Collective movements, initiation and stops: Diversity of situations and law of parsimony

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ABSTRACT

The environment of animals is often heterogeneous, containing zones that may be dedicated specifically to resting, drinking or feeding. These functional zones may spread over a more or a less extensive area. Thus, mobile animals may have to move from one patch to another when resources are locally depleted or when they need to change activity. The mechanisms involved in collective movement appear simple at first glance, but a brief reflection shows the real difficulty of the problem in terms of the numerous environmental, physical, physiological and social parameters involved. This review is mainly concerned with collective movements, which are characterised by a directional and temporal coordination, where individuals mutually influence each other, meaning this coordination mainly depends on social interactions (Huth and Wissel, 1992; Warburton and Lazarus, 1991; Couzin and Krause, 2003; Couzin et al., 2002). In literature, two types of movement are discussed: large-scale movement and small-scale movement. First, we define these types of movement and then discuss the behavioural mechanisms involved. Secondly, we show that short and long movement but also moving and stopping may result from the outcome of parameters modulation underpinning collective decision-making.

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1. Types of movement

It is very difficult to categorise these two types of movement, because many parameters (or variables) may be used to characterise them, and, moreover, these movements are often associated with different activities.

Woolf et al. (1970) considered two types of daily movements as a function of ecological contexts (habitat use and group activity): large-scale oriented movements to a specific location during seasonal migration (e.g. lobster; fish: Reesb, 2000), homing to reproduce in natal areas (fish: Rich et al., 2006; ungulates: Dubois et al., 1994), joining new functional area (water points: Fischhoff et al., 2007; resting areas) and small-scale feeding movement within the same feeding area or between different feeding areas (ungulates: Dumont et al., 2005). Woolf et al. (1970) also stressed that movements can involve another activity like grazing, depending on the velocity. For example, short slow movements can include grazing, whereas long movements at high velocity preclude grazing.

Bourjade et al. (2009) classified movements into single bout movements, consisting of a unique moving period at the end of which all individuals eventually engage in new activities or disperse, and multiple-bout movements comprising collective stops during which the groups keep a conspicuous moving shape. In their definition, Bourjade et al. (2009) do not take into account the modulation of velocity in function of movement type.

These two definitions and classifications highlight a modulation of some physical parameters among many others, which can be used to characterise movements (distance, duration, velocity, modulation of velocity, distribution of velocity, etc.).

2. Why and when moving

Before undertaking a movement, animals may be confronted with a choice of direction, different foraging sites or different resting sites (Couzin et al., 2005) and/or the moment to start (migrating geese, wildebeest: Camazine et al., 2001).

Such choices depend on many physiological, social and environmental parameters and the distributions of these parameters (e.g. number of individuals).

Because individuals in groups are often not equivalent regarding reproductive state, energetic reserves, age, health and local environment (Conradt, 1998; Ruckstuhl, 1998; Rands et al., 2003; Couzin et al., 2005; Fischhoff et al., 2007), they may differ in their spatial and temporal choice. Temporal coordination corresponds to an adjustment of individual rhythms (influenced by the physiological state), and individual goals may be affected by conforming
to collective choice. When they are moving through habitat, there is a wide range of information available to animals. Individuals in a group can directly interact with their environment to generate ‘personal information’ derived from environmental cues (e.g. local landmarks), and can also obtain social or public information from the behaviour of conspecifics (velocity, distance, posture, etc.) (Dall et al., 2005 and citations therein; Valone, 1989). Their physiological status modulates the interaction and the behaviour. Moreover, when a start attempt occurs it may not be possible for individuals to know if the initiator possesses pertinent information and the incentive to move. How individuals manage to reach a collective decision and which interactions allow synchronisation of individual rhythms is a central issue.

3. Collective decision-making

To remain cohesive, individuals have to make a rapid communal decision (Conradt and Roper, 2009) either to move together or refuse to move. If there is no following, giving up is an important mechanism (feral horses: Berger, 1977, mountain baboons: Byrne et al., 1990, golden tamarins Leontopithecus rosalia: Menzel and Beck, 2000; Petit et al., 2009). In the case when the initiator moves without being followed or partially followed, groups split (Michelena et al., 2009). Thus, it is important to consider several steps such as pre-departure, movement initiation and adhesion when we study collective movement. These different steps are often considered as involving qualitatively distinct mechanisms (Leca et al., 2003; Conradt and Roper, 2005) (personal versus distributed leadership, shared versus unshared decision, ...). Do decision and behaviour fall in qualitatively different categories or do they form part of a continuum? In the last case, collective outcome results from the modulations of parameters influencing individual decision, the behavioural algorithms remaining the same. For example, leadership may arise as a simple modification of physiological parameters, which may vary individually, some individuals having a higher probability per unit of time to initiate a movement. In such cases, the shift from democratic decision-making to despotic decision-making results from the distribution of these individuals’ probabilities among the group. The distributed leadership corresponds to an intermediate situation between democratic and despotic decision-making.

Moreover, do moving and stopping imply the same mechanisms or are these mechanisms qualitatively different? Few authors are interested in the comparison of these two processes of large-scale oriented movement or small-scale feeding movement, and it is evident that the frequency of movements and their scale depend on the individual probability of moving and stopping. Two factors could account for the relative distance moved by animals. Short or long movements could either be owed (1) to a qualitative modulation, i.e. typical patterns corresponding to each type of movement, or (2) to the outcome of quantitative modulation of parameters underpinning decision-making.

There is a wide variety of parameters which influence the type/length of collective movement. In this paper, we consider just one of them, the duration of movement and resting.

4. Two families of mechanisms

4.1. Qualitative modulation

Under this hypothesis, each type of movement is characterised by a specific sequence of behaviour. For a given species, long movements, more expensive in energy and time than a short movement, could require shared decision-making, i.e. a majority of individuals decide to move. Moreover, movements may be preceded by a negotiation phase between all individuals of the group, during which they decide whether to move or not and, if they move, in which direction (Petit et al., 2009). Alternatively, short-distance movements, less expensive in energy or associated with risk reduction (to avoid a predator), can arise from a deterministic following, where all group members systematically follow the initiator whatever its identity and wherever it goes and the initiator shows a low probability of giving up (Petit and Bon, this issue). The mechanisms initiating a long movement could thus be more elaborated than the ones used for a short movement, because the consequences of a wrong choice at the individual level are not the same. To our knowledge, no experimental study highlights this hypothesis. Quantitative modulation of the parameters, however, may account for the decision of individuals to initiate a long movement instead of a short movement. In fact, a simple modulation of both the imitation or giving-up parameters can lead to a different type of movement with either a shared or an unshared system.

4.2. Quantitative modulation

The hypothesis of quantitative modulation assumes that a modulation of the same external or physiological parameters is sufficient to explain why groups decide to move or stop, and in consequence modulate the length of the movement. A simple model based on our experiments with sheep (Pilott et al., 2009, in preparation), incorporating one parameter representing the fluctuation of the physiological state or the environment, can lead either to short or long movement. In a group of size N, M individuals can either be moving and R resting (non-moving) (N = M + R; M and R can vary from 0 to N), and the probability to switch between the two behaviours depends on the number of individuals in the two states, P(M, R):

\[
P_M = \alpha + \frac{\beta M}{R + 1} \\
P_R = \alpha + \frac{\beta R}{M + 1}
\]

where \(P_M\) is the probability to switch between resting and moving and \(P_R\) is the probability to switch between moving and resting. \(\alpha\) corresponds to the spontaneous probability to switch and \(\beta\) the imitation factor. Individuals in a group differ. Individual \(i\) is characterised by its own value of \(\alpha_i\) and \(\beta_i\). However for simplicity, we consider that the transitions \(M\) to \(R\) and \(R\) to \(M\) are symmetrical and the same for all individuals (\(\alpha_1 = \cdots = \alpha_M, \beta_1 = \cdots = \beta_R\)).

When individuals are independent, i.e. their activities are not influenced by the behaviour of detectable conspecifics, \(\beta = 0\), \(P_M = P_R = \alpha\). Independent individuals would change from \(R\) to \(M\) only on the basis of their physiological status and personal information, excluding social or public information. Such individuals occurring in a group may depart and proceed either followed or not by group members.

In the case where individual decision is influenced by the activity of neighbours, \(\beta > 0\). Assuming \(\beta > 0\), a collective movement can emerge. During a start attempt, the initiator can be confronted with two situations, either no individuals follow and he gives up, or all or parts of group members follow the initiator who goes on. If the decision to move depends on a modulation of endogenous and/or exogenous parameters, the mathematical equation may apply to group stopping, but with an inverse relation, reflecting the reversibility of the system. For example, local food resources, represented by the parameter \(\lambda\) in the equation, produce an effect on \(P_M\) and \(P_R\) and accordingly provoke one type of behaviour rather than another type. The function \(F(\lambda)\) increases with \(\lambda\) and \(P_M\) decreases with \(\lambda\), and there is a switch of behaviour for a particular value of \(\lambda\) (Fig. 1). In our example, the less the food resource, the greater the probability of moving and the less the probability of...
Fig. 1. Examples of response function, i.e. number of individuals in movement in function of parameter $\lambda$, corresponding to a variation of the food resource. Population $= (M+R) = 10$ individuals. Dotted line corresponds to a weak mimetic behaviour ($\alpha = 1$ and $\beta = 1.2$); black/dashed line corresponds to a strong mimetic behaviour ($\alpha = 1$ and $\beta = 4$). The dashed line corresponds to an unstable solution.

Alternatively, we can also obtain a classical effect of hysteresis and collective memory. In this case, the parameter $\lambda$, corresponding, for example, to the food resources or a physiological state triggers a movement when it reaches the value $\lambda_1$. With effects of imitation and interaction between conspecifics, the group stay in movement, until the parameter $\lambda$ (local food resource) decreases to a second value $\lambda_2 = \lambda_1$. In this case, the collective response (number of moving or resting individuals) obtained with an increasing $\lambda$ and the one obtained with decreasing $\lambda$ are not superimposable: there are two thresholds characterising the switch between two states (Fig. 1).

Considering that movements can be initiated by 'tunable' parameters raises the question whether a short movement only corresponds to an aborted long movement. The previous example was mainly focused on switches induced by environmental parameters. The collective movement can also result from the coupling between 'personal information' corresponding to physiological variables and 'public information'. Often physiological status depends on the time spent in a state and this dependence was not included in Eqs. (1) and (2).

When moving, group members also need to eat and rest. The time ($t_i$) spent in a state may influence the individual probability ($P_i$) to change state following a sigmoidal function:

$$P_i = \frac{a t_i^n}{K^n + t_i^n}$$

where $t_i$ is the time elapsed since the start of resting or moving, $a$ is the maximum probability. $K$ is a constant and corresponds to the threshold, and $n$ represents the determinism of the response. These parameters $a, K$ and $n$ depend on the activity and external parameters (e.g. if the environment is poor, $K$ may be large). Fig. 2A shows that the greater $t_i$ is, the greater is the probability of changing, and the greater $n$ is, the more deterministic the individual response is. When $n = 0$, $P_i$ is independent of time $t$ and constant ($= 0.5 a$) and when $n$ is very large $P_i$ is a step-function (if $t < K$: $P_i = 0$; $t = K$: $P_i = 0.5 a$; $t > K$: $P_i = a$).

Coupling Eq. (1), the probability to switch between two states independently of the time, and Eq. (3), include the influence of the time spent in the state, gives:

$$P_{Mi} = \frac{a t_i^n}{K^n + t_i^n} \left( \frac{\alpha + \beta M}{R + 1} \right)$$

$$P_{Ri} = \frac{a t_i^n}{K^n + t_i^n} \left( \frac{\alpha + \beta R}{M + 1} \right)$$

where $t_i$ corresponds to the personal information and the imitation to the social information (Valone, 1989). Fig. 2B–D shows that the greater $n$ is, the greater is the synchronisation in the
group, and the lower the frequency, the more regular is the activity pattern.

If $\beta = 0$, there is no synchronisation in the group because there is no imitation effect; if $\beta > 0$ we have synchronisation (Goss and Deneubourg, 1988).

Fig. 2B–D illustrates how with the modulation of one parameter (e.g. $n$), different patterns of movements are generated. Moreover, for the same set of parameters, different durations are generated. A synchronised initiation and cessation of motion may result from mimetic behaviour resulting from interactions between group members, producing amazing behaviour (Fig. 3).

5. Conclusion

The toy models analysed in this paper show that different types of movement and initiation and stopping may result from the same set of behavioural rules. Modulations of the equation’s parameters expressing exogenous factors (Eq. (2)) and endogenous factors (Eq. (3)) and those associated with interactions between individuals generate different types or patterns of collective movements (e.g. synchronisation, collective memory, ...). The coupling of these models with explicit movements and spatial heterogeneities must be able to generate a diversity of collective decision-making (including the abortion of such decisions) that are often assumed to result from different behavioural algorithms.

An individual in a group, suddenly attracted by a patch of grass, which decides to stop may break a long move into two shorter moves. In the same environmental conditions, however, owing to the physiological status of the individuals, this long move could not be interrupted. Moreover, depending on the collective memory effects and the history of the group (see Fig. 1), different collective responses may be observed for the same environmental and physiological conditions.

The two main messages of this modelling respectively concern the experimental procedure and the a priori often guiding the study of the biological systems diversity. The first message stresses the importance of experiments performed under standardised and controlled conditions. The second one suggests avoidance of the classical trap where the analysis is ‘governed’ by a qualitative one-to-one relationship between individual behaviour and collective responses.

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