Collective strategies and cyclic dominance in asymmetric predator-prey spatial games

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A B S T R A C T

Predators may attack isolated or grouped prey in a cooperative, collective way. Whether a gregarious behavior is advantageous to each species depends on several conditions and game theory is a useful tool to deal with such a problem. We here extend the Lett et al. (2004) to spatially distributed populations and compare the resulting behavior with their mean-field predictions for the coevolving densities of predator and prey strategies. Besides its richer behavior in the presence of spatial organization, we also show that the coexistence phase in which collective and individual strategies for each group are present is stable because of an effective, cyclic dominance mechanism similar to a well-studied generalization of the Rock-Paper-Scissors game with four species, a further example of how ubiquitous this coexistence mechanism is.

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1. Introduction

There are a myriad of foraging strategies that predators utilize to increase their success rate. Among them, prey may be attacked in a cooperative, coordinated way by a group of predators employing similar spatially and temporally correlated actions. When different and complementary behaviors are involved, it is also called a collaboration (Bailey et al., 2013). Examples of animals that exhibit coordinated or collaborative hunting include lions (Heinsohn and Packer, 1995; Legge, 1996; Stander, 1992) (also the pair of man-eater lions of Tsavo Yeakel et al., 2009), hawks (Bednarz, 1988), crocodiles (Dinets, 2015), spiders (Nentwig, 1985; Vakanas and Krafft, 2001), ants (Dejean et al., 2010), and several other species (Bailey et al., 2013). Interspecies collaborations exist as well, for example, between fishermen and dolphins in the south of Brazil (Daura-Jorge et al., 2012; Pryor et al., 1990), honey hunter men and honeyguide birds (Isack and Reyer, 1989; Spottiswoode et al., 2016), coyotes and badgers (Minta et al., 1992), among others (Bshary et al., 2006). Hunting in groups may bring several benefits and has been widely discussed (for a review, see Bailey et al., 2013 and references therein). For example, it increases the probability of capturing large prey (Bednarz, 1988; Creel and Creel, 1995; Dejean et al., 2010; Malan, 1998), helps prevent the carcass from being stolen by other predators (Brockmann and Barnard, 1979; Vucetich et al., 2004), allows for faster food location (Pitcher et al., 1982) and more complex distracting, tracking and chasing tactics, helps related conspecifics that may be unable to hunt or are in the process of acquiring hunting skills (Galef and Giraldeau, 2001; Malan, 1998), etc. On the other hand, there may be setbacks as it also increases the competition between members of the group while feeding, concentrates the search for food to a smaller territory that may decrease the availability of prey, etc. Collective tactics may also benefit prey (Garay, 2009). Surveillance is more efficient when done in parallel by several individuals while others have more time to feed themselves (Beauchamp, 2008; Pays et al., 2007; Pulliam, 1973). The probability of being caught is smaller (Hamilton, 1971; Ioannou et al., 2012) and the group may take advantage of group distracting (Cresswell and Quinn, 2010), intimidating and escaping techniques. Conversely, a group of prey may be more easily spotted than an individual and the resources should be shared by all members (Giraldeau, 1988; Ritz and Hamner, 1997). In addition to those factors, for both prey and predators, collective decision making can be improved in larger groups (Conradt and List, 2009; Couzin, 2009) (but information sharing may involve costs Barbier and Watson, 2016 and benefits van der Post and Semmann, 2011 as well).

Despite mounting experimental results, much less attention has been dedicated to model coordinate hunting (Packer and Ruttan, 1988). Over a decade ago, Lett et al. (2004) introduced a game theoretical model, hereafter referred to as the LAG model, in which the abundance of prey and predators were assumed constant and only the fractions of each populations using either an individual or

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Table 1
Model parameters (Lett et al., 2004) along with the default value considered here.

	Definition and default value
p	Probability of a predator in a group capturing a lone prey (0.5)
G	Gain per captured prey per unit of time (1)
n	Number of predators in a group (3)
e	Number of prey captured by a group of predators (2)
α	Preying efficiency reduction due to grouped prey
β	Preying efficiency reduction when hunting alone
γ	Reduction of prey resources due to aggregation (1)
F	Gain for isolated prey per unit of time (1)

a collective strategy coevolved (see, however, Mchich et al., 2006). The LAG model takes into account some of the advantages and disadvantages for both prey and predators choosing a grouping strategy. More specifically, it is assumed that grouping lowers the risk of being preyed at the cost of increasing the competition for resources, while predators have a greater probability of success at the expense of having to share the prey with others, sometimes referred to as the "many-eyes, many mouths" trade-off (Giraldeau, 1988; Ritz and Hamner, 1997). Prey and predators were modeled by assuming a fully mixed (no spatial structure), mean-field approach, and the temporal evolution of both densities being described by replicator equations (Hofbauer and Sigmund, 1998).

A complementary approach, based on a less coarse grained description, explicitly considers the spatial distribution of individuals and groups. The local interactions between them introduce correlations that may translate into spatial organization favoring either grouping or isolated strategies, raising a number of questions. For instance, do these strategies coexist within predators or prey populations? If yes, is this coexistence asymptotically stable? How does the existence of a local group induce or prevent grouping behavior on neighboring individuals? Do gregarious individuals segregate, forming extended regions dominated by groups? In other words, how spatially heterogeneous is the system? Does the replicator equation provide a good description for both the dynamics and the asymptotic state? If not, when does it fail? If many strategies persist, which is the underlying mechanism that sustains coexistence? We try to answer some of these questions with a version of the LAG model in which space is explicitly taken into account through a square lattice whose sites represent a small subpopulation. Each of the sites is large enough to contain only a single group of predators and prey at the same time. If any of these groups is ever disrupted, their members will resort to a solitary strategy, hunting or defending themselves alone.

The paper is organized as follows. We first review, in Section 2.1, the LAG model (Lett et al., 2004) and summarize the main results obtained with the replicator equation, and then describe, in Section 2.2, the agent based implementation with local competition. The results obtained in the spatial framework are presented in Section 3. Finally, we discuss our conclusions in Section 4.

2. The model

2.1. Replicator equations

Lett et al. (2004) considered, within a game theoretical framework, grouping strategies for prey and predators. Both can choose between single and collective behavior and each choice involves gains and losses for the individuals, as discussed in the introduction. The relevant parameters of the model are defined in Table 1. The size of both populations is kept constant during the evolution of the system; only the proportion of cooperative predators, $x(t)$, and the fraction of gregarious prey, $y(t)$, evolve in time (see, however, Ref. Mchich et al., 2006 for a version that also considers population dynamics). Variations depend on how the subpopulation's

payoff compares with the average payoff of the respective population. If collective behavior leads to a larger payoff than the average, the associated density increases, otherwise it decreases. This dynamics is then described by the replicator equations (Hofbauer and Sigmund, 1998).

For the fraction x of predators hunting collectively, the payoff is (Lett et al., 2004)

$$P_x = \frac{e\alpha pG}{n}y + \frac{pG}{n}(1-y).$$

The first contribution comes from the interaction of these predators with the fraction y of prey that organize into groups for defense. By better defending themselves, prey reduce the hunting efficiency by a factor $0 \le \alpha < 1$; nonetheless, e prey are captured with probability p and the gain G per prey is shared among the n members in the group of predators. The second term is the gain when the group attacks an isolated prey, whose density is $1-y$, and shares it among the n predators as well. When the remaining $1-x$ predators hunt solely, they are limited to a single prey and an efficiency that is further reduced by a factor $0 \le \beta < 1$, what is somehow compensated by not having to share with others. This information is summarized in the payoff matrix:

$$A = \begin{pmatrix} e\alpha pG/n & pG/n \\ \alpha\beta pG & \beta pG \end{pmatrix}. \tag{1}$$

As isolated prey consume the available resources, the gain per unit time is, on average, F. Once aggregated, the resources are shared and the individual gain reduced by a factor $0 \le \gamma < 1$. The fraction of prey that aggregates becomes less prone to be preyed on by a factor α. If the grouped prey are attacked by a group of predators, e prey are captured and Lett et al. (2004) considered that the payoff coefficient is $1 - e\alpha p$ (imposing $e\alpha p \le 1$). On the other hand, a lone predator has its efficiency reduced by a factor β, thus the surviving probability is $1 - \beta p$ or $1 - \alpha\beta p$ for an individual or a group of prey, respectively. The payoff for the fraction y of prey that remain grouped is then written as

$$P_y = (1-e\alpha p)\gamma Fx + (1-\alpha\beta p)\gamma F(1-x).$$

A similar consideration can be done for isolated prey (Lett et al., 2004), whose payoff matrix is

$$B = \begin{pmatrix} (1-e\alpha p)\gamma F & (1-\alpha\beta p)\gamma F \\ (1-p)F & (1-\beta p)F \end{pmatrix}. \tag{2}$$

It is the difference between the payoff P and its average, $\overline{P}$, that drives the evolution of both x and y. Indeed, the replicator equations, $\dot{x} = x(P_x - \overline{P_x})$ and $\dot{y} = y(P_y - \overline{P_y})$, which give the rate at which these two densities evolve in time, are (Lett et al., 2004)

$$\frac{\dot{x}}{x} = (1\ 0)A\begin{pmatrix} y \\ 1-y \end{pmatrix} - (x\ 1-x)A\begin{pmatrix} y \\ 1-y \end{pmatrix}$$

$$\frac{\dot{y}}{y} = (1\ 0)B\begin{pmatrix} x \\ 1-x \end{pmatrix} - (y\ 1-y)B\begin{pmatrix} x \\ 1-x \end{pmatrix}. \tag{3}$$

These equations describe an asymmetric game and can be rewritten as (Hofbauer and Sigmund, 1998):

$$\dot{x} = x(1-x)[\alpha_{12}(1-y) - \alpha_{21}y]$$
$$\dot{y} = y(1-y)[\beta_{12}(1-x) - \beta_{21}x], \tag{4}$$

where

$$\alpha_{12} = -p(\beta - 1/n)G$$
$$\alpha_{21} = \alpha p(\beta - e/n)G$$
$$\beta_{12} = [\gamma - 1 + \beta p(1 - \alpha\gamma)]F$$
$$\beta_{21} = [1 - \gamma - p(1 - e\alpha\gamma)]F. \tag{5}$$