Individual differences and cooperation

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Symposium on “The Theory of Cooperation”
Adelboden, 11-13 August, 2011

Outline of the talk

1. Cooperation: concepts and consequences
2. Variation: fundamental aspect of life
3. Case studies
4. General conclusions

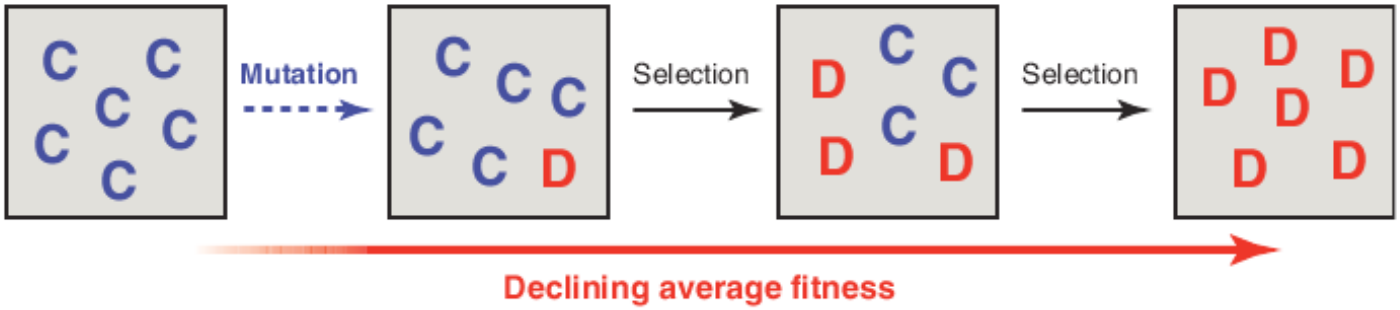
Outline

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

Many models of cooperation proposed.

Many models of cooperation proposed.

Most of them, however,

NEGLECT

individual variation!

BUT!

Outline

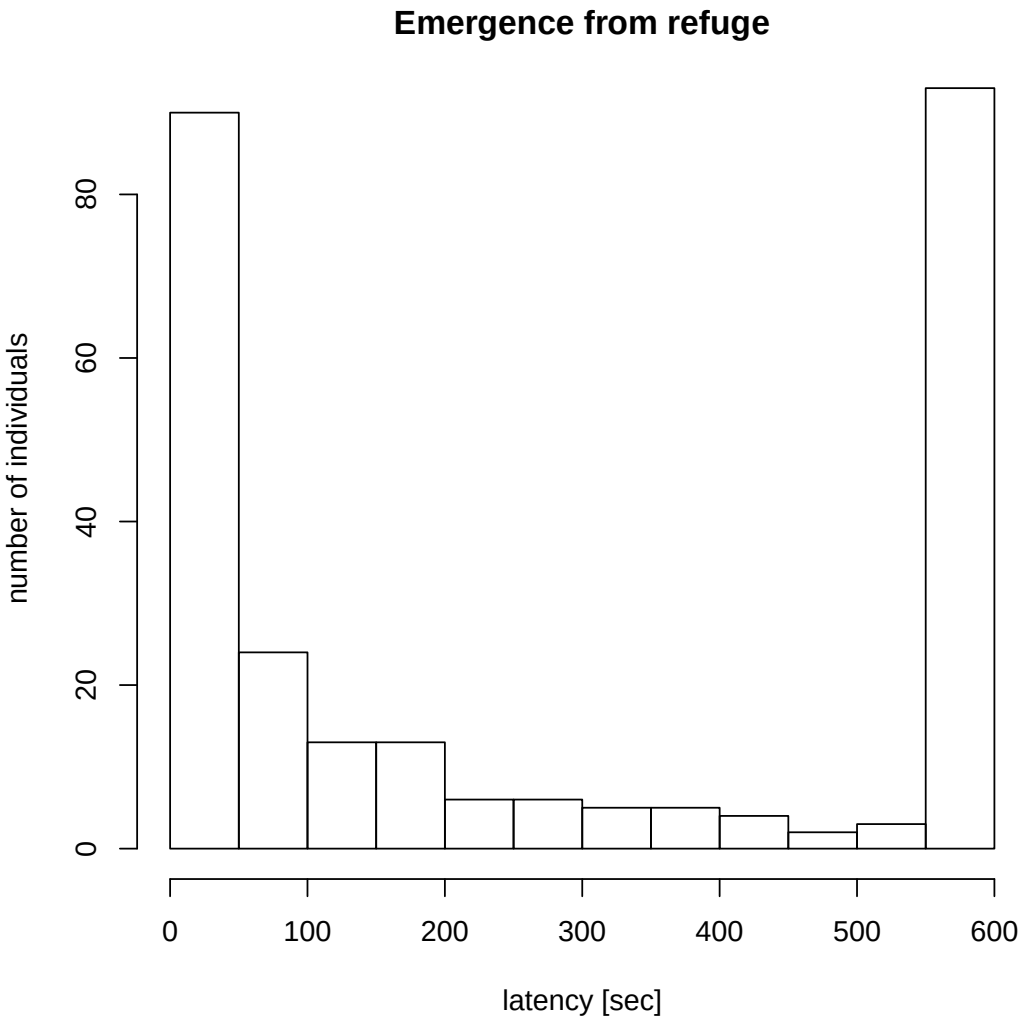
Biodiversity

Individual variation: morphology

Emlen et al. 2007 PNAS

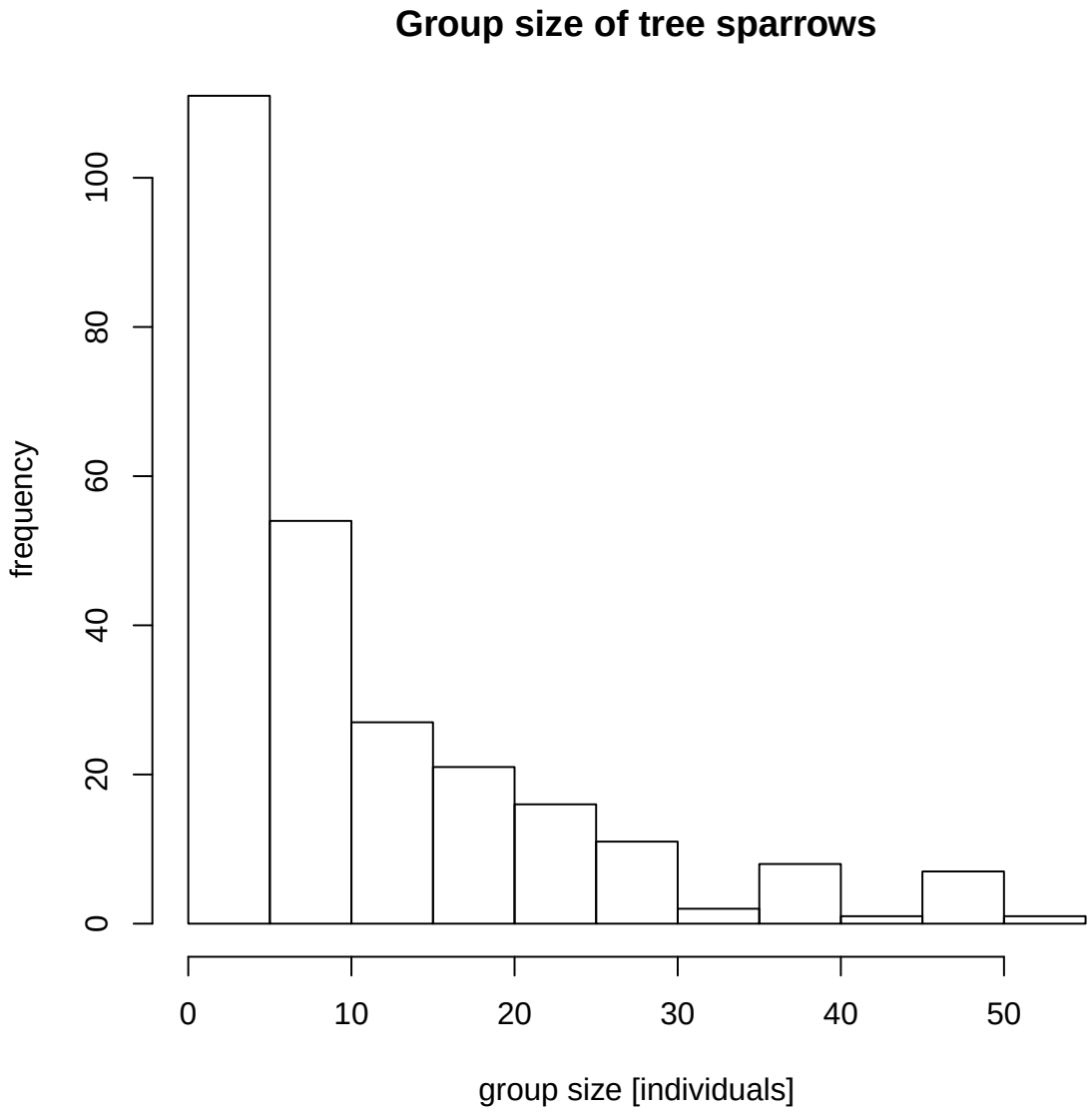
www.sfu.ca/biology/wildberg/ruff.html

Individual variation: behaviour



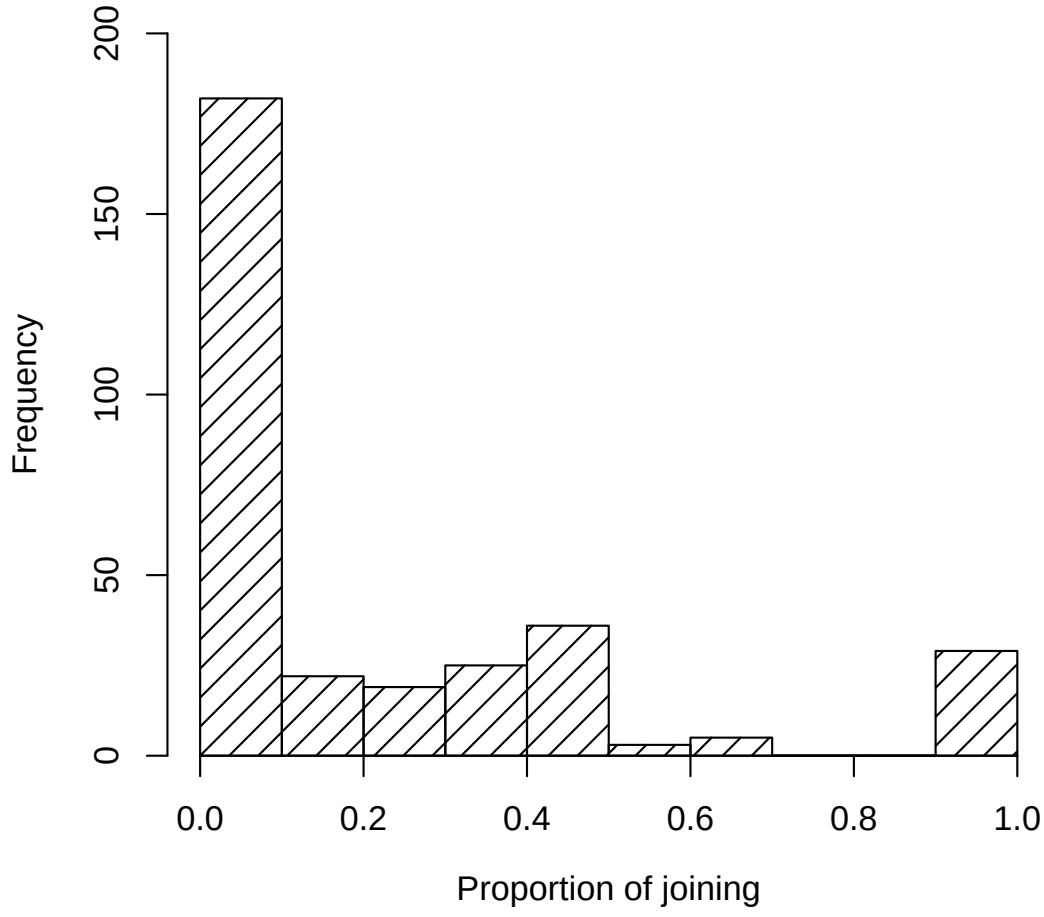
Gyuris et al. 2011 Proc. R. Soc. B

Individual variation: social behaviour



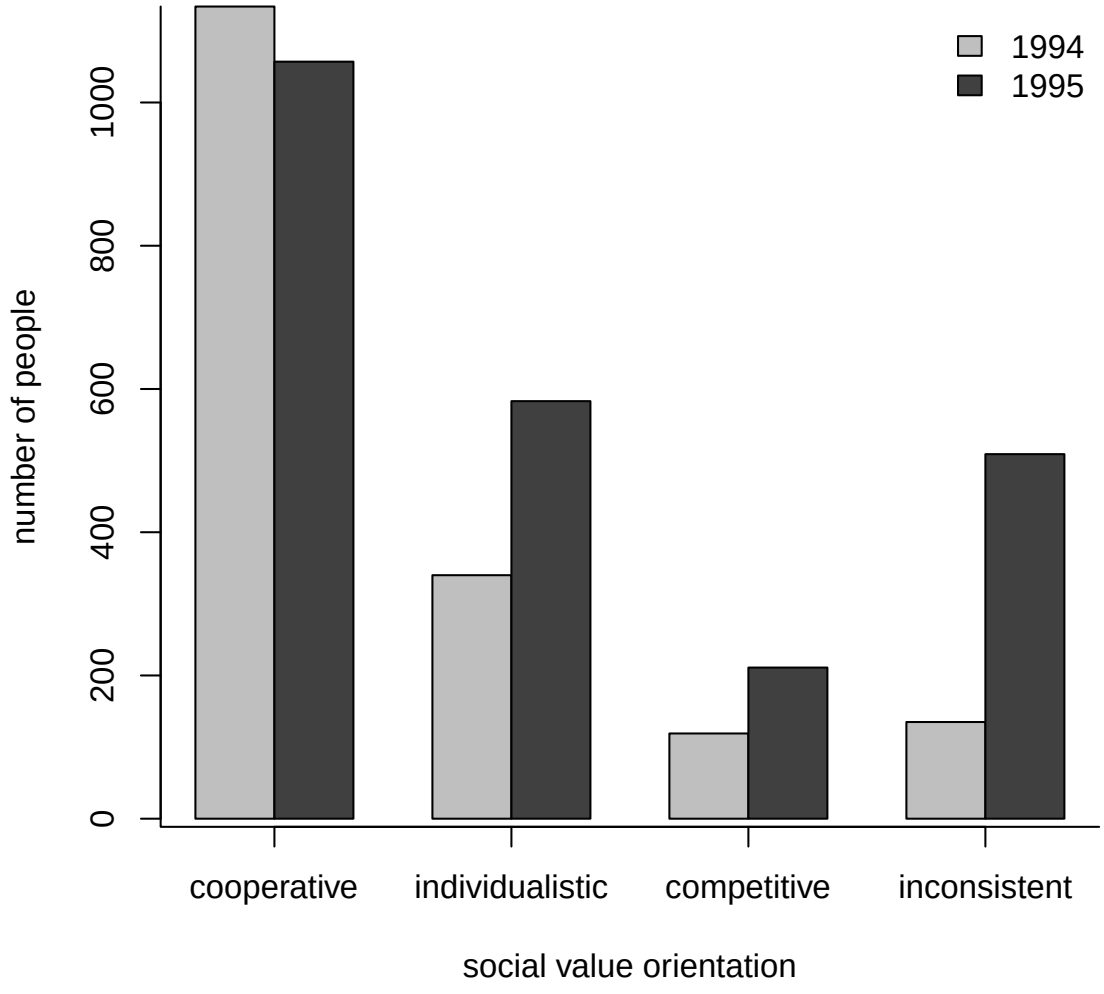
Mónus & Barta 2011 Int. Stud. Sparrows

Individual variation: social behaviour



Barta et al. 2004 Anim. Behav.

Individual variation: social behaviour



Bekkers 2004 in prep.

Sources of individuality

- Random effects
  - mutation
  - developmental noise
- State
  - environmental stochasticity
  - history

Why is individual variation important?

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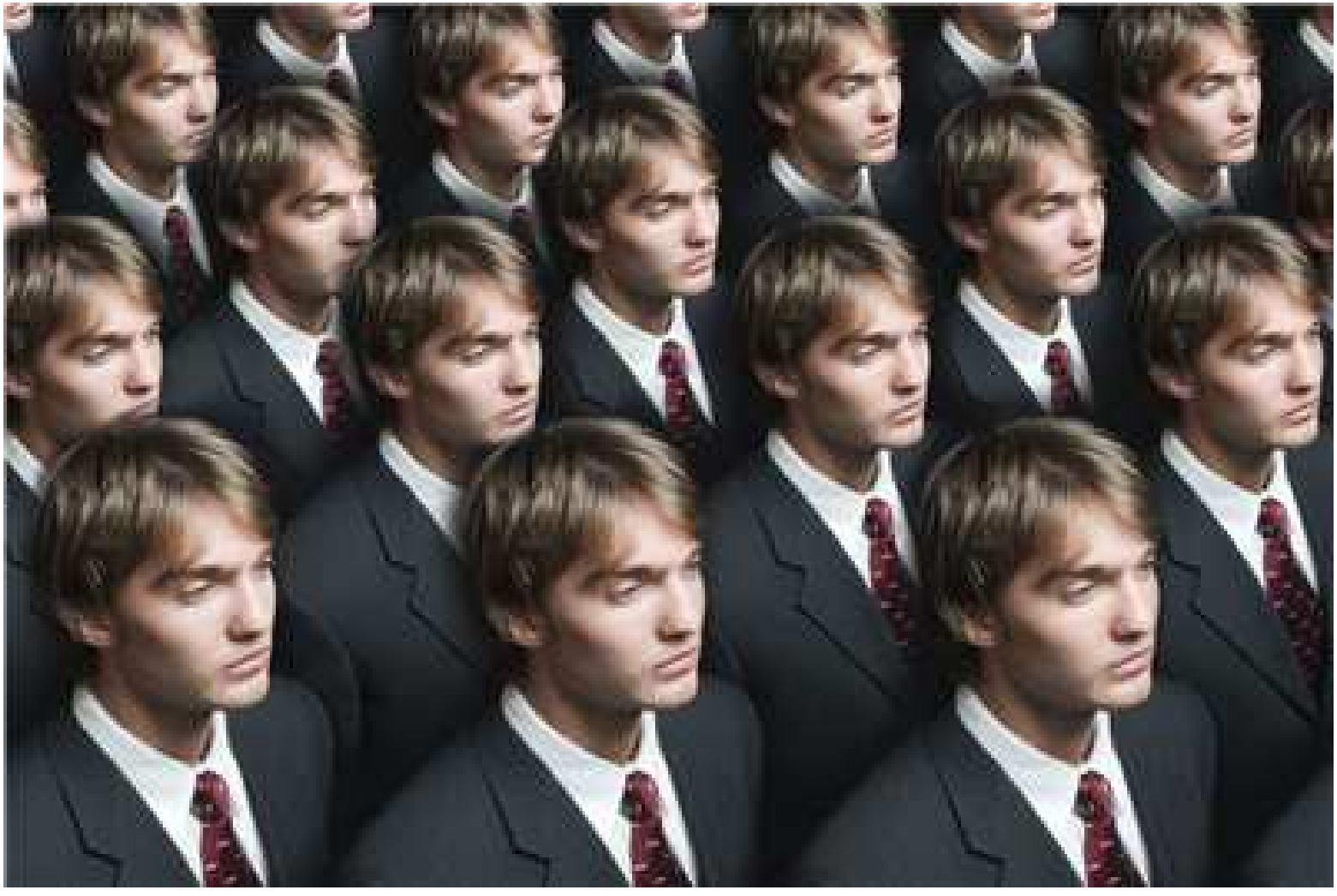


partner choice is meaningless

www.markpeterdavis.com/getventure/

Why is individual variation important?

make sense to choose among partners

Why is individual variation important?

possibility of specialisation

Question

How does individual variation affect the evolution of cooperation?

Question

How does individual variation affect the evolution of cooperation?

Specifically:

- random effects
  - getting off
  - partner choice
- state
  - generalised reciprocity
  - specialisation

Outline

Outline

Variation and cooperation

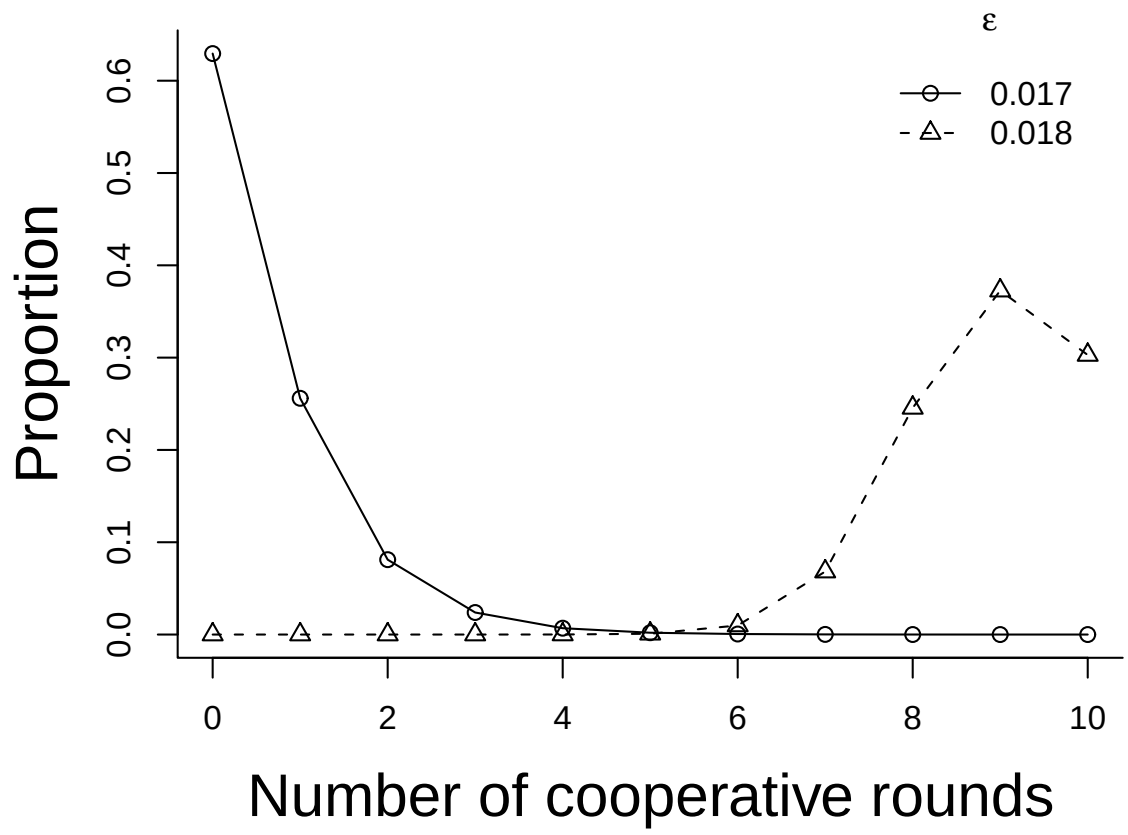
	D	C
D	1	5
C	0	3

The model

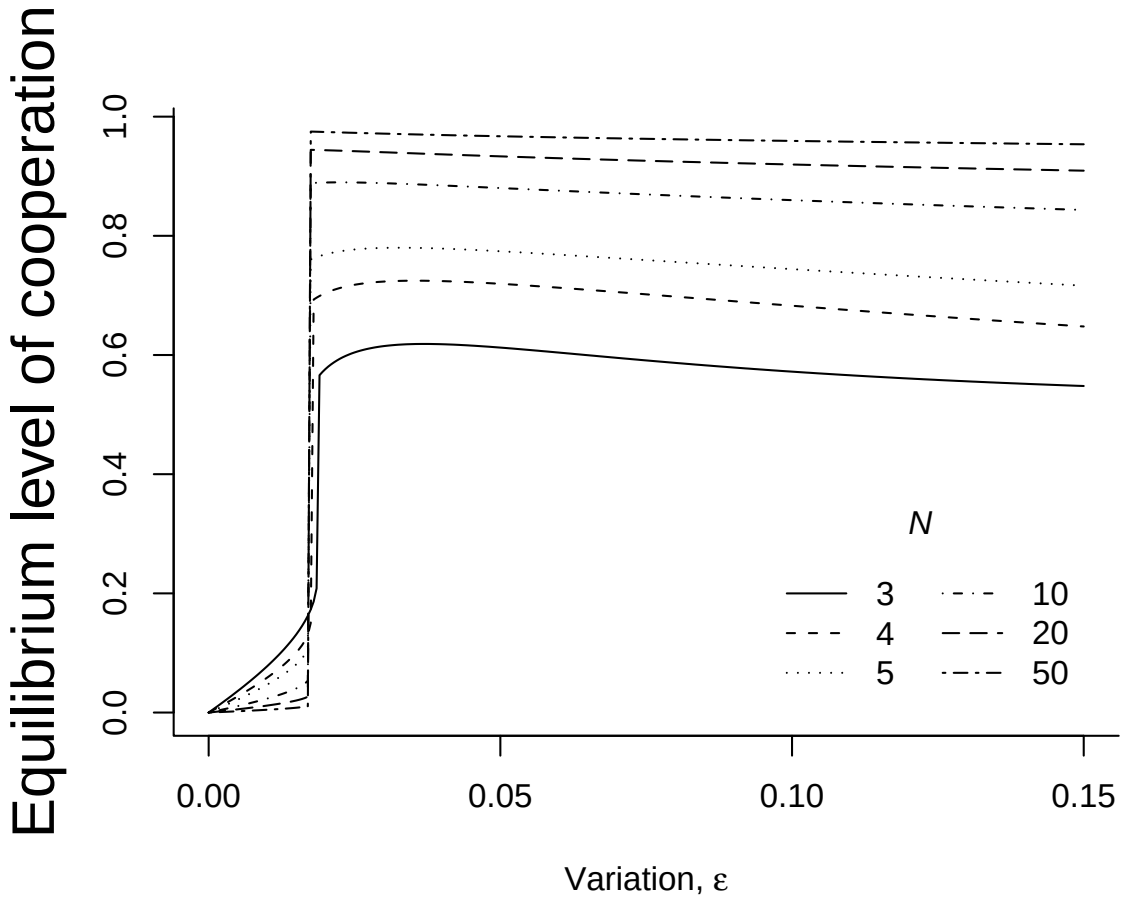
- The game:
  - iterated Prisoner's Dilemma, between two players
  - number of rounds, N, fixed
  - if anybody cheats, the game ends
  - the total pay-off is the sum of pay-offs from the rounds
- The strategy:
  - number of cooperative rounds, n, before cheating
  - variation is maintained by mutation
    - ϵ is the probability that a parent with n will have offspring with either $n-1$ or $n+1$

McNamara et al., 2004, *Nature*

Evolutionary stability



Effects of the maximum number of rounds, N



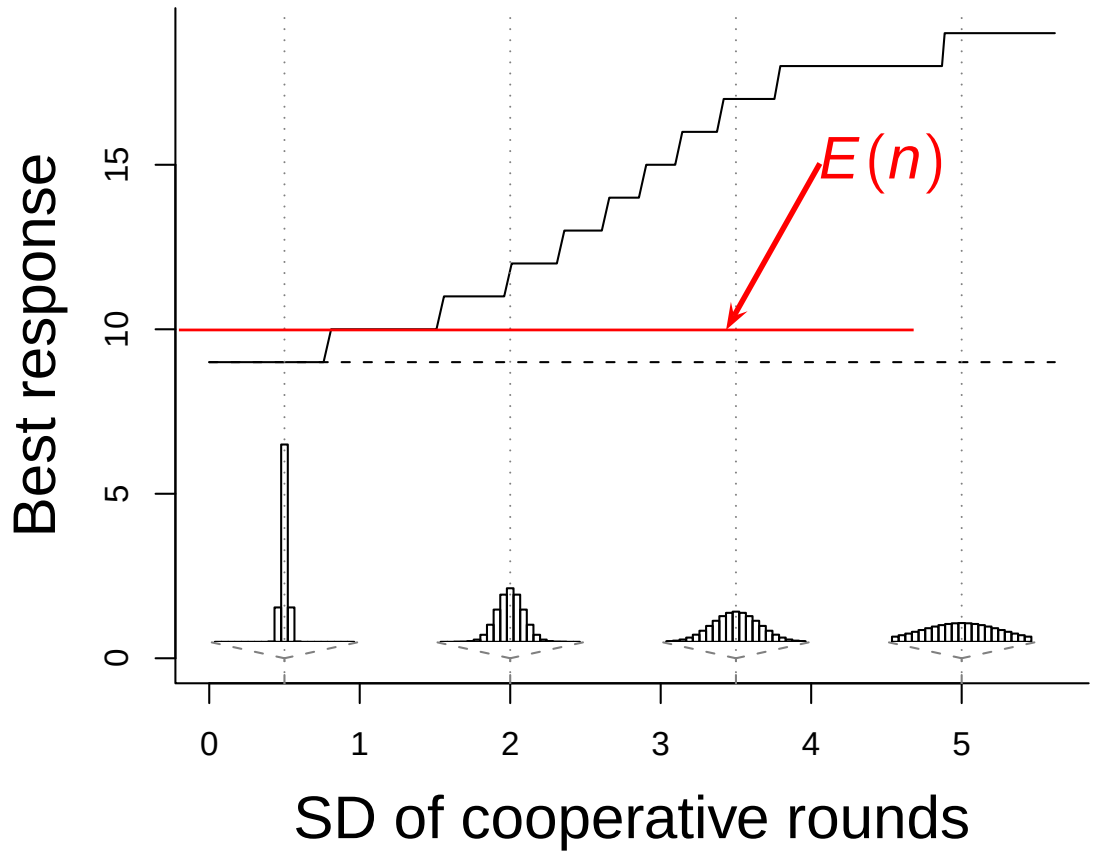
NO variability

- the opponent cooperates for n rounds and defect on the $n+1$th round
- the best is to pre-empt the opponent's defection by cooperating for $n-1$ rounds and defecting on the nth round
- all population members have n (no variation) ☞ a mutant best response, $\hat{n}$, is $\hat{n} = n - 1$
- the ESS is $n^* = 0$ ☞ no cooperation

Variation

- population consists of a mixture of individuals with different n
- let $E(n)$ is the population mean
- variation ☞ some of the individuals cooperate for less than $E(n)$ some for more than $E(n)$
- 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

The best response



Conclusions

- Variation allows to leave non-cooperators.
- Variation makes benefitial to cooperate more.
- Variation promotes cooperation.

Outline

Variation, choosiness and cooperation

The model:

- individuals characterised by 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
  - continuous Prisoner's Dilemma: $B(x')$
  - continuous snowdrift game: $B(x + x')$
- infinite population for many time steps
- a time step is five stages

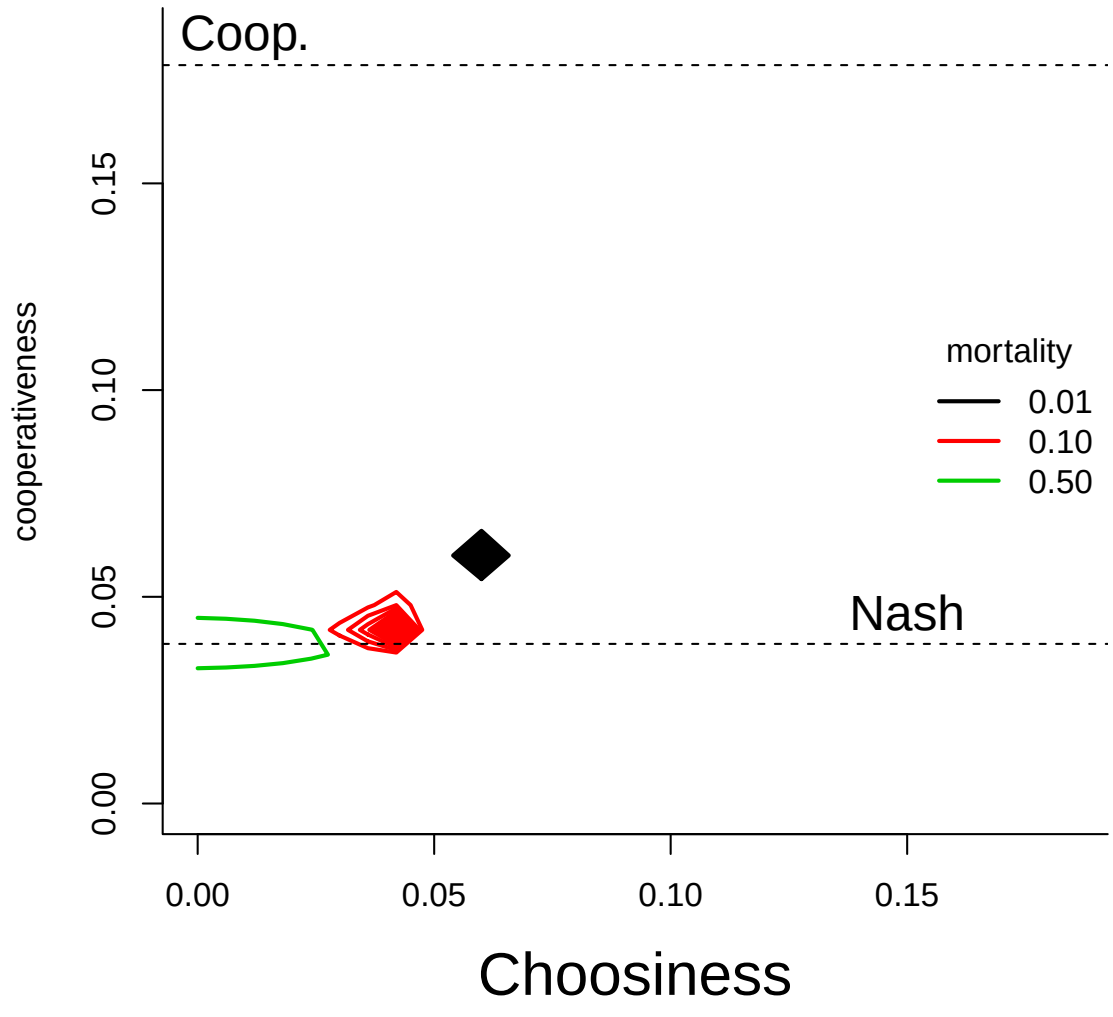
McNamara et al., 2008, *Nature*

Stages

- **Stage 1**: mate search, costly
- **Stage 2**: play the game with partner
- **Stage 3**: reproduction
  - success proportional to gain from the game (Stage 2)
  - mutation may occur
- **Stage 4**:
  if $x' < y$ then “divorce”
  else stay together forever
- **Stage 5**: mortality; death occurs with a given probability

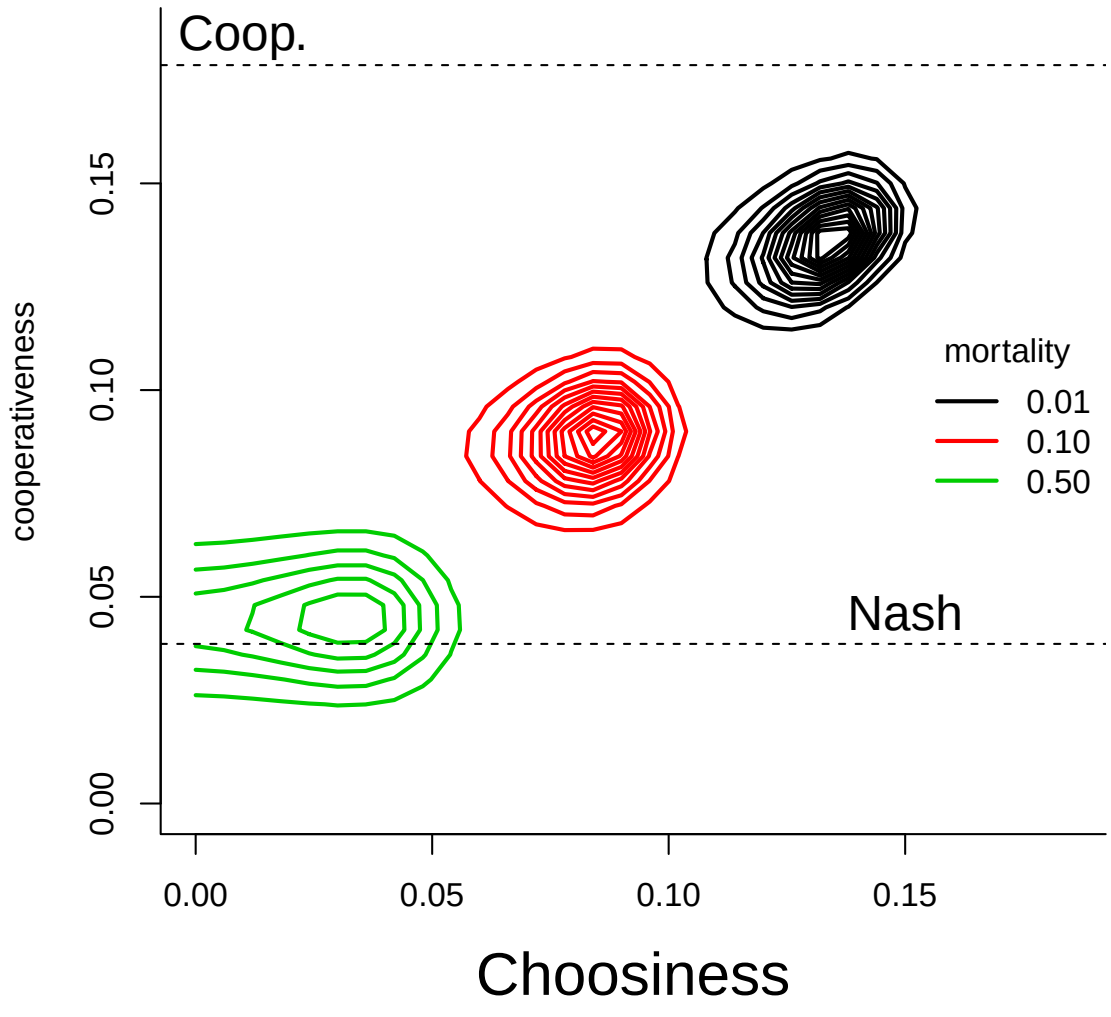
Results: continuous snowdrift game

Mutation rate: 0.001

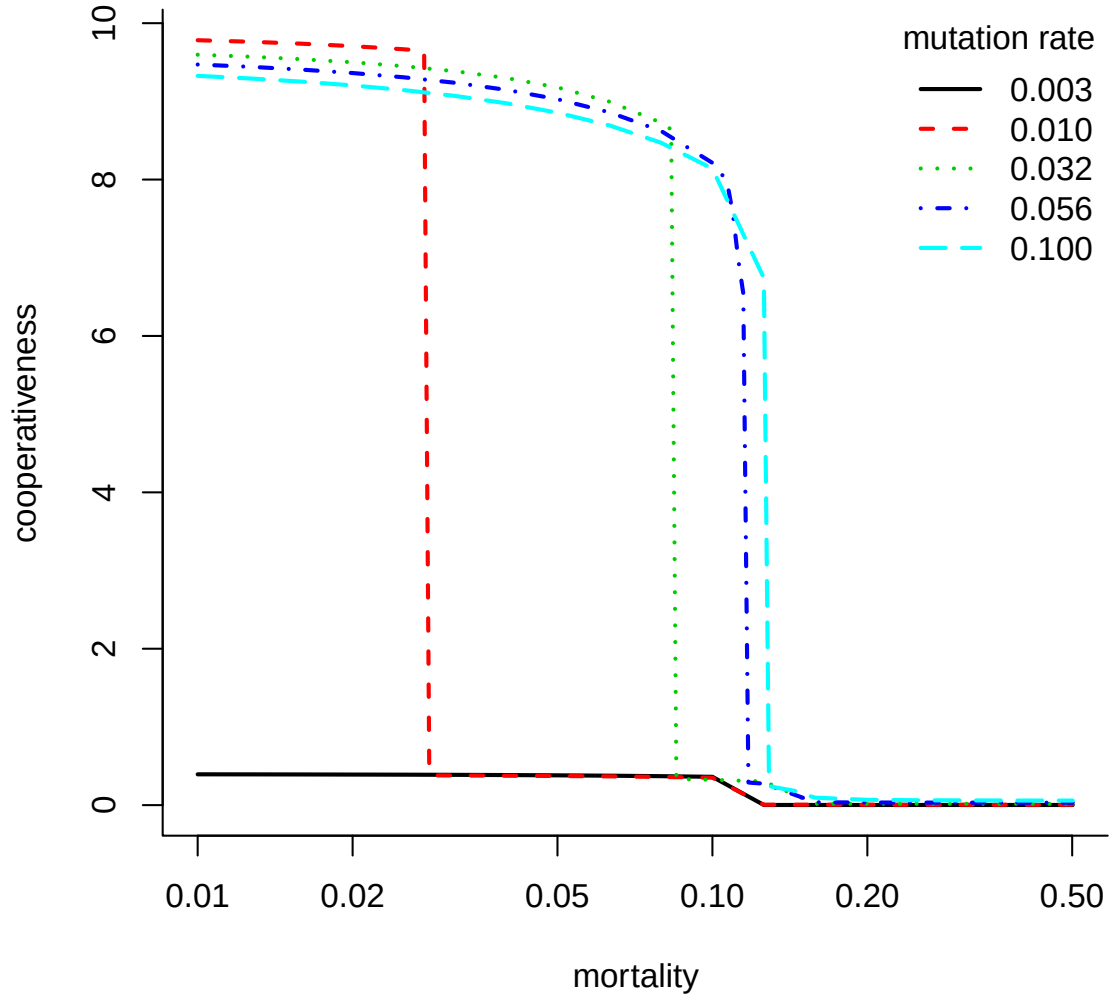


Results: continuous snowdrift game

Mutation rate: 0.05



Results: continuous Prisoner's Dilemma



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

Variable population

- mutation maintains significant variation in cooperativeness
- more cooperative individuals can be found  worth divorcing
- cooperative individuals enjoy an advantage by not being divorced
  - NOTE: high mortality destroy this advantage
- run-away process starts: both cooperativeness and choosiness increase
- stable state: choosy and cooperative population

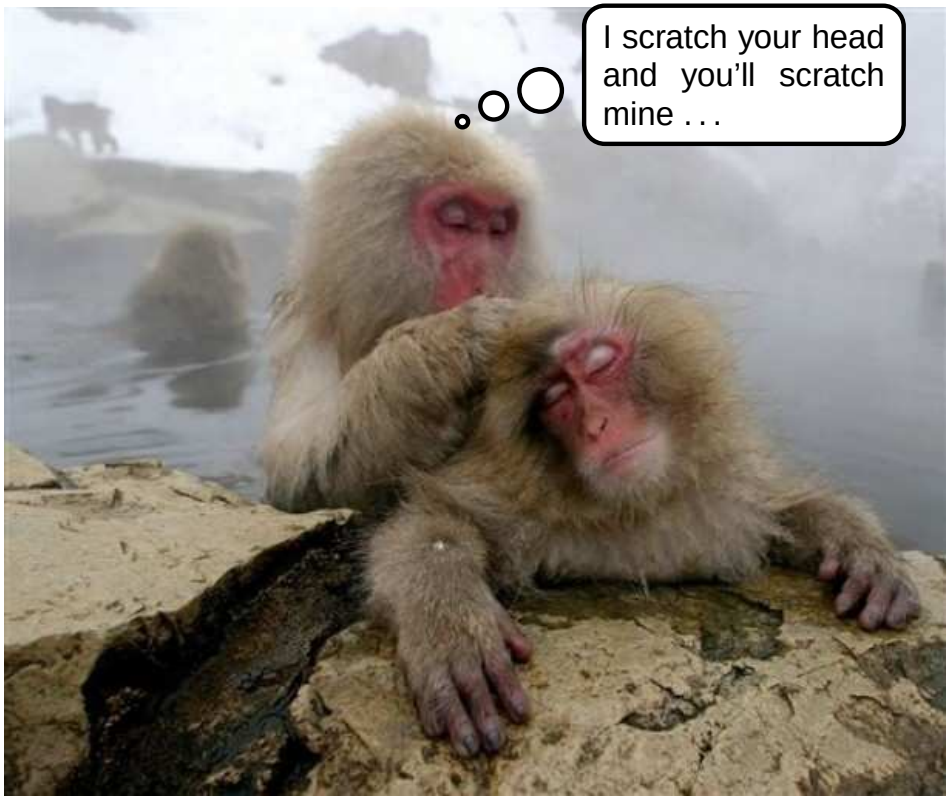
Conclusions

- Variation makes worth being choosy.
- Assortment of cooperators.
- Cooperation evolves.

Outline

Reciprocity

Direct reciprocity



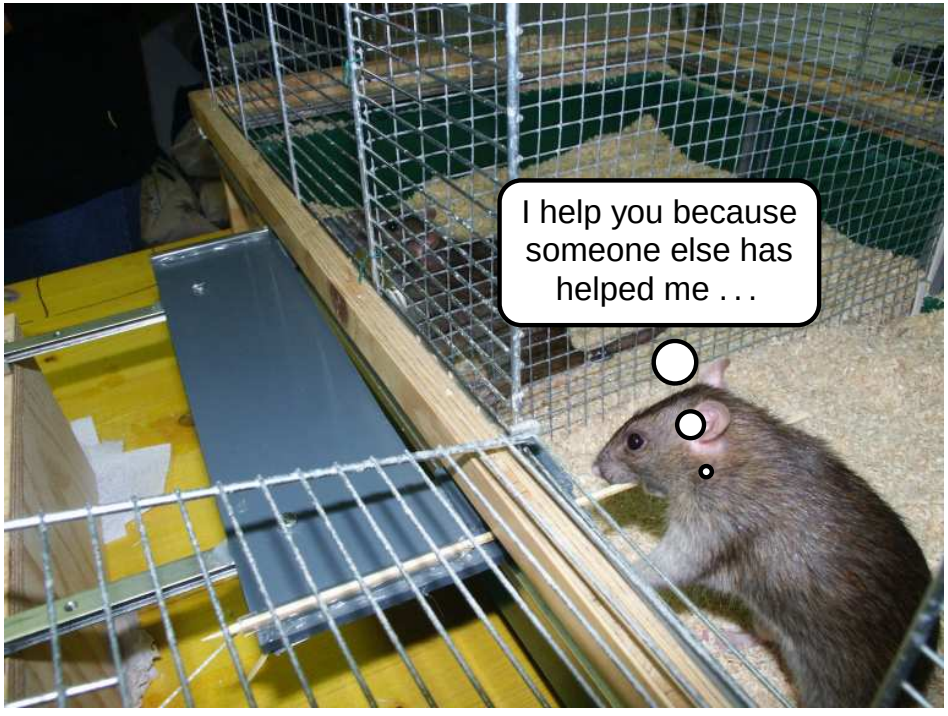
Indirect reciprocity

- back and forth helping between non-kins
- based on reputation

advanced cognitive capabilities ☞ minor importance in animals

New kid on the block

Generalised reciprocity



Rutte & Taborsky, 2007, PLoS Biol.

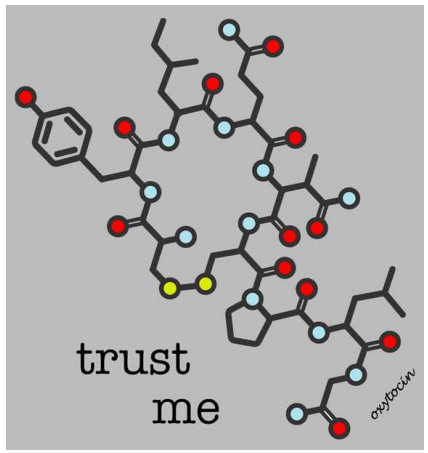
- among anonymous partners
  ☞ simple mechanism
- the role of internal state???

A neglected constraint: internal state

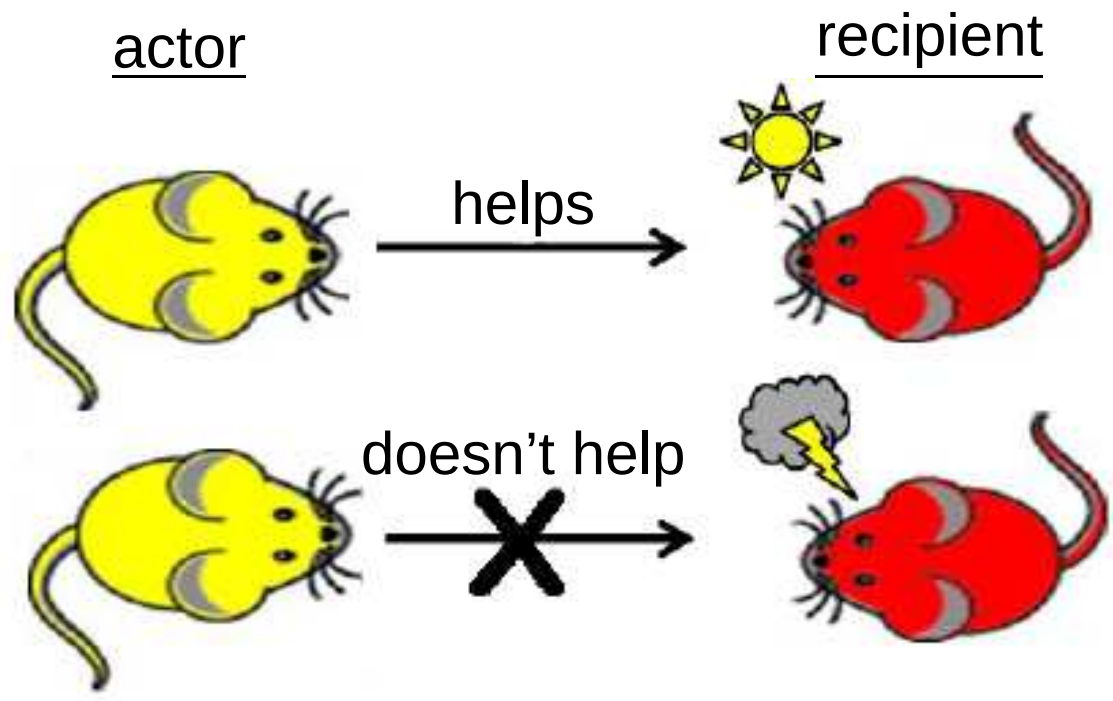
Internal state can influence social behaviour.

- mental mood: gratitude, hate, anger…
- neurotransmitters/hormones
  - oxitocin
  - serotonin

Models of cooperation usually neglect these.



Simple model of generalised resiprocity



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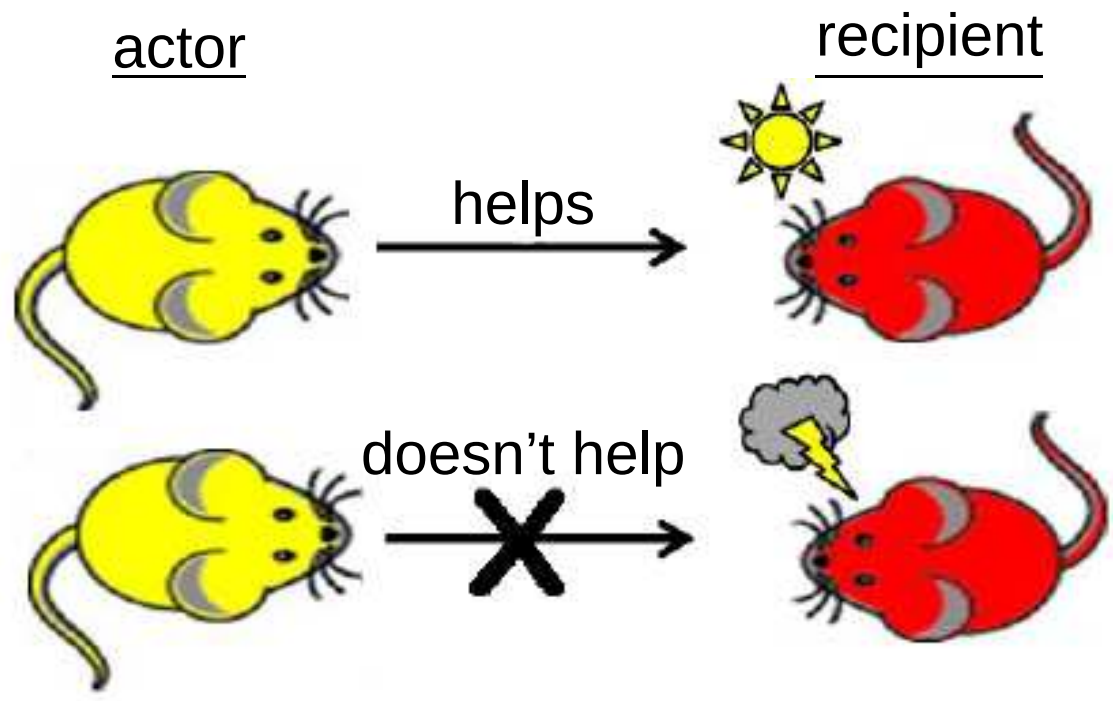
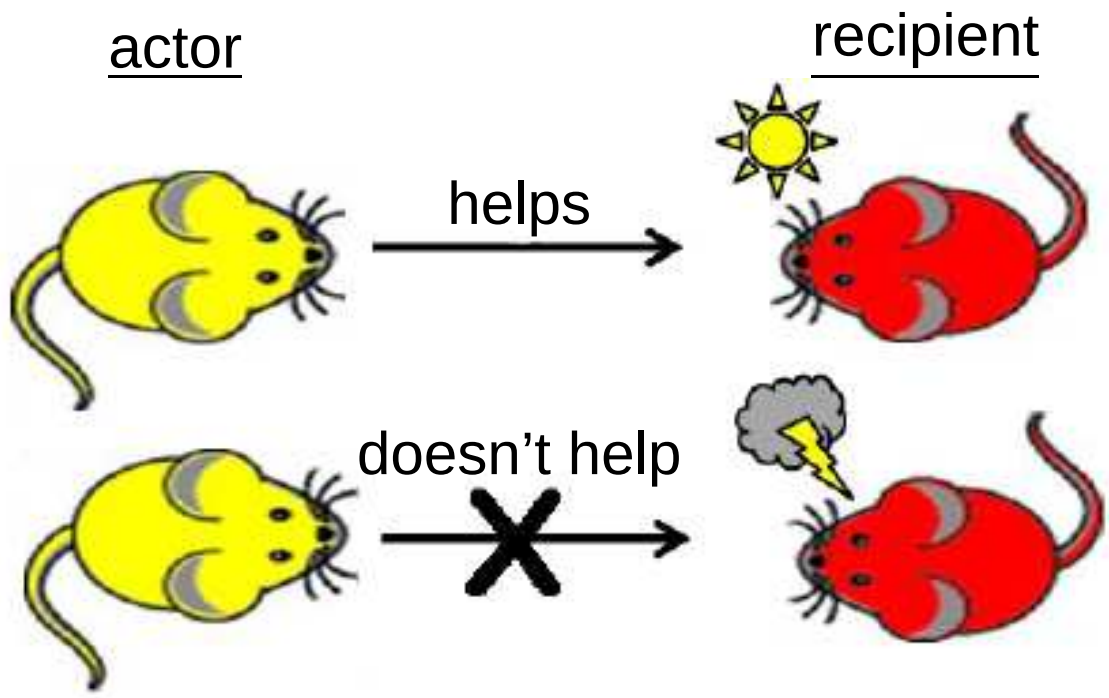


No state, no cooperation!

Simple model of generalised resiprocity

I) $K_{act} \geq 0.5$

II) $K_{act} < 0.5$



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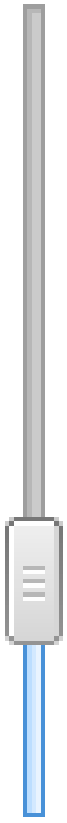

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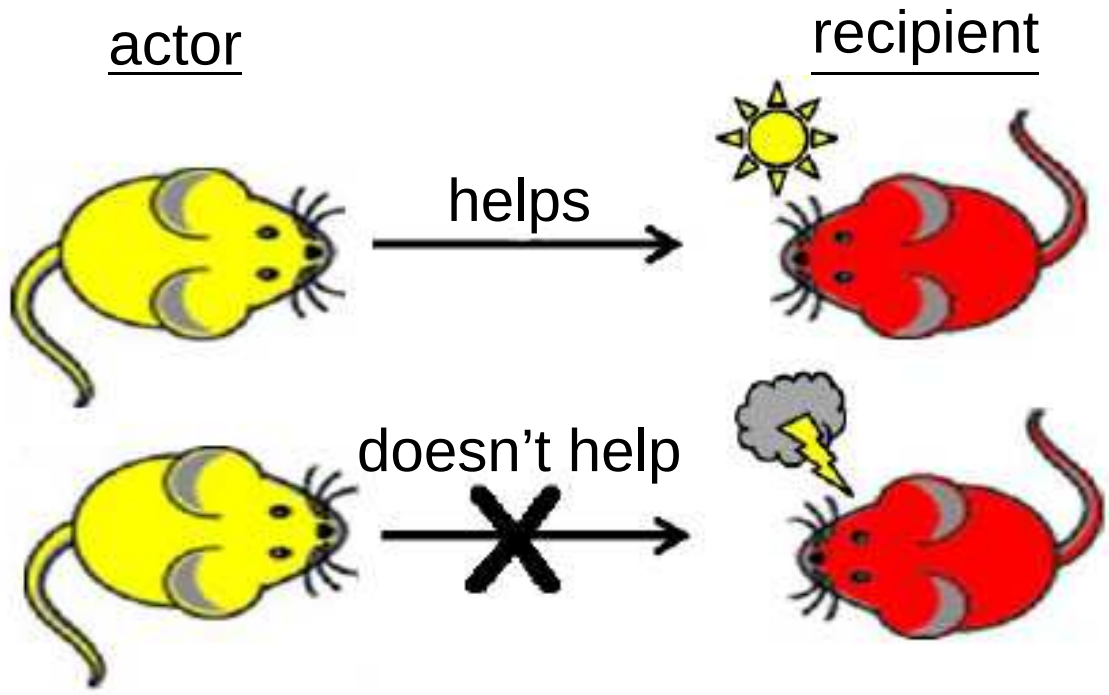
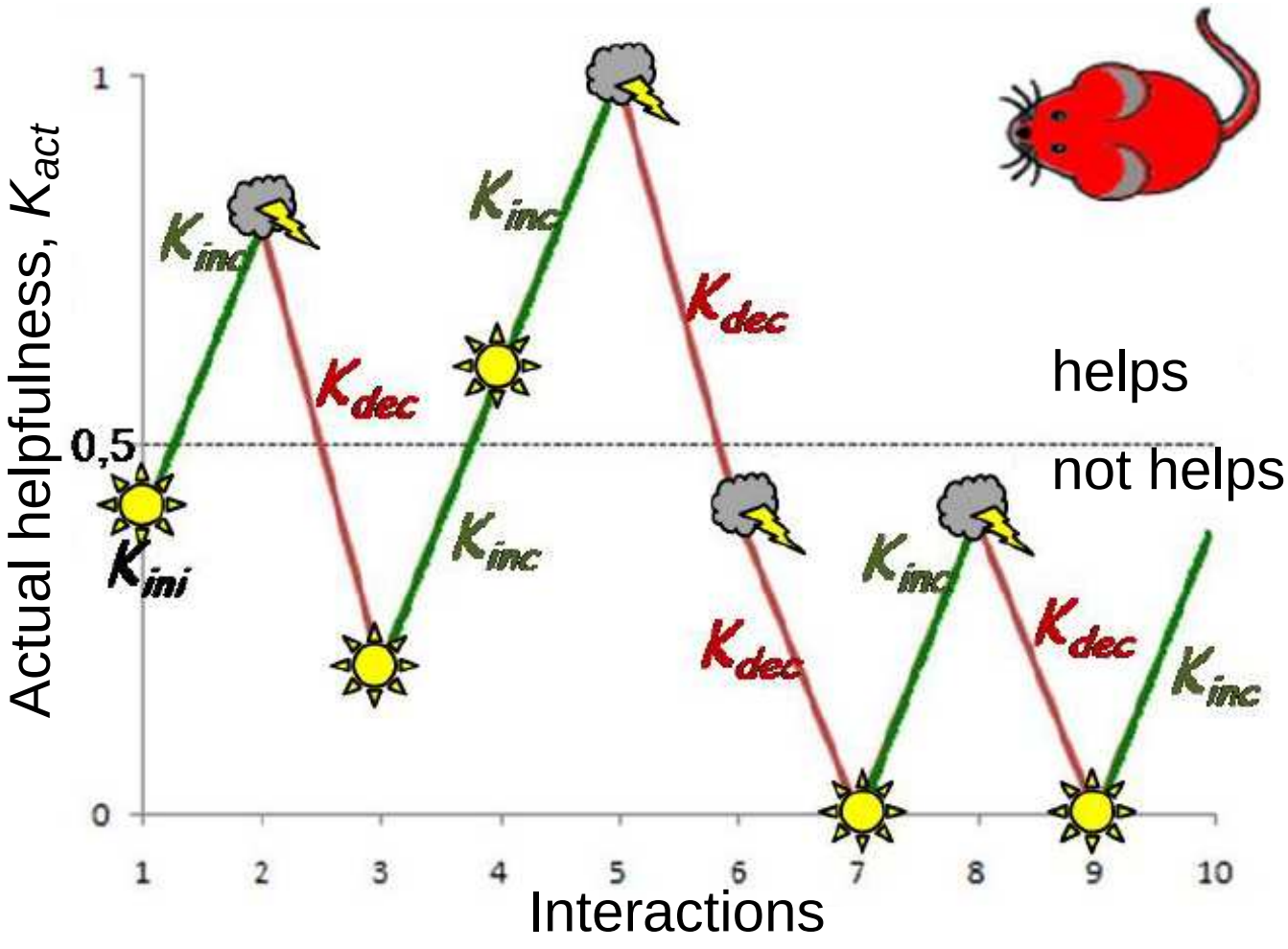


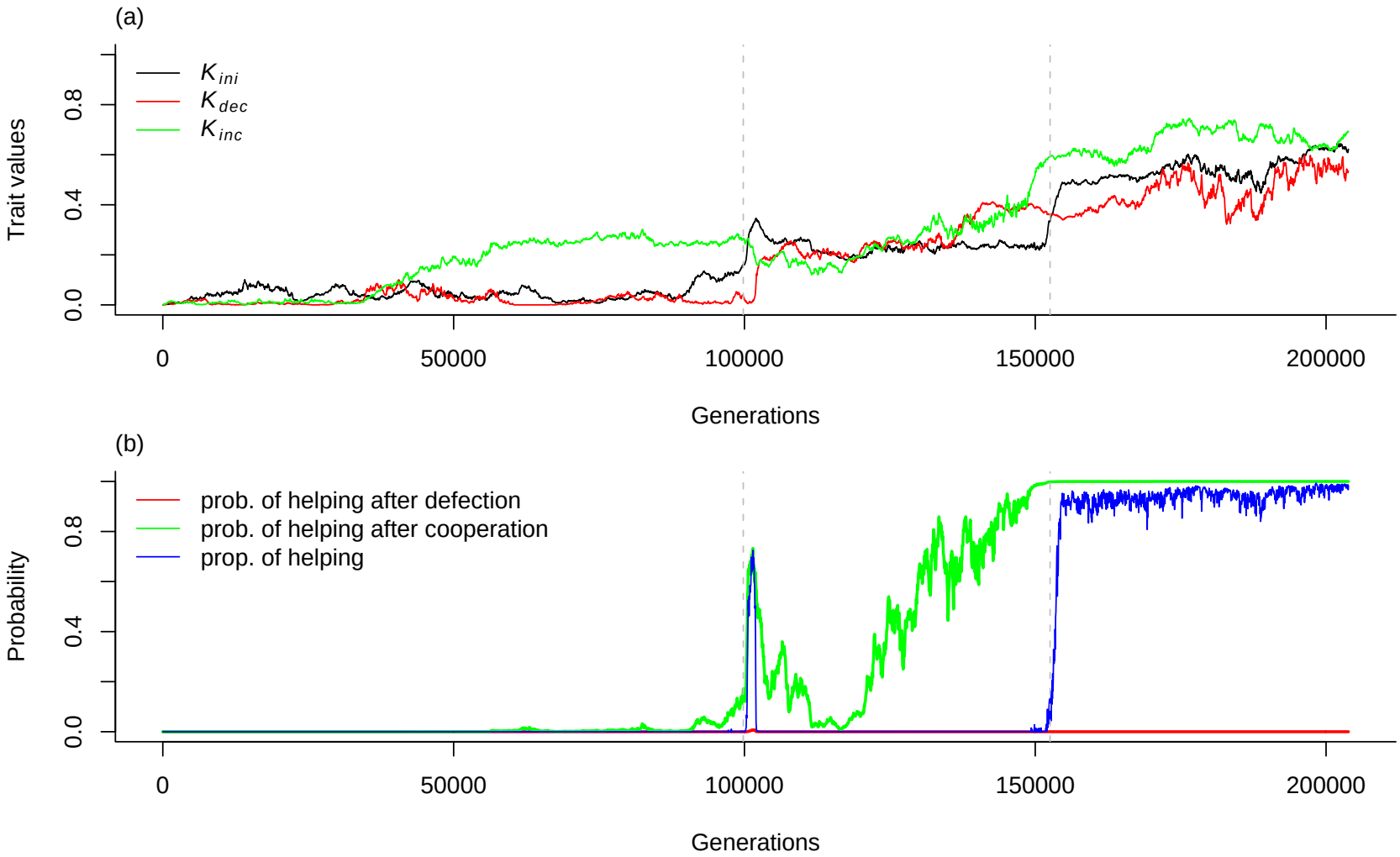
State-dependent model of generalised reciprocity



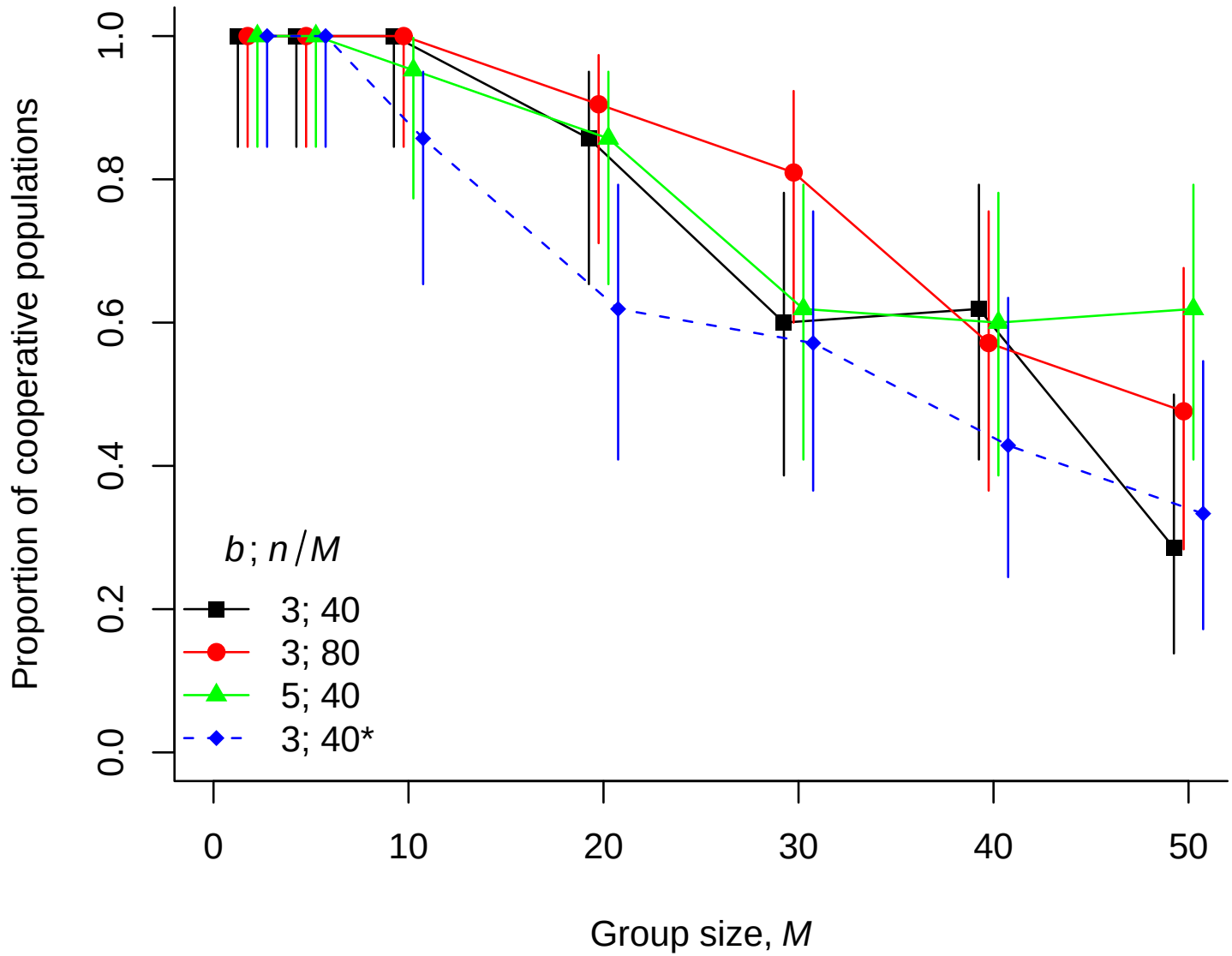
Traits:

- K_{ini}: initial helpfulness;
- K_{dec}: decrement of helpfulness (it has not been helped);
- K_{inc}: increment of helpfulness (it has been helped)

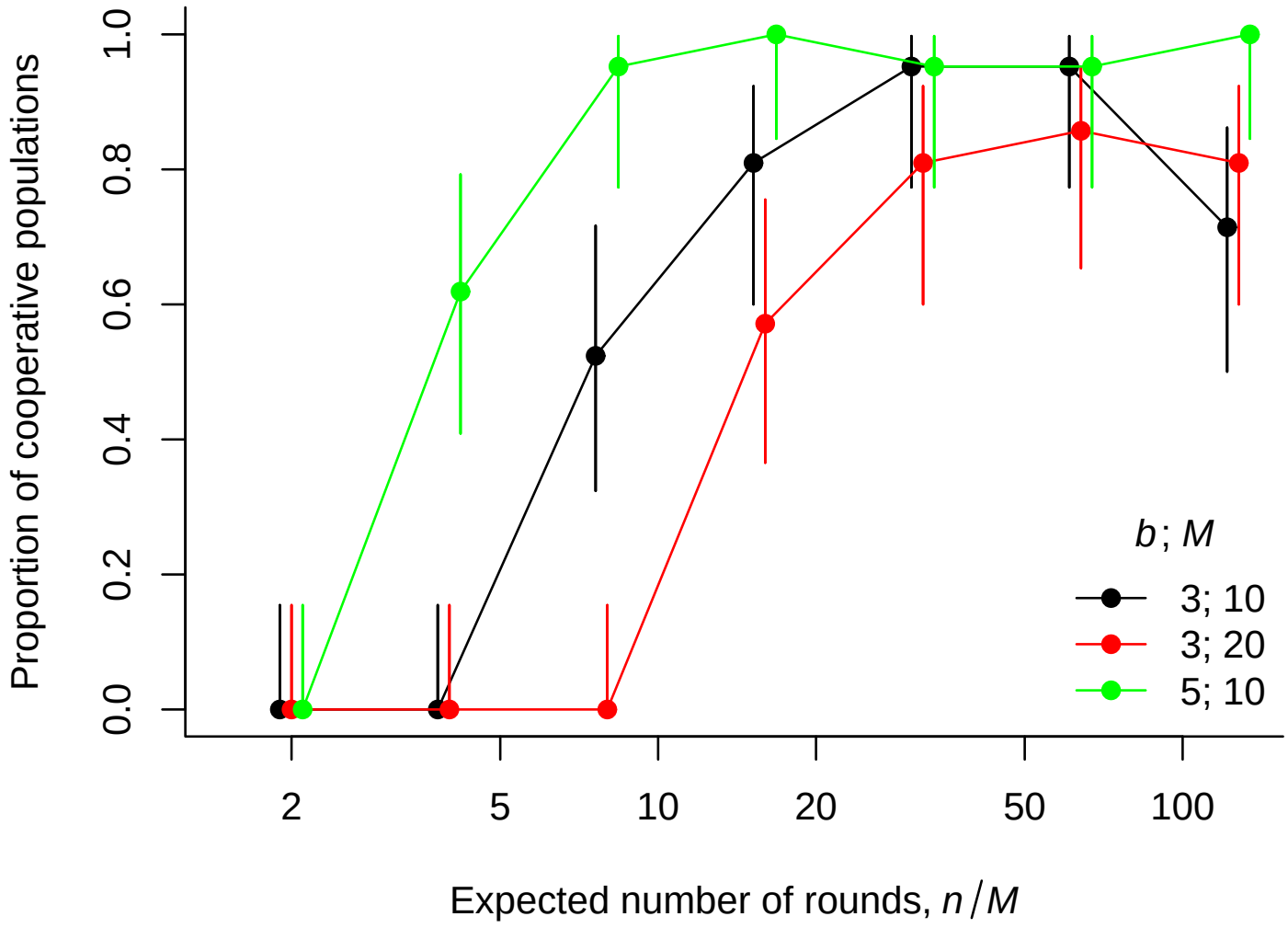
The rise of cooperation



Effect of group size

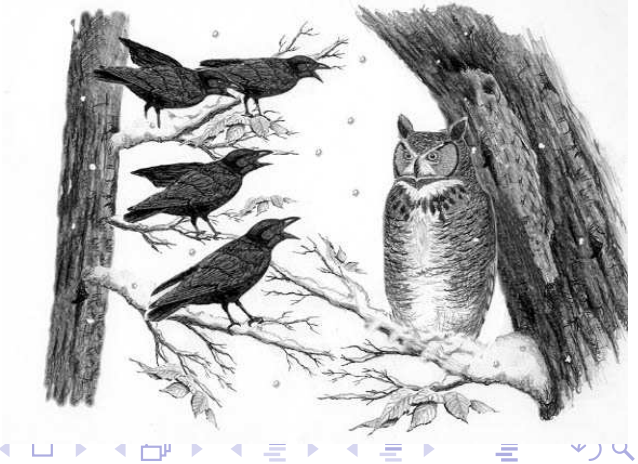


Effect of number of interactions



Conclusions

- cooperation under a wide range of conditions
  - anonymous players
  - large groups
  - moderate number of interactions
- very simple framework
  - one internal state variable
  - update rules through gradual evolutionary steps
  - no advanced cognitive abilities



Outline

Parental care

Species	biparental care[a]	male-only care[a]	female-only care[a]	biparental desertion[a]	Reference
Birds					
Little Egret	40.0	44.0	4.0	12.0	Fujioka 1989
Snail Kite	22.2	50.0	27.8	0.0	Beissinger & Snyder 1987
Kentish Plover	9.1	81.8	9.1	0.0	Székely & Lessels 1993
Penduline Tit	0.0	17.9	47.8	34.3	Persson & Ohrström 1989
Amphibians					
E. johnstonei	0.0	64.3	35.7	0.0	Bourne 1998
Fish					
St Peter's fish	74.7	8.1	17.2	0.0	Balshine-Earn 1995
I. nebulosus	56.2	39.3	4.5	0.0	Blumer 1986

a: percentage of broods

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?

Parental conflict about care

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What happens if care involves distinct types of activities?

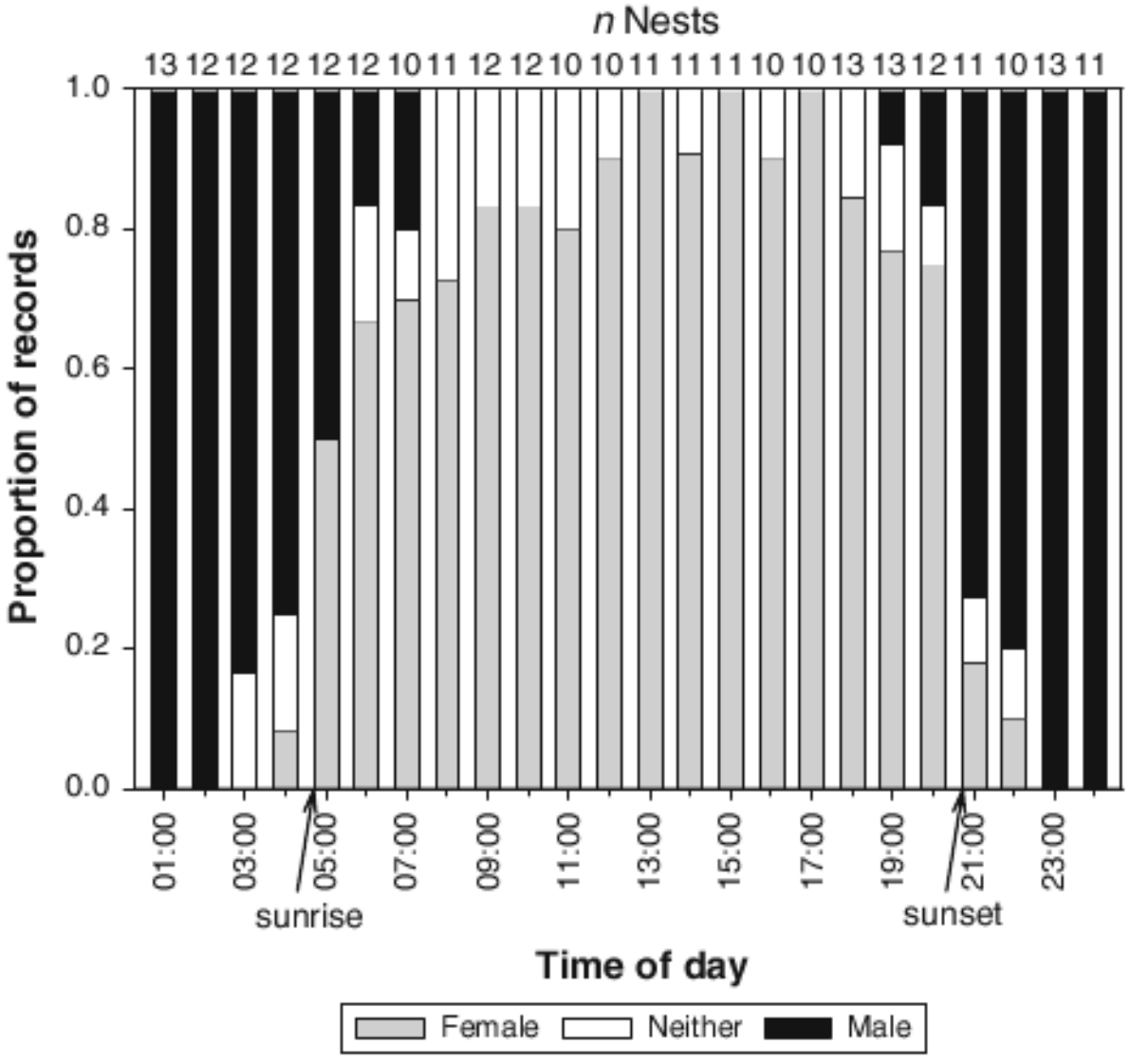
- distinct types of activities ☞ task specialisation possible

Task specialisation

- both parents care but each performs different task
- each task is necessary to raise the young
- examples:

build the nest	$\Leftrightarrow$	incubate
incubate	$\Leftrightarrow$	feed the incubating parent
incubate during daylight	$\Leftrightarrow$	incubate during night
feed the young	$\Leftrightarrow$	guard the nest
hunt insects	$\Leftrightarrow$	search for seeds

Task specialisation



Two-banded plover, St Clair et al. 2010, J. Ornithol.

Question

Does task specialisation promote cooperation between parents?

Evolutionary simulation

Behaviour

Two tasks:

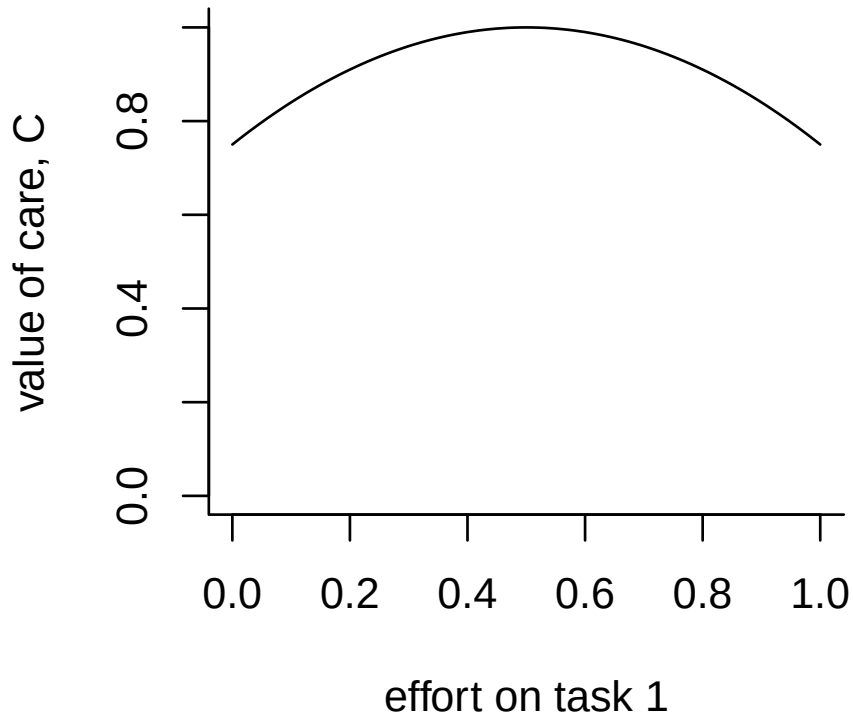
- T1 (e.g. feeding the young)
- T2 (e.g. guarding the nest)

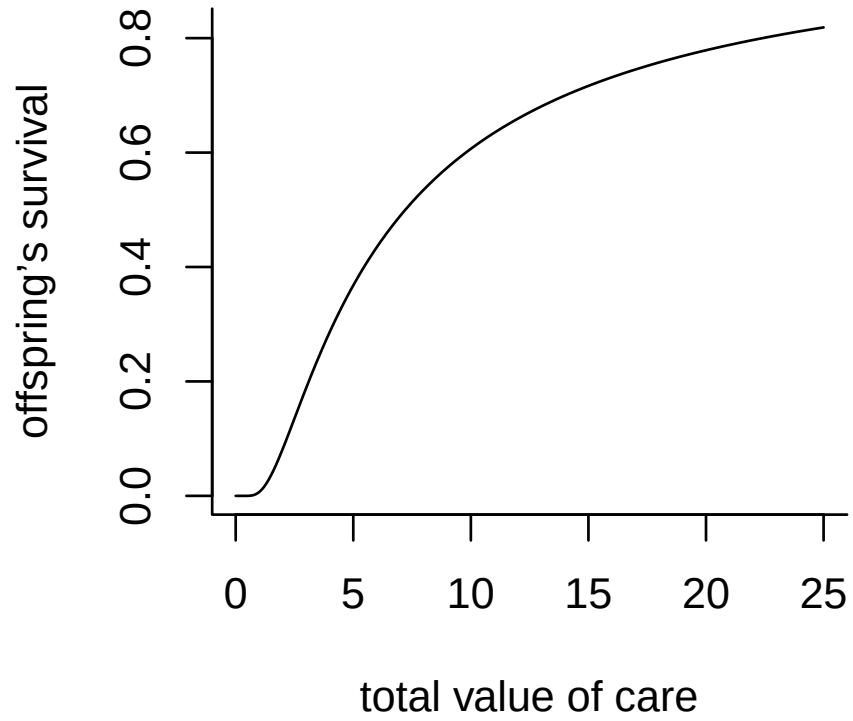
Two decisions:

1. division of parental effort between tasks
   - E_1^m: male effort on task 1
   - E_2^m: male effort on task 2
   - E_1^f: female effort on task 1
   - E_2^f: female effort on task 2

   $E_1^m + E_2^m = 1$ and $E_1^f + E_2^f = 1$
2. length of care
   - L^m: male's care
   - L^f: female's care

Both tasks needed by the young



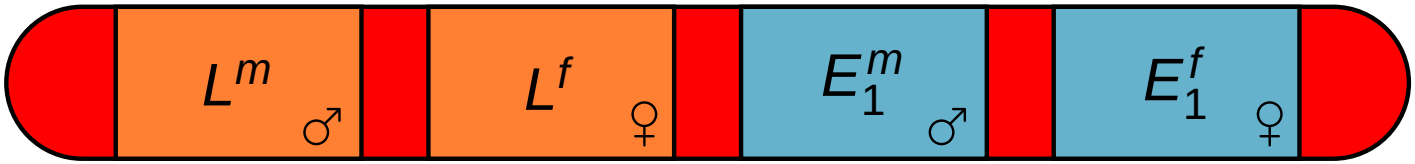


value of care: $C^m = B_1 E_1^m + B_2 E_2^m + B_3 E_1^m E_2^m$

total value of care: $T_C = L^m C^m + L^f C^f$

Population and genetics

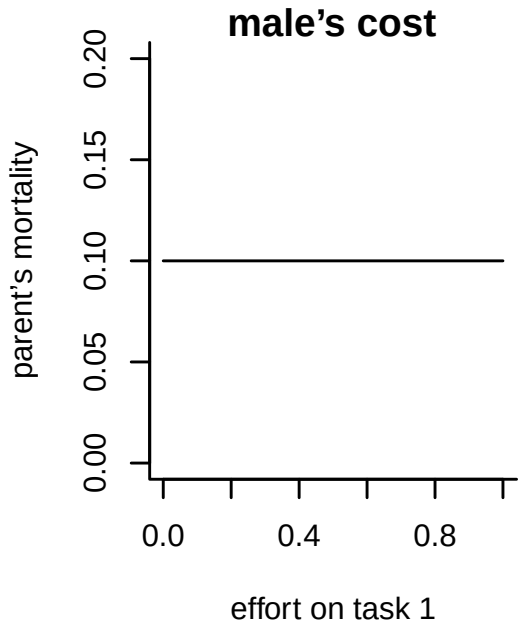
- diploid individuals
- four loci per artificial chromosome

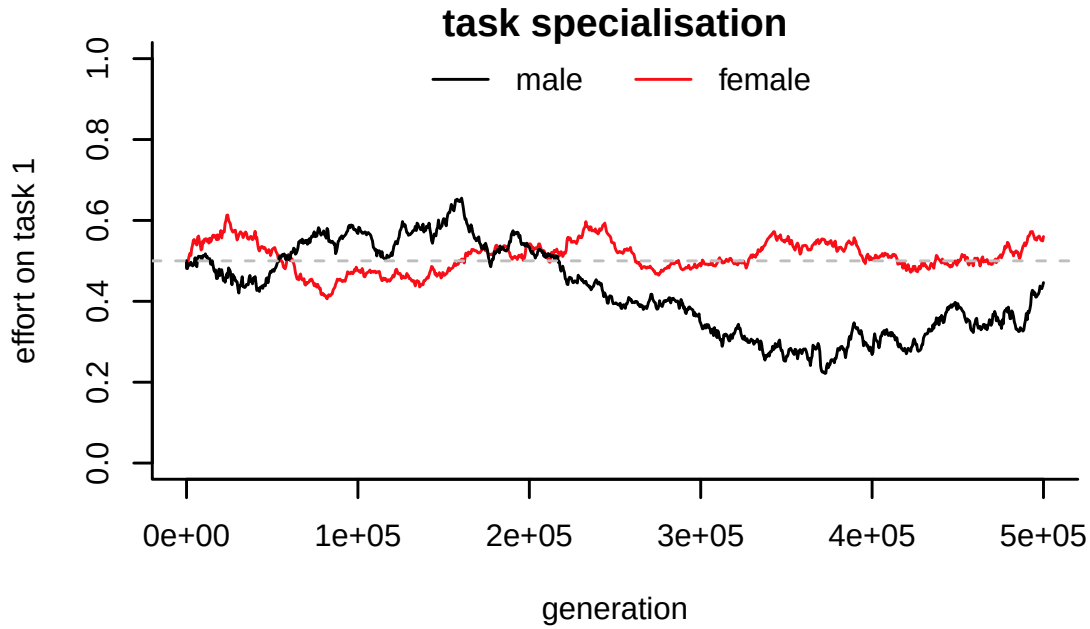


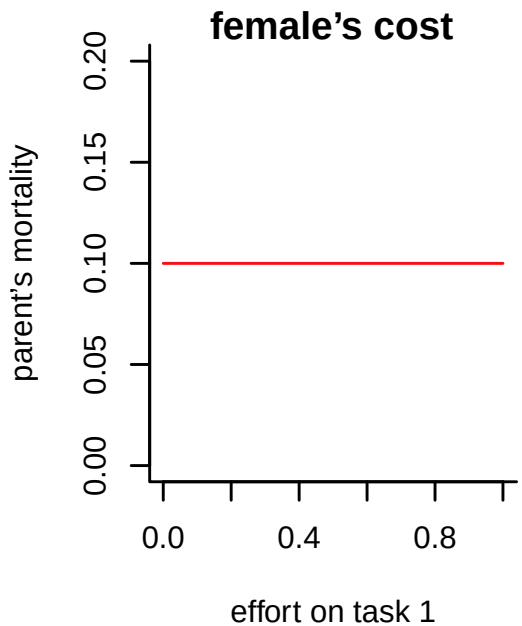
  - ♂ loci are expressed only in males
  - ♀ loci are expressed only in females
- recombination, mutation
- sex ratio at birth is 1:1
- self-consistent, full population model with Fisherian condition

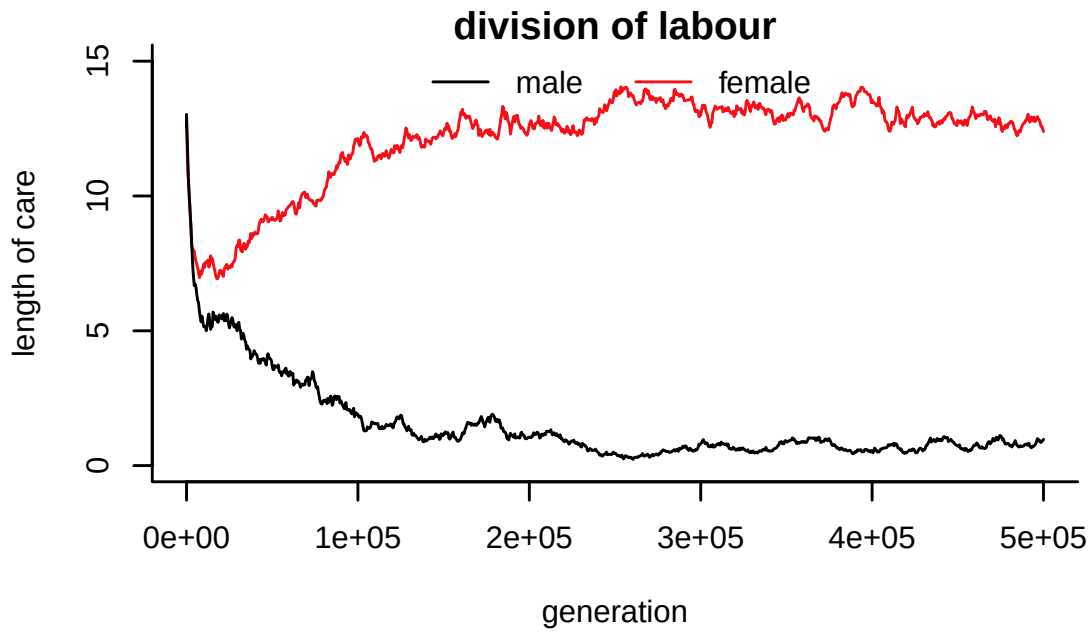
Kokko & Jennions, 2008, J Evol Biol

Two sexes similar: no need to specialise

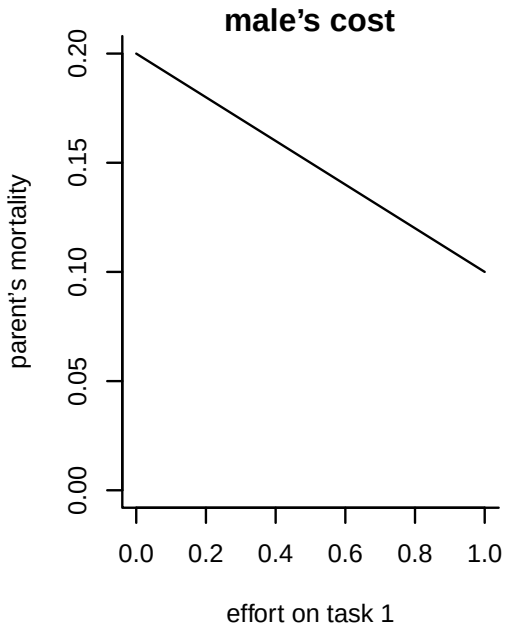


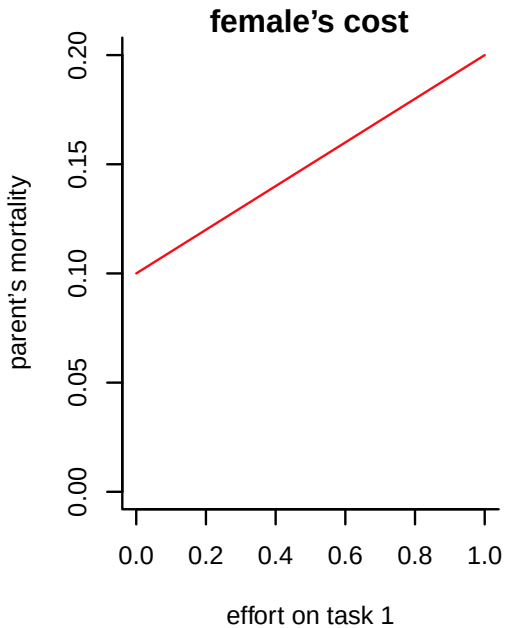






The sexes differ





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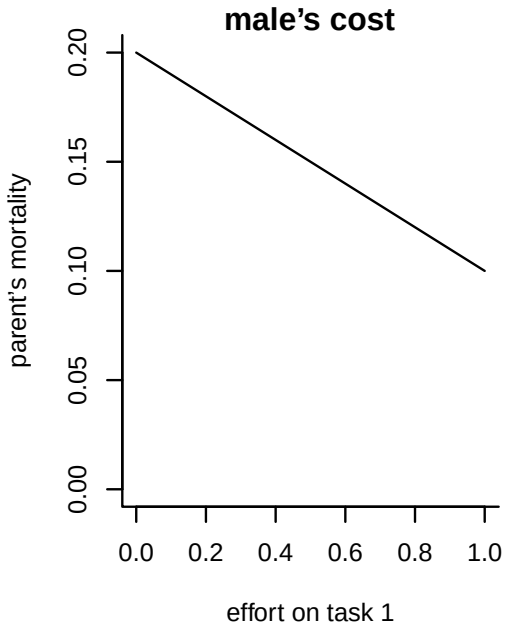
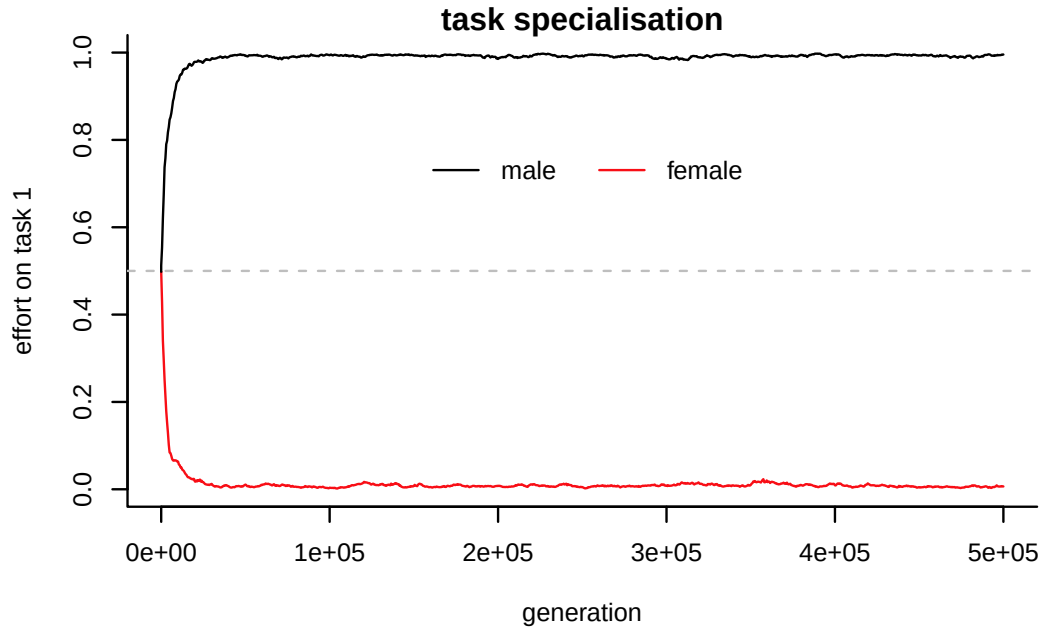
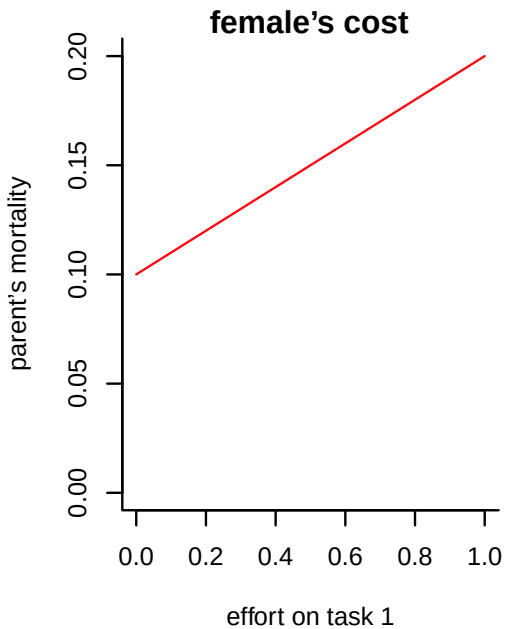
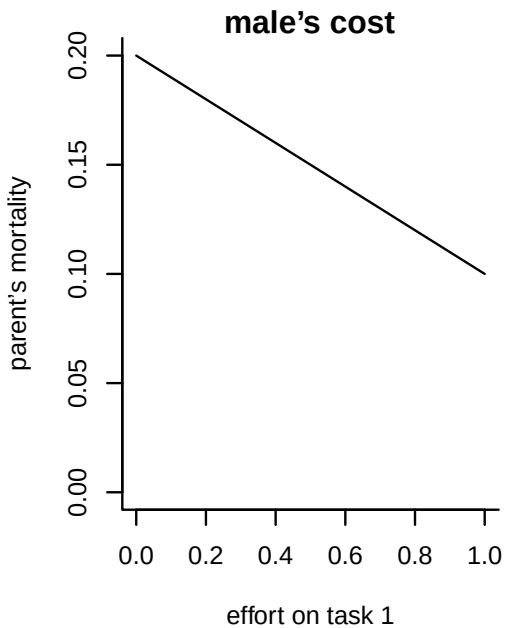
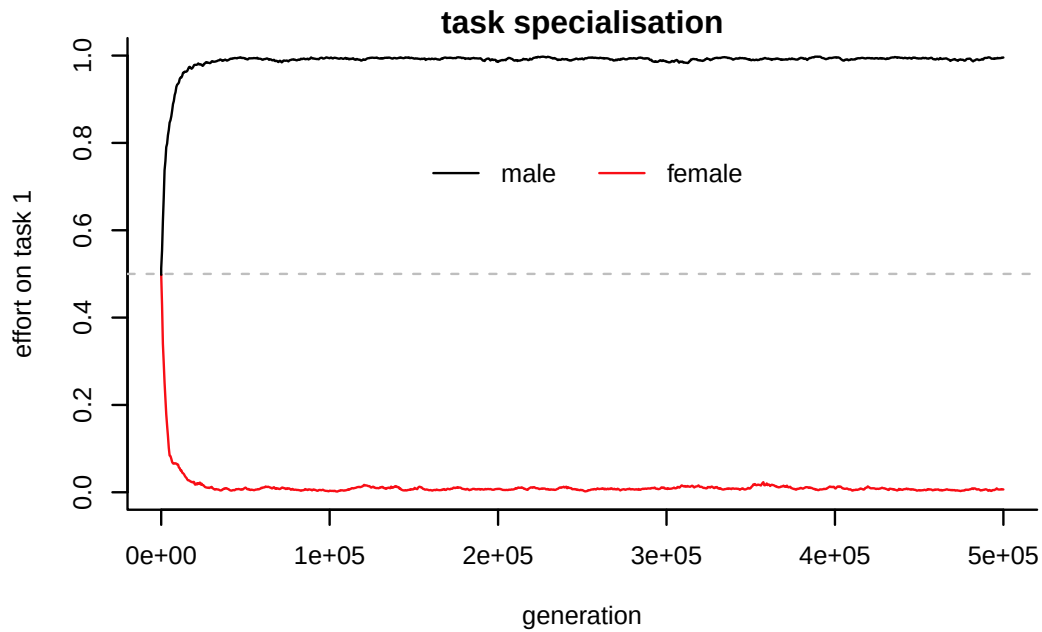


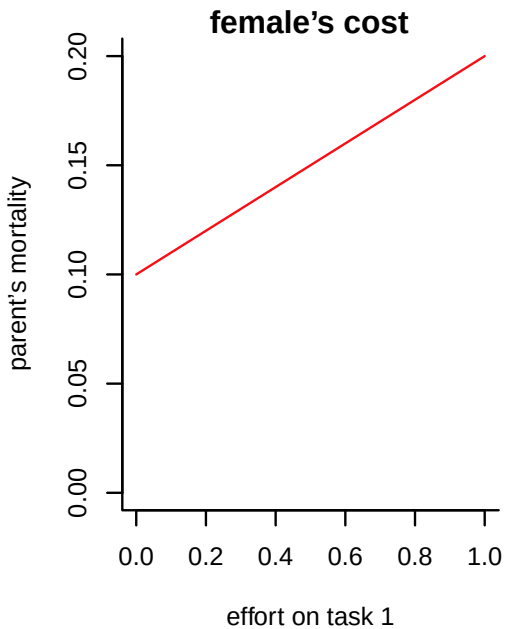


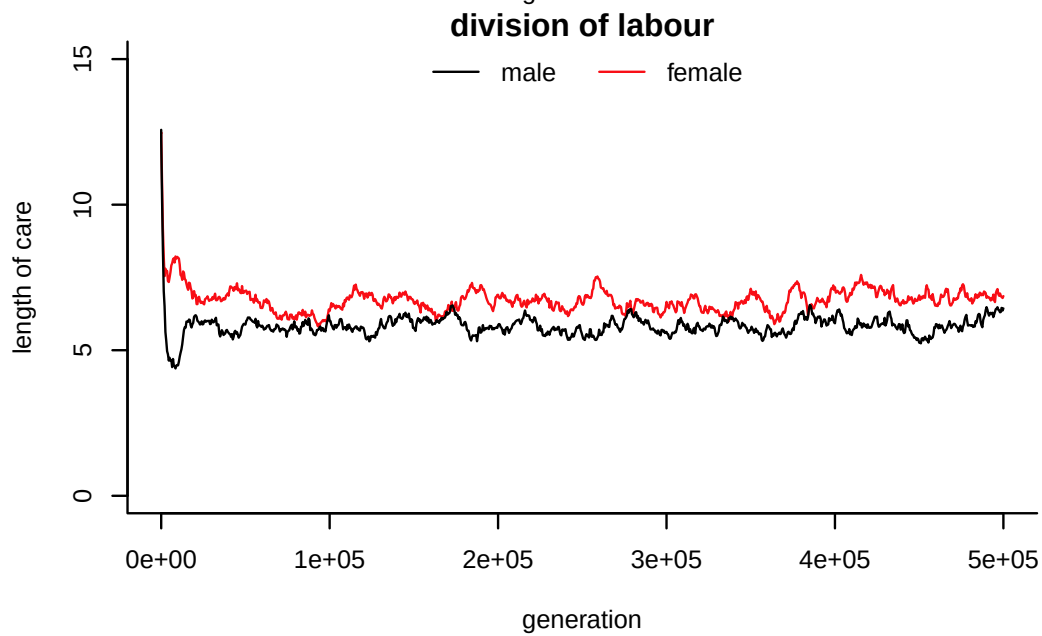


The sexes differ

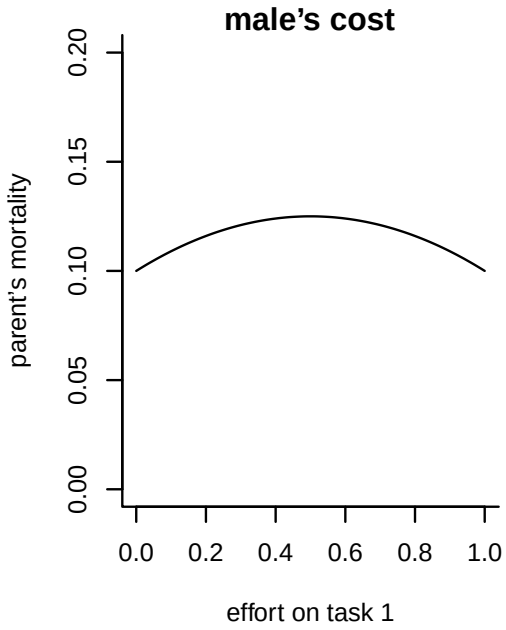


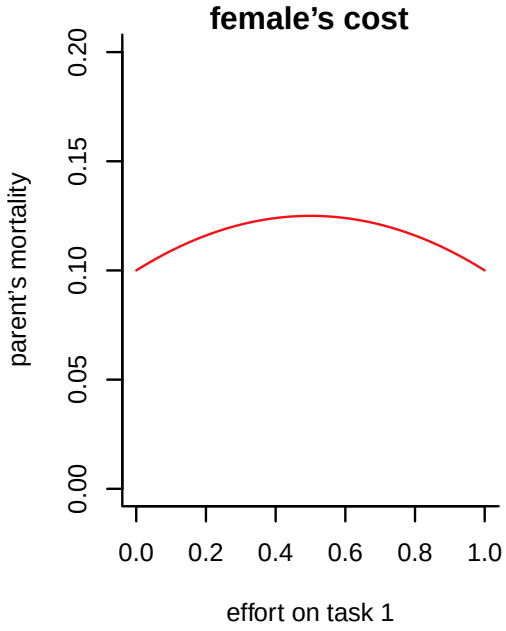




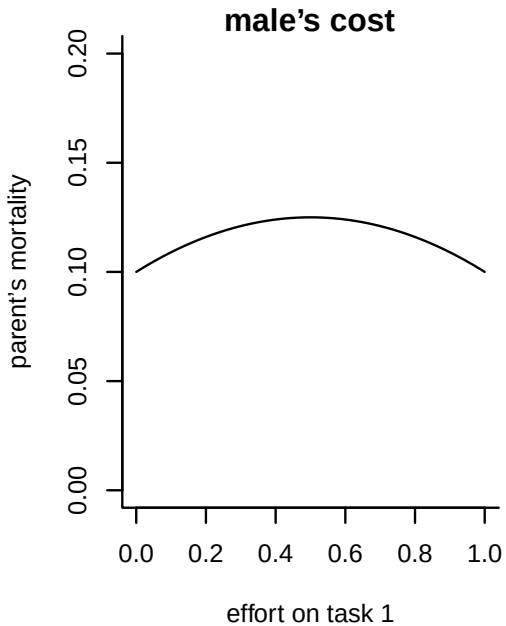


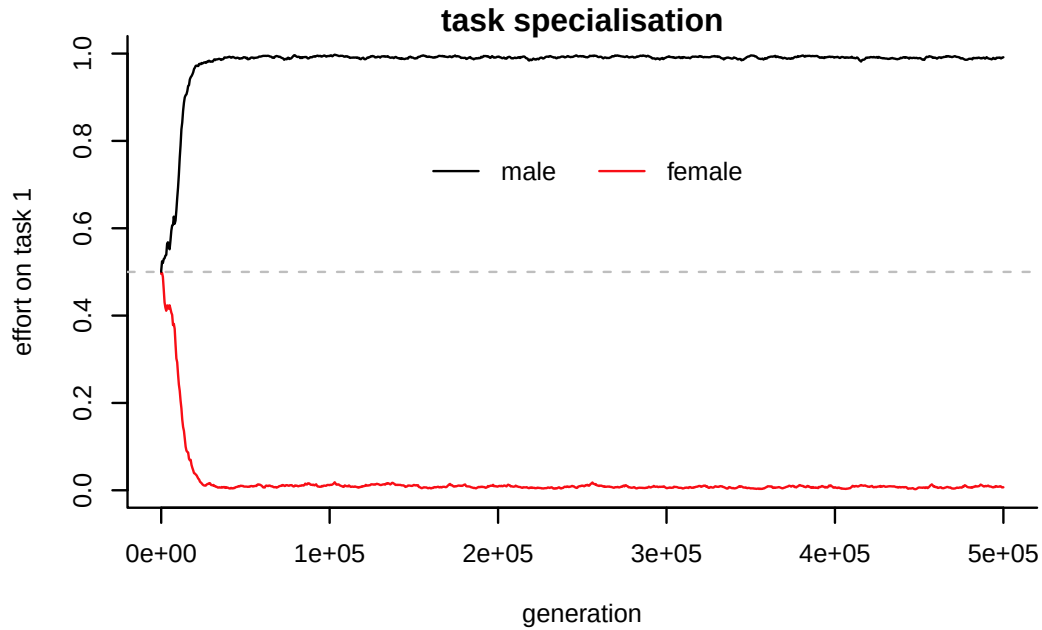
The sexes similar: worth specialising

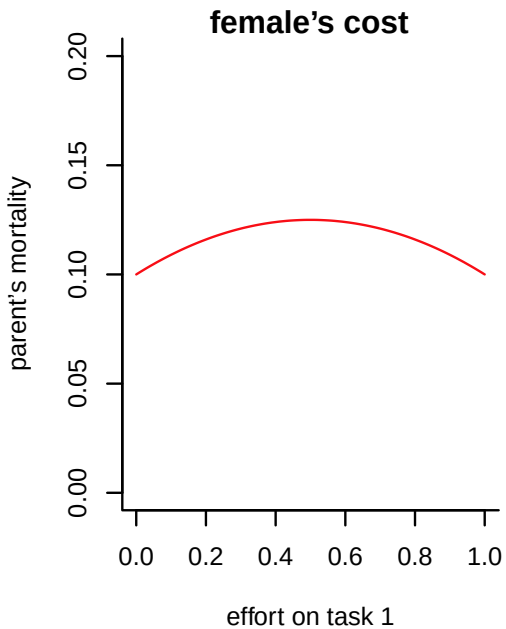




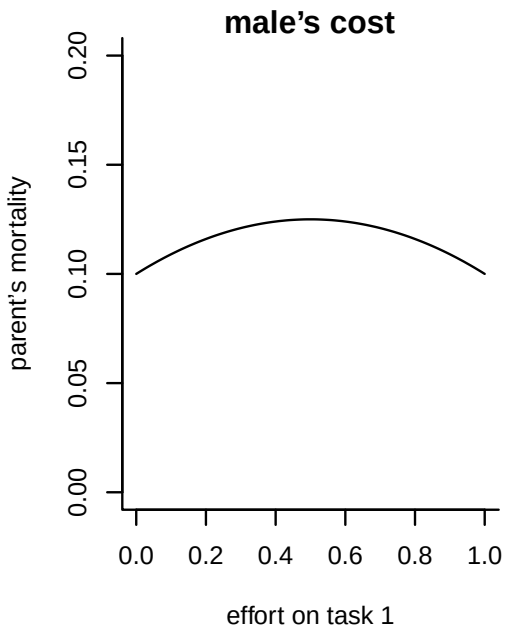
The sexes similar: worth specialising

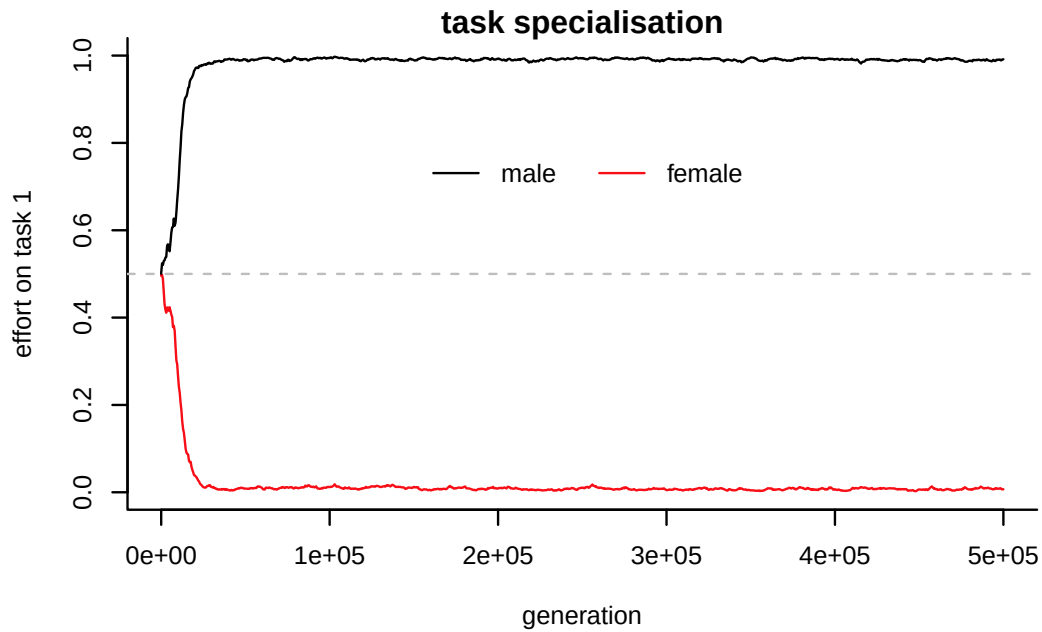


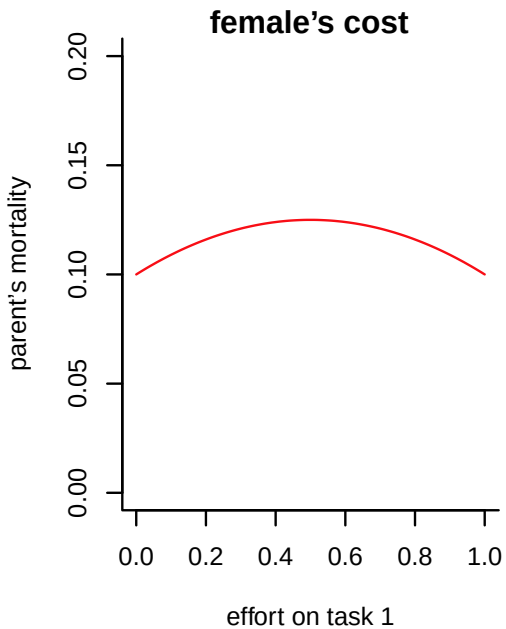


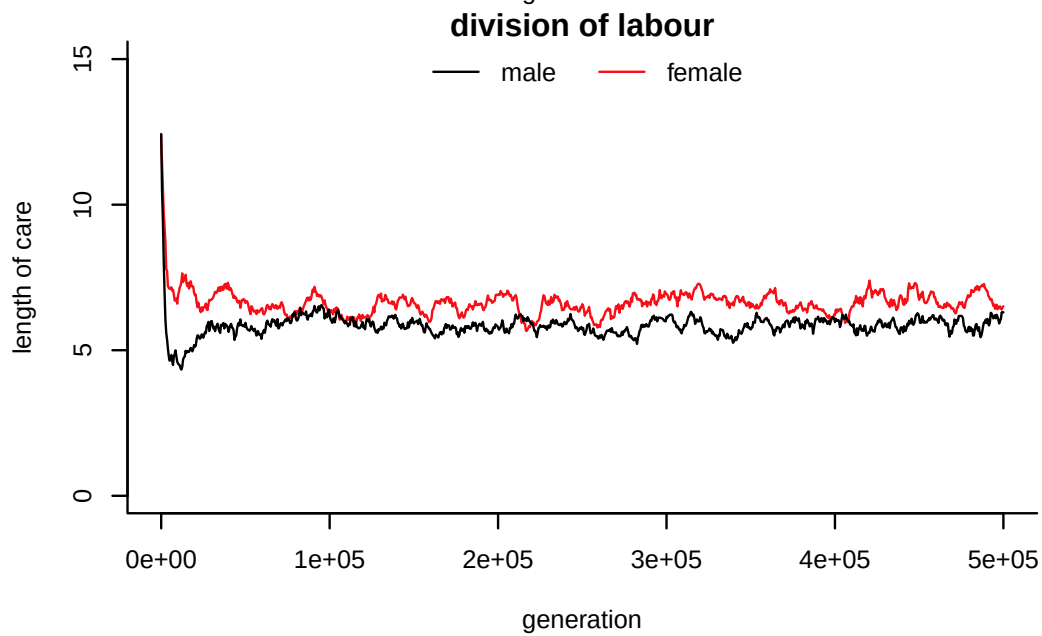


The sexes similar: worth specialising









Conclusions

- differential costs, i.e. skill differences for males and females, promotes cooperation
- role specialisation evolves if
  - offspring need *both* types of care
  - parents pay much for providing both types of care *simultaneously*
- conditions favouring role specialisation also favours cooperation
  - evolutionary correlation expected between them

Outline

General conclusions

- Variation changes a lot of things.
- Variation allows the work of several new mechamisms.
  - getting off
  - choosiness
  - generalised reciprocity
  - specialisation
- Variation promotes cooperation.
- Variation cannot be neglected.

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Variation is important!

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