FEEDING SKILLS AND THE EFFECT OF INJURY ON WILD CHIMPANZEES

Emma Jane Stokes

A Thesis Submitted for the Degree of PhD
at the
University of St Andrews

1999

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Dissertation submitted to the University of St Andrews
for the degree of Doctor of Philosophy

School of Psychology,
University of St Andrews
September 1999

DECLARATION

i) I, Emma Stokes, hereby certify that this thesis, which is approximately 65, 000 words in length, has been written by me, that it is the record of work carried out by me and that it has not been submitted in any previous application for a higher degree.

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ii) I was admitted as a research student in October, 1996 and as a candidate for the degree of Doctor of Philosophy in October, 1996; the higher study for which this is a record was carried out in the University of St. Andrews between 1996 and 1999.

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iii) I hereby certify that the candidate has fulfilled the conditions of the Resolution and Regulations appropriate for the degree of Doctor of Philosophy in the University of St. Andrews and that the candidate is qualified to submit this thesis in application for that degree.

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ACKNOWLEDGEMENTS

I wrote the acknowledgements for my PhD on the first day I spent in Budongo Forest. Without even having yet seen a chimpanzee I made a mental note to thank over and over again all the people who had helped make it all possible and who had helped in lessening the impact of a '3-year essay on monkeys' - and to think that wasn't even a third of the way through.

I would like to say a big thank you to my supervisor Dick Byrne, for his constant encouragement and guidance throughout, but mostly for helping me see the wood through all those trees in sorting through my data and writing up.

I am extremely grateful to the Biological and Biotechnological Sciences Research Council for my studentship and field costs, and to the Uganda National Council for Science and Technology, the Presidents Office and the Forestry Department for enabling me to carry out research in Uganda. I am indebted to Professor Vernon Reynolds and the Budongo Forest Project for allowing me to study the Sonso chimpanzees, and to NORAD, the National Geographic Society and Conservation International's Margot Marsh Fund for their continued support of chimpanzee research in Budongo.

In St Andrews I must say a huge thank you to Jason for being such a good friend throughout and one of many people who fell victim to my statistics-induced irrational side. During the first year, thanks to Simon, Michael and especially Ralph – wherever you may be – for brightening up a less than rosy start. I hope that by now you have found your seventh wife. Thanks also to Penny and Jeremy for helping to while away the office hours in those weeks of itchy feet prior to fieldwork, and to Nathan, in particular, for introducing me to St Andrews domesticity! A big thank you goes to Andy, Jamie, Janice, Jenny, Trisha, Richard, and Hazel for making St Andrews unrecognisable when I returned from the field, and to Andy and Jamie in particular for making my third year only a fraction of the nightmare I thought it would be. Thanks also to Mark Mon-Williams and Paul Gardener for their advice on the analyses, to Nadia for understanding how

annoying flow diagrams are and for essentially teaching me how to write a PhD, and to Kate, Heather and everyone in the Scottish Primate Research Group and Behaviour Discussion Group for being a safety blanket amidst the unknown recesses of the Psychology Department. I would also like to thank John Henderson, from IT Services, for his help in designing a program to make sense of my data, and John Galloway, from the Anatomy department, for investing his talents and time in the drawings of the injured chimpanzees as well as showing me my first dead body!

In Budongo, heartfelt thanks to my field assistant James Kakura, not only for his valued contribution to the data collection but also for his company, enthusiasm and never-ending supply of energy during long days in the forest. Thanks to him and all the other field assistants, Geresomu Muhumuza, Zephyr Tuka Kiwede, Tinka John, Joseph Karamaji and Kennedy Andama, for their knowledge, patience and good humour. In making day-to-day life run (almost) smoothly thanks must go to the multitude of project directors - with the obvious exception of one - Chris Bakuneeta, Jeremy Lindsell, Lucy Beresford-Stooke, Mark Attwater and Fred Babweteera, and to all the staff, Joy, Mary, Evace, Kahawa, Richard, Gino, Sebe and the trail cutters, who boosted my morale on a daily basis just by being around. For their friendship, advice and goodness knows what else thanks to all the various students (and helpers!) that drifted in and out, in particular Cath, Lucy – second time round – Paula, Donna, Glenn, Eric, Mnason, BB and lastly Katie and Clea, whose friendship, advice and goodness knows what else has extended way beyond the realms of Budongo. The 'original four' was a huge comfort during the more turbulent times - if anyone wanted to employ Katie as personal agony aunt, mentor, nurse, friend and all-round nice person then they wouldn't go far wrong.

The Forestry College played a far more important role than I'm sure it would have ever imagined, not least in being the nearest reliable source of cold beer, but also in its 24-hour nation-wide transportation and breakdown services – thanks to Ronald and Douglas for being on constant call-out alert. An immense debt of gratitude goes to the incredibly generous sugar daddies at Kinyara who exchanged a large piece of their – slightly more sophisticated - world for a brief glimpse into ours, each with their own unique brand of hidden dangers! A big thank you to all those remaining people - too many to mention – that I befriended throughout my stay in Uganda and who helped fuel my addiction to Africa and all it has to offer. A particular thanks to the chimpanzees of Budongo for never failing to dazzle the humble observer, and providing that all important impetus to continue when things got tough.

A special thanks goes to Mark whose patience, during my adjustment to life in St Andrews, and understanding, of a girlfriend's desire to leave him for 14 months in favour of a hermit's existence in the middle of the African rainforest, kept me together through some awkward moments. He has gone through this PhD with me and to have seen him watching the chimpanzees in the forest and the monkeys in the trees around camp at tea made it all worthwhile.

For being in the enviable position to study chimpanzees in their natural habitat I owe everything to the love and support of my family, especially my parents. They have encouraged – and endured - my far-fetched ideas for as long as I can remember, and have made me into who I am. When I had bored everyone with tales from Africa I knew that they would always be there wanting to hear more. For this, and everything, thank you.

To my parents

ABSTRACT

While gorillas and orangutans have been shown to display considerable manual skill in obtaining certain plant foods, complex feeding skills in chimpanzees have only been described in the restricted context of tool use. This thesis provides the first study of plant-processing skills in a non-tool using community of chimpanzees in Budongo Forest, Uganda. Furthermore, this community contains over 20% of individuals with upper or lower limb injuries. The strategies used by injured individuals in compensating for injury were investigated through a comparison of feeding skill between the able-bodied and injured population. A cognitive approach to feeding behaviour in chimpanzees was adopted, with respect to the implications this may have for overcoming the effects of injury.

Chimpanzees were found to employ a broad range of skills in feeding, reflecting variation in their environment and in their diet. Three food types were examined, each illustrating a particular aspect of feeding skill. In processing leaves of *Broussonettia papyrifera*, chimpanzees use complex multi-stage feeding techniques, employ bimanual co-ordination at several stages and elicit behaviour that is hierarchical in overall organisation. Able-bodied individuals show considerable standardisation in their feeding with a preference for two techniques. In contrast, when feeding on figs, chimpanzees rely upon simple processing techniques but at the same time employ strategies that serve to minimise the effects of feeding competition. In the case of *Ficus mucuso* chimpanzees co-ordinate several handfuls of food simultaneously between limbs, and with *Ficus sur*, chimpanzees display a range of dynamic feeding postures and positions in order to access food patches and increase relative food availability. No significant hand preferences were found in any of the three feeding tasks.

Even the most severe of injuries does not result in a decline in feeding efficiency, and the possible mechanisms contributing to this were addressed. Injured individuals were found not to invent novel solutions to familiar tasks, but instead to modify their existing repertoire in order to work around their injuries, thus sharing the program-level organisation observed in able-bodied individuals

and compensating at the level of individual actions. However, the physical limitations imposed by the injured limb considerably reduce bimanual co-ordination and manoeuvrability in the tree, which may have long-term negative implications.

CONTENTS

Part 1
Introduction

Until recently, 'skill' in primate foraging has been regarded as a matter of learning how to identify and locate edible items (Clutton-Brock & 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 in chimpanzee insect gathering and nut-cracking (e.g. McGrew 1992a; Teleki 1974) and orangutan frugivory (van Schaik et al. *1996; Fox* et al. *1999) has it been recognised that technical abilities are also important*

However, detailed analyses of both gorilla (Byrne & Byrne 1993) and orangutan manual feeding (Russon 1998; Galdikas & Vasey 1992) have now shown that eating leaves, stems and fruit may also involve considerable technical skill. These feeding techniques reveal a number of features characteristic of skill, for example the ordered sequencing of actions, bimanual co-ordination, hierarchical organisation and strong behavioural laterality. As yet, little is known of the non-tool plant-feeding abilities of the chimpanzee. Medicinal plant-use in chimpanzees is an obvious exception (e.g. Huffman & Wrangham), but this is a rare and non-subsistence activity. Elsewhere, reports of skilled plant processing in chimpanzees are derived at best from anecdotal observations in the field:

> *"The pods of Diplorynchus condylocarpon were placed upside down between the incisors after being cracked with the molars and then pulled open with one or two hands, using the thumb and forefinger"* [at Gombe: Wrangham 1977]

> *"[In feeding on the pith of Landolphia owariensis] they peel the bark of the woody vine with teeth, holding the shoot with their hands and biting at the internal pith with their incisors. The white pith is pulled with the incisors and extracted skilfully with teeth, fingers and lips"* [at Mahale: Nishida et al. 1983]

> *"leaves were stripped off the stem and immediately chewed, although exceptions were Aspilia sp. and Ficus urceolaris. The latter [rough-surfaced leaves] were sometimes piled together and rolled into a crude cigar shape before being chewed"* [at Gombe: Wrangham 1977]

> *"When feeding on the seeds of Brachystegia bussei, Mahale chimpanzees hold a single pod (10cm long) between upper and lower frontal teeth, and then crack it open by jerking the outer edge of the fixed pod up and/or down with the palm of one hand"* [Nishida et al. 1983]

> *"[When feeding on fruits of Diospyros mannii] processing was the same in all cases: the fruits was plucked by hand and rubbed and rolled against a branch to remove the hairs; the chimpanzee then bit into the fruit and fed, taking both seeds and outer flesh into the mouth but dropping the fruits skin"*
> [at Lopé Reserve, Gabon: Tutin et al. 1996]

The potential for complex plant processing by chimpanzees is thus apparent, and these observations only exacerbate the need for a systematic analysis of manual food processing comparable to that performed on gorillas and orangutans.

I propose to investigate the feeding skills of a community of chimpanzees in which over 20% suffer from some form of upper or lower limb injury. If complex plant processing is indeed an important component of chimpanzee feeding behaviour, as is suggested, then the ability of an injured individual to overcome their injuries is paramount to their survival. The fact that such a large proportion of this community has sustained and survived major limb trauma suggests that these individuals are able to compensate for their injuries. In the absence of developmental data on acquisition of feeding behaviour both prior and following injury, this thesis will investigate both the nature and extent to which feeding skills in the injured population differ from those shown by able-bodied individuals.

There are two possible: either injured chimpanzees show novel ways of processing food, or they share the existing repertoire as seen in the able-bodied population, and work around their injuries. Through a direct comparison of feeding techniques between the able-bodied and injured individuals, we can attempt to provide indirect evidence of the means through which compensation in the injured population is achieved.

This study, therefore, has two linked objectives: to perform a detailed analysis of feeding skill in able-bodied chimpanzees and, in doing so, define the problems faced by an injured individual and analyse the strategies used by individuals in order to overcome these problems.

Chapter 1

COMPLEX PLANT PROCESSING IN GREAT APES

In this chapter I will discuss the factors that might have selected for skilled plant feeding in great apes, and in doing so, review the current evidence of feeding skill in great apes and its implications for the design of this study.

Chimpanzee diet

Complete descriptions of the diets of wild primates are not easy, because the number of food items recorded for a species varies with duration of study and habitat. The habitat defines the potential diet of the species, and floristic variation is often so great as to limit the validity of inter-site comparisons. Chimpanzees however, can be confidently classed as frugivorous. For all populations of chimpanzees studied to date, fruit dominates the diet both in terms of percentage of feeding time and mass ingested (Hladik 1977; Wrangham 1977). This primarily fruit-based diet is supplemented with leaves and leaf-buds, and a miscellany of seeds, blossoms, stems, pith, bark, resins and fungi. Animal foods such as insects, birds' eggs, birds, and small and medium-sized mammals enrich the vegetable diet, and chimpanzees are also observed to visit rock outcrops for use as 'salt-licks', and to consume various substances such as soil, presumably for their mineral content (Goodall 1986; Hladik 1977; McGrew & Baldwin 1988; Nishida & Uehara 1983; Reynolds & Reynolds 1965; Mahaney *et al.* 1996). A high degree of diversity is therefore a common theme in chimpanzee diet. However, their feeding behaviour suggests that chimpanzees are highly selective feeders. Wrangham (1977) found that in spite of seasonal changes in food availability diet composition was similar from month to month, and Teleki (1981) noted that selected food items make up only a fraction of the potential resource availability. Food choice patterns can be influenced by a number of factors; energetic needs and nutrient requirements (Pulliam 1975); constraints of the digestive system and cranio-dental anatomy

(Chivers, *et al.* 1984; Milton 1984); avoidance of particular plant secondary compounds (Freeland & Janzen 1974) and additional factors such as degree of food clumping, dispersal, intra- and interspecific competition (Janson 1988) and predation.

Hladik (1977) suggested that food choice in the chimpanzee is affected by variation in the levels of specific nutrients in different foods rather than by variation in secondary compounds. His findings indicated that only a combination of different food categories could give a balanced diet. Energy is found in the lipids of seeds and arils and in the glucids or sugars of fruits, with young leaves and shoots supplementing protein intake, and invertebrates providing digestible protein (without the digestion-inhibiting effects of plant fibre and tannins) and essential amino acids. Little evidence existed to suggest that plants containing alkaloids were selected against, and it appears more likely that the alkaloids were not toxic or at least did not occur in sufficient quantities to exert a toxic effect. Phenolic and tannin content was not measured in this particular study, but Bouquet (1972) found that whereas phenolics occur in few species eaten by the chimpanzees, tannins occur frequently in the leaves and bark of many species, and are likely to interact with feeding. Resources yielding maximum nutrients have a patchy distribution both temporally and spatially. Hladik concluded this to be a contributing factor to the exceptional size of the range of the chimpanzee compared to that of other frugivorous primate species.

By contrast, Wrangham *et al.* (1993) argued that feeding rate appeared to be a more important influence than absolute nutrient levels on the rate of nutrient intake. In a comparison with a classic sugar-rich primate fruit, e.g. *Mimusops bagshawei*, Wrangham stressed the importance of figs to the Kanyawara chimpanzee population of Kibale Forest, Uganda as an energy rich food with adequate protein containing essential amino acids - in the form of dead fig wasps contained inside them. He concluded that by maximising fig intake, more energy and nutrients could be gathered per unit time, and could therefore promote social activity, long distance travel, or other activities normally constrained by time and energy.

When fruit is scarce however, chimpanzees, like other frugivores, must migrate to more productive areas (Nishida 1979), reduce energy expenditure (Wrangham, 1977) or broaden their diet (Isabirye-Basuta 1990). Wrangham *et al.* (1991) specifically investigated the use of terrestrial herbaceous vegetation (THV, defined here as terrestrial pith and leaves) by the chimpanzees of the Kibale Forest, and found them to eat more THV when fruits were scarce, and when rainfall - and thus plant growth - was higher. Nutritional analysis revealed piths to be typically low in free sugars and protein, but when compared with fruit and young leaves, consistently high in hemicellulose and cellulose. These insoluble fibres are partly digestible by chimpanzees, and Wrangham *et al.* concluded that fibrous herbaceous piths provide an alternative energy source to the chimpanzees when fruits are scarce.

In a comparative study with bonobos in the Lomako Forest, Zaire, Malenky & Wrangham (1994) found herbaceous vegetation to be more abundant in the bonobo habitat, and faecal analysis showed THV to constitute quantitatively a far more important dietary component of bonobos than is apparent from similar analyses with chimpanzees. Moreover, bonobos appear to consume THV all year round, independent of fruit availability. Dental morphology of bonobos shows a greater shearing efficiency of the upper and lower molars (Malenky & Stiles 1991), which also suggests that bonobos may have evolved to depend on non-reproductive plant parts (food items other than fruit e.g. leaves, shoots, stems and pith) more extensively than chimpanzees. Furthermore, bonobos were found to preferentially choose the new shoots and young pith of *Haumania liebrechtsiana* (Marantaceae) over other species of THV. Nutritional analysis showed that *H liebrechtsiana* had considerably more protein, with similar levels of digestible complex carbohydrates, than the mean for species of herbaceous food eaten by the chimpanzees of Kibale Forest. Wrangham *et al.* (1996) designated *H. liebrechtsiana* as an example of *high-quality* THV (H-THV) which they defined as being protein-rich, of sufficient nutritional value to allow growth and reproduction, preferable to typical fig fruits and occurring ubiquitously at low-density. They suggest that these food patches allow for relatively stable foraging parties by reducing the intensity of feeding competition'. A similar effect is observed with the diet of the mountain gorillas in the Virungas, which is based on herbaceous vegetation and dominated by the consumption of a few species ubiquitously distributed throughout the habitat (Watts 1984). The stems of these herbs would qualify as another example of H-THV in that they are high in digestibility and together with the leaves provide a nutrient-rich source that can be processed relatively rapidly (Waterman *et al.* 1983). Mountain gorillas feed as part of a semi-permanent, non-fragmenting group of individuals. Dietary niche therefore, may have been an important factor in the evolution of the fission-fusion society of chimpanzees for dealing with fluctuating levels of food abundance and within-group competition.

In a comparative study of the foraging profiles of sympatric populations of gorillas and chimpanzees in the Lopé Reserve, Gabon, Tutin *et al.* (1991) found that during the dry season gorillas eat large quantities of vegetative foods, some of which are permanently available but are usually ignored due to their high levels of indigestible fibre. Wrangham *et al.* (1996) labelled these foods as *low-quality* THV (L-THV) - defined as cellulose-rich, of insufficient quality to allow growth and reproduction by chimpanzees and bonobos and thus less preferable than most fig fruits. L-THV typically occurs in high-density patches, and is eaten only annually. Chimpanzees, on the other hand, increase their consumption of the fruit of *Elaeis guineenis* during the dry season, in addition to the pith and young leaves of herbaceous plants. The presence of entodiniomorph ciliates is ubiquitous in the faeces of lowland gorillas (Goussard *et al.* 1991). These micro-organisms are efficient cellulose digestors, and live symbiotically in the gut of their host. The nature of their intestinal flora, combined with their larger gut size, means that unlike chimpanzees, lowland gorillas are capable of surviving on a totally folivorous diet of poorer quality than their gut morphology may suggest. This pattern is also observed in sympatric populations of eastern lowland gorillas and chimpanzees in the Kahuzi-Biega National Park, Zaire (Yamagiwa *et al.* 1996). The hypotheses still remain to be tested that THV densities are higher in areas containing gorillas or bonobos than in areas with only chimpanzees, or if competition between gorillas and chimpanzees limit the year round availability of high-quality THV for chimpanzees.

A complicated diet is regarded by many as a causal factor in the evolution of primate intelligence. This forms one of the two major lines of speculation about selection pressures leading to the evolution of intelligence, namely foraging behaviour and complex social life. Social intelligence, including kin recognition and prediction of future interactions, has received considerable attention over the past four decades (Humphrey 1976; Jolly 1966; Kummer & Goodall 1985). The several versions of this concept were more recently revived and reviewed by Byrne & Whiten (1988; Whiten & Byrne 1997) under the banner term "Machiavellian Intelligence" (see Byrne 1997). This thesis however, will focus on the alternative hypothesis for the evolution of intelligence, that of the relationship between foraging behaviour and cognitive ability in the great apes.

Evolution of intelligence

Apes have large brains, but this does not come without severe costs. Along with gut tissue, the brain has the highest metabolic costs regardless of wake or sleep state (Aiello & Wheeler 1995). Moreover, this demand for energy is remorseless, unlike other organs the supply to the brain has to be constant; if the supply of energy is interrupted, brain tissue will be irreparably damaged after about 4 minutes. The costs argue that an increase in brain size must have come with strong selective advantages.

Milton (1981; 1988) proposed that the need to search for patchily distributed food in the tropical forest was the critical stimulus for the development of increased cranial capacity and mental development in higher primates. She compared the foraging behaviour between populations of howler (*Alouatta palliata*) and spider monkeys *(Ateles geoffroyi*), and noted that spider monkeys, which eat fruit with a patchy distribution, have a greater relative brain size and degree of neural complexity as well as longer periods of maternal dependence than howler monkeys, which are primarily folivorous. Clutton-Brock & Harvey (1980) found that the trend of greater cerebral expansion among more frugivorous species as opposed to more folivorous ones held across the Primate Order, and that this also extended to Chiroptera (Eisenberg & Wilson 1978) and some rodents (Mace *et al.* 1981).

Parker & Gibson (1977; 1979) examined the means by which food is located and processed. They proposed that primate intelligence evolved in response to the need for locating and processing food encased in a shell or embedded in a solid matrix such as the earth. Such behaviour is termed extractive foraging, examples of which include digging up underground roots or social insects such as termites and opening hard-shelled fruits. It is argued that extractive foraging supplies a year round high calorie diet essential for the support of a large brain, and may have provided a powerful stimulus for complex processing skills (Gibson 1986).

Technical skills in manual food processing have been reported both in orangutans (Russon, 1998) and in mountain gorillas (Byrne & Byrne 1991; 1993). In some cases, these techniques exhibit a considerable logical complexity.

To the orangutans studied by Russon in East Kalimantan, the coconut palm, *Borassodendron borneensis* provides a permanent food source, and despite being one of their most difficult food items to process, the new leaf is a preferred food when available. New leaves emerge as a tightly closed fan of leaflets from the centre of the palm's crown. Palms can grow up to 7-10 m and a veritable fence of razor-sharp mature leaf stalks surrounds the new leaves. Russon divided the technique for obtaining the new leaves into four phases. The first phase is described as an active search for a suitable palm, which involves identifying a likely plant, planning an entry route into its crown, and once entered, checking for a good, new leaf. The second phase involves active preparation for extraction. Preparation comprises some subset of making a "workseat", moving obstructing mature leaf stalks out of the way, and removing debris from around the new leaf spear. The third phase integrates extracting the spear with eating its base. Repetitively, the spear is subdivided into small sections, each extracted and its base eaten. Sometimes the base is eaten in several stages, between which sections are stored. The final phase denotes leaving the palm. This includes selecting an exit direction (often continuing the previous travel direction), planning an exit route, and executing the plan (including modifying it to handle problems of error). However, this data was obtained from rehabilitated rather than wild orangutans. Populations of rehabilitated orangutans are unlikely to exhibit *traditions* of behaviour that are seen with tool-use in wild populations of chimpanzees (McGrew *et al.* 1979), and plant feeding in the population of mountain gorillas studied by Byrne in the Virunga Volcanoes. Consequently, Russon's analysis was based upon a single individual only.

Byrne & Byrne (1993) found that the mountain gorillas use several different techniques for dealing with all their major food plants, and investigated these in a study population of 38 adults and juvenile individuals. Although nutritious and chemically innocuous, the herbaceous vegetation in their diet is protected by various physical defences such as stings, tiny hooks, spines and hard outer casing. Before they can be eaten, the gorilla has to neutralise the defences in some way. The technique used in feeding on wild nettle *Laportea alatipes,* shows this clearly. First the soft leaves at a stem top are gently held to bring the stem into reach, then one hand is half-cupped at the stem base and stripped upwards (sometimes requiring firm support at the base from the other hand). This detaches the leaves in a bunch with only the least-stinging undersurfaces in contact with the gorilla's hand. The bunch is then gripped firmly with both hands (a loose grip would make the stings more liable to hurt) and the two hands rocked or twisted against each other to detach the leaf stalks, which are discarded. Finally, the tight bundle of leaf blades is carefully folded over and held folded for insertion into the mouth, such that only the undersides possibly contact the tender lips. This is quite different to the technique used for eating bedstraw, *Galium ruwenzoriense*, which is covered in a dense mat of tiny hooks. In processing this particular plant a mass of tangled stems are pulled into reach and supported with one hand, whilst the other hand picks out the green stem and folds in any loose stems. This is repeated until the hand is full, at which point the supporting hand picks out any debris and the loosely held stems are gripped tightly and eaten as a tight bundle.

These methods prove effective, at least in juveniles and adults, and are quite different again to those techniques involving extractive foraging, such as obtaining pith from the stalks of wild celery and thistle stems. In the case of wild celery, the stem must first be bitten or snapped into manageable segments. Then, a segment is partly peeled by biting the outer case and stripping it off with a pull against the teeth. The exposed pith can then be carefully picked out with delicate finger work. With a large 10m stalk, stripping may then continue for up to 15 minutes. The stems of thistle pose an additional problem in the form of sharp spines. The outer layer of skin - to which the spines are attached - must first be peeled off and discarded before the edible portion of the stem is revealed.

In chimpanzees, comparable studies of innovative and inventive behaviours of the type indicated by Gibson (1986), are largely limited to observations of tool-use.

Tool-use – an example of skilled feeding by chimpanzees

Goodall (1963) first reported tool-use by wild chimpanzees over 30 years ago, and much has been added to our knowledge since, going beyond the level of description to focus on a social, cultural and evolutionary interpretation of tool-using behaviour (e.g. McGrew, 1992a; McGrew *et al.* 1979). At its technical level, tool-use in chimpanzees is a useful paradigm of the skills employed in complex plant processing by gorillas and orangutans, with earlier studies revealing the chimpanzee's capacity to solve practical problems. This capacity goes beyond the use of the tool itself, to include manufacture of tools, precise selection of raw material and transport of tools (Boesch & Boesch 1985; 1990; McGrew 1974; McGrew & Collins 1985; Nishida 1973).

Tool-making

In a tropical forest environment, twigs and grasses are more commonly available than stones, and accordingly, chimpanzees use sticks much more frequently than stones. Similarly, the ease to modify a material decreases from a stick to a large branch and a stone, and thus decreases the tendency of chimpanzees to modify them; stones are used unmodified.

In the forests of West Africa, the presence of stones suitable for use as a hammer-tool to crack nuts is few and far between. These chimpanzees show high faculties in representation of space in finding the rare stones at previous nut-cracking sites (Boesch & Boesch 1984). The transport of tools from one site to another can be interpreted as a highly goal-directed form of behaviour, and individuals have been observed to carry a favoured anvil- or hammer-stone hundreds of metres to a nut-cracking site (Boesch & Boesch 1983).

By contrast, when the availability of raw material is not a limiting factor, chimpanzees usually make their tools at arm's reach, rarely searching further. This has been documented for the use of sticks as tools in bone marrow extraction (Boesch & Boesch, 1990) termite fishing (McGrew *et al.*, 1979), and arboreal ant-gathering (Nishida, 1973). Holes to reach ants are larger and deeper than holes to extract marrow from bone. The latter tool should therefore be finer and shorter than the former, and data on the lengths and thickness of tools used for these two tasks shows this to be so. Within a particular tool-using task, there exist even finer levels of distinction in the preparation of tools. Nishida recorded five variants of a poking tool used to obtain arboreal ants of *Camponatus* and *Crematogaster* spp. Discrimination between each appeared to be conditioned by both the size of the entrance to the ants nest and the nature of material used. Thus, for a very small entrance to a nest, a slender and elastic tool is required, which will penetrate the opening smoothly. Tools therefore have to be made to conform to specific physical requirements, which may involve cutting to the correct length by breaking with the hands, and shaping the stick by removing leaves or bark and sharpening the ends with the teeth. Similarly for termite fishing, tools are selected, and if necessary, modified according to the nature of the material used. McGrew & Collins (1985) noted that in the use of sedges as a fishing tools, the chimpanzees stereotypically removed one of three ridges of the stem, usually along its entire length, changing its cross-sectional shape from a triangle to a trapezoid, presumably making the tool either easier to insert, or easier for the termites to bite onto. Various modifications can be applied to very simple objects and these modifications may allow the individual to be less selective in choosing the raw material, and thus become less dependent on the environment.

Tool-using

In nature, most primate tool-use is one-handed, such as fishing for termites with a probe. Asymmetrical and bimanual tool-use is apparently limited to great apes and capuchin monkeys (in captivity). In one form, the tool is held in one hand, usually in a precision grip, and the object of action is held in the other, often in a power grip, e.g. using a twig to pick out bone marrow (Boesch & Boesch 1989) or a handful of leaves to scoop out the ripe pulp of hard shelled fruits (Wrangham, 1977). More impressive is what occurs in ant-dipping (McGrew 1974). One end of the wand is held tightly in a power grip (in either hand or foot), while the other hand quickly slides the length of the wand in a loose precision grip (the 'pull through'). This is remarkably similar to the 'stripping' action used by mountain gorillas, in avoiding the painful stings of the nettle *Laportea alatipes.* As a result of the 'pull through' ants have collected on the sides of the thumb and forefinger and are shovelled into the mouth and rapidly chewed before they have a chance to bite.

The complex behaviour shown in chimpanzee tool-use and plant-processing by gorillas and orangutans, shows a number of features that suggest a level of cognitive ability comparable to that seen in technical skills of humans. For example, the ability of chimpanzees to make tools specific for a particular task suggests that they have an advanced understanding of the causal relations between objects. In order to test these observations from the field, Visalberghi *et al.* (1995) measured performance in a laboratory-controlled tool-using task by chimpanzees, bonobos, an orangutan and capuchin monkeys. Among monkeys, capuchins are most noted for their use of tools (Beck 1980; Visalberghi 1990), and like great apes, show flexible use of tools. The task set involved obtaining a food treat placed inside a clear tube. The animal was initially presented with a straight stick, and then with bundles of sticks or misshapen sticks, which both required some modification in order to access the food. Although all species could solve the tasks set, only the performance of the great apes showed emerging representational capabilities, consistent with the avoidance of errors in the more complex tasks. Continuing research on *Cebus* however, (Westergaard *et al.* 1997; Westergaard 1994) together with a recent interest in other species (e.g. Hauser *et al.* 1999), still leaves in some doubt the true extent of cognitive ability in primates other than the great apes. Rather, a mechanism that is emerging as critical in distinguishing great ape and human cognition from that of other non-human primates is hierarchical organisation of behaviour.

Hierarchical organisation of behaviour

Lashley (1951) was the first to argue that complex serial behaviour could not be explained in terms of associations between contiguous acts, and that order must be generated by some higher level organisation. Continuing work on the intellectual abilities of the great apes (Byrne 1995;1997; Gibson 1993; McGrew 1992b; Russon, 1998) suggests the application of hierarchical mental construction skills, which involve keeping a number of mental, perceptual or motor elements in mind simultaneously, and combining several of these elements into new wholes which can then be used as subunits of other constructions. Behaviour therefore appears to be organised as interconnected clusters, rather than isolated units.

Examining these cognitive mechanisms through indices of behaviour can assess the role of hierarchical organisation. The latter include iteration to criterion, routine and subroutine structure (routines are behaviour complexes that function as integrated units rather than chained sequences of individual actions; subroutines are routines used as elements of other routines-i.e. lower level units within higher level behavioural structures), optional and alternative subroutines, inter-co-ordination between routines and recovery from interruption or error, so as to resume the original routine from the point of disruption. Examples of these mechanisms are exhibited in the complex behaviour of gorillas and orangutans (Byrne & Russon 1998).

To illustrate these phenomena in chimpanzee feeding behaviour, I have represented the complex multistage processes of tool-using behaviours as three alternative notations derived from descriptive accounts in the literature.

The first is adapted from Fushimi *et al.*'s observations of nut-cracking behaviour by wild chimpanzees at Bossou, Guinea (Fushimi *et al.* 1991) shown in **Figure 1.1**. Here, a conventional flowchart of computer science, as used by Byrne & Byrne (1991; 1993) in describing the food processing techniques of mountain gorillas, is used. The sequence of behavioural elements (which begins when an animal arrives at a nut cracking site) starts at the top and moves down; rectangular boxes show elements (with 'element' here referring to an action or suite of actions that results in a visble change to plant material), described by the words in them. Brackets show actions that are optional depending on environmental conditions. Actions are vertically aligned according to whether the 'hammer-hand' or the 'nut-anvil-hand' is used. Diamonds represent branch points, with the approximate criteria for the decision indicated in words in the diamond; thus iteration of a process may be required until the appropriate conditions are met. The sequence ends with putting the processed food in the mouth.

The second notation (**Figure 1.2**) is a representation of Goodall's recorded observations of termite fishing by the chimpanzees of the Gombe Stream Reserve (Goodall, 1963). This uses an adaptation of Russon's notation to describe the palm-leaf processing skills of the orangutan. This notation shows similar features to the ALGOL computer programming language designed specifically for programming scientific computations. ALGOL creates blocks of statements for the scope of variables and the extent of influence of control statements. In addition, parameters can be passed to subprograms (the equivalent of subroutines in hierarchically organised behaviour), calling by value or by name. Furthermore, structured control statements: if – then – else, and the use of a general condition for iteration control, are also features of the language. The termite fishing-technique of chimpanzees can be subdivided into a distinct four-phase structure. Each phase (or block) is shown in CAPITALS. Within each phase, complex combinations of manipulations with a

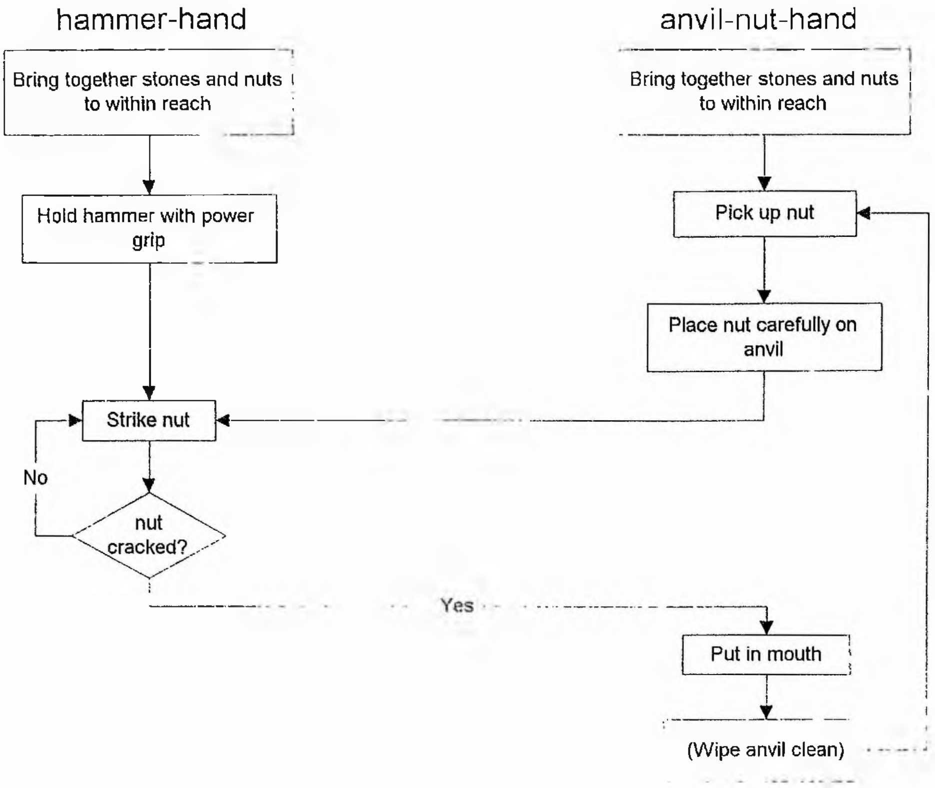

Figure 1.1 Hierarchical organisation of nut-cracking behaviour

unified focus are shown in *ITALIC CAPITALS*, and action elements are shown in UNDERLINED type. Selected actions only are described in detail (i.e. for TOOL-USING) so as to overcome the idiosyncratic variability in technique shown at this level of organisation. Optional elements (i.e. some do, most don't) are shown in **bold.**

The third representation of chimpanzee tool-using behaviour uses a notation popular in artificial intelligence, known as "production systems". This was explored by Byrne (1995) who examined its capacity to formulate what (minimally) needs to be represented in the brain in order to explain observed behaviour, without weighing down empirical data with theoretical baggage. Production systems are composed of elements that are conventionally written (pattern) → (procedure). When the specified pattern matches the objects perceived in the world-and so encoded in the individual's working memory-then that particular procedure is executed. As a result, both the contents of working memory and the external world

ACTIVE PREPARATION
PLAN feeding routine to incorporate termite feeding during first few weeks of rainy season
optional: *SELECT* suitable tool in advance
  ***TRANSPORT* tool to termite mound**
IDENTIFY termite mound
INSPECT termite mound for sealed off entrance holes
PREPARE sealed off entrance holes
  SCRATCH surface layer of soil

TOOL-MAKING
SELECT suitable fishing tool
  if there is no previously used tool lying available:
PREPARE raw material
  DETACH from surrounding vegetation
  STRIP/PEEL bark to produce smooth surface
  REMOVE outer leaves, side branches and/or attachments such as seed heads or rhizomes

  else go straight to:
INSERT

TOOL-USING - iterate until satiated
INSERT tool in entrance hole,
  GUIDE the tool into the hole using a repeated precision pinch grip between thumb and forefinger starting near the distal end of the tool, and regrasping higher up as the tool is inserted
PAUSE with tool remaining in the hole
  OSCILLATE tool slowly from side to side, holding in a firm pad-to-pad pinch grip
WITHDRAW tool
  If no termites are attached to tool then back to:
INSERT
  else:
EAT collected termites
  SUPPORT tool on back of wrist of the other hand and
  DRAW tool sideways through protruding lips of the mouth, with the tool still held in a precision grip at its proximal end
optional: *MOP* up fallen termites on the ground with the back of the hand
  ***PICK* off directly with the lips**
EXAMINE state of tool
  If tool is damaged then go to:
REPAIR
  else back to:
INSERT

TOOL MODIFICATION
REPAIR damaged tool
  PINCH off frayed end or
  REVERSE tool and use opposite end

Figure 1.2 Hierarchical organisation of termite-fishing behaviour

will change, so that a different production matches, and so on until no productions have matching patterns or the goal is reached. In this instance, I have applied production system notation to the ant dipping technique used by chimpanzees at the Gombe Stream Reserve, as first described by McGrew (1974), and shown in **Figure 1. 3.**

1. (ant mass accumulated on the side of flexed thumb and forefinger) &
   (distal end of tool held just below the mouth) &
   (long straight sturdy tool without side branches in hand) → (transfer to mouth and gnash jaws frantically)

2. (distal end of tool held just below the mouth) &
   (ants streamed 3/4 of the way up the tool) &
   (long straight sturdy tool without side branches in hand) &
   (moving stream of ants in view)

3. (ants streamed 3/4 of the way up the tool) &
   (long straight sturdy tool without side branches in hand) → (withdraw tool from hole)

4. (long straight sturdy tool without side branches in hand) &
   (moving stream of ants in view) → (insert tool in hole)

5. (moving stream of ants in view) → (make ready a dipping tool)

Figure 1.3 Hierarchical organisation of ant-dipping behaviour

From research done in captivity or in the laboratory many are of the opinion that the highest levels they can achieve resemble those of human children under 3.5 or 4 years of age (Greenfield 1991; Premack 1988). From field data, all great apes appear capable of performing hierarchically organised tasks. McGrew (1992b) noted that chimpanzees in the wild are unique in having *tool-sets* in which two tools are used sequentially on a given object. For example, Sugiyama and Koman (1979) observed chimpanzees using a stone to strike a nut placed on an anvil. McGrew concluded that this level may be the non-human primate limit on cognitive skills. However, Matsuzawa (1991; 1996) has reported *meta-tool use* in wild chimpanzee nut-cracking behaviour at Bossou, Guinea, using a stone hammer and anvil and a third stone used as a wedge to keep the surface of the anvil stone flat and stable. This involves 'additive construction' in tool manufacture i.e. the combination of two objects into a tool subassembly that can then act on a third object outside the chimpanzee's own body. Thus, the full potential of hierarchical organisation of food processing behaviour in the great apes may still to be realised.

Plant food-processing skills

To understand the techniques used by chimpanzees in the manual processing of plant-foods, an understanding of the potential problems faced by a chimpanzee in dealing with food is required. Descriptions of the diet, comparisons with the feeding techniques of other species of great ape, and a testing of foraging hypotheses for the evolution of intelligence all assist in anticipating these problems and identifying likely situations where complex skills may be put to good use.

The majority of chimpanzee foods are arboreally located (Goodall, 1986; Reynolds & Reynolds, 1965), which by their very nature will tend to restrict technique to monomanual processing as one hand will be used in postural support (Nishida, 1973). The minimal food processing costs afforded by ripe tree fruits in itself makes them an attractive food source to frugivorous primates. There are however, some notable exceptions, where a degree of complexity in the processing of arboreal fruits is required. The fruit of *Strychnos* sp. is smashed against the trunk or branch of a tree to crack the hard rind (Goodall 1986), and fruits of the oil-nut palm *Elaeis guineenis* must be carefully poked out from between the spiny tips of the florescence (Wrangham 1977). This procedure is similar in principle to that described in orangutans in extracting the new leaves from the spiny-palm *Borassodendron borneensis*, where a skilful and highly organised technique was required just to access the food and prepare for processing.

These exceptions aside however, two broad types of food processing appear to offer likely tasks that would require a degree of complex manipulation by the chimpanzees. Firstly, *pith extraction*, or by extension, the processing of terrestrial herbaceous vegetation, and secondly *seed predation*, which is particularly interesting in its role as a possible contributor to the origins and diversification of the early hominids.

McGrew & Baldwin (1988) predicted a positive correlation to exist between extent of grassland and the extent of low-quality or hard-to-process foods in the diet of wild chimpanzees (see also Suzuki 1969). Wrangham *et al.* (1991) described the monocotyledonous herbaceous vegetation in the Kibale Forest as having thick, tough protective stems, restricting many animals from harvesting piths. A similar problem is faced by the mountain gorillas in the Virungas in extracting the pith from the stalks of wild celery, which is a common food in their diet. A number of anatomical features assist in enabling great apes to include these food items in their diet. African apes have thin-enamelled teeth, which are particularly effective at shearing stems and extracting the soft pith inside (Wrangham *et al.* 1991). The manipulative abilities of the ape hand are also important. The Opposability Index of gorillas is the highest of all the great apes (Napier 1980), which suggests their manipulative skill be the best developed. These anatomical features evolved hand in hand with increasing terrestriality. In relation to the other great apes gorillas are predominately ground living animals and, as a consequence, they have to an extent become secondarily adapted to a ground-living way of life; adept at dealing with, for example, the mechanically defended terrestrial herbs that dominate their montane forest habitat. A similar method of eating pith from the inside of tough stems is found in vervet monkeys, although they lack the deliberately structured approach seen in mountain gorillas. Harrison (1996) found that vervets (*Cercopithecus aethiops*) process sugar cane by holding the cane in both hands, biting into the outer case with the incisors and tearing back with a jerking movement of the head against a forward push with the hands. Even among strepsirhines there are close similarities in basic technique. Studies of food preparation skills of the hapalemurs (*Hapalemur griseus*) in captivity have revealed that these animals remove the outer casing in a similar way to monkeys (Stafford *et al.* 1993), and moreover their actions are highly structured into an organised sequence, in a sense reminiscent of gorillas eating celery. This led Byrne (1999a) to suggest that stem-processing skills are more primitive than for example the leaf-

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processing skills documented in gorillas. Some aspects of the former process may be found in a wide range of primates, as part of a genetically coded repertoire of basic feeding methods. It is plausible therefore that great apes may depend on rather more general primate abilities in order to process these stems, and this should be taken into account when analysing these techniques as performed in the wild.

By contrast, paleontological and archeaological studies have implicated nut-cracking adaptations as present in the earliest hominids (Jones *et al.* 1992). In the light of this, Peters (1987) recognised the need for "a systematic analysis of the ecology and physical properties of the relevant nuts as a prerequisite to the development of sound evolutionary interpretations". Forest tree species do not as a rule produce fruits with edible mesocarps. In contrast, the woodland savannah species characteristically provide a valuable whole fruit, i.e. a nutritious mesocarp in addition to edible oil-rich nut seeds. These fruits drop from the tree before they are fully mature and go through the final ripening phase of the ground. These are important seasonal foods for a variety of vertebrates, including primates, elephants and antelope. Peters concluded, from strength measurements, that the woodland nuts are not as tough as those of the tropical forest and that it was the former that were probably available on a seasonal basis to the earliest hominids. The role of seed predation in the feeding ecology of extant primates provides another indirect source of information to test this hypothesis. In one of the few published studies that attempt to systematically define the problems faced by forest-dwelling chimpanzees in dealing with food items, Tutin *et al.* (1996) describe the protection afforded by the developing seeds of *Diospyros mannii*, both directly in terms of a hard testa and the presence of toxins in the cotyledons, and indirectly, via fruit characters such as cryptic coloration, distasteful pulp and the presence of irritant hairs and sharp spines. Out of eight species of primates acting as potential predators on the immature seeds, only gorillas and chimpanzees were capable of breaching the defences to extract the protein-rich seed inside. This was achieved by plucking the fruit by hand, rubbing and rolling it against the branch to remove all the hairs, and then ingesting both seeds and outer flesh but dropping the fruit skin. Tutin *et al.* suggested that monkeys were unable to manipulate the large fruit painlessly due to their small hands. Furthermore, as the fruit ripens and seed defences diminish, abscission occurs, and arboreal monkeys are unable to take full advantage of the fallen fruit. This particular task bears similarities to the so-called habitual tool-use reported in wild Sumatran orangutans, in processing the fruits of *Neesia* sp. (Fox *et al.* 1999). The husks of these large fruits (c. 15 x 10cm) split partly open when ripe, but edible seeds remain difficult to extract and are embedded in a mass of irritating hairs. Breaking off twigs and stripping the bark with teeth makes small tools. Holding the tool in their mouth, they inserted it into the cracks between two valves, scraped out the hairs by moving it towards the fruit apex and then removing the accumulated hairs from the tool by blowing and wiping with a fingernail. In this way the seeds could be pushed towards the apex of the fruit, and scooped out with one finger or the hand-held tool. The best documented examples of dealing with formidable seed defences come from the nut-cracking behaviour of chimpanzees in West Africa (Boesch & Boesch 1983; Hannah & McGrew 1987), but again, this relies on the use of technology.

Current archaeological and fossil evidence is challenging the view that the early phases of the hominisation process were dependent upon the ability to make and use tools. (Wynn 1988). The question now remains, do non-tool tasks in chimpanzees require mentally demanding problem-solving abilities, as demonstrated by gorillas, and orangutans. Moreover, do they parallel the skills, both cognitive and technical, documented for tool-use. Through an investigation of plant processing skills in able-bodied chimpanzees, this study deals with both of these issues.

Chapter 2

FIELD METHODOLOGY

The principal objective of the field study was to record and describe the manual food processing skills of both able-bodied and injured chimpanzees. Data on feeding skill was collected by Byrne & Byrne (1991, 1993) for the mountain gorillas in the Virunga Volcanoes, Rwanda. To further a comparative study on manual food processing in great apes, it was proposed to use their methods to collect similar data from a community of chimpanzees in the Budongo Forest, Uganda. However, ecological differences between the two species combined with a difference in vegetation between the two study sites and degree of habituation between the two study populations, forced a number of changes to be made in the methodology.

This chapter describes the field site and some of the factors, both economic and ecological, which have shaped the flora and fauna over time. With the study placed in context, the remainder of the chapter will describe the various data collection methods used.

Study site

Budongo Forest Reserve

The Budongo Forest Reserve lies if the western Rift Valley, near Lake Albert (see **Figure 2.1**). The Reserve covers a total area of 793 km², of which 482 km² is continuous forest cover, and is situated between 1° 35' - 1°55' N and 31° 18' - 31°42' E at a mean altitude of 1050m (Eggeling 1947). To the north of the forest, bush and grassland stretch to the end of the rift and is contiguous with Murchison Falls National Park. The forest is classified by Eggeling as medium altitude semi-deciduous, and is Uganda's largest remaining block of tropical rainforest.

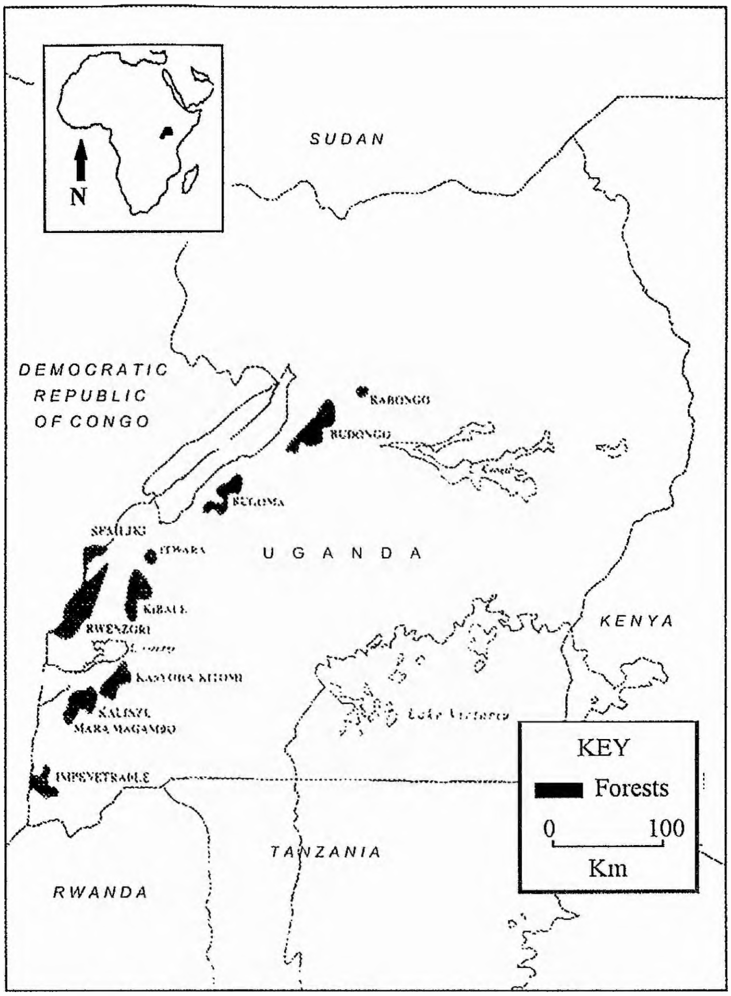


Figure 2.1 Map showing location of Budongo Forest and other chimpanzee inhabited forests in Uganda

The area receives a plentiful supply of rainfall throughout the year, with the exception of a pronounced dry season from December through February. Mean annual rainfall recorded at different locations throughout the reserve varies from 1454mm (recorded at Busingiro close to the edge of the forest 1933 – 1945 by Eggeling) to1680mm (Budongo Forest Project Research Station 1993-1998) to 1842mm (centre of forest 1945 by Eggeling). During the study period 1997-1998, annual rainfall peaked at 2187mm, due to the effect of the El Nino weather system, with 1253mm falling between October and December of 1997.

The forest consists of several distinct yet successive vegetation communities (described by Eggeling, 1947, see **Figure 2.2**). According to Eggeling, these comprise two types of climax forest and two distinct series. The climaxes are the ironwood (*Cynometra*) forest and the swamp forest, which is an edaphic or arrested climax. The series are colonising forest – of which there are two forms: *Maesopsis* and woodland forest – and mixed forest. The ironwood forest is dominated by *Cynometra alexandrii,* which accounts for up to 35% of all trees and as much as 90% of all large trees. Two genera, *Lasiodiscus* and *Lipidoturus*, are common as understorey trees although they do not occur in association. The swamp forest is the least common forest type. Here the forest grows on soils that are flooded for part of the year and waterlogged for the remainder. Consequently, its composition constantly fluctuates depending on the level of water present, and the structural detail and species diversity of this forest is very high (Eggeling 1947). The two forms of colonising forest are distinct in make-up. The *Maesopsis* forest is dominated by *Maesopsis eminii*, *Cordia milleni* and *Diospyros abyssinca* and is generally found in large blocks along the forest edge. The woodland forest is generally found on poorer soils, often in the sides of ridges, and forms an uneven broken canopy (Patterson 1991). Mixed forest is dominated by *Celtis mildbraedii, Celtis zenkeri, Khaya anthotheca, Chrysophllum albidum* and *Funtumia elastica*. This is the most common forest type (Plumptre & Reynolds 1994), and economically is the most important due to the presence of the mahoganies *Khaya anthotheca, Entandrophragma cylindricum, E. utile* and *E. angolense.*

Logging history

Budongo Forest serves as the largest mahogany producing forest in Uganda, and produced timber on a sustainable basis from the mid-1920s until the decline of the sawmill in the 1970s. The Uganda Forestry department divided the forest into 47 compartments. Selective logging was conducted on a compartment by compartment basis, leaving one compartment set aside, at the outset, as a Nature Reserve (see **Figure 2.3**). For each compartment, extensive records were kept of

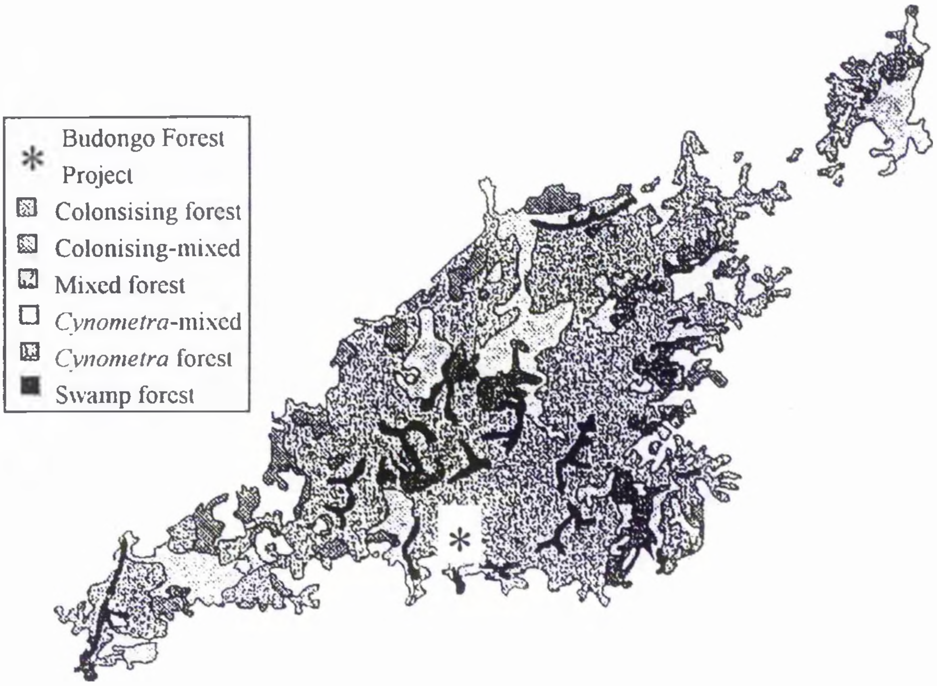


Figure 2.2 Forest types in Budongo Forest Reserve as of 1990 (from Plumptre & Reynolds 1994)

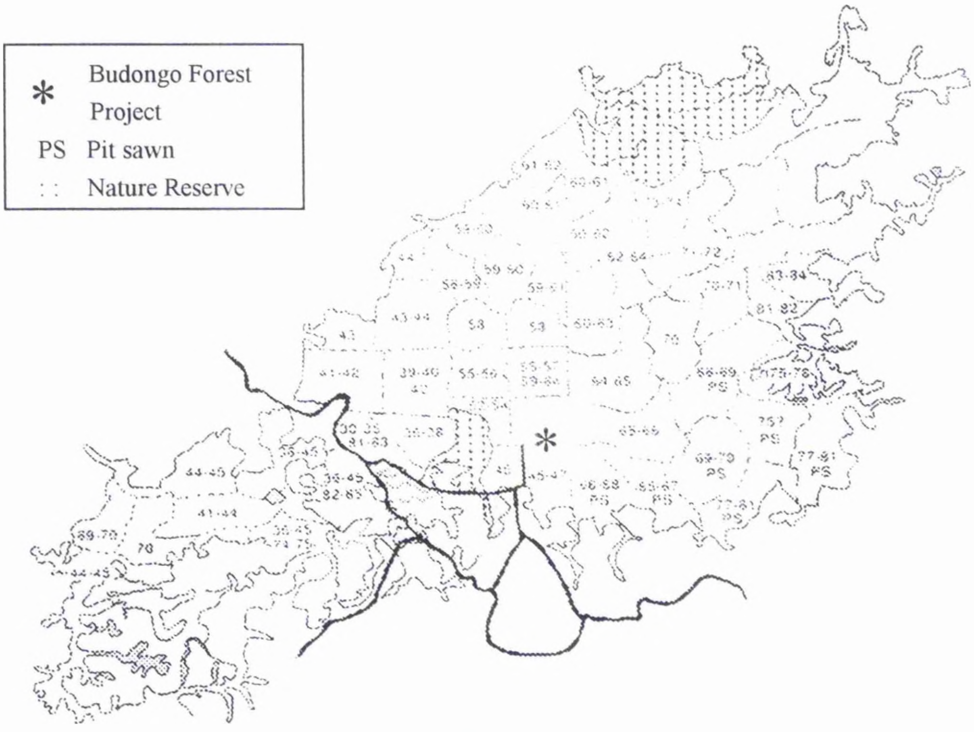


Figure 2.3 History of logging operations in Budongo Forest; numbers represent logging dates, in years (from Plumptre & Reynolds 1994)

logging dates, management practices and amount of timber extracted (see (Plumptre 1996). Almost 80% of this area has now been logged, and Synnott (1985) argues that the only areas of the forest undergoing long-term succession are those unlogged areas, now protected by the Nature Reserve. The remainder has been managed for commercial purposes, using various methods that encourage the growth of those species characteristic of mixed forest. The prime focus of management policy therefore was to reduce the area of climax forest, which it was thought, competed directly with the timber-rich mixed forest. Following an attempt at a mahogany replanting scheme in the 1950s, which resulted in a mass elephant control programme in order to protect the plantations (Patterson 1991), a refining operation was implemented using arboricide to kill trees that were known as 'weed species'. This operation was aimed at removing *Cynometra* trees in particular in order to favour the regeneration of mahoganies (Plumptre & Reynolds 1994).

Current situation

Of the four sawmills that once operated in Budongo, only one is still active, operating a concession in the north-eastern part of the forest. The sawmills fell victim to the general collapse of the country's infrastructure under Idi Amin in the 1970s. During this time, mechanised logging was overtaken by pit sawing, which proved a far more economical alternative (see **Figure 2.3**). Pit sawing is the local logging technique, whereby trees are felled, heaved onto constructed platforms and then cut into planks over a pit. Although less destructive than mechanised extraction, it is less easy to monitor as many separate trees are being felled in different locations at the same time.

The logging trade at Budongo attracted large numbers of employees from not only Uganda but also what was then Zaire, and Rwanda. Many of the people remained following the winding down of the sawmill factory, and their numbers increased with mass immigration during the civil unrest in the 80's. This all led to human occupation of the grasslands surrounding the forest with increased pressure on the forest resources and their consequent misuse. In the last 30 years, illegal pit sawing has damaged the forest in patches by systematic removal of all the largest and most precious trees, and now seriously threatens both the economic and ecological future of Budongo Forest. In addition to and not unrelated to illegal logging, poaching of wildlife and the encroachment of human settlements and agricultural land into the forest are evident (pers. obs). During the study period I personally recovered over 11 snares from pit sawing camps deep in the forest as well as the perimeters of cultivated fields. The nature of these snares and the 'accidental' injuries they cause to chimpanzees in particular is discussed in detail in **Chapter 3.**

Fauna

There are five species of diurnal primate in the forest: chimpanzee, olive baboon *Papio cynocephalus anubis*, black and white colobus *Colobus guereza*, red-tailed monkey *Cercopithecus ascanius* and blue monkey *C. mitis*. The nocturnal species of primates in Budongo are unknown, but during the study period there were two independent sightings of pottos *Perodicticus potto*. Estimates of the number of chimpanzees in the Budongo Forest range from 675 to 2046 depending on the censusing methods used (Plumptre & Reynolds 1996), with figures of 906 or 950 based on nest counts corrected for those individuals which do not build nests and for the proportion of nests re-used (Plumptre & Reynolds *ibid*).

Other large mammals include bushbuck *Tragelaphus scriptus*, red duiker *Cephalophus rubidus*, blue duiker *C. monticola* and bushpig *Potamochoerus larvatus*. Buffalo *Synceros caffer*, lion *Panthera leo* and leopard *P. pardus* are still found in the northern most part of the forest only. Many other smaller mammals can be found, including genets, civets, tree hyraxes, squirrels, the African tree pangolin *Manis tricuspis* and many species of rodent including the brush-tailed porcupine *Hystrix atherurus*.

The forest is also home to a huge diversity of bird species, many of which are endemic to the Albertine Rift (J. Lindsell pers. com.). The crowned hawk eagle

Stephanoaetus coronatus, which can be found here, is a known predator of primates (J. Lindsell pers. com.). A vast array of reptiles and amphibians, many of which remain to be documented, live in and around the forest, including many venomous species of snake as well as large pythons.

Budongo Forest Project

The Budongo Forest Project was set up in 1990 by Professor Vernon Reynolds, in order to assess the problems faced by the Budongo Forest, and suggest ways in which it can be exploited economically at the same time as preserving its status as a refuge for biodiversity. The Project is located in the Sonso region of Budongo, named after the River Sonso that flows through this part of the forest. The research station is in a small clearing adjacent to the now largely defunct Sonso sawmill, and is close to the centre of the compartment termed N (Nyakafunjo) 3, selectively logged between 1947 and 1952 and now comprising typical Mixed forest (see **Figure 2.2** and **2.3**). In 1998, the Ugandan Forestry Department named this compartment a Site of Special Scientific Interest (SSSI).

In 1991 the Project secured funding from the Overseas Development Agency (ODA) in order to investigate the effects of logging practice on forest ecology, and the importance of frugivorous primates to forest regeneration. This study was conducted primarily by Dr A J Plumptre, co-director of the project from 1992 – 1997. This work formed a platform from which a number of diverse studies, relating to all aspects of forest ecology, sprung. In 1997, the Project secured a three-year grant from the Norwegian forestry organisation NORAD. This funding was intended primarily to support studies that investigated the importance of the forest's resources, including behavioural studies on its wildlife, and their impact on the local community. In response to this, my study on the effects of injury on chimpanzees will assess the long-term impact of the current levels of snaring on chimpanzee populations, and thus evaluate the consequences for both the growth of tourism within the area and the development of conservation measures.

Trail System

At the outset of the Project, a primate census study selected eight compartments (including N3), in each of which was cut five transects of at least 2km in length (Plumptre & Reynolds 1994). In N3 at least, these transects have been developed by the Project as an intricate grid system which enables rapid access through the forest, for chimpanzees and human observers alike, as well as a means of orientating oneself in relation to the research station (see **Figure 2.4**).

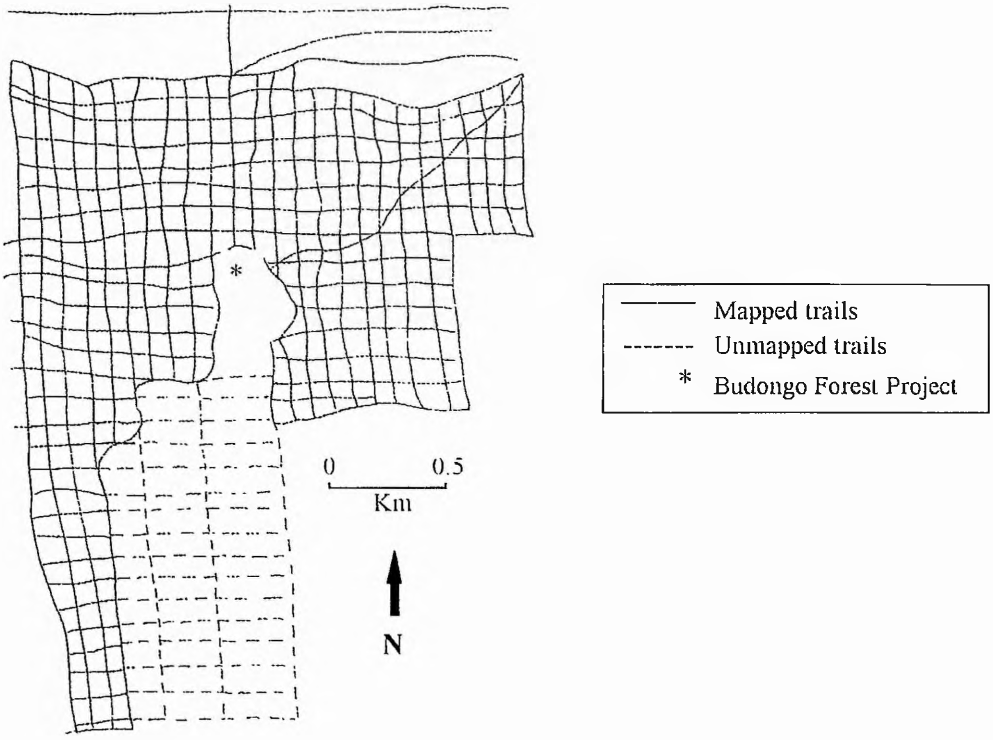


Figure 2.4 Trail system in the Sonso area of Budongo Forest

The current trail system consists of north-south and east-west trails which intersect to give 'blocks' measuring roughly 100m by 100m, the accuracy of which depends primarily on physical obstacles such as swamp forest or small valleys, which often lead to a deviation from the true compass bearing. To the east, the trail system is crossed by the main logging road, and to the west, trails cut at 200km interval connect to the Nature Reserve. To the south-west, the boundary running north-south between mapped and unmapped trails, marks the main road leading out of the forest, and to the south-east lies primarily swamp forest, which reflects the discontinuation of the grid system in this area, as fluctuating water levels severely hinder the cutting of trails. In addition to the trail system designed by the Project there a number of well-trodden paths leading in from the forest edge that are used by local villagers for collecting firewood, as well as meandering trails deep within the forest used primarily by pit sawyers for transporting cut timber.

Study community

The chimpanzees of the Budongo Forest were first studied in the 1960's by Vernon and Frankie Reynolds (Reynolds & Reynolds 1965) and by Yukimaru Sugiyama (Sugiyama 1968; 1969). Vernon Reynolds resumed work on a continuing basis when he initiated the Budongo Forest Project in 1990. In 1990, habituation of a single community of chimpanzees began. This was termed the Sonso community, whose range encompasses compartment N3. At the beginning of the study this community totalled 52 named individuals, which had risen to 53 by the end of the study. These chimpanzees have never been artificially provisioned, thereby offering the ideal situation for a valid study on naturally acquired manual feeding skills in the wild. **Table 2.1** gives a breakdown of the study community by age and sex and presence of injury.

A number of demographic changes occurred during the study. Immediately prior to the study, two births occurred, and there was a further birth during the study period. In addition, a previously unknown juvenile female was recognised and named. It is likely that she is an immigrant to this community. There was one presumed death in the community: an adult male disappeared in September 1997 and was not seen again. One major new injury occurred during the study period: a juvenile female lost her hand to a snare.

Table 2.1 Demographic distribution of the Sonso community

		Able-bodied		Injured	
Age-class	**Sex**	**Aug 97**	**Sept 98**	**Aug 97**	**Sept 98**
Adult	Males	9	8	4	4
	Females	8	8	4	4
Adolescents	Males	3	4	0	0
	Females	4	4	1	1
Juveniles	Males	6	5	0	0
	Females	5	5	0	1
Infants	Males	4	4	0	0
	Females	4	5	0	0
Total		**43**	**43**	**9**	**10**

Sampled individuals

This study focused on all adult and adolescent individuals in the community. Two adult females were peripheral to the group and were seen infrequently. On occasions when these females were observed they were extremely nervous and could not be followed. Consequently, these individuals were not used as focal subjects. In order to omit age-dependant variation in feeding skill, dependants (juveniles and infants) were not sampled. **Table 2.2** gives a detailed breakdown of the sampled animals, providing names and identity codes for each individual. For this study, injured individuals are restricted to those with major limb deformities, and those individuals with missing parts of single digits (Maani) were considered able-bodied by comparison. The total number of sampled individuals therefore totals 30, with 22 able-bodied and 8 injured individuals.

Table 2.2 Breakdown of sampled individuals

[breakdown is as of August 1997. † denotes mother with dependant offspring; * denotes mother with infant not yet weaned; known or putative mothers of each individual are placed in brackets]

Able-bodied				**Injured**			
Name	**Code**	**Name**	**Code**	**Name**	**Code**	**Name**	**Code**
Adult males		***Adult females***		***Adult males***		***Adult females***	
Black	BK	Kutu †	KU	Kikunku	KK	Banura †	BN
Bwoya	BY	Kwera †	KW	Muga (NB?)	MU	Kigere †	KG
Duane	DN	Nambi †	NB	Tinka	TK	Kalema †	KL
Jambo	JM	Ruda †*	RD			Zana †	ZA
Maani	MA	Ruhara †*	RH				
Magosi	MG	Zimba †*	ZM				
Nkojo	NJ						
Vernon	VN						
Zesta	ZT						
Sub-adult males		***Sub-adult females***		***Sub-adult males***		***Sub-adult females***	
Andy (NB)	AY	Janie	JN			Kewaya (ZM?)	KY
Nick (RH)	NK	Mukwano	MK				
Zefa	ZF	Sara	SR				
		Vita	VT				

Habituation

Work to habituate the Sonso community of chimpanzees began in 1990. By 1995, all the individuals currently recognised in the community had been named and had reached a sufficient level of habituation to permit the presence of human observers, at least whilst they were in the trees. My arrival at Sonso coincided with that of three other researchers who would also be observing this particular community of chimpanzees over the course of the next 14 months. At the beginning of the study period a number of individuals, in particular females, were still noticeably shy when on the ground, and attempts to follow these individuals proved futile, as they would rapidly seek refuge in dense undergrowth within the blocks. The males were far more amenable to pursuit on the ground and in the presence of males, females could be followed with relative ease. As the study progressed, the continual presence of four researchers and their field assistants with the chimpanzees began to pay dividends, and after the first six months we were able to observe and follow individuals on the ground at distances of 3-4 metres. Lone females with infants still appeared nervous on the ground however, evidence of a past legacy when poachers often shot mothers in order to capture their young. These individuals were best observed when in large groups.

Data collection

A pilot study was conducted between March and May 1997, which I used to refine my field methods and learn how to identify individual chimpanzees. During this time, Budongo Forest Project assigned me a field assistant, James Kakura, whose intended role was primarily that of a tracker and a source of expertise on tree identification. All field assistants at the Project had previously received training in plant identification from samples orginally sent to the herbarium at Makerere University in Uganda. The main period of data collection was carried out between August 1997 and September 1998. During this time chimpanzees were observed on 229 days amounting to over 850 hours contact time.

Chimpanzees were located each morning either by calls or by visiting areas in which chimpanzees had recently been sighted. Failure to locate chimpanzees using these two methods prompted a tour of known fruiting trees within the home range. If we were still unsuccessful in locating chimpanzees using these methods then a backup method was used which involved waiting at major junctions of the trail system, which maximised our chances of hearing and following calls from any direction. From May to July 1998, chimpanzees were ranging far from base camp and were frequently difficult to locate. It is thought that the heavy rains and prolonged wet season in the latter part of 1997 had a major effect on the food availability and consequent ranging patterns of Sonso chimpanzees. This is reflected in the paucity of data collected during these three months.

Once chimpanzees were located an attempt was made to stay with the group for as long as possible. Sporadic searches for other groups were often conducted by my field assistant whilst I collected data on the current group. In this way we could monitor the activity of more than one group of chimpanzees and collect data from as many individuals as possible throughout the day. Following the chimpanzees as they travelled was aided by the trail system but impeded by the thick undergrowth as soon as the chimpanzees moved within the block or travelled beyond the limits of the cut trails. Consequently, chimpanzees were followed whenever possible, but often we were forced to either wait or 'head them off' as they moved into a more accessible area. Observations of chimpanzees were made with binoculars (Zeiss - Dialyt 10 x 40B T* for myself, and Nikon 10 x 50 for my field assistant), and when terrain permitted, a tripod-balanced telescope (Opticron HR. 66) with angled eyepiece.

Two methods of data collection after Altmann (1974) were used: sequence sampling (continuous) and scan sampling (instantaneous).

Sequence sampling

Bakeman & Gottman (1986) perform a thorough review of sequential data collection techniques and conclude that focal sampling, where the sample is of a particular individual for an allotted time period, is extremely limiting when the interaction occurs at the beginning or end of the sample, where parts of the interaction sequence will inevitably be lost to the observer. Consequently, event based coding was used to record feeding sequences. This is referred to by Altmann (1974) as sequence sampling, where the focus of the observation is the interaction sequence, in this instance between animal and food item, rather than any particular individual. This method was tried and tested by Harrison (1996) in her study of food processing skills in vervet monkeys. The primary advantage of using this method is that it allows for large samples of data to be collected: because the observer takes the next available interaction in the group once the previous interaction has terminated, time is seldom spent without available data. This is particularly pertinent to field studies where the number and location of subjects is unpredictable from one day to the next.

Sequence sampling differs from focal animal sampling in that behaviour-dependant rules determine the beginning and the end of a sample. It is important, therefore, that these rules be precisely defined so that the beginning and end of an interaction sequence can be clearly identified in the field. The sample period therefore began when an interaction started, in this case the touching of the food item. The sample ended when the interaction sequence was interrupted or terminated. This was identified by switching to another activity or moving away from the food item, when movement involved the whole body changing position only, and periods of inactivity of 20 seconds or more. In addition, these criteria ensured that samples were independent of one another. These independent interaction sequences were termed feeding *bouts*. Chimpanzees tend to accumulate leaves into the hand before placing into the mouth. This was termed a *handful* and formed the basic unit of sequential analysis. A bout therefore may contain several handfuls. It is important to note here that using handfuls as units of analyses are not appropriate for all food types. In Byrne & Byrne's study on plant gathering techniques in gorillas (Byrne & Byrne 1993), handfuls formed the most useful measure in leaf processing tasks, but not, for example, in stem-processing tasks, where processing involves iterative loops spanning across several handfuls of food. A handful is therefore tentatively adopted here as the unit of sequentially analyses, and food specific variations in this methodology are addressed in the appropriate chapters.

Data collected

Data on food processing was collected using two recording methods: tape recording and hand-held computer. Irrespective of method used, all recorded bouts contained the animal's name, date and time of observation, food species, part of food ingested and feeding posture. For both tape-recorded and computerised bouts, posture was also recorded, as the use of limbs in postural support whilst feeding may constrain choice of feeding technique. With this in mind postures were categorised on the basis of how many limbs were 'used' up in postural support, and by default how many limbs that left 'free' for food processing'. Posture could easily be recorded at the beginning of each bout as, unlike Russon reports for orangutans for example (Russon pers. com.), chimpanzees change posture by *interrupting* food processing rather than simultaneously changing posture and processing food.

The following categories of posture were distinguished:

Seated (SE)	animal seated and feeding within arms reach
Seated-reaching (SL/R)	animal seated but leaning over, with one hand in support, to bring food item into range
Bipedal support (2L/R)	animal bipedal, and supporting with one upper limb, whilst feeding with the remaining upper limb
Tripedal support (3L/R)	animal suspended by three limbs (upper or lower) with only one limb (upper or lower) available for feeding
One-arm support (1L/R)	animal suspended by one limb only (typically upper), with remaining limbs available for feeding.

Additionally, for every female sampled, the oestral state and/or presence of a dependant were recorded. A three point scale was used to describe the anogenital swelling of a female: 0 (no swelling); 1 (some swelling); 3 (full swelling). Both the presence of a swelling and the presence of a dependant are likely to introduce additional postural constraints during feeding.

Tape Recording

Using a voice operated Sony Dictaphone, records were taken of the sequence of behavioural elements used to process each handful. Individual *elements* were described at the level of detail such that each resulted to a visible change in plant material (see Byrne & Byrne 1993). A full catalogue of elements can be found in **Appendix I**. It is recognised that certain elements comprise a suite of actions that could be argued as forming a small subroutine (eg. 'strip up'). However, for the purpose of this study, an individual element was considered to form the basic building block of complex behaviour. Any regularly used sequential ordering of individual elements, was defined as a *technique*.

For each element, two additional data components were recorded. The first of these was the body part used, recorded as left or right hand, both hands, left or right foot or mouth. Secondly, the grip type used was noted. Due to differences in gross anatomy of the hand between gorillas and chimpanzees (primarily concerned with the relative length of fingers and thumb), discrepancies between this study and that of Byrne & Byrne's study on mountain gorillas were anticipated in the terminology of particular actions. In recognition of these differences in hand morphology, I used the grip classification of Marzke & Wullstein (1996), which was designed specifically for chimpanzees, based upon their observations of locomotor and manipulative behaviour in captivity.

All tape recorded samples were transcribed into text files on a laptop computer (Gateway 2000 Colorbox) at the field station, and indexed by animal name and food type.

Hand-held computer

A hand-held computer (Hewlett Packard HP200LX) was programmed to record timings using the Observer software package. At the beginning of each bout the computer prompted for the name of the plant part and the feeding posture. During the bout, key presses were used to record the time at which each handful of processed food was placed in the mouth, as well as any change in posture. In the case of the former, the designated key also recorded the hand used: L (left), R (right), B (both) or O (other). The programme also enabled notes to be added after each handful. In this way, exceptionally long or short handfuls could be identified as such. When the bout was terminated, the computer logged the total bout length.

At the end of each day, all samples were downloaded onto the computer at the field base and saved in the appropriate project directory according to the animal's name.

Data was collected for each subject on all observed bouts of feeding. For both recording methods, an attempt was made to collect equal amounts of data per individual in terms of handfuls. This was not always easy due to the fission-fusion nature of chimpanzee society and the difficulties this raises in terms of finding a particular individual from one day to the next. In addition, the dense undergrowth and variable levels of habituation across individuals often posed problems of visibility, particularly when feeding on food items located on the ground or high in the canopy. This problem was exacerbated for sequential data collected using the Dictaphone recording method, where details of individual hand movements needed to be observed. Consequently when visibility permitted collection of feeding sequence data, this method was favoured above that of the hand-held computer. Considerable variation was therefore anticipated in both observation times across subjects, and visibility conditions across different food items. In order to deal with this, a minimum of ten handfuls of a particular food type was set as the criterion for each individual (see **Table 2.3**).

Table 2.3 Amount of data collected for each individual, by recording method

Ind	Dictaphone recording method			Hand-held recording method		
	Total no. bouts	Total no. handfuls	Median no. handfuls/food type	Total no. bouts	Total no. handfuls	Median no. handfuls/food type
AY	27	117	5.5	64	502	45
BK	38	204	29	32	410	52
BN	6	42	15	10	160	34.5
BY	25	136	12	23	192	52
CL	5	15	7.5	9	97	15.5
DN	43	309	32.5	44	635	31
JM	9	67	3.5	10	104	28
JN	20	74	4	25	310	34.5
KG	15	119	15	35	375	41
KK	71	353	8.5	44	632	59
KL	53	299	25	48	510	43
KU	4	55	27.5	21	157	45
KW	18	98	18.5	38	406	27
KY	44	170	16	56	715	38
MA	35	283	9	49	536	36.5
MG	14	93	14	27	291	25
MU	6	46	5	29	247	51
MK	35	338	32	43	642	65
NB	32	297	13	19	383	42
NJ	21	96	13	32	373	39
NK	7	25	5.5	7	58	10
RD	12	139	26	17	200	100
RH	1	10	10	15	259	129.5
SR	4	25	12.5	12	174	87
TK	87	579	69	75	758	83
VN	25	238	12	47	460	31
VT	7	31	31	1	16	16
ZA	37	348	23.5	42	448	35
ZF	10	71	32	20	118	30
ZM	21	123	12	17	417	16
ZT	27	156	24	51	456	31.5

Scan sampling

In addition to data on food processing skills, it was considered appropriate to collect data on the daily activities of the community as a whole. This would allow any discussion on the effects of injury in feeding skill to be placed in context. For example, if an injured chimpanzee is unable to process a food type efficiently, we need to know if that food type plays an important part in the diet of Sonso chimpanzees before we can predict the likely long-term effects of injury. In addition, this data will provide useful information as to the broader effects of injury on chimpanzee behaviour.

Instantaneous sampling is defined by Altmann (1974) as "a technique in which the observer records an individual's current activity at preselected moments in time…it is a sample of states not events". Instantaneous sampling of large numbers of group members, by observing each in turn within a very short time period, is referred to as scan sampling (Altmann 1974). This is recommended in studies of the amount of time an individual devotes to a particular activity, and from this we can infer the relative importance of a particular activity to an individual. I chose a sample interval of fifteen minutes, a compromise between temporal dependence between successive samples (shorter time interval) and the risk of missing short-duration behaviour patterns (longer time intervals).

The collection of this data would potentially jeopardise the collection of sequential data, which is the primary aim of this study. To overcome this problem I enlisted the help of my field assistant, who was responsible for collecting the scan samples whilst I collected sequence samples. This was a simple and routine task for the field assistants at the Project, and James's experience in identifying both trees and individual chimpanzees were realised in his work, which was without fail meticulous and accurate.

Data collected

Data was recorded on checksheets designed specifically for this study. These data sheets were A4 sized paper and carried into the field on a clipboard. The design was extremely simple and consisted of only four columns. The first column contained the time of the sample, the second column contained the animal's name, the third column the activity of the named animal and the final column contained the position in which that animal was performing the activity. All visible group members were sampled on each scan. **Table 2.4** shows the total number of individual scans, per month, over the main study period.

Table 2.4 Total number of scans across individuals

Month (1997 – 1998)												
Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep
295	2467	2385	1328	1012	682	1753	1796	781	690	620	1531	128

Each completed sheet was indexed by the name of the observer (either James or myself) and the date. Activity and position was coded; the precise method of which was agreed between my field assistant and myself. The following behaviour patterns were distinguished:

Activity

Feeding (species and plant part)	ingesting any food item
Terrestrial locomotion	any whole body movement on the ground which implies travel - generally quadrupedal
Moving within tree	arboreal locomotion within a single tree – generally involves relocating to

	a different food patch within a feeding tree or else climbing up/down from ground
Moving between trees	arboreal locomotion from one tree to another - generally involves movement into or out of a feeding tree without coming down to the ground
Self grooming	an individual grooms oneself (grooming includes combing through the hair with fingers as well as scratching)
Allo-grooming (receiver)	individual is groomed by another
Allo-grooming (actor)	individual is grooming another
Resting	individual is not actively engaged in any other behaviour
Other	any behaviour other than that listed above – includes nesting, copulations and play
Position	
Canopy	apical branches of the tress
Lower	main trunk of the tree and the first branch fork
Middle	default position – neither canopy nor lower

Ground	on the ground, or else a level surface that is not in the tree i.e. fallen log

General analysis methods

Details of analysis methods particular to each chapter are described therein. Parametric statistics were used only when the data approximated a normal distribution. This was assessed by visual assessment of histograms and probability plots, and by the use of a test of skew, contained within the statistical computer software used. In cases where the data failed to approximate to a normal distribution using these methods, non-parametric statistics were applied. All tests are two tailed unless otherwise stated.

The majority of analyses were conducted using SPSS for Windows 95 Version 7.5. Microsoft Excel 97 was used for limited statistical analysis and graphical output. Additional statistical procedures were carried out with the aid of Zar (1996) and Siegel and Castellan (1988). In order to calculate individual usage of element actions a DOS version of a programme designed by John Henderson, of IT Services at the University of St Andrews, was used. This converted sequences of elements into long strings of unique codes and for each animal feeding on each food type calculated the total number of times each unique code was used.

Part 2

Classifying and measuring the effect of injury

The following two chapters present empirical data designed to give a broad introduction to injury and its effects on chimpanzee behaviour.

***Chapter 3** describes the nature and extent of injury in the study population and discusses suitable ways in which this can be measured in the field.*

***Chapter 4** highlights different aspects of feeding behaviour in Sonso chimpanzees and identifies those most likely to be affected by injury.*

These two chapters set the scene for a directed approach towards the analysis of feeding skills and the effect of injury on Sonso chimpanzees.

Chapter 3

INJURY IN CHIMPANZEES

Approximately one quarter of the Sonso community of chimpanzees in Budongo Forest, Uganda suffers from some form of major limb injury. In the majority of cases these injuries involve either the complete loss of a hand or foot or partial and complete paralysis of at least one limb without loss to the extremity. In all but one instance these injuries are the likely result of having encountered snares set for small antelope and other prey on the forest floor.

The most common snares are those consisting of steel wire nooses. Simple yet effective, the wire is of a high tensile strength so that when sprung, the noose embeds itself deeply in the flesh where it may stay on until it rusts off, or until natural amputation occurs, or the individual dies. Three juveniles were found trailing wires from their wrists when first observed in 1994, and all three have since lost the wires, and not only survived but completely recovered. Two other types of snare are also reported as being employed within the forest: the spring snare and the 'man-trap' or 'land-mine' (Waller 1995). The spring snare is more sophisticated than the wire noose in that the limb is wrenched upwards due to the tension in the sprung tree stem. This produces sufficient force to cause breakages and fractures in the limb. The 'man-trap' is the most severe of the reported trapping devices. The snare is triggered by stepping on a plate lying between two parallel steel jaws which when sprung bite deeply into the limb. This is likely to result in amputation of the limb. No evidence of either of these two snares was found during the study period and thus while it is conceivable they were employed in the past it appears that they are no longer widely used.

At the time of writing, there are eight adult chimpanzees and one juvenile with upper or lower limb injuries. These injuries are permanent, and in all but one case were present when the individuals were first seen in the community, so that it is impossible to tell for certain whether these chimpanzees are the unlucky few who got caught in snares, or whether many more died than survived. The exception is the juvenile, a female, who was first observed trailing a wire in June 1998. By July, the hand had become completely amputated from the wrist. This is the only new injury to have occurred within the community since the project began in 1990. The high incidence of adult chimpanzees with injuries, is probably best regarded as part of the legacy of economic destruction and biodiversity loss that the present government inherited from Idi Amin and his successors.

In the absence of life-history data little can be deduced about the extent of recovery since the initial injury, but it is both impressive and intriguing that these individuals survived at all. The injuries sustained by these individuals will have initially produced extensive open wounds, and a consequently high risk of death from excessive blood loss and infection. In his Masters thesis, Waller (1995) explores some of the behavioural and physiological aspects as to why an injured chimpanzee might have what can be described as an unusually good prognosis.

Factors contributing to survival following injury

From a physiological stance, it has been suggested that non-human primates display significant resistance to infection (Fowler 1986). There is little doubt that without the technology of modern medicine, a human in a similar situation to that in which a snare' chimpanzee finds itself, would not fare nearly so well. Both humans and chimpanzees are similar in that it is considered important to debride necrotic tissue from the site of injury. For chimpanzees, natural blood flow as opposed to primary suture, is effective in cleaning the wound and reducing the risk of infection. Waller (1995) extrapolated from this to instances of limb injury in humans, suggesting that failure to apply a suture following severe limb trauma may not overly endanger the injured individual.

The use of medicinal plants by wild chimpanzees has been reported in a number of studies (e.g. Huffman & Wrangham 1994; Newton 1991; Wrangham & Nishida 1983). Many of these plants contain compounds also used in traditional (and modern) human medicine for the healing of wounds. The idiosyncratic and very deliberate execution of feeding techniques associated with the use of these plants leaves little doubt as to the purpose of consumption. Whether this ability to diagnose and treat one's own ailments requires conscious decision-making however, is a moot point. Of the tree species with known medicinal properties linked to chimpanzees elsewhere, the leaves of *Commelina* spp., and the bark and fruit of *Ficus exasperata* are part of the diet of the Sonso community of chimpanzees. The first of these has been shown to be effective against bleeding. In her thesis on the use of Budongo Forest's products by the local people, Johnson (1993) reports the use of leaves of *Erythrophleum suavelons* to treat wounds, and also the use of plants as anti-inflammatory agents, eg. *Terminalia* spp. Although these species are recorded in the diet of chimpanzees at Budongo, they have not been observed to feed on those particular plant parts.

The change in behaviour of conspecifics elicited by the presence of an injured individual may also affect chances of survival. Boesch (1991a) describes how a chimpanzee with serious injuries, incurred as a result of a fight with a leopard, was surrounded by conspecifics who proceeded to remove particles of dirt and blood with fingers or mouth, before licking the wound clean, and presumably reducing the chance of infection. This particular chimpanzee was receiving attention two months after the attack. Changes in group behaviour towards an injured individual are not limited to observations on chimpanzee society. In their study of a brain damaged infant in a free-living troop of Japanese monkeys Fedigan & Fedigan (1977) reported that during provisioning, the infant would often feed on or next to the alpha male's food pile. After threatening and chasing away the mother, the alpha male seldom continued to persist in threatening the infant, so long as he maintained a low profile. In this way, the alpha male and the infant fed from a large food pile, whilst the other members of the troop ate from smaller neighbouring piles. Reports such as these can prove useful in understanding issues of a similar nature in human evolution. Quiatt *et al.* (1994) refer to evidence of physical disability in the hominid fossil record, and how this can be used to infer the level of social organisation, and the type of social and physical support that would have been required for that individual to have survived. For hominids of the Plio-Pleistocene, *Homo habilis*, *Homo erectus* and perhaps even for Neanderthal peoples, they suggest the key to survival of disabled individuals was the free flow of information concerning local resources. Thus, the issue was not one of physical care or special kinds of social support, as we see in modern *Homo sapiens*, but rather communication and undifferentiated responses across able-bodied and disabled individuals alike. In human communities this would be identified as 'tolerance' or 'respect'. They suggest that this may also be the case for disabled chimpanzees, referring in particular to the severe limb injuries shown by the Sonso community.

It is perhaps telling that there are so few studies documenting incidences of major limb injury in non-human primates. Arboreal primates live in an environment where physical injuries can easily occur, and the territoriality of many primate species can result in a high risk of injury as a result of intraspecific conflict. It seems that the ephemeral nature of the majority of these injuries enables the individual to survive long enough for the wound to completely heal. Furthermore, there is an almost total absence of studies reporting injured individuals surviving to adulthood in non-human primates other than great apes. The few instances that have been reported have been limited to injury in infants (as in the Fedigan's study) and juveniles, where mothers are found to provide care well above the level directed at normal infants (Chapman & Chapman 1987; Nakamichi *et al.* 1983). In addition to maternal care, both behaviour and the natural healing processes of the body are likely to show greater plasticity at an earlier age. Longitudinal studies on Japanese monkeys however, have shown that individuals with severe traumas are unlikely to survive beyond four years of age.

The fact that over 20% of the adult population in the Sonso community of chimpanzees have survived a major limb injury is therefore quite remarkable. Injury to chimpanzees as a result of snares occurs at many field sites across Africa (Stokes *et al.* 1999), and their apparently high rate of survival stands out among great apes. Even then, the frequency and severity of injury in the Sonso community is particularly striking, and worthy of further investigation.

In this chapter I will discuss ways in which the effect of injury can be systematically measured in a wild population of chimpanzees. In a broad treatment of the effects of injury on everyday activities, I will use some of these measures to illustrate the nature and extent of the relationship between injury and behaviour in the Sonso community of chimpanzees.

Concepts of impairment, disability and handicap

In order to investigate the effect of injury on chimpanzees in a systematic way, I turned to the literature on health psychology in studies on humans. The effect of injury can be measured at three different levels: *impairment, disability* and *handicap*.

The International Classification of Impairment, Disability and Handicap (ICIDH: World Health Organisation, 1980) proposes a theoretical model that encompasses these three concepts of injury or 'disease'. Rather than implying a direct relationship between the cause of the 'disease' and its manifestation, it offers different dimensions of the consequence of 'disease'. The proposed model is shown in **Figure 3.1**

The definitions of each of these concepts (Wood 1980) are as follows:

Impairment, in the context of health experience is any loss or abnormality of psychological, physiological or anatomical structure or function (whether or not due to a disease, provided it is *exteriorised)*.

Disability in the same context is any restriction or lack (resulting from impairment) of ability to perform an activity in a manner or within the range considered normal for a human being in his or her environment. Clearly, other dimensions are added here: disability is not merely the consequence of disease, but an interaction with the habits, training, skills and expectations of that individual.

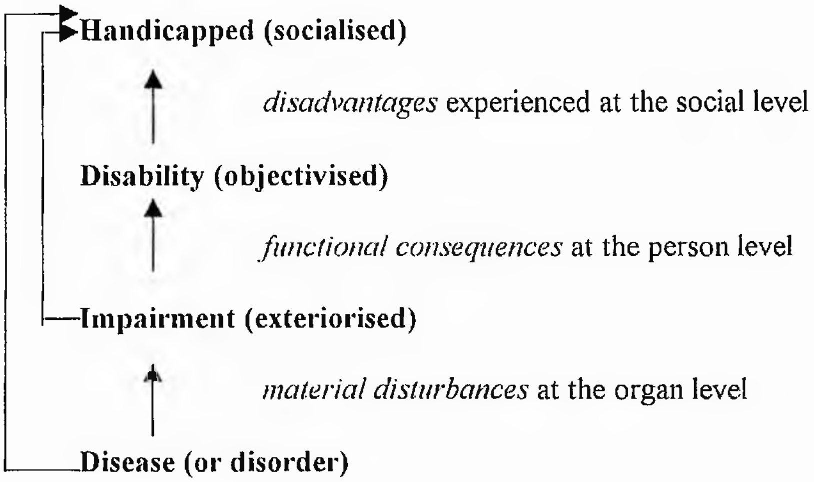


Figure 3.1 The ICIDH model of sequential/parallel grouping

Handicap is a disadvantage for a given individual, often (although not always) resulting from an impairment or disability that limits or prevents the fulfilment of a role that is normal, depending on age, sex and social or cultural factors, for that individual. This is a much more complex level which is difficult to rate objectively for the purpose of clinical trials as many variables, which are personal to that individual, such as the level of previous achievement, the expectations of the family and of the community, and the financial context, all contribute to the overall handicap.

This model can be applied to our community of wild chimpanzees, with some modification. Most straightforwardly, the 'disease' - or in this case initial injury - will result in an impairment. Impairments were documented by Waller (in prep.), describing the nature and extent of each individual injury, extrapolating from clinical conditions in humans to those of the chimpanzee.

The impairment in turn may have functional consequences, which would lead to disability in everyday activities such as feeding or locomotion. For example, Reynolds *et al.* (1996) found injured individuals to be disabled with respect to positional behaviour in fruiting trees. In a comparison with able-bodied individuals, injured chimpanzees fed higher up in the tree where there are more branches to lean against for support. However, Quiatt *et al.* (1994) found injured individuals to be well integrated spatially with their able-bodied counterparts in both terrestrial *and* arboreal feeding groups, which brings into question the extent of this particular disability.

Disability, in turn, may have implications at the third level of this model, that of handicap. It is at this point, however, that the analogies between human and chimpanzee populations begin to break down. To a wild community of chimpanzees external factors such as maternal and community support are likely to play less of a role than in human populations in determining the outcome of injury once the chimpanzee reaches adulthood. Furthermore, at this level of the model, the disadvantages are likely to be more extreme for a wild chimpanzee. In human populations, a handicap may affect the quality of life, whereas in a chimpanzee community a handicap will tend to exert its effect through lower reproductive success, and ultimately a decrease in fitness of the individual. This has been suggested by Reynolds *et al.*, (1996) who found limb injuries in chimpanzees at Budongo tend to reduce an individual's dominance status in the group.

For these chimpanzees, it is apparent that there are potentially heavy costs stemming from injury, and that the key to survival must be in overcoming these costs. Furthermore, the nature and extent of injury varies across individuals, and this will inevitably influence behaviour. One likely consequence of these injuries would appear to be feeding difficulties - specific to those foods requiring a degree of manual processing. It may be, however, that chimpanzees are able to compensate partially if not fully for their injuries, and that as a result, the *disabling* effect of injury on feeding skill, and the operation of such injuries as selective factors in intraspecific competition is minimised.

Studies on mountain gorillas and bonobos support the view that great apes are able to survive injuries by compensating for them. In his observations of limb abnormalities among wild bonobos, Kano (1984) concluded that "social position appears to be far more important than small differences in locomotor ability with regard to accessibility to food". He suggested that that the abnormalities he observed "were very likely maintained at a high rate because their effects on individual survival were negligible in [bonobo] social structure".

In a more systematic analysis, Byrne & Byrne (1991) were able to show these compensatory strategies at work in the plant processing skills of gorillas. They investigated the feeding behaviour of an adult female, Pandora, with extensive injuries in both hands. In the right, the little finger is flexed rigid and both digits 2 and 3 are non-functional. All that remains of the left hand is part of the thumb, which still retains some function. Despite these injuries, comparison with the population of non-injured female gorillas revealed no significant difference in food processing efficiency.

The nature of these compensatory strategies, however, at both a cognitive and motor level of organisation, remains largely unknown. An understanding of both the nature and extent of these strategies is not only important in accurately assessing the viability of chimpanzee populations, but also holds interest to clinical practice in humans. In the absence of external factors such as community support and financial context in chimpanzee society, we can more accurately assess the direct relationship between level of impairment on one hand and disability and handicap on the other; this may have particular relevance for the design of rehabilitation programmes.

For the remainder of this chapter, I will describe the level of impairment in the Sonso community, and based upon this discuss the design of a suitable instrument that is able to measure the extent of disability in a wild population of chimpanzees.

Nature and extent of injury in the Sonso Chimpanzees

Waller (1995; in prep.) distinguished two broad morphological categories of snare injury: claw-hands and wrists, and missing digits and entire segments of limbs. The descriptions below are taken from Waller (1995; in prep.) and modified to the extent where improved levels of habituation during the period of this study facilitated a more accurate account. Two individuals have sustained injuries to both of their upper limbs on presumably separate occasions. One of these individuals has a different category of injury to each hand. In order to emphasise the idiosyncrasy in both nature and extent of injury, I have grouped injuries according to individual rather than morphological category. Drawings are courtesy of John Galloway or, where stated, taken from original figures in Waller (1995).

Tinka (TK)

Both the left and the right hand of Tinka exhibit severe deformities. In the left hand (**Figure 3.2a**) most of the muscles of the wrist are paralysed, which allows a limited axis of movement, but in its relaxed posture the wrist is hooked and weakened. Digits 1-4 are incapable of assuming any other posture than that shown although the thumb has retained some function (**Figure 3.2b**). The right hand (**Figure 3.3a**) exhibits a deformity even more debilitating than that of the left. The paralysis of the wrist and hand is complete and voluntary movement impossible, although the digits can be passively extended (**Figure 3.3b**).

Zana (ZA)

Just as in the case of Tinka, both hands of the adult female Zana exhibit deformities (**Figure 3.4**). The left hand exhibits a combination of claw-hand and hooked wrist deformity. The hand is extremely wasted and the fingers are partially to totally clawed and incapable of voluntary movement. Waller stated that the thumb had retained normal function. However, on no occasion did I see the thumb used independently although the orientation of the hand may have prohibited this.

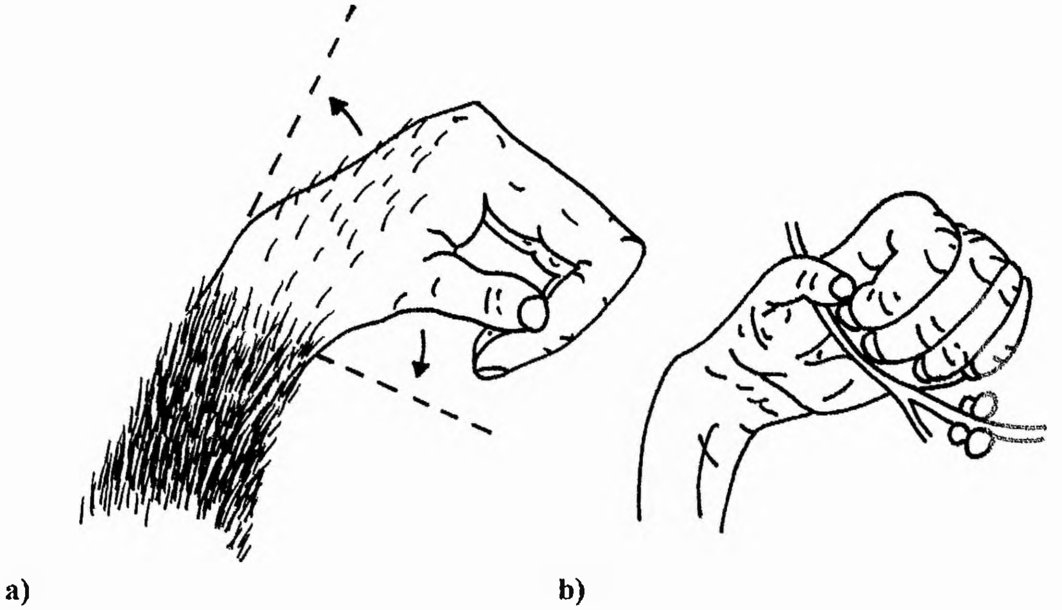


Figure 3.2 The left hand of Tinka, illustrating a) permanent flexion of the joints of the fingers and the degree of movement of the wrist within the axis shown, and b) normal functioning of the thumb in precision grip

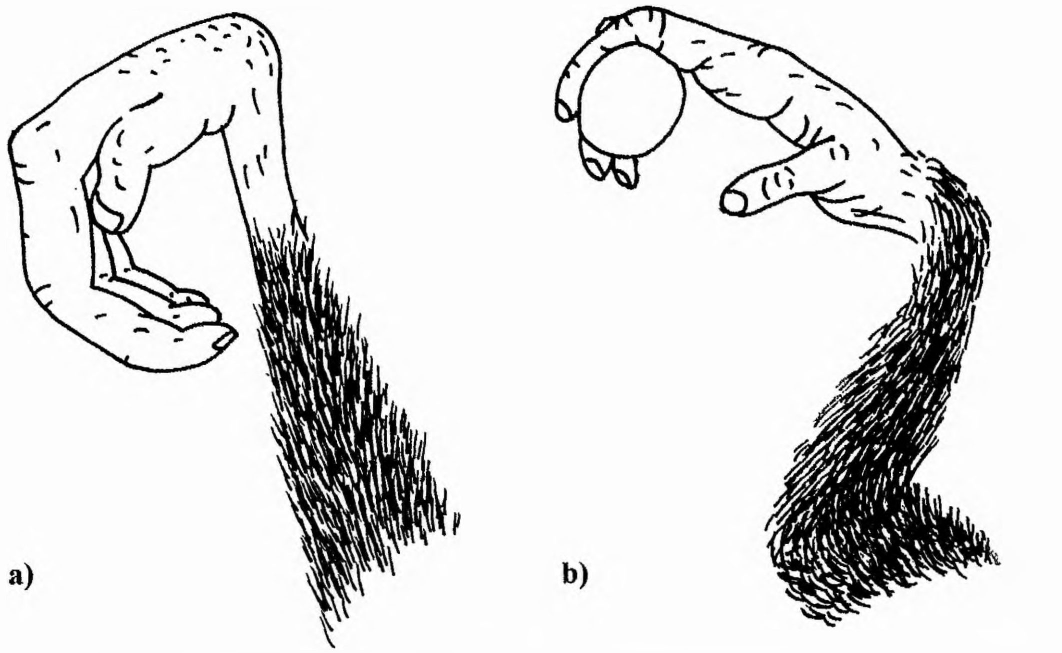


Figure 3.3 The right hand of Tinka, illustrating a) wasted wrist, adducted thumb, flexed joints of the digits and tilt of the hand downwards towards the little finger, and b) passive extension of digits

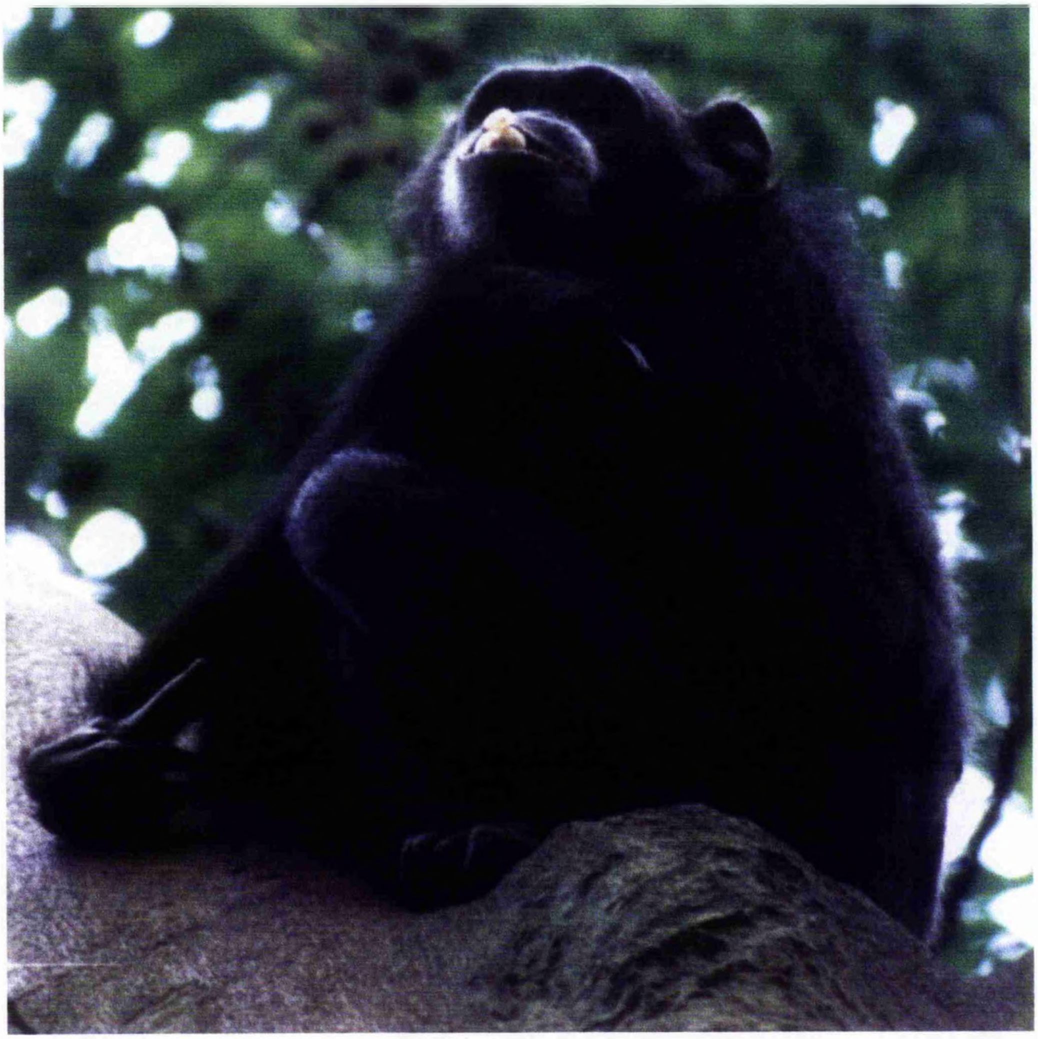


Figure 3.4 The left and right hand of Zana, illustrating the hooked wrist and degree of flexion in the digits of the left hand, and the missing digits of the right hand, with only the thumb prominent

The digits are configured so that the middle finger is abducted towards the forefinger, with both of these digits clawed to a lesser degree than digits 3 and 4. Although the wrist is obviously weakened it is has retained most - if not all – movement about its axis. The right hand exhibits an injury of a different morphological category to that of the left hand. It appears to have retained normal function at the wrist, but of the digits only the thumb is complete and appears to function normally. Of the remaining digits, all are barely visible, and the musculature of the hand is greatly reduced. Waller considered this to be the most elusive of all the injuries in terms of aetiology, although he concluded that the scarring of the wrist suggests a leg-hold trap or wire snare was responsible.

Kewaya (KY)

Figure 3.5 shows the extremely deformed hand of the sub-adult female Kewaya. The hand is totally paralysed, but still capable of a certain amount of passive movement - swinging limply about the wrist, with movement confined to a small axis. The wrist is extremely hooked at all times, stretched and folded over to such a degree that if the forearm is held upright, then the index and middle finger overlap the lower side of the arm. The hand is adducted and the fingers arranged in a highly distinctive fashion, with the middle finger so contorted that it lies in a position overlapping the forefinger. In pulling against the wire, Kewaya managed to fracture most of the wrist bones and probably snapped the extensor tendons of the wrist and thumb. This gives a powerful indication of the potency of a wire snare when pulled on by a chimpanzee.

Kalema (KL)

Kalema, another adult female, shows a similar claw-hand deformity to that of Kewaya. The right hand is rigidly hooked at the wrist (**Figures 3.6a** and **3.6b**), and the fingers are flexed and immobile The whole hand is emaciated and wasted.

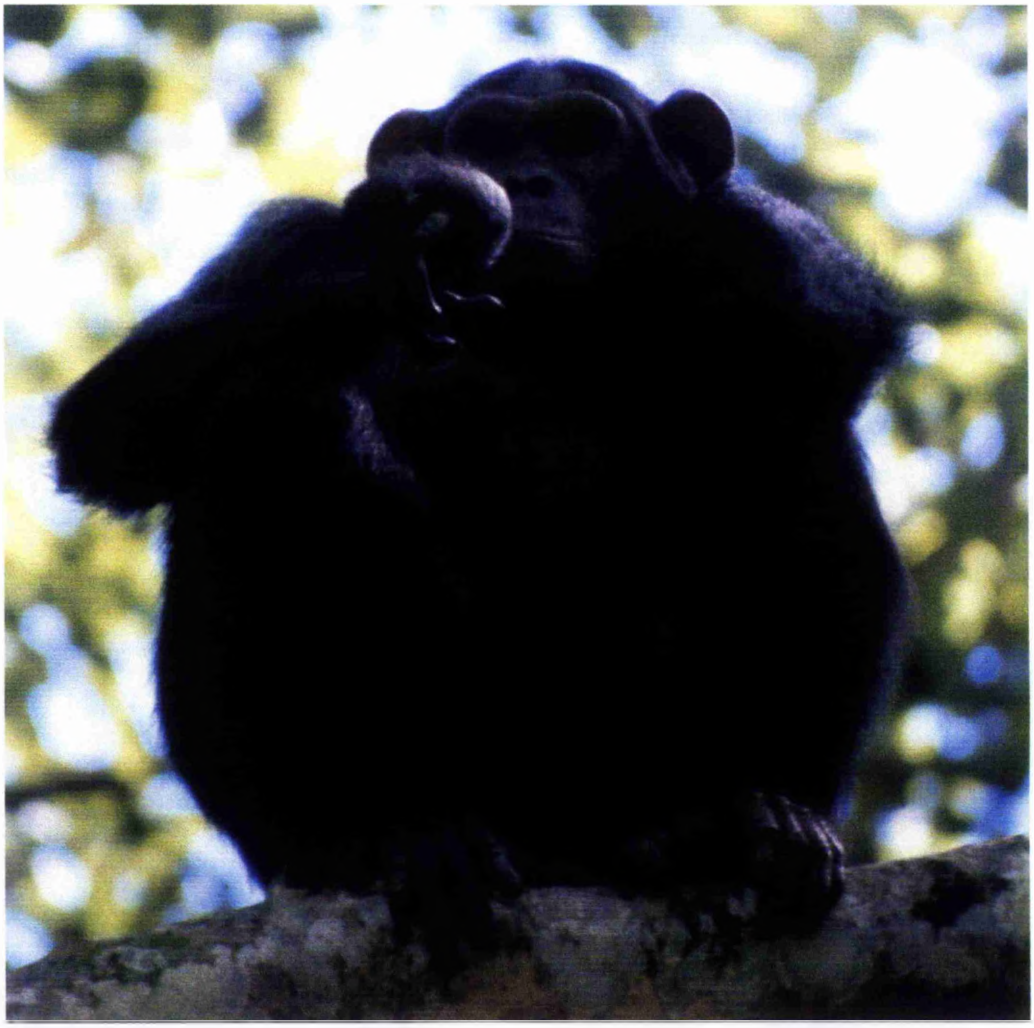


Figure 3.5 The right hand of Kewaya, illustrating the degree of twisting back of the hand

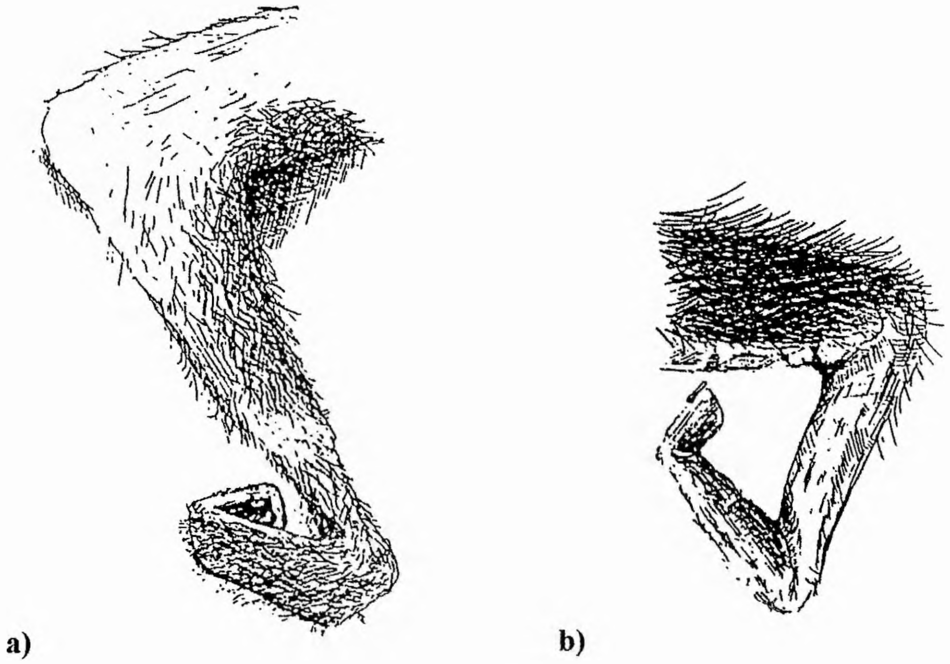


Figure 3.6 The right hand of Kalema, illustrating a) the clawed fingers, hooked wrist and adducted hand, and b) the little finger showing degree of flexion at the digital joints (from Waller 1995, with permission)

Kikunku (KK)

The adult male Kikunku has completely lost his left hand. The point of amputation is proximal to the wrist, and no element of the wrist joint is present (**Figure 3.7**). A complete loss of hair at the distal end of the remaining forearm is an indication of the considerable stress experienced as a result of the injury.

Muga (MU)

Muga, an adult male, is also missing a limb; his right hand. However, unlike Kikunku, the point of amputation is distal to the wrist (**Figure 3.8**) and consequently he has retained the majority of the wrist joint, which appears to function as normal.

Figure 3.7 The truncated left forelimb of Kikunku

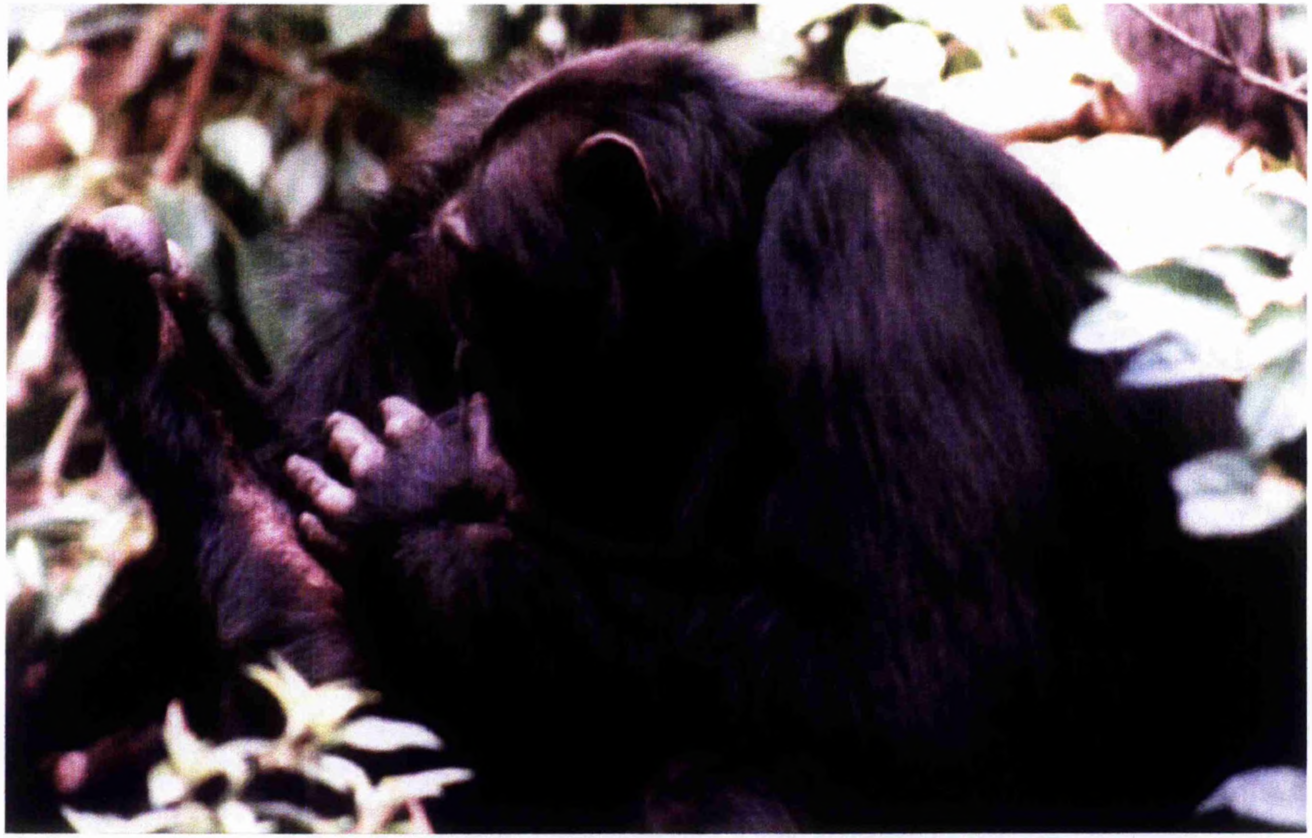


Figure 3.8 Muga's amputated right hand, illustrating the remaining wrist joint

Kigere (KG)

The adult female Kigere is missing her right foot from above the ankle.

Banura (BN)

Banura, an adult female, is the only one of the injured chimpanzees whose injury is the result of a congenital deformity rather than a snare. She has a considerably enlarged left foot, upon which two malformed digits lie contralaterally **(Figure 3.9)**. Waller confidently diagnosed the deformity as being akin to cleft foot. The existence or otherwise of any muscle action is difficult to determine by observation alone, but in agreement with Waller, neither the foot below the ankle nor the digits themselves were seen to move voluntarily.

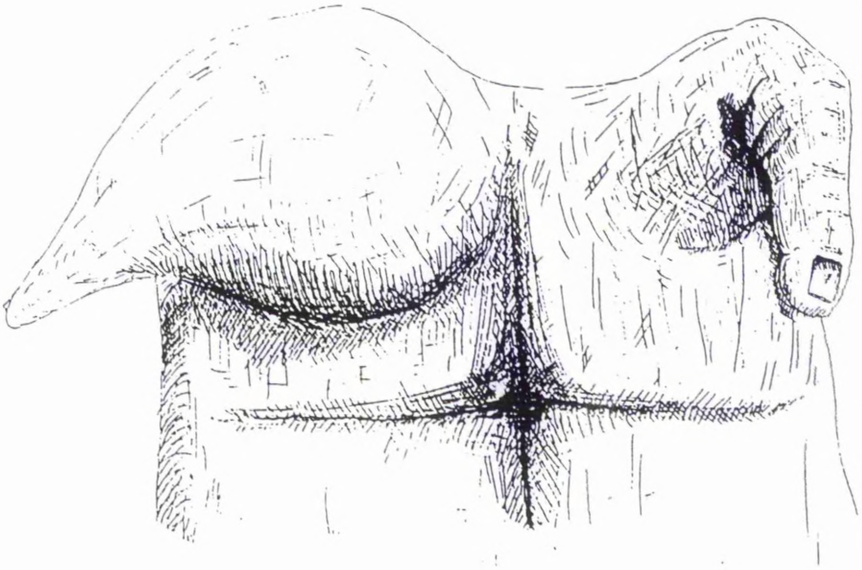


Figure 3.9. The left foot of Banura, illustrating the orientation of the remaining digits (from Waller 1995, with permission)

Nature and extent of disability in the Sonso chimpanzees

Because of the highly idiosyncratic nature of the injuries, a measure is required that can both encompass all of these different conditions, as well as being sensitive enough to capture the limitations of each individual injury. Behavioural measures of disability are becoming increasingly popular in studies of health care in humans, preferred over psychological and biological measures in that they address these very issues. In this section I wish to illustrate the utility in extraoplating measues originally employed in human studies to studies on animal behaviour, by employing a general measure of disability to the Sonso community of chimpanzees. In addition this will give a broad overview of the relationship between impairment and disability.

When developing a suitable procedure applicable to a wild population of chimpanzees, a number of factors must be taken into account. In the discussion that follows, I refer to the guidelines set by Johnston *et al.* (1995) in selecting an appropriate measure.

In deciding upon the type of item to be included in the measure, we first need to distinguish between what the individual *can* do, and what they *actually* do. Observational studies of animals in the wild require a number of different assumptions to those made in studies on human populations, where questionnaires tend to rely on the honesty and accuracy of the interviewee. For the purpose of this study measures will be taken of what the animal is *observed* to do, assuming that the absence of a particular activity in an individual's behavioural repertoire, that is otherwise a part of the normal repertoire of an able-bodied individual, is due to disability and not a result of individual preference.

A sufficient range of activities need to be sampled so as to discriminate between individuals with different levels of disability, but at the same time avoiding activities that cannot be reliably observed or else fluctuate so rapidly that they cannot be used to describe the current state of functioning. In studies on human patients, activities-of-daily-living are frequently chosen as items representative of an individual's ability. The injuries that are of particular interest to this study are those involving the upper limb and how these effect feeding. However, lower limb injuries may also have an effect on access to food items and locomotion between feeding patches. For the purpose of this chapter, it was considered appropriate to apply an independent measure that would encompass all those activities *other* than feeding that require some degree of dexterity by the limbs. Feeding will be covered in detail in later chapters, and for the time being we are concerned primarily with illustrating a methodological concept in addition to providing a broad introduction to the extent of disability amongst Sonso chimpanzees. These activities therefore comprise terrestrial locomotion, arboreal locomotion, self-grooming and allo-grooming. In addition, these activities compare favourably with those distinguished for the measurement of activity budgets as described in **Chapter 2.**

The measure used here, as proposed by Williams *et al.* (1976), assumes that disabilities do not occur in random patterns, but instead follow a linearly ordered hierarchy. Thus, if key disabilities are identified, then inability to perform a certain activity implies that individual will be unable to perform the more difficult activities, which are further up in the hierarchy. This measure was applied to all activities excluding feeding in order to provide a somewhat subjective yet very broad-based gauge of disability in the population.

For each of the items of terrestrial locomotion, arboreal locomotion, self-grooming and allo-grooming, a scale of 0-5 was constructed which represented increasingly difficult activities to perform. Able-bodied individuals are assumed to obtain the maximum score for each item, and for injured individuals the scale follows the hierarchical model of disability. For example, an individual scoring 3 for a particular item is assumed to also score for activities 1-2, but not 4 or 5. This assumption was inadvertently tested during the study when Tinka sustained a sprain to his ankle. His path of recovery in the two items arboreal and terrestrial locomotion followed the hierarchical model proposed. In order to increase the reliability of the measure, scoring was repeated for each injured individual across each item once a month, and the mean score taken. The validity of the measure can be tested by the hypothesis that individuals with the most severe injuries should score consistently lower across all four items.

Figure 3.10 shows the design of the measure. This measure was taken into the field each month and every individual was marked against the appropriate activity level for each item. This data was collected independently of all other data. For items that involve bimanual co-ordination i.e. both self-grooming and allo-grooming, each *hand* was scored independently, and a mean of the two hands taken to give a score for the individual.

The scores for each individual across each item are given in **Table 3.1.** Each score is expressed as a 'disability co-efficient' (individual score/total possible score), between 0 and 1, with 1 being able-bodied.

Table 3.1 Disability co-efficients for injured individuals in daily activities.

Item	**BN**	**KG**	**KK**	**KL**	**KY**	**MU**	**TK**	**ZA**
Terrestrial Locomotion	Not sampled	0.8	0.8	0.8	0.8	0.8	0.6	0.8
Arboreal Locomotion	0.6	0.8	0.8	0.8	0.8	0.8	0.6	0.6
Self-grooming	1	1	0.7	0.7	0.7	0.8	0.6	0.6
Allo-grooming	1	1	0.7	0.6	0.6	0.8	0.6	0.5
Mean	**0.87**	**0.9**	**0.75**	**0.73**	**0.73**	**0.8**	**0.6**	**0.63**

At a glance, it can be seen that individuals can roughly be divided into three groups depending on the nature of their injuries. As expected, those that are least disabled are those with lower limb injuries – Banura and Kigere - with locomotor activities only affected. Individuals with upper limb injuries can be divided into two

Figure 3.10 Measure used to scale disability in daily activities of chimpanzees

A TERRESTRIAL LOCOMOTION

1 - Cannot move on ground
2 - Getting left behind group
3 - Stops for rest, yet staying with the group
4 - Efficient locomotion with odd style
5 - Able-bodied

B ARBOREAL LOCOMOTION

1 - Cannot arboreally travel
2 - Slow, and unable to reach all areas of tree
3 - Can reach all areas of tree but much slowed
4 - Efficient locomotion with odd style
5 - Able-bodied

C SELF-GROOMING

1 - Cannot self-groom
2 - Self-groom restricted parts of body only
3 - Limited role in grooming
4 - Efficient grooming yet with odd style
5 - Able-bodied

D ALLO-GROOMING

1 - Cannot groom others
2 - Used only in bimanual grooming
3 - Mono-manual grooming but with limited role
4 - Efficient grooming yet with odd style
5 - Able-bodied

groups, those with one hand injured, i.e. Kalema, Kewaya, Kikunku and Muga, and those with both hands injured, Tinka and Zana.

However, even within these groups there are further differences across items. Kalema and Kewaya seem to be more affected in grooming activities than Muga and Kikunku, and Tinka appears to be more affected in terrestrial locomotion than Zana. These individual differences are to be expected from the individual variations in degree of impairment. Not only does a relationship exist between impairment and extent of disability, but also between impairment and the activities in which that individual is likely to be disadvantaged. One might predict that individuals would spend less time in social activities that they have most difficulty with, e.g. grooming, in order to spend more time in activities necessary for survival, i.e. feeding.

This measure illustrates one way in which injury can be systematically measured in the field. Although it is useful in revealing the extent of disability in the population, it is extremely limited in its ability to uncover the degree to which individuals *compensate* for their injuries. To further investigate the difficulties an injured individual might experience in feeding and how their behaviour changes as a result, a more detailed measure is required. For this purpose a measure is proposed, which will compare criterion groups, i.e. injured chimpanzees with age-matched controls in the able-bodied population. As for the measure illustrated in this chapter, a sufficient range of feeding activities should be sampled in order to capture the true scope of behaviour that is likely to be affected by injury. This is investigated in the following chapter.

Chapter 4

FEEDING BEHAVIOUR OF ABLE-BODIED AND INJURED CHIMPANZEES IN BUDONGO FOREST

INTRODUCTION

The purpose of this chapter is to provide a broad overview of the feeding behaviour of able-bodied chimpanzees of the Sonso community, so that we can identify likely aspects of behaviour that might pose difficulties for injured individuals. In addition, with a general knowledge of Sonso chimpanzee feeding ecology, we can place these difficulties in a broader context by predicting when, where and with what food items an individual is likely to experience the greatest effect on behaviour as a result of injury. In this way, we can assess the relative impact of feeding difficulties on everyday life.

METHODS

Data on activity and positional behaviour were collected by scan sampling methods as described in **Chapter 2**. Individuals for whom less than 100 scans were collected over the 14-month period were omitted from further analysis. A net total of 19,182 scan samples were collected (total number of scans for able-bodied individuals = 15,270, median number of scans per able-bodied individual = 577.5; total number of scans for injured individuals = 3,912; median number of scans per injured individual = 485).

Postural data was obtained from sequence samples recorded on hand-held computer (**see Chapter 2 for details**). Postural data was collected from a total of 1,231 feeding bouts across 33 individuals. Only data collected from feeding bouts on those plant species that constitute more 5% of the diet are included here for analysis (total number of bouts for able-bodied individuals = 804, median number of bouts/able-bodied individual across all analysed food items = 20, median number of bouts/able-bodied individual/food item = 2.4; total number of bouts for injured individuals = 427, median number of bouts/injured individual across all analysed food items = 43.5, median number of bouts/injured individual/food item = 7). Because postural data was obtained from independent feeding bouts as opposed to scan sampling, it is based upon a much smaller data set.

RESULTS

Time spent feeding

Activity budgets were calculated from scan sample data, and are shown in **Figure 4.1** for both the able-bodied and injured population (n = no. of individuals).

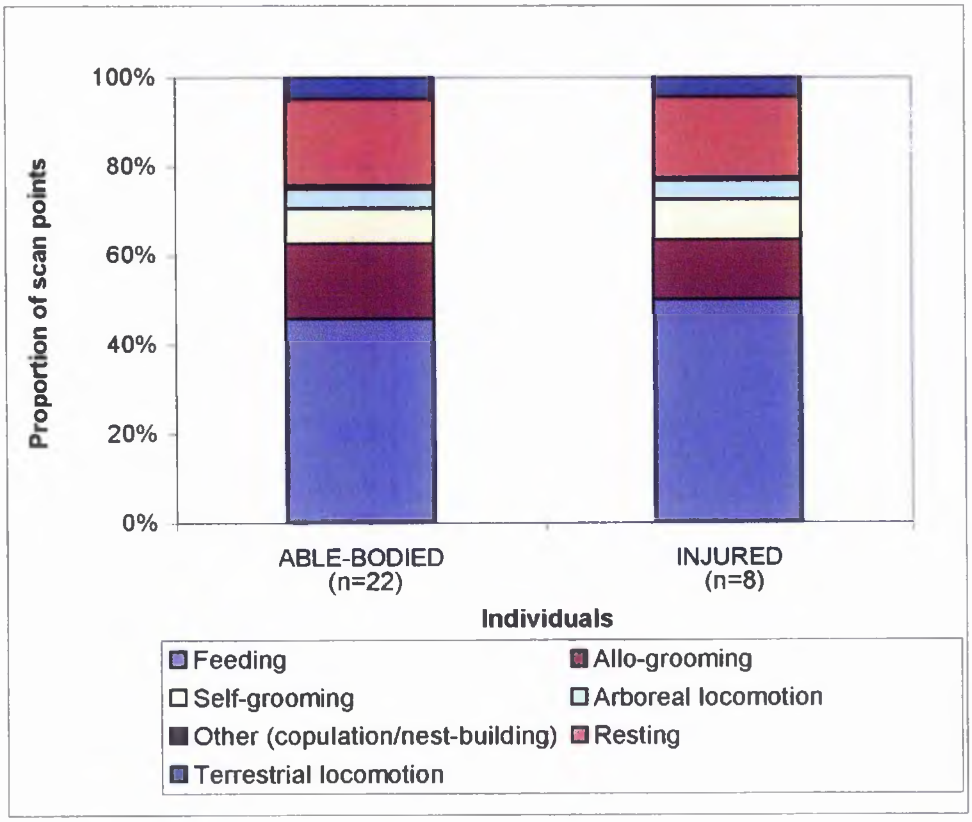


Figure 4.1 A comparison of activity budgets between able-bodied and injured individuals

In order to test whether injury had a significant effect on the time engaged in particular activities, the Chi-squared statistic was applied to raw scan counts for both injured and able-bodied individuals across all activities. Injury does have a significant effect on activity budget ($\chi^2 = 37.7712$, df = 5, $p < 0.001$). Post-hoc inspection of the data reveals this effect to be primarily located to a reduction in allo-grooming (Chi-squared test of allo-grooming scan counts against all other categories collapsed, corrected for continuity: $\chi^2 = 23.8767$, df = 2, $p < 0.001$). In addition, a concomitant increase is seen in feeding, although this does not reach significance at the $p = 0.05$ level (Chi-squared test of feeding scan counts against all categories collapsed excluding allo-grooming, corrected for continuity: $\chi^2 = 5.93782$, df = 2, ns).

This result agrees with the prediction that injured individuals will spend less time in social activities that they find difficult (i.e. those activities that scored low on the disability scale), and tend towards spending more time in those activities necessary for survival, i.e. feeding. If we now compare the diet of injured chimpanzees with that of their able-bodied counterparts we can ask whether injured chimpanzees concentrate their extra effort in feeding on particular food types or whether their feeding time is distributed evenly across the diet. If their efforts are concentrated on one particular food type at the expense of another, we are able to identify possible food items that are avoided by injured chimpanzees and highlight properties about these food items that might pose difficulties in feeding to an individual with severe limb injuries. Conversely, food types that show an increase in time spent feeding will enable us to identify those foods that are important in the diet of injured chimpanzees, and investigate what properties of these food items are being selected for by injured individuals.

Diet

Chimpanzees were observed feeding on 44 plant species, comprising 61 plant food items (**see Appendix II**). In addition, at least two vertebrate species and one invertebrate species were consumed. The feeding budget of able-bodied chimpanzees was calculated from scan samples, and is shown in **Figure 4.2.** Only

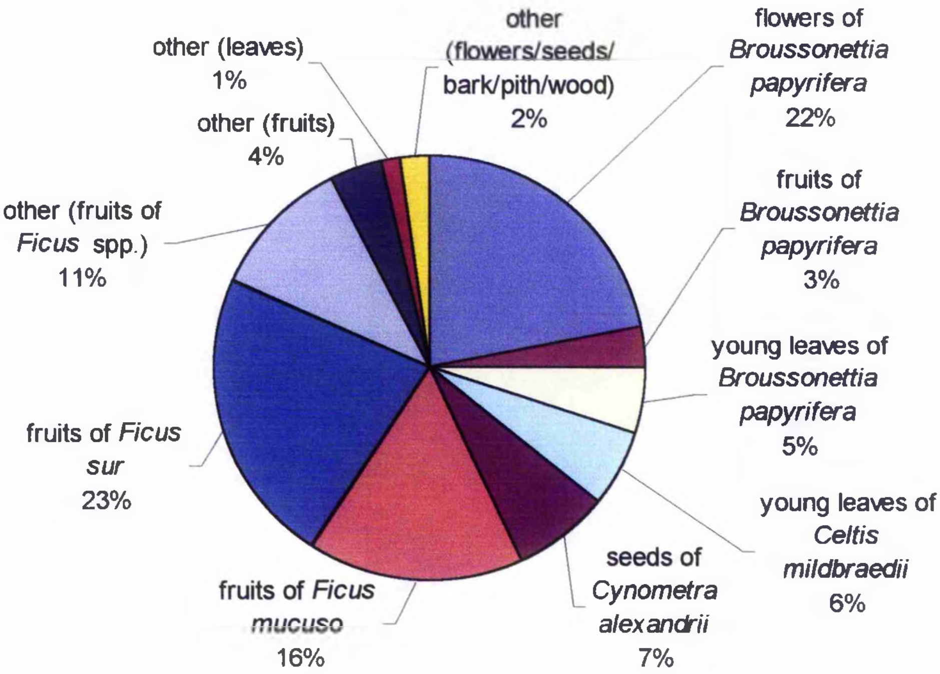


Figure 4.2 Feeding budget of able-bodied chimpanzees

those food items that constitute more than 2% of feeding scans are included for further analysis. All other species are pooled.

Figure 4.2 shows the diet of chimpanzees to be dominated by figs. Figs represent 50% of feeding time, of which 39% is taken up by only two species, namely *Ficus sur* and *Ficus mucuso*. Flowers, young leaves, seeds and other fruits, supplement the remainder of the diet. Terrestrial herbaceous vegetation comprises only 0.4% of feeding time. Figs are a valuable food item as by maximising fig intake, chimpanzees can maximise both energy and nutrient intake (Wrangham *et al.* 1993). In addition the high density and asynchronous fruiting of the several species of fig make them a year-round keystone resource. However, although figs are important for maximising nutrient and energy intake at any one time, it is apparent that chimpanzees select food items other than figs throughout the year. **Figure 4.3** shows considerable seasonal variation in the diet of able-bodied chimpanzees. At certain times throughout the year, able-bodied chimpanzees appear to prefer particular food items to figs when they are available.

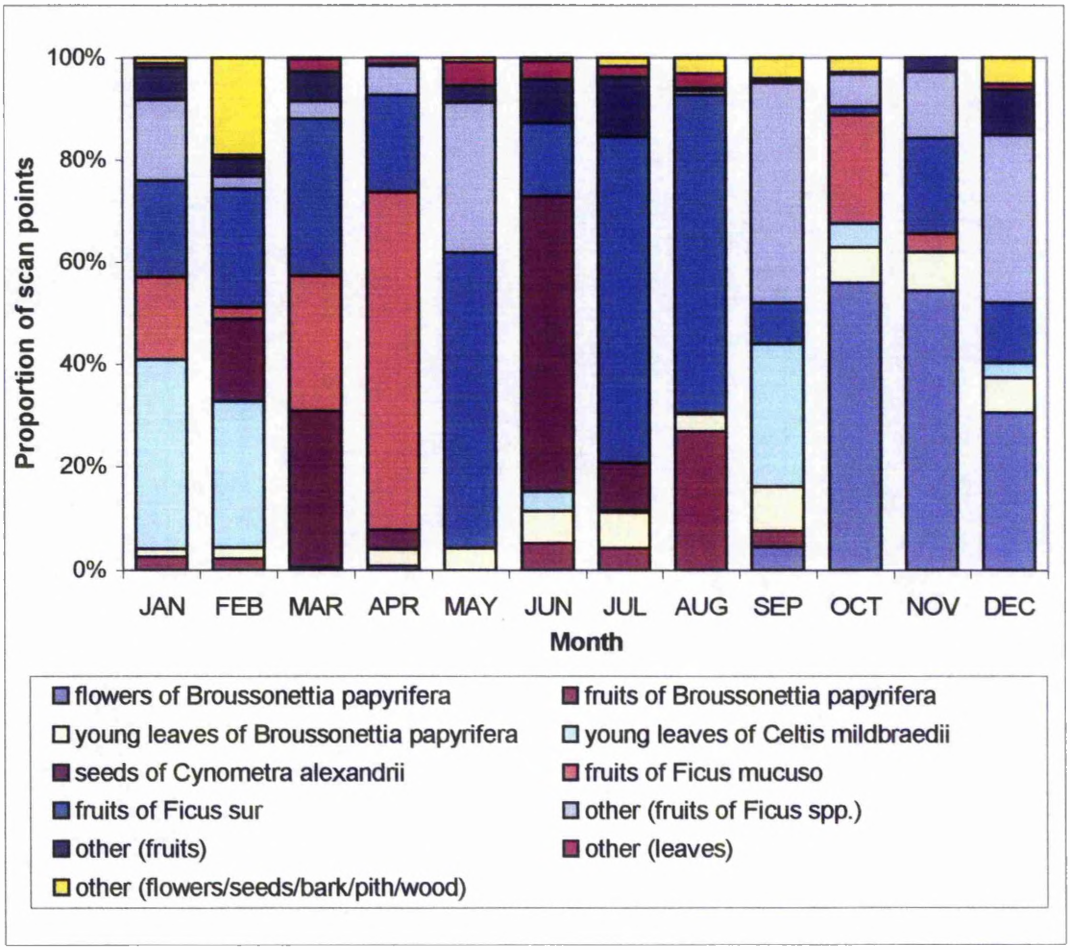


Figure 4.3 Seasonal variation in the diet of able-bodied chimpanzees

Broussonettia papyrifera is an important plant species for able-bodied chimpanzees in this respect. This is an exotic species that was introduced from Asia with the advent of the sawmill in the 1950's. It colonises forest edges and provides chimpanzees with ripe fruits in August and succulent flowers in September through December.

Young leaves of *Broussonettia*, although not constituting a major proportion of the diet, are eaten throughout the year and it is possible that they provide an important nutritional supplement as opposed to a substitute for figs. Elsewhere, the seeds of *Cynometra alexandrii*, when available, are a preferred food, and young leaves of *Celtis mildbreadii* are an important component of the diet in September and January through to February.

An injured chimpanzee is therefore faced with a number of different options. They may choose to concentrate the diet on figs. Figs are simple foods to process, and the key to efficient feeding appears to me maximising intake rather than food preparation skills. For most of the year, ripe figs are available, but food patches are dispersed in space and time. Any one fruiting tree at any one time will be highly competed over for ripe fruit, and a single tree may carry food for the entire community over the fruiting period of just a few days. Alternatively, an injured chimpanzee has the option of exploiting seasonal food items such as *Cynometra alexandrii*, *Celtis mildbraedii*, or flowers and fruits of *Broussonettia papyrifera*

The feeding budget of injured chimpanzees is compared with that of able-bodied chimpanzees in **Figure 4.4.**

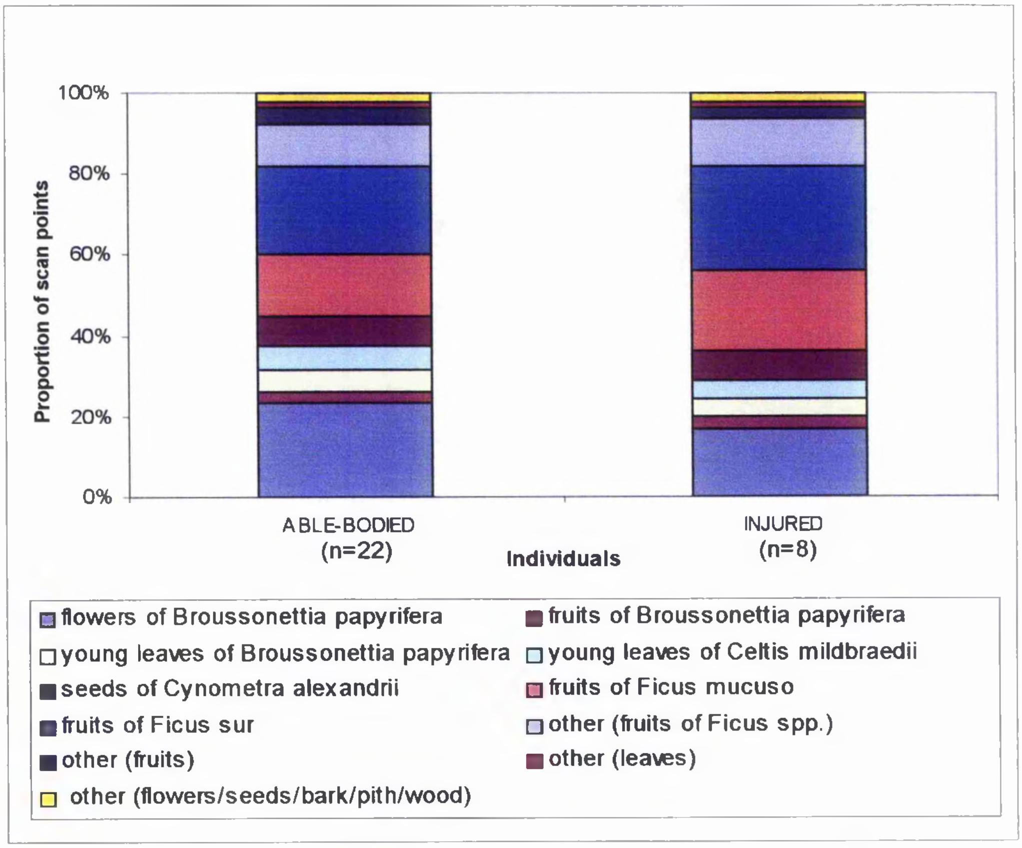


Figure 4.4 A comparison of feeding budgets between able-bodied and injured individuals

Figure 4.4 shows that injured individuals feed on the same food items as able-bodied individuals. In order to see whether time spent feeding on particular foods is affected by injury, the Chi-squared statistic was applied to raw counts of feeding scans for both injured and able-bodied individuals across all food types. Injury does have a significant effect on the frequency with which particular food items are eaten ($\chi^2 = 69.3978$, df = 10, $p < 0.001$). Post-hoc analysis reveals that this effect can be located primarily to a decrease in time spent feeding on flowers of *Broussonettia papyrifera* (Chi-squared test on scan counts for *Broussonettia papyrifera* flowers against all other categories collapsed, corrected for continuity: $\chi^2 = 34.3193$, df= 2, $p < 0.001$). At the same time, a significant increase is seen in time spent feeding on ripe fruits of *Ficus mucuso* (Chi-squared test on scan counts for *Ficus mucuso* against all other categories collapsed excluding flowers of *Broussonettia papyrifera,* corrected for continuity: $\chi^2 = 10.1906$, df= 2, $p < 0.01$). An increase is also seen in time spent feeding on *Ficus sur,* although this does not reach significance at the $p = 0.05$ level (Chi-squared test on scan counts for *Ficus sir* against all other categories collapsed excluding *Broussonettia* flowers and *Ficus mucuso*, corrected for continuity: $\chi^2 = 4.6487$, df= 2, ns).

It seems, therefore, that injured individuals devote more of their time to feeding, and in turn concentrate this extra effort in feeding on figs of *Ficus mucuso,* and to a lesser extent, *Ficus sur*. In particular, they tend to feed on figs at the expense of *Broussonettia papyrifera* flowers. By concentrating their efforts on figs, injured individuals gain maximum energy and nutrients and at minimum processing cost. However, in the long-term, the fact that able-bodied individuals elect to feed on flowers of *Broussonettia papyrifera* when they are available, and injured individuals do not, presumably places the latter at a disadvantage. If able-bodied individuals were to choose a year-round diet of figs, then presumably they would select figs over seasonal foods such as *Broussonettia,* and **Figure 4.3** suggests that this is not the case. For an injured individual, the benefits of figs must outweigh the costs associated with flowers of *Broussonettia*. There must, therefore, be a problem associated with feeding on *Broussonettia* flowers that is specific to injured individuals and forces them to choose this particular strategy. Two possible factors, feeding position and feeding posture, will be considered.

Positional behaviour in feeding trees

Different food items require different feeding positions, depending on the vertical distribution of the food. **Figure 4.5** shows how the food item affects the feeding position of able-bodied individuals.

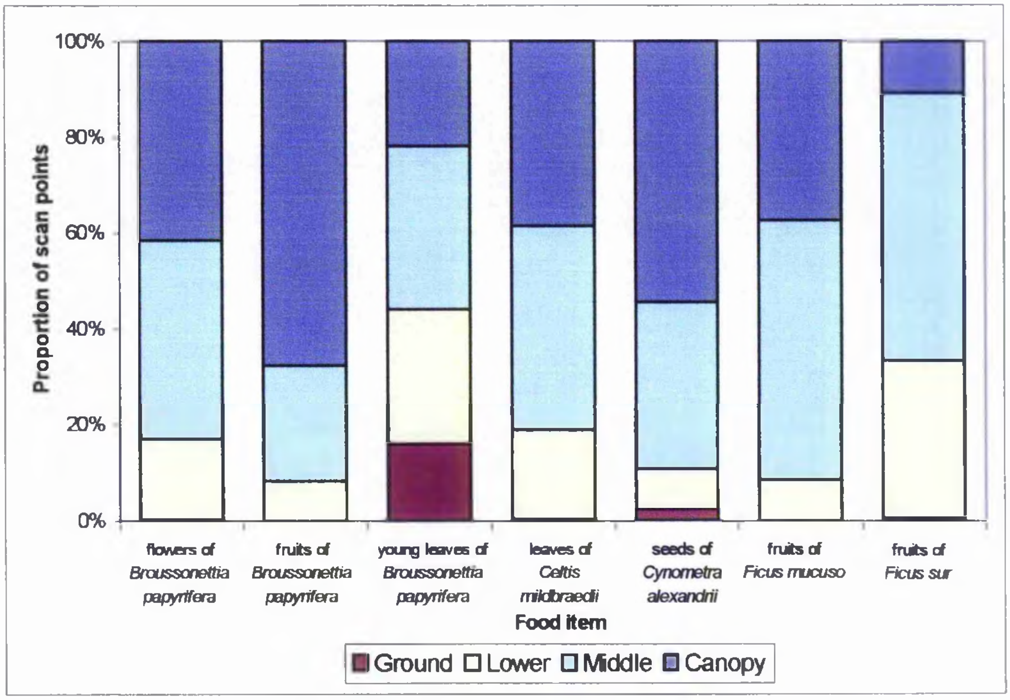


Figure 4.5 Positional behaviour of able-bodied individuals on different foods

The majority of food items in the diet of Sonso chimpanzees are arboreal. Whereas some food items such as flowers of *Broussonettia papyrifera* and leaves of *Celtis mildbraedii* are evenly distributed throughout the tree, certain food types are concentrated at a particular point within the vertical strata, seedpods of *Cynometra alexandrii*, for example, are usually found on the apical branches in the canopy.

Chimpanzees are large-bodied, arboreal feeders; manoeuvring both within and between trees requires a considerable amount of skill. Exit and entry routes to a particular food patch have to be planned carefully so that the individual does not risk falling. For an injured individual with severe limb impairment, the problem is amplified (**see Table 3.1**). **Figure 4.6** shows a comparison of able-bodied and injured individuals' feeding positions across the same food types.

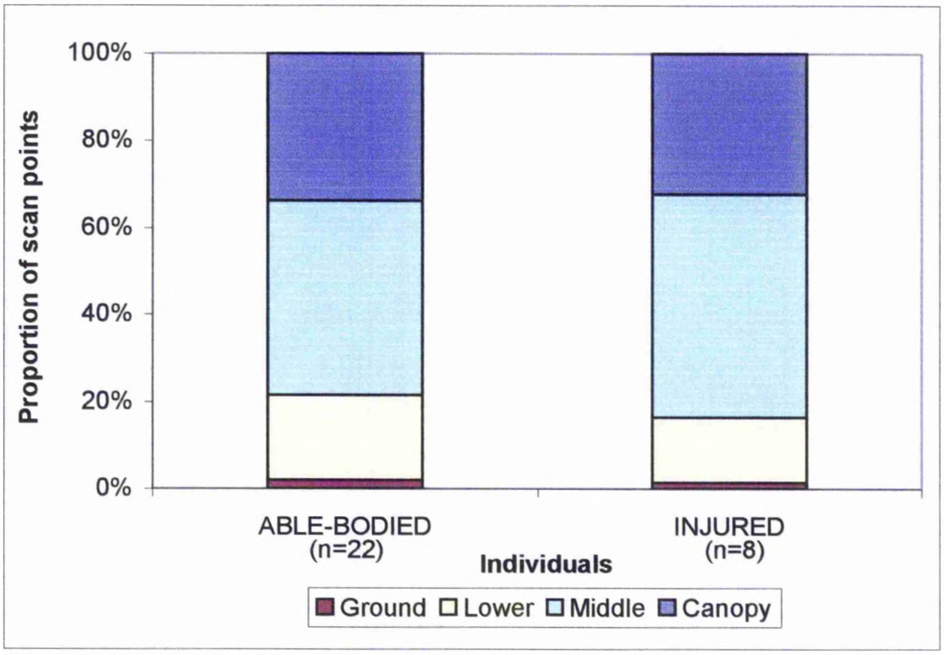


Figure 4.6 A comparison of positional behaviour between able-bodied and injured individuals

To investigate whether injured chimpanzees are constrained in their feeding position, a Chi-squared test was performed on raw counts of feeding scans for both able-bodied and injured individuals across all feeding positions. Injury does have a significant effect on feeding position ($\chi^2 = 29.2994$, df = 3, $p < 0.001$). Post-hoc analysis reveals this effect to be primarily due to a reduction in use of the lower part of the tree (Chi-squared test of scan counts for lower position against all other categories collapsed, corrected for continuity: $\chi^2 = 17.1247$, df = 2, $p < 0.001$). In addition, there is a concomitant increase in the use of the middle part of the tree (Chi-squared test of scan counts for middle position against all other categories collapsed excluding lower positions, corrected for continuity, $\chi^2 = 10.4569$, df = 2, $p < 0.01$.

This agrees with the findings of Reynolds *et al.* (1996) that injured individuals are more likely to feed higher in the trees where additional branches can provide support. An injured individual is therefore likely to be constrained in their choice of food items that are located in the lower part of the tree, and limited primarily to those food items in the middle and upper portion of the tree. Consequently, particular food items are likely to pose more of a problem in an injured chimpanzee's positional behaviour than others. As none of the food items in a chimpanzee's diet are eaten exclusively in the lower part of the tree, an injured individual is not going to be excluded from feeding on a particular food by this limitation alone. However, the choice of which particular food patch to access within the tree will be affected.

In addition to manoeuvring within a tree, a chimpanzee must provide postural support whilst feeding, again to avoid the risk of falling. Where we see variation in the vertical position of food items within a tree, there is also variation in the orientation of particular foods that requires precise postural readjustment in order to provide access. **Figure 4.7** shows the frequency of feeding postures used by able-bodied individuals for different food items.

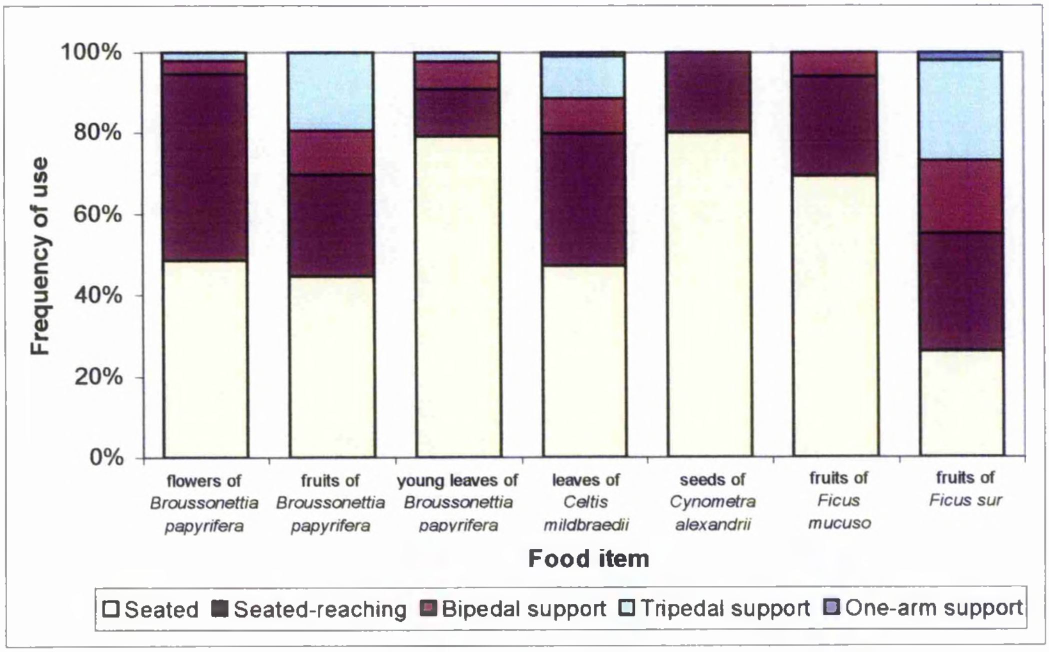


Figure 4.7 Feeding postures used by able-bodied individuals for different foods

The majority of foods are eaten from a predominately seated posture. However, *Ficus sur,* and to a lesser extent, the flowers and fruits of *Broussonettia papyrifera* and leaves of *Celtis mildbraedii* employ some form of limb support (shown in **Figure 4.7** by colours other than yellow) in more than 50% of postures, with *Ficus sur* demanding the greatest range of feeding postures.

As for feeding position, postural readjustment within the tree is likely to be affected by severe limb injury. **Figure 4.8** shows the frequency of postures used by able-bodied and injured chimpanzees across the same food types.

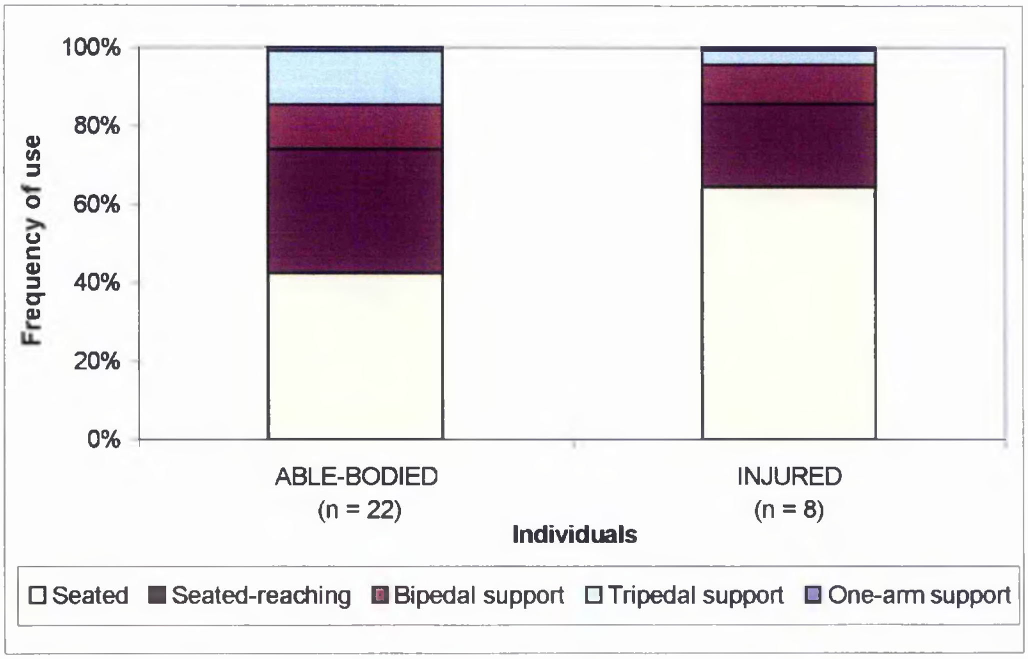


Figure 4.8 A comparison of feeding postures used by able-bodied and injured individuals

In order to see whether injury constrained the range of feeding postures available to a chimpanzee, a Chi-squared test was applied to raw counts of posture for able-bodied and injured individuals. Injury does have a significant effect on the feeding posture used ($\chi^2 = 69.677$, df = 4, $p < 0.001$). Post-hoc analysis reveals the majority of this effect is due to an increase in the use of the seated posture (Chi-squared test of raw counts of seated posture against all other categories collapsed, corrected for continuity: $\chi^2 = 59.1394$, df = 2, $p < 0.001$). In this posture, chimpanzees feed on food items within arms reach only, and no upper limbs are used in postural support. At the same time, there is a decrease in the use of the tripedal support posture (Chi-squared test of raw counts of tripedal support posture against all other categories collapsed excluding seated posture, corrected for continuity: $\chi^2 = 12.2878$, df = 2, $p < 0.005$).

As for feeding position, the constraint on posture whilst feeding is likely to have a greater effect on some food types than on others. Similarly, this will not eliminate certain food types altogether but will restrict access to certain food patches within any one feeding tree.

In addition to feeding position and postural support, the density of food patches on a tree also varies from one food item to another. Fruits of Ficus *mucuso* typically occur in large clumps, producing concentrated food patches within the tree. Conversely, flowers and fruits of *Broussonettia papyrifera* are dispersed throughout the feeding tree, and this typically involves continual manoeuvring and postural readjustment in order to gain a sufficient quantity of food. **Figure 4.9** shows the mean bout length for able-bodied chimpanzees feeding on different foods.

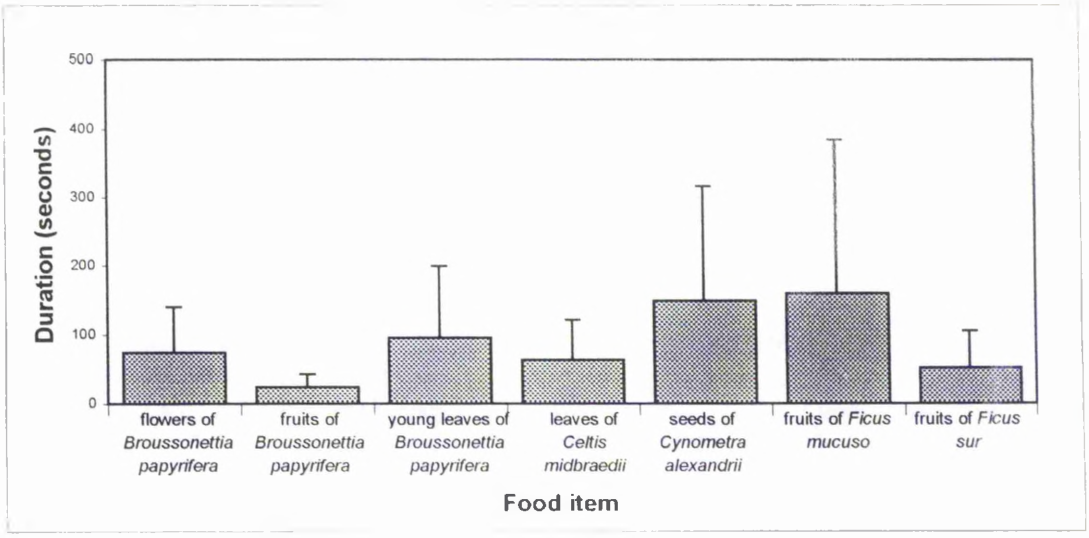


Figure 4.9 Mean bout length for able-bodied individuals feeding on different foods

In addition to density of food patches, bout length will also be affected by orientation of food on the tree. Individuals will be able to feed for much longer in a seated posture than if hanging by one arm, as this arm will soon become tired. Thus whilst *Ficus sur* has high-density food patches, bout lengths are typically shorter as feeding posture is most likely to require limb support.

For an injured chimpanzee, postural and positional constraints imposed by limb impairment are likely to favour high-density food patches that can be reached from a predominately seated position in the upper part of the tree or where additional branches are available for support, for example *Ficus mucuso*, young leaves of *Broussonettia papyrifera* and seed pods of *Cynometra alexandrii*. The extent to which these criteria are met for any one food must be a trade-off with nutrient and energy intake rates. Thus, *Ficus sur*, whilst demanding a range of postural behaviours, is still a preferred food item. Conversely, the flowers of *Broussonettia papyrifera* do not apparently offer a high enough reward to justify the combination of postural adjustment and low-density food patches that must be negotiated. Finally, seasonal availability of food will act further to determine food choice at any one time.

DISCUSSION

As Sonso chimpanzees feed predominately on figs, food processing will be reduced to a minimum as the high rate of nutrient and energy intake provided by figs makes them a preferred food source. Thus, in a study of manual processing skills, we must look elsewhere in the diet for a suitable food item that poses a technical problem in its preparation prior to eating. Furthermore, the seasonal variation in diet will determine the extent of data that can be collected for any one food item, and thus to some extent dictate those food items that can and cannot be used for systematic analysis across individuals. An alternative approach to seeking non-seasonal, hard-to-process food items, is to broaden our definition of ‘feeding skills’, to encompass aspects of feeding behaviour in addition to manual processing of foods, that require problem-solving capabilities using limb dexterity and co-ordination.

Feeding competition over figs is high and able-bodied chimpanzees have developed highly co-ordinated strategies that seek to minimise the effects of competition. Injured individuals channel a greater proportion of their time into feeding on figs, which suggests they are subjected to greater pressures from feeding competition. In the case of *Ficus sur*, intense feeding competition is combined with the need for postural readjustment and manoeuvrability whilst feeding. The postural constraints of injured chimpanzees may also help to account for the extra feeding time directed at this particular food item.

One food item that does pose technical difficulties in processing is the young leaves of *Broussonettia papyrifera*. This provides a year-round food source, distributed ubiquitously along the forest edge. Sonso chimpanzees consume these young leaves throughout the year, independent of the proportion of figs in their diet. In both their temporal and spatial distribution, leaves of *Broussonettia papyrifera* occupy a similar niche to THV in both the diet of bonobos (Wrangham & Malenky 1994) and that of mountain gorillas (Watts 1984). In the absence of any biochemical analysis of this food type we can speculate that *Broussonettia*, like THV, provides an easily digested protein rich food source, and that feeding on this particular food item would reduce the intensity of direct feeding competition. Furthermore, like THV, feeding on *Broussonettia* leaves requires a complex processing technique akin to that described by Byrne & Byrne (1993) in the leaf-preparation skills of mountain gorillas. The fact that injured chimpanzees spend the same amount of time feeding on this food item as able-bodied individuals suggests that they have developed compensatory strategies that overcome the technical demands of this food type.

Part 3

The effect of injury on feeding skill

The previous chapter highlighted a number of different areas of feeding behaviour that have shown, or are likely to show, an effect of injury. The following three chapters investigate each of these areas in turn, illustrating each with a particular food type. Each chapter is based upon the analyses of sequential data collected on each of the three food types, and although the findings of each chapter are independent of one another, they have a unified focus in investigating the effect of injury on feeding skill.

***Chapter 5** looks at the processing technique used in feeding on young leaves of* Broussonettia papyrifera, *and investigates the effect of injury on technique.*

***Chapter 6** analyses the strategies used by able-bodied individuals in minimising the effects of fluctuating levels in feeding competition, using* Ficus mucuso *as an example, and investigates the effect of injury on executing these strategies efficiently.*

***Chapter 7** investigates the role of posture in feeding, and extent to which by injured chimpanzees can overcome their positional and postural deficiencies, using* Ficus sur *as an example.*

By encompassing different aspects of feeding skill, we can investigate the extent to which patterns of disability are likely to vary across tasks. It is likely that different tasks will present very different outlooks as to what an injured individual can or cannot do. In this way we can determine the flexibility and variability of behaviour in injured chimpanzees in dealing with food types that require different components of skill.

Chapter 5

THE EFFECT OF INJURY ON FOOD PREPARATION TECHNIQUE: BROUSSONETTIA PAPYRIFERA

The young leaves of the paper mulberry – *Broussonettia papyrifera*, have large fleshy leaf blades with a rough hairy surface. The leaf petioles are tough and are removed before the leaves are eaten in order to aid digestion and palatability. In order to process these leaves, chimpanzees use a variety of complex techniques. These techniques have a number of different stages, each stage requiring a distinct set of elements, involving bimanual co-ordination and delicate manipulation. Within the able-bodied population, the majority of these techniques hinge around a single solution to the task at hand. This involves stripping up 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. The direction in which the leaves are stripped further determines the sequence of elements required and hence the particular technique used. 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. This chapter investigates the structure of techniques in the able-bodied population, and looks at how injury affects an individual's ability to process this food item efficiently.

Classification of techniques within the able-bodied population

Techniques that differed in their sequential organisation of individual elements were distinguished and labelled 1 – 15 for those used solely for processing leaves, and i –vi for those occasionally used to feed on young leaves together with flowers **(see Appendix III)**. These techniques were classified across individuals according to the number of times they appeared in an individual's repertoire. They were then further categorised according to the hand/body part used at each stage of processing (**see Table 5.1**).

Laterality aside, pathways were ranked in order of frequency of use by each individual; as shown in **Table 5.2.**

Table 5.2 Techniques for processing leaves of Broussonettia papyrifera ranked in order of frequency of use

[only individuals with no. of handfuls > 10 are included for analysis, techniques representing > 5% of handfuls only are included; techniques recorded as processing young leaves together with flowers are omitted]

RANK	ABLE-BODIED									INJURED					
	AY	BK	BY	DN	MA	NB	NJ	ZM	ZT	KG	KK	KL	KY	MU	TK
1	i	2,3	4	4	13	4	1	1	4	i	i	2	4	7,3	ii
2	3,2		1	3	1,i,4	1	i	2,3,7	2	4	4	8	2		4
3		i	3,1,9	i		8	ii,iii,iv		3		ii	4		8,2	i
4	4	4,1		2,5		3,2			i		2,5	7			2
5					ii,3							3		3,4	
6		8		iii		i	9								
7					11									iv	
8														12,2	
Total no. techniques:	4	6	5	6	7	6	6	4	4	2	5	5	2	9	4
% handfuls processed by commonest technique:	40	23.3	48	26.7	15.6	29.4	23.1	57.1	53.8	93.3	35.7	35.6	73.9	13.8	39.7
Total no. handfuls:	20	43	25	60	45	17	26	21	26	15	42	43	22	65	58

Some individuals seem to have a strong preference for a single pathway, with 4 individuals processing 50% or more of handfuls with a single sequence of elements (mean 40.6, range 13.8 – 93.3%), from a mean repertoire of 5 pathways (range 2 – 9). However, this trend is by no means followed rigidly across all individuals. Flexibility in choice of pathway is important in order to respond to environmental variations in food efficiently. Additionally, linear regression of the number of pathways from the number of handfuls reveals a good deal of the

Table 5.1 Classification of techniques for able-bodied individuals feeding on young leaves of *Broussonettia papyrifera*

[refer to **Appendix III** for techniques; n is the number of occurrences of a particular pathway for each individual; N is the total number of handfuls recorded for each individual (only individuals with N > 10 are included here); * denotes swap-hand; ** denotes flowers eaten together with young leaves; mn denotes mature/new leaves or leaf buds; ( ) indicate an optional element - all recorded options are included, demarked by / and listed in order of frequency they occur; within a single sequence consecutive elements of the same action are listed within a single bracket - ie, (reach reach) - elements of the same action interspersed with a different action are

IND.	TECH.	SEQUENCE						n	%N	N	% N yl	N yl	% N yl/fl	N yl/fl	% N mn	N mn
AY	3	(R)	(R)	L	M			4	12.5	32	20.0	20		12		0
	2	L	L	M				3	9.4		20.0					
		-	(B)	M				1								
	ii	-	(L)	M	R	-	R	1	3.1		5.0					
	ii**	(R)	(R)	M	R	-	R	2	9.4				25.0			
		(L)	(L)	M	L*	-	R	1								
	i	(L) RL	(L)	M				8	25.0		40.0					
	i**	(R)/(LR)	(R)	M				9	28.1				75.0			
	4	(R)*	(L)	R	(R)	R		2	6.3		10.0					
	7	R	R	R	M			1	3.1		5.0					
BK	3	(R)	(R)	L	M			2	23.3	43		43		0		0
		-	-	R	M			8								
	1	(L)/(L)*	(L)/(R)	L	(R)	L	L	2	9.3							
		-	-	R	-	R	R	2								
	2	L	L	M				1	23.3							
		R	R	M				5								
		-	B	M				2								
		RL	L	M				2								
	12	-	-	R	R			2	9.3							
		(R)	(R)	L	L			2	4.7							
	4	-	-	R	-	(R)	R	2	9.3							
		-	-	L	-	(L)	L	2								
	10	-	-	R	(R)	R	M	2	4.7							
	8	-	-	L	-	L		3	7.0							
	7	R	R	R	M			1	2.3							
	i	(L)	(L)	M				1	11.6							
		(R)	(R)	M				2								
		(-),(L)	(R),(B)	M				1								

		(-),(R)	(L),(B)	M						1							
BY	i**	(R)	(R)	M						8	25.0	36		26	90.0	10	0
		(L)	(L)	M						1							
	i	(R)	(R)	M						6	16.7		23.1				
	2	R	R	M						1			3.8				
	3	-	-	L	M					1	5.6		7.7				
		-	-	R	M					1							
	4	(L)	-	L	(L)	(L)	L			6	36.1		50.0				
		(LR),(R)	(L),(R)	L	(L)	(L)	L			1							
		-/(R)'*	(L)/(RF)	R	(R)	(R)	R			5							
		-	-	L	(L)												
		(L)*	(RF)	L	(L)	(L)	L*R			1							
	1	-	-	L	-	L	L			2	5.6		7.7				
	ii**	(R)	(R)	M	R	(R)	R			1	2.8				10.0		
	9	-	-	R	-	R	R			2	5.6		7.7				
DN	3	(R)	(R)	L	M					11	13.6	88	19.7	61		27	0
		(RL)	(L)	R	M					1							
	1	(R)/(L)	(R)	L	(L)	L	L			3	3.4		4.9				
	2	R	R	M						4	5.7		8.2				
		-	B	M						1							
	iii	(L)	(L)	R	R	M	R			4	4.5		6.6				
	4	-	(L)	R	(R)	(R)	R			11	19.3		27.9				
		-	(LF)	L	(L)	(L)	L			6							
	6	-	-	R	(R)	(R)	M	R	R	1	1.1		1.6				
	5	(RL)	(L)	R	-	M				5	5.7		8.2				
	i	(R)	(R)	M						5	8.0		11.5				
		(L)/(RL)	(L)	M						2							
	i**	(-),(R)	(L),(B)	M						2	25.0				81.5		
		(R)	(R)	M						6							
		(LF),(L)	(LF),(B)	M						1							
		(L)/(RLL)/(RL	(L)	M						11							
		(-),(L)	(R),(B)	M						1							
		-	-	M						1							
	8	-	-	L	-	L				1	1.1		1.6				
	10	(L)	(L)	R	-	R	M			1	1.1		1.6				
	ii**	(RL)	(L)	M	L	-	L			1	1.1				3.7		
	iii**	-	-	R	R	M	R			3	3.4				11.1		
	v**	R	R	R						1	1.1				3.7		
	iv	-	-	R	M	R	-	R		1	1.1		1.6				

	v	R	R	R					2	2.3		3.3				
	11	-	-	R	R				2	2.3		3.3				
MA	1	-	-	R	-	R	R		5	11.5	52	13.0	46		6	0
		-	-	L	(L)	L	L		1							
	i**	(L)	(L)	M					6	11.5				100.0		
	4	(L)	(L)	R	(R)	(R)	R		6	13.5		15.2				
		(RLB)	(B)	L	(L)	(L)	L		1							
	12	-	-	R	R				1	1.9		2.2				
	ii	(L)	(L)	M	R	-	R		1	5.8		6.5				
		(L)	(L)	M	L	-	L		1							
		(RLBR)	(R)	M	R	-	R		1							
		(-),R	(L),(B)	M	L	-	L		1							
	i	(R)	(R)	M					3	11.5		13.0				
		(LL).(R)	(L).(B)	M					1							
		(L)/(LRL)	(L)	M					2							
	iii	-	-	R	R	M	R		1	1.9		2.2				
	9	-	-	R	-	R	M		1	1.9		2.2				
	13	(R)	(R)	M	R	R			4	13.5		15.2				
		(L)	(L)	M	L	L			3							
	3	(L)	(L)	R	M				3	7.7		8.7				
		(R)	(R)	L	M				1							
	iv	(L)	(L)	R	M	R	-	R	2	3.8		4.3				
	2	RR	R	M					1	1.9		2.2				
	11	-	(L)	R	R				1	1.9		6.5				
		-	-	L	L				2							
	7	R	R	R	M				2	3.8		4.3				
	8	-	-	R	-	R			1	1.9		2.2				
NB	1	(R)	(R)	L	-	L	L		3	16.7	18	23.5	17		1	0
		-	-	R	-	R	R		1							
	8	-	-	R	-	R			3	16.7		17.6				
	2	L*	LFL	M					1	11.1		11.8				
		R*	RFR	M					1							
	i**	(R)	(R)	M					1	5.6				100.0		
	4	-	-	L	-	(L)	L		2	27.8		29.4				
		-	-	R	(R)	(R)	R		3							
	i	(R)	(R)	M					1	5.6		5.9				
	3	(R)	-	R	M				2	11.1		11.8				
NJ	3	(B)	-	L	M				1	3.8	26		26		0	0
	ii	(R)	(R)	M	R	-	R		3	11.5						

	iv	-	-	R	M	R	-	R	2	11.5							
		-	-	L	M	L	-	L	1								
	vi	L*	LF*L	M	L	L			1	3.8							
	i	(R)	(R)	M					4	19.2							
		(L)	(L)	M					1								
	v	L	L	L					1	3.8							
	1	-	-	L	-	M			4	23.1							
		-	-	R	-	M			2								
	9	-	-	L	-	L	(L)		2	7.7							
	iii	-	-	L	M	L			3	11.5							
	4	(L*)	(LF)	L	-	-	L		1	3.8							
VN	i**	(-).(L)	(R).(B)	M					2	25.0	12		3	100.0	3		6
		(R)	(R)	M					1								
	3	(LRLR)	(R)	L	M				3	25.0							
	imn	(L)	(L)	M					1	8.3						16.7	
	2mn	R	R	M					1	33.3						66.7	
		RL*	R	M					1								
		LRL	L	M					1								
		L	L	M					1								
	9mn	-	-	R	-	R	-		1	8.3						16.7	
ZM	1	-	-	L	-	L	L		10	41.4	29	57.1	21		8		0
		-	-	R	-	R	R		2								
	2	RL	L	M					1	13.8		19.0					
		-.R	L.B	M					1								
		L	L	M					2								
	3	(L*)	(RF)	L	M				1	3.4		14.3					
		-	-	R	M				2	6.9							
	7	L	L	L	M				3	10.3		14.3					
	i**	(L)	(L)	M					7	24.1				87.5			
	iii**	-	-	L	L	M	L		1	3.4				12.5			
ZT	2	L	L	M					5	20.0	30	22.2	27		3		
		R	R	M					1								
	3	-	-	L	M				3	13.3		14.8					
		-	-	R	M				1								
	4	(L)	(L)	R	(R)	(R)	R		6	50.0		55.6					
		(R)/(R*)	(R)/(RFR)/(RFR*LF)	L	(L)	(L)	L		9								
	ii**	(R)	(R)	M	R	R	R		2	10.0				100.0			
		(R)	(R)	M	L	-	L		1								
	i	(R)	(R)	M					2	6.7		7.4					

variance in the number of pathways in a repertoire is accounted for by the sample size (R = 0.62, p = 0.01).

Within the able-bodied population, 6 out of 9 individuals employ Techniques 1 or 4 as their preferred technique, accounting for a mean of 39.7% of handfuls processed (SD 14.97, range 23.1 – 57.1). Out of the remaining 3 individuals, all use one or other of these two techniques to process > 5% of handfuls. Both these techniques employ the 'strip-up' element in order to detach leaves. Technique 1 (preferred by 2 out of 6 individuals) requires the leaves to be 'stripped-towards' the individual and Technique 4 (preferred by 4 out of 6 individuals) requires leaves to be 'stripped-away' from the individual. Remaining techniques show variation on frequency of use across individuals, but Techniques 3 and i account for > 5% of processing in all individuals, with the one exception of Nkojo (NJ). Technique 3 again employs the strip-toward element, but the leaves are stripped and held and the blades folded over and detached with the lips rather than the hand. Technique i is used primarily for processing leaves together with flowers.

One important feature of all of these individual techniques is the existence of shared behavioural units or clusters of elements. As a result of this, a composite flow diagram can be created which incorporates all the possible pathways used by able-bodied chimpanzees in processing a handful of young leaves of *Broussonettia* **(see Figure 5.1).** Factors governing the choice of pathway have had to be deduced in the majority of cases, and those instances in which the decision-making process remains questionable are likely to be relatively rare options explored when dealing with particularly awkward plants to process.

This flow diagram illustrates that in order to successfully complete the task; an ordered sequence of directed elements is required, with bi-manual co-ordination at several stages. In addition, the organisation appears hierarchical. There are a number of principles that serve to characterise the underlying hierarchical structure of complex behaviour that appears as individual linear sequences of elements, or as illustrated here, as individual techniques. The following principles are taken from

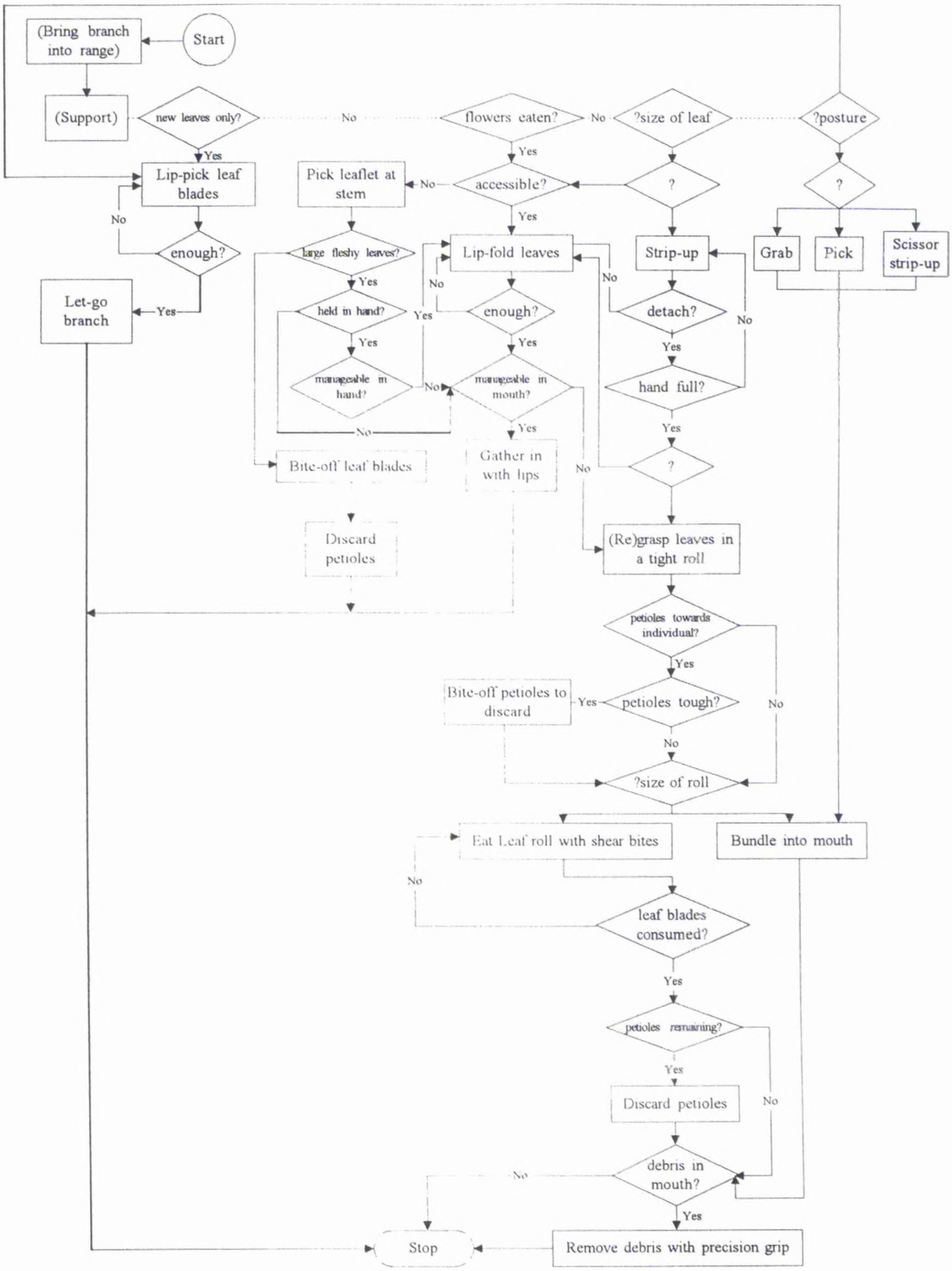


Figure 5.1 Able-bodied individuals feeding on *Broussonettia papyrifera*

[Flow diagram begins at the top and works down. Boxes represent actions and diamonds represent decision processes; a question mark indicates that the factors governing decisions have not been inferred; brackets around text indicates that these actions are optional. Vertically aligned shapes are performed with the same hand or the mouth; dashed horizontal lines between columns represents bimanual co-ordination]

Byrne (1999b) and used to illustrate hierarchical organisation of behaviour in processing *Broussonettia* leaves:

Subroutines: Modules - as subroutines - occur in which the elements seem more tightly bound together, whereas at a junction between modules the link is weaker. Interruption at these junction points will permit smooth resumption once the distraction is past, whereas interruption within a module will force the animal to "begin at the beginning again". In feeding on *Broussonettia*, subroutines can be identified in, for example, "strip up leaves with the hand - hold in tight roll". Interruptions between these elements typically result in aborting the handful whereas interruptions between subroutines usually have no effect on progression of the sequence.

Optional subroutines: Unnecessary stages or modules can be omitted on the basis of local circumstance. If petioles are not tough for example, this stage is skipped. This signals the underlying modular structure and highlights where bonds between elements are weakest.

Iteration to criterion: Modules used as subroutines may be employed iteratively until some criterion is reached, for example, stripping leaves and accumulating before holding in a tight roll. This gives a series of short sequences of elements embedded within the main sequence.

Alternative subroutines: In minor and trivial ways every execution of behaviour is different, but those characteristics that always occur, in regular position leading to the same outcome, can be identified as necessary ones, whereas those that do not can be revealed are unnecessary. In processing *Broussonettia* leaves, the existence of a wide repertoire of subroutines that are used at low frequency can be deemed as unnecessary or alternative subroutines - appropriate perhaps in particular environmental circumstance. Conversely, the more widely used strip-up subroutines appear necessary in their standardisation of use across the able-bodied population.

Inter co-ordination of subroutines: A subroutine may be used in more than one program, or a program may be used as a subroutine in another. For example, individual techniques are related by sharing particular modules or discrete sequences of elements - so-called behavioural units or clusters.

The integrity of this structure and processing technique in general can be tested further in the case of injury.

Effect of injury on choice of technique

As for able-bodied individuals, techniques were classified across injured individuals according to frequency of use and the hand/body part used at each stage of processing (**see Table 5.3**).

The effect of injury on choice of technique was analysed at two different levels. Firstly it was important to see whether the injured population as a whole showed any difference in their choice of techniques. Having established any population effects, injured individuals were then investigated on a case-by-case basis.

Injured population v able-bodied population

Table 5.4 compares the frequency of use for each pathway for the able bodied population as a whole, with frequencies for each injured individual. For each pathway, the median value for frequency of use across the able-bodied population was taken. The median is less sensitive than the mean to outliers and the high frequency of zero scores for certain techniques combined with a few extreme values for other techniques by certain individuals therefore dictated this choice of statistic. Individuals were then subdivided into four groups based on their frequency of use of a particular technique – those above and below the median - and those injured or able-bodied. A Chi-squared test (corrected for continuity) was applied to these frequencies in order to see whether the pattern of choice of technique in the injured population differed from that seen in the able-bodied

Table 5.3 Classification of techniques for injured individuals feeding on young leaves of Broussonettia papyrifera

[refer to **Appendix III** for techniques; see **Table 5.1** for key; for injured individuals, *italics* denotes passive use of the injured limb, and ***bold italics*** denotes active use of the injured limb]

IND.	TECH.	SEQUENCE							n	%N	N	% N yl	N yl	% N yl/fl	N yl/fl	% N mn	N mn
KG	i	(R)/(RR)	(R)	M					11	93.3	15		15		0		0
		(R*),(R)	(LF),(LFR)	M					1								
		(R)	(LFR)	M	(R)				2								
	4	-	-	R	(R)	(R)	R*L		1	6.7							
KK	1	-	-	R	-	R	R		2	3.5	57	4.8	42		15		
	i**	(R)	(R)	M					11	19.3				73.3			
	12	-	-	R	R				2	3.5		4.8					
	7	R	R	R	M				1	1.8		2.4					
	ii**	(R)	(R)	M	R	-	R		1	1.8				6.7			
	8	-	-	R	-	R			1	1.8		2.4					
	iii**	-	-	R	R	M	R		3	5.3				20.0			
	2	R	R	M					3	5.3		7.1					
	i	(R)	(R)	M					15	26.3		35.7					
	4	(R*)	(RF)	R	(R)	(R)	R		6	10.5		14.3					
	11	-	-	R	R				1	1.8		2.4					
	v	R	R	R					1	1.8		2.4					
	iv	-	-	R	M	R	-	R	1	1.8		2.4					
	ii	-/(RF)	(R)/(RF)	M	R	-	R		4	7.0		9.5					
	3	-	-	R	M				1	3.5		4.8					
		-	-	R	M				1								
	5	-	-/(RF)	R	-	M			3	5.3		7.1					
KL	2mn	L	L	M					11	20.3	59		43		0	75.0	16
		L*	LFL	M					1								
	8mn	-	-	L	-	L			4	6.8						25.0	
	2	L	L	M					9	15.3		20.9					
	8	-	-	L	(L)	L			10	16.9		23.3					
	3	-	-	L	M				1	6.8		9.3					
		(L*)	*(R)*	L	M				3								
	7	L	L	L	M				6	11.9		16.3					
		R	*R*	*R*	M				1								
	1	-	-	L	-	L	L		2	3.4		4.7					
	5	-	-	L	-	M			1	1.7		2.3					
	4	(L*)	(LF)/*(R)*	L	(L)	(L)	L		9	15.3		20.9					
	12	-	-	L	L				1	1.7		2.3					

KY	4	*(R)*/(L*)	*(R)*	L	-	(L)	L		8	73.9	23		22		1	0
		(L*)	(RF)	L	(L)	(L)	L		2							
			(LF)/(L*LF)	L	(L)	(L)	L		4							
		-/*(R)*	(L*RF)/*(R)*	L	(L)	(L)	L		3							
	2	L	L	M					2	17.4						
		LL	L	M					1							
		R L	L	M					1							
	3	-	-	L	M				1	4.3						
	i**	(L)	(L)	M					1					100.0		
MU	2	L	L	M					7	12.3	65		65		0	0
		L*R*	*B*	M					1							
	ii	(L)	(L)	M	L	(L)	L		4	6.2						
	8	-	*(R)*	L	-	L			8	12.3						
	4	*(R)*	*(R)*	L	-	(L)	L		6	9.2						
	1			L	-	L	L		9	13.8						
	7	L	L	L	M				8	13.8						
		R L	L	L	M				1							
	12	-	-	L	L				4	6.2						
	3	(L*)	*(R)*	L	M				4	7.7						
		(L*R*)	-	*B*	M				1							
	iv	-	-	L	M	L	(L)	1	1	1.5						
	iii	-	-	L	L	M	L		7	10.8						
	vi	L	I	M	L	L			1	1.5						
	i	(L)	(L)	M					2	3.1						
	5	-	-	L	-	M			1	1.5						
TK	ii**	***(L)***	*(L)*	M	*L*	-	*L*		3	4.2	71		57	21.4	14	
	2	*L*	*L*	M					2	2.8		3.5				
	i**	***(L)***	*(L)*	M					6	8.5				42.9		
	8	-	-	*L*	-	*L*			2	2.8		3.5				
	v**	*L*	*L*	*L*					5	7.0				35.7		
	iii	-	-	*L*	*L*	M	*L*		1	1.4		1.8				
	i	***(L)***	*(L)*	M					6	15.5		19.3				
		(-),***(L)***	*(R)*,*(B)*	M					3							
		(L*),***(L)***	(LF),(LF*L*)	M					1							
		(L*),***(L)***	(RF),(RF*L*)	M					1							
	ii	***(L)***/LF*L*)	*(L)*	M	*L*	-	*L*		13	32.4		40.4				
		(-),***(L)***	*(R)*,*(B)*	M	*L*	-	*L*		3							
			(LF*L*)	M	*L*	-	*L*		1							
		(L*),***(L)***	(RF),(RF*L*)	M	*L*	-	*L*		1							
		(-),***(L)***	(RF),(RF*L*)	M	*L*	-	*L*		1							
		(-),***(L)***	(RF*),*(L)*	M	*L*	-	*L*		1							
		(LR)	*(B)*	M	*L*	-	*L*		3							
	4	(-),***(L*)***	*(R*)*,*(R)*/(R)	*L*	***(L)***	*L*			2	23.9		29.8				
		-	*(R)*/*(RF)*/*(R* RF)	*L*	***(L)***	*(L)*	*L*		15							
	14	-	*(R)*	*L*	M	*L*	*L*		1	1.4		1.8				

population. The test was repeated for each technique. It is hypothesised that those 'technically more difficult' pathways would be reduced in frequency amongst the injured population, and as a result the injured population would rely on 'easier to perform' techniques which they could execute efficiently.

Table 5.4 Frequency of use of technique (%) for processing leaves (young, mature and new) of *Broussonettia papyrifera*

[individuals with no. of handfuls < 10 are not included for analysis, sequences recorded as processing young leaves together with flowers are omitted]

	ABLE-BODIED						INJURED					
TECH	N	Mean	Median	SD	Min	Max	KG	KK	KL	KY	MU	TK
1	9	15.4	9.3	17.86	0	57.1	0	4.8	3.4	0	13.8	0
2	9	11.8	11.8	8.89	0	23.3	0	7.1	35.6	18.2	12.3	3.5
3	9	13.8	14.3	6.44	3.8	23.3	0	4.8	6.8	4.5	9.2	0
4	9	22.4	15.2	19.90	0	55.6	6.7	14.3	15.3	77.3	9.2	29.8
5	9	0.9	0	2.73	0	8.2	0	7.1	1.7	0	1.5	0
6	9	0.2	0	0.53	0	1.6	0	0	0	0	0	0
7	9	2.9	0	4.73	0	14.3	0	2.4	11.9	0	13.8	0
8	9	3.2	0	5.88	0	17.6	0	2.4	23.7	0	12.3	3.5
9	9	2.0	0	3.34	0	7.7	0	0	0	0	0	0
10	9	0.7	0	1.59	0	4.7	0	0	0	0	0	0
11	9	1.1	0	2.30	0	6.5	0	2.4	0	0	0	0
12	9	1.3	0	3.10	0	9.3	0	4.8	1.7	0	6.2	0
13	9	1.7	0	5.07	0	15.2	0	0	0	0	0	0
14	9	0	0	00	0	0	0	0	0	0	0	1.8
i	9	14.6	11.6	11.73	0	40	93.3	35.7	0	0	1.5	19.3
ii	9	2.8	0	4.51	0	11.5	0	9.5	0	0	6.2	40.4
iii	9	2.3	0	4.11	0	11.5	0	0	0	0	4.6	1.8
iv	9	1.9	0	3.87	0	11.5	0	2.4	0	0	7.7	0
v	9	0.8	0	1.57	0	3.8	0	2.4	0	0	0	0
vi	9	0.4	0	1.27	0	3.8	0	0	0	0	1.5	0

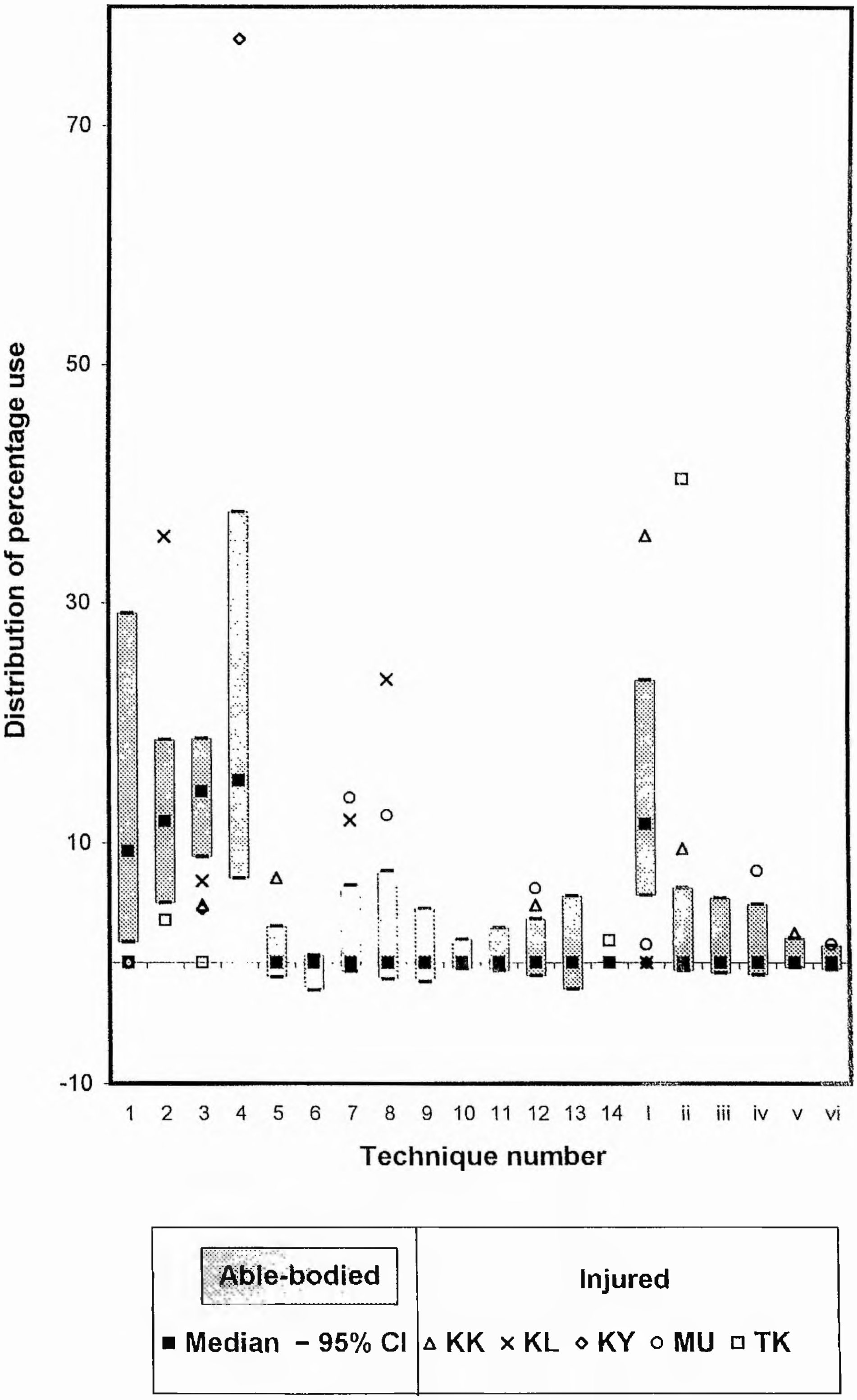
Only Technique 3 showed a significant reduction in frequency of use in the injured population ($\chi^2 = 7.4186$, df = 1, $p < 01$), although Technique 1 showed a non-significant tendency in the same direction. Both of these techniques share the 'strip-toward' element. Technique 5 significantly increased in frequency of use across the injured population ($\chi^2 = 6.5464$, df = 1, $p < .05$).

Not all injured individuals fall to the same side of the median however, which suggests that individual differences are powerful. From differences in both the nature and extent of individual injuries this would be expected. These individual differences are worthy of further investigation and the following case studies will examine each injured individual in turn.

Injured individual v able-bodied population

When investigating the repertoire of an injured individual compared to the repertoire 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 quantity of data collected between an injured *individual* on one hand and an able-bodied *population* on the other. In general, data sets collected for injured individuals tended to be larger than those collected for able-bodied individuals. This was in a deliberate attempt to try and distinguish between compensatory strategies and idiosyncrasy in choice of technique by an injured chimpanzee. However, this in itself creates the additional problem of whether the presence of a particular technique observed in an injured individual be regarded as 'novel' merely as a result of its 'absence' in the repertoire of the able-bodied population. Statistical testing is further compromised by the high concentration of zero scores for certain techniques. A simple solution was sought in order to address these problems. 95% confidence intervals for the frequency of use of each technique were calculated from scores obtained from able-bodied individuals. These intervals formed the control against which the injured individuals were compared. Injured individuals whose score fell outside these intervals were considered to vary significantly in their use of that technique. **Figure 5.2** shows the distribution of scores within the able-bodied population for each technique. Only those injured individuals whose score falls outside the 95% confidence intervals set by the able-bodied population are shown.

Figure 5.2 Frequency of use of technique



From the results presented in **Figure 5.2,** case studies were performed on all individuals with upper limb injuries for whom 10 or more handfuls were recorded. Each case study investigated the extent of departure from the pattern observed in the able-bodied population. The findings from each case study are illustrated in the form of a flowchart, which represents the choice of pathways available to each injured individual. Each flowchart is based upon a template created from the repertoire of the able-bodied population **(Figure 5.1)** then subsequently modified in order to produce the behaviour observed in the injured individual.

Tinka (TK)

Technique 1 is missing from the repertoire, as are Techniques 3 & 7, although the latter is not outside the limits set by the able-bodied population. All these techniques require the 'strip-towards' element. This pathway is not completely lost however, as TK employs a variant of Technique 3 which involves regrasping the leaves once lip-pick folded from the strip-up hold (Technique 14). The technique is therefore an extended version of Technique 3, and is unique to Tinka. It is used at low frequency however - 1.8% - and is therefore not thought to be a preferred pathway. Technique 7 is considered as a separate technique on the assumption that individuals with one hand injured, would tend to rely more on the mono-manual 'reach-slide-and-strip' variation of Technique 3. With TK at least, this does not seem to be the case. Bearing in mind that Tinka has severe injuries to both hands this is perhaps to be expected. Technique 4 is maintained at a similar frequency to that observed in the able-bodied population, but again a slight variant of the technique occurs – this time at the level of the 'strip-away' element. Only one leaf is stripped at a time, and leaves are either accumulated or else eaten individually. Stripping up multiple leaves is reserved exclusively for Technique 14 where the leaves are not detached but merely held. As already mentioned, this technique is rare, and the regrasping of leaves once detached suggests that the original strip action may not have been sufficiently tight for the bundle of leaves to be manageable in the mouth.

Techniques 5, 6, 9, 10, 11, 12, 13, iv and vi are all missing from the repertoire, although for these techniques, 'absence' still falls within the confidence intervals of the able-bodied population. Of all the techniques, Technique ii is the only - yet markedly so - technique to show an increase in frequency of use. By folding the leaves over the petioles with the lips and then detaching in the mouth, Technique ii effectively bypasses the 'strip multiple leaves with hand' element seen in able-bodied Technique 4.

From the flow diagram seen in **Figure 5.3** it is apparent that the overall organisation of the techniques that Tinka employs is essentially the same as that used by the able-bodied population. Tinka is however severely limited in his choice of technique, which appears to be ultimately governed by the nature of his injuries. It seems that there are certain techniques that he cannot perform at all. A further decision must then be made between a narrow repertoire of efficient techniques and a wider repertoire of semi-efficient techniques. Tinka appears to have chosen the former strategy, processing 40% of handfuls with a single pathway, Technique ii, from a repertoire of 4 pathways (accounting for > 5% of processing).

Kalema (KL)

Technique 3 is reduced in frequency of use and falls below the confidence limits set by the able-bodied population. Similarly for Technique 1, frequency is reduced to 3.4% from an able-bodied median of 9.3%. This however remains within the acceptable range of the able-bodied population. Technique 7 however shows an increase in frequency of use, which supports the hypothesis that a mono-manual 'strip and hold' would be expected to increase in frequency at the expense of Technique 3. The essential difference between Technique 1 on one hand and Techniques 3 & 7 on the other is that the former technique requires the leaves to be detached whereas the latter requires them only to be held. By comparison, Technique 4 – 'strip-away-and-detach' – is maintained at a similar frequency to that observed in the able-bodied population. In addition to Technique 7, Techniques 2 and 8 show a significant increase in frequency of use. Both these

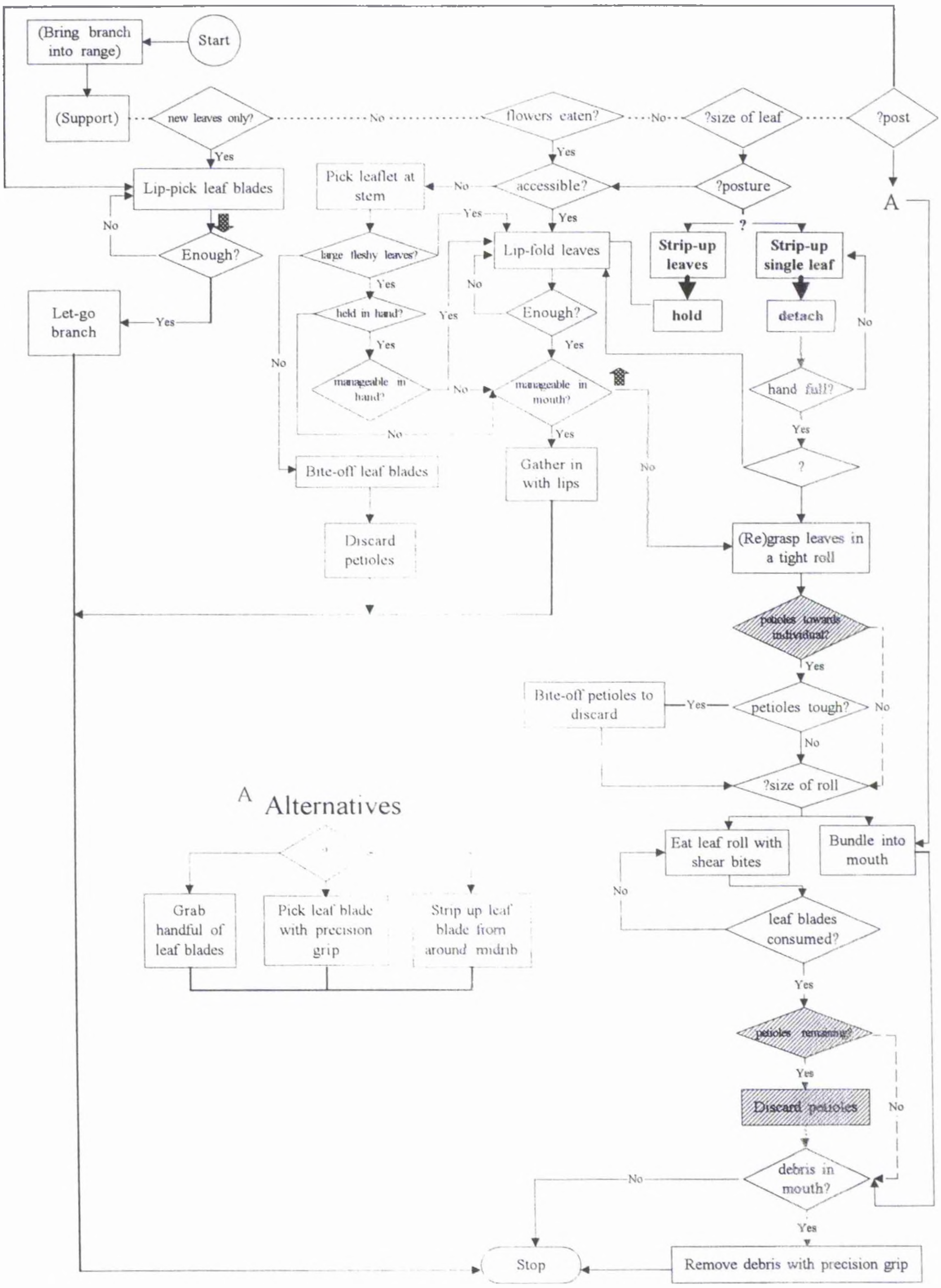


Figure 5.3 Tinka feeding on *Broussonettia papyrifera*

[see **Figure 5.1** , bold indicates modification to technique, hashed arrows indicate pathway in which a significant change in frequency is seen, hashed shapes and long dashed lines represent stages that are missing] techniques involve a simple two-stage process; 'reach-lip-pick' in the case of Technique 2 and 'reach-pick' in the case of Technique 8. Techniques 6, 9, 10, 11, 13, i, ii, iii, iv & vi are all missing from the repertoire; of these absences only that of Technique i is significant. This is possibly due to the fact that no data was recorded for Kalema feeding on young leaves together with flowers.

From the flow diagram in **Figure 5.4** it can be seen that the overall organisation of techniques is essentially the same as that employed by able-bodied individuals. Kalema is however, more constrained in her choice of pathway, with those techniques involving the 'strip-toward' element performed at a much lower frequency. Conversely, simple, two-stage techniques such as 2 and 8, or a monomanual variant of an otherwise complex bimanual task such as Technique 7, show an increase in frequency of use. 36% of Kalema's handfuls are processed by the commonest pathway, Technique 2, from a repertoire of 5 pathways (accounting for > 5% processing). From this evidence alone it appears that Kalema has reverted to a repertoire consisting primarily of 'easy-to-perform' techniques. By comparison with Tinka however, Kalema does not rely as heavily on a single technique for processing. She can therefore afford to be more flexible in her choice of pathway.

Kewaya (KY)

Again, Technique 1 is missing from the repertoire and Technique 3 is much reduced in frequency. Both of these frequencies fall outside the limits set by the able-bodied population. Unlike the case of Kalema, however, Technique 3 is not compensated for by an increase in Technique 7. This technique is also missing from the repertoire. In contrast, Technique 4 shows an overwhelming increase in frequency of use above that shown by able-bodied individuals. Techniques 5, 6, 8, 9, 10, 11, 12, 13, ii, iii, iv, v and vi are all 'missing' but do not exceed the 95% confidence intervals. The only significant result comes from Technique i, which although recorded for feeding on young leaves together with flowers, is not recorded for young leaves only.

The flow diagram in **Figure 5.5** shows a similar picture to that presented by

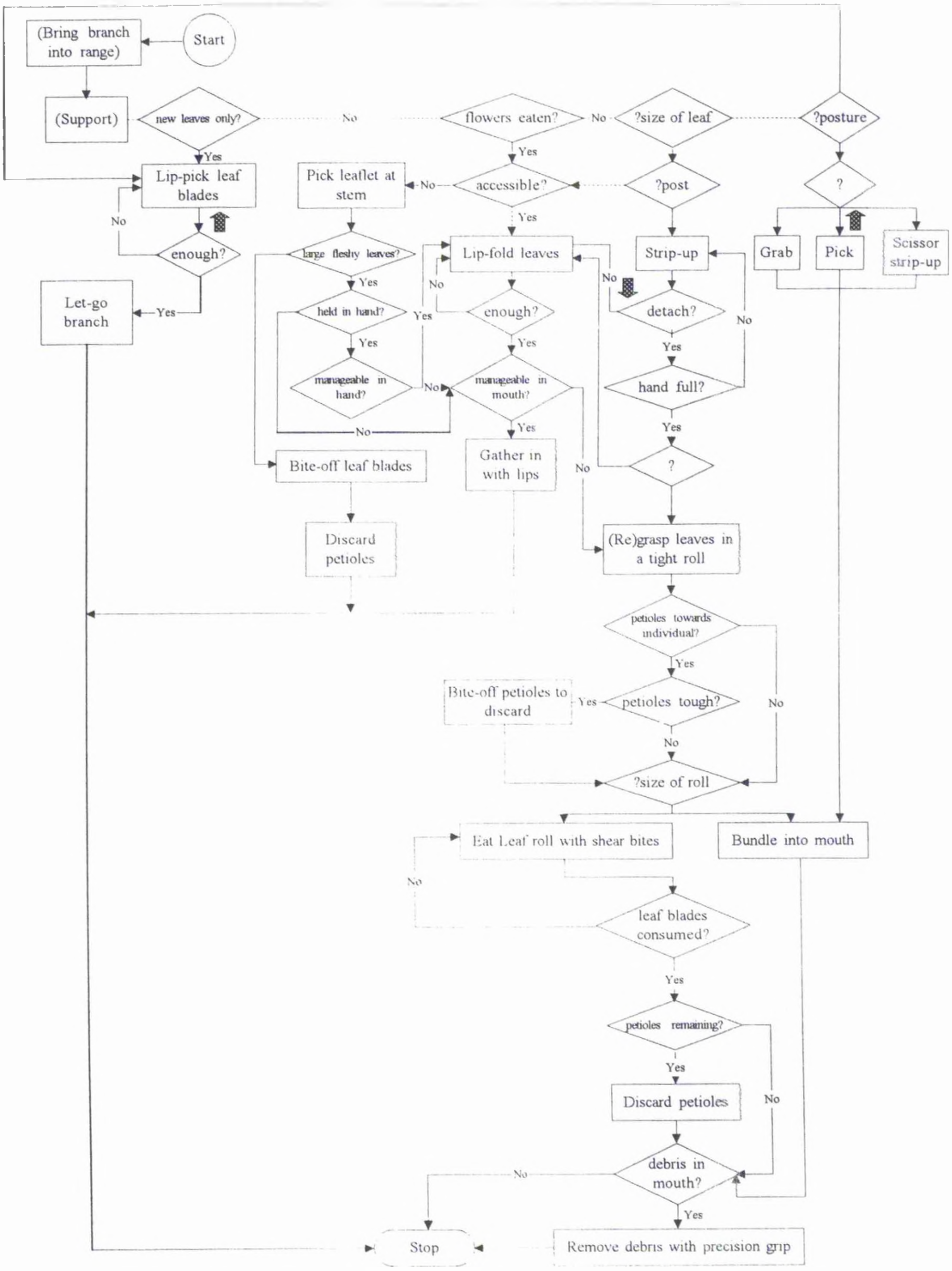


Figure 5.4 Kalema feeding on *Broussonettia papyrifera*

[see **Figure 5.1** & **Figure 5.3** for key]

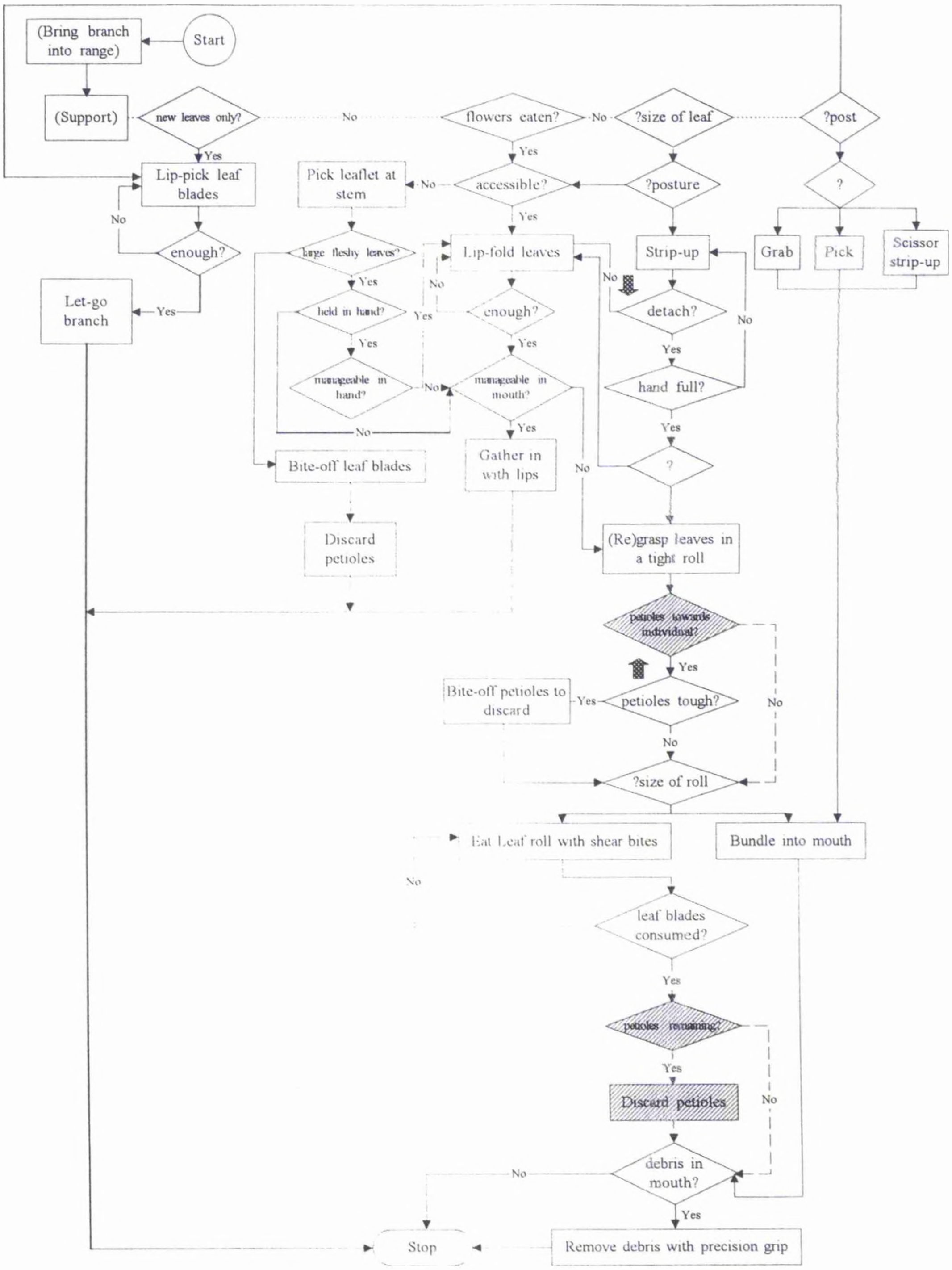


Figure 5.5 Kewaya feeding on *Broussonettia papyrifera*

[see **Figure 5.1** & **Figure 5.3** for key]

Kalema and Tinka, in so far as those techniques involving the 'strip-toward' element appear to be missing altogether or else reduced in frequency. However, rather than revert to simpler techniques as shown by Kalema, Kewaya has increased the frequency of a more complex technique involving the 'strip-away' element, Technique 4. This technique accounts for 73.9% of all handfuls processed out of a repertoire of only 2 techniques (accounting for < 5% processing).

Kikunku (KK)

Kikunku shows a slightly different picture again. Technique 3 is significantly reduced in frequency, which is to be expected from the pattern we have already seen in the injured population. However, this is not matched by an increase in Technique 7, which remains within the boundaries of the able-bodied population. Technique 1, although below the able-bodied median, is within the 95% confidence intervals of the able-bodied population. Techniques 5, 12, i, ii and v all show a slight increase in frequency over that seen in the able-bodied population, with Technique i being the most marked.

The flow diagram in **Figure 5.6** shows that Kikunku not only retains the overall organisation of pathways observed in the able-bodied population, but also shows little constraint in his choice of technique. Only Technique 3 shows a significant decrease in frequency of use with 5 techniques showing a slight increase.

Despite such a broad repertoire however, **Table 5.2** shows that although Technique 1 being maintained at a frequency within the limits set by the able-bodied population, it accounts for less than 5% of processing. Kikunku seems to favour a number of other techniques over and above these, namely Techniques i, ii and 4. Technique i accounts for 36% of processing, out of a repertoire of 5 pathways, and involves a simple two-stage monomanual process. However whilst reverting to a 'simple-to-perform' technique as his most preferred, Kikunku, unlike Kalema, Kewaya and Tinka, still maintains a number of other pathways in his repertoire at low frequency. Therefore, in the choice of pathways available to him

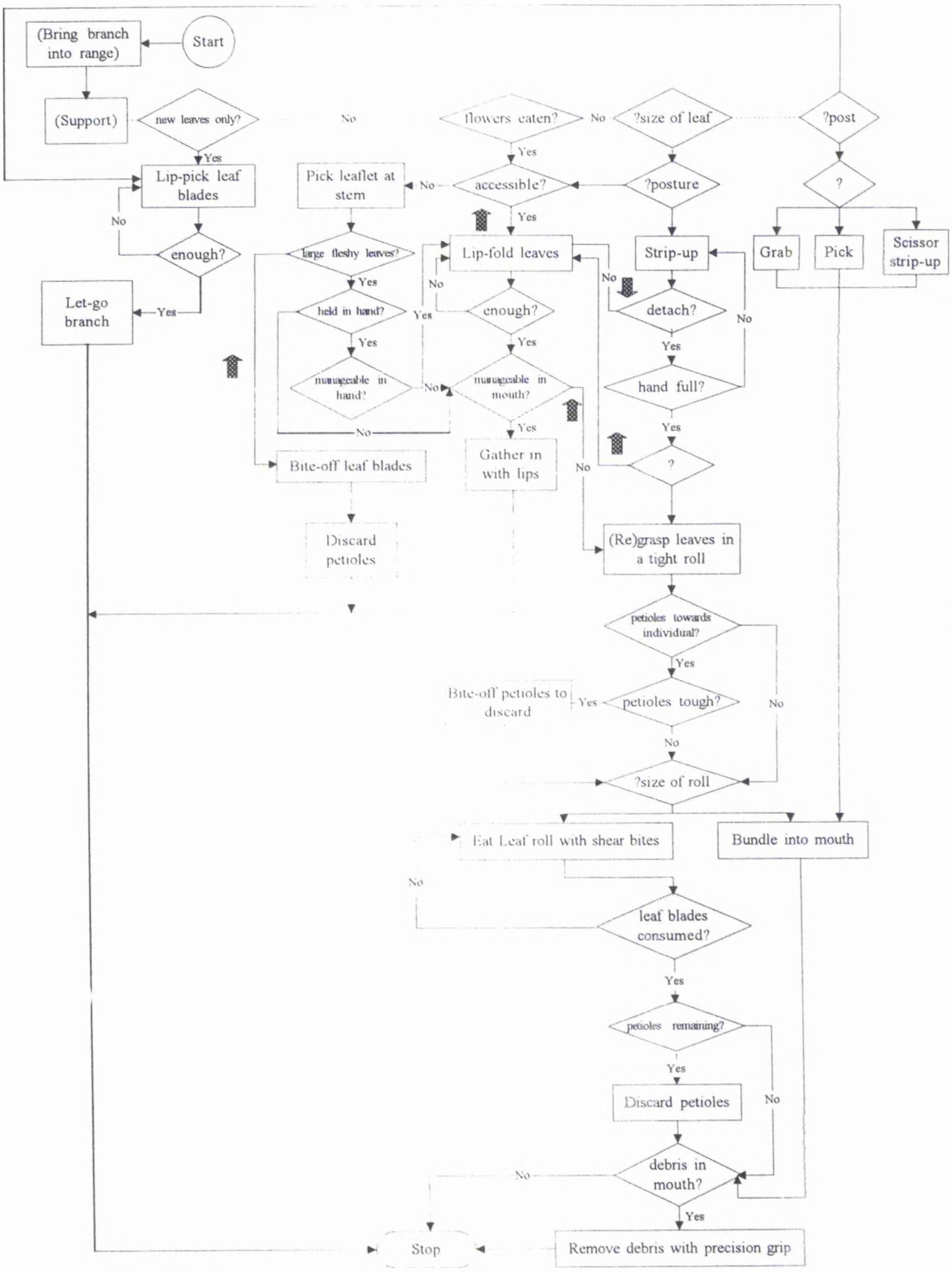


Figure 5.6 Kikuuku feeding on ***Broussonettia papyrifera***

[see **Figure 5.1** & **Figure 5.3** for key]

he more closely resembles an able-bodied individual, but his preferred pathways are similar to those seen in other injured individuals

Muga (MU)

Muga shows an even closer conformity to the pattern seen in able-bodied individuals. No technique shows a significant reduction in frequency, with both Techniques 1 and 3 occurring at similar frequencies to that observed in the able-bodied population. Although there is no significant reduction in the use of Technique 3, Technique 7 shows a significant increase in use. Technique 4 remains at a similar frequency to that seen in able-bodied individuals. Elsewhere, Techniques 8, 12, i and iv show a slight increase in frequency of use; of which 8 is the most marked. Technique 6, 9, 10, 11 and 13 are missing from the repertoire but all still fall within the limits set by the able-bodied population.

From the flow diagram in **Figure** 5.7 it can be seen that the overall organisation of techniques that Muga employs is essentially the same as that used by the able-bodied population, with no constraint upon choice of technique. However, on closer inspection Muga shows yet a different strategy again from other injured individuals. Muga has retained use of Techniques 1, 3 and 7, which include the 'strip-toward' element. Moreover, he has retained them at markedly higher frequencies than seen in all other injured individuals, with Techniques 1 used almost 3 times as often as is the case with Kikunku, who has the next highest score for this technique. The most striking difference between Muga and the remaining injured population however, is that Muga retains Techniques 1, 3 and 7 as preferred techniques (see **Table 5.2**). However, only 13.8% of handfuls are processed by the commonest technique, in this case both Techniques 1 and 7. Therefore although these techniques are retained as preferred pathways, Muga does not rely heavily on them and is able to choose from a repertoire of 9 pathways accounting for over 5% of processing.

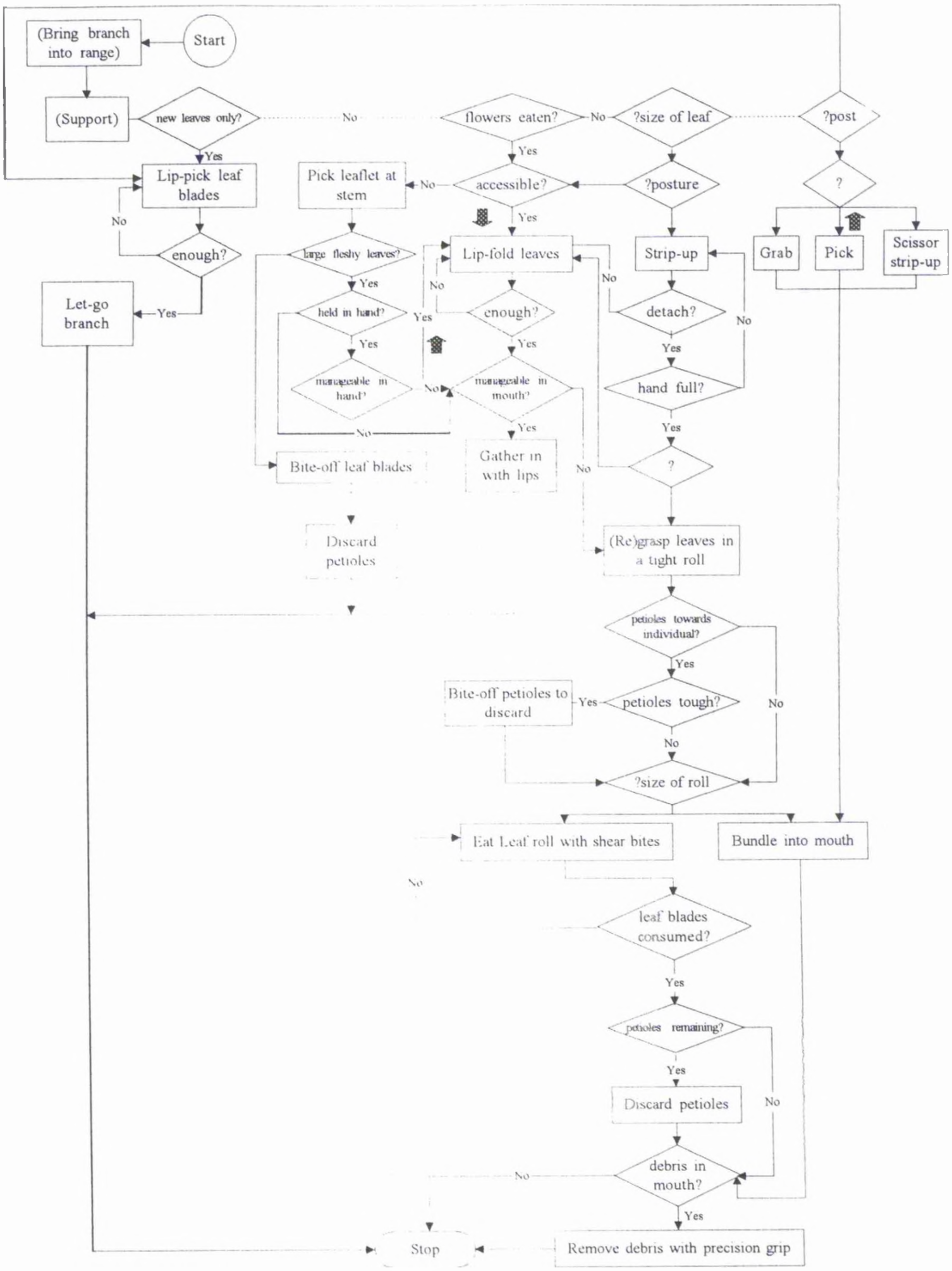


Figure 5.7 Muga feeding on *Broussonettia papyrifera*

[see **Figure 5.1 & Figure 5.3** for key]

Relationship between choice of technique and nature and extent of injury

Upper limb injury does exert an effect on the technique used to process leaves of *Broussonettia papyrifera*. Whereas the program-level organisation of technique is the same for able-bodied and injured individuals - as indicated by the similarity of flowchart template produced by the behaviour of both able-bodied and injured individuals - injury appears to determine the particular pathway chosen.

Within the injured population, a group effect or trend is seen in the absence or significant reduction of techniques employing the 'strip-towards' element – namely Techniques 1 and 3, but excluding Technique 7. Injured individuals can be graded according to their departure from the pattern seen in the able-bodied population. This 'grading' appears to conform to the severity of the injuries.

Tinka shows the most severe of injuries with both limbs affected. Accordingly Tinka shows the strongest departure from the pattern shown by the able-bodied population and is severely limited in his choice of pathway (see **Figure 5.3**). Techniques 1 and 3 are missing from the repertoire and although Tinka is still able to perform Technique 4 he is limited by the number of leaves he can detach in one handful. Tinka shows a significant increase in Technique ii which is the preferred technique. Technique ii effectively bypasses the multiple-leaf strip favoured by able-bodied individuals in Technique 4.

Kalema shows severe paralysis of the right hand, with the left hand unimpaired and functioning normally. Technique 1 and 3 show a reduction in frequency of use from the able-bodied median, although this is only significant for Technique 3. Many of the techniques that appear idiosyncratic in the repertoire of able-bodied individuals are absent in Kalema's repertoire. Two-stage or monomanual techniques are increased in frequency.

Kewaya' also shows paralysis of the right hand which is of a similar nature to Kalema's injury but perhaps even more severe – with the hand being almost completely twisted back on itself. Kewaya shows a significant reduction in use of Technique 3 and Technique 1 is absent from the repertoire. A marked increase is seen in the frequency of Technique 4, on which Kewaya is heavily reliant.

Like both Kalema and Kewaya, Kikunku has lost the use of one hand – in this instance the left hand is completely severed above the wrist. Like Kalema, Kikunku shows a reduction in frequency of Techniques 1 and 3 although of these, only Technique 3 is significant. Again, like Kalema, Kikunku uses a two-stage monomanual technique as his preferred pathway, but retains a broad repertoire of less-preferred techniques at low frequency.

This apparent division in functional limitation between Kalema and Kewaya on one hand and Kikunku on the other is interesting in that all three have lost the use of one hand. In the case of Kalema and Kewaya it seems that the presence of the injured hand is actually more disadvantageous than losing it altogether. This phenomenon is also observed in human patients with limb impairments (M. Mon-Williams pers. com.). For example, children with 'mild' movement disorders sometimes perform a task at a lower level than children with more severe impairments. This is presumably because they persist in using strategies more appropriate for people without impairment, whereas those children with a more profound disability have learned that they need to adopt novel strategies

Like Kikunku, Muga is also missing a hand. The right hand is missing from below the wrist. The point of amputation is important as it means that Muga has retained his wrist joint, which appears fully functional. Consequently, Muga seems to be the least disabled of all the chimpanzees. He has retained both Techniques 1 and 3 as well as Technique 4. Unlike the other injured individuals however, Technique 1 is a preferred pathway. However, it accounts for only 13% of handfuls processed. Therefore, although Muga's use of Technique 1 exceeds that of all other injured individuals, he is not as reliant on this as the commonest technique as an able-bodied individual would be, and like Kikunku, retains a broad repertoire of techniques albeit at slightly higher frequencies.

In order to address the initial hypothesis of whether injured individuals rely on 'easier to perform' techniques at the expense of those 'technically more difficult' pathways, we need to consider what to an injured individual comprises a 'technically difficult' pathway. It appears that Techniques 1 and 3 present difficulties to most injured chimpanzees. Technique 4 on the other hand, which also involves a complex sequence of stripping and detaching, appears to pose little problem. The crucial distinction between these two techniques however is the direction in which the strip is performed. The fact that Technique 7 is uncorrelated in frequency with Technique 3 indicates that there must be some additional feature of Technique 7, which facilitates the performance of this pathway. Technique 7 is a monomanual technique. Techniques 1 and 3 are bimanual. Thus a bimanual task involving a 'strip-towards' element poses significant difficulties to all injured individuals with the exception of Muga, and even then he is not completely reliant on this technique as a preferred pathway. A bimanual task involving a 'strip-away' element however can be confidently grouped with the simple two-stage, monomanual tasks as 'easy to perform'. The one exception here is Tinka who experiences difficulties with detaching multiple leaves at once. This element is incorporated into both 'strip-away' and 'strip-toward' techniques and so Tinka bypasses this altogether and prefers a technique that uses neither.

Now that we have seen that injury affects the choice of technique, it is important to determine further whether the effects we have seen are compensatory strategies as a result of injury and not merely individual idiosyncrasy. This can be addressed by investigating feeding skills at a finer level of detail. By analysing technique at the level of individual sequences and finer still at the level of individual elements, we may be able to pick out subtle aspects of behaviour that may not be apparent at the program-level of organisation. Three measures were used to investigate compensatory strategies of injured individuals further. The first is an analysis of the repertoires of elements employed to make up a sequence. The second looks at the properties and dimensions of each sequence, and the third is a systematic measure of feeding efficiency.

Repertoire of elements used in processing

All elements used in processing leaves only (and not leaves together with flowers), by individuals with 10 or more complete handfuls were identified and placed into functional categories. In order to investigate fully the functional limitations of the injured limbs fully, element use was broken down into left and right hand, or when used simultaneously for the same action – both. Use of the mouth (lips/teeth) was also included to see if this bore any relationship to injury (see **Table 5.5a** for able-bodied individuals and **5.5b** for injured individuals).

Within the able-bodied population, these data clearly show the highly idiosyncratic usage of elements within each functional category. As the number of handfuls varies between animals, it is evident that the full set of elements has not reached asymptote for all animals (see **Figure 5.8**). Linear regression for the number of elements from the number of handfuls supports this (elements = 0.614 x handfuls + 9.010, $r^2 = 0.795$, F (1,7) = 27.187, p = 001).

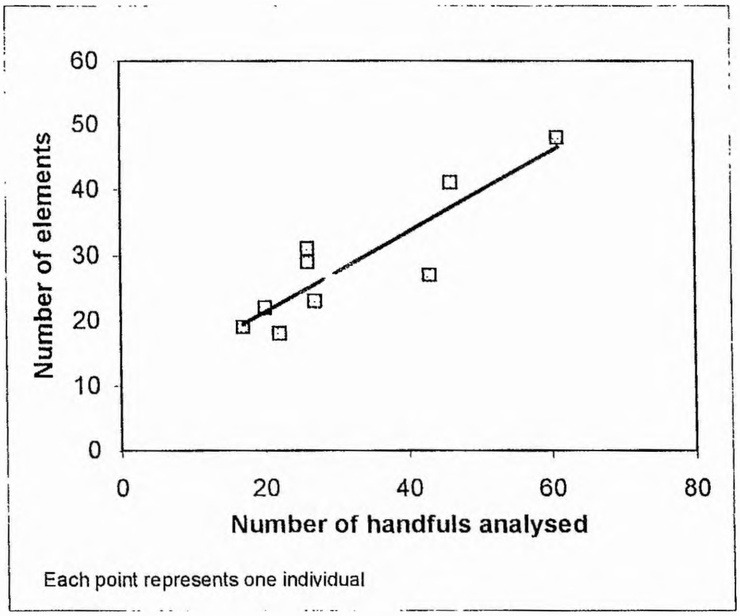


Figure 5.8 Relationship between amount of data analysed and number of elements in an able-bodied individual's repertoire

Table 5.5a Elements used by able-bodied individuals in processing young leaves of *Broussonettia papyrifera*

[elements recorded in the processing of young leaves only are included, and not those used for processing young leaves together with flowers. L or R refers to hand used, B refers to both hands used together and M refers to mouth. For Two-hand A and foot-hand elements, hand used refers to the second grip in brackets. Combinatorial/accumulation elementsare included for hands only and not for actions performed by mouth]

Element	AY				BK				BY				DN				MA				NB				NJ				ZM				ZT			
	L	R	B	M	L	R	B	M	L	R	B	M	L	R	B	M	L	R	B	M	L	R	B	M	L	R	B	M	L	R	B	M	L	R	B	M
Pull into range																																				
Reach (TH)	4	2			3	10				5			5	8			8	7			1	3				1			9	1			4	5		
Reach (DH)	4								1	3				2			3	4				1			1	1							1	4		
Reach (1,2,3 & 4)																		1																		
Reach (1,2 & 3)										1				2			1																			
Reach (PS)					2					1																			1	1						
Hook (2& 3)		2							1				1	2				2															1	2		
Hook (2,3 & 4)	1	2			1	3								1				1							1	3										
Yank																			2																	
Stem-break	2				1				1	1			2	3			3	1				1				1	1		1							
Foot																																				
Slide-adjust	1	1				1												2											3							
Manoevering items																																				
Swap-to hand	2					1			1																											
Swap-to foot										3															1					1			1	1		
Support																																				
Transverse hook	6	3			3	9	2		1	3			6	11			7	4	2			2				1			8				5	4		
Diagonal hook	1		1						1	3				3			6	2				1			1	2								4		
TH (1,2,3 & 4 only)														1				1																		
TH (1,2 & 3 only)														1			2																			
Hook (2 &3)		1											1	2	1			2							1								1	2		
Hook (2,3 & 4)	4	4			1	4	2		1					1				1								5										
Precision grip (1 2IMP)														2																						
Precision grip (PS)	1				2					1				3				1							2				3		1					
Precision grip (SG)																																				
Two-hand A (TH/PS)													1																							
Two-hand A (2 3:4/2 3)														1																						
Two-hand A (TH/2 3 4)																																				
Foot										3			1												2					1			1			
Foot-hand (L/DH)													1																							
Foot-hand (L/PS)																					1															
Foot-hand (R/TH)																						1												1		
Mouth																												1								
Strip (1)	3	1			2	9			1	1			11	1			1	5				2			1				4	1			3	1		
Detaching items																																				
Grab (whole hand)					2	2												1																		
Pick (2:3:Pm)													1																							
Pick (1:2IMP)														3																						
Pick (PS)					3									3				3				3			6	2			1							

Pick (SG)											1																
Pick (1:3)														1													
Lip-pick			5			18			2			18			8			5						14			14
Lip-pick x n leaves			5			14			3			13			1						1			3			6
Lip-pick fold			14			3			5			23			6			3			12			2			2
Lip-pick fold x n leaves			4			3			6			4			9			2			5			9			5
Strip (5) single leaf w/o petioles		2									2			2												1	
Strip (5) x n leaves w/o petioles										1	4			1											6	1	
Strip (5) x n leaves					2		2	2		1	5					2	3		1						2	2	
Strip (5) single leaf					4		6	3		4	7		1	2											1	2	
Strip (1) single leaf					3					2			1	5								1					
Strip (1) x n leaves				1			2	2		1						3	1		4	2		9	2				
Strip (1) x n leaves w/o petioles														1													
Strip (SG)											2		2	1													
Strip (SG) x n leaf blades																			2								
Accumulate																											
Combine (3 4 5 Pm/hook)							1																				
Combine (3 4 5 Pm/Strip 5 single)					6		12	8		10	5		1	6			2								3	2	
Combine (3 4 5 Pm/Strip 5 x n)		2					2	2			2																
Combine (3 4 5 Pm/Strip 1 single)					4					1			1														
Combine (3 4 5 Pm/Strip 1 x n)										1																	
Maneovring items																											
Swap-to foot																			1								
Swap hand to			1					1	1			1			2				1		4						2
Adjust	2	2					1				2		5	8					3	5					1	4	
Removing parts from items																											
Bite-off						4			13			8			3			5									8
Putting in mouth																											
Shear bite(R)		4		2	2		6	7		6	13		6	13		2	3		3	5					10	8	
Shear bite (S)				1	5		2			3	1		1	5		3	1		4	2		10	2				
Bite (S)							1																				
Eat x n				2	2									2													
Eat				3						1				1			3										
Eat (CH)											2		2	1													
Bite-off								2			2								3								
Lip-fold x n leaves												3			1						3			1			
Lip-fold												4									1						
Retain nucleus									1		1	1									1						
No. of different elements used*	**22**			**27**			**31**			**48**			**41**			**19**			**29**			**18**			**23**		
No. of handfuls	**20**			**43**			**26**			**61**			**46**			**17**			**26**			**30**			**30**		

(* hand insensitive)

Table 5.5b Elements used by injured individuals in processing young leaves of *Broussonettia papyrifera*

[elements recorded in the processing of young leaves only are included, and not those used for processing young leaves together with flowers. L or R refers to hand used, B refers to both hands used together and M refers to mouth. For Two-hand A and foot-hand elements, hand used refers to the second grip in brackets. Combinatorial/accumulation elements included for hands only and not for actions performed by mouth]

Element	KG				KK				KL				KY				MU				TK			
	L	R	B	M	L	R	B	M	L	R	B	M	L	R	B	M	L	R	B	M	L	R	B	M
Pull into range																								
Reach (TH)		8							21				4				19							
Reach (HK:GS)																					24			
Reach (DH)		2				5			4								1							
Reach (1,2,3 & 4)																								
Reach (1,2 & 3)																								
Reach (PS)		2							1				1				2				3			
Hook (2& 3)		1				13			3				1				1							
Hook (2,3 & 4)		1																						
Index hook		1																						
Yank																								
Stem-break		1				2			1				1				1				1			
Foot						1															1			
Reach (wrist-wrap)																						1		
Reach (back of wrist)										1				3										
Reach (lateral wrist)																					3			
Reach (wrist grasp)																		3						
Slide-adjust						1			6	1							9							
Manoevering items																								
Swap-to hand										2				1				1			2	1		
Swap-to foot	1					2			2				1	2							1	2		
Support																								
Transverse hook		5				6			13				2				10							
Diagonal hook		1				6			4								1							
TH (1,2,3 & 4 only)																								
TH (1,2 & 3 only)																								
Hook (2 &3)		1				6			1				1											
Hook (2,3 & 4)		1																						
Index hook		1																						
Precision grip (1:2IMP)																								
Precision grip (1:2:3IMP)																	1							
Precision grip (PS)		2							3								10							
Precision grip (SG)																								
Back of wrist										1				3										
Wrist-hook										1														
Lateral wrist																					1			
Wrist-wrap																						18		
HK:GS																					22			
Wrist grasp																		8						
Two-hand A (TH/PS)																								
Two-hand A (2:3:4/2:3)																								
Two-hand A (TH/2:3:4)																								
Two-hand A (bow/PS)													1											
Two-hand A (GS/2:3)																	1							
Two-hand A (ww/HK:GS)																					5			
Two-hand A (ww/PS)																					3			
Two-hand A (ww/lw)																								
Foot	3					4			3				4	3							2	9		
Foot-hand (L/DH)		3																						
Foot-hand (L/PS)									1															
Foot-hand (R/TH)																								
Foot-hand (R/GS:HK)																						1		
Foot-hand (L/HK:GS)																					2			
Foot-hand (R/HK:GS)																					3			
Mouth																								
Strip (5)						1																		
Strip (1)						2			9				1				13		1		1			
Strip (1 bow/side of body)										1														
Detaching items																								
Grab (whole hand)						2			1								4							

Pick (2:3:Pm)			1									
Pick (2:3:4:Pm)												
Pick (1:2IMP)												
Pick (1:2:3IMP)									1			
Pick (PS)			1		12				15		2	
Pick (SG)			1									
Pick (1:3)												
Lip-pick				10		50		10		40		3
Lip-pick x n leaves				1		11				14		3
Lip-pick fold		27		30						3		25
Lip-pick fold x n leaves		1		5		1				2		17
Strip (5) single leaf w/o petioles											8	
Strip (5) x n leaves w/o petioles												
Strip (5) x n leaves			3		2		8		6			
Strip (5) single leaf	1		3		7		9				9	
Strip (1) single leaf					1				1			
Strip (1) x n leaves			3		2				9			
Strip (1) x n leaves w/o petioles			2									
Strip (SG) single leaf blade												
Strip (SG) x n leaf blades			1									
Accumulate												
Combine (3:4:5:Pm/hook)												
Combine (3:4:5:Pm/Strip 5 single)	2		2		8		24					
Combine (HK:GS:Pm/Strip 5 single)											12	
Combine (3:4:5:Pm/Strip 5 x n)			1				2					
Combine (3:4:5:Pm/Strip 1 single)												
Combine (3:4:5:Pm/Strip 1 x n)												
Combine (3:4:5/pick PS)					3							
Maneovring items												
Swap-to foot												
Swap hand to		1		1						1		
Manipulate											1	
Adjust	1 1		5						6		26	
Removing parts from items												
Bite-off		1		2		8		20		9		6
Putting in mouth												
Shear bite(R)	1		11		9		17		12		41	
Shear bite (S)			2		2				9			
Bite (S)	1											
Eat x n			3		3				4			
Eat			1		12				8		2	
Eat (CH)												
Bite-off			1									
Lip-fold x n leaves				3						3		
Lip-fold						1				17		4
Retain nucleus				1			1					
Removing debris from mouth												
Pick-out (PS)	1											
No. of different elements used*	**26**		**37**		**36**		**21**		**34**		**32**	
No. of handfuls	**15**		**42**		**59**		**23**		**65**		**57**	

(*hand insensitive)

Within the injured population, the number of elements performed by the injured limb is drastically reduced. However, through a limited number of compensatory actions, the injured limb can still be incorporated into techniques, albeit to a lesser extent and for the most part limited to passive/support actions (see **Table 5.6**).

Element	KK	KL	KY	MU	TK	
					L	R
Pull into range						
Reach (HK:GS)					/	
Reach (PS)					/	
Stem-break					/	
Reach (wrist wrap)						/
Reach (back of wrist)		/	/			
Reach (lateral wrist)					/	
Reach (Wrist grasp)				/		
Support						
Back of wrist		/	/			
Wrist-hook		/				
Lateral wrist					/	
Wrist-wrap						/
HK:GS					/	
Wrist grasp				/		
Two-hand A (bow/PS)			/			
Two-hand A (GS/2:3)				/		
Two-hand A (ww/HK:GS)						/
Two-hand A (ww/PS)						/
Two-hand A (ww/lw)					/	/
Foot-hand (R/GS:HK)						/
Foot-hand (L/HK:GS)					/	
Foot-hand (R/HK:GS)					/	
Strip (1)					/	
Strip (1 bow/side of body)		/				
Detaching items						
Pick (PS)					/	
Strip (5) single leaf w/o petioles					/	
Strip (5) single leaf					/	
Accumulate						
Combine (HK:GS:Pm/Strip 5 single)					/	
Maneovring items						
Manipulate					/	
Adjust					/	
Putting in mouth						
Shear bite (R)					/	
Eat					/	
Total number of elements	**0**	**4**	**3**	**3**	**16**	**6**

Table 5.6 Elements used by the injured limb

From **Table 5.6**, a number of features relating element use to nature and extent of injury are apparent. It is clear that similarities exist between the functional capacities of both Kalema and Kewaya's injured limb. This is in agreement with findings from the previous section. The injury in both these cases is so severe as to render the hand incapable of any voluntary movement from the wrist down. Reaching actions are achieved through movement from either the elbow or the shoulder – and the 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 majority of cases, the able limb reaches for and places the item in the support of the injured limb, thus minimising any effort required from the latter.

Kikunku shows no use of the injured limb in any of the functional categories. This is perhaps not surprising since the hand is missing from above the wrist. Muga however appears to still retain some function of his right limb despite also missing his hand. As previously noted, the point of severance distal to the wrist joint clearly makes a difference, as the wrist joint itself is capable of 'grasping' items. With the injured limb capable of performing an adequate supporting role the able limb is free to perform more dextrous tasks – and in a sense retains some semblance of bimanual control over processing.

Of course 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 the disabled functions of the other, Tinka still retains bimanual control (see **Table 5.6**). 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 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 must accumulate individual items. As a result the 'grab' and 'strip x n' elements are absent from the repertoire of elements which manifests itself in the absence of Technique 12 and the restricted variant of Technique 4 respectively. He is also unable to perform finely controlled actions with individual digits. For example, the absence of the '2:3 scissor-strip' element explains why Technique 11 is missing from the repertoire.

The right limb is used mainly to support plant parts during feeding in a similar way to the injured limbs of Kalema and Kewaya. In addition, the digits of the right hand can be extended merely by the effect of gravity and a tight hold can be placed on branches/stems in this way.

The limited number of elements available to Tinka explains his limited choice of pathway. In the case of Kikunku, the redundancy of the injured limb in processing also helps to explain his choice of preferred pathway. Technique i, which accounts for 36% of all handfuls processed by Kikunku, requires no bi-manual co-ordination. The branch is held by one hand and the leaves folded over and detached by the lips.

Although an injured individual does not exclude itself from any of the functional categories listed in **Tables 5.5a** and **5.5b**, the range of manipulations that can be performed is severely restricted in one hand, and in the case of Tinka in both hands to differing extremes. Certain actions such as the 'strip-toward' element not only require bimanual control but also necessitate precise positioning of the individual with respect to the food item in order to perform the action correctly. Whilst an injured individual may be theoretically capable of performing individual elements with a particular hand, co-ordinating these elements into a feeding technique may not be a feasible option, and hence these elements are not incorporated into the repertoire.

In contrast to able-bodied individuals therefore, linear regression for the number of elements from the number of handfuls does suggest that something other than the amount of processing analysed is accounting for the variation in the data (see **Figure 5.9** elements = 0.233 x handfuls +20.895, $r^2 = 0.600$, one-way ANOVA F (1,4) =5.991, ns).

In order to understand more fully the nature of the compensatory strategies at work, an attempt should be made to place each sequence in a postural context. All further analyses will take this into account.

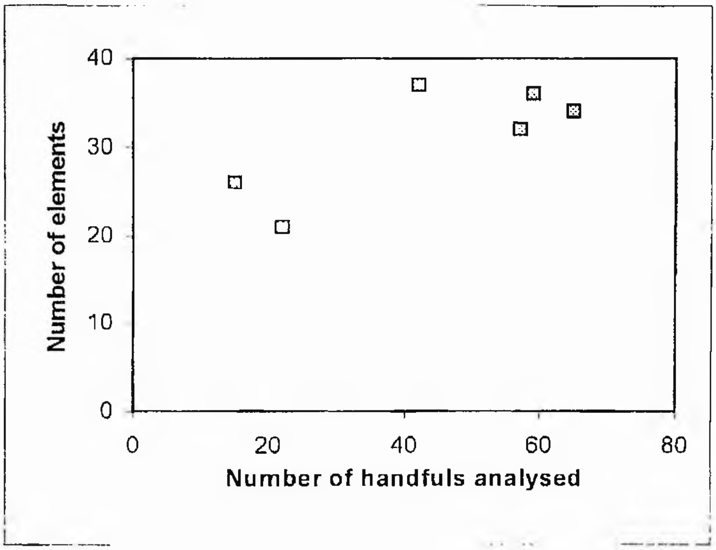


Figure 5.9 Relationship between amount of data analysed and number of elements in an injured individual's repertoire

Extended sequences

It has already been seen that the injured limb plays a predominately passive role in bimanual processing. It was also mentioned in the case of Kewaya and Kalema for example, that the able limb was frequently observed to reach towards and hand over an item for the injured limb to support. Additionally, Tinka's limb injuries permit a limited yet complementary range of functions with each hand, and thus food items need to be passed from one hand to the other in order to be processed correctly. As a result of this 'hand-swapping' strategy it is suggested that sequences belonging to injured individuals would be extended in length. These sequences achieve a common goal through a recognised pathway but via a roundabout route of actions involving a number of hand changes.

The percentage of sequences in which 'swap-hand' occurred was recorded for both injured and able-bodied individuals. If one arm is involved in postural support, then any 'swap-hand' that occurred could conceivably be as a direct result of this, and this applies equally to able-bodied and injured individuals. Distinguishing sequences in which one upper limb was used in postural support therefore controlled for posture. As a result only 'swap-hand' actions in a seated posture were used for further analysis. **Figure 5.10** shows the frequency of use for the swap-hand element across all individuals both before and after controlling for posture.

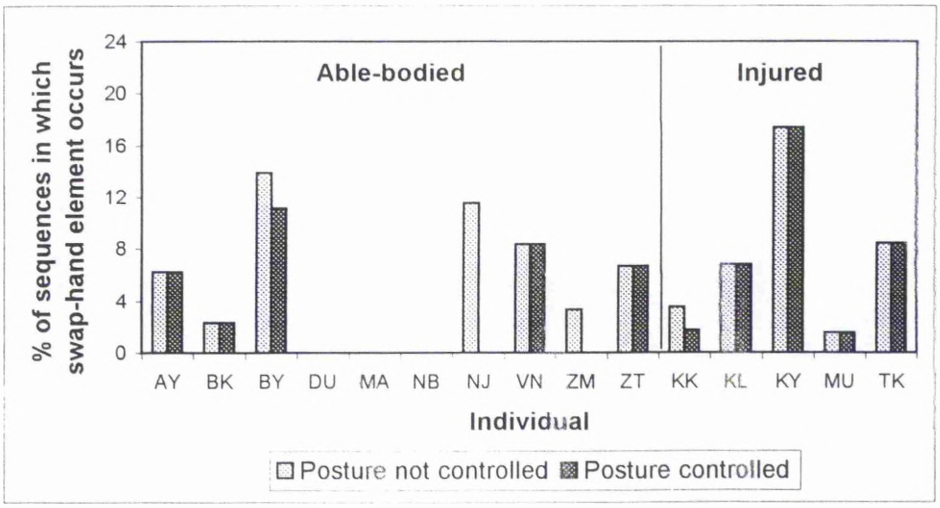


Figure 5.10 Frequency with which food items are swapped between hands within a single handful

The median value for 'swap-hand' in the able-bodied population was taken (see **Table 5.7**). Individuals were subdivided into four groups – those above and below the median and those injured or able-bodied. The Chi-squared test (corrected for continuity) was applied to these frequencies to see whether injury had an effect on the frequency the swap-hand element was used. Only individuals with upper limb injuries were used.

Table 5.7 Frequency with which 'swap-hand' element occurs within a handful (posture controlled)

ABLE-BODIED						INJURED					
N	Mean	Median	SD	Min	Max	KG	KK	KL	KY	MU	TK
10	3.27	0.17	4.34	0	11.11	6.67	1.75	6.78	17.39	1.54	8.45

The swap-hand element was used at a significantly greater frequency across the injured population ($\chi^2 = 6.1667$, df = 1, $p < .05$).

Mean length of sequence was then calculated across individuals and is shown in **Figure 5.11** (with standard deviation).

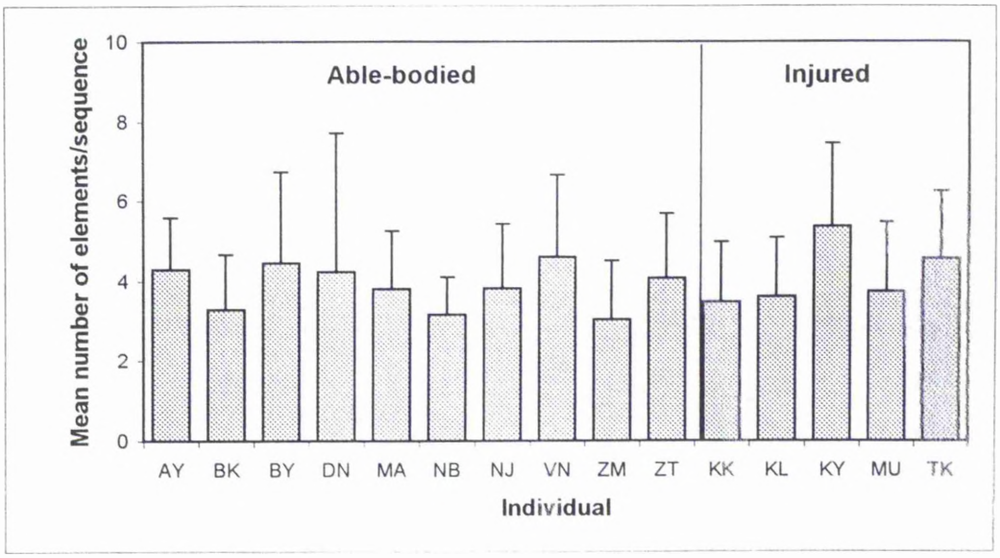


Figure 5.11 Number of sequential elements used to process a single handful

Differences in length of sequence were found across individuals (one-way ANOVA F (1,16) = 3.133, $p < 001$), although this difference was not primarily between injured and able-bodied populations. ($t = -1.276$ - controlling for unequal variance, ns.). In spite of this, a dependant relationship does appear to exist between the frequency of 'swap-hand' and the length of sequence (**Figure 5.12** length = 009 x swap-hand + 3.495, $r^2 = 0.60$, one-way ANOVA F (1,14) = 26.6121, $p < 001$).

Within the injured population, Tinka and Kewaya seem to be producing the majority of this effect. In general, 'swap-hand' appears to be a reasonably good predictor of disability, whereas length of sequence does not. Sequence length can be influenced by a number of factors including choice of pathway. There is little evidence to suggest that the relationship between swap-hand and length of sequence is a direct effect of injury.

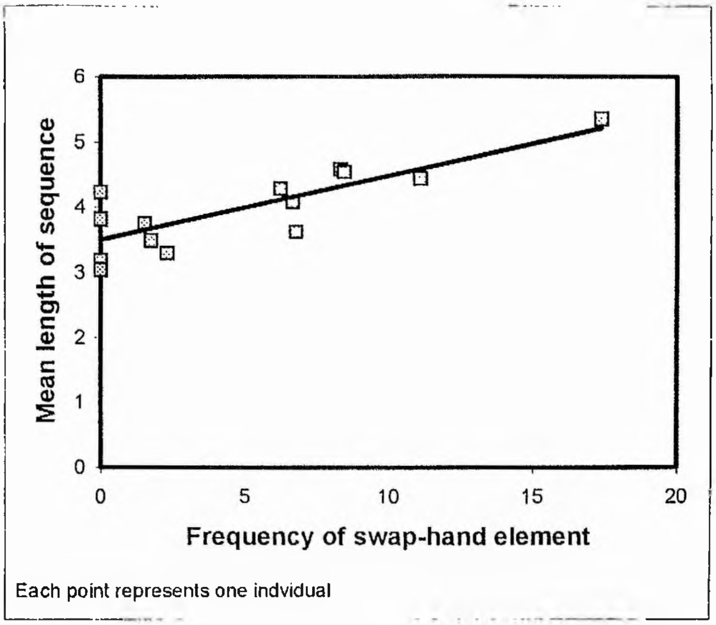


Figure 5.12. Relationship between number of sequential elements in a handful and the frequency of 'swap-hand' element

Use of feet

Chimpanzees are remarkably dextrous with their feet – in both arboreal locomotion and in feeding. From **Tables 5.5a** and **5.5b**, it can be seen that feet are used in a number of different functional categories, particularly in support. From this evidence, it is suggested that injured individuals might use their feet as 'substitute limbs'. In addition, the injured limb may lack strength to fully support the actions of the able-bodied limb. Using the feet as an 'aid' in conjunction with the injured limb may alleviate this problem.

As for 'swap-hand', the use of feet had to be placed in a postural context. **Figure 5.13** shows the frequency with which feet were used in processing across all individuals both before and after controlling for posture:

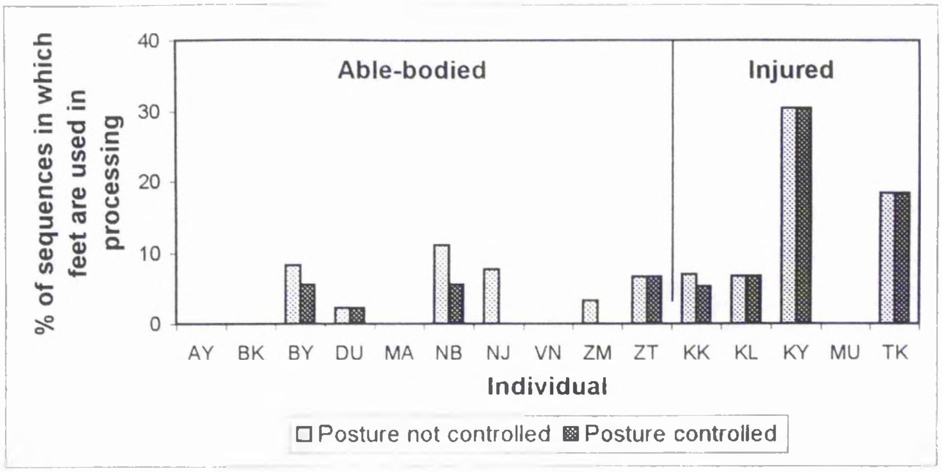


Figure 5.13 Frequency with which feet are used in processing a single handful

As for swap-hand, the median value for foot use in the able-bodied population was taken (see **Table 5.8**). Individuals were subdivided into four groups – those above and below the median and those injured or able-bodied. . The Chi-squared test (corrected for continuity) was applied to these frequencies to see whether injury has a significant effect on the frequency of foot-use. Only individuals with upper limb injuries were used.

Table 5.8 Frequency with which the feet are used in processing a handful (posture controlled)

ABLE-BODIED						INJURED					
N	**Mean**	**Median**	**SD**	**Min**	**Max**	**KG**	**KK**	**KL**	**KY**	**MU**	**TK**
10	2.01	0	2.81	0	6.67	0	5.26	6.79	30.43	0	18.3

There was no difference in the frequency of 'foot-use' between able-bodied and injured populations ($\chi^2 = 1.7292$, df = 1, ns). However, both Kewaya and to a lesser extent Tinka show an unusually high use of their feet. Within the injured population, the use of feet in an active role was recorded in only two sequences. Both Kikunku and Tinka used their feet to reach for a branch and bring into range – but only one instance of this was recorded for each individual. Within the able-bodied population, one occurrence of active reaching with the feet was also recorded for Duane.

In both able-bodied and injured populations, feet are used in a predominately passive or supportive role, and there is no evidence to suggest that within the injured population, the feet be used in a novel way to act as a 'substitute able-limb'. The data indicate that feet are used as 'optional supports' across individuals, regardless of any injury. However, individual trends within the injured population do suggest that some rely more on the use of their feet than others. The existence of individual variation can be related to the extent of injury in the sense that Tinka is injured in both limbs and would therefore be expected to rely more on his feet in processing. It does not explain however, why Kewaya should be more reliant on her feet than say Kalema, who shares a similar type of injury. This can be investigated further by looking at the second of the two hypotheses.

Snare injuries typically result in the severance of a number of muscles, tendons and nerves in both the wrist and the hand. As a direct result both hand and wrist are weakened. Exactly which muscle and nerves were severed will determine the extent of wasting and atrophy. It is possible that this could explain the difference between Kewaya and Kalema mentioned previously. The second of the two hypotheses suggests that feet may be used as 'aids' to the injured limb in order to enhance their performance. Evidence of this will manifest itself in 3-limb co-ordinated sequences. A 'foot-hand-reach/hold' involving simultaneous use of injured limb and the foot, supporting processing by the able-limb or in the case of Tinka the alternative limb.

Figure 5.14 depicts both able-bodied and injured individuals for whom incidences of foot-use are recorded (after controlling for posture). The frequency of 3-limb co-ordination is calculated from the number of occurrences of 'foot-hand' reach/support, and graphically represented as a proportion of total foot-use (from **Figure 5.13**).

Within the able-bodied population, 3-limb co-ordination accounts for between 50 and 100% of foot-use, and within the injured population between 0 and 48%. Sample sizes are too small to permit statistical analysis between injured and able-bodied populations, but there is no discernible trend to support the claim that feet are used as an 'aid' in conjunction with the injured limb. No occurrence of 3-

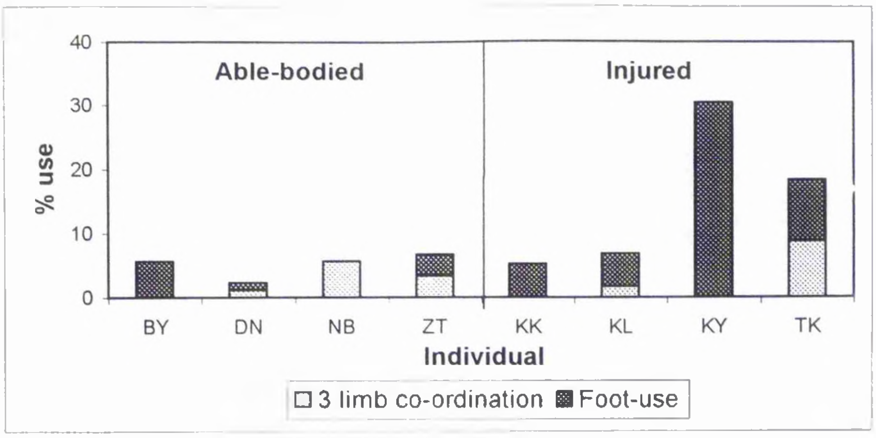


Figure 5.14 Frequency with which feet are used to aid injured limbs

limb co-ordination was recorded for Kewaya. Tinka shows 3-limb co-ordination at a frequency of 8.7%, which is noticeably higher than all other individuals. However, this accounts for only 48% of total foot-use. It is clear that other factors in addition to posture and extent of injury are responsible for individual variation in foot-use.

Feeding efficiency

Ultimately, the aim of all compensatory strategies used by injured individuals must be to maintain feeding efficiency at optimal levels. A reduction in feeding efficiency is indication that not only does injury have a disabling effect on an individual's ability to feed, but that the individual is handicapped as a result. This is turn may have serious repercussions on their day-to-day lives. Feeding efficiency therefore provides the fourth measure by which to assess the effect of injury on individuals – and is really the final outcome of all the other measures that we have looked at so far.

Feeding efficiency was calculated from processing rates recorded on the hand-held computer using the Observer program (see **Chapter 2** for full details of method used). The 'end-point' in a handful was recorded as the point at which the food item was placed in the mouth. Intervals between successive 'end-points' were calculated. These intervals included changes of posture within a bout but excluded relocation between bouts. The former was considered pertinent to feeding efficiency, as particular techniques by their very nature, may require a change in orientation of the individual. The latter – although relevant - could be influenced by too many factors such as presence and proximity of other individuals in the group, to make it a reliable measure. Complete handfuls only were included in the analysis – consecutive sequences separated by other activities such as resting for periods longer than 30secs or grooming, were discounted. Although processing rates in themselves provide a useful measure of feeding efficiency; a more accurate approach was desired. For example, two individuals may have the same processing rate per handful but one individual may have a much larger handful than the other. This is particularly pertinent to injured individuals who through the nature of their injuries cannot necessarily process as large a handful as their able-bodied counterparts. From sequence data, the mean number of leaves processed in a single handful was calculated for each individual for whom data was obtained. Individual leaf counts were facilitated by the large size of the leaves combined with the systematic way in which leaf blades were aligned parallel, thus enabling a reliable count to be made merely by observation. 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.

A significant variation was found in feeding efficiency across all individuals (Kruskall-Wallis, $\chi^2 = 216.177$, df = 13, $p < 0.001$). This result can be primarily located to a difference between able-bodied and injured individuals, with injured individuals being significantly less efficient (Mann-Whitney, U = 11628, $p < 0.001$). Post-hoc analysis however (modified Tukey HSD) reveals significant differences within able-bodied and injured populations. In the able-bodied population individuals can be classified as ‘inefficient’ or ‘efficient’ on the basis of their feeding efficiency. Similarly, within the injured population, individuals can be classified as inefficient or efficient, or in terms of their behaviour, as handicapped or compensated respectively. In terms of their feeding efficiency, compensated individuals in the injured population are not significantly different from efficient individuals in the able-bodied population, and similarly, handicapped individuals in the injured population are not significantly different from inefficient individuals in the able-bodied population.

Figure 5.15 shows feeding efficiencies across all individuals, different coloured bars represent groups of individuals that are significantly different from one another at the 0.05 level.

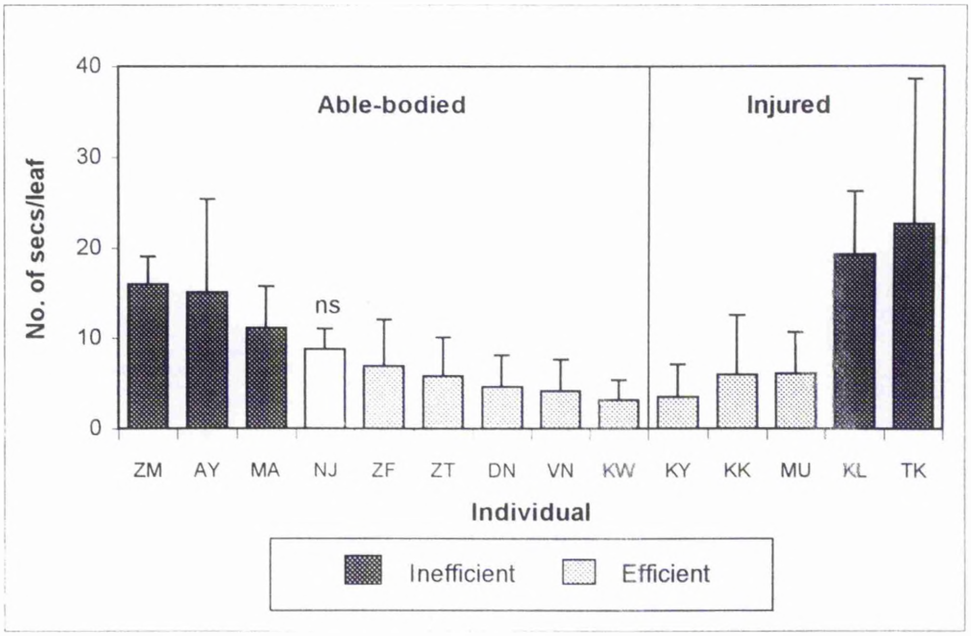


Figure 5.15 Feeding efficiency across individuals

For all individuals, there are degrees by which they can be confidently classed as 'efficient' or 'inefficient'. For example, Kwera (KW) and Kikunku (KK) show a much weaker effect than the remainder of individuals classed as 'efficient'. Similarly, amongst those individuals classed as 'inefficient' in **Figure 5.15**, Maani (MA) shows a much weaker effect than Zimba (ZM) and Andy (AY). Nkojo (NJ) is the only individual that cannot be classed as either 'efficient' or 'inefficient' as he does not show any significant effect in post-hoc comparisons.

The subdivision of able-bodied individuals is surprising, particularly as there appears to be no coherent pattern - with one adult female, one subadult male and to a lesser extent one adult male, showing a significantly lower feeding efficiency than both the remaining able-bodied individuals and some injured individuals. In the case of Zimba, the presence of a dependant infant is likely to have an effect on feeding behaviour. For both Andy and Maani, a possible explanation may be environmental factors such as time of day and feeding location. However, the data set is representative of the study period as a whole rather than clumped from a single recording session, and any particularly awkward plants to process represent isolated events, which are unlikely to exert a dramatic effect on the data set as a whole. It is possible that these individuals are concentrating their energy on processing food types other than young leaves of *Broussonettia*. Alternatively, the variation in feeding efficiency seen in able-bodied individuals may simply be a result of low feeding competition over this particular food type.

The variation among injured individuals is particularly interesting as it follows a similar pattern to that seen already in choice of technique. This therefore enables us to relate the measures of disability that we have tested so far to that of feeding efficiency.

It was suggested that choice of technique followed a particular pattern according to nature and extent of injury. Departure from the pattern seen in able-bodied individuals appeared to be graded according to injury. Muga was seen as the least affected by injury as he retained and preferred those techniques favoured by the able-bodied individuals, but did not rely on them quite so heavily. Correspondingly, in terms of feeding efficiency he falls into the same class as the majority of able-bodied individuals.

Tinka was at the other extreme in being the most affected by his injuries. As a result he is severly limited in his choice of pathway and has lost a number of techniques preferred by able-bodied individuals. To compensate for this he is forced to increase his use of a less-preferred technique from the able-bodied repertoire. Correspondingly he falls into the 'inefficient' class in terms of feeding efficiency.

In between these two extremes the interaction between choice of pathway, feeding efficiency and nature of injury is less clear-cut but obvious correlations still exist. After Muga, Kikunku was considered to be the next most affected by injury in his choice of pathway, retaining the pathways used by the able-bodied population but preferring to use other techniques. Consequently he remains in the same class as Muga for feeding efficiency, but shows a weaker effect in post-hoc comparisons.

Kalema and Kewaya show similar injuries to each other, with that of Kewaya apparently more severe in terms of muscle and nerve damage. The results from the feeding efficiency analysis do not however match this impression. Kewaya appears fully compensated in terms of feeding efficiency, and is placed in the same class as Muga and Kikunku. Furthermore, Kewaya shows a stronger effect than either Muga or Kikunku in post-hoc comparisons with 'inefficient' individuals. Kewaya relies heavily on a single technique to process the majority of her food. This technique employs the 'strip-up' component favoured by able-bodied individuals. Kalema on the other hand shows a severe handicap in her feeding efficiency. Although not as limited as Tinka in her choice of technique, Kalema has significantly reduced in frequency those techniques preferred by the able-bodied population, relying instead on several simple stage pathways.

The discordance of this result from that expected given the apparent severity of Kewaya's injury highlights the extent to which injured individuals are able to compensate for their injuries. An interesting feature of Kewaya's compensatory strategy was found in that she relied much more heavily on the use of her feet in processing than other injured individuals. In spite of the similarities in th. nature of injury between Kalema and Kewaya it is possible there are subtle differences which have a profound effect on the functional capacities of the limb. This is turn may require radically different compensatory strategies.

For an injured individual, the ability to successfully perform at least one of the two stripping techniques seems to be the key to feeding efficiently on *Broussonettia* leaves. However, even when this is not the case, injured individuals have modified their behaviour to the extent that even the most severe of injuries does not result in a significant decline in feeding efficiency below that of the most casual feeder in the able-bodied population.

Observations of complex preparation techniques used for other food items.

In addition to the young leaves of *Broussonettia* a number of *ad libitum* samples of feeding technique were collected on a number of other food items. These data did not prove sufficient to enable a systematic analysis akin to that performed for *Broussonettia*. However, they do show additional examples of complex plant-preparation skills in chimpanzees and thus descriptions of the technique, at whatever level of detail available, were considered relevant for inclusion here.

A number of observations were made on feeding techniques used to process the young leaves of *Ficus varifolia* and *F. natalensis*. Like *Broussonettia* these leaves have a rough hairy upper surface, and as for *Broussonettia* they are aligned parallel in the palm before eating. However, unlike *Broussonettia,* the technique does not appear distinguished by the direction in which leaves are stripped, nor do the presence of petioles appear to effect the sequence of action. However, this is interesting in that it does seem to point to a shared solution - or subroutine - to the problem of dealing with certain physical properties of plant foods.

The seeds of the ironwood *Cynometra alexandrii* are an important seasonal food item in the diet of Sonso chimpanzees. These seeds are enclosed in a flat pod located on the apical branches of the canopy, which needs to be prised open at one end and split into two halves – much like the action involved in opening an oyster – before the seed can be taken with the lips and eaten. However, this food item is typically located on the apical tips of branches in the uppermost canopy of the tree and thus reliable observations were hampered by visibility

Terrestrial herbaceous vegetation also provided a number of *ad libitum* samples to be taken. Although the majority of these observations were made of individuals feeding on the ground, the sampling problem was to do with quantity of observations as oppose to quality. Terrestrial herbaceous vegetation does not constitute an important food item in the diet of Sonso chimpanzees and as a result, the majority of observations approximated to opportunistic foraging rather than concentrated feeding bouts. **Figure 5.16** shows a flow diagram representing the technique used to feed on rattan *Calamus deeratus*, based on observations of two individuals. Rattan is a climber, of which only the soft white pith of the stem is eaten. To access this pith the chimpanzee must first negotiate a spiny outer casing - very similar to the thistle-stem task described by Byrne & Byrne (1991) - before removing successive inner layers in order to expose the edible pith below. The technique can readily be divided into firstly *segments*, then *sections*, and finally *portions*, which are bitten off and eaten. Each stage represents a more advanced stage of processing, and latter stages are embedded within earlier ones as indicated by the iteration loops.

A similar stem-processing technique was observed in feeding on the herb *Costus dubious*. These are tall leafy green stems, of which again only the soft white inner pith is eaten. The leaves are first removed using a slicing action with the side of the hand and then similar to the technique used in feeding on rattan, the stem is divided into segments of which the outer green casing is removed in a whole-arm stripping action. A manageable section is then detached from this stripped segment and successive layers are stripped off and discarded until a thin pink 'tissue-layer' is reached. This is then unravelled with an action similar to that in unravelling string from around a stick, which exposes the white pith underneath. A portion of this exposed pith is then bitten off and chewed before returning to the unfinished section and when this is processed, to the unfinished segment.

A slightly different technique again is used to process the pith of a broad-leaved herb of the family Marantaceae. Compared to both *Costus* and rattan, the stems of this particular plant are pencil thin and the teeth are used to perform delicate stripping actions by holding the base of the plant steady and pulling back with the head. This exposes an area of pith in the centre of the stem, which is pulled out with the teeth and grasped by the hand. The extracted pith fronds are then fed into the mouth using a zigzag action, which involves a deliberate side-to-side movement of the hand. They are then wadged and eventually spat out with the fibrous pith frond still in an obvious concertina shape. Presumably this is the most effective way of manipulating thin pith strips into a sufficiently compact substrate for wadging.

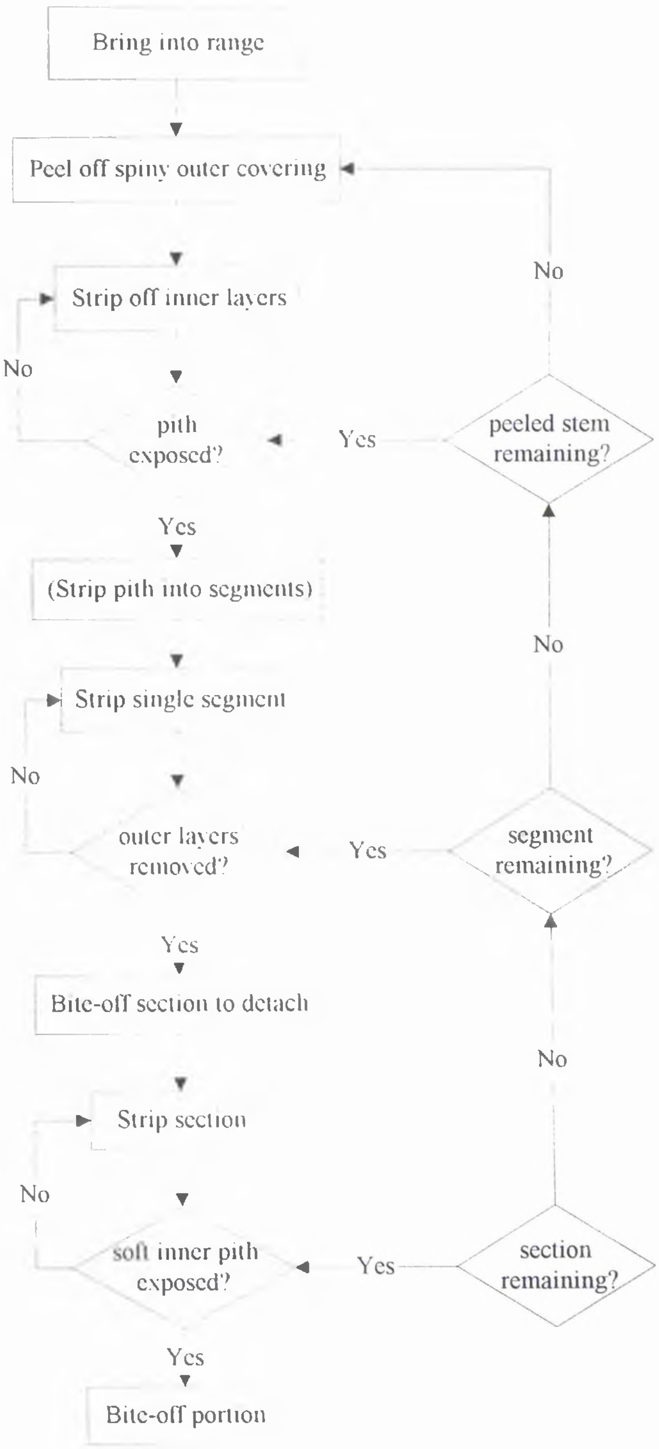


Figure 5.16 Flow diagram showing stem processing of rattan *Calamus deeratus*

Out of these additional food items, only rattan provided observations on both able-bodied and injured individuals. Both Kewaya and Kigere were observed feeding on rattan, and for both these individuals the same overall structure of technique as shown in **Figure 5.16** For the able-bodied population was observed. Differences were seen in the use of feet as supporting structures - particularly in the case of Kewaya - or as a brace against which the teeth were used in a stripping action. In addition, Kewaya was observed to combine a number of different elements - such as holding of a segment of stem during concomitant processing of a section of pith - with her able hand. Although only anecdotal, these observations do at least agree with the general pattern of behaviour shown by injured chimpanzees in processing *Broussonettia* leaves.

Chapter 6

THE EFFECT OF INJURY ON LIMB CO-ORDINATION IN FEEDING: FICUS MUCUSO

The fruits of *Ficus mucuso* are a preferred food item amongst the Sonso community of chimpanzees. The figs are smooth round fruits about the size of a golf ball, and require little processing beyond picking and placing in the mouth. Fruits typically hang in clumps along wide smooth horizontal branches. The trees are large with a broad canopy, and can hold as many as 40 chimpanzees at peak fruiting periods. The behaviour shown when feeding on these particular figs suggests that chimpanzees will try to defend their feeding patch as best they can. This is achieved by picking as many food items as is possible before transferring them to a 'shelf' and processing each item individually.

A *shelf* refers to any part of the animal's body (usually an upper or lower limb) that is enlisted in holding a food item whilst another food item is being processed. A shelf can constitute any number of limbs holding any number of food items at any one time and does not necessarily have to be a different limb to that involved in simultaneous processing. For a food item to be considered shelved rather than merely held, concomitant *manual* processing of another food item must occur, thus holding food items whilst wadging, for example, does not constitute shelving.

Wadging is frequently observed with fleshy fruits and in particular figs, but also bark, leaves and pith. It involves use of the lips and palate to squeeze or rub the food item so as to form a wadge of skin, seeds or fibres, from which the juices are extracted by leisurely squeezing or sucking. For the fruits of *Ficus mucuso,* wadges were often savoured and when dry, were placed on a shelf before accumulating fruits in the mouth and then retrieving the old wadge to pad out the mouthful. Wadging was not considered here as a separate activity. However, the shelving and retrieval of wadges was frequently co-ordinated with fruit processing prior to eating and in this instance, *manual* handling of the wadge was incorporated into the feeding technique.

This chapter investigates the nature of 'shelving' behaviour in processing fruits of *Ficus mucuso*, and looks at the effect of injury on an individual's ability to reproduce this behaviour.

Classification of techniques within the able-bodied population

Both fruits and wadges can be shelved and retrieved at various stages within a particular sequence of elements. Because the individual can be processing a number of different food items at any one time, and each food item may be at a different stage of processing, *handfuls* ie. processing of individual fruits, may, at times, be nested within one another. Thus for clarity, individual *techniques* were not subdivided on this basis. Rather, individual techniques followed the fate of a particular fruit from the point at which it is detached until the point at which it enters the mouth, including all intervening elements that may involve several different handfuls.

All techniques that differed in their sequential organisation of individual elements between picking a fruit and placing it in the mouth were recorded and labelled 1 – 34 (see **Appendix IV**). Techniques that used the same sequence of elements were further distinguished if these elements involved bimanual or monomanual co-ordination within a single handful (e.g. Techniques 2 and 3). Similarly, techniques with the same sequence of elements that disrupt the processing of a particular fruit by shelving and processing another handful were further distinguished if there was more than one item on the shelf (e.g. Technique 28 and 29). It was thought that these features demanded additional dexterity and skill and thus warranted an independent technique. All techniques were then classified across individuals according to the number of times they appeared in an individual's repertoire. They were then further categorised according to the hand/foot part used at each stage of processing (see **Table 6.1**).

Table 6.1 Classification of techniques for able-bodied individuals feeding on fruits of *Ficus mucuso*
[refer to **Appendix IV** for techniques; see **Table 5.1** for key]

IND	TECH	SEQUENCE	n	%N	N
BY	2	- - R - - R (R)	15	53.6	28
		- - L (M) (L) L (L)	10	35.7	
	8	- - R R R R*RF R RF*R R	1	3.6	
	9	- - R R R R*RF R	1	3.6	
	15	(R)* (L) R R L - L - R - R -	1	3.6	
DN	15	- - L L*LF L - L - LF*L - L -	1	7.7	13
	2	- - L (L) - L (L)	7	53.8	
		- - R - - R -	3	23.1	
	14	- - L L R - R R - R L L*R*RF*R (R) R R*L (R) R R - R	1	7.7	
	23	- - R R R*L (R) R R - - R L L (L)	1	7.7	
JM	2	(R) (R) L - (L) L (L)	21	55.3	38
		- - R (R) - R -	14	36.8	
	17	- - R R L L R*RF M*R L - L L - L L - L L - L L M*L R*M RF*R R	1	2.6	
	16	- - L L (R*RF) M*R L	1	2.6	
	18	- - L L M*L R*M RF*R R L L	1	2.6	
MA	15	- - L L*LF R - R - LF*R - R -	1	3.7	27
	2	- - R - - R -	7	25.9	
		- - L - (M) L -	15	55.6	
	4	- - L L	1	3.7	
	25	- - L - L L L (R) - L L	1	3.7	
	20	- - L L L L*R L - L M*R (L) L L - - L L - (L) L R*L L	1	3.7	
	10	- - L L L L*R L - L M*R (L) L	1	3.7	
MG	2	- - R - - R -	1	7.1	14
		- - L - - L -	4	28.6	
		- - R*L - - L -	1	7.1	
	3	(R) (R) L (R) - L (R)	2	14.3	
	15	- - R R*L R - R - L*R - R -	1	7.1	
	9	(L) (L) R R R R*L R	1	7.1	
	7	(L) (L) R R R R*L R L L - R L	1	7.1	
	21	- - L (L) L L*RF R - R L L	1	7.1	
	24	- - L (L) L L*RF R - R L L RF*L L	1	7.1	
	12	- - R R L L RF*L L R R	1	7.1	
NB	2	- - L - - L (L)	24	70.6	34
		- - R - - R (R)	5	14.7	

	6	-	-	L	(M)	-	L	-										3	8.8	
	13	L	L	M														1	2.9	
	16	-	-	L	L	-	M*R	L										1	2.9	
NJ	2	-	-	L	-	-	L	-										8	80.0	10
		-	-	R	-	-	R	-										1	10.0	
	22	-	-	L	L*RF	L	L	R*M	L	L	R	R	RF*R	R				1	10.0	
RD	2	(R)	(R)	L	-	(L)	L	-										13	50.0	26
		(L)	(L)	R	-	-	R	-										8	30.8	
	16	-	-	L	L	-	M*L	L										3	11.5	
		(L)	(L)	R	R	-	M*L	R										2	7.7	
RH	15	-	-	R	R*RF	R	-	R	-	RF*R	-	R	-					1	10.0	10
	2	-	-	R	-	-	R	-										9	90.0	
VN	2	-	-	R	(R)	-	R	(R)										7	24.1	29
		-	-	L	-	-	L	(L)										13	44.8	
	6	-	-	R	(M)	-	R	-										2	6.9	
		-	-	L	(M)	-	L	-										1	3.4	
	1	-	-	R	-	R	R	-										1	3.4	
	11	L	L	L	-	L												2	6.9	
		R	R	R	(M)	R												3	10.3	
IT	2	(R)	(R)	R	-	-	R	(R)										10	32.3	31
		-	-	L	-	-	L	(L)										17	54.8	
	6	-	-	R	(M)	-	R	(R)										1	3.2	
	5	-	-	R	R	(R)												1	3.2	
	1	-	-	L	-	L	L	-										1	3.2	
	16	-	-	L	L	-	M*RF	L										1	3.2	
ZM	2	-	-	R	-	-	R	(R)										10	83.3	12
	15	-	-	R	R*LF	R	-	R	-	R	-	R	-	LF*R	-	R	-	1	8.3	
		-	-	R	R*LF	R	-	R	-	LF*R	-	R	(R)					1	8.3	
ZT	2	-	-	R	-	-	R	-										16	88.9	18
	6	-	-	R	(M)	-	R	-										1	5.6	
	4	-	-	R	R													1	5.6	

Because of the way in which technique has been defined for this particular food type, the number of potential sequences is vast. From the point at which a fruit is picked, the options open to an individual is almost entirely dependent upon the level of risk they consider their food patch to be at. In addition, the length of time they have been at a particular food patch will also be a factor. For example, when feeding begins at a particular patch there will be no wadge to transfer to the hand and no fruits on the shelf to transfer to the mouth. A *bout* of feeding at a particular food patch can be represented by a composite flow diagram representing all possible techniques within that bout (see **Figure 6.1**). The flow diagram therefore starts when an animal arrives at a feeding patch, i.e. with all shelves empty, and stops when the animal leaves, again with all shelves empty. Within the bout, techniques will always start with picking a fruit, and end with eating the same fruit. Decision nodes governing choice of pathway will most likely be dependant upon feeding competition and length of time spent at a particular food patch at any one time.

Unlike the processing technique used for leaves of *Broussonettia,* the technique used in processing fruits of *Ficus mucuso* is seemingly stimulus dependant and does not an employ an ordered sequence of directed elements. For *Ficus mucuso* each technique does not strictly represent a learnt solution to the task - processing the fruit - at hand. Rather, technique depends primarily upon external factors prevalent at the time of processing a particular handful, be it either feeding competition or the presence of semi-processed handfuls that have been shelved. The factors governing choice of a particular pathway or a particular sequence of elements are therefore dynamic, and there is not a fixed set of rules as we saw with *Broussonettia papyrifera*. In spite of this, however, a chimpanzee must still deal adeptly with these fluctuations in circumstance. Thus rather than investigate the organisation of technique, we can tease out aspects of technique which have functional significance.

By shelving fruits in the face of feeding competition, a chimpanzee can be displaced from their feeding patch yet still have reaped the benefits. Similarly, in shelving wadges, a chimpanzee can prolong and maximise nutrient extraction. A

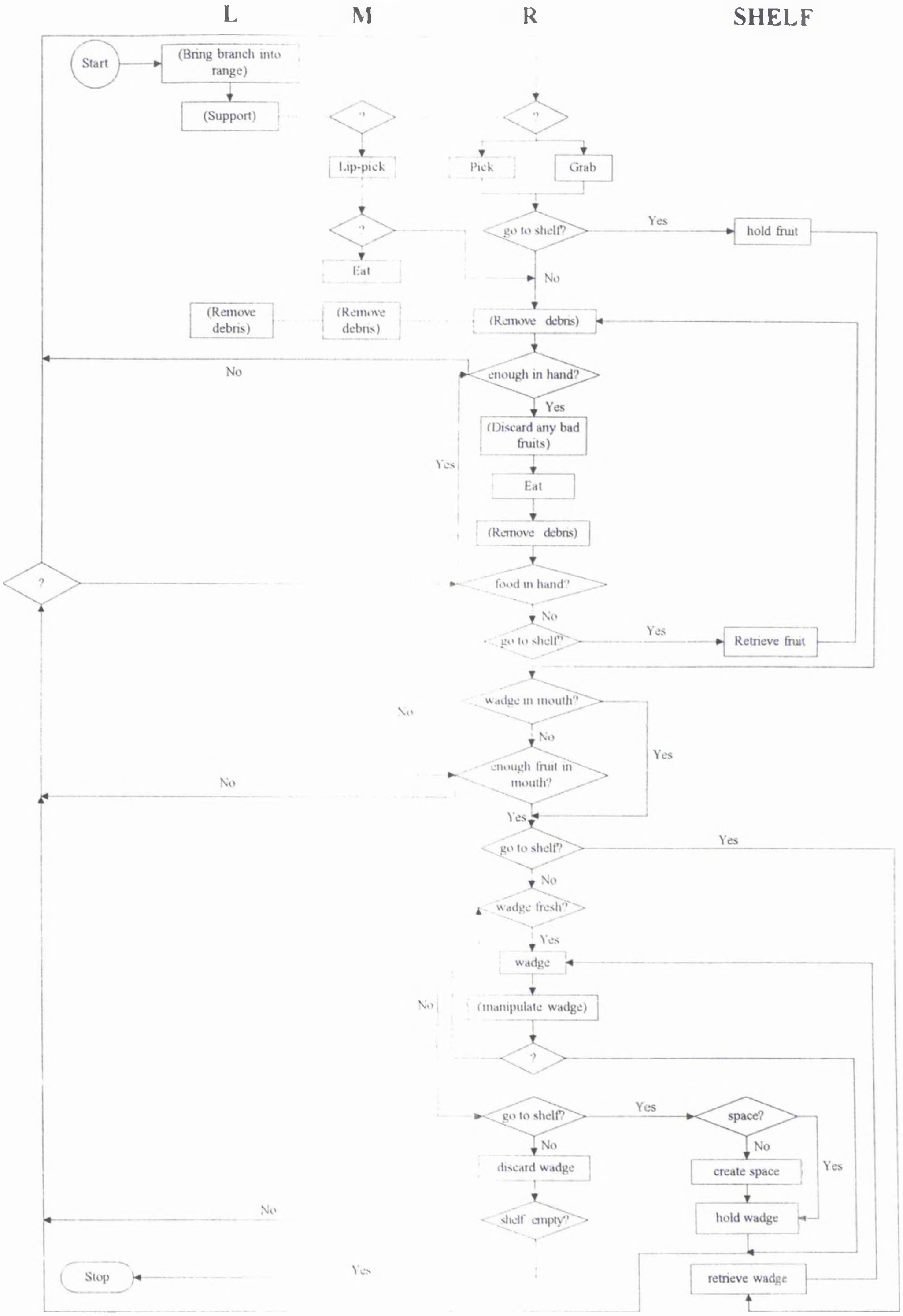


Figure 6.1 Able-bodied individuals feeding on fruits of *Ficus mucuso*

[Flow diagram begins at the bottom and works down. Boxes represent actions and diamonds represent decision processes; a question mark indicates that the factors gocerning decisions have not been inferred; brackets around text indicates that these actions are optional. Vertically aligned shapes labelled L M R at the head of each column indicate that these actions are performed with either left L or right R hand or the mouth M. Left and right is used arbitrarily here and merely indicates bimanual co-ordination as represented by a dashed horizontal line between columns. The right column indicates use of a shelf in processing. This can constitute any body part (left of right) and is represented on the flow diagram in abstract rather than spatial form] third option is to eat fruits one by one as quickly as possible before being displaced. Techniques can therefore be grouped according to function. Four groups were identified; 1) techniques that do not employ a shelf, 2) techniques that shelve fruits, 3) techniques that shelve wadges and 4) techniques that shelve both fruit and wadges.

Able-bodied individuals process a mean 87.84% of their handfuls without shelving fruits (range 57.1-100%). A mean 8.22% of handfuls involved shelving fruit whilst another food item was processed (range 0-42.6%), a mean 2.15% of handfuls involved shelving wadges during processing (range 0-19.2%) and a mean 1.74% of handfuls shelved both fruit and wadge whilst another food item was processed (range 1-10%). This implies that able-bodied individuals prefer to eat individual fruits one by one, and that shelving fruits is a relatively rare phenomenon. However, in interpreting these results we need to remember that handfuls are nested, and thus we need to take into account the context of the particular handful we are analysing. For example, five fruits may be picked and eaten one by one, whilst a fruit is being shelved in the other hand. Therefore, although these five fruits are being processed monomanually both hands are actually employed simultaneously, albeit in processing separate handfuls. Processing fruits of *Ficus mucuso* is not therefore a primarily monomanual technique as the above results imply. Rather, as for processing leaves of *Broussonettia papyrifera*, it involves bimanual co-ordination in an asymmetric task. The difference being that for *Ficus mucuso*, this task represents separate yet simultaneously processed handfuls. With this in mind, we can investigate the limitations that limb injury might impose.

Effect of injury on choice of technique

As for able-bodied individuals, techniques were classified across injured individuals according to frequency of use and the hand/body part used at each stage of processing (see **Table 6.2**). For the four functional groups of technique, frequency of use was analysed both at the population level and at the individual level.

Table 6.2 Classification of techniques for injured individuals feeding on fruits of Ficus mucuso

[refer to **Appendix IV** for techniques; see **Table 5.1 & 5.3** for key]

IND	TECH	SEQUENCE																			n	%N	N
GN	2	-	-	R	(R)	(R)	R	(R)													15	60.0	25
		(R)	(R)	L	L	-	L	(L)													4	16.0	
	6	-	-	R	(M)	-	R	(R)													1	4.0	
		-	-	L	(M)	-	L	(L)													1	4.0	
	28	-	-	L	(L)	L*LF	R	-	R	LF*R	R										1	4.0	
	29	-	-	L	(L)	L*LF	R	-	R	LF*R	R	-	R	L	L						1	4.0	
	30	(R)*	(L)	R	(R)	R	R*LF	R	R	LF*R	R										1	4.0	
	31	-	-	R	(R)	R	R*LF	R	R												1	4.0	
KG	6	-	-	L	(M)	-	L	-													2	13.3	15
	2	-	-	L	-	-	L	-													8	53.3	
		-	-	R	-	-	R	-													3	20.0	
	3	-	-	L	(R)	-	L	-													1	6.7	
	16	-	(R)	L	L	-	M*R	L													1	6.7	
KK	2	-	-	R	(R)	(R)	R	(R)													53	89.8	59
	1	-	-	R	-	R	R	(R)													2	3.4	
	6	-	-	R	(M)	-	R	-													2	3.4	
	11	R	R	R	-	R															1	1.7	
	16	-	-	R	R	-	M*R*LF	R													1	1.7	
KL	15	-	-	L	L*LF	L	-	L	-	LF*L	-	L	-								1	1.3	76
	2	(L)*	(LF)/(*R*)	L	-	-	L	(L)													65	85.5	
		-	-	L*LF	-	-	LF*L	-													1	1.3	
	6		(LF)	L	(M)	-	L	-													9	11.8	
KY	2	-	-	L	-	-	L	(L)													18	85.7	21
		-	-	L*LF	-	-	LF*L	-													1	4.8	
	6	-	-	L	(M)	-	L														1	4.8	
	3	(L)*	(*R*)	L	(*R*)	-	L	-													1	4.8	
MU	2	-	-	L	(L)	-	L	-													12	80.0	15
	11	L	L	L	-	L															3	20.0	
TK	2	(L)*	(R)	L	-	-	L	(L)													49	84.5	58
	15	-	-	L	L*RF	L	-	-	-	RF*L	-	L	-								1	1.7	
		-	-	L	L*R	L	-	L	-	R*L	-	L	-								1	1.7	
	32	-	-	L	L*R	L	L	M*L	L	L	R*L	L									1	1.7	
		-	-	L	L*RF	L	L	M*L	L	L	RF*L	L									1	1.7	
	33	-	-	L	L*R	L	L*R	L	L*RF	L	L	M*L	L	L	RF*L	L	R*L	L	R*L*R*L	L	1	1.7	
		-	-	L	L*R	L	L*RF	L	L	M*L	L	L	RF*L	L	R*L	L					1	1.7	

	34	-	-	L	L	M*L	L	L																						3	5.2	
ZA	2	(LF)	(LF)/(RF)/(L)	R	-	-	R	(R)																						61	66.3	92
		-	-	RF	-	-	RF	-																						1	1.1	
		-	-	LF	-	-	LF	-																						2	2.2	
		-	-	LF*R	-	-	R	-																						4	4.3	
		-	-	LF	-	-	B	-																						3	3.3	
		-	-	LF*B*R	-	-	R	-																						2	2.2	
	6	-	-	R	(M)	-	R	-																						11	12.0	
		-	-	RF*R	(M)	-	R	-																						1	1.1	
		-	-	LF*B*R	(M)	-	R	(R)																						1	1.1	
	27	R	R	M	R	R																								1	1.1	
	15	-	-	R	R*RF	R	-	R	-	R	-	R	-	RF*R	-	R	-													1	1.1	
	21	(R)*	(LF)	R	-	R	LF	-	LF	R	R																			2	2.2	
	26	-	-	LF	LF	R	R	-	R	R	-	R	R	(R)	R	R	-	R	R	(R)	R	R	-	R	R	(R)	LF*R	R	-	1	1.1	
	12	-	-	LF	LF	R	R	LF*R	R																					1	1.1	

Injured population v able-bodied population

Table 6.3 compares the frequency of each group for the able bodied population as a whole, with frequencies for each injured individual. For each group, the mean frequency for the able-bodied population was taken. Individuals were then subdivided according to whether their frequencies were above or below the mean and whether they were injured or able-bodied. The Chi-squared test (corrected for continuity) was applied to these frequencies to see whether injury has an effect on choice of technique. It is hypothesised that limb injuries will reduce shelf options, and thus favour one-step ‘easy-to-process’ techniques, that do not require the use of a shelf.

Table 6.3 Frequency of use of technique (%) for processing fruits of *Ficus mucuso*

[techniques 1-34 grouped according to function; individuals with no. of handfuls < 10 are not included for analysis]

TECH	ABLE-BODIED						INJURED							
GROUP	N	Mean	Med	SD	Min	Max	BN	KG	KK	KL	KY	MU	TK	ZA
No shelf	13	87.84	90	11.61	57.1	100	84	93.3	98.3	98.6	100	100	89.7	94.7
Fruit shelved	13	8.22	0	12.84	0	42.6	16	0	0	1.3	0	0	10.2	5.5
Wadge shelved	13	2.15	0	5.28	0	19.2	0	6.7	1.7	0	0	0	0	0
Fruit & wadge shelved	13	1.74	0	3.1	0	10	0	0	0	0	0	0	0	0

The only group that showed a significant effect was techniques that shelved both fruit and wadge whilst another food item was processed. The injured population showed a significant reduction in their use of these techniques (χ^2 = 3.7719, df = 1, p = 0.05). At the population level there was no concomitant increase in the use of non-shelf techniques. Within the injured population however, individual differences are seen across the four groups and these shall be dealt with in detail.

Injured individual v able-bodied population

In comparing individuals against a population, the same method as used in **Chapter 5** was employed. **Figure 6.2** shows the distribution of scores within the able-bodied population for each of the four functional groups of technique. Only those injured individuals whose score falls outside the 95% confidence intervals set by the able-bodied population are shown.

On the basis of the frequency with which they use particular groups of technique, injured individuals fall into two groups. The first group shows an increase in their use of simple pick-and eat techniques without employing a shelf. At the same time these same individuals show a significant decrease in their use of techniques that require fruits to be shelved. This agrees with the original hypothesis that limb injury will favour 'easy' one-step processing. The second group does not conform to this hypothesis. Rather, they exhibit similar frequencies as seen in the able-bodied population and hence are not represented in **Figure 6.2.** These two groups of individuals correlate with extent of injury. In the first group are individuals with limb injuries to one hand, leaving only one able upper limb. This includes Kewaya (KY), Kalema (KL), Muga (MU) and Kikunku (KK). In the second group are individuals with limb injuries to one foot, leaving two able upper limbs, namely Banura (BN) and Kigere (KG), and individuals with injuries to both hands, leaving no able upper limbs, namely Tinka (TK) and Zana (ZA). Only Kigere uses a technique that requires wadges to be shelved, and no individuals within the injured population use a technique that requires both wadge and fruit to be shelved. However at the individual level none of these frequencies fall outside of the distribution of the able-bodied population.

Within each functional group of techniques, we can elicit further differences by reverting to the 34 individual techniques originally identified. Again, injured individuals were compared against the able-bodied population using the same method as above. **Figure 6.3** shows the distribution of scores within the able-bodied population for each technique. Only those injured individuals whose

Figure 6.2 Frequency of use of techniques - grouped according to function

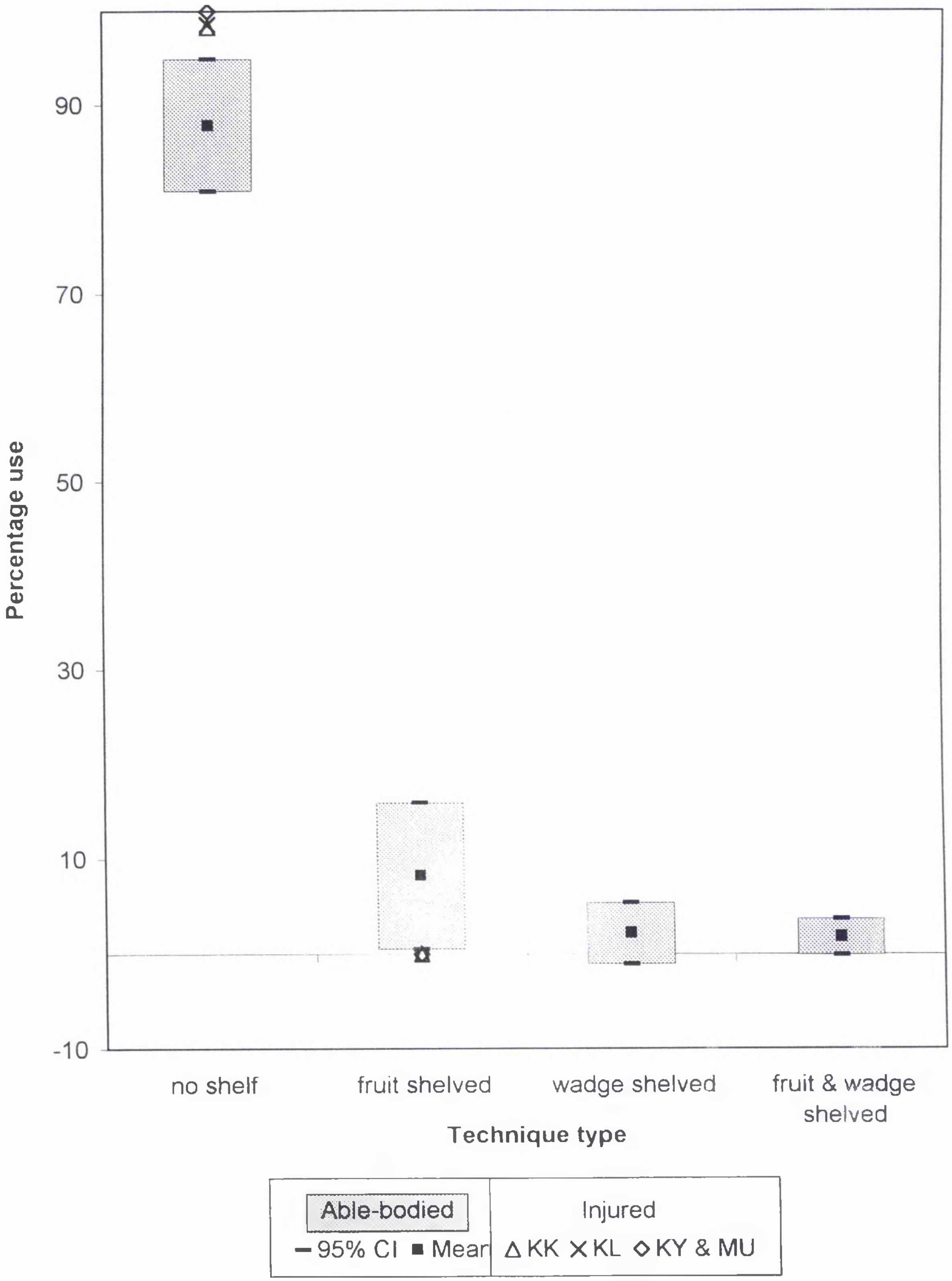
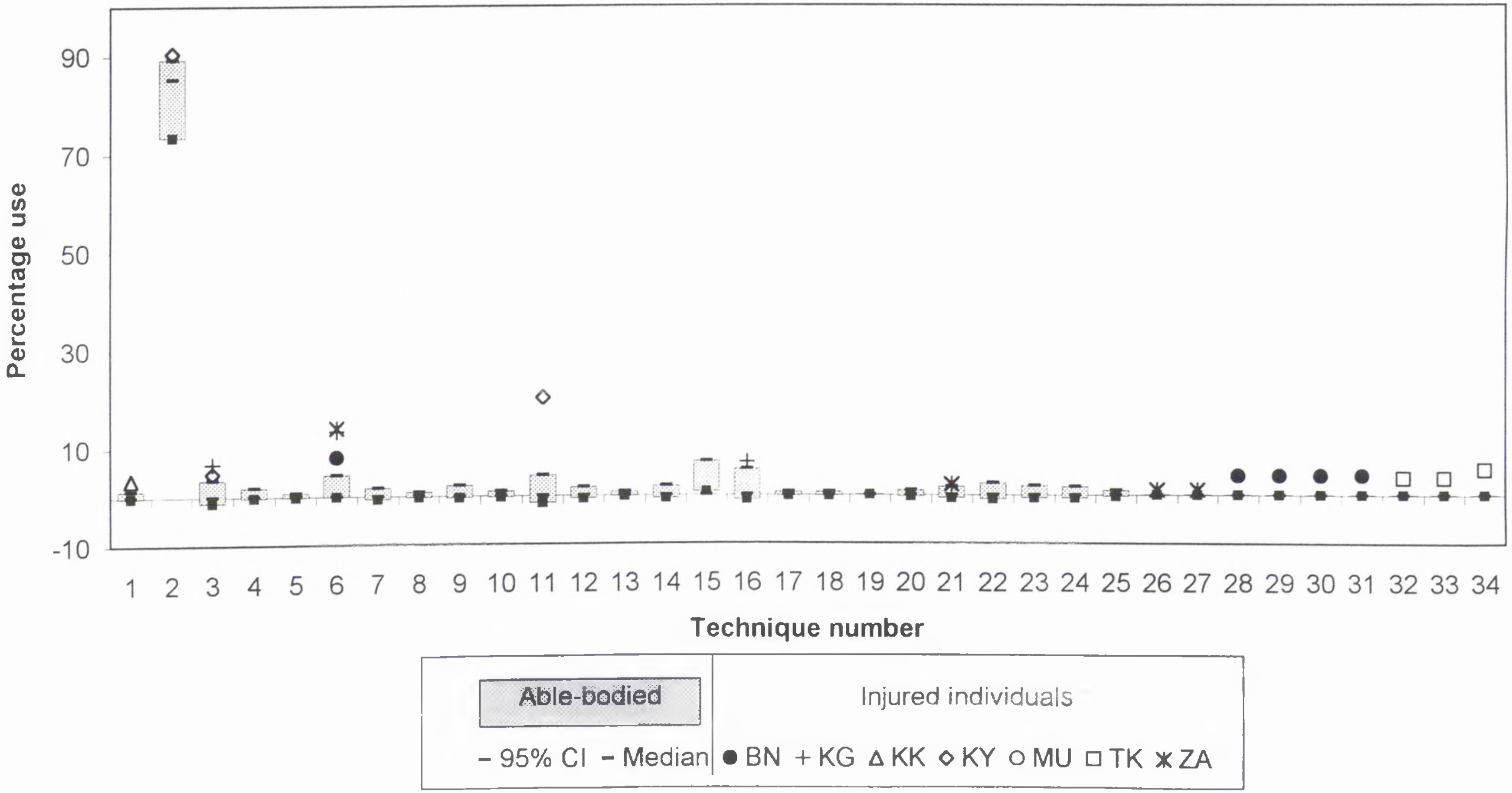


Figure 6.3 Frequency of use of technique



score falls outside the 95% confidence intervals set by the able-bodied population are shown.

The greatest difference in frequency of use of a particular technique from that seen in the able-bodied population is within those techniques that require no shelf, as would be predicted from **Figure 6.2.** There is a further subdivision within this group into monomanual and bimanual processing of a single handful. A preference for mono-manual processing of a single handful is shown by injured individuals. Kikunku and Kewaya show an increase in their use of Techniques 1 and 2 respectively. Both of these require debris be removed by the same hand that is holding the fruit, ie an individual's digits are performing separate elements. Banura and Zana show an increase in their use of Technique 6. This again requires mono-manual processing, but rather than individual digits of the same hand performing separate elements, the mouth is used in conjunction with the hand. Zana also shows an increase in Technique 27, which require the branch to be brought into range, a fruit picked off with the lips and then re-grasped with the hand, again a mono-manual process. Muga shows an increase in Technique 11. Here the branch is brought into range and the same hand slide-adjusts itself up the branch in order to detach the fruit. Technique 34 is unique to Tinka. After picking the fruit, the wadge is spat out and discarded before the fruit is eaten. Within the able-bodied population, the wadge would normally be transferred to a shelf before eating the fruit rather than discarded altogether. Only Kewaya and Kigere show an increase in their use of a technique requiring bimanual processing of a single handful, namely Technique 6, in which one hand removes debris from a fruit held in the other.

Within other functional groups of techniques, only those individuals with both hands injured or with one foot injured show an effect on frequency of use. Again, this is to be expected from inspection of **Figure 6.2.** For techniques requiring fruits to be shelved, Tinka shows an increase in Techniques 32 and 33. As for Technique 34, these techniques are unique to Tinka and involve discarding the wadge from the mouth before retrieving fruits from the shelf. Zana shows a slight increase in Techniques 21 and 26, and Banura shows an increase in Techniques 28 – 31. For techniques requiring shelving of wadges, Kigere shows an increase in Technique 16. This technique involves creating space on the shelf before the wadge can be placed there.

In looking at the effect of injury on choice of technique, two patterns emerge. Firstly, injuries to the upper limbs have a greater effect on feeding technique than injuries to the lower limb, as would be expected. Secondly, of those individuals with upper limb injuries, the greatest effect results from having one hand injured rather than both. This is in sharp contrast to the pattern seen in processing *Broussonettia* leaves, where individuals with the most severe of injuries, ie. both hands injured, showed the greatest departure from the pattern seen in the able-bodied population.

In order to understand how individuals with both hands injured are compensating in a way that they couldn't with *Broussonettia* leaves, there are two factors to consider. The first is the degree of manual dexterity required in the two tasks. In processing leaves of *Broussonettia*, individual digit manipulation was required for a number of elements, which limited the particular pathway available to those individuals with no able hands. Conversely, processing *Ficus mucuso* requires no fine-level manipulation, other than manoeuvring fruits and wadges between limbs. Depending to an extent upon the exact nature of the injury, the range of techniques open to injured individuals will in general be comparatively greater. In order to investigate this I will look at the elements used by each limb, and in particular the injured limb. The second factor involves limb co-ordination in processing separate yet simultaneous handfuls. The greater effect on choice of technique shown by individuals with one injured hand may be as a result of overcompensation with the able limb at the expense of the injured limb. The findings from **Figure 6.3** suggest that this may be the case. In addition to monomanual processing of a single handful, monomanual processing of concomitant handfuls may occur, by combining functions with different digits of the same hand. For example, fruits and wadges may be shelved on the same hand that is carrying out simultaneous processing of another handful. At the same time, individuals with both hands injured do not have this option and therefore must gauge compensation according to the severity of the injury in each hand. When the effect of injury on each hand is similar, ie. both retain similar function, the two hands would be expected to be used in a similar way to an able-bodied individual. If loss of function is greater in one hand than the other, then individuals may bias compensation towards one hand only or else rely more on their feet to counterbalance the most affected hand. In order to investigate this, we shall look at patterns of limb use and co-ordination in processing concomitant handfuls. Of course, these two measures are not mutually exclusive but are instead complementary in understanding the nature of compensatory strategies.

Repertoire of elements used in processing

All elements used in processing fruits by individuals with 10 or more complete handfuls were identified and placed into functional categories, which correspond with the four functional groups of technique. Element use was broken down into left and right hand, or when used simultaneously for the same element – both. Use of the mouth (lips/teeth) was also included to see if this bore any relationship to injury (see **Table 6.4a** for able-bodied individuals and **6.4b** for injured individuals).

Even for a relatively simple food item to process such as *Ficus mucuso*, able-bodied individuals show highly idiosyncratic usage of elements within each functional category. As the number of handfuls varies between individuals, it is evident that the full set of elements has not reached asymptote for all animals (**Figure 6.4**). Linear regression for the number of elements from the number of handfuls supports this (elements = 1.391 x handfuls - 3.586, $r^2 = 0.739$, F (1,11) = 31.154, $p < 0.001$).

The same story is seen for injured individuals, with the amount of data analysed accounting for most of the variation seen in size of element repertoire (**Figure 6.5** elements = 3.221 x handfuls - 19.3, $r^2 = 0.743$, F (1,6) = 17.363, p = 0.006). The relationship appears even stronger when only individuals with upper limb injuries are considered.

Table 6.4a Elements used by able-bodied individuals in processing fruits of *Ficus mucuso* [see Table 5.5a for key]

Element	BY				DN				JM				MA				MG				NB				NJ				RD				RH				VN				VT				ZM				ZT			
	L	R	B	M	L	R	B	M	L	R	B	M	L	R	B	M	L	R	B	M	L	R	B	M	L	R	B	M	L	R	B	M	L	R	B	M	L	R	B	M	L	R	B	M	L	R	B	M	L	R	B	M
Pull into range																																																				
Reach (TH)																													2																							
Reach (DH)																																																				
Hook (2:3:4)										1											1								4								1	3														
Hook (2:3)		1															1	1											1								1				1											
Combine (hold wadge CH/reach PS)																														1																						
Foot																																																				
Slide-adjust																																					2	3														
Manoevering items																																																				
Swap to hand	1																																																			
Support																																																				
Transverse hook																													3																							
Diagonal hook																																																				
Hook (2·3)	1									4							1	1											1												1											
Hook (2 3 4)										7											1								5																							
Adjust										1																																										
Combine (hold wadge CH/ precision grip PS)																														1																						
Detaching items(may/may not inc. Pm)																																																			
Pick (PS)	8	15			6	2			13	10			15	7			7	4			10	3			8	1			12	7				10			13	9			1	4				4				12		
Pick (2 3·Pm)	2				1	1			1	1				1			1				10	1																			9	o				4						
Pick (1.2IMP)																													5								3															
Pick (1.3)									3				2								8	1																								4						
Pick (1 3IMP)									3																1												1	2														
Pick (1 2 3)		1			1				1	1																												1												1		
Pick (1 2 3IMP)																																																		1		
Pick (SG)					1																																															
Pick (1 4)									1																																											
Twist-off		1																																																		
Grab x n (whole hand)													1																													1								1		
Lip pick single fruit																																																				
Combine (support 2.3/pick 4 5 Pm)																																										1										
Combine (hold wadge CH/pick PS)																														3																						
Accumulate																																																			
Combine (hold fruit CH/pick 2 3)																	1																								1											
Combine (hold fruit CH/pick PS)	1	1			1	1			1				4				1	1																			2	1												1		
Combine (hold fruit 4·5 Pm/pick 2 3 Pm)																																																				
Combine (hold fruit CH/pick 1 2IMP)																													1																							
Removing parts from items																																																			
mouthpeel				5																				5																3				1								1
Pick-off																																						1														
Pick-at																																										1										
Twist-off														1				1																																		
brush																																																				
biteoff																2																																				
Combine (hold fruit CH/biteoff)													1																																							
Combine (hold fruit CH/POF PS)						1																																														
Maneovring items (fruits)																																																			
Manipulate					1					4											1																					1										
Rotate						1																																														
Adjust																																						1														
Swap-to foot					1					1			1													1								1											2							

Swap to hand		1		1	2			1			1		3	1						1						1				1					2				
Combine (hold fruit CH/SH RF PS)		1			1								1																										
Combine (hold fruit CH/SH PS)					1					1				1																									
Combine (hold wadge CH/SH PS)											1																												
Storing items																																							
Foot		1		1	1			1		1				1		1				1						1						1		2					
Mouth																																							
Cup-hold	3	6		2			3	3		1	3		3	1		4	3			2		7	8		1						1								
Precision grip (PS)																																							
Precision grip (1:3)																																							
Combine (hold fruit CH/hold fruit PS)																																							
Combine (hold fruit PS/hold wadge CH)											1												1																
Combine (hold fruit 1:3/hold wadge 4:5:Pm)							1																																
Combine (hold wadge CH/hold wadge 2:3:Pm)																	1																						
Putting in mouth																																							
Bite																																							
Bite (S)																																1			1				
Bite (R)		2					5	12		5						8						2	3					4	8			6						4	
Eat x n					1					1																1					1							1	
Eat	10	15		9	3		17	3		13	8		11	3		20	5		8	2		11	4			9		13	4		9	5			11			13	
Retain nucleus																													1										
Combine (hold fruit CH/ BR PS)										2																		1	1			1							
Combine (hold fruit PS/eat 4:Pm)							1																																
Combine (hold fruit CH/eat 1 2IMP)																						1																	
Combine (hold fruit CH/eat PS)	1									1																		1										1	
Combine (hold wadge CH/BR PS)																							1																
Combine (hold wadge CH/eat PS)																						1	2																
Removing debris																																							
Pick-out (PS)	2	8		2			1							1		11	5											3	1		1	2			2				
Pick-out (SG)																																							
Pick-out (1 3)																1																							
Maneovring items (wadge)																																							
Wadge			17			2			5			7			3			9			2			19			1			5			20			2			2
Adjust		7		2									1																		2	3			1				
Manipulate	1	2																													6	1							
Rotate																															2								
Swap mouth to	4	7					2	1		2	2					4	3					11	7		1			1			8	1						1	
Swap mouth to foot																																1							
Swap hand to			10						3		1	3						4			1			10		1	1			1			10						1
Swap to foot		1																																					
Combine (hold fruit CH/SH mouth PS)																																							
Combine (hold fruit 1:3/SH 4.5:Pm)							1																																
Combine (hold fruit PS/ SH 4:5:Pm)																						1																	
Combine (hold wadge 2 3:Pm/SH mouth Pm)																	1																						
Removing items																																							
Discard		1														1																							
Knock														1																									
Foot discard		1																																					
No. of different elements used*	**25**			**19**			**26**			**23**			**17**			**20**			**9**			**23**			**10**			**21**			**25**			**11**			**13**		
No. of handfuls	**28**			**13**			**38**			**27**			**14**			**34**			**10**			**26**			**10**			**29**			**31**			**12**			**18**		

(* hand insensitive)

Table 6.4b Elements used by injured individuals in processing of fruits of *Ficus mucuso* [see Table 5.5b for key]

Element	BN				KG				KK				KL				KY				MU				TK				ZA			
	L	R	B	M	L	R	B	M	L	R	B	M	L	R	B	M	L	R	B	M	L	R	B	M	L	R	B	M	L	R	B	M
Pull into range																																
Reach (TH)																	1															
Reach (DH)		1																														
Reach (PS)													1																			
Hook (2:3:4)		1																														
Hook (2:3)										1			1								3											
Hook (1)																														2		
Combine (hold wadge CH/reach PS)																																
Reach (HK:GS)																									1							
Foot													1																2			
Slide-adjust										1			1								3											
Manoevering items																																
Swap to foot																													1			
Swap to hand	1													1				1								1						
Support																																
Transverse hook	1																															
Diagonal hook		1																														
Hook (2 3)						1																										
Hook (2 3 4)																																
Hook (1)																														1		
Elbow-hook														3																		
Back-of-wrist																		1														
Wrist-wrap																										1						
Lateral-wrist																										1						
Knuckles																													1			
Foot													6																8	2		
Adjust																																
Combine (hold wadge CH precision grip PS)																																
Detaching items(may/may not inc. Pm)																																
Pick (PS)	5	14			6	3				14			16				16				8				51							
Pick (2 3 Pm)	1	2			1					15			28				5				7											
Pick (2 3 4 Pm)													1																			
Pick (1 2IMP)		1																														
Pick (1:3)		1																														
Pick (1:3IMP)					2																											
Pick (1:2:3)													1																			
Pick (1:2.3IMP)																																
Pick (SG)																																
Pick (1:4)																																
Pick (HK:GS)																									2							
Pick (1:Pm)																														72		
Pick (foot)																													14	2		
Twist-off																									1							
Grab x n (whole hand)																																
Lip pick single fruit																																1
Combine (support 2:3/pick 4 5 Pm)																																
Combine (hold wadge CH/pick PS)																																
Accumulate																																
Combine (hold fruit CH/pick 2:3)		1								3																						
Combine (hold fruit CH/pick PS)	1	3								3			1																			
Combine (hold fruit 4:5:Pm/pick 2:3:Pm)																																
Combine (hold fruit CH/pick 1:2IMP)																																
Removing parts from items																																
mouthpeel				2				2				2				17				1												13
Pick-off																					1											
Pick-at																														3		
Twist-off						1																										
brush																		1														
biteoff																																1
Combine (hold fruit CH/biteoff)																																
Combine (hold fruit CH/POF PS)		1								2																						
Maneovring items (fruits)																																
Index-probe																														1		

Manipulate																								
Rotate		1						2		2			4			2								
Adjust																							1	
Pick-out																			1					
Swap-to foot										1			1							1			1	
Swap to hand		2								1			1					1	6	3			8	
Swap to hand (foot/ support L lateral wrist)																							2	
Combine (hold fruit CH/SH RF PS)																								
Combine (hold fruit CH/SH LF) PS)	1	1																						
Combine (hold fruit CH/SH PS)																								
Combine (hold wadge CH/SH PS)																								
Storing items																								
Foot	2						1			1										2		5	2	
Mouth																								
Cup-hold	1			1	1			1																
Precision grip (PS)																								
Precision grip (1·3)																								
(1:Pm)																							6	
Crook of elbow							1																	
Wrist-hook											3													
'Grasp-hook'																								
'Grasp-hook' x n																				1				
Combine (hold fruit CH/hold fruit PS)																								
Combine (hold fruit PS/hold wadge CH)																								
Combine (hold fruit 1:3/hold wadge 4:5 Pm)																								
Combine (hold wadge CH/hold wadge 2 3 Pm)																								
Putting in mouth																								
Bite																								
Bite (S)																							5	
Bite (R)	1	1		4	1			1		13						2			13				49	
Eat x n								3																
Eat	5	16		8	2			55		16			21			12			45				30	
Eat (foot)																						2	1	
Eat (foot/support L lateral wrist)																						3		
Retain nucleus																								
Combine (hold fruit CH/ BR PS)																								
Combine (hold fruit PS/eat 4 Pm)																								
Combine (hold fruit CH/eat 1 2IMP)																								
Combine (hold fruit CH/eat PS)		3						1		1														
Combine (hold wadge CH/BR PS)																								
Combine (hold wadge CH/eat PS)																								
Removing debris																								
Pick-out (PS)	1	2						6		10			2						2					
Pick-out (1)																							1	
Pick-out (SG)																								
Pick-out (1.2IMP)																								
Pick-out (1.3)										1														
Maneovring items (wadge)																								
Wadge			6			2			11			18			6			1			12			11
Adjust		2					1			6	1								3					
manipulate										2														
Rotate																								
Swap mouth to					1		1	2		4	3								3				3	
Swap mouth to foot																						2	1	
Swap hand to						1		2	3	2		7												
Swap foot to										1													1	4
Swap to foot										1												1	1	
Swap to mouth (foot/support R 1:Pm)																						1		
Combine (hold fruit CH/SH mouth PS)																								
Combine (hold fruit 1:3/SH 4:5:Pm)																								
Combine (hold fruit PS/ SH 4:5:Pm)																								
Combine (hold fruit 3:4:5:Pm/SH LF PS)								1																
Combine (hold wadge 2:3:Pm/SH mouth Pm)																								
Removing items																								
Discard																								
Knock																								
Foot discard																								
Combine (hold fruit HK:GS/knock 1)																			3					
No. of different elements used*	**24**			**12**			**21**			**30**			**13**			**10**			**19**			**31**		
No. of handfuls	**25**			**15**			**59**			**76**			**21**			**15**			**58**			**92**		

(* hand insensitive)

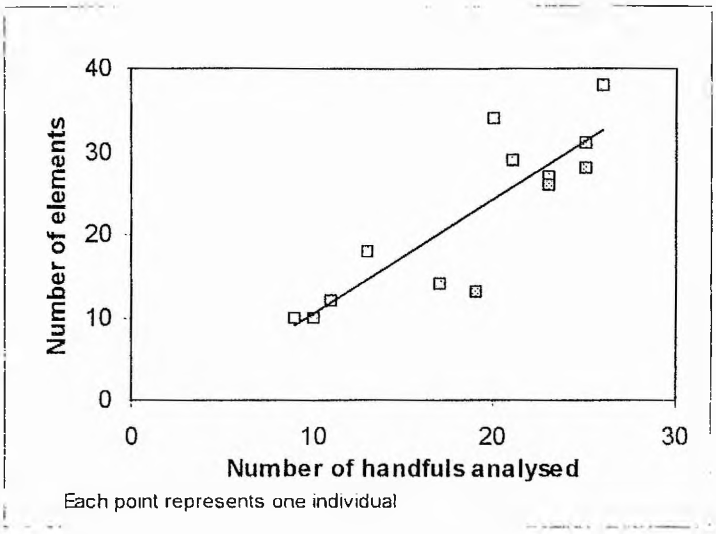


Figure 6.4 Relationship between amount of data analysed and number of elements in an able-bodied individual's repertoire

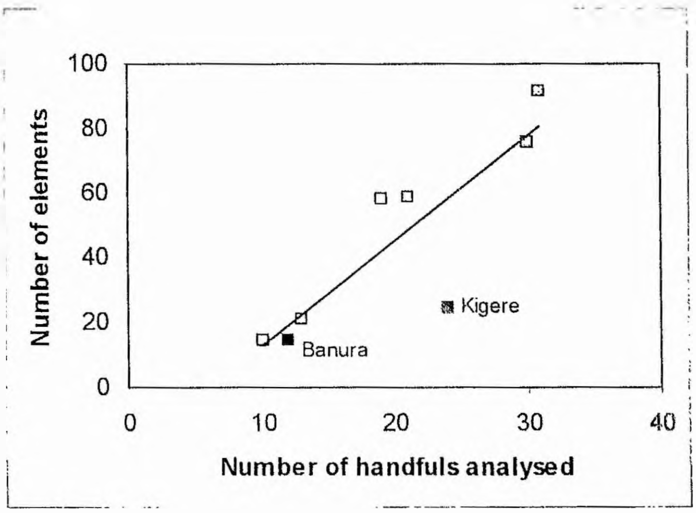


Figure 6.5 Relationship between amount of data analysed and number of elements in an injured individual's repertoire (named individuals indicate lower limb injuries)

This is in sharp contrast to that seen in processing *Broussonettia* leaves. For an injured individual the repertoire of elements used in processing *Broussonettia* leaves is constrained by the skilled nature and multi-stage organisation of the task. The repertoire of elements used in processing *Ficus mucuso* is constrained only by how many fruits can be processed at once.

One effect of injury that is seen on processing both *Broussonettia* and *Ficus mucuso* however, is the reduction in number of elements performed by the injured limb, at least for those individuals that have only one hand injured. As for *Broussonettia*, the injured limb can still be used in processing *F. mucuso* through a number of compensatory actions, but its role is limited to passive or support actions. (see **Table 6.5**). Despite *Ficus mucuso* posing a relatively simple task in terms of manual dexterity, the range of elements performed by the injured limb seems no greater than that seen in a complex leaf-processing task such as *Broussonettia.*

It is clear from **Table 6.5** that individuals with one injured hand do not rely on their injured limb in processing. In order to investigate whether they overcompensate with their able limb, we can look at the frequency of 'combine' elements that are performed with the able hand, or in other words the frequency with which two elements are performed simultaneously with individual digits of one hand (see **Tables 6.4a** & **6.4b**). For able-bodied individuals, a mean of 20.5% (SD 20.27, range 0-69.67%) of elements require combined functions of individual digits. This represents elements performed by both hands. For individuals with one injured hand, the frequency with which the able hand performs 'combine' elements is 42.86% for Kikunku, 6.67% for Kalema, and 0% for both Kewaya and Kalema. Only for Kikunku can we say that the able-limb may be compensating for the loss of function in the injured limb, and even then 89% of all 'combine' elements performed by Kikunku involve accumulating fruits in techniques that do not use a shelf. Thus, our hypothesis that 'one-handed' individuals might over-compensate with the able limb in co-ordinating the processing of separate handfuls can be rejected.

Table 6.5 Elements used by the injured upper limb

Element	KK	KL	KY	MU	TK		ZA	
	L	R	R	R	L	R	L	R
Pull into range								
Reach (HK:GS)					/			
Hook (1)								/
Manoeuvring items								
Swap to hand		/	/			/		
Support								
Hook (1)								/
Elbow-hook		/						
Back-of-wrist			/					
Wrist-wrap						/		
Lateral-wrist						/		
Knuckles							/	
Detaching items (may/may not inc. Pm)								
Pick (PS)					/			
Pick (HK:GS)					/			
Pick (1:Pm)								/
Twist-off					/			
Removing parts from items								
Brush			/					
Manoeuvring items (fruits)								
Index-probe								/
Pick-out					/			
Swap to hand					/	/		/
Swap to hand (foot/ support L lateral wrist)								/
Storing items on shelf								
(1:Pm)								/
Crook of elbow	/							
Wrist-hook		/						
'Grasp-hook'								
'Grasp-hook' x n						/		
Putting in mouth								
Bite (S)								/
Bite (R)					/			/
Eat					/			/
Eat (foot/support L lateral wrist)							/	
Removing debris								
Pick-out (PS)					/			
Pick-out (1)								/
Manoeuvring items (wadge)								
Adjust	/	/			/			
Swap mouth to	/	/			/			/
Swap foot to								/
Swap to mouth (foot/support R 1:Pm)								/
Removing items								
Combine (hold fruit HK:GS/knock 1)					/			
Total number of elements	3	5	3	0	12	5	2	14

In the case of individuals with both hands injured, an interesting difference between Tinka and Zana emerges. As we have already seen, the injuries to each of Tinka's hands are sufficiently different such that each complements the other's loss of function. The same is true with *Ficus mucuso*. The left hand is responsible for picking fruits and transferring them to shelves. Importantly, Tinka is able to use his injured right hand as a shelf. The right hand is incapable of voluntary movement, but because the digits can be passively extended, the left hand is capable of shelving any number of fruits in the palm of the right hand. This is in contrast to what we have seen in the case of Kewaya, Muga and Kikunku, primarily because the injuries to their limbs are such that food items cannot physically be shelved. Kikunku was once observed to transfer a wadge to the crook of his left elbow, and Kalema to transfer a wadge to the hooked wrist of the right hands, but these are presumably precarious shelves, unlike the snug fit of Tinka's right hand. This ability to shelve fruits must be the crucial factor in why Tinka's behaviour conforms so well to that seen in the able-bodied population. His one limitation is in accumulating food items in the left hand, the same limitation that was incurred in stripping up multiple leaves of *Broussonettia*. This may also explain why Techniques 32-34 are unique to Tinka. These involve discarding the wadge from the mouth when able-bodied individuals would normally have shelved it. With food items already held in the left hand, Tinka would not be able to accumulate the wadge.

A similar pattern however, is not observed in the case of Zana, whose injured hands do not perform complementary roles in processing. Each hand differs in the nature of injury. The right hand is missing all digits but retains the thumb which functions normally as a 'precision grasping' limb. However, as for Tinka, this hand is not capable of accumulating food items, and instead fruits must be picked and processed individually. The paralysis to the left hand however is so complete as to render the hand useless. However Zana, like Tinka, still conforms well in choice of technique to the pattern shown by the able-bodied population. **Table 6.4b** suggests that Zana may rely on her feet in conjunction with the left hand, in co-ordinating processing with the more 'able' right hand. In order to investigate this in more detail we can look at the second of the proposed measures – that of limb-co-ordination in processing concomitant handfuls.

Patterns of limb co-ordination

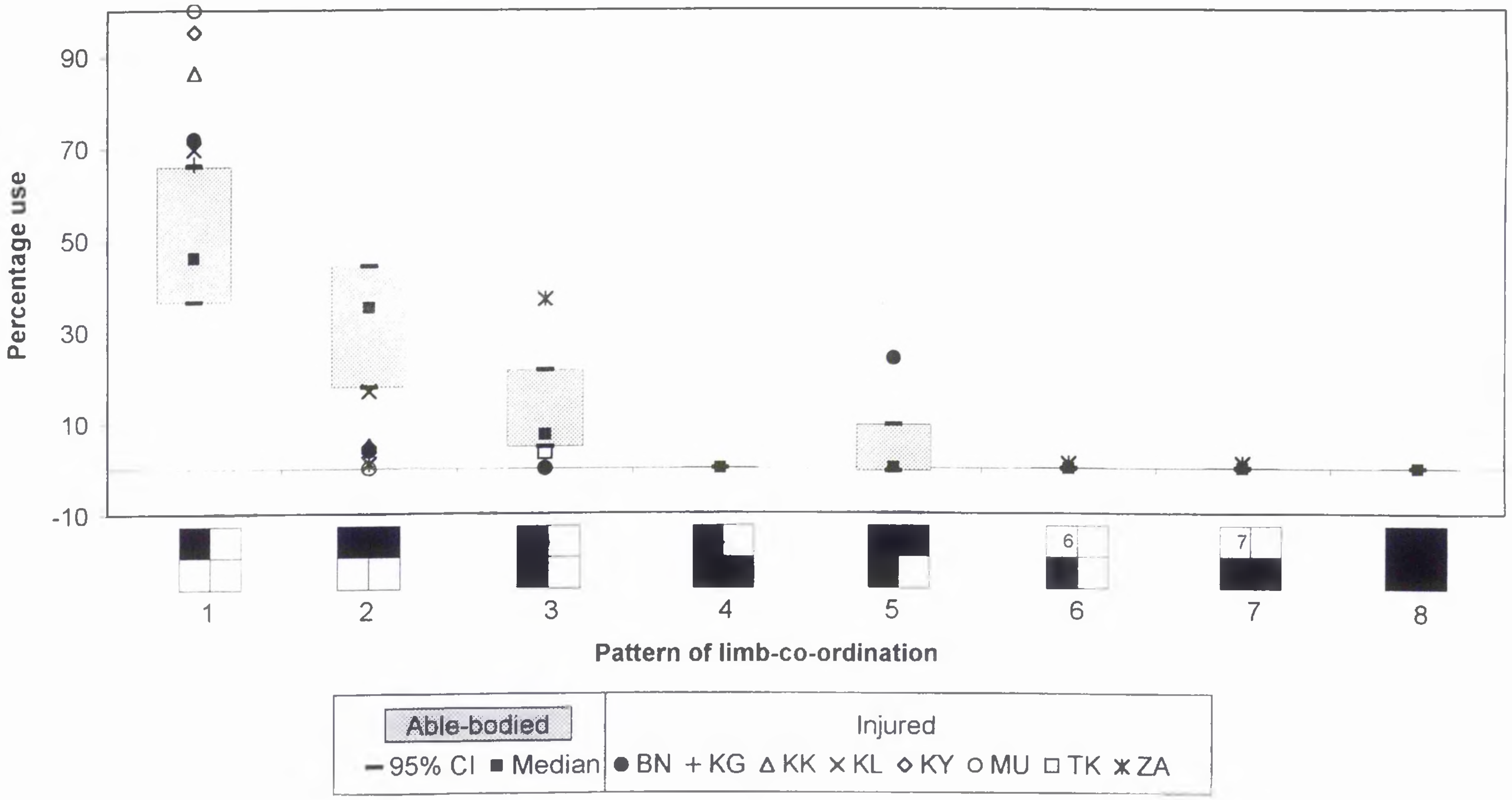
Figure 6.6 shows which of the two upper and two lower limbs are involved in food processing at any one time, within the time period of a particular handful across all individuals. Seven possible patterns are identified according to the combination of upper and lower limbs that are employed. This particular measure does not distinguish what each limb is doing, ie. whether it is picking fruit, shelving fruits or shelving wadges. Neither does it distinguish how many handfuls are being processed simultaneously, ie. two upper limbs may be involved in processing a single handful as well as three handfuls concomitantly. The distribution of scores within the able-bodied population is shown for each pattern. Only those injured individuals whose score falls outside the 95% confidence intervals set by the able-bodied population are shown.

Interestingly, no individuals, either able-bodied or injured are observed to use all four limbs simultaneously in processing. Presumably, constraints of arboreal feeding require at least one limb be used for postural support.

For individuals with lower limb injuries, Kigere (KG) shows a very slight increase in her use of Pattern 1 (mono-manual processing with the upper limb), and a concomitant decrease, but again only very slight, in her use of Pattern 2 (bi-manual processing with the upper limbs). Banura (BN) shows a much larger effect in the same direction. However, at the same time, Banura shows a marked increase in her use of Pattern 5, which involves co-ordination of 3 limbs in processing simultaneous handfuls.

For individuals with one hand injured, the pattern is what we might expect given the results shown in **Table 6.5.** Kikunku (KK), Kalema (KL), Kewaya (KY) and Muga (MU) all show a significant increase in mono-manual processing and a reduction in bimanual co-ordination of the two upper limbs. It is also clear that these same individuals do not show an increase in the use of their feet in processing and therefore they are disadvantaged in the number of fruits that are processed at any one time.

Figure 6.6 Limb-coordination in processing Ficus mucuso



For individuals with both hands injured, Tinka (TK) falls within the limits set by the able-bodied population in both monomanual and bimanual processing with the upper limbs. Again, this is to be expected from what we have already seen. Unexpectedly, Tinka shows a slight reduction in his use of Pattern 3, which involves co-ordinating the upper limb with the lower limb.

In contrast, Zana (ZA) shows a decrease in bimanual co-ordination of the two upper limbs and instead prefers to co-ordinate handfuls between the right hand and the foot. Interestingly, Zana is the only individual observed to rely exclusively on the feet in processing handfuls (Patterns 6 and 7).

Within the injured population, only individuals with one hand injured are disadvantaged in the number of handfuls they can process simultaneously, and therefore in the number of food items that can be shelved at any one time. We can now look at the effect that this might have on feeding efficiency.

Feeding efficiency

For the fruits of *Ficus mucuso*, feeding efficiency is influenced by two major factors. The first is the processing rate, which was recorded using the methods described in **Chapter 5.** However, if fruits are shelved, then the rate at which successive fruits enter the mouth will decrease as a result of simultaneous processing of handfuls. The second factor therefore is the number of handfuls that are processed simultaneously This factor is interesting in its own right. If an individual were to be displaced from a food patch midway through a feeding bout, that individual is likely to be at an advantage if fruits are shelved, as processing could continue away from the food patch. **Figure 6.7** shows the number of fruits processed simultaneously within the time period of a particular handful. The results were averaged for each individual, and the mean taken for both able-bodied and injured populations.

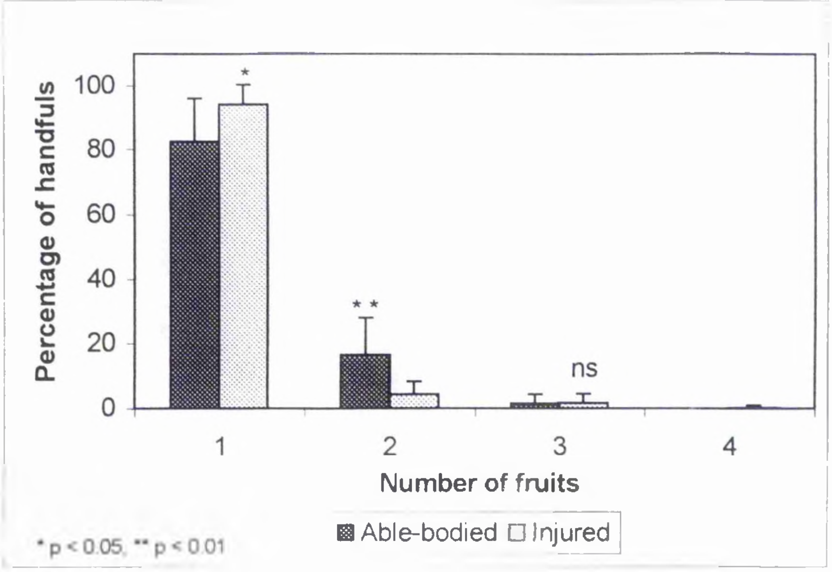


Figure 6.7 Mean number of fruits processed simultaneously across able-bodied and injured populations

The number of fruits processed simultaneously is dependent upon the number of limbs that are acting in concert. We have already seen that individuals with one hand injured are primarily mono-manual in technique, and do not compensate for this my combining a number of food items in the able hand. Not surprisingly then the results in **Figure 6.7** show injured individuals are more likely to process a single fruit at a time than able-bodied individuals, and show a significant reduction in processing more than one fruit simultaneously. Again, this effect can be primarily located to individuals with only one hand injured.

It should be re-iterated at this point that able-bodied individuals prefer to process one fruit at a time rather than shelving them, as this reduces processing rate for a single handful and hence maximises intake. However, when feeding competition is high, and the likelihood of being displaced from a food patch increases, processing rate may increase, but only to the point at which the mouth is full. In these circumstances, shelving fruits becomes the preferred option, and the animal is able to maximise its food intake by continuing processing, albeit at a lower rate.

Bearing this is mind, and taking the two factors into account, feeding efficiency was calculated for each individual using the formula: mean processing rate for successive mouthfuls/mean number of fruits processed simultaneously. This gave a comparative measure of feeding efficiency as feeding time/handful.

A significant variation was found in feeding efficiency across all individuals (Kruskall-Wallis, $\chi^2 = 50.407$, df = 19, $p < 0.001$). This result can be primarily located to a difference between able-bodied and injured individuals, with injured individuals being significantly less efficient (Mann-Whitney, U = 48426, $p < 0.001$). However, a post-hoc analysis (modified Tukey HSD) of the data reveal that this difference between the injured and able-bodied population can be localised further to a single individual. The results of the post-hoc test are shown in **Figure 6.8.** Mean values with standard deviation are presented for each individual, and from left to right, individuals are placed in order of increasing q values in pair-wise comparisons with Kewaya.

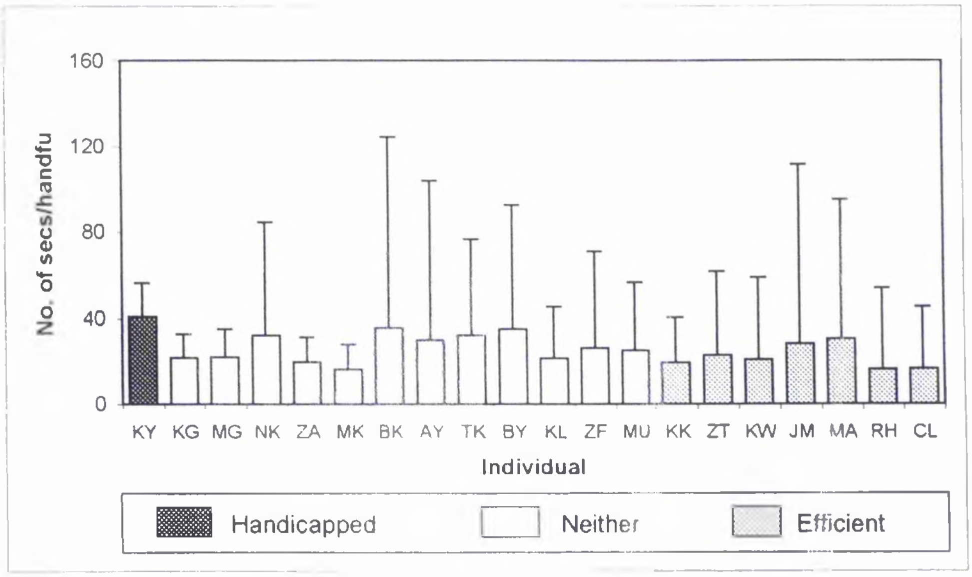


Figure 6.8 Feeding efficiency across individuals

Within the injured population, only Kewaya shows a significant reduction in feeding efficiency when compared with able-bodied individuals, and is shown by the dark hatched bar in **Figure 6.8.** Kewaya can therefore be termed handicapped in terms of her feeding efficiency. Even then, Kewaya is only significantly different from some, and not all, able-bodied individuals. Those individuals who are significantly more efficient than Kewaya are shown by the pale hatched bars in **Figure 6.8,** and these able-bodied individuals are termed efficient. Interestingly, there is one injured individual who is also significantly more efficient than Kewaya. Kikunku is also represented by a pale hatched bar, and belongs to this group of efficient feeders. The remaining individuals, both injured and able-bodied, show no difference in their feeding efficiency to either the handicapped or the efficient group, and can be placed in a category mid-way between the two.

Within the able-bodied population, there appears to be no chimpanzee performing significantly worse than others. This is in contrast to the pattern observed with *Broussonettia papyrifera*, where able-bodied individuals showed a significant divide between efficient and inefficient feeders. This lends support to the suggestion that feeding competition plays an important role in driving performance.

Within the injured population we might have expected that individuals with one hand injured performed less efficiently than those individuals with both hands injured. Although this is the case for Kewaya, it does not apply to Kalema and Muga, and even less so for Kikunku, who performs significantly more efficiently than Kewaya. It is not clear as to why Kewaya should be the only chimpanzee out of the four with one injured hand, to produce a significant result, when she has not been shown to behave significantly differently in her feeding technique. Kewaya was in full oestrus for the full ten days during peak fruiting of one particular *Ficus mucuso* tree in the home range. Oestral swellings seem to be an additional postural constraint whilst feeding, and this may have influenced processing rate. The placing of Kikunku in the same group as efficient able-bodied feeders is also surprising. Kikunku was the only individual in this group of four that showed an increase in his use of 'combine' elements by the able-bodied limb. Although this was not shown to be as a result of overcompensation for the injured limb, it did result in an increase in the number of fruits that were processed in a single handful, and this is likely to have an effect on overall feeding efficiency.

Furthermore, **Figure 6.8** does not show Tinka and Zana placed closer to the able-bodied individuals in terms of their q values, again as we might have expected.

The size of the error bars – for able-bodied individuals in particular - indicates that this measure of feeding efficiency varies considerably within individuals. This is to be expected, as the feeding behaviour varies according to the level of competition at any one time and averaging across all incidences of feeding is likely to disguise the most extreme effects of injury on feeding efficiency when competition is at its greatest. For the majority of feeding bouts however, injury has little effect on feeding efficiency. Individual fruits can be processed monomanually and efficiently without the need to shelve food items. The results presented throughout this chapter however indicate that injury, at least in one hand, may pose problems when feeding competition is high. Then, injury will reduce the number of limbs available to co-ordinate processing, which in turn will tend to limit the choice of technique to those that do not require the use of a shelf. This in turn will reduce the number of fruits that can be processed at any one time, thus reducing food intake in the case of displacement from the feeding patch.

Injured chimpanzees are therefore less flexible to sudden changes in their immediate feeding environment than able-bodied chimpanzees, and the trend towards smaller error bars for injured individuals (see **Figure 6.8)** suggests less variation in behaviour than that seen in able-bodied chimpanzees. This effect, however, is greatly influenced by nature of injury, being generally confined to individuals with single limb injuries. As a result of their injuries, these individuals are less adept at finding short-term solutions to fluctuations in external conditions than their able-bodied counterparts and this may have long-term implications for feeding efficiency.

Chapter 7

THE EFFECT OF INJURY ON FOOD ACCESSIBILITY: FICUS SUR

The fruits of *Ficus sur* are an important food item in the diet of Sonso chimpanzees. As in the case of *Ficus mucuso,* these figs are simple to process, and are strongly competed for. The fruits are much smaller than those of *Ficus mucuso* however, having an approximate diameter of 15mm. Consequently, there would seem to be no limit to the rate of ingestion and individual fruits at particular food patches do not tend to be prized and hoarded as was observed with *Ficus mucuso.* Rather, the strategy employed by able-bodied individuals appears to employ short but continuous bursts of feeding from a large number of suitable food patches distributed about the feeding tree. Consequently, able-bodied chimpanzees are seen to use a variety of postures to access different food patches, and these postures are continually adjusted as the chimpanzee relocates from one food patch to another. **Chapter 4** revealed that injured individuals perform a significantly smaller repertoire of feeding postures compared to their able-bodied counterparts. In addition, they are constrained in their feeding position within the tree. In spite of this, *Ficus sur* remains an important food item in their diet. This chapter investigates the role of feeding posture and postural adjustment in feeding on the fruits of *Ficus sur*, and asks to what extent are injured individuals able to overcome the postural constraints imposed by their injuries and minimise feeding competition.

Classification of techniques within the able-bodied population

Techniques that differed in sequential organisation of individual elements were distinguished and labelled 1 – 6 (see **Appendix V**). These techniques were classified across individuals according to the number of times they appeared in an individual's repertoire. They were then further categorised according to the hand/body part used at each stage of processing (see **Table 7.1**).

Table 7.1 Classification of techniques for able-bodied chimpanzees feeding on fruits of Ficus sur.

[refer to **Appendix V** for techniques: see **Table 5.1** for key]

IND	TECH	SEQUENCE							n	%N	N
AY	1	L	L	M	(M)	M			1	2.27	44
		R	R	M	(M)	M			8	18.18	
	2	(RF)/(L)*	(RF)	L	-	-	L	-	8	18.18	
		-	-	R	-	-	R	-	26	59.09	
	5	-	L	L	L	L			1	2.27	
BK	2	(L)*	(LF)	L	-	(L)	L	-	35	49.30	71
		-	-	R	-	-	R	-	26	36.62	
	4	-	-	R	R				2	2.82	
	1	R	R	M	(M)	M			2	2.82	
		L	L	M	(M)	M			4	5.63	
	5	-	R	R	R	R			2	2.82	
BY	2	(RF)	(RF)	R	-	(R)	R	-	32	50.00	64
		-	-	L	-	-	L	-	27	42.19	
	1	R	R	M	(M)	M			3	4.69	
		L	L	M	(M)	M			1	1.56	
	4	-	-	L	L				1	1.56	
DN	2	-	-	L	-	(L)	L	-	15	27.78	54
		-	(LF)	R	-	(R)	R	-	37	68.52	
	4	-	-	R	R				1	1.85	
	1	L	L	M	(M)	M			1	1.85	
JN	1	R	R	M	(M)	M			1	2.17	46
	2	(R)*	(LF)	R	-	-	R	-	19	41.30	
		(L)*	(LF)	L	-	-	L	-	23	50.00	
	5	-	L	L	L	L			1	2.17	
	4	-	(LF)	L	L				2	4.35	
KU	2	-	-	L	-	-	L	-	7	28.00	25
		-	-	R	-	-	R	-	14	56.00	
	5	-	R	R	R	R			3	12.00	
	4	-	-	R	R				1	4.00	
KW	2	-	-	R	-	(R)	R	-	26	44.83	58
		-	-	L	-	(L)	L	-	27	46.55	
	1	R	R	M	-	M			5	8.62	
MA	2	-	R/(L*R)	L	-	(L)	L	-	57	69.51	82
		(L)	(L)	R	-	(R)	R	-	14	17.07	
	5	-	L	L	L	L			7	8.54	
	6	-	L	L	L	L			3	3.66	
	1	L	L	M	(M)	M			1	1.22	
MG	1	L	L	M	(M)	M			3	3.85	78
	2	-	-	L	-	(L)	L	-	27	34.62	
		(R)*	(RF)	R	(R)	R			46	58.97	
	5	(RF)	L	L	L	L			2	2.56	
MK	2	-	-	R	-	-	R	-	9	36.00	25
		-	-	L	-	-	L	-	8	32.00	
	1	L	L	M	-	M			2	8.00	
		R	R	M	(M)	M			6	24.00	
NB	2	-	-	R	-	-	R	-	49	36.84	133
		(RF)/(L)*	(LF)/(RF)	L	(M)	-	L	(L)	77	57.89	
	1	L*,L	RF.RFL	M	(M)	M			1	0.75	
		R	R	M	-	M			2	1.50	
	5	(LF)	L	L	L	L			3	2.26	
	4	-	(LF)	L	L				1	0.75	
RD	2	-	-	L	-	(L)	L	-	56	50.91	110
		-	-	R	-	(R)	R	-	41	37.27	
	1	L	L	M	(M)	M			3	2.73	
		R	R	M	-	M			4	3.64	
	5	-	R	R	R	R			1	0.91	
		-	L	L	L	L			5	4.55	

VN	2	-	-	R	-	-	R	-	26	27.37	95
		(R)/(L)*	(R)/(RF)	L	-	(L)	L	(L)	65	68.42	
	5	-	R	R	R	R			1	1.05	
	1	R	R	M	-	M			1	1.05	
	4	-	-	R	R				1	1.05	
	3	-	-	R	(L)	-	R	-	1	1.05	
ZT	2	(L)	(L)	R	-	-	R	-	11	23.40	47
		-	(L*R)	L	-	-	L	-	32	68.09	
	1	L	L	M	-	M			2	4.26	
	4	-	-	L	L				1	2.13	
		-	(L)	R	R				1	2.13	
ZM	2	(R)	(R)	L	-	(L)	L	-	34	64.15	53
		-	-	R	-	-	R	-	19	35.85	

The six techniques can be represented in a composite flow-diagram, which incorporates all possible pathways used by able-bodied chimpanzees in processing a single handful of food (see **Figure 7.1**). The striking feature of this flow diagram when compared with those describing feeding in young leaves of *Broussonettia papyrifera* or fruits of *Ficus mucuso*, is the relative simplicity of technique. Processing figs of *Ficus sur* does not employ a complex multi-stage technique as we saw for *Broussonettia papyrifera*, nor does it involve limb co-ordination between separate yet simultaneously processed handfuls as was the case for *Ficus mucuso*. These small figs are a preferred food source just *because* rates of ingestion can be maximised at minimal processing cost. Thus simplicity of technique will give a selective advantage in feeding on this particular food type. In addition, postural support will tend to limit processing to primarily mono-manual hand to mouth co-ordination. In spite of this, bimanual co-ordination is an optional element in all techniques other than Technique 1. Thus, whilst not all individuals use bimanual co-ordination in every handful when using Techniques 2-6, some certainly employ this strategy for some of the time.

Able-bodied chimpanzees use Technique 2 to process a mean 89.11% of all handfuls (range 69–100%) although only 4 out of 15 individuals were observed to use bimanual co-ordination. For these 4 individuals using this particular technique, bimanual co-ordination was used in a mean 12.2% of handfuls (range 5.4–16.98%). Of the remaining 4 techniques where bimanual co-ordination is an option (Techniques 3 – 6), only 1 individual was observed to use both hands, and on only one occasion when using Technique 3. These 4 techniques represent less than 5% of all handfuls. Technique 1, which requires mono-manual processing only, accounts for a mean 6.59% of handfuls (range 0–32%).

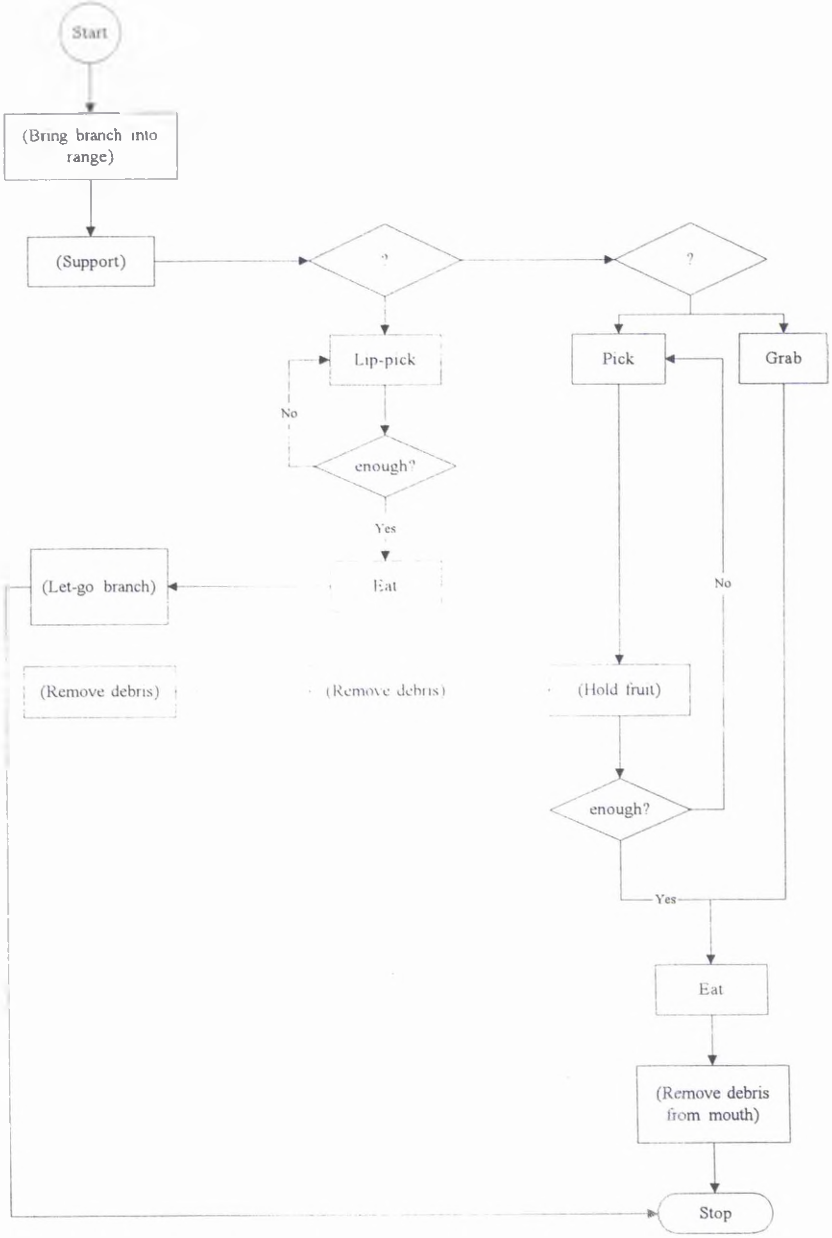


Figure 7.1 Able-bodied individuals feeding on fruits of *Ficus sur*

[See **Figure 5.1** for key]

Therefore, in spite of the postural demands of feeding on fruits of *Ficus sur*, able-bodied individuals do not prefer the explicitly mono-manual Technique 1 at the expense of bimanual Techniques 2-6. Although bimanual co-ordination comprises an optional rather than obligatory element in these techniques, bimanual processing is still observed more frequently than use of Technique 1. Thus there appear to be two factors operating in the feeding strategies of able-bodied individuals. The first of these is a postural factor, determined by the level of competition at any one food patch, together with the distribution and orientation of food patches at any one tree. The second is a processing factor, which involves the option of bimanual co-ordination. Bimanual processing of figs typically requires one hand to bring a branch into range and support the branch whilst individual fruits are picked off with the other hand. Bimanual co-ordination in processing has two immediate advantages. Firstly, it increases the relative size of the food patch by allowing food items to be brought in from outside the animal's immediate range. Secondly, it is a much more efficient means of obtaining these food items than say using a single hand to reach in and slide-adjust up the stem to detach the fruit. Thus, Technique 2, which requires one hand to bring in the branch and support whilst the other hand detaches a fruit, is preferred over Techniques 5 and 6, which employ the reach-slide-adjust-pick subroutine. However, using both hands in processing fruits will leave no upper limbs for postural support, and thus the benefits of bimanual co-ordination must be weighed against those of postural readjustment. Technique 3 is a variant of Technique 2 in that there are two independent options for bimanual co-ordination. The first, as for Technique 2, is support-pick, and the second is hold fruit-remove debris – which in Technique 2 is done with the mouth and the hand rather than both hands. It is possible, that Technique 2 represents something of a compromise between bimanual co-ordination and postural change, in that after the first stage of the technique the hand is then available for postural support. With Technique 3, the 'other' hand would be required in a later stage of processing. Hence, Technique 2 is preferred over Technique 3.

These two factors therefore are not mutually exclusive, and choice of technique and resultant feeding strategy will be a trade-off between the two. We can now investigate how the choice of strategies used by injured individuals compares with that of their able-bodied counterparts.

Effect of injury on choice of technique

Just as for able-bodied individuals, techniques were classified across injured individuals according to frequency of use and the hand/body part used at each stage of processing (see **Table 7.2**).

Table 7.2 Classification of techniques for injured individuals feeding on fruits of Ficus sur

[refer to **Appendix V** for techniques; see **Table 5.1 & 5.3** for key]

IND	TECH	SEQUENCE							n	%N	N
KG	2	-	-	L	-	-	L	-	59	76.62	77
		(L)	(L)	R	-	-	R	-	14	18.18	
	1	L	L	M	(M)	M			4	5.19	
KK	1	R	R	M	(M)	M			17	12.88	132
	2	(L)/(RL)/(R)*	(L)/(LF)	R	-	(R)	R	-	89	67.42	
	4	-	(*L*)	R	R				25	18.94	
	5	-	R	R	R	R			1	0.76	
KL	2	(LF)/(L)*	(LF)/(R)	L	-	-	L	-	53	85.48	62
	1	L	L	M	-	M			4	6.45	
		-	LF	M	-	M			1	1.61	
		L*R*	*B*	M	-	M			1	1.61	
		R	*R*	M	(M)	M			1	1.61	
	5	-	L	L	L	L			2	3.23	
KY	2	(LF)/(L)*/(R)	(RF)/(LF)/(R)	L	-	(L)	L	-	80	76.92	104
	1	*R*	*R*	M	-	M			1	0.96	
		L	L	M	(M)	M			6	5.77	
		-,L	LF,LFL	M	-	M			1	0.96	
		-,L	LF,*B*	M	(M)	M			1	0.96	
		-,L	RF,RFL	M	(M)	M			8	7.69	
		-,*R*	L,*R*	M	(M)	M			1	0.96	
	5	(RF)	L	L	L	L			6	5.77	
MU	2	(RF)	(RF)	L	-	(L)	L	-	93	75.61	123
		-	-	L*	-	-	*R*	-	1	0.81	
	1	RF	RF	M	-	M			1	0.81	
		L	L	M	-	M			10	8.13	
		R	*R*	M	(M)	M			9	7.32	
	5	-	L	L	L	L			5	4.07	
	4	-	-	L	L				4	3.25	
TK	2	(LF)/(L)*/(R)	(R)/(LF)/R*RF/RF	*L*	-	-	*L*	-	152	91.57	166
	1	*L*	*L*	M	(M)	M			13	7.83	
		-,*L*	L*R*L,L	M	(M)	M			1	0.60	
ZA	2	(L)/(**R**)*/(LF)/(RF)	(*L*) (LF)/(RF)	R	-	-	R	-	161	80.10	201
	1	R	R	M	(M)	M			33	16.42	
		RFR	R	M	-	M			1	0.50	
		L	*L*	M	-	M			4	1.99	
	5	-	R	R	R	R			2	1.00	

As with young leaves of *Broussonettia papyrifera* and fruits of *Ficus mucuso*, choice of technique was analysed at both the population and individual level.

Injured population v able-bodied population

Table 7.3 shows the frequency with which the able-bodied population as a whole used each technique compared with frequency used by each injured individual. For each technique, the median value for the able-bodied population was taken. Individuals were then subdivided according to whether their frequencies were above or below the median, and whether they were injured or able-bodied. A Chi-square test (corrected for continuity) was then applied to these frequencies in order to investigate whether or not injury influenced choice of technique. Independent of posture, injured individuals are limited in their use of bimanual co-ordination in food processing (see **Chapters 5 & 6**). It is therefore hypothesised that injured chimpanzees will prefer Technique 1 at the expense of the other five techniques that employ bimanual co-ordination.

Table 7.3 Frequency of use of technique (%) for processing fruits of *Ficus sur*
[individuals with no. of handfuls < 10 are not included for analysis]

	ABLE-BODIED						INJURED						
TECH	N	Mean	Med.	SD	Min	Max	KG	KK	KL	KY	MU	TK	ZA
1	15	6.59	3.85	8.72	0	32	50.19	12.88	11.28	17.3	20.33	8.43	18.91
2	15	89.11	91.38	8.11	68	100	94.8	67.42	85.48	76.92	75.61	91.57	80.1
3	15	0.07	0	0.27	0	1.05	0	0	0	0	0	0	0
4	15	1.38	0.75	1.69	0	4.35	0	18.94	0	0	3.25	0	0
5	15	2.61	2.17	3.54	0	12	0	0.76	3.23	5.77	4.07	0	1.0
6	15	0.24	0	0.95	0	3.66	0	0	0	0	0	0	0

A significant increase is seen in the use of Technique 1 by the injured population ($\chi^2 = 6.3370$, df = 1, $p < 0.05$). However, no significant decrease is seen in any particular one of the five techniques that use bimanual processing. Within the injured population, individual differences are seen in choice of technique, and these are worthy of further investigation.

Injured individual v able-bodied population

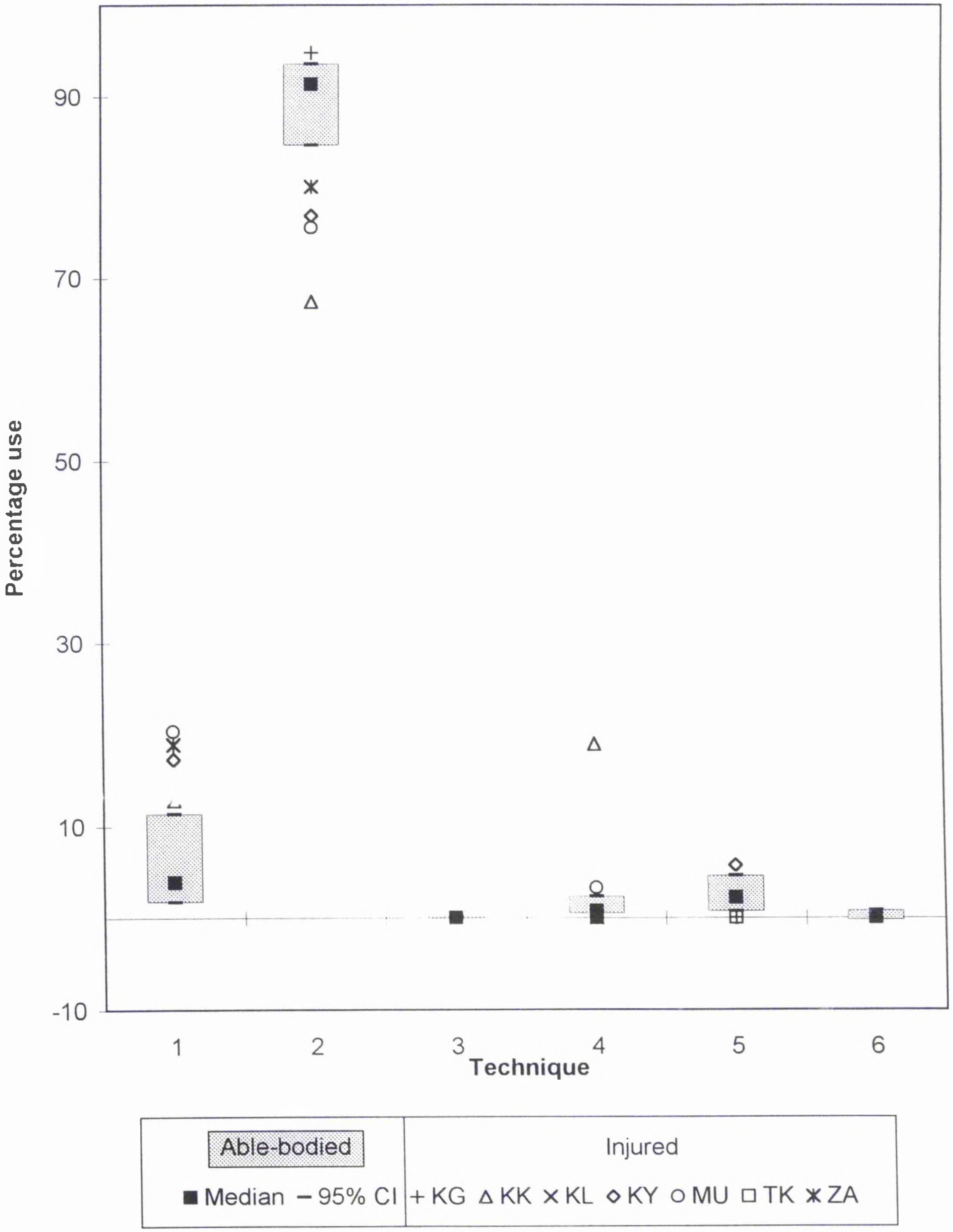
In comparing individuals against a population, the same method as employed in **Chapters 5 & 6** is used here. **Figure** 7.2 shows the distribution of scores within the able-bodied population for each of the six techniques. Only those injured individuals whose score falls outside the 95% confidence intervals set by the able-bodied population are shown.

On the basis of the frequency with which they use Techniques 1 and 2, two groups of injured individuals can be identified. The first group shows a significant increase in Technique 1, and a concomitant decrease in Technique 2, as originally predicted. This group comprises Kewaya, Muga, Kikunku and Zana. The second group conforms to the pattern seen in the able-bodied population for these two techniques and is thus not shown in **Figure 7.2.** Tinka and Kalema represent this group. This result is interesting because these two groups do not correlate with extent of injury, with each group containing individuals with injuries to both single and two limbs. This is in contrast to the pattern observed with both *Broussonettia papyrifera* and *Ficus mucuso*, where nature and extent of injury were distinctly correlated with choice of technique

Of the individuals with lower limb injuries, only Kigere is represented here. Kigere actually shows a slight increase in her use of Technique 2. Kigere would be expected to conform more closely to able-bodied individuals, as she is not constrained by injury in bimanual processing. Both Kigere and Tinka also show a slight reduction in their use of Technique 5. This is primarily, but not exclusively a mono-manual technique.

Further differences exist within the two groups of individuals with upper limb injuries. Kikunku shows a marked increase in his use of Technique 4. This involves grabbing multiple food items at once. For processing leaves of *Broussonettia papyrifera* and fruits of *Ficus mucuso*, Kikunku also shows an increase in his use of those techniques that involve grabbing multiple food items simultaneously. Furthermore, Kikunku was also shown to increase the use of

Figure 7.2 Frequency of use of technique



'combine' elements with the able limb in processing fruits of *Ficus sur*. This use of the able-limb in compensation for the injured limb therefore appears to be a strategy that Kikunku has generalised across a number of different food items. Muga shows a similar but much smaller effect with Technique 4. Again, this strategy is repeated in foods other than *Ficus sur*, but with leaves of *Broussonettia papyrifera* only.

With *Ficus sur* we see a pattern with the injured population that is different again to that seen for both *Broussonettia papyrifera* and *Ficus mucuso*. Lower limb injuries appear to exert little effect on choice of technique, as we would expect. Upper limb injuries however, appear to exert a selective effect, and this does not seem to be determined by the extent of injury. Individuals with one hand injured appear to be split in their choice of strategy, and this is not in accordance with amputation of the limb, with only Kalema showing a similar strategy to able-bodied chimpanzees. Individuals with both limbs injured are also divided in their choice of strategy, with Tinka behaving more like an able-bodied chimpanzee.

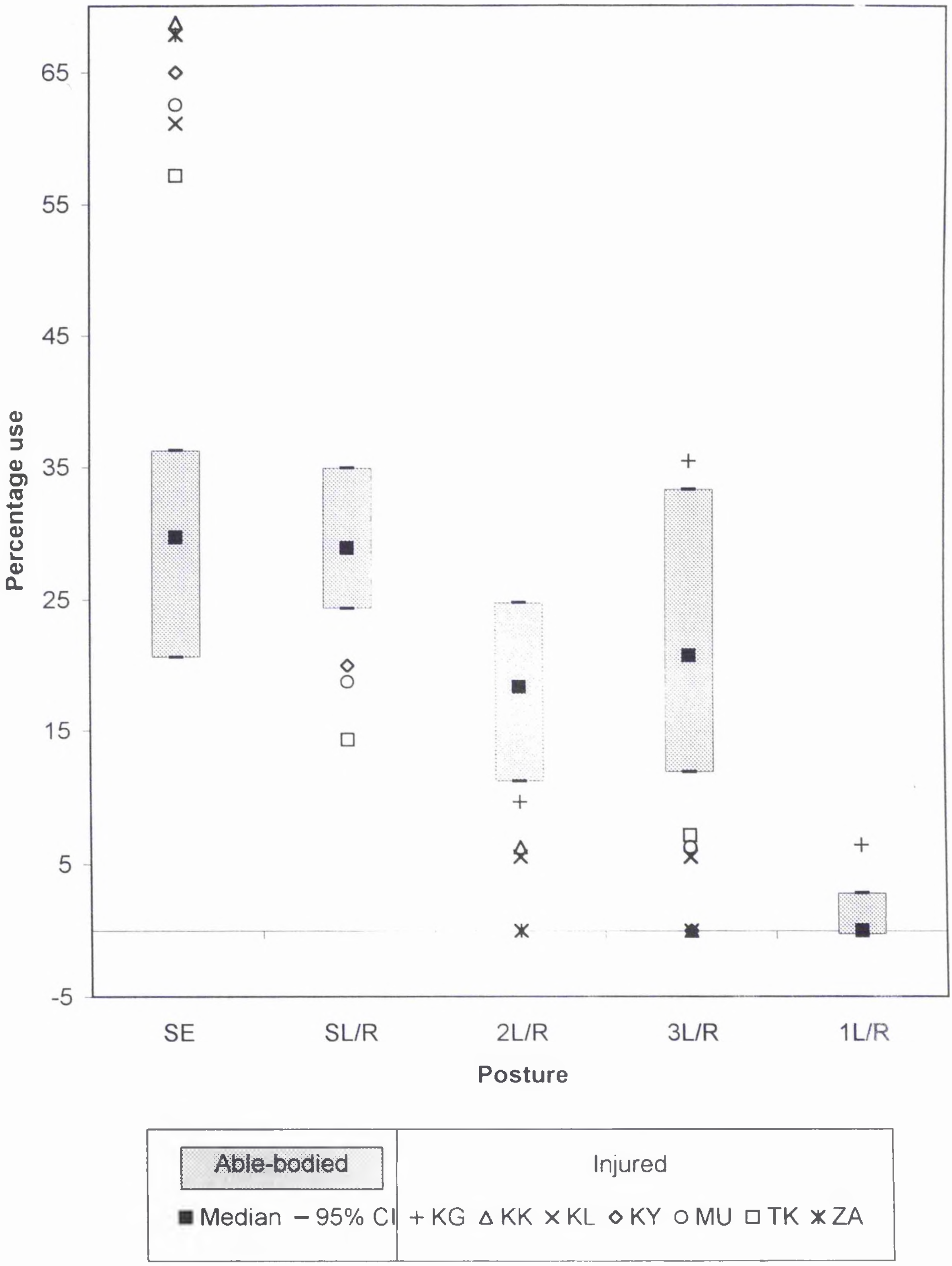
In order to explain the choice of strategy by an injured individual, we need to first look at the effects of injury on posture. In this way we can determine the extent to which an individual is limited in their access to a particular feeding patch, and the extent to which they need to rely on efficient processing technique, in order to minimise feeding competition

Postural constraints in feeding

Figure 7.3 shows the distribution of values for frequency of use of five postures by able-bodied chimpanzees whilst feeding on *Ficus sur* (see **Chapter 2** for details on terminology). Only those injured individuals that fall outside of the 95% confidence intervals set by the able-bodied population are shown.

All six of the sampled individuals with upper limb injuries show a significant increase in their use of the seated (SE) posture. At the same time, all six

Figure 7.3 Frequency of use of feeding posture



individuals do show a concomitant reduction in their use of tripedal-support (3L/R) posture. In addition, Kewaya, Muga and Tinka show a decrease in frequency of seated-reaching (SL/R) posture, and Kikunku, Kalema and Zana show a reduction in their use of bipedal-supported (2L/R) posture. Where individuals show a similar direction of change in use for a particular posture, there is considerable variation in the size of the effect between individuals. Zana uses only two postures whilst feeding (seated and seated-reaching), Kewaya and Kikunku use three postures (seated, seated-reaching and bipedal-support), and Muga, Tinka and Kalema retain four postures (seated, seated-reaching, bipedal-support and tripedal support).

Of the sampled individuals with lower limb injuries, Kigere differs from the six individuals above in that she does not show an increase in her use of the seated posture, nor a reduction in the use of seated-reaching. In this sense, she resembles an able-bodied individual. However, the lower limb injury does exert an effect on bipedal-supported postures as one might expect. Consequently, Kigere shows a reduction in her use of this posture, and shows a concomitant increase in her use of tripedal-support (3L/R) and one arm-support (1L/R) postures.

In general, individuals with upper limb injuries show an increase in the seated posture and a reduction in postures that require a degree of support and manoeuvrability. Furthermore, they are limited in the total number of feeding postures in their repertoire. However, the degree of difference varies between individuals, with Zana showing the most extreme effect, Muga, Tinka and Kalema the least effect, and Kewaya and Kikunku falling midway between. As for the pattern seen with choice of technique, this pattern does not correlate with extent of injury. A bifurcation of strategies is seen both in individuals with one injured hand and in individuals with both hands injured. In the case of lower limb injury, Kigere shows a decrease in bipedal-support but at the same time increases her use of other postures that require limb support. Consequently, she maintains manoeuvrability whilst feeding.

A reduction in both manoeuvrability about the tree and postural adjustment from one feeding patch to another will tend to increase the length of time an individual spends at a single food patch. **Figure 7.4** compares the mean bout lengths of able-bodied and injured individuals

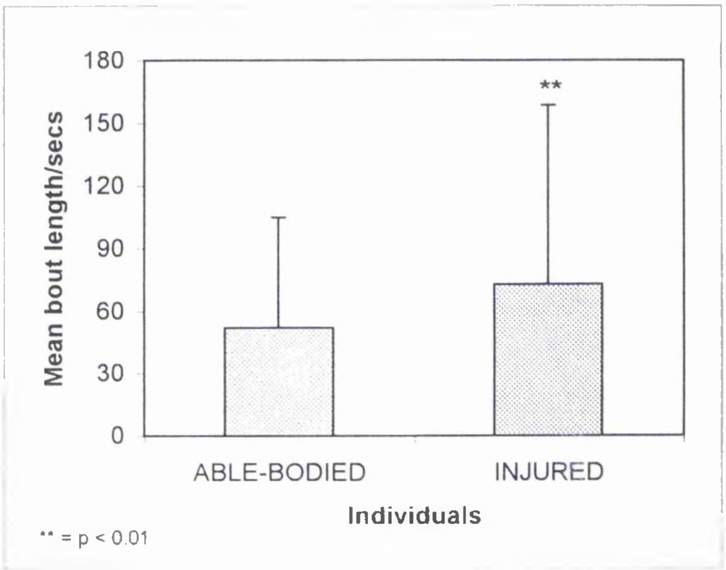


Figure 7.4 A comparison of bout length between able-bodied and injured individuals

Injured individuals have significantly longer feeding bouts than their able-bodied counterparts (Mann –Whitney U = 21197.5, two-tailed p = 0.007). The effect of injury on feeding posture broadly conforms to the pattern that was seen with choice of technique. Within the injured population, those that are most constrained in their repertoire of techniques are also most constrained posturally. Thus the trade-off between efficient processing and manoeuvrability that was inferred from the behaviour of the able-bodied population would seem not to be operating within the injured population in the most extreme of cases. In these instances, injured individuals that are forced to remain in a seated posture do not have the option of bimanually processing food. Rather, those individuals who show the greatest difference to able-bodied chimpanzees, both in technique and posture, are likely to be limited in their choice of strategy, and will consequently be under greater pressure from feeding competition.

In order to test this hypothesis further we need to look at the efficiency of processing technique in both able-bodied and injured individuals. In order to do that, we can first examine technique at the level of individual elements so as to establish any compensatory strategies that might be operating at a finer level of detail than that which we have already investigated. Secondly, we can measure processing rate of a single handful. That is, the efficiency with which these individual elements are co-ordinated together in a single sequence.

Repertoire of elements used in processing

All elements used in processing fruits by individuals with 10 or more complete handfuls were identified and placed into functional categories. As for leaves of *Broussonettia papyrifera* and fruits of *Ficus mucuso*, element use for *Ficus sur* was broken down into left and right hand, or both hands together. Use of the mouth for elements was also distinguished. Element use for able-bodied individuals is shown in **Table 7.4a**, and for injured individuals, in **Table 7.4b**.

As for other food types, able-bodied individuals show highly idiosyncratic use of elements within each category. Much of this idiosyncrasy can be accredited to grip type used for each element and it is clear that we are still underestimating the full repertoire of elements for each chimpanzee (**Figure 7.4**). Linear regression for the number of elements from the number of handfuls reveals that the full set of elements has not reached asymptote fo. all animals (elements = 0.1245 x handfuls + 10.291, $r^2 = 0.529$, F (1,13) = 14.578, $p < 0.005$).

With injured individuals, only those with injuries to the upper limbs were considered. For individuals with injury to a single limb, element use is as equally idiosyncratic for the able limb, as that seen in able-bodied individuals. For individuals with both limbs injured however, there is a considerable reduction in idiosyncrasy, and this is especially true for Zana. Linear regression suggests that there is no direct relationship between amount of data analysed and number of elements in an individual's repertoire (elements = -0.0498 x handfuls +

Table 7.4a Elements used by able-bodied individuals in processing fruits of *Ficus sur* [see Table 5.5a for key]

Element	AY				BK				BY				DN				JN				KU				KW			
	L	R	B	M	L	R	B	M	L	R	B	M	L	R	B	M	L	R	B	M	L	R	B	M	L	R	B	M
Pull into range																												
Clear																	2	1										
Hook (2:3)	2	5				3			1	2			1															
Hook (2:3:4)		1			1					1								1										
Reach (DH)		3																								1		
Reach (TH)	1	1			1	1											1									1		
Reach (1,2 and 3)																												
Reach (1,2,3 and 4)																												
Reach (PS)					1																	3				1		
Index hook					1																							
Hook (5 only)																												
Slide-adjust	1					1											1					3						
Foot		1								2																		
Manoueuvering items																												
Swap to foot		1			1												3											
Swap to hand																												
Index probe														1														
Adjust		1															1											
Foot adjust																												
Support																												
Transverse hook	1	1				6																				3		
Diagonal hook		3																								1		
Foot		2			4					5			1				6											
Hook (2 3)		6			1	1			1	3			1															
Hook (2 3 4)					1													1										
Index hook					1																							
TH (1,2 and 3 only)																												
TH (1,2,3 and 4)																												
Precision grip (PS)					1																					1		
Detaching items (may/may not inc. Pm)																												
Pick (1:3IMP)	3	1			3	1			4	1			8	6			6	2										
Pick (1:3)		1				1			1					1			1								3	4		
Pick (2:3)	2	3			6	7			3	2			1	2			1				3	9				5		
Pick (PS)	4	21			19	13			18	26			1	12			14	16			3	8			18	16		
Pick (PT)																												
Pick (1:2IMP)		4			3	2			1	3			4	10			3								1			
Twist off																												
Pick (SG)		2			1									2				1								1		
Lip-pick				17				11				11				2				3								5
Lip-pick x n																												
Pick (1:2:3)					1	1								4							1				5			
Pick (1:2:3IMP)																												
Grab x n						2			1				1	1			2					1						
Pick (3:4)					2																							
Accumulate																												
Combine (hold 3:4:5:Pm/pick PS)					2					1															1	1		
Combine (hold 4:5:Pm/pick 1:2.3IMP)														1														
Combine (hold 3:Pm.pick PS)																												
Combine (hold 4:5:Pm/pick 2:3 Pm)																												
Combine (hold 4:5:Pm/pick 1:3)													1	1														
Remove debris																												
Pick-off																												
mouthpeel																												
Putting in mouth																												
Eat	9	32			33	28			27	31			14	38			26	19			7	17			26	25		
Eat x n					2	2			1	1			1	3			1					1			1	1		
Combine (hold 3:4:5:Pm/eat PS)																	1											
Manoevering items																												
Wadge				1																								
Remove debris																												
Pick-out																												
No. of different elements used*	**21**				**26**				**15**				**17**				**19**				**7**				**15**			
No. of handfuls	**44**				**71**				**64**				**54**				**46**				**25**				**58**			

Element	MA				MG				MK				NB				RD				VN				ZM				ZT			
	L	R	B	M	L	R	B	M	L	R	B	M	L	R	B	M	L	R	B	M	L	R	B	M	L	R	B	M	L	R	B	M
Pull into range																																
Clear						1							1																			
Hook (2:3)	10				1				1				2				6	1				3				3						
Hook (2:3:4)						1																										
Reach (DH)										1																1			1			
Reach (TH)	1					3			1	3			5	1			2	2			1					1			1			
Reach (1,2 and 3)	1				2					2																						
Reach (1,2,3 and 4)																																
Reach (PS)													1	1				2											1			
Index hook																						1										
Hook (5 only)						1																										
Slide-adjust	10				1	1							3				5	1														
Foot														4																		
Manoeuvering items																																
Swap to foot						5							1	4								1										
Swap to hand		1																												1		
Index probe														1			1															
Adjust										1																						
Foot adjust						2																										
Support																																
Transverse hook	5								1	4				1			2	2				1							7	1		
Diagonal hook																									2	2			1			
Foot						41							42	24								2										
Hook (2 3)					2				1								1	1				5				5						
Hook (2:3.4)																																
Index hook																																
TH (1,2 and 3 only)	2				2					2																						
TH (1,2,3 and 4)																																
Precision grip (PS)		3											1	1				1				1							1			
Detaching items (may may not inc. Pm)																																
Pick (1 3IMP)	12	3			2	3			2	3			8	11			6	3			12	2			9	5			12	8		
Pick (1 3)	4	2			1	2				1			1	2			1	10			2	1										
Pick (2 3)					2	1				2			6	11			17	3			1	1			7	2						
Pick (PS)	37	12			18	39			6	3			58	21			27	22			38	22			11	6			17	3		
Pick (PT)														1												1						
Pick (1.2IMP)	3	5			2	1							1				7	4			5	1			4				3			
Twist off														1																		
Pick (SG)													1	2							2				1	3						
Lip-pick				2								12				2				9				1								2
Lip-pick x n																2																
Pick (1:2:3)													2								4				1	1						
Pick (1:2:3IMP)																					1					1						
Grab x n	3												1									1							1	1		
Pick (3:4)																																
Accumulate																																
Combine (hold 3:4:5:Pm/pick PS)	1																3				1				1							
Combine (hold 4:5:Pm/pick 1:2.3IMP)																																
Combine (hold 3:Pm.pick PS)	2																															
Combine (hold 4:5:Pm/pick 2:3 Pm)					2																											
Combine (hold 4:5:Pm/pick 1:3)		1				1												1														
Remove debris																																
Pick-off																					1											
mouthpeel																6																
Putting in mouth																																
Eat	58	21			27	46			8	9			81	49			60	42			65	28			34	19			30	11		
Eat x n	1	1			1	1											1												1	1		
Combine (hold 3:4:5:Pm/eat PS)	5												1				2	1			1	1			1							
Manoevering items																																
Wadge				1																				1								1
Remove debris																																
Pick-out													1								2											
No. of different elements used*	**21**				**22**				**14**				**27**				**19**				**23**				**16**				**15**			
No. of handfuls	**82**				**78**				**25**				**133**				**110**				**95**				**47**				**53**			

Table 7.4b Elements used by injured individuals in processing fruits of *Ficus sur* [see Table 5.5b for key]

Element	KG				KK				KL				KY				MU				TK				ZA			
	L	R	B	M	L	R	B	M	L	R	B	M	L	R	B	M	L	R	B	M	L	R	B	M	L	R	B	M
Pull into range																									1			
Clear																						1						
Hook (2:3)	2					3			5				3				4											
Hook (2.3:4)						3							8															
Reach (DH)	2					4							1				2											
Reach (TH)	1					9			1				1				6											
Reach (1,2 and 3)									1				6															
Reach (1,2,3 and 4)																												
Reach (PS)													1				2				2							
Index hook													1															
Hook (5 only)																												
Reach (thumb only)													1													35		
Slide-adjust						1			2				1				5								2	2		
Foot									6				1					2			1				1	2		
Stem-break						1																						
Grasp-hook																						1						
Hook-grasp																					11							
Back of wrist														3											2			
Lateral wrist										2															3			
Grasp					2													9										
Manoeuvering items																												
Swap to foot					1				1					2								1			2			
Swap to hand					1				1									1			3	2						
Index probe						1			3																			
Foot probe									1																			
Adjust						1							5				1				1							
Rotate									1																			
Foot adjust																												
Support																												
Transverse hook	1					1			1				1				5											
Diagonal hook	10					1							1				2											
Foot					1				8				12	31				3				23			7	1		
Hook (2:3)	2					4			2								2											
Hook (2:3:4)						2							2															
Index hook																						1						
TH (1,2 and 3 only)									1				2															
TH (1,2,3 and 4)																												
Precision grip (PS)													1				1				1							
I:Pm																										32		
Wrist-wrap																						2						
Grasp					5													9										
Back of wrist														3											5			
Lateral wrist										3															4			
Hook-grasp																					15							
Grasp-hook																						2						
Two-hand A (1:2:3/lateral wrist)										1																		
Two-hand A (1:2:3/back of wrist)														1														
Foot-hand (L/2:3:4)													1															
Foot-hand (R/1:2:3)													2															
Foot-hand (R/2:3)													2															
Foot-hand (R/2:3:4)													4															

Detaching items (may/may not inc. Pm)														
Pick (1:3IMP)	2		14		3		6		25					
Pick (1:3)	1		10		2		4		8					
Pick (2:3)	32		5		14		13		12					
Pick (PS)	41	14	49		27		53		32		88			
Pick (PT)			2								4			
Pick (PP)											11			
Pick (TT)											3			
Pick (1:2IMP)	5		2		7		2		8		3			
Twist off											40			
Pick (SG)	1								1					
Lip-pick		7		17		10		37		33		27		63
Lip-pick x n				3								2		
Pick (1:2:3)	6				1		1		6					
Pick (1:2:3IMP)			8						4					
Grab x n			25						3					
Pick (1:2.3:4)									2					
Pick (3:4)	1													
Pick (1:Pm)													166	
Pick (hook-grasp)											2			
Accumulate														
Combine (hold 3 4 5 Pm pick PS)			4				1		3					
Combine (hold 4 5 Pm/pick 1 2 3IMP)														
Combine (hold 3 Pm pick PS)														
Combine (hold 4 5 Pm/pick 2 3 Pm)							1							
Combine (hold 4 5 Pm pick 1 3)			1											
Remove debris														
Pick-off														
mouthpeel														
Putting in mouth														
Eat	80	11	85		51		--		98	1	153		165	
Eat x n			30				2		2					
Combine (hold 3 4 5 Pm eat PS)									4					
Manoeuvering items														
Wadge		1										1		
Remove debris														
Pick-out														
No. of different elements used*	**18**		**31**		**26**		**36**		**30**		**25**		**14**	
No. of handfuls	**77**		**132**		**62**		**104**		**123**		**166**		**201**	

31.731, $r^2 = 0.097$, F (1,5) = 0.534, ns), although any lack of effect can be largely attributed to Zana and Tinka. (**Figure 7.5**).

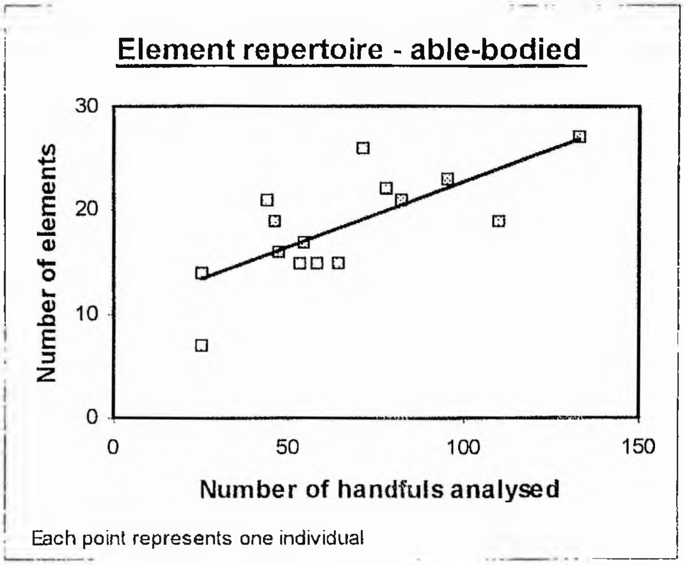


Figure 7.4 Relationship between amount of data analysed and number of elements in an able-bodied individual's repertoire

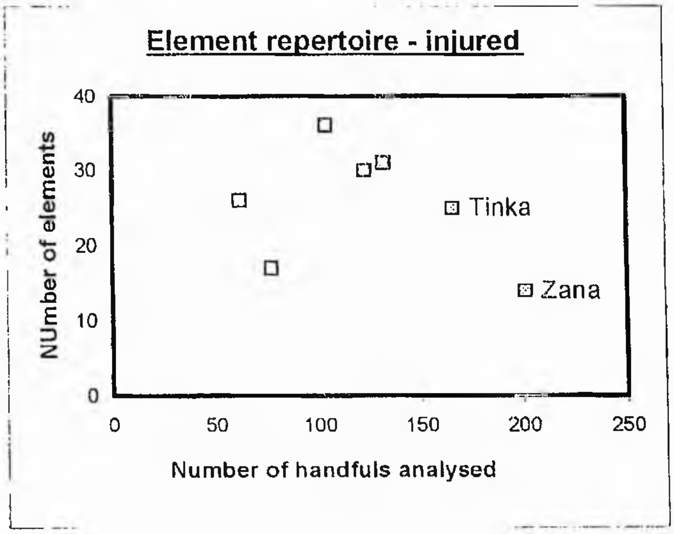


Figure 7.5 Relationship between amount of data analysed and number of elements in an injured individual's repertoire (upper limb injuries only – named individuals indicate injuries to both limbs)

The repertoire of elements performed by the injured limb is shown in **Table7.5.**

Table 7.5. Elements used by the injured limb

Element	KK	KL	KY	MU	TK		ZA	
	L	R	R	R	L	R	L	R
Pull into range								
Reach (thumb only)								/
Slide-adjust							/	/
Grasp-hook						/		
Hook-grasp						/		
Back of wrist			/				/	
Lateral wrist		/					/	
Grasp	/			/				
Manoeuvring items								
Adjust					/			
Support								
Index hook						/		
Precision grip					/			
1:Pm								/
Wrist-wrap						/		
Grasp	/			/				
Back-of wrist			/				/	
Lateral wrist		/					/	
Hook-grasp					/			
Grasp-hook						/		
Two-hand A (1:2:3.lateral wrist)		/						
Two-hand A (1:2:3.back of wrist)			/					
Detaching items (may/may not inc. Pm)								
Pick (PS)					/			
Pick (PT)					/			
Pick (PP)					/			
Pick (TT)					/			
Pick (1:2IMP)					/			
Twist off					/			
Pick 1:Pm								/
Pick (hook-grasp)					/			
Putting in mouth								
Eat				/	/		/	
Total number of elements	**2**	**3**	**3**	**3**	**11**	**5**	**6**	**4**

Although individuals with one hand injured have a repertoire of elements comparable to an able-bodied individual, these elements are for the most part restricted to one hand, and thus in spite of a number of compensatory elements performed with the injured limb, their options for bimanual co-ordination are limited. When using Technique 2, 5/6 injured individuals were observed using bimanual co-ordination. However, for these individuals using this particular technique bimanual co-ordination represented only a mean of 2.49% handfuls (range 1.24 – 3.37%). Therefore, not only do injured individuals use Technique 2 less than is observed within the able-bodied population, but when they do use this technique; they tend not to exploit the option of bimanual co-ordination. Consequently, they restrict themselves primarily to monomanual techniques.

For those individuals with both hands injured, the problem is potentially compounded, as they show a reduction in elements performed by both hands. Therefore these chimpanzees are not only restricted in their options for bimanual processing, as is the case with Muga, Kewaya, Kikunku and Kalema, but they are also hindered in the alternative option of monomanual processing, due to an incomplete repertoire of elements capable of being performed by either hand. While this is largely true for Zana, Tinka still retains some idiosyncrasy in his use of elements with the injured limbs, even to the point of maintaining a range of grip types. Consequently, Tinka can be expected to show much greater flexibility than Zana in responding to particular difficulties associated with individual food items, and this may account for both the similarities between Tinka and able-bodied individuals, and the differences between Tinka and Zana in choice of technique. As was the case for *Ficus mucuso*, a combination of the simplicity of task involved and the nature of each hand's injury, has greatly favoured Tinka's ability to overcome the effects of injury on food processing.

The disabilities shown by each injured limb go part way in explaining the choice of technique shown by each individual. However, Kalema differed from other individuals with one hand injured in that she, together with Tinka, conformed more closely to the pattern observed in the able-bodied population. That is, they did not show an increase in use of mono-manual techniques and a concomitant decrease in bimanual techniques that was predicted, and has been shown to occur with the other injured chimpanzees. In order to understand what particular strategy Kalema is using in contrast to other individuals with one injured limb, we need to look elsewhere. If Kalema is not using bimanual co-ordination between the two upper limbs, then it is possible she is using her feet to substitute for the injured hand.

Use of feet

Chapters 5 & 6 investigated the use of feet in processing by injured individuals and found that feet played an important albeit idiosyncratic role in processing within the injured population. In feeding on *Ficus sur* therefore it is possible that injured individuals may use their feet as a substitute for the injured limb in bimanual feeding. In this way, injured individuals could feed more efficiently from a seated posture through access to food items that might not be reached by using a monomanual feeding technique alone. **Figure 7.6** shows the frequency with which feet were used in processing across all individuals, with postural effects both present and removed (i.e. seated).

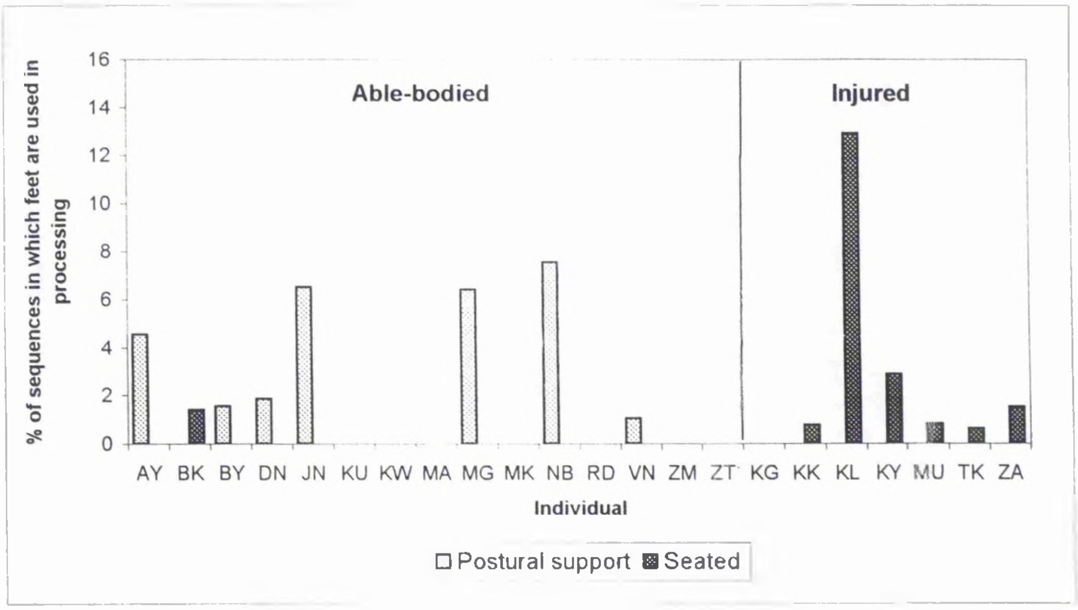


Figure 7.6 Frequency with which feet are used in processing a single handful

Figure 7.6 shows postural context to have an important effect on the use of feet by able-bodied individuals on one hand, and injured individuals on the other. For able-bodied chimpanzees, the use of upper limbs in postural support will on occasion demand use of the feet in supporting a branch whilst feeding. Injured individuals have decreased their use of postures that demand postural support and thus an absence of foot use in this context was expected. Rather, the interesting effect is the use of feet between injured and able-bodied chimpanzees whilst seated. All individuals with upper limb injuries (i.e. with the exception of Kigere, KG) were observed using their feet in processing whilst in a seated posture; this is in contrast to only 1 out of 15 able-bodied individuals tested. In order to test whether injury has a significant effect on the frequency of foot-use when seated, the median value for foot use whilst seated in the able-bodied population was taken (see **Table 7.6**). Individuals were then subdivided into four groups – those above and below the median and those injured or able-bodied. The Chi-squared test (corrected for continuity) was then applied to these frequencies

Table 7.6 Frequency with which feet are used in processing a handful (in seated posture only)

ABLE-BODIED						INJURED						
N	**Mean**	**Median**	**SD**	**Min**	**Max**	**KG**	**KK**	**KL**	**KY**	**MU**	**TK**	**ZA**
15	0.09	0	0.4	0	1.4	0	0.8	13.0	2.9	0.8	0.6	1.5

Injury does have a significant effect on foot-use whilst seated (χ^2 = 16 4625, df = 1, p < 0.001), and thus the suggestion that injured individuals use their feet to substitute for bimanual co-ordination in accessing food items is certainly feasible. This hypothesis is further strengthened by the fact that Kalema shows the greatest use of feet and accordingly conforms closest to the pattern shown by able-bodied chimpanzees in their choice of technique. In other words, Kalema uses bimanual techniques at roughly equal frequency to able-bodied chimpanzees, but rather than using both upper limbs she substitutes the injured limb with the feet. Kalema in particular, therefore, has used this strategy to broaden her feeding options whilst seated, and thus go part way in compensating for her lack of manoeuvrability about the tree.

This chapter sought to investigate the effect of injury on access to food, and used two measures with which to gauge this. The first was the range of feeding postures and the manoeuvrability of an individual around the tree. The second was the use of bimanual co-ordination in accessing food from a seated position in which no postural support was required. Able-bodied individuals use both these strategies in order to access food and minimise feeding competition at any one feeding patch. Within the injured population, all individuals are constrained in their postural behaviour, and were found to be limited in the first of the two measures. For the second measure, that of bimanual co-ordination, only two individuals have compensated their behaviour to the extent where choice of technique remains relatively unchanged from that of able-bodied individuals. These two individuals show different strategies in dealing with the same problem. Kalema relies heavily on the use of her feet as a substitute for the injured limb in bimanual co-ordination, and Tinka fares well in bimanual processing on the strength of the nature of his injuries alone. These strategies will assist in providing access to food at a single feeding patch that would be unavailable to a seated individual restricted to monomanual processing.

In general therefore, injured individuals are limited in the food available to them. In order to minimise feeding competition at their restricted feeding sites the simple processing technique and the small size of this particular food item holds potential for increasing food-processing rate. Rather than avoid competition by constantly changing feeding patch, an injured chimpanzee may simply choose to feed faster at the same patch. The next section will test this hypothesis.

Rate of food processing

Processing rates were recorded using the methods described in **Chapter 2.** However, a change was made to the analysis used for both *Broussonettia* leaves and *Ficus mucuso* in that intervals between successive ‘end-points’ were excluded for those cases where postural change within a bout occurred. In other words, we are specifically interested in the rate of processing at a single feeding patch in the absence of postural adjustment. In this way, we can address the hypothesis that injured chimpanzees increase their processing rate in order to compensate for their limited manoeuvrability.

A significant variation was found in feeding efficiency across all individuals (Kruskall-Wallis, $\chi^2 = 175.829$, df = 21, $p < 0.001$). However, this difference was not located between able-bodied and injured populations (Mann-Whitney, U = 2641660, ns). Moreover, post-hoc comparisons revealed no discernible pattern in processing rate across individuals. **Figure 7.7** shows the mean processing rates (with standard deviation) for all individuals, placed in order of increasing mean.

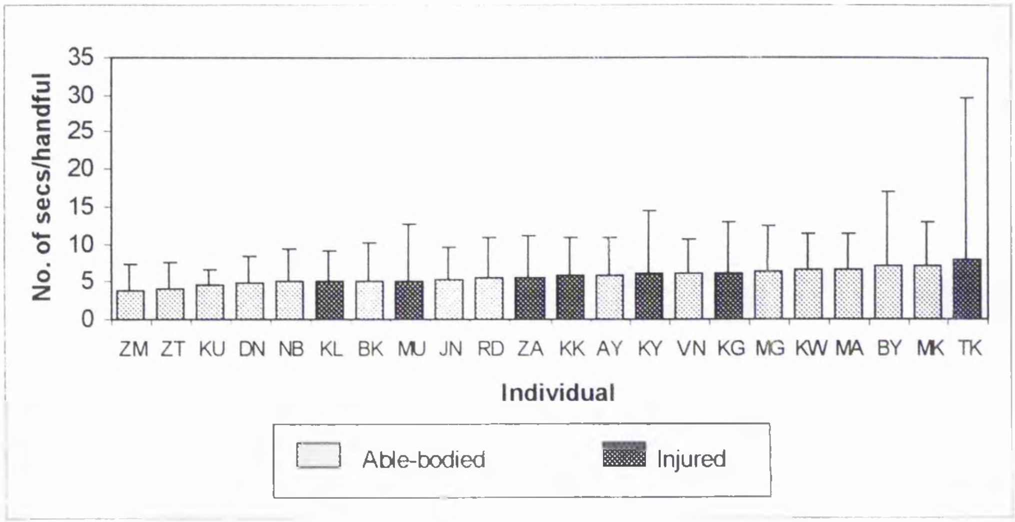


Figure 7.7 Mean processing rate across all individuals

Figure 7.7 shows that the significant difference found across all individuals can be largely attributed to the variance rather than the mean. What is immediately apparent is the large variance of Tinka (TK), and to a lesser extent that of Bwoya (BY), Kewaya (KY) and Muga (MU). These individuals are not consistently feeding at a lower rate than other chimpanzees in the community, but they do have periods when their processing is distinctly slower – as shown in **Figure 7.7** by the gradual change in mean, and the more abrupt spikes in variance.

It is tempting to say that these occasional periods of slow processing are a direct effect of injury. This is however, unlikely, as those individuals that have temporary lapses in their performance are at all other times processing at a similar rate to those individuals that do not. In addition, whereas Tinka, Kewaya and Muga do represent almost half of the injured population that was analysed, there is no accounting for Bwoya's performance, who is an able-bodied adult male, and also no accounting for the remaining injured individuals whose variance is not notably high. An alternative explanation may be a distraction of attention from feeding – for example, increased vigilance, directed towards both observers and other chimpanzees. Assuming that Reynolds *et al* (1996) are correct in that injury does reduce social status within the group, then injury may act indirectly on processing rate by increasing time spent monitoring other individuals in the group at the expense of food intake. This phenomenon would be particularly prevalent when feeding on *Ficus sur*, as the large group size in the tree at any one time, couple with the continual relocation and postural readjustment of able-bodied individuals around the feeding tree would suggest the need for continual reassessment of individuals' positions by an injured chimpanzee. Furthermore, the fact that injured individuals are unable to manoeuvre about the tree to the same extent as able-bodied chimpanzees would exacerbate the need for visual monitoring in keeping track of another individual's movements.

This aside, my initial hypothesis can be disproved on the grounds that injured individuals are not seen to increase their processing rate above that seen in able-bodied individuals at any one feeding patch. We have already established that injured individuals are restricted in their access to feeding patches throughout the tree and in their access to food items within a particular feeding patch. Furthermore, it is suggested that rate of food intake (as oppose to rate of processing) may also be constrained as a result of injury.

Part 4

Laterality in feeding skill

Laterality of hand-use is recognised as an important component of manual skill, no more so than in humans where the origins of handedness are believed to lie in the complex behaviour associated with tool-use and manufacture. MacNeilage et al. *(1987) rekindled the debate as to whether non-human primates show true handedness, and since then interest in the topic has mushroomed. Of particular interest has been the extent of manual lateralisation in the apes. In the current literature, tool-use in chimpanzees and complex food preparation techniques in gorillas have elicited levels of laterality approaching that observed in humans, but non-tool feeding in chimpanzees is represented only by simple reaching and picking tasks. In order to investigate laterality across a variety of different food types that present tasks of varying complexity, laterality of hand-use and the effect of injury on hand preferences in feeding are considered separately in the following chapter.*

Chapter 8

THE EFFECT OF INJURY ON HAND PREFERENCES IN FOOD PROCESSING

INTRODUCTION

In trying to find an evolutionary explanation as to why an organism should ever depart from random symmetry, or indeed why a whole population of organisms should do so in concert, it is perhaps telling that there is no agreed theory of what underlies laterality of behaviour. That a primate should constrain the manipulatory function of its limbs in such a way, in the face of a dynamic and decidedly unlateralized environment, begs the question of what benefits this must convey via natural selection. In the absence of an accepted theory, there are instead a number of models of varying power and conviction.

MacNeilage *et al.*'s "postural origins theory" is by far the most enterprising and comprehensive of these models (MacNeilage *et al.* 1987). This suggests that an ancestral, arboreal primate gained adaptive advantage from using one hand more powerfully than the other in postural and locomotion behaviour, since it thereby became stronger and more practical. Arbitrarily, for unknown developmental reasons, this was the right hand. By default, this left the other hand, the left, preferentially available for visibly guided reaching and grasping. This pattern is seen in prosimian species, which feed in an upright position and use the left hand for grabbing and the right for postural support. Greater success was thereby achieved by consistently using one hand over the other for the ballistic reach where a large quantity of sensory information had to be processed in order to catch the rapidly moving insects. Manipulative specialisations developed in the continuing course of primate evolution with the development of the opposable thumb. As this development occurred a second, right-hand, specialisation may have come to coexist with the original left-hand specialisation for reaching. This may also have been an adaptation primarily for feeding, but in this instance for foraging and processing foods prior to eating. The specialisation is therefore likely to have developed partly in the context of bimanual co-ordination. MacNeilage *et al.* (1987) suggest the postural preadaptation of the right arm, as a versatile gripping device capable of precision movement, may have predisposed later evolving animals, less dependant upon postural support, to prefer the right limb for tasks requiring fine sensorimotor control. From this emerged a generalised right-hand bias for all manual tasks, as shown most clearly in humans. Although this theory still leaves many questions unanswered, such as the fundamental reason why the original manual specialisation should have been towards visio-spatial left and postural support right and not vice versa, it does make the testable hypothesis that laterality of hand-function, in specific directions, is the norm for all primates.

In contrast, Warren (1980) has argued that primates show no intrinsic signs of lateralisation. Rather, individual lateralisation of hand-use is learned over a lifetime of experience and is shaped by environmental forces. Population-level lateralisation is therefore a myth or an artefact of poor experiments. This ‘theory’ however, requires asymmetries in the neural structure of non-human primates (Falk 1987) to be unrelated to behavioural asymmetries, which is perhaps unlikely.

Fagot and Vauclair (1991) attempted a compromise between these two lines of reasoning. They divided hand function, according to degree of skill employed, into low-level and high-level types. Low-level tasks include habitual simple activities such as reaching for food. No individual lateralisation is necessarily invoked, but if individual preferences do occur, these are expected to be symmetrically distributed between right and left at the population level. High level tasks include novel, finely-tuned motor actions that are demanding both spatio-temporally and in cognitive complexity. Individuals are expected to be strongly lateralised and preferences asymmetrically skewed at the population level. Consequently, they proposed that these tasks provided the only situations in which to expect behavioural laterality in hand-use. Although Fagot and Vauclair (1991) are careful to point out that their dichotomy is really a graded continuum, they do not provide gradations. Each category of task (high or low-level) is a composite of several variables, and thus a routine but complex act like nut-cracking in chimpanzees, or a novel but simple act like reaching for food overhead, poses a problem in defining as high or low-level from the criteria given. However, the message of manual specialisation from increasing task complexity is a useful one.

Although these models could be useful in helping us to understand how asymmetries in hand use might have come into being, evidence of hand asymmetries in non-human primates must be the first step to answering some of the more pertinent evolutionary questions outlined at the outset. This evidence in itself is hard to establish unequivocally and studies in the past have been dogged by problems of methodology. McGrew and Marchant comprehensively reviewed these issues in their recent meta-analysis on laterality of hand function in non-human primates (McGrew & Marchant 1997a). In studies on apes alone, they found that of the 86 published data papers, only 18 met acceptable methodological criteria. By far the biggest problem was with over 40 studies that lacked the minimum of 6 subjects, with the second most common problem, in earlier studies in particular, being no assurance of any steps taken to guarantee independence of data points.

Many problems arising from methodology can, to a large extent, be avoided by adopting an ethological approach. Recording spontaneous (as opposed to induced) motor patterns, rigorously defined (preferably in exhaustive and inclusive repertoires or ethograms), is challenging and often frustrating but it does have the overriding benefit of high validity. Furthermore, by using naturally posed problems in the wild, one neatly side-steps practical issues such as the artefactual results produced by environmental asymmetries often found in cage testing, either from interaction with humans or limited amount of space, which have bedevilled tasks used in laboratory studies of hand preference. In nature, tasks are presented entirely at random with respect to the animal's orientation and prior activities.

In addition to methodological issues, McGrew and Marchant (1997a) singled out three factors that deserve special attention in any study of laterality, which are considered below.

Preference vs. performance

Natural selection would favour more lateralised individuals if they had a greater rate of success when using the preferred hand. In their study on hand preferences in skilled feeding tasks by mountain gorillas, Byrne and Byrne (1991) found a slight advantage in processing rate for celery stems, to animals having a stronger hand preference, regardless of direction. However, no other task showed such an effect.

It is possible that the strength and direction of preference may be quite distinct factors in patterns of hand-use. Bryden (1987) found that in humans, there is only limited heritability for direction of handedness, but there is strong heritability for the degree or strength of handedness. One major distinction among humans may therefore be how willing they are to shift hands to the so-called 'mirror-form' of asymmetric sequences of actions as a function of environmental demands. Byrne & Byrnes' work hints that this may also be the case in the gorillas. Although they found no tendency for overall strength or direction of preference to run in families, strength of preference was greater in females, suggesting a possible genetic influence.

Posture

The issue of posture was first brought to the attention of those in laterality research by Macneilage *et al.* (1987) as an evolutionary precursor to primate handedness. In extant primates, for whom postural control is important, posture is pertinent to studies of laterality of hand function because broadly speaking a limb providing postural support is not available to do anything else. If a behaviour is performed in a tree rather than on the ground then positional behaviour will be more constrained by the three-dimensionally structured environment and this in turn will influence the strategy employed to perform the task at hand (Hopkins and Morris 1993). On these grounds Marchant and McGrew (1996) hypothesise that arboreal individuals should be more lateralised in their behaviour than terrestrial ones, although their particular study on chimpanzees at Gombe found no apparent differences in laterality across these two conditions. Studies rarely record what the 'other' hand is doing whilst the operative hand performs a one-handed task. Marchant and McGrew (1996) found for wild chimpanzees that one hand was idle in only 10% of bouts of manual activity; in all remaining cases both hands were active or the other hand provided support.

In more contrived settings, individuals that are tested in atypical human-like bipedal postures on the ground display indications of human-like handedness (Hopkins *et al.* 1993; Hopkins 1993). In the wild however, these postures are generally avoided. It may be that settings conducive to bipedalism may somehow lateralise the "freed hands" of captive apes. Ideally, ethological studies need to look at both captive and wild apes performing their full repertoire of manual behaviour in a range of postures if we are to establish the true implication of posture on laterality of hand-use.

Bimanuality

In addition to postural support, the 'other hand' may be co-opted as part of a two-handed task, or even used in a separate task altogether. Marchant and McGrew (1996) state that bimanual combinations of hand-use should be more lateralised than cases in which only one hand was used whilst the other hand was idle. This is to be expected on the grounds that two-handed activities are more constrained by task requirements than are one-handed activities. Bimanuality can take a number of forms, of which most attention has been paid to the condition in which both operate simultaneously but complimentarily on the same object. In such cases the hand performing the more gross, less skilled component, often with some form of power grip, is termed the subordinate hand, whilst the dominant hand is often the one doing the finer, more skilful component, often with a precision grip. In nature, this is common in grooming but less so in feeding. The exceptions are found in plant gathering by mountain gorillas (Byrne & Byrne 1991; 1993), and tool-use in chimpanzees (e.g. McGrew 1992). Marchant and McGrew (1996) found that most bouts of bimanual feeding by wild chimpanzees consisted of the individual consuming one food item held in the dominant hand while the subordinate hand held other, yet to be eaten food stuffs. Bimanuality requires explicit and precise operational definitions of the roles of each hand, and care should be taken when any of the four limbs act simultaneously.

Classifying laterality

In assessing the data on laterality of hand use, it is important to define clearly the term used for each phenomenon observed. This is by no means adhered to in the literature and so a standardised terminology, as presented by McGrew & Marchant (1996), will be used here. *Handedness* is reserved for the most robust and comprehensive case, when most subjects show consistency for many types of hand use. Consistency for one task at the level of the individual is a case of *hand preference*. For the intermediate conditions, *hand specialisation* refers to the individual's same hand being used for many tasks, while *task specialisation* refers to many subjects using the same-sided hand for some particular task.

In reviewing the literature it is useful to have some classification framework into which all the data on laterality of hand function can be fitted. In their meta-analysis on the laterality of hand use in great apes, McGrew and Marchant (1996) classify lateralisation into five categories as shown by great apes (see **Figure 8.1**). This was subsequently modified to encompass patterns of laterality shown by all non-human primates (McGrew & Marchant 1997a; 1997b).

Level 1 is when the majority of individuals are ambipreferent (ratio of left to right hand-use does not differ from 50:50) and the minority of individuals are lateralised to either side to varying degrees. This is assumed to be the baseline from which all ontogenetic and phylogenetic biases emerge.

Level 2 is when most of the subjects are significantly but incompletely (i.e. not 100%) lateralised, but their collective distribution of left vs. right does not depart from 50:50.

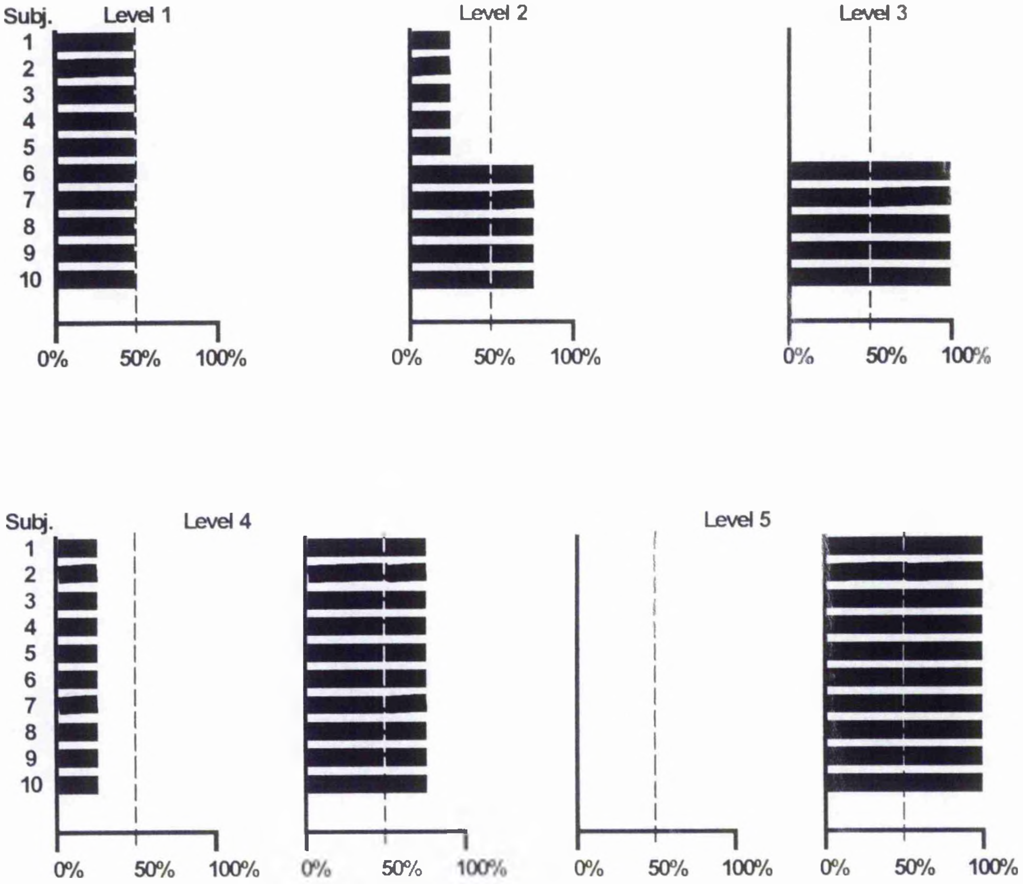


Figure 8.1 Levels of right-sided laterality: hypothetical extreme distribution of ten subjects through five levels of lateralisation (McGrew & Marchant 1996)

Level 3 is when most subjects use only one hand for a task, but again at the population level, the distribution of left vs. right does not depart from 50:50. All subjects therefore show an exclusive preference for one hand. This extreme lateralisation is a logical extension of Level 2.

Level 4 is when the majority of individuals are significantly but incompletely lateralised and when the population distribution is significantly skewed to either the left or the right.

Level 5 is when the majority of individuals are completely lateralised and when their distribution is significantly skewed to the left or the right. All subjects always use the same hand and the population's distribution is maximally asymmetrical. As Level 3 is a logical extension of Level 2, the extreme manual commitment shown in Level 5 is a logical extension of Level 4.

This 5-level model is not sequential but instead is intended to be viewed as two alternative evolutionary pathways; one that goes to Level 2 and then on to Level 3, where most subjects show hand preference for a task but the population distribution is not skewed to the left or the right, or another that goes to Level 4 and then on to Level 5, where the majority of individuals are completely lateralised and the population distribution is asymmetric. It is also not designed to be an exact match to that which is seen in reality, but rather a useful guide by which hand laterality in non-human primates can be classified.

Current data on laterality of hand-use in great ape feeding behaviour

In their meta-analysis, McGrew & Marchant (1997a), found that the chimpanzee, *Pan troglodytes*, represented over half of the data sets, and is unusual in that more studies have been done in the wild than for any other species of non-human primate. Because we are interested here in seeking an evolutionary explanation for asymmetries of hand-use in non-human primates, I shall concentrate on studies performed in nature, as these are most likely to reflect the environmental conditions for evolutionary adaptedness and will therefore provide the most valid measures. Reliable published data on laterality in the wild comes from Gombe (McGrew & Marchant 1996) and Mahale (e.g. Nishida & Hiraiwa 1982) in Tanzania, Bossou in Guinea (e.g. Sugiyama *et al.* 1993), and Tai in Ivory Coast (e.g. Boesch 1991b).

McGrew and Marchant found that most simple feeding activities in free-ranging or semi-free ranging chimpanzees are remarkably unlateralised. Picking up food, whether attached (McGrew & Marchant 1996; Sugiyama *et al.* 1993) or detached (Boesch 1991; Tonooka & Matsuzawa 1995) is dispersed across Levels 1 and 2. All data that reach level 3 lateralisation concern tool-use by wild chimpanzees: using sticks or stones to crack open nuts on root or stone anvils (Boesch 1991b; Sugiyama *et al.* 1993); using fruit fibre as a wadge to sponge up water (Boesch 1991b); using flexible probes of vegetation to fish for termites (McGrew & Marchant 1996); using stones or roots as anvils to smash open hard-shelled fruits (McGrew *et al.* 1997). Furthermore, chimpanzees showing exclusive use of one hand in termite fishing are more efficient than are those who use either hand (McGrew & Marchant 1997c). However, no field studies on chimpanzees have reported data reaching Levels 4 and 5 in either tool-use or non-tool tasks.

These results can be compared to the data on laterality from studies on the other great apes. In contrast to chimpanzees, there are no published data on hand laterality in free-ranging bonobos or lowland gorillas. For orangutans, Rogers and Kaplan (1996) provide the only major study, on a group of rehabilitated but free-ranging individuals. They found little convincing evidence of laterality in feeding, with data on monomanual holding of food and bimanual feeding spanning Levels 1 and 2 respectively. However, no individual scores were provided in the study, one of the methodological criteria set by McGrew and Marchant (1997a). The only dependable field data on laterality in great apes other than chimpanzees focuses on herbaceous plant processing by mountain gorillas (Byrne & Byrne 1993). All eight tasks produced results at Level 2 and above – showing strong hand preferences at each stage. Furthermore, manual processing reaches Level 3 for several of the food items, (nettle, thistle leaves, galium and wild celery), with Byrne & Byrne (1991) reporting a weak population effect in asymmetric hand use (Level 4) for all three leaf-processing tasks. One food type produced a clear Level 5 result; McGrew and Marchant (1997a) noted that in the bimanual processing of spiny thistle leaves 16 out of 33 mountain gorillas used *exclusively* their right hands to do the fine manipulation.

In summary, the majority of simple feeding activities of wild great apes are relatively unlateralised and tend to cluster at Level 1. Tool-use in chimpanzees reaches Level 3 and complex multi-stage plant processing in mountain gorillas reaches Levels 4 & 5. Both of these behaviours are derived from specialised activities that contrast sharply with the simple scratching, reaching plucking and pick-up tasks seen in Levels 1 and 2. This lends considerable support to Fagot and Vauclair's dichotomous view of high and low-level tasks, and strongly suggests that laterality may be linked to task complexity. However, complexity alone was found insufficient to elicit asymmetry in the eating of thistle stem in mountain gorillas (Byrne & Byrne 1991) in which the hands reverse roles regularly within a bout of processing, apparently to avoid the difficulty of manoeuvring a long spiny stem. Conversely, the simple technique for undefended leaves was found to elicit significant hand preferences.

As yet there is no compelling evidence to suggest that great apes or indeed any of the non-human primates are lateralised at the population level. In 1973 Nishida, amongst others, placed the origin of Level 5 hominid handedness to lie in tool-use, and in particular tool manufacture. He suggests that handedness evolved with higher skill, probably at the level tool making activities shown by early hominids, implying that patterns of hand-use hominids and especially *Homo sapiens* are a unique characteristic. However, the current evidence from field studies on extant apes contests this theory. The only reports of Level 5 laterality comes not from studies on tool use, but from Byrne & Byrne's work on the plant processing tasks, thistle leaf in particular, of mountain gorillas.

Laterality of skilled plant processing in chimpanzees

For chimpanzees, an 'evolutionary gap' in feeding hand-preferences exists between Level 1 manual tasks involving simple-reach-and-pick activities and Level 3 tool-use. At the same time however, there exists a similar gap in the literature on laterality: a study on chimpanzee hand preferences in manual tasks in the wild other than tool-use, incorporating naturally-acquired tasks that demand complex and bimanual solutions, is overdue. This chapter reports a study that meets these requirements and determines whether or not the current status of knowledge on laterality of hand function in chimpanzees is really the whole story.

Three tasks were investigated, which represent food items in the diet that demand varying levels of complexity in processing. Of increasing complexity, these tasks were *Ficus sur*, a small fig that employs simple mono-manual processing (see **Chapter** 7), *Ficus mucuso*, a medium-sized fig that also requires simple mono-manual processing, but at the same time demands a degree of co-ordination between limbs which may constrain hand-use in feeding (see **Chapter 6**), and leaves of *Broussonettia papyrifera*, which requires multi-stage sequences of processing with bimanual co-ordination at several stages (see **Chapter 5**). Choice of task was further constrained in that only food items were used for which sufficient data could be collected for all individuals. Data on food items other than the three specified tasks were collected on an *ad-libitum* basis. The majority of these other food items offered relatively simple tasks that required little more than pick-and-eat processing. For each individual, these data were pooled and included by way of a control measure.

The plan of the analyses is as follows. For each task we can first ask whether there is a significant bias towards an asymmetric style of processing in each individual. If there is a bias we then ask whether that individual has a preference for performing the task in one way and how the presence of upper limb injury may affect this preference. Having established hand preferences within the able-bodied population, we can compare among tasks for any given animal, compare animals on a single task and relate an animal's degree of preference to its sex and age. Finally, we can look at the effects of hand preference on performance, as measured by processing rates, and look at the effect of posture and arboreality on patterns of hand-use.

METHODS

Hand-use was recorded using two different methods (see **Chapter 2** for details). Dictaphone recording of feeding sequences logged the hand-used for each element in the sequence, whereas the hand-held computer logged only the hand used to place the item in the mouth, i.e. the last element in the sequence. Either one or the other recording method was used exclusively during any one sample, and thus in subsequent analyses, with the exception of hand performance, the two sets of data are pooled.

There are two major issues to consider in analyses of laterality, which are not mutually exclusive of one another: statistical independence of data points needs to be guaranteed whilst at the same time ensuring sufficiently large data sets for each individual (see McGrew & Marchant 1997a). For example, individual follows, that is, a single day's data on a subject, might be considered independent of one another, but would considerably reduce the data set. More practically, we can use the feeding bout as our unit (see **Chapter 2**) since bouts can still be relied upon to be statistically independent of one another in terms of laterality. Handfuls are not independent of one another, but are included here for comparability.

In their study of mountain gorillas, Byrne & Byrne (1993) found that degree of laterality within sequences of elements increases from start to finish and thus if chimpanzees show hand preferences in feeding, then this is most likely to be identified in the final stage of the sequence. The final element in the sequence before the food item was eaten was therefore chosen as the marker for laterality. For each of the three feeding tasks analysed here, this represents the hand that places the food item in the mouth, or else the hand that brings the plant item towards the mouth before it is bitten off by the lips. For both Dictaphone and hand-held computer recorded bouts, a criterion of more than 2/3 of handfuls with one hand was set for scoring each bout left or right, else the bout was scored as mixed (see Byrne & Byrne 1991). Inspection of sequential data revealed that the final element in the sequence was nearly always performed with one hand, and therefore analysis of laterality is not likely to be affected by bimanual co-ordination. All feeding postures during the bout were recorded in order to investigate the effect of posture on laterality. (see **Chapter 2**).

Hand performance, or rate of processing, was assessed using timings of intervals between successive handfuls recorded using the hand-held computer (see **Chapter 2**). Because hand preferences were obtained from sequential data recorded using the Dictaphone in addition to the hand-held computer, these are based on a much larger sample than that on rates of processing.

RESULTS

Existence of single-hand preferences

The first level of analysis is to determine whether individuals prefer to use just one hand within a bout of processing one food item (asymmetric), use both types at random or consistently use both hands alternatively (symmetric).

Table 8.1 shows raw scores for each food type across all individuals for single-handed bouts. For both able-bodied and injured individuals, instances in which other than the left of right hand were recorded (i.e. both hands together) were rare, particularly in the three named tasks, and was consequently disregarded in further analysis.

For each individual on the three tasks, and the one condition of all remaining food items pooled, an index was calculated of the tendency towards using both hands in a bout (the number of mixed-hand bouts expressed as a percentage of all recorded bouts); this is shown in **Table 8.2**. For all animals for whom a sufficient data set is available, the index is low across all three tasks – indeed it is most often at 0, which implies strong consistency in asymmetric processing within bouts. For all remaining food types other than the three specified tasks the result is similar although there is greater variation. This is not surprising considering this condition involves data pooled from many tasks, which although similar in processing technique, are different in other variables such as size and location.

In order to investigate whether these results were produced by animals whose hand choice was random for each handful needs careful specification of what this null hypothesis predicts. The criterion for recording a bout as “mixed” was less than 2/3 handfuls either left or right. The ratio of mixed hand to one-hand bout

Table 8.1 Laterality of hand-use

[Results at the level of bout and individual sequence are given. Two numbers separated by a hyphen indicate frequency of left versus right. Numbers in parentheses indicate frequency of mixed hand-use for bouts and frequency of hand-use other than left or right, ie. mouth, both hands together, hand and foot together, for sequences. Frequency of hand-use other than left, right or mixed for bouts are rare and are consequently omitted. Females are in italics; * indicates mother with infant not yet weaned; - indicates no data]

	Ficus sur		*Ficus mucuso*		*Broussonettia papyrifera*		**Remaining food types combined**	
Ind	**Bouts**	**Sequences**	**Bouts**	**Sequences**	**Bouts**	**Sequences**	**Bouts**	**Sequences**
AY	15-19(2)	84-196	1-1	13-5	6-8(1)	26-39	34-13(4)	178-49(12)
BK	13-8(1)	118-68	3-3(1)	14-22	3-4(2)	15-26(2)	19-16(3)	190-154(9)
BN	1-1	11-43	-	-	-	-	5-0(7)	59-55(7)
BY	7-11	37-101	1-6(1)	12-46	0-4(2)	11-25	12-12(3)	78-74(6)
CH	5-5	30-56(1)	-	-	-	-	4-1	19-3
CL	4-5	24-51	1-0(1)	15-6	0-3	0-5	1-2	1-13
DN	16-18(1)	161-198	3-1	16-5	7-6(1)	59-54(2)	20-21(7)	256-187(12)
JM	-	-	3-3	28-39	-	-	13-4(2)	72-36(6)
JN	14-18	158-117	1-1	3-5	2-0	3-1	7-10(3)	30-57(7)
KG	16-19	186-209	3-1	12-3	1-1	1-14	13-8	64-27(1)
KK	0-31	3-463(10)	0-13	0-120	0-19	0-65(1)	1-48(2)	10-300(4)
KL	24-3	324-10(3)	27-0	159-0	27-0	102-1(1)	28-3	208-13(15)
KU	4-2	39-36	-	-	-	-	5-15(3)	41-100(1)
KW	19-23(1)	139-161	4-1	33-17	1-0	5-0	19-11	79-74(1)
KY	33-0	433-3(2)	9-0	36-0	15-1	40-2(2)	43-1(2)	386-6(14)
MA	11-5(3)	170-64	6-5(1)	48-33	2-5(1)	24-51	34-25(7)	216-232(10)
MG	13-7	124-105(3)	4-1(2)	27-11			8-9(3)	63-39(7)
MK	13-8	94-61(3)	2-5	11-13	0-1	0-2	11-11(2)	69-46(4)
MU	23-3	348-19(2)	16-0	144-0	18-0(1)	105-6(4)	23-1(6)	325-57(28)
NB	14-12	153-246(16)	3-3	30-7	3-5	5-12(1)	9-13(4)	90-126(7)
NK	1-0	8-0	3-1	14-4	-	-	8-5	35-20
NJ	3-4	13-46(4)	2-0(1)	8-2	4-4(3)	20-15	23-14(2)	202-170(3)
*RD**	10-16(1)	116-194(1)	0-0(1)	17-10	-	-	0-1(1)	2-6
*RH**	4-14(1)	62-159	1-2(1)	21-30	-	-	-	-
SR	10-11	73-98	1-0	3-1	-	-	1-3	8-17
TK	24-2	314-3(3)	33-0	151-0	23-0	143-0	106-3	703-12(21)
VN	7-7(2)	171-102	3-0(1)	21-10	3-2(2)	18-16	23-21(7)	205-149(7)
VT	0-3	0-17(1)	3-4	18-15	-	-	-	-
ZA	1-39	4-508(1)	0-21(1)	115-0(11)	0-2	0-7	0-21	0-148(14)
ZF	8-6(2)	26-51	0-6	0-19	0-3(2)	2-17	3-4	45-33
*ZM**	12-9	246-137	0-1	0-12	5-1(2)	31-6	11-6	65-48(2)
ZT	14-7(1)	129-49	1-3	2-20	6-10(3)	22-24(1)	25-17(7)	233-127(10)

Table 8.2 Symmetry of processing

[The figures under each task name indicate the percentage of all recorded bouts labelled as "mixed-hand bouts" (i.e. a symmetric process), with N giving the total number of bouts for each individual. An asterisk indicates that deviation from 50% was significant at the level of p=0.05 or less following two-tailed testing on raw frequencies]

Ind	*Ficus sur*	N	*F mucuso*	N	*Broussonettia papyrifera*	N	Remaining food types combined	N
AY	5.56 *	36	0.00 -	2	0.00 *	15	8.00 *	50
BK	4.55 *	22	14.29 ns	7	22.22 ns	9	8.57 *	35
BN	0.00 -	2	- -	-	- -	-	53.33 ns	12
BY	0.00 *	18	12.50 ns	8	33.33 ns	6	12.00 *	25
CH	0.00 *	10	- -	-	- -	-	0.00 -	5
CL	0.00 *	9	50.00 -	2	0.00 -	3	0.00 -	3
DN	2.86 *	35	0.00 -	4	7.14 *	14	14.58 *	48
JM	- -	-	0.00 *	6	- -	-	10.53 *	19
JN	0.00 *	32	0.00 -	2	0.00 -	2	10.00 *	30
KG	2.78 *	36	0.00 -	4	0.00 -	2	0.00 *	21
KK	0.00 *	31	0.00 *	13	0.00 *	19	3.92 *	51
KL	0.00 *	27	0.00 *	27	0.00 *	27	0.00 *	31
KU	0.00 *	6	- -	-	- -	-	13.04 *	23
KW	2.33 *	43	0.00 -	5	0.00 -	1	0.00 *	30
KY	0.00 *	33	0.00 *	9	0.00 *	16	0.00 *	46
MA	15.79 *	19	8.33 *	12	12.50 ns	8	10.61 *	66
MG	0.00 *	20	28.57 ns	7	- -	-	15.00 *	20
MK	0.00 *	21	0.00 *	7	0.00 -	1	8.33 *	24
MU	0.00 *	26	0.00 *	16	5.26 *	19	20.00 *	30
NB	0.00 *	26	0.00 *	6	0.00 *	8	15.38 *	26
NK	0.00 -	1	0.00 -	4	- -	-	0.00 *	13
NJ	0.00 *	7	33.33 -	3	27.27 ns	11	5.56 *	36
RD	3.70 *	27	100.00 -	1	- -	-	66.67 -	3
RH	5.26 *	19	25.00 -	4	- -	-	0.00 -	2
SR	0.00 *	21	0.00 -	1	- -	-	0.00 -	4
TK	0.00 *	26	0.00 *	33	0.00 *	23	0.00 *	109
VN	12.50 *	16	25.00 -	4	28.57 ns	7	14.29 *	49
VT	0.00 -	3	0.00 *	7	- -	-	0.00 -	0
ZA	0.00 *	40	4.55 *	22	0.00 -	2	0.00 -	22
ZF	12.50 *	16	0.00 *	6	40.00 -	5	0.00 *	7
ZM	0.00 *	21	0.00 -	1	25.00 ns	8	0.00 *	17
ZT	4.55 *	22	0.00 -	4	15.79 *	19	14.29 *	49

frequencies expected from the null hypothesis will depend on the distribution of bout lengths; assuming a binomial then the predicted ratio of one-hand/both hand bouts varies from 50 to nearly 100 as bout length increases. As the most conservative estimate, I tested against a null hypothesis of 50% single-handed bouts. When 10 or more bouts were recorded, the Chi-squared statistic (two-tailed, 1 d.f, using Yates correction) was applied to the raw counts of single hand and mixed hand bouts to test for departure from equal use of both. For smaller samples with at least 6 bouts, the Binomial test (two-tailed) was applied. Significance at the p=0.05 level is indicated in **Table 8.2.**

For *Ficus sur*, the tendency towards asymmetry in hand-use is overwhelming: all testable cases are significantly asymmetric. For *Ficus mucuso,* a similar – yet slightly weaker - effect is seen with 12 out of 15 animals with sufficient data for analysis showing asymmetric processing. Similarly for *Broussonettia papyrifera,* 9 out of 15 animals show significant asymmetry in hand-use. A convincing trend towards asymmetry is also seen in the pooled data on remaining food items, with 24 out of 25 testable individuals reaching significance.

The overall tendency towards single-hand preference was deemed sufficient to proceed with examining the relative direction of preference.

Relative hand preference for right or left

The scores for left and right-handed bouts across individuals are shown in **Table 8.1**. The results are highly consistent across both levels, for example subjects who are left-predominant for bouts also show left-predominance for sequences. This is not surprising considering the embedding of levels but it is encouraging to know that the results analysed at the bout level are representative of the animals' behaviour as a whole.

For each individual on each task, an index of tendency towards right-hand preference was calculated (the number of right-handed bouts, expressed as a percentage of the sum of left and right-handed bouts). The same was calculated for pooled data on all recorded food types. When 10 or more bouts were recorded, the Chi-squared statistic (two-tailed, 1 df, using Yates correction) was applied to the raw frequencies of left and right-handed bouts to test for departure from equal use of both. For smaller samples with at least 6 bouts, the Binomial test (two-tailed) was applied. The results are summarised in **Table 8.3.**

Table 8.3 Direction of hand preferences

[In all cases where data on 6 or more bouts were available, the figures for each task give the preference indices. The 'preference index' is the proportion of all asymmetric (left- and right-handed bouts) that were right-handed, expressed as a percentage: thus 100% implies that asymmetric bouts were entirely right-handed, and 0% that they were entirely left-handed. In the second column are hand preferences shown significant on two-tailed tests. R represents a hand index between 80 and 100%, L a hand index between 0 and 20%, r an index between 70 and 79% and l an index between 21 and 30%; - indicates no evidence of preference, either because of insufficient data to test or an index between 31 and 69%. Hand preferences are followed by the level of significance: *** corresponds to p=0.001 or less, ** to p=0.01 or less, * to p=0.05 or less. Females are in italics and if followed by * indicates a mother with infant not yet weaned]

Ind	_Ficus sur_	Pref.	_F. mucuso_	Pref.	_Broussonettia papyrifera_	Pref.	All recorded food items	Pref.
AY	55.88	- ns	50.00	- -	57.14	- ns	42.71	- ns
BK	38.10	- ns	50.00	- ns	57.14	- ns	46.97	- ns
_BN_	50.00	- -	-	- -	-	- -	14.29	- ns
BY	61.11	- ns	85.71	- ns	100.00	- -	64.71	r *
CH	50.00	- ns	-	- -	-	- -	40.00	- ns
_CL_	55.56	- ns	0.00	- -	100.00	- -	62.50	- ns
DN	52.94	- ns	25.00	- -	46.15	- ns	50.00	- ns
JM	-	- -	50.00	- ns	-	- -	30.43	- ns
_JN_	56.25	- ns	50.00	- -	0.00	- -	46.30	- ns
_KG_	54.29	- ns	25.00	- -	50.00	- -	46.77	- ns
KK	100.00	R ***	100.00	R ***	100.00	R ***	99.11	R ***
_KL_	11.11	L ***	0.00	L ***	0.00	L ***	5.36	L ***
_KU_	33.33	- -	-	- -	-	- -	65.38	- ns
_KW_	54.76	- ns	20.00	- -	0.00	- -	44.87	- ns
_KY_	0.00	L ***	0.00	L **	6.25	L ***	1.96	L ***
MA	31.25	- ns	45.45	- ns	71.43	- ns	43.01	- ns
MG	35.00	- ns	20.00	- -	-	- -	40.48	- ns
_MK_	38.10	- ns	71.43	- ns	100.00	- -	49.02	- ns
MU	11.54	L ***	0.00	L ***	0.00	L ***	4.76	L ***
_NB_	46.16	- ns	50.00	- ns	62.50	- ns	63.46	r *
NK	0.00	- -	25.00	- -	-	- -	33.33	- ns
NJ	57.14	- ns	0.00	- -	50.00	- ns	43.14	- ns
_RD_*	61.54	- ns	-	- -	-	- -	62.96	- ns
_RH_*	77.78	r *	66.67	- -	-	- -	76.19	r **
_SR_	52.38	- ns	0.00	- -	-	- -	53.85	- ns
TK	7.69	L ***	0.00	L ***	0.00	L ***	2.62	L ***
VN	50.00	- ns	0.00	- -	40.00	- -	46.88	- ns
_VT_	100.00	- -	57.14	- ns	-	- -	57.14	- ns
_ZA_	97.50	R ***	100.00	R ***	100.00	- -	97.65	R ***
ZF	42.86	- ns	100.00	R *	100.00	- -	63.33	- ns
_ZM_*	42.86	- ns	100.00	- -	17.00	- ns	37.78	- ns
ZT	33.33	- ns	75.00	- -	62.50	- ns	44.45	- ns

For the three tasks, only 19 of the 54 cases, which were statistically examined, showed a significant hand preference (at the 0.05 level) for left or right hands. Of these 19, 17 encompassed all individuals with upper limb injuries for whom sufficient data was available. In each of these 17 cases, across all three tasks, injured individuals showed a significant preference (at the p=0.001 level) for the able hand, or when both hands are injured for the hand retaining precision grip function. The remaining two cases that showed a significant hand preference were able-bodied individuals. One was an adult female with a young infant, who showed a right hand preference for *Ficus sur*, and the other was a sub-adult male who showed a right-hand preference for *Ficus mucuso*. No able-bodied individuals exhibit hand preferences in processing *Broussonettia papyrifera*. A similar pattern was seen in the pooled data on all remaining food items. Out of the 32 individuals with sufficient data to be analysed, only 9 showed a significant hand preference. Out of these 9 subjects, 6 were chimpanzees with upper limb injuries, again showing a preference for the able or precision functioning hand. The remaining three cases of significant hand preferences were able-bodied individuals. Two were adult females with young infants not yet weaned, and the other was an adult male.

In order to take into account the larger data set available for the injured population, I repeated the test using only those individuals with a sample size of 20 bouts or more. Hand preferences in able-bodied individuals for whom a substantial data set was available are no more apparent, with only 8 out of 21 cases reaching significance, and all 8 of these cases belonging to individuals with upper limb injuries. Thus, strong hand preferences in chimpanzee manual food processing are not the norm. Rather, tasks involve single-handed bouts, which are as likely to be performed by either hand.

In their study on mountain gorillas Byrne and Byrne (1991) found that hand injury masked the presence of existing hand preferences. In the absence of any existing hand preferences as shown by able-bodied chimpanzees in this study, strong hand preferences exhibited by injured chimpanzees are an artefact of hand injury, and distort the underlying ambipreference of the able-bodied population.

Table 8.3 however, shows that not all indices fall on exactly 50% and consequently it is worth looking at the consistency both across the three tasks and across subjects in order to tease out any effect in both strength and direction of preference that may be hidden within the data. In addition, the exceptional cases of significant hand preferences in mothers with young infants, and to a lesser extent in sub adults over adult suggests effects of both age and sex on hand preference.

Consistency across tasks

Able-bodied individuals

Although an able-bodied individual may not show a significant hand preference for any one task it is possible that that individual may show a consistent predominance to left or right across tasks. **Table 8.3** however does not immediately reveal any obvious similarities in the particular hand chosen for different tasks, and indeed when Pearson correlations were calculated between tasks in the indices of hand preference, no significant correlations were found between any of the three tasks (*Ficus sur* and *Ficus mucuso*: R = 0.521, ns; *Ficus sur* and *Broussonettia papyrifera*: R = -0.305, ns; *Ficus mucuso* and *Broussonettia papyrifera*: R = -0.0929, ns). In addition, intercorrelations between the strengths (i.e. the absolute value of the index's deviation from 50%) of preference on each task were calculated. Here, a significant correlation was found to exist between *Ficus sur* and *Ficus mucuso* (R = 0.804, p = 0.05), but not between either of these and *Broussonettia papyrifera* (*Ficus sur* and *Broussonettia papyrifera*: R = -0.090, ns; *Ficus mucuso* and *Broussonettia papyrifera*: R = 0.929, ns). This suggests that there may be a difference in patterns of hand preference between processing fruits and processing leaves, which would be expected judging by the relative complexity involved in processing these two food types. However, in the absence of any more leaf-processing tasks of similar complexity to *Broussonettia* these results are by no means conclusive.

Injured individuals

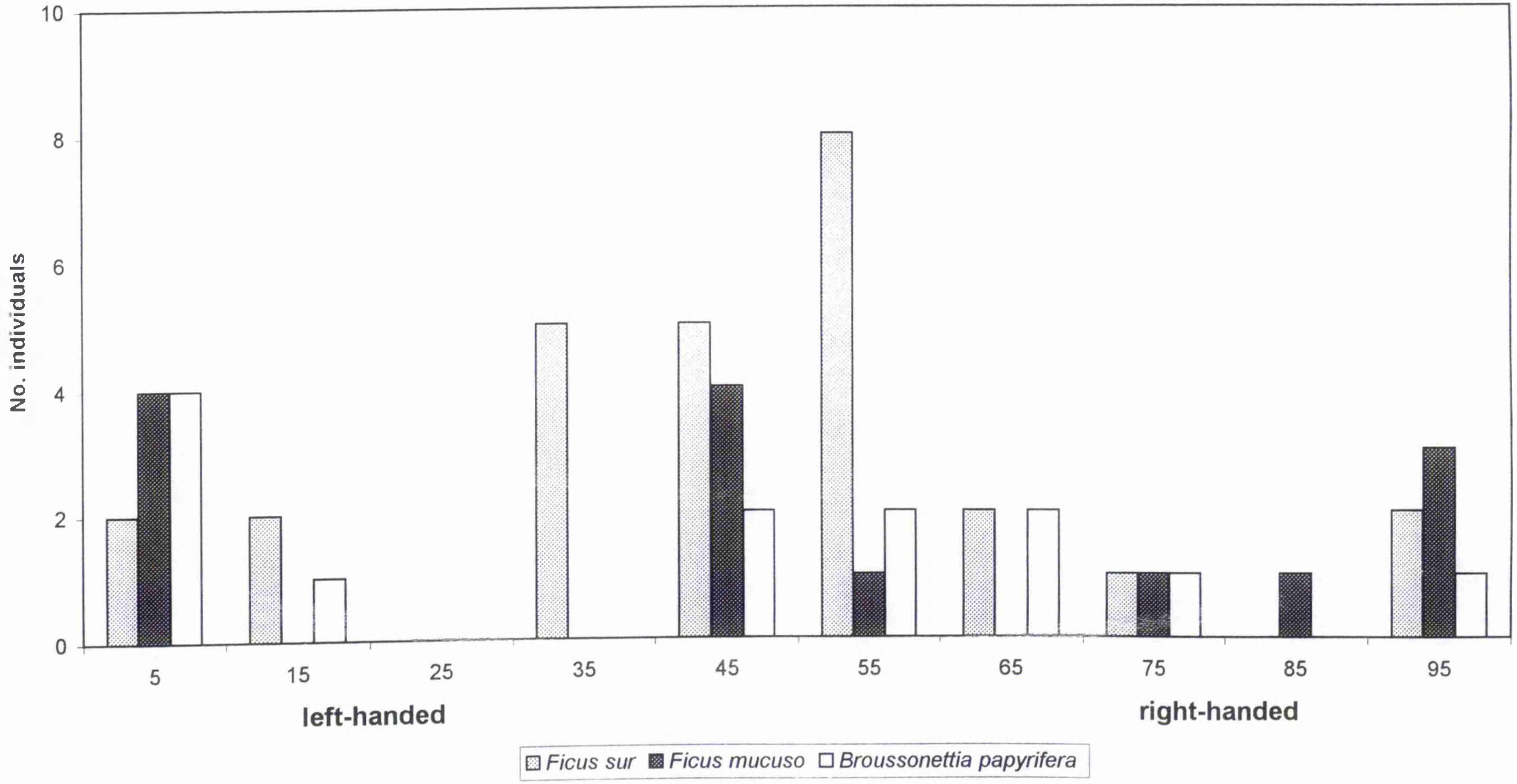
In the case of injured individuals, Pearson correlations calculated between tasks in the indices of hand preference revealed significant correlations between all tasks (*Ficus sur* and *Ficus mucuso*: $R = 0.0996$, $p < 0.0001$; *Ficus sur* and *Broussonettia papyrifera*: $R = 0.0985$, $p < 0.005$; *Ficus mucuso* and *Broussonettia papyrifera*: $R = 0.998$, $p < 0.0001$). This result is not surprising as preference is always for the able limb or, in the case of two injured hands, for the least disabled limb. Intercorrelations were then calculated between the strengths of preference for each task. Significant correlations were found between the two fig species, but only between one of these figs, *Ficus mucuso*, and *Broussonettia papyrifera* (*Ficus sur* and *Ficus mucuso*: $R = 1$, $p = 0$; *Ficus sur* and *Broussonettia papyrifera*: $R = -0.591$, ns; *Ficus mucuso* and *Broussonettia papyrifera*: $R = 1$, $p = 0$). Strength of preference in processing *Ficus sur* is thus considerably lower than for the other two food types, which suggests that this food presents a very different task to injured individuals.

Consistency across individuals

The distribution of individuals' hand preferences on each task is shown in **Figure 8.2.** If we exclude injured individuals, whose hand preferences are represented by the extreme 15% at either end of the distribution, the remaining distribution of preference indices of able-bodied individuals does suggest slight population bias in laterality of hand use for each of the three tasks. In order to examine this further, we can test both the *number* of chimpanzees found with a right or left predominance against a null hypothesis of 50:50 sorting, as well as testing the hand preference *indices* against a null hypothesis of a 50% mean.

The number of individuals with a left or right predominance does not significantly differ from 50:50 (*Ficus sur* 9L:12R $z = 0.50$ ns, *Ficus mucuso* 4L:7R

Figure 8.2 Hand preferences: distribution across tasks



z = 0.86 ns, *Broussonettia papyrifera* 3L:7R z = 1.00 ns). In processing *Broussonettia*, there exists a trend of individuals towards right-hand predominance, but analysis is hampered by a small sample size.

Indices of preference of *Ficus mucuso* and *Broussonettia papyrifera* average above 50% with mean values at 63.7 and 53% respectively – indicating a right-handed bias. *Ficus sur* gave a mean value of 47.6%, indicating a slight left-hand bias.

The Chi-squared statistic was used to test whether or not individual preference indices deviate from a symmetrical distribution. Expected frequencies were calculated on the basis of equiprobable L/R at each of four levels of preference index (20-35%, 36-49%, 51-65% and 66-80%), giving eight bands. Due to the relatively small number of subjects for two of the tasks, four groups were the maximum number permitted. Difference from symmetry do not reach significance on any task (*Ficus sur* χ^2 = 1.649 df = 3 ns, *Ficus mucuso* χ^2 = 1.000 df = 3 ns, *Broussonettia papyrifera* χ^2 = 2.2857 df = 3 ns; all two-tailed).

Relationship of hand preference to age and sex of individuals

Excluding injured individuals, independent samples t-tests of both hand preference indices and strength of preference against sex of animal revealed no effects. However, for pooled data on all foods combined, females did tend towards a right-hand bias and a greater strength of preferences (preference indices: *Ficus sur* male 46.1 female 54.0 t = 1.682, *Ficus mucuso* male 66.2 female 60.0 t = -0.432, *Broussonettia papyrifera* male 57.4 female 39.8 t = 1.395, pooled data on all recorded foods male 45.3 female 52.3 t = -1.373, all non-significant; strength; *Ficus sur* male 8.7 female 8.5 t = -0.067, *Ficus mucuso* male 18.1 female 9.5 t = -0.583, *Broussonettia papyrifera* male 8.7 female 22.8 t = -1.906, pooled data on all recorded foods male 8.9 female 11.7 t = -0.866, all non-significant).

Table 8.3 suggests the slight but non-significant trend towards a right-hand bias and greater strength of preference in females can be located primarily to those mothers with dependant infants. Again, as with the injured individuals, significant hand preferences in feeding shown by these individuals may be artefacts generated for example by left-hand preferences in infant cradling as shown by Manning *et al.* (1994).

In omitting juveniles and infants from this study, age-dependant effects were minimised. However, sub-adults were included in the data set, and this may have had an effect on hand preference. Consequently only two age groups, sub-adult and adult, are tested against hand preference indices and strength of preference. Again, no effect on either direction of strength of preference was found. For the pooled data there was a trend towards left-hand bias and a greater strength of preference in adults, but sample sizes for sub-adults are small (preference indices: *Ficus sur* sub-adult 50.1 adult 49.8 t = 0.067, *Ficus mucuso* sub-adult 76.2 adult 56.2 t = 1.477, *Broussonettia papyrifera* sub-adult 57.1 adult 52.4 t = 0.810, pooled data on remaining foods sub-adult 50.3 adult 48.1 t = 0.399, all non-significant; strength; *Ficus sur* sub-adult 6.5 adult 9.5 t = -0.930, *Ficus mucuso* sub-adult 26.2 adult 8.1 t = 1.387, *Broussonettia papyrifera* sub-adult 7.1 adult 12.9 t = 0.648, pooled data on all recorded foods sub-adult 7.9 adult 11 7 t = -1.137, all non-significant).

Relationship of hand preference to hand performance

Processing rates were obtained using methods described in **Chapters 2** and **5. Table 8.4** compares processing rates with preference indices and strengths of preference for each of the three tasks for those individuals for whom sufficient data was available.

For each task, Pearson correlations were computed between rates of processing and both preference indices and strengths of preference. Injured individuals were excluded from this analysis as injury can independently affect processing rate (see **Chapters** 5 – 7). No correlation was found between processing

Table 8.4 Hand preference vs. performance

[see Table 8.3 for key]

	Ficus sur			*Ficus mucuso*			*Broussonettia papyrifera*		
Ind	**Rate**	**Pref index**	**Pref strength**	**Rate**	**Pref index**	**Pref strength**	**Rate**	**Pref index**	**Pref strength**
AY	5.94	55.58	5.58	37.57	-	-	30.18	57.14	7.14
BN	5.12	-	-	-	-	-	-	-	-
BK	5.11	38.10	11.90	51.41	50.00	0.00	-	57.14	7.14
BY	7.03	61.11	11.11	39.13	85.71	35.71	-	-	-
CH	7.21	50.00	0.00	16.72	-	-	-	-	-
CL	3.90	55.56	5.56	-	-	-	-	-	-
DN	4.76	52.94	2.94	-	-	-	13.79	46.15	3.85
JM	-	-	-	32.84	50.00	0.00	-	-	-
JN	5.25	56.25	6.25	-	-	-	-	-	-
KL	5.07	11.11	38.89	18.66	0.00	50.00	38.79	0.00	50.00
KY	5.99	0.00	50.00	40.81	0.00	50.00	13.87	6.25	43.75
KG	6.19	54.29	4.29	22.16			-	-	-
KK	5.90	100.00	50.00	20.35	100.00	50.00	17.68	100.00	50.00
KU	4.46	-	-	-	-	-	-	-	-
KW	6.47	54.76	4.76	23.96	-	-	9.38	-	-
MA	6.55	31.25	1.25	34.90	45.45	4.55	22.29	71.43	21.43
MG	6.29	35.00	15.00	28.12	-	-	-	-	-
MU	5.18	11.54	38.46	22.76	0.00	50.00	18.19	0.00	50.00
MK	7.05	38.10	11.90	16.33	71.43	21.43	-	-	-
NB	4.99	46.16	3.84	6.50	50.00	0.00	-	62.50	12.50
NK	3.05	-	-	40.82	-	-	-	-	-
NJ	6.77	57.14	7.14	-	-	-	26.39	50.00	0.00
RD*	5.50	61.54	11.54	-	-	-	-	-	-
RH*	4.99	77.78	27.78	16.89	-	-	-	-	-
SR	4.22	52.38	2.38	7.38	-	-	-	-	-
TK	7.92	7.69	42.31	38.14	0.00	50.00	45.15	0.00	50.00
VN	6.00	50.00	0.00	-	-	-	12.29	-	-
VT	10.20	-	-	-	57.14	7.14	-	-	-
ZA	5.64	97.50	47.50	24.17	100.00	50.00	-	-	-
ZF	4.30	42.86	47.14	46.81	100.00	50.00	20.73	-	-
ZT	4.02	33.33	16.67	36.11	-	-	17.44	62.50	12.50
ZM*	4.03	42.86	7.14	36.11	-	-	47.79	17.00	33.00

rate and either preference index or strength of preference (Pearson's R for preference index: *Ficus sur* 0.028 ns, *Ficus mucuso* 0.353 ns, *Broussonettia papyrifera* –0.340; Pearson's R for strength of preference *Ficus sur* 0.068 ns, *Ficus mucuso* 0.133 ns, *Broussonettia papyrifera* –0.178, ns).

Ideally, we would compare the rate of processing when using the preferred hand against the rate of processing when using the non-preferred hand. However, within the able-bodied population there are no significant hand preferences with which to test this theory, and in the injured population the preferences are too strong to give sufficient samples or processing rates by the non-preferred or injured hand. In any case, we have already seen that use of both able and injured limb in bimanual processing results in a decline in feeding efficiency, and so the animal is not likely to further disadvantage their performance by habitually using the injured limb alone. Furthermore, it is difficult to argue that preferred forms of sequence would not be faster as a practice effect alone. We can however, apply this test to the able-bodied population, in order to see if there is any processing advantage in showing a left or right-hand bias, even if this is not a significant preference. For *Ficus sur* the processing rates for the predominant form (defined by the direction of departure from a 50% preference index) averaged 5.43 secs/handful (2069 cases, SD 5.13) and for the non-predominant form 5.23 secs/handful (1345 cases, SD 4.51). For *Ficus mucuso*, the predominant form averaged 35.30 secs/handful (86 cases, SD 69.24), and the non-predominant form 25.85 secs/handful (33 cases SD 41.04). Neither of these two food types show a significant difference in processing rate between the predominant and non-predominant hand (Independent samples t-test: *Ficus sur* t = 1.231, ns; *Ficus mucuso* t = 0.734, ns). *Broussonettia papyrifera* was the only task which showed faster processing by the predominant form with and average of 22.63 secs/handful (81 cases SD 16.11) compared to an average of 26.82 secs/handful (30 cases, SD = 19.50) for the non-predominant form. However, the difference in processing rate is not significant (independent samples t-test: t = -1.150 ns).

Effect of posture on hand preferences

For each bout, posture was noted as one of the seven codes described in **Chapter 2**: seated (SE), seated-reaching (SR/L), bipedal-support (2R/L), tripedal-support (3L/R) and one arm-support (1L/R). Whilst it is appreciated that hanging suspended by three limbs imposes far greater constraints on hand use in feeding than, say, seated with just one limb supporting, to analyse the effect of posture at each of the five levels recorded demands a far greater data set than is provided here. Therefore only two conditions were considered. The first is no limbs involved in postural support – i.e. seated either arboreally or on the ground, and the second is the use of at least one upper limb in postural support, which encompasses the remaining conditions.

Controlling for the effect of injury, the significance of posture was tested against the preference index and strength of preference on each task. Posture had no effect on the preference index (independent samples t-test: *Ficus sur* postural support 50.5% no support 47.7% t = 0.876 ns, *Ficus mucuso* postural support 71.1% no support 65.5% t = 0.324 ns, *Broussonettia papyrifera* postural support 33.33% no support 48.5% t = 0.727 ns). However postural effects did emerge in the strength of preference. This effect was limited to *Broussonettia papyrifera* only (independent samples t-test: *Broussonettia papyrifera* postural support 50.0% no support 19.7% t = -5.732 p < 0.01, *Ficus mucuso* postural support 37.8% no support 22.1% t = -1.490 ns, *Ficus sur* postural support 10.66% no support 16.5% t = -1.652 ns).

DISCUSSION

Laterality in able-bodied chimpanzees

Figures 8.3 – 8.6 show hand preference indices for each of the three tasks for all individuals for whom sufficient data was available, as well as data pooled across all recorded food items. Significant hand preferences are marked as such.

Injured individuals aside, these data conform most closely to Level 1 in McGrew and Marchants' classification framework (McGrew & Marchant 1996), with virtually all members of the able-bodied population showing no hand-preferences. This is in agreement with the majority of studies that have looked at hand-use in simple non-tool feeding tasks of chimpanzees in the wild. However, unlike these studies, the data presented here encompasses tasks of increasing complexity. Processing young leaves of *Broussonettia papyrifera* shows similarities to techniques described for plant gathering in mountain gorillas in that both

Figure 8.2 Hand preferences: *Ficus mucuso*

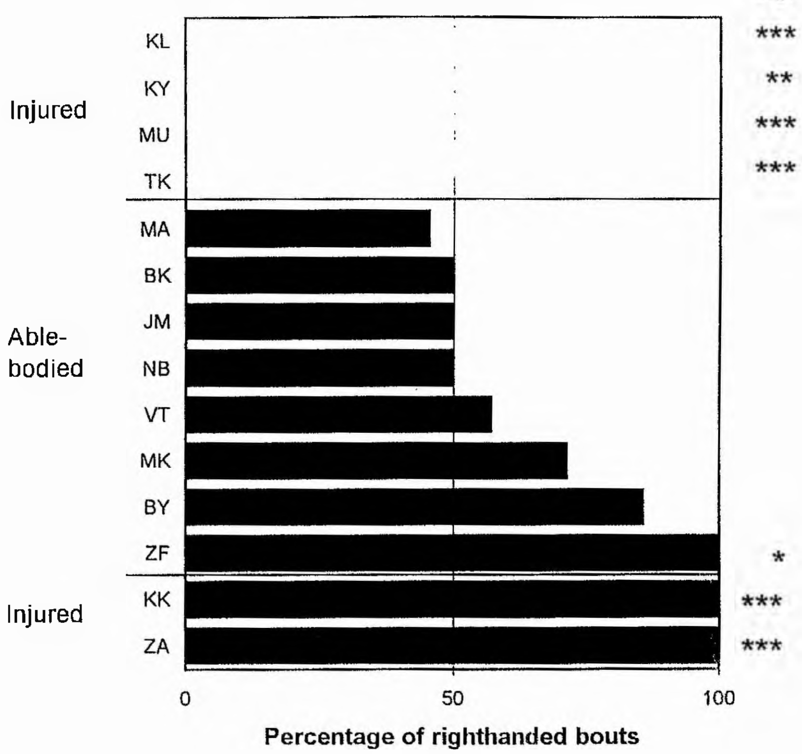


Figure 8.3 Hand preferences: *Broussonettia papyrifera*

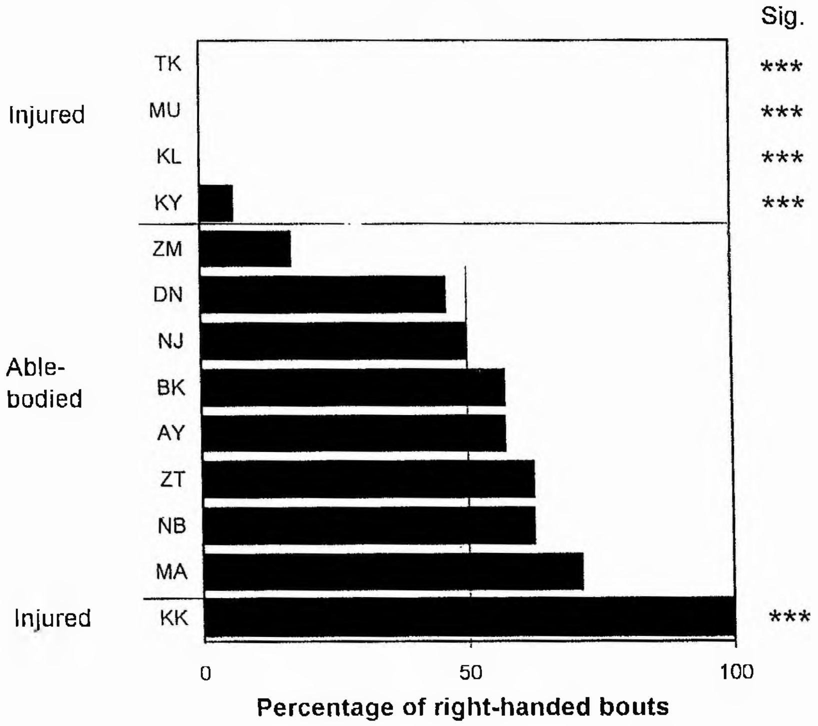


Figure 8.5 Hand preferences· *Ficus sur*

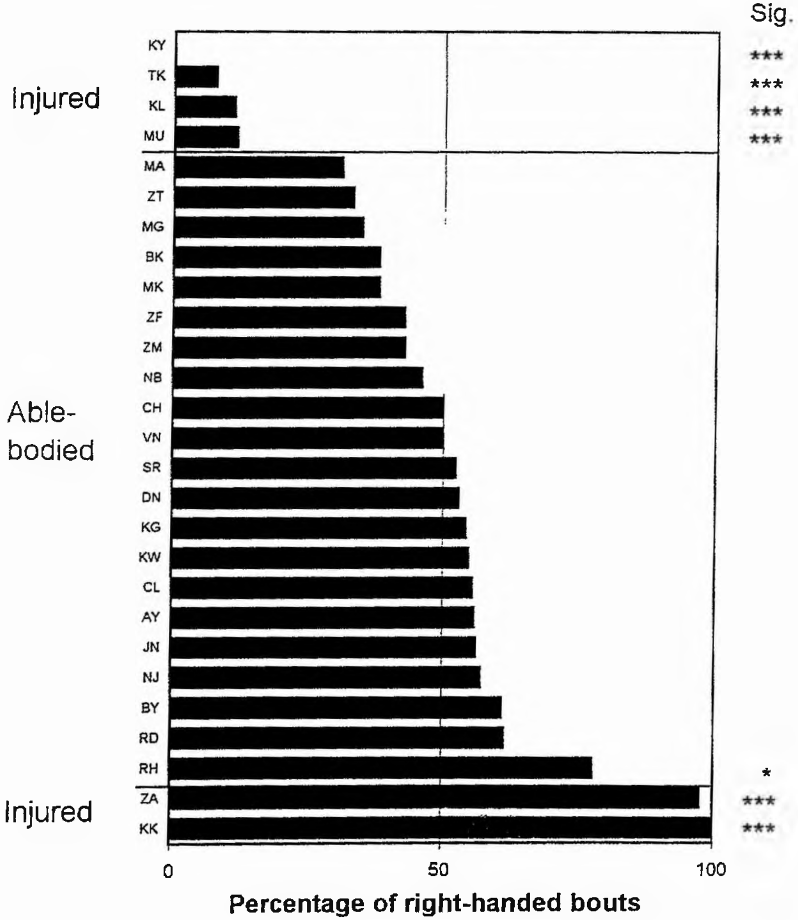


Figure 8.6 Hand preferences across all recorded food items

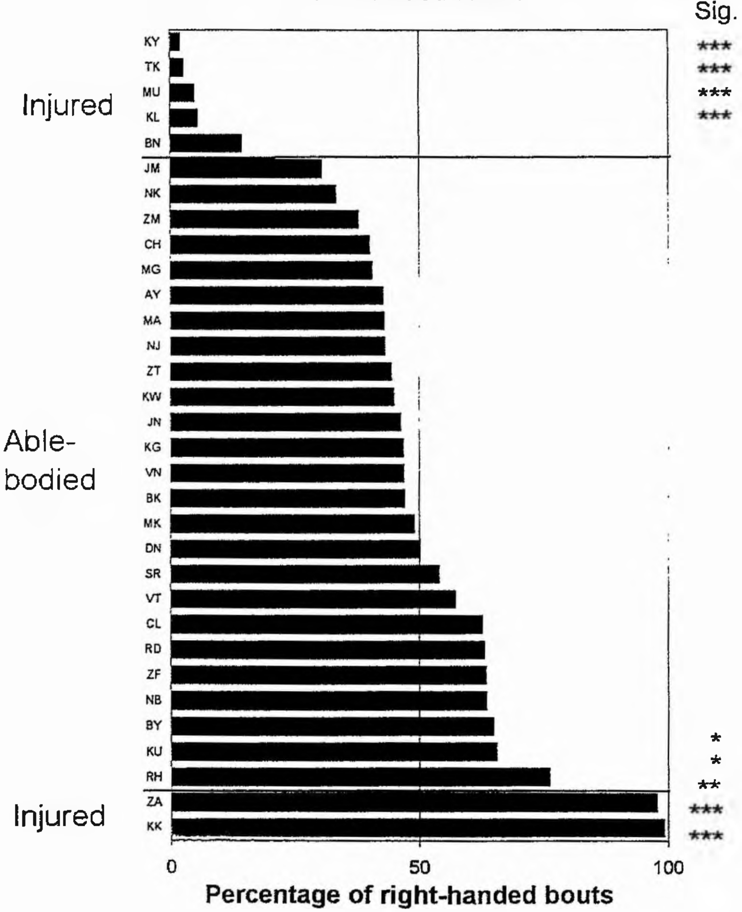


exhibit ordered sequences of directed elements, bimanual co-ordination and hierarchical organisation of behaviour. In the case of food processing in gorillas however, a number of tasks reached Level 3 in the strength of individual hand preferences, which by Fagot & Vauclairs' reasoning suggests that food processing in gorillas shows greater complexity in technique. It is also possible that there are true differences between mountain gorillas and chimpanzees to the extent in which individual hand preferences are shown in manual food processing. Byrne and Byrne (1991) recorded the mirror form of asymmetric sequences of processing using the stage of least variation within this mirror form as a marker for examining hand-preferences. Processing young leaves of *Broussonettia papyrifera* by chimpanzees also requires asymmetric use of the hands, and similarly, the stage of least variation i.e. leaf roll put in mouth, was used as a marker . However, although there is a preference for asymmetric processing of *Broussonettia* amongst able-bodied chimpanzees, a total of 15 possible techniques was recorded, of which many show monomanual or symmetric processing. Ideally, the mirror form of asymmetric techniques would have been analysed separately from symmetric techniques. The data set did not permit such an analysis however, but this is worth considering before any inter-specific differences amongst plant processing in great apes are suggested.

There is no clear evidence for a population level task specialisation of hand use. There was a tendency towards a right-hand predominance in processing *Ficus mucuso* and *Broussonettia papyrifera*, but small sample sizes hindered interpretation of the data. For hand specialisation across tasks, the only significant result was a correlation in *strength* of preference between the two fig tasks. Not only does this suggest that direction and strength of preference are indeed operating independently of one another, it also suggests that there may be a difference in patterns of hand preference between processing fruits and processing leaves. However, in the absence of additional leaf-processing tasks of similar complexity to *Broussonettia* these results are by no means conclusive.

In looking for an evolutionary explanation as to why non-human primates should have ever departed from symmetrical hand use, our first step was in assessing whether or not laterality of hand function does or does not exist in nature. The evidence from this study indicates that in chimpanzee food processing without tools the answer is a provisional no. This finding alone perhaps precludes our need to look any further. For a non-human primate to constrain the use of its hand, there must be considerable gain involved. This study explored the theory that an increase in task complexity would provide such a gain in terms of successful completion of the task. We examined an asymmetric multi-stage task used by chimpanzees to process the leaves of *Broussonettia papyrifera*. The absence of any significant hand preference within the able-bodied population suggests that any advantage of laterality in successful completion of this task is offset by other factors. In Budongo Forest, figs are a year-round staple food item in the diet of chimpanzees. Figs require simple, symmetric processing. All figs are arboreally located and food patches are heavily contested at peak fruiting periods. In contrast, the young leaves of *Broussonettia papyrifera* comprise a much smaller proportion of the diet. This food item is prevalent year round in large patches distributed around the forest edge. Feeding bouts are usually solitary and subdued affairs, occurring both on the ground and in the tree. Ambipreference is favoured by subsistence on arboreally located food items that require symmetric processing and continual postural re-adjustment in the face of intense feeding competition. Conversely, this will tend not to favour subsistence on ubiquitous year round terrestrial food items that require asymmetric processing. This is suggested by a significant effect of posture on the strength of preference in processing *Broussonettia*. Postural constraints on an asymmetric task are likely to have a profound effect on patterns of hand-use. Presumably, the fact that *Broussonettia* leaves occupy a relatively small proportion of the diet in comparison to figs means that these potential costs are offset by the nutritional value of the food. Mountain gorillas in the Virunga Volcanoes subsist on a diet of ubiquitously distributed, non-seasonal terrestrial vegetation which requires skilled processing in order to circumvent a variety of mechanical plant defences. These apes have adapted to their environment by showing strong hand preferences to deal with these food items efficiently. Similarly, the environment may dictate the pattern of hand-use shown by chimpanzees.

Rather than blindly strive to prove the existence of laterality of hand function in non-human primates, it is important to consider the evolutionary and adaptive significance of laterality at both the species and the population level. For example, it may be that lowland gorillas subsisting on a fruit enriched diet do not show the degree of hand preference that is seen in mountain gorillas. Similarly, pygmy chimpanzees tend to rely more on terrestrial herbaceous vegetation in their diet than their common chimpanzee counterparts. One would predict that their degree of hand preference in the wild would have increased accordingly.

Laterality in injured chimpanzees

Individuals with an injury therefore, are at a disadvantage in showing strong hand preferences, albeit these preferences are artificially induced. It follows, however, that individuals with upper limb injuries would show less disadvantage in processing *Broussonettia* leaves over figs, as asymmetric processing required by the former will benefit from dominant hand-use. The findings in **Chapters** 5 – 7 strongly suggest that this is the case. Furthermore, this may also explain why individuals with single limb injuries are particularly disadvantaged in feeding on figs; injury to one hand will exacerbate the contrast between dominant (able) and sub-dominant (injured) hand far more so than injury to both hands. Conversely, strong hand preference may well be a contributing factor as to why injured individuals that perform poorly in fig processing are apparently fully compensated in processing *Broussonettia* leaves. A further point of interest resides in the difference between the two fig processing tasks. Although both of these tasks are relatively simple in comparison to *Broussonettia papyrifera*, injured individuals show a significant reduction in strength of hand preference when processing *Ficus sur*. *Ficus sur* is more heavily influenced by postural factors in processing than is *Ficus mucuso*. *Ficus sur*, therefore, is likely to pose a comparatively larger problem to an injured chimpanzee with a preference for a single hand in processing. Accordingly, where injured chimpanzees are unable to change the direction of hand preference, they are observed to minimise the effects of injury by reducing the strength of preference when feeding on this particular food type.

Chapter 9

CONCLUSIONS

This thesis provided a systematic analysis into some of the feeding skills used by chimpanzees in the wild to process plant foods, and investigated the ways in which individuals with severe limb injuries are affected in their ability to perform these tasks efficiently. In the light of current evidence on manual skill in other great apes, the results from this study can be used to evaluate some of the cognitive and technical abilities of chimpanzees and, in doing so, gain an insight into the manner and extent to which chimpanzees are capable of using these abilities in overcoming the disabling effects of injury.

Prior to any discussion of manual feeding skills, the term ‘feeding skill’ must be precisely defined, and this needs to be done in the light of the natural history of the animal under study. The major studies on feeding skill in great apes (other than analyses of tool-use in feeding) have focussed on the processing technique used for feeding on herbaceous vegetation in the case of gorillas (Byrne & Byrne 1991; 1993), and on both processing technique and the difficulties of feeding arboreally for orangutans (Russon 1998).

The chimpanzee, whilst not as extreme an arboreal specialist as the orangutan, is neither as terrestrial in behaviour as the mountain gorilla nor capable of subsisting on its primarily herb-dominated diet. In its positional behaviour at least, the chimpanzee rests somewhere between the two, and whilst primarily feeding on food items located in the trees, is also observed to feed on the ground. Analyses of feeding, on items located on the ground on the one hand and in trees on the other, suggests different aspects of skill may be for required for efficiency in the two cases. On the ground, where postural constraints are lifted, chimpanzees are able to deal with food items that require bimanual co-ordination in order to prepare them for eating; whereas in trees, food items must be relatively simple to process but nevertheless require postural readjustment and correct orientation of feeding position in order to access food patches. Chimpanzees are primarily frugivorous, and as fruits are typically seasonal (or, in the case of figs, aseasonal but highly preferred), feeding competition is likely to be high in any one tree at any one time, so any strategies that reduce levels of competition would be favoured.

This eclectic mix of feeding skills is important to bear in mind during any discussion of the plant processing abilities of the chimpanzee and when drawing any implications these may have for our understanding of the evolutionary factors that led to the technical sophistication seen in the hominid line. Compared to the mountain gorillas studied by Byrne & Byrne, the Sonso chimpanzees are not as dependant in their diet upon difficult-to-process plant food items - that is, those that require complex solutions in the form of asymmetric multi-stage processing techniques - and thus it is perhaps unlikely that manual skill alone was a unitary selective force towards advanced cognition. Rather, these skills, together with those involved in accessing and retaining food items, are likely to have evolved in concert.

However, manual processing skills comparable to those seen in gorillas and orangutans do exist in chimpanzees, and they provide a useful tool with which to explore the cognitive processes underlying feeding behaviour in chimpanzees.

Complex stem and leaf-processing in chimpanzees

Examination of the literature highlights a number of feeding tasks particularly likely to invoke a degree of complex processing in chimpanzees, namely pith extraction and seed predation. During the study, chimpanzees were observed performing both of these tasks, although feeding on these food items was by no means habitual in the case of the former or readily visible in the case of the latter; hence, anecdotal records only were made. Nevertheless, some conclusions can be drawn. In the case of stem-processing at least, the food preparation skills of chimpanzees appear to exhibit the same characteristics shown in the technique of gorillas, vervet monkeys and *Hapalemur griseus*, as regards the motor actions involved in stripping away the outer layers in order to access the soft pith inside. This lends support to Byrne's theory (Byrne 1999a) that some stem-processing skills are a primitive characteristic among primates. Byrne (1999a) highlights the fact that *Hapalemur* spp. tend to specialise on one species of bamboo only, and whilst the particular species of bamboo varies from one species of *Hapalemur* to another, stem-processing technique may well remain identical in structure. Byrne goes on to suggest that this could reflect an innate specification for the organisation of actions, in addition to the motor actions themselves, which would be effective given the structural similarity of all bamboos. In contrast, the variety and flexibility of gorilla techniques, together with their very localised use, would tend to argue against such 'hard-wiring'. Chimpanzees share a highly structured approach to stem processing, and as with gorillas this is unlikely to be hard-wired. Furthermore, I found that those primitive characteristics retained in the chimpanzees' stripping action seem to be elaborated by incorporating stages or perhaps subroutines particular to each particular food item, which makes innate specification in general seem unlikely. For example, in processing rattan, the spiny casing is removed by a delicate push-down action from the inside in order to avoid coming into contact with the spines as would happen if the typical primate stripping action was employed; with *Costus dubious* the tissue-paper layer needs to be carefully unravelled rather than stripped, and in the case of the Marantaceae herb the pith is zigzagged into the mouth rather than bitten off and chewed. In this way, the basic stripping action is augmented to provide individual solutions to particular tasks.

A systematic analysis of the technique used for a difficult-to-process food was feasible with only a single food item, the young leaves of the paper mulberry *Broussonettia papyrifera*. Analysis of the behaviour of able-bodied chimpanzees, processing the young leaves of *Broussonettia papyrifera*, revealed an ordered sequence of directed elements, organised into routine and subroutine structures which included iteration loops, , optional and alternative subroutines and inter-co-ordination between subroutines. All of these behavioural indices imply a hierarchically structured process under voluntary control, of the sort illustrated in Chapter 1 for gorilla and orangutan plant feeding and chimpanzee tool-use. The goal structure illustrated in **Figure 9.1** displays the *minimum* hierarchical complexity that is implied by these behavioural indices as shown in the preferred stripping technique of able-bodied chimpanzees.

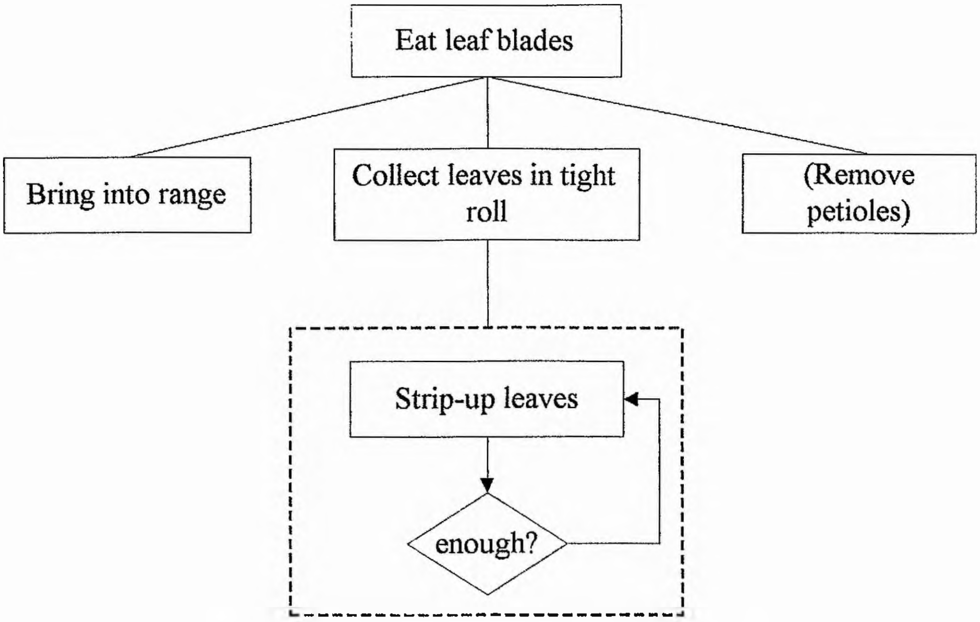


Figure 9.1 Goal hierarchy for young leaves of *Broussonettia papyrifera*

Individuals also possess a number of other less commonly used techniques in their repertoire of stem and leaf-processing that reflect the continual variation within their feeding environment. This variation is in sharp contrast to that found with mountain gorillas where low seasonal variation in their diet, and as a result relatively low feeding competition, combined with primarily terrestrial feeding habits enables them to develop remarkable standardisation in their major feeding techniques. Chimpanzees, on the other hand, experience seasonal and spatial variation in their diet with consequently greater feeding competition and this is often combined with the positional and postural constraints of feeding arboreally. Thus, chimpanzees' considerably greater variation in feeding techniques is most likely a response to environmental demands.

An advantage of the hierarchical structure of the program used to process *Broussonettia* leaves (shown in **Figure 9.1**) is that it enables this type of low-level decision making to be incorporated. For example, if postural constraints prevent leaves being collected using the bimanual stripping element (the behavioural sequence normally used to collect leaves), then leaves may instead be collected by lip-folding and then regrasping in the hand. At a lower level still (not shown in

Figure 9.1) there is considerable variation in the nature of individual elements used, as well as the preferred hand, but with little functional significance apparent. By confining variation in technique primarily to these lower levels, the integrity of the main sequence of processes is retained, thus enabling the ultimate goal of eating the leaves (as represented by the top row) to be achieved efficiently. At the same time, however, the organisation of behavioural sequences is not inflexible. For example, if petioles are not sufficiently tough to warrant removing then this sub-process is not evoked.

The leaf-processing skills shown by the Sonso chimpanzees thus bear a number of similarities to those shown by mountain gorillas (Byrne & Byrne 1993), both in structural organisation and degree of complexity. Byrne & Russon (1998) concluded that gorilla food preparation appeared to be organised into shallow hierarchies, with gorillas capable of keeping track of at least two embedded goals. A two level hierarchy is seen in chimpanzee leaf-processing as shown in **Figure 9.1**, suggesting at least one embedded goal can be tracked in this case. Byrne & Russon argued that a linear chain-like structure was not sufficient to explain the behaviour observed in mountain gorilla food preparation, as this could not account for the optional processes observed – which in a linear model would interrupt a link in the chain and thus lose track of the sequence altogether. Furthermore, in gorilla food preparation, where certain behavioural routines exist as subroutines used for other food, a linear structure could result in confusion as to which path to follow when a point of overlap between two food types is reached. Neither of these difficulties were observed in gorilla behaviour, which is thus better described by a hierarchical organisation. Applying these guiding principles to chimpanzee food preparation forces a similar conclusion. In leaf-processing skills, and as much as can be inferred from the anecdotal reports of stem-processing skills, behaviour does appear to operate as interconnected clusters rather than isolated units. In stem-processing at least, chimpanzees appear to be able to generalise their behaviour by combining particular behavioural clusters - the routine employed in the stripping action - into different techniques that are used to address different food types. In addition, *ad libitum* observations on the techniques used to process the young leaves of *Ficus natalensis* and *F. exasperata* suggest that the same may be true of certain leaf processing tasks.

Integration of food processing with arboreality and competition from conspecifics

When feeding on the fruits of *Ficus mucuso*, chimpanzees can process up to four separate handfuls simultaneously: a strategy apparently beneficial in reducing levels of feeding competition. This behaviour requires that the chimpanzee be able to keep track of where each handful has progressed to, as well as which limbs are in use at any one time. Here, different aspects of feeding skill are combined, namely food processing technique and limb co-ordination. This facility, apparently amounting to cognitive integration of seemingly independent skills, (*viz.* Russon 1998), is also shown by chimpanzees when feeding on *Ficus sur*. Here both limbs and behaviour need to be co-ordinated, not between several concomitant handfuls but between food processing and postural support whilst feeding. Again it appears that the function is to enable the chimpanzee to access a variety of food patches, increasing the relative amount of food available, and thus reduce local feeding competition. Russon (1998) reports a similar phenomenon in the behaviour shown by orangutans in feeding on arboreal difficult-to-process foods. Here, in addition to apparently hierarchical organisation of orangutan food processing, Russon identified several signs of hierarchical organisation in orangutans' techniques for accessing arboreal foods. For example iteration loops, where individuals climb into 'vehicle' trees and repeat a swaying action until the vehicle tree comes sufficiently close to the target tree in order to enter; subroutines, such as 'sway' that is also used in play; and disruption, where the vehicle tree is swaying in the wrong direction, and this is corrected by pulling in additional vegetation to alter the direction of swing, and then resuming the swaying action. Russon argues that if both complex processing and arboreality are cognition-enhancing evolutionary pressures in the Hominidae in their own right, then the two pressures acting together should exert pressures for even more complex cognition. In the case of chimpanzees, *Ficus sur*, whilst not a difficult food to process, is arboreally located and requires precise positioning and manoeuvrability in order to feed with reduced competition. There is thus a three-way interaction of processing, arboreal positioning and support, and behavioural devices to avoid intense feeding competition, all of which need to be co-ordinated in order to feed efficiently. In the light of what we know of the cognitive abilities of chimpanzees from their food preparation skills, and in the absence of a systematic analysis of arboreality in chimpanzees, it is reasonable to suggest that similar cognitive processes to those shown by orangutans may be operating.

Coping with injury

Severe limb injuries to chimpanzees represent yet another independent factor, which needs to be integrated with the skills found in able-bodied individuals in order to feed efficiently. The three food types investigated in this study demand skills that require a considerable degree of manual dexterity and control, whether in food preparation, manipulation of simultaneous handfuls, or postural support whilst feeding. The severity of limb injuries investigated here pose severe limitations to both dexterity and control in the injured limb. However, feeding efficiency measures of the three food types revealed remarkable compensation in feeding ability, independent of nature and extent of injury sustained.

Hypotheses on the response to injury

All injuries belonging to the adult individuals analysed in this study were already in place when the Budongo Forest Project was initiated in 1990. Therefore we can be sure that all techniques currently used by these individuals represent 'complete compensation' and are not likely to be in the process of changing further. In the absence of any direct developmental data, three possible mechanisms of compensation seem feasible, which broadly relate to the mode of acquisition of feeding skills in able-bodied chimpanzees. The first hypotheses assumes that individuals were injured late in life after already having learnt the technique, whereas the second two hypotheses both assume individuals were injured young, but with differing predictions according to the role of social learning in acquisition of technique.

1) Late injury - no essential change in behaviour

This hypothesis assumes that individuals were injured late in life after already having learnt the processing technique as an able-bodied individual. Our results would therefore show dramatic crystallisation of behaviour, with injured individuals seemingly unable to learn any new techniques that might presumably prove more efficient than that shown by able-bodied individuals. 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 on in life before any knowledge of processing technique is acquired (see Chapter 3 for a more detailed discussion). All new injuries in the nine years following the initiation of the Project have occurred to juveniles below the age of four, who by their very nature are inquisitive and therefore most likely to fall victim to snares on the ground. In addition, the idea that chimpanzees, as adults, are unable to learn new behavioural patterns is an unparsimonious one given our current knowledge of great ape mental abilities. Consequently, this hypothesis can be provisionally rejected.

2) Early injury - environmental channelling

This hypothesis makes the far more parsimonious assumption that individuals were injured early normally acquire the techniques they do because the constraints of the environment, in interaction with the affordances of the chimpanzee's hand or body, guide their attempts towards a particular organisation. Tomasello & Call (1997) 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 from direct observation of another individual's behaviour. On this hypothesis, an injured chimpanzee would be expected to learn a new technique that suits the surviving functionality of the hands, in order to feed on a particular food item efficiently. As both the nature and extent of injury varies considerably between individuals, one would expect feeding technique to differ not only between able-bodied and injured individuals, but also between individuals with different injuries.

3) Early injury - observational learning

As for hypothesis 2, this hypothesis assumes that individuals were most likely injured at an early age. However, in this case individuals would normally acquire their processing technique through observation of other chimpanzees. Byrne & Byrne (1993) suggested that the more complex gorilla feeding techniques are acquired by means of observation of others in the population, normally the mother. Individuals show great idiosyncratic variation at the detailed level of elements used, but remarkable standardisation in technique, and this was argued to imply that "the logical ordering of elements and the interrelationship of processing stages is copied by program-level imitation." Thus, the basic approach to the problem is demonstrated by the mother, whilst the detailed actions of individual elements may be learnt by trial and error exploration. Byrne & Russon (1998) have argued that this may apply also to other complex behaviours seen in great apes. In Tomasello *et al.*'s, experiment of observational learning of tool use by young chimpanzees (Tomasello *et al.* 1987), young chimpanzees saw demonstrators get out-of -reach food with a rake-tool. Chimpanzees who saw these demonstrations did use the rake to bring food into reach, but did not show some details of the technique demonstrated. Tomasello *et al.* had originally attributed the social learning of these behavioural strategies to emulation: that is, the observational learning of the goal or result that the demonstrator is seen to achieve, and not the technique they use to achieve it. Byrne & Russon however, point out that in using the rake, chimpanzees displayed an understanding of the relation between rake and food, and furthermore used the rake in a similar way – i.e. raking, rather than poking, throwing or any other manipulation – to produce a behavioural strategy similar in essence to that demonstrated. Byrne & Russon concluded that chimpanzee behaviour on these tasks was consistent with program-level imitation but not with emulation. Since the chimpanzee's copying was successful in obtaining the food rewards it was unsurprising that imitation at lower hierarchical levels, including the details of raking actions, were not copied.

On this hypothesis of acquisition by program-level imitation, injured chimpanzees would have no option but to copy the basic approach of the technique shown by the able-bodied population, i.e. conform to the goal hierarchy shown in

Figure 9.1. However, at the same time these individuals would then have to “work around” the disabling effect of their injuries by modifying the way each stage in the process was achieved, or fail at the task. Thus a shared repertoire of techniques between able-bodied and injured chimpanzees is predicted, but with considerable variation in details of execution.

Evidence from patterns found in injured adult chimpanzees

The paper mulberry *Broussonettia papyrifera* is an exotic species introduced from Asia in the 1950’s by sawmill operators. Consequently, just as for the plant-preparation skills of the isolated population of mountain gorillas in Rwanda, there is little doubt that the technique used by the Sonso chimpanzees in processing *Broussonettia* leaves is learnt.

In processing the leaves of *Broussonettia papyrifera*, we find that injured chimpanzees do not demonstrate a specialised range of techniques appropriate to their individual injuries, but instead share the overall structure of technique as seen in the able-bodied population. Just as the goal hierarchy, illustrated for able-bodied chimpanzees in processing *Broussonettia* leaves (see **Figure 9.1**), enables low-level variation in technique in response to environmental conditions, 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. Tinka is the most severely injured of the chimpanzees and as a result is incapable of using certain behavioural subroutines in order to achieve the subgoal represented as ‘collect leaves in tight roll’ in **Figure 9.1.** As a result he relies more heavily on an alternative subroutine, used less frequently by the able-bodied population, in order to achieve the same goal. At the other end of the scale, Muga, who shows least impairment, is seen to use all the alternative subroutines observed in the able-bodied population; rather than show a preference for a single one, however, these are used at roughly equal frequencies. Similarly, all other injured individuals favour particular behavioural subroutines that suit their individual injuries, whilst sharing the same overall organisation of technique as performed by able-bodied chimpanzees. In a comparative study on the effects of limb injury on chimpanzees and gorillas

(Byrne & Stokes in prep), Pandora, an adult female gorilla with snare injuries comparable to those seen in the Sonso chimpanzees, showed a similar manner of compensation in processing nettle leaves. The nettles are apparently more problematic to deal with than *Broussonettia* leaves, since the able-bodied population uses only a single technique. Pandora shared the technique shown by able-bodied individuals but, as with injured chimpanzees, modified the fine details 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.

Ficus mucuso and *Ficus sur* are not difficult-to-process foods; however, they provoke high levels of feeding competition and require postural support to enable feeding. Recall that, for *Ficus mucuso,* able-bodied individuals "shelve" food items in order to reduce competition and, for *Ficus sur,* they increase both access to and relative availability of food patches by their manoeuvrability about the tree. In the same way as seen for *Broussonettia* leaves, injured individuals did not develop novel strategies in order to deal with this problem; rather, they share the basic strategy seen in the able-bodied population.

However, in able-bodied individuals, competition avoidance, together with both postural and positional adjustments, are dynamic processes that depend upon a particular food item at a particular time; in other words, what is good for one particular food patch may not necessarily be appropriate for another. Consequently, in the manner in which these overall goals are achieved, there is much greater freedom for individual learning by trial and error and as a result a considerable degree of idiosyncrasy. This is in contrast to the processing technique used for *Broussonettia* leaves, where, in spite of a degree of flexibility in choice of technique, either one of two techniques was generally preferred by the able-bodied population. Injured individuals are, according to nature of injury, extremely limited in the range of elements (and therefore options open to them) in fig processing, and whilst capable of modifying their behaviour they show a considerable reduction in behavioural flexibility. In the long-term, therefore, injured individuals are likely not to be as capable of feeding efficiently on these food types as able-bodied chimpanzees. This may therefore explain why injured individuals spend comparatively more time feeding on both *Ficus sur* and *Ficus mucuso* than their able-bodied counterparts.

For all three feeding tasks, injured chimpanzees have developed a number of novel elements in order to achieve the intermediate stages in the process and hence employ the same basic technique as able-bodied chimpanzees. These elements include using the feet as a substitute for the injured limb, as well as innovative use of the remaining functional properties of the injured limb particularly in supporting roles to enable bimanual co-ordination. These actions are "novel" in the sense that they are not observed in the able-bodied population. The feet are used in feeding by both able-bodied and injured alike, but injured individuals also use their feet in a way that is not shown by their able-bodied counterparts, for example, Zana's extensive use of feet in both active and passive roles in processing *Ficus mucuso*. Novel use of the injured limb was not restricted to food processing; elbows were often hooked over a branch in order to support the animal in the tree and free the able limb for processing. Similarly, when feeding on *Ficus mucuso*, elbow joints and wrist were seen to be used for shelving food items whilst the able limb engaged in concomitant processing. In addition to novel elements, and in food preparation tasks in particular, injured individuals compensate through their use of familiar elements at novel stages of processing, for example, combining functions with the able-limb at a stage which is normally performed bimanually, using the lips to detach multiple leaves at once where the injured limb is unable to do so, and swapping food items between hands for reasons other than postural constraints. Further evidence of compensation at the level of individual elements is seen in the hand used at each stage. Injured chimpanzees show strong hand preferences as a result of injury, which is in sharp contrast to able-bodied individuals who show ambipreference in their hand-use. It is suggested that strong hand preferences are advantageous in complex asymmetric processing skills, but disadvantageous in arboreal feeding on simple-to-process food items. Injured individuals showed relatively weak hand preference when feeding on *Ficus sur*, an arboreally located food item that requires considerable postural control on feeding, but strong preference when feeding on both *Broussonettia papyrifera* and *Ficus mucuso,* where postural constraints are less prominent and bimanual processing skills more so. The variation in use of elements seen *between* able-bodied and injured chimpanzees parallels the idiosyncratic use of individual elements *among* the able-bodied population. A similar phenomenon was found in our preliminary analysis of the effects of injury in gorilla feeding skill (Byrne & Stokes in prep.) Here, the injured female Pandora was found to show unique variation in precisely those features that show idiosyncrasy amongst able-bodied individuals.

It is also at this level of individual elements that we see the greatest variation, not only across chimpanzees with different injuries, but for each injured chimpanzee across different feeding tasks. Individuals have therefore developed novel actions according to the nature of the task as well as the nature of their injuries. This strongly suggests that at the level of individual elements, each individual is learning from their own experiences, supporting the interpretation made earlier regarding the acquisition of feeding skills in chimpanzees, and the manner of compensation in the case of injury. On this hypothesis, feeding skills are copied at the program-level, and the basic strategy is duplicated by individuals regardless of the type of injury. At the same time, details of individual elements are learnt through trial and error and so consequently bear the hallmark of each particular injury.

The fact that injured chimpanzees share the skeletal structure of complex behavioural routines with able-bodied individuals and fill in the details according to their own predicament enables them 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 capable of generalising learnt skills to individual circumstances, which so far has only been observed in the great apes and humans. This 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. However, there are physical limitations to the ability of chimpanzees, at least, to compensate fully for the effects of injury, and these may manifest themselves, for example, in times of extreme feeding competition. At the same time the fission-fusion nature of chimpanzee society may be a contributory factor in enabling injured chimpanzees to devote more feeding time to those food items that cannot be fed on efficiently, thus overcoming any adverse effects resulting from injury. In addition, possible changes in group behaviour towards an injured member may have implications, for example, towards access to food items that would otherwise not be tolerated.

Further work

Although this study has provided evidence to suggest that program-level imitation is the most parsimonious explanation of how compensation is achieved, a long term and comparative study of the development of feeding skills in infants with able-bodied mothers on the one hand, and injured mothers on the other, would lend further evidence to the role of social learning and ecological constraints in the acquisition of chimpanzees feeding skills in the wild. Furthermore, observations on the juvenile female irreversibly injured during the course of this study would shed considerable light on the acquisition of behaviour following injury, and further help to resolve the alternatives.

Additionally, complementary studies on the long-term effects of injury with regard to feeding efficiency, together with the short-term social implications of injury, including group behaviour and association patterns between able-bodied and injured individuals, would enhance our understanding of the cognitive abilities of chimpanzees involved in withstanding and coping with potentially disabling injuries.

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Appendix I

CATALOGUE OF ELEMENTS USED IN FOOD PROCESSING

General terminology

Combine	ability to carry out separate functions simultaneously, with the digits of one hand
Grasp	a general functional term but specific to injured individuals, which involves the use of the injured limb. This may manifest itself in a variety of novel ways (specify), distinguishable from the designated grips of the able-bodied

Grips and supports

Transverse hook	grip for enclosing and firmly holding cylindrical objects perpendicular to the long axis of the hand by flexion of the fingers. The amount of flexion at the interpharangeal joints and the degree of involvement of the distal palm depend upon the diameter of the object. Thumb may be adducted or opposed.
Diagonal hook	grip for enclosing and firmly holding cylindrical objects by the flexed fingers alone, oriented away from the transverse axis of the hand. Meta-carpopharangeal flexion is greatest for digits 4-5 and least for digit 2. Abducted thumb may oppose fingers on objects of large diameter.
Index finger hook	Grip for enclosing and firmly holding cylindrical objects by the flexed index finger used during knuckle-walking locomotion on the third and fourth fingers.
Power grip	potentially strong, closed-hand grip (varying as to whether whole hand or 1+ fingers only) on cylindrical object (often stem) for support or for procurement, or on a bundle whilst accumulating items.
Cup hold	grip for holding large spherical/irregularly-shaped objects or many small objects at once, in which they are cupped in upturned palm propped by flexed fingers and by the opposed thumb. The number of fingers involved depends upon the size and shape of the object. The cup-hold may also be inverted.
Pad-to-pad	grip for retrieving and holding small-medium sized objects in which the distal pads of the thumb and finger(s) (specify) are opposed
Pad-to-side	grip for retrieving and holding small, relatively flat or cylindrical objects in which the pad of the thumb props or holds the object against the lateral surface of the distal phalange of the index finger
Tip-to-tip	grip for retrieving and holding small objects between distal volar tips of thumb and index finger
Pad-to-tip	grip for retrieving and holding small objects between the distal pad of the thumb and the distal volar tip of the index finger (and *vice versa*)
Scissor grip	grip for retrieving and holding small objects between the lateral surfaces of digits 2 and 3. Digits may be fully, partly or non-flexed

Pencil grip	closed hand (tight) grip of one hand on cylindrical object (usually stem) with object caught between pair of fingers and resting on thumb (specify fingers), usually for support
Imprecise grip	grip for retrieving and holding small objects between the distal volar pad of the thumb an any aspect of the middle and proximal phalanges of 2/3/4/5.
Two-hand	two hands simultaneously holding object. May be symmetrical grip (S), or asymmetrical (A) in which one hand usually plays a major supporting role and the other hand a minor and more manipulative role to bring the food item closer to the mouth
Crossed-hands	both hands held flat/cupped and palm up, crossed at right angles to support scraping/biting with greater

Procuring/retrieving items

Part	1 or 2 hands used to pull parts of material to each side (without detaching) so that lips can go between and take out food (Commonly 2-handed symmetrical – not to be confused with *Clear*)
Clear	1 or 2 hands used to push vegetation to one side so that food item can be brought into range (Commonly 1-handed or 2 hands alternatively)
Hook	used to bring item into range (specify hook grip)
Reach	1 or 2 hands used to pull an item into range (Commonly 2 hands alternatively – specify grips)
Yank	tight grip used to apply force on an 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)
Stem-bend	use of the hand to bend the central portion of a stem (supported by its natural attachment at one or both ends) without breaking it off, to have the effect of bringing into range or reducing to manageable size

Detaching items

Pick	precision grip on clearly defined object, which is pulled against force of natural attachment
Pick-up	grip (specify) on clearly defined object which is lying free on the ground
Lip pick	delicately pluck directly from point of natural attachment with lips
Lip pick-fold	item is detached by folding over with the lips and pulling against force of natural attachment in single movement (used for eating leaves)
Grab	detach several items at once from point of natural attachment
Twist-off	rotation at the wrist to detach food item against force of natural attachment (Commonly seen for large or unripe fruits)
Prise	use of fingertips to lever an object from its natural attachment, in an action similar to removing a lid from sealed box (Commonly used in detaching pieces of bark from trunk)
Strip-up	half-open power grip (specify whether constricted at little finger or thumb) around leafy stem, slid up stem to detach bundle of leaves against force of substrate or other hand's supporting grip

Lever-apart	on objects held in both hands, leverage of the hands in symmetrical fashion against one another (often with thumb as pivot) to detach two objects from same point of attachment
Tooth-pull	pull with object held in teeth against bracing of limbs

Detaching parts from items

Pick-at	single digit used to pick or loosen item, e.g. to remove excess debris
Pick-off	debris removed from item held in the other hand and then discarded
Pick-out	debris removed from item already placed in the mouth and then discarded (distinguish from that under **manoeuvring items**)
Brush-off	debris/dirt removed from item held in the other hand by sweeping/wiping action
Roll	debris/dirt removed from a (spherical) item held in the hand by rolling against substrate, e.g. branch with the flat of the palm (see *wipe* also)
Wipe	latex removed from the petioles of picked leaves (and sometimes fruits) by wiping against substrate (see *roll* also)
Bite-off	use teeth to cut off portion of naturally attached or hand-held item. May be either discarded (e.g. petioles of leaves) or else retained as manageable portion for further processing (e.g. stem-processing)
Snap	bend long object (e.g. stem) in order to make a break – supported by both hands wither side of break, or by one hand and point of natural attachment
Snip-case	use of incisor teeth to clip off hard outer casing, in order to discard or else expose free end
Strip	grip with one hand to pull off covering with gross movement of arm – supported by other hand and/or point of natural attachment
Push-down	use of whole hand or single digits to remove unwanted against force of substrate or support of other hand e.g., in removing spiny covering of rattan stems by pushing away from the inside out
Peel	precision grip with one hand used to pull off covering (often with a twisting back action), whilst other hand supports. Distinguishable from *strip* in the more delicate and precisely0defined nature of the action
Tooth-strip	part-close incisors around stem and pull covering against support of hands – an action like that of wire strippers
Mouth-peel	use of lips/teeth to pull of covering (e.g. hard rind of fruit) while hand supports item – usually discarded
Unravel	remove outer covering by circular motions of the object held in hand – to resemble action of unwinding string wrapped around a pencil

Manoeuvring items

Accumulate	ability to carry out separate functions with different digits of the same hand. E.g. pick items with pad-side grip to add to items already held in hand with digits 3-5
Index finger probe	movement of index finger independently of thumb and other fingers in probing recesses and moving objects

Manipulate	rearranging, simply using the fingers, the position or shape of an item(s) held in one hand, without using the other hand.
Rotate	special case of *manipulate* in which in which the orientation of an item is changed – usually used with round items such as fruits, but also seen for stems
Adjust	delicately adjusting the position of an item held in the other hand or mouth, using specified grip, a push with the knuckles or just with a single finger
Slide-adjust	re-locate firm grip on different portion or item by sliding hand up stem, whilst supported with mouth, other hand or point of natural attachment
Knock	single digit used to remove item held in the other hand – e.g. for removing less ripe fruit from handful
Swap-hand	transfer object or handful from one hand to the other
Pick-out	pull single item out with one hand from among a mass of items held in the other hand, requiring discrimination of one item from among many
Lip-fold	use of the lips to fold over and item held in the hand – e.g. used with leaves in order to reduce leaf blades to a more manageable handful
Zigzag	with object held in mouth at one hand, horizontal movements of the hand holding stem at other end fold strand into mouth in concertina shape – implies loosening and regrasping with teeth.

Eating/biting food

Eat	implies single food item is placed in mouth
Bite	handful of food is not eaten whole, but either a single bite is taken (S) and the remains discarded, or else repeated bites are taken until the handful is finished (R)
Sausage-feed	repeated loosening and regrasping of object in order to feed it into the mouth (usually a cylindrically-shaped bundle)
Shear bite	shearing bites used to slice off parts of large compact handful with teeth, either single bite (S) and remains discarded unless *retain nucleus*, or else repeated bites until handful finished (R)
Retain nucleus	using the remains of the last handful as a basis for starting to accumulate the next
Wadge	use of the lip and palate to squeeze/rub ingested food item so as to form a wad of skin, seeds or fibres from which the juices are extracted by leisurely squeezing/sucking
Tooth-scrape	use of the incisors to scrape away surface or inner layer of food item – may be supported by point of natural attachment, e.g. hardened resin on trunk, or held by either/both hands e.g. in scraping the inner layer of a large piece of bark
Lick	liquid resin/sap removed directly from bark of trunk

Appendix II

PLANT FOOD ITEMS RECORDED FOR SONSO CHIMPANZEES DURING THE STUDY PERIOD

[F = fruit, L = leaves, Fl = flowers, B = bark, W = wood, S = seeds, P = pith, R = resin]

Family	Food species	Plant	Part eaten	J	F	M	A	M	J	J	A	S	O	N	D	Total no. months
Anacardiaceae	Lannea welwitschii	Climber	F, B	1										1	1	3
	Pseudospondias microcarpa	Tree	F,L			1	1	1	1	1						5
Annonaceae	Cleistopholis patens	Tree	W	1	1						1			1	1	5
	Monodora myristica	Tree	F											1		1
Apocynaceae	Alstonia boonei	Tree	B							1						1
Boraginaceae	Cordia millenii	Tree	F		1	1	1	1	1	1	1	1	1	1		10
Ixonanthaceae	Klainedoxia gabonensis	Tree	F								1	1				2
Leguminosae, Caesalpinioideae	Cynometra alexandri	Tree	S, B,	1	1	1		1	1	1			1	1	1	9
	Dialium excelsum	Tree	F			1										1
	Erythrophleum suaveolens	Tree	S									1	1	1		3
	Mildbraediodendron excelsum	Tree	F			1	1	1	1	1	1					6
Marantaceae	Marantochloa leucantha	Shrub	P			1									1	2
Meliaceae	Entandophragma cylindricum	Tree	S										1			1
	Khaya anthotheca	Tree	B,R,L,Fl,							1	1	1				11
Moraceae	Antiaris toxicaria	Tree	F, L		1	1									1	3
	Broussonetia papyrifera	Tree	F, L, Fl	1	1	1	1	1	1	1	1	1	1	1	1	12
	Ficus barteri	Tree	F		1		1	1				1	1	1	1	7
	Ficus exasperata	Tree	F, L	1	1	1	1	1	1	1	1	1	1	1	1	12
	Ficus mucuso	Tree	F,L,B	1	1	1	1	1	1	1	1	1	1	1	1	12
	Ficus natalensis	Tree	F		1		1	1			1	1	1	1		6
	Ficus polita	Tree	F		1								1	1	1	4

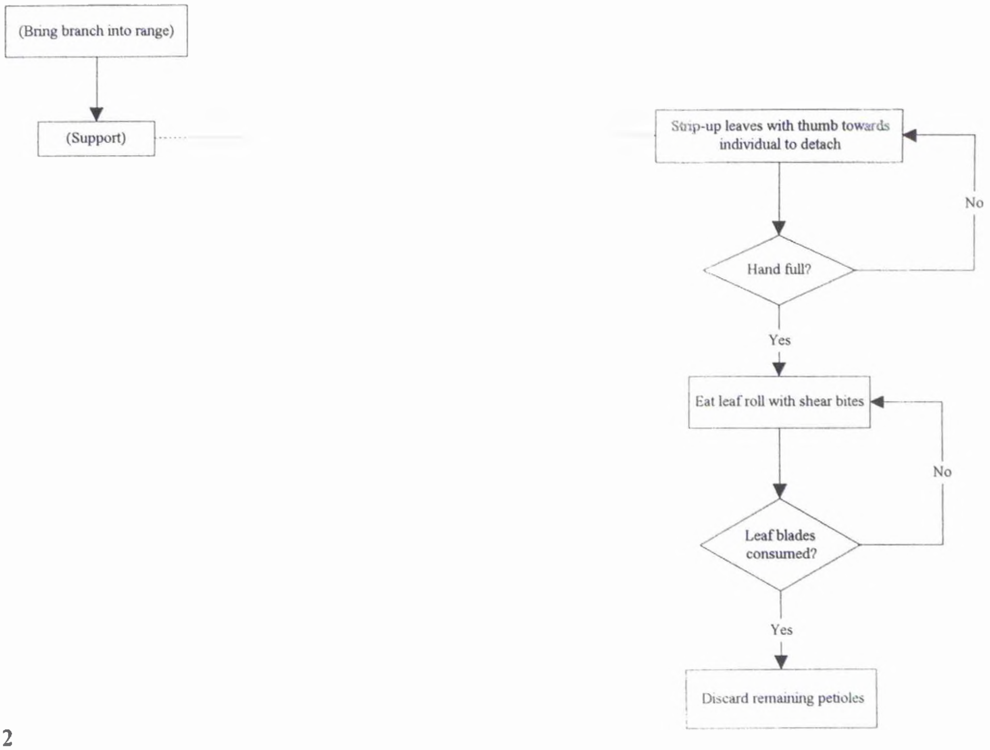
Family	Food species	Plant	Part eaten	J	F	M	A	M	J	J	A	S	O	N	D	Total no. months
Moraceae cont.	Ficus sansibarica (brachylepis)	Tree	F	1		1		1	1				1	1	1	6
	Ficus saussureana (dawei/lutea)	Tree	F, B	1		1	1		1					1	1	5
	Ficus sur (capensis/vogelana)	Tree	F, L	1	1	1	1	1	1	1	1	1	1	1	1	12
	Ficus thonningii	Epiphyte	F								1	1	1			2
	Ficus variifolia	Tree	L,F		1		1			1		1	1		1	6
	Ficus ottoniaefolia	Tree	F	1												1
	Milicia excelsa	Tree	F, L	1	1		1	1								4
	Morus lactea	Tree	F	1	1	1		1								4
	Myrianthus holstii	Tree	F,L			1	1	1	1	1	1	1				7
Palmae	Calamus deerratus	Climber	P						1							1
	Raphia farinifera	Tree	W			1	1	1	1	1	1					2
Polypodiaceae	Platycerium angolense	Epiphyte	L			1							1			2
Rhamnaceae	Lasiodiscus mildbraedii	Tree	L												1	1
	Maesopsis eminii	Tree	F				1	1	1	1	1					5
Sapotaceae	Chrysophyllum albidum	Tree	F		1	1								1	1	4
	Mimusops bagshawei	Tree	F										1	1		2
Tiliaceae	Desplasia deweii	Tree	F,L	1			1			1	1	1		1		6
Ulmaceae	Celtis milbraedii	Tree	L,Fl	1	1	1	1	1	1	1	1	1	1	1	1	12
	Celtis wightii	Tree	L, Fl	1		1	1	1			1				1	6
	Celtis zenkeri	Tree	L		1	1	1	1	1	1	1	1	1	1	1	11
Urticaceae	Urera cameroonensis	Climber	L,Fl,P	1	1					1					1	4
Zingiberaceae	Afromomum sp.	Shrub	F,P			1		1	1	1	1	1	1	1	1	9
	Costus dubious	Herb	P	1												1
?Meliaceae	Trichillia rubescens	Tree	L		1				1							2
?	Palisota schweinfurthii	Herb	P			1										1
?	Alaphia laudolphoides	Climber	F	1	1							1	1	1		5

Appendix III

TECHNIQUES USED FOR EATING BROUSSONETTIA PAPYRIFERA

Young leaves only

1



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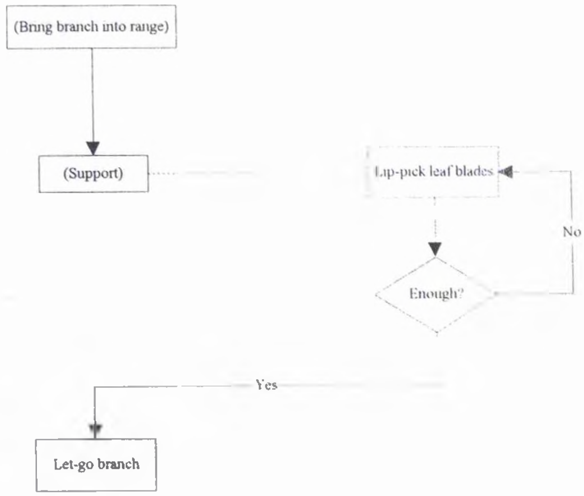

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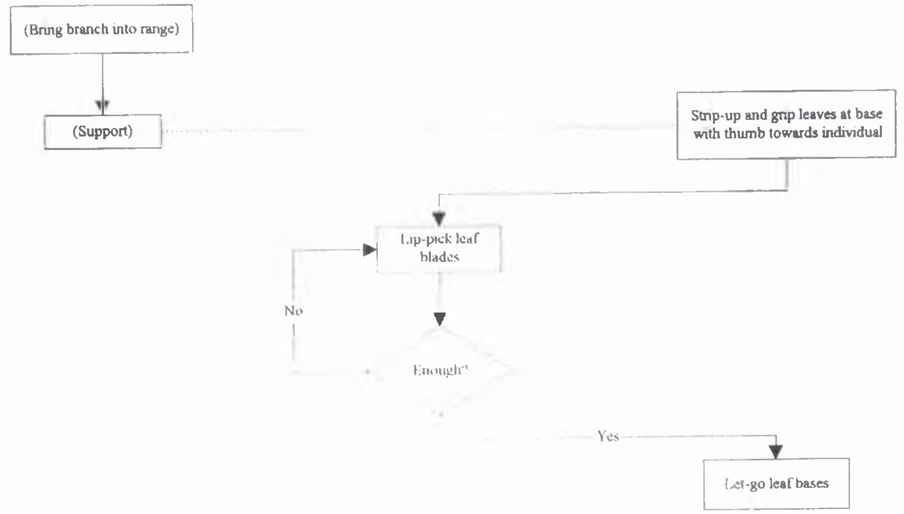
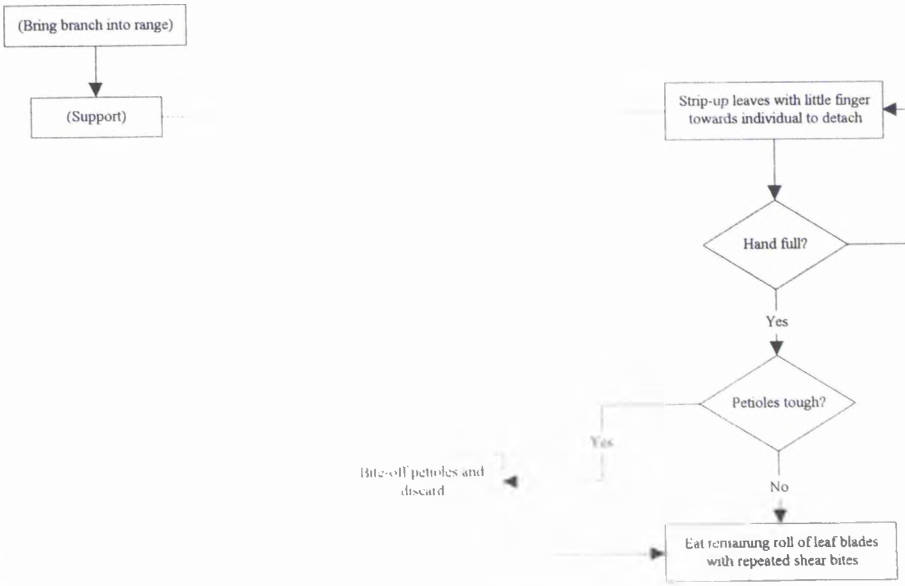
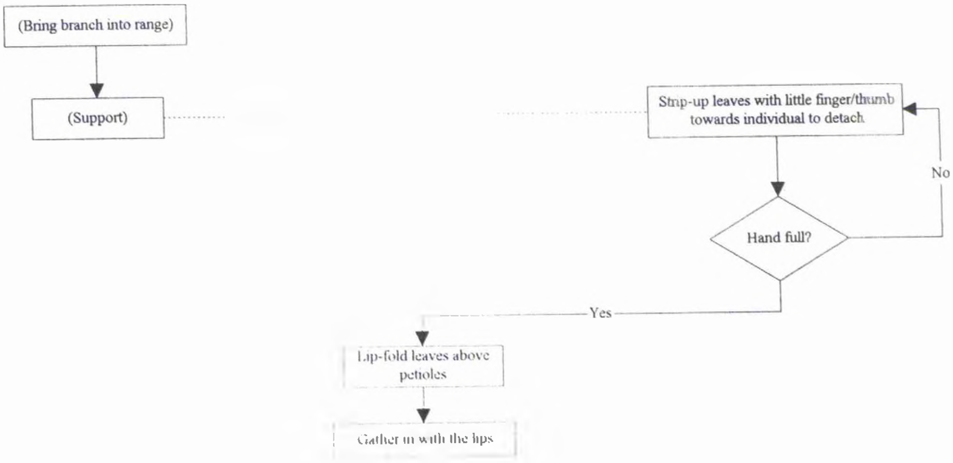

(Bring branch into range)
(Support)
Strip-up and grip leaves at base with thumb towards individual
Lip-pick leaf blades
No
Enough?
Yes
Let-go leaf bases

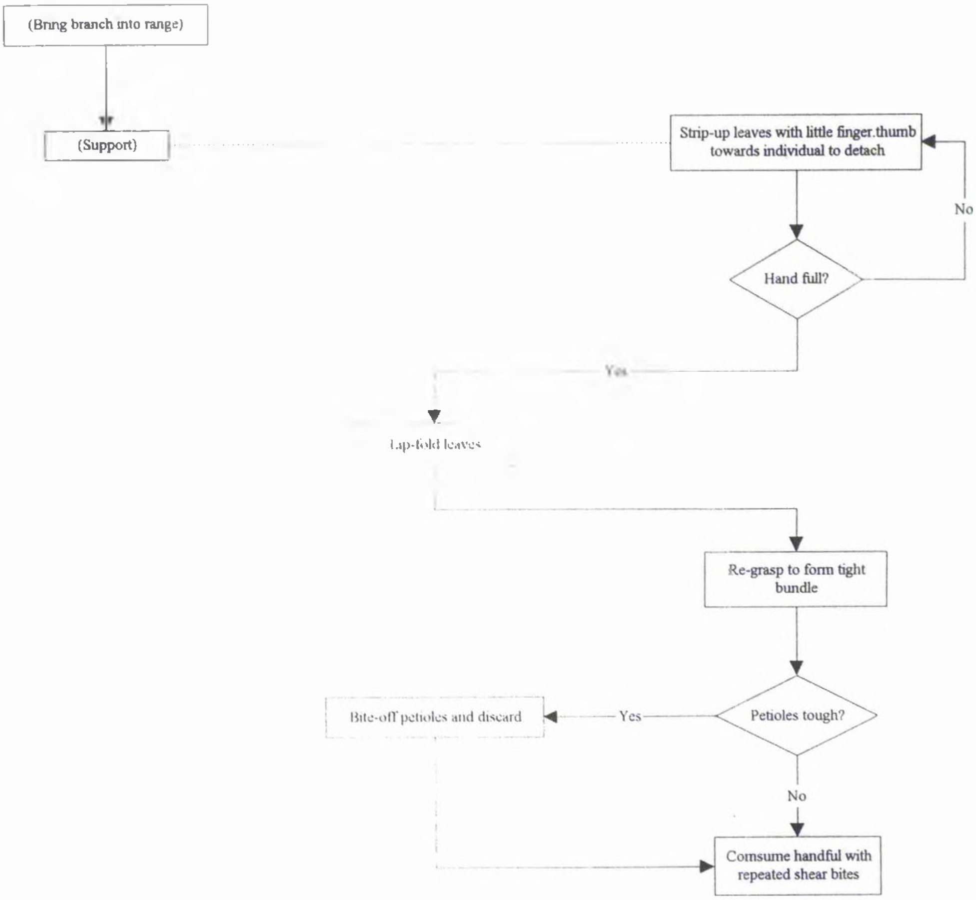
4


(Bring branch into range)
(Support)
Strip-up leaves with little finger towards individual to detach
No
Hand full?
Yes
Petioles tough?
Yes
Bite-off petioles and discard
No
Eat remaining roll of leaf blades with repeated shear bites

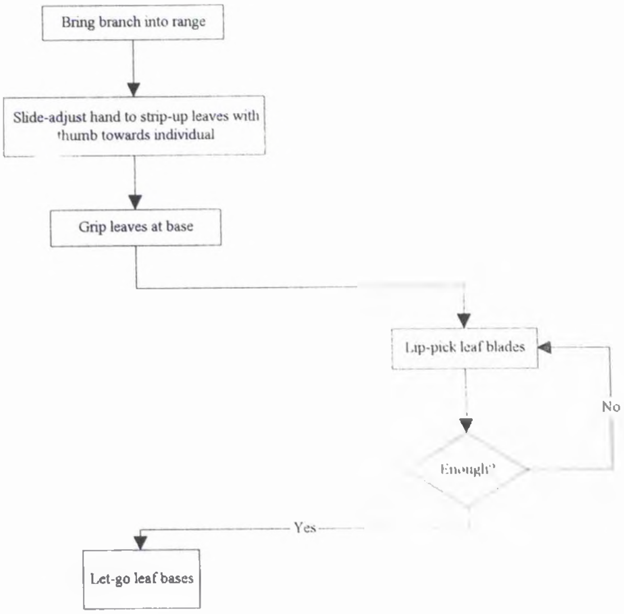
5


(Bring branch into range)
(Support)
Strip-up leaves with little finger/thumb towards individual to detach
No
Hand full?
Yes
Lip-fold leaves above petioles
Gather in with the lips

6


(Bring branch into range)
(Support)
Strip-up leaves with little finger.thumb towards individual to detach
Hand full?
No
Yes
Lip-fold leaves
Re-grasp to form tight bundle
Petioles tough?
Yes
Bite-off petioles and discard
No
Consume handful with repeated shear bites

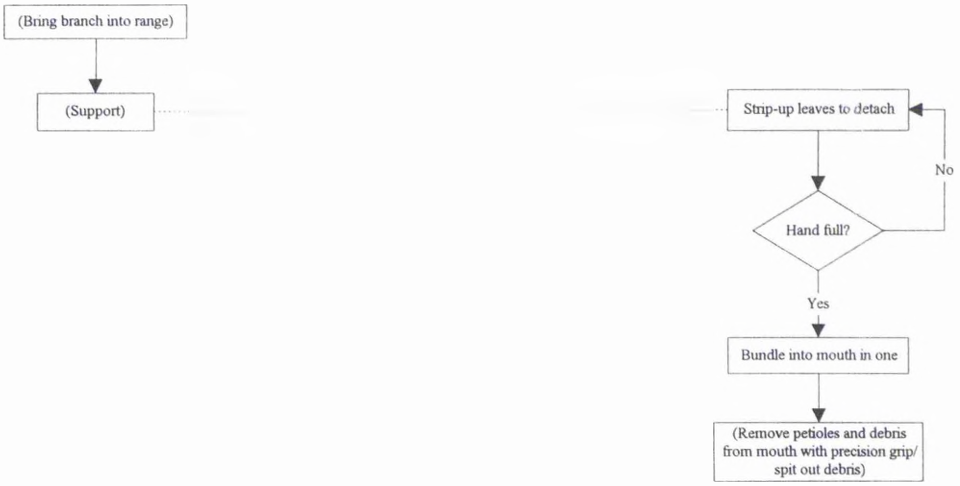
7


Bring branch into range
Slide-adjust hand to strip-up leaves with thumb towards individual
Grip leaves at base
Lip-pick leaf blades
Enough?
No
Yes
Let-go leaf bases

8


(Bring branch into range)
(Support)
Pick individual leaf blade with precision grip
Hand full?
No
Yes
Eat in one

9


(Bring branch into range)
(Support)
Strip-up leaves to detach
Hand full?
No
Yes
Bundle into mouth in one
(Remove petioles and debris from mouth with precision grip/ spit out debris)

10


(Bring branch into range)
(Support)
Strip-up leaves to detach
Hand full?
No
Yes
Comsume leaf roll with shear bites
(Remove petioles and debris from mouth with precision grip/spit out debris)

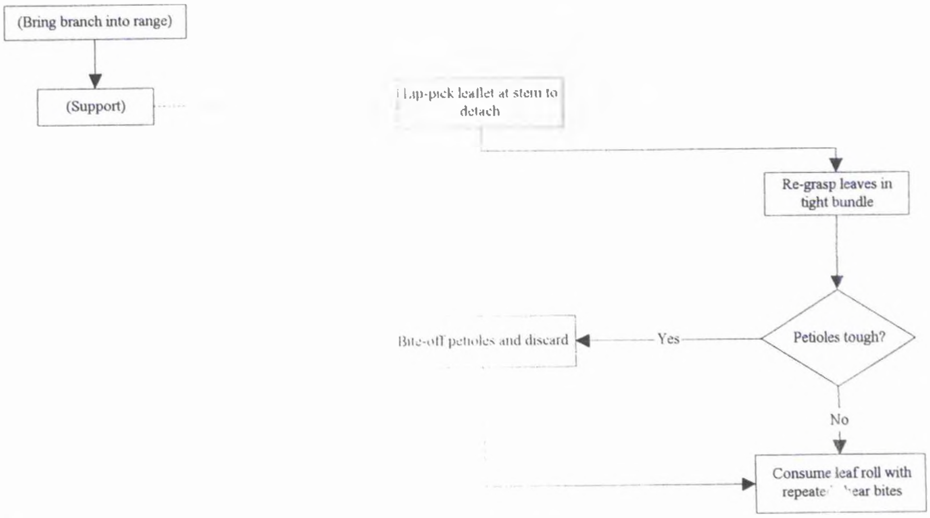
11


(Bring branch into range)
(Support)
Strip-up leaf blade from around midrib/petiole to detach
Bundle leaf blade into mouth in one

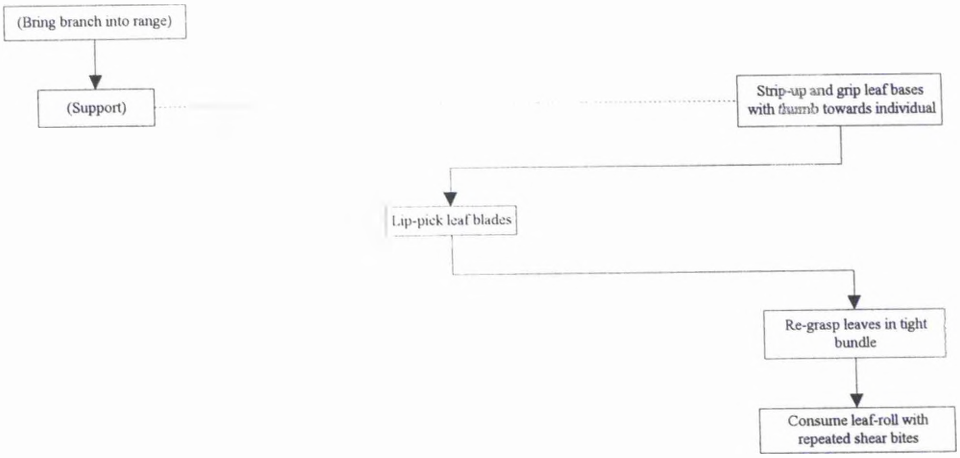
12


(Bring branch into range)
(Support)
Grab handful of leaf blades
Bundle into mouth in one

13

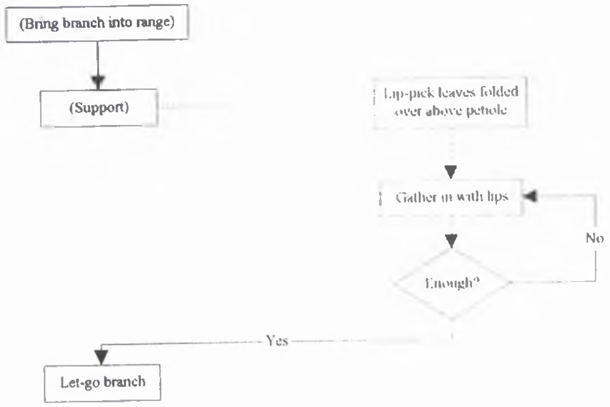

(Bring branch into range)
(Support)
Lip-pick leaflet at stem to detach
Re-grasp leaves in tight bundle
Petioles tough?
Yes
Bite-off petioles and discard
No
Consume leaf roll with repeated shear bites

14

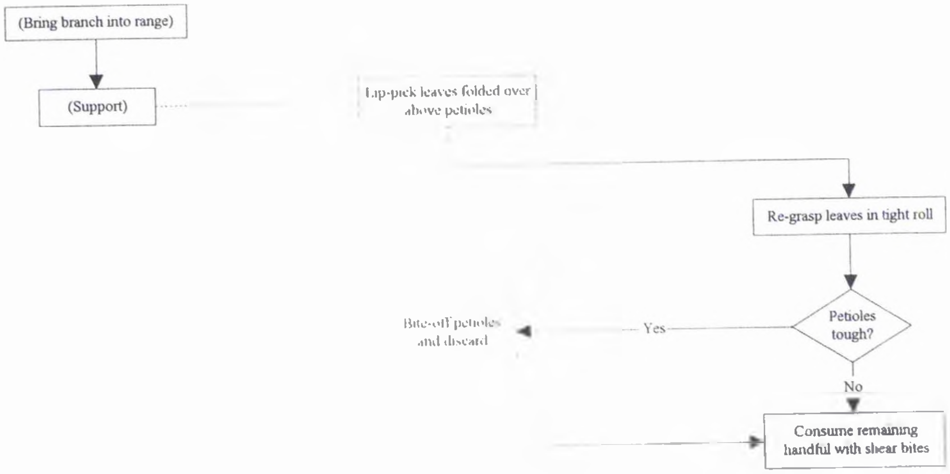

(Bring branch into range)
(Support)
Strip-up and grip leaf bases with thumb towards individual
Lip-pick leaf blades
Re-grasp leaves in tight bundle
Consume leaf-roll with repeated shear bites

Young leaves facultatively eaten with flowers

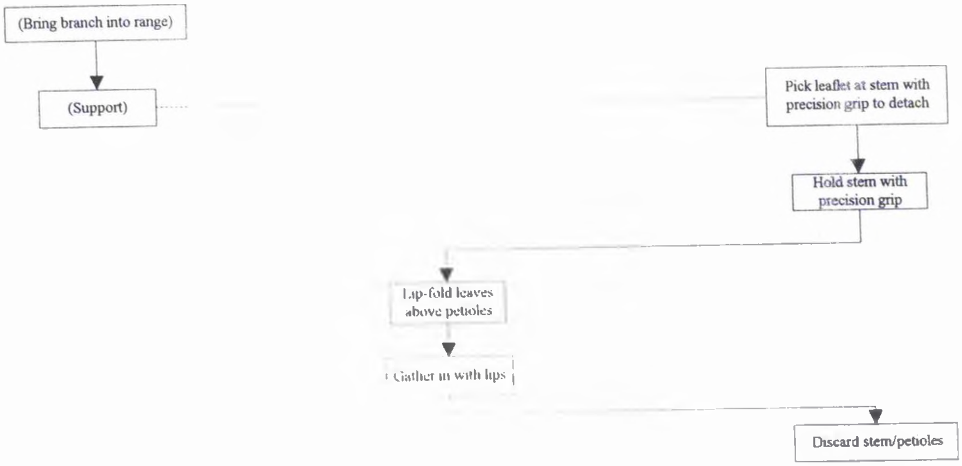
i



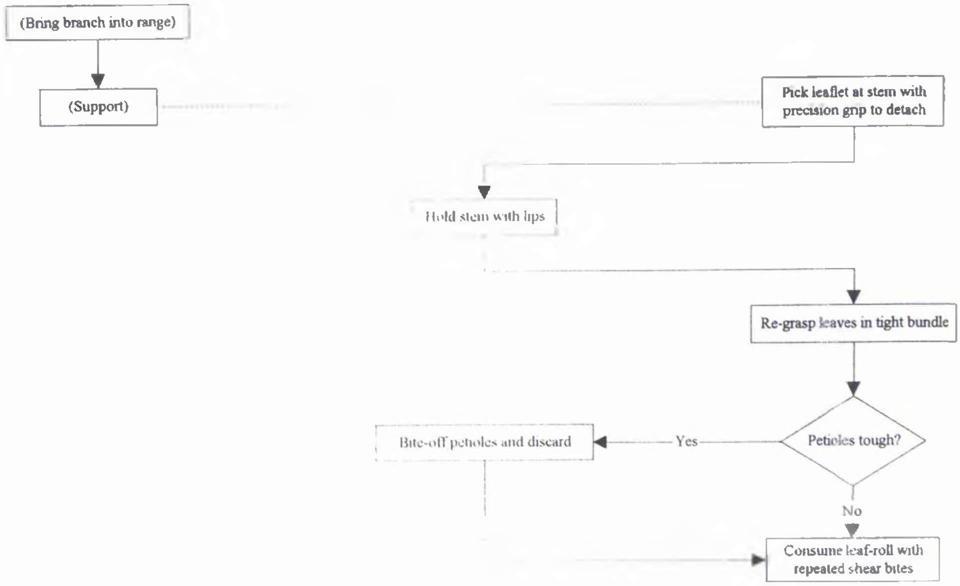
ii



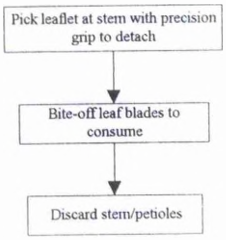
iii



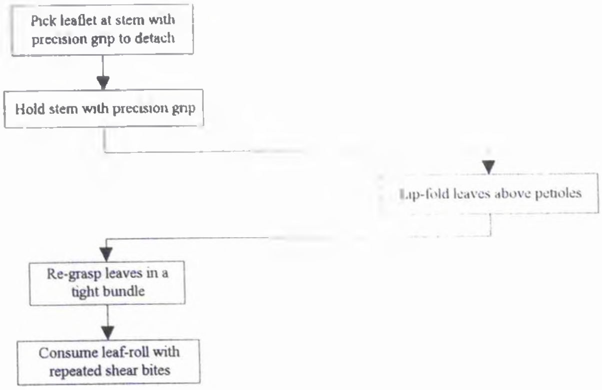
iv


(Bring branch into range)
(Support)
Pick leaflet at stem with precision grip to detach
Hold stem with lips
Re-grasp leaves in tight bundle
Petioles tough?
Yes
Bite-off petioles and discard
No
Consume leaf-roll with repeated shear bites

v


Pick leaflet at stem with precision grip to detach
Bite-off leaf blades to consume
Discard stem/petioles

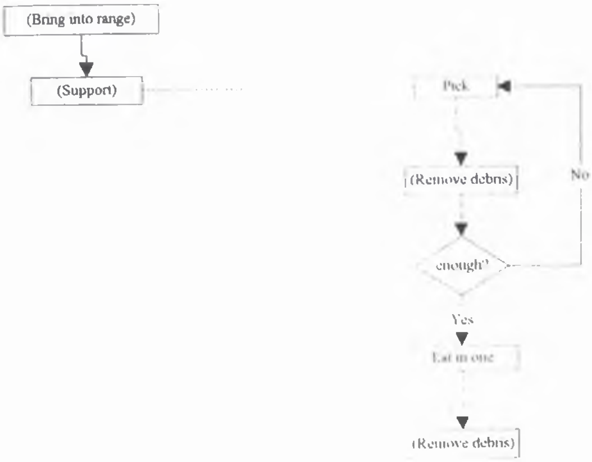
vi


Pick leaflet at stem with precision grip to detach
Hold stem with precision grip
Lip-fold leaves above petioles
Re-grasp leaves in a tight bundle
Consume leaf-roll with repeated shear bites

Appendix IV

TECHNIQUES USED FOR EATING FRUITS OF FICUS MUCUSO

1



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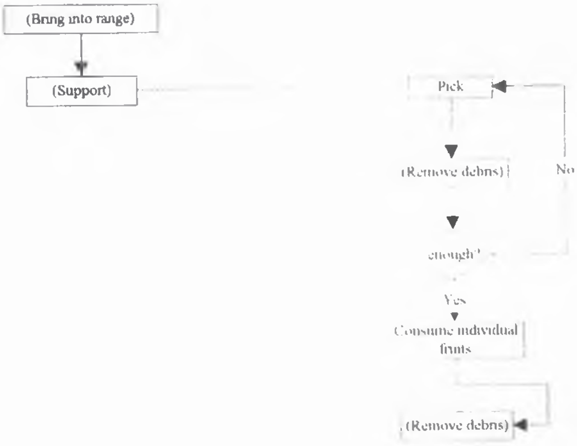

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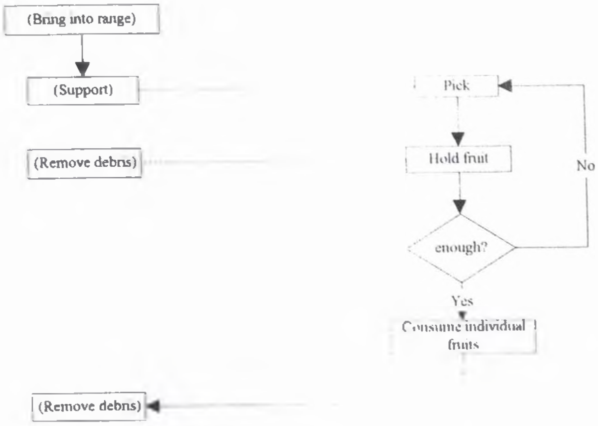


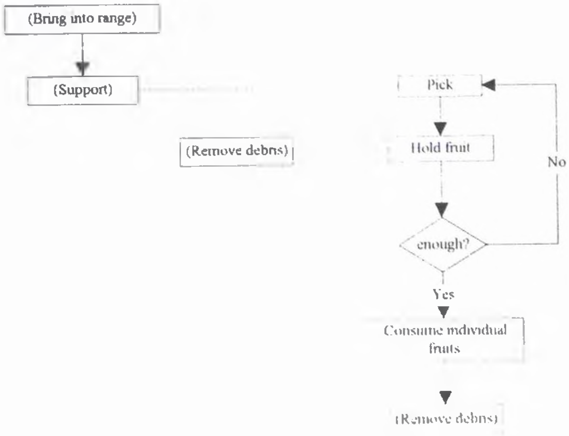
4


(Bring into range)
(Support)
Grab
Eat in one

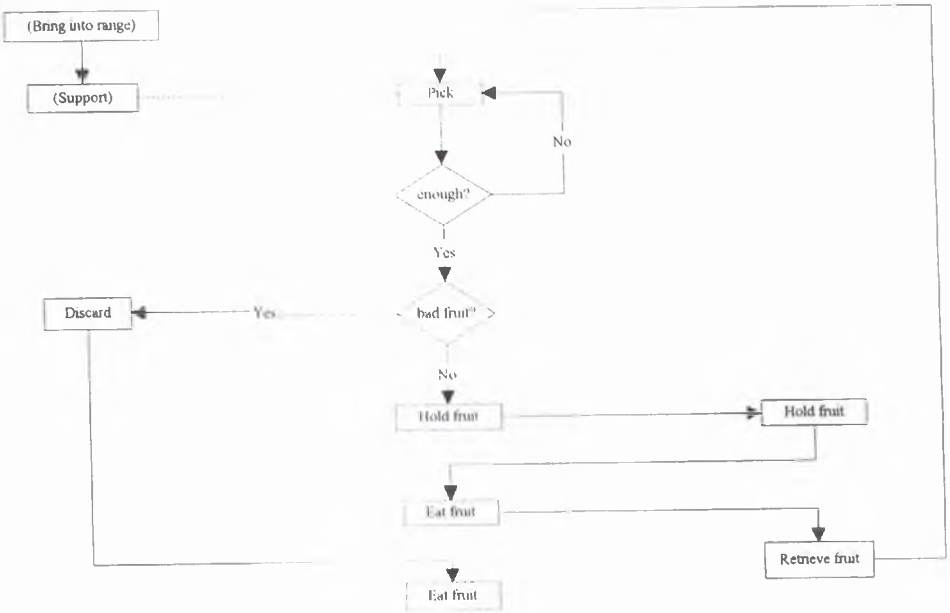
5


(Bring into range)
(Support)
Grab
Eat individual fruits
(Remove debris)

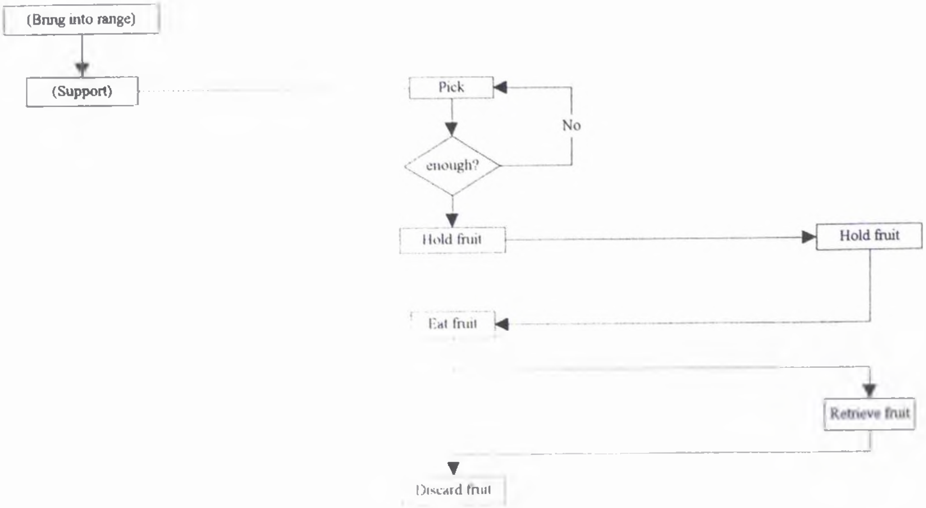
6


(Bring into range)
(Support)
(Remove debris)
Pick
Hold fruit
No
enough?
Yes
Consume individual fruits
(Remove debris)

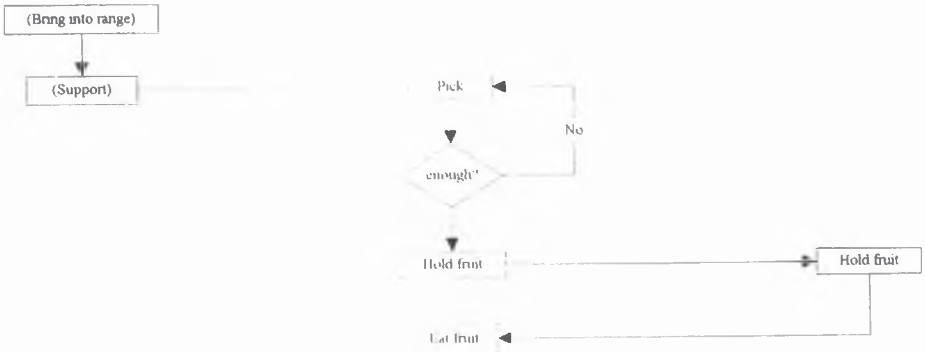
7


(Bring into range)
(Support)
Pick
No
enough?
Yes
Discard
Yes
bad fruit?
No
Hold fruit
Hold fruit
Eat fruit
Retrieve fruit
Eat fruit

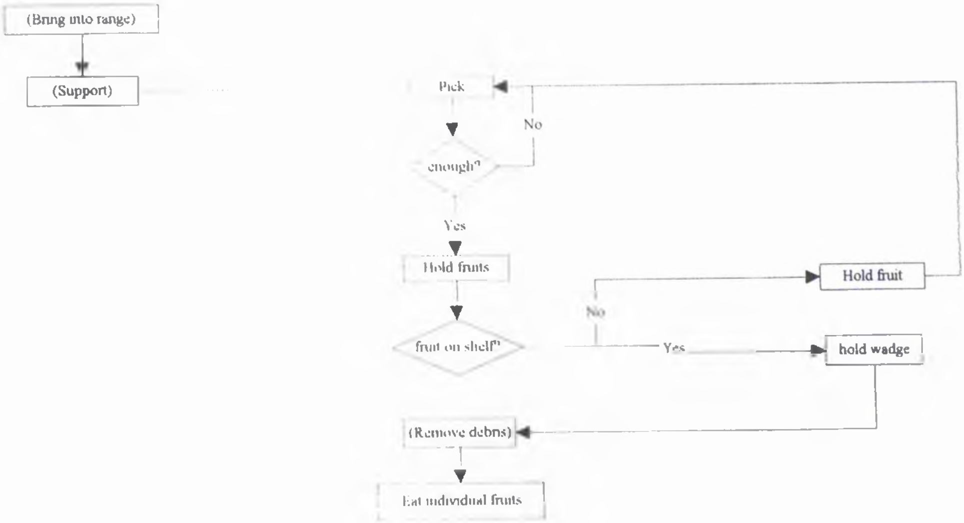
8


(Bring into range)
(Support)
Pick
No
enough?
Hold fruit
Hold fruit
Eat fruit
Retrieve fruit
Discard fruit

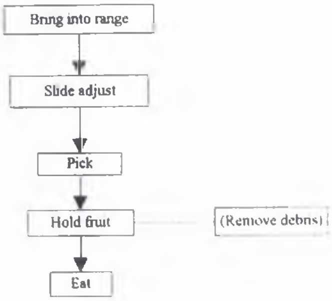
9


(Bring into range)
(Support)
Pick
No
enough?
Hold fruit
Hold fruit
Eat fruit

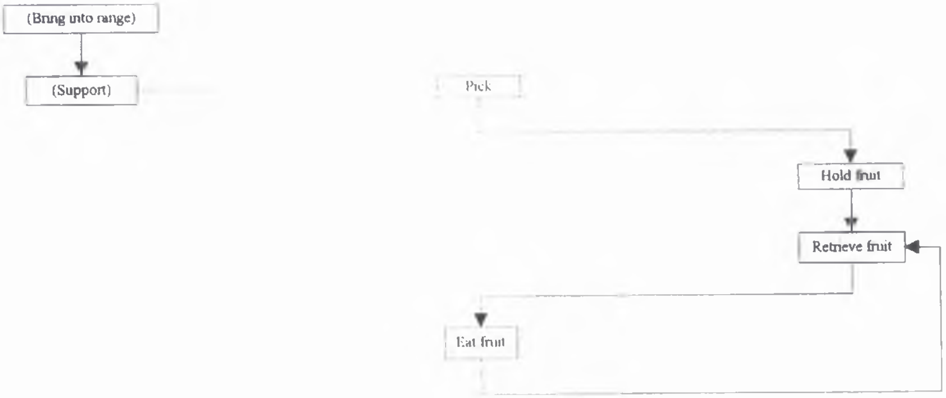
10


(Bring into range)
(Support)
Pick
No
enough?
Yes
Hold fruits
Hold fruit
No
fruit on shelf?
Yes
hold wadge
(Remove debris)
Eat individual fruits

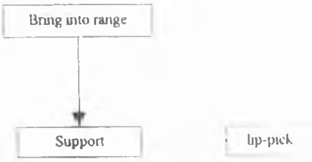
11


Bring into range
Slide adjust
Pick
Hold fruit
(Remove debris)
Eat

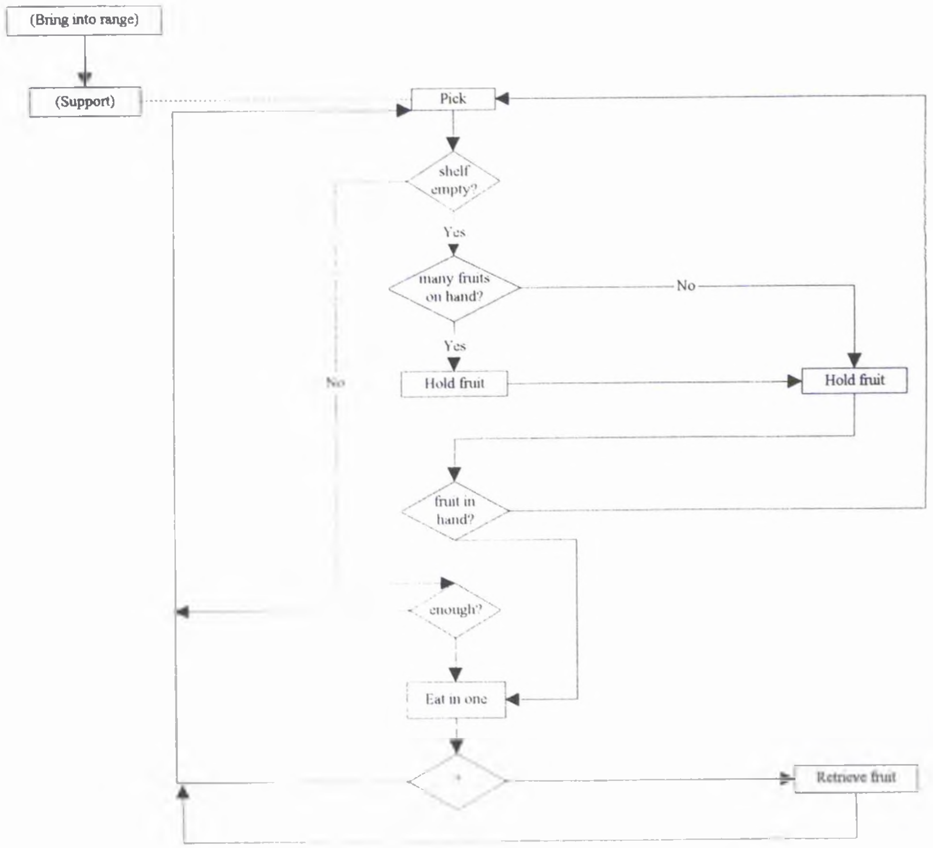
12


(Bring into range)
(Support)
Pick
Hold fruit
Retrieve fruit
Eat fruit

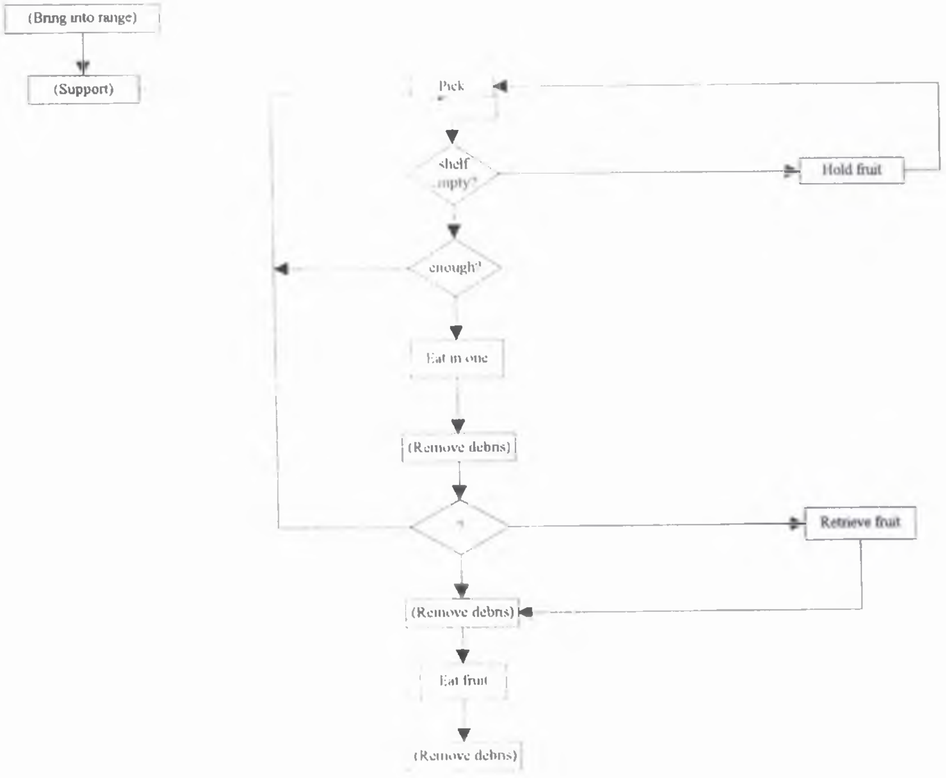
13


Bring into range
Support
lip-pick

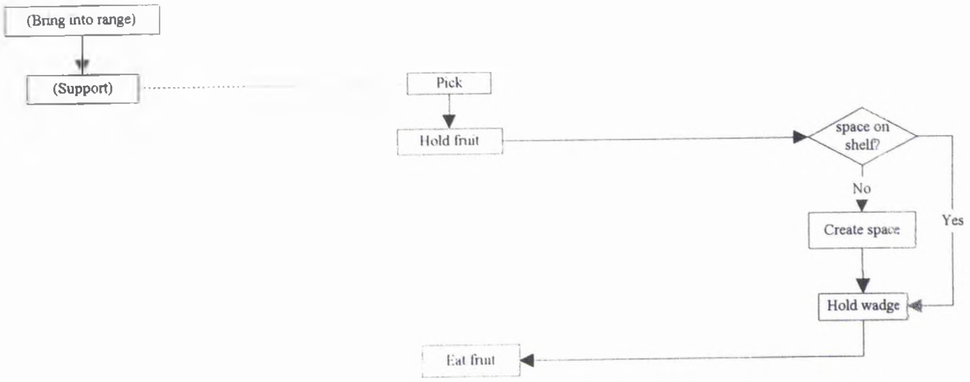
14


(Bring into range)
(Support)
Pick
shelf empty?
Yes
many fruits on hand?
No
Yes
Hold fruit
Hold fruit
No
fruit in hand?
enough?
Eat in one
?
Retrieve fruit

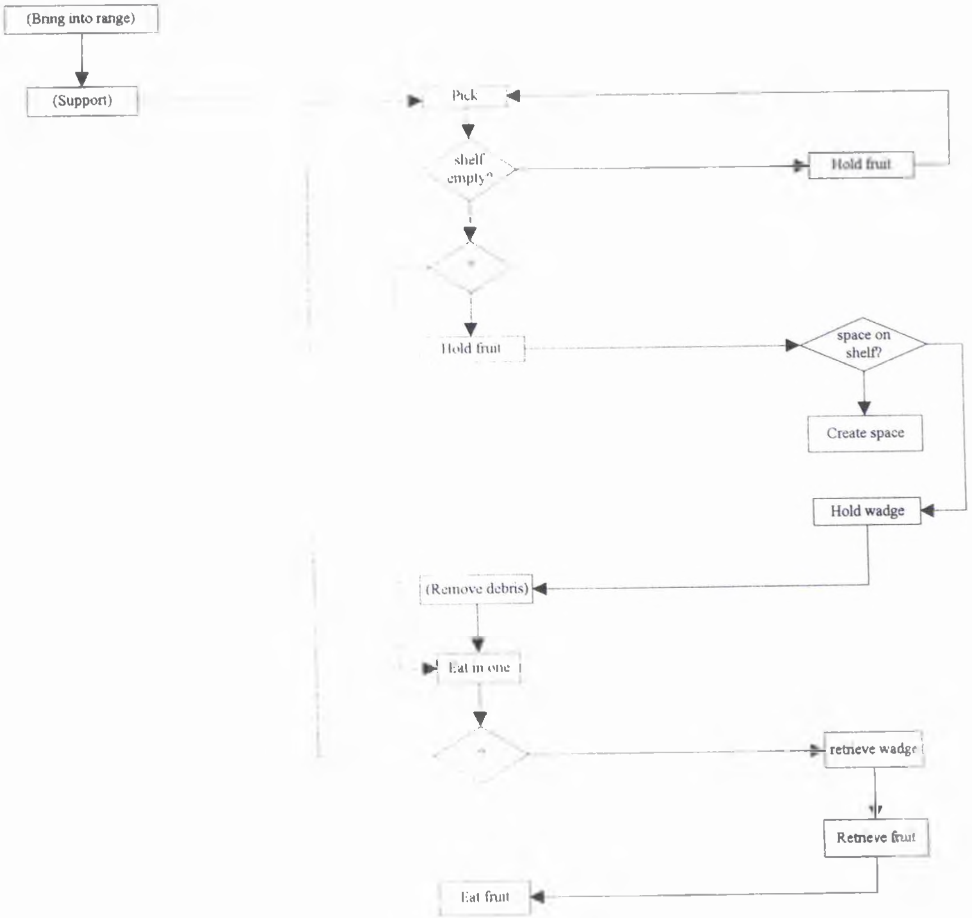
15


(Bring into range)
(Support)
Pick
shelf empty?
Hold fruit
enough?
Eat in one
(Remove debris)
?
Retrieve fruit
(Remove debris)
Eat fruit
(Remove debris)

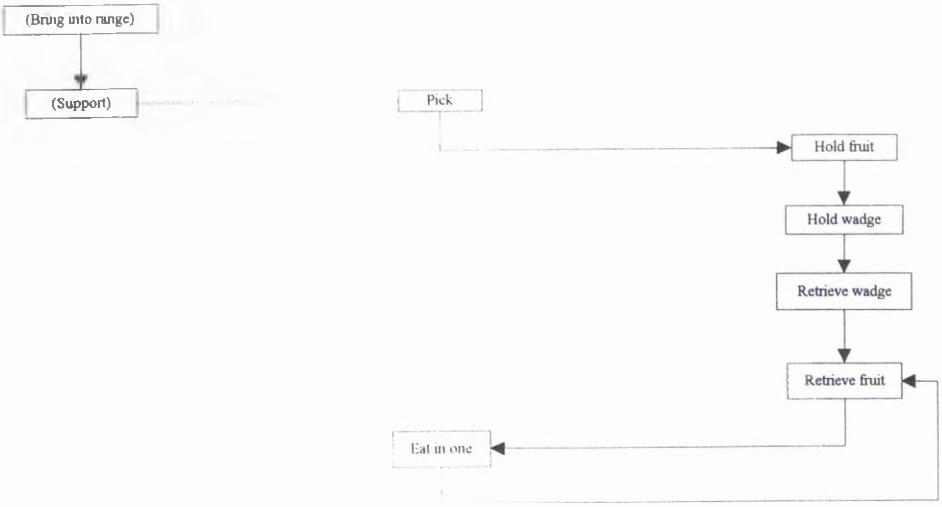
16


(Bring into range)
(Support)
Pick
Hold fruit
space on shelf?
No
Create space
Yes
Hold wadge
Eat fruit

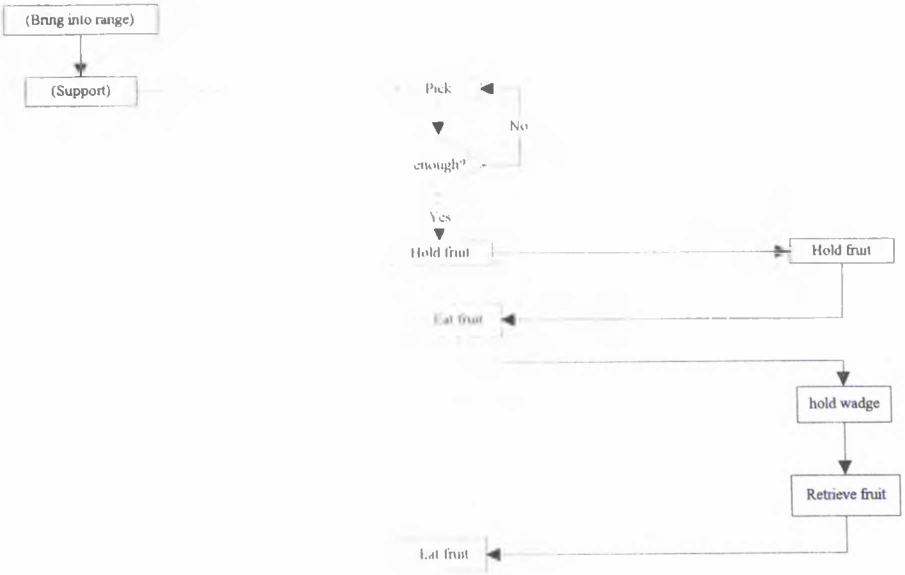
17


(Bring into range)
(Support)
Pick
shelf empty?
Hold fruit
Hold fruit
space on shelf?
Create space
Hold wadge
(Remove debris)
Eat in one
retrieve wadge
Retrieve fruit
Eat fruit

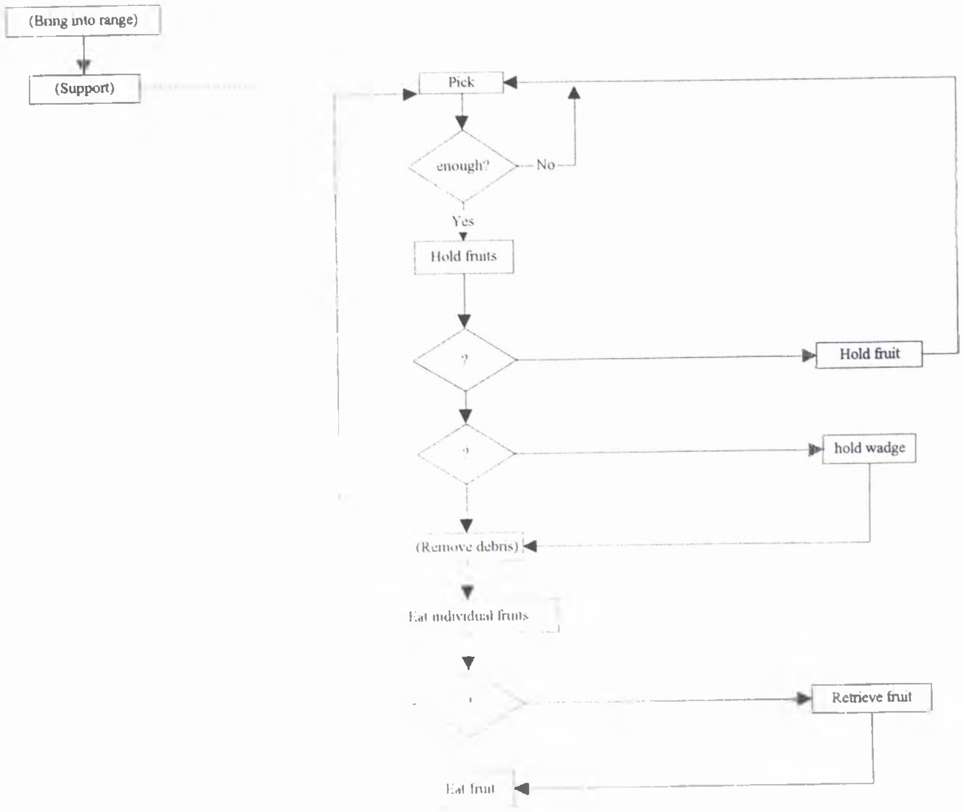
18


(Bring into range)
(Support)
Pick
Hold fruit
Hold wadge
Retrieve wadge
Retrieve fruit
Eat in one

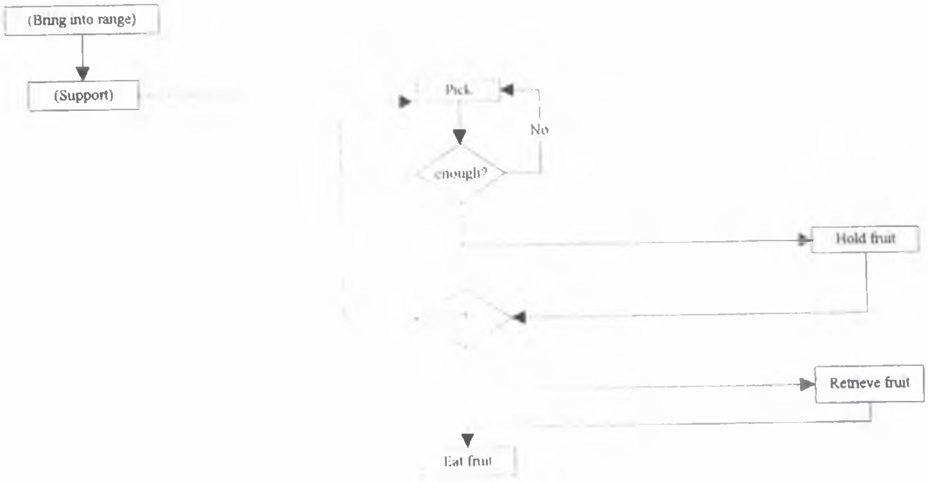
19


(Bring into range)
(Support)
Pick
No
enough?
Yes
Hold fruit
Hold fruit
Eat fruit
hold wadge
Retrieve fruit
Eat fruit

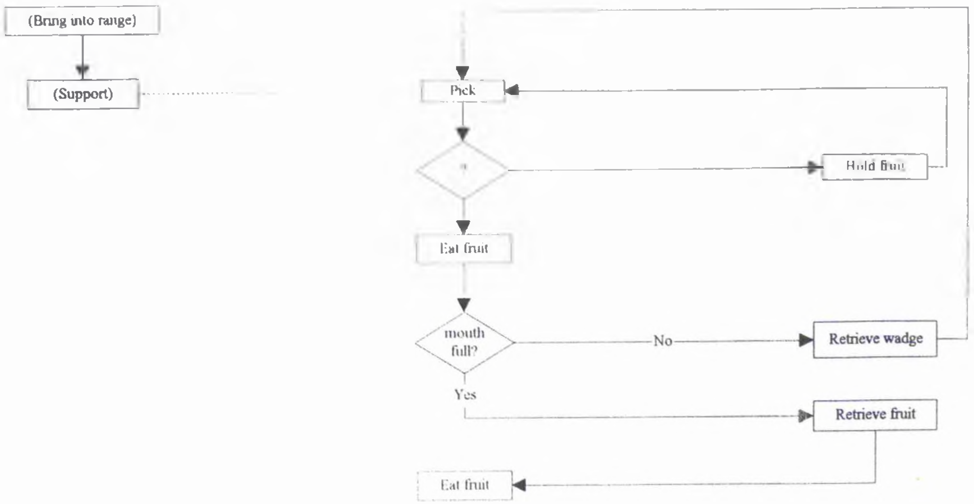
20


(Bring into range)
(Support)
Pick
enough?
No
Yes
Hold fruits
?
Hold fruit
?
hold wadge
(Remove debris)
Eat individual fruits
?
Retrieve fruit
Eat fruit

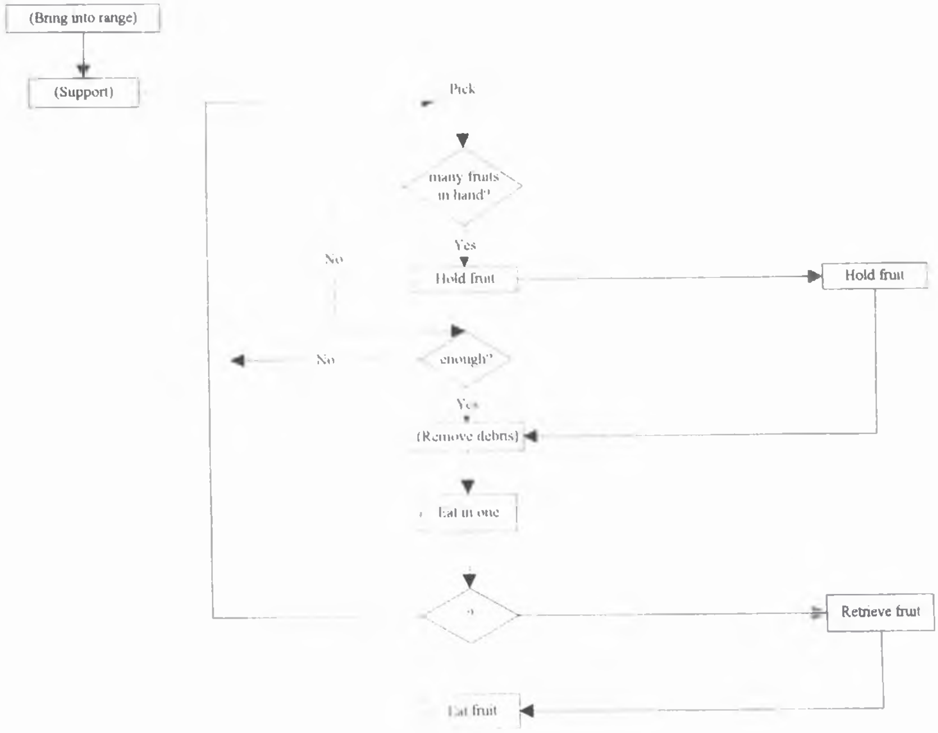
21


(Bring into range)
(Support)
Pick
No
enough?
Hold fruit
?
Retrieve fruit
Eat fruit

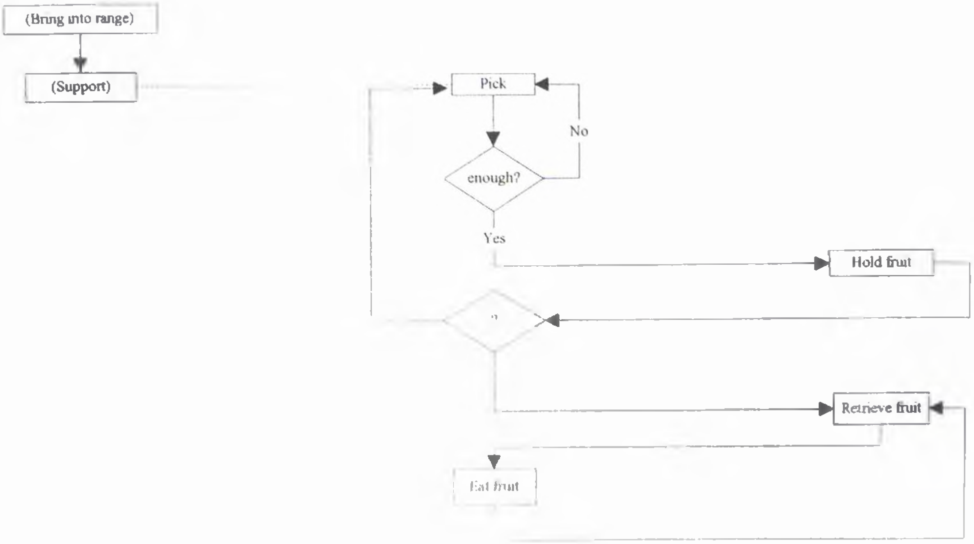
22


(Bring into range)
(Support)
Pick
?
Hold fruit
Eat fruit
mouth full?
No
Retrieve wadge
Yes
Retrieve fruit
Eat fruit

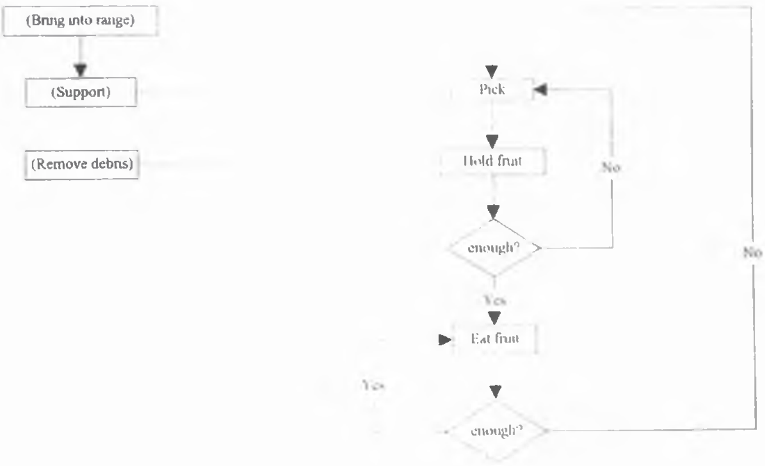
23


(Bring into range)
(Support)
Pick
many fruits in hand?
Yes
No
Hold fruit
Hold fruit
No
enough?
Yes
(Remove debris)
Eat in one
?
Retrieve fruit
Eat fruit

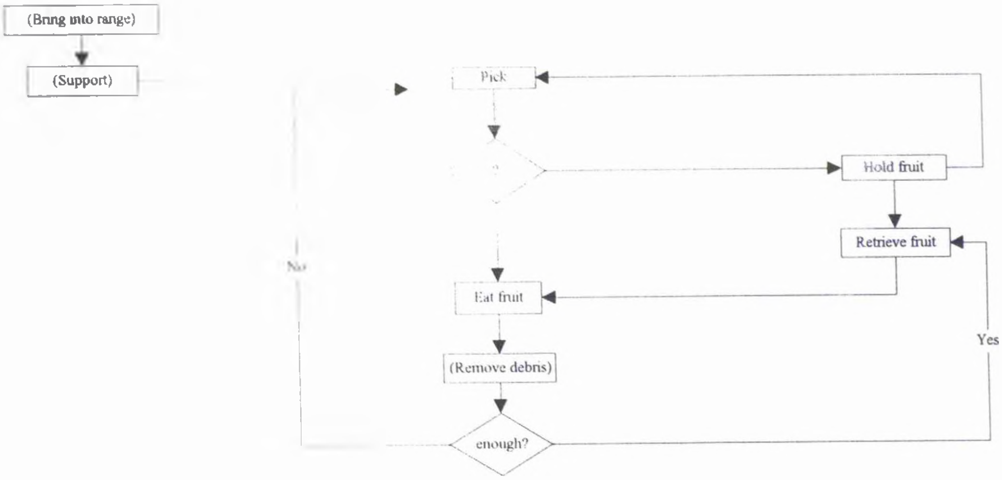
24


(Bring into range)
(Support)
Pick
No
enough?
Yes
Hold fruit
?
Retrieve fruit
Eat fruit

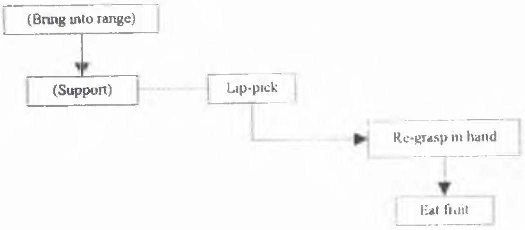
25


(Bring into range)
(Support)
(Remove debris)
Pick
Hold fruit
No
enough?
No
Yes
Eat fruit
Yes
enough?

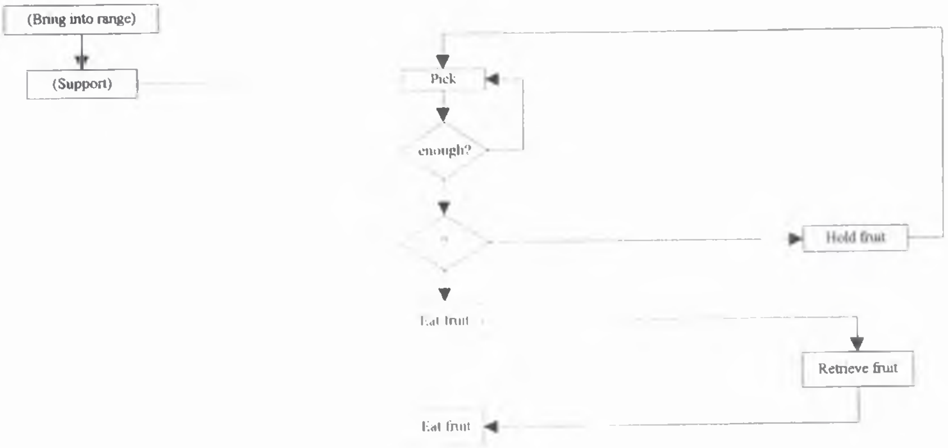
26


(Bring into range)
(Support)
Pick
?
Hold fruit
Retrieve fruit
No
Eat fruit
(Remove debris)
Yes
enough?

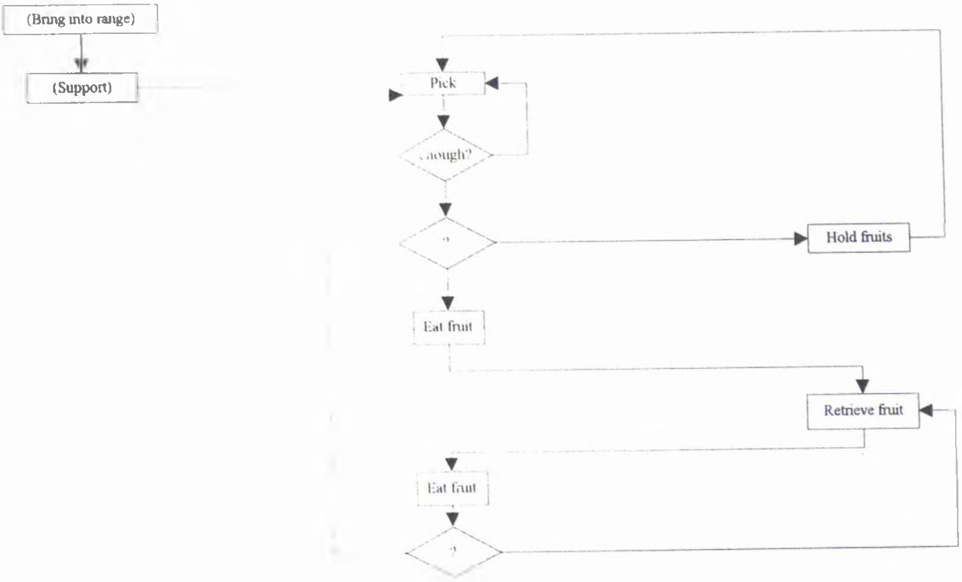
27


(Bring into range)
(Support)
Lip-pick
Re-grasp in hand
Eat fruit

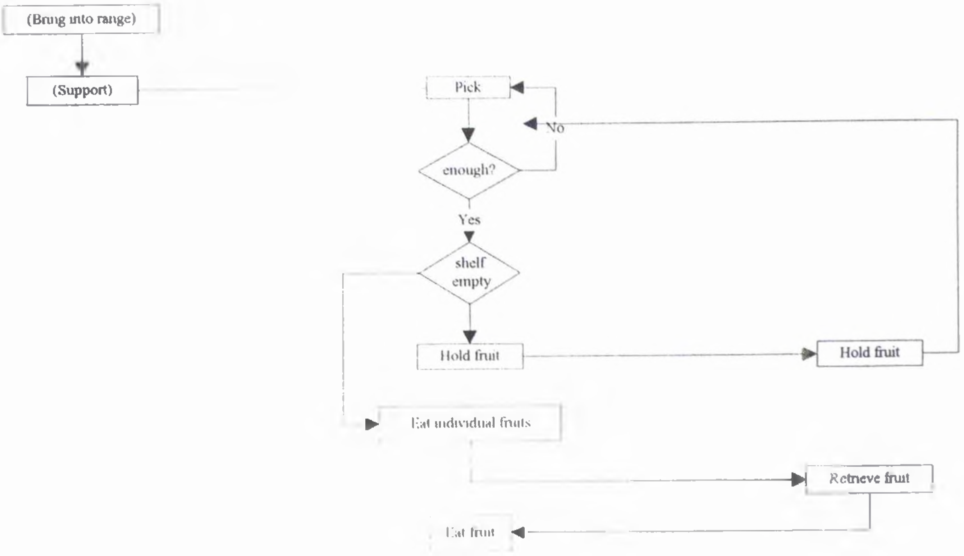
28


(Bring into range)
(Support)
Pick
enough?
?
Hold fruit
Eat fruit
Retrieve fruit
Eat fruit

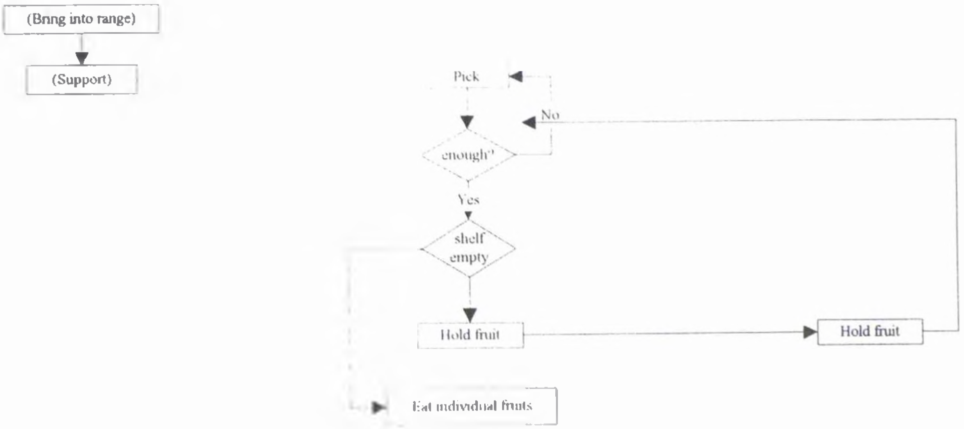
29


(Bring into range)
(Support)
Pick
enough?
?
Hold fruits
Eat fruit
Retrieve fruit
Eat fruit
?

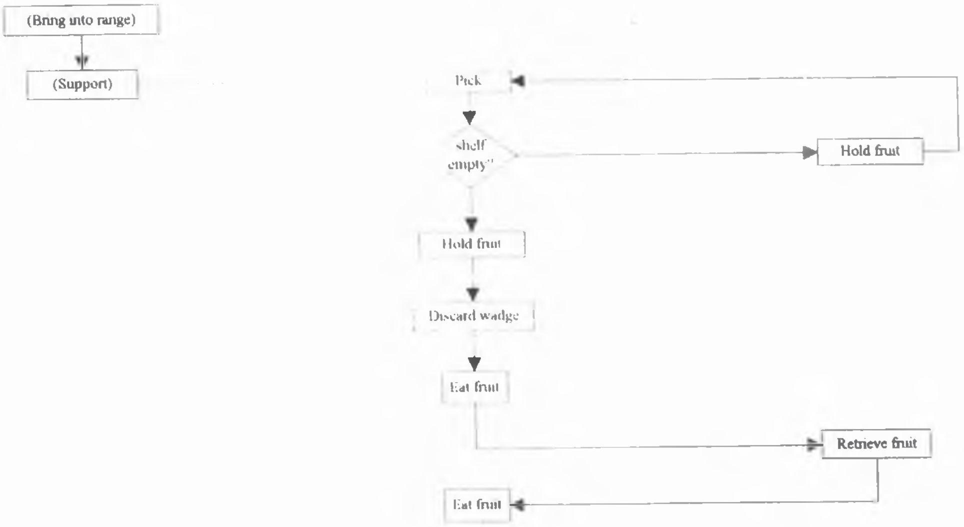
30


(Bring into range)
(Support)
Pick
No
enough?
Yes
shelf
empty
Hold fruit
Hold fruit
Eat individual fruits
Retrieve fruit
Eat fruit

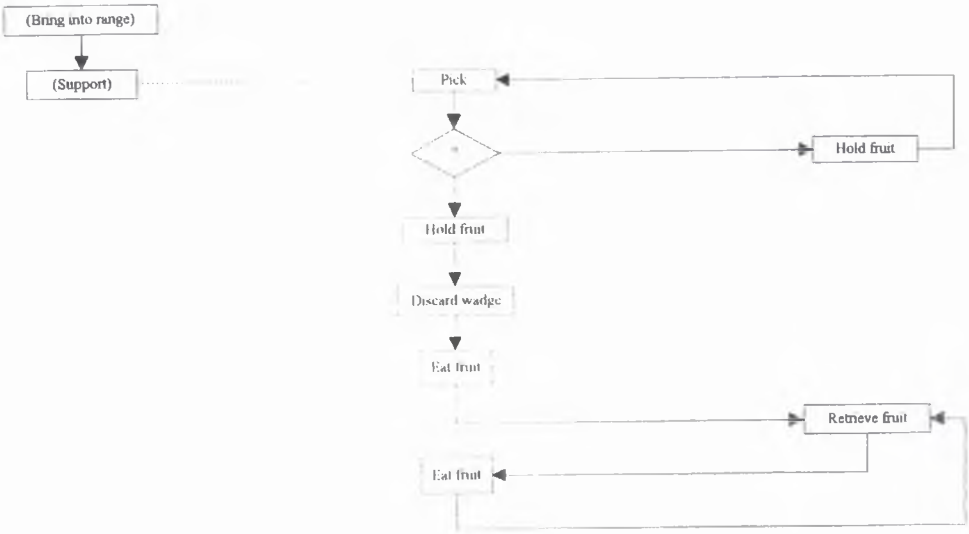
31


(Bring into range)
(Support)
Pick
No
enough?
Yes
shelf
empty
Hold fruit
Hold fruit
Eat individual fruits

32


(Bring into range)
(Support)
Pick
shelf
empty?
Hold fruit
Hold fruit
Discard wadge
Eat fruit
Retrieve fruit
Eat fruit

33


(Bring into range)
(Support)
Pick
Hold fruit
Hold fruit
Discard wadge
Eat fruit
Retrieve fruit
Eat fruit

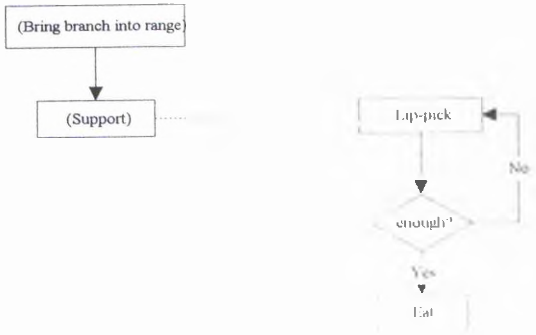
34


(Bring into range)
(Support)
Pick
Hold fruit
Discard wadge
Eat fruit

Appendix V

TECHNIQUES USED FOR EATING FRUITS OF FICUS SUR

1



2

3

4


(Bring branch into range)
(Support)
Grab fruits
Eat in one

5


(Support)
Bring branch into range
Slide adjust
Pick
Eat

6


(Support)
Bring branch into range
Slide adjust
Grab fruits
Eat in one