Intelligence in Animals and Machines

Seminar, Week 5

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Intro things

Human collective decision-making

Ant collective decision-making

Discussion

Intro things

- Any questions about last week/the lecture?

Assessment 1

- Two options – paper report or modelling report

- Module is designed around modelling report
  - 2 x lab classes
  - 1 x seminar

- Template can be found on Canvas

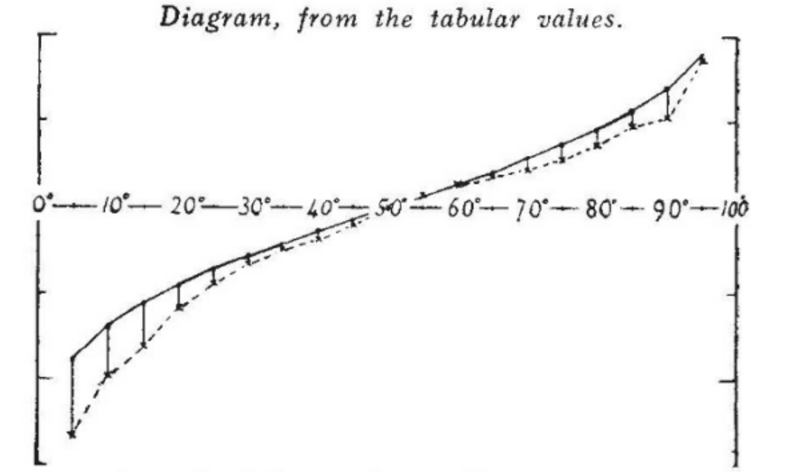
Wisdom of the crowds

Aristotle

For it is possible that the many, though not individually good men, yet when they come together may be better, not individually but collectively

Galton (1907), *Nature*

- Guess the weight of the ox
- Correct response was 1198lbs
- Average response was 1207lbs (error = 0.75%)



The continuous line is the normal curve with p.e.=37.
The broken line is drawn from the observations.
The lines connecting them show the differences between the observed and the normal.

Human collective decision-making

<u>Very difficult to study (properly):</u>

- Verbal vs non-verbal communication
- Different biases, varying degrees of (domain-specific!) competence
- Ability to express one's confidence varies too

Easier to study in species without language

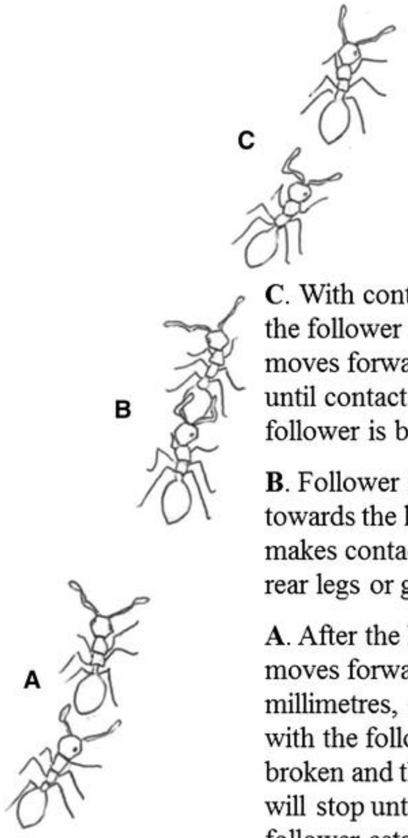
See Bahrami et al (2012). *Phil Trans B if* you're interested

Rock ants

- Temnothorax albipennis (rock ant)
- Nest in rocky areas e.g. rock cavities in cliffs or under stones
- Queen (reproduces); lots of workers (F); males are for reproduction
- Some workers are idle; some are generalists; some are specialists. High variability in work ethic!

Tandem runs

- One ant (leader) leads a naïve ant (follower) to a new resource/nest site (or sometimes to raid other colonies)
- First recorded 1896, present in many ant species
- Differs from using pheromone trails (ants follow -> return to nest with food, dropping more pheromones)
- Seems more common in colonies too small to use the above



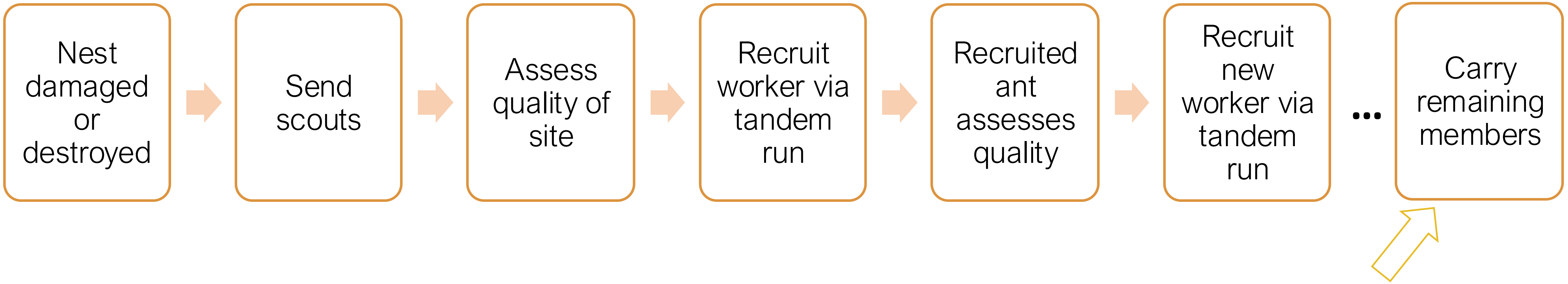
C. With contact from the follower the leader moves forward again until contact with the follower is broken.

B. Follower moves towards the leader and makes contact with her rear legs or gaster.

A. After the leader moves forward a few millimetres, contact with the follower is broken and the leader will stop until the follower establishes contact.

e.g. Franklin (2013), *Insects Sociaux*

Moving house

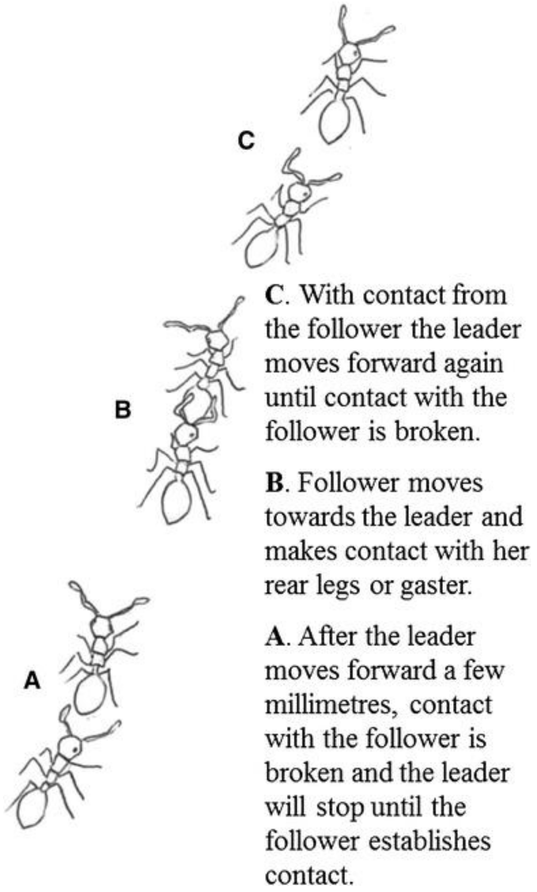


Switch to carrying = quorum number

e.g. Franklin (2013), *Insects Sociaux*

House-hunting

- Model for collective decision-making
- Race to quorum? (Mallon et al, 2001)
  - Multiple sites with multiple tandem runs
  - When members start being carried, terminate search
  - Quorum sensing via encounters with nest mates? (Pratt, 2005)
- But sometimes nests far away still win!



e.g. Franklin (2013), *Insects Sociaux*

Paper (optional reading)

PROCEEDINGS OF THE ROYAL SOCIETY B

Proc. R. Soc. B (2009) **276**, 2635–2641
doi:10.1098/rspb.2009.0350
Published online 22 April 2009

Do ants make direct comparisons?

Elva J. H. Robinson*, Faith D. Smith, Kathryn M. E. Sullivan and Nigel R. Franks

School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, UK

Research question

How do ants select new nests?

1. Direct comparison (compare the quality of two nests against each other)
2. Sequential comparison (compare the quality of each encountered nest against an internal threshold)
3. Recruitment latency

Method

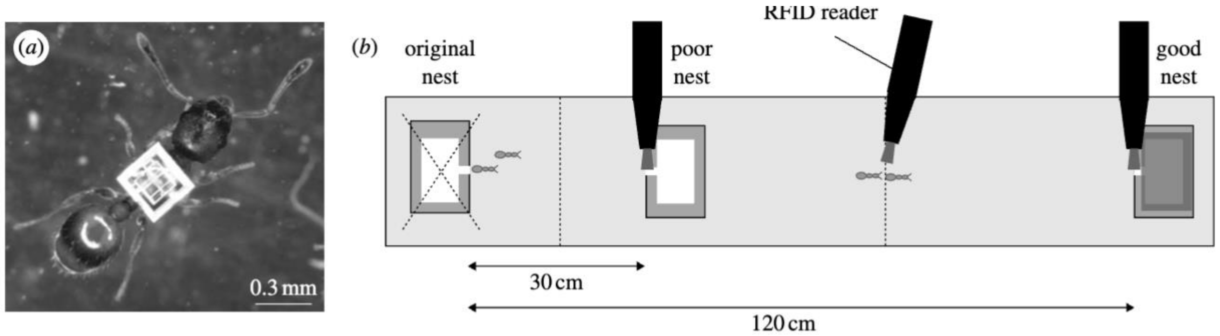


Figure 1. Experimental procedure using RFID technology. (a) *Temnothorax albipennis* worker with RFID tag. (b) Experimental arena (18×180 cm) with original nest (destroyed at the start of the trial) and two new nests. The good nest has a red filter making the interior dark. Dashed lines indicate recording points for tandem runs (at 15 and 45 cm).

- 9 x colonies; 100-200 workers each
- Conditions: Light nest (clear lid) & dark nest (red filter)
- Experiment lasted until migration was complete OR 5hrs had elapsed
- Control condition: both nests are identical (the good nest)
- Recruitment latency = time from entering a nest to when the same ant leads a tandem run to that nest

Question

What behaviours or patterns would you expect to see if ants make:

- direct comparisons?
- sequential comparisons?
- or if recruitment latency determines nest selection?

Results

- 4/9 colonies chose the (far) good nest; 3/9 chose the (near) bad nest; 2/9 were split
- Control condition: 14/15 chose the near nest; 1 chose the far nest; 0 were split
- Significantly different from control, BUT was good > bad?
- No difference in recruitment latencies between near & far nests
- 27 +/- 11% of ants visited more than 1 nest

Results

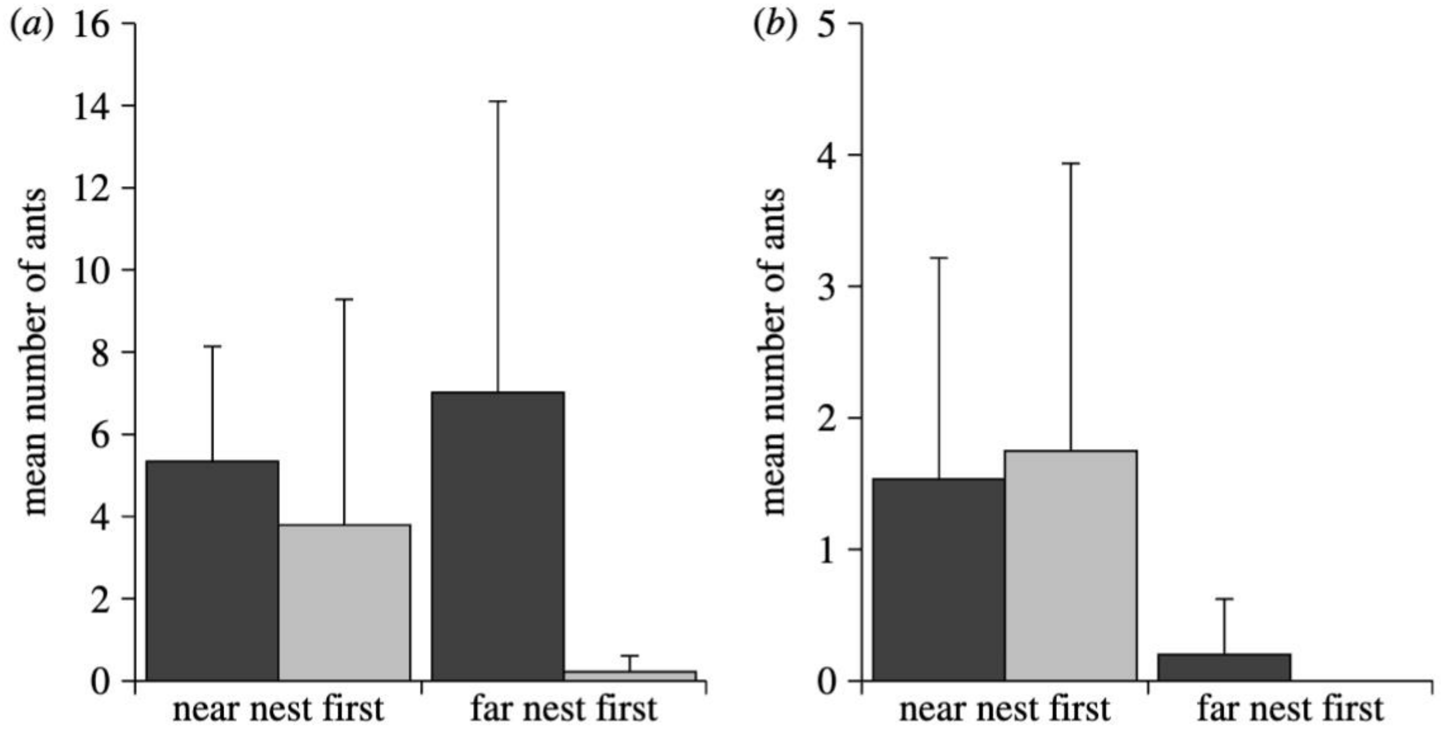


Figure 2. Direction of uninformed switching. (*a*) Ants that make an independent visit to one nest, and then either continue to visit that nest only (black bars, stay) or visit the other nest (grey bars, switch). (*b*) Ants which make an independent visit to one nest and begin recruitment by tandem running to that nest, then either continue to visit that nest only (black bars, stay) or visit the other nest (grey bars, switch). Nine colonies, mean + s.d.

Results

Why is switching informative?

Results

Table 1. Informed ants that visited both nests before leading a tandem run. (TR, tandem run.)

	near nest first		far nest first		
	lead TR to near	lead TR to far	lead TR to near	lead TR to far	Fisher's exact probability test
discover both nests independently	5	3	1	1	$p=0.99$
discover first nest independently and follow TR to other	0	2	0	1	$N=3$, no test performed

Paper

PROCEEDINGS OF THE ROYAL SOCIETY B

rspb.royalsocietypublishing.org

Research

Cite this article: Robinson EJH, Feinerman O, Franks NR. 2014 How collective comparisons emerge without individual comparisons of the options. *Proc. R. Soc. B* **281**: 20140737. http://dx.doi.org/10.1098/rspb.2014.0737

How collective comparisons emerge without individual comparisons of the options

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[2]Department of Physics of Complex Systems, Weizmann Institute of Science, Rehovot, Israel

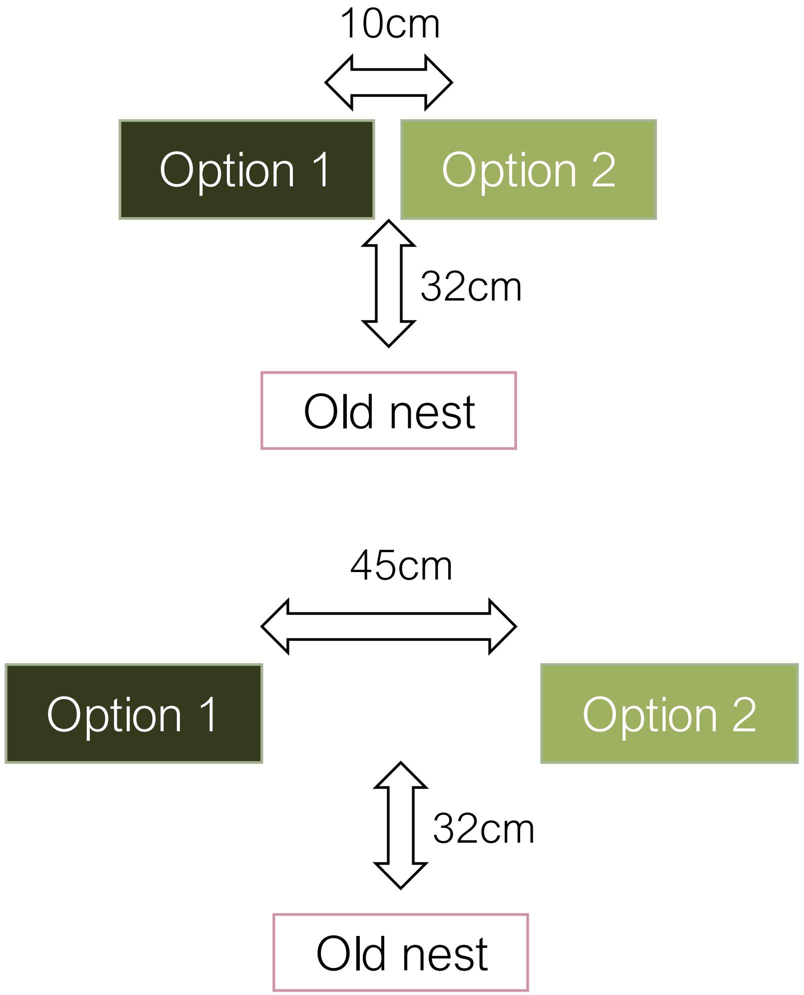
Collective decisions in animal groups emerge from the actions of individuals who are unlikely to have global information. Comparative assessment of options can be valuable in decision-making. Ant colonies are excellent collective decision-makers, for example when selecting a new nest-site. Here, we test the dependency of this cooperative process on comparisons conducted by individual ants. We presented ant colonies with a choice between new nests: one good and one poor. Using individually radio-tagged ants and an automated system of doors, we manipulated individual-level access to information: ants visiting the good nest were barred from visiting the poor one and

Method

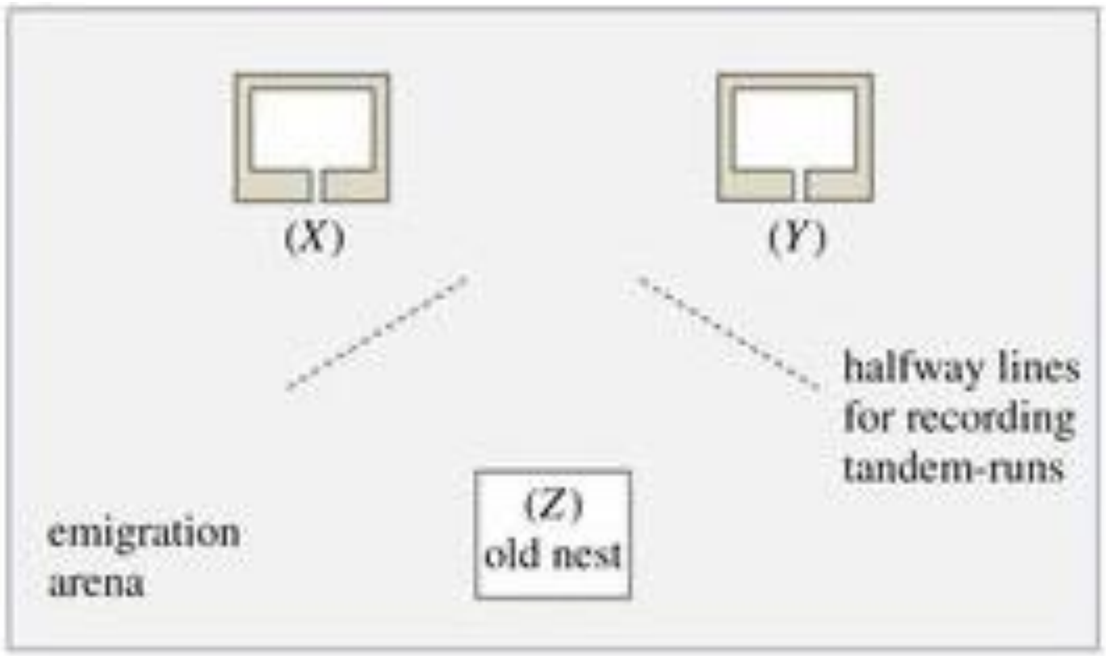
- 6 x colonies
- 70-150 workers each

Conditions:

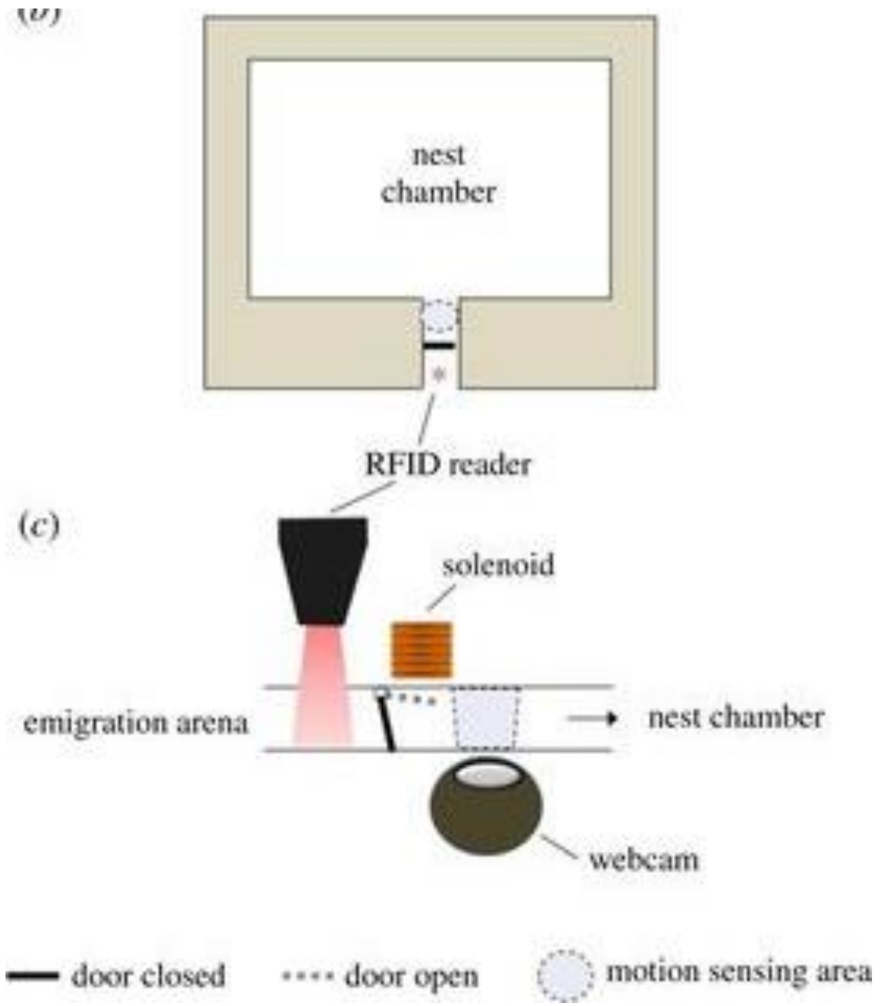
- No comparisons vs Comparisons possible
  - Within-subjects, 1 week apart (counterbalanced)
- Near vs Far
  - 3 colonies in each
  - Far – more unanimous choices; few ants go to both in the control
  - Near – many go to both; sometimes colony is split



Method



(X)
(Y)
halfway lines
for recording
tandem-runs
emigration
arena
(Z)
old nest



nest
chamber
RFID reader
(c)
solenoid
emigration arena
nest chamber
webcam
door closed
door open
motion sensing area

Method

- Recorded:
  - Initial choice (number of ants in each nest once all have emigrated)
  - Location of queen
  - Final choice (number of ants in each nest after 24hrs)

Colony-level decision-making

Decision accuracy

Far away nests: 3/3 chose the good nest in both treatment & control

Close together nests: 3/3 were split in the control, 2/3 were split in the treatment

Decision speed

Control: median = 38 min (25-175)

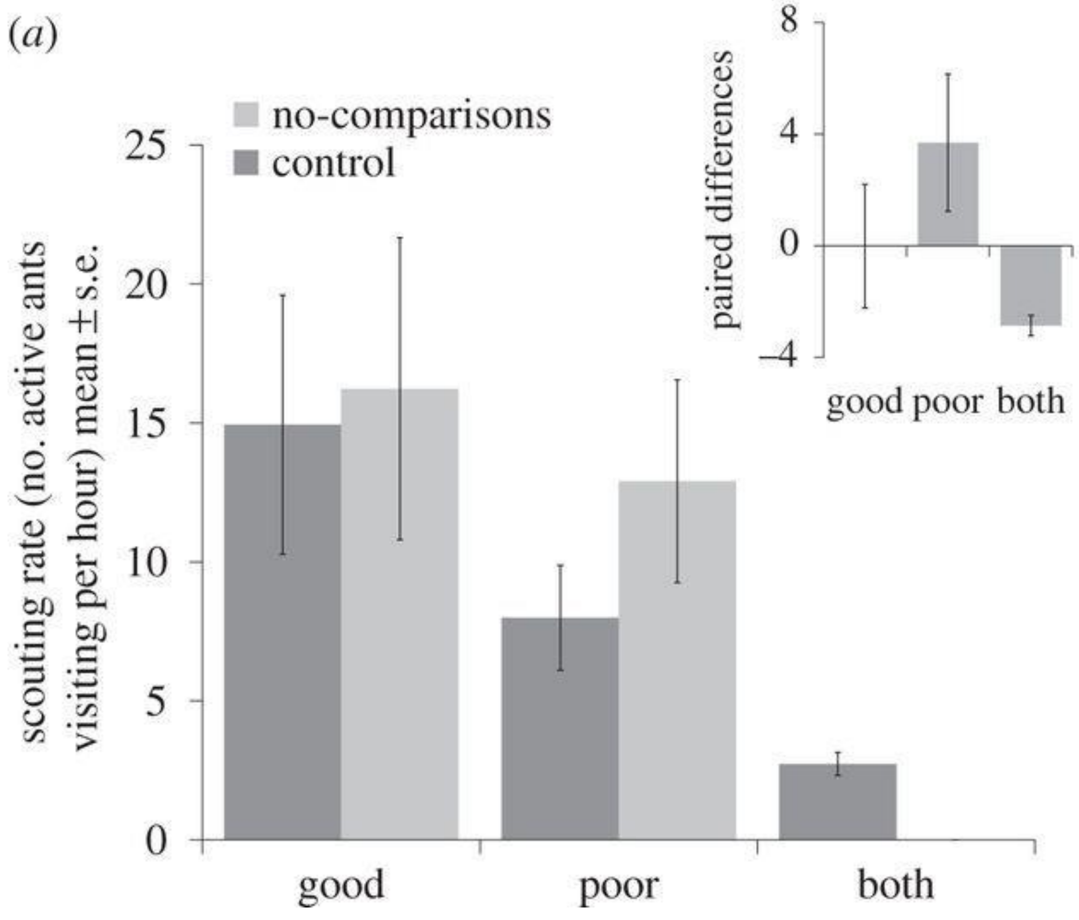
Treatment: median = 38 min (21-107)

Thoughts so far?

- Any differences between real-world house-hunting and the experiment?

- What results would you expect to see if ants do/do not need to compare?

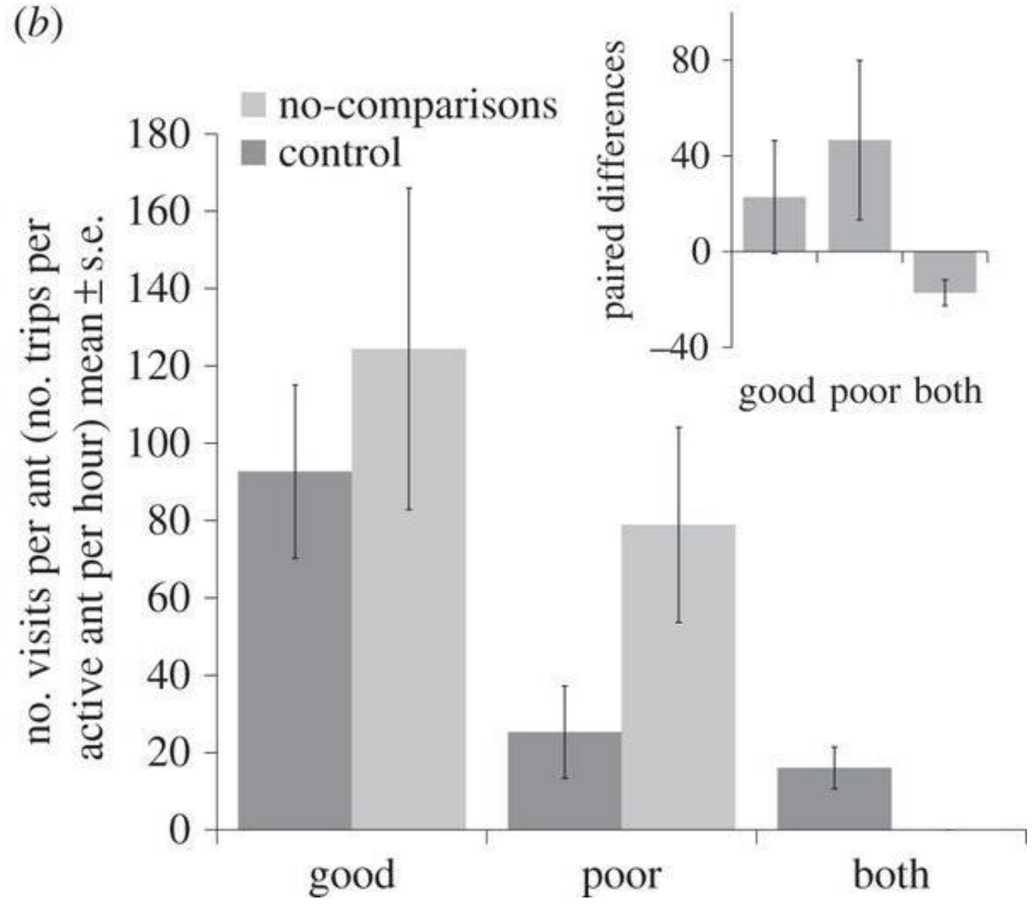
Individual-level decision-making



Similar number of ants visited the good nest

Fewer ants visited the bad nest when ants could compare

Individual-level decision-making



Ants visited the good nest a similar number of times

When they couldn’t compare, they visited the bad nest more often

Individual-level decision-making

- No significant difference in which nest was discovered first, or in number of scouts
- Overall, more ants went to the good nest
- Number of ants trying to switch nests was similar across conditions (24% vs 30%), though they persevered more in the treatment condition.
- Ants that scouted more in session 1 also did so in session 2

Thoughts so far?

- What did the authors show?
- What does this mean wrt collective decision-making?
- Do the results coincide with what you thought they'd be?
- What cognitive abilities are needed for:
    - Direct comparison
    - Evaluation against a threshold

Modelling paper

OPEN ACCESS Freely available online

PLoS one

A Simple Threshold Rule Is Sufficient to Explain Sophisticated Collective Decision-Making

Elva J. H. Robinson[1,2]*, Nigel R. Franks[1], Samuel Ellis[1], Saki Okuda[1], James A. R. Marshall[3]

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Abstract

Decision-making animals can use slow-but-accurate strategies, such as making multiple comparisons, or opt for simpler,

Goal

Three proposals for how an ant decides to recruit to a new nest:

1. Comparison
2. Recruitment latency (hesitation time before recruiting)
3. Threshold rule

Goal of paper: test #3

Model

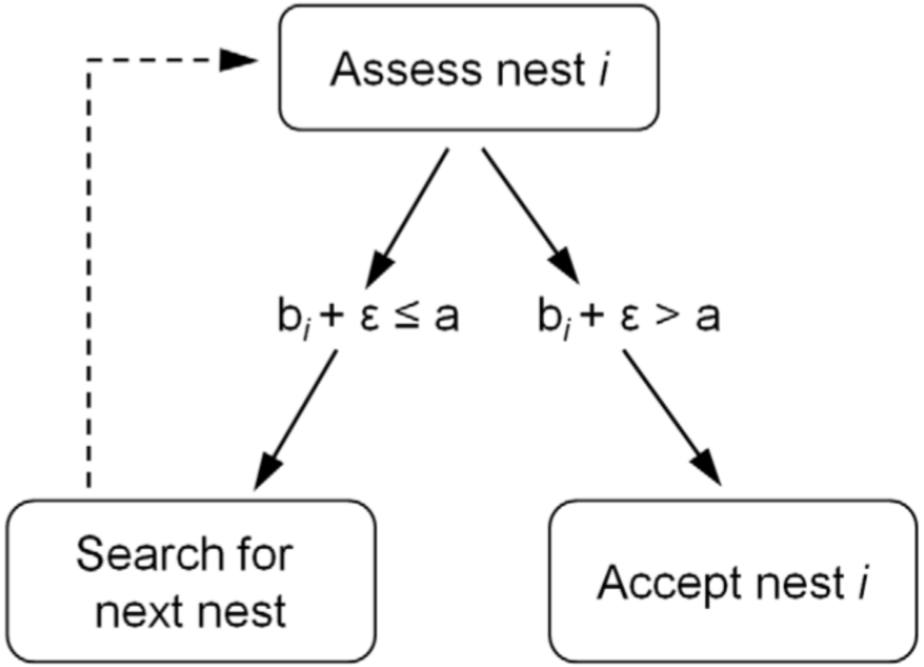


Figure 2. Schematic of model. A simulated ant continues searching until it encounters a nest of a quality (*b*) exceeding the ant's individual threshold (*a*), taking into account assessment error (ε). Ants may revisit the same nest (with probability *r*), and do not have any memory of previously visited nests.
doi:10.1371/journal.pone.0019981.g002

i Nest number (1, 2, 3, …)

b_i Quality of the i^{th} nest

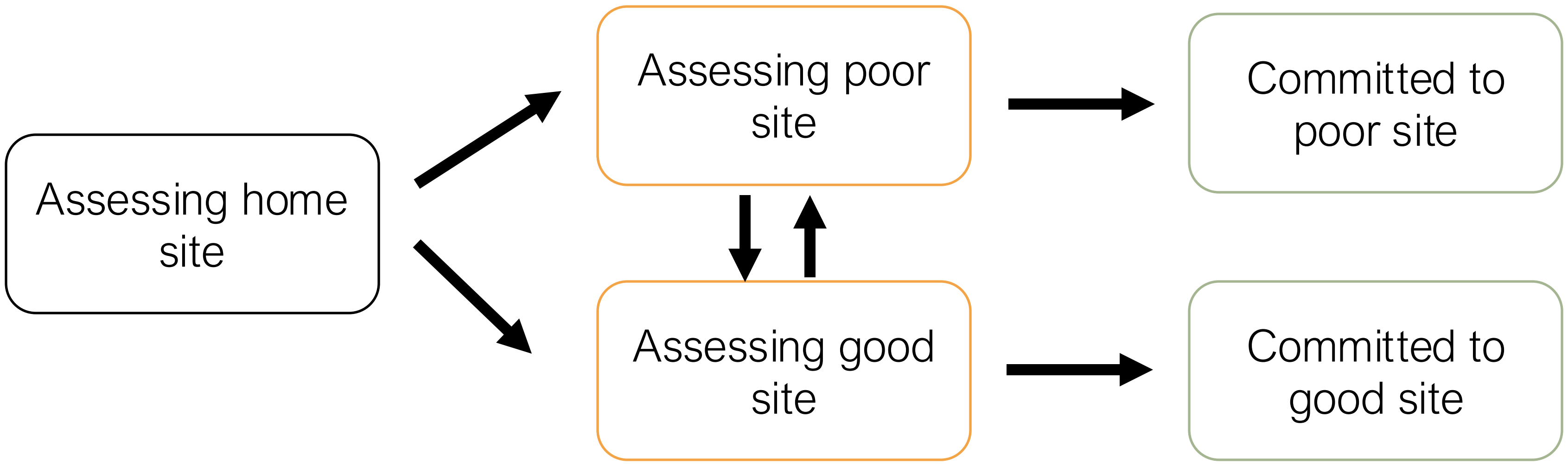
a Ant's threshold (constant over all *i*s)

Markov process

Describes a sequence of events

The probability of the current state depends only on previous state (no memory)

It's a random process (i.e. non-deterministic; based on probabilities)



Model parameters

The threshold, *a*, for each ant is normally distributed A ~ N(5, 1)

Distance between current nest and other nests (only matters for recruitment latencies)

Probability of finding a new nest site from the current nest

Nest quality (old = -inf; poor = 4; good = 6)

The probability of rediscovering a nest when randomly searching, *r*

Steps

1. Ant has to find a nest (depends on probability of finding one)

2. Ant assesses quality (objective quality + assessment noise)

3. Compare assessed quality to threshold, a

4. Commit or keep searching

State transition matrix

$$Q = \begin{pmatrix} (1-p)r & (1-g)(1-r) & 0 & 0 \\ (1-p)(1-r) & (1-g)r & 0 & 0 \\ p & 0 & 1 & 0 \\ 0 & g & 0 & 1 \end{pmatrix},$$

A matrix (table) of probabilities that tell you the chance of moving from state *n-1* to state *n*

State transition matrix

p = probability that the ant accepts the poor site.

g = same but for good site

FROM

$$
Q=\begin{array}{c}
\begin{array}{cccc} \multicolumn{2}{c}{\text{Assessing …}} & \multicolumn{2}{c}{\text{Commit to…}} \\ \text{Poor} & \text{Good} & \text{Poor} & \text{Good} \end{array} \\
\begin{pmatrix}
(1-p)r & (1-g)(1-r) & 0 & 0 \\
(1-p)(1-r) & (1-g)r & 0 & 0 \\
p & 0 & 1 & 0 \\
0 & g & 0 & 1
\end{pmatrix},
\end{array}
\begin{array}{l}
\\ \\
\text{Assessing poor} \\
\text{Assessing good} \\
\text{Commit to poor} \\
\text{Commit to good}
\end{array}
\quad \text{TO}
$$

State transition matrix

p = probability that the ant accepts the poor site.

g = same but for good site

$$
\begin{array}{cccccc}
 & \multicolumn{4}{c}{\text{FROM}} & \\
 & \multicolumn{2}{c}{\text{Assessing …}} & \multicolumn{2}{c}{\text{Commit to…}} & \\
 & \text{Poor} & \text{Good} & \text{Poor} & \text{Good} & \\
\end{array}
$$

$$
\begin{array}{cl}
Q=\begin{pmatrix}
(1-p)r & (1-g)(1-r) & 0 & 0 \\
(1-p)(1-r) & (1-g)r & 0 & 0 \\
\boxed{p} & 0 & 1 & 0 \\
0 & g & 0 & 1
\end{pmatrix}, &
\begin{array}{l}
\text{Assessing poor} \\
\text{Assessing good} \\
\text{Commit to poor} \\
\text{Commit to good}
\end{array}
\end{array}
\quad \text{TO}
$$

Move from assessing a poor site to committing to a poor site with probability p

State transition matrix

p = probability that the ant accepts the poor site.

g = same but for good site

FROM

Assessing … Commit to…

$$
\begin{array}{rcl}
 & \begin{array}{cccc}\text{Poor} & \text{Good} & \text{Poor} & \text{Good}\end{array} & \\
Q= & \begin{pmatrix}
(1-p)r & (1-g)(1-r) & 0 & 0 \\
(1-p)(1-r) & (1-g)r & 0 & 0 \\
p & 0 & 1 & 0 \\
0 & \boxed{g} & 0 & 1
\end{pmatrix}, & \begin{array}{l}\text{Assessing poor}\\ \text{Assessing good}\\ \text{Commit to poor}\\ \text{Commit to good}\end{array}
\end{array}
$$

TO

Move from assessing a good site to committing to a good site with probability g

State transition matrix

p = probability that the ant accepts the poor site.

g = same but for good site

$$
\begin{array}{cccccc}
 & \multicolumn{4}{c}{\text{FROM}} & \\
 & \multicolumn{2}{c}{\text{Assessing …}} & \multicolumn{2}{c}{\text{Commit to…}} & \\
 & \text{Poor} & \text{Good} & \text{Poor} & \text{Good} & \\
Q= & \left(\begin{matrix} (1-p)r \\ (1-p)(1-r) \\ p \\ \boxed{0} \end{matrix}\right. & \begin{matrix} (1-g)(1-r) \\ (1-g)r \\ 0 \\ g \end{matrix} & \begin{matrix} 0 \\ 0 \\ 1 \\ 0 \end{matrix} & \left.\begin{matrix} 0 \\ 0 \\ 0 \\ 1 \end{matrix}\right), & \begin{matrix} \text{Assessing poor} \\ \text{Assessing good} \\ \text{Commit to poor} \\ \text{Commit to good} \end{matrix} \quad \text{TO}
\end{array}
$$

Never move from assessing poor site to committing to good site

State transition matrix

p = probability that the ant accepts the poor site.

g = same but for good site

FROM

Assessing … Commit to…

$$
\begin{array}{rcl}
 & \begin{array}{cccc}\text{Poor} & \text{Good} & \text{Poor} & \text{Good}\end{array} & \\
Q= & \begin{pmatrix} (1-p)r & (1-g)(1-r) & 0 & 0 \\ (1-p)(1-r) & (1-g)r & 0 & 0 \\ p & 0 & 1 & 0 \\ 0 & g & 0 & \boxed{1} \end{pmatrix}, & \begin{array}{l}\text{Assessing poor}\\ \text{Assessing good}\\ \text{Commit to poor}\\ \text{Commit to good}\end{array}
\end{array}
$$

TO

If you’ve committed to a good site, stay there

State transition matrix

p = probability that the ant accepts the poor site.

g = same but for good site

$$
\begin{array}{cccccc}
 & \multicolumn{4}{c}{\text{FROM}} & \\
 & \multicolumn{2}{c}{\text{Assessing …}} & \multicolumn{2}{c}{\text{Commit to…}} & \\
 & \text{Poor} & \text{Good} & \text{Poor} & \text{Good} & \\
Q= & \left(\begin{array}{c} (1-p)r \\ (1-p)(1-r) \\ p \\ 0 \end{array}\right. & \begin{array}{c} (1-g)(1-r) \\ \boxed{(1-g)r} \\ 0 \\ g \end{array} & \begin{array}{c} 0 \\ 0 \\ 1 \\ 0 \end{array} & \left.\begin{array}{c} 0 \\ 0 \\ 0 \\ 1 \end{array}\right), & \begin{array}{l} \text{Assessing poor} \\ \text{Assessing good} \\ \text{Commit to poor} \\ \text{Commit to good} \end{array} \quad \text{TO}
\end{array}
$$

Move from assessing good site to assessing good site with "rediscovery" probability x probability you didn't commit last time

State transition matrix

p = probability that the ant accepts the poor site.

g = same but for good site

FROM

$$
\begin{array}{c|cccc|l}
 & \multicolumn{2}{c}{\text{Assessing …}} & \multicolumn{2}{c|}{\text{Commit to…}} & \\
 & \text{Poor} & \text{Good} & \text{Poor} & \text{Good} & \\
\hline
 & (1-p)r & \boxed{(1-g)(1-r)} & 0 & 0 & \text{Assessing poor} \\
Q= & (1-p)(1-r) & (1-g)r & 0 & 0 & \text{Assessing good} \\
 & p & 0 & 1 & 0 & \text{Commit to poor} \\
 & 0 & g & 0 & 1 & \text{Commit to good}
\end{array}
$$

TO

?

(Hint: 1-x means “not”)

State transition matrix

$$E(\text{time to accept any site}) = \frac{4(1-r)+2r(p+g)-p-g}{2((2r-1)pg+(1-r)(p+g))}. \quad (2)$$

Equation (2) will be used below to examine the sensitivity of acceptance time to changes in site qualities. Note that, technically, we should be interested in the latency between discovering a particular site, and recruiting to that site, however in general per-state latencies are difficult to calculate in Markov-chains, and the overall expected latency given in equation 2 is an acceptable simplification (see Text S1).

Results (simulations vs real data)

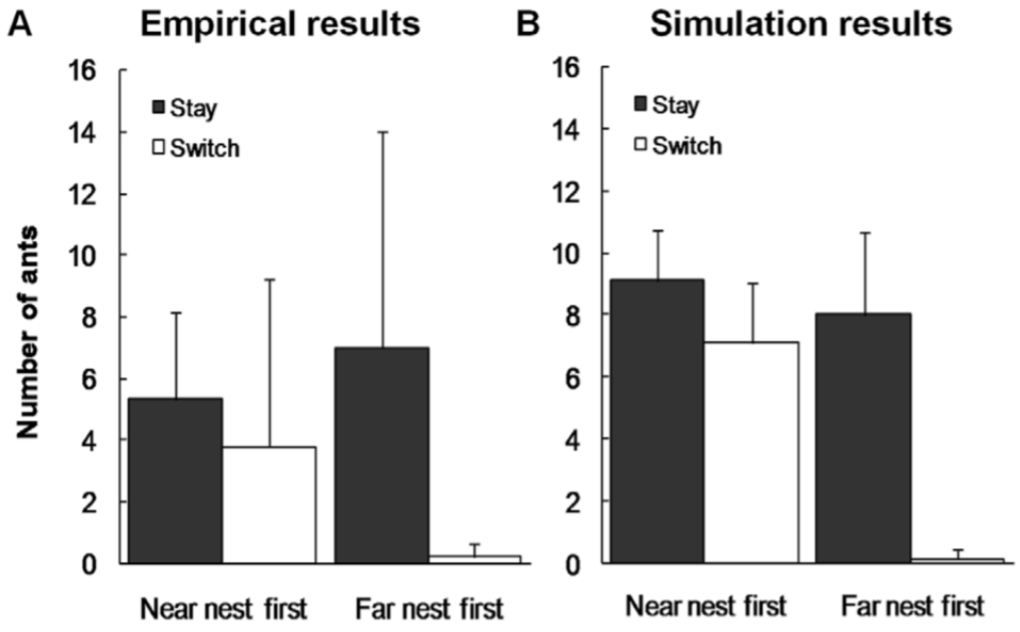


Figure 3. Comparison of empirical and simulated emigration behavior. Number of ants continuing to visit the same nest (stay) or going on to visit the other nest (switch), depends on the quality of the first nest visited. (A) Empirical results, 9 colonies, mean + SD. ($\chi^2_1 = 86.6$, $P < 0.001$), reproduced from Figure 2a, Robinson et al. [26] with permission from Royal Society Publishing. (B) Simulation results, 9 replicates, mean + SD ($\chi^2_1 = 42.0$, $P < 0.001$). A sample set of 9 replicates are shown here for comparability with the empirical data. Running 100 repeat sets gave the same pattern, statistically significant in 100% of cases.

Results (simulations vs real data)

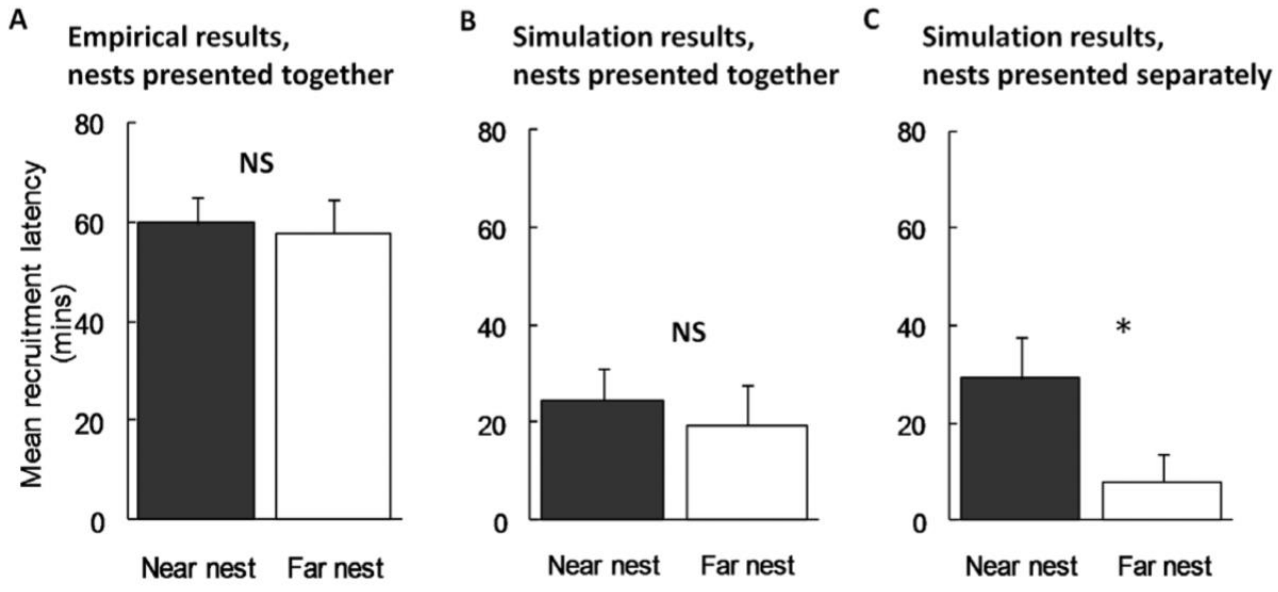


Figure 4. Comparison between empirical and simulated recruitment latency results where the higher quality is further away. Recruitment latencies to the near (poor) and far (good) nests, mean + SE. (A) Empirical data [26]; nests presented together, n = 9 colonies. No significant differences in recruitment latencies: GLMM: $t_{39} = 0.08$, $P = 0.93$. (B) Simulation data; nests presented together, n = 9 replicates. No significant differences in recruitment latencies: GLMM: $t_{39} = 0.71$, $P = 0.48$. Sample set of 9 replicates shown; of 100 repeat sets, 90% showed no significant difference in recruitment latencies. (C) Simulation data; nests presented separately, n = 9 replicates. Recruitment latencies to poor nest significantly greater: GLMM: $t_{88} = 2.19$, $P < 0.05$. Sample set of 9 replicates shown; of 100 repeat sets, 70% showed significantly greater recruitment latencies to poor nest.

Model parameters

Table 1. Parameterisation used in simulations of Monte-Carlo model.

Parameter	Comparison with [26]	Comparison with [20]	Comparison with new multiple-nest experiment	Derivation
Number of nests	3	3	4	From experiments
Arena size and shape	See Fig. 1a	See Fig. 1b	See Fig. 1c	From experiments
Position of nests	Good nest (A) further than poor nest (B) (Fig. 1a)	New nests equidistant from old (Fig. 1b)	New nests equidistant from old (Fig. 1c)	From experiments
Mean travel time between nests (sec) from column nest to row nest (SD = 1/5 mean)	$\begin{array}{cc} & \begin{array}{ccc}\text{Old} & \text{A} & \text{B}\end{array} \\ \begin{array}{c}\text{Old}\\ \text{A}\\ \text{B}\end{array} & \begin{pmatrix}1 & 36 & 143\\ 36 & 1 & 116\\ 143 & 116 & 1\end{pmatrix}\end{array}$	$\begin{array}{cc} & \begin{array}{ccc}\text{Old} & \text{A} & \text{B}\end{array} \\ \begin{array}{c}\text{Old}\\ \text{A}\\ \text{B}\end{array} & \begin{pmatrix}1 & 54 & 54\\ 54 & 1 & 81\\ 54 & 81 & 1\end{pmatrix}\end{array}$	$\begin{array}{cc} & \begin{array}{cccc}Old & A & B & C\end{array} \\ \begin{array}{c}Old\\ A\\ B\\ C\end{array} & \begin{pmatrix}1 & 46 & 46 & 46\\ 46 & 1 & 80 & 80\\ 46 & 80 & 1 & 80\\ 46 & 80 & 80 & 1\end{pmatrix}\end{array}$	From walking speed 8.4 mm/s [74]
Probabilities of finding nests (from column to row)[1]	$\begin{array}{cc} & \begin{array}{ccc}\text{Old} & \text{A} & \text{B}\end{array} \\ \begin{array}{c}\text{Old}\\ \text{A}\\ \text{B}\end{array} & \begin{pmatrix}0.91 & 0.15 & 0.03\\ 0.06 & 0.80 & 0.06\\ 0.03 & 0.05 & 0.91\end{pmatrix}\end{array}$	$\begin{array}{cc} & \begin{array}{ccc}\text{Old} & \text{A} & \text{B}\end{array} \\ \begin{array}{c}\text{Old}\\ \text{A}\\ \text{B}\end{array} & \begin{pmatrix}0.70 & 0.15 & 0.15\\ 0.15 & 0.70 & 0.15\\ 0.15 & 0.15 & 0.70\end{pmatrix}\end{array}$	$\begin{array}{cc} & \begin{array}{cccc}Old & A & B & C\end{array} \\ \begin{array}{c}Old\\ A\\ B\\ C\end{array} & \begin{pmatrix}0.76 & 0.08 & 0.08 & 0.08\\ 0.08 & 0.82 & 0.05 & 0.05\\ 0.08 & 0.05 & 0.82 & 0.05\\ 0.08 & 0.05 & 0.05 & 0.82\end{pmatrix}\end{array}$	From arena size, arena shape & nest positions; see Text S1.
Number of ants	27 (Fig. 3); 49 (Fig. 4)	29 (Table 2); 12–63 (Fig. 5)[2]	13 (test 1); 20 (test 2)	From experiments
Acceptance threshold distribution (A)[3]	Normal distribution: mean = 5, SD = 1	Normal distribution: mean = 5, SD = 1	Normal distribution: mean = 5, SD = 1	Arbitrary
Nest qualities (b)[3]	Old = −inf; Poor = 4; Good = 6	Old = −inf; Poor = 4; Good = 6	Old = −inf; Poor = 4; Poor = 4; Good = 6	Arbitrary
Assessment error (from which ε is drawn)[3]	Normal distribution: mean = 0, SD = 1	Normal distribution: mean = 0, SD = 1	Normal distribution: mean = 0, SD = 1	Arbitrary

Model parameters

Table 1. Parameterisation used in simulations

Parameter	**Comparison with [26]**
Number of nests	3
Arena size and shape	See Fig. 1a
Position of nests	Good nest (A) further than poor nest (B) (Fig. 1a)
Mean travel time between nests (sec) from column nest to row nest (SD = 1/5 mean)	$\begin{array}{cccc} & \text{Old} & \text{A} & \text{B} \\ \text{Old} & 1 & 36 & 143 \\ \text{A} & 36 & 1 & 116 \\ \text{B} & 143 & 116 & 1 \end{array}$
Probabilities of finding nests (from column to row)[1]	$\begin{array}{cccc} & \text{Old} & \text{A} & \text{B} \\ \text{Old} & 0.91 & 0.15 & 0.03 \\ \text{A} & 0.06 & 0.80 & 0.06 \\ \text{B} & 0.03 & 0.05 & 0.91 \end{array}$
Number of ants	27 (Fig. 3); 49 (Fig. 4)
Acceptance threshold distribution (A)[3]	Normal distribution: mean = 5, SD = 1
Nest qualities (b)[3]	Old = −inf; Poor = 4; Good =
Assessment error (from which ε is drawn)[3]	Normal distribution: mean = 0, SD = 1

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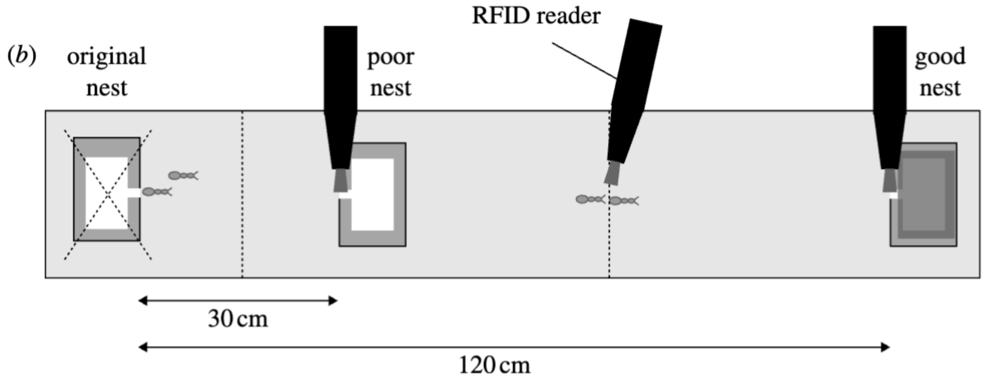
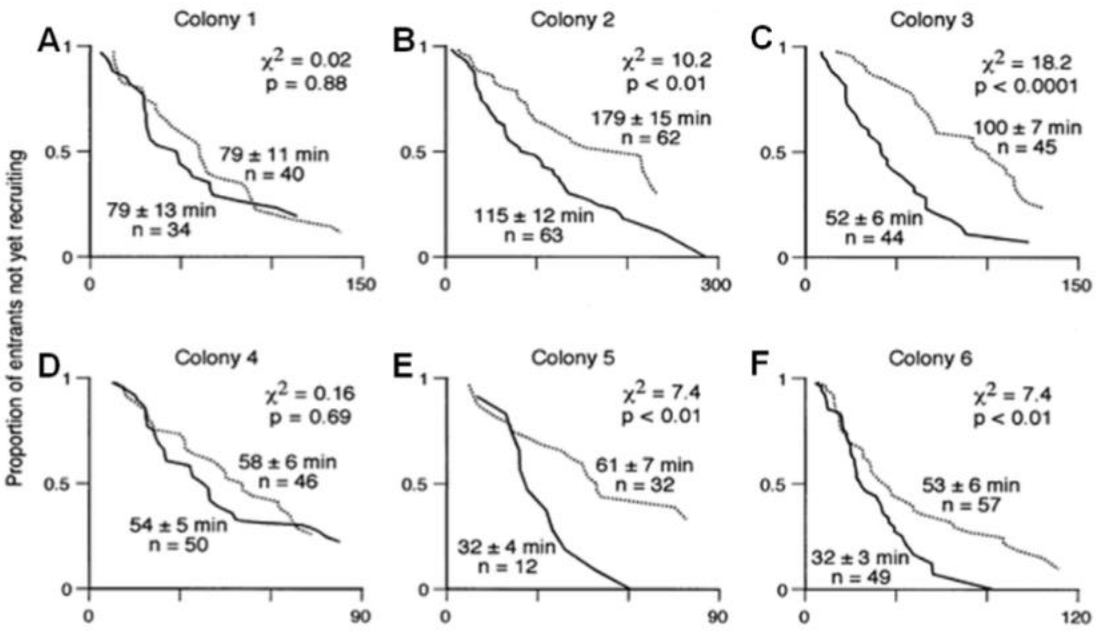
Do ants make direct comparisons?

Elva J. H. Robinson*, Faith D. Smith, Kathryn M. E. Sullivan and Nigel R. Franks



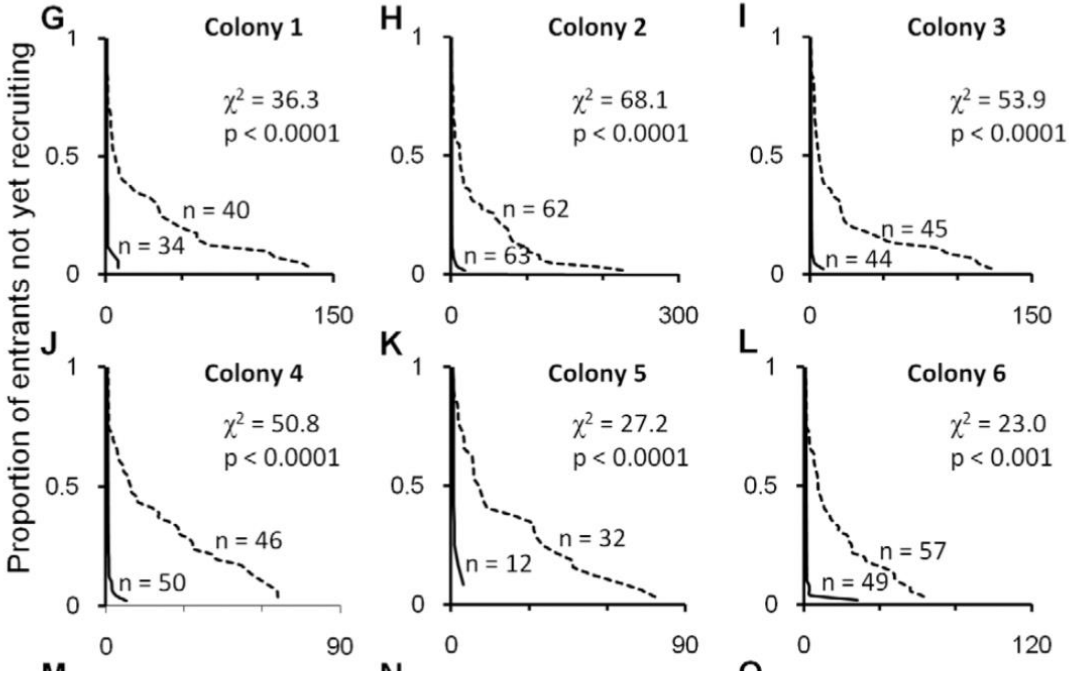
Reproducing results

Empirical results in [20]



Latency between first entry & first recruitment

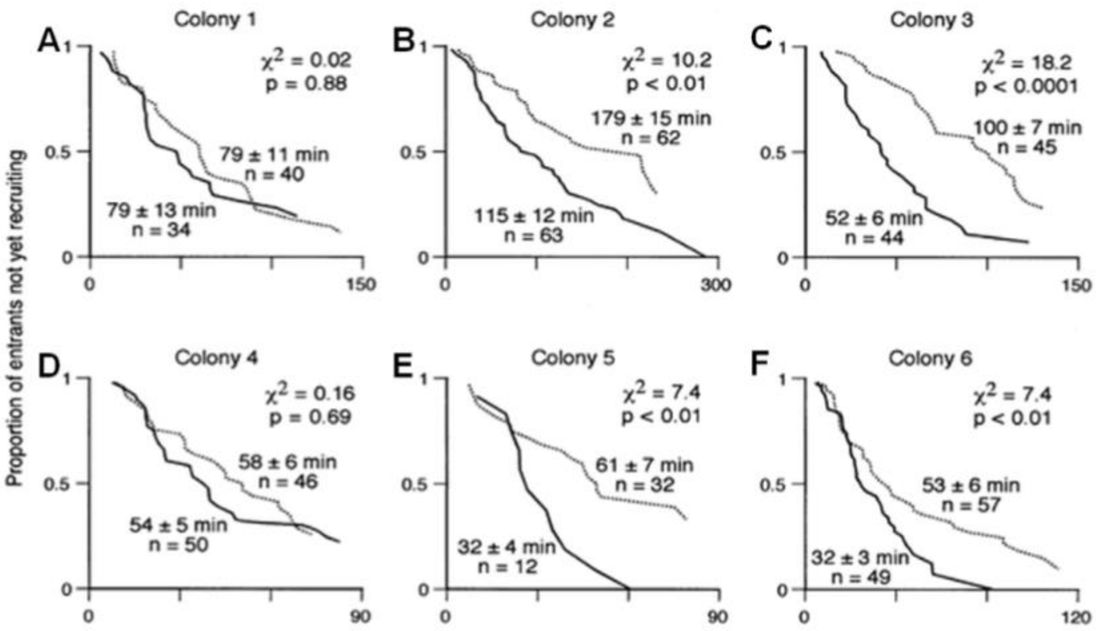
Simulated results (nests presented separately)



Good nest Poor nest

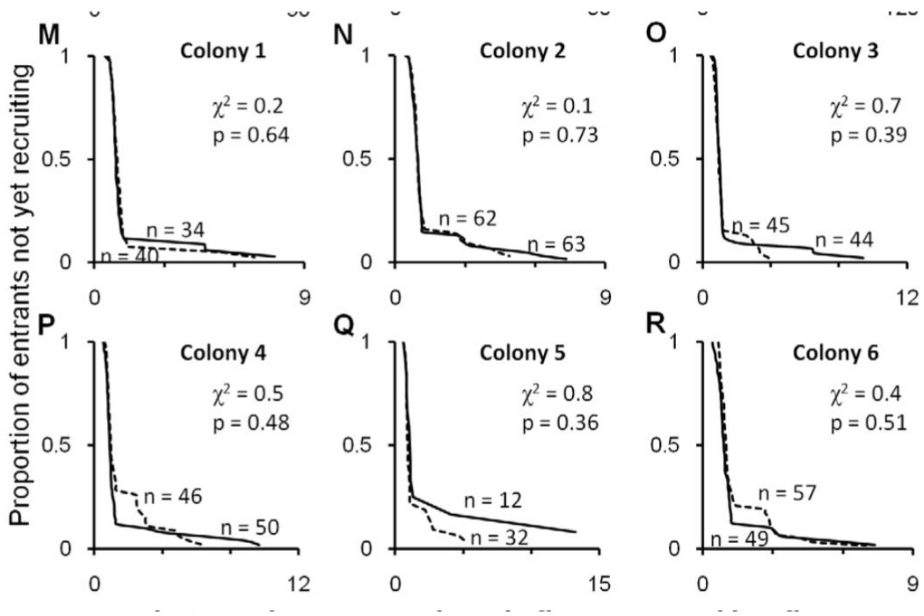
Reproducing results

Empirical results in [20]



Latency between first entry & first recruitment

Simulated results (nests presented together)



Good nest Poor nest

Questions

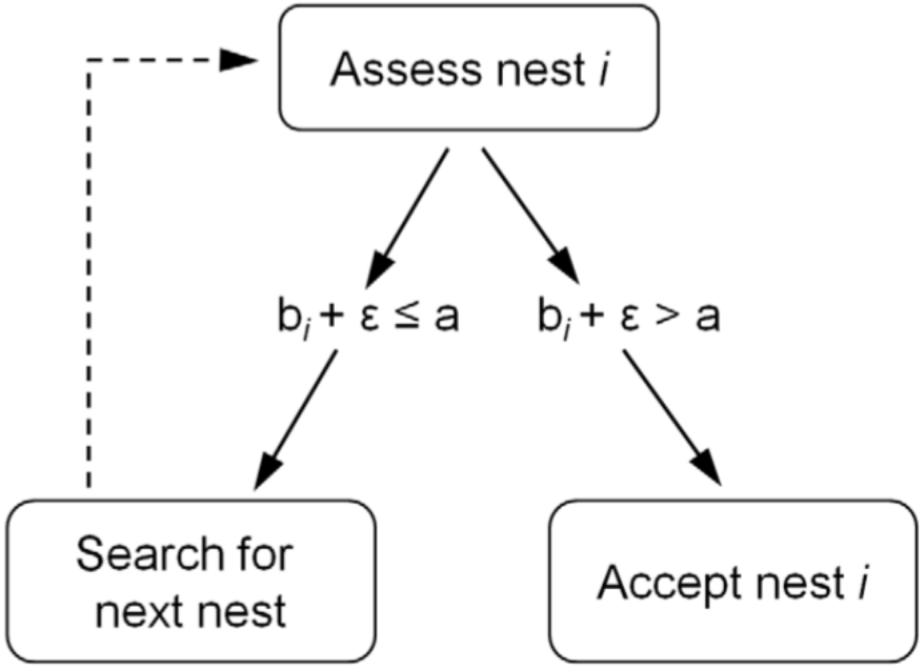


Figure 2. Schematic of model. A simulated ant continues searching until it encounters a nest of a quality (*b*) exceeding the ant's individual threshold (*a*), taking into account assessment error (ε). Ants may revisit the same nest (with probability *r*), and do not have any memory of previously visited nests.
doi:10.1371/journal.pone.0019981.g002

1. How well does the model reproduce ant behaviour?
2. What cognitive abilities does it assume ants have?

See you next week!