Negative feedback may suppress variation to improve collective foraging performance

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Abstract

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

1 Introduction

Collectively-foraging social insects need to use feedback mechanisms in order to robustly and efficiently satisfy the nutritional requirements of the colony. Positive feedback signal usage by such foraging social insects are well known, such as mass-recruitment via pheromone in various ant species [1], and recruitment of small numbers of individuals such as via the honeybees' waggle-dance [2], or rock ants' tandem-running [3]. The use of negative feedback signals in these systems has, however received comparatively little attention. Negative feedback was predicted to be important for collectively foraging species [4, 5], and subsequently discovered in diverse systems such as Pharaoh's ants [6, 7] and honeybees [8, 9]. Several studies have interpreted negative feedback as a mechanism to reduce recruitment to a resource based on some aspect of its quality, for example allowing unrewarded trails to be shut down [6, 7], to allow recruitment to a crowded source of forage to be reduced [10], or transferring information that a forage patch may have an increased predation risk [8, 11]. Subsequent theoretical studies have similarly focussed on the role of negative feedback in dealing with time-varying forage patches [12].

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

Foraging theory is an active and complex research area, and our results do not rely on assumptions about the nature of the colony's target distribution, other than it can be achieved by agents with access only to local information at both the forage source, and the colony. Thus, the target distribution may be akin to an Ideal Free Distribution, in which agents are distributed such that none can improve

		WITHOUT NEGATIVE SOCIAL FEEDBACK	WITH NEGATIVE SOCIAL FEEDBACK
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 [23].

overall foraging efficiency by switching to a different forage patch [13, 14]. Alternatively, the target distribution may be based on the requirement of the colony for different micro- and macro-nutrients [15, 16, 17, 18]. Or, the target distribution may be based on some other objective entirely, or on combinations of objectives such as those just discussed. In ignoring the nature of the distribution, therefore, our focus is purely on the dynamics of foraging, and how negative feedback can improve this.

For our analysis we adapt our model from a simple model of negative feedback for foraging in honeybee colonies [12], in itself inspired by models of negative feedback in house-hunting honeybee swarms [19, 20, 21]; however since other social insect species such as Pharaoh's Ants also make use of negative feedback during foraging [6], we argue that the model is generally applicable.

2 Methods

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

$$x_i^* \approx \frac{q_i}{\sum_{j \in n} q_j}, \qquad i \in \{1, \ldots, n\}\,, \tag{1}$$

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

We assume that social recruitment (positive feedback) is much more efficient than independent discovery, so $r_i \gg q_i$. The model with only positive feedback is easy to solve for the desired equilibrium distribution of foragers, with a simple parameterisation of individuals' rates (see Supplementary Text). The model with negative feedback, however, requires a heuristic individual parameterisation based on site qualities, which we perform numerically (see Supplementary Text). However, this heuristic has a simple functional form (see Supplementary Text) so could easily be approximated by real foragers.

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

The mean-field model assumes an infinitely-large population size S and provides deterministic system dynamics in the absence of any noise from finite population effects. On the other hand, stochastic simulation of the master equation ([22]) gives a probabilistically correct simulation of dynamics of finite populations of size S.

3 Results

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

Through numerical integration of the master equations, we investigate the effect of stochastic fluctuations on the system dynamics [22]. The fluctuation size is inversely proportional to the system size S, *i.e.* there are no fluctuations in very large groups (*i.e.* $S \to \infty$) and large fluctuation in small groups. The effect of the system-size noise can be appreciated in the two bottom panels of Figure 1. They show 30 representative trajectories for a system of size $S = 200$. The higher variance can also be appreciated in the boxplots on the right of each bottom panel of Figure 1, in which the average of 1,000 simulations hits the target value in both models, however, the variance is reduced considerably with the introduction of negative social feedback.

Large deviations from the target distribution could compromise the ability of the colony to intake the necessary nutrients for survival and reproduction, thus decreasing colony fitness. Figure 2 shows how the cumulative error in achieving the target distribution is significantly higher without negative social feedback. Similarly, the speed of adaptation to environmental changes is an important factor in the survival of the colony. The system without negative feedback can be incapable of adapting to changes in a timely manner because its temporal dynamics vary significantly depending on the initial commitment (see top-left inset of Figure 1). The system with negative feedback, instead, displays a constant convergence time regardless of the initial state of the system (see Supplementary Material). Figure 3 shows how the convergence speed and the deviation from the target distribution are influenced by the strength of the negative feedback; the strength of negative feedback can tune a speed-robustness trade-off, similarly to the tuning of speed-value and speed-coherence trade-offs in consensus decisions [20, 21, 24].

4 Discussion

Negative feedback has been considered in collective decisions, particularly as a means of symmetry breaking [19, 20, 21, 25], and in foraging, as a means of adapting to dynamically changing environments [10, 7, 12]. Other than in entomology, negative feedback as been observed as a tool for noise reduction in gene networks [26, 27, 28] and in electronic systems [29, 30]. Here we have shown that negative feedback may play an important role in reducing variance in colony foraging performance. For example, considering the honeybee system that inspired our model, field observations have reported that levels of stop signalling increase in response to changes such as dangerous, overcrowded, or depleted food patches [31, 11, 10]; however, it has not yet been fully understood why, even in static conditions, honeybees always deliver a small quantity of stop signals to foragers visiting the same forage patch [10]. Our analysis gives an interpretation for such observed behaviour.

Our results suggest a further progression in the evolution of collective foraging behaviour; solitary foraging by members of social insect colonies evolved first, but was comparatively inefficient due to the need for foragers to repeatedly and independently discover forage sites [32, 33]. Subsequently, positive social feedback evolved to improve foraging efficiency [34, 35], but this came at the expense of robustness of the foraging outcome, through increased variance in foraging performance (see Supplementary Material). Finally, negative feedback evolved not only to respond better to changing environments, but also to reduce variance in foraging performance. The re-use of negative feedback signals, such as in the case of honeybee stop-signals which are used in both foraging [10] and house-hunting [19] life history stages, would facilitate performance-enhancing innovations in signalling behaviours; however, it is not clear whether stop-signalling first arose in foraging or in house-hunting contexts.

Some species have not evolved negative signalling mechanisms but rely on natural decay of feedback, such as pheromone evaporation. For instance, *Lasius niger* ants rely on the downregulation of positive feedback (*i.e.* pheromone deposition) in order to let pheromone decay take over [36, 37]. It is worth noting that this is not technically negative feedback; given the time taken from the first understandings of the positive-feedback signals in colonies of honeybees and ants [3, 38, 39] to that of the corresponding negative feedback signals [6, 40], it may be worth further exploring social insects in which explicit negative feedback has not been observed, to search for expected negative feedback mechanisms, or explain why their life history means they would not be beneficial. As a motivating example, decaying waggle dance durations in honeybee swarms were taken to be due to decay processes

internal to scout bees [41], but the negative stop-signal was subsequently discovered to be significant in these swarms [19].

We conclude by noting that our study highlights the importance of using multiscale modelling to understand collective behaviour [42, 43, 44]. In fact, through mean-field analysis we could not observe the dynamics that justify the use of the negative feedback. Instead, complementing the analysis with probabilistic models, we have been able to identify the systems dynamics that corroborate the appearance of stop signalling as a mechanism for variance reduction. Multiscale modelling is a valuable framework which combines the use of a set of modelling techniques to analyse the system at various levels of complexity and noise. In this study, we only employed noise-free mean-field analysis and master equations with system-size dependent noise. However, further analysis could include the impact of spatial noise, and time-correlated information and/or interactions [42].

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Author contributions

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

Competing interests

The authors declare no competing interests.

Code availability

A Mathematica notebook reproducing the analyses presented herein is available in the GitHub repository `https://github.com/DiODeProject/VarianceSuppression`.

This is supplemented by a notebook for MuMoT [42], an open-source tool for multiscale modelling, which reproduces similar results to those presented herein. The notebook is available online at `https://mybinder.org/v2/gh/DiODeProject/MuMoT/master?filepath=DemoNotebooks%2FVariance_suppression.ipynb`.

References

[1] B. Hölldobler and E. O. Wilson, *The Ants*. Harvard University Press, 1990.

[2] T. D. Seeley, *Honeybee Democracy*. Princeton University Press, 2010.

[3] M. Möglich, U. Maschwitz, and B. Hölldobler, "Tandem calling: A new kind of signal in ant communication," *Science*, vol. 186, no. 4168, pp. 1046–1047, 1974.

[4] T. R. Stickland, N. F. Britton, and N. R. Franks, "Models of information flow in ant foraging: the benefits of both attractive and repulsive signals," in *Information Processing in Social Insects*, pp. 83–100, Basel: Birkhäuser Basel, 1999.

[5] C. Detrain and J.-L. Deneubourg, "Self-organized structures in a superorganism: do ants "behave" like molecules?," *Physics of Life Reviews*, vol. 3, no. 3, pp. 162–187, 2006.

[6] E. J. H. Robinson, D. E. Jackson, M. Holcombe, and F. L. W. Ratnieks, "'No entry' signal in ant foraging," *Nature*, vol. 438, no. 7067, pp. 442–442, 2005.

[7] E. J. H. Robinson, F. L. W. Ratnieks, and M. Holcombe, "An agent-based model to investigate the roles of attractive and repellent pheromones in ant decision making during foraging," *Journal of Theoretical Biology*, vol. 255, no. 2, pp. 250–258, 2008.

[8] J. C. Nieh, "A negative feedback signal that is triggered by peril curbs honey bee recruitment," *Current Biology*, vol. 20, no. 4, pp. 310–315, 2010.

[9] P. M. Kietzman and P. K. Visscher, "The anti-waggle dance: use of the stop signal as negative feedback," *Frontiers in Ecology and Evolution*, vol. 3, no. February, pp. 1–5, 2015.

[10] C. W. Lau and J. C. Nieh, "Honey bee stop-signal production: temporal distribution and effect of feeder crowding," *Apidologie*, vol. 41, no. 1, pp. 87–95, 2010.

[11] K. Tan, S. Dong, X. Li, X. Liu, C. Wang, J. Li, and J. C. Nieh, "Honey bee inhibitory signaling is tuned to threat severity and can act as a colony alarm signal," *PLOS Biology*, vol. 14, no. 3, p. e1002423, 2016.

[12] S. Bidari, O. Peleg, and Z. P. Kilpatrick, "Social inhibition maintains adaptivity and consensus of honeybees foraging in dynamic environments," *Royal Society Open Science*, vol. 6, no. 12, p. 191681, 2019.

[13] L.-A. Giraldeau and T. Caraco, *Social foraging theory.* Princeton University Press, 2000.

[14] A. Lamb and J. Ollason, "Foraging wood-ants formica aquilonia yarrow (hymenoptera: formicidae) tend to adopt the ideal free distribution," *Behavioural Processes*, vol. 28, no. 3, pp. 189 – 198, 1993.

[15] J. M. McNamara, A. I. Houston, and E. J. Collins, "Optimality models in behavioral biology," *SIAM Review*, vol. 43, no. 3, pp. 413–466, 2001.

[16] O. Olsson, J. S. Brown, and K. L. Helf, "A guide to central place effects in foraging," *Theoretical Population Biology*, vol. 74, no. 1, pp. 22–33, 2008.

[17] A. Dussutour and S. J. Simpson, "Communal nutrition in ants," *Current Biology*, vol. 19, no. 9, pp. 740–744, 2009.

[18] A. I. Houston and J. M. McNamara, "Foraging currencies, metabolism and behavioural routines," *Journal of Animal Ecology*, vol. 83, no. 1, pp. 30–40, 2014.

[19] T. D. Seeley, P. K. Visscher, T. Schlegel, P. M. Hogan, N. R. Franks, and J. A. R. Marshall, "Stop signals provide cross inhibition in collective decision-making by honeybee swarms," *Science*, vol. 335, no. 6064, pp. 108–111, 2012.

[20] D. Pais, P. M. Hogan, T. Schlegel, N. R. Franks, N. E. Leonard, and J. A. R. Marshall, "A mechanism for value-sensitive decision-making," *PLoS ONE*, vol. 8, no. 9, p. e73216, 2013.

[21] A. Reina, J. A. R. Marshall, V. Trianni, and T. Bose, "Model of the best-of-N nest-site selection process in honeybees," *Physical Review E*, vol. 95, no. 5, p. 052411, 2017.

[22] D. T. Gillespie, "A general method for numerically simulating stochastic time evolution of coupled chemical reactions," *Journal of Computational Physics*, vol. 22, pp. 403–434, 1976.

[23] R. T. Jack-McCollough and J. C. Nieh, "Honeybees tune excitatory and inhibitory recruitment signalling to resource value and predation risk," *Animal Behaviour*, vol. 110, pp. 9–17, 2015.

[24] N. Franks, T. Richardson, N. Stroeymeyt, R. Kirby, W. Amos, P. Hogan, J. Marshall, and T. Schlegel, "Speed–cohesion trade-offs in collective decision making in ants and the concept of precision in animal behaviour," *Animal Behaviour*, vol. 85, no. 6, pp. 1233–1244, 2013.

[25] N. Zabzina, A. Dussutour, R. P. Mann, D. J. T. Sumpter, and S. C. Nicolis, "Symmetry restoring bifurcation in collective decision-making," *PLoS computational biology*, vol. 10, no. 12, p. e1003960, 2014.

[26] I. Lestas, G. Vinnicombe, and J. Paulsson, "Fundamental limits on the suppression of molecular fluctuations," *Nature*, vol. 467, no. 7312, pp. 174–178, 2010.

[27] A. S. Howell, M. Jin, C.-F. Wu, T. R. Zyla, T. C. Elston, and D. J. Lew, "Negative feedback enhances robustness in the yeast polarity establishment circuit," *Cell*, vol. 149, no. 2, pp. 322–333, 2012.

[28] L. Laurenti, A. Csikasz-Nagy, M. Kwiatkowska, and L. Cardelli, "Molecular filters for noise reduction," *Biophysical Journal*, vol. 114, no. 12, pp. 3000–3011, 2018.

[29] C. D. Motchenbacher and J. A. Connelly, *Low noise electronic system design.* Wiley, 1993.

[30] D. Pan, X. Ruan, C. Bao, W. Li, and X. Wang, "Capacitor-current-feedback active damping with reduced computation delay for improving robustness of LCL-type grid-connected inverter," *IEEE Transactions on Power Electronics*, vol. 29, no. 7, pp. 3414–3427, 2014.

[31] S. Dong, K. Tan, Q. Zhang, and J. C. Nieh, "Playbacks of asian honey bee stop signals demonstrate referential inhibitory communication," *Animal Behaviour*, vol. 148, pp. 29–37, 2019.

[32] F.-X. Dechaume-Moncharmont, A. Dornhaus, A. I. Houston, J. M. McNamara, E. J. Collins, and N. R. Franks, "The hidden cost of information in collective foraging," *Proceedings of the Royal Society B: Biological Sciences*, vol. 272, no. 1573, pp. 1689–1695, 2005.

[33] C. Grüter and E. Leadbeater, "Insights from insects about adaptive social information use," *Trends in Ecology & Evolution*, vol. 29, no. 3, pp. 177–184, 2014.

[34] J. C. Biesmeijer and T. D. Seeley, "The use of waggle dance information by honey bees throughout their foraging careers," *Behavioral Ecology and Sociobiology*, vol. 59, no. 1, pp. 133–142, 2005.

[35] C. Grüter, E. Leadbeater, and F. L. Ratnieks, "Social learning: The importance of copying others," *Current Biology*, vol. 20, no. 16, pp. R683–R685, 2010.

[36] T. J. Czaczkes, C. Grüter, and F. L. W. Ratnieks, "Negative feedback in ants: crowding results in less trail pheromone deposition," *Journal of The Royal Society Interface*, vol. 10, no. 81, p. 20121009, 2013.

[37] S. Wendt, N. Kleinhoelting, and T. J. Czaczkes, "Negative feedback: ants choose unoccupied over occupied food sources and lay more pheromone to them," *Journal of The Royal Society Interface*, vol. 17, no. 163, p. 20190661, 2020.

[38] K. v. Frisch and R. Jander, "Über den schwänzeltanz der bienen," *Zeitschrift für vergleichende Physiologie*, vol. 40, no. 3, pp. 239–263, 1957.

[39] B. Hölldobler, R. C. Stanton, and H. Markl, "Recruitment and food-retrieving behavior in novomessor (formicidae, hymenoptera): I. chemical signals," *Behavioral Ecology and Sociobiology*, vol. 4, pp. 163–181, 1978.

[40] J. C. Nieh, "The stop signal of honey bees: reconsidering its message," *Behavioral Ecology and Sociobiology*, vol. 33, no. 1, pp. 51–56, 1993.

[41] T. D. Seeley, "Consensus building during nest-site selection in honey bee swarms: the expiration of dissent," *Behavioral Ecology and Sociobiology*, vol. 53, no. 6, pp. 417–424, 2003.

[42] J. A. R. Marshall, A. Reina, and T. Bose, "Multiscale modelling tool: Mathematical modelling of collective behaviour without the maths," *PLoS ONE*, vol. 14, no. 9, p. e0222906, 2019.

[43] T. Biancalani, L. Dyson, and A. J. McKane, "Noise-induced bistable states and their mean switching time in foraging colonies," *Physical Review Letters*, vol. 112, no. 3, p. 038101, 2014.

[44] Y. Khaluf, C. Pinciroli, G. Valentini, and H. Hamann, "The impact of agent density on scalability in collective systems: noise-induced versus majority-based bistability," *Swarm Intelligence*, vol. 11, no. 2, pp. 155–179, 2017.

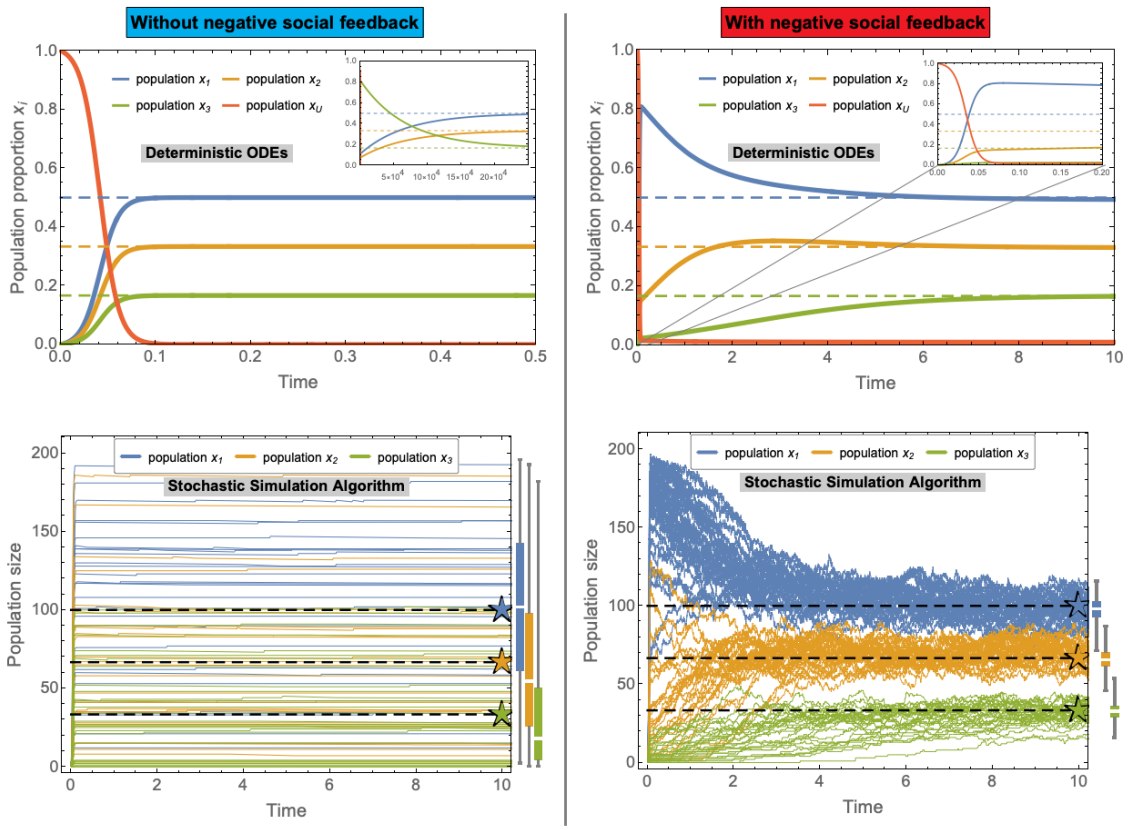

Figure 1: Temporal evolution of the models without (left) and with (right) negative social feedback in an environment with $n = 3$ food patches with qualities $q_1 = 0.75, q_2 = 0.5, q_3 = 0.25$. The top panels show the dynamics of the ODEs for systems of infinite size $S \to \infty$. The bottom panels show the trajectories of 30 representative runs of the stochastic simulation algorithm by Gillespie (SSA) 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 $a = 10^{-3}$, recruitment strength $\rho = 100$, 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 fluctuation 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 ODEs model for the system without negative social feedback are due to the symmetric initial conditions. In the left inset, we show that a small random perturbation of the initial population (*i.e.* $x_1, x_2 = 0$ and $x_3 = 0.05$) delays the convergence of more than 5 orders of magnitude. Such a fragility to random fluctuations is made evident by the stochastic trajectories. The right inset shows a zoom of the larger plot.

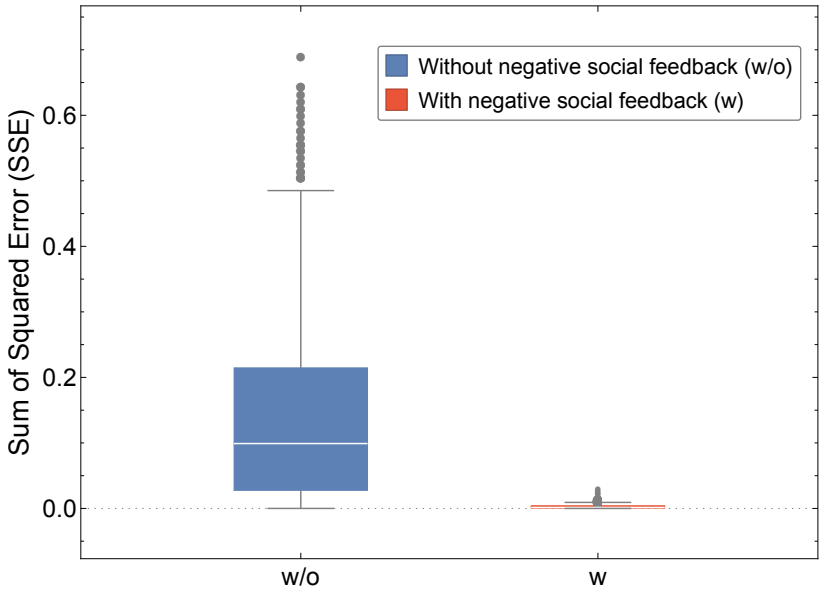

Figure 2: Sum of squared errors (SSE) computed as the sum for $n = 2$ food patches of the square of the difference between the subpopulation size at time 1000 (convergence) and the target distribution to that patch (see Supplementary Text). The boxplots show the distribution of the SSE for 10^3 numerical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

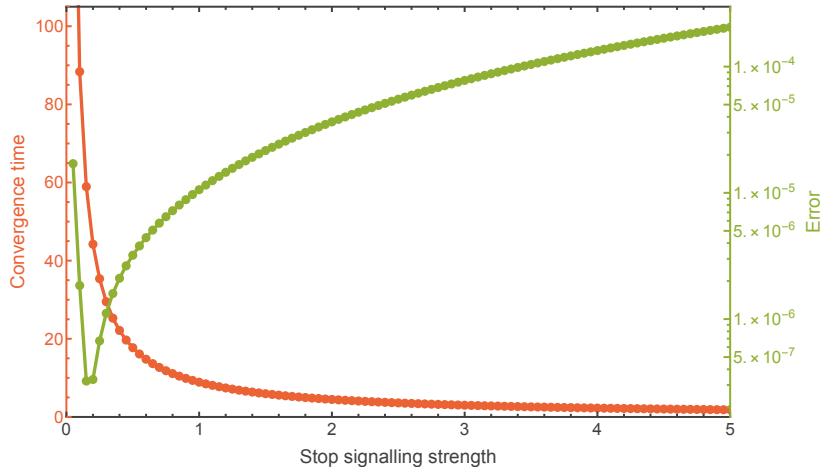

Figure 3: The stop signalling strength can be the control parameter in a speed-robustness trade-off. Stronger stop signalling speeds up the convergence of the system (orange curve) but also increases the predicted error from the target distribution (green curve). These results are in agreement with field observations that documented an increase in stop signalling when a quick response to environmental changes was necessary [10]. The error is computed as the sum for every foraging population of the squared distance R^2 from the target at large time (convergence). The convergence time (red 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 when the R^2 error becomes smaller than 10^{-4}.