

# Evaluation of Breeding Strategies of Eusocial Species by Gene Extinction Probability

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## 1 Introduction

Understanding eusociality in the view of Hamilton rule [1] is fundamentally important. Here, using a simple branching processes of gene propagation, we evaluate the extinction probability of genes in different cooperative breeding strategies of eusocial species [2, 3]. We discuss the relationship between the propagation advantage of breeding strategy and Hamilton rule.

## 2 Gene Propagation and its Extinction in Solitary Species

Consider a gene which controls the breeding behavior of solitary species. The foundress lives an exponential time with the death rate  $d_1$ , and during her life span she produces offspring according to Poisson process with the rate  $b_1$ . In solitary species, each emerged offspring is supposed to disperse and to produce her own offspring, who start their own lineage independently as a continuous-time branching process. Suppose the focal solitary gene in the foundress is shared by her offspring with probability  $r$  independently. See Figure 1 for an example of branching process representation of gene propagation when  $rb_1 = 0.12$  and  $d_1 = 0.10$ . It is important to see that there are many extinctions (the extinction probability is  $rb_1/d_1 = 5/6$  in this case as we see below) in the case when  $b_1$  is slightly larger than  $d_1$ .



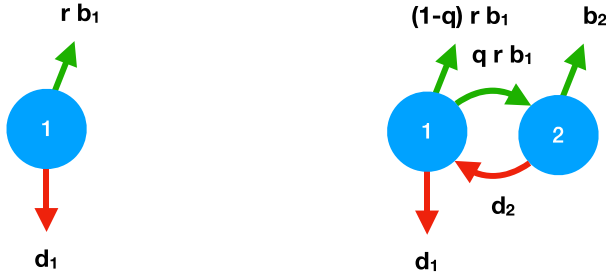


Figure 2: Solitary (left) and Two-Eusocial Species (right)

as a worker with the probability  $q$ , and then starts helping queen's breeding. When the worker emerges, the nest is cooperatively maintained by the foundress queen and this daughter worker, and it produces their offspring all dispersing with the faster rate  $b_2$  until the worker dies with the rate  $d_2$ . Both rates  $b_2$  and  $d_2$  are supposed to be larger than  $b_1$  and  $d_1$  respectively, because the worker works harder than solitary mother. After the worker's death, the remaining queen produces new offspring on her own with the rate  $b_1$  again, and a new offspring may become her new worker with the probability  $q$ . This process is repeated until the queen's death. As in the previous section, we assume that the focal gene in mother is shared among her daughters with the probability  $r$ .

See Figure 3 for an example of the propagation of 2-eusocial gene. We can see that the most of the nests are failed unless they can recruit workers.

As shown in [2], the probability generating function of the number of dispersed offspring  $X$  is calculated by

$$\phi(z) = E[z^X] = \frac{1}{1 + \{1 - (1 - q)z - q\phi_2(z)\}rb_1/d_1},$$

$$\phi_2(z) = \frac{1}{1 + (1 - z)rb_2/d_2}.$$

As a special case when the parameters are linear to the group size as  $b_2 = 2b_1$  and  $d_2 = 2d_1$ , the extinction probability is the same as the solitary species, i.e., when  $rb_1 > d_1$ ,

$$p = \frac{d_1}{rb_1},$$

as expected, because the linear case can be regarded as the aggregation of

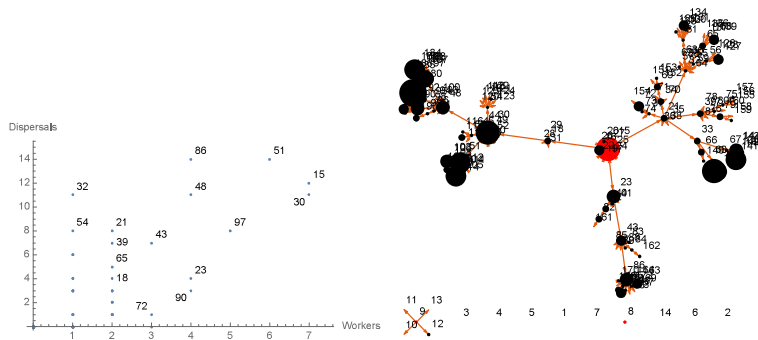


Figure 3: A simulation of branching process of 2-eusocial gene propagation of first 100 individuals. Each lineage starts from the red node, and the size of nodes represent the number of workers the foundress got.  $rb_1 = 0.12$  and  $d_1 = 0.1$ ;  $b_2 = 3b_1$  and  $d_2 = 2d_1$ ;  $q = 1$ .

independent solitary groups. On the other hand,

$$E[X] = \frac{(1-q)rb_1}{d_1} + \frac{qrb_1rb_2}{d_1d_2} > \frac{rb_1}{d_1}.$$

This shows that the extinction probability  $p$  is a good performance measure of eusociality while the basic reproductive number  $E[X]$  is not.

## 4 Daughter's Gene and Hamilton's Rule

Consider a gene in a daughter, and her sisters share the same gene with probability  $r_s$  (sister to sister relatedness). Assume that all dispersed gene-lineage extinct independently with the identical extinction probability  $p$ , regardless they are on sisters or daughters.

First, suppose the daughter disperses and starts her own new nest producing her daughters with your gene. Then, the distributed genes in the first generation can be decomposed into two independent parts: genes in her daughters in the new nest  $X_d$  and genes in her sisters in the mother's nest  $X_s$ . The extinction probability of her gene is obtained as:

$$p_{e,d}(d) = E[p^{X_d+X_s}] = \frac{1}{1 + (1-p)rb_1/d_1} E[p^{X_s}].$$

Next, suppose the daughter stays as a worker and help her mother produce the daughter's sisters with the rate  $b_2$  until the daughter's death with

the rate  $d_2$ . After the daughter's death, her mother produces her sisters with the rate  $b_1$ . Then, the gene distribution through the sisters can be decomposed into two independent parts: the genes  $X_s$  on the sisters produced without help and the genes  $X_{s,2}$  produced by the daughter's help:

$$p_{e,d}(s) = E [p^{X_s+X_{s,2}}] = E [p^{X_s}] \frac{1}{1 + (1-p)r_s b_2/d_2}.$$

Note that we assume the worker to die first. It is easy to see that staying is better decision avoiding the extinction ( $p_{e,d}(s) < p_{e,d}(d)$ ) if and only if

$$\frac{r_s b_2}{r d_2} > \frac{b_1}{d_1},$$

regardless of the baseline extinction probability  $p$ . This is indeed a kind of Hamilton's rule:  $rB > C$ , where  $r = r_s/r$  is the relative relatedness,  $B = b_2/d_2$  is the benefit of cooperation per unit time, and  $C = b_1/d_1$  is the cost of cooperation per unit time.

## References

- [1] W.D. Hamilton. The genetical evolution of social behaviour. ii. *Journal of theoretical biology*, 7(1):17–52, 1964.
- [2] Jeremy Field and Hiroshi Toyoizumi. The evolution of eusociality: no risk-return tradeoff but the ecology matters. *Ecology Letters*, 2020. doi: 10.1111/ele.13452. URL <https://onlinelibrary.wiley.com/doi/abs/10.1111/ele.13452>.
- [3] Feng Fu, Sarah D Kocher, and Martin A Nowak. The risk-return trade-off between solitary and eusocial reproduction. *Ecology letters*, 18(1):74–84, 2015.