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Research Focus

Many wrongs: the advantage of group navigation

Andrew M. Simons

Department of Biology, College of Natural Sciences, Carleton University, 1125 Colonel By Drive, Ottawa, ON, Canada K1S 5B6

Research into the puzzling phenomena of animal navigation and aggregation has proceeded along two distinct lines. Study of navigation generally focuses on the orientation ability of the individual without reference to the implications of group membership. A simple principle (the 'many wrongs principle'), first proposed by Bergman and Donner in 1964, and developed by both Hamilton and Wallraff three decades ago, provides a link between these lines of current interest by suggesting that navigational accuracy increases with group size. With unprecedented scope for testing the hypotheses it generates, it is now time that the many wrongs principle is exhumed.

Animal navigation has been a source of fascination to humans for centuries. Navigation directly affects dispersal patterns, which influence conservation efforts as well as population and evolutionary dynamics. In spite of intense recent research that has improved our understanding of the navigational tools used by animals, a consensus has yet to be reached on explanations for the accuracy with which migration is accomplished [1–5]. In a seemingly unrelated area, scientists continue to seek explanations for why animals tend to form groups, with recent work focusing on group decision making [6–8] and complexity theory [9]. Although migrating animals often occur in groups, the studies of navigation and aggregation have persisted as independent lines of research. A largely unnoticed idea that was first suggested 40 years ago might hold the key to solving the current impasse: it could account for unexplained navigational accuracy and simultaneously offer an explanation for aggregation.

Bergman and Donner first made the intriguing suggestion that we should not expect to account for accuracy of migration by studying individual navigational error rates [10]: we should expect group error to be lower than that of individual members because group migration 'increases the accuracy of the orientation mechanism' [10]. Hamilton [11] and Wallraff [12] then placed the original suggestion within a solid theoretical framework. Inadequacies in both the technology for tracking migratory animals and datasets available to test the principle might explain why the papers received little attention at the time of publication. They now offer an appropriate null model and general framework on which to base empirical tests of the advantage of group navigation.

Corresponding author: Andrew M. Simons (asimons@ccs.carleton.ca).

(Dis)orientation

Experimental and observational work has refined our knowledge of a wide array of orientation cues that are available to long-distance migrants including geomagnetic and solar information in combination with an internal circadian clock, stellar rotation, geographical topology, olfactory cues and complex interactions or cross-calibration of these cues (*c.f.* [13–18]). However, navigational imprecision has many sources. For example, geomagnetic compass precision is reduced near the equator and the poles; stellar rotational cues are unavailable for much of the year in polar regions; and solar cues vary with season and location [2,16]. Navigation error introduced by limitations that are inherent to the orientation cues themselves is compounded by additional hazards such as wind drift [18]. Correction mechanisms serve to reduce directional bias, but add a further source of random error. Even if orientation cues were absolutely reliable, flawless navigation would require perfect sensory interpretation and integration of cues by individuals. This inherent individual error is at the heart of the current controversy over whether orientation mechanisms, as they are currently understood, are sufficient to explain the accuracy with which animals navigate [1–5].

Error rates measured on individual birds are implicitly assumed to result in a corresponding dispersion of individuals around the target migration destination. This scatter is traditionally described (using circular distribution statistics) in terms of a mean migration direction and directional concentration. The three focal papers show how the failure of orientation systems to account for observed navigational accuracy could be the result of an unnoticed but flawed assumption about how individual error rates should determine directional scatter [10–12].

When many wrongs do make a right

The many wrongs principle is based on the idea that the pooling of information from many inaccurate compasses yields a single more accurate compass (Box 1) because individual orientation error is suppressed by group cohesion [10–12]. Renewed attention to the principle might provide a vital step toward a fuller understanding of observed navigational accuracy.

The simplest, or null model can be envisioned as one in which there are no innate differences in accuracy among individuals within a flock, and individuals contribute equally to the mean flock direction. Under this null model, expected flock accuracy is a function of flock size; smaller flocks are expected to miss their target more often (Box 1). Recent work on the

Box 1. The many wrongs principle

Given that it is the individual rather than the group that has tools for navigation, it is at this level that studies of navigation have traditionally focused. Interindividual variation in flight paths is an appropriate measure of scatter for birds in solitary flight [2,3], but flocks are cohesive units that share a single path, and groups must be viewed as random samples of *n* individuals drawn from the population.

On the scale of linear measurements, for example, the standard deviation of the mean (or the standard error) is given by $\frac{s}{\sqrt{n}}$. Standard error decreases as sample size, n, within each group increases. Variation among flight trajectories must be measured on an angular rather than linear scale because orientation is a compass direction that is taken from a circular distribution that has neither true zero, nor true high or low values. Analogously to the linear scale, it is the angular sampling distribution of flock means rather than that of individuals that determines directional scatter [12,24]. Therefore, all else being equal, individuals flying within larger flocks will arrive more reliably at their destination than will individuals within smaller flocks, because of the declining relationship between flock size and standard error of flight trajectories (Figure I). Thus, the assumption that error rates of flight trajectories are given by individual error rates is erroneous when individuals navigate in groups constrained by their cohesiveness to follow a single trajectory.

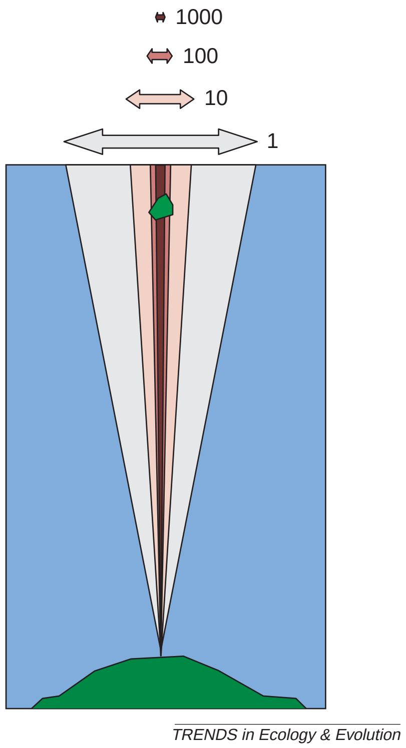

Figure I. The advantageous effect of large group size on navigational accuracy. Shaded areas depict 95% confidence intervals of trajectories for groups of 1, 10, 100, and 1000 individuals of equal navigational ability. The trajectory of a cohesive group is given by the angular mean of the individual navigators comprising the group as calculated using angular statistics [24]. The mean angular deviation is given by $s = \frac{180}{\pi}\sqrt{2(1-r)}$, where *r*, the angular concentration, is given by the length of the mean vector. The 95% angular confidence interval of group orientation is then calculated as 2*s*. Here, a fixed value chosen for *r* results in an angular deviation $s = 10.36°$ for animals navigating alone; $s = 3.43°$ when participating in groups of size 10; $s = 1.07°$ in groups of 100; and $s = 0.34°$ in groups of 1000. In a manner analogous to this simultaneous vector summation for many individuals, accuracy can also be gained from sequential trajectory summation (*c.f.* [25]) if a trajectory is chosen only at the beginning of each stage of a migration that occurs in multiple stages.

evolutionary advantage of aggregation posits superior group decisions based on consensus or democratic vote counting [6,8], and requires communication of information among individuals. The elegance of the many wrongs principle lies in its simplicity: the navigational advantage is gained automatically through group cohesion alone.

This flock size advantage can be generalized to more complex scenarios. Variation in navigational abilities among individuals is expected, and has several sources. For example, adult and juvenile raptors differ in their ability to compensate for wind drift [18]. Similarly, naïve migrants might orient correctly [19], but only experienced individuals can adjust this vector navigation if displaced from the correct route. When differences in ability are recognized by fellow flock members, navigational responsibility might be weighted unequally among individuals. The effective sample size of a flock for navigation would then be smaller than the bird count, but the correct expectation for directional scatter among groups must still consider the general group size advantage.

The sampling distribution of flocks converges on that of individuals only if a single individual assumes exclusive navigational responsibility for an entire flock. However, even at this logical extreme, flocks will show little scatter if experienced individuals lead the flocks. Thus, the use of individual error to predict directional scatter is reasonable only for solitary flight or under the unreasonable assumption that a single individual of average navigational ability leads.

Tests and implications

Thus far, the scant references to the original papers, with few exceptions, do not directly test the navigational advantage of aggregation. Important exceptions do exist. A comparison of orientation ability in homing pigeon *Columba livia* pairs that were manipulated to differ in orientation abilities shows that the trajectory of the flock of two birds is a result of a compromise between the paths that the birds would have taken individually [20]. Randomly assembled flocks of three–six homing pigeons showed a reduction in both directional scatter and homing times compared with single birds [21] although, in another study comparing one- and four-member pigeon flocks, no significant group advantage was detected [22]. Navigational accuracy increases with flock size in the skylark *Alauda arvensis* [23], providing support for the many wrongs principle.

With the development of tracking technology and the accumulation of large datasets, several testable predictions based on the automatic grouping advantage should provide fruitful avenues for research. The most basic prediction is that, within species, directional scatter among groups will decrease with increasing group size. Furthermore, if the 'correct' direction can be inferred, larger flocks will deviate less from the correct direction than will smaller flocks. Species characterized by small group sizes are predicted to either have more efficient navigational tools, or to suffer greater losses during migration. Grouping is predicted to be more prevalent in danger zones or if environmental factors limit the efficacy of orientation tools. If overwintering and breeding destinations differ in size, flock size is predicted to differ accordingly during spring migration compared with migration in the autumn. Finally, flight paths will deviate from the shortest path if perilous habitat (e.g. open ocean) occurs on one side of this path. Smaller flocks will hedge their bets by deviating landward because the fitness cost of a random deviation oceanward from the flight path is high.

The interpretation of observational data might be confounded by factors that are themselves amenable to study. First, the size of a group in nature might be determined by the navigational abilities of its members, in that group size might increase until a critical group orientation threshold is reached. If so, little variation in error will be found among groups in spite of differences in group size. Furthermore, if there is a cost to large group size, recognized navigational ability might influence group membership decisions. Although difficult, ideal tests of the many wrongs principle would follow randomly assembled aggregations of different sizes.

Early work recognized that the standard error of group trajectories is lower than the scatter that is predicted based on individual error rates [10–12]. The navigational advantage is general in that it applies in principle to all cohesive animal groups that exhibit any degree of random individual orientation error and subsumes, as special cases, scenarios in which navigational responsibilities are unequally divided among group members.

The automatic advantage of group navigation helps to reconcile the difference in expected and observed migratory accuracy, and provides an additional explanation for the widespread phenomenon of animal aggregation. Given the current interest in both subjects, the research orientation advocated by Wallraff in 1978 [12] now merits amplification: the 'influence of social relationships on migratory orientation of birds deserves, in my opinion, more attention than it has received so far'.

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