Conflict and cooperation in animal societies

the role of internal state

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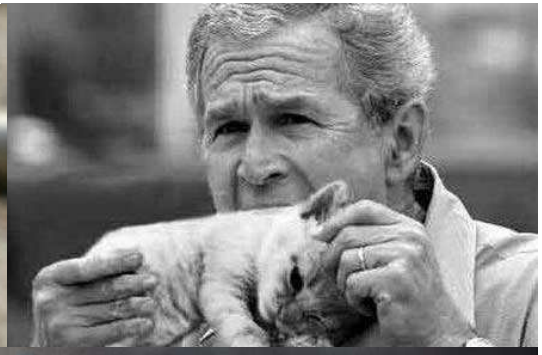
Conflicts









Cooperation









Conflict and cooperation

- social dilemma
  - gain depends on collective investment
  - investment is costly

☞ conflict of interest

everybody likes the others to invest more in public goods

- two solutions of social dilemma:
  - **conflict**
    - exploitation
      - ☞ exploited loose a lot, exploiter gain a lot
  - **cooperation**
    - everybody invests, everybody enjoys the benefits
      - ☞ everybody gain some
- **conflict** and **cooperation** are the two sides of the same coin

What's this talk about?

Internal state is important.

- hungry – well-fed
- lean – fat
- low – high level of testosterone

$\Leftrightarrow$

Internal state is often neglected.

How does the internal state influence the outcome of social dilemma?

Three case studies:

- parental care vs. reserves
- social foraging vs. reserves
- cooperation vs. helpfulness

Defence against exploitation: parental care vs. energetic reserves

The distribution of care patterns – a few example

Species	bipar. care[a]	male only care[a]	female only care[a]	bipar. 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

The parental conflict about care

- parental care *improves* offspring's survival
- care is *costly*
  - reduced future survival
  - reduced chance of remating
- cost of care can be avoided by *deserting* the brood if
  - one parent can raise the brood
  - partner will continue to care
- conflict of interest: *which of the parents should care?*
  - the sex deciding first can force the other sex to care by deserting

Simultaneous vs. sequential decisions

- members of the pair decide independently of each other

male:

		female: care	female: desert
male	care	**5**	**3**
	desert	4	2

female:

		female: care	female: desert
male	care	5	**6**
	desert	**3**	2

- male decides first, female then decides on the basis of the male's decision

male:

		female: care	female: desert
male	care	5	**3**
	desert	**4**	2

female:

		female: care	female: desert
male	care	5	**6**
	desert	**3**	2

Why do we need a dynamic modell of parental care?

- previously: arbitrary pay-offs
- in reality the pay-offs depend on
  - behaviour of current mate
  - own future behaviour
  - past and future behaviour of others in the population
- need to model the past and future of the population to get the pay-offs

Solution

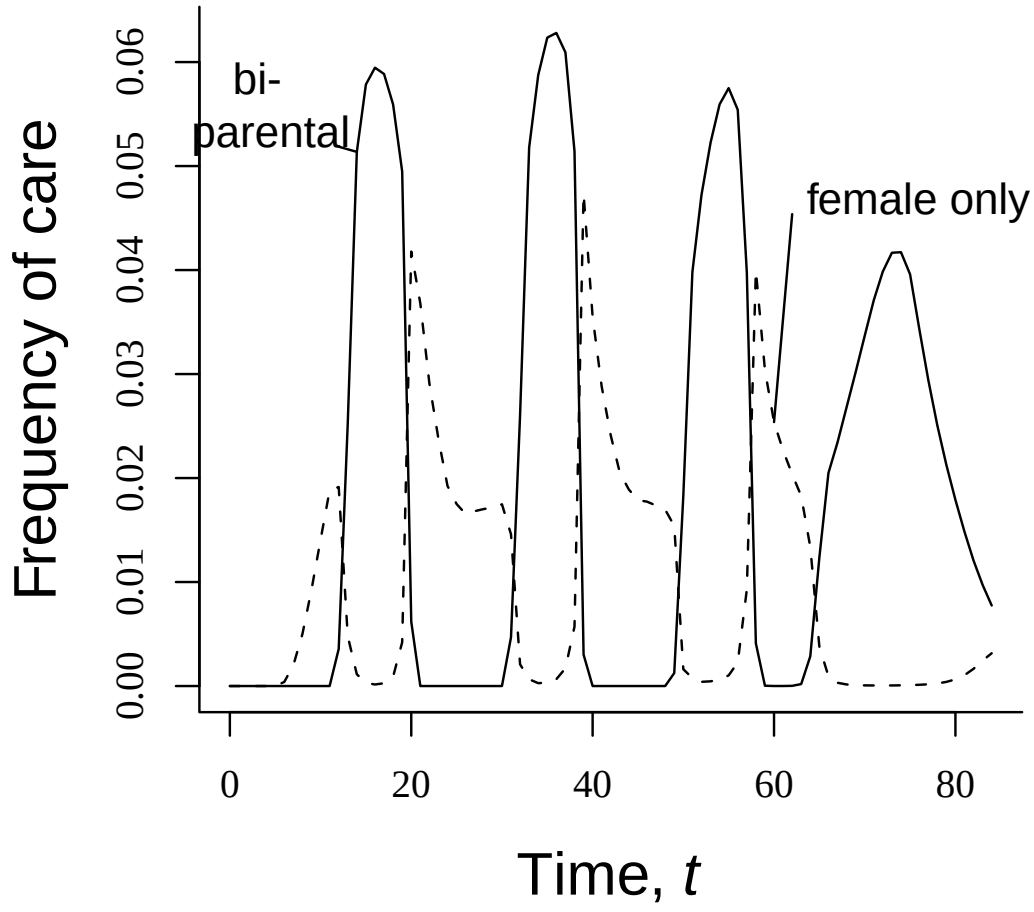
state-dependent dynamic game model of parental care

The outline of the model

- time scale: one breeding season of $T = 100$ days.
- state variables: marital status, own and mate's energy reserves.
- behavioural actions:
  - *unmated individuals* : rest, forage or search for a mate,
  - *mated individuals* : after producing a batch of offspring the parents either cares or deserts.
- decision about care: sequential, the male decides first
- cost of care: energy and time
- uni- and biparental care similarly efficient

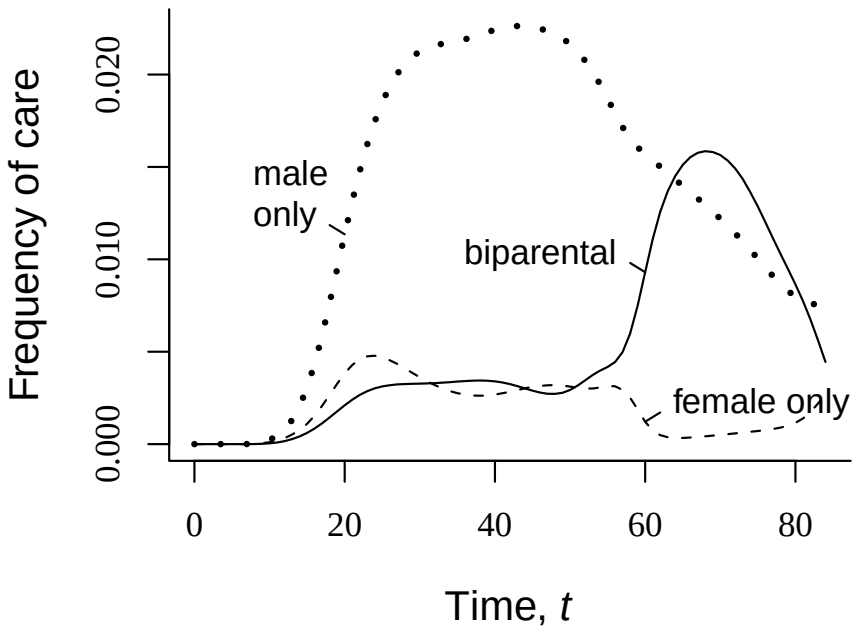
  ☞ strong conflict of interest about who should care

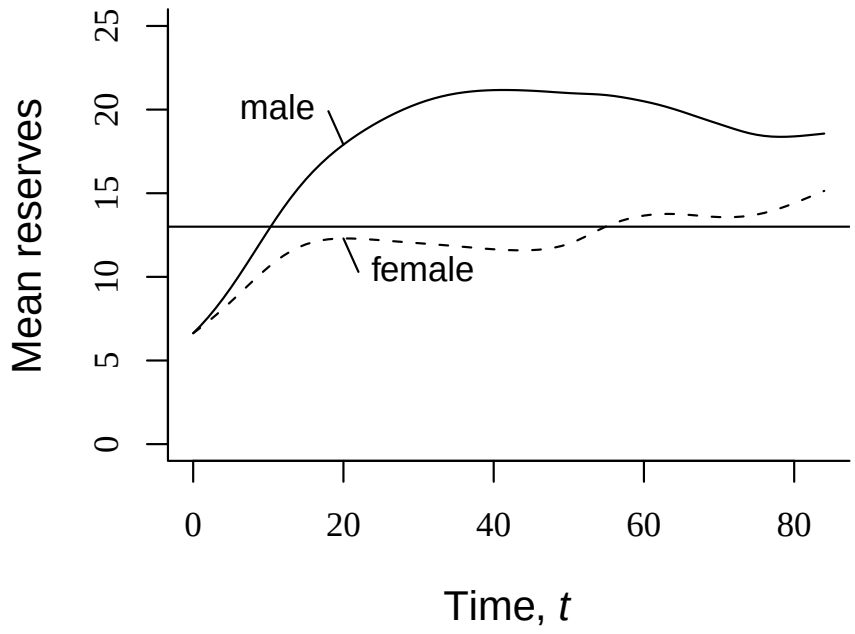
Results: no effects of reserves



The male forces the female to care by deserting her.

Results: reserves are important





The female circumvent the male's behaviour by keeping her reserves below the cost of care.

Parental care game: conclusions

- The sequence is important!
- Only credible threat works.
  - low energy reserves guarantees credibility
- Strategic regulation of body mass can be important in parental conflict about care.

Social foraging:
from exploitation to insurance

Social foraging: foraging in groups

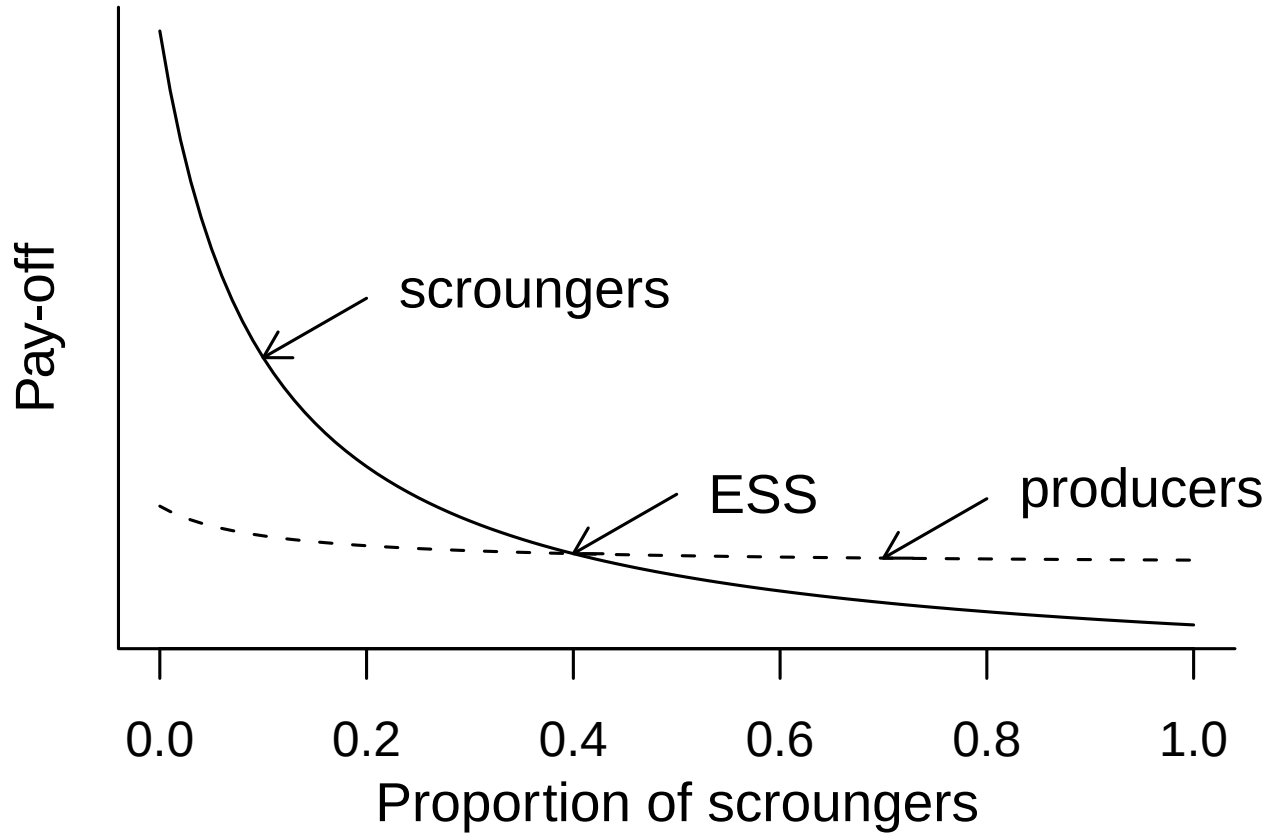
- group mates ☞ chance to exploit others
- common in ground-feeding passerines
- two food finding behaviour in the group:

producing

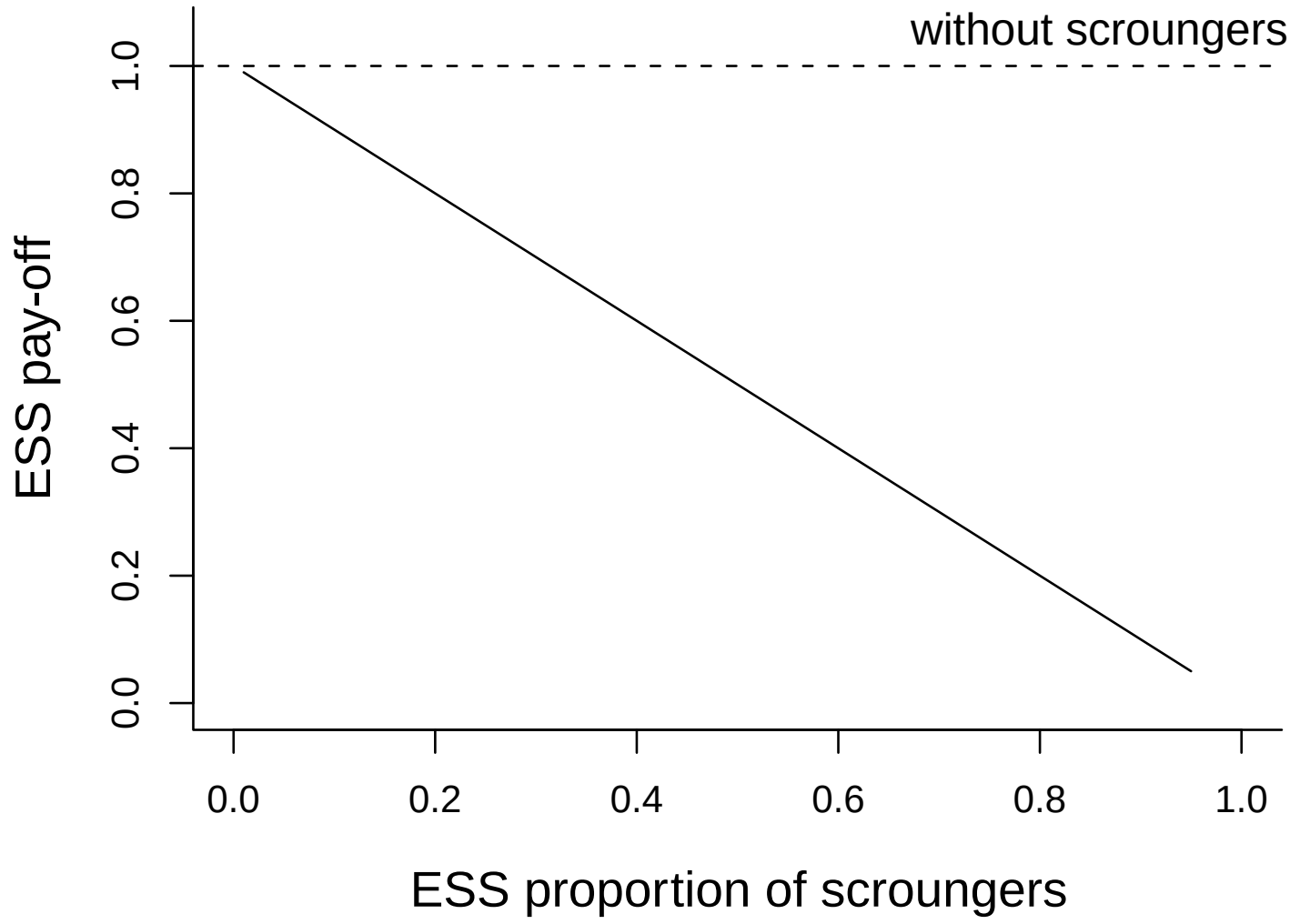
scrounging

The basic model

- strong negative frequency dependence of scroungers' payoff
- evolutionarily stable strategy (ESS)



Basic model: exploitation



Problems with the basic model

Assumptions		Consequences
• simplistic environment		• predation? • stochasticity in food?
• everybody is the same		• dominance? • spatial position? • reserves?

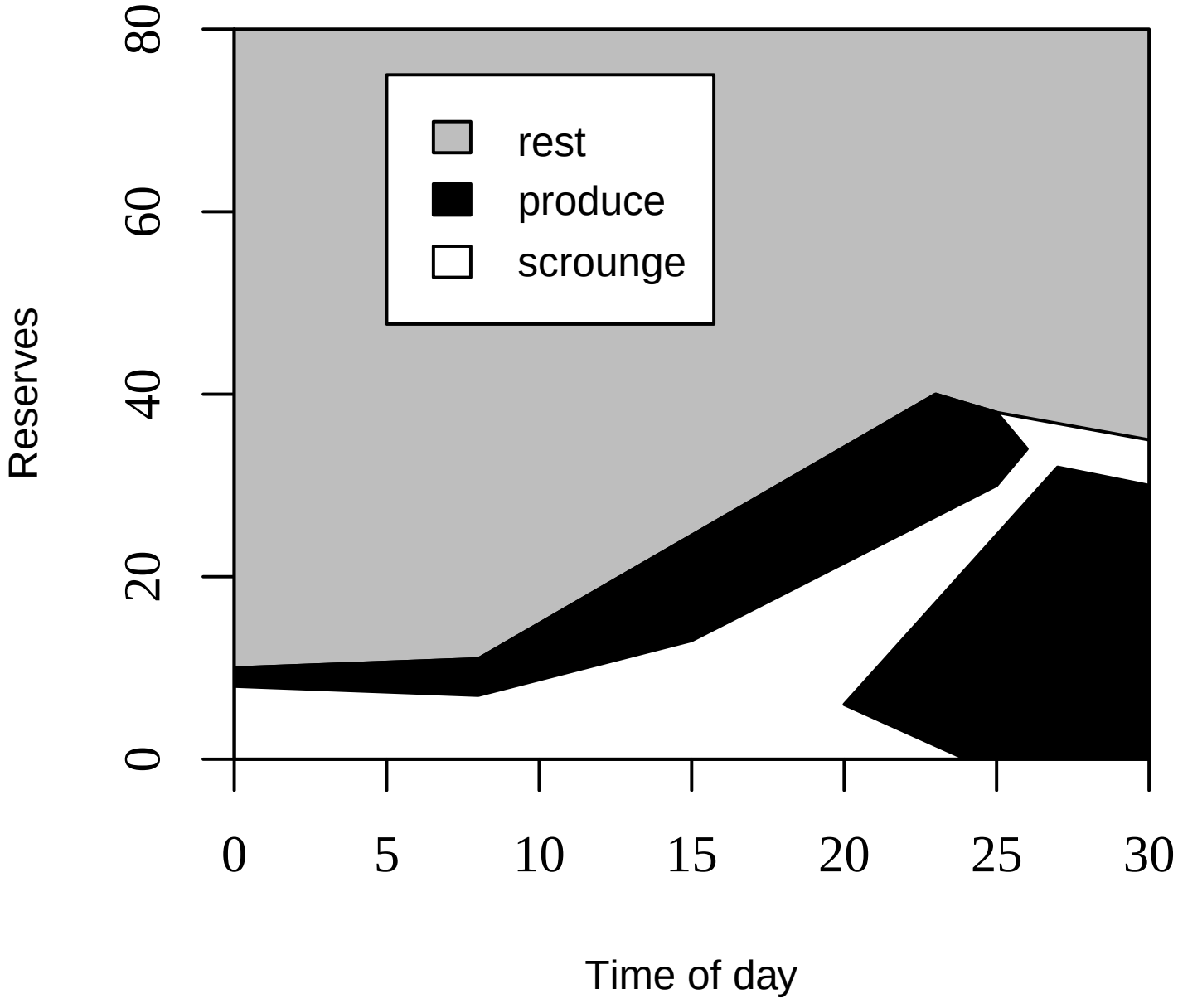
Solution

state-dependent stochastic dynamic game model of producing-scrounging

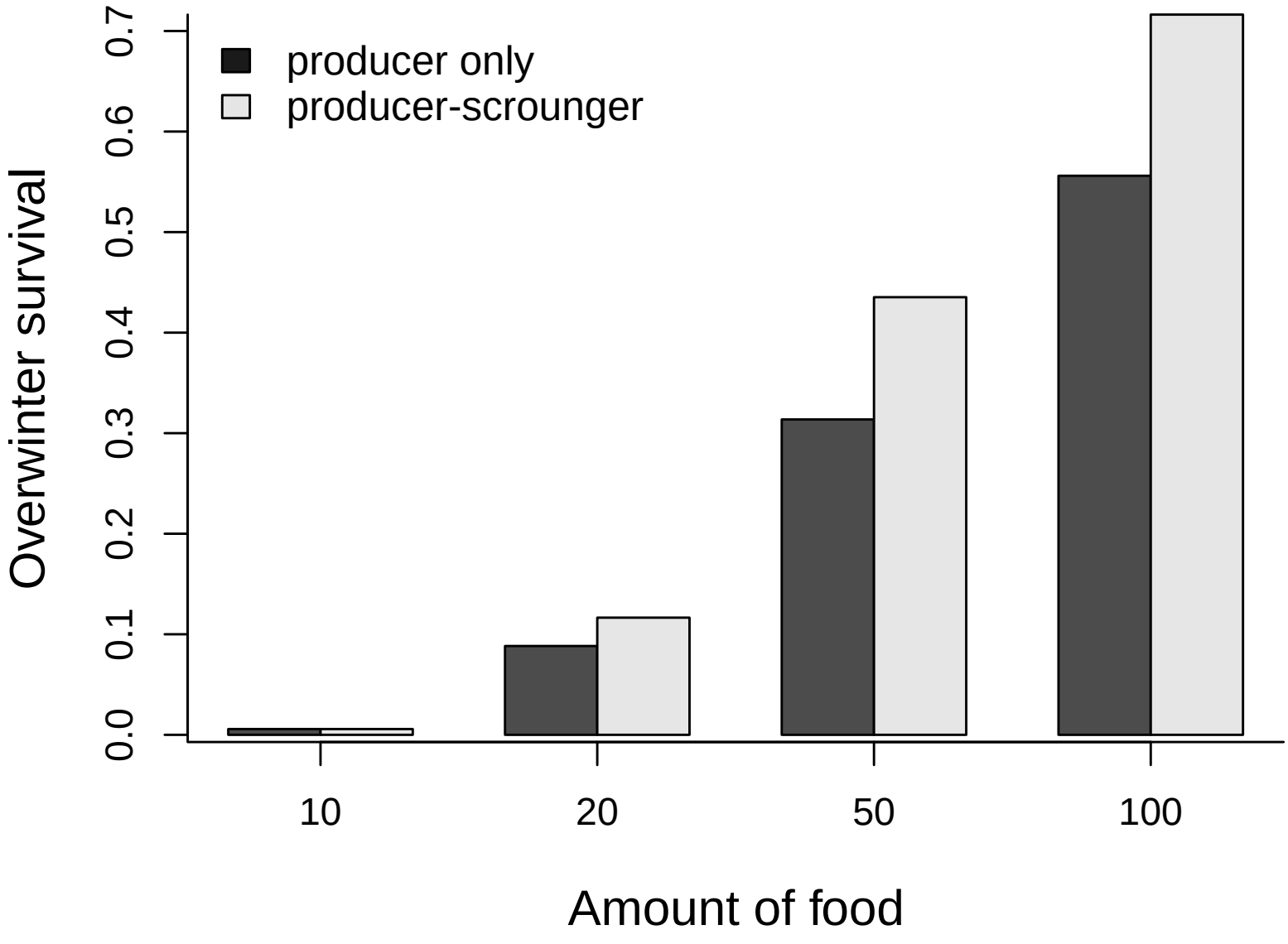
The model

- social foraging over a couple of winter days
- maximising daily survival
- behaviour
  - *daytime*: rest, forage (produce, scrounge)
  - *night*: rest
- state variable: energy reserves

Results: optimal strategy



Results: overwinter survival



Use of scrounging improves winter survival.

Producing - scrounging: conclusions

- use of scrounging depends on internal state
- scrounging as explorative strategy?
  - yes: its use decreases others' gain
  - BUT: the possibility of scrounging increases everybodies' survival

The rise of cooperation: state-dependent generalised reciprocity

Cooperation

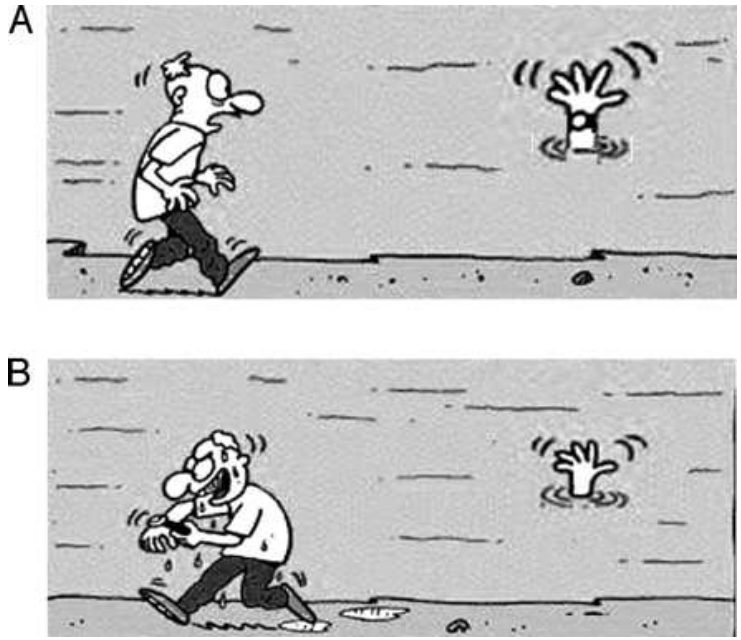
- benefitial, but risky
- big temptation to cheat

Cooperation

- cooperators are more successful than non-cooperators

BUT

- among cooperators *cheating* is the best

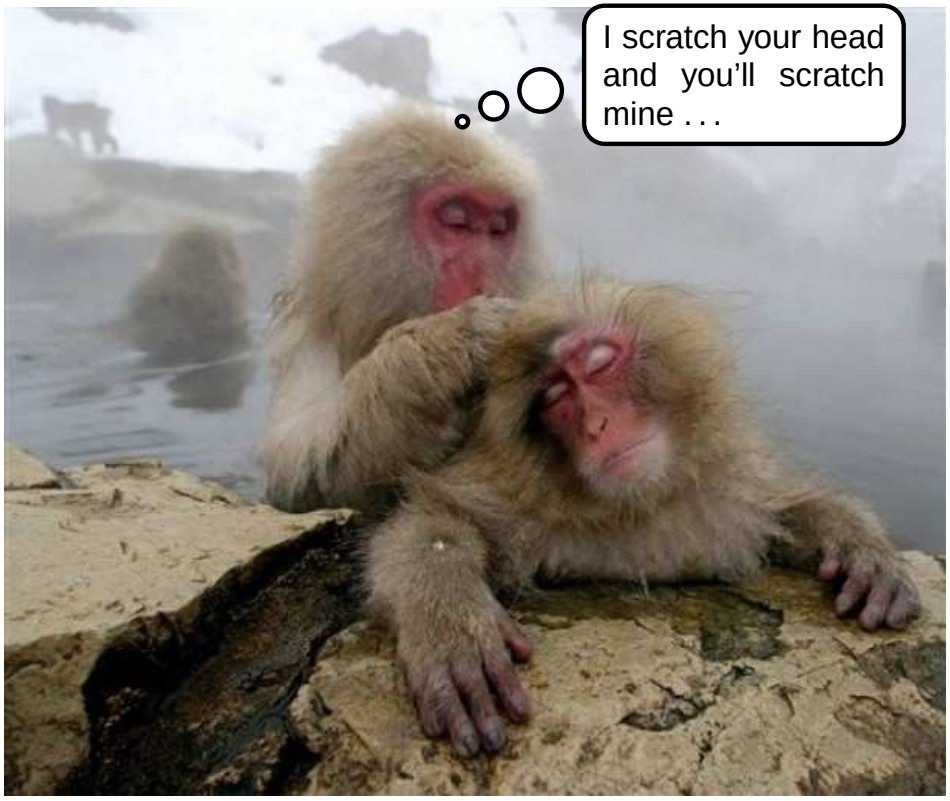


How can cooperation evolve?

Cooperation among non-kins needs some “helping” mechanism.

Reciprocity

Direct reciprocity



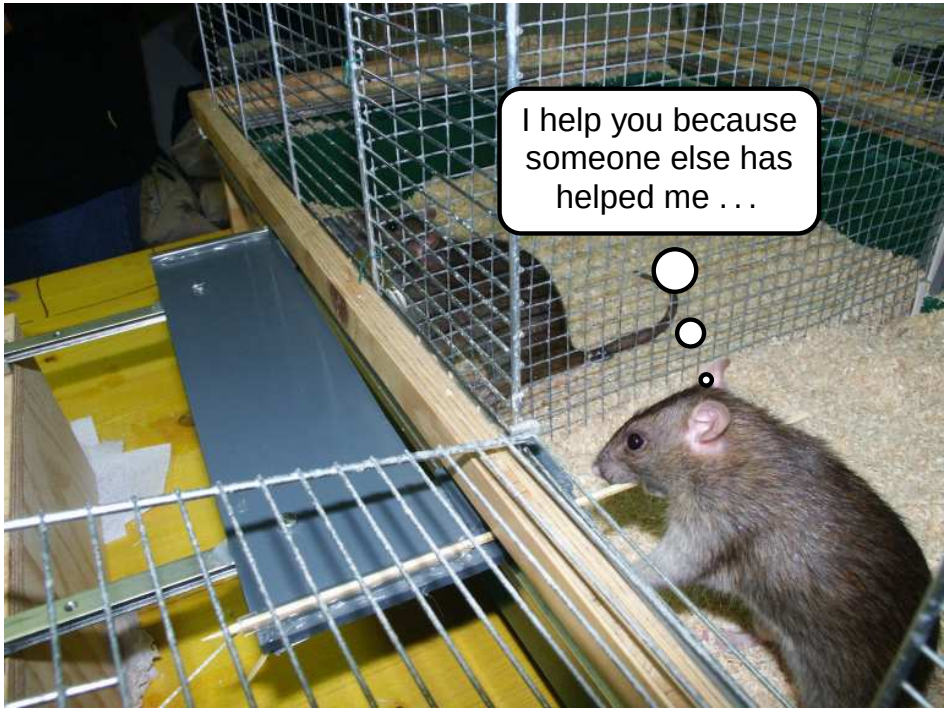
Indirect reciprocity

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

advanced cognitive capabilities ☞ minor importance in animals

New kid on the block

Generalised reciprocity



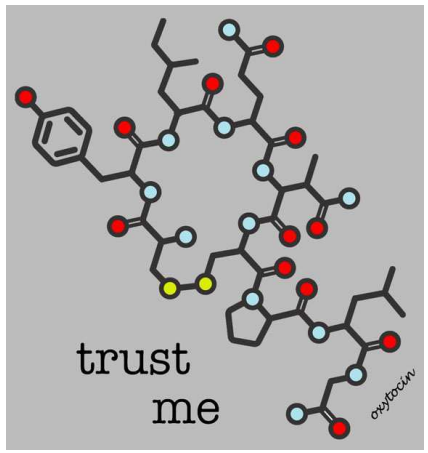
- among anonymous partners
  ☞ simple mechanism
- the role of internal state???

A neglected constraint: internal state

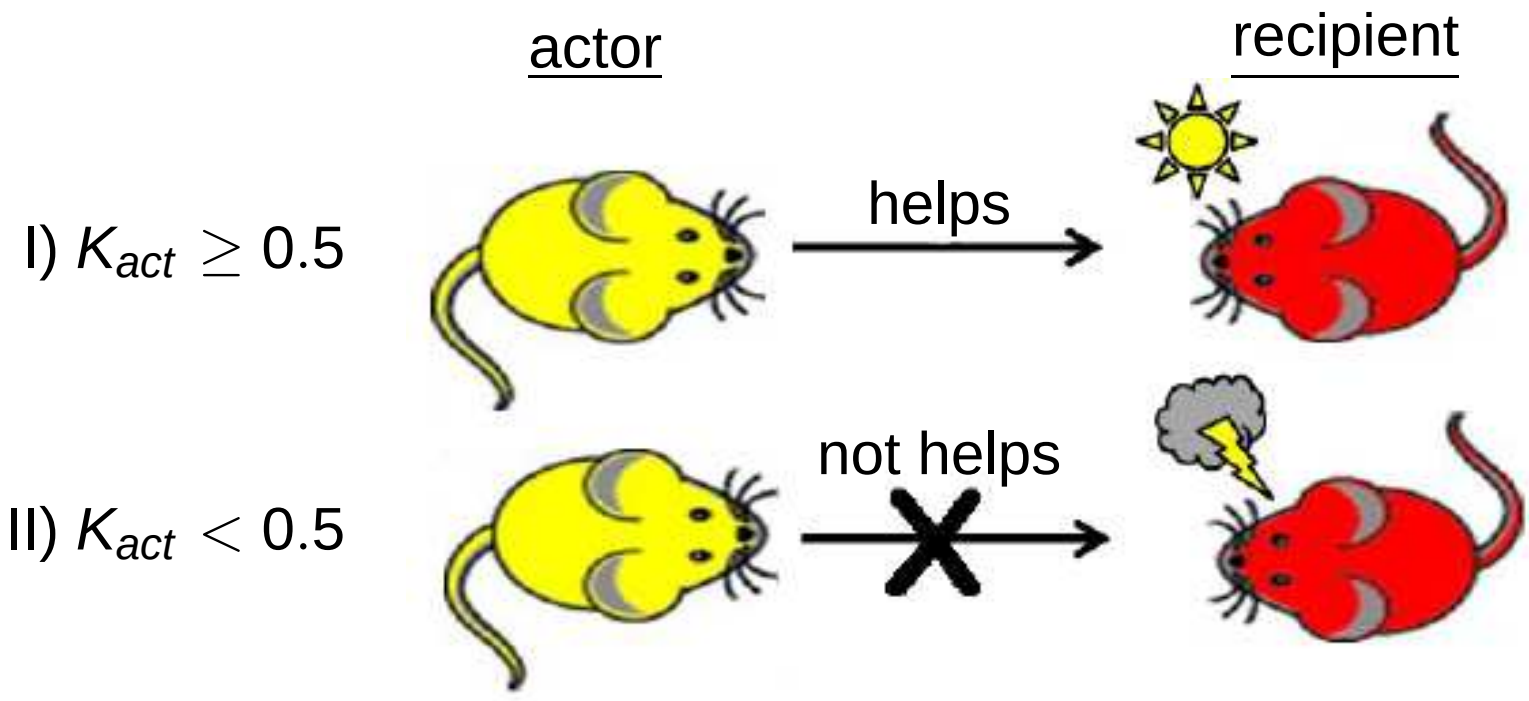
Internal state can influence social behaviour.

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

Models of cooperation usually neglect these.

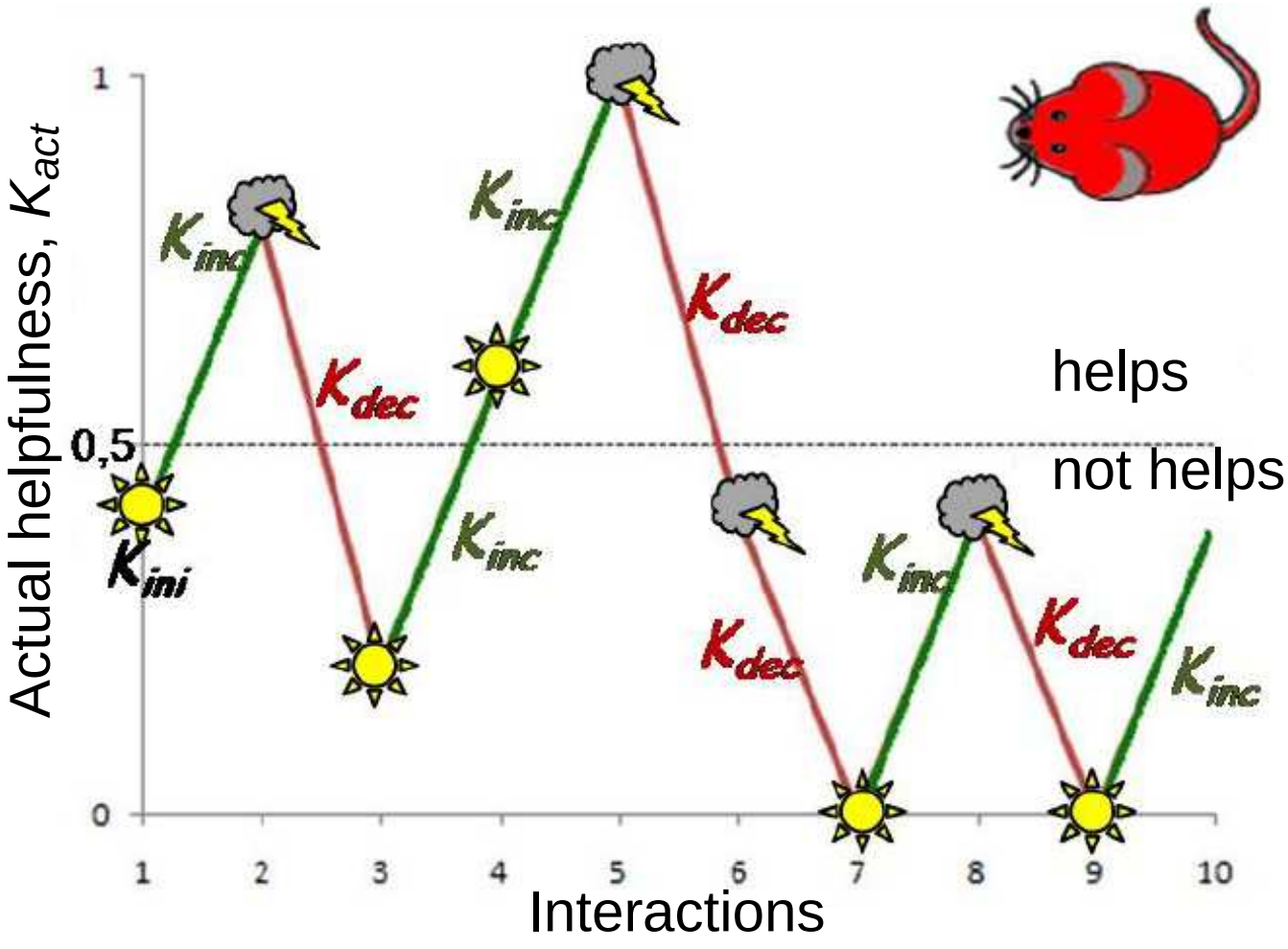


Simple model of generalised resiprocity



no cooperation

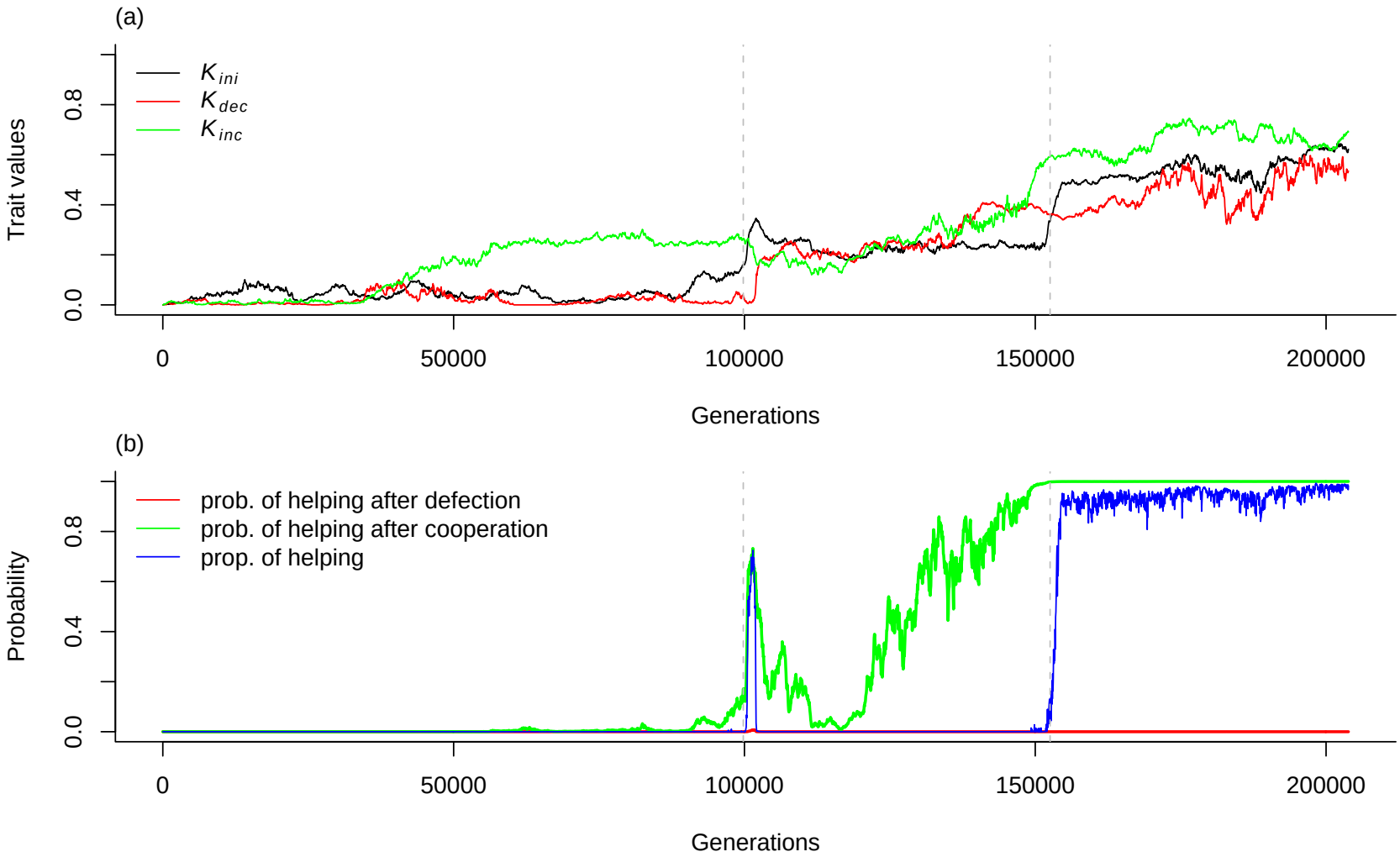
State-dependent model of generalised reciprocity



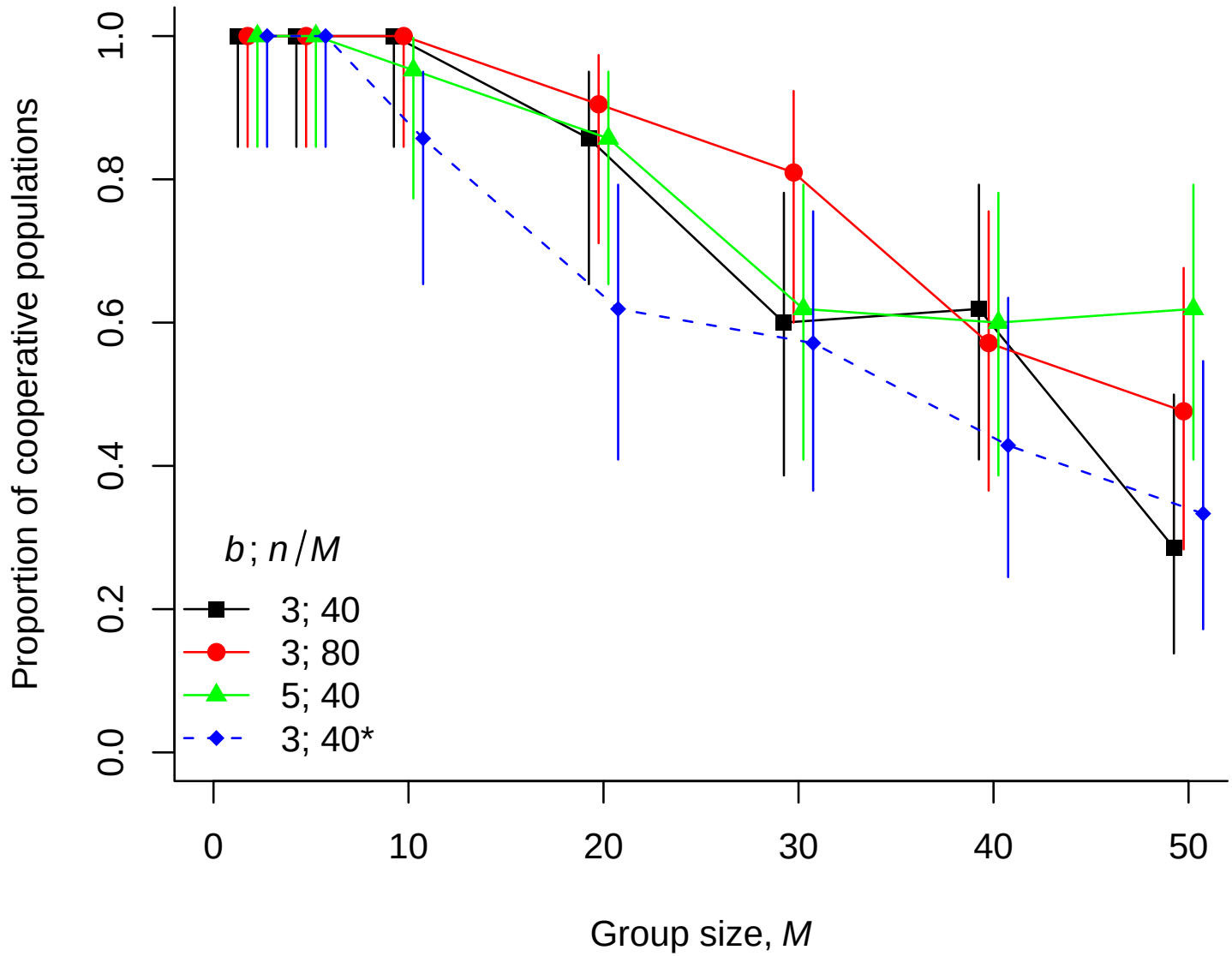
Traits:

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

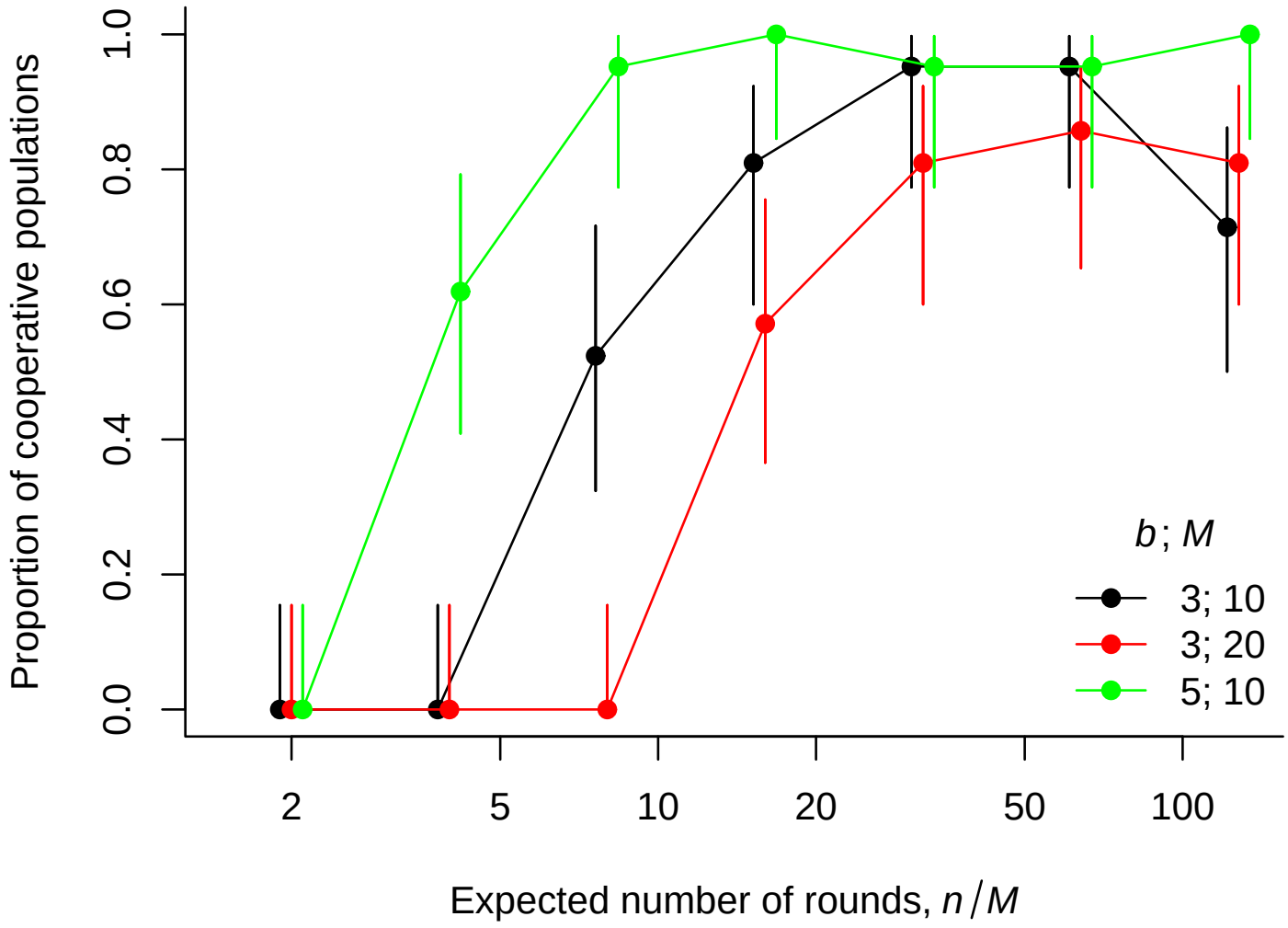
The rise of cooperation



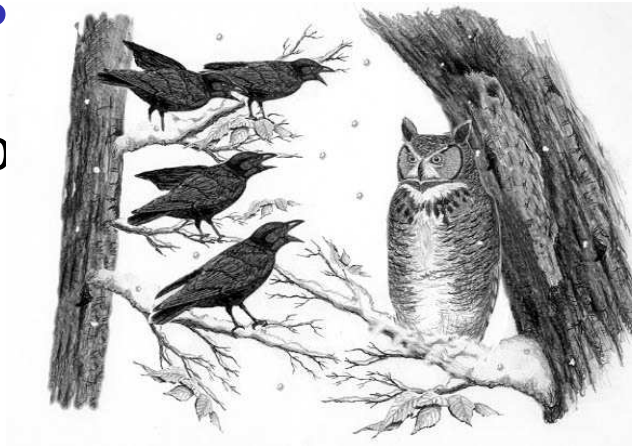
Effect of group size



Effect of number of interactions



Generalised reciprocity: conclusions



- cooperation under a wide range of conditio
  - 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

state-dependent generalised reciprocity:
a basis for the evolution of complex social behaviour???

General conclusions

Internal state may have an important role in determining the outcome of social dilemma.

- avoiding force, credible threat
- insurrance instead of exploitation
- cooperation through simple, gradual evolutionary steps

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