

1 Negative feedback may suppress variation to improve collective 2 foraging performance

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8 **Abstract**

9 Social insect colonies use negative as well as positive feedback signals to regulate foraging
10 behaviour. In ants and bees individual foragers have been observed to use negative pheromones
11 or mechano-auditory signals to indicate that forage sources are not ideal, for example being
12 unrewarded, crowded, or dangerous. Here we propose an additional function for negative feedback
13 signals during foraging, variance reduction. We show that while on average populations will
14 converge to desired distributions over forage patches both with and without negative feedback
15 signals, in small populations negative feedback reduces variation around the target distribution
16 compared to the use of positive feedback alone. Our results are independent of the nature of the
17 target distribution, providing it can be achieved by foragers collecting only local information. Since
18 robustness is a key aim for biological systems, and deviation from target foraging distributions
19 may be costly, we argue that this could be a further important and hitherto overlooked reason
20 that negative feedback signals are used by foraging social insects.

21 **1 Introduction**

22 Collectively-foraging social insects use feedback mechanisms in order to robustly and efficiently
23 satisfy the nutritional requirements of the colony. Positive feedback signal usage by such foraging
24 social insects is well known, such as mass-recruitment via pheromone in various ant species [1], and
25 recruitment of small numbers of individuals such as via the honeybees' waggle-dance [2], or rock ants'
26 tandem-running [3]. The use of negative feedback signals in these systems has, however received com-
27 paratively little attention. Negative feedback was predicted to be important for collectively foraging
28 species [4, 5], and subsequently discovered in diverse systems such as Pharaoh's ants [6, 7] and honey-
29 bees [8, 9]. Several studies have interpreted negative feedback as a mechanism to reduce recruitment

30 to a resource based on some aspect of its quality, for example allowing unrewarded trails to be shut
31 down [6, 7], allowing recruitment to a crowded source of forage to be reduced [10], or transferring
32 information that a forage patch may have an increased predation risk [8, 11]. Subsequent studies have
33 similarly focussed on the role of negative feedback in dealing with time-varying forage patches [12, 13],
34 or with the amount of available comb storage space [14].

35 Here we propose an alternative function for negative feedback mechanisms in collective foraging,
36 suppression of costly variation in the colony's foraging performance. In the following, we present simple
37 models of collective foraging with positive and negative feedback, and with positive feedback only.
38 We show how both models are able to approach a desired target distribution over forage patches on
39 average, when forager populations are assumed to be infinite. However, when finite forager populations
40 are modelled, the two foraging systems differ in the robustness with which they achieve the target
41 distribution; with positive feedback only, stochastic fluctuations can lead to the forager population
42 being far from its target distribution at any point in time, however by adding negative feedback
43 the forager distribution becomes more robust. We argue that this will increase colony-level foraging
44 success [15, 16], and thus may represent a new functional explanation for the observation of negative
45 feedback in foraging by social insect colonies.

46 Foraging theory is an active and complex research area, and our results do not rely on assumptions
47 about the nature of the colony's target distribution, other than it can be achieved by agents with access
48 only to local information at both the forage source, and the colony. Thus, the target distribution may
49 be akin to an Ideal Free Distribution, in which agents are distributed such that none can improve
50 overall foraging efficiency by switching to a different forage patch [16, 17]. Alternatively, the target
51 distribution may be based on the requirement of the colony for different micro- and macro-nutrients
52 [18, 19, 20, 21]. Or, the target distribution may be based on some other objective entirely, or on
53 combinations of objectives such as those just discussed. In ignoring the nature of the distribution,
54 therefore, our focus is purely on the dynamics of foraging, and how negative feedback can improve
55 this.

56 For our analysis we adapt our model from a simple model of negative feedback for foraging in
57 honeybee colonies [12], in itself inspired by models of negative feedback in house-hunting honeybee
58 swarms [22, 23, 24]; however since other social insect species such as Pharaoh's Ants also make use of
59 negative feedback during foraging [6], we argue that the model is generally applicable.

60 2 Methods

61 We assume a target distribution of the individuals to the n patches in quantities proportional to
62 the relative patch quality arbitrarily defined:

$$x_i^* \approx \frac{q_i}{\sum_{j \in n} q_j}, \quad i \in \{1, \dots, n\}, \quad (1)$$

63 where q_i is the quality of patch i . In our models an individual's state can be either uncommitted
64 (X_U) or committed to patch i (X_i) with $i \in \{1, \dots, n\}$. Therefore, based on the number of patches
65 n , the commitment of the population will be split among $n + 1$ subpopulations; we represent the
66 subpopulation proportions as x_U and x_i , in the closed interval $[0, 1]$. Note that, in a finite population
67 of S individuals, it will be impossible for the colony to achieve exactly the desired target distribution
68 if $x_i S$ is not an integer number.

69 We analyse the population dynamics of the two systems parametrised to reach the same target
70 distribution (with and without negative social feedback) using mean-field models of infinite and finite
71 populations, using ordinary differential equations (ODEs) and stochastic simulation of the master
72 equation respectively. Both types of analyses can be performed for models derived from chemical
73 reaction equations, which specify how individuals in the system interact and change state (see Table 1).

74 The ODE model assumes an infinitely-large population size S and provides deterministic system
75 dynamics in the absence of any noise from finite population effects. On the other hand, stochastic
76 simulation of the master equation (Gillespie's SSA [25]) gives a probabilistically correct simulation of
77 dynamics of finite populations of size S .

78 While previous research has documented that collective foraging is regulated by the actions and
79 interactions that we included in our models, the relationship between their frequency (transition rates)
80 and the estimated nest-site quality are still debated. Table 1 reports the best functions we obtained
81 through numerical optimisation to approximate the target distribution. Including negative inevitably
82 feedback inevitably requires a change also in the recruitment function, from constant to linearly pro-
83 portional to the quality. In the Supplementary Text ST1 we show the numerical optimisation analysis
84 and results for a variety of assumptions. Here, we assume that social recruitment (positive feedback)
85 is much more efficient than independent discovery, so $r_i \gg q_i$, as has been documented in a large
86 variety of social insect species [26, 27, 28, 29]. For fair comparison, the average recruitment strength
87 r is equalised between the two models so that quality-sensitive recruitment transitions—model with
88 negative feedback—happens on average at the same rate of quality-insensitive recruitment—model
89 without negative feedback (see Supplementary Text ST2). The model with only positive feedback
90 is easy to solve for the desired equilibrium distribution of foragers, with a simple parameterisation
91 of individuals' rates (see Supplementary Text ST3). The model with negative feedback, however,
92 requires a heuristic individual parameterisation based on site qualities, which we perform numerically.
93 However, this heuristic has a simple functional form (see Supplementary Figure SF2) so could easily
94 be approximated by real foragers.

95 **3 Results**

96 The two top panels of Figure 1 show the time dynamics of the two models for representative values
97 and $n = 3$ patches. Both models asymptotically approximate the target distribution of Eq. (1).

98 Through numerical integration of the master equations, we investigate the effect of stochastic

		WITHOUT NEGATIVE FEEDBACK	SOCIAL	WITH NEGATIVE FEEDBACK	SOCIAL
Independent discovery	$X_U \xrightarrow{q_i} X_i$	Quality-sensitive		Quality-sensitive	
Independent abandonment (leak)	$X_i \xrightarrow{a} X_U$	Constant		Constant	
Recruitment (positive social feedback)	$X_U + X_i \xrightarrow{r_i} 2X_i$	Constant		Quality-sensitive	
Stop signalling (negative social feedback)	$X_i + X_i \xrightarrow{z} X_U + X_i$			Constant	

Table 1: The two analysed models can be described in terms of transitions between commitment states by individuals. The commitment states are ‘committed to foraging patch i ’ (X_i) or ‘uncommitted’ (X_U). Both models have the same positive and negative feedback for *independent transitions*: quality-dependent discovery and constant abandonment (leak a). The difference lies in the social feedback; one model (blue) has quality-insensitive recruitment ($r_i = \rho$) but no negative social feedback ($z = 0$). The other model (red) has both quality-sensitive recruitment ($r_i = \rho q_i$) and quality-insensitive self-inhibition ($z > 0$), as reported by field observations [30]. In these representative models, we set rates as constant and (linear) quality-sensitive functions of the quality according to the best function we obtain with numerical optimisation (see Supplementary Text ST1).

99 fluctuations on the system dynamics [25]. The fluctuation size is inversely proportional to the system
100 size S , *i.e.* there are no fluctuations in very large groups (*i.e.* $S \rightarrow \infty$) and large fluctuation in small
101 groups. The effect of the system-size noise can be appreciated in the two bottom panels of Figure 1.
102 They show 30 representative trajectories for a system of size $S = 200$. The higher variance can also
103 be appreciated in the boxplots on the right of each bottom panel of Figure 1, in which the average of
104 1,000 simulations hits the target value in both models; however, the variance is reduced considerably
105 with the introduction of negative social feedback. These results are not specific to the representative
106 example of Figure 1, but are consistent throughout the wide parameter space (see analysis in the
107 Supplementary Text ST4). Additionally, increasing abandonment, which is a form of independent,
108 asocial negative feedback, is not sufficient to reduce variance (see Supplementary Text ST5).

109 Large deviations from the target distribution could compromise the ability of the colony to in-
110 take the necessary nutrients for survival and reproduction, thus decreasing colony fitness. Figure 2
111 shows how the error in achieving the target distribution is significantly higher without negative social
112 feedback. Similarly, the speed of adaptation to environmental changes is an important factor in the
113 survival of the colony [31, 32]. The system without negative feedback can be incapable of adapting to
114 changes in a timely manner because its temporal dynamics vary significantly depending on the initial
115 commitment (see top-left inset of Figure 1). The system with negative feedback, instead, displays
116 a constant convergence time regardless of the initial state of the system (see Supplementary Text
117 ST6). Figure 3 shows how the convergence speed and the deviation from the target distribution are
118 influenced by the strength of the negative feedback; the strength of negative feedback can tune a
119 speed-robustness trade-off, similarly to the tuning of speed-value and speed-coherence trade-offs in
120 consensus decisions [23, 24, 33]. In agreement with field observations of honeybees, which increase
121 stop signalling when a quick response is necessary [10], our analysis also predicts a speed-up of the
122 group dynamics for higher levels of negative feedback.

123 4 Discussion

124 Negative feedback has been considered in collective decisions, particularly as a means of symmetry
125 breaking [22, 23, 24, 34], and in foraging, as a means of adapting to dynamically changing environments
126 [10, 7, 12, 13]. Other than in entomology, negative feedback has been observed as a tool for noise
127 reduction in gene networks [35, 36, 37] and in electronic systems [38, 39]. Here we have shown that
128 negative feedback may play an important role in reducing variance in colony foraging performance. For
129 example, considering the honeybee system that inspired our model, field observations have reported
130 that levels of stop signalling increase in response to changes such as dangerous, overcrowded, or
131 depleted food patches [13, 40, 11, 10]; however, it has not yet been fully understood why, even in
132 static conditions, honeybees always deliver a small number of stop signals to foragers visiting the
133 same forage patch [13, 10]. This pattern is consistent with our model, and the analysis presented is
134 an interpretation for such observed behaviour.

135 Our results suggest a further progression in the evolution of collective foraging behaviour; solitary
136 foraging by members of social insect colonies evolved first, but was comparatively inefficient due to
137 the need for foragers to repeatedly and independently discover forage sites [41, 42] (see Supplementary
138 Text ST8). Subsequently, positive social feedback evolved to improve foraging efficiency [43, 44, 45],
139 but this came at the expense of robustness of the foraging outcome, through increased variance in
140 foraging performance (see Supplementary Text ST9). Finally, negative feedback evolved not only to
141 respond better to changing environments, but also to reduce variance in foraging performance. The
142 re-use of negative feedback signals, such as in the case of honeybee stop-signals which are used in
143 both foraging [10] and house-hunting [22] life history stages, would facilitate performance-enhancing
144 innovations in signalling behaviours; however, it is not clear whether stop-signalling first arose in
145 foraging or in house-hunting contexts (intuitively, we suggest the former, a more common life history
146 event).

147 Some species have not evolved negative signalling mechanisms but rely on natural decay of feed-
148 back, such as pheromone evaporation. For instance, *Lasius niger* ants rely on the downregulation
149 of positive feedback (*i.e.* pheromone deposition) in order to let pheromone decay take over [46, 47].
150 It is worth noting that this is not technically negative feedback; given the time taken from the first
151 observations of the positive-feedback signals in colonies of honeybees and ants [3, 48, 49] to that of
152 the corresponding negative feedback signals [6, 50], it may be worth further exploring social insects
153 in which explicit negative feedback has not been observed, to search for expected negative feedback
154 mechanisms, or explain why their life history means they would not be beneficial. As a motivating ex-
155 ample, decaying waggle dance durations in honeybee swarms were taken to be due to decay processes
156 internal to scout bees [51], but the negative stop-signal was subsequently discovered to be significant
157 in these swarms [22].

158 We conclude by noting that our study highlights the importance of using multiscale modelling to
159 understand collective behaviour [52, 53, 54]. In fact, through mean-field analysis we could not observe

160 the dynamics that justify the use of the negative feedback. Instead, complementing the analysis with
161 probabilistic models, we have been able to identify the system dynamics that favour the appearance of
162 stop signalling as a mechanism for variance reduction. Multiscale modelling is a valuable framework
163 which combines the use of a set of modelling techniques to analyse the system at various levels of
164 complexity and noise. In this study, we only employed noise-free mean-field analysis and master
165 equations with system-size dependent noise. However, further analysis could include the impact of
166 spatial noise, and time-correlated information and/or interactions [52].

167 **Acknowledgements**

168 The authors thank Gianni Di Caro, Ulrike Feudel and David Wagg for useful discussions. This
169 study was funded by the European Research Council (ERC) under the European Union’s Horizon
170 2020 research and innovation programme (grant agreement number 647704). A.R. also acknowledges
171 support from the Belgian F.R.S.-FNRS, of which he is a Chargé de Recherches.

172 **Code availability**

173 All data, simulation code, and a Mathematica notebook reproducing the analyses presented herein
174 is available in the GitHub repository <https://github.com/Di0DeProject/VarianceSuppression>.

175 This is supplemented by a notebook for MuMoT [52], an open-source tool for multiscale modelling,
176 which reproduces similar results to those presented herein. The notebook is available online at
177 https://mybinder.org/v2/gh/Di0DeProject/MuMoT/master?filepath=DemoNotebooks%2FVariance_suppression.ipynb.

178 **Author contributions**

179 Both authors conceived the original idea, performed mathematical analyses, and wrote the paper.
180 A.R. generated the simulation data, and figures.

181 **Competing interests**

182 The authors declare no competing interests.

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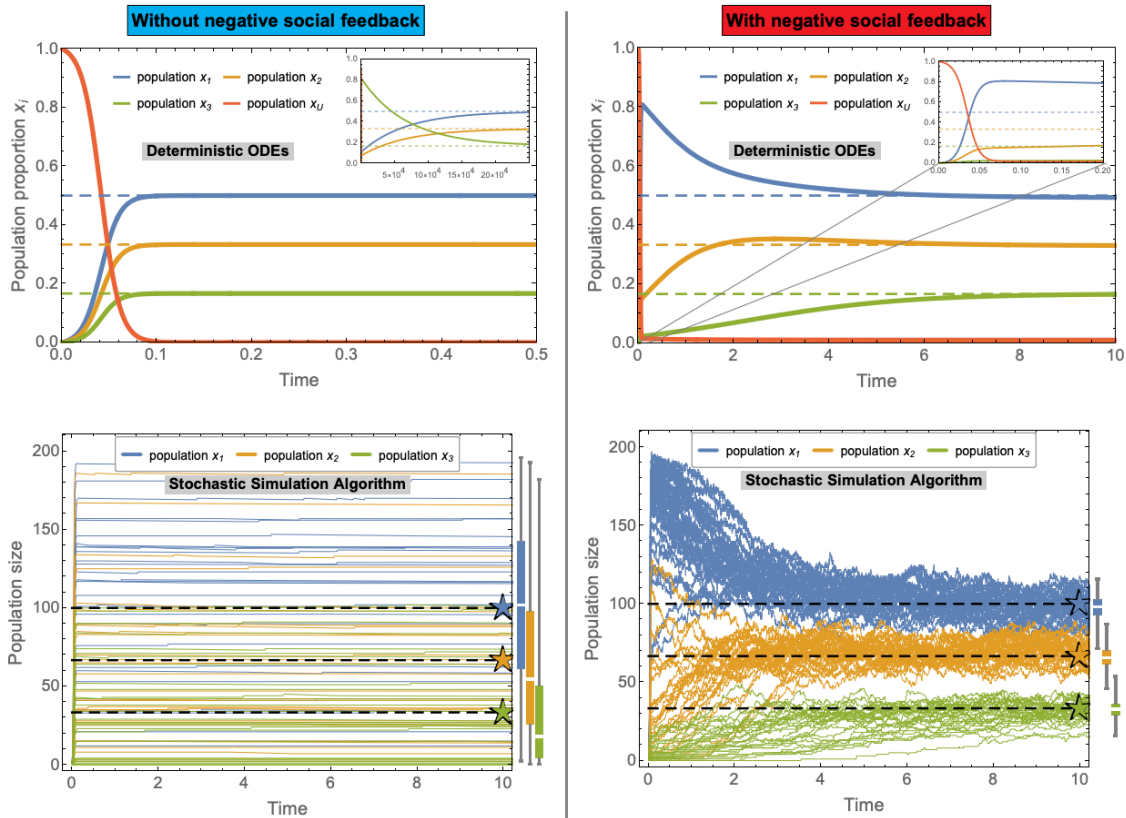


Figure 1: Temporal evolution of the models without (left) and with (right) negative social feedback in an environment with $n = 3$ food patches with qualities $q_1 = 0.75, q_2 = 0.5, q_3 = 0.25$. The top panels show the dynamics of the ODEs for systems of infinite size $S \rightarrow \infty$. The bottom panels show the trajectories of 30 representative runs of the stochastic simulation algorithm (SSA, [25]) for a system comprised of $S = 200$ individuals. The boxplots on the right of each bottom panel show the statistical aggregate at time 400 for 1000 runs of the SSA. (Other simulation parameters are: constant abandonment $a = 10^{-3}$, average recruitment strength $r = 100$, and stop signal strength $z \simeq 3.1$.) While the infinite size dynamics predict convergence to the target distribution of Eq. (1) (dashed lines) for both models, the stochastic trajectories show different results for the two models. The system without negative social feedback has smaller fluctuations over time but frequently stabilises at values far from the target distribution (bottom-left panel). The system with negative social feedback fluctuates more but always remains relatively close to the target distribution (bottom-right panel). The apparently quicker dynamics of the ODE model for the system without negative social feedback are due to the symmetric initial conditions. In the left inset, we show that a small perturbation of the initial population (*i.e.* $x_1, x_2 = 0$ and $x_3 = 0.05$) delays the convergence by more than 5 orders of magnitude. Such a susceptibility to random fluctuations is made evident by the stochastic trajectories. The right inset shows a zoom of the larger plot.

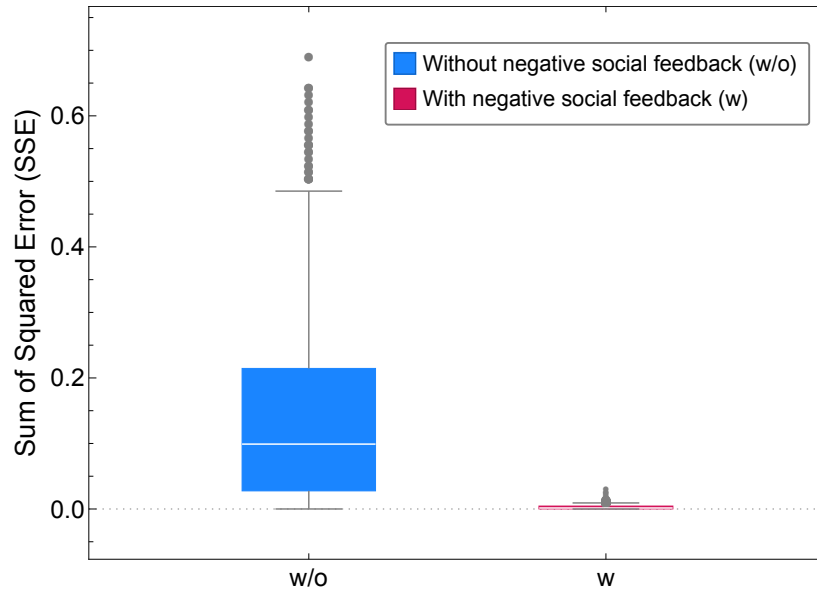


Figure 2: Sum of squared errors (SSE) computed as the sum for $n = 2$ food patches of the square of the difference between the subpopulation size at time 1000 (convergence) and the target distribution to that patch (see Supplementary Text ST7). The boxplots show the distribution of the SSE for 10^3 numerical simulations for swarm size $S = 200$, average recruitment strength $r = 100$, and qualities $q_1 = 0.75$ and $q_2 = 0.5$.

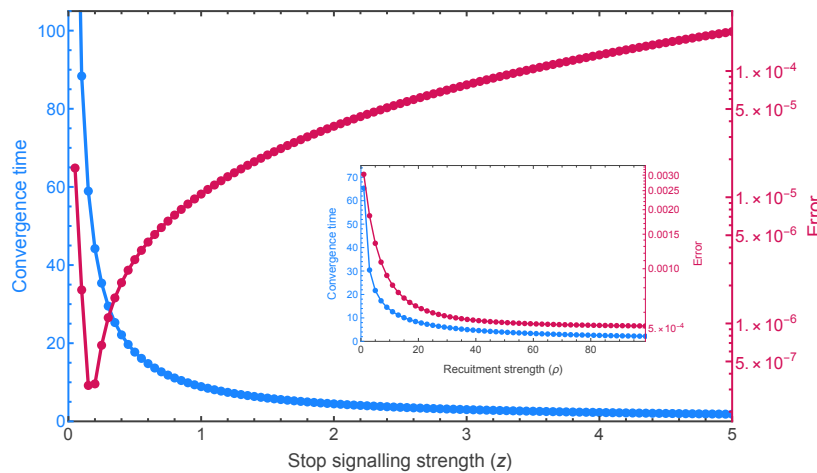


Figure 3: The stop signalling strength can be the control parameter in a speed-robustness trade-off. Stronger stop signalling speeds up the convergence of the system (magenta curve) but also increases the predicted error from the target distribution (blue curve). These results are in agreement with field observations that documented an increase in stop signalling when a quick response to environmental changes was necessary [10]. Both error and convergence time are computed from the infinite population model (ODE). The error is computed as the sum for every foraging population of the squared distance R^2 from the target at large time (convergence, computed analytically as the ODE's stable fixed point in the unit-simplex). The convergence time (magenta curve) is computed as the time necessary to reach the (numerically computed) fixed point. As the system has an asymptotic convergence, the reported time corresponds to the R^2 error becoming smaller than 10^{-4} .