Balancing direct and indirect sources of navigational information in a leaderless model of collective animal movement

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Abstract

Navigation is an important movement process that enables individuals and groups of animals to find targets in space at different spatio-temporal scales. Earlier studies have shown how being in a group can confer navigational advantages to individuals, either through following more experienced leaders or through the pooling of many inaccurate compasses, a process known as the 'many wrongs principle'. However, the exact mechanisms for how information is transferred and used within the group in order to improve both individual- and group-level navigational performance are not fully understood. Here we explore the relative weighting that should be given to different sources of navigational information by an individual within a navigating group at each step of the movement process. Specifically, we consider a direct goal-oriented source of navigational information such as the individual's own imperfect knowledge of the target (a 'noisy compass') alongside two indirect sources of navigational information: the previous movement directions of neighbours in the group (social information) and, for the first time in this context, the previous movement direction of the individual (persistence). We assume all individuals are equal in their abilities and that direct navigational information is prone to higher errors than indirect information. Using computer simulations, we show that in such situations giving a high weighting to either type of indirect navigational information can serve to significantly improve the navigation success of groups. Crucially, we also show that if the quality of social information is reduced, e.g. by an individual's limited cognitive abilities, the best navigational strategy for groups assigns a considerable weighting to persistence, a behaviour that is neither social, nor directly aimed at navigating.

Keywords: Animal Movement, Collective Behaviour, Many Wrongs Principle, Navigation, Persistence

1. Introduction

Navigation towards a target in space is an important ecological process for many animals. The navigation process can range from short time-scale processes such as finding localised food patches in foraging (Bell, 1991), to much larger spatial and temporal scales such as in seasonal migrations (Bergman & Donner, 1964). At the individual level, navigation processes can be classified as either 'allothetic' or 'idiothetic' (Whishaw & Brooks, 1999). An alliothetic navigation process uses the relationships between one or more external cues (which could be visual, auditory, olfactory, or other cues such as geo-magnetic forces) and geometrical calculations about the observed landscape to locate targets in space (Whishaw & Brooks, 1999). In contrast, an idiothetic navigation process relies on cues generated by internal movement processes (proprioceptive cues, cues from optic, auditory, and olfactory flow, or efference copy of motor commands) and subsequent path integration ('dead reckoning') to locate a target in space given the known starting location (Whishaw & Brooks, 1999). In this context, an alliothetic process can be considered to use 'direct' (external) goal-oriented navigational information about the target, while an idiothetic process relies on 'indirect' (internal)

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navigational information.

Alliothetic and idiothetic navigation processes for an individual animal can be modelled using standard random walk theory (Codling et al., 2008). Specifically, an alliothetic movement process is equivalent to a biased random walk (BRW), where the animal directly reorientates towards a fixed target in space (or a target direction, which is equivalent to a target 'point at infinity') at each step of the random walk process (Benhamou, 2004, 2006; Codling et al., 2008, 2010). An idiothetic movement process is equivalent to a correlated random walk (CRW) with an initial facing towards the target direction (Cheung et al., 2007). In a CRW the animal has a tendency to continue moving in the same direction as the previous step, and hence exhibits 'forward persistence' (Kareiva & Shigesada, 1983; Bovet & Benhamou, 1988; Benhamou, 2004; Codling et al., 2008). It is also possible to combine the external navigation (alliothetic) and forward persistence (idiothetic) processes together into a single random walk model known as a biased and correlated random walk (BCRW). In such cases the external navigation and forward persistence components are usually combined in a simple weighted vectorial sum (Benhamou & Bovet, 1992; Benhamou, 2004; Codling et al., 2008), but more complicated models are also possible (Codling & Hill, 2005a).

It can easily be shown using a mathematical argument that relying on idiothetic cues alone is a poor navigation strategy in the long term, and that an external cue is necessary for long-term navigation success (Cheung et al., 2007, 2008). This is because without reference to any external cues, small errors at each time step in the CRW process are not corrected and propagate forwards in time such that, in the long-term, the net expected movement towards the target in a single time step will tend towards zero (Kareiva & Shigesada, 1983; Bovet & Benhamou, 1988; Benhamou, 2004, 2006; Codling et al., 2008). In fact it is easy to show that the expected long term cumulative displacement towards the target direction in a CRW that is initially orientated towards the target (equivalent to a classic 'dead reckoning' task) is always bounded and finite unless there is zero error in the movement process (Cheung et al., 2007, 2008). In contrast, in a BRW there is always an external cue available to the random walker (albeit with possible error) and hence the expected net displacement towards the target direction increases linearly with time (Benhamou, 2004, 2006; Codling et al., 2008, 2010). Given this fact, it is perhaps surprising that Benhamou & Bovet (1992) were able to show that when combining both idiothetic path-integration and alliothetic external navigation in a vector-weighted BCRW, the most efficient navigation strategy is to give a low (c10%) weighting to the alliothetic navigation component. It should be noted however, that this result is based on the assumption that the only source of error in the BCRW is in the external alliothetic cue (the 'noisy compass') and there is no error assumed on the idiothetic path-integration element of the movement process.

Many animal species move and make decisions as part of a collective group (Krause & Ruxton, 2002). Group membership is known to confer advantages to individuals such as protection from predators, sharing of resources, mate availability, and fulfilling social need (Krause & Ruxton, 2002). In addition, previous theoretical studies have shown how navigating as part of a social group can improve navigation performance. For example, Grünbaum (1998) developed an individual-based model for group-level taxis in a noisy environment based on individuals modifying their turning rates in response to the movements of their neighbours. Couzin et al. (2005) demonstrated a 'leader-follower' model for navigation where informed individuals with high levels of navigational knowledge can successfully lead a group where the majority of individuals are uninformed. In general, group navigation arises when individuals in the group directly or indirectly share navigational information. The exact mechanisms for how information is most effectively transferred and used within the group are not well understood, although recent empirical and theoretical work has given some insights into this problem. For example, Berdahl et al. (2013) showed how group taxis can occur even without direct navigation behaviour at the individual level, while Couzin et al. (2011) demonstrated how uninformed individuals within the group can help a consensus to form when some individuals have conflicting target directions. Additionally, Ioannou et al. (2015) found that informed leaders in a school of golden shiners (*Notemigonus crysoleucas*) need to carefully balance goal-oriented (navigation) cues and social (group cohesion) cues in order to maintain a cohesive group that confers a navigational benefit to all individuals.

The composition of a navigating animal group can range from a majority of naive or uninformed individuals directly following a few 'leaders' who have relatively strong navigational knowledge (e.g. Couzin et al., 2005; Mirabet et al., 2008), through to a group where all individuals are effectively homogeneous (there are no leaders) and are equally well (or poorly) informed about the location of the target. It is this 'leaderless' case that we investigate here. Simons (2004) termed this strategy the 'many wrongs principle' where group navigation performance is improved through 'the pooling of many inaccurate compasses' and group cohesion acts to suppress navigation errors. The many wrongs principle has been confirmed empirically in both birds and humans (Bergman & Donner, 1964; Dell'Ariccia et al., 2008; Faria et al., 2009). In reality, it is likely that many animal groups will not be entirely homogeneous (as the simplest interpretation of the many wrongs principle assumes) and individuals may have different levels of experience and motivation resulting in leaders emerging within the group. In such cases the many wrongs principle may still act as an effective navigation method at the group level. Nevertheless, there are certain animal groups that do fit the basic assumption of group homogeneity, an example being cohorts of recruiting juvenile coral reef fish larvae that have been hypothesised to navigate in groups and use the many wrongs principle to reach a target reef to settle upon (Codling et al., 2004; Simpson et al., 2013).

The many wrongs principle has been explored theoretically using computational models. For example, Hancock et al. (2006) considered a localised search problem and explored how the many wrongs principle might evolve in a population of foraging mammals. Guttal & Couzin (2010) and Torney et al. (2010) used simulations to conceptually demonstrate how both the 'leader-follower' and the 'many-wrongs' model for group navigation can evolve in animal populations where individual fitness is obtained by balancing navigation success against costs of investment into navigation or social abilities. Bode et al. (2012a) illustrated how leaderless group navigation can be improved through an internal social network structure within the group. Codling et al. (2007) demonstrated a basic mechanism for information transfer within a group navigating using the many wrongs principle but assumed an equal weighting between individuals using their individual (noisy) compass and copying the directions of movement of their nearest neighbours at each step of the movement process. Codling & Bode (2014) generalised this model and explored the optimal weighting given to the (direct) navigational information provided by the individual compass and the (indirect) information provided by copying the movements of group neighbours. In particular, they demonstrated the somewhat counter-intuitive result that the best navigation performance is obtained by giving only a low ($c10-20\%$) weighting to direct navigational cues. This can be compared to the finding of Benhamou & Bovet (1992) who showed that alliothetic cues should be given a similar weighting when balanced with idiothetic cues (persistence) in a BCRW model of navigation for individual animal movement. However, Codling & Bode (2014) did not directly include persistence in their group navigation model.

It is possible to create forward persistence in a movement path by restricting the turns of individuals at each step using a maximimum turning angle (sometimes termed *rotational* or *directional inertia*). At the most basic level, this process is essentially a variation of a CRW where the introduction of a maximum turning angle means one is effectively drawing turns from a truncated (uniform) circular distribution, rather than a unimodal continuous circular distribution (such as the von Mises or wrapped normal) as is typically used in a standard CRW (Codling et al., 2008). In the context of collective animal group movement, a maximum turning angle has typically only been included for purposes of biological realism, so that individuals do not turn unrealistically quickly. Couzin et al. (2002) considered a range of maximum turning angles (between 10 and 100 degrees per time step) but only in the context of exploring the form and structure of a non-navigating animal group. Couzin et al. (2005) and Mirabet et al. (2008) both used a maximum turning angle in the context of an 'informed leader' navigation problem, but neither study explored how the maximum turning angle affected navigational efficiency, or considered the role of forward persistence as an indirect navigational cue that could be balanced against other cues.

In this study we explore the relative weighting that should be given to different sources of navigational information by an individual within a homogeneous navigating animal group at each step of the movement process in order to achieve the maximum group-level navigational efficiency. Specifically, we consider a direct (alliothetic) source of navigational information such as the individual's own imperfect knowledge of the target (a 'noisy compass') alongside two indirect sources of navigational information: the movement directions of neighbours in the group (social information) and the previous movement direction of the individual (persistence). In a similar manner to Benhamou & Bovet (1992) and Codling & Bode (2014), we assume that the error in the noisy compass is the main source of directional uncertainty. Introducing individual persistence (an idiothetic cue and a non-social behaviour) within the group navigation context is the key novelty of this work.

2. Methods

We use a discrete time individual-based group movement model based closely on the models given in Codling et al. (2007) and Codling & Bode (2014), which are themselves modified versions of more general collective movement models (Aoki, 1982; Couzin et al., 2002; Gregoire et al., 2003; Couzin et al., 2005; Viscido et al., 2005). In the model, movement is governed by a hierarchy of behavioural rules applied at the individual level. We are specifically interested in the case where there are no 'leaders' in the group and all individuals are equally good (or poor) at navigation. Time steps and distances in the simulations are given in arbitrary units, have no physical meaning, and are used for comparative purposes only. Simulations were coded in the Java programming language (https://www.java.com/).

2.1. Simulation framework and model structure

At the start of the simulation individuals in our navigating group are placed uniformly at random within a square of side length 100 units centred at $(x, y) = (0, 0)$. The initial movement direction of individuals is randomly chosen from a uniform circular distribution. The virtual two-dimensional environment is assumed to be homogeneous and empty except for a single target site situated at $(x_T, y_T) = (0, 1000)$. We assume that the group are required to navigate towards this target while also (in general) maintaining group cohesion. Based on the findings of Codling & Bode (2014), we assume a group size of $N = 40$ individuals. Codling & Bode (2014) showed that, in this type of virtual navigation experiment, the overall size of the group has little effect once a minimum viable group size is reached (e.g. $N > 10$). Instead, it is the number of influential neighbours (k) that individuals interact with when copying directional movements that are important (Codling & Bode, 2014).

At each unit time step every individual in the group simultaneously updates its position and movement direction according to the hierarchical rules of movement as described in Section 2.2; the exact movement behaviour of each individual is determined by the distance of the nearest influential neighbours in the previous time step. For simplicity, the group is assumed to be homogeneous and all individuals use the same movement parameters and follow the same hierarchical rules. Hence, in contrast to studies where one or more of the group act as 'leaders' (Couzin et al., 2002, 2005; Conradt et al., 2009), we assume the group is 'leaderless' and all individuals have the same navigational knowledge, motivation and experience (as in Codling et al., 2007; Codling & Bode, 2014). Each individual moves with an *average* speed of 1 distance unit per time step; the exact distance moved is subject to the addition of a random noise term and hence the realised speed at each time step can be slightly higher or lower than 1, see Section 2.3).

Each simulation is run for 500 time steps. This implies that the theoretical maximum distance that the group can reach *on average* is 500 distance units away from the centre of the target (this is on average since fluctuations in speed can be introduced through the additive random noise term mentioned previously). We do not model movement within the local vicinity of the target and hence concentrate on the large scale navigation stage of the movement process. Similar to Codling & Bode (2014), we define the *group-level* navigational efficiency as

$$E = \frac{1000 - d_T}{500}, \tag{1}$$

where d_T is the distance from the centre of mass of the group to the centre of the target after 500 time steps of the simulation. Using this definition the group navigational efficiency, E, ranges in value from 1 (movement in a straight line directly towards the target), through 0 (no net movement towards or away from the target), to -1 (movement in a straight line directly away from the target). Note that because of the random noise term added to the movement of each individual (Section 2.3), it is theoretically possible for E to lie slightly outside the range $(-1, 1)$ but in practice we found this did not occur in our simulations.

An alternative *individual-based* definition of navigational efficiency is also possible. In this case, the distance between the final position of each individual and the target is calculated, and these values are then averaged over the group. In the case of navigation towards a target direction (equivalent to the target being a 'point at infinity') the two definitions are exactly equivalent. However, close to a fixed target the two definitions can give different results, particularly if individuals are not cohesive and are widely dispersed about the centre of mass of the group. In general, because our simulations are based on the initial navigation stage where the target is far away, the two defintions give very similar results (for mean navigational efficiency) and hence we present results for the group-level efficiency only. However, it should be noted that the variance in navigational efficiency is obviously higher when considering the individual-based definition.

As we are interested in group-level navigation, it is important to also consider the relative cohesiveness of the group during the navigation process. To determine cohesiveness we consider the relative dispersal (spread) of individuals within the group in both the x (non-navigation) and y (navigation) directions. We consider dispersal in each direction separately as it is not immediately obvious whether the dispersal within the group will be symmetric (see for example Codling et al., 2010). The relative dispersal within the group is measured by calculating the mean squared displacement (MSD) about the group centre for each individual and averaging over the group:

$$MSD_x = \frac{1}{N}\left(\sum_{i=1}^{N}(x_i - \bar{x})^2\right),$$

$$MSD_y = \frac{1}{N}\left(\sum_{i=1}^{N}(y_i - \bar{y})^2\right), \tag{2}$$

where $N = 40$, and (x_i, y_i) and $(\bar{x}, \bar{y})$ are respectively the positions of the i-th individual and the centre of mass of the group at the end of 500 simulation time-steps.

A description of the parameters and the typical values used in the simulations are given in Table 1. For each simulation scenario and parameter combination 100 replicate simulations were completed and the mean and variance in group navigation efficiency calculated.

2.2. *Hierarchical individual rules of movement*

Similar to standard models in the literature (e.g. Aoki, 1982; Couzin et al., 2002; Gregoire et al., 2003; Couzin et al., 2005; Viscido et al., 2005; Codling et al., 2007; Guttal & Couzin, 2010) we assume that individual-level interactions and movement decisions are based on a hierarchy of behavioural rules based on the distance to the nearest influential neighbours. We assume each individual in the group has a radius of collision avoidance, R_C, and a radius of orientation interaction, R_O, which are assumed to be the same for all individuals in the group (Table 1). At any given time step the movement behaviour of individual i at position (x_i, y_i) is dependent on the distance, d, between itself and its *nearest* neighbour j at position (x_j, y_j), where $d = \|(x_i - x_j, y_i - y_j)\|$.

2.2.1. *Collision avoidance*

If $d < R_C$, then collision avoidance is assumed to take priority and hence individual i will attempt to move directly away from individual j. The preferred movement direction is then given by the unit vector

$$\mathbf{r} = \frac{(x_i - x_j, y_i - y_j)}{\|(x_i - x_j, y_i - y_j)\|}. \tag{3}$$

Note that no noise or error term is added to the collision avoidance direction vector at this stage.

2.2.2. *Navigation, persistence, and neighbour-copying*

If $R_C < d < R_O$, then navigation takes priority and individual i will attempt to navigate towards the target based on a weighted vectorial sum of i) the movement directions of its k nearest neighbours,

Parameter	Description	Value(s) or range
N	Total group size	40
k	Number of influential neighbours	$1, 3, 5, 7, 15$
R_C	Radius of collision avoidance	2
R_O	Radius of orientation / navigation	15
w_{nav}	Weighting given to individual navigation	$(0, 1)$
w_{soc}	Weighting given to copying neighbours' directions	$(0, 1)$
w_{per}	Weighting given to individual persistence	$(0, 1)$
ϵ	Standard deviation of individual navigation error	$0, 0.1, 0.2, 0.5, 1, 1.5, 2, 3, 5, 10$
ξ	Standard deviation of added environmental movement noise / error	0.1

Table 1: Parameter values used in the simulations of group navigation. Simulations were run across 201 equally spaced values of w_{nav} and w_{soc} between 0 and 1 (where $w_{per} = 1 - w_{nav} - w_{soc}$). Five values for k and ten values for ϵ were also considered. All other parameter values were fixed for all simulations at the values shown.

ii) a target vector based on its own navigational knowledge, and iii) a persistence vector given by the direction of movement of the individual in the previous time step. The preferred movement direction is then given by the unit vector

$$\mathbf{r} = \frac{w_{nav}\mathbf{r}_{nav} + w_{soc}\mathbf{r}_{soc} + w_{per}\mathbf{r}_{per}}{\|w_{nav}\mathbf{r}_{nav} + w_{soc}\mathbf{r}_{soc} + w_{per}\mathbf{r}_{per}\|}, \tag{4}$$

where w_{nav} is the weighting given to individual navigation, w_{soc} is the weighting given to the movement directions of the k nearest neighbours, w_{per} is the weighting given to the previous direction of movement of the individual, and $w_{nav} + w_{soc} + w_{per} = 1$. Note that this model can be considered as a more generalised version of the weighted vectorial sum used within both Benhamou & Bovet (1992) and Codling & Bode (2014).

The direction vector corresponding to individual navigation is given by

$$\mathbf{r}_{nav} = \frac{(x_T - x_i + e_x, y_T - y_i + e_y)}{\|(x_T - x_i + e_x, y_T - y_i + e_y)\|}, \tag{5}$$

where (x_T, y_T) is the centre of the navigation target, and $e_x \sim N(0, \epsilon^2)$ and $e_y \sim N(0, \epsilon^2)$ are normally distributed error terms. Note that the form of this 'noisy compass' is similar to Codling & Bode (2014) but we have directly included the noise term before normalising the direction vector. Hence in this model large levels of navigational noise / error will have less of a disruptive effect than in Codling & Bode (2014), who applied the noise term after the normalisation of the direction vector.

The direction vector corresponding to copying the movement directions of neighbours is given by

$$\mathbf{r}_{soc} = \frac{\sum_{j=1}^{k} \mathbf{v}_j}{\|\sum_{j=1}^{k} \mathbf{v}_j\|}, \tag{6}$$

where $\mathbf{v}_j$ gives the movement directions of the k nearest neighbours to individual i in the previous time step. In equation (6) we assume for simplicity and consistency across simulations that there is no restriction on the distance to the nearest neighbour in order for it to influence the movement of individual i. Hence, when copying the movement directions of neighbours we assume topological rather than metric interactions (Ballerini et al., 2008). Note that no noise or error term is added to the $\mathbf{r}_{soc}$ vector at this stage, so we assume that individuals are able to determine the average of the movement directions of their k nearest neighbours perfectly. However, we do vary the quality of this social information in a biologically relevant way by adjusting the number of nearest neighbours, k, that individuals respond to. Low values of k imply individuals only have imperfect information of the movement of the group as a whole, while high values of k imply more complete information about the group movement. We have previously argued that k should not be interpreted literally (Codling & Bode, 2014), but that it instead provides a simple way for implementing different levels of social information about the movement of the group which could be linked to the cognitive abilities of each individual.

The direction vector corresponding to persistence, $\mathbf{r}_{per}$, is simply given by the final movement direction of individual i in the previous time step. No noise or error term is added directly to the $\mathbf{r}_{per}$ vector at this stage. Note however that an individual moving purely through persistence ($w_{nav} = w_{soc} = 0$) will still have errors in their movement due to the addition of a final external (non-navigational) movement error term (see below).

Note that the form of Equation (4) means that we are able to directly control the relative balance between forward persistence (directional inertia) and other navigational cues in order to explore the relative efficiency of different combinations of cue weightings. In principle, one would obtain qualitatively similar results by using a maximum turning angle at each step (Couzin et al., 2002, 2005; Mirabet et al., 2008) to constrain turns and introduce some level of forward persistence to the movement. At the extremes, the two approaches of modelling forward persistence are exactly equivalent: a maximum turning angle of 0 rads directly corresponds to $w_{per} = 1$ and $w_{nav} = w_{soc} = 0$ (straight line movement); a maximum turning angle of 2π rads directly corresponds to $w_{per} = 0$ (no restriction on turns, but no additional forward persistence contribution to each move). However, for intermediate values it is not clear how the maximum turning angle would relate to w_{per} (and hence to w_{nav} and w_{soc}), making it difficult to directly compare navigational efficiency across different combinations of weightings within the study and with results elsewhere (Benhamou & Bovet, 1992; Codling & Bode, 2014).

2.2.3. Group cohesion

If $d > R_O$, then group cohesion takes priority and individual i will attempt to rejoin the group by moving directly towards the centre of mass of the group. The preferred movement direction is given by the unit vector

$$\mathbf{r} = \frac{(x_C - x_i, y_C - y_i)}{\|(x_C - x_i, y_C - y_i)\|}, \tag{7}$$

where $(x_C, y_C) = \frac{1}{N}\sum_{j=1}^{N}(x_j, y_j)$ is the centre of mass of the group at the end of the previous time step (calculated including the position of individual i for consistency across simulations). Note that no noise or error term is added to the group cohesion direction vector at this stage.

2.3. Implementing movement

As with Codling & Bode (2014) (and in contrast to Codling et al. (2007)) we do not include an additional radius of cohesion outside which individuals are assumed to have left the group (and as such would navigate and move independently). In addition we have not assumed any 'blind regions' (e.g. Couzin et al., 2005). Essentially we are assuming that all individuals stay within sight of the rest of the group at all times. We use values of $R_C = 2$ and $R_O = 15$ (Table 1) that are similar to earlier studies (Codling et al., 2007; Codling & Bode, 2014), although this choice is arbitrary. As with Codling & Bode (2014), our aim is to use values for the interaction radii that ensure globally polarised and cohesive group movement in the absence of navigation.

We assume that individuals are subject to an additional noise/error term (corresponding to short-scale information processing or movement errors, or environmental turbulence) when they attempt to move in their chosen preferred direction. If, after the hierarchical interaction rules have been applied, the preferred movement direction is $\mathbf{r}$ (corresponding to either Eqs. (3), (4) or (7), depending on the nearest neighbour distance) then we calculate the actual movement direction implemented as follows

$$\mathbf{v}_i = \mathbf{r} + (m_x, m_y), \tag{8}$$

where $m_x \sim N(0, \xi^2)$ and $m_y \sim N(0, \xi^2)$ are normally distributed error terms. The standard deviation, $\xi = 0.1$, is fixed and represents the (low) level of error present due to short time-scale information processing errors or environmental turbulence (Codling et al., 2007). Finally, the new spatial position of individual i is updated to be $(x_i', y_i') = (x_i, y_i) + \mathbf{v}_i$ (and hence the speed of movement is variable due to the introduced movement error/noise).

3. Results

Figure 1 illustrates how the mean group navigational efficiency relates to the weighting given

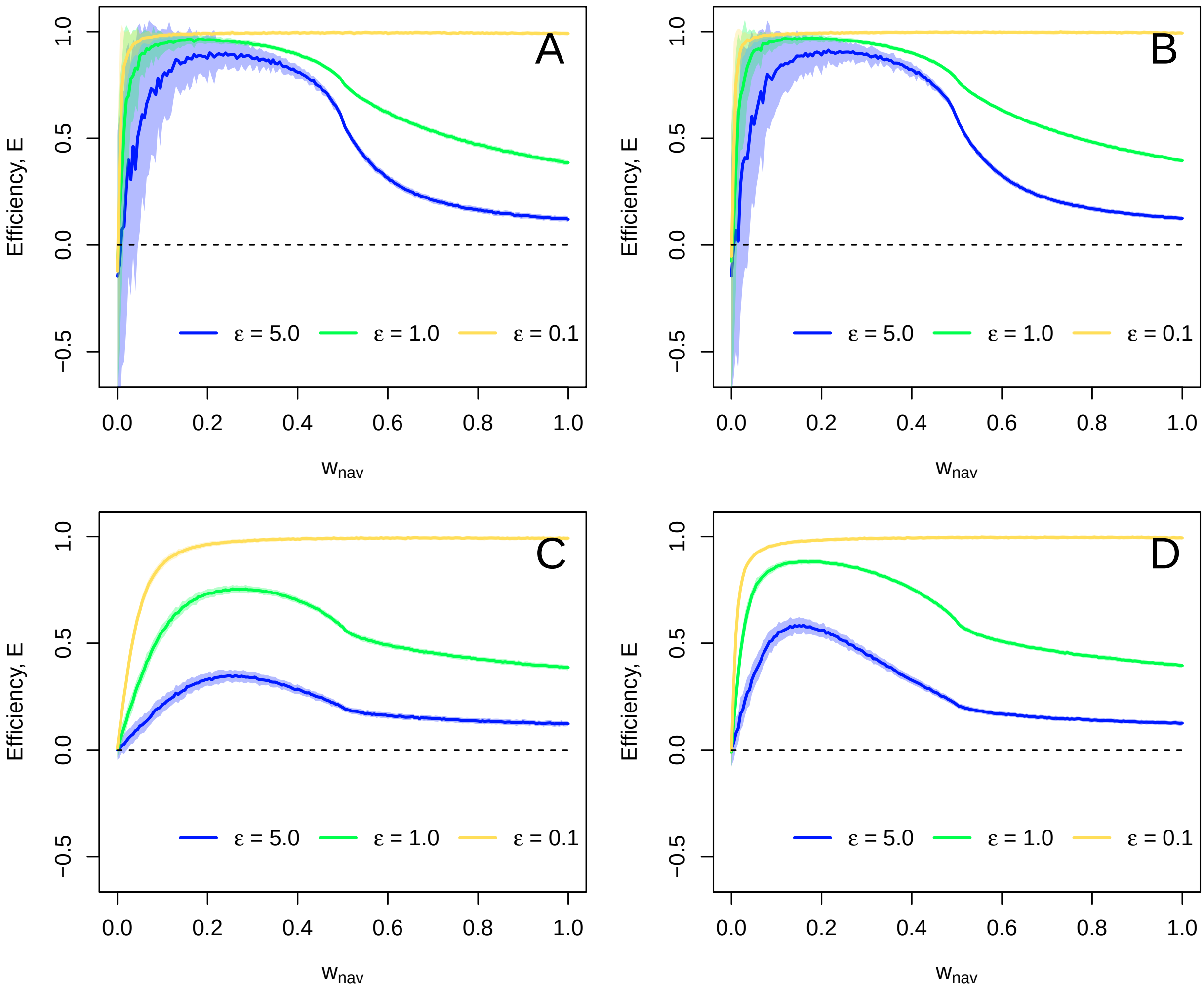

Figure 1: Group-level navigational efficiency against weighting towards individual navigation, w_{nav} for different levels of navigational noise/error, ϵ, after 500 simulation time-steps. In A and B, we set $w_{soc} + w_{nav} = 1$ and thus $w_{per} = 0$ (as in Codling & Bode, 2014). In C and D, we set $w_{nav} + w_{per} = 1$ and thus $w_{soc} = 0$. Individuals in A and C maintain group cohesion (attraction) and avoid collisions (repulsion), while individuals in B copy group neighbours but do not maintain group cohesion or avoid collisions, and individuals in D move entirely independently from each other (no copying of neighbours, cohesion or collision avoidance, as in Benhamou & Bovet, 1992). The mean group level navigation efficiency over 100 replicate simulations is given as solid lines, while the shaded regions show one standard deviation above and below the mean. The number of influential neighbours is set to seven ($k = 7$). Results for other non-trivial values of k are qualitatively very similar and are not shown here. Simulations were performed for 201 equally spaced values of w_{nav} between 0 and 1.

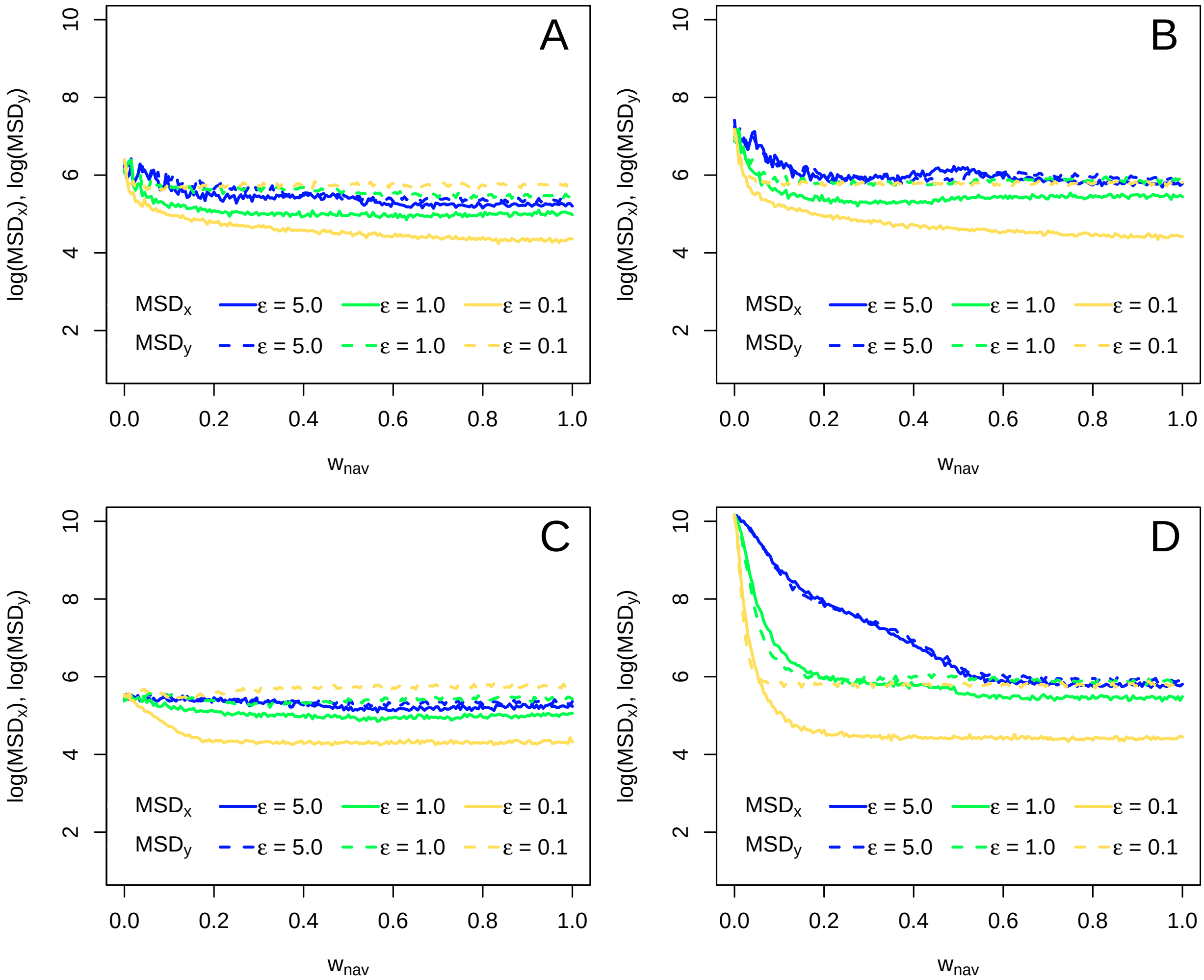

Figure 2: Log of mean-squared displacement (log(MSD)) about the group centre of mass in the x (non-navigation, solid lines) and y (navigation, dashed lines) directions after 500 simulation time-steps. The MSD gives a measure of the level of cohesion of the group with lower values corresponding to higher cohesion. As with Figure 1, the labels A and B refer to simulations with $w_{soc} + w_{nav} = 1$, while in C and D, $w_{nav} + w_{per} = 1$. Similarly, A and C include group cohesion and collision avoidance rules, while B and D do not include these rules. The number of influential neighbours is set to seven ($k = 7$) and simulations were performed for 201 equally spaced values of w_{nav} between 0 and 1.

to individual navigation, w_{nav}. In Figure 1:A, $w_{per} = 0$, so that there is no weighting given to persistence (and hence $w_{soc} + w_{nav} = 1$). This is essentially the same scenario as Codling & Bode (2014) and qualitatively similar results are obtained. The highest navigational efficiency is achieved when using a low weighting for individual navigation ($w_{nav} \approx 0.2$ for all levels of navigation uncertainty. The value of $w_{nav} \approx 0.2$ is slightly higher than that found in Codling & Bode (2014) (who observed $w_{nav} \approx 0.1$ to give the highest navigational efficiency), but this can be explained by the fact that, in contrast to Codling & Bode (2014), we normalise the navigational error term in Equation (5) which results in the additive error term having less of an impact on navigation performance. Figure 1:B also has $w_{per} = 0$ and shows very similar results, but in this case we do not include the collision avoidance and group cohesion social interaction rules. The collision avoidance and group cohesion rules can be considered as potential sources of navigation error (since the directions specified by these rules may not be towards the target). However, comparing Figure 1:A and Figure 1:B, it is clear that there is very little difference in terms of group-level navigation performance between the two cases. This result could be interpreted as the collision avoidance and group cohesion rules having little or no effect. For the collision avoidance rule this may be true, but with the group cohesion rule there is also the possiblity that group cohesion gives the group some navigational benefits by keeping individuals close to neighbours (the closer an individual is to a neighbour, the more likely they are to share the same direction vector towards the target since our target is not a point at infinity), but this benefit is then cancelled out by the potential source of additional navigational error for the steps when the collision and cohesion rules are implemented.

Figure 2:A and Figure 2:B show how the log of the mean squared displacement (MSD) about the group centre of mass in the x (non-navigation) and y (navigation) directions varies for the same scenarios and range of parameters as Figure 1:A and Figure 1:B. The MSD is a suitable measure for determining the group cohesion, with low values of MSD corresponding to a highly cohesive group. Comparing Figure 2:A and Figure 2:B, it is clear that (unlike the results for navigational efficiency) the simulation results differ with, as expected, groups that include the cohesion rule having a lower MSD (Figure 2:A) than when the cohesion rule is dropped (Figure 2:B). However, there are also some additional results worth commenting on. For high values of navigational error ($\epsilon = 5$) it is clear that there is very little difference between MSD_x and MSD_y in both Figure 2:A and Figure 2:B, and hence the spread around the group centre of mass is effectively isotropic (the group has a circular shape with no elongation). In contrast as the navigational error decreases there is a clear pattern where $MSD_y > MSD_x$ (for both Figure 2:A and 2:B), and hence the group has a more elliptical shape and is more elongated in the navigation direction (anisotropic spread). This result is related to the additional observation that MSD_y seems to approach approximately the same value as w_{nav} increases for all values of ϵ. In contrast, MSD_x, appears to decrease as ϵ decreases. This result is not surprising, as it simply indicates that for lower navigational error the group is less dispersed perpendicular to the navigation direction. These results are consistent with the observations of anisotropic diffusion in a BCRW with no group interactions in Codling et al. (2010).

In Figure 1:C and 1:D we consider two scenarios involving $w_{soc} = 0$ (so that $w_{per} + w_{nav} = 1$). Firstly, in Figure 1:C individuals in the group follow the rules for collision avoidance and group cohesion but do not give any weighting to the movement directions of neighbours when navigating (since $w_{soc} = 0$). In contrast, in Figure 1:D individuals in the group move entirely independently of each other and there are no social interactions or collision avoidance at all. The scenario in Figure 1:D is directly equivalent to the BCRW model explored by Benhamou & Bovet (1992) and our results closely match Figure 1 from Benhamou & Bovet (1992). Comparing Figure 1:C and 1:D (where $w_{soc} = 0$ in both cases), including the collision avoidance and group cohesion rules has a detrimental effect on the group-level navigational efficiency. This is explained by the fact that in 1:C, individuals in the group are effectively paying a navigational cost through the implementation of the collision and cohesion rules but gain no navigational benefit from being in the group as they do not copy directional information from group neighbours ($w_{soc} = 0$). This is in contrast to the results in Figures 1:A and B where $w_{soc} \neq 0$

and the cost of the collision avoidance and cohesion rules is balanced by a gain in navigation performance through copying directional information from neighbours.

In Figure 1:C and Figure 1:D we show the mean and variance of the *group-level* navigational efficiency. If we consider the *individual-level* navigation performance (results not shown) then the mean individual-level navigational efficiency is very similar to the group-level efficiency. However, the variance in navigational efficiency is different for the individual- and group-level cases. For the same levels of individual navigation error, ϵ, the inclusion of basic (non-navigational) social interactions such as collision avoidance and group cohesion reduces the variance of the individual-level navigational efficiency (as well as reducing the mean individual-level efficiency, similar to Figure 1:C and Figure 1:D for the group-level results). Hence, at the individual-level, the inclusion of social interactions results in a reduced navigational efficiency but a more consistent navigational performance, which could be important depending on the ecological context. This result matches with the results in Figure 2:C and Figure 2:D, where the group cohesion is much lower when the collision and cohesion social rules are not included (Figure 2:D), particularly for low values of w_{nav}. When the group is much more spread out (low cohesion), one would expect the navigational efficiency at the individual-level to have higher variance.

It is worth noting that for $w_{nav} > 0.5$ the results for MSD_x and MSD_y are qualitatively and quantitatively similar for all plots in Figure 2. In other words, for larger values of w_{nav}, groups navigating entirely non-socially but sharing a common target (as in Figure 2:D) do not appear to split and are just as cohesive as a group moving fully socially (as in Figure 2:A). This is in contrast to empirical results in Ioannou et al. (2015), where a careful balance between individual navigation and cohesion was required in order to avoid the group splitting. However, the key difference between these studies is that in our simulations all individuals in the group are actively navigating to a common target. In contrast, in Ioannou et al. (2015) it is only the informed leaders that actively navigate, meaning the group is more likely to split when cohesion is low as the leaders leave naive individuals behind. The problem of distinguishing between a social and non-social group in the context of navigation towards a common target is very much an open one and is explored in more detail in Bode et al. (2012b).

Figure 3 illustrates the average group navigational efficiency across the parameter space $w_{soc} + w_{nav} + w_{per} = 1$ for low, medium and high social information quality ($k = 1, 7, 15$, respectively) and low, medium and high navigational error ($\epsilon = 0.1, 1.0, 5.0$, respectively). We also completed simulations for additional values of k and ϵ (see Table 1), but results were qualitatively similar and are only shown in summarised form in Figure 4. In each plot in Figure 3 the main diagonal corresponds to $w_{soc} + w_{nav} = 1$ (i.e. $w_{per} = 0$) and is hence equivalent to the results shown in Figure 1:A. Similarly, results shown on the lower horizontal edge of the triangular region (where $w_{soc} = 0$) directly correspond to the results shown in Figure 1:C; the results inside the triangular region correspond to both $w_{per} > 0$ and $w_{soc} > 0$. If $w_{nav} = 0$ (results shown on the left-hand vertical edge of the triangular region), then navigational efficiency is always zero. In each plot we show the location in parameter space and the value for the maximal navigational efficiency across these simulations, as well as the contour line at 95% of the maximal navigational efficiency.

The results in Figure 3 show that as the navigational error, ϵ, increases (top to bottom), the highest achievable group navigation performance is reduced and the peak in group navigation performance for low values of w_{nav} becomes more pronounced and narrower (see also Figure 4:A and 4:B). As the quality of social information decreases (decreasing k, right to left), the contour line at 95% of the maximal level for group navigation performance moves away from the leading diagonal, suggesting that non-zero persistence weightings, w_{per}, are required to achieve the highest levels of group navigation efficiency (see Figures 3:B1 and 3:C1, in particular).

Figure 3 also shows that, aside from the scenarios with very low levels of navigational error (where navigational efficiency is consistently high as long as $w_{nav} > 0.1$), the group navigation performance is more robust to changes in the balance between the two indirect sources of information (w_{soc} v w_{per}) than to variation in

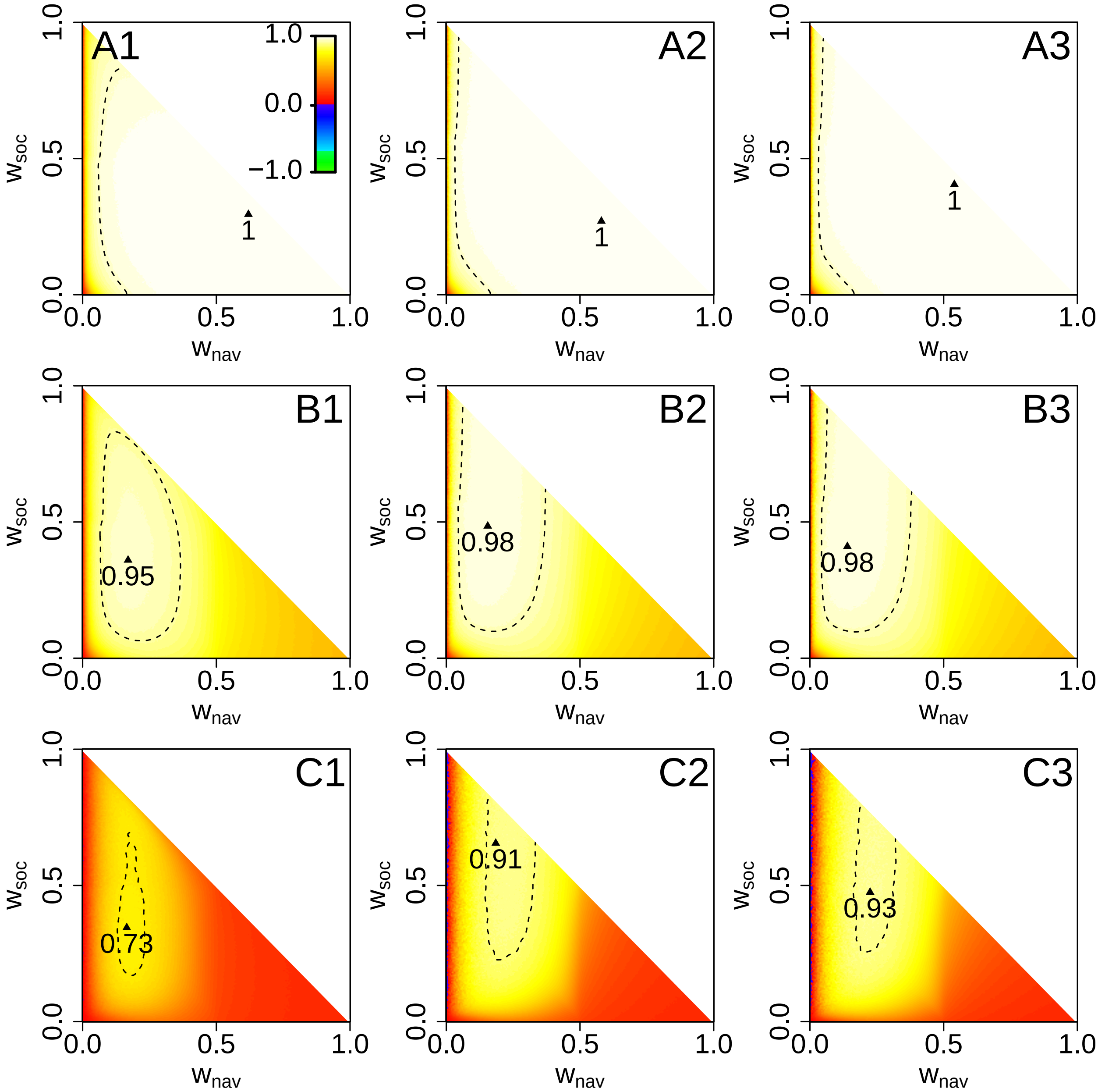

Figure 3: Group-level navigational efficiency across the parameter space $w_{soc} + w_{nav} + w_{per} = 1$ for different group sizes (left-to-right $k = 1, 7, 15$) and navigational noise/error (top-to-bottom $\epsilon = 0.1, 1.0, 5.0$) after 500 simulation time-steps. Parameter combinations underneath the leading diagonal, $w_{soc} + w_{nav} = 1$, include values of $w_{per} > 0$. Values of the navigational efficiency are colour-coded according to the scale shown in the top right hand corner of A1. We simulated values for the weighting parameters on a regular 201×201 grid in $w_{nav} \times w_{soc}$ space and interpolated the results between adjacent parameter combinations to obtain a smooth plot. We show the mean navigational efficiency over 100 replicate simulations. The maximal value for navigational efficiency across our simulations, E_m, is indicated with a triangle and the dashed line shows the contour line at 95% of this maximal value. Note that when $w_{nav} \ll 1$ it is possible for the navigational efficiency to be negative (corresponding to movement away from the target on average).

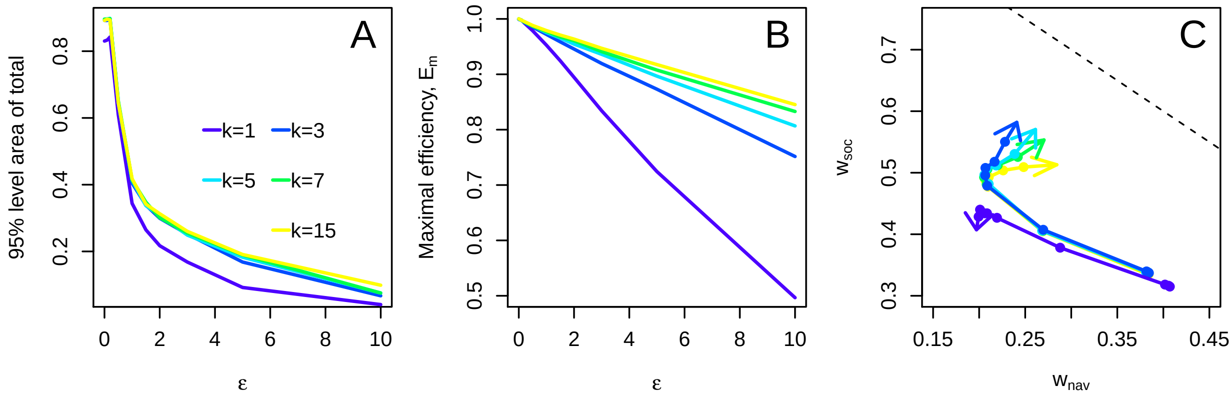

Figure 4: Summary plots illustrating the relationship between navigational efficiency, the number of influential group neighbours (k), the individual navigation error (ϵ), and the relative weightings w_{nav}, w_{soc}, and (indirectly) w_{per}. In A we show how the relative area contained within the 95% maximal efficiency contour line in (w_{nav}, w_{soc}) space (as shown in the plots in Figure 3) changes as ϵ increases for $k = 1,\ 3,\ 5,\ 7,\ 15$. In B we show how the maximal group-level navigational efficiency, E_m, changes as ϵ increases for the same values of k. Plot C shows trajectories corresponding to the position of the centre of mass of the area contained within the 95% maximal efficiency contour line in (w_{nav}, w_{soc}) space as ϵ increases from 0.1 to 10 (the starting point for all trajectories is at approximately $(0.38, 0.35)$; all trajectories initially move up and to the left with the final direction at $\epsilon = 10$ indicated with the arrows). Since $w_{per} = 1 - (w_{nav} + w_{soc})$, any points below the diagonal correspond to $w_{per} > 0$ (note that the plot is shown 'zoomed-in' to the area of interest for clarity). In all plots, the data points represent information extracted from 100 replicate simulations for each parameter combination on a regular 51×51 grid in (w_{nav}, w_{soc}) space.

the balance between direct and indirect sources of navigation information (w_{soc} or w_{per} v w_{nav}; the 95% contour level extends further along the y-axis than it does along the x-axis). Equivalently, for a given value of w_{nav}, there is very little difference in navigation performance as w_{soc} and w_{per} are changed, until w_{soc} gets smaller than approximately 0.2 at which point the navigation perfomance starts to be impaired. This suggests that as long as w_{soc} is sufficiently large, then the weighting given to w_{per} does not negatively affect navigational performance and may in fact improve it slightly in some cases (Figures 3:B1 and 3:C1). However, if w_{soc} is too low then a large value of w_{per} does not give as efficient navigation. One explanation for this result could be the fact that the value of the information contained in individual persistence will be less useful over longer time-scales, whereas the information contained within the movement directions of neighbours is more dynamic and is continually updated from a number of group neighbours rather than one individual.

Figure 4 summarises some of the more general trends that can be extrapolated from Figure 3 and includes results from simulations with additional values of k and ϵ (Table 1). In Figure 4:A we show how the proportion of the area within the triangular region that is bounded by the contour line corresponding to 95% of the maximal navigational efficiency (as shown in Figure 3) decreases as ϵ increases. This measurement is essentially a proxy for the sensitivity of a particular scenario to different navigation strategies (weightings given to w_{nav}, w_{soc} and w_{per}). In other words, when the area bounded by the 95% contour line is large (as in Figure 3:A1 - A3), nearly all combinations of w_{nav}, w_{soc} and w_{per} (with the exception of very low values of w_{nav}) produce navigational performance close to the maximal value. This is in contrast to Figure 3:C1, where the region inside the 95% contour line is much smaller and only a narrow range of w_{nav}, w_{soc} and w_{per} values give navigational efficiency values close to maximal. In general in 4:A, the results for $k \geq 3$ are very similar with little quantitative difference in the size of the bounded region for each value of k as ϵ increases; only the results for $k = 1$ give a significantly lower bounded region for all ϵ.

Figure 4:B illustrates how the value of the maximal navigational efficiency, E_m, decreases as the individual navigational error, ϵ, increases for different values of k. It is clear that for larger values of k there is an increase in navigational performance but a limit is quickly reached after

which the gains are minimal. I.e. the difference in navigational efficiency between $k = 1$ and $k = 3$ is substantial (particularly for large error levels), but the difference in navigational efficiency between $k = 7$ and $k = 15$ is negligible for all ϵ. This result is also observed by Codling & Bode (2014) and suggests an upper limit for how many neighbours it is worth trying to copy information from (particularly given the fact that animals are likely to have cognitive limitations to the number of other individuals they can respond to which we have not accounted for in our simulation model).

Figure 4:C shows trajectories in parameter space for the location of the *centre of mass* of the region bounded by the contour line corresponding to 95% of the maximal navigational efficiency. We plot the location of the centre of mass of the bounded region rather than the location of the maximal navigational efficiency itself, as the latter is more noisy and the pattern of movement within the trajectories is not clear (see results in Figure 3 for example). It should be noted that the centre of mass of the bounded region always corresponds to a navigational efficiency that is within a few percent of the maximal navigational efficiency value and hence this approach is valid. When $\epsilon = 0.1$ results for all values of k are similar with the initial centre of mass being located at approximately $(w_{nav}, w_{soc}) = (0.4, 0.3)$ (and hence $w_{per} \approx 0.3$). As ϵ initially increases, the trajectories for all values of k initially move upwards and to the left. This indicates that for slightly larger individual navigation error, the centre of mass of the maximal efficiency region moves towards both a higher value of w_{soc} and a lower value of w_{nav}, while the value of w_{per} appears to be approximately constant (as the distance from the diagonal of the triangle stays approximately constant). However, for increasingly larger values of ϵ the trajectories for $k > 1$ start to move upwards and right towards the diagonal (indicating a lower value of w_{per} and higher values of w_{nav} and w_{soc}). The trajectory for $k = 1$ is slightly different; for the largest ϵ the trajectory moves down and (very) slightly to the left (indicating a decreased value of w_{soc} and an increased value of w_{per}). Although the exact position of this point could be interpreted as something of an outlier, it is certainly the case that the $k = 1$ trajectory does not move closer to the diagonal for increasing ϵ as with the other trajectories. A general interpretation of these results is that when the quality of social information is high ($k > 1$) and the individual navigation error increases initally (i.e. low ϵ), the best strategy is to give an increasing weighting to social information (w_{soc}) at the expense of w_{nav}, and then at larger values of ϵ at the expense of w_{per}. The rate at which the weighting moves towards w_{soc} also appears to depend on k: for higher k it seems that a lower value of w_{soc} is sufficient, while if k is small, a higher weighting needs to be given to w_{soc}. This suggests that there is in effect a tuning of the mechanisms of social information transfer (either copy more neighbours or give more weighting to the information from the neighbours who you do copy) in order maximise the navigational efficiency; this is an outcome that was also observed by Codling & Bode (2014). Finally, when the quality of social information is low ($k = 1$), it is less useful to rely on this as a navigational cue and the potential navigational information that can be obtained from persistence comes into play (see also Figure 3:C1).

4. Discussion

We have used an individual-based simulation model to explore the most efficient movement strategy for individuals within a leaderless social animal group navigating towards a fixed target. We assume individuals balance three different sources of information when navigating. In common with previous work (Codling & Bode, 2014), we consider the balance between individual navigational knowledge of the target location and socially mediated information about the target (via copying the movement directions of k nearest neighbours). The key novelty of our work is the introduction of individual forward persistence as a third source of (indirect) navigational information. Persistence behaviour is intrinsically non-social and, on its own, does not lead to efficient navigation (Benhamou & Bovet, 1992; Cheung et al., 2007). However, in the context of leaderless animal group navigation we have shown that persistence could play an important role in how individuals in groups should collectively navigate towards a target in the most efficient way.

Specifically, we find that when the quality of social information is likely to be lower (k=1) and the error in individual navigation is high (high

ϵ) then the inclusion of persistence behaviour at the individual level can serve to improve group navigation (Figures 3:C1 and 4:C). In general, the precise weightings of the three different sources of direct and indirect navigational information that lead to the highest group navigation performance depend on their relative quality (size of error). If the direct navigation error at the individual level is high (high ϵ; Figures 3B:1-3 and 3C:1-3), then the most efficient group navigation performance occurs when individuals assign high weights to indirect sources of navigation information (w_{per} or w_{soc}). The converse is not true however. When the individual navigation error is low (low ϵ; Figures 3A:1-3), there is no disadvantage to having a high weighting on w_{per} or w_{soc} (see also Figure 4:A). Once the weighting for direct navigation behaviour exceeds a minimum threshold ($w_{nav} \approx 0.3$ for our simulations), little is gained from investing more into this behaviour, as the information about the target is more efficiently distributed across the group via indirect mechanisms (social information or persistence). This leads to the rather counter-intuitive conclusion that improved navigation at the group level is achieved by individuals within the group giving a low (but non-zero) weighting to direct navigational cues when making decisions about which direction to move (Benhamou & Bovet, 1992; Codling & Bode, 2014). Of course, these results should be considered in the context of the relative errors assigned to the different sources of information, but our results suggest that individuals in the group may use behaviours that are not goal-directed in order to improve overall group navigation performance (Ioannou et al., 2015).

Ultimately, group navigation is a problem of how information should be transferred between individuals and how individuals should balance different types of information. Although we don't directly explore how an optimal navigation strategy for leaderless group navigation may have evolved, it would be possible to do so in a future study using techniques similar to Wood & Ackland (2007), Guttal & Couzin (2010) and Torney et al. (2010). One can hypothesise that, in this context, a sensible strategy may be for individuals to invest some time in using both of the indirect sources of navigational information (persistence and social) in order to 'hedge their bets' against high levels of error in either. This is particularly true since simulation results show that, as highlighted by Codling & Bode (2014), there is little disadvantage in using indirect cues when individual navigation error is low (Figure 3A:1-3 and Figure 4) and potentially strong advantages in doing so when navigation error is high (Figures 3B:1-3, 3C:1-3 and Figure 4), and that social information and persistence appear to be exchangeable across a wide range of relative weightings without reducing group navigation efficiency. These conclusions are supported by Figure 4:A where it is clear that there are a wide range of navigation strategies (meaning parameter combinations of w_{nav}, w_{soc}, and w_{per}) that get close to the maximal navigational efficiency if the error is low, but when the error increases the range of navigation strategies near the maximal efficiency narrows.

In our simulation model we make a number of assumptions considering the specific implementation of individual movement behaviour. It is likely that adjusting these assumptions will produce results that differ quantitatively from those shown here. A key model assumption is that a direct error term is only added to the $\mathbf{r}_{nav}$ vector in Equation (5) and hence individuals have 'perfect' knowledge of the movement directions of neighbours and of their own previous movement direction. This is a parsimonious assumption that simplifies this explorative study and allows us to compare our results directly to Benhamou & Bovet (1992) and Codling & Bode (2014) who also made the same assumption, but this may not be realistic in general. Future studies should explore the effect of direct errors on the persistence or social information used within individual navigation. Although no error is directly applied to persistence in the first instance, the addition of the external movement error (as described in Section 2.3) means that relying on persistence alone with no further navigation cues is not an efficient strategy within our model. It would be possible to implement peristence through a maximum turning angle (Couzin et al., 2002, 2005; Mirabet et al., 2008) and similar results would be obtained, although it would be much more difficult to directly relate the weightings given to each navigaitional cue within the study and when comparing to earlier results (Benhamou & Bovet, 1992; Codling & Bode, 2014). Although we don't apply a direct error to the social navigation information, we have indirectly explored the relative quality of the information available to an individual through the number of neighbours that individuals interact with, k (where a higher value of k is likely to lead to a more accurate estimate of the target direction from a larger proportion of the group). However, using a different approach for implementing social interactions, e.g. based on individuals' visual perception (Strandburg-Peshkin et al., 2013), may well change the relative quality of this social information, possibly making it more robust. We have assumed that the preferred direction of each individual is computed via a weighted vectorial sum. In an alternative approach individuals could undertake a single behaviour, such as navigation or interacting with others, at each time step in a probabilistic way by selecting one behaviour at a time with a certain, possibly dynamically varying probability (Bode et al., 2012a).

In order to test our predictions about the most efficient navigation strategies for leaderless animal groups it is important that the models used are critically evaluated in relation to empirically observed movement data, although we do not try to do this here. Arguably the key open question in the study of empirical navigation and collective motion is how to determine the underlying movement and decision-making processes in observed data. In the context of individual animal navigation we now have a better understanding of how the sampling and observation process used by the observer may affect the apparent properties of a CRW or BCRW movement path (Bovet & Benhamou, 1988; Codling & Hill, 2005b). An additional key open problem is how to distinguish between the localised directional bias in a CRW and the global directional bias towards a target in a BRW, particularly when the target may be different across a group of individuals and only a short movement path is available. Benhamou (2006) proposed a path-analysis method to address this problem but the approach has a reasonably high potential for misclassification. The problem of identifying the underlying movement process used by individuals is arguably even harder in the context of group navigation. For example, Bode et al. (2012b) explored the difficult problem of distinguishing between a social and non-social navigating group in empirical data when there is a common target (e.g. the social and non-social groups in Figure 2 appear very similar for $w_{nav} > 0.5$). Bode et al. (2012b) proposed a method based on the components of the directions of movement of each individual throughout the movement. By comparing the components of movement towards the target and towards other group members it is possible to determine the relative level of sociality of a group as a whole, as well as the relative sociality of individuals within the group (so that 'leaders' and 'followers' could be distinguished). Similar statistically based methods (e.g. Del Mar et al., 2014) may offer the potential to make progress with identifying the underlying movement and decision-making processes observed in empirical data. Nevertheless, further research in this area is clearly needed, particularly if we are to determine the weightings that real animals give to cues such as goal-oriented navigation, persistence, or social information, as in our model.

Carefully controlled experiments completed in the laboratory are one promising way to explore the role of individual behaviour in collective animal groups while avoiding many of the problems inherent in trying to track or observe complete animal groups undergoing collective movement and navigation in the wild (e.g. Dell'Ariccia et al., 2008). For example, Faria et al. (2009) used instruction cards to control the information and target preference in a group of humans when testing predictions of the 'many wrongs principle' from Codling et al. (2007). One of the observations from this study was that individual humans did not always interpret the instructions in the same way and hence the group was not as homogeneous as perhaps was required in order to match the assumptions of the theoretical model (and this is possibly why only weak evidence for the many wrongs principle was found). Rather than using humans, Berdahl et al. (2013), Strandburg-Peshkin et al. (2013) and Ioannou et al. (2015) used schools of golden shiners (*Notemigonus crysoleucas*) to explore group decision-making. In particular, in Strandburg-Peshkin et al. (2013) and Ioannou et al. (2015) 'informed' individuals were those trained to associate a target with a food source, and hence acted as leaders when placed within a larger group of uninformed individuals. Meanwhile, Berdahl et al. (2013) explored the mechanisms for group-level taxis through the natural tendency of golden shiners to avoid light and seek refuge in dark areas. Similar experimental approaches may provide a way to gain further empirically-based insights into the group navigation problem we have considered here.

Theoretical navigation studies of individual animals have typically considered the interplay between alliothetic (external direct goal-oriented cues) and idiothetic (internal indirect cues such as persistence) (Benhamou & Bovet, 1992; Codling & Hill, 2005b; Cheung et al., 2007, 2008), while group navigation studies have typically only considered the balance between goal-oriented direct navigation and social information or interactions (Couzin et al., 2005; Codling et al., 2007; Guttal & Couzin, 2010; Codling & Bode, 2014). In this study we have brought together important concepts from both individual-level navigation (persistence) and collective group navigation (social information) and illustrated how leaderless group navigation can reach maximal efficiency when both factors are included in the movement decisions made at the individual-level. Our results suggest one possible way in which real animals may transfer information within groups in order to gain navigational advantages through the 'many wrongs principle' (Simons, 2004). Our findings should now be explored and tested in more detail through further theoretical and empirical studies.

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Conflicts of Interest

The authors declare that they have no conflicts of interest.

Author Contributions

Both authors contributed to the design, implementation and interpretation of the simulation study. Both authors wrote the paper and have approved the final article.

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*Highlights (for review)

Highlights

- Individual-based simulations are used to explore leaderless animal group navigation.
- We consider the balance between indirect and direct navigational cues.
- Indirect cues include individual persistence and social information.
- Giving a high weighting to indirect cues gives the maximal navigation efficiency.
- Including persistence may improve leaderless group navigation.