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.

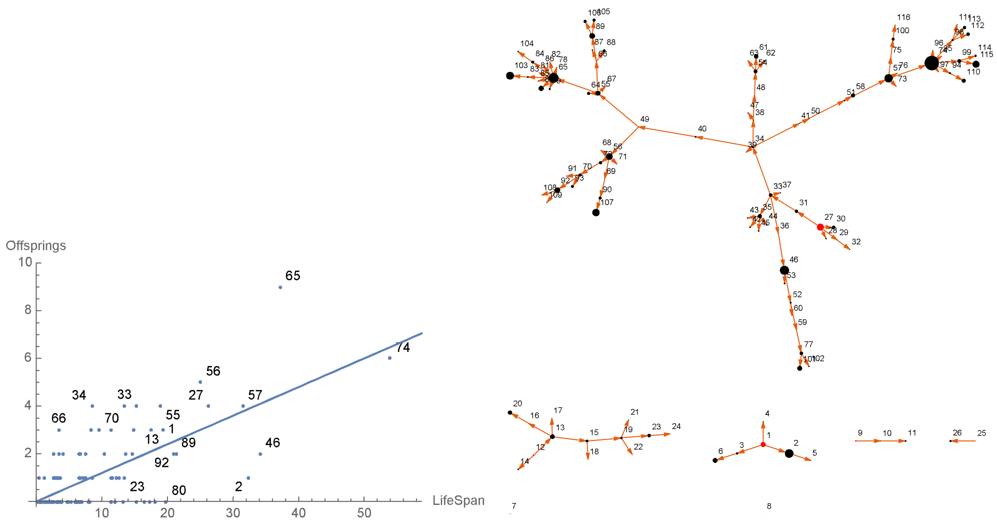

Figure 1: The graph of lifespan vs the number of offspring (left) and the solitary gene propagation of first 100 individuals (right). Each lineage starts from the red node, and the size of nodes represent the lifespan. $rb_1 = 0.12$ and $d_1 = 0.1$. When an extinction happens, we restart the simulation runs.

Let X be the number of dispersed offspring carrying the focal gene. In this paper, we assume all X lineages breed their offspring independently, and the extinctions (the focal gene is no longer propagated in this lineage) happen independently with an identical baseline probability p. Then, the extinction probability of this focal solitary gene is obtained by

$$p_s = E[p^X] = \frac{1}{1 + (1-p)rb_1/d_1},$$

using a simple application of the probability generating function of Poisson process.

3 Two-Eusocial Species: One Queen and One Worker

Consider a foundress who has 2-eusocial gene, which controls a specific breeding behavior of 2 individuals (a mother queen and her daughter worker) as follows (see Figure 2). Like solitary species, the foundress lives an exponential time with the death rate d_1, and she produces her offspring according to Poisson process with the rate b_1 up to the time when one of her offspring stays

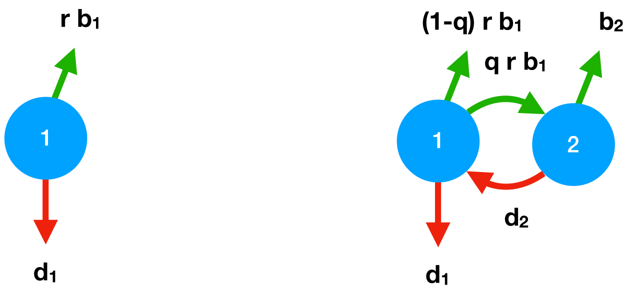

Figure 2: Solitary (left) and Two-Eusocial Species (right)

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

$$\phi(z) = E\left[z^X\right] = \frac{1}{1 + \{1 - (1-q)z - q\phi_2(z)\} r b_1 / d_1},$$
$$\phi_2(z) = \frac{1}{1 + (1-z) r b_2 / d_2}.$$

As a special case when the parameters are linear to the group size as $b_2 = 2b_1$ and $d_2 = 2d_2$, 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

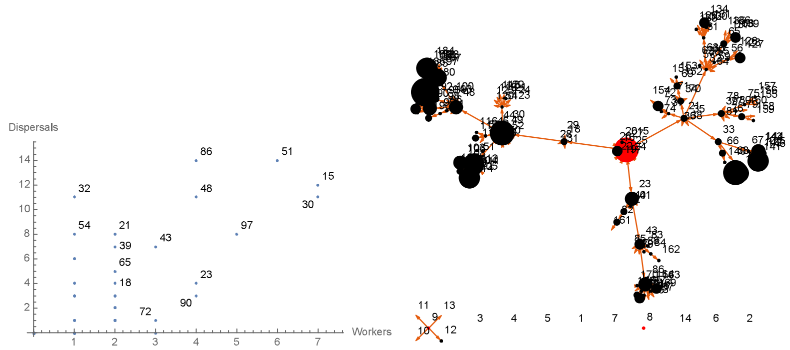

Figure 3: A simulation of branching process of 2-eusocial gene propagation of first 100 individuals. Each lineage starts from the red node, and the size of nodes represent the number of workers the foundress got. $rb_1 = 0.12$ and $d_1 = 0.1$; $b_2 = 3b_1$ and $d_2 = 2d_1$; $q = 1$.

independent solitary groups. On the other hand,

$$E[X] = \frac{(1-q)rb_1}{d_1} + \frac{qrb_1}{d_1}\frac{rb_2}{d_2}. > \frac{rb_1}{d_1}.$$

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:

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

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:

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

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

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

regardless of the baseline extinction probablity 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

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[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.