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## Pulsed perturbations in population dynamics

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# Pulsed perturbations in population dynamics

MOMI 2023

Ludovic Mailleret

M2P2, UMR ISA, INRAE, CNRS, Université Côte d'Azur  
Macbes (ex Biocore), Inria d'Université Côte d'Azur

*with:* S. Nundloll, N. Bajeux, B. Ghosh, F. Aubree,  
V. Calcagno, F. Hamelin, V. Lemesle & F. Grogard

INRAE



UNIVERSITÉ  
CÔTE D'AZUR



Inria

# Institut Sophia Agrobiotech

UMR INRAE, CNRS, Université Côte d'Azur



200 pp. working on plant health issues

- interactions b. plants, pests/symbionts
- interactions b. pests and enemies
- population dynamics in time and space
- development of ecological pest management programs

## Methods

- comparative and functional genomics
- population and community ecology
- mathematical and computer modelling



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# Population dynamics modelling

Understand how/why population sizes change with time and space

- predict plant pest and disease dynamics and evolution
- design control actions: external perturbations of population sizes

Main applications

- efficient and sustainable use of plant resistance
- optimization of biological control programs



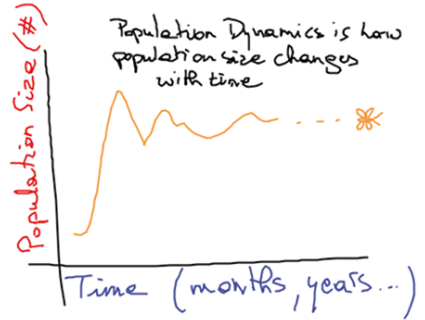
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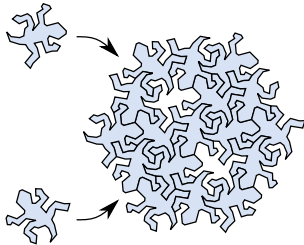
- efficient and sustainable use of plant resistance
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# External perturbations of population size

Two main types of perturbations

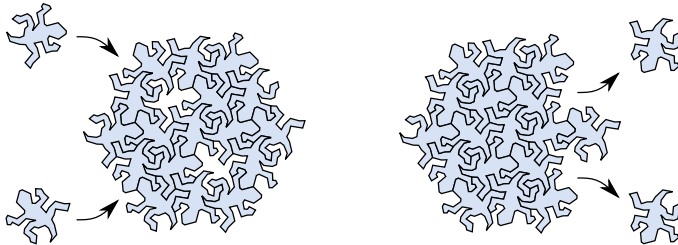
- increase population size (introductions of individuals)  
→ immigration, reintroduction biology, biological control
- decrease population size (removal of a fraction of the population)  
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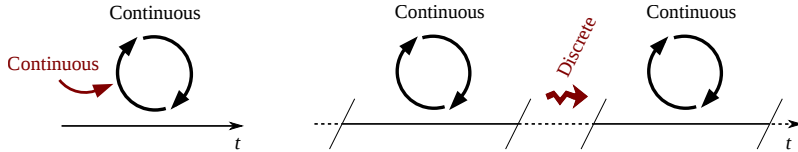




# Continuous or pulsed perturbations

Both types of perturbation may occur:

- continuously over time
- as pulses at discrete time instants

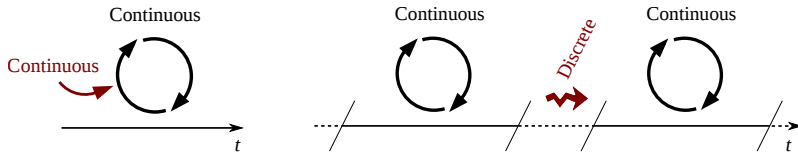


- intensity of perturbations significantly influences population dynamics
- role of the temporal pattern of perturbations has been much less studied

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# Outline

Framework to study the influence of pulsed perturbations on population dynamics

- for a given perturbation effort
- role of temporal pattern (magnitude / frequency)

Investigate the two main perturbation types

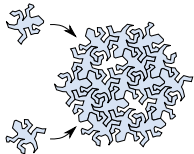
- pulsed introductions
- pulsed removals
- if time: pulsed introductions & removals

# Pulsed introductions

with special emphasis on  
augmentation biological control & adaptation under pulsed migration



# Framework for studying pulsed introductions



Compare different patterns of introductions for a given introduction effort  $\mu$

Continuous introductions<sup>1</sup>

$$\left\{ \begin{array}{l} \dot{x} = f(x) + \mu. \end{array} \right.$$

1: Kermack, McKendrik (1932), Kostitzin (1937)

Pulsed introductions<sup>2</sup>

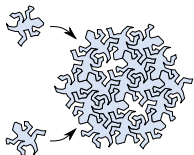
$$\left\{ \begin{array}{l} \dot{x} = f(x), \\ x(kT^+) = x(kT) + \mu T. \end{array} \right.$$

2: Mailleret, Grogard (2006, 2009), Mailleret, Lemesle (2009)

Both models account for the same mean rate of introduction

- comparison of different introduction patterns through introduction period
- pulsed model reduces to continuous one as  $T \rightarrow 0$

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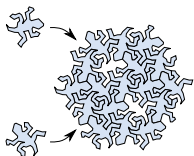
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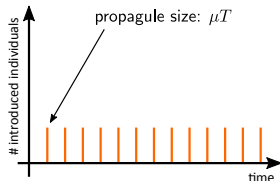
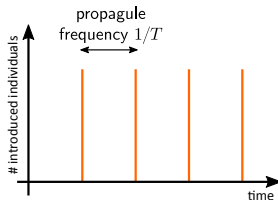
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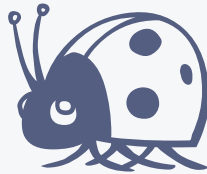
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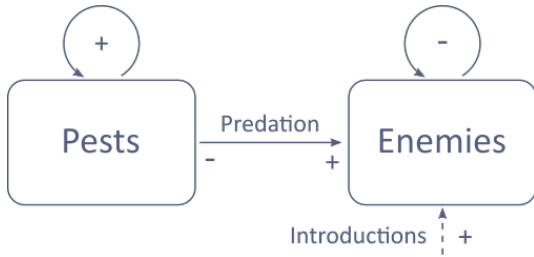
# Augmentation biological control



Created by Pencil from the Noun Project



# Augmentation biological control



Fight pests through regular introductions of natural enemies

- parasitoids or predators
- supplied by biofabrics

- General predator-prey model

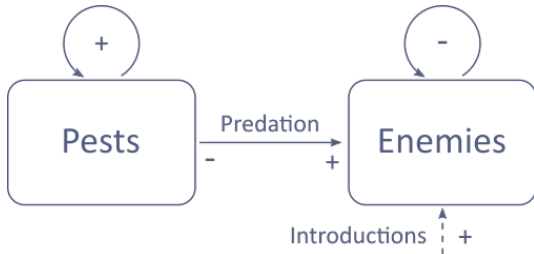
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$$\{ y(kT^+) = y(kT) + \mu T, \forall n \in \mathbb{N} \}$$

How different introduction strategies affect pest control ?

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Null model : no density dependence in BCA population

Pest control is achieved provided<sup>a</sup> :

$$\mu > S = \sup_{x \geq 0} \frac{mf(x)}{g(x)}$$

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<sup>a</sup>Mailleret, Grogard (2009)

- pest control always possible
- threshold intro. rate increases w.  $m$  et  $f(\cdot)$ , decreases w.  $g(\cdot)$
- introduction strategy ( $T$ ) does not impact stability

What about transient dynamics ?

- time for pest to fall below some damage threshold  $\bar{x}$

$$\Pi(T, x_0, t_0) = \int_{t_0}^{t_f} (\tau - t_0) d\tau, \quad x(t_f) \triangleq \bar{x}$$

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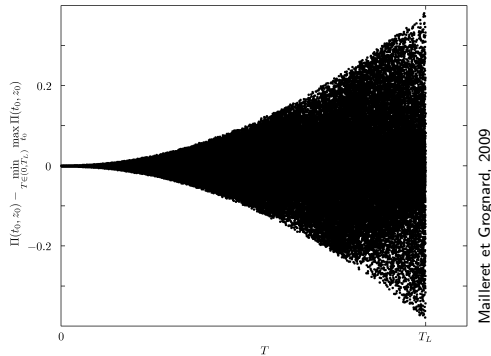
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- $\mathbb{E}_{t_0 \in (0, T)} [\Pi(t_0, x_0)] = \min_T \left( \max_{t_0} \Pi(t_0, x_0) \right) (= \text{constant})$
- $\text{Var}_{t_0 \in (0, T)} [\Pi(t_0, x_0)]$  increases with  $T$

- mean transients not influenced by intro. strategy
- variance increases with larger/less frequent introductions

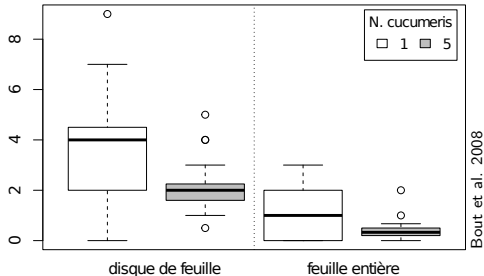


anomaly of  $\Pi(t_0)$  w.r.t  $T$ ,  $t_0 \in (0, T)$

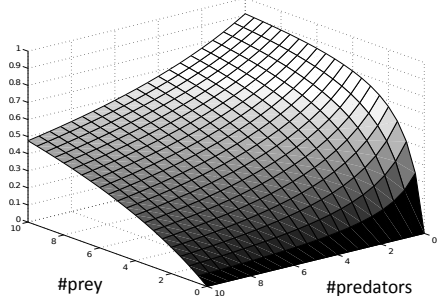
# Augmentation biological control (2)

## Negative density dependence in BCA population

Prédation *per capita* sur 24h de L1 de *F. occidentalis* par *N. cucumeris*



Réponse fonctionnelle de prédateurs qui interfèrent



*Per capita* predation decreases with BCA population size

$$\begin{cases} \dot{x} = f(x) - g(x, y)y \\ \dot{y} = h(x, y)y - m(\cdot)y \end{cases}$$

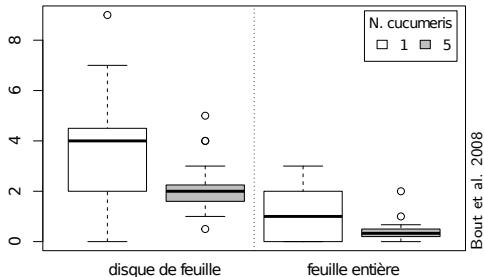
$$g(x, y) = g \left( \frac{x}{\theta y + (1 - \theta)} \right)$$

$g(\cdot) \nearrow$ ;  $\theta \in (0, 1]$ :  $-DD$  index

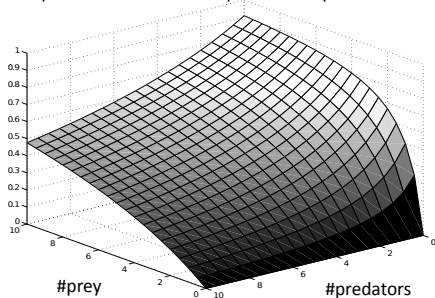
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## Augmentation biological control (2)

### Negative density dependence in BCA population

Pest control is achieved iff<sup>a</sup>:

$$f'(0) < \frac{g'(0)}{\theta} \quad \text{and} \quad \mu > \frac{1 - \theta (1 - e^{-m \frac{\theta f'(0)}{g'(0)} T}) (1 - e^{-mT})}{(e^{-m \frac{\theta f'(0)}{g'(0)} T} - e^{-mT})}$$

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<sup>a</sup>Nundloll et al. 2010

A biological and a strategy condition

- negative DD shall not be too strong
- threshold introduction rate increases with  $T$  ( $\rightarrow +\infty$ )
- too large  $T$  makes pest suppression impossible
- transients: the smaller the  $T$ , the faster pests are suppressed

When DD comes into play, introduction pattern has major impacts

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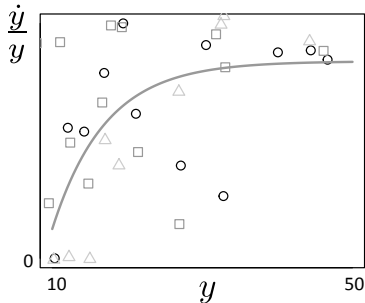
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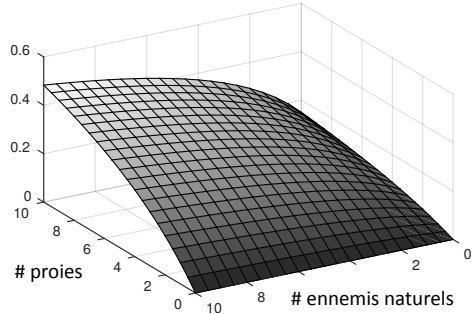
# Augmentation biological control (3)

## Positive density dependance in BCA population

Taux de croissance de trichogrammes



Réponse fonctionnelle avec DD positive



*Per capita* predation/natality increases with BCA population size

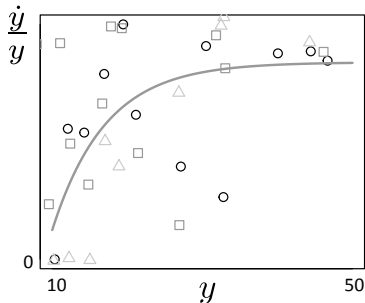
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Component Allee effects :  
 $q_f(\cdot), q_r(\cdot)$  increasing

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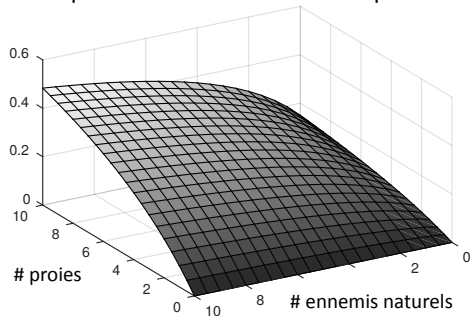
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data: Elodie Vercken

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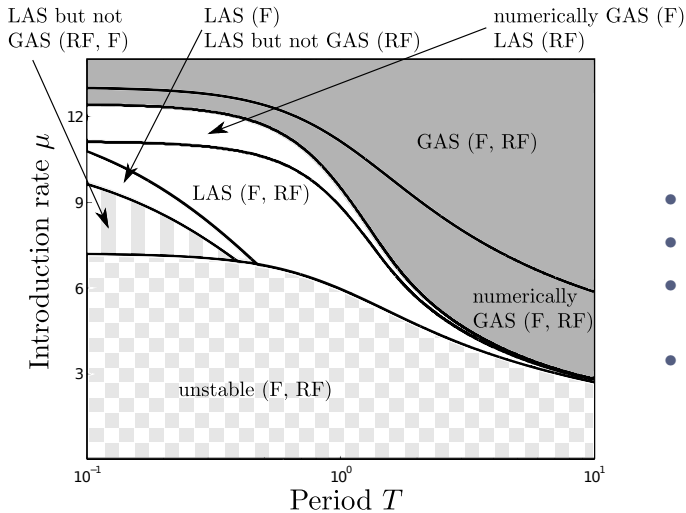
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## Augmentation biological control (3)

### Positive density dependence in BCA population



Bajeux et al. 2017

- reverted results compared to negative DD
- pest control facilitated by  $T$  large
- transients: the larger the  $T$ , the faster pest suppression
- what positive DD influences matters

## Pulsed migration and adaptation

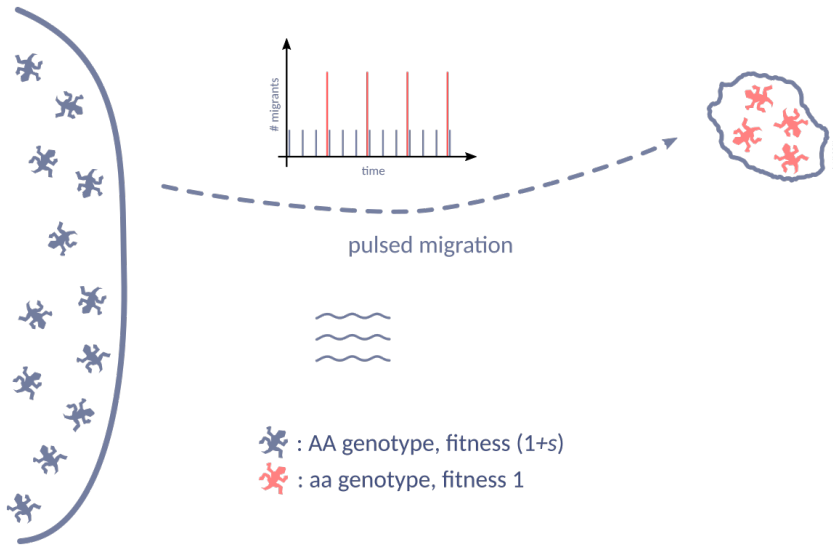


# Pulsed migration from mainland to island<sup>1</sup>



<sup>1</sup>Aubree et al. 2023

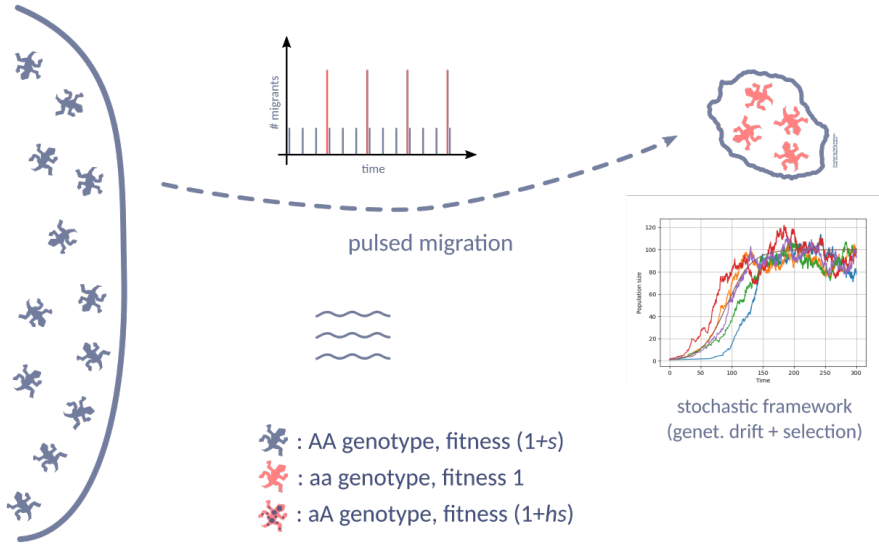
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## Pulsed migration from mainland to island (2)

In the long run AA genotype will overtake the island population

- is it faster (or not) with pulsed migration ?

AA fixation is (initially) faster with pulsed migration when:

$$s < \frac{-(K+1)^2}{2K^2(1+h(K-1))} < 0$$

In a nutshell:

- sufficiently deleterious alleles favored by migr. pulsedness
- neutral and beneficial alleles disfavored

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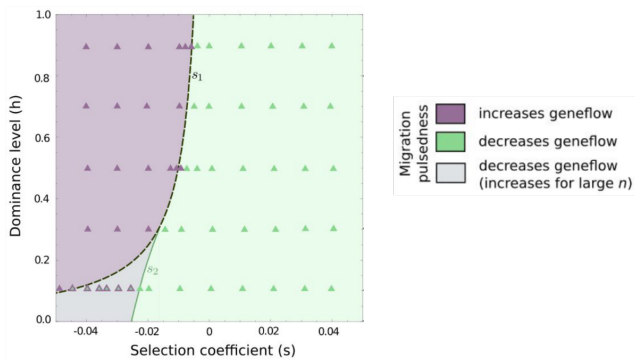
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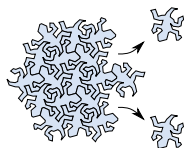


## Pulsed removals

with special emphasis on harvesting and vaccination



# Framework for studying pulsed removals (1)



Compare different patterns of removals for a given taking effort  $E$

Continuous removals<sup>1</sup>

$$\left\{ \begin{array}{l} \dot{x} = f(x) - Ex. \end{array} \right.$$

1: Schaefer (1954)

Pulsed removals (first attempt)<sup>2</sup>

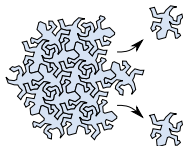
$$\left\{ \begin{array}{l} \dot{x} = f(x), \\ x(kT^+) = x(kT) - \tilde{E}x. \end{array} \right.$$

2: from Lu *et al.* (2003)

- Mean taking effort in the continuous model

$$\langle E_c \rangle = \frac{\dot{x}_E}{x} = \frac{Ex}{x} = E$$

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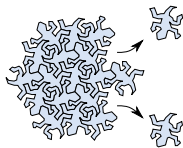
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## Framework for studying pulsed removals (2)



Compare different patterns of removals for a given taking effort  $E$

- Mean taking effort in the pulsed model:

$$\langle E_p \rangle = \frac{1}{T} \int_{kT}^{(k+1)T} \frac{\dot{x}_E}{x} d\tau = \frac{1}{T} \int_{kT}^{kT^+} \frac{\dot{x}_E}{x} d\tau = \frac{1}{T} \int_{x(kT)}^{x(kT^+)} \frac{dx_E}{x},$$

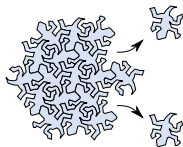
so that:

$$\langle E_p \rangle = \frac{1}{T} \ln \left( \frac{1}{1 - \tilde{E}} \right) \neq E$$

In Lu *et al.* (2003) framework, the mean taking effort varies with  $T$



## Framework for studying pulsed removals (3)



Desired property: mean taking effort constant to allow comparisons

Solve:

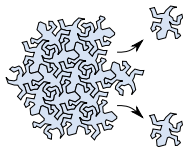
$$\langle E_p \rangle = E = \frac{1}{T} \ln \left( \frac{1}{1 - \tilde{E}} \right) \Rightarrow \tilde{E} = 1 - e^{-ET}$$

$\Rightarrow$  more frequent removals shall be smaller...

A well-posed pulsed taking model reads:

$$\begin{cases} \dot{x} = f(x), \\ x(kT^+) = e^{-ET} x(kT). \end{cases}$$

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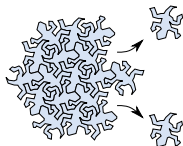
$$\langle E_p \rangle = E = \frac{1}{T} \ln \left( \frac{1}{1 - \tilde{E}} \right) \Rightarrow \tilde{E} = 1 - e^{-ET}$$

$\Rightarrow$  more frequent removals shall be smaller...

A well-posed pulsed taking model reads:

$$\begin{cases} \dot{x} = f(x), \\ x(kT^+) = e^{-ET} x(kT). \end{cases}$$

## Framework for studying pulsed removals (3)



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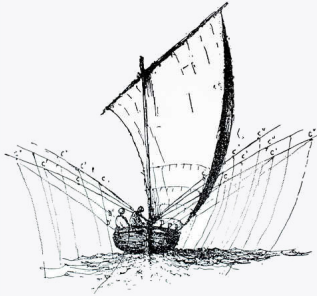
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## Pulsed harvests



## Pulsed harvesting

Assuming logistic growth, we get the 'pulsed Schaefer model'

$$\begin{cases} \dot{x} = rx \left(1 - \frac{x}{K}\right), \\ x(kT^+) = e^{-ET} x(kT). \end{cases}$$

Properties:

- periodic solution  $x_p^*(t)$ , GAS if  $E < r$
- $x^* = 0$  is GAS if  $E > r$ .

(i.e. similar to continuous model)

## Pulsed harvesting

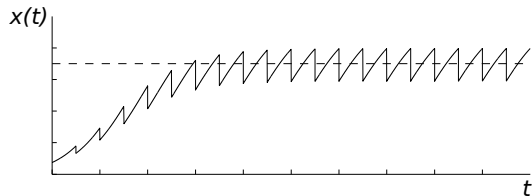
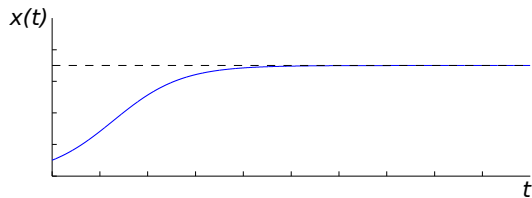
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## Pulsed harvesting (2)

Compute the mean yield over a time period  $T$ :

$$Y_p(T) = \frac{(1 - e^{-ET})(1 - e^{(E-r)T})}{(1 - e^{-rT})} \frac{K}{T}$$

This can be compared to continuous harvesting yield:

$$Y_c = KE \left(1 - \frac{E}{r}\right) = \lim_{T \rightarrow 0} Y_p(T)$$

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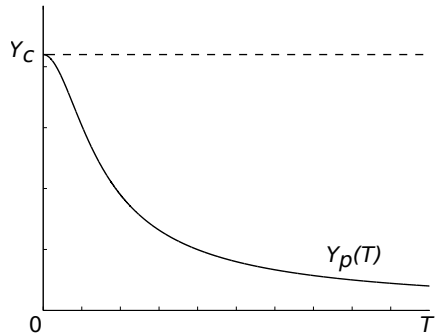
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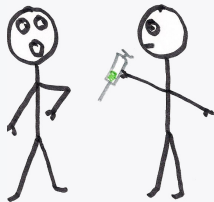
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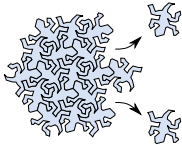




## Pulsed vaccination



## Pulsed vaccination (1)



Vaccination of individuals is also a form of removal of  $S$  individuals

Continuous vaccination at rate  $\Psi$  in the susceptible population<sup>2</sup>

$$\begin{cases} \dot{S} = b - \mu S - \beta SI - \Psi S \\ \dot{I} = \beta SI - \mu I - \alpha I \end{cases}$$

In such a model

$$\mathcal{R}_{\text{eff}} = \frac{\beta S_c^*}{\alpha + \mu} = \frac{\beta}{(\alpha + \mu)} \frac{b}{(\Psi + \mu)}$$

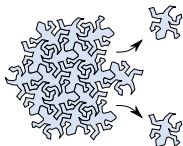
Vaccination prevents disease spread when

$$\Psi > \frac{b\beta}{\alpha + \mu} - \mu$$

---

<sup>2</sup>model adapted from Onyango & Müller, 2014

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## Pulsed vaccination (2)

A comparable pulsed vaccination model reads<sup>3</sup>

$$\begin{cases} \dot{S} = b - \mu S - \beta SI \\ \dot{I} = \beta SI - \mu I - \alpha I \\ S(kT^+) = e^{-\Psi T} S(kT) \end{cases}$$

$T$ -periodic infection free solution  $S^*(t, \Psi)$ , so that:

$$\mathcal{R}_{\text{eff}} = \frac{\beta}{(\alpha + \mu)} \frac{1}{T} \int_0^T S^*(\tau, \Psi) d\tau$$

---

<sup>3</sup>pulsed vaccination has originally been introduced by Agur *et al.*, 1993. Advocated as a more efficient vaccination strategy, a statement which is still debated today.

## Pulsed vaccination (3)

Pulsed vaccination prevents disease spread when:

$$\frac{1}{T} \int_0^T S^*(\tau, \Psi) d\tau < \frac{(\alpha + \mu)}{\beta}$$

unfortunately, isolating  $\Psi$  is difficult, and ultimately uninformative

Yet, numerics show vaccination may fail for large

## Pulsed vaccination (3)

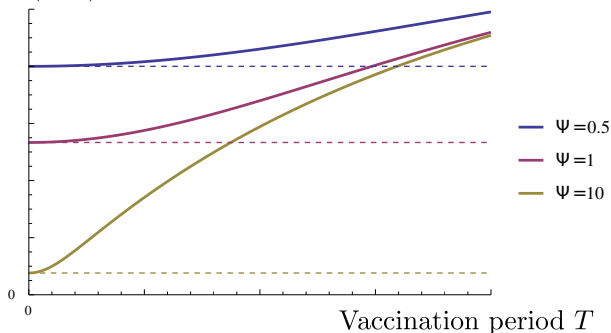
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$T$

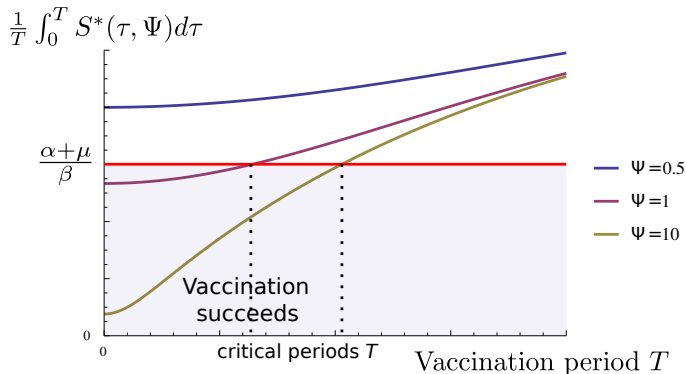
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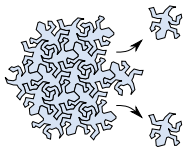
## Mixing: pulsed migration



Created by Parakei Digital Studio from the Noun Project

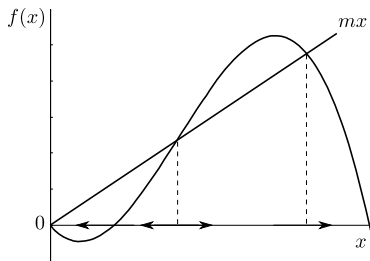


## Pulsed migration and the Allee effect (1)



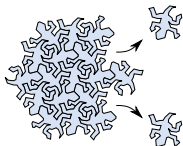
Emigration from a habitat is also a form of removal

- emigration is harmful to populations
- even more in species subjected to Allee effects



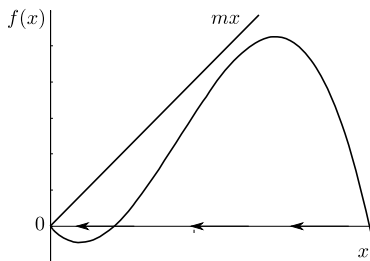
Pulsed emigration more harmful than continuous emigration:

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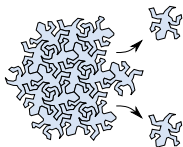
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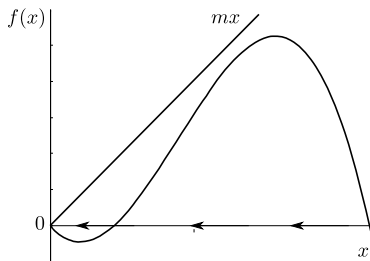
$$\begin{cases} \dot{x} = rx \left( \frac{x}{K_a} - 1 \right) \left( 1 - \frac{x}{K} \right), \\ x(kT^+) = e^{-mT} x(kT). \end{cases}$$

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Emigration from a habitat is also a form of removal

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Pulsed emigration more harmful than continuous emigration:<sup>4</sup>

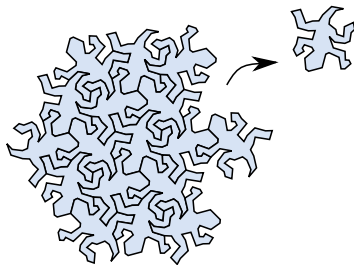
- for any  $m > 0$ , large  $T$  will always lead to pop. extinction

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<sup>4</sup>Mailleret and Lemesle, 2009

## Pulsed migration and the Allee effect (2)

In nature, migration is usually a bi-directional process



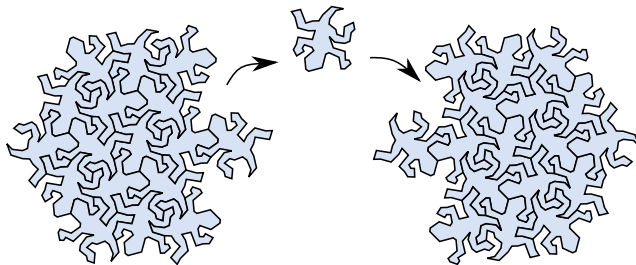
emigration & immigration

- emigration harmful, pulsed even more than continuous
- immigration beneficial, pulsed even more than continuous

How do pulsed migration, migration period and Allee effects interact at the metapopulation scale?

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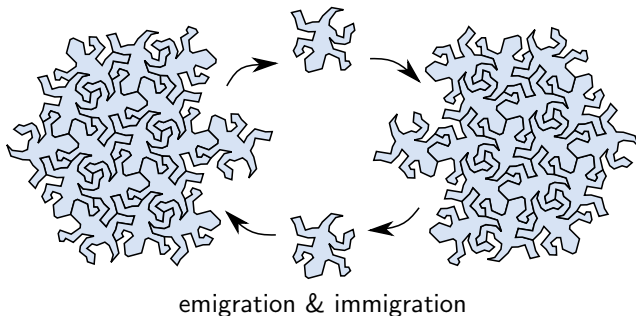
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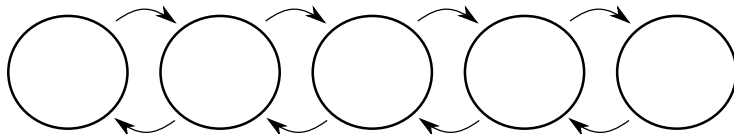
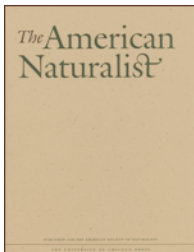


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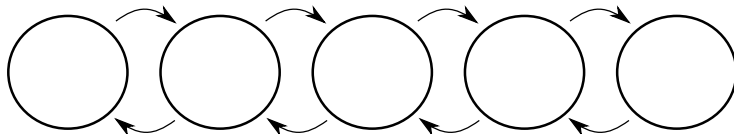
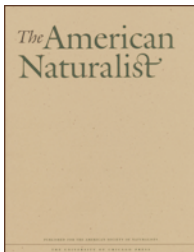
Keitt *et al.* (2001): populations 'pinned' at intermediate migration



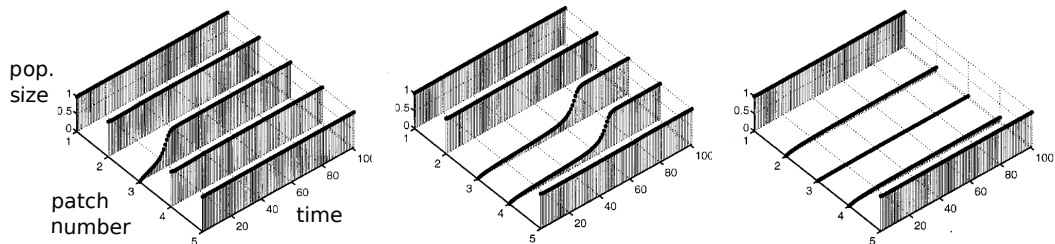
Stepping stone, continuous migration

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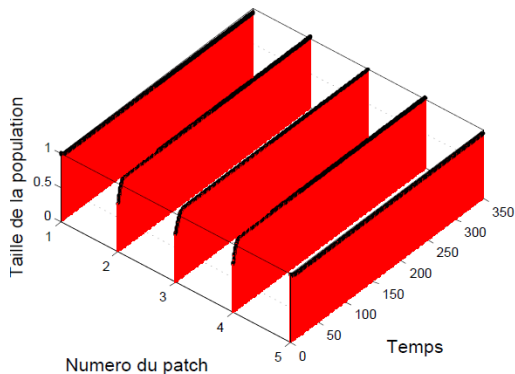
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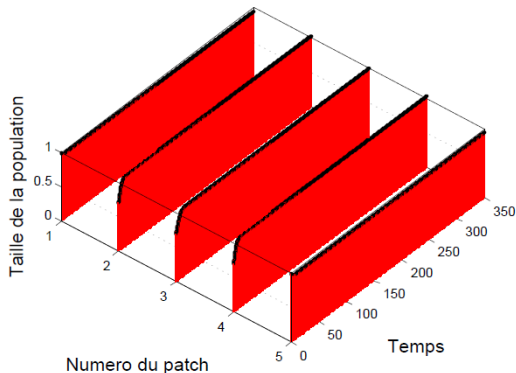


## Pulsed migration and the Allee effect (4)

The effects of pulsed migration, and migration period  $T$



**pulsed** migration

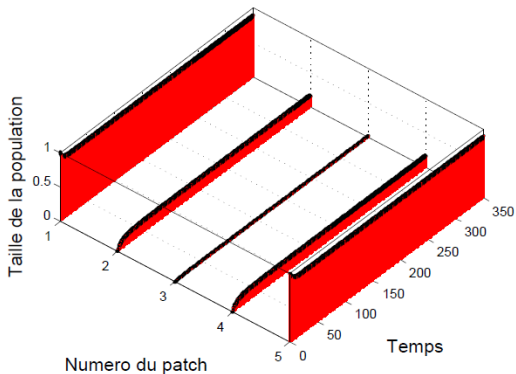


**continuous** migration

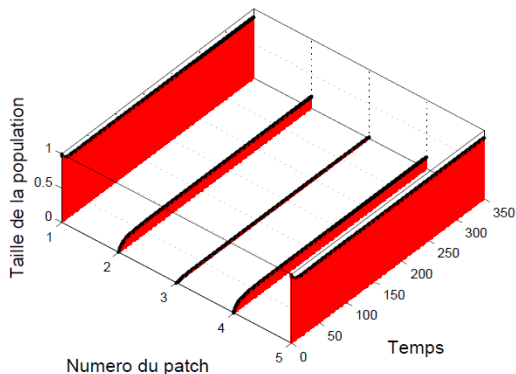
same effects as continuous migration: population stable

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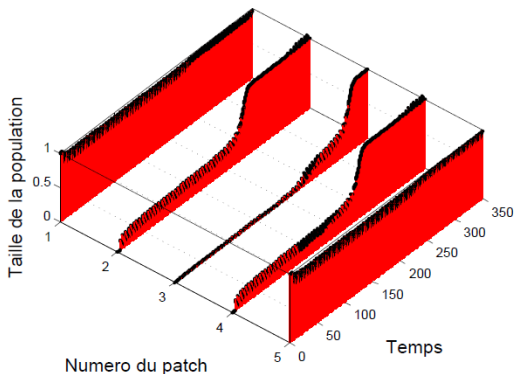


**continuous** migration

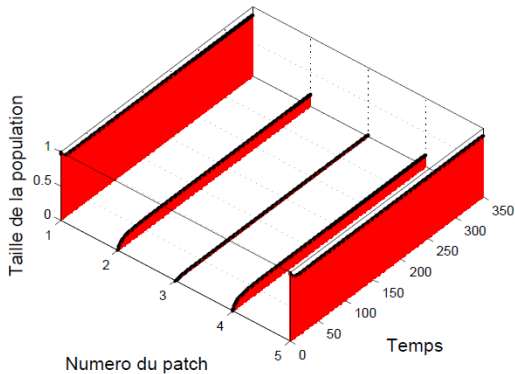
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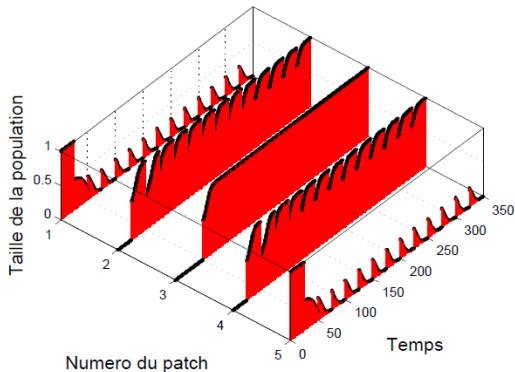


**continuous** migration

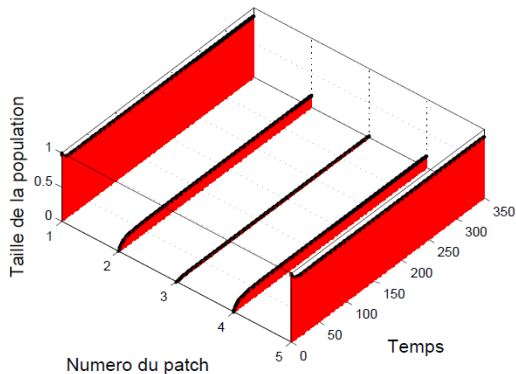
emerging patterns for larger periods  $T$ : invasion succeeds

## Pulsed migration and the Allee effect (4)

The effects of pulsed migration, and migration period  $T$



**pulsed** migration

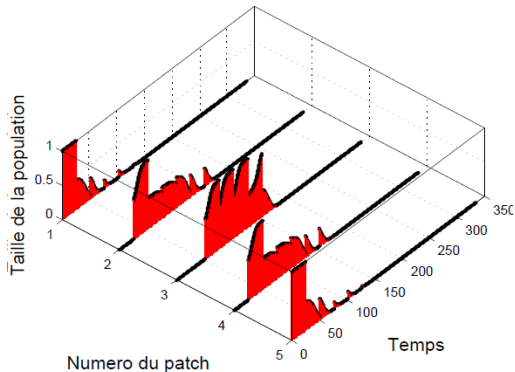


**continuous** migration

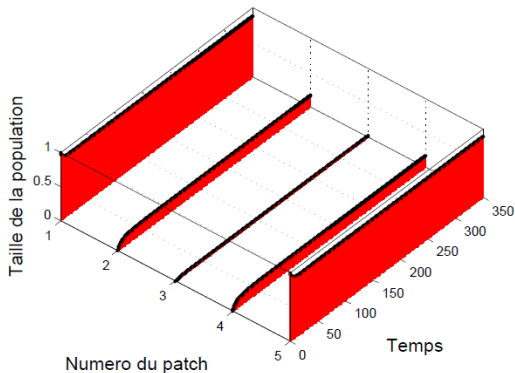
emerging patterns for larger periods  $T$ : pop-up effect

## Pulsed migration and the Allee effect (4)

The effects of pulsed migration, and migration period  $T$



**pulsed** migration



**continuous** migration

emerging patterns for larger periods  $T$ : global extinction

# Conclusion



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## Take home messages

- Many populations are perturbed by pulsed introductions or/and removals, but this is rarely taken into account
- Temporal pattern of occurrence of perturbations may have different impacts on population dynamics:
  - none (or almost none)
  - quantitative effects
  - qualitative effects, up to the emergence of new dynamical patterns
- General conclusions: not restricted to population dynamics *per se* (e.g. therapies against diseases)

Thank You !



Do you have any questions?



# Pulsed migration examples

Behavior



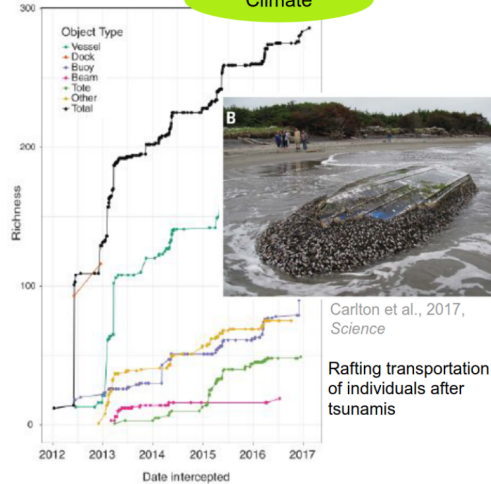
Ballooning dispersal  
© Barnett

Human activities



Ballast waters © W.Carter

Climate



## Pulsed vaccination revisited (1)

(F. Grognard incognito)



Some disagree on the pulsed vaccination framework

↪ Comparing vaccinations on the basis of  $\Psi$  is unfair

Only the **number of vaccines delivered** over  $T$  can be compared

$$\Psi \int_0^T S_c^* d\tau = \frac{\Psi b T}{(\Psi + \mu)}$$

Pulsed vaccinations should verify:

$$S(kT^+) = S(kT) - \frac{\Psi b T}{(\Psi + \mu)}$$

With

$$\mathcal{R}_0 = \frac{\beta}{(\alpha + \mu)} \frac{1}{T} \int_0^T S^*(\tau, \Psi) d\tau$$

## Pulsed vaccination revisited (2)



Some disagree on the pulsed vaccination framework  
↔ Comparing vaccinations on the basis of  $\Psi$  is unfair

Further computations show that

$$\frac{1}{T} \int_0^T S^*(\tau, \Psi) d\tau = \frac{b}{\Psi + \mu}$$

so that, vaccination prevents disease spread when

$$\Psi > \frac{b\beta}{\alpha + \mu} - \mu$$

condition independent on  $T$ , coincides with cont. vaccination.

Only nonlinear incidence rates<sup>5</sup>, or density dependence, would discriminate between continuous and pulsed vaccination.

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<sup>5</sup>e.g. Liu *et al.* (1986)