

Social Patch Foraging Theory in an Egalitarian Group

Lisa Blum Moyse^{✉*} and Ahmed El Hady[†]

Centre for the Advanced Study of Collective Behavior, [University of Konstanz](#), Konstanz, Germany



(Received 18 December 2024; accepted 2 July 2025; published 22 July 2025)

Foraging is a widespread behavior. Specifically, social foraging can bring several benefits compared to solitary foraging, such as collective pooling of information and reducing environmental uncertainty. Based on an evidence accumulation framework, we developed a model of patch-leaving decisions in a large egalitarian group, going through two intertwined paradigms: in which habitat to forage and, inside habitats, how to balance exploration and exploitation in patches. In this paper, we define patches as small areas that are rapidly depleted, in contrast to habitats, defined as larger areas, almost nondepleted. Across these two environments, we used numerical simulations and analytical tools to quantify the collective foraging dynamics. We showed that three variables—the cohesion of a group, the mean residence times, and the accuracy in finding the best habitat—are relevant metrics to characterize the collective processes. In particular, cohesion, a less studied aspect in classical foraging approaches, characterizes the initial nonstationarity of the dynamics and is ecologically relevant as it provides risk dilution in the presence of threat. These metrics are shaped by different environment statistics, such as reward probabilities, travel time between areas, or the depletion rate. They also enable the quantification of the impact of social information. We found that these metrics are strongly modulated by social interactions and that different types of information sharing mechanisms give rise to a variety of emergent collective patterns. In particular, most interaction types increase accuracy, but have nontrivial and various effects on cohesion and exploration-exploitation tradeoff. The effects of these social interactions were similar in habitats and patches. We expect this flexible and quantitative model to be relevant for analyzing large scale foraging datasets and formulating hypotheses.

DOI: [10.1103/mqxr-1nyv](https://doi.org/10.1103/mqxr-1nyv)

I. INTRODUCTION

Foraging is a widespread decision-making process [1], which constitutes complex multilevel behavior on different spatial and time scales. This process entails two main questions: where to forage and how long to exploit a certain resource [2]. For the first question, the associated process corresponds to “habitat choice” [3], where individuals choose a large area in which to forage, without significant modifications to the environment. Once a habitat is chosen, animals exploit resources in smaller regions within, patches, which are depleted by their activity. We refer to this process as “patch exploitation.” For both processes, the foraging areas can be conceptualized as patches. The difference lies in the depletion rate of resources in these regions.

Within these environments, many animal species forage socially. For example, eusocial insects [4], birds [5], rats [6], meerkats [7], or baboons [8] forage collectively. Although

social foraging affects resource availability [9], being part of a group brings several benefits compared to solitary foraging, such as safety against predators [10], enhanced ability to capture prey [11], or collective sharing of information [12,13]. In fact, for the latter, the sharing of social information can lead to greater foraging success [14,15].

To investigate the underlying processes of social foraging, several theories and quantitative models have been developed. A theory such as ideal free distribution predicts the distribution of foraging individuals among patches with different amounts of food so that fitness is optimized and competition is minimized [16]. However, empirical data often show a deviation from these predictions [17]. Another model uses the marginal value theorem, modified to study the residence times of groups, compared to solitary ones [18]. Agent-based models are a useful framework for implementing complex individual and interaction rules [19], as well as reinforcement learning models [20,21]. Some game-theoretic approaches have also been applied to social foraging [22,23], which allows the study of competitive and cooperative behaviors between agents, or the impact of a group’s size. The way agents integrate their personal and social information to increase their knowledge of their environment has been studied in Bayesian models [24]. Movement decisions in groups can also be studied theoretically, to understand the impact of the proportion of informed individuals [25].

However, the aforementioned approaches are often coarse grained, implying general interaction rules, or are too

*Contact another: lisa.blum-moyse@ens-lyon.fr

†Present address: Department of Collective Behaviour, Max Planck Institute of Animal Behaviour, Konstanz, Germany.

Published by the American Physical Society under the terms of the [Creative Commons Attribution 4.0 International](#) license. Further distribution of this work must maintain attribution to the author(s) and the published article’s title, journal citation, and DOI.

complex to be treated analytically. Another limitation is that uncertainty and noise in decision processes are often not taken into account, which can strongly shape the agents' patch departure statistics [26,27]. This calls for the development of an analytically tractable framework, including inherent stochasticity, to study the mechanisms underlying social foraging under a variety of social and environmental conditions.

Our aim in this study is to develop a new framework for describing quantitatively collective patch foraging dynamics, focusing on collaborative foraging. Our model is built on a widespread stochastic decision-making framework based on the evidence accumulation process, drift-diffusion models, which can be applied to patch-leaving tasks [26]. Such processes have related neural correlates [28,29], and have been useful in understanding the neural basis involved in binary perceptual choices [30].

So far, such mechanistic models have focused only on one [26] or two foragers [31]. The latter model introduced a theoretical framework to study coupled agents for different interaction mechanisms [31]. In this paper, the model is generalized to larger groups, with more interaction mechanisms. To investigate with precision the effects of social information, we rely on the following classification of these social interactions [32,33]. They can be broadly divided into two categories: environmental information actively shared through specific signals between agents or social information observed by others. In addition to these directed signals, social foraging can also be based on information-bearing cues [33]. Inside this category, two types of social information can be distinguished: social cues, which expose the internal belief of an individual, and public information, when the behavior of another agent reveals information about the environment.

With our framework, we investigate quantitatively the emergent foraging properties in different behavioral tasks—habitat choice and patch exploitation—and how they are shaped by social information.

II. METHODS

A. Environments: Habitats and patches

All variables and parameters are summarized in Tables I. and II. N agents move between different habitats or patches identified by a number k , separated by a travel time T_{tr} . For a two-habitat environment in Sec. III A, $k = 0$ is the initial habitat, and $k = 1$ is the highest quality habitat. For successive patches in Sec. III B, the patches are numbered from 1 to K , and $k = 1$ is the initial patch.

For both situations, the local foraging area, habitat or patch, can be conceptualized as a 'patch'; the key difference is whether or not the foragers affect the resource availability.

In a given habitat/patch k , at each time step an agent i has a probability p^k of receiving rewards according to a time-dependent reward function $r_i(t)$, equal to 1 s^{-1} if a piece of food is received, 0 s^{-1} otherwise. This quasicontinuous situation (small time step) can be reproduced in a laboratory, with experiments controlling the reward rate provided, or in natural landscapes where the possibilities of receiving pieces of food are numerous. This quasicontinuous approximation

TABLE I. Variable and parameter definitions of the model.

Variable or parameter	Definition
i	Index of an agent
k	Index of a patch
x_i	Decision variable
α	Cost of foraging
$r_i(t)$	Food reward
B	Noise parameter
$W(t)$	Wiener process
θ	Decision threshold
T_{tr}	Travel time between patches
$p^k(t)$	Probability of reward
p_{in}	Initial probability of reward
A_m	Maximum amount of food
$n^k(t)$	Number of agents in a habitat/patch
$c_{ij}(t)$	Coupling term
κ_r	Reward strength
κ_{diff}	Diffusive strength
κ_d	Departure strength
κ_a	Arrival strength
κ_c	Counting strength
η	Counting threshold

also makes the comparison easier with the marginal value theorem, which assumes continuous rewards.

In habitats, this reward probability is constant, while in patches it decreases as the amount of food consumed. In the latter case, the reward probability is updated as $dp^k(t) = -\sum_{i \in k} r_i(t)/A_m$, with A_m the maximum amount of food that can be contained in a patch.

Animals integrate this personal food availability information, which in turn modulates their departure decision process.

B. Habitat/patch leaving decision process

In this model, we provide a mechanistic description of when to leave a habitat/patch based on the actual experience of rewards [34–37]. Motivated by models of decision making [38,39], which have already been applied to patch-leaving decisions [26], we represent this using a drift-diffusion process

TABLE II. Variable and parameter definitions of the analysis.

Variable or parameter	Definition
$\mu^k(t)$	Effective drift term
$\Psi^k(t)$	Unit probability density of leaving
$\Omega^k(t)$	Unit probability to be in the patch
$P^k(t)$	Probability density of leaving
$Q^k(t)$	Fraction of agents
$P_{nc}^k(t)$	$P^k(t)$ for noncoupled agents
$Q_{nc}^k(t)$	$Q^k(t)$ for noncoupled agents
μ_s^k	$\mu^k(t)$ in a steady state
P_s^k	$P^k(t)$ in a steady state
Q_s^k	$Q^k(t)$ in a steady state (accuracy)
$\bar{T}^k$	Mean residence time (exploitation)
γ	Cohesion parameter (cohesion)

through a patch decision variable x_i . Upon entering a patch, $x_i = 0$, and changes in x_i occur with evidence accumulation from a constant drift α and time-dependent rewards $r_i(t)$. The forager decides to leave the patch when the threshold of $x_i = \theta$ is reached. This decision variable evolves according to the following stochastic differential equation:

$$dx_i(t) = (r_i(t) - \alpha)dt + \sum_{j \neq i} c_{ij}(t)dt + \sqrt{2B}dW_i(t) \quad (1)$$

The stochastic part of the equation is composed of $W_i(t)$, the standard Wiener process, and B the noise amplitude. In addition to the individual parts, we include the sum of social information from other agents j in the same habitat/patch, $\sum_{j \neq i} c_{ij}(t)$, extending preliminary results with two interacting agents [31].

C. Integrated social information

In this paper, we consider four different social information gathering mechanisms; see Fig. 2(a). One way to convey information is through actively shared signals [15,32,33].

1. Signaling (diffusive)

An example of active signals is vocalization, used to communicate in species such as capuchin monkeys [40] or bats [41]. In bees, information about patch locations can be communicated through the waggle dance [42]. Another mechanism, trophallaxis—the exchange of liquid food by mouth—allows honeybees to learn associations between nectar odors and rewards [43]. In this paper, we focus on continuous belief signaling, sometimes referred to as diffusive coupling. This mechanism has already been studied in a patch-leaving task with two agents [31], as well as in some “ideal groups” of decision makers [44,45], and in models of migrating animal groups [46,47]. It is mathematically described as the coupling of decision states between agents:

$$c_{ij}(t) = \frac{\kappa_{\text{diff}}}{N} [x_j(t) - x_i(t)]. \quad (2)$$

The parameter κ_{diff} is the diffusive coupling strength. It is normalized by the size of the group N , so that the sum in Eq. (1) represents the averaged social information over all agents in the same habitat/patch. Please see Fig. 8 in Appendix G for the scaling by the number of agents in a habitat/patch $n^k(t)$, which assumes an additional computation for the animals to evaluate this variable.

Signaling is a direct way to communicate one’s belief, but social information can also be inferred through inadvertent social information, such as social cues whereby an animal’s behavior reveals their internal beliefs. [15,33]. For example, the presence of other individuals constitutes a social cue that may attract the observer to a habitat/patch location. This process is known as local enhancement [32]. Examples of this phenomenon can be found in various species, such as birds that tend to move to places where other birds are feeding [48], or in Norway rats, that follow each other from their burrows to food or water locations [49]. In this paper, we focus on

two different underlying mechanisms that could lead to local enhancement.

2. Local enhancement (counting)

A possible mechanism of local enhancement could be through counting the number of conspecifics and finding where the highest fraction of the group is. We refer to this process as counting coupling. It is mathematically represented as the difference between the fraction of agents in a habitat/patch k and a counting threshold η . For clarity reasons, we write this term without the sum in Eq. (1):

$$c_i(t) = \kappa_c \left(\frac{n^k(t)}{N} - \eta \right), \quad (3)$$

where κ_c is the counting coupling strength.

If many agents are in the same patch, $n^k(t)/N > \eta$, so $c_i(t) > 0$, i.e., the agent accumulates evidence to stay in the habitat/patch; inversely for $n^k(t)/N < \eta$.

Counting coupling is thus based on the computation of the group’s proportion at one place at any time t . Other mechanisms may underlie local enhancement without this continuous evaluation, such as the observation of others’ movements between habitats/patches.

3. Local enhancement (pulsatile)

This alternative relies on pulsatile information, shared only when a departure decision is made [31,50,51], or when another agent enters the habitat. We refer to these processes as departure and arrival pulsatile couplings. The latter is studied only in a habitat choice task; in fact, the arrival information in successive patch foraging is less relevant since individuals do not go back to the previous patches.

The departure coupling is mathematically described as

$$c_{ij}(t) = -\frac{\kappa_d}{N_d dt} \delta(x_j(t) - \theta), \quad (4)$$

where κ_d is the departure coupling strength. When the agents j ’s decision variable reaches the threshold θ , i.e., the agent leaves, then $c_{ij}(t) < 0$. This means that the observing agent i is more likely to follow this leaving individual. The scaling by dt is related to the discrete effect of this coupling (nonzero Dirac), which means that it is modifying the differential equation Eq. (1) with $-\kappa_d$ (without the dt in the decision equation). The coupling term is normalized either by the size of the group $N_d = N$, or by the number of other individuals in the habitat/patch $N_d = n^k - 1$. The second normalization assumes an additional computation for the animals to evaluate this variable.

Inversely, if an agent j is arriving in the habitat (after the decision to leave the previous one, plus a travel time T_{tr}), then

$$c_{ij}(t) = \frac{\kappa_a}{N_a dt} \delta(x_j(t - T_{tr}) - \theta), \quad (5)$$

where κ_a is the arrival coupling strength. In this case $c_{ij}(t) > 0$, which means that the observer i is more likely to remain in their current habitat/patch. The coupling term is normalized either by the size of the group, $N_a = N$, or by the number of other individuals in the other habitat/patch, $N_a = N - n^k - 1$.

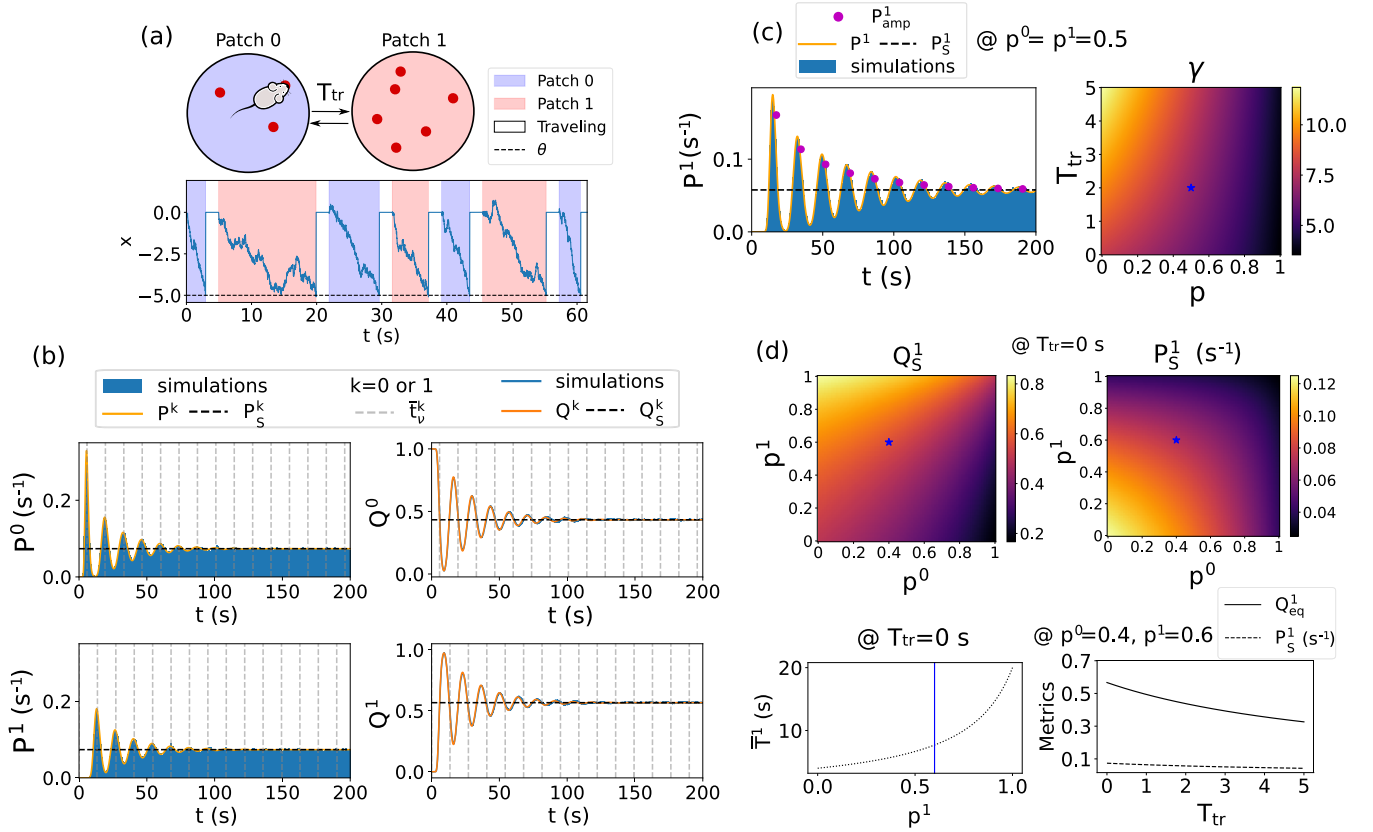


FIG. 1. Habitat choice dynamics is shaped by environmental statistics. (a) Schema of the two-habitat environment. Foraging agents accumulate evidence in a habitat (e.g., habitat 0, shaded in blue), and leave it when their decision variable x reaches the threshold θ . They then go to the other habitat (e.g., habitat 1, shaded in red), after a travel time (nonshaded area). This process is repeated during the duration of the experiment. (b) Distribution density of leaving times $P^k(t)$ (left) and fraction of agents $Q^k(t)$ (right) in habitats $k = 0$ (top) and $k = 1$ (bottom) show oscillations converging to a steady state (2×10^4 simulations). (c) Damped oscillations quantification. Left: $P^k_{A,v}$ amplitudes diminish with time (2×10^4 simulations). Right: The cohesion parameter γ decreases with the reward probability $p = p^0 = p^1$ and increases with T_{tr} . The blue star corresponds to the set of parameters in (b). (d) Steady states and mean residence time quantification. Top left: Steady state fraction in the best habitat Q^1_S increases with p^1 and decreases with p^0 . Top right: Steady state leaving probability of the best habitat P^1_S decreases with p^0 and p^1 . In this noninteracting situation, $P^1_S = P^0_S$. The blue star corresponds to the set of parameters in (b). Bottom left: Mean best habitat residence time $\bar{T}^1$ increases with p^1 . The blue vertical line corresponds to the set of parameters in (b). Bottom right: Q^1_S, P^1_S decrease with the travel time T_{tr} .

Social cues enable observers to catch information about others' beliefs. Another type of inadvertent social information may be directly related to the characteristics of the environment. This information is provided when the behavior of individuals makes some environmental cues available to observers [32]. For example, this phenomenon has been observed in starlings [52], where the observation of the success of others in foraging provides information on the current patch [53].

4. Public information (reward)

Focusing on this example, we study the effect of observing others' food catches, which constitutes a form of public information. We name this mechanism reward coupling. It is mathematically represented as

$$c_{ij}(t) = \kappa_r \frac{r_j(t)}{n^k(t) - 1}, \quad (6)$$

where κ_r corresponds to the reward coupling strength. When an individual receives a reward, $c_{ij}(t) > 0$, which means the observer is more likely to remain in the current habitat/patch. It is normalized by the number of conspecifics in the habitat/patch. Please see Fig. 9 in Appendix G for the scaling by the number of agents in the group N , which highlights similar results.

D. Simulations details

The stochastic differential equation (1) of the decision variable is solved numerically with an Euler method, with $dt = 0.01$ s. Other variables are updated at every time step.

In figures in the habitat choice section III A, except in the theoretical plots, nonsocial parameters remain constant: $\theta = -5$, $\alpha = 1.25$ s $^{-1}$, $B = 0.1$ s $^{-1}$; and the reward probabilities in each habitat are $p^0 = 0.4$, $p^1 = 0.6$. $T_{tr} = 1$ s in Fig. 1 and $T_{tr} = 0$ s otherwise. For the γ plots, $p^0 = p^1 = 0.5$.

In Fig. 6, numerical parameters are $\theta = -5$, $\alpha = 1.25$ s $^{-1}$, $B = 0.1$ s $^{-1}$, $K = 10$, $N = 10$, $A_m = 8000$, and $p_{in} = \frac{2}{3}$.

III. RESULTS

Foraging constitutes a multilevel process across different spatial scales, which considers two questions: where to forage (in which habitat) and how long to exploit a certain resource (in a patch) [3]. We first consider the habitat choice problem in Sec. III A; following this, we consider the patch leaving problem in Sec. III B.

A. Where to forage? Collective movements and stationary states during habitat choice

In large areas, foraging activity may not significantly affect the amount of available resources. In this habitat choice process [3], animals are accumulating evidence in different places to choose where they will remain to forage. In this paper, we focus on a two-habitat choice process. We first define the dynamics of noninteracting agents, to subsequently study how it is modulated by social information.

1. Dynamics of noninteracting animals: Exploitation, accuracy, and cohesion

To characterize the movements in the environment, we quantify the leaving dynamics and repartition over time of the agents between the initial, low yielding ($k = 0$) habitat and the highest yielding one ($k = 1$). In this situation of noninteracting agents, there is independence of dynamics in each habitat. Then, the probability density of leaving a habitat k is given by a convolution between the unit distribution densities for each habitat:

$$P^k(t) = \sum_{v=1}^{\infty} (\Psi_v^0 * \Psi_{v-1+k}^1) [t - (2v - 2 + k)T_{tr}]. \quad (7)$$

For $t \leq (2v - 2 + k)T_{tr}$, the convolution is equal to zero.

The unit distribution density is defined by

$$\Psi_v^k(t) = \frac{-v\theta}{\sqrt{4\pi Bt^3}} \exp\left(-\frac{(v\theta + \mu^k t)^2}{4Bt}\right) \quad (8)$$

for $v \geq 1$. $\Psi_0^k(t) = 1$ for all t . See Appendix B for the calculation details.

μ^k is the effective drift term. Since rewards arrive quasi-continuously, it is possible to approximate the time irregular function $r_i(t)$ by the average reward rate, equal to $p^k \text{ s}^{-1}$ in habitats. We can then define the effective drift term $\mu^k = \alpha - p^k$. See Appendix A for more details. Indeed, since the reward sampling time is small compared to the timescale of the decision equation, it is possible to decouple both dynamics using a slow-fast analysis. Please note that this variable must satisfy the condition $\mu^k \geq 0$.

The probability of being in the habitat k , or the fraction of individuals in this habitat, is given by

$$Q^k(t) = 1 - k + \int_0^t d\tau [P^{k'}(\tau - T_{tr}) - P^k(\tau)]. \quad (9)$$

Figure 1(b) shows an example of these analytical distributions, $P^k(t)$ and $Q^k(t)$ that reproduce the results of numerical simulations. Both $P^k(t)$ and $Q^k(t)$ show an oscillatory pattern. The agents first leave their initial habitat $k = 0$ to go to the habitat $k = 1$, then go back, and so on. The vertical

gray dotted lines indicate the mean residence times for each passage. This variable constitutes an important metric used in behavioral ecology, especially defined in the marginal value theorem [54]. Our model allows us to define precisely these mean residence times, to quantify how long animals spend exploiting a habitat before leaving.

Exploitation. The mean residence time is mathematically defined as

$$\bar{T}^k = -\theta/\mu^k. \quad (10)$$

Figure 1(d) shows that $\bar{T}^1$ is increasing for a higher reward probability p^1 . In fact, foragers remain longer in better habitats. In this case of noninteracting individuals, the oscillations are periodic with period $\bar{T}^0 + \bar{T}^1 + 2T_{tr}$.

However, these oscillations are also damped [see Fig. 1(b)], which is related to the progressive desynchronization of individuals. This aspect is of particular importance because cohesion is a collective protective behavior in the presence of threats such as predation, as it provides increased collective vigilance and risk dilution [10,55]. To quantify this synchronization feature, we introduce a cohesion metric; see below.

Cohesion. The damping of P^k oscillations can be exactly characterized in the case of identical habitats, with $p^0 = p^1 = p$; see Fig. 1(c). The cohesion parameter is defined as (see Appendix B for calculation details)

$$\gamma = \sqrt{\frac{\mu}{B}(\mu T_{tr} - \theta)}. \quad (11)$$

The larger γ values are, the more cohesive the group is (i.e., the less damped the oscillations are).

Figure 1(c) highlights how cohesion is shaped by environmental properties. A higher reward probability p leads to a less cohesive group (smaller γ values). In fact, more abundant resources are associated with more dispersed residence times. Another feature of the habitat environments is the travel time separating them. We observe that a longer travel time T_{tr} leads to a more cohesive group (larger γ values). Indeed, this introduces a timescale difference that delays the desynchronization and stationary repartition of agents between the habitats.

Then, after an oscillatory period, where the collective movements between the two habitats are still coherent, the oscillations converge toward stationary values; see the horizontal black dotted lines in Fig. 1(b). Among these different steady state values, the fraction of agents in the best habitat, Q_S^1 , is a metric of particular significance. In fact, it is a measure of the group's accuracy in finding the best habitat, which reflects the foraging success.

Accuracy. The fraction of agents in a habitat k in a steady state can be found after computing the entering and leaving fluxes (see Appendix C):

$$Q_S^k = \frac{1}{-\frac{2\mu^k T_{tr}}{\theta} + 1 + \frac{\mu^k}{\mu^{k'}}}. \quad (12)$$

The steady state leaving probability density P_S^k is mathematically described as

$$P_S^k = \frac{\mu^k}{2\mu^k T_{tr} - \theta(1 + \frac{\mu^k}{\mu^{k'}})}. \quad (13)$$

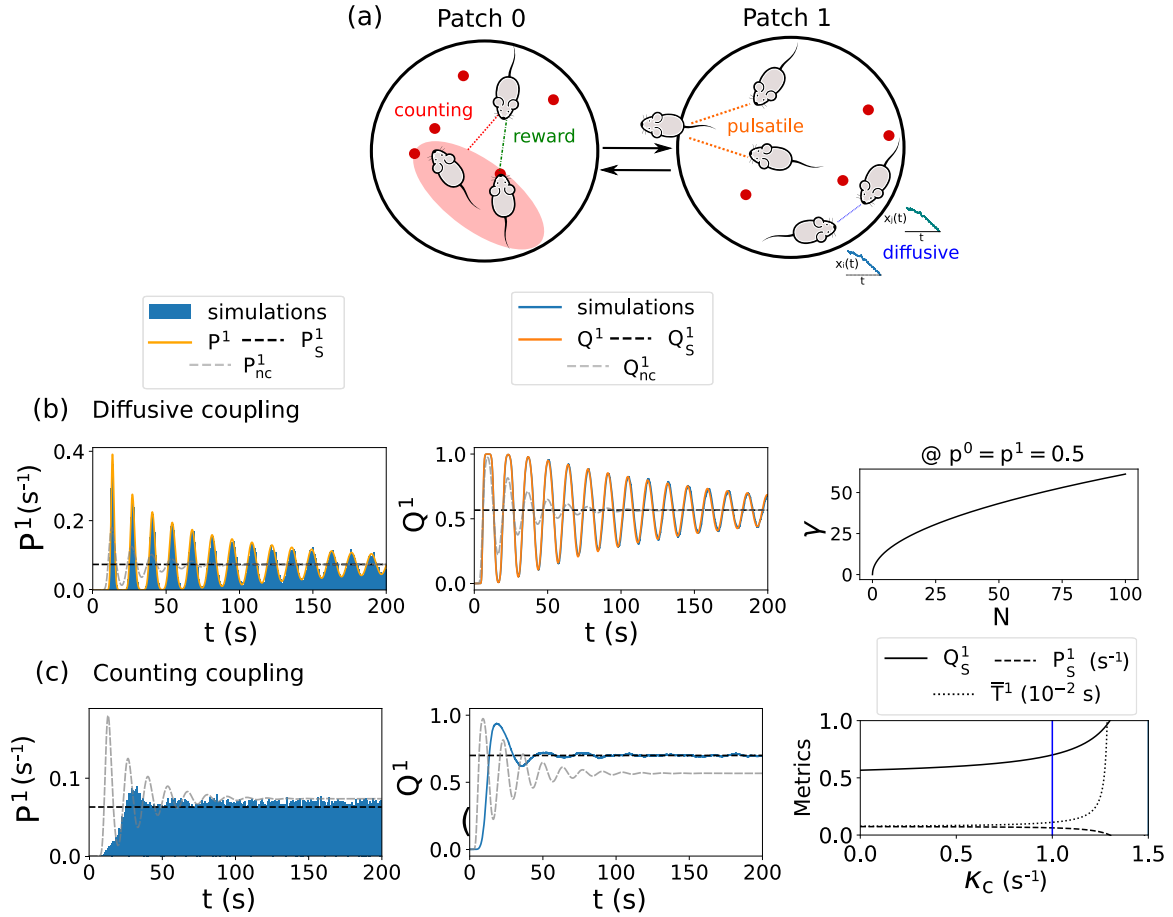


FIG. 2. Collective social dynamics for a group with active communication and local enhancement (counting coupling) in a habitat choice process. (a) Schema of a group with interacting agents in a two-habitat environment. Individuals interact with their conspecifics in different ways. Information can come from the observation of others' food rewards (reward coupling). Individuals can also observe others' beliefs about a habitat quality, by communicating continuously (diffusive), through agents' arrivals or departures observation (pulsatile), or by observing the number of agents in their current habitat (counting). (b) Continuous belief sharing (diffusive) leads to more cohesion, with no accuracy and exploitation modifications. Left: Distributions of leaving times $P^1(t)$ and fraction of agents $Q^1(t)$ in the best habitat show less damped oscillations, and no change in steady states and periodicity compared to a noncoupled situation $[P_{nc}^1(t), Q_{nc}^1(t)]$. Parameters are $N = 5$, $\kappa_{diff} = 10 \text{ s}^{-1}$ (2×10^3 simulations). Right: The cohesion parameter γ increases with the group's size N . (c) Observation of the proportion of agents in a habitat (counting) increases accuracy and exploitation, and reduces cohesion. Left: Distributions of leaving times $P^1(t)$ and fraction of agents $Q^1(t)$ in the best habitat show more damped oscillations, later departure times, and a higher fraction of agents in the best habitat compared to a noncoupled situation $[P_{nc}^1(t), Q_{nc}^1(t)]$. Parameters are $N = 5$, $\kappa_c = 1 \text{ s}^{-1}$ (2×10^3 simulations). Right: Increased κ_c values lead to higher Q_S^1 , $\bar{T}^1$ values and decreased P_S^1 values. The blue vertical line corresponds to the set of parameters in the left figure.

Figure 1(d) shows how these stationary values change for different environmental characteristics. Accuracy increases with a larger ratio p^1/p^0 , when the two habitats are easier to distinguish. Independently of this ratio, the leaving probability density decreases with higher reward probabilities in both habitats, as animals remain more in better habitats. On the other side, increasing travel times T_{tr} decrease both accuracy and leaving probability density, meaning that a greater fraction of agents travel and are not in the habitats.

The distributions and metrics (exploitation, cohesion, accuracy) defined above constitute useful analytical tools to quantify the collective foraging dynamics. Applying these different methods to more complex situations, we now study how this collective dynamics is modulated by social information. The different types of information gathering mechanisms are schematized in Fig. 2(a), and we begin

by analyzing the effects of active signaling between individuals.

Please note that, for readability reasons, the travel time is set to zero ($T_{tr} = 0 \text{ s}$) in the next parts of the paper.

2. Continuous active signaling (diffusive) increases cohesion

How would the continuous signaling of beliefs, for example through vocalizations, modulate the collective dynamics? To analytically predict the different distributions and metrics for agents interacting through diffusive coupling (see Sec. II, Methods), we study the case of perfectly coupled individuals, in the strong limit $\kappa_{diff} \rightarrow \infty$. This analysis extends previous predictions made for 2 agents [31] to an arbitrary number of agents N . The resulting dynamics is equivalent to the noninteracting situation, but with the noise amplitude scaled by the

size of the group, B/N (see Appendix D for the calculation details).

Figure 2(b) shows the modification of the analytical and simulated distributions in the best habitat, $P^1(t)$ and $Q^1(t)$, with perfect diffusive coupling, compared to the noncoupled ones, $P_{nc}^1(t)$ and $Q_{nc}^1(t)$. As the noise amplitude B has no effect on the steady state values $P_S^k(t)$, $Q_S^k(t)$, and $\bar{T}^k$ [see Eqs. (10), (12), and (13)], the effect of diffusive coupling can only be observed on the modulation of cohesion, which increases with the number of agents N . Please note that an alternative to mathematically describe the diffusive coupling, by normalizing by the number of agents in a habitat instead of the size of the group, highlights similar results; see Fig. 8 in the Appendix G.

Let us now move to the study of less direct belief sharing mechanisms, through the observation of social cues. In the following, we analyze the effects of local enhancement.

3. Local enhancement (counting) increases accuracy and exploitation, and reduces cohesion

The presence of other individuals constitutes a social cue that can attract the observer to a habitat location. We study here the collective consequences of foragers that prefer to be surrounded by a large number of conspecifics.

Analytical predictions of distributions are not possible in this coupling case; however, estimates of metrics in a steady state can be calculated via the effective drift term. For $N \gg 1$, the steady state effective drift term is mathematically described as

$$\mu_S^k = \frac{2\alpha - (p^k + p^{k'}) - \kappa_c(1 - 2\eta)}{2} \times \left[1 + \frac{(p^{k'} - p^k)}{2\alpha - (p^k + p^{k'}) - 2\kappa_c(1 - \eta)} \right]. \quad (14)$$

Figure 2(c) shows the modification of the simulated distributions in the best habitat, $P^1(t)$ and $Q^1(t)$, with counting coupling, compared to the noncoupled ones, $P_{nc}^1(t)$ and $Q_{nc}^1(t)$. In these plots, we observe more damped oscillations with counting coupling, i.e., less cohesion. Quantification of steady state metrics in the best habitat shows increased accuracy, mean residence time, and decreased leaving probability density with increasing coupling strengths κ_c .

These results are strikingly different from the collective consequences of active signaling. But would a closer social information type, another local enhancement mechanism, result in more similar emergent processes? Instead of looking at the number of neighbors in a habitat, we investigate the effects of another way to collect information about others' beliefs, through the observation of leaving and arriving movements.

4. Local enhancement (pulsatile) increases cohesion, and has various effects on accuracy and exploitation

This alternative relies on pulsatile information, shared only when an individual enters or leaves a habitat. Analytical predictions of distributions are possible only for perfect pulsatile coupling ($\kappa_d \rightarrow \infty$). In that case, all agents move together; the first one to leave is immediately followed by the others. So the number of agents in any habitat k is $n^k(t) = N$. The

unit distribution of residence times becomes

$$\Psi_{\kappa_d \rightarrow \infty}(T) = \Psi(T)\Omega(T)^{N-1} \quad (15)$$

and can be used to compute $P^k(t)$ and $Q^k(t)$ (see Appendix B). Otherwise, the effective drift term μ^k is time-dependent and predictable with difficulty [50,51]. However, steady state predictions are possible. The two normalization possibilities (see Sec. II, Methods) are studied below, starting with normalization by the total number of agents.

$\mathcal{N}_d = \mathcal{N}_a = N$. For a large number of agents $N \gg 1$, the effective drift term in a steady state can be written as

$$\mu_S^k = \frac{-a_2^k \pm \sqrt{(a_2^k)^2 - 4a_1a_3^k}}{2a_1} \quad (16)$$

with $a_1 = 2 + \frac{\kappa_d - \kappa_a}{\theta}$, $a_2^k = (p^k - p^{k'})(1 + \frac{\kappa_d - \kappa_a}{\theta}) - 2(\alpha - p^k)$, and $a_3^k = -(\alpha - p^k)(p^k - p^{k'})$. See Appendix E for the calculation details. Please note that μ_S^k depends on the difference $\kappa_d - \kappa_a$ here.

The second normalization, by the number of agents in the habitat, is slightly different, as it assumes an additional computation for the individuals to evaluate this variable.

$\mathcal{N}_d = n^k - 1$, $\mathcal{N}_a = N - n^k - 1$. Similarly, for a large number of agents $N \gg 1$, the effective drift term in a steady state can be written as

$$\mu_S^k = \frac{1}{2} \left[\frac{2\alpha - (p^k + p^{k'})}{1 + (\kappa_d - \kappa_a)/\theta} - \frac{(p^k - p^{k'})}{1 + (\kappa_d + \kappa_a)/\theta} \right]. \quad (17)$$

See Appendix E for calculation details.

Figure 3 shows the modification of the simulated distributions in the best habitat, $P^1(t)$ and $Q^1(t)$, with pulsatile coupling, compared to the noncoupled ones, $P_{nc}^1(t)$ and $Q_{nc}^1(t)$. For normalization by the total size of the group, these graphs highlight more cohesive movements for both types of coupling. Quantification of steady state metrics in the best habitat shows decreased accuracy and mean residence time, and an increased probability density of leaving for higher κ_d values compared to κ_a .

For normalization by the number of agents in a current habitat, the oscillatory behaviors are similar, and therefore the effects on cohesion are similar (see Fig. 9 in Appendix G). The effects on steady state metrics are also similar, except that increased κ_d values lead to increased accuracy and mean residence time.

In summary, pulsatile coupling is responsible for various collective patterns, which are qualitatively different from the ones observed with the other local enhancement mechanism (counting). First, observation of others' arrivals or departures leads to more cohesion. Then, arrivals observation increases collective accuracy and exploitation, while departure observation diminishes exploitation and may decrease or increase accuracy depending on the individual reference: the whole group, or only agents in the observer's current or other habitat.

So far, we have investigated a wide range of collective modifications induced by different social information types, either active signaling or inadvertent social cues. Let us now study the changes generated by the last information gathering mechanism modeled in this paper: public information. This information is provided when the behavior of agents provides some environmental cues, here rewards, to others.

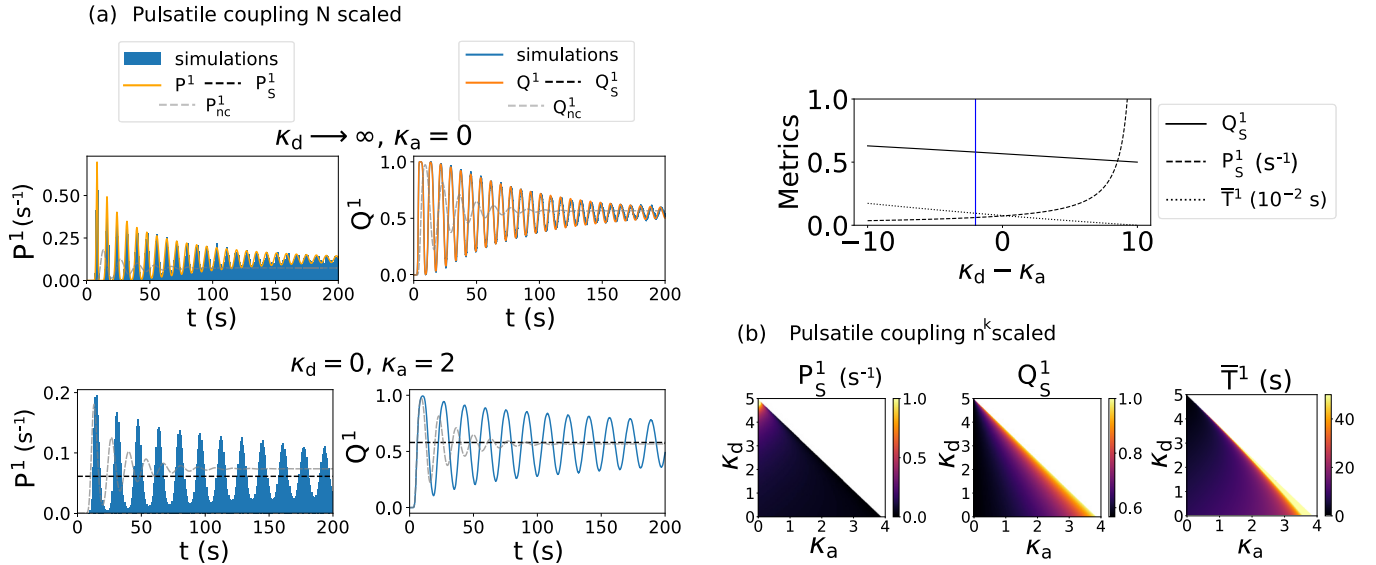


FIG. 3. Collective social dynamics for a group with local enhancement (pulsatile coupling) in a habitat choice process. (a) Pulsatile coupling scaled by the group's size N . Top left: Observation of others' departures leads to less accuracy, less exploitation, and more cohesion. Distributions of leaving times $P^1(t)$, and fraction of agents $Q^1(t)$ in the best habitat show less damped oscillations, earlier departure times and a smaller steady state fraction of agents in the best habitat. Parameters are $N = 50$, $\kappa_d = 100$, $\kappa_a = 0$ (1×10^3 simulations). Bottom left: Observation of others' arrivals leads to more accuracy, more exploitation, and more cohesion. Distributions of leaving times $P^1(t)$ and fraction of agents $Q^1(t)$ in the best habitat show less damped oscillations, later departure times, and a higher steady state fraction of agents in the best habitat compared to a noncoupled situation [$P^1_{nc}(t)$, $Q^1_{nc}(t)$]. Parameters are $N = 50$, $\kappa_d = 0$, $\kappa_a = 2$ (1×10^3 simulations). Right: An increased $\kappa_d - \kappa_a$ difference leads to higher P^1_s values and decreased Q^1_s , $\bar{T}^1$ values. The blue vertical line represents the value used in Fig. 3(a) bottom. (b) Pulsatile coupling scaled by the number of other agents in the observer's current or other habitat. An increased κ_d parameter leads to higher P^1_s , Q^1_s values and decreased $\bar{T}^1$ values, except close to the upper boundary, where the tendency is reversed for P^1_s and $\bar{T}^1$. For readability reasons P^1_s and $\bar{T}^1$ values are bounded respectively to 1 and 50 s, and the upper part corresponds to sets of parameters beyond the limits corresponding to $\mu^k_S = 0$.

5. Public information (reward) increases accuracy and exploitation, and decreases cohesion

This information gathering mechanism comes from the observation of food rewards that other agents in the same habitat receive. Distributions and metrics can be easily analytically predicted by including the additional coupled reward rate in the effective drift term:

$$\mu^k = \alpha - p^k(1 + \kappa_r). \quad (18)$$

Figure 4 shows the impact of public information gathering through reward coupling on analytical and simulated distributions $P^1(t)$, $Q^1(t)$ compared to noncoupled ones $P^1_{nc}(t)$, $Q^1_{nc}(t)$. First, cohesion decreases with the coupling strength κ_r . Quantification of steady state metrics in the best habitat shows increased accuracy and mean residence time, and decreased probability density of leaving, with increasing coupling strengths κ_r . Interestingly, the observed collective patterns are similar to the ones described for local enhancement with counting coupling, although these two mechanisms are inherently different.

All in all, the two-habitat environment represents a useful framework to investigate collective foraging dynamics. All the tools developed to quantify these emergent patterns—probability density of leaving, fraction of agents in a habitat, and the metrics mean residence time, cohesion, and accuracy—have been especially useful to understand more

complex social situations. These measures in fact highlighted the large diversity of collective properties shaped by different social information gathering mechanisms.

Let us now consider a patch foraging task within a given habitat. Both habitats and patches are conceptually similar; their only differences lies in their time and spatial scales (not addressed here) and nature of depletion. Moving from habitat choice to an exploration-exploitation tradeoff, as a consequence of the depleting nature of patches, we seek to quantify the dynamics in a succession of patches.

B. How long to exploit a resource? Exploration-exploitation tradeoff

Inside a habitat, animals forage through patches of food. During this process, animals deplete the patches they are exploiting and have to decide when to leave, to explore further. In this section, agents go through K successive patches of identical initial reward probabilities p_{in} , without going back to the previous patch [see Fig. 5(a)].

Similarly to the previous section, we first define the dynamics of noninteracting agents, to subsequently investigate how it is modulated by social information.

1. Dynamics of noninteracting agents: Exploitation and cohesion

To characterize the movements of a single agent ($N = 1$) in the environment, we quantify the leaving dynamics and

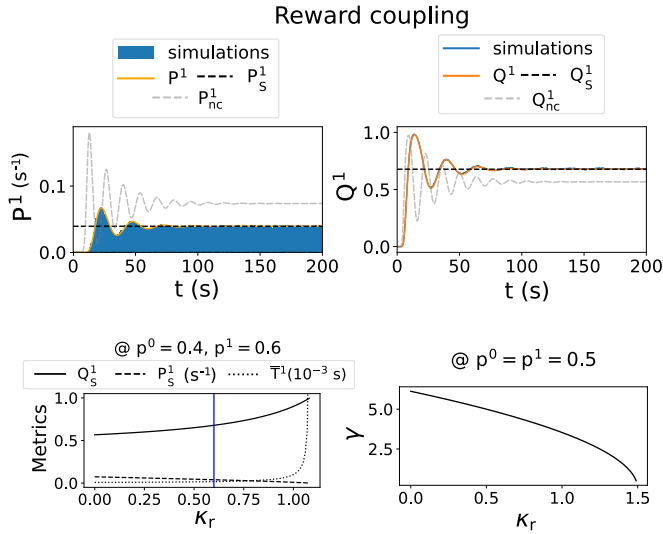


FIG. 4. Collective social dynamics for a group with public information (reward coupling) in a habitat choice process. Others' rewards observation increases accuracy and exploitation, and decreases cohesion. Top: Distribution density of leaving times $P^1(t)$ and fraction of agents $Q^1(t)$ in the best habitat show more damped oscillations, later departure times, and an increased steady state accuracy compared to a noncoupled situation [$P_{nc}^1(t)$, $Q_{nc}^1(t)$]. Parameters are $N = 50$, $\kappa_r = 0.6$ (2×10^3 simulations). Bottom left: An increased κ_r parameter leads to increased Q_s^1 , $\bar{T}^1$ values and decreased P_s^1 values. The blue vertical line corresponds to the set of parameters in the top figure. Bottom right: The damping factor γ decreases with κ_r .

repartition over the time spent by the agents in the different patches. The total probability density of leaving any patch is given by

$$P_{\text{tot}}(t) = \sum_{k=1}^K (\Psi * \dots * \Psi)[t - (k-1)T_{\text{tr}}]. \quad (19)$$

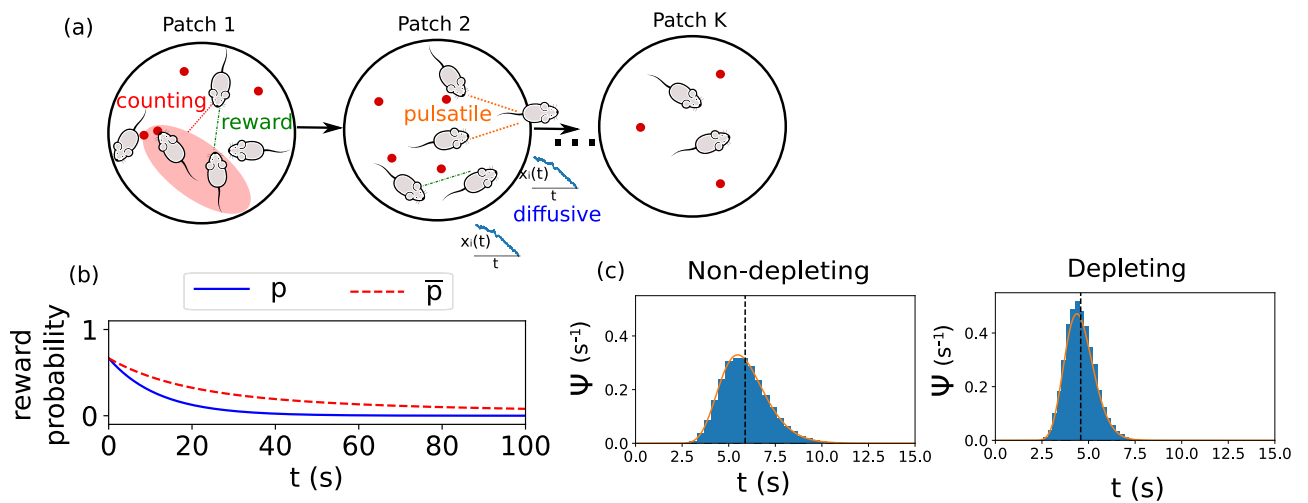


FIG. 5. Foraging in a depleting environment (patch) increases cohesion and decreases exploitation compared to a nondepleting area. (a) Schema of a K successive patches environment. Individuals all start from patch 1, and move to the next patch without going back. The same information sharing mechanisms can be used to interact (reward, diffusive, pulsatile, counting). (b) Reward probability $p(t)$ and average reward probability $\bar{p}(t)$ decrease exponentially in a perfectly cohesive group. (c) Unit probability densities of leaving for nondepleting and depleting patches. The vertical black dotted line corresponds to the mean residence time. Depletion decreases mean residence times and increases cohesion (less dispersed distribution).

For $t \leq (k-1)T_{\text{tr}}$, the convolution is equal to zero.

The unit distribution density is defined by

$$\Psi(t) = \frac{-\theta}{\sqrt{4\pi Bt^3}} \exp\left(\frac{-(\theta + \mu(t)t)^2}{4Bt}\right). \quad (20)$$

We can then define the effective drift term $\mu(t) = \alpha - \bar{p}(t)$. If the depletion rate is slow enough, the average reward rate $\bar{p}(t)$ can be used as a slow variable to evaluate the unit distribution density of leaving. This time-averaged rate is mathematically calculated as follows:

$$\bar{p}(t) = p_{\text{in}} A_m dt \frac{1 - e^{-\frac{t}{A_m dt}}}{t}. \quad (21)$$

with A_m the maximum amount of food in a patch. See Appendix A for calculation details. Figure 5(b) shows the evolution of the reward probability, and the averaged equivalent over time. The probability of being in the patch k ($1 < k < K$), or the fraction of individuals in this patch, is given by

$$Q^k(t) = \int_0^t d\tau [P^{k-1}(\tau - T_{\text{tr}}) - P^k(\tau)] \quad (22)$$

with $Q^1(t) = 1 - \int_0^t d\tau P^1(\tau)$ and $Q^K(t) = \int_0^t d\tau P^{K-1}(\tau - T_{\text{tr}})$ for the first and last patches.

Please note that analytical predictions for $N > 1$ in this noninteracting case are difficult to compute, due to the complicated estimate of the average reward rate. Figure 5(c) shows that foraging in a depleting environment reduces the mean residence time and increases cohesion (less dispersed distribution).

The distributions defined above and metrics defined in the previous section (exploitation, cohesion) constitute as well useful analytical tools to quantify the dynamics in the patch environment. Similarly to the previous section, we study the effects of social information with these methods. The different types of information gathering mechanisms are schematized

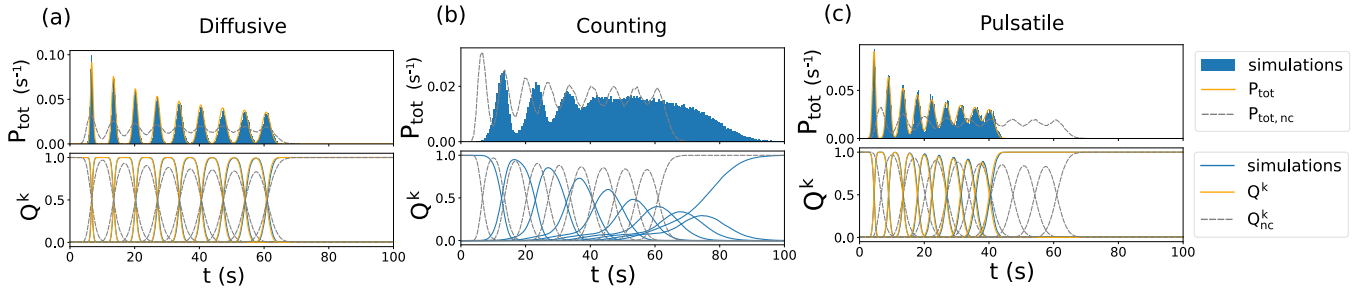


FIG. 6. Collective social dynamics in successive patches. (a) Continuous belief sharing (diffusive) leads to more cohesion, with no exploitation modifications. Distributions of leaving times $P_{\text{tot}}(t)$ (top) and fraction of agents $Q^k(t)$ (bottom) show less damped oscillations and no change in periodicity compared to a noncoupled situation $[P_{\text{tot}, \text{nc}}(t), Q_{\text{nc}}^k(t)]$. $\kappa_{\text{diff}} = 100$ (2×10^3 simulations). (b) Observation of the proportion of agents in a patch (counting) increases exploitation and reduces cohesion. Distributions of leaving times $P_{\text{tot}}(t)$ (top) and fraction of agents $Q^k(t)$ (bottom) show more damped oscillations and later departure times compared to a noncoupled situation $[P_{\text{tot}, \text{nc}}(t), Q_{\text{nc}}^k(t)]$. $\kappa_c = 1$ (2×10^3 simulations). (c) Observation of others' departures leads to more cohesion and less exploitation. Distributions of leaving times $P_{\text{tot}}(t)$ (top) and fraction of agents $Q^k(t)$ (bottom) show less damped oscillations and earlier departure times compared to a noncoupled situation $[P_{\text{tot}, \text{nc}}(t), Q_{\text{nc}}^k(t)]$. N scaled, $\kappa_d = 20$, $\kappa_a = 0$ (2×10^3 simulations).

in Fig. 5(a). Public information with reward coupling is not detailed here, the results being similar and corresponding to an increased perceived reward probability [see Eq. (18)]. We begin by analyzing the effects of active signaling between individuals in the patch environment.

2. Active signaling (diffusive)

Similarly to the previous section, it is possible to study the dynamics with diffusive coupling analytically in the strong limit of the coupling parameter κ_{diff} . In that case, all agents move together. That is, the number of agents in any patch k is $n^k(t) = N$. The distributions are then equivalent to a noninteracting one, with the noise parameter scaled by the size of the group, B/N . In addition, as the amount of food is depleted by N agents together in a patch, the average reward rate corresponds to $\bar{p}(Nt)$; see Eq. (21).

Figure 6(b) shows the modification of the analytical and simulated distributions, $P_{\text{tot}}(t)$, $Q^k(t)$ with perfect diffusive coupling compared to the noncoupled ones $P_{\text{tot}, \text{nc}}(t)$, $Q_{\text{nc}}^k(t)$. We observe that an increasing number of agents N leads to less damped oscillations, with no periodicity change. Similarly to the previous section, continuous belief sharing leads to more cohesion, without exploitation modifications.

Let us now move to the study of less direct belief sharing mechanisms, through the observation of social cues. We begin with the counting mechanism of local enhancement.

3. Local enhancement (counting)

Except for the perfect counting case ($\kappa_c \rightarrow \infty$), for which all agents remain in the initial patch, analytical distributions are not computable here.

Figure 6(c) shows the modification of the simulated distributions $P_{\text{tot}}(t)$, $Q^k(t)$ with counting coupling compared to the noncoupled ones $P_{\text{tot}, \text{nc}}(t)$, $Q_{\text{nc}}^k(t)$. These plots highlight that counting coupling enhances cohesion and increases departure times. Similarly to the previous section, observation of the proportion of agents in a patch increases exploitation and reduces cohesion.

Let us now move to another mechanism of local enhancement, through pulsatile coupling. Instead of looking at the number of neighbors in a patch, this alternative consists of collecting information about others' beliefs to observe their leaving and arriving movements.

4. Local enhancement (pulsatile coupling)

Since agents do not go back to a previous patch, the arrival information from that previous patch is less relevant here. Here we study only the departure pulsatile coupling case ($\kappa_d > 0$ and $\kappa_a = 0$).

It is possible to study the dynamics with pulsatile coupling analytically in the strong limit of the coupling parameter κ_d . In that case, all agents move together; the first one to leave is immediately followed by the others. So, the number of agents in any patch k is $n^k(t) = N$. The average reward rate is therefore $\bar{p}(Nt)$.

Figure 6(d) shows the modification of the simulated and analytical distributions $P_{\text{tot}}(t)$, $Q^k(t)$ with pulsatile coupling compared to noncoupled ones $P_{\text{tot}, \text{nc}}(t)$, $Q_{\text{nc}}^k(t)$. These plots highlight that pulsatile coupling increases cohesion and is associated with earlier departure times. Observation of others' departures leads to more cohesion and reduces exploitation.

A successive depleting patches environment represents a useful framework to study how different information sharing mechanisms and social structures lead to different effects on the group cohesion and the exploration-exploitation tradeoff. Depletion leads to a decrease in the mean residence time and increased cohesion. However, a key result is that social information has the same effect on collective dynamics in habitats and in patches.

IV. DISCUSSION

Group foraging is a complex collective behavior observed in a large variety of species [1]. Throughout this paper, we quantified the foraging dynamics with time-dependent functions: the probability density of leaving, the fraction of agents in a patch, and the time-independent metrics cohesion, mean residence time, and accuracy. These tools allowed us to investigate the emergent foraging properties in different

TABLE III. Classification of the effects ($\nearrow$ increasing, $\searrow$ decreasing, $\emptyset$ no effect, – not relevant) of the environment (patch quality, depletion, travel time), individual (individual learning; see Appendix F), and information sharing mechanisms (diffusive, counting, pulsatile, reward) on emergent collective characteristics (cohesion, accuracy, exploitation). This accuracy column is only relevant for the two-habitat section.

Feature	Cohesion γ	Accuracy Q^1	Exploitation $\bar{T}$
Quality p	$\searrow$	$\nearrow$ (ratio)	$\nearrow$
Depletion A_m	$\nearrow$	–	$\searrow$
Travel T_{tr}	$\nearrow$	$\searrow$ (fraction)	$\emptyset$
Ind. learning y	–	$\nearrow$	$\nearrow$
Diffusive κ_{diff}	$\nearrow$	$\emptyset$	$\emptyset$
Counting κ_c	$\searrow$	$\nearrow$	$\nearrow$
Pulsatile κ_d	$\nearrow$	$\searrow$ (N) or $\nearrow$ (n^k)	$\searrow$
Pulsatile κ_a	$\nearrow$	$\nearrow$	$\nearrow$
Reward κ_r	$\searrow$	$\nearrow$	$\nearrow$

environments (two habitats, successive patches) and how they are shaped by social information, as summarized in Table III.

A. Effects of the environment on the collective dynamics features

In an ecological context, habitat choice activity (nondepleting area) and patch exploitation (depleting area) constitute an intertwined foraging behavior, where an individual decides where to forage and how long to exploit a certain resource.

1. Habitats

For habitat choice, the strategic behavior is to spend most of the time in the highest-yielding habitat. Our model showed that, when the ratio between the food reward probabilities of the two habitats increases, accuracy increases as it becomes easier to distinguish the two patches. Indeed, in better habitats, the number of agents is higher [56]. This is qualitatively similar to the ideal free distribution [16], but here the ratio between the fractions of agents in habitats is not equal to the quality ratio and depends on other factors such as the cost of foraging. Please note that the addition of individual learning, by inferring which habitat is the best, has a significant positive impact on collective accuracy (see Appendix F), which is consistent with empirical observations of foraging success [57,58]. In addition, the mean residence time increases for an increased reward probability, i.e., animals exploit a habitat more if food is abundant. This is consistent with the predictions of the marginal value theorem [54]. Finally, we noted that increased reward probabilities are associated with a decrease in cohesion, as the variance of residence times increases.

We also observed that increased travel times between habitats lead to increased cohesion and a smaller fraction in the best patch, as more agents are between habitats, but do not change the exploitation behaviors. As longer travel times are associated with longer residence times [59], this effect would have to be added in future works.

2. Patches

Within a given habitat, an animal exploiting patches must consider the exploration-exploitation tradeoff, due to the depleting feature of the foraging areas. This aspect leads to increased cohesion, with more exploration. This is consistent with the marginal value theorem [54]. We may note that in our model animals always end up exploring other places. In fact, even if the areas do not deplete like habitats, exploration could be adaptive to increase information and reduce boredom [60,61].

But despite the differences between habitats and patches and their different associated questions, we showed that the collective dynamics was modulated similarly in both environments by social information.

B. Effects of the information sharing mechanisms on the collective dynamics features

We observed a variety of emergent processes associated with the different information sharing mechanisms studied.

In particular, for a two-habitat environment, it is more advantageous for the group to spend more time in the habitat with the highest reward rate. In that case, cooperative behaviors are crucial to increase the fraction of agents in the best patch. All information sharing mechanisms studied here increase accuracy, except for departure (negative effect) and diffusive coupling (no effect). These findings are consistent with empirical observations that information sharing increases foraging success [14,15].

The impact of these interaction rules between foragers was more diverse when considering the cohesion of the group. Indeed, cohesion increased with diffusive and pulsatile couplings and decreased with reward and counting couplings. As greater cohesion can be important in the presence of threats, since it provides increased collective vigilance and risk dilution [10,55], it could be hypothesized that animals would communicate with active social signals (diffusive) and pay more attention to the decisions to leave and arrive of others (pulsatile) in the presence of a predator. Inversely, in the absence of threat, agents can focus more on increasing the group's accuracy, through collecting information about the environment by observing others' catches (reward) or by looking at others' beliefs regarding the best patch (counting), which have a strong positive impact on both accuracy and exploitation, but decrease the group's cohesion. Interestingly, the pulsatile and counting couplings do not produce similar effects on the group's features, suggesting that the way agents infer others' beliefs has a strong impact on the collective dynamics, and thus one mechanism might be preferred over the other depending on the context (for example predation). Furthermore, pulsatile departure and arrival couplings do not produce the same effects. Arrival observation increases collective accuracy and exploitation, while departure observation diminishes exploitation and may decrease or increase accuracy depending on the individual frame of reference: the whole group, or only agents in the observer's current or other patch. It will be interesting to infer such underlying mechanisms from observed global movement dynamics [62].

Finally, the quantification of mean residence times offers a way to address the balance between exploration and exploitation [61,63,64]. Our model showed that while some cooperative information sharing mechanisms lead to more exploitation (reward, arrival pulsatile, and counting couplings), others favor exploration (departure pulsatile coupling). More precisely for reward coupling, for example, the use of public information can improve the estimation of patch quality and prevent the underutilization of resources [65].

All these different collective behaviors might be more or less advantageous depending on the context, and the same group can display various group dynamics depending on the context. Famous examples are the fission-fusion dynamics in macaques [66] or dolphins [67], or locusts that can be gregarious or social [68]. Depending on the habitat [67], or the composition of the group (young or not, for example) [69], the modes of collective behavior are different and are modulated contextually.

Altogether, our theoretical framework for social habitat/patch foraging highlighted a diversity of dynamics emerging from the variations of a mechanistic model. This core structure could later be further developed to account for more diverse foraging situations.

C. Limitations and future directions

Among the limitations of the framework presented here, one is constituted by the fact that all the theoretical distributions were derived using the approximation of a constant drift term. This was calculated with a continuous reward rate, which is also the assumption of the marginal value theorem [54]. Such calculations are not possible for more time-spaced and noisy food intakes [70]. However, analytical predictions such as the mean residence times or steady state rates, as well as numerical investigations, are still possible. Another limitation of the environments implemented in our model is that fixed travel times were considered, while these can be distributed [71]. And since longer travel times are correlated with longer residence times [59], the model should be modified to study this effect. Other environmental limitations include the configuration of areas. An environment with multiple habitats/patches, where a leaving agent could go into any of them, would be an important further development to relate to existing experimental [63,72] and field [8] work with multiple patches.

In addition to these environmental constraints, the social organizations studied in this paper could be extended in many ways. Some information sharing mechanisms have been studied in this paper, but more could be added. Another social cue example is the chemical trails left by foraging bees in the food patches they already exploited. These marks may lead other bees to avoid these flowers [73]. In addition, under certain circumstances, the use of public information can be suboptimal and misleading [74], or foraging agents (songbirds) use only social cues about the location of potential food sources but not their profitability [75]. Furthermore, since social cohesion can be counterproductive in some cases [76], the model should be further developed to explain the possible detrimental effects of cooperative patch foraging. Further developments also include a complexification of social organizations to make

them closer to real foraging groups. This model studied an egalitarian group; however, there are more complex social structures [77,78]. Including hierarchies in the model is the next step in the social foraging framework. Another important possibility would be to study competitive behaviors [79,80], to link our theoretical framework with producer-scrounger models [81]. Extending this idea, it would be realistic to include agents following different social rules in these nonegalitarian groups [82].

The scripts used to generate the results of this article are freely available online [83].

ACKNOWLEDGMENTS

We would like to thank Jacob Davidson and Zachary Kilpatrick for insightful discussions. All authors acknowledge support from the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) under Germany's Excellence Strategy, EXC 2117-422037984.

Authors L.B.M. and A.E.H. developed the study, derived the results, and wrote the manuscript.

DATA AVAILABILITY

The data that support the findings of this article are openly available [83].

APPENDIX A: SINGLE HABITAT/PATCH

We consider the small reward time step Δ_r . In main text, $\Delta_r = dt$; here we detail the general case. Since the reward time step is small ($\Delta_r \ll 1$), we use a quasicontinuous reward approximation. Then it is possible to replace the reward term $r(t)$ by the average rate $\bar{p}(T)$ and consider the effective drift term $\mu(T) = \alpha - \bar{p}(T)$. This average rate $\bar{p}(T)$ has different expressions, depending on the nondepleting or depleting feature of the foraging area.

1. Habitat (nondepleting environment)

In this case, the average rate can be written as

$$\bar{p} = \frac{p dt}{\Delta_r}. \quad (A1)$$

If $\mu > 0$, the mean residence time $\bar{T}$ can be obtained by integrating Eq. (1) from 0 to θ :

$$\bar{T} = -\frac{\theta}{\mu}. \quad (A2)$$

With this constant drift μ , the probability of leaving a habitat at time T is an inverse Gaussian distribution [84],

$$\Psi(T) = -\frac{\theta}{\sqrt{4\pi BT^3}} \exp\left(\frac{-(\theta + \mu T)^2}{4BT}\right), \quad (A3)$$

And the probability of being in the habitat at a time T is

$$\Omega(T) = \Phi\left(\frac{-\theta - \mu T}{\sqrt{2BT}}\right) - \exp\left(\frac{-\mu\theta}{B}\right) \Phi\left(\frac{\theta - \mu T}{\sqrt{2BT}}\right) \quad (A4)$$

with the standard normal integral

$$\Phi(y) = \frac{1}{\sqrt{2\pi}} \int_{-\infty}^y \exp\left(-\frac{z^2}{2}\right) dz. \quad (\text{A5})$$

In contrast to a habitat, in a depleting environment the average rate is not constant.

2. Patch (depleting environment)

We can write the evolution of the probability of receiving a reward as $p(t) = \frac{p_{\text{in}} dt}{\Delta_r} \times e^{-\frac{t}{A_m \Delta_r}}$. The average reward rate is estimated as

$$\bar{p}(T) = \frac{\int_0^T \frac{p_{\text{in}} dt}{\Delta_r} e^{-\frac{t}{A_m \Delta_r}} dt}{T} = p_{\text{in}} dt A_m \frac{1 - e^{-\frac{T}{A_m \Delta_r}}}{T}. \quad (\text{A6})$$

The term $\bar{p}(T)$ can be used in Eqs. (A2)–(A4).

To find the value of $\bar{T}$, the self-consistent equation (A2) should be solved numerically.

APPENDIX B: CALCULATION OF DISTRIBUTIONS

1. $P^k(t)$ and $P_{A,v}^k$

The probability density of leaving a habitat k at time t , $P^k(t)$, is given by the convolution over $\Psi^0(t)$ and $\Psi^1(t)$:

$$\begin{aligned} P_v^0(t) &= \int_0^{t-T_{\text{tr}}} d\tau_{v-1} \Psi^0(t - (\tau_{v-1} + T_{\text{tr}})) \\ &\times \int_0^{\tau_{v-1}-T_{\text{tr}}} d\tau_{v-2} \Psi^1(\tau_{v-1} - (\tau_{v-2} + T_{\text{tr}})) \\ &\dots \int_0^{\tau_2-T_{\text{tr}}} d\tau_1 \Psi^0(\tau_2 - (\tau_1 + T_{\text{tr}})) \\ &\times \int_0^{\tau_1-T_{\text{tr}}} d\tau_0 \Psi^1(\tau_1 - (\tau_0 + T_{\text{tr}})) \Psi^0(\tau_0). \end{aligned} \quad (\text{B1})$$

This probability can be found after using the Laplace transform of Ψ to compute the convolution of functions with the same drift term in one compartment.

Through the Laplace transform,

$$\tilde{\Psi}^k(s) = \exp\left[\frac{\theta}{B}(\mu^k - \sqrt{\mu^{k^2} + 2sB})\right]. \quad (\text{B2})$$

The successive v convolutions over distributions with the same effective drift term lead to the term $(\tilde{\Psi}^k(s))^v = \exp[\frac{v\theta}{B}(\mu^k - \sqrt{\mu^{k^2} + 2sB})]$. Going back to the real domain,

$$P_v^0(t) = (\Psi_v^0 * \Psi_{v-1}^1)[t - 2(v-1)T_{\text{tr}}] \quad (\text{B3})$$

with

$$\Psi_v^k(t) = \frac{-v\theta}{\sqrt{4\pi B t^3}} \exp\left(\frac{-(v\theta + \mu^k t)^2}{4Bt}\right) \quad (\text{B4})$$

for $v \geq 1$. $\Psi_0^k(t) = 1$ for all t .

The same reasoning for habitat 1 gives the following:

$$P_v^1(t) = (\Psi_v^0 * \Psi_v^1)[t - (2v-1)T_{\text{tr}}]. \quad (\text{B5})$$

$P_v^k(t)$ can be written compactly as

$$P_v^k(t) = (\Psi_v^0 * \Psi_{v-1+k}^1)[t - (2v-2+k)T_{\text{tr}}]. \quad (\text{B6})$$

$P^k(t)$ is then obtained by the sum over v from 1 to ∞ of Eqs. (B6). The amplitude series $P_{A,v}^k$ in the case of $p^0 = p^1$ corresponds to P^k computed at times $\bar{t}_v^k$.

Since $\bar{t}_v^k = (2v-1+k)(\bar{T} + T_{\text{tr}}) - T_{\text{tr}}$, it is not convenient to simplify the equation due to the last $-T_{\text{tr}}$. A shift of T_{tr} of the distributions can be used to define an alternative threshold θ' , such that $\bar{T} + T_{\text{tr}} = -\frac{\theta'}{\mu}$. So $\theta' = \theta - \mu T_{\text{tr}}$, and the alternative peak times are instead $\bar{t}_v^{k'} = (2v-1+k)(\bar{T} + T_{\text{tr}})$.

Rewriting the amplitude $P^k(t)$ for each peak v gives

$$\begin{aligned} P_{A,v}^k &= \sum_{m=1}^{\infty} \frac{2m-1+k}{\sqrt{4\pi(2v-1+k)^3}} \\ &\times \frac{\mu^2}{\gamma B} \exp\left(-\frac{(v-m)^2 \gamma^2}{2v-1+k}\right). \end{aligned} \quad (\text{B7})$$

Please note that, for $v \rightarrow \infty$, $P_{A,v}^k$ tends to the steady state value P_S^k . The resulting expression (B7) enables extracting the parameter γ (11).

2. Identical habitats

In the special case $p^0 = p^1$, the distributions are

$$P^k(t) = \sum_{v=1}^{\infty} \Psi_{2v-1+k}^k(t - (2v-2+k)T_{\text{tr}}) \quad (\text{B8})$$

and

$$\begin{aligned} Q^k(t) &= \sum_{v=1}^{\infty} [\Omega_{2v-1+k}^k(t - (2v-2+k)T_{\text{tr}}) \\ &- \Omega_{2v-1+k'}^k(t - (2v-1+k')T_{\text{tr}})] \end{aligned} \quad (\text{B9})$$

with

$$\Omega_v^k(T) = \Phi\left(\frac{-v\theta - \mu^k T}{\sqrt{2BT}}\right) - \exp\left(\frac{-\mu^k v\theta}{B}\right) \Phi\left(\frac{v\theta - \mu^k T}{\sqrt{2BT}}\right). \quad (\text{B10})$$

APPENDIX C: COMPUTING Q_S^k WITH ENTERING AND DEPARTING FLUXES

We compute the balance of four agent fractions in a steady state: in habitat 0 (Q_S^0), in habitat 1 (Q_S^1), traveling from 0 to 1 (W_S^{01}), and traveling from 1 to 0 (W_S^{10}). These terms are

linked by

$$Q_S^0 + Q_S^1 + W_S^{01} + W_S^{10} = 1. \quad (C1)$$

With steady state departure rates equal to $-\alpha_{\text{eff,eq}}/\theta$, the balance system can be written as

$$\begin{aligned} -\frac{\alpha_{\text{eff,eq}}^0}{\theta} Q_S^0 + \frac{1}{T_{\text{tr}}} W_S^{10} &= 0, \\ -\frac{1}{T_{\text{tr}}} W_S^{10} - \frac{\alpha_{\text{eff,eq}}^1}{\theta} Q_S^1 &= 0, \\ -\frac{\alpha_{\text{eff,eq}}^0}{\theta} Q_S^0 + \frac{1}{T_{\text{tr}}} W_S^{10} &= 0, \\ -\frac{1}{T_{\text{tr}}} W_S^{10} - \frac{\alpha_{\text{eff,eq}}^1}{\theta} Q_S^1 &= 0. \end{aligned} \quad (C2)$$

Solving the system of equations (C1) and (C2) gives the general equation

$$Q_S^k = \frac{1}{-\frac{2\mu^k T_{\text{tr}}}{\theta} + 1 + \frac{\mu^k}{\mu^{k'}}}. \quad (C3)$$

and P_S^k is estimated to be $P_S^k = \frac{Q_S^k}{T^k}$.

APPENDIX D: PERFECT DIFFUSIVE COUPLING

The mean $\bar{x} = \frac{\sum_{i=1}^N x_i}{N}$ and the half-difference between two agents, $x_{ij}^- = \frac{x_i - x_j}{2}$, evolve as

$$d\bar{x} = (p^k - \alpha)dt + \sqrt{2B} \left/ N \sum_{i=1}^N dW_i, \quad (D1)$$

$$dx_{ij}^- = -\frac{\kappa_{\text{diff}}}{N} x_{ij}^- dt + \sqrt{B/2} (dW_i - dW_j) \quad (D2)$$

With the Ornstein-Uhlenbeck process of x_{ij}^- , it is possible to show that, for $\kappa_{\text{diff}} \rightarrow \infty$, $\langle x_{ij}^- \rangle = 0$, $\langle (x_{ij}^-)^2 \rangle = 0$ [85]. Thus,

in this limit all x_i are considered equal, and the equivalent averaging equation can be described by

$$d\bar{x} = (p^k - \alpha)dt + \sqrt{\frac{2B}{N}} dW(t). \quad (D3)$$

APPENDIX E: PULSATILE EFFECTIVE DRIFT TERMS

We start with normalization by the total number of agents.

$$1. \mathcal{N}_d = \mathcal{N}_a = N$$

For a large number of agents $N \gg 1$, the effective drift term in a steady state can be written as

$$\mu_S^k = \alpha - p^k + \frac{\kappa_a - \kappa_d}{\theta} \frac{\mu_S^k \mu_S^{k'}}{\mu_S^k + \mu_S^{k'}}. \quad (E1)$$

Solving the system gives Eq. (16).

The second normalization, by the number of agents in the habitat, is slightly different, as it assumes an additional computation for the individuals to evaluate this variable.

$$2. \mathcal{N}_d = n^k - 1, \mathcal{N}_a = N - n^k - 1$$

Similarly, for a large number of agents $N \gg 1$, the effective drift term in a steady state can be written as

$$\mu_S^k = \alpha - p^k - \kappa_d \frac{\mu_S^k}{\theta} + \kappa_a \frac{\mu_S^{k'}}{\theta}. \quad (E2)$$

Solving the system of two equations gives Eq. (17).

APPENDIX F: INDIVIDUAL LEARNING

Equation (1) and the reset of x_i 's at every departure do not include a memory effect throughout the different habitats. In the two-habitat situation, agents with a long-term belief of which habitat has the highest quality are studied.

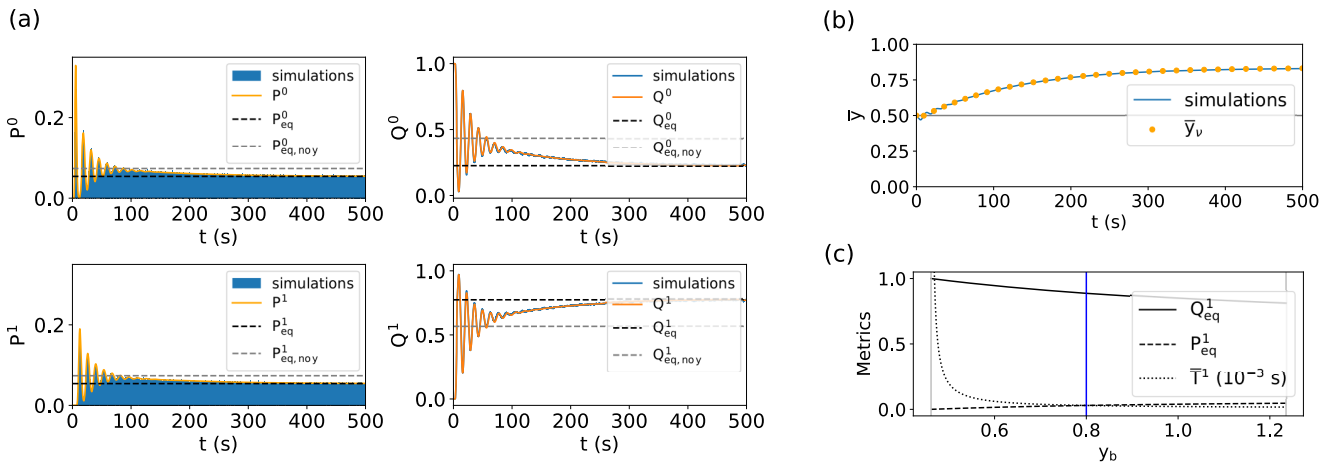


FIG. 7. Best habitat individual inference improves collective accuracy and exploitation times in the best habitat. (a) Distributions of leaving times $P^k(t)$ (left), and fraction of agents $Q^k(t)$ (right) in habitats $k = 0$ (top) and $k = 1$ (bottom) show damped oscillations and different steady states compared to agents without best habitat inference. $y_b = 0.8$ (2×10^4 simulations). (b) The average best habitat inference $\bar{y}(t)$ converges to a value $> \frac{1}{2}$, corresponding to a correct best habitat inference ($k = 1$). (c) Fraction in the best habitat Q_S^1 and mean habitat residence time $\bar{T}^1$ decrease with y_b , while P_S^1 increases. The two vertical gray lines represent the two limits in Eq. (F8), and the vertical blue line corresponds to the numerical y_b value used in (a). Please note that, for all y_b values, the steady state accuracy Q_S^1 is higher than the situation without best habitat inference [see Fig. 1(b)].

To represent this long-term belief dynamics, the variable y_i is introduced. This variable represents the inference of which habitat has the highest reward probability p^k . It evolves as

$$\tau_y dy_i(t) = [k - y_i(t)] r_i(t) dt. \quad (F1)$$

The variable y_i converges towards the value $k = 0$ or $k = 1$, at a rate $r_i(t)$. Then, as more rewards are received in a habitat k , the convergence rate increases. This happens in the best habitat ($k = 1$), as the reward rate is higher and the animals spend more time in this habitat. These dynamics depend here only on the individual food catches. At $t = 0$, $y_i(0) = \frac{1}{2}$. τ_y is the timescale of the differential equation.

The variable y_i determines the evolution of the factor ω_i^k , modifying the effective drift term as $\mu_i^k(t) = \alpha \times \omega_i^k(t)$. When an agent i is leaving a habitat at time t , the factor ω_i^k is updated with $y_i(t)$:

$$\omega_i^k(t) = \frac{y_b + y_i(t)(1 - 2k) + k}{y_b + \frac{1}{2}}. \quad (F2)$$

For example, if $y_i(t) > \frac{1}{2}$ (that is, the best estimated habitat is $k = 1$), $\omega_i^k < 1$ in habitat $k = 1$ and $\omega_i^k > 1$ in habitat $k = 0$. So $\alpha \times \omega_i^k$ decreases in $k = 1$, implying that the agent stays longer in this best estimated habitat, and inversely for the other habitat $k = 0$.

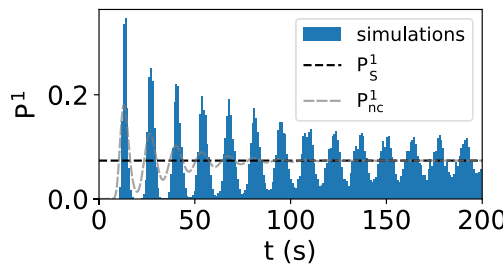
The average value of y at the departure time $t_{y,v}^k$ can be estimated with $\bar{y}_v^k$.

It is possible to solve Eq. (F1) using solutions for $k = 0$ and $k = 1$ to estimate the mean value of y when leaving a habitat k for the time v :

$$\begin{aligned} y_v^0 &= y_v^1 \exp\left(\frac{p^0 t_v^0}{\tau_y}\right), \\ y_v^1 &= 1 + (y_v^0 - 1) \exp\left(\frac{p^1 t_v^1}{\tau_y}\right), \end{aligned} \quad (F3)$$

with $t_v^k = -\frac{\theta}{\alpha \omega_v^k - p^k}$ and

$$\begin{aligned} \omega_v^0 &= \frac{y_b + \bar{y}_v^1}{y_b + \frac{1}{2}}, \\ \omega_v^1 &= \frac{y_b + 1 - \bar{y}_v^0}{y_b + \frac{1}{2}}, \end{aligned} \quad (F4)$$



since ω_v^k in habitat k is updated with the last $\bar{y}_m^{k'}$ from the other habitat k' . Writing the detailed terms in Eq. (F3) gives the recurrence relation in Eq. (F6).

For $v \in \{1, 2, \dots\}$,

$$y_v^0 = y_{v-1}^1 \exp\left(\frac{p^0 \theta (y_b + \frac{1}{2})}{\tau_y [\alpha (y_b + y_{v-1}^1) - p^0 (y_b + \frac{1}{2})]}\right), \quad (F5)$$

$$y_v^1 = 1 + (y_v^0 - 1) \exp\left(\frac{p^1 \theta (y_b + \frac{1}{2})}{\tau_y [\alpha (y_b + 1 - y_v^0) - p^1 (y_b + \frac{1}{2})]}\right), \quad (F6)$$

with $y_0^1 = \frac{1}{2}$.

The average best habitat inference is $\bar{y}_v = \frac{y_v^0 + y_v^1}{2}$, plotted with $\bar{t}_v = \frac{t_{y,v}^0 + t_{y,v}^1}{2}$:

$$\begin{aligned} t_{y,v}^0 &= t_{y,v-1}^1 - \frac{\theta (y_b + \frac{1}{2})}{\alpha (y_b + y_{v-1}^1) - p^0 (y_b + \frac{1}{2})}, \\ t_{y,v}^1 &= t_{y,v}^0 - \frac{\theta (y_b + \frac{1}{2})}{\alpha (y_b + y_v^0) - p^1 (y_b + \frac{1}{2})}. \end{aligned} \quad (F7)$$

From condition $\alpha \omega_{y_{\max}}^k - p^k > 0$, with $y_{\max} = 1$, two limits are derived for y_b :

$$\frac{p^1}{2(\alpha - p^1)} > y_b > \frac{2\alpha - p^0}{2(\alpha - p^0)} \quad (F8)$$

It is possible to compute $P^k(t)$, $Q^k(t)$ with the updated $\mu^k \times \omega_v^k$, and Q_{eq}^k , P_{eq}^k for $\tau_y \gg 1$.

Figure 7 shows how the distributions are changed with the best habitat inference. The steady state fraction of agents in the best habitat is progressively increasing as the mean best habitat inference variable $\bar{y}$ increases. Figure 7(c) highlights higher accuracy and habitat residence times in the best habitat, as well as a smaller value P_S^1 for small values of the boundary parameter y_b . The individual inference of the best habitat improves collective accuracy and the exploitation of the best habitat.

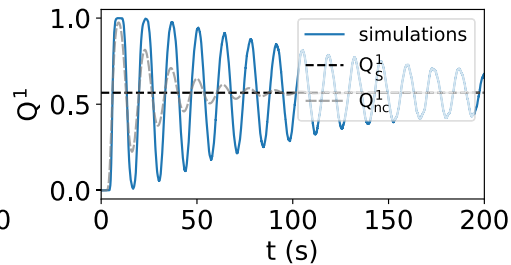


FIG. 8. Diffusive coupling normalized by the number of other agents in the observer's current or other habitat. Continuous belief sharing (diffusive) leads to more cohesion, with no accuracy and exploitation modifications. Left: Distributions of leaving times $P^1(t)$ and fraction of agents $Q^1(t)$ in the best habitat show less damped oscillations, and no change in steady states and periodicity compared to a noncoupled situation. Parameters are $N = 5$, $\kappa_{\text{diff}} = 1 \text{ s}^{-1}$ (2×10^3 simulations).

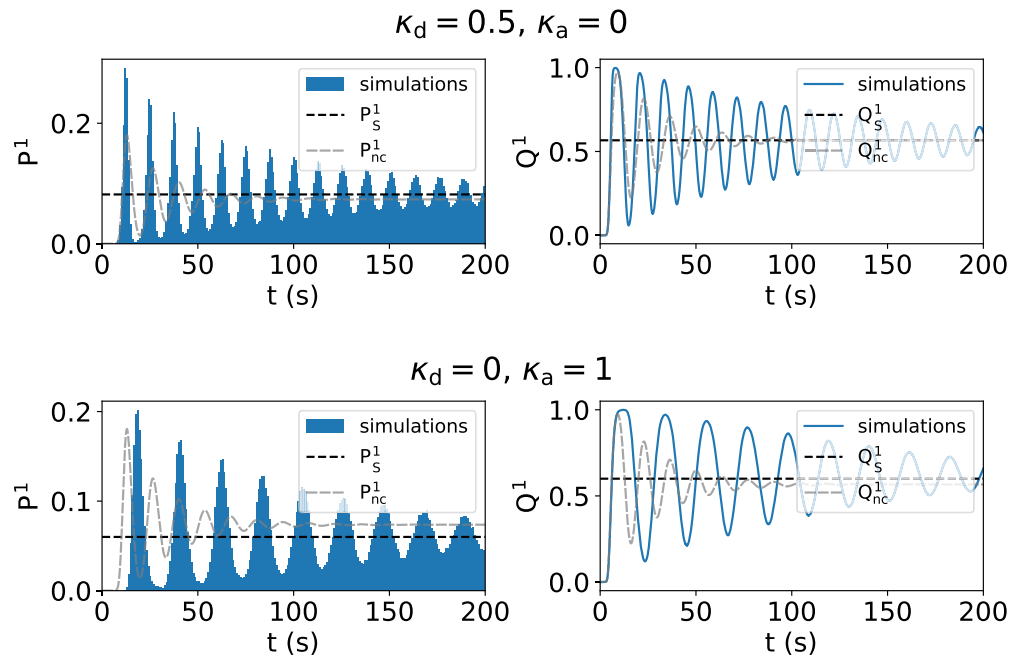


FIG. 9. Pulsatile coupling scaled by the number of other agents in the observer's current or other habitat. Top: Observation of others' departures leads to more accuracy, less exploitation, and more cohesion. Distributions of leaving times $P^1(t)$ and fraction of agents $Q^1(t)$ in the best habitat show less damped oscillations, earlier departure times, and a higher steady state fraction of agents in the best habitat. Parameters are $N = 50$, $\kappa_d = 0.5$, $\kappa_a = 0$ (1×10^3 simulations). Bottom: Observation of others' arrivals leads to more accuracy, more exploitation, and more cohesion. Distributions of leaving times $P^1(t)$ and fraction of agents $Q^1(t)$ in the best habitat show less damped oscillations, later departure times, and a higher steady state fraction of agents in the best habitat. Parameters are $N = 50$, $\kappa_d = 0$, $\kappa_a = 1$ (1×10^3 simulations).

APPENDIX G: SUPPLEMENTARY FIGURES

See Figs. 8 and 9 for plots of diffusive coupling normalized by the number of other agents in the observer's current or

other habitat, and pulsatile coupling scaled by the number of other agents in the observer's current or other habitat, respectively.

- [1] D. W. Stephens, J. S. Brown, and R. C. Ydenberg, *Foraging: Behavior and Ecology* (University of Chicago Press, Chicago, 2007).
- [2] K. McGarigal, H. Y. Wan, K. A. Zeller, B. C. Timm, and S. A. Cushman, Multi-scale habitat selection modeling: A review and outlook, *Landsc. Ecol.* **31**, 1161 (2016).
- [3] D. W. Stephens, Decision ecology: Foraging and the ecology of animal decision making, *Cogn. Affect. Behav. Neurosci.* **8**, 475 (2008).
- [4] C. Detrain and J.-L. Deneubourg, Collective decision-making and foraging patterns in ants and honeybees, *Adv. Insect. Physiol.* **35**, 123 (2008).
- [5] L. M. Aplin, D. R. Farine, R. P. Mann, and B. C. Sheldon, Individual-level personality influences social foraging and collective behaviour in wild birds, *Proc. R. Soc. B: Biol. Sci.* **281**, 20141016 (2014).
- [6] L. Alfaro, F. Sanabria, and R. Cabrera, The role of outcome unit size in the social foraging strategies of rats, *Int. J. Comp. Psychol.* **32** (2019).
- [7] G. E. C. Gall and M. B. Manser, Group cohesion in foraging meerkats: Follow the moving 'vocal hot spot', *R. Soc. Open Sci.* **4**, 170004 (2017).
- [8] A. Strandburg-Peshkin, D. R. Farine, I. D. Couzin, and M. C. Crofoot, Shared decision-making drives collective movement in wild baboons, *Science* **348**, 1358 (2015).
- [9] E. Fernandez-Juricic, Flock density, social foraging, and scanning: An experiment with starlings, *Behav. Ecol.* **15**, 371 (2004).
- [10] W. Siegfried and L. Underhill, Flocking as an anti-predator strategy in doves, *Anim. Behav.* **23**, 504 (1975).
- [11] M. Dumke, M. E. Herberstein, and J. M. Schneider, Advantages of social foraging in crab spiders: Groups capture more and larger prey despite the absence of a web, *Ethology* **124**, 695 (2018).
- [12] C. W. Clark and M. Mangel, The evolutionary advantages of group foraging, *Theor. Popul. Biol.* **30**, 45 (1986).
- [13] T. J. Pitcher, A. E. Magurran, and I. J. Winfield, Fish in larger shoals find food faster, *Behav. Ecol. Sociobiol.* **10**, 149 (1982).
- [14] R. Martínez-García, J. M. Calabrese, T. Mueller, K. A. Olson, and C. López, Optimizing the search for resources by sharing information: Mongolian gazelles as a case study, *Phys. Rev. Lett.* **110**, 248106 (2013).

- [15] S. Dall, L. Giraldeau, O. Olsson, J. McNamara, and D. Stephens, Information and its use by animals in evolutionary ecology, *Trends Ecol. Evol.* **20**, 187 (2005).
- [16] S. D. Fretwell and H. L. Lucas, On territorial behavior and other factors influencing habitat distribution in birds: I. Theoretical development, *Acta Biotheor.* **19**, 16 (1969).
- [17] M. Kennedy and R. D. Gray, Can ecological theory predict the distribution of foraging animals? A critical analysis of experiments on the ideal free distribution, *Oikos* **68**, 158 (1993).
- [18] B. Livoreil and L.-A. Giraldeau, Patch departure decisions by spice finches foraging singly or in groups, *Anim. Behav.* **54**, 967 (1997).
- [19] E. Wajnberg, T. S. Hoffmeister, and P. Coquillard, Optimal within-patch movement strategies for optimising patch residence time: An agent-based modelling approach, *Behav. Ecol. Sociobiol.* **67**, 2053 (2013).
- [20] A. Falcón-Cortés, D. Boyer, and G. Ramos-Fernández, Collective learning from individual experiences and information transfer during group foraging, *J. R. Soc. Interface.* **16**, 20180803 (2019).
- [21] R. C. Löffler, E. Panizon, and C. Bechinger, Collective foraging of active particles trained by reinforcement learning, *Sci. Rep.* **13**, 17055 (2023).
- [22] L.-A. Giraldeau and T. Caraco, *Social Foraging Theory* (Princeton University Press, Princeton, 2000).
- [23] R. Cressman, V. Křivan, J. S. Brown, and J. Garay, Game-theoretic methods for functional response and optimal foraging behavior, *PLoS ONE* **9**, e88773 (2014).
- [24] A. Perez-Escudero and G. De Polavieja, Collective animal behavior from Bayesian estimation and probability matching, *Nat. Precedings* **1** (2011).
- [25] I. D. Couzin, J. Krause, N. R. Franks, and S. A. Levin, Effective leadership and decision-making in animal groups on the move, *Nature (London)* **433**, 513 (2005).
- [26] J. D. Davidson and A. El Hady, Foraging as an evidence accumulation process, *PLoS Comput. Biol.* **15**, e1007060 (2019).
- [27] Z. P. Kilpatrick, J. D. Davidson, and A. El Hady, Uncertainty drives deviations in normative foraging decision strategies, *J. R. Soc. Interface.* **18**, 20210337 (2021).
- [28] T. Liu and T. J. Pleskac, Neural correlates of evidence accumulation in a perceptual decision task, *J. Neurophysiol.* **106**, 2383 (2011).
- [29] A. C. Huk and M. L. R. Meister, Neural correlates and neural computations in posterior parietal cortex during perceptual decision-making, *Front. Integr. Neurosci.* **6**, 00086 (2012).
- [30] J. I. Gold and M. N. Shadlen, The neural basis of decision making, *Annu. Rev. Neurosci.* **30**, 535 (2007).
- [31] S. Bidari, A. El Hady, J. D. Davidson, and Z. P. Kilpatrick, Stochastic dynamics of social patch foraging decisions, *Phys. Rev. Res.* **4**, 033128 (2022).
- [32] E. Leadbeater and L. Chittka, Social learning in insects—from miniature brains to consensus building, *Curr. Biol.* **17**, R703 (2007).
- [33] B. G. Galef and L.-A. Giraldeau, Social influences on foraging in vertebrates: Causal mechanisms and adaptive functions, *Anim. Behav.* **61**, 3 (2001).
- [34] J. McNamara, Optimal patch use in a stochastic environment, *Theor. Popul. Biol.* **21**, 269 (1982).
- [35] P. Haccou, S. J. D. Vlas, J. J. M. V. Alphen, and M. E. Visser, Information processing by foragers: Effects of intra-patch experience on the leaving tendency of *Leptopilina heterotoma*, *J. Anim. Ecol.* **60**, 93 (1991).
- [36] G. Driessen and C. Bernstein, Patch departure mechanisms and optimal host exploitation in an insect parasitoid, *J. Anim. Ecol.* **68**, 445 (1999).
- [37] D. E. Taneyhill, Patch departure behavior of bumble bees: Rules and mechanisms, *Psyche J. Entomol.* **2010**, 1 (2010).
- [38] P. L. Smith and R. Ratcliff, Psychology and neurobiology of simple decisions, *Trends Neurosci.* **27**, 161 (2004).
- [39] R. Ratcliff, P. L. Smith, S. D. Brown, and G. McKoon, Diffusion decision model: Current issues and history, *Trends Cognit. Sci.* **20**, 260 (2016).
- [40] S. Boinski, Vocal coordination of troop movement among white-faced capuchin monkeys, *Cebus capucinus*, *Am. J. Primatol.* **30**, 85 (1993).
- [41] J. E. Kohles, G. G. Carter, R. A. Page, and D. K. N. Dechmann, Socially foraging bats discriminate between group members based on search-phase echolocation calls, *Behav. Ecol.* **31**, 1103 (2020).
- [42] K. V. Frisch, T. D. Seeley, and L. E. Chadwick, *The Dance Language and Orientation of Bees* (Harvard University Press, Cambridge, 2013).
- [43] M. Gil and R. J. De Marco, Olfactory learning by means of trophallaxis in *Apis mellifera*, *J. Exp. Biol.* **208**, 671 (2005).
- [44] V. Srivastava and N. E. Leonard, Collective decision-making in ideal networks: The speed-accuracy tradeoff, *IEEE Trans. Control Netw. Syst.* **1**, 121 (2014).
- [45] R. D. Sorkin, C. J. Hays, and R. West, Signal-detection analysis of group decision making, *Psychol. Rev.* **108**, 183 (2001).
- [46] D. Pais and N. E. Leonard, Adaptive network dynamics and evolution of leadership in collective migration, *Physica D* **267**, 81 (2014).
- [47] C. J. Torney, S. A. Levin, and I. D. Couzin, Specialization and evolutionary branching within migratory populations, *Proc. Natl. Acad. Sci. USA* **107**, 20394 (2010).
- [48] T. A. Waite and T. C. Grubb, Copying of foraging locations in mixed-species flocks of temperate-deciduous woodland birds: An experimental study, *Condor* **90**, 132 (1988).
- [49] J. B. Calhoun, *The Ecology and Sociology of the Norway Rat* (U.S. Department of Health, Education, and Welfare, Public Health Service, Bethesda, MD, 1963).
- [50] R. J. Caginalp and B. Doiron, Decision dynamics in groups with interacting members, *SIAM J. Appl. Dyn. Syst.* **16**, 1543 (2017).
- [51] B. Karamched, S. Stolarczyk, Z. P. Kilpatrick, and K. Josić, Bayesian evidence accumulation on social networks, *SIAM J. Appl. Dyn. Syst.* **19**, 1884 (2020).
- [52] J. J. Templeton and L.-A. Giraldeau, Patch assessment in foraging flocks of European starlings: Evidence for the use of public information, *Behav. Ecol.* **6**, 65 (1995).
- [53] T. J. Valone and L.-A. Giraldeau, Patch estimation by group foragers: What information is used? *Anim. Behav.* **45**, 721 (1993).
- [54] E. L. Charnov, Optimal foraging, the marginal value theorem, *Theor. Popul. Biol.* **9**, 129 (1976).
- [55] G. Powell, Experimental analysis of the social value of flocking by starlings (*Sturnus vulgaris*) in relation to predation and foraging, *Anim. Behav.* **22**, 501 (1974).

- [56] M. M. Food competition and foraging party size in the black spider monkey (*Ateles paniscus chamek*), *Behaviour* **105**, 117 (1988).
- [57] N. J. Lemanski, C. N. Cook, C. Ozturk, B. H. Smith, and N. Pinter-Wollman, The effect of individual learning on collective foraging in honey bees in differently structured landscapes, *Anim. Behav.* **179**, 113 (2021).
- [58] S. Eliassen, C. Jørgensen, M. Mangel, and J. Giske, Quantifying the adaptive value of learning in foraging behavior, *Am. Nat.* **174**, 478 (2009).
- [59] A. Kacelnik and I. A. Todd, Psychological mechanisms and the marginal value theorem: Effect of variability in travel time on patch exploitation, *Anim. Behav.* **43**, 313 (1992).
- [60] J. D. Cohen, S. M. McClure, and A. J. Yu, Should I stay or should I go? How the human brain manages the trade-off between exploitation and exploration, *Philos. Trans. R. Soc. B* **362**, 933 (2007).
- [61] K. Mehlhorn, B. R. Newell, P. M. Todd, M. D. Lee, K. Morgan, V. A. Braithwaite, D. Hausmann, K. Fiedler, and C. Gonzalez, Unpacking the exploration–exploitation tradeoff: A synthesis of human and animal literatures, *Decision* **2**, 191 (2015).
- [62] P. Michelena, A. M. Sibbald, H. W. Erhard, and J. E. McLeod, Effects of group size and personality on social foraging: The distribution of sheep across patches, *Behav. Ecol.* **20**, 145 (2009).
- [63] 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, *Anim. Behav.* **85**, 1233 (2013).
- [64] C. T. Monk, M. Barbier, P. Romanczuk, J. R. Watson, J. Alós, S. Nakayama, D. I. Rubenstein, S. A. Levin, and R. Arlinghaus, How ecology shapes exploitation: A framework to predict the behavioural response of human and animal foragers along exploration–exploitation trade-offs, *Ecol. Lett.* **21**, 779 (2018).
- [65] T. J. Valone, Group foraging, public information, and patch estimation, *Oikos* **56**, 357 (1989).
- [66] F. Amici, J. Call, J. Watzek, S. Brosnan, and F. Aureli, Social inhibition and behavioural flexibility when the context changes: A comparison across six primate species, *Sci. Rep.* **8**, 3067 (2018).
- [67] B. Würsig and H. C. Pearson, Dusky dolphins: Flexibility in foraging and social strategies, in *Primates and Cetaceans*, edited by J. Yamagiwa and L. Karczmarski (Springer Japan, Tokyo, 2014), pp. 25–42.
- [68] I. Petelski, Y. Günzel, S. Sayin, S. Kraus, and E. Couzin-Fuchs, Synergistic olfactory processing for social plasticity in desert locusts, Zenodo (2024), doi: [10.5281/zenodo.10931393](https://doi.org/10.5281/zenodo.10931393).
- [69] E. Sorato, P. R. Gullett, S. C. Griffith, and A. F. Russell, Effects of predation risk on foraging behaviour and group size: Adaptations in a social cooperative species, *Anim. Behav.* **84**, 823 (2012).
- [70] L. Real and T. Caraco, Risk and foraging in stochastic environments, *Ann. Rev. Ecol. Syst.* **17**, 371 (1986).
- [71] E. Wajnberg, P. Bernhard, F. Hamelin, and G. Boivin, Optimal patch time allocation for time-limited foragers, *Behav. Ecol. Sociobiol.* **60**, 1 (2006).
- [72] W. A. Roberts and T. J. Illersich, Foraging on the radial maze: The role of travel time, food accessibility, and the predictability of food location, *J. Exp. Psychol. Anim. Behav. Process.* **15**, 274 (1989).
- [73] D. Goulson, S. A. Hawson, and J. C. Stout, Foraging bumblebees avoid flowers already visited by conspecifics or by other bumblebee species, *Anim. Behav.* **55**, 199 (1998).
- [74] L.-A. Giraldeau, T. J. Valone, and J. J. Templeton, Potential disadvantages of using socially acquired information, *Philos. Trans. R. Soc. London B* **357**, 1559 (2002).
- [75] F. Hillemann, E. F. Cole, B. C. Sheldon, and D. R. Farine, Information use in foraging flocks of songbirds: No evidence for social transmission of patch quality, *Anim. Behav.* **165**, 35 (2020).
- [76] R. Stutz, U. Bergvall, O. Leimar, J. Tuomi, and P. Rautio, Cohesiveness reduces foraging efficiency in a social herbivore, *Anim. Behav.* **135**, 57 (2018).
- [77] M. C. Baker, C. S. Belcher, L. C. Deutsch, G. L. Sherman, and D. B. Thompson, Foraging success in junco flocks and the effects of social hierarchy, *Anim. Behav.* **29**, 137 (1981).
- [78] W. Lee, E. Yang, and J. P. Curley, Foraging dynamics are associated with social status and context in mouse social hierarchies, *PeerJ* **6**, e5617 (2018).
- [79] E. Ranta, H. Rita, and K. Lindstrom, Competition versus cooperation: Success of individuals foraging alone and in groups, *Am. Nat.* **142**, 42 (1993).
- [80] M. Laguë, N. Tania, J. Heath, and L. Edelstein-Keshet, The effects of facilitation and competition on group foraging in patches, *J. Theor. Biol.* **310**, 88 (2012).
- [81] W. L. Vickery, L.-A. Giraldeau, J. J. Templeton, D. L. Kramer, and C. A. Chapman, Producers, scroungers, and group foraging, *Am. Nat.* **137**, 847 (1991).
- [82] J. P. Scott, The analysis of social organization in animals, *Ecology* **37**, 213 (1956).
- [83] Lblummoy/social-foraging-theory-in-an-egalitarian-group, <https://github.com/lblummoy/social-foraging-theory-in-an-egalitarian-group>.
- [84] D. Cox and H. Miller, *The Theory of Stochastic Processes* (Chapman and Hall, New York, 1965).
- [85] C. W. Gardiner, *Handbook of Stochastic Methods for Physics, Chemistry, and the Natural Sciences*, 3rd ed., Springer Series in Synergetics (Springer-Verlag, New York, 1985).