Plasticity of insect social behavior

Tamar Keasar
University of Haifa – Oranim
tkeasar@research.haifa.ac.il

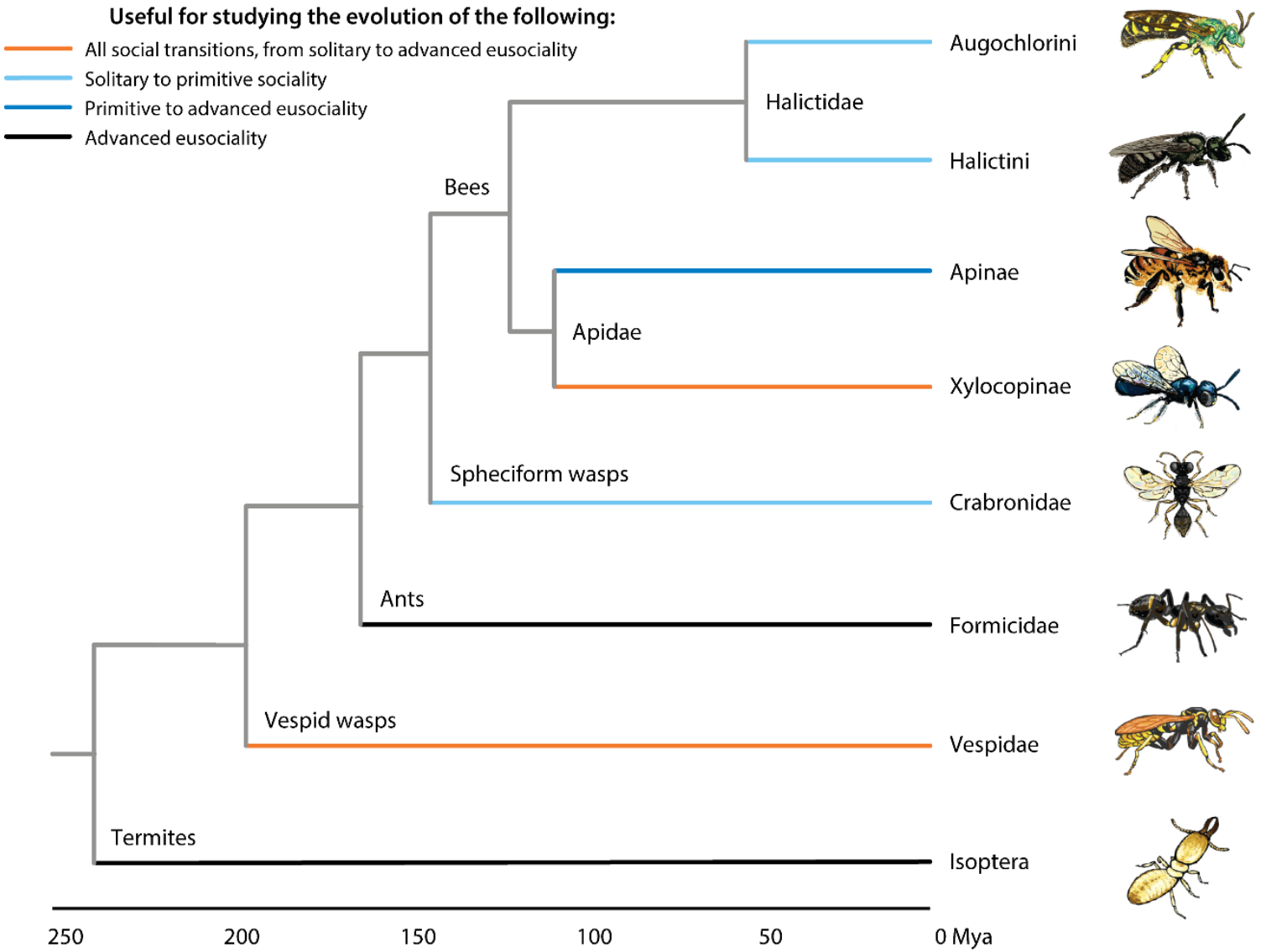
A major evolutionary transition

TABLE 1 The major transitions[1]

Replicating molecules to populations of molecules in compartments
Unlinked replicators to chromosomes
RNA as gene and enzyme to DNA and protein (genetic code)
Prokaryotes to eukaryotes
Asexual clones to sexual populations
Protists to animals, plants and fungi (cell differentiation)
Solitary individuals to colonies (non-reproductive castes)
Primate societies to human societies (language)

Szathmary & Maynard Smith, 1995

Insects exhibit a wide range of sociality patterns



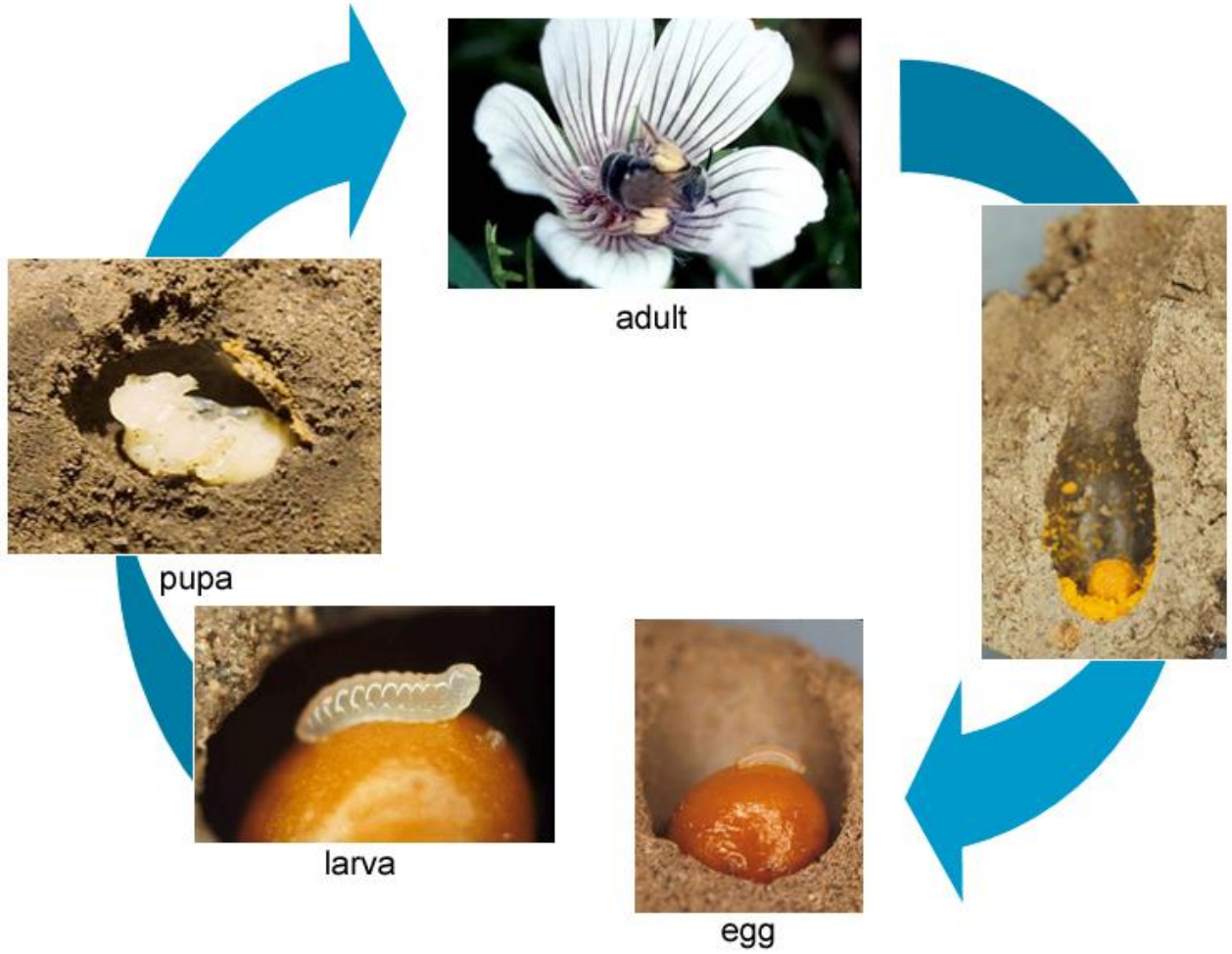
Toth & Rehan 2017

Aspects of insect social life

Table I. Social terminology—adapted from Rehan and Toth 2015

Stage	Social class	Cooperative brood care	Overlapping generations	Division of labor	Facultative sociality	Examples—with genomes
Early	Solitary	No	No	No	No	*Megachile rotundata*, *Dufourea novaeangliae*, *Habropoda laboriosa* (Kapheim et al. 2015)
	Subsocial	No	Some	No	Yes	*Ceratina calcarata* (Rehan et al. 2016)
	Incipiently social	Yes	Some	Some	Yes	*Ceratina australensis* (Rehan et al. unpub. data)
Late	Primitively eusocial	Yes	Some	Yes	Yes	*Lasioglossum albipes* (Kocher et al. 2013); *Bombus terrestris*; *Bombus impatiens* (Sadd et al. 2015)
	Advanced eusocial	Yes	Yes	Yes	No	*Apis mellifera*, *Apis florea*, *Melipona quadrifasciata* (Kapheim et al. 2015)

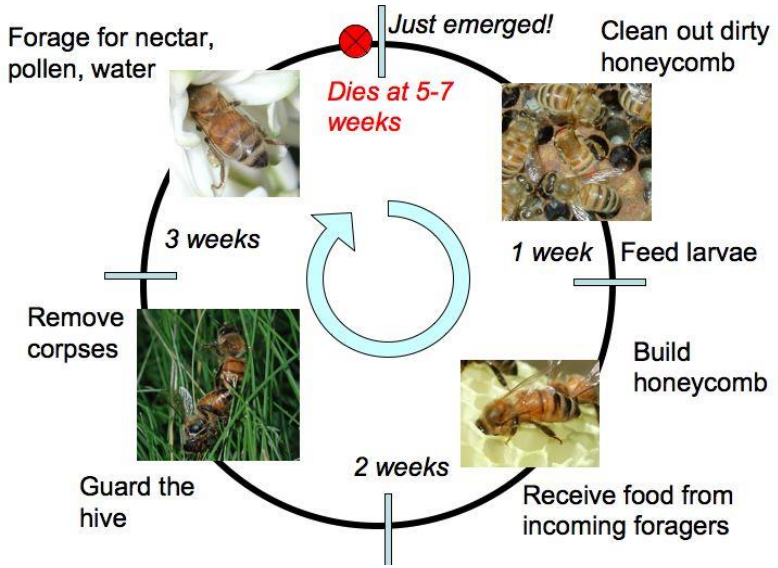
Solitary living



- Each female lays eggs in own nest
- No brood care after egg-laying
- One-generation nests
- Obligatory

Eusocial living

- Reproductive castes
- Division of labor, cooperative brood care
- Large, long-lived colonies
- Obligatory



Yet, many lineages show social transitions…

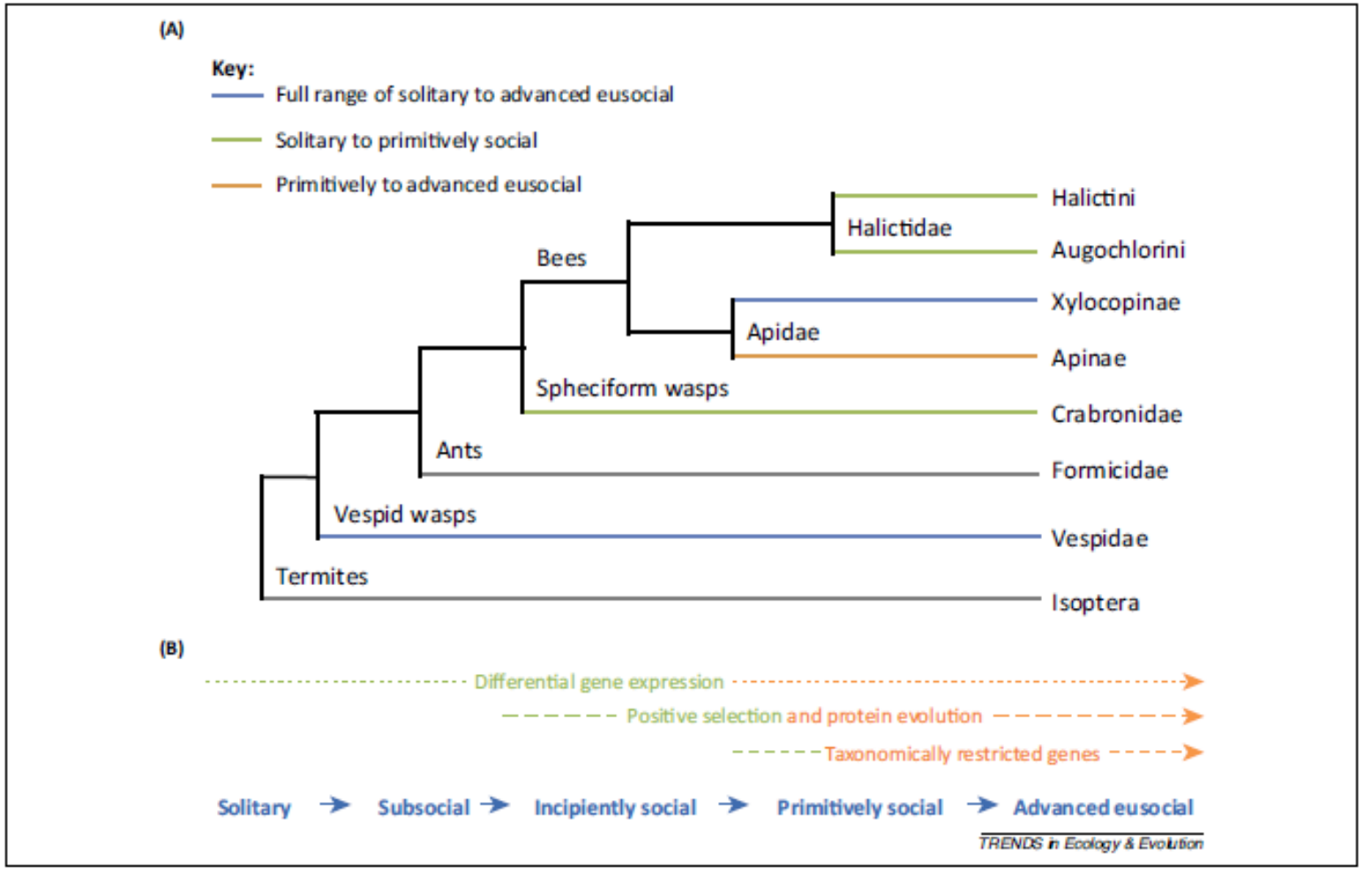
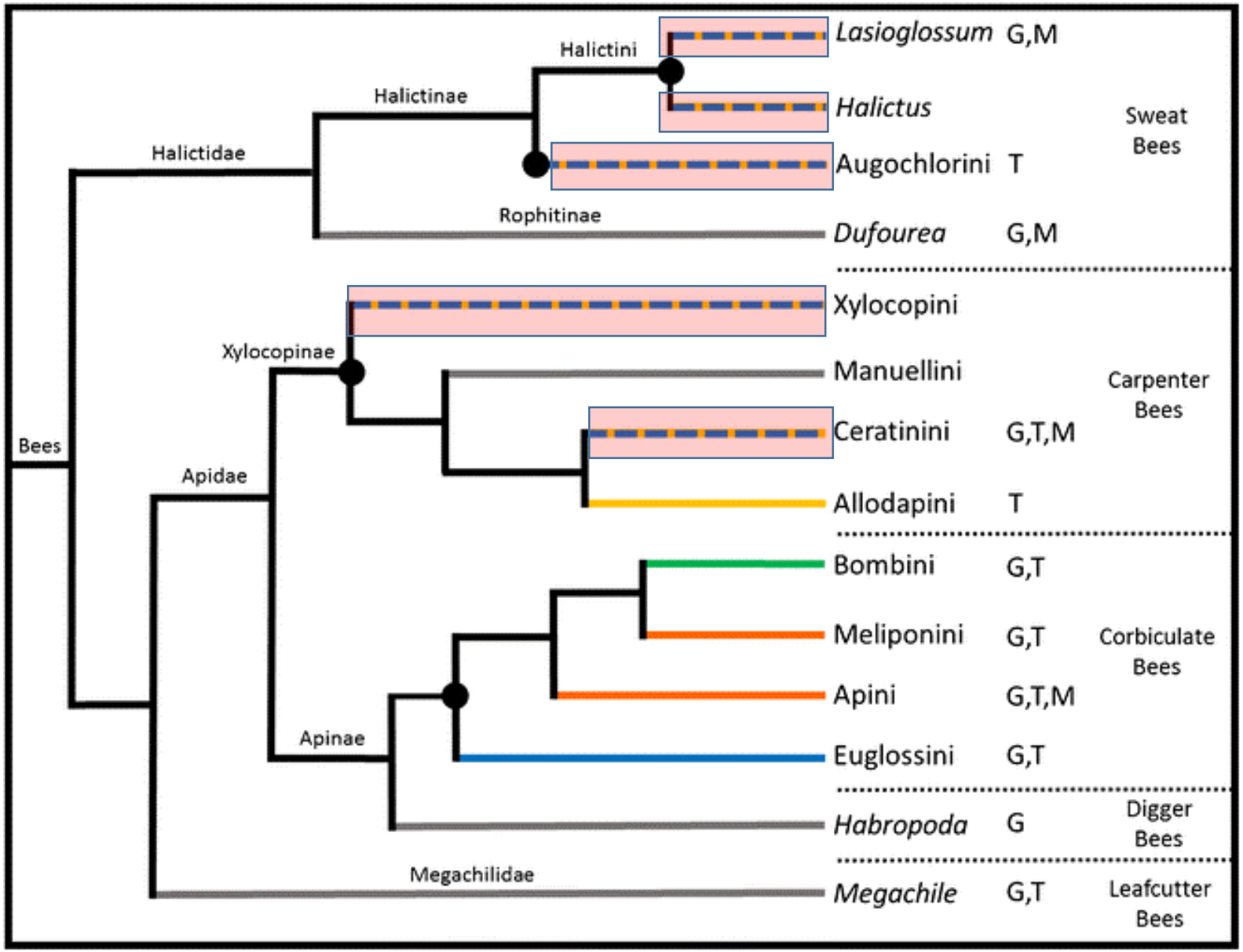


Figure 1. **(A)** Overview of phylogeny of aculeate Hymenoptera (with the nonhymenopteran but eusocial termites as an outgroup), highlighting independent origins of sociality (colored branches), groups with species ranging from solitary to primitively social (green), primitively social to advanced eusocial (orange), solitary to advanced eusocial (blue), and all species advanced eusocial (grey). **(B)** The full range of the solitary to eusocial spectrum (blue) and predictions of which genomic mechanisms are hypothesized to operate at different transitional stages of social evolution (broken arrows).

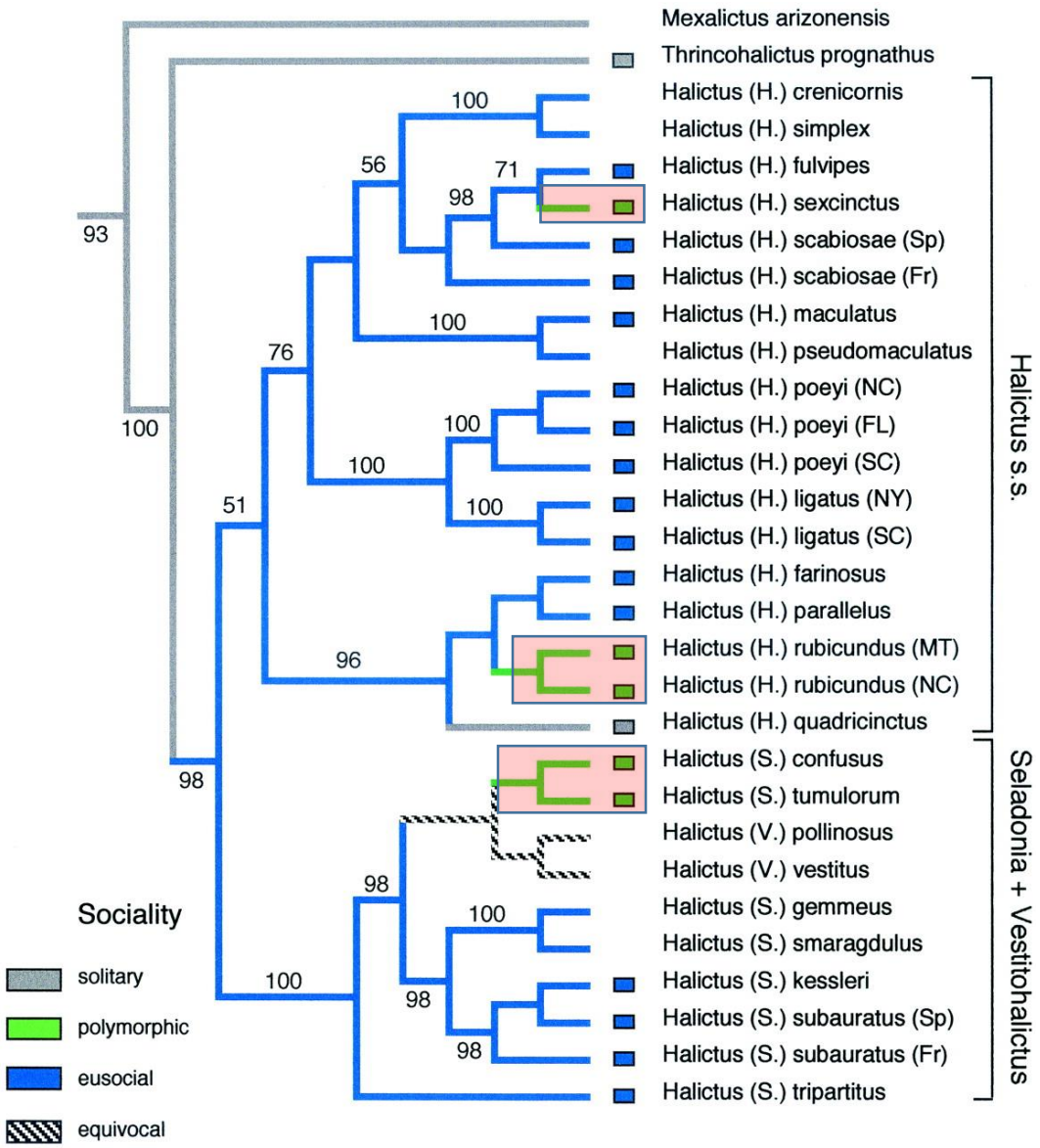
Rehan & Toth, 2015

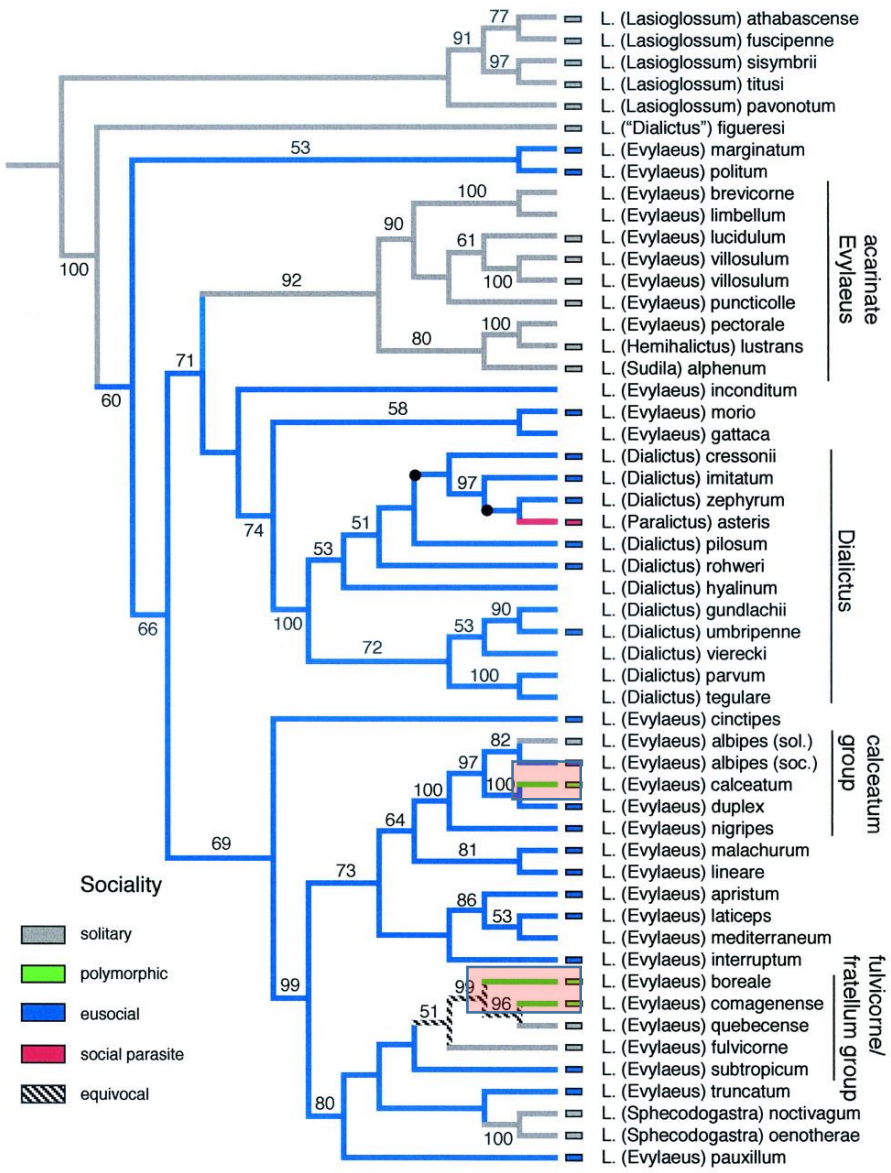
And some lineages contain socially polymorphic species



Shell & Rehan, 2018

Some socially polymorphic lineages in greater detail





Danforth, 2002

Learning from facultative social insects: Potential selective forces for sociality

- High genetic relatedness (haplodiploidy/monogamy/inbreeding)
- Difficult dispersal
- Difficult-to-handle food sources?

Learning from facultative social insects: Two local examples

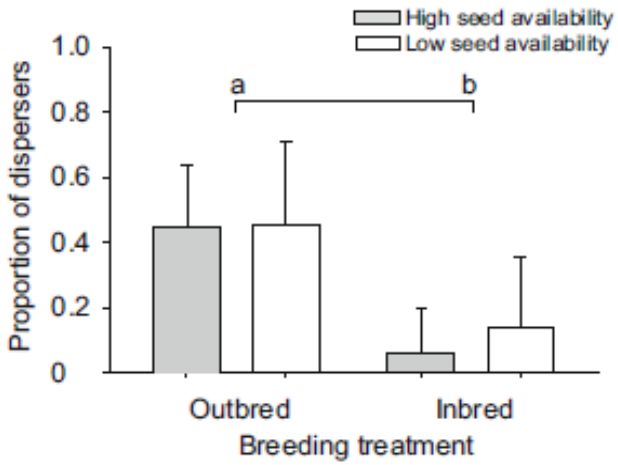
- Date stone beetles (*Coccotripes dactyliperda*)
- Carpenter bees (*Xylocopa spp.*)

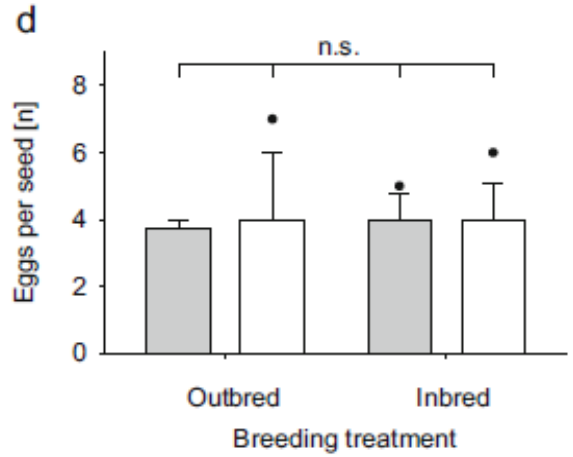
Social flexibility in date stone beetles

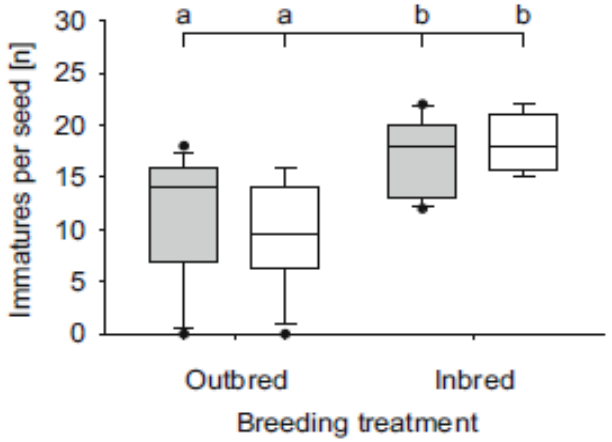
- Founder digs gallery in a date stone and lays several eggs
- Offspring remain in the seed and extend the gallery
- Little dispersal until the seed is completely consumed (up to 6 generations)
- Haplodiploid and highly inbred
- Highly female-biased sex ratio
- Communal breeding and brood guarding

High relatedness inhibits dispersal and improves offspring survival

High inbreeding Abundant seeds	**High inbreeding Limited seeds**
Low inbreeding Abundant seeds	**Low inbreeding Limited seeds**







Sitkov-Sharon et al., 2017

Social flexibility in carpenter bees

- Founder digs nest in wood and lays several eggs
- Emerging daughters may:
- Found new nest
- Take over mothers' nest
- Remain in mother's nest as guard
- Nesting season March-September
- More social nesting in summer

Ali et al., 2017

Nest and pollen shortage favor sociality

1990	Mild environmental constraints March–May 1990			Severe environmental constraints June–September 1990		
	Solitary	Social		Solitary	Social	
Days	804	160		845	663	
Eggs	185	54		95	181	
Average eggs/day	0.230	0.338	**	0.112	0.273	**
Brood mortality	36	32		40	61	
Net reproduction/day	0.185	0.138	*	0.065	0.181	**
% Cells lost	19.5%	59.3%	***	42.1%	33.7%	n.s.
Cells lost through:						
pollen robbery	5.4% (10)	1.9% (1)	n.s.	20.0% (19)	0.6% (1)	***
take over by nestmate	0 % (0)	29.6% (16)	***	0 % (0)	18.2% (33)	***
take over by intruder	7.0% (13)	13.0% (7)	n.s.	11.6% (11)	6.6% (12)	n.s.
other reasons	7.0% (13)	14.8% (8)	n.s.	10.5% (10)	8.3% (15)	n.s.

Hogendoorn & Velthuis, 1993

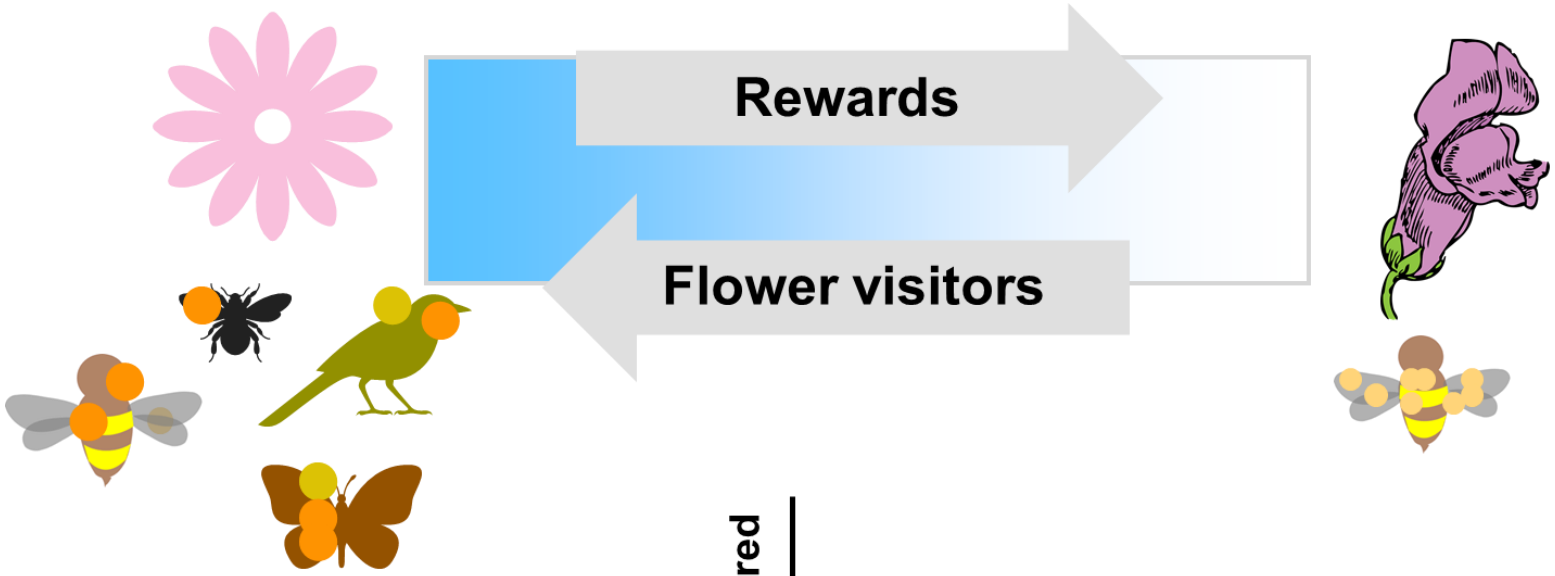
Summing up so far

- Social organization in insects ranges from solitary to eusocial.
- Some species show flexible levels of sociality.
- Experiments and observations on such species point to genetic relatedness and resource shortage as evolutionary drivers of sociality.
- Bees are attractive models for understanding social evolution.

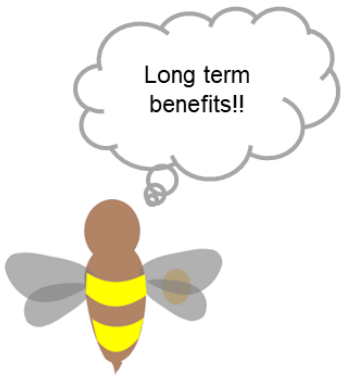
Can difficult-to-handle flowers promote sociality in bees?

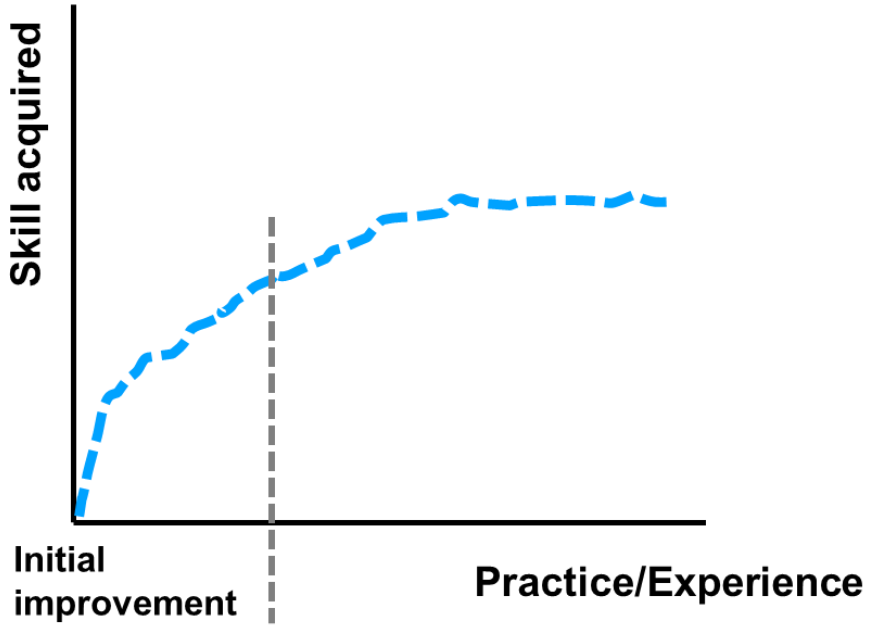
Floral food sources come in many shapes

Complex flowers: highly rewarding, but only after practice



Higher handling times
Higher energy to handle





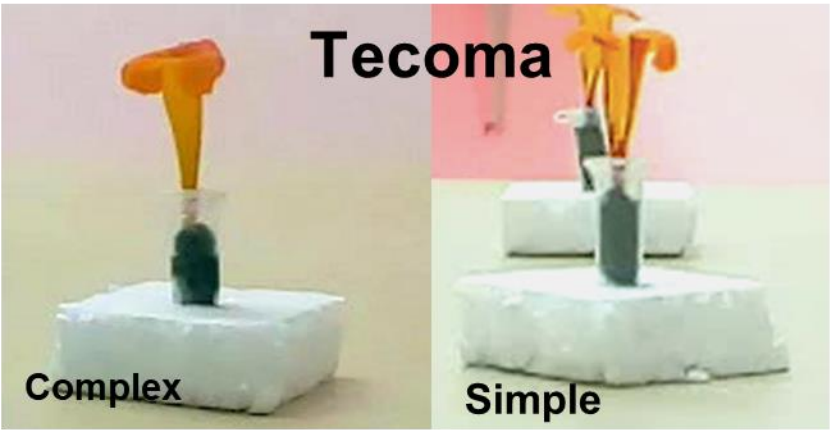
How do bumblebees persist on complex flowers?

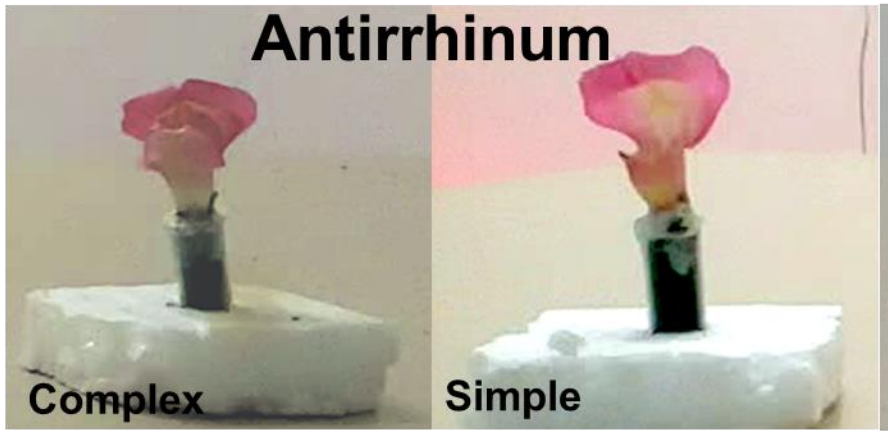
Bumblebee sociality:

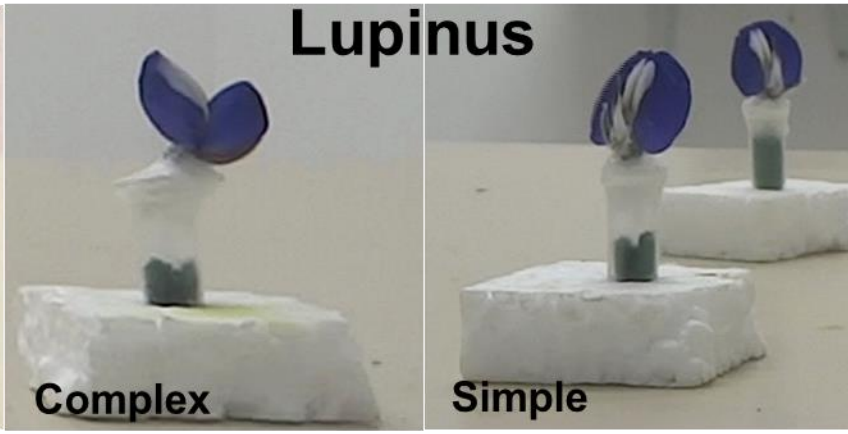
- Annual colonies of <300 bees
- Communal brood care
- Division of labor:
  - Reproductives vs. workers
  - Foragers vs. household workers
  - Temporary foraging specializations
- Obligatory

Real-flower experiment

- Allow single, naïve bee to forage on complex vs. simplified flowers of one species
- Identical rewards in both flower types
- Record choices and time budgets
- Study three flowers of increasing complexity

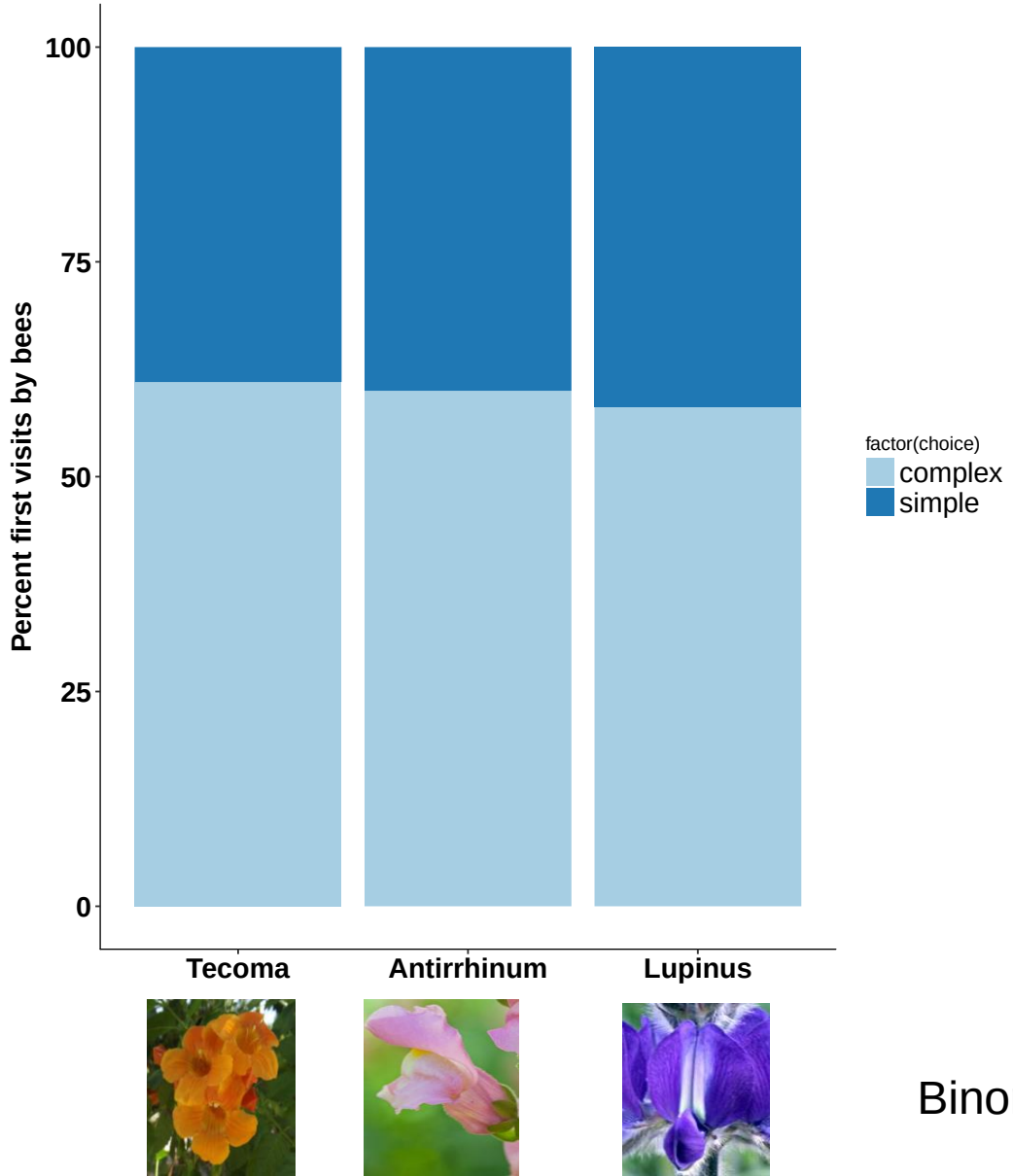






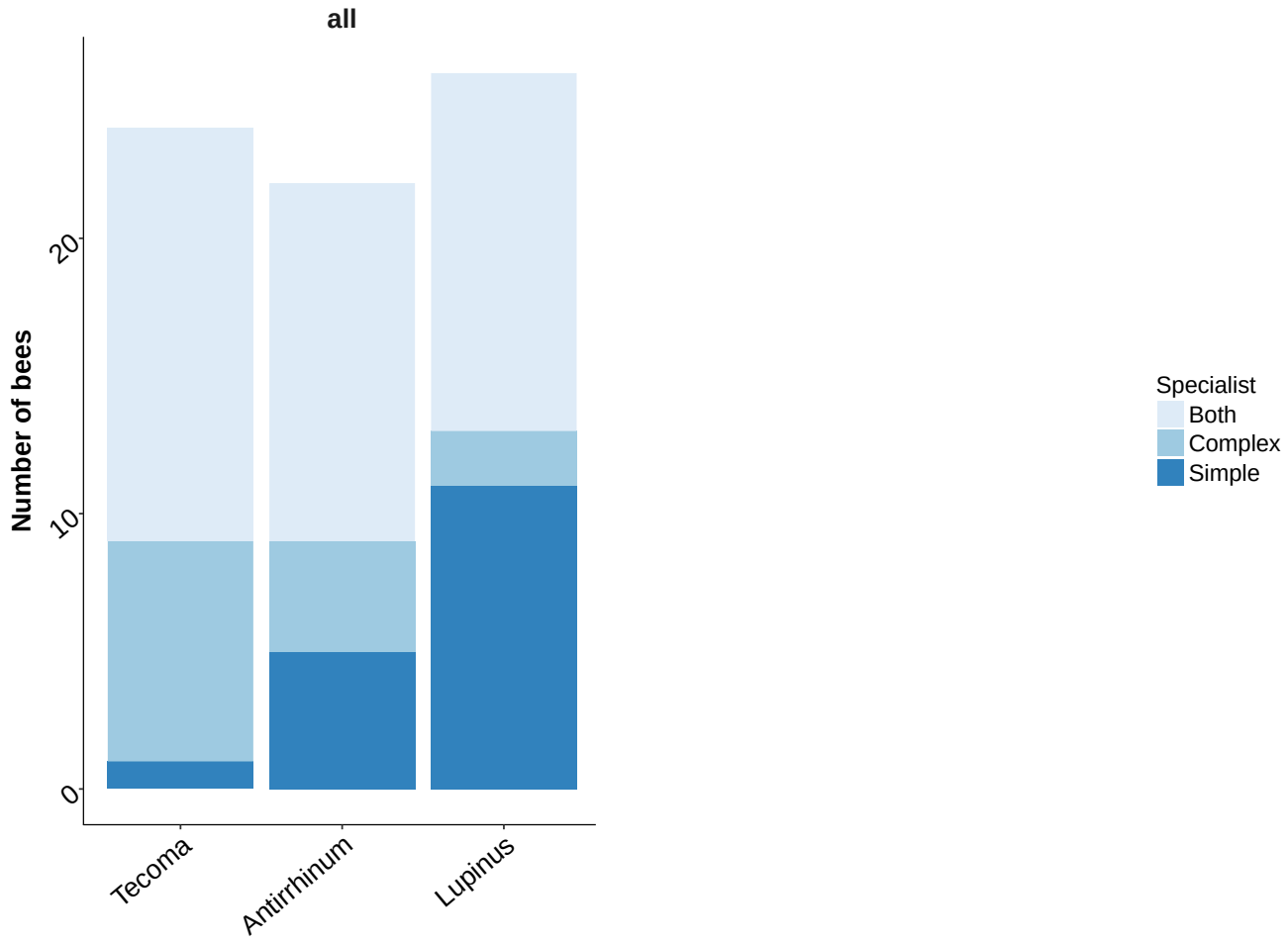
Krishna & Keasar, 2019

Initial preference for complex flowers

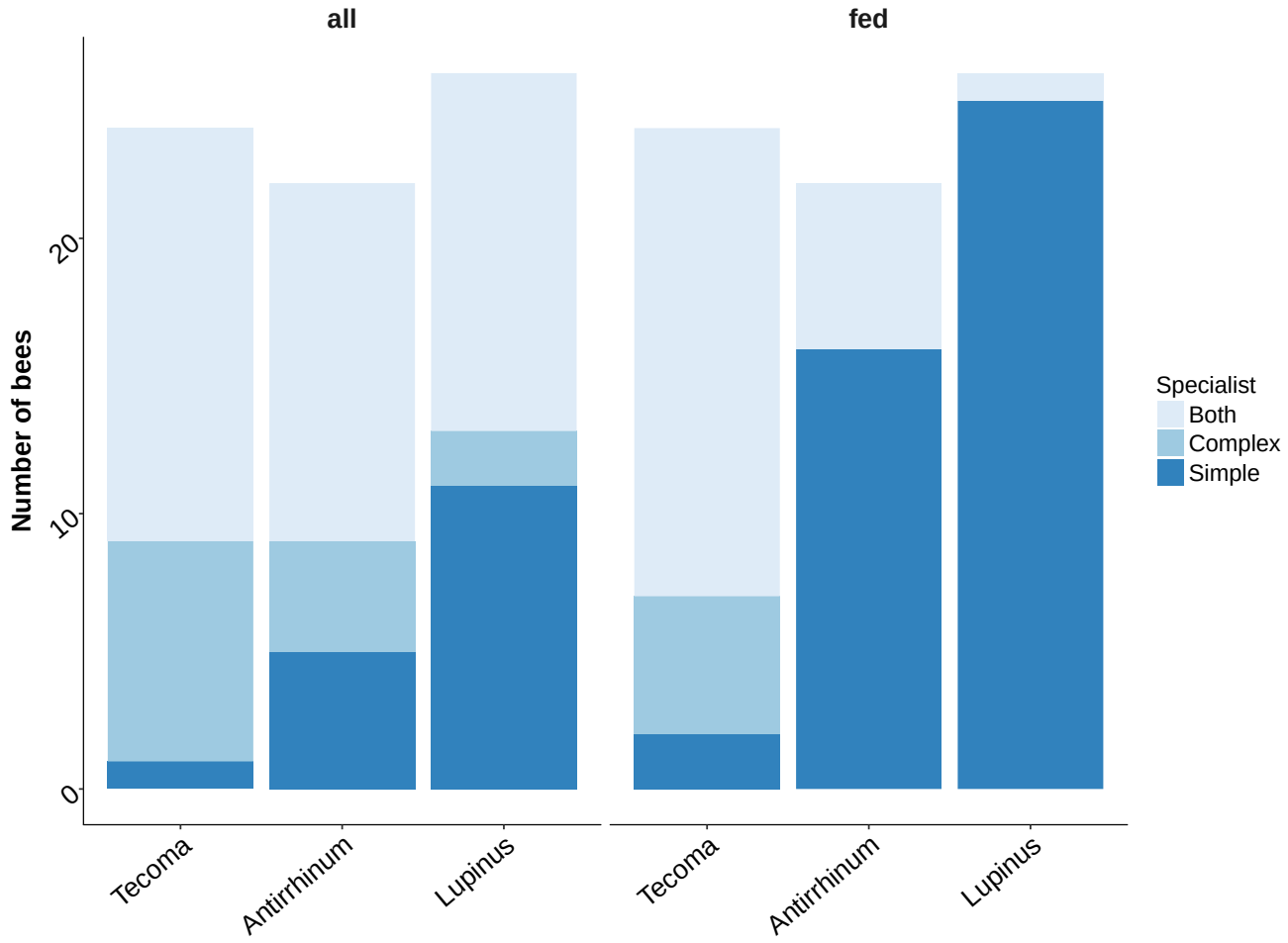


Binomial test: p = 0.007, N = 144

Some foragers specialized on complex flowers…

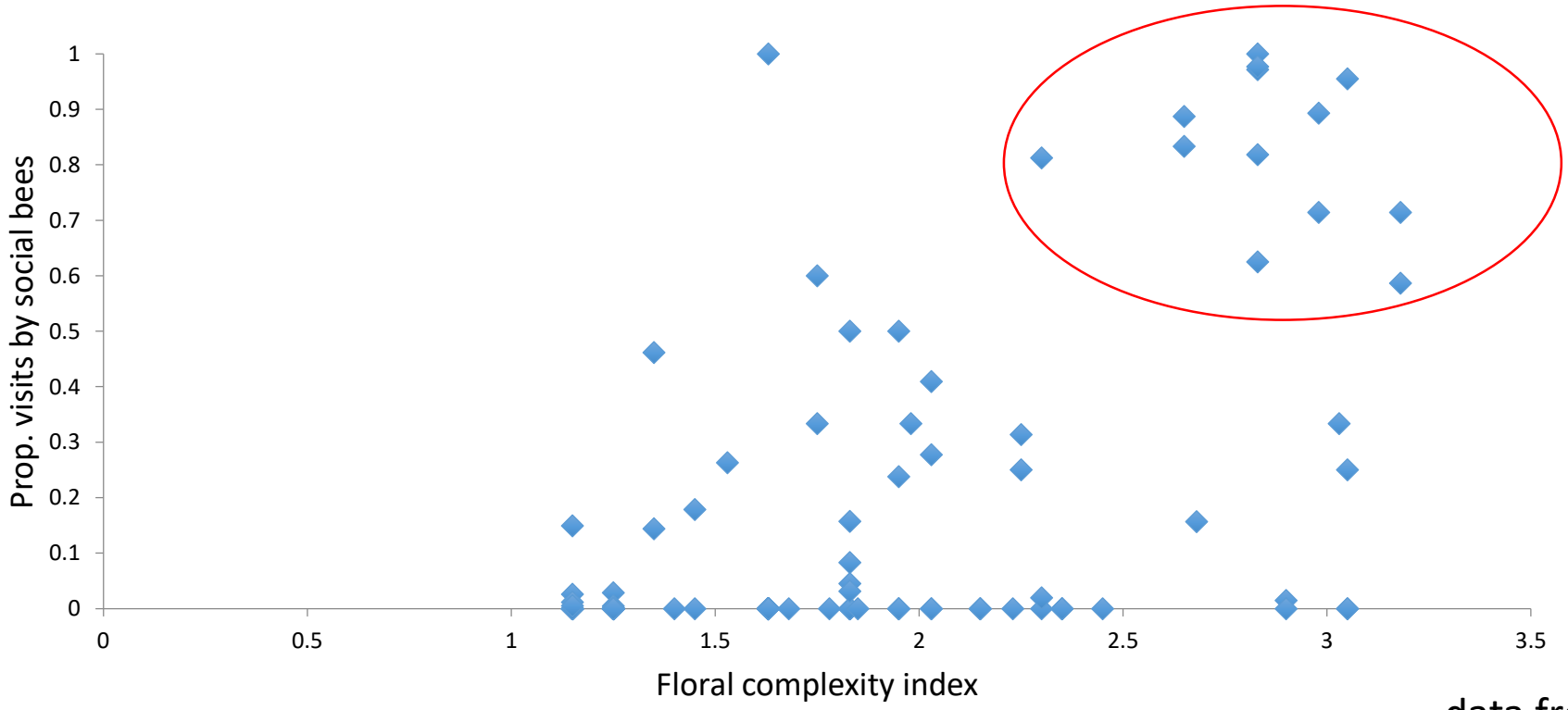


… in spite of very low feeding success



Hypothesis: sociality buffers against initial failures of foragers that specialize on complex flowers

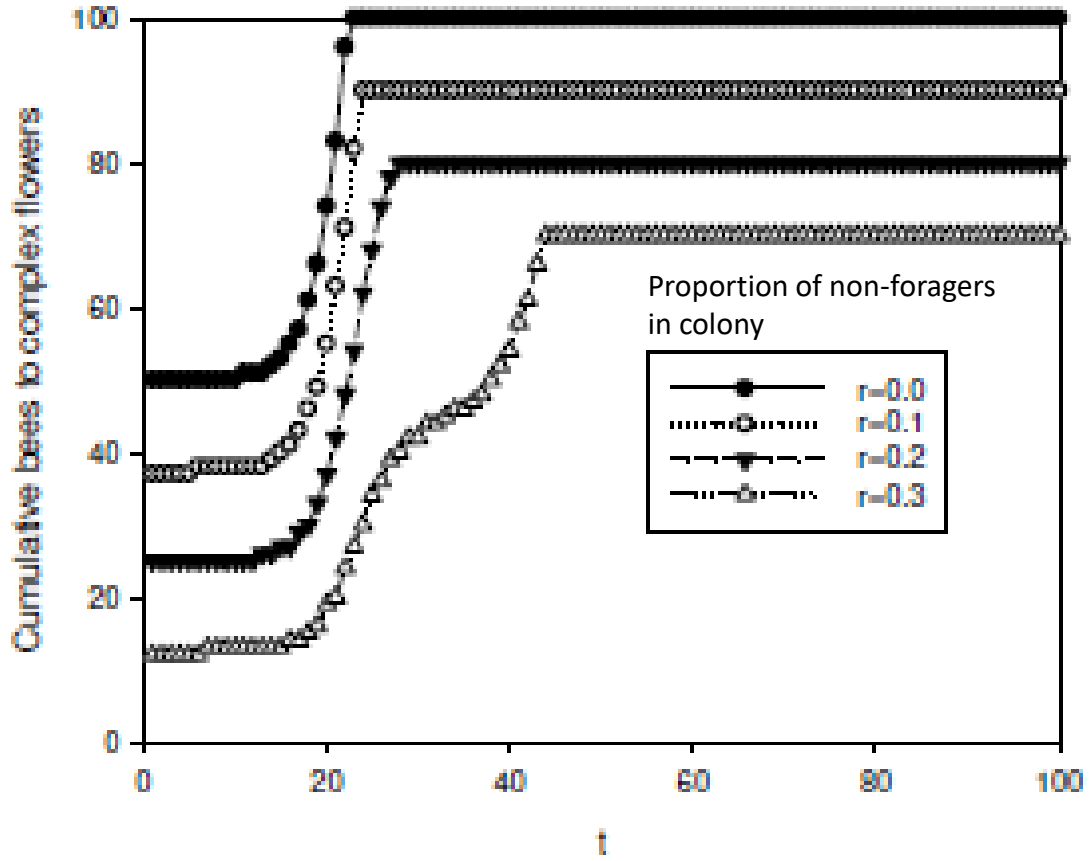
- Preliminary evidence: Social bees mainly visit complex flowers in an alpine community



data from Benadi et al., 2014

Hypothesis: sociality buffers against initial failures of foragers that specialize on complex flowers

- Preliminary evidence: Theoretical model predicts higher exploitation of complex flowers as workforce increases



Krishna, Wajnberg, Pourtallier & Keasar, unpublished

Connecting to our workshop: towards higher sociality levels in human societies?

Characterized by increasing:

- Group size
- Longevity (~generation overlap)
- Communal offspring care
- Reproductive bias
- Task specialization

Promoted by increasing:

- Kinship
- Resource limitation
- Learning difficulty of high-quality resources