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The Effects of Permanent Injury on the Behavior and Diet of Commensal Chacma Baboons (*Papio ursinus*) in the Cape Peninsula, South Africa

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Abstract Primates may suffer injury from both natural (fights with conspecifics, predators) and human-induced (snares, power-lines and guns) causes. Though behavioral flexibility may allow primates to compensate for injuries, permanent disabilities, such as the loss of a limb, may adversely affect both foraging and locomotory efficiency and ultimately the survival and fitness of individuals. In the Cape Peninsula, South Africa, members of the chacma baboon population (*Papio ursinus*) experience chronic levels of conflict with humans that manifests in high levels (15%) of disabled baboons in groups that overlap with residential areas. In this study we investigate the potential impact of such disabilities by comparing the behavior and diet of disabled baboons with uninjured baboons matched closely for age, sex, and social status from groups of a similar size and composition for 8 mo, from May to December 2005. Disabled baboons spent more time resting and traveling and less time feeding than uninjured baboons. Disabled and uninjured baboons had similar diets but the former consumed fewer food items with high handling costs and fed more on high return foods than the latter. There was no difference in the frequency of grooming or social vigilance behaviors, as might be expected if disability had compromised either competitive ability or predation risk. Further, there was no difference in the survival of disabled or uninjured individuals in each group. Together these results suggest that while permanent injury may affect the behavior and diet of Peninsula baboons, that these constraints may be offset by access to anthropogenic food sources and the lack of natural predators. Disability in baboons may lead to obligate raiding of high-return anthropogenic foods, which is an important challenge for the ongoing management of this population.

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Introduction

Primates often suffer injury to their limbs and bodies through both natural causes such as predation (Cheney *et al.* 2006; Cowlishaw 1994; Smuts 1985, 1987), fights with conspecifics (baboons: Drews 1996; macaques: Dittus and Ratnayeke 1989; Whitten and Smith 1984), or accidental falls (Beamish 2010; Teleki 1973) and human-induced causes such as snares (Goodall 1968; Kano 1984; Stokes *et al.* 1999), predation (Strum 1994), disease (polio: Goodall 1968; leprosy: Kano 1984; Köndgen *et al.* 2008), vehicles (Pyle 1980), high-voltage wires (Printes 1999), or contaminants that produce congenital deformities, e.g., pesticides (Turner *et al.* 2008).

Human-induced causes of injury in primates have been documented in chimpanzees (*Pan troglodytes*: Goodall 1968; Quiatt *et al.* 2002), bonobos (*Pan paniscus*: Kano 1984), and Japanese macaques (*Macaca fuscata*: Turner *et al.* 2008). These injuries are often permanent and typically result in the partial or complete loss or paralysis of a hand and/or a foot or limb. Snares are the most common cause of injury in chimpanzees (Waller and Reynolds 2001) as well as bonobos (Kano 1986) and are used by subsistence hunters and bush meat traders. The prevalence of human-induced limb injuries may reach alarmingly high percentages, as exemplified by studies in Uganda that report >20% of the chimpanzees having some form of severe limb injury (Byrne and Stokes 2002; Munn 2006).

A permanent injury may adversely affect the fitness of an individual by impeding its locomotory, foraging, and parenting skills. The loss or deformity of a limb adversely affected terrestrial locomotion in chimpanzees (Quiatt 1996; Goodall 1968) and arboreal locomotion in spider monkeys (*Ateles geooffroyi:* Chapman and Chapman 1987). Some species of primate can adapt well to physical injuries by modifying their locomotor techniques, although the movement is reported as more awkward and slower than their uninjured counterparts, e.g., chimpanzees (Goodall 1968; Munn 2006) and bonobos (Kano 1984).

Where complex manual processing of food is required the loss of, or injury to, a forelimb poses severe limitations to dexterity and control that may adversely affect an individual's ability to forage efficiently. Studies of the feeding patterns of gorillas and chimpanzees with snare injuries reveal that while they use feeding techniques that resemble those of able-bodied individuals, they introduce novel compensatory actions that vary depending on the nature and extent of the injury (Byrne and Stokes 2002; Stokes and Byrne 2001). The ability to compensate through the modification of existing behaviors resulted in individuals with forelimb loss or injury showing no reduction in overall feeding efficiency (Stokes 1999).

While behavioral plasticity in primates allows injured animals to meet their specific dietary needs adequately, injuries still influence their ability to socialise. Injured female chimpanzees in Uganda showed a preference for arboreal rather than terrestrial space and consequently spent more time foraging alone than uninjured chimpanzees (Munn 2006). Injured male baboons avoided interactions with other males, even emigrating temporarily (Drews 1996; Harding 1980), thus reducing their social and reproductive activity (Smuts 1985). Injury may influence the ability to provide parental care as observed in chimpanzees where impaired arboreal agility resulted in females carrying their offspring less often than uninjured females (Munn 2006). Reduced parental care may have long-term adverse effects on the social development of young and increase the risk of injury or death from a fall. Severe injury is known to cause a reduction in dominance rank in chimpanzees (Reynolds and Reynolds 1965) and baboons (Altmann 1980; Drews 1996), suggesting that injury may reduce an individual's competitive ability and thus impact negatively on their social status.

In the Cape Peninsula, South Africa, the chacma baboon (*Papio ursinus*) has a history of conflict with humans dating back 350 yr to when the first settlers established vegetable gardens on the slopes of Table Mountain (Gerber 2004). Subsequent loss of productive low-lying land to urban and rural developments has resulted in chronic levels of conflict between residents and baboons (Hoffman and O'Riain 2012), with the latter regularly raiding both rural (van Doorn *et al.* 2010) and urban (Kaplan *et al.* 2011) areas in search of high-return food items. This conflict manifests in a variety of human-induced injuries and deaths to baboons including shootings, domestic dog bites, vehicle accidents, and burns from exposed high-voltage wires (Beamish 2010).

Chacma baboons are omnivorous and feed on a broad array of food items acquired by foraging in diverse habitats (arboreal, subterranean, and the seasonally productive herb and shrub layer). Accessing such a broad menu is greatly facilitated by both manual dexterity and limb strength (Byrne *et al.* 1993; Norton *et al.* 1987; Oftedal 1991; Whiten *et al.* 1991). Given that Peninsula baboons are characterized by a diverse range of permanent injuries to limbs including the loss or partial paralysis of limbs, feet, and/or hands it is an ideal population and species in which to study whether such injuries adversely affect their behavior, survival, and reproduction.

In this study we investigate the influence of permanent limb injury, i.e., disability, on the behavior, diet, survival, and number of live offspring produced by free-ranging commensal baboons. We predict that 1) the loss of a limb or the distal elements of a limb will adversely affect locomotion, resulting in more time spent traveling and resting and less time climbing; 2) the disabled baboons will spend more time foraging because of increased handling time for foods that require manual dexterity and limb strength to process and therefore less time socializing; and 3) the disabled baboons would have higher levels of social vigilance and self-grooming as a result of anxiety due to reduced competitive ability, when compared to their uninjured counterparts.

Methods

Study Site

The Cape Peninsula lies between 18°E–19°E and 32°S–33°S, with a range in altitude from sea level to 1000 m, covering an area of 470 km^2. More than half the total land mass of the Peninsula, encompassing the central mountain chain and the southern portion (Cape of Good Hope [CoGH] Reserve), falls within the Table Mountain National Park (TMNP). The lower elevations outside the TMNP are mostly developed for residential land use, with small pockets of rural land remaining. The dominant vegetation in the Peninsula is fynbos, a key component of the Cape Floral Kingdom (Cowling *et al.* 1996). Fynbos is an indigenous, species-rich but nutrient poor flora, resulting in relatively low numbers of endemic mammal species (Fraser 1994). Interspersed with the fynbos are pockets of exotic plantations and large tracts of land that are infested by a variety of invasive trees and shrubs. Exotic vegetation is readily exploited by baboons (Davidge 1978a; Hoffman and O'Riain 2011, 2012; van Doorn *et al*. 2010) both as a food resource, and, in the case of pine trees, as a safe refuge for sleeping. There are no natural baboon predators on the Peninsula, with the last leopard shot in the late 1800s.

Focal Groups and Habitat Characterization

At the commencement of this research in 2005 a total of 350 baboons lived in 11 groups within the Cape Peninsula (Beamish 2010). Seven of these groups ranged outside the CoGH Reserve and exhibited substantial home range overlap with urban and rural land use (Hoffman and O'Riain 2012) while the remaining four groups range exclusively within the CoGH Reserve. The groups within the Reserve had no disabled members while the groups outside the Reserve included baboons that were disabled. We selected focal individuals from the two Peninsula groups, Da Gama (DG) and Plateau Road (PR), which had the highest number of disabled individuals. The two groups have similar group size, composition, and home range size (Table I), and both home ranges have similar habitat composition characterized by indigenous fynbos vegetation (including endemic *Protea*, *Restio*, and *Erica* species) interspersed with a variety of exotic tree species (*Pinus*, *Eucalyptus*, and *Acacia* species), areas of cleared exotic species, and both residential and rural land use areas (van Doorn *et al*. 2010). Fynbos is the predominant vegetation type covering the home ranges of both DG (55.1%) and PR (77.6%), and exotic vegetation accounts for similar areas in DG (9.7%) and PR (8.9%). The home range of the DG group has a higher percentage of overlap (9.2%) with urban development than the PR group (2.5%), and the group is actively discouraged from urban raiding by "baboon monitors." Monitors are people employed to herd groups away from the urban edge (van Doorn *et al*. 2010). The central part of the DG home range is composed of natural vegetation within the TMNP while most of the peripheral areas are urbanized. The home range of the PR group borders the TMNP and overlaps predominantly with low-density agricultural small holdings including an ostrich farm that the group visits regularly to raid feed pellets (van Doorn *et al*. 2010). The low density of human dwellings negates the need for a monitor program in PR but the group is nevertheless actively chased away from the farms and dwellings by the respective land owners/residents and their dogs.

Table I Composition of the two focal groups of baboons (*Papio ursinus*) in Da Gama and Plateau Road groups, Cape Peninsula, South Africa, January 2005

Group	Home range (km^2)	Count	No. of males[a]	No. of females[a]	No. of juveniles	No. of permanently injured baboons
Da Gama	10.9	35	4	14	17	4
Plateau Rd	9.1	36	2	14	20	3

[a] Includes subadults

Focal Individuals

A total of seven individuals in the two groups had sustained permanent limb injuries and together formed the disabled group. We matched each disabled individual as closely as possible with respect to age, social status, and estrous state (in the case of females) with an uninjured individual of the same sex and from the same group (Table II) before data collection. We used focal and *ad libitum* observations recorded in a parallel study (van Doorn 2009) to create a winner–loser matrix using submissive behaviors and active supplants to infer winners and losers in dyadic interactions. Following the method of De Vries and Appleby (2000) we calculated dominance

Table II The name, group, rank, injury type, age category, sex, hours observed, and a description and cause of the permanent injury of the seven study pairs of baboons (*Papio ursinus*) from the Da Gama and Plateau Road groups, Cape Peninsula, South Africa, 2005

Pair no.	Name	Group	Rank	Injury	Age	Sex	Hours observed[a]	Description and cause of injury
1	Paula	PR	1	Hand	Adult	F	49.60	Missing right forearm from point midway up the forelimb. High-voltage power line burn.
1	Olivia	PR	3	Uninjured	Adult	F	45.60	None
2	Beatrice	PR	2	Hand	Adult	F	51.00	Left hand paralyzed. Fingers and wrist withered and immobile. Snare injury.
2	Nanda	PR	4	Uninjured	Adult	F	45.90	None
3	Pedro	PR	unk	Hand and foot	Juvenile	M	39.10	Left hand and right foot missing from midway up the forelimb and hind limb. High-voltage power line burn.
3	Manuel	PR	unk	Uninjured	Juvenile	M	34.80	None
4	Penny	DG	14	Hand	Adult	F	41.00	Missing right forearm from a point midway up the forelimb. High-voltage power line burn.
4	Marilyn	DG	10	Uninjured	Adult	F	33.90	None
5	Crook	DG	4	Hand	Adult	F	47.90	Left hand paralyzed. Fingers are clawed and immobile. Trap or snare suspected.
5	Kate	DG	1	Uninjured	Adult	F	46.60	None
6	Ellie	DG	3	Leg	Adult	F	41.70	Leg amputated at the hip joint. Gunshot, fell and broke leg, fracturing pelvis.
6	Lucy	DG	5	Uninjured	Adult	F	39.30	None
7	Thami	DG	11	Leg	Adult	F	28.00	Leg amputated at the hip joint. Gunshot injury.
7	Amy	DG	12	Uninjured	Adult	F	24.70	None

Rank indicates the relative position in the group hierarchy, with 1 being most dominant. DG = Da Gama; PR = Plateau Road; unk = unknown

[a] Hours observed = the actual hours that an individual was observed and that exclude the time during the observation that the individual was not visible

hierarchies for both focal groups that we used to match the rank of uninjured individuals with that of our disabled individuals. We also matched the estrous state of females where possible and our final pairings included: 2 lactating; 3 pregnant, and 1 pair with a cycling and a lactating female. The 7 pairs comprised 12 females (10 adults, 2 subadults) and 2 males (juveniles). We determined the sex and age classes based on the classification of Altmann *et al.* (1977).

Data Collection

We habituated the focal individuals to the close proximity (≥5 m) of researchers, allowing for detailed behavioral observations. Two observers performing simultaneous, continuous focal observations (Altmann 1974) collected data from May to December of 2005. On a given day each observer focused on one individual from a matched pair in the same group. After finding the group (typically after sunrise at the sleeping site) and locating the focal individuals the observers commenced with data collection, which typically continued for an entire day. Data collection ended when the baboons had returned to their sleeping site or if one or both of the observers lost sight of their focal individual for ≥30 consecutive minutes. We observed one pair of individuals on a given day using focal observation and did not observe them on consecutive days. We randomized the order of selection of focal pairs within a group and the observers switched groups only when all pairs in a given group had been observed. We ensured that observers collected similar amounts of data for disabled and uninjured baboons to reduce the potential effects of observer bias on the two categories of focal individual.

The observers recorded the behavior of the focal pair on a Palm Psion hand held computer that had been programmed with the Pendragon® Forms software and we included detailed behavioral subcategories within the broad-scale behavioral categories of feed, move, rest, and socialize (*sensu* Altmann 1974) (Table III). We recorded the type of food eaten (exotic vegetation, annual plants, fynbos, human-derived food, and other which are food items that fell outside of the major groups, e.g., mushrooms, insects), the part of the plant eaten (flower, stem, or bulb), and the location of the food source (i.e., above or below ground or in arboreal space). We recorded climbing events to determine whether injury compromised a baboon's ability to utilize arboreal space for foraging and resting bouts.

We recorded life history data *ad libitum* over a 4-yr period from January 2004 to December 2007 and included the survival, reproductive state, and all births and deaths of offspring to female focal individuals.

Data Analyses

As there was a disparity in the amount of time that members of each pair were visible during observation sessions (Table II), we calculated the time that each individual allocated to different behaviors as a proportion of the total time that each individual was visible (Fig. 1). We calculated an activity budget using the mean percentage time that the seven disabled individuals and the seven uninjured individuals spent on a given activity. We used sign tests to test whether disabled individuals consistently spend more or less of their total time engaged in each behavior than their uninjured counterpart. The sign test does not explore the mean but rather the consistency of the relationship

Table III An ethogram of the four main behavioral categories and their associated subcategories including a description of each subcategory

Behavioral category	Behavioral subcategory	Description of the behavioral subcategory
Feed	Feed	Ingesting food, including check pouch feeding but not while traveling.
	Forage	Searching for food while stationery or moving small distances when the predominant activity is foraging.
	Food handling	Processing and handling food items by hand or mouth. For broad scale analysis this is included with forage.
	Drink	Drinking water.
	Raid	Searching for and acquiring human derived food.
Move	Travel	Directional walking and running.
	Climb	Climbing.
Rest	Rest	Sleeping or lying down and the eyes may be closed.
	Inactive	Inactive with eyes open and no social interactions.
	Self-groom	Autogrooming but excluding scratching.
	Vigilant social Vigilant other	Passive scanning of the group. Passive scanning of the environment, e.g., ostrich/car / monitor
Social	Affiliative Aggressive Submissive	Including the specific behavior, the partner and the response.
	Social infant	Including the behavior and the partner.
	Groom another	Includes the partner that initiated the response.
	Being groomed	Includes the partner, which initiated the grooming and response.

between paired individuals within the two groups that are independent of each other. We use separate tests for each behavior category, although the subcategories within an activity budget sum to 100% of the time.

For detailed analysis of feeding behavior, we included the behavioral categories of raid and food handling in the feeding and foraging subcategories respectively. In our analysis of grooming behavior we excluded infant grooming bouts, as maintenance of social bonds was not the primary motivation. To determine whether disabled individuals had higher levels of anxiety than uninjured baboons, as a result of reduced competitive ability from their injury, we analyzed the time spent on social vigilance (and on autogrooming) as indicators of increased anxiety levels. To assess whether disability influenced the time spent feeding on a particular food we compared the time allocated to feeding on food types and dietary items that are the major components of the diet. In addition, to assess whether diminished manual dexterity and strength influenced the ability to dig for and process underground food items we compared the time spent foraging on underground food items vs. items obtained above ground.

Ethical Note

We collected the data according to protocols approved by the University of Cape Town and the South African National Parks and that adhered to the legal requirements of the Republic of South Africa.

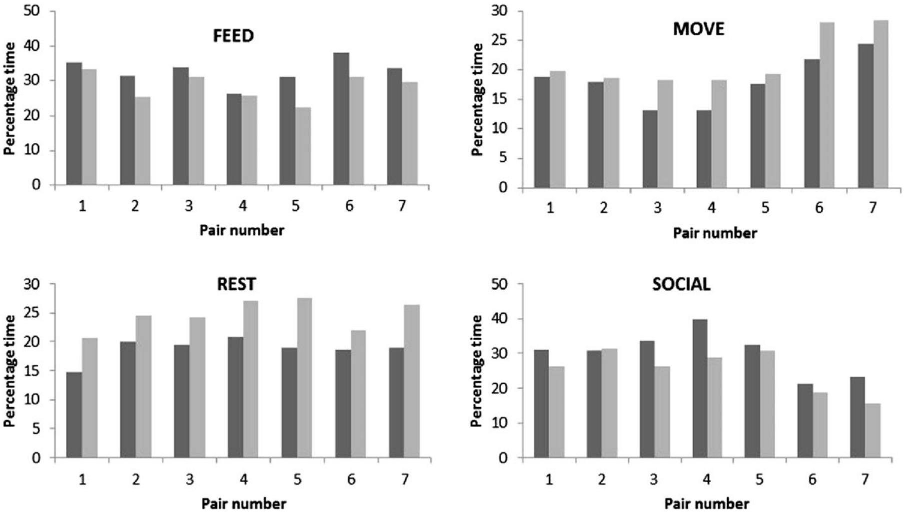

Fig. 1 The total percentage time that matched pairs of uninjured (dark bars) and disabled (light bars) baboons (*Papio ursinus*) engaged in the four main behavioral categories that together comprise the activity budget. See Table II for the details of each pair of baboons in the Da Gama and Plateau Road groups, Cape Peninsula, South Africa.

Results

Distribution and Extent of Permanent Injuries on the Peninsula

In 2005 we recorded 9 disabled baboons in 4 of the 7 groups outside the CoGH Reserve and no disabled baboons in the 4 groups that range exclusively within the reserve. Of these nine disabled individuals, 7 came from the 2 focal groups in this study (see Table II). In 2007 the number of disabled baboons had increased to 17 individuals in 6 groups outside the CoGH Reserve, with the conservation authorities euthanizing a further 8 severely injured individuals, bringing the total to 25 for 2007. Thus in 2007 12% of the total number of baboons ($N = 207$) in these 6 groups suffered disability or euthanasia as a result of human-induced injuries. These injuries had a substantial skew toward adults and subadults (72%) with a strong female bias (75%).

Behavioral Differences Between Disabled and Uninjured Individuals

The activity budgets for disabled and uninjured individuals had a similar trend, with individuals in both groups allocating the most time to feeding and socializing followed by resting and travelling. The sign test revealed that disabled baboons spent significantly less time feeding than uninjured baboons and rested and traveled for significantly longer periods than uninjured baboons. However, disabled and uninjured baboons showed no difference in the time allocated to social activities (Table IV). The feeding subcategories for disabled and uninjured baboons showed no difference but in the behavioral subcategories associated with travel, disabled baboons spent significantly more time traveling than uninjured individuals whereas injured and uninjured individuals spent the same time climbing. Within the rest subcategories, disabled baboons spent significantly more time inactive than uninjured baboons (Table IV).

Diet

Disabled baboons spent significantly more time consuming raided foods and significantly less time consuming exotic plants than uninjured individuals and showed no difference in the time spent feeding on annual plants, fynbos, or other food types by disabled and uninjured baboons (Table V). Disabled baboons fed less on pine cones and more on raided food than uninjured baboons. Disabled and uninjured baboons fed a similar amount of time on all other food types including exotic seeds, exotic other exotics, fynbos bulbs, fynbos flowers, fynbos other, grass, and other (Table V). A more detailed analysis of foraging showed that disabled and uninjured individuals spent the same amount of time feeding on pine cones found on the ground vs. in trees and allocated a similar amount of time to feeding on above vs. below ground food items (Table V).

Table IV A statistical comparison (sign test: *z*-score) of the proportion of time that disabled ($N = 7$) and uninjured ($N = 7$) baboons (*Papio ursinus*) engaged in the four main behaviors and their respective subcategories in the Da Gama and Plateau Road groups, Cape Peninsula, South Africa in 2005

Behavior	Subcategory	*z*	*P*-level
Feed		2.268	**0.023**
	Drink	0.756	0.450
	Feed	0.756	0.450
	Food handling	0	1
	Forage	0.756	0.450
Rest		2.268	**0.023**
	Inactive	2.268	**0.023**
	Rest	1.512	0.131
	Self-groom	0.756	0.450
	Vigilant other	0	1
	Vigilant social	0.756	0.450
Social		1.512	0.131
	Social affiliative	0	1
	Social aggressive	0	1
	Social submissive	0.756	0.450
	Being groomed	0.756	0.450
	Groom another	0.756	0.450
Move		2.268	**0.023**
	Climb	0.756	0.450
	Travel	2.268	**0.023**

Significant difference in bold (sign test: $P <. 0.05$)

Table V A statistical comparison (sign test: *z*-score) of the proportion of time that disabled and uninjured baboons (*Papio ursinus*) ate food types in the Da Gama and Plateau Road groups, Cape Peninsula, South Africa, 2005

Food types	*z*	*P*-level
Exotic vegetation	2.268	**0.023**
Annual	0	1
Fynbos	0	1
Raid – human-derived food	2.268	**0.023**
Other	0	1
Food subtype		
Exotic pine cone	2.268	**0.023**
Exotic seed	0	1
Exotic other	0	1
Fynbos bulb	0	1
Fynbos flower	0	1
Fynbos other	1.512	0.131
Grass	0	1
Raided food	2.268	**0.023**
Other	0	1
Location		
Above ground	1.512	0.131
Below ground	1.512	0.131

Significant difference in bold (sign test: $P <. 0.05$)

Survival and Reproductive History

None of our disabled or uninjured focal individuals died during the study period (2004–2007) and each group each had a mean of 2.5 (SD = 2.08) live offspring born per annum. A single uninjured female had two stillborn offspring born in consecutive pregnancies. Both the disabled and uninjured subadult females had their first birth in 2005 and the uninjured subadult gave birth again in 2006 after infanticide to her first offspring. In another pair both the disabled and uninjured females lost their second offspring to infanticide (Table VI).

Discussion

Permanent injury to a limb or portion thereof influences the behavior of free-ranging chacma baboons on the Cape Peninsula. Disabled baboons rested and traveled for longer periods and fed for shorter periods than uninjured baboons of the same group and sex and of similar age and social rank. However, disabled and uninjured individuals showed no difference in the time spent performing social activities. These findings support our predictions that disability may influence traveling and resting behaviors but are contrary to our predictions for feeding and social behaviors.

Baboons are group-living and movement patterns are largely dictated to by the dominant group members, even if these movements are not in the interests of the majority of the group members (Kaplan *et al.* 2011; King *et al.* 2008). Thus disabled

Table VI A summary of the reproductive history of disabled and uninjured female baboons (*Papio ursinus*) from the Da Gama and Plateau Road groups, Cape Peninsula, South Africa: 2004 – 2007

Focal pair	Group name	Individual name	Reproductive state across years				No. of live births	Birth rate	No. and cause of infant deaths	No. of infants surviving to 1 yr
			2004	2005	2006	2007				
1A	PR	Paula	Birth	Lactating	Birth	Lactating	2	0.5	0	2
1B	PR	Olivia	Birth	Lactating	Birth	Lactating	2	0.5	0	2
g										
2A	PR	Beatrice	Birth	Lactating	Birth	Lactating	2	0.5	0	2
2B	PR	Nanda	Birth	Lactating	Birth	Lactating	2	0.5	0	2
3A	DG	Ellie	Pregnant: miscarriage	Cycling	Birth	Lactating	1	0.25	1: Miscarriage	1
3B	DG	Lucy	Birth	Lactating	Birth	Lactating	2	0.5	0	2
4A	DG	Crook	Cycling	Birth: HI death	Birth: infanticide	Pregnant	2	0.5	1: HI death 1: Infanticide	0
4B	DG	Kate	Birth: stillborn	Birth: stillborn	Cycling	Pregnant	0	0	2: Stillborn	0
5A	DG	Penny	Lactating	Birth	Birth: infanticide	Pregnant	2	0.5	1: Infanticide	1
5B	DG	Marilyn	Lactating Lactating	Birth	Birth: infanticide	Pregnant	2	0.5	1: Infanticide	1
6A	DG	Thami	Cycling	Birth	HI death	Pregnant	1	0.25	1: HI death	0
6B	DG	Amy	cycling	birth: infanticide	birth: infanticide	pregnant	2	0.5	2: Infanticide	0

A = disabled; B = uninjured; HI death = human-induced death individuals are forced to travel the same distance as uninjured group members if they are to benefit from the advantages associated with group living (Dunbar 1988). Our results suggest that disabled individuals respond by increasing their total travel time and resting (inactive) time. Similar result are reported from studies on chimpanzees where chimpanzees with deformed limbs had difficulty in keeping up with traveling groups (Goodall 1968) while those with hind limb deformities had slow and awkward movements (Quiatt 1996).

There are no other studies on the effect of disability on chacma baboons, and the data available for injury in natural baboon populations are mostly for adult males engaged in male-on-male contest (Archie *et al.* 2012; Drews 1996). These injuries are almost always temporary in nature with median healing times of 25 d (Archie *et al.* 2012). The study by Archie *et al.* (2012) reported 423 injuries in 144 adult male baboons over a 27-yr period in the Amboseli. Comparison of data sets are difficult because our study recorded human-induced injury in all age and sex classes and did not record male injuries from challenges for alpha status. However, a study of injury in chimpanzees (Munn 2006; Stokes 1999) found that disabilities did not have a significant influence on movement or foraging time. This may reflect the quality and distribution of food resources, in the habitats of these two primates, as these are known to influence the daily distances traveled to meet energetic needs. In periods of food scarcity baboons travel farther than when food is abundant (Anderson 1981; Barton *et al.* 1992; Davidge 1978b; Henzi *et al.* 1992; Hoffman and O'Riain 2011) with provisioned baboons (Altmann and Muruthi 1988), macaques (Fa 1998), and vervets (Saj *et al.* 1999) all traveling less than nonprovisioned groups. Peninsula baboons travel a mean of 6.2 km/d (Hoffman and O'Riain 2012) compared to chimpanzees, which travel only between 3 km (Wrangham 1977) and 3.9 km (Goodall 1968) per day. Injured chimpanzees in the tropical Budongo Forest may therefore not have to travel as far or as fast on a daily basis as baboons on the Cape Peninsula because tropical forests have a much higher primary productivity than the temperate fynbos biome (Cowling *et al.* 1996; Rebelo *et al.* 2006). Thus the effect of permanent injuries may be mitigated in more productive environments. Another possible explanation for the differences between this study and those of Munn (2006) and Stokes (1999) may be found in the type and severity of the injuries. Five of the seven disabled baboons in our study had either partial or complete loss of a limb or limbs. In contrast, only one of the five females had lost a hand in Munn's study (2006), and three of the eight chimpanzees had a hand or foot missing in Stokes' study (1999), with the most severely injured individuals halving their travel budget relative to the group (Munn 2006).

Given that limb loss impedes locomotion and results in disabled baboons spending more time inactive and traveling than uninjured individuals, it follows that they may be subject to higher predation risk. The baboons in our study showed no difference in the overall survival of disabled and uninjured individuals, and this finding may be attributed to both the lack of natural predators and the remarkable climbing ability of disabled baboons, which used the arboreal space equally as much as uninjured baboons. Chimpanzees with a forelimb injury are also known to move successfully in arboreal space using modified locomotory techniques (Munn 2006; Quiatt 1996). Humans and their dogs do kill baboons on the Peninsula but there is no correlation between disability and human-induced mortality (Beamish 2010). However, in predator-rich environments such as Moremi (Cheney *et al.* 2006) or Amboseli

(Altmann and Altmann 1970), disabled baboons would be predicted to experience much lower survival rates, which may explain their rarity in such areas. In a study of chimpanzees in the Budongo Forest, Uganda, severe injuries did not result in a reduction in time spent feeding (Munn 2006) and the feeding efficiency showed no significant difference (Stokes 1999). These injured individuals achieved efficient feeding and maximized their energy intake by targeting food items with minimum processing costs (Stokes and Byrne 2006). The disabled baboons in our study fed less but appeared to compensate by feeding significantly more on high-return anthropogenic foods compared to their uninjured counterparts. Such foods require less handling time and are more easily digested than food items from either indigenous or exotic vegetation (Altmann and Muruthi 1988; Forthman Quick 1986; Forthman Quick and Dement 1998). Thus injured baboons adopted a similar strategy to injured chimpanzees and maximized their energy intake by targeting foods with minimal processing costs, including high-return anthropogenic foods. Raiding is, however, a risky behavior for it often leads to conflict with humans and may result in either further injury or death (Beamish 2010; Kansky and Gaynor 2000; Strum 2005). It is possible that similar to other studies (Altmann and Altmann 1970; Hill 2000; Strum 1987) our presence may have reduced threats to the baboons including retributive attacks by raided humans, which in turn may have encouraged disabled baboons to raid more than uninjured baboons during the study.

Accessing the seeds within pine cones requires considerable manual dexterity and forelimb strength, and it is thus not surprising that disabled individuals spent less time feeding on this nutritionally valuable exotic food source. Baboons have dexterous feet, and when baboons with limited forelimb functionality fed on pine cones they compensated by using their feet to support the cones, while processing the item with the uninjured hand and/or teeth. Similarly Stokes (1999) noted that chimpanzees rarely use their feet in bimanual processing but individuals with an injured upper limb used their feet significantly more than their able-bodied counterparts. Grasses, by comparison, require little manipulation and are consumed at similar rates by disabled and uninjured baboons alike.

A small overall sample size compounded by infanticide ($N = 3$) and stillbirths ($N = 2$) prevented a statistical comparison of either interbirth intervals or the average number of offspring successfully weaned by disabled vs. uninjured females. However, the females in both groups had the same mean number of offspring born during the study (2.5 offspring/ female), suggesting that disability may not have a large impact on female reproductive fitness on the Peninsula although more data are needed to test the robustness of this finding, particularly during periods of food stress. Injured baboons fed equally on food items found above ground vs. below ground food despite the observations by Hill and Dunbar (2002) that foraging for food items above ground rather than digging for them yielded a higher energy return on foraging effort.

Disabled and uninjured baboons engaged for a similar amount of time in social behavior, suggesting that the maintenance of social bonds is equally important to both categories of baboons. Allogrooming is regarded as a strategy to reduce anxiety in primates (Shutt *et al.* 2007; Wittig *et al.* 2008), and self-grooming is part of a suite of self-directed behaviors (yawning, scratching) that correlate positively with anxiety and may be indicators of stress in nonhuman primates (Castles *et al.* 1999; Maestripieri *et al.* 1992; Stephenson *et al.* 2008). Our finding that the time allocated to self-grooming or to all grooming behaviors in disabled and uninjured baboons did not differ significantly is surprising, as one might expect disabled baboons to have higher levels of social vigilance and anxiety as a result of reduced competitive ability (Castles *et al.* 1999; Drews 1996; Stokes 1999). Though the reasons for this are not clear, it is possible that where food is not scarce or clumped and competition for food is not high that group members are tolerant of disabled individuals.

In conclusion, our results suggest that though disability may affect the behavior of baboons, the behavioral plasticity, absence of natural predators, and access to anthropogenic food sources may together reduce the impact on survival and the number of offspring born to baboons with disabilities. Contrary to our predictions, disabled baboons appeared to conserve their social budget and compensated for the reduced time spent foraging by consuming fewer foods with high handling costs and foraging for high-return anthropogenic foods. Our study was biased toward females, which inherit their social rank (Cheney 1977). The consequences of injury for social rank and reproduction may be higher for males, which compete for rank (Gesquiere *et al.* 2011; Palombit *et al.* 2000) and have rank-related reproductive success (Alberts *et al.* 2003; Palombit *et al.* 2000) than for females. Of relevance to ongoing management of the Peninsula population is the finding that disabled baboons consume significantly more raided food items than uninjured baboons, suggesting a possible relationship between injuries sustained and subsequent further raiding behavior to meet their energy demands with reduced locomotory and feeding capabilities. Permanent injuries are unique to groups living outside the CoGH Reserve, suggesting that they are a consequence of a commensal lifestyle and that management efforts need to focus on reducing the spatial overlap between baboons and both residential and agricultural areas.

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