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Drinking frequency in wild lactating chimpanzees (*Pan troglodytes schweinfurthii*) and their offspring

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Abstract

Maintaining water balance is essential for organismal health, and lactating females must balance individual needs with milk production and offspring hydration. Primate milk is dilute and presumed to be the primary source for infant hydration for a considerable time period. Few studies have investigated the hydration burden that lactation may place on female primates. In this study, we investigated sources of variation in female and offspring drinking frequency among wild chimpanzees (*Pan troglodytes*). We hypothesized females would experience seasonal and lactation hydration burdens and adjust their drinking behavior to accommodate these, but this hydration burden would vary between females of different dominance ranks. We also predicted that parity would relate to maternal drinking frequency since primiparous females are still investing in their own growth. Finally, we predicted that offspring would drink more in the dry season and as they aged and lost milk as a water source, but that offspring of high-ranking females would be buffered from these effects. Using 41 years of long-term data on the behavior of mothers and offspring of Gombe National Park, we found that mothers drank more in the dry season, but there was no significant difference between mothers of different ranks during this period. Low-ranking females drank significantly more than mid- and high-ranking females during late lactation. Offspring also drank more in the dry season and as they aged, but there was no evidence of buffering for those with high-ranking mothers. While chimpanzees in our study population drank infrequently, they do demonstrate noticeable shifts in drinking behavior that suggests seasonal and reproductive hydration burdens.

KEYWORDS

chimpanzees, dominance rank, drinking, Gombe National Park, lactation

1 | INTRODUCTION

Hydration is essential for maintaining organismal health. Some ecological or reproductive conditions may present more intense hydration challenges, and many animals demonstrate behavioral shifts to mitigate dehydration. Lactating females must balance their own needs with the water requirements for milk production and offspring hydration. Milk has deep evolutionary roots in hydration; the first "milk" may have been a watery substance secreted by female synapsids to keep their eggs moist (Oftedal, 2012). Of the primates, ape milk is the most dilute, consisting of 85%–90% water (Hinde & Milligan, 2011) and is presumed to be the primary source of infant hydration for a considerable time period. While the production of dilute milk mitigates the daily energetic costs of lactation, this may place a hydration burden on females. Indeed, in humans, health practitioners recommend a three-fold increase in water consumption during lactation (Institute of Medicine, 2005), and a failure to do so can lead to maternal dehydration (Bethancourt et al., 2021; Rosinger, 2015).

The extent to which lactation presents a hydration burden has been understudied in nonhuman primates (NHP). Based on average human milk yields (approximately 750 ml/day; Kent, 2007) and the water content of ape milk (85%–90% water; Hinde & Milligan, 2011), it can be estimated that ape mothers lose approximately 640–675 ml water/day through milk. Starin (2002) investigated drinking behavior in Gambian Red Colobus (*Piliocolobus basius temminckii*), and found that while drinking was a rare occurrence, it occurred more often in the rainy season, even when fruits and young leaves with higher water contents were more readily available. Additionally, lactating females and young colobus drank more frequently than other age-sex classes. Conversely, mantled howler monkeys (*Alouatta palliata Gray*) are recorded to drink more water when their diet consists mostly of foods with lower water contents, and they tend to choose more succulent food items when free-standing water sources are scarce (Glander, 1978). Thus, environmental conditions, diet, and reproduction may affect water balance and water consumption in complex and variable ways. Recent work by Pontzer et al. (2021) demonstrated water turnover (the daily gain and loss of water by an individual) in great apes is 30%–50% higher than in humans, and apes consume more water per unit of metabolized food energy, despite an increased capacity for sweating in humans. Additionally, chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) had the highest water turnover of the great apes. These results indicate a lower capacity to conserve water and suggest water balance in great apes is more complicated than previously thought.

In the present study, we investigated how drinking behavior relates to parity, lactation stage, and dominance rank in wild female eastern chimpanzees (*Pan troglodytes schweinfurthii*) and their offspring at Gombe National Park, Tanzania. Chimpanzees live in fission–fusion societies in which party size and composition change frequently (Boesch 1996; Goodall 1986). While this is thought to reduce feeding competition, it may also allow females to change their behavior to maintain water balance. Chimpanzees specialize on ripe fruits but have a wide dietary breadth that can change flexibly based on food availability (Matthews et al., 2019; Watts et al., 2012). Chimpanzees can inhabit a wide range of environments in part because of this flexible social structure and omnivory. Most populations live in rainforests but some inhabit savannah landscapes which may present additional physiological challenges (Pruetz & Bertolani, 2009). A recent study (Wessling et al., 2018) found that chimpanzees living in a savannah habitat (Fongoli) and lowland forest (Taï) both showed markers of dehydration, suggesting that water is limiting for chimpanzees across varied ecologies, regardless of water availability in a habitat. Both populations also demonstrated a positive relationship between stress hormones and physiological markers of dehydration, but this relationship was stronger at Taï, which suggests the Fongoli chimpanzees are employing behavioral adaptations to overcome dehydration in savannah environments. One such adaptation includes the use of caves, which is thought to assist in thermoregulation and prevent further water loss (Boyer Ontl & Pruetz 2020). These results highlight the complex relationship between ecology, social structure, and hydration in chimpanzees.

Female chimpanzees invest substantially in each offspring, and experience long interbirth intervals (IBI), due to both the length of the lactational period and the need to recover a positive energy balance to resume cycling (Thompson et al., 2012). The average IBI at Gombe National Park is approximately 5 years, though there is considerable variation (Goodall 1986; Jones et al., 2010). Chimpanzee infants develop slowly and are exclusively dependent on their mothers for the first 6 months of life when they slowly begin adding solid foods (Goodall 1986; Lonsdorf et al., 2014). The average weaning age of chimpanzees is between 4 and 5 years of age, but there is considerable variation between and within populations. Additionally, maternal dominance rank can impact weaning patterns, with low-ranking mothers less likely to wean their offspring early as compared to high-ranking mothers (Lonsdorf et al., 2020). Research has demonstrated that immatures develop adult-like diet breadth and composition by juvenility (Bray et al., 2018; Lonsdorf et al., 2021). Acquisition of adult-like drinking patterns, as well as obtaining enough water from their diet may also be an important transition after weaning.

No study has yet investigated how water consumption varies based on lactation stage, though studies suggest that lactating females are more challenged by thermoregulation and water balance than other age-sex classes. For example, Boyer Ontl & Pruetz (2020) reported that lactating females use caves more often than males and non-lactating females. However, that study classified females with clinging infants as lactating and females with juvenile offspring as nonlactating, which did not allow for elucidation of cave-dwelling behavior during different stages of lactation. Lee (1987) argues that peak milk yield and metabolic demand on mothers should occur during the period when infants are growing most rapidly. Indeed, milk yield increases in rhesus macaques (*Macaca mulatta*; Hinde et al., 2009) and baboons (*Papio cynocephalus* and *Papio anubus*; Roberts et al., 1985) as infants increase in size and become more active. Studies of captive chimpanzee infants indicate that the highest peak velocity curve of body length occurs during the first 2 years of life (Hamada & Udono, 2002). Stable isotopic studies of infant chimpanzees at Kibale and Taï National Parks indicate a decrease in the amount of milk consumed after 1 and 2 years, respectively (Bădescu et al., 2017; Fahy et al., 2014). As such, early lactation may present the greatest hydration challenge to females, when infants are more reliant on milk.

In addition to lactation stage, no studies have examined whether differences in dominance rank, core area quality, and parity impact the extent to which lactation presents a hydration burden to females. There are several reasons to predict that higher-ranking eastern female chimpanzees may be under less hydration stress; they occupy the highest quality core areas in terms of food resources, have higher quality diets, and are heavier than low-ranking females, which may reflect greater fat reserves to draw on when under water stress (Foerster, Zhong, et al., 2016; Murray et al., 2006, 2007; Pusey et al., 2005). Dominance rank may also impact the hydration burden present at each lactation stage, given previous research demonstrating the effect of maternal rank on offspring weaning and developmental patterns. Indeed, in many animal species and populations, high maternal rank is correlated with faster-developing offspring, shorter inter-birth intervals, and earlier weaning (e.g., olive baboons [*Papio anubis*]: Smuts & Nicolson, 1989; savannah baboons [*Papio cynocephalus*]: Altmann & Alberts, 2005; chimpanzees: Lonsdorf et al., 2020; mountain gorillas [*Gorilla beringei beringei*]: Wright et al., 2020; spotted hyenas [*Crocuta crocuta]*: Holekamp et al., 1996). Faster-developing infants may require less milk as they incorporate solid foods during later stages of lactation, and wean faster, decreasing water stress for high-ranking mothers. Finally, parity may also affect drinking frequency, as younger, first-time mothers are still investing in their own somatic growth and have less fat reserves to combat water stress (Pusey et al., 2005). As such, it can be expected that low-ranking and/or primiparous mothers may need to drink more frequently than high-ranking or multiparous mothers to mitigate differences in diet quality and body mass.

Here we use a long-term data set of mother and offspring behavior from the wild chimpanzees of Gombe National Park, Tanzania, to investigate how parity, season, dominance rank, and lactation stage relate to drinking frequency. Food-based water consumption is assumed to be adaptive given that water-borne illnesses pose an acute risk to primates (Bakuza & Nkwengulila, 2009; Deere et al., 2019). Thus, understanding the context and extent to which chimpanzees consume free-standing water sheds light into both hydration stressors and potential disease risks. We hypothesized that mothers adjust their drinking behavior to accommodate seasonal and reproductive hydration burdens, but this will differ between mothers of different ranks and parity. Based on differences in the core area feeding quality (Murray et al., 2006) and body mass (Pusey et al., 2005), we predicted higher-ranking females would be buffered from seasonal and lactation stage effects. Specifically, we predicted that higher-ranking females would drink less during the dry season and during early lactation than low-ranking mothers. We also predicted parity would have an independent effect on maternal drinking, with primiparous mothers drinking more frequently than multiparous mothers. Finally, we tested our prediction that milk consumption would buffer offspring from seasonal effects. Specifically, we predicted that younger infants would show no or smaller seasonal effects than older infants that are in the process of weaning or are fully weaned. However, we predicted that offspring of high-ranking females would be buffered from seasonal and age effects.

2 | METHODS

2.1 | Ethics statement

The Government of Tanzania, Tanzania National Parks, and the Tanzania Wildlife Research Institute granted permission to conduct this study. All behavioral data were collected noninvasively, and data collection adhered to the American Society of Primatologists Principles for the Ethical Treatment of Nonhuman Primates. Because this study is purely observational in nature, it was exempted from IACUC approval.

2.2 | Study population

We analyzed behavioral data collected on wild chimpanzees in the Kasekela community at Gombe National Park, Tanzania, from 1975 to 2016. Gombe is a small park (35 km^2) bordering Lake Tanganyika. Elevation varies throughout the park, from the shores of Lake Tanganyika at 766 m above sea level to 1622 m above sea level at the eastern ridges of the park. Vegetation is also diverse; the northern and central areas of the park are characterized by dense forests, and the eastern areas located in higher elevations consist of shrubs and grasslands (Pintea, 2007). The dry season at Gombe is from May to October (Clutton-Brock & Gillett, 1979). June and July are the driest months of the year, while November and December receive the most precipitation (Wallis, 2002). During the course of the study, the Kasekela community size varied but had a maximum of 25 adult females, 14 adult males, and 29 immatures at any time. We included all offspring under the age of 4.5 ($N = 60$) and all mothers with offspring under the age of 4.5 ($N = 25$). We defined infants as 0–4.5 years old because the average weaning age in this population is between 4 and 5 (Lonsdorf et al., 2020). We also included weaned juvenile offspring aged 4.5–6 years who had younger siblings as a sample of fully weaned immatures ($N = 17$).

2.3 | Behavioral data collection and summation

These data come from the long-term mother–infant project that collects behavioral data from mothers, their infants, and their next oldest sibling if possible (see Lonsdorf et al., 2014 for a more detailed ethogram). When a focal individual (either mother, infant, or sibling) was out of sight on the scan, they were marked as "bad observation." Throughout the study period, researchers collected detailed behavioral data on mothers and offspring. These data include 1-minute point samples on the behavior of the mother, infant, and next oldest sibling. Researchers aim to conduct 1 monthly follow for at least 6 hours on each mother in the study community. During behavioral follows, all occurrences of drinking were recorded (Altmann, 1974); drinking is defined as the ingestion of freestanding water. The final data set for our analyses included 10,517 hours of good observation time of mothers and 10,680 h for offspring.

To measure the effect of the lactation stage on offspring and maternal drinking, offspring and mothers were categorized based on offspring age and split into three lactation stages. Early lactation included offspring less than 1.5 years old. Middle lactation included offspring between the ages of 1.5 and 3 years. Late lactation included offspring between the ages of 3 and 4.5 years. We chose these age categories to divide lactation into three equal stages that correspond to offspring developmental milestones. During early lactation (0–1.5

years), offspring are mostly dependent on mothers for nutrition and are in close proximity to their mothers (Goodall, 1986; Lonsdorf et al., 2014), which may impact how much milk they are consuming. Offspring in middle lactation (1.5–3 years of age) increasingly incorporate solid food into their diets, but still depend on supplemental milk (Bray et al., 2018; Lonsdorf et al., 2021). Offspring in late lactation (3–4.5 years of age) are nearing weaned age, and as such might be less dependent on milk for hydration. Juveniles in our data set (4.5–6 years of age) were observed as older siblings, and therefore were fully weaned.

We also separated mothers by parity (primiparous or multiparous), dominance rank, and age. Dominance ranks were continuously calculated by pooling all available pant-grunt (a formal signal of subordination) data collected throughout the data set. Ranks were calculated based on the Elo method but also categorically (high, mid, and low) based on Jenks natural breaks of continuous scores (Foerster, Franz, et al., 2016; Foerster, Zhong, et al., 2016). This is an optimization method that minimizes variance within categories and maximizes variance between categories. To analyze patterns of drinking based on our predictions, mothers were separated by season (dry or wet), lactation stage (early, middle, or late), dominance rank (low, mid, or high), and parity (primiparous or multiparous). Age was used as a control because declining renal function, glucose control, and other age-related conditions can occur in older chimpanzees (Lowenstine et al., 2016; Videan et al., 2008) and may impact drinking frequency. Mothers aged 12–20 years were classified as young, 21–35 as prime, and older than 35 as old. Offspring were separated by lactation stage, season, and maternal dominance rank. We then calculated the total number of observations drinking in the bin of interest as the number of point samples at which a female or offspring was recorded drinking. These data were pooled over multiple births for mothers.

2.4 | Statistical analyses

We conducted all analyses in R version 4.0.2 (R Core Team, 2020) and RStudio version 2.0.2 (RStudio Team, 2020) using the glmmTMB version 1.0.2.1 (Brooks et al., 2017), DHARMA version 0.3.3 (Hartig, 2020), car version 3.0-10 (Fox & Weisberg, 2019), and emmeans version 1.5.3 (Lenth, 2020) packages. To test our predictions, we fitted generalized linear mixed models (GLMMs) to each response variable using the glmmTMB function in the glmmTMB package with a Poisson error structure. We fit separate models for maternal drinking frequency and offspring drinking frequency, using only individuals who had been observed for 600 min or more within a given combination of variables. Six hundred minutes corresponds to at least 10 h of observation, or at least one full follow day. For both models, we used total good observation time for each individual (log-transformed) as an offset term in the model (McCullagh & Nelder, 1989) to control for differences in observation time between individuals. For both mothers and offspring, we expected the data to be zero-inflated as drinking was a rare event, and as such, we used a zero-inflation model. For offspring, however, we specified the zero-inflation term to lactation stage. We expected infants in early lactation would drink very rarely due to their age, resulting in false zeroes (zeroes due strictly to age and not hydration requirements), which are different from zero counts of drinking for older offspring. To assess the stability of our models, we omitted random effect level one at a time and compared model estimates against those of the full model. We also used the testResiduals function in the DHARMa package to verify that our models satisfied model assumptions and the testDispersion function in the DHARMa package to confirm that our models did not exhibit overdispersion. As an initial test of significance, we first compared both the maternal and offspring full models with all predictors and their respective null models. Using a likelihood ratio test (R function analysis of variance [ANOVA] with argument "test" set to "χ^2"), we tested if the full model was significant against the null model. If this was true, we then evaluated the effects of our predictors on maternal and offspring drinking.

2.5 | Maternal model

For our first model analyzing patterns in maternal drinking frequency, we evaluated the effect of our predictor variables (age, season, lactation stage, rank, and parity) on our response variable (maternal drink proportion). To test our prediction that high-ranking females would be buffered from seasonal and lactation stage effects, we also considered interaction terms between rank and season, and rank and lactation stage. Maternal ID was included as a random effect because the same individual could be represented in multiple seasons, lactation stages, ranks, and measures of parity. To eliminate the possibility of collinearity, we first determined variance inflation factors (VIF) using the function check_collinearity in the package performance (Lüdecke et al., 2021) on a model lacking interactions (maximum VIF = 4.16). Our final, simplified models were selected based on the Akaike information criterion (AIC). To do this, we compared AIC between a full model with interactions between both rank and season and rank and lactation stage with reduced models with just one of these interactions and selected the simplest model with the best fit. With this model, if the interaction between rank and season and/or rank and lactation stage was significant, we conducted pairwise post hoc comparisons between seasons (wet vs. dry) within each rank, and between lactation stages (early vs. middle vs. late) within each rank using the pairs and emmeans functions in the emmeans package. If the interaction was not significant, it was removed, and the model was refit with those terms as independent predictors.

2.6 | Offspring model

For our second model analyzing patterns in offspring drinking frequency, we evaluated the effect of our predictor variables (season, lactation stage, and maternal dominance rank) on our response variable (offspring drink proportion). To test our prediction that the offspring of high-ranking females would be buffered from seasonal and lactation stage effects, we also considered interaction terms between maternal rank and season and maternal rank and lactation stage. We included offspring identity as a random effect because the same individual could be represented in multiple seasons and lactation stages. We considered using maternal identity as a nested random effect in the offspring model, as data were pooled over multiple births for mothers, but this was eliminated as it explained almost zero variance and caused model convergence issues. We checked for collinearity by determining VIF (maximum VIF = 1.05). Our final, simplified models were selected based on AIC. If the interaction between maternal rank and season and/or maternal rank and lactation stage was significant, we conducted pairwise post hoc comparisons between seasons (wet vs. dry) within each rank, and between lactation stages (early vs. middle vs. late) within each rank using the pairs and emmeans functions in the emmeans package. If the interaction was not significant, it was removed, and the model was refit with these terms as independent predictors (Table 1).

3 | RESULTS

There were 788 and 352 recorded drinking point samples for mothers and offspring, respectively (Table 2). Drinking made up less than 1% of point samples for both mothers and offspring.

3.1 | Maternal drinking patterns

Parity was not a significant predictor of drinking frequency, so it was excluded from the final model (SI Table 1). AIC comparisons indicated the best model fit was one that included season as an independent predictor, with an interaction between rank and lactation stage. Thus, the final model included age, season, the interaction between rank and lactation stage, and a random intercept for individual ID, which was a significantly better fit than the null model ($\chi^2 = 182.23$, $df = 11$, $p < 0.001$) and the model with an interaction between season and rank with lactation stage as an independent effect ($\chi^2 = 21.40$, $df = 2$, $p < 0.001$; Table 3). This model was also a significantly better fit than the model excluding the random intercept of individual ID ($\chi^2 = 169.88$, $df = 1$, $p < 0.001$). Season had a significant independent effect on drinking proportion; females drank more in the dry season. Post hoc analysis of the interaction between rank and lactation stage revealed that there was no significant difference in drinking frequency between ranks during early and middle lactation. Low-ranking females drank significantly more during late lactation than mid- and high-ranking females (Figure 1; SI Table 2).

3.2 | Offspring drinking patterns

AIC comparisons indicated the best fit model was one that excluded interactions between maternal rank and season, and maternal rank and lactation stage (SI Table 3). When we removed infants in early lactation from the data (while refitting the model with a regular zero-inflation term, instead of specified to lactation stage), AIC comparisons indicated the best fit model was one that included season as an independent predictor, with the interaction between maternal rank and lactation stage (SI Table 4). We, therefore, chose to run a model with only offspring in middle and late lactation and juveniles, with the season as an independent predictor, and a random intercept on individual ID (Table 4). The full model was a significantly better fit than the null model including only individual ID ($\chi^2 = 83.283$, $df = 9$, $p < 0.001$), as well as a model excluding the random intercept on individual ID ($\chi^2 = 131.93$, $df = 1$, $p < 0.001$). Season had an independent effect on offspring drinking, with offspring drinking more in the dry season. Post hoc analysis of the interaction between maternal rank and lactation stage revealed no significance difference between offspring of different maternal ranks (SI Table 5).

4 | DISCUSSION

Most studies emphasize that wild great apes, including chimpanzees, can meet their water requirements through their diet (e.g., Pontzer et al., 2021; Wrangham, 1977). While food-based water consumption may be adaptive to avoid water-borne illnesses (Bakuza & Nkwengulila, 2009; Deere et al., 2019), it is important to consider the consumption of free-standing water to understand how primates meet their hydration requirements, as well as potential disease risks. Our results demonstrate that while drinking was a relatively rare occurrence in this population, mothers and offspring varied in their drinking frequency in response to seasonal and reproductive hydration challenges, and this varied between mothers of different

TABLE 1 Models and model parameters for generalized linear analyses

Model	Response variable	Fixed effects	Random effects
Maternal drinking	Drinking proportion	Age Parity Rank × Lactation stage Rank × Season	Individual ID
Offspring drinking	Drinking proportion	Maternal rank × Lactation stage Maternal rank × Season	Individual ID

TABLE 2 Sample size, average number of observation minutes, drink count, mean drink count (±SD), and mean drink proportion (±SD) mothers and offspring in each lactation stage

Lactation stage	N	Average observation minutes	Drink count	Mean drink count (±SD)	Mean drink proportion (±SD)
Maternal					
Early lactation	25	2852	301	3.5 (±6.6)	0.001 (±0.002)
Low-rank	13				
Mid-rank	17				
High-rank	8				
Middle lactation	25	3069	297	4.0 (±5.9)	0.001 (±0.002)
Low-rank	11				
Mid-rank	15				
High-rank	10				
Late lactation	22	2265	190	2.7 (±4.5)	0.001 (±0.002)
Low-rank	9				
Mid-rank	16				
High-rank	8				
Total		2743	788	3.4 (±5.8)	0.001 (±0.002)
Offspring					
Early lactation	48	2420	17	0.20 (±0.94)	0.0001 (±0.0005)
Low-rank	15				
Mid-rank	20				
High-rank	17				
Middle lactation	47	2519	115	1.35 (±3.01)	0.0005 (±0.001)
Low-rank	11				
Mid-rank	18				
High-rank	18				
Late lactation	44	2083	134	1.89 (±4.22)	0.001 (±0.003)
Low-rank	9				
Mid-rank	21				
High-rank	14				
Juvenile	17	2276	86	2.77 (±4.82)	0.001 (±0.001)
Low-rank	1				
Mid-rank	5				
High-rank	11				
Total		2347	352	1.29 (±3.31)	0.0006 (±0.002)

Note: The same female or offspring is often included in multiple bins.

dominance ranks. Both mothers and offspring drank more in the dry season, as was predicted based on studies of other chimpanzee populations (Nishida, 1980). However, we found no support for our hypothesis that high maternal dominance rank would buffer mothers and offspring from seasonal water stress; there was no difference in drinking frequency by rank during the dry season. Furthermore, there was no evidence that high-ranking mothers buffered their offspring from weaning-associated water stress. It is important to note that we only had one juvenile with a low-ranking mother. Because female rank increases with age, most females have surpassed low rank before they have juvenile offspring (Foerster, Franz, et al., 2016), which may explain the lack of significant results for juvenile drinking patterns between different maternal ranks. Nonetheless, our analyses did reveal unexpected interactions discussed below.

Our results indicate that a hydration burden may be present during different lactation stages, dependent on a female's dominance rank. Our prediction that early lactation would present the strongest hydration burden to females was not supported, with drinking peaking during middle lactation for mid- and high-ranking females. Drinking in low-ranking females, however, peaked during late lactation. While infant dependence on milk exclusively during early lactation may impact water balance, maternal energy balance (measured via urinary C-peptide of insulin) is lowest during this time (Thompson et al., 2012), which may play a role in their ability to find and consume free-standing water. Conversely, research in rhesus macaques (*Macaca mulatta*) shows that milk yield increases with infant age (Hinde et al., 2009), which supports the idea that milk production increases even as infants introduce solid foods into their diets and may explain why middle or late lactation are more challenging to mothers than early lactation.

TABLE 3 Model summary from maternal analysis investigating the influence of season (dry and wet), lactation stage (early, mid, and late), and rank (low, mid, and high)

Predictors	Estimate	SE	*z*	Pr(>|z|)
Intercept	−6.510	0.280	−23.244	-
Age (prime)	0.451	0.157	2.873	**0.004**
Age (young)	0.358	0.217	1.654	0.098
Season (wet)	−1.060	0.109	−9.772	**<0.001**
Rank				
Mid	−0.448	0.213	−2.099	-
High	−0.287	0.260	−1.104	-
Lactation stage				
Middle	−0.315	0.190	−1.656	-
Late	0.438	0.193	2.266	-
Dominance rank × Lactation stage				
Mid-rank: middle lactation	0.666	0.239	2.787	**0.005**
High-rank: middle lactation	0.604	0.234	2.585	**0.010**
Mid-rank: late lactation	−0.364	0.253	−1.438	0.150
High-rank: late lactation	−0.814	0.266	−3.059	**0.002**

Note: The reference value for all age variables is old. The reference value for all season variables is the dry season. The reference value for all dominance rank variables is low. The reference value for all lactation stage variables is early lactation. Significance (Pr(>|z|) ≤ 0.05) is indicated in bold. (−) indicates the value is not shown because it does not have a meaningful interpretation.

TABLE 4 Model summary from offspring analysis investigating independent effects of season and interaction between maternal dominance rank and lactation stage

Predictors	Estimate	SE	*z*	Pr(>|z|)
Intercept	−6.081	0.347	−17.522	**<0.001**
Season (wet)	−1.199	0.175	−6.859	**<0.001**
Maternal rank				
Low	−0.355	1.242	−0.286	-
Mid	−1.213	0.527	−2.302	-
Lactation stage				
Middle lactation	−1.308	0.297	−4.407	-
Late lactation	−1.142	0.345	−3.306	-
Maternal rank × Lactation stage				
Low-rank: middle lactation	−0.220	1.307	−0.169	0.866
Mid-rank: middle lactation	1.008	0.451	2.234	**0.025**
Low-rank: late lactation	0.272	1.321	0.206	0.837
Mid-rank: late lactation	1.526	0.482	3.165	**0.002**

Note: The reference value for all dominance rank variables is high. The reference value for all lactation stage variables is juvenile. Significance (Pr(>|z|) ≤ 0.05) is indicated in bold. (−) indicates the value is not shown because it does not have a meaningful interpretation.

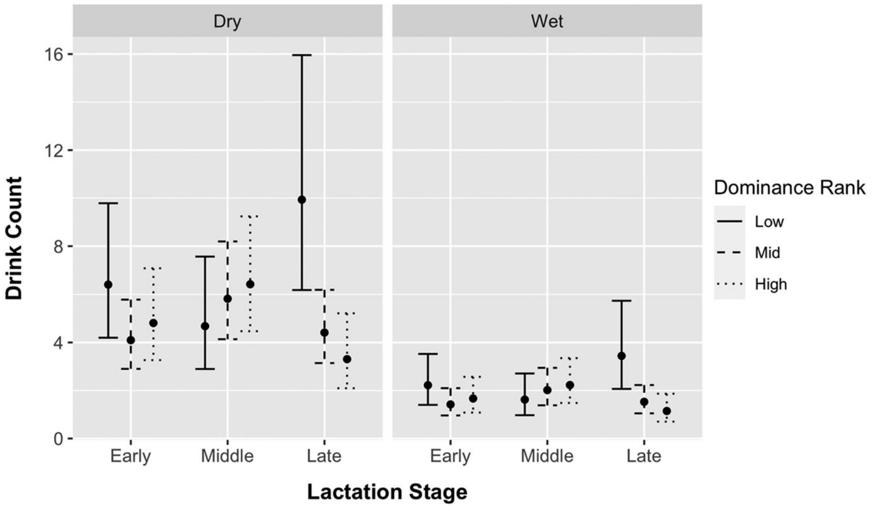

FIGURE 1 Model predicted maternal drink counts ± SE by dominance rank, lactation stage, and season.

Interestingly, we found that low-ranking females drink significantly more in late lactation than mothers of higher ranks. This result requires future study, but we suggest it may reflect different developmental trajectories and life histories of females and their offspring based on individual characteristics. Varying developmental rates of offspring between mothers of different ranks have been demonstrated in studies of wild savannah baboons (*Papio cynocephalus*); offspring of high-ranking mothers are born larger and develop faster than offspring of low-ranking mothers (Altmann & Alberts, 2005). Studies in chimpanzees have similarly found offspring of high-ranking mothers have higher muscle mass than offspring of low-ranking mothers (Samuni et al., 2020). High-ranking female chimpanzees are more likely to wean their infants earlier than low-ranking females (Lonsdorf et al., 2020), but evidence for shorter IBIs for high-ranking mothers is mixed (Jones et al., 2010; Stanton et al., 2017). Recent work has found chimpanzee infants obtain adult-like feeding patterns between 4 and 6 years of age (Bray et al., 2018; Lonsdorf et al., 2021), however, variation in feeding development between offspring based on maternal rank has not been investigated. If the offspring of high-ranking females develop and reach adult-like diets faster, late lactation may present less of a hydration burden as compared to low-ranking females with slower developing offspring.

Our analyses also tested the hypothesis that primiparous females may face an extra hydration burden associated with supporting somatic and reproductive effort. This was not born out in our results as there was no significant difference between primiparous and multiparous female drinking frequencies. Multiparous female rhesus macaques produce more milk than primiparous mothers, both in early and peak lactation (Hinde et al., 2009), and this increased with each additional parity. While primiparous female chimpanzees have been found to nurse more frequently than multiparous mothers during the first year of the infant's life (Stanton et al., 2014), differences in milk yield between primiparous and multiparous female chimpanzees have yet to be explored.

The random effect of individual identity significantly improved model fit for both our maternal and offspring analyses. This suggests that individual characteristics, or phenotype, are a significant source of variation in drinking frequency, in addition to the season, maternal dominance rank, and lactation stage. Future studies should investigate potential sources of phenotypic variation, such as early life experiences. For example, there is some evidence in rats and sheep that maternal dehydration during pregnancy can lead to changes in offspring water balance mechanisms (Ross & Desai, 2005).

Our analyses here focused on a behavioral measure of hydration status; future analyses should include physiological measures of hydration in mothers and offspring to assess the extent to which drinking behavior prevents dehydration. Wessling et al. (2018) found that both savannah and forest chimpanzees had higher physiological markers of dehydration (creatinine) during the dry season, suggesting that diet and increased drinking may not be enough to compensate for arid conditions, and hydration presents a challenge to chimpanzees inhabiting varying ecosystems.

Another potential future direction is to consider how the water content of food varies, and the extent to which diet quality relates to drinking frequency. As mentioned previously, lactating chimpanzees lose an estimated 640–675 ml of water per day through milk, and water ingestion through food can also provide explanations for how females mitigate this increased water loss. Some ape foods consist of 80% or more moisture content, providing a robust source of water (Rogers et al., 1990; Rothman et al., 2006). Because of this, it is likely that chimpanzees are gaining most of their water requirements from preformed water in foods, and decrease their drinking frequency when consuming foods with higher water contents, similarly to other primate species (Glander, 1978; Newton, 1992). More research is required to examine whether lactating females increase their consumption of water-heavy foods as compared to nonlactating females to accommodate for this increased water loss.

Our result that low-ranking females drank more during late lactation than mid- and high-ranking females may be related to differences in diet and access to preformed water in foods. Previous research has demonstrated high-ranking females have increased access to high-quality foods and higher-quality core areas as compared to low-ranking females (Foerster et al., 2016; Murray et al., 2006, 2007). This might suggest that high-ranking females are buffered from lactation's hydration challenge, not through consumption of free-standing water, but rather their increased diet quality and consumption of foods with high water contents. Further research is needed to determine variation in water consumption through food and physiological measures of hydration between females of different ranks.

Understanding hydration and the extent to which it varies based on ecological, social, and reproductive contexts, as well as how chimpanzees meet their water requirements is important to the conservation of this and other primate populations that face changing environments. Infectious disease poses the highest risk to the Gombe chimpanzees (Williams et al., 2008), and climate and anthropogenic change are predicted to have a high impact on disease prevalence in primates in the future, especially through water-borne diseases (Chapman et al., 2005). Studies of chimpanzee water consumption also have important public health implications, especially given that Gombe National Park is home to 5 monkey species in addition to chimpanzees and is bordered by human villages to the north, south, and east. Given the myriad of ways these species interact, including through the shared use of water sources, it is important to understand how chimpanzees utilize these water sources for mitigating potential zoonotic disease transmission.

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CONFLICT OF INTERESTS

The authors declare there are no conflict of interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the supplemental materials.

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