

Predators-prey models with competition: the emergence of territoriality

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Abstract

We introduce a model aiming at shedding light on the emergence of territorial behaviors in predators and on the formation of packs. We consider the situation of predators competing for the same preys (or spatially distributed resource). We analyze the influence of different factors on the predictions of our model. We focus our attention on the effects of the segregation of the population of predators into competing, hostile packs on the overall size of the population of predators. The model allows us to give an economics interpretation of territoriality (in the sense of Brown 1964). We thus give a purely evolutionary interpretation of territorial and social behaviors. We present some numerical simulations that allow us to describe our counter-intuitive and most important conclusion: lethal aggressiveness among hostile packs of predators may actually lead to an increase of their total population.

Introduction

A long standing and major problem in ecology is to understand the emergence of territoriality, and in particular, its competitive advantage. Any theory on animal behavior regarding territoriality has to indicate how the relative fitness increases for individuals that adopt territorial behavior. A common and unifying theory of territoriality may be difficult (if not impossible) to formulate due to the large variety of environments that host such organisms. This is confirmed by a *reductio ad absurdum* based on the simple observation that not all species are territorial.

Among specific theories that have been proposed we can recall for instance the settlement in familiar sites to increment the efficiency of food-retrieval and decrease mortality (Johnson and Gaines 1990; Larsen and Boutin 1994), the regulation of the population density (Wynne-Edwards 1962), provision and allocation of resources (Brown 1964; Wilson 1975), the avoidance of contagious diseases by the formation of buffer zones between different territories (Krebs 1971).

A general theoretical framework for territorial behaviors should satisfy two prerequisites: *aggressiveness* among the con-specifics and *economic defendability* of the territory (Brown 1964). In this direction, a good approach to analyze the problem is to adopt an economic viewpoint. That is, first, aggressive behaviors are favored if they help to increase the survival of the organism and its likelihood of reproduction, and thus a territory will form if there is an advantage in increasing the food availability, the mating probability, or the survival of the animal or of its offspring. In this context, it has been pointed out that a key aspect could be the relative –and not absolute– increase of the fitness of the individual that adopt a specific strategy, that is, the establishment of a territory may also favor the occupier by limiting the access to the resources (food and possible encounters with mates) of those that do not possess a territory, and not necessarily by increasing the net availability of the needed resource (Verner 1977). Secondly, the territory should be *defendable* in economics terms, that is, the benefits gained from territoriality should offset the energy invested in the active defense against invaders. For instance one can consider the problem of the allocation of time and energy by predators (Hixon 1980). In this approach, the main insight is that predators have to spend time in warding off competitors, which time cannot be used to catch preys. By taking into account the different contributions to the allocation of time and energy, one can also derive an estimate of the optimal size of territory.

On the other hand, a different problem is the emergence of co-operation and sociability (Alexander 1974; Allee 1958; Bergstrom 2002; Hamilton 1964; Jones 2014), and in particular in the formation of large groups of predatory animals in a competitive environment. While it may seem easy to see the advantages of a social behavior in some species (e.g. the nurturing of the newborns by the whole pack, the possibility to adopt efficient hunting strategies or the establishment and the defense of a territory), when dealing in particular with predators, all the obvious benefits seem to require an already established and well functioning social structure. Thus these features cannot be used to explain the emergence of sociability in an evolutionary context. Even though explanations have been suggested in order to fit the Darwinian point of view with the predominant selfishness that characterizes the fundamental state prior to the evolution of social features (such as cooperation and “altruism”), a crucial point remains: how can a social behavior flourish in an environment composed by only selfish individuals?

Finally, a vast part of the scientific literature in mathematical biology concerns the study of competition as a promoter for heterogeneity and persistence in the environment (see for instance, Comins and Blatt 1974; Shigesada et al. 1979). Here the focus is on the implications that a strong

selfish-competing behavior has on the spatial distribution of the species under consideration. The goal in that work is to analyze populations of preys competing for a common resource. Then, the aggressiveness of the predators may favor a richer diversification in the population of preys and also in the populations of predators that occupy the same region. Regarding models with competition between predators, we wish to bring to the reader's attention an article of Kuang et al. (2003) that considers a system of ordinary differential equations (with no space variable). It analyses mainly the situation of internal competition between members of the same species, while extra-specific competition is mild. It shows that this situation can be a promoter of biological diversity among predators for the same resource.

The aim of this paper is to present a relatively parsimonious mathematical model that contains the three aspects above. Our starting point, which we feel is also the strength of our approach, is to consider an environment occupied by preys and predators that interact between each other but have no a priori social structure imposed on them. By varying the degree of aggressiveness among predators of some individuals towards others, we see that the separation of the territory occurs spontaneously and, moreover, in many cases the aggressiveness between groups is self-sustained by a strong increase in the *economic defendability* of the territory, as a new consequence of the formation of the territory itself.

Thus, we see in many cases that the emergence of very hostile and competing groups, meaning lethal encounters between individuals of different groups, even though they lead to an increase of mortality, may result in many cases in a global increase of the population and a better defendability.

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Methods

Reaction-diffusion equations play a fundamental role in mathematical biology, and in particular in the study of population dynamics. Many models have been introduced in the literature in order to give more precise and succinct explanations of phenomena that are well documented in these domains. In this perspective, our approach is not dissimilar to the established one, but the novelty, as it will be clear later, stands on the questions to which we want to give an answer with the models, and thus the mathematical instruments we use. An aspect that is crucial in our analysis is the spatial distribution of the individuals of both the population of preys and predators. For this reason, an approach based on a sole system of ordinary differential equations is not sufficient for our scopes: we will need also to introduce a spatial component in the analysis.

Overview of the theoretical framework

Interactions between organisms (or groups of organisms) can be very complex, in particular in highly differentiated environment, but we can mostly divide them in three different categories: cooperative, competitive or predator-prey. A cooperative interaction benefits (directly or indirectly) both the agents, a competitive interaction affects negatively the two actors of the interaction, and finally a predator-prey interaction benefits the predator while hurting the prey.

Competitive interactions between predators can be again divided into two sub-categories (Holomuzki et al. 2010; Lang and Benbow 2013): interference competition and exploitative competition (in this paper we will not consider apparent competition, as it mainly concerns preys). In the case of interference competition, each organism directly influences negatively the fitness of the other; this is the case, for instance, of territorial predators, that actively defend their territory from the invasion of another predators. Differently, exploitative competition is characteristic of two agents that compete indirectly and only because they consume the same resource; this is the case of herbivores that eat the same plants, or predators that hunt the same prey.

From a modeling point of view, we adopt the paradigm suggested by Volterra (1928) and Lotka (1932) to model all interactions between groups. The rationale behind the interaction proposed by Volterra and Lotka is that, given two populations, the effects of the interaction between the two is proportional to the probability of such interaction. This translates into quadratic terms in the differential equations that describe the dynamics, given by the product of the densities of the interaction species.

Overview of the literature

To our knowledge, Dancer and Du (1994) were the first to analyze the effect of strong competition between two different populations: the authors propose to study the model of two competing populations, occupying the same territory. The most important aspect of their work is to establish a precise description of the solutions of this model when the competition parameter diverges; in particular, they are able to show that it makes sense, from a precise mathematical point of view, to consider the case of infinite competition, a case which, they show, implies a complete segregation of the species and thus partition of the original region in two subregions –territories– each of which contains only one of the two populations. A main aspect of their model is that competition has always negative effects on the two groups: it can be shown, indeed, that the highest total population is achieved only if the competition is absent in their model. As a result, the adaptive significance of strong competition, in this case, can be explained only as an augmentation of the relative fitness: more precisely, aggressiveness is a defensive response that will have only detrimental effects on the two populations.

Dockery et al. (1998) proposed a different yet relevant model. The focus is on what is the optimal dispersion strategy for groups of individuals competing for the same resource: the authors show, quite remarkably, that if the distribution of the food source is heterogeneous (that is, non constant in the region) and sufficiently abundant, then all the solutions of their proposed model converge for large time to the solution that has a unique group of individuals, the one that had the smallest diffusion rate. This lead to the famous result “slow diffusion wins”, that had been substantially verified in empirical observations, for instance in asian carps, an invasive species of the great lakes (DeGrandchamp et al. 2008). Under some assumptions, we can show that our model is deeply linked to the model proposed by Dockery et al., though there is a crucial difference, that is underlined more specifically in the appendix: unlike our model, the model of Dockery et al. considers only exploitative competition, that is, competition for the food source. This, as we shall see, will reflect in radically different results about the stability and the convergence of solutions.

Finally, we mention the literature involved in the study of the territorial mechanisms that characterize wolves and coyotes, initiated by the seminal contribution (Lewis and Murray 1993) and further developed in a series of works (Giuggioli et al. 2011; Hamelin and Lewis 2010; Lewis

et al. 1997; Moorcroft et al. 2006; Potts et al. 2012; Potts and Lewis 2014, 2016a,b; White et al. 1996a). By introducing a coupled system of equations to model location, deposition and expiration of markings, Lewis and Murray succeed in describing the shape of the territories and the disposition of the markings left by the different individuals, and in particular they manage to describe the insurgence of some *buffer zones* that separate the territories occupied by the groups: these zones can in fact be found in nature, and one expects to find more preys therein. Indeed, preys can use these locations as safe areas. A subsequent refinement (White et al. 1996b) introduces in this system a coupling between scent markings left by predators, predators and preys (in this case, wolves and deers), by assuming that the deposition of markers by predators is influenced by the presence of preys, and that densities of predators and preys follow some laws similar to the Lotka-Volterra system. These modifications result in a model that describes with more detail the buffer zones in between different territories, showing for instance a higher concentration of preys in these corridors. Although the model is quite different from the one we present here, their results suggest possible future directions of refinement of our own model.

Derivation of the model

We propose a model that is motivated in view of the previous remarks: we consider a region (denoted henceforth with the letter \mathcal{R}) occupied by a population of preys denoted by u and n groups of predators denoted by w_1, \dots, w_n . All the parameters introduced are to be considered positive.

The individuals of the population of preys u , in their natural dynamics, diffusive in the region \mathcal{R} , reproduce and perish, and are hunted by the predators. As a result, the population u follows the dynamics

$$(\partial_t - D\Delta)u = \left(r - \frac{r}{K}u - \sum_{i=1}^n p_i w_i \right) u \quad (1a)$$

where D is the diffusion rate of the preys, r is the growth rate, K is the (local) carrying capacity of the region \mathcal{R} and finally p_i are the predation efficiency coefficients, that is how an encounter with a predator (whose probability is proportional to uw_i) affects negatively the population of preys in average. Similarly, the predators diffuse, starve in absence of preys, hunt preys, compete internally and, more importantly, compete actively with each other (interference competition). To accommodate these characteristics, we propose to model the dynamics of each density w_i by the equation

$$(\partial_t - d_i\Delta)w_i = \left(-l_i + p_i u - a_{ii}w_i - \beta \sum_{j \neq i} a_{ij}w_j \right) w_i. \quad (1b)$$

Here, d_i is the diffusion rate of the i -th population, l_i is the loss (mortality) rate in absence of preys, p_i is the predation efficiency coefficient for group i , a_{ii} is the competition term among individuals of the same group, a_{ij} is in general the competition rate seen as how an encounter with the j -th group affects negatively the i -th group, and β is the strength of this competition. In the model we leave open the possibility of coefficient a_{ij} being different from a_{ji} , since predators may have asymmetric responses to a confrontation (Adams 1990). We emphasize the dependence of the coefficients on the index i to point out that we can take into consideration different models at once. Indeed, this system of equation can either describe groups of con-specifics (e.g., packs of

predators), that is of the same species, or different species in competition. The former case corresponds to a situation in which the coefficients in the system do not depend on i . Mathematically this distinction does not affect our analysis, though the results that we will describe can be used to draw different conclusions depending on the settings.

Value	Description
i, j	indices corresponding to a particular group/density of predators
\mathcal{R}	region/environment occupied by the preys and predators
D	diffusion coefficient of preys u
d_i	diffusion coefficient of preys w_i
r	reproduction rate of the preys
K	(mean) prey-carrying-capacity of the region \mathcal{R}
p_i	rate of success of predation of a given encounter prey/predator
l_i	loss rate/starvation rate of the predators in the absence of preys
a_{ii}	competition among individuals of the same group of predators
a_{ij}	competition among individuals of the groups of predators i and j , modulated by
β	characteristic size of inter-group competition

Table 1: Short description of the parameters of our model

We complete the model with non negative initial conditions which states that, at the time we start the observation, the region \mathcal{R} is occupied by predators and preys

$$u(x, 0) = u_0(x) \geq 0, \quad w_i(x, 0) = w_{i,0}(x) \geq 0 \quad \text{for any } x \in \mathcal{R}.$$

As for the boundary conditions, we consider here the case in which the region \mathcal{R} is isolated from the surrounding environment: there is no flux of individuals across the boundary $\partial\mathcal{R}$. Mathematically the no flux condition is translated into:

$$\nabla u(x, t) \cdot \nu = \nabla w_i(x, t) \cdot \nu = 0 \quad \text{for any } x \in \partial\mathcal{R} \text{ and } t > 0$$

where ν is the outward normal vector at the boundary. The Neumann boundary condition has also the advantage of minimizing spurious effects of the boundary.

Our insulation assumption on \mathcal{R} does not play a particular role for the properties of this system. Indeed, numerical simulations have extensively confirmed that one obtains most of our conclusions with different types of boundary condition, for instance, when the boundary is permeable or under Dirichlet conditions (i.e., no density on the boundary). Note that we have conducted the mathematical analysis of the model under this boundary condition (Berestycki and Zilio 2017).

We wish here to point out what we think is the main difference between the approaches previously introduced and our approach to the problem. In considering a system that describes both the preys and the predators, our aim is to show that a very simple mechanism, such as the predation and the competition in the Lotka-Volterra frameworks, are sufficient to explain why the predators establish territories and why they may adopt social behavior. As a result, we do not include in our model sophisticated behaviors such as the interactions with the territory markings. Nonetheless, the model is sufficient to describe territoriality as an emergent property of the system not given a priori.

Results

In this section we discuss the properties of the model and the predictions that can be drawn from it. We shall concentrate here only on the ecological consequences, leaving most of the mathematical discussion of the model and the complete proofs of the results to a dedicated paper (Berestycki and Zilio 2017). One of the striking features of our model here is that it describes a variety of circumstances, from hostile to favorable environments, from a single population of predators to the segregation in packs with territorial behavior in predators. Thus we can compare various situations with different numbers of packs and different territorial configurations. As we will see, we can also use it to provide reasonable estimates on the maximum number of territories that can be formed in a region by the predators as a function of various ecological parameters.

To start with, we can observe that standard mathematical arguments show that our model is well-posed, that is, for any non negative initial data (i.e., feasible densities of predators and preys), there exists a unique solution of the system (1).

Weak versus strong territorial behavior

The strength of the competition parameter β has a strong influence on the spatial distribution of predators. In particular, while for small values of β the various components of the predators can overlap, for very large values of β we find

$$w_i(x, t)w_j(x, t) \rightarrow 0 \quad \text{as } \beta \rightarrow +\infty, \quad i \neq j \quad (2)$$

for all $t > 0$ and $x \in \mathcal{R}$. The term $w_i w_j$ has two interpretations. Firstly, heuristically, as in the Lotka-Volterra theory, the quantity $w_i(x, t)w_j(x, t)$ is proportional to the probability of individuals the density w_i of encountering individuals from density w_j at location x and time t . Secondly, the product $w_i(x, t)w_j(x, t)$ describes the superposition of the densities. In order to illustrate this more clearly, let us assume that at the location and at time (x, t) we find $w_i(x, t)w_j(x, t) = 0$: the, this clearly entails that at least one of the two densities $w_i(x, t)$ or $w_j(x, t)$ is equal to zero. That is, the populations do not overlap at (x, t) . Thus we can rephrase the conclusion in (2) as follows. Increasing the value of the competition β has two effects: the encounters between the groups become more rare and the territories more clearly separated. The parameter β represents the intensity of the competition. Our result shows that this parameter can be used to tune the model in order to describe predators that have weak territorial behavior, and home ranges that overlap extensively (small values of β) (Getty 1981; Stamps 1990) or predators that exhibit strong territorial behavior tendencies and whose territories have sharp boundaries (large values of β) (Askenmo et al. 1994; Eason et al. 1999; Nursall 1977).

Hostile environment

In considering the behavior of the solutions as a function of time, we already have the following result: if it happens that for some index i the inequality $Kp_i \leq l_i$ is verified, then independently of the initial configuration, the i -th group of predators in (w_1, \dots, w_n) goes extinct. That is, in mathematical terms,

$$Kp_i \leq l_i \quad \text{implies} \quad \lim_{t \rightarrow +\infty} w_i(x, t) = 0.$$

Let us explain the biological meaning of this result. The carrying capacity K is, by definition, the maximum amount of preys that can be locally sustained by the region \mathcal{R} , so that Kp_i is the per capita maximum amount of preys that can be caught by a predator in the i -th group. On the other hand, l_i is the per capita loss rate in the i -th group of predators i . It follows that the previous inequality can be interpreted as an energy balance for the i -th group: if the per capita maximum intake of preys (read, energy) is not greater than the minimum amount necessary for survival, the population will starve. As a consequence, we have

Principle 1 (Extinction) *Keeping all the other parameters fixed, if the carrying capacity K is sufficiently small (precisely, less than or equal to $\min_{i=1,\dots,n} l_i / p_i$), then the environment cannot sustain any predator.*

As a particular case, if the densities w_i correspond to the same species of predator (and thus the coefficients do not depend on the subscript i), the previous result implies that for small enough K the environment cannot carry at all the particular species.

It should be pointed out that this estimate of the threshold for survival of predators does not depend on the region \mathcal{R} . Moreover, there is no threshold for the survival of the preys. One aspect of this shortcoming is that, in the model we proposed, the populations of preys and predators have continuous and not discrete values (Durrett and Levin 1994). Finer models could solve this issue, at the cost of make the subsequent analysis less clear.

Exclusive environment

Next, we analyze the spatial behavior of the solutions of our model, with a particular emphasis on long time asymptotic. To this end, we first introduce a characteristic number for the dynamics, defined as

$$\sigma := \mathcal{D} - \mathcal{G} \quad (3)$$

where $\mathcal{D} = \min\{D, d_i\}\gamma_1$ and $\gamma_1 > 0$ denotes the first non zero eigenvalue of $(-\Delta)$ in \mathcal{R} with homogeneous Neumann boundary conditions

$$\begin{cases} -\Delta\varphi = \gamma_1\varphi & \text{in } \mathcal{R} \\ \partial_\nu\varphi = 0 & \text{on } \partial\mathcal{R}, \end{cases} \quad (4)$$

D and d_1, \dots, d_n the diffusion coefficients, and \mathcal{G} is the Lipschitz constant of the right-hand side of the system. The constant σ is the combination of two opposing driving mechanisms of the system: the (linear) diffusion term and the (non-linear) reaction term. In order to describe these two more explicitly, let us first assume that the populations are subject to diffusion only, that is, the individuals neither die, nor reproduce, but they only disperse on the entire region \mathcal{R} . Then, by the theory of diffusion processes, we have that for each equation the quantity $D\gamma_1$ (or $d_i\gamma_1$) represents the time scale of spatial homogenization, that is the following convergence rate holds true

$$\left| u(t, x) - \frac{1}{\text{area}(\mathcal{R})} \int_{\mathcal{R}} u_0(x) \right| \leq Ce^{-\gamma_1 Dt}$$

where $C > 0$ and $\gamma_1 > 0$ (and similarly for each w_i). Thus \mathcal{D} summarizes the tendency of the populations to spread uniformly all over the region \mathcal{R} , the parameter $\min\{D, d_i\}$ is the (minimum) local diffusion rate and γ_1 is a global index of the geometrical properties of \mathcal{R} ,

depending on its size and shape. For instance, we observe that, if the domain is subject to an homothetic expansion ($\mathcal{R} \mapsto \lambda \mathcal{R}$ for $\lambda > 1$), then γ_1 (and thus \mathcal{D}) decreases.

The constant \mathcal{G} , on the other hand, sums up the character of the system: as it varies, the system changes from the purely diffusion case (when $\mathcal{G} = 0$), to a reaction (i.e. reproduction, death and hunting) one (when $\mathcal{G} > 0$). The larger the coefficient \mathcal{G} , the stronger the non-linear effects. Among other factors, we know that if the carrying capacity K or the strength of the competition β are very large, so is the parameter \mathcal{G} .

A classical result by Conway et al. (1978) says that, if $\sigma > 0$, then the diffusion wins against the reaction and the solutions of the model converge, as time increases, to the solutions of the corresponding ordinary differential equation system, that is

$$\begin{cases} \dot{U} = \left(r - \frac{r}{K}U - \sum_{i=1}^n p_i W_i \right) U, \\ \dot{W}_i = \left(-l_i + p_i U - a_{ii} W_i - \beta \sum_{j \neq i} a_{ij} W_j \right) W_i. \end{cases}$$

In particular, the averaged of the solutions of the system satisfy the above equation up to correction terms that decrease exponentially in time. Therefore, there is a spatial homogenization. The corresponding homogeneous (space-independent) model falls under the general framework introduced by Kuang et al. (2003) in order to study biodiversity as a result of interference competition. In particular, a straightforward analysis of the equilibria of the system implies that if the competition β is small compared to the competition inside each group a_{ii} , then mixed solutions (i.e., solutions with more than one component not identically zero) are stable and attractive, while if β is large enough compared to a_{ii} , the only stable solutions of the system are the so called simple solutions, that is solutions where all the components of (W_1, \dots, W_n) but one are equal to zero. As a result, if homogenization occurs and the competition is strong enough, at most one population of predators will settle in the region \mathcal{R} . We have

Principle 2 (Competitive exclusion) *Keeping fixed all the other parameters, there exists K' and a' such that if $K < K'$ and $a_{ii} < a'$, even if the environment can sustain some predators, due to the competition they will exclude one another. That is, a stable equilibrium has at most one group of predators present in the environment.*

Favorable environments

Depending on the initial conditions and on the choices of the parameters, the model predicts the existence of many stationary solutions that can be reached at equilibrium for large times. A crucial factor here for this is the strength of the competition between predators. To illustrate this, let us consider the case of the 1 + 2 model, that is the model of one group of prey and two (identical) groups of predators; looking for the possible equilibria of the system, we analyze the following stationary version of the model:

$$\begin{cases} -D\Delta u = \left(r - \frac{r}{K}u - pw_1 - pw_2 \right) u \\ -d\Delta w_1 = (-l + pu - \beta w_2) w_1 \\ -d\Delta w_2 = (-l + pu - \beta w_1) w_2. \end{cases}$$

For simplicity, we have discarded here the internal competition in the equation of the predators. First of all, we can show that in some cases, even if the carrying capacity is sufficiently high,

we may not have a heterogeneous solution, that is a solution with well separated groups of predators: this circumstance is very similar to the Principle of Competitive exclusion. Here is the precise statement.

Principle 3 (Homogenization) *If the strength of competition β is too small or the diffusion d of the predators is too large, the two groups of predators cannot separate and form distinct territories.*

The precise quantitative statement in this principle involves the following parameter:

$$\sigma' := d\gamma_1 - \frac{1}{1 + \frac{2p^2K}{r\beta}}(Kp - l).$$

We recall that here γ_1 is the first non zero eigenvalue of $(-\Delta)$ in \mathcal{R} with homogeneous Neumann boundary conditions (see (4) above). Notice that again σ' is of the form $\mathcal{D} - \mathcal{G}$ and is a counterpart of the homogenization threshold σ in (3). Note that, owing to the slightly different definitions, it can happen that $\sigma' > 0$ while $\sigma < 0$, in which case further mathematical considerations have to be developed. In particular, if the inequality $\sigma' < 0$ is satisfied, we can show that the model predicts the existence of separated solutions, and, depending on how strong the competition β is and how large the gap between the two sides of the inequality is, there may be more than one possible spatial configuration. Let us point out again that if K is too small, precisely $Kp \leq l$, we have extinction of all the predators. In order to ensure the existence of solutions with separated groups, it is sufficient to consider the case of β large: taking then the limit as $\beta \rightarrow +\infty$ in the inequality $\sigma' < 0$ we find the following

Principle 4 (Separation of the Groups) *Let us assume that the inequality*

$$d\gamma_1 < Kp - l$$

holds. Then if the strength of the competition β is sufficiently large, there are solutions with at least two distinct groups of predators.

This result can be interpreted as follows. From the *Principle of Extinction* we know that if $Kp - l \leq 0$, then the preys will never be enough to sustain the population of predators, which will consequently starve. Thus, $Kp - l > 0$ is a necessary condition for the survival of the predators. On the other hand, if $d\gamma_1$ is too large, $\sigma > 0$ and by the *Principle of Competitive Exclusion* and the spatial homogenization phenomenon, territorial behaviors will never emerge, since the diffusion is too large to allow it. The *Principle of Separation of the Groups* addresses as it were the case in between these two scenarios, that is, when the diffusion of the predators is relatively small and the habitat is abundant in preys, a strong competition between different groups will lead to a region that is partitioned into different territories.

Finally, we point out that the solutions persist for β very large, that is, in the limit $\beta \rightarrow +\infty$ the groups of predators segregate, that is they will not overlap in \mathcal{R} . One particular feature of the model is that, in the mathematical limit of segregation ($\beta \rightarrow +\infty$), it is possible to give a precise description of the location of the boundaries of the different territories. As an example, it follows that on the boundary between the territories occupied by w_i and w_j , the pressure exerted by the two groups is equal and opposite (mathematically, this translates in the equation $a_{ji}\partial_\nu w_i = a_{ij}\partial_\nu w_j$ for the exterior normal derivatives –here ν is the outward unit normal– of the

respective concentrations of predators in the two territories), and thus the model suggests that the boundaries of the territories can be found by matching the pressure of the competing predators (Adams 1998, 1990, 2001; Maynard Smith 1974). Moreover, in the case in which no strong asymmetry is present in the behaviors among the groups (that is, the groups tend to have the same behavior with each other), at the junction of three territories, these will divide the angle in three equal parts, thus predicting territories of hexagonal shapes in homogeneous environments, see Figure 8 and the discussion of the numerical investigations below. This conclusion is supported by the statistical analysis of the shape of territories that singles out hexagonal shapes as the most frequent configuration (Grant 1968) and it is also suggested by some simple behavioral models (Maynard Smith 1974). In contradistinction with these works, we start here from our general PDEs model and derive these qualitative properties of the solutions in a general manner. These works further mention observations exhibiting these features and thus our derivation is also in agreement with these observations.

Maximal capacity of predators groups

At this junction, a natural question is to know whether our model yields a qualitative information on the maximal number of groups that can survive in a given domain. This is made clearer in the extreme case of segregation of the groups, when the strength of the competition β is sent to infinity, that is, when the members of each pack do not trespass other groups territories. We introduce \mathcal{P}_{\max} as the maximal number of groups of predators that can be hosted in a region \mathcal{R} .

Principle 5 (Maximum number of group) *We consider an environment \mathcal{R} which hosts a population of preys and some groups of predators. The maximum number of groups \mathcal{P}_{\max} of predators that can persist in \mathcal{R} is always finite and moreover it holds asymptotically*

$$\mathcal{P}_{\max} \lesssim \frac{\text{area}(\mathcal{R})}{4\pi} \max_i \frac{Kp_i - l_i}{d_i} =: \Lambda$$

where the coefficients are described in Table 1, and the maximum is taken over the coefficient of the densities involved.

In this statement, the notation $\mathcal{P}_{\max} \lesssim \Lambda$ is understood to mean that $\mathcal{P}_{\max} \leq \Lambda + o(\Lambda)$ and $o(\Lambda)/\Lambda \rightarrow 0$ as $\Lambda \rightarrow \infty$.

We now give a biological interpretation of the result, by analyzing the dependence of the upper bound on the various parameters of the model. We recall that Λ stands for right hand side of the previous inequality.

First of all, if the region \mathcal{R} increases in size, then the maximal number of groups increases accordingly. For instance, if \mathcal{R} doubles in size, so does $\bar{\mathcal{P}}_{\max}$; this justifies the intuition that a larger region will host a larger number of groups than a small one.

If the carrying capacity K of the region increases, then $\bar{\mathcal{P}}_{\max}$ increases too. In particular, we find again that if K is too small, then we may have no groups of predators, or only one group, giving a different interpretation of the principles of extinction and competitive exclusion that we mentioned previously.

If the predation efficiency (p_i) increasing or the starvation coefficient (l_i) decreases, again \mathcal{P}_{\max} increases, implying for instance that smaller or more efficient predators can cover the region with a large number of groups.

Although the upper estimate of Λ is an asymptotic one, we conjecture that it is rather sharp. As a result, we can use it to infer an estimate on the minimal size of the packs territory, as predicted by our model. For instance, in the case of indistinguishable groups, that is groups formed by animals belonging to the same species, we claim that the average territory size (ATS) satisfies

$$\text{ATS} \propto \frac{d}{Kp - l}.$$

Thus, our model predicts a lower bound on the size of the territory of a predator/group of predators once the values of d , K , p and l are known. The relationship between K and the size of the territory is reminiscent of some empirical observations: indeed, as K is a rough upper estimate of the density of preys, from the formula we infer that the size of the territories are (at most) inversely proportional to the abundance of preys, a relation that has been already confirmed in some observations (Hixon 1980; Meyers et al. 1979; Temels 1987).

As a final remark, we observe that as the diffusion coefficient is smaller and smaller, the environment can sustain more and more groups of predators.

Aggressiveness and Economical Defendability

We can state the second fundamental result of the paper, which is concerned with the case of very large K . Fixing all the parameters of the model but the carrying capacity K , and taking the competition strength β very large, we have

- (i) if the carrying capacity K is small enough, then the only stationary solutions of the model contain at most one group of predators. This is a consequence of the Extinction Principle;
- (ii) if the carrying capacity K is larger than a threshold, then there are solutions that contain also a group of predators, but, depending on the other parameters, the solutions with more than one group of predators either do not exist or are very small and converge to 0 as the strength of the competition β diverges. This is a consequence of the Competitive Exclusion Principle;
- (iii) for even larger values of K , there are co-existing solutions, that is, solutions with more than one group of predators;
- (iv) finally, if K is sufficiently large, the co-existing segregated solutions, that is, the solutions with more than one group of predators and with β very large, have a larger total population of predators than the solutions with just one group of predators.

In particular we have that (i) is a consequence of the Extinction Principle; (ii) is a consequence of the Competitive Exclusion Principle; (iii) follows from the Separation of the groups Principle. The last point (iv) deserves some comments: we already recalled that, in the model of Dancer and Du (1994), the competition has only negative effects on the population, in terms of the total number of individuals. On the contrary, what the last scenario with K very large implies is the following. In the model of combined dynamics of predators and preys, the total number of predators in the case of very strong competition (the predators are strongly territorial and very aggressive in the defense) is higher in the case of a division of the population into two (or more) groups than in the case in which the territory is occupied by only one group of predators friendly to each other.

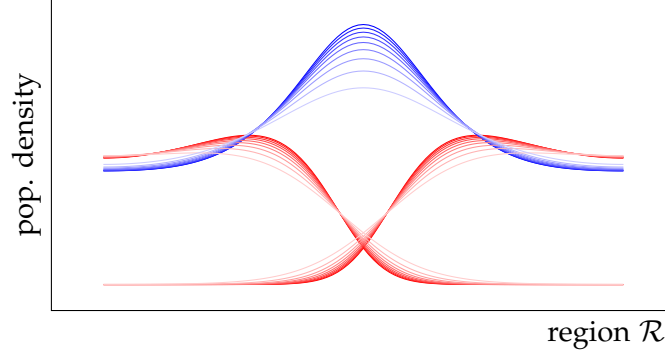


Figure 1: numerical simulations of the model, showing the impact of the competition parameter β on the distribution of predators (red) and preys (blue). Lighter colors correspond to small values of β , and darker colors to higher values. We see that the two groups of predators separate more clearly as β increases.

Moreover this result, when combined with the estimate of the maximal capacity, implies that (in the limit of strong competition) there exists a solution that maximizes the total number of predators in the region \mathcal{R} , and that if the parameters are correctly chosen, this solution has necessarily more than one group of predators.

This translate to the following principle

Principle 6 (Aggressiveness generates Economic Defendability) *If the competition rate β and the carrying capacity K are sufficiently large, the population of predators is maximized by a solution that has more than one group of predators.*

In Figures 1 and 2 we illustrate with the aid of some numerical simulations and a graphical schematization the content of the previous results. Figures 3, 4 and 5 allow us to give a more intuitive interpretation of this as a succession of three distinct phenomena: peaceful predators engage in aggressive behaviors (Figure 3), a buffer zone is created between the two and the preys thrive in it (Figure 4), the net increase of the population of preys is beneficial to the two antagonistic populations of predators (Figure 5).

An important question, that remains open, is to give an estimate on the size of the territories that maximize the total population of predators. Even though as of now we do not have rigorous mathematical results in this direction, extensive numerical simulations suggest that, if the predators are indistinguishable, then the average size of the territories that maximizes the total population of predators (ASmp) satisfies

$$\text{ASmp} \propto \frac{d}{Kp - l}.$$

This is the same asymptotic expression that we have conjectured for the minimal territory size, up to the proportionality constant that in this case is greater. Therefore we believe that this estimate for the average territory size is rather precise. This question calls for further research.

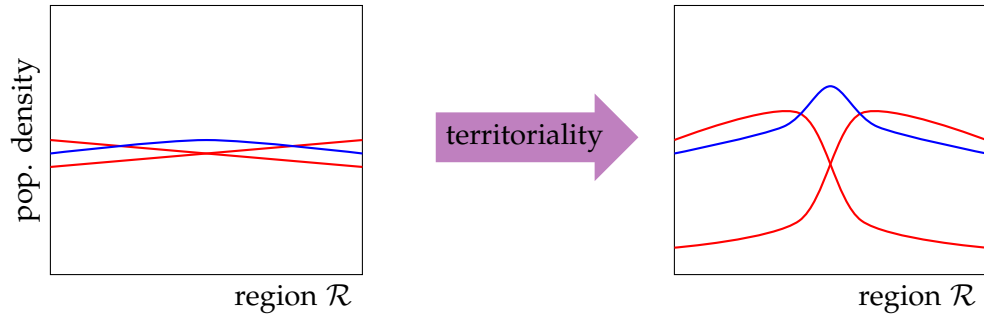


Figure 2: a graphical representation of the Principle *Aggressiveness generates Economic Defendability*: if the conditions are correct, the insurgence of territorial behaviors in predators can augmented the total predator population.

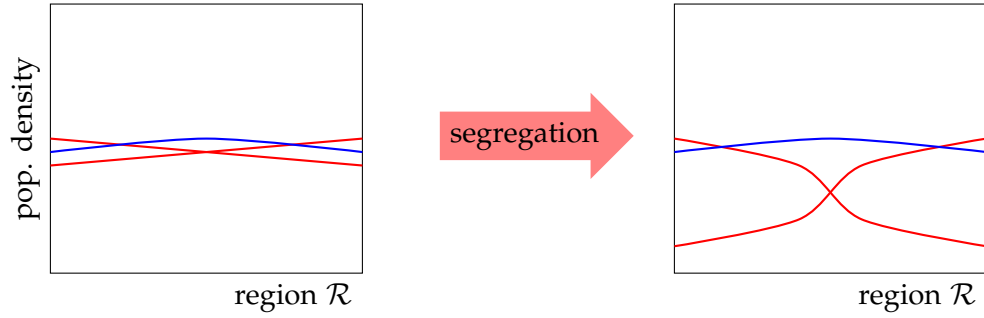


Figure 3: when the strength of the competition increase, the densities of predators segregated (as in Equation (2)). If there were no feedback from the population of preys, the segregation would have a negative impact on the total population of predators.

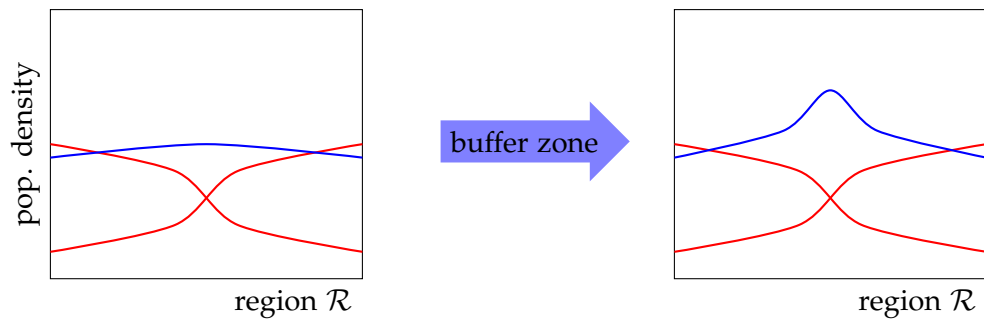


Figure 4: in the area between two territories, the predators are less abundant. A buffer zone is then created, where the preys can thrive and their total population increases.

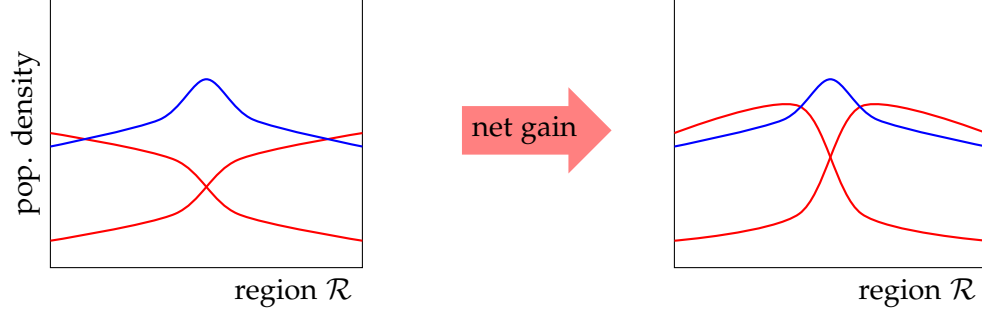


Figure 5: the predators hunt the local peak of population of preys, and this results in a net gain.

Numerical investigations for the system of 1 or 2 predators in dimension 1

Some numerical simulations illustrate the predictions resulting from the facts that we have established mathematically. We start by analyzing the behavior of the solutions of system of 1+2 components, that is, the case of one population of preys and two of indistinguishable predators, and we also consider the one dimensional version of the model in the region $(-L, L)$ with $L > 0$: this circumstance is not only indicative of the one dimensional case, but it can also be used to draw conclusions for the two (or higher) dimensional model; indeed, once we have a solution in $(-L, L)$ it can be extended to a solution in the square $(-L, L) \times (-L, L)$ just by considering it constant in the new dimension. The system is described altogether by 7 parameters and by the physical dimension of the domain. However, up to a scaling and a change of variables, we can reduce the system to involve only 4 parameters. This system reads:

$$\begin{cases} -u'' = \bar{r} \left(1 - \frac{1}{\bar{K}}u - w_1 - w_2\right) u, \\ -w_1'' = \bar{l} (-1 + u - \bar{\beta}w_2) w_1, \\ -w_2'' = \bar{l} (-1 + u - \bar{\beta}w_1) w_2, \end{cases} \quad \text{in } \mathcal{R} = (-1, 1)$$

(here the notation h'' stands for spatial derivatives of the second order of the function h) where the new effective coefficients are defined as

$$\bar{r} = \frac{rL^2}{D}, \quad \bar{l} = \frac{lL^2}{d}, \quad \bar{K} = \frac{Kp}{l}, \quad \bar{\beta} = \beta \frac{r}{lp}.$$

This system possesses some obvious constant solutions, whose stability can be inferred by a simple linearization. Since the computations are rather lengthy, here we only report the results, leaving the full details to the mathematical paper (Berestycki and Zilio (2017)). Indeed we have the solution

$$u = w_1 = w_2 = 0$$

which corresponds to an empty environment, and it is unstable, as the intuition suggests: preys introduced in a fertile but unoccupied territory will rapidly thrive in it. The solution

$$u = K, \quad w_1 = w_2 = 0$$

that is, an environment occupied only by preys and no predators, is stable in $\bar{K} \leq 1$ (a consequence of the *Principle of Extinction*) while it is unstable if $\bar{K} > 1$, since new predators will hunt

the abundant preys and thrive. The solution

$$u = 1, w_1 = 1 - \frac{1}{\bar{K}}, w_2 = 0 \quad (5)$$

(and the one obtained by interchanging w_1 and w_2) which is meaningful only if $\bar{K} > 1$ (that is $Kp - l > 0$) corresponds to the case of an environment occupied by a population of preys hunted by a unique group of predators. This solution is stable if $\bar{\beta} > 0$, since the predominant predators would defend their environment from external competitors. Finally, we have the solution

$$u = \frac{\bar{K}(2 + \bar{\beta})}{\bar{\beta} + 2\bar{K}}, w_1 = w_2 = \frac{\bar{K} - 1}{\bar{\beta} + 2\bar{K}}$$

which describes the case of one group of preys and two groups of predators that are in competition with each other, but when territoriality has not emerged, since the two groups are spatially undifferentiated: this suggests that the solution is always unstable, as we eve int the mathematical paper.

Here we are focus our attention on solution (5), that is one group of preys and one group of predators. We can use this solution in comparison with the solution with two groups. According to our results, for \bar{K} and $\bar{\beta}$ very large, the solution with two groups of predators has a larger total population. To see this, we have conducted some numerical simulation, that are reported in Figure 6, of the limit system that one obtains by letting \bar{K} and $\bar{\beta}$ go to $+\infty$. We have plotted the ratio of the total population of the predators (top) and preys (bottom) as a function of the remaining free parameters \bar{r} and \bar{l} . As the graphs show, the ratio is always greater than one (as from the *Principle of Aggressiveness generates Economic Defendability*) but large values of \bar{l} and small value of \bar{r} seem to enhance this phenomenon: in particular for $\bar{r} \simeq 3.5$ and $\bar{l} \simeq 0.1$, the ratio is 1.5, meaning that in this case the population of predators is 50% higher than if there was only one group of (non competing) predators. The first plot in Figure 6 shows also a striking property of the model: by keeping fixed all the parameters in the original formulation but L , we see that the scaled parameter \bar{K} and $\bar{\beta}$ are constant in L , while \bar{r} and \bar{l} both depend linearly on L^2 . It follows that varying L corresponds to moving on the plane (\bar{r}, \bar{l}) along lines passing from the origin. The concavity of the isolines of the total population of predators translates then into the the existence of a (unique) length L of the territory that maximizes the total population of predators. In a sense, we then obtain a result that is similar to the ideas of Hixon (1980).

We now turn to the study of the dependence in \bar{K} and $\bar{\beta}$. We choose for instance the values $\bar{r} = 3.5$ and $\bar{l} = 0.1$ for the other parameters and look at the behavior of the solution for large values of the other two parameters. In Figure 7 we have represented again the ratio of the population in comparison with the reference case: the non monotonic behavior of the solution for small values of \bar{K} and $\bar{\beta}$ is a consequence of the *Principle of Homogenization*: in fact, for some ranges of the parameters, the diffusivity of the populations is too strong for them to separate. Beyond some threshold value, the two groups separate and start to gain in the total number of individuals as they sharply segregate.

Next we look at the shape of territories predicted by the model. Figures 8 and 9 show a representation of a solution to the system with 9 indistinguishable groups of predators competing in the same region for the same prey. On the left, we show the distribution of predators, on the right the distribution of preys. In order to separate clearly the territories, we have chosen very aggressive predators (β large). It can be shown mathematically that the lines dividing the

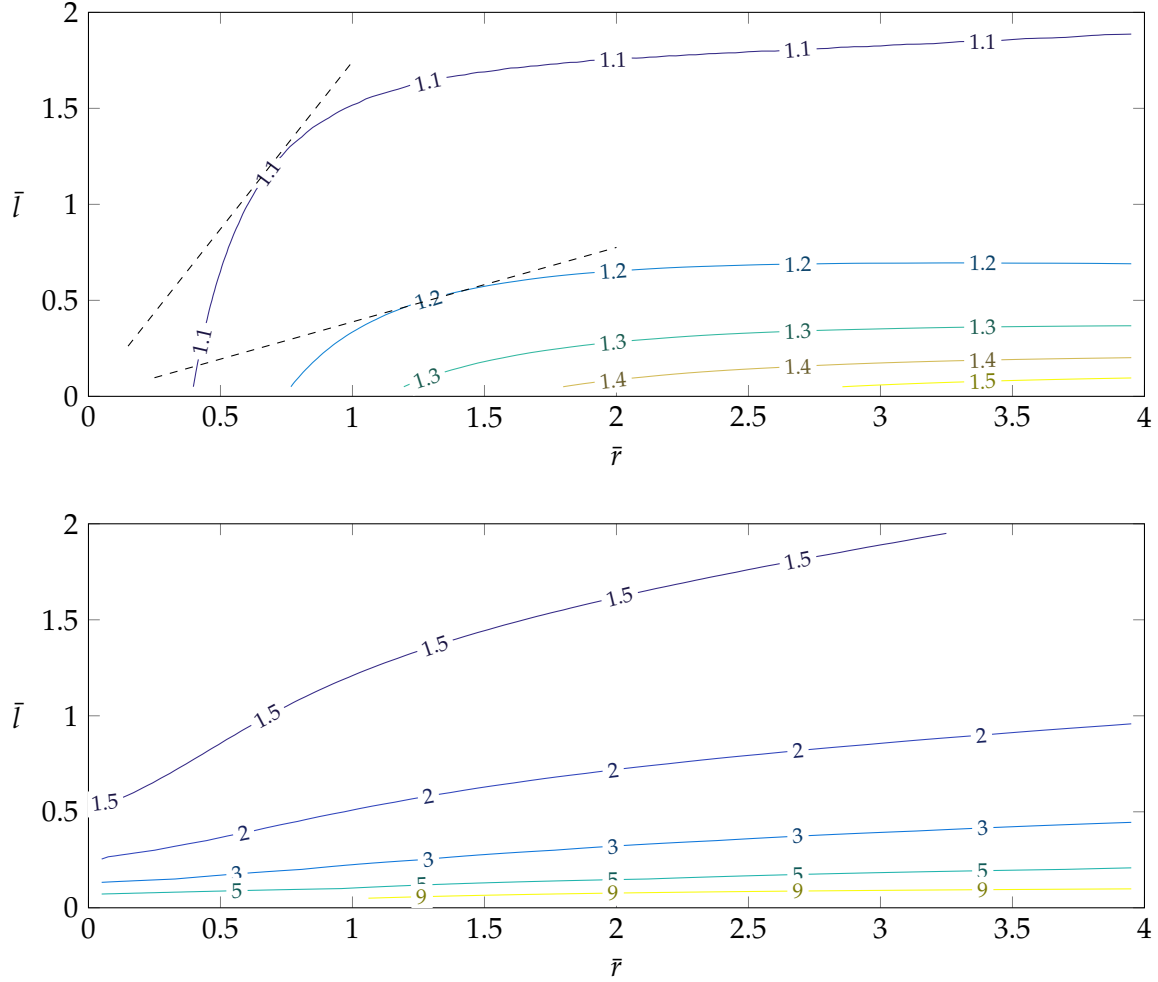


Figure 6: Isolines of ratio of the total population of predators (top) and preys (bottom) for the solution with two groups over the corresponding quantity for the solution with only one group. The parameters \bar{r} and \bar{l} are plotted in the axes. In the predators plot, we have also included some lines emanating from the origin. These correspond to what happens when we set all the other parameters in the model but we vary the length L . By the convexity of the isolines we can deduce that there exists one value of L that maximizes the total population of predators.

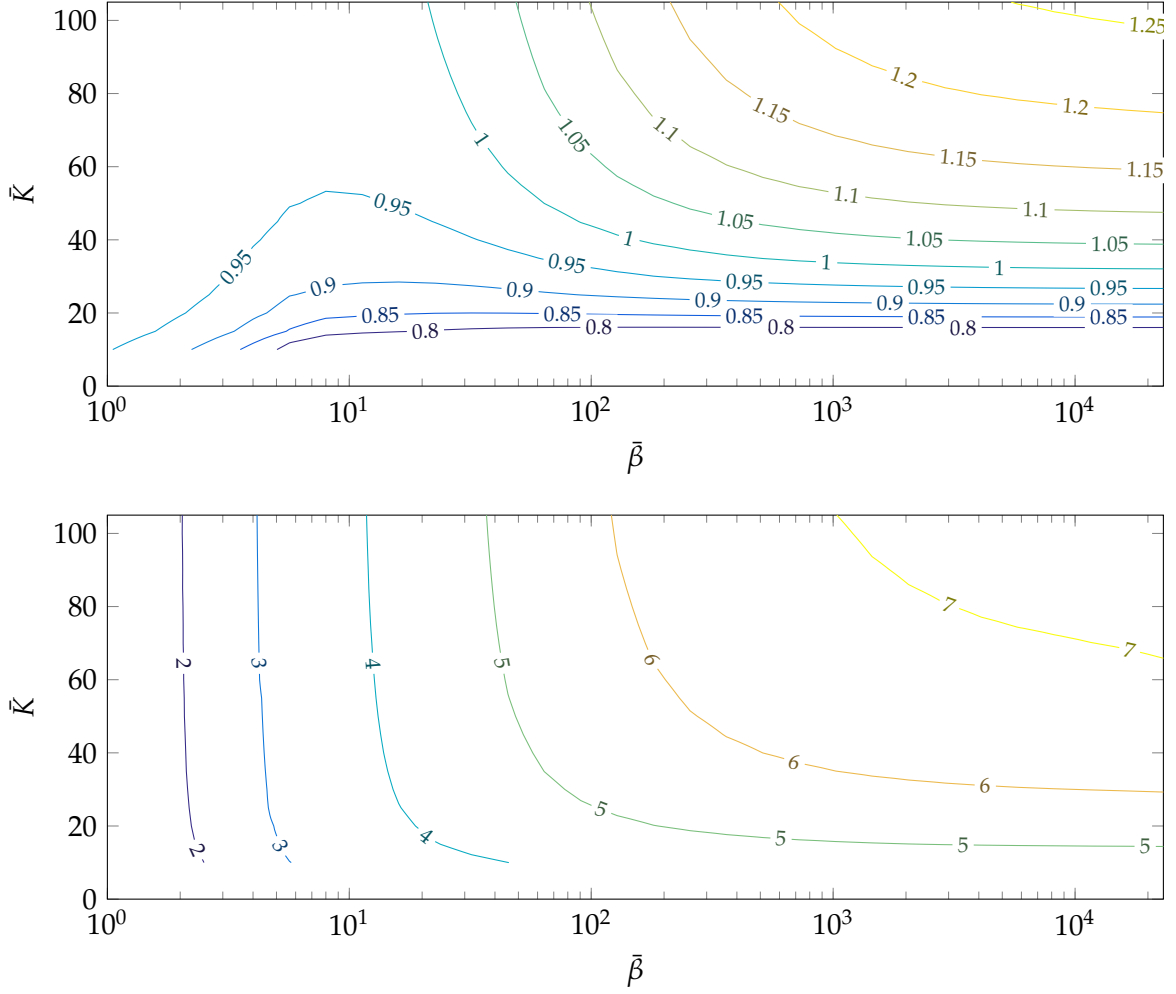


Figure 7: Isolines of the ratio of the total population of predators (top) and preys (bottom) in the solution of the model with $\bar{r} = 3.5$ and $\bar{l} = 0.1$ and \bar{K} and $\bar{\beta}$ as parameters.

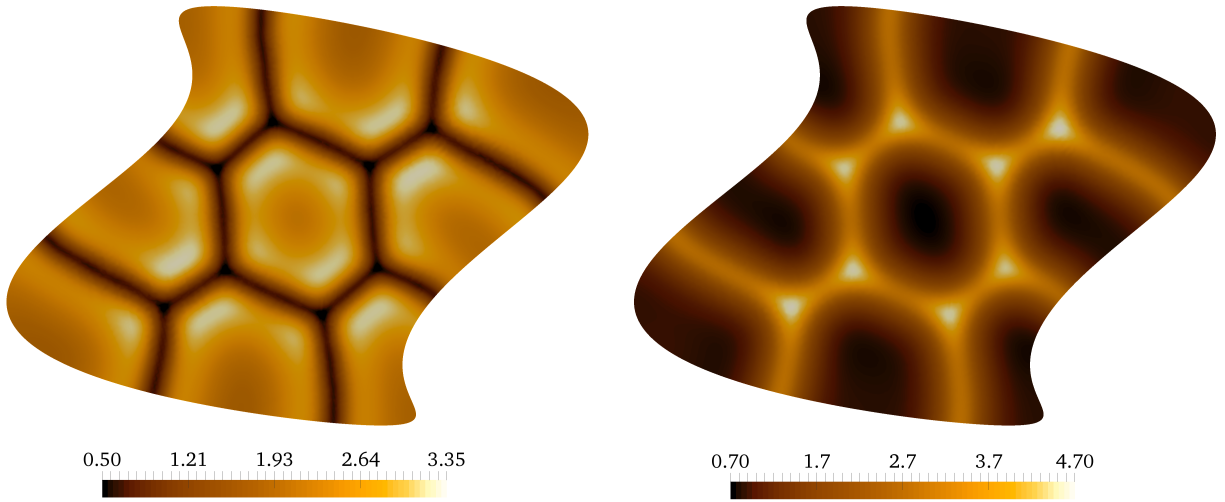


Figure 8: Shape of the territories predicted by the model in an homogeneous environment. On the left, the distribution of 9 groups of predators, on the right the corresponding distribution of preys. Under each plot, the color scale: darker colors correspond to lower densities, brighter colors to higher densities.

different territories are regular, and when more than two regions meet, the curves reaching the common boundary point divide the angle in equal parts: in this example the angles are all of $2\pi/3$, and thus the territories look hexagonal in homogeneous environments (Grant 1968; Maynard Smith 1974). As it is evident from the picture, the preys tend to accumulate on the buffer zones that are formed at the boundary of the territories: there the predators are fewer than elsewhere and the preys can reproduce more. Consequently, also the distribution of the predators tends to increase along the boundary of the territories, since it is there that the preys are more abundant. These two effects combined explain the augmentation of the total population of predators, even though the predators are very competitive. We also point out that in Figure 9 the diffusion coefficients are different, but the aggressiveness promotes diversity: indeed the solution does not converge (as in the model of Dockery et al. 1998) to the solution with only one non trivial component (the one with the lowest diffusion). On the contrary it seems that the most diffusive groups are the ones that gain territory, while the ones with lower diffusion retreat (in this case, for instance, the center territory is occupied by the lowest diffuser in the region).

Discussion

Our model suggests that the main factor that discriminates between the different scenarios is the carrying capacity of preys K for the region. For small values of K , the region cannot sustain predators, for larger values it can sustain a single group of predators, and if K is sufficiently large it can sustain more than one group, and these can maximize their total population by adopting territorial behaviors. As a result, our model predicts that territorial behaviors should be more common in environments rich in preys, while territory should be spread out in inhospitable environment, and it also suggests a inverse proportionality between the average size of the territories

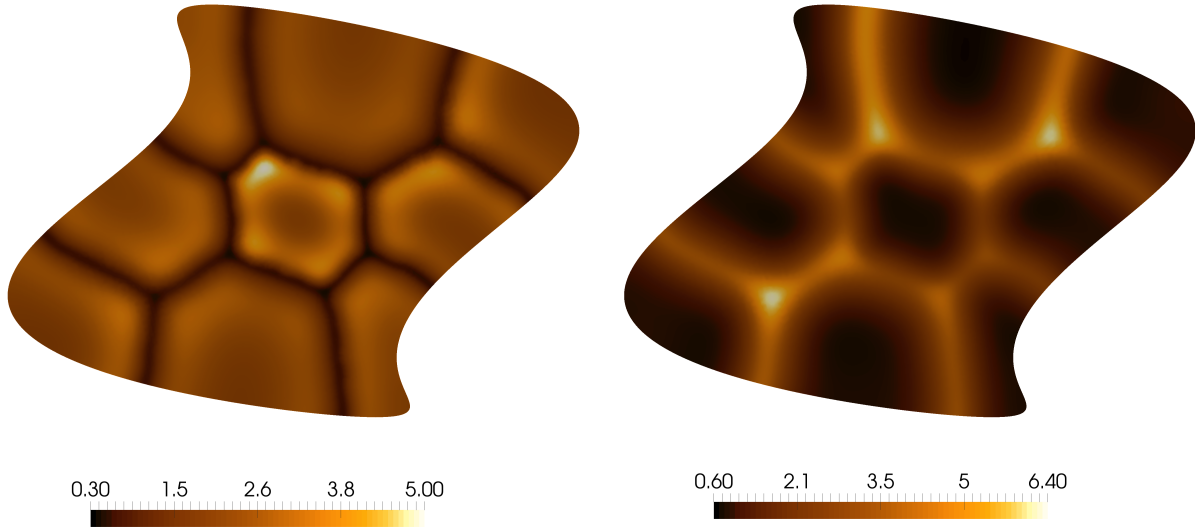


Figure 9: Same as Figure 8 but with different diffusion coefficients for each group.

and the abundance of preys. Thus, our model provides a theoretical framework that accounts for observations reported in earlier works (Hixon 1980; Meyers et al. 1979; Temels 1987). We indicate some directions of alternative possible observations that could be used to test the validity of our theory.

From the presence of territorial animals in deserts (Costa 1995) we infer that the principle of *Aggressiveness generates Economic Defendability* is not the only factor responsible for the emergence of territoriality. For instance the relative increase of the fitness of the individuals that adopt territorial strategies can play an important role.

It should be pointed out that our model suggests that the segmentation of the population in competing groups yields a clear advantage for the total population. This advantage is a consequence of the aggressive behavior because it leads to the formation of *buffer zones* between different territories. And in these buffer zones, preys thrive, providing a more favorable environment as well to the predators who feast on them. Once these zones are established, other mechanisms (such as the deposition of markings) can take over, thus justifying a posteriori the models of Lewis and Murray (1993) and White et al. (1996b). As a matter of fact, the deposition of markings can be interpreted as a proxy for the direct competition between individuals.

Moreover, a key mechanism that we recognize through our model is a positive feedback loop between the spatial distribution of predators (territorial behavior) and local abundance of preys. If, for some reason, the preys (read, the main spatially distributed resource of the predators) is not strongly affected by the distribution of the predators, this mechanism would not be in place and thus our model would fail to predict the emergence of territorial behaviors. In this case, that is when the distribution of preys is a given datum (see for instance the Appendix), the model can still be used to understand the shape of the territories, but the emergence of any territorial behavior can not be as easily inferred.

There are two key aspects that we have not yet analyzed: the impact of the landscape inhomogeneities or natural boundaries, such as mountains and rivers, and the dynamic evolution of territories. Regarding the former, for instance, the presence of less hospitable areas in the region

may boost or impede the feedback loop, by forcing the boundaries of the territories in some specific locations (Eason et al. 1999). In practical terms, this can be accomplished by (a) changing the diffusion component of the model, by making it more difficult to the animals to reach some of the areas, (b) letting the parameters of the models, in particular the reproduction rate and the prey-carrying-capacity, depend on the location x .

Evidently, these adjustments are specific to the particular case, but numerical simulations suggests a natural sensitivity of the location of the boundaries to these factors. With respect to the dynamic evolution of the territories, the model the we have proposed here is by its nature dynamical, and thus it can be used to address questions like how territories change as a result of a decline in the population of predators (Potts et al. 2013).

Conclusion

In this paper, we propose a model that gives a possible explanation of why territoriality of hostile groups is formed by certain predators. In some sense this is simplest one to describe this phenomenon.

We consider a predator-prey situation in which there is a single prey (representing an array of resources) and in which the predators may break up into several highly hostile groups. In the limit of very strong aggressiveness, the different groups divide up the spatial environment into segregated territories. Here we further analyze the outcomes of such segregation. We are thus able to compare the total sizes of the population in the case when there is no hostility between the groups and the cases when the population is divided up into very hostile groups.

Our first finding is that a given environment can only support a certain maximal number of groups. We further derive a bound on this maximal number of groups that depends on the various parameters of the model. In particular we show that this bound increases with respect to the carrying capacity of the environment for the preys, the predation efficiency, and the available surface while it decreases with respect to the mobility of predators and the decay rate of the predators in absence of preys .

The second finding is a principle that we call here: *aggressiveness generates economic defendability*. By analyzing the dependence of the solutions of our model with respect to the different parameters, we establish that if the prey carrying capacity is sufficiently large, the total number of predators hosted in a region is maximized when the predators split into several highly competing groups. This is related to the effect that territories generate buffer zones where the preys strive and can then generate an overall positive effect on the size of the population that offsets the losses caused by the strong hostility between groups. It has been argued (Brown 1964) that in order for territoriality to emerge, there need to be aggressiveness between con-specifics and an economics advantage in having divided territories. What we show here is that the con-specific aggressiveness between groups yields an economic gain in the sense of the total size of the population. Thus, we consider here aggressiveness and selfishness of the predators as the only explaining factors, and maximization of the total population of predators as a driving mechanism. Within this framework, the formation of several highly hostile groups dividing up the environment into several well defined territories (as observed in nature) appears to be advantageous.

Acknowledgments

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Appendix: A link with the model of Dockery et al. (1998)

We point out here the link of our model to the model of Dockery et al. (1998). In particular we want to emphasize the crucial difference that makes it so that our model predicts a different behavior for the dynamics of the densities.

The model here reads as the following system of differential equations

$$\begin{cases} (\partial_t - D\Delta)u = \left(r - \frac{r}{K}u - \sum_{i=1}^n p_i w_i\right) u \\ (\partial_t - d_i\Delta)w_i = \left(-l_i + p_i u - a_{ii}w_i - \beta \sum_{j \neq i} a_{ij}w_j\right) w_i \\ \nabla u \cdot \nu = \nabla w_i \cdot \nu = 0. \end{cases}$$

Let us consider the system when introducing a simplifying assumption: the density of preys u evolves very rapidly but diffuses much slower than the predators. As a result, we assume that at each $t > 0$ the density u solves

$$r - \frac{r}{K}u - \sum_{i=1}^n p_i w_i = 0 \quad , \text{ that is, } u = \frac{K}{r} \left(r - \sum_{i=1}^n p_i w_i \right).$$

Substituting this formula in the equation satisfied by w_i yields

$$(\partial_t - d_i\Delta)w_i = \left(Kp_i - l_i - a_{ii}w_i - \frac{Kp_i}{r} \sum_{j=1}^n p_j w_j - \beta \sum_{j \neq i} a_{ij}w_j \right) w_i$$

We can further simplify the equation for instance by assuming that the groups of predators are similar. That is, we let $p_i = p$ and $l_i = l$, and moreover we assume that the internal competition in each group is negligible, which corresponds to $a_{ii} = 0$. By doing so, up to a scaling, we find that the densities satisfy the system

$$(\partial_t - d_i\Delta)w_i = \left(a - \sum_{j=1}^n w_j - \beta \sum_{j \neq i} \bar{a}_{ij}w_j \right) w_i$$

where we let $a = Kp - l$.

We start by observing that if the strength of the competition β is set to 0, we have then obtained exactly the model of Dockery et al. (1998). This tells us that the case of non direct competition corresponds to agents that are engaged only in exploitative competition, as they compete only through the interaction with the preys (or food), while the term related to β is exactly responsible for the description of interference competition.