The Evolution of Eusociality

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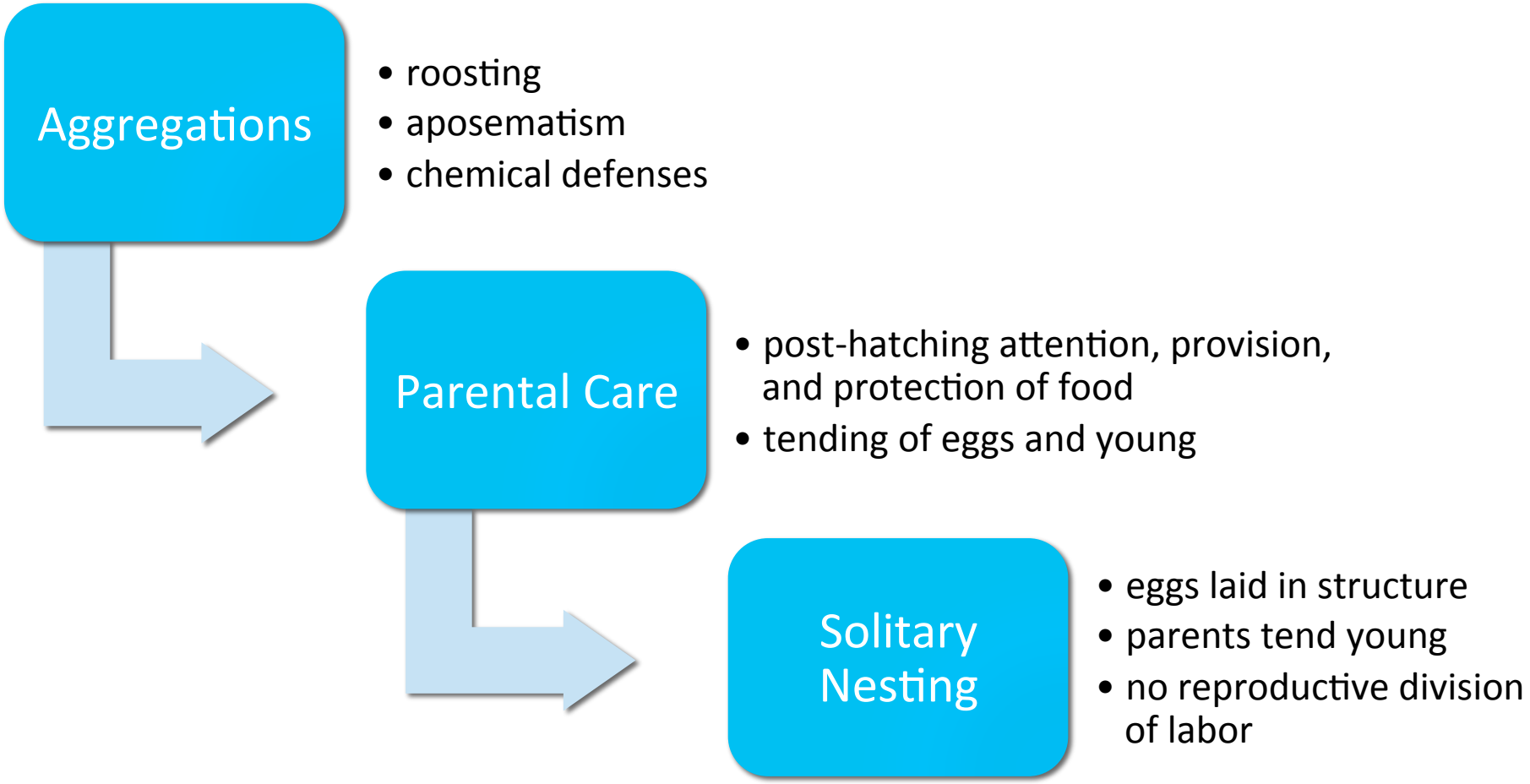
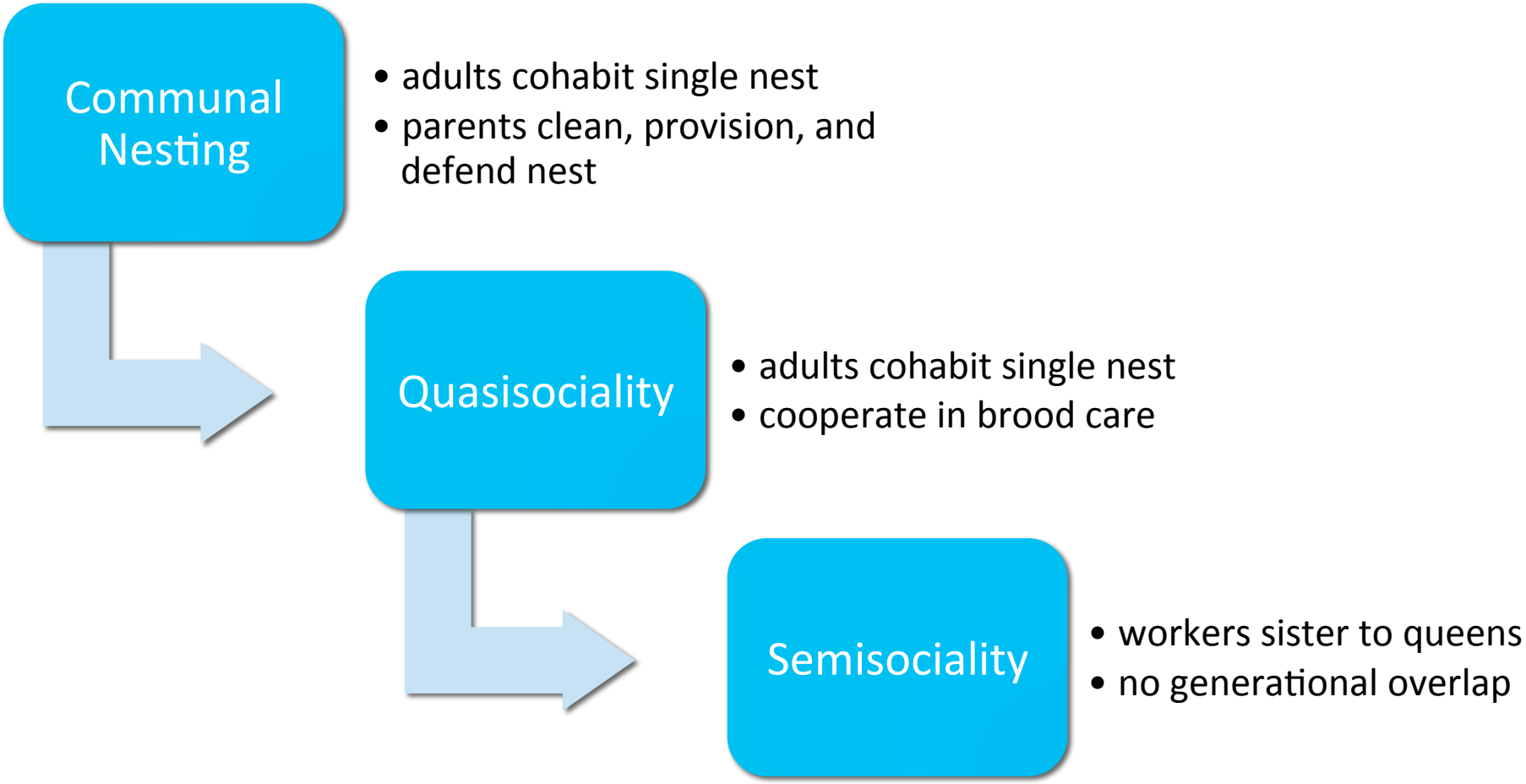
Stages of Social Behavior



Stages of Social Behavior



Eusociality

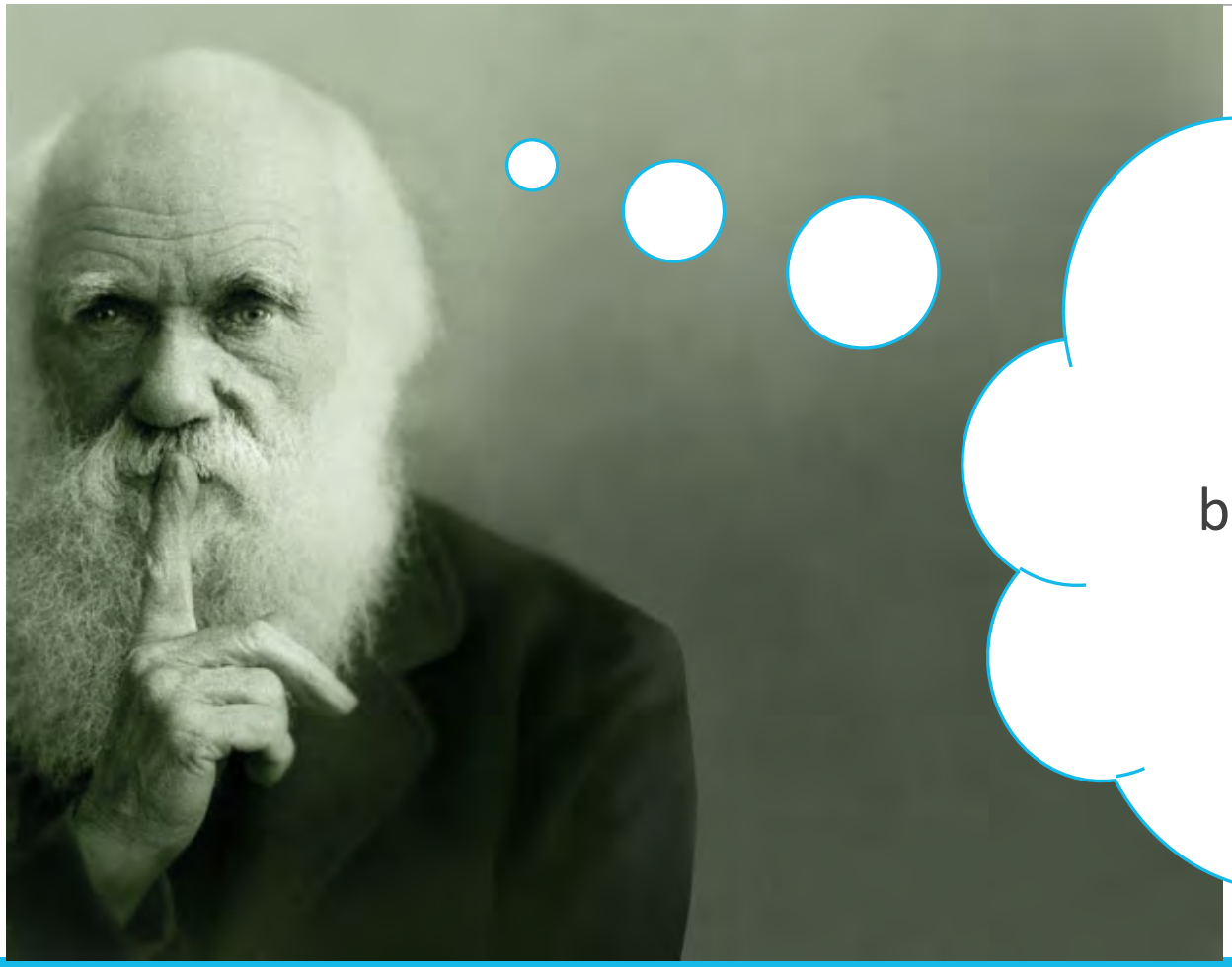
Defining Properties:

1. division of reproductive labor
2. cooperative parental care
3. multigenerational colonies

Advanced Eusociality:

- polyphenism: morphological differences between queen and workers
- polyethism: behavioral differences between queen and workers
- caste system: can include reproductives, workers, and soldiers
  - subcastes possible

Darwinian Dilemma

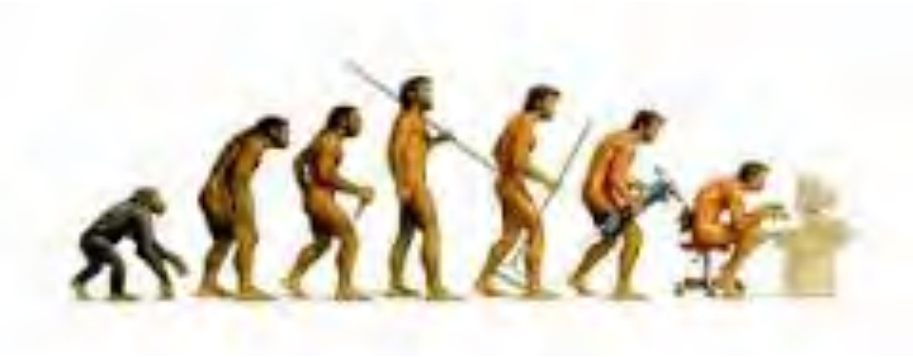


How can genetically prescribed selfless behavior arise through natural selection?

Prior Understandings

1859: Charles Darwin – *The Origin of Species*:

- if sterility can be carried but not expressed and sterile individuals help reproductive individuals, then the sterile trait can persist



Prior Understandings

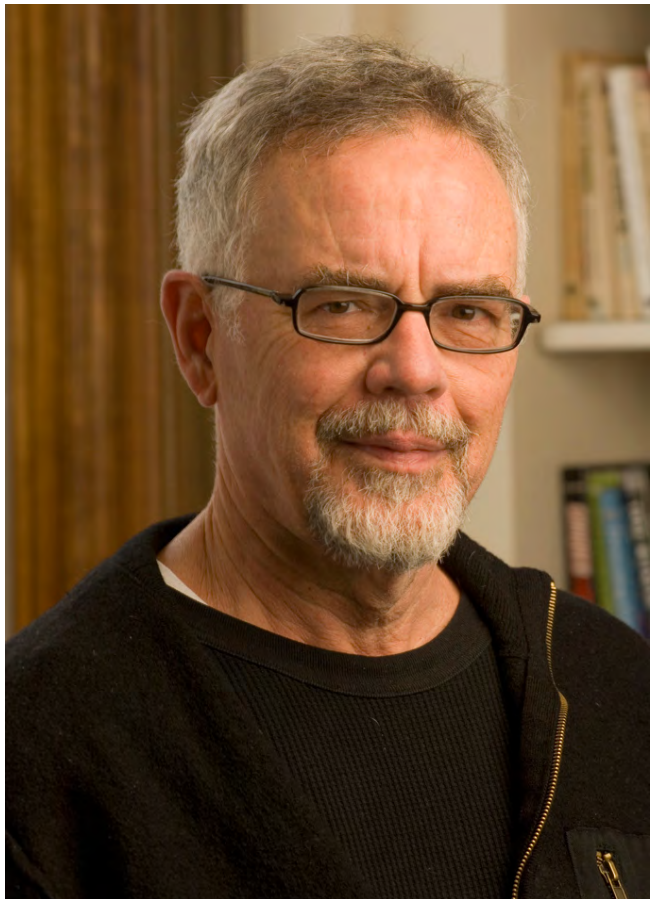
1964: W.D. Hamilton:

- inclusive fitness: individual reproductive success + reproductive success of others with similar genes
- kin selection: favoring of collateral relatives by an individual
- Hamilton's rule: altruism is advantageous if rB > C

Prior Understandings

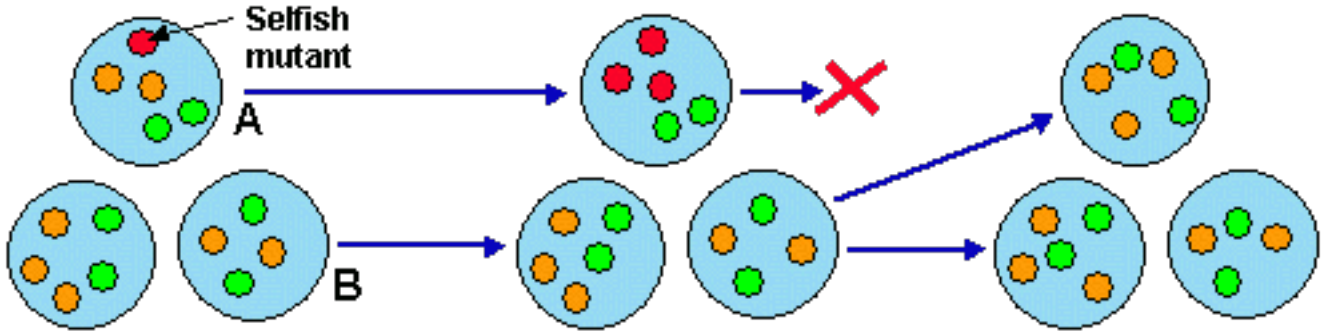
1971: R.L. Trivers:

- reciprocal altruism: the cost of altruism may be beneficial if there is a chance of being in a reverse situation
  - explains how selection can operate against a cheater



Different Selective Forces

- individual direct selection: differential personal survival and reproduction of each colony member
- kin selection: (dis)favoring of collateral relatives by an individual
- group selection: differential survival and reproduction of entire cooperative groups



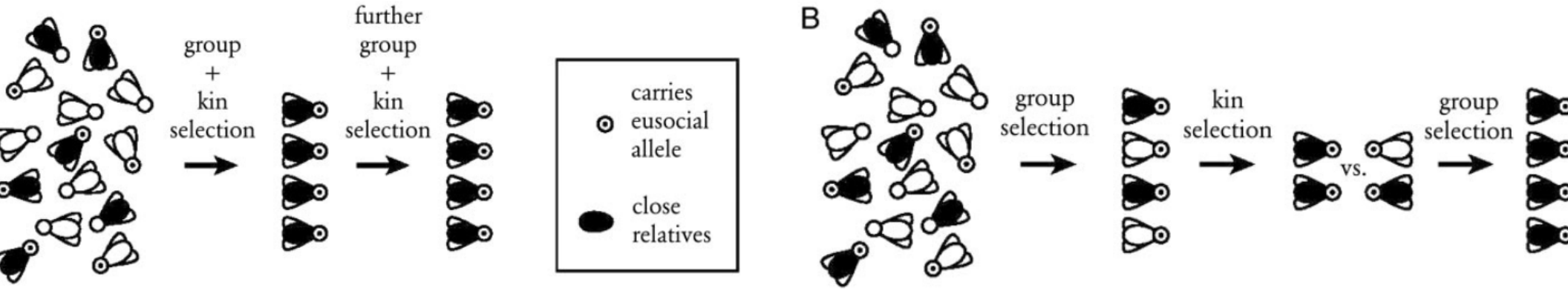
The Debate

Is the evolution of eusociality influenced more by kin selection or by group selection?

Wilson & Hölldobler (2005)

Model A	Model B
altruism originates by selection of its prescribing alleles through **kin network**	• altruism originates by **group selection** of its phenotypically flexible prescribing alleles
group selection from environmental pressure and kin selection drive evolution of system	• kin selection is absent, weakly binding or weakly dissolutive
close relatedness precedes origin of eusociality	• relatedness arises from eusociality bu is not necessary condition

Wilson & Hölldobler (2005)



Discussion

Question: Both hypotheses mention prescribing “eusociality” alleles. What might be the mechanism behind these alleles, i.e. what is the result of having them?

Answer:

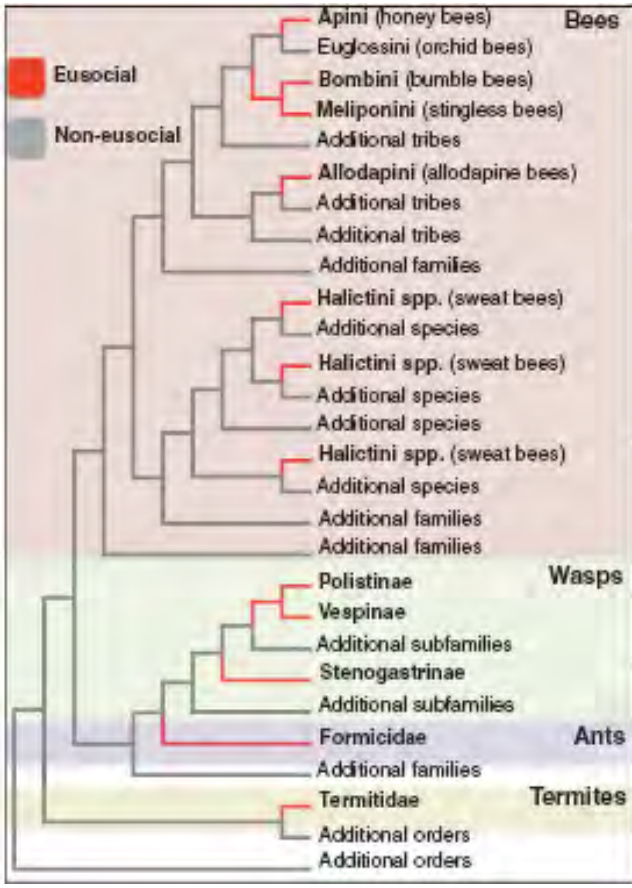
- promotes altruism
- promotes cooperation
- causes daughters to stay in the colony rather than dispersing

Support for Model B

1. relatedness can have "dissolutive effects"
   - relatedness causes group-wide divisions → competition amongst each other
   - ex. in Xylocopine carpenter bee pairs, subordinates only prefer to stay if unrelated
   - ex. primitively eusocial wasps don't favor close over distant relatives when founding colonies
   - ex. lack of favoring bias by workers of their respective mother in colonies with multiple queens
2. phylogenetic rarity of eusociality
3. ecological success of extreme eusociality

Support for Model B

1. relatedness can have "dissolutive effects"
2. phylogenetic rarity of eusociality
   - only 12 known origins in arthropods
   - nature has set "high bar" for development of eusociality
   - plasticity of genome helps it be molded by group selection
3. ecological success of extreme eusociality



Discussion

Question: If kin selection is a driving factor in the evolution of eusociality, why hasn't it evolved more in other lineages that live in related groups?

Answer:

- hyperrelatedness may also be a necessary condition
- presumably requires perfect set of environmental circumstances

Discussion

Question: Wilson & Hölldobler mention that “extraordinary circumstances” are necessary to “vault the bar,” but what might these be?

Answer: ????? but possibly:

- occupy habitat that is easily defended
- reside in location with abundant resources to support large populations

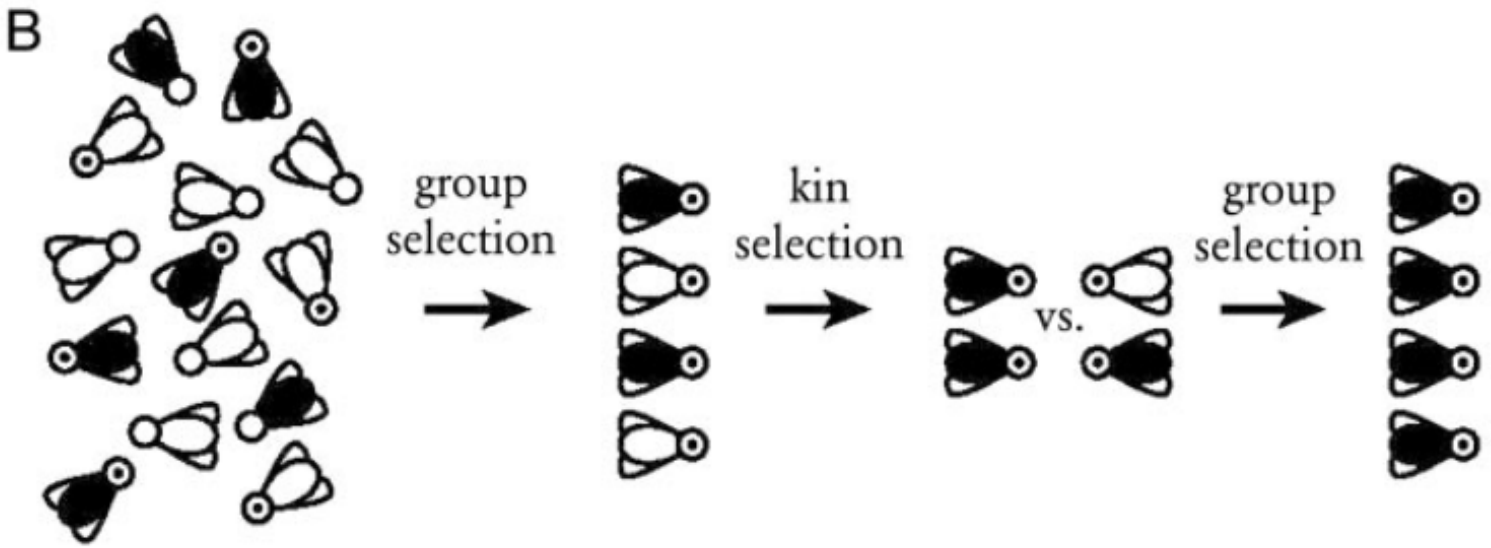
Support for Model B

1. relatedness can have "dissolutive effects"
2. phylogenetic rarity of eusociality
3. ecological success of extreme eusociality
   - ants and termites: 2% of insect species but >1/2 total insect biomass
   - groups can dominate central, stable areas of habitat
   - better to live in a group and sacrifice reproduction than to live as a solitary reproductive individual

Wilson & Hölldobler (2005) Conclusions

If their alternative hypothesis (Model B) is correct:

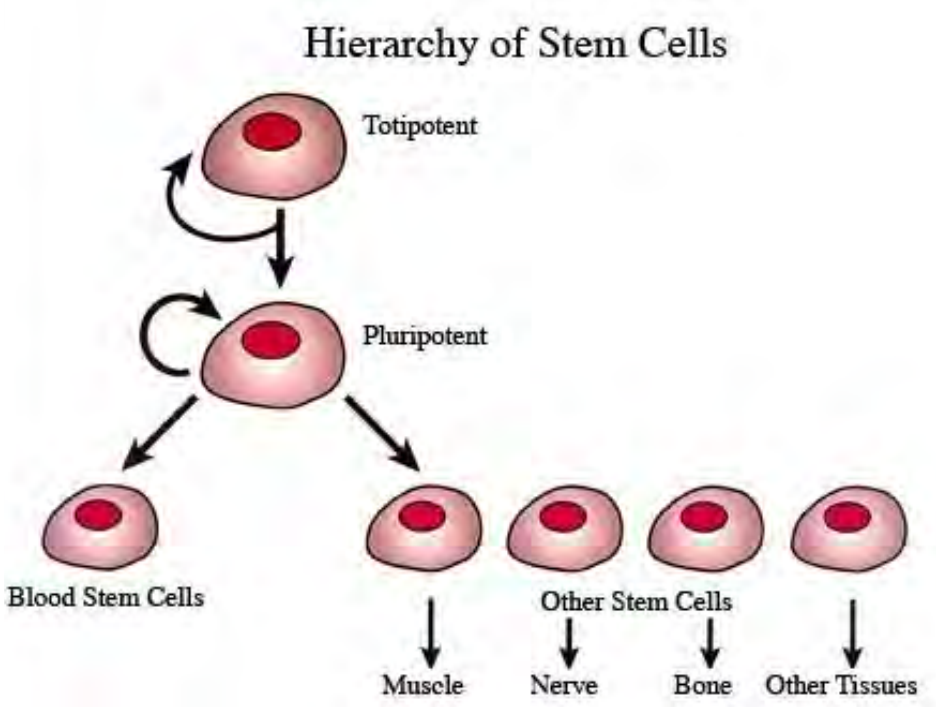
- **the evolution of eusociality is driven by group selection** rather than kin selection
- **relatedness is a consequence rather than a cause of eusociality**



Wilson & Hölldobler vs. Hughes et. al.

Hughes et. al. (2008) Terminology

- polygyny: one male mating with multiple females
  - reduces relatedness among siblings
- polyandry: one female mating with multiple males
  - reduces relatedness among siblings
- monandry: female with one mating partner
- totipotency: ability of a cell to differentiate into any other cell type



Hughes et. al. (2008) Predictions

IF Wilson & Hölldobler are INCORRECT that group selection > kin selection and high relatedness is not a necessary condition for the evolution of eusociality, THEN:

- monandry should be ancestral state
- polyandry should only evolve after workers have lost reproductive totipotency
- functional polygyny should not be ancestral state

Discussion

Question: The authors hypothesized that polyandry should only evolv if workers had already lost reproductive totipotency. Why is this? What is the evolutionary advantage of developing polyandry as a derived state?

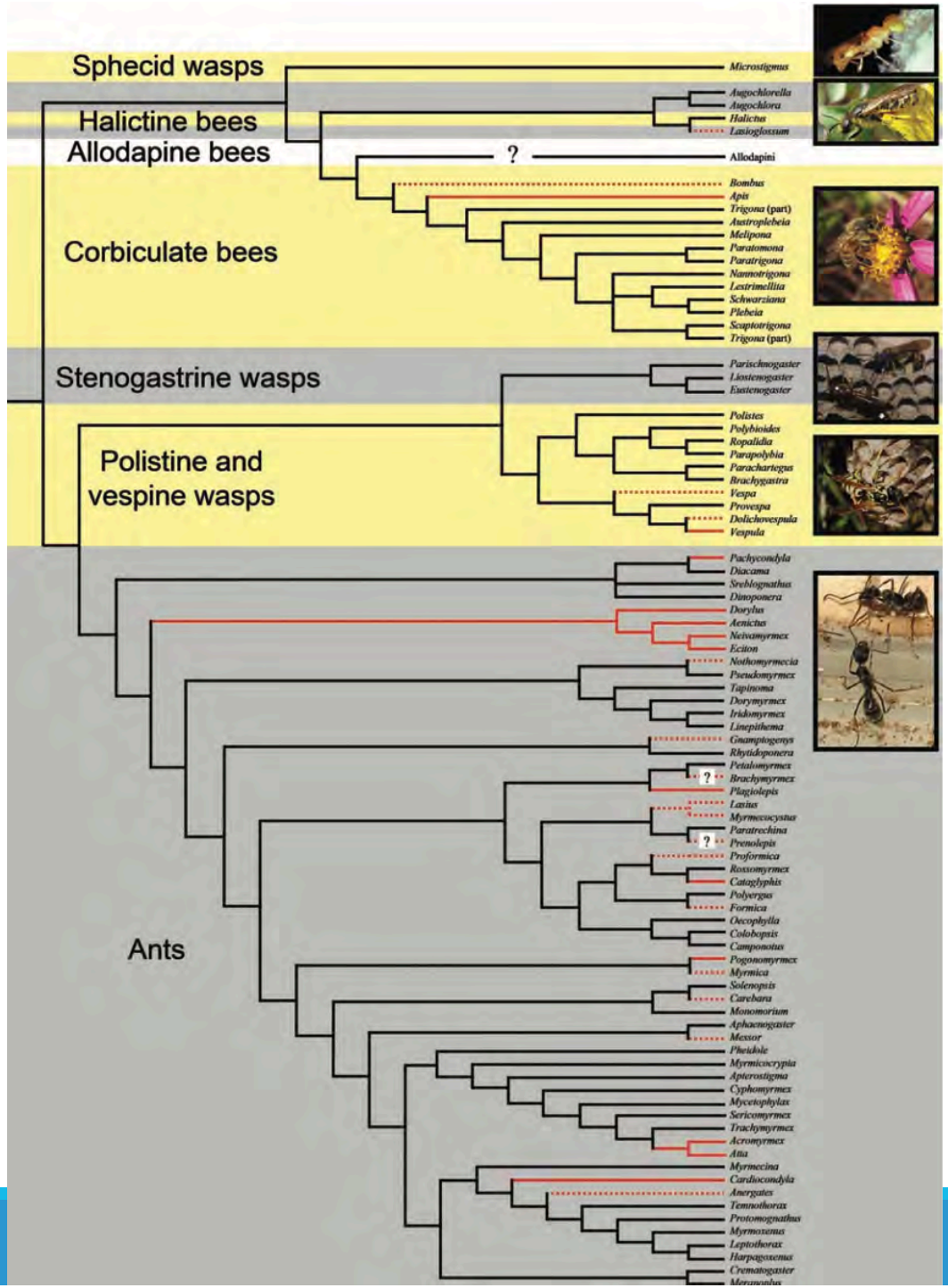
Answer: Polyandry reduces relatedness of sisters. If kin selection is important, then workers would be more likely to undermine the quee and reproduce on their own if their sisters were no longer hyperrelated. However, mating multiply allows queens to introduce genetic variation into the colony.

Hughes et. al. (2008) Methods

- collected data set of female mating frequencies and worker reproductive totipotency for 267 species of social Hymenoptera
- mapped data onto phylogeny
- carried out ancestral state reconstruction for:
  - monandry/polyandry
  - polygyny
- used phylogenetic independent contrasts to analyze relationship between totipotency and polyandry

Hughes et. al. (2008) Conclusions

- monandry was ancestral state for all eight independent origins of eusociality
- worker reproductive totipotency associated with monandry
  - obligate or high polyandry are derived and occur only in species whose workers lack the ability to become primary breeders
- functional polygyny was derived state


Sphecid wasps
Halictine bees
Allodapine bees
Corbiculate bees
Stenogastrine wasps
Polistine and vespine wasps
Ants
Microstigmus
Augochlorella
Augochlora
Halictus
Lasioglossum
?
Allodapini
Bombus
Apis
Trigona (part)
Austroplebeia
Melipona
Paratomona
Paratrigona
Nannotrigona
Lestrimellita
Schwarziana
Plebeia
Scaptotrigona
Trigona (part)
Parischnogaster
Liostenogaster
Eustenogaster
Polistes
Polybioides
Ropalidia
Parapolybia
Parachartegus
Brachygastra
Vespa
Provespa
Dolichovespula
Vespula
Pachycondyla
Diacama
Streblognathus
Dinoponera
Dorylus
Aenictus
Neivamyrmex
Eciton
Nothomyrmecia
Pseudomyrmex
Tapinoma
Dorymyrmex
Iridomyrmex
Linepithema
Gnamptogenys
Rhytidoponera
Petalomyrmex
Brachymyrmex
Plagiolepis
Lasius
Myrmecocystus
Paratrechina
Prenolepis
Proformica
Rossomyrmex
Cataglyphis
Polyergus
Formica
Oecophylla
Colobopsis
Camponotus
Pogonomyrmex
Myrmica
Solenopsis
Carebara
Monomorium
Aphaenogaster
Messor
Pheidole
Myrmicocrypta
Apterostigma
Cyphomyrmex
Mycetophylax
Sericomyrmex
Trachymyrmex
Acromyrmex
Atta
Myrmecina
Cardiocondyla
Anergates
Temnothorax
Protomognathus
Myrmoxenus
Leptothorax
Harpagoxenus
Crematogaster
Meranoplus

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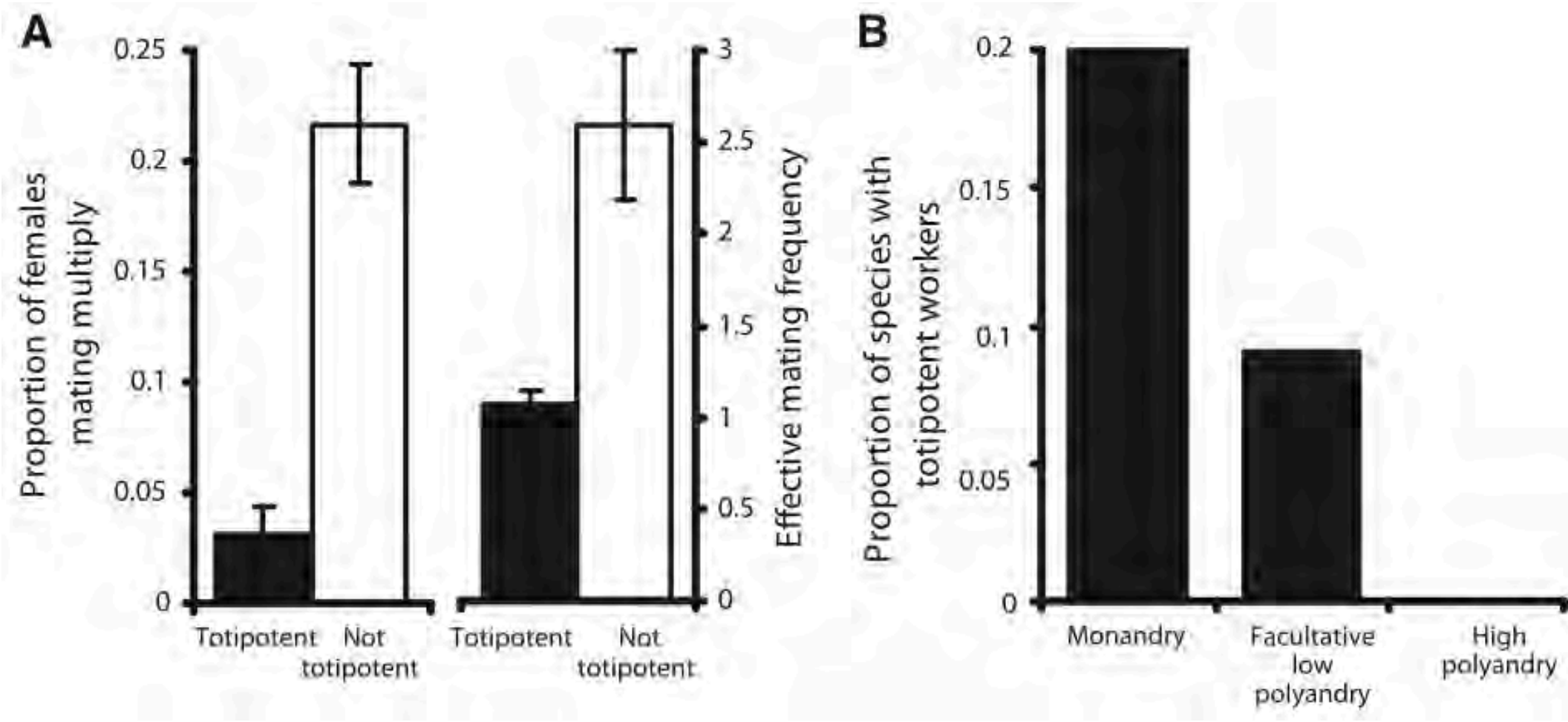

A
Proportion of females mating multiply
0.25
0.2
0.15
0.1
0.05
0
Totipotent
Not totipotent
Totipotent
Not totipotent
Effective mating frequency
3
2.5
2
1.5
1
0.5
0
B
Proportion of species with totipotent workers
0.2
0.15
0.1
0.05
0
Monandry
Facultative low polyandry
High polyandry

Hughes et. al. (2008) Conclusions

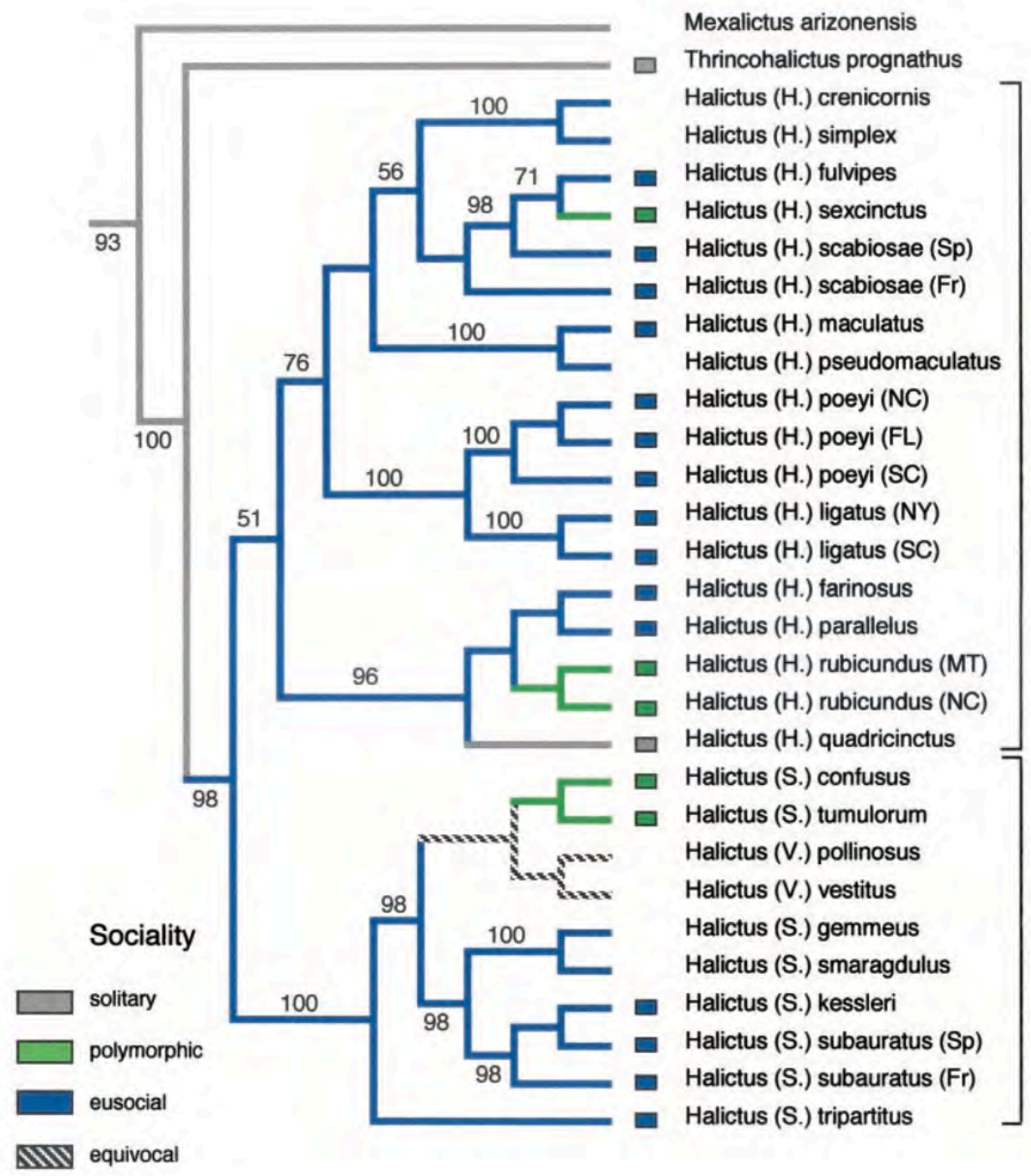
- monandry was ancestral state for all eight independent origins of eusociality
- worker reproductive totipotency associated with monandry
  - obligate or high polyandry are derived and occur only in species whose workers lack the ability to become primary breeders
- functional polygyny was derived state

Kin selection and high relatedness have played a decisive role in the evolution of eusociality

Taxa	Eusocial origins	Eusocial species	Evidence
Sphecid wasps	1	1	This study; $P < 0.0001$; $P < 0.0001$
Halictid bees (*Augochlorella/Augochlora*)	1	Many of 140	This study; $P = 0.0014$; $P < 0.0001$
Halictid bees (*Halictus*)	1	Most of 217	This study; $P = 0.0014$; $P < 0.0001$
Halictid bees (*Lasioglossum*)	1	Most of 544	This study; $P = 0.003$; $P < 0.0001$
Allodapine bees	1		No data
Corbiculate bees	1	≈1000	This study; $P = 0.015$; $P = 0.0007$
Stenogastrine wasps	1	≈50	This study; $P = 0.0026$; $P < 0.0001$
Polistine and vespid wasps	1	≈860	This study; $P = 0.043$; $P < 0.0001$
Ants	1	≈12,000	This study; $P = 0.034$; $P = 0.0007$
Ambrosia beetle	1	1	Monoandry thought probable but no data (*19*)
Aphids	≈17	≈50	Eusocial colonies produced parthenogenetically by single female (*4*, *23*)
Termites	1	≈2800	Generally monoandrous, with only a few species exhibiting low polyandry (*4*)
Thrips	1	7	Normally monoandrous (*4*, *23*, *24*)
Snapping shrimps	3	6	Monoandrous (*20*)
Mole rats	2	2	Facultative low polyandry (*21*, *22*)

Danforth (2001)

- when reversals from primitive eusociality to solitary nesting do occur, they correspond with decreases in relatedness



Discussion

Question: Wilson & Holldobler attempted to provide an alternative hypothesis for the evolution of eusociality, but it was shot down by Danforth (2001) and Hughes et. al. (2008).
What did Wilson & Holldobler do wrong?

Answer: “From observing the growth of a hair, can we learn anything concerning the generation of a man?” – David Hume

- cherry-picked examples
- ignored evolutionary history
- used only qualitative analyses

Publishing and Reputation

E.O. Williams:

- "father of sociobiology"
- developed theory of island biogeography
- Harvard University graduate → professor
- two-time winner of Pulitzer Prize for General Non-Fiction
- three-time *New York Times* bestseller

Takeaway Points

- no single trait or model is sufficient to conclusively explain the evolution of eusociality
  - the origins likely involved combination of pre-conditions, environmental/ ecological factors, and genetic influences
- phylogenies and evolutionary history must always be used when trying to discern cause/effect
- even scientific literature should be taken with a grain of salt and regarded with a certain degree of skepticism

Works Cited

Danforth, B. N. 2002. Evolution of sociality in a primitively eusocial lineage of bees. Proceedings o the National Academy of Sciences 99:286–290.

Darwin, C. 2003. The Origin of Species: 150th Anniversary Edition. Signet.

Hamilton, W. D. 1964. The genetical evolution of social behavior. Journal of Theoretical Biology 7:1–16.

Hughes, W. O. H., B. P. Oldroyd, M. Beekman, and F. L. W. Ratnieks. 2008. Ancestral Monogamy Shows Kin Selection Is Key to the Evolution of Eusociality. Science 320:1213–1216.

Trivers, R. L. 1971. The Evolution of Reciprocal Altruism. The Quarterly Review of Biology 46:35–57.

Wilson, E. O., and B. Hölldobler. 2005. Eusociality: Origin and consequences. Proceedings of the National Academy of Sciences of the United States of America 102:13367–13371.