CHAPTER FIFTEEN

Effects of Injury on the Locomotion of Free-Living Chimpanzees in the Budongo Forest Reserve, Uganda

Julie Munn

INTRODUCTION

Locomotion is a fundamental component of a chimpanzee's survival in the wild. Moving around in the canopy and on the ground is a skill much needed in the everyday life of chimpanzees in order to gain access to food and social partners, to assist young and to flee from potential danger. That chimpanzees in Uganda and elsewhere have survived disabling injury to one or more limbs suggests they are able to cope with locomotor deficiencies. In Uganda, at least 22% of chimpanzees (*Pan troglodytes schweinfurthii*) from five study sites have injuries that are known or suspected to have resulted from "snares" (Munn, 2003).

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Hunting of wildlife in all Ugandan forest reserves is illegal (Howard, 1991), but is nonetheless a common practice. The snaring of chimpanzees in the majority of cases has been assumed as "accidental" as chimpanzees are not typically target species for hunters in Uganda, in part because primate meat is not a traditional food item (Johnson, 1996a). Methods for hunting all bush meat include the setting of both snares and traps; wire nooses and spring snares are the most frequently used devices for catching terrestrial forest quadrupeds in the Budongo Forest Reserve. These snaring methods involve placing a length of wire or cord over a small hand built pit, which is then camouflaged with forest litter. The loop is either attached to a bent over sapling, or is secured by upright branches (Waller, 1995). Animals that subsequently tread on a snared pit invariably pull and, as a result, the snare tightens and embeds deeper into the victim's flesh. Steel jaw traps (or man-traps) are another trapping method less commonly used. The victim places weight on a metal plate that springs two parallel jaws together with great force, firmly trapping the limb. The force of the steel jaws is great enough to sever the limb completely (Waller, 1995). Throughout this text, the term "snare" is used throughout to describe all trapping methods including spring snares, wire nooses and steel jaw traps, except where otherwise stated.

Injuries are not unique to chimpanzees. Nonhuman primates, throughout their ranges, are exposed to the dangers of injury to limbs whether by accident (e.g., falling from a tree), disease, predation, through an aggressive interaction, or from being caught in a hunter's snare. Limb defects are also caused by congenital deformities. These injuries, regardless of their cause, will have impacts on various aspects of an individual's behavior.

Locomotion

Chimpanzees in the wild spend approximately 14% (Taï National Park, Côte d'Ivore) and 18% (Gombe National Park, Tanzania) of their time in locomotor activities (Doran, 1993). Chimpanzees are adapted to travel both on the forest floor and in the canopy, and the mode and pattern of locomotion differs depending on the substrate utilized. In Taï National Park, arboreal activities were found to account for 16%, and terrestrial activities for 84%, of all locomotor activities (Doran, 1993).

Very little has been documented about the effects of injuries on the types of locomotion used by chimpanzees. Ghiglieri (1988) and Goodall (1986) both describe cases of chimpanzees with deformed limbs having difficulty keeping up with traveling groups. In Gombe National Park, Tanzania, six individuals with limb paralysis (almost certainly from poliomyelitis) were described as adapting well to their injuries (Goodall, 1968b). A study on bonobos (*Pan paniscus*) at Wamba, Democratic Republic of Congo, reported changes in locomotion techniques for individuals that had physical abnormalities (Kano, 1984). Reports from Kibale National Park, Uganda, describe an injured female with a stump as a right hand as an "unbelievable daredevil" (Ghiglieri, 1988:147). Despite her injury she seemed both an excellent climber and an acrobatic one, although there is no mention of her behavior prior to injury. Finally, in a study focusing on the effects of snare injury on the locomotion of the Sonso community, it was found that individuals with injuries to the forelimbs used modified, but very successful adaptations for arboreal locomotion. Those individuals with injuries to the hind limbs were more awkward and slow (Quiatt, 1996).

Here, I examine and descried how locomotor and behavior patterns differ between injured and noninjured chimpanzees. Aspects reported here are types of locomotion used, the time individuals spent moving both in the trees and on the ground, and the ability to carry dependants while traveling.

METHODOLOGY

Study Site and Subjects

The Budongo Forest Reserve, the study site for this research, lies in the west of Uganda between the latitudes of 1°37′ and 2°00′ N, and between the longitudes 31°22′ and 31°46′ E (Plumptre, 1996). The ground is undulating with an average altitude of about 1100 m (3600 ft) (Eggeling, 1947). The Budongo Forest Reserve covers an area of 793 km^2 of both moist, semideciduous forest and grassland; 428 km^2 of the area is forested (Howard, 1991). The ecology of this forest is detailed in an extensive study by W. J. Eggeling (1947). Five species of diurnal primates are found in Budongo, including the eastern subspecies of common chimpanzees, *Pan troglodytes schweinfurthii.*

The subjects of my study are habituated chimpanzees of the Sonso community, in the Budongo Forest Reserve, Uganda. Habituation began in 1991 and all members of the Sonso community were identified and named by July 1995 (Newton-Fisher, 1997). The community contained 49 individuals during the study period, of which 10 had serious deformities. One of these was possibly congenital, and the other nine were as a result of entrapment in snares (Waller, 1995). Adult females with dependants from the Sonso community were the focus of my study because at the onset of the study they were the age–sex class with the most injuries (since that time two males, plus a very young female, have been wounded seriously from snares). Only one age–sex class was chosen to study, as this greatly reduces natural variation in the data caused by behavioral differences seen between individuals. Five adult females with dependants were observed, and their injuries are outlined below:

Kalema had an injury resulting from a wire snare on her right hand; there are reports that she bore the remains of a wire snare on her wrist for some time after the injury (Waller, 1995). Her hand was paralyzed and hooked from the wrist, with the fingers bent so far forward they almost touched the inner part of the lower forearm. Her fingers were curled right over, and came together at a point; they appeared to have no strength or mobility.

Kewaya's right hand was injured from a wire snare (Waller, 1995). The hand was extremely deformed being both twisted and hooked. The wrist was so twisted that the fingers of her right hand pointed out to the side. The fingers came together at a point (similar to Kalema). Her hand was paralyzed in this position so her fingers lacked any function.

Kigere was missing the entire foot of her right leg. The injury was likely to have been caused by a wire snare that became gangrenous, or by a larger metal trap (Waller, 1995).

Both of Zana's hands were injured as a result of snares (Waller, 1995; Waller & Reynolds, 2001). Zana's left hand resembled the injury of Kewaya's right hand. The wrist was twisted and the fingers deformed, pointing out sideways and very floppy, seeming to lack any voluntary movement. Zana's right hand had only one finger, the forefinger, and she had the remaining stump of her thumb. The missing digits, or perhaps the snare itself, have caused a great weakening in the wrist (Waller, 1995).

Banura's left foot was considerably enlarged (appeared swollen), not capable of much movement, and had only two digits. One digit was like a small finger or thumb, and seemed to have some ability to grip. The other digit was larger and folded over toward the centre of the sole of the foot.

Banura was the only individual in the Sonso community thought to have a congenital deformity (Waller, 1995; Waller & Reynolds, 2001). She is included here because she has a physical disability, and this shows signs of affecting her

Table 1. Level of habituation of study individuals (injured individuals in bold)

Level of habituation			
1—High (relaxed)	2	3	4—Low (shy)
Nambi NB	Kwera KW	**Kigere KG**	**Zana ZA**
Zimba ZM	**Kalema KL**	Ruda RD	Ruhara RH
	Kewaya KY	**Banura BN**	Kutu KU
	Janie JN		

behavior. The main difference between her disability and the snare wounds is that she would have been born with her deformity. She is designated as "injured" in this chapter.

Habituation levels affected the amount of time I was able to observe individuals moving (and resting) on the ground. In this study the level of habituation for the 12 females did differ, with some individuals being relaxed in the company of researchers, and others shy. Table 1 shows my judgment of the level of habituation for the study females to both myself, and my field assistant, over the study period.

Definition of Terms

A dependant refers to the youngest offspring of the mother. Dependant is divided into four age categories: Infant 0, Infant 1, Infant 2, and Juvenile 1. Infant 0 refers to the youngest infants, less than 12 months of age. Infant 1 refers to young chimpanzees between 1 and 2 years, Infant 2 those between 2 and 4 years, and Juvenile 1 those 4–6 years old. No dependant changed age category during the study period, so any effects owing to the change in age of the dependant during the 8 months of this study are not determined in these results.

Moving and traveling (here treated synonymously)—the transit from one feeding or resting location to another, whether to a neighboring branch, an adjacent tree, or a site some distance away.

For some analyses, severity of injury has been included. Zana, with injuries to both hands, and Kigere, who was missing a whole foot, were regarded as having the most severe injuries. Kewaya and Kalema had only one hand injured, and Banura had a swollen foot: these three are seen as having less severe injuries. Zana and Kigere both showed difficulties in balancing when moving and feeding, which also led to their being included in the category of most severe injuries.

Data Collection

Data were collected during both wet and dry seasons from October 1999 to June 2000, with a brief intermission between 18th December 1999 and 4th January 2000. Data were collected for 3 months in the dry season (219 observation periods) and 5 months in the wet season (232 observation periods).

Chimpanzees were found each day either by calls heard early in the morning, by visiting the place that chimpanzees were last seen on the evening before, or by visiting known fruiting trees (a large system of trails surrounds the field station at Sonso and covers a large proportion of the community's home range).

Chimpanzees were observed for half-hour observation periods, using both focal animal sampling and scan sampling. Focal animal sampling (Altmann, 1974) was used to determine the amount of time a mother spent carrying her dependant. If a mother was recorded as not carrying her dependant, the dependant was traveling without assistance from its mother or from any other chimpanzee in the group. Focal animal sampling was also used to determine the amount of time individuals spent traveling. Total time spent in arboreal space (regardless of behavior) was calculated using scan sampling (Altmann, 1974), with data collected at 5-min intervals during the observation period. At each 5-min interval it was recorded if a focal subject was on the ground, or in the trees. Ad libitum sampling was used to describe the different methods of locomotion used by injured chimpanzees at Sonso. Number of observation periods, number of 5-min scans and total time observed are shown in Table 2.

Observation periods were rotated among focal subjects. Sampling rules were made to determine the order in which subjects were observed. The sampling rules and the rotation of focal subjects aimed to enable observations to be spread equally between all individuals, and for all times of the day, over the study period. To reduce dependence in the data, no individual was observed more frequently than once every 90 min, that is, a full hour was allowed to pass before the end of one observation period and the beginning of the next.

Data Analysis

Linear models were applied to each set of data (Davidian & Giltinan, 1995; McCullagh & Nelder, 1989). Continuous data collected during focal animal sampling were analyzed using mixed linear models. All data were analyzed as a proportion (e.g., time chimpanzee spent moving/total time chimpanzee

Table 2. Number of observation periods, scan samples, and total time each focal subject was observed during the study period

Focal subject (dependant)	Number of 30-min observation periods	Number of 5-min scans	Total time observed (min)
Injured females			
Banura (Infant 2)	33	231	990
Kewaya (Infant 0)	44	308	1320
Kigere (Infant 1)	36	252	1080
Kalema (Juvenile 1)	41	287	1230
Zana (Juvenile 1)	39	273	1170
Total	*193*	*1351*	*5790*
Noninjured females			
Janie (Infant 0)	38	266	1140
Kutu (Infant 1)	31	217	930
Kwera (Juvenile 1)	45	315	1350
Nambi (Juvenile 1)	38	266	1140
Ruda (Infant 2)	34	238	1020
Ruhara (Infant 2)	29	203	870
Zimba (Infant 2)	43	301	1290
Total	*258*	*1806*	*7740*
Combined total	451	3157	13530

Age category of focal subject's youngest dependant is included in brackets.

observed). Proportions are not usually normally distributed, so the proportions were transformed to the logit scale to normalize the data. Discrete data, collected by means of scan sampling, were analyzed using a binomial Generalized Linear Model. The statistics used in both cases were the Change in Deviance Statistic (F test) or the Wald Statistic, which are characterized by a chi-square distribution. Factors used in the models include injury status of the mother, severity of her injury (see Definition of Terms, above), habituation level of the mother, age of her dependant, and the season during which the observation was taken. It was appropriate in the data analysis to determine the effect different seasons had on the results; however it must be noted that data were not collected for a full 12-month period.

Significance levels of $P < 0.05$ were used throughout, except where simultaneous tests were carried out on the same data set (e.g., time spent moving and time moving in arboreal space). In these cases the Bonferroni correction method was used to change the significance level (Howell, 1997) using the formula: α/m, where α = normal significance level (0.05), and m = the number of simultaneous tests. The resulting significance level is 0.025. Only significant results are reported here.

RESULTS

Methods of Locomotion Used by Injured Chimpanzees of the Sonso Community

Results demonstrate that injured chimpanzees of the Sonso community used modified forms of the locomotor patterns typical of noninjured chimpanzees and showed a tendency to avoid some locomotor patterns altogether. The use of modified forms of locomotion affected the balance needed for arboreal travel in some individuals, as well as the speed at which individuals traveled, especially when attempting to move quickly on the ground. In general, injured females were more awkward in their locomotion when compared to able-bodied chimpanzees. A description of the locomotor patterns of individual chimpanzees with injuries follows.

Banura

Banura walked on the ground using quadrupedalism, placing weight on her deformed foot as she moved. She usually placed weight on the tips of the deformed digits, rather than on the sole of her left foot. She has also been observed walking tripedally, holding her left (deformed) foot off the ground. This always occurred when she was trying to move quickly. Banura's hips tilted in order to compensate for both the awkwardness of her step and the different lengths of her legs. When climbing and scrambling in arboreal space, Banura could not use her injured foot to cling or grasp. This foot was instead used for balance, by placing it alongside a branch or holding it outwards at varying angles. When moving in arboreal space along wide horizontal branches she was able to use her foot as she did when moving on the ground.

Kalema

Kalema used both knuckle walking and tripedalism when traveling on the ground. She used a modified version of knuckle walking with her right (injured) hand; it was placed with the back of the wrist touching the ground, rather than the back of the middle phalanges. While in the trees she used tripedal locomotion when moving along a wide horizontal branch. When climbing and scrambling, Kalema used her injured hand, which had no ability to clasp, for balance by holding it out at varying angles or by placing it against the trunk of a tree or branch. She also used the crook of her right elbow, or her right hand hooked over a branch when climbing down, for balance, or to help pull her up. She was unable to use brachiation, as she could not grasp with her right hand.

Zana

When terrestrial, Zana walked quadrupedally. She used the back of her left wrist as the point of contact with the ground in a modified form of knuckle walking, with the fingers splayed out to the side. Zana moved very slowly and deliberately in the trees. Many times she was seen to hesitate when crossing from the extremity of one tree to the next (bridging and tree swaying); on one occasion she lost balance and hesitated five times before making it across on the sixth attempt. She was never seen to be involved in any suspensory behavior. She was observed walking tripedally along wide horizontal branches, holding her left hand up. When climbing and scrambling in arboreal space she used the back of her left hand against branches to help with balance. She also used her forearms and elbows to assist by leaning against them or using them to pull herself up.

Kewaya

When terrestrial, Kewaya used quadrupedalism. She used a modified version of knuckle walking on the right (injured) side, using the point just above the right wrist as the contact point with the ground, with her fingers splayed out to the side. When vertical climbing, Kewaya used the back of her injured hand, placed against the trunk, to help her balance. When climbing and scrambling she held her injured hand out at an angle to help with her balance. She also used her injured hand as a hook to support herself. She was unable to brachiate, as she could not grasp with her right hand.

Kigere

When moving on the ground, Kigere used knuckle walking, placing even weight on both her injured and noninjured leg. As a consequence her hips tilted considerably as she walked, compensating for the shortness of her injured leg. When observed moving quickly on the ground she was tripedal, with her right leg bent up toward her chest. When moving in trees she used her stump during quadrupedalism (as when terrestrial), or for balance (by lightly touching against branches), or held it out of the way. Twice, when arboreal, Kigere was observed to lose her balance.

Time Spent Moving

On average, adult females in this study spent 10.5% of their time in locomotor activities. Two injured individuals, Zana and Kigere, spent approximately 4% of their time in locomotion whereas all other individuals spent 8% or more (up to 15%) of their time in locomotion (Figure 1).

A linear mixed model revealed that both severity of injury (Wald statistic = 18.81, df = 2, $P < 0.001$) and season (Wald statistic = 16.90, df = 1, $P < 0.001$) significantly affected the time spent moving. The most severely injured individuals spent less time moving than either less injured or noninjured individuals. Both injured and noninjured chimpanzees moved less in the wet season, and more in the dry season, possibly because they were forced to travel extensively to locate food sources. All seasonal differences are based on the 8 months studied, not an entire year.

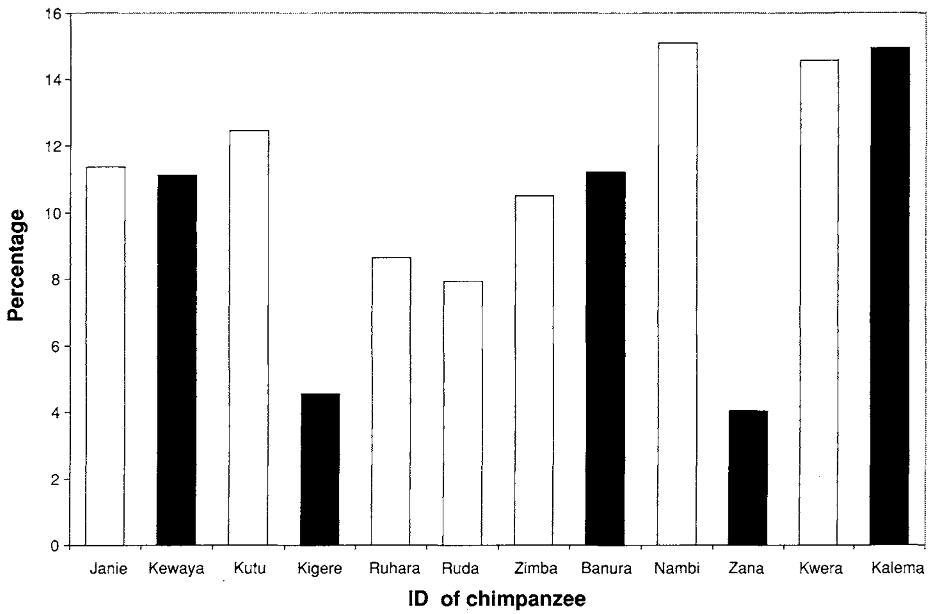

Figure 1. The percentage of total observation time that each focal subject spent in locomotion. Females are ordered from left to right along the base of the graph, with the female with the youngest dependant on the left through to the female with the oldest dependant on the right. Injured females are indicated by the black bars.

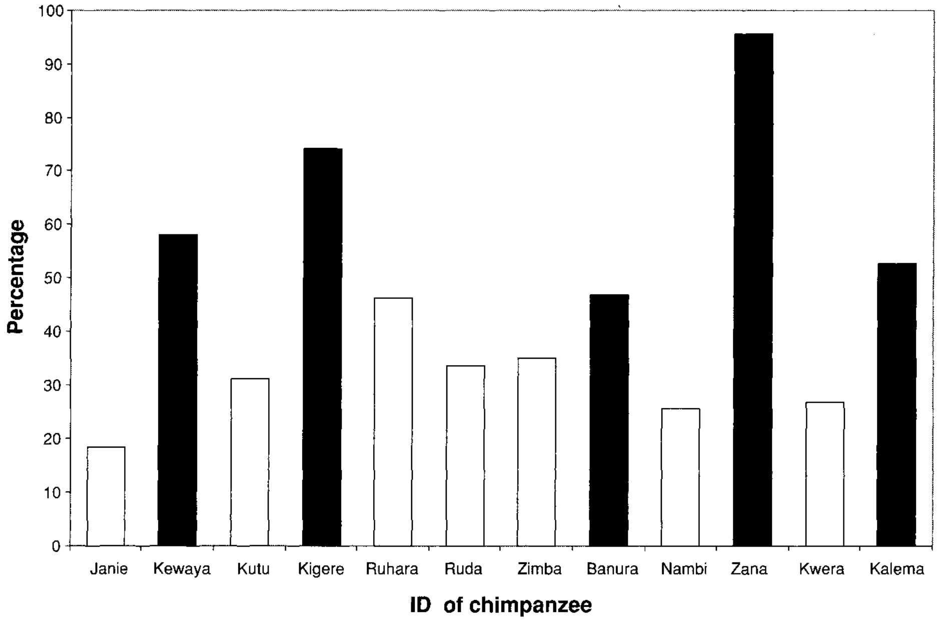

Figure 2. The time spent in arboreal locomotion as a percentage of the total time spent in locomotion. Females are ordered from left to right along the base of the graph, with the female with the youngest dependant on the left through to the female with the oldest dependant on the right. Injured females are indicated by the black bars.

The injured chimpanzees also spent more time moving in arboreal space, as a percentage of the total time spent moving, than did noninjured chimpanzees (Figure 2). A linear mixed model revealed that both severity of injury (Wald statistic $= 10.58$, df $= 2$, $P = 0.005$) and season (Wald statistic $= 17.31$, df $=$ 1, $P < 0.001$) significantly affected the time spent in arboreal locomotion. The greater the severity of injury the larger the proportion of traveling time spent in arboreal locomotion (Figure 3). All individuals spent more time moving in the trees in the wet season than in the dry (Figure 3). A high number of *Cynometra* seeds were eaten off the forest floor in the dry season. *Cynometra* pods burst in the heat of the dry season, scattering hundreds of seeds to the ground. The time spent searching for *Cynometra* seeds was recorded as feeding, not moving, although the presence of these seeds meant that chimpanzees spent more time on the ground. Chimpanzees also tended to travel further distances to find food in the dry season.

These results show that when moving, injured chimpanzees move proportionally more in trees and proportionally less on the ground than noninjured

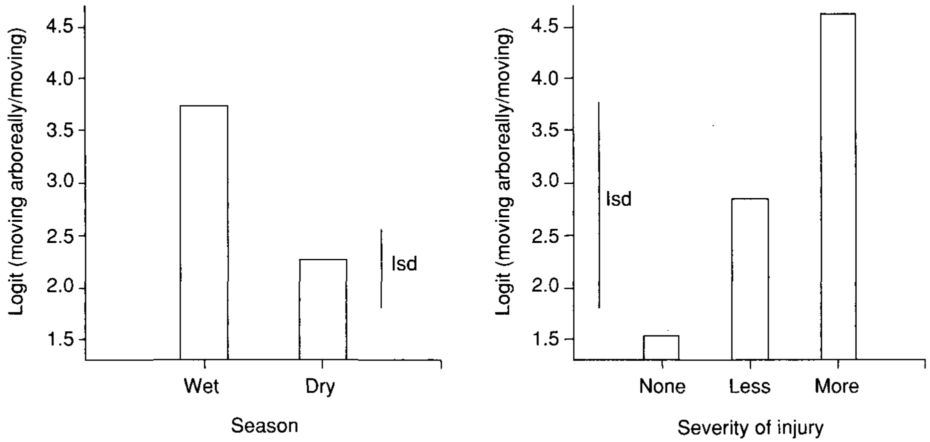

Figure 3. Time spent moving arboreal as a proportion of the total time spent moving. This graph explains the results found in the linear mixed model. The measure of error used in this figure is the least significant difference (lsd), which refers to the minimum distance needed to have a significant difference. Black shading indicates terrestriality.

chimpanzees. Injured chimpanzees, however, spent more time in arboreal space than noninjured chimpanzees, although there was some overlap (Zimba, Kutu, Ruhara). Kigere and Zana once again show the most distinct result, spending almost all of their time in the trees, and the least time on the ground (Figure 4).

A binomial GLM revealed that both the severity of injury ($F = 26.80$, df$=$ $2, 422$, $P < 0.001$) and the degree of habituation ($F = 8.92$, df$= 3, 422$, $P < 0.001$) significantly affected the proportion of time spent arboreal or terrestrial (Figure 5). The more severely injured individuals, as well as the least habituated individuals, spent the greatest proportion of time arboreal. This means that severely injured chimpanzees with low habituation are spending the most time arboreal, and noninjured chimpanzees with a higher level of habituation are spending the least amount of time in arboreal space. Injured chimpanzees are both high and low on the habituation scale (Table 1).

Mother Carrying Dependant during Locomotion

Injury may also affect a mother's ability to carry her offspring. Figure 6 shows a general decrease in the time a mother carries her dependant as the age of

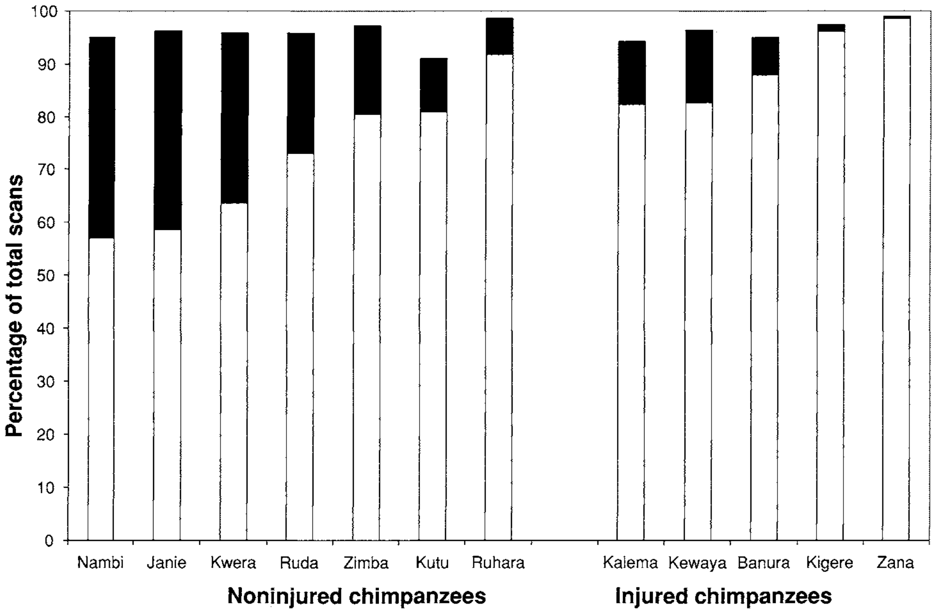

Figure 4. The percentage of 5-min scans that each individual was arboreal or terrestrial. The remainder of time not included on the graph represents time out of sight. The noninjured females are grouped on the left of the graph and injured females grouped on the right.

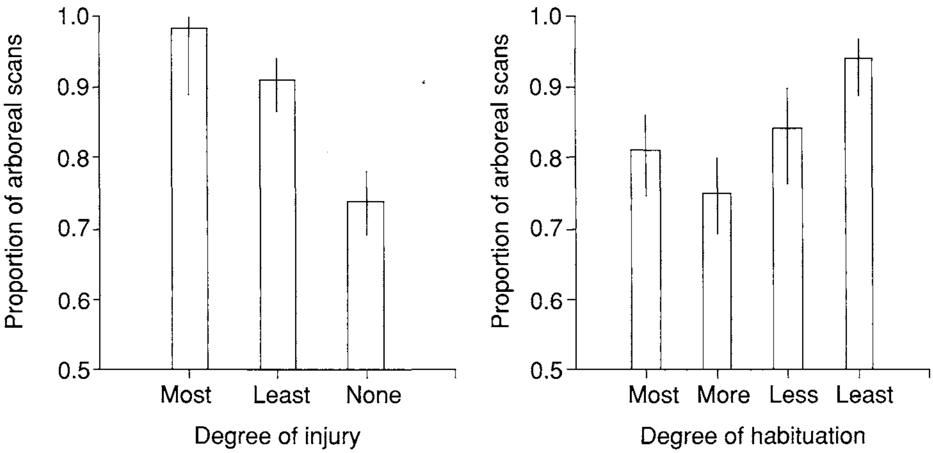

Figure 5. The proportion of scans spent arboreal, showing the effects of both severity of injury and habituation. This graph explains the results found in the binomial GLM. Error bars used in this figure refer to 95% confidence intervals.

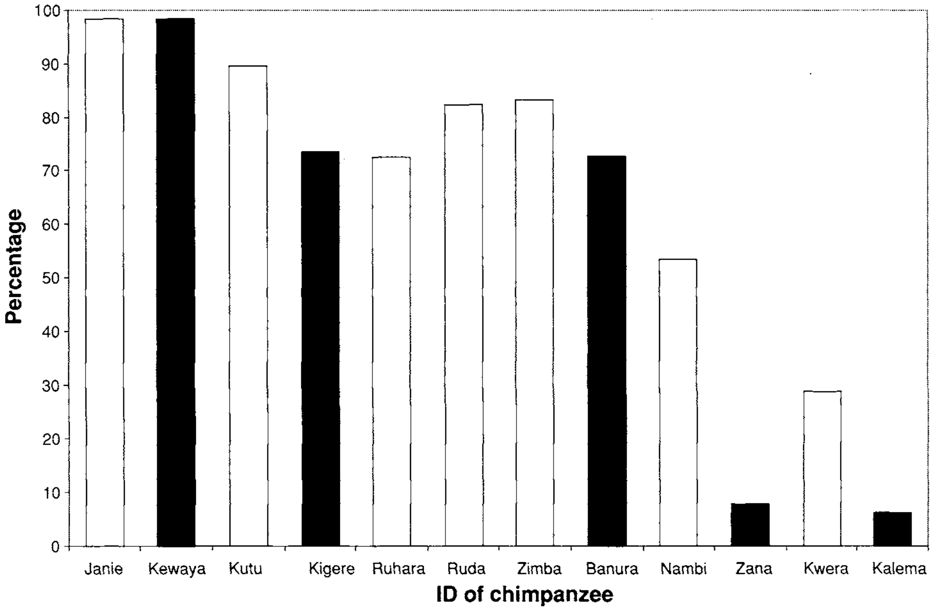

Figure 6. The time each mother spent carrying her youngest dependant as a percentage of the total time spent in locomotion. The mothers are ordered by age of dependant, with the youngest dependant on the left hand side of the graph and the oldest on the right. Injured females are indicated by the black bars.

the dependant increased. Two mothers (Janie and Kewaya) carried their infants (Infant 0) for almost 100% of their time during locomotion; these two mothers have the youngest offspring in the community. The mothers with Infant 1 and Infant 2, shown in the centre of the graph (Kutu through to Banura), show a small difference between injured and noninjured mothers, with injured mothers carrying their offspring for less time than noninjured mothers (with the exception of Ruhara). The four mothers with juvenile offspring (on the right of the graph) show a marked difference between the amounts of time that mothers spent carrying them, the injured mothers carrying their dependants for less time than the noninjured mothers. It appears that the effect of injury on the time a mother carries her dependant is more evident as the offspring gets older.

The linear mixed model revealed that both the age of the dependant (Wald Statistic $= 40.43$, df $= 2$, $P < 0.001$) and the injury status of the mother (Wald Statistic $= 4.37$, df $= 1$, $P < 0.05$) significantly affected the time a mother spent moving without carrying her dependant. The time the mother

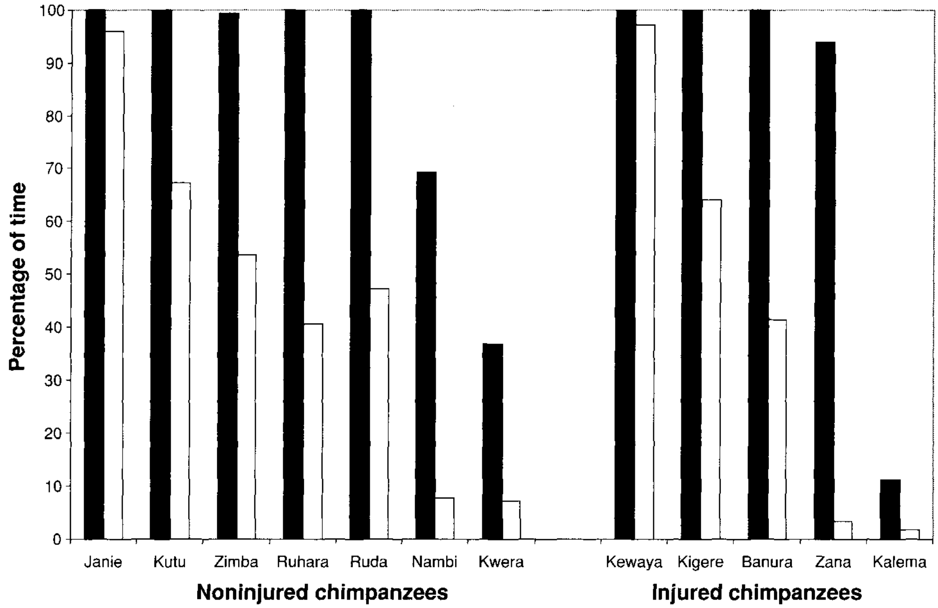

Figure 7. The percentage of time that each mother carried her youngest dependant in terrestrial and arboreal space. The noninjured females are grouped on the left of the graph and injured females on the right. Black shading indicates terrestriality.

spent moving without carrying her dependant increased significantly with the age of the offspring. Injured mothers spent significantly more time moving without carrying their dependant than noninjured mothers. Infant 0 group was found to be significantly different from other age classes (Wald Statistic = 66.90, df = 1, $P < 0.001$) with respect to the time they were carried by the mother.

Injured mothers may have more difficulty carrying their dependants, depending on whether they are traveling on the ground or in the trees. Figure 7 shows the percentage of time a mother carried her dependant, out of the total time she was moving, in both arboreal and terrestrial space. As the age of the dependant increased, the amount of time the mother spent carrying it decreased. The age at which an infant began traveling alone was different in arboreal and terrestrial space. Mothers continued to carry infants and juveniles in terrestrial space for far longer than in arboreal space; even Infant 0 moved on its own in the trees. This may be because long distances are most commonly traveled on the ground. There appears to be no difference between injured and noninjured mothers.

DISCUSSION

Methods of Locomotion Used by Injured Chimpanzees of the Sonso Community

Injured adult female chimpanzees of the Sonso community were more cumbersome in their locomotion, used many modified forms of locomotion, and employed novel methods to assist in locomotion in comparison to their non-injured counterparts. The character of each injury determined the type of accommodation adopted, and the number of injuries also affected the level of locomotor disability. A casual observer is likely to conclude that chimpanzees who survive their injuries, and any subsequent infection, can learn to cope adequately with their disability. That injured chimpanzees can move adequately is also reported in earlier studies (Ghiglieri, 1988; Goodall, 1968; Kano, 1984). Only after watching the injured females for the length of this study period did I witness events such as Kigere losing balance and Zana struggling with bridging and tree swaying. These two individuals are the most severely injured, and seem to be at the greatest risk of losing balance and falling, which is potentially fatal. This result could have serious repercussions for the individual, her dependant offspring, and her community. For example, a population modeling simulation of chimpanzees in Uganda determined that in a population of 100 individuals the annual removal, by human-caused mortality, of one single female and her dependant offspring could have "a real detrimental effect on the growth potential of chimpanzee populations" (Edroma *et al.*, 1997:71).

Time Spent Moving and Preference for Arboreal Space

Adult female chimpanzees at Sonso spent, on average, less recorded time in locomotion than has been recorded at other field sites (Doran, 1993). It is, however, difficult to compare these data, as the records from other field sites include both males and females, and females are known to travel less than males (Wrangham & Smuts, 1980).

The two females with the most severe injuries (Zana and Kigere) spent significantly less time moving than all other females in this study. They were often seen feeding by themselves, either remaining in the feeding tree after other group members moved off, or foraging alone. They may have been avoiding long-distance travel on the ground because of their more cumbersome locomotion.

All injured chimpanzees spent a significantly larger proportion of their traveling time in arboreal locomotion. This is likely a function of the general tendency for these individuals to be more frequently observed in trees. Injured chimpanzees may spend more time in arboreal space as they may move between feeding and resting sites in the trees, rather than come to the ground (although this was rarely observed for long distances), or they may spend more time feeding (mostly an arboreal activity). It may also be because they feel more vulnerable on the ground. The threat from predators and the avoidance of snares (which are all set at ground level) are two reasons why the ground could be perceived as more dangerous for injured individuals.

Feeding

The majority of food items in the diet of the Sonso chimpanzees are found in arboreal space (Stokes, 1999), so an increase in time spent feeding may be the reason why injured chimpanzees spent more time in the trees. No significant difference was found when proportion of time spent feeding was compared for injured and noninjured females (Munn, 2003). Also in results relating to feeding efficiency from Stokes' (1999) study of the Sonso community, feeding efficiency was reduced for only some injured individuals, and not for all food types. Therefore it is unlikely that injured chimpanzees spent more time in arboreal space because of time spent feeding.

That injured females did not spend more time feeding than noninjured females suggests they had a similar ability to process foods. However, they may have had physical difficulty in gaining access to the best foods when in the presence of a large group. Some foods, such as *Ficus sur*, a common fig species used by the chimpanzees at Sonso, were difficult for injured females to feed on since the figs are suspended from a branch in large clumps. Able-bodied chimpanzees commonly hang from the large clump by one hand, and one or two feet, while using the other hand to process the figs. An injured female may require a seated position to access these figs, and may be more confident doing this when other chimpanzees are not attempting to feed off the same clump. For other food types, it may be that injured females have one or two fewer limbs to help with balance in arboreal space, and so it is easier to access food when in the presence of fewer competitors. It is possible that injured chimpanzees spent more time in arboreal space to reduce feeding competition because of the physical difficulties associated with a limb injury; in this case, a lack of balance. Reducing feeding competition by foraging alone has been discussed elsewhere as a strategy used by female chimpanzees to increase food intake (Wrangham & Smuts, 1980). Injured females may behave in this way even more than noninjured females to further reduce their competition for food.

Threat from Predators

Whether arboreal space is "safer" than terrestrial is difficult to determine. Predators of chimpanzees include leopards (Hiraiwa-Hasegawa *et al.*, 1986; Boesch, 1991; Poppenwimer, 1999–2000), lions (Tsukahara, 1993), and humans. In many primate habitats, predation risk from terrestrial felids decreases as height above the ground increases (Boinski *et al.*, 2000), and one of the most common reactions of chimpanzees to feline predators is to climb up into a tree (Hiraiwa-Hasegawa *et al.*, 1986; Tutin & Fernandez, 1991; Tsukahara, 1993). Since raptors are not reported to be major predators of chimpanzees (Treves, 1999), these reports suggest that chimpanzees are safer from predators in the trees than on the ground.

No attacks by large carnivores on chimpanzees have been recorded for the Sonso community, and a recent survey of large mammals across the Budongo Forest found no evidence of large carnivore dung (Plumptre *et al.*, 2001), suggesting that these species are now rare. Lions do occur in the far northeast of the Budongo Forest at Kanyo-Pabidi, the site of one of the two tourist facilities within the reserve. On one known occasion in 2003, a lion was sighted within the Sonso campsite (Z. Kiwede, personal communication), and a lion has been heard from the Sonso campsite in 1992, although it was an extremely dry season and it was thought that the lions might have been looking for water (A. Plumptre, personal communication). Historically leopards were found in the Budongo Forest (Reynolds, 1965), and it is possible that some still exist, although they have not been sighted near Sonso for many years.

Although there are apparently very few feline predators in the area surrounding the Sonso community, it is possible that chimpanzees still respond to the potential risk of an attack by a predator. Dunbar (1988) commented that mortality due to predation can sometimes be low or negligible in primates, and he therefore proposes that it has little effect on social systems and group behavior. He argued that it is not the actual mortality rate that is important; rather it is the potential risk of encountering a predator that may be important in affecting the behavior of the prey species (Dunbar, 1988). It is possible, then, that injured chimpanzees in this study are responding to a potential risk of predation. Supporting this possibility, it has been found that male chimpanzees nest lower than female chimpanzees at Budongo. One explanation given for this behavior was that males strategically locate their nests so as to protect the females and young from ground predators (Brownlow *et al.*, 2001).

Injured chimpanzees at Sonso may be particularly vulnerable to predation owing to their more cumbersome locomotion and their difficulty moving quickly. Injured female chimpanzees at Sonso have been found to spend more time, than noninjured females, in small groups, and alone with their dependants (Munn, 2003); this may make them even more acutely sensitive to any risk of predation. It has been suggested elsewhere that female chimpanzees might be more vulnerable to attack by predators, as their habits are more solitary (Tsukahara, 1993).

Avoidance of Snares

Another factor that could be responsible for injured chimpanzees spending less time on the ground, and proportionally less time moving on the ground, is that they are avoiding snares. Injured chimpanzees may relate spending time on the ground with the painful experience of becoming trapped, and possibly avoid ground travel where possible for this reason. People with their wire snares and traps can be seen as yet another type of ground predator.

Mother Carrying Dependant during Locomotion

Injured mothers may find it more difficult to carry a dependant owing to their modified and sometimes more cumbersome locomotion.

The two youngest dependants (Infant 0) were carried for almost 100% of their mothers' traveling time, regardless of the mother's injury. Younger infants are more dependent on their mother and usually do not travel on their own until about 2 years of age (Hiraiwa-Hasegawa, 1990). Young infants also stay in close proximity to their mother; the two youngest infants in the Sonso community stayed within 1 m of their mother for more than 85% of their time (Munn, 2003). The results in this chapter show that differences in carrying are only apparent when infants become older.

Injured mothers may carry older dependants less because of the extra weight. As offspring weight increases, the effort imposed on the mother to carry must also increase. Furthermore, older dependants move around on the mother during locomotion—changing from ventral carrying to dorsal, reaching out to grab at passing-by objects, or by jumping on and off as the mother moves, creating a potentially unbalanced weight.

Results here show that as dependants get older and heavier, and able to travel independently, injured mothers are more likely to travel without them. One of the juvenile dependants with an injured mother (Zana) was observed being pushed off his mother while she was traveling along thin branches at the outer edge of a fig tree. It is possible that the mother was simply weaning the juvenile, but in context with the difficulties of arboreal travel it is also possible that the mother was avoiding carrying him. Once she reached the wider and more stable branches lower down in the fig tree, she carried the juvenile.

Injured mothers did not show any preference for carrying their dependants in arboreal or terrestrial space. All mothers carried their dependants until an older age when on the ground compared to when they were arboreal. This may be because there are fewer dangers in arboreal space (as described above), or may be because long-distance travel is more common on the ground and mothers are more likely to carry dependants over long distances. It may also be because dependants find it easier, or more fascinating, to clamber freely in trees, than on the ground, or because mothers find it easier to carry dependants when on the ground.

Snare Injuries vs. Congenital Deformity

Of the five injured chimpanzees in this study, four have injuries from snares and one, Banura, has a presumed congenital deformity. Banura's disability was equivalent to that of the snare-injured chimpanzees; she had no use of the digits of her foot, or the actual foot itself. This affected her movement and her balance, and made her locomotion more cumbersome, as was the case for the other handicapped chimpanzees. Socially, her disability may have been different. Since she was born with her injury, other community members might have accepted her to a greater or lesser degree, than mothers who received their injuries later in life. This was not the case. All handicapped chimpanzees, Banura included, were well accepted into the broader community. A lack of tolerance by other community members was argued not to be the causal factor of the differences seen between injured and noninjured chimpanzees' behavior (Munn, 2003).

Conservation Implications of Snaring

There are many threats to the survival of chimpanzees in Africa. Some, such as the bush meat trade in west and central Africa, result in the death of countless chimpanzees. In contrast, snaring has resulted in only a few known deaths in Uganda (Munn & Kalema, 1999–2000; Wrangham & Mugume, 2000). The low incidence of deaths is probably because the snaring of chimpanzees has mostly been accidental. All hunting of vertebrate species living within Uganda's forest reserves is against the law (Howard, 1991), and it is considered culturally unacceptable to eat primate meat for almost all Ugandans (Johnson, 1996). Snaring may, unfortunately, be on the increase in Ugandan forests. Firstly, this is because of the expanding human population. Uganda has an annual rate of population growth (without regard for migration) of 3% (Population Reference Bureau—World Population Data Sheet, 2002). The population in Uganda in mid-2002 was 24.7 million. This is expected to almost double to 48.0 million by 2025, and then by 2050 an expected 84.1 million people will be living in Uganda (Population Reference Bureau—World Population Data Sheet, 2002). Population pressure creates an increasing demand for all forest resources, including bush meat, and the accidental snaring of chimpanzees is likely to increase as a result. Secondly, there has been an influx of new ethnic groups into Uganda. The instability in the Democratic Republic of Congo (DRC) has led to hundreds of refugees crossing the Ugandan border in the hope of finding security. Nearly one-third of immigrants from the DRC living in a village near the Budongo Forest Reserve are known to eat primates (Johnson, 1996), although it is unclear if this includes chimpanzees. Until recently, no known deliberate hunting of chimpanzees for trade or meat in Uganda had been recorded. A recent unpublished report tells the tale of two bush meat traders who were arrested carrying chimpanzee carcasses in western Uganda (Moeller, 2000). It is possible that the bush meat traders were Congolese, and so hunting for themselves. Alternatively, they could have been hunting to supply a new market that may be opening in Uganda that reflects the traditions and habits of refugees, the eating of primate meat being one of them.

Deaths and injuries to chimpanzees will certainly increase as the human population increases, and as more immigrants, with no cultural taboo on eating primates, arrive in Uganda. Chimpanzees with existing injuries face the possibility of receiving further injuries, placing huge pressure on their ability to survive. Whether because of their more cumbersome locomotion, the potential threat from ground predators, or a reduction in feeding competition, injured female chimpanzees from the Sonso community are showing a preference for arboreal space. This leads to injured females spending more time alone or in small groups (Munn, 2003). Consequently, a reduction in social opportunities, less protection from other group members, and fewer opportunities to gain group knowledge, such as feeding sites, may occur. Injured mothers also carry their offspring less than a noninjured mother, particularly as the offspring gets older—this may have long-term behavioral implications for the offspring.

Finally, since snare wounds affect the behavior, survival (Boesch & Boesch-Achermann, 2000; Munn & Kalema, 1999–2000; Wrangham & Mugume, 2000), and the general welfare of chimpanzees, efforts must be made in order to reduce, or eliminate, the occurrence of snaring in Ugandan forests.

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