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Analysis of Transmission of Infection in Epidemics: Confined Random Walkers in Dimensions Higher Than One

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Abstract

The process of transmission of infection in epidemics is analyzed by studying a pair of random walkers, the motion of each of which in two dimensions is confined spatially by the action of a quadratic potential centered at different locations for the two walks. The walkers are animals such as rodents in considerations of the Hantavirus epidemic, infected or susceptible. In this reaction-diffusion study, the reaction is the transmission of infection, and the confining potential represents the tendency of the animals to stay in the neighborhood of their home range centers. Calculations are based on a recently developed formalism (Kenkre and Sugaya in Bull Math Biol 76:3016-3027, 2014) structured around analytic solutions of a Smoluchowski equation and one of its aims is the resolution of peculiar but well-known problems of reaction-diffusion theory in two dimensions. The resolution is essential to a realistic application to field observations because the terrain over which the rodents move is best represented as a 2d landscape. In the present analysis, reaction occurs not at points but in spatial regions of dimensions larger than 0. The analysis uncovers interesting nonintuitive phenomena one of which is similar to that encountered in the one-dimensional analysis given in the quoted article, and another specific to the fact that the reaction region is spatially extended. The analysis additionally provides a realistic description of observations on animals transmitting infection while moving on what is effectively a two-dimensional landscape. Along with the general formalism and explicit one-dimensional analysis given in Kenkre and Sugaya (2014), the present work forms a model calculational tool for the analysis for the transmission of infection in dilute systems.

Keywords Smoluchowski \cdot Interacting random walks \cdot Diffusion \cdot Infection transmission \cdot Epidemics \cdot Hantavirus

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1 Background and Motivation for the Investigation

Random walks are ubiquitous in physics (Wax 1954) and biology (Berg 1983). Within the vast field of their investigation is the difficult and important area of *confined* random walks. We present below analysis and practically usable results for random walkers moving under a confinement potential and interacting when they arrive within the influence of one another. We develop the theory as an extension of work we have published recently (Kenkre and Sugaya 2014) where we have provided a general formalism and illustrated it explicitly for a specific one-dimensional case. The application in mind here, as in Kenkre and Sugaya (2014), is to the description of transmission of epidemics such as the Hantavirus (Yates et al. 2002), wherein rodents moving randomly on the terrain passing on infection on encounter.

The reason for providing the two-dimensional analysis in the present paper is twofold. The first is that the rodents involved in the spread of the Hantavirus do move on an effectively two-dimensional (2-d) landscape and, although the detailed calculations in Kenkre and Sugaya (2014), hereafter referred to as KS, have unearthed interesting results in a one-dimensional (1-d) model, it is important to study whether the generalization to 2-d is straightforward or whether it changes significant features. There is, however, an additional reason for this study. In the continuum, the dimensionality of the region in which the reaction event occurs (in many instances trapping, in our present case the transmission of infection via contact) may be different from (smaller than) that in which the over-all motion of the walker(s) occurs. Thus, the analysis presented in KS had the over-all motion occurring on the one-dimensional line but the encounter (reaction) occurred at a point, i.e., a zero-dimensional region. Reaction-diffusion theory in a spatial continuum of dimensions larger than 1 suffers from peculiar blowups if the reaction occurs at points. Whereas our development in KS was naturally built on point encounters on a line, motion in a plane such as in the terrain over which rodents execute their random walks can result in singular behavior for point encounters. An explicit resolution of the familiar blowups must be therefore implemented for *realistic* 2-d and higher-dimensional systems.

The theory in the present paper has been constructed in two parts, one in which a straightforward extension of KS is presented but with both the reaction event and the diffusion occurring in higher-dimensional space, particularly 2-d as appropriate to rodents on the landscape. In the second part, we will display the blow-up problem for point encounters that fortuitously does not occur for one-dimensional (over-all) motion but does in a plane and also show an explicit resolution of the problem by taking the reaction (passing of infection from one walker to another) to occur in an *extended* region rather than at a point. In both parts, we obtain usable expressions for the description of transmission of infection, recover a certain interesting non-monotonicity phenomenon presented in the 1-d analysis of KS and, additionally, find here another phenomenon worthy of note that arises from the introduction of a new distance that characterizes the extent of the reaction region.

An analytic theory of the transmission of infection is a challenging undertaking and is needed at this time because of recent developments in observations. Description of the transmission of infection in an epidemic derives its importance from human relevance as well as the theoretical difficulties of its intellectual challenge. Original contributions (Anderson and May 1991; Okubo and Levin 2001; Hethcote 2000; Brauer and Castillo-Chávez 2001; Dickmann et al. 2000) beginning with the study of Anderson and May (1991) involved concepts such as mass action, SIR, and the basic reproductive rate. Spatial considerations were introduced into the investigations independently by various authors (Dickmann et al. 2000; Okubo and Levin 2001; Abramson and Kenkre 2002; Aguirre et al. 2002; Cantrell and Cosner 2003; Kenkre 2004, 2005; McKane and Newman 2004; Kenkre 2003; Kenkre et al. 2007; MacInnis et al. 2008). Missing from all those studies was confinement features that arise in animal motion from the existence of home ranges. That these confinement considerations cannot be ignored became clear from the analysis of field observations (Giuggioli et al. 2005; Abramson et al. 2006; Giuggioli et al. 2006; MacInnis et al. 2008). Typically, the mean square displacement of the rodents extracted from mark-recapture experiments is found to saturate as time progresses rather than always growing linearly as unconfined random walks would predict. The saturation area represents the home ranges of the animals which, unmistakably, perform their random walks in a tethered manner, tending to return repeatedly to their shelters. Therefore, it became necessary to undertake a fundamental study of the transmission of infection in terms of interacting random walks specially under confinement.

Such a theory that takes explicit consideration of confinement has been developed (Kenkre and Sugaya 2014) by the present authors in KS on the basis of pairwise interactions in a dilute system of random walkers (representing infected and susceptible animals) moving in m dimensions. The model calculation is restricted to the time evolution of a representative pair of animals, one infected and one not, and is thus especially appropriate to a dilute system of random walkers. The motion of each animal pair is taken to obey a Smoluchowski equation in 2m-dimensional space that combines diffusion with confinement of each animal to its particular home range. This passage to a space of twice the number of dimensions follows the formalism introduced by one of the present authors for the study of Frenkel exciton annihilation in molecular crystals (Kenkre 1980). The new feature of the present analysis (as that of KS) is the existence of home ranges, i.e., attractive centers for the walkers. An additional (reaction) term that comes into play when the animals are in close proximity describes the process of infection. Analytic solutions are obtained, confirmed by numerical procedures, and shown (Kenkre and Sugaya 2014) to predict a surprising effect of confinement (Spendier et al. 2013). The effect is that infection spread has a non-monotonic dependence on the diffusion constant and/or the extent of the attachment of the animals to the home ranges. Optimum values of these parameters exist for any given distance between the attractive centers. Any change from those values, involving faster/slower diffusion or shallower/steeper confinement, hinders the transmission of infection. A physical explanation has been provided in KS. Reduction to the simpler case of no home ranges has been demonstrated in full detail. Effective infection rates have been calculated, and it has been pointed out how one might use them in complex systems consisting of dense populations.

2 Analysis in Higher Dimensions when the Dimensionality of Motion Equals that of Reaction

Let the dimensionality of the over-all motion as well as that of the transmission of infection be the same and denoted by *m*. We denote the locations of the disease-carrying mouse, which we refer to as infected, and the one without but susceptible to the disease, which we refer to as susceptible, by $\mathbf{r}_1 = (x_1^1, x_1^2, \dots, x_1^m)$ and $\mathbf{r}_2 = (x_2^1, x_2^2, \dots, x_2^m)$, respectively, where the subscripts denote whether the mouse is infected or susceptible, and the superscripts denote the dimension. The probability density to find the walkers at their respective positions at time *t* is denoted by $P(\mathbf{r}_1, \mathbf{r}_2, t)$. The mice are considered to be random walkers attracted to their home locations, $\mathbf{R}_1 = (h_1^1, h_1^2, \dots, h_1^m)$ and $\mathbf{R}_2 = (h_2^1, h_2^2, \dots, h_2^m)$, where h_i^j is the home coordinate in each dimension.

2.1 General Expression for the Infection Probability

The equation of motion for the probability density is as in KS but now with an extended reaction region,

$$\frac{\partial P(\mathbf{r}_{1}, \mathbf{r}_{2}, t)}{\partial t} = \nabla_{1} \cdot \left[\gamma \left(\mathbf{r}_{1} - \mathbf{R}_{1} \right) P(\mathbf{r}_{1}, \mathbf{r}_{2}, t) \right] + \nabla_{2} \cdot \left[\gamma \left(\mathbf{r}_{2} - \mathbf{R}_{2} \right) P(\mathbf{r}_{1}, \mathbf{r}_{2}, t) \right] + D \left(\nabla_{1}^{2} + \nabla_{2}^{2} \right) P(\mathbf{r}_{1}, \mathbf{r}_{2}, t) - \mathcal{C} \int^{\prime} d\mathbf{r}_{1}^{\prime} d\mathbf{r}_{2}^{\prime} \, \delta(\mathbf{r}_{1} - \mathbf{r}_{1}^{\prime}) \delta(\mathbf{r}_{2} - \mathbf{r}_{2}^{\prime}) P(\mathbf{r}_{1}, \mathbf{r}_{2}, t),$$
(1)

where the primed integral is over the reaction region covered by \mathbf{r}'_1 and \mathbf{r}'_2 . The third term on the right-hand side describes the random motion of the random walkers with D being the diffusion constant. Their motion due to the attraction to their homes is described by the first two terms, where γ is the strength of the attraction. Thus, the walkers' motion is given by the Smoluchowski equation. Their infection-transmission interaction is given in the fourth term. The infection rate is denoted by C and has the unit [1/time].

We focus on the homogeneous propagator, $\Pi(\mathbf{r}_1, \mathbf{r}'_1, \mathbf{r}_2, \mathbf{r}'_2, t)$, and obtain from it, the homogeneous solution,

$$\eta(\mathbf{r}_1, \mathbf{r}_2, t) = \int \int d\mathbf{r}_1' d\mathbf{r}_2' \Pi(\mathbf{r}_1, \mathbf{r}_1', \mathbf{r}_2, \mathbf{r}_2', t) P(\mathbf{r}_1', \mathbf{r}_2', 0),$$
(2)

with $P(\mathbf{r}'_1, \mathbf{r}'_2, 0)$ being the initial condition, and the integral being over all space. This allows us to obtain the infection probability, $\mathcal{I}(t)$, the probability that the susceptible mouse is infected at time t, precisely as in KS,

$$\mathcal{I}(t) = 1 - \int \int d\mathbf{r}_1 d\mathbf{r}_2 P(\mathbf{r}_1, \mathbf{r}_2, t), \qquad (3)$$

where the integral is over all space. With this definition, $\mathcal{I}(t)$ is obtained in the Laplace domain as

$$\widetilde{\mathcal{I}}(\epsilon) = \frac{1}{\epsilon} \left[\frac{\widetilde{\mu}(\epsilon)}{1/\mathcal{C} + \widetilde{\nu}(\epsilon)} \right],\tag{4}$$

where tilde denotes Laplace transform and ϵ is the Laplace variable. The functions $\mu(t)$ and $\nu(t)$ are given in terms of homogeneous quantities, $\eta(\mathbf{r}_1, \mathbf{r}_2, t)$ and $\Pi(\mathbf{r}_1, \mathbf{r}_1', \mathbf{r}_2, \mathbf{r}_2', t)$ by

$$\mu(t) \equiv \int' d\mathbf{r}_1 \mathbf{r}_2 \eta(\mathbf{r}_1, \mathbf{r}_2, t), \tag{5}$$

$$\nu(t) \equiv \frac{\int' d\mathbf{r}'_1 d\mathbf{r}'_2 \int' \mathbf{r}_1 d\mathbf{r}_2 \Pi(\mathbf{r}_1, \mathbf{x}'_1, \mathbf{r}_2, \mathbf{r}'_2, t)}{\int' d\mathbf{r}'_1 d\mathbf{r}'_2}.$$
 (6)

Here, $\mu(t)$ is the probability to find the walkers within the infection region at time *t* given their initial conditions, in the *absence* of the infection phenomenon. Because of the extended reaction region, $\nu(t)$ here is obtained via the ν -function method (Kenkre 1982; Kenkre and Parris 1983), where an ensemble average of the probability to find the walkers within the region at *t* given that they were within the region initially, over the infection region. All these results are straightforward generalization of those in KS for arbitrary dimensions.

2.2 Introduction of the Relative Coordinate

A realistic scenario for an infection-transmission event is for it to occur when the mice come within a certain distance of one another. In such a case, it is useful to make a coordinate transformation to the center of mass (CM) and relative coordinate system. To illustrate this explicitly, we refer the reader to Fig. 1. The one-dimensional position phase-space in the original coordinate (labeled with $x_1^1 \equiv x_1$ and $x_2^1 \equiv x_2$) and CMrelative coordinate (labeled with x_+ and x_-) is superimposed. The gray region lying



diagonal to the original coordinate indicates the infection region. Notice that this region lies parallel to the CM coordinate and perpendicular to the relative one, indicating that the transmission of infection occurs only dependent on the relative coordinate.

Thus, let the CM and the relative coordinates be denoted by r_+ and r_- , respectively. The specific transformation between r_1 , r_2 and r_+ , r_- is given by

$$\mathbf{r}_{\pm} = \frac{1}{\sqrt{2}} \left(\mathbf{r}_1 \pm \mathbf{r}_2 \right) \quad \Longleftrightarrow \quad \mathbf{r}_{1,2} = \frac{1}{\sqrt{2}} \left(\mathbf{r}_+ \pm \mathbf{r}_- \right), \tag{7}$$

where the factor of $1/\sqrt{2}$ is chosen to preserve the form of the motion part of the equation. With this transformation, the equation of motion becomes

$$\frac{\partial P(\mathbf{r}_{+},\mathbf{r}_{-},t)}{\partial t} = \nabla_{+} \cdot \left[\gamma \left(\mathbf{r}_{+} - \mathbf{R}_{+} \right) P(\mathbf{r}_{+},\mathbf{r}_{-},t) \right] + D\left(\nabla_{+}^{2} + \nabla_{-}^{2} \right) P(\mathbf{r}_{+},\mathbf{r}_{-},t) \\ - \mathcal{C} \int^{\prime} d\mathbf{x}_{+}^{\prime} d\mathbf{x}_{-}^{\prime} \,\delta(\mathbf{x}_{+} - \mathbf{x}_{+}^{\prime}) \delta(\mathbf{x}_{-} - \mathbf{x}_{-}^{\prime}) P(\mathbf{x}_{+},\mathbf{x}_{-},t), \qquad (8)$$

where R_{\pm} are given by

$$\boldsymbol{R}_{\pm} = \frac{1}{\sqrt{2}} \left(\boldsymbol{R}_1 \pm \boldsymbol{R}_2 \right). \tag{9}$$

Following the same procedure as in the system of original coordinates, we find

$$\nu(t) \equiv \frac{\int' d\mathbf{r}'_{+} d\mathbf{r}'_{-} \int' d\mathbf{r}_{+} d\mathbf{r}_{-} \Pi(\mathbf{r}_{+}, \mathbf{r}'_{+}, \mathbf{r}'_{-}, \mathbf{r}'_{-}t)}{\int' d\mathbf{r}'_{+} d\mathbf{r}'_{-}},$$
(10)

and

$$\mu(t) \equiv \int' d\mathbf{r}_+ d\mathbf{r}_- \,\eta(\mathbf{r}_+, \mathbf{r}_-, t). \tag{11}$$

The propagator in this coordinate, $\Pi(\mathbf{r}_+, \mathbf{r}'_+, \mathbf{r}_-, \mathbf{r}'_-, t)$, is given by

$$\Pi(\mathbf{r}_{+},\mathbf{r}_{+}',\mathbf{r}_{-},\mathbf{r}_{-}',t) = \left(\frac{1}{\sqrt{4\pi DT(t)}}\right)^{2m} \prod_{\beta=1}^{m} e^{-\frac{\left(x_{+}^{\beta}-h_{+}^{\beta}-(x_{+}'^{\beta}-h_{+}^{\beta})e^{-\gamma t}\right)^{2} + \left(x_{-}^{\beta}-h_{-}^{\beta}-(x_{-}'^{\beta}-h_{-}^{\beta})e^{-\gamma t}\right)^{2}}{4DT(t)}},$$
(12)

where $T(t) = (1/2\gamma)(1 - e^{-2\gamma t})$. Since the entire CM coordinate is part of the infection region as explained above, the primed integral is appropriately written as

$$\int' d\mathbf{r}_{+} d\mathbf{r}_{-} \to \int_{\text{all space}} d\mathbf{r}_{+} \int' d\mathbf{r}_{-}.$$
 (13)

Using this relation and performing the first integral in the numerator of the definition of v(t) given in Eq. (10) results in

$$\int_{\text{all space}} d\mathbf{r}_{+} \int' d\mathbf{r}_{-} \Pi(\mathbf{r}_{+}, \mathbf{r}'_{+}, \mathbf{r}_{-}, \mathbf{r}'_{-}, t) = \int_{\text{all space}} d\mathbf{r}_{+} \int' d\mathbf{r}_{-} \left(\frac{1}{\sqrt{4\pi DT(t)}}\right)^{2m} \prod_{\beta=1}^{2m} e^{-\frac{\left(\frac{x^{\beta}}{4} - h^{\beta}_{+} - (x^{\prime\beta}_{+} - h^{\beta}_{+})e^{-\gamma t}\right)^{2} + \left(\frac{x^{\beta}_{-} - h^{\beta}_{-} - (x^{\prime\beta}_{-} - h^{\beta}_{+})e^{-\gamma t}\right)^{2}}{4DT(t)}} = \int' d\mathbf{r}_{-} \left(\frac{1}{\sqrt{4\pi DT(t)}}\right)^{m} \prod_{\beta=1}^{m} e^{-\frac{\left(\frac{x^{\beta}_{-} - h^{\beta}_{-} - (x^{\prime\beta}_{-} - h^{\beta}_{-})e^{-\gamma t}\right)^{2}}{4DT(t)}}.$$
 (14)

Since we see clearly that the CM coordinate is integrated entirely out of the problem, we need to focus only on the relative coordinate. Let us define the integrand of Eq. (14) as

$$\Pi(\mathbf{r}_{-},\mathbf{r}_{-}',t) \equiv \left(\frac{1}{\sqrt{4\pi DT(t)}}\right)^{m} \prod_{\beta=1}^{m} e^{-\frac{\left(x_{-}^{\beta}-h_{-}^{\beta}(x_{-}')^{\beta}-h_{-}^{\beta})e^{-\gamma t}\right)^{2}}{4DT(t)}}.$$
 (15)

With this result, the ν -function can be written as

$$\nu(t) = \frac{\int_{\text{all space}} d\mathbf{r}'_{+} \int' d\mathbf{r}'_{-} \int' d\mathbf{r}_{-} \Pi(\mathbf{r}_{-}, \mathbf{r}'_{-}, t)}{\int_{\text{all space}} d\mathbf{r}'_{+} \int' d\mathbf{r}'_{-}}.$$
 (16)

The propagator does not depend on r'_+ . The integrals over r'_+ in the numerator and the denominator cancel, leading to

$$\nu(t) = \frac{\int' d\mathbf{r}'_{-} \int' d\mathbf{r}_{-} \Pi(\mathbf{r}_{-}, \mathbf{r}'_{-}, t)}{\int' d\mathbf{r}'_{-}}.$$
(17)

Let us consider a delta-function initial condition of the walkers for the rest of this paper, i.e., $P(\mathbf{r}_1, \mathbf{r}_2, 0) = \delta(\mathbf{r}_1 - \mathbf{r}_1^0) \delta(\mathbf{r}_2 - \mathbf{r}_2^0)$, which translates to $P(\mathbf{r}_+, \mathbf{r}_-, 0) = \delta(\mathbf{r}_+ - \mathbf{r}_+^0) \delta(\mathbf{r}_- - \mathbf{r}_-^0)$ according to Eq. (7). Therefore, $\mu(t)$ becomes

$$\mu(t) = \int' d\boldsymbol{r}_{-} \Pi(\boldsymbol{r}_{-}, \boldsymbol{r}_{-}^{0}, t).$$
(18)

Most actual situations correspond to a two-dimensional space because the mice that transmit the infection move about on the open terrain which can be considered flat for all practical purposes. Therefore, we give further analysis in two dimensions.

2.3 Reaction Region as a Disk in the Plane

For the ease of notation, we let the relative coordinate in the first dimension be denoted by $x_{-}^{1} \equiv x$, that of the second dimension by $x_{-}^{2} \equiv y$, the initial condition by $x_{-}^{0,1} \equiv x^{0}$ and $x_{-}^{0,2} \equiv y^{0}$, the relative home-center coordinate in the first dimension by $h_{-}^{1} \equiv h$, and that of the second dimension by $h_{-}^2 \equiv f$. The propagator corresponding to Eq. (15) then becomes

$$\Pi(x, x', y, y', t) = \left(\frac{1}{4\pi DT(t)}\right) e^{-\frac{\left(x-h-(x'-h)e^{-\gamma t}\right)^2 + \left(y-f-(y'-f)e^{-\gamma t}\right)^2}{4DT(t)}},$$
 (19)

and v(t) and $\mu(t)$ are given by

$$v(t) = \frac{\int dx' dy' \int dx dy \,\Pi(x, x', y, y', t)}{\int dx' dy'},$$
(20)

and

$$\mu(t) = \int' dx dy \Pi(x, x^0, y, y^0, t).$$
(21)

Suppose that the infection is transmitted to the susceptible mouse at a rate C when the mice come within a distance *b* of one another. This means that the infection region is described by $x^2 + y^2 \le b^2$. Hence it is clear that the primed integral over the infection region is expressed simpler in the corresponding polar coordinate, where it becomes a circular disk of radius *b*, i.e.,

$$\int' dxdy = \int_0^b dr \int_0^{2\pi} r d\phi.$$
⁽²²⁾

Since the polar variables, r and ϕ , are given by

$$\begin{cases} r^2 = x^2 + y^2 \\ \phi = \tan^{-1}(y/x) \end{cases} \iff \begin{cases} x = r \cos \phi \\ y = r \sin \phi \end{cases},$$
(23)

the relative home-center coordinates transformed as

$$\begin{cases} H^2 = h^2 + f^2\\ \omega = \tan^{-1}(f/h) \end{cases} \iff \begin{cases} h = H \cos \omega\\ f = H \sin \omega \end{cases}$$
(24)

In these polar coordinates, the propagator takes the form

$$\Pi(r, r', \phi, \phi', t) = \frac{1}{4\pi D\mathcal{T}(t)} e^{-\frac{r^2 + \mathcal{F}^2(r', \phi', t) - 2r\mathcal{F}(r', \phi', t) \cos(\phi - \Phi(r', \phi', t))}{4D\mathcal{T}(t)}}.$$
 (25)

Here, the functions \mathcal{F} and Φ are given in terms of γ , H, and $\mathcal{T}(t)$ as

$$\mathcal{F}^{2}(r',\phi',t) = r'^{2} - 2\gamma \left[r'^{2} + H^{2} - 2r'H\cos(\phi'-\omega) \right] \mathcal{T}(t),$$
(26)

$$\Phi(r',\phi',t) = \tan^{-1}\left(\frac{(r'\sin\phi' - H\sin\omega)e^{-\gamma t} + H\sin\omega}{(r'\cos\phi' - H\cos\omega)e^{-\gamma t} + H\cos\omega}\right).$$
 (27)

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In computing, the important quantity v(t) is given by

$$v(t) = \frac{\int_0^b dr' \int_0^{2\pi} r' d\phi' \int_0^b dr \int_0^{2\pi} r d\phi \Pi(r, r', \phi, \phi', t)}{\int_0^b dr' \int_0^{2\pi} r' d\phi'}$$
(28)

requires the calculation of the integral over ϕ of $\Pi(r, r'\phi, \phi', t)$. The analytic evaluation of this integral is, which is nothing other than the propagator to find the walkers somewhere within the disk, being separated by a distance $r \leq b$ at t, given that they were separated by $r' \leq b$ and angle ϕ' at the beginning, straightforward. Calling this integral as $\Pi(r, r', \phi', t)$, we see that

$$\Pi(r, r', \phi', t) \equiv \int_0^{2\pi} d\phi \,\Pi(r, r', \phi, \phi', t)$$
⁽²⁹⁾

$$=\frac{1}{4\pi D\mathcal{T}(t)}e^{-\frac{r^2+\mathcal{F}^2(r',\phi',t)}{4D\mathcal{T}(t)}}\int_0^{2\pi} d\phi \, e^{\frac{2r\mathcal{F}(r',\phi',t)\cos(\phi-\Phi(r',\phi',t))}{4D\mathcal{T}(t)}}$$
(30)

$$=\frac{1}{2DT(t)}e^{-\frac{r^{2}+\mathcal{F}^{2}(r',\phi',t)}{4DT(t)}}I_{0}\left(\frac{r\mathcal{F}(r',\phi',t)}{2DT}\right),$$
(31)

where $I_0(z)$ is the zeroth-order modified Bessel function of the first kind. This expression is similar to, and a generalization of, the expression obtained recently by and Kenkre (Spendier and Kenkre 2013) for reaction–diffusion theory.¹ Then, in terms of $\Pi(r, r', \phi', t)$, $\nu(t)$ and $\mu(t)$ are given by

$$\nu(t) = \frac{1}{\pi b^2} \int_0^b dr' \int_0^{2\pi} d\phi' \int_0^b dr \ rr' \Pi(r, r', \phi', t), \tag{32}$$

$$\mu(t) = \int_0^b dr \ r \Pi(r, r^0, \phi^0, t).$$
(33)

We now examine the short-time behavior of v(t) by taking limit $t \to 0$ in Eq. (32). When $t \to 0$, the functions $\mathcal{T}(t)$ and $\mathcal{F}(r', \phi', t)$ become

$$\mathcal{T}(t \to 0) \to t \tag{34}$$

$$\mathcal{F}^2(r',\phi',t\to 0)\to r'^2,\tag{35}$$

which in turn makes $\Pi(r, r', \phi', t)$ to become

$$\Pi(r, r', \phi', t \to 0) \to \frac{1}{2Dt} e^{-\frac{r^2 + r'^2}{2Dt}} I_0\left(\frac{rr'}{2Dt}\right).$$
(36)

Furthermore, the argument of the Bessel function diverges and it is appropriate to express $I_0(z)$ in terms of its asymptotic form Abramowitz and Stegun (1970), which is

¹ It has also appeared earlier in the context of heat conduction (Carslaw and Jaeger 1959).

$$I_0(z) \sim \frac{1}{\sqrt{2\pi z}} e^z$$
, for large z. (37)

With this, $\Pi(r, r', \phi', t \to 0)$ becomes

$$\Pi(r,r',\phi',t\to 0)\to \frac{1}{\sqrt{rr'}}\frac{1}{\sqrt{4\pi Dt}}e^{-\frac{(r-r')^2}{4Dt}}\to \frac{1}{\sqrt{rr'}}\delta(r-r').$$
 (38)

Using this result, $v(t \rightarrow 0)$ is

$$\nu(t \to 0) \to \frac{1}{\pi b^2} \int_0^b dr' \int_0^{2\pi} d\phi' \int_0^b dr \ rr' \sqrt{\frac{1}{rr'}} \delta(r - r') \\ = \frac{1}{\pi b^2} \int_0^b dr' \int_0^{2\pi} d\phi' \int_0^b dr \ r' = 1.$$
(39)

We thus see that v(t) is well behaved at short times and its Laplace transform does exist.

Further calculations to arrive at the infection probability $\mathcal{I}(t)$ require numerical means: first, v(t) and $\mu(t)$ given in Eqs. (32) and (33) are calculated by numerically evaluating the integrals. Then they are numerically Laplace transformed, and the result is used to obtain the infection probability in the Laplace domain, $\tilde{\mathcal{I}}(\epsilon)$, through Eq. (4). Finally, this $\tilde{\mathcal{I}}(\epsilon)$ is numerically inverted to obtain $\mathcal{I}(t)$.

2.4 Non-monotonicity in the Dependence of the Strength of the Confinement

The infection probability, obtained numerically, shows the non-monotonic effect of the home ranges of the walkers. On panel (a) of Fig. 2, the infection probability against time (scaled to the diffusive time, $\tau_H = H^2/2D$) is given. As the magnitude of the confinement of the walkers to their respective homes is increased from $\gamma \tau_H = 0.5$ (asterisks), 1.2 (solid line), to 2.0 (circles), the infection curve behaves non-monotonically, as observed in the one-dimensional result given in KS.

In addition to $\mathcal{I}(t)$, as explained in KS, the effective rate of infection, α , can be generally defined to efficiently characterize the effect of the confining potentials on $\mathcal{I}(t)$. In order to find such a quantity, if it exists, we asked: what would the rate α be in terms of v(t) and $\mu(t)$, if $\mathcal{I}(t)$ were a decaying exponential of the form² $\mathcal{I}(t) = 1 - e^{-\alpha t}$? In the Laplace domain, such $\mathcal{I}(t)$ is given by $\widetilde{\mathcal{I}}(\epsilon) = \alpha / [\epsilon(\epsilon + \alpha)]$, which is equated to the right-hand side of Eq. (4) to be solved for ϵ -dependent quantity, $\widetilde{\alpha}(\epsilon)$. An Abelian theorem was applied to define the effective rate: $\alpha \equiv \lim_{\epsilon \to 0} [\epsilon \widetilde{\alpha}(\epsilon)]$, which results in

$$\alpha = \frac{\mu(\infty)}{1/\mathcal{C} + 1/\mathcal{M}},\tag{40}$$

 $^{^2}$ See Kenkre and Sugaya (2014) for a detailed discussion. Section 5 is devoted entirely to this exponential representation. See particularly Equations (15)–(17).



Fig. 2 a The non-monotonic effect of infection probability as a function of increasing $\gamma \tau_H$. The latter dimensionless parameter characterizes the strength of confinement. The infection probability $\mathcal{I}(t)$ is plotted against time in units of the diffusive time, τ_H , for the walkers to traverse the inter-home distance H. Infection curves are produced for the values of $\gamma \tau_H = 0.5$, 1.2, and 2.0. **b** The effective rate α scaled to $1/\tau_H$ plotted against $\gamma \tau_H$, whose peak indicates the optimal value of $\gamma \tau_H$ for infection. The rate of infection C is kept constant at 0.05 in units of $1/\tau_H$

where \mathcal{M} , which we call the motion parameter, is defined as

$$\frac{1}{\mathcal{M}} = \int_0^\infty dt \, \left[\nu(t) - \mu(t) \right]. \tag{41}$$

In panel (b) of Fig. 2, α scaled to $1/\tau_H$ is plotted against $\gamma \tau_H$. The peaking behavior of α as a function of $\gamma \tau_H$ shows, *transparently*, that the degree of the confinement of the random walkers to their respective homes affects the infection probability non-monotonically.

This result reconfirms the generalization of the effect of confinement found in one dimension in KS. The existence of the home ranges of the walkers makes their probability density to become Gaussians in the steady state. As seen in the expressions of $\tilde{\mathcal{I}}(\epsilon)$ in Eq. (4) and α in Eq. (40), the effects of confinement enter these quantities through the homogeneous probabilities, $\mu(t)$ and $\nu(t)$, to find the walkers within the infection region at time *t*, given their initial conditions, and given that they were within the region initially, respectively. The probability density to find the walkers together, in the steady state, varies non-monotonically as a function of the confinement strength, and thus gives rise to the non-monotonic effect in $\mathcal{I}(t)$ and α .

We now discuss a more general situation, where the dimensionality of the infection region and that of the motion of walkers differ.

3 Analysis in Higher Dimensions When the Dimensionality of Motion Exceeds that of Reaction

Although the above analysis is based on the assumption that the dimensionality of the walker equals that of the infection region, practical situations exist in which this is not true. A clear example is a pair of walkers each executing a 1-d random walk and transmitting infection on encounter at a point. This example indeed underlies the situation in our earlier analysis (Kenkre and Sugaya 2014). A mathematical problem arises if each of the walkers executes a 2-d random walk but the infection region is still a point. Singularities appear in the short-time behavior of the ν -function causing its Laplace transform impossible to be evaluated.

Generally, for a point infection-region in *m*-dimensions, v(t) is given by (Kenkre and Sugaya 2014)

$$\nu(t) = \frac{\int_{\text{all space}} d^m \mathbf{r}_1' \int_{\text{all space}} d^m \mathbf{r}_1 \ \Pi(\mathbf{r}_1, \mathbf{r}_1', \mathbf{r}_1, \mathbf{r}_1', t)}{\int_{\text{all space}} d^m \mathbf{r}_1'}$$
(42)

$$= \left(\frac{1}{\sqrt{8\pi DT(t)}}\right)^{m} \prod_{\beta=1}^{m} e^{-\frac{\left[\left(h_{1}^{\beta}-h_{2}^{\beta}\right)\left(1-e^{-\gamma t}\right)\right]^{2}}{8DT(t)}}.$$
(43)

In the limit $t \to 0$, this v-function behaves as

$$\nu(t \to 0) \to t^{-m/2} \tag{44}$$

to the lowest order of t. As a consequence, the Laplace transform of v(t) exists only when m = 1, and does not exist for m > 1. What this means is that while 1-d walkers transmitting infection on meeting at a point do not raise any problems for the theory as developed in KS, an extension of the theory to 2-d walkers doing the same presents a singularity problem.

We show how this problem can be solved by expanding the dimensionality of the infection region and give an example in two dimensions.

3.1 Resolution of Point Encounter Problems by Expansion of the Reaction Region

Consider a situation where infection transmission occurs when the walkers are within a certain region of dimensionality θ that is smaller than that of the motion: $\theta < 2m$. For such a case, we write, for the equation of motion for $P(\mathbf{r}_1, \mathbf{r}_2, t)$,

$$\frac{\partial P(\mathbf{r}_{1}, \mathbf{r}_{2}, t)}{\partial t} = \nabla_{1} \cdot \left[\gamma \left(\mathbf{r}_{1} - \mathbf{R}_{1} \right) P(\mathbf{r}_{1}, \mathbf{r}_{2}, t) \right] + \nabla_{2} \cdot \left[\gamma \left(\mathbf{r}_{2} - \mathbf{R}_{2} \right) P(\mathbf{r}_{1}, \mathbf{r}_{2}, t) \right] \\ + D \left(\nabla_{1}^{2} + \nabla_{2}^{2} \right) P(\mathbf{r}_{1}, \mathbf{r}_{2}, t) \\ - \mathcal{C}_{(2m-\theta)} \int^{\prime} d^{\theta_{1}} \mathbf{r}_{1}^{\prime} d^{\theta_{2}} \mathbf{r}_{2}^{\prime} \, \delta^{m} (\mathbf{r}_{1} - \mathbf{r}_{1}^{\prime}) \delta^{m} (\mathbf{r}_{2} - \mathbf{r}_{2}^{\prime}) P(\mathbf{r}_{1}, \mathbf{r}_{2}, t).$$
(45)

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The first three terms on the right-hand side describe the motion of the random walkers precisely as in Eq. (45). The departure from Eq. (45) is seen in the fourth term, in the dimensionality of the differential elements, $d^{\theta_1} r_1$ and $d^{\theta_2} r_2$, and the infection rate $C_{(2m-\theta)}$. The dimensionalities of the infection region for infected and susceptible mice are given by θ_1 and θ_2 , respectively, where $\theta = \theta_1 + \theta_2$. The infection rate is denoted by $C_{(2m-\theta)}$ to reflect its dimensionality: [length^(2m-\theta)/time].

We follow the previous arguments to arrive at the expression of the infection probability in the Laplace Domain. In terms of the propagator, $\Pi(\mathbf{r}_1, \mathbf{r}_1', \mathbf{r}_2, \mathbf{r}_2', t)$, the solution in the Laplace space is given by

$$\widetilde{P}(\mathbf{r}_1, \mathbf{r}_2, \epsilon) = \widetilde{\eta}(\mathbf{r}_1, \mathbf{r}_2, \epsilon) - \mathcal{C}_{(2m-\theta)} \int' d^{\theta_1} \mathbf{r}_1' d^{\theta_2} \mathbf{r}_2' \, \widetilde{P}(\mathbf{r}_1', \mathbf{r}_2', \epsilon) \widetilde{\Pi}(\mathbf{r}_1, \mathbf{x}_1', \mathbf{r}_2, \mathbf{r}_2', \epsilon),$$
(46)

where $\eta(\mathbf{r}_1, \mathbf{r}_2, t)$ is the homogeneous solution given in Eq. (2). The definition of the infection probability [Eq. (3)] yields

$$\widetilde{\mathcal{I}}(\epsilon) = \frac{\mathcal{C}_{(2m-\theta)}}{\epsilon} \int' d^{\theta_1} \mathbf{r}'_1 d^{\theta_2} \mathbf{r}'_2 \, \widetilde{P}(\mathbf{r}'_1, \mathbf{r}'_2, \epsilon). \tag{47}$$

Applying the defect technique (Montroll and West 1979) to Eq. (46), we integrate in the variables r_1 and r_2 over the infection region, i.e.,

$$\int d^{\theta_1} \boldsymbol{r}_1 d^{\theta_2} \boldsymbol{r}_2 \widetilde{\boldsymbol{P}}(\boldsymbol{r}_1, \boldsymbol{r}_2, \epsilon) = \int d^{\theta_1} \boldsymbol{r}_1 d^{\theta_2} \boldsymbol{r}_2 \widetilde{\eta}(\boldsymbol{r}_1, \boldsymbol{r}_2, \epsilon) - \mathcal{C}_{(2m-\theta)} \int d^{\theta_1} \boldsymbol{r}_1' d^{\theta_2} \boldsymbol{r}_2' \widetilde{\boldsymbol{P}}(\boldsymbol{r}_1', \boldsymbol{r}_2', \epsilon) \int d^{\theta_1} \boldsymbol{r}_1 d^{\theta_2} \boldsymbol{r}_2 \widetilde{\boldsymbol{\Pi}}(\boldsymbol{r}_1, \boldsymbol{r}_1', \boldsymbol{r}_2, \boldsymbol{r}_2' \epsilon).$$
(48)

We define $\nu_{2m-\theta}(t)^3$ by the use of the ν -function method (Kenkre 1982; Kenkre and Parris 1983):

$$\nu_{(2m-\theta)}(t) \equiv \frac{\int' d^{\theta_1} \mathbf{r}'_1 d^{\theta_2} \mathbf{r}'_2 \int' d^{\theta_1} \mathbf{r}_1 d^{\theta_2} \mathbf{r}_2 \Pi(\mathbf{r}_1, \mathbf{r}'_1, \mathbf{r}_2, \mathbf{r}'_2, t)}{\int' d^{\theta_1} \mathbf{r}'_1 d^{\theta_2} \mathbf{r}'_2},$$
(49)

and also define $\mu_{(2m-\theta)}(t)$ as

$$\mu_{(2m-\theta)}(t) \equiv \int' d^{\theta_1} \boldsymbol{r}_1 d^{\theta_2} \boldsymbol{r}_2 \eta(\boldsymbol{r}_1, \boldsymbol{r}_2, t).$$
(50)

Replacing the integral over the propagator in Eq. (48) with $\widetilde{\nu}_{(2m-\theta)}(\epsilon)$ yields

$$\int' d^{\theta_1} \boldsymbol{r}_1 d^{\theta_2} \boldsymbol{r}_2 \widetilde{P}(\boldsymbol{r}_1, \boldsymbol{r}_2, \epsilon) = \frac{\widetilde{\mu}_{(2m-\theta)}(\epsilon)}{1 + \mathcal{C}_{(2m-\theta)}\widetilde{\nu}_{(2m-\theta)}(\epsilon)},$$
(51)

³ Note that when $(2m - \theta) = 0$ the *v*-function is denoted simply by v(t) (the original definition Kenkre 1982; Kenkre and Parris 1983). In a couple of recent publications (Spendier and Kenkre 2013; Kenkre and Sugaya 2014), the symbol v(t) has been applied to a function with varying dimensions according to the dimension of the motion and the trap.

which is an approximate result. Consequently, substituting this result into Eq. (47) gives

$$\widetilde{\mathcal{I}}(\epsilon) = \frac{1}{\epsilon} \left[\frac{\widetilde{\mu}_{(2m-\theta)}(\epsilon)}{1/\mathcal{C}_{(2m-\theta)} + \widetilde{\nu}_{(2m-\theta)}(\epsilon)} \right].$$
(52)

This is the generalized form of the infection probability (in the Laplace domain) given in Eq. (4), to cases with differing dimensionality between the infection region and motion of the walkers. The effective rate of infection is given by

$$\alpha = \frac{\mu_{(2m-\theta)}(\infty)}{1/\mathcal{C}_{(2m-\theta)} + 1/\mathcal{M}_{(2m-\theta)}},\tag{53}$$

with

$$\frac{1}{\mathcal{M}_{(2m-\theta)}} = \int_0^\infty dt \, \left[v_{(2m-\theta)}(t) - \mu_{(2m-\theta)}(t) \right].$$
(54)

We proceed to derive $\nu_{(2m-\theta)}$ and $\mu_{(2m-\theta)}$ in CM-relative coordinates. This leads to

$$\nu_{(2m-\theta)}(t) \equiv \frac{\int' d^{\theta_+} \mathbf{r}'_+ d^{\theta_-} \mathbf{r}'_- \int' d^{\theta_+} \mathbf{r}_+ d^{\theta_-} \mathbf{r}_- \Pi(\mathbf{r}_+, \mathbf{r}'_+, \mathbf{r}'_-, \mathbf{r}'_- t)}{\int' d^{\theta_+} \mathbf{r}'_+ d^{\theta_-} \mathbf{r}'_-}, \qquad (55)$$

and

$$\mu_{(2m-\theta)}(t) \equiv \int' d^{\theta_+} \boldsymbol{r}_+ d^{\theta_-} \boldsymbol{r}_- \eta(\boldsymbol{r}_+, \boldsymbol{r}_-, t).$$
(56)

It was shown in the last section that the geometry of the infection region does not depend on the CM coordinate when we consider infection transmission to take place as a function of the relative distance of walkers. This means that $\theta_+ = m$, while θ_- remains to be determined for a specific scenario at hand. Thus, the primed integral is written as

$$\int' d^{\theta_+} \mathbf{r}_+ d^{\theta_-} \mathbf{r}_- \to \int_{\text{all space}} d^m \mathbf{r}_+ \int' d^{\theta_-} \mathbf{r}_-, \qquad (57)$$

and $2m - \theta = 2m - \theta_+ - \theta_- = m - \theta_-$. Performing the first integral in the numerator of the definition of $v_{(2m-\theta)}(t)$ given in Eq. (55) results in

$$\int_{\text{all space}} d^m \mathbf{r}_+ \int' d^{\theta_-} \mathbf{r}_- \Pi(\mathbf{r}_+, \mathbf{r}'_+, \mathbf{r}_-, \mathbf{r}'_-, t) = \int' d^{\theta_-} \mathbf{r}_- \Pi(\mathbf{r}_-, \mathbf{r}'_-, t), \quad (58)$$

where $\Pi(\mathbf{r}_{-}, \mathbf{r}'_{-}, t)$ is given in Eq. (15). With this result, the ν -function can be written as

$$\nu_{(2m-\theta)}(t) = \nu_{(m-\theta_{-})}(t) = \frac{\int' d^{\theta_{-}} \mathbf{r}'_{-} \int' d^{\theta_{-}} \mathbf{r}_{-} \Pi(\mathbf{r}_{-}, \mathbf{r}'_{-}, t)}{\int' d^{\theta_{-}} \mathbf{r}'_{-}}.$$
 (59)

For a δ -function initial condition, $\mu_{(2m-\theta)}(t)$ becomes

$$\mu_{(2m-\theta)}(t) = \mu_{(m-\theta_{-})}(t) = \int' d^{\theta_{-}} \mathbf{r}_{-} \Pi(\mathbf{r}_{-}, \mathbf{r}_{-}^{0}, t).$$
(60)

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3.2 Specific Example of a Reaction Region as a Ring

We present here the simplest example in two dimensions, where the transmission of infection is assumed to occur when the mice are *at* a certain distance from each other. We call this distance the infection range. In polar coordinates, such geometry of the infection region becomes a ring of a given radius *b*, with $b^2 = (x_-^1)^2 + (x_-^2)^2$. The dimensionality of the ring infection-region in the relative coordinate is 1. Thus, the subscript $(2m - \theta)$ becomes $(2m - \theta) = m - \theta_- = 2 - 1 = 1$.

Note that, for a ring infection-region of radius b, the primed integral is explicitly written as

$$\int' d^{1}\mathbf{r}_{-} \to \int_{0}^{\infty} dr \int_{0}^{2\pi} r d\phi \, \frac{1}{r2\pi} \delta\left(r-b\right) = \int_{0}^{\infty} dr \int_{0}^{2\pi} d\phi \, \frac{1}{2\pi} \delta\left(r-b\right),\tag{61}$$

in the polar coordinates. We calculate $v_1(t)$ and $\mu_1(t)$ from the definitions given in Eqs. (59) and (60).

$$\nu_{1}(t) = \frac{\int_{0}^{\infty} dr' \int_{0}^{2\pi} d\phi' \frac{1}{2\pi} \delta\left(r'-b\right) \int_{0}^{\infty} dr \int_{0}^{2\pi} d\phi \frac{1}{2\pi} \delta\left(r-b\right) \Pi(r,r',\phi,\phi',t)}{\int_{0}^{\infty} dr' \int_{0}^{2\pi} d\phi' \frac{1}{2\pi} \delta\left(r'-b\right)} = \frac{1}{2\pi} \int_{0}^{2\pi} d\phi' \Pi(b,b,\phi',t),$$
(62)

and

$$\mu_1(t) = \int_0^\infty dr \int_0^{2\pi} d\phi \, \frac{1}{2\pi} \delta\left(r-b\right) \, \Pi(r, r^0, \phi, \phi^0, t) = \frac{1}{2\pi} \Pi(b, r^0, \phi^0, t). \tag{63}$$

Here $\Pi(r, r', \phi, \phi', t)$ and $\Pi(r, r', \phi', t)$ are given in Eqs. (25) and (29), respectively.

The ring infection-region in two dimension is analogous to a point infection-region in one dimension in the following way. The analysis provided at the beginning of this section shows that the ν -function for the point infection in one dimension behaves as $t^{-1/2}$ for small times. It is straightforward to demonstrate $\nu_1(t)$ given in Eq. (62) exhibits the same time dependence for small times. As $t \rightarrow 0$, the argument of the Bessel function becomes large where its asymptotic form is appropriate, as given in Eq. (37), and $\nu_1(t)$ behaves as, at short times,

$$\nu(t \to 0) \to \frac{1}{2\pi} \int_0^{2\pi} d\theta' \left(\frac{1}{4\pi Dt}\right) e^{-\frac{b^2}{2Dt}} \sqrt{\frac{2Dt}{b^2}} e^{\frac{b^2}{2Dt}} \sim t^{-1/2}.$$
 (64)

3.2.1 Recovery of Non-monotonicity and Appearance of a Resonance Effect

To obtain the infection probability, the integral over ϕ' of $\nu_1(t)$ given in Eq. (62) is done numerically. Then this result and $\mu_1(t)$ of Eq. (33) are numerically Laplace



Fig. 3 a The non-monotonic variation in the infection probability $\mathcal{I}(t)$ as a function of increasing strength of confinement, γ . Here γ is scaled to $1/\tau_H$, the diffusive time for the walker to traverse the inter-home distance H. The infection probability $\mathcal{I}(t)$ is plotted against time in units of τ_H . Each infection curve corresponds to a different value of $\gamma \tau_H$. **b** The effective rate α in units of $1/\tau_H$ is plotted against $\gamma \tau_H$. The peak indicates the optimal value of $\gamma \tau_H$ for transmission of infection. The rate of infection C_1 is illustrative and kept constant at 9 in units of 2D/H

transformed and substituted into Eq. (52) to obtain $\tilde{\mathcal{I}}(\epsilon)$. Finally, $\tilde{\mathcal{I}}(\epsilon)$ is numerically Laplace inverted to obtain the result, $\mathcal{I}(t)$, in the time domain.

The resulting infection curve and the effective rate showing the non-monotonic behavior due to the effect of confinement are shown in Fig. 3. In panel (a), the infection curve is plotted against time. The latter is scaled to the diffusive time $\tau_H = H^2/2D$. Each curve corresponds to a value of the unitless parameter $\gamma \tau_H$, effectively to a given potential strength γ . Panel (b) of Fig. 3 shows the effective rate α scaled to $1/\tau_H$, plotted against $\gamma \tau_H$ again showing the non-monotonic effect. Intuitively, one can think of this effect arising from the changing probability of the walkers finding one another given their inter-home distance H and the degree of their confinement to respective homes, in the contact-limited case. The steady-state Smoluchowski width σ essentially gives the degree of confinement. When these lengths are balanced, i.e., $H = \sigma$, the probability for the walkers to find each other is maximized, which in turn is reflected in the maximized infection probability.

The infection range, b, is a new length scale in addition to H and σ . It arises from the extension of the infection influence to a finite region and enters the dynamics in a manner to effectively modulate the role of H per given σ . In other words, when the walkers live at homes that are separated by H and if the infection happens at range b, then part of the problem becomes equivalent to a co-location infection with |H - b| as the home separation distance. For this reason, when H = b, i.e., when the inter-home



Fig. 4 Optimal value of the confining potential steepness γ (scaled to $1/\tau_H$) for maximum infection rate as a function of (b/H). The divergence of $\gamma \tau_H$ at b/H = 1 signals the *resonant* phenomenon. Values given here are accurate for a large value of the infection rate

distance and infection range are the same, infection occurs as if the walkers share a home. In such a situation, increasing the strength of confinement only helps the infection transmission. We refer to this phenomenon as "resonant" behavior.

We show this effect in Fig. 4 for the simplest case where an infection range is introduced in one dimension. The optimal value of γ (scaled to $1/\tau_H$) for infection transmission is plotted as a function of the ratio between the infection range and interhome distance, b/H. The resonant behavior is indicated by the diverging value of $\gamma \tau_H$ at b/H = 1. We provide a detailed analysis to determine the optimal value of $\gamma \tau_H$ in "Appendix".

4 Discussion

The mathematical analysis of transmission of infection in an epidemic such as the Hantavirus, which propagates by contact of animals moving over a landscape, was begun in KS (Kenkre and Sugaya, 2014) and is completed in the present paper. The essential theory is in KS where many fundamental insights into infection spread were obtained through a simplified one-dimensional study. However, the present extension to two (and higher) dimensions also plays a non-trivial, indeed essential, role in an understanding and description of the phenomenon of infection spread. This is so not only because the realistic situation in cases such as that of the Hantavirus is best described in two dimensions (the landscape over which the rodents move) but also because reaction diffusion in dimensions higher than 1 inevitably presents singularities in description. We have described these singularities in Sect. 3 of the present paper, particularly in Eq. (44), where the crucial quantity v(t), central to the KS formalism,

is shown to vary with time t as $t^{-m/2}$. The dimensionality being m here, the Laplace transforms of v on which the KS theory is built exist for m = 1 but not for m > 1, i.e., for 2 and higher dimensions.

The present study resolves this problem by expanding the dimensionality of the infection region, thereby avoiding point encounters which are the source of the singularities. The detailed theory is shown in Sects. 3.1 and 3.2 with results displayed graphically in Figs. 3 and 4. Of these, the former reconfirms the curious non-monotonicity effect introduced in KS, now for higher dimensions as well, whereas the latter shows our findings on an *additional* phenomenon we call the *resonant effect*. The present analysis thus generalizes the KS theory and adds to it new predictions.⁴

The present paper has two different types of infection spread description: one in which the singularity problems stemming from point encounters are eliminated by expanding the dimensionality of the infection region as explained above; but also another in which the dimensionality of the infection region and that of the motion of walkers is the same. Singularity problems do not arise in this case as point regions are avoided entirely. The analysis which is more straightforward is given in Sect. 2 of this paper, and results in the infection plots are displayed in Fig. 2. The plots show a simple generalization of the KS theory in higher dimensions. Thus, the analysis in the present paper along with the KS formalism completes, in the sense of model calculations, the theory of infection spread of epidemics such as the Hantavirus for the case of dilute concentration of rodents.

Appendix: Analysis in One Dimension: Introduction of Infection Range

We consider that the infection is transmitted *at* a range *b*, while the mice move in one dimension, and start the analysis in CM-relative coordinates. The equation of motion for $P(x_+, x_-, t)$, the probability density to find the walkers at CM and relative coordinates x_+ and x_- , respectively, at time *t* is

$$\frac{\partial P(x_{+}, x_{-}, t)}{\partial t} = \frac{\partial}{\partial x_{+}} \gamma (x_{+} - h_{+}) P(x_{+}, x_{-}, t) + \frac{\partial}{\partial x_{-}} \gamma (x_{-} - h_{-}) P(x_{+}, x_{-}, t) + D \left(\frac{\partial^{2}}{\partial x_{+}^{2}} + \frac{\partial^{2}}{\partial x_{-}^{2}} \right) P(x_{+}, x_{-}, t) - C_{1} \delta (x_{-} - b) P(x_{+}, x_{-}, t) - C_{1} \delta (x_{-} + b) P(x_{+}, x_{-}, t).$$
(A.1)

The first three terms represent the Smoluchowski motion. The infection transmission is described in the last two terms; the arguments of the δ -functions indicate that the infection is transmitted to the susceptible mouse from the infected one when they are at distance *b* apart, i.e., when $x_{-} = \pm b$. The infection rate is given by C_1 .

⁴ We mention here in passing that if the motion of the rodents (in the absence of the transmission of infection) is not Gaussian as concluded in Hantavirus observations in Refs. Giuggioli et al. (2005), Abramson et al. (2006), and MacInnis et al. (2008) but rather anomalous in nature, the time dependence of infection curve $\mathcal{I}(t)$, can be quite complex making it definition of the effective rate α impossible.

The symmetry and simplicity of this infection region allows for an exact calculation of $\tilde{\nu}(\epsilon)$, without the approximation of the ν -function method. The propagator for this problem is given by

$$\Pi(x_{+}, x_{+}', x_{-}, x_{-}', t) = \frac{1}{4\pi D\mathcal{T}(t)} e^{-\frac{\left(x_{+} - h_{+} - (x_{+}' - h_{+})e^{-\gamma t}\right)^{2} + \left(x_{-} - h_{-} - (x_{-}' - h_{-})e^{-\gamma t}\right)^{2}}{4D\mathcal{T}(t)}}.$$
(A.2)

In terms of this propagator, the solution to Eq. (A.1) in the Laplace domain as

$$\tilde{P}(x_{+}, x_{-}, \epsilon) = \tilde{\eta}(x_{+}, x_{-}, \epsilon) - C_{1} \int_{-\infty}^{\infty} dx'_{+} \tilde{\Pi}(x_{+}, x'_{+}, x_{-}, -b, \epsilon) \tilde{P}(x'_{+}, -b, \epsilon) - C_{1} \int_{-\infty}^{\infty} dx'_{+} \tilde{\Pi}(x_{+}, x'_{+}, x_{-}, b, \epsilon) \tilde{P}(x'_{+}, b, \epsilon).$$
(A.3)

From its definition given in Eq. (3), the infection probability in the Laplace domain is given in Eq. (A.3) by

$$\widetilde{\mathcal{I}}(\epsilon) = \frac{\mathcal{C}_1}{\epsilon} \left[\int_{-\infty}^{\infty} dx_+ \widetilde{P}(x_+, b, \epsilon) + \int_{-\infty}^{\infty} dx_+ \widetilde{P}(x_+, -b, \epsilon) \right].$$
(A.4)

The use of the defect technique, i.e., setting $x_{-} = \pm b$ and integrating x_{+} over all space, after some algebra, yields

$$\begin{split} &\int_{-\infty}^{\infty} dx_{+} \widetilde{P}(x_{+}, b, \epsilon) + \int_{-\infty}^{\infty} dx_{+} \widetilde{P}(x_{+}, -b, \epsilon) \\ &= \frac{1}{\mathcal{C}_{1}} \frac{\left[1/\mathcal{C}_{1} + \widetilde{v}_{1}^{++}(\epsilon) - \widetilde{v}_{1}^{+-}(\epsilon) \right] \widetilde{\mu}_{1}^{-}(\epsilon) + \left[1/\mathcal{C}_{1} + \widetilde{v}_{1}^{--}(\epsilon) - \widetilde{v}_{1}^{-+}(\epsilon) \right] \widetilde{\mu}_{1}^{+}(\epsilon)}{\left[1/\mathcal{C}_{1} + \widetilde{v}_{1}^{--}(\epsilon) \right] \left[1/\mathcal{C}_{1} + \widetilde{v}_{1}^{++}(\epsilon) \right] - \widetilde{v}_{1}^{-+}(\epsilon) \widetilde{v}_{1}^{+-}(\epsilon)}, \end{split}$$
(A.5)

where

$$\mu_1^+(t) = \int_{-\infty}^{\infty} dx_+ \eta(x_+, b, t) = \frac{1}{\sqrt{4\pi D\mathcal{T}(t)}} e^{-\frac{\left(b - H - (x_-^0 - H)e^{-\gamma t}\right)^2}{4D\mathcal{T}(t)}}$$
(A.6)

$$\mu_1^{-}(t) = \int_{-\infty}^{\infty} dx_+ \eta(x_+, -b, t) = \frac{1}{\sqrt{4\pi DT(t)}} e^{-\frac{\left(b + H + (x_-^0 - H)e^{-\gamma t}\right)^2}{4DT(t)}}$$
(A.7)

$$\nu_1^{++}(t) = \int_{-\infty}^{\infty} dx_+ \Pi(x_+, b, x'_+, b) = \frac{1}{\sqrt{4\pi DT(t)}} e^{-\frac{\left[(b-H)(1-e^{-\gamma t})\right]^2}{4DT(t)}}$$
(A.8)

$$\nu_1^{+-}(t) = \int_{-\infty}^{\infty} dx_+ \Pi(x_+, b, x'_+, -b) = \frac{1}{\sqrt{4\pi DT(t)}} e^{-\frac{\left[b - H + (b+H)e^{-\gamma t}\right]^2}{4DT(t)}}$$
(A.9)

$$\nu_1^{-+}(t) = \int_{-\infty}^{\infty} dx_+ \Pi(x_+, -b, x'_+, b) = \frac{1}{\sqrt{4\pi DT(t)}} e^{-\frac{\left[b + H + (b - H)e^{-\gamma t}\right]^2}{4DT(t)}}$$
(A.10)

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$$\nu_1^{--}(t) = \int_{-\infty}^{\infty} dx_+ \Pi(x_+, -b, x'_+, -b) = \frac{1}{\sqrt{4\pi DT(t)}} e^{-\frac{\left[(b+H)(1-e^{-\gamma t})\right]^2}{4DT(t)}}.$$
 (A.11)

In the calculation of the $\mu_1(t)$'s, a δ -function initial condition was assumed. The infection probability in the Laplace domain is then given exactly by

$$\widetilde{\mathcal{I}}(\epsilon) = \frac{1}{\epsilon} \frac{\left[1/\mathcal{C}_{1} + \widetilde{\nu}_{1}^{++}(\epsilon) - \widetilde{\nu}_{1}^{+-}(\epsilon)\right] \widetilde{\mu}_{1}^{-}(\epsilon) + \left[1/\mathcal{C}_{1} + \widetilde{\nu}_{1}^{--}(\epsilon) - \widetilde{\nu}_{1}^{-+}(\epsilon)\right] \widetilde{\mu}_{1}^{+}(\epsilon)}{\left[1/\mathcal{C}_{1} + \widetilde{\nu}_{1}^{--}(\epsilon)\right] \left[1/\mathcal{C}_{1} + \widetilde{\nu}_{1}^{++}(\epsilon)\right] - \widetilde{\nu}_{1}^{-+}(\epsilon) \widetilde{\nu}_{1}^{+-}(\epsilon)}.$$
(A.12)

The non-monotonic effect is explained in detail in Ref. (Kenkre and Sugaya 2014) in the steady state and in the contact limit where $1/C_1$ is much greater than any of the $v_1(t)$'s and $\mu_1(t)$'s in its effect. In these limit, $\mathcal{I}(t)$ approximately becomes

$$\mathcal{I}(t) \sim \mathcal{C}_1\left(\mu_1^+(\infty) + \mu_1^-(\infty)\right) \cdot t, \qquad (A.13)$$

where we note that $\nu_1^{++}(\infty) = \nu_1^{+-}(\infty) = \mu_1^+(\infty)$ and $\nu_1^{--}(\infty) = \nu_1^{-+}(\infty) = \mu_1^-(\infty)$. The condition for the optimal value of $\gamma \tau_H$ value found from this result yields the transcendental relation,

$$\frac{1 - 2\gamma \tau_H (1 - b/H)^2}{1 - 2\gamma \tau_H (1 + b/H)^2} = -e^{-4\gamma \tau_H (b/H)}.$$
(A.14)

The value of $\gamma \tau_H$ for given value of b/H found from this equation is plotted in Fig. 4.

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