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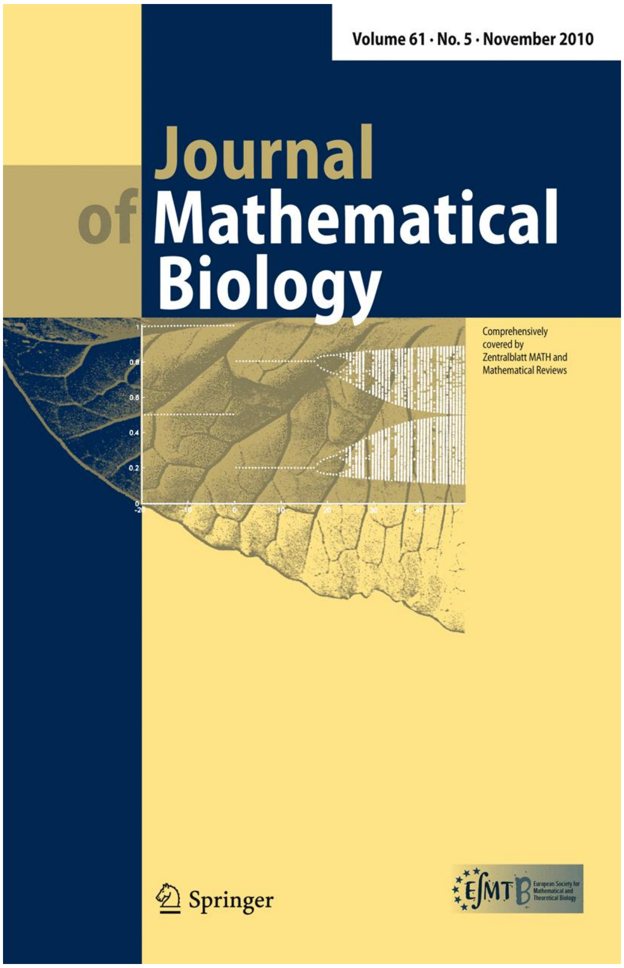

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A differential game theoretical analysis of mechanistic models for territoriality

Frédéric M. Hamelin · Mark A. Lewis

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Abstract In this paper, elements of *differential* game theory are used to analyze a spatially explicit home range model for interacting wolf packs when movement behavior is uncertain. The model consists of a system of partial differential equations whose parameters reflect the movement behavior of individuals within each pack and whose steady-state solutions describe the patterns of space-use associated to each pack. By controlling the behavioral parameters in a spatially-dynamic fashion, packs adjust their patterns of movement so as to find a Nash-optimal balance between spreading their territory and avoiding conflict with hostile neighbors. On the mathematical side, we show that solving a nonzero-sum differential game corresponds to finding a non-invasible function-valued trait. From the ecological standpoint, when movement behavior is uncertain, the resulting evolutionarily stable equilibrium gives rise to a *buffer-zone*, or a no-wolf's land where deer are known to find refuge.

Keywords Spatial ecology · Behavioral ecology · Home range analysis · Evolutionary games · Function-valued traits

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F. M. Hamelin · M. A. Lewis
Centre for Mathematical Biology, Mathematical and Statistical Sciences,
University of Alberta, 632 Central Academic Building, Edmonton, AB T6G 2G1, Canada

Present Address:
F. M. Hamelin (✉)
Écologie et Sciences Phytosanitaires, AGROCAMPUS OUEST, 65 rue de Saint Brieuc,
CS 84215, 35042 Rennes Cedex, France
e-mail: fhamelin@agrocampus-ouest.fr

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1 Introduction

Territories take the form of distinct space-use patterns, many of which persist over long periods of time (Moorcroft and Lewis 2006). For example, some wolf territories are separated by long-lasting *buffer-zones*, areas between territories that each pack avoids, which constitute a deer sanctuary (Mech 1977). There is also evidence that, in these buffer zone regions, the deer density is higher than in surrounding wolf territories (Hoskinson and Mech 1976). It is intriguing to ask how such buffer zones can arise and be maintained as stable entities, when wolf packs could gain much-needed additional prey by trespassing into the buffer zones and depleting them of prey. An early theoretical investigation assumed hexagonal territories with intervening buffer zones and Lotka-Volterra predator prey dynamics, concluding that such buffer zones should be susceptible to invasion by adjacent packs, thus having limited stability (Taylor and Peters 1991). However, a partial answer to the issue of buffer zone persistence stems from the observation that wolf scent-mark densities can be high at territorial boundaries where interpack aggression is also high (Peters and Mech 1975). When these ideas are included in a mechanistic territorial model with fixed behavioral rules for movement and scent-marking, buffer zones and *bowl-shaped* scent mark densities (with the edges of the bowl corresponding to territorial boundaries) can arise spontaneously under the joint assumptions of (i) positive feedback with regard to overmarking foreign scent marks and (ii) spatial avoidance of foreign scent marks (Lewis and Murray 1993) (Fig. 1).

Mechanistic models for territorial movement of the form analysed in Lewis and Murray (1993) provide a framework, based on mathematical modelling and real data analysis, for determining how animal space-use behaviors shape observed territorial

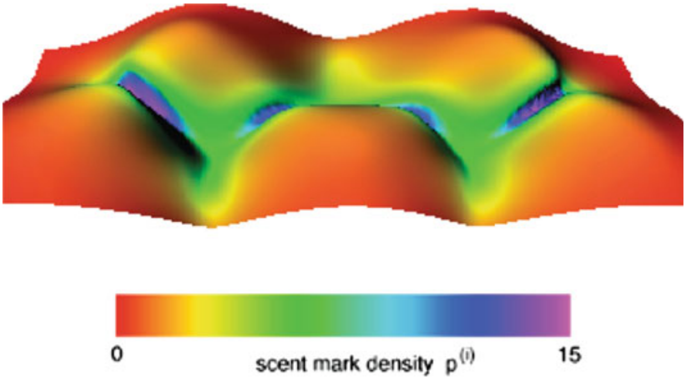

Fig. 1 Sharp territorial boundaries arise from mechanistic models with scent marking rules. The mathematical model describes 5 interacting packs. The height of the surface indicates total space-use density and the gradation indicates scent-mark density. Note the existence of buffer zones and heightened scent mark density. For details of the underlying mathematical model see Moorcroft and Lewis (2006). This figure is based on color plate six of Moorcroft and Lewis (2006)

patterns (Moorcroft and Lewis 2006). The mechanistic models start from a biased random walk, with behavioral rules formulated to describe how individuals respond locally to environmental conditions. The long-term space use of the territorial individuals can, in turn, be approximated by steady states of Fokker-Planck equations that are derived from the random walk model. The Fokker-Planck equations have coefficients that vary spatially, depending on locally varying conditions such as scent mark density, terrain slope, or prey density. Predictions from the Fokker-Planck approximations for space use have been rigorously tested against radio-tracking data, and have shown to be more powerful than typical statistical models (Moorcroft et al. 1999). The reasons for this are two-fold. First they can replicate the complex patterns of space use observed in radio-tracking data using very few model parameters, and second they can accurately predict territorial shifts under changing conditions (such as removal of a competing pack). For example, the mechanistic modelling Fokker-Planck approach can determine how interpack scent marking and prey resource availability govern territorial patterns of animals in heterogeneous environments, such as coyotes in Yellowstone (Moorcroft et al. 2006). [For a test of a model predictions for territorial shifts under changing conditions, see, for example, color plate 15 of Moorcroft and Lewis (2006)].

One limitation of the mechanistic models, as originally formulated, lies in the assumption of fixed behavioral rules, that do not respond to the behaviors of individuals from adjacent packs. Space-use behavior is expected to result from a tradeoff between expanding a territory (so as to maximize prey intake, prevent intra-pack competition, provide mating opportunities, etc.) and avoiding conflict with hostile neighbors (Adams 2001). Thus, although the ecological determinants of home-range pattern formation are, in the light of such models, much better understood, a new question arises: that of the evolutionary relevance of the underlying space-use behavioral rules.

The simplest approach to evolutionary significance of space-use does not use mechanistic models at all. It simply asks how adjacent packs can occupy space so as to individually maximize space occupancy while avoiding neighbors (Adler and Gordon 2003). When two adjacent packs attempt to do this simultaneously, it can be formulated as a game. We refer to this as a u-game because this game is with respect to the expected density of packs u. As we will show, a simple analysis of the u-game gives rise to a distinct partitioning of space with no territorial overlap. Indeed this pattern is sometimes seen in some territorial mammals, such as badgers (Kruuk 1989; Moorcroft and Lewis 2006).

How, then, do buffer zones arise as evolutionarily stable strategies? Assuming each location in space a priori has the same value (as opposed to a resource-continuum version of the ideal-free-distribution, see Rowell (2009) and references therein), one possibility is that buffer zones are a response to wolf movement patterns that are unknown or uncertain. Such uncertainty will arise from behaviors that are unpredictable a priori, being dependent upon stochastic individual components (such as gut fullness) or variable environmental cues (such as deer scent patterns). In this case, if interactions are aggressive then it may be advantageous to avoid regions that are close to another pack.

It is this possibility of uncertainty in behavior driving the formation of buffer zones as evolutionarily stable strategies that we investigate in the paper. Uncertainty can be incorporated into the mechanistic behavioral rules. In the context of mechanistic

Fokker-Planck movement models, the random component of movement is summarized by a diffusion coefficient and the directed component by an advection term. If movement terms retain uncertainty or randomness, then the ratio of advective to diffusive movement will remain bounded. A more precise definition of this ratio will be described by the term β in Sect. 3.

In an initial attempt at investigating the question of evolutionary significance of space-use in a mechanistic territorial model, (Lewis and Moorcroft 2001) consider an evolutionary game between wolf packs (Maynard Smith 1982), where each wolf pack is assumed to operate as a cohesive unit, maximizing the expected number of offspring produced in a single year by the alpha female (Schmidt and Mech 1997). An interesting and ecological implication of the model is that the Evolutionarily Stable Strategy (ESS) gives rise to an *overlap* of the territories rather than formation of a buffer-zone. Thus it still remains to be explained how such a no wolf's land can be evolutionarily stable (Adler and Gordon 2003; Mesterton-Gibbons and Adams 2003; Morrell and Kokko 2005; Börger et al. 2008).

One limitation of the Lewis and Moorcroft (2001) analysis is the assumption of space-use strategies that are static in space, thus limiting the territorial shaping possibilities. In other words, the rules in Lewis and Moorcroft (2001) cannot be modified to vary as a function of distance from the den site. Hence the following question: *can allowing for spatially-dynamic space-use strategies that maintain an uncertain component give rise to a buffer-zone?* In this paper, we aim to apply differential game theory (Isaacs 1965; Başar and Olsder 1999) as an appropriate and powerful framework for addressing this issue. As a preliminary approach, we initially review the approach of Lewis and Moorcroft (2001) by assuming that behavioral rules are invariant in space (Lewis and Moorcroft 2001). We then extend this model to allow strategies that vary spatially as a function of distance from the den site.

The paper is organized as follows. Section 2 addresses the above mentioned u-game. Section 3 introduces the ecological model. Section 4 deals with a game for the simple spatially invariant model, and points out the limits of this static theory. Section 5 then states the open-loop nonzero-sum differential game that corresponds to a spatially-dependent extension of the earlier static one. Section 6 summarizes the results and finally, Sect. 7 is a discussion oriented towards future directions.

2 Definition and analysis of the u-game for space use

An initial investigation as to how territorial animals allocate space asks how space use is allocated between two adjacent packs, when both packs are expected to individually maximize space occupancy while avoiding neighbors.

Consider two equal-sized wolf packs, **1** and **2**, moving on the segment [0, 1] (our length unit), whose end points 0 and 1 are the locations of packs **1** and **2**'s densities, respectively.

2.1 Phenotypic evolution and game theory

According to Diekmann (2004), "*The theory of phenotypic evolution comes in two brands. The earliest is based on direct interaction and game theory, with evolution-*

ary success being measured in terms of (*an often rather mysterious*) *pay off*", see Maynard Smith (1982). The body of the present paper enters in this category, so as to express the central issue in the simplest possible way. A possible game-theoretical shortcut consists in assuming that each pack is interested in minimizing the overlap with itself and even more in minimizing the overlap with the other pack. 'Minimizing the overlap with itself' means avoiding over-occupying a given location, as, for example, it may negatively affect resource density in this area. This can be expressed as the following game

$$\mathcal{P}_1 : \min_{u_1(\cdot)} J_1(u_1(\cdot), u_2(\cdot)) = \int_0^1 u_1(x)(u_1(x) + \vartheta u_2(x))\mathrm{d}x, \tag{1}$$

$$\mathcal{P}_2 : \min_{u_2(\cdot)} J_2(u_1(\cdot), u_2(\cdot)) = \int_0^1 u_2(x)(u_2(x) + \vartheta u_1(x))\mathrm{d}x, \tag{2}$$

where $\vartheta > 1$, subject to the constraints

$$\int_0^1 u_1(x)\,dx = \int_0^1 u_2(x)\,dx = 1. \tag{3}$$

The second brand, Adaptive Dynamics, makes phenotypic interactions indirect, *via* an ecological feedback loop. (see Diekmann 2004 for an introduction to concepts, ideas and methods developed by the authors of Dieckmann and Law 1996; Metz et al. 1996; Geritz et al. 1998 and others.) The latter brand incorporates density dependence in a Darwinian fashion. In this way, "payoffs" are dynamic and endogenous to the model, itself ecologically consistent and explicit.

Note that the replicator equation in evolutionary game theory nonetheless naturally arises from frequency dependent population growth rates (see, e.g., Bernhard and Hamelin 2009), and that "refined" game dynamics incorporating density dependence also are very relevant (e.g., Vincent and Brown 2005; see Dercole and Rinaldi 2008 for a comparative analysis, and Auger and Pontier 1998 for an alternate approach, accounting for behavioral plasticity).

Anyhow, even the "rough" game theoretical modelling shortcut is not necessarily to be opposed to self-contained Adaptive Dynamics. Appendix A introduces an ecological feedback loop and derives a "non-invasibilty" (Diekmann 2004) criterion that includes prey, natural mortality, reproduction and interpack aggression. This results in the same game (1)–(3), but with the interaction term given as

$$\vartheta = 1 + \frac{\alpha}{\sigma\psi}\frac{r}{\psi}, \tag{4}$$

where r is the maximum growth rate for prey, α is the mortality rate arising from hostile interactions from adjacent packs, ψ is the rate of prey consumption and σ is the conversion efficiency from prey into predators. Based on parameters for wolf populations in Minnesota the interaction term is estimated as $\vartheta \approx 3$ (Appendix A). The non-invasibility condition then defines a Nash equilibrium (see below) for the game (1)–(3). Both modelling approaches thus lead to the same mathematical problem.

2.2 Solution to the u-game

Any pair $(u_1^\star, u_2^\star)$ that satisfies the following inequality is a Nash equilibrium:

$$\begin{aligned} \forall u_1(\cdot) \in \mathcal{U}, &\quad J_1(u_1^\star(\cdot), u_2^\star(\cdot)) \leq J_1(u_1(\cdot), u_2^\star(\cdot)), \\ \forall u_2(\cdot) \in \mathcal{U}, &\quad J_2(u_1^\star(\cdot), u_2^\star(\cdot)) \leq J_2(u_1(\cdot)^\star, u_2(\cdot)), \end{aligned}$$

where $\mathcal{U}$ is the set of admissible $u_i(\cdot)$'s, $i = 1, 2$, i.e., those which sum to unity (having $u_i : [0, 1] \mapsto \mathbb{R}^+$).

A straightforward application of the minimum principle shows that a nontrivial Nash equilibrium to the above u-game is a solution with constant total density $u(x) = u_1(x) + u_2(x) = 2$, and no overlap $\mathcal{O}(u_1, u_2) = 0$ (Appendix B). This solution, corresponding to Pack **1** on the left and Pack **2** on the right, is thus given as

$$\left(u_1^*(x) := \begin{cases} 2 \text{ if } x \in [0, 1/2), \\ 0 \text{ if } x \in [1/2, 1]. \end{cases}, \qquad u_2^*(x) := \begin{cases} 0 \text{ if } x \in [0, 1/2). \\ 2 \text{ if } x \in [1/2, 1]. \end{cases} \right).$$

Thus, the u-game gives rise to equitable partitioning of space, and no buffer zone arises.

3 The ecological model

We now develop a mechanistic approach to movement modelling, based on the Fokker–Planck equation. This will allow us to incorporate a new element into the game, that of intrinsic unpredictabilty in the movement behavior. As we will show in later sections, it is this element that is key to the formation of buffer zones. The Fokker–Planck equation can be derived as an approximation for a large class of general mechanistic models whose qualitative behavior is captured in the infinitesimal mean (advection) and variance (diffusion) moments of a movement function describing step sizes and directions. Details of this approximation are given in Moorcroft and Lewis (2006).

3.1 Wolves' space-use dynamics

Following the approach of Moorcroft and Lewis, movement of each pack is modeled by a Fokker–Planck equation, with spatially varying diffusion coefficients d_i and advection coefficients c_i (Moorcroft and Lewis 2006). This arises from a random walk governing individual behavior with bias towards the den-site. Packs **1** and **2**'s probability distributions u_1 and u_2 are given by: $\forall x \in (0, 1)$,

$$\begin{aligned}\frac{\partial}{\partial t}\mathsf{u}_1(x,t) &= \frac{\partial^2}{\partial x^2}(d_1(x)\mathsf{u}_1(x,t)) + \frac{\partial}{\partial x}(c_1(x)\mathsf{u}_1(x,t)),\\ \frac{\partial}{\partial t}\mathsf{u}_2(x,t) &= \frac{\partial^2}{\partial x^2}(d_2(x)\mathsf{u}_2(x,t)) - \frac{\partial}{\partial x}(c_2(x)\mathsf{u}_2(x,t)),\end{aligned} \tag{5}$$

where the d_i's and the c_i's are functions that map space to $\mathbb{R}^+$, respectively C^2 and C^1. They respectively correspond to the random and directed (towards the den-site) components of motion. Each of the above PDE's is subject to zero-flux boundary conditions at $x = 0, 1$:

$$\begin{aligned}\frac{\partial}{\partial x}(d_1(x)\mathsf{u}_1(x,t)) + c_1(x)\mathsf{u}_1(x,t) = 0,\\ \frac{\partial}{\partial x}(d_2(x)\mathsf{u}_2(x,t)) - c_2(x)\mathsf{u}_2(x,t) = 0,\end{aligned} \tag{6}$$

indicating that individuals remain in the [0, 1] spatial domain.

Lastly, as each probability density function, u_1 and u_2 must sum to one:

$$\forall t, \quad \int_0^1 \mathsf{u}_1(x,t)\mathrm{d}x = 1 \quad \text{and} \quad \int_0^1 \mathsf{u}_2(x,t)\mathrm{d}x = 1. \tag{7}$$

3.1.1 Pattern of space-use, definition

We define a *pattern of space-use* u_1 as a stationary solution of Eq. (5):

$$0 = \frac{\mathrm{d}^2}{\mathrm{d}x^2}(d_1(x)u_1(x)) + \frac{\mathrm{d}}{\mathrm{d}x}(c_1(x)u_1(x)), \tag{8}$$

subject to zero-flux boundary conditions

$$\frac{\mathrm{d}}{\mathrm{d}x}(d_1(x)u_1(x)) + c_1(x)u_1(x) = 0, \tag{9}$$

for $x = 0, 1$. Similar equations hold for Pack **2**'s stationary distribution u_2, *mutatis mutandis*.

Equations (8) and (9) yield: $\forall x \in [0, 1]$,

$$0 = \frac{\mathrm{d}}{\mathrm{d}x}(d_1(x)u_1(x)) + c_1(x)u_1(x), \tag{10}$$

and one can equivalently consider: $\forall x \in [0, 1]$,

$$0 = \frac{\mathrm{d}}{\mathrm{d}x}u_1(x) + \beta_1(x)u_1(x), \tag{11}$$

where $\beta_1(x) = (\mathrm{d}d_1(x)/\mathrm{d}x + c_1(x))/d_1(x)$ is a C^1 function, provided d_1 is not zero, which we assume. The coefficient β_1 can be considered as Pack **1**'s control variable. In other words, one may assume without loss of generality that d_1 is a constant, in which case the variation on β_1 would reflect that of the advection coefficient c_1. We shall refer to the latter interpretation when discussing the ecological implications (Sect. 7).

We restrict ourselves to the biologically reasonable case where there is a net bias towards the den-site (Moorcroft and Lewis 2006) and hence $\beta_1, \beta_2 \geq 0$. It is also natural to assume that, when movement retains an unpredictable nature, β_1 will be bounded from above by some maximum possible value, a, so that $0 \leq \beta_1, \beta_2 < a$. Estimates can be made for β for red fox and coyotes for the simple case where both the c_1 and d_1 are constant. These estimates can be found by taking the dimensional values of β in Chapter 3 of Moorcroft and Lewis (2006) (with units km^{-1}) and rescaling them by the half width of a territory for a red fox (1 km) and a coyote (2 km): $\beta \approx 2$ for red foxes and $\beta \approx 24$ for coyotes. To the best of our knowledge, β has not been estimated explicitly for wolves.

3.1.2 Expressing $u_1(x)$ in terms of an ODE

We introduce the notation $\dot{u}_1 = \mathrm{d}u_1/\mathrm{d}x$. Equations (11) and (7) now read

$$\dot{u}_1 = -\beta_1 u_1, \quad u(0) = u_1^0, \quad \text{s.t.} \int_0^1 u_1(x)\mathrm{d}x = 1.$$

Hence,

$$u_1(x) = u_1^0 \exp\left(-\int_0^x \beta_1(y)\mathrm{d}y\right),$$

where u_1^0 is given by the integral constraint (7).

For instance, if β_1 is a constant, one obtains

$$u_1^0 = \begin{cases} 1 & \text{if } \beta_1 = 0, \\ \beta_1/(1 - \mathrm{e}^{-\beta_1}) & \text{otherwise,} \end{cases}$$

so that

$$u_1(x) = \begin{cases} 1 & \text{if } \beta_1 = 0, \\ \beta_1 \mathrm{e}^{-\beta_1 x}/(1 - \mathrm{e}^{-\beta_1}) & \text{otherwise.} \end{cases}$$

The case $\beta_1 > 0$ describes the so-called Holgate–Okubo home-range model where space-use drops off exponentially with distance from the den-site (Moorcroft and Lewis 2006). As it is clear that u_1 is continuous with respect to β_1, we shall omit to specify the above singularity ($\beta_1 = 0$ case) in what follows.

4 The static game

In this section, we model wolf pack interactions as a *static* game, i.e., where the control variables β_1 and β_2 are assumed invariant in space. We show that this provides only limited insight as to the underlying behavioral mechanisms.

The game is thus the following:

$$\begin{aligned} \mathcal{P}_1 &: \min_{\beta_1 \in \mathbb{R}^+} J_1(\beta_1, \beta_2) = \int_0^1 u_1(u_1 + \vartheta u_2)\mathrm{d}x, \\ \mathcal{P}_2 &: \min_{\beta_2 \in \mathbb{R}^+} J_2(\beta_1, \beta_2) = \int_0^1 u_2(u_2 + \vartheta u_1)\mathrm{d}x, \end{aligned} \quad \text{where} \quad \begin{aligned} u_1(x) &= \frac{\beta_1 \mathrm{e}^{-\beta_1 x}}{1 - \mathrm{e}^{-\beta_1}}, \\ u_2(x) &= \frac{\beta_2 \mathrm{e}^{\beta_2 x}}{\mathrm{e}^{\beta_2} - 1}. \end{aligned} \tag{12}$$

Note that $J_1(\beta_1, \beta_2) = J_2(\beta_2, \beta_1)$. We are interested in finding a Nash equilibrium $(\beta_1^\star, \beta_2^\star)$.

4.1 Game solution

Equation (12) yields

$$J_1(\beta_1, \beta_2) = \begin{cases} \dfrac{\beta_1}{2} \dfrac{\mathrm{e}^{2\beta_1} + 2\vartheta\beta_1 \mathrm{e}^{\beta_1} - 1}{\mathrm{e}^{2\beta_1} - 2\mathrm{e}^{\beta_1} + 1} & \text{if } \beta_1 = \beta_2, \\ \dfrac{\beta_1}{2} \dfrac{(\beta_2 - \beta_1)(\mathrm{e}^{\beta_1 + \beta_2} + \mathrm{e}^{\beta_2} - \mathrm{e}^{\beta_1} - 1) + 2\vartheta\beta_2(\mathrm{e}^{\beta_2} - \mathrm{e}^{\beta_1})}{(\beta_1 - \beta_2)(\mathrm{e}^{\beta_1} + \mathrm{e}^{\beta_2} - \mathrm{e}^{\beta_1 + \beta_2} - 1)} & \text{otherwise,} \end{cases}$$

symmetrically for J_2. The limit of the second term when $\beta_1 \to \beta_2$ coincides with the first term; the payoff functions are thus continuous. Define

$$B_1(\beta_2) = \arg\min_{\beta_1} J_1(\beta_1, \beta_2) \quad \text{and} \quad B_2(\beta_1) = \arg\min_{\beta_2} J_2(\beta_1, \beta_2),$$

as the best-response functions. Note that $B_2(\beta_1) = B_1(\beta_1)$, due to the symmetry.

As we are interested in fixed territorial patterns, already resulting in pairs of wolf distributions, let us focus on *pure* (non-randomized) equilibria only, and thus omit this adjective from now on.

Numerically solving $\partial J_1/\partial \beta_1 = 0$ allows one to plot these best-response functions, as shown in Fig. 2. A nontrivial intersection of the best-response curves exists for $\vartheta > 2$, but for $\vartheta \leq 2$, there is no intersection other than $(0, 0)$. As the Nash equilibria are precisely given by the intersections of the best-response curves (Fudenberg and Tirole 1991), this means that when $\vartheta \leq 2$, $(0, 0)$, a pair of spatially uniform territorial patterns, is the unique Nash equilibrium of the game. On the other hand, when $\vartheta > 2$, $(0, 0)$ may not be the most relevant equilibrium, in the sense that the evolutionary dynamics of space use could have converged to the Holgate-Okubo home-range equilibrium. (The evolutionary dynamics of space use are as yet unspecified, and are

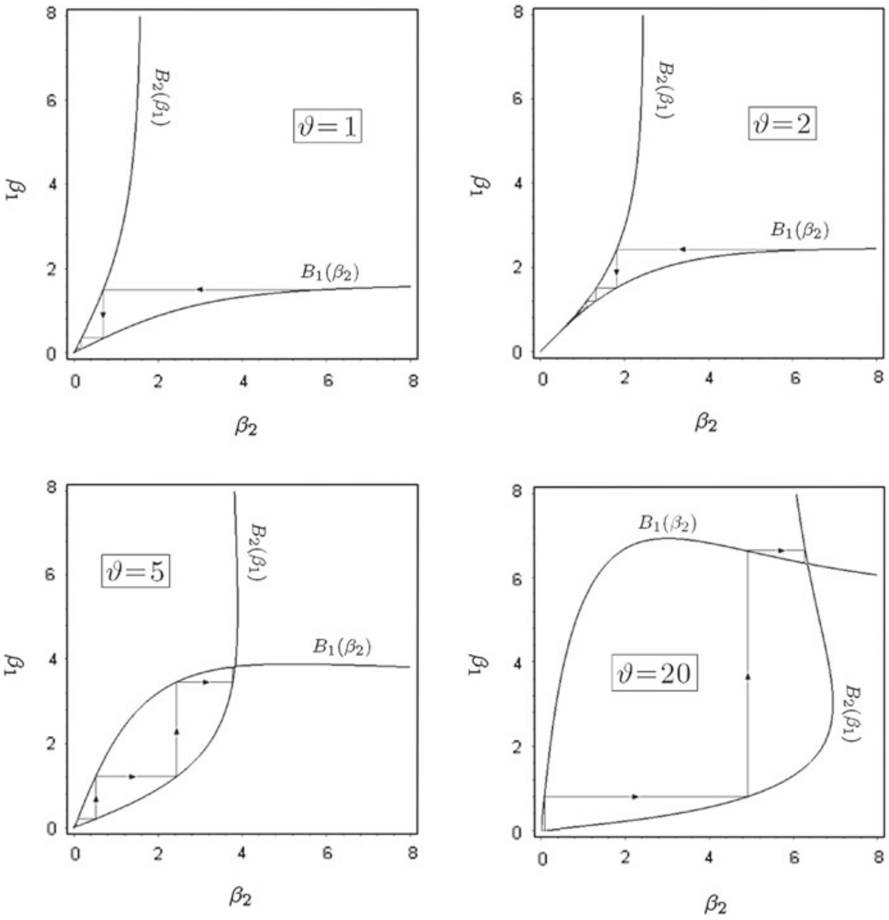

Fig. 2 Best-responses curves of the game stated in Sect. 4, for several values of ϑ. The *arrows* represent the best-response dynamics, as a caricature of evolutionary dynamics. $\vartheta = 20$ is a rather extreme value that was chosen to stress the general shape of the curves

caricatured in Fig. 2 by best-response dynamics; this point is further discussed in Sect. 7). We are interested in this case because it corresponds to the emergence of territories.

Rather than further analyzing this game, plotting the best-response curves reveals an apparent paradox in the game. Figure 2 shows best-response curves that are increasing functions over much of their domain. It means that, in this model, when one's opponent draws back (or increases its β), then one also has to do so (most of the time). Yet, it would have been expected that one spreads itself a bit more (or lowers its β) to conquer the space left by its opponent. Moreover, a similar observation can be drawn from Lewis and Moorcroft's model (Lewis and Moorcroft 2001). Thus this seemingly paradoxical feature is not particular to our model. The explanation lies in the fact that when the opponent concentrates its forces on its side, the other pack cannot invade the territory left at the center without also increasing its presence at the place where the opponent is very likely to be encountered. This is likely due to the fact that the pack's pattern of space use belongs to a one-parameter family of curves (see Eq. (12)). Thus, the pack cannot cleverly modulate its distribution. However, animals likely adjust their propensity to retreat as a function of the distance they are from their den-site. To take this into account, one has to allow β for depending on x, and this amounts to considering a differential game.

4.2 On open- and closed-loop formulations

One may point that β, or the propensity wolves have to retreat, should also be allowed to depend on u (and h) the densities of competing packs (and prey, possibly, see Appendix A), rather than on the independent variable x (the distance from the den-site) alone. Control theoreticians refer to a *closed-loop*, or state-feedback, control, as opposed to an *open-loop* one (see, e.g., Olsder 2001). By doing so, one would allow for *dynamic information* (Başar and Olsder 1999). In this way, players would be able to exert an influence on their opponents actions (yet not on their sovereign strategies) through partially controlling the information. The point is that it would change the nature, thus likely the outcome, of the game.

Unfortunately, in this particular case, the dynamics are to be stated as a two-point-boundary-value-problem (see Eq. (13) in Sect. 5), and such a formulation does not immediately fit into the Hamilton–Jacobi–Bellman/Isaacs theory (see, e.g., Hamelin and Bernhard 2008). Addressing the game in closed-loop is thus left for future research (see the end of Appendix B for a starting point).

In this paper, we aim to show that considering the propensity wolves have to retreat β as a *function-valued trait* (Dieckmann et al. 2006; Parvinen et al. 2006) (depending on the distance from the den-site x only) is sufficient to explain the occurrence of a buffer-zone.

5 A nonzero sum differential game in open-loop

We now consider the case where the spatial control variables β_1 and β_2 depend explicitly on space. In this case each pack can modulate its spatial movement as a function of location.

5.1 Game statement

In what follows, we use new variables u_3 and u_4 to ensure that $u_1(x)$ and $u_2(x)$ integrate to unity over the domain (7). Let

$$u_3(x) = \int_0^x u_1(z)\mathrm{d}z \quad \text{and} \quad u_4(x) = \int_0^x u_2(z)\mathrm{d}z.$$

Consider the following dynamics $\mathrm{d}u/\mathrm{d}x = \dot{u} = f(u, \beta_1, \beta_2)$:

$$\begin{cases} \dot{u}_1 = -\beta_1 u_1, & u_1(0) = u_1^0, \quad u_1(1) = u_1^1, \quad \beta_1 \in [0, a], \; u_1^0 > 0, \\ \dot{u}_2 = +\beta_2 u_2, & u_2(0) = u_2^0, \quad u_2(1) = u_2^1, \quad \beta_2 \in [0, a], \; u_2^1 > 0, \\ \dot{u}_3 = u_1, & u_3(0) = 0, \quad u_3(1) = 1, \\ \dot{u}_4 = u_2, & u_4(0) = 0, \quad u_4(1) = 1, \end{cases} \tag{13}$$

where u_1^0, u_1^1, u_2^0, u_2^2 are the names given to the boundary values associated to u_1 and u_2, as they result from the above equation.

The game is the following:

$$\begin{aligned} \mathcal{P}_1 : \min_{\beta_1(\cdot)} J_1(\beta_1(\cdot), \beta_2(\cdot)) &= \int_0^1 \ell_1(u(x))\mathrm{d}x, \quad \ell_1(u) = u_1(u_1 + \vartheta u_2), \\ \mathcal{P}_2 : \min_{\beta_2(\cdot)} J_2(\beta_1(\cdot), \beta_2(\cdot)) &= \int_0^1 \ell_2(u(x))\mathrm{d}x, \quad \ell_2(u) = u_2(u_2 + \vartheta u_1), \end{aligned} \tag{14}$$

subject to (13) and where $\vartheta > 1$. Define the Hamiltonian associated to each player's control problem as follows:

$$\begin{aligned} H_1(u, \beta_1, \beta_2, \lambda) &= \langle \lambda, f(u, \beta_1, \beta_2) \rangle + \ell_1(u), \\ &= -\lambda_1 \beta_1 u_1 + \lambda_2 \beta_2 u_2 + \lambda_3 u_1 + \lambda_4 u_2 + u_1(u_1 + \vartheta u_2), \\ H_2(u, \beta_1, \beta_2, \mu) &= \langle \mu, f(u, \beta_1, \beta_2) \rangle + \ell_2(u), \\ &= -\mu_1 \beta_1 u_1 + \mu_2 \beta_2 u_2 + \mu_3 u_1 + \mu_4 u_2 + u_2(u_2 + \vartheta u_1). \end{aligned} \tag{15}$$

The manifolds $\mathcal{M}_i$, $i = 0, 1$, define the boundary conditions for u_3 and u_4 by $\mathcal{M}_i = \{u_3 = i, \; u_4 = i\}$ (see Eq. 13). We use the $\star$ superscript to denote optimal policies or trajectories.

Given a continuous $\beta_2^\star(\cdot)$, Pontryagin's minimum principle (PMP) (Pontryagin et al. 1962) states that if a policy $\beta_1^\star(\cdot)$ generating a trajectory $u^\star(\cdot)$ is to be optimal, then there exists an absolutely continuous adjoint trajectory $\lambda(\cdot)$ such that

$$\begin{aligned} &\dot{\lambda}(x) = -\nabla_u H_1(u^\star(x), \beta_1^\star(x), \beta_2^\star(x), \lambda(x)), \quad \lambda(0) = \nu_0, \quad \lambda(1) = \nu_1, \\ &\quad \text{s.t. } \forall x \in [0, 1] \quad \text{where } \beta_1^\star(\cdot) \text{ is continuous}, \\ &\quad H_1(u^\star(x), \beta_1^\star(x), \beta_2^\star(x), \lambda(x)) = \min_{\beta_1 \in [0,a]} H_1(u^\star(x), \beta_1, \beta_2^\star(x), \lambda(x)), \end{aligned}$$

and where the ν_i's are normal to the $\mathcal{M}_i$'s manifolds (their nonzero components are to be determined). Similar equations hold for player **2**.

The above minimization condition translates into the following switch-functions

$$\begin{aligned} \sigma_1 &= \partial H_1 / \partial \beta_1 = -\lambda_1 u_1, \\ \sigma_2 &= \partial H_2 / \partial \beta_2 = +\mu_2 u_2, \end{aligned} \tag{16}$$

and the *bang-bang* optimal policy:

$$\beta_1^\star = \begin{cases} a & \text{if } \sigma_1 < 0, \\ \text{any } \beta_1 \in [0, a] & \text{if } \sigma_1 = 0, \quad \text{(singular control)} \\ 0 & \text{if } \sigma_1 > 0, \end{cases}$$

similarly for player **2**.

Based on our previous discussion, it turns out that two of our modelling assumptions regarding continuity of movement terms with respect to space may technically be violated. However, we do not expect this pose a problem with the analysis, as explained below.

(i) the assumption made in Sect. 3 that β_1 is, through c_1 and d_1, C^1. As argued by White et al. (1996), although allowing for a discontinuity in the advection term technically violates a flux conservation law, the connection with Eq. (8) can always been made, at the end of day, through smoothing β_1 around its possible discontinuity. Stating the game with such a smoothness constraint on the control would thus add unworthy difficulties, as the present game makes sense.

(ii) the assumption that $\beta_2^\star(\cdot)$ is continuous in the above PMP statement. Indeed, the difference with a classical control problem lies in the fact that the opponent is very likely to induce endogenous discontinuities in the dynamics (13). However, as players are assumed to use *open-loop* controls (as defined in Sect. 4.2), no discontinuity in the adjoint variables is to be expected (see, e.g., Olsder 2001).

We continue by writing the adjoint equations associated to player **1**,

$$\begin{cases} \dot{\lambda}_1 = -\partial H_1/\partial u_1 = +\lambda_1\beta_1 - \lambda_3 - 2u_1 - \vartheta u_2, & \lambda_1(0) = 0, \quad \lambda_1(1) = 0, \\ \dot{\lambda}_2 = -\partial H_1/\partial u_2 = -\lambda_2\beta_2 - \lambda_4 - \vartheta u_1, & \lambda_2(0) = 0, \quad \lambda_2(1) = 0, \\ \dot{\lambda}_3 = -\partial H_1/\partial u_3 = 0, & \lambda_3(0) = \gamma_0, \quad \lambda_3(1) = \gamma_1, \\ \dot{\lambda}_4 = -\partial H_1/\partial u_4 = 0, & \lambda_4(0) = \varepsilon_0, \quad \lambda_4(1) = \varepsilon_1, \end{cases} \tag{17}$$

and to player **2**,

$$\begin{cases} \dot{\mu}_1 = -\partial H_2/\partial u_1 = +\mu_1\beta_1 - \mu_3 - \vartheta u_2, & \mu_1(0) = 0, \quad \mu_1(1) = 0, \\ \dot{\mu}_2 = -\partial H_2/\partial u_2 = -\mu_2\beta_2 - \mu_4 - 2u_2 - \vartheta u_1, & \mu_2(0) = 0, \quad \mu_2(1) = 0, \\ \dot{\mu}_3 = -\partial H_2/\partial u_3 = 0, & \mu_3(0) = \zeta_0, \quad \mu_3(1) = \zeta_1, \\ \dot{\mu}_4 = -\partial H_2/\partial u_4 = 0, & \mu_4(0) = \delta_0, \quad \mu_4(1) = \delta_1. \end{cases} \tag{18}$$

One sees that $\gamma_0 = \gamma_1 = \gamma$, $\delta_0 = \delta_1 = \delta$, $\varepsilon_0 = \varepsilon_1 = \varepsilon$, $\zeta_0 = \zeta_1 = \zeta$, thus $\lambda_3 = \gamma$, $\lambda_4 = \varepsilon$, $\mu_3 = \zeta$ and $\mu_4 = \varepsilon$. Rewrite the adjoint Eqs. (17),

$$\begin{cases} \dot{\lambda}_1 = +\lambda_1\beta_1 - \gamma - 2u_1 - \vartheta u_2, & \lambda_1(0) = 0, \quad \lambda_1(1) = 0, \\ \dot{\lambda}_2 = -\lambda_2\beta_2 - \varepsilon - \vartheta u_1, & \lambda_2(0) = 0, \quad \lambda_2(1) = 0, \end{cases} \tag{19}$$

and (18),

$$\begin{cases} \dot{\mu}_1 = +\mu_1\beta_1 - \zeta - \vartheta u_2, & \mu_1(0) = 0, \quad \mu_1(1) = 0, \\ \dot{\mu}_2 = -\mu_2\beta_2 - \delta - 2u_2 - \vartheta u_1, & \mu_2(0) = 0, \quad \mu_2(1) = 0. \end{cases} \tag{20}$$

As u_1 and u_2 are strictly positive, we shall refer to $\varsigma_1 = -\lambda_1$ and $\varsigma_2 = \mu_2$ as the switch-functions associated with players **1** and **2** respectively (instead of σ_1 and σ_2, see Eq. (16)).

5.2 Game solution

First, notice that if Pack **2** plays 0 at any $x \in [0, 1]$ (is uniformly distributed), then there is no incentive for Pack **1** to attempt avoiding Pack **2** (each location being at the same risk level). Since the uniform distribution is the one which allows Pack **1** for minimizing the overlap with itself (or maximizing space occupancy, see Sect. 2.1), it follows that $(0, 0)$ (the pair of uniform distributions) is a Nash equilibrium. Yet, as already mentioned in Sect. 4, addressing the static game, this may not be the most relevant equilibrium; otherwise territories would not be observed. A preliminary analysis (Appendix C.1) shows that among *nonsingular* solutions, the only possible alternative is both packs play a for every $x \in [0, 1]$.

In this section, we investigate possible one-switch bang-bang *singular* solutions of the game stated in Sect. 5, see Eqs. (13) and (14). More accurately, we address the existence of a solution in which player **1** switches from a singular control $\tilde{\beta}_1(\cdot)$ to $\beta_1 = a$ forward in space (moving to the right), and player **2** conversely. Two scenarios are to be considered: either players' singular control x-range overlap, in which case we shall refer to an *overlap* scenario, or there is no bisingular component in the solution, in which case we shall refer to a *buffer* scenario.

In other words, the buffer-zone is defined as a separating region where both packs play full "advection" a, i.e., that each pack avoids.

Let us divide the $[0, 1]$ spatial domain into three parts: $[0, x^{\mathtt{l}}]$ (Pack **1**'s territory, to the left), $[x^{\mathtt{l}}, x^{\mathtt{r}}]$ (the possible buffer-zone or overlap region, at the center) and $[x^{\mathtt{r}}, 1]$ (Pack **2**'s territory, to the right).

5.2.1 To the left

Consider the dynamics (13), where $\beta_1 = \tilde{\beta}_1$ (a singular control to be determined) and $\beta_2 = a$. As $\varsigma_1 = -\lambda_1$ has to be zero on the singular arc followed by player **1**, one must have $\dot{\lambda}_1(0)$, which yields, after Eq. (19),

$$\gamma = -2u_1^0 - \vartheta u_2^0. \tag{21}$$

Equation (19) then reads

$$\dot{\lambda}_1 = 2(u_1^0 - u_1) + \vartheta(u_2^0 - u_2) = 0. \tag{22}$$

Therefore, despite the fact that $\tilde{\beta}_1$ is not yet determined, one gets an explicit expression of Eq. (13):

$$\begin{cases} u_1(x) = u_1^0 + \vartheta(u_2^0 - u_2(x))/2, \\ u_2(x) = u_2^0 \mathrm{e}^{ax}, \\ u_3(x) = u_1^0 x + \vartheta u_2^0(x + (1 - \mathrm{e}^{ax})/a)/2, \\ u_4(x) = u_2^0(\mathrm{e}^{ax} - 1)/a. \end{cases} \tag{23}$$

We shall also make use of the following explicit solution of Eq. (20) in the sequel:

$$a\mu_2(x) = (\delta + \vartheta u_1^0)(\mathrm{e}^{-ax} - 1) + u_2^0(\mathrm{e}^{-ax}(1+\vartheta^2/4) - \mathrm{e}^{ax}(1-\vartheta^2/4) - \vartheta^2/2). \tag{24}$$

Characterizing the singular control. Since Eq. (22), we know that the singular control is such that $2u_1 + \vartheta u_2$ is invariant. Using Eq. (13), this reads $0 = 2\dot{u}_1 + \vartheta \dot{u}_2 = -2\tilde{\beta}_1 u_1 + \vartheta a u_2$, hence:

$$\tilde{\beta}_1(x) = a\frac{\vartheta}{2}\frac{u_2(x)}{u_1(x)}, \tag{25}$$

where u_1 and u_2 are given by Eq. (23). Notice that $\mathrm{d}\tilde{\beta}_1(x)/\mathrm{d}x > 0$.

5.2.2 To the right

Consider the dynamics (13), where $\beta_1 = a$ and $\beta_2 = \tilde{\beta}_2$ (a singular control to be determined). Proceeding as in Sect. 5.2.1, one gets

$$\delta = -2u_2^1 - \vartheta u_1^1, \tag{26}$$

an explicit expression of Eq. (13)

$$\begin{cases} u_1(x) = u_1^1 \mathrm{e}^{a(1-x)}, \\ u_2(x) = u_2^1 + \vartheta(u_1^1 - u_1(x))/2, \\ u_3(x) = 1 + u_1^1(1 - \mathrm{e}^{a(1-x)})/a, \\ u_4(x) = 1 + u_2^1(x-1) + \vartheta u_1^1((\mathrm{e}^{a(1-x)} - 1)/a + x - 1)/2, \end{cases} \tag{27}$$

an explicit solution of Eq. (19) that we shall use later

$$\begin{aligned} a\lambda_1(x) = (\gamma + \vartheta u_2^1)(1 - \mathrm{e}^{a(x-1)}) + u_1^1(\mathrm{e}^{a(1-x)}(1 - \vartheta^2/4) \\ - \mathrm{e}^{a(x-1)}(1 + \vartheta^2/4) + \vartheta^2/2), \end{aligned} \tag{28}$$

and the expression of the singular control

$$\tilde{\beta}_2(x) = a\frac{\vartheta}{2}\frac{u_1(x)}{u_2(x)}, \tag{29}$$

where u_1 and u_2 are given by Eq. (27). Notice that $\mathrm{d}\tilde{\beta}_2(x)/\mathrm{d}x < 0$.

5.2.3 *At the center: buffer scenario*

Consider the dynamics (13), where $\beta_1 = a$, $\beta_2 = a$ and $x \in [x^{\mathtt{l}},\ x^{\mathtt{r}}]$. We shall use a superscript $\mathtt{l}$ or $\mathtt{r}$ to denote the value taken by a given variable at points $x^{\mathtt{l}}$ or $x^{\mathtt{r}}$, respectively.

We are interested in solving the following system of equations, whose first part below translates the connection of (23) to (27) through the buffer-zone (as the dynamics (13) can be decomposed in two autonomous systems of ODEs, according to odd and even subscripts):

$$u_1^1\mathrm{e}^{a(1-x^{\mathtt{l}})} = u_1^0 + \vartheta(u_2^0 - u_2^{\mathtt{l}})/2 \quad \text{where } u_2^{\mathtt{l}} = u_2^0\mathrm{e}^{ax^{\mathtt{l}}}, \tag{30}$$

$$u_2^0\mathrm{e}^{ax^{\mathtt{r}}} = u_2^{\mathtt{l}} + \vartheta(u_1^1 - u_1^{\mathtt{r}})/2 \quad \text{where } u_1^{\mathtt{r}} = u_1^1\mathrm{e}^{a(1-x^{\mathtt{r}})}, \tag{31}$$

$$1 + u_1^1(1 - \mathrm{e}^{a(1-x^{\mathtt{l}})})/a = u_1^0 x^{\mathtt{l}} + \vartheta u_2^0(x^{\mathtt{l}} + (1 - \mathrm{e}^{ax^{\mathtt{l}}})/a)/2, \tag{32}$$

$$u_2^0(\mathrm{e}^{ax^{\mathtt{r}}} - 1)/a = 1 + u_2^1(x^{\mathtt{r}} - 1) + \vartheta u_1^1((\mathrm{e}^{a(1-x^{\mathtt{r}})} - 1)/a + x^{\mathtt{r}} - 1)/2. \tag{33}$$

The second part consists in maintaining the continuity of the adjoint variables all along the trajectory followed, as required by Pontryagin's minimum principle (Sect. 5.1). After Eqs. (20) and (24), one obtains the following equality

$$\begin{aligned} a\mu_2(x^{\mathtt{l}}) &= -\delta(1 - \mathrm{e}^{a(x^{\mathtt{r}}-x^{\mathtt{l}})}) - u_2^{\mathtt{r}}(\mathrm{e}^{a(x^{\mathtt{l}}-x^{\mathtt{r}})} - \mathrm{e}^{a(x^{\mathtt{r}}-x^{\mathtt{l}})}) \\ &\quad + a\vartheta u_1^{\mathtt{r}}(x^{\mathtt{r}} - x^{\mathtt{l}})\mathrm{e}^{a(x^{\mathtt{r}}-x^{\mathtt{l}})}, \\ &= (\delta + \vartheta u_1^0)(\mathrm{e}^{-ax^{\mathtt{l}}} - 1) + u_2^0(\mathrm{e}^{-ax^{\mathtt{l}}}(1 + \vartheta^2/4) - \mathrm{e}^{ax^{\mathtt{l}}}(1 - \vartheta^2/4) - \vartheta^2/2), \end{aligned} \tag{34}$$

where $u_2^{\mathtt{r}} = u_2^0\mathrm{e}^{ax^{\mathtt{r}}}$. Similarly, Eqs. (19) and (28) yield

$$\begin{aligned} a\lambda_1(x^{\mathtt{r}}) &= \gamma(1 - \mathrm{e}^{a(x^{\mathtt{r}}-x^{\mathtt{l}})}) + u_1^1(\mathrm{e}^{a(x^{\mathtt{l}}-x^{\mathtt{r}})} - \mathrm{e}^{a(x^{\mathtt{r}}-x^{\mathtt{l}})}) + a\vartheta u_2^{\mathtt{l}}(x^{\mathtt{l}} - x^{\mathtt{r}})\mathrm{e}^{a(x^{\mathtt{r}}-x^{\mathtt{l}})}, \\ &= (\gamma + \vartheta u_2^1)(1 - \mathrm{e}^{a(x^{\mathtt{r}}-1)}) + u_1^1(\mathrm{e}^{a(1-x^{\mathtt{r}})}(1 - \vartheta^2/4) \\ &\quad - \mathrm{e}^{a(x^{\mathtt{r}}-1)}(1 + \vartheta^2/4) + \vartheta^2/2), \end{aligned} \tag{35}$$

where $u_1^{\mathtt{l}} = u_1^1\mathrm{e}^{a(1-x^{\mathtt{l}})}$. We take ε and ζ such that λ_2 and μ_1, respectively, are continuous (γ and δ were fixed by Eqs. (21) and (26), respectively). There are

- six equations: (30), (31), (32), (33), (34), (35), and
- six unknowns: $x^{\mathtt{l}} \in [0,\ 0.5]$, $x^{\mathtt{r}} \in [0.5,\ 1]$ and $u_1^0,\ u_2^0,\ u_1^1,\ u_2^1 \in \mathbb{R}^+$.

One can perform numerical computations and see whether there is an admissible solution. If so, one has moreover to verify that

(i) the switch-functions have the right sign, i.e. $\varsigma_1 = -\lambda_1$, which is zero to the left, must be negative elsewhere, symmetrically for player **2**,
(ii) the singular controls are admissible, i.e. $\forall x \in [0,\ x^{\mathtt{l}}],\ \tilde{\beta}_1(x) \in [0,\ a]$, symmetrically for player **2** (see Eqs. (25) and (29)),

to claim a Nash equilibrium in open-loop.

5.2.4 A numerical example

For instance, taking $\vartheta = 5$ and $a = 5$ yields $u_1^0 = 2.45$, $u_1^1 = 0.05$, $u_2^0 = 0.05$, $u_2^1 = 2.45$, $x^{\mathrm{l}} = 0.25$ and $x^{\mathrm{r}} = 0.75$ as an approximate solution. To our knowledge, there is no other admissible solution to the above system of equations for these parameter values. Figure 3 (left column) illustrate this result. The superscript $\star$ denotes the trajectory of a given variable under the scenario associated to the considered solution. The vertical lines correspond to $x = x^{\mathrm{l}}$ and $x = x^{\mathrm{r}}$. After Fig. 3 (lower center panel), we see that the switch functions $\varsigma_1 = -\lambda_1$ and $\varsigma_2 = \mu_2$ have the right sign. Moreover, one sees through Fig. 3 (lower left panel) that the singular controls are admissible. There is no contradiction, hence the Nash equilibrium.

We proceeded to do the same computations for a wide range of parameters and it turned out that each time a solution was admissible, it was unique and symmetric, i.e., such that $u_1^0 = u_2^1$, $u_1^1 = u_2^0$ and $x^{\mathrm{l}} = 1 - x^{\mathrm{r}}$.

5.2.5 A focus on symmetric solutions

Assuming $u_1^0 = u_2^1$, $u_1^1 = u_2^0$ and $x^{\mathrm{l}} = 1 - x^{\mathrm{r}}$, the above system of six equations reduces to a three equations one, whose solution can be expressed as follows:

$$\begin{aligned} u_1^1 &= a/((1 + ax^{\mathrm{l}})\mathrm{e}^{a(1-x^{\mathrm{l}})} + \vartheta(1 + (ax^{\mathrm{l}} - 1)\mathrm{e}^{ax^{\mathrm{l}}})/2 - 1), \\ u_1^0 &= u_1^1(\mathrm{e}^{a(1-x^{\mathrm{l}})} + \vartheta(\mathrm{e}^{ax^{\mathrm{l}}} - 1)/2), \end{aligned} \tag{36}$$

where x^{l} is solution of

$$\begin{aligned} 0 = a\vartheta(2x^{\mathrm{l}} - 1)\mathrm{e}^{a(2x^{\mathrm{l}}+1)} + (\vartheta - 2)\mathrm{e}^{a(x^{\mathrm{l}}+1)} + \mathrm{e}^{2a} + \left(1 - \frac{\vartheta^2}{4}\right)\mathrm{e}^{2ax^{\mathrm{l}}} \\ + \frac{\vartheta}{2}(\vartheta - 2)\mathrm{e}^{3ax^{\mathrm{l}}} - \frac{\vartheta^2}{4}\mathrm{e}^{4ax^{\mathrm{l}}}. \end{aligned}$$

Define the *width of the buffer zone* as $w = 1 - 2x^{\mathrm{l}}$. The reason why we introduce the above awkward implicit form is that it nonetheless allows one to see that when $\vartheta = 2$, $x^{\mathrm{l}} = 0.5$ (or equivalently $w = 0$) is solution of the above equation whatever the value of a. This can be guessed from Fig. 4, which shows that w is decreasing in a, and increasing in ϑ. No solution arises for $\vartheta < 2$. Another guess can be drawn from Fig. 4: when $a \to \infty$, $w \to 0$, whatever ϑ (see also Fig. 3, upper center panel). This is consistent with the u-game analysis made in Appendix B.

5.2.6 The $\vartheta = 2$ case

Figure 3's right column illustrate the $\vartheta = 2$ case. The superscript $\star$ and the vertical lines keep the same meaning as before. First, one sees that there is no discontinuity in $\beta_1^\star(x)$ and $\beta_2^\star(x)$, thus neither in $u_1^\star(x)$ and $u_2^\star(x)$. Indeed, as seen earlier, $x^{\mathrm{l}} = 0.5$ whatever a. Moreover, one has $u_1^1 = \mathrm{e}^{-a/2}$ and $u_1^0 = 2 - x_1^1$, hence $\tilde{\beta}_1(.5) = a$ (after Eqs. (36) and (25)). Second, notice that $\forall x \in [0, 1]$, $u_1^\star(x) + u_2^\star(x) = 2$. Indeed,

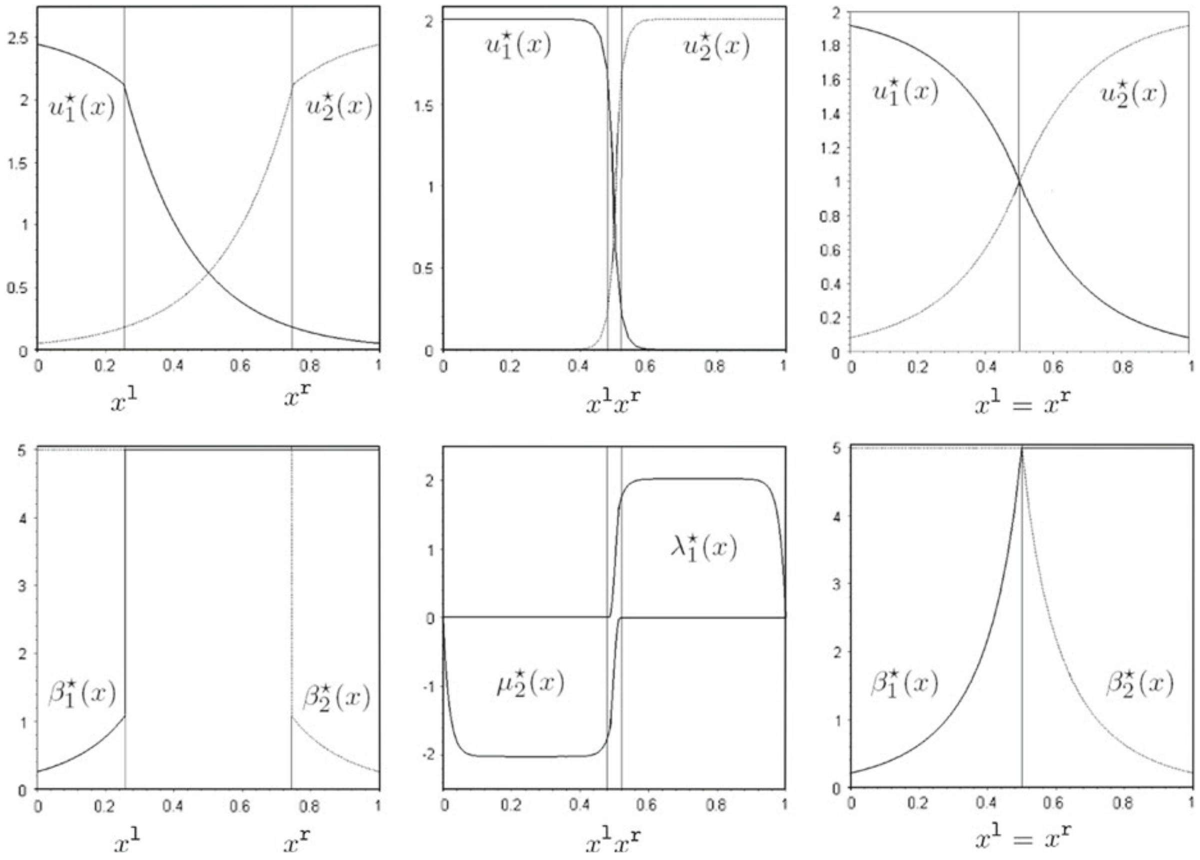

Fig. 3 Nash-optimal trajectories for several parameter values, according to the solution considered in Sect. 5.2.4. *First column* $a = 5$ and $\vartheta = 5$. *Second column* $a = 55$ and $\vartheta = 3$. *Third column* $a = 5$ and $\vartheta = 2$

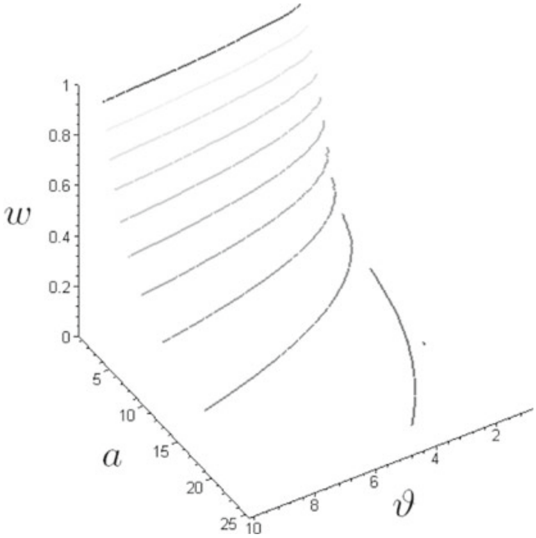

Fig. 4 After Sect. 5.2.5: the width of the buffer zone w as a function of a and ϑ

one has $\forall a \in \mathbb{R}^+$, $\forall x \in [0, 0.5]$, $u_2(x) = \mathrm{e}^{a(x-1/2)}$ and $u_1(x) = 2 - u_2(x)$, symmetrically for $x \in [0.5, 1]$. Lastly, it appears that $\lambda_1^\star(x)$ and $\mu_2^\star(x)$ are zero all along the trajectory, whose half only was deliberately singularized. Appendix C.2, which excludes the possibility of an overlap, substantiates this observation also.

6 Summary

In this paper, our aim was to overstep the limit that faces the static game theoretical approach in analyzing mechanistic models for territoriality. Stating the simplest of the territorial games as a differential one, we showed that its solution-range is significantly richer than that of its static counterpart. More accurately, we considered two parameters

- a, the maximum retreating speed relative to the uncertainty (randomness) associated with animal movement
- ϑ, a penalty for encountering hostile conspecifics

as determinants of territorial space use. Several kinds of territorial patterns arise:

- either $\vartheta < 2$ and there is a unique, trivial, equilibrium, which results in a pair of spatially *uniform* distributions,
- or $\vartheta \geq 2$ and other equilibria appear:
  - either $\vartheta = 2$ and any pair of strategies which yields a *uniform overall wolf density* ($\forall x \in [0, 1]$, $u_1(x) + u_2(x) = 2$) constitutes a Nash equilibrium (this includes both the trivial equilibrium and the territorial pattern drawn in Fig. 3, upper right panel),
  - or $\vartheta > 2$ and a *buffer-zone* takes shape; ϑ and a have antagonistic (positive and negative, respectively) effects on the width of the no-wolf's land, although the greater a, the more pronounced the territories boundaries.

The fact that there is a bifurcation at $\vartheta = 2$ in terms of the appearance of another equilibrium makes sense since it also happened in the static game (see also Appendix B, addressing an oversimplified version of this game).

We do not claim having found all the possible Nash equilibria. Yet, the picture we draw is quite rich, makes sense, and has no empty space.

Have we solved the apparent paradox found in the static game i.e., the fact that if one's opponent draws back, then one also has to draw back, see Sect. 4)? In a sense, as we saw that if a was allowed to go to infinity, then the dynamic framework would allow for enough flexibility to conquer the space left by the opponent without biting into its reinforced territory. Yet, the fact that a is actually finite still allows for such a phenomenon. The resulting territorial buffer zones arise from the limited ability of packs to draw back abruptly at the edge of their territorial boundary. The dynamic analysis thus substantiates the static game's seemingly paradoxical feature.

Considering the non generic $\vartheta = 2$ case as a limiting one, the main ecological implication of our model is that allowing for spatially dynamic motion strategies gives rise to a buffer-zone. More accurately, let us refer to the ecological definition of a buffer-zone, i.e., a separating area where the overall wolf density $u_1 + u_2$ is reduced. As the static game also yielded a so defined buffer-zone, how can we hold such an assertion? Is not the dynamic analysis just a refinement over the static one? It is not, as the static game formulation a-priori assumed a buffer-zone (it is easy to see that $u_1 + u_2$ is convex whatever the game solution, see Eq. (12)). As the dynamic formulation clearly allows for a concave overall wolf density, our model *gives rise* to a buffer-zone.

7 Discussion

This paper shows how buffer zones can arise as solutions to spatial games, provided there is sufficiently large penalty for interacting with neighboring packs, rather than fellow pack members. The strict threshold of $\vartheta = 2$ arises from the quadratic nature of the objective function. In turn, this objective function can be built from first principles, as outlined in Appendix A. As shown in Eq. (43), $\vartheta > 2$ is equivalent to the condition $\pi > 1$ (Eq. (42)). This inequality can be interpreted as

$$\frac{\alpha}{\sigma\psi} > \frac{\psi}{r}. \tag{37}$$

In other words, the buffer zone can arise if the cost to reward ratio associated with buffer zone interactions exceeds the impact of wolf predation on deer resource in the core region of the territory.

Given that the buffer zone exists, its width depends upon the maximum possible value a for the movement bias term β. This can be interpreted as the maximum possible level of directed component of animal movement $c(x)$, relative to the uncertainty (randomness) associated with animal movement $d(x)$. The limiting case, where a becomes large, gives rise to a solution with distinct non-overlapping territories exhibiting abrupt edges (see Fig. 3, upper center panel).

Also, let us stress that our model can be tested *via* estimating the value of $\vartheta = 1+\pi$, as done in Appendix A, where we found $\vartheta \approx 3$ for wolves. For this value of ϑ, our model predicts territories should be separated by a buffer-zone, and the width of the buffer zone is a function of the maximum possible value a that the movement bias term β can attain. Reports of buffer zones for wolves in Minnesota indicate that they can take up to $1/4$ of the total region (Mech 1977). Based on Fig. 4, this would suggest a value of a close to 10 for wolves.

It is interesting to contrast territorial patterns of Minnesota wolves (with wide buffer zones comprising up to 25% of the total area) (Mech 1977) to those of badgers (where there are distinct and abrupt edges to territories, marked by a distinct trail, and with little of either overlap or buffer zone between territories) (Kruuk 1989) (and Figure 5.6 of Moorcroft and Lewis 2006, compare also with Fig. 3, upper center panel). Contributing factors may be that (i) badger territories are much smaller than wolf territories relative to movement rates, taking only minutes to travel across as opposed to several hours (ii) badgers typically eat prey with little mobility (e.g., earthworms) (Kruuk 1989), rather than the highly mobile deer that may actively evade capture. The first of these factors suggests that, for badgers, $c(x)$ may be large relative to typical length and time scales; the second that $d(x)$ may be less pronounced for badgers grazing on earthworms than for wolves possibly engaged in pursuit and evasion dynamics with highly mobile prey. The result is a larger likely value of a for badgers.

An alternative to the mechanistic random walk approach is to simply calculate optimal spatial allocation of foraging effort between competing groups. This approach, given in Sect. 2, yields an equitable partitioning of space with neither a buffer zone nor territorial overlap. Moreover, we would not expect such an approach to have led to the same explanation for buffer zones. Buffer zones of significant width rely on there being a constraint in the mechanistic model. That is, the ratio of directed to random movement β must not exceed an upper bound a. In other words, movement patterns cannot be entirely predictable. There must be a random component d that describes the inherent uncertainty in how individuals move around their territories. When this component is sufficiently large then β will remain bounded.

There are several unusual aspects to the approach we have taken in this paper. First, the progression from a mechanistic random walk model for individual behavior to a partial differential equation model for space use to an ordinary differential equation with an integral constraint for the resulting space use is unusual (but see Moorcroft and Lewis 2006). Interpreted in the context of a spatial game, this ordinary differential equation with an integral constraint is then transformed to a two-point boundary value problem, whose dynamics form the foundation for a nonzero sum differential game in open-loop. Finally, bilateral application of the Pontryagin's minimum principle gives rise to conditions for formation of buffer zones via spatial games.

Possibilities for future research include:

- In the static game: specifying the evolutionary game dynamics so as select an equilibrium, i.e., so as to determine the circumstances under which there one observes the emergence of territories (see Sect. 4.1). However, the fact that the strategy set is a continuum makes the replicator dynamics approach rather challenging (see, e.g., Shaiju and Bernhard 2009, for an insight on the induced difficulties). Nevertheless, Adaptive Dynamics theory would definitely deal with such a continuous trait, provided one specifies an ecological feedback loop. We did so in Appendix A to prepare a non-invasibility analysis. Future work could extend non-invasibility to include the evolutionary dynamics (see, e.g. Diekmann 2004).

- A closely related issue is that of territories emergence as a game solution if one relaxes the a-priori den-site hypothesis (Briscoe et al. 2002). In our model, it consists in relaxing the $\beta_1, \beta_2 \geq 0$ hypothesis (see Sect. 3.1.1), by allowing $\beta_1, \beta_2 \in [-a, a]$. In this way, there is no bias towards an a-priori determined direction. Notice that, although the preliminary discussion (eliminating some possible solutions, see Sect. C.1) no longer holds, the Nash Equilibrium we find in this paper still does hold in this context (as the singular control cannot saturate to zero, see Eqs. (25) and (29)). Moreover, the trivial equilibrium consisting of two uniform distributions corresponds to a bisingular trajectory along which zero is never played as a lower bound.
- Considering an asymmetry between the wolf packs. Actually, relaxing the symmetry (or the equal-sized/strength packs) hypothesis is not a difficulty: it suffices to introduce a discrimination between the two packs, e.g., distinct ϑ_1 and ϑ_2 throughout the paper. The resulting equations hold as, actually, no symmetry was required. Although the solution analysis is more complicated, this issue may typically be of some relevance regarding wolves–coyotes interactions (see Moorcroft and Lewis 2006, Chapter 9).
- Allowing the prey to enter the game. If the prey were allowed to move, then the way they would do so should depend on the local predator density, and *vice-versa*, which would result in introducing a third player.
- Allowing the prey-capture/adjacent-pack-encounter rates to depend on the rates at which location changes occur (which involve the advection and diffusion coefficients), as in McKenzie et al. (2009).
- Including explicit scent-marking in the game. As argued in Sect. 4.2, the fact that the packs communicate on their respective positions may have an incidence on the territorial conflict outcome. It is not clear whether scent-marking-related behavior would still (as compared to Lewis and Moorcroft 2001) promote overlapping territorial patterns if it was considered as a function-valued trait. As Lewis and Moorcroft (2001) suggested, scent-marking behavior might result in a “bluffer-zone.”

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Appendix A: An ecological feedback loop

In this section, our aim is to make explicit the way wolf pack interactions affect wolf dynamics, so as to refer to Darwinian evolutionary (or adaptive) dynamics as a process having possibly shaped territorial patterns.

More accurately, we are interested in finding a *non-invasible* trait (Diekmann 2004), say $\beta^{\star}$, which describes the ratio of directed to random movement as a function of distance from den site. In other words, given a resident population (Pack **2**) with trait $\beta_2(x) = \beta^\star(1-x)$, which, in turn, defines the resident's territorial space use pattern $u_2^\star(x)$, a mutant neighbor (Pack **1**) that deviates from $\beta_1 = \beta^\star(x)$ will not grow. At this equilibrium point, wolf densities are assumed to be stationary, distributed according to territorial patterns $u_1^\star$ and $u_2^\star$, and the packs are assumed to be of equal size. Symmetry in the problem translates to $u_1^\star(x) = u_2^\star(1-x)\ \forall x \in [0, 1]$. Our focus is on identifying this non-invasive equilibrium point. The broader question is whether evolutionary dynamics would converge to such an equilibrium point. This is beyond the scope of this paper and is raised as future research possibilities.

Deer are the primary food item for wolves in northeastern Minnesota, where the territorial buffer zones have been most widely observed (Hoskinson and Mech 1976). Thus the growth-rate of a wolf pack is related to the number of deer it captures over a year. We assume the deer population grows logistically in absence of wolf-induced predation and that the predation rate is bilinear in the wolf and deer abundances. Given a *predation pressure* $u_1 + u_2$, the deer density h follows:

$$\forall x \in [0,1], \quad \frac{\mathrm{d}}{\mathrm{d}t}\mathsf{h}(x,t) = r\mathsf{h}(x,t)\left(1 - \frac{\mathsf{h}(x,t)}{K}\right) - \psi(u_1(x) + u_2(x))\mathsf{h}(x,t), \qquad (38)$$

where r is the Malthusian parameter (rate of maximum population growth), K is the carrying capacity, and ψ a predation rate. This model is the continuous-time equivalent of the one used previously by researchers (Lewis and Murray 1993; Lewis and Moorcroft 2001) (see, for example, de Vries et al. 2006 for a connection between the Beverton–Holt model used in Lewis and Murray 1993; Lewis and Moorcroft 2001 and the logistic equation used here). The deer are territorial and are not assumed to shift territories in response to wolf predation. This is consistent with available observations (Hoskinson and Mech 1976).

Reproductive success through to the next generation takes several years, as it requires sufficient food through conception, gestation, weaning survival and juvenile survival periods. Thus the long-term growth rate of the pack depends on deer intake averaged over several years. However, the deer population density may also adjust to wolf predation on the same time scale, so that wolf foraging decisions made early may affect the availability of deer later. A fully detailed model would include these time scales and the reproduction events. However, for the sake of producing an analytically tractable and transparent formulation, we consider two possible simplifications (i) deer density is assumed to respond quickly to the predation pressure exerted, relative to the time scale of reproduction of wolves (ii) deer density is assumed to respond slowly to the predation pressure exerted relative to the time scale of reproduction of wolves.

The first case, that of rapid response of the deer density to wolf predation is modelled by a quasi-steady state assumption for (38) (see also Lewis and Moorcroft 2001). We define $h^*(x) = h(x)/K$ to be a stationary solution of the above equation, scaled by the carrying capacity K, that maps predation pressure to a deer density. Dropping the asterisk for notational simplicity, we have

$$h(u_1(x) + u_2(x)) = \min\left\{0, 1 - \frac{\psi}{r}(u_1(x) + u_2(x))\right\}. \qquad (39)$$

Then, given a pair of territorial patterns $(u_1(x), u_2(x))$ and the corresponding deer stationary distribution $h(x)$, Pack **1**'s relative growth rate can be expressed as follows:

$$G_1 = \int_0^1 \sigma\psi u_1(x) h(u_1(x) + u_2(x))\mathrm{d}x - \int_0^1 \alpha u_1(x)u_2(x)\mathrm{d}x - \mu_0, \tag{40}$$

where μ_0 is the wolves' natural mortality rate, α is a death rate associated to inter-pack aggression, and σ is the rate of conversion of prey into offspring.

The second case, that of slow response of deer density to wolf predation would ignore the feedback between the behavior of Pack **1** and the deer density, assuming that the environmental conditions are as set by the resident $u_2(x)$ only. This corresponds with substituting Eq. (40) by

$$\tilde{G}_1 = \int_0^1 \sigma\psi u_1(x) h(u_2(1-x) + u_2(x))\mathrm{d}x - \int_0^1 \alpha u_1(x)u_2(x)\mathrm{d}x - \mu_0.$$

For the purposes of this paper, we choose the first simplification and, using Eq. (39), obtain

$$G_1 = -\mu_0 + \sigma\psi - \int_0^1 u_1(x)\left(\frac{\sigma\psi^2}{r}u_1(x) + \left(\frac{\sigma\psi^2}{r} + \alpha\right)u_2(x)\right)\mathrm{d}x.$$

Definition We shall say that u_2 is *non-invasible*, and will denote it by the superscript $\star$, if $u_1(x) = u_2(1-x)$ locally maximizes (among the set of admissible $u_1(\cdot)$'s) the above growth rate, or equivalently locally minimizes the following criterion:

$$J_1 = \int_0^1 u_1(x)\left(u_1(x) + \left(1 + \frac{\alpha r}{\sigma\psi^2}\right)u_2(x)\right)\mathrm{d}x. \tag{41}$$

Note: In our formulation, the wolf growth rate is based on the quasi-steady state assumption for deer. In other words, it is calculated based on the updated stationary distribution of deer, assuming the transient deer dynamics does not affect packs' densities. Thus, strictly speaking, "*the environmental conditions* [are not] *as set by the resident*" only. This is a deviation from Diekmann (2004)'s definition of non-invasibility, but the two definitions become similar under the assumption given for Eq. (41), that is, the characteristic time for deer density equilibration is much shorter than for wolf reproduction.

Rather than focusing on an instantaneous growth rate, another possibility would have been to consider the expected number of offspring produced in a single year by the alpha female, as Lewis and Moorcroft (2001) do, in a semi-discrete framework. In other words, they consider the number of prey that will be captured as a function of the deer and wolf distributions just after reproduction in spring, *times* the probability that the alpha female survives the year, given a pair of territorial patterns. Our criterion is, as opposed to that of Lewis and Moorcroft (2001), *additive*, and thus fits into the existing differential game theoretical framework. Although Lewis and Moorcroft (2001)'s formulation makes more sense for wolves, the above formulation may nevertheless be relevant for other, continuous-time reproduction processes species, such as ants for instance (Adler and Gordon 2003). Also, Lewis and Moorcroft (2001)'s formulation and ours', yield, at least in the static game, qualitatively similar results (see Sect. 4).

In addition, our criterion depends on a unique parameter,

$$\pi = \frac{\alpha}{\sigma\psi}\frac{r}{\psi}. \tag{42}$$

It can be interpreted as a penalty for encountering foreign-pack members; the greater the deer recovery rate r/ψ and the greater the cost over reward ratio $\alpha/\sigma\psi$, the lower it is worthy taking the risk to encounter a hostile conspecific. Moreover, π is quantifiable. Indeed, according to Lewis and Moorcroft (2001), one gets the following estimates for wolves (*Canis lupus*) interacting with white-tailed deer (*Odocoileus virginianus*) populations in Minnesota: $\alpha = 0.69$, $\psi = 0.15$, $r = 0.69$ and $\sigma\psi = \log(5)$, which yields $\pi \approx 2$. The value of π is likely highly variable across the numerous species that show territorial behavior (Adams 2001).

Lastly, notice that the connection with the body of the paper is given by the relation

$$\vartheta = 1 + \pi. \tag{43}$$

Appendix B: A brief analysis of an elementary companion game

In this section, we address a u-game (see below) as an oversimplified version of the β-game addressed in the body of the paper. Our aim is to check whether the u- and β-games' solutions are consistent.

We call u-game the following problem:

$$\mathcal{P}_1 : \min_{u_1(\cdot)} J_1(u_1(\cdot), u_2(\cdot)) = \int_0^1 u_1(x)(u_1(x) + \vartheta u_2(x))\mathrm{d}x,$$

$$\mathcal{P}_2 : \min_{u_2(\cdot)} J_2(u_1(\cdot), u_2(\cdot)) = \int_0^1 u_2(x)(u_2(x) + \vartheta u_1(x))\mathrm{d}x,$$

subject to

$$\dot{u}_3 = u_1, \quad u_3(0) = 0, \quad u_3(1) = 1,$$
$$\dot{u}_4 = u_2, \quad u_4(0) = 0, \quad u_4(1) = 1,$$

where $u_1, u_2 \in \mathbb{R}^+$ are the players' controls, u_3, u_4 being state variables whose dynamics ensure that u_1 and u_2 both sum to unity. We are interested in finding a Nash equilibrium $(u_1^\star, u_2^\star)$.

Proceeding as in the body of the paper, we define the Hamiltonians as follows

$$\begin{aligned} H_1 &= u_1(u_1 + \vartheta u_2) + u_1\lambda_1 + u_2\lambda_2, \\ H_2 &= u_2(u_2 + \vartheta u_1) + u_1\mu_1 + u_2\mu_2, \end{aligned}$$

the λ_i's and μ_i's, $i = 1, 2$, being adjoint variables. As the Hamiltionians have to be minimized all along the trajectory, we introduce

$$\begin{aligned} \sigma_1 &= \partial H_1/\partial u_1 = 2u_1 + \vartheta u_2 + \lambda_1, \\ \sigma_2 &= \partial H_2/\partial u_2 = 2u_2 + \vartheta u_1 + \mu_2, \end{aligned}$$

from which we see that each u_i is such that $\sigma_i = 0$, $i = 1, 2$, (unless it yields a negative value, in which case the control saturates to zero). We also introduce the following adjoint equations

$$\begin{aligned} \dot{\lambda}_1 &= -\partial H_1/\partial u_3 = 0, \quad \lambda_1(1) = \gamma, \\ \dot{\mu}_2 &= -\partial H_2/\partial u_4 = 0, \quad \mu_2(1) = \delta, \end{aligned}$$

(λ_2 and μ_1 will not reappear anymore in the analysis). We thus get $\lambda_1 = \gamma$ and $\mu_2 = \delta$.

We then get the following relationship:

$$u_1^\star = \max\left\{0, -\frac{1}{2}(\vartheta u_2^\star + \gamma)\right\}, \quad \text{and} \quad u_2^\star = \max\left\{0, -\frac{1}{2}(\vartheta u_1^\star + \delta)\right\}.$$

Let us temporarily restrict our attention to possible solutions where no control saturates to zero. Using the above relationship, and finding δ and γ using the fact that $u_1^\star$ and $u_2^\star$ both sum to unity, we get that if $\vartheta = 2$, then any pair (u_1, u_2) such that $u_1 + u_2 = 2$ is a Nash equilibrium. Otherwise ($\vartheta \neq 2$), the only possible solution is the pair of uniform distributions, i.e., $\forall x \in [0, 1]$, $u_1(x) = u_2(x) = 1$.

Now, our aim is to show that the pair

$$\left(u_1^*(x) = \begin{cases} 2 \text{ if } x \in [0, 1/2), \\ 0 \text{ if } x \in [1/2, 1]. \end{cases}, \quad u_2^*(x) = \begin{cases} 0 \text{ if } x \in [0, 1/2), \\ 2 \text{ if } x \in [1/2, 1]. \end{cases}\right)$$

is a Nash equilibirum, so as to complete the picture suggesting that $\vartheta = 2$ is a bifurcation point giving rise to an additional solution.

Regarding player **1**, the following relationship has to be satisfied:

$$-\frac{1}{2}\gamma = 2 \quad \text{and} \quad -\frac{1}{2}(2\vartheta + \gamma) \leq 0,$$

as, when $u_2^\star = 0$, $u_1^\star = 2$, and, when $u_2^\star = 2$, $u_1^\star = 0$ implies the above inequality (symmetrically for player **2**). This indeed translates in the $\vartheta \geq 2$ requirement for (u_1^*, u_2^*) being a Nash equilibrium.

A more thorough analysis, addressing the existence of other equilibria, is left for future research. A closed-loop formulation of the above u-game will typically be investigated, since in this framework, given the policies $u_1(\cdot)$ and $u_2(\cdot)$, there is no need of using conditions at both extremities ($x = 0, 1$) to compute a trajectory (as opposed to what happens in the β-game, see Eq. (13)).

Appendix C: Control-theoretical considerations

C.1 Preliminary discussion

Consider the game stated in Sect. 5.1.

If playing $\beta_1 = 0$ at $x = 1$ is optimal, one must have $\varsigma_1 = -\lambda_1 > 0$ to the left neighborhood of $x = 1$, which translates in:

$$\dot{\lambda}_1(1) = -\gamma - 2u_1^1 - \vartheta u_2^1 > 0. \tag{44}$$

As long as $\beta_1 = 0$ backward in space (moving to the left), one has

$$\dot{\lambda}_1 = -\gamma - 2u_1^1 - \vartheta u_2 \geq -\gamma - 2u_1^1 - \vartheta u_2^1 > 0,$$

after (44). Hence there is no switch.

Similarly, if playing $\beta_1 = 0$ at $x = 0$ is optimal, one must have $\varsigma_1 = -\lambda_1 > 0$ to the right neighborhood of $x = 0$, which translates in:

$$\dot{\lambda}_1(0) = -\gamma - 2u_1^0 - \vartheta u_2^0 < 0. \tag{45}$$

As long as $\beta_1 = 0$ forward in space (moving to the right), one has

$$\dot{\lambda}_1 = -\gamma - 2u_1^0 - \vartheta u_2 \leq -\gamma - 2u_1^0 - \vartheta u_2^1 < 0,$$

after (45). Hence there is no switch. By symmetry, these observations also hold for player **2**.

Therefore, there is no (non strictly-singular) solution in which one of the players would play 0 at one of the extremities (0 and 1) of the x domain, except the pair of uniform distributions. By strictly-singular, we mean a solution in which controls that belong to (0, 1) are used. This terminology is necessary as actually, playing (0, 0) for all x makes the trajectory follow a *bisingular* arc (see Appendix C.2).

What does it leave to us? A plateau (i.e., switching from a to 0 to a, possibly n times) can be excluded through a very similar reasoning: if switching from a to 0 at $x = \xi \in (0, 1)$ is optimal, then simply substitute the superscript 0 (meaning $x = 0$) by the superscript ξ in Eq. (45) and notice that there will be no further switch.

C.2 On a possible overlap

In this section, we address the existence of a bisingular solution, i.e. a solution in which both players simultaneously play singular controls. Consider the dynamics (13), where $\beta_1 = \bar{\beta}_1, \beta_2 = \bar{\beta}_2$ and $x \in [x^{\mathrm{l}}, x^{\mathrm{r}}]$. Proceeding as in, and extending, Sects. 5.2.1 and 5.2.2 (dealing with the unisingular components of the solution, and where γ and δ were determined), one gets two (coupled) equations, respectively ensuring $\dot{\varsigma}_1 = -\dot{\lambda}_1 = 0$ and $\dot{\varsigma}_2 = \dot{\mu}_2 = 0$:

$$\begin{aligned} 0 &= 2(u_2^1 - u_2) + \vartheta(u_1^1 - u_1), \\ 0 &= 2(u_1^0 - u_1) + \vartheta(u_2^0 - u_2). \end{aligned} \tag{46}$$

Two cases are to be considered: either $\vartheta = 2$ and the above equation is satisfied iff

$$\forall x \in [x^{\mathrm{l}}, x^{\mathrm{r}}], \quad u_1^0 + u_2^0 = u_1(x) + u_2(x) = u_1^1 + u_2^1,$$

(see Sect. 5.2.6 for instance) or $\vartheta \neq 2$ and Eq. (46) has for unique solution:

$$\forall x \in [x^{\mathrm{l}}, x^{\mathrm{r}}], \quad u_1(x) = \bar{u}_1 \quad \text{and} \quad u_2(x) = \bar{u}_2,$$

where

$$\bar{u}_1 = (-4u_1^0 + \vartheta^2 u_1^1 - 2\vartheta u_2^0 + 2\vartheta u_2^1)/(\vartheta^2 - 4), \tag{47}$$

$$\bar{u}_2 = (-4u_2^1 + \vartheta^2 u_2^0 - 2\vartheta u_1^1 + 2\vartheta u_1^0)/(\vartheta^2 - 4). \tag{48}$$

From now on, let us consider the generic case $\vartheta \neq 2$ only. Proceeding as in Sect. 5.2.3, we are interested in solving the following system of equations, whose first part below translates the connection of (23) to (27) through the overlap zone, where u_1 and u_2 are constant (a kind of plateau);

$$\bar{u}_1 = u_1^1 \mathrm{e}^{a(1-x^{\mathrm{r}})}, \tag{49}$$

$$u_2^0 \mathrm{e}^{ax^{\mathrm{l}}} = \bar{u}_2, \tag{50}$$

where $\bar{u}_1$ and $\bar{u}_2$ are given by Eqs. (47) and (48). We do not need specifying the two other equations (related to u_3 and u_4) for what follows. The second part consists in maintaining the continuity of the adjoint variables all along the followed trajectory, as required by Pontryagin's minimum principle. Equations (28) and (24) here read:

$$\begin{aligned} 0 = (\gamma + \vartheta u_2^1)(1 - \mathrm{e}^{a(x^{\mathrm{r}}-1)}) + u_1^1(\mathrm{e}^{a(1-x^{\mathrm{r}})}(1 - \vartheta^2/4) \\ - \mathrm{e}^{a(x^{\mathrm{r}}-1)}(1+\vartheta^2/4) + \vartheta^2/2) \end{aligned} \tag{51}$$

$$\begin{aligned} 0 = (\delta + \vartheta u_1^0)(\mathrm{e}^{-ax^{\mathrm{l}}} - 1) + u_2^0(\mathrm{e}^{-ax^{\mathrm{l}}}(1 + \vartheta^2/4) \\ - \mathrm{e}^{ax^{\mathrm{l}}}(1 - \vartheta^2/4) - \vartheta^2/2), \end{aligned} \tag{52}$$

where are γ and δ given by Eqs. (21) and (26), respectively. Using Eqs. (49) and (50), Eqs. (51) and (52) yield

$$0 = 2(u_2^1 - u_2^0) + \vartheta(u_1^1 - u_1^0),$$
$$0 = 2(u_1^1 - u_1^0) + \vartheta(u_2^1 - u_2^0),$$

which is true iff $u_1^1 = u_1^0$ and $u_2^1 = u_2^0$. Hence the above system of equations has for unique solution the trivial one: $x^1 = 0,\ x^r = 1,\ u_1^0 = 1,\ u_2^0 = 1,\ u_1^1 = 1,\ u_2^1 = 1$, which was already known as a Nash equilibrium in any event, see Sect. C.1.

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