Supplementary Materials for

Extraordinary Self-Sacrifice

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Overview of Models

All models are set in an infinitely large, Malthusian (i.e. inelastic) population composed of asexual, haploid individuals distributed over a large number of islands. There are n breeding vacancies on each island, and each breeder produces a large number of offspring. After this, all breeders die.

I assume a small probability d that an offspring will grow wings. Offspring are paired at random with another individual from the same island and pay a fecundity cost C to give a fecundity benefit B to the recipient. Following this, winged individuals disperse, landing on a random island with probability $1–k$, where k is small. All individuals then compete for a breeding vacancy on their island. The n winners acquire a breeding vacancy and the remaining individuals die.

Working from Taylor (*8*), the probability that two randomly selected individuals drawn from the same island, with replacement, bear copies of the focal allele identical by descent is

$$r = \frac{1}{n} + \frac{n-1}{n}\hat{r},$$

where $\hat{r}$ is the probability that two randomly selected breeders drawn from the same island, without replacement, bear copies of the focal allele identical by descent. If we let h be the probability that a breeder is native to the island on which it breeds, then $\hat{r} = h^2 r$. With substitution, we can calculate $\hat{r}$ from the recursion

$$\hat{r} = h^2\left(\frac{1}{n} + \frac{n-1}{n}\hat{r}\right).$$

Expanding and solving for $\hat{r}$ gives

$$\hat{r} = \frac{h^2}{n - h^2(n-1)}.$$

Finally, let us calculate h. There is a $1–d$ probability that an individual is sedentary, of a total of $1–d$ natives and $(1–k)d$ migrants on the island. Thus,

$$h = \frac{1-d}{1-d+d(1-k)} = \frac{1-d}{1-dk}.$$

To study the effects of actor dispersal (Model 1), recipient dispersal (Model 2), and kin recognition (Model 3), I calculate the inclusive fitness effect W of a mutant actor playing $(B + b, C + c)$ for small increments of b and c. Next, I find the evolutionarily stable (ES) marginal cost-benefit ratio, c/b. Finally, I translate this into an actual cost-benefit ratio,

C/B. I assume diminishing returns, such that $C = B^2$. Given that c/b can be approximated by the derivative dC/dB, $c/b = 2C/B$. For instance, if the ES $c/b = 1$, then the ES $C/B = 0.5$. In the numerical simulations, I assume that $n = 10$ and $k = 0.1$, and I study dispersal within the range $0 \leq d \leq 0.1$, allowing r to vary with it. I define extraordinary self-sacrifice as $c/|b| > 1$ for the marginal effects and $C/|B| > 1$ for the actual effects.

Model 1: Effect of actor dispersal

In Model 1, the actor knows whether it has grown wings, it also knows whether it will disperse or remain at home with complete certainty. A dispersing individual will successfully arrive on a new, random island with probability $1-k$. An individual remains on the natal island with probability $1-d$ and the same is true of its neighbors.

Let us first consider the case of a dispersing actor, denoted as D. Because the actor disperses, it has a $1-k$ probability of landing on a new island and competing for a breeding vacancy. The recipient will be kin of consanguinity r; it will compete on the natal island with probability $1-d$ and will compete on a new island with probability $(1-k)d$. The actor's neighbors will be relatives of consanguinity $\bar{r} = 0$ and the recipient's neighbors will be relatives of the actor of consanguinity $(1-d)r$ if the recipient remains on the natal island (also with probability $1-d$) or they will be relatives of consanguinity $(1-k)d\bar{r}$ if the recipient disperses. The inclusive fitness effect is thus $W_{\mathrm{D}} = -(1-k)c + \left[(1-d)+(1-k)d\right]rb + (1-k)\bar{r}c - (1-d)^2 rb - (1-k)d\bar{r}b$, which is evolutionarily stable when $W_{\mathrm{D}} = 0$. With simplification and rearrangement, this yields

$$\frac{c}{b} = \frac{(1-kd)r - (1-d)^2 r}{1-k}. \tag{S1}$$

In the case that of a sedentary actor, denoted as S, the logic is identical to that above, except that the actor will compete on the natal island with complete certainty. Thus, the inclusive fitness effect for a sedentary actor is
$W_{\mathrm{S}} = -c + \left[(1-d)+(1-k)d\right]rb + (1-d)rc - (1-d)^2 rb - (1-k)d\bar{r}b$, which is evolutionarily stable when $W_{\mathrm{S}} = 0$. With simplification and rearrangement, this yields

$$\frac{c}{b} = \frac{(1-kd)r - (1-d)^2 r}{1-(1-d)r}. \tag{S2}$$

Let us now compare eqs. (S1) and (S2), which differ only in their denominators. If we assume that d and k are small and, consequently, that r is large, then the ES c/b for a sedentary actor (eq. (S2)) is smaller than that of a dispersing actor (eq. (S1)). Thus, altruism will tend to evolve more easily when actors are sedentary than when they disperse.

Model 2: Effect of recipient dispersal

I now study the effect of recipient dispersal. As in Model 1, the actor knows whether it has grown wings, and so knows whether it will disperse. However, it can also tell whether the recipient has grown wings, and so knows whether the recipient will disperse. Thus, we have four conditions to analyze.

First, let us consider a dispersing actor interacting with a dispersing recipient, denoted as DD. Following the logic applied in Model 1, the inclusive fitness effect is $W_{\mathrm{DD}} = -(1-k)c + (1-k)rb + (1-k)\bar{r}c - (1-k)\bar{r}b$. With simplification and rearrangement, this gives the ES marginal cost-benefit ratio

$$\frac{c}{b} = r\,. \tag{S3}$$

This is Hamilton's classic result for the evolution of altruism (*1*).

Second, let us consider a dispersing actor interacting with a sedentary recipient, denoted as DS. The inclusive fitness effect is $W_{\mathrm{DS}} = -(1-k)c + rb + (1-k)\bar{r}c - (1-d)rb$. This gives the ES marginal cost-benefit ratio

$$\frac{c}{b} = \frac{r-(1-d)r}{1-k}\,. \tag{S4}$$

Third, let us consider a sedentary actor interacting with a dispersing recipient, denoted as SD. The inclusive fitness effect is $W_{\mathrm{SD}} = -c + (1-k)rb + (1-d)rc - (1-k)\bar{r}b$. This gives the ES marginal cost-benefit ratio

$$\frac{c}{b} = \frac{(1-k)r}{1-(1-d)r}\,. \tag{S5}$$

Finally, let us consider a sedentary actor interacting with a sedentary recipient, denoted as SS. The inclusive fitness effect is $W_{\mathrm{SS}} = -c + rb + (1-d)rc - (1-d)rb$. This gives the ES marginal cost-benefit ratio

$$\frac{c}{b} = \frac{r-(1-d)r}{1-(1-d)r}\,. \tag{S6}$$

As expected, the largest ES *c*/*b* is for the condition of a sedentary actor interacting with a dispersing recipient (eq. (S5)). This condition exceeds the $c/|b| \leq 1$ limit. Conversely, the smallest *c*/*b* is for the condition of a dispersing actor and a sedentary recipient (eq. (S4)). Thus, altruism evolves most easily when actors are sedentary and recipients disperse.

Model 3: Effect of kin recognition

Finally, I study the effect of kin recognition. As in Models 1 and 2, the actor knows whether it and the recipient have grown wings. Thus, it knows whether it and the recipient will disperse. In addition, let us suppose that, before interaction, offspring learn a song from their parents (*15*). This song is shared among all individuals born on the same island. Consequently, breeders born on the same island sing one same song, but immigrant breeders born on another island sing a different one. At the point of interaction with a random partner, all offspring sing their parent's song. If the actor and recipient sing the same song, then consanguinity between them is 1. If they sing different songs, then consanguinity between them is 0.

We now have eight conditions to analyze. First, let us consider a dispersing actor interacting with a dispersing recipient who sings the same song, denoted as DD|1. The inclusive fitness effect is $W_{\mathrm{DD}|1} = -(1-k)c + (1-k)b + (1-k)\bar{r}c - (1-k)\bar{r}b$. With simplification and rearrangement, this gives the ES marginal cost-benefit ratio

$$\frac{c}{b} = 1 . \tag{S7}$$

Second, let us consider a dispersing actor interacting with a dispersing recipient who sings a different song, denoted as DD|0. The inclusive fitness effect is $W_{\mathrm{DD}|0} = -(1-k)c + (1-k)\bar{r}c - (1-k)\bar{r}b$. This gives the ES marginal cost-benefit ratio

$$\frac{c}{b} = 0 . \tag{S8}$$

Third, let us consider a dispersing actor interacting with a sedentary recipient who sings the same song, denoted as DS|1. The inclusive fitness effect is $W_{\mathrm{DS}|1} = -(1-k)c + b + (1-k)\bar{r}c - (1-d)rb$. This gives the ES marginal cost-benefit ratio

$$\frac{c}{b} = \frac{1-(1-d)r}{1-k} . \tag{S9}$$

Fourth, let us consider a dispersing actor interacting with a sedentary recipient who sings a different song, denoted as DS|0. The inclusive fitness effect is $W_{\mathrm{DS}|0} = -(1-k)c + (1-k)\bar{r}c - (1-d)rb$. This gives the ES marginal cost-benefit ratio

$$\frac{c}{b} = -\frac{(1-d)r}{1-k}. \tag{S10}$$

Fifth, let us consider a sedentary actor interacting with a dispersing recipient who sings the same song, denoted as SD|1. The inclusive fitness effect is $W_{\mathrm{SD}|1} = -c + (1-k)b + (1-d)rc - (1-k)\bar{r}b$. This gives the ES marginal cost-benefit ratio

$$\frac{c}{b} = \frac{1-k}{1-(1-d)r}. \tag{S11}$$

Sixth, let us consider a sedentary actor interacting with a dispersing recipient who sings a different song, denoted as SD|0. The inclusive fitness effect is $W_{\mathrm{SD}|0} = -c + (1-d)rc - (1-k)\bar{r}b$. This gives the ES marginal cost-benefit ratio

$$\frac{c}{b} = 0. \tag{S12}$$

Seventh, let us consider a sedentary actor interacting with a sedentary recipient who sings the same song, denoted as SS|1. The inclusive fitness effect is $W_{\mathrm{SS}|1} = -c + b + (1-d)rc - (1-d)rb$. This gives the ES marginal cost-benefit ratio

$$\frac{c}{b} = 1. \tag{S13}$$

Finally, let us consider a sedentary actor interacting with a sedentary recipient who sings a different song, denoted as SS|0. The inclusive fitness effect is $W_{\mathrm{SS}|0} = -c + (1-d)rc - (1-d)rb$. This gives the ES marginal cost-benefit ratio

$$\frac{c}{b} = -\frac{(1-d)r}{1-(1-d)r}. \tag{S14}$$