Drivers of high infant mortality in *Propithecus edwardsi*: The role of resource availability

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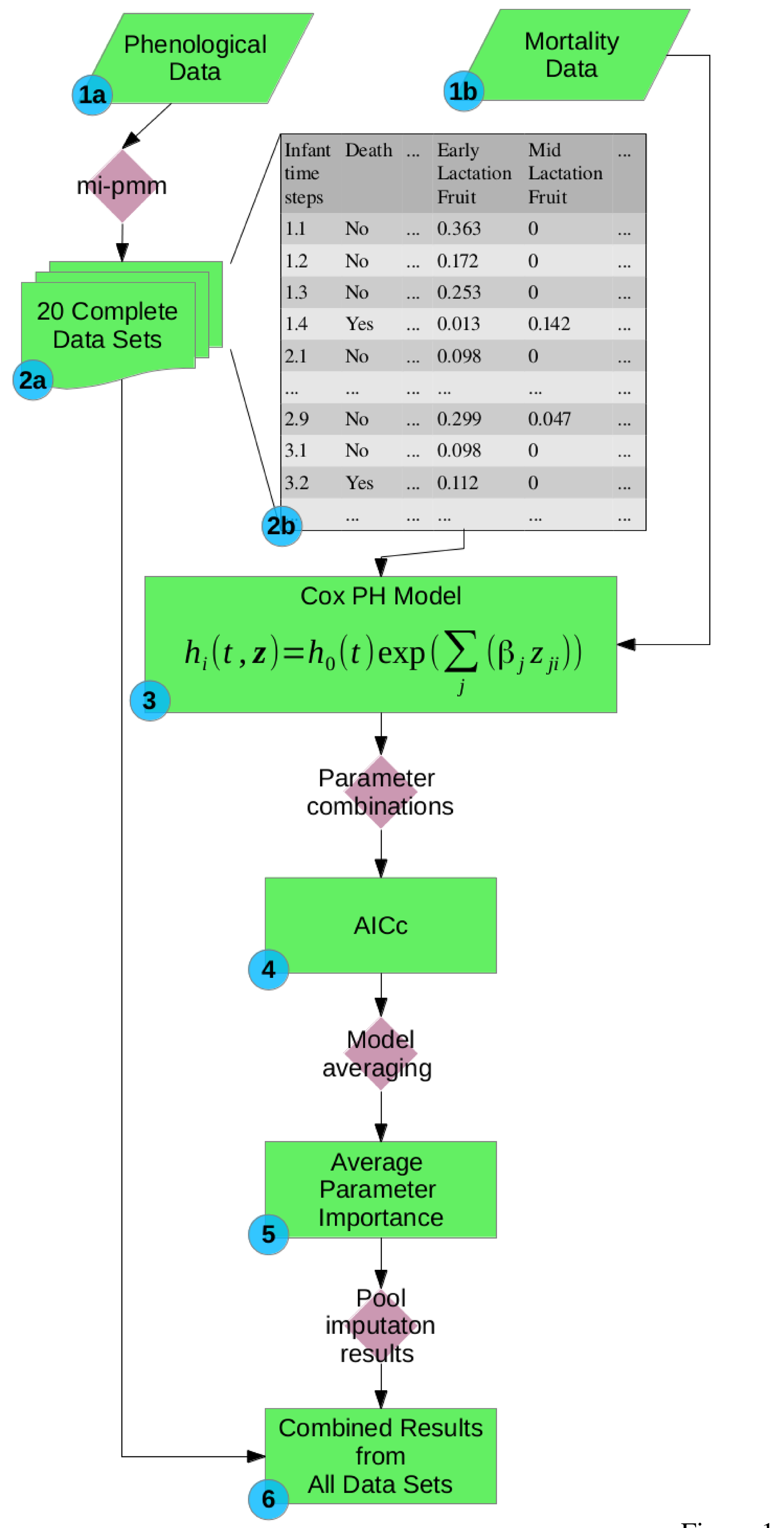
Introduction:

The primary drivers of infant mortality in *Propithecus edwardsi* are currently unknown. Birth is seasonal, with 98% of *P. edwardsi* infants born during the months of May, June, and July, and only around 50% of these infants survive past weaning. The reproductive season of *P. edwardsi*as well as at least 8 other lemur species in Ranomafana National Park may be timed to correspond to a period of peak fruit abundance[13]. Fruit may therefore be a key resource for *P. edwardsi* infant survival.

While *P. edwardsi* have gut and tooth morphology characteristic of a folivorous diet, fruit makes up approximately 30-40% of their diet[4,13]. Since they otherwise fit the profile of relaxed income breeders, which use mostly concurrent resource intake to support pregnancy and infants rather than relying on stored resources[2], fruit may be a key resource supporting infant success.

We performed a Survival Analysis of 50 infants born between 1992 and 2009 in Ranomafana National Park. To simultaneously test the importance of fruit and leaf abundance on infant mortality, and determine if *P. edwardsi* are Capital or Income Breeders, we evaluated the effects of fruit and leaf abundances during gestation. If *P. edwardsi* are Capital Breeders, fruit and/or leaf abundance should be important during the gestation period. If they are Income Breeders, fruit and/or leaf abundance should be important throughout gestation and lactation. We also included instantaneous abundance parameters to determine if infants that die were starving.



Infant time steps	Death	...	Early Lactation Fruit	Mid Lactation Fruit	...
1.1	No	...	0.363	0	...
1.2	No	...	0.172	0	...
1.3	No	...	0.253	0	...
1.4	Yes	...	0.013	0.142	...
2.1	No	...	0.098	0	...
...	...	...	...	...	...
2.9	No	...	0.299	0.047	...
3.1	No	...	0.098	0	...
3.2	Yes	...	0.112	0	...
...	...	...	...	...	...

Figure 1

Materials:

Tree phenology and *P. edwardsi* infant mortality data were collected from 1988 to 2010, and have continued to be collected through the present.

1.a. Trees in the Talatakely trail system of Ranomafana National Park were scored by the presence of fruit (ripe and unripe) and leaves (immature) during once-monthly visits.

1.b. Infant mortality data were drawn from a data set of daily group follows; each group was followed throughout the day to record group membership and feeding behavior. Infants were considered to have survived and have reached independence at 9 months.

2.a. For those months when phenology and/or feeding data were not collected, we replaced the missing data using multiple imputation with predictive mean matching (mi-pmm)[5], creating 20 complete data sets. **2.b.** All further analyses were performed on each data set separately.

3. We used a Cox Proportional Hazards model for the Surivival Analysis. The Cox PH model is nonparametric and makes no assumptions about the likelihood of death ("hazard"), and allows the use of time-censored data (in this case, infants that survive past the 9 month cut off) to calculate the probability of mortality. These attributes make it an appropriate model for this kind of mortality data[7].

The mortality risk ($h_i(t,z)$) of infant i at time t depends the mortality risk shared by all individuals, ($h_0(t)$). This risk is modified by the sum of each parameter (z) multiplied by its coefficient (β).

Parameters were formative periods: Early Gestation (EG), Late Gestation (LG), Early Lactation (EL), Mid Lactation (ML), and Late Lactation and Weaning (LL/W; LL and W were highly correlated and were lumped for analysis). The abundance value for each period is the geometric mean of the each month in that period, to upweight months with low abundance. We used the Survival package in R to run the time-dependent Cox PH model[10].

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4. We used an Information Theoretic Approach (via Akaike's second order information criterion; AICc) to compare and rank these various models to find the set of parameters that best approximate any underlying influences on infant mortality in the context of the Cox PH model[3,8]. We ran the AICc procedure on models including all formative periods, and either the parameter of current fruit and/or leaf abundance for each time step, or the parameter of the previous month's fruit and/or leaf abundance parameter for each time step[1].

5. Prior to pooling all of the data imputations together for a final result, we averaged the resulting AICc models with delta < 2 for each data set[8].

6. We then used the mi.inference() command in the norm package in R to pool imputations across the 20 data sets[9], resulting in a set of coefficients and significance values for each parameter.

We repeated the entire procedure on the feeding proportion data to determine if the mother's feeding behavior had a different effect than the raw resource abundance.

* R-specific methods[1,6,10,12] and code available at https://github.com/lauterbur/Infant-Mortality

Ledger

Results:

50 *P. edwardsi* infants were born from 1992 to 2009, and 44% (22) died before being weaned. AICc and model averaging showed that none of the included parameters were significant across all imputed data sets for either model.

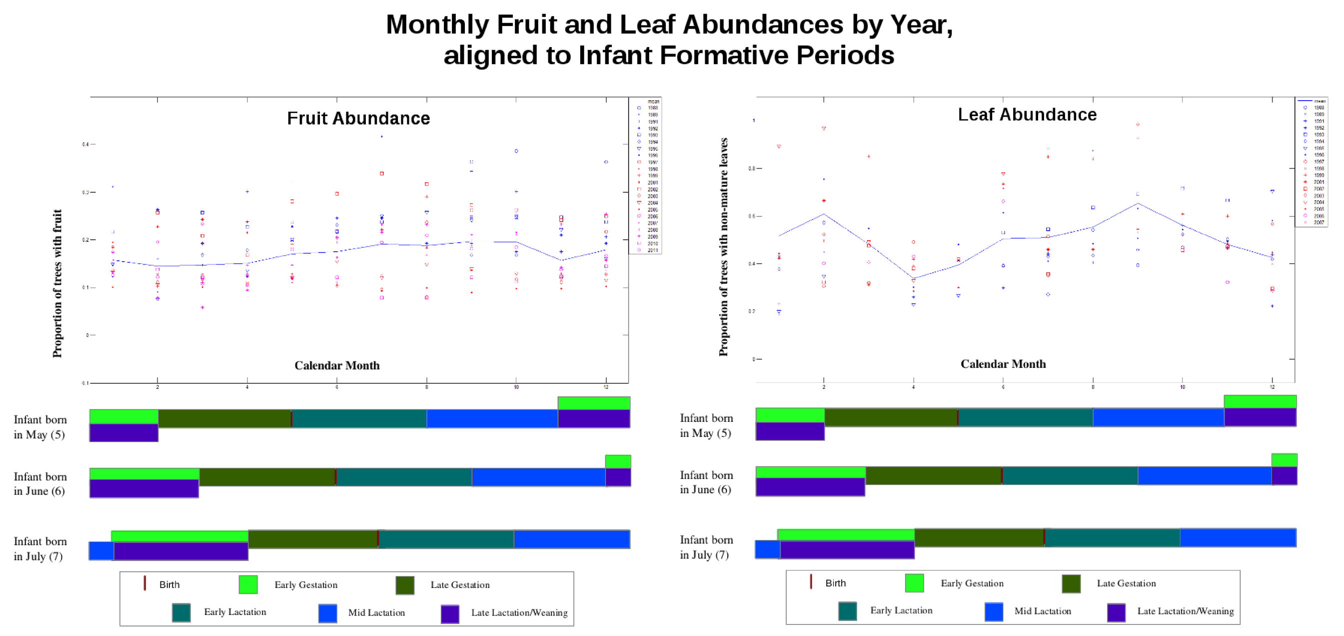

Figure 2. 98% of infants are born in May, June, and July. Gestation lasts approximately six months, and infants are weaned approximately nine months after birth. Fruit and leaf abundances vary between months and years.

However mothers' time spent feeding on fruit during late gestation approached significance ($p = 0.057$), with a negative correlation with mortality risk.

There was thus no influence of fruit or leaf abundance, or mothers' feeding time, either immediately or cumulatively, on infant mortality.

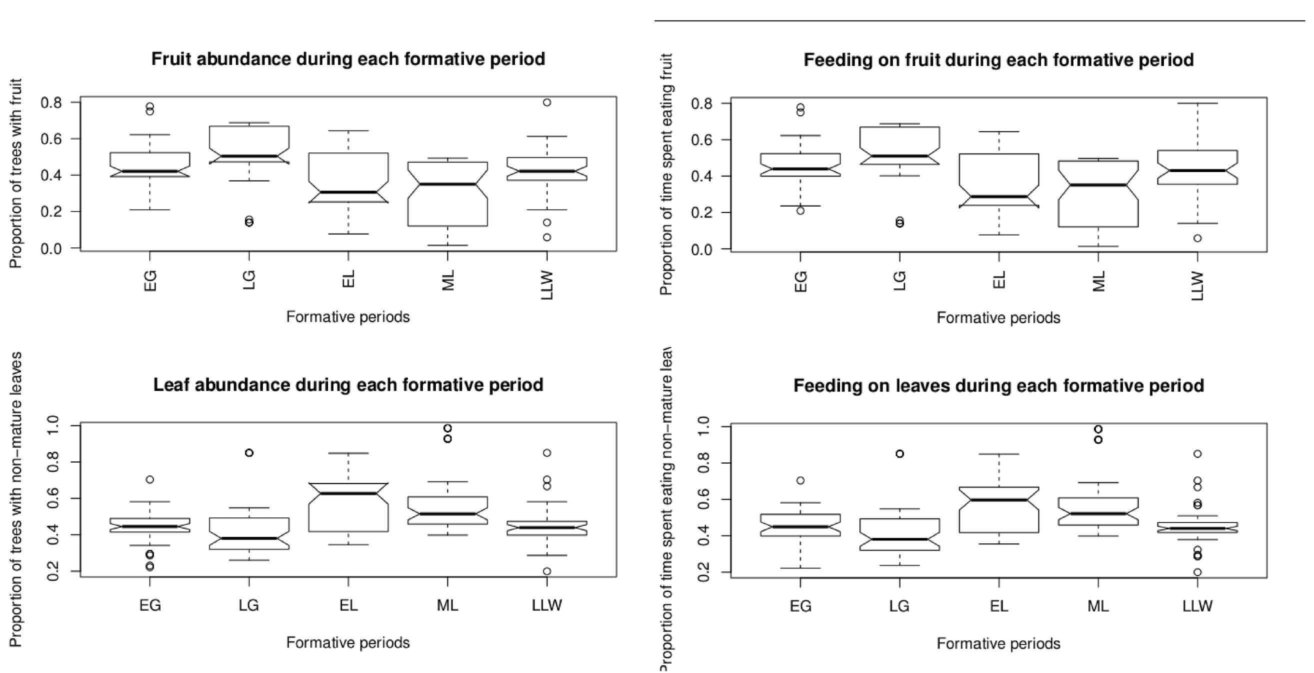

Figure 3. Fruit and leaf abundances vary between formative periods (ANOVA; $p < 0.0001$ for both fruit and leaf abundances), as does mothers' time spent feeding on fruit or leaves (ANOVA; $p < 0.0001$).

Conclusions:

This is the first simultaneous, comprehensive analysis of these two long-term data sets, and is the strongest argument to date that resource abundance (as calculated from general measures of forest phenology) and mothers' feeding choices are not the drivers of infant mortality in *P. edwardsi*. We tested the effect of immediate and cumulative fruit and leaf abundances, immediate and cumulative, as well as the effect of mothers' feeding choices, on infant mortality using nearly 20 years of data. These infants are neither starving nor being fatally stunted during lean times.

In addition, the lack of influence of resource abundance coupled with the lack of influence of mother's feeding time suggests that mortality is not caused by mothers taking unusual risks to access food during lean times.

We provide a new analytical model with which to test the Capital Breeder-Income Breeder distinction. Infant survival in Capital Breeders should be dependent on the resources available to mothers during gestation, while infant survival in income breeders should be dependent on resources available after birth. This framework can be used in those cases in which infant mortality and resource abundance data exist.

However in the case of *P. edwardsi,* not only do we need to look elsewhere to discover what biotic and/or abiotic factors are causing infants to die before weaning, we need to rethink the importance of the Capital Breeder-Income Breeder distinction.

Literature Cited:

1. Bartoń, K. (2013). MuMIn: Multi-model inference. R package version 1.9.13. http://CRAN.R-project.org/package=MuMIn
2. Brockman, D., and van Schaik, C. (2005). Seasonality in Primates. (D. Brockman and C. van Schaik, Eds.). Cambridge: Cambridge University Press.
3. Burnham, K., Anderson, D., and Huyvaert, K. (2010). AIC model selection and multimodel inferencein behavioral ecology: some background, observations, and comparisons. Behavioral Ecology and Sociobiology, 65(1), 23–35.
4. Hemingway, C. (1996). Morphology and phenology of seeds and whole fruit eaten by Milne-Edwards' sifaka, *Propithecus diadema edwardsi*, in Ranomafana National Park, Madagascar. International Journal of Primatology, 17(5), 637–659.
5. Marshall, A., Altman, D., and Holder, R. (2010). Comparison of imputation methods for handling missing covariate data when fitting a Cox proportional hazards model: a resampling study. BMC Medical Research Methodology, 10(1), 112.
6. Mo, Q., Gonen, M. and Heller, G. (2012). CPE: Concordance Probability Estimates in Survival Analysis. R package version 1.4.4. http://CRAN.R-project.org/package=CPE
7. Muenchow, G. (2013). Ecological Use of Failure Time Analysis. Ecological Society of America, 67(1), 246–250.
8. Nakagawa, S., and Freckleton, R. (2010). Model averaging, missing data and multiple imputation: a case study for behavioural ecology. Behavioral Ecology and Sociobiology, 65(1), 103–116.
9. Schafer, J. (2013). norm: Analysis of multivariate normal datasets with missing values. R package version 1.0-9.5. http://CRAN.R-project.org/package=norm
10. Therneau, T. (2014). A Package for Survival Analysis in S. R package version 2.37-7, http://CRAN.R-project.org/package=survival.
11. Therneau, T. and Grambsch, P. (2000). Modeling Survival Data: Extending the Cox Model. Springer, New York. ISBN 0-387-98784-3.
12. van Buuren, S., and Groothuis-Oudshoorn, K. (2011). mice: Multivariate Imputation by Chained Equations in R. Journal of Statistical Software, 45(3), 1-67. URL http://www.jstatsoft.org/v45/i03/.
13. Wright, P., Vololontiana, R., and Pochron, S. (2005). The Key to Madagascar Frugivores. In Tropical Fruits and Frugivores: The Search for Strong Interactors (J. Dew and J. Boubli, Eds.) (pp. 121–138).

Acknowledgments

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