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Simulating predator attacks on schools: Evolving composite tactics

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ABSTRACT

One hypothesis about the origins and evolution of coordinated animal movements is that they may serve as a defensive mechanism against predation. Earlier studies of the possible evolution of coordinated movement in prey concentrated on predators with simple attack tactics. Numerous studies, however, suggest that to overcome the apparent defensive mechanisms which grouping and coordinated movement may provide to prey, predators in nature appear to use elaborate target selection and pursuit/hunting tactics. We here study predators that use composite tactics, (a) predators that in successive attacks based on probability choose one of several simple attack tactics, (b) predators that first disperse prey and then pick off isolated individuals. We develop an individual based model of a group of prey that is attacked by a solitary predator agent. By using genetic algorithms, we enable the predator agent to adapt (a) the probability that a specific tactic will be selected in the next attack, (b) the distance at which it stops dispersing the prey and the radius within which it searches for the most isolated prey. With a direct competition of the evolved predator agents we examine which is the better tactic against a group of prey moving in a polarized cohesive manner in three different settings. Our results suggest that, (a) a delayed response is an efficient advanced prey defence tactic, (b) predator confusion plays an important role in the evolution of composite tactics, and (c) when confusion is at play, the dispersing predator is a much better hunter, capable of at least partially diminishing the effectiveness of the prey's delayed response.

1. Introduction

Collective behaviour is a phenomenon that can easily be observed in nature, where the most typical examples are schools of fish, flocks of birds, swarms of insects, and herds of ungulates. Studies of collective behaviour are interesting not only because they give a better insight into the behaviour of animals, but also because humans behave in a similar fashion in a wide repertoire of situations. Similar behaviour (as in animal groups) can be seen in stop and start traffic jams, crowd behaviour at various events, e.g. at football games or music concerts (Silverberg et al., 2013), and even in the bureaucracy of the European Union (Sumpter, 2006). Comparable patterns can also be observed at much smaller scales like cancerous cells (Deisboeck and Couzin, 2009).

The literature about collective behaviour contains several hypotheses about why animals coalesce into groups. Some studies suggest that animal groups may increase the mating and foraging efficiency of their members (Krebs and Davies, 1997), or that grouping could save energy because of hydrodynamic or aerodynamic benefits (Lissaman and Shollenberger, 1970; Bill and Herrnkind, 1976; Partridge and Pitcher, 1979; Hemelrijk et al., 2014). Other studies propose that such groups might function as a defensive mechanism against predators (Pavlov and Kasumyan, 2000; Krause and Ruxton, 2002; Nishimura, 2002; Hart and Freed, 2005; Lebar Bajec and Heppner, 2009; Cresswell and Quinn, 2011; Larsson, 2012; Demšar and Lebar Bajec, 2014).

Collective behaviour in animals is in some cases (e.g. flocks of birds) quite large in scale and as such hard to enclose in a controlled environment in which scientists could then perform various test of hypotheses about the "whys" and "hows" of such behaviour of the animal groups (Lebar Bajec and Heppner, 2009). If we look at the case of a solitary predator attacking a group of prey, it is evident that in nature different predators with different hunting tactics exist in different environments, meaning that it is difficult to

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compare the tactics without the confounding effects of environmental context. As computational approaches usually remove the effects of the environment they proved to be a good tool for studying various hypotheses concerning collective behaviour (Vicsek et al., 1995; Couzin et al., 2002; Hildenbrandt et al., 2010), and the results obtained with such methods are usually more general.

Several computer models suggest that animal grouping may indeed act as a defensive mechanism against predators. Some models (Reluga and Viscido, 2005; Wood and Ackland, 2007; Olson et al., 2013a, 2013b) focused on the selfish herd theory (Hamilton, 1971) and its effect on the safety of prey individuals. The selfish herd theory suggests that individuals try to reduce their predation risk by reducing their domain of danger, where an individual's domain of danger is defined as the area in which any point is nearer to the observed individual than it is to any other individual (Hamilton, 1971). A number of studies (Nishimura, 2002; Zheng et al., 2005; Kunz et al., 2006; Olson et al., 2013b) suggest that predator confusion might play an important role in defence against predators and evolution of grouping behaviour. Ruxton and Beauchamp (2008) and Haley et al. (2014) investigated the many eyes theory, which suggests that as the size of the group increases the amount of time an individual has to scan the environment decreases. As larger groups are usually more conspicuous to the predator, Tosh (2011) concentrated on density dependant selection of individuals in prey aggregations and the dilution of risk theory, which suggests that the chance of a single prey to be targeted is lower in larger groups. Some models (Ward et al., 2001; Oboshi et al., 2003; Demšar and Lebar Bajec, 2014), however, did not focus on a specific hypothesis about why animals are safer in groups.

Natural observations (Hector, 1986; Forsman and Appelqvist, 1998; Nøttestad et al., 2002; Gazda et al., 2005; Lopez, 2006; Cresswell and Quinn, 2010; Handegard et al., 2012; Rutz, 2012; Kane and Zamani, 2014) suggest that predators can decrease the defensive advantages of grouping by using sophisticated target selection and pursuit/hunting tactics. In turn prey can also use sophisticated escape manoeuvres to increase their chances of survival (Domenici et al., 2011a, 2011b). For example a fish school often delays its escape response to a later point in time, and then tries to outsmart the predator with rapid movement such as the flash expansion or the fountain effect (Partridge, 1982).

To enhance their chances of a successful hunt goshawks (*Accipiter gentilis*) in large flocks of feral pigeons (*Columba livia*) single out odd-coloured birds as target prey, presumably because targeting rare coloured birds in large uniform flocks might help them overcome confusion (Rutz, 2012). Once a target is selected, some predators in nature also use various pursuit tactics, for example as a recent experimental study reported (Kane and Zamani, 2014) some species of falcons during pursuit use the technique of motion camouflage. They either camouflage themselves against a fixed background object so that the prey observes no relative motion between them and the fixed object or they approach the prey so that, from the point of view of the prey, they always appear to be on the same bearing (Justh and Krishnaprasad, 2006). While peregrine falcons (*Falco peregrinus*) normally attack from the open and use aerial pursuit, sparrow hawks (*Accipiter nisus*) prefer to ambush prey from cover (Cresswell and Quinn, 2010). To increase their hunting success several species have even evolved to hunt their prey by working together with other members of the species (Alcock, 1979; Packer and Ruttan, 1988; Handegard et al., 2012). Bottlenose dolphins (*Tursiops truncatus*) have distinctive behavioural roles during group feeding, one individual herds the attacked fish towards the remaining dolphins, to make them leap into the air and become easy prey for the team (Gazda et al., 2005; Lopez, 2006). Killer whales (*Orcinus orca*) congregate in large groups, dive to the limit of their capacity, force tens of tonnes of herring (*Clupea harengus*) out of their safe deep-water habitat by coordinated action, and split large aggregations of fish into small, dense schools before attacking them (Nøttestad et al., 2002). On the other hand, some predator species that often hunt alone (for example swordfish, *Xiphias gladius*) use a different tactic, and approach the centre of the school to disperse it and when it does, they lock on isolated individuals (Pavlov and Kasumyan, 2000; Larsson, 2012). Lett et al. (2014) showed that predators can efficiently disturb fish schools if they attack them with a high enough frequency, however they did not measure how these disturbances influence the predator's hunting success.

Since several empirical studies suggest that predator animals in nature use very elaborate hunting techniques, the simple attack tactics used in previous computer models might be naïve. This research focuses on how a solitary predator might adapt its attack tactic to overcome the defensive benefits provided by collective behaviour and increase its hunting success. To the best of our knowledge, this has been investigated (to some degree) by Nishimura (2002), Demšar and Lebar Bajec (2014), Kunz et al. (2006), and Olson et al. (2013a,b, in press), but all of these studies concentrated on simple attack tactics. In this study we use *genetic algorithms* (Holland, 1992) to investigate the adaptation of a solitary predator that uses composite tactics. First we study the adaptation of a predator that on each individual attack chooses between three simple tactics (attack nearest prey, attack central prey, attack peripheral prey). With this we analyze to which tactic an evolved solitary predator will resort to use the most when released to attack a group of prey moving in a polarized cohesive manner (*mixture of simple tactics*). Next we study the adaptation of a predator that initially chases the nearby group of prey in order to disperse it and then locks on the most peripheral prey (*the dispersing tactic*). More specifically we investigate how the predator adapts the parameters of this composite tactic (i.e. the distance at which to stop dispersing and the radius in which to search for the most peripheral target) in order to increase the hunting success. Note that in the case of predators that use the dispersing tactic, the line between target selection and hunting/pursuit tactic becomes less clear, as the predator intentionally defers the decision about its target to a later point in time.

2. Methods

Scientists that use computational approaches to study collective behaviour usually design computer models in which the behaviour of the modelled animals is in most cases constructed around *drives* (Reynolds, 1987; Lebar Bajec and Heppner, 2009; Vicsek and Zafeiris, 2012). These are designed so that the behaviour of artificial animals in the computer model resembles the behaviour of their counterparts in nature. The drives are implemented in various ways and the parameters of the drives that govern the behaviour of individuals are usually pre-set by hand (i.e. *pre-set models*); some researchers, as in our case, however, use genetic algorithms (Holland, 1992) to let certain parameters evolve through time (i.e. *evolvable models*) and by means of that the authors study the possible evolution of collective behaviour or attack tactics.

Since several studies (Huth and Wissel, 1992, 1994; Kunz and Hemelrijk, 2012) showed that the dimensionality of the model minimally affects the results of the simulations of schooling systems without a predator, our model is for computational simplicity also two-dimensional. It consists of two types of agents – a solitary predator and a group of prey. The behaviour of an individual depends on its nearby neighbours. The goal of prey individuals is to survive, while the predator tries to catch as many prey individuals as possible. In our model the behaviour of prey is not a part of the evolutionary process, it is pre-set so that the group of prey moves in a polarized cohesive manner; only the behaviour of the predator evolves.