University of Sheffield | Centre for Machine Intelligence

Opteran®

Negative feedback as a noise suppression mechanism in collective foraging

James A. R. Marshall, University of Sheffield & Opteran Technologies Ltd.

Mathematics of Intelligences Programme - Workshop IV: Modeling Multi-Scale Collective Intelligence

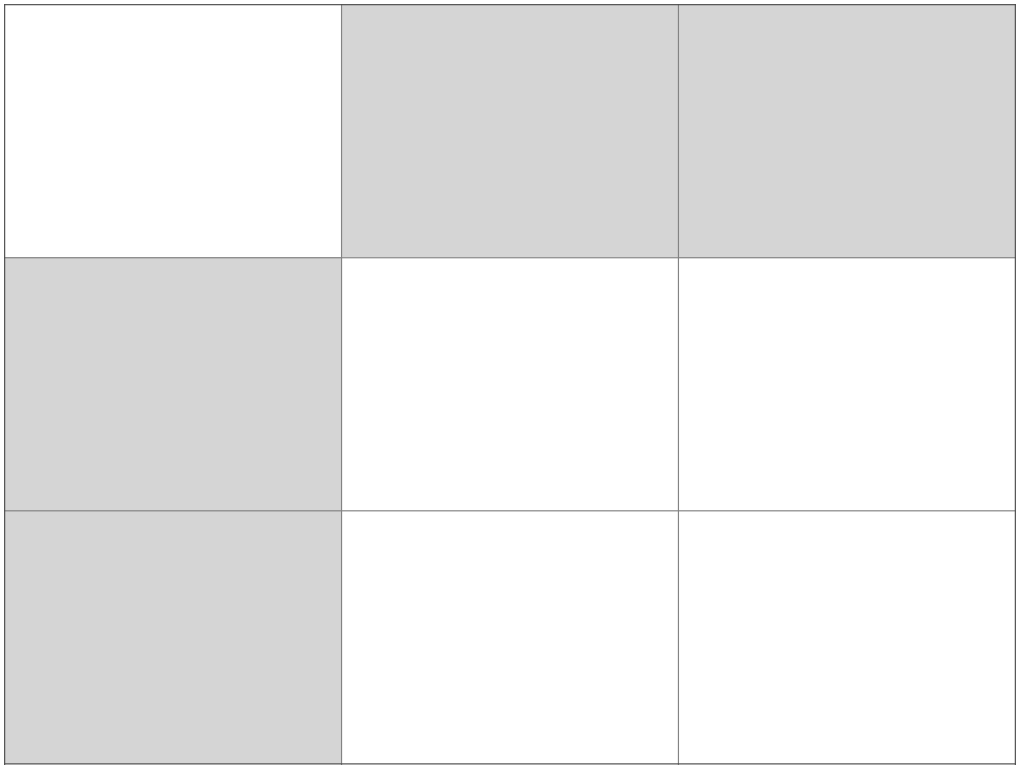
A talk in two parts

Part one: how can we think about collective animal behaviour?

Wikipedia

An evolutionary framework for collective behaviour

Tinbergen, Behavioural Ecology, and Collective Behaviour



An evolutionary framework for collective behaviour

Tinbergen, Behavioural Ecology, and Collective Behaviour

Proximate View		

An evolutionary framework for collective behaviour

Tinbergen, Behavioural Ecology, and Collective Behaviour

Proximate View		
Ultimate View		

An evolutionary framework for collective behaviour

Tinbergen, Behavioural Ecology, and Collective Behaviour

	Dynamic View	
Proximate View		
Ultimate View		

An evolutionary framework for collective behaviour

Tinbergen, Behavioural Ecology, and Collective Behaviour

	Dynamic View	Static View
Proximate View		
Ultimate View		

An evolutionary framework for collective behaviour

Tinbergen, Behavioural Ecology, and Collective Behaviour

	Dynamic View	Static View
Proximate View	Behavioural development	
Ultimate View		

An evolutionary framework for collective behaviour

Tinbergen, Behavioural Ecology, and Collective Behaviour

	Dynamic View	Static View
Proximate View	Behavioural development	Behavioural mechanism
Ultimate View		

An evolutionary framework for collective behaviour

Tinbergen, Behavioural Ecology, and Collective Behaviour

	Dynamic View	Static View
Proximate View	Behavioural development	Behavioural mechanism
Ultimate View	Behavioural evolution	

An evolutionary framework for collective behaviour

Tinbergen, Behavioural Ecology, and Collective Behaviour

	Dynamic View	Static View
Proximate View	Behavioural development	Behavioural mechanism
Ultimate View	Behavioural evolution	Behavioural function

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Marshall & Reina, 2024

Question A: What quantity should be optimised?

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Question C: At what level should behaviour be optimised?

Marshall & Reina, 2024

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Marshall & Reina, 2024

A Dog a Day

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Marshall et al., 2017

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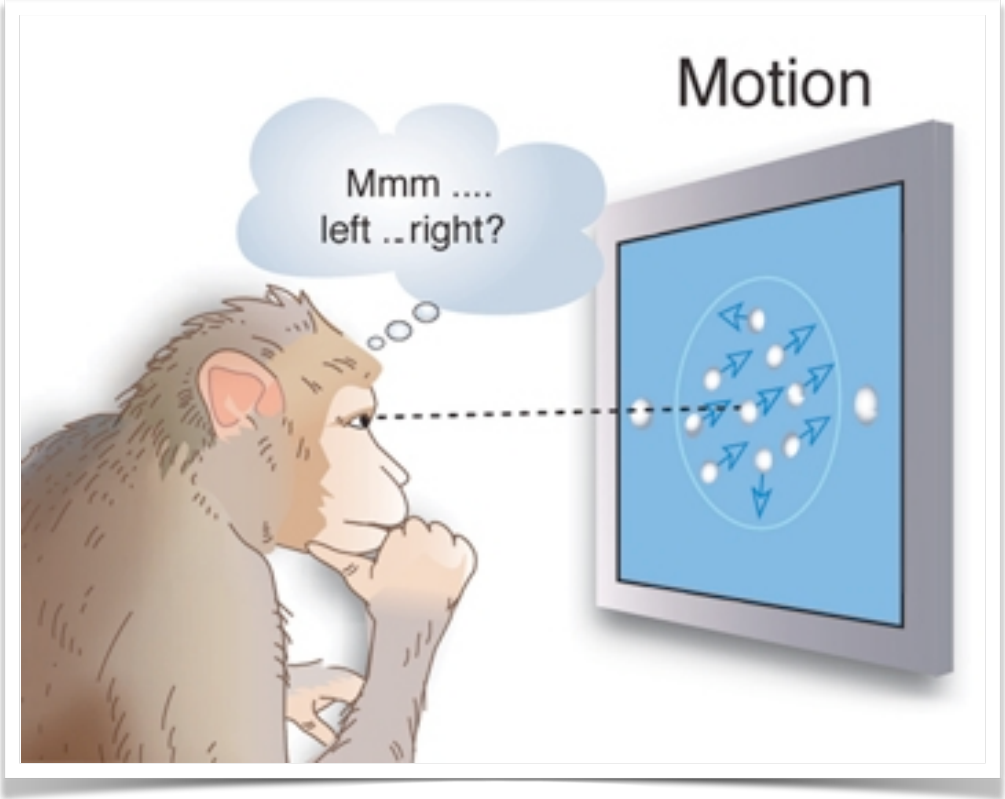
Optimisation tools

Behavioural function

What quantity should be optimised?

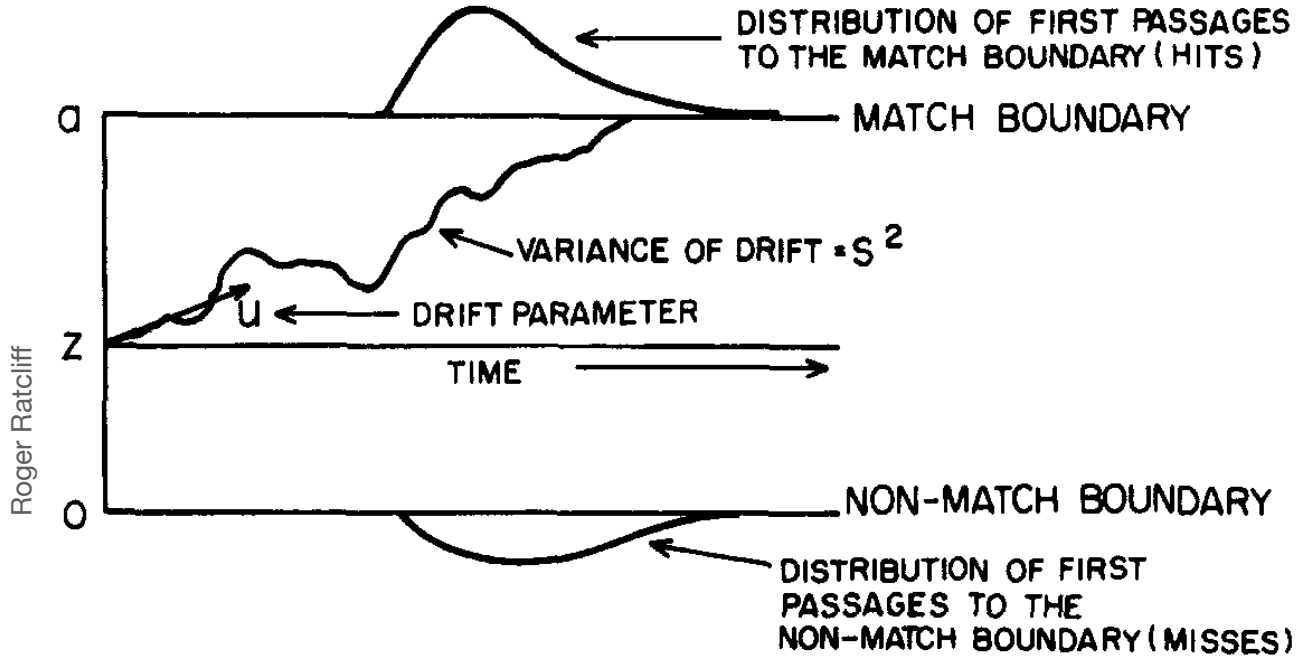
Tom Seeley



Nature Neuroscience

Optimal statistical tests

Drift-Diffusion Model (DDM): based on likelihood ratio test



Roger Ratcliff

SCIENCE

BEHAVIOR

How Honeybees Break a Decision-Making Deadlock

During the search for a new nest site, use of an inhibitory signal enables honeybees to reach a decision.

Jeremy E. Niven

For a honeybee swarm of potentially thousands of individuals, choosing a home is a momentous decision. Failing to choose a single location may cause the swarm to split and the queen to be lost (*1*); choosing poorly may limit the swarm's growth or expose it to freezing temperatures during the winter (*2*). Studies over the past 60 years have shown that honeybee swarms use quorum sensing, a form of decentralized decision-making, to choose a suitable nest site, but many gaps remain in our understanding of this process. On page 108 in this issue, Seeley *et al*. (*3*) show that an inhibitory signal between bees advocating different locations allows them to make a decision even when potential nest sites are equally favorable.

Honeybee colonies reproduce through budding, whereby the queen and some workers leave the nest and bivouac on a branch. Some of the most experienced workers leave to locate suitable nest sites (*4*). Upon their return, these scouts advertise potential locations and their qualities by performing a waggle dance. During the dance, the scout walks straight across the bivouacking bees, making side-to-side waggles of her body. She then stops, turns left or right, and walks a semicircular return path to her starting point. The waggle run's duration and orientation encode the length and the angle of the outward flight, respectively, whereas the number of dance circuits encodes the quality of the potential nest site (*5*). Waggle dances recruit additional scouts to a site until a quorum number is reached and the swarm prepares to move to its new home (*2*).

Scouts advocating less attractive sites produce fewer dance circuits and make fewer trips to the site (*6*). Along with the recruitment of uncommitted scouts to more attractive sites, this was assumed to be sufficient to enable the bees to reach a quorum, thereby deciding which site to choose (*2*). However, foraging workers use an additional type of signal to communicate with other bees. Upon returning from a feeder that is crowded or where a predator is present, forager bees produce a brief vibrational signal that discourages other bees from producing waggle dances that advertise the location of that feeder (*7*). Hypothesizing that a similar signal may be used by house-hunting bees, Seeley *et al*. set out to observe scout behavior. They found that scouts received "stop" signals—head butts mainly to their head and thorax—from other bees during the return run of the waggle dance (see the figure). These stop signals occurred more frequently just before a scout stopped dancing.

The authors next established swarms on Appledore Island (Maine), which lacks natural nest sites, and gave them a choice of two identical nest boxes. Scouts visiting one box were marked with yellow paint; those visiting the other were marked with pink paint. Most of the bees giving "stop" signals selection process, dancing scouts with yellow paint received many more stop signals from scouts with pink paint and vice versa, showing that scouts from one site preferentially inhibit the dances of those advertising a competing site (see the figure, panel A). Once the scouts started implementing the decision, dancing scouts received stop signals from scouts that had visited either site. When swarms were given only one nest box, scouts received few stop signals during the decision phase but many during the implementation phase. This general inhibition of dancing during the implementation phase presumably ensures that all the bees are present when the swarm takes flight.

To demonstrate a role for the observed cross inhibition between scouts advertising competing sites, Seeley *et al*. constructed a series of computational models of the collective decision-making process, based on the interaction rules they had observed among the scouts. Models that incorporated no or indiscriminate stop signaling predicted that the scouts would reach a stable deadlock, failing to choose between two

Cease and desist. (**A**) Seeley *et al*. have found that during house hunting, scouts advertising one nest site preferentially inhibit scouts advertising another site during the decision-making process. Inhibition is conveyed by a "stop" signal, given mainly to the head and thorax of a scout during the return phase of the waggle dance. (**B**) Stop signals from scout bees inhibit other scouts, discouraging them from advertising a potential site. These

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School of Life Sciences, University of Sussex, Falmer, Brighton BN1 9QG, UK. E-mail: jen23@sussex.ac.uk

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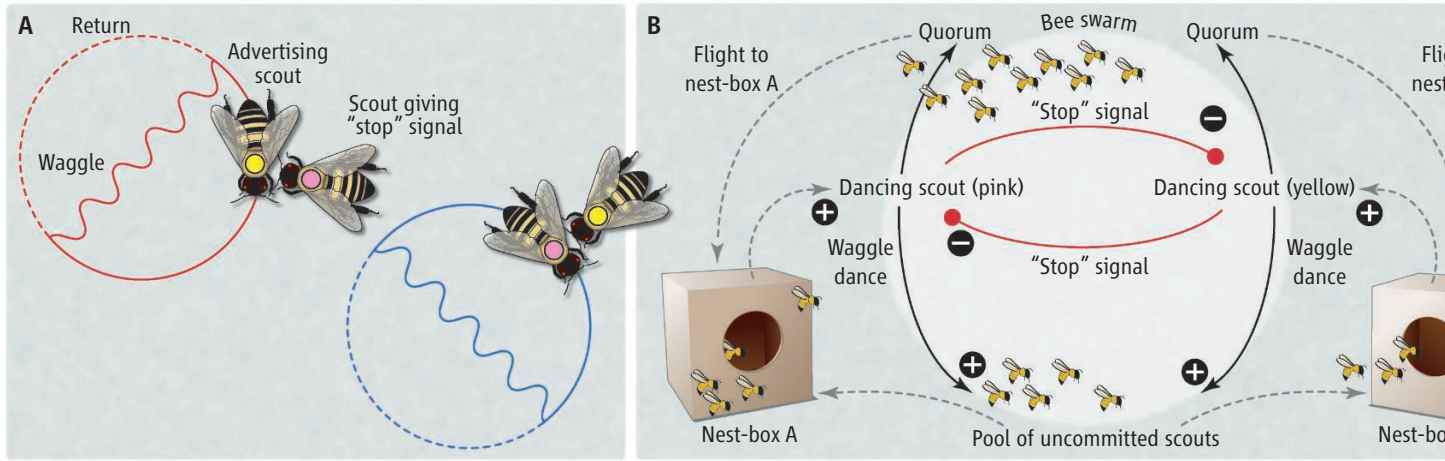

CREDIT: P. HUEY/*SCIENCE*

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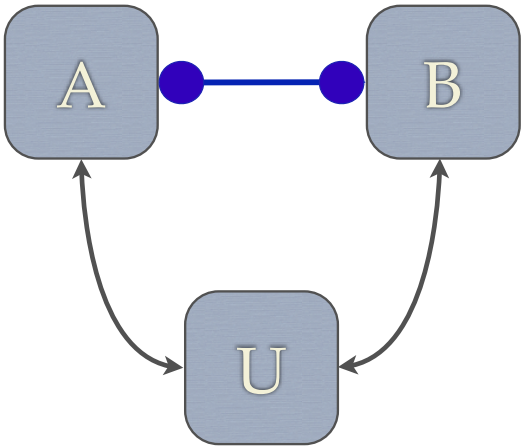
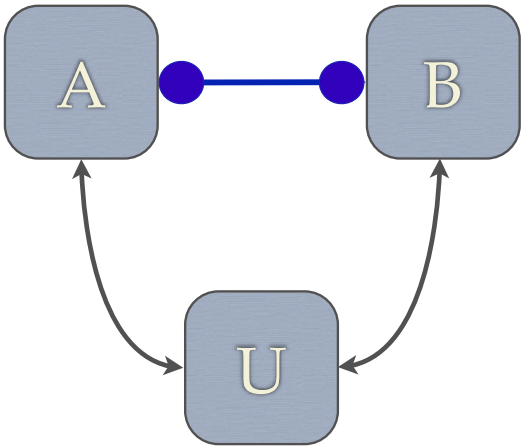
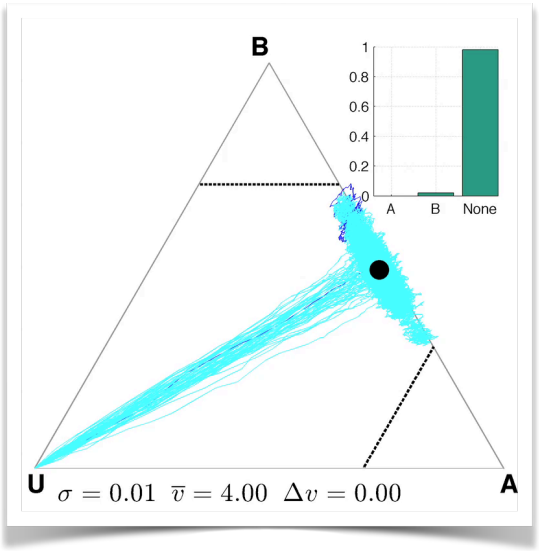


Pais et al. (2013)





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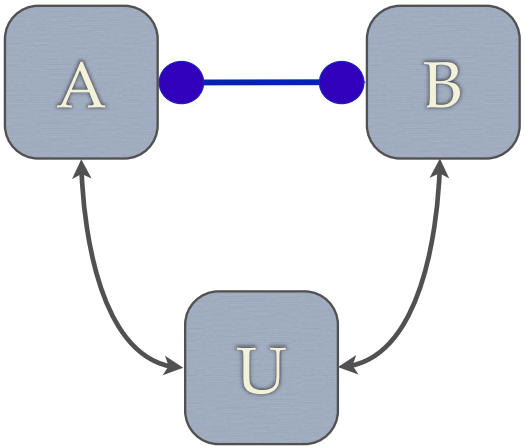

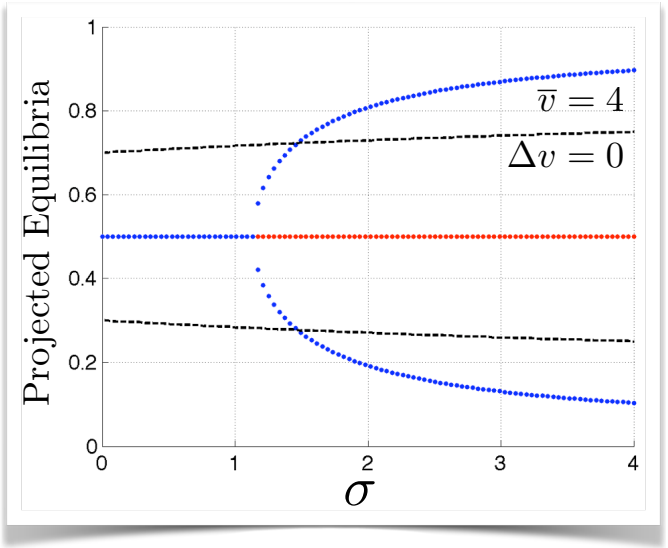

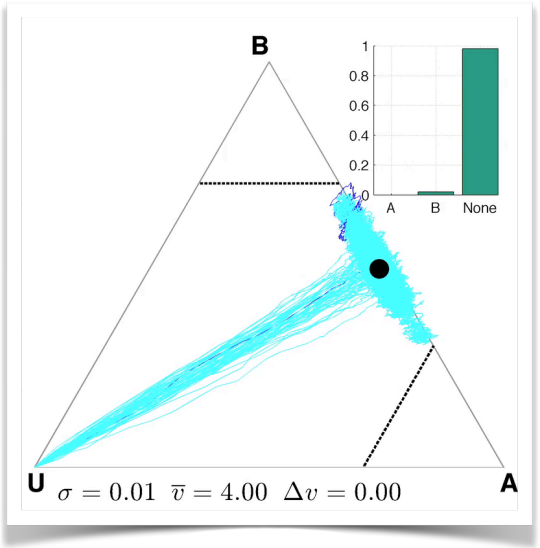

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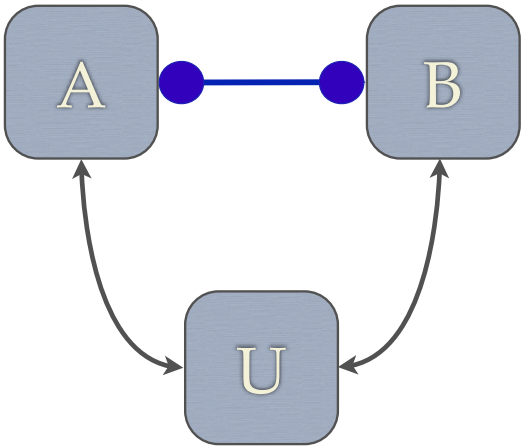
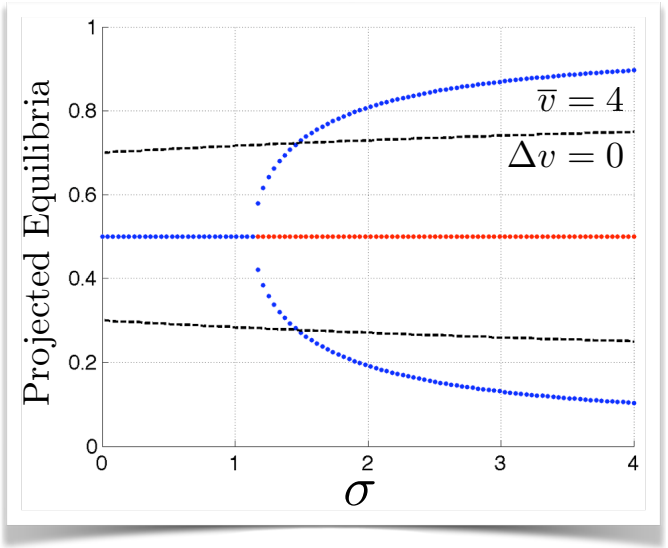
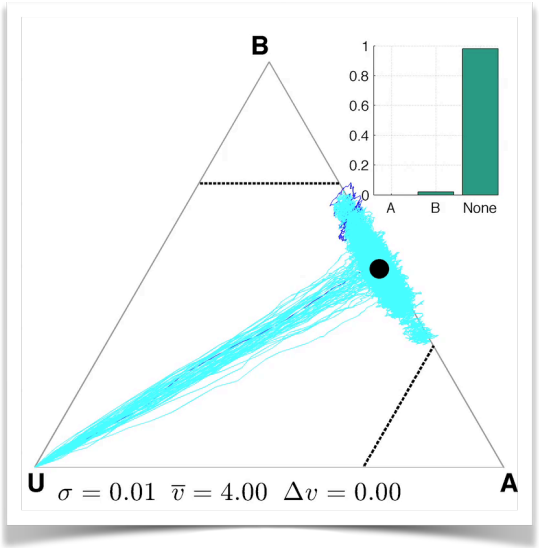
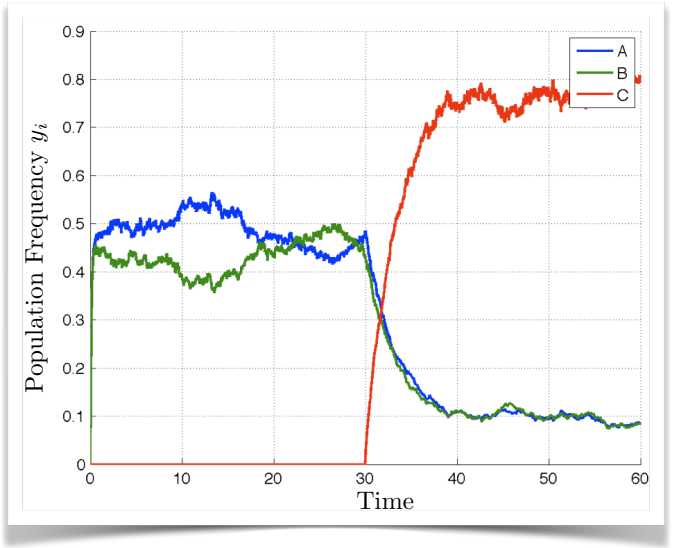






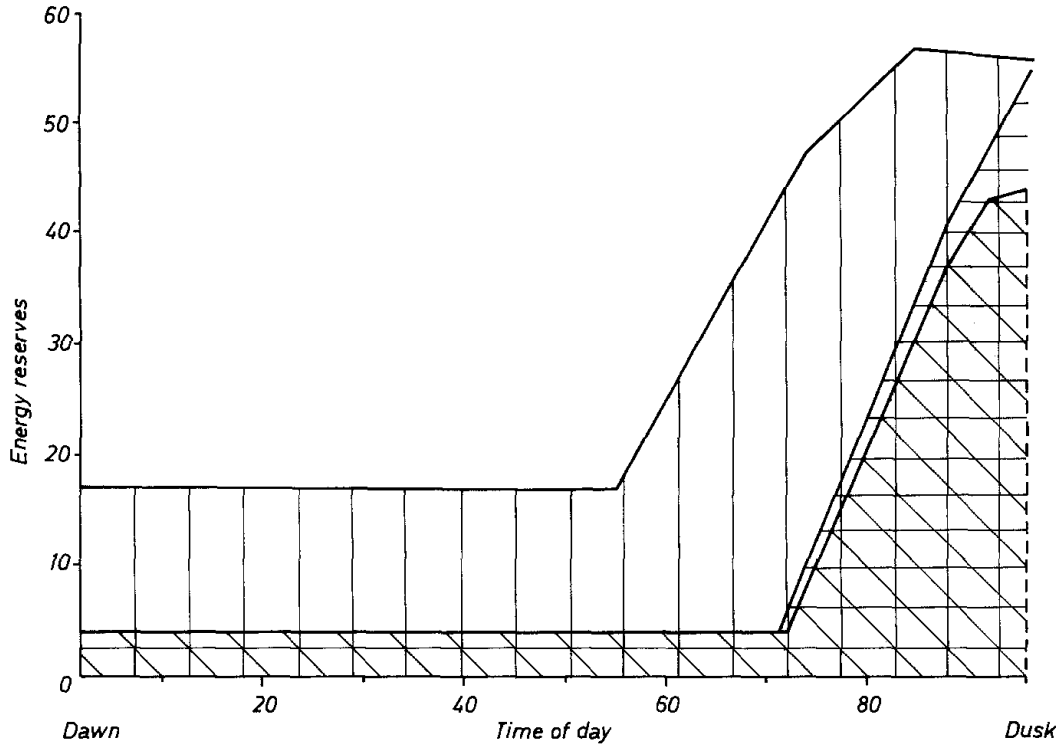


Pais et al. (2013)

But how do we *know* this strategy is optimal?

Stochastic dynamic programming

A classic optimisation tool applied in behavioural ecology



McNamara, Mace & Houston

Dynamic program for decision making

Tajima *et al.*

Dynamic program for decision making

Tajima *et al.*

- Solved the Bellman equation for decisions:

Dynamic program for decision making

Tajima *et al.*

- Solved the Bellman equation for decisions:

$$V(t, \hat{r}_1, \hat{r}_2) = \max \{ V_{\mathrm{d}}(\hat{r}_1, \hat{r}_2), \\ \langle V(t + \delta t, \hat{r}_1(t + \delta t), \hat{r}_2(t + \delta t)) \mid \hat{r}_{1,2}(t) = \hat{r}_{1,2} \rangle - c \ \delta t \}.$$

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VALUE OF SAMPLING

COST OF SAMPLING

Dynamic program for decision making

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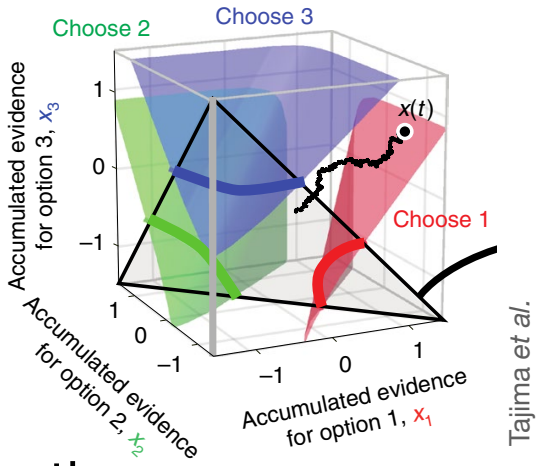

- Found DDMs with decision boundaries that collapse over time
  - Optimise speed-accuracy tradeoffs
  - No magnitude-sensitive deadlock-breaking

Dynamic program for decision making

Marshall *et al.*

$$V(t, \hat{r_1}, \hat{r_2}) = \max\{V_d(\hat{r_1}, \hat{r_2}),$$
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Dynamic program for decision making

Marshall *et al.*

- Solved the *geometric* Bellman equation for decisions:

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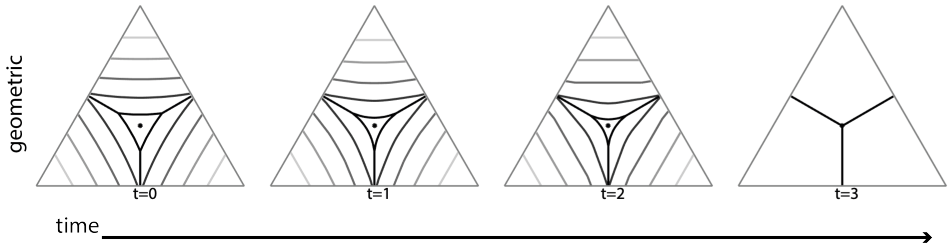
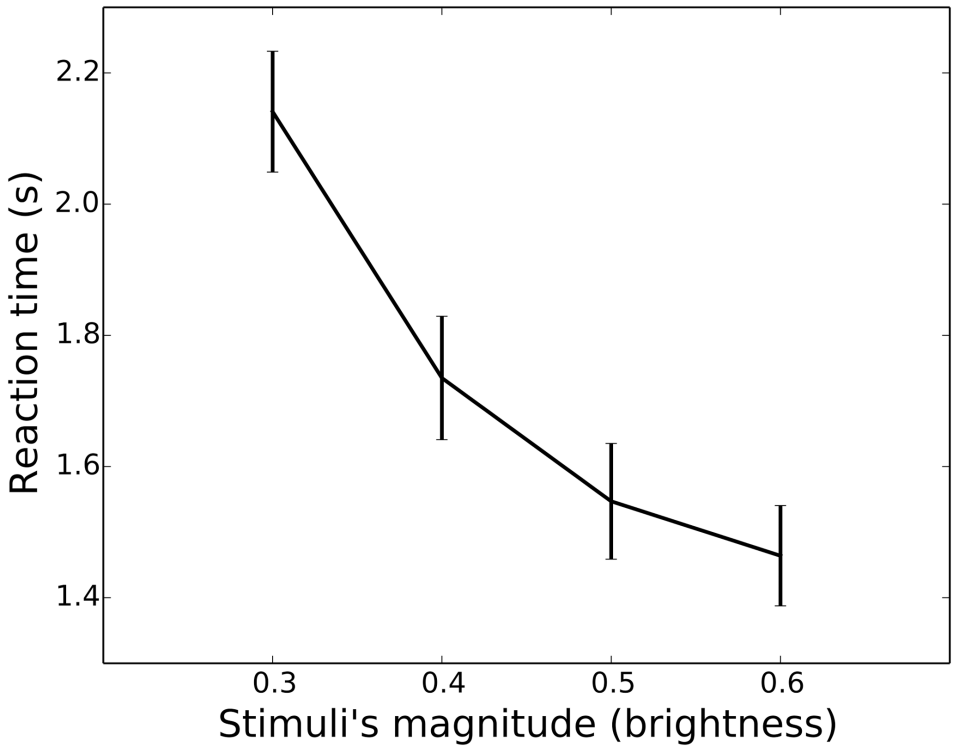
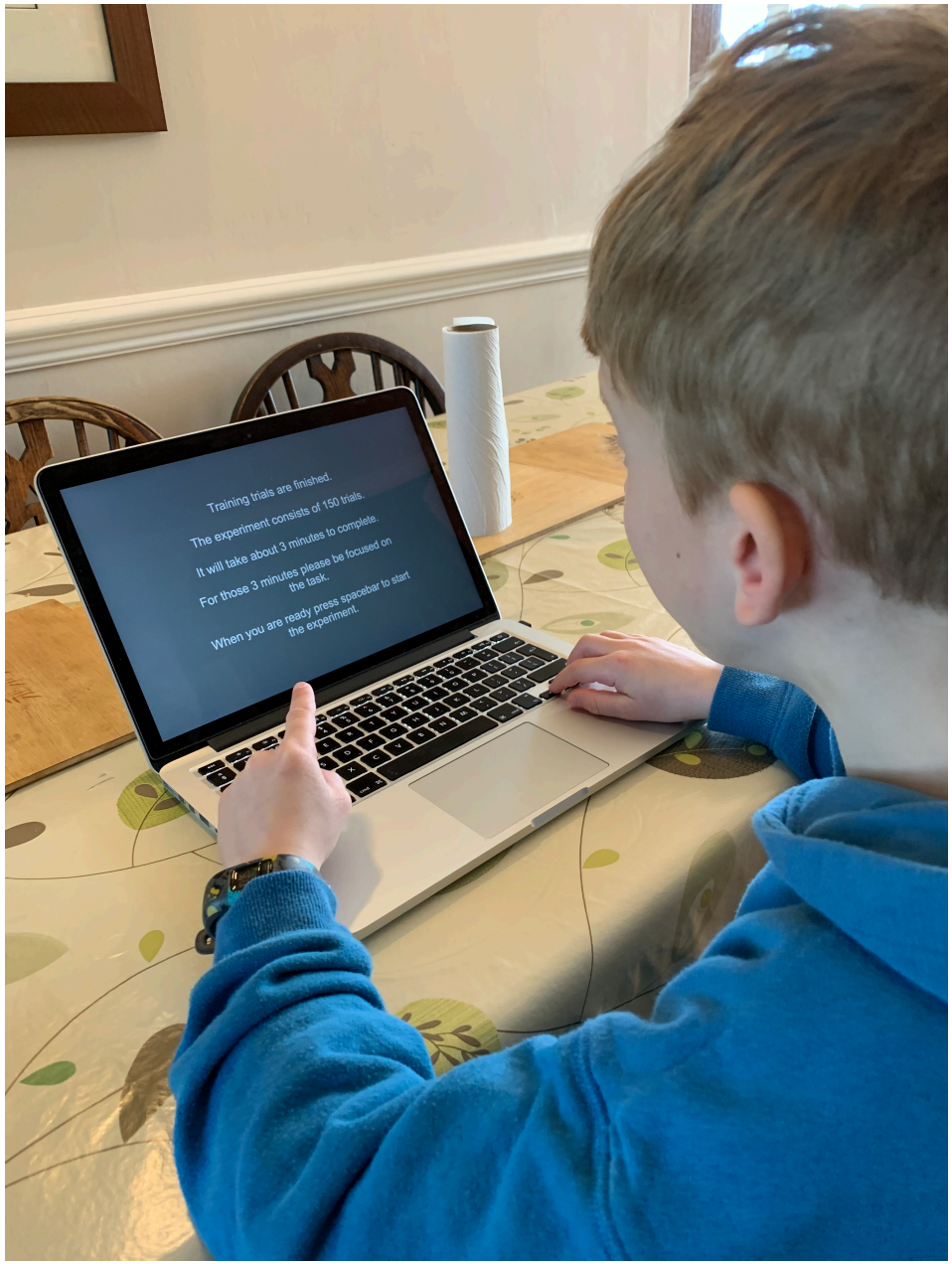
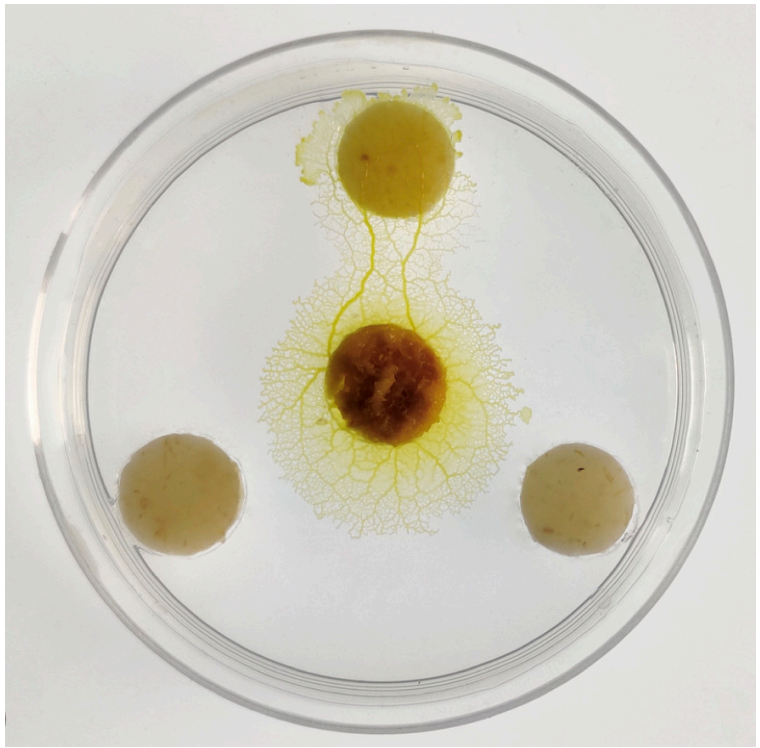
COST OF SAMPLING VALUE OF SAMPLING

- Found time and magnitude-varying decision boundaries
  - *Optimise speed-value trade-off*
  - *Magnitude-sensitive deadlock-breaking*

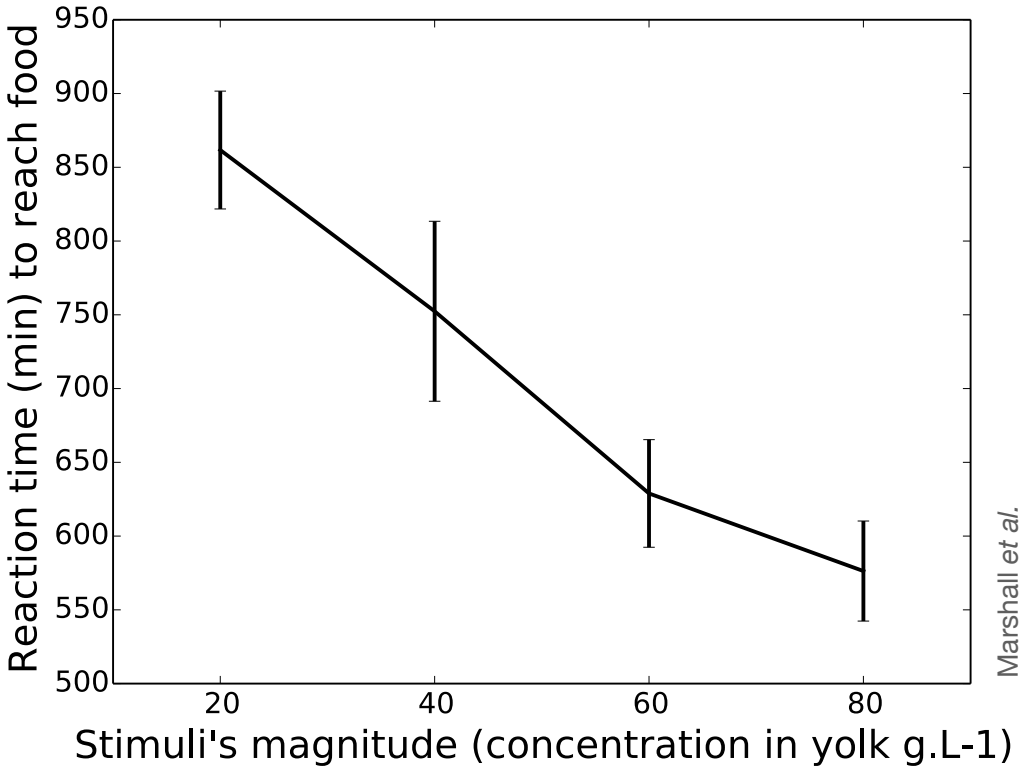



Reaction time (s)
2.2
2.0
1.8
1.6
1.4
0.3
0.4
0.5
0.6
Stimuli's magnitude (brightness)


Training trials are finished.
The experiment consists of 150 trials.
It will take about 3 minutes to complete.
For those 3 minutes please be focused on the task.
When you are ready press spacebar to start the experiment.



Audrey Dussutour



Marshall *et al.*

Part two: noise suppression in collective foraging

An evolutionary framework for collective behaviour

Tinbergen, Behavioural Ecology, and Collective Behaviour

	Dynamic View	Static View
Proximate View	Behavioural development	Behavioural mechanism
Ultimate View	Behavioural evolution	Behavioural function

An evolutionary framework for collective behaviour

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Signalling mechanisms in social insect colonies

Signalling mechanisms in social insect colonies

Positive feedback

Stephen Pratt

Signalling mechanisms in social insect colonies

Positive feedback

Stephen Pratt

Christoph Grüter

Signalling mechanisms in social insect colonies

Positive feedback

Stephen Pratt

Christoph Grüter

Negative feedback

Duncan Jackson

Signalling mechanisms in social insect colonies

Positive feedback

Stephen Pratt

Christoph Grüter

Negative feedback

Duncan Jackson

Thomas Schlegel

Negative feedback

Negative feedback

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- Unrewarded (time-varying environment) [Robinson *et al. Nature* 2005; Bidari *et al. R.Soc.OS* 2019]

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We propose an alternative function for negative feedback signals,
variance reduction

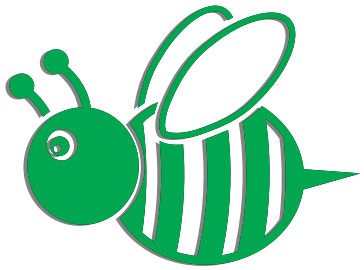
Behavioural evolution

What quantity should be optimised?

Bob Peterson

Collective ~~emigration~~ foraging model

Honeybee foraging

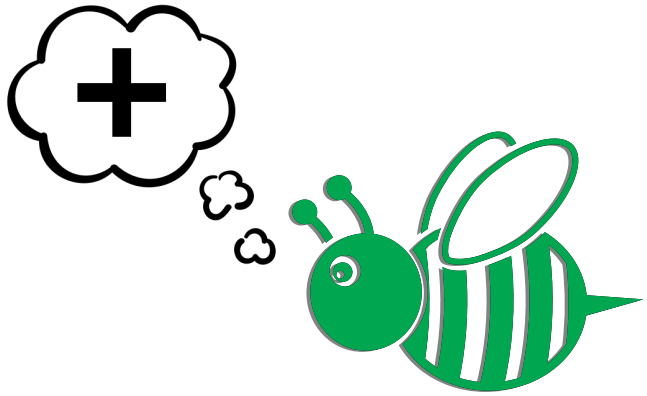


[Bidari *et al. R.Soc.O.S.* 2019, Seeley *at al. Science* 2012]

Collective ~~emigration~~ foraging model

Honeybee foraging

Discovery



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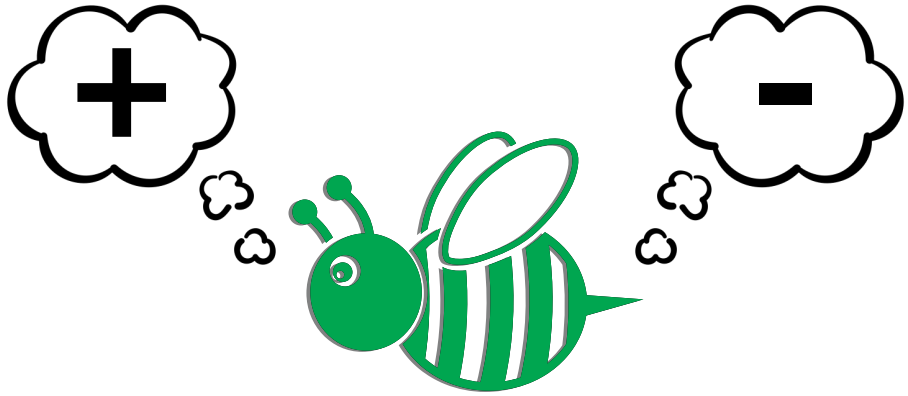
Collective ~~emigration~~ foraging model

Honeybee foraging

Discovery



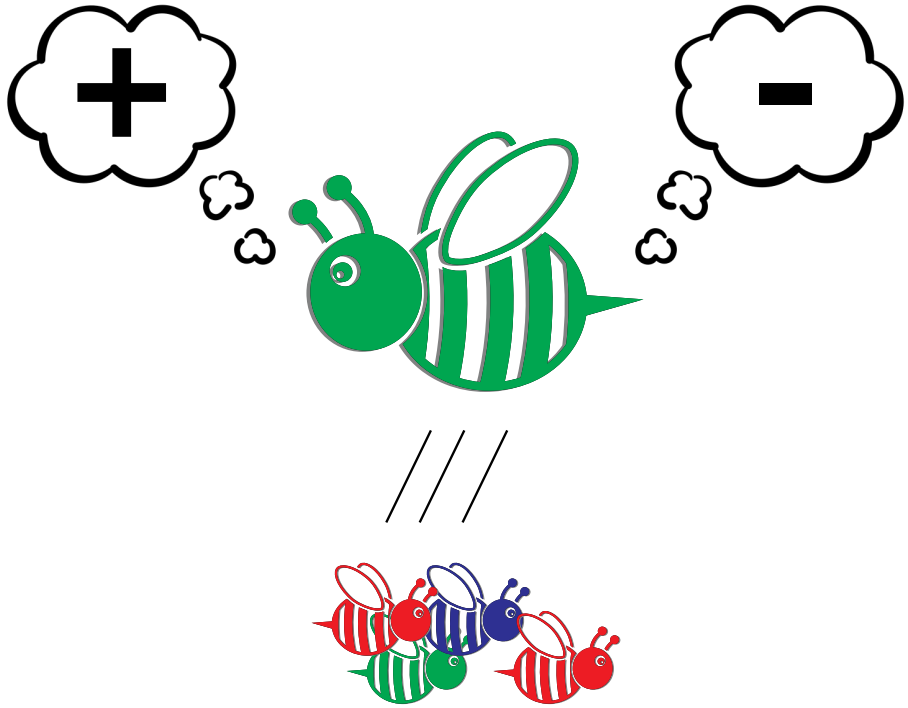
Abandonment

[Bidari *et al. R.Soc.O.S.* 2019, Seeley *at al. Science* 2012]

Collective ~~emigration~~ foraging model

Honeybee foraging

Discovery



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Collective ~~emigration~~ foraging model

Honeybee foraging

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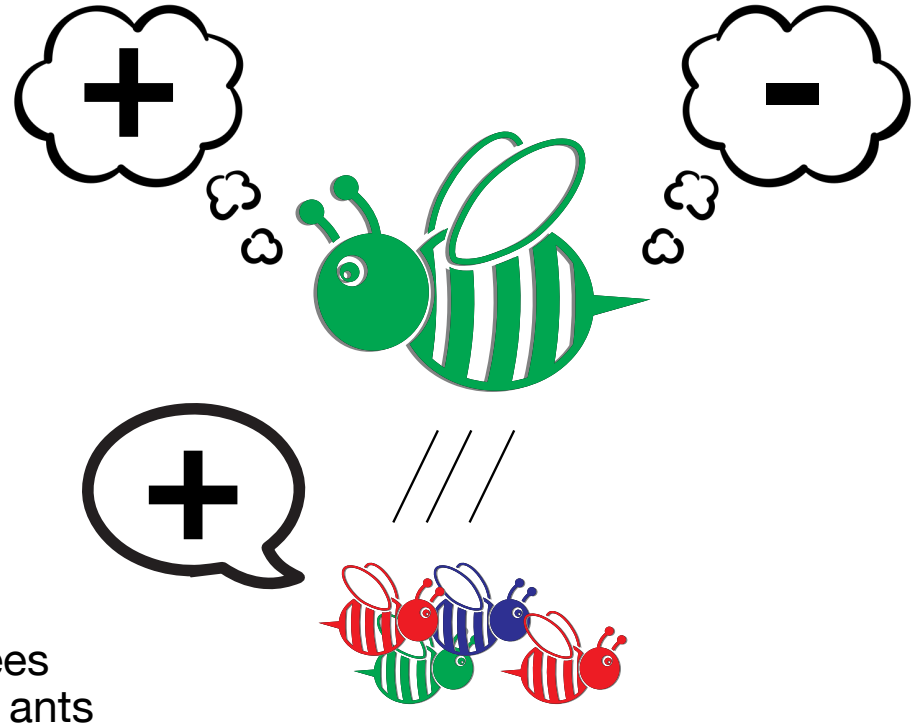


Abandonment

Recruitment

Positive feedback

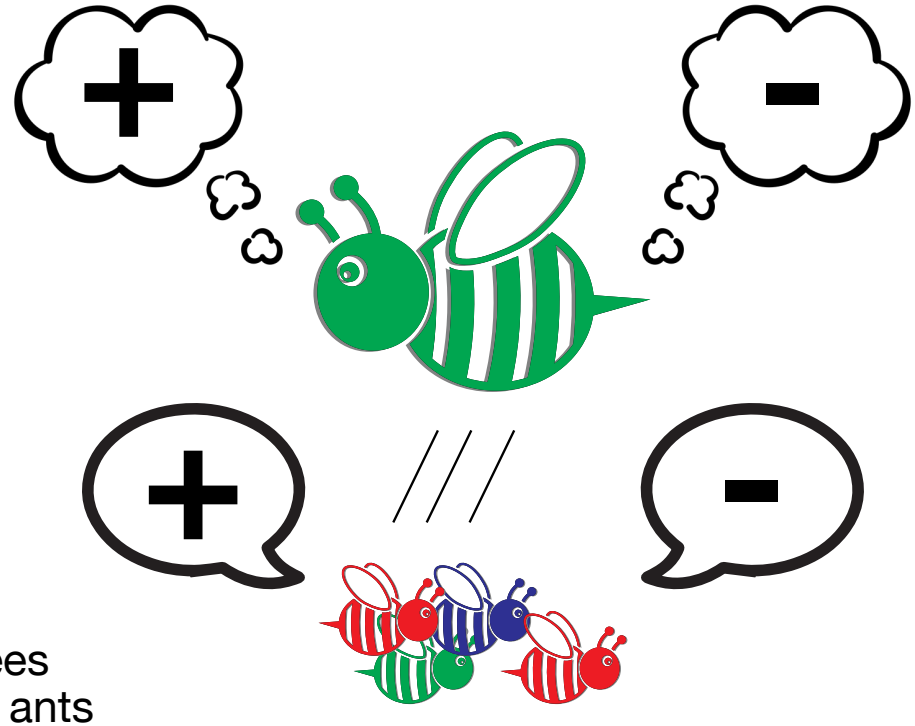
e.g. waggle dance in bees
pheromone trails in ants

[Bidari *et al. R.Soc.O.S.* 2019, Seeley *at al. Science* 2012]

Collective ~~emigration~~ foraging model

Honeybee foraging

Discovery



Abandonment

Recruitment

Positive feedback

e.g. waggle dance in bees
pheromone trails in ants

Inhibition

Negative feedback

e.g. stop signals in bees
repellent pheromone in ants

[Bidari *et al. R.Soc.O.S.* 2019, Seeley *at al. Science* 2012]

Collective foraging model

Chemical reaction model

Collective foraging model

Chemical reaction model

Insect committed to food source 

Collective foraging model

Chemical reaction model

Insect committed to food source 

Uncommitted 

Collective foraging model

Chemical reaction model

Insect committed to food source 

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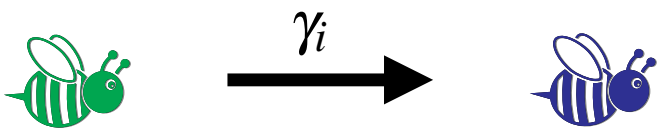
Discovery 

Collective foraging model

Chemical reaction model

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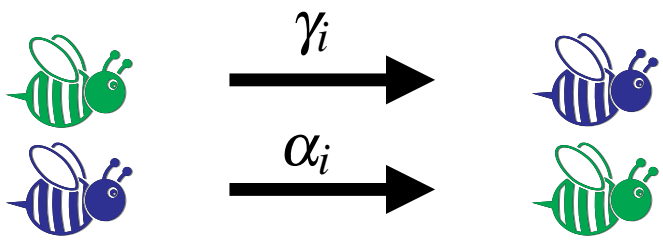
Discovery

Abandonment

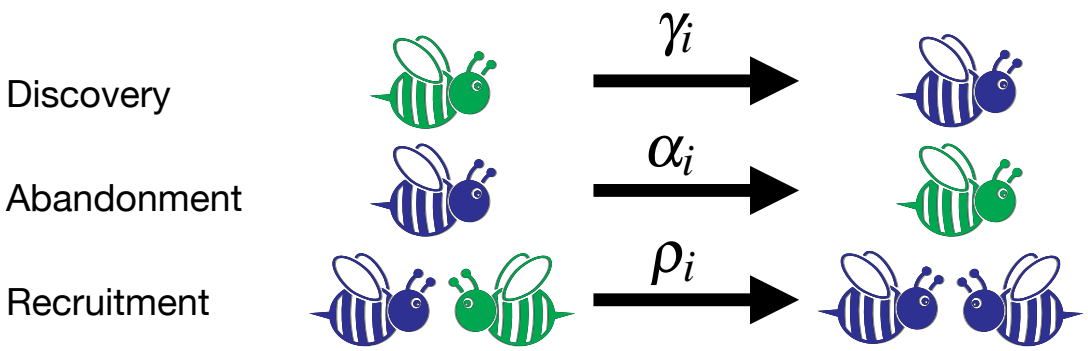


Collective foraging model

Chemical reaction model

Insect committed to food source

Uncommitted



Collective foraging model

Chemical reaction model

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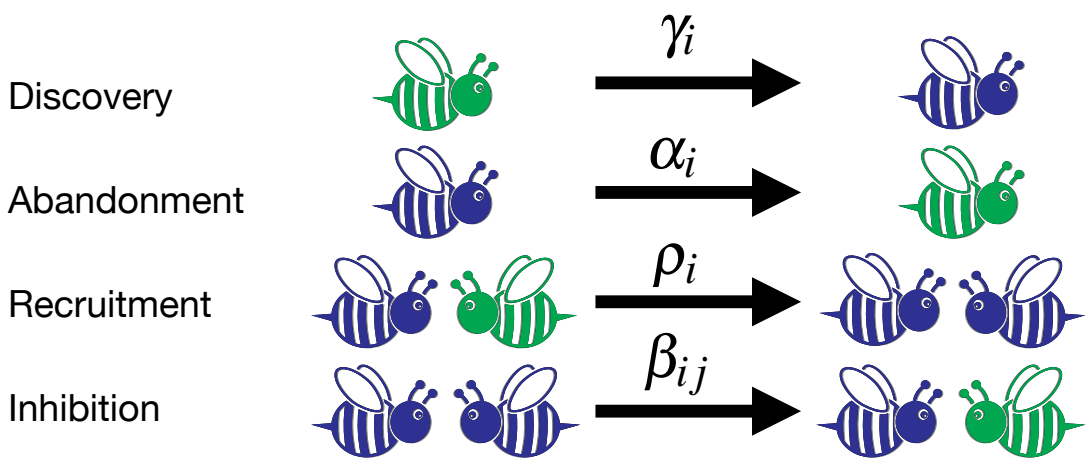


Collective foraging model

Chemical reaction model

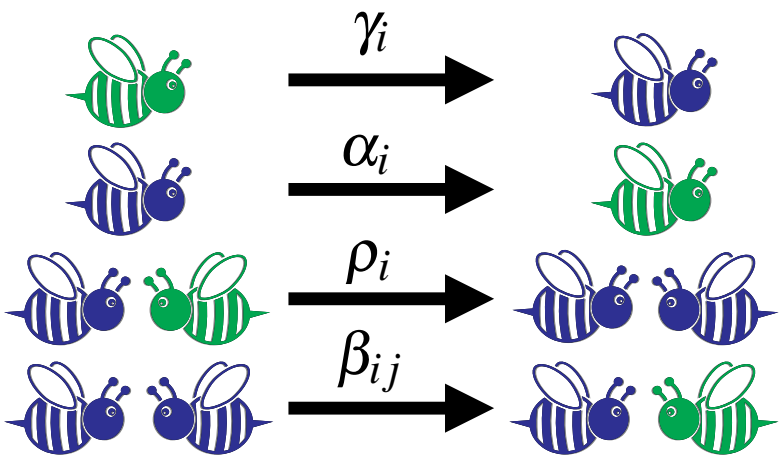
Insect committed to food source  Uncommitted 

Discovery

Abandonment

Recruitment

Inhibition



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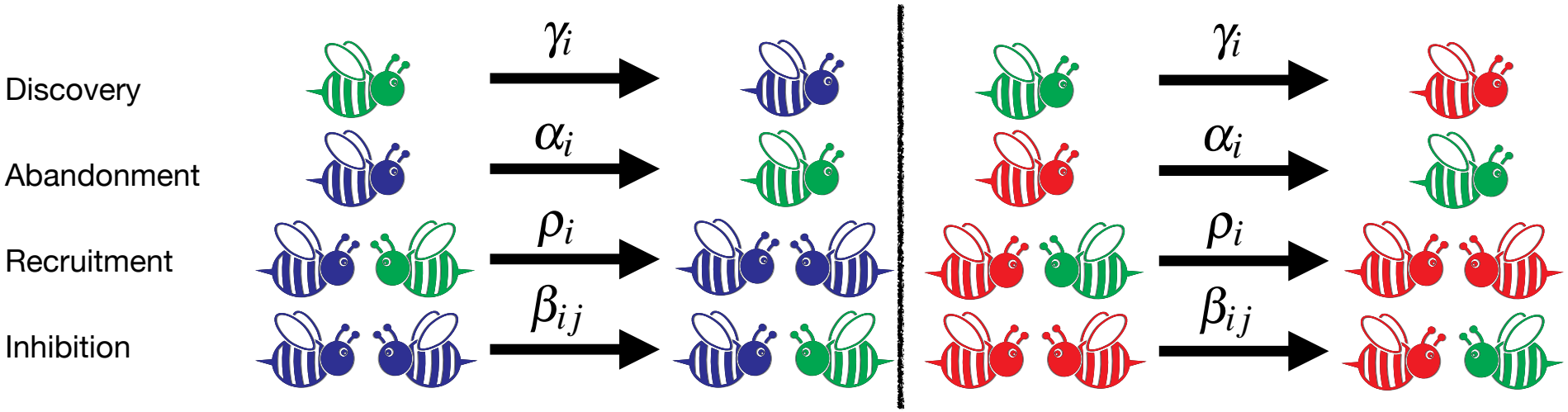
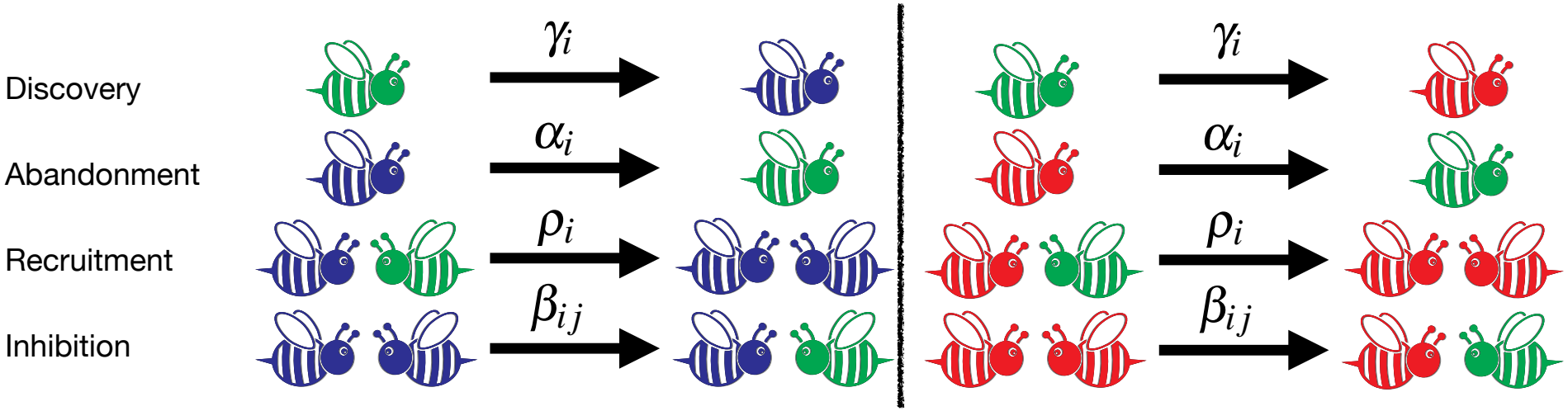


Collective foraging model

Chemical reaction model

Insect committed to food source  Uncommitted 

with quality: q_1 q_2



Collective foraging model

Chemical reaction model

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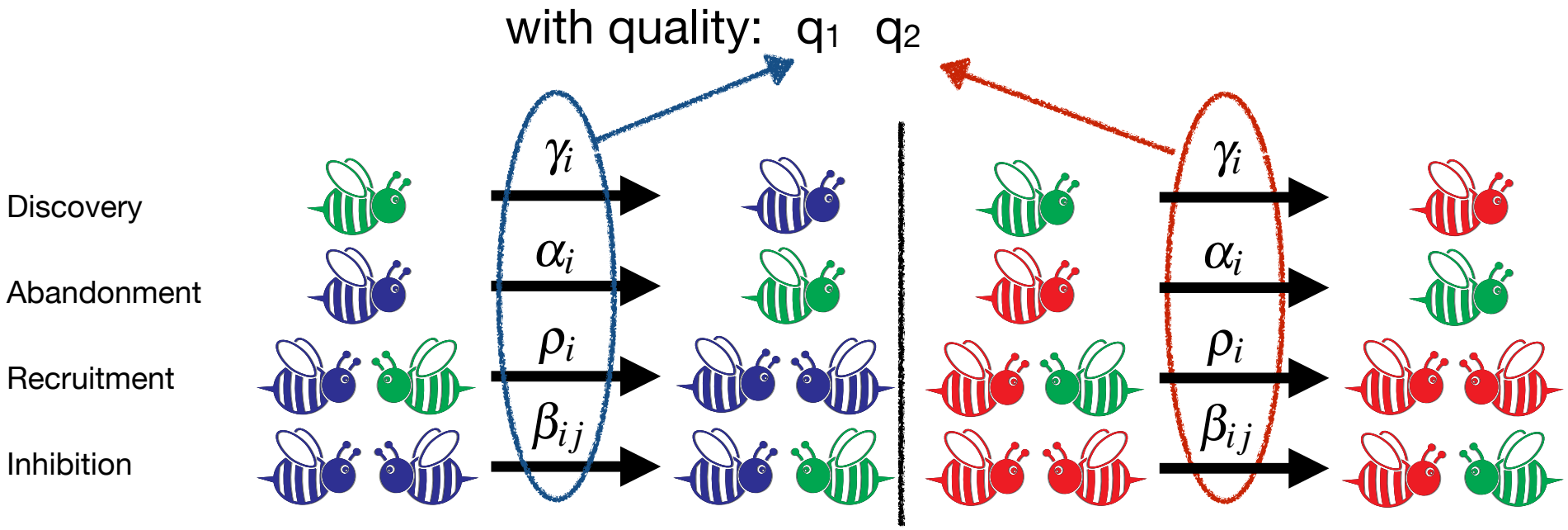
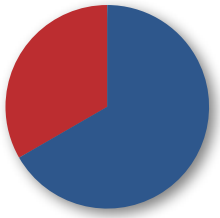


Collective foraging model

Chemical reaction model

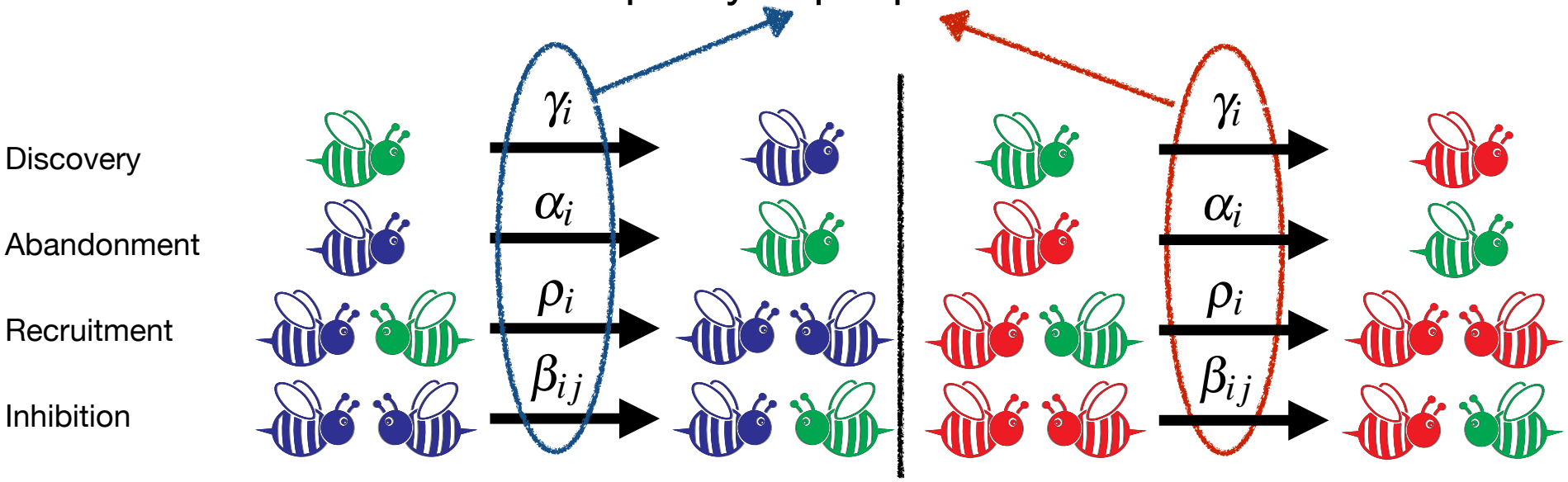
Group distribution



Insect committed to food source

Uncommitted

with quality: q_1 q_2



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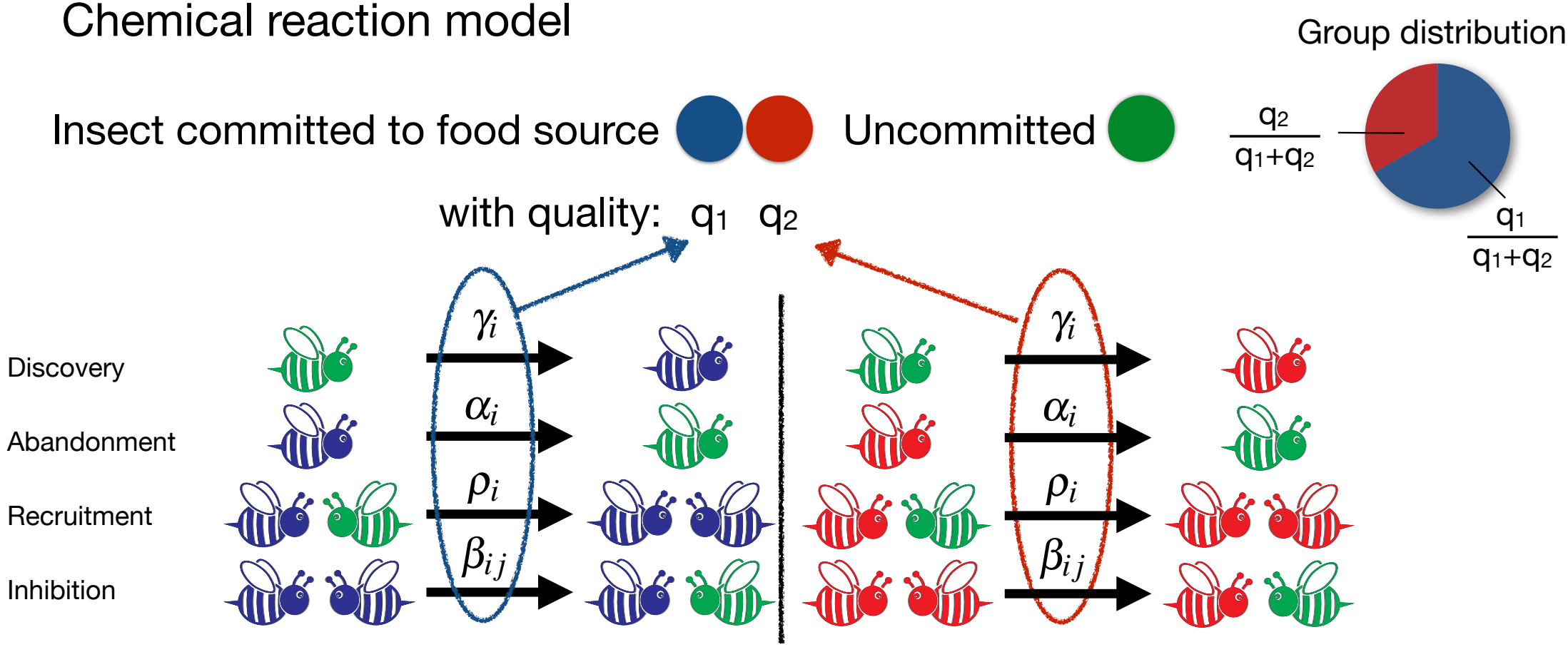
Chemical reaction model



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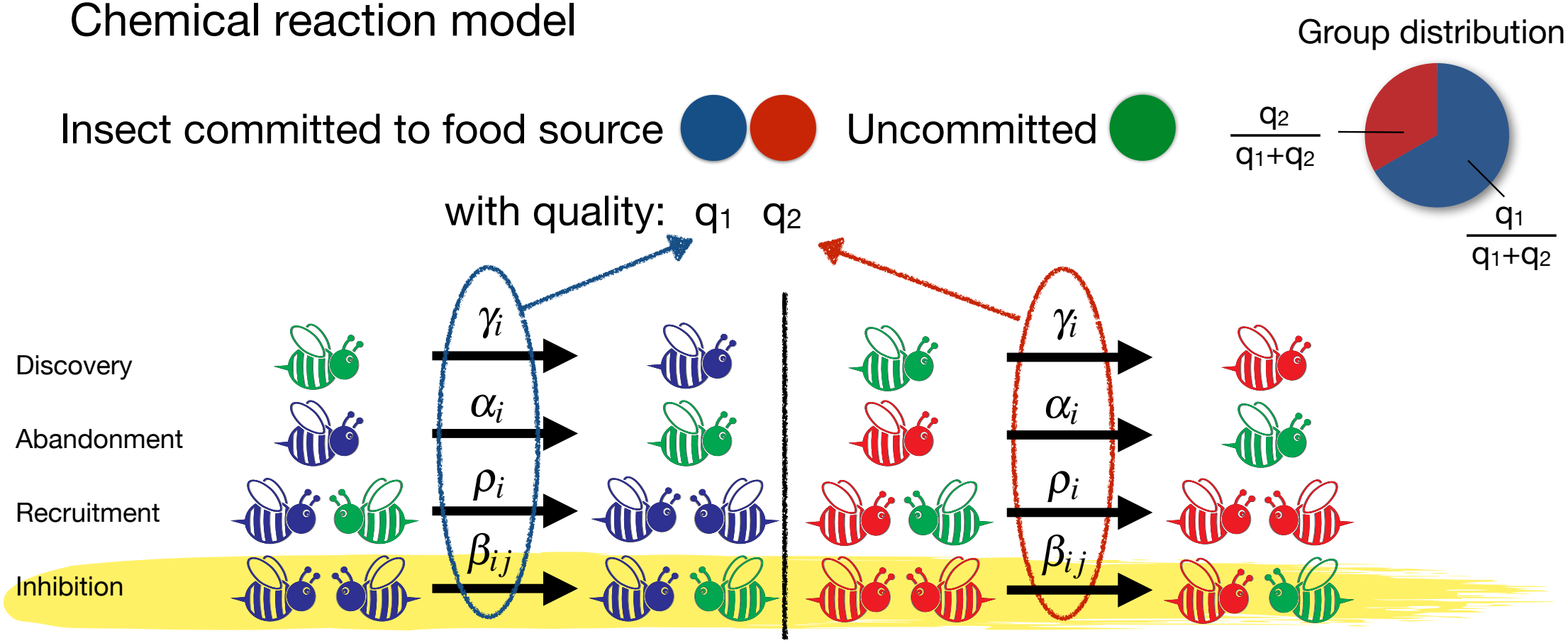
Chemical reaction model



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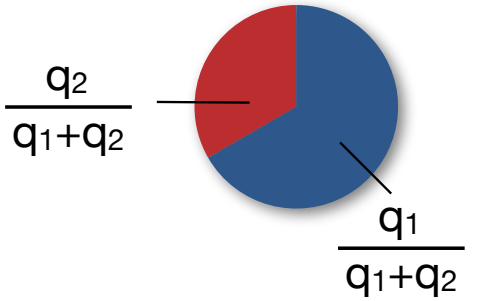
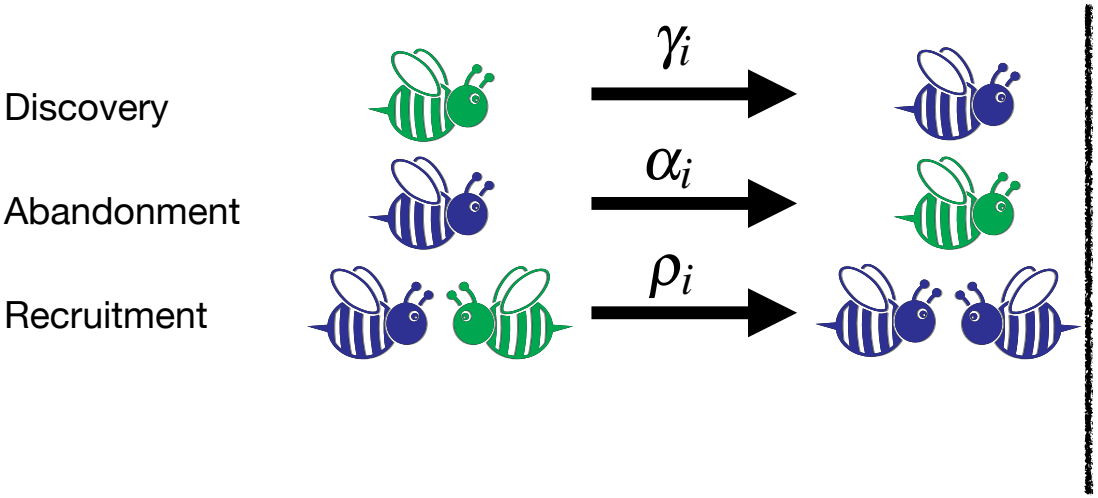


Model **without** negative feedback



Collective foraging model

Chemical reaction model

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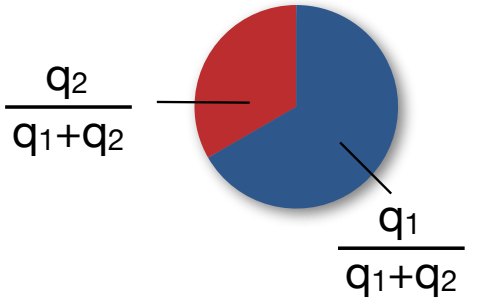
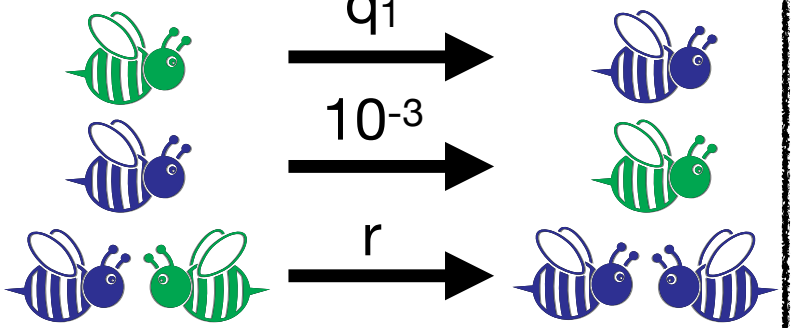


Model **without** negative feedback

Discovery

Abandonment

Recruitment



$q_1 \in [0,1]$

$r > 1$

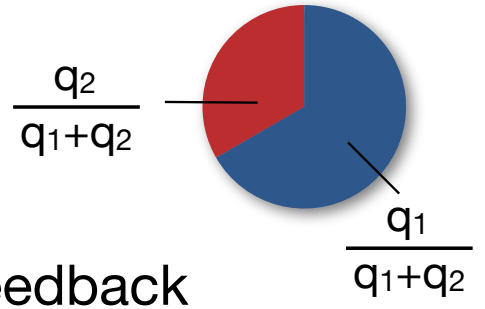
Collective foraging model

Chemical reaction model

Insect committed to food source

Uncommitted

Group distribution



Model **without** negative feedback

Discovery

Abandonment

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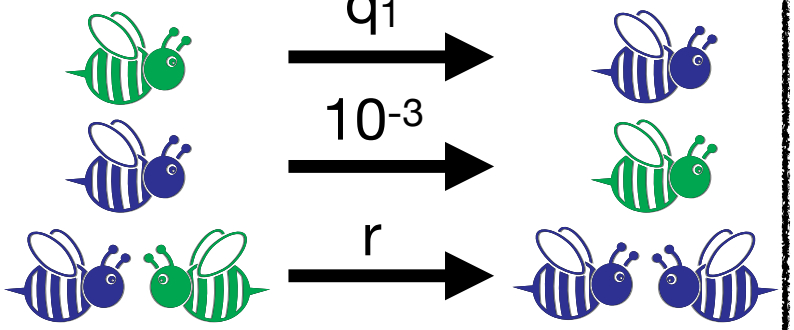


$q_1 \in [0,1]$

$r > 1$

Model **with** negative feedback

Collective foraging model

Chemical reaction model

Insect committed to food source

Uncommitted

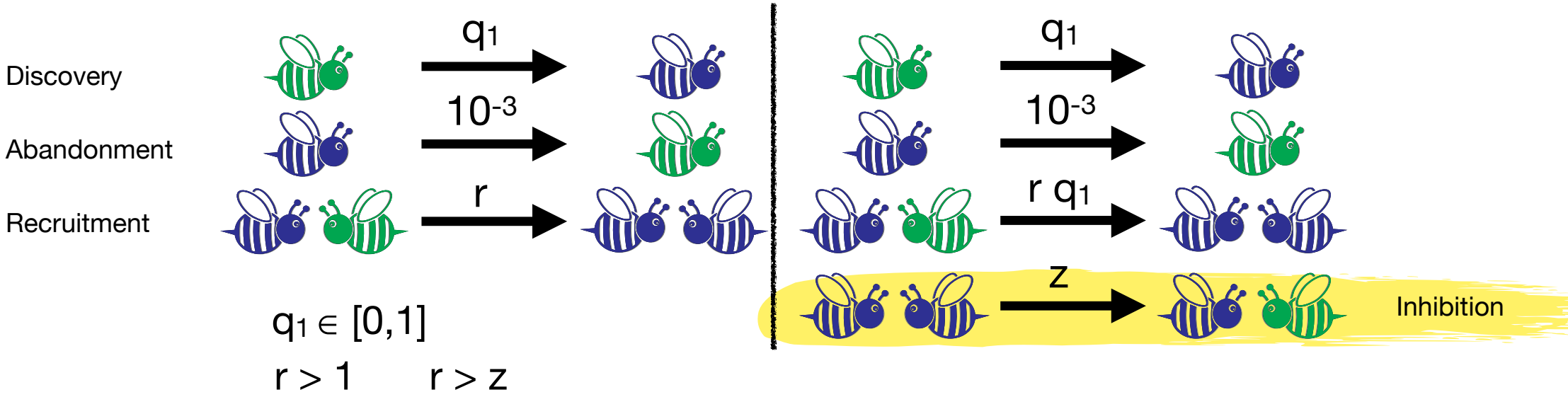
Group distribution

$\frac{q_2}{q_1+q_2}$

$\frac{q_1}{q_1+q_2}$

Model **without** negative feedback

Model **with** negative feedback



$q_1 \in [0,1]$

$r > 1 \qquad r > z$

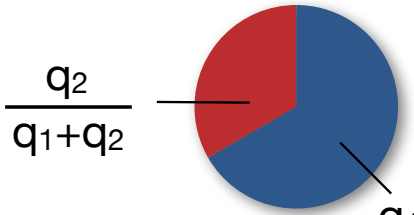
Collective foraging model

Chemical reaction model

Insect committed to food source

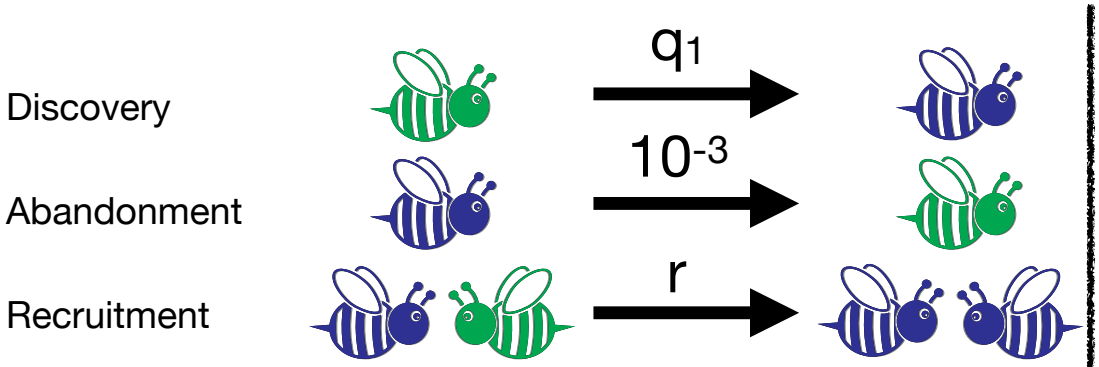
Uncommitted

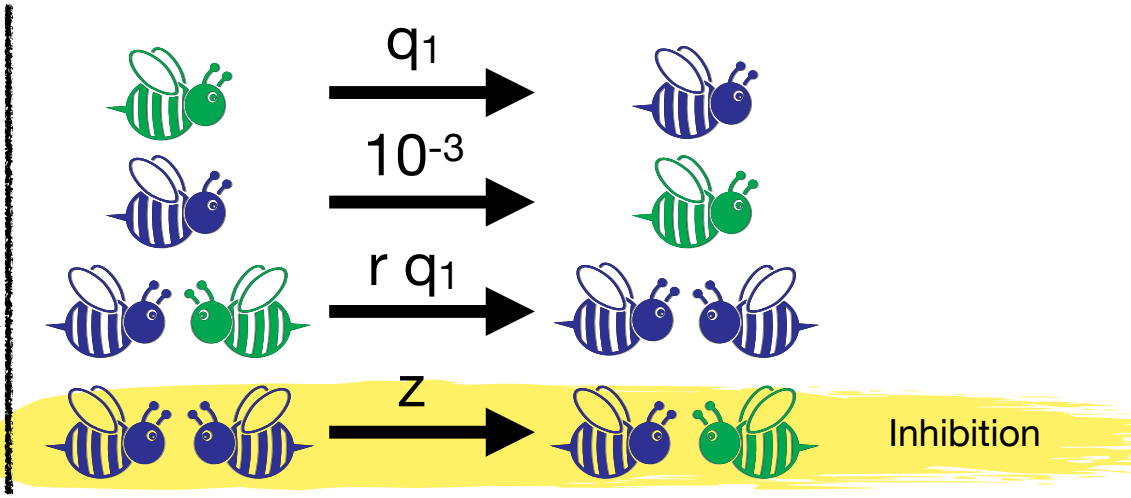
Group distribution



Model **without** negative feedback

Model **with** negative feedback





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$r > 1$ $r > z$

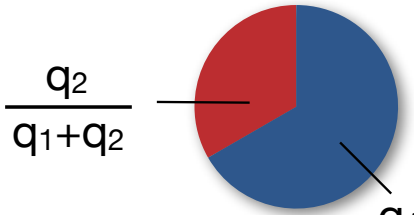
Collective foraging model

Chemical reaction model

Insect committed to food source

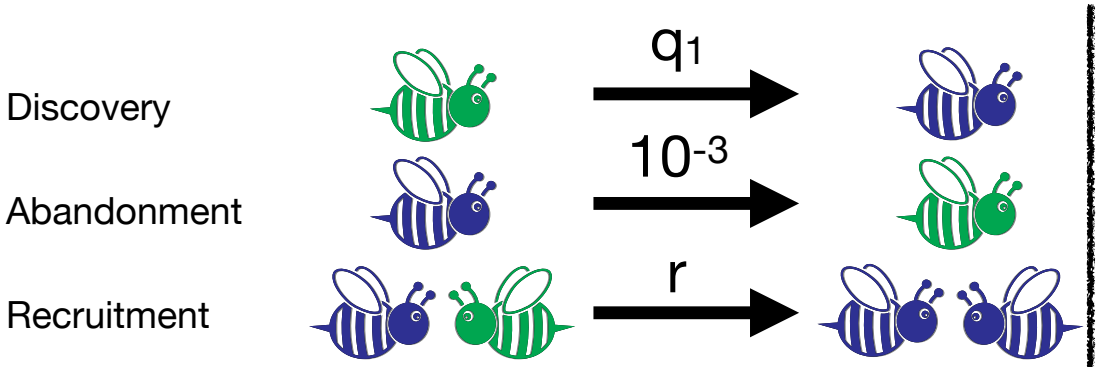
Uncommitted

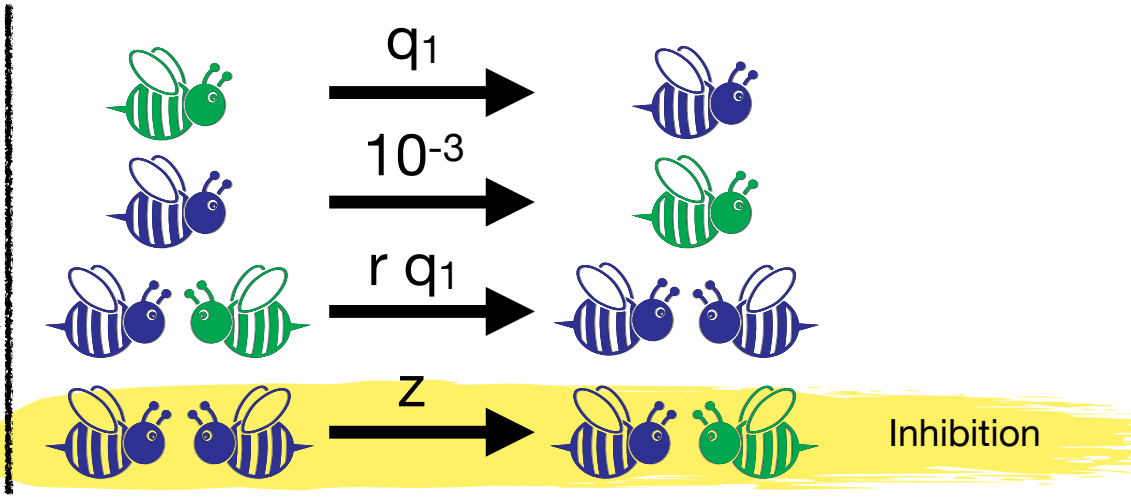
Group distribution



Model **without** negative feedback

Model **with** negative feedback





$q_1 \in [0,1]$

$r > 1$ $r > z$

Our analysis

Mean-field model of collective foraging

mumot.readthedocs.io

Model **without** negative feedback

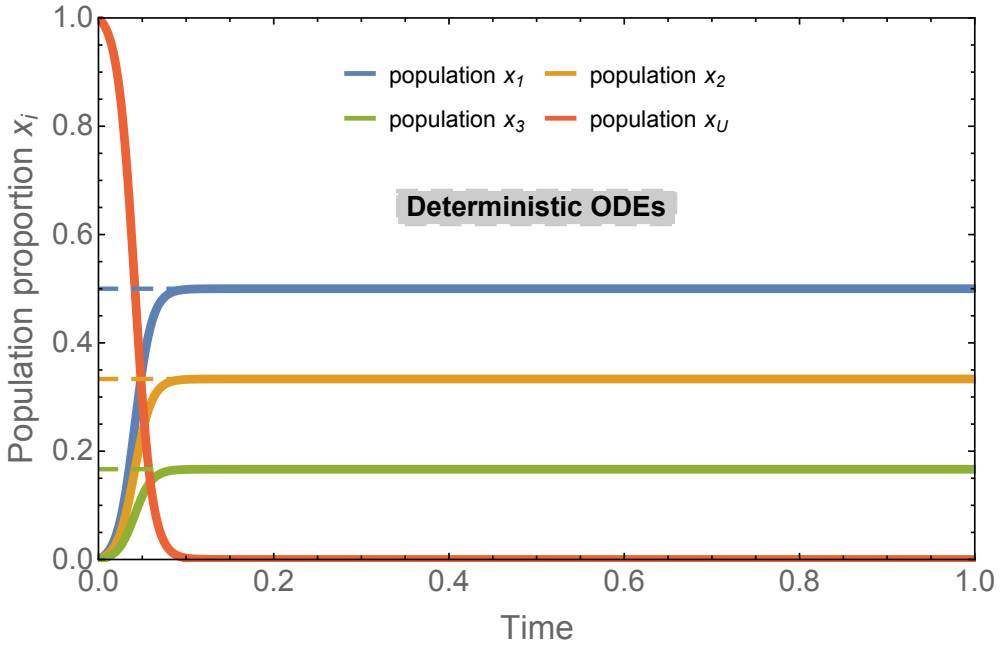
Model **with** negative feedback

Our analysis

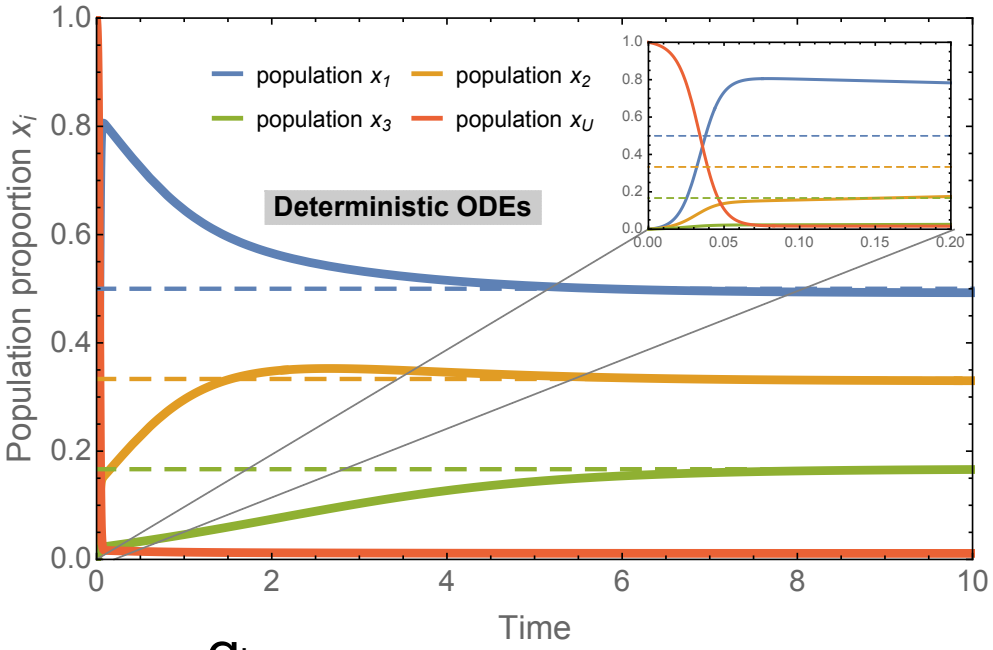
Mean-field model of collective foraging

mumot.readthedocs.io

Model **without** negative feedback

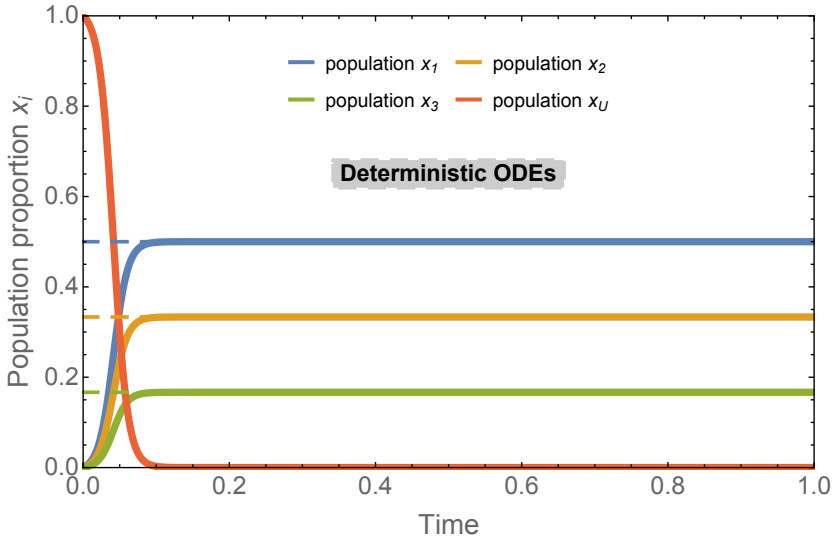


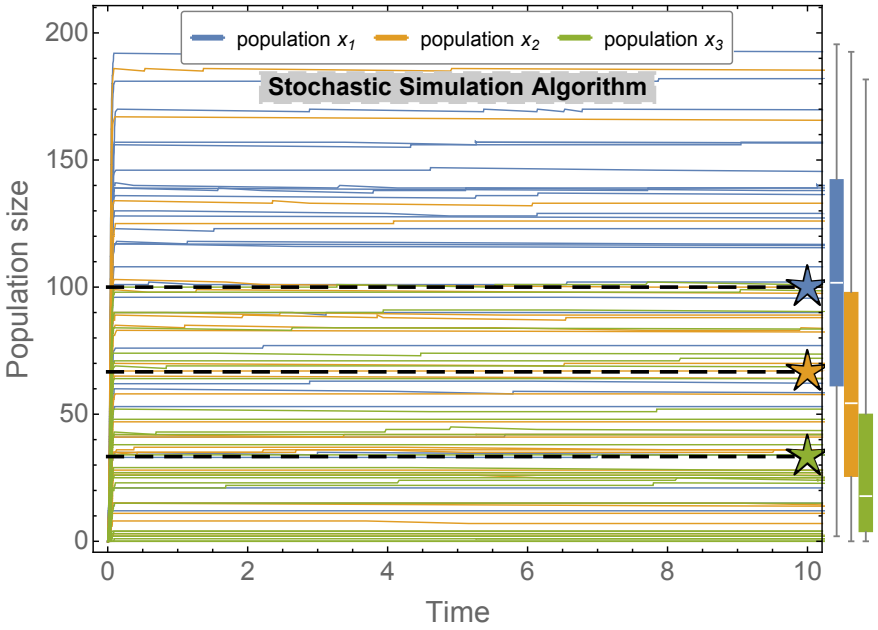
Model **with** negative feedback



$$\text{Final distribution} = \frac{q_i}{\sum_j q_j}$$

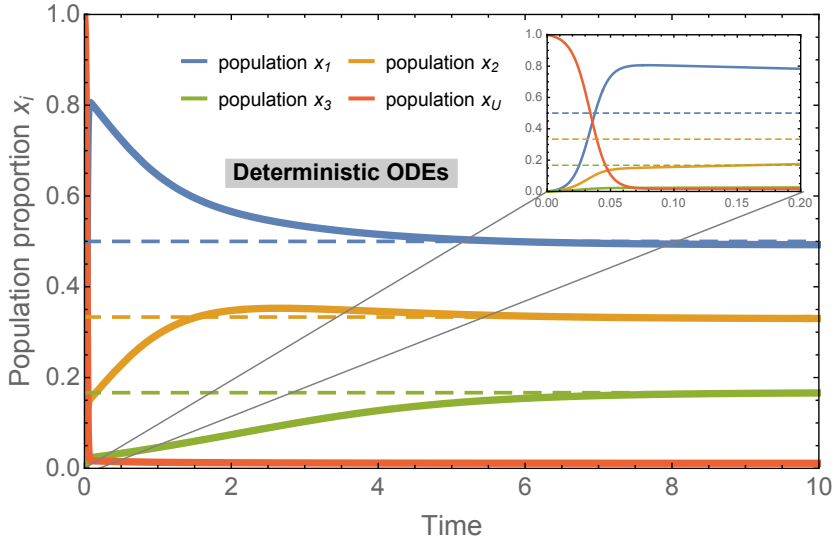
Model **without** negative feedback

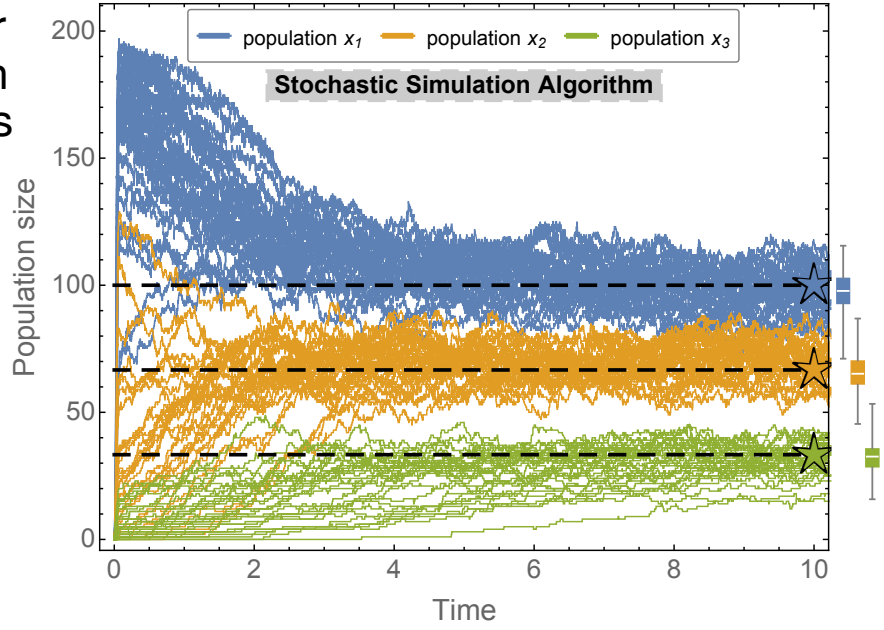




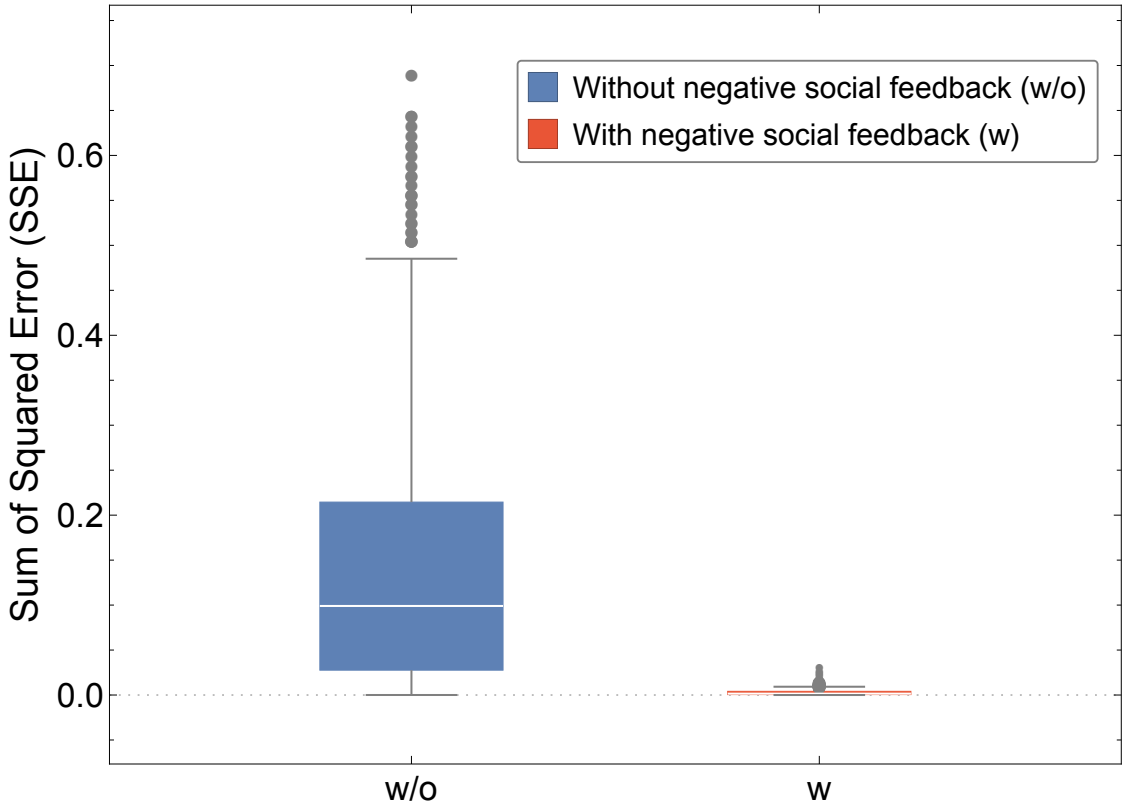
Results for model with 200 insects

Model **with** negative feedback



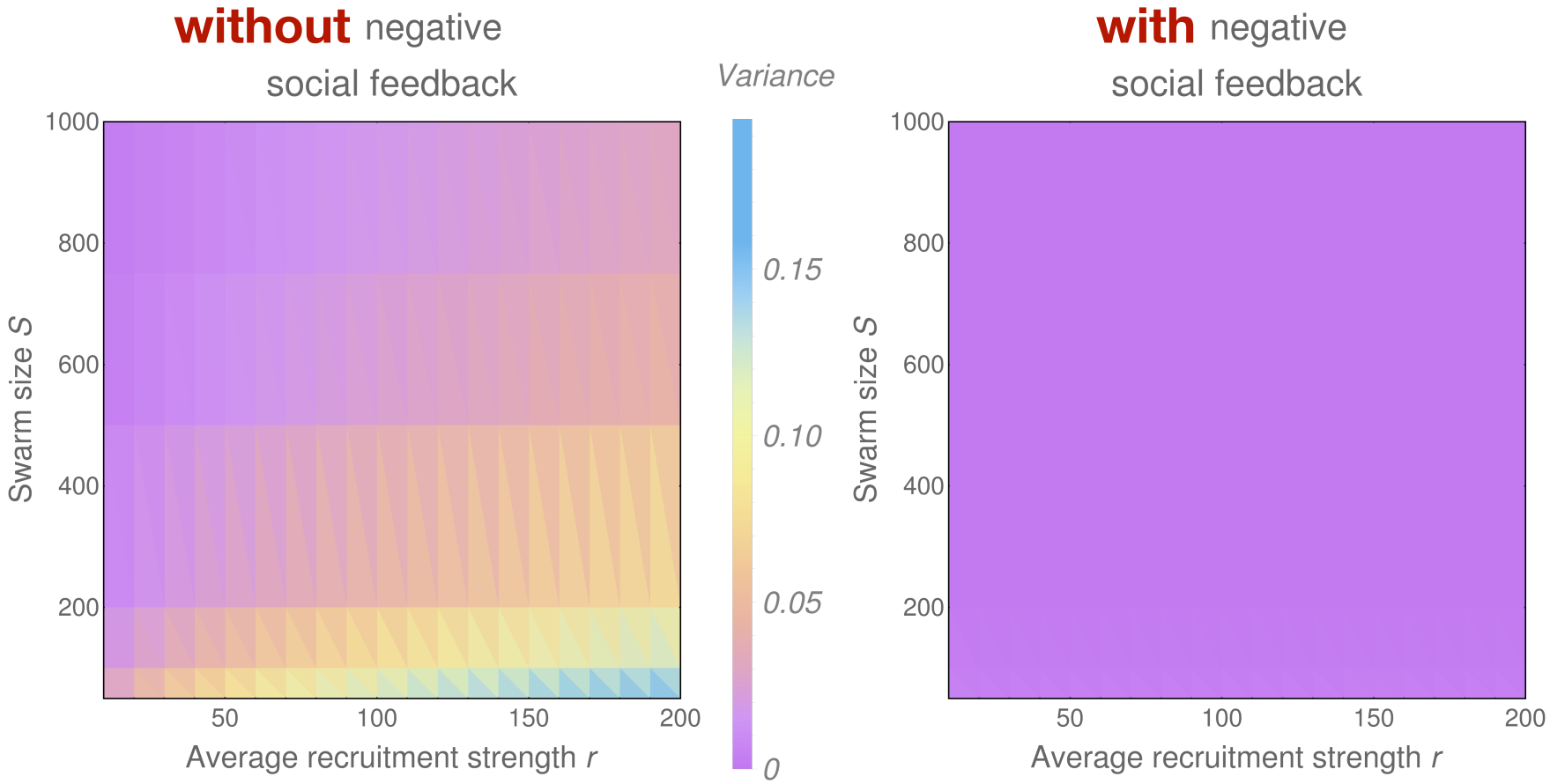


Sum of Squared Error



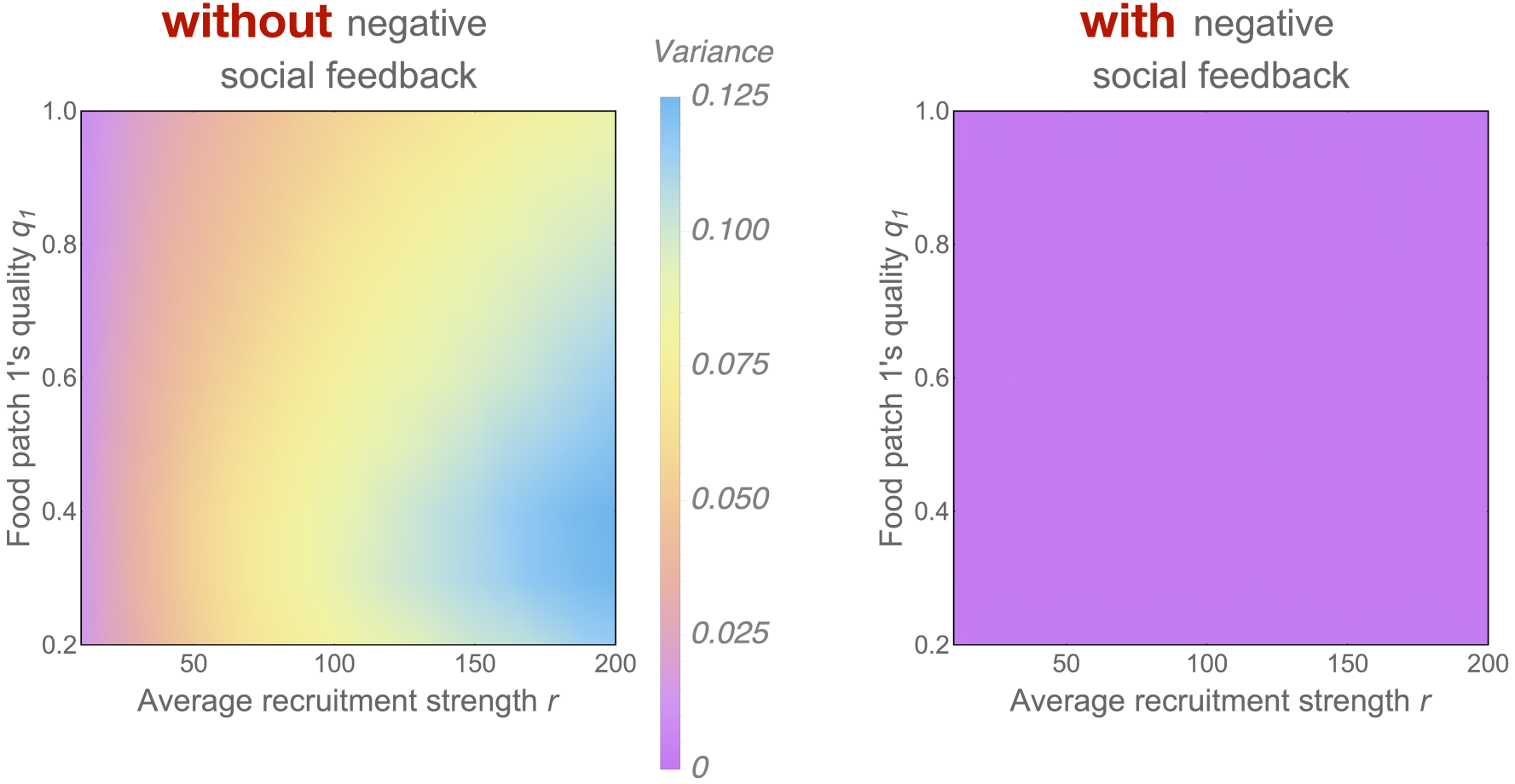
Sensitivity analysis

Varying the recruitment strength and system size



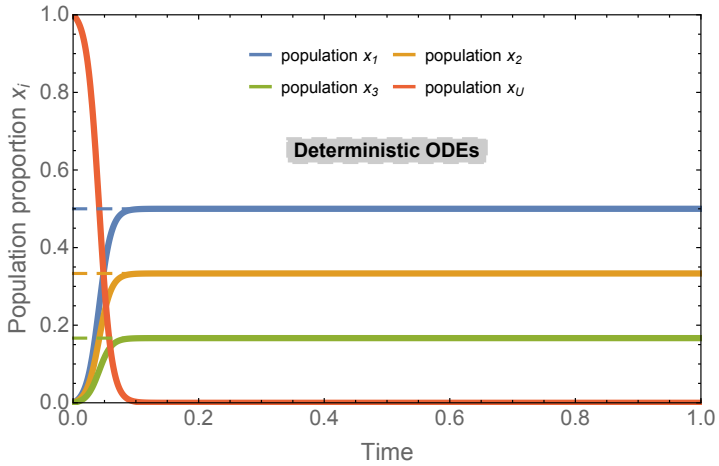
Sensitivity analysis

Varying the recruitment strength and food patch quality

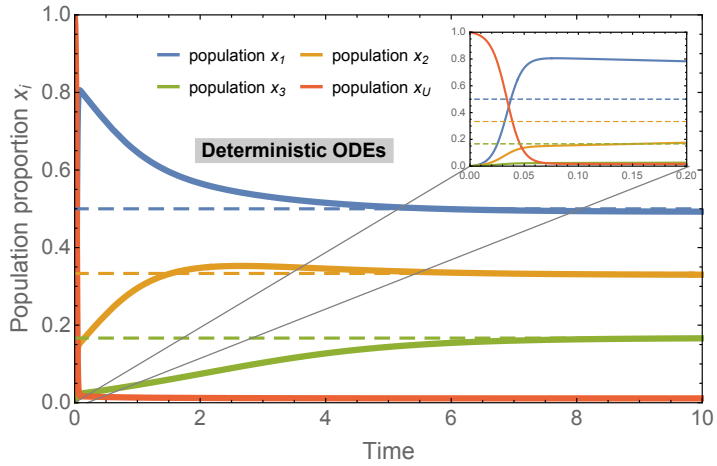


Speed of convergence

Model **without** negative feedback



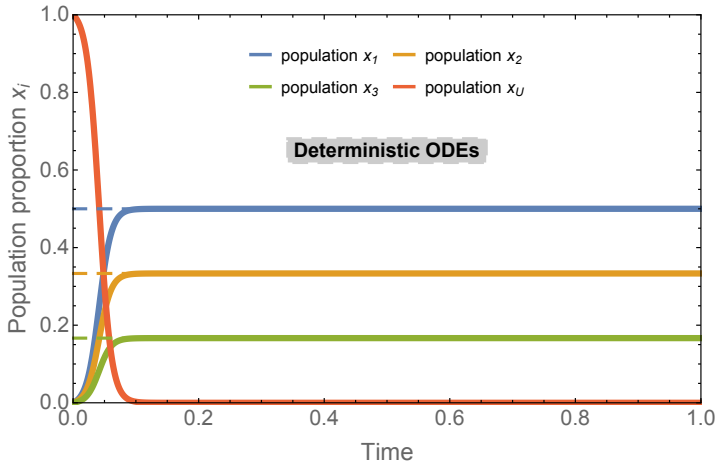
Model **with** negative feedback



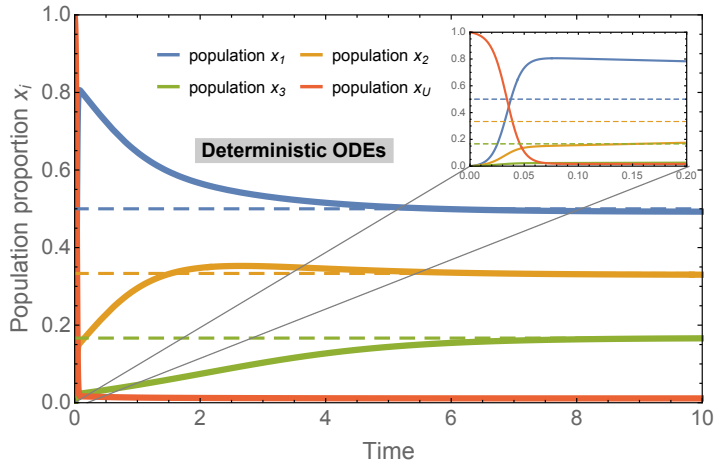
Speed of convergence

The model without negative feedback looks quicker

Model **without** negative feedback



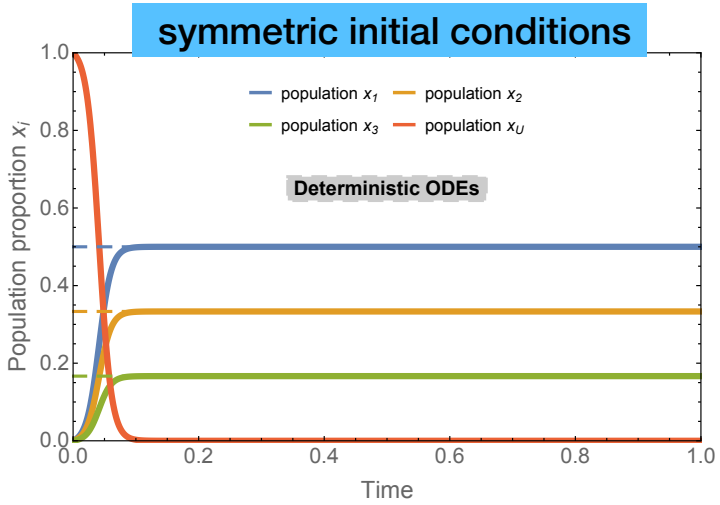
Model **with** negative feedback



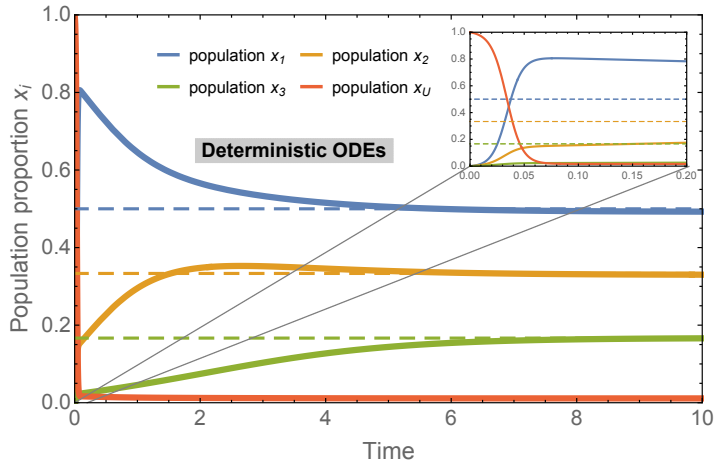
Speed of convergence

The model without negative feedback looks quicker

Model **without** negative feedback



Model **with** negative feedback



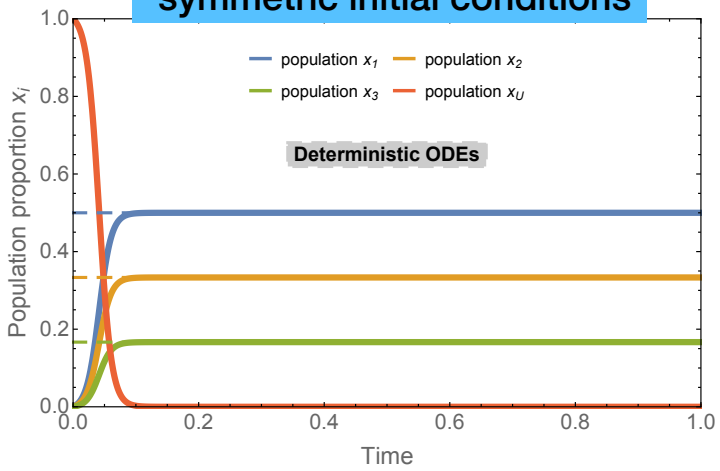
Speed of convergence

The model without negative feedback looks quicker

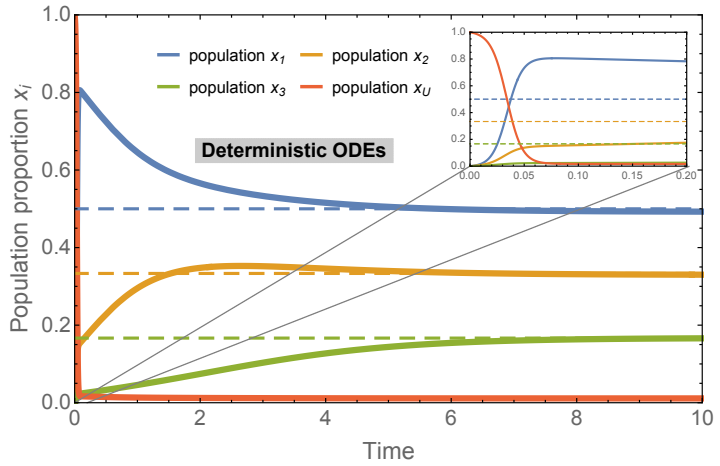
symmetric initial conditions

asymmetric initial conditions

Model **without** negative feedback



Model **with** negative feedback



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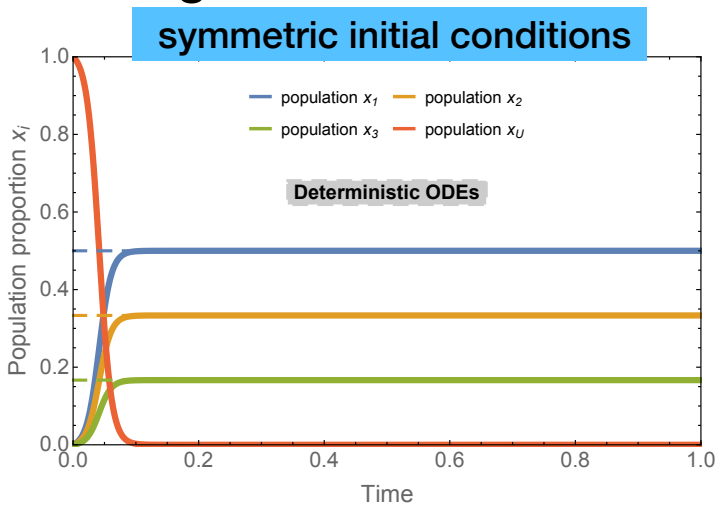
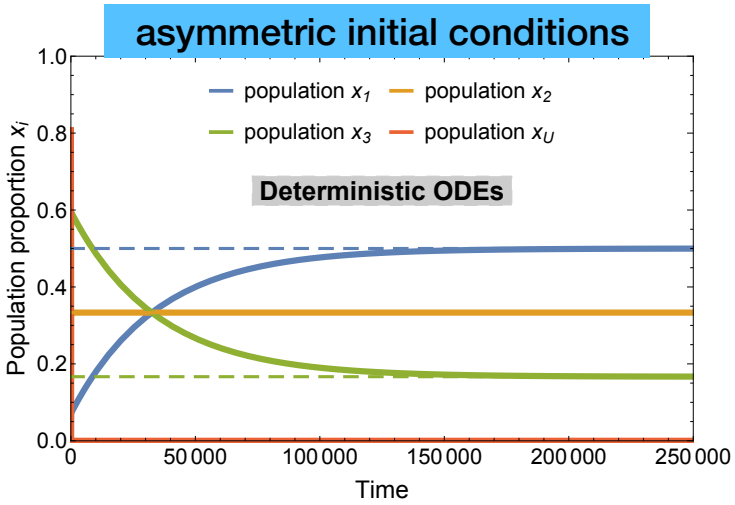
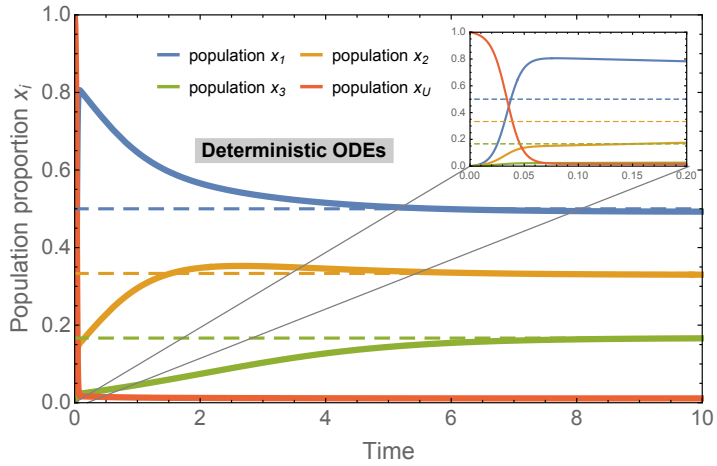
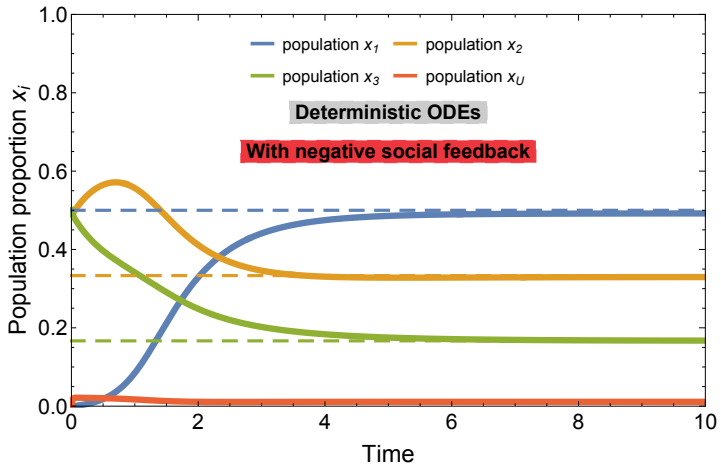






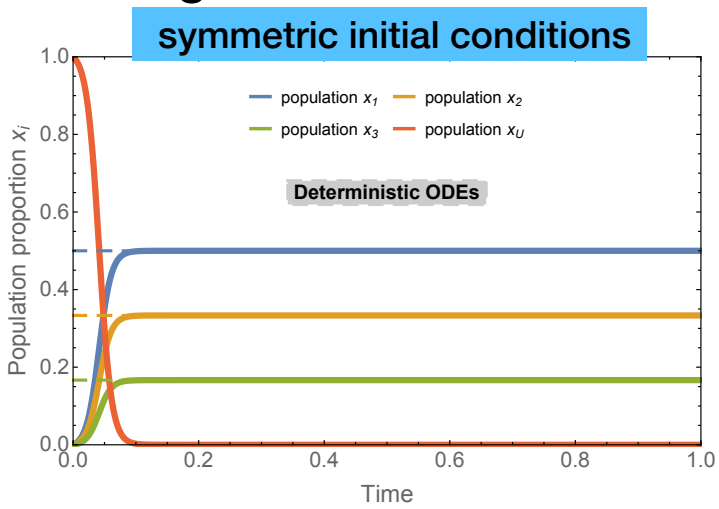


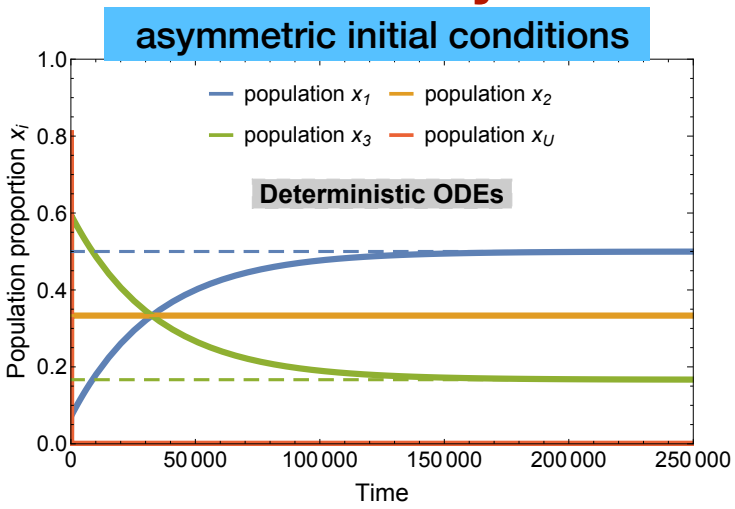
Speed of convergence

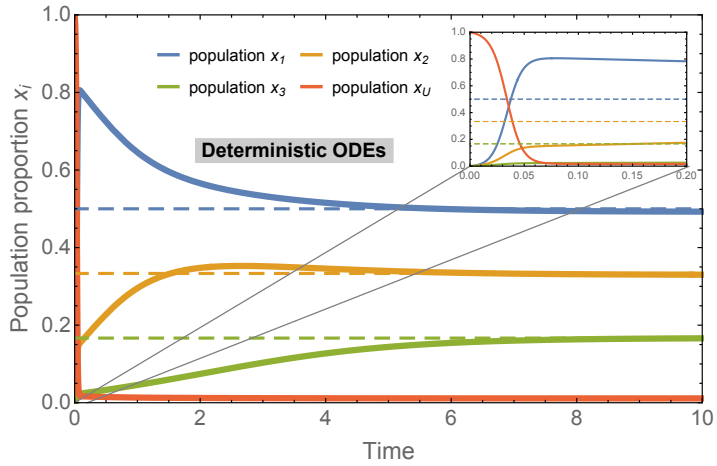
The model without negative feedback looks quicker **but it is actually slower**

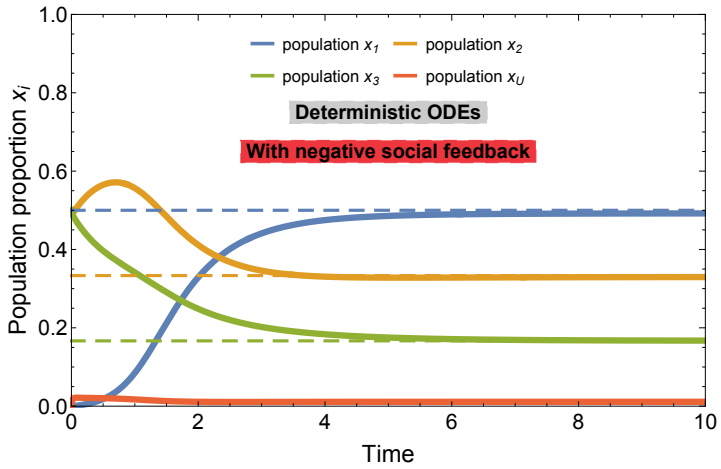
Model **without** negative feedback

Model **with** negative feedback



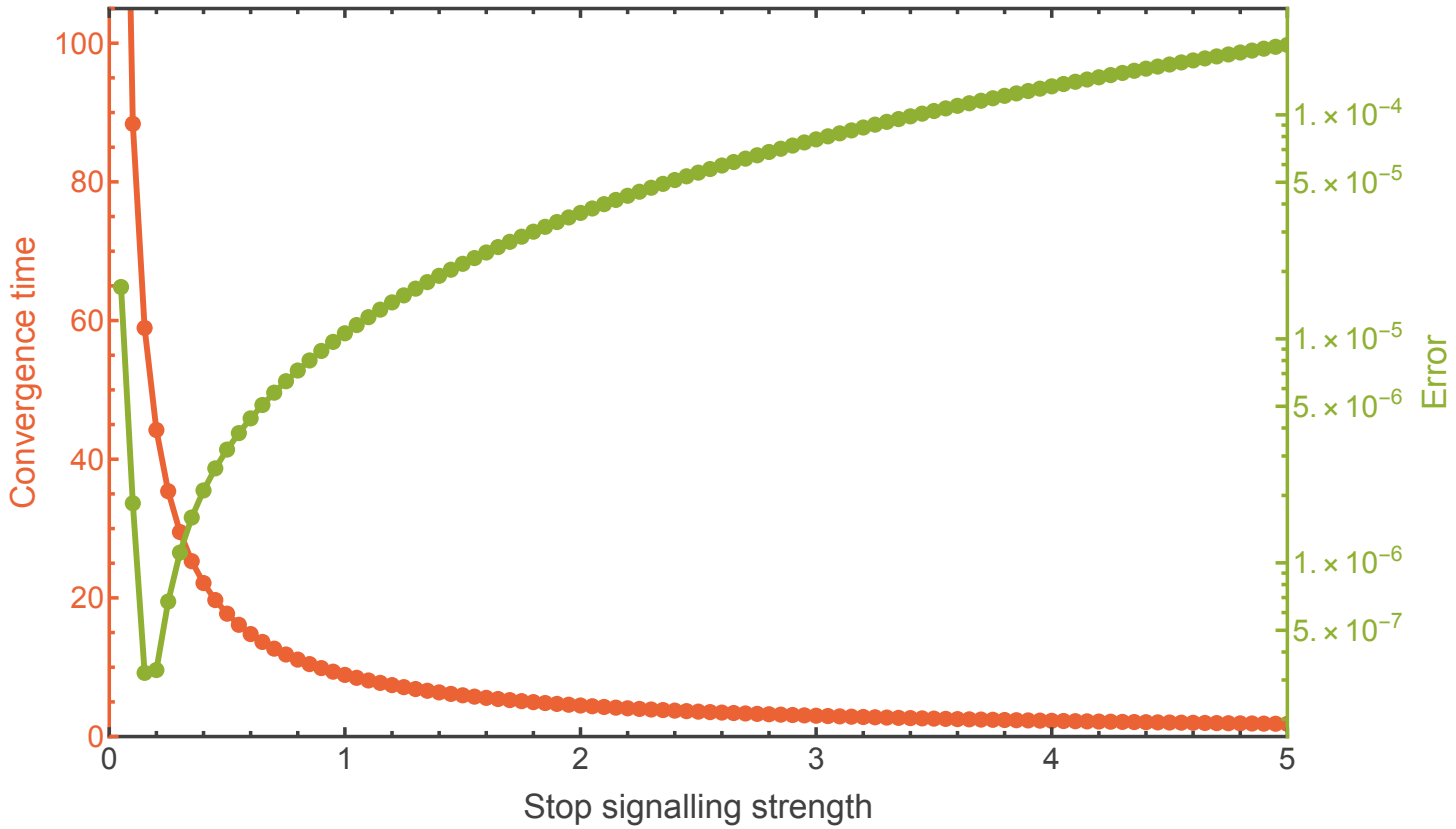






Speed-robustness trade-off

Negative feedback strength regulates the trade-off



Negative feedback

as a variance reduction mechanism

Negative feedback

as a variance reduction mechanism

We know negative feedback is an efficient mechanism to allow social insects:

- **break symmetry** in collective decisions [Seeley *et al.* Science 2012, Reina *et al.* PhyRev. E 2015]
- **adapt** to time-varying environments [Nieh *Curr. Biol.* 2010, Robinson *et al. Nature* 2005,…]

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as a variance reduction mechanism

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We find an additional important role of negative feedback: **variance reduction**

- similar strategy found in **gene networks** or **electronics**
- it could explain why, even in static conditions, honeybees **always deliver** a small quantity of stop signals to foragers visiting the same forage patch [Lau & Nieh *Apidologie* 2010]

An evolutionary framework for collective behaviour

Tinbergen, Behavioural Ecology, and Collective Behaviour

	Dynamic View	Static View
Proximate View	Behavioural development	Behavioural mechanism
Ultimate View	Behavioural evolution	Behavioural function

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Negative feedback

Progression in the evolution of collective foraging

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Individual foragers
—no feedback—

low efficiency

Negative feedback

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Recruitment
—positive feedback—

efficient but noisy

Negative feedback

Progression in the evolution of collective foraging

Individual foragers
—no feedback—

low efficiency

Recruitment
—positive feedback—

efficient but noisy

Inhibition
—negative feedback—

low variance + adaptive

Thanks

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- Angelo Pirrone, University of Liverpool
- Papers: bet-lab.sites.sheffield.ac.uk

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