# The Perturbation Effect in wildlife species

**JC Prentice[1*], G Marion[2], RS Davidson[1], PCL White[3], MR Hutchings[1]**
1) Disease Systems, SRUC, Edinburgh, 2) Process & Systems Modelling, BioSS, Edinburgh, 3) Environment Department, University of York, York
* Email: jamie.prentice@sruc.ac.uk

## Introduction

**Population reduction** is often used as a control strategy when managing infectious diseases in wildlife populations in order to reduce host density below a critical threshold. However, it can disrupt existing social and demographic structures[1] leading to changes in observed host behaviour[2,3], which may result in enhanced disease transmission[4,5]. This may lead to the counterintuitive **perturbation effect**, whereby disease levels increase, or disease is stabilised where it would otherwise be unstable.

Several mechanisms have been suggested for the perturbation effect, including a change in behaviour, the **vacuum effect**, and territorial disruption, which may lead to increased movement, contact rates, and ranging behaviour[6,7]. Here we characterise the fundamental properties of disease systems for which such effects undermine the disease control benefits of population reduction.

Our interest lies in the effect that changing the population size has on the rate that animals become infective; we therefore design appropriate disease models, and perform sensitivity analysis, looking for situations when a decrease in the population gives an increase to the rate of change of infective animals.

European badger (*Meles meles*)

Wild boar (*Sus scrofa*)

## Methods

We first demonstrate the potential for the perturbation effect, by explicitly enhancing disease transmission during population reduction, using a generic parameter *k* to represent all possible mechanisms that might lead to an increase.

$$\dot{S} = N(1 - N/c) - (d + p)S - (\beta + kp)SI$$
$$\dot{I} = -(d + e + p)I + (\beta + kp)SI$$

Deterministic non-spatial *SI* model. *S*(*t*) is the number of susceptibles, *I*(*t*) is the number of infectives, *N* is the total population size. *r* is the intrinsic reproductive rate, *c* is the site carrying capacity, *d* and *e* are the natural and disease induced mortality rates, *β* is the horizontal transmission rate, *p* is the population reduction rate, and *k* represents disease enhancement.

Next we demonstrate how the perturbation effect can emerge naturally from basic disease models, and we look for mechanics which can allow for the perturbation effect to be *a direct consequence of the disease dynamics*.

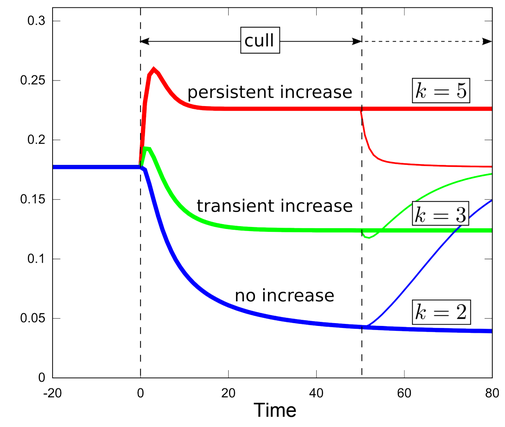
Structure of a population is important to the stability of a disease. Animal populations are not homogeneous, and stochasticity has a strong influence on the stability of small populations, we therefore design equivalent event based stochastic disease models (see the table below for events and corresponding rates), and use simulations to see if the effect predicted by the deterministic analysis occurs as expected. We look at spatial organisation of animals, particularly those who live in discrete groups, in order to find how movement between groups can aid in the spread of disease.

| **Event** | **Rate** | $\delta S_i$ | $\delta I_i$ | $\delta S_j$ | $\delta I_j$ |
|---|---|---|---|---|---|
| Birth of $S_i$ | $rN_i(1 - N_i/c)\delta t$ | $+1$ | $0$ | $0$ | $0$ |
| Death of $S_i$ | $dS_i\delta t$ | $-1$ | $0$ | $0$ | $0$ |
| Death of $I_i$ | $(d + e)I_i\delta t$ | $0$ | $-1$ | $0$ | $0$ |
| Infection of $S_i$ | $(\beta_w I_i + \beta_b \sum_j I_j)S_i\delta t$ | $-1$ | $+1$ | $0$ | $0$ |
| Movement of $S_i$ to site $j$ | $mS_i f(N_j)\delta t$ | $-1$ | $0$ | $+1$ | $0$ |
| Movement of $I_i$ to site $j$ | $mI_i f(N_j)\delta t$ | $0$ | $-1$ | $0$ | $+1$ |

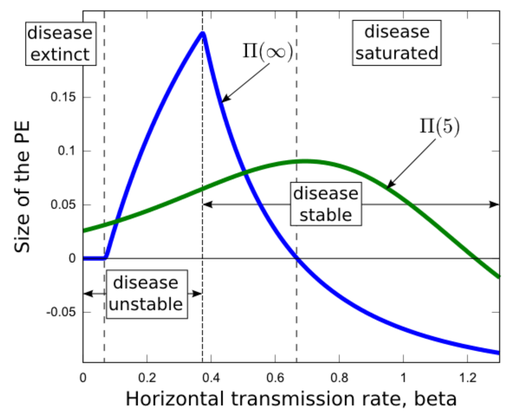
Event rates at time $t$ in the stochastic spatial *SI* model, and corresponding change in the state space. Sites are indexed by $i$, neighbouring sites by $j$. $S_i$ and $I_i$ are the number of susceptible and infective animals in site $i$ respectively, while $N_i$ is the total population size in site $i$. $r$ is the intrinsic reproductive rate, $c$ is the site carrying capacity, $d$ and $e$ are the natural and disease induced mortality rates, $\beta_w$ and $\beta_b$ are the within and between-group horizontal transmission coefficients, $m$ is the weighted dispersal rate between groups, and $f(N)$ is the density dependence function for dispersal that depends on the neighbour's population size.

## Results

In the non-spatial model, there is a threshold of enhanced transmission, $k$, above which the perturbation effect can be observed, whereby the number of infected individuals increases during the period when population reduction is applied. However, sufficient population reduction *will* reduce numbers of infectives in the area it is applied.

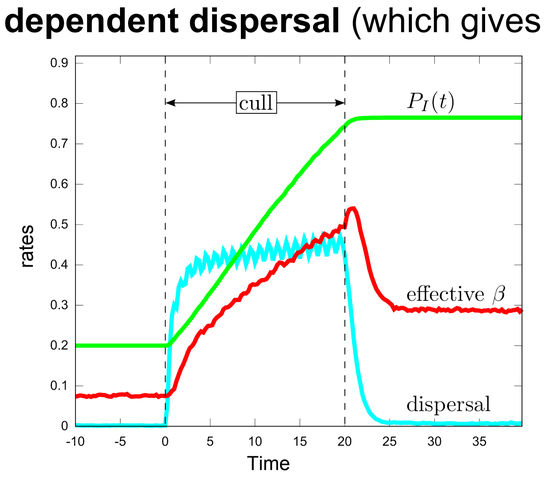



Emergent disease, for varying levels of disease enhancement *k*. While population reduces disease for low *k*, for moderate *k*, a transient disease increase is observed, which persists for large k.

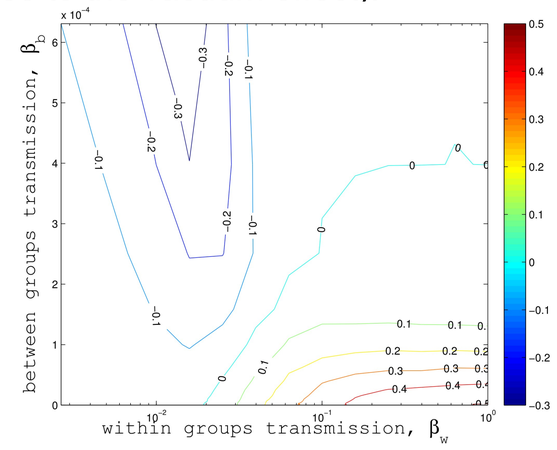



Sensitivity analysis of horizontal transmission, $\beta$, for both endemic and emergent disease. For endemic disease, the maximum PE occurs when $\beta$ is low enough that it causes the disease to become unstable, however this may maximise emergent disease spread.

Disease systems with **low levels of disease** are more sensitive to the impacts of enhanced transmission. For endemic disease systems, the perturbation effect is greater with increased natural and disease induced mortality rates and reduced by horizontal disease transmission (due to reduced levels of endemic disease). The trend is reversed in emergeing disease, as higher mortality removes cases caused by enhanced transmission, however the perturbation effect is maximised by intermediate disease transmission, as higher rates can cause the disease to reach equilibrium sooner, reducing the duration of the pertubation effect. This effect is mirrored in emergent disease in the spatial model, where the perturbation effect is driven by **density dependent dispersal** (which gives rise to the vacuum effect).




Emergent disease, showing how dispersal and effective disease transmission increase during population reduction, leading to an increase in the proportion of infected groups $P_I(t)$.




Sensitivity analysis of within and between groups transmission, $\beta_w$ and $\beta_b$. The maximum occurs for high $\beta_w$, but drops off rapidly with $\beta_b$ due to **saturation** of disease leaving no further groups for the disease to reach.

## Conclusions

Our results suggest that the impact of population reduction on social and demographic structures is likely to undermine disease control in many systems, and in severe cases leads to the perturbation effect. Social and demographic mechanisms that enhance transmission following population reduction should therefore be routinely considered when designing control programmes.

## Acknowledgements

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