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Simultaneous use of different communication mechanisms leads to spatial sorting and unexpected collective behaviours in animal groups

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HIGHLIGHTS

- We model the simultaneous use of two communication mechanisms in animal aggregations.
- We examine the effect of initial population size on the types of patterns displayed.
- The use of multiple communication mechanisms leads to unexpected group behaviours.
- The use of multiple communication mechanisms leads to spatial sorting of individuals.

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ABSTRACT

Communication among individuals forms the basis of social interactions in every animal population. In general, communication is influenced by the physiological and psychological constraints of each individual, and in large aggregations this means differences in the reception and emission of communication signals. However, studies on the formation and movement of animal aggregations usually assume that all individuals communicate with neighbours in the same manner. Here, we take a new approach on animal aggregations and use a nonlocal mathematical model to investigate theoretically the simultaneous use of two communication mechanisms by different members of a population. We show that the use of multiple communication mechanisms can lead to behaviours that are not necessarily predicted by the behaviour of subpopulations that use only one communication mechanism. In particular, we show that while the use of one communication mechanism by the entire population leads to deterministic movement, the use of multiple communication mechanisms can lead in some cases to chaotic movement. Finally, we show that the use of multiple communication mechanisms leads to the sorting of individuals inside aggregations: individuals that are aware of the location and the movement direction of all their neighbours usually position themselves at the centre of the groups, while individuals that are aware of the location and the movement direction of only some neighbours position themselves at the edges of the groups.

1. Introduction

Self-organised biological aggregations have been an area of intense study and growth, as a result of an increased interest in understanding and controlling the complex spatial and spatio-temporal patterns formed by these aggregations. Generally, biological aggregations can be formed of individuals belonging to different species (as in herds of ungulates Sinclair, 1985 or fish shoals Krause et al., 2005), or can be formed of same-species individuals that have different physiological characteristics (e.g., different age or different health states Barber, 2003). The heterogeneity of these aggregations translates also into a heterogeneity of inter-individual communication (see, for example, the discussion in Seyfarth et al. (1980) on age-related alarm calls in vervet monkeys), which likely has implications on the formation and structure of aggregations. In fact, Bro-Jørgensen (2010) suggests that species that use multiple signals are more likely to be prone to speciation (and implicit spatial divergence), since they could adapt their response more flexibly to the local environment. Moreover, recent studies on the directionality of animal communication showed that different bird species communicate with conspecifics using signals with various degrees of directionality (Yorzinski and Patricelli, 2010). This raises the question of the effect of directional communication between individuals on the group-level behaviour in aggregations formed of multiple species. In addition, Yorzinski and Patricelli (2010) suggested that birds might

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shift the directionality of their calls depending on the intended receiver. This shift would generate a heterogeneity of inter-individual communication, with possible effects on the structure of large flocks of birds.

The structure of various biological aggregations has been investigated intensively in the past years, both from experimental and theoretical (i.e., statistical and mathematical) points of view. Studies have shown that spatial sorting of individuals can be associated with individuals' size (Parrish, 1989), parasite infections (Barber, 2003), hunger level (Krause, 1993), predator type (Romey and LaBuda, 2010), sex preferences in non-mating groups (Romey and Wallace, 2007), swimming speed (Muzinic, 1977; Couzin et al., 2005), turning rate (Couzin et al., 2005), personality traits (Kurvers et al., 2009) or perception ranges (Couzin et al., 2005). However, despite evidence of language-based segregation in human communities (Hellerstein and Newmark, 2008), or information-based formation of mixed-species aggregation (Goodale et al., 2010), the effect of inter-individual communication on the structure and movement of animal aggregations has not been investigated much. As mentioned previously, this aspect could be particularly relevant in understanding animal speciation and its connection with multiple signalling and environmental variability (Bro-Jørgensen, 2010). The use of multiple sensory modalities has been previously associated with accuracy in decision making (Johnstone, 1996). However, the potential role of multiple signalling on group structure or spatial segregation is still an open problem. While an experimental investigation of this aspect is still a difficult task, mathematical modelling can propose hypotheses regarding the effects of multiple communication mechanisms on the spatial structure of stationary and moving groups.

The mathematical models for self-organised animal aggregations focus mainly on the social interactions among individuals: repulsion from near-by individuals, attraction towards individuals further away and alignment with individuals positioned at intermediate distances (see, for example, Couzin et al., 2005; Sumpter, 2006; Eftimie, 2012 and the references therein). The majority of these models also assume that all individuals in a population have similar characteristics and behave in a similar manner. An exception to this is models investigating leader–follower dynamics (Couzin et al., 2002; Codling et al., 2007; Guttal and Couzin, 2010) and models investigating spatial sorting (Couzin et al., 2005). (In many species, leadership and spatial sorting are actually correlated phenomena, with some leaders being positioned at the front of the moving groups (Bumann and Krause, 1993; Burns et al., 2010).) While the leader–follower models assume that some individuals in the population have more knowledge about a particular movement direction (i.e., they are "informed"), they do not actually investigate the communication mechanisms used to transmit this knowledge. One of the first models to investigate the effect of communication mechanisms on animal aggregations and the interplay between communication and social interactions was introduced in Eftimie et al. (2007a). However, even this study considered homogeneous populations, with all individuals communicating (i.e., emitting and receiving information) in the same way.

The goal of this paper is to investigate the role of multiple communication mechanisms on the sorting of individuals within aggregations, and on the types of patterns displayed by these aggregations. The communication mechanisms considered here differ slightly from each other. This allows us to investigate and formulate hypotheses on two types of aggregations: (a) aggregations formed of different species which communicate using slightly different signals, and (b) aggregations formed of only one species, but where a few individuals have difficulties in emitting/receiving information to/from their neighbours. These differences in the communication mechanisms allow us to refer to individuals as being "fully aware" (if they receive information about the position and the movement direction of all their neighbours within a certain spatial range) or "partially aware" (if they receive information about the position and the movement direction of only some of their neighbours; e.g., only neighbours positioned ahead). Note that this approach is different from the approach in Couzin et al. (2002), where the "informed" individuals are those that move in a preferred direction.

We will consider the mathematical framework introduced in Eftimie et al. (2007a), where a nonlocal mathematical model for movement in 1D is coupled with different communication mechanisms among individuals. The framework takes into consideration three types of social interactions: short-range repulsion, medium-range alignment and long-range attraction. These interactions are influenced by how individuals communicate with each other via unidirectional signals (e.g., auditory or tactile) or via omnidirectional signals (e.g., chemical signals or combinations of signals, such as visual and auditory signals). To investigate the effect of multiple communication mechanisms used by individuals belonging to the same population, we will assume that this population is formed of individuals perceiving/emitting signals from/to *all of their neighbours* located within a certain spatial range (i.e., omnidirectional reception and emission), and individuals perceiving/emitting signals only from/to *some of their neighbours* located within a certain spatial range (unidirectional reception or emission).

Since our focus here is on the use of multiple communication mechanisms, we will assume that all individuals have similar motility characteristics (i.e., same speed and turning rates), same hunger levels, same body size, and no birth and death processes occur during the time frame investigated.

2. Model description

To derive the mathematical model, we follow the general approach taken in Eftimie et al. (2009), where a nonlocal model for self-organised aggregations and one-dimensional movement incorporated not only social interactions (attraction, repulsion and alignment), but also different communication mechanisms among individuals in a population. However, in Eftimie et al. (2009) the whole population used the same communication mechanisms (i.e., all individuals emitted and received communication signals in the same manner; see Fig. 1 for a description of these mechanisms). Here, we build up on that approach and assume that individuals in a population communicate via *two different mechanisms*, depending on their own physiological characteristics. For example, some individuals can receive information only from a certain direction (e.g., from ahead through visual signals, as in model M3, Fig. 1), while others can receive information from all directions (e.g., through a combination of visual, sound and chemical signals, as in model M2, Fig. 1). The emission of signals also influences inter-individual communication, especially when the emitted signals cannot be understood by the receiving individuals (due to environmental effects or to particular physiological characteristics; see Endler (1993) for a summary of factors that can affect signal emission and reception).

The use of two different communication mechanisms by an animal population splits the population into two subpopulations, u and v (each communicating via one mechanism). For simplicity, we assume that the spatial domain is much longer than wide and we focus only on one spatial dimension. In 1D, the evolution of densities of left-moving (u^-, v^-) and right-moving (u^+, v^+) individuals belonging to the two subpopulations u and v is described by the following equations:

$$\frac{\partial u^+}{\partial t} + \gamma \frac{\partial u^+}{\partial x} = -\lambda_u^+[u^+, u^-, v^+, v^-]u^+ + \lambda_u^-[u^+, u^-, v^+, v^-]u^-, \tag{1a}$$