Cooperation and Construction

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Eusociality

Eusociality is a form of social organization where some individuals do not reproduce but raise the offspring of others.

Different origins of eusociality

Eusociality is characterized by

- overlapping generations
- division of labor
- division of reproduction

- Ants
- Termites
- Wasps
- Bees
- Australian ambrosia beetle
- Aphids
- Thrips
- Snapping shrimp
- Naked mole rats


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Paradox of eusociality

- Why would individuals forego their own reproduction to help others reproduce?
- Why is eusociality so rare given that it is so successful?

New idea

"I would jump into the river to save two brothers or eight cousins".

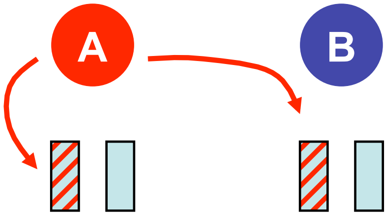
– J.B.S. Haldane (ca. 1930)

What is inclusive fitness?

"Inclusive fitness may be imagined as the personal fitness which an individual actually expresses in its production of adult offspring as it becomes after it has been first stripped and then augmented in a certain way. It is stripped of all components which can be considered as due to the individual's social environment, leaving the fitness which he would express if not exposed to any of the harms or benefits of that environment. This quantity is then augmented by certain fractions of the quantities of harm and benefit which the individual himself causes to the fitnesses of his neighbours. The fractions in question are simply the coefficients of relationship appropriate to the neighbours whom he affects; unit for clonal individuals, one-half for sibs, one-quarter for half-sibs, one-eighth for cousins,....and finally zero for all neighbours whose relationship can be considered negligibly small."

(Hamilton 1964)

Inclusive fitness:



$$W_{IF} = \sum_j (\text{effect of actor on } j) \times R_j$$

where R_j is the relatedness of the actor to individual j.

The haplodiploid hypothesis

- in haplodiploid species sisters are more related to each other (3/4) than mothers are to daughters (1/2)
- hence it makes more sense to invest in sisters than in daughters
- this hypothesis has been refuted
  - theoretically (Evans 1977, Andersson 1984, Strassmann and Queller 1989, Alexander et al 1991, Queller and Strassmann 1998)

...and empirically: more eusocial species were found that are not haplodiploid

- Ants
- Termites
- Wasps
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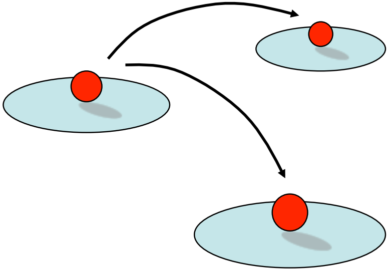
Origin of Eusociality

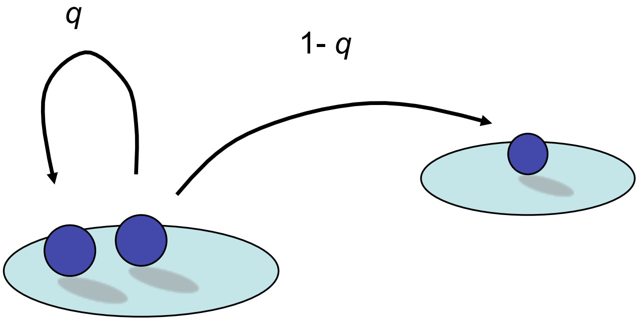
Precursor state: “solitary"



- valuable and defensible nest
- dependable food source within foraging distance
- progressive provisioning = fertilized female builds nest, gathers food, feeds young. The young then leave.

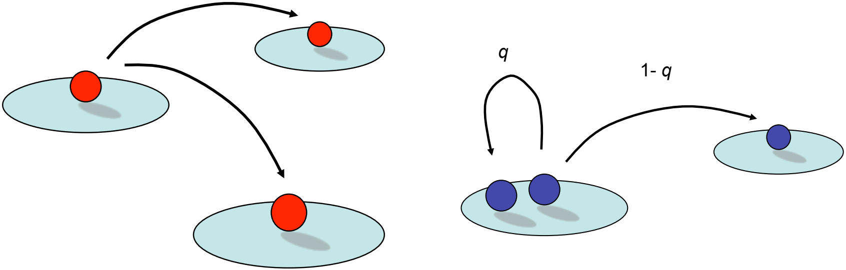
A simple step

- Consider a mutation that prevents some of the offspring from leaving the nest (in some environments).
- Those young that stay with the nest begin to work on tasks that need to be done. (**“Spring-loaded preadaptation"**)
- Born is the “eusocial" strategy.



$q \cdots$ probability that daughter stays with the nest

Solitary versus eusocial

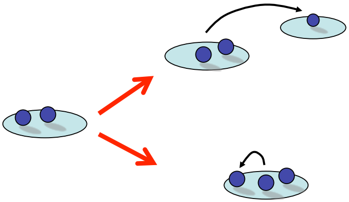


Solitary

$$\dot{x}_0 = (b_0 - d_0)x_0$$

- $b_0 \cdots$ birth rate of solitary female
- $d_0 \cdots$ death rate of solitary female
- $x_0 \cdots$ number of solitary females

Eusocial



$$\dot{x}_1 = \sum_{i=1}^{\infty} b_i(1-q)x_i - b_1 q x_1 - d_1 x_1$$

$$\dot{x}_i = b_{i-1} q x_{i-1} - b_i q x_i - d_i x_i$$

- $b_i \cdots$ birth rate of queen in colony of size i
- $d_i \cdots$ death rate of queen in colony of size i
- $x_i \cdots$ number of colonies of size i
- $q \cdots$ probability that daughters stay at the nest

Solitary versus eusocial

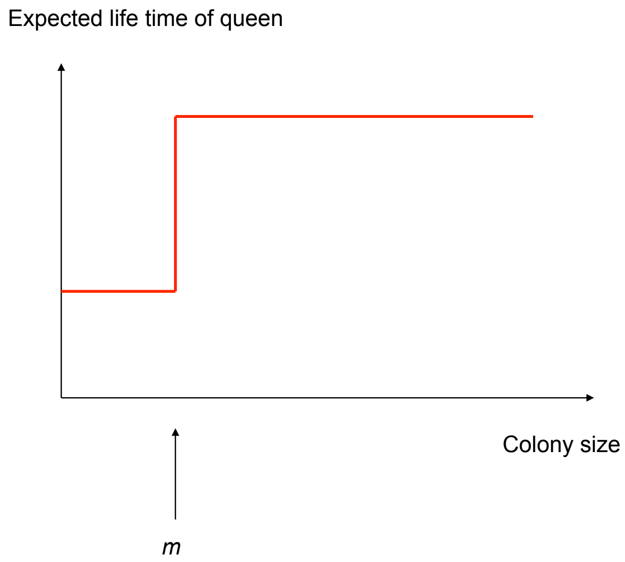
$$\dot{x}_0 = (b_0 - d_0)x_0$$

$$\dot{x}_1 = \sum_{i=1}^{\infty} b_i(1-q)x_i - b_1 q x_1 - d_1 x_1$$

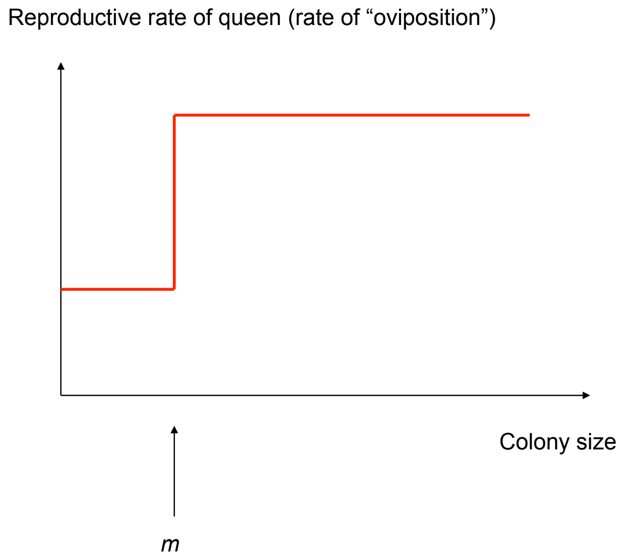
$$\dot{x}_i = b_{i-1} q x_{i-1} - b_i q x_i - d_i x_i \qquad i = 2, 3, \cdots$$

- a linear selection equation
- whoever reproduces faster wins

Longevity benefits



Reproductive benefits



Results

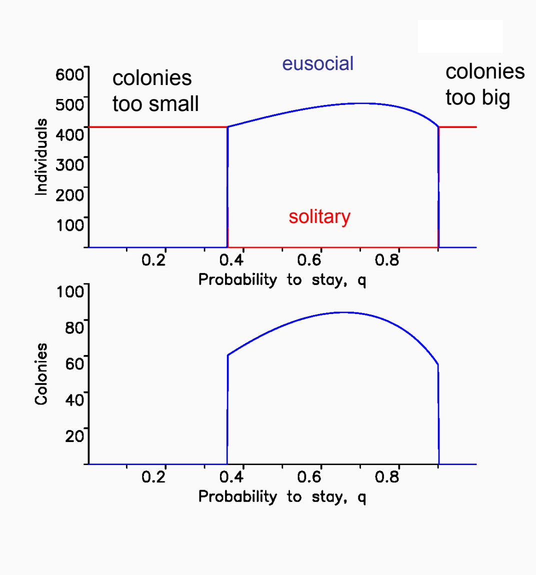
- A necessary condition for the evolution of eusociality is

$$b - k_m d > k_m(b_0 - d_0)$$

  The number k_m depends on the critical colony size, m, where the advantages of eusociality arise. It turns out that k_m grows exponentially with m.

- The above condition is necessary but not sufficient. If it holds then there exist values of q that allow eusociality to win. There is a lower bound, q_{min}, and an upper bound, q_{max}. Eusociality wins if $q_{min} < q < q_{max}$.

Results



$$b_0 = 0.5$$

$$d_0 = 0.1$$

$$m = 3$$

$$b = 4$$

$$d = 0.01$$

$$\alpha = 0.1$$

Eusociality wins

- if the advantages of eusociality (increased life expectancy and reproductive rate of the queen) arise for small colony size
- and if the probability to stay is within a certain range

A haplo-diploid model

females		males		fertilized females (queens)
AA	+	A	$\rightarrow$	AA,A
AA	+	a	$\rightarrow$	AA,a
Aa	+	A	$\rightarrow$	Aa,A
Aa	+	a	$\rightarrow$	Aa,a
aa	+	A	$\rightarrow$	aa,A
aa	+	a	$\rightarrow$	aa,a

Queen's offspring

queens		females		males
AA,A	$\rightarrow$	AA	+	A
AA,a	$\rightarrow$	Aa	+	A
Aa,A	$\rightarrow$	AA + Aa	+	A + a
Aa,a	$\rightarrow$	Aa + aa	+	A + a
aa,A	$\rightarrow$	Aa	+	a
aa,a	$\rightarrow$	aa	+	a

- If the mutation is **dominant**, then **Aa** and **aa** daughters stay with probability q.
- If the mutation is **recessive**, then **aa** daughters stay at the nest with probability q.

A haplo-diploid model

$$\dot{X}_{AA\text{-}A,1} = \beta x_{AA} y_A - b_1 q_1 X_{AA\text{-}A,1} - d_1 X_{AA\text{-}A,1} + \alpha X_{AA\text{-}A,2}$$

$$\dot{X}_{AA\text{-}A,i} = q_1 (b_{i-1} X_{AA\text{-}A,i-1} - b_i X_{AA\text{-}A,i}) - d_i X_{AA\text{-}A,i} - \alpha(i-1) X_{AA\text{-}A,i} + \alpha i X_{AA\text{-}A,i+1}$$

$$\dot{X}_{AA\text{-}a,1} = \beta x_{AA} y_a - b_1 q_2 X_{AA\text{-}a,1} - d_1 X_{AA\text{-}a,1} + \alpha X_{AA\text{-}a,2}$$

$$\dot{X}_{AA\text{-}a,i} = q_2 (b_{i-1} X_{AA\text{-}a,i-1} - b_i X_{AA\text{-}a,i}) - d_i X_{AA\text{-}a,i} - \alpha(i-1) X_{AA\text{-}a,i} + \alpha i X_{AA\text{-}a,i+1}$$

$$\dot{X}_{Aa\text{-}A,1} = \beta x_{Aa} y_A - b_1 \frac{q_1 + q_2}{2} X_{Aa\text{-}A,1} - d_1 X_{Aa\text{-}A,1} + \alpha X_{Aa\text{-}A,2}$$

$$\dot{X}_{Aa\text{-}A,i} = \frac{q_1 + q_2}{2} (b_{i-1} X_{Aa\text{-}A,i-1} - b_i X_{Aa\text{-}A,i}) - d_i X_{Aa\text{-}A,i} - \alpha(i-1) X_{Aa\text{-}A,i} + \alpha i X_{Aa\text{-}A,i+1}$$

$$\dot{X}_{Aa\text{-}a,1} = \beta x_{Aa} y_a - b_1 \frac{q_2 + q_3}{2} X_{Aa\text{-}a,1} - d_1 X_{Aa\text{-}a,1} + \alpha X_{Aa\text{-}a,2}$$

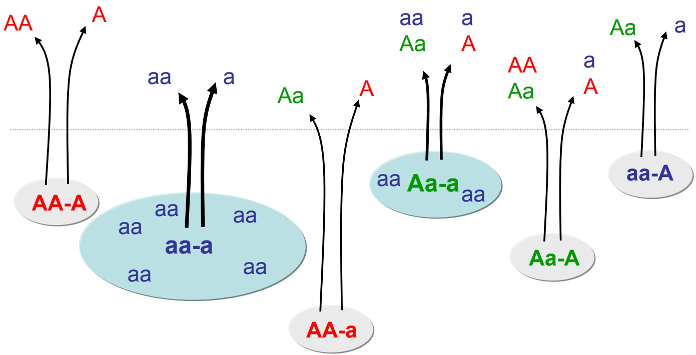
$$\dot{X}_{Aa\text{-}a,i} = \frac{q_2 + q_3}{2} (b_{i-1} X_{Aa\text{-}a,i-1} - b_i X_{Aa\text{-}a,i}) - d_i X_{Aa\text{-}a,i} - \alpha(i-1) X_{Aa\text{-}a,i} + \alpha i X_{Aa\text{-}a,i+1}$$

$$\dot{X}_{aa\text{-}A,1} = \beta x_{aa} y_A - b_1 q_2 X_{aa\text{-}A,1} - d_1 X_{aa\text{-}A,1} + \alpha X_{aa\text{-}A,2}$$

$$\dot{X}_{aa\text{-}A,i} = q_2 (b_{i-1} X_{aa\text{-}A,i-1} - b_i X_{aa\text{-}A,i}) - d_i X_{aa\text{-}A,i} - \alpha(i-1) X_{aa\text{-}A,i} + \alpha i X_{aa\text{-}A,i+1}$$

$$\dot{X}_{aa\text{-}a,1} = \beta x_{aa} y_a - b_1 q_3 X_{aa\text{-}a,1} - d_1 X_{aa\text{-}a,1} + \alpha X_{aa\text{-}a,2}$$

$$\dot{X}_{aa\text{-}a,i} = q_3 (b_{i-1} X_{aa\text{-}a,i-1} - b_i X_{aa\text{-}a,i}) - d_i X_{aa\text{-}a,i} - \alpha(i-1) X_{aa\text{-}a,i} + \alpha i X_{aa\text{-}a,i+1}$$


AA
A
AA-A
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Aa
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AA-a
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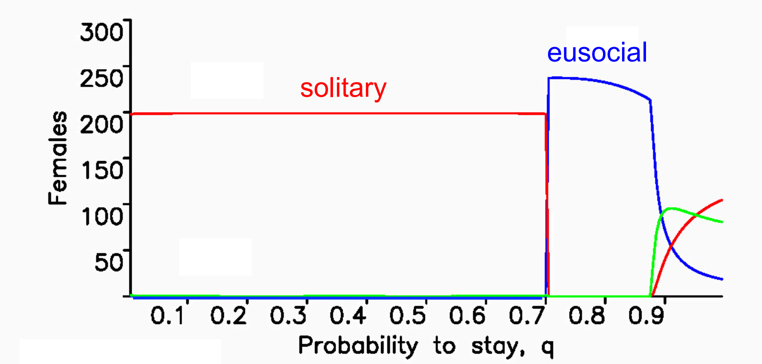
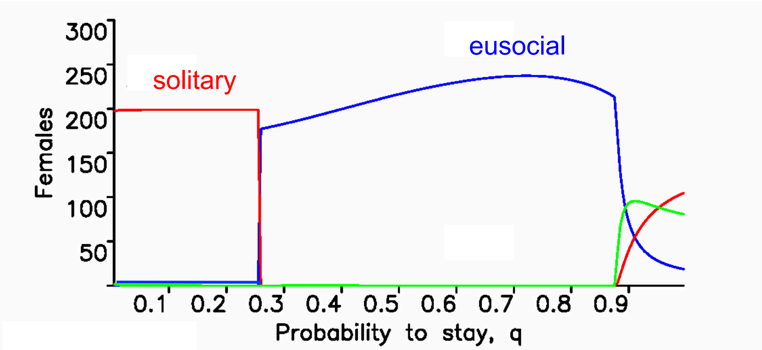
Aa
A
aa Aa-a aa
AA
a
Aa
A
Aa-A
Aa
a
aa-A

Eusociality is hard to evolve…



AA = solitary; aa – a = eusocial (full); Aa – a = eusocial (half)

…but easy to maintain



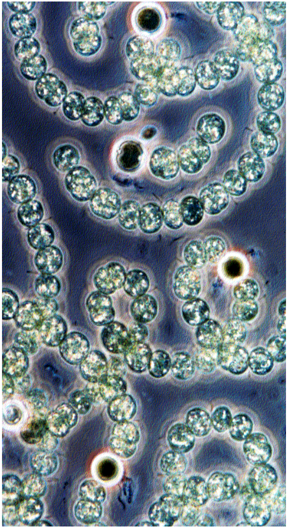
AA = solitary; aa – a = eusocial (full); Aa – a = eusocial (half)

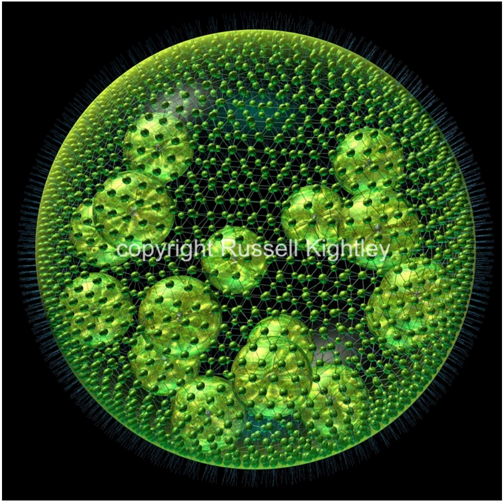
Model results and predictions

- Despite obvious advantages it is not easy for eusociality to be selected over solitary.
- Its success depends on how the queen's **lifetime** and **birth rate** increase with colony size.
- Advantages have to arise for small colony size.
- Daughters must have the right probability to stay.
- It is easier to maintain eusociality than to evolve it (bistability).

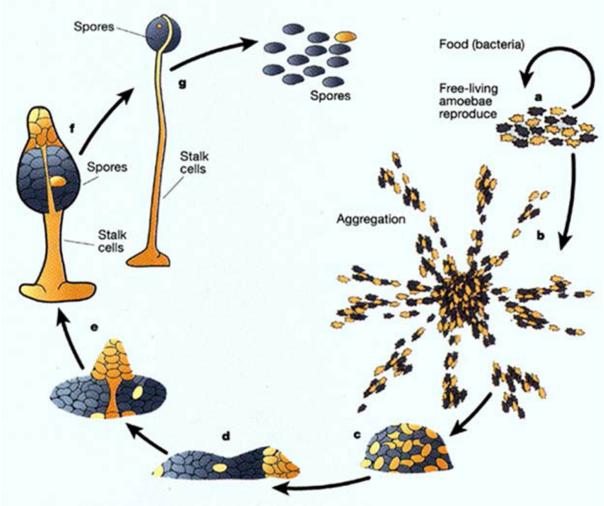
Eusociality represents a different form of cooperation.

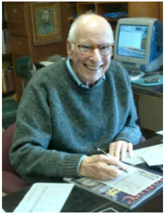
Multicellularity



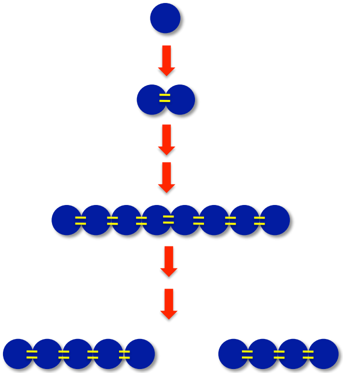


Another way to construct - Aggregation

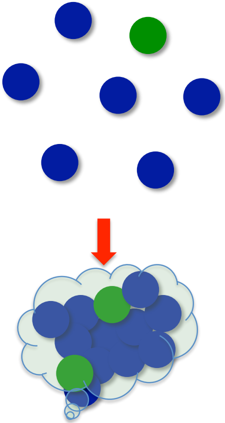




Staying together



Aggregation



Protocells, Endosymbiosis, Eusociality and Sociality