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Again, the positive equilibrium $u_þ^2$ is stable and the negative equilibrium u^2 is unstable. On t [T, T +), (t) = 0 and $a(t \quad t) ¼ a$, equilibria satisfy $0 = (1 \quad u) u \quad u$, so

$$u_0^3 ¼ 0 \quad \text{and} \quad u_1^3 ¼ \frac{b \quad g}{b},$$

and on t [T + , 2T), (t) = (t) = 0, so $0 ¼ (1 \quad u)bu \quad gu \quad rau^2$ and

$$u_0^4 ¼ 0 \quad \text{and} \quad u_1^4 ¼ \frac{b \quad g}{b þ ra}:$$

Both pairs of equilibria have associated eigenvalues

$$l_0 ¼ b \quad g \quad \text{and} \quad l_1 ¼ g \quad b,$$

so the zero equilibria $u_0^3 ¼ u_0^4 ¼ 0$ are stable when > and the non-zero equilibria u_1^3 and u_1^4 are positive and stable when > . Thus, to ensure no bees continue foraging when there is no food, abandonment should be stronger than recruitment .

We deem $u :¼ u_þ^2$ the consensuslevel, as it is the upper limit on the fraction of the bees foraging at the feeder, when it supplies food. The eigenvalues $l_{on} :¼ l_þ^2$ and $l_{off} :¼ l_0^4$ define the adaptivity of the colony, or the rates of arrival to/departure from the feeder when it does/does not supply food.

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Long-term periodic solutions to equation (2.3) result from switching the food quality (t) between *a* and 0 every T min. These are obtained by solving equation (2.3) iteratively using separation of variables. For example, when *a*(t) ; *a* and (t) 0 we can separate variables and factor the resulting fraction

$$\frac{du}{u \quad u_þ} \quad \frac{du}{u \quad u} ¼ \quad (b þ ra)^{p} D\, dt,$$

where D is defined in equation (A 1). Integrating, isolating u and applying $u(0) = u_0$, we find

$$u(t) ¼ \frac{u_þ (u_0 \quad u) \quad u (u_0 \quad u_þ) e^{\ (bþra)^{p} Dt}}{u_0 \quad u \quad (u_0 \quad u_þ) e^{\ (bþra)^{p} Dt}}, \qquad \text{(A 2)}$$

consistent with our equilibrium analysis showing $\lim_{t! \ 1} u(t) ¼ u ¼ u_þ^2$. Now, taking *a*(t) ; *a* on t [2nT, (2n + 1)T) for n = 0, 1, 2, 3,... and *a* ; 0 otherwise, we will have

$$\underline{u} ¼ (1 \quad u)(a(t) þ bu) \quad gu \quad R(t)u^2, \qquad \text{(A 3)}$$

where R(t) ; *ra* for t [2nT + , (2n + 1)T +) and R(t) 0 otherwise. The periodic solution to equation (A 3) can be derived self-consistently by starting with an unknown initial condition $u(0) = u_0$, and then requiring $u(2T) = u_0$. Thus, withi f y s t a r t i . Thus, withi f y s t a r t i . Thus, wit u r e s e v t h n s 3 0 6 . 8 2 2 (i) 0 1 T f 3 (2

for , and the limit as is $u(t) = u_2/(1 + u_2\ t)$, which can both be evaluated at $t = T +$ to yield

$$u_3 := u(T + t) = \begin{cases} \dfrac{u_2(b - g)}{bu_2 - (bu_2 + g - b)e^{(g-b)t}} & : b = g \\ \dfrac{u_2}{1 + u_2 bt} & : b = g. \end{cases} \qquad \text{(A 7)}$$

At $t = T +$, self-inhibition returns since $(t -) > 0$, increases the negative feedback acting on foragers. The long-term steady state is determined by the balance of abandonment and recruitment: $(u_+, u_-) = (b - g/b + ra, 0)$ if $>$ and $(u_+, u_-) = (0, b - g/b + ra)$ if $<$. Thus,

$$u(t) = \frac{u_3(b - g)}{(b + ra)u_3 - ((b + ra)u_3 + g - b)e^{(g-b)t}}$$

for , and in the limit , $u(t) = u_3/(1 + u_3(b + ra)t)$. Both expressions can be evaluated at $t = 2T$, and self-consistency of the periodic solution requires $u_4 - u_0$,

$$u_0 = u_4 := u(2T) = \begin{cases} \dfrac{u_3(b - g)}{(b + ra)u_3 - ((b + ra)u_3 + g - b)e^{(g-b)(T-t)}} & : b = g \\ \dfrac{u_3}{1 + u_3(b + ra)(T - t)} & : b = g \end{cases} \qquad \text{(A 8)}$$

equations (A 4), (A 6), (A 7) and (A 8) can be solved explicitly for (u_0, u_1, u_2, u_3), although the expressions

In the long interval lim $_T$ and short delay lim $_0$ (omitting the intermediate delay equilibria) limits, we can simplify the expression as

$$J \frac{u}{2} (a \quad c) \; 1 \quad \frac{1 \quad e^{\; l_{on} T}}{l_{on} T} \qquad c \frac{1 \quad e^{\; l_{off} T}}{l_{off} T} \; ,$$

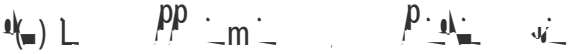
where $u = u^2$, $l_{on} = l^2 = l_{þ}^2$ and $_{off} = {}^4 = {}_0$, as written in equation (2.6). For the specific case in which $a = 2$ and $c = 1$, we can write this more cleanly as

$$J(a(t), b, g, r) = \frac{u}{2} \quad 1 \quad \frac{1 \quad e^{\; l_{on} T}}{l_{on} T} \qquad \frac{1 \quad e^{\; l_{off} T}}{l_{off} T} \; :$$

Clearly, increasing consensus (1) and adaptivity ($_{on/off}$) increases the RR.

As 0, $_{off} =$, $u = 2=[2 þ g]$, with $_{on} = (2 +)$. Increasing the rate of abandonment decreases consensusu

a [[0:5, 20] (at D*a* ¼ 0:1 steps) and T [1, 200] (at T = 1 min). See figure 5 for direct switching and figures 8 and 9 for discriminate and indiscriminate stop-signalling model, respectively. For the self-inhibition model, the optimal strategy is low abandonment (= 0.01 min ^{1}) with high recruitment and social inhibition (= = 10 min ^{1}). The maximum RR is plotted for each of the four models in a given environmental condition (food quality *a* and switching period T) in figure 4.



To compute consensus and adaptivity, we derived a linear approximation to the period solution in the two-feeder case. Feeder qualities started with $a_A(t) = a$ and a_B

Considering the single-feeder foraging colony model without nonlinear negative feedback (= 0 so delays are irrelevant), we can explicitly compute the RR J as a function of other parameters. We found that the best strategies do not use recruitment (= 0), so the abandonment rate is the only parameter that needs to be tuned with the environmental switching time T and food quality *a*.

Thus, equation (2.3) is linear and so the linear approximation of the periodic solution is exact, described by

$$u(t) = \begin{cases} A + (u_0 - A)e^{-(a+g)t}, & t \in [0, T) \\ u_1 e^{-g(t-T)}, & t \in [T, 2T), \end{cases}$$

where $u_0 = A(1 - e^{-(a+g)T})/(e^{gT} - e^{-(a+g)T})$ and $u_1 = A(e^{gT} - e^{-aT})/(e^{gT} - e^{-(a+g)T})$. As such, we can explicitly compute the RR equation (2.4),

$$J = \frac{a - c}{2T} - AT + \frac{u_0 - A}{a + g}(1 - e^{-(a+g)T}) - \frac{c}{2T} - \frac{A}{g}(1 - e^{-gT}),$$

determining the maximum with respect to the abandonment rate by solving J= 0 (figure 7). The optimal abandonment rate increases with the feeder quality and decreases with the switching time T of the environment. Thus, the negative feedback process should adapt to the dynamics of the environment, and discounting can be more rapid when the evidence for feeder quality is stronger.

Similar to figure 5, we optimized interactions for the discriminate stop-signalling and indiscriminate stop-signalling model to yield the highest RR equation (2.2).

In the discriminate stop-signalling model, weak recruitment

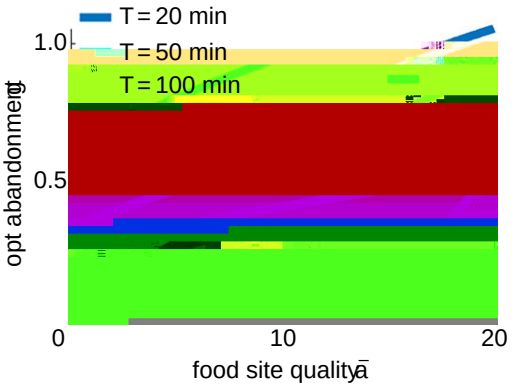


Figure 7. R , (2.4), m m b m ( ) p m ( ) p (T) m . m m J b b b m m m m . (min)

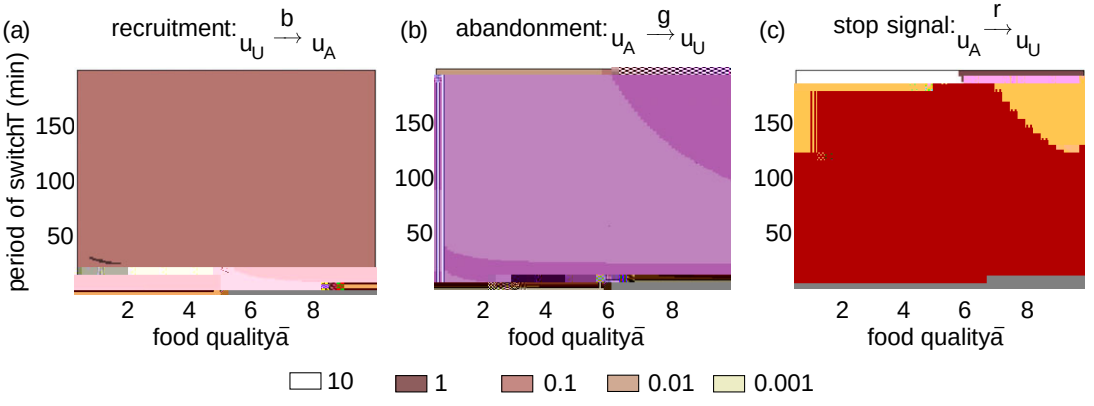
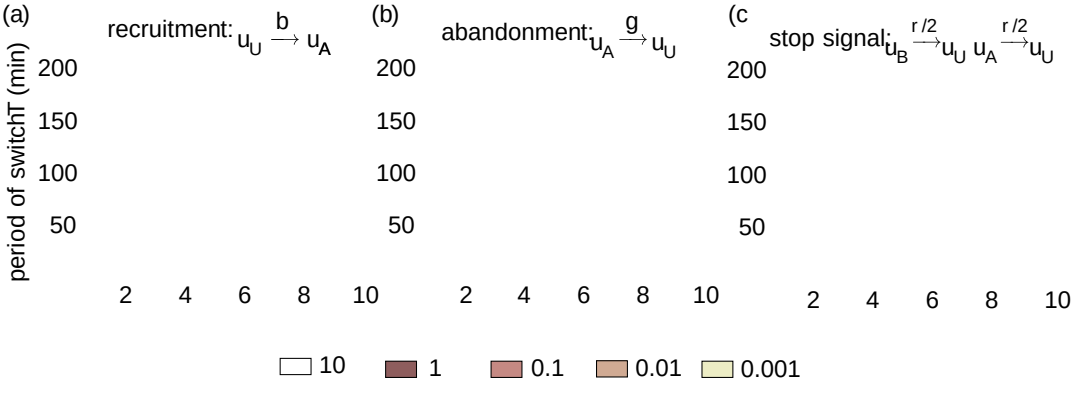
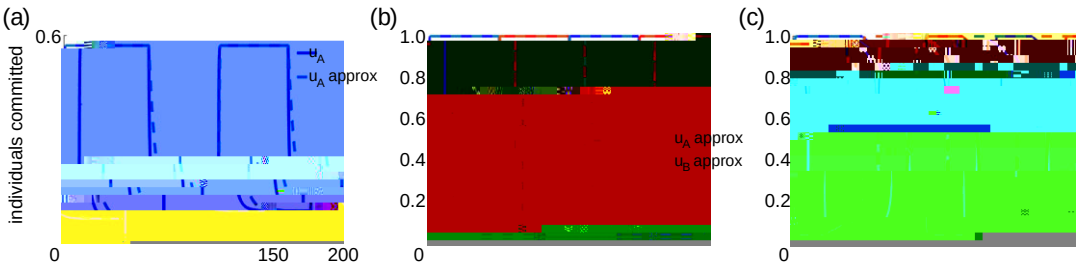


Figure 8. T (a) m ; (b) b m ; (c) b m m (RR) ((2.2)), m p m . (a) R m (b) b m b m (c) b b m p (T) a m .



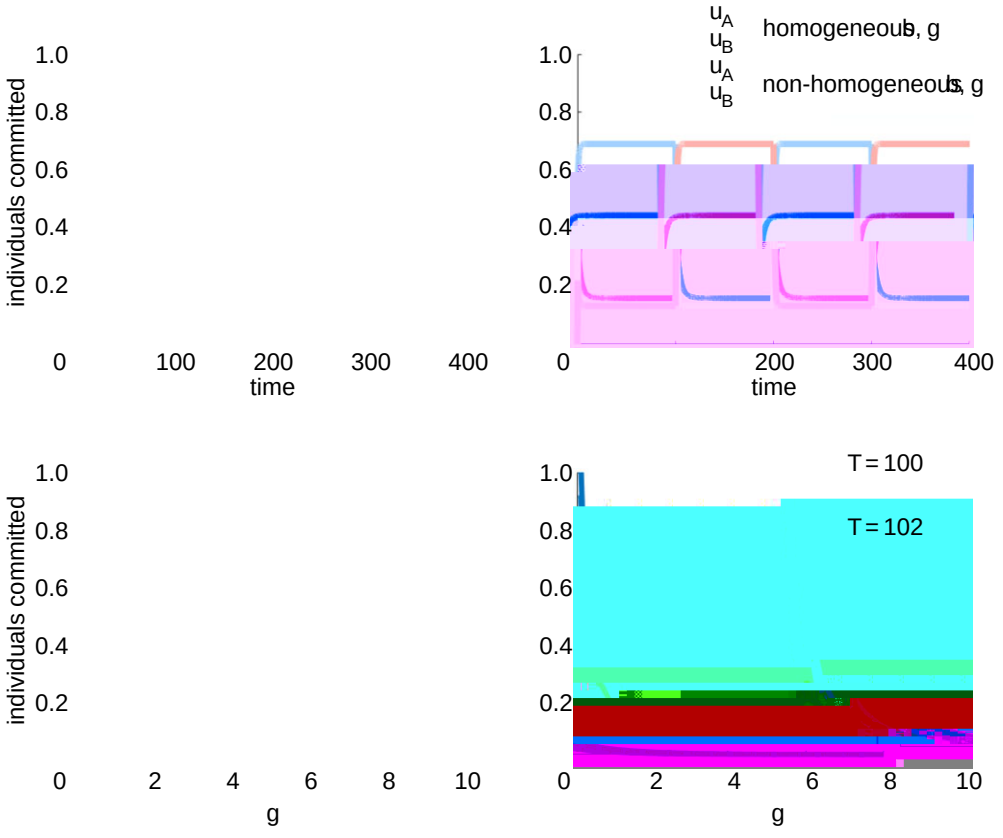
social inhibition (for example, figure 10 a,b). If the system is not poised close to a bifurcation, the dynamics between switches roughly linearly decays to the stable equilibrium. However, in the discriminate stop-signalling model, the system can lie close to the saddle-node bifurcation beyond which the model exhibits bistability (figure 10 c). In this case, the ghost of the saddle-node slows the solution trajectory, a nonlinear effect which is not well characterized by a linear approximation [70].



Here, we calculate consensus u and adaptivity across a wider range of environments as the abandonment rate (figure 11) and social inhibition rate (figure 12) are varied. The general trends observed in figure 6b,c are preserved. For strong enough abandonment , adaptivity increases as u decreases, and direct switching tends to balance this trade-off best (figure 11). Indiscriminate stop-signalling presents a similar trade-off as social inhibition strength is increased (figure 12), while the other social inhibition mechanisms eventually show increases in both consensus u and adaptivity , but again direct switching tends to provide higher levels of both overall.

Here, we introduce and simulate a model of a colony whose bees have recruitment and forgetting rates drawn from a distribution p(,). Here, each parameter and is drawn independently

from a gamma distribution (a, b) with shape a and rate b whose mean a/b is set equal to the



In the case of the single-feeder model, the master equation for the probability $p(n, t)$ of finding n bees committed to foraging at time t is

$$\dot{p}(n, t) = r_+(n-1)p(n-1, t) + r_-(n+1)p(n+1, t) - [r_+(n) + r_-(n)]p(n, t), \qquad (C\ 2)$$

for integer $n = 0, 1, 2, \ldots, N$ with boundary conditions $p(-1, t) = p(N+1, t) = 0$ and forward and backward transition rates

$$r_+(n) = (N-n)(a(t) + bn) \quad \text{and} \quad r_-(n) = gn + \kappa(a - a(t-\tau))n^2$$

for system size (total bee number) N. To obtain the mean-field equation (2.3) as $N \to \infty$ [26,71], one must define $a(t) = a(t)/N$, $b = b/N^2$, $g = g/N$ and $\kappa = \kappa/N^2$. Note, the scalings correspond to the power of the population count appearing in the interaction term, ensuring the transition terms remain bounded in the thermodynamic limit. We used the stochastic simulation algorithm by Gillespie [72] to evolve the stochastic system for the statistic plotted in figure 14*a*,*b*. We make two remarks about our findings. First, the colony generally increases the fraction of committed foragers when food is present at the feeder and decreases when food is removed. Second, the amplitude of fluctuations in individual simulations decreases with system size, as typically expected [71], as evidenced by the narrower standard deviations in the solution trajectories in the $N = 1000$ versus the $N = 100$ simulations.

In the case of the two-feeder model, the master equation is more complicated as it must track the probability of transitions between uncommitted bees, bees committed to feeder A, and those committed to feeder B. Indeed, we can write the model down for any of the four forms of social

inhibition, but we just provide the discriminate stop-signalling model here. Others can be written similarly. The probability $p(n_A, n_B, t)$ of finding n_A bees committed to A and n_B committed to B at time t given system size N is (dropping the argument in t for brevity):

$$\dot{p}(n_A, n_B) = r_{0A}(n_A - 1, n_B)p(n_A - 1, n_B) + r_{0B}(n_A, n_B$$

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