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Mathematical Modelling of an Advection-driven Interspecific Competition

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Abstract: An advection-driven interspecific competition model is constructed, which we believe is more physically realistic as the movements of competing species are usually aimed at a target. Standard analysis using the travelling wave approach was employed, and the results show that the equilibrium points are independent of the advection velocities and the wave speed. However, the stability of each steady state depends on the wave speed and the advection velocities of the competing species. Conditions for the extinction and coexistence of the species were also obtained and illustrated using numerical simulations. The implication for ecological resource management is also highlighted.

Keywords: Competition, travelling wave, advection velocity, stability

1 Introduction

Mathematical modelling of interspecfic competition has been at the centre of mathematical ecology. The classic Lotka-Volterra interspecific competition model is a reference point, despite its shortcomings such as non-capturing of the random movement of the interacting species. A lot of research work has been carried out on the Lotka-Volterra competition model. Prominent among them are the works of Fassoni, etal [1], who established the effects of parameters on the size of the basin of attraction of the equilibrium points in an interspecific competition model. The works of Barabas, et al [2], Gerhard, et al [3], Gavina, et al [4] and Cushing, et al [5] are relevant references as far as interspecific competition is concerned. However, critics of some of the interspecific models are of the view that most of the models do not capture certain biological features such as environmental effects and spatial heterogeneity. This is the focus of this research work. However, many researchers have addressed some aspects of spatially structured competition models. For instance, Okubo [6] addressed the effect of diffusion on a two-species competition model. Ryabov and Blasius [7] in a review paper, noted that advection is the directed movement of species from one region to the other. They stated that the dynamics of a

population involving the spatial movement of organisms due to diffusion and advection is given by

$$\frac{\partial p(x,t)}{\partial t} + v\frac{\partial p}{\partial x} = \mu(x,p)p + \frac{\partial}{\partial x}\left(D\frac{\partial p}{\partial x}\right),$$

where $p(x,t)$ is the population density, μ is the intrinsic growth rate, v is the advection velocity and D is the diffusion coefficient. Specifically, the advection term is given by $v\frac{\partial p}{\partial x}$. Similarly, Lam and Ni [8] considered a reaction-diffusion-advection system for two competing species and examined the effects of both diffusion and advection on the coexistence of the species, similar to the works of Zhao and Zhou [9] and Xu and Jiang [10]. Averill, et al [11] on the other hand studied the effect of intermediate advection on the dynamics of a reaction-diffusion-advection competition model and concluded that the species cannot coexist under weak advection, but that they only coexist in the presence of strong advection. Mackenzie, et al [12], though did not approach their work from a mathematical perspective, submitted that the movement of animals is a combination of diffusion and advection. While diffusion measures the random movement of animals, advection captures the component in a specified direction, such as the movement towards a food resource. In species interactions in a

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competition, movement is more directed towards the food resource, rather than random movement. The effects of advection on the dynamics of competition models have not been adequately addressed by researchers, hence the focus of this work. Advection is certainly not the only form of movement among competing species as captured above and as described by Smouse, et al [13], but no doubt the dominant form of movement. The current research intends to investigate only the effects of advection on the dynamics of the competing species with the assumption that random movement is negligible. The remaining parts of this work is structured as follows: section 2 is dedicated to the mathematical formulation of the model, section 3 centres on the analysis and numerical simulations, while section 4 deals with the results and discussion.

2 Mathematical Formulation

We consider two competing species p and q such that the interactions are governed by the equations

$$\frac{\partial p}{\partial t} + u_1 \frac{\partial p}{\partial x} = r_1 p \left(1 - \frac{p}{K_1} - \frac{\alpha_{12}}{K_1} q \right) \tag{1}$$

$$\frac{\partial q}{\partial t} + u_2 \frac{\partial q}{\partial x} = r_2 q \left(1 - \frac{q}{K_2} - \frac{\alpha_{21}}{K_2} p \right) \tag{2}$$

where u_1 and u_2, r_1 and r_2, K_1 and K_2 are respectively the advection velocities, the linear birth rates and the carrying capacities of the environment of species p and q, while α_{12} and α_{21} measure the competitive pressures on p and q respectively. Using the scalling variables

$$p = K_1 p^*, q = K_2 q^*, t = \frac{t^*}{r_1}, x = Lx^*,$$

we obtain after dropping asterisks, the non-dimensional system

$$\frac{\partial p}{\partial t} + v_1 \frac{\partial p}{\partial x} = p(1 - p - \alpha q) \tag{3}$$

$$\frac{\partial q}{\partial t} + v_2 \frac{\partial q}{\partial x} = \theta q(1 - q - \beta p) \tag{4}$$

where $v_1 = \frac{u_1}{r_1 L}, v_2 = \frac{u_2}{r_1 L}, \alpha = \frac{\alpha_{12} K_2}{K_1}, \beta = \frac{\alpha_{21} K_1}{K_2}$ and $\theta = \frac{r_2}{r_1}$. Assuming the wave variable $\tau = x - ct$, where c is the wave speed, we obtain the equations

$$(v_1 - c)\frac{dp}{d\tau} = p(1 - p - \alpha q) \tag{5}$$

$$(v_2 - c)\frac{dq}{d\tau} = \theta q(1 - q - \beta p) \tag{6}$$

3 Stability Analysis of the Equilibrium Points

The steady states of (5)-(6) are obtained as $E_0 = (0,0), E_1 = (0,1), E_2 = (1,0)$ and $E_3 = \left(\frac{\alpha - 1}{\alpha\beta - 1}, \frac{\beta - 1}{\alpha\beta - 1} \right)$. The equilibrium points are however the same as in the competition model without advection, hence the equilibrium points are independent of the advection velocities. The Jacobian matrix of the system is given by

$$J(p,q) = \begin{pmatrix} \frac{(1-2p-\alpha q)}{v_1 - c} & -\frac{\alpha p}{v_1 - c} \\ -\frac{\beta\theta q}{v_2 - c} & \frac{\theta(1-2q-\beta p)}{v_2 - c} \end{pmatrix} \tag{7}$$

Hence $J(E_0) = \begin{pmatrix} \frac{1}{v_1 - c} & 0 \\ 0 & \frac{\theta}{v_2 - c} \end{pmatrix}$, with eigenvalues $\lambda_1 = \frac{1}{v_1 - c}$ and $\lambda_2 = \frac{\theta}{v_2 - c}$. Thus, E_0 is unstable when $v_1, v_2 > c$ and stable for $v_1, v_2 < c$. However, E_0 is a saddle point for $v_1 < c < v_2$ and $v_2 < c < v_1$. This clearly shows the effects of advection on the stability of the equilibrium point. The table below shows the equilibrium points E_0, E_1 and E_2 and the conditions for stability or otherwise.

The analysis of the interior equilibrium point $E_3 = \left(\frac{\alpha - 1}{\alpha\beta - 1}, \frac{\beta - 1}{\alpha\beta - 1} \right)$ is more complex than the other three and is considered separately. The Jacobian matrix corresponding to this steady state is given by

$$J(E_3) = \begin{bmatrix} -\frac{1}{v_1 - c}\left(\frac{\alpha - 1}{\alpha\beta - 1} \right) & -\frac{\alpha}{v_1 - c}\left(\frac{\alpha - 1}{\alpha\beta - 1} \right) \\ -\frac{\beta\theta}{v_2 - c}\left(\frac{\beta - 1}{\alpha\beta - 1} \right) & -\frac{\theta}{v_2 - c}\left(\frac{\beta - 1}{\alpha\beta - 1} \right) \end{bmatrix} = \begin{bmatrix} A & \alpha A \\ \beta D & D \end{bmatrix} \tag{8}$$

where $A = -\frac{1}{v_1 - c}\left(\frac{\alpha - 1}{\alpha\beta - 1} \right)$ and $D = -\frac{\theta}{v_2 - c}\left(\frac{\beta - 1}{\alpha\beta - 1} \right)$. The eigenvalues are obtained as

$\lambda_1 = \frac{(A+D) + \sqrt{(A+D)^2 + 4AD(\alpha\beta - 1)}}{2}$ and $\lambda_2 = \frac{(A+D) - \sqrt{(A+D)^2 + 4AD(\alpha\beta - 1)}}{2}$. We note that for the interior equilibrium point $E_3 = \left(\frac{\alpha - 1}{\alpha\beta - 1}, \frac{\beta - 1}{\alpha\beta - 1} \right)$ to be physically meaningful, $\alpha < 1, \beta < 1 \Rightarrow \alpha\beta < 1$ and $\alpha > 1, \beta > 1 \Rightarrow \alpha\beta > 1$. Hence two cases arise:

Case 1: $\alpha < 1, \beta < 1$ and $\alpha\beta < 1$

For case 1, we have four conditions to consider, $v_1, v_2 > c, v_1, v_2 < c, v_1 < c < v_2$ and $v_2 < c < v_1$. If $v_1 > c$ and $v_2 > c$, then $A < 0, D < 0, AD > 0$ and $\alpha\beta - 1 < 0$. Hence

$$(A+D)^2 > (A+D)^2 + 4AD(\alpha\beta - 1) \Rightarrow (A+D) + \sqrt{(A+D)^2 + 4AD(\alpha\beta - 1)} < 0.$$

Thus, $\lambda_1 < 0$ or $Re\lambda_1 < 0$. Similarly, $(A+D) - \sqrt{(A+D)^2 + 4AD(\alpha\beta - 1)} < 0$ which implies $\lambda_2 < 0$ or $Re\lambda_2 < 0$. Hence E_3 is a stable point. For $v_1 < c$ and $v_2 < c$, $A > 0, D > 0, AD > 0$ and $\alpha\beta - 1 < 0$,

$$(A+D) + \sqrt{(A+D)^2 + 4AD(\alpha\beta - 1)} > 0,$$

Table 1: Summary of Equilibrium Points and their Stability

Equilibrium point	Eigenvalues	Conditions	Stability
$E_0 = (0,0)$	$\lambda_1 = \frac{1}{v_1-c}$ $\lambda_2 = \frac{\theta}{v_2-c}$	$v_1, v_2 > c$	Unstable node
		$v_1, v_2 < c$	Stable node
		$v_1 < c < v_2$	Saddle
		$v_2 < c < v_1$	Saddle
$E_1 = (0,1)$	$\lambda_1 = \frac{1-\alpha}{v_1-c}$ $\lambda_2 = -\frac{\theta}{v_2-c}$	$\alpha < 1, v_1, v_2 > c$	Saddle
		$\alpha < 1, v_1, v_2 < c$	Saddle
		$\alpha < 1, v_1 < c < v_2$	Stable node
		$\alpha < 1, v_2 < c < v_1$	Unstable node
		$\alpha > 1, v_1, v_2 > c$	Stable node
		$\alpha > 1, v_1, v_2 < c$	Unstable node
		$\alpha > 1, v_1 < c < v_2$	Saddle
		$\alpha > 1, v_1 < c < v_2$	Saddle
$E_2 = (1,0)$	$\lambda_1 = -\frac{1}{v_1-c}$ $\lambda_2 = \frac{\theta(1-\beta)}{v_2-c}$	$\beta < 1, v_1, v_2 > c$	Saddle
		$\beta < 1, v_1, v_2 < c$	Saddle
		$\beta < 1, v_1 < c < v_2$	Unstable node
		$\beta < 1, v_2 < c < v_1$	Stable node
		$\beta > 1, v_1, v_2 > c$	Stable node
		$\beta > 1, v_1, v_2 < c$	Unstable node
		$\beta > 1, v_1 < c < v_2$	Saddle
		$\beta > 1, v_2 < c < v_1$	Saddle

therefore $\lambda_1 > 0$ or $Re\lambda_1 > 0$. Consequently,

$$(A+D) - \sqrt{(A+D)^2 + 4AD(\alpha\beta - 1)} > 0$$

and so $\lambda_2 > 0$ or $Re\lambda_2 > 0$, which shows that E_3 is an unstable point in this case. For $v_1 < c < v_2$, $A > 0, D < 0, AD < 0$. If $A + D > 0$, then

$$(A+D) + \sqrt{(A+D)^2 + 4AD(\alpha\beta - 1)} > 0 \Rightarrow \lambda_1 > 0.$$

Also,

$$(A+D) - \sqrt{(A+D)^2 + 4AD(\alpha\beta - 1)} < 0 \Rightarrow \lambda_1 < 0.$$

However, if $A + D < 0$, then

$$(A+D) + \sqrt{(A+D)^2 + 4AD(\alpha\beta - 1)} > 0 \Rightarrow \lambda_1 > 0$$

and

$$(A+D) - \sqrt{(A+D)^2 + 4AD(\alpha\beta - 1)} < 0 \Rightarrow \lambda_2 < 0.$$

Hence E_3 is a saddle point. For $v_2 < c < v_1$, $A < 0, D > 0, AD < 0$ and $4AD(\alpha\beta - 1) < 0$.
This is similar to the last condition above, hence E_3 is a saddle point.

Case 2: $\alpha > 1, \beta > 1$ and $\alpha\beta > 1$
Four conditions will be examined under this case. For $v_1, v_2 > c$, $A < 0, D < 0, AD > 0$ and $\alpha\beta - 1 > 0$. Hence

$$(A+D) + \sqrt{(A+D)^2 + 4AD(\alpha\beta - 1)} > 0 \Rightarrow \lambda_1 > 0.$$

Similarly,

$$(A+D) - \sqrt{(A+D)^2 + 4AD(\alpha\beta - 1)} < 0 \Rightarrow \lambda_2 < 0,$$

thus E_3 is a saddle. For $v_1, v_2 < c$, $A > 0, D > 0, AD > 0$ and $\alpha\beta - 1 > 0, \lambda_1 > 0$ and $\lambda_2 < 0$, therefore, E_3 is again a saddle point. Considering $v_1 < c < v_2$, $A > 0, D < 0, AD < 0$ and $\alpha\beta - 1 > 0$. Hence $A + D > 0$ or $A + D < 0$. If $A + D > 0$, we have

$$(A+D) + \sqrt{(A+D)^2 + 4AD(\alpha\beta - 1)} > 0 \Rightarrow \lambda_1 > 0$$

or $Re\lambda_1 > 0$ and

$$(A+D) - \sqrt{(A+D)^2 + 4AD(\alpha\beta - 1)} > 0 \Rightarrow \lambda_2 > 0$$

or $Re\lambda_2 > 0$. Thus, E_3 is an unstable node or spiral. But, if $A + D) < 0$,
$(A+D) + \sqrt{(A+D)^2 + 4AD(\alpha\beta - 1)} < 0$ and $(A+D) - \sqrt{(A+D)^2 + 4AD(\alpha\beta - 1)} < 0$, hence $\lambda_1 < 0$ and $\lambda_2 < 0$ and so E_3 is a stable node or spiral. In a similar vein, for $v_2 < c < v_1$, E_3 is an unstable node or spiral.

Numerical simulations are carried out to confirm the stability of the steady states contained in the analysis done above. Each figure is based on some conditions already stated in the stability analysis.
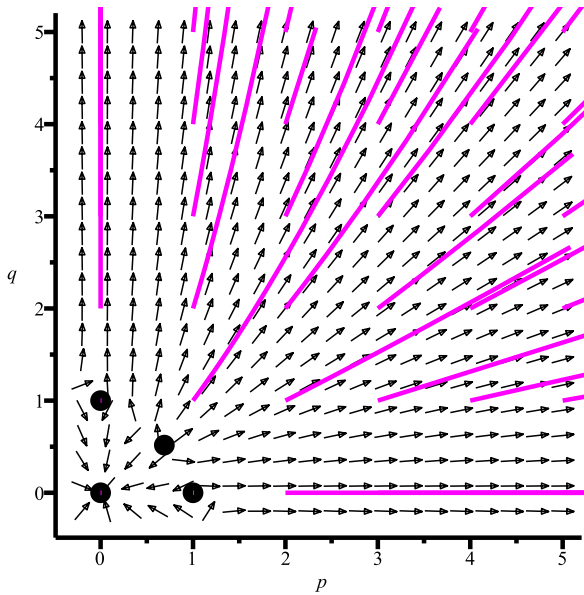
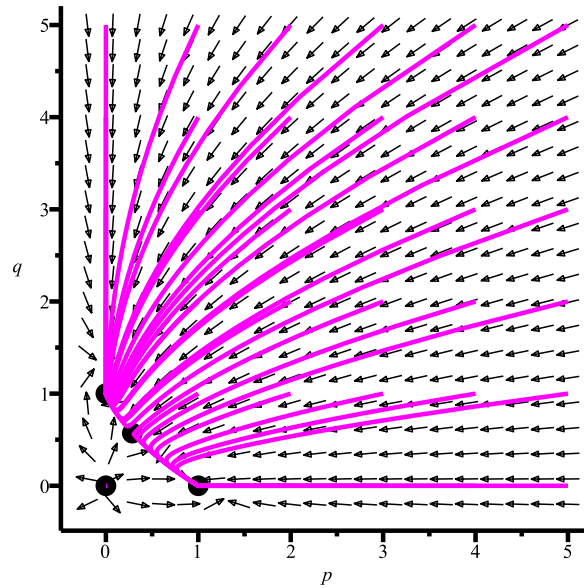**Fig. 1:** $\alpha < 1$, $\beta < 1$, $v_1 < c$ and $v_2 < c$

Fig. 3: $\alpha > 1$, $\beta > 1$, $v_1 > c$ and $v_2 > c$

Fig. 2: $\alpha < 1$, $\beta < 1$, $v_1 < c < v_2$
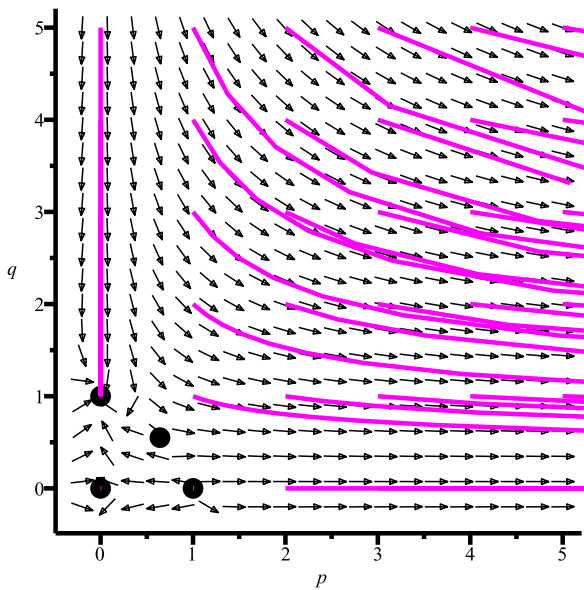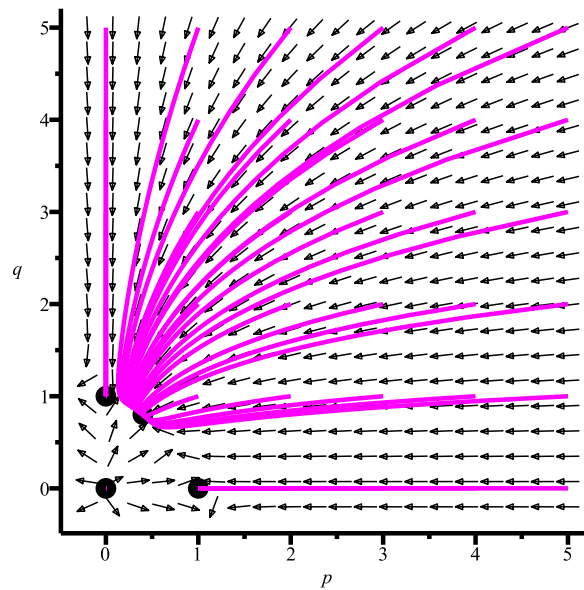

Fig. 4: $\alpha < 1$, $\beta < 1$, $v_1 > c$ and $v_2 > c$

4 Results and Discussion

This research work is targeted at investigating the effects of advection on the dynamics of two competing species. In any competition, the competitors direct their movements towards a target, rather than random movement, hence the need to examine the effects of such targeted movements in a competition model. An advection-driven competition model involving two species is considered. The results show that the equilibrium points are independent of the advection velocities of the species, but not their stability. The stability of each steady state depends on the advection velocities of the competing species and the wave speed. The results of theoretical analysis summarised on Table 1 and the numerical simulations both agree, as can be seen from Figures 1-4 below. Figure 1 indicates that for $v_1 < c$ and $v_2 < c$, E_0 is stable, which implies that competing species go into extinction when they both compete weakly with low advection velocities. Under the same conditions, E_1 and E_2 are unstable as can be seen from table 1. However, E_1 is stable when $\alpha < 1$ and $v_1 < c < v_2$, which physically implies that species p goes into extinction when it competes at advection speed less than that of q. E_1 is also stable when $\alpha > 1$, $v_1 > c$ and $v_2 > c$. This means that species p also dies out under strong competitive pressure from q, in the presence of high advection speeds from both species. A similar scenario occurs in the case of E_2, when species q goes into extinction. For $v_1 < c < v_2$, $\alpha < 1$ and $\beta < 1$, E_0 is a saddle point, E_1 is a stable node or spiral, which shows that species q wins in this case. The result is depicted on Figure 2. Figure 3 on the other hand, indicates the phenomenon of bistability, when both species compete strongly at high advection velocities. The species however coexist when they compete weakly, but at advection speeds higher than the wave speed. This is shown on Figure 4.

In conclusion, we have shown that advection affects the dynamics of competing species. Secondly, conditions for the stability of all the equilibrium points were obtained and the numerical results agree with theoretical analysis. These results show that the targeted movement of species as they compete for food in an ecosystem has effects on the stability of species population as well as implication for ecological resource management. The various stability conditions are indicators of when one or both species go into extinction or coexist and the role of the advection velocity, which is the measure of the rush for food.

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Conflict of Interest

The authors declare that they have no conflict of interest.

References

[1] A.C. Fassoni, L.T. Takahashi, L.J. dos Santos, Basins of attraction of the classic model of competition between two populations, *Ecol. Complex.*, **18**,39-48 (2014). https://doi.org/10.1016/j.ecocom.2013.12.004

[2] G. Barabas, M.J. Michalska-Smith and S. Allesina, The Effect of Intra- and Interspecific Competition Coexistence in Multispecies Communities, *Am. Nat.*, **188**, E1-E12 (2016).

[3] C.C. Gerhard, P. Karewa, M.A. Lewis, J.D. Murray (1996), Competition in a Spatially heterogeneous Environment: Modelling the Risk of Spread of a Genetically Engineered Population, *Theoretical Population Biology*, **49**,1-38 (1996).

[4] M. K. A. Gavina, T, Tahara, K. Tainaka, H. Ito, S. Morita, G. Ichinose, T. Okabe, T. Togashi, T. Nagatani and J. Yoshimura, Multi-Species Coexistence in Lotka-Volterra Competitive Systems with Crowding Effects, *Scientific Report*, **8** (2017).

[5] J.M. Cushing, S. Levarge, N. Chitnis and S.M Henson, Some Discrete Competition Models and the Competitive Exclusion Principle, *J. Differ. Equ. Appl.*, **10**, 1139-1151 (2004).

[6] A. Okubo, P.K. Maini, M.H. Williamson and J.D. Murray, On the Spatial Spread of the Grey Squirrels in Britain, *Proc. R. Soc. B*, **238**, 113-125 (1989).

[7] A. B. Ryabov and B. Blasius, Population Growth and Persistence in a Heterogeneous Environment: the Role of Diffusion and Advection, *Math. Model. Nat. Phenom.*, **3**, 42-86 (2008). http://dx.doi.org/10.1051/mmnp:2008064

[8] K-Y. Lam and W-M. Ni, Advection-Mediated Competition in General Environments, *J. Differential Equations*, **257**, 3466-3500 (2014).

[9] X-Q. Zhao and P. Zhou (2016), On a Lotka-Volterra competition model: the Effects of Advection and Spatial Variation, Calc. Var. Partial Differ. Equ., **55**, 73 (2016). Doi: 10.1007/s00526-016-1021-8

[10] Benlong Xu and Hongyan Jiang, Dynamics of Lotka-Volterra diffusion-advection competition system with heterogeneity vs homogeneity. J. Nonlinear Sci. Appl., **10**, 6132 - 6140 (2017). doi:10.22436/jnsa.010.11.46

[11] I. Averill, K-Y. Lam and Y. Lou, *The Role of Advection in a Two-Species Competition Model: A Bifurcation Approach*, Memoirs of the American Mathematical Society, **245** (1161) (2017).

[12] H.W. Mckenzie, M.A. Lewis and E.H. Merrill,First Passage Time Analysis of Animal Movement and Insights into the Function Response, *Bull. Math. Biol.*, **71**, 107-129 (2009).

[13] P.E. Smouse, S. Forcardi, P.R. Moocroft, J.G. Kie, J.D. Forester and J.M. Morales, Stochastic Modelling of Animal Movement, *Phil. Trans. R. Soc. B*, **365**, 2201-2211 (2010).

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