

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

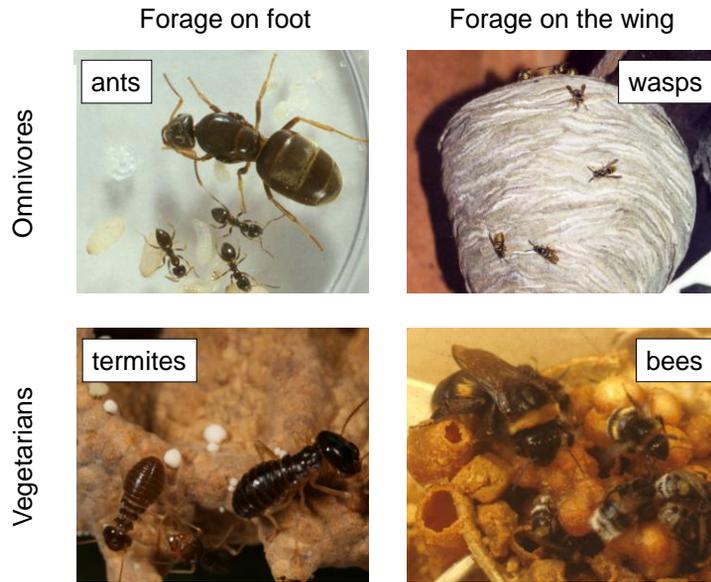
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Taking stock

- 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



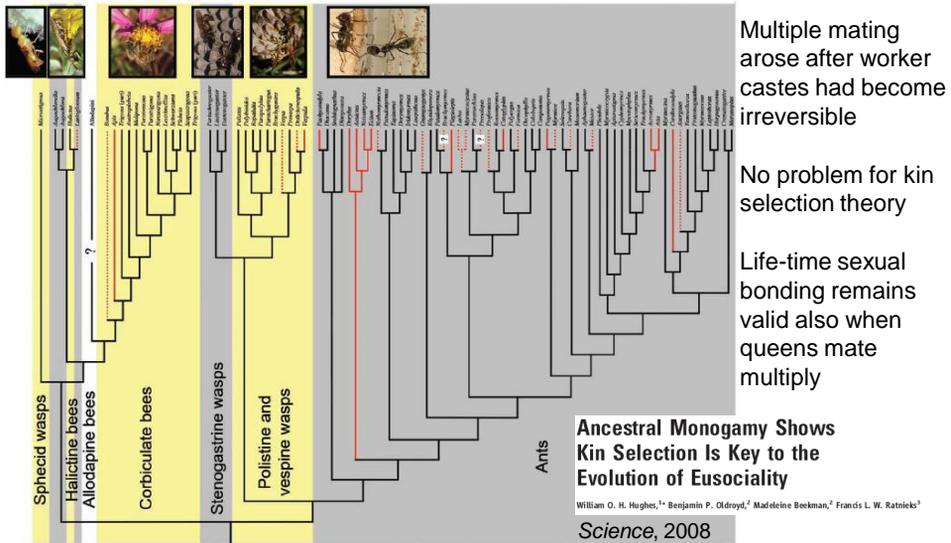
- Hymenopteran males survive only as stored sperm and queens never re-mate later in life (no remating promiscuity)



- 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

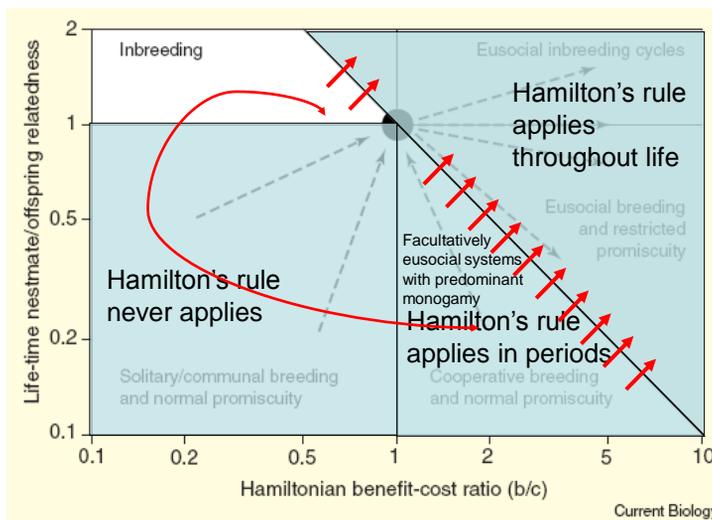
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The absence of re-mating promiscuity is key

- 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



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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

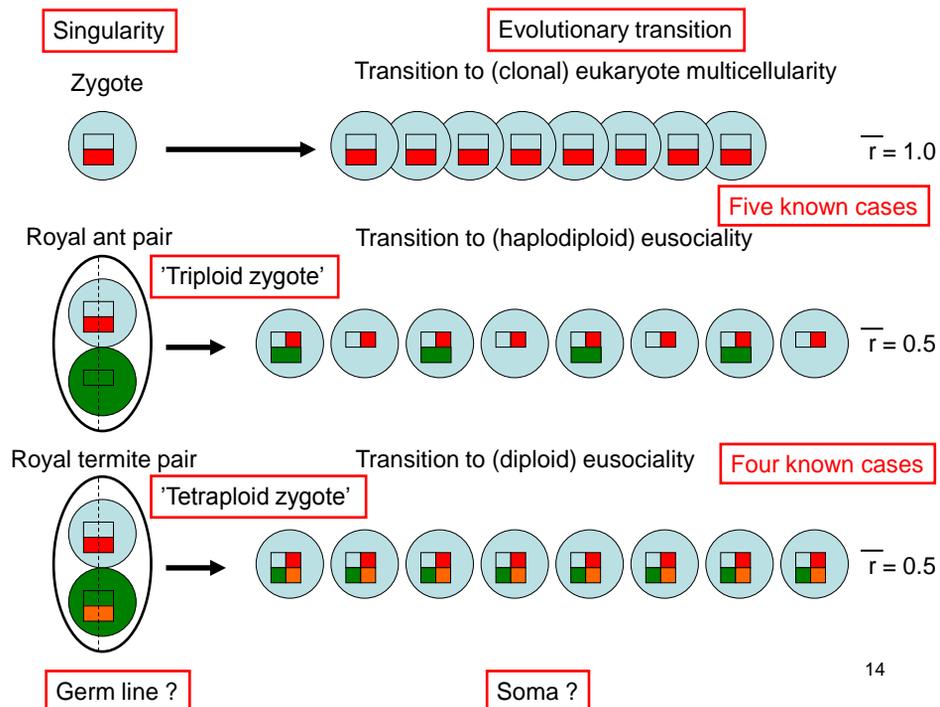
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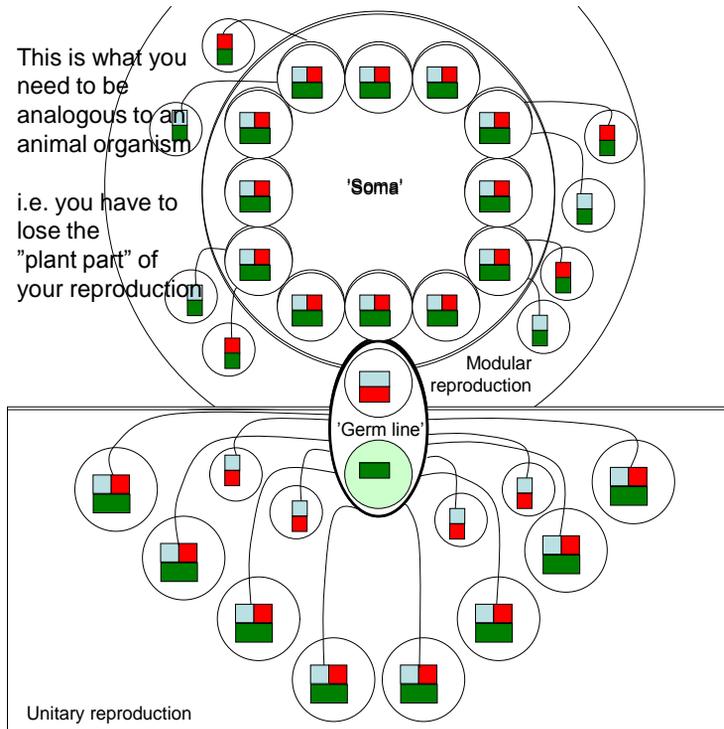
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Eusociality and cooperative breeding as domains

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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