

# Populations with Higher Sociality Lead to Higher Long-term Population Growth in Time-Dependent Environments

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## Background

An organism's vital rates and fitness are often significantly influenced by the within and between group social interactions (Lucas 2020). One such social interactive mechanism, cooperative breeding, may enhance the reproductive success of organisms through resource allocation optimization (Koykka & Wild 2016). Recent developments in evolutionary research hypothesize humans as ‘cooperative breeders’. Hrdy (2006) defines cooperative breeding as a “system in which group members, other than the genetic parents (alloparents), help one or both parents rear their offspring.”

Human social relationships and cultural niches are rooted in elevated degrees of selflessness and sociality, often marked by the willingness to share food and information and cooperate with others (Batson 1991; Kaplan et al. 2000). Sociality refers to association among conspecifics, whereas advanced sociality refers to group living involving individual relationships between members depending on their status and relatedness (Ozgul et al. 2010; Taborsky et al. 2021). Studies show that in highly social species, such as humans, group cooperation and association of varying degrees have implications for individual fitness (Dunbar and Shultz 2010). Asocial populations are at a selective disadvantage, particularly in oscillating or poorly favored environments (Philip 1957). Studies also argue that sociality is likely a key factor that shapes the potential for phenotypic plasticity (Komdeur and Ma 2021).

There is ample evidence suggesting the presence of kin benefits fitness outcomes. Human mothers receive considerable help and care in provisioning for their young (Hrdy 2009) from grandparents, aunts, uncles, siblings, older kids, and distantly related kin. Maternal grandparents and older siblings are found to improve child survival (Sear et al. 2000). The care providers vary according to the culture and the setting, especially in terms of male involvement (Hill, 1982). The studies so far have been context-specific and deterministic.

The current study aims to understand the impact of sociality, measured in terms of kinship structure, on long-term population growth rates. We hypothesize that human Populations with higher levels of sociality, defined in terms of kinship structure, lead to higher long-term population growth in time-dependent environments. As an improvement over the existing works, we measure the said effect by considering sociality as a stochastic environment to which the vital rates respond across all world countries. Using the United Nations’s World Population Prospects (WPP, hereafter) 2024 revision, we estimate the kinship structure of the focal woman in every country

and assign the vital rates matrices to these kinship environments at each time point. Asymptotic stochastic growth rate and their sensitivities to different environments are estimated by projecting the matrices.

## Methods and Materials

To test the cooperative breeding hypothesis, we devised a quantitative methodology involving classifying levels of sociality into different environmental states. We define the groups of countries based on the levels of sociality, to which selected demographic outcomes will be calculated and compared. Following this, we construct population projection matrices (PPMs, hereafter) for each vital rates response matrix corresponding to each sociality state. Later, we consider a Markovian environment.

## Data Inputs

We extracted multiple data variables from the WPP 2024 revision (WPP, hereafter) to test the impact of wider levels of kinship networks on long-term population growth. The input variables in constructing both sociality environments and PPMs are age-specific population size, survival rates, & fertility rates, sex ratio at birth (SRB, hereafter), and distribution of ages of mothers. These data for 237 countries/areas are extracted from 1950 to the present and projected for 500 years (transient analysis) and 10,000 years (asymptotic analysis).

## Matrix Population Models (MPMs)

Matrix population models are widely used in population ecology (van Groenendael et al. 1988; Crone et al. 2011) and demography (Caswell 2001, 2019) to inform population management (Ezard et al. 2010), conservation strategies (Ferson et al. 2010; Fieberg & Ellner 2001), extinction (Gotelli & Ellison, 2006; Sanz 2019), and other applications. We adopt the (discrete chronological) age-based MPMs, commonly called the Leslie Matrix (Leslie 1945, 1948), to estimate population stochastic growth rate in response to varying environmental states, defined in terms of sociality levels. Assume a structured population divided into age classes 1 to  $k$ . A Leslie matrix, an  $n \times n$  matrix with non-zero elements on the sub-diagonal (survival rates) and first row (fecundity), projects the population growth rate and change in age structure from one-time point to the next as follows:

$$n(t+1) = \mathbf{A}n(t) \quad (1)$$

Where  $n(t)$  is a population vector describing the number of individuals in a given age at time  $t$ , for age classes  $i = 1, \dots, k$ . The projection matrix  $\mathbf{A}$  is an  $18 \times 18$  matrix, owing to the number of age classes from ages 0 to 85+.

To construct the Leslie matrices for 237 countries/areas, we utilized age-specific survival probabilities from abridged life tables (1971-2023), age-specific fertility rates, and SRB provided by WPP 2024.

## Sociality Environments

We classify sociality into  $E_y$  distinct environmental states defined based on the focal's kin type: mothers (M), daughters (D), grandmother (G), siblings(S), aunts (A), and cousins through aunts(C). The considered environmental states are multiple combinations of focal's kins: **E1** = M alone, **E2** = M & D, **E3** = M, D & G, **E4** = M, D, G & S, **E5** = M, D, G, S, and A and **E6** =M, D, G, S, A & C. The environment states are ranked as per the number of kin. E1 represents the lowest state of sociality, whereas E6 is the highest. The classification is based on kinship nodes provided by Caswell (2019).

The Leslie matrix corresponding to each environmental state is averaged by calculating the element-by-element arithmetic mean of all matrices over the considered duration and is denoted as  $\mathbf{A}(E_1)$ , ...,  $\mathbf{A}(E_y)$ . As a result, every country will have a single MPM for an environmental sequence.

## Stochastic Population Growth Rate

A stochastic population model constitutes a model for environmental dynamics and the response of vital rates to these environments (Cohen 1979; Tuljapurkar 1990). Estimating stochastic growth rate is based on the assumption of a finite set of discrete environmental states (Tuljapurkar and Orzack 1980). We calculate the stochastic growth rate for each environmental state to test the hypothesis that a higher level of sociality leads to a larger population growth rate. Let the population under consideration grow as per

$$\mathbf{n}(t+1) = \mathbf{A}(t)\mathbf{n}(t) \quad (2)$$

$\mathbf{A}(t)$  is the projection matrix generated by the ergodic stochastic environments and the set of corresponding vital rates. Then, with a probability of one, the asymptotic long-term growth rate is obtained as,

$$\log \lambda_s = \lim_{T \rightarrow \infty} \log |A(T - 1) \dots A(0)n_0| \quad (3)$$

## Environment-specific sensitivities of growth rates to vital rates

We calculated environment-specific sensitivities of vital rates to  $\log \lambda_s$  to understand the contribution of different environmental states and the response of vital rates to these states to the difference in  $\log \lambda_s$ . Assume  $\theta$  to be a vector of parameters determining the projection matrix  $\mathbf{A}$ , where the vectors  $\theta_1, \dots, \theta_y$  corresponds to environmental states form  $E = 1, \dots, n$ . The set of vital rates can be written as,

$$\theta = \{\theta_1, \dots, \theta_y\} \quad (4)$$

If we write  $\mathbf{A}(t) = \mathbf{A}[\theta(t)]$ , the stochastic growth rate becomes,

$$\log \lambda_s[P, \theta] = \lim_{T \rightarrow \infty} \frac{1}{T} \log |A[\theta(T - 1)] \dots A[\theta(0)]n_0| \quad (5)$$

Writing  $\log \lambda_s$  as an explicit function of  $P, \theta$  reiterates that the model depends on both environmental states and the vital response (Caswell 2019). To calculate the environment-specific

stochastic sensitivities, the derivatives of  $\log \lambda_s$  with respect to each vector  $\theta_i$  in  $\theta$  is calculated as

$$\frac{d \log \lambda_s}{d \theta^\top} |_{u=i} = \lim_{T \rightarrow \infty} \frac{1}{T} \sum_{t=0}^{T-1} J_t \frac{[w(t)^\top \otimes v(t+1)^\top]}{R_t v^\top(t+1) w(t+1)} \frac{d \text{vec} A[\theta(t)]}{d \theta^\top} \quad (6)$$

(7)

Vectors  $w(t)$  and  $v(t)$  are the right and left eigenvectors of this stochastic model, describing age distribution and reproductive value, respectively.  $R_t$  is the total population growth between times  $t$  to  $t+1$ . An indicator variable  $J_t$  defined as

$$J_t = \begin{cases} 1 & \text{if } u(t) = i \\ 0 & \text{otherwise} \end{cases} \quad (7)$$

is incorporated to make the sensitivity environment-dependent.

### Expected Results

It is expected that higher levels of sociality will show higher stochastic growth rates, as seen by larger family networks and cooperative breeding systems. This expectation arises from the theory that stronger social support networks—such as those of large kin networks, including mothers, grandmothers, aunts, and siblings—offer more substantial aid with childrearing, enhancing survival and increasing the likelihood of successful reproduction. We anticipate notable variations in population growth rates among varied environmental states characterized by different levels of sociality. Populations with high levels of social support, represented by the E6 environmental state, should grow faster over the long run than the E1 sociality state.

Matrix representations of these high-sociality states (e.g., systems with many alloparents) should show greater average growth rates than matrices representing less complex social structures. We predict that different sociality levels will result in different sensitivity of stochastic growth rates to vital rates (e.g., fertility and survival rates). More specifically, compared to low-sociality situations, it is anticipated that changes in vital rates will have less of an impact on growth rates in high-sociality environments. This is so that long-term growth rates can be more steady and possibly even greater because of the stabilizing influence of strong kin support, which can act as a buffer against variations in essential rates.

We anticipate that the asymptotic growth rates will steadily favor high-sociality environments over long time horizons (10,000 years). The idea that sociality has a major influence on long-term population dynamics should be supported by the increasing favorable effects of cooperative breeding and strong kin networks on population increase and stability. Given that the model considers various social surroundings and demographic characteristics, the results should hold well in various geographical and cultural contexts. Regardless of geographical or cultural variations, persistently greater growth rates in high-sociality states will prove this robustness.