Limited resources and evolutionary learning may help to understand the mistimed reproduction in birds caused by climate change

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ABSTRACT

We present an agent-based model inspired by the Evolutionary Minority Game (EMG), albeit strongly adapted, to the case of competition for limited resources in ecology. The agents in this game become able, after some time, to predict the *a priori* best option as a result of an evolution-driven learning process. We show that a self-segregated social structure can emerge from this process, i.e., extreme learning strategies are always favoured while intermediate learning strategies tend to die out. This result may contribute to understanding some levels of organization and cooperative behaviour in ecological and social systems. We use the ideas and results reported here to discuss an issue of current interest in ecology: the mistimings in egg laying observed for some species of bird as a consequence of their slower rate of adaptation to climate change in comparison with that shown by their prey. Our model supports the hypothesis that habitat-specific constraints could explain why different populations are adapting differently to this situation, in agreement with recent experiments.

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1. Introduction

Minority games (Challet and Zhang, 1998), and more recently Evolutionary Minority Games (EMG) (Johnson et al., 1999a, 2000; de Cara et al., 2000; Johnson et al., 2003; Hod and Nakar, 2002; Hod, 2003; Sysi-Aho et al., 2003; Johnson et al., 1999b; Lo et al., 2000), have received widespread attention in recent years as a useful model to describe competition for highly limited resources in complex systems, especially in economics. These games are essentially based on a minority rule (Challet and Zhang, 1998) according to which N agents compete repeatedly for some resources by choosing between two options A or B. Each agent makes its choice, and those agents belonging to the less (most) frequently chosen option are considered the winners (losers), so they are rewarded (fined). So, the idea behind this game is that the agents must always try to be in the minority: few individuals choosing the same option as yourself means fewer competitors, so it should be easier to obtain the resource. The decisions taken by the agents are chosen according to a pool of strategies available, and these strategies are based on the m previous outcomes in the game, as that information is assumed to be accessible to all of the agents. To give a simple example, a specific strategy in a minority game with $m = 2$ has the form

$$S = \{(A, A) \to A, (A, B) \to B, (B, A) \to A, (B, B) \to A\}.$$

This means that if the two previous winning options in the game were (A,A), an agent following strategy S will choose option A the next time; if the last winning options were (A,B), that agent will choose B, and so on. At the beginning of the game several strategies are assigned to each agent, and the agent tends to choose from among them the strategy that gave better results in the past; however, many different versions of the minority game exist, where the rules that determine the strategies chosen by the agents are different. Here, we will skip the minor details on the mechanisms of the minority game, since that is outside the scope of the current work; an exhaustive compilation of works on minority games can be found in http://www.unifr.ch/econophysics.

In the evolutionary version (EMG) of the game (Johnson et al., 1999a), all the agents are assigned the same strategies but they can (i) follow that given strategy with probability p_k or (ii) do exactly the opposite with probability $1 - p_k$, where p_k is different for each agent (the subindex k denotes the kth agent). Those agents performing the worst (losing many times) are forced to change their value of p_k; so, in the EMG there is an implicit learning process based on *trial and error*. As a consequence, the system tends towards an optimal distribution of p_k values for which the number of winners is as close to $N/2$ as possible (note that, by definition, in a minority game the number of winners cannot be higher than $N/2$). As reported in Johnson et al. (1999a), the most striking result arising from the EMG is the natural emergence of segregated behaviour: those agents that behave in an extreme way ($p_k \to 0$ and $p_k \to 1$) perform better

than those with intermediate behaviour, so that the individuals tend to segregate into two groups: those who always follow the given strategy and those who never follow the strategy. From the point of view of complex systems, it has been claimed that this result may help to understand some levels of organization such as crowding (Johnson et al., 2000; Cont and Bouchaud, 2000) and cooperation (de Cara et al., 2000), which are common in many social and biological systems. Specifically, within the context of the EMG some authors have coined the term *unintentional* or *indirect cooperation* to illustrate the behaviour observed (Quan et al., 2003; Hod and Nakar, 2004). This concept refers to the fact that in the EMG many agents tend to behave similarly (either $p_k \rightarrow 0$ or $p_k \rightarrow 1$), but not consciously, but rather because the global winning probability is higher that way. This is different from other games (for example, the well-known Prisoner's Dilemma) where cooperation is a conscious option given to the agents (Nowak et al., 2004; Nowak, 2006).

2. Minority games in ecology

In general, minority games are helpful to describe multi-agent systems where each agent (individual) is able to analyze the history of the system (i.e., the success of the different strategies used before) in order to make its next decision. For this reason they have been especially designed and used to explain the complex dynamics of some financial markets (Johnson et al., 2003), albeit some authors have stated that similar ideas could also hold within an ecological context; probably the best example being foraging behaviour (Hod and Nakar, 2002; Hod, 2003). However, as far as we know very few real efforts have been made to extend minority games to ecological situations. In Tella et al. (2001) the authors presented a model, inspired by the rules of the minority game, to explore the *colonial versus solitary* behaviour in birds as a function of predation pressure, and some discussions on the connection between minority games and ecological evolution were provided in de Cara et al. (2000) and Sysi-Aho et al. (2003).

The apparent lack of interest by ecologists in these games is probably due to the fact that the most interesting and dramatic situations concerning decision-making in animals are not well described by such concepts as *trial and error* and *pool of strategies* involved in minority games. Instead, in ecology most of the interest lies in understanding those situations where individuals perform just one or a few critical decisions throughout their whole life (concerning, for example, timing in reproduction or choice of habitat); these decisions have been called 'fitness-critical actions' in a very recent work by Heesch and Little (2006). Intuitively, decision-making in these 'fitness-critical actions' follows quite simple mechanisms (compared to the complex rules of minority games): the individuals need to use their skills or their experience to predict the *a priori* best option. By *a priori* best option we mean that option which would be the winning one in the case where half of the agents choose A and the other half choose B. In the basic minority game described above we have considered that the agents choose between two identical options A or B, so there is no *a priori* best option. However, it is easy (and more realistic) to consider a game where A and B are intrinsically different. For example, in the case of habitat selection, individuals usually need to choose between different options with different habitat qualities. Some individuals may be able, from past experience, to know in advance which the best choice is e.g. that where the availability of food is higher. But if all the individuals are able to do this, then all of them will choose the same option and the availability of food will decrease there; in that case the *a priori* best option is not necessarily the winning option. Those individuals that are not able to determine what the *a priori* best option is will probably behave *randomly* or *persistently* (always choosing the same option). The

role of evolution and natural selection is thus expected to be crucial in these processes, as stated in Heesch and Little (2006).

We note that these decision-making mechanisms are also common in human behaviour. For instance, drivers who have to choose between two alternative routes in order to avoid traffic jams do not analyze every past experience and make a decision according to a pool of strategies (contrary to what is suggested by some authors (Hod, 2003)), but mainly use simpler strategies like *persistent* behaviour (they always choose the same route because they do not like to take risks) or they may simply listen to the traffic news to find out what the *a priori* best route is.

According to these arguments, some essential elements which are absent in the EMG must be considered in order to get a realistic implementation of minority games in ecology. So, the aim of this work is to present a new game where competition for resources is also introduced by means of a minority rule, but the dynamics and strategies followed by the agents aim to capture the dynamics of some ecological systems. In what follows, we will refer to this new model as the Evolutionary Learning Game (ELG).

3. Mistiming in predator-prey systems caused by climate change

We now introduce a specific problem that has attracted the interest of ecologists in recent years (van Noordwijk et al., 1995; Visser et al., 1998; Grieco et al., 2002; Visser et al., 2004; Gienapp and Visser, 2006) and has strongly motivated our approach. In many species of bird, individuals must face the problem of choosing the correct time for egg laying. This choice becomes dramatic if the availability of food is restricted to a very short period of time. So, for survival in breeding, the correct timing of egg laying is necessary, so that the feeding period matches the food peak. This process has been studied in recent decades for some species, such as great tits (*Parus major*) and blue tits (*Parus caeruleus*), whose main prey (caterpillar) is only available for two or three weeks in the late spring (Visser et al., 2004). At the moment of egg laying (approximately one month before), the birds do not know when the food peak will happen. The problem is partially overcome by the way many of these birds develop with age the ability to follow some cues (based on climate and other environmental parameters) to predict the right time for laying (van Noordwijk et al., 1995; Grieco et al., 2002; Gienapp and Visser, 2006). In general, this capacity of an individual to adapt its behaviour to the environmental conditions is known as phenotypic plasticity, and is usually a heritable trait. Specifically, it has been demonstrated (Nussey et al., 2005) that plasticity in egg laying for birds is heritable.

The effects of global climate change, however, have put many biological species to the test (Parmesan, 2006). As a consequence of warmer springs, caterpillars have advanced their hatching date in many habitats (Visser et al., 1998, 2004), so those birds with a higher plasticity in laying are expected to adapt better to the new situation. According to the observational data, some bird populations have become adapted, but in some other cases a very weak response to the new situation has been observed (Visser et al., 2004; Gienapp and Visser, 2006). In the latter case, the mismatching between the feeding period and the food peak will probably lead to a decline in the number of individuals (Both et al., 2006) or the habitat fitness (Visser, 2007). Although different explanations have been provided, there is no clear understanding of why different populations show different responses to the changing conditions (Gienapp and Visser, 2006). As we discuss below, our model provides some arguments that support the idea that resource constraints from each specific habitat may be responsible for these differences.