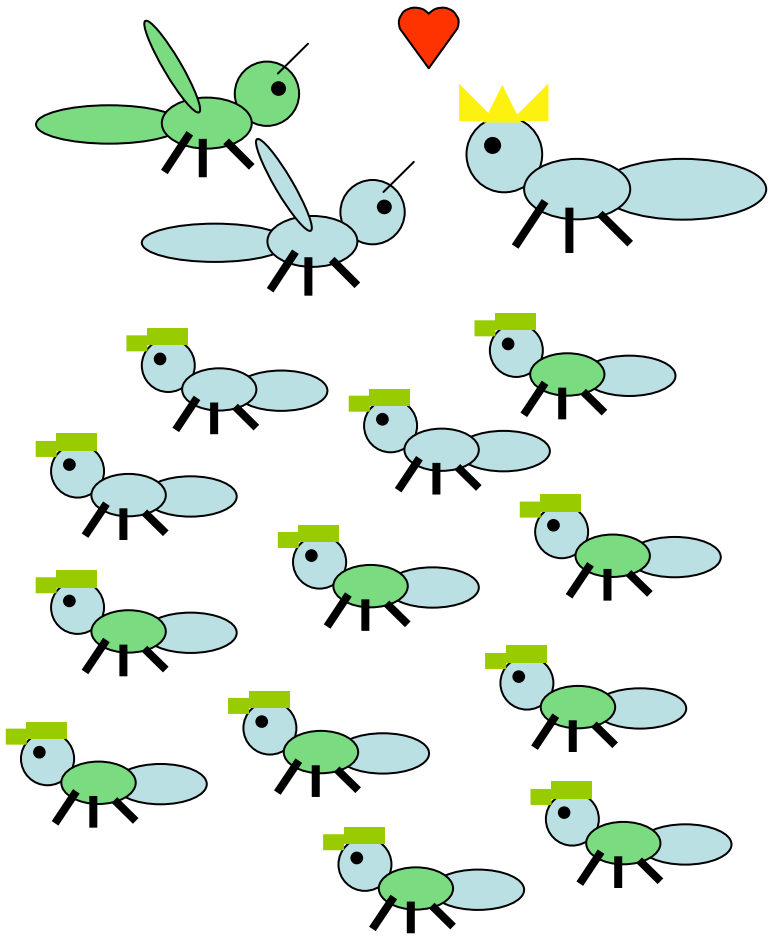
The Evolution of Colony Structure

in the Social Hymenoptera

DANIEL KRONAUER

COLONY KIN-STRUCTURE

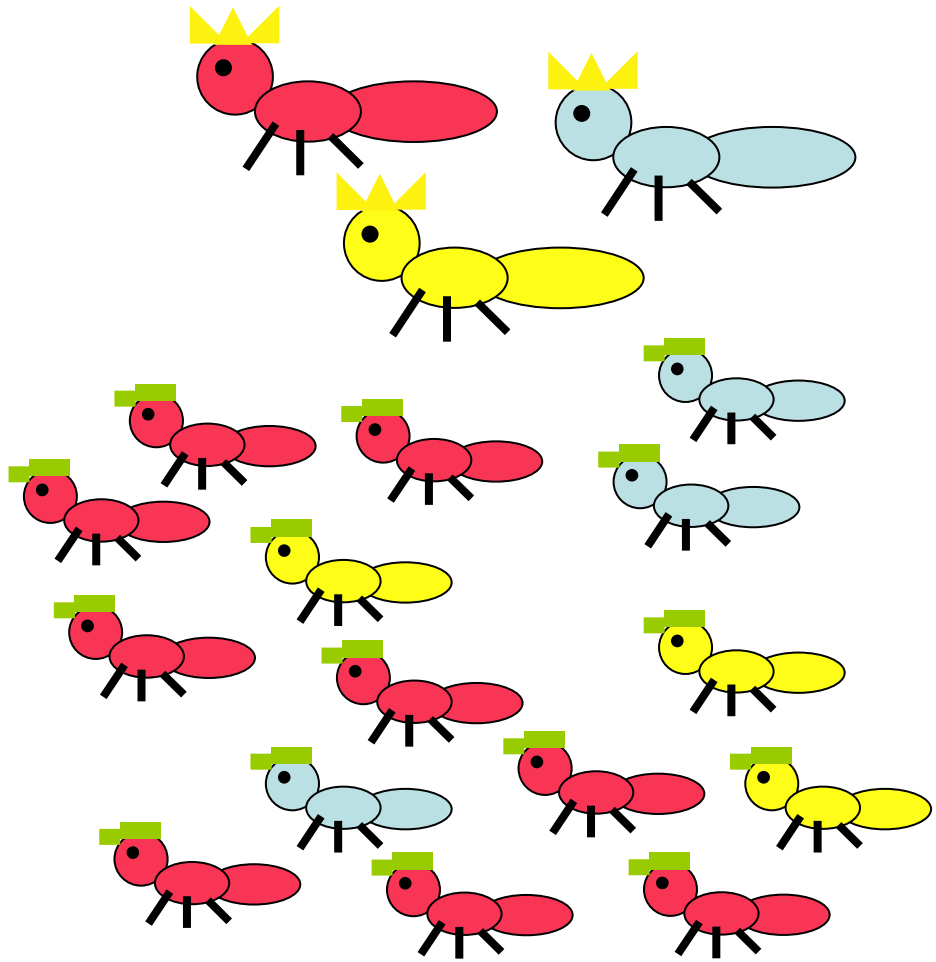
Queen mating frequency



Relatedness between mates / inbreeding

Reproductive skew

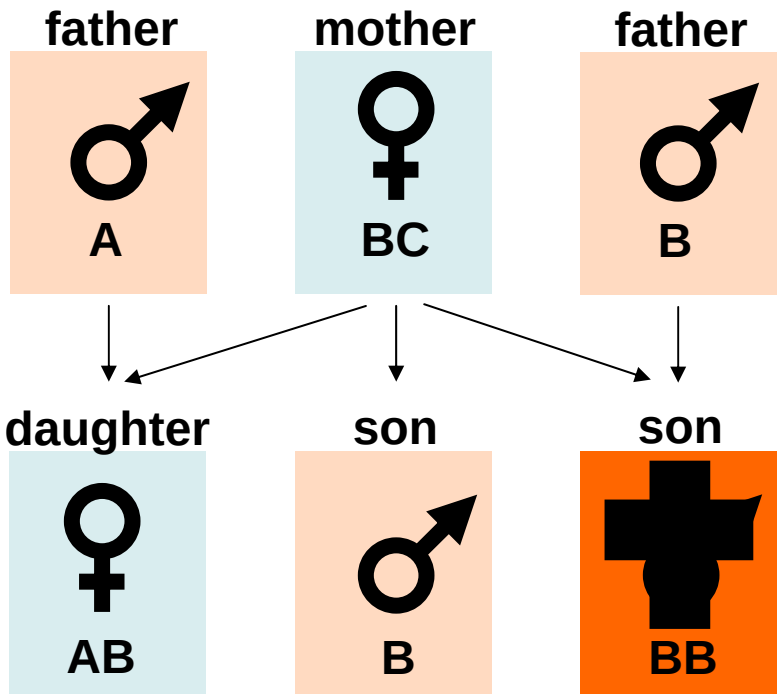
Queen number



Relatedness between queens

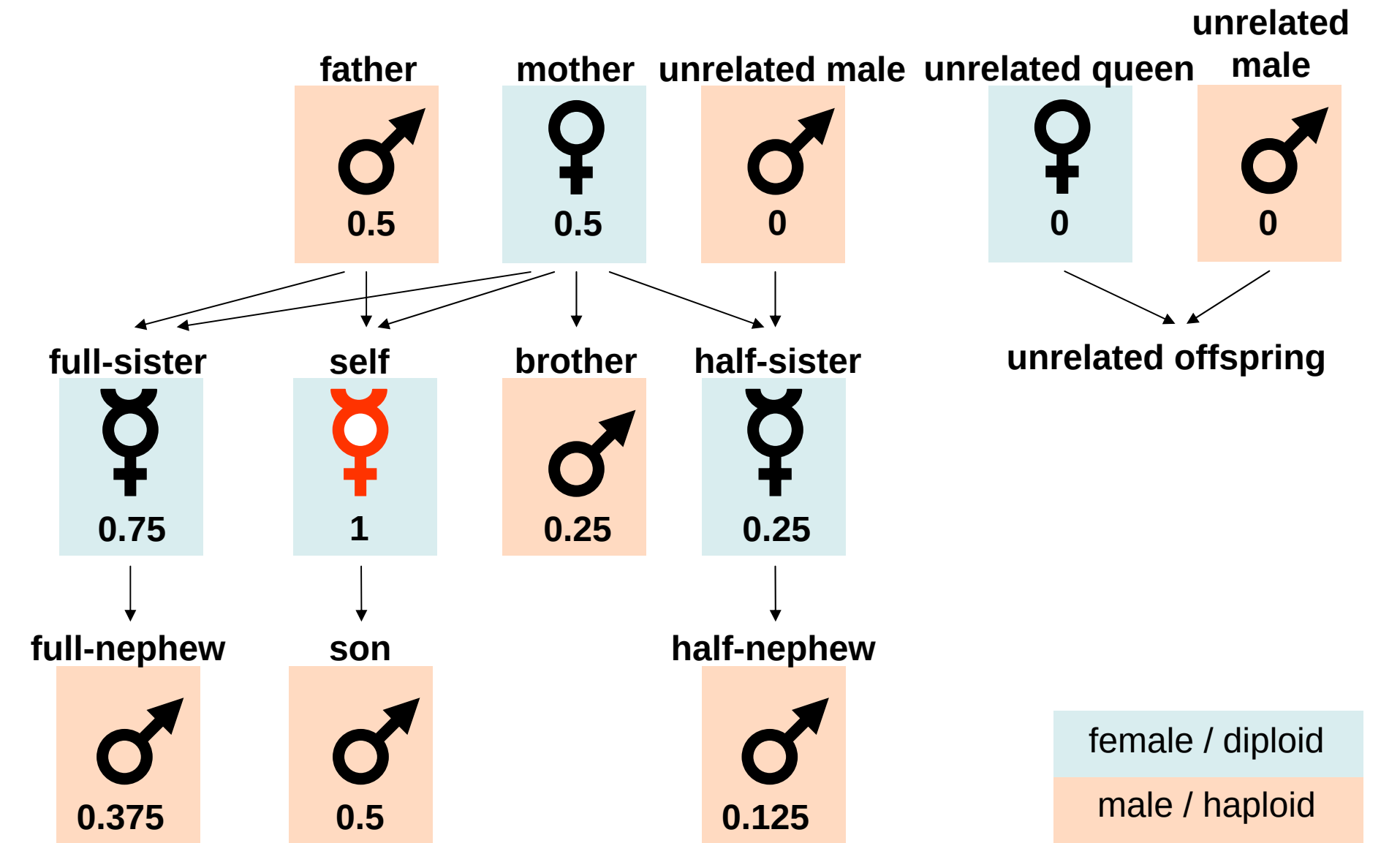
Reproductive skew

COLONY KIN-STRUCTURE

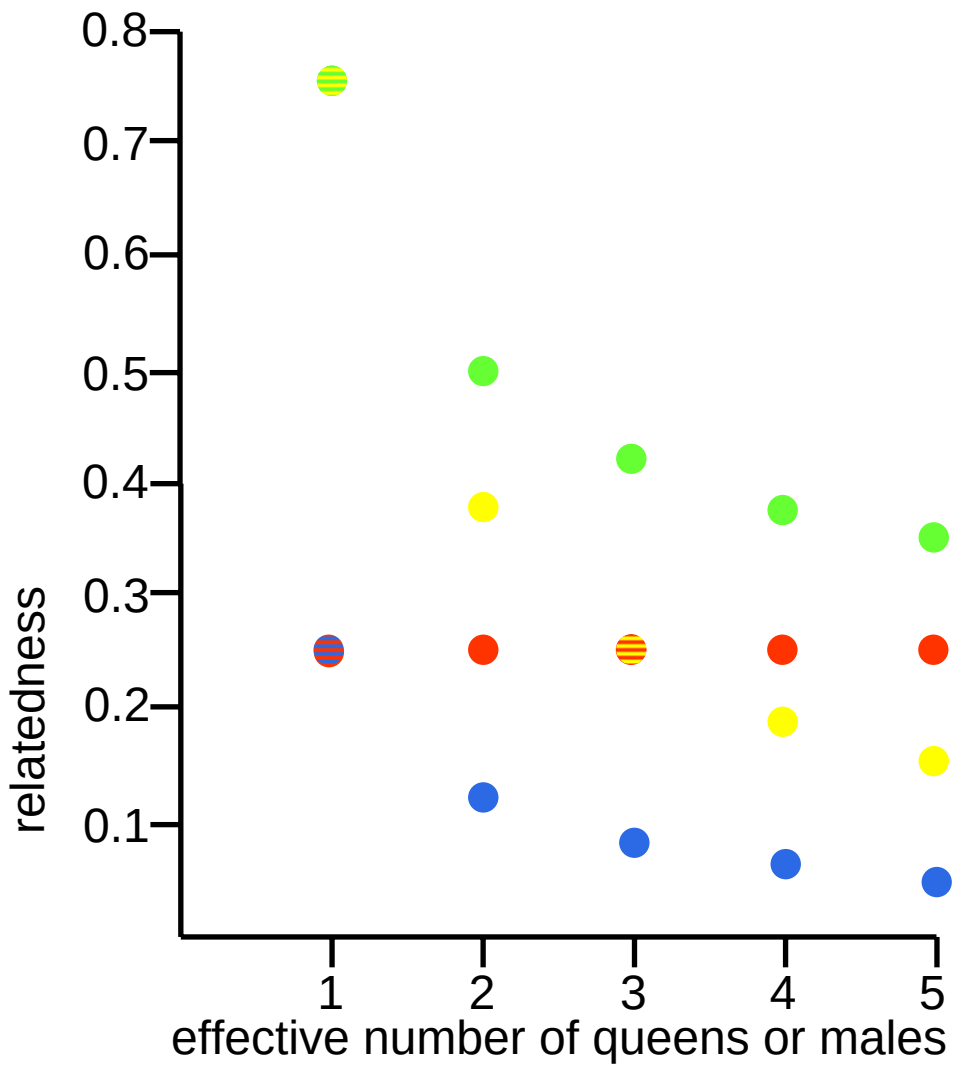


- Females are diploid, males are haploid
- Females can produce male offspring without having mated
- Females control offspring sex
- Matched matings lead to diploid, sterile males
- Special pattern of genetic relatedness

COLONY KIN-STRUCTURE



COLONY KIN-STRUCTURE



Worker-male relatedness under monogyny

Worker-gyne relatedness under monogyny

Worker-male relatedness under monandry

Worker-gyne relatedness under monandry

Queen perspective:

- no effect of mating frequency
- r divided by number of queens

COLONY KIN-STRUCTURE

- Mating is assumed to be costly
- Monandry is ancestral and polyandry is rare in social Hymenoptera
- No material gain or broodcare from males
- Long-term sperm storage, time lapse before reproduction, and colony effects
- Special set of adaptive hypotheses:

    Sperm limitation

    Genetic polyethism

    Herd immunity

    Sex-locus load

COLONY KIN-STRUCTURE

- Queens need more sperm than a single male can provide
- Particularly in species with large colonies
- Requires constraints on male sperm production or transfer efficiency of queens
- A consequence of polyandry rather than a cause?

COLONY KIN-STRUCTURE

- Genetic task “specialization”

  caste determination, foraging, scouting for food or nest sites, tending larvae, fanning…

- Genetic diversity contributes to colony fitness

  differences in foraging rates, food storage, colony growth

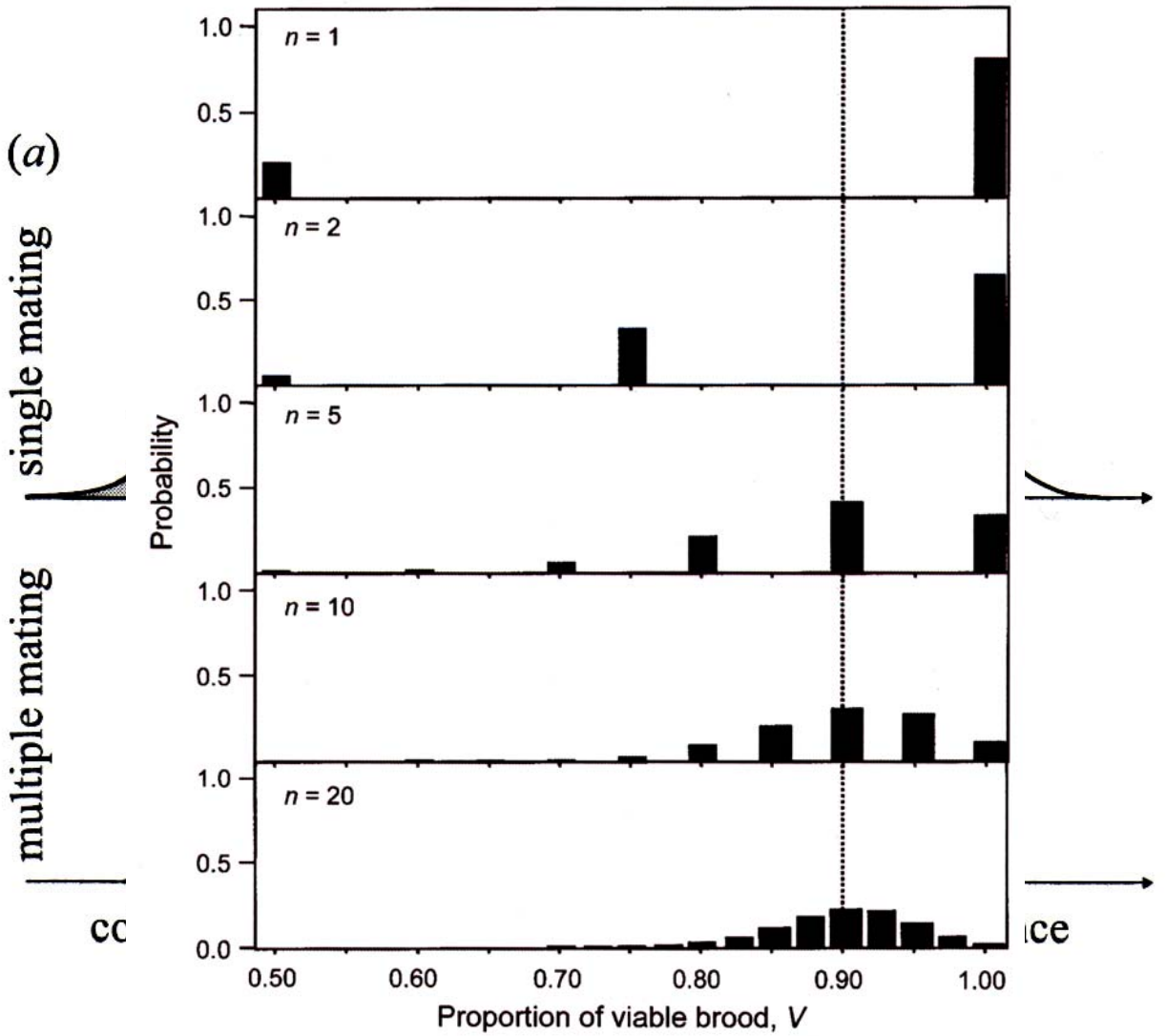
- Positive relationship between genetic diversity and division of labor / colony homeostasis

- Phylogenetic correlation between polyandry and colony complexity

COLONY KIN-STRUCTURE

- Susceptibility to infections has a genetic component
- Increased likelihood that some genotypes are resistant
- Genetic diversity slows down transmission within colonies

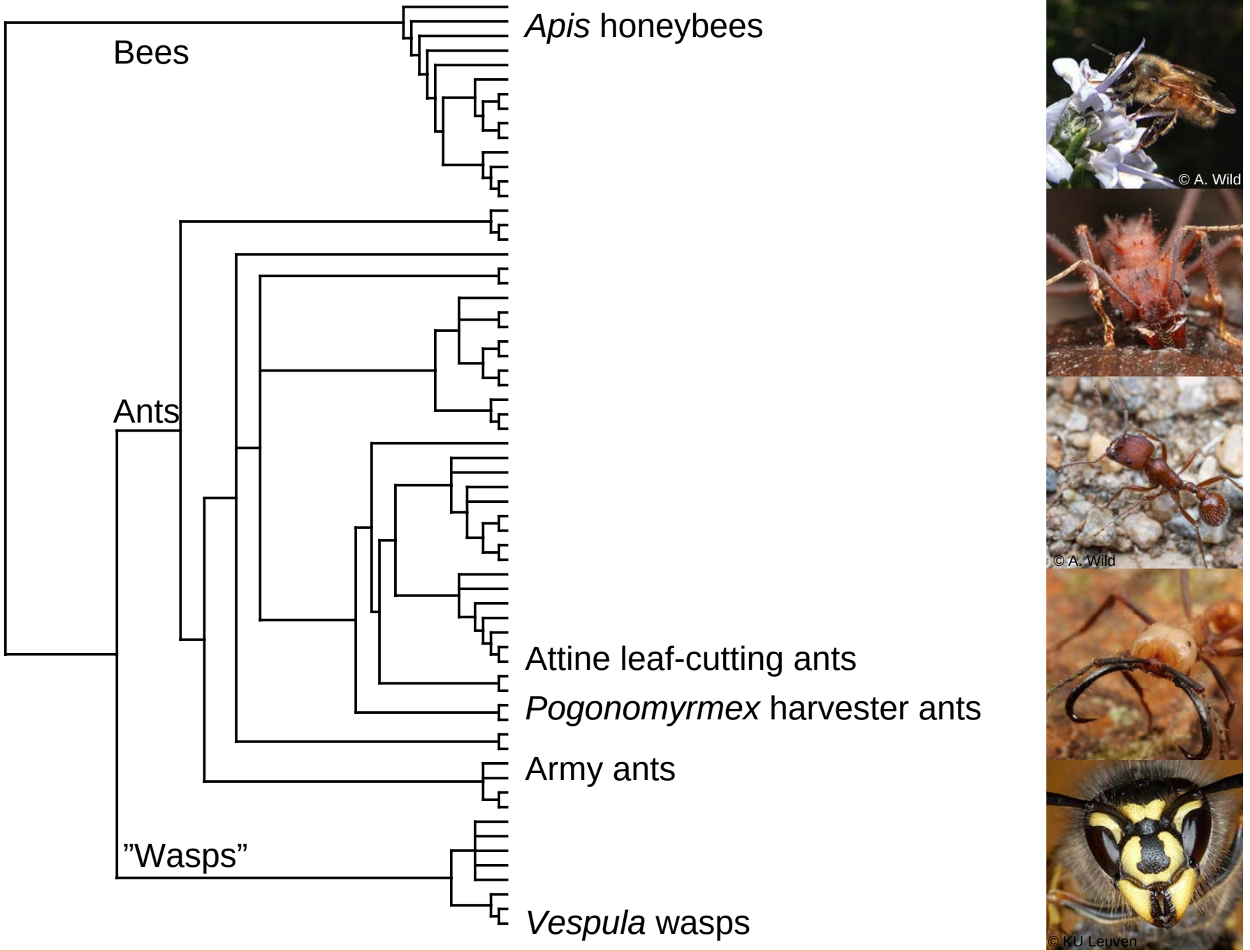
COLONY KIN-STRUCTURE



Tarpy & Page 2001

Rüppell et al. 2008

Mate number – Sex-locus load / Colony variance


Bees
Ants
”Wasps”
Apis honeybees
Attine leaf-cutting ants
Pogonomyrmex harvester ants
Army ants
Vespula wasps
© A. Wild
© A. Wild
© KU Leuven

Mate number

COLONY KIN-STRUCTURE

Different types of polygyny:

Primary polygyny from colony-founding associations (pleometrosis)

Secondary, multicolonial polygyny (extra queens are adopted)

Secondary, unicolonial polygyny

Functional monogyny (several mated queens but only one reproduces)

COLONY KIN-STRUCTURE

Reproduction by a mix of winged sexuals and colony budding

Polygynous queens are typically smaller and weaker fliers, correlated with adoption and low dispersal

Polygynous queens reproduce earlier and have a shorter lifespan

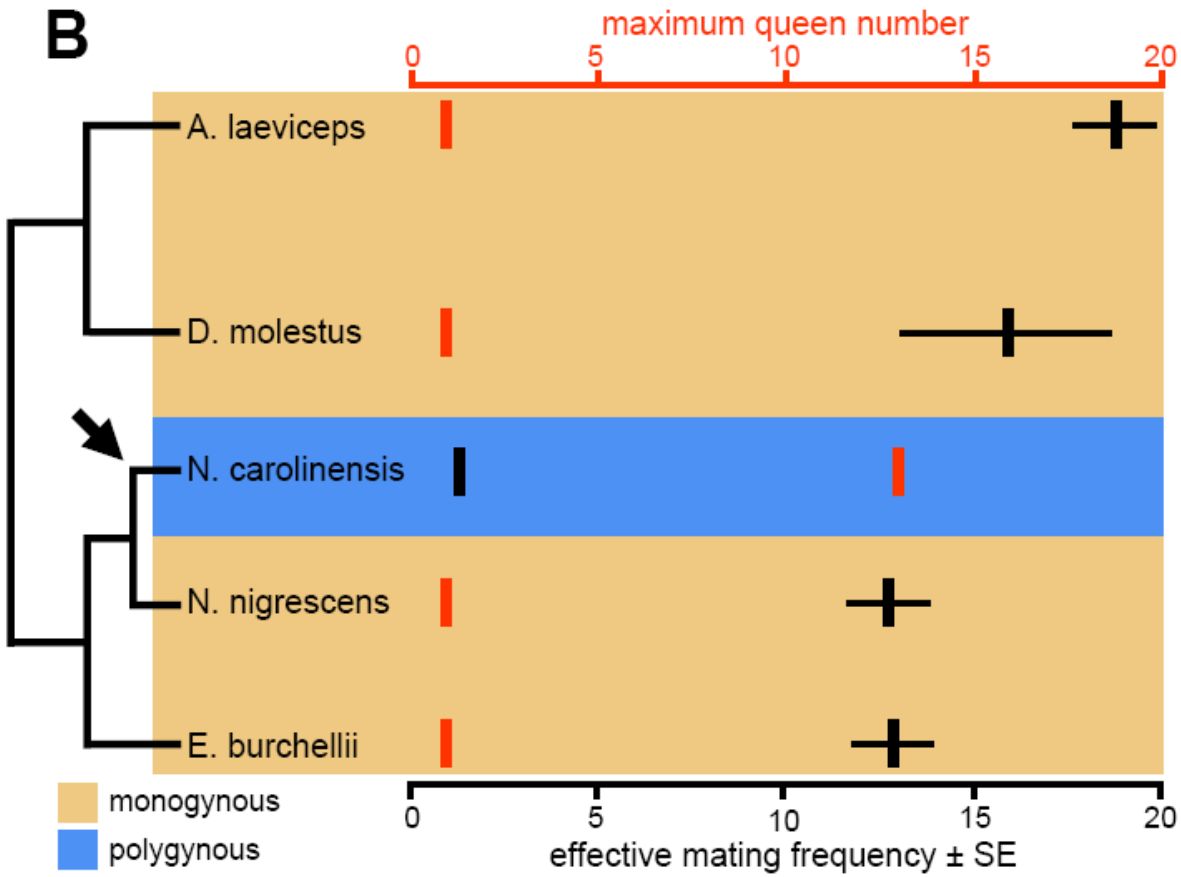
COLONY KIN-STRUCTURE

- Sharing reproduction reduces individual reproductive success
- Foundress associations can be more competitive (often revert to monogyny later)
- Re-adoption under ecological constraints on independent breeding (predation, habitat patchiness and saturation)
- Polygyny can buffer against colony mortality due to predation or harsh winters
- Overall, polygyny is thought to evolve in response to ecological parameters

COLONY KIN-STRUCTURE

- Multiple mating probably evolves to increase genetic diversity within colonies
- Multiple mating probably has some cost
- Polygyny also increases the genetic diversity within colonies, although it probably does not evolve for this purpose
- Multiple mating should be lost in species with multiple queens

COLONY KIN-STRUCTURE



Kronauer & Boomsma 2007

Mate number vs queen number

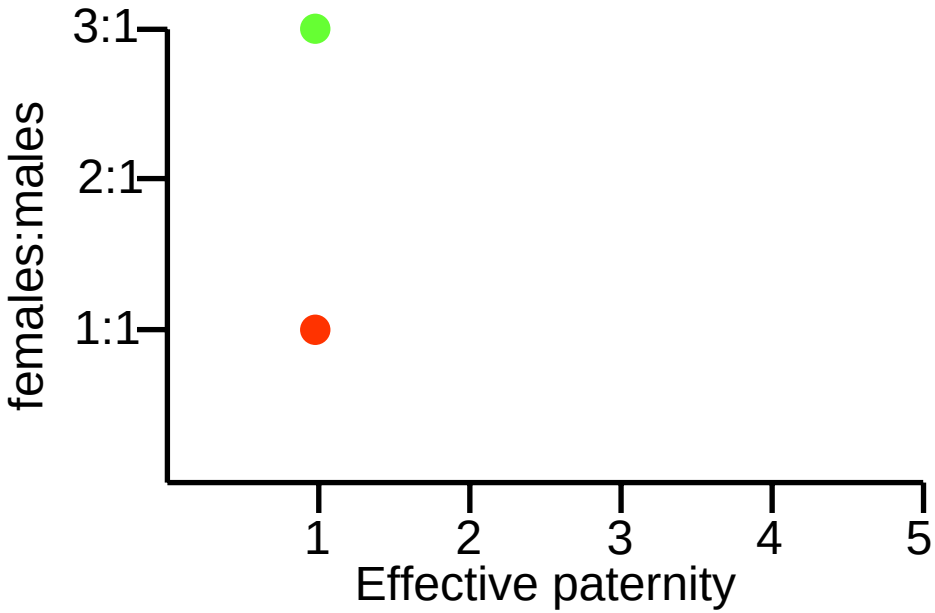
SOCIAL CONFLICT

Unlike cells in conventional organisms, workers in superorganisms are not genetically identical and conflicts over reproductive allocation arise:

- Should a female stay and help vs leave and reproduce independently; who monopolizes reproduction (only in primitively eusocial species)?
- How should a colony allocate investment into offspring?
- Should a female larva develop into a queen or a worker?
- Should a worker lay haploid eggs or forego reproduction?
- Should a worker behave nepotistically?

At r<1, social groups are vulnerable to exploitation by group members who free ride on group resources – tragedy of the commons

The **optimal decision** is not a conscious decision of the individual, but the **evolutionary optimum** (the behaviour is assumed to be instinctive and genetically determined)



Polyandry alleviates conflict over sex allocation

worker allocation

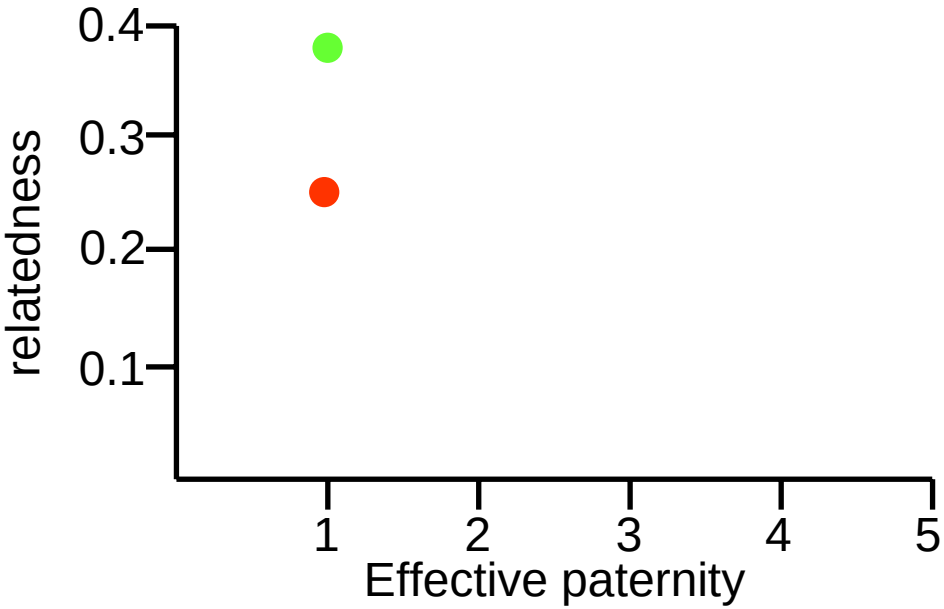
queen allocation

Sex-investment ratio in monandrous species is often female biased, which implies worker control; power can be shared which results in intermediate sex-ratios

Queens control the primary sex-ratio; workers ofton control secondary sex-ratio by selectively rearing female larvae

Split sex-ratios: monandrous colonies rear females, polyandrous colonies rear males

SOCIAL CONFLICT



queen sons

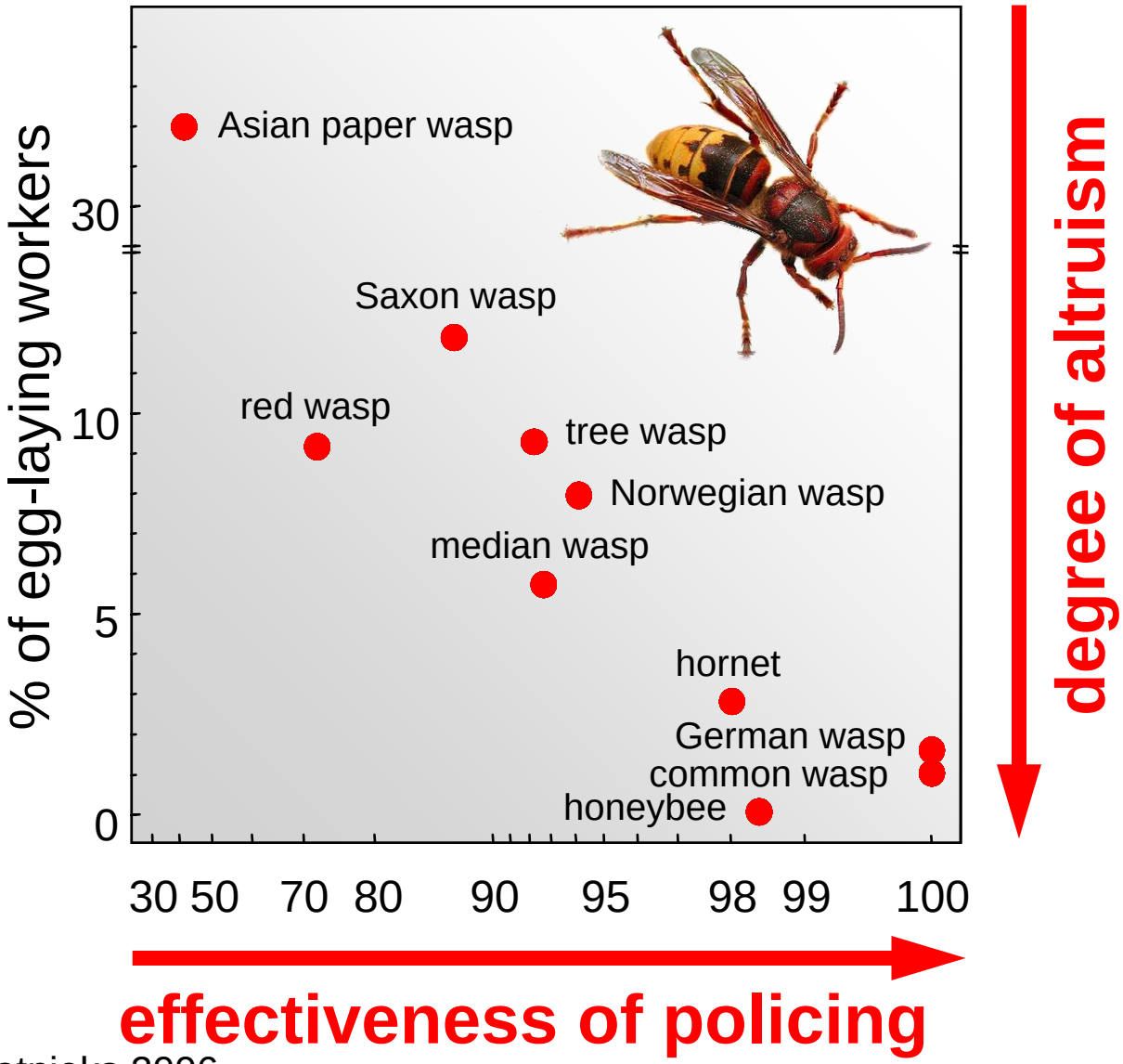
worker sons

Workers in many species can lay unfertilized eggs that could develop into males

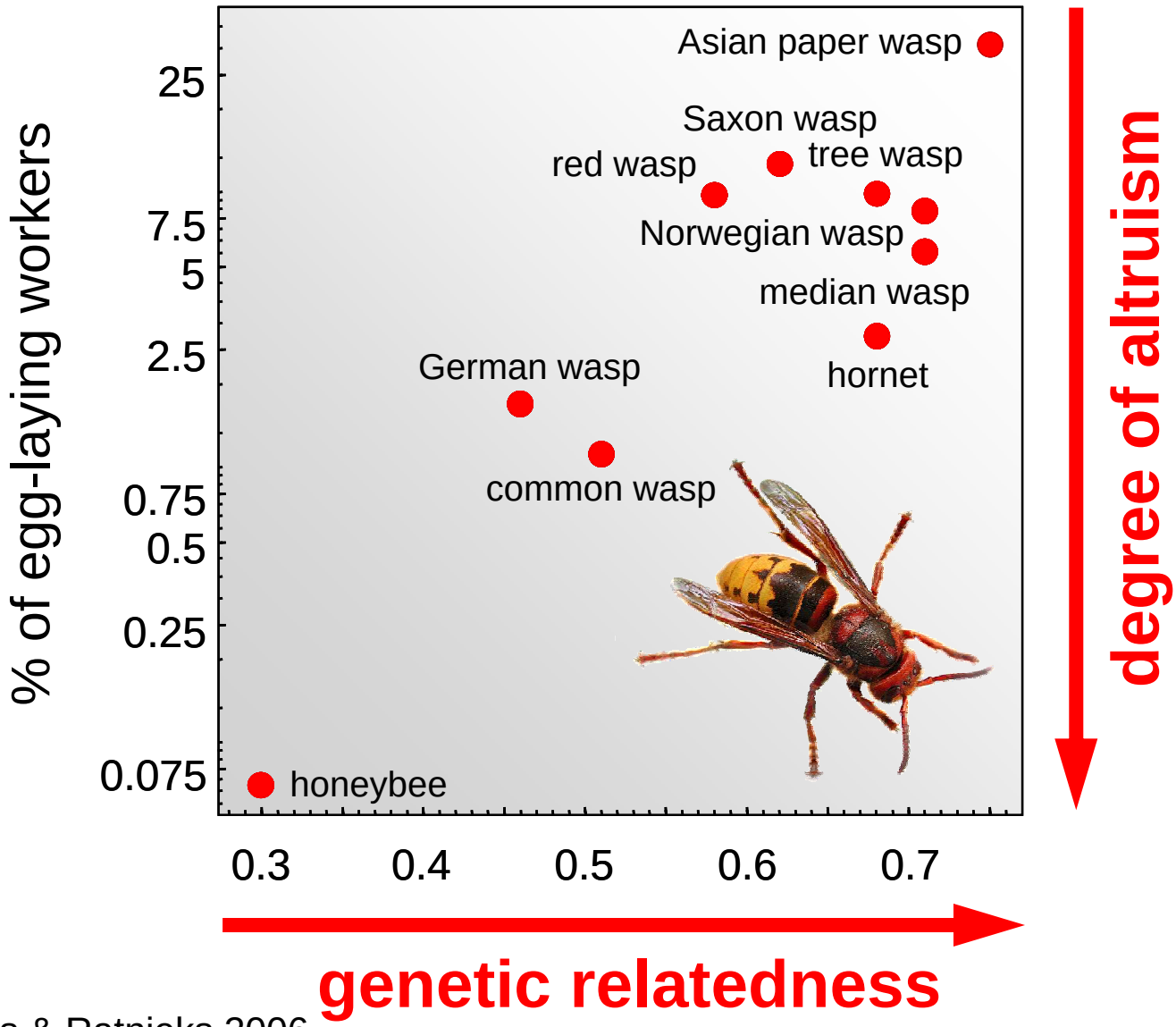
Queen policing efficient in small societies but inefficient in large societies

Reproductive workers work less and worker policing can evolve if it increases total colony fitness

Worker policing is selected under polyandry

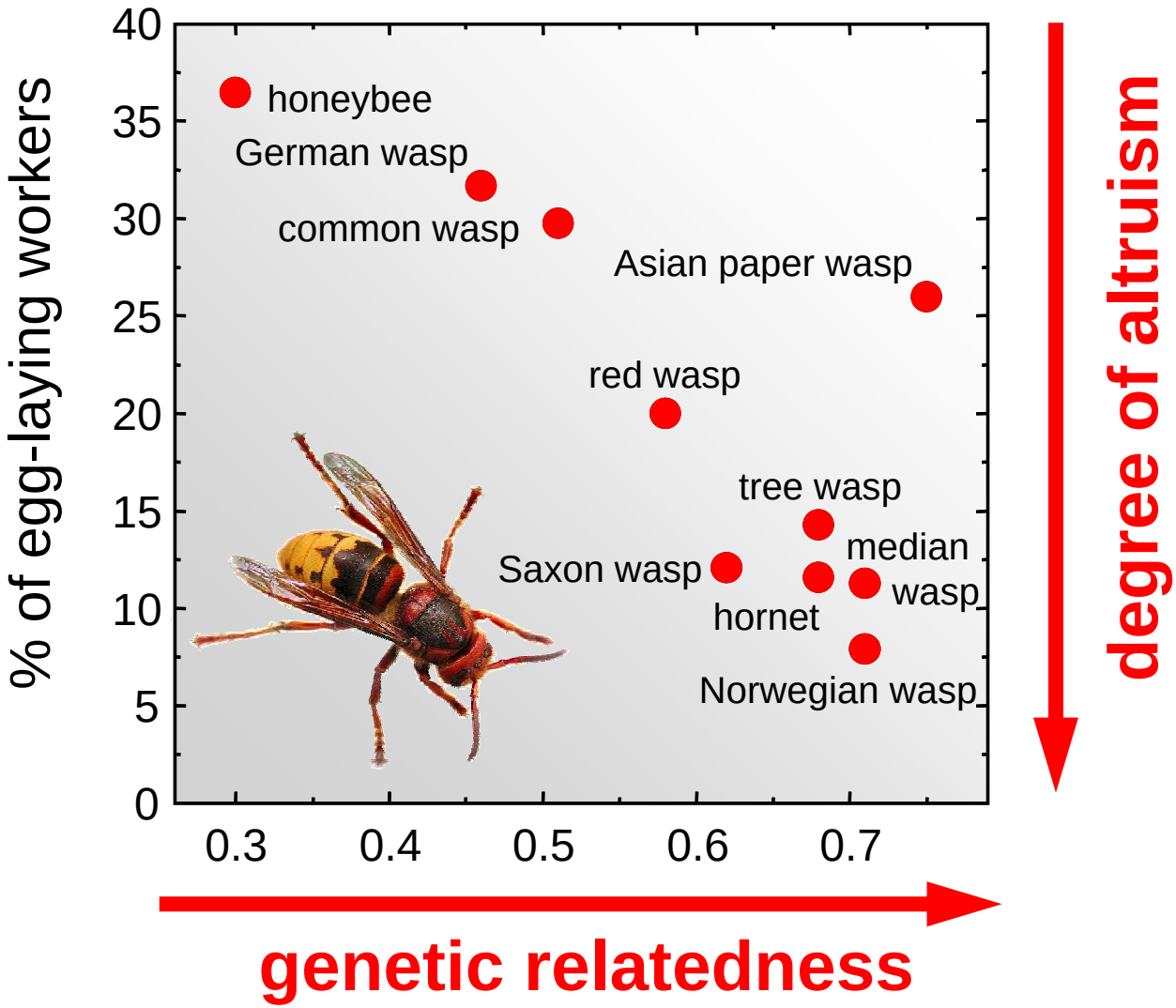


Wenseleers & Ratnieks 2006



Wenseleers & Ratnieks 2006

SOCIAL CONFLICT

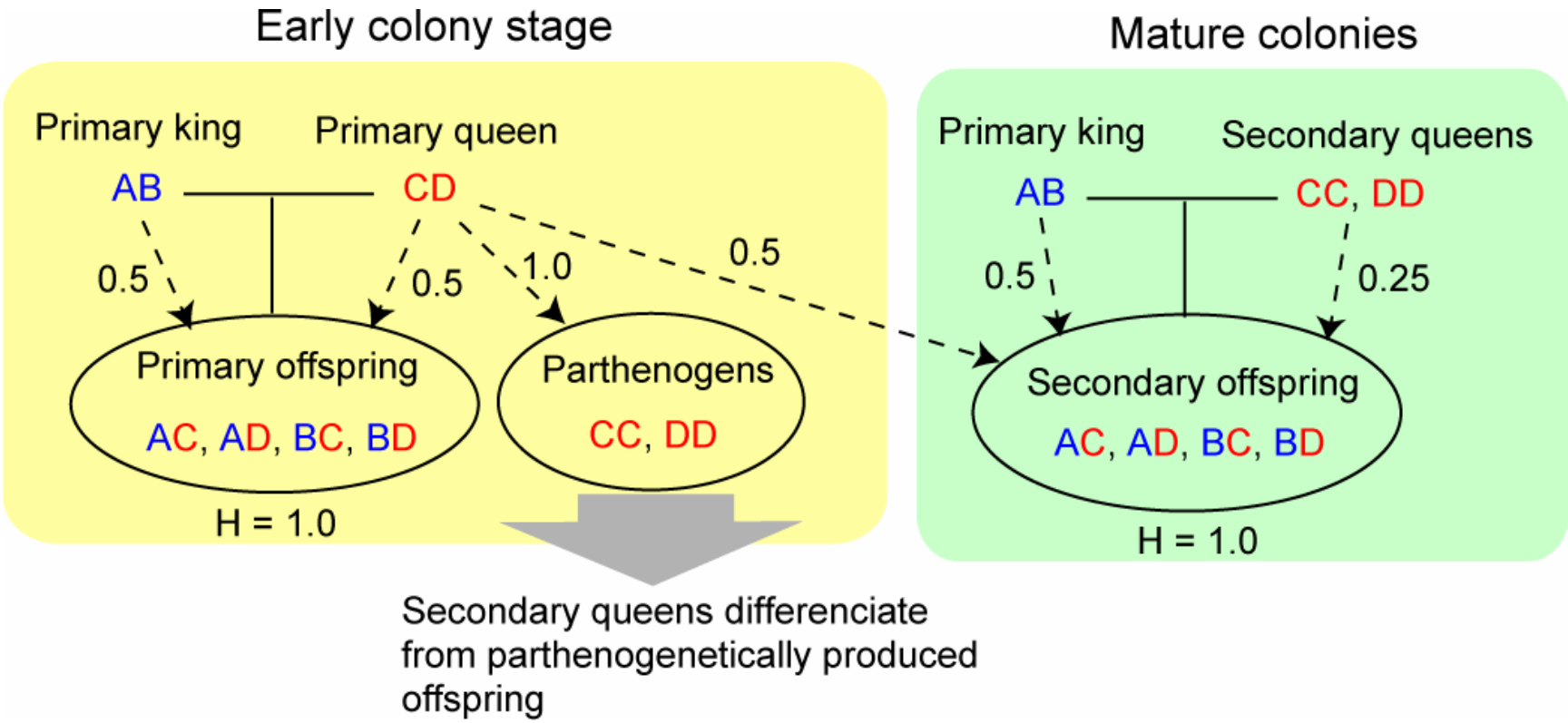


In queenless colonies: no policing / enforcement; simple Hamiltonian prediction recovered

Wenseleers & Ratnieks 2006

Conflict over male parentage

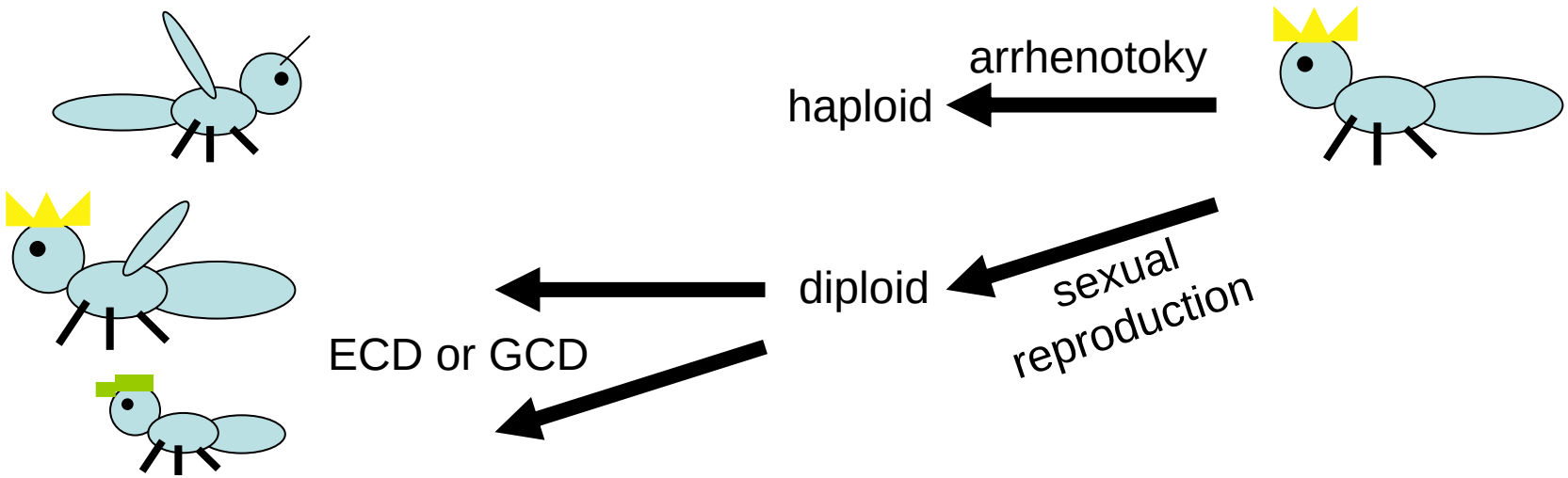
Asexual queen succession in termites



- Automixis with terminal fusion
- Queens retain the transmission rate of their genes to descendants even after death
- Complete avoidance of inbreeding for entire colony life

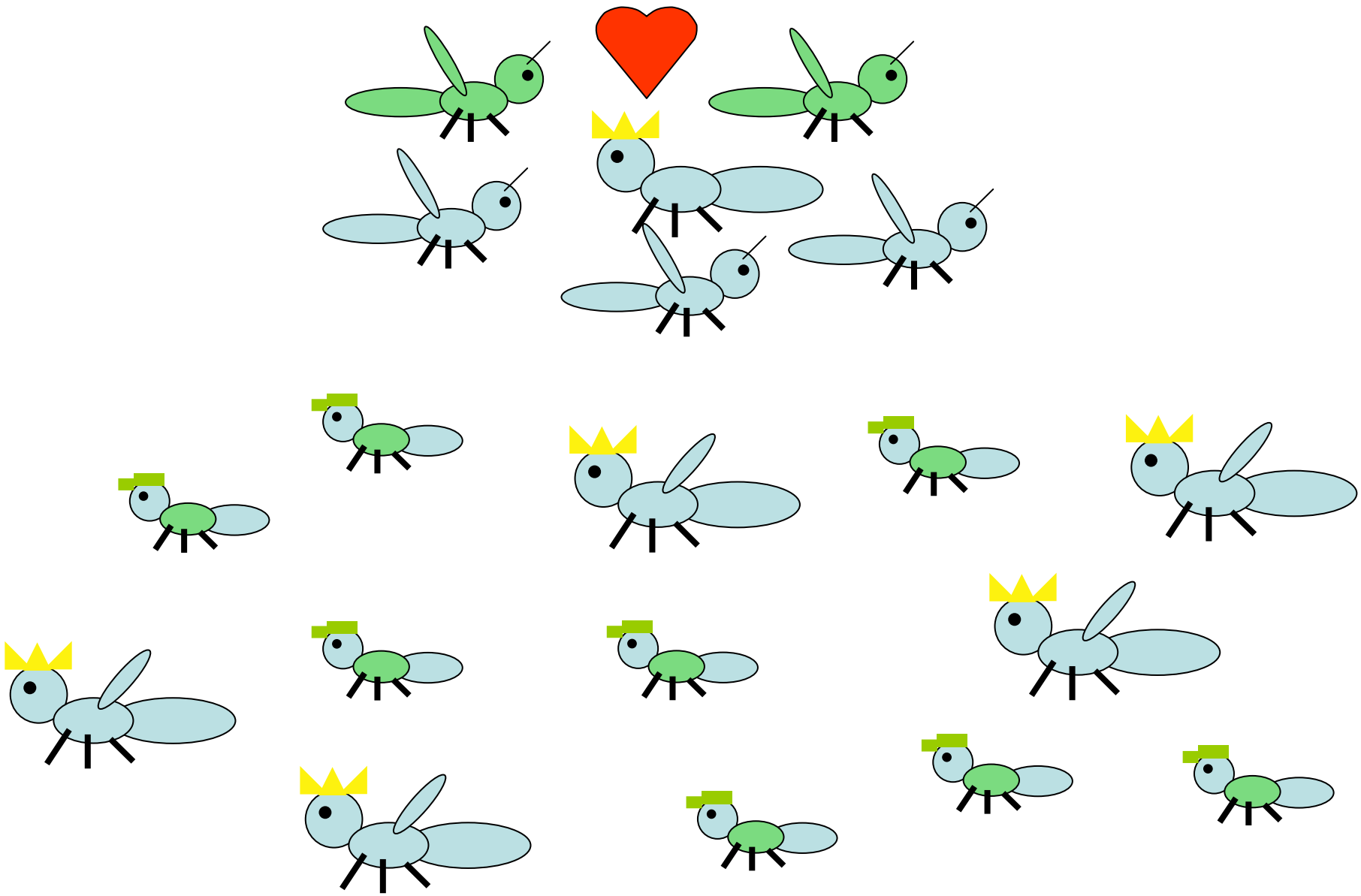
Relatedness
Paternal gene
Maternal gene
H: Heterozygosity

Matsuura et al., *Science* (2009)



- Hybrid sterility in workers has minimal fitness costs
- Queens with hybrid matings will still produce non-hybrid sons

UNUSUAL REPRODUCTIVE SYSTEMS



Hybridization and GCD in *Pogonomyrmex*

CONCLUSIONS

- Queen number, queen-mating frequency, reproductive skew and inbreeding determine colony kin-structure
- Multiple mating evolves to increase genetic diversity
- Multiple queen societies evolve in response to ecological factors
- Queen number and queen-mating frequency interact
- Colony kin-structure effects social conflicts
- Eusociality allows for the evolution of unusual reproductive systems

The Evolution of Colony Structure

in the Social Hymenoptera

DANIEL KRONAUER