Understanding fission-fusion dynamics in social animals through agent-based modelling

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Abstract

This paper describes the way in which we have employed agent-based models to understand fission-fusion dynamics (FFD), a collective pattern of behavior in many social animals. Groups with a high degree of FFD split into subgroups that vary in size, cohesion and composition, often within short temporal scales. These dynamics are thought to be more complex than those of other species with cohesive, stable groups, leading to hypotheses about the origin of social intelligence. Also, a flexible grouping pattern is supposed to be an adaptive solution to the temporal and spatial variation in feeding resources. We have used models where relatively simple agents forage in realistic, heterogenous environments and have shown that, for intermediate levels of heterogeneity in the size of food patches, agents form subgroups that vary in size and composition in a similar fashion as they do in species with a high degree of FFD. We have also explored the idea that by splitting in subgroups that vary in size, animals can exploit a heterogeneous environment with ephemeral food sources more efficiently than cohesive groups. Agent-based models have provided ways to test hypotheses and develop predictions about social and ecological dynamics.

Fission-fusion dynamics (FFD) is a property of many groups of animals that split in subgroups of variable size, composition and degree of cohesion (Kummer, 1971; Aureli, et. al. 2008). Species that show this property, to different degree, include, among mammals: baboons (*Papio* spp), chimpanzees (*Pan* spp), spider monkeys (*Ateles* spp), African elephants (*Loxodonta africana*), hyenas (*Crocuta crocuta*), dolphins (*Tursiops truncatus*), bats (*Myotis bechsteinii*) and several species of birds (Aureli, et al. 2008; Silk, et al. 2014).

A proposed adaptive function of FFD is that it allows for an efficient exploitation of resources that are distributed heterogenously in time and space, adjusting the size of the foraging units to the local density of resources (Kummer, 1971; Aureli, et.al. 2008). While there have been some partial tests of this idea, the complexity of environmental variables and the different ways in which a particular behavior could be adaptive have provided contradictory results (Chapman, et al. 1995; Newton-Fisher, et. al. 2000; Symington 1988).

In terms of the mechanistic basis of FFD at the level of individual behavior, it has been proposed that, because species with FFD confront a greater diversity of social situations than species with cohesive groups, they should be subject to selection for higher cognitive abilities. These would underlie processes of information sharing or withholding and special social interactions that allow for individuals to cope with the constant fissioning and fusioning of subgroups (Aureli, et. al. 2008).

We have used agent-based models to complement field observations of the social behavior of spider monkeys (*Ateles geoffroyi;* Ramos-Fernández, et. al. 2003) in order to understand their movement and grouping patterns. We extended an agent-based model initially aimed at understanding the movement trajectories of a single forager in heterogenous environments (Boyer, et al. 2006), by incorporating several foragers (Ramos-Fernandez et al. 2006). Our goal was to understand the minimum conditions that would give rise to a fission-fusion grouping pattern among foragers. We set up an environment where discrete food patches vary in size according to an inverse power-law (as real trees do in many tropical and temperate forests: Enquist and Niklas, 2001) with some large patches and many small patches. Here, a set of foragers moves according to a local optimality rule, maximizing the size of the next visited patch and minimizing the distance traveled to it. In each iteration of the simulation, a forager takes a step or reduces the food content of a patch by one unit. In addition, foragers do not come back to a previously visited patch.

Even though the model does not specify any interaction among foragers, it does have an implicit fission-fusion mechanism: when two foragers coincide in the same patch, they form a temporary aggregation that can continue as they forage together in other patches, whereas they can also split due to their previous history of visits. Figure 1 shows a summary of the different situations observed in the model: for certain values of the parameter that controls patch size heterogeneity, the foraging trajectories and the size of the temporary aggregations are similar to those described in field studies of spider monkeys (Symington 1988; Ramos-Fernandez & Ayala-Orozco 2003). Particularly, intermediate values of patch size heterogeneity led to the longest foraging trajectories and the largest aggregations. This is because foragers traveled long distances to reach large patches that were neither rare nor scarce, coinciding with others more often at these large patches (Ramos-Fernandez et al. 2006).

These results show that an important ecological influence on FFD could be the relative abundance of patches of different size, in contrast with the usual measures of overall food abundance or average patch size. This can be taken as a prediction for field studies in which the size of visited patches can be measured.

We then developed a simpler version of this model, aimed at testing the idea that groups with FFD could be more

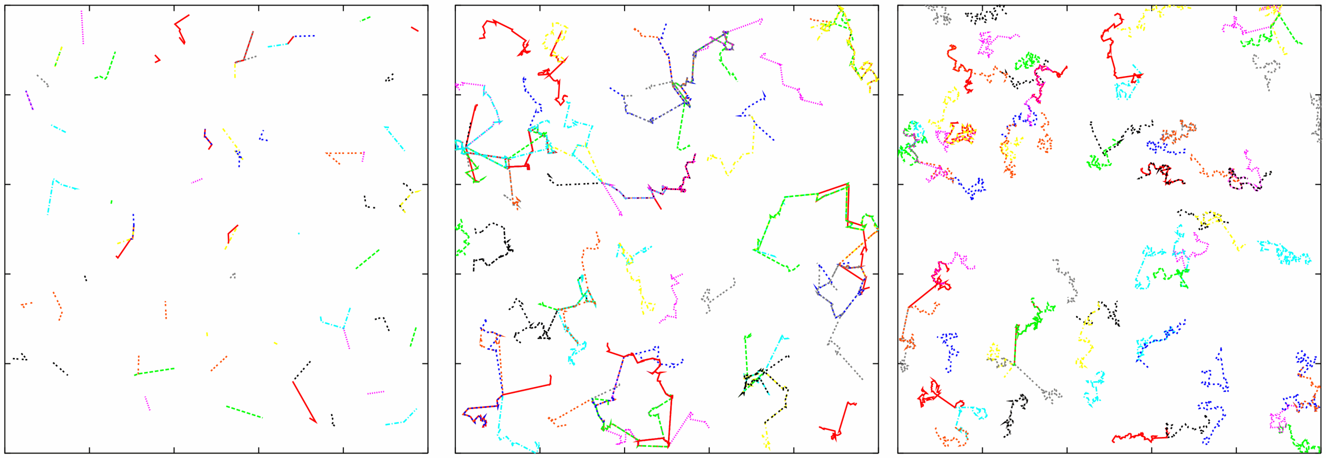

Figure 1. Movement trajectories described by foragers in the agent-based model by Ramos-Fernández et al. (2006). Each line (in different color) represents a different forager. Starting from randomly assigned positions, foragers move to the nearest and largest food patch available (points not visible in the figure). The left panel corresponds to a situation with maximum heterogeneity in patch size and thus a comparatively large proportion of large patches. In this situation, foragers find a large patch very close and the simulation "freezes" with very little interaction between foragers. On the contrary, the panel on the right represents a situation with minimum heterogeneity in patch size, and thus very few large patches. Here, foragers simply visit the nearest patch, describing long trajectories with many changes in direction. They may coincide with others but they mostly forage locally. The situation in the middle panel represents an intermediate level of heterogeneity in patch size, with some large patches that are often worth visiting even when they are far. The trajectories described by foragers are longer, with a combination of small and long "steps" between patches. This is the situation when foragers formed the largest subgroups with others with whom they coincided in these large patches.

efficient than cohesive groups at exploiting ephemeral and unpredictable patches, such as tropical trees, which have short fructification periods, each species with fruit at different times of year (Rathcke and Lacey, 1985). In this environment, food patches have a randomly assigned amount of food, which is present for a randomly chosen period of time. Foragers search for food using a correlated random walk, and they can be either cohesive (all agents move together) or separate (all agents move independently, as subgroups of spider monkeys do: Ramos-Fernández et al. 2011). The foraging efficiency is calculated as the number of food units obtained over the distance traveled by each forager. In order to control for the effect of group size on the foraging efficiency, the same number of foragers are present in both conditions. Preliminary results show that the efficiency of separate foragers is in fact greater than that of the cohesive foragers.

We have successfully used agent-based models to explore the minimum, simplest conditions that could produce a collective pattern out of local interactions between agents and their environment. Also, these models have served to develop predictions to be tested with further fieldwork and to test hypotheses about the adaptive function of FFD.

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