Maternal social position and survival to weaning in arid-country vervet monkeys

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Abstract

Objectives

We consider the relative contributions of maternal rank and sociability to the survival of infant vervet monkeys (*Chlorocebus pygerythrus*) to nutritional independence (~210 days) in a generally resource-poor environment.

Methods

We analysed survival data from 153 infants born to 60 mothers across three free-ranging troops and 10 yearly birth cohorts at a South African research site experiencing general but variable resource scarcity. i

Results

The population was characterised by a pre-weaning mortality of 30% (Range: 9%-85%), with a median age at death of 50 days. In addition to the consequences of resource availability, increased infant survival was independently and equivalently positively associated with higher maternal rank and a greater number of maternal spatial partners.

Discussion

We use this outcome to suggest that apparent discrepancies across sites and species in the relative importance of different maternal attributes in determining reproductive outcomes may be resolved by considering more closely local sources of infant mortality.

KEY WORDS: Maternal effects, infant survival, weaning, vervet monkeys

1. Introduction

Reproductive success hinges fundamentally on the survival of offspring to reproductive maturity. Within the constraints imposed by the need to balance current and future investment (Parker et al., 2002), female mammals contribute directly to this through the postpartum provision of milk, the quantity and quality of which has direct consequences for offspring growth and survival well beyond weaning (Lee, 1987; Hinde & Milligan, 2011). Nevertheless, the pre-weaning period is critically important to a female's reproductive success for the simple reason that the likelihood of infant survival is maximally under maternal control during this period. In this regard, early infant death is relatively common, occurring when offspring are still totally reliant on their mothers for both food and protection (Kerhoas et al., 2014; Henzi et al., 2010; McLean et al., 2019). Weaning therefore constitutes a watershed for both mother and infant, marking as it does the time from which maternal influence, while it may continue to be very significant, is less immediate for nutritionally independent offspring (Blomquist, 2013; Borries et al., 2014; Zipple et al., 2021). Consequently, in addition to buffering vulnerable offspring against external threats, a mother's minimal post-partum objective must be to sustain lactation so as to ensure infant survival to independence.

To this end, maternal diet is critical, as it underpins the dependent infant's viability, through both initial gestational growth and subsequent milk composition and availability (Butte et al., 1984; Lummaa & Clutton-Brock, 2002; Blomquist et al., 2017). As the provision of milk also carries energy and time costs (Lee, 1996), maternal performance is likely to be contingent on optimising access to relevant resources, especially where these are limited and contested. In gregarious animals, such as primates, this resource holding potential (RHP: Parker, 1974) is usually indexed by within-group dominance relationships, where higher ranking animals are more competitively successful and presumed to be able to forage more efficiently and target higher quality foods when this is advantageous (Koenig, 2002).

Not surprisingly, therefore, there has been a long-standing presumption of a relationship between female rank and reproductive success (Ellis, 1995), at least under circumstances where RHP is relevant (Lee, 1996), and/or where high rank enables mothers to buffer young infants against social or environmental threats (Clutton-Brock & Huchard, 2013). Despite its intuitive appeal, however, the generality of the link between female rank and reproductive success is uncertain, especially once phylogeny is accounted for (Majolo et al., 2012), and may, in part, be traced back to mixed evidence for a relationship between rank and RHP (Majolo et al., 2012; Clutton-Brock & Huchard, 2013).

More recent evidence of links between female social integration and reproductive success also highlights the explanatory ambiguity of rank. That both higher rank and sociability can be beneficial for mothers (Silk et al., 2003; Ostner & Schülke, 2018), or that social integration, but not rank, predicts infant survival (Silk et al., 2009; Cameron et al., 2009; McFarland et al., 2015), points to the possibility that it is sociability that is of primary importance, especially since rank and social connectivity can be strongly correlated (Silk et al., 2009). At the same time, however, analyses flagging the importance of sociability do not always model maternal rank (see, for example, Kalbitzer et al., 2017; Menz et al., 2020), while those emphasising rank effects may not consider social integration (Wright et al., 2020; Arlet et al., 2021). All of this suggests a continued need to model explicitly the contributions of both rank and indices of social integration to reproductive success in order to account for the drivers of infant survival across circumstances where the relative value of each may vary (Clutton-Brock & Huchard, 2013), not only spatially but also temporally.

We have been working on a population of vervet monkeys (*Chlorocebus pygerythrus*) that is detectably vulnerable to several features of the local environment (McFarland et al., 2014; Ducheminsky et al., 2014; Young et al., 2019). In this population, female dominance hierarchies are relatively shallow (Henzi et al., 2013), and the adaptive responses that have been measured point to the explanatory primacy of social integration over rank (Josephs et al., 2016; McFarland et al., 2015). Here, we consider whether this extends similarly to infant survival, or if the ecological constraints that characterise the region (Pasternak et al., 2013) leads to the benefits of high rank (i.e., greater RHP and more access to resources) manifesting more prominently. To do so, we first account for the possible effects of maternal experience and reproductive history (Hinde et al., 2009; Menz et al., 2020; Arlet et al., 2021), and then model survival to weaning in relation to maternal rank, socio-spatial connectivity, and food availability.

2. METHODS

2.1 Study species and research site

We have collected data from three fully habituated groups (RBM, RST since 2008; and PT from 2012; Table 1 indicates the number of adults in each troop, and the size of each birth cohort) of wild vervet monkeys at Samara Private Game Reserve, South Africa ($32^{0}22$’S, $24^{0}52$’E). The study area is semi-arid riverine woodland (Pasternak et al., 2013), with a declining annual average rainfall of 386 mm, and average minimum and maximum temperatures of 6.1 C and 21.2 C respectively. While rainfall is generally low, the area is also characterised by periods of severe drought (Young et al., 2019).

2.2 Births and Deaths

TABLE 1. Numbers of adult females/adult males/infants across the study period for each of the three study troops. Adult numbers indicate the maximum recorded for each sex in any month of the year. Infant numbers indicate the size of the birth cohort for infants conceived in that year.

Year	Troop: RST	Troop: RBM	Troop: PT
2010	22 / 19 / 15	15 / 11 / 11	—
2011	22 / 17 / 5	13 / 14 / 1	—
2012	20 / 22 / 2	8 / 18 / 1	10 / 10 / 1
2013	17 / 14 / 12	10 / 16 / 10	12 / 11 / 7
2014	16 / 14 / 11	13 / 16 / 13	11 / 6 / 10
2015	18 / 14 / 11	13 / 11 / 10	10 / 4 / 2
2016	16 / 16 / 9	12 / 8 / 9	9 / 8 / 2
2017	11 / 9 / 3	8 / 10 / 3	10 / 14 / 6

As at other locations (Butynski, 1988), vervet females in our study population experience a moderately circumscribed birth season with a peak centred on October. We classified infants into cohorts based on the year of conception (e.g. 2018), given that a birth season can extend into the next calendar year. Gestation in vervet monkeys has been estimated at ~163 days (Kavanagh et al., 2011) and infants in our population are considered to have completed weaning by the age of seven months (Sashaw, 2012). While we recorded all births for two troops (RBM, RST) from 2008 through 2018, we only tracked individual infant survival (with the addition of one animal in 2009) for the 2010-2017 cohorts (2012-2017 cohorts for PT). We considered only live births. Where births or deaths occurred on a weekend, when the animals were not under observation, we allocated Saturday’s date to the event. Age at death (days) was used to model the temporal distribution of those infant deaths that occurred before weaning.

2.3 Behavioural data and female dominance hierarchies

Each group was followed for five days each week, and data collected for 10 hours each day by three to five observers. We used data on nearest adult neighbours and grooming partners, collected during scan samples conducted every 30 minutes to construct social networks. We used ad libitum observations of agonistic interactions to estimate the dominance rank of each female over the period of each of her births. Given male-female co-dominance in this population (Young et al., 2017), we generated a single matrix that included all decided agonistic interactions, and extracted an interdigitated hierarchy. To enable direct comparison across groups of different size and interaction rates, dominance ranks were expressed as standardized David's scores using the package “compete” in R (Curley, 2016).

2.4 Female social networks

We used the “igraph” package (Csardi & Nepusz, 2006) in R 3.5.2 (R-Core-Team, 2018) to construct female grooming and nearest-neighbour spatial networks. As the presence of young infants alters maternal social interactions in the short-term (Henzi & Barrett, 2007), and because network structure is broadly consistent over the longer-term in this species (Blaszczyk, 2018), we used data from the two months prior to each birth. Doing so allowed us to target social structure at the time of the increased metabolic demand of the last trimester and the transition to lactation. Model outcomes were not affected by increasing the gestational period used to construct networks. In order to describe the structure of these networks, with individuals represented as ‘nodes ’ connected by ‘edges’, we estimated three network parameters: (i) degree (the number of connections a node has), (ii) node strength (the sum of link weights of a given individual), and (iii) eigenvector centrality (a measure of the influence of each node in the network). We did so because all three measures have been implicated, in either their spatial or social configurations, in one or other aspect of the study population’s social engagement (McFarland et al., 2014; Ducheminsky et al., 2014; Young et al., 2019), making it difficult to offer a principled specification of a reduced set, which would be preferable (Webber et al., 2020). At the same time, posterior pairwise comparisons indicated acceptable collinearity across the six measures, as they also do with estimates of rank.

2.5 Food availability

We quantified food availability in each troop's home range by calculating the Normalized Difference Vegetation Index (NDVI) every 16 days (Young et al., 2019) from MODIS data collected by Earth Observing System (EOS) satellites Terra (EOS AM-1) and Aqua (EOS PM- 1). Using Moderate Resolution Imaging Spectroradiometer MOD13Q1 vegetation indices at a 250-meter resolution (Didan, 2015), NDVI estimates biomass by calculating the difference between the visible red and near infrared bands divided by their sum, generating a range of values between -1 and 1. This is a reliable measure of food availability in this species (Willems et al., 2009) and at this site (Jarrett et al., 2020). We assigned a value for each day in the 16-day period and calculated total NDVI over a four-month period for the two months prior to birth and the two months following this. We chose this period, following the results presented in Figure 1 below, because it captured the last trimester of gestation as well as the transition to lactation prior to infant mortality.

2.6 Statistical analyses

All statistical analyses were undertaken in a Bayesian framework, using the "brms" package (Bürkner, 2017) in R. Relevant behavioural data were initially only collected on adult females and network estimates were consequently unavailable for 10 of the 40 primiparous females. Similarly, we lacked sufficient data to estimate networks for the single, multiparous PT female who gave birth in 2012. We took advantage of brms's capacity to impute these values during model fitting, via the 'mi()' function, making it possible to fit a single multilevel, multivariate model to the data that used all the data and generated an outcome qualitatively the same as the model with a truncated data set.

We constructed a model with a Bernoulli distribution, where the response variable was survival to weaning (yes/no). The fixed effects, consequently, were parity (primiparous, multiparous), infant the previous year (yes/no), maternal rank, food availability (NDVI), and spatial and grooming network measures (degree, strength, eigenvector centrality). We included an interaction term between rank and NDVI to account for the possibility that high rank may be disproportionately influential during periods of drought. Similarly, to account for a possible interaction between our two statistical controls we also ran the model with an interaction between parity and infant last year. Maternal ID, nested in troop, was specified as a random effect. Continuous variables were scaled and mean centred. We conducted prior predictive checks and specified weakly informative priors (normal (0, 1)). We ran models with four chains and 4000 iterations. Chain convergence was confirmed ($\hat{R}$=1.0), and model goodness-of-fit was assessed using the 'pp_check()' function from the "bayesplot" package (Gabry & Mahr, 2017). We used the 'bayes_R2 'function to generate conditional and marginal R^2 values for each model (Gelman et al., 2019).

We present summary statistics for posterior slopes, standard errors and 95% credible intervals (CIs) for the main effects, and indicate effective sample sizes (ESS). Interpretation of outcomes is guided by the extent to which CIs depart from zero (effect size) and the span between the lower and upper CI values (precision of the posterior estimate). We augment the CIs by providing probability of direction (PD) estimates as these, together with the specification of 95%, while not prescriptive (McElreath, 2016), are intuitively helpful for non-Bayesian interpretation (Henzi et al., 2021). To aid interpretation, we generated whole model predictions using brms's 'fitted()' function to extract the fitted values of the variables in our model. Variables that were not the specific focus of the prediction were either fixed to their means, if continuous, or held constant, if categorical. These predictions were then used to construct predictive posterior plots.

2.7 Ethical statement

All protocols were noninvasive and adhered to the laws and guidelines of South Africa and Canada. Procedures were approved by the University of Lethbridge Animal Welfare Committee (Protocols 0702 and 1505).

3 RESULTS

3.1 Infant mortality

Of the 154 live births across the nine years—from 60 mothers—for which we have appropriate survival data, 47 (30%) died prior to weaning. The mean age at death was 73.95 days (median: 50 days) and the probability density was markedly right-skewed (Figure 1), with the peak in mortality occurring while infants were still spending most of their time ventral and on the nipple (Sashaw, 2012). Excluding 2009, for which we have a single datum from a larger cohort, annual cohort mortality ranged from 0.09 (1/11) to 0.85 (17/20).

3.2 Predictors of survival to weaning

Table 2 presents the results of the model, which identifies moderately strong but relatively imprecise effects for three variables (see also Figure 2). Survival to weaning was positively and

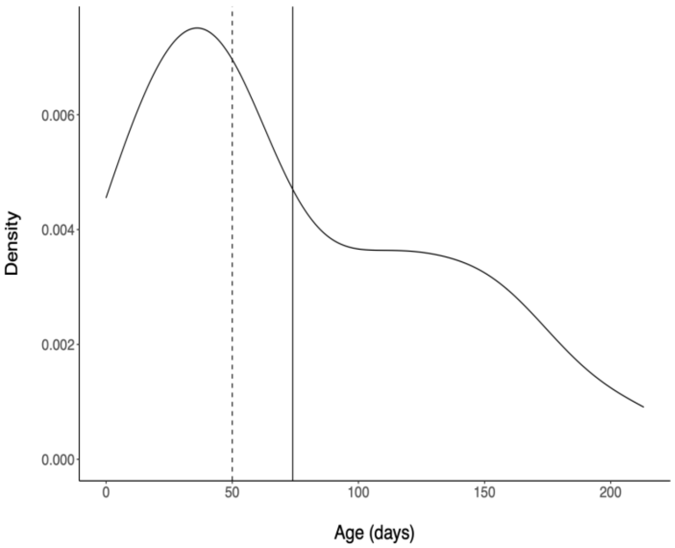

Figure 1. Probability density of age at death for infants who died prior to nutritional independence (N=46). Median age: dashed line; mean age: solid line.

independently associated with increasing maternal rank, resource availability, and the number of other monkeys that constituted a mother's spatial network (Median number of unique nearest neighbours: 22 ± 6.4 S.D.; Range: 4-41). There was, however, no indication that the influence of maternal rank on infant survival was contingent on resource availability. Similarly, there was little to indicate that a mother's recent reproductive history, nor any of the remaining network measures, were implicated in infant survival.

4 DISCUSSION

Our results confirm that infants in our population were subject to substantial mortality at an age when they were very much still dependent on their mothers for food and safety. In this context, it is revealing that rising maternal rank, spatial degree, and NDVI independently predicted an increased probability of infant survival to nutritional independence. Examination of the slopes of the three variables suggests a generally equivalent contribution by each, while the spreads illustrated in Figure 2 point to increased uncertainty of outcome associated with low values, whereas predictions for high values were far more precise. Interestingly, since one might expect the RHP of high rank to be even more influential when resources are scarce, we could detect no interaction between rank and resource availability. The answer here is likely to lie in the fact that, although we tailored our NDVI estimates to each birth, the variation in NDVI across birth cohorts was simply far greater than any variation across females within years. There is support for this in the observed variation of mortality across cohorts.

TABLE 2. Posterior density estimates of population level predictors of infant survival to weaning.

	β	SE	Lower 95% CI	Upper 95% CI	Bulk_ESS	Tail_ESS	PD
Intercept	0.92	0.84	-0.88	2.45	3974	4573	0.8644
Infant previous year? (Ref: No)	-0.3	0.79	-1.82	1.24	8401	6077	0.647
Parity (Ref: Multiparous)	0.58	0.64	-0.67	1.87	10256	5728	0.8184
Maternal rank	0.89	0.37	0.21	1.66	4322	4387	1
NDVI	1.2	0.34	0.58	1.91	4548	4926	0.996
Maternal rank*NDVI	-0.28	0.29	-0.88	0.28	7340	6227	0.6466
Infant previous year*Parity	-0.3	0.78	-1.86	1.21	8307	6514	0.8364
Grooming degree	-0.27	0.51	-1.23	0.74	4337	5222	0.7074
Grooming strength	0.6	0.57	-0.54	1.7	3804	4729	0.8517
Grooming eigenvector centrality	-0.11	0.36	-0.81	0.59	5211	5484	0.6152
Spatial degree	1.03	0.38	0.35	1.82	3550	4254	0.999
Spatial strength	-0.26	0.48	-1.18	0.72	4294	4676	0.7139
Spatial eigenvector centrality	0.12	0.35	-0.57	0.82	5772	5840	0.627

Subject ID, nested in Troop was entered as a random effect. β : slope of the predictor; SE: standard error of the estimate of β ; CI: credible interval; ESS: effective sample size; PD: probability of direction. $R^2_{Marginal}$: 0.31; $R^2_{Conditional}$: 0.39.

While we were not able to specify network measures *a priori*, the finding that increased spatial degree is associated with increased infant survival does confirm that social integration can make an independent contribution to infant survival, even in resource-stressed environments, and emphasises the need to consider both RHP and sociability in analyses of survival outcomes. At the same time, it also suggests that future analyses might consider more precisely the intersection of maternal attributes and the proximate basis of adaptive outcomes (Ostner & Schülke, 2018). We were generally unable to differentiate the causes of infant mortality but this is a population at sustained risk of predation (Henzi et al., 2021; see also Isbell et al., 2009 for sources of infant vervet mortality in another population), where increased maternal sociability—but not rank—is associated with reduced 'domains of danger' (Josephs et al., 2016). That is, intrinsic and extrinsic threats to infant survival may independently promote different maternal attributes (see also McFarland et al., 2017). In summary, and from the perspective of an infant in our population, it would be best to be born to a high-ranking, spatially central mother, at a time when resources were plentiful.

Interestingly, while not the principal focus of this study, we found little evidence that parity and recent reproductive history were influential in structuring infant survival in our population. The absence of an effect for reproductive history may be tied to the relatively fast life history of species under risk of higher mortality in marginal habitats (Isbell et al., 2009), even in a clade generally characterised by slow lives (Charnov & Berrigan, 1993). That is, a female who misses a year is not subsequently in any better state than a female who has not, and may perhaps have been worse off, consequently needing longer to recover from the previous birth (see Cheney et al., 1988). While infants of primiparous mothers may be at greater risk of early death in both wild (Glander, 1980) and provisioned populations, including vervets (Fairbanks & McGuire, 1985), this is not universal (Watanabe et al., 1992; Cords & Chowdhury, 2010; Nuñez et al., 2015). To the extent to which the effects of parity are assumed to be tied into maternal capacity and the ability to sustain early infant growth (Nuñez et al., 2015), it is worthwhile noting that we also found no effect of parity on juvenile growth rates in our population (Jarrett et al., 2020; see also Nuñez et al., 2015). Whether primiparous mothers have more restrictive mothering styles that channel infant energy into growth, as suggested by Nuñez et al. (2015), remains to be determined.

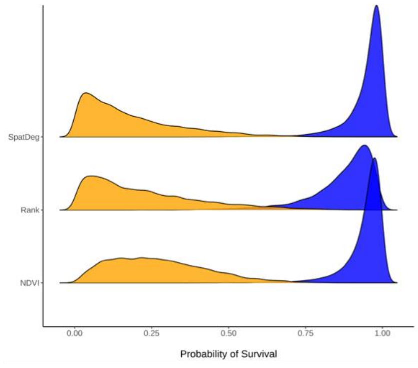

Figure 2. Changes in the mean probability of survival in relation to spatial degree, maternal rank, and NDVI. Density plots indicate probability as predicted by the model, with the values of the continuous predictor variables dichotomously categorised as ‘Low ’(Orange) or ‘High ’(Blue) for the purposes of visualisation. The spread of each curve indicates the relative uncertainty of the prediction.

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AUTHOR CONTRIBUTIONS

Rosemary Blersch: Formal analysis (lead); data collection (equal); visualization (equal); writing - review and editing (supporting). **Tyler Bonnell**: Formal analysis; writing - review and editing (supporting). **Madison Clarke**: data curation (equal); writing - review and editing. **Marcus Dostie**: Data collection (equal); formal analysis (supporting); data curation (supporting); writing - review and editing (supporting). **Miranda Lucas**: Data collection (equal); writing - review and editing (supporting). **Jon Jarrett**: conceptualisation (supporting); data collection (equal); writing - review and editing (supporting). **Richard McFarland**: Data collection (equal); ; writing - review and editing (supporting). **Christina Nord**: Data collection (equal); writing - review and editing (supporting). **April Takahashi**: Data collection (equal); writing - review and editing (supporting). **Stephanie Varsanyi**: Conceptualisation (supporting); formal analysis (supporting). **Chloé Vilette**: Data collection (equal); Data curation (equal); writing - review and editing (supporting). **Chris Young**: Data collection (equal); Data curation (equal); writing - review and editing (supporting). **Louise Barrett**: Funding acquisition (equal); project administration (equal); Conceptualisation (equal); writing - review and editing (supporting). **Peter Henzi**: Funding acquisition (equal); project administration (equal); conceptualisation (equal); writing - original draft (lead); writing - review and editing (lead).

CONFLICT OF INTEREST

All authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data and code that support the findings of this study have been uploaded to Zenodo. https://doi.org/ 10.5281/zenodo.7500113

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Figure legends

Figure 1. Probability density of age at death for infants who died prior to nutritional independence (N=47). Median age: dashed line; mean age: solid line.

Figure 2. Changes in the mean probability of survival in relation to spatial degree, maternal rank, and NDVI. Density plots indicate probability as predicted by the model, with the values of the continuous predictor variables dichotomously categorised as ‘Low ’(Orange) or ‘High ’(Blue) for the purposes of visualisation. The spread of each curve indicates the relative uncertainty of the prediction.

Figure 2 (Greyscale). Changes in the mean probability of survival in relation to spatial degree, maternal rank, and NDVI. Density plots indicate probability as predicted by the model, with the values of the continuous predictor variables dichotomously categorised as ‘Low ’(Light grey) or ‘High ’(Dark grey) for the purposes of visualisation. The spread of each curve indicates the relative uncertainty of the prediction.