CHAPTER SIXTEEN

Effect of Snare Injuries on the Fig-Feeding Behavior of Chimpanzees of the Budongo Forest, Uganda

Behavioral Adaptations and Long-Term Implications

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INTRODUCTION

Permanent injuries to chimpanzees (*Pan troglodytes*) as a result of snares have been recorded across their geographic range (Quiatt *et al.*, 2002). In August 1997, over 20% of the Sonso community of chimpanzees in the Budongo Forest, Uganda, showed some form of upper or lower limb injury. These injuries are extreme in the sense that they involve either the loss of a hand or foot or else partial or complete paralysis of at least one limb (Waller & Reynolds, 2001). The ability of an injured individual to overcome their injuries is paramount to

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their survival, and the fact that such a large proportion of this community has sustained and survived major limb trauma suggests that these individuals are indeed able to compensate for their injuries.

A particularly important consequence of upper limb injuries would be feeding difficulties, likely to be specific to those foods that require a degree of manual skill in order to process. Studies on complex plant processing by gorillas and chimpanzees injured by snares (Stokes & Byrne, 2001; Byrne & Stokes, 2002) have shown them to be capable of implementing novel actions with their injured limb to execute feeding techniques that resemble those of able-bodied individuals in their overall structure. This was interpreted to mean that feeding techniques require learning, by program-level imitation, from the mother, who is normally able-bodied. In contrast, individual actions can be flexibly modified by individual learning, so compensation following injury is at the level of specific actions rather than overall plan. As a result of their ability to compensate, injured individuals were not found to show a significant reduction in feeding efficiency. The behavioral flexibility needed to compensate so effectively may be relatively unusual among animals. All simian primates are large-brained (Passingham, 1981), and there is now a growing body of evidence to suggest that environmental pressures have acted specifically on great apes to enhance their cognitive flexibility. Observations of skills shown when apes hunt (e.g., Teleki, 1973; Nishida, 1979; Boesch & Boesch, 1989), make tools (e.g., Goodall, 1964; Nishida 1973; Boesch & Boesch, 1983; McGrew 1992), manually process physically defended plants (Russon, 1998; Byrne *et al.*, 2001; Stokes & Byrne, 2001; Corp & Byrne, 2002;), or overcome locomotor problems associated with large body size (Povinelli & Cant, 1995), lend empirical support to the possibility of an unusual flexibility in behavior among great apes.

Arboreal fruit feeding by able-bodied chimpanzees has also been shown to demand skill (Stokes & Byrne, in review). While relatively simple to process, arboreal fruit presents a problem of a different sort for chimpanzees, one that is largely determined by environmental conditions such as quality and size of the fruit patch and the physical characteristics of the fruiting tree. These, in turn, are exacerbated by the large body size of chimpanzees and the social costs to them of foraging with conspecifics. In feeding on arboreal fruits, chimpanzees were found to show considerable behavioral flexibility in positioning themselves in relation to the constraints of the particular species of tree in which they were foraging (Stokes & Byrne, ibid). Injury is likely to exacerbate the problems of accessing arboreal food resources that are faced by able-bodied individuals, and preliminary studies have found that injured individuals exhibit significant differences in their positional behavior while feeding, compared with able-bodied individuals: injured chimpanzees preferring the canopy over the middle or lower portions of the tree, in which there are fewer secondary branches available for support (Reynolds *et al.*, 1996).

In this paper we systematically examine the effects of injury on arboreal fruit feeding by chimpanzees. We focus our attention on figs (*Ficus* sp.), which are a year-round staple food source for the Sonso community of chimpanzees, representing 50% of feeding time; of which 39% is taken up by two species, *Ficus mucuso* and *Ficus sur* (Stokes, 1999; see also Newton-Fisher, 1999a). Figs are a valuable food item, energy-rich with adequate protein, containing essential amino acids—in the form of dead fig wasps contained within the fig (Wrangham *et al.*, 1993). Figs are straightforward to process, and the key to efficient feeding is almost certainly maximizing food intake rate rather than special food preparation skills. In spite of largely asynchronous fruiting cycles, food patches are highly dispersed in space and time, and feeding competition within a single tree is likely to be high. Furthermore, within a particular fruiting tree, the size, orientation, and location of fruit varies considerably.

We present here new data on the fig-feeding behavior of injured individuals and compare with existing data on able-bodied chimpanzees (Stokes & Byrne, in review). We examine behavioral adaptations to injury through a descriptive analysis of postural and positional behavior and feeding technique (*sensu* Stokes & Byrne, 2001). In addition, we assess the extent to which injured individuals have compensated for injury, through a comparison of feeding efficiency with able-bodied individuals. Finally, we discuss the long-term implications for reproductive fitness.

METHODS

Study Site

The Budongo Forest Reserve lies in Western Uganda between 1°35′–1°55′ N and 31°18′–31°42′ E at an altitude of 1050 m. It is described as medium-altitude, semideciduous forest (Eggeling, 1947). Budongo Forest serves as the primary production forest in Uganda, and produced timber on a sustainable basis from the mid-1920s until the decline of the sawmill in the 1970s. The Sonso study site is found in the N (Nyakafunjo) 3 logging concession, and was last exploited between 1947 and 1952. It is composed of typical mixed-species forest, largely the result of previous forest management practices, and dominated by *Celtis mildbraedii*, *C. zenkeri*, *Khaya anthotheca*, *Chrysophyllum albidum*, and *Funtumia elastica* (Eggeling, 1947; Plumptre, 1996).

Study Community

The study was conducted between August 1997 and September 1998, at the beginning of which the study community consisted of 51 known individuals: 25 adults (13 males and 12 females), 8 subadults (3 males and 5 females), 11 juveniles (6 males and 5 females), and 8 infants (4 males and 4 females). Age classes were determined according to Goodall (1986). Eight individuals have permanent injuries to the hands, forelimbs, or feet. These comprise seven adults (three males and four females) and one subadult female. In all but one case, these injuries are the likely result of encounters with snares set on the forest floor. The one exception is an adult female with a congenital deformity to the foot (Waller, 1995). During the study a new injury was sustained by a juvenile female who lost her hand to a snare (personal observation). Certain adult females were irregularly observed on the periphery of the known community range, and are not considered here. Moreover, in order to set aside age-dependant variation in feeding skill (Corp & Byrne, 2002), juveniles and infants were not sampled. In total, 23 able-bodied individuals (15 adults [9 males and 6 females] and 8 subadults [4 males and 4 females]) and all 8 injured individuals were sampled.

Nature and Extent of Injuries

The nature and extent of injuries is highly idiosyncratic across the populations and described in detail elsewhere (Stokes, 1999; Stokes & Byrne, 2001). Table 1 provides a brief summary of each individual injury and classifies the nature of injury in three groups: injuries to (a) one upper limb, (b) both upper limbs, and (c) to one lower limb. However, it should be noted that these categories are largely based on morphology rather than functional limitations.

Feeding Tasks

We consider here two fig species, *F. sur* and *F. mucuso*, each of which illustrates a suite of relatively independent feeding tasks.

Fruits of *F. mucuso* are about the size of a golf ball and distributed in large drupes hung along wide horizontal branches. Processing is simple procurement,

Table 1. Description and classification of individual injuries

Category	Age–sex	Description
Injuries to one upper limb		
Kalema	Adult female	Right hand paralyzed. The hand is rigidly hooked at the wrist and the fingers are flexed and immobile. The whole hand is emaciated and wasted.
Muga	Adult male	Missing right hand from point distal to the wrist. Majority of the wrist joint is retained and capable of some flexion.
Kikunku	Adult male	Missing left forelimb from point midway up the forearm.
Kewaya	Subadult female	Right hand paralyzed. The wrist is extremely hooked and considerably stretched and twisted round the forearm. The hand is wasted and the fingers contorted so that the middle finger lies overlapping the forefinger. No voluntary movement of the hand.
Injuries to two upper limbs		
Zana	Adult female	Left hand is extremely wasted and the fingers are partially clawed and incapable of voluntary movement. Thumb has retained some function, but is incapable of flexion. Right wrist functions normally but the hand is missing digits 1–4. Thumb retains normal function.
Tinka	Adult male	Most of the muscles of the left wrist are paralyzed, the wrist is hooked and weakened and movement severely restricted. Digits 1–4 are in permanent flexion although the thumb has retained some function. Paralysis of the right wrist and hand is complete and voluntary movement impossible, although the digits can be passively extended.
Injuries to one lower limb		
Kigere	Adult female	Missing right foot from point just above the ankle
Banura	Adult female	Congenital deformity of left lower limb below the ankle, akin to "club foot." Foot enlarged and incapable of voluntary movement.

Description of injuries taken from Stokes (1999) and Stokes (2001), and from original drawings by Waller (1995).

but the relatively large size of the fruit appears to limit ingestion rate. To maximize fig intake, chimpanzees pick several figs from a particular patch and transfer them either to the other hand or to a foot while more fruits are accumulated. A chimpanzee may hold up to four fruits at any one time, which are subsequently retrieved to be processed individually. If displaced from a feeding patch, a chimpanzee will carry the accumulated fruit with them. Wadging is frequently observed and wadges are also transferred to another part of the body, while more fruits are accumulated. By retaining wadges, a chimpanzees can prolong and maximize nutrient extraction.

The fruits of *F. sur* are smaller than *F. mucuso* (~15 mm diameter), and thus food ingestion rate is less tightly constrained. Moreover, patches of figs are distributed vertically along the main trunk of the tree and thus limbs are required for postural support rather than for accumulating fruits. Chimpanzees exhibit short concentrated bouts of feeding, using a variety of feeding postures to access different parts of the tree. Processing is also simple procurement, but chimpanzees may elicit bimanual food processing in order to pull out-of-reach, fruit-bearing branches into range, although this is achieved at the expense of postural support.

Data Collection

Observations were made on the behavior of chimpanzees consuming both fig species. We used three different measures of feeding behavior: (a) position within the tree, (b) posture, and (c) structure of feeding technique.

Position

Scan sampling (Altmann, 1974) was used to record the activity and position of each individual in the feeding group every 15 min. The subject's position was distinguished as either canopy, apical branches of the tree, lower, main trunk of the tree and the first branch fork, and middle, all other parts of the tree.

Posture

Body posture was noted at the beginning of each feeding bout. We defined a feeding bout as beginning when an individual first touched the food, and ending when interrupted or terminated by switching to another activity, by moving away from the food item, or periods of inactivity of 10 s or more (see Appendix of Stokes & Byrne, 2001, for full glossary of terms). Feeding activities included procuring, manipulating, ingesting, and wadging food items.

We categorized posture on the basis of how many limbs were occupied in postural support. The following categories of posture (in order of decreasing stability) were distinguished: seated (SE), animal seated and feeding within arms reach; seated-reaching (SR), animal seated but with one hand in support while leaning to bring food item into range; one-arm support (1), animal suspended by one upper limb only, with remaining limbs available for feeding; bipedal support (2), animal bipedal and supporting with one upper limb while feeding with the other upper limb; and tripedal support (3), animal suspended by three limbs (upper or lower), with only one limb available for feeding.

Feeding Technique

Sequence sampling (Altmann, 1974) was used to record individual actions during feeding. A handful formed the basic unit of sequential analysis, comprising the sequence of events between picking a fruit and placing it in the mouth. For any one handful, processing was considered to be made up of sequences of individual elements (Byrne & Byrne, 1993). For each handful, we recorded the sequence of elements, and for each element the body part used: left or right hand, both hands together, left or right foot, or mouth. Any regularly used sequence of elements, co-coordinated so that the whole performance serves to process a handful of food, was defined post hoc as a technique (*sensu* Stokes & Byrne, 2001).

For *F. sur*, we further distinguished among techniques, according to whether the elements involved bimanual or monomanual co-ordination within a single handful. Techniques were also subdivided on the basis of postural support. In the case of *F. mucuso*, another part of the animal's body (usually an upper or lower limb) was frequently enlisted in holding a food item while another food item was being processed; this included both fruits and wadges, and we use the term "shelf" for this. Techniques were distinguished by the extent to which food items were shelved in a single handful (no shelf, fruit only, wadge only, fruit and wadge) and by the number of food items shelved during any one handful. More than one body part could be used as a shelf at a single time, and simultaneous use of limbs for shelving and processing were recorded during each handful.

Table 2. Summary of data collected

	Ficus mucuso		*Ficus sur*	
	Able-bodied	Injured	Able-bodied	Injured
Feeding posture				
N(individuals)[a]	16	8	23	7
N(bouts)	65	76	341	145
Median no. bouts/individual	4.5 (1–7)	5.5 (1–14)	15.0 (1–36)	14.0 (2–23)
Feeding position				
N(individuals)[a]	23	8	23	8
N(scans)	750	303	882	410
Median no. scans/individual	32.6 (4–53)	36.5 (18–68)	38.3 (12–141)	39.5 (1–58)
Feeding sequence				
N(individuals)[a,b]	13	8	15	7
N(handfuls)	290	361	985	865
Median no. handfuls/individual	26 (10–38)	41.5 (15–92)	58 (25–133)	123 (77–201)

[a] *F. sur* was more common than *F. mucuso* and more frequently fed on, thus more individuals were sampled on this food type.
[b] Only sampled individuals with 10 or more handfuls were included here for analysis of feeding sequence.

For analysis of feeding technique for both food types, we subdivided injured chimpanzees into those with injuries to one upper limb, those with injuries to both upper limbs, and those with injuries to lower limbs. Table 2 summarizes the sample size available for able-bodied and injured individuals for each feeding task and for each behavioral measure.

Feeding Efficiency

In addition to feeding behavior, feeding efficiency was measured by calculating rates of processing from data collected on a hand-held computer (Hewlett Packard 200LX). Key presses were used to record the time at which each handful of processed food was placed in the mouth, and intervals between successive key presses were used to measure the time taken to process a single handful in any given bout. The total bout length was also recorded. In the case of *F. mucuso*, the processing rate for each handful was divided by the mean number of fruits processed simultaneously (as recorded during observations of feeding technique), to indicate relative rates of food intake. However, the combination of two data sets reduced the total sample size in calculation of feeding efficiency for this food type.

Data Analysis

Goodness of fit tests were used to compare postural and positional patterns between able-bodied and injured individuals for each food type. Comparison of feeding techniques between able-bodied and injured individuals presents a number of statistical problems largely concerned with small sample sizes (see Stokes & Byrne, 2001, for discussion). To avoid these problems, variation in usage of a technique among the able-bodied population was used to estimate the likelihood of a deviant frequency occurring by chance in an injured individual. For the frequency of use of each technique, 95% confidence intervals were calculated from scores obtained from able-bodied individuals. Injured individuals whose score fell outside these intervals were considered to vary significantly in their usage of that technique.

RESULTS

Feeding Position and Posture

Injured individuals differ significantly from able-bodied individuals in their feeding position when feeding on *F. sur* ($X^2 = 16.841$, df $= 2$, $P < 0.0001$, Figure 1A). Injured individuals concentrate their feeding in the middle section of the tree (68%, compared to 55% by able-bodied individuals) and spend less time feeding in the canopy and in lower sections. In contrast, no significant difference in feeding position were found between injured and able-bodied individuals when feeding on *F. mucuso* ($X^2 = 0.388$, df $= 2$, $P = 0.824$, Figure 1B).

A significant difference was also found between able-bodied and injured individuals in their use of postures when feeding on *F. sur* ($X^2 = 39.425$, df $= 4$, $P < 0.0001$, Figure 2A). Injured individuals show a reduction in their use of different feeding postures and spend more time feeding from a seated posture (55%), than do able-bodied individuals (27%). As with feeding position, no significant difference in feeding posture was found between injured and able-bodied individuals when feeding on *F. mucuso* ($X^2 = 2.401$, df $= 2$, $P = 0.301$, Figure 2B).

When feeding on *F. sur*, bout length was significantly longer for injured individuals than for able-bodied individuals (mean bout length: injured $= 90 \pm 75$ s, able bodied $= 57 \pm 18$ s, t-test corrected for unequal variance $t = -2.261$, df $= 34$, $P < 0.05$). Injured individuals therefore relocate or change their

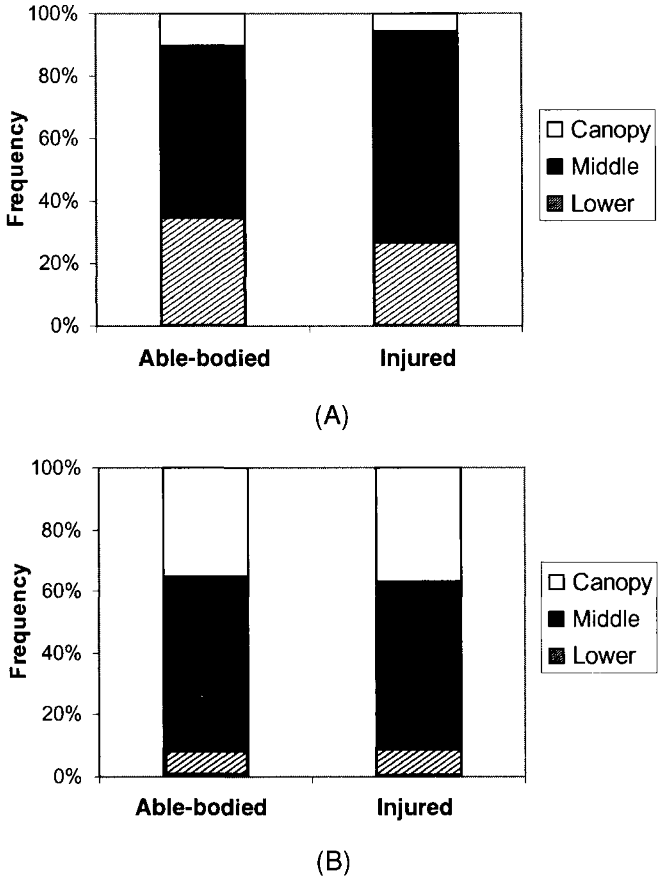

Figure 1. (A) Effect of injury on positional behavior when feeding on *F. sur*. (B). Effect of injury on positional behavior when feeding on *F. mucuso*.

feeding posture less frequently than able-bodied individuals, indicating reduced maneuverability in the tree. Once again, there was no significant difference in bout length between able-bodied and injured individuals when feeding on *F. mucuso* (mean bout length: injured = 159 ± 105 s, able-bodied = 203 ± 107 s, *t*-test $t = 1.070$, df = 26, $P = 0.294$).

Feeding Technique

Ficus sur

A total of six different techniques for processing *F. sur* have been identified for able-bodied individuals, five of which incorporate bimanual coordination. The

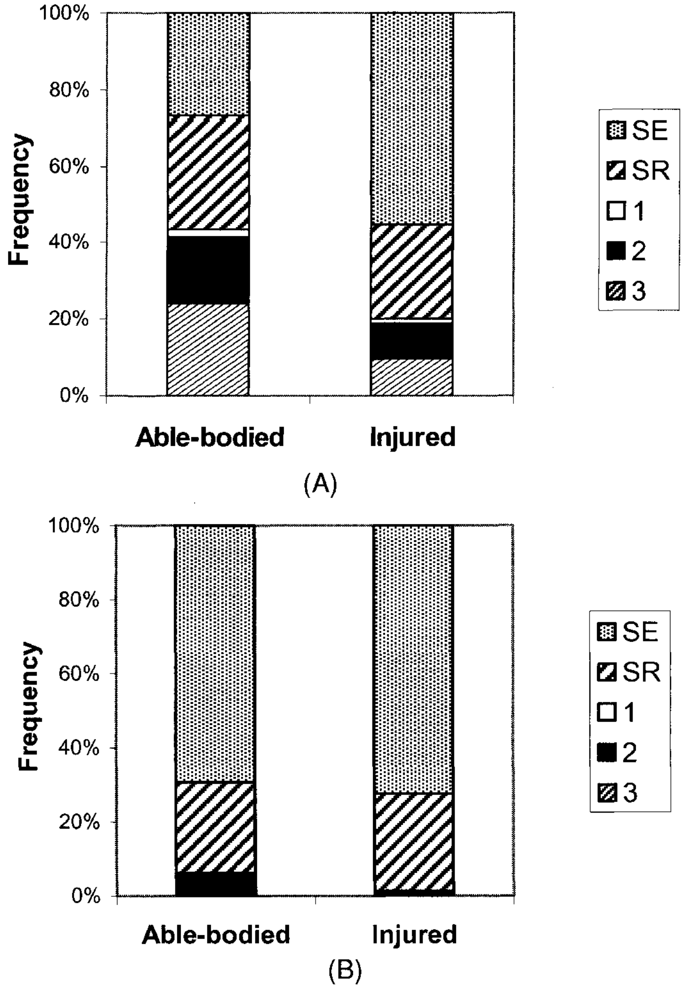

Figure 2. (A) Effect of injury on postural behavior when feeding on *F. sur*. See text for details: SE: seated; SR: seated-reaching; 1: one-arm support; 2: bipedal support; 3: tripedal support. (B) Effect of injury on postural behavior when feeding on *F. mucuso*. See text for details: SE: seated; SR: seated-reaching; 1: one-arm support; 2: bipedal support; 3: tripedal support.

frequency of use of each of monomanual and bimanual techniques by injured individuals is shown in Figure 3. Individuals with injuries to one and both upper limbs show a significant reduction in their use of bimanual techniques compared to able-bodied individuals. What is perhaps more surprising is that these individuals still incorporate bimanual processing into the majority of their techniques (mean 85% of techniques for all injured individuals pooled).

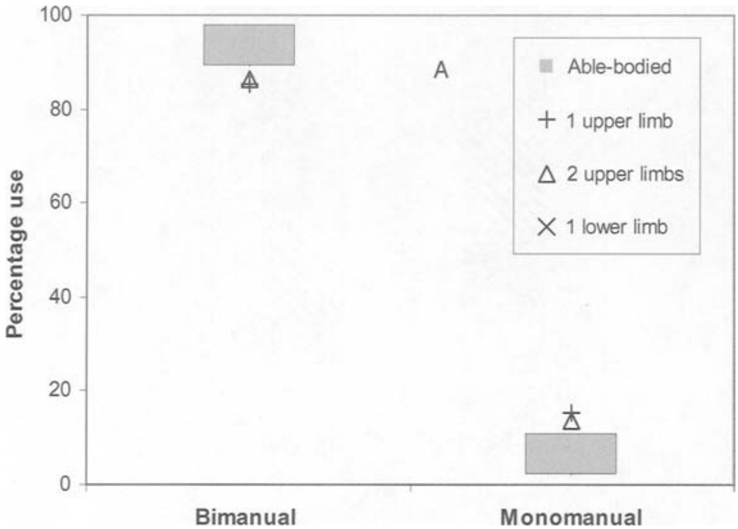

Figure 3. Effect of injury on the use of monomanual and bimanual techniques in processing fruits of *F. sur*. Injured individuals are divided into three categories according to nature and extent of injury. Grey bars represent 95% confidence intervals for frequency of use by able-bodied individuals. Only scores of injured individuals that fall outside these intervals are shown.

Able-bodied individuals rarely use their feet in bimanual food processing. In only 2.1% (0.5–3.7) of sequences were the feet used in combination with an upper limb, always to support a fig branch or bring a fig branch into range while the hand picked off individual fruits and almost exclusively (95%) when the other upper limb was tied up in postural support. Individuals with injuries to one or both upper limbs use their feet significantly more than able-bodied individuals (5.4%) and, perhaps more important, use their feet in food processing exclusively from a seated posture (100%), when no postural support is required. Furthermore, we observed injured individuals implementing novel elements with the injured limb to execute a bimanual feeding technique. In feeding on *F. sur*, injured chimpanzees used their injured upper limbs to pull a branch into range by the crook of the elbow and to support the branch between the forearm and the side of the body while the able limb picked off individual fruits (95% of all bimanual sequences).

Ficus mucuso

A total of 34 different sequences for processing *F. mucuso* have been identified for able-bodied individuals. We distinguished techniques for injured individuals

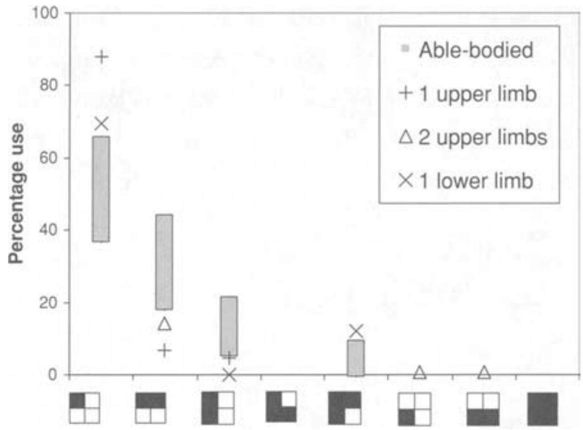

Figure 4. Effect of injury on limb coordination in processing fruits of *F. mucuso*. Each pattern represents the combination of upper and lower limbs used in feeding at any one time during a particular handful for all techniques. Left and right are used ambiguously. See figure for explanation of bars.

in processing fruits of *F. mucuso* and classified each according to the degree of shelf-use (no shelf, fruit shelved, wadge shelved, fruit and wadge shelved). The use of each group of techniques by injured individuals varies with the nature of injury. Individuals with one upper limb injury prefer to utilize a simple pick-and-eat process rather than techniques that shelve fruits (able-bodied: mean = 87.8%, 80.8–94.6; single upper limb injuries: 99.2%). However, individuals with injuries to both upper limbs shelve fruits and wadges at similar frequencies to able-bodied chimpanzees (fruit shelved: mean = 8.2%, 0.5–16.0; wadge shelved: 2.1%, –0.1–5.3; fruit and wadge shelved: 1.7%, –0.1–3.6).

Figure 4 shows the role of each limb in processing fruits of *F. mucuso*. Injured individuals differ in their use of a particular pattern of limb coordination according to injury types. Those individuals with injuries to one upper limb almost exclusively (88%) use their able upper limb in processing. In contrast, individuals with both upper limbs injured use their feet more, always to shelve fruits (1% of sequences for two individuals with both upper limbs injured, compared to zero occurrence for 23 able-bodied individuals).

Feeding Efficiency

No significant effect of injury on processing times was found for either *F. sur* or *F. mucuso* (*F. sur*: able-bodied individuals mean $= 6 \pm 1$ s/handful, injured individuals pooled mean $= 6 \pm 1$ s/handful, *t*-test $t = -0.871$, $df = 20$, $P = 0.39$;

F. mucuso: able bodied individuals mean = 22 ± 7 s/fruit, injured individuals pooled mean = 25 ± 8 s/handful, *t*-test $t = -0.713$, df = 11, $P = 0.491$). Sample sizes were too small to statistically examine feeding efficiency by injury type. In the case of *F. mucuso*, able-bodied individuals can process up to four fruits simultaneously, although 84% (±14) of handfuls are processed without shelving fruits (i.e., one fruit processed at a time). As expected, injury reduces the number of fruits that can be processed at the same time, and injured chimpanzees process a mean 94% (±6) of handfuls with only one fruit.

DISCUSSION

Injured individuals compensate remarkably well in processing complex foods (Stokes & Byrne, 2001). However, the analyses of this chapter have shown that in a feeding task that requires agility and maneuverability in order to rapidly procure fruits that are by themselves relatively simple to process, injured individuals show a marked deviation from their able-bodied counterparts. The breadth of feeding postures available to an injured chimpanzee is reduced, as is the number of limbs available for temporarily holding fruits before processing ("shelving") when feeding on *F. mucuso* and consequently the number of fruits that can be processed simultaneously.

In feeding on the leaves of *Broussonetia papyrifera*, injured chimpanzees retained the basic structure of the feeding technique observed in the able-bodied population, and compensated at the level of individual elements, where they employed novel use of the injured limb in order to execute each stage of the overall program (Stokes & Byrne, 2001; Byrne & Stokes, 2002). Fig processing does not require a complex program of actions, but instead presents a suite of dynamic challenges. In dealing with these challenges, injured individuals were able to modify their behavior to an extent, although no individual successfully compensated for reduced flexibility in postural behavior. Compensation was largely through the use of novel elements by the injured limb in bimanual processing. These novel elements require neither considerable muscle strength nor manual dexterity, and are likely to play an important role in enabling injured individuals to exploit bimanual processing techniques. Feet were also used more frequently than is observed in able-bodied individuals, both as a shelf for processing *F. mucuso* and to complement an upper limb in processing fruits of *F. sur*. For able-bodied chimpanzees feeding on *F. sur*, adapting to the constraints of a particular tree represents a trade-off between bimanual processing and postural support. Both strategies serve to effectively increase access to food patches, the former by bringing food into the range of the animal, and the latter by bringing the animal into the range of the food. The trade-off between the two strategies therefore provides an opportunity for injured individuals to compensate for their reduced maneuverability in the tree, by increasing their usage of bimanual techniques. However, in most cases, the frequency of use of bimanual techniques fell below even that of able-bodied individuals and was frequently at the expense of postural support. In general, therefore, injured chimpanzees showed a considerable reduction in their behavioral plasticity to environmental constraints.

Perhaps by their very nature, feeding tasks of this sort produce a great deal of idiosyncrasy in behavioral response. Here, behavioral variation within the injured population were observed in the preferred choice of technique and the nature of individual elements, but not in the structure of the technique itself, probably because the nature of the fruit largely determined what little needed to be done to process it. For injured chimpanzees, this variation was largely associated with the nature and extent of injury. In feeding on *F. mucuso*, chimpanzees with injury to a single upper limb appeared to "overcompensate" with the able limb and repertoires of feeding techniques were notably reduced as a result. In contrast, individuals with injuries to both upper limbs showed a more diverse repertoire of techniques, either through increasing the use of feet in bimanual processing and "shelving," or the use of novel elements with the injured limb. In the two cases of double upper limb injury examined here—Tinka and Zana—this was facilitated by the fact that both injured limbs retained some able functions, and that these functions were complementary across the two hands. For example, the right hand of Tinka retained a passive grasping and support function, while the left hand retained precision control of the thumb and index finger. In this way Tinka could pick an individual fruit with the left hand and place it into the passive grip of his right hand as a "shelf," before accumulating a second fruit. In this way he functioned as an able-bodied individual.

In measures of feeding efficiency, however, injured individuals did not show significantly lower processing rates than their able-bodied counterparts. Given that processing is a simple pick-and-eat process, at least for *F. sur*, this is perhaps not surprising. However, for *F. mucuso* feeding efficiency also takes into account the number of fruits that can be processed simultaneously, which we know to be lower for injured individuals, and thus it is perhaps at first glance surprising that this was not reflected in the results. It is worth noting here that able-bodied chimpanzees process the majority of handfuls of *F. mucuso* with a simple pick-and-eat sequence. Although shelving does occur, it is relatively rare and most likely a direct response to scramble competition within the tree. If levels of feeding competition are driving performance, then the disparity between able-bodied and injured individuals will most likely be observed at times of peak scramble competition over food. A similar argument can be made for *F. sur*, in that accessibility to food patches will be at a premium when levels of scramble competition in a tree are high. Those individuals who are able to make the most accurate judgments with regards to how to position themselves and adapt their feeding strategy, both with respect to the amount of food available and the presence of conspecifics are likely to have the highest success in feeding. Accordingly, the two males with the highest social ranking in the population (both able-bodied) recorded the two highest averages for the number of fruits of *F. mucuso* processed simultaneously. With the physical limitations imposed by injury, and limited capacity to compensate manually for loss of function, injured individuals have a higher risk of losing access to high quality food patches when scramble competition is high, and individual fitness will likely be compromised as a result.

Preliminary studies on injured individuals suggest that injury does reduce the social ranking of chimpanzees (Reynolds *et al.*, 1996). The effects of injury on feeding efficiency are therefore likely to be compounded 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 *F. sur*, as the large group size in the tree at any one time, coupled 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. Furthermore, the fact that injured individuals are unable to maneuver about the tree to the same extent as able-bodied chimpanzees would exacerbate the need for visual monitoring in keeping track of a conspecific's movements.

The long-term implications of injury on fig feeding may be mitigated to an extent by the prevalence of figs in the diet of Budongo chimpanzees. Figs are considered a staple, rather than fallback, food at Budongo and are consumed year-round (Newton-Fisher, 1999). From studies on activity budgets over a period of 14 months, injured chimpanzees were found to spend significantly more time feeding on *F. sur* than did able-bodied individuals (Stokes, 1999)—this flexibility in daily activity largely facilitated by the dynamics of a fission–fusion society. Therefore, while injury has a profound effect on positional and postural capabilities, the long-term negative implications for reproductive fitness may be buffered by the relative spatial and temporal abundance of figs in the Budongo Forest.

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