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The Chimpanzee That Never Drank: Re-Evaluating the Ecological Impact of Water on the Behaviour of Wild Rainforest-Living Chimpanzees

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Abstract

Climate change is predicted to negatively impact global water availability. For effective conservation, research on the ecological role of water is essential – to date, especially little is known about it in mesic environments. In this thesis, I explore the ecological impact of water availability on the behaviour of a community of wild eastern chimpanzees (*Pan troglodytes schweinfurthii*), a species often assumed to be independent of surface water outside of arid environments, living in an equatorial rainforest in Uganda. Using long-term observational, phenology, and climate data, fieldwork observational data, and camera trap videos, I re-evaluate previous findings on the presence of drinking and water-contact behaviour in rainforest chimpanzees and add new knowledge on how water acts on chimpanzee space use and social behaviour. The chimpanzees studied drank water daily and showed no hydrophobia. While they drank more often in the dry season, daily drinking behaviour was present regardless of season. All regularly observed chimpanzees above the age of 2.5 years were seen drinking. Low water availability corresponded with constrained female space use around a fallback water source, with individual home ranges significantly smaller during the dry season. Core area structure also changed with water availability: interindividual overlap increased during the dry season, and core area centres shifted between the wet and dry season. Additionally, all 50% core areas included a fallback water source during the dry season compared to chance level during the wet season, the use of which increased as water scarcity intensified. Female social behaviour and networks were also characterised by high seasonal variability corresponding to water availability. Females were more gregarious in the dry season, but had more constrained proximity and grooming networks, characterised by a reduction in the number of partners, while maintaining even bond

strength. The findings provide an example of water being a major shaper of behaviour in a mesic environment and have broader implications for behavioural ecology, conservation, and human evolution.

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Az elmúlt öt év szintén nem lett volna lehettséges a családom nélkül. Mindig is tudtam hogy ha teljes munkaidős majomkodásra adom a fejem, annak az ára a kétlakiság, a döntés egy még valamennyire funkcionális akadémia rendszer és a közelség között. Köszönöm, és csodálom, hogy ezt milyen könnyen elfogadtátok, sőt, támogattátok, még ha ez azt is jelentette hogy akár évekig nem láttok, borzasztó jószágokkal szórakoztatlak titeket (mangólégy és társai), vagy unokák helyett kiscsimpánzokról mesélek. Nem mindenki van még itt hogy lássa és velem ünnepelje ennek az igen hosszú útnak a végét, de el nem tudom mondani mennyire örülök hogy amíg lehetett, mind részesei voltatok.

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To the forest

Author's Declaration

I confirm that this thesis is my own work, except where indicated otherwise. The thesis was written by myself, with comments from my supervisors, Dr Nicholas Newton-Fisher and Dr Sarah Johns. Long-term climate, phenology, and observational data was collected by the employees of the Budongo Conservation Field Station, and was used in this thesis with the full knowledge and approval of the Field Station. Camera trap data was collected by various Budongo Conservation Field Station employees and visiting researchers, Walter John Akankwasa, Dr Catherine Hobaiter, and Hella Péter. Fieldwork data was collected by Hella Péter. All data analyses were run by Hella Péter. All images and figures were generated by Hella Péter, except for Figure 2, which has been generated by and is used with the permission of Dr Catherine Hobaiter. Risk assessment and ethical approval were provided by the University Kent, and permission to conduct research in Uganda was provided by the Uganda Wildlife Authority and the Uganda National Council for Science and Technology.

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Aims of the Thesis

“Biology has forgotten water, or never discovered it. […] the last thing a deep-sea fish would discover is water.”

(Albert Szent-Györgyi, Biology and Pathology of Water, 1971)

Research on the ecological importance of free water in mesic environments is scarce. While recent research from South and Central American (e.g.: Chaves et al., 2021; Dávila et al., 2020) and Southeast Asian forests (e.g.: Pin et al., 2020) supports its crucial nature in those ecosystems, especially little is known about the ecological role of water in equatorial Africa, a region both rich in biodiversity (Orme et al., 2005), including several endangered species (DeGroot et al., 2023; Strindberg et al., 2018), and predicted to undergo drastic changes in water availability due to climate change (Bush et al., 2020; Jiang et al., 2019).

In this thesis, I explore the importance of water as a resource for eastern chimpanzees (*Pan troglodytes schweinfurthii*), an endangered (Amsini et al., 2010) species living in equatorial Africa, commonly thought of as rainforest-adapted and independent of surface water outside of marginal habitats (Lindshield et al., 2017; Pontzer et al., 2021; Wessling et al., 2018a). The study focuses on the Waibira community of wild eastern chimpanzees living in the Budongo Forest, Uganda. The community, despite living in a warm tropical rainforest, experiences an annually recurring shortage of surface water during the dry season due to the topography of their home range, making them suitable for studying the impacts of naturally occurring water scarcity in the wild.

In Chapter 1, I review the literature on the physiological and ecological role of water, the threat climate change poses to global water availability, and highlight how water as a resource has received little focus in studies both on wild chimpanzees and mesic environments. In the subsequent chapters I evaluate whether drinking behaviour is present in the chimpanzees living in the Waibira community, and how the availability of surface water shapes their space use and social behaviour. My analyses rely on long-term data on chimpanzee behaviour, phenology, and climate, collected by the employees of the Budongo Conservation Field Station between 2015 and 2022; my fieldwork data on chimpanzee behaviour collected between November 2021 and March 2022; and camera trap data collected at a major water source of the Waibira community between 2013 and 2022. In Chapter 3, using the camera trap and fieldwork data, I provide a detailed descriptive account of the drinking behaviour and water-contact behaviour of the community, showing that rainforest-living chimpanzees drink free water on a regular, daily basis across seasons, with an increased use of arboreal water sources when those are available. Additionally, while the chimpanzees are generally averse to water contact, that aversion does not qualify as fear of water – they regularly interact with water sources during drinking and various water-contact behaviours. In Chapters 4 and 5, I focus on the behaviour of female chimpanzees: as they are more sensitive to changes in resource availability and levels of competition compared to males (Hashimoto & Furuichi, 2015; Pusey & Schroepfer-Walker, 2013; Wrangham, 1979), studying their behaviour allows for the identification of key resources. In those two chapters, I use long-term data, fieldwork data, and camera trap data to examine changes in female chimpanzee behaviour corresponding to water availability, providing further evidence that free water is an important and limiting resource to chimpanzees. In Chapter 4, I

focus on the space use of the female chimpanzees of the Waibira community. I show that their space use is constrained by water availability, with core areas clustering around the remaining terrestrial water source during periods of water scarcity, with high inter-individual overlap. The use of a small natural feature, the remaining terrestrial waterhole, also intensifies as the dry season and with it, the shortage of water, progresses. In Chapter 5, I evaluate if periods of low water availability result in increased female-female competition, specifically water competition, and/or increased stress levels by looking at seasonal changes in gregariousness, agonistic interactions between females, female-female social relationships, and social structure. Females are more gregarious during periods of low water availability, traveling and foraging in larger parties, and the rate of agonistic interactions is seasonally stable. However, females prioritise specific relationships when water availability is low, focusing their social effort on fewer partners. While the females of the Waibira community did not respond to periods of low water availability by increasing water competition, changes in their social behaviour suggest that low water availability can be a significant stressor even to rainforest-living chimpanzees.

Overall, I show that chimpanzees in rainforest habitats are dependent on free water in addition to the water in their fruit-rich diet to meet their hydration needs and maintain water balance, providing an example of the importance of free water and small natural water sources in a mesic environment in equatorial Africa. Rainforest-living chimpanzees drink regularly, and seasonal changes in their space use and social behaviour correspond to changes in water availability. Water is a key resource for chimpanzees across all habitat types, not just in species range edge populations, and its availability shapes multiple aspects of wild chimpanzee behaviour. These findings have broader implications for chimpanzee conservation and human-wildlife

coexistence, the conservation of small water bodies, and behavioural ecology, specifically foraging ecology.

Chapter 1

Water – An Essential Resource

- Water is a key resource for terrestrial life
- Little is known about its importance in mesic environments
- Little is known about its importance for chimpanzees

Water is essential for life and the normal functioning of a body (Jéquier & Constant, 2010; Lang & Waldegger, 1997). It is an important part of cells, of chemical reactions within the body, it transports nutrients and waste, and aids with thermoregulation and protective cushioning and lubricating (Jéquier & Constant, 2010). The renal system (Johnson et al., 2016), digestion, circulation, as well as the nervous system are all impaired when dehydration, where an individual loses more water from their system than what is entering it, occurs (Popkin et al., 2010; Thomas et al., 2008). As a result, dehydration negatively impacts cognitive (Wilson & Morley, 2003) and physical performance (Adams et al., 2019a). Severe dehydration where lost body water exceeds 5% of body weight in humans can lead to delirium (Lieberman, 2007), and if it increases to 15-25%, it can ultimately result in death (Byard & Riches, 2005; Goldberger, 1962; Lacey et al., 2019; Popkin et al., 2010). To keep their hydration levels at optimum and avoid dehydration, individuals need to achieve water balance, where the amount of water entering their system is equal to the amount of water leaving their system by breathing, cutaneous evaporation, sweating, urination, and defecation (Pontzer et al., 2021; Popkin et al., 2010). How much water an individual needs for water balance can be estimated by looking at their water turnover, the total amount of water moving through their body in a given

time period, comprised of water formed during metabolic processes, and water consumed by drinking liquids and eating food; or their water intake, the total amount of water consumed as liquids and as water contained in foods.

For humans, water turnover is estimated to be 3-7 L per day, depending on individual and environmental factors like activity levels, age, sex, body composition, humidity, or temperature (Yamada et al., 2022). Daily water intake values are slightly lower than water turnover, as some water is produced during metabolic processes (Popkin et al., 2010), but are similarly context-dependent. For adults with low activity levels, doing sedentary work, 2-2.7 L is recommended for women and 2.5-3.7 L for men (EFSA, 2010; Sawka et al., 2005), with higher activity levels and temperatures further increasing daily water intake (Sawka et al., 2005). Even higher values, 4.6-4.9 L per day, have been documented in the hunter-gatherer Tsimane' people living in Bolivia (Rosinger & Tanner, 2015). While women in general have a lower water intake than men, pregnancy and lactation temporarily increases water needs (EFSA, 2010) and with it the risk of dehydration (Bethancourt et al., 2021; Rosinger, 2015). There is also a large variation in the proportion of water intake from liquids versus foods. In Europe, 70-80% of water intake is from liquids (EFSA, 2010), while in Japan, only 50% (Tani et al., 2015). Besides cultural differences in diet, practical reasons like avoiding drinking contaminated water can also increase the consumption of water in food over liquids - getting a higher proportion of one's water needs from food lowers the risk of ingesting waterborne parasites or pathogens (Rosinger & Tanner, 2015). But regardless of variation in the exact amount and sources of water one needs, humans must consume a large quantity of water every day for their health and survival, some percentage of which must be liquids, making free water an essential resource for us.

As evidenced by diet changes to include more water-rich foods when available drinking water is contaminated, besides having a sufficient quantity of water to drink, the quality of it is also crucial (Hadley & Wutich, 2009; Wutich et al., 2020). Low-quality, stagnant water sources can have a build-up of faecal material (Nunn et al., 2014), be a breeding ground for parasites (Perry, 1999), bacteria (Felföldi et al., 2010), and function as a malaria vector (Nkuo-Akenji et al., 2006). Globally, access to water and specifically, good quality drinking water is insufficient: in 2005, 35% of the population faced chronic water shortage (Kummu et al., 2010). The negative consequences of this shortage range in severity, and disproportionally affect women and children: from children missing out on education due to time spent carrying water for their households (Sorenson et al., 2011) and musculoskeletal strain in those carrying water over long distances (Geere et al., 2018), to lower birth weights, earlier births and higher infant mortality (Rocha & Soares, 2015), and additional stress for mothers due to worries about the cessation of lactation caused by dehydration (Collins et al., 2019). In the most severe cases, lack of access to clean and safe water can lead to death, with an estimated 4.2-6.3% of all deaths per year due to illness, infections, and malnutrition caused by poor water quality (Bartram & Cairncross, 2010; Prüss-Üstün et al., 2008).

Water as a Resource for Animals

Insufficient hydration also results in adverse health consequences for nonhuman animals, including growth reduction in immatures (fat sand rats (*Psammomys obesus*): Kam & Degen, 1994; house crickets (*Acheta domesticus*): McCluney & Date, 2008), reduced lactation (hopping mice (*Notomys* spp.), plains rats (*Pseudomys australis*), house mice (*Mus musculus*): Baverstock et al., 1976; fat sand rats: Kam & Degen, 1994), increased offspring mortality and pregnancy loss

(white-faced capuchins (*Cebus capucinus imitator*): Campos et al., 2020a; baboons (*Papio* hybrid): Morishima et al., 1975), the cessation of reproduction (Geoffroy's spider monkeys (*Ateles geoffroyi*): Campos et al., 2020a; zebra finches (*Poephila guttata*): Vleck & Priedkalns, 1985), slower body mass increase and fat accumulation (blackcaps (*Sylvia atricapilla*): Tsurim et al., 2008), stress (western chimpanzees (*Pan troglodytes verus*): Wessling et al., 2018b), thermoregulation issues (Arabian oryx (*Oryx leucoryx*): Ostrowski et al., 2003; desert birds: Riddell et al., 2019), and in cases of extreme, sustained dehydration, death (koalas (*Phascolarctos cinereus*): Gordon et al., 1988; desert birds: Riddell et al., 2019; vervet monkeys (*Chlorocebus pygerythrus*): Wrangham, 1981). Besides maintaining hydration levels, some insect species and amphibians with aquatic life stages are also dependent on surface water for their reproduction (common frogs (*Rana temporaria*), common toads (*Bufo bufo*), alpine newts (*Mesotriton alpestris*): Plăiaşu et al., 2010; insects: Tauber et al., 1998). The primary form of water intake and the relative importance of metabolic water, water in food, and free water for survival varies between species, depending on their physiology, diet, and the climate of their habitat, all of which can impact the amount of body water lost during the course of normal activities, and the maximum possible water intake an individual can have from each form.

Natural sources of free water include both terrestrial and arboreal water bodies, and can be permanent, containing water year-round, or ephemeral, with hydroperiods ranging from a few days to several months depending on precipitation and temperatures. Terrestrial water bodies are dependent on direct precipitation, surface runoff, and groundwater and are further differentiated as either flowing or standing ones, depending on the presence of water flow. Arboreal water bodies are formed by direct precipitation or stemflow (Kitching, 1971; Paradise & Dunson, 1998)

filling junctions and divots in trunks, flowers, leaves, and most often, tree holes (Blakely & Didham, 2008), with the latter also called dendrotelmata. Though less common, free water can also be consumed from other sources besides arboreal or terrestrial water bodies, including the consumption of ice (Andersen & Nielsen, 1983), dew and rainwater collected on surfaces (Asa & Wallace, 1990; Geffen et al., 1992a), and rainwater or soil moisture accessed by moisture harvesting, the cutaneous absorption of water (Cartledge et al., 2006; Comanns et al., 2016). Water availability in a specific area is then dependent on the topography and spatial distribution of free water sources, the loss of water from evotranspiration and infiltration, and the input of water from precipitation and irrigation (Belnap et al., 2005).

Maintaining an optimal hydration status can be improved via physiological adaptations such as minimising the amount of water leaving the body through sweating, panting, urination, defecation, and for female mammals, lactation; or having a reserve of body water which can act as a buffer during periods of low water availability. Relying on heat storing (Arabian oryx: Ostrowski et al., 2003) or high body heat conductivity (coyotes (*Canis latrans*), kit foxes (*Vulpes macrotis*): Golightly & Ohmart, 1983) instead of evaporative cooling can reduce water needs by minimising thermoregulatory water loss, with some desert-adapted species completely independent of free water (kit fox: Golightly & Ohmart, 1983, 1984; Arabian oryx: Ostrowski et al., 2003). On the other hand, species with less efficient thermoregulation processes are more likely to require free water, and consume it more often (birds: Bartholomew & Cade, 1963). Increasing the concentration of urine (sandhill frogs (*Arenophryne rotunda*): Cartledge et al., 2006; Arabian oyx: Ostrowski et al., 2006), less water-dependent urea excretion processes (birds: Bartholomew &

Cade, 1963), and decreasing the water content of faeces (Arabian oryx: Ostrowski et al., 2006; kangaroo rats (*Dipodomys* spp.): Schmidt-Nielsen & Schmidt-Nielsen, 1951) also helps minimise the amount of water exiting the body, and with it, the necessary water intake for survival. Instead of minimising water loss, ungulates rely on their high gut water content to avoid dehydration (donkeys (*Equus asinus*): Kasirer-Izraely et al., 1994; Shkolnik et al., 1980; equids: Sneddon & Argenzio, 1998), which can be reabsorbed into their body to act as a buffer during dry periods, allowing some species to go several days or even weeks without drinking (sable antelope (*Hippotragus niger*): Cain III et al., 2012; Marwari goat (*Capra hircus*): Khan et al., 1979; dromedaries (*Camelus dromedarius*): Macfarlane et al., 1963). However, once those gut water reserves are depleted, they cannot be refilled from food water content only: individuals must drink free water (bighorn sheep (*Ovis canadensis mexicana*): Gedir et al., 2020; mouflon (*Ovis orientalis*), Najafi et al., 2019; khulan (*Equus hemionus*): Payne et al., 2020; dromedaries: Schmidt-Nielsen et al., 1956).

The diet of an animal determines the proportion of water in food and free water in their water intake. Species with a primary diet of water-rich foods like succulents, leaves, fruits, and meat or insects, do consume free water occasionally, but are generally less dependent on it compared to granivores, or grazing herbivores (Table 1). Foraging with the primary aim of hydration also occurs in arid environments and during periods of low water availability regardless of diet, and includes the increased consumption of fruits (Blanford's foxes (*Vulpes cana*): Geffen et al., 1992a), flowers (brown howler monkeys (*Alouatta guariba clamitans*): Chaves et al., 2021; vervet monkeys: Wrangham, 1981), bark (Barbary macaques (*Macaca sylvanus*): Ciani et al., 2001), and other water-rich plant parts (bearded capuchins

(*Sapajus libidinosus*): Castro et al., 2017). However, for species which primarily rely on water in food to meet their water needs, their maximum foraging capacity also limits the maximum amount of water in food they can consume, and increased or novel consumption of free water might be necessary if food competition (kit foxes: Hall et al., 2013) or individual water needs (cheetahs (*Acinonyx jubatus*): Laurenson, 1995) increase beyond that limit.

Table 1

Studies Documenting Free Water Consumption Across Diet Types

Diet	Species	Study
Folivores –	Fat sand rats	Kam & Degen, 1994
succulents	Chuckwallas (*Sauromalus obesus*)	Nagy, 1972
	Kangaroo rats	Tracy & Walsberg, 2002
Folivores – tree	Koalas	Clifton, 2010; Mella et al., 2020
foliage	Black howler monkeys (*Alouatta pigra*)	Dias et al., 2014
	Common brown lemurs (*Eulemur fulvus*)	Sato et al., 2014
Frugivores	Red-fronted lemurs (*Eulemur rufifrons*)	Amoroso et al., 2020a
	Spider monkeys (*Ateles* spp.)	Campbell et al., 2005
	White-faced capuchins	Freese, 1978
	White-winged doves (*Zenaida asiatica mearsnii*),	Wolf & Martinez del Rio, 2000
	Collared peccaries (*Dicotyles tajacu*)	Zervanos & Day, 1977
Carnivores &	Sechuran desert foxes (*Dusicyon sechurae*)	Asa & Wallace, 1990
insectivores	Leopards (*Panthera pardus*)	Bothma, 2005; Najafi et al., 2019
	Coyotes, Kit foxes	Golightly & Ohmart, 1984
	Lions (*Panthera leo*)	Hayward & Hayward, 2012
	Diamond-backed rattlesnakes (*Crotalus atrox*)	Murphy & DeNardo, 2019
	Gila monsters (*Heloderma suspectum*)	Wright et al., 2013
Granivores	Red-headed finches (*Amadina erythrocephala*)	Abdu et al., 2018
	Cape buntings (*Emberiza capensis*)	Lee et al., 2017
	Budgerigars (*Melopsittacus undulatus*)	Votto et al., 2020
	California quails (*Callipepla californica*)	Williams & Koenig, 1980
Grazers	Zebras (*Equus quagga*), Sable antelopes	Cain III et al., 2012
	Khulan	Kaczensky et al., 2010
	Przewalski's horses (*Equus ferus przewalskii*)	Scheibe et al., 1998

The dietary proportion of free water consumed, and with it, dependence on surface water also increases with higher temperatures and lower precipitation, as

animals lose more water through evaporative cooling to maintain optimal body temperatures (desert bighorn sheep: Cain III et al., 2008; birds: Lee et al., 2017; Smit et al., 2019; Votto et al., 2020). This increased dependence on surface water can manifest as increased visitation of water sources during hotter and drier periods (black howler monkeys: Dias et al., 2014; birds: Lee et al., 2017; Votto et al., 2020; roe deer (*Capreolus capreolus*): Wallach et al., 2007), or seasonal drinking behaviour, with animals only consuming free water during summers (collared peccaries: Zervanos & Day, 1977) and dry seasons (birds: Williams & Koenig, 1980), when foraging enough water-rich food to achieve water balance might not be possible (kit foxes: Hall et al., 2013) due to the thermoregulatory costs of foraging outweighing the hydration benefits gained from it (pied babblers (*Turdoides bicolor*): du Plessis et al., 2012; Blanford's foxes: Geffen et al., 1992b; common lizards (*Lacerta vivipara*): Lorenzon et al., 1999), or reaching maximum foraging capacity (koalas: Mella et al., 2019, 2020). Some species' ability to increase their intake of free water to sufficiently cope with high temperatures might be limited (birds: Smit & McKechnie, 2015), which can lead to population collapse, especially for species normally independent of surface water (prairie falcon (*Falco mexicanus*), turkey vulture (*Cathartes aura*), northern mockingbird (*Mimus polyglottos*): Riddell et al., 2019).

Extreme weather events, such as droughts or cyclones, impact the water needs of animals and the availability of surface water more suddenly and severely than regular seasonal changes in temperature and precipitation. Milder cases of sudden water shortage and resulting chronic dehydration, while not lethal, can lead to health issues, like lower birth weights (rats (*Rattus norvegicus domestica*): Ross & Desai, 2005; American alligators (*Alligator mississipiensis*): Tate et al., 2012),

reduced immune function (Barrow Island euros (*Macropus robustus isabellinus*): King & Bradshaw, 2010) and growth (yellow baboons (*Papio cynocephalus*): Levy et al., 2023), and increased stress levels (vervet monkeys: Young et al., 2019). In some species, such as Milne Edward's sifakas (*Propithecus edwardsi*) (Dunham et al., 2008), vervet monkeys (Wrangham, 1981), Northern muriquis (*Brachyteles hypoxanthus*), woolly monkeys (*Lagothrix lagotricha*) (Wiederholt & Post, 2011) and Geoffroy's spider monkeys (Campos et al., 2020a), droughts negatively impact population growth by causing a temporary cessation of or decrease in reproduction.

In severe cases, extreme water shortages can lead to mass mortality (koalas: Gordon et al., 1988; chacma baboons (*Papio ursinus*): Hamilton, 1985; eland (*Taurotragus oryx*), gnu (*Connochaetes taurinus*), red hartebeest (*Alcelaphus buselaphus caama*): Knight, 1995; vervet monkeys: Wrangham, 1981), especially in females and immatures (white-faced capuchins: Campos et al., 2020a; African elephants (*Loxodonta africana*): Foley et al., 2008; ring-tailed lemurs (*Lemur catta*): Gould et al., 1999). Lactation increases water needs, and with it, the risk of dehydration (humans: Bethancourt et al., 2021; Rosinger, 2015), while immatures are more vulnerable to dehydration because of their higher body water content (Adolph & Heggeness, 1971) and being dependent on their mother for hydration pre-weaning (Bethancourt et al., 2021; eastern chimpanzees (*Pan troglodytes schweinfurthii*): Nelson et al., 2022). Extreme weather events can also cause high mortality indirectly – while a species might get sufficient water to survive, their primary food source can be more heavily impacted by the water shortage, leading to drought-induced starvation (yellow baboons: Altmann et al., 1985; Geoffroy's spider monkeys: Campos et al., 2020a; aardvarks (*Orycteropus afer*): Rey et al., 2017).

Besides their immediate impacts on health and survival, extreme weather events can have long-lasting effects on populations, as the sudden death of multiple group members can impact a group's sex ratio (chacma baboons: Hamilton, 1985) and population growth (white-faced capuchins, Geoffroy's spider monkeys: Campos et al., 2015). They can also interfere with conservation efforts, as animals leave protected areas in search of water (O'Farrill et al., 2014), start to rely on human water sources (Hanuman langurs (*Semnopithecus entellus*): Waite et al., 2007), exposing them to hunting or retaliatory killings for endangering humans or crop raiding (Mukeka et al., 2019; Baird's tapir (*Tapirus bairdii*): Pérez-Flores et al., 2021), and previously suitable habitats dry out irreparably leading to the failure of reintroduction projects (white-headed ducks (*Oxyura leucocephala*): Bajomi, 2004; Molnár, 1987). Case studies of populations experiencing resource bottlenecks due to extreme weather event-induced water shortages demonstrate the importance of water, specifically surface water, as an essential resource for the given species.

Dependence on free water, in addition to regular consumption of it and adverse health effects in its absence, is further evidenced by changes in behaviour to facilitate access to water. If a species needs to drink on a regular basis, that need is reflected in their space use: the extent of their ranging is constrained by the distance they can travel away from water sources without risking dehydration (olive baboons (*Papio anubis*): Barton et al., 1992; mountain sheep (*Ovis canadensis*): Bleich et al., 2010; mule deer (*Odocoileus hemionus*): Boroski & Mossman, 1996; chacma baboons: Hamilton, 1985; Tana River red colobus (*Piliocolobus rufomitratus*): Kimanzi et al., 2019; American badgers (*Taxidea taxus*): Piper, 2021; African elephants: Purdon & van Aarde, 2017), and activity often centres on water

sources during periods of increased reliance on free water (red-fronted lemurs: Amoroso et al., 2020a; white-faced capuchins: Campos & Fedigan, 2009).

Social interactions around water sources, during water shortages, and specifically over accessing water can also inform us about whether water is perceived as a high-value or monopolisable resource, and the presence of any competition for water. Dominant individuals within groups having priority access to water sources (chacma baboons: Hamilton, 1985; siamangs (*Symphalangus syndactylus*): Sharma et al., 2016; vervet monkeys: Wrangham, 1981), and intergroup interactions around water sources ranging from blocking access to and displacement from the water source to chases and physical attacks (yellow baboons: Markham et al., 2012; vervet monkeys: Wrangham, 1981) support that water is a valuable, limited resource in a given environment, with the risks of competition outweighing the benefits of accessing water. However, a lack of agonistic interactions does not necessarily mean that water is not a limiting factor, only that overt water competition is not present, evidenced by peaceful intergroup encounters at water sources during periods of water scarcity (Hanuman langurs: Beck & Tuttle, 1972; patas monkeys (*Erythrocebus patas*): Struhsaker & Gartlan, 1970; yellow baboons: Washburn & DeVore, 1961).

Finally, extractive foraging to access water can also serve as evidence for its importance. Both non-tool use behaviours, like digging wells in order to reach the water table (e.g.: warthogs (*Phacochoerus africanus*), African elephants, zebras, yellow baboons: Stommel et al., 2016; feral horses (*Equus ferus caballus*) and donkeys: Lundgren et al., 2021, khulan: Payne et al., 2020), and the use and construction of tools to access water (e.g.: bearded capuchins: Castro et al., 2017; orangutans (*Pongo pygmaeus*): Russon et al., 2010; chimpanzees: Whiten et al.,

1999) are costly with regards to time and energy. Their presence in a population then suggests that animals derive some water-related benefit from them that outweigh the costs, either by providing access to a key resource (Yamakoshi, 1998), or improving its quality (Sanz & Morgan, 2013).

Water & Climate Change

Trying to maintain their water balance in the face of seasonal changes in temperature and precipitation as well as extreme weather events will become even more challenging for animals with climate change predicted to impact the availability and quality of free water. Dry seasons (Bush et al., 2020; Chou et al., 2013; Padrón et al., 2020) and summers (Heimann & Sept, 2000; Venäläinen et al., 2020) are becoming drier and last longer in most areas (Fu et al., 2013; Jiang et al., 2019; Ruosteenoja et al., 2016), increasing the time water sources spend cut off from waterflow or replenishment from precipitation, and being stagnant. The chance and magnitude of extreme weather events impacting water availability and quality, like cyclones (Zhu et al., 2014), hurricanes (Paerl et al., 2001), heat waves (Lhotka et al., 2018), and droughts (Trenberth et al., 2014), are also increasing (Schlaepfer et al., 2017; Venäläinen et al., 2020), especially in areas with high human water use (Wanders & Wada, 2015). Previously permanent, year-round water sources can disappear due to more intense dry seasons (Liu et al., 2008), droughts (Altmann et al., 1985), or increased human activity, such as getting drinking water and agricultural irrigation (Mtahiko et al., 2006; Poudel & Duex, 2017). With less water sources available, connectivity between them also decreases (O'Farrill et al., 2014). Besides the threat of complete evaporation, water sources can become unsafe to drink from due to algae blooms brought on by cyclones and hurricanes (Michalak,

2016) or high microbial and faecal loads caused by a cessation of waterflow (Gereta & Wolanski, 1998).

In addition to decreased rates of precipitation, climate change further impacts water availability via increasing temperatures, present across biomes (Bush et al., 2020; Duffy & Tebaldi, 2012; Freychet et al., 2021; Heimann & Sept, 2000) and seasons (Almazroui et al., 2012; Laing & Binyamin, 2013; Ruosteenoja et al., 2016). Periods with significantly higher temperatures than the running average, heatwaves, are also predicted to become more frequent and last longer (Fischer & Schär, 2010; Lhotka et al., 2018). With higher temperatures, the evaporation of moisture from the surface layer of the soil accelerates, contributing to droughts and the disappearance of water sources (Ndiaye et al., 2021; Padrón et al., 2020), even in areas where precipitation is otherwise predicted to increase (Ruosteenoja et al., 2018).

The reduction in the number of available water sources paired with higher temperatures then impacts where animals can access water to achieve a sufficient water intake, how much water they need to avoid dehydration, and whether they are dependent on free water. For species dependent on any amount of free water to maintain their water balance or for reproduction, their distribution will be restricted with the reduction in the number of available water sources, and will centre on remaining water sources (insects: Chown et al., 2011; night parrots (*Pezoporus occidentalis*): Kearney et al., 2008). These range shifts resulting from the disappearance of water sources can lead to animals leaving protected areas (Erasmus et al., 2002; O'Farrill et al., 2014), being more exposed to anthropogenic risks like vehicles and hunting (khulan: Payne et al., 2020; Baird's tapirs: Pérez-Flores et al., 2021), and humans and animals increasingly sharing the remaining water sources (Abrahms et al., 2023; Ocholla et al., 2013; sleepy lizards (*Tiliqua*

rugosa): Leu & Bull, 2016; African elephants: Mariki et al., 2015; Baird's tapirs: Pérez-Flores et al., 2021). Sharing water sources creates risks for both parties, including injury and death both for humans (Acharya et al., 2017; Dunham et al., 2010; Mukeka et al., 2019) and animals (Mariki et al., 2015; Pérez-Flores et al., 2021), and disease transmission through the consumption of contaminated water (eastern chimpanzees: Deere et al., 2019; banded mongooses (*Mungos mungo*): Pesapane et al., 2013) or due to disease vector insect species increasingly breeding in water sources near humans as alternatives disappear (Chown et al., 2011). Visiting water sources near human settlements also provides animals crop raiding and livestock depredation opportunities (Mariki et al., 2015; Mukeka et al., 2019; Pérez-Flores et al., 2021), further worsening human-wildlife conflict. Increased use of waterholes by different species can also expose animals to aggressive interference competition interactions from species previously not a threat (Perera-Romero et al., 2021).

With increasing temperatures, animals will increase thermoregulatory behaviour, including evaporative cooling, to maintain optimal body temperature, which elevates their water needs (Wolf & Walsberg, 1996). Therefore, as temperatures increase globally, species will likely become more dependent on free water (Smit & McKechnie, 2015). For species that regularly consume free water, higher temperatures result in more frequent drinking, and therefore a stronger dependence on free water (birds: Lee et al., 2017). Species which only rely on free water during dry seasons or summers, above a certain temperature (night parrots: Kearney et al., 2016; roe deer: Wallach et al., 2007; collared peccaries: Zervanos & Day, 1977), will be reliant on it for longer periods of time within the year with rising temperatures across all seasons (Kearney et al., 2016). Water availability can also

become a completely novel constraining factor for species which normally rarely or never consume free water as they begin drinking to avoid overheating (mountain gorillas (*Gorilla beringei beringei*): Wright et al., 2022), and can no longer increase foraging effort to get sufficient water from food (kit foxes: Hall et al., 2013; koalas: Mella et al., 2019). In worst case scenarios, the combination of lower water availability and increased water needs leads to a resource bottleneck, where animals can no longer adjust to the temperature-induced increase in their water needs, resulting in catastrophic population crashes and extinction (Maron et al., 2015; white-faced capuchins: Campos et al., 2015; *Drosophila birchii*: Hoffmann et al., 2003; birds: McKechnie & Wolf, 2009; Riddell et al., 2019).

Given the predicted changes in global precipitation and temperature patterns, xeric areas where year-round water access is already challenging are expected to deal with a further worsening of water shortages and resulting problems. Typically water-rich, mesic areas, with plenty of stable year-round water sources are also at risk, being increasingly likely to face periods of limited water availability - possibly even more at a risk than drier areas, as coping with water shortage is a novel situation both for humans and wildlife there (Rakovec et al., 2022), for which species might not have physiological (*Drosophila birchii*: Hoffmann et al., 2003; rufous-collared sparrows (*Zonotichia capensis*): Sabat et al., 2006) or behavioural adaptations. However, studies on the impacts of water deprivation and water shortage have either focused on captive individuals (e.g.: Hiley, 1976; Morishima et al., 1975; Ostrowski et al., 2006; Vleck & Priedkalns, 1985), or populations living in areas with low annual precipitation rates like the Midwest and Southern United States and Mexico, Southern Africa and other African savannahs, Central Asia, Australia, the Mediterranean, and the Middle East (Table 2). While there is an

increasing focus on water as a resource in tropical rainforest and monsoon climates in South and Southeast Asia and in South and Central America (Table 2), suggesting that water is an essential and limiting resource in mesic environments, there are very few studies from continental climates in Europe, with the exception of dendrotelmata as microhabitats for insects (e.g.: Gossner, 2018), and tropical climates in equatorial Africa where the ecological role of free water is considered (Table 2). This disproportionate representation has led to minimal research existing on the water needs and hydration strategies of species in mesic environments and how the availability of free water impacts their behaviour, yet documenting how they respond to water constraint and the extent of their dependence on surface water is essential for the effective conservation of those species under climate change.

Table 2

Studies on Water as a Resource Across Geographic Areas

Location	Studies
Midwestern & Southern United States and Mexico	Adams & Thibault, 2006; Boroski & Mossman, 1996; Cain III et al., 2008; Campbell et al., 2005; Delgado-Martínez et al., 2022a, 2022b, 2023; Dias et al., 2014; Gehrt & Fritzell, 1998; Golightly & Ohmart, 1984; Hall et al., 2013; Harris et al., 2015; Hill et al., 2023; Lundgren et al., 2021; Marshal et al., 2006; Murphy & DeNardo, 2019; O'Farrill et al., 2014; Pérez-Cortez et al., 2012; Pérez-Flores et al., 2021; Piper, 2021; Riddell et al., 2019; Vernes & Devos, 2022
Southern Africa	Amoroso et al., 2020a, 2020b; Bothma, 2005; Crosmary et al., 2012; Du Preez, 1997; Farrell et al., 2022; Ferry et al., 2016; Fox, 2015; Kasiringua et al., 2017; Knight, 1995; Lee et al., 2017; Mpakairi, 2019; Ndaimani et al., 2016; Ndlovu et al., 2018; Ramey et al., 2013; Redfern et al., 2003; Smit & McKechnie, 2015; Stommel et al., 2016; Sutherland et al., 2018; Valeix, 2011; Valeix et al., 2009; Wrangham, 1981; Young et al., 2019; Zvidzai et al., 2013
Other African savannahs	Altmann et al., 1985; Ayeni, 1977; Gould et al., 1999; Hamilton, 1985; Henty & McGrew, 2014; Kimanzi et al., 2019; Lindshield et al., 2017; Levy et al., 2023; Maguju, 2022; McGrew, 1977; McGrew et al., 2007; Nishida, 1980; Ogutu et al., 2014; Sapolsky, 1986; Sharma et al., 2016; Struhsaker & Gartlan, 1970; Wessling et al., 2018a; Wrangham, 1981
Central Asia	Kaczensky et al., 2008, 2010; Payne et al., 2020; Zhang et al., 2023
Australia	Cartledge et al., 2006; Clifton, 2010; Davies et al., 2013; Dawson et al., 1983; Ellis et al., 1995; Fisher et al., 1972; Gordon et al., 1988; James et al., 1999; King & Bradshaw, 2010; McKechnie &

	Wolf, 2009; Mella et al., 2019, 2020; Votto et al., 2020; Webb et al., 2022; Wright et al., 2013
Mediterranean	Amorim et al., 2018; Ciani et al., 2001; Grenot et al., 1987; Lorenzon et al., 1999; Palomares et al., 2001; Rosalino et al., 2005; Santos et al., 2011; Wallach et al., 2007
Middle East	Edwards et al., 2017; Geffen et al., 1992a, 1992b; Najafi et al., 2019; Ostrowski et al., 2003; Sapir et al., 2004; Tsurim et al., 2008; Wakefield et al., 2008
South & Southeast Asia	Beck & Tuttle, 1972; Gray et al., 2015; Pin et al., 2020; Sharma et al., 2016; Waite et al., 2007; Yoshiba, 1968
South & Central America	Burger, 2001; Campbell et al., 2005; Campos et al., 2020a; Campos & Fedigan, 2009; Chaves et al., 2021; Dávila et al., 2020; Freese, 1978; Gilbert & Stouffer, 1989; Montalvo et al., 2019; Moreira-Ramírez et al., 2016; Moro-Rios et al., 2008; Nagy & Milton, 1979
Europe – continental climate	Burston, 2006; Holá et al., 2015; Kirsch et al., 2021; van Apeldoorn et al., 2006
Equatorial Africa	Lanjouw, 2002; Outtara et al., 2019; Wright et al., 2022

Water as a Resource for Chimpanzees

Chimpanzees, alongside bonobos (*Pan paniscus*), are the closest living relatives to humans, having diverged from our last common ancestor 7 – 8 million years ago (Langergraber et al., 2012). The high genetic relatedness is responsible for generally similar body composition between *Pan* and *Homo* (Zihlman & Bolter, 2015), with the notable exception of lower body fat percentage and higher muscle mass (Angus, 1971) and less efficient water conservation in chimpanzees (Pontzer et al., 2021). They are ripe-fruit specialist omnivores (Goné Bi & Wittig, 2019; Newton-Fisher, 1999a; Piel et al., 2017), with the majority of their diet comprised of

fruits (Matsumoto-Oda & Hayashi, 1999; Moore et al., 2018; Piel et al., 2017; Pruetz, 2006), a typically water-rich food item. While they are primarily regarded as a rainforest-dwelling species, living in forested areas with high annual precipitation, their species range in equatorial Africa also extends to mosaic forests and savannahs (van Leeuwen et al., 2020a). As large-brained (Herndon et al., 1999), long-lived species (Matsuzawa, 2018; Nishida et al., 2003; Wittig & Boesch, 2019), they possess a high degree of behavioural flexibility (Boesch & Boesch, 1990; Pruetz et al., 2015; Stokes & Byrne, 2001; Whiten et al., 1999), which enables them to cope with limited resource availability in open, arid habitats (Hernandez-Aguilar et al., 2007; McGrew et al., 1981; Pruetz & Bertolani, 2009; Wessling et al., 2018a). The first scientific description of wild chimpanzee behaviour dates from the 1930s (Nissen, 1931), followed by several projects initiated in the 1960s and 1970s (Boesch-Achermann & Boesch, 1994; Goodall, 1965a; Kortlandt, 1962; Nishida, 1968; Reynolds & Reynolds, 1965; Sugiyama & Koman, 1979), with a significant proportion of them evolving into long-term research stations, running continuously since then (Boesch, 2019; Granier, 2016; Nakamura et al., 2020; Wilson et al., 2020).

Despite several decades of research on the behaviour of wild chimpanzees encompassing different habitat types and subspecies, the importance of water has received little attention, and the assumption that free water, with the exception of populations in arid, marginal habitats (Boyer-Ontl & Pruetz, 2020; Lindshield et al., 2017; Wessling et al., 2018b), is a resource of little to no ecological relevance to chimpanzees is still present (Pontzer et al., 2021; c.f.: Wessling et al., 2018a). First, frugivores (spider monkeys: Campbell et al., 2005; white-faced capuchins: Freese, 1978) and folivores (koalas: Clifton, 2010; Mella et al., 2020; howler monkeys:

Chaves et al., 2021) obtain a substantial proportion of their water intake from water in food, with some initial accounts reporting a complete lack of drinking and reliance on free water (howler monkeys: Nagy & Milton, 1979; koalas: Ellis et al., 1995). Given their diet rich in fruit and foliage, it has been reasonable to assume chimpanzees would follow this pattern and consume little to no water. However, more recent studies report frequent drinking by those species originally assumed to consume water only by food (howler monkeys: Bicca-Marques, 1992; Chaves et al., 2021; Dias et al., 2014; koalas: Mella et al., 2020).

Besides their fruit-specialist diet, the assumption of water being ecologically irrelevant for rainforest chimpanzees also stems from chimpanzees commonly regarded as hydrophobic. The statement first appeared in Yerkes' (1943) comprehensive account on captive chimpanzee behaviour, in which he stated that chimpanzees avoid touching water or becoming wet, motivated by a strong fear of water itself. Early studies on wild populations then interpreted wild chimpanzees' reluctance to wade into or touch water or mud as motivated by hydrophobia, and concluded that chimpanzees generally avoid interacting with water (Goodall, 1986; Kortlandt, 1962; McGrew, 1977, c.f: Nishida, 1980). As the observation of water sources allows for the simultaneous study of both water contact and drinking behaviour, early accounts from wild and captive populations often focused on both (Angus, 1971; McGrew, 1977; Nishida, 1980). However, this approach carries the risk of conflating the two behaviours, and the extension of the assumption of hydrophobia to drinking as well. Even when the original authors acknowledged that the low number of recorded drinking events reflects low habituation and poor visibility rather than actual non-drinking (Reynolds & Reynolds, 1965), partial observer presence throughout the day (Nishida, 1980), or when the time spent drinking was

reported as a proportion of total feeding time (Teleki, 1977), the findings have nevertheless been interpreted in some studies as a complete hydrophobic avoidance of water, including for drinking (e.g.: Pontzer et al., 2021). As a result, water availability, with the exception of some studies on populations inhabiting arid, savannah environments (e.g.: Lindshield et al., 2017; Wessling et al., 2018a, 2018b), has not been factored into models of chimpanzee behavioural ecology, leading to a gap in our knowledge about water needs, consumption of free water, and behavioural changes due to water availability in wild chimpanzees, especially in rainforest populations.

In addition to the conflation of water contact behaviour and drinking, evidence for true hydrophobia is weak. Yerkes' (1943) original experiment consisted of throwing immature chimpanzees into water against their will, which does not replicate voluntary contact with water. Later both Nishida (1980) and Angus (1971) observed chimpanzees voluntarily reaching or wading into water to access high-value foods or escape harassment. Instead of hydrophobia, Nishida (1980) proposed water aversion in chimpanzees, but his theory has not managed to fully counter that of Yerkes, and after the initial wave of field studies on wild chimpanzees in the 1960s and 1970s, little attention has been paid to the relationship of chimpanzees and water until the 2000s, when a long-term project on a population of savannah chimpanzees in Fongoli, Senegal began (Pruetz, 2006).

Since the start of the Fongoli Savanna Chimpanzee Project, interest in the role of free water as a resource potentially limiting chimpanzee behaviour is slowly picking up again. The water-contact behaviour and drinking behaviour of the Fongoli community of chimpanzees is well-studied (Pruetz & Bertolani, 2009; Wessling et al., 2018a, 2018b), with individuals in the community distinctly lacking any fear of water

(Pruetz & Bertolani, 2009), and drinking regularly (Lindshield et al., 2017). While targeted research interest is returning to the topic of chimpanzees and water in the recent decade (Nelson et al., 2022, 2024; Péter et al., 2022; Wessling et al., 2018a, b), with Wessling and colleagues (2018a) calling for the study of it across various chimpanzee habitat types, focus has primarily been on marginal savannah or mosaic forest populations. Whether free water is an essential, regularly consumed resource by all chimpanzee populations, including rainforest-living chimpanzees, is still not known.

Broader Relevance

Research on the water needs of species (Kearney et al., 2016) and how water as a resource shapes their behaviour (Abrahms et al., 2023; McCluney et al., 2012) is essential for accurately predicting population dynamics and effective conservation planning with increased likelihoods of lower precipitation, higher temperatures, extreme weather events, and the resulting changes in water availability due to climate change. Especially little is known about how water impacts species inhabiting mesic environments, which are nonetheless predicted to experience novel water shortage situations (Kirkpatric Baird et al., 2023).

Studies on the water needs of animals, how water shortages impact them, how they behave, congregate, or use other resources around water sources, and resulting human-wildlife conflict have also mainly focused on species living in and adapted to arid environments (Clifton, 2010; Hamilton, 1985; Kasiringua et al., 2017; Knight, 1995), or populations facing extreme weather events (Campos et al., 2020a; Gould et al., 1999). For chimpanzees, the majority of human-chimpanzee coexistence research so far has focused on education (Njukang et al., 2019), practical solutions to reduce crop raiding (Garriga et al., 2018; Hockings &

McLennan, 2016), and how to safely share and utilise the same foraging areas and food resources (Hockings et al., 2020; Waller & Pruetz, 2016). However, no attention has been paid to shared water sources, specifically. Researching whether rainforest chimpanzees are dependent on surface water and how they utilise water sources can help in the management of human-chimpanzee conflict, and highlight potential further venues for conservation research, such as the potential impact of anthropogenic disturbance and threats such as hunting, vehicles (Kaczensky et al., 2010), and noise pollution (Domer et al., 2021) shown to decrease the use of water sources in other species, on chimpanzees.

Studying water as a resource can also highlight the importance of small water bodies (1 m^2-5 ha for standing waters (Biggs et al., 2005, 2017)) as small natural features, which have an ecological importance larger than their size (Hunter et al., 2017), in equatorial Africa. Such small water bodies include lakes, ponds (Biggs et al., 2005), springs (Davis et al., 2017), ephemeral streams (Acuña et al., 2017), waterholes (Beck & Tuttle, 1972; Moreira-Ramírez et al., 2016), cenotes (Vernes & Devos, 2022), and dendrotelmata (Delgado-Martínez et al., 2022b; 2023; Kirsch et al., 2021), all of which provide hydration and foraging ground to several species (Delgado-Martínez et al., 2023; Pin et al., 2020), serve as important ‘refuelling points’ for migratory birds (Dávila et al., 2020), contribute to animals staying within protected areas (O’Farrill et al., 2014), and are common species refuges due to lower likelihood of contamination owing to their smaller catchment areas (Biggs et al., 2017). As Biggs et al. (2017) highlight, policy and decision making currently does not fully recognise how crucial these water sources are, with those smaller than 100 m^2 not even included in most legislations on the protection and conservation of water sources. While due to their smaller size, small natural features are easier to manage

and protect from a conservation viewpoint, they are easier to overlook and are more vulnerable to complete disappearance (Hunter et al., 2017).

On a broader level, research on water as a limiting resource in mesic environments can also help with the decoupling of climate and water availability and lead to more accurate descriptions of water availability in ecology. Oftentimes water availability at a specific habitat is extrapolated from the general climate of the area, or annual average precipitation. However, the microclimate of the habitat might differ from that of the general area, while the geography of the habitat also contributes to actual water availability through the speed of runoff and evotranspiration (e.g.: Boroski & Mossman, 1996; Lanjouw, 2002). Detected differences in the behaviour of species or populations in arid versus mesic environments therefore might not be due to water availability, but simply to higher temperatures and lower humidity.

Chimpanzees, alongside bonobos as members of the genus *Pan,* diverged from early humans approximately 7 – 8 million years ago (Langergraber et al., 2012). A large part of early hominin evolution, and resulting behavioural and physiological differences from *Pan*, are theorised to be due to habitat shifts from mesic forests to more arid climates, including a drastic shift in African hydroclimate approximately 300,000 years ago, corresponding to the emergence of modern *Homo sapiens* (Gosling et al., 2022). These arid habitats then posed the challenge of more drastic and unpredictable variability of resources and environmental conditions, including the availability of water (Potts, 1999, 2012). Most studies on the role of water in human evolution and this range shift focus on the intersection of bipedality, thermoregulation, and how they relate to maintaining a water balance (e.g.: Hora et al., 2019; Kamberov et al., 2018; Lieberman, 2015; Mitchell et al., 2009). With regards to the evolution of human drinking behaviour itself, physiological water

conservation, or the evolutionary role of water availability on behaviour, little is known. Physiologically, humans are more effective at utilising water consumed, with a reduced water turnover rate compared to captive great apes (Pontzer et al., 2021). Palaeohydrology and -climatology has also been used to model ancient hydroscapes, and the role of hydro-refugia, areas with reliable water availability, as a geographical feature shaping ancient hominin distribution and dispersal (e.g.: Cuthbert & Ashley, 2014; Cuthbert et al., 2017; Larrasoaña et al., 2013). However, as Pontzer and colleagues (2021) highlight, studies on the drinking behaviour of great apes are essential for understanding the evolutionary pressure water posed to early humans. Establishing whether drinking behaviour and water dependence is present in wild rainforest chimpanzees, as well as documenting any behavioural changes corresponding to water availability can help set an evolutionary baseline for water needs and behavioural adaptations already present in our lineage prior to its divergence from *Pan.* Focusing on water availability in mesic areas, in this case, equatorial African rainforests, can also help determine whether water scarcity was a novel environmental challenge to early hominins, unique to mosaic forests and savannahs, or did they still frequently encounter it, and potentially had to adapt to it, in rainforests.

With an increased focus on how water can be a limited resource impacting animal behaviour in mesic environments too, the field of ecology can hopefully leave behind the general assumption that only arid environments are water-restricted and that all such environments have poor water availability. Joined with growing knowledge on a diverse range of water sources, this perspective switch on water as a resource will hopefully result in more behavioural ecology studies incorporating water as its own variable, and more specific measures of water availability,

describing the number, size, spatial distribution, and seasonality of water sources available to study populations, both of which are essential for effective conservation in the face of climate change. Such additional level of detail will also improve our understanding of early hominin evolution, and the role water availability and maintaining a water balance has played the evolutionary history of the lineage.

Chapter 2

Study Site, Population, & General Methodology

Study Site

The Budongo Forest Reserve lies in the Western Rift Valley of Uganda, at 1050 m mean altitude (1°35′-1°55′ N, 31°18′-31°42′ E). Four rivers run through the forest – the Waisoke, the Sonso, the Kamirambwa, and the Siba. The forest has a warm tropical climate, with an annual three-month dry season centred on January and February and extending into December or March depending on the year, and heavy rains between April and June and August and November (Eggeling, 1947; Newton-Fisher, 1999a) (Figure 1). The annual mean precipitation between 1993 and 2021 was 1659 mm, with some inter-annual fluctuation: the driest year on record, 2016, had 1227 mm of rainfall, while the wettest, 1997, had 2187 mm.

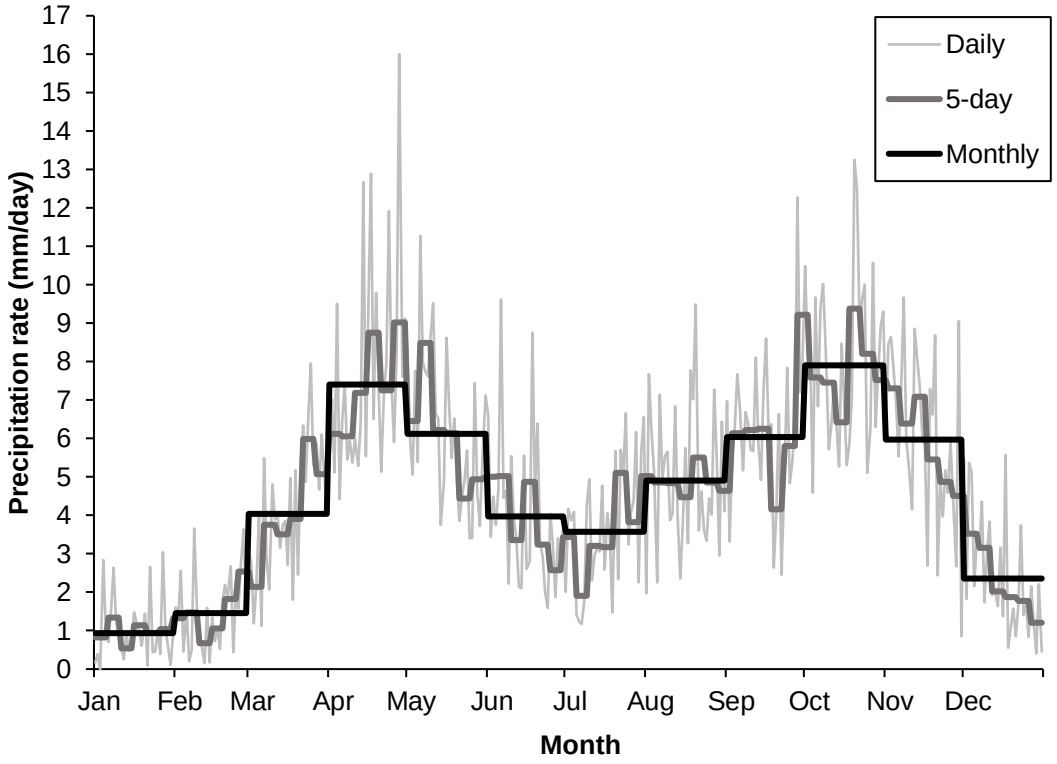


Figure 1

Pluviogram of Mean Daily, 5-Day, and Pentad Precipitation Rates Throughout the Year, Calculated Using Rainfall Data Available from 1993 to 2021.

The Budongo Forest is a medium-altitude, semi-deciduous forest (Eggeling, 1947). Between 1930 and 1970 extensive logging activity took place in the forest, including arboricide treatments (Bahati, 1995), which caused the dominant forest type to switch from *Cynometra* forest (Eggeling, 1947) to mixed forest (Plumptre, 1996). Despite the shift in forest type and the intense logging activity causing it, the forest still has a high number of plant species consumed by primates (Tweheyo et al., 2004), providing a consistent and abundant food source to various primate species, including chimpanzees (Newton-Fisher, 1999a; Newton-Fisher et al., 2000; Plumptre & Reynolds, 1996; Villioth, 2018). The Budongo Forest Reserve is home to a large chimpanzee population, with an estimated population size of 674-2046 individuals (Plumptre & Reynolds, 1996) in the 1990s, though Newton-Fisher (1997)

gives close to 1000 as a more realistic number. Initial research activity in the area started in the 1960s (Reynolds & Reynolds, 1965; Sugiyama, 1968, 1969), stopped due to political unrest in Uganda during the 1970s and 1980s, and have been continuous since 1990, when the Budongo Forest Project was started, later renamed as the Budongo Conservation Field Station (BCFS) (Newton-Fisher, 1997; Reynolds, 2005).

The Budongo Conservation Field Station is located inside the Forest Reserve, regularly monitoring and providing research access to two communities of eastern chimpanzees (*Pan troglodytes schweinfurthii*) – the fully habituated Sonso community, where habituation started in 1990 (Newton-Fisher, 1997; Reynolds, 2005), currently numbering 64 individuals (C. Hobaiter, pers. comm.), and the neighbouring Waibira community, numbering an estimated 120 chimpanzees, in which habituation started in 2011 (Samuni et al., 2014). For both communities, a north-south east-west transect line grid-system has been cut, dividing the chimpanzee territories into ‘blocks’ of roughly 100 m x 100 m or 200 m x 200 m. Besides primatology, the BCFS also focuses on phenology, ornithology, and herpetology, veterinarian research & interventions, and community-based conservation in partnership with the villages bordering the Forest Reserve (Jackson, 2024; Reynolds, 2005).

The Waibira Community

This study focuses on the Waibira community, which at the end of the fieldwork data collection period in March 2022 had 98 named individuals (19 adult males, 30 adult females, 49 immatures). The total estimated community size is likely larger than that number, at ~120 individuals. Female chimpanzees take longer to fully habituate (Bertolani & Boesch, 2008; Langergraber et al., 2014), and despite habituation underway with an almost-daily presence of BCFS research staff in the

community since 2011 (Samuni et al., 2014), occasional encounters with unknown adult females and their dependent offspring within the community home range as well as camera trap data of them suggests the presence of several unhabituated resident females present in the community. The Waibira community is neighboured by other chimpanzee communities on all sides – the Sonso community to the south-west, and at least three other, unhabituated communities to the other directions – and therefore has no access to human settlements or crops (Villioth et al., in prep.). There is demonstrated gene flow between the Sonso and Waibira communities, with at least three Sonso-born females migrating to Waibira as adults to date (Samuni et al., 2014).

In the transect line grid-system covering the Waibira community home range, lines running north-south are denoted with numbers, increasing further east from the research station. Lines running east-west are denoted with numbers if they are south of the research station, increasing further south from the research station with the line directly at the latitude of the research station denoted 0, and with letters in alphabetical order north of the research station, increasing the further north they are. Intersections of the transect lines are named using the joint name of the specific north-south line followed by the specific east-west line, e.g.: the junction of north-south line 27 and east-west line N is named junction 27-N. Blocks formed by the transect lines are named after the junction in their south-west corner, e.g.: the block enclosed by the north-south lines 27 and 29 and the east-west lines N and P is block 27-N (Figure 2).

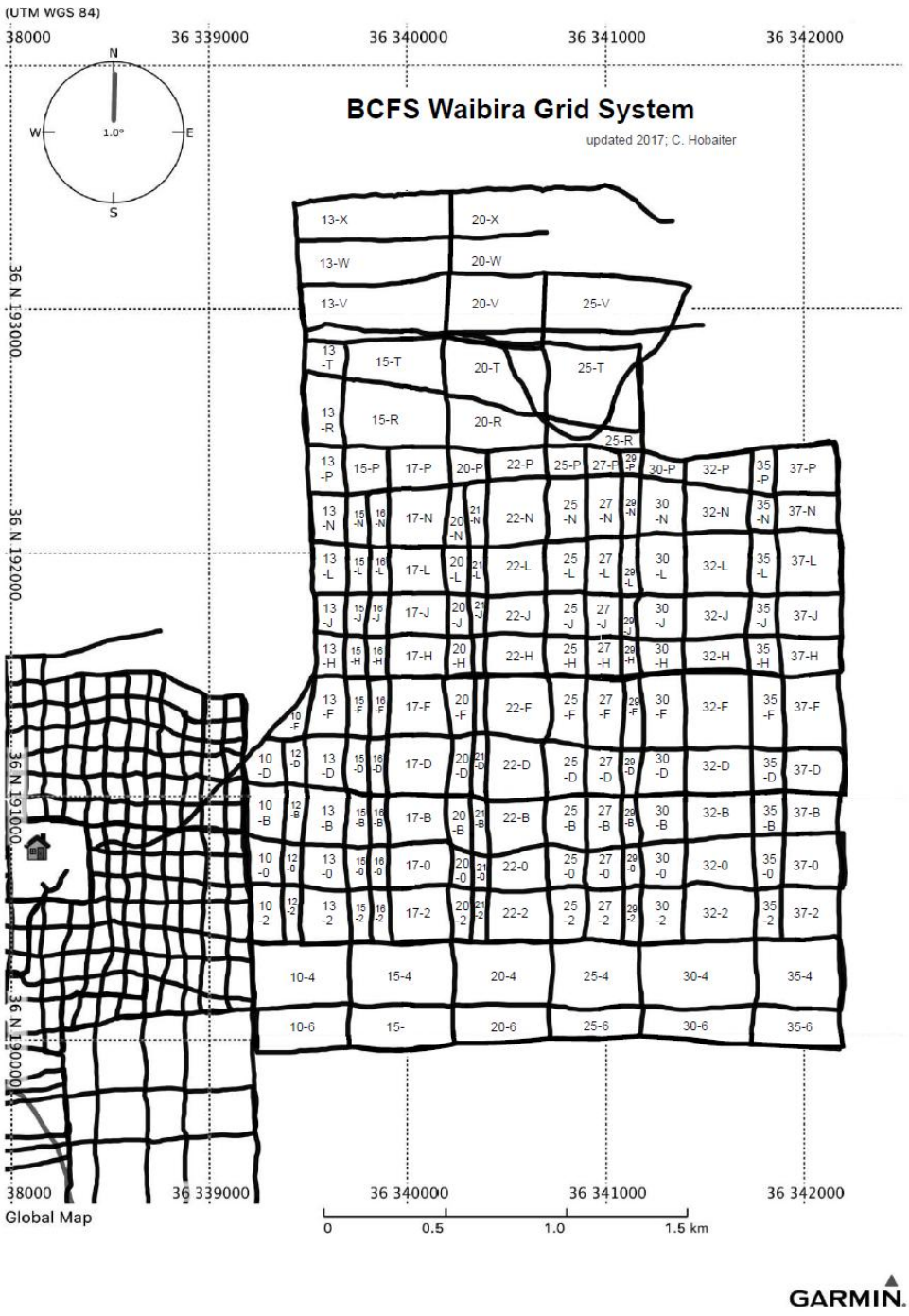


Figure 2

The Waibira Transect Line Grid-System

Note. Image courtesy of C. Hobaiter.

The Central Waterhole

While the Sonso community's home range includes the Sonso river, the Waibira community has no year-round flowing water available. During wet season months, the chimpanzees of the Waibira communtiy have access to an intermittent creek running through their home range, as well as small ephemeral terrestrial and arboreal water sources like puddles and dendrotelmata. During the dry season, the creek and all ephemeral water sources gradually dry out, leaving the Waibira chimpanzees with three waterholes as their only source of drinking water. Two of those are located on the eastern and southern borders of their home range respectively, shared with neighbouring chimpanzee communities, which makes visiting them, especially for solitary individuals or smaller parties, risky due to the potential of violent intercommunity encounters common in chimpanzees (Goodall, 1986; Watts et al., 2006). The third waterhole is located at the centre of the Waibira community home range (from now on, central waterhole), at block 25-L, and is the primary water source of the community during dry season months.

The central waterhole is located in a valley running north-south through the community home range and is the deepest part of the intermittent creek's bed. As the dry season progresses, waterflow to the area stops, leaving water only in a 5-10 m straight section of the creek bed, and a ~10 m x 10 m area connected to the straight section where the main bed separates into smaller branches and pools interspersed with terrestrial herbaceous vegetation before converging again at the other end. The exact size of the central waterhole is not fixed during the dry season: the straight section gradually recedes from the intermittent creek bed and reduces in length as precipitation ceases, while the broader area's smaller branches lose connectedness with each other, separating into pools and puddles. As rainfall returns at the end of the dry season, the straight section increases in length, the

smaller branches become connected again, and water begins to extend into the original creek bed on both ends of the waterhole. Waterflow to the creek is then restored as the wet season returns. The soil in the straight section of the creek bed is a firm, red silt, while the 10 m x 10 m area has mixed soil types, containing firm sand and silt patches, as well as clay mud (Figure 3).


a
b

Figure 3

The Central Waterhole on February 25 2022

[a] The straight section of the creek bed that retains water during the dry season. [b] The broader area where the creek bed divides. [c] The red silt of the creek bed visible in a dried-out section. [d] The mixed soil type of clay, silt, and sand present at the broader area of the central waterhole.

Besides chimpanzees, the central waterhole is also visited during the dry season by other species including blue duikers (*Cephalophus monticola*), red forest duikers (*C. natalensis*), bushbucks (*Tragelaphus scriptus*), honey badgers (*Mellivora capensis*), two mongoose species (*Atilax paludinosus* and *Crossarchus alexandri*), black and white colobus (*Colobus guereza*), olive baboons (*Papio anubis* or hybrids of it), red-tail monkeys (*Cercopithecus ascanius*), blue monkeys (*C. mitis*), and various bird species during the day, and red river hogs (*Potamochoerus porcus*), brush-tailed porcupines (*Atherurus africanus*) and other rodents, tree hyrax (*Dendrohyrax* spp.), genets (*Genetta genetta*), civets (*Civettictis civetta*), pottos (*Periodicticus potto*), unidentified bat species, and giant pangolins (*Smutsia gigantea*) during the night.

Camera Trap Data Collection

Camera trap data was collected with Bushnell Aggressor camera traps – the exact model number and year of make is not known, as cameras malfunctioned, were moved to different field sites, or updated to newer models throughout the years without those details being recorded. The camera traps monitor the central waterhole, aiming to encompass the annual dry season. Video data is available for every dry season from January 2013. Due to year-to-year variation in the start and end dates of the dry season, some monitoring periods also have videos from the end or start of the wet season, and/or do not fully cover the dry season. Camera trap 1 (CT1) monitors the same area of the waterhole every year – the straight section of the original creek bed, which is used by the chimpanzees for drinking throughout the dry season (Figure 4). There are minor changes in the camera location and angle of CT1, as suitable tree trunks for attaching the camera trap might fall or become overgrown between monitoring periods. Camera trap 2 (CT2) has been in use since February 2017, monitoring other sections of the waterhole that fluctuate in water

availability and chimpanzee usage throughout the dry season. As the main purpose of CT2 is to monitor these short-term high intensity drinking spots at the central waterhole, it has more changes in camera location and angle, following recent chimpanzee activity in the area (Figure 4). The cameras are set to record videos both day and night with the highest sensitivity level of infrared detection, filming for 1 min after activation during the day, and 15 s during the night, with a 1 s interval between consecutive videos. The videos are time and date stamped. Batteries were changed and videos were downloaded to more permanent storage every five to two days depending on capture frequency and resulting battery drainage speed by BCFS primatology research staff, visiting researchers, including myself during the 2018-19 and the 2021-22 dry seasons, Walter John Akankwasa, and Catherine Hobaiter to ensure the camera traps always remain active. However, due to equipment failures and public holidays some days within a monitoring period are occasionally missing (103 out of 750 total days camera traps were deployed).


a
b

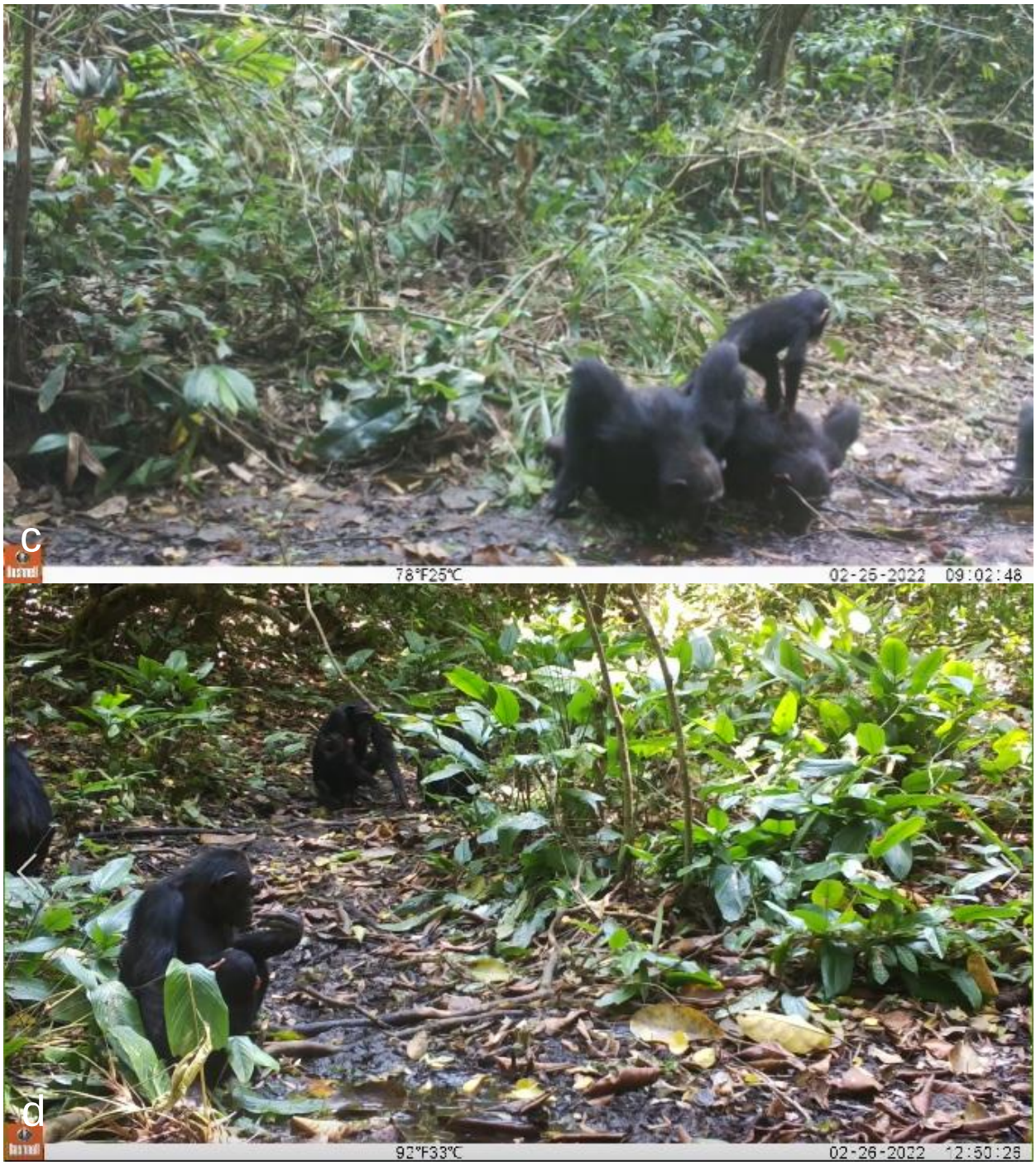


Figure 4

Example Locations and Views of the Camera Traps in the 2021-2022 Dry Season

Note. Photographs were taken February 25 2022. The locations of the camera traps are indicated by black circles. Screenshot *c* is from February 25 2022. Screenshot *d* is from February 28 2022.

[a] The location of CT1 during the 2021-2022 dry season. [b] The location of CT2 between February 24-April 10 2022 for the 2021-2022 dry season. [c] The view of CT1 during the 2021-2022 dry season. [d] The view of CT2 between February 24-April 10 2022 for the 2021-2022 dry season.

Sampling effort varied between monitoring periods, both on the level of the earliest and latest dates camera traps were active in each period, as well as the number of videos recorded and days sampled per period (Table 3). The number of days camera traps were active was defined as days with at least one camera trap active and represent general monitoring presence in the area – for monitoring periods with two camera traps, a day was counted as active if at least one of the two camera traps was active. If two camera traps were active, the day was not counted as double. Hours of potential footage was calculated by counting the number of days a camera trap was active, then multiplying it by 12.5. For days where two camera traps were active, hours of potential footage were calculated for each trap, then added for the day, to represent how the amount of potential footage that could contain chimpanzees on a given day increases with two camera traps active. 12.5 hr per day per active camera trap was used to calculate the hours of potential footage instead of 24 hr, as the earliest and latest 30 min bins when Waibira chimpanzees were recorded on camera trap were 7 am and 7:30 pm respectively (Chapter 3). Limiting hours of potential footage to that time period also reflects the diurnal behaviour of chimpanzees – while nocturnal activity has been observed in savannah-dwelling chimpanzees (Pruetz, 2018), it is an adaptation to extremely high daytime temperatures in open habitats, and no chimpanzee activity has been recorded on camera trap outside daylight hours in the Waibira community.

Table 3

Camera Trap Sampling Effort at the Central Waterhole

Monitoring period	Start	End	Days active	Hours of potential footage	Number of videos
2012-2013	January 13 2013	April 12 2013	78	975	858
2013-2014	December 17 2013	February 12 2014	36	450	501
2014-2015	January 23 2015	April 4 2015	42	525	992
2015-2016	January 21 2016	April 14 2016	49	612.5	165
2016-2017	January 13 2017	February 28 2017	43	675	2626
2017-2018	December 5 2017	March 4 2018	74	1612.5	5375
2018-2019	December 13 2018	February 25 2019	75	1737.5	4476
2019-2020	December 12 2019	March 11 2020	58	787.5	797
2020-2021	January 29 2021	April 6 2021	67	1500	2589
2021-2022	December 5 2021	April 10 2022	125	2862.5	8842
Total			647	11,737.5	27,221

Note. CT2 active from February 11 2017.

Unhabituated Resident Females

At the BCFS, all chimpanzees older than 6 months and identifiable consistently and without disagreement by primatology research staff are given a unique identifying name. For chimpanzees born to a named resident female, their name also starts with same letter as their mother's. In the Waibira community all adult and subadult males and most resident females are already named, however, there is evidence of the presence of several unhabituated, and thus unnamed, resident females as well. First, primatology research staff occasionally encounters unhabituated adult females and their dependent offspring in the centre of the community home range that is not shared with other communities and where visiting

would mean substantial risk for a non-resident individual (Martínez-Íñigo et al., 2021; Watts et al., 2006). Second, two subadult males in the community, *Bright* and *Lillo,* have no known mothers, and were first sighted in mixed-sex parties as a juvenile and subadult respectively, at the age when male chimpanzees decrease their association with their mothers and increasingly interact with other males (Sandel et al., 2020). As males are the philopatric sex in chimpanzees (Nishida et al., 1985; Pusey, 1980), it is also highly unlikely *Bright* and *Lillo* transferred from another community. Whether they are orphaned, or their mothers are still alive, they were not seen as infants and do not interact with any of the named resident females in a manner that would suggest a mother-offspring relationship (e.g. travel together frequently, groom preferentially, share high value food). The most likely explanation is that they are the sons of unhabituated resident females. Third, unhabituated females commonly appear on camera trap, where habituation levels to human observers do not impact detection (Boyer-Ontl & Pruetz, 2014). Most of them are also accompanied by dependent offspring and all interact with named individuals of the community in a peaceful manner, supporting that they are residents of the Waibira community, but have not been habituated to the presence of human observers since 2011.

As several of those females are recorded on camera trap across multiple years, unambiguous identification in video data, if not official naming in line with BCFS rules, is possible. To maximise the available camera trap data on female behaviour, I have included all identified females in data collection, that is, both named, and unnamed, but regularly recurring females (Table 4). Unnamed but identified females received a temporary identifying name for this study. One of them, a female with the temporary name *Alfmother* was repeatedly sighted by observers

over the 2021-2022 dry season with her juvenile daughter and was named *Elodie* in June 2022.

Table 4

List of Unhabituated Identified Females and Their Offspring

Bright's mom: First seen February 7 2013 with infant *Bright*. Not seen since January 9 2018, presumed dead alongside *BRM2* in the 2017-2018 dry season respiratory outbreak.
Bright (2010 ± 1 year) ♂: First seen February 7 2013, regularly seen by observers since January 2018. Named July 2018.
BRM2 (2016 August ± 1 month) ♀: First seen January 13 2017. Not seen since January 9 2018, presumed dead.
Dada's daughter (2010 ± 6 months) ♀: First seen February 17 2013 with mother *Dada,* a named resident female. Her older brother *Dun-Edin* and younger brother *David* are also named. Last seen March 15 2022, occasionally seen by observers in the 2021-2022 dry season.
Elodie (prev. *Alfmother*): First seen February 27 2013 with juvenile *ELD1*. Last seen February 24 2022. Regularly seen by observers since the 2021-2022 dry season, named July 2022.
ELD1 (2008 ± 1 year) ♂: First seen February 27 2013.
Esther (2015 ± 6 months) ♀: First seen January 21 2017. Regularly seen by observers with *Elodie* since the 2021 - 2022 dry season, named July 2022.
ELD3 (December 6 2021 ± 3 days) ?: Infanticide by Waibira males December 16 2021.
Long-hair adult female: First seen February 9 2013 with juvenile *LHA1*, last seen March 10 2022. Seen by observers March 2022.
LHA1 (2005 ± 1 year) ♂: First seen February 9 2013.
LHA2 (September 2013 ± 1 month) ♂: First seen February 4 2014.
Mittens: First seen February 9 2013, last seen March 17 2022. Seen by observers February 2022.
MTS1 (December 2018) ♀: First seen January 5 2019

Note. Camera trap data available January 13 2013-April 10 2022. Birth dates are estimated based on body size.

Video Coding

Out of a total 27,221 camera trap videos available, 8288 were of chimpanzees. Using BORIS video coding software (v. 7.13.6, Friard & Gamba, 2016), I coded every camera trap video containing at least one chimpanzee drinking for Chapter 3, and any identified adult or subadult female chimpanzee present for Chapter 4 and 5.

For Chapter 3, I recorded all occurrences of chimpanzees drinking on screen by direct drinking, dipping a hand or finger in the water, or drinking tool use, including the identity, sex, and age category of the chimpanzee drinking. *Age categories* used followed Reynolds (2005), and were *adult* (Females: 14+ years, Males: 15+ years), *subadult* (Females: 10-14 years; Males: 10-15 years), *juvenile* (5-< 10 years), and *infant* (< 5 years). Unidentified individuals or individuals with indeterminable identity due to poor light conditions or being only partially visible were recorded as their age-sex category. Individuals with no identifiable age and sex were recorded as *unknown*. Relying on the video date and time stamp, I also recorded the date for all videos with chimpanzees drinking, as well as the time for videos after 2016. Errors in time stamps were frequent for videos before 2016, and only allowed for determining the time elapsed between videos.

For Chapter 4 and 5, I coded videos where at least one identified adult or subadult female was present at any point during the video. For each video, I recorded the date, then for each identified independent female appearing on-screen at any point during a video I recorded the time she spent on-screen to the nearest second (1-60 s). If a female went off-screen then returned within the same video, I recorded it as continuous presence, using her last on-screen appearance during the video as the end point – within a 1 min video, it is impossible for a chimpanzee to leave the central waterhole and its immediate area and return. I also recorded her

current *reproductive status*: depending on the presence and age of any infants, as well as the presence or absence of a perineal swelling, the tumescence of which roughly correlates with ovulation (Emery & Whitten, 2003; Emery Thompson, 2005), one of four reproductive status categories were assigned. *Without a swelling*, for females with no infant and no perineal swelling, *with swelling*, for females with a perineal swelling, *young infant*, for females with an infant aged < 2 years, and *old infant*, for females with an infant aged 2-< 5 years. Infants were split into two categories to capture the differences in the energetic (Emery Thompson et al., 2012) and hydration demand (Nelson et al., 2022) of lactation as infants age. Where the female had a young infant but was recorded as having a perineal swelling, the category *young infant* was assigned to her. While some females might have shorter interbirth intervals between offspring, the median interbirth interval in case of a surviving offspring is 5.2-6.6 years across wild chimpanzee populations (Emery Thompson et al., 2007a). Having a less than three year reproductive turnover, and therefore resuming ovulation with a still-dependent infant, is extremely rare (Emery Thompson et al., 2007a, 2012; but see: Cibot et al., 2019a) and has not been observed in the Waibira community during 13 years of research presence.

At the start of each video, I took a scan sample of the number and identity of female party members of each female on-screen, that is, all other independent identified females also on-screen at the start of the video, and 5 m party members, that is, all other independent identified females also on-screen and within 5 m of the given female at the start of the video, used to calculate *dyadic association indices* and *proximity indices* between females in Chapter 5.

I also coded all-occurrence data on pant-grunts between females and agonistic female-female interactions, including the identity of the recipient and actor. For bi-directional events, I recorded the event once as individual A as recipient and

individual B as actor and once with the roles switched. Ethograms of all specific behaviours coded from camera trap videos for Chapters 3, 4, and 5 can be found in Table 5.

Table 5

Ethograms of Behaviours Recorded

Behaviour	Description
Drinking	A chimpanzee consuming water either by direct drinking; by dipping; or by using a drinking tool made of soft vegetation
Drinking tool use	Dipping a drinking tool made of soft vegetation into the water, inserting it into the mouth fully or partially, and sucking the water out of it (Goodall, 1965b). The drinking tool can be fabricated by the individual, or fabricated by another chimpanzee, discarded, then reused by the individual (Hobaiter et al., 2014).
Dipping	Dipping a hand into the water, then licking off the clinging water from the fur and fingers (Reynolds & Reynolds, 1965).
Direct drinking	Putting the mouth to the surface of water and sucking it up with the lips (Goodall, 1965b; Nishida, 1980).
Pant-grunt	Short, repeated cough-like vocalisations given upon encounters (Goodall, 1986) – they are usually given by the lower ranking individual of a dyad, though bidirectional pant-grunts do sometimes occur (e.g.: Newton-Fisher, 2006).
Approach-leave interaction	One individual using a resource at a given sublocation within 3 s of another individual stopping its use of the resource at that spot and moving away from it. I purposefully do not use the term ‘displacement’ for these interactions, as they might simply reflect waiting or turn taking to use a resource, a behaviour chimpanzees are capable of (Martin et al., 2017), instead of an intentional ousting of a competitor.
Vocal threat	Harsh, low-frequency vocalisation given by one individual towards another, ranging from a soft bark to a bark, waa bark, and screaming (Goodall, 1986).

Gestural threat	One individual flinging their arm or hand in the direction of another, shaking, slapping, or punching an object, or punching the ground (Hobaiter & Byrne, 2014), tipping their head towards another, or hunching sitting or standing up, accompanied by piloerection (Goodall, 1986)
Physical aggression	One individual hitting, slapping, or biting another – as hitting, slapping, and biting can also happen in a play context (Hayaki, 1985), the lack of a play face and the presence of a negative reaction from the recipient, such as screaming or fleeing, is also necessary.

Limitations of Camera Trap Video Data

While camera traps were active throughout the day, the length of videos recorded is pre-set, and even if the camera trap is immediately re-triggered as soon as it finished recording, there is at least 1 s delay between consecutive videos. As such, camera traps cannot provide truly continuous data on activity in the monitored area, but rather a series of snapshots which are continuous within themselves, but are separated by a variable amount of delay within the activity they are a record of. Compared to direct observation, camera traps are also limited by their fixed viewshed, unable to be triggered by activity outside their trigger area, or record activity outside their viewable area (Moeller et al., 2023). These characteristics then pose two methodological issues that need addressing when encoding information from camera trap videos: first, the uncertainty of what animals do in the gaps between videos, and second, the uncertainty about how representative a sample based on on-screen behaviour is.

For events, recorded at their onset (Altmann, 1974), both the potential gap between videos and the limited view means that compared to direct observation of the central waterhole, the number of them will likely be lower when coded from camera trap videos, as some events unavoidably take place in the few seconds

between consecutive videos or just outside the view of the camera traps. For this reason, I will assume throughout this thesis that frequencies and rates of various types of events recorded from camera trap videos represent the minimum number of them, and actual frequencies and rates might be higher. However, studies comparing data from camera trap videos and direct observation on chimpanzees have shown that while camera traps underestimate numbers, general trends detected are consistent between the two methods (McCarthy et al., 2018; van Leeuwen et al., 2020b; Vink et al., 2020). For CT2, the location of the camera trap was also moved within the central waterhole depending on chimpanzee activity reported by observers to minimise the chance of events of interest occurring off-screen and going undetected.

For states, where the length of the behaviour is also of interest (Altmann, 1974), gaps between videos and potential off-screen behaviour pose an additional problem, as it cannot be determined with certainty if the animal continued a specific behaviour between videos, even if they engage in it during the videos. To address this, I have calculated the time elapsed between the current on-screen behaviour and the previous on-screen behaviour of an individual, and recorded it as part of the same state or a new one depending on a predetermined cut-off point. The cut-off point was calculated as the shortest duration which would have resulted in the termination of the state during continuous data collection. For drinking behaviour in Chapter 3, the cut-off point was 1 min, as drinking bouts within a minute-long video were coded as the same state. For waterhole visitations in Chapter 4, the cut-off point was 3 min 50 s, based on the minimum amount of time it would have taken for a chimpanzee to leave block 25-L from the central waterhole then return.

While continuous observational monitoring of the central waterhole could have addressed the above limitations, and have been done in past studies (e.g.: Beck &

Tuttle, 1972; Ferry et al., 2016), it also could have acted as a deterrent towards less habituated or unhabituated chimpanzees and other animals. As the central waterhole is one of the few remaining water sources within several km^2 during the dry season and as such likely a small natural feature with high ecological importance (Hunter et al., 2017), I prioritised minimising disturbance to wildlife accessing water, and chose camera traps as the primary way of monitoring chimpanzees at the central waterhole, in accordance with suggestions monitoring unhabituated chimpanzees (Boyer-Ontl & Pruetz, 2014; Ibnou et al., 2018) and waterholes (Hayward & Hayward, 2012).

Fieldwork Data Collection

I conducted fieldwork between November 4 2021 and March 17 2022, encompassing the end of the wet season and the entire dry season, collecting data on the drinking behaviour, space use, and social behaviour of the independent female chimpanzees of the Waibira community. Field days consisted of observational data collection 7 am-5 pm between November 2021 and January 3 2022, 7 am-12 pm between January 4 and February 21 2022, and 7 am-3 pm between February 22 and March 2022, due to changing field site COVID-19 health protocols limiting observation hours per day. Due to the same health protocols, between January 4 and February 21 2022, the maximum amount of time observers could spend with one subgroup of chimpanzees was also restricted to maximum 30 min. The general schedule of field days was four field days followed by two days off, unless interrupted by public holidays, with any field days falling on a Sunday and the fourth field day being a ‘half day’, working between 7 am-1 pm only.

For Chapter 4 and 5, I conducted focal individual follows of named adult and subadult females of the Waibira community. I collected 132 hr of focal individual follow data across 75 days – 94 hr 50 min across 28 days in the wet season, and 37

hr 10 min across 27 days in the dry season. Working together with Vincent Kizza, a trained BCFS primatology research staff, we located female chimpanzees primarily by visiting currently fruiting trees, or locations the chimpanzees were last seen during the previous day. Female chimpanzees are less likely to use travel vocalisations compared to males (Crunchant et al., 2021; Kalan, 2019), so locating a focal individual primarily by following those vocalisations could have led to an uneven sampling of more social or currently cycling females, who are more likely to travel with males (Newton-Fisher, 2014). If no females were found at fruiting trees or the location chimpanzees were last seen the previous day, listening for travel vocalisations was an alternative way to locate a subgroup which potentially had a female individual. Once a female was encountered, she was chosen as the day's focal individual unless she has been sampled within the same four day working period. If more than one female was encountered, the one with less observation hours on record was chosen as the focal individual. When health protocols allowed for it, we tried to follow focal individuals all day, but switched to a new focal individual if the current one could not be located for 2 hr. During focal individual follows, I recorded the focal female's identity and her current *reproductive status* (*without swelling*, *with swelling*, *young infant*, *old infant*), and took scan samples at 10 min intervals, recording the identity of all independent identified female individuals within the same party as her, the identity of her 5 m female neighbours, and her location on the grid cell level. A party was defined as all adults and subadults within a roughly 35 m radius from the party centre (Newton-Fisher, 1997). I also collected data on her daily travel route using a handheld Garmin 60CSx GPS device set to record a waypoint every 5 min.

Parallel to focal individual follows, I also conducted focal group follows of parties including at least one independent identified female. The majority of focal

group follows were of the party of our focal individual during focal individual follows, but on some days we have lost our focal individual too close to the end of working hours (< 2 hr) to allow us to find her or to pick a new focal individual, or only found females who have already been chosen as focal within the same four day working week, and I only collected data on the focal group. Finding a second or suitable focal female was further limited by the number of working hours restricted between January and March 2022. I collected 146 hr 28 min of focal group data across 56 days – 100 hr 43 min across 28 days in the wet season and 45 hr 45 min across 28 days in the dry season. During focal group follows, I recorded *ad libitum* data on any observed instance of drinking, recording the identity of the individual drinking, the date, and whether the individual drank from a terrestrial or arboreal water source for Chapter 3; any pant-grunts between independent identified females for Chapter 4 and 5; and any agonistic behaviour between independent identified females for Chapters 3 and 5 (Table 5). I also recorded data on the daily first sighting of independent identified females according to a fixed protocol for Chapter 4 - when I encountered any of them for the first time during the day, I recorded where the encounter happened on the grid cell level.

Long-Term Data

Trained BCFS primatology research staff Gideon Atayo, Robert Eguma Yikii, Vincent Kizza, and Steven Mugisha conduct daily focal individual follows in the Waibira community, and record *ad libitum* data on social behaviour, which includes pant-grunts and agonistic interactions. Except for public holidays or illness, there is always at least two research staff collecting observational data on the chimpanzees on a given day. They are in the forest 7 am-5 pm, locating chimpanzees by listening for travel vocalisations, visiting locations they were last seen in the previous afternoon, or currently fruiting feeding trees. Focal individuals are always

independent named individuals and are chosen to ensure an even sampling of individuals, with no chimpanzee followed for two days in a row. When research staff loses a focal subject, a new one is chosen if it cannot be located after more than 2 hr.

From long-term focal follow data available 2015-2022, I extracted 15 min interval party composition data, which is a scan sample including the identity of all independent individuals within the focal individual's party and the party's location on the grid cell level for Chapters 4 and 5. There are 22,771 party composition scan samples available, across 1601 days and 5742 hr 15 min of observation, with an average 19.5 days per month. From focal follow data on female individuals only, I also extracted the identity of all adults and subadults within 5 m of the focal individual, if any, recorded at 15 min intervals alongside party composition for Chapter 5.

From *ad libitum* long-term data available 2015-2022, I extracted all recorded pant-grunt events between females for Chapters 4 and 5 and all agonistic interactions between females for Chapter 5. BCFS primatology research staff also records health monitoring data at the end of all observation days, recording which chimpanzees were seen, any injuries, births, and data on the presence and tumescence of perineal swellings for all adult and subadult females encountered that day. Health monitoring data was also available 2015-2022, from which I extracted data on the reproductive status of independent females, which I used it to determine individuals' *reproductive status* at a given timepoint (*without swelling*, *with swelling*, *young infant*, *old infant*) for Chapters 4 and 5 and calculating the *number of sexually available females* on a given day for Chapter 5.

Phenology Data

Phenology data were available 2015-2022, collected by trained BCFS phenology research staff James Ahebwa, Moses Businge, Gophine Ericsson, and Nelson Orijabo. Each month, the same common chimpanzee feeding trees are visited, and research staff records the amount of young leaves, mature leaves, unripe fruit, ripe fruit, flowers, and other, unclassified plant parts the tree has at the moment, assigning it a score between zero and four. Zero represents the tree not having any of the given element when it was visited, while four represents the tree being at its maximum capacity for producing the given element when it was visited. Basal area measurements (B) for each of the trees, representing their potential fruit yield, was updated in 2022, and was calculated as

$$B = (1/2DBH)^2 \times \pi$$

where DBH is the diameter of the tree trunk at breast height, or above any buttress roots if they reach to breast height. Extracting the number of trees surveyed and the number of trees with any ripe fruit per month from the long-term phenology data, I calculated a monthly *food availability index* (*FAI*) for Chapter 5 based on Basabose's (2005) method:

$$FAI_m = \frac{N_{m\ fruiting}}{N_{m\ surveyed}} \times B_{m\ surveyed}$$

where the proportion of surveyed trees fruiting in a given month are multiplied by the total basal area of the trees surveyed in that month. As opposed to Basabose (2005), who used the proportion and basal area of all trees he regularly monitored, I used proportion and basal area of all trees surveyed in a given month to account for months when not all regularly monitored trees were visited by the phenology team – including them as nonfruiting without knowing if they were in fruit or not could have potentially lowered *FAI*s. Mean monthly food availability between 2015 and 2022

was 22,666.6, with considerable monthly fluctuation (Figure 5). Food availability was at 0 in 15 months, in November 2015, April and August 2016, January, May, and July 2018, August and December 2019, October to December 2020, July 2021, and March, June, and September 2022, and the highest, 125,521 in April 2017. Mean wet season monthly food availability was 21,559.6 ± 26,669.9, while mean dry season monthly food availability was 25,736.3 ± 24,954.1.

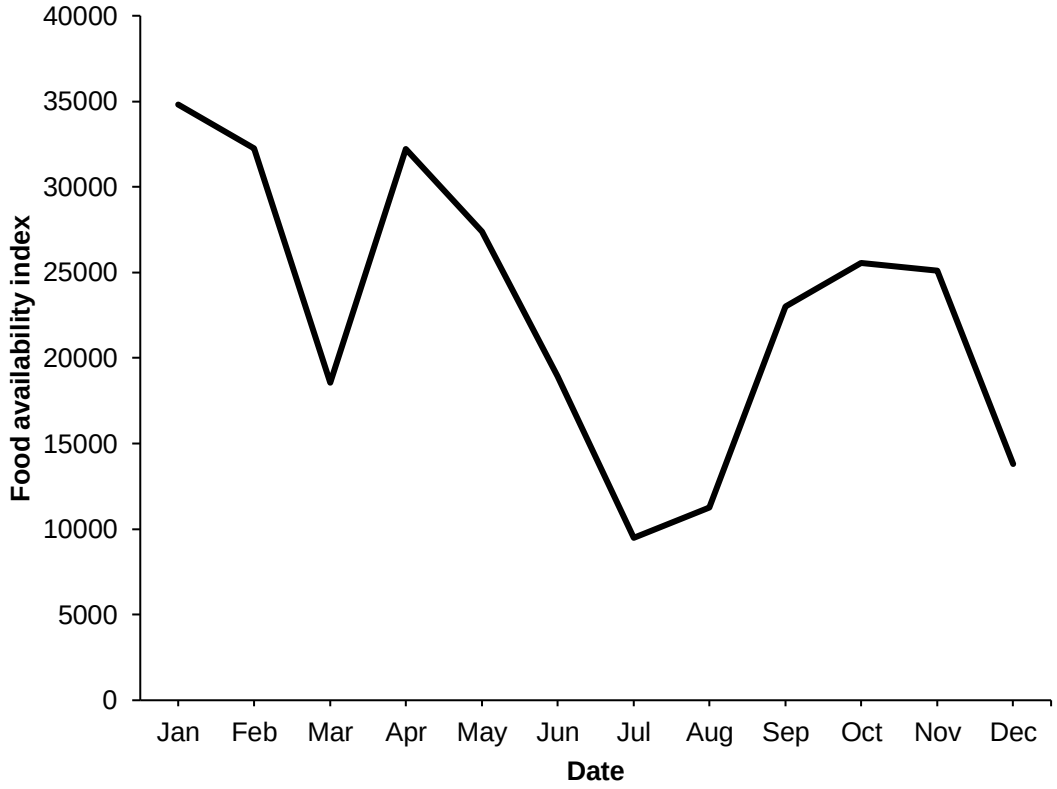


Figure 5

Mean Food Availability Throughout the Year, Calculated Using Phenology Data Available from 2015 to 2022

Weather Data & the Onset of Dry Seasons

Long-term data on rainfall and minimum and maximum daily temperature from BCFS is available 1993-2022. Rainfall is recorded with a rain gauge located in an open area near the forest edge. It is recorded in mm, and was used to calculate the

onset, end date, and duration of dry seasons. While using a nominal, binary wet-dry categorisation of entire months is common in primatology (e.g.: Murray et al., 2006; Pruetz, 2018; Reynolds, 2005), giving the dry season a flexible start and end date, commonly used in meteorology and phenology (Chou et al., 2013; Fu et al., 2013; Jiang et al., 2019; Kousky, 1988) results in a more sensitive measure and captures interannual variation in the timing and intensity of the dry season (Valeix, 2011). Following Kousky (1988) and Fu et al. (2013), I chose a pentad-based approach, which divides the year into five-day units, starting from January 1. For leap years, February 29 is included in a pentad alongside February 28. I defined the start of the dry season as the first day of the first pentad which has both less than half the average rainfall per pentad for the year and is then followed by five out of eight pentads having < 1 mm total rainfall. For 2022, where rainfall data was only available until November 1, the per pentad average was calculated based on the available pentads. The end of the dry season was the last day of the last pentad which has both less than half the average rainfall per pentad for the year and is the being preceded by five out of eight pentads with < 1 mm total rainfall (Table 6, Appendix A). The first day was numbered one, and all consecutive days then numbered sequentially within each season, providing a variable which captures the increasing ‘intensity’ of the dry season as temporary water sources dry up and evaporate and humidity decreases.

Table 6

Dry Season Start and End Dates

Dry season	Start date	End date
2012-2013	January 1 2013	March 6 2013
2013-2014	November 27 2013	March 1 2014
2014-2015	November 27 2014	March 16 2015
2015-2016	December 22 2015	March 16 2016
2016-2017	December 07 2016	February 24 2017
2017-2018	November 27 2017	March 6 2018
2018-2019	December 12 2018	February 19 2019
2019-2020	December 17 2019	February 14 2020
2020-2021	December 7 2020	March 16 2021
2021-2022	January 1 2022	March 16 2022

Female Rank

Pant-grunts are thought to be a reliable indicator of dominance relationships between chimpanzees, with the subordinate individual vocalising to the dominant one (Goodall, 1986). Relying on *ad libitum* fieldwork and long-term data on pant-grunts exchanged between females, I assigned a rank to females for Chapters 4 and 5 based on the proportion of other females in the group who pant-grunted to them, taking the arcsine of the square root of the proportion to calculate dominance values (DV) (Beilharz & Mylrea, 1963), then assigning one of four *rank* categories (*high, mid, mid-low, low*) based on DV following Newton-Fisher (2006) (Table 7). Females who were not recorded giving or receiving a pant-grunt were assigned *unknown*. While more precise rank calculation methods are available (eg.: Elo-ranks), pant-

grunt vocalisations are rare between female chimpanzees (e.g.: Murray et al., 2007; Perspectives Collective, 2023), and collecting a sufficient sample size is extremely time consuming. Additionally, more precise rank estimation methods also require that ranks remain stable, and that individuals do not disappear during the data collection period, assumptions which such a lengthy data collection period makes difficult to fulfil.

Table 7

Female Dominance Values and Categorical Ranks

Individual	Dominance value	Categorical rank
Rita	0.46	High
Lotty	0.46	High
Monika	0.41	High
Bahati	0.37	Mid
Ndito-Eve	0.37	Mid
Kidepo	0.32	Mid
Kipepeo	0.32	Mid
Liran	0.32	Mid
Nora	0.32	Mid
Ketie	0.26	Mid
Akiki	0.18	Mid-low
Arua	0.18	Mid-low
Daima	0.18	Mid-low
Penelope	0.18	Mid-low
Shay	0.18	Mid-low
Tatu	0.18	Mid-low
Tibu	0.18	Mid-low
Eili	0	Low
Jinja	0	Low
Liz	0	Low
Masindi	0	Low
Onyofi	0	Low
Rachna	0	Low
Santa	0	Low
Spini	0	Low

Ethical Note

This research has received ethical approval from the Animal Welfare and Ethical Review Body of the University of Kent, and was conducted with full approval from BCFS, Uganda Wildlife Authority, and the Uganda National Council for Science and Technology. All fieldwork conformed to the International Primatological Society Code of Best Practices for Field Primatology. Site rules by BCFS are in place to minimize disturbance and possible disease transmission to chimpanzees, such as keeping a minimum 7 m distance between chimpanzees and observers, wearing a surgical mask while in the forest, not entering the forest when experiencing any signs of respiratory or gastrointestinal illness, and undergoing a 10-day total quarantine upon arrival to the research station.

Chapter 3

Drinking & Water-Contact Behaviour in Rainforest Chimpanzees

- Rainforest chimpanzees drink water daily, year-round
- They drink more often during the dry season, but drinking behaviour is not induced by the dry season
- They show a context-dependent aversion towards water-contact, not fear
- Water is a regularly consumed resource by chimpanzees regardless of climate

Most animals depend on surface water to meet their hydration needs. Whether they drink, from which water sources, how often, and when depends both on necessity – how much liquid water they need to consume to avoid dehydration – and opportunity – the availability and distribution of free water sources they can utilise. As a result, drinking behaviour can vary not just between- but within-species as well, as individuals navigate changing seasons, fear of predators or humans, and major life events. Knowledge of the basic foraging ecology of a species, including whether they regularly consume or otherwise rely on a resource and in what contexts, is an important part of behavioural ecology and essential for effective conservation. With climate change increasingly disrupting water availability and quality, such studies of foraging ecology should extend their focus to water as well. In this chapter, I provide a comprehensive account of the drinking and water-contact behaviour of a rainforest-living community of eastern chimpanzees (*Pan troglodytes schweinfurthii*), detailing drinking frequency, daily patterns of drinking behaviour, water sources utilised, as well as variation between seasons and demographic

categories, to describe the water-consumption patterns of chimpanzees in mesic environments.

The presence and extent of drinking behaviour shows high variation between species, shaped by necessity and opportunity. Carnivores (coyotes (*Canis latrans*), kit foxes (*Vulpes macrotis*): Golightly & Ohmart, 1984; Hall et al., 2013; cheetahs (*Acinonyx jubatus*): Laurenson, 1995) and frugivores (mantled howler monkeys (*Alouatta palliata*): Nagy & Milton, 1979, spider monkeys (*Ateles* spp.): Campbell et al., 2005; collared peccaries (*Dicotyles tajacu*): Zervanos & Day, 1977) have a diet rich in foods with high water content, resulting in a lower need for liquid water and less frequent drinking compared to granivores (birds: Abdu et al., 2018) or grazing folivores (khulan (*Equus hemionus kulan*): Kaczensky et al., 2010; Przewalski's horses (*Equus przewalskii*): Scheibe et al., 1998). As thermoregulatory responses rely on evaporating body water (Hiley, 1976), species in hotter environments also face a higher necessity to drink (ring-tailed lemurs (*Lemur catta*), red-fronted lemurs (*Eulemur rufifrons*): Amoroso et al., 2017, 2020a; African elephants (*Loxodonta africana*): Fox, 2015; vervet monkeys (*Chlorocebus pygerythrus*): Wrangham, 1981). However, in extremely arid environments, where individuals do not reliably have the opportunity to access free water, species often evolve to be independent of surface water (Blanford's foxes (*Vulpes cana*): Geffen et al., 1992a, 1992b; Arabian oryx (*Oryx leucoryx*): Ostrowski et al., 2003) (Chapter 1).

As necessity and opportunity are not constant across space, time, and individuals, drinking behaviour also varies within species. Depending on their availability and distribution, water sources used range in size and permanence from rivers and large lakes (birds: Lee et al., 2017; red lemurs (*Eulemur rufus*): Scholz & Kappeler, 2004) to seasonal waterholes (eland (*Tragelaphus oryx*): Kasiringua et al., 2017; white-lipped peccaries (*Tayassu pecari*): Moreira-Ramírez et al., 2016;

lowland paca (*Cuniculus paca*): Paredes et al., 2017), rainwater collected in puddles, tree boles, or between branches (white-nosed coatis (*Nasua narica*): Delgado-Martínez et al., 2022b; bearded capuchins (*Sapajus libidinosus*): Castro et al., 2017; vervet monkeys: Wrangham, 1981) and licking dew or rainwater off of surfaces (eastern chimpanzees: Goodall, 1986). Depending on the topography of their habitat, different populations might primarily rely on different types of water sources (e.g.: eastern chimpanzees: Lanjouw, 2002).

However, the availability and importance of water sources can change with seasonal shifts in precipitation and temperature, leading to within-population changes in drinking behaviour. As smaller, ephemeral water sources can evaporate or be fully exploited during longer periods of high temperatures and low precipitation, the main water source of a population can change. The remaining larger water sources are visited by an increased number of species (birds: Dávila et al., 2020; ungulates: Sutherland et al., 2018) and individuals (white-lipped peccary: Moreira-Ramírez et al., 2016; Nubian ibex (*Capra nubiana*): Wakefield et al., 2008), arboreal species can show high terrestrial activity due to increased reliance on terrestrial water sources (spider monkeys: Campbell et al., 2005; white-fronted capuchins (*Cebus albifrons*)*:* Defler, 1979; Teminck's red colobus (*Piliocolobus badius temminckii*): Hilyer et al., 2015; siamangs (*Symphalangus syndactylus*): Sharma et al., 2016), and wildlife might venture into human settlements, seeking out human water sources which are more stable and actively maintained (Temnick's red colobus: Hillyer et al., 2015; Baird's tapirs (*Tapirus bairdii*): Pérez-Flores et al., 2021; Hanuman langurs (*Semnopithecus entellus*): Yoshiba, 1968). Besides evaporation, seasonal changes in water quality brought on by the cessation of waterflow (Sutherland et al., 2018) can also render them unusable. The levels of minerals (Ayeni, 1977), salinity, dung content (Wolanski & Gereta, 2001), bacteria (Stommel

et al., 2016), and parasites (Mugoya et al., 2019) worsen during dry seasons, and drinking from these stagnant water sources can negatively impact health (Hereford cows (*Bos taurus*): Willms et al., 2002). In response, low quality water sources might be completely avoided, even in droughts, risking dehydration (various lemur species: Amoroso et al., 2017; African elephants: Ndlovu et al., 2018), or animals might adapt their drinking behaviour to improve water quality by filtration (warthogs (*Phacochoerus africanus*): Ramey et al., 2013; African elephants: Stommel et al., 2016).

The necessity to drink can also change seasonally, with increased thermoregulation and lower food water contents leading to increased drinking frequency in species which drink regularly (brown howler monkeys (*Alouatta guariba clamitans*): Chaves et al., 2021; black howler monkeys (*Alouatta pigra*): Dias et al., 2014; white-faced capuchins (*Cebus capucinus*): Freese, 1978; koalas (*Phascolarctos cinereus*): Mella et al., 2019), and the appearance of drinking behaviour in species otherwise independent of surface water (kit foxes: Hall et al., 2013; mountain gorillas (*Gorilla beringei beringei*): Watts et al., 2022; collared peccaries: Zervanos & Day, 1977). High seasonal temperatures can also impact the within-day temporal patterns of drinking. Some species drink most often during the hottest periods of the day to improve evaporative cooling (yellow baboons (*Papio cynocephalus*): Altmann & Altmann, 1970; white-lipped peccaries: Moreira-Ramírez et al., 2016), while others shift their activity, including drinking, outside of daily peaks of temperature (Hanuman langurs: Beck & Tuttle, 1972).

Water sources are common locations of interspecies interactions, including human-wildlife ones. Besides environmental variables, animals also adjust their drinking behaviour to navigate predation protection, fear of humans, and interspecies competition. In addition to availability and quality, perceived safety is also taken into

consideration when choosing a water source. Predators visit terrestrial water sources to drink or to hunt congregating prey (fossa (*Cryptoprocta ferox*), Madagascar harrier hawks (*Polyboroides radiatus*): Amoroso et al., 2020b; jaguars (*Panthera onca*): Chaves et al., 2021; bobcats (*Lynx rufus*), coyotes: Harris et al., 2015). For prey species, terrestrial water sources are therefore sites of increased predation risk, resulting in behavioural adaptations impacting where, how often, and when animals drink. Water sources with low vegetation cover (yellow baboons: Altmann & Altmann, 1970) and good visibility are preferred (white-nosed coatis, white-faced capuchins (*Cebus capuchinus*): Burger, 2001), and animals might visit in large groups, have a staggered drinking order (yellow baboons: Altmann & Altmann, 1970; white-faced capuchins: Freese, 1978; patas monkeys (*Erythrocebus pata*): Henty & Mcgrew, 2014), shorter drinking bouts (Hanuman langurs: Beck & Tuttle, 1972; white-faced capuchins: Burger, 2001), and visit depending on when predator presence is lowest (red-fronted lemurs: Amoroso et al., 2020b; Sirot et al., 2016) for increased protection. For arboreal or semi-arboreal species, arboreal water sources allow individuals to remain in the safety of the trees while drinking (white-faced capuchins: Freese, 1978).

Compared to the presence of predators, human activity can serve both as a deterrent and attractant. Water sources with high human activity like cattle grazing and water carrying are avoided by some species, even at the cost of incurring heat stress or travelling further to undisturbed water sources (bantengs (*Bos javanicus*), giant ibises (*Thaumatibis gigantea*): Pin et al., 2020; leopards (*Panthera pardus*), European wild cats (*Felis silvestris*): Najafi et al., 2019; African wild dogs (*Lycaon pictus*): Ndaimani et al., 2016). For other species, human water sources serve as an attractant, especially in periods of low water availability (Temnick's red colobus: Hillyer et al., 2015; Baird's tapirs: Pérez-Flores et al., 2021; Hanuman langurs:

Yoshiba, 1968). With regards to other interspecies interactions, temporal partitioning, visiting water sources at different times of the day, to reduce between-species drinking competition as well as feeding competition for food sources around it is a common adaptation in species with similar diets, as seen in bats (Adams & Thibault, 2006), or savannah-living ungulates (plains zebras (*Equus burchelli*): Du Preez, 1977; gemsbok (*Oryx gazella*): Kasiringua et al., 2017; impalas (*Aepyceros melampus*), white rhinoceros (*Ceratotherium simum*): Sutherland et al., 2018).

Finally, individual variation in drinking behaviour can also occur, as age and female reproductive status can impact water requirements. In mammals, milk provides infants with a source of hydration, being composed of a varying percentage of water and other nutrients, as well as non-nutritional components (Prentice, 1996; Stead et al., 2021) – infants do not have to fully rely on water as their primary source of liquids until fully weaned. Lactating mothers, on the other hand, need to increase their water intake to compensate for the extra water output of producing milk – lactating female African leopards drank more often than nonlactating females or males (Bothma, 2005), while female red deer (*Cervus elaphus*) increased the amount of water drunk during lactation (Archer et al., 2013).

Water & Chimpanzees

Chimpanzees (*Pan troglodytes*) are the closest living relatives of humans alongside bonobos (*Pan paniscus*) (Langergraber et al., 2012). Their species range across equatorial Africa encompasses a diverse range of habitats from rainforests through mosaic forests to savannahs (van Leeuwen et al., 2020a; Wessling et al., 2020). These various types of chimpanzee habitats have different amounts of yearly precipitation, maximum and average temperatures, humidity levels, and even annual dry seasons of differing length (Itoh, 2015; Pruetz, 2007; Reynolds, 2005), posing a wide range of water availability and water requirement scenarios chimpanzees have

to adapt to. However, little is known about the drinking behaviour of chimpanzees, especially rainforest populations, with no clear consensus on their exact water needs, how often they drink, and if they even need to regularly consume liquids in addition to water in their fruit-rich diet (Goné Bi & Wittig, 2019; Newton-Fisher, 1999a; Piel et al., 2017) to meet their water needs (Pontzer et al., 2021; Wessling et al., 2018a, 2018b).

The first published observational account of wild chimpanzees, in Guinea, reports only two occasions of drinking across 49 days of observation, and concludes they need very little drinking water (Nissen, 1931). More than 30 years later, Reynolds and Reynolds (1965) report no terrestrial drinking events across 300 observation hours among the group of chimpanzees they studied in the Budongo Forest, Uganda, and only one case of a chimpanzee drinking from a tree bole. As opposed to the reasoning of Nissen (1931), they note that the low number was likely due to poor visibility and low habituation levels, and not reflective of the actual drinking frequency of the group. Later accounts document slightly higher numbers and support that drinking behaviour is present in chimpanzees, though the relative frequency of it, and with it, assessment of the water dependency of chimpanzees, varies between accounts, even ones from the same chimpanzee community. The majority of studies focusing on or mentioning drinking behaviour in chimpanzees are from the Gombe National Park, Tanzania, a mosaic forest habitat. Teleki (1977) groups drinking with the consumption of other miscellaneous items and measures the frequency of it as the proportion of the feeding budget, giving 0.2-1% of the chimpanzees' feeding activity spent on it depending on season. McGrew (1977) documents 23 occasions of chimpanzees drinking with leaf sponges within the span of a year, and 'a few' occasions of direct drinking from Lake Tanganyika. Goodall (1986) writes that the same population of chimpanzees drink 'often' from streams,

and while during the wet season they seem to be able to go without drinking for a few days, in the dry season they drink up to two to three times a day. A more recent account from Gombe, compiling 1140 drinking events across more than 20,000 observation hours, sets their frequency at less than 1% of all activity, defining them as ‘rare’ events (Nelson et al., 2022). The rest of the existing studies are also from forest mosaic or savannah habitats: Nishida (1980) reports 43 cases of drinking observed across 14 months of study in Mahale, another Tanzanian chimpanzee community, while chimpanzees in the savannah environment of Fongoli, Senegal drank water in 89% of the days observed (Lindshield et al., 2017).

While the drinking behaviour of captive chimpanzees are easier to observe and measure than that of wild conspecifics, studies on it are similarly scarce. Angus (1971) reported that half of a group of captive chimpanzees drank from the moat surrounding their enclosure at some point during the study. Captive chimpanzees drink ‘occasionally’ in Chester and Dudley Zoo, and ‘often’ in Colchester and Edinburgh, with staff at Chester reporting the chimpanzees’ particular fondness of sugar-free squash, of which they can drink ‘litres of’ at a time (Chester Zoo, Colchester Zoo, Dudley Zoo, Edinburgh Zoo, pers. comm). Besides the limited nature of data available on whether and how often captive chimpanzees drink, findings also cannot fully be generalised to wild chimpanzees, as zoo-housed captive individuals have a comparably drier diet than wild ones (Pontzer et al., 2021), requiring them to meet more of their water needs from liquids and therefore drink more. Human drinking behaviour and water needs also cannot be generalised to wild chimpanzees, despite our close genetic relatedness (Langergraber et al., 2012): chimpanzees have a lower body fat percentage (Angus, 1971), and are less efficient at water conservation than humans (Pontzer et al., 2021), which both impact how much water they need and how often they need to drink.

Spatial, temporal, and individual variation in chimpanzee drinking behaviour is similarly understudied, though potential cultural variation in the use of soft vegetation tools to drink has received some attention (Goodall, 1965a, 1965b; Hobaiter et al., 2014; Matsusaka et al., 2006; Péter, 2019; Sousa et al., 2009). In addition to sipping the water directly, chimpanzees make and use tools made of chewed or crumpled leaves or moss to drink water across all long-term chimpanzee field sites (Hobaiter et al., 2014; Lanjouw, 2002; Matsusaka et al., 2006; Ohashi, 2006; Whiten et al., 1999). Hand-dipping, briefly submerging the hand or fingers then licking off the water clinging to hair is another common method of drinking (McGrew, 1977; Reynolds & Reynolds, 1965). Regarding water sources used by wild chimpanzees, they range from terrestrial sources like lakes, streams, and waterholes, to arboreal ones like rainwater collected in tree boles (Goodall, 1986; McGrew, 1977; Nishida, 1980; Sharma et al., 2016; Sousa et al., 2009; Teleki, 1977). Licking rainwater or dew from fur or leaves was also noted as a potential source of water (Goodall, 1986). Mahale chimpanzees drank more often from streams over lakes (Nishida, 1980) and dendrotelmata (Sharma et al., 2016), while chimpanzees in Gombe sponged water mostly from dendrotelmata over water from lakes (McGrew, 1977). It is unclear whether this avoidance of lakes is a risk-related preference, with streams and tree boles posing a lower or non-existent risk of drowning, or a hygiene-related one, with flowing water sources being cleaner than standing water and small, ephemeral tree boles evaporating before becoming stagnant. Similar to what has been documented for waterholes in the Serengeti (Wolanski & Gereta, 2001), standing water sources frequently used by chimpanzees without sufficient water flow have an increased parasitic and pathogen content, posing a health risk to them (Bakuza & Nkwengulila, 2009).

Only a single account of within-day variation in drinking activity in chimpanzees exists (Nishida, 1980), which suggests that the timing of drinking can be a thermoregulation strategy, with a peak in drinking activity during the early afternoon coinciding with the highest daily temperature, similar to what has been seen in other species (yellow baboons: Altmann & Altmann, 1970; white-lipped peccaries: Moreira-Ramírez et al., 2016). Seasonal variation is better documented – the number of drinking events increased during dry (compared to wet) seasons in Mahale (Nishida, 1980), as well as in Gombe (Goodall, 1986; Nelson et al., 2022; Teleki, 1977) and Fongoli (Wessling et al., 2018b). Both savannah- and forest-living chimpanzees (Gombe: Nelson et al., 2024; Fongoli, Taï: Wessling et al., 2018a, 2018b) experienced dehydration and a related elevation in stress levels during dry seasons, suggesting that chimpanzees face an increased necessity to drink during dry seasons, either because of higher overall water needs caused by high temperature, or because of a lower amount of water-rich foods being available and consumed by them.

Besides temporal variation in drinking behaviour, there is variation between individuals as well. Lactation, especially during the later stages, increases the water needs of female chimpanzees by an estimated 640-675 ml/day (Nelson et al., 2022), which is reflected in higher drinking frequency compared to non-lactating females (Nelson et al., 2022), and more severe dehydration in females compared to males (Nelson et al., 2024). For infants, milk is their main hydration source until weaning at approximately four years of age (Samuni et al., 2020), with it having an estimated 85-90% water content (Hinde & Milligan, 2011). Water is increasingly drunk as individuals approach weaning (Nelson et al., 2022), with Nishida (1980) noting 2.5 years of age for the first direct drinking event, and generally shorter drinking event durations for infants compared to adults. Finally, idiosyncratic variation in drinking

frequency, not explained by age, rank, or reproductive status, might also be present in chimpanzees (Nelson et al., 2022; Edinburgh Zoo, pers. comm.).

While they are not specifically about drinking behaviour, accounts of chimpanzee behavioural adaptations to water shortages and arid environments at the edge of their species range further support the importance of water for their wellbeing and survival. Despite being a primarily rainforest-dwelling species, their high degree of behavioural flexibility buffers them from the negative effects of water shortage to a certain extent. Even without terrestrial, open water sources available, they can access collected rainwater in small tree boles where direct drinking is not possible by using aforementioned drinking tools (e.g.: Lanjouw, 2002). Digging wells in dried out riverbeds to reach the water table has also been documented in Mahale (Nishida et al., 1999) and Toro-Semliki, Uganda (McGrew et al., 2007). Increased consumption, in some cases associated with tool-assisted digging up, of water-rich tubers can also help meet chimpanzees' water needs when free-standing water is scarce (Hernandez-Aguilar et al., 2007; Hockings et al., 2010a; Lanjouw, 2002). Thermoregulatory adaptations, like partially submerging themselves into water (Pruetz, 2007), nocturnal foraging and travelling (Pruetz, 2018), and using caves during high daytime temperatures (Pruetz, 2007) can also help them cope with water scarcity by keeping the amount of water lost during sweating and panting to keep their body temperature low (Hiley, 1976), and with it the amount of water they need to consume.

Water-Contact Behaviour

Besides the above accounts on chimpanzee drinking behaviour, research on chimpanzees and water has mostly focused on water-contact behaviour, including their ability and propensity to swim, enter water, exploit aquatic resources, or even make contact with water. As discussed in Chapter 1, chimpanzees are commonly

regarded as hydrophobic, afraid of water and avoiding interacting with it as much possible, likely related to their low buoyancy and resulting inability to swim (Angus, 1971). There are three theories about the origins and extent of their purported hydrophobia. The first is the theory of *innate hydrophobia*, which proposes genetic fear of water, present from birth without any social learning or previous negative experience with water. It was posited by Yerkes (1943), based on his behavioural observations and experiments on captive chimpanzees. The chimpanzees of his captive colony never crossed water-filled moats, while immature chimpanzees he has thrown into water responded with screaming in distress, behaviours he accredited to fear of water. Early accounts from wild populations supported his theory, writing about chimpanzees avoiding becoming wet, whether by being rained on or stepping into water, and crossing terrestrial water sources by jumping over them or brachiating in order to avoid contact with water and mud (Goodall, 1986; Kortlandt, 1962).

However, occasional instances of voluntary, positive water-contact cast doubt on the theory of innate hydrophobia. In Gombe, immature chimpanzees have been observed engaging in water play, splashing and making manual contact with water, without being stopped or discouraged by their mothers (McGrew, 1977); in Mahale, one chimpanzee repeatedly waded into a 50 cm deep stream to access a high value food item, while three others immersed their hands and arms to do so (Nishida, 1980). In captivity, despite several of their group members drowning in the same moat, two females regularly waded into it to avoid aggression from males (Angus, 1971). McGrew (1977) proposed a *learned hydrophobia* to account for these exceptions, arguing that given the strong conservatism of chimpanzees (Hopper et al., 2011), even a few past negative experiences a community might have with water, such as a group member drowning, can produce a strong aversion lasting for

generations, with individuals avoiding entering even shallow, narrow streams, with no risk of aquatic predators or drowning. Immature individuals will initially be without fear towards water, evidenced by voluntary water-contact or water play being most common in infants, then begin avoiding water-contact as they age and learn from other community members.

Another explanation for voluntary water-contact is the theory of *context-dependent aversion*. Angus (1971) points out that regardless of whether the hydrophobia of chimpanzees is innate or learned, mature chimpanzees still enter or make contact with water if social or ecological factors, like the two captive females avoiding aggression, make it beneficial. Nishida's (1980) field experiment, which showed chimpanzees are willing to wade or reach into water to reach high value food supports her argument. Nishida (1980) argues against labelling chimpanzees as universally hydrophobic altogether, pointing out that humans show a similar avoidance of stepping into water or getting wet. Chimpanzees might not fear water, but instead show distaste towards becoming wet or soiled by mud that they can overcome depending on social and ecological factors (Angus, 1971; Nishida, 1980).

Recent studies on various types of water-contact behaviour in chimpanzees support learned hydrophobia or context-dependent aversion. Well-digging, where chimpanzees dig small holes into dried-out riverbeds or next to existing water sources to access or filter water (McGrew et al., 2007; Nishida et al., 1999; Péter et al., 2022), requires manual contact with mud and water. Exploitation of aquatic resources, like algae fishing using sticks (Boesch et al., 2017) or hunting for crabs (Koops et al., 2019), has been documented in western chimpanzees (*Pan troglodytes verus*). Both activities require the chimpanzees to stand very near or in water sources, and hands or arms being occasionally submerged in water. The

savannah chimpanzees of Fongoli are even less averse to water, and regularly dip in naturally occurring pools of water for thermoregulation (Pruetz, 2007).

The Current Study

To date, there is no clear consensus on whether wild chimpanzees need to consume liquid water in addition to water in food and how often they drink. Their aversion to water-contact is better-documented, and while there is some between-group variation in the extent of their aversion, attitudes towards water are consistent within chimpanzee communities. However, aversion towards water-contact does not necessarily mean aversion towards interacting with water sources or a lack of drinking – while research on water-contact and drinking both focus on water sources, the presence, frequency, and variation of drinking behaviour in chimpanzees need to be assessed independently from that of water-contact behaviour.

Closing the gap in the literature about whether water is a regularly consumed resource by chimpanzees is becoming more and more pressing in the era of climate change. Chimpanzees are doubly at risk: first, as large bodied mammals, with adults weighing 30-50 kg (Uehara & Nishida, 1987), they need more water to avoid dehydration and thermal stress compared to smaller species, potentially making them more vulnerable to any changes in water availability and temperature (Fuller et al., 2016; Hetem et al., 2014). Dehydration during dry seasons is already present in both forest and savannah populations, elevating stress levels regardless of compensatory behaviours (Wessling et al., 2018a, 2018b). Second, their species range in equatorial Africa is predicted to be highly impacted by climate change. The area is likely to get hotter and dryer across all habitat types, with minimum and maximum temperatures predicted to increase, as well as the intensity of wet and dry seasons, increasing the chances of floods, dry spells, and droughts (Jiang et al., 2019; Makula & Zhou, 2021; Ndiaye et al., 2021; Ojara et al., 2020). Vicinity to

humans further increases the chance of chimpanzee populations having to face lower water availability and extreme weather events, with human activity exacerbating the effects of droughts (Desbureaux & Damania, 2018; Wanders & Wada, 2015). Studies specifically focusing on the drinking behaviour of wild chimpanzees are needed to fully explore the role of water as a resource for them.

Additionally, existing studies on the drinking behaviour of chimpanzees have somewhat limited generalisability. As for captive chimpanzees, they differ from wild chimpanzees in the water content of their diets and general activity levels (Pontzer et al., 2021). Being provided with multiple sources of water within their enclosures, most of which are regularly topped up with clean drinking water (Chester Zoo, Colchester Zoo, Dudley Zoo, Edinburgh Zoo, pers. comm), they also do not have to consider the costs of travelling to access water or drinking low quality, contaminated water when deciding whether and how often to drink. Given these differences between the waterscape of wild and captive chimpanzee populations, research on the drinking behaviour of captive chimpanzees are essential for captive primate welfare but are less generalisable to wild chimpanzees.

Accounts from wild populations are primarily of eastern chimpanzees living in the Gombe (Goodall, 1986; McGrew, 1977; Nelson et al., 2022; Teleki, 1977) and Mahale National Parks (Nishida, 1980), in Tanzania. Both field sites are strongly seasonal with dry seasons lasting five to six months and are classified as forest mosaics (van Leeuwen et al., 2020a). In Gombe, vegetation cover consists of mosaic forests, dry woodlands, and open grasslands, with average annual rainfall of 1540 mm (Teleki, 1977), and a dry season lasting May to October (Lonsdorf et al., 2011). Mahale has a similar climate, with an average annual rainfall of 1700mm and a dry season lasting May to September (Itoh, 2015), but more forest coverage (Carvalho et al., 2022). The chimpanzees of Fongoli are western chimpanzees, but

also live in a savannah environment commonly considered the northern edge of the species range and the most arid conditions chimpanzees can cope with (Wessling et al., 2020). Dry seasons last six months, with an average annual precipitation of 900-1100 mm (Bá et al., 1997). Vegetation cover is majority woodlands and grasslands with occasional small gallery forests (Pruetz, 2006). While being located on the banks of Lake Tanganyika (Nishida, 1980) protects both Tanzanian sites from severe water shortage, all three sites experience long periods of elevated temperatures and lower rainfall and humidity during dry seasons, environmental conditions which increase water needs (Yamada et al., 2022) and the frequency of drinking in other primate species (Chaves et al., 2021; Wright et al., 2022). Patchy tree cover can also contribute to an increase in water needs, with less shade available to help regulate body temperature (Lopes & Bicca-Marques, 2017; Stelzner, 1988). Therefore, chimpanzees occupying mosaic forest and savannah habitats might have higher water needs and drink more often than conspecifics in less arid, rainforest environments; findings on their water dependence and drinking behaviour cannot be fully generalised to chimpanzees inhabiting more mesic environments.

While there is a general need for more research on the drinking behaviour of wild chimpanzees, it needs to include a more diverse range of chimpanzee habitats, having predominantly focused on arid environments (Wessling et al., 2018a). Little is known about the ecological role of free water in mesic environments in general (Schlaepfer et al., 2017; Trenberth et al., 2014), and studies on the drinking behaviour of rainforest-dwelling chimpanzee communities, who seem to be more sensitive to dehydration compared to savannah-dwelling conspecifics (Wessling et al., 2018a), are necessary for describing the full extent of chimpanzee behavioural

diversity and effective conservation but are completely missing from the current literature.

In this chapter, I provide a comprehensive account of the drinking behaviour of the forest-dwelling Waibira community of eastern chimpanzees, from the Budongo Forest Reserve, Uganda to evaluate whether water is a commonly consumed resource by rainforest chimpanzees. Using five months of observational and ten years of camera trap data, I will describe the community's general drinking behaviour, daily temporal variation, the frequency of drinking and the types of water sources used, seasonal variation in drinking frequency and usage intensity of water sources, and demographic patterns of drinking, such as sex differences in drinking frequency and the age of onset. I will also provide a description of water-contact behaviour observed in the group to evaluate whether aversion towards water-contact is necessarily connected to low drinking frequency.

Regarding water-contact behaviour, I will additionally evaluate the three possible theories about the origins of chimpanzees' reluctance to touch water – they are the theories of *innate hydrophobia* (Yerkes, 1943), *learned hydrophobia* (McGrew, 1977), and *context-dependent aversion* (Angus, 1971; Nishida, 1980) (Table 8). If chimpanzees are *innately hydrophobic,* in addition to a reluctance to stepping into water or mud or becoming wet, I expect to see fear and vigilance behaviour directed at the water and no voluntary water-contact by any individuals of the community outside of drinking. If they have a *learned hydrophobia*, individuals will show vigilance and fear behaviour towards water and avoid making contact with it outside of drinking, except immature individuals, who will engage in voluntary water-contact, like water play. Finally, if individuals are not fearful or vigilant towards water, but only show a general reluctance to make contact with it that is occasionally

voluntarily overcome both by mature and immature individuals, *context-dependent aversion* is the most likely explanation (Table 8).

Table 8

The Three Water-Contact Theories Evaluated

Theory	Behaviour towards water		
	Vigilance towards water	Voluntary water-contact by immatures	Voluntary water-contact by all ages
Innate hydrophobia	✓	×	×
Learned hydrophobia	✓	✓	×
Context-dependent aversion	×	✓	✓

Note. ✓ denotes that the given behaviour will be observed, while × denotes that the given behaviour will not be observed.

The Waibira community occupies a dense, equatorial semi-deciduous forest (Eggeling, 1947), with an average of 1659 mm of annual rainfall (1993-2022) and a three-month annual dry season, placing them firmly in the forest-habitat category (van Leeuwen et al., 2020a). Similar to trends in equatorial Africa in general, climate predictions for Uganda include increased temperatures, longer dry seasons, and extreme weather events (Nsubuga et al., 2014; Nsubuga & Rautenbach, 2018; Ojara et al., 2020). Unlike Gombe, Mahale, and Fongoli, the Budongo Forest provides practically complete tree coverage, and while Mahale receives a similar amount of yearly rainfall, the length of dry seasons at Budongo are much shorter than at either of those three sites. The exact geographical features of the Waibira community's home range make them especially suited for studying drinking behaviour, as during the three-month long dry season, the central waterhole is the only stable water source within their home range (see detailed description in Chapter 2). Monitoring it

by direct observation or camera traps in this time period allows for easy censusing and all-occurrence sampling (Beck & Tuttle, 1972; Washburn & DeVore, 1961; Weir & Davidson, 1965), in this case for recording the majority of the chimpanzees' interactions with water.

The findings of this chapter could improve captive ape welfare and enrichment, providing drinking opportunities as close to natural usage patterns as possible, and refine our models of the evolution of human water dependency and consumption. Assessing the water dependence of wild chimpanzees and any variation in their drinking behaviour can also inform conservation planning, with a particular focus on habitat suitability assessments, which so far has mostly focused on the disappearance of forest cover (e.g.: Carvalho et al., 2022; Fotang et al., 2021; McLennan et al., 2021), and managing human-wildlife conflict around shared water sources to lower the risk of chimpanzee attacks on humans (Hockings et al., 2010b; McLennan & Hill, 2012; McLennan & Hockings, 2016), and disease transmission (Adams et al., 2001; Deere et al., 2019) .

Methods

Camera Trap Videos

Camera trap videos were available for every year from February 2013 to April 2022, centring on the annual dry season. As the onset and end of dry seasons show annual fluctuations both in Budongo (Newton-Fisher, 1997) and the general Lake Victoria area (Kizza et al., 2009), camera traps were often operational for a few weeks before and after the exact start and end dates of the dry season. To maximise data available on drinking behaviour, camera trap videos from both wet and dry season dates were included in this chapter's dataset. To reflect the inclusion of wet season videos, as opposed to the use of dry-season-only videos as I have done in Chapters 4 and 5, in this chapter I will use 'monitoring period' instead of 'dry season'

to differentiate between the annual time periods when camera traps were active and video data were available from.

Camera trap videos were available from 10 monitoring periods, between February 2013 to April 2022. The central waterhole was monitored for a total of 647 days, with substantial variation between monitoring periods (36-125 days). During those 647 days, 27,221 videos have been recorded, with 8288 videos (30.45%) containing 118 different identified individual chimpanzees across 11,737.5 hours of potential footage. Between February 2013 and January 2017 only one camera trap was used (CT1); a second trap was added from February 2017 (CT2). More information on camera trap locations, models, battery change schedules, and the definition of hours of potential footage can be found in Chapter 2.

Video Coding

I coded the 8288 camera trap videos that included chimpanzees for all instances of drinking behaviour. Based on video timestamps, a drinking event was defined as an individual remaining on-screen between bouts of drinking behaviour, and the bouts taking place in the same minute and/or consecutive minutes (maximum 1 min apart). If more than a minute passed between videos of an individual drinking, they were recorded as separate drinking events. Consecutive minutes were chosen instead of consecutive videos as daytime and night-time video length differed – two night-time videos of an individual's drinking bouts might be separated by another without any drinking, but as those videos are only 15 s long, it is coded as the same drinking event, having taken place less than a minute apart. I classified fabricating a drinking tool as a drinking-related activity, and therefore as an activity that does not interrupt a drinking event.

For every drinking event, I recorded the identity of the individual drinking, their *age category* (*adult*, *subadult*, *juvenile*, *infant*) and their *sex* (*male*, *female*). If

individual identity was not determinable due to poor visibility or the individual was not one of the identified chimpanzees, only *age* and *sex* was recorded. If *age* and/or *sex* could not be determined, it was recorded as *unknown*. I also recorded the date of the drinking event, from the video timestamp. For videos between 2016 and 2022, I also recorded the time on the timestamp at the start of each video of the drinking event. Before 2016, while the date is accurate, timestamp errors regarding the correct hour are frequent, and only allow for determining the order of and time elapsed between different videos. A total 5923 drinking events were recorded.

For each drinking event, the exact time to the nearest minute during which the event happened was recorded, with the resulting data point called a *chimpanzee-minute*. For drinking events spanning several minutes, each of those minutes were recorded as separate data points to reflect differences in usage intensity – for example, a short drinking event spanning twenty seconds at 7:35 am was recorded as one *chimpanzee-minute* at 7:35 am, while a longer drinking event that spanned five minutes between 7:38 am and 7:43 am was recorded as five *chimpanzee-minutes*, one for each of those minutes. 7380 *chimpanzee-minutes* were coded in total.

Fieldwork

I conducted fieldwork between October 2021 and March 2022, collecting observational data on the drinking behaviour of the Waibira community, totalling 146 hr 28 min observation time and 77 observation sessions – 100 hr 43 min in the wet season and 45 hr 45 min in the dry season. Observation hours varied between seasons due to changing health & safety protocols due to the ongoing COVID-19 pandemic, limiting the hours that observers could spend in the forest, as well as the time observing a specific group of chimpanzees. Data on drinking behaviour within the focal party was collected using *ad libitum* sampling during focal group follows of

the Waibira community. For every observed instance of drinking, I recorded the identity of the individual drinking, the date of the event, later used to determine if the observation took place in the *wet* or *dry season* based on precipitation data, and whether the individual drank from a *terrestrial* or *arboreal* water source. I recorded 60 drinking events from 15 individuals.

Statistical Analyses

Data analysis was conducted in R (v. 4.3.1) (R Core Team, 2023) running in RStudio (v. 2023.6.0+421) (Posit Team, 2023), except for the exact binomial tests, which were calculated by hand.

To investigate variation between monitoring periods, I used the number of drinking events, the number of days camera traps were active that reflected general monitoring presence at the central waterhole, as well as the number of monitoring hours per monitoring period that reflected the amount of potential footage containing chimpanzee activity (see Chapter 2). To see if there is a relationship between monitoring effort and number of drinking events recorded, I determined the correlation between the number of drinking events for a given monitoring period with the number of days camera traps were active for the monitoring period, as well as the number of monitoring hours for the season, using Pearson's correlation.

To determine daily patterns of drinking behaviour by chimpanzees at the central waterhole, I used data from camera trap videos from the 2015-2016 monitoring period and onward. Dividing time into 30 min bins from 6 am to 7:30 pm, I calculated the intensity of drinking activity at the central waterhole during each 30 min time period by adding up the number of *chimpanzee-minutes* in that bin.

To determine water source usage patterns and seasonal differences in drinking behaviour, I used observational data collected during fieldwork, using exact binomial tests due to the relatively small sample size (N = 60). First, I compared the

number of drinking events from *terrestrial* versus *arboreal* water sources in the *wet* and *dry season* respectively to see if there is a type of water source with increased usage. Expected proportions were set to equal. To see if there was a seasonal difference in drinking frequency, I also compared the number of drinking events in the *wet* and *dry seasons*. Expected proportions were set based on the number of observation hours for each season, as observation protocols including the maximum number of daily contact hours with chimpanzees changed between seasons.

To determine whether there was a sex difference in the number of drinking events both across (a) all *age categories* and (b) when only including events from *adults*, I ran G-tests of goodness-of-fit using the GTest function of the package DescTools (Signorell, 2023). Events from individuals of *unknown sex* were excluded from the analyses. Expected proportions were set based on (a) the number of all identified males and females in the community and, separately, (b) the number of identified adult males and adult females in the community.

Results

Drinking Behaviour at the Central Waterhole

Out of the 8288 camera trap videos which contained chimpanzees, chimpanzees drank in 5459 videos, totalling 5923 drinking events. Across the 10 monitoring periods, there were a mean 592.3 ± 502.3 drinking events recorded per monitoring period (8-1466 events/monitoring period). However, sampling effort varied considerably between monitoring periods (36-125 days/monitoring period, mean = 64.7 ± 26.1), especially with the addition of a second camera trap from 2017 Feb (450-2862.5 hr of potential footage/monitoring period, mean = 1173.8 ± 757.6). There was a strong positive correlation between drinking events recorded per monitoring period and the number of days camera traps were active (Pearson's correlation, $R_{(8)} = 0.71$, $p = 0.022$), as well as hours of potential footage (Pearson's

correlation, $R_{(8)} = 0.81$, $p = 0.004$). While excluding the most intense, 2021-2022 monitoring period from the dataset makes the correlation with the number of active days nonsignificant (Pearson's correlation, $R_{(7)} = 0.45$, p = NS), the strong relationship between the number of hours of potential footage and events remains (Pearson's correlation, $R_{(7)} = 0.68$, $p = 0.042$) – the annual variation in the number of recorded drinking events is likely a result of differing sampling effort; the chimpanzees of the Waibira community do not show inter-annual changes in their drinking behaviour and the central waterhole is a consistently used water source.

Regarding within-day variation, chimpanzees drank water at the central waterhole throughout the day, being active exclusively during the daylight hours (range: 7:26 am-7:19 pm) with no chimpanzee ever sighted on camera trap outside those hours whether drinking or passing through, and a peak in activity during the afternoon and drinking most often in the early parts of it (mean: 1:58 pm ± 2.75 hr, median: 2:33 pm) (Figure 6).

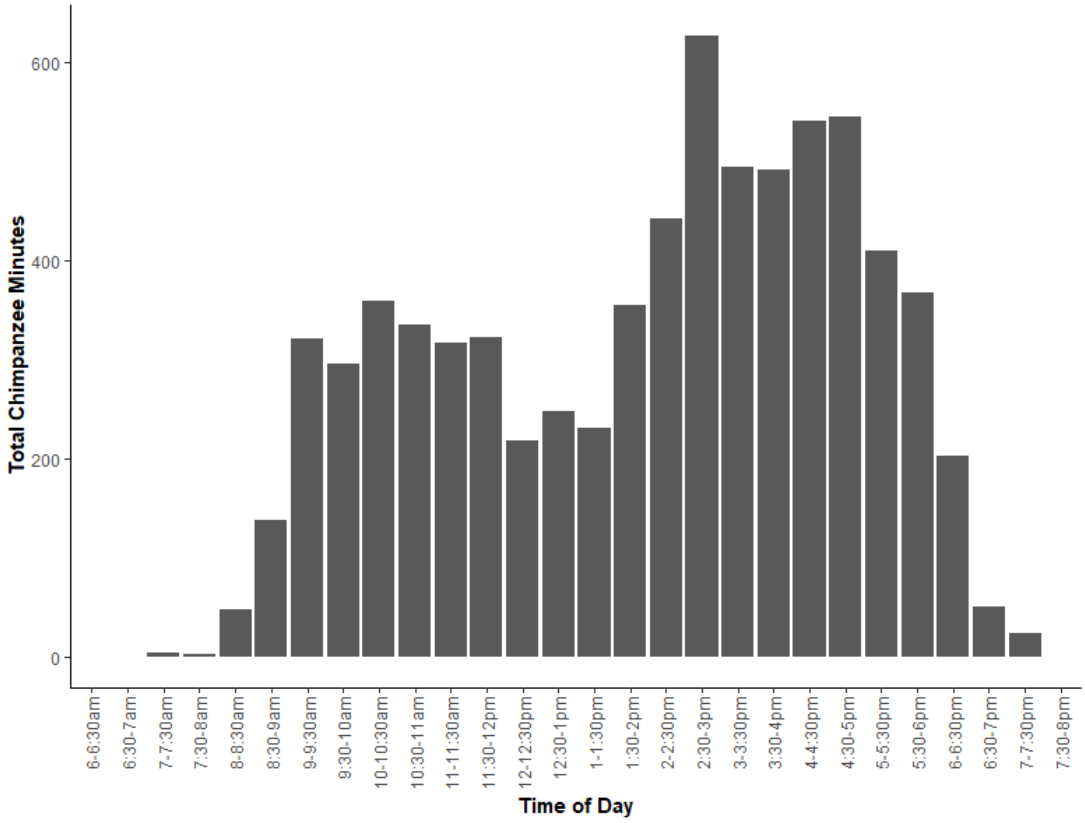


Figure 6

Chimpanzee-Minutes Across the Day, Pooled into 30 min Bins.

Note. No chimpanzees were ever sighted on camera trap outside 7:26 am-7:19 pm.

Based on camera trap videos and fieldwork observations, when visiting the central waterhole, the chimpanzees of the Waibira community enter the central waterhole on the ground, using a few paths on both sides of the valley in which the waterhole is located. These paths are visibly well-used, and can be easily followed by human observers, suggesting high frequency of use, as well as high year-to-year consistency. After briefly looking around on arrival, they immediately drink. When visiting in groups, chimpanzees spread themselves out along the edge of the original stream-bed section of the waterhole or across the broader area with puddles instead of waiting their turn to drink at a few preferred spots (Figure 7). However, with very large groups (> 10 individuals), especially at the end of the dry season when the waterhole has considerably shrunk, individuals occasionally have to wait for a

drinking spot to become free on the edge of the waterhole or at one of the puddles in the broader section. Agonism over access to water and preferred drinking spots is rare, and extends only to approach-leave interactions, and one occasion when a mid-ranking adult female, *Ketie*, was observed to give a gestural arm-fling threat and a vocal threat to *Onyofi*, a low-ranking adult female when the latter approached the part of the waterhole that *Ketie* and her infant son have been drinking from.

Figure 7

Chimpanzees Drinking Along the Edges of the Central Waterhole in the 2021-2022 Monitoring Period

[a] Screenshot from CT1, showing chimpanzees spread out along the banks of the stream-bed section of the central waterhole. [b] Screenshot from CT2, showing chimpanzees spread out across the broader area of the central waterhole.

When drinking, chimpanzees employ one of three methods: they either lean down to the surface of the water and sip the water, drinking directly, or sit upright,

dipping the water with a drinking tool made of soft vegetation, or their hands. Direct drinking occurred in 87.2% of all camera trap drinking events, while dipping water with a drinking tool in 20.4%, and with a hand in 0.7% of all camera trap drinking events. When drinking directly, individuals adapt one of three postures: they either bend all limbs, and lower themselves to the ground, with the stomach often touching it; only bend the arms to lower the head to the water, while the legs remain extended and the pelvis high; or support themselves leaning over the water holding onto a branch or liana with an arm. Switching from one method of drinking to the other within a drinking event also occurred, happening in 8.5% of all camera trap drinking events. Infants were also seen to directly drink while still clinging to their mothers, lowering their face to the water without dismounting. When mothers lean down to drink, infants are not actively repositioned, but usually climb onto the mother's back or fully dismount. Neonates remain clinging on the stomach or chest of the mother.

Based on camera trap and observational data, there is no evidence of predators in the community's home range, terrestrial or aquatic, that pose a danger to chimpanzees. No other chimpanzee communities use the central waterhole either. Black and white colobus (*Colobus guereza*), red-tail monkeys (*Cercopithecus ascanius*), and blue monkeys (*Cercopithecus mitis*), common prey species of the Waibira chimpanzees (Hobaiter et al., 2017), abandon and avoid the waterhole when chimpanzees visit. Red forest duikers (*Cephalophus monticola*), while also hunted by the Waibira chimpanzees (Hobaiter et al., 2017), were seen to venture down to the waterhole to drink when chimpanzees were present on three occasions, twice on camera trap, and once during fieldwork observation – immature chimpanzees attempted to chase them in all three cases. Chimpanzees and olive baboons (*Papio anubis*) also do not use the waterhole at the same time - smaller female chimpanzee parties or individual females travelling only with their dependent offspring were seen

leaving the waterhole with haste just before the arrival of baboons on camera trap videos. While responding with fear when encountering them in other parts of the forest, chimpanzees did not have any recorded encounters with red river hogs (*Potamochoerus porcus*) at the central waterhole, as red river hogs were primarily active in the area during the nighttime (~6 pm-8 am), and chimpanzees exclusively during the daytime (~7 am-7 pm).

Water-Contact Behaviour at the Central Waterhole

Based on camera trap videos and fieldwork observations, chimpanzees avoid contact with water and mud by placing their hands and feet on the dry waterhole edge, branches, wads of terrestrial vegetation, stones, conspecifics, or by hanging from a branch or liana when drinking at the central waterhole. The fabrication of leaf cushions to protect from mud has also been observed five times (Péter, 2019). Chimpanzees also avoid contact with water and mud when crossing the water – they step or jump across the stream part of the waterhole and keep to islands of sandy substrate and terrestrial herbaceous vegetation above the water line when navigating the broader part of it. Infants who cannot cross the stream on their own are carried across by their mothers: in one video the mother left her infant on the other side of the approximately 30 cm wide stream, the infant responded with whimpering, which only stopped when the mother turned back, allowing the infant to climb on her arm, then on her back to cross the water. A juvenile male also responded to being pushed into the shallow water (3-4 cm) during play with screaming.

However, occasional voluntary water-contact does occur in the Waibira community of chimpanzees. Infants and juveniles have been observed to engage in water play on camera trap (n_{CT} = 11), splashing the water with their hands using movements ranging from small waves at the wrist to large swings from the shoulder

with the arm fully extended. A play-face expression accompanies water play. Other exploratory behaviour aimed towards water also occurs in immatures (n_{CT}= 113), and consists of reaching towards the water, dipping fingers or hands into the water but not licking the water off them, or dipping objects like sticks, leaves, moss, and drinking tools discarded by other individuals into the water without drinking from them. Mothers or other individuals never intervened to stop immatures during water play or exploration. Adults voluntarily make manual contact with water and mud during well-digging, a habitual behaviour in the Waibira community (Péter et al., 2022). Reuse of discarded drinking tools is also present in the community (Péter, 2019), and depending on where the tool was discarded, requires the submerging of one's fingers or hand to retrieve it from the water.

Regarding general caution and vigilance at the central waterhole, both on camera trap videos and when directly observed, chimpanzees briefly look around on arrival, checking for conspecifics, and especially in the case of less-habituated adult females, for the presence of human observers. These females rarely descend to the waterhole to drink while observers are present, instead staying in the denser vegetation around the paths leading down to it. However, they show the same confidence as other adult females in the community on camera trap videos when there is no human presence. Following looking around, chimpanzees drink, either directly, or dipping water manually or with a drinking tool. General vigilance during drinking is low, consisting of occasional glances and maintaining visual contact while drinking, and is aimed at more dominant individuals drinking nearby or arriving to the waterhole and human observers. Infants also accompany their mothers to the water, either being carried, or travelling on their own, as opposed to being left a safe distance from the water, showing reluctance to approach the water, or actively prevented by their mother from approaching the water. No vigilance behaviour is

directed towards the water itself. After drinking, chimpanzees do not avoid spending time at the central waterhole and near water. They have been repeatedly observed resting, grooming, and playing at the edges of the waterhole and in the surrounding vegetation at the bottom of the valley.

Water Sources & Seasonal Variation

15 different individuals contributed to 60 drinking events across 146 hr 28 min of observation during fieldwork (Table 9). Drinking events were recorded both in the *wet* and *dry seasons*, and both from *terrestrial* and *arboreal* water sources. While chimpanzees drank from *terrestrial* water sources across all seasons and showed no increased use of either water source type in the *wet season* (exact binomial test, expected: $n_{arboreal} = 15.5$, $n_{terrestrial} = 15.5$, observed: $n_{arboreal} = 12$, $n_{terrestrial} = 19$, P = NS), they did not drink from *arboreal* water sources during the *dry season* (exact binomial test, expected: $n_{arboreal} = 14.5$, $n_{terrestrial} = 14.5$, observed: $n_{arboreal} = 0$, $n_{terrestrial} = 29$, $P < 0.001$, Table 9, Figure 8). However, the majority of *wet season* drinking events from *terrestrial* sources ($n = 17$) were recorded on March 17 2022, the first day of the 2022 wet season and therefore might not be fully representative of *wet season* water source usage patterns, as arboreal water sources might not have been replenished and available. After excluding events from March 17 2022, and only analysing data collected during the November – December part of the *wet season*, chimpanzees show an increased use of *arboreal* water sources compared to *terrestrial* ones in the *wet season* (exact binomial test, expected: $n_{arboreal} = 7$, $n_{terrestrial} = 7$, observed: $n_{arboreal} = 12$, $n_{terrestrial} = 2$, $P = 0.013$, Figure 8). Taking the difference in observation hours into account, chimpanzees drank more often in the *dry season* (exact binomial test, expected: $n_{wet\ season} = 41.3$, $n_{dry\ season} = 18.7$, observed: $n_{wet\ season} = 31$, $n_{dry\ season} = 29$, $P = 0.005$) (Table 9, Figure 8). The rate of drinking events per observation hours for fieldwork data (0.41 event/hr) was similar to that of camera

trap videos (0.50 event/hr) and suggests that drinking is a common behaviour in the Waibira community.

Table 9

Number of Drinking Events Across Seasons and Water Source Types

Season	Observation hours	Water source	Events	Frequency
Wet	100 hr 43 min	Arboreal	12	0.12 event/hr
		Terrestrial	19	0.19 event/hr
		Total	31	0.31 event/hr
Dry	45 hr 45 min	Arboreal	0	0 event/hr
		Terrestrial	29	0.63 event/hr
		Total	29	0.63 event/hr
Total	146 hr 28 min		60	0.41 event/hr

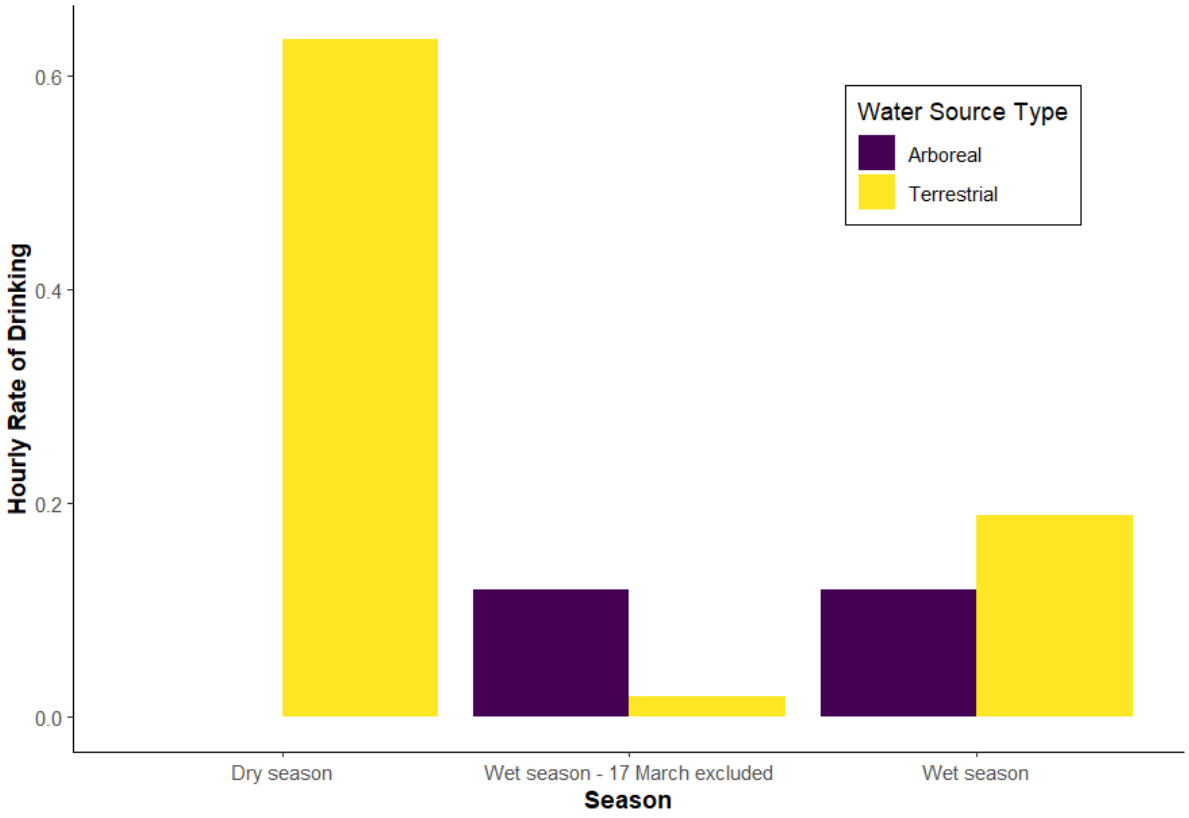


Figure 8

Hourly Rates of Drinking Events Across the Dry Season, the Wet Season, and the Wet Season With Events From 17 March 2022 Excluded, and Arboreal and Terrestrial Water Source Types

Demographic Variables

Out of the 8288 camera trap videos that contained chimpanzees, 5459 (65.9%) were of chimpanzees drinking. From those 5459 videos, I coded 5923 drinking events. 118 different identified individuals were recorded drinking, which included all but two of the independent named individuals of the Waibira community present during the data collection period, three identified unnamed females, and two of their offspring. The two missing named independent individuals were *Impia*, a subadult female who disappeared in 2015 (likely emigrated), and *Vesta*, a peripheral female named in 2019 but not yet seen on camera traps. Eight named infants who either died in early infancy or are still < 2 years old also have no recorded drinking events. The mean number of events per individual was 40.4 ± 31.3 (range: 1-130 events/individual). Chimpanzees from all demographic categories were recorded drinking (Table 10). Out of the 118 identified individuals, 60 were *males* and 58 were *females*. Out of the total 5923 drinking events, 2681 were by *females* and 2700 by *males* respectively. Expected proportions were corrected for the number of individuals in the community in each category – all *males* and *females* for the first test of goodness-of-fit, and all *adult males* and *adult females* for the second one. There was no difference between the number of drinking events recorded for *males* and *females* when all ages were included (G-test of goodness-of-fit: expected: n_{males} = 2736.2, $n_{females}$ = 2644.8, observed: n_{males} = 2700, $n_{females}$ = 2681, $G_{(1)}$ = 1.46, p = NS). However, *adult females* (n = 36) drank more frequently than *adult males* (n = 28) (G-test of goodness-of-fit: expected: n_{males} = 1545.3, $n_{females}$ = 1986.8, observed: n_{males} = 1465, $n_{females}$ = 2067, $G_{(1)}$ = 9.16, p = 0.002) (Table 10).

Table 10

The Number of Drinking Events Across Age and Sex Categories

Sex	Age				
	Adult	Subadult	Juvenile	Infant	Unknown [a]
Female	2067	137	268	209	NA
Male	1465	499	503	233	NA
Unknown [a]	84	20	234	159	45
Total	3616	656	1005	601	45

[a] Drinking events where the *sex* or *age category* of the individual was not clearly identifiable.

Discussion

Water is a regularly consumed resource by rainforest-living chimpanzees. The Waibira chimpanzees drink water from terrestrial and arboreal water sources, and while they drink more often in the dry season, the presence of drinking is not correlated with the dry season itself; they regularly drink water throughout the year. Drinking activity is most common in the early afternoon. Some demographic variation is present, with adult females drinking more often than adult males. Chimpanzees of the community start drinking water in infancy, and all stable community members above that age were seen drinking. While aversion towards water-contact is the dominant attitude of the Waibira chimpanzees, they do not show fear towards water, and both mature and immature individuals engage in voluntary water-contact on occasions. Their aversion is also not connected to low drinking frequency.

Regarding drinking behaviour, I observed 60 drinking events during five months of fieldwork, with a drinking rate of 0.44 event/hr for focal group follows and 0.11 event/hr for focal individual follows. These numbers do not only demonstrate that chimpanzees in rainforests regularly drink water but are higher than reported in Gombe (1140 drinking events from 21,197 hr of long-term focal individual follow

data, 0.05 events/hr (Nelson et al., 2022)) and Mahale (15 events from 869.5 hr of *ad libitum* sampling, 0.02 events/hr, but 12 events come from a two-month period covering 151.3 hr, 0.08 events/hr (Nishida, 1980)), and what an early study from another population in the Budongo Forest Reserve found (one drinking event during 170 days or 300 hr of *ad libitum* sampling, <0.01 events/hr (Reynolds & Reynolds, 1965)). The difference could either mean the Waibira chimpanzees do drink more than those chimpanzee communities or could be due to methodological differences. For the early Budongo study, the authors acknowledge that low habituation levels and poor visibility due to dense vegetation likely contributed to such a low number (Reynolds & Reynolds, 1965). While the Wabira community lives in the same dense rainforest environment, the group has been well-habituated by the time of the current study, with most individuals followable on the ground. That, in return, allows for recording terrestrial activities such as using terrestrial water sources, and also reduces vigilance towards human observers, which could have further prevented chimpanzees from drinking in the early study. However, the issue of poor visibility due to dense vegetation still remains as a limitation of the current study. While I recorded a good number of drinking events during fieldwork, there is still a chance of some of them being missed especially in dense tree crowns, like chimpanzees still in their nest in the morning licking residual dew, drinking from tree boles, or licking rainwater. Regarding differences between the drinking frequencies of the two mosaic forest chimpanzee populations and Waibira, the lower drinking rates in Mahale and Gombe are potentially a result of different group characteristics and sampling protocols. While Nishida (1980) employed a similar *ad libitum* sampling, his observation hours have not been adjusted for the number of individuals in the observed group. As the existing reports on chimpanzee drinking behaviour using *ad libitum* sampling of groups (Nishida, 1980; Reynolds & Reynolds, 1965) did not

correct for the number of individuals observed, this chapter followed a similar design in order to get as similar data as possible for ease of comparison. However, this leaves open the possibility of higher drinking rates in Waibira being an artefact of a larger group size than in Mahale.

While it is not possible to certainly know if the higher drinking rate in Waibira compared to Mahale reflects true higher drinking frequency, comparisons with Gombe do support that at least in certain rainforest communities, chimpanzees might drink more often than conspecifics in mosaic forests. Gombe long-term data, while employing an all-occurrence protocol, only recorded drinking by the focal individual (Nelson et al., 2022) as opposed to any members of the focal party, as done in this study. However, when only including drinking events recorded from the focal individual during focal follows (n = 17), the hourly rate of drinking still remains at 0.12/hr, more than double the drinking frequency of 0.05/hr in Gombe. Additionally, Nelson and colleagues (2024) also found severe and long-term dehydration in the Gombe population, suggesting the chimpanzees there might be drinking less than what is optimal to maintain water balance. While no hourly drinking rates are available from the Fongoli chimpanzee field site, one study reports drinking observed in 89% of observation days (Lindshield et al., 2017). As the study does not report the specific number of drinking events needed to calculate hourly drinking rates, comparison is difficult. If calculating a similar metric for the current study, the 60 drinking events were observed in ten out of 56, or 18% of observation days. However, maximum observation hours throughout the day and per focal group were severely limited in the second half of the current study making comparison possibly inaccurate.. While opportunity for comparison between chimpanzee field sites is limited with the current data, rainforest chimpanzees drink as often, or possibly even more so, as conspecifics inhabiting forest mosaic environments, but likely less often

than savannah chimpanzees. Drinking in chimpanzees is not an adaptation to arid environments, but is present across all habitat types. To move beyond establishing the universality of water dependence in all chimpanzee populations, which has been the main aim of this chapter, to inter-site comparisons, future studies must include the specific number of drinking events observed, as well as observation hours corrected for the number of individuals if using *ad libitum* data collection.

The Waibira chimpanzees relied both on terrestrial and arboreal water sources, though showed seasonal changes in usage frequency. Terrestrial water sources included the central waterhole and the seasonal stream within their home range, while arboreal water sources ranged from small divots of collected rainwater between two branches meeting to tree boles varying in depth from a few centimetres to the chimpanzees having to insert their entire arm to reach water with a drinking tool. During the wet season, they showed an equal usage intensity of both types, though once an outlier from the first day of the wet season was excluded, an increased use of arboreal water sources appeared. Whether they derive any hygiene, safety, or medicinal benefits (Castro et al., 2017; Parr et al., 2013; Sharma et al., 2016) from drinking from an arboreal source as opposed to a terrestrial one, or it is simply a question of convenience and minimising daily travel, being able to drink while foraging arboreally as opposed to having to travel to terrestrial water sources, can be tested in future studies investigating water quality and parasite load in arboreal and terrestrial water sources, and foraging decision making for drinking. However, arboreal water sources, comprised of collected rainwater, seem to disappear via evaporation and/or exploitation in the dry season, as I did not see any chimpanzees drinking from them during that period. The exclusive use of terrestrial water sources during the dry seasons most likely reflects availability and the use of the central waterhole as a fallback option, rather than preference.

Findings on the use and stability of arboreal and terrestrial water sources have implications for the conservation of species relying on arboreal water sources, as well as for the importance of small terrestrial water sources. Even a relatively short, three-month dry season was sufficient to make arboreal water sources disappear in a rainforest environment with almost complete tree coverage. While the Waibira chimpanzees were able to deal with this reduction in the number of available water sources by shifting to the exclusive use of terrestrial water sources, other species who predominantly rely on arboreal water sources, such as spider monkeys (Campbell et al., 2005; Campos et al., 2020a), mantled howler monkeys (Gilbert & Stouffer, 1989), Temnick's red colobus (Starin, 2002) or koalas (Gordon et al., 1988; Mella et al., 2019), might start experiencing water scarcity at an earlier point during periods of low precipitation, and benefit from interventions like tree-mounted drinkers (Mella et al., 2019). In addition to the water needs of a species, conservation plans must also include which water sources they utilise, and how vulnerable those sources are to evaporation.

Additionally, small terrestrial water sources (Biggs et al., 2005, 2017), like waterholes, have an increased importance during dry seasons as fallback options, as seen here in the Waibira community, as well as other species (white-lipped peccaries: Moreira-Ramírez et al., 2016; birds: Dávila et al., 2020; ungulates: Sutherland et al., 2018; Nubian ibex: Wakefield et al., 2008). The disappearance of these small water sources due to climate change can lead to species ranging outside of protected areas in search of water and relying on human-made water sources (e.g.: Hillyer et al., 2015), or in extreme cases, lead to catastrophic population crashes (e.g.: white-faced capuchins, Geoffroy's spider monkeys (*Ateles geoffroyii*): Campos et al., 2020a; koalas: Clifton, 2010; aardvarks (*Orycteropus afe*r): Rey et al., 2017; vervet monkeys: Wrangham, 1981). To prevent the disappearance of these

essential water sources, artificial deepening of waterholes has been proposed to make them more stable (Gray et al., 2015), while Biggs and colleagues (2017) call for policy to include them in water protection plans.

Water, Fear, and Aversion in the Waibira Community

The chimpanzees of the Waibira community showed a *context-dependent aversion* (Angus, 1971; Nishida, 1980) towards water-contact outside of drinking. Contact with water other than drinking directly or using tools was generally avoided, but the chimpanzees showed no vigilance, apprehension, or fear towards the water – vigilance, when present, was directed towards conspecifics or human observers. Occasional voluntary water-contact has also been observed. Immatures played with water, as seen in Gombe (McGrew, 1977), splashing it or waving their hands in it, and often engaged in exploratory behaviours targeting the water. They were not discouraged or stopped by their mothers, who otherwise intervene in dangerous situations (Reddy et al., 2024). Adults also make voluntary manual contact with water or mud when digging wells (Péter et al., 2022) or reusing drinking tools (Péter, 2019). Finally, the Waibira chimpanzees were occasionally seen resting right at the edges of the central waterhole, lying in damp, but not muddy soil. As the behaviour took place during the height of the dry season, when temperatures can exceed 40°C, it likely has a thermoregulatory function, similar, though more subtle than Fongoli chimpanzees' immersing themselves in water (Pruetz & Bertolani, 2007)

While occasional voluntary water-contact by mature individuals goes against the *innate* (Yerkes, 1943) and *learned hydrophobia* (McGrew, 1977) theories, the *context-dependent aversion* theory does not specify whether the source of the aversion is innate or learned, only that it is not a fear, but a distaste of water (Angus, 1971; Nishida, 1980). Despite the Waibira community having little access to water sources deep enough to pose the risk of drowning to a healthy adult chimpanzee,

with the central waterhole and the seasonal stream never more than ankle-deep and no aquatic predators, a past negative experience triggering *learned context-dependent aversion* is still possible. First, older or less mobile chimpanzees can still drown in shallow water following a fall or similar incident (Cibot et al., 2019b). Second, the southern edge of their home range is a swampy area, with water pools that can be deep enough to pose a drowning risk regardless of mobility. While those areas are overlapping with the home ranges of the Sonso community and the unhabituated South community, and therefore used less, the possibility is there regardless. Whatever the source of the aversion is, it does not impact the Waibira chimpanzees' propensity to drink, and they are able to overcome it when beneficial, like helping thermoregulation or accessing water from hand-dug wells, similar to what has been seen in Mahale (Nishida, 1980), Fongoli (Pruetz & Bertolani, 2007), and in a captive group (Angus, 1971).

Finally, while the central waterhole is located at the bottom of a valley, with thick surrounding vegetation, chimpanzees entering the central waterhole area and drinking only showed low levels of vigilance, except for less habituated females towards human observers. This is in contrast to what is seen in smaller primate species, like yellow baboons (Altmann & Altmann, 1970), Hanuman langurs (Beck & Tuttle, 1972), vervet monkeys (Henty & Mcgrew, 2014), and white-faced capuchins (Burger, 2001; Freese, 1978), in which staggered drinking order, short drinking bouts, and a preference for water sources with better visibility are common. Low level vigilance and avoidance behaviour has only been directed towards conspecifics, human observers, and olive baboon troops outnumbering the chimpanzee subgroup visiting the central waterhole. The Waibira chimpanzees' relaxed attitude is likely due to the low to non-existent predation risk in the Budongo Forest Reserve - while lions (*Panthera leo*) have been sighted at BCFS occasionally

during the 1990s (N. Newton-Fisher, pers. comm.), no proven predation of Sonso or Waibira chimpanzees by either lions or leopards has been documented since monitoring started (Reynolds, 2005). Nine years of camera trap monitoring at the central waterhole also did not record any sign of leopards or lions in the Waibira community range either. Leaning down to drink and entering a low-elevation area with poor visibility therefore does not increase predation risk for the chimpanzees of the Waibira community.

Variation in Drinking Behaviour in the Waibira Community

Regarding large-scale temporal variation, chimpanzees in the Waibira community drank more often in the dry season, as seen in other chimpanzee groups (Gombe: Goodall, 1986; Nelson et al., 2022; Teleki, 1977), other primate species (Chaves et al., 2021; Wright et al., 2022), and mammals in general (Harris et al., 2015; Mella et al., 2019). However, in contrast to another rainforest-living great ape species (mountain gorillas: Wright et al., 2022), drinking in the Waibira community was not a behaviour brought on by the dry season; the chimpanzees consume liquid water year-round. The seasonal increase in drinking frequency is also in line with Wessling et al.'s (2018a) findings about dry seasons and the resulting increase in water needs being a stressor both in savannah and rainforest chimpanzees. As the primary aim of the current study was to determine whether rainforest chimpanzees even consume liquid water regularly, specific measures of hydration were beyond the scope of it. Future research can combine the methods of the studies above to gain an accurate picture of the water intake and hydration management strategies of forest living chimpanzees under changing weather conditions, as suggested by Wessling and colleagues (2018a) too. Urine samples provide accurate measures of day-to-day hydration (Wessling et al., 2018a, 2018b), recording the duration of drinking events allows for an estimate of the amount of water drank (Dias et al.,

2014), while determining the water content of food species consumed allows for an estimate of the amount of water eaten in food (Wright et al., 2022).

Drinking showed within-day variation as well, with a smaller peak mid-morning, then a large one in the afternoon, similar to the high afternoon drinking activity seen in Mahale (Nishida, 1980). This temporal distribution roughly corresponds to daily fluctuations in temperature, and the chimpanzees' activity budget following it – temperatures are highest around midday, and in the middle of the dry season can exceed 40°C. Chimpanzees in Budongo also spend a lot of time resting and grooming on the ground around that time and avoid arboreal activities (Kosheleff & Anderson, 2008). The Waibira chimpanzees likely drink during the afternoon as a thermoregulatory strategy – they rest and minimise activity during the hottest times, similar to other species (white-faced capuchins: Campos & Fedigan, 2009; yellow baboons: Stelzner, 1988), then hydrate and return to arboreal activities as the afternoon cools down. While drinking behaviour in itself is likely not a response to high temperatures in rainforest chimpanzees, as evidenced by drinking in the wet season when temperatures are lower, it can nevertheless aid with thermoregulation. Additionally, there was no nocturnal activity seen on the camera traps – while high daytime temperatures impact their behaviour, the heat is not extreme enough to necessitate moving outside daylight hours as has been reported for savannah chimpanzees (Pruetz, 2018).

Mapping the temporal distribution of drinking activity in chimpanzees has implications for managing human-chimpanzee coexistence. Many households in low income countries lack access to piped water, and get their drinking water by members of the household fetching water from off-site water sources (Avotri & Walters, 1999; Sorenson et al., 2011; Tomberge et al., 2021). Children are often in charge of water carrying for their household (Sorenson et al., 2011), including in

Uganda (Asaba et al., 2013) and other chimpanzee range countries (Graham et al., 2016). Children are also more likely to be severely attacked and injured by chimpanzees compared to adults (Hockings et al., 2010b; McLennan & Hockings, 2016), putting them uniquely at risk at water points. Cattle and chimpanzees meeting at shared-use water points present an additional source of conflict (Fryns et al., 2021).

Knowing when chimpanzees are likely to make use of shared water sources can help reduce the number of encounters between humans and chimpanzees – in this case, the early morning hours just after sunrise seem to be consistently underutilised by the chimpanzees, while afternoons are the busiest, and therefore pose the highest risk to both sides. To avoid human-chimpanzee conflict at shared water sources, water carrying is safest to do in the early morning, up until 9 am, and should be avoided in the afternoon hours of peak chimpanzee activity, between 1:30 pm-6 pm. While unhabituated females in the Waibira community avoided human observers at the central waterhole, repeated encounters between humans and chimpanzees in anthropogenic environments can lead to chimpanzees becoming accustomed to human presence without targeted habituation efforts (McLennan & Hill, 2010), and initial fear-based avoidance by chimpanzees might not be a reliable, long-term conflict mitigation solution at shared water sources. However, chimpanzees are not the only species that could pose a danger to humans at water sources - future research on how different species use water sources is needed, especially for water sources that humans share with wildlife. For example, while chimpanzees were not active outside of daytime hours, in anthropogenic areas leopards shift from a mostly diurnal activity pattern to being active during the night (Havmøller et al., 2020; Van Cleave et al., 2018), making the nighttime also unsafe around water sources for humans. Additionally, human presence might alter natural

patterns of water use, with some species completely avoiding water sources with high human use (African wild dogs (*Lycaon pictus*): Ndaimani et al., 2016; Himalayan langurs (*Semnopithecus schistaceus*): Sharma et al., 2016). However, camera trap monitoring in areas with high human use has its own ethical caveats (see Sandbrook et al., 2021; Simlai & Sandbrook, 2021), and methods will need to be adjusted accordingly.

On the level of individuals, all but two of the adult chimpanzees of the community were seen drinking. As the camera traps do not provide 100% coverage of the waterhole area, and chimpanzees occasionally use one of the peripheral water sources which are not monitored, it is important to remember that the number of recorded drinking events only gives a representative sample of all drinking events in the community, but do not represent all the drinking events in the community. In the case of those two individuals, lack of data is likely due to sampling effort changing across years and being focused on the central waterhole, instead of them never drinking water. One of them, *Impia*, a subadult female, emigrated from the community shortly after camera trap monitoring began, and were not present for enough dry seasons where camera traps were active to have a recorded drinking event. The other, *Vesta*, is one of the less habituated females, only named in 2019. While *Impia* appears in a few camera trap videos, to date there is none of *Vesta*. In her case, it is likely that she rarely uses the central waterhole, and instead relies on some of the peripheral ones, either because she tries to avoid humans, or like in other East African chimpanzee communities (Emery Thompson et al., 2007b; Wakefield, 2008), she only uses certain parts of the group home range.

All the other individuals without any recorded drinking event were infants under the age of two. As infant chimpanzees are still heavily reliant on their mothers' milk at that age (Bădescu et al., 2017, 2022; Samuni et al., 2020), which has a high

water content (Hinde & Milligan, 2011), it is likely that their water needs are fully met by it until that age, from which point they gradually start shifting over to water. This shifting from milk to water as the primary liquid consumed as infant chimpanzees are shifting from milk to solid foods as the primary source of nutrition (Bădescu et al., 2017) is also supported by the Nelson and colleagues' (2022) findings in Gombe, where drinking frequency increased with infant age, as well as the onset of drinking tool use and fabrication happening around the same age in Waibria (Péter, 2019).

When comparing the drinking frequencies of adult males and females, females had more drinking events than expected. This difference could be due to the higher water requirements imposed by lactation, as Nelson et al. (2022; 2024) suggests and as seen in other mammal species (Archer et al., 2013; Bothma, 2005). However, neither the Gombe nor the current study recorded the number of sips taken or the duration of drinking events, similar to what Nishida has done (1980), so it is possible that the reason for the difference is different drinking strategies, rather than different water needs. Rather than a higher water intake, more drinking events could simply mean more interrupted drinking events due to higher vigilance towards conspecifics and humans, or more frequent, but shorter visits to water sources. Nevertheless, drinking was still a regular occurrence in adult males – all weaned chimpanzees of the community regularly consumed water.

General Conclusion

In conclusion, liquid water is a resource regularly consumed by rainforest chimpanzees. They drink water on a daily basis both in the wet and dry seasons, suggesting they cannot meet their full water needs from water in fruit. Drinking activity at the central waterhole was the highest during the early afternoon hours, and lowest in the early morning. The water sources they rely on can be arboreal or terrestrial, with an increased use of arboreal water sources when opportunity is

present. Arboreal water sources and small terrestrial ones however are quick to disappear in periods of low rainfall and high temperatures. All habituated community members older than two years of age were seen drinking, with adult females drinking more often than adult males. Chimpanzees were also not afraid of water, but showed *context-dependent aversion*. These findings have practical implications for captive primate welfare, conservation management, and future ecological research on species in mesic environments.

With regards to captive chimpanzee welfare, based on the drinking frequency of wild rainforest chimpanzees, the water needs of captive chimpanzees are sufficiently met, with water provided *ad libitum* and multiple water sources available within enclosures. However, given the Waibira chimpanzees' use of both arboreal and terrestrial water sources when both are available, providing different forms of water sources, such as artificial tree boles, Lixit drinkers placed higher off the ground, as well as providing foliage suitable for drinking tools, like chewable sticks, larger tree leaves, or moss, could serve as enrichment options and to encourage climbing. Drinking tool enrichment has been provided to captive chimpanzees in the Kyoto Primate Research Institute as part of an experiment and proved popular with the animals (Tonooka et al., 1997). As their aversion to water is not universal and fear-based, shallow surface water can also serve as water play enrichment or as a thermoregulatory option for chimpanzees living in warmer climates, but might not be sufficient in serving as a barrier keeping chimpanzees contained. However, when providing shallow water as water play enrichment, care should be taken to provide support such as ropes, netting, or grating next to and in the water to allow for the safe navigation of the water and slippery surfaces around it (Angus, 1971).

Documenting water-dependence and regular drinking in chimpanzees across all habitat types also adds to our theories about the importance of water and water-

dependence on hominid evolution. The drinking behaviour of the Waibira community support that relying on liquid water to meet their hydration needs was not a novel challenge for early hominid species shifting their species range towards more arid mosaic woodlands and savannahs (see also: Wessling et al., 2018a). However, with chimpanzees drinking daily even in a shaded, humid rainforest environment, a high water-dependence was likely present in our last common ancestor as well, and therefore still remains as a strong constraint on hominid behaviour and physiology, contributing to the evolution of improved thermoregulation mechanisms (Wheeler, 1984), water conservation (Pontzer et al., 2021) and possibly even bipedalism (Wheeler, 1991). Finally, the context-dependent aversion towards water contact seen in the chimpanzees of the community suggests, alongside findings of habitual algae (Boesch et al., 2017) and crab fishing (Koops et al., 2019) in western chimpanzees and opportunistic wading into water for high value food items in eastern chimpanzees (Nishida, 1980), that early hominids likely lacked strong hydrophobia, and were able to exploit aquatic resources successfully and regularly.

The findings of this study also have broader relevance for conservation, highlighting the importance of small water sources (Biggs et al., 2017). While several other studies do exist on the importance of waterholes as an essential source of food and water both in savannah environments in Africa and forest environments outside of it (e.g.: Epaphras et al., 2008; Gray et al., 2015; Moreira-Ramírez et al., 2016; Pin et al., 2020; Wright et al., 2010), this study provides an account of a seasonally important waterhole in an African rainforest environment. The central waterhole of the Waibira community is an ideal location for further studies on the same topic, even broadening the scope of species monitored and monitoring it as one ecological unit, documenting all visiting species, water quality, and vegetation status in an approach termed ‘waterhole studies’ by Beck and Tuttle (1972). Camera traps are an

effective tool for this approach (Boyer-Ontl & Pruetz, 2014; Montalvo et al., 2019; Pin et al., 2020), minimising human presence while maximising the hours of observation in an area. Monitoring can also be extended to the peripheral waterholes to see how chimpanzee communities use water sources where the risk of between-group encounters is present.

Finally, this chapter provides an example of free water being a regularly consumed resource by a species in a mesic environment. Despite having a water rich, fruit-specialist diet, and their habitat having high annual precipitation rates, the chimpanzees in the Waibira community consumed water daily all year, regardless of season. Their high drinking frequency and context-dependent aversion towards water contact is contrary to previous theories about chimpanzees, especially in rainforest environments, being independent of surface water (Pontzer et al., 2021) and hydrophobic (Yerkes, 1943; McGrew, 1977). The consumption of and dependence on free water of a species or a population therefore must not simply be equated with the water content of their solid diet or the climate of their habitat, but investigated and determined separately from those factors. In general, increased focus is needed on the drinking behaviour of species living in mesic environments, as water might be a yet-unknown factor shaping their behaviour.

Chapter 4

Water as a Driver of Female Chimpanzee Space Use

- Female space use in chimpanzees changes with water availability
- Female chimpanzees structure their ranging around terrestrial water sources during water scarcity, but not when the number of available water sources is high
- The usage intensity of terrestrial fallback water sources increases as water scarcity progresses

Across multiple taxa, animals structure their behaviour spatially (birds: Borrmann et al., 2019; reptiles: Congdon et al., 2011; Shimada et al., 2016; mammals: Pasch & Koprowski, 2006; Costello, 2010; amphibians: Meuche et al., 2011), resulting in the formation of home ranges, defined as the area traversed by an animal in its normal activities of foraging, mating, and raising offspring; and core areas, the most frequently used parts of home ranges (Burt, 1943). Concentrating their activity within a specific area has multiple benefits for animals through familiarity. Knowing where consumable resources are located and any seasonal changes in their availability reduces the time and energy spent searching for them (western chimpanzees (*Pan troglodytes verus*): Janmaat et al., 2013), improving foraging success (snow buntings (*Plectrophenax nivalis*): Smith & Metcalfe, 1994). With less time spent traveling between foraging locations (black-tailed deer (*Odocoileus hemionus columbianus*): Forrester et al., 2015) and familiarity with potential refuges and escape routes (eastern chipmunks (*Tamias striatus*): Clarke et al., 1993) the risk of predation decreases as well. Within-species resource competition is also lowered by ranging in a specific area. In case of species with

overlapping home range areas, fewer individuals rely on a given resource patch, reducing user density and with it both scramble and contest competition. Additionally, individuals with overlapping home ranges are familiar with each other: knowing the likely outcome of contest competition events minimises the need for them during encounters, further reducing stress, energy expended, and injury (colonial orb-weaving spiders (*Metepeira incrassata*): Jakob et al., 2001). Temporal partitioning, the use of resources in areas of overlap at different times is also facilitated by familiarity with conspecifics ranging in the same area, and further lowers the number of foragers at a resource patch at a given time (Geoffroy's spider monkeys (*Ateles geoffroyi*): Asensio et al., 2015). While for solitary species with distinct individual home ranges individuals have sole access to the resources within them (meadow voles (*Microtus pennsylvanicus*): Ostfeld & Canham, 1995), familiarity with neighbouring conspecifics and their fighting power similarly reduces the need for frequent contest competition over boundary areas and territory ownership (red-backed salamanders (*Plethodon cinereus*): Liebgold & Dibble, 2011; fish: Ward & Hart, 2003). More efficient foraging, less predation, and lower resource competition then lead to better energetic condition and better offspring survival, increasing reproductive success (common loons (*Gavia immer*): Piper et al., 2008; Magellanic penguins (*Spheniscus magellanicus*): Rebstock et al., 2022; piping plovers (*Charadrius melodus*): Saunders et al., 2012).

To maximise the fitness benefits of ranging in a specific area, animals should occupy the smallest home range that provides a sufficient foraging yield to meet their energetic requirements while minimising time and energy spent on travelling and, when applicable to the species, territorial defence, as well as avoiding injury or predation (Stephens & Krebs, 1986). Therefore, the size and spatial structure of home ranges depend on the amount and spatial distribution of key resources and

threats, as well as environmental and individual factors impacting energetic requirements. Core areas reflect which areas are most used within home ranges, and so give insight into which resources are used most frequently, which areas are avoided, and the socioecological factors most likely to impact which resources are available and visited, how often, and for how long. Studying the space use patterns of a species then allows for the identification of essential resources, relevant threats, and socioecological factors changing their relationship to those two.

The most studied essential resource shaping space use is food: home range size and structure, as well as core areas are impacted by how much food an animal needs, and how that food is distributed spatially. In general, a higher energy intake correlates to a bigger home range, as the foraging yield per area unit cannot be increased, leading to individuals having to increase the size of the area they regularly traverse and forage in to acquire an amount of food sufficient to cover their energetic needs (primates: Milton & May, 1976). However, the distribution and quality of food is not uniform across habitats, impacting how far animals need to travel between food patches and how much of their energetic needs they can meet from one patch. If the foraging yield per area unit is low, animals need to further increase the area they regularly cover during foraging to meet their energetic requirements (polar bears (*Ursus maritimus*): van Beest et al., 2016), leading to home range size increasing with low food availability and quality (western Hoolock gibbons (*Hoolock hoolock*): Akers et al., 2013; mountain lions (*Puma concolor*): Grigione et al., 2002; ring-tailed lemurs (*Lemur catta*): Kelley, 2013; wood bison (*Bison bison athabascae*): Larter & Gates, 1994; common ravens (*Corvus corax*): Roth et al., 2004; Iberian ibex (*Capra pyrenaica*): Viana et al., 2018). The same home range increase happens in fragmented habitats, where suitable habitat types are not continuous within the home range, and therefore food patches are also

further apart (Milne-Edwards' sifakas (*Propithecus edwardsi*): Gerber et al., 2012; wild turkeys (*Meleagris gallapovo silvestris*): Marable et al., 2012; bald-faced sakis (*Pithecia irrorata*): Palminteri & Peres, 2012). As animals aim to minimise travel distance and duration between available food patches, core areas are commonly centred on parts within the home range which have high food availability (moose (*Alces alces*): Cederlund & Okarma, 1988; eastern chimpanzees (*Pan troglodytes schweinfurthii*): Moore et al., 2018), leading to a patchy core area structure in fragmented habitats (ring-tailed lemurs: Kelley, 2013; eastern chimpanzees: McLennan et al., 2021). If seasonal fluctuations in food availability and distribution are present, core areas also not fixed throughout the year in several species, but change depending on the season or month (Père David's deer (*Elaphurus davidianus*): Ding et al., 2017; lions (*Panthera leo*): Kittle et al., 2016; Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*): Li et al., 2010; desert mule deer (*Odocoileus hemionus eremicus*): Marshal et al., 2006; Japanese macaques (*Macaca fuscata*): Tsuji & Takatsuki, 2009).

The availability and distribution of water, another essential and consumable resource, also shapes space use in species which are dependent on surface water. As opposed to food, where a higher individual intake requirement increases home range size, a higher need for water decreases home range size: animals must access water on a regular basis while also avoiding excessive travel distances between food patches and water sources (olive baboons (*Papio anubis*): Barton et al., 1992; mountain sheep (*Ovis canadensis*): Bleich et al., 2010; mule deer (*Odocoileus hemionus*): Boroski & Mossman, 1996; koalas (*Phascolarctos cinereus*): Davies et al., 2013; Iberian lynx (*Lynx pardinus*): Palomares et al., 2001; African elephants (*Loxodonta africana*): Purdon & van Aarde, 2017; white-naped mangabeys (*Cercocebus lunulatus*): Outtara et al., 2019), with the maximum distance they can

travel away from available water sources determined by how often they need to drink (khulan (*Equus hemionus*), Przewalski's horses (*Equus ferus przewalskii*): Kaczensky et al., 2008; khulan: Payne et al., 2020; buffalo (*Syncerus caffer*), wildebeest (*Connochaetes taurinus*): Redfern et al., 2003). During periods of low water availability, as the number and quality of available water sources decrease (Padrón et al., 2020; Strauch, 2013; Wolanski & Gereta, 2001), animals adjust their space use accordingly. Home ranges might shift in space (red-fronted lemurs (*Eulemur rufifrons*): Amoroso et al., 2020a; vervet monkeys (*Chlorocebus pygerythrus*): Wrangham, 1981) or have increased overlap with other individuals' or groups' home ranges (raccoons (*Procyon lotor*): Gehrt & Fritzell, 1998; vervet monkeys: Wrangham, 1981) as animals have to resort to using water sources located outside their usual ranging patterns (sleepy lizards: Leu & Bull, 2016; Baird's tapir (*Tapirus bairdii*): Pérez-Flores et al., 2021). To decrease time spent traveling, which can increase water needs (common lizards (*Lacerta vivipara*): Lorenzon et al., 1999), activity is commonly centred in the vicinity of the remaining water sources during dry periods, leading to a seasonal shift in core area locations to encompass water sources (bats: Amorim et al., 2018; red-fronted lemurs: Amoroso et al., 2020a; white-faced capuchins (*Cebus capucinus*): Campos & Fedigan, 2009; raccoons: Gehrt & Fritzell, 1998; parti-coloured bats (*Vespertilio murinus*): Safi et al., 2007).

While the distribution of food and water drive much of the spatial behaviour of animals, functioning as an attractant across taxa, other factors, such as anthropogenic disturbance (western Hoolock gibbons: Akers et al., 2013; white rhinoceros (*Ceratotherium simum simum*): Nhleko et al., 2022; Iberian lynx: Palomares et al., 2001; banteng (*Bos javanicus*), Eld's deer (*Rucervus eldii*), giant ibis (*Thaumatibis gigantea*): Pin et al., 2020) or predation risk (feral cats (*Felis catus*): Gehrt et al., 2013), can instead trigger avoidance of otherwise resource-rich

areas due to fear (Brown et al., 1999). Depending on the species' strategy to navigate a landscape of fear, home range size can either decrease when threats are present so the individual can stay near shelter (common octopus (*Octopus vulgaris*): Mather & O'Dor, 1991) and restrict their space use to areas with low threat levels (coyotes (*Canis latrans*): Atwood et al., 2004; bobcats (*Lynx rufus*): Riley, 2006), or increase to allow for the individual to memorise and access multiple shelter and escape options (common pheasants (*Phasianus colchicus*): Heathcote et al., 2023; common degus (*Octodon degus*): Lagos et al., 1995), while areas that offer more shelter (steephead parrotfish (*Chlorurus microrhinos*): Welsh & Bellwood, 2012) or are harder to access by predators, like steep slopes (desert mule deer: Marshal et al., 2006) are used more. Increased spatial overlap between individuals can also be a result of high levels of threat, having to share existing shelter opportunities (green razorfish (*Xyrichtys splendens*): Nemtzov, 1997) or relying on joint predation protection efforts with conspecifics (western chimpanzees: Boesch, 1991).

Individual characteristics can further impact space use, as they change the energetic requirements of the individual, how sensitive they are to risks and threats, and how important energetic optimisation is for them. Mating strategies and the energetic costs of reproduction differ between the sexes, with male reproductive success mostly dependent on access to mating opportunities, and female reproductive success on body condition (brown trout (*Salmo trutta*): Birnie-Gauvin et al., 2023; birds: Drent & Daan, 1980; primates: Dunbar, 1988; mammals: Uphouse, 2011). For males, seeking out (puff adders (*Bitis arietans*): Glaudas et al., 2020), attracting (wolf spiders (*Hygrolycos rubrofasciata*): Kotiaho et al., 1998) or defending access to females (whiptail lizards (*Aspidoscelis costata*): Ancona et al., 2010; Japanese macaques: Matsubara, 2003) increases energy expenditure, and exposes them risk of injury from conspecifics (fig wasps (*Sycoscapter australis*): Bean &

Cook, 2001; Barbary macaques (*Macaca sylvanus*): Kuester & Paul, 1992) and predation (*Hyalella azteca*: Cothran, 2004; moustached tamarins (*Saguinus mystax*): Huck et al., 2004; wolf spiders: Kotiaho et al., 1998). While good energetic condition and optimisation is necessary for ensuring mating success for males (North American red squirrels (*Tamiasciurus hudsonicus*): Lane et al., 2010), long-term maintenance of it, in the absence of sexually available females, is not essential for the survival of the resulting offspring in species without paternal care (Namaqua rock mouse (*Aethomys namaquensis*): Fleming & Nicolson, 2004; damselflies (*Calopteryx splendens xanthostoma*): Plaistow & Siva-Jothy, 1997). For females, while also engaging in mate-seeking behaviour (eastern chimpanzees: Newton-Fisher, 2014) or contest competition over mating opportunities (Japanese medaka (*Oryzias latipes*): Grant & Foam, 2002; Qinghai toad-headed agamas (*Phrynocephalus vlangalii*): Wu et al., 2018), the increase in energetic costs due to reproduction is present after successful mating as well: gestation, lactation (mammals: Clutton-Brock et al., 1989; eastern chimpanzees: Emery Thompson et al., 2012; house mice (*Mus musculus*): König & Markl, 1987), provisioning (tree swallows (*Tachycineta bicolor*): Bonier et al., 2011) and carrying offspring (chimpanzees: Pontzer & Wrangham, 2006) all increase energy expenditure. Engaging in overt competition or risking predation can also harm female reproductive success more than that of males – the resulting stress can interfere with conception (mammals: Uphouse, 2011; humans (*Homo sapiens*): Valsamakis et al., 2019), and offspring might also be killed (banded mongooses (*Mungos mungo*): Gilchrist, 2006; white-faced capuchins: Kalbitzer et al., 2017; chimpanzees: Townsend et al., 2007). In general, female reproductive success requires good energetic condition and optimisation in the long term, covering the period of mating, producing offspring, and in species with maternal care, offspring dependence as well (Gadgil & Bossert, 1970). As a result, females are generally

more sensitive to changes in resource availability, threats, and factors impacting energetic condition than males, including changing their space use patterns (e.g.: parti-colored bats: Safi et al., 2007).

For example, while males increase their home range size during mating periods to have access to more females and cover their increased energetic needs (Namaqua rock mice: Fleming & Nicolson, 2004; California voles (*Microtus californicus*): Salvioni & Lidicker, 1995; bottlenose dolphins (*Tursiops aduncus*): Sprogis et al., 2016), female home ranges also show changes during periods of offspring dependence. Depending on food availability and the landscape of fear, females might range broader to meet their reproduction-related energetic needs (moose: Cederlund & Sand, 1994; pig-nosed turtles (*Carettochelys insculpta*): Doody et al., 2002; northern fulmars (*Fulmarus glacialis*): Edwards et al., 2016a; king rails (*Rallus elegans*): Kolts & McRae, 2017; wood bison: Larter & Gates, 1994), or restrict their ranging to safer and well-known areas to avoid risks such as infanticide (mountain lions: Grigione et al., 2002; polar bears: van Beest et al., 2016) or predation (mule deer: Boroski & Mossman, 1996; Iberian ibex: Viana et al., 2018).

Age can also influence energetic requirements and risk aversion, and with it, space use patterns. In some species, younger independent individuals range broader to familiarise themselves with their habitat (black rhinoceros (*Diceros bicomis*): Goddard, 1967) or seek out mates (wood bison: Larter & Gates, 1994), while being less likely to already have dependent offspring vulnerable to predation and restricting the distance and speed they can travel (wild boars (*Sus scrofa*): Keuling et al., 2008), resulting in larger home ranges. In other species, age positively correlates with home range size (European badgers (*Meles meles*): Cresswell & Harris, 1988; coyotes: Holzman et al., 1992; black bears (*Ursus americanus*): Reynolds & Beecham, 1980), with older individuals traversing a larger area either

due to increased body size and with it energetic requirements (black bears: Reynolds & Beecham, 1980) or an increased familiarity with the area and potential foraging locations within it (coyotes: Holzman et al., 1992).

Space Use in Chimpanzees

Chimpanzees have a large body size, with adults weighing 30-50 kg (Uehara & Nishida, 1987), and a long life span of up to 40-50+ years in the wild (Boesch & Boesch-Achermann, 2000; Goodall, 1986; Matsuzawa, 2018). They are ripe fruit specialists (Potts, 2004), preferring energy-rich *Ficus* species (Matsumoto-Oda & Hayashi, 1999; Moore et al., 2018; Piel et al., 2017; Pruetz, 2006) or crop-raiding if able to access human settlements (Bersacola et al., 2021; Hockings & McLennan, 2012). They also consume leaves and other soft vegetation (Matthews et al., 2019), comprising a large part of their diet in habitats where the density of fruit trees is low (Yoshikawa et al., 2022), various small animals (arboreal monkeys: Boesch, 1994; duikers: Hobaiter et al., 2017; tortoises: Pika et al., 2019), insects (McGrew et al., 1979), tubers (Hernandez-Aguilar et al., 2007), honey (Bermejo & Illera, 1999), or tree bark (Lapuente et al., 2020).

As long-lived, large-bodied fruit-specialist omnivores, chimpanzees benefit from high site fidelity and the resulting familiarity with their foraging grounds, memorising the location of fruit trees and regularly monitoring their fruiting status (Janmaat et al., 2013). They live in multi-male, multi-female highly fission-fusion communities (Sugiyama, 1968; Goodall, 1986), which allows for flexible managing of within-group resource competition by the community dividing into smaller parties or individuals foraging alone when food availability is low, and re-grouping when it is high (Van Schaik, 1983). The home ranges of communities have little overlap (Moore et al., 2018; Newton-Fisher, 2003) and are defended by the community members patrolling the peripheral areas, which can turn into violent or lethal intercommunity

encounters (Goodall, 1986; Watts et al., 2006, but see Hashimoto et al., 2020 for an example of peaceful intercommunity encounters). Intercommunity transfers are most commonly adolescent females, dispersing from their natal community then permanently settling in a new one to avoid inbreeding (Pusey, 1980; Walker & Pusey, 2020), or in the remaining cases, adult females and their dependent offspring whose community has dissolved (Emery Thompson et al., 2006; Nishida et al., 1985). Within the community home range, individual chimpanzees also have their own area of primary ranging (females: Kahlenberg et al., 2008a; Nishida et al., 1985; Wakefield, 2008; Wrangham, 1979; males: Chapman & Wrangham, 1993; Newton-Fisher, 2000), which are stable over time (Emery Thompson et al., 2007b; Murray et al., 2006). These individual home ranges overlap between community members (Emery Thompson et al., 2007b; Fawcett, 2000; Newton-Fisher, 2000; Wakefield, 2008). Aggression over individual space use is rare (Miller et al., 2014), most commonly resident females aggressing recently immigrated females still establishing their individual home ranges (Kahlenberg et al., 2008b).

Research on individual home ranges in chimpanzees has mostly focused on females. First, the structure of their individual home ranges within the community home range is of theoretical interest to unpick chimpanzee social and grouping structure: whether space use patterns support a male-only community model (Lehmann & Boesch, 2005; Wrangham, 1979), where smaller female ranges are equally distributed, and independent of larger male ranges and the community home range (c.f.: Martínez-Íñigo et al., 2021; Pusey, 1980; Wilson et al., 2004); a male-bonded model (Lehmann & Boesch, 2005; Wrangham, 1979), where smaller female ranges are contained within larger male ranges and the community home range (Kanyawara, Uganda: Emery Thompson et al., 2007b; Ngogo, Uganda: Wakefield, 2013; Gombe, Tanzania: Williams et al., 2002a); or a bisexually-bonded one

(Lehmann & Boesch, 2005; Wrangham, 1979), where females and males range throughout the entire community home range (e.g.: Sonso, Uganda: Fawcett, 2000; Kalinzu, Uganda: Hashimoto & Furuichi, 2015; Taï, Côte d'Ivoire: Lehmann & Boesch, 2005; Bossou, Guinea: Sakura, 1994). Extensive variation in female space use between field sites and even within subspecies (eastern chimpanzees: Fawcett, 2000; Wakefield, 2013) further fuelled interest in the topic. Additionally, focusing on the space use of female chimpanzees as opposed to that of males allows for an easier identification of key resources for the species. Female chimpanzees have to balance the high energetic requirements of the long pregnancy, extended lactation, and infant carrying typical for the species, with offspring highly dependent on the mother for the first three to five years (Emery Thompson et al., 2012; Murray et al., 2009) and are therefore more sensitive to any change in the availability of variables impacting their energetic status and body condition (Hashimoto & Furuichi, 2015; Van Schaik, 1989; Wrangham, 1979).

Acquiring a sufficient quality and quantity of food is essential for female chimpanzee reproductive success (Emery Thompson et al., 2012; Murray et al., 2009), leading to food availability and the levels of food competition theorised to be the primary shapers of female primate behaviour (Van Schaik, 1989; Wrangham, 1979). High and stable food availability or lower chimpanzee density in an area result in lower levels of competition for food, leading to more tolerance and a higher overlap between individual home ranges as seen in Taï (Lehmann & Boesch, 2005), Ngogo (Wakefield, 2013), and Sonso (Fawcett, 2000). As food competition increases with fluctuating or low food availability, as well as high chimpanzee density, spatial segregation of females becomes stricter, as seen in Gombe (Murray et al., 2006) and Kanyawara (Emery Thompson et al., 2007b). The clustering of individual home ranges into so-called ‘cliques’ or ‘neighbourhoods’, where females selectively

overlap their space use and associate with only a few other females is also more common in larger communities (Kanyawara: Emery Thompson et al., 2007a; Ngogo: Wakefield, 2013; Gombe: Williams et al., 2002), allowing individuals to keep the number of competitors for food within their home range low while still enjoying the benefits of socialisation (Wakefield, 2013).

Similar to other species, predation protection and avoidance of risk also shape the space use patterns of female chimpanzees. Like other great ape species, they have very few natural predators (African leopards (*Panthera pardus pardus*): Boesch, 1991; lions: Tsukahara, 1993), though hunting by humans for the bushmeat and pet trade is an ever-present threat (Hicks et al., 2010; Ogunjemite & Ashimi, 2010). In Taï, predation and injury by leopards is one of the leading causes of death (Boesch, 1991; Wittig & Boesch, 2019). Spending time travelling and foraging with other community members offers some protection from leopard attacks, and increases the size and rate of overlap of individual home ranges of the females in the communities there (Lehmann & Boesch, 2005). Besides predators, other chimpanzee communities are also perceived as a risk, as individuals risk injury, death, or for females with dependent offspring, infanticide during intergroup encounters (Kirchhoff et al., 2018; Martínez-Íñigo et al., 2021; Watts et al., 2006). Female chimpanzees adjust their space use accordingly, and avoid settling in peripheral areas of the community home range, regardless of food quality there, as seen in Kanyawara (Emery Thompson et al., 2007b) and Sonso (Fawcett, 2000). However, female participation in community defence along the edges of the community range occurs in small communities with a female-biased sex ratio, where only a small number of adult or subadult males are present, leading to broader ranging and larger individual home ranges (Lehmann & Boesch, 2003; Lemoine et al., 2020). Finally, for females with dependent infants, within-community infanticide is

also a risk, both from males and females (Lowe et al., 2020; Townsend et al., 2007; Walker et al., 2021; Watts & Mitani, 2000). The non-uniform, clustered female space use found in several communities (Kanyawara: Emery Thompson et al., 2007b; Ngogo: Wakefield, 2013; Gombe: Williams et al., 2002) has been theorised to serve as an infanticide protection measure by increasing female-female coalition opportunities (Wakefield, 2013).

Individual home range size and structure can also differ between females in the same community, owing to slightly different energetic needs and strategies depending on individual factors. Specifically age related space use differences in female chimpanzees are difficult to unpick, as their age and tenure in a community are strongly correlated with their rank (Foerster et al., 2016; Mielke et al., 2019). New immigrants used peripheral areas more in Mahale (Uehara, 1981), while in Sonso both peripheral females were old (Fawcett, 2000). The correlation between home range size and rank is similarly variable, with higher ranking females ranging broader in Taï (Riedel et al., 2011) and Sonso (Fawcett, 2000), but having smaller home ranges in Gombe (Murray et al., 2006, 2007). However, the pattern of high-ranking females using higher quality areas more often is consistent: their home ranges are either more central and therefore safer from other chimpanzee communities (Gombe: Murray et al., 2006, 2007), or have higher food availability and quality (Kanyawara: Emery Thompson et al., 2007b; Kahlenberg et al., 2008a; Gombe: Murray et al., 2006, 2007), which in turn leads to better reproductive success (Kanyawara: Emery Thompson et al., 2007b; Gombe: Williams et al., 2002a). Reproductive status also impacts space use, with pregnant and lactating females travelling less, either due to being hindered by infant carrying, conserving energy (Murray et al., 2009), or having to adapt their pace to their juvenile offspring who is not carried, but still travels with the mother (Pontzer & Wrangham, 2006). In contrast,

cycling females range broader compared to non-cycling females, either to look for mating opportunities (Newton-Fisher, 2014) or to flee from conspecific aggression (Matsumoto-Oda & Oda, 1998). Besides the size of the area females traverse, which parts of the community home range they use can also be impacted by their reproductive status. Lactating females were less likely to range in the peripheral, more risky areas of the community home range, likely to avoid stress, injury to self, or infanticide (Bates & Byrne, 2009).

The Current Study

Female space use in chimpanzees is highly flexible, showing variation between and within communities depending on resource availability, risk, and individual factors impacting energetics. This flexibility in turn allows for the identifying of key resources for their survival and reproductive success: in this study, to test if water, a regularly consumed resource, is also an essential resource for rainforest-dwelling chimpanzees, as well as how female chimpanzees balance acquiring enough food and water in an environmental water shortage. The impact of water availability and the spatial distribution of water sources on space use is well-studied in species inhabiting arid environments, with activity centring on water sources and spatial overlap between individuals and groups increasing as the number of available water sources decreases (e.g: red-fronted lemurs: Amoroso et al., 2020a; raccoons: Gehrt & Fritzell, 1998; African elephants: Purdon & van Aarde, 2017; red lemurs (*Eulemur rufus*): Scholz & Kappeler, 2004; vervet monkeys: Wrangham, 1981). However, little is known about how water availability impacts the space use of species in mesic environments, including rainforest-dwelling chimpanzees, and in general, if water is even a limiting resource in those habitats.

Chimpanzees in arid, water-scarce environments also show several behavioural adaptations to deal with lower hydration levels and heat stress, like

drinking tool-use (Lanjouw, 2002), digging for tubers (Hernandez-Aguilar et al., 2007; Hockings et al., 2010a; Lanjouw, 2002), night-time travelling (Pruetz, 2018), cave use (Boyer-Ontl & Pruetz, 2020), and the lack of water-contact aversion prominent in other chimpanzee groups (Pruetz, 2007). Alongside evidence of elevated stress levels due to dehydration in both savannah- and forest-living chimpanzees (Wessling et al., 2018a; 2018b), as well as evidence from Chapter 3 that rainforest chimpanzees regularly drink water, it is reasonable to expect changes in female chimpanzee space use with changing water availability. Besides the higher flexibility in their individual ranging depending on extrinsic and intrinsic factors, dehydration and the stress caused by it may pose greater risks for female chimpanzees compared to males. Evidence from other primate species suggests that stress due to dehydration might interfere with successful conception and gestation (Morishima et al., 1975; Nepomnaschy et al., 2006; Valsamakis et al., 2019), while severe dehydration can negatively impact lactation (Rosinger, 2015).

In the Waibira community, despite living in an equatorial rainforest, the number of available water sources reduces drastically during the dry season: the ephemeral creek in their home range dries out with the exception of the central waterhole, while terrestrial water sources similarly disappear due to evaporation or exploitation. Other factors which can impact female space use patterns are well-documented. Food availability, despite logging activity changing the predominant forest type, is high and stable (Tweheyo et al., 2004; Villioth, 2018), and can likely support high chimpanzee density while keeping female food competition low (Villioth et al., 2022). While lions have been sighted at BCFS occasionally during the 1990s (N. Newton-Fisher, pers. comm.), no proven predation of chimpanzees by either them or leopards has been documented in the area used by the Waibira community or the neighbouring Sonso community since monitoring started (Reynolds, 2005),

and no lions or leopards have ever been sighted in the Waibira community range by direct observation or on camera trap. Chimpanzees are not targeted by human hunting in the area either, though accidental injuries from wire snares targeting duikers are common (Quiatt et al., 2002; Waller & Reynolds, 2001). The large community size of Waibira (100 individuals with 19 adult males in March 2022) also reduces the risk and pressure of intercommunity encounters (Lemoine et al., 2020), as well as the need for females to extend their ranging and partake in boundary patrols (Riedel et al., 2011), though depending on the individual, they have been observed to so (pers. obs.).

If water is a key resource for rainforest chimpanzees, then the decrease in the number of water sources during the dry season is likely to pose a resource constraint to the female chimpanzees in the Waibira community. Similar to changes in the space use patterns of species inhabiting arid environments in response to water scarcity, I expect to see increased spatial overlap between the females during the dry season, as well as a greater likelihood of including the central waterhole within their core areas during the dry season. As distance from water sources can limit ranging depending on the maximum distance animals can travel without drinking, I will also test if female ranging shrinks in the dry season as alternative water sources, available during the wet season, disappear. With the drying up of arboreal water sources and the creek in the community home range, I also predict an increase in the usage intensity of the central waterhole as the dry season progresses, reflected in increased visitation frequency and length, with possible impacts of reproductive status on an individual level.

The findings from this chapter will help understand the relative importance of water as a resource for chimpanzees and species living in water-rich environments, as well as the importance and ecological role of waterholes in African rainforests.

Early hominin evolution is theorised to be characterised by a high degree of environmental variability (Potts, 2012), including highly variable hydroperiods of water sources & precipitation. Research on extant great apes' responses to water shortages across a variety of environments – here, on ranging patterns - can improve our understanding of the dispersal patterns of early hominins within Africa, and later for early *Homo* species, outside of Africa, as well as palaeoclimatological models of habitat suitability. Studying specifically water availability-related changes in the space use of chimpanzees will also aid conservation, including the creation and evaluation of protected areas, and managing human-wildlife conflict around shared water sources.

Methods

Space Use Data

I conducted fieldwork between November 2021 and March 2022, encompassing the end of the 2021 wet season, the entire 2021-2022 dry season, and the start of the 2022 wet season. I collected data on the space use of the female chimpanzees of the Waibira community by recording the current date and the location of our first encounter with any identified adult or subadult females during the day using a handheld Garmin 60CSx GPS device. Further first encounter data on the grid cell level was extracted from long-term focal follow data of named adult and subadult members of the community available June 2015-November 2022, during which scan samples of the focal individual's party are recorded at 15 min intervals. Besides first encounter data on females, I also extracted data on the location of each 15 min party composition scan, regardless of whether there were any females present. Grid cell level long-term data was then converted to a point coordinate at the centre of the given grid cell with ArcGIS Pro (v. 2.7). More information on fieldwork data collection and long-term data can be found in Chapter 2.

First encounter location was used to calculate individual home ranges and core areas, as it is independent of the frequency of the individual being chosen as a focal, and is therefore less biased towards more habituated females (Murray et al., 2007; Williams et al., 2002a). As several named females in the Waibira community are habituated enough to be seen when travelling or feeding with a party, but rarely can be followed on the ground for longer periods of time, minimising or at least accounting for potential bias towards more habituated females who can be chosen as focal individuals was an important factor in choosing space use estimation methods. Additionally, while alone first encounter location is more commonly used, especially in studies from Gombe (e.g.: Murray et al., 2007; Williams et al., 2002a), it assumes low gregariousness and exclusive core area usage of females, which is relatively rare across chimpanzee communities (Fawcett, 2000; Lehmann & Boesch, 2005; Sakura, 1994; Wakefield, 2008). As this is the first targeted study on the sociality and space use of the Waibira females, those assumptions of low gregariousness and minimal spatial overlap cannot be made, and therefore all first encounters were included in the dataset, whether the female was alone or traveling with a party. The locations of the 15 min party composition scans were used to calculate the community home range.

Minimum sample size per individual for inclusion in spatial analyses was determined by incremental area analysis conducted in Ranges 9 (Kenward et al., 2014). Asymptotes were reached around 105 first encounter locations, therefore only females with at least 105 first encounters recorded were included in calculations of general ranging patterns. In total, 6997 first encounters were included from 22 different adult or subadult females, recorded between June 2015 and November 2022. The number of first encounters ranged from 106-616 between females, with an average of 318 and median of 352 (Table 11).

Table 11

Females Included in General Ranging Analyses

Individual	First encounters
Akiki	125
Arua	260
Bahati	462
Eili	106
Jinja	301
Ketie	434
Kidepo	282
Kipepeo	347
Liran	397
Lotty	380
Monika	484
Masindi	119
Ndito-Eve	441
Nora	616
Onyofi	282
Penelope	367
Rachna	242
Rita	376
Shay	130

Spini	115
Tatu	379
Tibu	352
Total	6997

For seasonal space use analyses, minimum sample size per individual was determined by the same incremental area analysis method: females needed to have a minimum 95 first encounters from both the wet and dry season. 16 different adult or subadult females were included, contributing 4228 first encounters across nine wet seasons, and 1892 first encounters across eight dry seasons. The number of first encounters ranged from 145-432 with a mean of 264 and median of 266 for wet seasons, and 96-184 with a mean of 118 and median of 114.5 for dry seasons (Table 12).

Table 12

Females Included in Seasonal Ranging Analyses

Individual	Dry season first encounters	Wet season first encounters
Arua	101	159
Bahati	128	334
Jinja	96	205
Ketie	114	320
Kipepeo	126	221
Liran	129	268
Lotty	112	268
Monika	138	346
Ndito-Eve	121	320
Nora	184	432
Onyofi	115	167

Penelope	103	264
Rachna	97	145
Rita	115	261
Tatu	111	268
Tibu	102	250
Total	1892	4228

22,639 15 min party composition scans, also recorded between June 2015 and November 2022, were available. However, as they were recorded at 15 min intervals within the day, as opposed to first encounter locations which were taken once per day, there is a possibility that data points were not independent of each other (Mitchell et al., 2020). To address this issue of temporal autocorrelation and ensure the independence of data points, I calculated the maximum time it would take the Waibira chimpanzees to travel in a straight line between any two points on the grid system at the median chimpanzee travel speed of 0.44 m/s (Jang et al., 2019), following Newton-Fisher (2003). A minimum of three hours between consecutive data points was then set and starting at the first party composition scan of a given day, any party composition scans recorded less than three hours from the previous scan were excluded from community home range estimates, leaving a total of 2909 15 min party composition scans.

Besides recording daily first sightings of females, I also conducted focal individual follows of the named independent females of the community, recording their presence on the grid cell level every 10 min. GPS data were also collected on the daily travel route of focal females, with the Garmin set to record a waypoint every 5 min. Unfortunately, due to changing COVID-19 health protocols at the field station restricting the time we could spend in the forest and observing specific chimpanzee parties, daily travel routes and 10 min focal locations are only available November-

December 2021 and 22 February-March 2022, resulting in 12 days recorded during the dry season, and as such are not sufficient for analyses of seasonal changes in space use patterns, given that the dry season lasted from January 1 to March 16 2022 that year. More information on focal individual follows and COVID-19 restrictions during fieldwork can be found in Chapter 2.

Camera Trap Videos

Camera trap videos from the central waterhole were available every year from February 2013 to April 2022, centring on the annual dry season, but depending on the year, also including the end and/or the start of the wet season as well. As the current chapter focuses on variation in the usage of the central waterhole within the dry season, videos from the wet season were excluded from this chapter's dataset. Camera trap videos were available from all ten dry seasons between February 2013 and April 2022. More information on camera trap monitoring can be found in Chapter 2.

Video Coding

Using BORIS video coding software (v. 7.13.6, Friard & Gamba, 2016), I extracted data from every camera trap video showing at least one identified adult or subadult female chimpanzee (N = 4219), recording for each female: their *identity*, *reproductive status* (*without swelling*, *with swelling*, *young infant*, *old infant*), the date, which dry season the video was from, as well as the time spent on-screen to the nearest second (1-60 s). If a female went off-screen then returned within the same video, I recorded it as continuous presence, using her last on-screen appearance within that video as the end point, as it was impossible for her to leave the central waterhole and its immediate area and return within the duration of a one-minute video. Records of on-screen presence were then used to calculate *waterhole visitations*: a *waterhole visitation* was defined as a state (Altmann, 1974) starting at

the first on-screen appearance of a given female and concluding at her last on-screen appearance. If the female was on-screen for multiple videos within the same day, a *waterhole visitation* started at her first on-screen appearance in the earliest video, and was counted as ongoing throughout videos of her recorded within maximum 3 min 55 s of each other, ending at her last on-screen appearance within those videos. If more than 3 min 55 s passed between on-screen appearances of the same female within the same day, the first *waterhole visitation* was concluded at the last on-screen appearance of her before the 3 min 55+ s gap between videos, then a new *waterhole visitation* started at her first on-screen appearance after the gap. 3 min 55 s was chosen as cut-off point as it is the average time it takes to reach grid lines 25, 27, L, and N, or junctions 25-L, 25-N, 27-L, or 27-N, making up the edges of grid cell 25-L, and by that leaving the vicinity of the central waterhole then returning to it, travelling in a straight line at the highest chimpanzee travel speed of 1.10 m/s (Jang et al., 2019). More on the limitations of camera trap data and the Waibira grid line system can be found in Chapter 2.

For each day an identified female visited the central waterhole at least once, I calculated three measures of *waterhole visitation* for that individual. First, the *number of days elapsed* since that specific female last had at least one recorded *waterhole visitation*, calculated by subtracting the date of her current visitation(s) from the date of her most recent previous visitation(s). *Number of days elapsed* was not calculated for the first day a female visited the central waterhole for a given dry season. Second, *visitation count*, which is the total number of *waterhole visitations* by a specific female on a given day. Finally, *mean on-screen time*, for which I divided the total duration of a specific female being on-screen in a given day with her *visitation count* for the same day. *Mean on-screen time* was used instead of total on-screen time to avoid autocorrelation with *visitation count*. 1465 *waterhole visitations* by 40

different identified females across 273 days and ten dry seasons were recorded from the camera trap videos.

Ecological Variables

Days were categorized as *wet* or *dry season* days depending on rainfall using the pentad-based approach described in Chapter 2. *Dry season* days were also consequently numbered within dry seasons starting with one for the first day of the respective dry season. First encounter data points were then categorised as *wet* or *dry season* data points depending on the date, while data extracted from camera trap videos was categorised using *dry season day number*.

Individual Variables

Rank category (*high, mid, mid-low, low*) was calculated using long-term *ad libitum* data on female-female pant-grunts available 2014-2022, and additional *ad libitum* data collected during fieldwork between November 2021-March 2022. Descriptions of the specific method and exact individual dominance values can be found in Chapter 2. Where the female was not recorded to give or receive any pant-grunts, she was assigned *unknown* as *rank*. *Age category* was assigned as *adult* for females older than 14 years and as *subadult* for females aged 10-14 years (Reynolds, 2005). *Reproductive status* (*without swelling*, *with swelling*, *young infant*, *old infant*) was retrieved from long-term health monitoring data available July 2015-July 2022 and where available, camera trap videos and fieldwork observations. Where the female had no infant, anogenital swelling, or the lack of it recorded, she was assigned *unknown* as reproductive status. More information on long-term health monitoring data and assigning reproductive status can be found in Chapter 2.

Statistical Analyses

Ranging estimates, dyadic overlaps, and nearest neighbour analysis were calculated using Ranges 9 (Kenward et al., 2014). All other statistical analyses were

conducted using R (v. 4.3.1) (R Core Team, 2023) running in RStudio (v. 2023.6.0+421) (Posit Team, 2023), except exact tests of goodness-of-fit which were calculated by hand.

Individual female home ranges and core areas were calculated from first encounter locations. Individual home ranges were defined as the area in which the individual spent 100% of their time (following Fawcett, 2000 and Lehmann & Boesch, 2005). Two types of individual core areas were calculated: 80% core areas, defined as the smallest area containing 80% of all fixes, and 50% core areas, the smallest area containing 50% of all fixes. While 80% core areas are more commonly used in studies on chimpanzee ranging (e.g.: Fawcett, 2000; Newton-Fisher, 2002, 1997), utilisation distributions had no clear inflection point which would indicate a clear home range – core area distinction, and I therefore also chose to include estimates of 50% core areas, which are commonly used in non-primate spatial ecology (e.g.: Atwood et al., 2004; Borrmann et al., 2019; Cavalcanti & Gese, 2009). Individual home ranges and 80% and 50% core areas were calculated first using all fixes to gain an estimate of general, year-round ranging patterns, then separately for the *wet* and *dry season* using only fixes from the respective season to estimate seasonal ranging patterns. For community-level space use, only all-year home range was calculated.

Two different range estimation methods were used to calculate each type of individual range, the Minimum Convex Polygon method (MCP) and Kernel Density Analysis using the Fixed Kernel method (FKD) (Worton, 1989). The MCP estimation method draws the smallest convex polygon area that encompasses all data points. It captures the extent of ranging and it is the only range estimation method that allows for direct comparison between studies (Harris et al., 1990), but does not inform about patterns of space use within its boundaries, including utilisation intensity or areas

avoided. Kernel Density Analysis calculates the probability of finding the animal at a given location based on the recorded fixes, adds these probabilities across the map, then draws the boundaries of the range around them depending on a smoothing parameter *h* which determines how closely is the boundary line fitted to locations (Worton, 1989). In FKD, this smoothing parameter is constant across the range, irrespective of the concentration of recorded fixes in an area. While least squares cross-validation (h_{LSCV}) has been recommended as the best practice for finding an optimal smoothing parameter (Worton, 1989), it can have a high failure rate when fixes have a high concentration in specific areas and at large sample sizes (Hemson et al., 2005; Wauters et al., 2007). As that was the case with this dataset as well, I have chosen to use the other commonly used smoothing parameter estimation method, the reference smoothing method (h_{ref}) (Worton, 1989), with a multiplier of 1 and a grid size set to 50 x 50 cells in Ranges 9 for FKD estimates. Community home range was estimated using MCP, including all 15 min party composition scans recorded at least 3 hr apart. Accuracy for all space use estimates was assumed to be 50-100 m, given the average grid cell size on the Waibira grid system (See Chapter 2). Nearest neighbour analysis (Clark & Evans, 1954) compared the mean distance between FKD range centres, as those depend on utilisation density rather than the geometric centre of the range as opposed to MCP range centres. Overlap percentage was calculated separately for each type of individual range for each female, once for general ranging, once for wet season ranging, and once for dry season ranging, and was defined as the mean of her dyadic overlap percentages with all other females. To investigate how range centre spacing impacts the overlap of 50% FKD core areas, I use an independent samples t-test to compare the dyadic overlap scores between dyads within the same range centre cluster (‘neighbourhood’) and those in different clusters.

To assess concordance between the two different range estimation methods I used (Boyle et al., 2008), I ran Pearson correlations between MCP and FKD general home range, 80%, and 50% core area sizes. MCP and FKD home range sizes were only moderately correlated, while core area sizes were strongly correlated between the two methods. As a result, I included both MCP and FKD home range sizes as dependent variables in subsequent models, but only FKD core area sizes. The impacts of *season* and *rank* on the extent and spacing of female individual ranges were investigated with linear mixed effect models (LMEs) using *lme4* (Bates et al., 2015). Dependent variables were FKD home range size, MCP home range size, 80% FKD core area size, 50% FKD core area size, FKD home range overlap, 80% FKD core area overlap, and 50% FKD core area overlap. Fixed variables were *season* (*wet*, *dry*) and *rank* (*low*, *mid-low*, *mid*, *high*), and *identity* (N = 16) was set as random factor. Model selection included checking that none of the fixed variables were correlated ($r > 0.5$), then setting up a model including all factors, a null model including only the random factor, and all other possible candidate models, covering the full combination of fixed factors (Thomas et al., 2017; Zuur et al., 2009). Candidate models were then evaluated based on Akaike Information Scores (AIC) and weighted AIC (wAIC) (Wagenmakers & Farrell, 2004) with the *bblme* package (Bolker & R Development Core Team, 2023). Models within 2 ΔAIC of each other were averaged using the *MuMIn* package (Bartoń, 2023). Exact tests of goodness-of-fit were used to see if female 80% and 50% FKD core areas are more likely to include the central waterhole during the *wet* and *dry season*.

To analyse within-season and between-individual changes in the use of the central waterhole, I have used LMEs or Generalised Linear Models (GLM) and Generalised Linear Mixed Models (GLMM) with a Poisson distribution with the R package *lme4* (Bates et al., 2015). Model type was decided based on the distribution

of the dependent variable and any issues with model singularity, following suggestions by Bolker et al. (2009). *Mean on-screen duration* was log transformed to achieve normal distribution, while *dry season day number* was z-transformed for easier interpretability. The model for *mean on-screen duration* was a LME, with *age* (*subadult*, *adult*), *reproductive status* (*without swelling*, *with swelling*, *young infant*, *old infant*), *rank* (*high*, *mid*, *mid-low*, *low*, *unknown*), and *dry season day number* as the fixed factors, and individual *identity* (*N* = 40) as random factor. The model for *visitation count* was a GLM, including only the fixed factors, while the model for *number of days elapsed* was a GLMM, including both the fixed factors and the random factor of identity. Model selection procedure was the same as for models of seasonal and monthly ranging.

Results

General Space Use

Mean individual home range size was 8.3 $km^2 \pm 1.0$ when calculated with MCP, and 7.4 $km^2 \pm 0.6$ when calculated with FKD (Table 13). Both 80% and 50% core areas were smaller than home ranges, with a mean 80% core area size of 4.0 $km^2 \pm 0.5$ for MCP and 4.6 $km^2 \pm 0.4$ for FKD, and a mean 50% core area size of 1.7 $km^2 \pm 0.4$ for MCP and 2.6 $km^2 \pm 0.5$ for FKD (Table 13). The different space use estimation methods yielded different values for the same individual: for home ranges, there was only a moderate correlation between area estimates by MCP and FKD (Pearson's correlation: $R_{(20)} = 0.34$, p = NS). However, core area estimates both at 80% (Pearson's correlation: $R_{(20)} = 0.81$, $p < 0.001$) and 50% (Pearson's correlation: $R_{(20)} = 0.75$, $p < 0.001$) were strongly correlated between the two methods, suggesting that while exact values might differ, detected trends are consistent between them.

Table 13

Descriptive Statistics of Home Range and Core Area Characteristics

Range type	Mean size ± SD (Range)	Mean overlap ± SD (Range)
MCP home range	8.3 ± 1.0 (6.1-9.6)	85.3 ± 4.2 (78.8-93.4)
FKD home range	7.4 ± 0.6 (6.0-8.5)	86.6 ± 3.5 (71.2-86.8)
MCP 80% core area	4.0 ± 0.5 (3.2-4.9)	72.6 ± 5.6 (62.8-84.0)
FKD 80% core area	4.6 ± 0.4 (4.1-5.5)	81.4 ± 4.1 (71.2-86.8)
MCP 50% core area	1.7 ± 0.4 (1.0-2.5)	42.9 ± 3.5 (29.5-54.9)
FKD 50% core area	2.6 ± 0.5 (1.8-3.9)	61.7 ± 6.0 (47.2-69.5)

Note. Home range and core area sizes are in km^2, while dyadic overlap is in percentages. Home range areas were calculated using MCP and FKD including all first sightings, while individual core areas captured the smallest area containing 80% and 50% of all first sightings.

Community home range size was estimated to be 11.2 km^2. The females of the Waibira community range broadly, utilising a large part, 73.9% ± 8.7, of the of the community home range, with almost all of their activity taking place within it: all MCP home ranges were fully contained by the community home range, except for *Jinja* and *Ketie* whose home ranges slightly extended outside the northern edge of it, and *Onyofi*, whose home range slightly extended outside the eastern edge (Figure 9). While several FKD individual home ranges were also slightly outside the boundaries of the community home range (Figure 9), it is likely due to the different boundary estimations of the two methods (Boyle et al., 2008; Worton, 1989). As a result of their broad ranging, the home ranges of the Waibira females show a high degree of dyadic overlap (85.3% ± 4.2 for MCP, 86.6% ± 3.5 for FKD, Table 13, Figure 9).

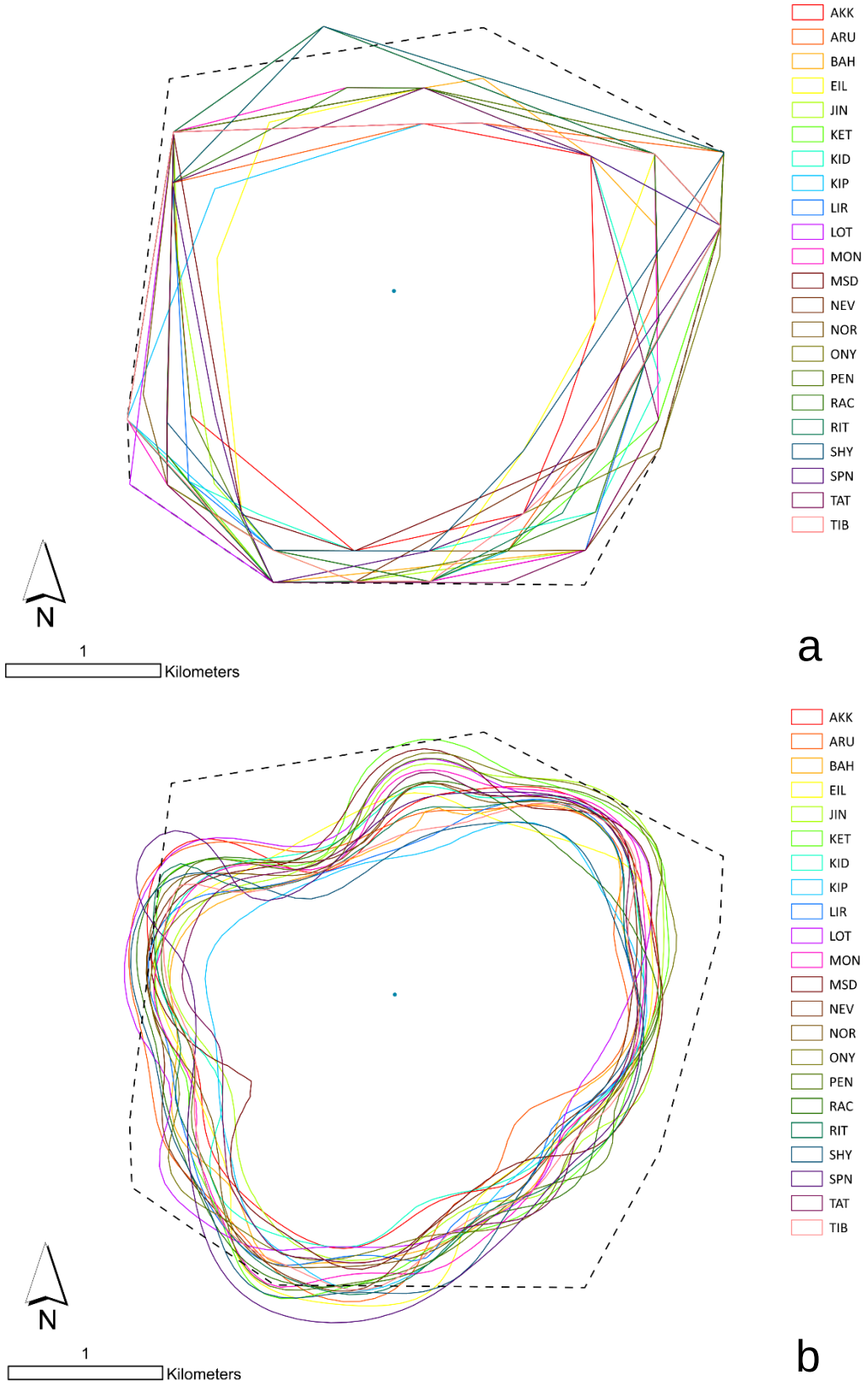


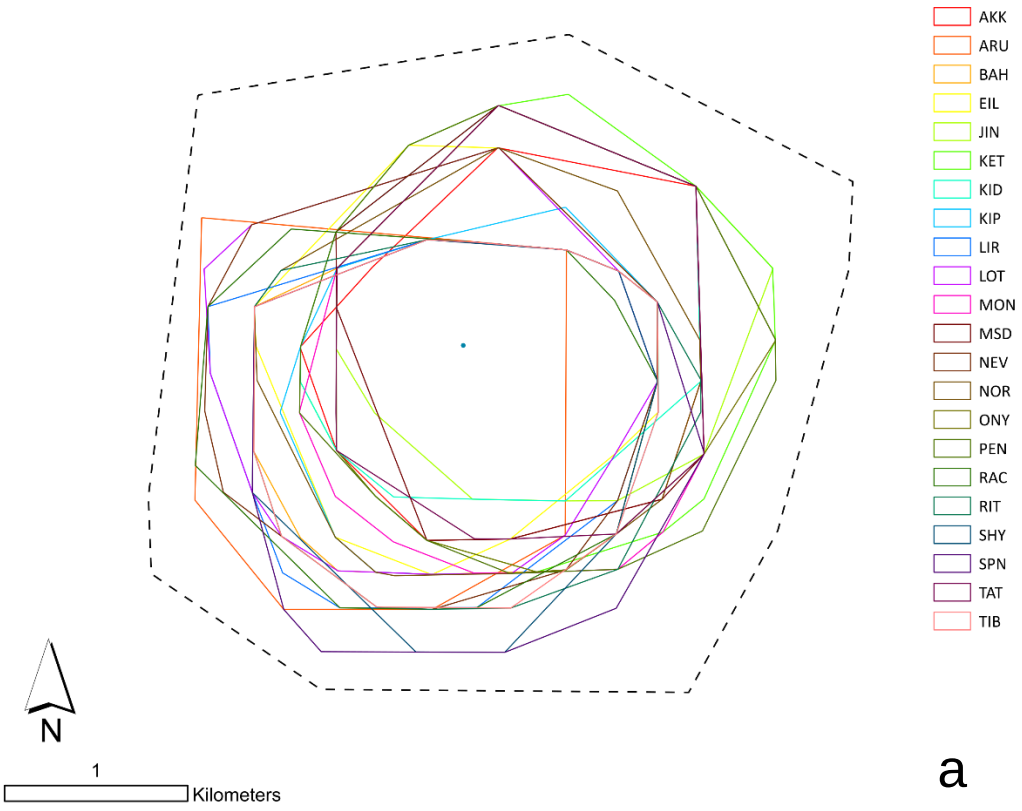
Figure 9

MCP Community Home Range and MCP and FKD Individual Home Ranges

Note. Community home range is outlined in dashed grey, while individual home ranges are outlined in colour. The blue dot marks the central waterhole.

[a] Individual home ranges calculated with MCP. [b] Individual home ranges calculated with FKD.

The core areas of the Waibira females were located fully within the community home range, except for *Spini*'s 80% FKD core area, which extended slightly outside the southern edge of it (Figure 10). While the females do traverse the majority of the community home range, resulting in large individual home ranges, regular activity, at 80% and 50% of all fixes, is concentrated in increasingly smaller areas, encompassing on average 35.4% ± 4.2 and 15.1% ± 3.3 of the community home range respectively. However, mean dyadic overlap is still high (72.6% ± 5.6 for MCP 80%, 81.6% ± 4.1 for KFD 80%, 42.9% ± 7.8 for MCP 50%, and 61.7% ± 6.0 for FKD 50%, Table 13, Figure 10), with core areas concentrated in the more central areas of the community of home range (Figure 10). The females of the Waibira community do restrict their primary ranging to a smaller area within the community home range, however, the use of their core areas is not exclusive, and core area structure is characterised by high interindividual overlap and low activity in the peripheral areas.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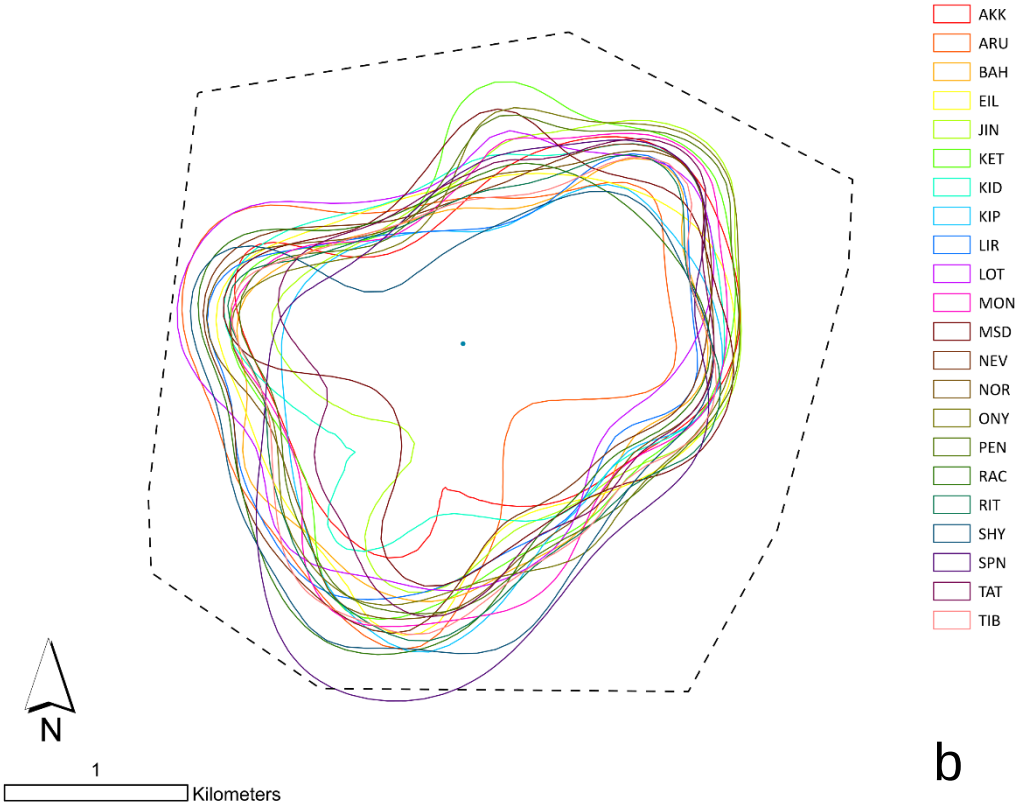
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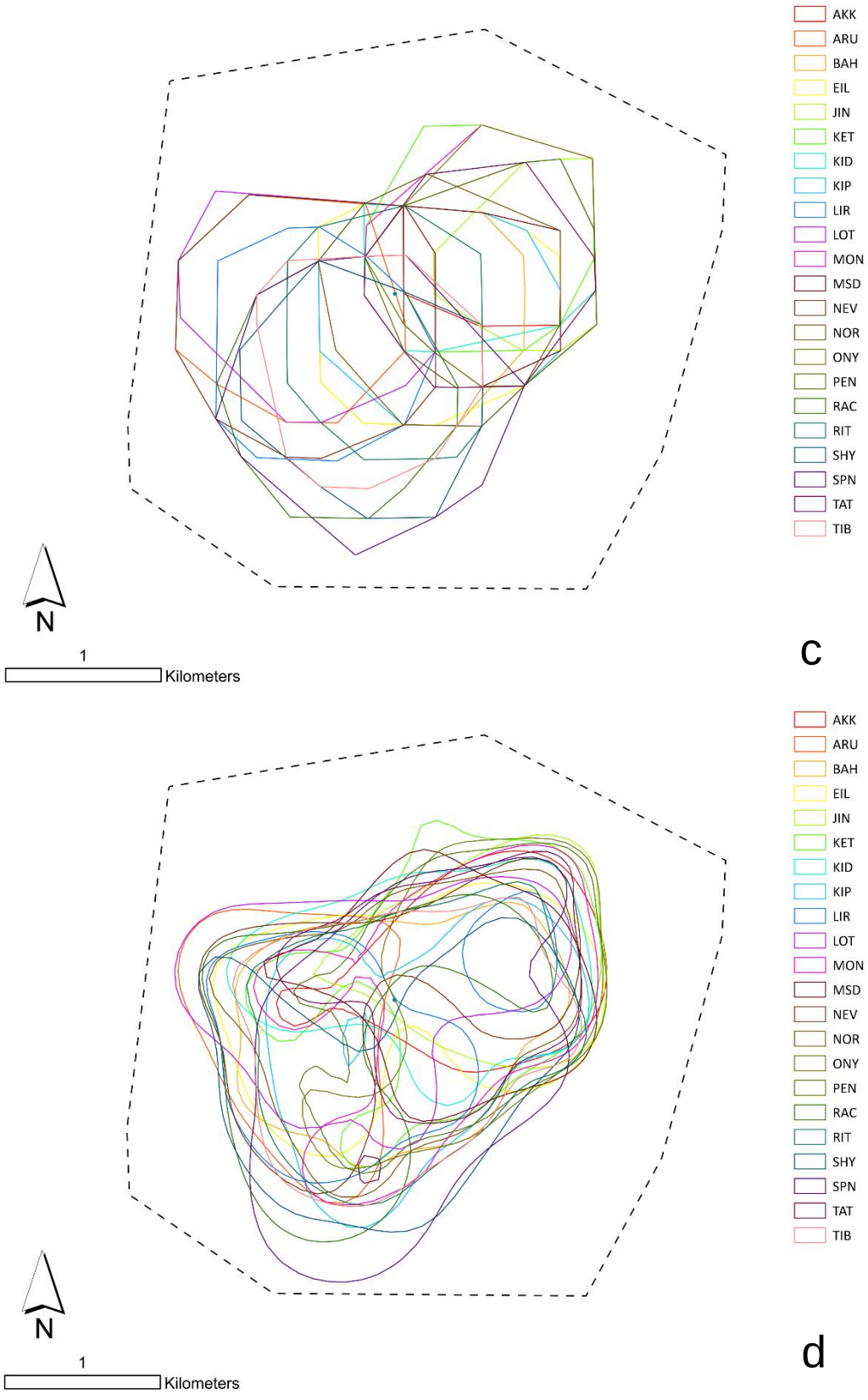


Figure 10

MCP Community Home Range and MCP and FKD 80% and 50% Individual Core Areas

Note. Community home range is outlined in dashed grey, while individual home ranges are outlined in colour. The blue dot marks the central waterhole.

[a] Individual 80% core areas calculated with MCP. [b] Individual 80% core areas calculated with FKD. [c] Individual 50% core areas calculated with MCP. [d] Individual 50% core areas calculated with FKD.

The location of FKD range centres also supports that the Waibira females predominantly use the central areas of the community home range, with the spacing of them significantly different from random (nearest neighbour analysis: $R = 0.35$, $p < 0.001$, Figure 11). Within the centre of the community home range, female range centres also form four loose 'neighbourhoods' to the south, centre, north, and west. The 50% core areas of females within the same neighbourhood overlapped more with each other (76.9% ± 11.6) compared to females not in the same neighbourhood (59.4% ± 17.4, independent samples t-test: t (396.84) = 12.63, $p < 0.001$). *Rank* was a strong predictor of neighbourhood residence (*Cramer's V* = 0.29), with no *low-ranking* females in the west, and no *high-* or *mid-ranking* females in the south.

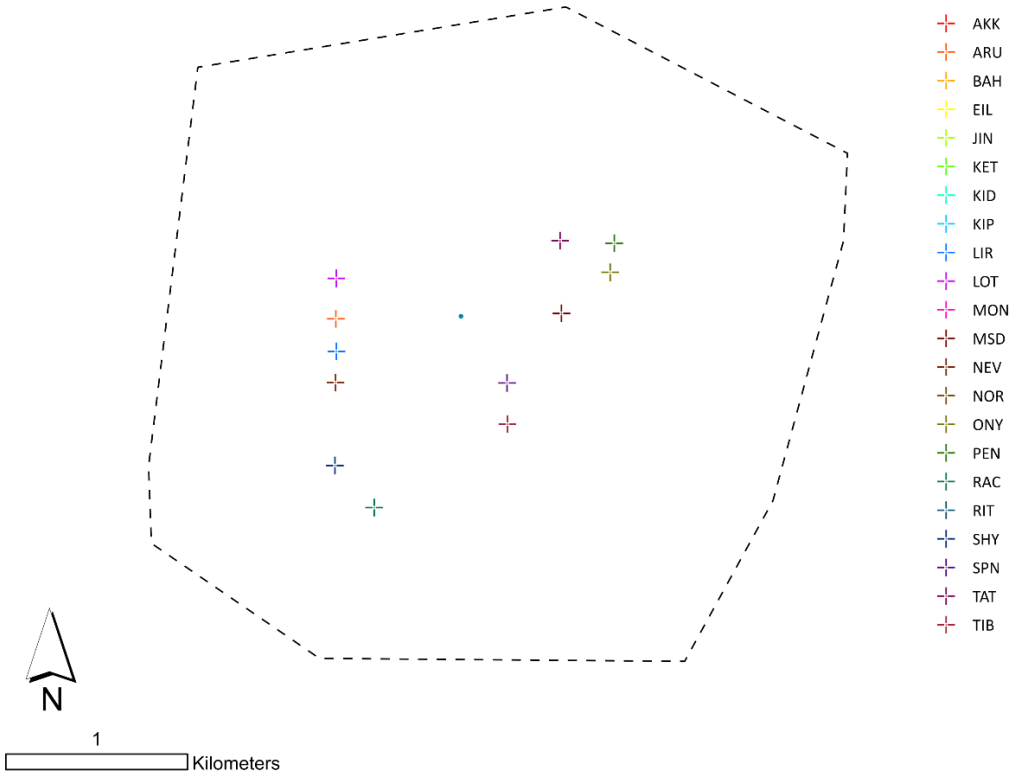


Figure 11

Individual FKD Range Centres Within the MCP Community Home Range

Note. Community home range is outlined in dashed grey. The central waterhole is marked by a blue dot. Range centres are indicated by + marks.

Seasonal Space Use

Mean home range sizes were larger in the *wet season* (MCP: 8.0 km^2 ± 0.8, FKD: 7.3 km^2 ± 0.8) compared to the *dry season* (MCP: 6.8 km^2 ± 0.5, FKD: 7.1 km^2 ± 0.5, Table 14). While the size of 80% core areas were relatively similar between seasons (MCP_{wet}: 3.8 km^2 ± 0.5, MCP_{dry}: 3.8 km^2 ± 0.4, FKD_{wet}: 4.4 km^2 ± 0.5, FKD_{dry}: 4.6 km^2 ± 0.3, Table 14), mean FKD 50% core area size was smaller in the *wet season* (2.2 km^2 ± 0.4) than in the *dry season* (2.7 km^2 ± 0.4, Table 14).

Table 14

Descriptive Statistics of Home Range and Core Area Sizes Across Seasons

Range type	Mean Wet season size ± SD (Range)	Mean Dry season size ± SD (Range)
MCP home range	8.0 ± 0.8 (6.5-9.3)	6.8 ± 0.5 (5.6-7.4)
FKD home range	7.3 ± 0.8 (5.8-8.6)	7.1 ± 0.5 (5.8-7.7)
MCP 80% core area	3.8 ± 0.5 (3.0-4.6)	3.8 ± 0.4 (3.1-4.3)
FKD 80% core area	4.4 ± 0.5 (3.5-5.0)	4.6 ± 0.3 (4.0-5.0)
MCP 50% core area	1.5 ± 0.4 (0.9-2.4)	1.7 ± 0.3 (1.1-2.0)
FKD 50% core area	2.2 ± 0.4 (1.6-2.9)	2.7 ± 0.4 (1.9-3.2)

Note. Home range and core area sizes are in km^2. Individual home ranges were calculated with MCP and FKD including all first sightings for a given season, while individual core areas captured the smallest area containing 80% and 50% of all first sightings for a given season.

Overlap between home ranges remained consistent across seasons (MCP_{wet}: 83.5% ± 3.7, MCP_{dry}: 84.2% ± 2.9, FKD_{wet}: 83.3 % ± 4.5, FKD_{dry}: 86.3% ± 3.0, Table 15), but increased in the *dry season* across all core area sizes (Table 15).

Table 15

Descriptive Statistics of Home Range and Core Area Overlaps Across Seasons

Range type	Mean Wet season overlap ± SD (Range)	Mean Dry season overlap ± SD (Range)
MCP home range	83.5 ± 3.7 (77.3-89.0)	84.2 ± 2.9 (80.1-90.3)
FKD home range	83.3 ± 4.5 (76.1-90.2)	86.3 ± 3.0 (81.8-92.1)
MCP 80% core area	67.8 ± 6.6 (58.6-80.6)	79.5 ± 3.2 (75.5-87.2)
FKD 80% core area	75.3 ± 4.5 (68.8-81.5)	83.4 ± 2.9 (77.4-87.8)
MCP 50% core area	37.1 ± 5.5 (27.9-46.6)	51.3 ± 9.5 (35.1-62.2)
FKD 50% core area	50.1 ± 5.3 (36.3-56.9)	73.0 ± 3.2 (65.9-76.9)

Note. Dyadic overlaps are in percentage. Individual home ranges were calculated with MCP and FKD including all first sightings for a given season, while individual core areas captured the smallest area containing 80% and 50% of all first sightings for a given season.

Models of range sizes and overlaps with $AIC_w \geq 0.01$ are summarised in Table 16. Two models were chosen then averaged for FKD and MCP home range size ($\Delta AIC \leq 2$, $w_i \geq 0.27$, Table 16): the null model and the model with only *rank* as a fixed factor for FKD home range size, averaged to include *rank* as a fixed factor, and a model with *season* and one with *season* and *rank* as fixed factors averaged to include *rank* and *season* as fixed factors for MCP home range size. One model was chosen for each core area size and measure of overlap respectively ($w_i \geq 0.76$, Table 16): the null model for 80% FKD core area size, a model with *season* as a fixed factor for 50% FKD core area size, and models with *season* and *rank* as fixed factors for all three measures of overlap. Model parameters for averaged and top models are shown in Table 17.

Table 16

Summary of Candidate Models of Seasonal Space Use Change With AIC Weights ≥ .01

Model	K[1]	AIC[2]	ΔAIC	w_i[3]
FKD home range size				
Null model	3	61.1	0.0	0.67
Rank	6	62.9	1.8	0.28
Season + Rank	7	66.3	5.2	0.05
MCP home range size				
Season	4	71.2	0.0	0.73
Season + Rank	7	73.2	2.0	0.27
FKD 80% core area size				
Null model	3	38.6	0.0	0.76
FKD 50% core area size				
Season	4	40.2	0.0	0.98
Null model	3	49.4	9.1	0.01
Season + Rank	7	50.7	10.5	0.01
FKD home range overlap				
Season + Rank	7	162.5	0.0	0.98
Rank	6	170.7	8.2	0.02
FKD 80% core area overlap				
Season + Rank	7	162.9	0.0	1
FKD 50% core area overlap				
Season + Rank	7	175.2	0.0	0.96
Sason	4	181.4	6.1	0.05

Note. Dependent variables for each model are **bolded.** Candidate model structure is listed underneath each dependent variable. All models are LME models.

[1] Number of parameters. [2] Akaike Information Criterion. [3] AIC weights.

Table 17

Model Parameters for Top and Averaged Models of Seasonal Space Use Change

Parameters	Coefficient	CI 95%	SE
FKD home range size			
Intercept	7.36	6.82-7.90	0.27
Mid rank	-0.92	-1.67- -0.16	0.38
Mid-low rank	-0.34	-1.10-0.41	0.37
Low rank	-0.03	-0.87-0.81	0.41
MCP home range size			
Intercept	7.00	6.22-7.77	0.39
Wet season	1.23	0.91-1.55	0.16
Mid rank	-0.92	-1.68- -0.17	0.37
Mid-low rank	-1.07	-1.83- -0.31	0.37
Low rank	-0.60	-1.45-0.25	0.41
FKD 80% core area size			
Intercept	4.49	4.29-4.70	0.10
FKD 50% core area size			
Intercept	2.74	2.56-2.92	0.09
Wet season	-0.53	-0.76- -0.29	0.16
FKD home range overlap			
Intercept	84.55	81.77-87.32	1.54
Wet season	-3.04	-4.74- -1.34	0.84
Mid rank	5.13	1.76-8.51	1.87
Mid-low rank	1.41	-1.97-4.78	1.87
Low rank	-1.50	-5.27-2.27	2.09
FKD 80% core area overlap			
Intercept	81.95	79.26-84. 63	1.49
Wet season	-8.10	-9.88- -6.32	0.88
Mid rank	4.65	1.41-7.90	1.80

Mid-low rank	1.31	-1.94-4.56	1.80
Low rank	-1.97	-5.60-1.66	2.01
FKD 50% core area overlap			
Intercept	72.79	68.83-76.75	2.20
Wet season	-22.88	-24.81- -20.95	0.96
Mid rank	2.42	-2.47-7.32	2.71
Mid-low rank	0.26	-4.63-5.16	2.71
Low rank	-3.43	-8.90-2.05	3.03

Note. All models are LME models. Factors included are *season* and *rank*. Baseline value for *season* is *dry*, and *high* for *rank*.

Overall, *season* was a predictor of changes in MCP home range size, 50% FKD core area size, and all measures of overlap. In the *dry season*, MCP home ranges were smaller: the extent of the female's general ranging was restricted compared to the *dry season* (Table 17, Figure 12). However, 50% FKD core area size increased, suggesting that while the maximum extent of their ranging is smaller in the *dry season*, they regularly utilise a larger subsection of their home range during it (Table 17, Figure 13). All measures of overlap also increased in the *dry season*, but especially between 50% core areas (Table 17, Figure 14). Together with smaller home range size and increased 50% core area size, it suggests that in the *dry season* the Waibira females restrict their general ranging to a specific area within the community home range, which they all utilise at a high frequency.

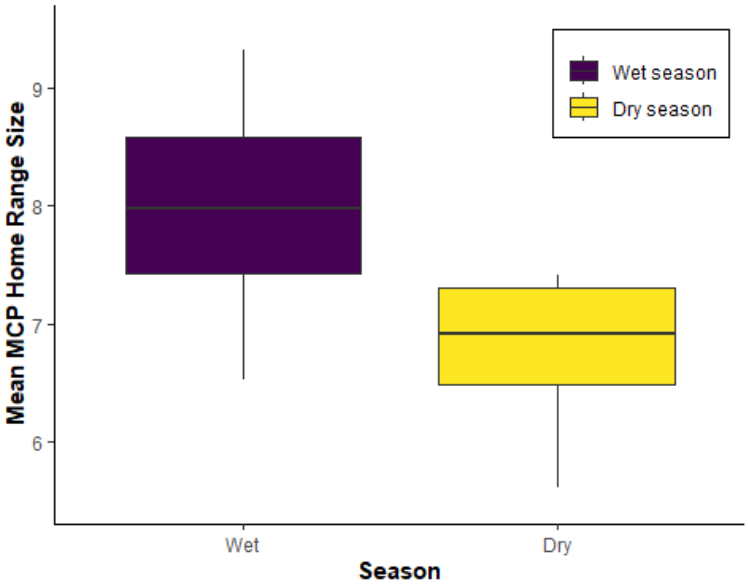


Figure 12

Mean MCP Home Range Sizes Across the Wet and Dry Seasons

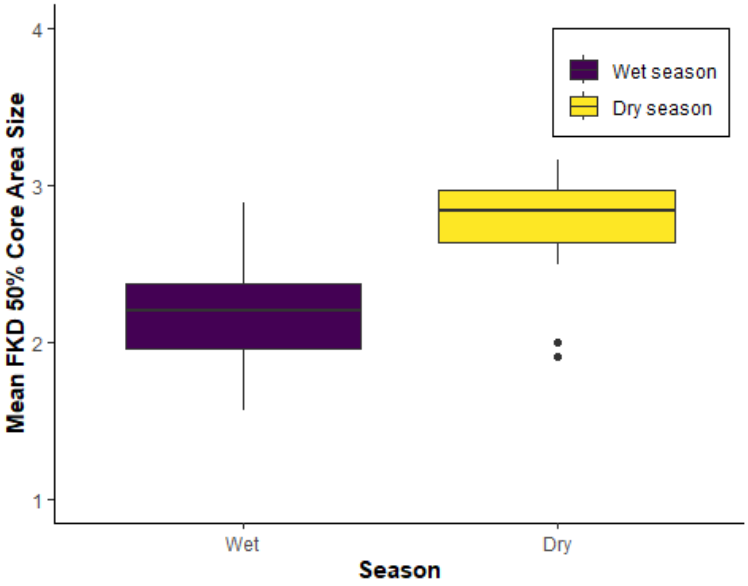


Figure 13

Mean FKD 50% Core Area Sizes Across the Wet and Dry Seasons

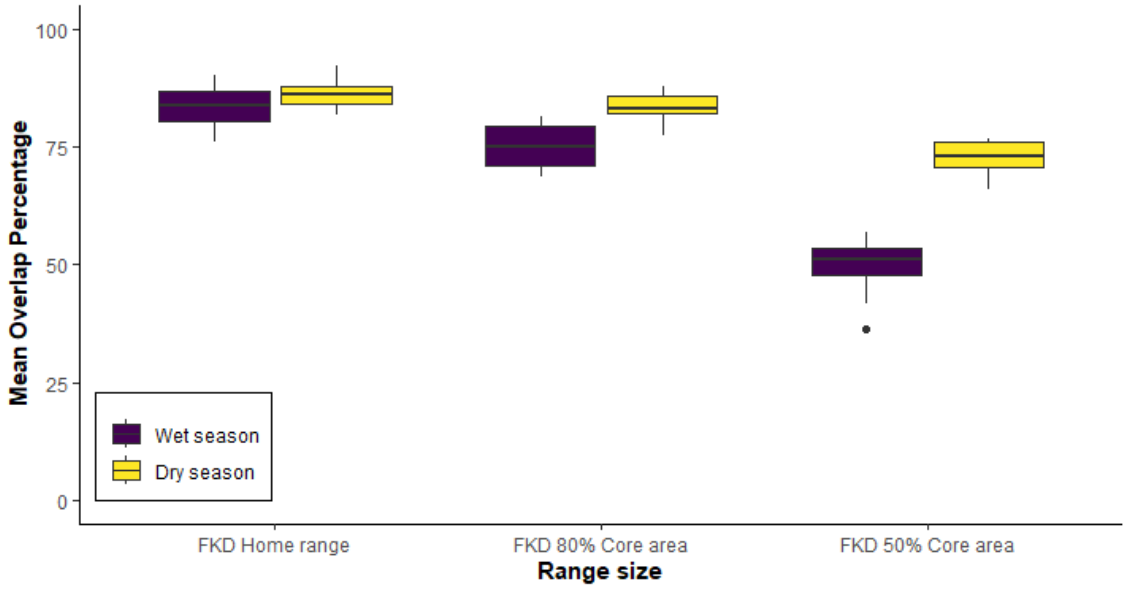


Figure 14

Mean Dyadic Space Use Overlap Percentage for FKD Home Ranges, 80%, and 50% Core Areas Across the Wet and Dry Seasons

Besides *season*, *rank* was also present as a predictor in some models. The *rank* of a female impacts the size of her home range, as well as how much her ranging at all levels overlaps with other females, with *mid-* and *mid-low-ranking* females generally ranging in smaller areas (Table 17, Figure 15) and *mid-ranking* females ranging more in areas shared with other females on the home range and 80% core area level (Table 17, Figure 16).

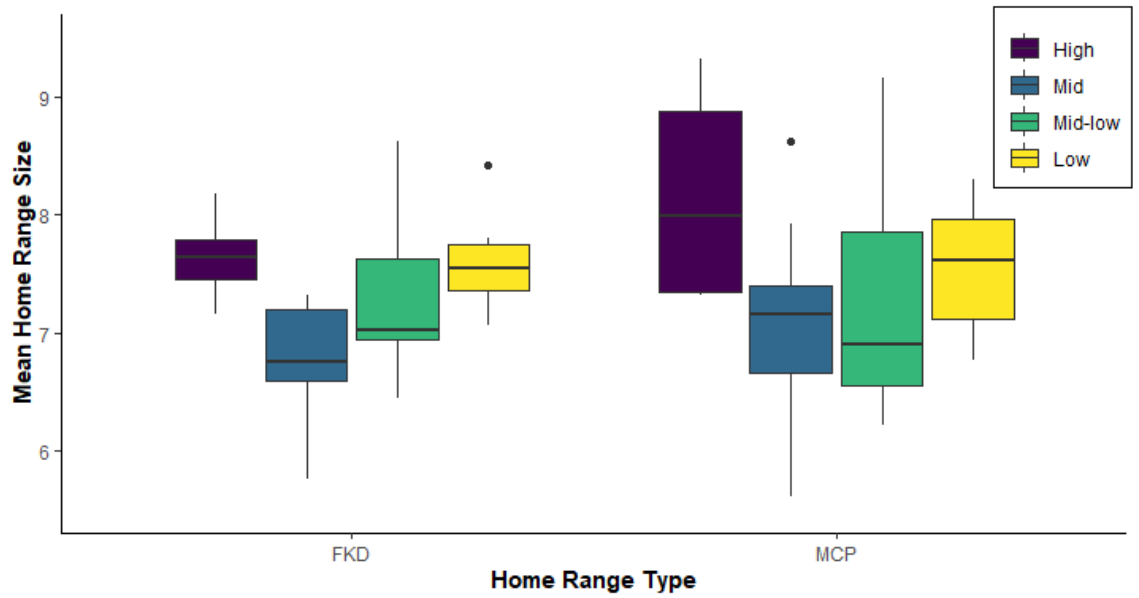


Figure 15

Mean FKD and MCP Home Range Sizes Across Rank Categories High, Mid, Mid-low, and Low

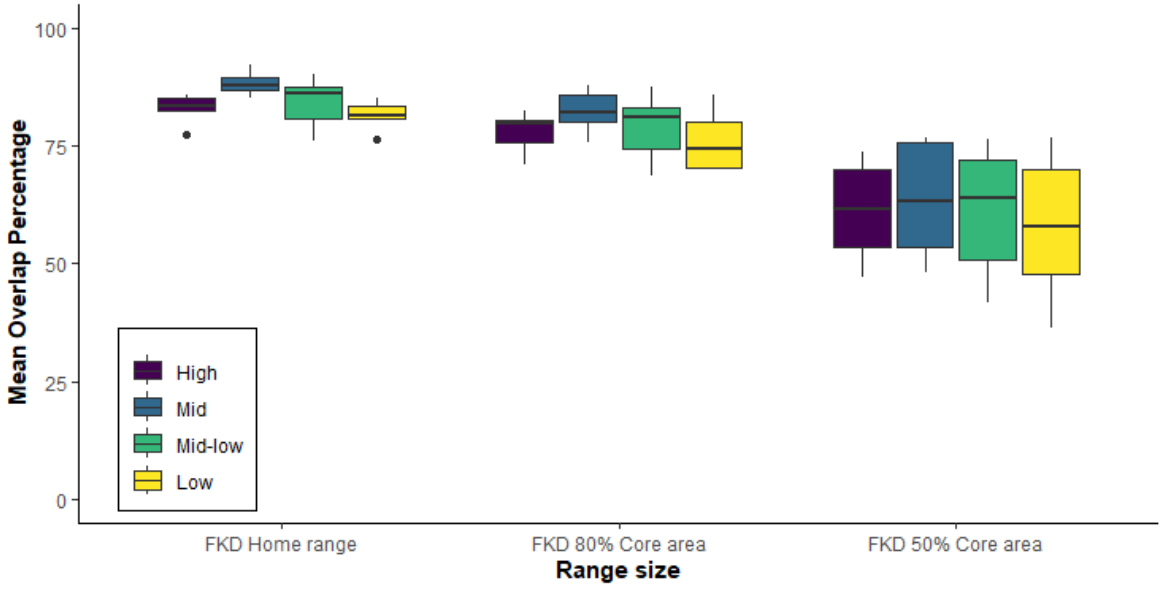
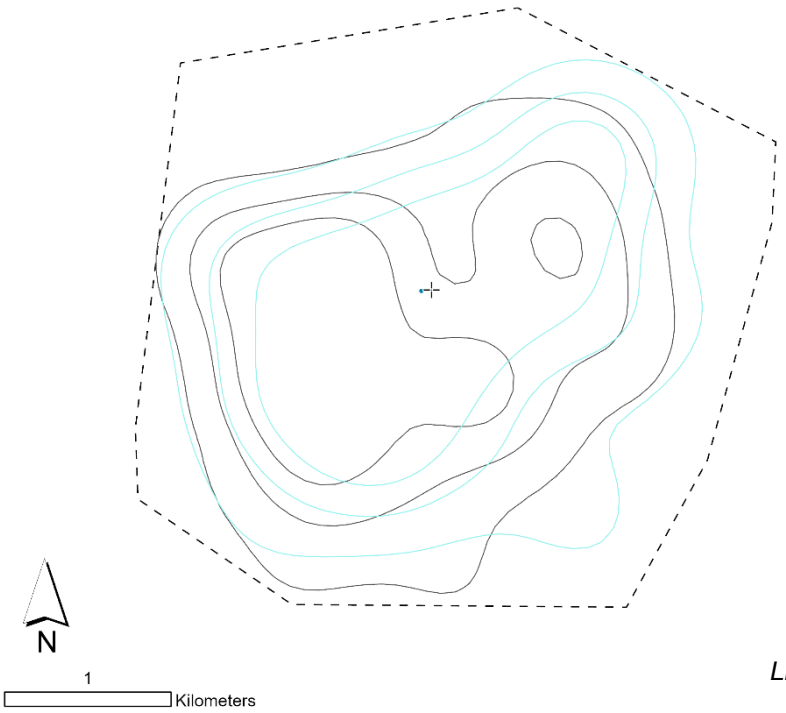


Figure 16

Mean Dyadic Space Use Overlap Percentage for FKD Home Ranges, 80%, and 50% Core Areas Across Rank Categories High, Mid, Mid-low, and Low

Stemming from 50% FKD core area sizes and spatial overlap between females increasing during the *dry season*, the overlap between the same female's *wet* and *dry season* 80% and 50% core area was not complete, especially for FKD

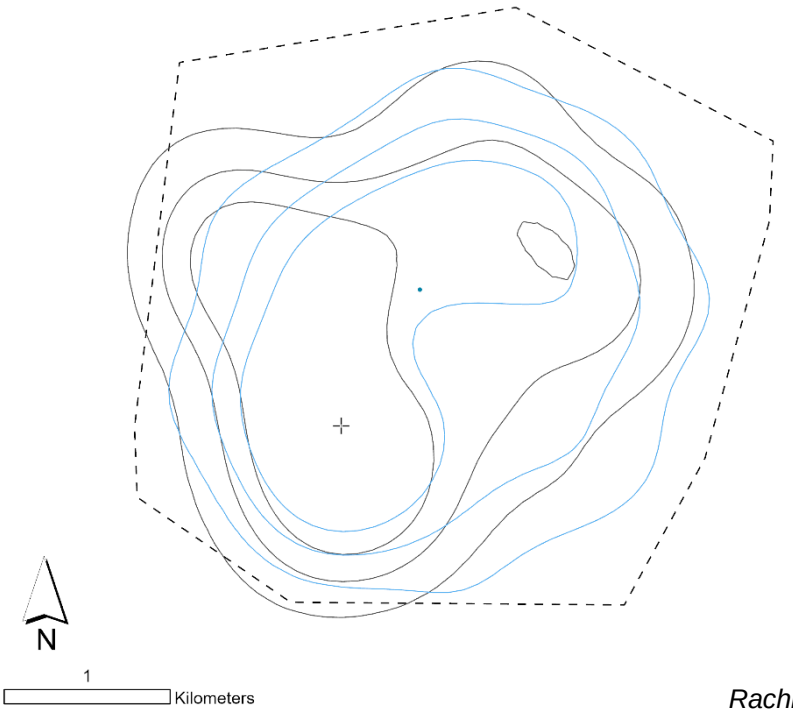
core areas (Figure 17). While their overlap with the central waterhole was variable during the *wet season*, all individual 50% FKD core areas shifted to include the central waterhole during the *dry season*. The inclusion of the waterhole in individual FKD 50% core areas did not differ from the expected 1:1 chance ratio during *wet seasons* (exact test of goodness-of-fit: expected: n_{yes} = 8, n_{no} = 8, observed: n_{yes} = 8, n_{no} = 8, *P* = NS), while it did during *dry seasons* (exact test of goodness-of-fit: expected: n_{yes} = 8, n_{no} = 8, n_{yes} = 16, n_{no} = 0, *P* = 0.001, Figure 18). The location of range centres also changes between seasons: the four neighbourhoods to the north, west, south, and centre are present during the *wet season*, but during the *dry season* shift into two lose clusters around the original north and south neighbourhoods, with one female, *Kipepeo,* remaining central (Figure 18). Several females also shift neighbourhoods: *Ndito-Eve* and *Arua,* originally in the west, *Onyofi,* originally in the north, and *Rita* and *Tibu,* originally central, are in the south cluster during the *dry season*, while central *Bahati* and western *Liran* and *Lottie* shift their range centres to the north. Together with the restricted general ranging and high interindividual overlap during the *dry season*, the inclusion of the central waterhole in the 50% core area of all females and the seasonal shift of range centres suggests that water availability, and specifically the dry season disappearance of alternative water sources like dendrotelmata (see Chapter 3), is a significant shaper of female ranging in the Waibira community, with females centring their space use around the remaining water source during the *dry season*.



Liran

Onyofi

Penelope



Rachna

Figure 17

Examples of Overlap of Wet and Dry Season FKD Home Ranges, 80%, and 50% Core Areas for Individual Females

Note: Wet season ranges are outlined in continuous grey, while *dry season* ranges are outlined in colour. The community home range is outlined in dashed grey. *Dry season* range centre is indicated by a + mark, while the central waterhole is marked with a blue dot. Female identity is indicated in the bottom left corner.

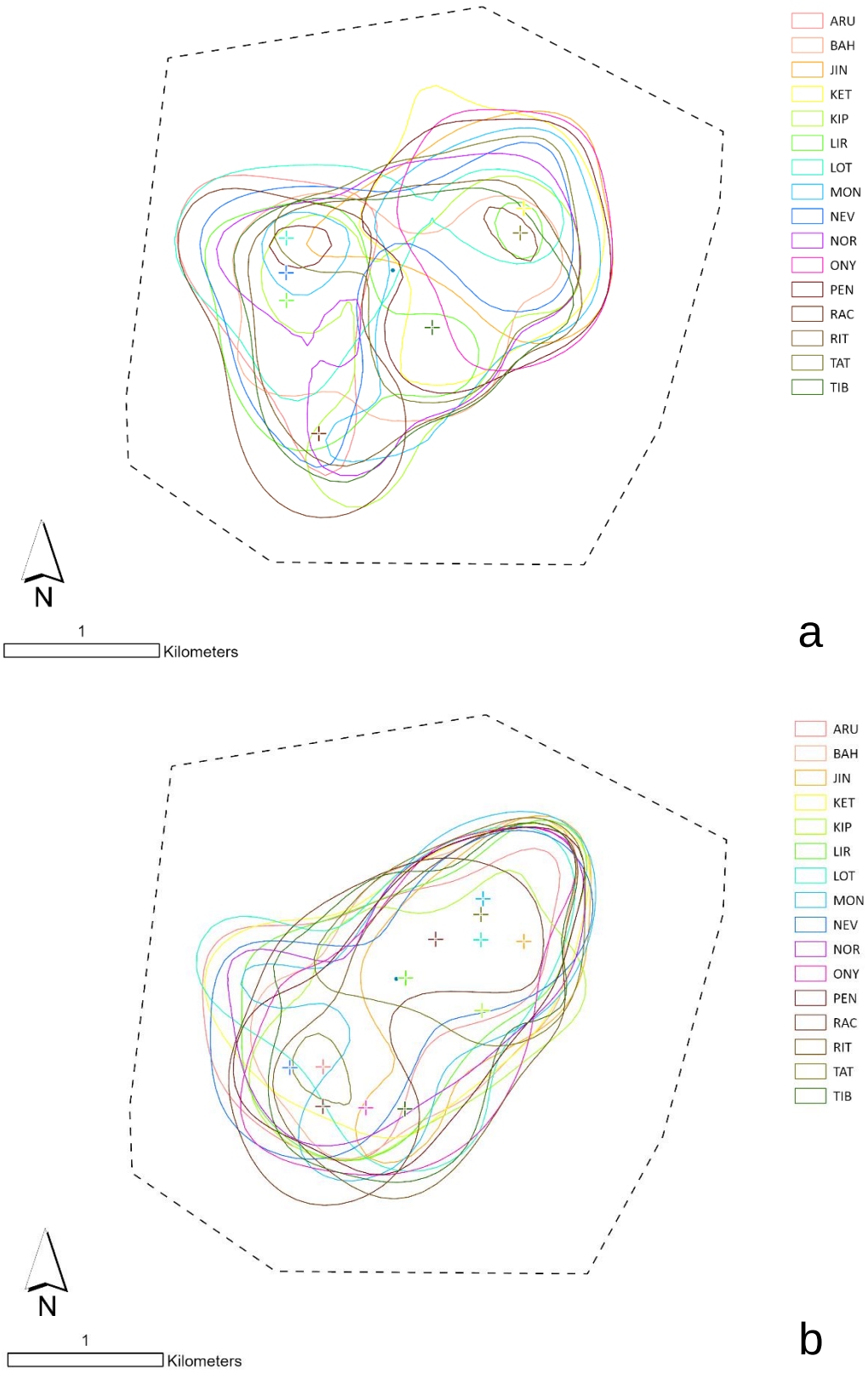


Figure 18

The Location of the Central Waterhole Relative to 50% FKD Core Areas and Range Centres in the Wet and Dry Season

Note: Range centres are indicated by a + mark. The central waterhole is indicated by a blue dot. The community home range is outlined in dashed grey. Outline and + mark colours correspond to female identity.

[a] *Wet season* 50% FKD core areas. [b] *Dry season* 50% FKD core areas.

Use of the Central Waterhole

Females were recorded visiting the central waterhole in the dry season every 5.6 days ± 6.8. On days they visited the waterhole, they made an average 1.4 ± 0.8 visitations, and spent 110.4 s ± 135.9 on-screen during each visit. Models of waterhole visitation with $AIC_w \geq 0.01$ are summarised in Table 18. Three models were chosen then averaged for *visitation count* ($\Delta AIC \leq 2$, $w_i \geq 0.16$, Table 18): one with *dry season day number* as fixed factor, one with *dry season day number* and *rank*, and one with *dry season day number* and *age*. Two models were averaged for *days since last visitation* ($\Delta AIC \leq 2$, $w_i \geq 0.27$, Table 18): one with *dry season day number*, *reproductive status* and *age* as fixed factors, and one with *dry season day number* and *age*. One model was selected for *mean on-screen duration* ($w_i \geq 0.86$, Table 18), including *dry season day number* as the only fixed factor. Model parameters for averaged and top models are shown in Table 19.

Table 18

Summary of Candidate Models of Waterhole Visitation With AIC Weights ≥ .01

Model	K [1]	AIC [2]	ΔAIC	w_i [3]
Mean on-screen time [4]				
Dry day	4	5063.6	0.0	0.86
Dry day + Age	5	5067.3	3.7	0.13
Dry day + Reproductive status	7	5073.4	9.8	0.01
Visitation count [5]				
Dry day	2	3671.4	0.0	0.42
Dry day + Reproductive status	5	3672.5	1.1	0.24
Dry day + Age	3	3673.3	1.9	0.16
Dry day + Reproductive status + Age	6	3674.2	2.8	0.10
Dry day + Rank	6	3676.8	5.4	0.03
Dry day + Reproductive status + Rank	9	3677.8	6.4	0.02
Dry day + Rank + Age	7	3678.7	7.4	0.01
Dry day + Reproductive status + Rank + Age	10	3679.6	8.2	0.01
Number of days elapsed [6]				
Dry day + Reproductive status + Age	7	10362.6	0.0	0.68
Reproductive status + Age	6	10364.5	1.9	0.27
Dry day + Reproductive status + Rank + Age	11	10368.4	5.9	0.04
Reproductive status + Rank + Age	10	10370.2	7.6	0.02

[1] Number of parameters. [2] Akaike Information Criterion. [3] AIC weights. [4] LME. [5] GLM. [6] GLMM.

Table 19

Model Parameters for Top and Averaged Models of Waterhole Visitation

Parameters	estimate	CI 95% [1]	SE [2]
Mean on-screen time [3]			
Intercept	4.00	3.91-4.08	0.04
Dry day	0.17	0.10-0.24	0.04
Visitation count [4]			
Intercept	0.30	0.20-0.40	0.05
Dry day	0.08	0.03-0.12	0.02
With swelling	0.07	-0.08-0.12	0.07
Young infant	0.14	-0.01-0.27	0.07
Old infant	0.03	-0.11-0.17	0.07
Subadult	0.03	-0.16-0.22	0.10
Number of days elapsed [5]			
Intercept	1.92	1.79-2.05	0.07
Dry day	0.03	0.01-0.05	0.01
With swelling	-0.18	-0.26- -0.10	0.04
Young infant	-0.16	-0.24- -0.08	0.04
Old infant	-0.24	-0.32- -0.16	0.04
Subadult	0.43	0.28-0.58	0.08

Note. Factors included are *reproductive status* and *age*. Baseline value for *reproductive status* is *without swelling*, and *adult* for *age*.

[1] 95% Confidence Interval. [2] Standard Error. [3] LME. [4] GLM. [5] GLMM.

Dry season day number was present as a predictor for all three measures of waterhole visitation – females made longer visitations to the central waterhole (Table 19, Figure 19), and more often within the same day as the dry season progressed

(Table 19, Figure 20). However, the *number of days elapsed* since their last visitation also increased with *dry season day number* (Table 19, Figure 21).

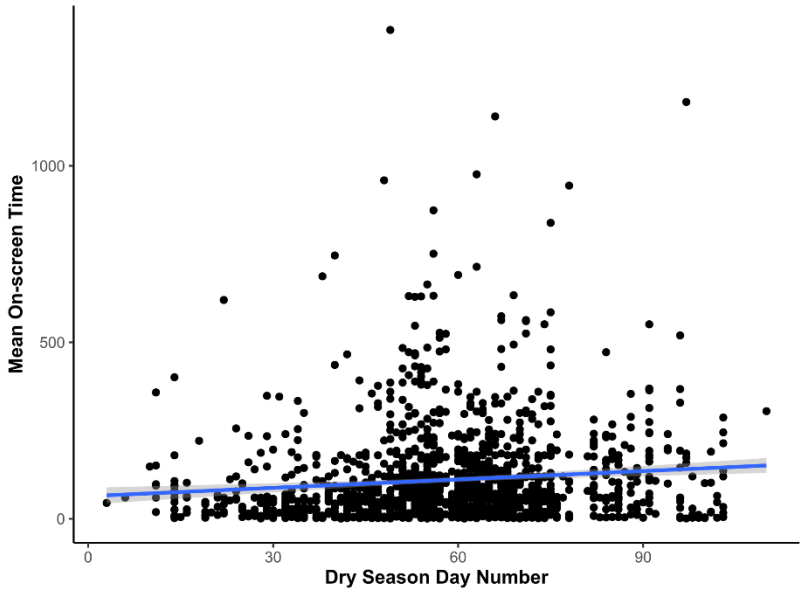


Figure 19

Mean On-Screen Time in Relation to Dry Season Day Number Throughout the Dry Season

Note. Mean on-screen time is in seconds.

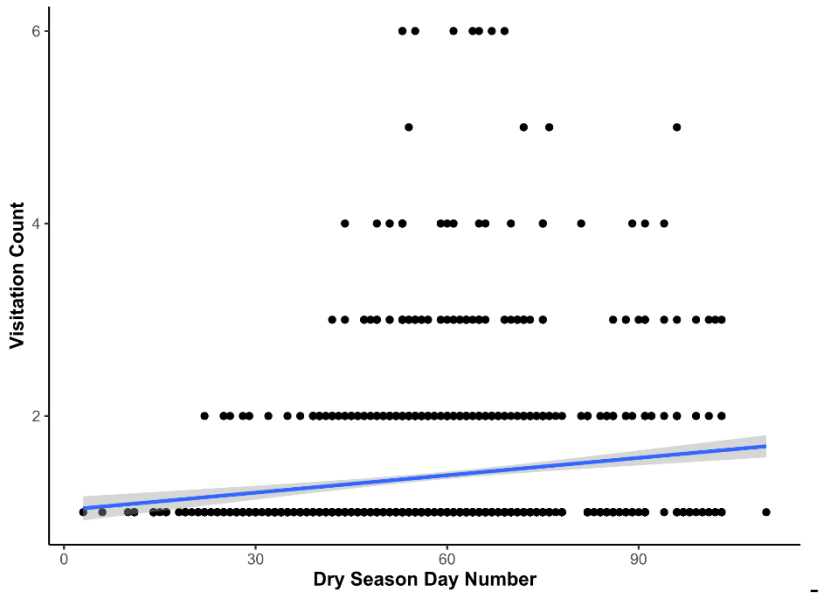


Figure 20

Visitation Count in Relation to Dry Season Day Number Throughout the Dry Season

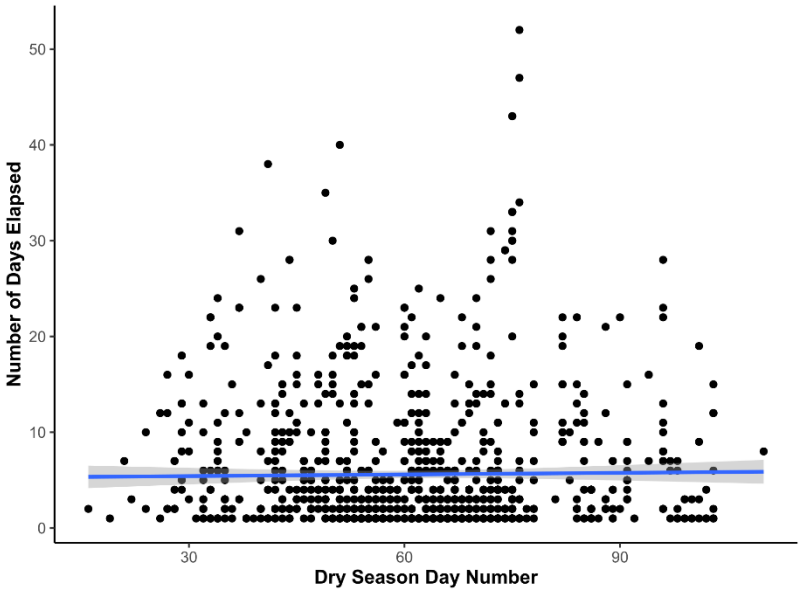


Figure 21

Number of Days Elapsed Shown in Relation to Dry Season Day Number Throghout the Dry Season

Age category and *reproductive status* were also present in models for *visitation count* and *number of days elapsed* (Table 19). *Visitation count* was slightly higher for females with *young infants* (Figure 22) and *subadult* females (Figure 23) compared to the other *reproductive status* and *age* categories, but 95% confidence intervals suggest a weak connection only (Table 19). Regarding *number of days elapsed*, females with *young* or *old infants* and females *with swellings* had fewer days between visitations compared to females *without swellings* (Figure 24, Table 19). *Subadult* females also went longer without visits to the waterhole compared to *adult* females (Figure 25, Table 19).

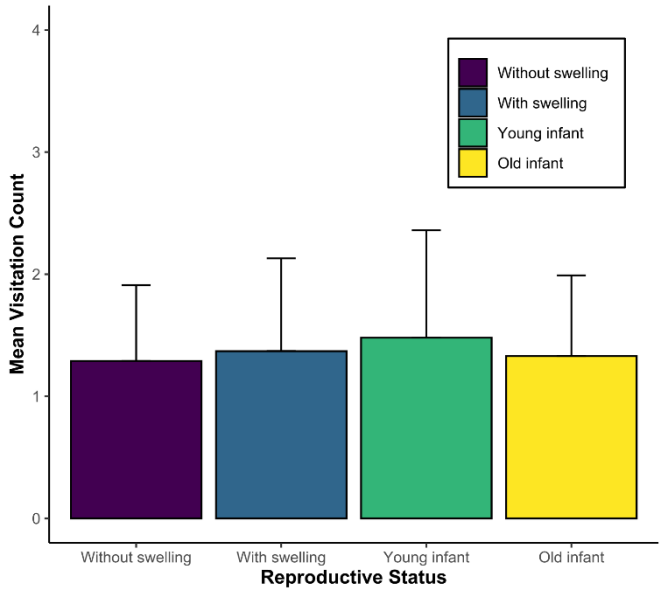


Figure 22

Mean Visitation Count Across Reproductive Status Categories Without Swelling, With Swelling, Young Infant, and Old Infant

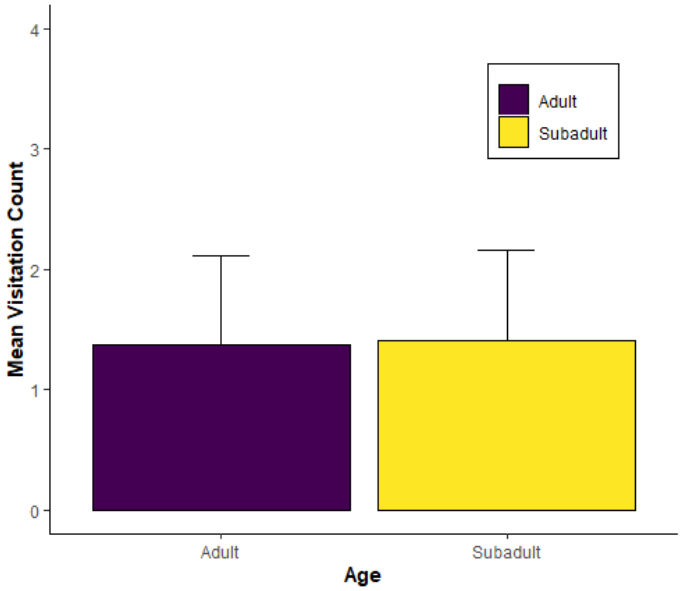


Figure 23

Mean Visitation Count Across Age Categories Adult and Subadult

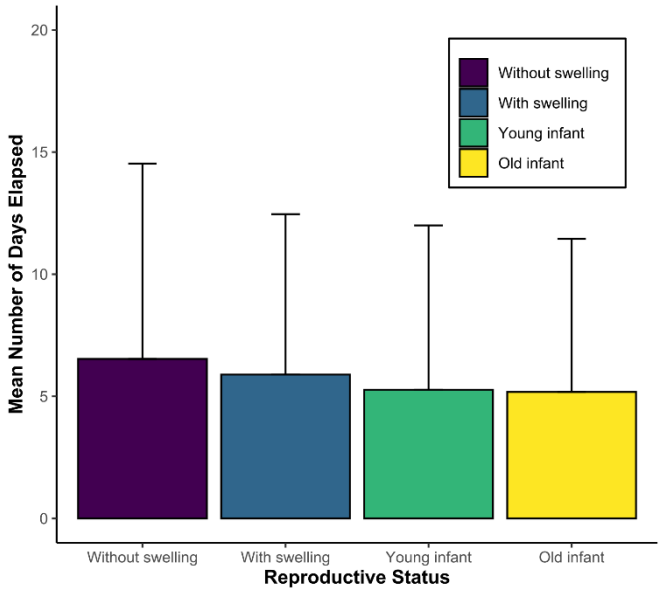


Figure 24

Mean Number of Days Elapsed Across Reproductive Status Categories Without Swelling, With Swelling, Young Infant, and Old Infant

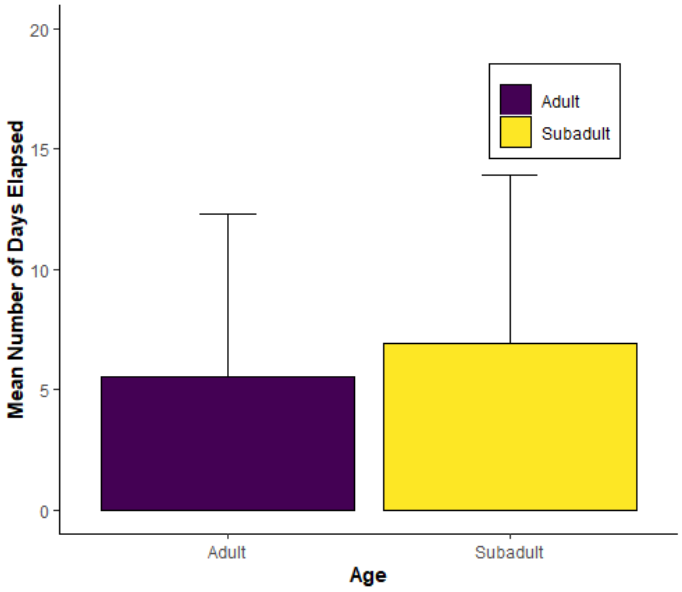


Figure 25

Mean Number of Days Elapsed Across Age Categories Adult and Subadult

Discussion

The space use of the female chimpanzees of the Waibira community is characterised by large home ranges, overlapping almost fully with each other and

the community home range, and core areas located at the more central areas of the community home range, away from peripheries shared with neighbouring communities. Core areas also have a high degree of overlap and are clustered into four subgroups or ‘neighbourhoods’ within which female core areas overlap even more. Range sizes and overlaps show seasonal variation between the wet and dry season, corresponding to changes in water availability. Home range size decreases, while core areas shift to include the central waterhole during the dry season, resulting in increasing overlap between individual home ranges and core areas and the temporary dissolution of two of the four neighbourhoods. Small scale space use patterns, at the level of individual use of the central waterhole, further support that the central waterhole is utilised at a high intensity during the dry season. As the dry season progresses, females visit the waterhole less frequently, but on the days they do so, they make longer, repeated visits to the waterhole, returning to it several times during the day. Patterns of seasonal ranging suggest that water is a resource that shapes female space use behaviour in the Waibira community of rainforest-dwelling chimpanzees, supporting its essential nature to chimpanzees and in mesic environments.

General Space Use

The females of the Waibira community use the entire community home range, and their individual home ranges have a high degree of dyadic overlap. Both 80% and 50% core areas also overlap with each other a lot – while the Waibira females have specific areas within their home range where they range preferentially, the use of those areas are not exclusive but shared between multiple females. This broad and highly overlapping ranging is similar to what has been found in two other rainforest-dwelling East African chimpanzee communities, the neighbouring Sonso community, and Ngogo in the Kibale National Park, Uganda (Wakefield, 2008, 2013),

and in the western chimpanzees of Taï (Lehmann & Boesch, 2005), also living in a rainforest, but does not reflect female ranging patterns in Gombe, Tanzania, a forest mosaic habitat (Murray et al., 2006; Williams et al., 2002a) and Kanyawara, also in the Kibale National Park (Kahlenberg et al., 2008a), characterised by more restricted ranging and distinct core areas with low overlap.

While female home ranges in the Waibira community do extend to the edges of the community home range, showing that females do visit the peripheral areas, core areas are all in the central areas of the community home range, with none of the females included in the current study preferentially ranging the peripheries. This is unlike the core area structure of females in Mahale (Uehara, 1981) and Gombe (Murray et al., 2006, 2007), where core areas were also located along the edges of the community home range, but similar to Kanyawara (Emery Thompson et al., 2007b) and Sonso (Fawcett, 2000). As preferences for central areas persist year-round, even when alternative arboreal and terrestrial water sources are available throughout the community range, the permanent central concentration of female core areas is not due to limitations posed by water availability. Instead, risk-driven avoidance is more likely, as the community is neighboured by other chimpanzee communities on all sides. While the Waibira community is relatively large, at ~120 individuals, and has a high fighting power with 19 adult males at the time of this study, females travelling alone or in smaller parties, whether all-female or mixed-sex, could be at risk of violent intercommunity encounters (Martínez-Íñigo et al., 2021; Watts et al., 2006). To date, no proven intercommunity killings of independent females occurred in the Waibira community, however, out of the 27 immatures who disappeared since 2011 while still dependent on their mother, two were killed by neighbouring chimpanzee communities. One of them, *Queen*'s unnamed first infant, was killed by the Sonso group during an intercommunity encounter, and another,

Nalala, Nora's juvenile son, was last seen during an intercommunity encounter with Sonso before his disappearance. In both cases, the Sonso community was involved, who have a smaller number of individuals and adult males than Waibira, showing that even neighbouring groups with a lower fighting power can pose a significant risk, especially to females with dependent offspring. It is likely that core area locations in the Waibira community are driven by avoidance of the areas of the community home range where intercommunity encounters can occur. However, females still occasionally range in the peripheral areas, evidenced by their large individual home ranges, including boundary patrols (pers. obs.), suggesting that the presence of several other individuals might mitigate the risk of intercommunity infanticides at least to some degree.

Female core areas in the Waibira community also showed selective overlap with some other females, and were organised into four neighbourhoods, similar to Ngogo (Wakefield, 2013), Kanyawara (Emery Thompson et al., 2007b), and Gombe (Williams et al., 2002a). The function of such clustering is debated, including lowering food competition while still remaining social with a select few individuals (Emery Thompson et al., 2007b; Williams et al., 2002a), and within-community infanticide protection via female-female coalitions (Wakefield, 2013) proposed as possible benefits. While overlap of 50% core areas was lower within the same neighbourhood, females in different neighbourhoods still overlapped considerably with each other (76.9% vs 59.4% mean overlap between dyads). If neighbourhood formation in the Waibira community functions as a way of lowering the number of competitors in the area to an optimum, a small degree of overlap decrease between neighbourhoods seems to be sufficient for it. Studies on the foraging decisions of the Waibira chimpanzees also suggest that the females of the group might not be particularly constrained by foraging optimisation due to a relatively abundant food

availability in the Budongo Forest compared to other long-term chimpanzee field sites (Villioth, 2018; Villioth et al., 2022, 2023), and the same might explain their highly overlapping core areas.

Coalition opportunities, specifically against within-community infanticide, could also benefit the females of the Waibira community and be facilitated by increased spatial overlap between specific females. Out of the 27 disappearances of dependent offspring, two, the unnamed first infant of *Monika*, and the unnamed third infant of *Elodie,* were observed to be due to male-led within-community infanticide, while one, the unnamed third infant of *Byazi,* was killed in a female-led infanticide by *Monika.* Records of those infanticide events as well as any attempted infanticides could be investigated to see if there were any interventions or intervention attempts from other females, and whether the targeted female and the intervenor(s) were from the same neighbourhood.

Regarding individual differences in the size and overlap of individual ranges, the females of the community likely pursue different strategies based on rank category. In other chimpanzee communities, high-ranking females either have smaller ranges compared to low-ranking ones, as they occupy areas with higher quality food and are able to meet their foraging needs in a smaller area, while low-ranking females forage in broader, less used areas to minimise feeding competition (Murray et al., 2006, 2007), or larger ones, due to participating in intercommunity encounters (Riedel et al., 2011) or having access to more feeding patches via contest competition (Fawcett, 2000). Curiously, both high- and low-ranking females had larger, less overlapping home ranges and core areas compared mid and mid-low-ranking ones in the Waibira community. As core areas do not extend into the peripheral areas, yet rank-related size differences were still present at core area level as well, it is unlikely the differences were driven by high-ranking females

participating in boundary patrols more often compared to mid- and mid-low-ranking females. Instead, it is possible that female space use patterns arise from a mixture of the strategies observed at other field sites: high-ranking females maintain larger, less overlapping core areas with good resource availability by winning contest competitions over lower ranking females more often which allows for them to maximise their foraging intake (Dunbar, 1988), while low-ranking females chose avoidance, and instead range broader in lower quality, less used areas and incur higher travel costs to reduce feeding competition (Murray et al., 2007). Mid- and mid-low-ranking females who are not able to ensure priority access to high quality areas instead range narrower, foraging in areas with a good enough resource availability that does not necessitate broad ranging and high travel costs low-ranking females face (Dunbar, 1988), but paying increased food competition costs compared to high-ranking females. The three high-ranking females of the community likely have an advantage in contest competitions: *Lottie* and *Monika* have a high rate of agonistic interactions (Chapter 5), with *Monika* being responsible for the community's only recorded female-led infanticide so far and *Lottie* even aggressing adult males on occasions, while both *Lottie* and *Rita* are large bodied for females. *Rita* also has an adult parous daughter, *Tibu* (Vigilant et al., unpublished BCFS data), who remained in the community and serves as a frequent coalition partner (pers. obs.).

While neighbourhood membership was somewhat correlated with rank category in the Waibira community, with the west having no low-ranking females and the south only low- and mid-low-ranking ones, and some neighbourhoods had more females than others, it is important to note that in the current study only 22 out of the 40 independent identified females of the community had enough fixes to allow for stable home range and core area estimates. As habituation progresses and more of those females will be habituated enough for focal follows, rank-neighbourhood

relationships might become more pronounced, and neighbourhoods that currently appear sparsely occupied might turn out to be equally utilised as the other ones.

In summary, the general space use patterns of the females in the Waibira community are characterized by broad general ranging, core areas within the centre of the community home range, and high interindividual overlap. They are likely shaped by the risk posed by other chimpanzee communities, leading to the avoidance of habitual ranging in the peripheral areas of the community home range, as well as the relatively abundant food availability of their habitat (Villioth, 2018), which allows for a high overlap between individual core areas (as seen in Taï (Lehmann & Boesch, 2005), Ngogo (Wakefield, 2013), and Sonso (Fawcett, 2000)), without females having to face a trade-off between reducing food competition or avoiding intercommunity encounters posing a risk to their dependent offspring. Rank-related variation is present in the size and overlap of individual ranges; the patterns of it correspond to female space use strategies used to navigate feeding competition documented at other field sites.

Seasonal Space Use

While the wet season space use patterns of the females of the Waibira community correspond to general, year-round ones, during the dry season the extent of the maximum ranging shrinks slightly, the overlap between individual ranges increases, and core areas shift to include the central waterhole. These space use changes correspond to a drastic drop in water availability in the community caused by the decrease in precipitation (Chapter 2, Appendix A) and the drying up of ephemeral terrestrial and all arboreal water sources (Chapter 3) during the dry season months. As food availability is similar between the seasons (FAI_{wet} = 21,560 ± 26,670, FAI_{dry} = 25,736 ± 24,954, Chapter 2), the chance of these seasonal changes being driven by it is also extremely low. Water is not only regularly

consumed by the rainforest chimpanzees of Waibira (Chapter 3), but the availability of it likely shapes female space use.

The size of female home ranges is slightly smaller in the dry season compared to the wet season. As maximum ranging has been documented to be constrained by distance from water sources in other species (eg. olive baboons: Barton et al., 1992; mountain sheep: Bleich et al., 2010; mule deer: Boroski & Mossman, 1996; African elephants: Purdon & van Aarde, 2017), being reliant on the central waterhole during dry season months could be the reason behind the slight restriction in home range sizes. In addition to balancing acquiring sufficient food while using the least amount of energy and staying safe, females in the dry season also would have to factor in regularly visiting the central waterhole to stay hydrated and avoid dehydration stress (Wessling et al., 2018a), potentially leading to shorter travel distances from it. To further unpick how chimpanzees balance energetic and hydration needs, future research could investigate their foraging decisions about visiting food patches and water sources during and outside periods of low water availability.

Core areas undergo more apparent seasonal changes: all 16 females included in seasonal space use analyses shifted their space use to include the central waterhole, when during the wet season, inclusion of it in their 50% core areas was at the level of chance. This pattern is similar to what has been found in other primate species, who centre their activity around water sources when experiencing water scarcity (red-fronted lemurs: Amoroso et al., 2020a; white-faced capuchins: Campos & Fedigan, 2009), and resulted in a higher degree of interindividual overlap during the dry season. Increased overlap between core areas then could lead to increased food competition during the dry season, simply by a higher number of females utilising the same areas. While the Waibira chimpanzees occasionally visit

the two peripheral waterholes in their community home ranges (pers. obs.; unpubl. data, BCFS), none of the females shifted their core areas to include either of those two waterholes, even if those were located within their individual home range. Extending camera trap monitoring to the peripheral waterhole in future projects could inform us about how different chimpanzee communities utilise shared waterpoints, high value resources with an extremely patchy distribution, with a specific focus on group dominance and temporal partitioning.

The observed seasonal space use patterns suggest that the Waibira females prioritised safety and energy-efficient access to water over minimising food competition during the dry season. Females structured their dry season core areas in a way that could ensure short travel distances to the single remaining safe water source, even if it increased food competition, instead of reducing food competition by only including the central waterhole in their 80% core areas or home ranges and travelling more to access it, or by including one of the peripheral waterholes shared with neighbouring communities in their core area. This high level of tolerance for shared space use during the dry season is likely enabled by the lack of food scarcity during the dry season in the community home range of the Waibira community, as opposed to other long-term field sites (Doran, 1997; Murray et al., 2007). While it is neither ethically nor logistically feasible to create a scenario where wild chimpanzees have to choose between prioritising access to food or water, the case of one of the Waibira females suffering a severe injury limiting her mobility during the dry season did create similar conditions. *Kidepo,* a female in her forties, severely injured, likely broke, one of her legs during the 2017-2018 dry season. Her travel speed and efficiency were reduced both on the ground and arboreally, and she also had a two-year-old dependent infant. Field staff reports *Kidepo* spending an increased amount of her time in the immediate vicinity of the central waterhole that dry season (G.

Atayo, R. Eguma, S. Mugisha, V. Kizza, pers. comm.), and while she lost a visible amount of weight, both she and her infant survived.

Besides a dry season increase in the overlap of 50% core areas and a restriction of broader ranging, females had increased 50% core area sizes in the dry season, suggesting their primary ranging covered a slightly larger area than in the dry season. Increasing core area size is theorised to aid with lowering food competition in Gombe (Murray et al., 2006). It could serve a similar function in the Waibira community as well, mitigating some of the increase in food competition potentially caused by clustering around the central waterhole, alongside the decrease in the number of social partners females were in close proximity with or groomed during the dry season (Chapter 5).

Finally, seasonal changes also occurred on the level of neighbourhoods. With shifting their core areas, females also shifted their range centres, resulting in the temporary disappearance of the west and central neighbourhoods. While due to the highly overlapping, central general ranging of the Waibira females none of them have to forage in completely unknown areas during the dry season, lowering foraging success, similar as with the increase of overlap between core areas, they are in a less efficient foraging scenario compared to the wet season. Whatever exact benefits neighbourhood formation carries for female chimpanzees, it seems that access to water is more important than those for the Waibira females.

In conclusion, seasonal changes in female space use in the Waibira community show that water availability can and does correspond to changes space use in rainforest chimpanzees. It does so by restricting the maximum extent of ranging away from remaining water sources, and increasing spatial overlap between individuals as they centre their activity around water sources. Access to water also

seems to be prioritised over food competition by the females of the community, further supporting the status of water as an essential resource for chimpanzees.

Use of the Central Waterhole

The central waterhole is predominantly used during the dry season, as dendortelmata and other arboreal sources, the predominantly used water source type of the Waibira chimpanzees (Chapter 3), dry up. However, the usage intensity of it is not uniform throughout the dry season: as the dry season intensified, the pattern of visitations by females also changed. They made longer, repeated visitations within the same day, but more days elapsed between days where they visited the central waterhole. Within-season changes in the use of the waterhole could reflect the females balancing meeting their hydration needs with other needs, such as ranging further enough from the central waterhole to cover a sufficient number of food patches to meet their energetic needs, minimising the energetic costs of travelling to and from the central waterhole, and avoiding the potential risk of within-community aggression at the central waterhole as conspecifics also increase their use of it.

The length of visitation events could reflect increased water intake. At the start of the dry season, smaller terrestrial water sources and dendrotelmata are still not dried up, therefore the central waterhole is not Waibira chimpanzees' only water source within the central areas of their community home range. But as the dry season goes on, they do dry up, meaning that chimpanzees must get all their liquid water needs met from the central waterhole or one of the peripheral waterholes. In that case, consuming more water during a visit is expected, leading to a longer duration of time spent at the central waterhole.

The rate of visitation events within a day also increases with the intensity of the dry season. In addition to an increased reliance on and therefore consumption of

water from the central waterhole, frequent visitation events can also reflect avoidance of or interruption by risks. Besides spending more time at the central waterhole per visit, on-screen party sizes also go up as the dry season progresses (Péter, 2019), increasing the chance of encountering other individuals at a visitation to the waterhole. As the chances of experiencing aggression increase with the number of males in a chimpanzee party (Shibata et al., 2022), visitations further into the dry season could also mean a higher risk of agonistic encounters causing females to leave pre-emptively or due to being aggressed.

Alternatively, and joined with an increase in the number of days elapsed between females visiting the central waterhole as the dry season goes on, more frequent returns to the central waterhole could also reflect energetic optimisation. While the concentration of core areas around the central waterhole reduces the amount of travel to it, the waterhole itself is still located in a steep valley. Chimpanzees (Green et al., 2020), similar to other species (African elephants: Wall et al., 2006), generally avoid steep slopes due to the energetic cost of traversing them (Newmark & Rickart, 2012). Additionally, travelling increases water needs, especially in high temperatures (Lorenzon et al., 1999; Ostrowski et al., 2003). The increase in temperature and restricted water availability towards the middle and end of the dry season then could make the costs of travelling to the central waterhole, descending into the valley, then climbing out of it outweigh the benefits if done too frequently, resulting in more days elapsed between sightings of females at the central waterhole. With regards to individual hydration levels, females likely incur a dehydration cost with this potential strategy on days spent away from the waterhole, followed by a higher water intake to achieve optimum hydration again, suggested by increased returns on the days they do visit, balancing dehydration stress with travel costs and all other factors in the competitive landscape. However, it is important to

note that this strategy of more spaced out visitation days later on in the dry season, with a higher number of visitations, do not reflect hydrating in advance, or water storing, which chimpanzees are not physiologically capable of, simply a compensation of already existing dehydration, similar to increased thirst and increased drinking quantities in dehydrated humans (Rolls et al., 1980).

Based on camera trap data, females visited the central waterhole and therefore consumed water on average every 5.6 days, which is a measure of drinking frequency that does not line up with the observed rate of drinking frequency of 0.15 events/hr recorded during focal individual follows in Chapter 3. This discrepancy of the two measures is most likely due to the limited viewpoint of the camera traps discussed in Chapter 2 – while camera traps focus on areas of high frequency use, they do not cover the entire central waterhole. Occasional visits to any of the peripheral waterholes are also unaccounted for in camera trap data. Based on the current study, camera traps can also provide valuable data on the use of water sources with minimal human disturbance (Delgado-Martínez et al., 2022a; Edwards et al., 2016b; Perera-Romero et al., 2021) for chimpanzees, and provide an excellent tool for inspecting general trends in behaviours. However, as discussed in Chapter 2 and evidenced here, care should be taken with interpreting observed frequencies of a given behaviour as the true frequency of the same behaviour.

To unpick behavioural changes in addition to changes in visitation patterns during the dry season and to gain more accurate measures of drinking frequency, establishing a camera trap monitoring grid covering the entire central waterhole, instead of areas of high usage intensity, and its immediate vicinity on both sides of the valley it is located in would be particularly useful. Additionally, collecting urine samples, similar to the methods employed by Wessling and colleagues (2018a, 2018b) can also inform us of the exact hydration status, energetic condition, and

stress levels of the sampled individuals, and further clarify how rainforest chimpanzees prioritise their various needs during seasonal water scarcity.

Finally, individual variation was also present in waterhole visitation patterns. Females with infants of any age and cycling females with anogenital swellings went fewer days between visiting the central waterhole, suggesting that accessing water was more important for them compared to cycling females without anogenital swellings. For mothers of infants, decreased time between visits to the waterhole likely reflects the increase in hydration needs due to lactation, especially for mothers of young infants: chimpanzee mothers produce more and higher quality milk during the first years of infancy (Bădescu et al., 2022; Emery Thompson et al., 2012), which at a 85-90% water content (Hinde & Milligan, 2011) could mean an additional 640-675 ml to their water needs (Nelson et al., 2022). Travelling, which cycling females with anogenital swellings as they seek out mating opportunities do at increased rate (Matsumoto-Oda & Oda, 1998; Newton-Fisher, 2014), increases water needs, especially during high temperatures (Lorenzon et al., 1999; Ostrowski et al., 2003), and load carrying, such as carrying infants, while travelling in high temperatures further increases the risk of dehydration (Adams et al., 2019b), thereby also contributing to the lower number of days elapsing between waterhole visits for females with anogenital swellings and mothers of infants. Different reproductive states contribute differently to female chimpanzees hydration burden, similar to what has been found in Gombe (Nelson et al., 2022). While subadult females also spent more days away from the central waterhole between visits, this is likely a byproduct of them being nulliparous instead of any age-related changes in water needs and energetic optimisation.

While water is the primary constraint acting on the space use behaviour of the Waibira females throughout the dry season, the specific usage patterns of the

remaining water sources during periods of low water availability might also depend on the availability of and competition for other resources, energetic optimisation, and risk avoidance. The increased use of arboreal water sources shown in Chapter 3 allows for a more flexible balancing of those factors with hydration needs, as arboreal water sources, while smaller, are more densely spaced in forest environments (Blakely & Didham, 2008) and therefore require less travel to access.

General Conclusion

The females of the Waibira community occupy large, highly overlapping individual home ranges and core areas, characterised by an aversion of intercommunity risk at the peripheral areas of the community, and a concentration of activity around the central waterhole, the remaining water source of the group, during the dry season. Pronounced changes in the size, overlap, and exact locations of individual female ranges demonstrate that water shapes female space use in the Waibira community, suggesting it is an essential resource to chimpanzees, even in water-rich, rainforest habitats. The impact of low water availability on female space use is also distinct from that of low food availability: while low food availability correlates to less overlapping female core areas (Wakefield, 2008, 2013), low water availability led to high overlap, as females clustered around the central waterhole. The importance of the central waterhole as a small natural feature (Hunter et al., 2017) is also highlighted by this chapter.

The findings also can be useful for models of early hominin and human evolution. First, this chapter provides evidence of a highly variable hydroscape within an equatorial rainforest, an environment often thought not to pose major environmental challenges. As such, early hominins could have experienced spatially limited water availability not just in savannahs or mosaic forests, but across all habitat types, leading to the emergence of behavioural strategies to mitigate it, such

as the space use changes in the Waibira community. Second, space use changes around the central waterhole and seasonal usage patterns of it demonstrate that extremely small water sources can nevertheless hydrologically support a relatively large hominin population – the waterhole is approximately 10 m x 10 m at its largest point, yet the entire Waibira community, numbering 120 or so individuals, relies on it during the dry season. Therefore, palaeoclimatology and -hydrology models should not exclude the possibility of specific habitats being inhabited by hominins solely due to the lack of large, permanent waterbodies.

On a larger scale in the present, understanding and predicting chimpanzee space use behaviour in relation to water can aid in conservation efforts, especially when it comes to mitigating human-wildlife conflict. In anthropogenic habitats, where chimpanzees are sympatric with humans, shared water sources can pose the risk of human-wildlife conflict (Hockings et al., 2010b; McLennan & Hill, 2012) and disease transmission (Adams et al., 2001; Deere et al., 2019). With the future likelihood of droughts and water scarcity increasing due to climate change (Schlaepfer et al., 2017; Trenberth et al., 2014) and human activity (Desbureaux & Damania, 2018; Wanders & Wada, 2015), knowing that chimpanzees are dependent on and arrange their space use around water sources is essential for their continued survival, and their peaceful and safe coexistence with humans.

Additionally, there is little known about the importance of small water bodies, such as the central waterhole, in equatorial African rainforests. This chapter demonstrates that a small waterhole is essential for a community of eastern chimpanzees to cope with a recurring, dry season-induced water scarcity. Camera trap monitoring the use of the central waterhole by species other than chimpanzees, or any other small water body in the same biome, similar to studies from Central America (Moreira-Ramírez et al., 2016; Moro-Rios et al., 2008; Vernes & Devos,

2022) and Southeast Asia (Pin et al., 2020) can provide further evidence of the importance of water sources and water as a resource in the region, which can then be incorporated into species protection plans, habitat suitability assessments, and the demarcation of protected areas.

Chapter 5

Water and Competition– Water Availability Shapes Female Chimpanzee Social Behaviour

- Female chimpanzee gregariousness increases during periods of water scarcity
- Female chimpanzees focused their proximity and grooming interactions on a few specific relationships with low water availability
- Rates of female-female agonistic interactions do not increase significantly in periods of water scarcity or at water sources
- While overt competition for water is not present in the Waibira community, water scarcity still corresponds to changes in female chimpanzee social behaviour

Female mammals bear the majority of the energetic costs of reproduction compared to male conspecifics (Bonier et al., 2011; Clutton-Brock et al., 1989; Emery Thompson et al., 2012; König & Markl, 1987; Pontzer & Wrangham, 2006). As such, optimal energetic and body condition are essential to their reproductive success (Gadgil & Bossert, 1970). To achieve high reproductive success, they should (a) ensure a sufficient intake of essential consumable resources (McEwen & Wingfield, 2003) by prioritising access to them (Clutton-Brock, 2009), and (b) avoid or minimise stress, as it negatively impacts both energetic condition (Emery Thompson et al., 2010; Martí et al., 1994; McEwen & Wingfield, 2003; Taylor et al., 2000) and reproductive processes (Crockford et al., 2008; Uphouse, 2011; Valsamakis et al., 2019), negating the effects of an otherwise optimal energy intake (McEwen & Wingfield, 2003).

For group-living female mammals, consuming a sufficient quantity and quality of essential resources while keeping their stress levels low are both helped and hindered by conspecifics within their social group. Groups have increased resource holding potential compared to that of a single individual (Clutton-Brock, 1974; Krebs & Davies, 1993; Majolo et al., 2008; Wrangham, 1980), meaning females can defend resources from other groups (e.g.: domestic cats (*Felis catus*): Bradshaw, 2016) or oust them from high-quality foraging grounds (e.g.: red howler monkeys (*Alouatta seniculus*): Pope, 2000), thereby accessing more, and likely better quality, resources, with the investment of less energy compared to living alone. Group members' shared effort towards time- and energy-consuming activities like predation protection (Alexander, 1974; white-bellied spider monkeys (*Ateles belzebuth belzebuth*): Link & Di Fiore, 2013; crab-eating macaques (*Macaca fascicularis*): van Schaik et al., 1983) allows for the individual to engage more in other activities, like foraging, further improving their access to resources (e.g.: cliff swallows (*Hirundo pyrrhonota*): Brown & Brown, 1987). For females, allomothering (Hrdy, 2005, 2016), the carrying, nursing, or otherwise taking care of dependent infants by group members, is one such benefit as well (mouse lemurs (*Microcebus murinus*): Eberle & Kappeler, 2006; white-faced capuchins (*Cebus capucinus*): Kalbitzer et al., 2017; Perry, 1996; African elephants (*Loxodonta africana*): Lee, 1987; chacma baboons (*Papio ursinus*): Silk et al., 2010a; right whales (*Eubalaena australis*): Sprogis & Christiansen, 2024).

Being around conspecifics also provides opportunities for affiliative interactions, like allogrooming, the removal of parasites, dead skin, and debris (eastern chimpanzees (*Pan troglodytes schweinfurthii*): Goodall, 1986; vervet monkeys (*Chlorocebus pygerythrus*): Seyfarth, 1980). Affiliative interactions are directly linked to stress reduction, evidenced by a decrease in heart rate (horses

(*Equus caballus*): Feh & de Mazières, 1993) and glucocorticoid levels (chacma baboons: Wittig et al., 2008). Affiliation with group members may thus act as a buffer from stressors (rhesus macaques (*Macaca mulatta*): Ellis et al., 2019; chacma baboons: Engh et al., 2005), and so mitigate the negative physiological consequences of stress. Group living can also reduce stress indirectly, through joint vigilance and protection efforts reducing the risk of injury or death to the individual during stressful events like encounters with predators (white-bellied spider monkeys: Link & Di Fiore, 2013; crab-eating macaques: van Schaik et al., 1983).

However, living around conspecifics can equally lead to suboptimal resource access and elevation in stress levels, as it introduces within-group competition for resources (Isbell, 1991; Janson & van Schaik, 1988; Majolo et al., 2008). Females can experience agonism from other females in their group competing for the same resources, including food (sooty mangabeys (*Cercocebus atys*): Range & Noë, 2002; Geoffroy's spider monkeys (*Ateles geoffroyii*): Slater et al., 2009; Taiwanese macaques (*Macaca cyclops*): Su & Birky, 2007; western chimpanzees (*Pan troglodytes verus*): Wittig & Boesch, 2003), and access to mates (bonobos (*Pan paniscus*): Hohmann & Fruth, 2003; chacma baboons: Huchard & Cowlishaw, 2011). In mixed-sex groups females can also be the targets of harassment, aggression (horses: Cameron et al., 2009; South American sea lions (*Otaria flavescens*): Cappozzo et al., 2008; eastern chimpanzees: Goodall, 1986), and infanticide (southern sea lions (*Otaria byronia*): Campagna et al., 1992; Przewalski's horses (*Equus ferus przewalskii*): Feh & Munkhtuya, 2008; white-faced capuchins: Kalbitzer et al., 2017) from within-group males as they attempt to maximise their own reproductive success. These within-group agonistic interactions can then lead to losing access to monopolisable resources (mountain gorillas (*Gorilla beringei beringei*): Grueter et al., 2016, western chimpanzees: Wittig & Boesch, 2003),

increased stress (chacma baboons: Crockford et al., 2008), as well as to injury to self or offspring (yellow baboons (*Papio cynocephalus*): Archie et al., 2014), including infanticide (banded mongooses (*Mungo mungo*): Gilchrist, 2006; eastern chimpanzees: Lowe et al., 2020; Walker et al., 2021; African striped mice (*Rhabdomys pumilio*): Schradin et al., 2010), all detrimental to female reproductive success to a varying degree. Additionally, energetic costs of within-group competition are present even in the absence of overt competition: individuals in larger groups, while able to monopolise larger, better food sources as a group, generally have decreased foraging efficacy due to increased travel between sources (Majolo et al., 2008; Alaskan moose (*Alces alces gigas*): Molvar & Bowyer, 1994; crab-eating macaques: Van Schaik, 1983; eastern chimpanzees: Vilioth et al., 2022).

The costs and benefits of sociality change across time depending on shifts in the availability of resources and presence of stressors, as well as individual factors. The costs of group living can depend on dominance rank: high-ranking individuals have priority access to resources even with competitors present (red deer (*Cervus elaphus*): Appleby, 1980; blue monkeys (*Cercopithecus mitis*): Foerster et al., 2011) and are less likely to be targeted by agonism (chacma baboons: Huchard & Cowlishaw, 2011; white-faced capuchins: Perry, 1996) outside of periods of social or rank instability (olive baboons (*Papio anubis*): Sapolsky, 1983; 1992). In some species, older individuals show decreased levels of sociality, suggesting that the costs of broad & frequent socialisation might increase with ageing (Barbary macaques (*Macaca sylvanus*): Rathke & Fischer, 2021; eastern chimpanzees: Thompson González et al., 2021). Regarding female reproductive status, conception is especially vulnerable to stress (banded mongooses: Gilchrist et al., 2006; humans (*Homo sapiens*): Nepomnaschy et al., 2006), and while females with infants are at risk of infanticide (chacma baboons: Engh et al., 2006; white-faced capuchins:

Kalbitzer et al., 2017; eastern chimpanzees: Lowe et al., 2020), group members can also provide allomothering (mouse lemurs: Eberle & Kappeler, 2006; white-faced capuchins: Kalbitzer et al., 2017; chacma baboons: Silk et al., 2010a; right whales: Sprogis & Christiansen, 2024), and socialisation and learning opportunities for their offspring (chimpanzees: Lonsdorf et al., 2014; Van Schaik, 2003; Williams et al., 2002b).

In species with high fission-fusion dynamics, group members flexibly adjust the extent they are around conspecifics, how many of them, and which specific conspecifics they associate with and to what extent to minimise the costs and maximise the benefits of group living according to their specific socioecological and individual circumstances (e.g.: chimpanzees: Kawanaka, 1984; Bechstein's bats (*Myotis bechsteinii*): Kerth & Konig, 1999; spotted hyenas (*Crocuta crocuta*): Kolowski et al., 2007; black spider monkeys (*Ateles paniscus chamek*): Symington, 1988). They rarely spend all their time with the entire group, but leave and join temporary subgroups only including some group members called parties, or travel and forage alone (Kummer, 1971; Reynolds, 1963; Sugiyama, 1968) to balance foraging gain & travel costs (Asensio et al., 2009; Azuma & Toyoshima, 1961; Clutton-Brock, 1974; Sugiyama, 1968) and minimise within-group contest competition (Asensio et al., 2008; Janson, 1988; Wrangham, 1979).

Subtle & Overt Competition

Reduction of gregariousness – the general tendency to associate with other group members (Grassia, 1978) – is a common strategy employed by female mammals in fission-fusion groups to reduce within-group competition for consumable resources. Female mammals generally pursue a subtle, risk-averse competition strategy (Clutton-Brock & Huchard, 2013), as their reproductive success hinges on maintaining optimal body condition for the duration of conception, gestation, and

lactation and therefore the relative value of a positive payoff following an aggressive interaction is much lower compared to males, whose reproductive success primarily depends on the number of successful inseminations (Pusey et al., 2008). With subtle competition, avoidance and non-direct competition is preferred unless a sufficiently high payoff is present (Cant & Young, 2013; Stockley & Bro-Jørgensen, 2011). Fissioning into smaller subgroups or travelling solitary is then one common way of subtle competition (Stockley & Campbell, 2013), where females can adjust the number of direct foraging competitors they have and ensure optimal resource access through avoidance instead of overt competition (spectral tarsiers (*Tarsius spectrum*): Gursky, 2002; geladas (*Theropithecus gelada*): Jarvey et al., 2023; Bornean orangutans (*Pongo pygmaeus wurmbii*): Knott et al., 2008; Indo–Chinese gray langurs (*Trachypithecus crepusculus*): Pengfei et al., 2015; eastern chimpanzees: Wakefield, 2008). Therefore, examining individual or seasonal changes in the levels of gregariousness can help identify resources over which female individuals compete (bonobos: Fassbender et al., 2022; spectral trasiers: Gursky, 2002; western chimpanzees: Wittiger & Boesch, 2013), as well as individual and socioecological factors that might impact the level of competition a given female experiences (spectral tarsiers: Gursky, 2002; western chimpanzees: Wittiger & Boesch, 2013).

However, not all competitive situations can be managed by avoidance. While agonism is not without the risk of retaliation or escalation, if the payoff is sufficiently high, females are willing to take the cost of stress and risk that comes with it (Cant & Young, 2013). Agonistic interactions between females are predominantly non-aggressive, like passive deferrals (bonobos: Furuichi, 1997) and non-aggressive reproductive suppression (European badgers (*Meles meles*): Woodroffe & MacDonald, 1995), but can escalate to physical, and occasionally even lethal aggression (chacma baboons: Huchard & Cowlishaw, 2011, eastern chimpanzees:

Lowe et al., 2020; Bornean orangutans: Marzec et al., 2016). Agonism is more common and intense over important resources (mountain gorillas: Grueter et al., 2016; Hanuman langurs (*Semnopithecus entellus*): Koenig et al., 1998; sooty mangabeys: Range & Noë, 2002; Geoffroy's spider monkeys: Slater et al., 2009; Taiwanese macaques: Su & Birky, 2007), in periods of lower resource availability (geladas: Jarvey et al., 2023; Bornean orangutans: Marzec et al., 2016), higher population density and spatial cohesion (ring-tailed lemurs (*Lemur catta*), Verreaux's sifakas (*Propithecus verrauxi*), red-fronted lemurs (*Eulemur rufifrons*): Seex et al., 2022), and around important female life events impacting reproductive success like rank advance (bonobos: Furuichi, 1997; Toda & Furuichi, 2020; white-faced capuchins: Perry, 1996), settling in a new community (Geoffroy's spider monkeys: Asensio et al., 2008; muriquis (*Brachyteles arachnoides*): Printes & Strier, 1999; c.f.: bonobos: Toda & Furuichi, 2020), or the conception and birth of a new infant (chacma baboons: Archie et al., 2014; Huchard & Cowlishaw, 2011; eastern chimpanzees: Lowe et al., 2020). Increased rates of agonism generally reflect an increase in within-group competition and as such are a good indicator of whether within-group competition intensifies, for which resource, and for which individuals (African elephants: Archie et al., 2006; Hanuman langurs: Koenig et al., 1998; mountain gorillas: Watts, 1994).

Stress & Relationships

Besides improving their access to resources by subtle or overt competition, females can also improve their reproductive success by active lowering of stress. Frequent affiliative social interaction with specific group members, resulting in strong affiliative relationships, defined by the content, quality, and patterning of repeat interactions (Hinde, 1976), is one possible strategy to do so. Social activity acts on stress directly, with increased social effort lowering cortisol levels (Rosal et al.,

2004), general activity in the adrenal axis (Carter, 1998), and the heart rate of both individuals (rhesus macaques: Aureli et al., 1999; crested black macaques (*Macaca nigra*): Aureli & Yates, 2010), and indirectly as well, with repeat affiliative interactions building feeding (and general) tolerance between members of a dyad (chacma baboons: Silk et al., 2010a; vervet monkeys: Seyfarth, 1980; tufted capuchins (*Sapajus nigritus*): Tiddi et al., 2011) and providing a basis for cooperative behaviours like coalitionary support (white-faced capuchins: Kajokaite et al., 2022, eastern chimpanzees: Fox et al., 2023) or allomothering (bonobos: Cheng et al., 2022; Moscovice et al., 2017). It is also a low-risk activity with a high chance of a positive payoff, and as such proposed to be a common response to stress in females (Taylor et al., 2000). Increased, consistent social interaction with specific social partners by females is seen during stressful events and periods (Taylor et al., 2000; Tonkean macaques (*Macaca tonkeena*): De Marco et al., 2010; chacma baboons: Wittig et al., 2008), such as social unpredictability (Crockford et al., 2008; Wittig et al., 2008), or the loss of a social partner (Engh et al., 2005). Females who are highly social, either by selectively and intensely socialising with a few select partners, resulting in strong affiliative relationships (white-faced capuchins: Kajokaite et al., 2022; Kinda baboons (*Papio kindae*): Schneider-Crease et al., 2022; yellow baboons: Silk et al., 2003; chacma baboons: Silk et al., 2010b) or socialising with a broad array of conspecifics, resulting in a high number of relationships (*Papio* hybrids: Campos et al., 2020b; rhesus macaques: Ellis et al., 2019; chacma baboons: McFarland et al., 2017), also have higher lifetime reproductive success. The two are alternative strategies, as females are constrained in their social decisions by a limited time budget per day (Lehmann et al., 2007), as well as the social preferences of other group members (Newton-Fisher, 2002b).

Affiliative interactions which define relationships can contribute to stress reduction to a different extent depending on how costly they are with regards to time and energy (Engh et al., 2006; Crockford et al., 2008). Party-level association can be passive, with females congregating around resources of shared interest (Geoffroy's spider monkeys: Ramos-Fernández et al., 2009), or two females attempting to affiliate with the same social partner, but not each other (Newton-Fisher, 2002b). Two individuals being in close proximity marks a more active association: while individuals might be drawn to the same party regardless of social interest, they can control their proximity to each other within the party (Newton-Fisher, 2002b). Additionally, as proximity is both a prerequisite of grooming (Newton-Fisher, 2002b) and agonistic interactions (Houle & Wrangham, 2021), it follows that dyads that have a strongly affiliative relationship will remain within proximity of each other more often, while dyads that have a weak or agonistic relationship minimise the time spent in proximity to avoid direct conflict. Interactions and relationships built around allogrooming show the highest selectivity, as this is the most time-consuming affiliative behaviour (Barbary macaques: Almeling et al., 2016; sooty mangabeys: Range & Noë, 2002). An increase in overall grooming relationship strength, with individuals spending more time grooming with a few specific grooming partners (chacma baboons: Crockford et al., 2008; Wittig et al., 2008), or increasing both the time spent on grooming and their number of grooming partners (chacma baboons: Engh et al., 2005), is a common social stress-reduction strategy. Therefore, increased stress can cause changes in social networks, including the strength of various types of affiliative relationships between dyads or the number of social partners an individual might have.

Due to their reproductive physiology, female mammals are more sensitive to any fluctuation in resources impacting body condition or stress compared to males

(Isbell, 1991; Koenig et al., 1998; Sterck et al., 1997; Wrangham, 1979; c.f.: Sussman et al., 2011), and adjust their competitive strategies earlier compared to them. Therefore, if we look at changes in the social behaviour of females in fission-fusion groups across time, we can identify factors that could likely impact access to and competition for resources and stress levels. The extent of their gregariousness should not be universal across time points, but fluctuate over time as individuals seek to maximise their access to resources while minimising costs (Aureli et al., 2008; Asensio et al., 2009; Dunbar, 1988; Sterck et al., 1997), with lower gregariousness suggesting higher within-group competition and an avoidant competition strategy. Female-female agonism can serves as an indicator of factors impacting within-group competition: looking at the rates and contexts of agonistic interactions can help identify resources in short supply or high importance, individuals more impacted by competition, and any temporal changes in its levels (Archie et al., 2006; Huchard & Cowlishaw, 2011; Range & Noë, 2002; Slater et al., 2009; Su & Birky, 2007). Finally, looking at dyadic relationships and social structure can help identify any increased social effort, a common female behavioural adaptation to mitigate stress (Taylor et al., 2000). Therefore, studying gregariousness, agonistic interactions, as well as social relationships & structure and how they change over time does not only inform us about a species' social capacity, but about key resources, individual characteristics, and life events impacting survival and reproduction.

Female Sociality in Chimpanzees

Chimpanzees live in highly fission-fusion, multi-male multi-female groups that can number between 8-150 individuals (Goodall, 1986; Kawanaka, 1984; Sandel & Watts, 2021; Sugiyama & Koman, 1979). Females are the dispersing sex, with the majority leaving their natal community upon adolescence and settling into a new one

permanently (Pusey, 1980). Communities have closed membership, and intergroup encounters are characterised by aggression, which can be lethal (Martínez-Íñigo et al., 2021; Watts et al., 2006). They are large bodied (Uehara & Nishida, 1987), long-lived (Matsuzawa, 2018; Nishida et al., 2003), fruit-specialist omnivores (Matsumoto-Oda & Hayashi, 1999; Potts, 2004; Pruetz, 2006).

Reproduction is non-synchronised between females (Wallis, 1995), and is characterised by a semi-concealed ovulatory period during which females usually mate with multiple males (Emery & Whitten, 2003; Emery Thompson, 2005), long interbirth intervals and periods of infant dependency (Emery Thompson et al., 2012; Wallis, 1997), high energetic investment into individual offspring (Bădescu et al., 2022; Cibot et al., 2019a; Reddy et al., 2024), and minimal if any paternal investment (Murray et al., 2016). Infant mortality is also high (Nishida et al., 2003; Wittig & Boesch, 2019), partially due to infanticide both between (Goodall, 1977; Martínez-Íñigo et al., 2021; Watts & Mitani, 2000) and within communities (Lowe et al., 2020; Nishie & Nakamura, 2018; Walker et al., 2021). In summary, female chimpanzees need to maintain optimal body condition and stress levels for a sustained period of time to ensure the successful production and survival of even a single offspring (Pusey et al., 2008). However, being around and building relationships with other group members can also provide them with coalition opportunities against male harassment (Fox et al., 2023; Newton-Fisher, 2006), valuable socialisation (Lonsdorf et al., 2014; Williams et al., 2002a) and social learning opportunities for their offspring (Van Schaik, 2003), and even increase the chances of any orphaned offspring being adopted (Lehmann & Boesch, 2009).

Initial accounts based on the chimpanzees in Gombe, Tanzania assumed females were solitary most of the time due to high within-group food competition (Wrangham, 1979). However, later research from other field sites showed that there

is high variation in the extent of female chimpanzee gregariousness: females in some group behave similar to those in Gombe, predominantly foraging and traveling alone or in small parties (Mahale: Kawanaka, 1984; Kanyawara: Wrangham et al., 1996), while other communities have highly gregarious females, associating with other chimpanzees more often than not (Sonso: Fawcett, 2000; Reynolds, 1963; Taï: Lehmann & Boesch, 2008; Ngogo: Wakefield, 2013). Female chimpanzees, rather than permanently avoiding other competitors, flexibly adjust their level of gregariousness to minimise resource competition and maximise the benefits of being social as a subtle competition strategy (Pusey & Schroepfer-Walker, 2013; Wakefield, 2008).

Competition for consumable resources, specifically ripe fruit (Wrangham et al., 1996), is the most common correlate for between- and within-community variation in gregariousness, as females tend to increase their association with others during periods of high food availability, and forage alone during periods of scarcity (Nyungwe: Matthews et al., 2021; Gombe: Murray et al., 2006; Taï: Riedel et al., 2011; Wittiger & Boesch, 2013; Mahale: Sakura, 1994; c.f.: Ngogo: Wakefield, 2008), and in general are more gregarious in communities with higher year-round food availability (Sonso: Fawcett, 2000; Kanyawara: Machanda et al., 2013; Ngogo: Wakefield, 2008) and fewer members (Taï: Lehmann & Boesch, 2004). Individual factors also impact a female's access to resources and with it the extent of her gregariousness. Similar to other species, high-ranking females enjoy priority of access to resources, and can remain more gregarious during periods of low resource availability (Taï: Riedel et al., 2011), while aging is correlated with lower social interest (Ngogo: Thompson González et al., 2021). Cycling females are more likely to associate with others (Kanyawara: Machanda et al., 2013; Taï: Wittiger & Boesch, 2013), actively seeking out males (Sonso: Newton-Fisher, 2014), leading to a

correlation between party size and the number of sexually available females (Taï: Wittiger & Boesch, 2013; Kalinzu: Shibata et al., 2022; Nyungwe: Matthews et al., 2021). Mothers of young infants might avoid infanticidal individuals (Sonso: Lowe et al., 2019) and be less gregarious (Mahale: Sakura, 1994), especially around parturition (Mahale: Nishie & Nakamura; Gombe: Pusey et al., 2008), while those with older infants might seek out socialisation and play opportunities (Gombe: Williams et al., 2002a; c.f.: Taï: Wittiger & Boesch, 2013).

A long reproductive turnover increases the cost of any stress, injury, or infant death, making female chimpanzees less likely to engage in agonistic encounters compared to male chimpanzees (Gombe: Goodall, 1986; Kanyawara: Sabbi et al., 2021), and to generally pursue a risk-averse, subtle competition strategy (Cant & Young, 2013; Pusey & Schroepfer-Walker, 2013). Their competitive behaviour can range from passive deferrals and displacements to gestural and vocal threats (Houle & Wrangham, 2021; Wakefield, 2008) to physical aggression (Kahlenberg et al., 2008a, 2008b; Pusey, 1980) and within community infanticide (Goodall, 2001; Lowe et al., 2020; Townsend et al., 2007; Walker et al., 2021). Agonistic interactions are a good indicator of changes in the levels of within-group competition, as well as which females are more impacted by it, and which resource it is for. The rates of female-female agonistic interactions are higher over access to food (Houle & Wrangham, 2021; Miller et al., 2014; Wittig & Boesch, 2003), as well as towards recent immigrant females, as resident females attempt to deter them from establishing a core area with high resource quality, or permanently settling into the community, increasing the number of competitors (Kahlenberg et al., 2008b; Nishida et al., 1989; Pusey, 1980). Cycling females and those with young infants are targeted most often, as the chances of harming another female's reproductive success is the highest in those periods (Lowe et al., 2020; Pusey et al., 2008).. Killing another female's infant costs

her the time and energy she has invested into conception and gestation, and might be sufficient to oust her from her core area (Lowe et al., 2020; Muller, 2007; Walker et al., 2021), while elevated stress levels can prevent conception and cause spontaneous abortion in primates (Nepomnaschy et al., 2006; Valsamakis et al., 2019).

Selective association with other females on the level of party association, proximity, and grooming is lower in female chimpanzees compared to male conspecifics (Surbeck et al., 2017), suggesting a low rate of affiliative interactions with all other female group members (Kanyawara: Gilby & Wrangham, 2008), or the prioritisation of specific female partners (Taï: Lehmann & Boesch, 2008; Gombe: Surbeck et al., 2017). In addition to large variation in relationship strength between specific female-female dyads (Taï: Lehmann & Boesch, 2008; Gombe: Surbeck et al., 2017), the latter interpretation is supported by the presence of ‘cliques’, mutual affiliative interactions between a subset of individuals (Ngogo: Langergraber et al., 2009; Wakefield, 2008), in some communities. Focusing their social effort likely benefits female chimpanzees (Foerster et al., 2015), with stronger relationships linked to coalitionary support (Ngogo: Fox et al., 2023), cooperative behaviours (Taï: Samuni et al., 2018), and increased tolerance (Taï: Lehmann & Boesch, 2009), which contribute to lower stress levels. Male chimpanzees also increase their social effort during stressful periods of social instability (Kaburu & Newton-Fisher, 2013).

The Current Study

While studies on the impact on water availability on space use exist for some species, there is little known about how the availability and distribution of water affects social behaviour. Studies primarily focus either on solitary species (e.g.: mule deer (*Odocoileus hemionus*): Boroski & Mossman, 1996; koalas (*Phascolarctos cinereus*): Davies et al., 2013; aardvarks (*Orycteropus afer*): Rey et al., 2017), or

between-species interactions (e.g.: Adams & Thibault, 2006; Amoroso et al., 2020b; Cain III et al., 2012). When within-species interactions at water points are studied, they are primarily accounts of between-group encounters (Hanuman langurs: Beck & Tuttle, 1972; yellow baboons: Markham et al., 2013; patas monkeys (*Erythrocebus patas*): Struhsaker & Gartlan, 1970; chacma baboons: Washburn & DeVore, 1961).

However, what little is known about the role of hydration in reproduction, within-group encounters around water access, and dehydration and stress suggests that water scarcity might impact social behaviour, especially that of female mammals. First, dehydration is tied to reproductive complications from conception (Geoffroy's spider monkeys, white-faced capuchins: Campos et al., 2020a; baboons (*Papio* hybrid): Morishima et al., 1975) to lactation (hopping mice (*Notomys* spp.), plains rats (*Pseudomys australis*), house mice (*Mus musculus*): Baverstock et al., 1976; fat sand rats (*Psammomys obesus*): Kam & Degen, 1994), making water a resource essential for optimal female body condition and reproduction. Second, while the literature is relatively sparse, within-group competition also might be present over water access. Higher ranking individuals had priority access to water sources in Hanuman langurs (Beck & Tuttle, 1972), siamangs (*Symphalangus syndactylus*) (Sharma et al., 2016), chacma baboons (Hamilton, 1985), and vervet monkeys (Wrangham, 1981). Wittig & Boesch (2003) briefly mention female-female contest competition over dendrotelmata (water-filled tree holes), and Wrangham's (1981) account of vervet monkeys experiencing a catastrophic drought documents threats and aggression during encounters over water both within and between groups. Third, dehydration also impacts stress levels (Barrow Island euros (*Macropus robustus isabellinus*): King & Bradshaw, 2010; western chimpanzees: Wessling et al., 2018a, 2018b), further contributing to its detrimental impact on female reproductive success.

After a few initial studies focusing on or including how wild chimpanzees interact with and rely on water (Angus, 1971; McGrew, 1977; Nishida, 1980; Teleki, 1977), research interest has been low until recently. Newer studies point to water being a key resource for chimpanzees across all habitats: lower water availability increased stress levels in both forest- and savannah-dwelling chimpanzees (Nelson et al., 2024; Wessling et al., 2018a, 2018b), and water points are common locations of human-chimpanzee conflict in mosaic woodlands (Fryns et al., 2021). Lactating females are more at the risk of dehydration (Nelson et al., 2022, 2024), and occasional female-female contest competition also has been observed over access to water sources (Wittig & Boesch, 2003). The importance of water is further supported by the seasonal shifting of female core areas in the Waibira community shown in Chapter 4. However, it is not clear whether water availability also impacts social behaviour, either by increasing the levels of within-group competition, or by acting as a seasonal stressor. In Gombe, while chimpanzees were less gregarious during the dry season, the authors note that the dry season also corresponds with low food availability (Murray et al., 2006). The Issa chimpanzees, also in Tanzania, altered their party size depending on food availability and the number of sexually receptive females, but not water availability (Giuliano et al., 2022) – however, the study did not investigate changes in gregariousness for females specifically, who might be more impacted by low water availability than males due to the essential role of water for their reproductive success. Additionally, despite both communities occupying a mosaic savannah environment, their waterscape is comparatively rich with multiple waterpoints accessible, the majority of which remain active and flowing year-round (Giuliano et al., 2022, R. Nelson, pers. comm.). While the low vegetation cover and high temperatures during dry seasons do considerably increase the hydration burden of the chimpanzees living in those areas, it cannot be said that

water availability is limited at any point of the year or that they experience a water shortage per se.

The Waibira community of eastern chimpanzees is well-suited for a study on how an annually recurring water shortage impacts female social behaviour, and through which pathways. Besides the shortage of water faced by the community during dry seasons, when the number of water points within their home range drastically decreases and they mostly rely on the central waterhole, the Budongo forest chimpanzees enjoy relatively high and stable year-round food availability (Newton-Fisher et al., 2000; Reynolds, 2005), similar to the Ngogo chimpanzees (Wakefield, 2008), so even though Waibira is a large community, with ~120 individuals, within-group food competition levels likely do not reach the point where they significantly constrain female gregariousness (Villloth et al., 2022). Risk, such as vehicles (Sakura, 1994) and the presence of predators (Boesch, 1991) has been shown to increase female gregariousness. However, the Waibira community has no access to human settlements or roads, and while lions (*Panthera leo*) were occasionally sighted in the 1990s (N. E. Newton-Fisher, pers. comm.), BCFS researchers and ongoing camera trap monitoring has not detected the presence of any known predators of chimpanzees in the Waibira community's territory either.

To investigate how limited water availability acts on female chimpanzee sociality, I focus on three areas. First, the extent of gregariousness, measured as the number of individuals with whom a female associates, which is a reliable & commonly used measure for the extent of subtle competition. Second, the rate, context, and participants of female-female agonistic interactions, which are reliable markers of increased levels of overt competition, as well as the resource competed over. And third, the strength and structure of party association, proximity, and grooming relationships, with intensified social effort corresponding to stressful

periods both in other primate species (Crockford et al. 2008; Engh et al. 2005; Wittig et al., 2008) and male chimpanzees (Kaburu & Newton-Fisher, 2013). If social behaviour is impacted by increased within-group competition for water, I predict lower levels of gregariousness in the dry season, as well as higher rates of agonistic interactions, especially at the central waterhole. While the high degree of spatial overlap between females and the dissolution of wet season core areas during the dry season (Chapter 4) could increase within-group food competition and produce decreased gregariousness, any increase in agonism in the dry season would not be associated with water sources. Finally, the dry season water shortage could also act on broader social networks. Females could experience dehydration, increased social instability and food competition due to the seasonal space use changes (Chapter 4), or other seasonal factors which impact social behaviour via stress. If lower water availability impacts female social networks, I expect to see a decrease in the number of overall social partners, especially grooming partners, for females during the dry season, but an increase in relationship strength.

Methods

Subtle & Overt Competition

Gregariousness

Long-term focal individual follow data was available 2015-2022 (see Chapter 2). From it, I extracted every long-term 15 min party composition scan with at least one named independent female recorded (N = 17,600, 4400 hrs from 1449 days), and used those to calculate three measures of the extent a given female associated with other community members on a given day, using the daily weighted mean of associates, based on the work of Wittiger & Boesch (2013). The *daily weighted mean of associates* per female per day ($DWMA_{total}$) was calculated as:

$$DWMA_{total} = \sum \frac{(number\ a * duration\ a)}{total\ duration} + \frac{(number\ a_2 * duration\ a_2)}{total\ duration} \ldots \frac{(number\ a_n * duration\ a_n)}{total\ duration}$$

where the number of scans in which the female was recorded with *a* number of associates was multiplied by the *duration* she spent in parties with that number of associates, divided by the *total duration* of all party scans including her for the given day, then summed. Only named independent individuals were included in party size. *Daily weighted mean of female* ($DWMA_{female}$) and *male associates* ($DWMA_{male}$) were calculated using the same formula as *daily weighted mean of associates*, with the number of associates based only on the number of named independent females and males recorded in party scans respectively:

$$DWMA_{female} = \sum \frac{(number\ fa_1 * duration\ fa_1)}{duration\ total} + \frac{(number\ fa_2 * duration\ fa_2)}{duration\ total} \ldots \frac{(number\ fa_n * duration\ fa_n)}{duration\ total}$$

$$DWMA_{male} = \sum \frac{(number\ ma_1 * duration\ ma_1)}{duration\ total} + \frac{(number\ ma_2 * duration\ ma_2)}{duration\ total} \ldots \frac{(number\ ma_n * duration\ ma_n)}{duration\ total}$$

Females were included in analyses of gregariousness if they were recorded in party composition scans across at least 50 different days. Females with an *unknown rank* category were excluded from gregariousness analyses regardless of sample size, as well as data points from days with unknown *food availability*. 24 different females were included, resulting in a total of 7087 data points on d*aily weighted mean associates*, *female associates*, and *male associates each*, across 1364 days.

As I only recorded the exact numbers, and identities of, female party members during fieldwork and camera trap party composition scans, data from those scans were not used in gregariousness analyses.

Agonistic Interactions

Instances of female-female agonistic interactions were recorded on an *ad libitum* basis during long-term data collection between 2015-2022, and during fieldwork focal group follows between November 4 2021 and March 17 2022, and from camera trap videos available 2013-2022, coded with the BORIS video coding software (v. 7.13.6, Friard & Gamba, 2016).

Agonistic interactions recorded in long-term, fieldwork, and camera trap data included approach-leave interactions and passive deferrals; vocal threats, including soft barks, barks, waa-barks, and screams (Goodall, 1986); gestural threats ranging from an arm raise, hitting or flapping an arm toward the other individual to swaying, flailing, or throwing an object, most often a stick or branch at the other (Goodall, 1986); chases; displays; physical aggression like hitting, slapping, kicking, stomping, or biting; and pant-grunt vocalisation.

To calculate the hourly rate of female-female agonistic interactions for fieldwork data, the number of events was divided by the number of total focal group follow hours, while for camera trap data, the number of events was divided by the hours of potential footage. While long-term data only includes agonistic interactions recorded on an *ad libitum* basis, I still calculated hourly rates of aggression for it, using the number of 15 min party composition scans to determine hours of observation in total and across seasons. Additionally, female-female agonistic interactions have a reputation amongst BCFS primatology research staff of being rare, and are recorded in the majority of occasions, especially when including displays, chases, or physical aggression. 77 agonistic female-female interactions

were recorded across 5742 hr 15 min of long-term data collection, 15 across 146 hr 28 min of focal group follows during fieldwork, and 24 across 11,737 hr 30 min of potential camera trap footage. More details on the various data collection methods, the full ethogram of agonistic behaviour, and camera trap hours can be found in Chapter 2.

Relationships & Social Structure

Measures of dyadic relationships and social structure were calculated using long-term data, fieldwork data, and camera trap data. From long-term data, I extracted 15 min party composition scans with at least one named independent female; focal individual follow data with a female focal, where the identity of all independent named individuals within 5 m was recorded at 15 min intervals; and all *ad libitum* data on grooming interactions between females. 17,600 party composition scans had at least one independent named female, while 8602 focal 5 m neighbour scans were of female focal individuals and 247 grooming events were recorded, including 35 different females.

During fieldwork data collection, I conducted focal individual follows of the named independent females of the Waibira community. During those follows, I took a scan sample of all identified independent females within the focal female's party as well as the identity of all identified independent females within 5 m of her at 10 min intervals, and *ad libitum* data on grooming interactions between females. I collected 132 hr of focal individual follow data across 75 days – 94 hr 50 min across 28 days in the wet season, and 37 hr 10 min across 27 days in the dry season. 769 party compositions, 792 5 m neighbour scans, and 15 grooming events were recorded during fieldwork, including 30 different females.

From the camera trap videos, I coded every video with at least one independent identified female. A party scan involved all identified independent

females who appeared at some point during the 1 min video, while a scan sample of the 5 m female neighbours of a given female was taken at the beginning of the video. If more than one female was present at the beginning of a video, a 5 m neighbour scan was recorded for each of them. I also recorded all occurrences of grooming between females on camera trap. 3612 party composition scans, 5679 5 m neighbour scans, and 11 grooming events were recorded across 3612 videos, including 40 different females. As the sample size for camera trap videos from the wet season containing chimpanzees was too low for the construction of meaningful social networks, only videos from the dry season were used for analyses of sociality.

Party Association

Party association between female-female dyads was calculated using 15 min party composition scans from long-term data, 10 min party composition scans from fieldwork data, and 1 min party composition scans from camera trap data (*N* = 3612). A simple ratio-based *dyadic party association index* (DAI) (Cairns & Schwager, 1987; Ginsberg & Young, 1992), commonly used in studies of primate sociality (e.g.: Fox et al., 2023; Newton-Fisher, 1999b; Nishida, 1968; Wittiger & Boesch, 2013), and thus allowing for greater inter-site comparison, was calculated for each dyad that was seen in the same party per data collection method and season as the following:

$$DAI = \frac{party\ AB}{party\ A + party\ B - party\ AB}$$

where the number of party scans containing both individual A and B were divided by the number of party scans containing individual A plus the number of party scans containing individual B minus the number of party scans containing both A and B. As party scans were taken at specific intervals for all data collection methods, the number of party scans is directly proportional to the duration of both individual A and B, individual A, and individual B having been observed.

Proximity

To measure a female dyad's frequency of being in close proximity to each other, I used data on the 5 m neighbours of female focal individuals taken at 15 min intervals during long-term data collection, 10 min intervals during fieldwork, and at the beginning of each video for camera trap videos. A simple ratio-based *proximity index* (PI), commonly used in studies on chimpanzee sociality (e.g.: Fox et al., 2023; Machanda et al., 2013; Newton-Fisher, 2002b), was calculated for each dyad who were in close proximity with each other per each method and season as the following:

$$PI = \frac{A\ 5m\ B + B\ 5m\ A}{A\ focal\ party\ B + B\ focal\ party\ A}$$

where the number of scans where individual A was the focal and individual B was within 5 m of them and where individual B was the focal and individual A was within 5 m of them were divided by the number of scans where individual A was the focal and individual B was in their party and where individual B was the focal and individual A was in their party. As party scans were taken at specific intervals for all data collection methods, the number of scans is directly proportional to the duration which A or B was the focal individual with the other individual in the party, thus correcting for time spent together. Scans where individual A or B was the focal with the other in the party were used instead of all party scans where both A and B were in the party as proximity partners were only recorded for focal individuals, and to ensure greater cross-site comparability with existing studies ((e.g.: Fox et al., 2023; Machanda et al., 2013; Newton-Fisher, 2002b).

Grooming

Grooming interactions within the focal individual's party were recorded on an *ad libitum* basis during long-term data collection and during fieldwork and on an all-

occurrence basis from camera trap videos. *Grooming indices* (GI) were constructed for all females who groomed with each other per season per data collection method:

$$GI = \frac{A\ groom\ B + B\ groom\ A}{A\ focal\ party\ B + B\ focal\ party\ A}$$

where the number of grooming events where individual A groomed B and where individual B groomed A were divided by the number of scans where A was focal and individual B was in their party and where B was focal and individual A was in their party. As party scans were taken at specific intervals for all data collection methods, the number of scans is directly proportional to the duration which A and B spent within the same party, thus correcting for time spent together. Scans where individual A or B was the focal with the other in the party were used instead of all party scans where both A and B were in the party to ensure greater cross-site comparability with existing studies ((e.g.: Fox et al., 2023; Machanda et al., 2013; Newton-Fisher, 2002b).

All association indices were calculated separately for the three data collection methods, as the different methods of locating parties and focal individuals differed between them, as discussed in Chapter 2. Only females with a known *rank* category and neighbourhood membership were included in models of sociality, resulting in 954 party association indices, 634 proximity indices, and 158 grooming indices from 17 different females being included in analyses. Index values of zero between females were excluded, as the aim was to investigate the strength and patterns of existing relationships instead of those of average, population-wide relationships.

Social Structure

DAI, PI, and GI values from all females were used to construct social networks per each method and season and conduct social network analysis (Krause

et al., 2007; Wey et al., 2008) focusing on changes in the number of social partners and connectivity between females.

Ecological Variables

Season

Days were categorised as *wet* or *dry season* days depending on precipitation, using the pentad-based approach detailed in Chapter 2. DWMA values were categorised as *wet* or *dry season* values accordingly. Female-female agonistic interactions were also categorised as having taken part in the *wet* or *dry season* using the same approach. Party scan compositions, 5 m neighbour scans, and grooming events used to calculate DAI, PI, and GI values were categorised as *wet* or *dry season* data points and used to calculate separate *wet* and *dry season* indices for dyads, as well as separate seasonal social networks.

Food Availability Index

Food availability was included as a variable in models of gregariousness and was calculated as a monthly *food availability index* (FAI), using data on the presence of ripe fruit and the basal area of regularly monitored trees extracted from long-term phenology data collected at BCFS. Following Basabose (2005), *food availability* for a given month was calculated as:

$$FAI_m = \frac{N_{m\ fruiting}}{N_{m\ surveyed}} \times B_{m\ surveyed}$$

where the proportion of surveyed trees fruiting in the given month are multiplied by the total basal area of the trees surveyed in that month. More information on the long-term phenology data used and how FAI was calculated can be found in Chapter 2.

Number of Sexually Receptive Females

The *number of sexually receptive females* on a given day was included in models of gregariousness and was calculated using long-term health monitoring data (see Chapter 2 for more information). Females encountered during day-to-day monitoring by BCFS primatology research staff are assigned a score from zero to four depending on the presence and physical appearance of their anogenital swelling, with zero denoting complete detumescence, and four full tumescence. I only counted females rated four as sexually receptive, as maximum tumescence correlates to ovulation (Deschner et al., 2003; Emery Thompson, 2005), as well as the highest rates of copulation and sexual interest by males (Emery Thompson, 2005; Matsumoto-Oda, 1999; Wallis, 1992), while partial tumescence can also occur during non-fertile phases in a female chimpanzee's cycle, as well as in non-cycling, pregnant or lactating females (Clark & Birch, 1948; Wallis & Goodall, 1993).

As not even the most habituated females are encountered every day, gaps in health monitoring data, and therefore gaps in data on the tumescence of females are common. To account for females who are likely fully tumescent but have not been sighted during the full duration of it and to bridge these gaps, if a female was recorded with an anogenital swelling ranked four on a day, I counted her as remaining at that stage for 10 more days following the initial sighting. This resulted in 11 continuous days of full tumescence, equal to the average duration across several populations (Deschner et al., 2003; Hasegawa & Hiraiwa-Hasegawa, 1983; Matsumoto-Oda, 1999; Tutin & McGinnis, 2012). If the female was sighted again maximally tumescent outside those 11 days, but within 18 days from the first sighting, the maximum length of full tumescence recorded (Hasegawa & Hiraiwa-Hasegawa, 1983), I extended the duration of full tumescence to encompass the days between the two sightings. If the second sighting of the same female with full

tumescence was more than 18 days from the first sighting, a new 11-day period of maximum tumescence was started. If the female was sighted again within an 11-day period and was ranked only partially tumescent (rated one – three) or fully detumescent, the period of full tumescence only extended to the previous day. The *number of sexually receptive females* for a given day was then calculated by summing up the number of all named independent females rated four or maximally tumescent for that day.

Individual Variables

Rank

Ordinal female *rank* (*high*, *mid*, *mid-low*, *low*) was used in all analyses. It was calculated using long-term *ad libitum* data on female-female pant-grunts available 2014-2022, and additional *ad libitum* data collected during fieldwork between November 2021-March 2022. The specific method and exact individual dominance values can be found in Chapter 2. Where the female was not recorded to give or receive any pant-grunts, she was assigned *unknown* as *rank*. As pant-grunts were both used to calculate *rank* categories and included in the list of agonistic behaviours, analyses of agonistic interactions did not focus on individual rank or rank direction.

Age

Age was used in models of gregariousness and was calculated in years for all females. While more precise birth dates are available for infants born to habituated females, narrowing down their birth date to a few days, individuals born in the early years of habituation, before the start of habituation, or to less habituated females only have an estimated birth year or month based on dependence, tooth wear (Kilgore, 1989; Morbeck et al., 2002), body mass, body hair coloration, mobility (Goodall, 1986), and number of offspring. When only birth year was available,

January 1 was used as the birth date. For individuals with only an estimated birth month, the 15th of the month was used. *Age direction* was used in analyses of agonistic behaviour, and had three possible values: *younger*, if the recipient was at least five years younger than the actor; *same*, if the recipient was less than five years younger or older than the actor; and *older*, if the recipient was at least five years older than the actor.

Reproductive Status

Reproductive status (*without swelling*, *with swelling*, *pregnant*, *young infant*, *old infant*) was retrieved from long-term health monitoring data available from July 2015-July 2022 and where necessary, camera trap videos and fieldwork observations, and used in analyses of gregariousness and agonistic interactions. In contrast to Chapter 4, *pregnant* was added as a fifth category of *reproductive status*, encompassing the time 226 days prior to the estimated birth date of a female's offspring (Wittiger & Boesch, 2013), as pregnancy and the perinatal period has been documented to correspond to changes in gregariousness (Wittiger & Boesch, 2013). More information on long-term health monitoring data and categories of reproductive status can be found in Chapter 2.

Neighbour Status

Neighbour status was used in models of sociality, as female chimpanzee association and interactions correspond to space use overlap in some communities (Foerster et al., 2015; Machanda et al., 2013; Wakefield, 2013). Based on the results of Chapter 4, each female-female dyad per season was classified as *neighbours*, if they resided in the same neighbourhood for the given season, or *non-neighbours*, if they resided in different neighbourhoods. As neighbourhoods and neighbourhood memberships changed between the *wet* and *dry season*, *neighbour status* also

differs between seasons for dyads where individuals shifted their dry season range centres significantly.

Residency Status

Residency status was used in analyses of agonistic behaviour. Independent identified females were assigned as *resident* if they have already given birth at least once by the date the given agonistic interaction was recorded, regardless of being born in the Waibira community or emigrating as subadults, and the survival of the infant or infants. Nulliparous identified females who were seen as dependent offspring (infants or juveniles) in the community but were nulliparous on the date of the agonistic interaction were also given *resident* status. Females who were not seen as infants or juveniles in the community, but first sighted as adults or subadults and were nulliparous on the date of the given agonistic interaction were assigned as *immigrant*.

Statistical Analyses

All statistical analyses were run using R (v. 4.3.1) (R Core Team, 2023) running in RStudio (v. 2023.6.0+421) (Posit team, 2023), except exact binomial tests of goodness-of-fit, which were calculated by hand.

For all linear models, the model selection process included ensuring that none of the fixed variables were correlated ($r > 0.5$), setting up a global model including all fixed factors, interaction terms, and random factors, then z-transforming all numeric variables in the global model for easier interpretability with the *arm* package (Gelman et al., 2024). All possible candidate models, including the null model, were then compiled using the *MuMIn* package (Bartoń, 2023). Candidate models were then ranked based on Akaike Information Scores (AIC) and weighted AIC (wAIC) (Wagenmakers & Farrell, 2004) with the *bblme* package (Bolker & R Development Core Team, 2023). The model with the highest wAIC was chosen. If there were any

additional models within 2 ΔAIC of the top model, they, including the top model, were averaged using the *MuMIn* package (Bartoń, 2023). All confidence intervals were calculated using the package *lme4* (Bates et al., 2015).

Subtle & Overt Competition

Gregariousness

To investigate how ecological and individual variables, including *season*, impact gregariousness, I fitted three Linear Mixed Models (LMM) using the *lme4* package (Bates et al., 2015). The response variables for the models were $DWMA_{total}$, $DWMA_{female}$, and $DWMA_{male}$ respectively. Response variables were square root transformed to achieve normal distribution of residuals. For each model, *season* (*wet*, *dry*), *food availability*, *number of sexually receptive females*, *rank* (*high*, *mid*, *mid-low*, *low*), *age*, and *reproductive status* (*without swelling*, *with swelling*, *pregnant*, *young infant*, *old infant*) were set as fixed effects, while *identity* (*N* = 24) was set as random effect. An interaction term was also set between *food availability* and *rank*, as Riedel et al. (2011) found rank-dependent effects of food availability on gregariousness in western chimpanzees, and *reproductive status* and *age*.

Agonistic Interactions

To see if the rates of agonistic interactions between females changed between seasons, I compared the expected and observed hourly rates of female-female agonistic events between the *wet* and *dry season*. To see if any individual characteristics impact a female's likelihood of acting agonistic towards another female or receiving agonism from one, I also compared the expected and observed rates of those across *residency status* (*resident*, *immigrant*), *reproductive status* (*without swelling*, *with swelling*, *pregnant*, *young infant*, *old infant*), as well as the direction of agonistic interactions between *age direction* (*younger*, *same*, *older*). Expected hourly rates of agonism were calculated based on focal party follow hours

for fieldwork data and hours of potential footage for camera trap data. The expected rate of actor and recipient identity categories and interaction directions were calculated based on the relative proportion of specific identity categories throughout the data collection period. The observed rate was then compared to these expected rates using exact binomial tests of goodness-of-fit calculated by hand and exact multinomial tests of goodness-of-fit using the package *Xnomial* (Engels, 2015). To assess partner diversity for actors and recipients, I calculated the standardized Shannon-Weaver index (Henzi et al., 1997; Kaburu & Newton-Fisher, 2015; Silk et al., 1999) for each female committing or receiving agonism more than once, which informs about how biased the distribution is towards specific partners, with zero indicating a complete bias towards one partner, and one denoting a completely even distribution. The index is calculated as the following:

$$H' = \frac{-\sum_{i=1}^{n} p_i \ln p_i}{\ln (n-1)}$$

where *n* is the number of total potential actors or recipients, and p_i is the proportion of agonism directed towards or received from individual *i.*

Relationships & Social Structure

To see which factors impact dyadic relationships between females, I fitted three LMMs with DAI, PI, and GI values as response variables respectively, using the package *lme4* (Bates et al., 2015). All response variables were square root transformed to achieve normal distribution of residuals. Fixed effects in the global model were *season* (*wet*, *dry*), *method* (*long-term*, *fieldwork*, *camera trap*), *rank* (*high*, *mid*, *mid-low*, *low*) and *neighbour status* (*non-neighbours*, *neighbours*), while *identity* (*N* = 17) was set as a random effect. An interaction term was set between *season* and *rank* and *season* and *neighbour status*.

Social Structure

To investigate changes in the female social structure, I used social network analysis. Social network analysis inform us of an individual's sociality beyond a simple rate or frequency of dyadic interactions, including their connectedness and social integration as well as any substructures within a social group (Brent, 2015; Krause et al., 2007; Sueur et al., 2011) and is often used in studies of primate sociality (e.g.: Kajokaite et al., 2022; Ramos-Fernández et al., 2009; Rathke & Fischer, 2021; Thompson González et al., 2021; Wikberg et al., 2014). In the current study, I constructed separate female social networks based on DAI, PI, and GI values, using the R package *igraph* (Csárdi et al., 2024). A separate network was constructed for each *season-method* combination, including every independent identified female recorded with a given *method* in a given *season*. All networks, including grooming networks, were nondirected.

From each network, I extracted four measures for each female included in the network: degree, strength, transitivity, and eigenvalue centrality. Degree is the number of individual independent, identified females a given female has interacted with. Strength is calculated as the degree weighted by the relevant index values of each connection a given female has. Transitivity expresses what proportion of a female's social partners also interact with each other and can detect the presence of social 'cliques', while eigenvalue centrality captures how embedded a female is into her community's social network (Newman, 2003). Both transitivity and eigenvalue centrality were weighted by the relevant index values. All measures were calculated with the *igraph* package (Csárdi et al., 2024).

I then used the resulting values from females with a known *rank* category in various statistical models examining the role of ecological and independent variables on social structure. Models on DAI_{degree}, PI_{degree} and GI_{degree} were Generalised Linear

Mixed Models (GLMM) using a Poisson distribution. All other models of social network values were LMMs, with the exception of the model on $GI_{transitivity}$ which was a Linear Model (LM). Model type was selected based on the distribution of the dependent variable and any issues with model singularity, following suggestions by Bolker et al. (2009). All models were run using *lme4* (Bates et al., 2015). $DAI_{transitivity}$ and $PI_{transitivity}$ were cubed, while all measures of strength, eigenvalue centralities, and $GI_{transitivity}$ were square root transformed to achieve normal distribution of residuals. Global model structure for all models included *season* (*wet*, *dry*), *method* (*long-term*, *fieldwork*, *camera trap*), and *rank* (*high*, *mid*, *mid-low*, *low*) as fixed effects and *identity* (DAI models $N = 25$, $PI_{degree, strength, eigenvalue}$ $N = 25$, $PI_{transitivity}$ $N = 24$, GI models $N = 23$) as random effect.

Results

Subtle & Overt Competition

Gregariousness

Females were recorded in parties with an average 10.39 ± 7.72 associates across seasons, 9.59 ± 7.18 associates in the *wet season*, and 12.84 ± 8.74 associates in the *dry season*. Of their total daily associates, 3.63 ± 3.19 were female associates across seasons, 3.28 ± 2.89 in the *wet season*, and 4.71 ± 3.77 in the *dry season*, while 6.78 ± 5.31 were male associates across seasons, 6.30 ± 5.06 in the *wet season*, and 8.25 ± 5.75 in the *dry season* (Table 20). The females of the Waibira community are gregarious and join parties with other independent individuals throughout their day – females recorded as alone during the entire day, with zero associates, account for only 1% of all data points ($n = 67$). They associate both with other independent females and males, though days where a given female was only seen with other females (5%, $n = 373$) or males (6%, $n = 455$) do occur occasionally.

Table 20

Descriptive Statistics of Daily Weighted Mean Associates, Female Associates, and Male Associates Across Seasons

DWMA	Mean wet season party size ± SD (Range)	Mean dry season party size ± SD (Range)	Mean party size ± SD (Range)
Total	9.59 ± 7.18 (0-44.67)	12.84 ± 8.74 (0-40)	10.39 ± 7.72 (0-44.67)
Female	3.28 ± 2.89 (0-20.67)	4.71 ± 3.77 (0-19.67)	3.63 ± 3.19 (0-20.67)
Male	6.30 ± 5.06 (0-24.50)	8.25 ± 5.75 (0-23.00)	6.78 ± 5.31 (0-24.50)

Note. DWMA is calculated as the daily weighted mean per individual.

Models of $DWMA_{total}$, $DWMA_{female}$, and $DWMA_{male}$ with $AIC_w \geq 0.01$ are summarised in Table 21. One top model was chosen for the model on $DWMA_{total}$ ($w_i = 0.99$, Table 21), the model with *season, food availability, number of sexually receptive females,* and *age* as fixed factors, and one for the model on $DWMA_{female}$ ($w_i = 0.65$, Table 21), the model with *season, food availability, number of sexually receptive females, age,* and *reproductive status* as fixed factors. Two models were averaged for the model on $DWMA_{male}$ ($\Delta AIC \leq 0.08$, $w_i \geq 0.39$, Table 21), averaged to include *season, food availability, number of sexually receptive females, age,* and *reproductive status* as fixed factors. Model parameters for top and averaged models are shown in Table 22.

Table 21

Summary of Candidate Models of Seasonal Changes in Gregariousness with AIC Weights ≥ 0.01

Model	K[1]	AIC[2]	ΔAIC	w_i[3]
Daily weighted mean associates				
Season + Food availability + Receptive females + Age	7	22309.1	0.0	0.99
Season + Food availability + Receptive females	6	22319.4	10.3	0.01
Season + Food availability + Receptive females + Rank + Age	10	22319.9	10.8	0.01
Daily weighted mean female associates				
Season + Food availability + Receptive females + Age + Reproductive status	11	17479.8	0.0	0.65
Season + Receptive females + Age + Reproductive status	10	17482.0	2.2	0.21
Season + Food availability + Receptive females + Age	7	17484.2	4.4	0.07
Season + Food availability + Receptive females + Rank + Age + Reproductive status	14	17486.1	6.4	0.03
Season + Receptive females + Rank + Age + Reproductive status	13	17487.1	7.4	0.02
Season + Receptive females + Age	6	17487.4	7.6	0.01
Daily weighted mean male associates				
Season + Food availability + Receptive females + Reproductive status	10	21556.4	0.0	0.58
Season + Food availability + Receptive females + Age + Reproductive status	11	21557.1	0.8	0.39
Season + Food availability + Receptive females + Age + Reproductive status	15	21562.4	6.0	0.03

Note. Dependent variables for each model are **bolded.** Candidate model structure is listed underneath each dependent variable. All models are LME models.

[1] Number of parameters. [2] Akaike Information Criterion. [3] AIC weights.

Table 22

Model Parameters for Top and Averaged Models of Seasonal Changes in Gregariousness

Parameters	Coefficient	CI 95%	SE
Daily weighted mean associates			
Intercept	2.99	2.90-3.07	0.04
Dry season	0.35	0.27-0.41	0.04
Food availability	0.17	0.11-0.22	0.03
Receptive females	0.32	0.25-0.38	0.03
Age	-0.34	-0.63- -0.11	0.08
Daily weighted mean female associates			
Intercept	1.68	1.52-1.85	0.08
Dry season	0.28	0.23-0.33	0.03
Food availability	0.17	0.11-0.22	0.03
Receptive females	0.32	0.25-0.38	0.03
Age	-0.74	-0.97- -0.40	0.09
With swelling	-0.12	-0.18- -0.04	0.04
Pregnant	-0.05	-0.13-0.04	0.04
Young infant	0.03	-0.03-0.10	0.03
Old infant	0.08	0.02-0.15	0.03
Daily weighted mean male associates			
Intercept	2.30	2.23-2.37	0.04
Dry season	0.26	0.19-0.32	0.03
Food availability	0.13	0.08-0.19	0.03
Receptive females	0.26	0.20-0.32	0.03
Age	-0.11	-0.20- -0.02	0.05
With swelling	0.25	0.16-0.34	0.05
Pregnant	0.09	-0.02-0.20	0.05
Young infant	0.06	-0.02-0.14	0.04
Old infant	-0.05	-0.13-0.03	0.04

Note. All models are LME models. Factors included are *season*, *food availability*, *number of sexually receptive females*, *age*, and *reproductive status*. Baseline value for *season* is *wet*, and *without swelling* for *reproductive status*. *Food availability, number of sexually receptive females*, and *age* are transformed to z-scores.

Gregariousness showed seasonal changes, with the Waibira females associating with others in larger parties, which contained both more males and more females, during the *dry season* (Table 22, Figure 26). Females were also more gregarious, both towards males and females, when *food availability* was higher (Table 22), as well as when the *number of sexually receptive females* increased in the community (Table 22). Individual characteristics also influenced the number of associates a given female joined had the day. Older females were less gregarious, having fewer associates, both female and male (Table 22), and while *reproductive status* did not impact general gregariousness (Table 22), females *with swellings* associated with fewer females but more males, and mothers of *old infants* spent their time with a higher number of female associates (Table 22)

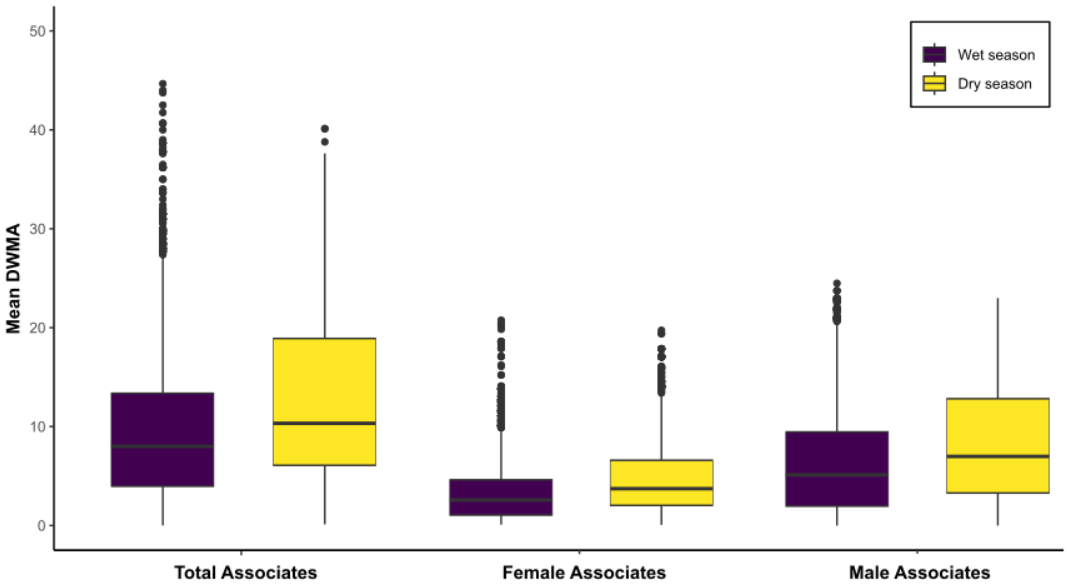


Figure 26

Daily Weighted Mean Associates, Female Associates, and Male Associates Across the Wet and Dry Seasons

Agonistic Interactions

During fieldwork, I recorded 15 agonistic interactions between females across 146 hr 28 min of focal group follows. Eight of them happened during the *wet season* (100 hr 43 min observation), and seven during the *dry season* (45 hr 45 min observation). Agonistic interaction rate was low, at 0.10/hr across both seasons, 0.08/hr in the *wet season* and 0.15/hr in the *dry season*. While the rate of agonistic interactions more than doubled in the *dry season* compared to the *wet season*, it was not a significant seasonal difference (exact binomial test of goodness-of-fit: expected: n_{wet} = 10,31, n_{dry} = 4.69, observed: n_{wet} = 8, n_{dry} = 7, *P* = 0.129, NS). 24 female-female agonistic events were coded from camera trap videos from across 11,737 hr 30 min of potential footage; 19 in the *dry season* and five in the *wet season*. Agonistic interaction rate on camera trap was 0.002/hr, both across and within seasons, suggesting that the waterhole was not a common location for conflict between females (exact binomial test of goodness-of-fit: expected: n_{wet} = 5.39, n_{dry} =

18.61, observed: n_{wet} = 4, n_{dry} = 19, *P* = 0.803, NS). Long-term data collection included 77 agonistic interactions across 5742 hr 15 min of observation. 57 happened in the *wet season* (4497 hr 15 min observation), 20 in the *dry season* (1245 hr). Agonistic interaction rate was low based on long-term data as well, at 0.01/hr across both seasons, 0.01/hr in the *wet season* and 0.02/hr in the *dry season* – similar to fieldwork observation, while there was a seasonal increase in the rate of agonistic interactions, it did not reach the level of significance (exact binomial test of goodness-of-fit: expected: n_{wet} = 60.30, n_{dry} = 16.69, observed: n_{wet} = 57, n_{dry} = 20, *P* = 0.336, NS).

Individual characteristics had a strong role in how likely a given female was likely to act agonistic towards another or be the target of agonism. *Age direction* in interactions was a significant predictor, with agonistic interactions more likely between females in the same age group, and less likely towards females in an older age group (exact multinomial test: expected: $n_{younger\ recipient}$ = 40.60, $n_{same\ age}$ = 34.80, $n_{older\ recipient}$ = 40.60, observed: $n_{younger\ recipient}$ = 42, $n_{same\ age}$ = 51, $n_{older\ recipient}$ = 23, *P* = 0.001). Besides *age*, *reproductive status* also influenced the rates of agonism given and received. Females *with swellings* and *pregnant* females were more likely to commit agonism, while females *without swellings* were less likely compared to expected rates (exact multinomial test: expected: $n_{without\ swelling}$ = 35.96, $n_{with\ swelling}$ = 5.8, $n_{pregnant}$ = 10.44, $n_{young\ infant}$ = 29, $n_{old\ infant}$ = 34.80, observed: $n_{without\ swelling}$ = 21, $n_{with\ swelling}$ = 9, $n_{pregnant}$ = 13, $n_{young\ infant}$ = 32, $n_{old\ infant}$ = 40, *P* = 0.026). Females *with swellings* were more likely to be the targets of agonism by other females, while *pregnant* females and those with *old infants* received less agonism than expected (exact multinomial test: expected: $n_{without\ swelling}$ = 35.96, $n_{with\ swelling}$ = 5.8, $n_{pregnant}$ = 10.44, $n_{young\ infant}$ = 29, $n_{old\ infant}$ = 34.80, observed: $n_{without\ swelling}$ = 33, $n_{with\ swelling}$ = 17, $n_{pregnant}$ = 4, $n_{young\ infant}$ = 39, $n_{old\ infant}$ = 22, *P* < 0.001).

The clear targeting of newly immigrated females by residents observed at other field sites (Kanyawara: Kahlenberg et al., 2008; Mahale: Nishida et al., 1989; Ngogo: Wakefield, 2008) also occurs in the Waibira community: while *residents* and *immigrants* act agonistic at a similar rate to expected (exact multinomial test, expected: $n_{resident}$ = 105.56, $n_{immigrant}$ = 10.44, observed: $n_{resident}$ = 111, $n_{immigrant}$ = 5, P = 0.102, NS), *immigrants* were targeted disproportionately (exact multinomial test, expected: $n_{resident}$ = 105.56, $n_{immigrant}$ = 10.44, observed: $n_{resident}$ = 85, $n_{immigrant}$ = 31, P < 0.001).

Besides variation dependent on individual characteristics, there was also high variation in the likelihood of engaging in agonistic interactions across females otherwise unexplained by age, rank, residency, or reproductive status. Actors and recipients were diverse, with 22 different females as actors, targeting 29 different females. Certain females were targeted more often than expected given their tenure and independent life span in the community. *Lottie*, *Onyofi*, and *Sula* received more than twice the expected rate of agonism, while *Spini* and *Tatu* were the most disproportionately targeted at 4.8 times of the expected rate. Females with an unexpectedly high rate of agonism directed towards other females were *Bahati*, *Ketie*, *Kipepeo*, *Lottie*, *Monika*, *Ndito-Eve*, *Nora*, and *Rita*, with *Monika* acting agonistic towards other females at 4.8 times and *Ketie* 5.3 times of that of the expected rate. For females who were the actor in more than one agonistic interaction recorded, the distribution of events across targeted females was low (standardized Shannon-Weaver index: H = 0.36 ± 0.20). Diversity of actors for females being targeted by more than one other female was also low (standardized Shannon-Weaver index: H = 0.25 ± 0.16).

Sociality

Mean DAI was 0.11 ± 0.09 across seasons, 0.13 ± 0.08 in the *dry season* and 0.10 ± 0.09 in the *wet season*. Mean PI was 0.19 ± 0.14 across seasons, 0.22 ± 0.14 in the *dry season* and 0.16 ± 0.13 in the *wet season*, while the mean GI was 0.05 ± 0.07 across seasons, 0.07 ± 0.11 in the *dry season* and 0.04 ± 0.04 in the *wet season* (Table 23). Overall, the Waibira females have numerous, but relatively weak relationships with other females of the community across various forms of interactions. However, when looking at individual dyads, the strength of party association, proximity, and grooming relationships can vary between them, with some dyads joining the same party, being in close proximity to each other, or grooming only very occasionally, while others do so often, as suggested by the large differences between mean, maximum, and minimum index values (Table 23).

Table 23

Descriptive Statistics of Index Values Across Seasons

Index type	Mean wet season value ± SD (Range)	Mean dry season value ± SD (Range)	Mean value ± SD (Range)
Party association	0.10 ± 0.09 (0.01-0.80)	0.13 ± 0.08 (0.01-0.57)	0.11 ± 0.09 (0.01-0.80)
Proximity	0.16 ± 0.13 (0.01-1)	0.22 ± 0.14 (0.02-1)	0.19 ± 0.14 (0.01-1)
Grooming	0.04 ± 0.04 (0.01-0.21)	0.07 ± 0.11 (0.01-0.56)	0.05 ± 0.07 (0.01-0.56)

Models of DAI, PI, and GI with $AIC_w \geq 0.01$ are summarised in Table 24. Two models were averaged for the model on party association ($\Delta AIC \leq 1.6$, $w_i \geq 0.31$, Table 24), one with *season, method,* and *neighbour status* as fixed factors and one with *season, method, neighbour status,* and the interaction of *season* and *neighbour status* as fixed factors, resulting in a model with *season, method, neighbour status,* and the interaction of *season* and *neighbour status* as fixed factors; for the model on

proximity (ΔAIC $\leq$ 1.6, $w_i \geq$ 0.30, Table 24), one with *method* as fixed factor and one with *method* and *neighbour status* as fixed factors, with the averaged model including *method* and *neighbour status* as fixed factors; and for the model on grooming (ΔAIC $\leq$ 1.5, $w_i \geq$ 0.31, Table 24), one with *method* and one with *season* and *method* as fixed factors, with the averaged model including *season* and *method* as fixed factors. Model parameters for averaged models are shown in Table 25.

Table 24

Summary of Candidate Models of Seasonal Changes in Sociality With AIC Weights ≥ 0.01

Model	K[1]	AIC[2]	ΔAIC	w_i[3]
DAI				
Season + Method + Neighbours	7	-1587.0	0.0	0.68
Season + Method + Neighbours + Season:Neighbours	8	-1585.4	1.6	0.31
Season + Method	6	-1577.6	9.3	0.01
PI				
Method	5	-787.0	0.0	0.67
Method + Neighbours	6	-785.4	1.6	0.30
Season + Method	6	-779.4	7.6	0.02
Season + Method + Neighbours	7	-778.8	8.2	0.01
GI				
Method	5	-325.0	0.0	0.67
Season + Method	6	-323.5	1.5	0.31
Method + Neighbours	6	-316.9	8.2	0.01
Season + Method + Neighbours	7	-316.0	9.0	0.01
Season + Method + Neighbours + Season:Neighbours	8	-315.9	9.2	0.01

Note. Dependent variables for each model are **bolded.** Candidate model structure is listed underneath each dependent variable. All models are LME models.

[1] Number of parameters. [2] Akaike Information Criterion. [3] AIC weights.

Table 25

Model Parameters for Averaged Models of Seasonal Changes in Sociality

Parameters		Coefficient	CI 95%	SE
DAI				
	Intercept	0.33	0.32-0.35	0.01
	Dry season	0.05	0.04-0.06	0.01
	Fieldwork	-0.01	-0.02-0.00	0.01
	Camera trap	-0.12	-0.15- -0.10	0.01
	Neighbours	0.03	0.02-0.05	0.01
	Neighbours:Dry season	-0.04	-0.07- -0.01	0.01
PI				
	Intercept	0.37	0.35-0.38	0.01
	Fieldwork	0.12	0.08-0.17	0.02
	Camera trap	0.16	0.13-0.18	0.01
	Neighbours	-0.03	-0.05- -0.01	0.01
GI				
	Intercept	0.18	0.16-0.19	0.01
	Dry season	0.04	0.01-0.07	0.01
	Fieldwork	0.20	0.14-0.27	0.03
	Camera trap	0.28	0.19-0.36	0.04

Note. All models are LME models. Factors included are *season*, *method*, and *neighbour status*. Baseline value for *season* is *wet*, *long-term* for *method*, and *non-neighbours* for *neighbour status*.

Party association

Female dyads' tendency to associate with each other on the party level showed seasonal changes: females were more likely to be in the same party during the *dry season* (Table 25, Figure 27). *Neighbour status* interacted with seasonality, as *neighbour* dyads were more likely to be in the same party during the *wet season*, while during the *dry season*, females within the same neighbourhood were less likely

to associate with each other (Table 25, Figure 28). Data collection method also impacted DAI values, with *fieldwork* and *camera trap* data collection yielding higher index values than *long-term* data (Table 25).

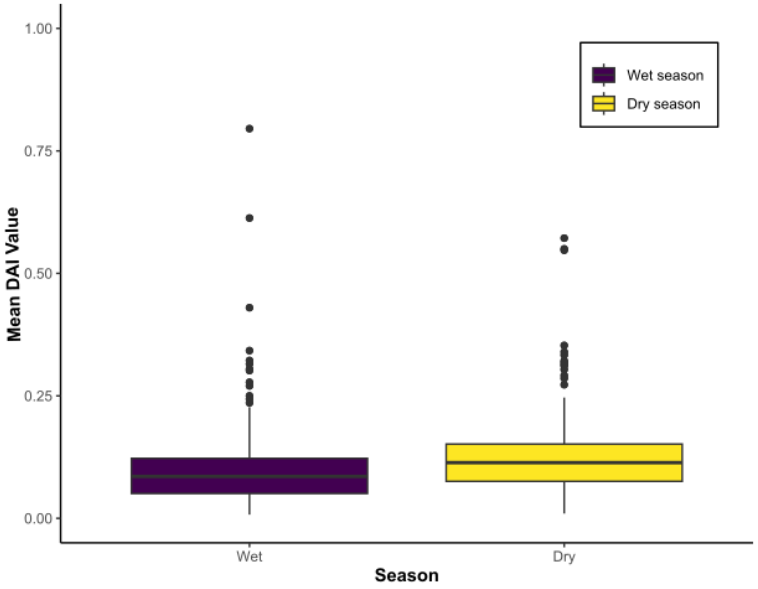


Figure 27

Mean Dyadic Party Association Index Values Across the Wet and Dry Seasons

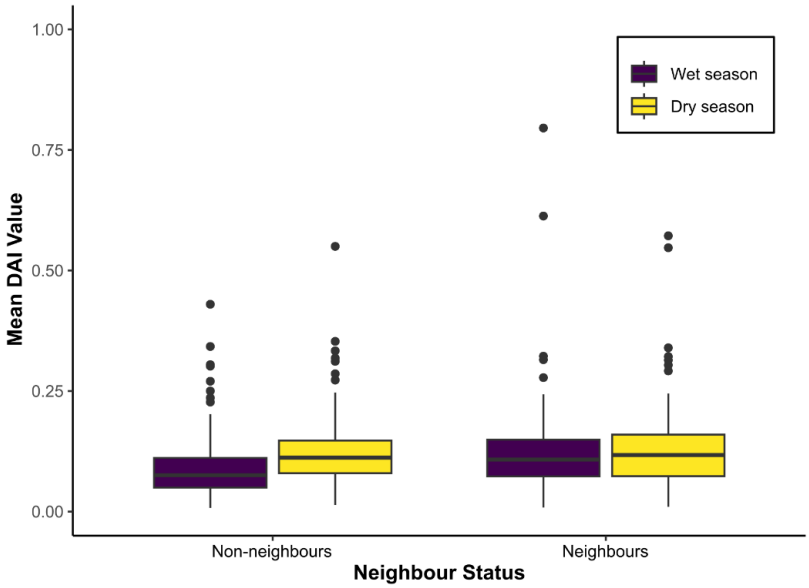


Figure 28

Mean Dyadic Party Association Index Values Across the Wet and Dry Seasons and Non-neighbours and Neighbours

Proximity

The propensity of female dyads to spend time in close proximity with each other remained stable across seasons (Table 25). When in the same party, *neighbour* dyads were less likely to be within 5 m of each other compared to *non-neighbour* dyads (Table 25). Data collection method also impacted PI values, resulting in lower values extracted from *fieldwork* and *camera trap* data (Table 25).

Grooming

Female dyads had more grooming interactions relative to the time spent in the same party during the *dry season* (Table 25, Figure 29), and grooming interactions were independent of spatial overlap (Table 25). GI values were higher in *fieldwork* and *camera trap* data (Table 25).

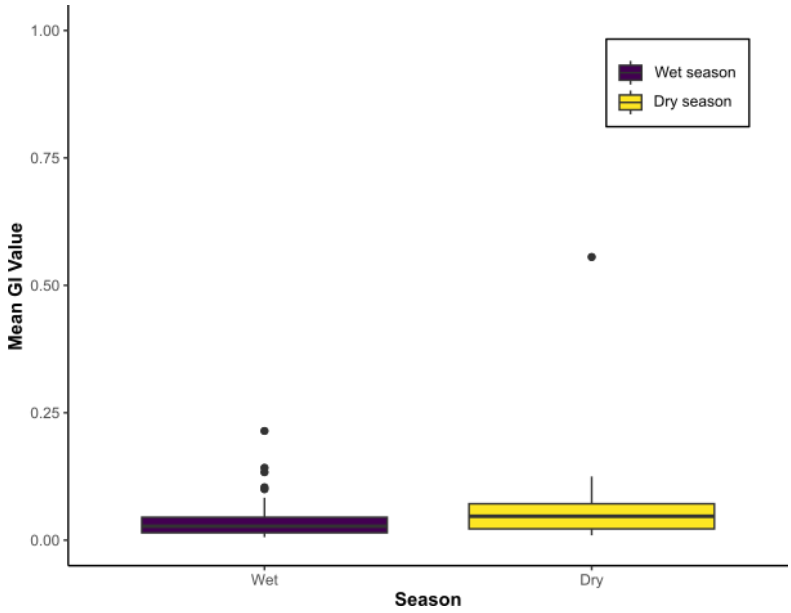


Figure 29

Mean Grooming Index Value Across the Wet and Dry Seasons

Social Structure

Party Association Structure. Females had on average 22.48 ± 7.49 social partners on the level of party association overall, 21.08 ± 8.59 in the *wet season* and 23.42 ± 6.56 in the *dry season*. Mean $DAI_{strength}$ was 1.60 ± 1.00 overall, 1.42 ± 0.64 in the *wet season* and 1.72 ± 1.16 in the *dry season*. Mean $DAI_{transitivity}$ was 0.80 ± 0.12 overall, 0.81 ± 0.12 in the *wet season*, and 0.80 ± 0.12 in the *dry season*, while mean $DAI_{eigenvalue}$ was 0.18 ± 0.08 overall, 0.18 ± 0.09 in the *wet season*, and 0.18 ± 0.07 in the *dry season*. The females in the Waibira community are connected to most other females in their community, as evidenced by their high number of social partners. However, their consistency of associating with the same specific partners across time is relatively low, as evidenced by the low weighted number of partners. Their party association network is characterised by a high number of weak bonds (Figure 30).

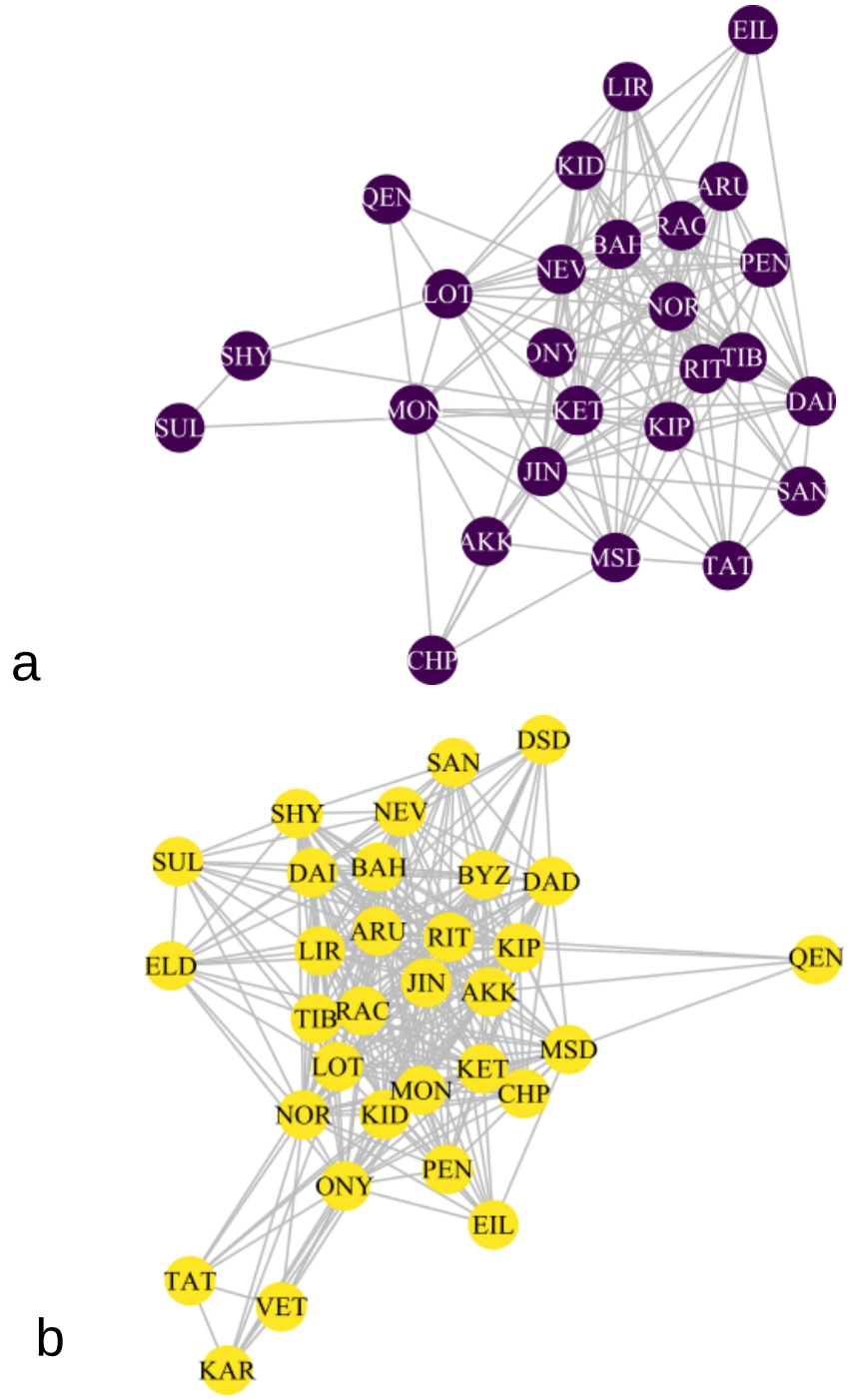


Figure 30

Example Party Association Networks Generated from DAI Values from Fieldwork Data Collection Across the Wet and Dry Seasons

Note. Edges between nodes represent undirected party associations. Edge thickness does not reflect party association frequency. Node placement determined by the Fruchterman-Reingold algorithm, resulting in less connected nodes being placed at a greater distance from each other.

[a] *Wet season* network. [b] *Dry season* network.

Models of DAI_{degree}, $DAI_{strength}$, $DAI_{transitivity}$, and $DAI_{eigenvalue}$ with $AIC_w \geq 0.01$ are summarised in Table 26. One model was chosen as the model on DAI_{degree} (w_i = 0.85, Table 26), including *season, method,* and *rank* as fixed factors; for the model on $DAI_{strength}$ (w_i = 0.84, Table 26), including *season* and *method* as fixed factors; for the model on $DAI_{transitivity}$ (w_i = 0.92, Table 26), including *method* as a fixed factor; and for the model on $DAI_{eigenvalue}$ (w_i = 0.98, Table 26): the null model. Model parameters for top models are shown in Table 27.

Table 26

Summary of Candidate Models of Seasonal Changes in Party Association Structure With AIC Weights ≥ 0.01

Model	K[1]	AIC[2]	ΔAIC	w_i[3]
DAI_{degree} [4]				
Season + Method + Rank	8	787.9	0.0	0.85
Season + Method	5	791.8	3.8	0.13
Method + Rank	7	795.3	7.3	0.02
$DAI_{strength}$ [5]				
Season + Method	6	27.0	0.0	0.84
Season + Method + Rank	9	30.2	3.3	0.16
$DAI_{transitivity}$ [5]				
Method	5	-65.7	0.0	0.92
Season + Method	6	-60.5	5.2	0.07
Method + Rank	8	-57.8	8.0	0.02
$DAI_{eigenvalue}$ [5]				
Null model	3	-231.1	0.0	0.98
Season	4	-222.3	8.8	0.01
Rank	6	-221.9	9.3	0.01

Note. Dependent variables for each model are **bolded.** Candidate model structure is listed underneath each dependent variable.

[1] Number of parameters. [2] Akaike Information Criterion. [3] AIC weights. [4] GLMM. [5] LME.

Table 27

Model Parameters for Top Models of Seasonal Changes in Party Association Structure

Parameters	Coefficient	CI 95%	SE
DAI_{degree} [1]			
Intercept	3.44	3.24-3.64	0.10
Dry season	0.13	0.05-0.22	0.04
Fieldwork	-0.51	-0.60--0.42	0.04
Camera trap	-0.29	-0.40- -0.18	0.05
Mid	0.01	-0.23-0.25	0.11
Mid-low	-0.11	-0.34-0.12	0.11
Low	-0.28	-0.52- -0.05	0.11
$DAI_{strength}$ [2]			
Intercept	1.33	1.22-1.44	0.05
Dry season	0.35	0.27-0.43	0.04
Fieldwork	0.04	-0.04-0.12	0.04
Camera trap	-0.87	-0.98- -0.77	0.05
$DAI_{transitivity}$ [2]			
Intercept	0.72	0.66-0.77	0.03
Fieldwork	-0.25	-0.31- -0.19	0.03
Camera trap	-0.31	-0.38- -0.24	0.04
$DAI_{eigenvalue}$ [2]			
Intercept	0.40	0.36-0.44	0.02

Note. Factors included are *season*, *method*, and *rank*. Baseline value for *season* is *wet*, *long-term* for *method*, and *high* for *rank*.

[1] GLMM. [2] LME.

The Waibira females associated with a higher number of female partners on a party level during the *dry season* compared to the *wet season* (Table 27, Figure 31). A similar seasonal increase in $DAI_{strength}$ suggests that the time they spent in the same party with other females also increased, independent of the change in DAI_{degree}

(Table 27, Figure 32). $DAI_{transitivity}$ and $DAI_{eigenvalue}$ was stable between seasons, suggesting no seasonal cliques or any females with fluctuating embededdness. *Method* impacted the number and weighted number of partners, as well as transitivity, with *fieldwork* and *camera trap* data collection identifying fewer partners for each female and yielding lower transitivity estimates, and fewer weighted partners for *camera trap* data collection (Table 27). Rank also impacted party level sociality, with *low-ranking* females having fewer social partners (Table 27), but not when weighted. Eigenvalue centrality was independent of any factor (Table 27).

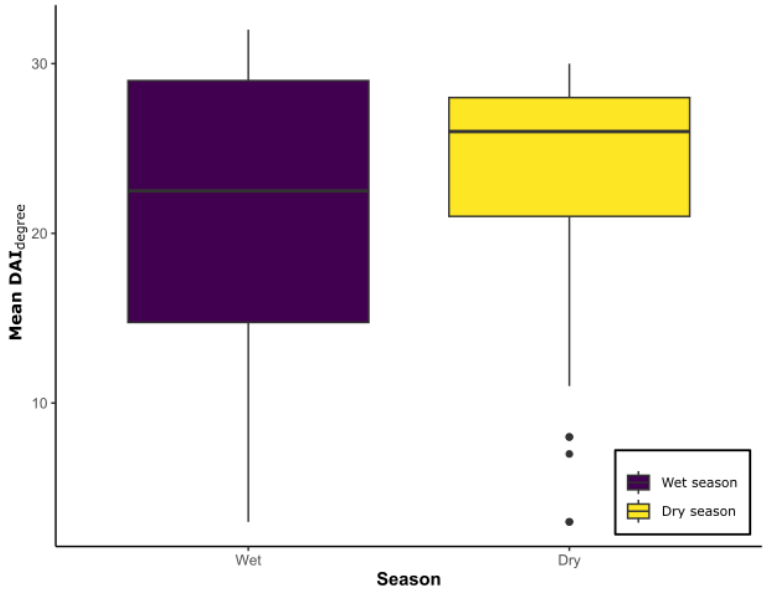


Figure 31

Mean Number of Party Association Partners Across the Wet and Dry Seasons

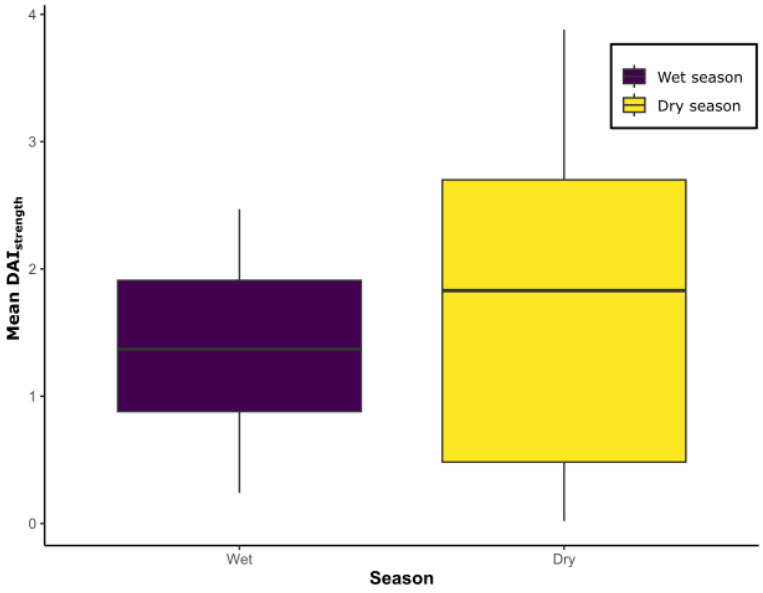


Figure 32

Mean Weighted Number of Party Association Partners Across the Wet and Dry Seasons

Proximity Structure. PI_{degree} was 11.08 ± 8.11 overall, 10 ± 8.45 in the *wet season*, and 11.86 ± 7.83 in the *dry season*. $PI_{strength}$ was 2.37 ± 1.84 overall, 1.73 ± 1.40 in the *wet season* and 2.42 ± 1.90 in the *dry season*. $PI_{transitivity}$ was 0.64 ± 0.24 overall, 0.66 ± 0.30 in the *wet season*, and 0.63 ± 0.18 in the *dry season*, while $PI_{eigenvalue}$ was 0.16 ± 0.12 overall, 0.16 ± 0.14 in the *wet season*, and 0.16 ± 0.11 in the *dry season*. The Waibira females have fewer proximity partners compared to party association partners – they do not come in close contact with every female they associate with on a party level. A smaller difference between number and weighted number of proximity partners suggests more consistent, stronger relationships between proximity partners as well, while transitivity is lower, indicating a less connected network (Figure 33).

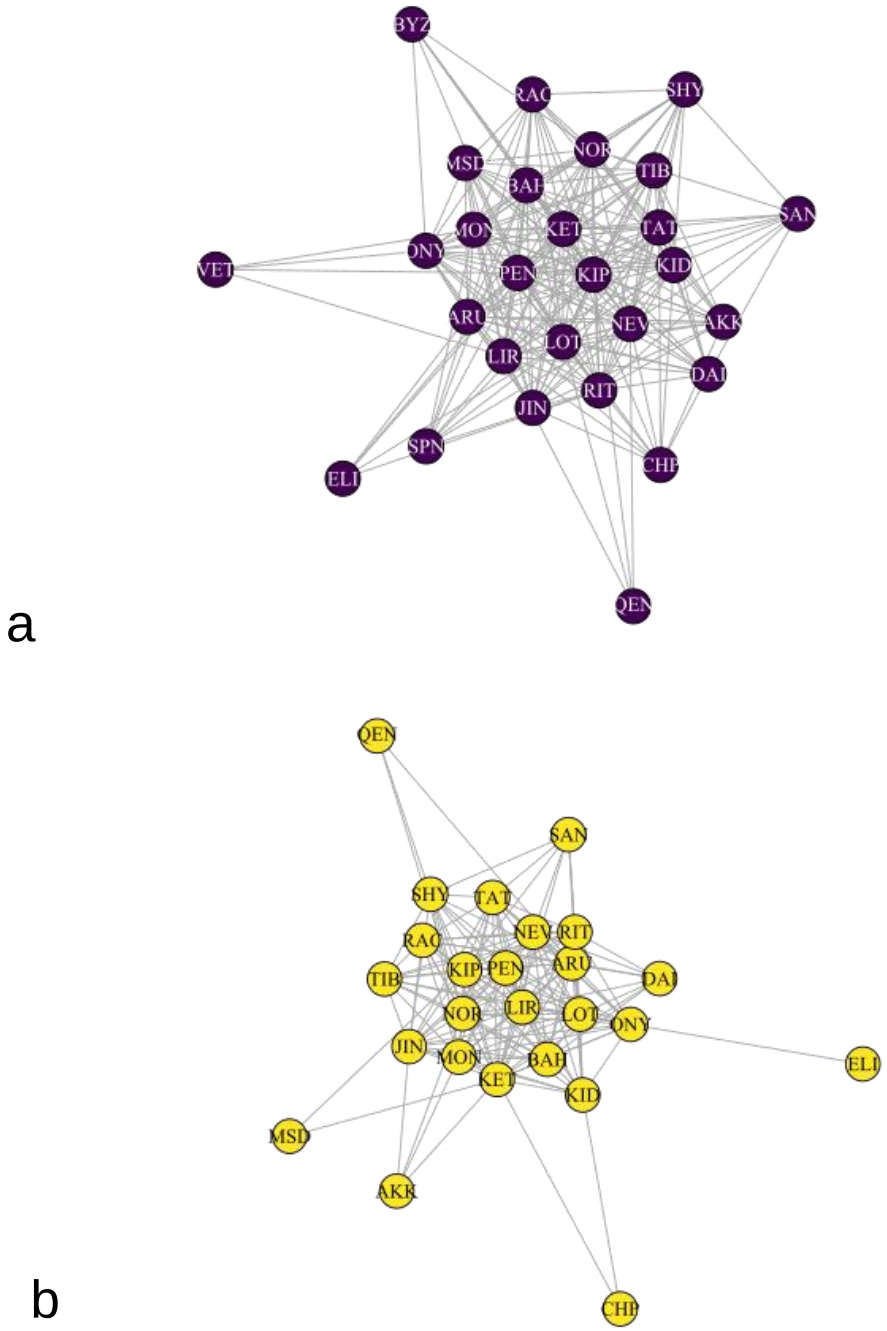


Figure 33

Example Proximity Networks Generated from PI Values from Long-term Data Collection Across the Wet and Dry Seasons

Note. Edges between nodes represent undirected proximity interactions. Edge thickness does not reflect proximity frequency. Node placement determined by the Fruchterman-Reingold algorithm, resulting in less connected nodes being placed at a greater distance from each other.

[a] *Wet season* network. [b] *Dry season* network.

Models of PI_{degree}, $PI_{strength}$, $PI_{transitivity}$, and $PI_{eigenvalue}$ on the level of proximity association with $AIC_w \geq 0.01$ are summarised in Table 28. One top model was chosen as the model on PI_{degree} ($w_i = 0.99$, Table 28), including *season, method,* and *rank* as fixed factors, and for the model on $PI_{strength}$ ($w_i = 0.85$, Table 28), including *method* as a fixed factor. Two models were averaged for the model on $PI_{transitivity}$ ($\Delta AIC \leq 0.8$, $w_i \geq 0.38$, Table 28), one with *season* and *method* and one with *method* as fixed factors, averaged to include *season* and *method* as fixed factors, and one top model was chosen for the model on $PI_{eigenvalue}$ ($w_i = 0.95$, Table 28), with *method* as a fixed factor. Model parameters for top and averaged models are shown in Table 29.

Table 28

Summary of Candidate Models of Seasonal Changes in Proximity Structure With AIC Weights ≥ 0.01

Model	K[1]	AIC[2]	ΔAIC	w_i[3]
PI_{degree}[4]				
Season + Method + Rank	8	543.8	0.0	0.99
Season + Method	5	552.3	8.4	0.01
$PI_{strength}$[5]				
Method	5	116.5	0.0	0.85
Season + Method	6	121.1	4.6	0.09
Method + Rank	8	121.8	5.3	0.06
Season + Method + Rank	9	126.5	9.9	0.01
$PI_{transitivity}$[5]				
Season + Method	6	15.6	0.0	0.55
Method	5	16.4	0.8	0.38
Null model	3	20.0	4.4	0.06
Season	4	22.4	6.8	0.02
$PI_{eigenvalue}$[5]				
Method	5	-47.2	0.0	0.95
Season + Method	6	-41.3	5.9	0.05

Note. Dependent variables for each model are **bolded.** Candidate model structure is listed underneath each dependent variable.

[1] Number of parameters. [2] Akaike Information Criterion. [3] AIC weights. [4] GLMM. [5] LME.

Table 29

Model Parameters for Top and Averaged Models of Seasonal Changes in Proximity Structure

Parameters	Coefficient	CI 95%	SE
PI_{degree}[1]			
Intercept	2.82	2.37-3.26	0.21
Dry season	-0.30	-0.45--0.15	0.07
Fieldwork	-2.16	-2.45- -1.89	0.14
Camera trap	0.33	0.18-0.48	0.33
Mid	0.01	-0.53-0.55	0.26
Mid-low	-0.24	-0.76-0.28	0.25
Low	-0.78	-1.36--0.28	0.26
$PI_{strength}$[2]			
Intercept	1.58	1.46-1.70	0.06
Fieldwork	-1.00	-1.17- -0.83	0.09
Camera trap	0.41	0.22-0.59	0.09
$PI_{transitivity}$[2]			
Intercept	0.55	0.47-0.62	0.04
Dry season	-0.16	-0.28- -0.04	0.06
Fieldwork	-0.30	-0.45- -0.14	0.08
Camera trap	-0.11	-0.25-0.04	0.07
$PI_{eigenvalue}$[2]			
Intercept	0.41	0.36-0.46	0.03
Fieldwork	-0.22	-0.29- -0.14	0.04
Camera trap	0.00	-0.08-0.08	0.04

Note. Factors included are *season*, *method*, and *rank*. Baseline value for *season* is *wet*, *long-term* for *method*, and *high* for *rank*.

[1] GLMM. [2] LME.

Females were in closer proximity with fewer other females during the *dry season* (Table 29, Figure 34). $PI_{strength}$ remained the same between seasons (Table

29), but $PI_{transitivity}$ decreased in the *dry season* (Table 29, Figure 35), resulting in a less connected social network during the *dry season*, where females spent an increased amount of time in close proximity with fewer specific other females. *Method* impacted all characteristics of proximity association. PI_{degree}, $PI_{strength}$, $PI_{transitivity}$, and $PI_{eigenvalue}$ were all lower in networks composed of *fieldwork data*, while *camera trap* networks had higher PI_{degree} and $PI_{strength}$ compared to networks from *long-term* data (Table 29). *Rank* also impacted social networks, with *low-ranking* females having fewer proximity partners (Table 29).

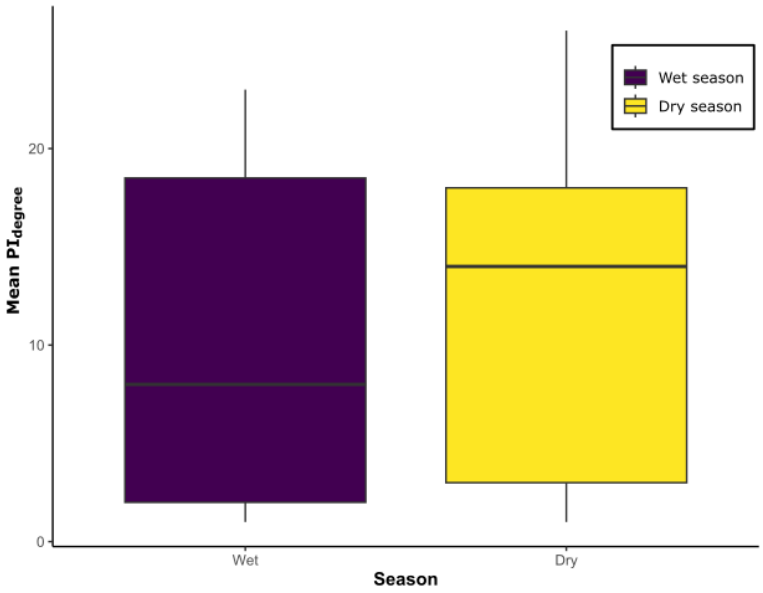


Figure 34

Mean Number of Proximity Partners Across the Wet and Dry Seasons

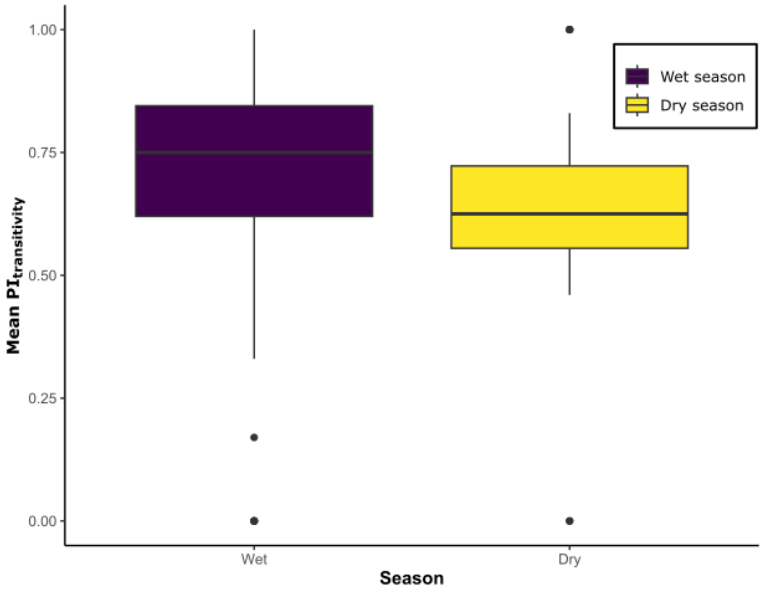


Figure 35

Mean Proximity Transitivity Across the Wet and Dry Seasons

Grooming Structure. Females groomed with a mean 3.77 ± 3.20 other females overall, 5.07 ± 3.60 in the *wet season* and 2.32 ± 1.84 in the *dry season*. $GI_{strength}$ was 0.21 ± 0.15 overall, 0.22 ± 0.14 in the *wet season* and 0.20 ± 0.17 in the *dry season*. $GI_{transitivity}$ was 0.44 ± 0.32 overall, 0.44 ± 0.25 in the *wet season*, and 0.44 ± 0.42 in the *dry season*, while $GI_{eigenvalue}$ was 0.20 ± 0.20 overall, 0.20 ± 0.18 in the *wet season*, and 0.19 ± 0.23 in the *dry season*. Females only have a few grooming partners, with weak grooming relationships and very low connectivity between individuals. Compared to party association and proximity, several females were not observed to give or receive any grooming and are therefore missing from the network (Figure 36).

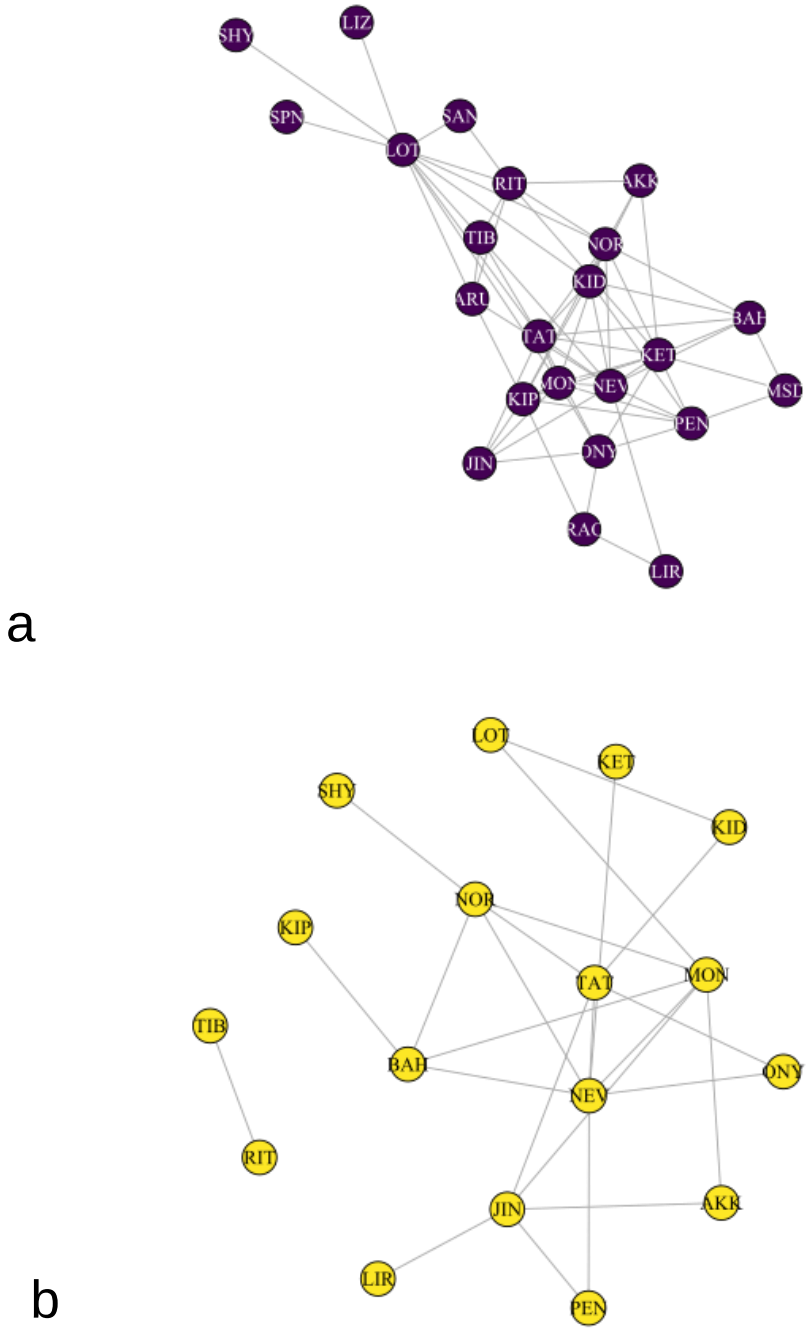


Figure 36

Example Grooming Networks Generated from GI Values from Long-term Data Collection Across the Wet and Dry Seasons

Note. Edges between nodes represent undirected grooming interactions. Edge thickness does not reflect grooming frequency. Node placement determined by the Fruchterman-Reingold algorithm, resulting in less connected nodes being placed at a greater distance from each other.

[a] *Wet season* network. [b] *Dry season* network.

Models of GI_{degree}, $GI_{strength}$, $GI_{transitivity}$ and $GI_{eigenvalue}$ with $AIC_w \geq 0.01$ are summarised in Table 30. One top model was chosen as the model on GI_{degree} (w_i = 0.82, Table 30), with *season, method,* and *rank* as fixed factors, and for the model on $GI_{strength}$ (w_i = 0.91, Table 30): the null model. Three models were averaged for the model on $GI_{transitivity}$ ($\Delta AIC \leq 1.8$, $w_i \geq 0.15$, Table 30): the null model, one with *season* and one with *method* as a fixed factor, averaged to include *season* and *method* as fixed factors, and one top model was chosen for the model on $GI_{eigenvalue}$ (w_i = 0.90, Table 30): the null model. Model parameters for top and averaged models are shown in Table 31.

Table 30

Summary of Candidate Models of Seasonal Changes in Grooming Structure With AIC Weights ≥ 0.01

Model	K[1]	AIC[2]	ΔAIC	w_i[3]
GI_{degree}[4]				
Season + Method + Rank	8	225.7	0.0	0.82
Season + Method	5	228.8	3.1	0.18
$GI_{strength}$[5]				
Null model	3	-29.3	0.0	0.91
Season	4	-24.0	5.3	0.06
Method	5	-21.7	7.7	0.02
$GI_{Transitivity}$[6]				
Null model	2	22.0	0.0	0.37
Method	3	23.8	1.7	0.16
Season	3	23.8	1.8	0.15
Rank	5	24.3	2.3	0.12
Season + Method	4	25.4	3.4	0.07
Method + Rank	6	25.7	3.7	0.06
Season + Rank	6	26.0	4.0	0.05
Season + Method + Rank	7	27.2	5.2	0.03
$GI_{eigenvalue}$[5]				
Null model	3	10.2	0.0	0.90
Season	4	15.6	5.5	0.06
Method	5	16.3	6.1	0.04

Note. Dependent variables for each model are **bolded.** Candidate model structure is listed underneath each dependent variable.

[1] Number of parameters. [2] Akaike Information Criterion. [3] AIC weights. [4] GLMM. [5] LME. [6] LM.

Table 31

Model Parameters for Top and Averaged Models of Seasonal Changes in Grooming Structure

Parameters	Coefficient	CI 95%	SE
GI_{degree}[1]			
Intercept	1.69	1.18-2.17	0.23
Dry season	-0.80	-1.13- -0.49	0.16
Fieldwork	-1.48	-2.20- -0.87	0.33
Camera trap	-1.19	-2.16--0.41	0.44
Mid	-0.10	-0.71-0.50	0.29
Mid-low	-0.37	-1.00-0.22	0.29
Low	-0.86	-1.56- -0.22	0.32
$GI_{strength}$[2]			
Intercept	0.42	0.38-0.47	0.02
$GI_{transitivity}$[3]			
Intercept	0.58	0.47-0.69	0.06
Season	-0.06	-0.29-0.18	0.11
Method	0.09	-0.31-0.49	0.20
$GI_{eigenvalue}$[2]			
Intercept	0.39	0.32-0.46	0.03

Note. Factors included are *season*, *method,* and *rank*. Baseline value for *season* is *wet*, *long-term* for *method*, and *high* for *rank*.

[1] GLMM. [2] LME. [3] LM.

The females of the Waibira community had fewer grooming partners (Table 31, Figure 37), and grooming networks were less connected (Table 31, Figure 38) in the *dry season* compared to the *wet season*, but $GI_{strength}$ stayed the same across seasons (Table 31), suggesting increased grooming interactions in a smaller number of relationships and the formation of grooming cliques during the *dry season*. *Method* also had an impact on grooming network measures – GI_{degree} was lower both in

fieldwork and *camera trap* grooming networks, while GIt$_{ransitivity}$ also varied between data collection types (Table 31). Regarding *rank*, *low-ranking* females had fewer grooming partners compared to others (Table 31).

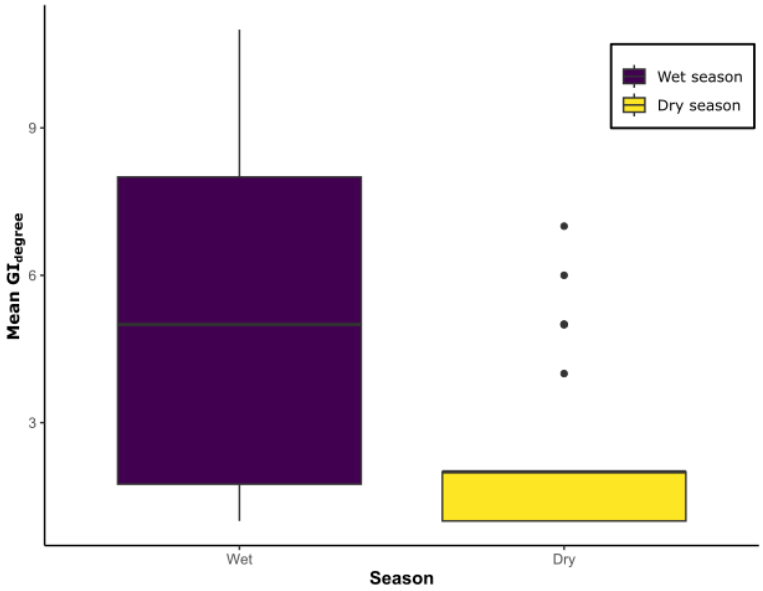


Figure 37

Mean Number of Grooming Partners Across the Wet and Dry Seasons

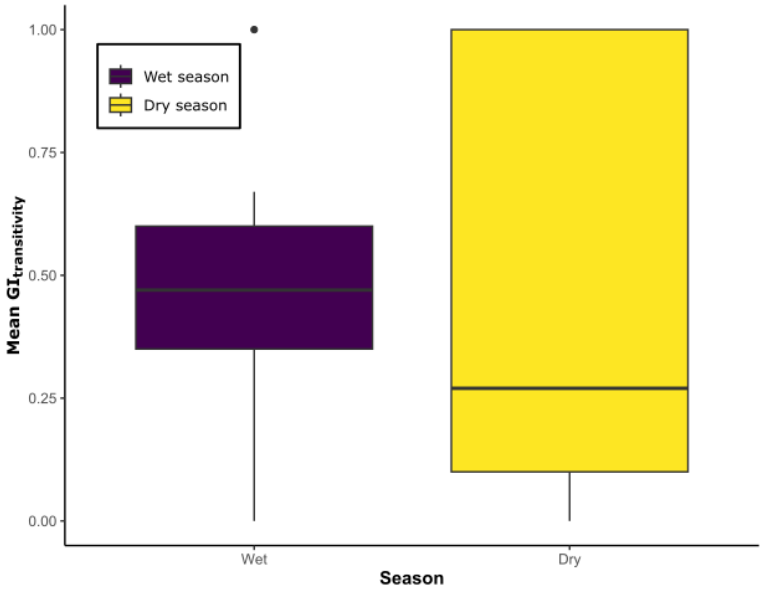


Figure 38

Mean Transitivity of Grooming Associations Across the Wet and Dry Seasons

Discussion

Female chimpanzee social behaviour changes in line with water availability. Gregariousness increased during the dry season water shortage, as females were in parties with both more male and female associates. The rates of agonistic interactions between females remained stable across seasons, both pooled across all contexts, and when looking at interactions at the central waterhole only. The increase in gregariousness, joined with seasonally stable agonism rates suggest that resource competition between females in the Waibira community does not increase significantly between seasons. Water shortage also corresponded to changes in female relationships and social structure. The females of the Waibira community interacted more often with a higher number of other females on the party level during the dry season, but focused their proximity and grooming interactions on a few specific relationships. They were in close proximity with fewer other females during the dry season, and groomed with fewer partners as well, resulting in lower social connectivity in those networks, or the formation of social ‘cliques’. Similar

prioritisation of a select number of relationships has been seen as a response to stressful situations in other primate species (Crockford et al. 2008; Engh et al. 2005; Wittig et al., 2008) and male chimpanzees (Kaburu & Newton-Fisher, 2013) and warrants further study.

Other ecological and individual variables also changed with sociality, in line with existing studies from other chimpanzee communities. Gregariousness increased with high food availability, as seen at several eastern and western chimpanzee sites (Nyungwe: Matthews et al., 2021; Gombe: Murray et al., 2006; Taï: Riedel et al., 2011; Wittiger & Boesch, 2013; Mahale: Sakura, 1994). A slight degree of social senescence (Thompson González et al., 2021) is also possibly present, with the females in the community showing a small, but steady continous decrease in gregariousness as they age. Females increased their gregariousness with mating competition and when tumescent, similar to those in Taï (Wittiger & Boesch, 2013) – this could be due to the femalesactively seeking out mating opportunities (Newton-Fisher, 2014), evidenced not only by a higher number of male associates, but a decrease in the number of female associates when sexually receptive. Mothers of old infants also had more female associates. However, water availability was present as a clear predictor for all models of gregariousness, models of DAI and GI values, and all models of social structure, highlighting that it is a key shaper of chimpanzee behaviour, even in a rainforest environment.

Gregariousness During a Water Shortage

As opposed to predictions about the dry season water shortage introducing subtle within-group competition for water, or indirectly for food, the females in the Waibira community were more gregarious during the dry season compared to the wet season. Despite their space use being restricted to a smaller area and a considerable increase in core area overlaps during the dry season (Chapter 4), they

did not show an increased avoidance, but rather the opposite. The first explanation is that increased gregariousness is simply due to increased spatial overlap at the location of the central waterhole between female core areas during the dry season, a passive association. Constraining their ranging to a smaller area increases the chances of encountering other individuals, especially if they all have to visit an essential resource location on a daily basis. However, core areas are still large enough and visits to the central waterhole short enough in duration (Chapter 4) to still allow females the option to forage alone for the rest of the day, suggesting that the observed increase in gregariousness is at least partially active, and that levels of within-group competition are not higher in the dry season.

The high level of gregariousness seen in the Waibira females, even with the dry season space use changes described in Chapter 4 effectively increasing population density, are likely due to the stable, year-round food availability in the community's home range (Villioth et al., 2022), and supports the view that food availability in the Budongo Forest might be high and/or stable enough not to restrict female behaviour to the extent seen at other long-term field sites (Villioth et al., 2022, 2023). However, further research is needed on why female gregariousness does not only remain high during the dry season, with higher spatial overlap, lower food availability, and lower water availability, but increases compared to the wet season. Besides general food availability, species diversity also contributes to optimal foraging group size in fission-fusion primate societies (Indochinese gray langurs: Pengfei et al., 2015) and could be one reason – recent research on the foraging ecology of the Waibira community shows high dietary diversity, with a high proportion of young leaves and seeds consumed depending on season (Villioth et al., in prep.). Specifically, the seeds of *Cynometra alexandrii* are a dominant food source for the community during the dry season, and have a less patchy distribution

across the Waibira community's home range compared to *Ficus* species (Villioth et al., in prep.). Joined with the central waterhole restricting the maximum extent of ranging during the dry season, seasonal changes in food patch distribution, instead of food availability, could also result in increased gregariousness.

Another possible explanation is that the Waibira females use gregariousness as a mitigation measure for dehydration stress experienced during the dry season. Wild chimpanzees experience significant increases in glucocorticoid levels during the dry season (Wessling et al., 2018a; Wessling et al., 2018a), even in forest environments with a high number of seasonally stable, flowing water sources (E. Wessling, pers. comm.) The stress the annual water shortage could pose in the Waibira community potentially outweighs that of any increase in within-group competition, with increased effort towards social opportunities more beneficial to reproductive success. Future research could focus on fine-scale foraging decisions, incorporating patch size and distribution both for food and water within a habitat, as well as collecting data on nutritional and hydration status and stress levels to unpick whether those contribute to increased dry season gregariousness and understand how the females in the community balance within-group competition, energetics, hydration, and stress.

Nevertheless the extent of active and passive association, alternative explanations, such as predation risk (Boesch, 1991) or visits to the central waterhole increasing gregariousness can be ruled out. To date there has been no observational or camera trap evidence for the presence of any lions or leopards (*Panthera pardus*), the natural predators of chimpanzees (Boesch, 1991; Tsukahara, 1993), in the Waibira community home range. The average duration and frequency of visits to the waterhole (Chapter 4) are also not sufficiently high to explain the increased number of associates during the dry season.

Other factors impacting gregariousness are in line with previous studies. Increased food availability corresponds to an increase in the number of both male and female associates (Nyungwe: Matthews et al., 2021; Gombe: Murray et al., 2006; Taï: Riedel et al., 2011; Wittiger & Boesch, 2013; Mahale: Sakura, 1994), with larger and higher quality food patches able to support a higher number of foragers (Stephens & Krebs, 1986). The number of sexually receptive females present in the community at a given time point is also positively correlated with female gregariousness (Taï: Wittiger & Boesch, 2013; Kalinzu: Shibata et al., 2022; Nyungwe: Matthews et al., 2021).

Rank had no impact on gregariousness, even in interaction with food availability, as opposed to the findings of Riedel et al. (2011). High-ranking females were not less constrained by subtle competition compared to females of other rank categories; females had a similar number of associates regardless of rank categories. The relatively high and stable food availability in Waibira (Villioth et al., 2022, 2023) could be one possible explanation of the lack of rank differences.

Females with anogenital swellings had more male associates, which can be explained by males being drawn to sexually available females. However, females with swellings also had fewer female associates, which suggests an active role in the sex distribution of associates, and a seeking out of mating opportunities (Newton-Fisher, 2014). Mothers of older infants had more female associates, likely seeking out the offspring socialising (Lonsdorf et al., 2014; Williams et al., 2002a) and allomothering benefits of being around other mothers (bonobos: Cheng et al., 2022; Moscovice et al., 2017). Interestingly, mothers of young infants did not decrease their number of either male or female associates, suggesting low infanticide avoidance efforts (Gursky et al., 2002; Lowe et al., 2019; Nishie & Nakamura, 2018). However, to date, within-community infanticide is relatively rare in Waibira, with only

two male-led infanticides, and one female-led infanticide, documented since 2011. The two male-led infanticides were against the third infant of *Elodie*, a less habituated resident female, and the first infant of *Monika,* a young, high-ranking immigrant from the Sonso community, while the female-led infanticide was committed by the same *Monika*, after the birth of her second infant, against the third infant of *Byazi,* a less habituated resident female with unknown rank. There has also been no rapid rank ascension by any Waibira males so far, which has been connected to an increased chance of male-led infanticide (Lowe et al., 2019). As such, females, especially multiparous, more habituated residents, either are not at risk of infanticide, or use gregariousness as a protective measure (Pusey et al., 2008; Wellens et al., 2022).

Agonism During a Water Shortage

The rate of female-female agonistic interactions remained stable across seasons for all three data collection methods. Joined with the lack of a seasonal decrease in gregariousness during the dry season, these findings suggest that the annual dry season water shortage does not significantly increase within-community competition either directly, for water, or indirectly, for food. The rate of agonistic interactions at the waterhole suggests that water competition also did not increase, even though high, daily drinking frequency (Chapter 3) and space use changes facilitating access to the central waterhole (Chapter 4) support that it is an essential resource for chimpanzees. Future research can incorporate recent methodological innovations in addition to camera trap data collection at the central waterhole, such as observational data collection from the crowns of feeding trees (Houle & Wrangham, 2021), to record more accurate rates of agonistic interactions, and get a more precise picture of how seasonal water shortage impacts female competition.

While there was no seasonal change in agonism rates, or an increase in agonism rates at the central waterhole, agonism did occasionally take place over water sources. The two recorded events that were over water were for priority access or access at convenient or more comfortable locations. In both cases, the target drank from the same water source as the aggressor once they finished drinking. In the first case, *Fiddich*, a low-ranking subadult male was threatened and displaced from a dendrotelmata by *Macallan*, a high-ranking adult male. *Macallan* then dipped water from the dendrotelmata using a drinking tool, alternating with *Monika*, a high-ranking female who had a newborn at the time. After the two were done drinking, *Fiddich* approached the dendrotelmata, reused a drinking tool, and drank until he left of his own volition, likely having slaked his thirst. When I have checked the dendrotelmata after his departure, it still contained water, approximately 15 cm deep. In the second case, *Ketie*, a mid-low-ranking female produced an arm swing threat and screamed at *Onyofi,* a low-ranking female approaching the location *Ketie* was drinking from at the broader part of the central waterhole. *Onyofi* retreated and drank directly from the central waterhole at a different location a few meters away, while *Ketie* and her infant son also drank directly after the interaction. The presence of occasional water competition suggests that, similar to leaves and grass, contest competition can occur for non-monopolisable resources (Jarvey et al., 2023; Koenig, 1998) due to varying quality of patches (Koenig, 1998). However, as severe agonism, including physical aggression has only been documented in a primate population undergoing catastrophic drought (Wrangham, 1981), it is likely that the dry season water shortage does not pose a sufficiently severe water competition scenario for females to engage in overt water competition.

With regards to patterns of agonistic interactions across individual characteristics, age, reproductive status, and residency status all had an impact.

Agonistic interactions between females of the same age group were also more common compared to targeting older or younger females. Reproductive and residency status also acted on the chances of receiving and committing agonism, in line with the changing importance of access to various resources at various life stages. Pregnant females and those with anogenital swellings were the most likely to target other females – pregnant females are the least constrained by risk of injury or death to their infants or physically hindered by infant carrying, while sexually available females can engage in overt mating competition. Females with swellings were also the most common targets. The clear targeting of immigrants seen in other communities was also present (Kahlenberg et al., 2008a, 2008b; Nishida et al., 1989), with the resident Waibira females making an active effort to either oust newly arrived females from their community or prevent them from settling in high quality areas, suggesting that some level of within-group competition is still present, despite the high, non-restrictive food availability (Villioth et al., 2022).

Finally, there was high individual variation in agonistic interactions, similar to what Furuichi (1997) noted between female bonobos – certain females were much more agonistic than expected, while others were more likely to be targeted. *Ketie,* a mid-low-ranking parous female, and *Monika,* a high-ranking parous female, were the most aggressive. *Monika* is responsible for the only female-led infanticide in the community so far, and is noticeably younger than the other two high-ranking females, being born in 2003 compared to *Lottie'*s 1984 or *Rita*'s 1980 estimated birth date. It is possible that both *Ketie* and *Monika* are pursuing a highly competitive rank attainment strategy, as seen in some female bonobos (Furuichi, 1997), instead of an age-related queueing for rank more common both in female chimpanzees (Foerster et al., 2016) and most female bonobos (Furuichi, 1997).

Tatu and *Spini* were disproportionately targeted, followed by *Lottie, Onyofi,* and *Sula.* Two of them, *Tatu* and *Onyofi,* are nulliparous, low-ranking immigrant females, who also have permanent disabilities due to snare injuries. *Spini* and *Sula* are two natal subadult females, with *Spini* orphaned since February 2018 and *Sula* the daughter of low-ranking *Shay.* In their case, persistent harassment is likely to 'encourage' emigration from the community – while daughters of high-ranking females were in a more beneficial position if remaining in their natal communities, daughters of low-ranking females, and especially orphaned females attained much worse reproductive success doing so in Gombe (Walker et al., 2018). While *Sula* is still regularly seen by observers in 2024, *Spini* was last seen March 2021 and presumed to have emigrated (C. Hobaiter, pers. comm.). *Lottie* however is neither a recent immigrant, nor a subadult, but a high-ranking resident female. In her case, the high chance of being targeted is likely due to a high chance of retaliation. This pattern is similar to what was seen in Chapter 4, with both high- and low-ranking females ranging more widely compared to mid- and mid-low-ranking females. As in that case, high-ranking females are likely to have a sufficient energetic status to easily take on the costs of being targeted without it particularly affecting their reproductive success, while low-ranking females take the costs of being targeted unwillingly. Long-term monitoring of the changes in agonistic interactions between females can determine whether persistent harassment of immigrants tapers after the birth of their first offspring, and known gene flow between the Sonso and Waibira communities (Samuni et al., 2014) could also allow for comparison of agonism received and committed in their natal and new communities, and whether maternal agonism styles are present.

Relationships & Social Structure

The Waibira females showed changes in their relationships and social structure with changing water availability. These patterns were similar to that seen in other primate species experiencing and successfully mitigating periods of stress (Crockford et al. 2008; Engh et al., 2006; Wittig et al., 2008) and male chimpanzees experiencing social instability (Kaburu & Newton-Fisher, 2013), with a decrease in the number of social partners, but increased interaction rates with them showing a focused effort towards specific relationships. Future studies should investigate whether an increase in stress is detectable during the dry season, and whether it correlates with dehydration, social instability, food competition, or other factors.

Dyadic party association interactions were more common in the dry season, which is most probably a product of increased gregariousness rates. While females were in the same party with other females in the same neighbourhood in the wet season, that pattern disappeared in the dry season: there, party association was less likely for females with a high spatial overlap, suggesting active dyadic party association, with high between-dyad variation, suggesting some females associating more frequently than others. Regarding structure, dyadic party association structure was characterised by many weak and few strong bonds, though there was a high variation in DAI values. Connectivity was high, with no evident subgrouping other than a peripheral-central structure. However, peripheral females were also less habituated, and their lower number of partners and weaker relationships could stem from their low habituation status preventing them from associating to other females to the full extent in front of observers. During the dry season, females had more partners, and spent more time with them, again, likely a consequence of higher dry season gregariousness. Low-ranking females had fewer partners, likely constrained from enjoying socialising by the observed higher rates of being targeted by agonism

(Markham et al., 2016), but spent more time with them as a compensatory strategy, leading to a similar level of weighted connections.

Proximity interactions were overall weaker than dyadic party association, suggesting that females were not in close proximity with every female they were in the same party with. Active choice of proximity partners (Newton-Fisher, 2002) is supported by PI values being not only independent of space use overlap, but being lower between neighbours. During the dry season, females focused their social effort by having fewer proximity partners, but were found more consistently in close proximity to them, leading to weighted relationship values remaining the same across seasons. Network connectedness also decreased during the dry season, with the centre-periphery divide increasing. Low-ranking females were in close proximity to fewer partners compared to the time they spent in parties. This could be driven by agonism avoidance, with low-ranking females attempting to avoid harassment by staying at a distance that does not allow for physical aggression and puts enough distance between them and potential aggressors to flee in time, or a form of extremely subtle food competition, where instead of the number of competitors within a party, females minimise the number of competitors within their immediate vicinity only (Saj & Sicote, 2007). The Waibira females spent more time in specific proximity relationships during the dry season, and while convenient access to water might draw them to the same party, proximity partnership provides a possibility for active control of social interactions.

Grooming interactions were relatively rare between females in the Waibira community, but showed seasonal changes. Prioritisation of specific grooming relationships was extreme during the dry season, with the number of grooming partner and overall network connectivity decreasing leading to the formation of clear ‘cliques’ of grooming unconnected to each other. One dyad, mother-daughter duo

Rita and *Tibu* were completely disconnected from the other females during the dry season. Grooming was an active form of association, negatively correlated with neighbour status. As grooming was less frequent between females with a higher spatial overlap, or more commonly done by low-ranking females, it is unlikely its function for the Waibira females is trading for feeding or general tolerance (Foerster et al., 2015). Based on studies in baboons (Crockford et al. 2008; Engh et al., 2006; Wittig et al., 2008), similar changes in grooming networks correlate to a lowering of stress hormones, which I propose as a likely function of the increased seasonal grooming effort by the Waibira females. However, future research on hormone levels between and within seasons would be necessary to determine the exact correlates and to confirm the seasonality of stress; whether it is dehydration (Wessling et al., 2018a, 2018b), or social instability (Engh et al., 2006; Newton-Fisher, 2002).

Finally, data collection method also had an impact on index values as well as social network measures. While studies cross-validating sociality measures between observational and camera trap data (McCarthy et al., 2018; 2019; van Leeuwen et al., 2020b) suggest generally similar trends detected by a two methods and only slight variation in values, fieldwork and long-term data in the current study yielded significantly different values. There are multiple possible reasons for this. First, fieldwork and long-term data collection employed different methods of locating chimpanzees, with fieldwork data collection aiming to locate female chimpanzees specifically, while long-term data collection aiming to locate any travel party of chimpanzees (Chapter 2). This could have led to recording more party composition scans where females were in the same party during fieldwork. Second, camera trap data collection could have yielded different measures of relationships and social structure by (a) having a limited view, and not capturing the entire party, (b) being located at a resource of high ecological importance that chimpanzees visit for a short

duration of time compared to feeding trees or during travel (Koops et al., 2024), where observational data is most often collected, or (c) genuinely capturing differences between how and which individuals female chimpanzees interact with at the central waterhole versus in other contexts. Compared to the studies of McCarthy et al. (2018, 2019), camera traps in Waibira are not placed in a grid system, ensuring equal sampling across the community home range, but so far has focused on specific high use areas of the central waterhole. While camera traps are extremely useful in monitoring chimpanzees that are not yet habituated or cannot be habituated for ethical reasons (Boyer-Ontl & Pruetz, 2014; Ibnou et al., 2018), or locations of high ecological importance (Boyerl-Ontl & Pruetz, 2020; Koops et al., 2019), including the waterhole in the current study, further cross-validation of methods is necessary in the future, comparing measures gained from observational data collection collected by various sampling approaches, as well as camera trap data collected at various types of locations within- and between field sites.

General Conclusion

This chapter further supports that water is a key resource for chimpanzees across all habitat types and as such should be included as a variable alongside other socioecological factors in models of chimpanzee, and in general, animal social behaviour. Water availability corresponds to changes in female gregariousness, relationships, and social networks, likely via increasing stress levels. Gregariousness increased, while proximity and grooming relationships showed higher prioritisation during the dry season water shortage. However, neither subtle or over competition, indicated by a decrease in gregariousness or increase in agonistic interaction rates, happened during the dry season; water competition is very rare and only extends to gestural threats over priority access to drinking locations. The exact mechanisms by which the water shortage leads to an increase in gregariousness and effort invested

into specific proximity and grooming relationships are still to be unpicked. Collecting urine samples in addition to observational data, similar to Wessling et al. (2018b) can measure how the hydration and stress levels of the Waibira chimpanzees vary between- and within-seasons, and test whether increased association aids in reducing potential stress experienced from dehydration. Adding fine-scale space use analyses can also detect if the stress is instead due to social upheaval and the seasonal dissolution of core areas, comparing changes in space use overlap degree and partners, as well as core area centres with fluctuations in stress levels. Inter-site comparisons on how water availability impacts female sociality are also necessary to uncover more about how water as a resource acts on chimpanzee behaviour.

The observed lack of competition for water also warrants further investigation, as it otherwise seems to be an important enough resource that a shortage of it impacts female core areas (Chapter 4), sociality and induces stress (Wessling et al., 2018a, 2018b). It could be that as the central waterhole did not run completely dry in any of the ten dry seasons covered by this study, the water was never sufficiently limited to provoke competition. Alternatively, chimpanzees' mental concept of water might be fundamentally different from that of other form of consumables, either due to previous experiences with water or cognitive limitations. The experience of consuming a food item in its entirety is different from completely consuming a water source, especially a terrestrial water source. While the former is frequently experienced by a chimpanzee, be it a fig, leaves, or a blue monkey, the latter is impossible to achieve for a single chimpanzee with the exception of shallower dendrotelmata. The different types of quantities could also pose a limit – fruit and leaves are distinct, individual physical objects, while water can only be quantified by area or volume, though captive chimpanzees performed equally well on tests of distinguishing different quantities of discrete and continuous quantities (Beran,

2010). In general, water, as a resource, acts on female chimpanzee sociality differently than food. As opposed to food shortages, water shortages increase their gregariousness, both measured as the likelihood of associating with other individuals and as party size, and while agonistic interactions increase with water shortages, it is not in the context of the resource of which there is a drastic shortage.

On a broader scale, this chapter demonstrates that water availability acts on hominid social behaviour even in mesic environments and highlights the need for assessing water availability in a habitat separately from habitat type. The findings challenge the notion that early hominins first faced difficulties maintaining their water balance and the need to develop adaptations after leaving rainforests to inhabit mosaic forest and savannah environments (Pontzer et al., 2021; Wheeler, 1993). The Waibira chimpanzee community, despite being a rainforest-living community, both experiences low water availability, even if only seasonally, and shows behavioural adaptations to cope with it, including altering their space use patterns (Chapter 4) and their social behaviour. Joining research on other behavioural strategies for managing water needs by savannah chimpanzees (Boyer-Ontl & Pruetz, 2020; Pruetz, 2018; Pruetz & Bertolani, 2007), it suggests that regardless of the timescale of species range shift in early human species from rainforests towards more arid environments, behavioural adaptations to water scarcity likely already existed in early hominins. Instead of dealing with a novel resource constraint, and according to some, a novel need to drink water (Pontzer et al., 2021), inhabiting hotter, more open environments likely only meant experiencing an increase in water constraint, as well as general water needs due to high temperatures and direct sun exposure (Wheeler, 1991, 1993), and therefore an increase in the extent and frequency of relying on spatial, social, and tool-use behavioural adaptations already present to manage their water balance instead of the appearance of completely

novel behavioural strategies. However, it is important to note that pre-existing behavioural adaptations to increased water needs or water scarcity do not negate the evolution of physiological adaptations to hotter, more open habitats that occurred during human evolution (Franciscus & Trinkaus, 1988; Lieberman, 2015; Pontzer et al., 2021; Wheeler, 1991).

Additionally, a decoupling of habitat type and water availability will also benefit evolutionary anthropology and archaeology, not just ecology and conservation. As demonstrated in this thesis, rainforest populations can experience extremely low water availability, despite high annual precipitation and high forest cover, while other studies on chimpanzees from marginal mosaic forest habitats report multiple flowing water sources available to their study community all year (Giuliano et al., 2022). While mosaic forest and savannah populations do experience higher temperatures, lower annual precipitation, and lower tree coverage, all of which increase thermoregulation and water needs (Lopes & Bicca-Marques, 2017; Stelzner, 1988), water availability at a specific habitat also depends on other geological properties (Belnap et al., 2005; e.g.: Boroski & Mossman, 1996; Lanjouw, 2002), leading to discrepancy between general mesic or arid habitat categorisation and local water availability. Therefore, early hominins might have had to adapt to high seasonal variation and resource constraints, theorised to be a driver behind the evolution of the genus *Homo* upon experiencing increased aridification and savannah expansion (aridity hypothesis: deMenocal, 1995; pulse climate variability hypothesis: Maslin & Trauth, 2009), to some extent prior to that timeframe. While paleoclimate and paleoenvironmental studies offer reconstructions of the environment of early hominins, in addition to vegetation cover (Carto et al., 2009), temperature, and precipitation (Sepulchre et al., 2006), modelling hypothetical water availability and the distribution of water sources in early human environments could help further

unpick the contribution of each of those factors to human evolution. Along with results from previous chapters, this chapter further emphasises the importance of including water as a discrete variable in models of animal behaviour, as it impacts social behaviour, but despite being a consumable resource, it does so in ways absolutely unlike food.

Chapter 6

Discussion

- Rainforest chimpanzees are dependent on free water
- Water availability corresponds to changes in chimpanzee behaviour in mesic environments
- Small terrestrial and arboreal water sources are important ecological features
- Water is a limiting resource in an equatorial rainforest in Africa

In this thesis, I have demonstrated that water is a regularly consumed resource by wild eastern chimpanzees (*Pan troglodytes schweinfurthii*) living in Waibira community of the Budongo Forest Reserve, Uganda. As evidenced by changes in their space use and social behaviour in line with water availability, I also showed that water is not only a regularly consumed resource, but a limiting one for them. Given that the Budongo Forest has one of the highest annual precipitation rates out of all long-term chimpanzee research sites (Wessling et al., 2018a), the findings support that water is a key resource for chimpanzees across all habitat types, and that its availability can considerably shape their behaviour even outside of extremely arid habitats at their species range edge (Wessling et al., 2020). On a broader level, the thesis also provides an example of water being an essential resource in a mesic environment in equatorial Africa.

Main Findings

The eastern chimpanzees of the Waibira community drink regularly, on a daily basis. While the chimpanzees drink more often in the dry season, frequent drinking behaviour is present year-round, and is not induced by higher temperatures as seen

in another rainforest-living great ape species (mountain gorillas (*Gorilla beringei beringei*): Watts et al., 2022). When available, the chimpanzees predominantly drink from arboreal water sources as opposed to terrestrial ones. The exclusive use of the terrestrial central waterhole during the dry season suggests that small arboreal water bodies, mostly dendrotelmata, evaporate and/or are fully exploited by the beginning of the dry season, and that terrestrial water bodies are important fallback options in equatorial rainforests.

Besides regular drinking behaviour by all regularly seen members of the community above the age of two, I also recorded several instances of voluntary water-contact behaviour, both in immature and mature individuals. Contrary to the hypothesis of chimpanzees being hydrophobic (McGrew, 1977; Yerkes, 1943), the chimpanzees in the Waibira community do not show any fear towards stepping or reaching into water or otherwise becoming wet, and rather respond with aversion (Angus, 1971; Nishida, 1980) that is easily overcome during play, the reuse of drinking tools (Péter, 2019), or manual well-digging (Péter et al., 2022). Similar to populations in savannah environments (Pruetz, 2007; Pruetz & Bertolani, 2009), rainforest chimpanzees frequently interact with water, mostly for the purpose of drinking, though non-drinking voluntary water-contact behaviour also occurs.

Space use and social behaviour also show major seasonal changes corresponding to variation in the availability and distribution of water sources within the community's home range. During the dry season, a period of low water availability, female chimpanzee space use is likely constrained by access to water. Maximum range size decreases, and core areas concentrate on the remaining terrestrial water source, the central waterhole. Spatial overlap between female core areas increases as well, suggesting that females prioritise access to water over lower levels of scramble competition for resources. Water acts as a spatial pull

factor, similar to what is seen in other species, constraining the maximum distance individuals can travel away from water sources (olive baboons (*Papio anubis*): Barton et al., 1992; American badgers (*Taxidea taxus*): Piper, 2021; African elephants (*Loxodonta africana*): Purdon & Van Aarde, 2017), and determining areas of high usage frequency (red-fronted lemurs (*Eulemur rufifrons*): Amoroso et al., 2020a; white-faced capuchins (*Cebus capuchinus*): Campos & Fedigan, 2009; Tana River red colobus (*Piliocolobus rufomitratus*): Kimanze et al., 2019; white naped mangabeys (*Cercocebus lunulatus*): Outtara et al., 2019) during periods of low water availability.

Gregariousness increases during periods of water shortage, with female chimpanzees being found in larger parties and associating with a broader scope of party-level associates during it. However, closer relationships show the opposite pattern: females have fewer social partners they are in close proximity with, or groom with, but interact with them more during the dry season. These seasonal patterns of sociality, joined with a stable female-female agonism rate, suggest that water scarcity does not increase the levels of competition between females, but it still corresponds to changes in sociality. One possible cause, to be investigated by future studies, could be the dry season increasing stress corresponds to elevated stress levels, either directly, via dehydration (Wessling et al., 2018a, 2018b), or indirectly, through the dissolution of wet season female core areas constituting some form of social instability (Kaburu & Newton-Fisher, 2013).

Regarding the general use of the central waterhole, chimpanzees drink throughout the day, and are active at the location 7:26 am-7:19 pm, with a peak in activity during the afternoon hours, 1:30 pm-6:00 pm. On the days they are recorded to visit the central waterhole, the female chimpanzees in the Waibira community generally make one or two short visits, spanning on average just under two minutes.

The central waterhole is used increasingly as the dry season progresses, and alternative water sources disappear – while days when females are recorded to visit are further apart, the number of visits per day and their duration go up, suggesting an increased reliance on that specific terrestrial water source. The central waterhole is not a common location of conflict and competition between females: rates of agonism are very low there, and remain stable between the wet and dry season, suggesting very low levels of competition for water.

Water, Conservation, & Human-Wildlife Coexistence

Findings about the water-dependence of rainforest chimpanzees have broader implications for conservation and the management of human-wildlife coexistence, especially findings about the temporal usage patterns of terrestrial water sources and space use changes in relation to water availability. In chimpanzee range countries households often rely on natural water sources to get water for drinking, cooking, and hygiene, with water carrying predominantly done by women and children (Asaba et al., 2013; Graham et al., 2016; Sorenson et al., 2011). While water sources might be shared between humans and chimpanzees in the wet season, chimpanzees' increased utilisation of terrestrial water sources and higher drinking frequency during the dry season will likely increase their reliance on such shared water sources, and cause a seasonal increase in human-chimpanzee interactions. Additionally, as seen in other species (Temminck's red colobus (*Piliocolobus badius temminckii*): Hillyer et al., 2015; African elephants: Mariki et al., 2015; Baird's tapirs (*Tapirus bairdii*): Pérez-Flores et al., 2021; Hanuman langurs (*Semnopithecus entellus*): Waite et al., 2007), chimpanzees that otherwise do not share a water source with humans might begin to do so in the dry season as a fallback option, as arboreal water sources disappear. Centring of chimpanzee ranging activity on remaining terrestrial water sources during the dry season can also

lead to overall increased chimpanzee presence in the broader vicinity of the shared water source, in areas of high human use.

Therefore, shared water sources can be potential locations of conflict between humans and chimpanzees during the dry season not just in savannah environments (Fryns et al., 2021), but in mesic, rainforest environments as well. The risks of increased activity and higher chances of encounters between humans and chimpanzees include injury and death both to chimpanzees (Cibot et al., 2019; Hyeroba et al., 2011; Reynolds, 2005; Waller & Reynolds, 2001) and humans, especially children (Hockings et al., 2010b; McLennan & Hockings, 2016), exposure to dogs (Hockings et al., 2012; McLennan & Hill, 2010) and vehicle collisions (Cibot et al., 2015; McLennan & Asiimwe, 2016), and disease transmission (Deere et al., 2019; McLennan et al., 2017) - the chimpanzees in the Budongo Forest have recently been found to regularly consume guano containing multiple viruses, including a betacoronavirus (Fedurek et al., 2024). More time spent in the general vicinity of shared water sources during periods of water scarcity could also increase the chance of chimpanzees relying on crops for foraging (Hockings & McLennan, 2012), and livestock depredation or harassment by chimpanzees (Hockings et al., 2016).

Some existing chimpanzee conservation projects already focus on the construction of boreholes and safe wells to provide safe, clean water: The Bulindi Chimpanzee & Community Project (2024) and the Bugoma Primate Conservation Project (Hobaiter et al., 2019), both in Uganda, are two examples where new boreholes are being installed to provide separate water sources for humans, while chimpanzees and other primates can continue to use natural water bodies. However, such projects are dependent on consistent, long-term funding; providing safe water options to a sufficient proportion of households that currently share their primary

water source with wildlife will likely be a long process. In the meantime, focused studies on the use of water sources shared between humans and chimpanzees and the effectiveness of conflict-mitigation solutions are needed: climate change is predicted to impact access to water especially for poor, rural households, and a large proportion of eastern (Hicks et al., 2014; McCarthy et al., 2015) and western chimpanzees (*Pan troglodytes verus*) (Garriga et al., 2019; Heinicke et al., 2019; Ndiaye et al., 2018) live outside of protected areas, near or overlapping with human settlements. As chimpanzees are not the only animals in the region with a high rate of human-wildlife conflict (Abrahms et al., 2023; Dunham et al., 2010; Mukeka et al., 2019; Ocholla et al., 2014), nor the only species regularly visiting the central waterhole, monitoring of shared water source use should also be extended to other species. Practical solutions reducing crop raiding (Garriga et al., 2018; Hockings & McLennan, 2016) and how to safely share and utilise the same foraging areas and food resources (Hockings et al., 2020; Waller & Pruetz, 2016) should be evaluated with their efficacy for shared water sources as well. Education outreach, an effective method to promote chimpanzee-human coexistence (Kuhar et al., 2010; Njukang et al., 2019), should also include information about chimpanzee activity at water sources, highlighting an increase in chimpanzee activity and presence during the dry season, and identifying safer hours for water carrying, which, based on the activity patterns of the Waibira community, are predominantly in the morning hours before 9 am, with afternoon hours to be avoided.

Knowing that chimpanzees are dependent on surface water even in mesic environments also has conservation implications for populations living in protected areas and/or in areas with no human contact. Delineation of protected areas and habitat suitability assessments should take into account not just the degree of tree cover and food availability (Carvalho et al., 2022; Chitayat et al., 2021), but water

availability as well. While water availability is recognised as a factor limiting the northern species range limit in sub-Saharan Senegal (Wessling et al., 2020), forest cover is not always directly correlated with on-the-ground water availability, and rainforest populations, well within the species range, can still experience periods of water scarcity due to the geographical properties of the area. One example is the Waibira community in this study, whose community home range does not overlap with any of the major, permanent rivers in the Forest Reserve. Another is the Tongo chimpanzee community in the Democratic Republic of the Congo, whose community home range is located on porous volcanic soil, which absorbs rainfall quickly. The chimpanzees of the Tongo community predominantly rely on dendrotelmata and extremely ephemeral rainfall runoff creeks for water, and water-rich tubers as fallback options (Lanjouw, 2002). The number, quality, and seasonal stability of water sources therefore should be included in habitat evaluations (e.g.: Kimanzi et al., 2019), as with the disappearance of water sources animals might leave protected areas in search of water (Erasmus et al., 2002; O'Farrill et al., 2014), and previously suitable habitats might become unable to hydrologically support populations (Bajomi, 2004; Molnár, 1987).

The Importance & Protection of Small Water Bodies

The Waibira chimpanzees increasingly used dendrotelmata during the wet season, and the terrestrial central waterhole, measuring 10 m x 10 m at its broadest part, as a fallback option during the dry season. They only drank from small water sources, with the central waterhole being the largest. These findings highlight the importance of small arboreal and terrestrial water sources in general, and specifically in mesic environments. Additionally, a wide range of mammal and bird species were also recorded at the central waterhole, further emphasising its ecological importance during the dry season.

Small water bodies are defined as ranging in size between 1 m^2 to 5 ha (Biggs et al., 2005, 2017), and are often small natural features with a larger ecological role than what is expected proportionate to their size (Hunter et al., 2017). Such small water bodies are also less likely to be contaminated due to having smaller catchment areas (Biggs et al., 2017), and their small size means complete protection is easier to achieve (Hunter et al., 2017). However, their small size also makes them more vulnerable to complete disappearance (Hunter et al., 2017), and they receive little focus in policy and decision making, especially water bodies smaller than 100 m^2 (Biggs et al., 2017).

To increase awareness and effective conservation of small water bodies, more focused research is needed on the utilisation of small water bodies, including dendrotelmata and waterholes in mesic environments. While more is known about the ecological role of small water bodies in South and Central America (e.g.: Dávila et al., 2020; Delgado-Martínez et al., 2022b, 2023; Freese, 1978; Moreira-Ramírez et al., 2016; O'Farill et al., 2014) and Southeast Asia (Beck & Tuttle, 1972; Gray et al., 2015; Pin et al., 2020), knowledge is especially fragmentary in the mesic areas of Europe (Kirsch et al., 2021) and Africa. Where studied, waterholes are common fallback options during drier periods, as seen here in the Waibira community, and other species (white-lipped peccaries (*Tayassu pecari*): Moreira-Ramírez et al., 2016; birds: Dávila et al., 2020; ungulates: Sutherland et al., 2018; Nubian ibex (*Capra nubiana*): Wakefield et al., 2008). Dendrotelmata have received especially little targeted attention in ecology (Delgado-Martínez et al., 2022b, 2023; Kirsch et al., 2021; Sharma et al., 2016), with the exception of entomology (e.g.: Kitching, 1971; Gossner, 2018; Gossner et al., 2020).

Systematic studies in areas of priority, in mesic environments in Europe and Africa, should focus on the scope of species relying on various types of small water

bodies, any temporal variation in the utilisation of those water bodies, as well as any potential between-species interactions, such as competition or temporal partitioning. A comprehensive, cross-disciplinary approach, termed ‘waterhole studies’ by Beck & Tuttle (1972), might be especially useful for early, exploratory studies: they advise for the comprehensive, interdisciplinary survey of waterholes, incorporating zoology, monitoring the use of the water source by animals; botany, surveying vegetation around the water source; as well as hydrology and geology, sampling the water for water quality, mineral, microbial, and parasitological analyses and describing the immediate surroundings of the water source to fully explore the role of a specific water body in an ecosystem. With the widespread use of camera traps, continuous monitoring of small water bodies is far from the exhausting in-person observation Beck & Tuttle (1972) envisioned. Camera traps are also the recommended best practice to monitor any small natural feature with a large ecological role – due to the natural features’ small size, it is easy to ensure almost complete coverage, while camera traps ensure minimal human disturbance, as seen here and in other studies (Boyer-Ontl & Pruetz, 2014; Delgado-Martínez et al., 2022a; Edwards et al., 2016b; Montalvo et al., 2019; Pin et al., 2020). Arboreal camera traps are also increasingly used (Chen et al., 2021; Moore et al., 2021), and allow for the extension of the ‘waterhole studies’ approach to arboreal water sources as well (Delgado-Martínez et al., 2023). In addition to camera trapping, eDNA sampling at waterholes has also been used to explore which species are visiting the location (Farrell et al., 2022).

Assessing Water-Dependence & Water Availability

The results of this thesis not only demonstrate that water availability can impact chimpanzee spatial and social behaviour to the same extent food availability does, but that it acts on those behavioural domains different from food availability. While food, especially ripe fruit, shows many similarities with water, both being a

consumable key resource with a patchy, seasonally changing distribution, and usually nonmonopolisable by a single individual, lower water availability decreased the extent of ranging, increased spatial overlap and gregariousness, and did not increase the rates of agonistic behaviour, the complete opposite of what is seen in female chimpanzees during periods of low food availability (Murray et al., 2006; Emery Thompson et al., 2007b; Riedel et al., 2011; Houle & Wrangham, 2021). Based on the current study and on patterns seen in other species (e.g.: red-fronted lemurs: Amoros et al., 2020; birds: Magaji, 2022), water sources present a strong spatial pull factor during periods of water scarcity. Competition for water was also extremely low, and did not increase during the dry season – overt, aggressive water competition seems to be a behaviour only present in catastrophic water shortage scenarios (vervet monkeys (*Chlorocebus pygerythrus*): Wrangham, 1981), and not an everyday feature in eastern chimpanzees.

Given these differences, the ecological role of water should be understood and investigated separately from that of food, instead of grouping drinking behaviour with all other foraging behaviour (e.g.: Geffen et al., 1992a; Teleki, 1977). Even when analysed separately, grouping water consumption with food consumption for visuals and descriptive statistics can hide its relative importance. Drinking behaviour usually constitutes a small percentage of overall foraging time budgets (Teleki, 1977); as seen here, most drinking events lasted a little under 2 min, while in Mahale, Tanzania, they were on average 2.5 min (Nishida, 1980). However, consuming the entirety of one's daily water intake takes much shorter than consuming one's daily food intake, and therefore the proportion of drinking in daily foraging budgets compared to that of various types of food is not an accurate representation of how important water is for a species.

Specific studies targeting or including water as a separate factor are desperately needed for species in mesic environments, including primates. Climate change is predicted to negatively impact water availability (Fu et al., 2013; Jiang et al., 2019; Ruosteenoja et al., 2016; Schlaepfer et al., 2017), and poses a high risk to primate species due to their large body size (Zhang et al., 2019) and specific time budgets (Lehmann et al., 2010). Knowing how water sources are utilised, how frequently, as well as how their distribution, size, and quality impact other travel and foraging decisions is essential for effective conservation and accurate models of foraging and spatial ecology. To conduct those studies, we also need (a) an accurate assessment of whether a species is dependent on surface water and (b) an accurate assessment of water availability at a specific habitat, going beyond a simple mesic-xeric division where water is not assumed to limit behaviour in the former, only in the latter.

With regards to accurate assessments of water-dependence in species, this thesis provides an example of a species with a water-rich diet, inhabiting a rainforest environment with high annual precipitation and humidity levels still showing high water-dependence. The findings highlight how water-dependence and the frequency of drinking behaviour cannot simply be extrapolated from the diet of a species or the climate of their habitat. Accurate assessments should focus on surveying a broad spectrum of potential drinking behaviours. Arboreality, for example, makes assessing accurate water needs and drinking frequency difficult due to poor visibility, as noted by Reynolds & Reynolds (1965). Therefore, care should be taken when declaring arboreal species independent of surface water. Dendrotelmata are usually small in size, and oftentimes located in the crown of a tree, not on more visible parts of the trunk or between the roots. Other drinking methods, such as licking dew or rainwater off surfaces is even more difficult to spot and record from the ground, and I am

certain even the current study did not record the true number of all drinking events that took place during fieldwork observations. As arboreal drinking is relatively common in primate species (Sharma et al., 2016), they are more at risk of inaccurate water-dependence assessments, thereby increasing their vulnerability to climate change. Besides eastern chimpanzees, other arboreal species have also been previously assumed to be independent of water (mantled howler monkeys (*Alouatta palliata*): Nagy & Milton, 1979), but once their water dependence has been re-evaluated with specific attention to arboreal water sources, were found to regularly consume free water (mantled howler monkeys: Chapman, 1988; koalas (*Phascolarctos cinereus*): Mella et al., 2020).

Arboreal camera trapping can help address the methodological issues of low tree-crown visibility (Chen et al., 2021; Moore et al., 2021), and aid with accurate water-dependency assessments. Additionally, Houle & Wrangham (2021) conducted a novel direct observation method, where the observer climbed up a potential feeding tree prior to the arrival of a group of habituated wild chimpanzees, and recorded rates of agonistic behaviour from the tree crown once the party arrived, noting higher rates compared to terrestrial observations. This arboreal observation method could also yield improved detection of arboreal drinking events, but requires high levels of habituation that can be logistically (Bertolani & Boesch, 2008) or ethically impossible (McLennan & Hill, 2010) at the time and location of a given study.

When assessing species-level water-dependence, assessments of water-dependency should also ideally focus on more than population (Wessling et al., 2018a). For example, savannah chimpanzees were thought to be the only ones experiencing high temperatures and water scarcity able to induce dehydration stress (McGrew et al., 1981). However, once Wessling and colleagues (2018a) investigated

seasonal dehydration and stress levels in western chimpanzees both in a savannah and in a rainforest population, they found similar dehydration-induced stress in both populations. The high discrepancy between the Waibira community's drinking frequency and that of the chimpanzees in Gombe, both eastern chimpanzees, also highlight the need for studying water-dependence across multiple habitats. The Gombe chimpanzees have a lower drinking rate (Nelson et al., 2022) than the Waibira ones, but have been the primary source of data on wild chimpanzee drinking frequency (Goodall, 1986; McGrew, 1977; Teleki, 1977; c.f.: Nishida, 1980), setting what is typically seen as the 'species standard'. However, they have recently been found to suffer from severe chronic dehydration (Nelson et al., 2024), suggesting that the observed drinking frequency is suboptimal for them, and likely not representative of an ideal drinking frequency for eastern chimpanzees.

Water availability also needs to be assessed accurately, incorporating the quantity, quality, and location of water sources animals can access, instead of extrapolating based on general climate. Besides precipitation and temperature, different rates of evaporation or the specific topography of an area can also impact water availability (Belnap et al., 2005). For forested areas, assessments of dendrotelmata density and distribution are also advisable (Blakely & Didham, 2008), while water quality can factor into the utilisation of water sources for some species (lemurs: Amoroso et al., 2017; African elephants: Ndlovu et al., 2018). Accurate description and assessment of the number and seasonal states of water sources allows for inter-site comparison and quantifying how much is water a limiting resource for different populations. For example, as seen in this thesis, gregariousness increases during the dry season in the Waibira community, as opposed to the savannah mosaic group of Issa, Tanzania, where it was independent of season (Giuliano et al., 2022). But once we consider specific seasonal changes in

water availability at the two habitats, it becomes clear that the dry season water availability in Waibira is much worse during the dry season than in Issa, likely leading to differences in seasonal patterns of gregariousness. While water levels did diminish in the dry season, the Issa chimpanzees still had multiple flowing water sources available to them throughout the year (Giuliano et al., 2022). In the Waibira community, even when including the peripheral waterholes, the total number of dry season water sources is still very low, with all off them cut off from waterflow. Wessling et al. (2018a) similarly warn against equating certain habitat types – in the case of chimpanzees, savannah habitats – with ecological marginality, and advise for assessing ecological marginality along several axes. By their definition, the Waibira population may be ecologically marginal with regards to water availability, despite living in a habitat with one of the highest annual rates of precipitation studied so far.

To conclude, this thesis provides an example of water being a limiting factor in a mesic environment in equatorial Africa. It does so through the example of eastern chimpanzees, a species in which water was assumed to have little to no ecological role, demonstrating that they drink water on a daily basis, and show significant changes in their space use and social behaviour in line with fluctuating water availability, concentrating their ranging on the primary remaining water source and prioritising access to water during periods of low water availability. The findings here join studies from other rainforest (e.g.: Beck & Tuttle, 1972; Delgado-Martínez et al., 2023; O'Farrill et al., 2014; Gray et al., 2022; Paredes et al., 2017; Pin et al., 2020; Outtara et al., 2019) and mesic regions (Holá et al., 2015; Kirsch et al., 2021) in highlighting the importance of water in mesic environments. Increased research focus is needed on the topic, especially in equatorial Africa and Europe, including the UK (Burston, 2006; Kirkpatrick Baird et al., 2023). Besides ecological research

focusing on water dependency, important water sources, and water availability, improved narratives, education, and communication around drought perception and risk is needed in regions experiencing water scarcity as a novel situation to enact effective protection of vulnerable species and areas (Antwi et al., 2022; Dessai & Sims, 2011; Greksch, 2021; McEwen et al., 2023).

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Appendix A

Per Pentad Rainfall Values Used to Determine the Onset and End of Dry Seasons

Pentad	Year									
	2013	2014	2015	2016	2017	2018	2019	2020	2021	2022
January 01-05	**0**	**0**	**0**	**1**	**0**	**0**	**0**	**0**	**2.8**	**0**
January 06-10	**22**	**0.6**	**0**	**0**	**0**	**0**	**0**	**1.8**	**0**	**0**
January 11-15	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**5.4**
January 16-20	**0**	**0**	**0**	**15**	**0**	**0**	**30.8**	**0**	**0**	**17.4**
January 21-25	**0**	**9.8**	**0**	**7.4**	**0**	**0**	**0**	**0**	**12.6**	**0**
January 26-30	**0**	**0**	**0**	**0**	**2**	**0**	**6**	**1.2**	**0**	**0**
January 31 - February 04	**0**	**8**	**0**	**0**	**2**	**0**	**0**	**33.8**	**0**	**0**
February 05-09	**2.2**	**3**	**0**	**0**	**0**	**0**	**0.8**	**8.8**	**0**	**1.2**
February 10-14	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
February 15-19	**34.4**	**0**	**5.2**	**0**	**33**	**9.4**	**2.6**	13.6	**2.4**	**0**
February 20-24	**5**	**0**	**0**	**0**	**9.2**	**52**	31.2	1.4	**0**	**0**
February 25-March 01	**0**	**3.6**	**15**	**16.2**	61.2	**17.4**	3.4	3.2	**0**	**24.4**
March 02-06	**0.8**	7.8	**9**	**1**	29.2	**4.6**	0	3.4	**3.2**	**15.2**
March 07-11	14.8	2.8	**0.4**	**25.6**	12.6	52	12.2	56.4	**30.8**	**0**
March 12-16	6.2	40.4	**3.8**	**0**	4.8	51.8	17.8	16.2	**1**	**1.8**
March 17-21	43	16.8	0	10.2	42.8	35.4	0	26.8	22.6	2.4
March 22-26	46.4	95.6	49.4	1	31	20.8	1.2	65	21	54.2
March 27-31	20.8	17.4	35.2	0	50	30.8	41.4	34.6	24.4	6.2
April 01-05	41.4	32.8	24.8	55.4	0	85	29	11.6	49.6	18
April 06-10	24.2	20.6	42.8	20.8	5.9	104.6	33.6	1.4	37.8	12
April 11-15	24.2	46	16.4	3.8	7.9	54.4	54.2	10.8	51.4	26
April 16-20	52	91	86	0	38.8	92.8	27	51.8	45.8	47.2
April 21-25	104.8	75	80	0	16.3	23.8	24.2	0	47.2	6.6
April 26-30	108.4	20	20.2	102.6	31.2	50.8	60.8	56.6	7.6	33.6

May 01-05	11	50.4	30.4	27.2	69.5	3	17.8	38.6	49.4	33.4
May 06-10	125.4	20.8	85	93.8	41	93.6	19.4	44.4	53.2	9
May 11-15	1.8	34	13.2	59.6	21.4	21.6	28	28.6	103.6	3.8
May 16-20	0	16.8	16.4	50.4	13.8	93.4	12.8	10.4	13.2	9
May 21-25	0	44	9	5.4	4.8	15	56.4	14.4	23.2	19
May 26-30	6.6	7.4	37.6	1.8	10	1.6	21.2	32.2	16.2	49.2
May 31-June 04	5.8	46.8	47.4	21.2	34.6	61	54	2.6	0	1.4
June 05-09	50.2	84.4	69.6	25.4	17.4	44	14.8	24.4	30.2	33.2
June 10-14	24.8	33.6	11.2	1.6	1.2	11.8	11.8	14	3.4	39.2
June 15-19	44.6	32.4	13.8	30.6	46.2	11	10	9	9.6	19.6
June 20-24	8	35	82	1.6	15.4	44.8	28.6	10.4	0	21.2
June 25-29	0	1.8	32.4	8.8	37	20.8	2.2	20.6	0.8	18.4
June 30-July 04	2.6	1.6	16.4	4.8	54.4	13.8	64	0	6.2	32.8
July 05-09	9.6	18.2	0	0	4	3.4	12.4	15.6	14	0
July 10-14	1	21	0	1.8	1.2	21	14.4	42.4	25.4	2
July 15-19	4	36.4	4.6	3.4	10	0	4.8	11.2	27.4	1
July 20-24	52.2	7.2	20.6	51.6	11.2	0	20.4	1.6	14.4	12.2
July 25-29	7	4.2	44.2	37.4	17.8	2.2	79.8	3.8	0	6
July 30-August 03	103.8	1.6	20.2	20.4	53.4	2.8	58.6	18.2	6.4	116.2
August 04-08	33.2	19.6	11	8.2	22.8	47	11.4	28.3	12.6	10
August 09-13	16.6	33.4	19.4	11.2	27.4	27.6	8.6	6.4	6.6	15.6
August 14-18	2.4	21	2.8	6	23.6	16.4	77.8	44.4	9.8	6.2
August 19-23	21.8	0.8	16	25	67.4	66.2	33.6	24	20.6	14.8
August 24-28	0	107	7.2	32	71.4	55.4	29	15.6	4.2	26.2
August 29-September 02	3.4	10	13.8	1.2	12.4	48.2	67.8	14.2	34.2	7.4
September 03-07	75	22.4	35	0.4	26.2	16.2	10.6	26.4	33.4	21.6
September 08-12	23	10	39.2	35.4	45	5.6	21	19.6	61	36.4
September 13-17	1	42.6	37.8	45.2	48.6	9.2	2	50	1.2	44.4
September 18-22	15.6	44.8	0	22.6	115.2	1.6	4	3.4	45.6	7.6
September 23-27	21.2	23	13.6	0	3.6	15.4	1.2	29.2	47.2	57

September 28-October 02	78.2	16.6	48	37	25.4	10	44.4	42	28.8	21.8
October 03-07	48.8	29	2	43.2	22.6	0	74.2	23.2	83.6	75.6
October 08-12	40.6	48.8	42.6	9.6	16.4	52.2	23.8	42.6	26.6	31.4
October 13-17	14	39.6	81.8	1	17.8	24.6	87.4	57	18.2	15
October 18-22	25.2	32.6	62.6	22.8	62.2	22.2	59.6	43.4	69	55.4
October 23-27	43.6	57.4	78.8	35.8	43.6	21.4	40.8	140.8	27.2	0
October 28-November 01	7.4	51.6	77	19	28.2	39	99.8	75	13.8	5
November 02-06	31	12.8	117.6	0	42.4	42.8	37.4	30	28.4	NA
November 07-11	58.4	23.6	82	34.6	24.6	4.8	49.2	31.8	22.4	NA
November 12-16	85.8	16.6	76	14.2	10	35.8	34.2	51.4	20.2	NA
November 17-21	14.2	57.8	71	31.2	0	36.2	65.4	7.6	12.6	NA
November 22-26	50.2	36.4	11.4	23.4	6.2	0	23.6	32	33.2	NA
November 27-December 01	**0**	**5.6**	153.6	19.6	**9.2**	0	42.4	34.6	23	NA
December 02-06	**6.8**	**5.4**	57.6	46	**6**	32.2	33.2	46.6	23.4	NA
December 07-11	**37.6**	**0**	4	**0.2**	**5.2**	16.4	65.4	**4.6**	5.4	NA
December 12-16	**1.8**	**0**	1	**3**	**0**	**9.4**	59.2	**0**	3.4	NA
December 17-21	**0**	**2**	17.2	**0**	**3**	**5.4**	**9.8**	**0**	0	NA
December 22-26	**0**	**0**	**0**	**0**	**0**	**0**	**5**	**16**	13.4	NA
December 27-31	**0**	**2.8**	**0**	**0**	**0**	**10.4**	**0.6**	**2.2**	23.2	NA
Mean rainfall/pentad	24.2	24.1	29.1	16.9	22.3	25.0	27.8	23.1	20.7	18.8
Mean rainfall/pentad ÷ 2	12.1	12.1	14.5	8.5	11.2	12.5	13.9	11.6	10.3	9.4

Note. Rainfall data recorded from 2013 to 2022. Half of per pentad rainfall was used to determine the onset and end date of dry seasons. Dry season pentads are marked as **bold.**