

Modeling the lowest-cost splitting of a herd of cows by optimizing a cost function

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Animals live in groups to defend against predation and to obtain food. However, for some animals — especially ones that spend long periods of time feeding — there are costs if a group chooses to move on before their nutritional needs are satisfied. If the conflict between feeding and keeping up with a group becomes too large, it may be advantageous for some animals to split into subgroups of animals with similar nutritional needs. We model the costs and benefits of splitting by a herd of cows using a cost function that quantifies individual variation in hunger, desire to lie down, and predation risk. We model the costs associated with hunger and lying desire as the standard deviations of individuals within a group, and we model predation risk as an inverse exponential function of group size. We minimize the cost function over all plausible groups that can arise from a given herd and study the dynamics of group splitting. We explore our model using two examples: (1) we consider group switching and group fission in a herd of relatively homogeneous cows; and (2) we examine a herd with an equal number of adult males (larger animals) and adult females (smaller animals).

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Although animals gain many advantages — such as protection from predators — from living in groups, they also incur considerable costs. For grazing animals, such as cows and antelopes, these costs include having to balance their own nutritional needs to stay in one place to feed with the need to keep up with a group and stop grazing when the rest of the herd moves on. If the nutritional needs of different individuals are sufficiently disparate, this can lead to the splitting of a group so that those with similar needs to graze, lie, and ruminant remain together. If a group of animals becomes too small, however, this can increase the risk of predation, as small groups are less able than large groups to defend themselves against predators. In this paper, we describe a cost function (CF) that balances predation risk (based on group size) with different individual needs for feeding and lying down to infer the sizes at which group splitting occurs. We model variation in hunger and lying desire using the standard deviation of individuals within a group, and

we model predation risk as an inverse exponential function of group size. By optimizing the CF for each individual in a group of animals, we examine when groups should split into smaller subgroups.

I. INTRODUCTION

Animals gain many advantages from grouping and synchronizing their behavior — including greater vigilance, coordinated defense against predators, and increased ability to find and defend food sources.^{1,2} However, living in large groups also carries disadvantages, such as increased risk of disease and parasitism,^{3,4} having food stolen,⁵ and interference with movement.⁶ A “perfect” synchronization requires animals to change their activities at a communal time rather than at individual ideal times, and this can be costly for individuals.

The balance between synchrony and risk of predation is complex,^{7,8} and one possible approach for examining such a balance is with a cost function with components from synchrony and risk. When a group of animals becomes very large, the cost incurred through synchrony tends to exceed that incurred through risk, as a significant number of individuals change their desired activities (like eating or lying) to conform with communal decisions. Because of the balance, a cost function (CF) with

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components from synchrony and risk of predation should have at least one optimum point, and one should expect animal groups to split if they are too large. However, an optimum group size is not necessarily a “stable” group size. Supposing that animals join a group one by one, a stable group size is a size at which one no longer observes either further switching of animals between groups or fission between groups.⁹ Even when a group is already at its optimum for existing individuals, extra individuals can still benefit from joining the group. At some point, however, the group can become sufficiently large that it splits into two groups, as this benefits its members more than the overloaded single group.⁹ A stable group size is therefore likely to be consistently larger than an optimum group size.^{9,10}

Sometimes grouping can be even more complicated, as individuals within a group differ in many ways that relate to their fitnesses. For example, males and females in a herd differ in their nutritional needs. However, although they can benefit from staying with a mixed-gender group, some individuals may have to interrupt valuable feeding or lying time to keep up with a herd when it moves.^{11,12} However, it can be costly for such individuals to synchronize their activities with others, as they are forced to switch between eating, lying down, or moving at a communal time rather than a time that is optimal for them as individuals.¹³ Alternatively, a group may split into subgroups that consist of individuals with similar switching times (such as all males and all females, or juveniles and adults), and then the costs of synchronization are lower.^{13–17} Such synchronization costs depend on the range of different activities of animals in a group, so some animals (e.g., baboons) break up into subgroups for foraging, particularly when food is scarce, and then come together into larger groups for sleeping.¹⁸

Social splitting between two categories (e.g., male–female or calves–adults) has been examined using an ordinary-differential-equation (ODE) model, whose performance was tested using data on inter-sexual splitting in red deer.¹² However, even for animals in the same category (e.g., males), activity synchronization can vary significantly, as it can depend on the age, body mass, and health of animals. Consequently, category-based splitting can create groups in which animals are still heterogeneous across many other categories. Splitting of animals in different categories can also be seasonal; for example, in nature, inter-sexual social splitting does not occur during the mating season.¹⁹

Communal decisions in herds are made either despotically by a dominant animal (or dominant animals) or democratically by the majority of individuals in a group,^{20–22} and the corresponding groups are called “despotic groups” and “democratic groups”, respectively. Modeling of synchronization costs has suggested that costs for despotic groups tend to be higher than those for democratic groups.²⁰

The rest of our paper is structured as follows. In Sec. II, we discuss biological modeling principles and the

construction of a CF, which encapsulates the demands of hunger and lying desire of cattle, for groups of cows to stay together or break apart. In Sec. III, we describe a method of determining demands for hunger and lying desire using a CF and an evolution scheme (ES) that describes the change in state (eating, standing, and lying down) of cows. In Sec. IV, we examine the dynamics of cows and study the cost function for various parameter values in our model. In Sec. V, we present two examples: in the first example, we examine switching dynamics of cows when a herd that consists of adults splits into a maximum of three groups; in the second example, we study a scenario in which a herd that consists of an even mixture of males and females splits into a maximum of two groups. In Sec. VI, we discuss our results and present ideas for future work.

II. BIOLOGICAL MODELING PRINCIPLES

We consider the behavior of cows (*Bos taurus*), which make many daily decisions regarding staying with or splitting from a herd. Cows have a two-stage feeding process that involves first grazing (standing up) and then ruminating (predominantly lying down). Together, lying down and ruminating can occupy up to 65% of a cow’s day.^{23,24} Both grazing and lying (including ruminating) are essential for successful digestion of grass,²⁵ but cows have to stop these actions if their herd decides to move to another area, which can occur 15–20 times a day.²⁴ Each individual cow has similar — but not identical — needs for lying and grazing,^{23,26} so keeping up with a herd each time it moves can be considerably costly because of interrupted grazing or lying times. This cost can include reduced growth rate in young cattle^{27,28} and physiological and behavioral symptoms of “stress” when a cow is deprived of adequate opportunities for lying down.^{29,30}

Reference 13 considered costs from synchronization, as animals often need to change their behavior (e.g., staying in one place versus moving to another place) at a communal time rather than at their ideal time. In our work, we consider both a synchronization cost and a cost due to predation risk. We assume that large groups encounter a large synchronization cost and small groups increase the cost of predation risk.^{7,8} Therefore, the “perfect” group size is neither too large nor too small. Moreover, we assume that the synchrony can vary within groups, so one set of cows can be eating while another set of cows is lying down or walking (in the neighborhood of others).

We construct a CF based on the following four principal assumptions:

- (i) Herds are fully democratic when cows take communal decisions, as this ensures a reduced cost.²⁰
- (ii) Cows are free to switch between groups, so groups freely form or dissolve.^{31–33}
- (iii) Fission of groups depends only on cows’ hunger, lying desire, and predation risk.

- (iv) The predation risk of a group is an exponential function of the inverse of the group size.

The decrease of predation risk with group size in assumption (iv) arises from the facts that more animals in a group contributes to greater vigilance,^{1,2,34} a higher dilution effect,^{35,36} and a higher confusion effect.^{37,38} Consequently, a larger group size tends to result in a lower predation risk. Motivated by empirical studies in Refs. 34, 39–41, which described an inverse exponential relationship between group size and predation risk, we use an inverse exponential relationship between group size and predation risk of cows in assumption (iv).

We model the CF, which we denote by C in Sec. III B 3, as a convex combination of the cost from hunger (h), desire to lie down (f), and predation risk (r). We thus write

$$C = \lambda h + \mu f + (1 - \lambda - \mu)r, \quad (1)$$

where $\lambda, \mu \in [0, 1]$ are parameters. In Eqn. (1), “hunger” refers to the grazing demand of hogs in a group, and “lying desire” is their demand to lie down. We compute their hunger and lying desire at each time step using a previously-introduced evolution scheme (ES)⁴² for cows to change their state (where eating, standing, and lying down are the three possible states), and we quantify synchronization cost based on cows’ hunger and desire to lie down. We assess the cost from hunger (respectively, lying desire) as the mean over all groups of the standard deviation of hunger (respectively, lying desire) within each group, and we model the cost from risk as a function of the group size. During each time step, we minimize the CF over all groups that one can construct from a given herd, where we specify a maximum number of groups, and determine the lowest splitting cost. We determine the optimum group sizes using the minimum of the CF, as it rewards groups with homogeneous demands for hunger and lying desire, and it entails perfect synchronization of activity within groups by construction. Our modeling framework is very flexible, and we can consider more general situations by considering different CFs, measuring synchrony in different ways, and other generalizations.

III. TEMPORAL EVOLUTION AND MODELING GROUP SPLITTING

As in Ref. 42, when considering a herd, we simulate cows’ hunger (i.e., desire to eat) and lying desire (i.e., desire to lie down) and change of states between eating, lying down, and standing. We then present a CF and optimize it to determine the lowest-cost splitting of the herd.

A. Temporal evolution and change of states of cows

Cows interact with each other through the ES, which thereby helps provide some understanding of their cooperative activities. We augment the ES in Ref. 42 by formulating it as an iterative scheme that we combine with our CF. In this model, each individual cow is a piecewise-smooth dynamical system, and a cow switches between three: discrete states eating (ε), lying down (\varkappa), and standing (s). There are also continuous variables, $x \in [0, 1]$ and $y \in [0, 1]$, that, respectively, represent cows’ desire to lie down and desire to eat. The dynamics of a single cow are given by the following differential equations:

$$\begin{aligned} \text{Eating state } (\varepsilon): & \begin{cases} \dot{x} = -\xi'' x, \\ \dot{y} = \zeta' y, \end{cases} \\ \text{Lying-down state } (\varkappa): & \begin{cases} \dot{x} = \xi' x, \\ \dot{y} = -\zeta'' y, \end{cases} \\ \text{Standing state } (s): & \begin{cases} \dot{x} = \xi' x, \\ \dot{y} = \zeta' y, \end{cases} \end{aligned} \quad (2)$$

where

- ξ'_i is the rate of increase of hunger,
- ξ''_i is the decay rate of hunger,
- ζ'_i is the rate of increase of desire to lie down, and
- ζ''_i is the decay rate of desire to lie down

of the i th cow. The parameters $\xi'_i, \xi''_i, \zeta'_i,$ and ζ''_i are all positive.

The parameters $\xi', \xi'', \zeta',$ and ζ'' can be different for different cows. If two cows have similar parameter values, we expect them to exhibit similar dynamics. Based on the hypothesis that it is good for cows to eat when other cows are eating and to lie down when other cows are lying down, one can extend the “single-cow model” in Eqn. (2) into a coupled dynamical system by allowing the individual cows to interact, and we use a time-dependent adjacent matrix to encode which cows are interacting with each other (see Sec. III C). In Eqn. (3) below, we express how coupling influences the dynamics of cows.

We modify the coupled system in Ref. 42 to produce an iterative scheme. To simplify our exposition (though at the cost of some technical correctness in the context of animal behavior), we sometimes use the terms “lying desire” to represent “desire to lie down” and “hunger” to represent “desire to eat.” Because we study the dynamics of the cows at each instant when the state variable changes from one state to another, we only keep records of x and y for the cows at those instants. Thus, for $t \in \{1, \dots, T-1\}$ and $i \in \{1, \dots, n\}$, the discrete-time variables $x_i^{(t)} \in [0, 1]$ and $y_i^{(t)} \in [0, 1]$, respectively, represent the level of hunger and desire to lie down of the i th cow when the discrete-time state variable $\theta_i^{(t)}$ changes

at time t . The variable $\theta_i^{(t)}$ represents the new state of cow i at time t ; it can be eating (\mathcal{E}), lying down (\mathcal{R}), or standing (\mathcal{S}).

As one can see from the paragraph above, the i th cow is described by three variables: $\theta_i^{(t)}$, $x_i^{(t)}$, and $y_i^{(t)}$. For times $t \in \{1, \dots, T-1\}$ and cows $i \in \{1, \dots, n\}$, the time-dependent coupling of cows is given by the differential equations

$$\begin{aligned} \dot{x}_i^{(t+1)} &= \left[\alpha_i(\theta_i^{(t)}) + \frac{\sigma_x}{d_i^{(t)}} \sum_{j=1}^n a_{ij}^{(t)} \chi_{\mathcal{E}}(\theta_j^{(t)}) \right] x_i^{(t)}, \\ \dot{y}_i^{(t+1)} &= \left[\beta_i(\theta_i^{(t)}) + \frac{\sigma_y}{d_i^{(t)}} \sum_{j=1}^n a_{ij}^{(t)} \chi_{\mathcal{R}}(\theta_j^{(t)}) \right] y_i^{(t)}, \end{aligned} \quad (3)$$

where

$$\begin{aligned} \alpha_i(\theta_i^{(t)}) &:= -\xi_i'' \chi_{\mathcal{E}}(\theta_i^{(t)}) + \xi_i' \chi_{\mathcal{R}}(\theta_i^{(t)}) + \xi_i' \chi_{\mathcal{S}}(\theta_i^{(t)}), \\ \beta_i(\theta_i^{(t)}) &:= \zeta_i' \chi_{\mathcal{E}}(\theta_i^{(t)}) - \zeta_i'' \chi_{\mathcal{R}}(\theta_i^{(t)}) + \zeta_i' \chi_{\mathcal{S}}(\theta_i^{(t)}), \end{aligned} \quad (4)$$

with

$$\chi_{\psi}(\theta_i^{(t)}) = \begin{cases} 1, & \theta_i^{(t)} = \psi, \\ 0, & \text{otherwise.} \end{cases} \quad (5)$$

The time-dependent adjacency matrix $A^{(t)} = [a_{ij}^{(t)}]_{n \times n}$ represents a network of cows at time t . Its components are

$$a_{ij}^{(t)} = \begin{cases} 1, & \text{if the } i\text{th cow interacts with} \\ & \text{the } j\text{th cow at time } t, \\ 0, & \text{otherwise.} \end{cases} \quad (6)$$

Thus, $d_i^{(t)} = \sum_{j=1}^n a_{ij}^{(t)}$ is the degree (i.e., number of interacting cows) of cow i . We will define this interaction in terms of grouping in Sec. III C. The nonnegative parameters σ_x and σ_y , respectively, represent coupling strengths with respect to hunger and desire to lie down.

The switching condition of the state variable $\theta_i^{(t)}$ of the i th cow at time step t is

$$\theta_i^{(t+1)} \rightarrow \begin{cases} \mathcal{E}, & \text{if } \theta_i^{(t)} \in \{\mathcal{R}, \mathcal{S}\} \text{ and } x_i^{(t)} = 1, \\ \mathcal{R}, & \text{if } \theta_i^{(t)} \in \{\mathcal{E}, \mathcal{S}\} \text{ and } x_i^{(t)} < 1, y_i^{(t)} = 1, \\ \mathcal{S}, & \text{if } \theta_i^{(t)} \in \{\mathcal{E}, \mathcal{R}\} \text{ and } x_i^{(t)} < 1, y_i^{(t)} = \delta \\ & \text{(or } x_i^{(t)} = \delta, y_i^{(t)} < 1), \end{cases} \quad (7)$$

where we use the parameter $\delta \in (0, 1)$ to exclude the point $(x_i^{(t)}, y_i^{(t)}) = (0, 0)$ from the variable domain (because it creates degenerate solutions).

We study the dynamics of cows at discrete times, so we can constrain our study to a Poincaré section that we construct by considering switches between different states. We construct the Poincaré section using Ref. 43, and we can thereby study the dynamics given by Eqns. (3) and

(7). See the schematic in Fig. 1. The boundaries of this Poincaré section are defined as

$$\begin{aligned} \partial\mathcal{E} &= \{(x, y, \theta) | x = 1, \delta \leq y \leq 1, \theta = \mathcal{E}\}, \\ \partial\mathcal{R} &= \{(x, y, \theta) | \delta \leq x < 1, y = 1, \theta = \mathcal{R}\}, \\ \partial\mathcal{S}_x &= \{(x, y, \theta) | \delta < x < 1, y = \delta, \theta = \mathcal{S}\}, \\ \partial\mathcal{S}_y &= \{(x, y, \theta) | x = \delta, \delta \leq y < 1, \theta = \mathcal{S}\}. \end{aligned} \quad (8)$$

These four boundaries arise from the switching conditions in (7); the first pair of conditions yields the first two boundaries, and the second pair yields the last two boundaries. At time t , the variables $x_i^{(t)}$, $y_i^{(t)}$, and $\theta_i^{(t)}$ of the i th cow are represented by one of the boundaries and then the cow switches to another boundary in the subsequent time step according to the switching condition in Eqn. (7).

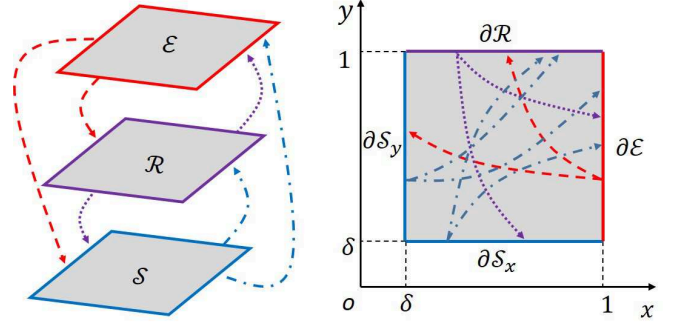


FIG. 1. Schematic of the switching dynamics of a cow. The left panel is a new version of the right panel of Fig. 1 in Ref. 42, and the right panel is an integrated version of the four panels from Fig. 2 of Ref. 42. The left panel shows three states ($\{\mathcal{E}, \mathcal{R}, \mathcal{S}\}$, where $\mathcal{S} = \mathcal{S}_x \cup \mathcal{S}_y$) and the potential switching between states. The edges of the square in the right panel represent boundaries of the domain of the continuous variables x and y [see Eqn. (8)]. We are interested only in the discrete dynamics of cows; they are given by $x_i^{(t)}$, $y_i^{(t)}$, and $\theta_i^{(t)}$ on the boundaries. The arrows represent all possible state switches of a cow. The same style and color of arrows between left and right panels refer to the same switches.

We solve the dynamical system in Eqn. (3) for n cows in T time steps together with the switching condition in Eqn. (7). The solution gives the discrete dynamics of the i th cow in terms of $x_i^{(t)}$, $y_i^{(t)}$, and $\theta_i^{(t)}$ at each time step t . We show the derivation of these solutions in Appendix A as an iterative scheme. As one can see in Fig. 1, at the t th time step, each cow is in one of three states (\mathcal{E} , \mathcal{R} , or \mathcal{S}) at the start of the time step, and it switches to one of the other two states, where it starts the $(t+1)$ th time step. The last two equations in Eqn. (8) collectively explain the standing state, so both the lower and the left boundaries of Fig. 1 represent the standing state. Thus, at the t th time of the iterative scheme, the starting point of each cow is one of four possibilities, each of which is represented by a boundary, and the end point is the new state that has two possibilities. We present the

corresponding iterative scheme of the solution in Table I, in which we use the following notation:

$$\begin{aligned}
 \eta'_i &:= \xi'_i + \frac{\sigma_x}{d_i^{(t)}} \sum_{j=1}^n a_{ij}^{(t)} \chi_{\mathcal{E}}^{(t)} \left(\theta_j^{(t)} \right), \\
 \eta''_i &:= -\xi''_i + \frac{\sigma_x}{d_i^{(t)}} \sum_{j=1}^n a_{ij}^{(t)} \chi_{\mathcal{E}}^{(t)} \left(\theta_j^{(t)} \right), \\
 \gamma'_i &:= \zeta'_i + \frac{\sigma_y}{d_i^{(t)}} \sum_{j=1}^n a_{ij}^{(t)} \chi_{\mathcal{R}}^{(t)} \left(\theta_j^{(t)} \right), \\
 \gamma''_i &:= -\zeta''_i + \frac{\sigma_y}{d_i^{(t)}} \sum_{j=1}^n a_{ij}^{(t)} \chi_{\mathcal{R}}^{(t)} \left(\theta_j^{(t)} \right),
 \end{aligned} \tag{9}$$

where $i \in \{1, \dots, n\}$ and $t \in \{1, \dots, T\}$.

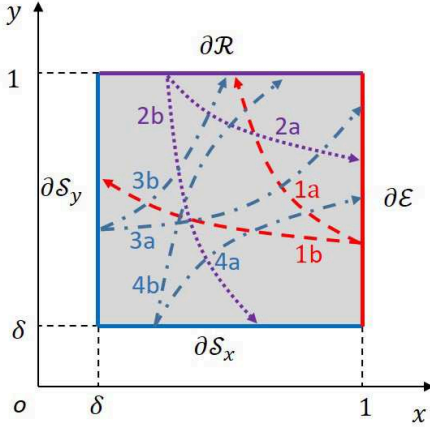


FIG. 2. All possible state switches of a cow in a single time step⁴². The states are $\{\mathcal{E}, \mathcal{R}, \mathcal{S}\}$ (eating, lying down, and standing), where $\mathcal{S} = \mathcal{S}_x \cup \mathcal{S}_y$. We show all possible state transitions in Table I. For example, “1a” refers to “case a” of “case 1” in the table. We use the same style and color of arrows as in Fig. 1.

B. Cost function (CF) determining the splitting of herds

In this section, we determine the lowest-cost grouping of cows by minimizing a CF. This gives the total number of groups and the number of cows in each group. We suppose that a herd of cows splits into a maximum of L distinct groups $N_1^{(t)}, \dots, N_L^{(t)}$, with $|N_l^{(t)}| = n_l^{(t)} > 0$ cows in the l th group (where $l \in \{1, \dots, L\}$), at each time step $t \in T$. If the herd splits into $L_1 < L$ groups at some time step t_1 , we set $|N_l^{(t_1)}| = 0$ for $l \in \{L_1 + 1, \dots, L\}$.

Our CF is the sum of two components: a synchronization component and a risk component. The synchronization component (SC) models the cost due to variation of the lying desire and hunger of cows, and the risk component (RC) models the cost from predation risk.

1. Synchronization component

Recall from Sec. III A that cow i 's hunger is $x_i^{(t)} \in [0, 1]$ and lying desire is $y_i^{(t)} \in [0, 1]$. We re-index the variables $x_i^{(t)}$ as $x_{k,l}^{(t)}$ and $y_i^{(t)}$ as $y_{k,l}^{(t)}$, respectively, to denote the hunger and lying desire of the k th cow in the l th group at the t th time step. Because hunger and lying desire are independent motivations in cows, we compute the two groupings independently, so that cows are optimally homogeneous with respect to hunger (case I) or optimally homogeneous with respect to lying desire (case II). Of these two groupings, we then select the one with the lower synchronization cost.

Case I: We sort cows according to increasing hunger, and we place the first $n_1^{(t)}$ cows into group $N_1^{(t)}$, the next $n_2^{(t)}$ cows into group $N_2^{(t)}$, and so on. In each group, the synchronization cost from hunger represents the heterogeneity of hunger within the group. As a simple way to quantify this cost, we use the mean of the standard deviations of cows' hunger within the groups and thus calculate

$$h_1^{(t)} = \frac{1}{L} \sum_{l=1}^L \sqrt{\frac{\sum_{k=1}^{n_l^{(t)}} \left(x_{k,l}^{(t)} - \sum_{k=1}^{n_l^{(t)}} x_{k,l}^{(t)} / n_l^{(t)} \right)^2}{n_l^{(t)}}} \tag{10}$$

to assess the SC due to hunger. Similarly, we quantify the heterogeneity of groups with respect to lying desire as the mean of the standard deviations of cows' lying desire in groups by calculating

$$f_1^{(t)} = \frac{1}{L} \sum_{l=1}^L \sqrt{\frac{\sum_{k=1}^{n_l^{(t)}} \left(y_{k,l}^{(t)} - \sum_{k=1}^{n_l^{(t)}} y_{k,l}^{(t)} / n_l^{(t)} \right)^2}{n_l^{(t)}}}. \tag{11}$$

Case II: Similar to case I, we sort cows according to increasing lying desire and place them into groups $N_1^{(t)}, \dots, N_L^{(t)}$. We again compute hunger and lying desire from the means of the standard deviations within the groups, and we denote them by $h_2^{(t)}$ and $f_2^{(t)}$, respectively.

From the cow groups that we found in cases I and II, we choose the grouping that yields the minimum SC. The hunger $h^{(t)}$ and the lying desire $f^{(t)}$ of the cow herd at time t are thus

$$h^{(t)} = \min \left\{ h_1^{(t)}, h_2^{(t)} \right\} \quad \text{and} \quad f^{(t)} = \min \left\{ f_1^{(t)}, f_2^{(t)} \right\}, \tag{12}$$

respectively.

2. Risk component

Unlike hunger and lying desire, a herd's predation risk is independent of individuals' states and depends only on the group size. Because the group size and the risk of

TABLE I. Iterative scheme for temporal evolution of cow dynamics that we obtain from solving the dynamical system in Eqn. (3) with the switching condition in Eqn. (7). We show the derivation of these solutions in Appendix A. For the i th cow in the t th time step, one of the cases 1, 2, 3, and 4 in this table represents the boundary of the Poincaré section (see Eqn. (8)) associated with the cow at the beginning of that time step. For each of the four cases, cases “a” and “b” represent the new state of the cow at the end of time step t . We illustrate all eight possible combinations in the Poincaré section in Fig. 2.

case 1: [Eqns. (A1) and (A4)]	If $x_i^{(t)} = 1$, $\delta \leq y_i^{(t)} \leq 1$, and $\theta_i^{(t)} = \varepsilon$		
	case a: if $y_i^{(t)} \geq \delta \frac{\gamma_i'}{\gamma_i''}$,	then	$x_i^{(t+1)} = \left[y_i^{(t)} \right]^{\frac{\gamma_i''}{\gamma_i'}}$, $y_i^{(t+1)} = 1$, and $\theta_i^{(t+1)} = \varepsilon$
	case b: if $y_i^{(t)} < \delta \frac{\gamma_i'}{\gamma_i''}$,	then	$x_i^{(t+1)} = \delta$, $y_i^{(t+1)} = \delta^{-\frac{\gamma_i'}{\gamma_i''}} y_i^{(t)}$, and $\theta_i^{(t+1)} = s$
case 2: [Eqns. (A2) and (A5)]	If $\delta \leq x_i^{(t)} < 1$, $y_i^{(t)} = 1$, and $\theta_i^{(t)} = \varepsilon$		
	case a: if $x_i^{(t)} \geq \delta \frac{\gamma_i'}{\gamma_i''}$,	then	$x_i^{(t+1)} = 1$, $y_i^{(t+1)} = \left[x_i^{(t)} \right]^{\frac{\gamma_i''}{\gamma_i'}}$, and $\theta_i^{(t+1)} = \varepsilon$
	case b: if $x_i^{(t)} < \delta \frac{\gamma_i'}{\gamma_i''}$,	then	$x_i^{(t+1)} = \delta^{-\frac{\gamma_i'}{\gamma_i''}} x_i^{(t)}$, $y_i^{(t+1)} = \delta$, and $\theta_i^{(t+1)} = s$
case 3: [Eqns. (A3) and (A6)]	If $x_i^{(t)} = \delta$, $\delta \leq y_i^{(t)} < 1$, and $\theta_i^{(t)} = s$		
	case a: if $y_i^{(t)} \leq \delta \frac{\gamma_i'}{\gamma_i''}$,	then	$x_i^{(t+1)} = 1$, $y_i^{(t+1)} = \delta^{-\frac{\gamma_i'}{\gamma_i''}} y_i^{(t)}$, and $\theta_i^{(t+1)} = \varepsilon$
	case b: if $y_i^{(t)} > \delta \frac{\gamma_i'}{\gamma_i''}$,	then	$x_i^{(t+1)} = \left[y_i^{(t)} \right]^{-\frac{\gamma_i'}{\gamma_i''}} \delta$, $y_i^{(t+1)} = 1$, and $\theta_i^{(t+1)} = \varepsilon$
case 4: [Eqns. (A3) and (A7)]	If $\delta < x_i^{(t)} < 1$, $y_i^{(t)} = \delta$, and $\theta_i^{(t)} = s$		
	case a: if $x_i^{(t)} \geq \delta \frac{\gamma_i'}{\gamma_i''}$,	then	$x_i^{(t+1)} = 1$, $y_i^{(t+1)} = \left[x_i^{(t)} \right]^{-\frac{\gamma_i'}{\gamma_i''}} \delta$, and $\theta_i^{(t+1)} = \varepsilon$
	case b: if $x_i^{(t)} < \delta \frac{\gamma_i'}{\gamma_i''}$,	then	$x_i^{(t+1)} = \delta^{-\frac{\gamma_i'}{\gamma_i''}} x_i^{(t)}$, $y_i^{(t+1)} = 1$, and $\theta_i^{(t+1)} = \varepsilon$

being attacked by predators are inversely related,^{1,2,34–38} we model the predation risk $r_l \in (0, 1]$ of the l th group (which has size $n_l > 0$) as an inverse exponential function of group size:^{34,39–41}

$$r_l = e^{-(1-n_l)/c}, \quad (13)$$

where c is a constant. We assume that the predation risk converges to a small value when a group has sufficiently many cows, and we use this condition to compute the constant c . We denote this sufficient group size (the so-called “safe size”) by n_s , and we denote the small risk that the risk function converges (the so-called “safety level”) at this size by τ . The constant c is thus $-(1 - n_s)/\ln \tau$, so the RC of the group is

$$r_l = \tau \left(\frac{1-n_l}{1-n_s} \right). \quad (14)$$

In Fig. 3, we show the relationship given by the Eqn. (14) for a group with safety level τ and safe size n_s .

We compute the predation risk of each group, and we treat its mean

$$r = \frac{1}{L} \sum_{l=1}^L \tau \left(\frac{1-n_l}{1-n_s} \right), \quad (15)$$

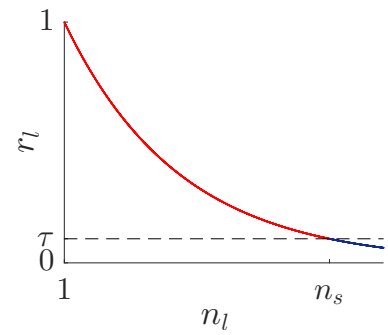


FIG. 3. We model predation risk as an inverse exponential function of group size. The red segment of the curve signifies a regime with an unsafe level of risk, and the blue segment signifies a regime with a safe level of risk.

as the risk of the herd.

In real situations, the safe size and safety level depend on the environment in which a herd lives. If the environment is either dense with predators or vulnerable to predation, the safe size should be comparatively large to achieve a significant safety level. As an example, we

use Eqn. (15) and compute the risk of splitting a herd of $n = 20$ cows into two groups with a safety level of $\tau = 1/30$ and safe sizes of $n_s = 10$, $n_s = 20$, and $n_s = 30$ (see Fig. 4). We thereby illustrate that large safety sizes model riskier situations for a herd than small safety sizes, independently of how the herd splits. For all safety sizes, we achieve the lowest cost when the herd remains intact (i.e., no splitting), because larger group sizes entail safer herds. We achieve the second-lowest cost when the herd splits into equal-sized groups.

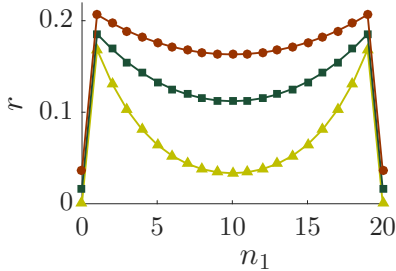


FIG. 4. Risk of splitting a herd of $n = 20$ cows into two groups of sizes n_1 and $n_2 = 20 - n_1$, where the safety level is $\tau = 1/30$ and the safe size is $n_s = 10$ (yellow triangles), $n_s = 20$ (green squares), and $n_s = 30$ (brown disks).

3. Cost function

We formulate the CF as a convex combination of the costs from hunger, lying desire, and risk of predation:

$$C^{(t)}(n_1^{(t)}, \dots, n_L^{(t)}) = \lambda h^{(t)} + \mu f^{(t)} + (1 - \lambda - \mu)r, \quad (16)$$

where $\lambda, \mu \in [0, 1]$. For a given herd, which we denote by the set N , and a maximum number L of groups into which it can split, we minimize (16) over all plausible groups that can be created, and we thereby determine the lowest-cost splitting.

C. Cost function and temporal evolution

We examine the CF simultaneously with the temporal ES for times $t \in \{1, \dots, T\}$. At each time step, we update the adjacency matrix $A^{(t)} = [a_{i,j}^{(t)}]_{n \times n}$ in the scheme so that it agrees with the best grouping provided by the optimization of the CF in the previous time step. That is,

$$a_{i,j}^{(t+1)} = \begin{cases} 1, & \text{if } i, j \in N_l^{(t)}, \\ 0, & \text{otherwise,} \end{cases} \quad l \in \{1, \dots, L\}. \quad (17)$$

At each time step, optimizing the CF outputs the lowest-cost grouping until it reaches a stopping criterion, which

we take to be the maximum time T . In Fig. 5, we show a flow chart of this process.

IV. EXAMINATION OF DYNAMICS

We explore the dynamics of cows with respect to coupling strength by examining hunger and lying desire on the boundary of a Poincaré section. We then study the cost function for different values of the parameters σ_x , σ_y , τ , and n_s .

We consider the splitting of a herd of $n = 15$ cows into maximum of three groups. We simulate hunger and lying desire using the ES (see Sec. III A) followed by computing the CF (16) and optimizing it to determine the lowest-cost grouping at each $t \in T$. As we discuss shortly, we draw some of the initial conditions and parameter values from probability distributions.

In the ES, we set the initial states of cows to be $\theta_i^{(0)} \in \mathbb{U}\{\varepsilon, \mathcal{R}, \mathcal{S}\}$ for $i \in \{1, \dots, n\}$, and we recall that \mathbb{U} denotes a uniform probability distribution over the set in its argument. We add noise sampled from a uniform distribution into the initial conditions and parameters, as it is the simplest type of noise to consider. We set the initial conditions $x_i^{(0)}$ and $y_i^{(0)}$ as follows:

$$\begin{cases} x_i^{(0)} = 1 \text{ and } y_i^{(0)} \in \mathbb{U}[\delta, 1], & \text{if } \theta_i^{(0)} = \varepsilon, \\ x_i^{(0)} \in \mathbb{U}[\delta, 1) \text{ and } y_i^{(0)} = 1, & \text{if } \theta_i^{(0)} = \mathcal{R}, \\ \begin{cases} x_i^{(0)} = \delta \text{ and } y_i^{(0)} \in \mathbb{U}[\delta, 1), \\ \text{or} \\ x_i^{(0)} \in \mathbb{U}(\delta, 1) \text{ and } y_i^{(0)} = \delta, \end{cases} & \text{if } \theta_i^{(0)} = \mathcal{S}. \end{cases} \quad (18)$$

For $\theta_i^{(0)} = \mathcal{S}$, each of the two subcases in Eqn. (18) has a 50% chance of being the initial condition. We also make the following parameter choices for the ES: $\xi_i', \zeta_i' \in \mathbb{U}[.0495, .0505]$, $\xi_i'' \in \mathbb{U}[.0995, .1005]$, $\zeta_i'' \in \mathbb{U}[.1245, .1255]$, and $\delta = .25$.

To examine the dynamics of the interacting cows, we first examine $\sigma_x = 0$ and $\sigma_y = 0$ (i.e., uncoupled cows) and run the ES for $T = 400$ and simulate hunger $x_i^{(t)}$ and lying desire $y_i^{(t)}$ for $i \in \{1, \dots, 15\}$ and $t \in \{1, \dots, 400\}$. We then consider $\sigma_x = 0.05$ and $\sigma_y = 0.05$ (i.e., weakly-coupled cows) and simulate $x_i^{(t)}$ and $y_i^{(t)}$ for $i \in \{1, \dots, 15\}$ and $t \in \{1, \dots, 400\}$ with the same initial conditions generated by Eqn. (18) and parameter choices that we discussed above. For each of the two examples above, we simulate one realization of the dynamics. In Fig. 6, we show the hunger and lying desire for cow $i = 1$. The uncoupled case is in panel (a), and the weakly-coupled case is in panel (b). By construction, we also observe similar dynamics for all of the other cows when they do not interact with each other, but this is not the case when they interact weakly with each other.

We now examine how the cost changes with respect to four parameters: hunger coupling strength σ_x , lying-desire coupling strength σ_y , safe size n_s , and safety level

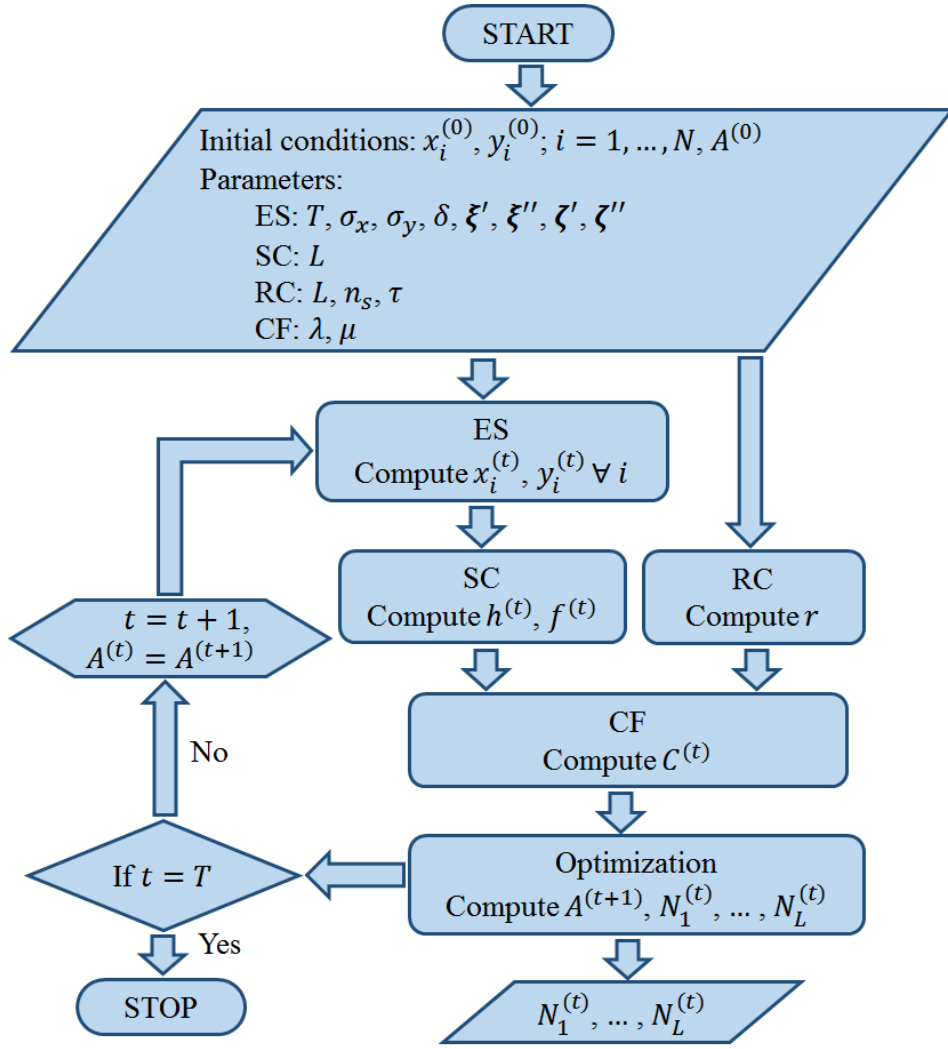


FIG. 5. Flow chart for our model. The inputs are (1) initial conditions for the variables for hunger and lying desire and (2) values for the parameters associated with ES, SC, RC, and CF. We explain these parameters in Secs. III A, III B 1, III B 2, and III B 3, respectively. At each time step, we adjust the adjacency matrix, which describes which cows interact with each other, using the new grouping information that we obtain by optimizing the CF. At each time step, our model outputs the groups of animals that correspond to the lowest-cost splitting, and it terminates upon reaching the stopping criterion (i.e., after a designated number of time steps).

τ . We do five realizations of the simulations, so we generate five sets of initial values using Eqn. (18) and five parameter sets $\xi'_i, \zeta'_i \in \mathbb{U}[.0495, .0505]$, $\xi''_i \in \mathbb{U}[.0995, .1005]$, $\zeta''_i \in \mathbb{U}[.1245, .1255]$. We set $\delta = .25$ in ES and run the simulation over each set of initial conditions and parameters for $n = 15$ cows through $T = 30$ time steps for coupling strengths $\sigma_x = \sigma_y = k/150$, where $k \in \{1, \dots, 30\}$. In Fig. 7(a), we see that the cost function decreases with σ_x (and hence with σ_y) until appearing to saturate once the coupling reaches a value of about 0.075. We then set the parameters in the CF to be $\lambda = .33$, and $\mu = .33$, and we simulate the system and compute the cost by setting $n_s = k_1$ (with $k_1 \in \{2, \dots, 20\}$) and $\tau = 0.05k_2$ (with $k_2 \in \{0, \dots, 20\}$). In Fig. 7(b), we show the cost as a function of n_s and τ . We observe that the cost is low

for small values of n_s and τ and that it increases with increasing parameter values until it appears to saturate.

V. BIOLOGICALLY-MOTIVATED EXAMPLES

We examine the CF (16) using two biological examples: a herd that splits into three groups, and a herd with half adults and half calves that splits into two groups.

A. Example 1

This example illustrates a scenario of a herd splitting into up to three groups. It also helps convey the effect of

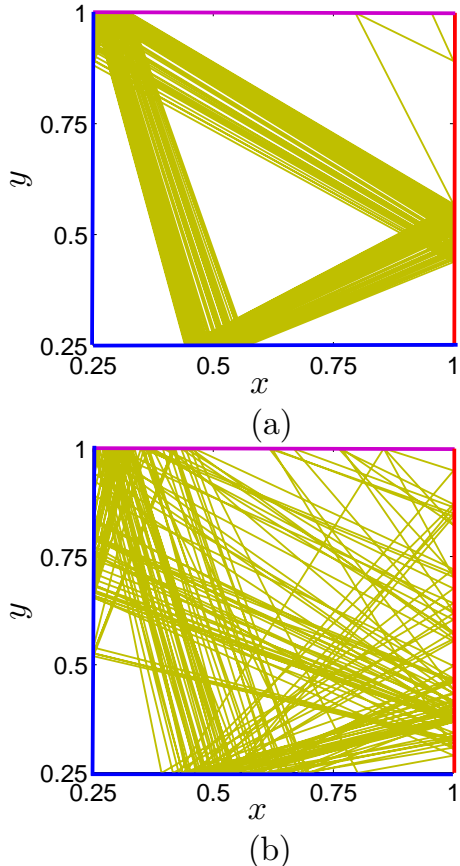


FIG. 6. Orbits of hunger and lying desire of the first cow for (a) $\sigma_x = \sigma_y = 0$ and (b) $\sigma_x = \sigma_y = 0.05$ in Eqn. (3). The red, purple, and blue boundaries, respectively, represent the eating, lying, and standing states. The colors of the boundaries are the same as those in Figs. 1 and 2.

choosing parameter values in Eqn. (16) and the relationship between groupings and their associated costs.

We consider a herd of $n = 12$ cows that we allow to split into a maximum of $L = 3$ groups during $T = 30$ time steps. We first simulate hunger and lying desire, then compute the cost function, and finally optimize the cost function to determine the lowest-cost grouping at each time. We consider a single realization of the model (i.e., one example herd) and use it to illustrate the general notion of trade-offs in the cost function.

In the ES, we set the initial states of cows to be $\theta_i^{(0)} \in \mathcal{U}\{\mathcal{E}, \mathcal{R}, \mathcal{S}\}$ for $i \in \{1, \dots, n\}$, and we recall that \mathcal{U} denotes a uniform probability distribution over the set in its argument. We set the initial conditions $x_i^{(0)}$ and $y_i^{(0)}$ according to Eqn. (18). We also make the following parameter choices for the ES: $\xi'_i, \zeta'_i \in \mathcal{U} [.0495, .0505]$, $\xi''_i \in \mathcal{U} [.0995, .1005]$, $\zeta''_i \in \mathcal{U} [.1245, .1255]$, $\delta = .25$, $\sigma_x = .05$, and $\sigma_y = .05$. We set the parameters in the CF and RC to be $n_s = 4$, $\tau = .2$, $\lambda = .33$, and $\mu = .33$.

A herd of 12 cows can be split into a maximum of 3

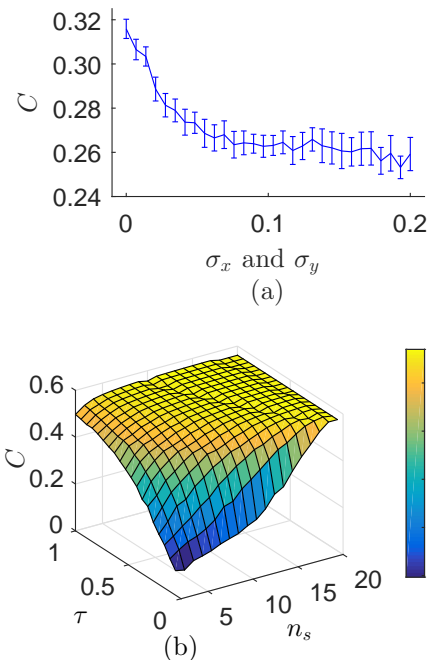


FIG. 7. Influence of parameters values on the cost function C . (a) The cost with equal coupling strengths σ_x and σ_y , which we compute by averaging over five realizations of simulations with the same initial conditions. The error bars indicate the standard deviations across the five realizations. (b) The cost of the herd versus the safe size n_s and safety level τ .

TABLE II. Possible group sizes for a herd of 12 cows that splits into a maximum of 3 groups.

Index	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
$n_1^{(t)}$	12	11	10	9	8	7	6	10	9	8	7	6	8	7	6	5	6	5	4
$n_2^{(t)}$	0	1	2	3	4	5	6	1	2	3	4	5	2	3	4	5	3	4	4
$n_3^{(t)}$	0	0	0	0	0	0	0	1	1	1	1	1	2	2	2	2	3	3	4

groups in 19 different combinations of group sizes (see Table II). We assign an index for each combination to simplify the labeling in our subsequent figures. We also run the ES together with the CF for another two instances of the CF parameters: $\lambda = .5$, $\mu = .25$ and $\lambda = .25$, $\mu = .5$. We show the result at time $t = 20$ for all three examples in Fig. 8. In the figure, the highest risk occurs for $n_{1,2,3}^{(20)} = 10, 1, 1$, in which two individual cows have separated from a herd. The second-highest risk occurs when $n_{1,2,3}^{(20)} = 0, 1, 11$, in which one cow has separated from a herd. In contrast, the lowest risk occurs when the entire herd stays together (index 1) or when it splits into equal groups (index 7), where we note that the group size of 6 is larger than the safety size $n_s = 4$. One can consider equally-weighted cost components in the convex combination that constitutes the CF [see Fig. 8(a)] or change

the importance of components by increasing the weight of hunger [see Fig. 8(b)], lying desire [see Fig. 8(c)], or risk.

Let's now examine the temporal grouping in the scenario with parameter values $\lambda = .33$ and $\mu = .33$. In Fig. 9(a), we see that cows freely switch their groups to achieve the optimum value of the CF (16). The cow that we represent with the red crosses remains in the same group during the entire simulation, whereas the cow represented by the green disk changes groups frequently. In Fig. 9(b), we show the total number of groups in the herd and see that the herd consists of a single group at times $t = 3$, $t = 12$, $t = 16$, and $t = 29$ and consists of three groups at time $t = 4$, $t = 6$, $t = 8$, $t = 25$, and $t = 27$. In Fig.9(c), we show the total cost and thereby reveal that it can be more costly for the herd to stay together as a single group (at times $t = 3$, $t = 12$, $t = 16$, and $t = 29$). We also note the low costs for $t = 15$, $t = 28$, and $t = 30$, when the herd consists of two or three groups. These specific trade-offs in the cost function arise specifically for the initial condition that we used in our example, and we expect to see qualitatively different trade-offs for different initial conditions and parameter values. (Note additionally that the “high” and “low” costs are not that different from each other.) However, the notion of such trade-offs is a rather general one.

B. Example 2

We now study the inter-sexual grouping dynamics of a herd that consists of two distinct categories of adult cows: males and females. This type of grouping is known to occur in some animal groups (e.g., red deer¹²), so we study the same phenomenon in our model of cow herds. Adult male cows require more energy and rest than female cows, as the former tend to have larger body weights.^{44,45} We therefore assume that the males' rates of change of hunger and lying desire are larger than those of females. Mathematically, we implement this assumption by using larger values of the parameters $\xi'_i, \xi''_i, \zeta'_i$, and ζ''_i of cows in the male group than for those in the female group.

We consider a herd of 10 cows that consists of two groups. The first group has five cows (where $i \in \{1, \dots, 5\}$ indexes the cow) with large body weights, and the second group has the remaining five cows ($i \in \{6, \dots, 10\}$), which have small body weights. As in Sec. V A, we simulate the hunger and lying desire of cows by the ES (see Sec. III A) and find the lowest-cost grouping by optimizing the CF (16). We set the initial states of cows in the first and second groups as eating and lying down, respectively. Within a group, the variables have very similar initial values. They are the same, except that we perturb them additively with a small amount of

uniform noise:

$$\begin{cases} \theta_i^{(0)} = \varepsilon \text{ and } (x_i^{(0)}, y_i^{(0)}) = [1, \delta + \phi_i], & i \in \{1, \dots, 5\}, \\ \theta_i^{(0)} = \varepsilon \text{ and } (x_i^{(0)}, y_i^{(0)}) = [\delta + \phi'_i, 1], & i \in \{6, \dots, 10\}, \end{cases} \quad (19)$$

where $\phi_i, \phi'_i \in 10^{-3}\mathbb{U}[0, 1]$ and $\delta = .25$. We use additive noise sampled from a uniform distribution in the above initial conditions and parameters, as it is the simplest type of noise to consider. We consider $\sigma_x = .2$ and $\sigma_y = .2$ in the ES, and we determine the other parameters so that the first group consists of cows with large body mass and the second group consists of cows with small body mass:

$$\begin{cases} \left\{ \begin{array}{l} \xi'_i, \zeta'_i \in \mathbb{U} [.2495, .2505], \\ \xi''_i \in \mathbb{U} [.2995, .3005], \\ \zeta''_i \in \mathbb{U} [.3995, .4005], \end{array} \right. & i \in \{1, \dots, 5\}, \\ \left\{ \begin{array}{l} \xi'_i, \zeta'_i \in \mathbb{U} [.0495, .0505], \\ \xi''_i \in \mathbb{U} [.0995, .1005], \\ \zeta''_i \in \mathbb{U} [.1225, .1255], \end{array} \right. & i \in \{6, \dots, 10\}. \end{cases} \quad (20)$$

We set the parameters in the CF and RC to be $n_s = 4$, $\tau = .2$, $\lambda = .33$, and $\mu = .33$. We run the ES for $T = 30$ time steps, and we consider the value of the CF at each step. As in our first example (see Sec. V A), we use only one realization, and we note that the noise in Eqn. (19) has a small magnitude. During time steps 0–11, 15, and 20–28, we see in Fig. 10(a) that all of the cows are in the groups with the other cows of their own gender (i.e., with others of similar sizes, hunger, and desire to lie down). However, during time steps 12–14 and 16–19, some cows are not in their “proper” group, and the cost becomes high [see Fig. 10(c)], although the CF minimizes the cost to achieve the lowest-cost grouping. We show the number of mismatched cows in the groups in Fig. 10(b). Observe that the cost is large when cows are in mismatched groups, but it is low when cows are in their proper (i.e., homogeneous-gender) groups.

VI. CONCLUSIONS AND DISCUSSION

We developed a framework for modeling the lowest-cost splitting of a herd of cows by optimizing a cost function (CF) that quantifies their hunger, desire to lie down, and predation risk. Lying in groups offers protection from predators,^{19,46–48} but synchronization can also be costly to individuals, as some portion of a herd has to change behavior to eat or lie down at a communal time rather than at an optimally beneficial time.^{11–13} In this paper, we examine situations in which cow herds split into groups such that cows' hunger and lying desire are relatively homogeneous within a group, while ensuring that further splitting does not result in overly small groups, which would be more vulnerable to predation.

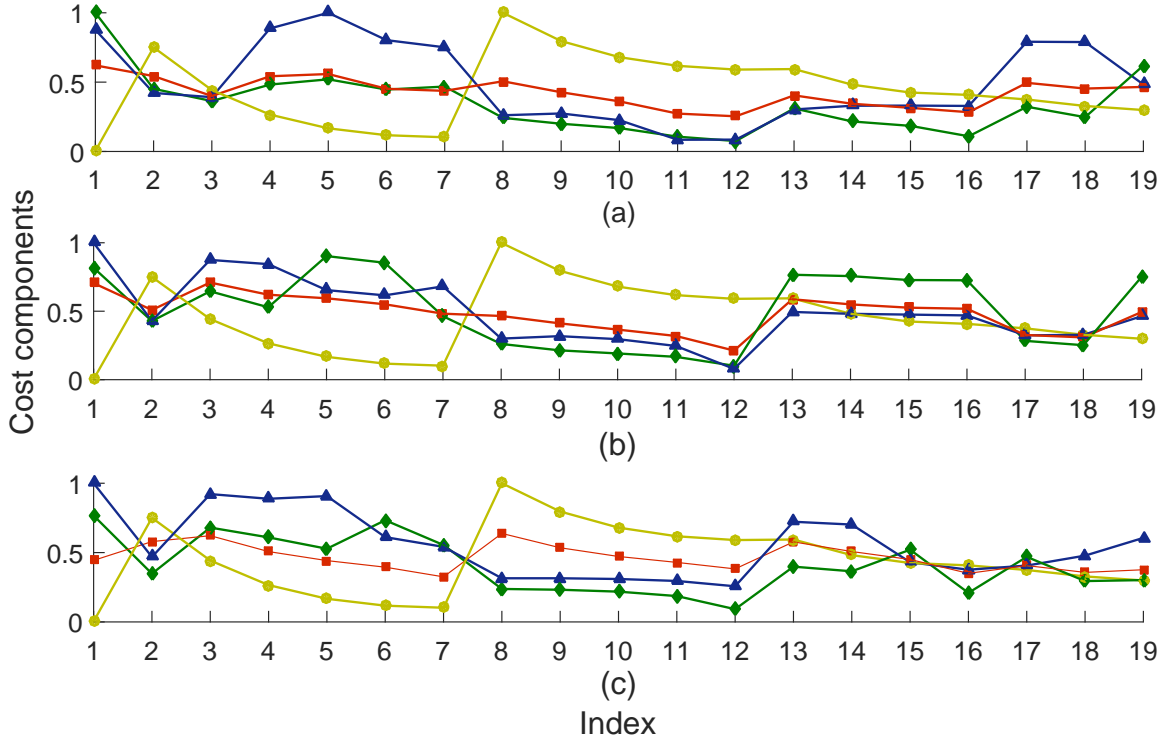


FIG. 8. Total cost (red squares) at time $t = 20$ and its components — hunger (blue triangles), lying desire (green diamonds), and risk (yellow disks) — versus the index that represents the different combinations of group sizes (see Table II). Total cost and its components for different parameters in the convex combination that constitutes the CF (16): (a) $\lambda = .33$ and $\mu = .33$; (b) $\lambda = .5$ and $\mu = .25$; and (c) $\lambda = .25$ and $\mu = .5$.

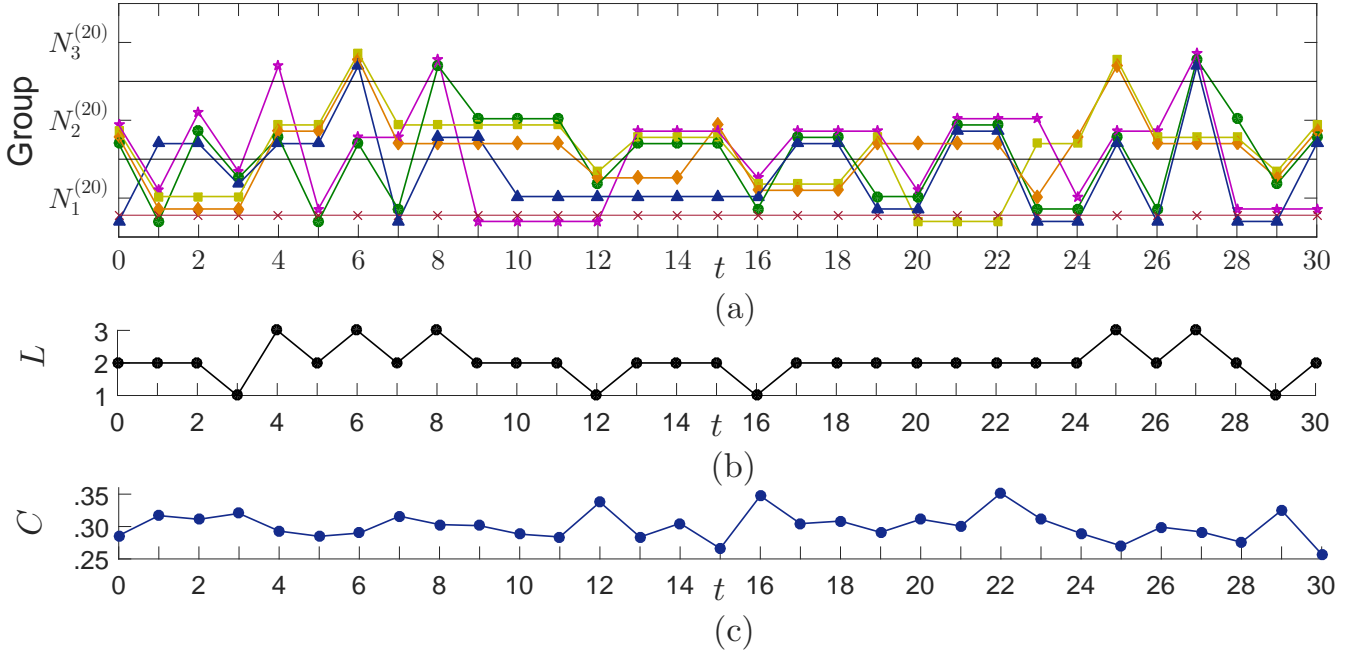


FIG. 9. Group changes and related costs as a function of time. (a) Group assignments $N_{1,2,3}^{(20)}$ of six cows (red cross, orange diamond, yellow square, blue triangle, green disk, and purple asterisk) in three groups. The (b) number of groups in which the herd splits is determined by (c) the total cost.

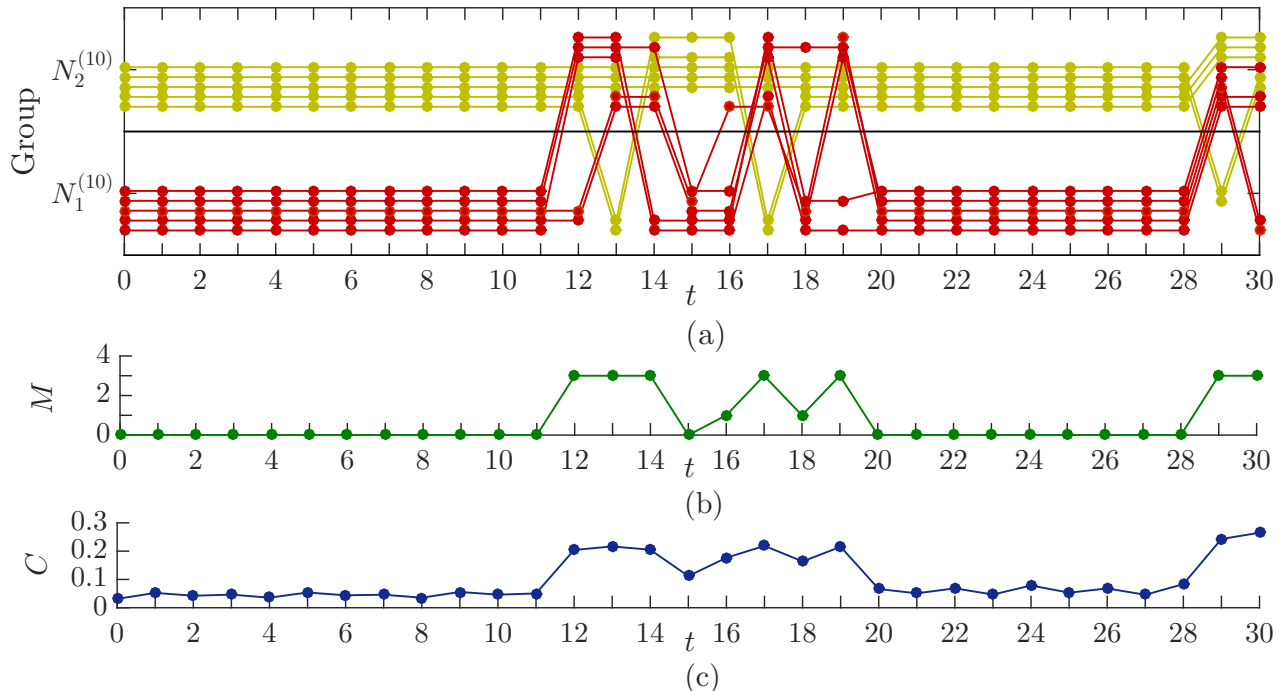


FIG. 10. Dynamics of a herd of 10 cows split in two groups and the cost as a function of time. (a) We color the first (“male”) 5-cow group in red, and we color the second (“female”) 5-cow group in yellow. (b) Number of cows that are not in their proper group. (c) Cost of the groups.

We employed the evolution scheme (ES) from Sun et al.⁴² and input cows’ time-dependent interactions in terms of an adjacency matrix $A^{(t)}$, which represents the lowest-cost grouping obtained by optimizing the CF. The adjacency matrix provides an interface between the CF and ES, and our framework can be used with arbitrarily intricate CFs, ESs, and interaction patterns. Because hunger and lying desire are two independent motivations of a cow, we optimize the CF separately for each one in each time step to obtain two different groupings, and we then use the grouping that has the lower total cost of the two possibilities. By imposing a maximum number of groups into which a herd can split, we reduce the computational complexity of our approach. For simplicity, we assess the cost contributed from hunger and lying desire using the standard deviation of the associated individual preferences in each group (although one can replace the computation of standard deviation by any measure of dispersion).

In Sec. IV, we examined the dynamics of interacting cows and the cost for different values of the model parameters. We simulated hunger and lying desire of cows for two sets of coupling strengths, $\sigma_x = \sigma_y = 0$ (i.e., uncoupled cows) and $\sigma_x = \sigma_y = 0.05$ (i.e., weakly-coupled cows), and observed different dynamics (see Fig. 6) in the two situations. Setting coupling strengths to 0 implies that each cow behaves independently [see Eqn. (3)]. Consequently, each cow oscillates as an independent dynamical system, which instead interact with each other

when the coupling strengths are nonzero. We then studied the influence of parameters (coupling strengths σ_x and σ_y , safe size n_s , and safety level τ) on the cost function. Increasing coupling strengths decreased the cost [see Fig. 7(a)], and it helps assure a grouping in which similar cows are assigned to the same group. In Fig. 7(b), we illustrated that setting the safe size and safety level to low values entails a low cost. Such parameter values allow cows to gather into small groups of similar cows without incurring significant risk for the herd.

We used one example to examine group fission and the dynamics of cows switching between groups. In that example, we set the initial states of cows arbitrarily, but one can also choose initial states to examine specific scenarios. To consider a relatively homogeneous herd, we used similar parameter values for different individuals, and we observed the dynamics that result from small differences in these parameter values. We considered a single realization of the model, as the other initial conditions and parameter values would yield different specific trade-offs but illustrate the same essential idea. Our primary hypothesis, that synchronization can be costly, is illustrated by Figs. 9(b) and 9(c). This occurs at times when the risk component of the CF gives a lower contribution to the total cost than does the synchronization component, which has contributions from hunger and the desire to lie down. However, this situation can be overcome by giving a stronger weight to the risk component in the CF (16). The herd then stays together to ensure safety rather than

splitting so that cows can eat or lie down at their optimal times.

One can customize the ES by changing the parameters for the rates of increase in hunger or desire to lie down. This versatility allowed us to model a scenario of inter-gender splitting in a herd. Adult male cows generally possess larger body masses and require more energy and lying time than adult female cows. We implemented this asymmetry among individuals by imposing larger values of the salient parameters for males than for females. At times, the heterogeneity in motivations for eating and lying down caused the optimal groups to be ones other than the single-gender groups [see Fig. 10(c)], but usually optimization of the CF yielded single-gender groups. Similar single-gender grouping occurs commonly in ungulates, such as deer and sheep, and are especially pronounced in species with the greatest body-size differences between males and females.^{11,12,14,15} In the second example, we added uniform noise to the initial conditions and parameters, as it is the simplest type of noise to consider. If we did not add any noise, each cow in group 1 has identical dynamics (because they are described by the same equations with the same parameter values), and each cow in group 2 also has identical dynamics.

One can adjust the CF so that it can be used for herding situations in different environments. A safe environment allows small groups in a herd, in contrast to an unsafe environment, which requires large groups to defend themselves against attacks. Our CF imitates a safe environment if the safe size n_s is large and the safety level is small. One can control the influence of the cost components (hunger, lying desire, and predation risk) on the CF by tuning parameters, and our approach thereby makes it possible to explore different grouping scenarios, such as analyzing the influence of one or more cost components over the others for group splitting. Our overall approach is also very flexible, and one can generalize our CF, the ES, and the interactions among animals (through a time-dependent adjacency matrix) to examine a wide variety of scenarios.

In our paper, we determined group size and splitting by optimizing a CF at each time step. However, because optimally-sized groups are not necessarily stable, it may be necessary in future work to introduce a learning process in which one keeps track of optimal group sizes during past time steps. In the present paper, we imposed a maximum number L of groups into which a herd can split. In our examples, the value of L was either obvious, as in the second example, where we used $L = 2$ (males and females), or hypothetical, as in the first example, where we used $L = 3$. However, instead of imposing a maximum number of groups in advance, it is also desirable to examine situations in which the number of groups is an unconstrained output to better reveal an optimal number of groups in herd splitting.

In summary, we developed a versatile model of lowest-cost splitting of a herd of animals that can admit numerous generalizations in a straightforward way. We il-

lustrated the utility of our model by exploring two plausible scenarios, and we believe that our approach can shed considerable insight on grouping behavior in animals in a wide variety of situations.

ACKNOWLEDGEMENTS

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Appendix A: Derivation of the discrete dynamics on the Poincaré section

We solve the differential equations given in Eqn. (8) using the boundary conditions in Eqn. (7). For convenience, we substitute Eqn. (9) into these differential equations and expand as follows:

when $\theta_i^{(t)} = \varepsilon$,

$$\begin{aligned} \dot{x}_i^{(t+1)} &= \eta_i'' x_i^{(t)}, \\ \dot{y}_i^{(t+1)} &= \gamma_i' y_i^{(t)}; \end{aligned} \quad (\text{A1})$$

when $\theta_i^{(t)} = \mathcal{R}$,

$$\begin{aligned} \dot{x}_i^{(t+1)} &= \eta_i' x_i^{(t)}, \\ \dot{y}_i^{(t+1)} &= \gamma_i'' y_i^{(t)}; \end{aligned} \quad (\text{A2})$$

when $\theta_i^{(t)} = \varepsilon$,

$$\begin{aligned} \dot{x}_i^{(t+1)} &= \eta_i' x_i^{(t)}, \\ \dot{y}_i^{(t+1)} &= \gamma_i' y_i^{(t)}. \end{aligned} \quad (\text{A3})$$

We then solve the differential equations in Eqns. (A1)–(A3) on the boundaries $\partial\mathcal{E}$, $\partial\mathcal{R}$, $\partial\mathcal{S}_x$, and $\partial\mathcal{S}_y$ given by Eqn. (8) as follows:

when $\theta_i^{(t)} = \varepsilon$ (i.e., on $\partial\mathcal{E}$ of the Poincaré section),

$$\left\{ \begin{array}{l} t\mathcal{E}\mathcal{R} = \frac{1}{\gamma_i'} \log\left(\frac{1}{y_i^{(t)}}\right), \text{ so} \\ \quad \left(x_i^{(t+1)}, y_i^{(t+1)}, \theta_i^{(t+1)}\right) = \left(\left(y_i^{(t)}\right)^{\frac{\eta_i''}{\gamma_i'}}, 1, \mathcal{R}\right); \\ t\mathcal{E}\mathcal{S}_y = \frac{1}{\eta_i'} \log\left(\frac{1}{\delta}\right), \text{ so,} \\ \quad \left(x_i^{(t+1)}, y_i^{(t+1)}, \theta_i^{(t+1)}\right) = \left(\delta, \delta^{-\frac{\gamma_i'}{\eta_i'}} y_i^{(t)}, \mathcal{S}_y\right); \end{array} \right. \quad (\text{A4})$$

when $\theta_i^{(t)} = \mathcal{R}$ (i.e., on $\partial\mathcal{R}$ of the Poincaré section),

$$\left\{ \begin{array}{l} t_{\mathcal{R}\mathcal{E}} = \frac{1}{\eta'_i} \log\left(\frac{1}{x_i^{(t)}}\right), \text{ so} \\ \quad \left(x_i^{(t+1)}, y_i^{(t+1)}, \theta_i^{(t+1)}\right) = \left(1, \left(x_i^{(t)}\right)^{\frac{\gamma'_i}{\eta'_i}}, \mathcal{E}\right); \\ t_{\mathcal{R}\mathcal{S}_x} = \frac{1}{\gamma'_i} \log\left(\frac{1}{\delta}\right), \text{ so} \\ \quad \left(x_i^{(t+1)}, y_i^{(t+1)}, \theta_i^{(t+1)}\right) = \left(\delta^{-\frac{\eta'_i}{\gamma'_i}} x_i^{(t)}, \delta, \mathcal{S}_x\right); \end{array} \right. \quad (\text{A5})$$

when $\theta_i^{(t)} = \mathcal{S}_y$ (i.e., on $\partial\mathcal{S}_y$ of the Poincaré section),

$$\left\{ \begin{array}{l} t_{\mathcal{S}_y\mathcal{E}} = \frac{1}{\eta'_i} \log\left(\frac{1}{\delta}\right), \text{ so} \\ \quad \left(x_i^{(t+1)}, y_i^{(t+1)}, \theta_i^{(t+1)}\right) = \left(1, \delta^{-\frac{\gamma'_i}{\eta'_i}} y_i^{(t)}, \mathcal{E}\right); \\ t_{\mathcal{S}_y\mathcal{R}} = \frac{1}{\gamma'_i} \log\left(\frac{1}{y_i^{(t)}}\right), \text{ so} \\ \quad \left(x_i^{(t+1)}, y_i^{(t+1)}, \theta_i^{(t+1)}\right) = \left(\left(y_i^{(t)}\right)^{-\frac{\eta'_i}{\gamma'_i}} \delta, 1, \mathcal{R}\right); \end{array} \right. \quad (\text{A6})$$

when $\theta_i^{(t)} = \mathcal{S}_x$ (i.e., on $\partial\mathcal{S}_x$ of the Poincaré section),

$$\left\{ \begin{array}{l} t_{\mathcal{S}_x\mathcal{E}} = \frac{1}{\eta'_i} \log\left(\frac{1}{x_i^{(t)}}\right), \text{ so} \\ \quad \left(x_i^{(t+1)}, y_i^{(t+1)}, \theta_i^{(t+1)}\right) = \left(1, \left(x_i^{(t)}\right)^{-\frac{\gamma'_i}{\eta'_i}} \delta, \mathcal{E}\right); \\ t_{\mathcal{S}_x\mathcal{R}} = \frac{1}{\gamma'_i} \log\left(\frac{1}{\delta}\right), \text{ so} \\ \quad \left(x_i^{(t+1)}, y_i^{(t+1)}, \theta_i^{(t+1)}\right) = \left(\delta^{-\frac{\eta'_i}{\gamma'_i}} x_i^{(t)}, 1, \mathcal{R}\right). \end{array} \right. \quad (\text{A7})$$

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