"Take me to your leader!" Inferring leadership in animal groups on the move

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Extended abstract

The topic of group living in animals (Krause and Ruxton, 2002), and especially the questions of how individuals share information, make collective decisions, and move as a group have been the focus of particular attention in recent scientific work (Couzin and Krause, 2003; Sumpter, 2006, 2010). An issue that is central to the problem of collective movement is how to quantitatively capture the influence of leaders, or indeed to determine whether leaders exist at all. Within a group, a leader is a key individual whose impact on the collective behaviour is significantly higher than that of other individuals (or "followers") (King et al., 2009). Studies now abound on the emergence and the role of leaders in collective behaviour, both from an experimental (Harcourt et al., 2009; Nagy et al., 2010; Lukeman et al., 2010; Tarcai et al., 2011; Couzin et al., 2011) and theoretical perspective (Grégoire et al., 2003; Rands et al., 2003, 2008; Grégoire and Chaté, 2004; Couzin et al., 2005; Conradt et al., 2009). However, a major challenge which is posed in the study of leaders and followers in animal groups is the identification of these leaders. Indeed, when animals move along a dynamical front whose shape and direction are subject to permanent changes and fluctuations, how to reliably determine who is leading the group? Moreover, may it be that in some contexts the effective group leader is situated within the group's core instead of at its rim, and in these cases how to capture its role? In this work we present new methods to infer and measure leadership in groups of entities moving collectively at variable speeds. We describe quantitative tools to study the synchronised trajectory of many individuals, and test these tools against simulated and measured collective movement data.

In a first step, we concentrate on the spatial dimension of leadership and ask the question of how to infer the dynamical progression order of a moving group. We present an algorithm to estimate a group's trajectory from that of its members, and expand on how to make the estimate robust to stop-and-go motion, or the alternation between dynamical movement periods (e.g. moving between food patches) and semi-static periods (e.g. foraging at a food patch), which are less relevant for the group's trajectory. The method is based on an estimation of the trajectory of the group's centroid, smoothed with a low-pass filter and protected against spurious directional changes due to noisy data.

We first apply this algorithm to the study of trajectories extracted from simulations of a multiplayer racing computer game and observe a strict correspondence between the ranking computed by the program from the progression along a known race circuit and our dynamically-computed ranking. We then use GPS tracks of human runners moving along a simple path at variable speeds and comment on the accuracy on the method. Finally, we apply our algorithm to the study of noisy trajectories coming from GPS sensors worn on a collar by individual meerkats (*Suricata suricatta* – illustrated in Fig. 1) and discuss the advantages of such a method to identify specific behaviours such as mate guarding.

In a second step, we present cases where studying leadership from a purely spatial perspective is irrelevant. This leads us to generalise our approach to leadership in moving groups by using information-theoretic measures, in particular conditional mutual information (CMI), to determine the directionality of the information flow between group members. The use of the CMI metric allows us to identify leaders and followers by inferring causality between the trajectories of individuals, thereby offering a richer definition of leadership which does not require leaders to be at the front of a moving group. Moreover, the method offers a time-dependent measure of leadership, which differs from previous work (see e.g. Nagy et al., 2010) in which aggregated measurements were averaged. We use surrogate data sets to generate synthetic uncorrelated trajectories; these provide a null model of interindividual crosscorrelation, which we use to quantify the significance of the CMI levels measured between dyads within the group. Finally, we apply this method to the set of meerkat GPS tracks used previously (illustrated in Fig. 2), and we study the influence of vocalisations (e.g. moving calls) emitted by individual animals on the flow of information between them.

These methods, and the insights obtained from them, are of relevance to the study of collective movement patterns in general. We expect that by drawing from other fields such as information theory and nonlinear time series analysis, these new tools will help to better understand the proximate factors underlying the synchronisation of behaviours between individuals within a group.

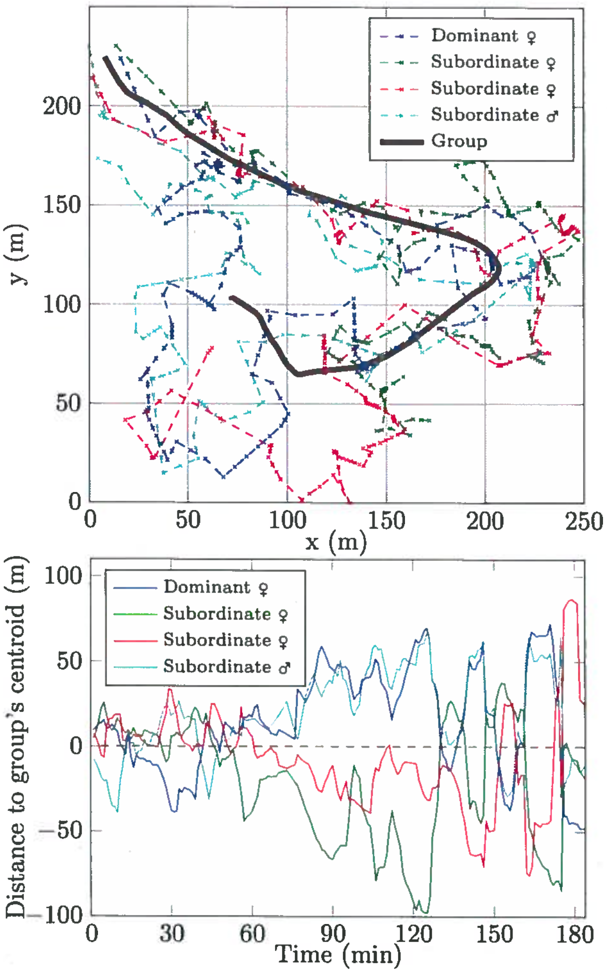

Figure 1: Application of the spatial leadership method to a group of 4 individual meerkats tracked over a period of 3 hours. (top) Thin lines: individual trajectories; thick line: group trajectory extracted from the individual trajectories. (bottom) Individual leading index, expressed as the signed distance between an individual's position projected on the group trajectory and the group's centroid.

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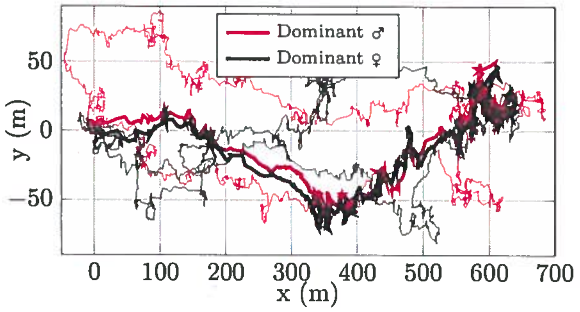

Figure 2: Trajectories of two different individuals (thick lines) followed over a period of 2h45m and an example of corresponding surrogate trajectories (thin lines – two iterates); all trajectories start at (0; 0). Whilst the real trajectories appear to be crosscorrelated (as the individuals move together), the surrogates ones are not; this provides a null model to test the values of conditional mutual information obtained.

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