Individual variation and social evolution

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MTA-DE „Lendület” Behavioural Ecology Research Group

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Outline of the talk

Outline

Social evolution

Natural selection

adaptive traits
fitness is maximised

Social evolution

Natural selection

adaptive traits
fitness is maximised

fitness gain depends only
on *own* behaviour

ordinary selection

Social evolution

Natural selection

adaptive traits
fitness is maximised

fitness gain depends only on *own* behaviour

ordinary selection

fitness gain also depends on *others'* behaviour

social selection

- group living
- cooperation
- biparental care

Many models of social evolution proposed.

Many models of social evolution proposed.

Most of them, however,

NEGLECT

individual variation.

BUT

Variation is a fundamental aspect of life!

Outline

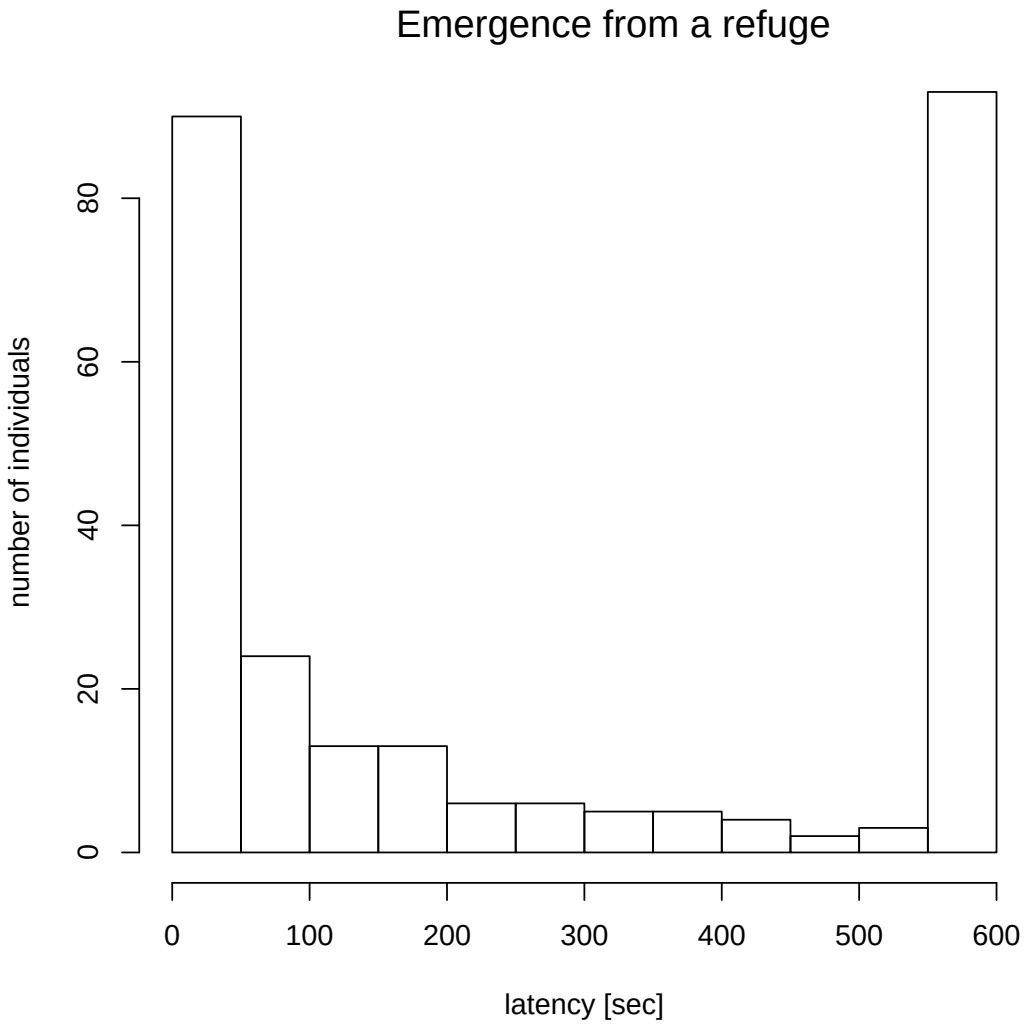
Biodiversity

Individual variation: morphology

Emlen et al. 2007 PNAS

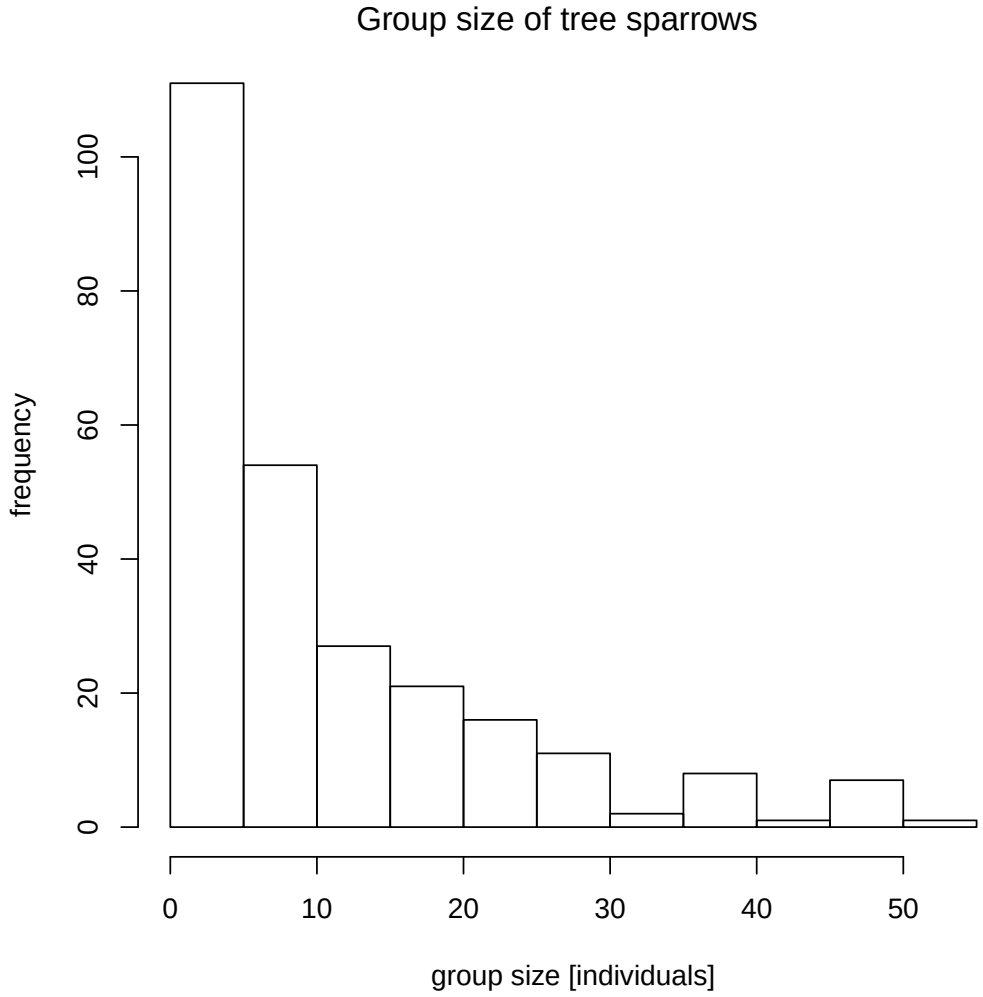
www.sfu.ca/biology/wildberg/ruff.html

Individual variation: behaviour



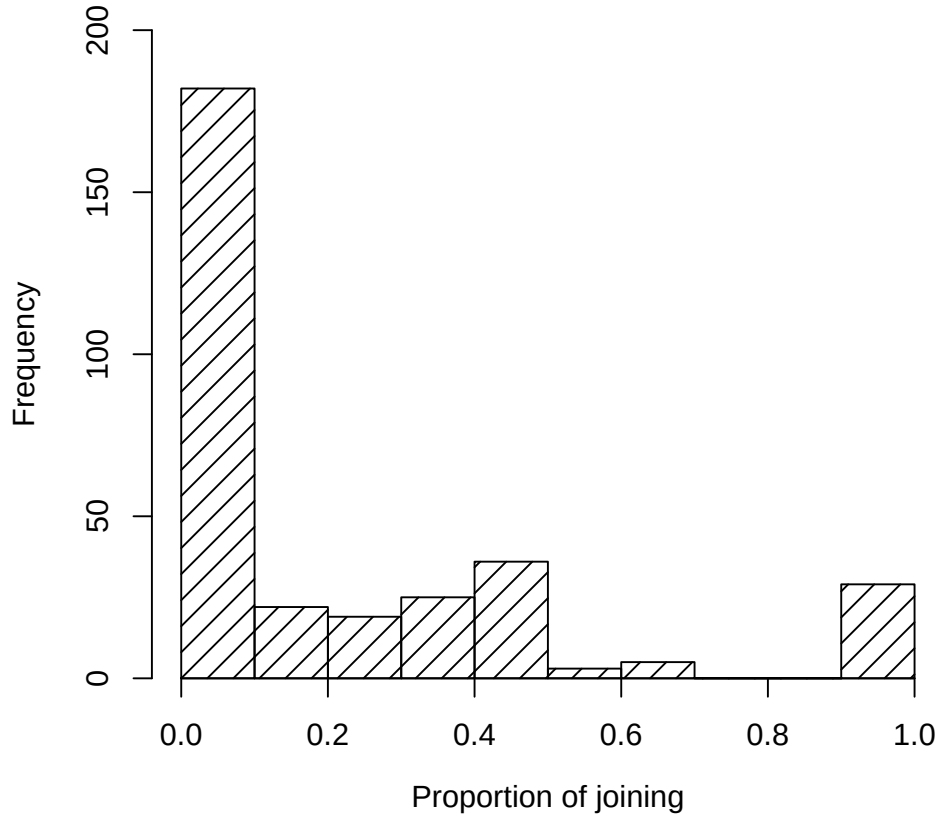
Gyuris et al. 2011 Proc. R. Soc. B

Individual variation: social behaviour



Mónus & Barta 2011 Int. Stud. Sparrows

Individual variation: social behaviour



Barta et al. 2004 Anim. Behav.

Outline

Animal personality: definition

Animal personality: consistent differences in individuals' behaviour across contexts and situations.

Dingemanse et al., 2010, TREE

- context: functional category of behaviour
  - feeding
  - predator avoidance
  - mating
  - parental care
- situation: set of conditions
  - *time*: morning, evening
  - *space*: in Cluj, in Debrecen
  - *environment*: in warm weather, in cold weather
  - *company*: small group, large group

Luttbeg & Sih, 2010, Phil. Trans. R. Soc. B

Consistency

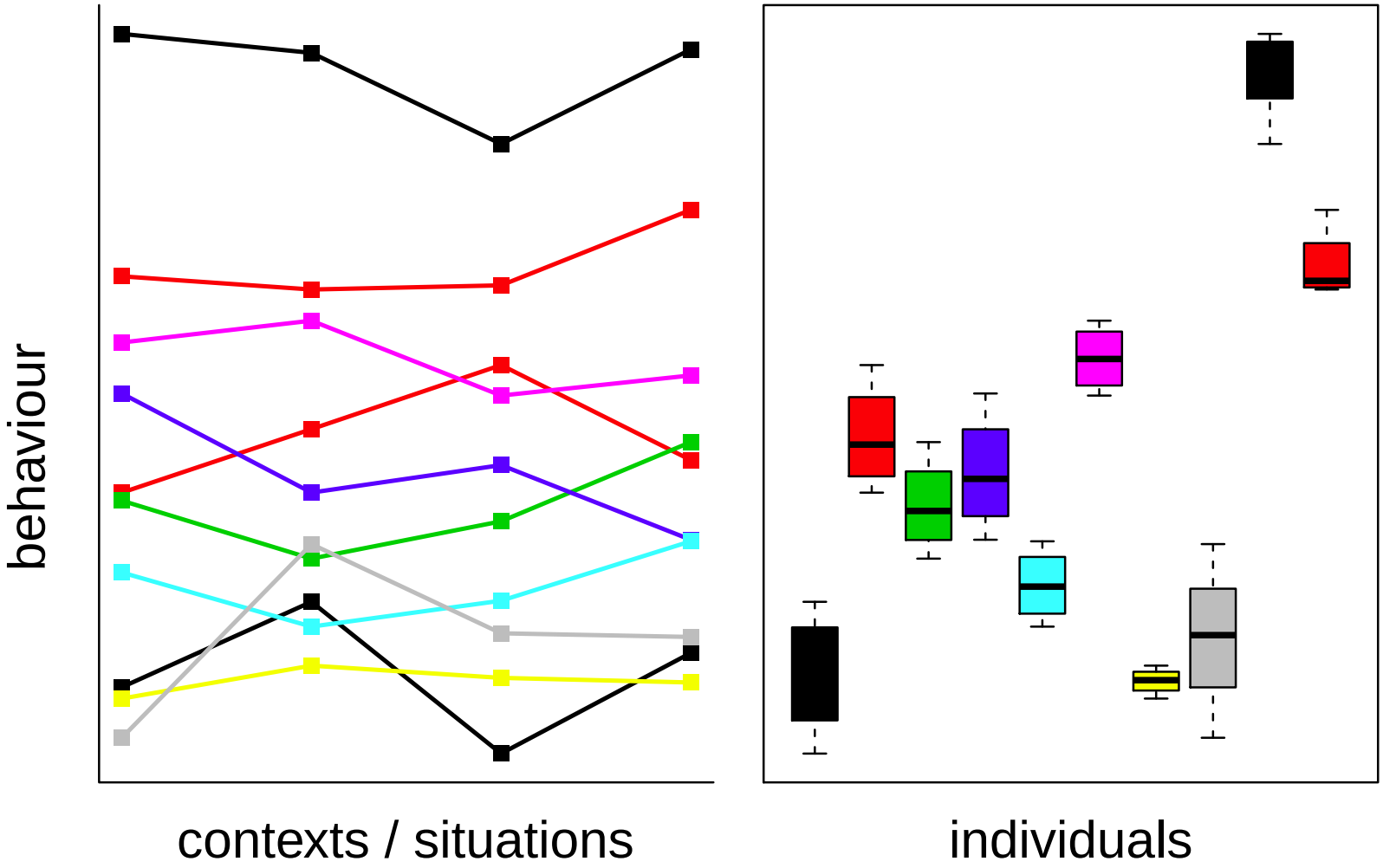
Two levels of consistency:

1. individual-level: individual behaviour stable across contexts or situations

Consistency

Repeatability: R = 0.936, p = 0.001

Kendall's concordance: W = 0.924, p = 0.001



Consistency

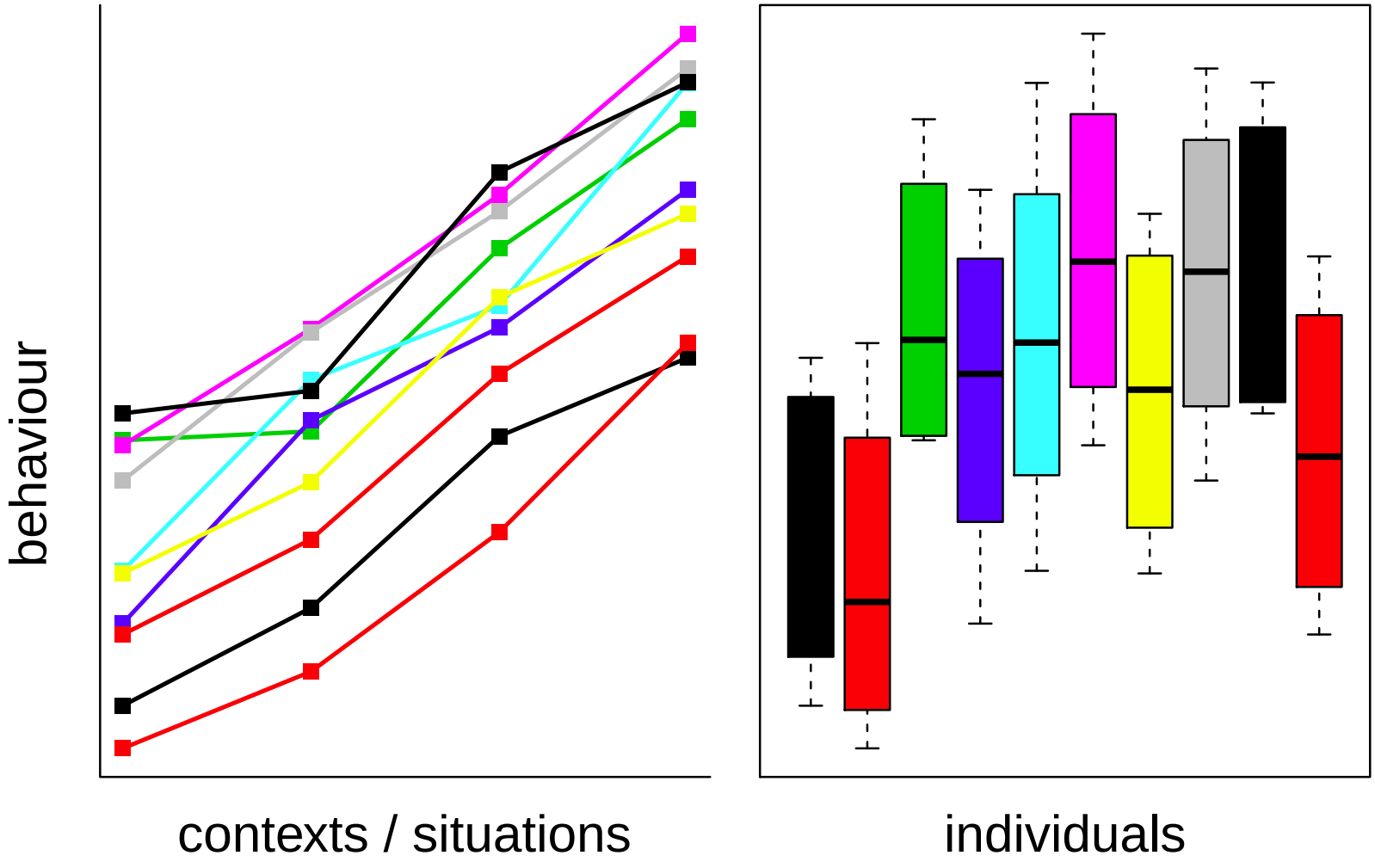
Two levels of consistency:

1. individual-level: individual behaviour stable across contexts or situations
2. group-level: rank-order consistency, the rank of an individual within group is stable

Consistency

Repeatability: R = 0.145, p = 0.147

Kendall's concordance: W = 0.9, p = 0.001



Consistency

Two levels of consistency:

1. individual-level: individual behaviour stable across contexts or situations
2. group-level: rank-order consistency, the rank of an individual within group is stable

Animal personality refers to the second case.

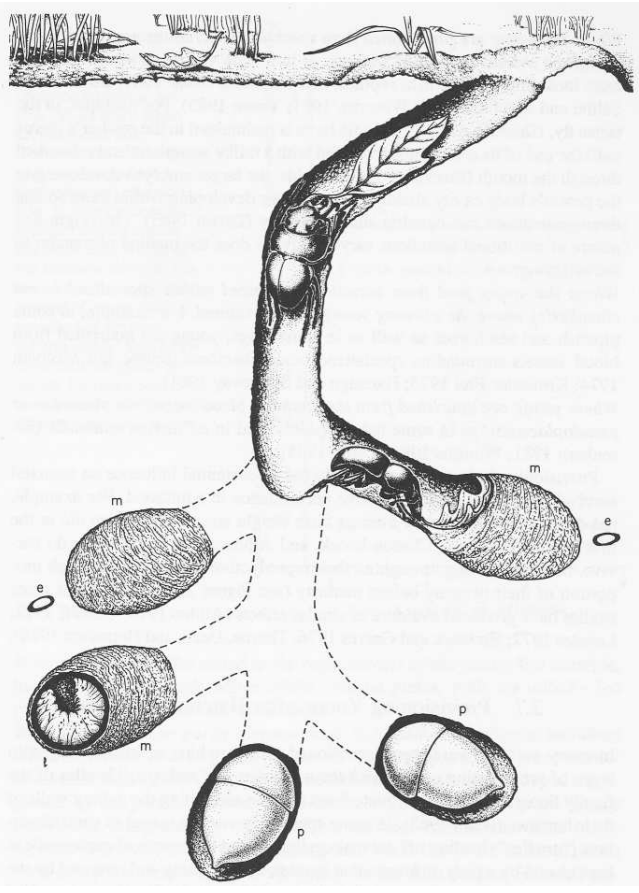
Two more concepts. . .

1. personality trait: correlated suite of behaviours
   - shyness – boldness
   - exploration – avoidance
   - activity
   - sociability
   - aggression
2. behavioural syndrome: correlation between personality traits

Herczeg & Garamszegi, 2012, Behav. Ecol. Sociobiol

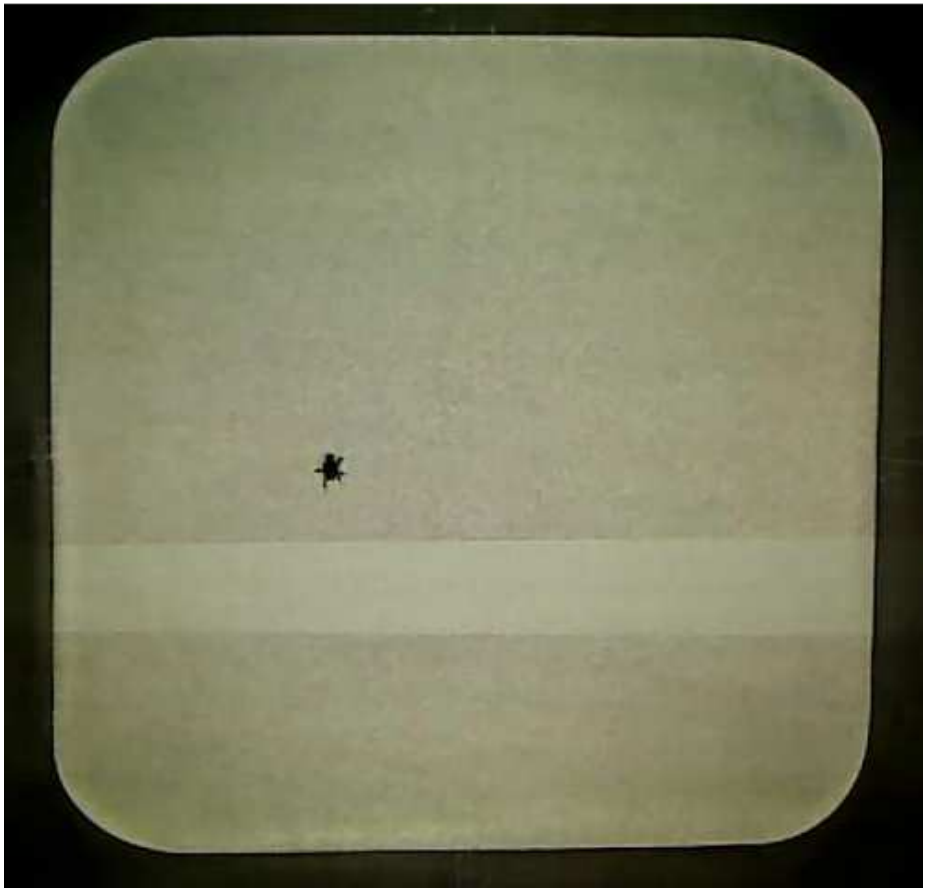
An example: *Lethrus apterus*

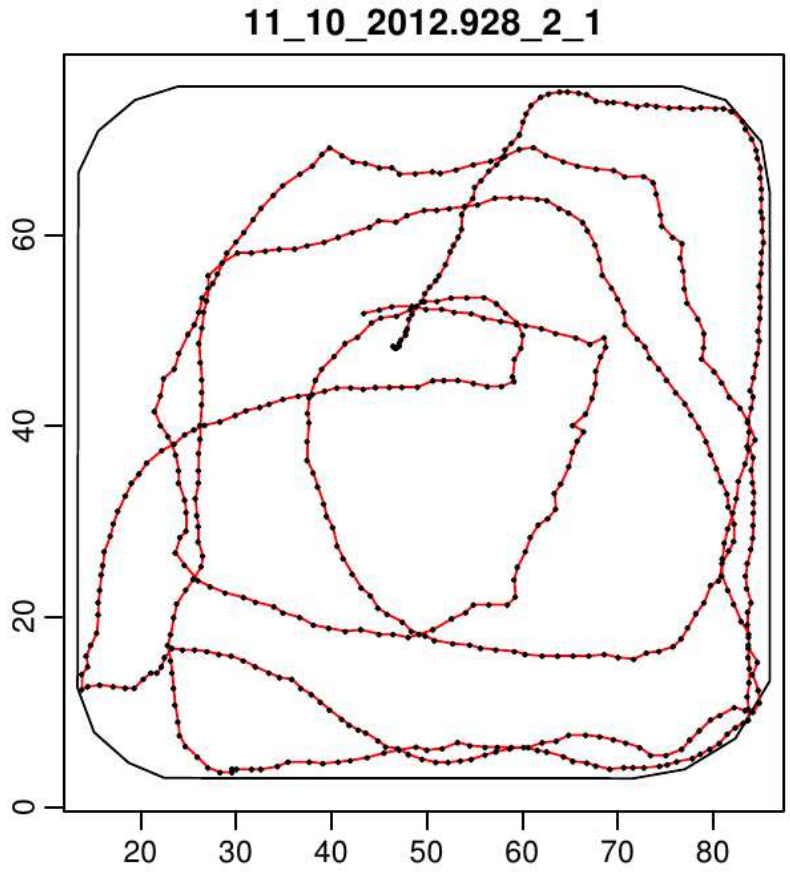
- large (~1.5 cm) beetle from Geotrupidae
- unique parental care pattern: male collects food, female prepares it for offspring



An example: *Lethrus apterus*

- open field arena for 10 min
- recording path
- 9 individuals for 3 occasions





An example: *Lethrus apterus*

Variables	Kendall's W	p
angular velocity	0.830	0.001
mean turning angle	0.733	0.004
duration of continuous movement	0.681	0.010
average speed	0.681	0.011
mean steps length	0.667	0.019
sd of steps length	0.663	0.016
wall latency	0.663	0.018
proportion of time rest	0.622	0.024
sd of duration of continuous movement	0.600	0.035
sd of turning angle	0.556	0.049
sidedness	0.474	0.148
duration of continous rest	0.367	0.367
move latency	0.355	0.416
proportion of time near wall	0.348	0.438
sd of duration of rest	0.304	0.553

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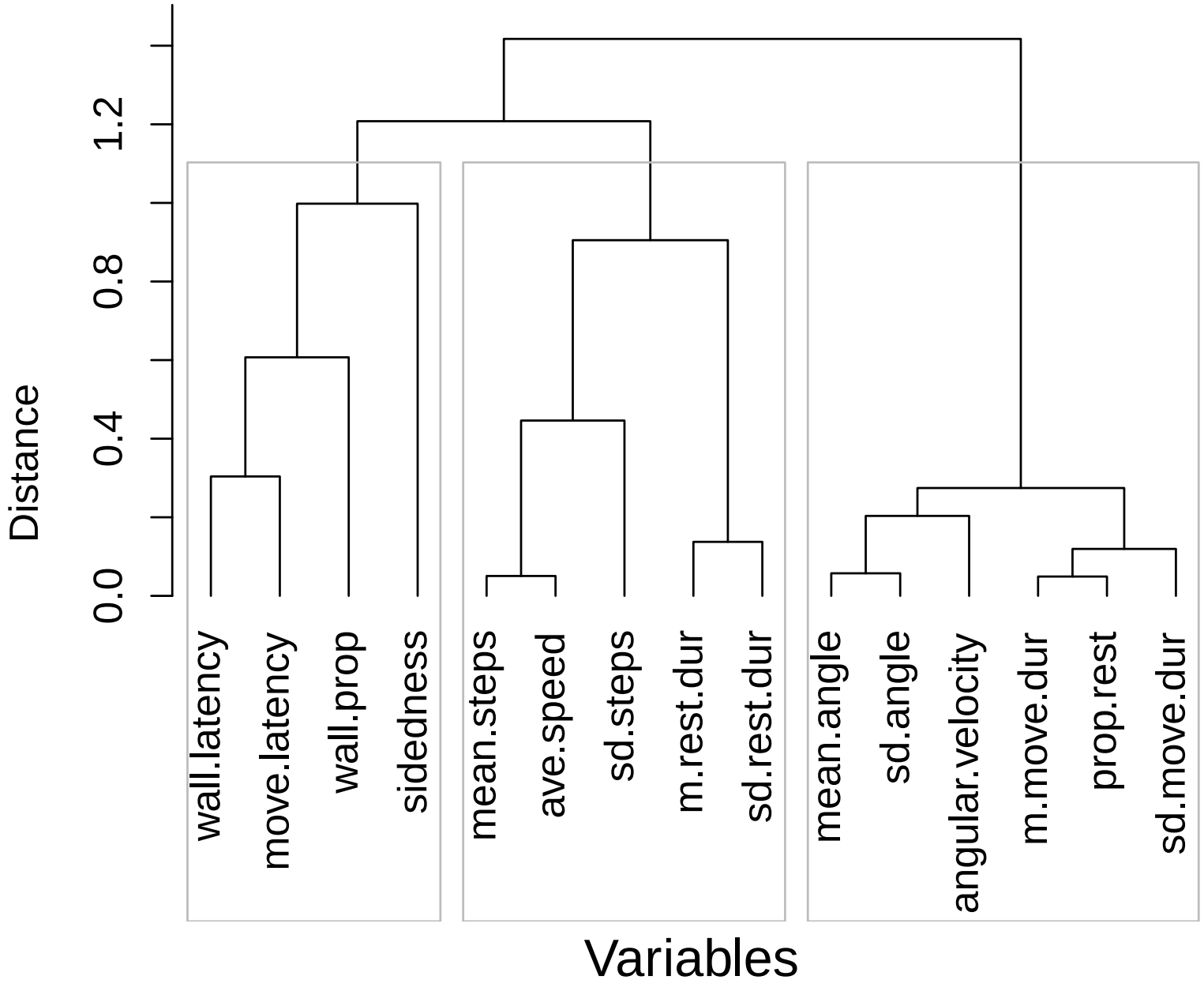


Questions about personality

1. Why is behaviour consistent?
   - constraints: hormonal effects, neural circuits – architecture of behaviour
   - adaptive explanation: effect of state

Wolf & Weissing, 2010, Phil. Trans. R. Soc. B

Questions about personality

1. Why is behaviour consistent?

Wolf & Weissing, 2010, Phil. Trans. R. Soc. B

2. How can multiple behavioural types coexist in a single population?
   - externally induced state differencies, e.g. sex determination, early ontogenic effects
   - frequency dependent effects
   - spatio-temporal environmental variation
   - non-equilibrium dynamics

Wolf & Weissing, 2010, Phil. Trans. R. Soc. B

Questions about personality

1. Why is behaviour consistent?

Wolf & Weissing, 2010, Phil. Trans. R. Soc. B

2. How can multiple behavioural types coexist in a single population?

Wolf & Weissing, 2010, Phil. Trans. R. Soc. B

3. What are the effects of personality differences?

Wolf & Weissing, 2012, TREE

An adaptive explanation and its test

Vol 447|31 May 2007|doi:10.1038/nature05835 nature

LETTERS

Life-history trade-offs favour the evolution of animal personalities

Max Wolf[1], G. Sander van Doorn[1]†, Olof Leimar[2] & Franz J. Weissing[1]

density dependent processes

different life history expectations

expect low future fitness

risk-prone

bold

expect high future fitness

risk-averse

shy

The species

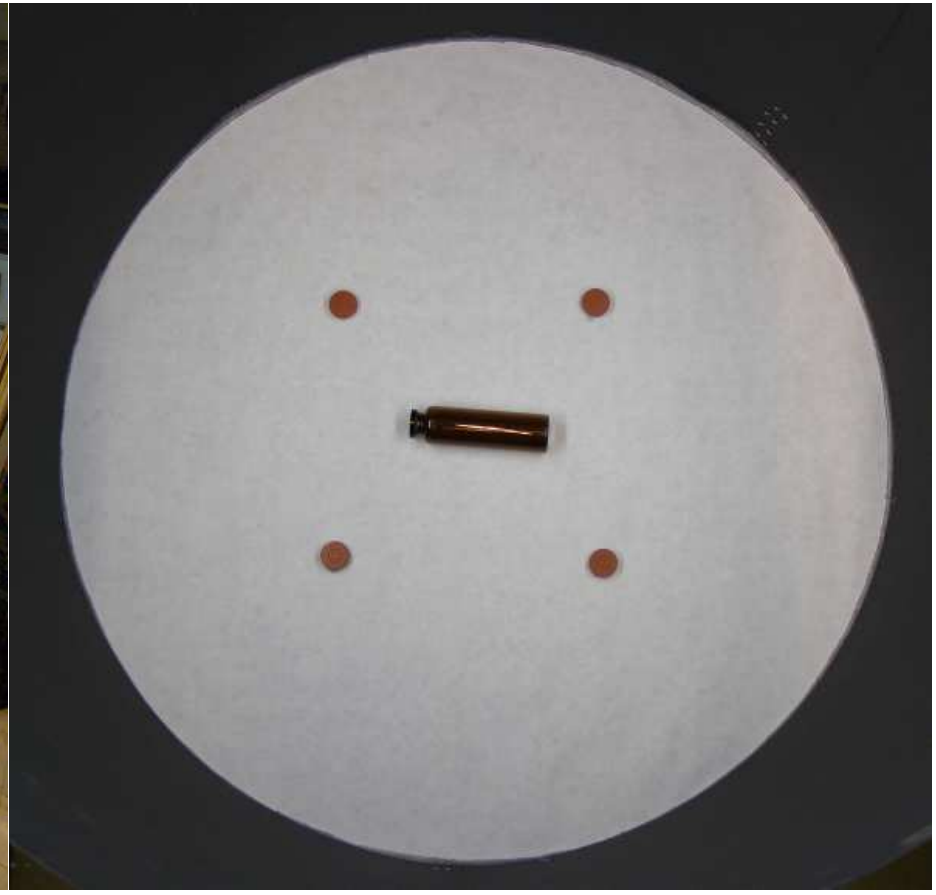
common firebug (*Pyrrhocoris apterus*)

The species

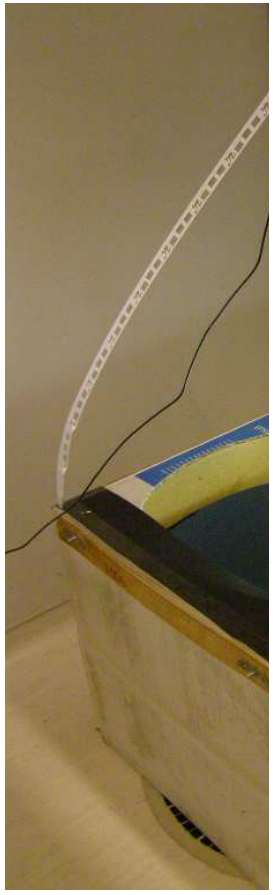
common firebug (*Pyrrhocoris apterus*)

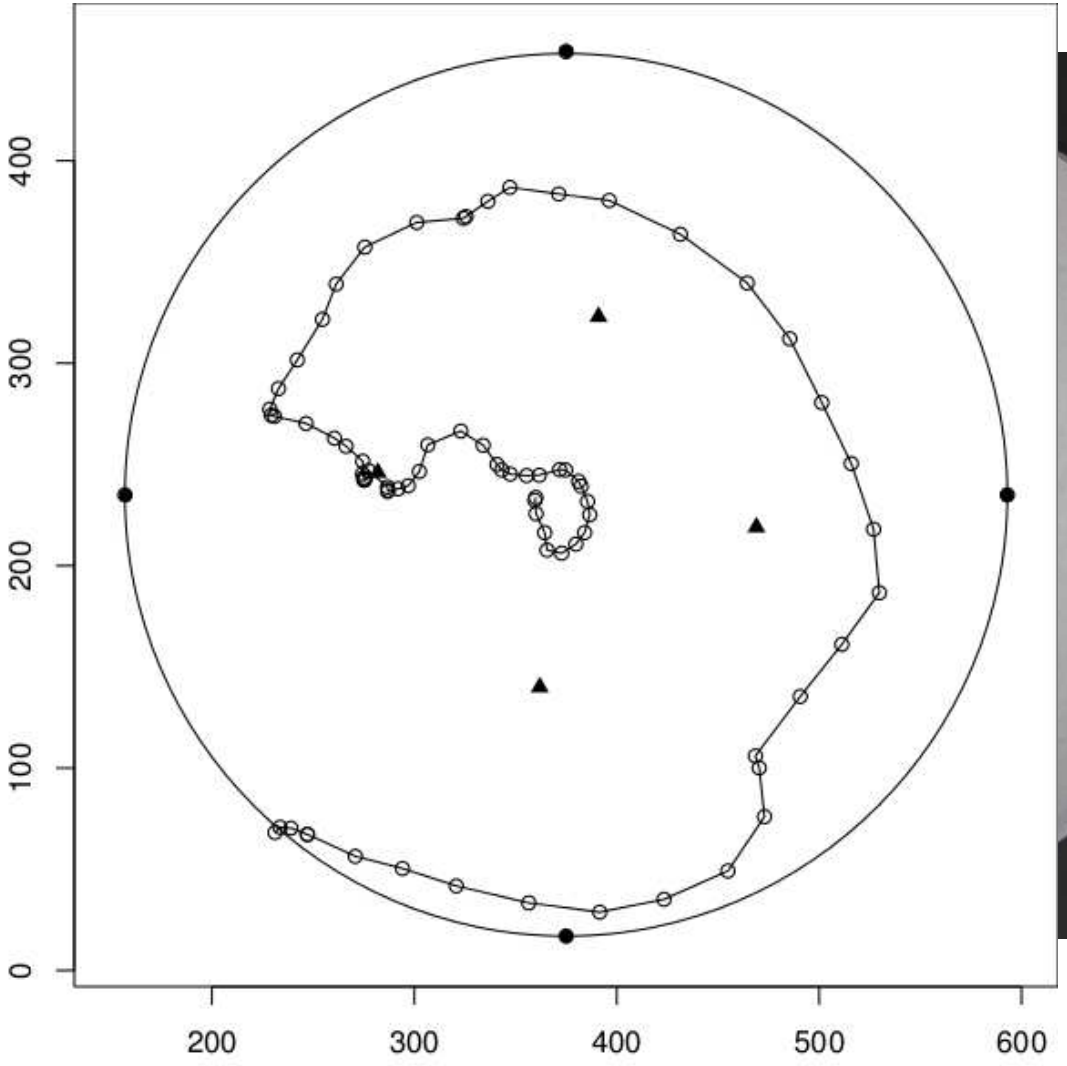
winged	unwinged
rover	sitter
low future expectations	high future expectations
bold	**shy**

Measuring firebug's personality

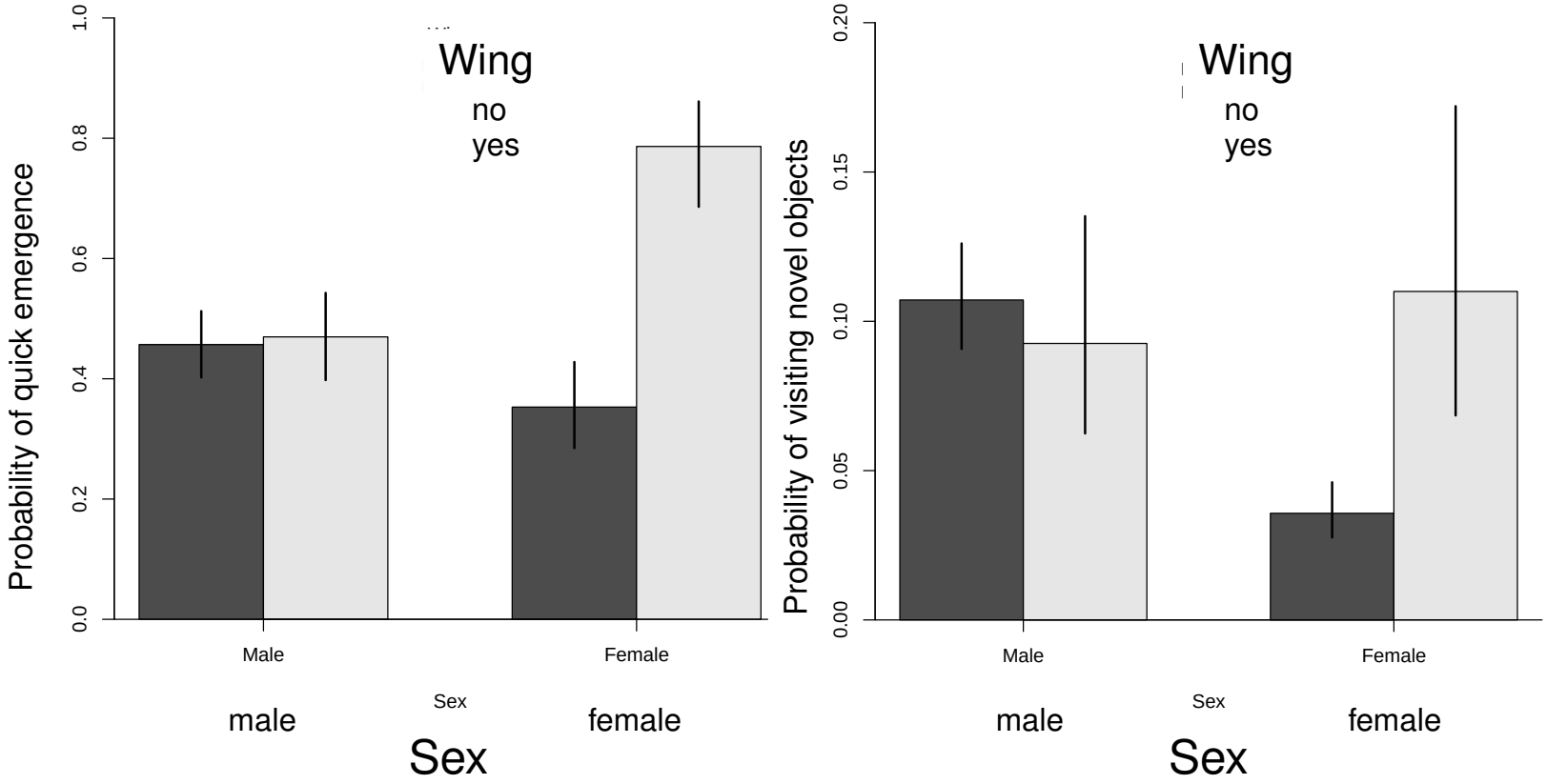


Measuring firebug's personality





Results



winged females are bolder
no effect in males

Gyuris et al., 2011, Proc. R. Soc. B

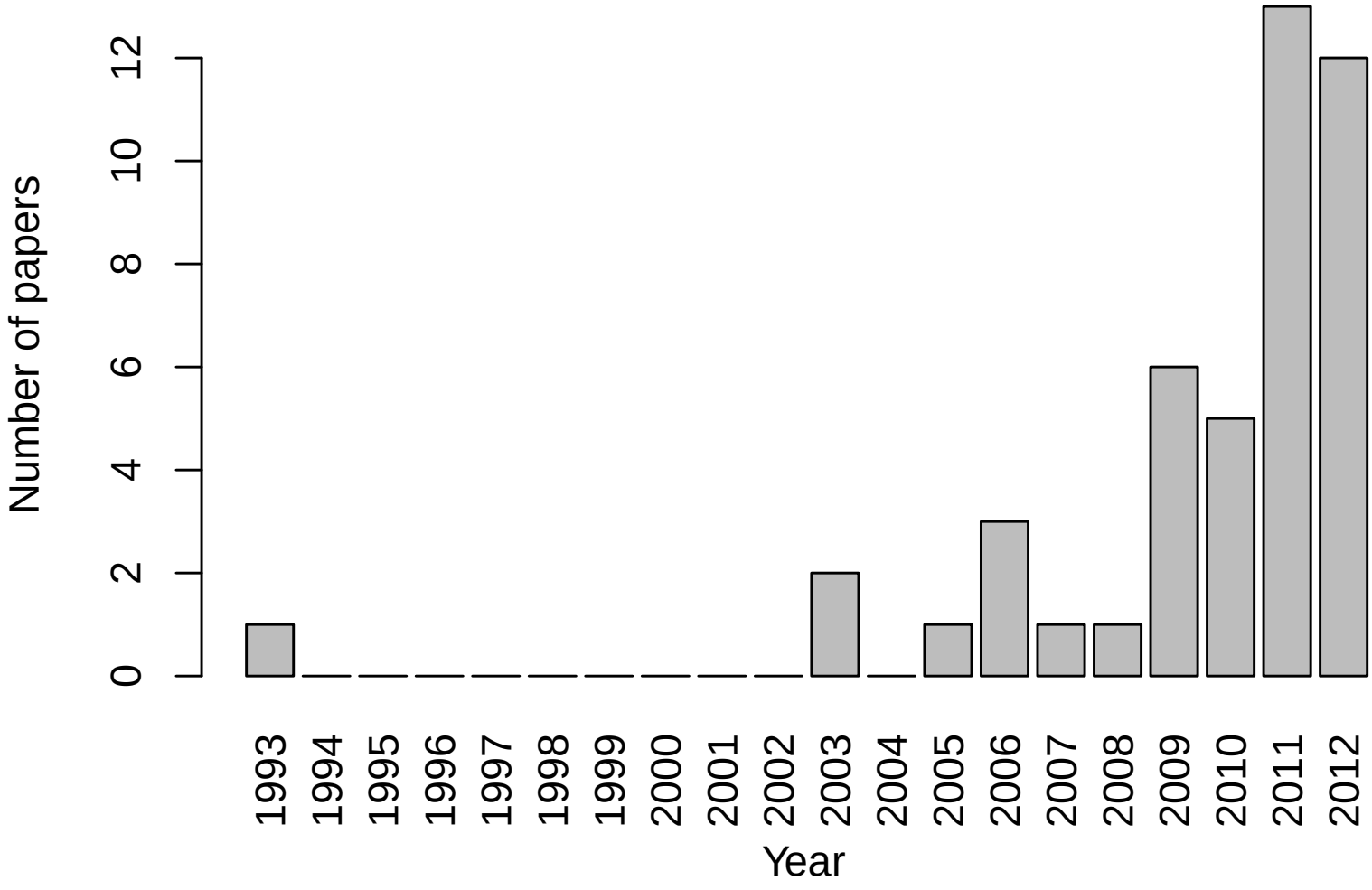
Outline

Literature search

- ISI Web of Knowledge
- 10 March 2013
- search term:
  ((animal NEAR personalit*) OR (behavioral NEAR syndrom*)) AND (insect* OR spider* OR arthropode*)

Journal	No. of papers
Animal Behaviour	11
Behav. Ecol. Sociobiol.	6
Functional Ecology	3
Proc. R. Soc. B	3
others	22
TOTAL	45

Number of papers published



Behaviours

Behaviour	Frequency
social tendency	11
boldness	10
activity	7
aggression	7
exploration	6
voracity	5
pollen-hoarding syndrome	3
sexual cannibalism	3
others	27

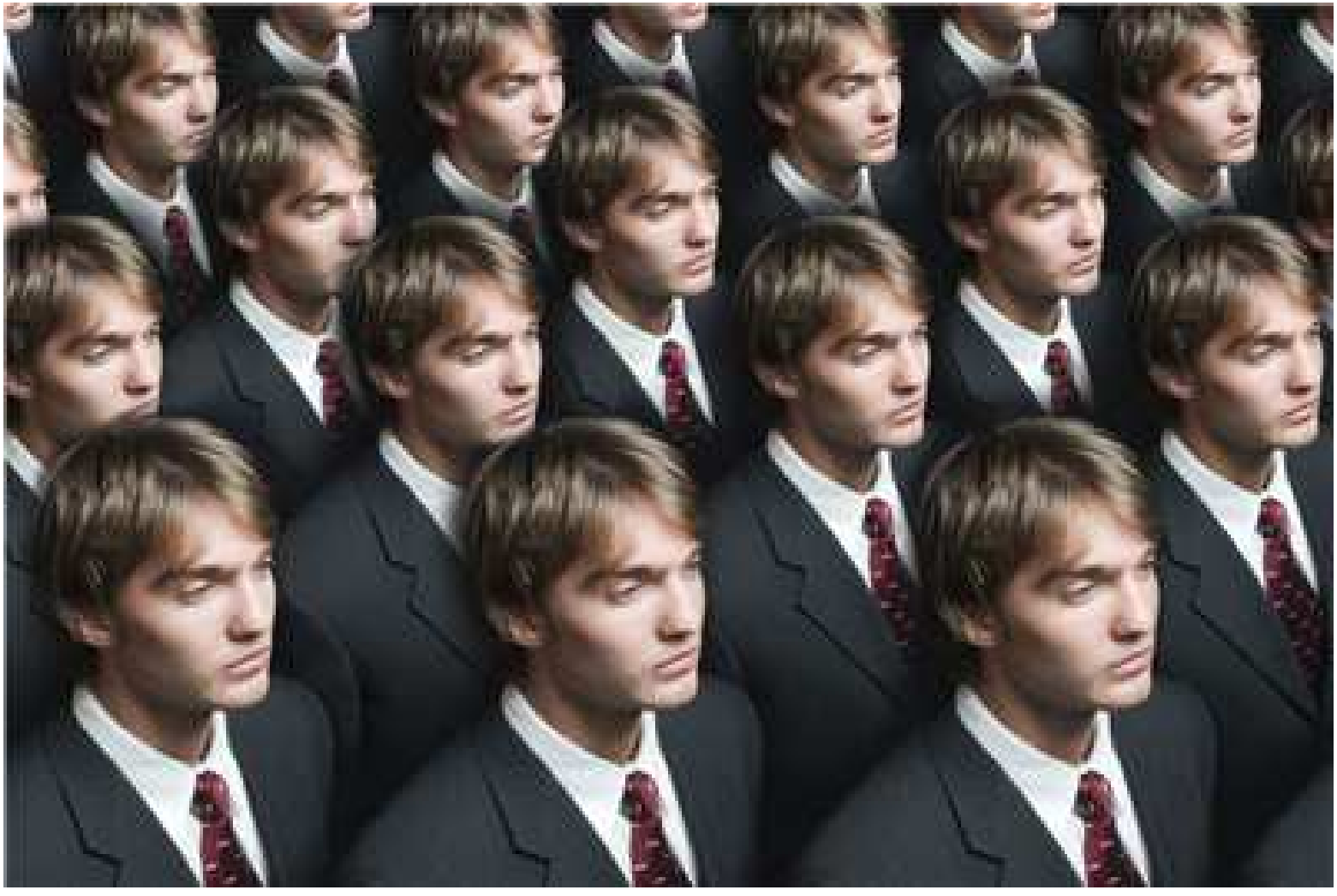
Taxons investigated

Taxon	Number of papers
spiders	22
honey bees	7
ants	4
bumblebees	3
firebugs	2
pea aphids	2
others	5

Outline

Outline

Why is individual variation important?



partner choice is meaningless

www.markpeterdavis.com/getventure/

Why is individual variation important?

make sense to choose among partners

Why is individual variation important?

possibility of specialisation

Bence Máté 2010

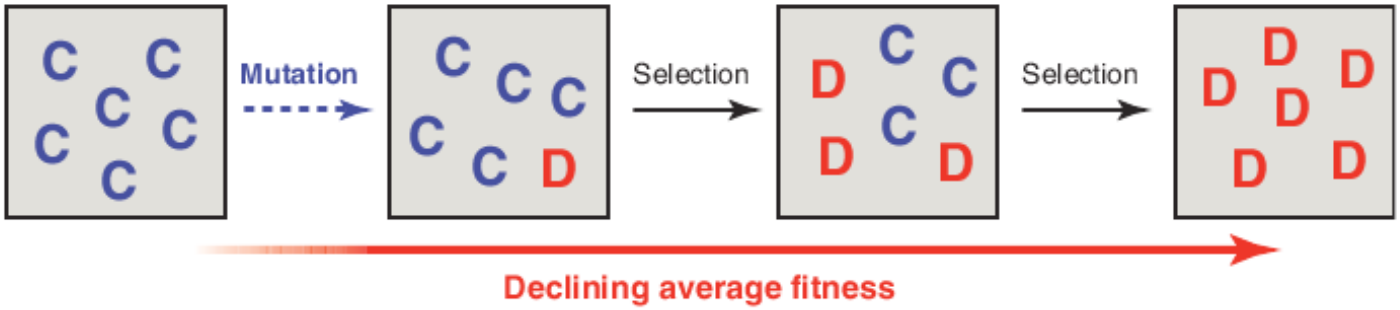
Outline

Cooperation: definitions

- Cooperative behaviour
  - incurs cost C
  - increases the success of another individual by B
  - $B > C$
- Gain
  - depends on the behaviour of others
  - risky
    - big temptation for cheating
  - **if** no cheating, then beneficial: $B > C$

Consequences

- cheaters can spread
- average fitness decreases



Nowak M, 2006, *Science*

- cooperation needs “help” to evolve

Variation and cooperation

Variation and cooperation: the model

rounds: 1 2 3 4 5 $N = 6$

- iterated Prisoner's Dilemma, between two players
- number of rounds, N, fixed
- strategy: number of cooperative rounds, n, before cheating
- strategy is subject of mutation

	D	C
D	1	5
C	0	3

Variation and cooperation: the model

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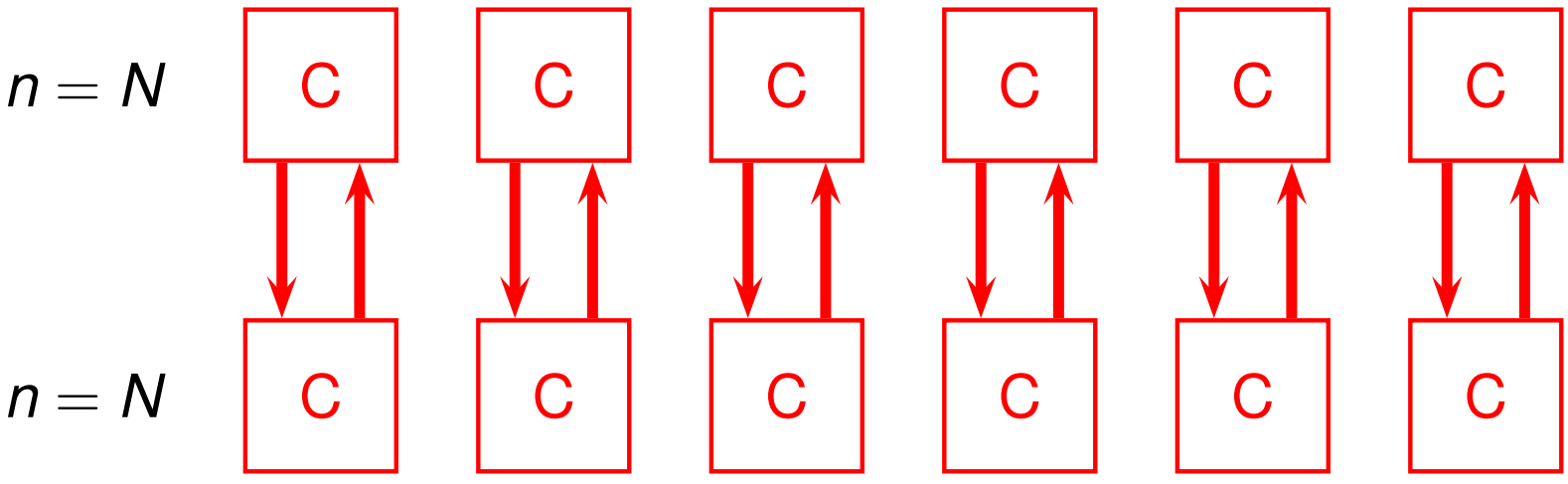

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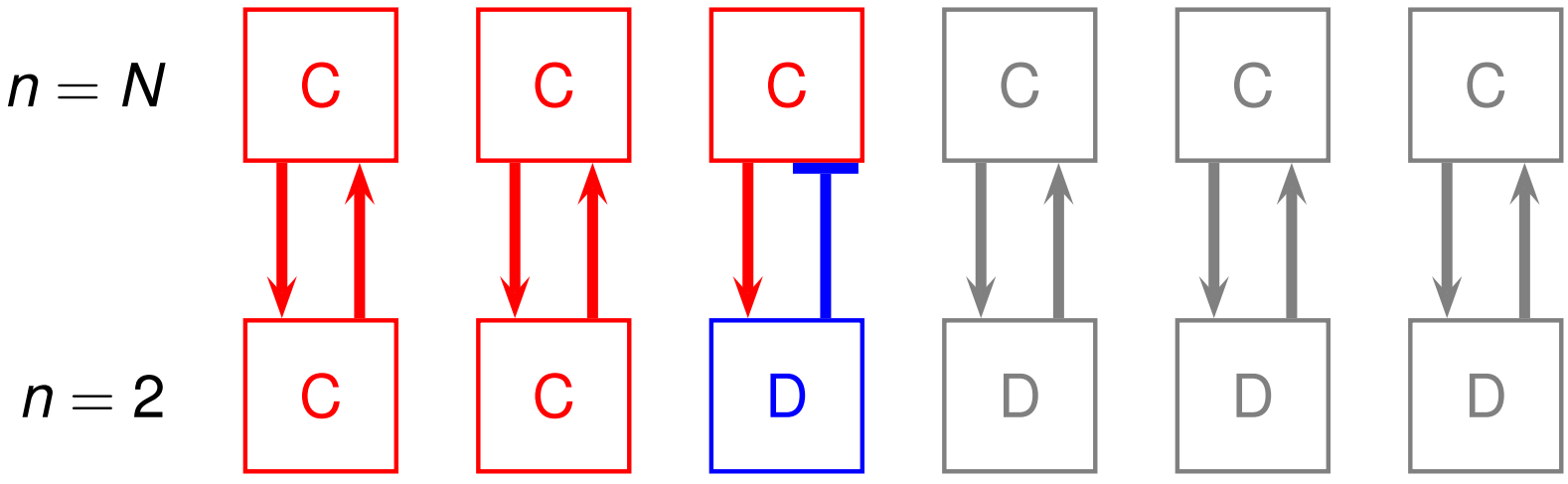

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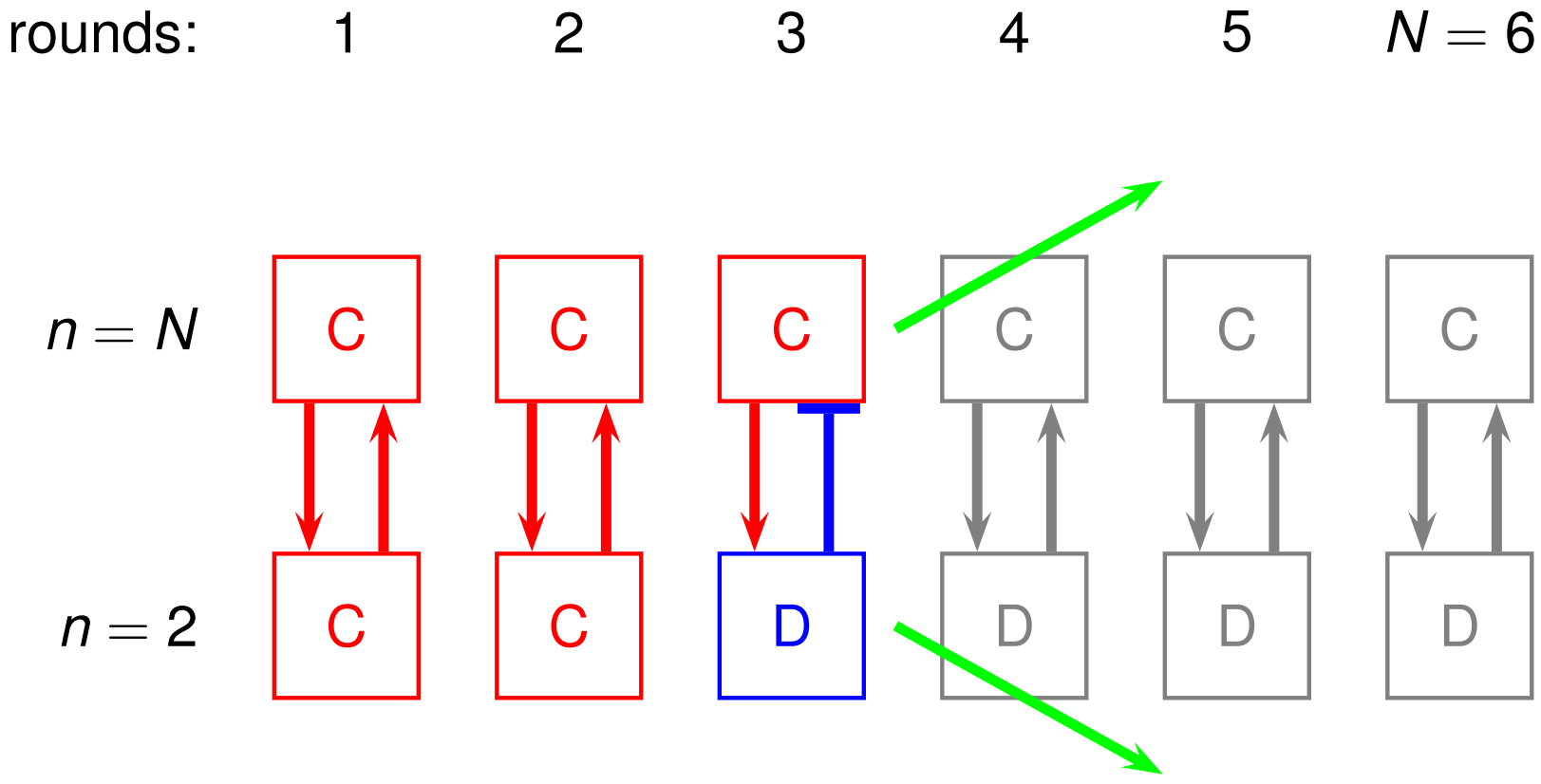

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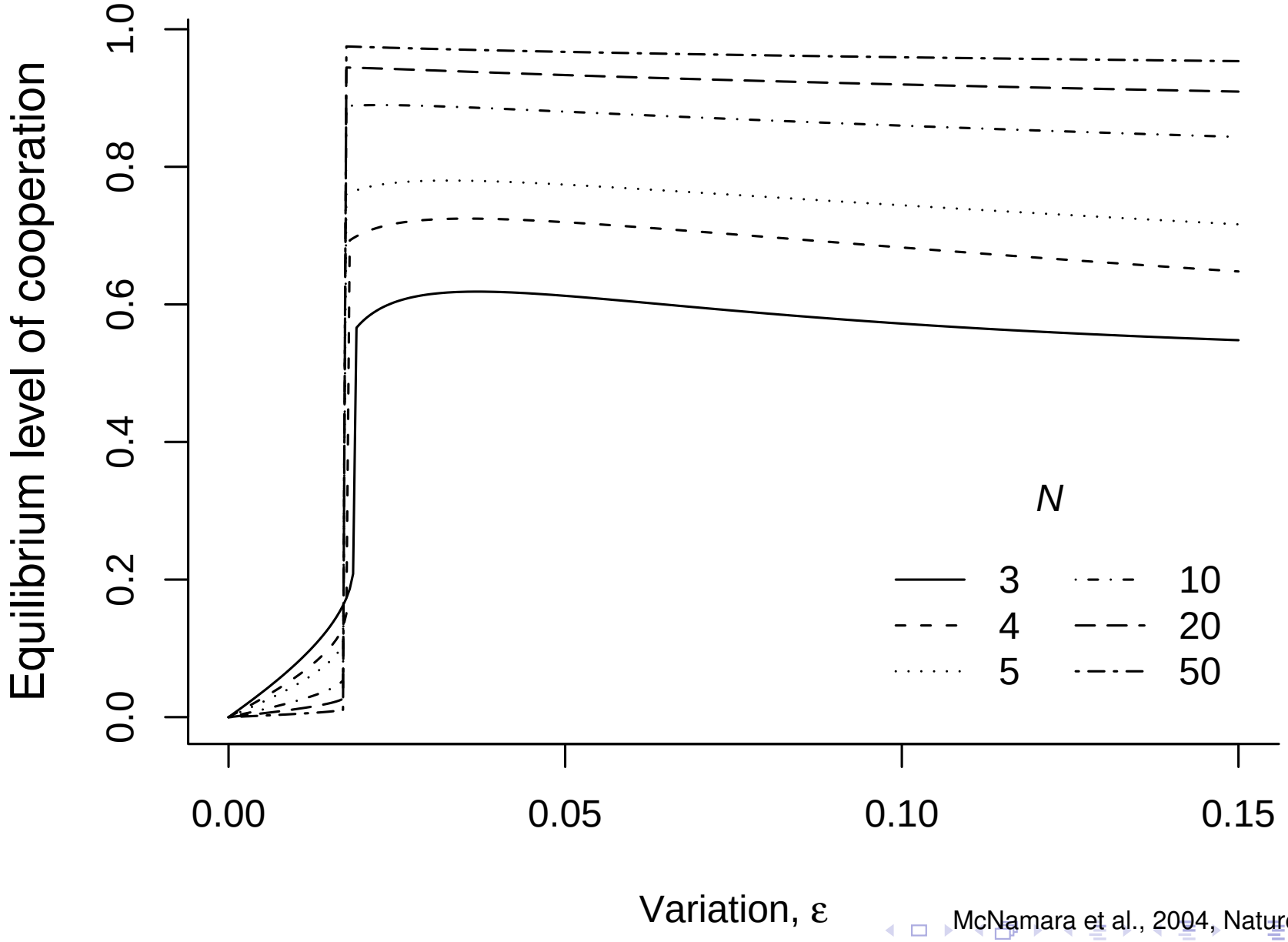
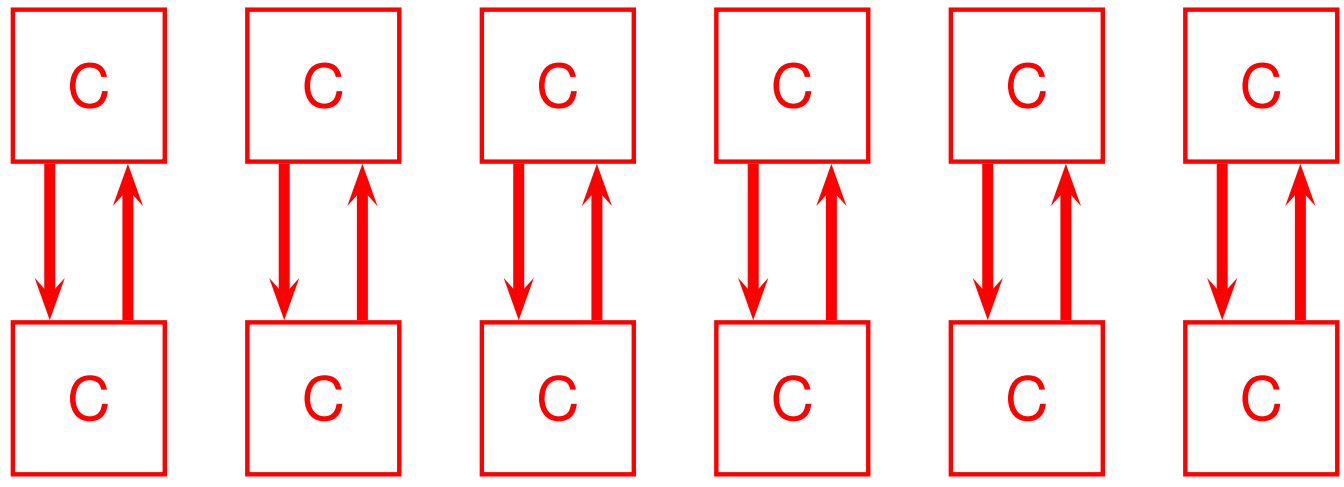
Evolutionary stability



McNamara et al., 2004, Nature

NO variability

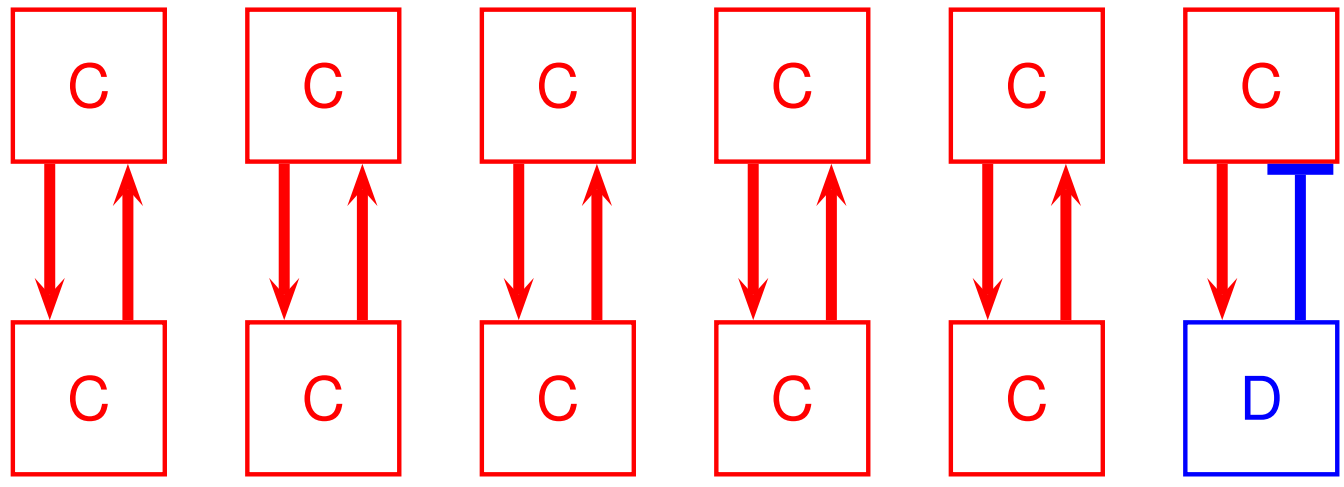
rounds:	1	2	3	4	5	$N = 6$	$\sum$
gain:	3	3	3	3	3	3	$3N = 18$
$n = N$	C	C	C	C	C	C	
$n = N$	C	C	C	C	C	C	
gain:	3	3	3	3	3	3	$3N = 18$



	D	C
D	1	5
C	0	3

NO variability

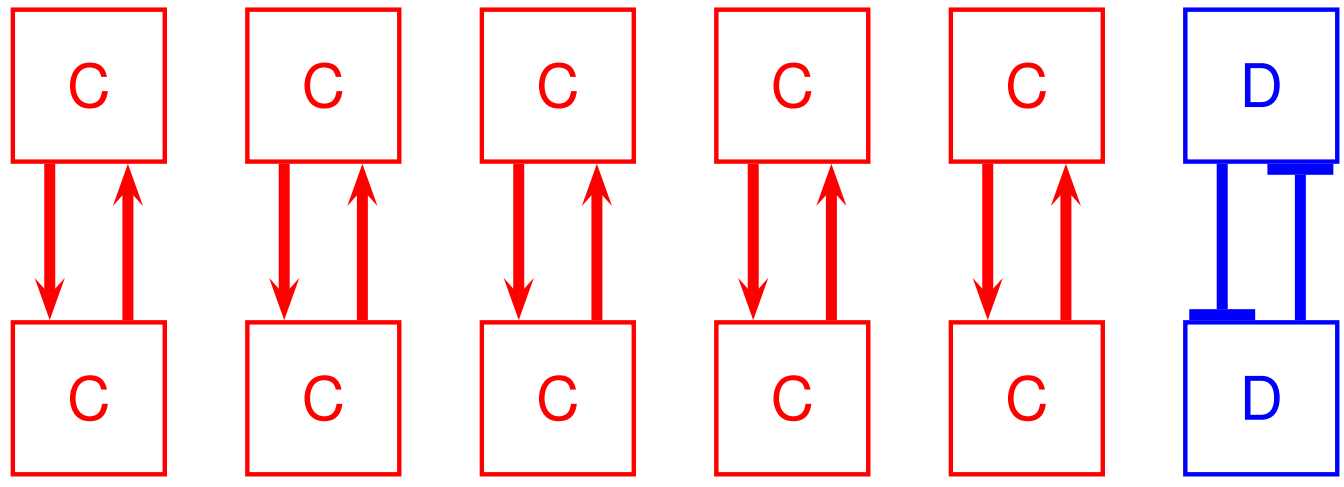
rounds:	1	2	3	4	5	$N = 6$	$\sum$
gain:	3	3	3	3	3	0	15
$n = N$	C	C	C	C	C	C	
$n = N - 1$	C	C	C	C	C	D	
gain:	3	3	3	3	3	5	20



	D	C
D	1	5
C	0	3

NO variability

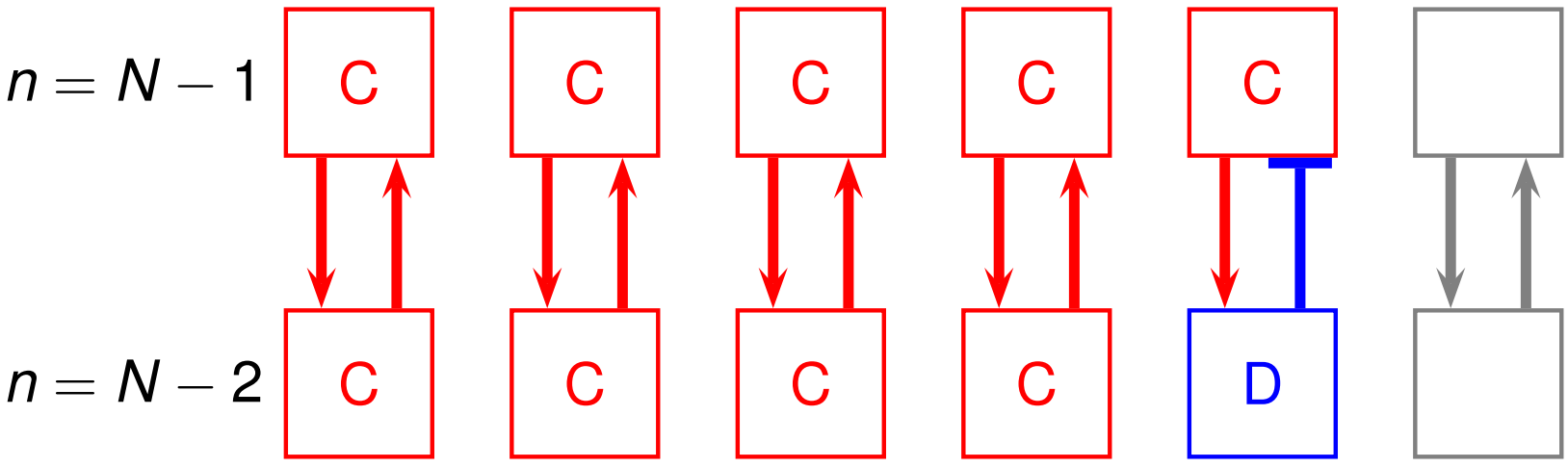
rounds:	1	2	3	4	5	$N = 6$	$\sum$
gain:	3	3	3	3	3	1	16
$n = N - 1$	C	C	C	C	C	D	
$n = N - 1$	C	C	C	C	C	D	
gain:	3	3	3	3	3	1	16



	D	C
D	1	5
C	0	3

NO variability

rounds:	1	2	3	4	5	$N = 6$	$\sum$
gain:	3	3	3	3	0		12



gain:	3	3	3	3	5		17

	D	C
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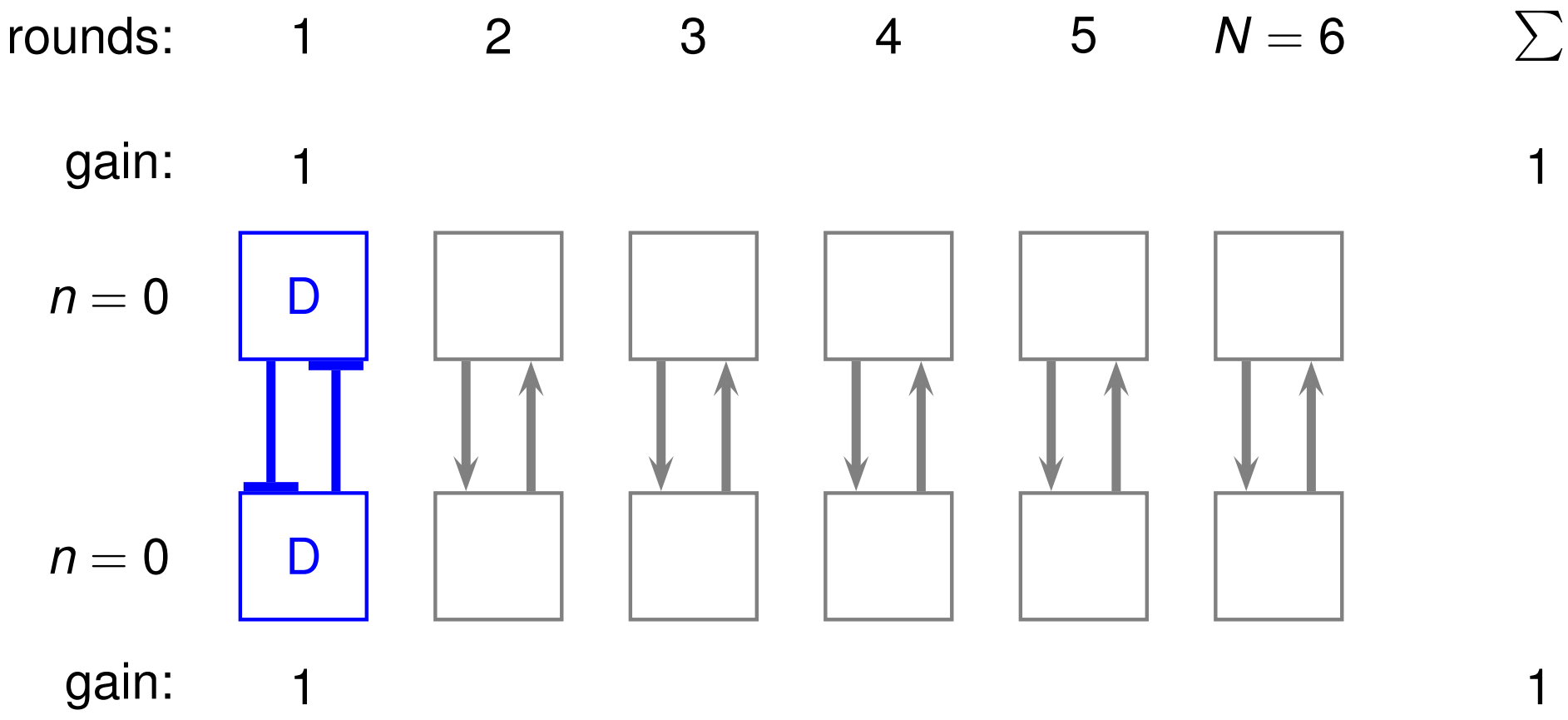
NO variability



- the ESS is $n^* = 0$ ☞ no cooperation

	D	C
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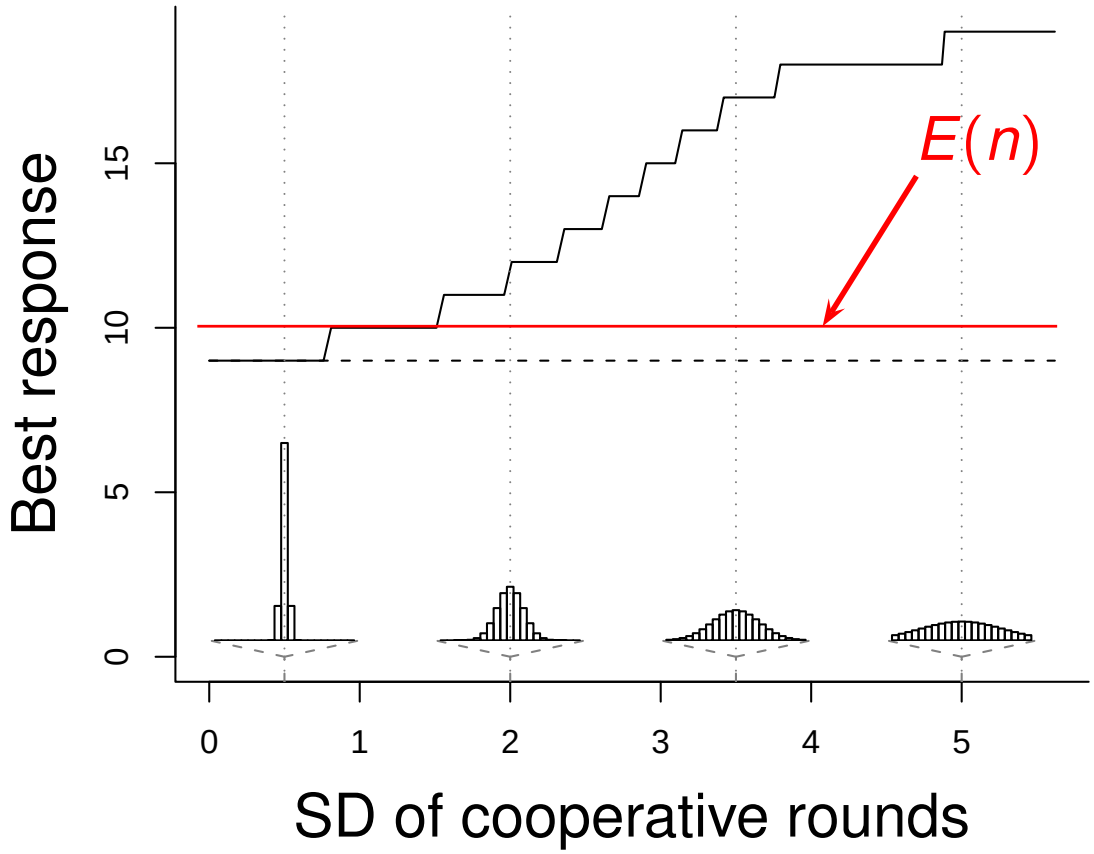
Variation: the best response



- best response, $\hat{n}$, can be $\hat{n} > E(n)$
  - large benefit from interacting individuals with $n' > E(n)$
  - small cost if $n' < n$
- cooperation arises if variation is large enough

Variation, choosiness and cooperation

Variation, choosiness and cooperation

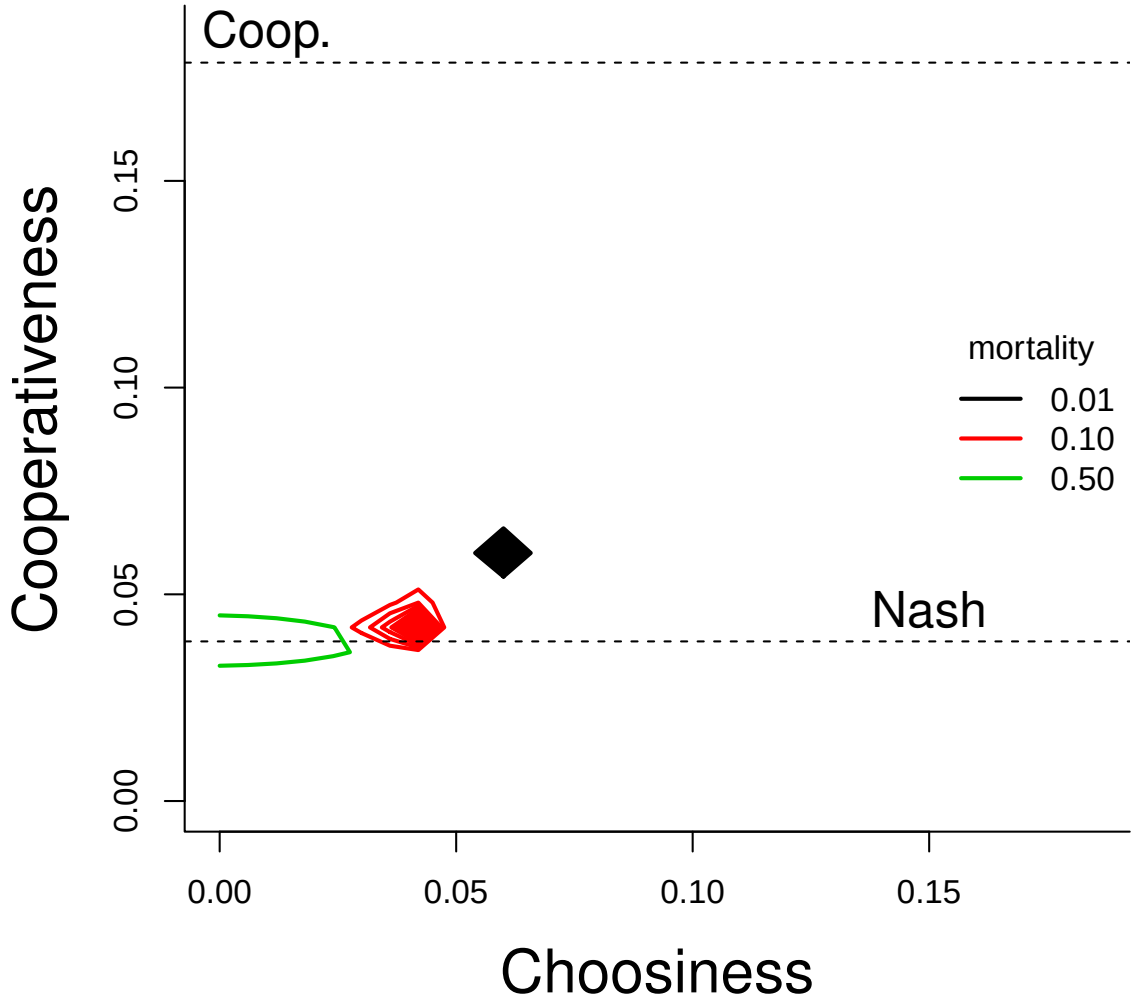
The model:

- two traits; traits genetically determined
  - cooperativeness, x: effort devoted to common goods
  - choosiness, y: minimum partner's cooperativeness x'
    if $x' < y$ then the interaction finished ("divorce")
- gain: $B(x, x') - C(x)$ ☞ social dilemma
- infinite population for many time steps

McNamara et al., 2008, *Nature*

Results

Mutation rate: 0.001

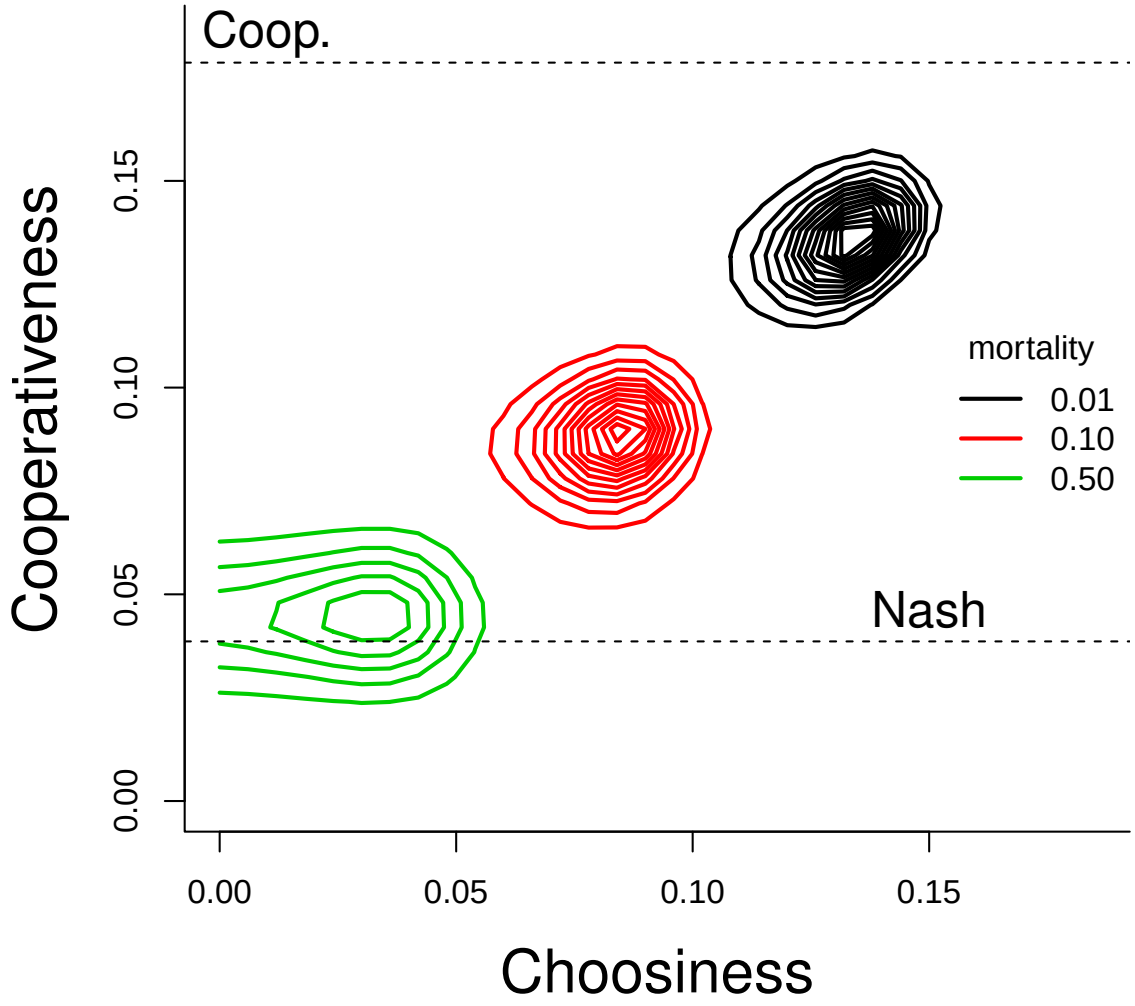


NO variation

- everybody is the same ☞ no gain by being choosy ☞ no choosiness
- no choosiness ☞ no risk of divorce ☞ not worth to invest cooperation
- the stable state: **non**-cooperative, **non**-choosy population

Results

Mutation rate: 0.05



Variable population

- more cooperative individuals can be found ☞ worth divorcing
- cooperative individuals enjoy an advantage by not being divorced
- run-away process starts: both cooperativeness and choosiness increase
- stable state: choosy and cooperative population

Task specialisation and cooperation

Parental conflict about care

- parental care *improves* offspring's survival
  ☞ both parents enjoy the benefit
- cost only paid by the *caring* parent(s)
- conflict of interest: *how much care each parent should provide?*
- large number of models, BUT usually unidimensional care

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What happens if care involves distinct types of activities?

- distinct types of activities ☞ task specialisation possible

Question

Does task specialisation promote cooperation between parents?

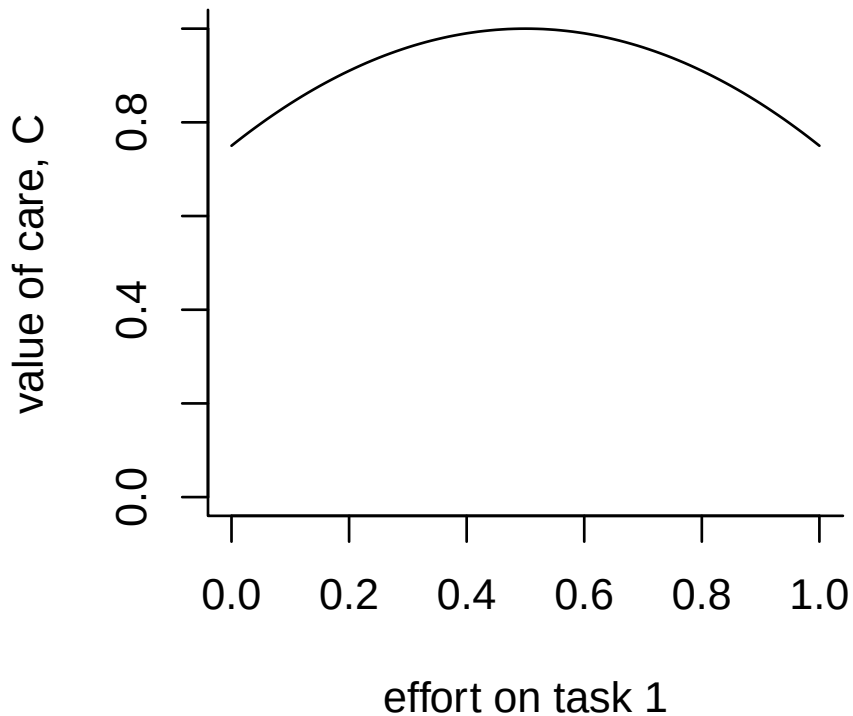
Model: behaviour

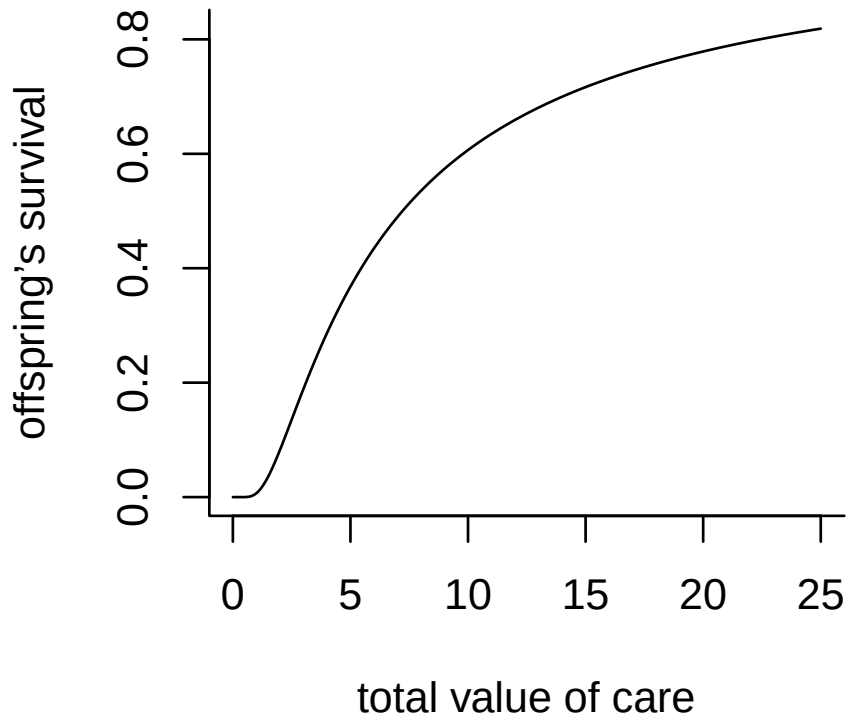
Two tasks:

- T1 (e.g. feeding the young)
- T2 (e.g. guarding the nest)

Two decisions:

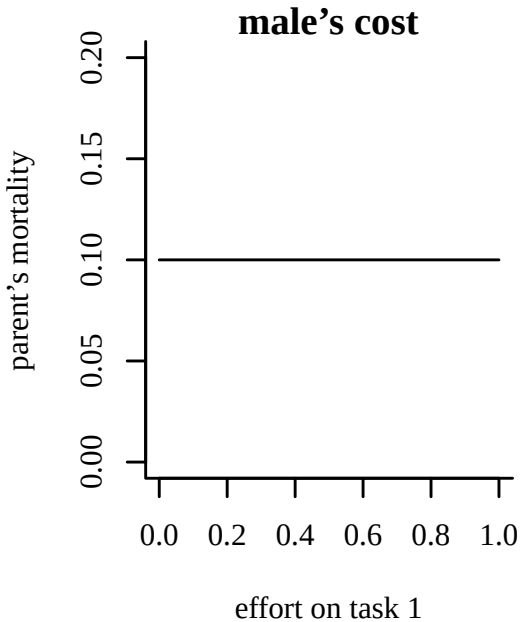
- division of parental effort between tasks
- length of care

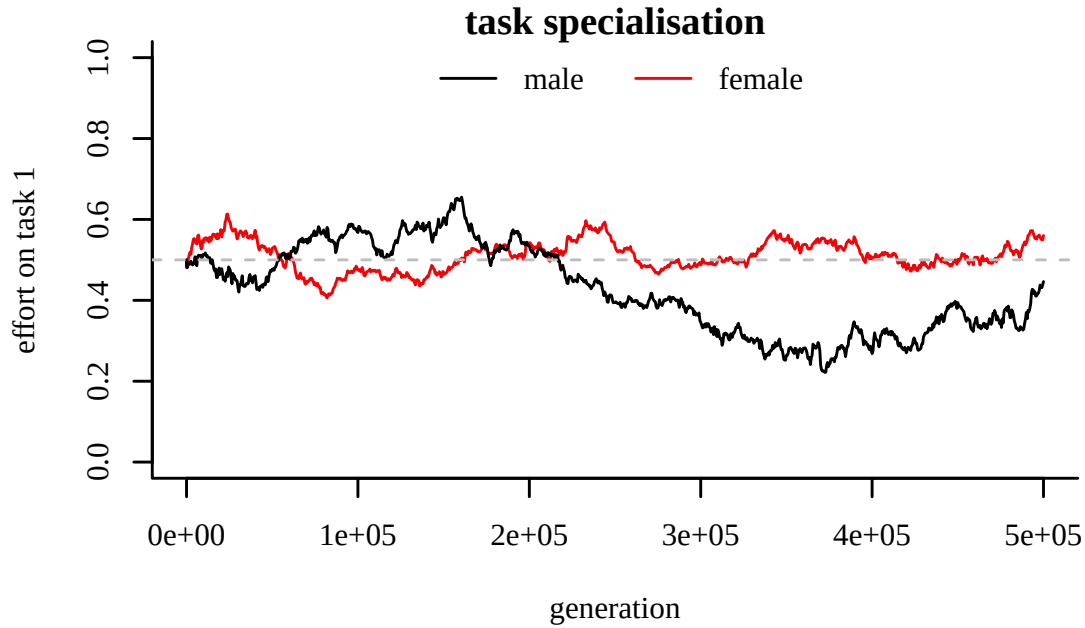


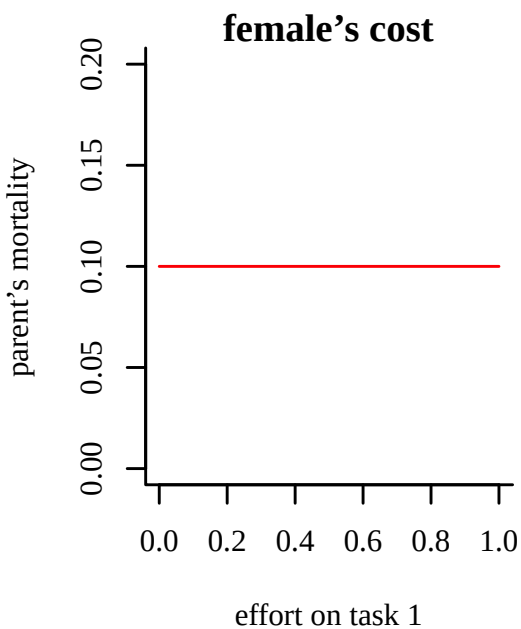


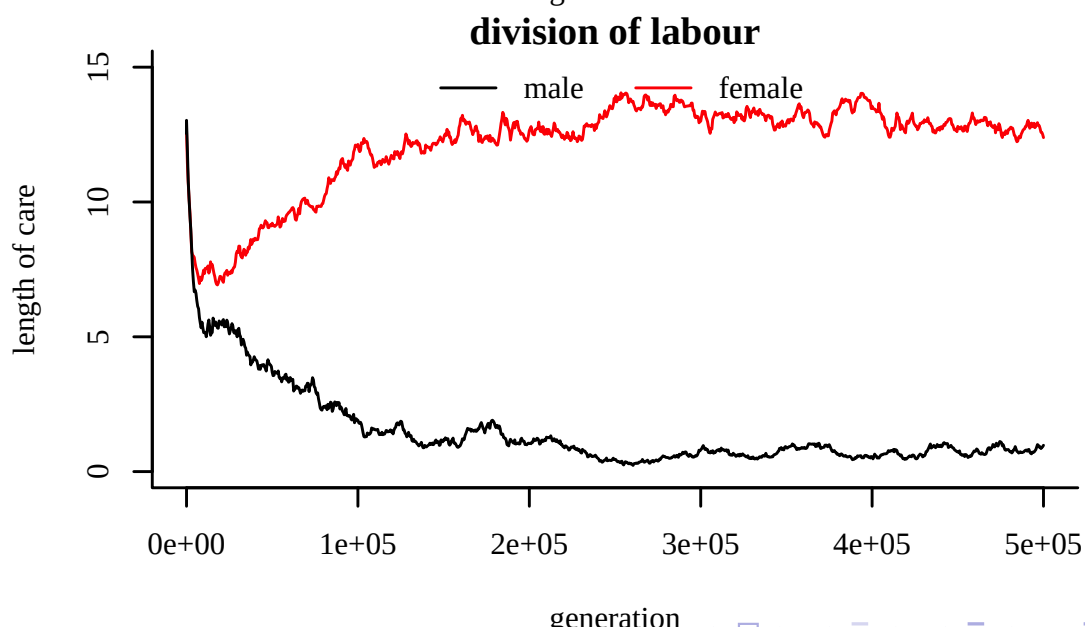
Two sexes similar: no need to specialise

strong sexual selection



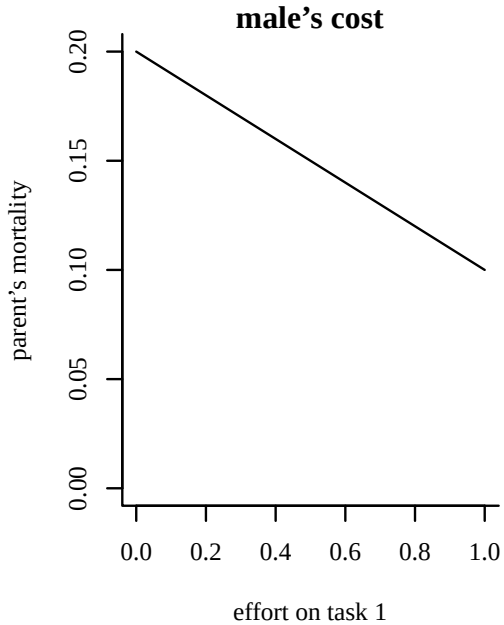


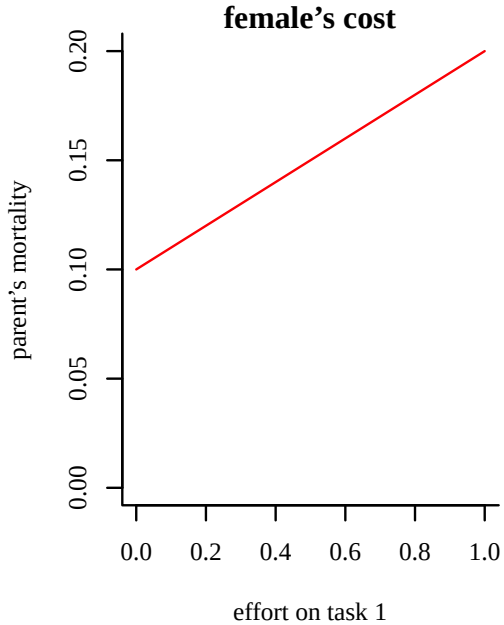




The sexes differ

strong sexual selection





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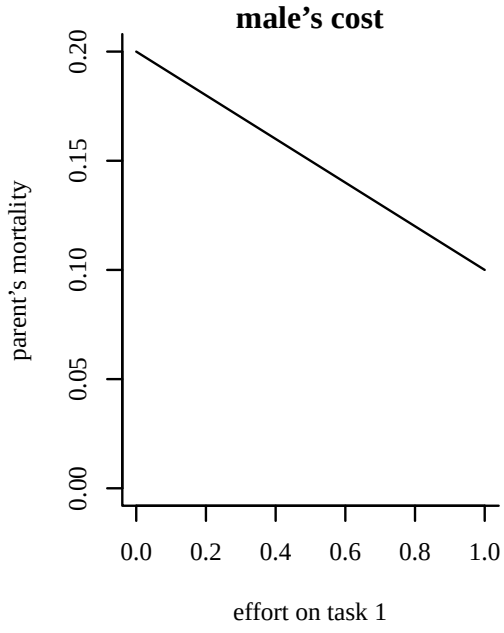

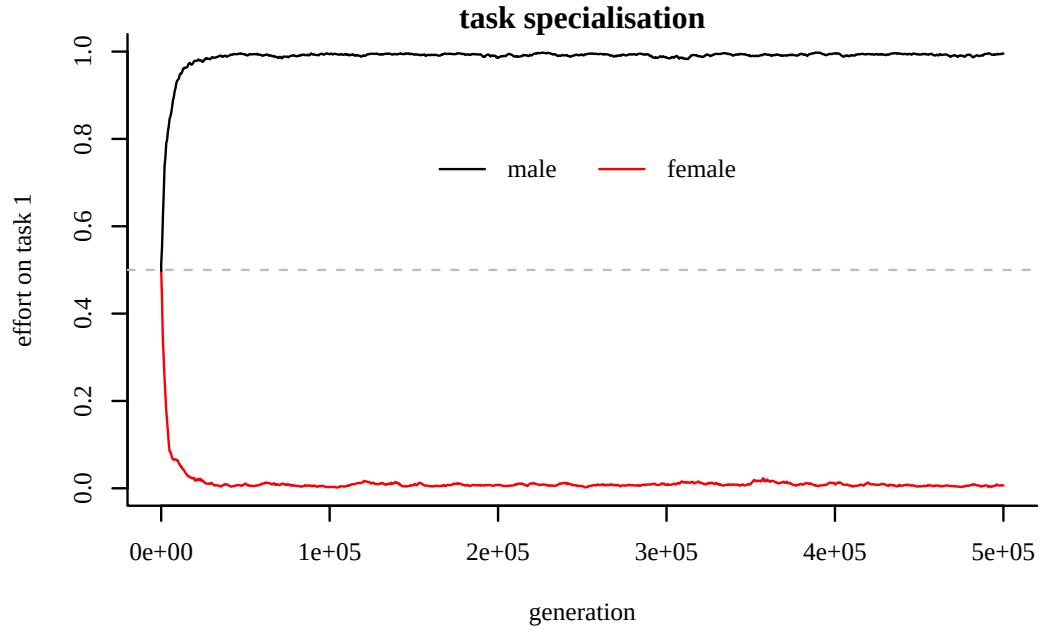

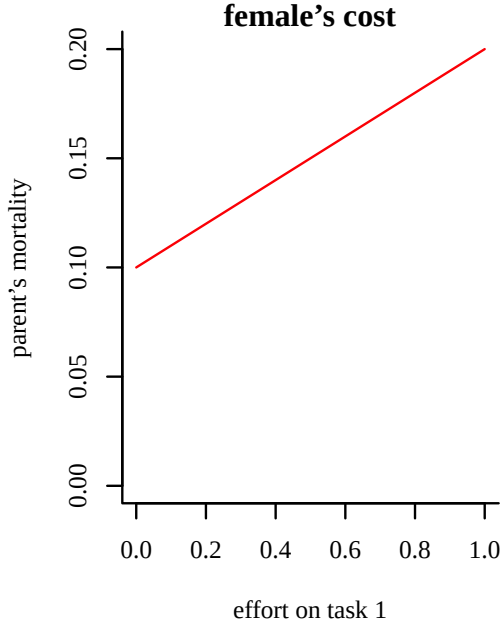

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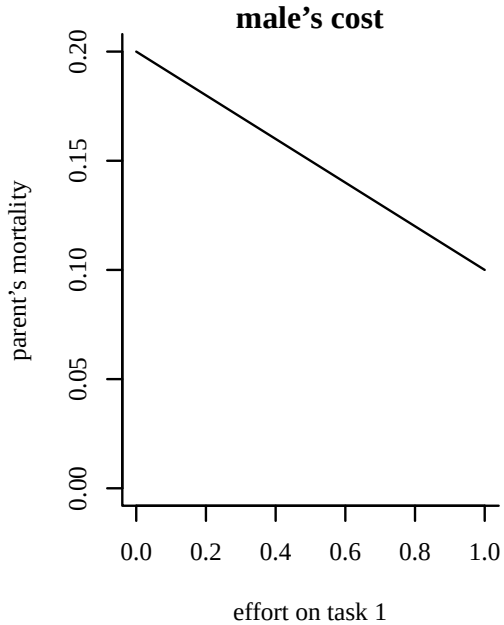

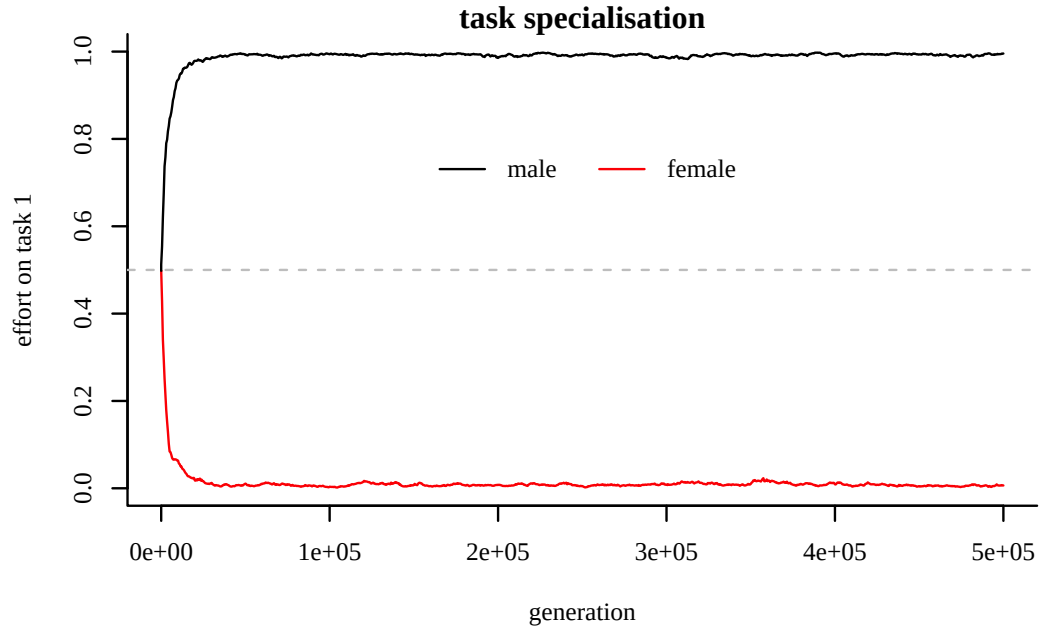

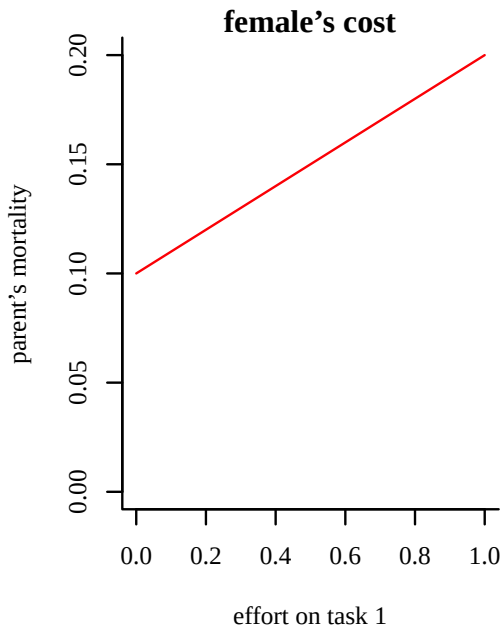

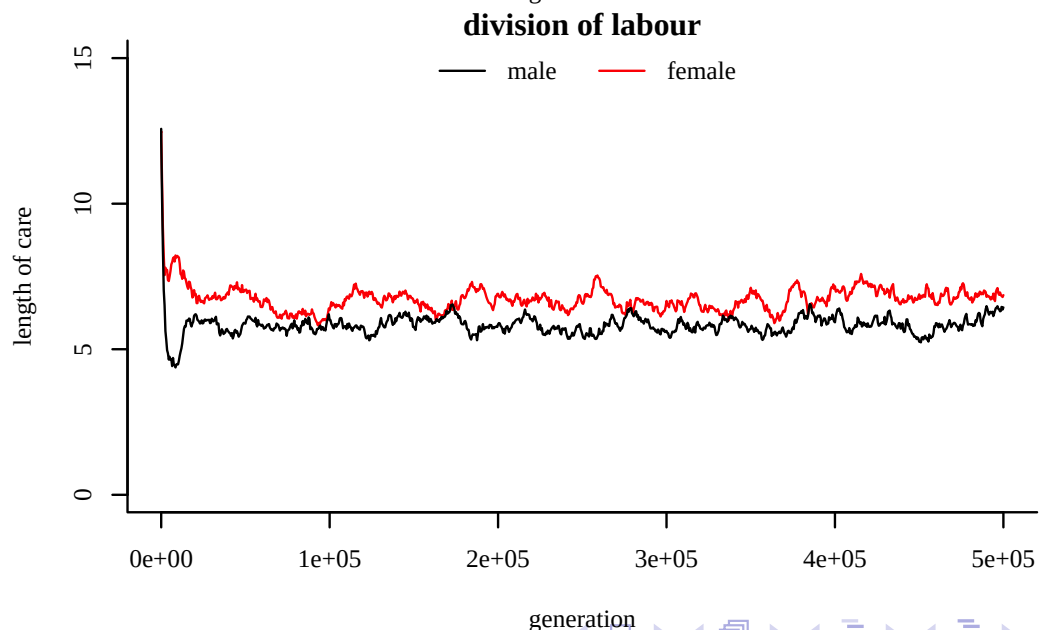

The sexes similar: worth specialising

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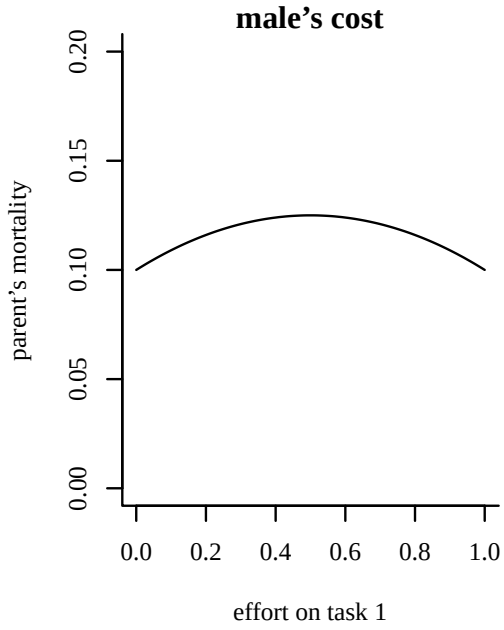

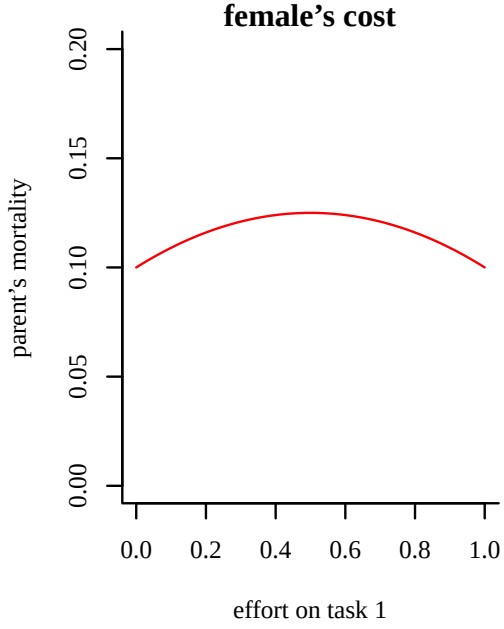

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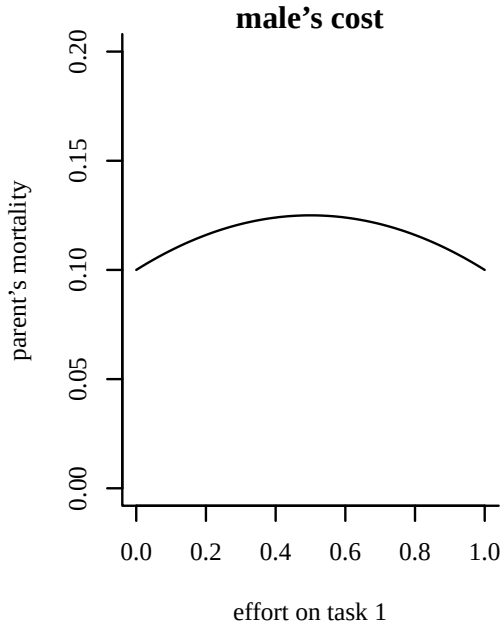

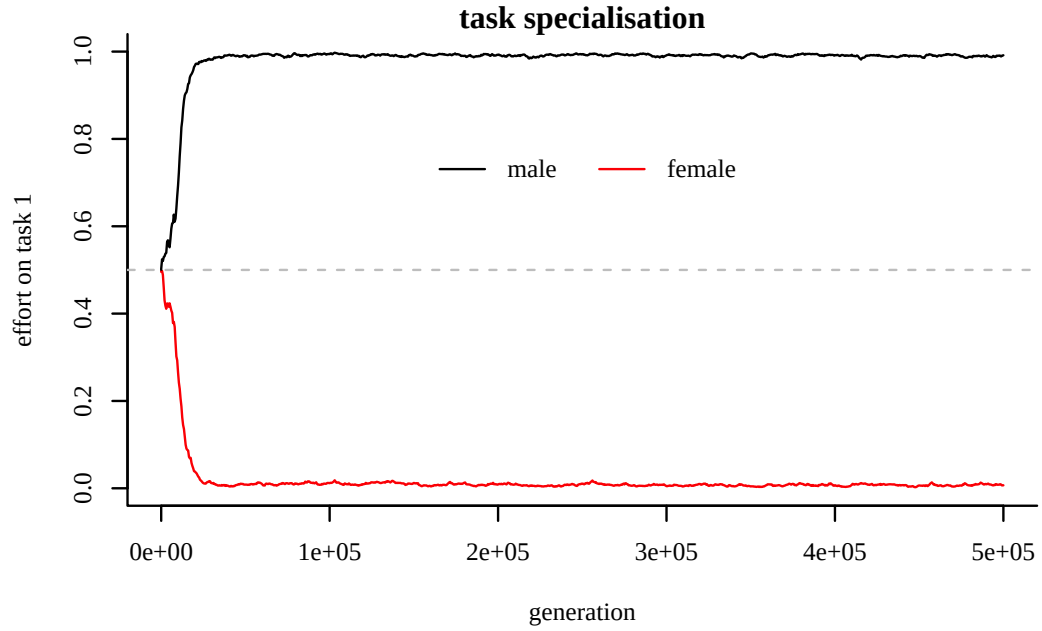

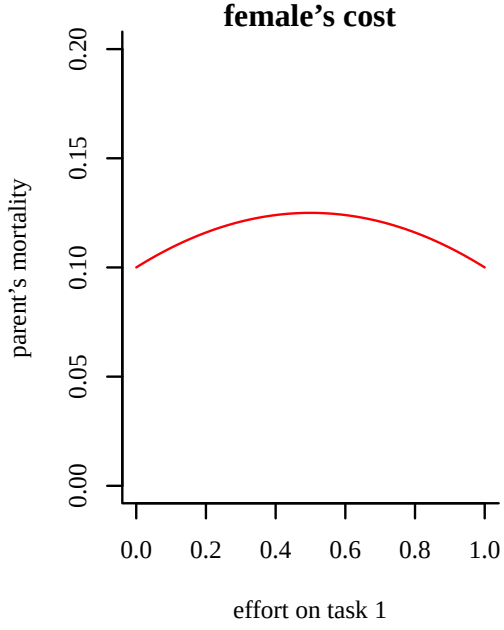

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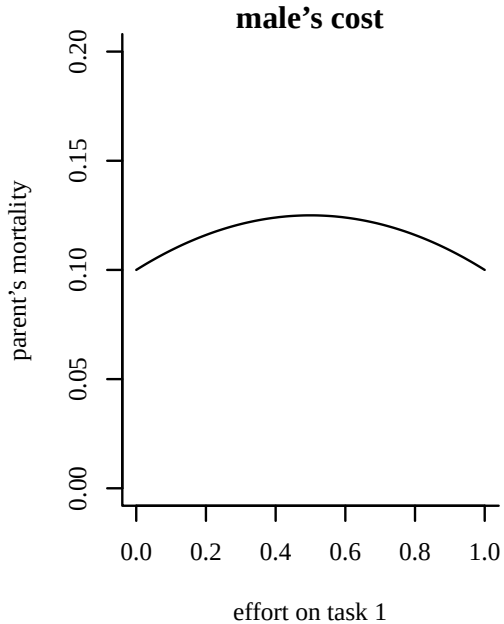
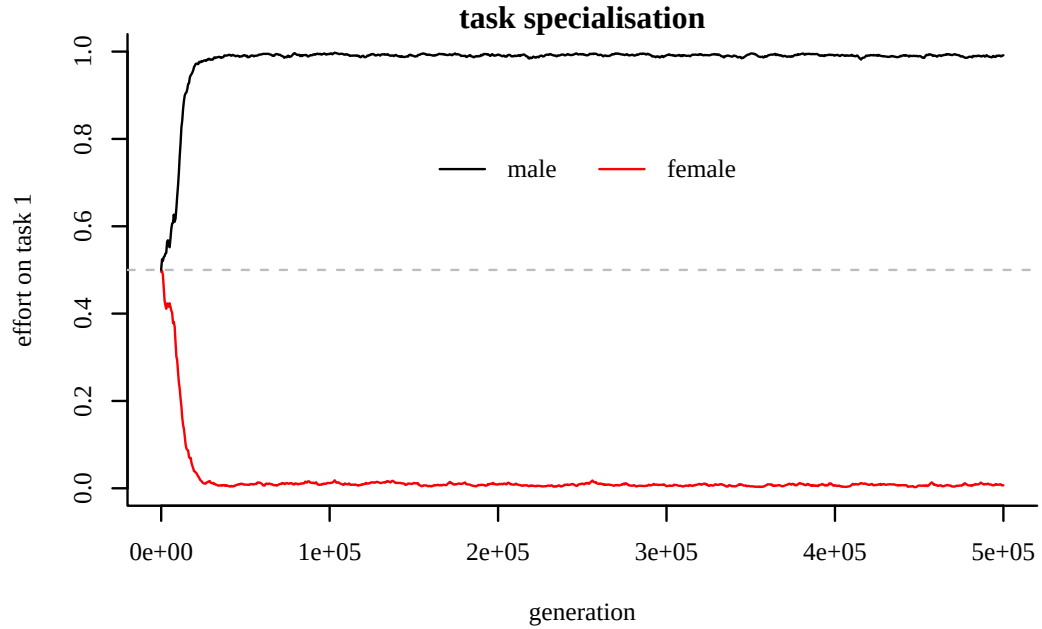
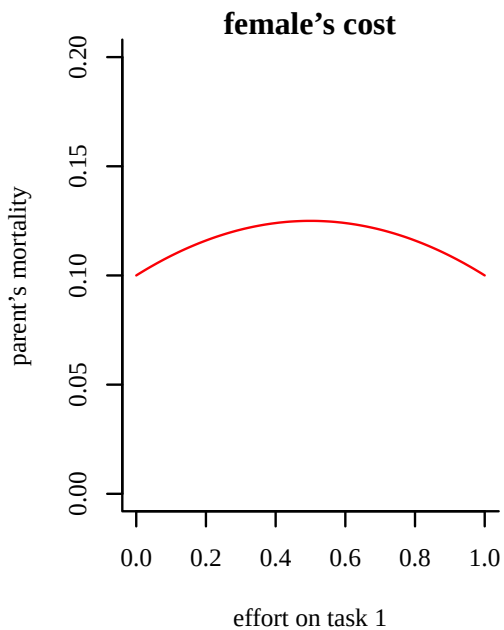
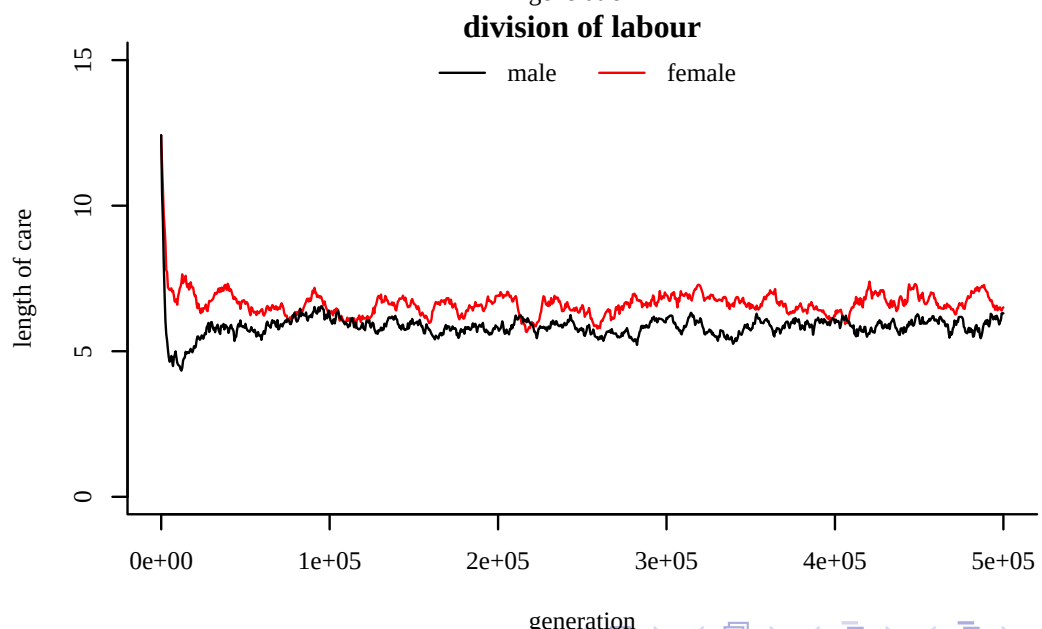








Outline

Question

Do individuals with different personality prefer different positions within groups?

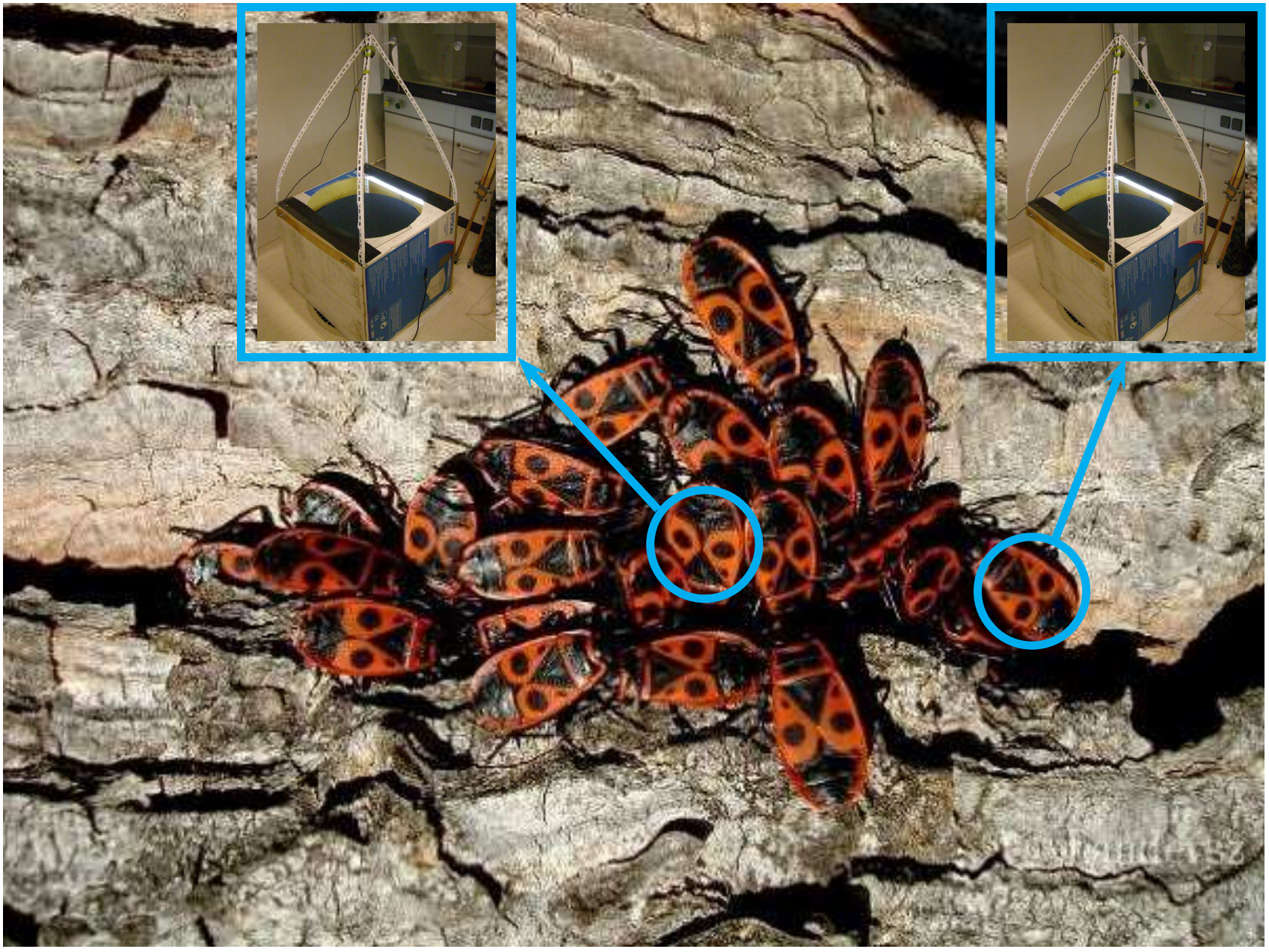
or

Does the personality of individuals on the edge of group differ from those on the centre?

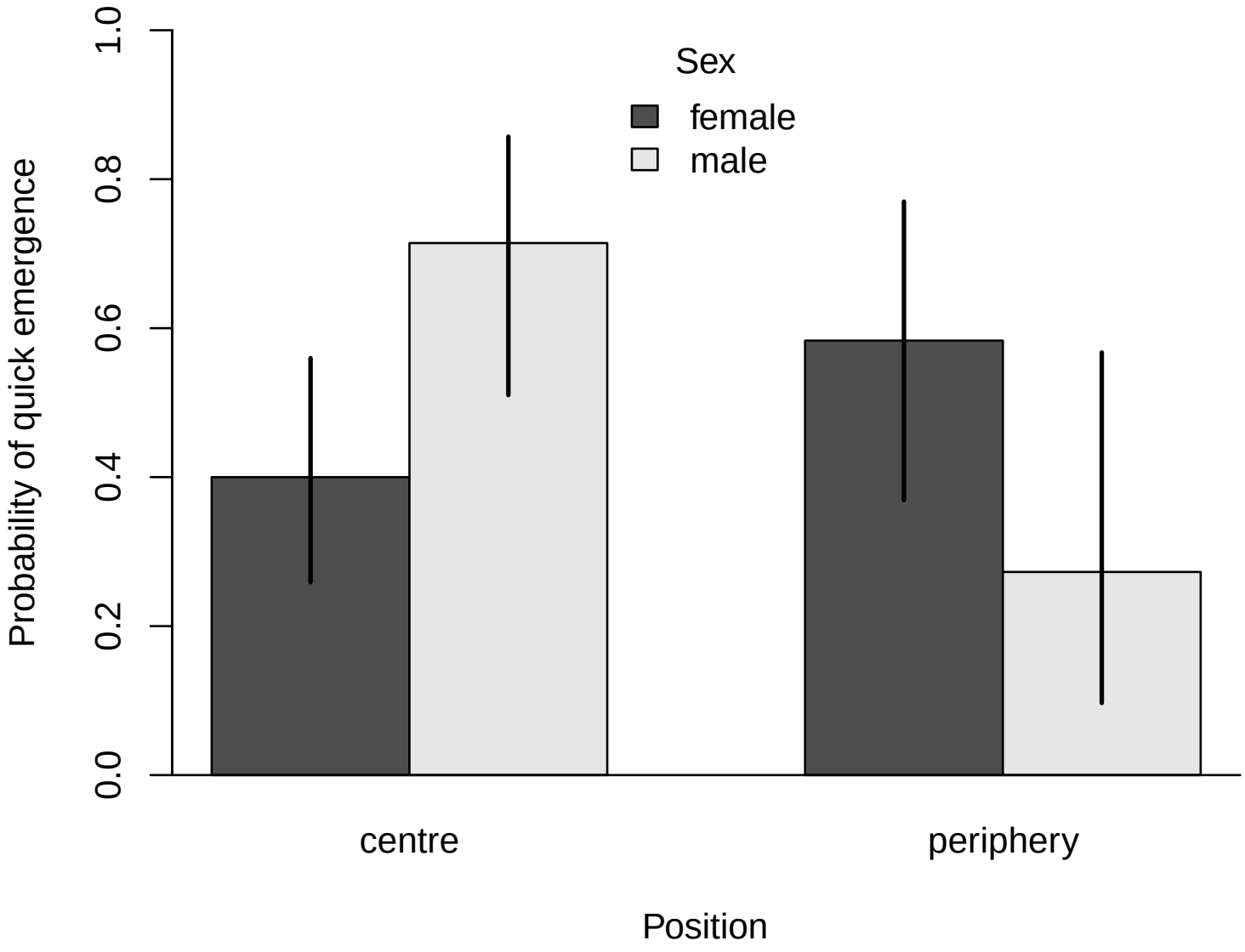
Setup

Setup

Setup



Preliminary result



Outline

General conclusions

- Consistent between individual variation is the rule rather than the exception.
  - even in arthropodes
  - BUT students of insects should catch up!

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General conclusions

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Variation is important!

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