Benefits of individual variation in collective systems:

individual efficiency, robustness, flexibility, and cost in social insects

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Social insects

- Diverse: group size 1-10 million, diverse lifestyles
- Distributed systems – no central control
- Cooperative: most individuals don't reproduce

Ants in the lab

(*Temnothorax rugatulus*)

Individually color-marked ants

Food

"Stone" wall

Water

Ants

Research areas

1. Communication & Information flow – push & pull, network structure, resource distribution, symmetry breaking, personal vs social information and reliability
2. Collective decision-making – individual vs collective, latent learning, colony size & consensus, speed & accuracy
3. Optimal search – adaptive random walks, group size effects
4. Spatial sorting – creates variation, stigmergy, self-organized group size effects
5. Division of labor – inactive workers, specialization, response threshold distributions, reserves, algorithms/mechanisms, task switching, elites
6. Individual vs collective intelligence – learning complex tasks without reward

socialinsectlab.arizona.edu

A broad picture of complex system organization

Why have particular strategies of communication, task allocation, search, etc. evolved in different complex systems?

In most of these, individuals differ

Why do systems produce/hire/implement variance?

Individual variation

In most of these, individuals differ

Why do systems produce/hire/implement variance?
Main hypothesis: benefits of specialization

Worker specialization

It is not obvious that specialization / individual variance is beneficial:

- Some specialization is null expectation from individual noise (and is costly to reduce)
- Why not – selection against specialization:
  - Loss of flexibility to envir. change
  - Loss of robustness to noise/indiv. error
  - Possible loss of predictability/coordination
  - Difficulty of predicting number of specialists needed

Worker specialization

Why does specialization evolve?

- Selection for specialization:
  - Efficiency of specialists
  - Reduction of switching costs
  - Enables new functionalities

} 'Classic' reasons *(Smith, Wilson)*

  - Difficulty of on-line reallocation of generalists
  - Differences in cost-benefit tradeoff among tasks

} New hypotheses *Dornhaus, Kelemen; Cornejo et al. 2014*

Worker specialization

Why does specialization evolve?

- Selection for specialization:
  - Efficiency of specialists **Not always**
  - Reduction of switching costs
  - Enables new functionalities

Dornhaus 2008
Dornhaus et al. in prep

Worker specialization

Why does specialization evolve?

- Selection for specialization:
  - Efficiency of specialists
  - Reduction of switching costs **Possibly**
  - Enables new functionalities

Goldsby et al. 2012
Leighton et al. in prep

Worker specialization

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Cornejo et al. 2014

Lemma 3.1. *For each round*
Then, all tasks are satisfied in

Proof. It suffices to show tha
round r. Assume to the cont
$\Phi(r)$ passive ants and each p
$\Phi(r) \leq \sum_{i \in U^{(r)}} (w_i^{(r+1)} - w_i^{(r)})$

Computation time to 'optimally' match workers with different skills to demand in different tasks may increase exponentially with number of workers or tasks (NP hard)

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Workers differ in other traits, such as cost and robustness -
If larger workers are costly and productive, only worth it for important tasks ➔ specialization

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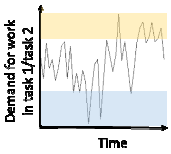


- *and*, we may have been looking at this too simplistically…
Workers may be a mixture of specialists and generalists, and still achieve near-optimal flexibility while increasing performance

Worker variation in bumble bees

Bumble bees

Workers differ in

- Body size (up to 10fold)
- Cost of production (food for larvae)
- Robustness (larger bees starve more quickly and have less fat)
- Task skills (larger bees are better)
- Task preferences (larger bees tend to forage, guard, and fan; smaller bees tend to nurse and incubate brood)
- Selfishness (larger bees are more likely to reproduce)

Couvillon et al. 2011, 2010a/b; Jandt & Dornhaus 2011, 2009; Couvillon & Dornhaus 2010&2009; Jandt et al. 2009

Worker variation in bumble bees

Bumble bees

Why do colonies produce a mix of workers that differ in body size?

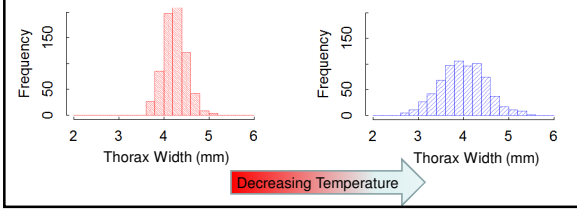
Assuming that body size is linked to production cost / robustness/ skills / selfishness, why should task preferences (i.e. allocation to tasks) differ?

Is worker variation just noise that can only be suppressed at a cost?

- Larvae only experience the environment that the workers produce
- Size variation may reflect a colony's ability to maintain a uniform nest environment

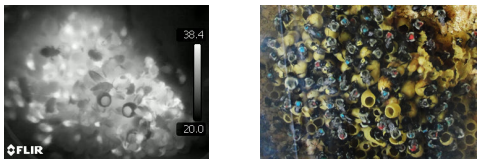
Stressors should increase noise because they increase suppression costs

Hypothesis: Increasing thermoregulatory demands should increase environmental heterogeneity → decreasing ambient air temperature will increase the amount of body size variation within a colony

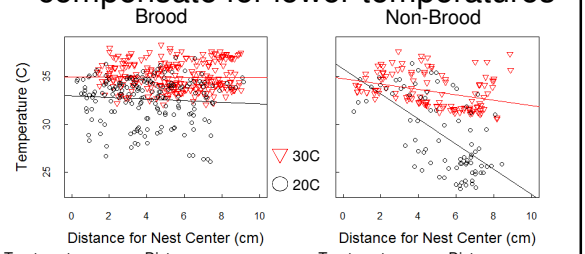


We measured the size distribution produced at different temperatures

- We kept colonies at 30ºC (n = 5) and 20ºC (n = 5)
- We measured the thorax width (mm) of all workers produced
- We took thermal images of each nest

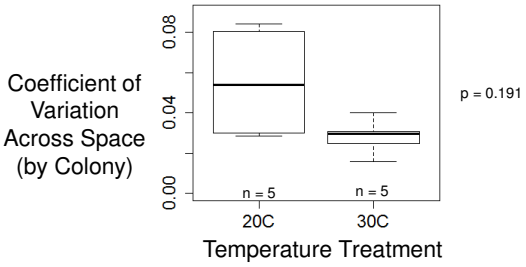


Colonies were not quite able to compensate for lower temperatures

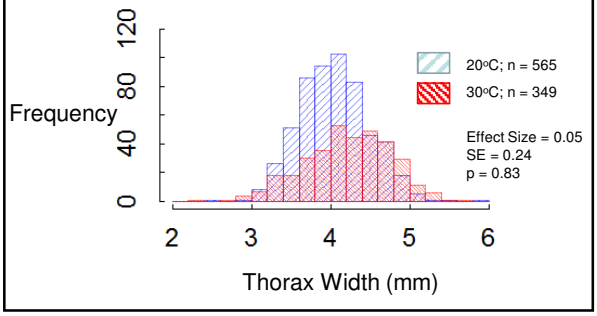


Brood		Non-Brood	
Treatment	Distance	Treatment	Distance
Effect Size = 2.78	Effect Size = -0.002	Effect Size = 4.49	Effect Size = -0.022
SE = 1.00	SE = 0.002	SE = 1.58	SE = 0.004
p = 0.027	p = 0.334	**p = 0.0248**	**p < 0.001**

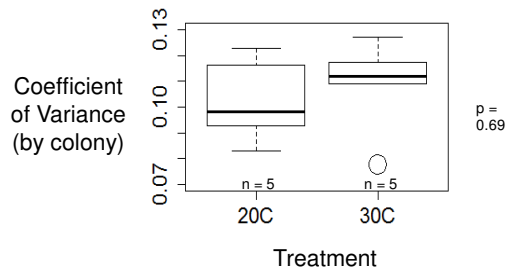
The spatial temperature variation experienced by the brood did not differ



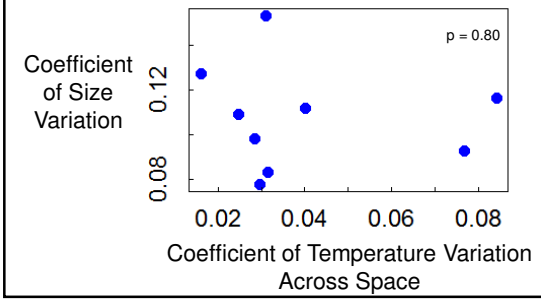
There was no difference in average size



Increased stress on the system did not affect body size variation



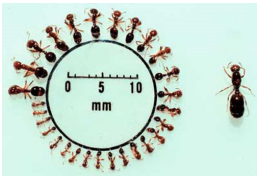
Environmental variation within the nest did not predict size variation



Conclusion

Why is there variation in complex systems?

- Bumble bees control temperature pretty tightly: even stressed, variation in temperature does not increase (nor does variance in worker size)
  - Variation among workers likely not noise caused by environmental heterogeneity
- Variation might be a conserved property
  - It could be due to constraints (e.g. resources)
  - It could be an adaptive trait



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Broad relevance

Why study collective behavior in social insects?

Many reasons!

- Philosophical: Complexity out of simpler parts
- Specific: Ecological (more biomass than vertebrates) and economic importance (pollinators, pests)
- Model for Cognition: (Collective) intelligence in tractable system
- and for Organismic traits: Evolutionary principles applied to different 'major transitions' or organizational levels (e.g. evolution of life history, intraspecific variation, etc.)
- Practical: Application to engineering