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Postural infant carrying adaptations by wild eastern chimpanzees (*Pan troglodytes schweinfurthii*) with limb disabilities

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Short running title: Infant carrying by disabled chimpanzees

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Abstract: Wild primates can become disabled due to congenital disabilities, illness, or injuries from falls and traps. Given their substantial behavioral flexibility, individuals are often able to adapt locomotion and foraging techniques to their needs, but likely incur increased energetic costs. For disabled primate mothers, the combination of altered locomotion, lactation, and infant carrying could pose a substantial energetic challenge that requires specific accommodation. Here, we describe the postural adaptations for infant carrying used by five eastern chimpanzee (*Pan troglodytes schweinfurthii*) mothers with significant limb disabilities caused by snare injuries and compare their technique to non-disabled mothers in the same community. We describe shifts in ventral and dorsal infant carry location, as well as additional support provided to infants. Disabled mothers had altered preferences towards specific infant carrying styles and positions, and novel carrying positions not seen in non-disabled mothers. We suggest disabled chimpanzee mothers use postural adaptations to mitigate the energetic costs of infant carrying while disabled, shifting their infants' weight to an individually specific position. We discuss the plasticity of infant carrying, with individual variation present in both disabled and non-disabled mothers. We highlight that this plasticity is not unlimited, and that certain types of limb disability appear to have a substantial impact on reproductive success.

Keywords: infant carrying; snare injury; *Pan troglodytes*; locomotion; disability

Introduction

Load carrying, including infant carrying, increases energy expenditure during locomotion, and reduces travel speed and foraging efficacy (Pontzer & Wrangham, 2006). Walking on sloping or uneven terrain such as the densely vegetated mountainous or forested environments typical of many primate habitats, adds to energetic burdens (Green et al., 2020). Infant carrying and its energetic costs falls to mothers in most primate species (Ross, 2001; c.f.: Tardif, 1994), along with the already substantial energetic costs of gestation and lactation (Clutton-Brock et al., 1989; Emery Thompson et al., 2012; Murray et al., 2009; Prentice & Prentice, 1988). While a range of studies have explored the impacts of disabilities on primate behavior (for example: food processing: Millette et al., 2009; Nakamichi et al., 1983; Stokes & Byrne, 2001; locomotion: Cibot et al., 2016; Turner et al., 2012; social behavior: Turner et al., 2014, review: Stewart et al., 2024), few studies have investigated how disabled primate mothers cope with the combined costs of being disabled and carrying their infants. We discuss the cases of five female chimpanzees living in the Budongo Central Forest Reserve, Uganda and their postural accommodations for carrying infants while having major limb disabilities.

Primates experience a range of different disabilities. They can sustain significant injuries leading to permanent disability from falls (chimpanzees (*Pan troglodytes*) Boesch & Boesch-Achermann, 2000; Fannin et al., 2024; Goodall, 1986; Teleki, 1973; Shimada & Yano, 2023), bites (bonobos (*Pan paniscus*): Kano, 1984, spider monkeys (*Ateles geoffroy*): Chapman & Chapman, 1987), and being caught in hunting snare traps (bonobos: Furuichi et al., 2012; chimpanzees: Quiatt et al., 2002; Waller & Reynolds, 2001); as well as through illnesses like polio (chimpanzees: van Lawick-Goodall, 1968)

64 or yaws (mountain gorilla (*Gorilla beringei beringei*): Levréro et al., 2007). They may
65 also have congenital disabilities from exposure to pesticides and arboricides
66 (chimpanzees: Krief et al., 2014; macaques (hybrids of *M. mulatta, thibetana, fuscata,*
67 and *nemestrina*: Burton & Chan, 1989), inbreeding (chimpanzees: Sugiyama, 1984), or
68 other genetic factors (chimpanzees: Matsumoto et al., 2016; Goodall, 1986). The most
69 frequently described disabilities largely affect limbs, with consequences for individuals'
70 range of motion and locomotion (chimpanzees: Waller & Reynolds, 2001; Japanese
71 macaques (*Macaca fuscata*): Turner et al., 2008, bonobos: Kano, 1984), although cases
72 of facial dysplasia have also been documented in mountain gorillas (Levréro et al.,
73 2007), eastern chimpanzees (Krief et al., 2014), and olive baboons (*Papio Anubis*)
74 (Struhsaker et al., 2011).

75 Of all human-induced causes, immature and adult primates most commonly
76 sustain permanent disability through being caught in hunting traps. The most common
77 type are snares, a wire, nylon, or natural fiber loop placed over a small pit and secured
78 to a bent sapling or branches. When an animal steps into the pit, the snare is sprung and
79 tightens around the limb—trying to pull free only causes the wire to tighten further
80 (Noss, 1998; Waller & Reynolds, 2001). Steel jaw traps or 'man-traps', composed of
81 two metal jaws that close once the trap is activated by weight, inflict very substantial
82 injury but are less commonly used or survived (Munn, 2006; Waller & Reynolds, 2001).
83 While snare-traps are often targeted at non-primate species, such as duiker or pigs, they
84 are a leading cause of disability in highly terrestrial primate species, including
85 chimpanzees (Munn, 2003; Quiatt et al., 2002; Waller & Reynolds, 2001), and result in
86 a range of permanent injuries from relatively minor impacts on a finger or toe, to a
87 complete loss of limb function or loss of the limb itself (Quiatt et al., 2002; Waller &

Reynolds, 2001). Individuals with snare-trap injuries experience substantial secondary costs, including higher parasite loads (Yersin et al., 2017), as well as reduced travel speed and distance (Munn, 2006) and foraging efficacy (Byrne & Stokes, 2002). Snare injuries can also lead to death: Reynolds (2005) attributed two or three chimpanzee fatalities per year to snares in the Budongo Forest. The mortality risk is highest immediately after the injury: necrosis from infection (Boesch & Boesch-Achermann, 2000) or falls from high trees due to loss of balance while adapting locomotion to the injury (Cibot et al., 2019) can lead to death, especially for immature or older individuals. After the initial injury heals, survival rates of disabled primates are similar to those of non-disabled ones (Beamish & O'Riain, 2014), although there is a small, but non-negligible risk of lethal accidents that may have been avoidable for non-disabled primates (Tokuyama, 2019).

Conspecifics, including mothers, typically respond to disabled infants in a neutral or positive way (De Marco et al., 2022; spider monkeys: Chapman & Chapman, 1987; Japanese macaques: Nakamichi, 1986; chimpanzees: Sugiyama, 1984; Matsumoto et al., 2016; Shimada & Yano, 2023), including providing extra support (Chapman & Chapman, 1987; Matsumoto et al., 2016; Nakamichi, 1986; Turner et al., 2005), though infant survival varies strongly depending on the disability in question (Goodall, 1986; Matsumoto et al., 2016; Nakamichi et al., 1997, Sugiyama, 1984). Disabled adults do not appear to be socially ostracized either (Struhsaker et al., 2011; Turner et al., 2014; c.f.: van Lawick-Goodall, 1971). Relative reductions in time socializing are more likely to be driven by them allocating more of their time to resting, rather than via weaker social bonds (Turner et al., 2014), and the social spread of adaptive techniques from disabled to non-disabled group members illustrates their

112 social integration (eastern chimpanzees: Hobaiter & Byrne, 2010; bonobos: Toda et al.,
113 2016). However, disabled primates might face challenges in everyday life including
114 locomotion, feeding, food processing, socialization, and tool use, requiring them to
115 modify their behavior or employ novel behavioral variants. Studying the behavioral
116 impacts of disabilities and the quality of life of disabled adult individuals can provide
117 insight into the adaptive capacities and behavioral flexibility of a species. For human-
118 induced disabilities, such as snare-trap injuries, investigating cumulative lifetime
119 impacts beyond survival can inform conservation efforts.

120 A fundamental feature of daily primate life is terrestrial and arboreal
121 locomotion. Despite delayed motor development, Japanese macaques with limb
122 differences were able to move independently by modifying their posture, for example
123 through walking on the end of their stumps, hopping, or habitual bipedalism
124 (Nakamichi, 1986; Nakamichi et al., 1983; Turner et al., 2012). Chimpanzees with limb
125 disabilities also adapt their locomotion (Cibot et al., 2016; Goodall, 1986; Kummer et
126 al., 1985), with the type and severity of disability impacting the extent of modification.
127 In the Sebitoli community, most disabled primates can climb to the same height as non-
128 disabled ones, with the exception of those with extensive hand disabilities, who hang
129 less and rely on larger branches for self-support (Cibot et al., 2016). Disabled bonobos
130 also modify their locomotion: depending on which limb is affected they brachiate more
131 or less frequently than those without a limb disability, and those with missing or
132 paralyzed legs often move by "crutching", swinging the lower body forward while
133 leaning on both arms (Kano, 1984).

134 While allowing them to access resources and remain with social partners,
135 disabled primates' altered posture and locomotion seems to increase the energetic costs

136 of moving around for disabled primates (Millette et al., 2009; Turner et al., 2014).
137 Besides locomotion, disabled primates might also have to employ behavioral
138 adaptations to acquire a sufficient quantity and quality of food, with the additional
139 energetic demands of adapted locomotion further impact the costs of foraging whilst
140 disabled (Millette et al., 2009; Turner et al., 2014). Two complementary strategies are
141 prevalent: allocating more of one's time budget to foraging and/or adjusting foraging
142 methods to optimize efficacy. The first strategy is present in chimpanzees with
143 extensive limb disabilities, who forage for longer durations (Byrne & Stokes, 2002;
144 Cibot et al., 2016; Stokes & Byrne, 2001), as well as in ring-tailed lemurs, who forage
145 while conspecifics rest (Millette et al., 2009). Japanese macaques with extensive
146 congenital limb disabilities adapt their style of foraging behavior, instead of engaging in
147 scramble competition for provisioned food or soliciting food from visitors like non-
148 disabled conspecifics did, they often solicited food from researchers (Nakamichi, 1986;
149 Nakamichi et al., 1983; Turner et al., 2012). Gorillas and chimpanzees with hand
150 disabilities adapt manual food processing and drinking techniques to access otherwise
151 inedible plants and water (Stokes & Byrne, 2001; Péter et al., 2025); however, their
152 efficiency rarely matches that of non-disabled individuals, and is typically lower for
153 primates with more extensive disabilities (Byrne & Stokes, 2002; Stokes & Byrne,
154 2001).

155 While accounts of primate mothers' reactions to disabled infants exist in the
156 literature, little is known about infant-carrying and infant care when it is the mother who
157 is disabled (Stewart et al., 2024). Gestation, lactation, and infant carrying are known to
158 present a substantial energetic challenge for primate mothers (Clutton-Brock et al.,
159 1989; Emery Thompson et al., 2012; Murray et al., 2009, Ross, 2001), and for disabled

160 mothers, this may create an energetic and reproductive bottleneck due to their increased
161 energetic baseline costs of locomotion and foraging. Disabled mothers are clearly able
162 to cope with the energetic demands of gestation and lactation in some cases (King et al.,
163 2005; Munn, 2003; Struhsaker et al., 2011); however, infant mortality is higher under
164 some environmental conditions (King et al., 2005), and some behavioral adaptations
165 come at an additional cost to their infants (such as stopping to carry them at a younger
166 age; Munn, 2003). While we know that non-disabled mothers adapt their infant carrying
167 style to accommodate their disabled infants (Matsumoto et al., 2016; Nakamichi, 1986;
168 Turner et al., 2005), to date there has been only one case report in Japanese macaques
169 (Nakamichi, 2016) on whether similar carrying style adaptations are present when the
170 mother herself is disabled. In the case in question, a disabled female Japanese macaque,
171 Yuki, had extensive congenital limb loss, being born without hands. She employed an
172 altered infant carrying position, where she walked bipedally and clutched the infant to
173 her side with her forearm. With this strategy, two of her five infants made it to at least
174 two years of age, though she is reported to have abandoned an infant that was not
175 willing to be repositioned to her preference (Nakamichi, 2016).

176 Chimpanzee mothers carry their infants until the birth of their next infant,
177 usually around four to six years (Goodall, 1986). This long period of dependency occurs
178 in combination with lactation and means that infant carrying is a substantial energetic
179 challenge at a time of high general energetic costs for chimpanzee mothers to bear
180 (Pontzer & Wrangham, 2006). As a result, chimpanzees are a particularly suitable study
181 species for investigating disabled mothers' accommodations for infant carrying. We
182 describe five disabled adult female eastern chimpanzees (*Pan troglodytes*
183 *schweinfurthii*) living in the Waibira community in the Budongo Central Forest

Reserve, Uganda, and the postural adaptations they employ when carrying their non-disabled infants, as well as comparing these to carry postures of non-disabled females with similar aged infants.

Methods

Camera trap data collection received ethical approval from the University of Kent and the University of St Andrews, as well as the Budongo Conservation Field Station, the Uganda Wildlife Authority, and the Uganda National Council for Science and Technology. The study conformed to the IPS Code of Best Practices for Field Primatology and the ASP Principles for the Ethical Treatment of Non-Human Primates.

Positionality Statement

We recognize that care must be taken when discussing and describing disability, whether in the context of people or other species, extending to using terminology that is up-to-date and commonly accepted within the disabled community and disability studies. To situate the paper in a specific epistemic position that discusses disability from a within-group viewpoint, we note that the first author of the study, HP, is herself disabled. We recognize that experiences and preferences within the community are not universal, and care must be taken to solicit other opinions, especially when writing about conditions other than one's own. For this reason, we also sought a sensitivity reader to provide a second viewpoint. While she does not experience the specific disability discussed in this paper, limb difference or loss, Alyssa Paparella is the founder of DisabledInSTEM, an online platform offering support, mentorship, and

community to disabled scientists (Bahumik & Paparella, 2025). Within the disabled community and in disability literature, there are two common approaches to describing individuals: people-first terminology (e.g. person with disability) and identity-first terminology (e.g. disabled person). Throughout this paper, we use identity-first terminology to discuss our study subjects and other primates, reflecting the personal preferences of HP.

Study Population

The Waibira community lives in the Budongo Central Forest Reserve, Uganda (1°35′-1°55′ N, 31°18′-31°42′ E, mean altitude 1050 m). The forest is a medium-altitude, semi-deciduous forest (Eggeling, 1947), with a warm tropical climate, receiving an annual mean precipitation of 1659 mm (1993-2021, BCFS unpublished data) The community numbers ~120 individuals, is surrounded by an estimated four other communities, and has no direct access to human settlements. Habituation started in 2011 (Samuni et al., 2014) and staff and researchers from the Budongo Conservation Field Station (BCFS) follow individuals daily between 6 a.m. and 6 p.m. while recording long-term behavioral data on activity, location, and party composition. Snare injuries are common in the Budongo Forest—while the chimpanzees themselves are not the target of hunting, they are caught in the wire snares used to hunt pigs and small antelopes (Quiatt et al., 2002). A snare removal team operates at BCFS, and removes an average of 220 snares per month from the forest, but snaring injuries still occasionally occur (Amati et al., 2008; Reynolds, 2005; Yersin et al., 2017).

Subjects

The subjects of this study were five adult females in the Waibira community with extensive disabilities (as classified by Cibot et al., 2016; Table 1): two with extensive foot disabilities and three with extensive hand disabilities. All five females became disabled prior to the beginning of observation in the community. All infants described were non-disabled. While the original injuries were not observed, the mothers' disabilities were considered most likely the result of snare-trap injuries as evidenced by bald patches on wrists, clean injury edges, as well as being in the form of common snare injury types, such as extensively contracted—'hooked' or 'twisted'—and immobile limbs (Waller & Reynolds, 2001).

1) Tatu is missing part of her lower left leg, with both the fibula and tibia cut around mid-shin. While she has full use of her intact right leg, she moves terrestrially by "crutching"—putting her body weight on her arms and swinging her lower body forward—which results in a more upright posture (Figure 1A, Video S1a). When moving arboreally, she crutches on vertical branches and climbs tree trunks by putting her tibia stump on her injured leg against the trunk.
2) Jinja is missing her right hand from the wrist, with no fingers or grasping capacity remaining, but an intact ulna and radius. When moving terrestrially, she holds the arm slightly bent towards her chest, not putting any weight on it (Figure 1B, Video S1b). Arboreally, she supports herself and climbs by hooking branches and tree trunks with her lower forearm.
3) Santa has a twisted right foot, with the entire foot facing backwards and upside down from the ankle, and with no grasping capacity apparent. The

first two segments of the fifth digit are also missing. She walks on the back of her foot and part of her tibia on that leg and occasionally 'crutches' (Figure 1C, Video S1c). She climbs tree trunks by putting her tibia and twisted foot against the trunk.

4) Chappati has an extensively contracted right hand. The arm is atrophied with no hair from mid-lower arm, the wrist permanently bent, and the fingers apparently fused together. She has no visible thumb, and no apparent range of movement in the wrist or fingers. She walks with the arm bent at the elbow, and the hand held out before her body with the back of the hand facing forward. She occasionally puts it down for support, walking on the metacarpals instead of the phalanges (Figure 1D, Video S1d). Arboreally, she occasionally uses the snare-injured hand for support by hooking branches with it.

5) Mathaai is missing her right hand at the wrist with intact ulna and radius, and has extensive finger loss on her left, with only the second digit remaining. Her left wrist and remaining finger are mobile, and she has been seen using them to pinch-grip drinking tools. However, her locomotion is severely impacted—while terrestrial, she either supports herself on one of her arms, walking on the stump instead of knuckle walking, or resorts to habitual bipedalism (Figure 1E, Video S1e).

Data Collection

Data collection was based on camera-trap videos. In doing so, we control for the potential impact of observers on female locomotion; as, despite habituation starting in

2011 (Samuni et al., 2014), some females in the community, including some of our subjects are only partially habituated and camera-trap based observations likely represent their typical locomotory behavior. While direct observations would have provided important additional context, they were not possible with these individuals. Mathaai is very rarely observed (directly observed only once or twice a year) and is likely to move more quickly or arboreally when in the presence of human observers. Santa and Chappati are less-well habituated females, and prefer to remain arboreal in the presence of human observers. Finally, infant carrying behavior is not recorded as part of the day-to-day observational data collection in the community, meaning no long-term observational data were available on either disabled or non-disabled individuals.

The camera trap videos used in this study are taken from the water hole at the center of the community's home range, which has been monitored with Bushnell No-Glow camera traps since January 2013 for every December to March dry season (2013–2017, single trap; 2017-present, two traps; Péter et al., 2022). The water hole is a seasonally important resource and provides information on both drinking and tool behaviour and of the presence of individuals in the community. The water hole itself is located in a valley, and consists of a 5 m long straight, shallow creek bed section, and a broader, 10 m x 10 m section with puddles and sandbanks. Videos used in this study were recorded between February 2013 and March 2022. The cameras were set to run 24 h/day, recording 60 s videos during the day, and 15 s videos during the night (infra-red), with a 1 s pause between successive videos and the sensor sensitivity set to high. Maintenance visits were scheduled every three to five days.

Data Analysis

We analyzed camera trap videos for each of the five disabled focal females and their non-disabled infants as well as for five control females and their infants. Control females and infants were selected by age-matching an infant born to a non-disabled female in the same year (Table 1 & 2). In one case (Chapatti and Chakka-mungo), there were no data on an infant born in the same year to a non-disabled female, and her carrying style was compared to an age-matched infant born in the previous year (Rita and Rwenzori).

We coded all videos in which the mother arrived at or left the waterhole while carrying her infant (we also made note of videos in which an infant under sixty months of age arrived at or left the waterhole without being carried; $n = 3$). Each carrying position observed within a video was treated as an individual data-point; however, observations of an infant being carried in two different positions within the same video were rare ($n = 2$).

For each observation, we recorded mother and infant identity, date, whether the infant was carried ventrally or dorsally, the lateral and longitudinal position of the infant being carried, and whether the mother provided additional support to the infant with a limb. If the lateral or longitudinal carrying position was not clearly visible, we only coded the dorsal/ventral for carrying position.

- We described three lateral positions: Left, Right, and Center; defined by whether the infant's line of spine was aligned with that of the mother or sat to the Left or Right of it. Cases where part of the infant's body larger than a single limb (e.g., leg or arm) was laterally shifted (for example their lower spine, legs, and pelvis

sat to one side of the mother's spine) as well as cases where the shift included the whole body of the infant were coded as shifted to the specific side.

- We described four longitudinal positions, Low, Middle, High, Very high; defined by the location of the infant's torso relative to the mother's. A Low position was defined as the infant's torso sat on or above the pelvis, just below the lower ribs of the mother. A Middle position was defined as the infant's torso sat above the pelvis, and overlapped with the ribcage of the mother. A High position was defined as the infant's torso sat fully on the ribcage of the mother, including up to and on the shoulder blades; and a Very High position was defined as the infant's torso sat on or above the shoulder blades of the mother, including on her head.

Videos were coded by HP, and inter-observer reliability was provided by CH as percentage agreement (as there was substantial skew in the distribution of the positions, making Cohen's Kappa unsuitable). Agreement was high across all three measures: ventral-dorsal = 93.75%, lateral position = 87.50%, longitudinal position = 75.00%).

Chi-square tests were used to compare the frequencies of behaviors observed in disabled mothers to that of non-disabled mothers. In one case, where the expected proportion was zero, a binomial test of goodness-of-fit was used. Chi-square and goodness-of-fit tests were calculated by hand. Observations where the specific positioning type was not clearly visible were excluded from the relevant analysis.

346 **Results**

347 We analyzed a total 255 camera trap videos, 100 of the five disabled focal
348 mothers and 155 of the control mothers. Videos of more than one infant were available
349 for two of the disabled focal mothers.

350 *General carry location*

351 Of the total 255 observations, mothers carried their infants ventrally in $n = 112$
352 cases (43.9% of observations; disabled mothers: $n = 66$; non-disabled mothers: $n = 46$)
353 and dorsally in 142 cases (55.7% of observations; disabled mothers: $n = 34$; non-
354 disabled mothers: $n = 108$; one video was excluded as play behavior with the infant
355 hanging off her mother's legs). Disabled mothers were more likely to carry their infants
356 ventrally rather than dorsally, as compared to non-disabled controls (Chi-square: X^2 (1,
357 N = 100) = 62.32, $p < 0.001$).

358 *Lateral and longitudinal shifts in carry location*

359 Lateral shifts in ventral carrying position were only observed in disabled
360 mothers (14.5% of observations; $\underline{n} = 37$, Table 3), though they did not preferentially
361 carry their infants shifted to the side when they were ventral (Chi-square: X^2 (1, N = 63)
362 = 1.92, $p = 0.166$, Figure 2A, Table 3).

363 All longitudinal locations (from Low to Very High) in ventral carrying position
364 were observed both in disabled and non-disabled mothers (Table 4). However, the
365 patterns within the two groups differed, with disabled mothers more likely to carry their
366 infant in a High position as compared to non-disabled mothers (Chi-square: X^2 (2, N =
367 58) = 59.83, $p < 0.001$; Figure 2B, Table 4). Both disabled (Chi-square: X^2 (2, N = 58) =
368 11.83, $p = 0.001$, Figure 2, Table 4) and non-disabled mothers (Chi-square: X^2 (2, N =

369 43) = 35.49, p < 0.001, Figure 2, Table 4) were most likely to carry their infants in a
370 Low longitudinal ventral carry position.

371 In contrast to the patterns seen in ventral carrying, lateral shifts in dorsal
372 carrying were seen both in disabled and non-disabled mothers (Table 5). Preferences
373 differed between the two groups (Chi-square: X^2 (1, N = 33) = 4.60, p = 0.016, Figure
374 2C, Table 5). Disabled mothers showed a stronger preference for Middle position
375 carrying when their infants were dorsal (Chi-square: X^2 (1, N = 33) = 25.49, p < 0.001,
376 Figure 2C, Table 5) as compared to non-disabled mothers (Chi-square: X^2 (1, N = 108)
377 = 40.33, p < 0.001, Figure 2C, Table 5).

378 The Very high dorsal longitudinal carrying position was only observed in
379 disabled mothers (Table 6). Across dorsal longitudinal carrying positions, disabled
380 mothers showed different carrying patterns as compared to non-disabled mothers, even
381 when observations of Very high locations were excluded (Chi-square: X^2 (2, N = 27) =
382 31.61, p < 0.001, Figure 2D, Table 6). Disabled mothers carried their infants higher than
383 non-disabled mothers, preferring High and Middle dorsal locations (Chi-square: X^2 (3,
384 N = 33) = 14.64, p < 0.001, Figure 2D, Table 6), while non-disabled mothers most often
385 carried their infants in Middle and Low dorsal locations (Chi-square: X^2 (2, N = 107) =
386 13.48, p < 0.001, Figure 2D, Table 6)

387

388 *Additional support*

389 Only disabled mothers were observed to provide additional support to their
390 infants while carrying them (disabled mothers: n = 36 of 100 observations, non-disabled
391 mothers: n = 0 of 155; exact binomial test of goodness-of-fit: p < 0.001). Four of the

five disabled mothers (all except Santa) provided additional support, and support was provided to infants up to three years old (2-27 months). Tatu, Jinja, and Mathaai used their snare-injured limb for support, while Chappati only used her non-injured hand. Additional support was only provided to infants being carried ventrally.

Tatu

We analyzed 37 videos for Tatu (disabled mother) and her infant Teddy, recorded between February 2021 and March 2022. Teddy was aged 15 months in the 2020/2021 observation season, and 26-27 months in the 2021/2022 observation season. Of the 37 observations, Teddy was carried ventrally in 22, dorsally in 14, and in both positions in one. Tatu showed postural adaptations in both. Ventral carrying: Teddy clung while shifted to the Left side of her mother in 14 out of 23 ventral carry observations (lateral position unknown: $n = 1$), with Tatu (disabled chimpanzee) supporting her with her injured left leg and knee in 19 observations (support unknown: $n = 3$; Video S2a). Dorsal carrying: Teddy sat further forward than control infants, typically with her body over Tatu's shoulder blades with the arms draped over her shoulders in a High ($n = 9$ of 15) or Very high ($n = 6$) position, with her body resting over Tatu's shoulders, arms circling her neck, and chin propped on her head. In both dorsal carry positions, Teddy's legs appear to be less bent at the knees and extended further down along her mother's body those of control infants (Video S2b).

Non-disabled control: We analyzed 31 videos for Ndito-Eve (control mother) and her fourth infant, Ngogo, recorded between February 2021 and March 2022. Ngogo was 16 months old in the 2020/2021 observation season, and 28-29 months old in the

2021/2022 observation season. Of the 31 observations, Ngogo was carried ventrally in two, and dorsally in 29. Ventral carrying: Ngogo clung in a Middle position in both observations, with no support from Ndito-Eve. Dorsal carrying: Ngogo typically sat in a Low position on Ndito-Eve's back, around the top of the pelvis (n = 12 out of 29 observations) or mid-back between the pelvis and the ribcage (n = 13; longitudinal position unknown: n =1). He sat in a High position (over Ndito-Eve's shoulder blades) in three observations, sitting upright in a jockey position in one of them, and clinging with bent legs in the other two.

Jinja

We analyzed 15 videos for Jinja (disabled mother) and her infant Jake, recorded between February 2021 and March 2022. Jake was 15 months old in the 2020/2021 observation season, and 25-26 months old in the 2021/2022 observation season. Jake was carried ventrally in all 15 observations. Jinja adapted her infant carrying style, Jake clung to the Right side and in a Middle position (around the height of Jinja's ribcage) in 13 out of 15 observations. Jinja supported Jake with her injured right arm in 10 out of 15 observations (support unknown: n = 15), holding him closer to her chest (Video S3).

Non-disabled control: We analyzed 25 videos for Ketie (control mother) and her infant Kalinzu, recorded between February 2021 and April 2022. Kalinzu was 14-15 months old in the 2020/2021 observation season, and 26-28 months old in the 2021/2022 observation season. Kalinzu was carried ventrally in 10 observations and dorsally in 15. Ventral carrying: Kalinzu was carried in a Central position in all ventral carry observations (lateral position unknown: n = 1), with no additional support from

Ketie. Dorsal carrying: Kalinzu was predominantly carried in a Middle (at mid-back height, $n = 9$ of 15 observations) or a Low position around the top of the pelvis ($n = 5$) during dorsal carries. He was carried in a High position on the shoulders once, clinging with bent legs.

Santa

We analyzed 22 videos for Santa (disabled mother), eight for her first infant, Sadaka, recorded between February 2015 and February 2017, and 14 for Scovia, her second infant, recorded between February 2021 and March 2022. Sadaka was 1 month old in the 2014/2015 observation season, 14 months old in the 2016/2017 observation season, and 26 months old in the 2017/2018 observation season. Scovia was 14-15 months old in the 2020/2021 observation season, and 26-27 months old in the 2021/2022 observation season. Sadaka was carried ventrally in three observations, and dorsally in five. He clung to the Right in one of three ventral carry observations, and sat Central in all five dorsal carry observations. The last observation of Sadaka being carried was at the age of 26 months in February 2018. The first observation of Sadaka travelling alongside Santa, without being carried was in January 2018, followed by two more in February 2018. Sadaka disappeared (likely died) in 2018. Scovia was carried ventrally in seven observations, and dorsally in seven. She clung in a Central position in in both ventral and dorsal positions ($n = 12$ of 14 observations, lateral position unknown: $n = 1$). Santa did not visibly adapt her infant carrying technique to her disability, but the last observation of Sadaka being carried is from a relatively young age (26 months).

Non-disabled control: We analyzed 20 videos for Ndito-Eve (control mother) and her third infant, Nimba, recorded between February 2016 and February 2018. Nimba was aged 5 months old in the 2015/2016 observation season, 17 months old in the 2016/2017 observation season, and 27-28 months old in the 2017/2018 observation season. Nimba was carried ventrally in six observations and dorsally in 14. Ventral carrying: Nimba clung in a Central position in all eight observations, with no additional support from Ndito-Eve. Dorsal carrying: Nimba predominantly sat in a Low (n = 10 of 14 observations) or a Middle position (n = 4). Nimba was carried shifted to the Left side in five of 14 dorsal carry observations. Ketie and Kalinzu, described above under Jinja, also served as a control for observations of Santa and Scovia.

Chappati

We analyzed 18 videos for Chappati (disabled chimpanzee), 14 for her second infant, Ciska, recorded between February 2014 and January 2019, and four for Chakka-mungo, her third infant, recorded between March 2021 and February 2022. Ciska was aged 15-17 months in the 2013/2014 observation season, 52-53 in the 2016/2017 observation season, 64-65 months old in the 2017/2018 observation season, and 75-77 months old in the 2018/2019 observation season. Chakka-mungo was 10-13 months old in the 2021/2022 observation season. Ciska was carried ventrally in nine observations, and dorsally in five, while Chakka-mungo was carried ventrally in two observations and dorsally in two. Both infants sat in a Central position while ventral and dorsal (n = 17 out of 18; ventral lateral position unknown: n = 1 observation). Chappati did not support either infant with her injured arm, only her intact one (support given n = 1 observation;

484 support unknown $n = 1$). The last observation of Ciska being carried was at 77 months
485 of age, after which she was only observed travelling independently.

486 Non-disabled control for Chappati-Ciska: We analyzed 45 videos for Byazi
487 (control female) and her infant Baraka, recorded between January 2013 and February
488 2017. Baraka was aged 8-11 months in the 2012/2013 observation season, 19-21 in the
489 2013/2014 observation season, 33-34 months old in the 2014/2015 observation season,
490 45 months old in the 2015/2016 observation season, and 56-57 months old in the
491 2016/2017 observation season. Baraka was carried ventrally in 12 observations, and
492 dorsally in 33. Ventral carrying: Baraka was carried in a Central position in all
493 observations, with no additional support from Byazi. Dorsal carrying: Baraka sat in a
494 Middle position in 18 out of 33 observations, and in a High position (clinging with his
495 body resting on Byazi's shoulder with bent legs) in 15 observations.

496 Non-disabled control for Chappati-Chaka-mungo: We analyzed 18 videos for
497 Rita (control female) and her infant Rwenzori, recorded between January 2017 and
498 February 2018. Rwenzori was 6-7 months old in the 2016/2017 observation season, and
499 16-18 months old in the 2017/2018 observation season. Rwenzori was carried ventrally
500 in three, dorsally in 13, and both ways in one. He hung from the back of Rita's legs in
501 one observation, holding onto her thighs and calves (excluded from analyses). Ventral
502 carrying: Rwenzori was carried in a Central position, with no additional support from
503 Rita in all four observations. Dorsal carrying: Rwenzori was most often carried in a
504 Low position ($n = 9$ of 14 observations), followed by a Middle position ($n = 5$). The last
505 observation of Baraka being carried was at 57 months of age. The next available video
506 was a year later, at which time Byazi had a new infant and Baraka was only observed to
507 travel independently.

508

509 Mathaai

510 We analyzed seven videos for Mathaai (disabled chimpanzee) and her first
511 infant, MAT1, recorded between February 2013 and February 2014. MAT1 was 2-3
512 months old in the 2012/2013 observation season, and 13-14 months old in the
513 2013/2014 observation season. Mathaai carried her infant ventrally in all seven
514 observations. MAT1 typically clung in a Middle position (n = 4 observations; lateral
515 position unknown n = 1) while Mathaai supported them with her right arm (n = 6
516 observations, support unknown n = 1; Video S4a). In February 2014 she was observed
517 using a similar technique to Jinja (disabled chimpanzee), shifting the infant to a High
518 ventral position slightly to the Right, and supporting them with her right arm, even
519 while walking bipedally (n = 2 observations; Video S4b). MAT1 disappeared (likely
520 died) in 2014.

521 Non-disabled control: We analyzed 15 videos for Bahati (control female) and
522 Balvenie, recorded between January 2013 and February 2014. Balvenie was 3-5 months
523 old in the 2012/2013 observation period, and 14-16 months old in the 2013/2014
524 observation period. Balvenie was carried ventrally in 12, and dorsally in three. Ventral
525 carrying: Balvenie was carried in a Middle and Low position, around the stomach, in
526 most observations (n = 7 of 12 observations, longitudinal location unknown: n = 2),
527 with no support from Bahati. Dorsal carrying: Balvenie was carried in a Middle position
528 in two observations, and in a High position on the shoulder blades in one. Balvenie
529 disappeared (likely died) in 2014.

530

Discussion

Disabled chimpanzee mothers employed various postural adaptations to infant carrying. These adaptations fell under two categories: first, altered preferences towards specific carrying styles and positions seen less frequently in non-disabled mothers, and second, novel carrying positions not seen in non-disabled mothers. Disabled mothers were more likely to carry their infants ventrally as compared with non-disabled mothers, as well as in a High longitudinal position both ventrally and dorsally, and a Middle position dorsally. Lateral shifting of infants during ventral carrying, dorsally carrying infants in a Very high position (at the height of the neck), and the provision of additional support were unique to disabled mothers in our sample. Their general preference for ventral infant carrying could also contribute to an earlier end of infant carrying, as documented by Munn (2003): as infants grow too large to be comfortably carried ventrally (disabled mothers' preferred position), disabled mothers may reach their energetic limit and stop carrying them at a smaller body size and weight than non-disabled ones.

Disabled chimpanzee mothers, who already face an increase in their baseline energetic needs as compared to non-disabled mothers (Millette et al., 2009; Turner et al., 2014), likely shift the weight of their infant to an individually preferred position to actively mitigate the increased locomotor costs of infant carrying while disabled. While a combined effort from mother and infant is needed to maintain a carrying position, it is unclear to what extent these postural adaptations are driven by the mother actively directing the infant to her preferred position, or by the infant shifting to a more stable or comfortable carrying position, or both. In Nakamichi's (2016) case report, he describes a potential conflict between maternal and infant positional preferences where, after four

555 days of unsuccessful repositioning attempts, the female macaque abandoned her infant.
556 To explore how postural adaptations are initiated and maintained by the mother-infant
557 dyad, as well as potential conflicts between the preferences of the two and how they
558 may be resolved, future research could incorporate repositioning attempts (successful or
559 unsuccessful), as well as whether they are initiated by the mother or infant, and compare
560 carrying behavior between offspring of multiparous disabled mothers.

561 Some disabled chimpanzee mothers are able to cope with the costs of infant
562 carrying, even with extensive limb disabilities: all but one of the disabled mothers in our
563 sample raised an infant to independence. However, there may be an upper limit to the
564 energetic or locomotory burden of disabilities for which they can effectively
565 compensate. Mathaai, who has extensive injuries to both hands, has been seen with at
566 least three separate infants; however, to date none have survived past the age of 11
567 months. While infant mortality is high in chimpanzees (Nishida et al., 2003; Wittig &
568 Boesch, 2019), and we were unable ascertain the exact cause of death of her infants, it is
569 likely that the joint demands of locomotion, foraging, and infant carrying with a double
570 major disability contributed to the high rate of infant mortality she has experienced. The
571 only pre-existing case report of infant carrying strategies by disabled primate mothers
572 features a female macaque with the same disability as Mathaai, who had two infants out
573 of five survive to at least two years of age (Nakamichi, 2016). It is possible that Mathaai
574 may at some point raise an infant to weaning age; however, the much longer period of
575 infant dependency in chimpanzees (as compared to macaques) increases the challenge
576 of doing so.

577 An overall increase in physiological stress is not a necessary outcome of
578 disability: in Japanese macaques, being a disabled mother did not correlate with

increased stress levels (Turner et al., 2023). A comparison of stress levels and body condition between disabled and non-disabled female chimpanzees could help us to better understand the demands of specific energetic landscapes at different reproductive states and identify possible thresholds for fitness and infant survival, as well as the ways in which chimpanzee mothers accommodate any additional costs.

While disabled chimpanzee mothers shared some forms of adjustment, we also observed substantial interindividual variation in infant carrying style, with each female appearing to alter her carrying posture to accommodate her specific disability. One example of this was the prevalence of Very high dorsal longitudinal carrying position in disabled mothers. This trend was likely driven by Tatu, the only mother in our sample who habitually moved by "crutching" when on the ground, which results in a more upright posture. Individual differences in carrying style were also present in non-disabled females, suggesting that a certain amount of variation is present in infant carrying behavior even when it is not constrained by accommodation of disabilities. Larger sample sizes across individuals and populations, as well as longitudinal observations of mothers with multiple infants are needed to begin to disentangle variation driven by the mother, from that shaped by the infant. Recent advances in automated pose-estimation in footage of wild apes (e.g., Wiltshire et al., 2023) will also allow for more nuanced and continuous measures of locomotion and carrying positions, allowing us to better quantify individual variations and similarities in infant carrying behavior in both disabled and non-disabled chimpanzees.

We describe the adaptations disabled mothers make to their carrying style to accommodate the additional costs of locomotion they bear. Most of the mothers in our sample appear to do so successfully, with only one individual—who has an extensive

603 disability impacting both hands—not observed to successfully raise an infant to
604 independence. We highlight the similarities and individual differences present in both
605 disabled and non-disabled mothers, demonstrating the substantial behavioral plasticity
606 in chimpanzee infant-carrying behavior. Studying the prevalence and adaptability of
607 disabled primates is also key for conservation efforts (Quiatt et al., 2002); 60% of all
608 published accounts of disability in wild primates connect its origins to human activity
609 (Stewart et al., 2024). Comprehensive accounts of the costs disabled primates
610 experience can help highlight the importance of protective measures such as snare trap
611 removal (Reynolds, 2006) and pesticide control (Burton & Chan, 1989), and in doing so
612 influence policy and funding priorities. Investigating the impact of specific categories
613 and extents of disability can also inform potential veterinary interventions by
614 quantifying the impact on quality of life. For example, when considering infant care, the
615 loss of fingers and motion in both hands (as experienced by Mathaai), appears to be
616 more challenging than the loss of most of a leg (as experienced by Tatu), highlighting
617 the importance of manual dexterity and mobility in chimpanzees. Finally, a richer
618 understanding of the range of adaptations present in other apes can shed light on the
619 evolution and presence of social care in early humans; for example: by determining the
620 degree of disability individual primates can compensate for without significant care or
621 assistance from conspecifics (Degusta, 2002; Tilley & Oxenham, 2011), and the
622 consequences of increased bipedalism on infant carrying.

623

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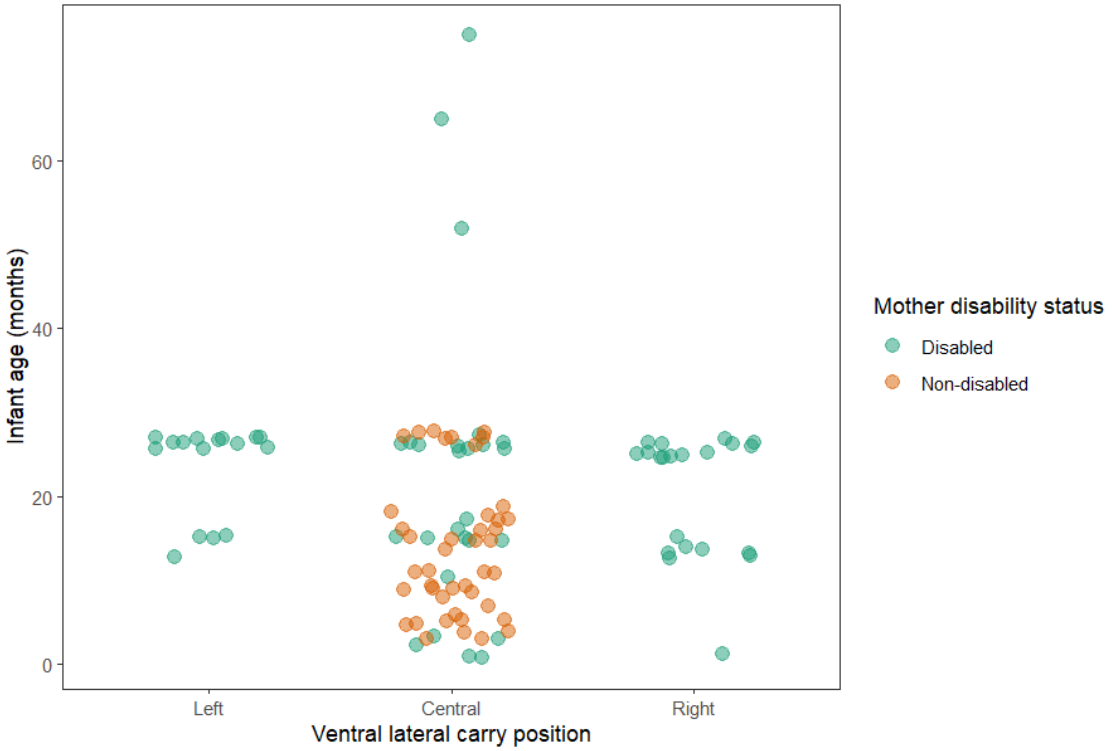
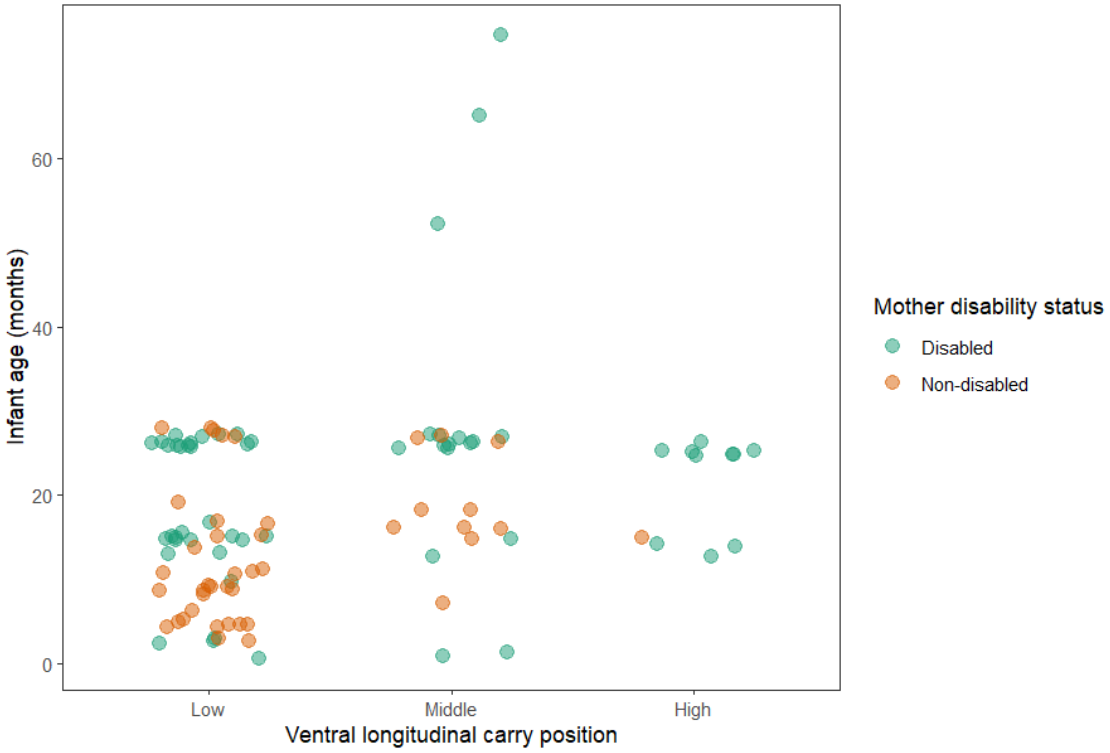
Fig. 1 Camera trap screenshot showing the extent of limb disabilities in the disabled mothers. A) Tatu, B) Jinja, C) Santa, D) Chappati, and E) Mathaai

Fig. 2 Jitter plot showing the number of observations in which a mother carried her infant in a specific position for disabled and non-disabled control mother across dorsal and ventral carry positions and lateral and longitudinal positions. Lateral positions are Left, Central, and Right, while longitudinal positions are Low, Middle, High, and Very high. A) ventral lateral carry positions, B) ventral longitudinal carry positions, C) dorsal lateral carry positions, D) dorsal longitudinal carry positions.





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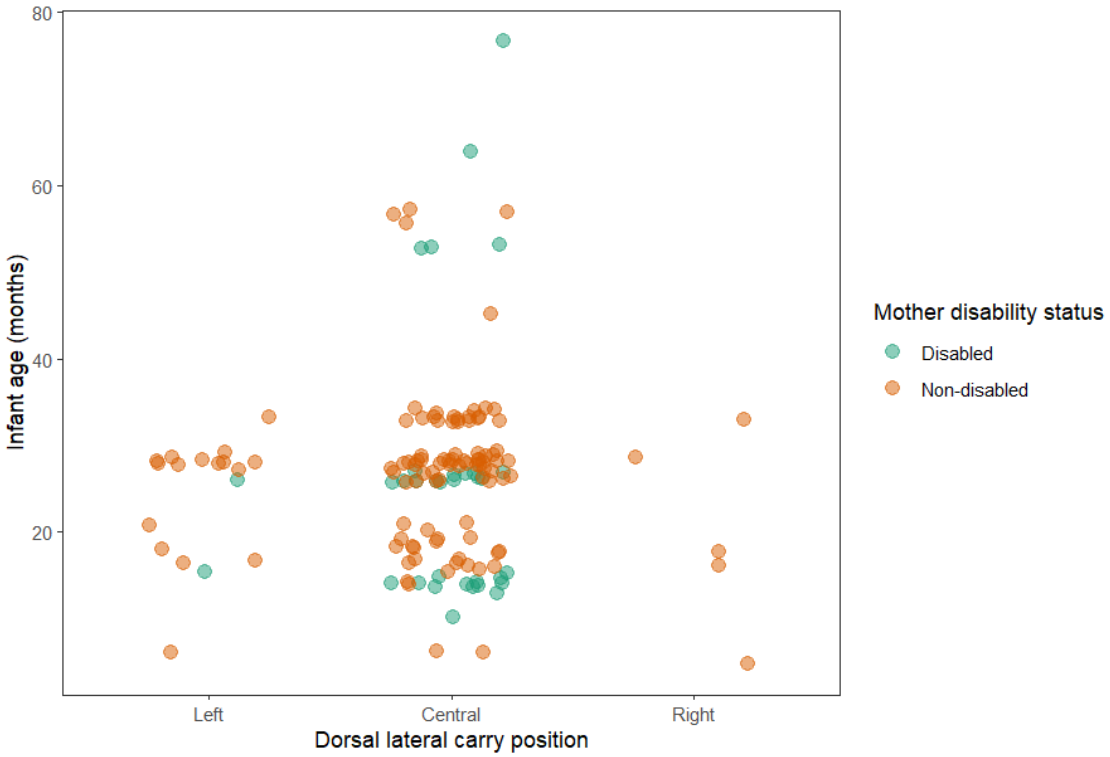

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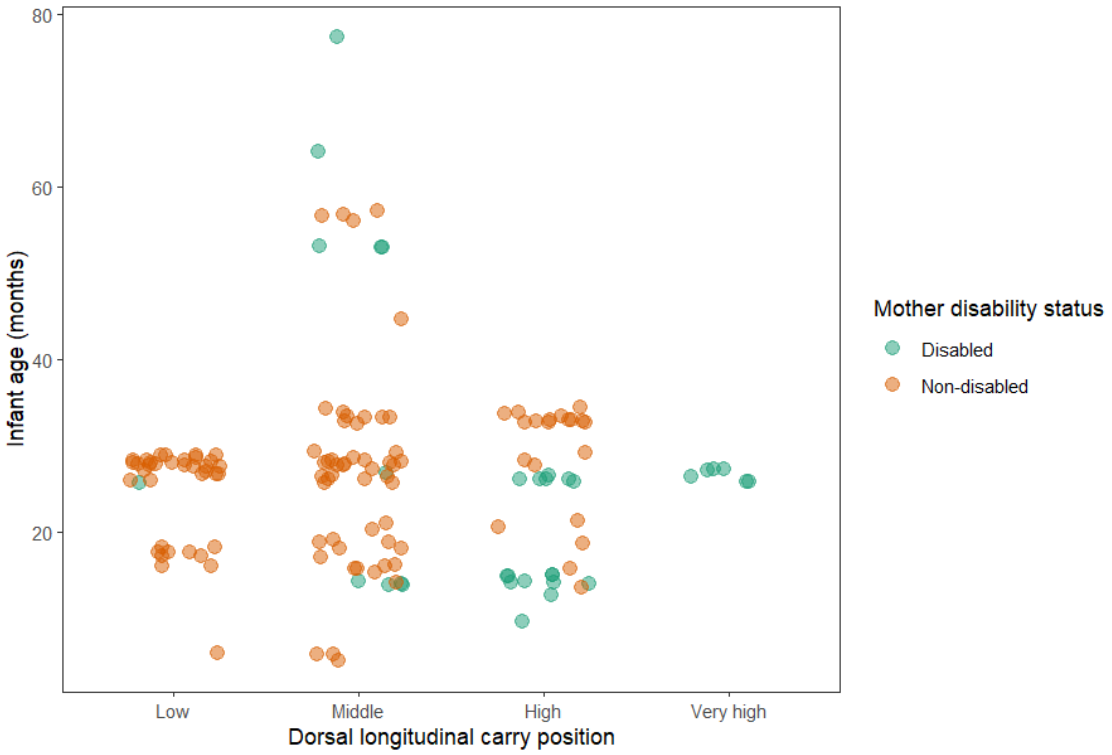

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876 **Table 1** The names, birth histories, and disabilities of the five disabled mothers. The

877 names, sex, estimated birth dates and age range in which data is available from; and

878 which control mother-infant dyad with which they were matched.

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Female	Age	Birth history	Disability	Infant	Infant birth date	Infant age	Paired
Tatu	1999±1yr	Primiparous	Left leg loss	Teddy ♀	Aug 2019	15-27 months	Ndito-Eve & Ngogo
Jinja	1988±3yrs	Primiparous	Left hand loss	Jake ♂	Oct 2019	13-26 months	Ketie & Kalinzu
Santa	2000±1yr	Primiparous	Twisted leg	Sadaka ♂	2015±6mths	1-26 months	Ndito-Eve & Nimba
		Multiparous		Scovia ♀	Dec 2019	14-27 months	Ketie & Kalinzu
Chappati	1990±5yrs	Multiparous	Twisted hand	Ciska ♀	Sept 2012	15-77 months	Byazi & Baraka
		Multiparous		Chakka-mungo ♂	May 2020	10-13 months	Rita & Rwenzori
Mathaai	1990±2yrs	Primiparous	Double hand loss	MAT1 UN	Dec 2012	2-14 months	Bahati & Balvenie

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Table 2 The names and birth histories of the control mothers. The names, sex, estimated birth dates, and age range in which data were available from of control infants; and the disabled mother-infant dyad with which they were matched. Control females and infants were selected by age-matching an infant born to a non-disabled female in the same year.

Control female	Birth history	Infant	Infant birth date	Infant age	Paired
Ndito-Eve	Multiparous	Ngogo ♂	Sept 2019	16-29 months	Tatu & Teddy
Ketie	Primiparous	Kalinzu ♂	Dec 2019	14-28 months	Jinja & Jake, Santa & Scovia
Ndito-Eve	Multiparous	Nimba ♀	Aug 2015	5-28 months	Santa & Sadaka
Byazi	Primiparous	Baraka ♂	Apr 2012	9-57 months	Chappati & Ciska
Rita	Multiparous	Rwenzori ♂	Jul 2016	6-18 months	Chappati & Chakka-mungo
Bahati	Primiparous	Balvenie ♂	Sept 2012	3-16 months	Mathaai & MAT1

895 **Table 3** Summary of lateral ventral carrying positions for disabled and non-disabled
896 mothers.

	Group	
Position	Disabled	Non-disabled
Left	16	0
Central	26	43
Right	21	0
Unknown	3	3
Total	66	46

897

898 **Table 4** Summary of longitudinal ventral carrying positions for disabled and non-
899 disabled mothers.

	Group	
Position	Disabled	Non-disabled
Low	31	32
Middle	17	10
High	10	1
Unknown	8	3
Total	66	46

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904 **Table 5** Summary of lateral dorsal carrying positions for disabled and non-disabled
905 mothers.

	Group	
Position	Disabled	Non-disabled
Left	2	16
Central	31	87
Right	0	5
Unknown	1	0
Total	34	108

906

907 **Table 6** Summary of longitudinal dorsal carrying positions for disabled and non-
908 disabled mothers.

	Group	
Position	Disabled	Non-disabled
Low	1	36
Middle	10	51
High	16	20
Very High	6	0
Unknown	1	1
Total	34	108

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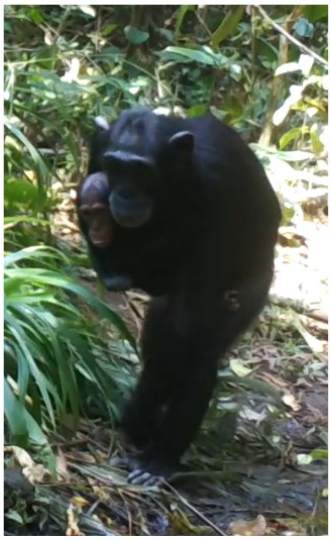
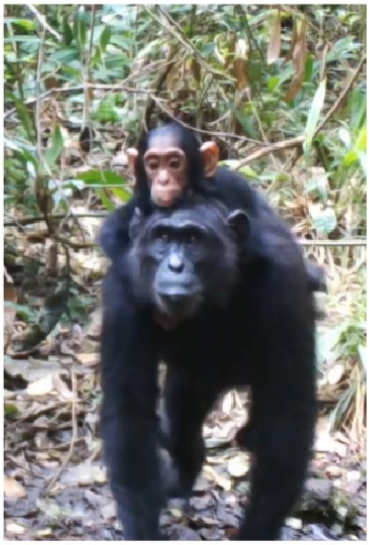
Disabled chimpanzee mothers use postural adaptations for infant carrying, with shifts in ventral and dorsal infant carry location, additional support provided to infants, and novel carrying positions





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