Accuracy versus efficiency in animal group movement

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Abstract
Animals that move in groups require mechanisms for effective decision making and information transfer to ensure, for example, that the group successfully reaches a food source or follows a migration route. Recent research has shown that effective leadership in animal groups can be explained by a simple model of information transfer that does not include explicit signalling and only requires a small proportion of informed individuals, the identities of which are unknown to other group members. Here we argue that the metric used in the model, group accuracy, overstates the level of effective leadership because it ignores group speed. We propose group efficiency as a better metric and demonstrate that group efficiency is consistently lower than group accuracy, especially when the proportion of informed individuals is small. We propose a modification to the simple model that raise group efficiency close to the level of group accuracy. Our results provide further insight into the mechanisms of leadership and effective decision making in animal groups.

INTRODUCTION

Animals that move in groups, such as zebras, ants (Franks *et al.* 2002) and shoaling fish (Reebs 2000), need to make decisions that will lead the group effectively in a preferred direction, such as towards a food source or along a migration route (Conradt & Roper 2003). In any given group, different animals will typically have different levels of information. Current research aims to understand the mechanisms whereby information is disseminated among such groups. Such research asks, for instance, whether individuals need to be able to recognise one another, or whether explicit signalling systems between individuals are necessary. Couzin et al. (2005) find that effective leadership in animal groups, as measured by the accuracy of group direction, can be explained by a simple model of information transfer that does not include explicit signalling and does not require group members to be able to recognise informed individuals.

We argue that the group accuracy demonstrated in the simple model of Couzin et al. (2005) is only one component of effective leadership—it measures how well information is transferred through the group, but it does not measure how well this information is utilised. A truer metric of effective leadership is group efficiency. To understand the distinction between accuracy and efficiency, consider that a group of animals may be accurate if it is moving in the preferred direction, but it may not be efficient because individual animals may be following paths that consistently wander either side of the preferred direction. Thus, accuracy may overstate the level of effective leadership.

Here we propose group efficiency as an alternative measure of effective leadership in animal groups. We reconstruct the model of Couzin et al. (2005) and investigate the differences between group accuracy and group efficiency. We propose mechanisms whereby the information transferred effectively through group accuracy may be propagated into group efficiency.

METHODS AND RESULTS

Following Couzin et al. (2005), we constructed a model in which groups of N individuals attempt to navigate towards a food source or other preferred location. At time t, each individual i has position vector $\mathbf{c}_i(t)$, unit direction vector $\mathbf{v}_i(t)$ and moves with speed s. Each individual attempts to avoid near neighbours by turning away from them:

$$\mathbf{d}_i(t+\Delta t) = \sum_{j \neq i} \frac{\mathbf{c}_j(t) - \mathbf{c}_i(t)}{\left|\mathbf{c}_j(t) - \mathbf{c}_i(t)\right|}$$

where $\mathbf{d}_i$ represents the desired direction of travel of individual i at time $t+\Delta t$, and the summation is over neighbouring individuals within a radius α. If there are no neighbours within this region, the individual will attempt to align itself with neighbours within a larger region:

$$\mathbf{d}_i(t+\Delta t) = \sum_{j \neq i} \frac{\mathbf{c}_j(t) - \mathbf{c}_i(t)}{\left|\mathbf{c}_j(t) - \mathbf{c}_i(t)\right|} + \sum_j \mathbf{v}_j(t)$$

where here the summation is over neighbouring individuals within a radius ρ, and $\rho > \alpha$. The desired direction is then normalised:

$$\hat{\mathbf{d}}_i(t+\Delta t) = \frac{\mathbf{d}_i(t+\Delta t)}{\left|\mathbf{d}_i(t+\Delta t)\right|}$$

A vector $\mathbf{g}$ is used to represent the direction of, say, a food source or a migration route. Individuals balance the tendency to move in the preferred direction with the social interactions described above:

$$\mathbf{d}'_i(t+\Delta t) = \frac{\hat{\mathbf{d}}_i(t+\Delta t) + \varpi_i \mathbf{g}}{\left|\hat{\mathbf{d}}_i(t+\Delta t) + \varpi_i \mathbf{g}\right|}$$

where $\mathbf{d}'_i(t+\Delta t)$ is the new desired direction of individual i, and ω_i is a weighting term. For uniformed individuals the weighting term $\omega_i = 0$ (representing no knowledge of the preferred direction); for a proportion p of informed individuals in the group, the weighting term $\omega_i = \omega > 0$.

We introduce an element of uncertainty by rotating the desired direction by an angle φ, which is drawn from a circular-wrapped gaussian distribution with mean zero and standard deviation $\sigma = 0.01$ radians:

$$\mathbf{d}''_i(t+\Delta t) = \begin{bmatrix} \cos(\varphi) & \sin(\varphi) \\ -\sin(\varphi) & \cos(\varphi) \end{bmatrix} \mathbf{d}'_i(t+\Delta t)$$

where $\mathbf{d}''_i(t+\Delta t)$ is the new desired direction of individual i.

Each individual then rotates its direction vector $\mathbf{v}_i(t)$ towards the desired direction $\mathbf{d}''_i(t+\Delta t)$. Individuals can rotate a maximum of $\theta\Delta t$ radians in each timestep:

$$\mathbf{v}_i(t+\Delta t) = \begin{cases} \mathbf{d}''(t+\Delta t), & |\gamma| < \theta \\ \begin{bmatrix} \cos(\theta') & \sin(\theta') \\ -\sin(\theta') & \cos(\theta') \end{bmatrix} \mathbf{v}_i(t), & \text{otherwise} \end{cases}$$

where γ is the angle from $\mathbf{v}_i(t)$ to $\mathbf{d}''_i(t+\Delta t)$, and $\theta' = \theta$ if γ is positive or $-\theta$ if γ is negative. The new position of individual i is then given by:

$$\mathbf{c}_i(t+\Delta t) = \mathbf{c}_i(t) + \mathbf{v}_i(t+\Delta t)s\Delta t$$

Following Couzin et al. (2005) we ran $M = 400$ replicates of each simulation to assess the effectiveness of group leadership. Also, following Couzin et al. (2005), we initially used group accuracy as a measure of effective leadership. Group accuracy is computed using vectors $\mathbf{h}_m$, where for each simulation m, $\mathbf{h}_m$ extends from the group centroid at time $t_f - 50\Delta t$ to the group centroid at time t_f. The formula for group accuracy is then:

$$accuracy = \sqrt{\left(\sum_m \sin(\psi_m)\right)^2 + \left(\sum_m \cos(\psi_m)\right)^2}$$

where ψ_m is the angle between $\mathbf{h}_m$ and $\mathbf{g}$, and the summations are over all simulation replicates. This formula comes from circular statistics (Batschelet 1981).

We used group efficiency as an alternative measure of effective leadership. Intuitively, group efficiency is the distance travelled by the group in the preferred direction as a proportion of the maximum distance it could have travelled in the preferred direction if all individuals were moving exactly in the preferred direction at all times. The formula used to calculate group efficiency is:

$$efficiency = \frac{1}{M}\sum_m \left(1 - \frac{|D\mathbf{g} - \mathbf{h}_m|}{D}\right)$$

where $D = 50\Delta ts$ is the maximum distance the group could have moved towards the target in time period of length $50\Delta t$.

We ran simulations with $\omega = 0.5$, $\alpha = 1$, $\rho = 6$, $\Delta t = 0.2$, $\theta = 2$ and $s = \alpha$. We used group sizes of $N = 10$, 30, 50, 100, and 200, and we varied the proportion of informed individuals p from zero to one by increments of 0.1. We ran M replicate simulations for each pair of values of N and p.

RESULTS

Group accuracy rapidly approached a maximum as the proportion of informed individuals increased (Figure 1). Group accuracy was higher in larger groups. Group efficiency behaved similarly (Figure 2), but was always lower than group accuracy (Figure 3).

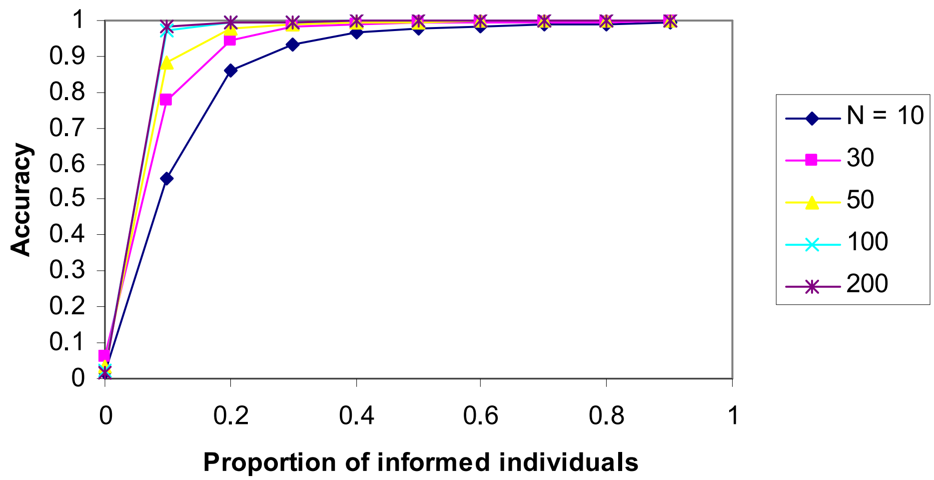

Figure 1 Group accuracy as a function of the proportion of informed individuals and group size. Model parameters were as described in the text.

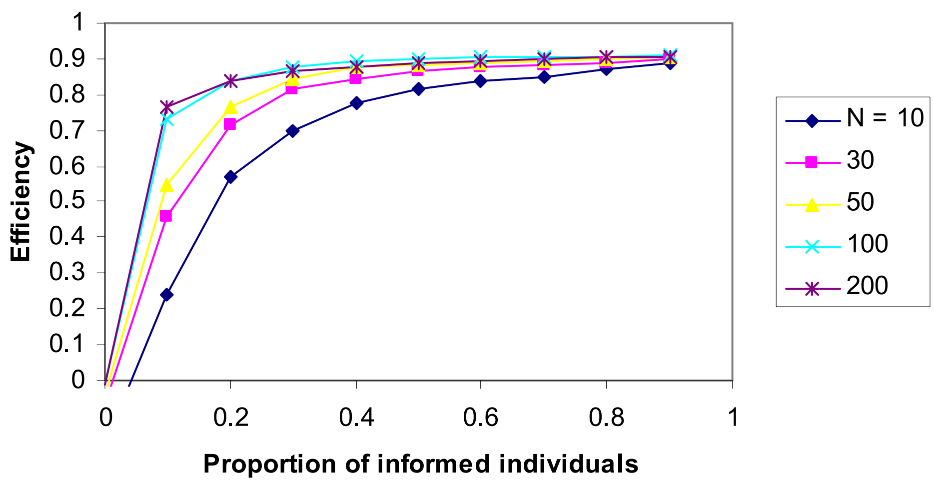

Figure 2 Group efficiency as a function of the proportion of informed individuals and group size. Model parameters were as described in the text.

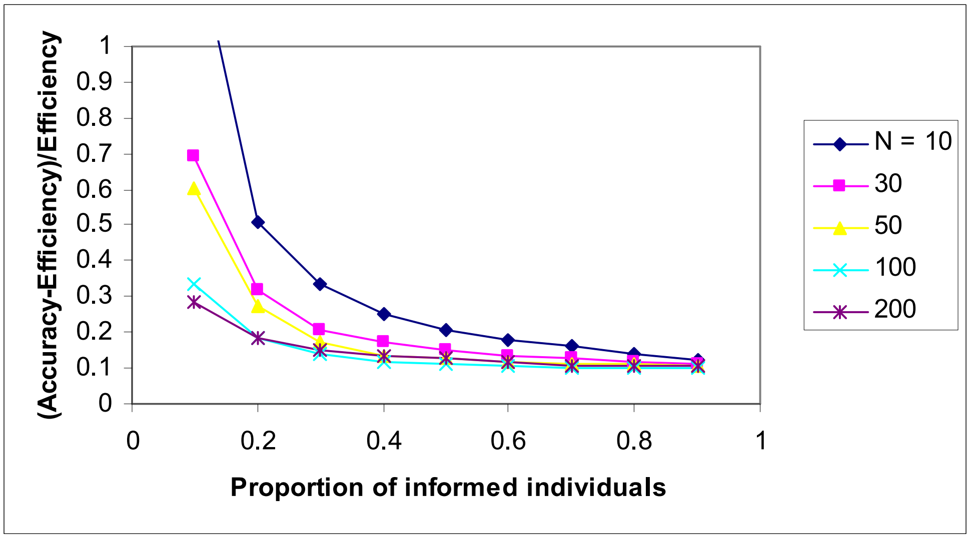

Figure 3 The difference between group accuracy and efficiency measured as a proportion of efficiency.

DISCUSSION

Our finding that group accuracy increases with increasing group size and increasing proportion of informed individuals is qualitatively consistent with those of Couzin et al. (2005). This suggests that effective information transfer in animal groups can be explained by a simple model that does not require explicit signalling.

Our new measure of effective leadership, group efficiency, is consistently lower than group accuracy. As argued in the introduction, this measure represents how well the information transferred through group accuracy is being utilised by the group. For groups that are moving accurately but inefficiently, the information required for efficient navigation is present, it is just not being used optimally.

Straightforward modifications to the model could allow the group to propagate information from group accuracy into group efficiency. For instance, individuals could periodically update their preferred direction vectors based on the group direction. In this way, uninformed individuals would gradually transition to being informed. This would require a one-parameter change to the model that would not introduce explicit signalling, thus retaining much of the simplicity and parsimony of the original model.

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