A model for demographic stochasticity in the demography of kinship

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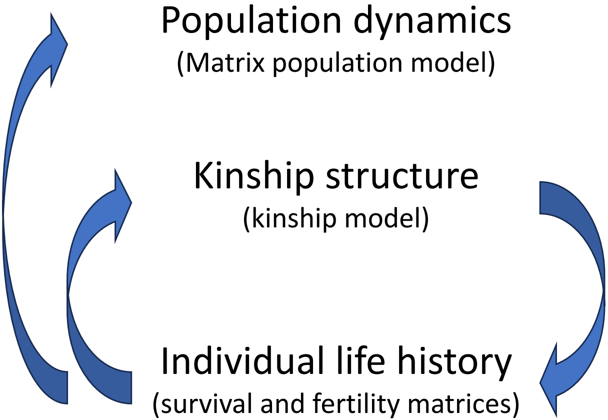
IBED

The conditions that present themselves in an actual population are always excessively complicated. Whoever has failed to grasp clearly the necessary relations among the characteristics of theoretical population, subject to simple hypotheses, will certainly be unable to manage in the much more complicated relations that exist in a real population.

A.J. Lotka (1939)

- summarize the model for demography of kin
- show a few results
- stochasticity!
- the stochastic kinship model
- a few stochastic results
- some uses of the model

Demography links individuals and populations



Kinship: Goodman, Keyfitz, and Pullum 1974

THEORETICAL POPULATION BIOLOGY 5, 1–27 (1974)

Family Formation and the Frequency of Various Kinship Relationships

LEO A. GOODMAN

The University of Chicago

NATHAN KEYFITZ AND THOMAS W. PULLUM

Harvard University

Received January 19, 1970

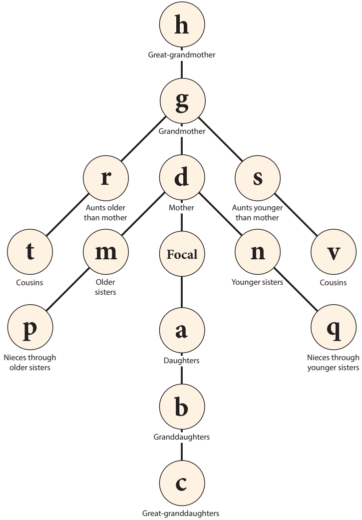
$(l_z/l_y)\, m_z$. In addition, the limits of the corresponding integration have to be altered; instead of α to y, they become y to $a + x + y$. Hence, we have

$$\int_\alpha^\beta \left[\int_\alpha^\beta \left\{\int_y^{a+x+y} \left(\int_\alpha^{a+x+y-z} l_w m_w \, dw\right) \frac{l_z}{l_y} m_z \, dz\right\} W(y) \, dy\right] W(x) \, dx, \quad (6.2.a)$$

for cousins whose mother is a younger sister of the mother of the girl aged a. The l_y in the denominator could be cancelled with the l_y contained in $W(y)$.

The sum of the two integrals would give the expected number of cousins

The Focal-centered kinship network[1]



[1] Keyfitz and Caswell 2005

The kin of Focal **are a population**

. . . so we might as well model them as one

The kinship model

The kin of Focal as a population

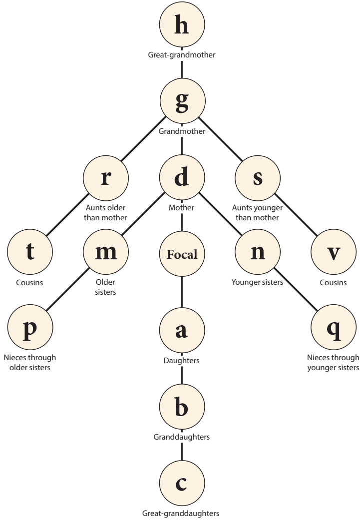
$\mathbf{k}(x) =$ age distribution of a (generic) kin at age x of Focal[2]

$$\mathbf{k}(x+1) = \mathbf{U}\mathbf{k}(x) + \begin{cases} \mathbf{0} & \text{no recruitment} \\ \mathbf{F}\,\mathbf{k}^*(x) & \text{recruitment from } \mathbf{k}^* \end{cases}$$

$$\mathbf{k}(0) = \mathbf{k}_0 \qquad \text{initial condition at birth of Focal}$$

[2] To be more precise, the expectation of the age distribution.

The kinship network[3]



[3] Keyfitz and Caswell 2005

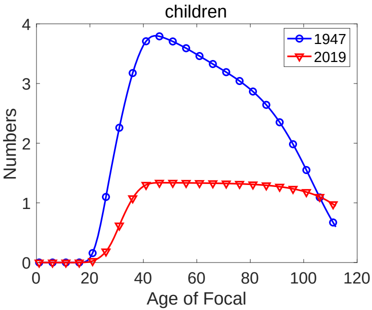
Dynamics of kin of Focal at age x

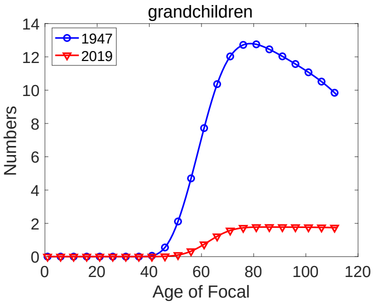
Symbol	Kin	i.c. $\mathbf{k}_0$	$\beta(x)$
a	daughters	$\mathbf{0}$	$\mathbf{Fe}_x$
b	granddaughters	$\mathbf{0}$	$\mathbf{Fa}(x)$
c	great-granddaughters	$\mathbf{0}$	$\mathbf{Fb}(x)$
d	mothers	$\boldsymbol{\pi}$	$\mathbf{0}$
g	grandmothers	$\sum_i \pi_i \mathbf{d}(i)$	$\mathbf{0}$
h	great-grandmothers	$\sum_i \pi_i \mathbf{g}(i)$	$\mathbf{0}$
m	older sisters	$\sum_i \pi_i \mathbf{a}(i)$	$\mathbf{0}$
n	younger sisters	$\mathbf{0}$	$\mathbf{Fd}(x)$
p	nieces via older sisters	$\sum_i \pi_i \mathbf{b}(i)$	$\mathbf{Fm}(x)$
q	nieces via younger sisters	$\mathbf{0}$	$\mathbf{Fn}(x)$
r	aunts older than mother	$\sum_i \pi_i \mathbf{m}(i)$	$\mathbf{0}$
s	aunts younger than mother	$\sum_i \pi_i \mathbf{n}(i)$	$\mathbf{Fg}(x)$
t	cousins from aunts older than mother	$\sum_i \pi_i \mathbf{p}(i)$	$\mathbf{Fr}(x)$
v	cousins from aunts younger than mother	$\sum_i \pi_i \mathbf{q}(i)$	$\mathbf{Fs}(x)$

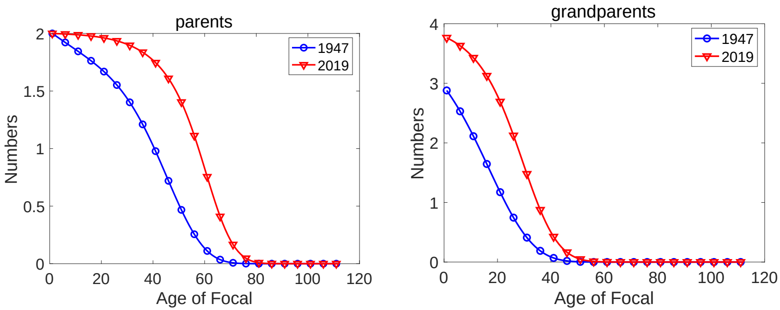
A demographic transition in Japan

	1947	2019
TFR	4.6	1.3
Life expectancy	54	87

Mean numbers



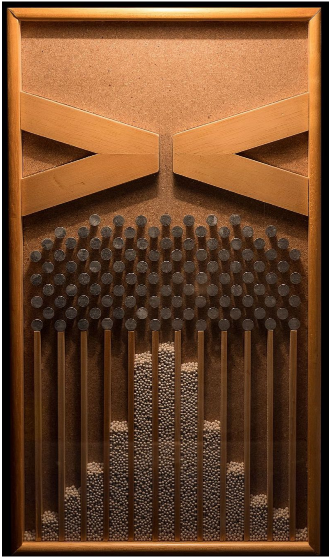



parents
Numbers
Age of Focal
1947
2019
0
0.5
1
1.5
2
0
20
40
60
80
100
120
grandparents
Numbers
Age of Focal
1947
2019
0
1
2
3
4
0
20
40
60
80
100
120

But what about . . . ?

I age-classified, time-invariant, deterministic, one-sex, living kin (Caswell 2019)
II age$\times$stage-classified (age$\times$parity) (Caswell 2020)
III time-varying (Caswell and Song 2021)
IV two-sexes (Caswell 2022)
V death of kin and bereavement (Caswell, Verdery, Margolis 2023)
VI stochastic (Caswell 2024)
VII overlap with kin (Caswell 2025)

Stochasticity



- survival is a sequence of random events
- reproduction is a sequence of random events
- $\Longrightarrow$ population growth is a random process

Kin of Focal are a population

...but they are a **small** population

- survival is a sequence of random events
- reproduction is a sequence of random events
- $\Longrightarrow$ population growth is a random process

the law of large numbers is not your friend

$$\bar{x} = \frac{1}{N}\sum x_i$$

$$\bar{x} \longrightarrow E(x) \text{ as } N \to \infty$$

$$SE(\bar{x}) = \frac{1}{\sqrt{N}} SD(x)$$

Demographic stochasticity

- population invasion
- epidemics
- mutation success or failure
- adaptive dynamics
- extinction and conservation

Galton-Watson branching process

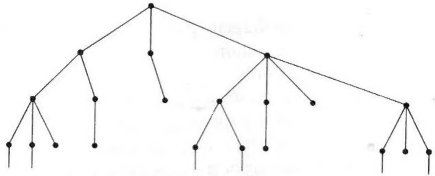


Figure 1.1 A realization of a branching process

$$
\begin{aligned}
X &= \text{number of offspring} \\
G_X(s) &= \text{probability generating function of } X \\
N(t) &= \text{population size at } t \\
G_{N(t)}(s) &= \text{probability generating function of } N(t)
\end{aligned}
$$

The result

$$G_{N(t+1)}(s) = G_X\left(G_{N(t)}(s)\right)$$

Branching process results

- probability distribution of $N(t)$ — essentially never
- moments of $N(t)$ — yes
- probability of extinction — actually pretty easy

Multitype branching processes

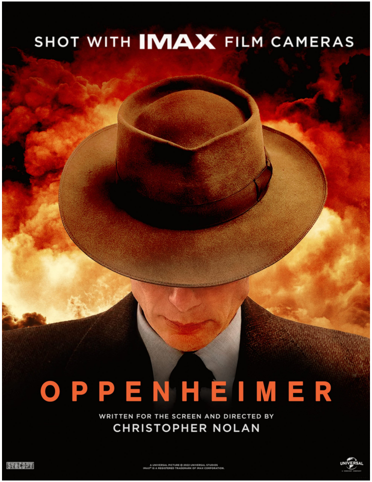
$$\mathbf{U} = \begin{pmatrix} 0 & 0 & 0 \\ p_1 & 0 & 0 \\ 0 & p_2 & 0 \end{pmatrix}$$

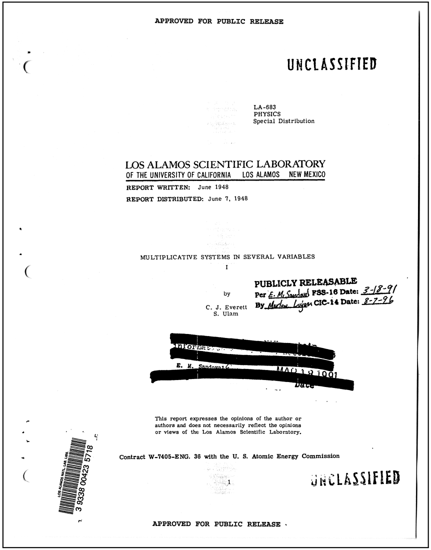
$$\mathbf{F} = \begin{pmatrix} f_1 & f_2 & f_3 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}$$

generating function for offspring

$$G_{\mathbf{X}}^{(j)}(\mathbf{s}) = G_{\mathbf{U}}^{(j)}(\mathbf{s})\, G_{\mathbf{F}}^{(j)}(\mathbf{s}) \qquad j = 1, \ldots, \omega$$

Multitype branching process





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MULTIPLICATIVE SYSTEMS IN SEVERAL VARIABLES

I

by

C. J. Everett
S. Ulam

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[redacted]

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- probability distribution of $\mathbf{k}(x)$ — worse
- moments (means, variances, etc.) — pretty easy
- extincition probability — also pretty easy

The kin vector for the stochastic model

$$\widetilde{\mathbf{k}}(x) = \left(\frac{E(\mathbf{k})}{\operatorname{vec}\mathbf{C}(\mathbf{k})}\right)(x)$$

with the covariance matrix

$$\mathbf{C}(\mathbf{k}) = \begin{pmatrix} V(k_1) & Cov(k_1, k_2) \\ Cov(k_1, k_2) & V(k_2) \end{pmatrix}$$

Apply the vec operator

$$\operatorname{vec}\mathbf{C}(\mathbf{k}) = \begin{pmatrix} V(k_1) \\ Cov(k_1, k_2) \\ Cov(k_1, k_2) \\ V(k_2) \end{pmatrix}$$

Dynamics of covariance[4]

$$\mathbf{C}(t+1) = \mathbf{A}\mathbf{C}(t)\mathbf{A}^{\mathsf{T}} + \sum_i E\left(k_i(t)\mathbf{V}_i\right)$$

Apply the vec operator

$$\operatorname{vec}\mathbf{C}(t+1) = (\mathbf{A}\otimes\mathbf{A})\operatorname{vec}\mathbf{C}(t) + \mathbf{D}E(\mathbf{k}(t))$$

[4] Everett and Ulam 1948, Harris 1963

Stochastic kinship model[5]

$$\left(\frac{E(\mathbf{k})}{\operatorname{vec}\mathbf{C}(\mathbf{k})}\right)(x+1) = \left(\begin{array}{c|c}\mathbf{U} & \mathbf{0}_{\omega\times\omega^2} \\ \hline \mathbf{D}_{\mathrm{U}} & \mathbf{U}\otimes\mathbf{U}\end{array}\right)\left(\frac{E(\mathbf{k})}{\operatorname{vec}\mathbf{C}(\mathbf{k})}\right)(x)$$

$$+ \left(\begin{array}{c|c}\mathbf{F} & \mathbf{0}_{\omega\times\omega^2} \\ \hline \mathbf{D}_{\mathrm{F}} & \mathbf{F}\otimes\mathbf{F}\end{array}\right)\left(\frac{E(\mathbf{k}^*)}{\operatorname{vec}\mathbf{C}(\mathbf{k}^*)}\right)(x)$$

which is to say

$$\widetilde{\mathbf{k}}(x+1) = \widetilde{\mathbf{U}}\widetilde{\mathbf{k}}(x) + \begin{cases}\mathbf{0} & \text{no recruitment} \\ \widetilde{\mathbf{F}}\,\widetilde{\mathbf{k}}^*(x) & \text{recruitment from } \mathbf{k}^*\end{cases}$$

[5] Pollard 1966, Caswell 2001

Outputs of the stochastic model

suppose

$$\mathbf{y}(x) = \mathbf{W}\,\mathbf{k}(x)$$

Then

$$\begin{aligned} E(\mathbf{y}) &= \mathbf{W}\,E(\mathbf{k}) \\ \mathbf{C}(\mathbf{y}) &= \mathbf{W}\mathbf{C}(\mathbf{k})\mathbf{W}^{\mathsf{T}} \end{aligned}$$

so that

$$\operatorname{vec}\mathbf{C}(\mathbf{y}) = (\mathbf{W}\otimes\mathbf{W})\operatorname{vec}\mathbf{C}(\mathbf{k})$$

and

$$\widetilde{\mathbf{y}}(x) = \left(\frac{E(\mathbf{y})}{\operatorname{vec}\mathbf{C}(\mathbf{y})}\right)(x).$$

An extended kinship model

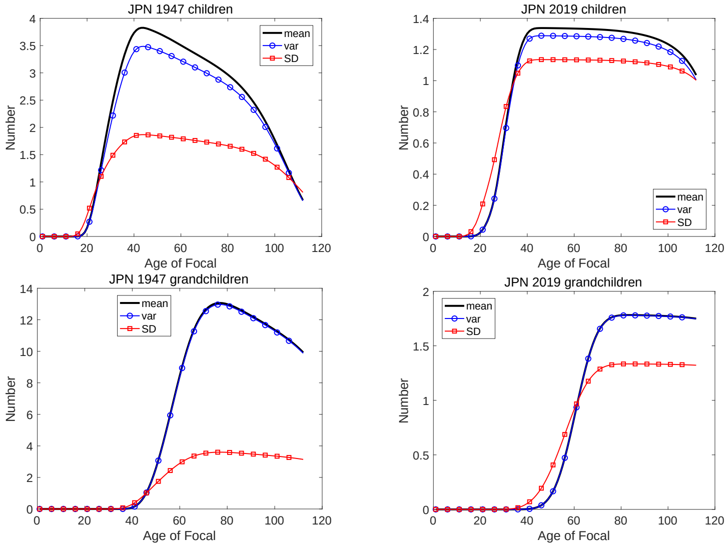
state equation

$$\tilde{\mathbf{k}}(x+1) = \tilde{\mathbf{U}}\tilde{\mathbf{k}}(x) + \begin{cases} \mathbf{0} & \text{no recruitment} \\ \tilde{\mathbf{F}}\,\tilde{\mathbf{k}}^*(x) & \text{recruitment from } \mathbf{k}^* \end{cases}$$

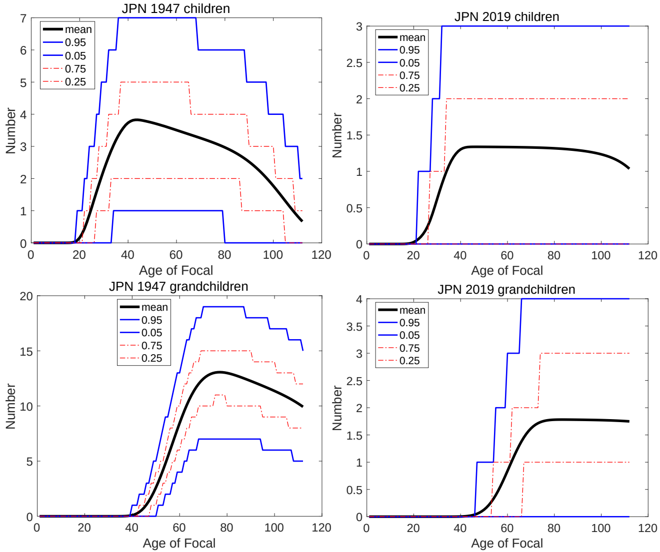
output equation

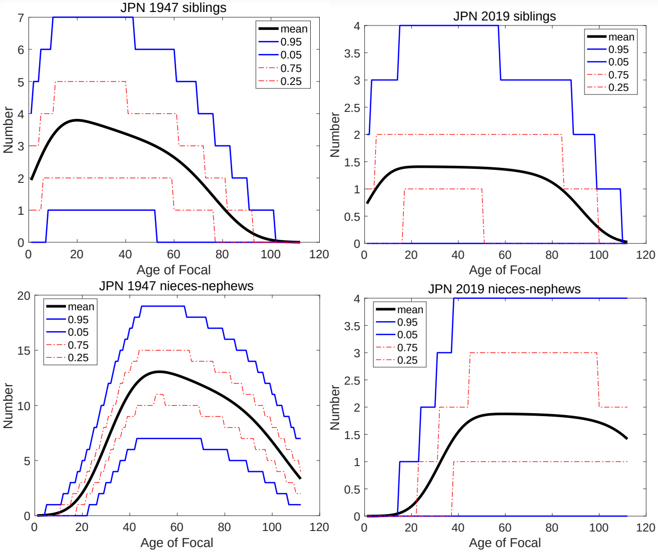
$$\tilde{\mathbf{y}}(x) = \left(\begin{array}{c|c} \mathbf{W} & \mathbf{0} \\ \hline \mathbf{D}_W & \mathbf{W} \otimes \mathbf{W} \end{array} \right) \tilde{\mathbf{k}}(x)$$

Means and variances



Prediction intervals




JPN 1947 siblings
JPN 2019 siblings
JPN 1947 nieces-nephews
JPN 2019 nieces-nephews
mean
0.95
0.05
0.75
0.25
Number
Age of Focal

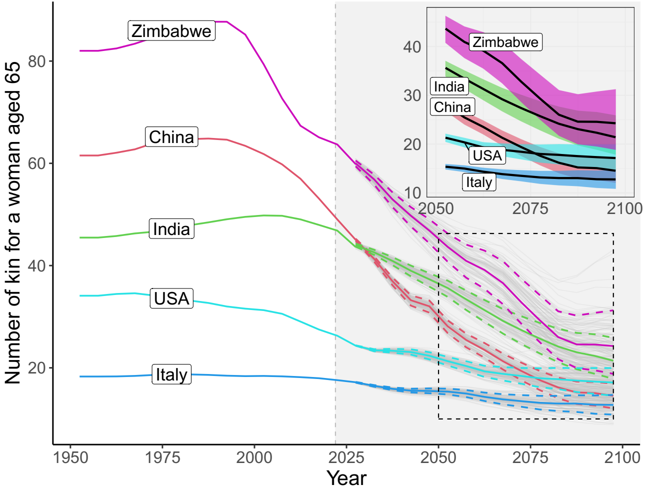
Some outputs

- age distributions, numbers of kin, weighted numbers of kin, ratios of weighted numbers, ...
- prevalence of conditions: disease, habitat occupancy
- numbers weighted by relatedness and reproductive value (inclusive fitness)

Evolutionary implications[6]

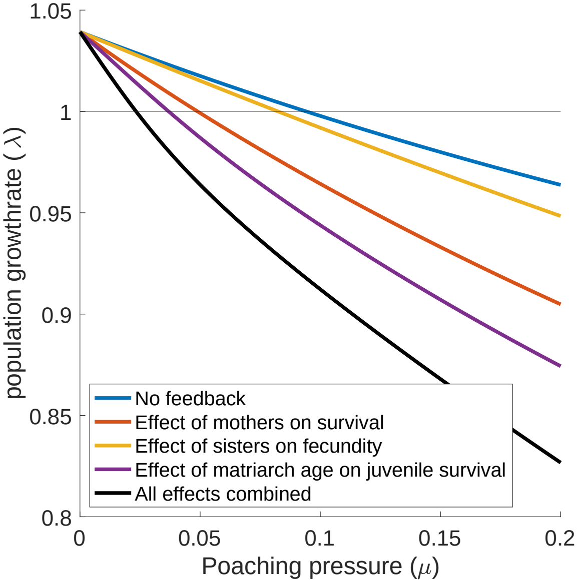
[6] Ellis et al. 2024, Nature

Global projections of kinship size[7]



[7] Alburez-Gutierrez et al. 2023

Conservation and disruption of kin[8]



[8] Croll and Caswell 2025

Questions?