



The Dynamics of Herds: From Individuals to Aggregations

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The dynamic behavior of small herds is investigated by means of simulations of two-dimensional discrete stochastic models. An individual-based approach is used to relate collective behavior to individual decisions. In our model, the motion of an individual in a herd is assumed to be the combined result of both density-independent and density-dependent decisions, in the latter case based on the influence of surrounding neighbors; assumed decision rules are hierarchical, balancing short-range repulsion against long-range attraction.

The probability of fragmentation of the model herd depends on parameter values. We explore the variety and characteristics of spatial patterns that develop during migration, for herds that are homogeneous or heterogeneous regarding intrinsic walking speeds. Group integrity can be maintained even in mixed populations, but fragmentation results for these more easily than for a homogeneous herd.

Observations of natural populations suggest that animals move away from individuals that intrude too closely into their environment, but are attracted to individuals at a distance. Between these extremes, there appears to be a neutral zone, within which other individuals engender no response. We explore the importance of this neutral zone, and offer evolutionary interpretations. In particular, the neutral zone, if not too large, permits the individual to remain in contact with the herd, while reducing the frequency with which acceleration or deceleration must be undertaken. This offers obvious energetic benefits.

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Introduction

In many animal species, individuals aggregate to form temporary or permanent groups. The reasons generally are fairly well understood. In most cases, sociality evolves because individuals derive anti-predator or foraging benefits that offset the automatic detriments of increased competition or disease transmission associated with aggregating (Alexander, 1974; Bertram, 1978; Rubenstein, 1978). Mating strategy provides the explanation in other situations. However, why groups assume particular shapes and exhibit characteristic dynamics and how group cohesion is maintained are less well understood.

Theory suggests that the risk of being preyed upon selects for individuals to join groups, and to avoid being on an edge; such individual behavior causes groups to form and then constrict (Hamilton, 1971). Observations of mammal herds (Underwood, 1982), bird flocks (Murton *et al.*, 1971; Barnard, 1980; Inglis & Lazarus, 1981), fish schools (Magurran *et al.*, 1986; Parrish, 1989) and insect swarms (Alexander, 1974) suggest that the dynamics are more complex than these simple rules would suggest, and that genetic and ontogenetic differences among individuals, as well as environmental factors including demographic and behavioral features of the population, all play a role. Groups composed of juveniles often differ in size, shape, structure and cohesion from those of adults because dietary needs and risks of being preyed upon differ (Rubenstein, 1978). Similarly, associations of

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individuals that are simply wandering appear to differ from those of individuals foraging (Major, 1978; Wittenberger, 1981; Bednarz, 1988). Conversely, even under constant ecological conditions, the features of a group appear to vary as its composition becomes less homogeneous (Black *et al.*, 1992).

In all of this variety of examples, spatial structure of groups emerges from the degree of coordination exhibited by the individuals that comprise them. Although there may exist counter-examples, most observations of the dynamics of small and large groups show that coordination is locally controlled, and that large-scale patterns can form spontaneously by the action of individuals in relation to only their neighbors or local environmental signals or markers; long-range information transfer, global knowledge and externally imposed forces are not necessary (Keenleyside, 1955; Partridge, 1982). From this perspective, the key to understanding how group cohesion is maintained is to investigate the role of individuals' social responses to neighbors, and to their local environments.

Models of group dynamics can be divided into two types: Eulerian and Lagrangian. Eulerian models, which suppress individual identities and measure only numbers of individuals per unit area or volume, usually (but not necessarily) treat space as a continuum. In this approach, the population is represented by a density function of the number of individuals in an area, and a set of equations is used to describe the dynamics of that function (see for example Okubo, 1986; Othmer *et al.*, 1988; Gueron & Liron, 1989; Alt & Hoffman, 1990; Grünbaum & Okubo, 1994). One advantage of continuous models is the diversity of readily available analytical tools that facilitate their study.

While the continuum assumptions may apply to the movement of large and dense aggregations of bacteria or small metazoans such as insects and krill (e.g., Grünbaum & Okubo, 1994), they are poor starting points for large bodied species, such as fish, birds and mammals, where schools, flocks or herds typically contain only dozens or hundreds of individuals and typical spacing is relatively large in terms of body lengths. For these situations, discrete individual-based (Lagrangian) models are more appropriate. Such models involve a finite number of individuals, and the rules governing the group's movements and cohesion result from a finite sequence of decisions made by individuals.

Even when continuum Eulerian models can be justified, an individual-based approach is helpful in deriving the correct limiting equations (Durrett & Levin, 1994; Grünbaum & Okubo, 1994). Most

published individual-based models for animal aggregation can be viewed as variants of an n -body dynamics problem (Okubo, 1986); in particular, the motion is controlled by Newton's second law, and computed by integrating Newton's equation

$$m_i \ddot{x}_i = \sum_k F_{ik} = F_i \quad i = 1, 2, \dots, n,$$

in which x_i is the position of individual i , and m_i is the mass of the individual.

F_i is the total force exerted on individual i and n is the total number of individuals. F_i is made up of components F_{ik} , which include (Grünbaum & Okubo, 1994) locomotory forces (viscous drag, constant swimming speed), aggregation or disaggregation forces (attraction or repulsion by neighbors), arrayal forces (tendency to match velocity or orientation of neighbors), deterministic environmental effects (gravity, fluid motions, chemical gradients, obstructions), and random forces (behavioral or environmental stochasticity). F_i is the sum of such forces (see for example Parr, 1927; Breder, 1954; Sakai, 1973; Suzuki & Sakai, 1973; Matsuda & Sannomiya, 1980, 1985; Aoki, 1982; Okubo, 1986).

In most "additive type" models (e.g., Warburton & Lazarus, 1991), social attraction or repulsion between individual i and j is represented by a continuous function that depends on the distance between them; all responses, attractive or repulsive, occur simultaneously. The resultant is the sum of all forces taken over all neighbors. In general, influences are discounted by distance, so that the influence of remote neighbors is dominated by the influence of nearer ones. Nonetheless, Huth & Wissel (1992) conclude from simulations of an additive type model that the weighted additive strategy yields a better description of fish schools than a strategy where each individual follows only a specific single neighbor.

Grünbaum (1992, 1994) presents a model for swarming that assumes that individuals seek a target density; that is, a desired number of neighbors in a predetermined neighborhood. This is achieved by assuming that individuals census their neighbors, and move in response to the gradient depending on how the observed density compares with the target density. Such a model is a variant on the additive theme.

Additive rules present one possibility; but for many natural situations, it seems more likely that animals make decisions according to a hierarchical decision tree based on responses to individuals. This claim is in part supported by our own field observations (DIR), but also reflects the recognition that typically

different types of biological influences—e.g. danger, resource acquisition, and social interactions—are important on different scales, and are not in general measurable in the same currency. Furthermore, since hierarchical rules permit decisions to be made on the basis of a single or small number of observations, they obviously are computationally simpler for the animal, and permit much more efficient decision-making than those that rely on weighted sums of the effects of large numbers of individuals. These points are, simply by way of motivating the assumptions that form our point of departure, and are not intended as proof. An important open problem in behavioral ecology is to compare various classes of decision rules through ecological and evolutionary analyses, and to ask which are adaptive under which conditions; we defer that investigation for future study.

In this paper, we develop a stochastic discrete model that is based on a hierarchical set of decisions taken by individuals. Instead of integrating cues from neighbors, each individual scans influence zones surrounding it to make decisions based only on the presence or absence of neighbors within these zones; the sizes of the influence zones govern the behavior of the model. In some configurations, information on the presence of neighbors within only part of the influence zones is sufficient to make a decision. The hierarchical structure of the model allows individuals to stop collecting information at that point; in this sense a hierarchical algorithm is thus more economical than an additive one. This is not proof that such decision rules would always be adaptive, since other factors may enter the equation.

Within the context of the model, we analyse the movements of individuals and examine how the shape and cohesion of groups change over time. In particular, we study the maintenance of group integrity, and attempt to determine the conditions under which groups become unstable or qualitatively change their characteristic shapes. In particular, we seek to determine how fragmentation depends upon assumed rules of behavior. Departing from the usual approach (e.g., Huth & Wissel, 1992) we allow groups to be heterogeneous for intrinsic walking speed. Such mixed populations can maintain integrity as a group; furthermore, not surprisingly, homogeneous populations can fragment. However, the trend is in the opposite direction. We explore these tendencies through analysis of fragmentation in relationship to the degree of heterogeneity.

Simulations of the type performed here cannot be the end of the story: analytical tools must be developed that allow exploration of the influence of varying the details of movement rules. Our investiga-

tions, however, provide an important starting point. An analytical theory of group size distributions is treated elsewhere (Gueron & Levin, 1995), and more work needs to be done relating fusion and fission rates to individual parameters. As for the development of hydrodynamic limits for such equations, the goal is a laudable one. However, it must be remembered that, in any limiting process, the zones over which individuals collect information would remain finite. Methods such as these introduced by Grünbaum (1992) can be invoked, e.g. by assuming that local densities are governed by Poisson distributions with appropriate means. These would be expected to lead to limiting equations of the form of partial differential integral equations. Given the existence of hierarchical decision rules, such limiting equations would be non-trivial to derive, and daunting to analyse. The issue remains, however, an attractive one for investigation.

The Simulation Model

UNDERLYING ASSUMPTIONS AND NOTATIONS

Our goal is to investigate the mechanisms that control herding behavior, and to determine conditions under which grouping can remain stable. Our basic assumptions assure that grouping is “self organized.” That is, the integrity of the herd is maintained entirely by individual movements, which in turn are affected only by the positions of neighbors within a restricted range.

The model conforms to the general class of n -body problems mentioned above, although we deal with an integrated version. For $i = 1 \dots n$, $r_i(t) = (x_i(t), y_i(t))$ denotes the location of the head of the i th individual, at time t . We also assume that each individual moves towards a “target”; with no loss of generality, we assume that the target is located at infinity in the direction of the y axis. The intrinsic velocity vector of individual i is \mathbf{w}_{i1} . The intrinsic velocity is complemented by a velocity component \mathbf{w}_{i2} representing responses to other individuals, so that

$$\dot{r}_i = \sum_{j=1}^2 \mathbf{w}_{ij} \quad i = 1, 2, \dots, n; \quad j = 1, 2. \quad (1)$$

where n is the number of individuals in the herd.

The model herd is embedded in the X, Y plane. We denote the body length of each individual by l and its half body width by w . Throughout the paper, to motivate parameter choices, we use the ratio $w = l/2$, which is roughly typical for grazing mammals. The time unit is set to be the time interval between

successive decisions, and velocities are measured in units of body lengths per unit time.

Real herds are non-homogeneous in a variety of aspects, for example their intrinsic walking speeds. Hence, in some of the simulations, we subdivide the population into subpopulations of “speeders” (e.g., dominant males searching for reproductive females, or nursing females searching for food and water) and “laggards” (e.g., juveniles). “Speeders” are assigned a walking speed that is a fraction k higher in the target direction than that of the others; the proportion of the (initially randomly distributed) speeders in the population is denoted by d . We study the maintenance of herd integrity in relation to variation in k .

INTRINSIC BEHAVIOR

In the absence of neighbors, we assume that each individual can move to the “left” ($-x$ axis direction), “forward” ($+y$ axis direction) or to the “right” ($+x$ axis direction), with respective probabilities p_1 , p_2 , p_3 at a given time step ($p_1 + p_2 + p_3 = 1$). If the animal knew exactly where the target was and could respond perfectly, p_2 would be equal to 1, and p_1 and p_3 would be zero. More generally, obviously, the ratios p_j/p_i reflect the individual’s sense of direction relative to the target, and ability to move in the preferred direction; relatively higher values of p_2 reflect a better orientation towards the target defined above. The intrinsic movement vector \mathbf{w}_{ii} is made up of intrinsic forward and lateral velocities or speeds, denoted v_i , u_i respectively; this implies that the step sizes in the respective directions, during a time step dt , are $v_i dt$ or $u_i dt$, depending on which direction is selected. We assume that individuals are capable of changing their walking speeds and directions at each time step, in response to the presence or absence of neighbors; these responses, which are discussed in the following section, define the components of \mathbf{w}_{i2} . Without them, there could be no cohesion, and heterogeneous herds would always fragment.

INFLUENCE ZONES AND INTERACTIONS WITH NEIGHBORS

The velocity component \mathbf{w}_{i2} is determined by a hierarchy of zones within which individuals detect neighbors and are influenced by them. These zones are defined below as rectangular regions, $[a, b] \times [c, d]$, where the notation $[a, b]$ represents an interval.

The stress zone

$$SZ = [x_i - a_1, x_i + a_1] \times [y_i - b_1, y_i + b_1] \quad (2)$$

The need for individual space causes individuals to be repelled by neighbors who enter their *personal* space (Hediger, 1950), here referred to as their stress zone. This repulsion is modeled as a biased change in speed and direction, intended to avoid stress zone “intruders.” If there is a neighbor in the stress zone, positioned in front of the individual i , the target individual reduces its speed to a fraction q_1 (to avoid potential collision). If, instead, a neighbor enters the stress zone laterally, i moves next in the opposite direction. If two (or more) neighbors enter the stress zone *on both sides* of i , the effects cancel and the individual does not move. Neighbors within the stress zone, positioned behind i and to one side, cause it to move in the opposite lateral direction, but not to change its speed. If rear zone neighbors are located on both sides, i is simply “pushed” in that it increases its forward speed by a fraction q_1 .

If there are neighbors in the stress zone, the other zones are irrelevant. If the stress zone is empty, the individual assesses the neutral zone.

The neutral zone

$$NZ = [x_i - a_2, x_i + a_2] \times [y_i, y_i + b_2] - SZ, \quad (3)$$

where $a_2 > a_1$ and $b_2 > b_1$. Note that the neutral zone has no component behind the individual.

This zone, intermediate between the stress zone and the attraction zone, is one in which individuals do not respond to neighbors unless all neighbors are on the same side. In the latter case, they display “selfishness,” moving towards the neighbors to reduce their chance of being eaten by predators (Hamilton, 1971; Parrish, 1989). Specifically, the response of an individual upon discovering that it has neighbors only to one side in the neutral zone is to bias its movement in the direction of those neighbors, with no change in speed.

If there are neighbors in the stress or neutral zones, the other zones are irrelevant. If the first two zones are empty, the individual assesses the attraction zone.

The attraction zone

$$AZ = [x_i - a_3, x_i + a_3] \times [y_i, y_i + b_3] - SZ - NZ, \quad (4)$$

where $a_3 > a_2$ and $b_3 > b_2$. Note that the attraction zone has no component behind the individual.

The need to avoid being too far from conspecifics, or on the “edge” of the herd where the risk of predation is highest (Hamilton, 1971), causes individuals to approach neighbors, interposing themselves between the “others” and the “edge.”

We model such attraction by a biased change in speed and direction towards neighbors within the attraction zone.

Neighbors positioned only on one side of an individual cause it to speed up to a multiple q_2 (of its intrinsic speed) and to move towards those individuals in an attempt to “fill in the gap.” The presence of attraction zone neighbors on both sides of the individual cause it to speed up to a fraction q_2 without changing direction.

If there are individuals in any of the three zones mentioned, the last zone is irrelevant. If, however, all are empty, the individual then assesses the rear zone.

The rear zone

$$RZ = [x_i - a_4, x_i + a_4] \times [y_i - b_4, y_i] - SZ, \quad (5)$$

where $a_4 > a_1$ and $b_4 > b_1$.

The presence of rear zone neighbors distinguishes trailers from leaders, as described in the next section.

Figure 1 provides a graphical heuristic representation of the zones, except for the rear zone.

LEADERS, TRAILERS AND THE HIERARCHY OF DECISIONS

If an individual has no neighbors within the first three zones, but has rear neighbors, it is a “leader”; otherwise, it is a “trailer.” Note that, a priori, there is no reason why, for example, laggards cannot be leaders, or speeders cannot be trailers. For reasons similar to those justifying the attraction zone, leaders, with probability s_1 , are assumed to reduce their intrinsic speed to a fraction q_3 ; trailers, in

contrast, speed up to a multiple q_4 . We define $s_2 = 1 - s_1$ and hence the ratio $s_1:s_2$ represents leaders’ “awareness” of the trailing herd behind them.

In real herds, being in the front might convey unique and specific benefits and costs. Leaders exhibit their uniqueness by having a preferred directionality possibly different from that of the rest of the herd. To that end, the parameters r_1, r_2, r_3 denote the probabilities for a leader to move to the left, forward or to the right, respectively, whereas the parameters p_1, p_2, p_3 remain the default probabilities for the rest of the herd.

Summarizing the order by which attraction and repulsion are implemented in the model recapitulates the description of the decision-making procedure. The individual (i) first senses (and reacts to) its stress zone neighbors, if there are any. In the absence of stress zone neighbors, i “searches” for neighbors within the neutral zone. If neutral zone neighbors are detected, i continues moving at its intrinsic pace or displays selfishness in the case that they are all on one side. If there are neither stress zone nor neutral zone neighbors, i seeks the protection of the herd by approaching neighbors within the attraction zone. Finally, if there are no individuals within any of the three zones, the individual increases or decreases its intrinsic speed, depending upon whether it is a “leader” or a “trailer.” In Fig. 2 we sketch a flowchart of this hierarchical procedure.

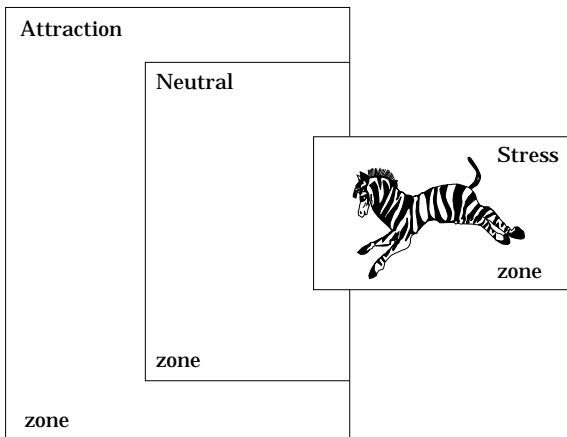


FIG. 1. Idealized stress, neutral and attraction zones for an individual.

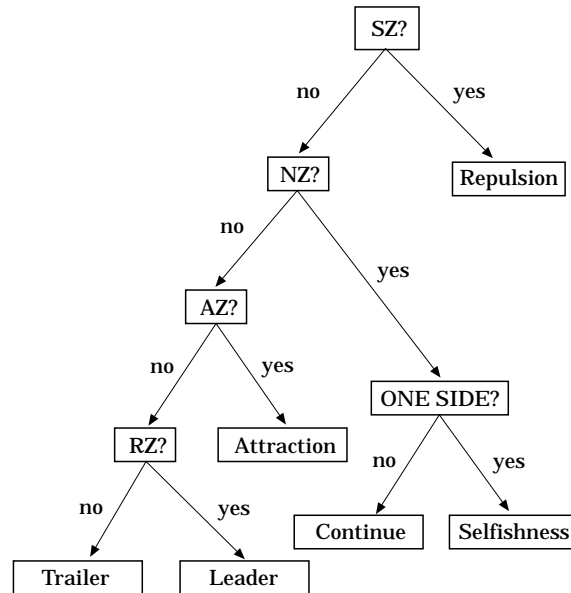


FIG. 2. Flowchart of the hierarchical decision algorithm for an individual.

TABLE 1
Default parameter values used for the simulations

Parameter	Short description	Default values	Units
a_1, b_1	stress zone dimensions	2, 4	body lengths
a_2, b_2	neutral zone dimensions	6, 12	body lengths
a_3, b_3	attraction zone dimensions	10, 20	body lengths
a_4, b_4	rear zone dimensions	10, 20	body lengths
$p_1:p_2:p_3$	intrinsic directionality	1:2:1	dimensionless
u, v	intrinsic velocity coordinates	1, 2	body lengths/time
q_1	slowing-down factor for repulsion	0.5	dimensionless
q_2	speeding-up factor for attraction	1.5	dimensionless
$r_1:r_2:r_3$	speeders' directionality	1:2:1	dimensionless
$s_1:s_2$	leaders' tendency to "wait"	10:7	dimensionless
q_3	leaders' relative velocity	0.5	dimensionless
q_4	trailers' relative velocity	2	dimensionless
k	speeders' relative velocity	1.4	dimensionless
d	proportion of speeders in heterogeneous herds	$\frac{1}{3}$	dimensionless
n	group size	25	individuals

Simulation Results

Through simulations, we examined the influence of variation of zone sizes, directionality, herd heterogeneity, and group size (for groups from 10 to 100 individuals); however, much more could be done to explore the very high dimensional parameter space. In Table 1, default parameters are given; the text describes deviations from these parameters. Zone dimensions are in body lengths, and speeds in body lengths per time step. Changing the time step would not change the qualitative behavior of the model, so this was not varied. The initial configuration was that of an approximately rectangular block of individuals, each with expected position (the exact position includes a random component) separated by a_3 (the attraction zone dimension) from neighbors to its left or right, and b_3 from neighbors ahead or behind. To the extent possible, the numbers of rows and columns were chosen approximately equal; for the default ($n = 25$), there were hence five rows of five individuals each.

We investigated herd pattern development through time, for up to 2000 timesteps. Based on our observations of terrestrial mammals (DIR), we would estimate a typical decision step size to be about 2 s, so that 2000 steps would represent a little more than an hour. Snapshots of herds shown in the figures are typically at $t = 250$, corresponding to early stages of pattern development.

HOMOGENEOUS HERDS

Before exploration of the dynamics of heterogeneous herds, it is important to understand homogeneous herds, i.e., those having no speeders ($d = 0$). For such herds, simulations show that, for a wide range of walking speeds, the simple hierarchical

implementation of the hypothesized behavior is sufficient for maintaining, for long periods of time, the integrity of homogeneous herds of as many as 100 individuals; even within this range, however, as group size increases, fragmentation occurs more easily (Fig. 3). The consequences of this dependence are explored further in Gueron and Levin (1995). In Fig. 3, the "fragmentation index" is the proportion of the population not in the largest subgroup. Individuals are defined to be in the same subgroup if they are within each other's attraction zones; this property is extended by transitivity, so that subgroups are distinct if no individual in one subgroup is in the attraction zone of any individual in the other. For small groups, only a few individuals get lost; for large groups, nearly 40% of the individuals exist outside of the main cluster. However, even 100 is not a large group when attention is focused, say, on wildebeest. It would be extremely interesting to extend the

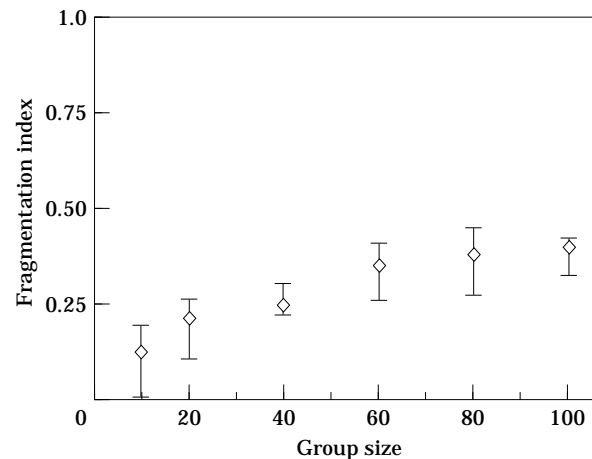


FIG. 3. Fragmentation (see text) in relation to group size. Diamonds show means; bars show minimum and maximum values.

dependence in Fig. 3 to even larger groups, but that must await more efficient algorithms and a later paper.

EFFECTS OF TARGET ORIENTATION AND VELOCITY

We define the (oriented) eccentricity of the herd [denoted $e(t)$] as the ratio of herd range along the x axis to its range along the y axis. Consequently, small values of $e(t)$ correspond to “column-like” patterns and large values of e correspond to “front-like” patterns.

Figure 4 displays snapshots of two herds with $n = 25$ individuals, which were started with the same initial conditions but with different values of v_i ($v_i = 2$ and $v_i = 12$). For comparison, the first is shown after 250 steps, the second (and faster) after 50 steps (and after 250 steps in Fig. 5). Figures 4 and 5 demonstrate the qualitatively different shapes that the herds can take, in relation to the degree to which intrinsic velocities are target-biased. In other simulations, the traveling fronts that appear with low values of v_i become thicker when n is increased. More importantly, the faster population ($v_i = 12$) obviously is beginning to develop more columnar structure, as shown in Fig. 5.

Figure 6 summarizes observed patterns for 500, 1000, 1500, and 2000 time steps, in relation to the

varying intrinsic speeds (that is, velocities v_i) in the direction of the target. The (oriented) initial eccentricity of all herds is 0.5, representing the ratio a_3/b_3 and the initial conditions described earlier. With time, however, eccentricity increases towards infinity for small values of v_i , and decreases towards zero for large values.

Target bias can be reflected in higher velocities when movement is in the target direction, or simply in a higher probability to move in that direction. We also studied the integrity and the evolving shape (and eccentricity) of the herds in relation to that probability, changing the ratio $p_1:p_2:p_3$ (larger values of p_2 represent more target-directed movement). Figure 7 presents snapshots (after 250 steps) of two homogeneous herds with $p_1:p_2:p_3 = 1:1:1$ and $1:10:1$, respectively (all other parameters are identical). As can be seen, as p_2 is increased, eccentricity is decreased, and more compact herds result. This is seen more clearly in Fig. 8, which shows the eccentricity after 250 steps in relations to p_2/p_1 , again for 25 individuals.

EFFECTS OF RELATIVE SIZES OF ZONES

To examine the importance of the different zones, we varied the size of the neutral zone (keeping its shape constant) from coincidence with the stress zone

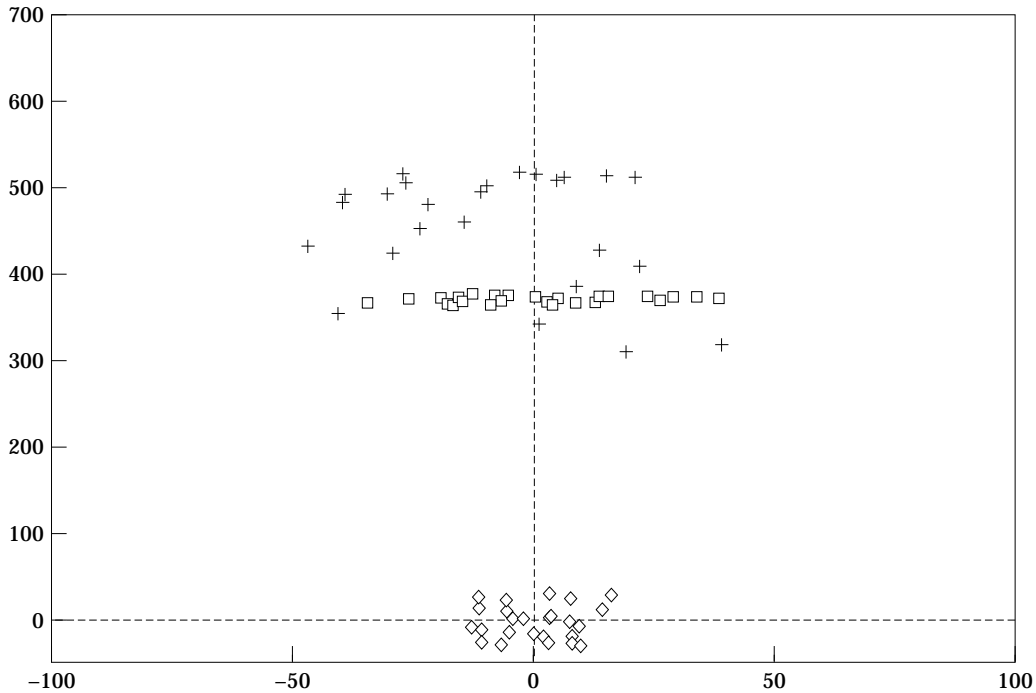


FIG. 4. Snapshot of homogeneous herds with $v_i = 2$ (\square), at time $t = 250$, and $v_i = 12$ ($+$) at $t = 50$. The axes in this and similar figures show the x and y coordinates of individual animals. \diamond denotes initial configuration. Note the looser organization at the higher speed.

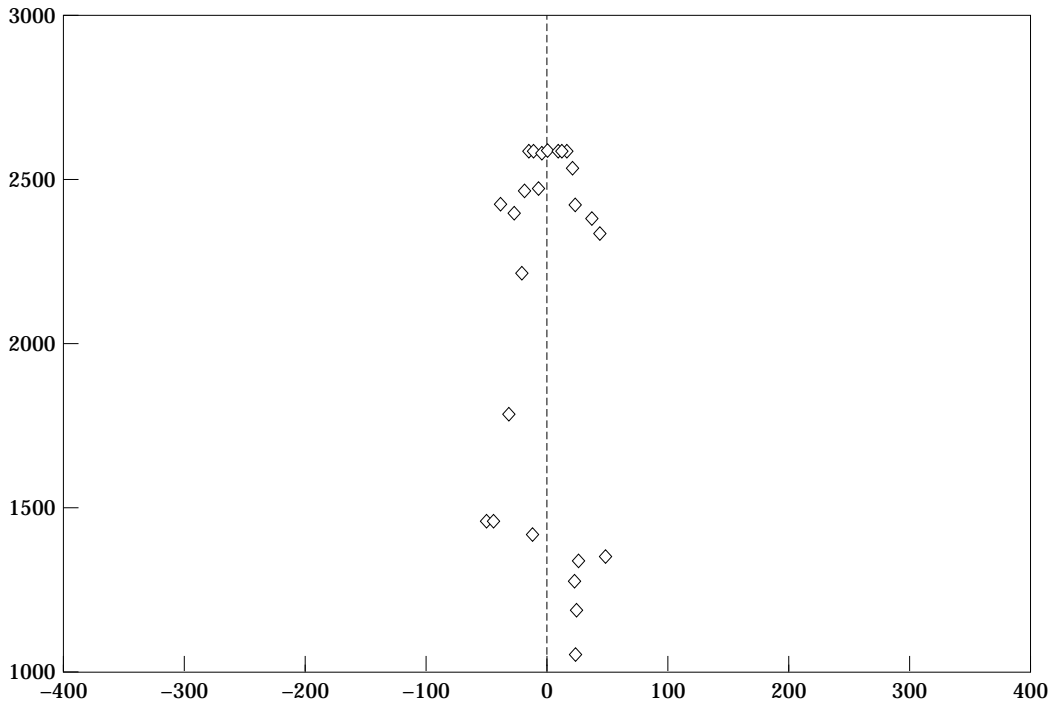


FIG. 5. A homogeneous herd with $v_i = 12$, at time $t = 250$. Column structure has developed.

(so that there was no neutral zone) to coincidence with the attraction zone (so that there was no attraction zone). Figure 9 describes the means of ten simulations, under these varying conditions. The neutral zone is shown as varying from zero to unity as a fraction of the attraction zone's outer linear dimension; thus, a value of one indicates no attraction zone, and a value of zero indicates no neutral zone. The potential for fragmentation does not seem affected by size of the neutral zone until the latter becomes large relative to the attraction zone.

Not surprisingly, when the attraction zone is made smaller (by increase in the neutral zone), herds are much more likely to fragment, and some individuals become lost. As a follow-up study, it would be interesting to explore how the eventual group size distribution varies with these parameters (Gueron & Levin, 1995). Variation in the stress zone size is not treated directly, since by rescaling of intrinsic walking speeds it can be made equivalent to variation of the other zones. Elimination of the neutral zone did not in general cause homogeneous herds to assume more front-like dynamics (but see Gueron & Levin, 1993).

In our simulations, the neutral zone was usually occupied. That meant that individuals were usually satisfied that they were not isolated, and tended therefore to accelerate less often than they otherwise

would. Figure 10 illustrates the fraction of time accelerating or decelerating as a function of relative neutral zone size, for 50 replicates run over 2000 time steps. In the no neutral-zone (knife-edge) model, individuals are always accelerating or decelerating. In contrast, when there is a neutral zone of the default size (relative size 0.6), in 78% of the cases an individual had no one in its repulsion zone, but someone in its neutral zone—that is, its movement rule was to move at the intrinsic speed. Therefore, observance of a neutral zone is energetically more efficient for an organism, because it reduces the necessity for individuals to change velocities. In the 22% of the cases when individuals did respond, they were attracted in 15% of the cases, and repelled in 7%. Comparison of Figs 9 and 10 shows that there are potential costs and benefits to increasing neutral zone size, and we suggest that these trade-offs provide the evolutionary determinants of neutral zone dimensions.

HETEROGENEOUS HERDS

We introduce herd heterogeneity, through consideration of mixed herds consisting of two sub-populations having different intrinsic walking speeds. We examine the effects that the presence of speeders has on the spatial configuration of the herd, and on tendencies for fragmentation.

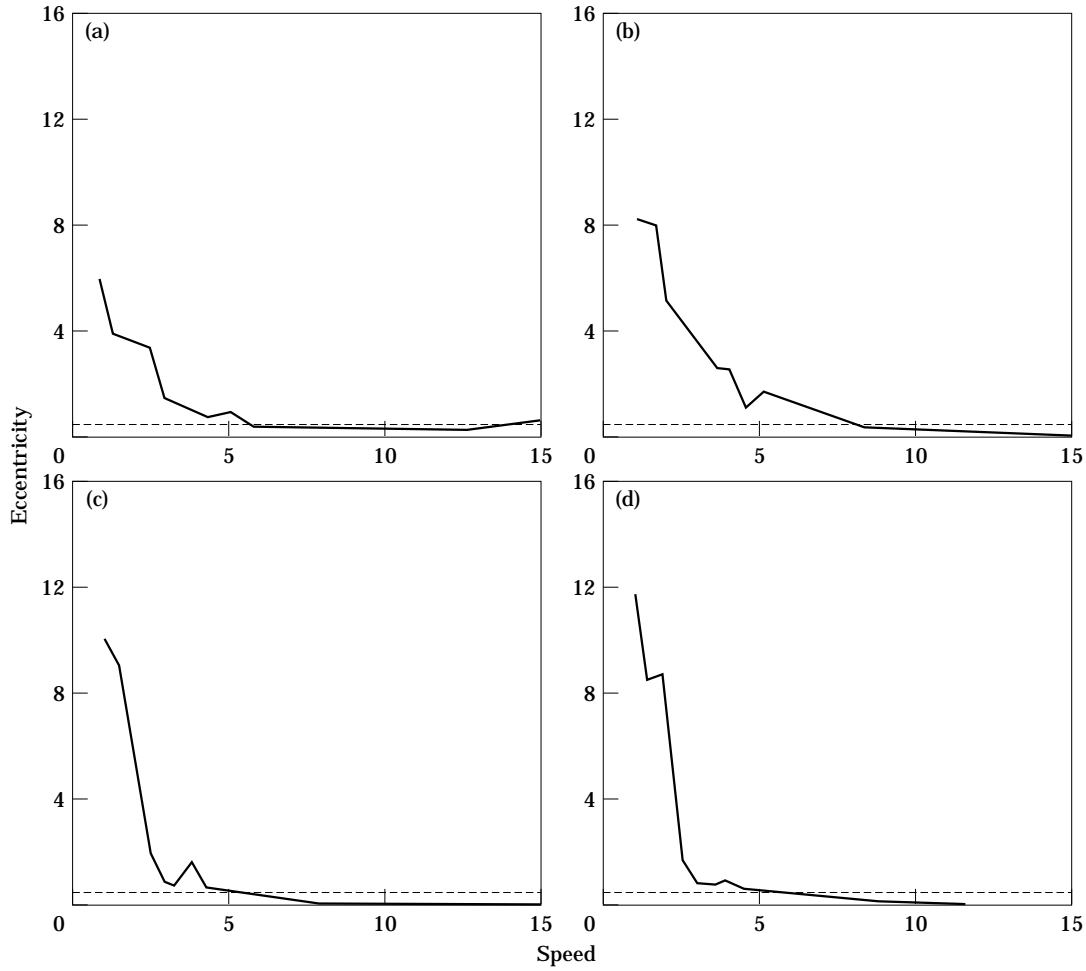


FIG. 6. The eccentricity of homogeneous herds as a function of the intrinsic (vertical) speed, after 500 (a), 1000 (b), 1500 (c), and 2000 (d) time steps. Initial configuration (dotted line in all figures) in all cases had eccentricity 0.5.

Simulations show that, even when speeders begin on the back of the initial cluster, they eventually become “leaders,” regardless of initial conditions. This is not proof, however, and there is no guarantee that this will happen under all conditions. The time it takes a speeder to attain a leading position depends on the ratio v_s/v_r , which reflects the extent to which it is faster than the slower individuals. In the simulations, we found that speeders, once they reach a leading position, remain at the front and eventually generate a “leading band” (see Fig. 11). Such bands of leading individuals are observed in nature, for example in large buffalo and wildebeest herds (Sinclair, 1977; Mloszewski, 1983; Scott, 1988). In the latter case, leading bands may be composed of a mixture of species (e.g. zebras and wildebeest or Grevy’s and plains zebras), consistent with the heterogeneous herds simulations in which leaders belong to a subpopulation.

Fragmentation will always occur without the rear zone behavior, in which leaders slow down for part of the time (i.e., $s_1 > 0$). Without this assumption, model herds consistently split into two distinct subgroups for values of $v_s/v_r > 1$ (see, for example, Fig. 12).

However, assuming $s_1 > 0$ does not necessarily ensure that the herd remains together as one group. If speeders are too fast, they eventually part and form a separate group (Fig. 13). In Fig. 14 we plot the eccentricity of the herd as a function of v_s/v_r , in the range where group cohesion is maintained.

Fragmentation also can be enhanced when speeders’ intrinsic sense of direction is different from that of the laggards. We demonstrate such fragmentation in Fig. 15, which is the result (after 250 steps) of a run with $v_s/v_r = 1.2$ and with the directionality parameters: $r_1:r_2:r_3 = 2:1:1$ for speeders and $p_1:p_2:p_3 = 1:2:1$ for laggards.

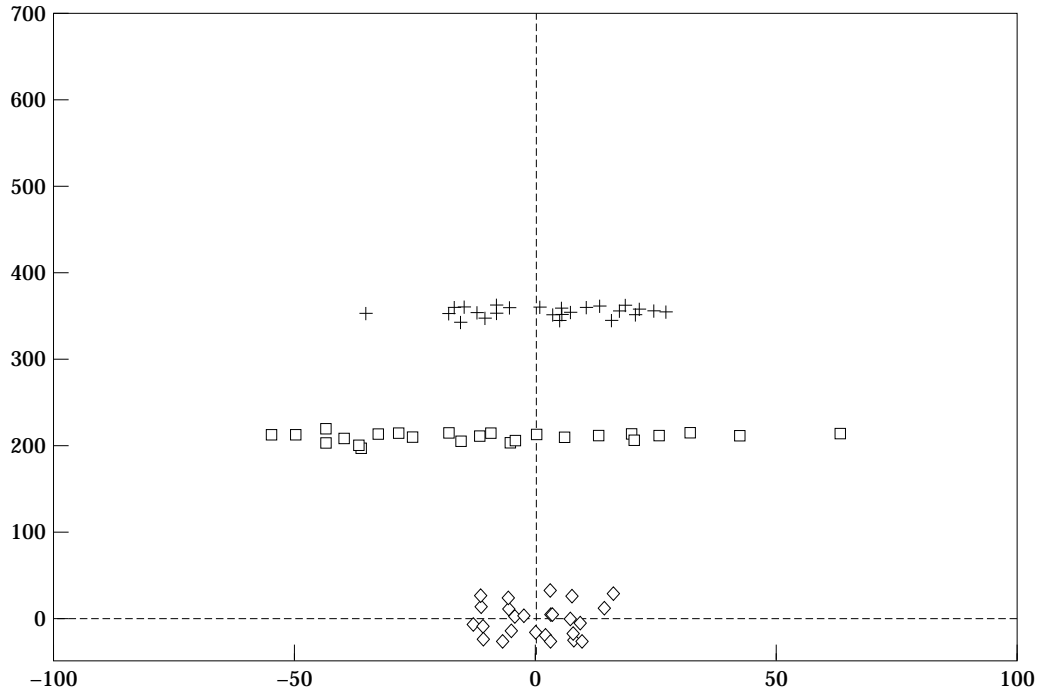


FIG. 7. Homogeneous herds with weak intrinsic directionality $p_1:p_2:p_3 = 1:1:1$ (□), and with strong intrinsic directionality $p_1:p_2:p_3 = 1:10:1$ (+), at time $t = 250$. Again, ◇ denotes initial configuration.

Again, for heterogeneous herds, we explored the consequences of varying the sizes of the zones. For a small or non-existent attraction zone, we again got increased tendency to fragment into subgroups, as intuition would suggest.

Discussion

Animal grouping patterns for particular populations can show a remarkable diversity of geometries, from single files to wave fronts, in response to changes

in the way individuals respond to cues. The model described in this paper produces such a range of geometries, and shows that a rich panoply of patterns can emerge from variation of a few basic parameters, in which individuals use information only about the location of a few of their nearest neighbors. The model involves a computationally simple hierarchical algorithm, by way of which individuals move away from neighbors too close, and towards distant ones.

For homogeneous groups composed of individuals endowed with identical intrinsic capabilities, cohesion

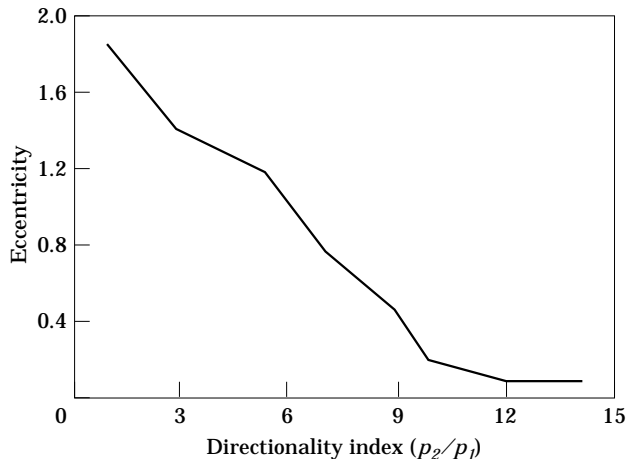


FIG. 8. Eccentricity as a function of directionality, after 2000 time steps.

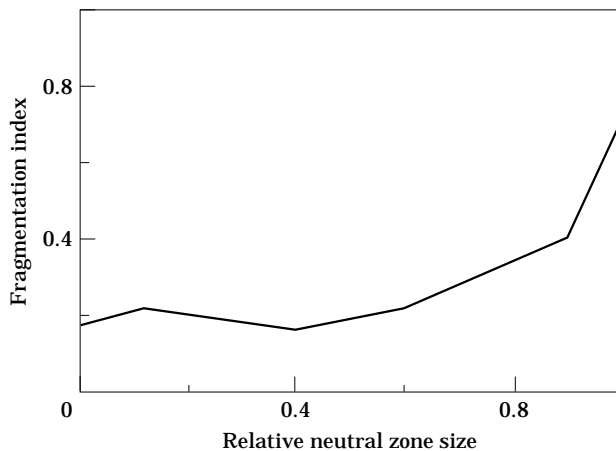


FIG. 9. Fragmentation as a function of relative neutral zone size (see text), after 2000 time steps.

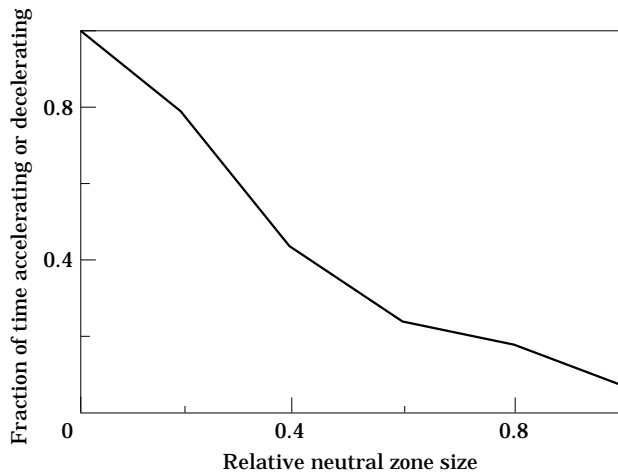


FIG. 10. Fraction of time accelerating or decelerating, as a function of neutral zone size.

and coordinated movements can be maintained essentially forever, for appropriate zone sizes, provided initial conditions are such that groups can form. The geometries of these cohesive groups depend fundamentally on the intrinsic walking speed in the target direction. When that speed is relatively slow, lines or bands form; when it is relatively fast, columns appear.

For heterogeneous groups composed of individuals with diverse walking speeds, initial aggregations tend to fragment when the difference between the normal

speed of fast individuals and the speed of slower ones increases sufficiently. Typically, and not surprisingly, faster individuals eventually become leaders. This organization is often seen in the wild, especially in fish shoals where hungry individuals swim faster, moving to the front edge of the group (Krause, 1993).

This sensitivity to group fragmentation is common in the natural world, where groups composed of different classes often split into subgroups. For both Grevy's zebras and Asiatic wild asses, herds composed of both lactating and non-lactating females segregate when walking rapidly towards or away from watering points (Rubenstein & Wrangham, 1986; Rubenstein, 1994). When herds travel more slowly, as is often the case when they are grazing, heterogeneous group walking persists.

Simulations of either homogeneous or heterogeneous groups show that shape, as measured by the index of eccentricity, also changes as environmental conditions change. When the risk of predation increases, in turn increasing the force of concealment, groups become more compact. In fact, as such hazards increase, greater variance in walking speed can be tolerated before groups fragment. Whether or not this occurs in the wild has yet to be determined.

A somewhat novel component of our model is the existence of a neutral zone, a buffer between the stress (repulsion) zone and the attraction zone. The neutral

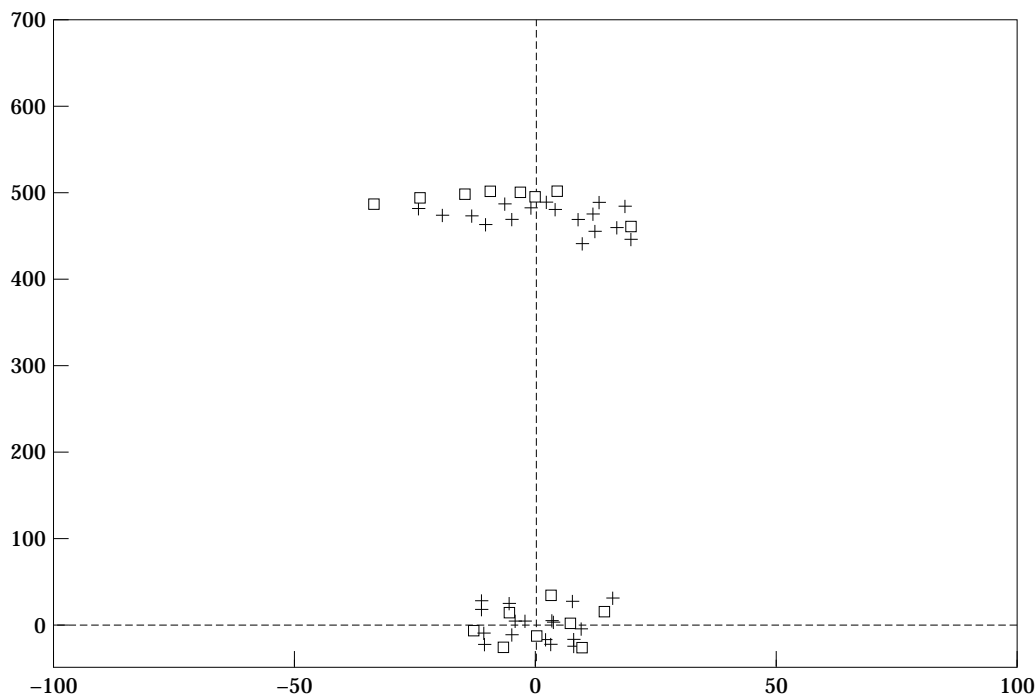


FIG. 11. Simulation of a heterogeneous herd ($v_s/v_r = 1.4$), at time $t = 250$ (and at time $t = 0$). A leading band is formed by the speeders (\square = speeders; $+$ = laggards).

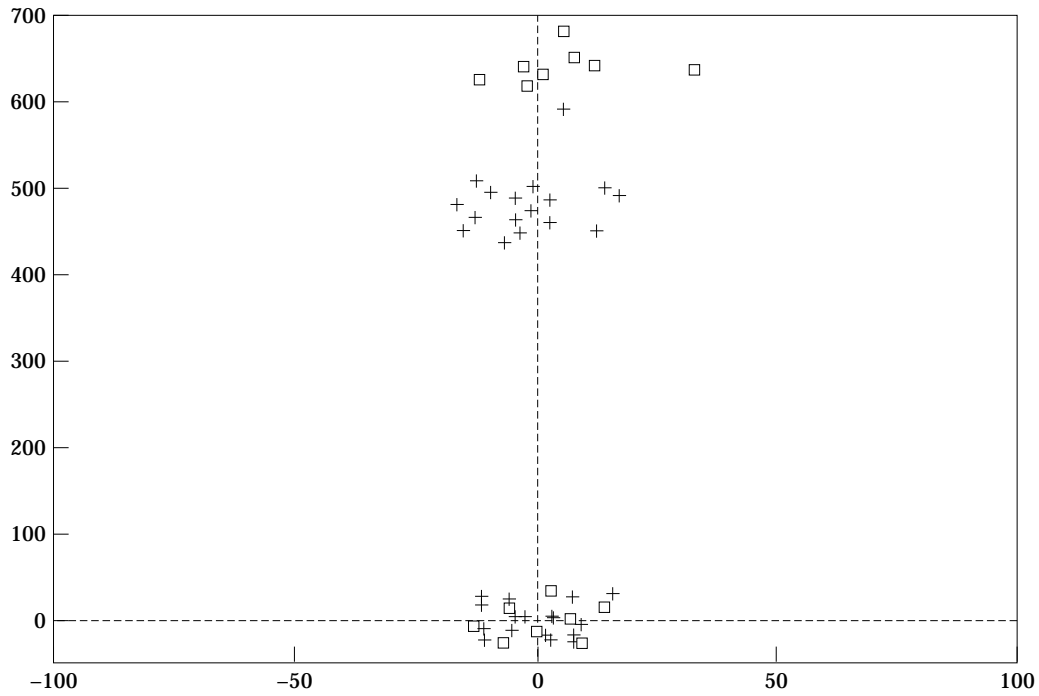


FIG. 12. A heterogeneous herd ($v_s/v_r = 1.4$), at time $t = 250$ (and at time $t = 0$). Fragmentation occurs because leaders do not “wait” for trailers (\square = *speeders*; $+$ = *laggards*).

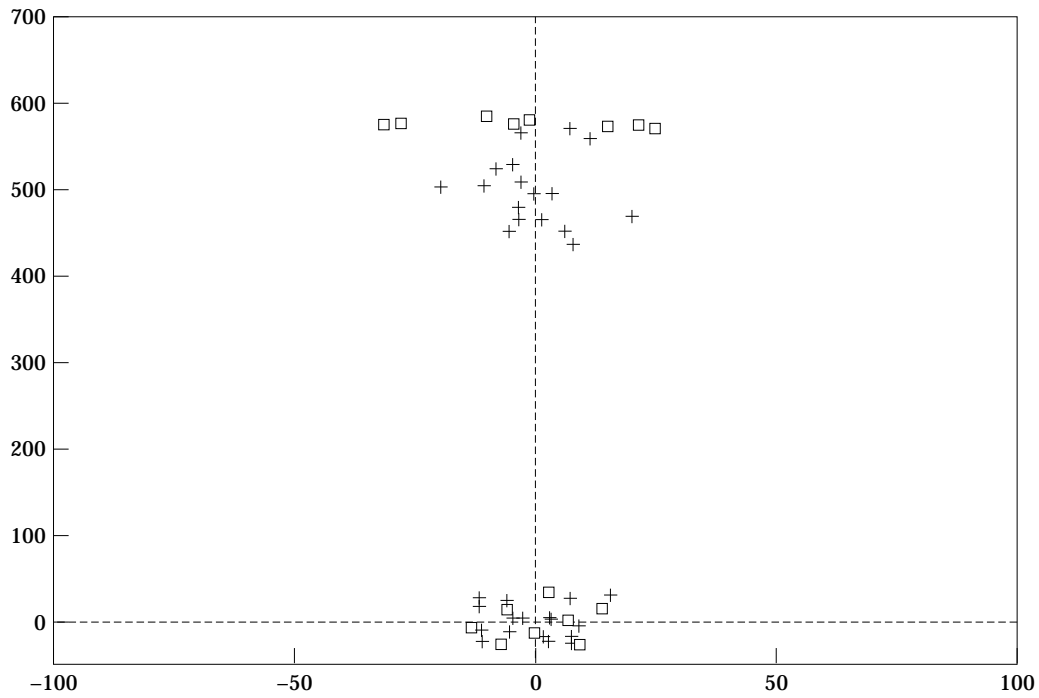


FIG. 13. Simulation of heterogeneous herd, at time $t = 250$ and at time $t = 0$. Fragmentation results because the ratio $v_s/v_r = 1.5$. Note that speeders (\square) are more eccentric in distribution.

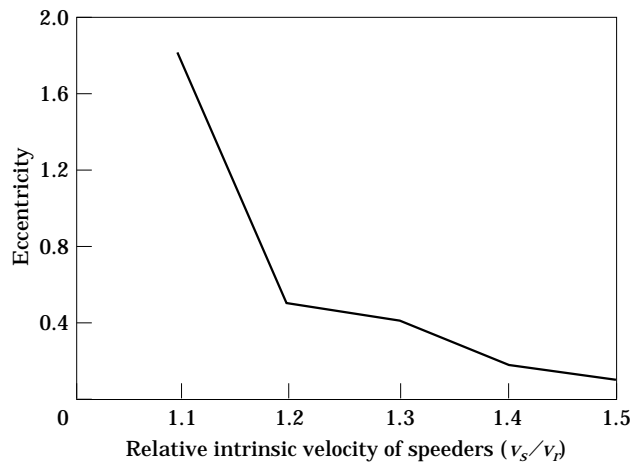


FIG. 14. Eccentricity displayed as a function of v_s/v_r for heterogeneous herds in the range where group cohesion is maintained.

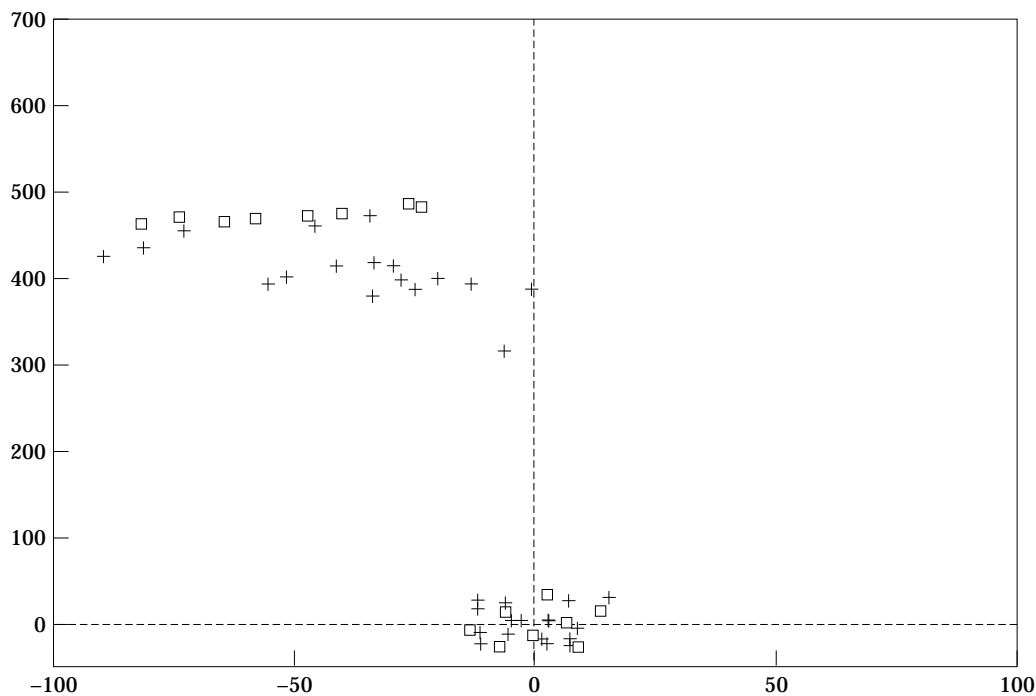


FIG. 15. Fragmentation at time $t = 250$, occurs in a heterogeneous herd when speeders and laggards have different directionalities (\square = speeders; $+$ = laggards).

zone is an energy saver for animals, in that it reduces the frequency with which they must accelerate or decelerate. The presence of the neutral zone does not appear to affect group coherence until the size of the zone becomes too large relative to the attraction zone.

The model described in this paper is admittedly crude, but illustrates the potential for individual-based models in representing observed patterns in the dynamics of herds.

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REFERENCES

- ALEXANDER, R. D. (1974). The evolution of social behavior. *Ann. Rev. Ecol. Syst.* **5**, 325–383.
- ALT, W. & HOFFMAN, G. (1990). *Biological Motion*. Lecture Notes in Biomathematics. Vol. 89. Berlin: Springer-Verlag.

- AOKI, I. (1982). A simulation study on the schooling mechanism in fish. *Bull. Japan. Soc. Sci. Fish.* **48**, 1081–1088.
- BARNARD, C. J. (1980). Flock feeding and time budgets in the house sparrow, *Passer Domesticus* L. *Anim. Behav.* **28**, 294–309.
- BEDNARZ, J. C. (1988). Cooperative hunting in Harris' hawks (*Parabuteo unicinctus*). *Science* **239**, 1525–1527.
- BERTRAM, B. C. R. (1978). Living in groups: predators and prey. In: *Behavioral Ecology*, (Krebs J. R. & Davies, N. B., eds), 1st Edn. pp. 64–96. Oxford: Blackwell Scientific.
- BLACK, J. M., CARBONE, C., WELLS, R. L. & OWEN, M. (1992). Foraging dynamics in goose flocks: The cost of living on the edge. *Anim. Behav.* **44**, 41–50.
- BREder, C. M., JR. (1954). Equations descriptive of fish schools and other animal aggregations. *Ecology* **35**, 361–370.
- DURRETT, R. T. & LEVIN, S. A. (1994). The importance of being discrete (and spatial). *Theor. Popul. Biol.* **46**, 363–394.
- GRÜNBAUM, D. (1992). Local processes and global patterns: Biomathematical models of bryozoan feeding currents and density dependent aggregations in Antarctic krill. Dissertation. Ithaca, NY: Cornell University.
- GRÜNBAUM, D. (1994). Translating stochastic density-dependent individual behavior with sensory constraints to an Eulerian model of animal swarming. *J. Math. Biol.* **33**, 139–161.
- GRÜNBAUM, D. & OKUBO, A. (1994). Modeling social animal aggregations. In: *Frontiers in Mathematical Biology*, Lecture Notes in Biomathematics, Vol. 100, (Levin, S. A., ed.), pp. 296–325. Heidelberg: Springer-Verlag.
- GUERON, S. & LEVIN, S. A. (1993). Self-organization of front patterns in large wildebeest herds. *J. theor. Biol.* **165**, 541–552.
- GUERON, S. & LEVIN, S. A. (1995). The dynamics of group formation. *Math. Biosci.* **128**, 243–264.
- GUERON, S. & LIRON, N. (1989). A model of herd grazing as a travelling wave, chemotaxis and stability. *J. Math. Biol.* **27**, 595–608.
- HAMILTON, W. D. (1971). Geometry for the selfish herd. *J. theor. Biol.* **31**, 295–311.
- HEDIGER, H. (1950). *Wild Animals in Captivity*. London: Butterworth.
- HUTH, A. & WISSEL, C. (1992). The simulation of movement of fish schools. *J. theor. Biol.* **156**, 365–385.
- INGLIS, I. R. & LAZARUS, J. (1981). Vigilance and flock size in brent geese: the edge effect. *A. Tierpsychol.* **57**, 193–200.
- KEENLEYSIDE, M. H. A. (1955). Some aspects of the schooling of fish. *Behaviour* **8**, 183–248.
- KRAUSE, J. (1993). The relationship between foraging and shoal position in a mixed shoal of roach (*Rutilus rutilus*) and chub (*Leuciscus cephalus*): A field study. *Oecologia* **93**, 356–359.
- MAGURRAN, A. E., OULTON, W. J. & PITCHER, T. J. (1986). Vigilant behaviour and shoal size in minnows. *A. Tierpsychol.* **67**, 167–178.
- MAJOR, P. F. (1978). Predator-prey interactions in two schooling fishes, (*Caranx ignobilis* and *Stolephorus purpureus*). *Anim. Behav.* **26**, 760–777.
- MATSUDA, K. & SANNOMIYA, N. (1980). Computer simulation of fish behaviour in relation to fishing gear. *Bull. Japan. Soc. Sci. Fish.* **46**, 689–697.
- MATSUDA, K. & SANNOMIYA, N. (1985). Computer simulation of fish behaviour in relation to a trap model. *Bull. Japan. Soc. Sci. Fish.* **51**, 33–39.
- MLOSZEWSKI, M. J. (1983). *The Behavior and Ecology of the African Buffalo*. New York: Cambridge University Press.
- MURTON, R. K., ISAACSON, A. J., & WESTWOOD, N. J. (1971). The significance of gregarious feeding behaviour and adrenal stress in a population of wood-pigeons (*Columba palumbus*). *J. Zool.* **165**, 53–84.
- OKUBO, A. (1986). Dynamical aspects of animal grouping: Swarms, schools, flocks and herds. *Adv. Biophys.* **22**, 1–4.
- OTHMER, H. G., DUNBAR, S. R. & ALT, W. (1988). Models of dispersal in biological systems. *J. Math. Biol.* **26**, 263–298.
- PARR, A. E. (1927). A contribution to the theoretical analysis of the schooling behavior of fishes. *Occas. Papers of the Bingham Oceanog. Coll.* **1**, 1–32.
- PARRISH, J. K. (1989). Re-examining the selfish herd: are central fish safer? *Anim. Behav.* **38**, 1048–1053.
- PARTRIDGE, B. C. (1982). The structure and function of fish schools. *Sci. Amer.* **246**, 114–123.
- RUBENSTEIN, D. I. (1978). On predation, competition, and the advantages of group living. *Perspectives in Ethology*. **3**, 205–231.
- RUBENSTEIN, D. I. (1994). The ecology of female social behavior in horses, zebras and asses. In: *Animal Societies: Individuals, Interactions and Organisation*. (Jarman, P. & Rossiter, A., eds), pp. 13–28. Kyoto: Kyoto University Press.
- RUBENSTEIN, D. I. & WRANGHAM, R. W. (1986) *Ecological Aspects of Social Evolution*. Princeton: Princeton University Press.
- SAKAI, S. (1973). A model for group structure and its behaviour. *Biophysics*. **13**, 82–90.
- SCOTT, J. (1988). *The Great Migration*. Emmaus: Rodale Press.
- SINCLAIR, A. R. E. (1977). *The African Buffalo, a Study of Resource Limitation of Population*. Chicago: The University of Chicago Press.
- SUZUKI, R. & SAKAI, S. (1973). Movement of a group of animals. *Biophysics* **13**, 281–292.
- UNDERWOOD, R. (1982). Vigilance behaviour in grazing African ungulates. *Behaviour* **79**, 82–107.
- WARBURTON, K. & LAZARUS, J. (1991). Tendency-distance models of social cohesion in animal groups. *J. theor. Biol.* **150**, 473–488.
- WITTENBERGER, J. F. (1981). *Animal Social Behavior*. Boston: Duxbury Press.