Relatedness and the fraternal major transitions

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Liberté, egalité, fraternité

	Fraternal	**Egalitarian**
Examples	Individuals in colonies, Cells in individuals, Same organelles in cells	Nucleus and organelles, Sex, Genes in chromosomes
Units	Like, exchange able	Unlike, not exchangeable
Reproductive division of labor	Yes	No
Initial advantage	Economies of scale	Division of labor
Control of conflicts	Kinship	Mutual dependence
Increase in complexity	Epigenesis	Symbiosis

Queller 1997 *Q. Rev. Biol.* 72:184-188

Ways to analyze social selection

- Inclusive fitness
- Neighbor-modulated fitness
- Multi-level selection
- Contextual analysis
- Indirect genetic effects
- Game theory
- Networks
- Population genetics
- Quantitative genetics

A simple exact kin selection model

Price's equation: $\overline{W}\Delta G = Cov(G,W)$

G = own breeding value

G' = partner's breeding value

$$W = \alpha + \beta_{WG.G'}G + \beta_{WG'.G}G' + \varepsilon$$

$$\Delta G = ~~Cov(\alpha,G)~~ + Cov(\beta_{WG.G'}G,G) + Cov(\beta_{WG'.G}G',G) + ~~Cov(\varepsilon,G)~~$$

$$\overline{W}\Delta G = \beta_{WG.G'}Cov(G,G) + \beta_{WG'.G}Cov(G,G')$$

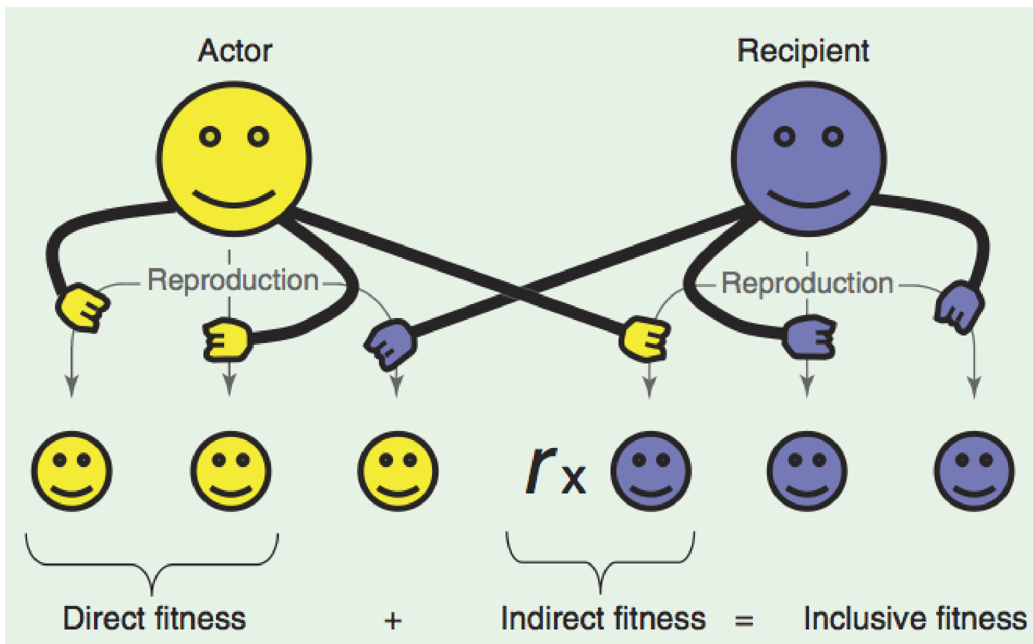
$\Delta G > 0$ when: $\beta_{WG.G'} + \beta_{WG'.G}\beta_{GG'} > 0$

for example: -c + br > 0

Inclusive fitness

$$\beta_{WG.G'} + \beta_{WG'.G}\beta_{GG'} > 0$$

switch to actor's perspective $$\beta_{WG.G'} + \beta_{W'G.G'}\beta_{G'G} > 0$$

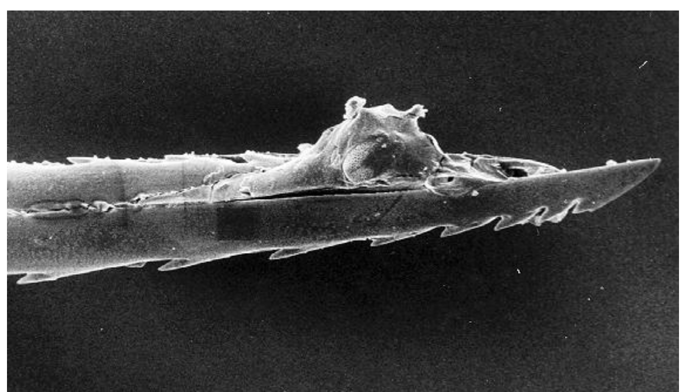


switch to phenotypes $$\beta_{WP.P'} + \beta_{WP.P'}\beta_{G'G} > 0$$

Social insects

Honeybee worker suicide

©Kathy Keatley Garvey



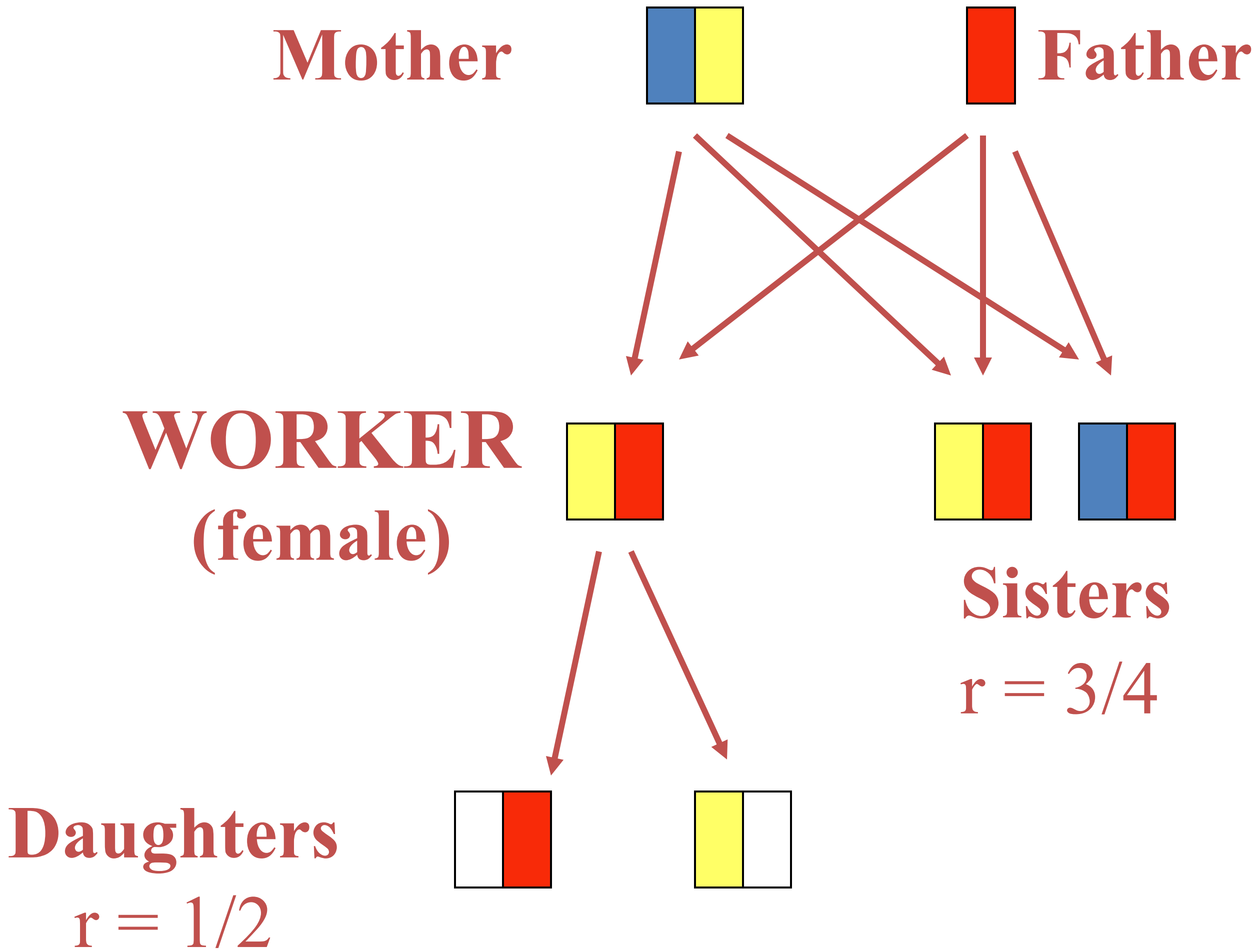
b >> c

Honeybee sister queen killing

b = c

photo: Francis Ratnieks

Haplodiploidy increases sister-sister relatedness in Hymenoptera



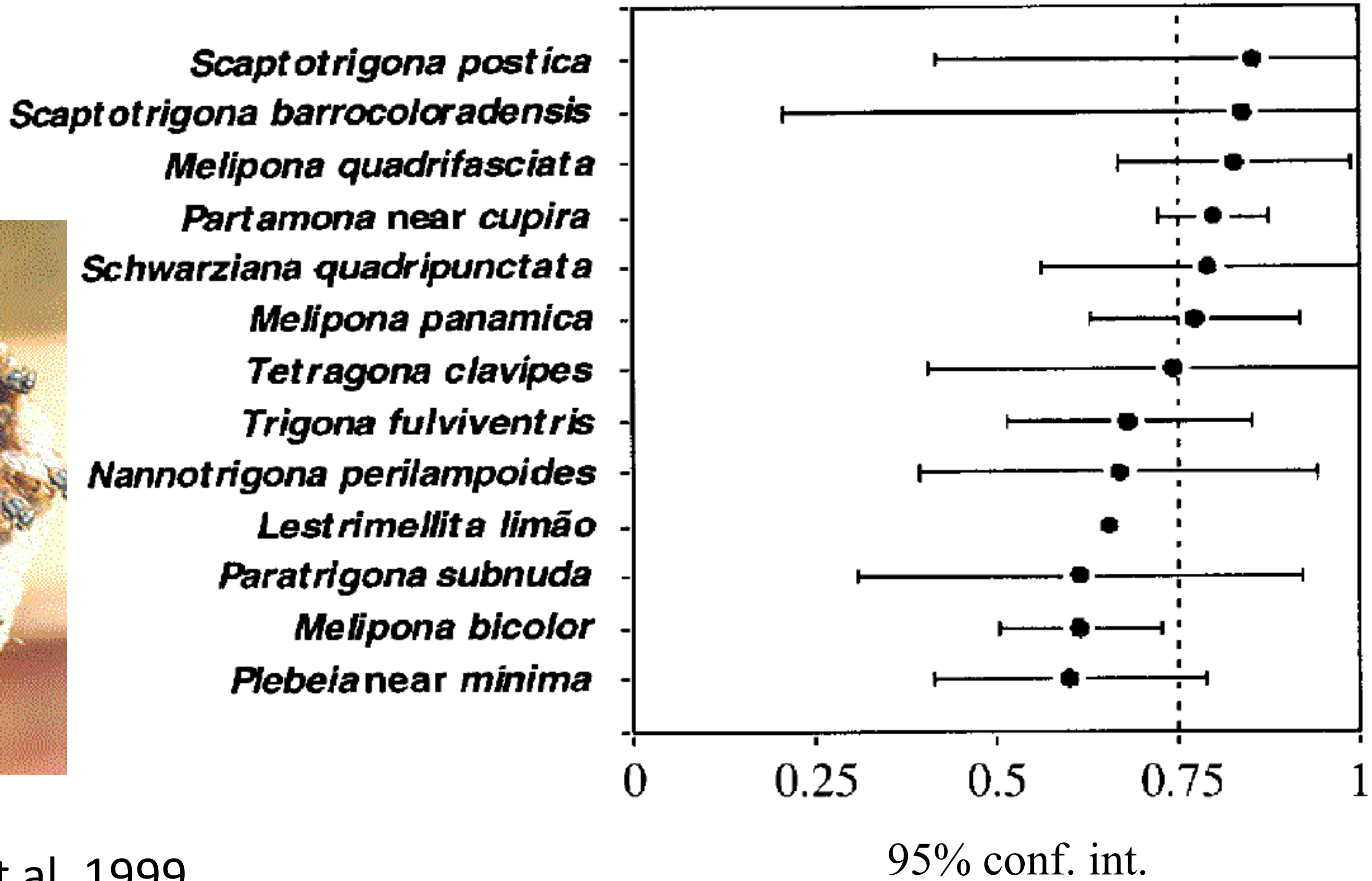
The haplodiploid hypothesis seems to explain:

More origins of sociality in haplodiploids than diploids

Only females are workers (except in diploids)

Workers produce male offspring only

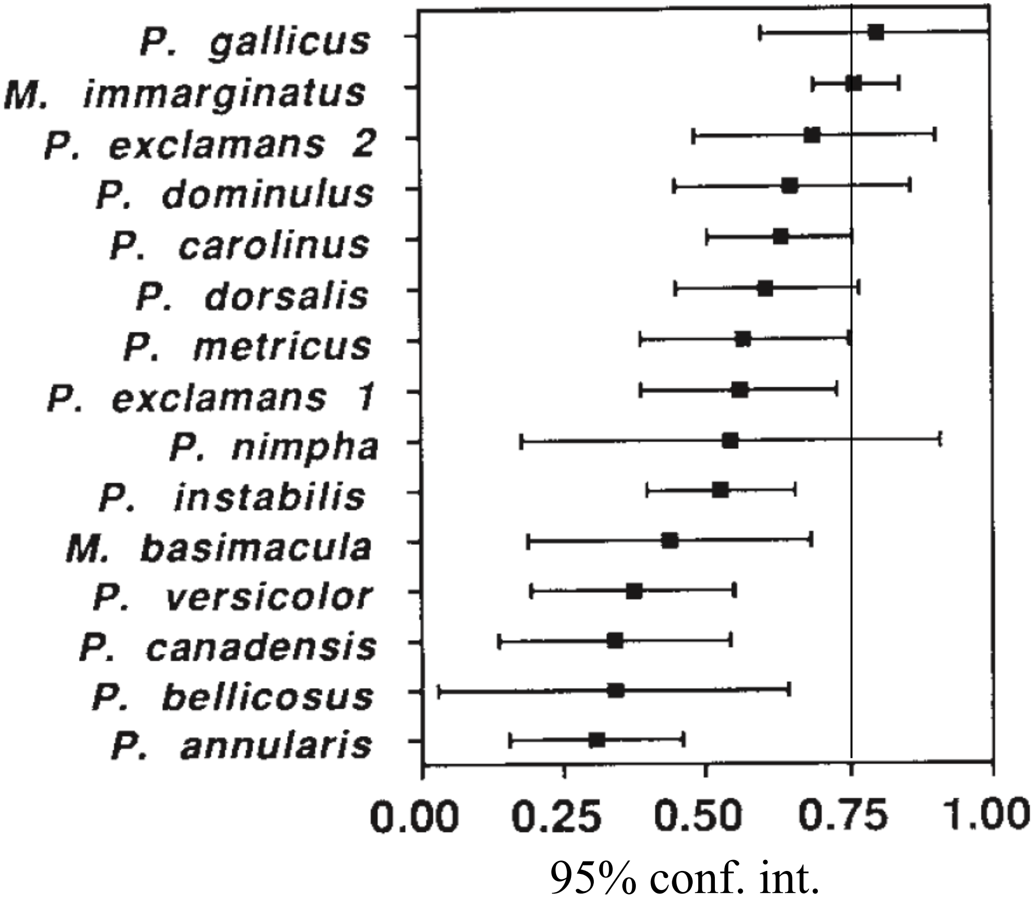
Relatedness in stingless bee colonies estimated with microsatellite markers



Peters et al. 1999

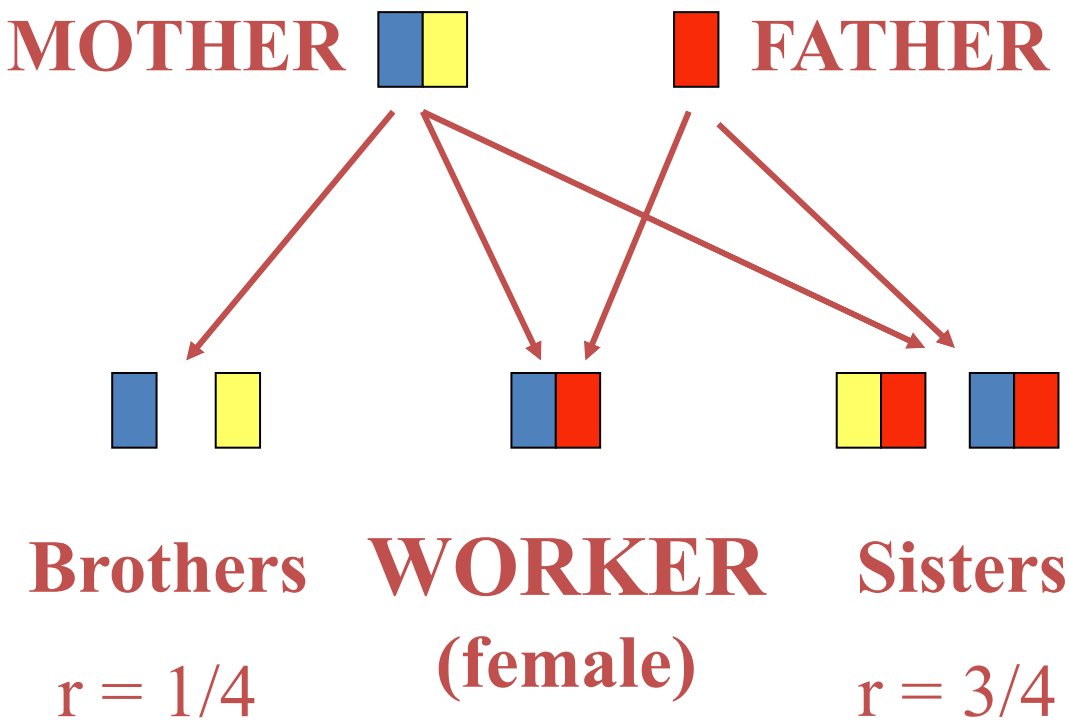
Female relatedness is sometimes below 3/4

Relatedness to sisters is often lower because of multiple mating or multiple queens



Strassmann et al. 1989

Problems with the haplodiploid hypothesis



If a worker rears equal numbers of sisters and brothers, average r is only 1/2

Alternative explanations for sociality in Hymenoptera

More origins of sociality in haplodiploids than diploids	Haplodiploid Hymenoptera have more parental care
Only females are workers (except in diploids)	Only females provide care in non-social Hymenoptera (sting)
Workers produce male offspring only	Workers can produce males without mating

The haplodiploid hypothesis requires kin selection, but not *vice versa*

$$r_c\, c < r_b\, b$$

c = fitness cost, r_c = relatedness to cost payer,
b = fitness benefit, r_b = relatedness to beneficiaries

Can be satisfied if either (or both):

$r_b > r_c$ e.g. haplodiploid hypothesis ¾ > ½

b > c many possible ways (same condition for multicellularity

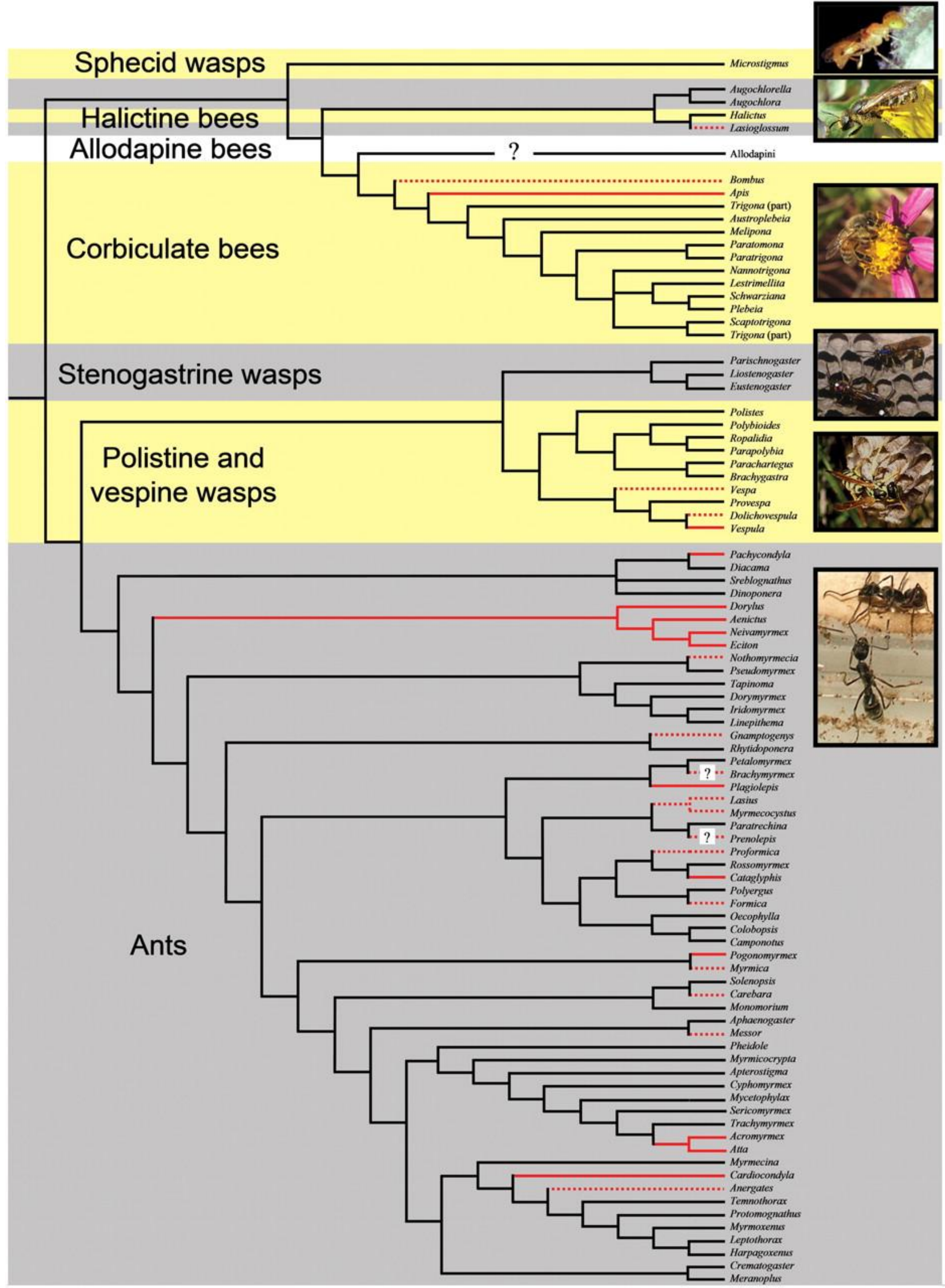
Relatedness matters

Singly mated

Multiply mated

267 species of eusocial bees, wasps, and ants

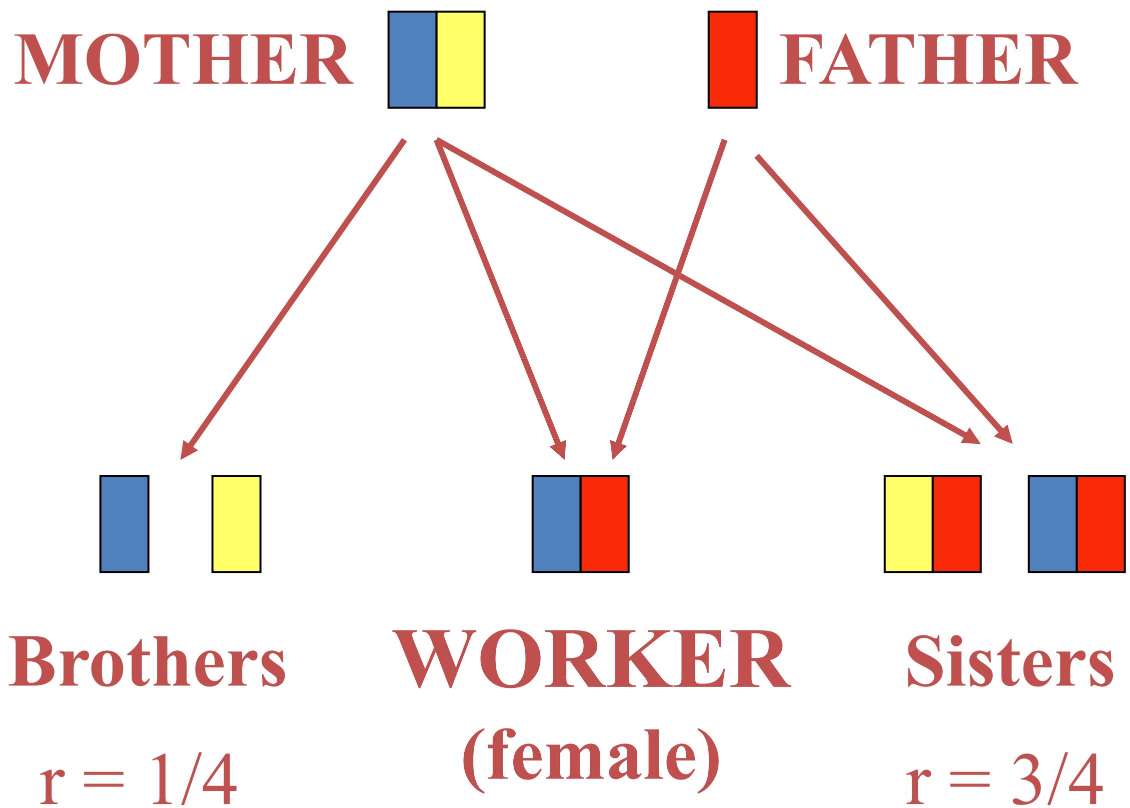
Hughes et al. Science 2008



High relatedness is not just incidental

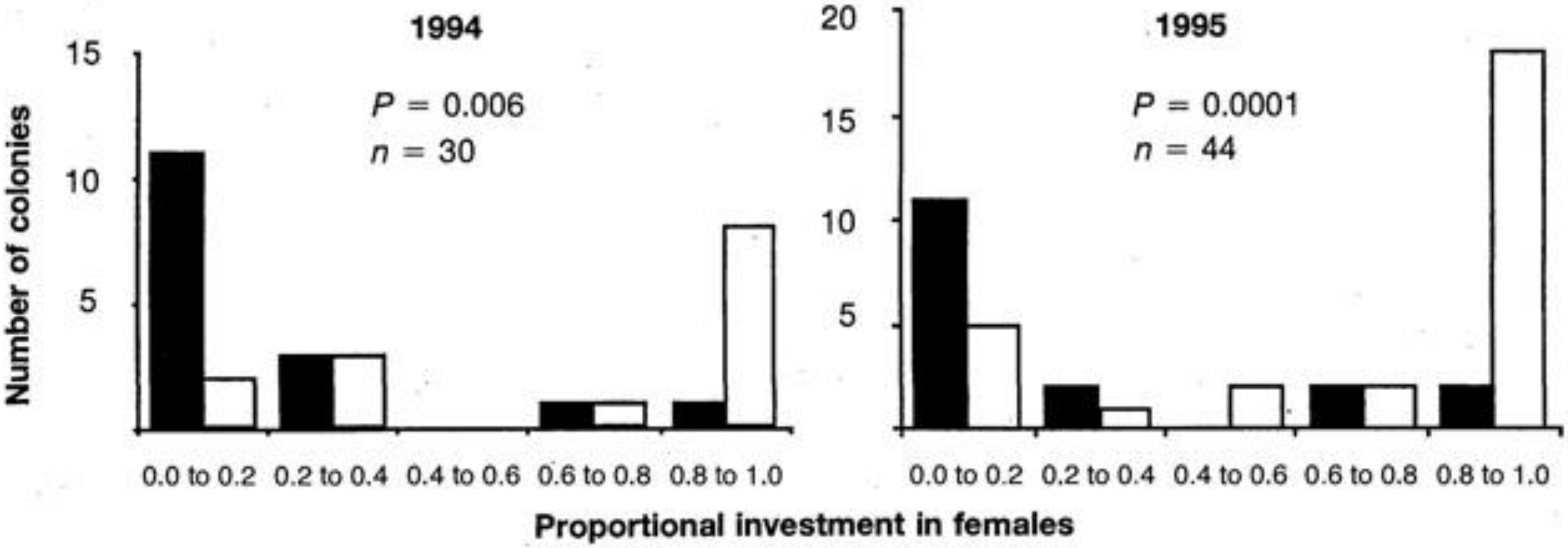
It is maintained by kin recognition and exclusion of non-relatives

Relatedness - sex ratios



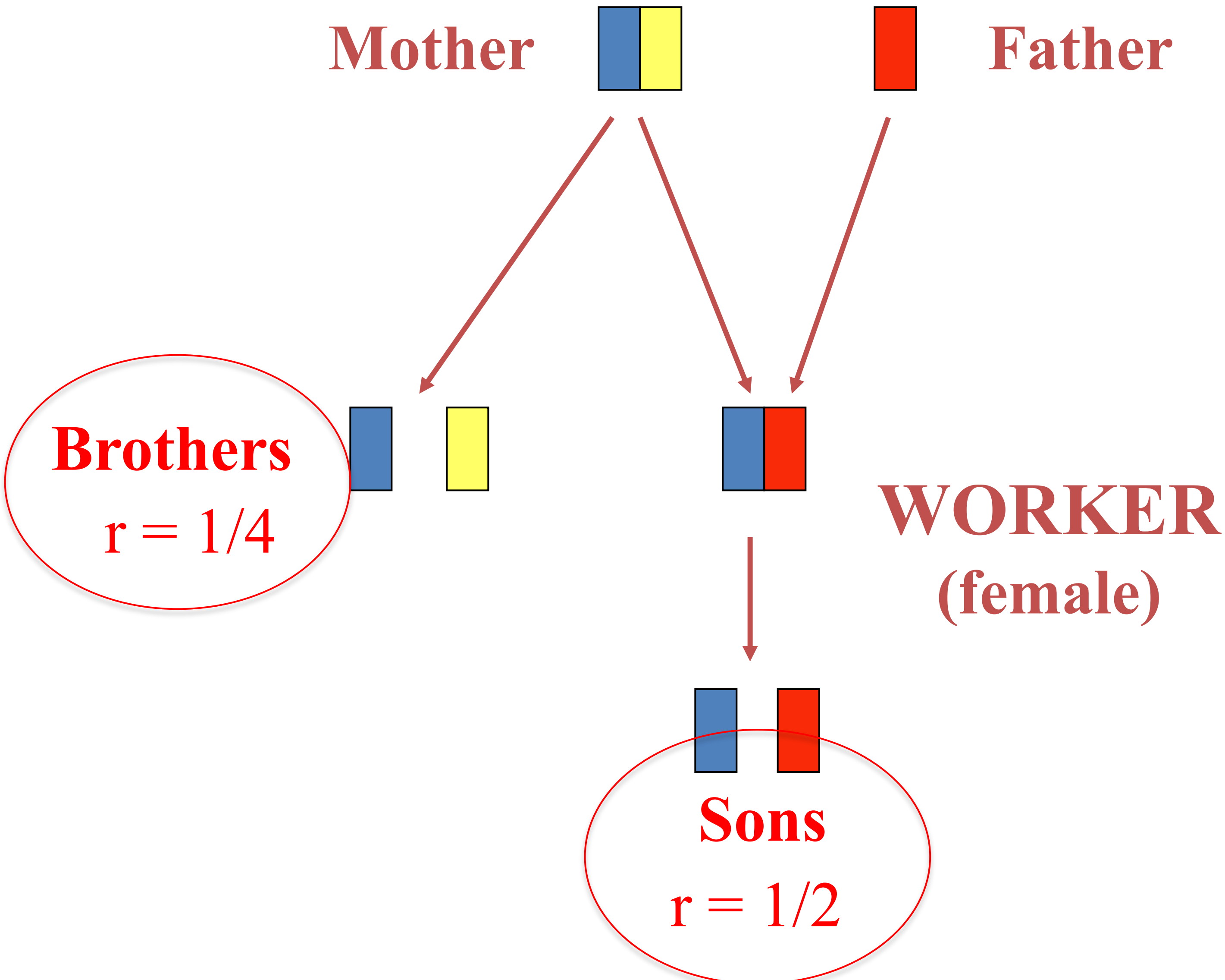
Prediction: workers of singly-mated queens favor 3:1 sex investment ratios

Split sex ratios - *Formica exsecta*
(Sundstrom et al. 1996)



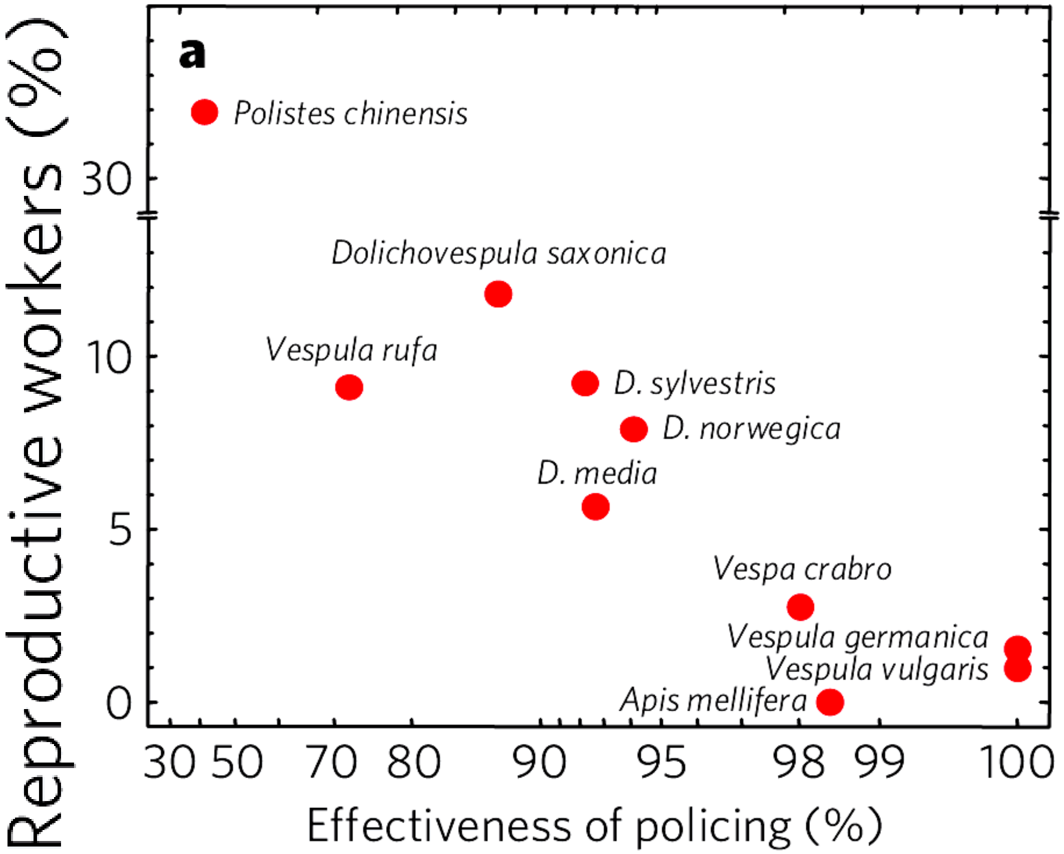
	single mating	multiple mating
Relatedness of workers to brood	$r_m = 1/4$	$r_m = 1/4$
	$r_f = 3/4$	$r_f = 1/4$

Relatedness matters?
Should workers produce the males?



Often workers do not reproduce – other workers eat worker-laid eggs (worker policing)

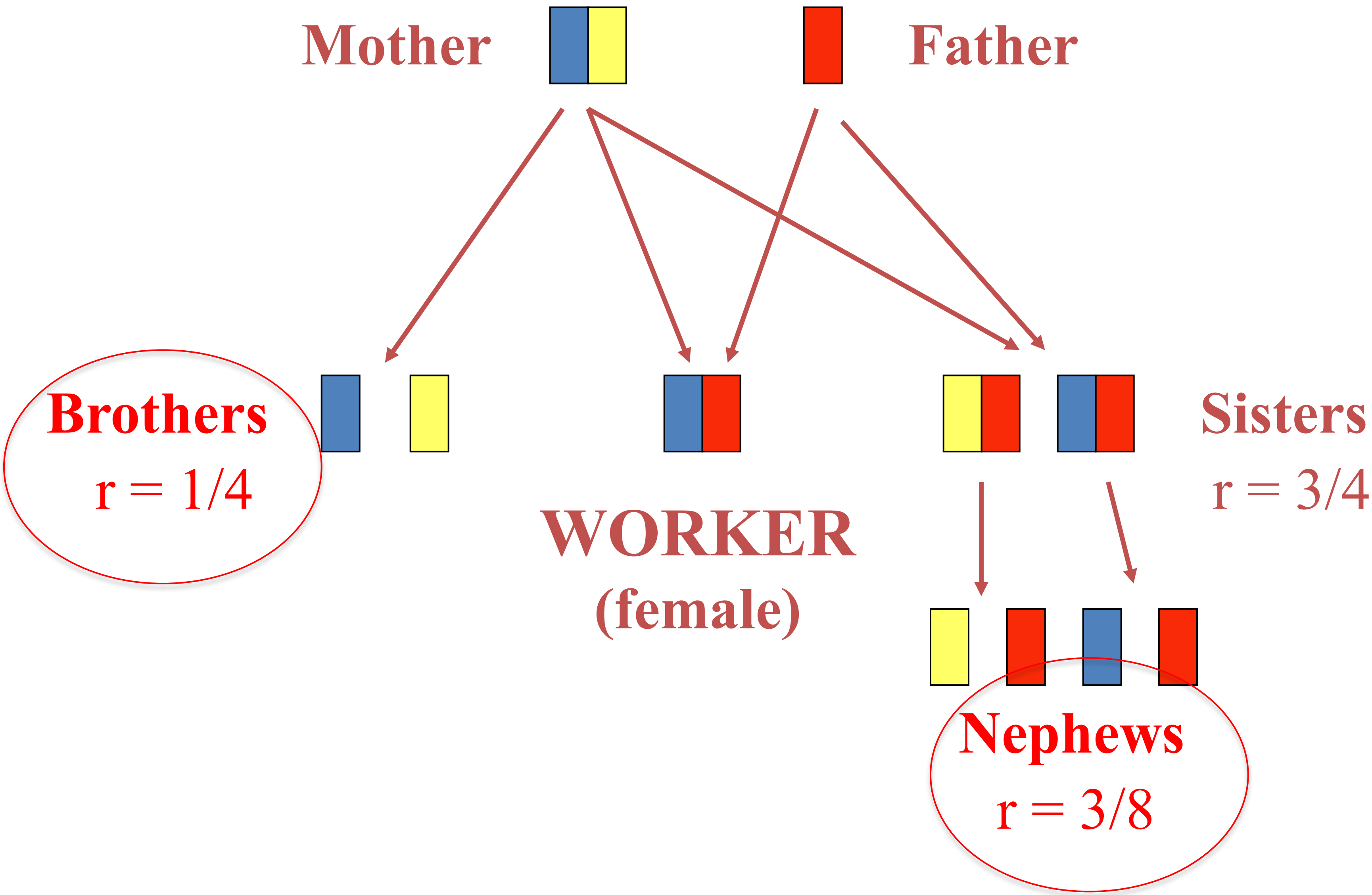
Effective policing reduces egg laying by workers – sensitivity to cost/benefit



Wenseleers and Ratnieks 2006

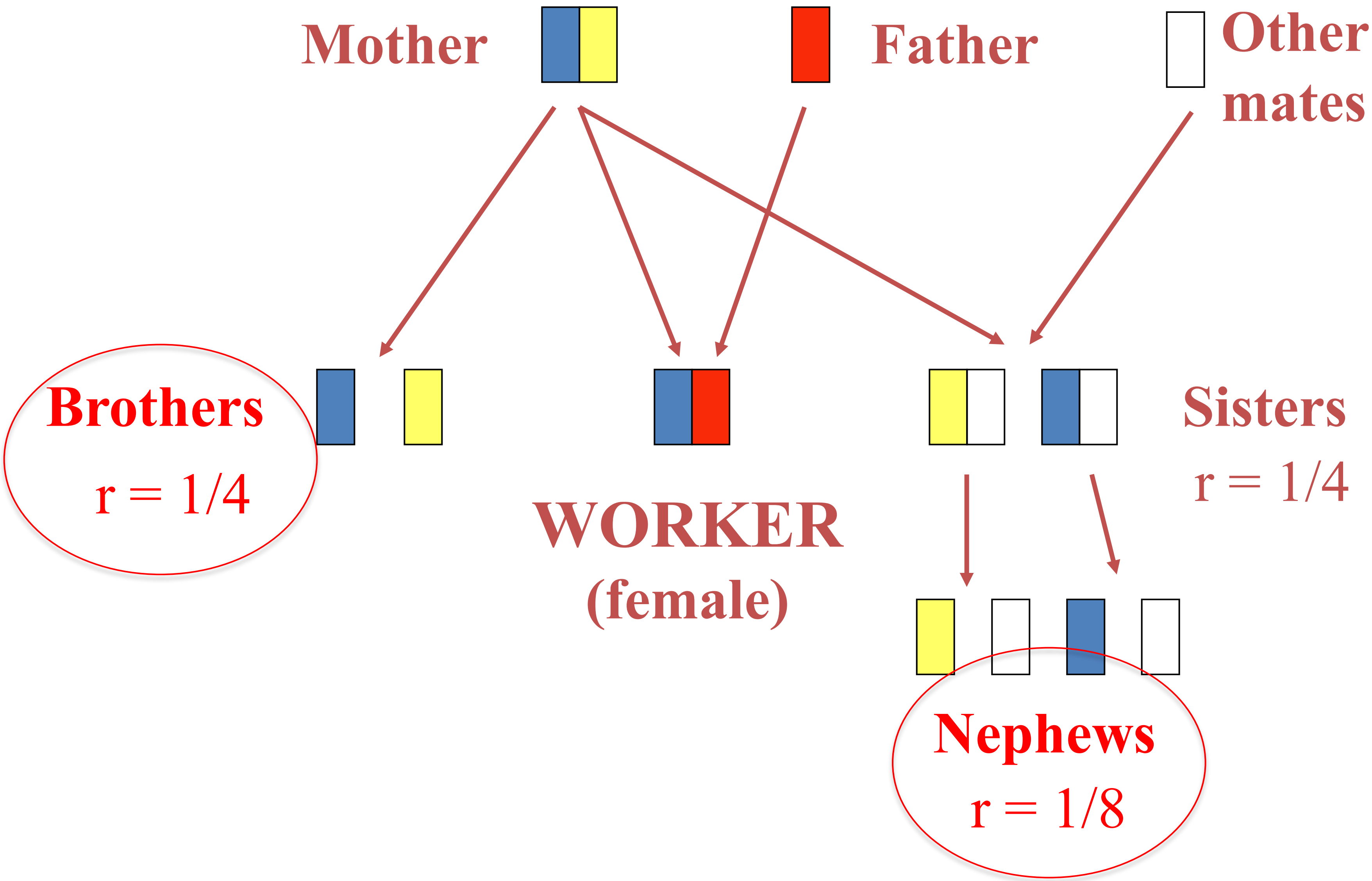
Single mating: workers prefer nephews

should not police

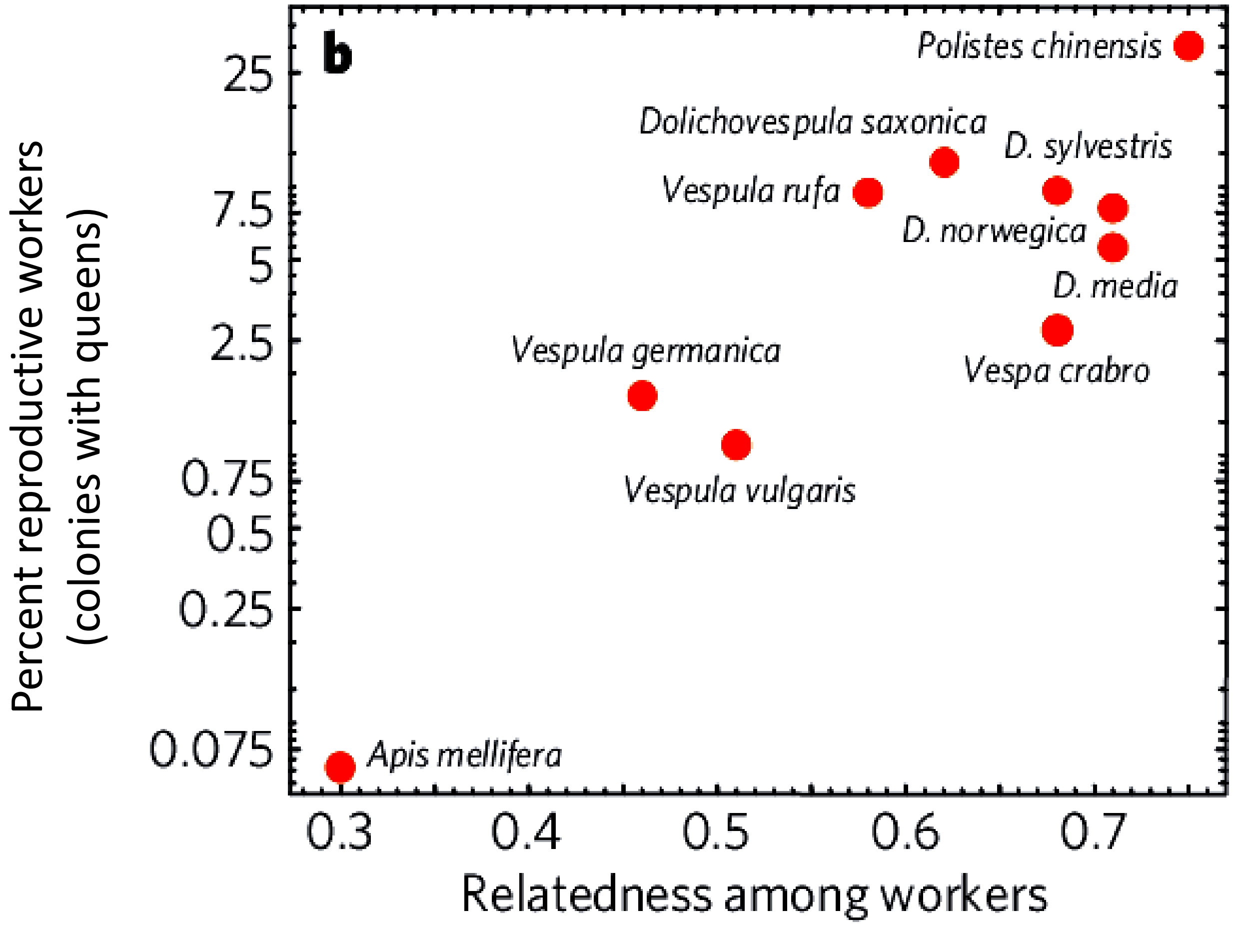


Multiple mating: workers prefer brothers

should police

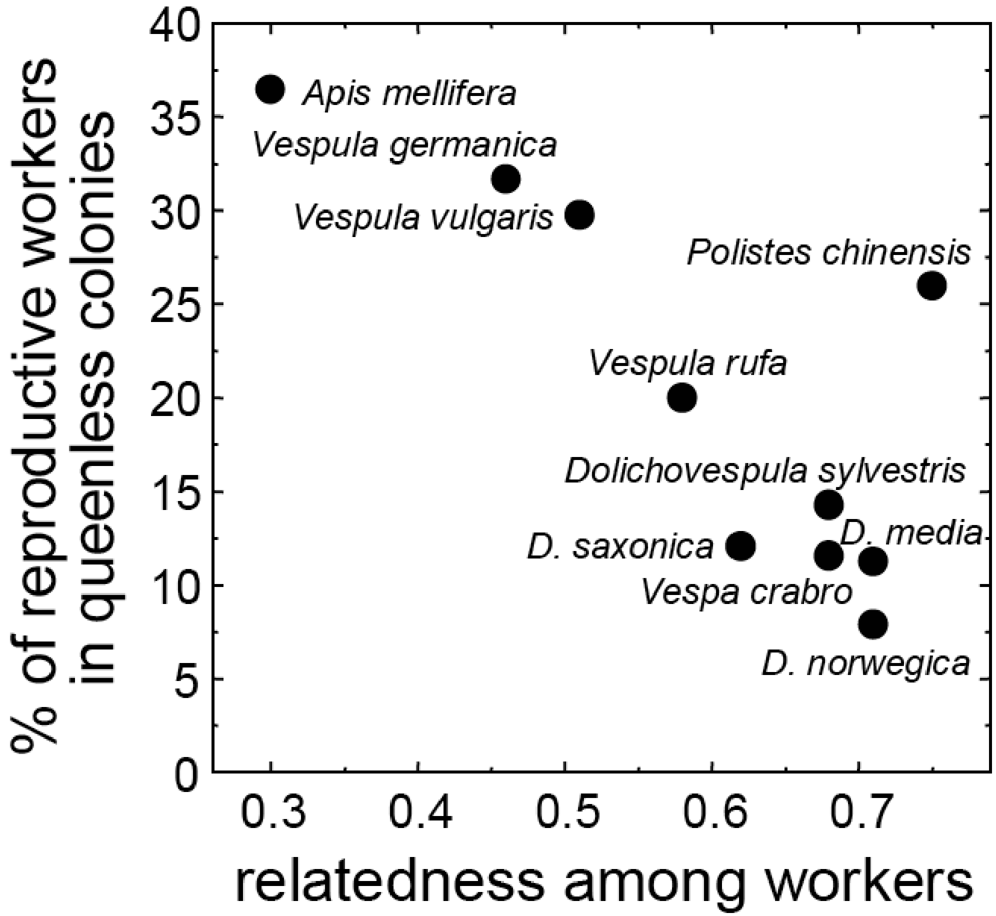


More reproductive workers allowed when workers are closely related colonies



Wenseleers and Ratnieks 2006

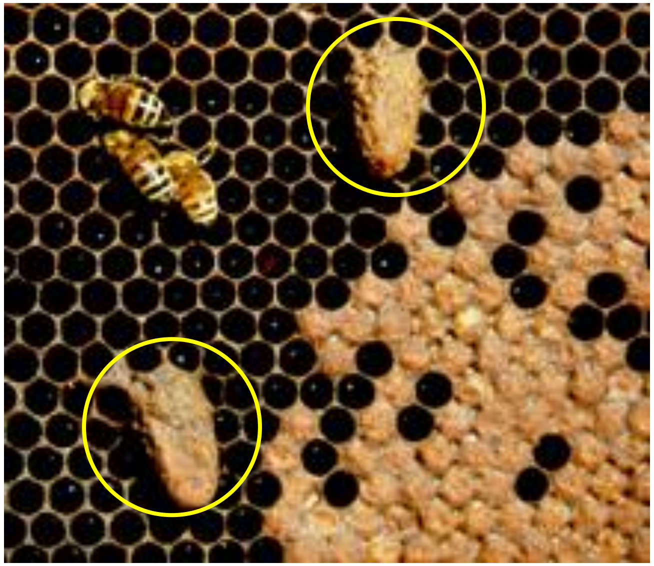
Experiment: same species, remove queens so no policing – fewer worker reproduce when more related



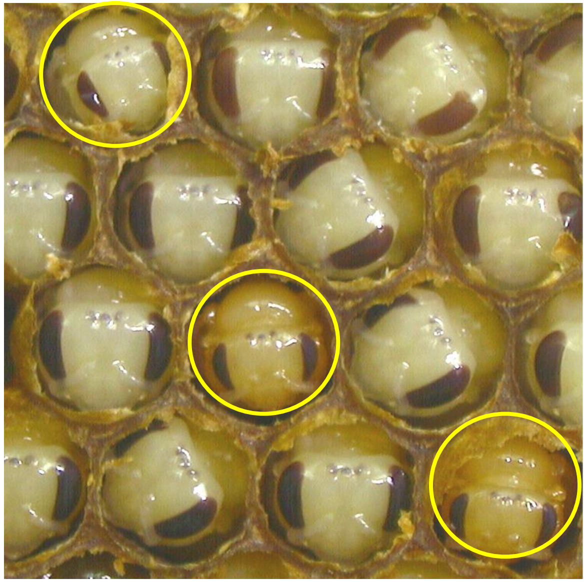
Wenseleers and Ratnieks 2006

Queen/worker caste determination

Honeybees "police" queenship by feeding differences



Melipona stingless bees feed larvae equally, so the larvae decide without constraint



In *Melipona beecheii* 15.8% of all females become queens

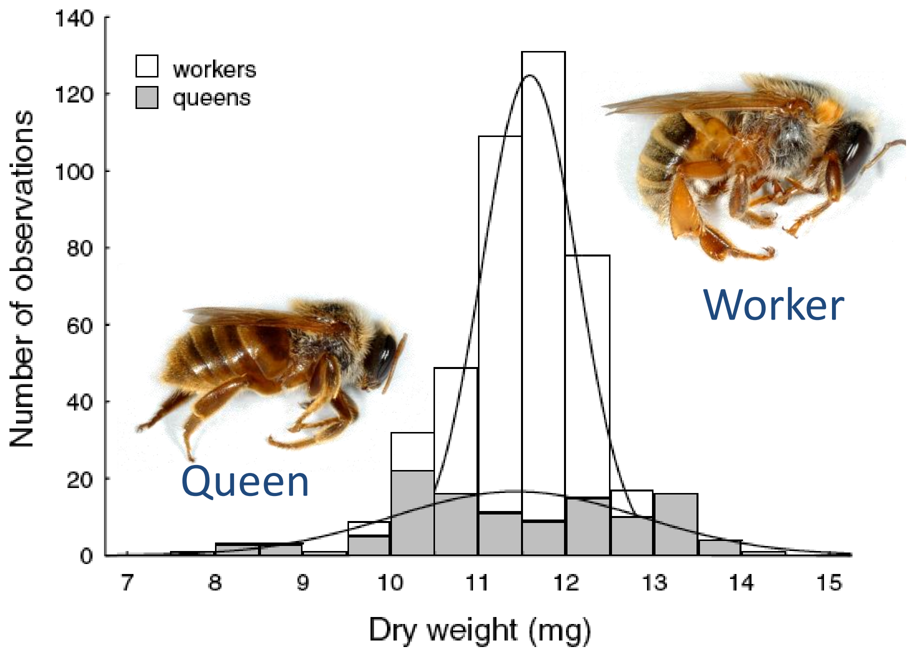
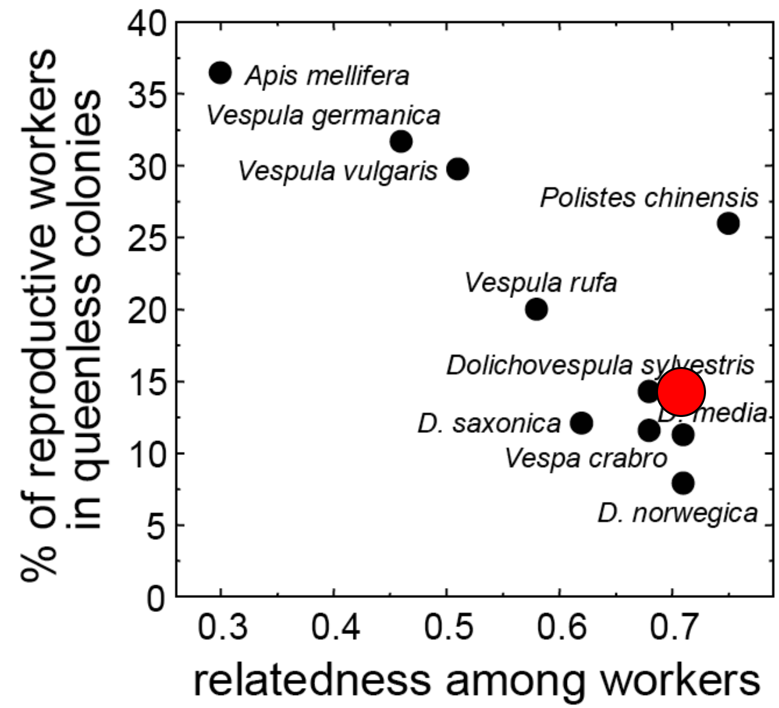


Fig. 1: Distribution of the dry weights of newly emerged queens and workers in *Melipona* (pooled data from three colonies)



Wenseleers et al. 2004

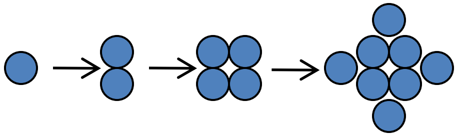
Nearly all of these queens are beheaded by workers within a day

Wenseleers et al. 2004

Multicellularity

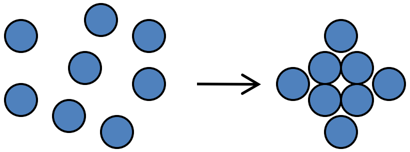
Single-cell bottleneck hypotheses: problems with chimeric development

Single-cell



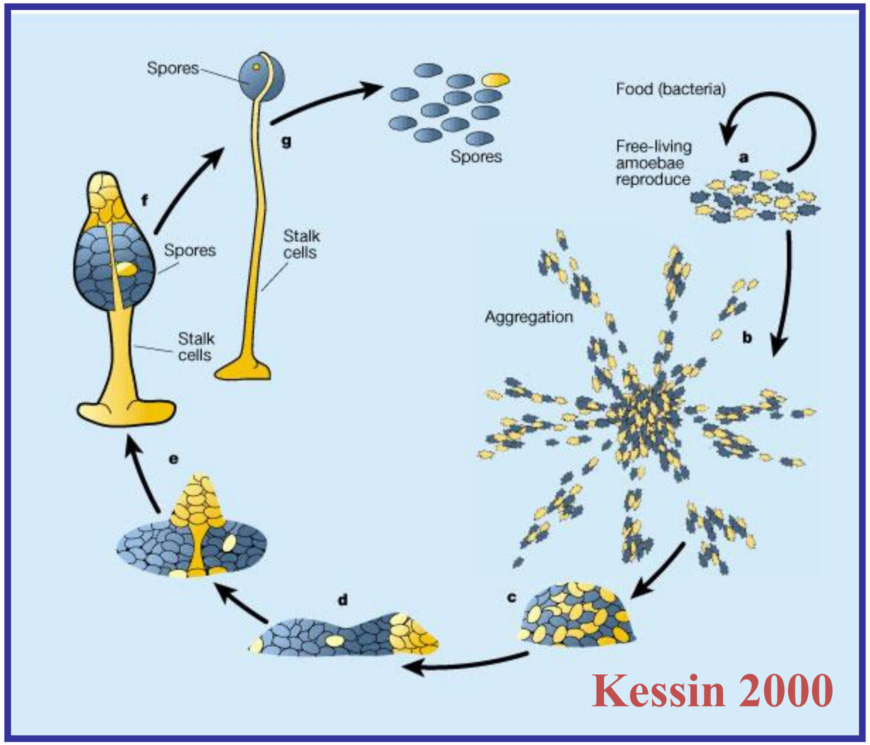
r = 1

Aggregative



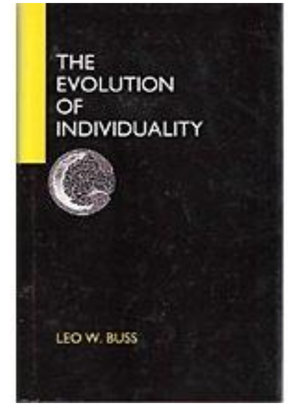
r = ?

Dictyostelium as a model system for development



Is conflict important?

Leo Buss

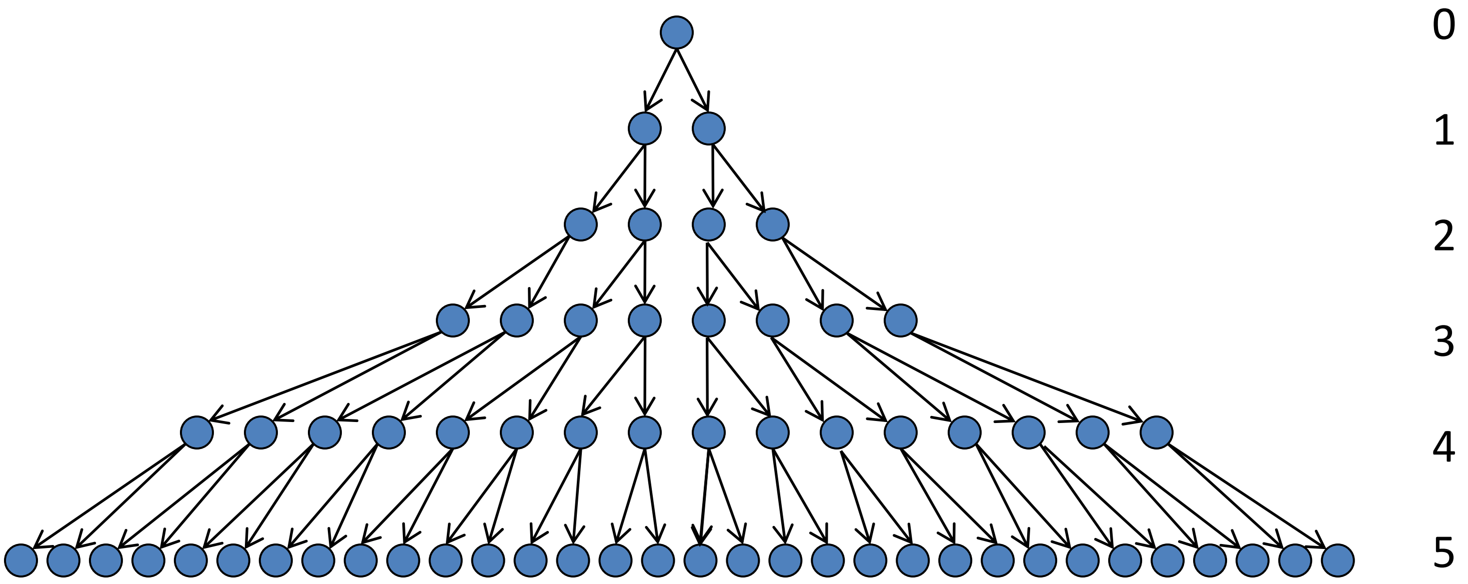


Competition among genetically different cell lineages within individuals has structured development:

- Policing of faster replication
- Morphogenetic movements to get into better position
- Forcing (induction) of other cells to adopt somatic function
- Evolution of controls e.g. germ line sequestration

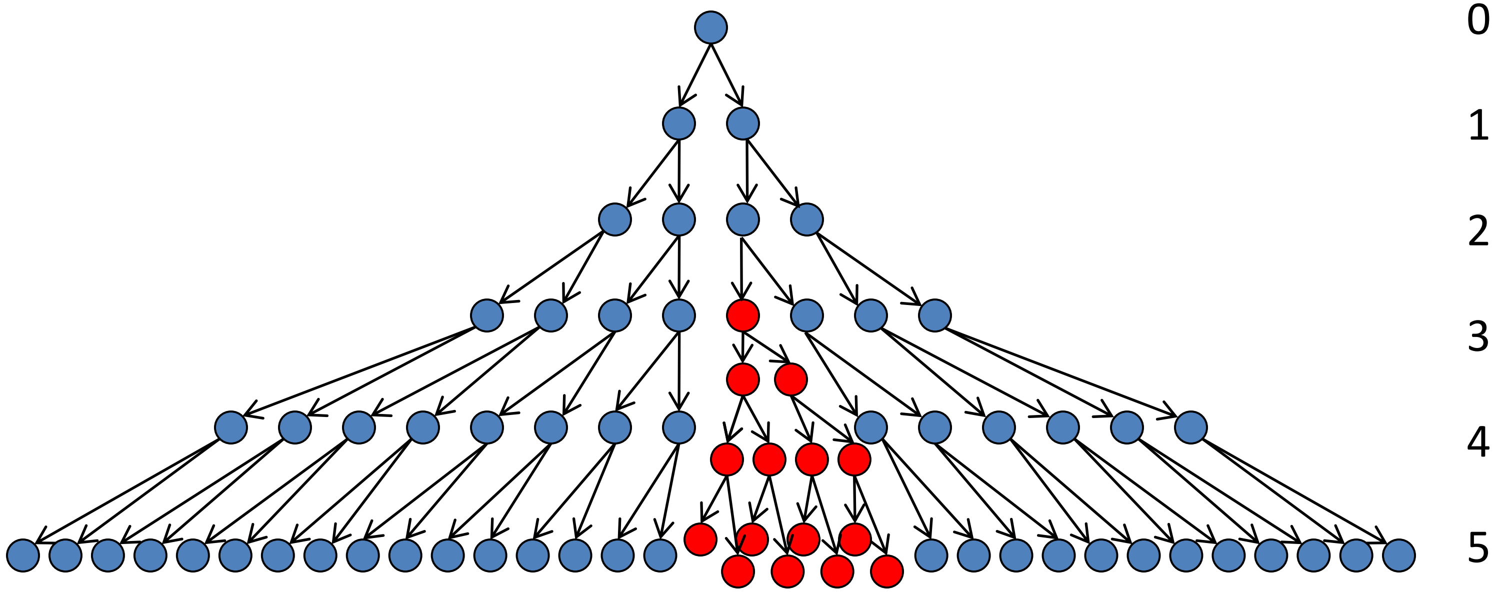
All of these are issues under aggregative development.
How about if there is a single-cell bottleneck?

Single-cell bottleneck



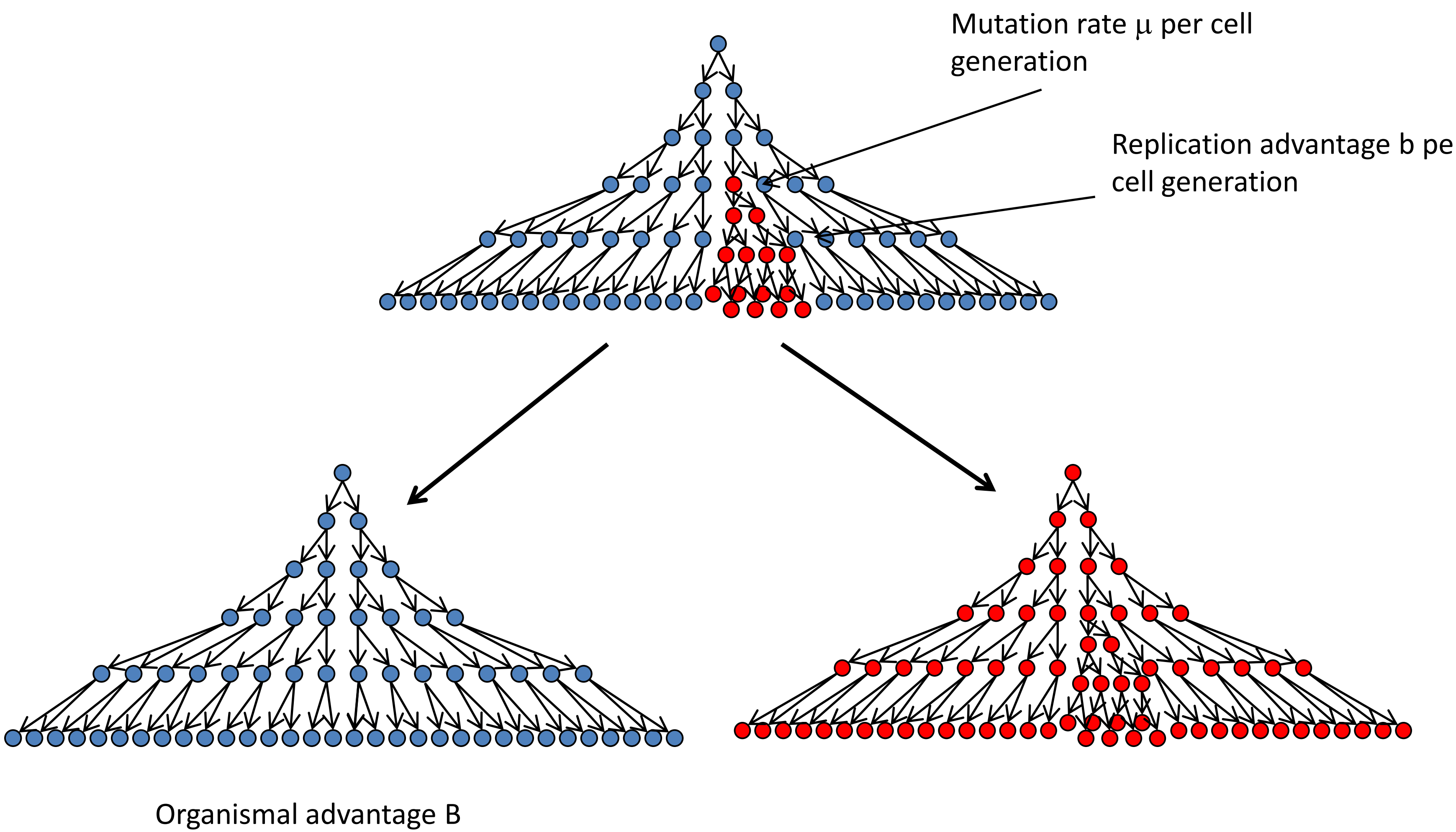
Relatedness = 1

Replication-rate cheater



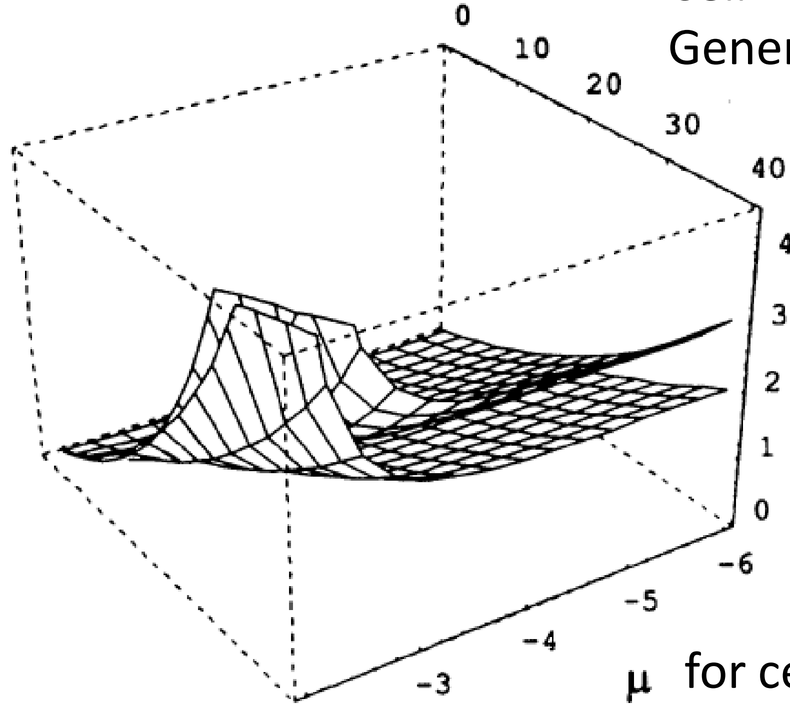
Relatedness ≠ 1

Replication-rate cheater



Selfish cell division mutants can be a problem

How large an organismal benefit is required to overcome a 5% selfish advantage per cell division?



Michod (1997) Amer. Nat. 149:607-645, Fig. 7

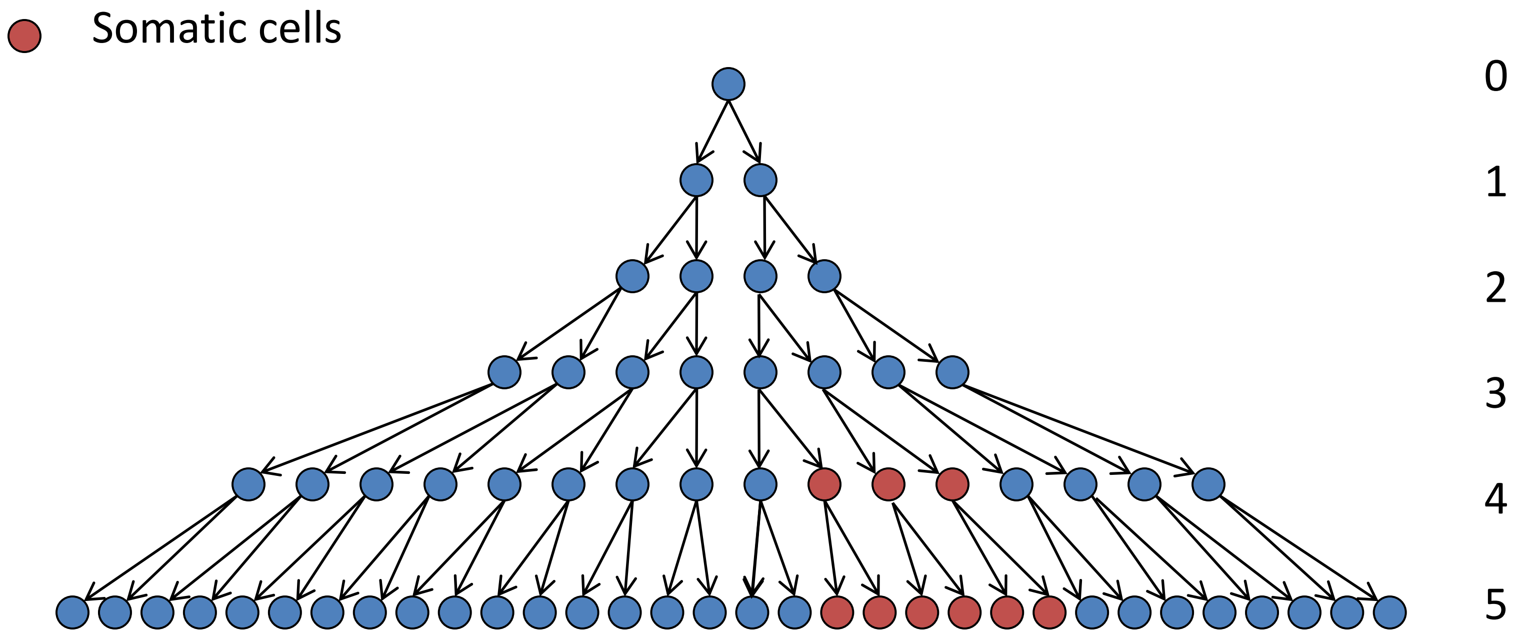
Single-time effects

e.g. Buss's mutants that move to germ line
or mutants that induce others to move out of germ line

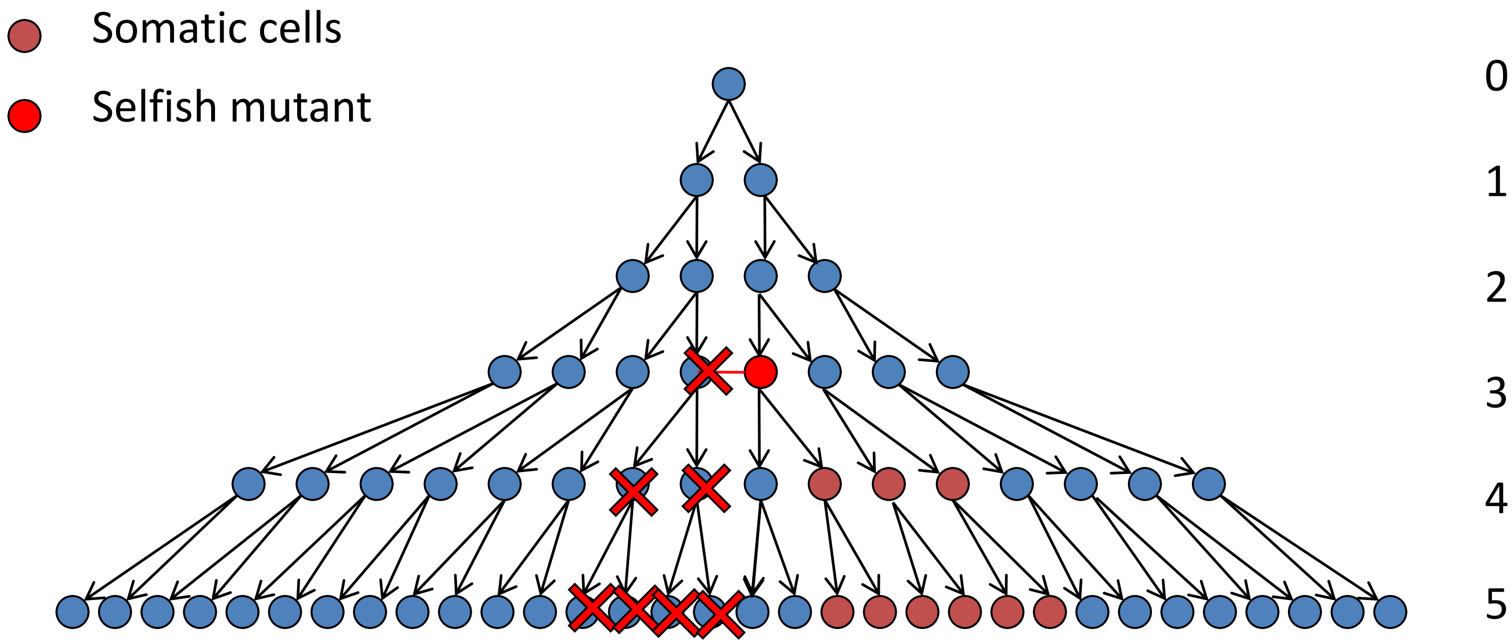
Harder to favor because:

1. Advantage is expressed once instead of accumulating every cell generation
2. Effective mutation rate lower because only some cells are in a position to express the behavior

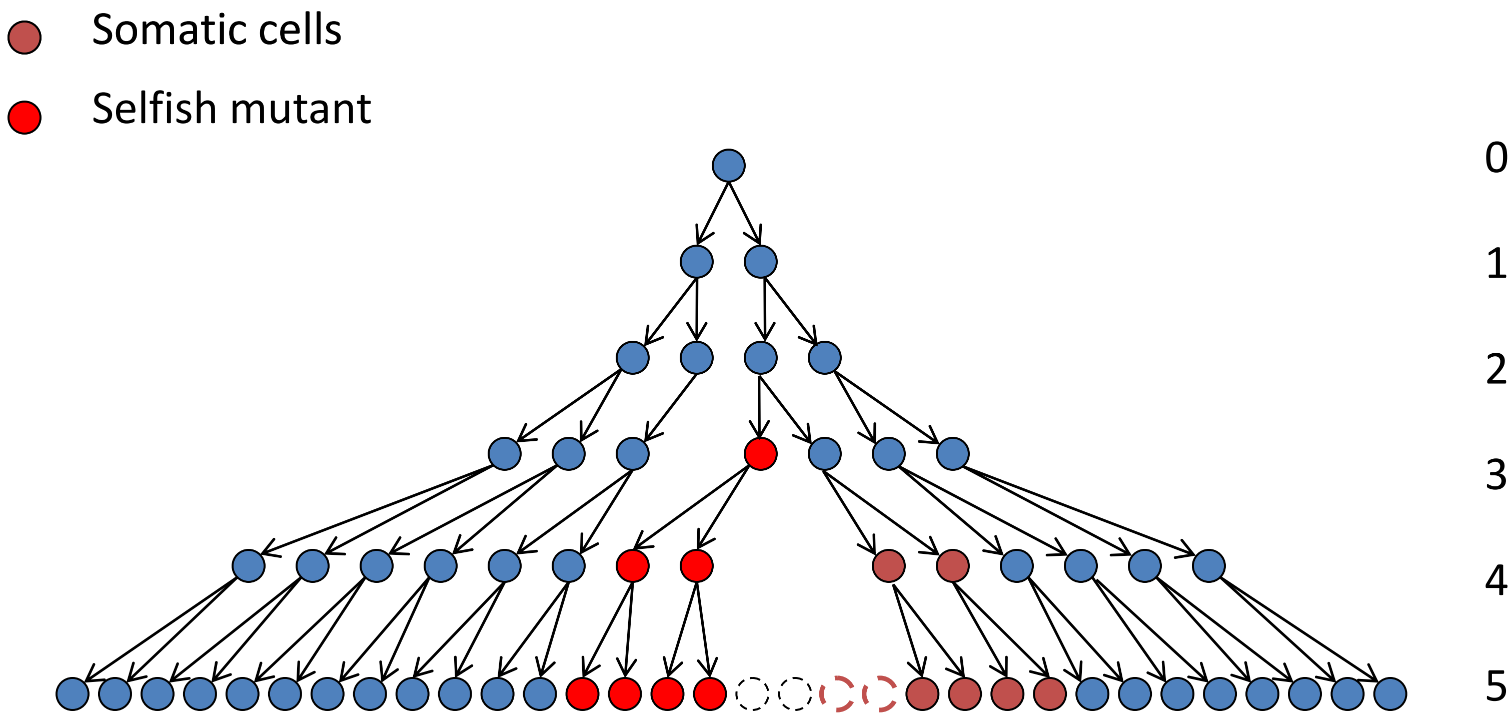
Single-time effects



Single-time effects



Single-time effects

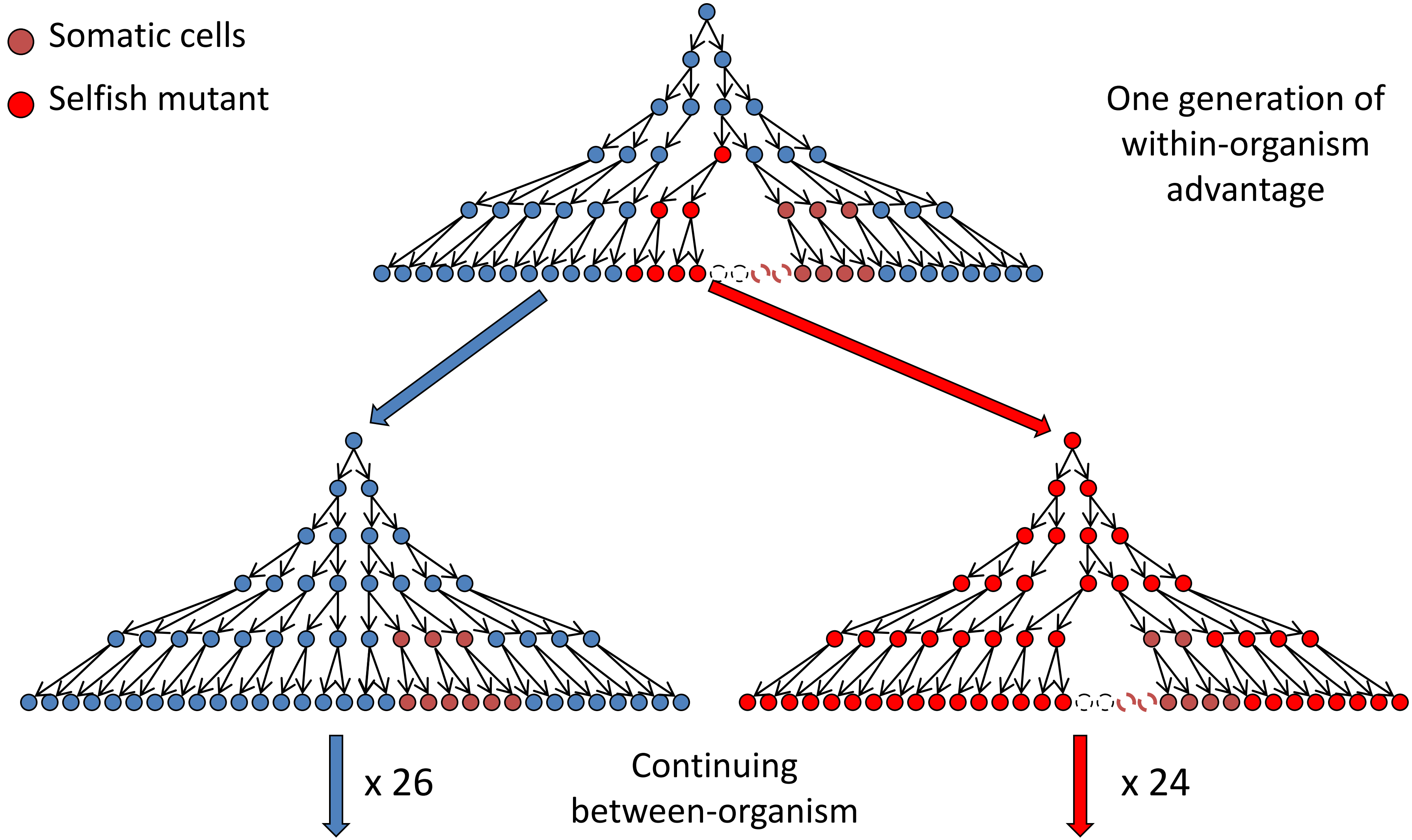


Mutant adds two reproductive descendants

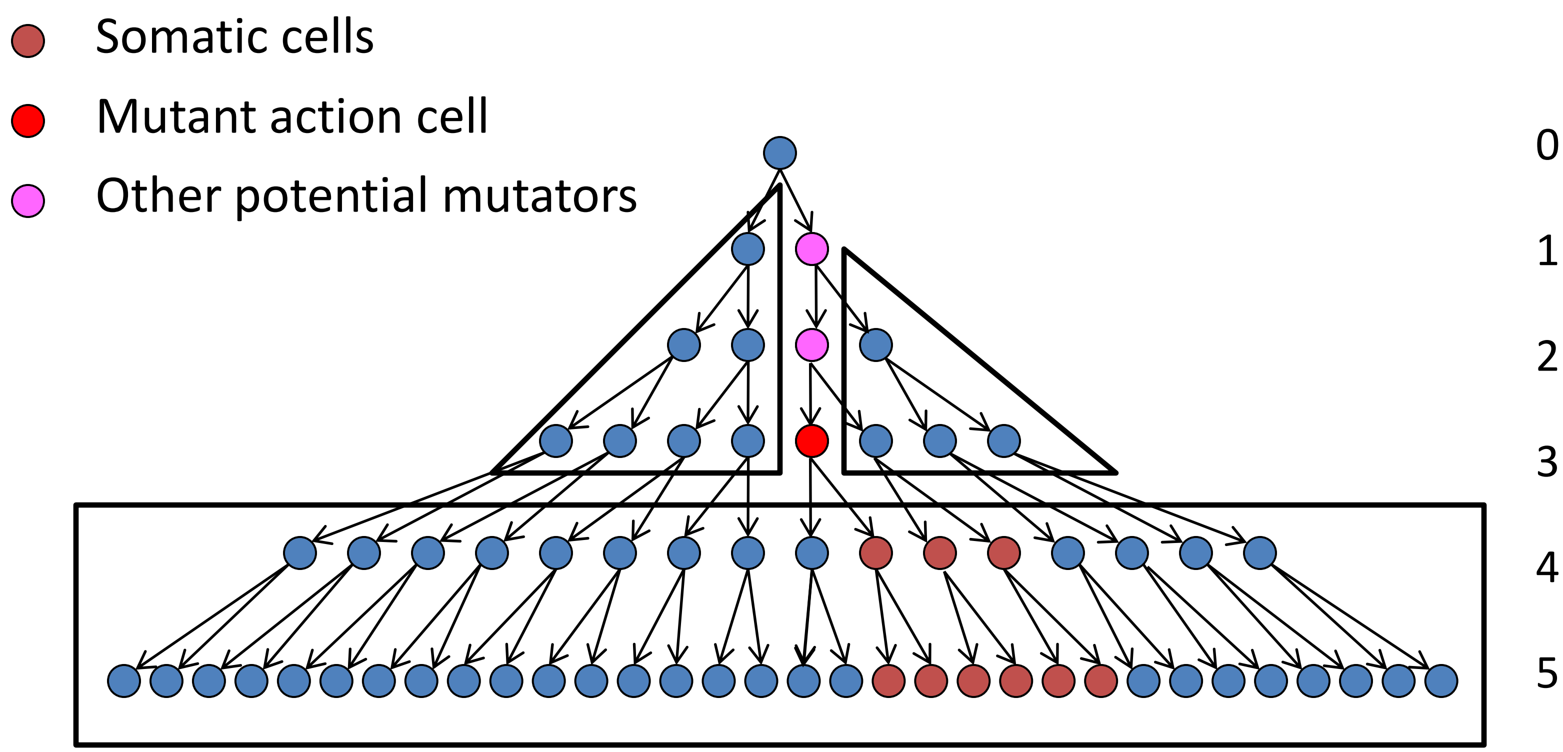
Cost to organism:

- Reduced somatic function
- Reduced reproductive cells

Single-time effects



Only some mutations can gain the even the one-time advantage



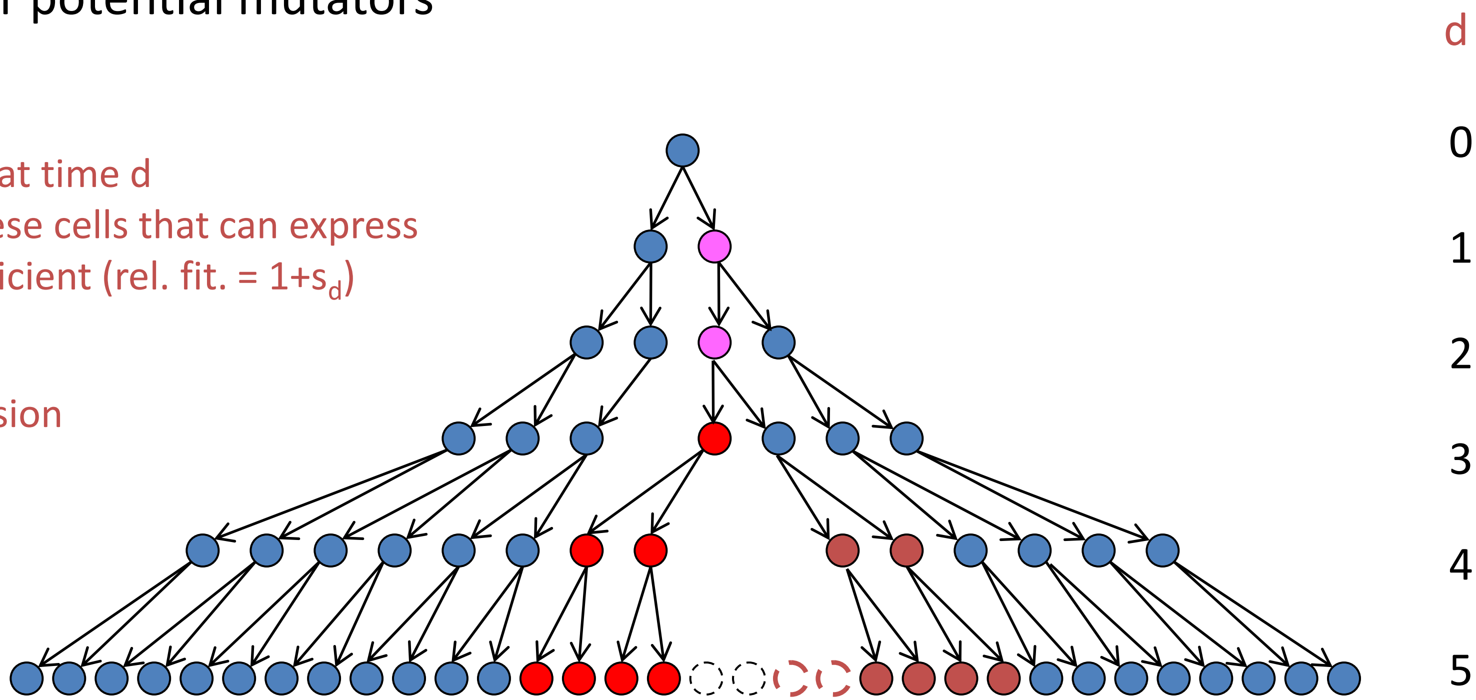
Model parameters

- Somatic cells
- Mutant action cell
- Other potential mutators

N_d = number cells at time d
e_d = fraction of these cells that can express
s_d= selection coefficient (rel. fit. = 1+s_d)

E = time of expression

D = total time of development



μ = mutation rate per division

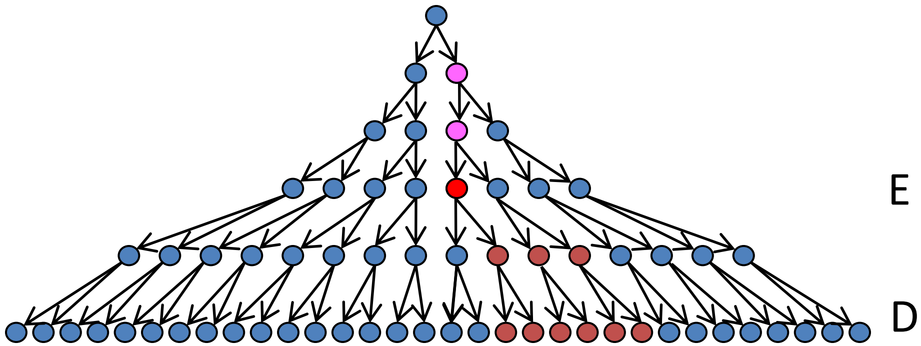
Within organism selection

$$\mu \sum_{d=1}^{D} \left(\frac{1 + e_d s_d}{1 + \cancel{\mu e_d s_d}} \right) + \mu \cancel{(D - E)}$$

Sum up to time of expression (mutation + selection)

Sum after time of expression (mutation pressure only)

$$\approx \mu E \left(1 + \overline{e_d s_d}\right)$$



Total selection

q = proportion non-cheaters

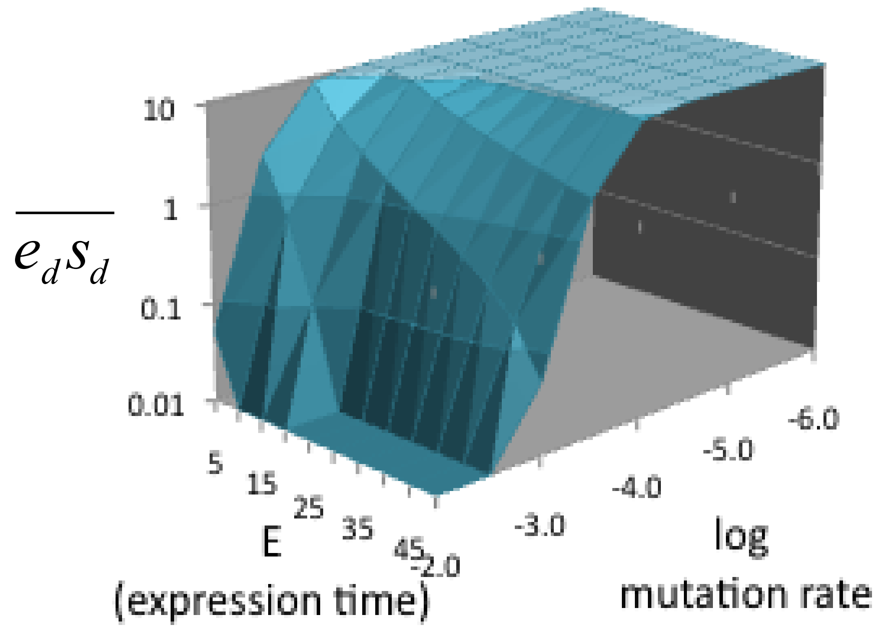
$$\Delta q < \frac{q(1-q)S}{1+qS} + (1-q)\mu E(1+\overline{e_d s_d})$$

Between-organism

Within-organism

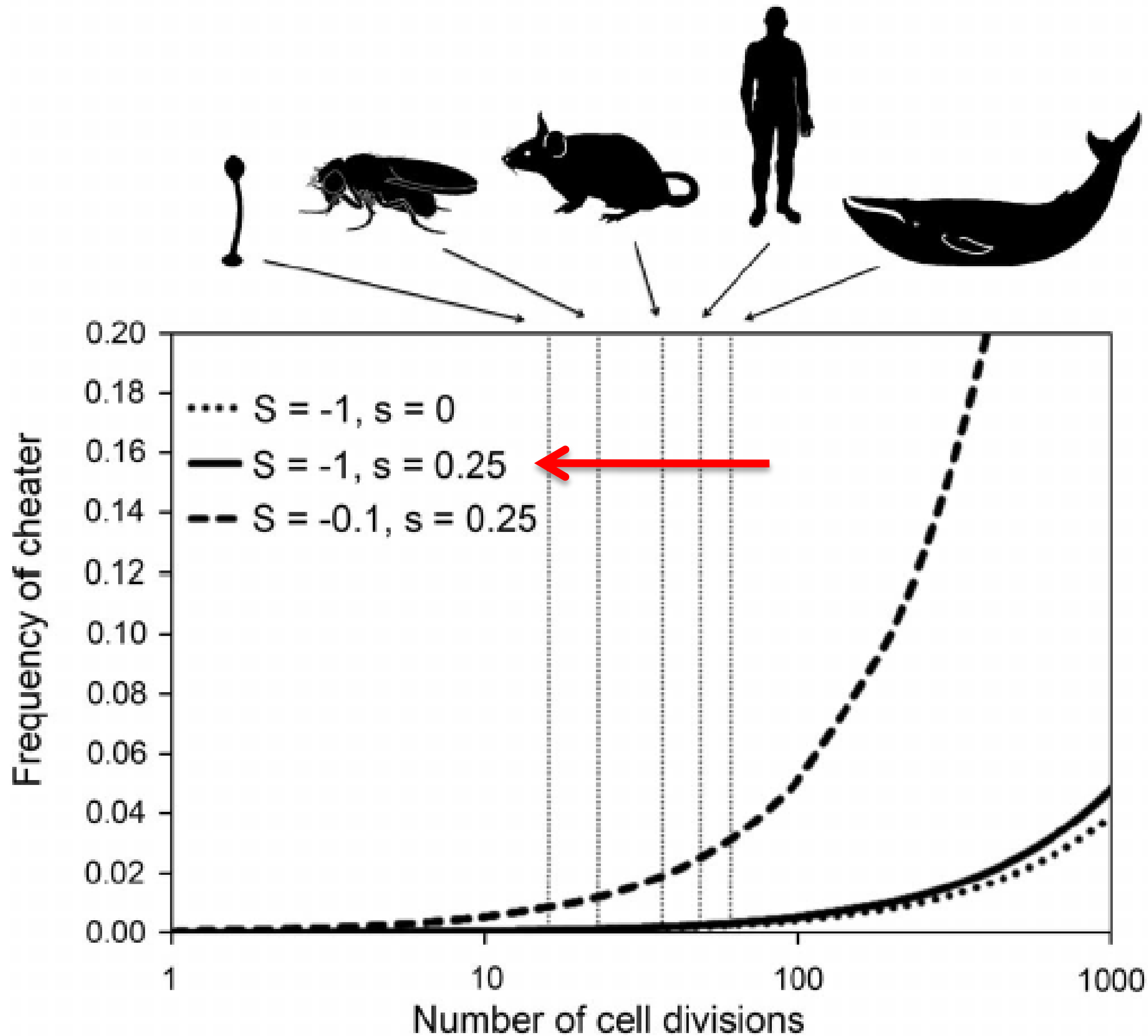
Single-time within-individual selection is very weak against between individual selection

How large an $e_d s_d$ is necessary to fix a selfish mutant imposing a cost of S = 0.05 on the organism?



Selfish mutants disfavored unless mutation rate is high and time of expression is late

Example: Suppose *Dictyostelium discoideum* is strictly clonal. How well could lethal cheaters spread for different numbers of cell divisions?



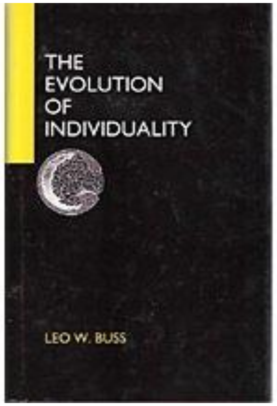
S = disadvantage of cheater when clonal

s = advantage of cheater in mixtures

$\mu < 4.1 \times 10^{-5}$

Is conflict important?

Leo Buss



All of these are these are issues under aggregative development. How about if there is a single-cell bottleneck?

Policing of faster replication Maybe

Morphogenetic movements to get into better position No

Forcing (induction) of other cells to adopt somatic function No

Evolution of controls e.g. germ line sequestration No, except to control replication mutants