

The origins and elaborations of eusociality
**Strict life-time monogamy as universal condition
 for transitions towards eusociality**

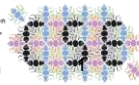
A new way of looking at Hamilton's rule



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Cooperation and conflict

- Mating pair
 - Making babies, but who does the work?
 - Strict monogamy promotes cooperation
 - Exit options induce conflict between sexes
- Cooperating group
 - Raising siblings, but for whose fitness benefit?
 - Obligate eusocial castes are committed altruists
 - Exit options towards independence exist in all cooperative breeders/facultative eusocial systems
- Obligate mutualism
 - Running a fungus-farm, but for whose profit?
 - Strict partner specificity promotes cooperation
 - Exit options induce conflict, but how to get "mutualistic monogamy" ?²



Hamilton's rule: $br > (0.5)c$



- Specifies the parameter space in which reproductive altruism can (should) evolve
- Does not specify the conditions for permanent loss of reproductive totipotency:
 - whether to become eusocial or a cooperative breeder
 - whether eusociality is the end point of a cooperative breeding continuum or a separate social evolution domain
- This has given a fair bit of confusion

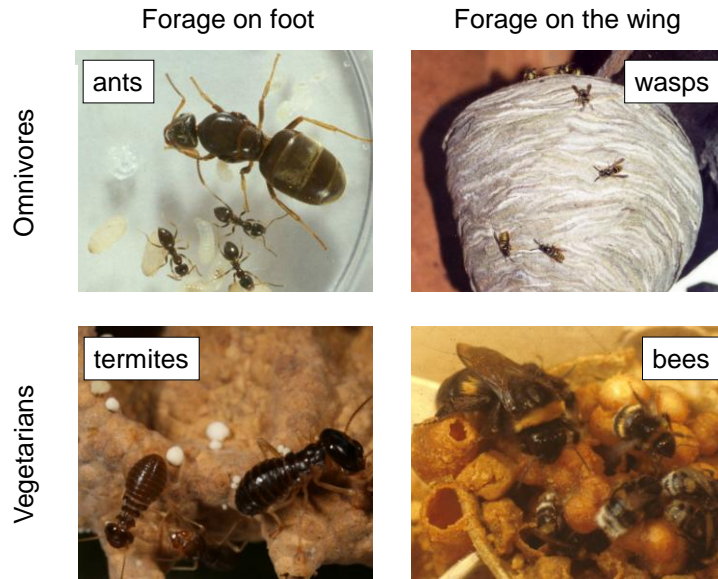
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Taking stock

- Eusocial Hymenoptera (ants, bees, wasps):
 - Multiple mating and polygyny common enough to be noticeable
 - Few believed these were derived conditions (but see Hamilton, 1964)
 - Haplodiploidy too cool not to give decisive $r > 0.5$ at origins
 - Alternative semi(para)-social transitional scenarios (without evidence that they have ever produced obligate eusociality)
- Termites:
 - Searching for >0.5 relatedness (inbreeding, ring chromosomes)
- The eusociality continuum idea (1980s) and group selection (2000s)
- Discovery of new 'shallow' cases of putative eusociality:
 - thrips, aphids, bark beetles, naked mole rats, snapping shrimps

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The obligate eusocial lineages



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Mating partners of all major eusocial clades commit for life

- Termites and *Cryptocercus* cockroaches are biparentally monogamous and almost all termites retained this



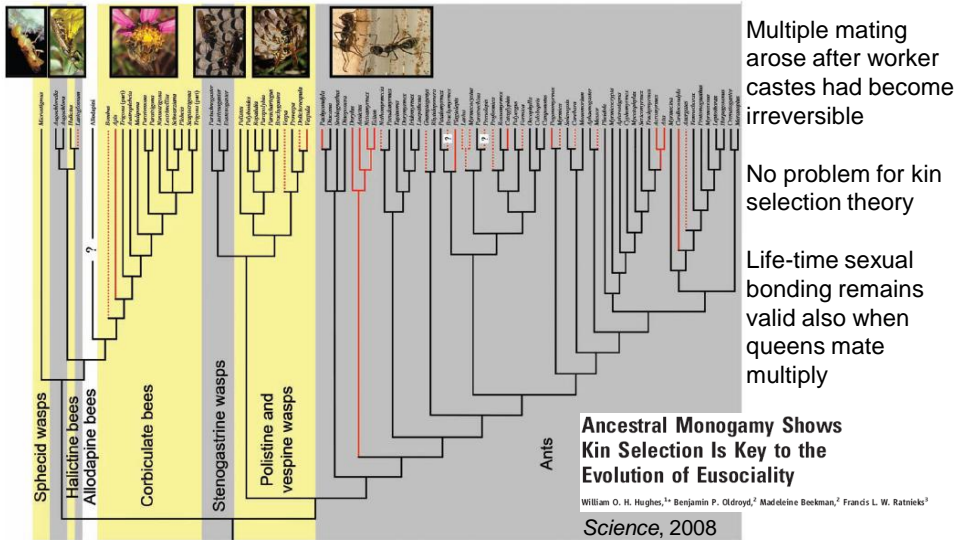
- Hymenopteran males survive only as stored sperm and queens never re-mate later in life (no remating promiscuity)



- Die with the only sexual partner you'll ever have
- Sex and society are completely separated



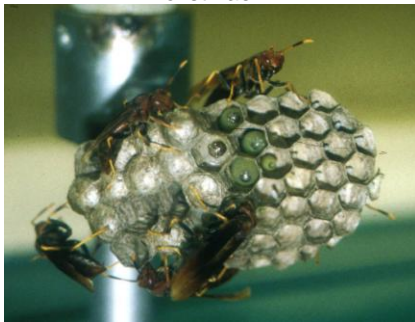
Comparative data show that single queen-mating is ancestral throughout eusocial ants, bees, wasps



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Both multiple mating and polygyny had to disappear before obligate eusociality could evolve

Polistinae



Advanced cooperative breeders

Vespinae



Obligatorily eusocial

'The life cycle of the vespines is basically similar to that of *Polistes*, except that the queen is not joined by auxiliaries during nest founding in spring'.

Wilson, 1971

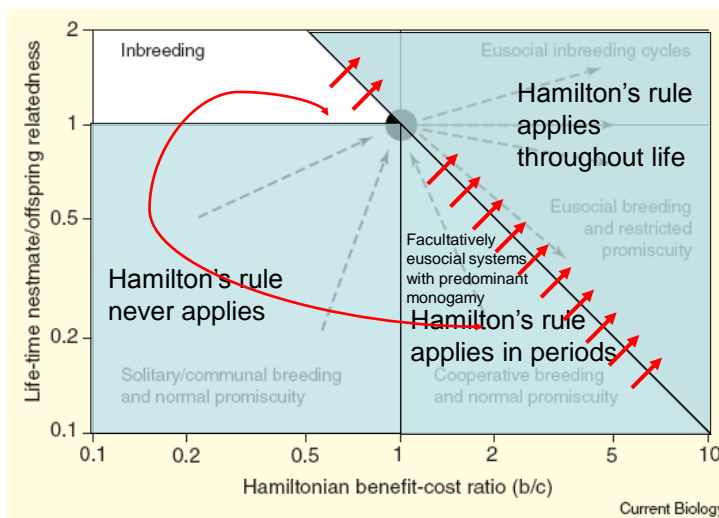
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The absence of re-mating promiscuity is key

- When queens **never** remate siblings are always full siblings, i.e. equivalent to offspring: $r = 0.5$ (termites) and $r = (0.75+0.25)/2 = 0.5$ (Hymenoptera)
- Origin obligate eusociality: $b/r > 0.5 c$, i.e. r cancels out of Hamilton's rule so that any marginal b/c benefit suffices
- $\bar{r} = 0.5$ appears to be a universal condition for the evolution of obligate eusociality
- Relatedness had to be constantly high (0.5) to be "irrelevant" for making the transition

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The monogamy window towards eusociality



Not supposed to happen

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Testable predictions

Comparative data and phylogenetics

- No obligate eusocial lineage has direct promiscuous ancestors
 - Consistent with the comparative data mapped on phylogenies
 - Lineages may be (mostly) monogamous long before becoming eusocial
- Cooperative breeders in which helpers obtain large indirect fitness benefits should be little promiscuous
 - Consistent with the comparative data (e.g. naked mole rates; cooperatively breeding birds)
- Male survival as stored sperm pre-adapted the Hymenoptera to evolve obligate eusociality
 - Consistent with the comparative data (ants, bees, wasps *versus* termites)

Boomsma (2009). *Phil. Trans. Roy. Soc.*

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Testable predictions

Genomics – EvoDevo - Proteomics

- Putative sexually antagonistic genes in eusocial lineages with multiple queen-mating ALL evolved independently
 - Testable in issues of ejaculate competition in ants, bees, wasps (we now have the first data on this)
- Nepotistic discrimination may occur in cooperative breeders (e.g. vertebrates, *Polistes* wasps, halictid bees), but got lost in monogamy windows and needed very special conditions to re-evolve in the obligate eusocial clades
 - Testable by comparing ponerine ant and *Polistes/Rhopalidia* dominance hierarchies
 - Expect convergent analogous gene expression pathways, not homologous ones

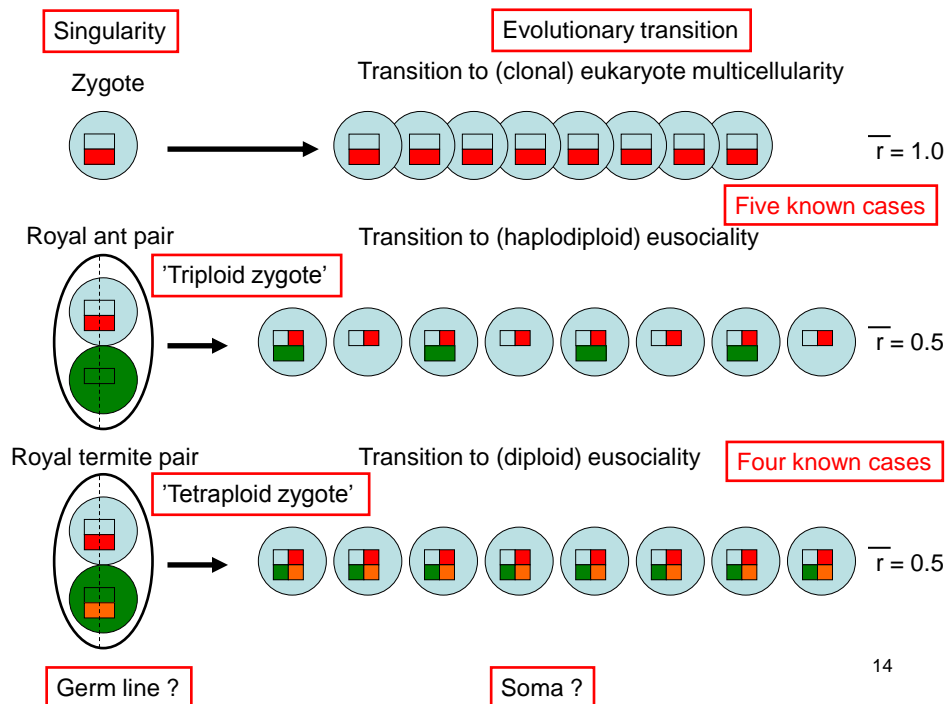
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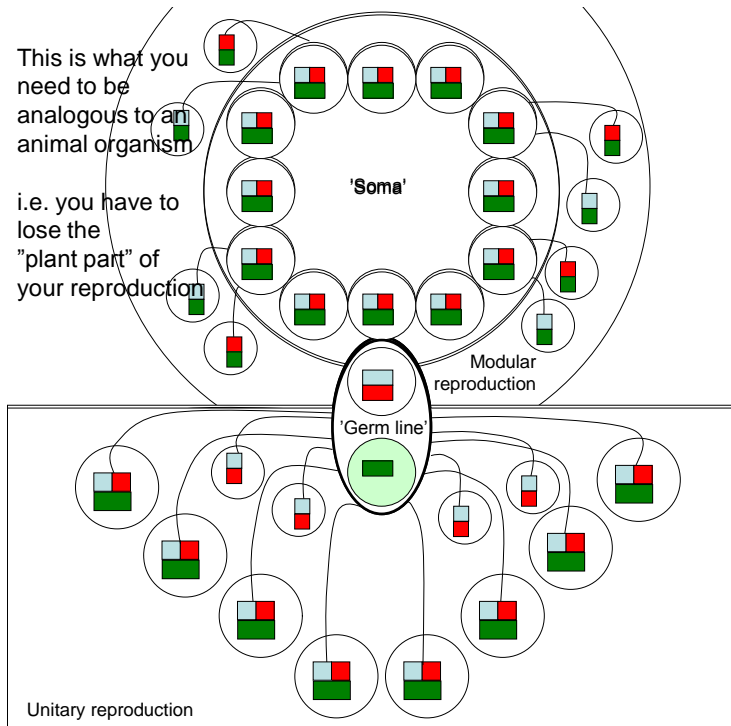
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Eusociality and cooperative breeding as domains

summary of arguments and further extension

- Eusociality (obligate/permanent) can evolve only when Hamilton's rule is fulfilled throughout the adult life of all helpers
- Cooperative breeding evolves when Hamilton's rule applies during some period of adult life; this includes facultative eusociality
- Re-mating promiscuity is compatible with cooperative breeding, but not with obligate eusociality
- These domains of social evolution are characterized by different sectors of parameter space for Hamilton rule
- The monogamy window is a singularity comparable to the $2n$ zygote; both can give rise to analogous evolutionary transitions¹³





Are there any obligate eusocial lineages that have become fully unitary?



Single queen + committed father(s)

Sterile workers

100% reproductive division of labor

Conclusions

- The evolution of eusociality may have been simpler than we thought:
 - Obligate eusocial lineages are old and have substantially radiated: ants, corbiculate bees, vespine wasps, higher termites
 - Cooperative breeding lineages are usually young and have recent solitary sister clades or within-clade reversals
 - If they are older they lack remating promiscuity (lower termites, most social wasps, halictid bees)
- Cooperative breeders and facultatively eusocial systems are THE direct testing ground for Hamilton's rule (b , r and c all vary)
- The eusocial domain provides indirect tests of Hamilton's rule; these were often most powerful because only r varied

Conclusions

The four origins of obligate eusociality are:

- "major transitions in evolution" – living in societies, i.e. being facultatively eusocial or advanced cooperative breeder is not
- rare because mating systems based on life-time commitments are unlikely to be evolutionary stable unless very special ecological conditions apply
- spectacular ecological successes, similar to the few eukaryote multicellular lineages that evolved
- highly sophisticated societies, with a number of (super-) organismic properties (e.g. for resource acquisition and communication), but without complete individuality

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