VOL. 193, NO. 3 THE AMERICAN NATURALIST MARCH 2019

Predator-Prey Models with Competition: The Emergence of Territoriality

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Submitted May 24, 2018; Accepted September 26, 2018; Electronically published January 14, 2019

Online enhancements: appendixes.

ABSTRACT: We introduce a model aimed 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 prey (or spatially distributed resource). We observe that strong competition between groups of predators leads to the formation of territories. At the edges of territories, prey concentrate and prosper, leading to a feedback loop in the population distribution of predators. 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. We present some numerical simulations that allow us to describe our counterintuitive and most important conclusion: lethal aggressiveness among hostile groups of predators may actually lead to an increase in their total population.

Keywords: emergence of territoriality, formation of packs, predator-prey interaction, systems of reaction-diffusion equations, competition, spatial distribution of populations.

Introduction

A long-standing major problem in ecology is to understand the emergence of territoriality, its mechanisms, and its ecological implications. A theory on territoriality has to indicate the impact that this behavior has on the population that adopts it. A common unifying theory of territoriality may be difficult (if not impossible) to formulate given the large variety of environments that host such organisms. This is confirmed by the simple observation that not all species are territorial. However, there are specific theories. For instance, it has been argued that some animals settle in familiar sites to increase the efficiency of food retrieval and decrease mortality (Johnson and Gaines 1990; Larsen and Boutin 1994). Other theory views competition for territories as a regulation mechanism for population density (Wynne-Edwards 1962) or as motivated by provision and allocation of resources (Brown 1964; Wilson 1975). Krebs (1971) pointed out that the creation of buffer zones between different territories is also a means to reduce the spread of contagious diseases.

Brown (1964) has argued that territorial behaviors should also include aggressiveness among conspecifics and economic defendability of territory. Aggressive behaviors are favorable if they help increase the chances of survival and the likelihood of reproduction. Thus, territories form if they increase the food availability, the mating probability, or the survival of the animal or its offspring (Brown 1964). Hixon (1980) argues that territories should also be defendable in economic terms. That is, the benefits gained from having a territory should offset the energy invested in the active defense against invaders.

An extensive ecological literature has focused on how aggressiveness and intra- and interspecific competition can lead to territoriality without invoking group selection arguments related to fitness or economic defendability. For instance, Okubo et al. (1989) introduced a model of two spatially distributed species that compete for the same given resource. The aim was to study the invasion of red squirrel territories in Britain by gray squirrels. In terms of rigorous mathematical analysis, Dancer and Du (1994) were the first, to our knowledge, to study the effect of strong competition between two populations occupying the same region of space. Particularly relevant for our investigation is the precise description they derive when the competition parameter becomes infinite.

The aim of this article is to show, through a relatively parsimonious mathematical model, that territoriality can emerge as a simple consequence of strong interference competition between predators. We start by considering an environment occupied by prey and predators interacting with each other. By varying the degree of aggressiveness among the predators, we see territories being formed spontaneously

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Am. Nat. 2019. Vol. 193, pp. 000–000.
DOI: 10.1086/701670

with some specific shapes. Further questions we address here are whether there is a limit to the number of groups and how this depends on the parameters and what is the effect on the overall population size of introducing lethal competition between rival groups.

Several authors have studied the territorial mechanisms that characterize specific species, such as wolves and coyotes. In a seminal work, Lewis and Murray (1993) proposed a model to describe wolf territories based on the dynamics of predators interacting with scent marks of the different predator groups. Their model does not involve competition between packs but rather avoidance. It takes the locations of centers of territories, the number of groups, and the total population of each one of them as given. By introducing a coupled system of equations to model location, deposition, and expiration of markings, Lewis and Murray succeeded in describing the shape of the territories and the disposition of the markings left by different individuals. In particular, they managed to describe the emergence of buffer zones that separate the territories occupied by the groups. Such zones are observed in nature, and one expects to find more prey there (Mech 1977, 1994; Mech et al. 1980).

A number of works have further developed this model (White et al. 1996*a*; Lewis et al. 1997; Moorcroft et al. 2006; Hamelin and Lewis 2010; Giuggioli et al. 2011; Potts et al. 2012; Potts and Lewis 2014, 2016*a*, 2016*b*). A subsequent refinement (White et al. 1996*b*) added a coupling between predators and prey (in this case, wolves and deer). It assumed that the deposition of markers by predators is influenced by the presence of prey and that prey density follows some laws similar to the Lotka-Volterra system, but with no feedback on the population of predators.

Unlike these models, the one we present here does not take the number of packs, their respective total populations, or the locations of centers as given. It does not assume a spatial variable like scent marks but rather derives territories from strong competition. We then find the total populations as resulting from territory formation and analyze the consequences of the number of packs.

The Model

We consider the spatial distribution of predators and prey as a key factor. We represent movement in the populations as resulting from random diffusion through Brownian motion. We are thus led to a system of reaction-diffusion equations.

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 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 of the groups.

We consider a region (henceforth denoted as $\mathcal{R}$) occupied by a population of prey, whose density we denote by u, and n groups of predators, whose densities we denote by $w_1, \dots, w_n$. All of the parameters introduced are to be considered positive.

Individuals of the population of prey u diffuse in region $\mathcal{R}$, reproduce and perish, and are hunted by predators. We propose describing population u by the equation

$$\underbrace{\partial_t u}_{\substack{\text{rate of local}\\ \text{population growth}}} - \underbrace{D\Delta u}_{\substack{\text{random}\\ \text{motion}}} = \underbrace{\left(r - \frac{r}{K}u\right)u}_{\substack{\text{intrinsic increase}\\ \text{in population}}} - \underbrace{u\sum_{i=1}^{n} p_i w_i}_{\text{predation}}. \tag{1a}$$

Here, D is the diffusion rate of the prey, r is the intrinsic growth rate, K is the (local) carrying capacity of region $\mathcal{R}$, and p_i are the consumption rates per predator based on a type I functional response: they describe how predator-prey encounters (whose probability is proportional to uw_i) negatively affects the prey population.

Similarly, predators diffuse, starve in the absence of prey, hunt prey, and compete. The new feature here lies in the competition between predators. We distinguish between internal competition in each group and interference competition between groups (or packs). By the Lotka-Volterra paradigm, we assume the former to be proportional to w_i^2 and the latter to be proportional to $w_i w_j$. Thus, we represent the dynamics of group i by the equation

$$\begin{aligned}\underbrace{\partial_t w_i}_{\substack{\text{rate of local}\\ \text{population growth}}} - \underbrace{d_i\Delta w_i}_{\substack{\text{random}\\ \text{motion}}} ={}& \\ \underbrace{(-l_i - a_{ii}w_i)w_i}_{\substack{\text{mortality and}\\ \text{intraspecific competition}}} + \underbrace{p_i u w_i}_{\text{predation}} - \underbrace{\beta w_i \sum_{j\neq i} a_{ij} w_j}_{\substack{\text{interference}\\ \text{competition}}}&.\end{aligned} \tag{1b}$$

Here, d_i is the diffusion rate of the ith population, l_i is the loss (mortality) rate in the absence of prey, p_i is again the consumption rate per predator 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 jth group negatively affects the ith 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 index i to point out that we can take into consideration different models at once. Indeed, this system of equations can describe either groups of conspecifics (e.g., packs of predators) 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, although the results that we will describe can be used to draw different conclusions depending on the settings. Descriptions and summary of model parameters are provided in table 1.

Thus, equations (1a) and (1b) represent a system of $1 + n$ equations in $1 + n$ unknowns $(u, w_1, \ldots, w_n)$. We complete the model with nonnegative initial conditions that assign the initial distributions at time $t = 0$:

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

As for the boundary conditions, we consider here the case in which region $\mathcal{R}$ is isolated from the surrounding environment and there are reflective boundary conditions. In other words, there is no flux of individuals across the boundary $\partial\mathcal{R}$. Mathematically, this translates 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. This Neumann boundary condition also has the advantage of minimizing spurious effects of the boundary. We have also considered other types of boundary conditions (see app. C; apps. A–G are available online), and we have found that our results are still valid if region $\mathcal{R}$ is sufficiently large.

Model Properties and Results

In this section we discuss the main ecological consequences that we draw from the model. Here we focus mainly on the effect of strong competition (large β) among predators and large carrying capacity of prey. In the appendixes we explore other dependencies, such as that on the diffusion coefficients and the carrying capacity. We assume throughout the presentation of our results that region $\mathcal{R}$ can sustain any of the groups of predators when taken separately, that is, it is the only group in the region. In the model this translates into the assumption $Kp_i > l_i$, which we impose for any group i of predators.

We describe the key mathematical arguments behind these results for a simplified formulation of the model in the appendixes. In a separate mathematical article (Berestycki and Zilio 2018), we establish rigorously these results for the general formulation. The main tools we employ in our analysis there are existence and long-time behavior results for solutions of semilinear parabolic equations, a priori estimates and singular perturbation analysis, free-boundary techniques, spectral properties, and shape optimization results. Besides the mathematical proofs, we have carried out several numerical simulations of the model, and we report here some of the most significant outcomes.

To start with, we observe that standard mathematical arguments show that the model is well posed—that is, for any nonnegative initial data (i.e., feasible densities of predators and prey), there exists a unique solution of system (1a) and (1b).

Weak versus Strong Interference Competition

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

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

for all $t > 0$ and $x \in \mathcal{R}$. The term $w_i w_j$ has two interpretations. First, as in the Lotka-Volterra theory, the quantity $w_i(x, t) w_j(x, t)$ is proportional to the probability of individuals from population i encountering individuals from population j at location x and time t. Second, the product $w_i(x, t) w_j(x, t)$ describes the overlap of the densities. To illustrate this more clearly, let us assume that at location and time (x, t) we find $w_i(x, t) w_j(x, t) = 0$; this then 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).

Table 1: Short description of the parameters of our model

Parameter	Description
i	Index corresponding to a particular group/density of predators
$\mathcal{R}$	Region/environment occupied by the prey and predators
D	Diffusion coefficient of prey u
d_i	Diffusion coefficient of prey w_i
r	Reproduction rate of the prey
K	Prey-carrying capacity (mean) of region $\mathcal{R}$
p_i	Consumption rates per predator based on a type I functional response
l_i	Loss rate/starvation rate of the predators in the absence of prey
a_{ii}	Competition among individuals of the same group of predators
βa_{ij}	Competition among predators in groups i and j
β	Characteristic size of intergroup competition

If the carrying capacity of prey is sufficiently large, when the competition parameter diverges ($\beta \gg 1$), the solutions persist and the groups of predators segregate. In the limit case of infinite competition ($\beta = +\infty$), region $\mathcal{R}$ is subdivided into smaller nonoverlapping regions (the territories). On each of these subregions only one group of predators is present. One particular feature of the model is that it gives a precise description of the location of the boundaries and the shapes of the different territories, as we discuss later.

Minimal Territory Size and Maximal Number of Predator Groups

A natural question is whether our model yields quantitative information on the minimal area of a territory and the maximal number of groups that can survive in a given region. This is made clearer in the extreme case of nonoverlapping territories, when the strength of competition β is infinity. Under this assumption, we have shown that our model yields a quantitative estimate of the minimal size of the territories.

> PROPERTY 1: *Minimal territory size.* Let TA_i be the area territory occupied by species i in the case of nonoverlapping territories ($\beta = +\infty$), such that the ith territory is surrounded by other territories and does not touch the boundary of $\mathcal{R}$. Then TA_i cannot be smaller than the threshold mTA_i (minimal territory area) given by
>
> $$\mathrm{mTA}_i = \chi \frac{d_i}{Kp_i - l_i},$$
>
> where the numerical constant χ is $\simeq 18.17$.

We can derive this estimate by assuming that the territory occupied by the group is a disk. Indeed, this is the best possible shape of a small territory, as the circle minimizes the perimeter of the territory (where the encounters with other hostile groups take place) for a fixed area. For this case, we can compute explicitly the value of the constant χ, which is the value appearing in the above statement.[1]

Thus, our model predicts a lower bound on the size of an enclosed territory of a group of predators once the values of d_i, K, p_i, and l_i are known.

A possible interpretation of this estimate is as follows. The diffusion coefficient can be viewed as the area covered by a single individual per unit of time, while the denominator ($Kp_i - l_i$) is the maximal possible growth rate of predators (again per unit of time). Thus, the minimal territory size corresponds to the area explored by a single individual during the amount of time necessary to produce an offspring (up to a multiplicative constant). For instance, this implies that, in principle, less motile predators could divide a region into many small territories, whereas a large diffusion coefficient would allow only for a few larger ones.

In the case where the competition strength parameter β is large but not infinite, the previous estimate is less meaningful, and we would need to specify the meaning of territory size. Alternatively, in the general case we have derived another estimate formulated in terms of the maximal number of groups $\mathcal{N}_{\max}$ of predators that can coexist in region $\mathcal{R}$. Here is the precise statement.

> PROPERTY 2: *Maximum number of groups.* We consider a flat region $\mathcal{R}$ that hosts a population of prey and some groups of predators that strongly compete between them ($\beta \gg 1$). The maximum number of groups $\mathcal{N}_{\max}$ of predators that can persist in $\mathcal{R}$ is always finite and satisfies
>
> $$\mathcal{N}_{\max} \leq \underbrace{\frac{\mathrm{area}(\mathcal{R})}{4\pi}}_{\substack{\text{geometrical}\\ \text{effect}}} \cdot \underbrace{\max_i\left(\frac{Kp_i - l_i}{d_i}\right)}_{\substack{\text{ecological}\\ \text{effects}}}$$
>
> up to small correction terms.

In the precise statement we need to discard some particular family of nearly extinct solutions that are biologically irrelevant. We give a sketch of the proof of this formula in the limit case of nonoverlapping territories ($\beta = +\infty$) in appendix C. The proof of this estimate for finite but large β is considerably more involved technically, and we have established it in the mathematical article (Berestycki and Zilio 2018).

At first, we see that the maximal number of groups that can be hosted in region $\mathcal{R}$ grows linearly in the area of region $\mathcal{R}$. This is sustained by the intuition that a larger region will host a larger number of groups than a small one. Similarly, we see that if the carrying capacity (K) or predation efficiency (p_i) increase or if the starvation coefficient (l_i) or diffusion coefficient (d_i) decrease, then more groups of predators can, in principle, live in the region. Note that if carrying capacity K of the region increases, then our upper estimate increases as well. In particular, we find again that if K is too small, then we may have no groups of predators or only one group (see app. A).

Aggressiveness and Ecological Consequences

We can now study the impact of strong competition on the overall population of predators. We fix all of the parameters of the model but carrying capacity K and take the competition strength β to be very large. We first state two simple facts: (i) if carrying capacity K is too small,

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[1] Mathematically, this is related to the Faber-Krahn inequality. We have detailed the computations in app. C.

then the only equilibria of the model contain at most one group of predators (see app. A); and (ii) for larger values of K, there are coexisting solutions, that is, solutions with more than one group of predators (this is the case of overlapping territories of predators).

We now look at the total population of predators that reside in $\mathcal{R}$, that is,

$$W = \int_{\mathcal{R}} \sum_i w_i .$$

We find that, in some situations, aggressiveness generates a positive feedback in the total size of the predators population. This hints at a possible new economic advantage of establishing a territory.

> Property 3: *Effects of territoriality on the total population.* If competition β and carrying capacity K are sufficiently large, the population of predators is maximized at an equilibrium that has more than one group of predators.

We interpret this result as follows. In spite of the lethal competition between different groups, the advantage gain in terms of increase in the total size of predators population can offset this loss.

We provide a proof of the previous result in appendix B) for the case $K = +\infty$. The result holds true even in the case of a large but finite K, but its proof is mathematically more delicate and available only in the case of a region $\mathcal{R}$ that is shaped like a rectangle.

In figure 1 we illustrate the previous results with the aid of some numerical simulations. We have already recalled that in the model of Dancer and Du (1994) competition has only negative effects on the population in terms of the total number of individuals. On the contrary, in the model of combined dynamics of predators and prey, 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 noncompeting predators. We can explain this difference by looking at the shape of the solutions, in particular in the area close to the interface between two different territories (see fig. 1). As the two territories separate more and more (when $\beta \to +\infty$), a buffer zone appears between the two. This buffer zone works as a refuge area for the prey. There, prey can reproduce more abundantly. As they diffuse, just close to the buffer zone, predators can find much more food. This feedback loop turns out to have a positive effect on the total population of predators if the carrying capacity of prey is large ($K \gg 1$).

The symmetric solutions in figure 1 appear to be unstable in numerical simulations if the length of region $\mathcal{R}$ is

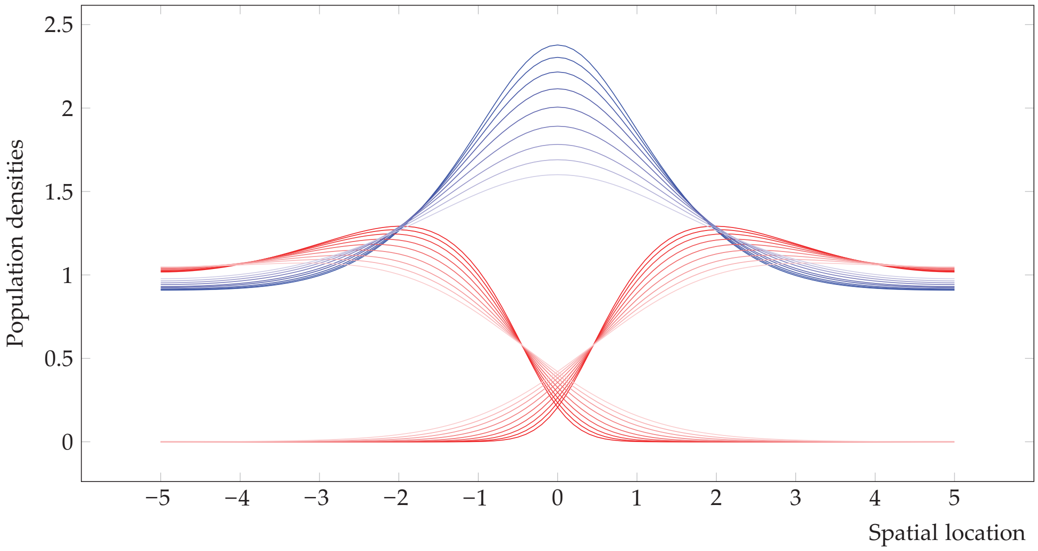

Figure 1: Numerical simulations of the model, showing the impact of the competition parameter β on the distribution of predators (red) and prey (blue) with the densities of prey and predators on the vertical axis. In this simulation, we have chosen the following values for the coefficients: $d = D = 1$, $r = l = 1$, $K = 1{,}000$, and $p = 1$. Lighter colors correspond to small values of β (from 2), and darker colors correspond to higher values (up to 35). We see that the two groups of predators separate more and more as β increases. At the boundaries, the solution converges to the Lotka-Volterra equilibria $u \simeq 1$, $w_i = 1$, and $w_j = 0$ for $j = i$. In the buffer zone, the density of prey reaches its maximum ($\simeq$2.4) for $\beta = 35$ (the largest value of β in these simulations). The densities of the predators reach their maximum ($\simeq$1.3) a little away from the buffer zone. The figure in dimension 1 illustrates the role of the buffer zones in creating a refuge zone for the prey.

too small or if the length of region $\mathcal{R}$ is too large. In the former case, perturbations will converge to a solution with only one density of predators. In the latter case, a perturbation yields a solution that will converge to a nonsymmetric solution, still with two densities of predators. In the intermediate range of domains $\mathcal{R}$, these symmetric solutions seem to be stable. The precise thresholds strongly depend on the values of the parameters, in particular on the strength of competition β. From a theoretical point of view, the question of stability is quite challenging, and very few results are known up to now.

Numerical Simulation for the System of One or Two Predators in One Dimension

We start by analyzing the behavior of the solutions of the system of 1 + 2 components—that is, the case of one density of prey and two of indistinguishable predators—and we also consider the one-dimensional version of the model in region $(-L, L)$ with $L > 0$. The system is described by seven parameters in addition to the characteristic length of the domain. However, up to scaling and change of variables, we can reduce the system so that it involves only four parameters. This scaled system reads

$$\begin{cases} -u'' = \bar{r}\left(1 - \dfrac{1}{\bar{K}}u - w_1 - w_2\right)u & \\ -w_1'' = \bar{l}(-1 + u - \bar{\beta}w_2)w_1 & \text{in } \mathcal{R} = (-1, 1) \\ -w_2'' = \bar{l}(-1 + u - \bar{\beta}w_1)w_2 & \end{cases} \tag{3}$$

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

$$\bar{r} = \frac{rL^2}{D},\ \bar{l} = \frac{lL^2}{d},\ \bar{K} = \frac{Kp}{l},\ \bar{\beta} = \beta\frac{r}{lp}. \tag{4}$$

This system possesses some obvious constant solutions whose stability can be inferred by a simple linearization. We are mostly interested in the solution

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

(and the one obtained by interchanging w_1 and w_2). This solution is meaningful only if $\bar{K} > 1$ (that is the condition $Kp - l > 0$). It corresponds to the case of an environment occupied by a population of prey 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. According to our results, for very large $\bar{K}$ and $\bar{\beta}$, the solution with two groups of predators has a larger total population. We illustrate this result with some numerical simulations that we report in figure 2. We look at the symmetric solution of the limit system that we obtain by letting both $\bar{K}$ and $\bar{\beta}$ go to $+\infty$. This limit system is given by

$$\begin{cases} -u'' = \bar{r}(1 - w_1)u & \\ -w_1'' = \bar{l}(-1 + u)w_1 & \text{in } \mathcal{R} = (0, 1) \\ u'(0) = u'(1) = 0, w_1(0) = w_{1'}(1) = 0. & \end{cases}$$

In the segment $(-1, 0)$, (u, w_2) satisfies a symmetric system. Note that the boundary condition is imposed at zero. This point is the boundary of the territory of w_1 in the case of segregation. A corresponding system holds for w_2 in $(-1, 0)$. We have plotted the ratio, with respect to the case of only one density of predators, of the total population of predators (*top*) and prey (*bottom*) as a function of the remaining free parameters $\bar{r}$ and $\bar{l}$. As the graphs show, these ratios are always greater than 1, but small values of $\bar{l}$ and large values of $\bar{r}$ do enhance this phenomenon. In particular, for $r \simeq 3.5$ and $l \simeq 0.1$, the ratio for predators is 1.5, meaning that in this case the total population of predators is 50% higher than if there was only one group of (noncompeting) predators.

The first plot in figure 2 also shows a striking property of the model. From equation (4), we see that $\bar{r}$ and $\bar{l}$ both depend linearly on L^2. It follows that by varying L and keeping the other parameters fixed, we move along lines coming from the origin in the plane $(\bar{r}, \bar{l})$. The concavity of the isolines of the total population of predators implies that there exists a (unique) length L of the territory that maximizes the total population of predators (we elaborate more on this in app. D).

We now turn to the study of the dependence in $\bar{K}$ and $\bar{\beta}$. For instance, we choose the values $\bar{r} = 3.5$ and $\bar{l} = 0.1$ and look at the behavior of the solution for large values of the other two parameters. In figure 3 we have represented again the ratio of the population in comparison with the reference case: the nonmonotonic behavior of the solution for small values of $\bar{K}$ and $\bar{\beta}$ is a consequence of the strong diffusivity of the populations that prevents them from separating. Beyond some threshold value, the two groups separate, and the total population starts to increase as the two groups sharply segregate.

Numerical Simulation for the System in Two Dimensions

Next we look at the shape of territories as they are predicted by the model. In figure 4 we represent a solution of the system with nine indistinguishable groups of predators and prey in dimension 2. On the left, we show the cumulative distribution of predators; on the right, the distribution of prey. To separate clearly the territories, we have chosen very aggressive predators ($\beta \gg 1$). Theoretical results imply that at the boundary between the territories occupied by w_i and w_j, the pressure exerted by the two groups is equal and opposite (this translates in the equation $a_{ji}|\partial_\nu w_i| = a_{ij}|\partial_\nu w_j|$

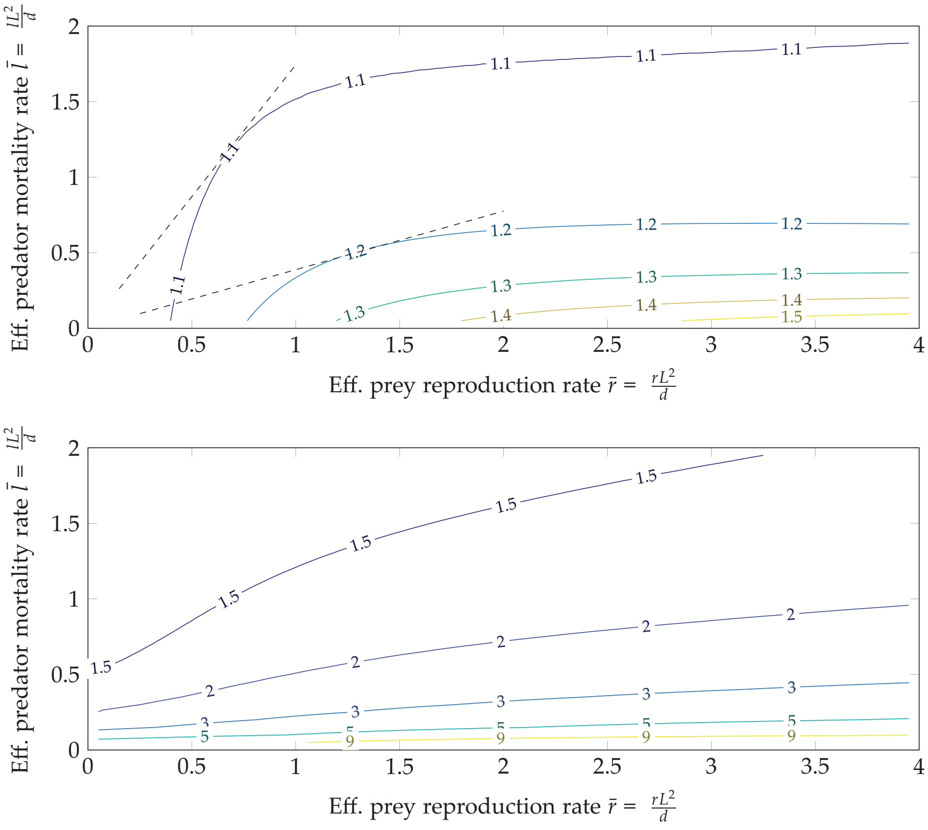

Figure 2: Isolines of the ratio of the total population of predators (*top*) and prey (*bottom*) for the solution with two groups to the corresponding quantity for the solution with only one group. The parameters $\bar{r}$ and $\bar{l}$ are plotted on the axes. In the predators plot, we have also included some lines emanating from the origin. These correspond to what happens when we set all of the other parameters in the model, but we vary 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.

across the boundary between two territories). Moreover, it can be shown that the lines dividing the different territories are regular, and when more than two regions meet, the curves reaching the common boundary point divide the angle into 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). Prey tend to accumulate on the buffer zones that are formed at the boundary of the territories: there predators are fewer than elsewhere, and prey can reproduce more. Consequently, the distribution of predators also tends to increase along the boundary of the territories, since it is there that prey are more abundant. These two effects combined explain the augmentation of the total population of predators, even though the predators are very competitive.

Model with Type II Functional Response

Many of the properties that we have seen for system (1a) and (1b), which has a type I functional response for predator-prey interaction, can be extended to models that are more realistic from an ecological point of view. To this end, we have explored the case of a type II functional response.

The new formulation reads as follows:

$$\begin{cases} \partial_t u - D\Delta u = \left(r - \dfrac{r}{K}\right)u - u\displaystyle\sum_{i=1}^{n} \frac{p_i}{1 + p_i T_i u} w_i, \\ \partial_t w_i - d_i \Delta w_i = (-l_i - a_{ii} w_i) w_i + \dfrac{p_i}{1 + p_i T_i u} u w_i \\ \qquad - \beta w_i \displaystyle\sum_{j \neq i} a_{ij} w_j. \end{cases} \tag{6}$$

We have imposed the same zero-flux conditions at the boundary. Here, the nonnegative parameters T_i are the handling time of each group i. Note that the handling times affect only the interaction of predators and prey.

First of all, the new model is well posed, meaning that for any nonnegative initial datum, the solution of equation (6) exists, is unique, is bounded, and is defined for all positive time. Furthermore, the qualitative description of separation of territories induced by strong competition $\beta \gg 1$ (in particular eq. [2] and its discussion) also holds in this case. The analytic techniques to derive these properties are similar.

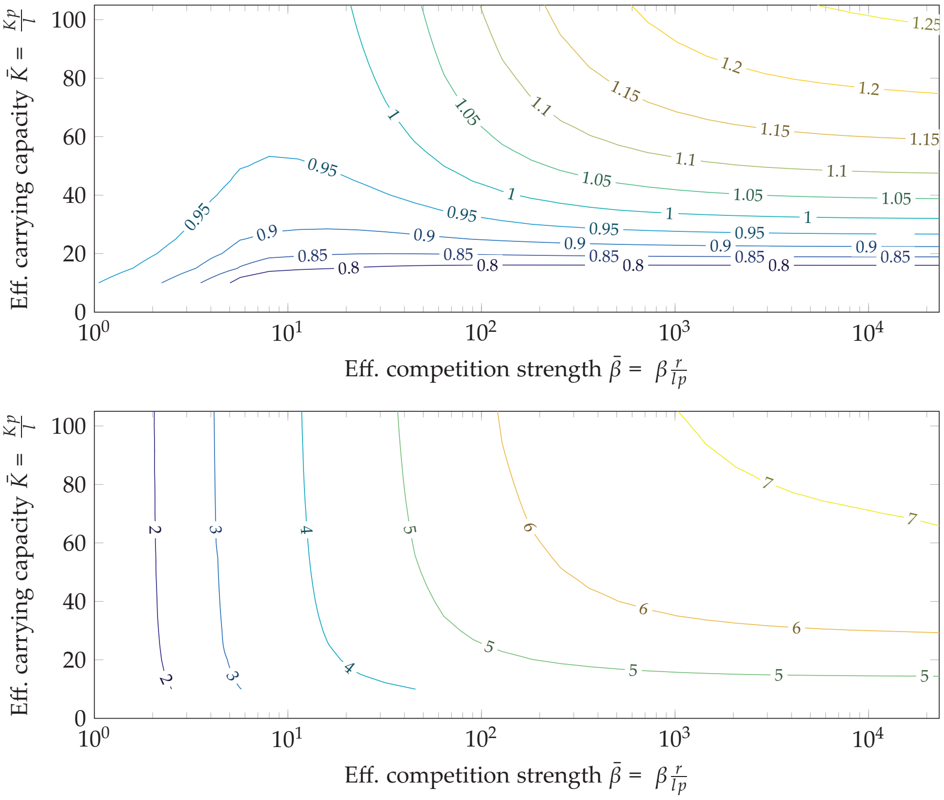

Figure 3: Isolines of the ratio of the total population of predators (*top*) and prey (*bottom*) in the solution of the model with $\bar{r} = 3.5, \bar{l} = 0.1$, and $\bar{K}$ and $\bar{\beta}$ as parameters to the corresponding quantity for the solution with only one group.

However, there are some notable differences between model (1a) and (1b) and model (5). To gain insight into these we have analyzed model (6) for different values of the handling times T_i. In particular, we have considered the effect of T_i on sizes of territories arising in the limit $\beta \to +\infty$.

In the case $T_i = 0$, model (6) is our original model. As simulations show, if the handling times are all small with respect to the other parameters, the solutions of model (6) are close to those of model (1a) and (1b). In particular, this implies that the properties of the original model are also valid in the presence of positive but small handling times.

For larger values of T_i, it is known that in space-independent predator-prey models, a type II functional response gives rise to an attractive limit cycle instead of an attractive equilibrium. We have observed in numerical simulations that if competition β is sufficiently small, large handling times T_i also induce oscillations in the space-dependent model.

On the other hand, strong competition and territoriality have a stabilizing effect, in particular through the formation of buffer zones. Again we have found that if the territories are sufficiently small and the buffer zones are not too scattered away from each other, the oscillations induced by large handling times are damped, and the solutions converge to equilibria that show similar characteristics to those of model (1b) and (1b).

Finally, if, on the contrary, territories are large enough, the damping effect of the buffer zones is not strong enough to compensate for the oscillations induced by type II functional responses (see app. G for some simulations on the aspect).

Thus, we have found that there is a remarkable interplay between the spatial effects of territoriality and dynamics induced by type II functional responses. These new features, as well as other modifications of the original model, open new perspectives and deserve more in-depth study.

Discussion

We have proposed a model for the interaction of predators and prey emphasizing the role of conspecific competition between predators. We have found that this competition plays a central role in the formation of territories. Indeed, we have shown that varying the strength of the competition yields different territorial behaviors. For small values of β, the model describes predators that have weak territorial behavior and home ranges that overlap extensively (Getty 1981; Stamps

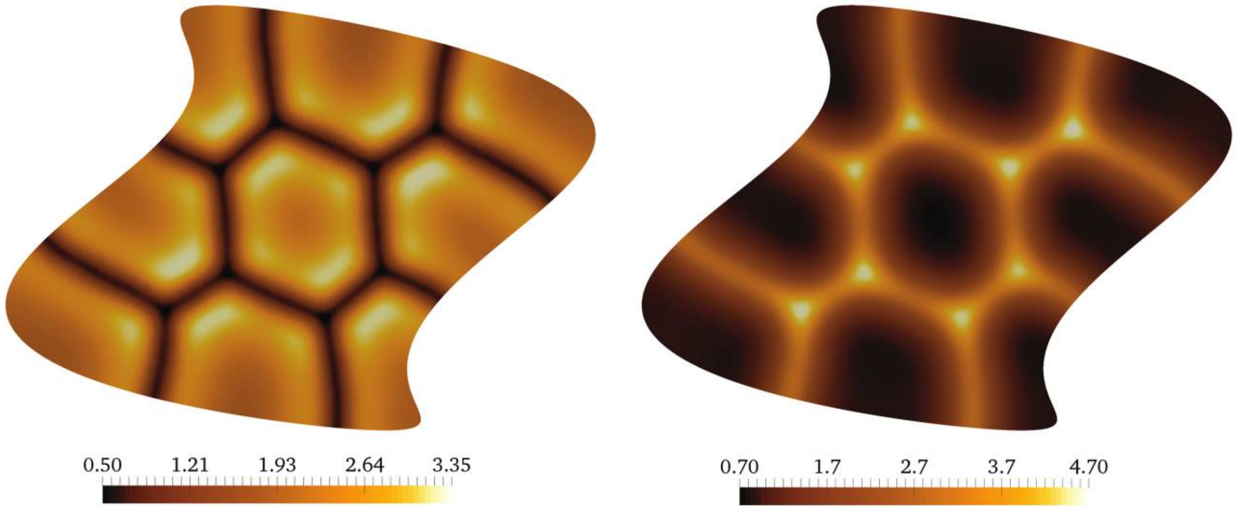

Figure 4: Shape of the territories predicted by the model in a homogeneous environment. Shown on the left is the distribution of nine groups of predators, and shown on the right is the corresponding distribution of prey. In the color scale under each plot, darker colors correspond to lower densities, and brighter colors correspond to higher densities.

1990). For large values of β, it yields predators with strong territorial behavior tendencies whose territories have sharp boundaries (Nursall 1977; Askenmo et al. 1994; Eason et al. 1999). Increasing the strength of competition β has two effects: encounters between groups become less frequent, and the territories become more distinctly separated.

Unlike some other models of spatially explicit territorial behaviors (e.g., Lewis and Murray 1993), we have not assumed any mechanisms in the establishment and defense of territories other than strong interference competition between groups. Thus, in this context territoriality emerges as a consequence of interference competition.

We have further analyzed the conditions for such spatial segregation. It depends on various parameters of the model. Strong inference competition will not lead to separated territories in the case of either (i) small regions or scarce prey (small carrying capacity K) or (ii) highly motile predators (large motility d_i). On the contrary, when the carrying capacity of prey is sufficiently larger than the abundance of prey expected at the predator-prey equilibrium, strong competition leads to territory formation.

Any territory must have a area larger than an explicit threshold and can support at most a certain maximal number of groups. In particular we have shown that the maximal number of groups may increase as the following quantities increase: the carrying capacity of the environment for the prey, the predation efficiency, and the available surface. It decreases when the mobility of predators and the decay rate of predators in the absence of prey increase. These relationships are reminiscent of some empirical observations. In particular, since carrying capacity K is a rough upper estimate of the density of prey, our formula suggests that the size of the territories is (at most) inversely proportional to the abundance of prey. Hixon (1980) predicted a similar dependence in time-allocation models. On the empirical side, several observations report such an inverse proportionality between territory size and resource/prey abundance. Empirical studies of ants (Adams 2016), seabirds (Myers et al. 1979), birds of prey (Temels 1987), river ducks (Ippi et al. 2018), migratory songbirds (Marshall and Cooper 2004), coyotes (Mills and Knowlton 1991), and African wild dogs (van der Meer 2014) report such inverse proportionality.

Next, we considered the effects on the total size of the population of predators. By analyzing the dependence of the solutions of our model with respect to the different parameters, we have established 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. It has been argued (Brown 1964) that in order for territoriality to emerge, there needs to be aggressiveness between conspecifics and an economic advantage in having divided territories. What we have shown here is that, under certain conditions, the conspecific aggressiveness between groups yields an increase of the total size of prey population due to buffer zones. This leads to an increase of the density of predators which in certain parameter regimes can offset the losses caused by the strong hostility between groups for the total population. Existence of buffer zones and their positive impact is well established. Several studies describe them, for example, between ants colonies (Adams

2016), wolf territories (Mech 1977, 1994; Mech et al. 1980), lions (Lehmann et al. 2008), and even human societies (Hickerson 1965; Watrall 1968).

The shape of territories predicted by our model reproduce some empirical observations. The model suggests that the boundaries of the territories can be found by matching the pressure of the competing predators (Maynard Smith 1974; Adams 1998, 1990, 2001, 2003). Moreover, it suggests that the hexagonal shape should be the most frequent in the absence of geographical disparities. 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).

The model we have proposed here opens up several new directions of investigation. First, it is important to further analyze its mathematical implications. The global structure of the set of solutions of this system remains to be fully understood. The stability of solutions is an essential criterion to discern realistic configurations. Therefore, stability needs to be further investigated, in particular when considering the impact of strong competition among predators on the total population. This is important in order to discard spurious (unstable) solutions. Another important development here would be a more general dynamical model that would involve the change in the number of groups or the aggressiveness between conspecifics as intrinsic variables that one seeks to determine. As we have seen, type II functional responses as well as other modifications of this model open many interesting perspectives.

Clearly, it will also be important in the future to carry out detailed comparisons of the consequences of the model or its generalizations with observations. Devising experiments to this end would be very useful. For instance, an experimental setting whereby one can vary the carrying capacity could shed light on the role this parameter plays in territory formation we notice here. All of this would make more precise one of our main findings here, namely, that a high level of aggressiveness between groups can benefit the total size of the predator populations.

Acknowledgments

This work was supported by a European Research Council (ERC) Advanced Grant 2013 (grant 321186, "ReaDi—Reaction-Diffusion Equations, Propagation and Modelling"), held by H.B. This work was also partially supported by the French National Research Agency (ANR), within project NONLOCAL ANR-14-CE25-0013. We are indebted to J. Murray for his inspiring lecture on wolf territories in Paris in 2001. We are grateful to M. Lewis and W. F. Fagan for many insightful comments and for pointing out some related literature. We thank E. Crooks for her useful comments on the manuscript. We are also much indebted to A. Winn, M. Cortez, Y. Michalakis, and two anonymous referees for the many exchanges and suggestions that helped to greatly improve the manuscript.

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