



# Self-organized spatial structures of locust groups emerging from local interaction



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## ABSTRACT

Collective movements are found in several taxa and many different scales. Locusts and grasshoppers are known for their formation of groups and collective movement. These groups exhibit self-organized characteristics of typical shapes and density gradients. Three different species-dependent characteristics of group structures can be distinguished in locusts and grasshoppers: spots (circular form), bands (large form), and ribbons (long form). In order to understand deeper the mechanisms leading to this diversity of structures, we aimed to reproduce the different spatial structures of locust and grasshopper groups by the mean of an agent-based model. The model describes the behaviour of individual insects by three simple processes of attraction, repulsion and cohesion – well known from classical flock models. The individuals' vision radius is updated according to their neighbours' density. Individuals update their direction and subsequent movement in response to local neighbours within the vision radius. The movement speed is irregular representing intermittent motion. Simulation experiments were applied to test the effects of the sequence of the processes of cohesion and alignment. As expected, the differences of group structures can be explained by differences in individual behaviours. More interestingly, the characteristic collective movements observed in locusts and grasshoppers need strong alignment behaviour of the individuals. We suggest that the different characteristic group structures found in grasshoppers and locusts depend on the strength of the aggregating behaviour exhibited by the different species. Our work shows that the high frontal densities observed in locust bands are the result of the turning back toward the group by the individuals in the front of the group. The specific behaviours needed to reproduce locust band structures suppose an adaptation to predation avoidance and eventually resource search.

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## 1. Introduction

Collective movement is a type of collective behaviour (Vicsek, 2001). It occurs in many natural scales and different taxa: mammals, birds, fish, insects, bacterial colonies or amoeba (Arboleda-Estudillo et al., 2010; Buhl et al., 2006; Hayakawa, 2010; Rappel et al., 1999; Sokolov et al., 2007; Sueur and Petit, 2008; Ward et al., 2008). Collective movement is also observed in physical and chemical systems (Blair et al., 2003; Deseigne et al., 2010; Kudrolli et al., 2008). Many studies have been conducted to under-

stand this universal phenomenon (Vicsek and Zafeiris, 2012 and literature therein). The first models to simulate collective movement of fish schools and birds' flocks (Aoki, 1982; Reynolds, 1987) were based on three types of interactions: avoidance (or repulsion) (tendency to keep a minimum distance to their mates), alignment (tendency to move in the same direction as the neighbours) and cohesion or attraction (tendency to stay in the group). Many other simpler variants have been developed later in order to find the simplest suitable description for such kind of collective behaviour. For instance, models were proposed with only two rules (Derzsi et al., 2009) (attraction-repulsion), with only the attraction rule (Strömbom, 2011), or based on a passive collision rule (inelastic collisions among unities) (Grossman et al., 2008).

Most of the models used to investigate collective movement are individual- or agent-based models (IBM/ABMs, we'll hereafter

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refer to ABM without distinction of the two). ABMs are characterized by self-governing agents who have the ability to interact with one another and with the environment (Epstein and Axtell, 1996; Gilbert and Troitzsch, 1999; Hemelrijk and Kunz, 2005; Hemelrijk and Hildenbrandt, 2008). Agents in an ABM are autonomous (control their own action), sociable (interact with each other via some kind of communication), reactive (perceive the environment and interact with it) and proactive (take an action to reach an objective) (Wooldridge and Jennings, 1995). The main feature of the ABM approach is to use individual traits and interactions to explain system complexity (Grimm and Railsback, 2005). Hence, ABMs are used to boost the understanding of complex systems in many disciplines such as policy fields (Carrillo-Hermosilla, 2006), natural sciences (Phillips, 2006) and social sciences (Sampson et al., 2002). In order to improve ABMs and to make ecological modelling more rigorous and comprehensive, the so-called pattern oriented modelling approach (POM) has been developed (Grimm and Railsback, 2005). POM proposes guidelines to develop structurally realistic models (Mooij and DeAngelis, 2003), which are able to reproduce multiple observed patterns in the context of the described ecological systems. The consideration of multiple patterns increases the complexity of models but plays an important role in filtering suitable parameter sets and essential processes. The realism of the model structure resulting from this process lead to models tuned to reproduce multiple patterns simultaneously (Grimm et al., 2005) and to detect the most reasonable ecological processes behind.

Among the organisms that generate collective movements, locusts form spectacular bands and swarms. Locusts are grasshoppers capable of both 1) phase polyphenism and 2) swarming (Pener and Simpson, 2009). Some locust species, such as *Schistocerca gregaria*, can migrate up to several kilometres per day (Uvarov, 1977). During bands migration, *S. gregaria* hoppers have a characteristic intermittent motion (individuals stop frequently, with motions lasting less than two seconds) (Stower, 1963). Intermittent motion is a primordial feature in the formation of locust bands, since it is suggested that moments of stops serve to decide whether or not to align (Ariel et al., 2014). Phase polyphenism confers to locust the capacity to switch between two extreme phases (1) a solitary one and (2) a gregarious one (But, there is intermediate phase between these two extreme phases named transiens). The phase of locusts can be identified by the body pigmentation and the body's morphology. The most striking difference, however, is in the behaviour. While the solitary locusts feed and move according to their own needs, the gregarious locusts aggregate (Pener and Simpson, 2009). Non-locust grasshoppers do not present this typical phenotypic plasticity. Many species of grasshoppers (e.g. the genus *Melanoplus*) tend to migrate in a collective movement despite their inability to exhibit phase polyphenism (Jago, 1985; Pener, 1991; Uvarov, 1966; Uvarov, 1977). Grasshoppers and locusts outbreaks are strongly correlated with the increase of population density (Buhl et al., 2006; Kennedy, 1961).

Moving bands of grasshoppers and locusts exhibit different spatial structures that vary between species (see Fig. 2 for illustration). Some of them create dense and large banana-shaped fronts. Banana-shaped bands are characterized by a large or amoeboid shape with a high frontal density (Buhl et al., 2011; Ellis and Ashall, 1957). This structure has been observed in different species (see Table 1). Generally, banana-shaped bands are characteristics of moving groups of locust species, particularly from third hopper instars to older (Buhl et al., 2011; Dean, 1967; Lecoq et al., 1999; Zakharov and Skalov, 1930). Other group structure may present a columnar form with a narrow front and a long and dense extent in the movement direction. These columns are described in some locust species but mostly in non-locust grasshoppers depicting a low aggregating behaviour (Heifetz and Applebaum, 1995; Pener and Yerushalmi, 1998). Hereafter, we will refer to the first spatial

**Table 1**

Some examples of locust and grasshopper species showing band or ribbon structures.

	Species	Reference
Band	<i>Nomadacris septemfasciata</i>	Dean (1967)
	<i>Rhammatocerus schistocercoides</i>	Lecoq et al. (1999)
	<i>Chortoicetes terminifera</i>	Buhl et al. (2011)
	<i>Schistocerca gregaria</i>	Ellis and Ashall (1957)
	<i>Calliptamus italicus</i>	Kirichenko (1926)
	<i>Dociostaurus maroccanus</i>	La Baume (1918)
	<i>Locusta migratoria</i>	Zakharov and Skalov (1930)
Ribbon	<i>Romalea microptera</i>	Watson (1941)
	<i>Phymateus aegrotus</i>	Kevan (1949)
	<i>Locustana pardalina</i>	De Wet and Webb (1952); Faure (1923)
	<i>Phymateus viridipes</i>	De Lotto (1951)

structure as “bands” (banana-shaped) and the second to “ribbon” (column-shaped) (Table 1). Furthermore, other group structures can appear according to the age or following some environmental factors. For instance, *Schistocerca gregaria* (Ellis and Ashall, 1957) and *Nomadacris septemfasciata* (Dean, 1967), generally creating bands, can form non-moving groups with a round or irregular shape and very high density in the centre. This structure is usually observed during resting time (Dean, 1967; La Baume, 1918). Hopper densities in resting groups are extremely high, and the area they cover can be two to four times smaller than that covered by the same band when marching (Ellis and Ashall, 1957). We will refer to this third type of non-moving group structure as “spots”. Hopper group structures are cohesive and stable since they are able to keep their properties in different landscape formations: in dense, sparse and in absence of vegetation (See Table 2).

Locust's collective motion has been frequently studied in the field, in laboratory and through modelling. The common goal of all these studies was to understand the onset and the mechanism of this phenomenon in locust species. Different hypotheses have been proposed. First, Uvarov (1977) suggested that the main mechanism leading to locust collective marching is the tendency for individuals to align with conspecifics in the group. This hypothesis is reinforced by recent studies, confirming a local scale of interactions between aligned individuals in moving groups (Buhl et al., 2006, 2011). Another hypothesis proposed cannibalism as a cause of collective marching (Bazazi et al., 2008; Simpson et al., 2006). Cannibalism is observed among orthoptera species such as *Schistocerca gregaria*, *Anabrus simplex* and *C. terminifera* (Bazazi et al., 2011; Hansen et al., 2011; Romanczuk et al., 2009; Simpson et al., 2006). According to this hypothesis, hoppers have the tendency to move towards conspecifics in front to cannibalize them and escape from others coming from behind. However, the cannibalism hypothesis has been recently criticized by Ariel and Ayali (2015) highlighting the non-consistence of the idea about the role of pursuit/escape in bands marching, since it suggests a continuous marching of individuals despite the intermittent motion (stop and go) characterizing locusts. Moreover, Buhl et al. (2012) have analysed and compared the spatial distribution of hoppers within *C. terminifera* bands between the field and computer simulations. They deduce that locusts have more a tendency to interact with all conspecifics around them, than following individuals in front and escaping from the ones behind.

The “social interactions” model of repulsion-attraction-alignment seems to be a promising tool for understanding collective motion, especially in locusts. The challenge for now is to scale this “social interactions” model up to large scale and try to explain the emergence of locusts' group structures in the field. One of the most characteristic locust band patterns is their spatial structure (shape & density distribution within the group). Locust

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