

Darwin's Special Difficulty: Worker Insects

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Honey Bee: Queen & Workers



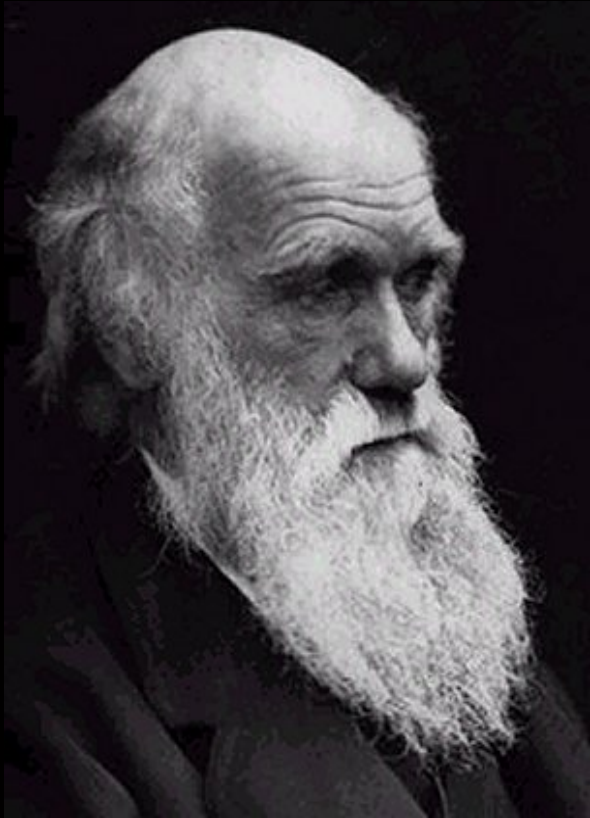
Darwin: 2009 Double Anniversary

200-Year Anniversary

1809 born

150-Year Anniversary

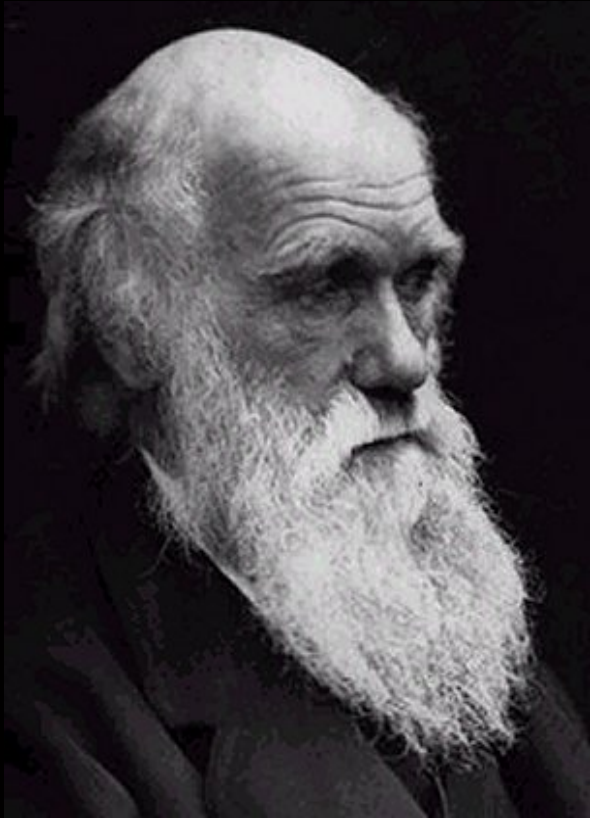
1859 Origin of Species published



Institute for Advanced Study, Berlin, 2004



Darwin 1859: Social Insects Frequently Mentioned



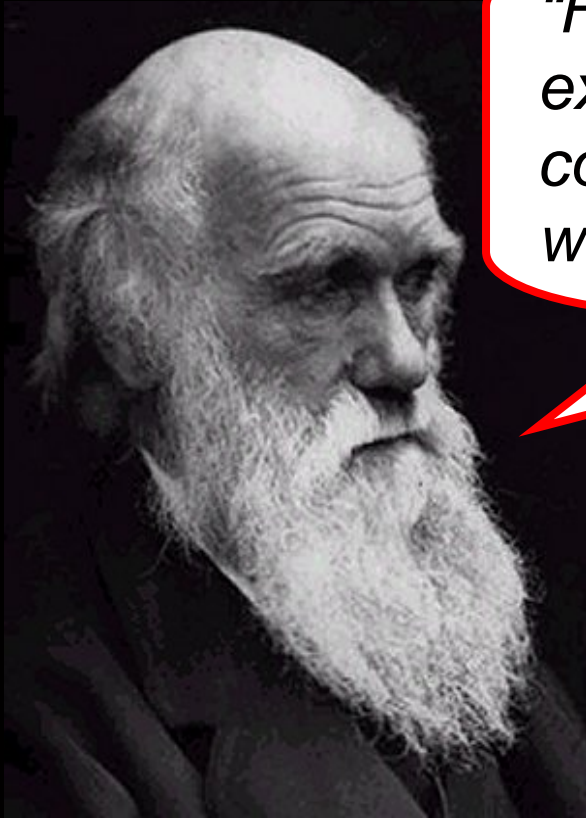
Charles Darwin
Origin of Species

*“We shall, perhaps, best understand how instincts in a state of nature have become modified by selection, by considering a few cases. I will select only three, ..., namely, the instinct which leads the cuckoo to lay her eggs in other birds' nests; **the slave-making instinct of certain ants; and the comb-making power of the hive-bee: these two latter instincts have generally, and most justly, been ranked by naturalists as the most wonderful of all known instincts.**”*

Chapter 6. Instinct

Don't Bee Dull

*“He must be a **dull man** who can examine the exquisite structure of a comb, so beautifully adapted to its end, without enthusiastic admiration.”*



Charles Darwin
Origin of Species



Natural Selection

Small inheritable changes

Profitable to bearer in the struggle for existence

Cause gradual change

Hardly Difficulties

Eye: Evolved Via Many Small Changes



*“To suppose that the eye, could have been formed by natural selection, seems, I freely confess, absurd.... Yet reason tells me, that if numerous gradations from a perfect and complex eye to one very imperfect and simple, each grade being useful to its possessor, can be shown to exist; if further, the eye does vary ever so slightly, and the variations be inherited, which is certainly the case;, then **the difficulty of believing that a perfect and complex eye could be formed by natural selection, though insuperable by our imagination, can hardly be considered real.**” Chapter 6*

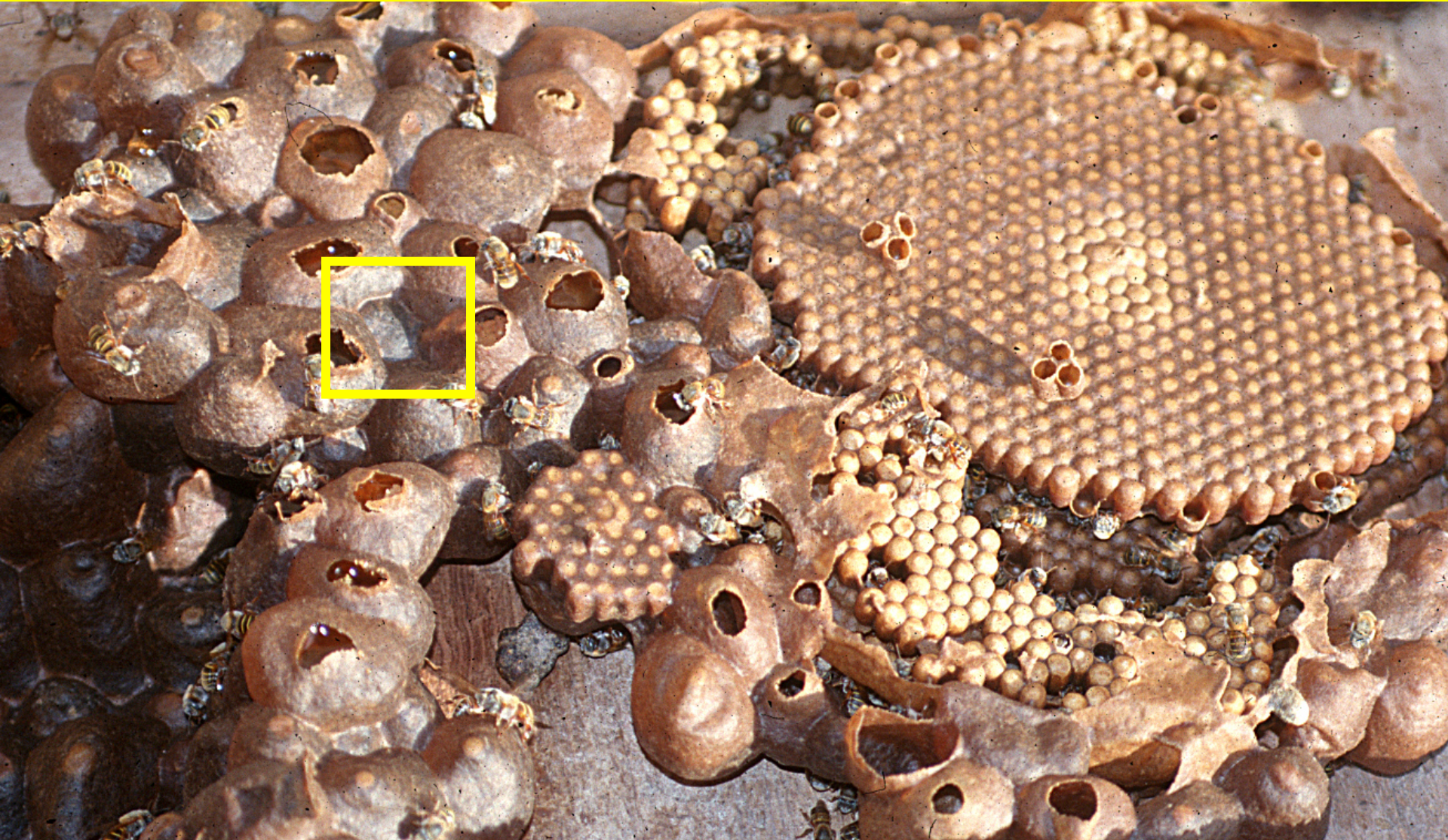
Cell Building in the Honey Bee



*“THE subject of instinct might have been worked into the previous chapters; but I have thought that it would be more convenient to treat the subject separately, especially as **so wonderful an instinct as that of the hive-bee making its cells will probably have occurred to many readers, as a difficulty sufficient to overthrow my whole theory.**”*

Chapter 7

Intermediate: Stingless Bee Honey Pots



Stingless bees have different types of cells for brood and food. The food, pollen or honey, is stored in egg-shaped pots. When clustered, these share walls and can take irregular polygonal shapes including hexagons.

The Special Difficulty

The SPECIAL Difficulty: Insect Workers



*“Iconfine myself to one **special difficulty**, which at first appeared to me insuperable, and actually fatal to my whole theory. I allude to the neuters or sterile females in insect-communities: for these neuters often differ widely in instinct and in structure from both the males and fertile females, and yet, from being sterile, they cannot propagate their kind.” Chapter 7, p. 236*

NOT The Evolution of Eusociality



“...How the workers have been rendered sterile is a difficulty; but not much greater than that of any other striking modification of structure; some insects and other articulate animals in a state of nature occasionally become sterile; and if such insects had been social, and it had been profitable to the community that a number should have been annually born capable of work, but incapable of procreation, I can see no very great difficulty in this being effected by natural selection. But I must pass over this preliminary difficulty.” Chapter 7 pp. 236-7

The GREAT Difficulty



“ The great difficulty lies in the working ants differing widely from both the males and the fertile females, If a working ant had been an animal in the ordinary state, I should have assumed that all its characters had been slowly acquired through natural selection; But we have an insect differing greatly from its parents, yet absolutely sterile; so that it could never have transmitted successively acquired modifications to its progeny. It may well be asked how is it possible to reconcile this case with the theory of natural selection”. Chapter 7 pp. 236-7

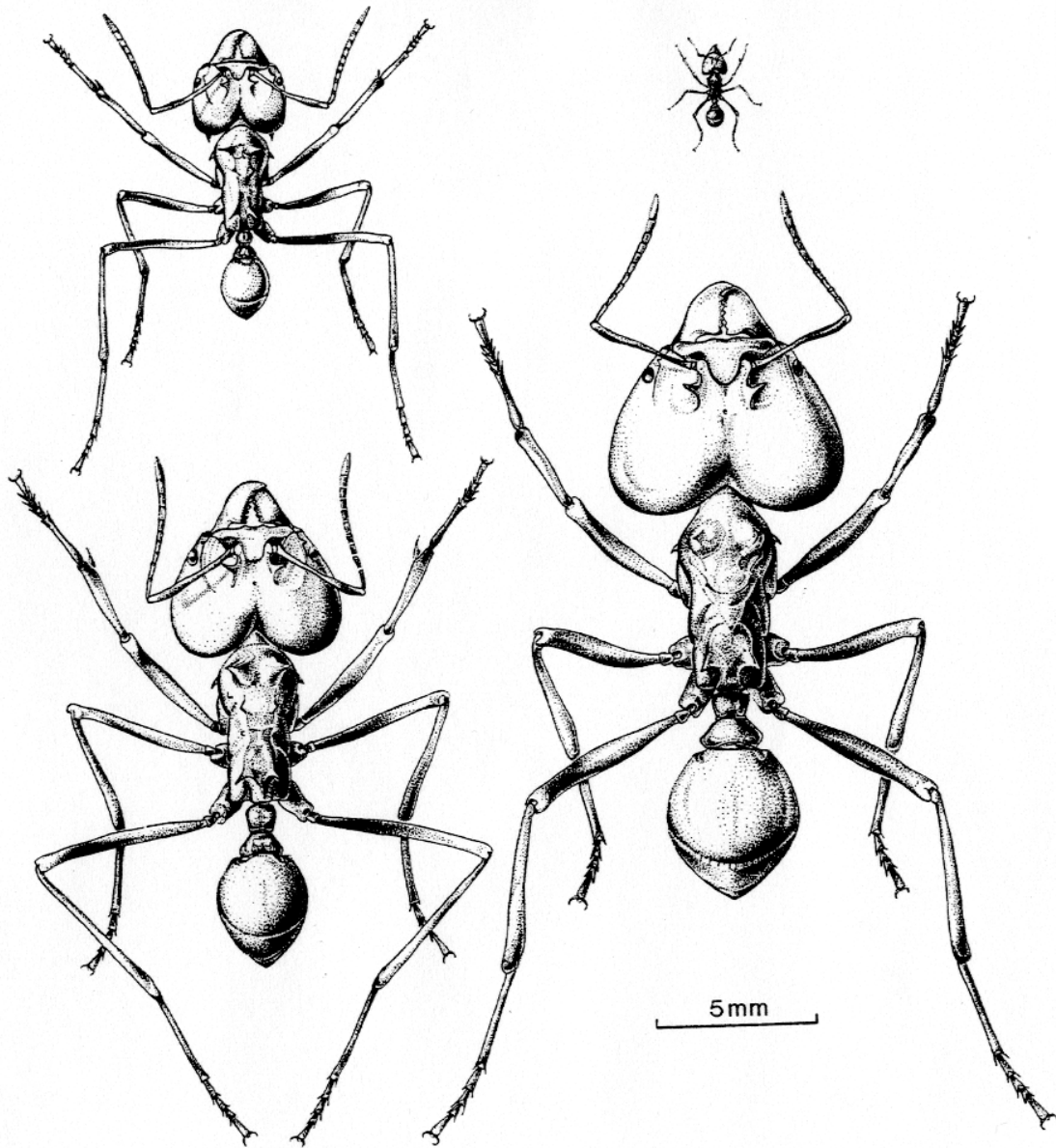
The CLIMAX of the Difficulty



*“...but we have not as yet touched on **the climax of the difficulty**; namely, the fact that the neuters of several ants differ, not only from the fertile females and males, but from each other, sometimes to an almost incredible degree, and are thus divided into two or even three castes. The castes, moreover, do not generally graduate into each other, but are perfectly well defined; being as distinct from each other, as are any two species of the same genus, or rather as any two genera of the same family....”*

Chapter 7 p 238

Workers of Different Sizes



Atta leafcutter
ant workers of
different sizes

A Big Worker



Workers Different to Queen



Atta cephalotes
leafcutter ant



Dorylus wilverthi
driver or army ant

Natural Selection Cannot Take a Leap



*“...natural selection can act only by taking advantage of slight successive variations; she **can never take a leap**, but must advance by the shortest and slowest steps.”*

Chapter 6.

“Natural selection can act only by the preservation and accumulation of infinitesimally small inherited modifications...”

Chapter 3

Problem Solved: Selection on Parents



*“...**natural selection, by acting on the fertile parents, could form a species which should regularly produce neuters**, either all of large size with one form of jaw, or all of small size with jaws having a widely different structure; or lastly, and this is our climax of difficulty, one set of workers of one size and structure, and simultaneously another set of workers of a different size and structure; a graduated series having been first formed, as in the case of the driver ant, and then the extreme forms, from being the most useful to the community, having been produced in greater and greater numbers through the natural selection of the parents which generated them; until none with an intermediate structure were produced....”*

Chapter 7 pp. 236-7

Problem Solved: Benefit to the Community



*“If we look at the sting of the bee,
.... **if on the whole the power of
stinging be useful to the
community, it will fulfil all the
requirements of natural selection,**
though it may cause the death of
some few members.”*

Chapter 7

At What Level Does Natural Selection Operate?

With no seeming difficulty, Darwin explains away the traits of individuals as being due to benefits at different levels or places, as convenient.

Individual

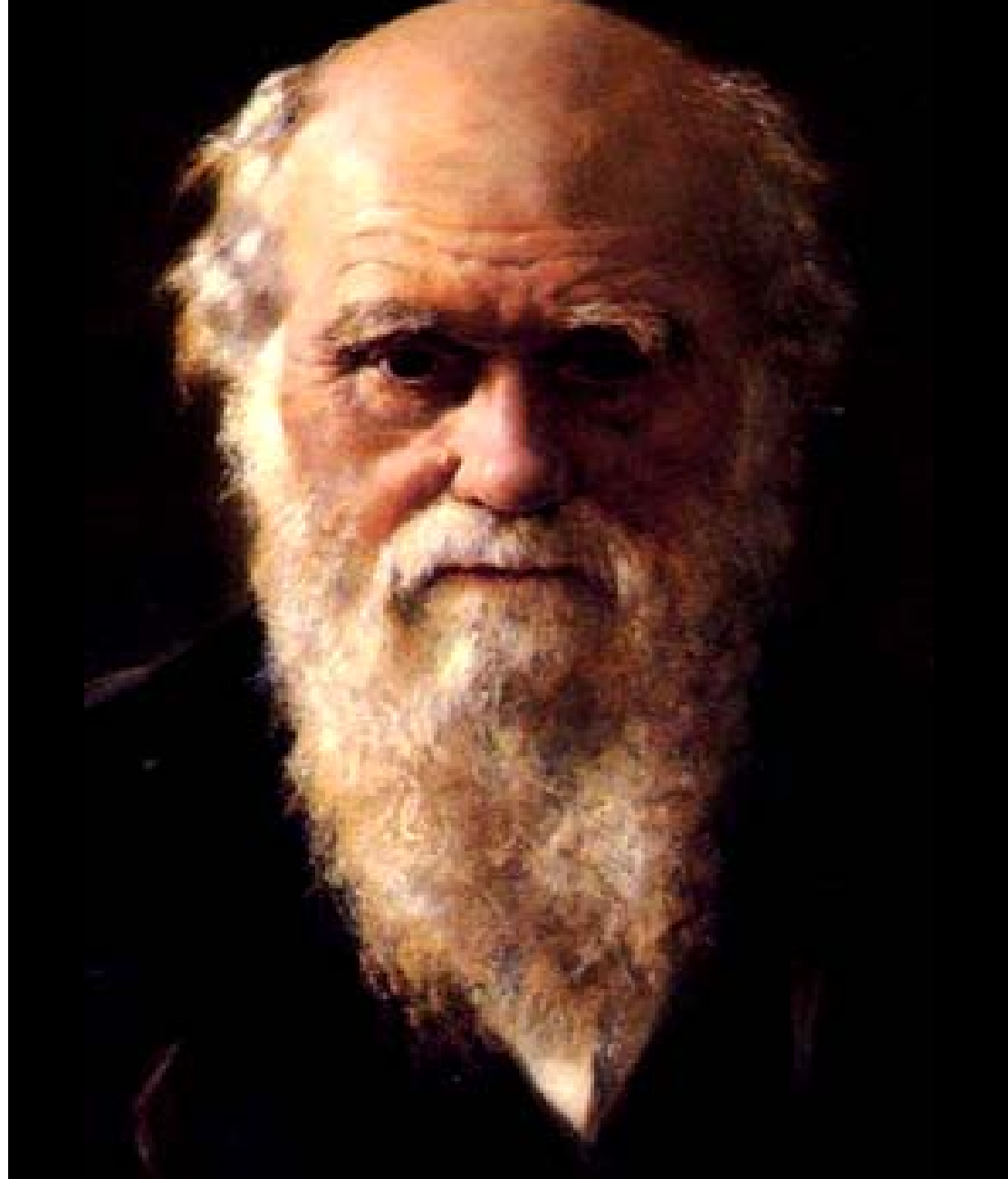
Community/Colony

Parents

Altruism: An Evolutionary Paradox?

Not to Darwin!

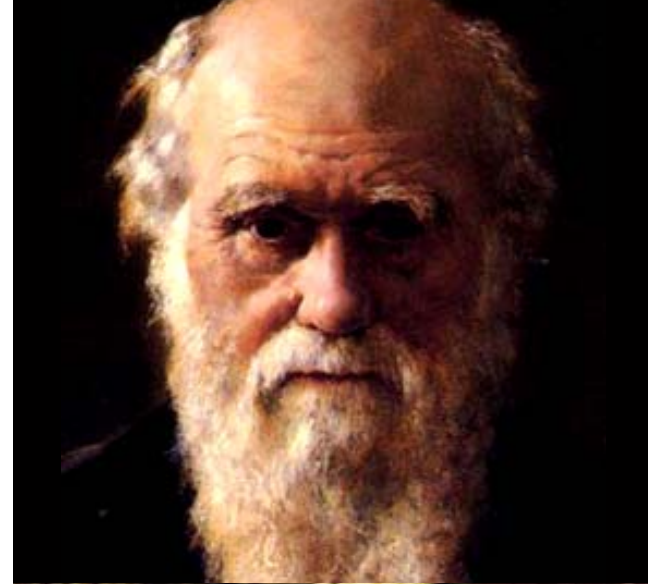
The evolution of
sterility is a minor
problem.



Evolutionary Paradox: Evolution of Altruism

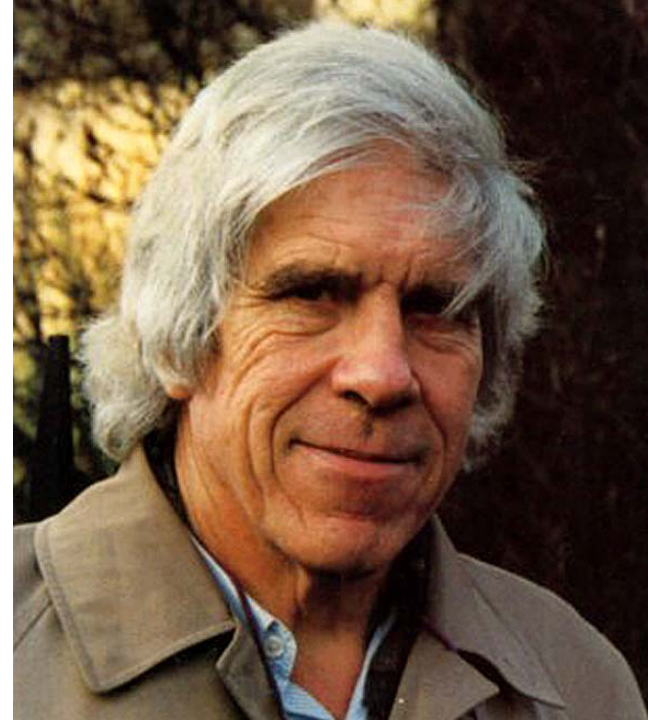
Charles Darwin (1859)

Sought to explain how natural selection could cause adaptations in insect workers. Did not seek to explain altruism (i.e., origin of workers)



William Hamilton (1964)

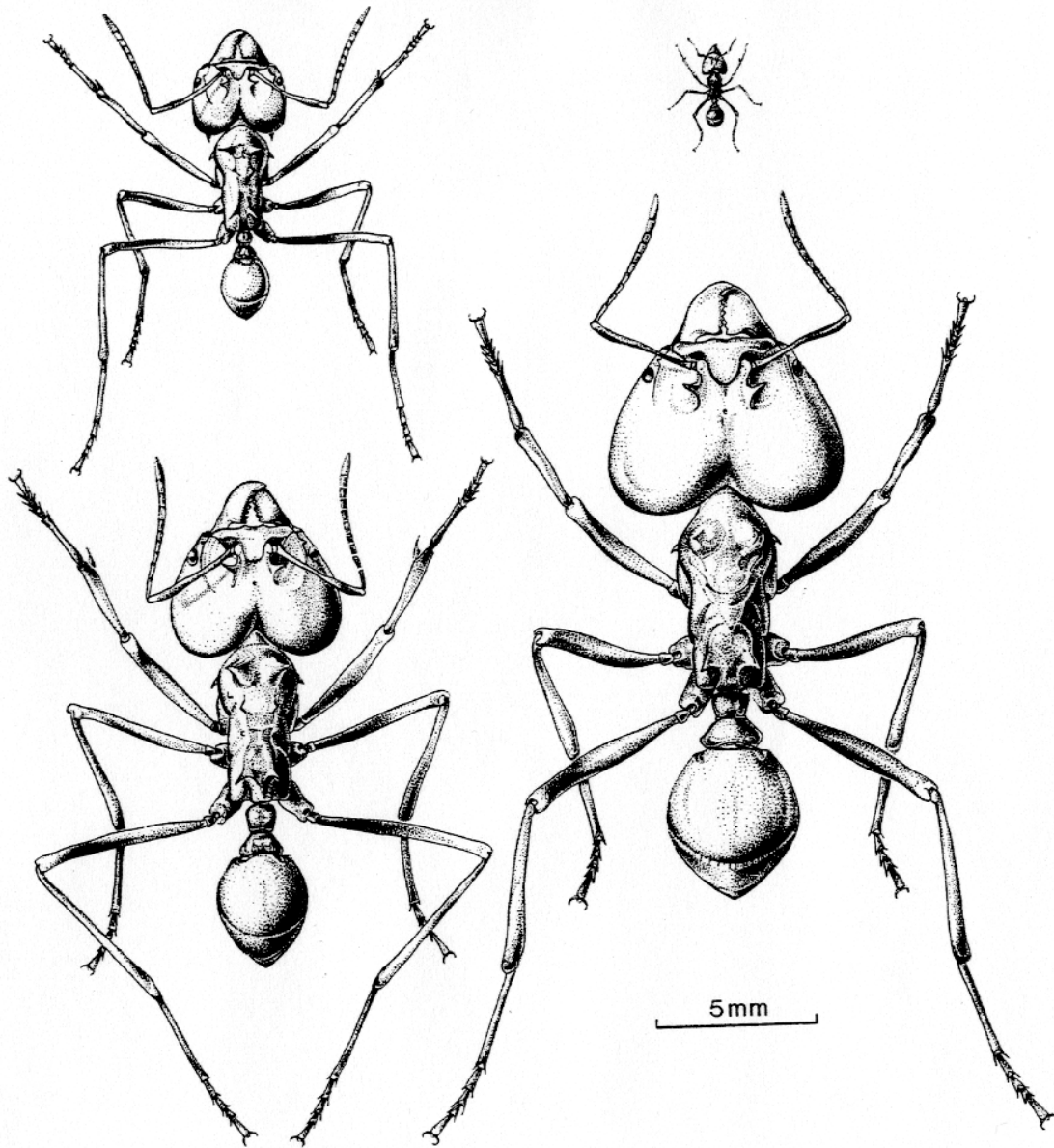
Sought to explain how natural selection could cause working itself (altruism).



Today: Benefit to the
Community & Parents

Increasing IF by Working
for the Benefit to the Colony

Value of Workers of Different Sizes



Atta leafcutter
ant workers of
different sizes

Medium Sized Workers



Large Workers

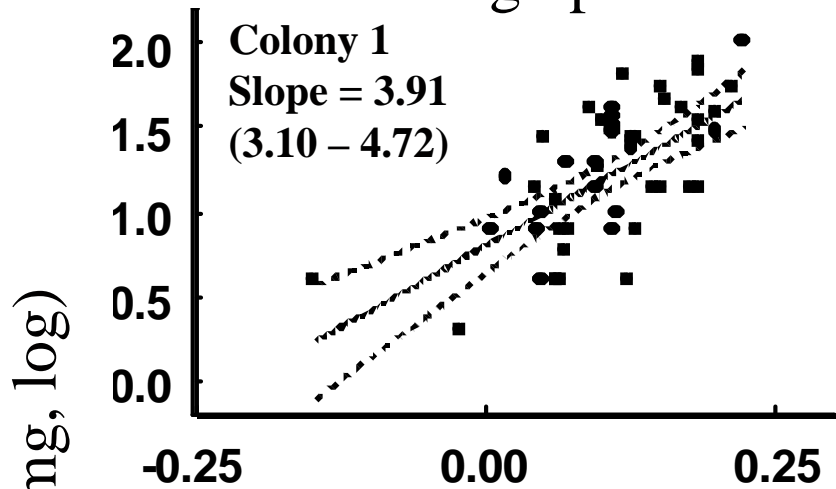


Large Workers

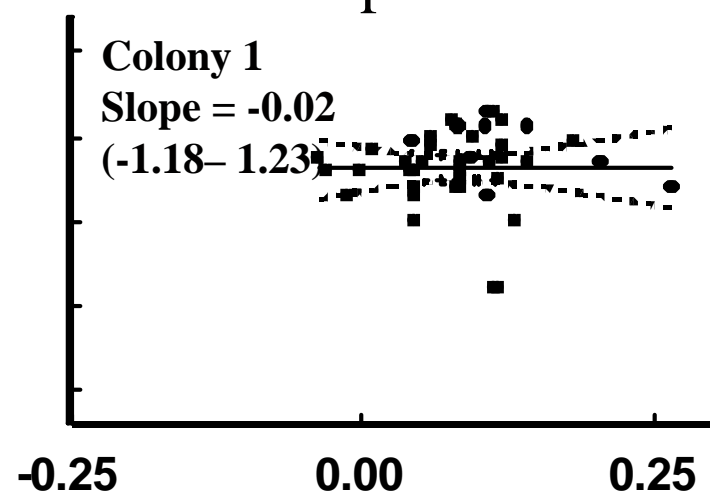


Geometry Hypothesis: Head Size & Food Cutting in Atta

Mango pieces

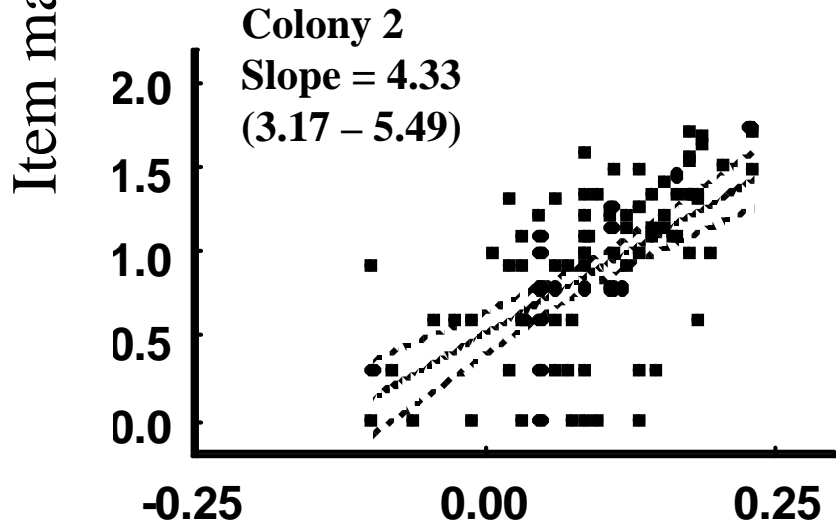


Leaf pieces



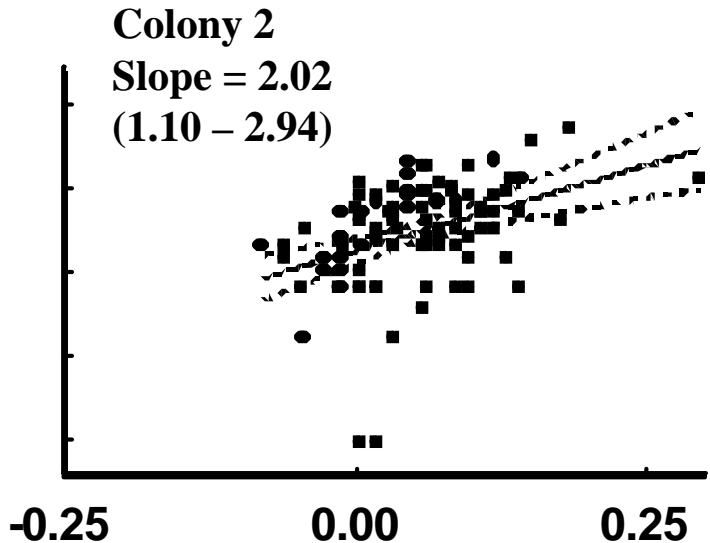
Colony 2

Slope = 4.33
(3.17 – 5.49)



Colony 2

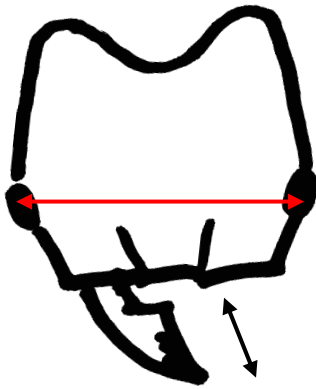
Slope = 2.02
(1.10 – 2.94)



Head Shape

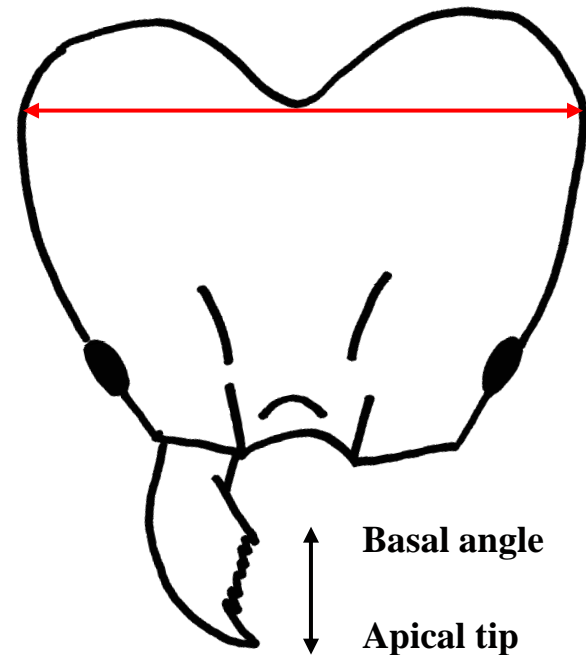
Media ants: oval head

Maximum headwidth 1.9 mm



Major workers: heart-shaped head

Maximum headwidth 6.6 mm



Why Should Working For
the Colony Be Favoured by
Natural Selection?

How Did Extreme
Altruism/Inequality Evolve?

Origin of Eusociality

Kinship & The Evolution of Eusociality

Ancestral State Reconstruction

8 independent origins of eusociality

Ants 1

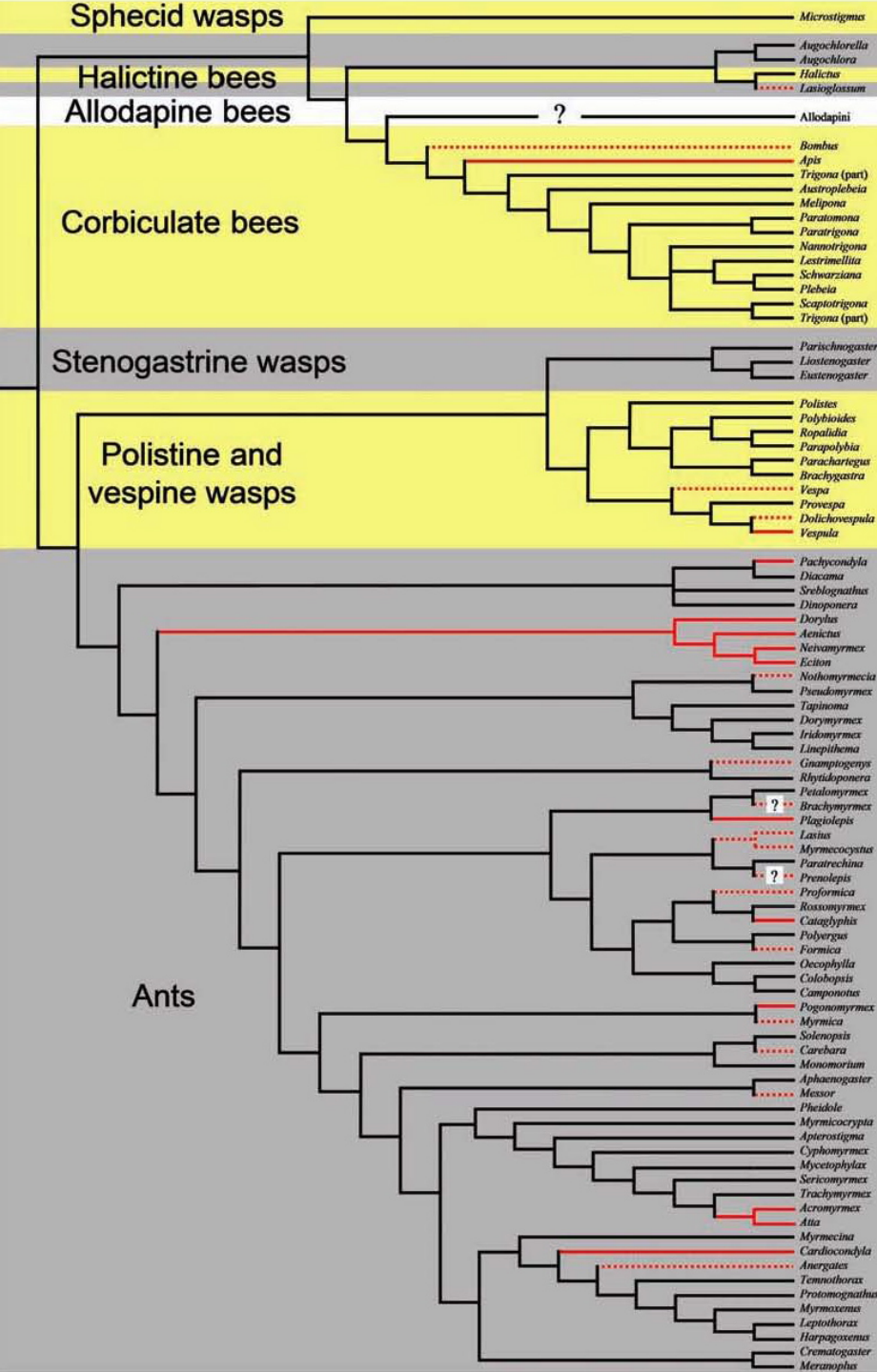
Wasps 3

Bees 5

When eusociality evolved kinship was high (monandry)

Low kinship (polyandry) is derived

Hughes, Beekman, Oldroyd, Ratnieks (2008) Science



How Did Extreme
Altruism/Inequality Evolve?

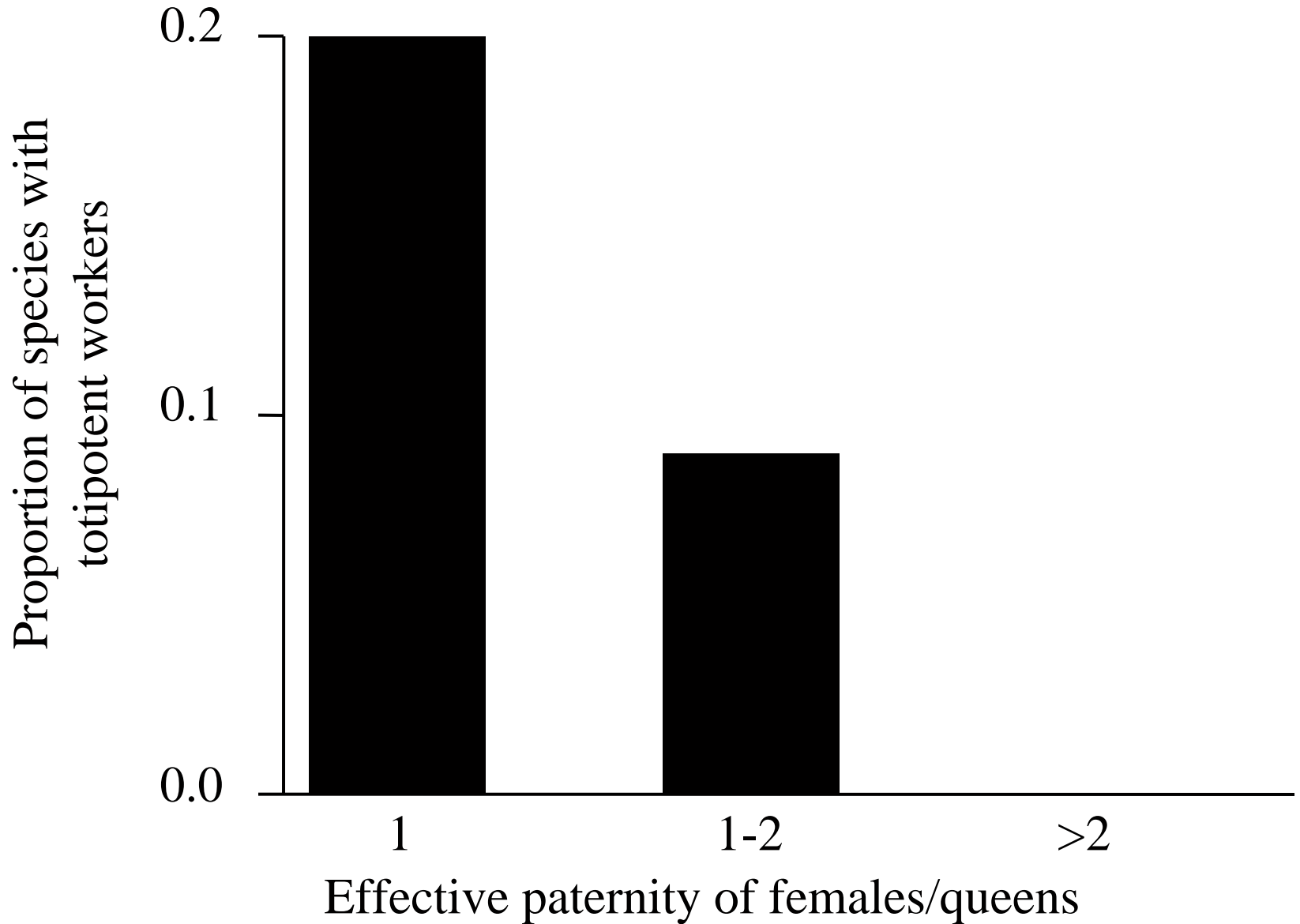
Elaboration of Eusociality

Females Morphologically Equal



Mischocyttarus sp., California

Kinship & The Evolution of Eusociality



Females Morphologically Unequal

Queen



Worker

Garden ant

Lasius niger

Honey bee

Apis mellifera

Common wasp

Vespula vulgaris

Only species with non-totipotent workers have high levels of polyandry (= low relatedness).

Point of “no return”. Workers cannot “opt out”

How Did Extreme Altruism/Inequality Evolve?

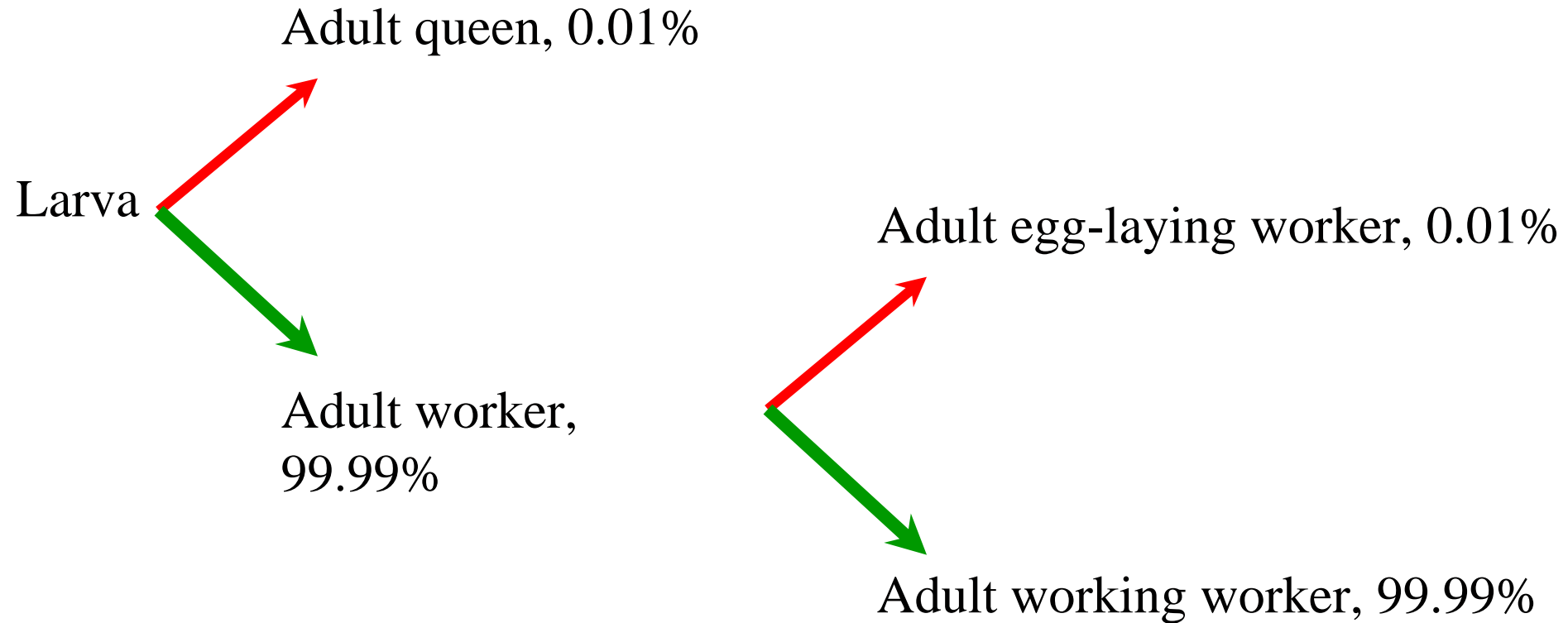
Modern Day Species

Altruism v. Selfishness

To Reproduce or to Help
Others Reproduce

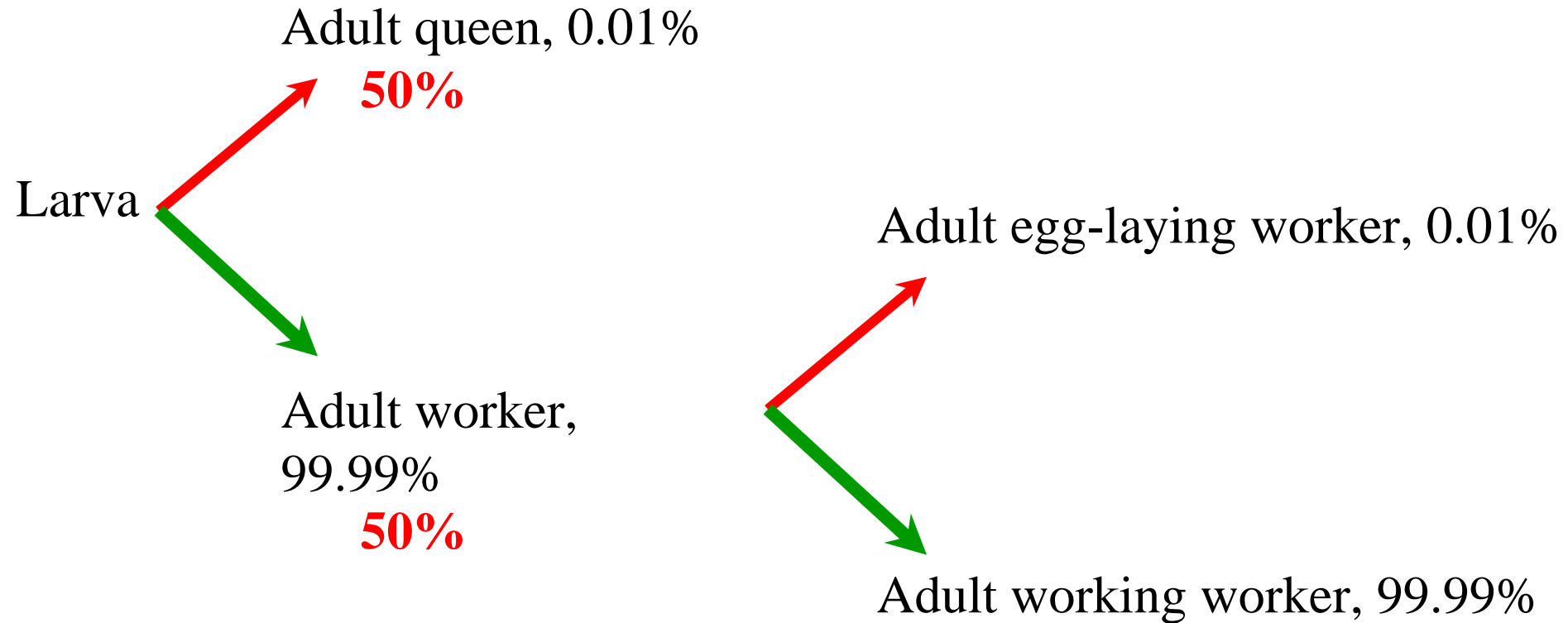
Altruism v. Selfishness

To lay eggs (selfish) or to work (altruism)?



Altruism v. Selfishness

To lay eggs (selfish) or to work (altruism)?



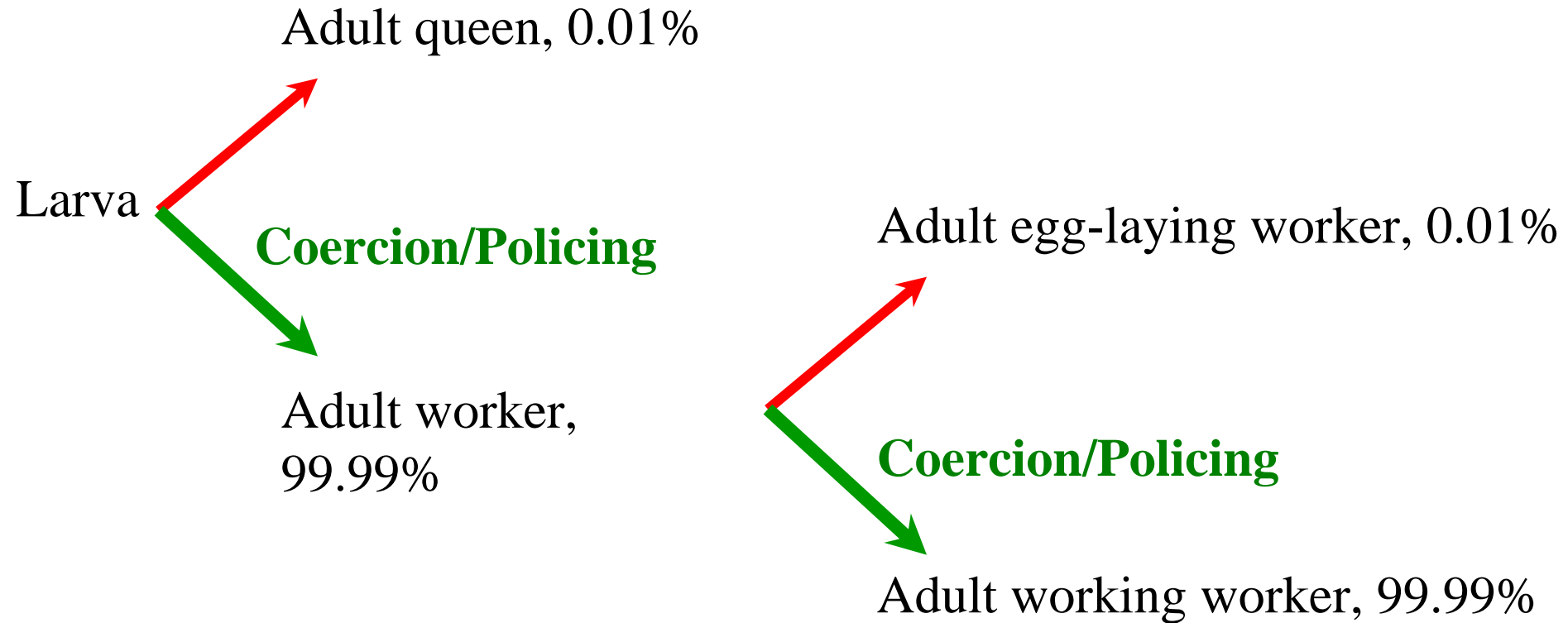
Levels of kinship alone cannot cause such extremes

Social Coercion/Policing

The Cause of Extreme
Altruism & Inequality

Altruism v. Selfishness

To lay eggs (selfish) or to work (altruism)?



Coercion/Policing can cause such extremes

Female Caste Fate: With Coercion



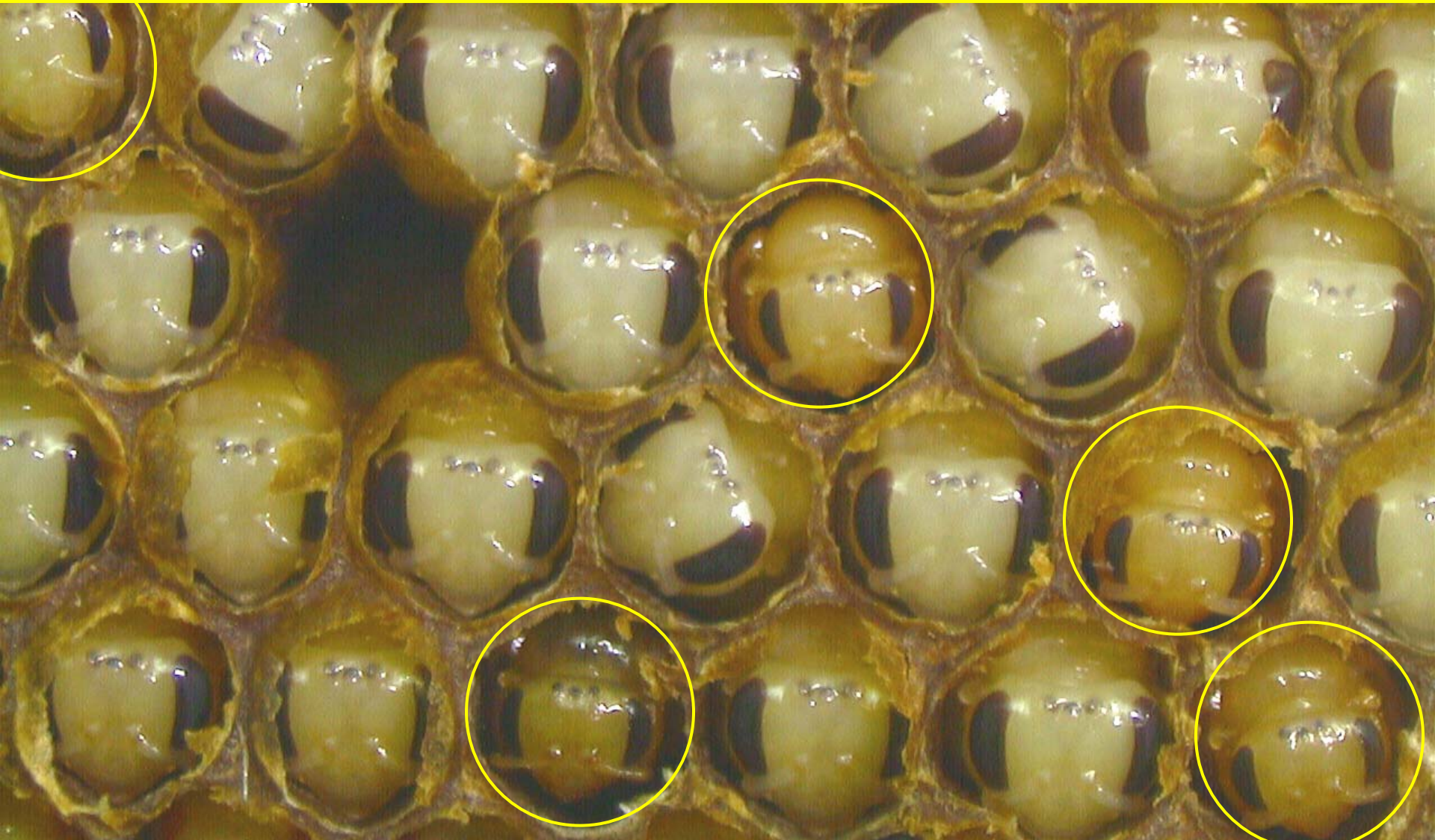
Queen honey bees are reared in special cells on royal jelly. Workers are reared in small cells. Adult workers can coerce larval caste fate.

Female Caste Fate: With Coercion



Worker honey bees are reared in hexagonal cells not on royal jelly. A larva in a worker cell cannot develop into a queen.

Female Caste Fate: Without Coercion



Queen *Melipona beecheii* (ringed) are reared in the same size sealed cells as workers. This prevents adult workers coercing larval caste

How *Melipona* Larvae Evade Coercion

Coercion difficult: queen not larger than workers

Melipona beecheii Queen



Melipona beecheii Worker



Although queen *Melipona* are morphologically distinct from workers, they are not larger as they are in most species. This means that adult workers cannot coerce larvae to become workers by providing less food.

How *Melipona* Larvae Evade Coercion

Coercion difficult: mass provisioning

*Melipona
beecheii*

Queen and male *Melipona* are reared in the same-sized sealed cells on a provision mass. This means that adult workers cannot coerce larvae to become workers by killing larvae that develop into queens.



Worker Reproduction: With Coercion



“Worker policing”. A worker honey bee *Apis mellifera* checks then kills a worker-laid egg. Policing workers kill few queen-laid eggs.

Worker Policing in the Honey Bee



Worker Policing in the Honey Bee



Worker-laid eggs removed

A close-up photograph of a honeycomb frame showing several rows of cells. The cells are filled with a brownish, textured substance, likely honey or wax. A red rectangular box highlights a row of cells where the contents have been removed, leaving the cells empty.



Queen-laid eggs not removed

A close-up photograph of a honeycomb frame showing several rows of cells. The cells are filled with a brownish, textured substance, likely honey or wax. A green rectangular box highlights a row of cells where the contents have not been removed, leaving the cells filled with the substance.

Worker Policing in the Saxon Wasp



A worker wasp *Dolichovespula saxonica* kills an egg laid by another worker. But these “policing” workers do not kill queen-laid eggs.

Queen Policing in Bumble Bees



A queen bumble bee, *Bombus terrestris*, kills a worker-laid egg.

Worker Reproduction: Without Coercion

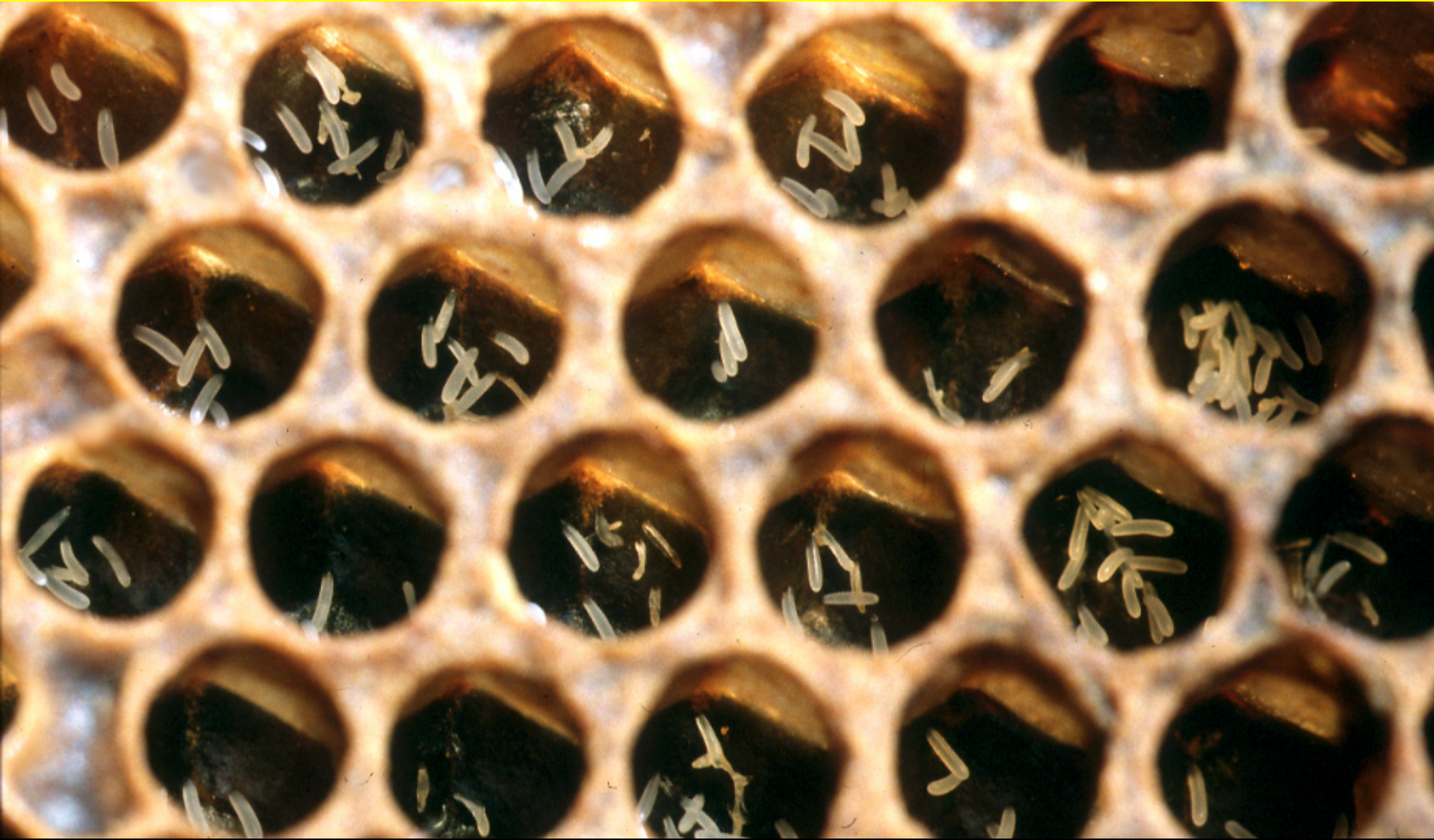


In queenless colonies (shown here the honey bee *Apis mellifera*) worker policing is switched off and many workers lay eggs, resulting in many eggs per cell.

There are more laying workers than needed to lay all the eggs that the colony could rear.

Beating the System by Evading Coercion

Evading Worker Policing of Eggs



In anarchistic honey bee colonies, and Cape honey bees, workers can lay eggs that evade worker policing.

Evading Caste Policing: Dwarf Queens

Stingless bee *Schwarziana quadripunctata*

Reared in

Normal queen



Royal cell (large)

Dwarf queen



Worker cell (small)

Worker



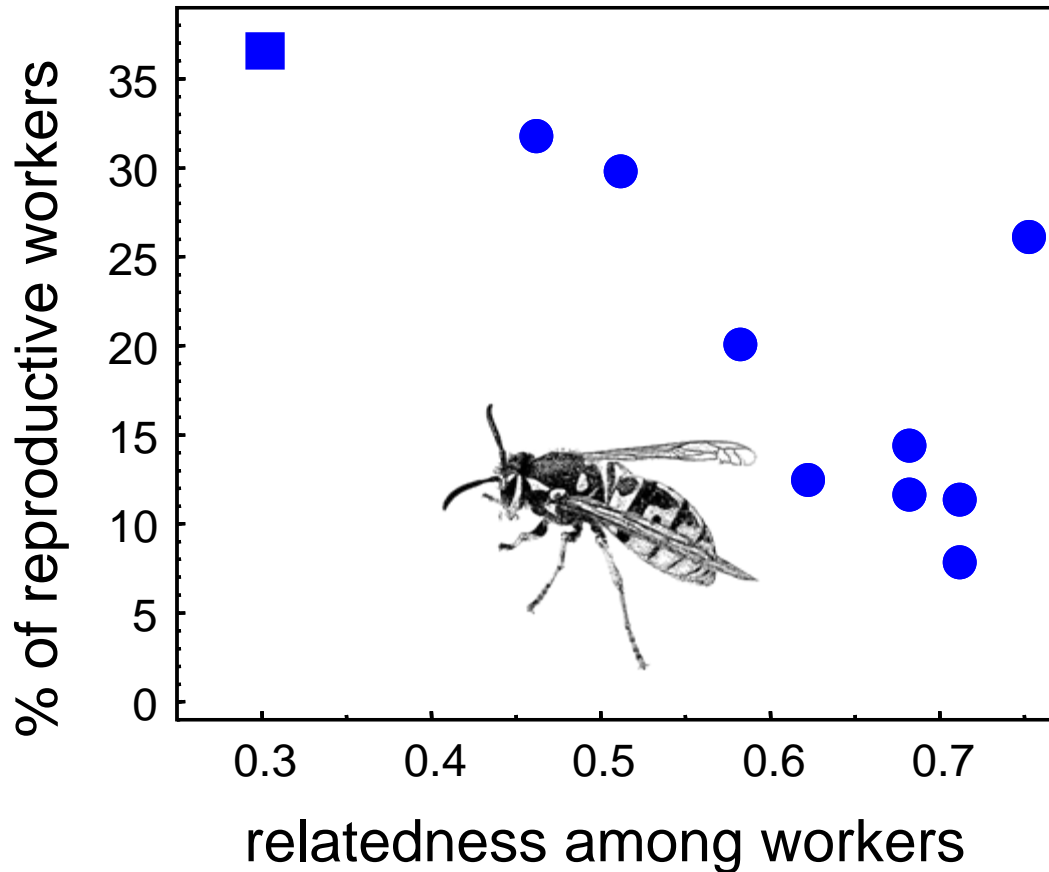
Worker cell (small)

In some stingless bee species, some female larvae reared in worker cells develop into queens. These dwarf queens can head colonies. By developing into dwarf queens, larvae evade coercion by adult workers.

Effects of Kinship & Coercion

Kinship Alone: Worker Reproduction in Queenless Colonies

Policing not possible in queenless colonies



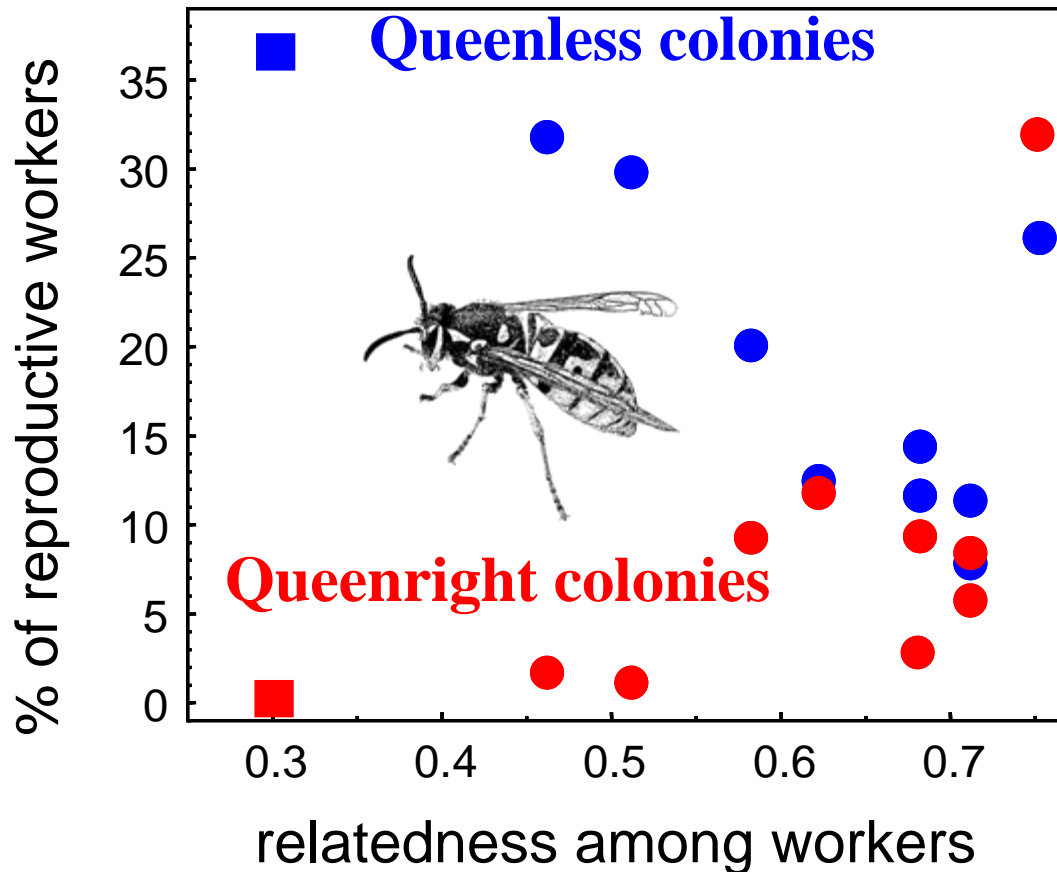
Conclusion

Higher relatedness leads to increased altruism in workers (more work).

In queenless colonies (without worker policing) of 9 species of Vespidae wasp and the honey bee (square), lower relatedness is correlated with lower altruism (Wenseleers & Ratnieks 2006 Nature).

+ Coercion: Worker Reproduction in Queenright Colonies

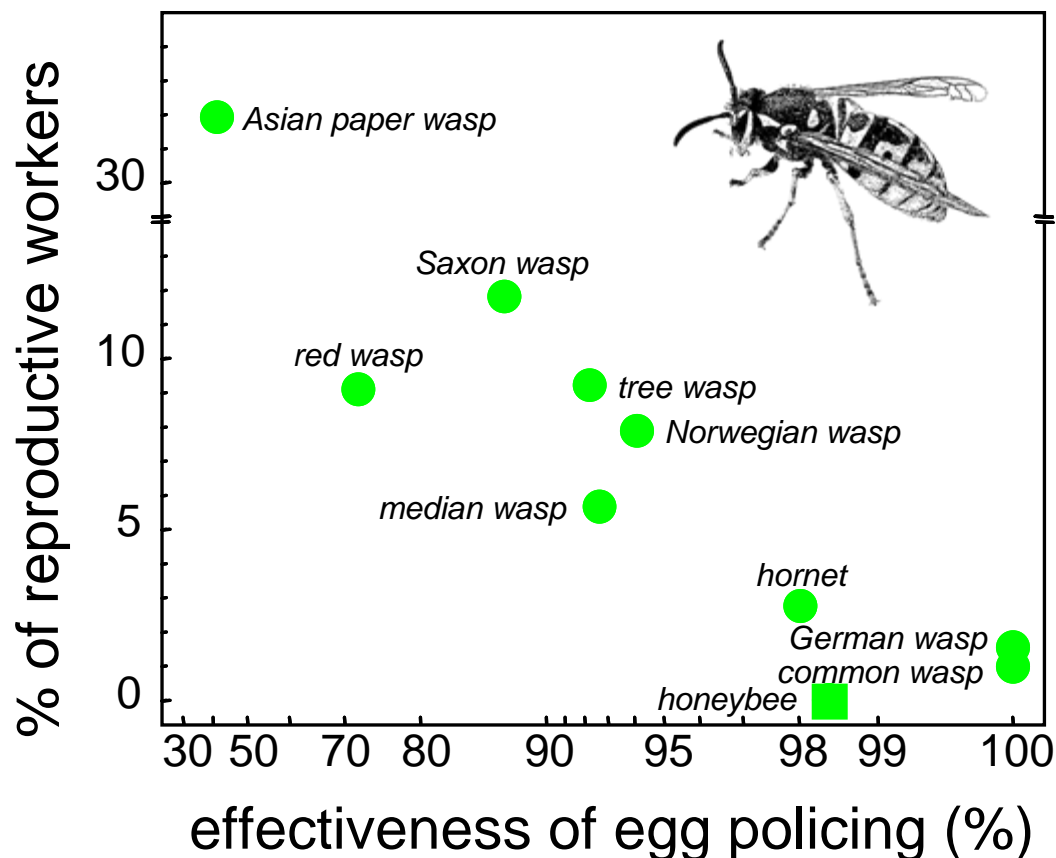
Policing is possible in queenright colonies



In queenright colonies (red) of 9 species of Vespidae wasp and the honey bee (square), lower relatedness is correlated with higher altruism. Why is this? (Wenseleers & Ratnieks 2006 Nature).

Effect of Coercion on Worker Reproduction

Worker reproduction in queenright colonies of 10 species



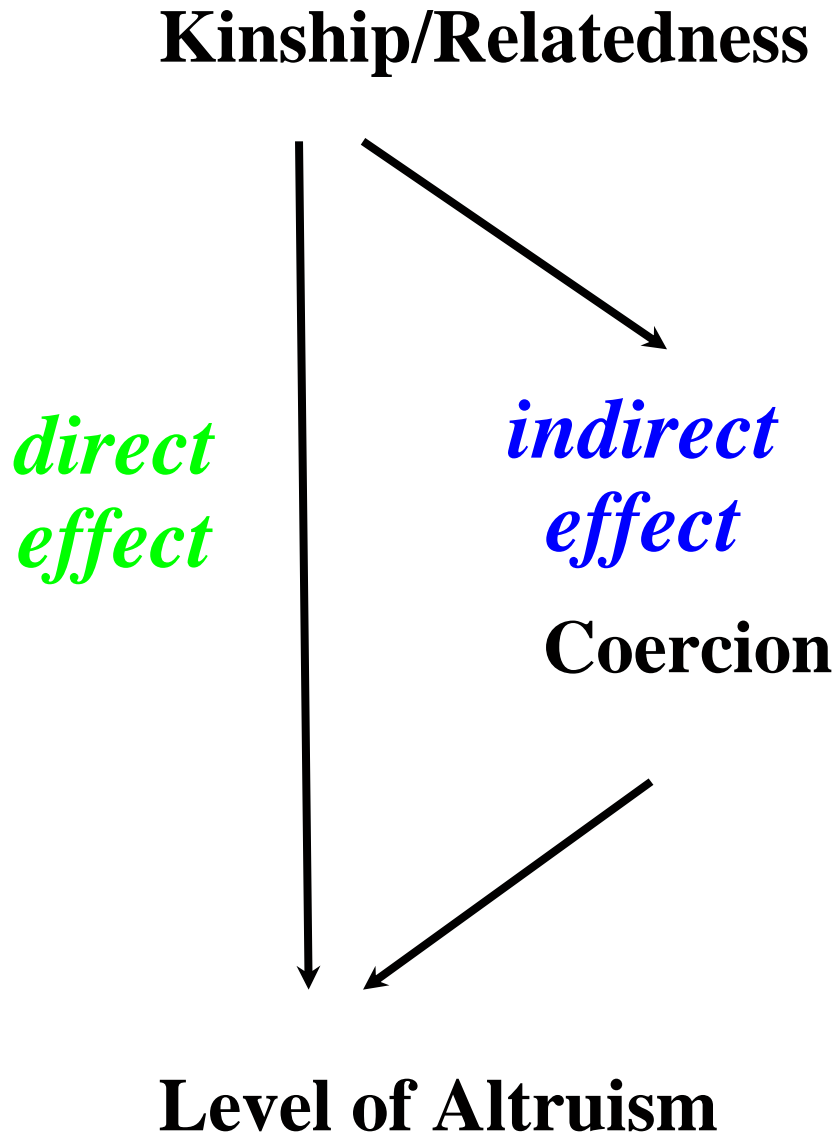
Conclusion

More effective policing leads to increased altruism in workers (more work).

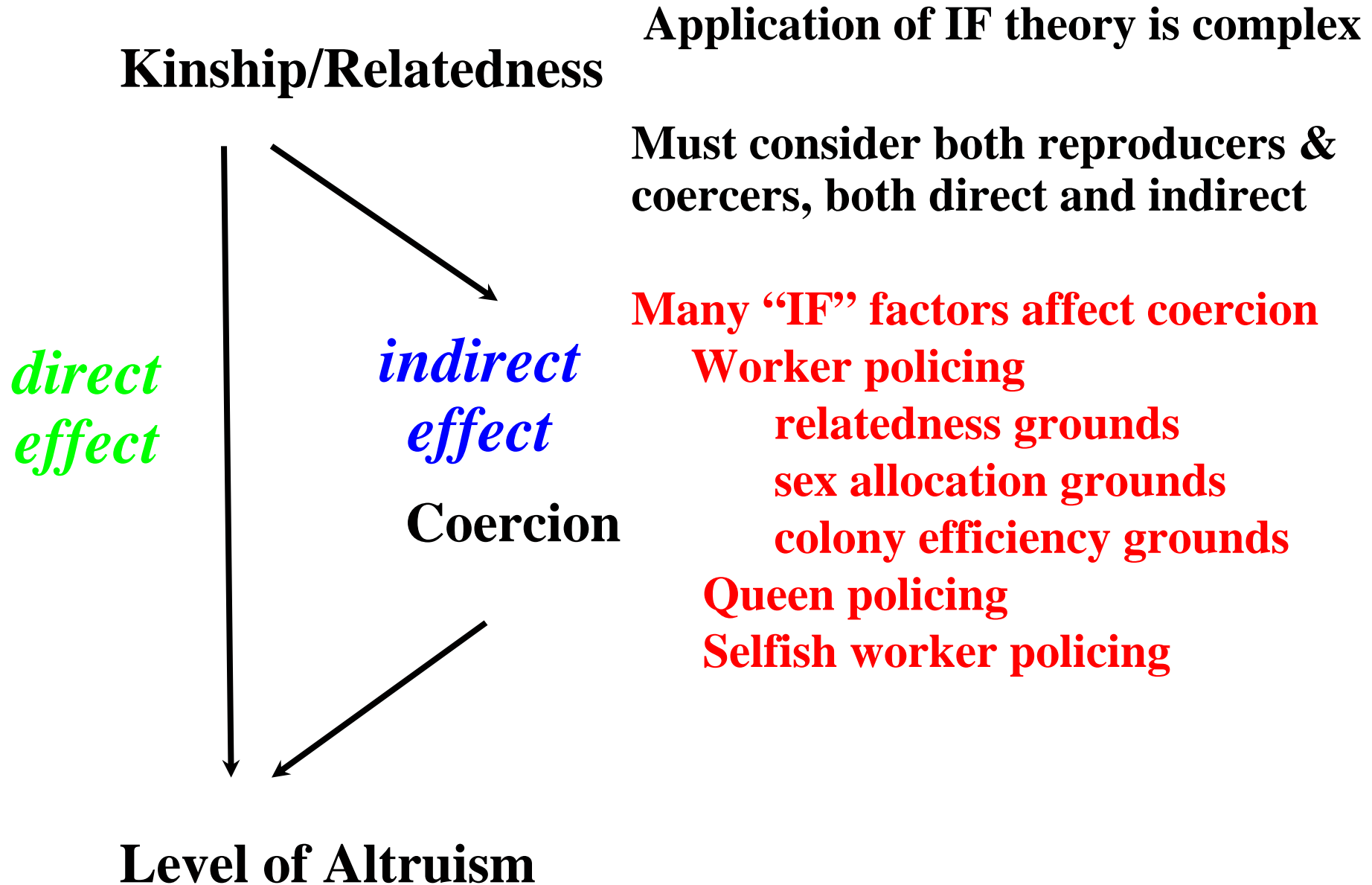
Effective policing is preventive.

In queenright colonies (red) of 9 species of Vespidae wasp and the honey bee (square), greater altruism is correlated with more effective policing of worker-laid eggs. (Wenseleers & Ratnieks 2006 Nature).

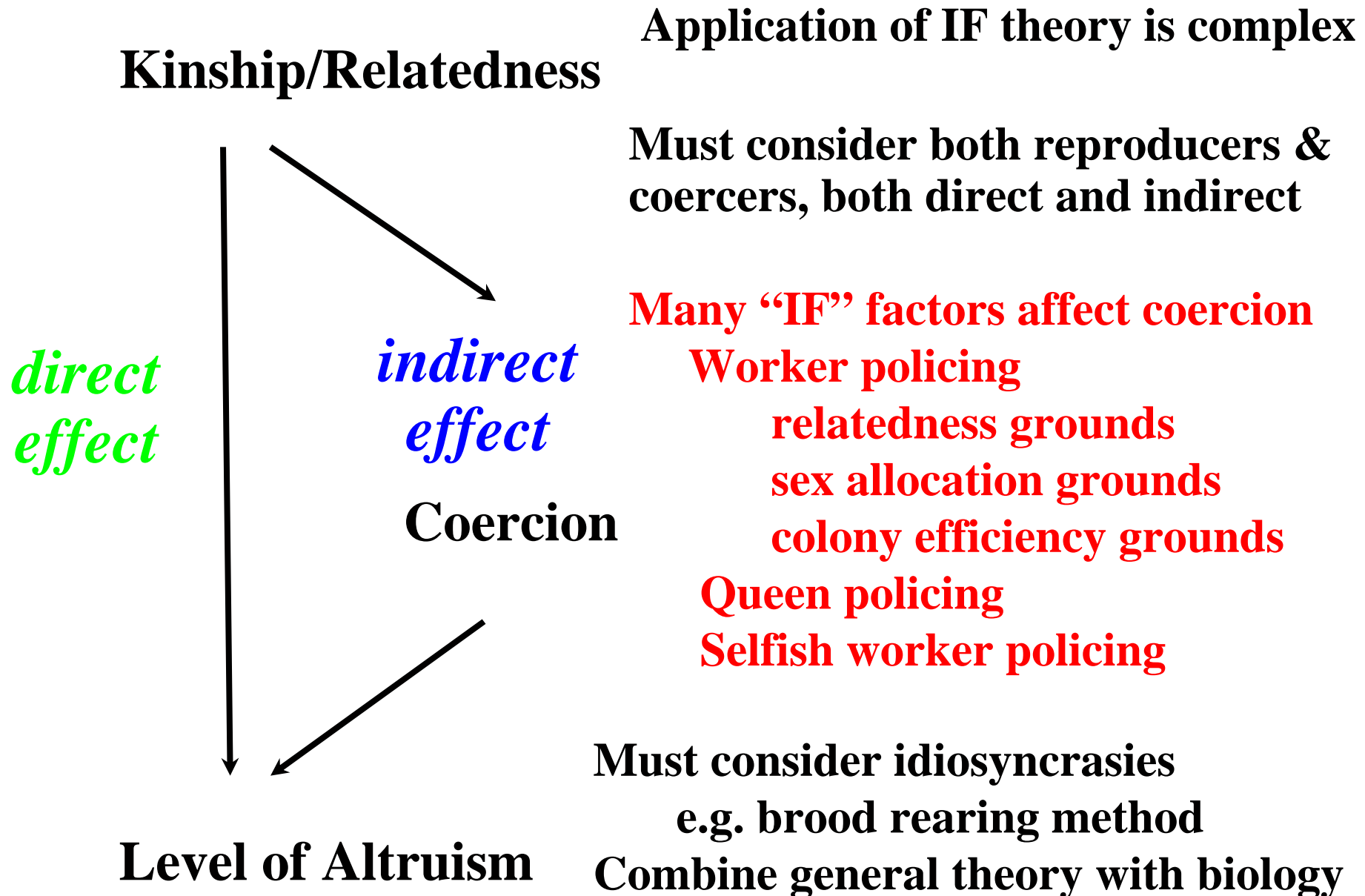
“Direct” and “Indirect” IF Theory Effects



“Direct” and “Indirect” IF Theory Effects



“Direct” and “Indirect” IF Theory Effects



Consequences

& Why Does it Matter?

Enforced Altruism & Acquiescence

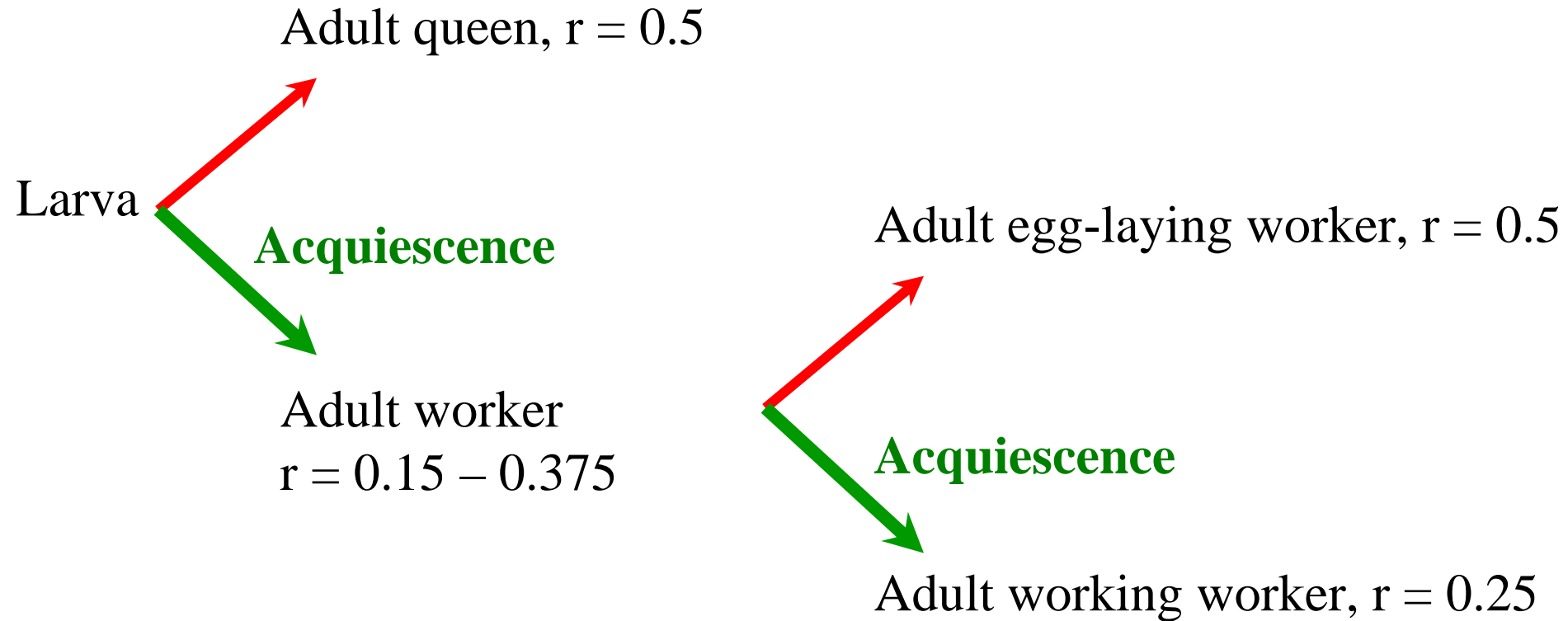
Enforced v. Voluntary Altruism

Voluntary altruism: altruism, or the level of altruism, favoured by natural selection acting on individuals in social groups **without coercion**.

Enforced altruism: altruism, or the level of altruism, favoured by natural selection acting on individuals in social groups **with coercion**.

Why Acquiesce to Coercion?

To lay eggs (selfish) or to work (altruism)?



Working is not the best option, but its not a disaster

Creating a Better Society

Building an Organism Made
of Many Individuals

Female Caste Fate: Without Coercion

Actual conflict wastes resources, reduces colony efficiency



Excess Queens are Swiftly Executed

Melipona quadrifasciata



Excess queens are killed soon after emerging from their cell. A colony needs just a few queens per year, to replace a failing mother queen or to permit colony fission. Vastly more than this are actually reared.

Selfishness Leads to Waste, Literally

Melipona beecheii



The body of a recently executed excess queen ends up on the waste heap.

