Unaffected Survivorship as a Result of Early Life Ecological Stress in Wild Chimpanzees (*Pan troglodytes schweinfurthii*) at Gombe National Park, Tanzania

by Sims Patton

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Carson M. Murray
Associate Professor of Anthropology

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Introduction

Nutritional Early Life Adversity

Numerous studies have demonstrated maternal effects on offspring outcomes (e.g. Altmann & Alberts 2005; Maestripieri 2018; Zipple et al. 2021). These effects are far-reaching and are often modulated by maternal behavior and physiology. One area of particular interest surrounds the impacts of maternal nutrition on offspring outcomes. Previous studies using rodent models *(Rattus norvegicus)* have provided valuable insight into the importance of proper maternal nutrition and potential outcomes for offspring who do not meet nutrient requirements in utero. For example, studies by Sullivan et al. (2014) and Batista et al. (2019) describe variations in maternal macronutrient consumption, both under and overconsumption, and the resulting negative impacts on offspring behavior and health. Rodent models allow researchers to not only control all aspects of maternal nutritional intake during gestation and lactation but also link genetic information to observed outcomes thus providing clear implications for impacts of early life nutritional adversity. Additional work in humans and non-human primates has supported the effects of early life nutritional deprivation on offspring providing meaningful insight into biological and behavioral responses to nutritional adversity.

The Dutch Hunger Winter represents seminal findings for how early life nutritional deprivation impacts offspring in humans. From November 1944 to May 1945, the German-occupied Netherlands experienced extreme food scarcity due to a German food embargo. Individual daily caloric intake went from 1800 cal/day in 1943 to less than 1000 cal/day, reaching as low as 400 cal/day (Roseboom et al., 2006 and Lumey et al.,

2007). While the famine resulted in a rapid increase in mortality rate due to malnutrition, babies gestated or born during this period provide unique insight into the long-term impacts of gestational nutritional adversity (Roseboom et al., 2006). Physiologically, the health outcomes of offspring differed based on timing of exposure; babies exposed to the famine during the first and second trimesters exhibited significantly decreased birth weights compared to those not exposed to famine and those exposed only in the third trimester. Infants also experienced different health outcomes based on the gestational timing of exposure (Roseboom et al., 2006). Adult glucose intolerance was associated with offspring exposed during all three trimesters while offspring exposed during in the first and second trimesters developed additional adverse health conditions like airways disease, increased microalbuminuria in the urine indicating poor renal function, and coronary heart disease (Roseboom et al., 2006). Due to the continued study of individuals from this cohort, a 2014 study by Ekamper et al. found an increase in mortality in men born between 1944 and 1945 who were exposed to the Dutch Hunger Winter particularly in early gestation compared to women who were also exposed and born during the same period. In addition to negative physiological outcomes, offspring also reported psychological and cognitive impacts such as mood disorders, schizophrenia, and poor performance on selective attention tasks when compared to unexposed peers (Susser and Lin, 1992; Brown et al., 1995; de Rooij et al., 2010). These findings are supported by more recent studies from Galler et al., (2011) and Jackson (2016) who reported increased instances of externalizing or aggressive behaviors and antisocial behaviors respectively among juveniles exposed to malnutrition during early life.

While the study above provides clear evidence for the impacts of early life nutritional adversity on health outcomes, human health is impacted by a broad range of factors affecting access to health care, including cultural and economic factors. Thus, investigating how adversity affects non-human primates provides a powerful comparative context. Captive non-human primate models allow for close monitoring of caloric and nutrient intake during gestation and easily manipulated social environments to control for and understand potential buffering factors to adversity. To complement human and rodent research on maternal consumption of a high fat diet during pregnancy, a captive primate study by Sullivan et al. (2010) found both physiological and behavioral impacts on Japanese macaque *(Macaca fuscata)* offspring. Female offspring born to mothers fed a high fat diet throughout their entire pregnancy exhibited increased levels of fear associated with novel objects and increased levels of inflammatory cytokines indicating fatty liver disease (Sullivan et al., 2010). All offspring in this study exhibited accelerated growth postpartum and had an increased percentage of body fat compared to control diet offspring (Sullivan et al., 2010). A study exploring the neurodevelopmental outcomes of offspring born to mothers fed a calorie restricted diet during gestation found evidence of affected activity levels and emotional arousal (Keenan et al., 2013). Juvenile offspring of female baboons *(Papio anubis)* fed a restricted diet were given a series of cognitive tests examining emotional arousal and reward motivation. Compared to offspring of mothers fed an ad libitum diet, the restricted offspring showed less emotional arousal and more varied activity levels (Keenan et al., 2013). Female offspring showed more varied levels of persistence and attention compared to control female offspring (Keenan et al., 2013).

In wild primates, poor early life nutrition has been found to have lasting impacts on offspring body size and behavior, and maternal behavior. For example, a study by Levy et al. (2023) on wild baboons *(Papio cynocephalus)* found prolonged exposure to drought in early life predicted shorter limb but not torso length. A study of wild Taihangshan macaques *(Macaca mulatta tcheliensis)* found as annual availability of oak seeds, an important source of fat and carbohydrates, varied, lactating female nutrient intake, activity levels were lower, and mothers spent more time nursing their offspring (Cui et al., 2020). A 2020 study by Campos et al. observing two primate species, white-faced capuchins (*Cebus capucinus imitator*) and Geoffroy's spider monkeys (*Ateles geoffroyi*) found varied primate responses to extreme drought. White-faced capuchin infants experienced exceptionally high rates of mortality during extreme drought but were buffered from death during periods of moderate water shortage (Campos et al., 2020). In contrast, female spider monkeys ceased reproduction during periods of extreme drought and thus infant mortality peaked later during periods of low fruit abundance and increased tree mortality as a result of the drought (Campos et al., 2020). A study on wild Assamese macaques (*Macaca assamensis*) found reduced immune function, accelerated offspring growth, and decelerated motor skill acquisition in offspring born to mothers with high levels of prenatal stress due to environmental factors like decreased food availability (Berghänel et al., 2016). Together, these studies of nutritional early life adversity in wild primates highlight the importance of quality prenatal maternal nutrition and its critical impact on offspring health and overall survival.

Buffering Factors

Studies in a range of mammals, including humans have demonstrated that the impact of early life adversity depends on 'buffering factors' that can mitigate the impacts of early life adversity. A comprehensive study of the impacts of early life adversity on humans and other social mammals found factors like social networks and economic status to be influential on later health outcomes (reviewed in Snyder-Mackler, 2020). In humans, as income and integration of social networks increased, survivorship overall increased and the susceptibility to chronic illnesses like asthma, heart disease, and bronchitis decreased (Snyder-Mackler, 2020). A similar pattern was found among savannah baboons as there was a positive correlation between maternal sociality and offspring survival. A strong social network is beneficial in its ability to increase coalitionary support, increase tolerance from more dominant individuals, and provide a positive environment for socializing offspring (Silk, et al., 2003). A 2018 review by Maestripieri highlighted that in primates with despotic dominance hierarchies, the transmission of maternal rank in the form of agonistic aid to offspring aids in offspring fitness and development (Maestripieri, 2018). As primate dominance rank is often correlated with improved access to quality resources and mating opportunities, it can be assumed during periods of resource stress, dominant individuals would still have access to quality food over low-ranking individuals (Kappeler and Silk, 2010). Buffering factors in primates like social integration, dominance rank, and priority access to quality resources can all be used to alleviate some of the stresses associated with early life adversity and improve offspring outcomes in later life.

Chimpanzee Behavior and Ecology

Chimpanzees are an interesting model to study early life adversity due to their fission-fusion social structure, protracted development period, and environmental seasonality.

Chimpanzees are frugivorous primates with ripe fruit making up the majority of their diet (Goodall, 1986). Other foods consumed include leaves and pith, insects, and small mammals on occasion. While less is known about the "ideal" chimpanzee diet, the nutritional value of various diet items is well understood, and extensive nutritional geometry studies have been conducted explaining macro and micronutrient values (Uwimbabazi et al., 2021). Because ripe fruit is high in carbohydrates but low in protein, young leaves serve as an important dietary component for maintaining protein and fiber balance and should not be ignored when considering what constitutes proper chimpanzee nutrition. In chimpanzee habitats, leaves and pith are often seen as "fallback foods" due to their relatively low preference and high abundance while fruit is considered a preferred food item due to its over-selection (Conklin-Brittain et al. 1998; Basabose 2002; Marshall and Wrangham, 2007).

Chimpanzees live in multimale, multifemale communities in which individuals form temporary subgroups or "parties" based on ecological factors like season, sexual status, and food availability (Goodall 1986). In East African chimpanzees (*P. t. schweinfurthii*), males are highly gregarious while mothers spend up to 40-70% of their time alone with their dependent offspring (Murray et al., 2007; Williams et al., 2002; Wrangham and Smuts, 1980). This fission-fusion social organization allows for individuals to spend time in both large group settings when food is abundant while also

choosing to spend time foraging for food alone when resources are scarce, making them an interesting study species for nutritional early life adversity research. While food resources are distributed heterogeneously throughout the environment, previous studies have found differences in chimpanzee behavior during periods of resource stress. During the dry season when fruit availability is low, female party sizes are smaller (Wrangham 1977; Boesch 1996; Doran 1997; Matsumoto-Oda et al., 1998), activity periods are longer (Lodwick et al., 2004), body mass decreases (Uehara and Nishida, 1987; Pusey et al., 2005) and consumption of lower quality foods increases (Richard 1985; Wrangham et al. 1991). The flexibility of fission-fusion social organization may serve as a buffering factor for young chimpanzees exposed to nutritional scarcity as mothers can choose to spend less time socializing to avoid competition for resources.

Despite spending much of their time alone foraging for food, eastern female chimpanzees have dominance hierarchies in which they compete for food and space use (Pusey et al., 1997; Murray et al., 2006). More dominant females are found to have higher quality core areas and be more efficient foragers (Murray et al., 2007; Murray et al. 2006). They also have shorter interbirth intervals and higher infant survival (Pusey et al., 1997). The influence of maternal rank of offspring survival will be considered in this thesis as a potential buffering factor for offspring born to high ranking mothers in periods of stress and a potential negative additive effect for offspring born to low ranking mothers during the same periods.

Like other primates and great apes in particular, chimpanzees have a protracted development period including a gestation period of 226.9 days (Wallis & Goodall, 1993; Wallis, 1997; Feldblum et al., 2022). Offspring are typically born as singletons with the

instance of twins being infrequent. Slow life histories and protracted development periods have the potential to buffer offspring from periods of resource scarcity by decreasing the speed of somatic growth and the nutrition it requires (Jones, 2011). Chimpanzee mothers have an average inter-birth interval of 2-5 years, varying by field site, characterized by lactational amenorrhea during which females do not have regular cycles and are temporarily infertile (Deschner & Boesch, 2007). At Gombe specifically, the average interbirth interval is 5.15 years (Wallis 1997). This allows chimpanzee offspring to avoid competion with close-in-age siblings for nutrition particularly during the lactation period when they are dependent on the mother for nutrient intake as only one offspring nurses at a time. Offspring experience weaning and are responsible for their own nutrition before a younger sibling is born.

Study Goals and Predictions

This study aims to analyze the survival outcomes of wild chimpanzees (*pan troglodytes schweinfurthii*) at Gombe National Park, Tanzania during periods of nutritional stress. Fruit consumption will be used as a proxy for food availability in determining years of interest for the study period. In particular, I predict that: (1) Offspring born during periods of low food availability will have lower overall survivorship compared to offspring born during periods of average or above average food availability; and (2a) The relationship between low food availability and survivorship will be more pronounced for offspring born to mothers of low dominance rank compared to offspring born to mothers of high rank and (2b) offspring born to high ranking mothers will experience less pronounced survival effects from nutritional adversity because they

are buffered. Alternatively, I predict that there may be no difference in infant survivorship since females have several 'tools' to mitigate the impacts of low food availability, including the fission-fusion social structure and slow life histories of chimpanzees.

Methods

Subjects and Study Site

This study investigates how early life nutritional "scarcity" (operationalized below) relates to infant survivorship in two communities of eastern chimpanzees (*Pan troglodytes schweinfurthii*) living in Gombe National Park (Tanzania). The two communities included in this study, Kasakela (KK) and Mitumba (MT), are fully habituated to human observation and have been studied since 1960 and 1985, respectively (Pusey et al. 2007). Using data from a long-term study site is important to the aims of this project to fully understand the long-term impacts that could arise due to low food availability. Gombe National Park covers 37.5 km^2 and shares 1622m with Lake Tanganyika on its western border. The terrain is complex with numerous ridges and valleys, grasslands, and semi-deciduous and evergreen forests. Gombe experiences distinct wet and dry seasons with the wet season lasting from November to April and the dry season from May to October (Clutton-Brock and Gillet, 1979). Average annual rainfall is estimated at 1190mm, an average of 178mm per month in the wet season and 6mm per month in the dry season (Schneider et al., 2011).

Detailed demographic data is available for the entire study period and detailed in Strier et al. (2010). These data include the following variables of interest: birthdates and depart dates and depart types. Depart types include individuals who are known to be dead (D), individuals still living and observable (O) as of 10/11/2020, and individuals who have permanently disappeared from the observation community but are not assumed to be dead (P). Individuals were not assigned depart type D until an identifiable corpse was found or there was strong circumstantial evidence like visibly poor health or violations of

population-specific behavior patterns before disappearance. In demographic analyses for this study, individuals with depart types O and P were right censored observations. Individuals within the population before the observation period with unknown birth and depart dates are given estimated minimum and maximum birth and death dates based on individual size, developmental characteristics, and parity in females (Strier et al., 2010). In some cases, estimated birth min and max dates created a window of several years limiting reliable survival calculations. These individuals were removed from the study sample.

Identifying Periods of Low Food Abundance

To identify periods of food "scarcity", I characterized yearly diet from long-term behavioral records focused on feeding behavior, including food species and part. Teams of field researchers conduct nearly daily focal follows on both chimpanzee communities, during which they follow and collect behavioral data on one adult member of the community each day. Information collected includes detailed data on subgroup composition and social behavior, as well as continuous records of feeding behavior, food species and part is also collected. Identified foods were characterized into four main categories: Fruit, Leaves and Pith, Fauna, and other. Food items in the "Leaves and Pith" category include leaves, stems, shoots, and saplings. Food items in the "Fauna" category include other small primates and invertebrates, including termites, ants, and caterpillars. Food items in the "Other" category include seeds, bark, sap, honey, and sprouts. Previous research has considered fruit as high-quality resources since chimpanzees are predominantly frugivorous (Wrangham, 1977; Matsumoto-Oda and Hayashi, 1999). A

study from Kanyawara (Kibale Forest, Uganda) found that habitat quality, measured based on non-fig fruit abundance, predicted ovarian hormone concentrations, and shorter inter-birth intervals for females that ranged in higher quality areas (Emery-Thompson et al. 2007). Despite having significantly more protein than fruits, leaves and pith consumption is negatively correlated to body mass (Gilby et al. 2013), lower levels of non-fibrous carbohydrates, an important source of energy, and thus, considered low quality (Matsumoto-Oda and Hayashi, 1999).

To characterize food availability for this thesis, diet proportions by food type were calculated using all focal feeding observations between 1973- 2015. Yearly diet proportions were calculated by taking the total duration of observed time spent feeding per food category divided by the total observed time spent feeding on all food categories for all chimpanzees each year **(Figure 1)**. For example, in 2015 the chimpanzees were observed feeding on fruit for 29,073 minutes and they were observed feeding on all food types for a total of 49,375 minutes. To calculate the proportion of time spent feeding on fruit in the year 2015, 29,073 was divided by 49,375 giving a fruit diet proportion of 0.588 for that year. Feeding observations where food type was recorded as "unknown" were removed from the study. Observations in which two food types were listed were classified into the food type category of the more valuable food type listed to avoid double counting the observation. For example, if an observation included both fruit and leaves, this observation was counted in the fruit category. Foods were classified as more valuable based on nutritional value and chimpanzee preference with the general rule being fruit > fauna > leaves and pith.

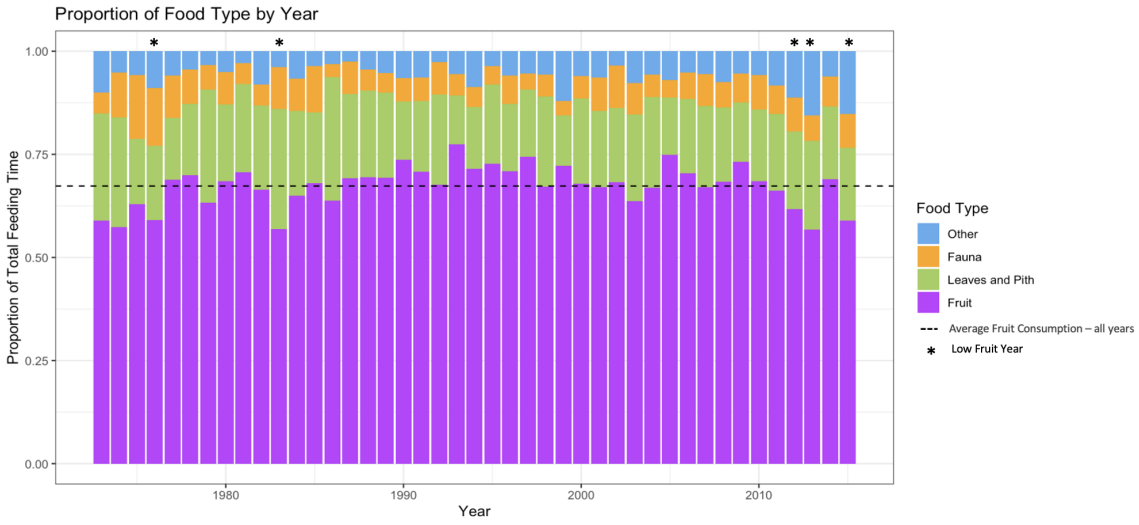

Figure 1: Proportion of each food type by year for all years included in the study period. The average annual fruit consumption is indicated by the dashed line (0.67).Low fruit years, i.e. years of fruit scarcity are indicated by * and include: **1976, 1983, 2012, 2013, 2015.**

To identify years in which diet proportions were significantly below the mean, the average proportion and standard deviation for each food type was calculated for all the years in the study period (**Table 1**). Years in which fruit consumption was greater than one standard deviation from the mean were classified as nutritional adversity years (**Table 2**).

	Fruit Consumption (Proportion of Diet)	Leaves and Pith Consumption (Proportion of Diet)	Fauna Consumption (Proportion of Diet)	Other Consumption (Proportion of Diet)
Average	0.6732	0.1924	0.0708	0.0636
Standard Deviation	0.0502	0.0409	0.0262	0.0294

Table 1: Average diet proportions for each food type calculated using all years in study sample (1973-2015).

Characterizing Infants Based on Fruit Scarcity

Individuals were considered to have experienced "Nutritional Scarcity" if they were gestated for at least four months or born and survived for at least four months during one of the low fruit years. Estimated conception dates were calculated by taking the birthdate and subtracting 8 months, 244 days. While the average chimpanzee gestation length is 226.9 days (Peacock and Rogers, 1959), an estimated conception time of 8 months was used to account for the uncertainty of birthdates within the sample. We excluded individuals who were victims of infanticide (N = 3) or had the same departure date as their mother (N = 4) were because we could not disentangle the effects of early life nutritional adversity from maternal loss or infanticide. Further, we excluded individuals with uncertain birthdates resulting in an estimated birth window of 365+ days (N = 43) from the study with the largest estimated birth window included being 84 days (2.8 months). In addition to birthdates and estimated conception dates, departure dates, departure types, maternal rank, and birth communities were also recorded and used for analysis. Individuals with no known birth community were also excluded from the study as birthdates could not be accurately calculated (N = 58). The previously mentioned parameters resulted in a study sample size of 185 individuals across the two fruit conditions, low and average, with lifespan ranges from 2 days to 49 years. (**Table 2**).

Maternal Dominance Rank

Female ranks were assigned based on the direction of pant grunts, a vocalization which is a formal indicator of subordination, and the decided outcomes of aggressive interactions. These interactions were used to assign a continuous dominance score, scaled

0 to 1, based on a modified version of the Elo rating method (see Foerester et al. 2016 for more detail). Continuous scores were then divided into categorical ranks using the Jenks natural break method. Maternal rank was recorded and used for analysis on the offspring's estimated birthdate in one of three categories: high, mid, or low. For the purposes of this study, offspring of high and mid ranking mothers were combined into one category, high, for maternal rank as survival differences between high and mid ranking offspring are minimal compared to differences between high/mid ranking offspring against low-ranking offspring (Pusey, 1997). During statistical analysis, this resulted two categories for maternal rank, high (N = 118) and low (N = 67).

Grouping	**Males**	**Females**	**Unknown**	**Total**
Nutritional Early Life Scarcity	9	10	0	19
No Nutritional Early Life Scarcity	88	64	14	166
Total	97	74	14	185

Table 2: Sample sizes by fruit abundance and sex.

Survival Analyses

To examine the relationships between poor nutrition during early life on chimpanzee overall survival, survival until adulthood, survival until age 5, and surviving until one year of age, Cox proportional hazards models and a Kaplan Meier survival curve were generated using the survival and survminer packages in R statistical software version 2023.03.0+386. Four separate Cox proportional hazards models were generated for chimpanzee survival throughout critical periods of development: 1 year of age, 5

years of age, 10 years of age (adulthood), and overall survival. Mortality during infancy is high but other key life history transitions include weaning (average age 4.2 years of age, Lonsdorf et al. 2020) and transition from adolescence to adulthood (age 10, Pusey, 1990). Offspring survival was the outcome variable in each of the four models with death before one of the four critical periods (separate for each model) as the event variable and exposure to nutritional scarcity and maternal rank as predictor variables. Each model was tested using the cox.zph function and all variables were found to meet all the assumptions of the cox proportional hazards model. Because research has demonstrated that high ranking females have higher body mass and increased infant survivorship than lower ranking females (Pusey et al. 1997; Pusey et al. 2005), maternal rank and exposure to nutritional scarcity were also modeled as interaction variables. We included maternal ID as a random effect to account for mothers of multiple offspring within the sample. To calculate lifespans, birth dates were subtracted from depart dates for individuals already deceased, depart type D in the demographic data. A Kaplan-Meier survival curve was generated for visualization purposes and 95% confidence intervals included to demonstrate potential uncertainty within the sample.

Results

Survival Analysis

There was no significant interaction between maternal rank and exposure to nutritional scarcity when estimating offspring survival to any age or overall (**Table 3**). We also did not detect significant differences in survivorship to any critical age or overall survival based on early life exposure to nutritional scarcity (**Table 3; Figure 2**) or maternal rank on its own (**Table 3**). Notably, while there was no effect of maternal rank at birth, the resulting hazard ratios do align with previous chimpanzee research indicating a relationship between low maternal rank and poor offspring survival (**Table 3**). The Kaplan-Meier curve created for visualization purposes highlights the overlap of the 95% confidence intervals also indicating no statistically significant difference between the two nutritional groups (**Figure 2**).

When looking at survival probabilities for each nutritional condition at four ages associated with critical periods in chimpanzee development, 6 months, 1 year, 5 years, and 10 years, they were non-significant with the adverse condition having the highest survival probability at each age (**Table 4**). These values were calculated by creating a summary of all study individuals who experienced the event by each of the age categories (0.5 years, 1 year, 5 years, and 10 years) and dividing that number of individuals by the total number in the sample. For example, at age 5, 62 individuals from the average fruit condition had died and 6 individuals from the low fruit condition had died. These number were divided by the total number of individuals in their sample groups, 151 and 19 respectively, to calculate the survival probability at age five for the two study conditions.

Model Investigating Survival Until Age:	Predictor Variables Included in Model	β	HR	SE(β)	*p*
1 year	Food Scarcity	-1.104	0.332	1.023	0.28
	Low Maternal Rank	0.211	1.235	0.335	0.529
	Food Scarcity * Low Maternal Rank	1.578	4.853	1.270	0.213
5 years	Food Scarcity	-0.843	0.431	0.597	0.158
	Low Maternal Rank	0.236	1.266	0.231	0.307
	Food Scarcity * Low Maternal Rank	0.977	2.657	0.849	0.25
10 years	Food Scarcity	-0.461	0.631	0.522	0.377
	Low Maternal Rank	0.345	1.419	0.228	0.124
	Food Scarcity * Low Maternal Rank	0.506	1.658	0.797	0.526
Overall Survival	Food Scarcity	-0.580	0.560	0.467	0.214
	Low Maternal Rank	0.314	1.369	0.198	0.113
	Food Scarcity * Low Maternal Rank	0.285	1.330	0.757	0.707

Table 3: Results of the Cox proportional hazards models examining the effects of nutritional early life adversity and low maternal rank on chimpanzee survival until different developmental stages compared to individuals not exposed to nutritional scarcity and born to mothers of high rank. * Indicates the interaction between two predictor variables within the model.

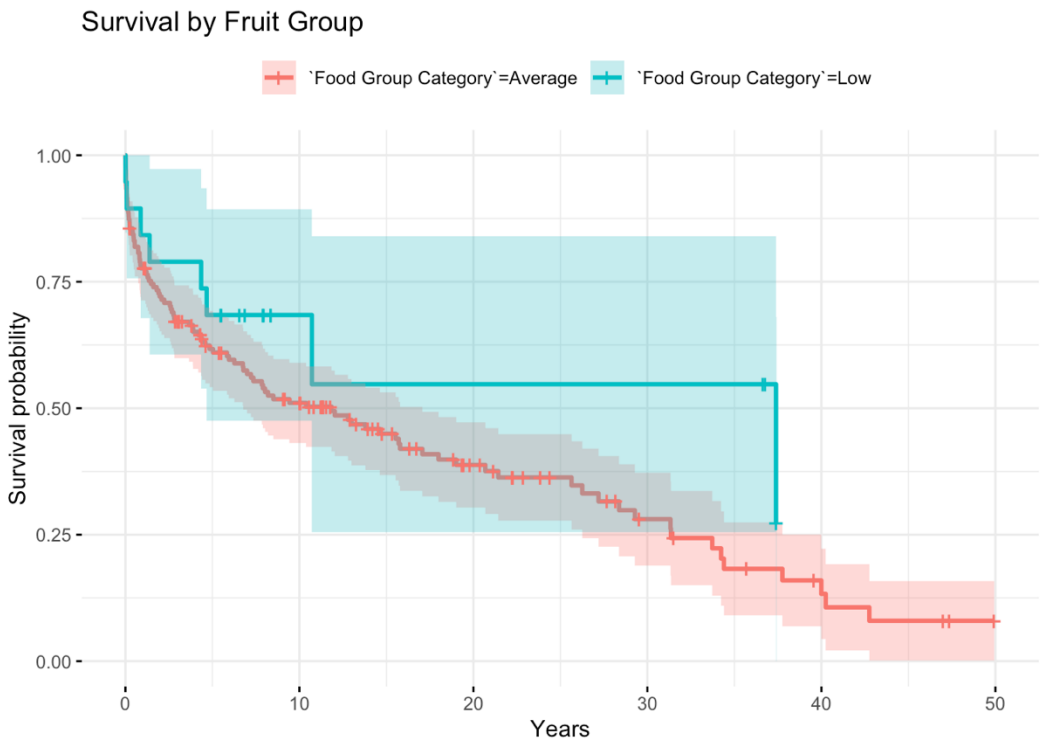

Figure 2: Kaplan-Meier survival curve by nutritional group: scarcity or non-scarce based on raw demographic data.

	Survival Probability at 6 months	**Survival Probability at 1 year**	**Survival Probability at 5 years**	**Survival Probability at 10 years**
Nutritional Early Life Scarcity	0.895	0.842	0.684	0.684
No Nutritional Early Life Scarcity	0.831	0.777	0.617	0.511

Table 4: Survival probabilities at different ages. Infant mortality is high but other key life history transitions include weaning (average age 4.2 years of age, Lonsdorf et al. 2020) and transition from adolescence to adulthood (age 10, Pusey, 1990).

Discussion

The long-term impacts of exposure to early life adversity are well- documented in a range of species (Brown et al., 1995; Roseboom et al., 2006; de Rooij et al., 2010; Sullivan et al., 2014; Keenan et al., 2013; Levy et al., 2023). In non–human primates, elegant work in baboons has demonstrated the impacts of maternal loss, drought exposure, and presence of close in age siblings on survival (Tung et al., 2016; Zipple et al., 2020; Zipple et al., 2021). We know less about how food scarcity relates to survivorship in great apes. Our results found no relationship between fruit scarcity for chimpanzee infants born into the study population. While we cannot eliminate the possibility that females are less likely to get pregnant or more likely to experience fetal loss, chimpanzees are an interesting system in which to consider how early ecological adversity impacts offspring given they have a more protracted developmental period and fission-fusion social dynamics. We suggest that these characteristics buffer offspring from mortality, at least in our study population, but future studies should investigate this relationship in other populations and the extent to which other aspects of development and health are impacted by reduced food availability during gestation and early lactation. While low maternal rank is found to negatively influence offspring survival overall, we found no additional negative effect on survival when combined with birth occurring during periods of fruit scarcity.

Fission-fusion social dynamics are observed in a wide range of species and thought to mitigate feeding competition (reviewed in Aureli et al. 2008). While this may limit competition among females in this study, especially during periods of food scarcity, it may also serve to buffer immature chimpanzees at key periods of early development

from food scarcity. However, this study only considered survivorship so future studies should consider other aspects of health and physical development, which are likely impacted by food availability during gestation and early development. Indeed, research has demonstrated a tradeoff in female chimpanzee reproductive rates and offspring growth, attributed to the effects of maternal energy depletion (Emery-Thompson et al. 2016). A similar mechanism could be at play based on extrinsic depletion associated with lower food abundance.

Future studies should also consider how reducing sociality during food scarcity may have other effects on the social development of offspring, particularly for immature chimpanzees that are starting to develop social relationships. Social exposure and play opportunities are important for chimpanzee development and could have negative impacts if not prioritized by mothers. As play is an important part of infant chimpanzee development (Lonsdorf et al., 2014), future studies should investigate how offspring are affected if forced to spend more time alone due to decreased food availability. Seminal research by Harlow highlights the importance of maternal attachment in infancy but also the need for social play in early life and the inability to overcome social isolation as an adult when exposed to prolonged periods of isolation as an infant (Harlow and Harlow, 1962; Harlow et al., 1965). Play is associated with benefits in motor function, social competency, and social and environmental learning (Poirier and Smith, 1974; Byers and Walker, 1995; Joffe, 1997; Graham and Burghardt, 2010).At Gombe specifically, young chimpanzees who engaged in higher amounts of social play reached developmental milestones like independent travel and spatial independence (Heintz et al., 2017). Chimpanzees have adjusted to their seasonal habitats by shifting their social

organizations possibly to mitigate some of the impacts of nutritional early life adversity (Wrangham 1977; Boesch 1996; Doran 1997; Matsumoto-Oda et al., 1998). This trade off may have some consequences for social development and should be considered for future studies.

It is important to note that while Gombe is a seasonal habitat with fruit availability varying during the wet and dry seasons, overall, food availability levels are relatively stable across time and "fallback foods" are often present in place of preferred food items. When analyzing 42 years of feeding data, only five years of significant food availability were identified. These years only differed from the mean by a maximum of two standard deviations and were rarely found to occur consecutively. Future studies should examine similar instances of primate nutritional stress in habitats with greater seasonal variation in food availability, temperature, and rainfall like savannah grassland ecosystems. This research could have an even greater impact in future years when the effects of global climate change become more pronounced. Research into the long-term impacts of decreased food availability will be important for management and conservation decisions in the future. As forest ecosystems across primate habitats experience decline as a result of deforestation and increased urban sprawl, it is only a matter of time before the Gombe chimpanzees experience similar events thus altering their food availability which in turn could affect aspects of their health and behavior long term.

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