Supplementary Information

Diminishing returns drive altruists to help extended family

Methods, analyses, and description of data collection are provided in the main text Methods section. In this Supplementary Information, we provide additional detail. Supplementary figures are provided in the Extended Data.

Contents

The following files are included as other supplementary data and code:

1. *"Model.R"* – R script for MCMC
2. *"intercept inits.txt"* – example initial values of intercepts
3. *"e array.txt"* – transitions data used in the model file
4. *"CovariatesData.txt"* – covariates data used in the model file
5. *"Mathematica Fig. 3.nb"* – Mathematica file for construction of Main Text Figure 3
6. *"MATLAB – Haplodiploid spatial simulation"* – MATLAB code for the individual-based model

1. Notation

Full description is provided in Section 1 of Methods. Tables of notation are provided below.

Table S1: Notation in theoretical models

Symbol	Model	Definition
G_i	*Bet-hedging maximand*	Genetic value for individual i, with population average $\bar{G}$
I_i	”	Absolute inclusive fitness of individual i. The total number of offspring-equivalents produced by individual $i's$ actions.
b_{ijt}	”	Additive effect of actor i on the absolute fitness of individual j in context (‘role’[1]) t
$\bar{w}$	”	Population average absolute fitness (reproductive success)
$\frac{I_i}{\bar{w}}$	”	‘Relative inclusive fitness’ of Grafen[1]
ω	”	State of the population, in the set Ω
$\mathbb{E}_\omega[I_i]$	”	Expected absolute inclusive fitness, $\mathbf{q}^\dagger\boldsymbol{\mu}$
v	”	Coefficient of variation in population average reproductive success $(\frac{\sigma_\omega[\bar{w}]}{\mathbb{E}_\omega[\bar{w}]})$. v functions as risk-aversion in the bet-hedging trade-offs of an organism.
ρ	”	Correlation, across states Ω, between I_i and $\bar{w}$ ($\rho_{I_i,\bar{w}}$)
$\sigma_\omega[I_i]$	”	Standard deviation of I_i, $\sqrt{\mathbf{q}^\dagger\mathbf{C}\mathbf{q}}$
$\mathbf{C}$	”	Variance-covariance matrix for the payoff rates of different investments made by a focal actor
$\mathbf{q}$	”	Vector of investment weights placed on different behaviours by a focal individual
$\boldsymbol{\mu}$	”	Vector of expected payoff rates from each behaviour choice, in terms of the expected number of offspring-equivalents produced per unit invested
$\mathbf{1}$	”	Vector of 1s
$\dagger$	”	Transpose
α	*Bet-hedging population size model*	Probability with which individuals are automatically paired with a genetically identical partner
N		Population size (since this model uses haploid asexuals, this is the number of ‘queens’)
P	”	Frequency of mutant allele
n_1	”	Number of workers on colony type 1
n_2	”	Number of workers on colony type 2, where $n_2 < n_1$
n_j	”	Number of workers on a colony belonging to queen j
$\bar{y}$	”	Resident drifting level (proportion of effort invested from a type 1 colony to a type 2 colony)
A	”	Constant determining the effect on queen fitness of adding additional workers
θ	”	Independent probability of a catastrophe occurring on a given colony
k	”	Effect of catastrophe occurring. If a catastrophe occurs on her colony, a queen’s absolute fitness is reduced to a proportion k of the value it would otherwise have.
w_j	”	Absolute fitness (reproductive success) of queen j ($w_j = An_j$)
w	”	Absolute fitness of a queen carrying the mutant allele. w can take the values w_2, w_1, kw_2, and kw_1
w_2	”	Absolute fitness of a queen carrying the mutant allele on a low-worker number colony on which no catastrophe occurs
w_1	”	Absolute fitness of a queen carrying the mutant allele on a high-worker number colony on which no catastrophe occurs

$w_{♀,s}$	*Indirect reciprocity and diminishing returns models*	Absolute fitness of an individual if it develops as female on a focal nest of type s
$w_{♂,s}$		Absolute fitness of an individual if it develops as male on a focal nest of type s
$\bar{w}$		Population average absolute fitness
W	”	Relative fitness $(\frac{w}{\bar{w}})$
z	”	Sex ratio (proportion of eggs that are male), with population average $\bar{z}$
x	”	Probability with which a focal individual develops as a sterile helper, with population average $\bar{x}$
y	”	Probability with which a focal individual invests its finite helping effort in a partner colony (‘drifting level’), with population average $\bar{y}$
Y_{f}	”	Average value of trait y among members of a focal individual’s colony
Y_{d}	”	Average value of trait y among members of a donor colony to a focal individual’s colony
K_j	”	Probability that individual j survives to reproductive maturity, given that they are a potential reproductive (i.e., not a sterile helper). $\bar{K}$ is the population average.
h	”	Amount of help received during development
p	”	Consanguinity
$c_{♀}$	”	Class reproductive value for females. For haplodiploids, $c_{♀} = \frac{2}{3}$
$c_{♂}$	”	Class reproductive value for males. For haplodiploids, $c_{♂} = \frac{1}{3}$
m	”	Willingness to accept drifters, with population average $\bar{m}$
M_{r}	”	Average value of trait m on a recipient colony to a focal individual’s colony
M_{f}	”	Average value of trait m among members of a focal individual’s colony
u	”	Correction factor for social heterosis. Help directed at an unrelated partner colony is amplified by a coefficient u.
a	”	Effect of help at home. Help directed at a worker’s own home colony is amplified by a coefficient a.
ψ	”	Worker-to-brood ratio, which we assume to be $0 \leq \psi \leq 1$.
T	”	Intensity of diminishing returns. Returns to cooperation are linear when $T = 1$. Higher values of T lead to stronger diminishing returns.
β	”	Constraint in model forcing $m = \beta y$
$d_{♀}$	”	Consanguinity to foreign female brood on a partner nest as a proportion of consanguinity to sister brood on the home nest
$d_{♂}$	”	Consanguinity to foreign male brood on a partner nest as a proportion of consanguinity to brother brood on the home nest
d	”	Value in Equation 3 of the main text, where we assume consanguinities to male and female brood are devalued to the same proportion, $d_{♀} = d_{♂} = d$

2. Supplementary information for Taylor-Frank model

For the indirect reciprocity and diminishing returns analyses, we consider a haplodiploid population and follow the framework for the evolution of eusociality in Davies *et al.*[2], which we summarise below. Notation is in **Table S1**. *See Sections 2 and 3 of Methods respectively for descriptions.*

Daughters become reproductives with probability $1 - x$ and workers with probability x. We therefore refer to x as the level of altruistic sterility.

We assume common sex ratio (z) and sterility (x) values for all colonies in the population. The absolute fitness of a female developing on colony type s is:

$$w_{♀,s} = (1 - x)K_s \qquad (S2.1)$$

where K_s is the probability of surviving to reproductive maturity for a potential reproductive developing on colony type s. We allow the fitness of a reproductive to follow a diminishing returns curve:

$$K_s = 1 - (1 - h_s)^T \qquad (S2.2)$$

where h_s denotes level of help experienced by brood on nest type s during its development. When there are no diminishing returns ($T = 1$), $K_s = h_s$. Higher values of T generate stronger diminishing returns.

The absolute fitness of a male developing on colony type s depends on the ratio of reproductive females to males:

$$w_{♂,s} = \frac{(1 - \bar{z})(1 - \bar{x})}{z} K_s \qquad (S2.3)$$

where z is the population average sex ratio and x is the population average altruistic sterility.

Female and male relative fitnesses ($W_{♀,s} = \frac{w_{♀,s}}{\bar{w}_{♀}}$ and $W_{♂,s} = \frac{w_{♂,s}}{\bar{w}_{♂}}$, respectively) simplify to $W_{♀,s} = W_{♂,s} = \frac{K_s}{\bar{K}}$. Assuming two nest types ($s = \{1,2\}$) of equal frequency in the population, relative fitness is $\frac{2K_s}{\bar{K}_1 + \bar{K}_2}$, where $\bar{K}_1$ and $\bar{K}_2$ are the average probabilities of survival to reproductive maturity on nests of each type respectively.

Selection favours an increase in a trait value y if an increase in y is associated with higher fitness overall, considering effects on female and male fitnesses[2]:

$$c_{♀}\frac{\mathrm{d}W_{♀}}{\mathrm{d}y} + c_{♂}\frac{\mathrm{d}W_{♂}}{\mathrm{d}y} > 0 \qquad (S2.4)$$

where $c_{♀}$ and $c_{♂}$ are, respectively, the class reproductive values of females and males (the relative contribution of each sex to the gene pool of the distant future). Class reproductive values in haplodiploids are $c_{♀} = \frac{2}{3}$ for females and $c_{♂} = \frac{1}{3}$ for males. Following the Taylor-Frank method[3], we expand the derivatives using the chain rule, as for instance:

$$\frac{\mathrm{d}W_i}{\mathrm{d}y_i} = \sum_j \frac{\partial W_i}{\partial y_j} \cdot \frac{\mathrm{d}y_j}{\mathrm{d}y_i} \qquad (S2.5)$$

where j denotes the actor role, i the recipient female, and y a genic value for a trait of interest (for trait value, we assume 1:1 genotype:phenotype mapping). In inclusive fitness models[4], the second fraction on the right hand side is regression relatedness (r). We follow Davies *et al.*[2] in writing conditions for selection in terms of consanguinities (p, the probability that randomly-chosen alleles at the focal locus in individuals j and i are identical by shared genealogy[5]), rather than regression relatedness (r):

$$r_{ji} = \frac{\mathrm{d}y_j}{\mathrm{d}y_i} = \frac{p_{ji}}{p_{ii}} \qquad (S2.6)$$

where p_{ji} is the consanguinity between j and i. The relevant consanguinity values for haplodiploids given in **Table S2** (see Table S1 of Davies *et al.*[2] for a list of consanguinity values in diploids and haplodiploids; see also Appendix B of Alpedrinha *et al.*[6]).

Table S2: Consanguinities in outbreeding monogamous haplodiploids

Consanguinity	**Value**
p_{sis}	$3/8$
p_{niece}	$3/16$
p_{bro}	$1/4$
p_{nephew}	$3/8$

3. Additional statistics information

Table S3: Mean residual deviance for each of the seven starting states and the aggregate model

	Total	$\boldsymbol{n_i}$	**Mean residual deviance**
Total residual deviance for entire fitted model (totresdev)	33551.9	24	2.97
Total residual deviance for intercepts-only model (totresdevIO)	71522.7	24	6.33
Total residual deviance for intercepts + random effects only model (totresdevREO)	47048.2	24	4.16
totresdevimodel[1]	10561.3	5	4.48
totresdevimodel[2]	5350.2	5	2.27
totresdevimodel[3]	4863.7	4	2.58
totresdevimodel[4]	4591.6	3	3.25
totresdevimodel[5]	1264.8	3	0.90
totresdevimodel[6]	4250.9	2	4.51
totresdevimodel[7]	2669.3	2	2.83

4. Work cited

1. Grafen, A. Optimization of inclusive fitness. *J. Theor. Biol.* **238**, 541–563 (2006).
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3. Taylor, P. & Frank, S. How to make a kin selection model. *J. Theor. Biol.* **180**, 27–37 (1996).
4. Alpedrinha, J., Gardner, A. & West, S. A. Haplodiploidy and the evolution of eusociality: Worker revolution. *Am. Nat.* **184**, 303–317 (2014).
5. Bulmer, M. *Theoretical Evolutionary Ecology*. (Sinauer Associates, 1994).
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