GROUP NAVIGATION AND THE "MANY-WRONGS PRINCIPLE" IN MODELS OF ANIMAL MOVEMENT

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Abstract. Traditional studies of animal navigation over both long and short distances have usually considered the orientation ability of the individual only, without reference to the implications of group membership. However, recent work has suggested that being in a group can significantly improve the ability of an individual to align toward and reach a target direction or point, even when all group members have limited navigational ability and there are no leaders. This effect is known as the "many-wrongs principle" since the large number of individual navigational errors across the group are suppressed by interactions and group cohesion. In this paper, we simulate the many-wrongs principle using a simple individual-based model of movement based on a biased random walk that includes group interactions. We study the ability of the group as a whole to reach a target given different levels of individual navigation error, group size, interaction radius, and environmental turbulence. In scenarios with low levels of environmental turbulence, simulation results demonstrate a navigational benefit from group membership, particularly for small group sizes. In contrast, when movement takes place in a highly turbulent environment, simulation results suggest that the best strategy is to navigate as individuals rather than as a group.

Key words: animal behavior; animal dispersal; animal grouping; animal movement; biased random walk; individual-based model; many-wrongs principle; navigation.

INTRODUCTION

The navigational ability of animals moving both as individuals and as groups can affect dispersal patterns and distances, population and evolutionary dynamics, and subsequent design and application of conservation efforts (Simons 2004). Navigational orientation cues used by long-distance migrating animals include geomagnetic and solar information, stellar rotation, geographical features and topology, and olfactory cues (e.g., Able and Able 1995, Weindler et al. 1996, Alerstam et al. 2001, Lohmann et al. 2001, Gould 2004). Cues used over shorter distances can include spatial memory and landmarks (e.g., Collett and Graham 2004, Gould 2004), chemical trails or gradients (e.g., Grunbaum 1998), visual cues, and sound (Codling et al. 2004, Simpson et al. 2004, 2005). However, navigational imprecision can arise through (1) limitations of the orientation cues themselves, and (2) sensory errors introduced through the imperfect interpretation and integration of cues by individuals (Gould 2004). Furthermore, the ability of the individual to overcome random environmental turbulence and factors such as wind or currents is critical to navigation success (e.g., migrating raptors, Thorup et al. [2003]; fish larvae settling on a reef, Codling et al. [2004]).

Recent studies of migrating birds do not reach a consensus as to how navigational accuracy is achieved; the observed accuracy of migrating flocks is greater than that predicted from individual navigational error rates (see references in Simons [2004] and Conradt and Roper [2005]). Simons (2004) correctly points out that migrating animals often occur in groups and it seems likely that some navigational benefit is gained thereby, in addition to other possible benefits such as predator avoidance (Hoare et al. 2004, Sword et al. 2005). This is known as the 'many wrongs principle,' described by Simons (2004:453) as when "...the pooling of information from many inaccurate compasses yields a single more accurate compass because individual orientation error is suppressed by group cohesion." The idea was first suggested by Bergman and Donner (1964) from observations of migrating ducks, and revisited theoretically by Hamilton (1967) and Wallraff (1978). Grunbaum (1998), uses a theoretical model to demonstrate how fish in a noisy

environment may improve their navigational ability by schooling, while Hancock et al. (2006) use a genetic algorithm to demonstrate how aggregation evolves as the optimal foraging strategy in a simulation study of the Bornean bearded pig (*Sus barbatus*). Field observations of bird movement also suggest that improved orientation and navigation ability can arise through flocking (Rabøl and Noer 1973, Tamm 1980, Guilford and Chappell 1996, Burt de Perera and Guilford 1999), while further biological examples are also given in Simons (2004) and Conradt and Roper (2005).

In this paper we concentrate on the many-wrongs principle as a mechanism for group navigation. We use individual-based simulations to demonstrate how the many wrongs principle works, and to investigate the effects of sensory error, group size, interaction radius, and environmental turbulence on the navigational performance of a group moving toward a fixed target.

METHODS

Simulation framework

We simulate a group of P individuals navigating through a two-dimensional environment toward a fixed target point. The simulation runs in discrete time: at every time step, τ, there is a "turning event" where each individual chooses a new direction of movement (as described in *Random-walk movement*, below), and then moves in this direction with a fixed speed, s. For simplicity we simulate a non-dimensionalized system where $\tau = s = 1$; distances are therefore measured in relative terms, so that our results should be considered in a qualitative sense only. A homogenous environment is assumed, although environmental turbulence and external fluctuations are implicitly modeled as part of the random-walk process used for the choice of direction at each turning event. A fixed target of radius R_T is situated at position (t_x, t_y); any individual reaching a position (x_i, y_i) such that $|(t_x, t_y) - (x_i, y_i)| < R_T$ is assumed to have successfully reached the target and is removed from the simulation. We assume that such individuals no longer contribute to group interactions (this may be overly simplistic in cases and/or species where such individuals still act as a source of orientation stimulus for other individuals; however, the effect is insignificant in the simulations presented here). Each individual is initially randomly distributed in a circular area of radius R_I centered on position (I_x, I_y), with a random direction of movement. Since we have a fixed target in space, the *target direction*, θ_0, (defined as the absolute direction from the individual's current position to the center of the target position, i.e., a global-navigation component) changes with spatial position and is different for each individual. This contrasts with models that have a fixed target direction or gradient (e.g., Grunbaum 1998, Couzin et al. 2005), although

differences between the models are only apparent when individuals are close to the target.

Random-walk movement

We use an uncorrelated and biased random-walk model for individual movement (see Okubo 1980, Benhamou 2006). At each turning event, the actual direction of movement of individual Z_i is given by

$$\theta_i = \gamma + \zeta_o \tag{1}$$

where γ is the *preferred direction* (the local direction chosen by the individual as the most desirable, taking into account both neighboring group interactions and global navigation, see *Group interactions and the preferred direction*, below) and ζ_o is a random variable [drawn from a wrapped normal distribution with angular variance σ_o^2 (Batschelet 1981, Mardia and Jupp 1999)] representing the error as each individual attempts to orientate toward its preferred direction. All angles θ_i are measured in radians, $-\pi \leq \theta_i < \pi$, where $\theta = 0$ is the positive y direction. The parameter σ_o^2 is fixed for all individuals in each simulation and can be considered as the turning ability of individuals relative to the inherent underlying environmental turbulence or stochasticity. We do not include a maximum turning angle or other correlation effects in this simple model. At each turning event, the new location of each individual is given by $(x_{n+1}, y_{n+1}) = (x_n, y_n) + s(\sin \theta_i, \cos \theta_i)$.

Group interactions and the preferred direction

Models of the individual-level interactions in animal groups are usually based on a hierarchy of simple rules (e.g., Okubo 1980, Aoki 1982, Huth and Wissel 1992, Grunbaum 1998, Couzin et al. 2002, 2005, Inada and Kawachi 2002, Parrish et al. 2002, Gregoire et al. 2003, Viscido et al. 2005) and we adopt a similar approach. We assume each individual, Z_i, has a "radius of collision avoidance," R_C; a "radius of orientation interaction," R_O; a "radius of group cohesion," R_G; and k influential neighbors N_j, where the nearest neighbor is denoted by N_j^*. Collisions between individuals are not considered and there is no limit to the number of individuals that can occupy a finite region of space (in practice the collision-avoidance rules given below act to maintain distance between individuals). Further details of the mathematical model and corresponding equations are given in the Appendix.

As shown in Fig. 1, group interactions are dependent on the position of the influential neighbors, N_j, and nearest neighbor, N_j^*, of the individual Z_i and this leads to different ways of calculating the preferred direction γ. The interaction rules are as follows: (a) *collision avoidance*: if N_j^* is within R_C then collision avoidance takes priority and γ is directly away from N_j^*; (b) *orientation*: if N_j^* is between R_C and R_O then γ is calculated from a vectorial sum of the average orienta-
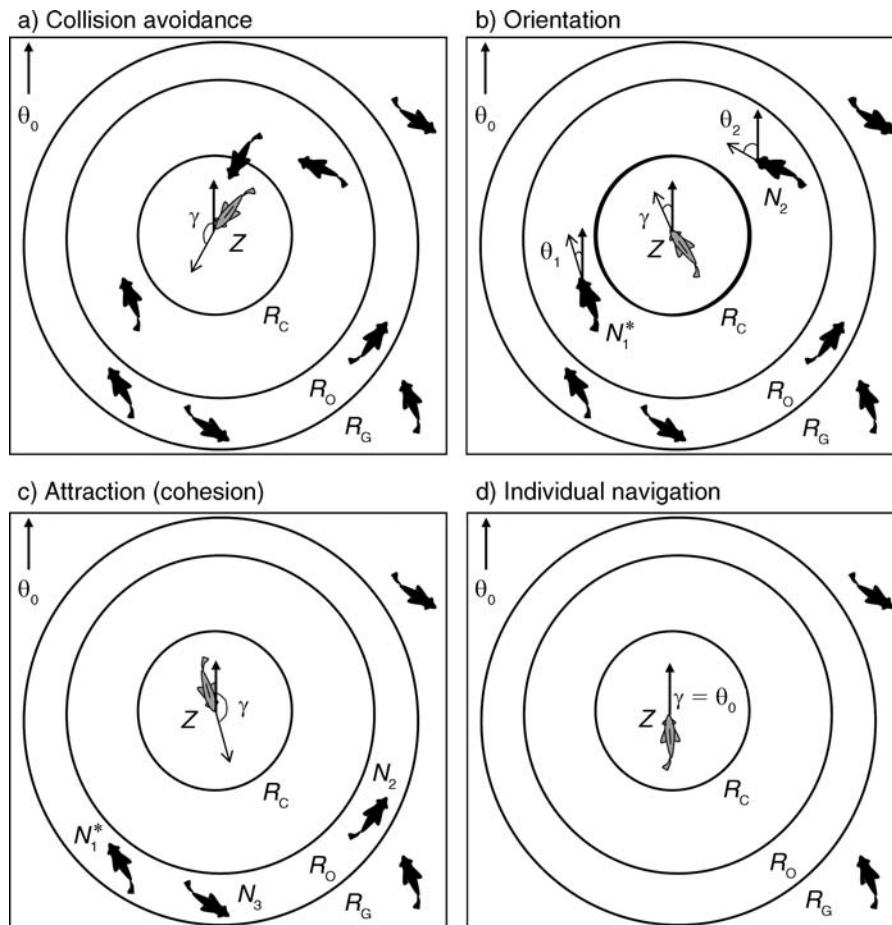
Fig. 1. Schematic illustration of the effects of group interactions on the preferred direction of an individual; Panels (a)–(d) correspond to behavioral rules (a)–(d) in *Methods: Group interactions and the preferred direction*. In all plots, Z is the individual of interest; θ_0 is the target direction (thicker arrow, pointing upward); γ is the preferred direction once all group interactions and navigation has been accounted for (thinner arrow, direction varies); R_C is the radius of collision avoidance; R_O is the radius of orientation interaction; and R_G is the radius of group cohesion. Since there are no group interactions in (d), the preferred direction is the same as the global target direction (the two arrows coincide).

tion of the influential neighbors of Z (α_a) and the perceived target direction ($\alpha_s = \theta_0 + \zeta_s$), see Eqs. A.2–A.5 in the Appendix; (c) *attraction (cohesion)*: if N_j^* is between R_O and R_G then the priority is to move toward other group members and γ points toward the center of mass of the influential neighbors, see Eq. A.7 in the Appendix; (d) *individual navigation*: if no neighbors are within R_G then γ is calculated from the navigation ability of the individual only (i.e., $\gamma = \alpha_s = \theta_0 + \zeta_s$).

Note that, similar to Eq. 1, in rules (b) and (d) the random variable ζ_s, drawn from a wrapped normal distribution with angular variance σ_s^2 (Batschelet 1980, Mardia and Jupp 1999), represents individual errors in correctly sensing the target direction (σ_s^2 is fixed at the same value for all individuals, so that all group members are equally "good" or "bad" at navigation).

In rules (b) and (c), we do not explicitly assume a maximum limit on k (the number of influential

neighbors), although recent work has shown this can have an influence on the emergent behavior of the group (Viscido et al. 2005). In practice, the behavioral rules described (particularly collision avoidance) effectively restrict the number of neighbors within the radius R_O. For simplicity, we also assume that individuals can sense all neighbors in their radii of interaction; we do not consider "blind regions" (in contrast with Couzin et al. (2002), Inada and Kawachi (2002), and others).

We consider two models of group movement in our simulations: the full model using interaction rules (a)–(d), where individuals attempt to stay as a group, avoid collisions, and balance their individual navigation with the behavior of their neighbors (*social group movement*), is compared to a null model where individuals navigate independently with no interactions except collision avoidance using rule (a) (*asocial movement*).

TABLE 1. Table of parameters used in the simulation model.

Parameter	Typical value	Range of values	Description
P	40	2–60	population size/number of individuals in group
s	1		speed of movement
τ	1		time step between turning events
(t_x, t_y)	(0, 0)		target position (center of target always set as the origin)
R_T	10		target radius (target is always a circle centered on origin)
(I_x, I_y)	(0, 300)		initial center of mass of group
R_I	20		radius of initial random distribution of individuals about center of mass
R_C	2		radius of collision avoidance
R_O	10	0–50	radius of social orientation interaction
R_G	15	0–75	radius of group cohesion interaction (in all simulations $R_G = 1.5\, R_O$)
σ_s^2	2	0–3	angular variance of random noise added to navigation component of movement (in radians)
σ_o^2	0.1	0–3	angular variance of random noise added to final orientation (in radians)

Notes: Typical values are used in the simulations unless the parameter is the test parameter, in which case the specified range of values is used. The system is nondimensionalized so that all units are on a relative scale only.

RESULTS

To measure the relative performance of the group under different scenarios and parameter values (Table 1) we compare the average time taken for the group to reach the target, n_T, averaged over 100 independent simulations. This statistic is more appropriate than comparing other group statistics such as mean direction (e.g., Couzin et al. 2005), because the target direction differs at every step for each individual.

Effect of navigation error (sensory variance)

Simulations of the null model (asocial movement) and the social group-movement model under different levels of navigational (sensory) error (σ_s^2) clearly illustrate the relative benefit of belonging to a group (Fig. 2a). When sensory error is small, then the relative navigational benefit of moving as a group is small (e.g., with $\sigma_s^2 = 0.2$, asocial $n_T = 376$; social $n_T = 342$; relative benefit ~10%). However, when individual sensory error is large, the relative benefit of moving as part of a group is much greater (e.g., with $\sigma_s^2 = 3$, asocial $n_T = 1480$; social $n_T = 533$; relative benefit ~178%). In fact, comparing the largest and smallest σ_s^2 values reveals only a relatively small decrease in performance of the social group movement model (e.g., relative decrease in performance when comparing $\sigma_s^2 = 0.2$ to $\sigma_s^2 = 3$ is ~42% for the social group model; for asocial movement this is ~294%). Moving as a group with social interactions clearly acts as a highly effective buffer to individual sensory error.

Effect of population size

From Fig. 2b, there is a striking benefit in increasing the group size, P, for small groups moving under the social group model (e.g., when $P = 2$, $n_T = 830$; when $P = 4$, $n_T = 498$; relative benefit ~ 67%). However, larger groups moving with social interactions gain little relative benefit from increasing the group size (e.g., when $P = 25$, $n_T = 440$; relative benefit compared to $P = 4$ is ~13%). In

fact the largest group sizes actually show a decrease in performance (e.g., when $P = 60$, $n_T = 458$). The same result applies to the asocial movement model where increasing the group size consistently impairs performance. This decrease in performance for both the social model (at large group sizes) and the asocial model can be attributed to the effect of the collision avoidance interactions. When there are no collision interactions and individuals move completely independently then group size is inconsequential ($n_T = 838$ for all P).

Effect of interaction radius size

From Fig. 2c, when orientation variance is low ($\sigma_o^2 \leq 0.5$) then increasing the radius of orientation interaction, R_O, ($R_G = 1.5\, R_O$ in all simulations) has a benefit to the performance of the group moving with social interactions (note that asocial movement is equivalent to $R_O = R_G = 0$). However, as with increasing the group size (Fig. 2b), there is a limited benefit to increasing the interaction radius above a certain size ($R_O \sim 10$ in our simulations). When orientation variance is high ($\sigma_o^2 \geq 1$) then a small interaction radius ($R_O = 5$) actually decreases group performance when compared to purely asocial movement ($R_O = 0$), since the cost of maintaining group cohesion outweighs the navigational benefit of group membership. In these cases, further increasing R_O results in improved performance as each individual has more neighbors and gains a greater navigational benefit from group membership.

Effect of environmental turbulence relative to turning ability (orientation variance)

Fig. 2d demonstrates that the relative benefit of moving in a social group decreases as the level of orientation variance, σ_o^2, increases (where orientation variance represents the turning ability of the individual relative to the level of environmental turbulence). For example, when $\sigma_o^2 = 0$, social $n_T = 418$, asocial $n_T = 872$, and the relative benefit of moving as a social group is
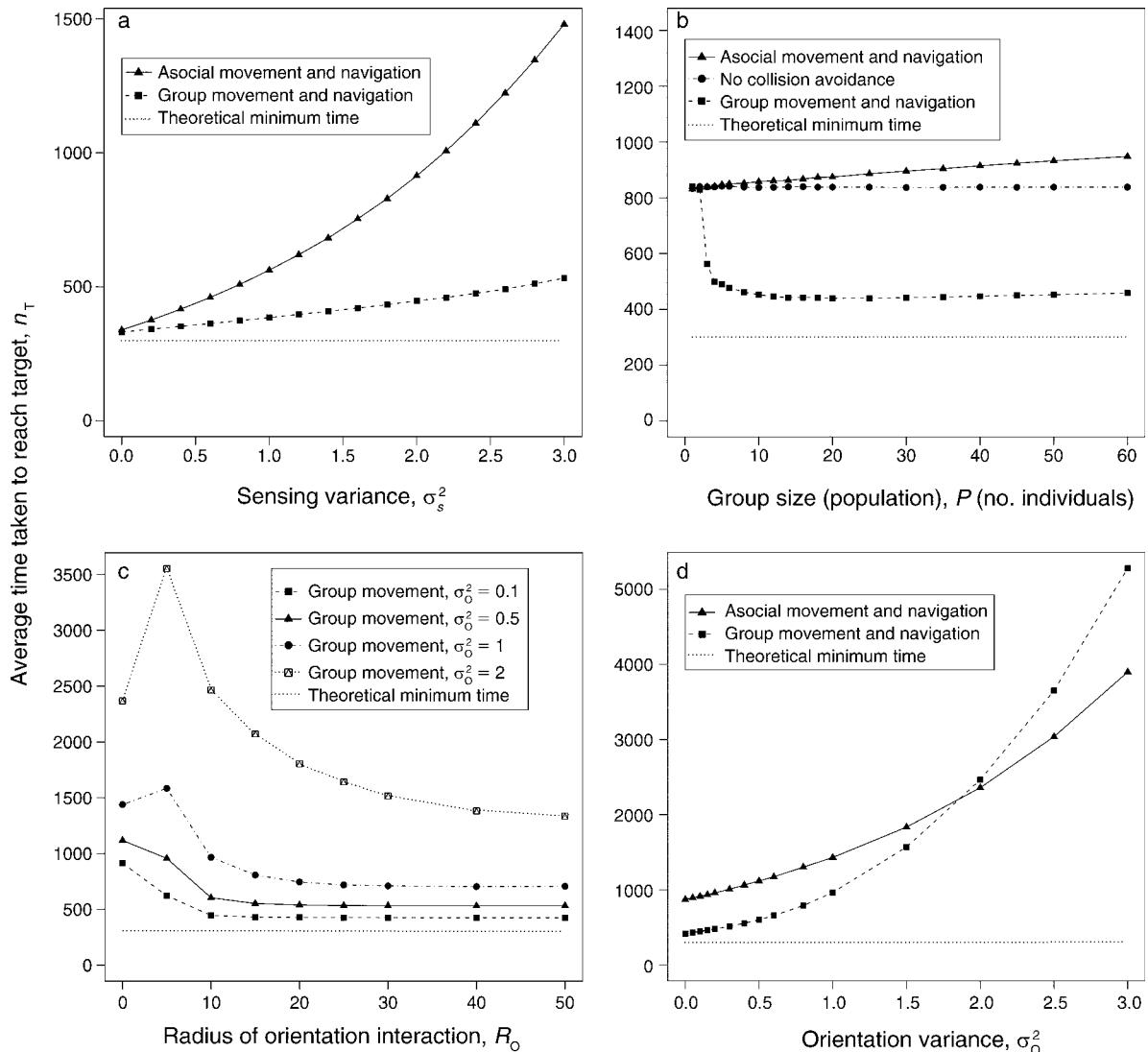
FIG. 2. Plots of average time taken, n_T, against (a) sensing variance, σ_s^2, for asocial movement and navigation (null model with collision avoidance and no other group interaction) and group movement and navigation; (b) group size (population), P, for zero interactions (no collision avoidance or other interactions), asocial movement and navigation, and social group movement and navigation; (c) radius of orientation interaction, R_O, for social group movement and navigation with a range of values of σ_o^2 (where the radius of group cohesion is given by $R_G = 1.5 R_O$); (d) orientation variance (turning ability relative to environmental turbulence), σ_O^2, for asocial movement and navigation, and for group movement and navigation. Marked points are the average of 100 iterative runs of the simulation. The theoretical minimum time of 300 arbitrary time units is marked as a dashed line.

~109%; when $\sigma_o^2 = 3$, social $n_T = 5279$, asocial $n_T = 3898$, and the relative cost of moving as a social group is ~35%. Thus when high environmental turbulence is present, our results suggest that moving completely independently (asocial movement) is a better strategy.

DISCUSSION AND CONCLUSIONS

The "many-wrongs principle" applies the "wisdom-of-crowds principle" (Surowiecki 2004) to animal movement and migration, where individual navigational errors are suppressed by group cohesion. Fig. 2 clearly

demonstrates how the many-wrongs principle can arise in an animal group moving toward a target where very simple group interactions (collision avoidance, average orientation, and attraction/cohesion) are balanced against an individual's ability to navigate to the target direction. Our simulation results confirm earlier theoretical results by Grunbaum (1998), who used a different model based on individual turning rates. Simons (2004) predicted that the many-wrongs principle (see also Gould 2004, Conradt and Roper 2005) would result in better navigational performance in larger groups (Rabøl

and Noer 1973, Tamm 1980, Guilford and Chappell 1996, Burt de Perera and Guilford 1999) and also that a threshold group size is likely to be reached. Fig. 2b confirms these predictions. It is also clear from our results that group repulsion mechanisms such as collision avoidance can result in groups larger than the optimum size having an impaired navigational performance, although it should be stressed that our simulation does not include other possible selective pressures acting on group size such as predator avoidance (Inada and Kawachi 2002, Hoare et al. 2004, Sword et al. 2005), foraging, or mating (Okubo 1980).

As discussed in Simons (2004) and Conradt and Roper (2005), it is probably too simplistic to assume that group-level dispersion and navigational accuracy can be predicted from individual navigational error rates. In fact, our results in Fig. 2a show that the relative benefit of moving as a social group (when compared to asocial movement) increases significantly as individual sensory error increases. An important result from our simulations that is not predicted by Gould (2004), Simons (2004), Conradt and Roper (2005), and others, is that the relative benefit of moving as a social group decreases as the orientation variance increases (Fig. 2d), so that in highly turbulent environments a better strategy is to move and navigate independently. Group movement models generally assume only a small amount of orientation variance [e.g., Couzin et al. (2002, 2005) assume $\sigma_o^2 \leq 0.2$ radians] so it is perhaps not surprising that this result has not been highlighted before. This apparently counter-intuitive result for high turbulence is an emergent property of the system; it was not predicted by consideration of the simple individual-based model, but a cost–benefit argument provides an explanation. When turbulence is high, group cohesion is impaired. This means that individuals attempting to move as a group do not gain the benefit of regular navigational corrections from a coherent set of neighbors (individual orientation error is not suppressed by the group), but rather experience a series of random interactions with other essentially isolated individuals. In effect, in high turbulence these social individuals waste navigational effort in attempting to stay as a group. In contrast, asocial individuals avoid this cost and navigate toward the target without interference (although Fig. 2d illustrates that such individuals are still relatively ineffective in comparison to social group movement in a nonturbulent environment).

An alternative to the many-wrongs principle in group navigation is the "informed-leader" model (Couzin et al. 2005), where a fixed proportion of group members are either uninformed (zero navigational knowledge or ability) or informed (high navigational knowledge or ability). For example, some social insects are known to have informed scouts that lead groups of unskilled workers to new nest sites or food sources (e.g., Seely

1995). Most real animal groups are likely to use a combination of mechanisms such as many wrongs and informed leader to move, navigate, and interact at the individual and group level (Conradt and Roper 2005), and our results should only be considered in a qualitative sense and relative to the various assumptions about individual behavior and group interaction that we have made. For example, when calculating the preferred direction in interaction rule (b) we assume equal weighting between an individual's sensing of the target direction and the average direction moved by its neighbors (see Eq. A.3 in the Appendix). This is a sensible (albeit arbitrary) initial weighting to use, but we have also simulated other weightings: in general, results were qualitatively similar to those in Fig. 2. However, when the weighting given to individual sensing becomes too low (approximately <20% for simulations with the typical parameters in Table 1), the group tends to aggregate and has a very low absolute velocity toward the target (compared to asocial movement), a result also noted by Viscido et al. (2005).

Similarly, we have assumed all individuals in the population have the same nondimensionalized parameter values and interaction rules governing their behavior. Our typical parameter values (Table 1) and the interaction rules used are similar to those in other group movement models (e.g., Inada and Kawachi 2002, Parrish et al. 2002, Couzin et al. 2002, 2005), but a more complex simulation model would allow each individual to use different behaviors or strategies when interacting as part of the group. A game-theoretic or evolutionary approach (e.g., Hancock et al. 2006) could then be developed to explore navigation success (at either a group or individual level) and search for successful strategies, but this is beyond the scope of the current paper.

As suggested by Simons (2004), experimental observations of animal behavior can be used to test the general ideas behind the many-wrongs principle (including the results generated from our theoretical model). However, this would require careful experimental design due to the relative difficulty in distinguishing between group interaction and orientation mechanisms in experiments—the same qualitative observed properties can emerge from very different theoretical models (e.g., there is little difference between results from the asocial and social-group models in both Fig. 2a [with low σ_s^2] and Fig. 2d [when $\sigma_o^2 = 2$], even though the underlying models are very different), see Parrish (2002) and Benhamou (2006). In such cases, a variety of group metrics are likely to be necessary to distinguish between possible different interaction mechanisms (Viscido et al. 2005).

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APPENDIX

A presentation of the mathematical model of group movement and navigation (*Ecological Archives* E088-111-A1).