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# A sex- and stage-structured model for pest control using the sterile insect technique



C. Kounoudji, S. Touzeau<sup>1,2</sup>, F. Grogard<sup>2</sup>, L. van Oudenhove<sup>1</sup>, L. Mailleret<sup>1,2\*</sup>

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# Fruit flies

- widespread polyphagous dipteran insects that lay their eggs in fruits
  - *Ceratitis capitata* : citrus, stone fruits...
  - *Drosophila suzukii* : berries, cherries...
- after hatching, maggots develop inside fruits, entailing massive damage
  - make them unfit for consumption
  - may cause early fruit drop
  - create entry points for diseases



# Fruit flies control

- control of fruit flies has long relied on chemicals
  - sustainability and health issues
  - development of resistant flies
  - more stringent state regulations (EU)



- alternative eco-friendly control means include
  - crop sanitation, mass trapping
  - biological control through natural enemies
  - taking advantage of sexual mode of reproduction through the sterile insect technique



# Sterile Insect Technique (SIT)

- flood agricultural plots with factory produced sterilized males
  - prevent matings between *wild males* and *wild females*



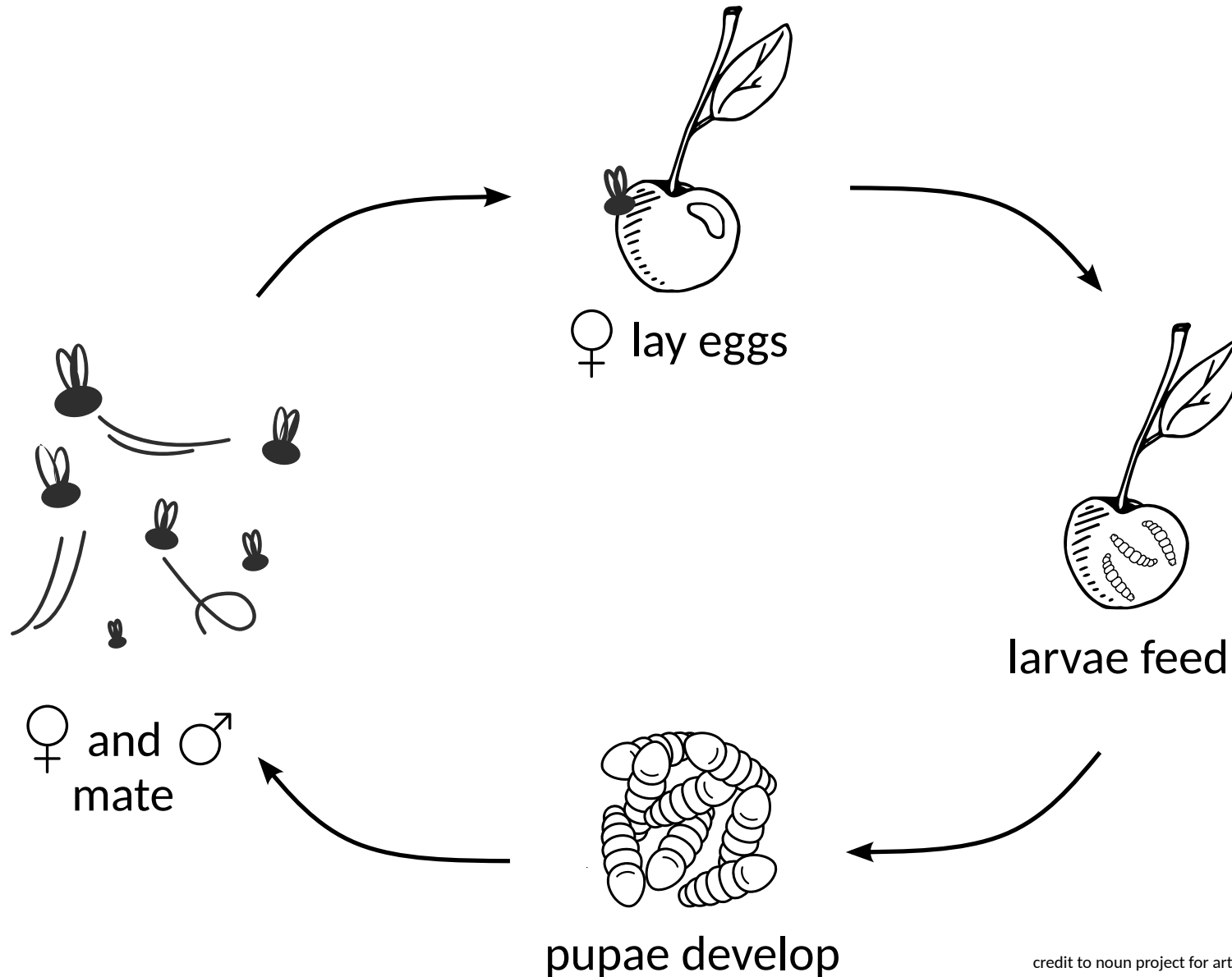
Where is  
Waldo?

SIT is like a football game with so many people on the ground  
you simply cannot find your teammates <sup>1</sup>

# Outline

- SIT model in an agricultural context relevant to fruit flies
- access to reliable estimates of crop damage caused by the larvae
- analyze influence of sterile male introductions on model dynamics and damage levels
- study if and how sterile male pattern of introduction can be optimized

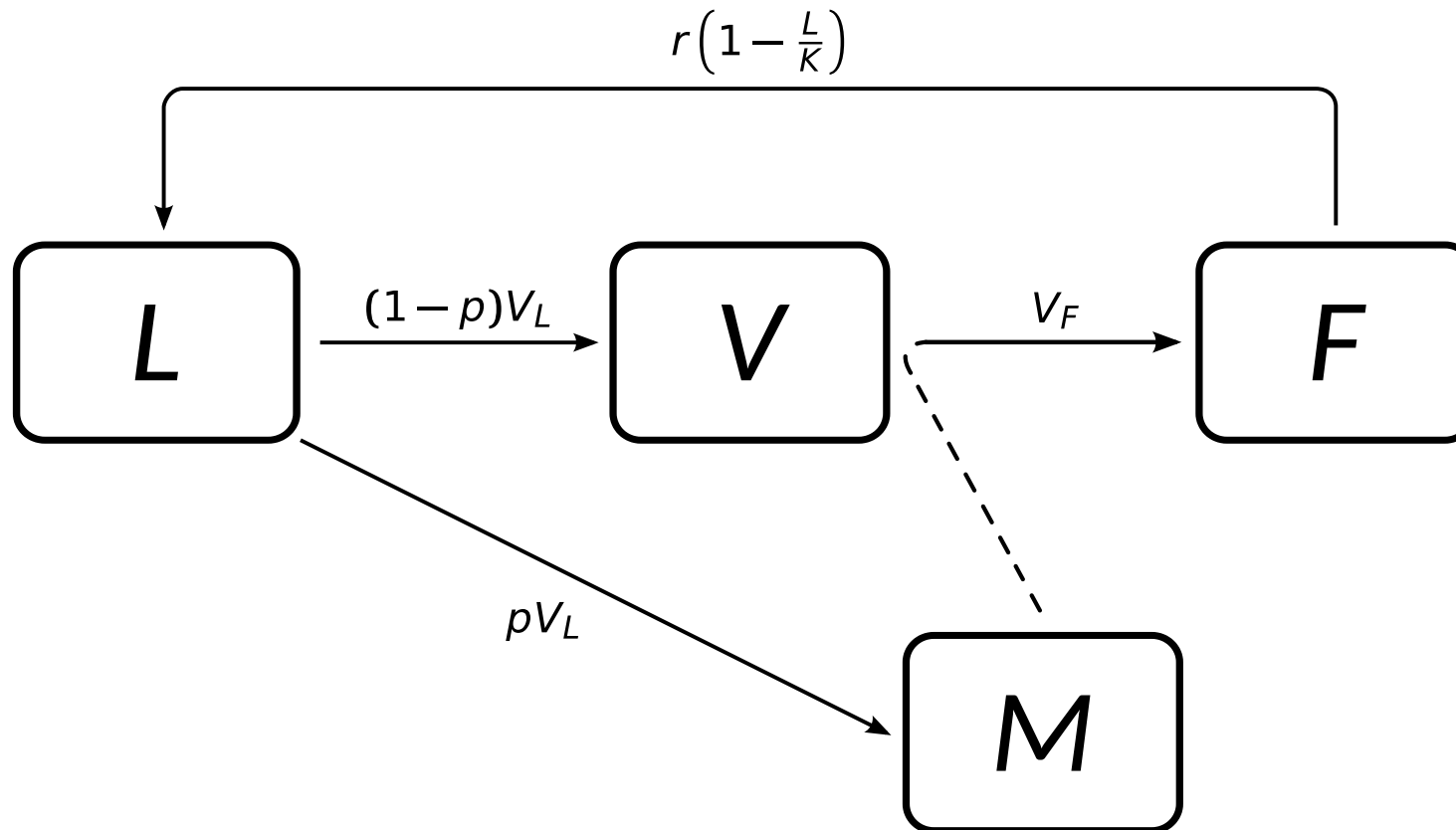
# Fruit flies life cycle



credit to noun project for art

# Model diagram

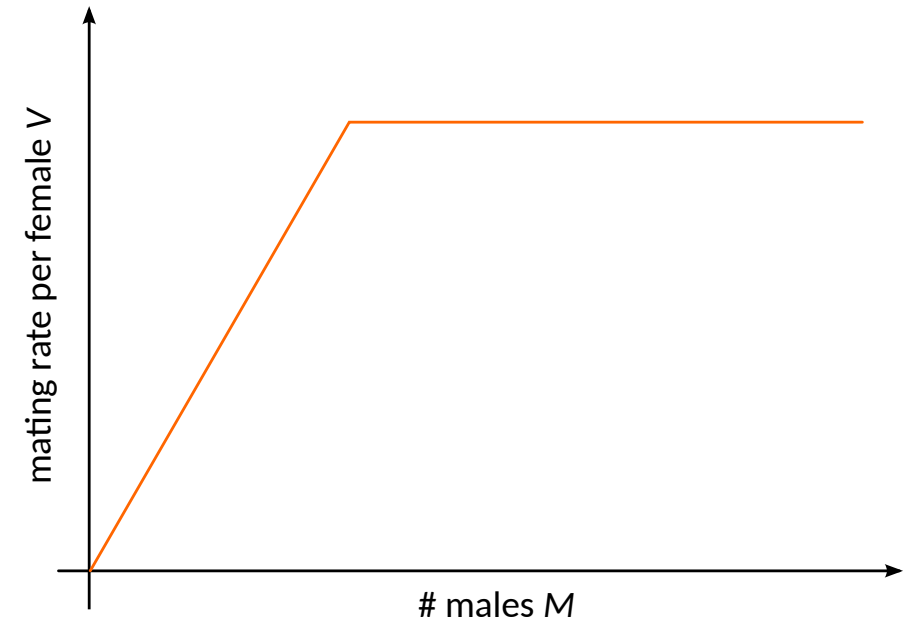
- 4 stages: eggs/larvae  $L$ , unmated females  $V$ , males  $M$ , mated females  $F$ <sup>1</sup>





# Mating model

- frequency dependent mating probability <sup>1</sup>
  - # males  $M$  abundant  
females  $V$  mated at rate  $v_F$
  - # males  $M$  limiting  
mating proba.  $\frac{\gamma M}{V}$ ,  $V$  mating rate  $\frac{\gamma M}{V} v_F$
- overall mating rate per unmated females  $V$



$$v_F \min \left( \frac{\gamma M}{V}, 1 \right)$$

# Population dynamics model

$$\begin{cases} \dot{L} = r \left(1 - \frac{L}{K}\right) F - v_L L - \mu_L L \\ \dot{M} = p v_L L - \mu_M M \\ \dot{V} = (1 - p) v_L L - v_F \min\left(\frac{\gamma M}{V}, 1\right) V - \mu_F V \\ \dot{F} = v_F \min\left(\frac{\gamma M}{V}, 1\right) V - \mu_F F \end{cases}$$

- in an agricultural context, the insect pest settles in crops at high densities s.t.

$$\eta_0 = \frac{r(1-p)v_L v_F}{\mu_F(\mu_F + v_F)(\mu_L + v_L)} > 1$$

- in that case, the positive equilibrium of the saturated submodel is GAS for the full model (Anguelov *et alii*, 2017)
- thus the  $\min(\cdot)$  necessarily saturates to 1 after some transient times

# Reduced model

- in what follows, we therefore concentrate on the simpler form

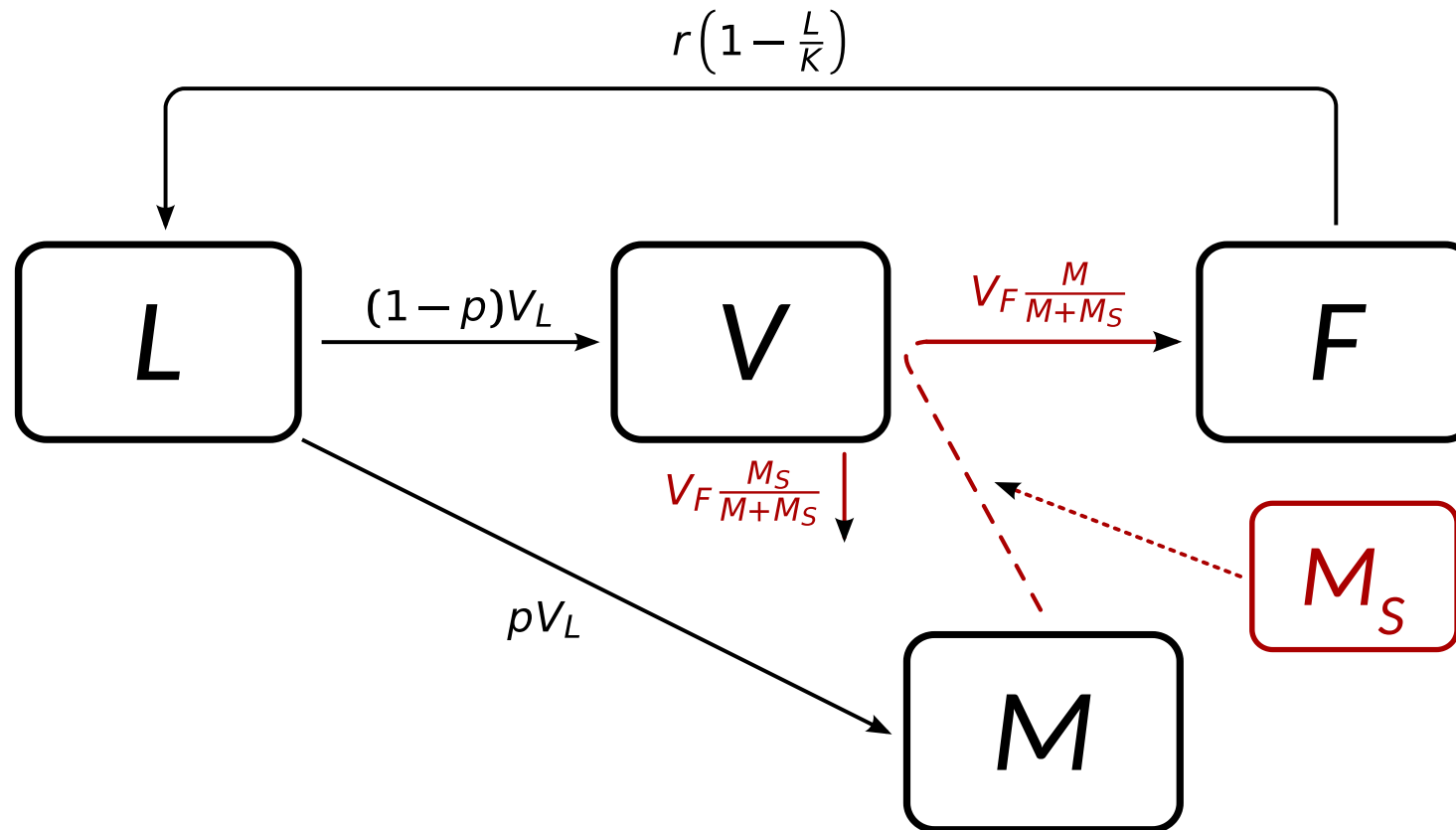
$$\begin{cases} \dot{L} = r \left(1 - \frac{L}{K}\right) F - v_L L - \mu_L L \\ \dot{M} = p v_L L - \mu_M M \\ \dot{V} = (1 - p) v_L L - v_F V - \mu_F V \\ \dot{F} = v_F V - \mu_F F \end{cases}$$

- assuming that the basic reproduction number

$$\eta_0 = \frac{r (1 - p) v_L v_F}{\mu_F (\mu_F + v_F) (\mu_L + v_L)} > 1$$

# Model diagram (with sterile males)

- 5th stage: sterile males  $M_S$  (= constant for now)



$M_S$  divert a part of unmated females  $V$  to *mated-with-sterile* females

# Model with sterile males

- only a proportion  $\frac{M}{M+M_s}$  of matings yield egg-laying females

$$\begin{cases} \dot{L} = r \left(1 - \frac{L}{K}\right) F - v_L L - \mu_L L \\ \dot{M} = p v_L L - \mu_M M \\ \dot{V} = (1 - p) v_L L - v_F V - \mu_F V \\ \dot{F} = v_F \frac{M}{M+M_s} V - \mu_F F \end{cases}$$

# Analysis: equilibria

- equilibria are solutions of

$$\left\{ \begin{array}{l} F = \frac{v_L + \mu_L}{r(1 - \frac{L}{K})} L \quad (\text{i}) \\ M = \frac{pv_L}{\mu_M} L \quad (\text{ii}) \\ V = \frac{(1-p)v_L}{v_F + \mu_F} L \quad (\text{iii}) \\ F = \frac{v_F}{\mu_F} \frac{M}{M + M_s} V \quad (\text{iv}) \end{array} \right.$$

- so that (0,0,0,0) is always an equilibrium
- and, using (i), (ii) and (iii) in (iv), other equilibria must verify

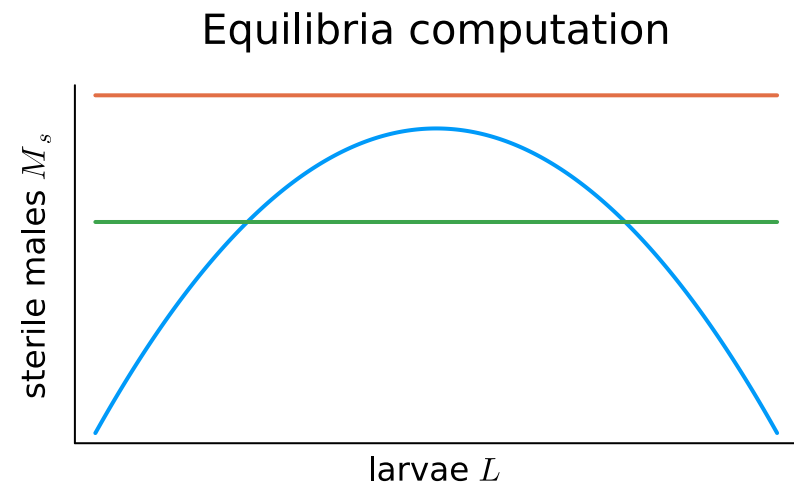
$$\frac{v_L + \mu_L}{r \left(1 - \frac{L}{K}\right)} = \frac{v_F}{\mu_F} \frac{\frac{pv_L}{\mu_M} L}{\frac{pv_L}{\mu_M} L + M_s} \frac{(1-p)v_L}{v_F + \mu_F}$$

# Analysis: equilibria

- rearranging, other equilibria must verify

$$1 = \eta_0 \left(1 - \frac{L}{K}\right) \frac{\frac{pv_L}{\mu_M} L}{\frac{pv_L}{\mu_M} L + M_s} \Leftrightarrow M_s = \frac{pv_L}{\mu_M} L \left(\eta_0 - 1 - \frac{\eta_0}{K} L\right)$$

- RHS term is a concave parabola in  $L$ , with roots: 0, and:  $K \left(1 - \frac{1}{\eta_0}\right) > 0$
- if  $M_s$  larger than max of parabola: no equilibrium other than 0
- if  $M_s$  smaller than max of parabola, there exists two positive equilibria with  $0 < L_1^* < L_2^* < K$



# Analysis: stability

- Jacobian matrix is 4D 😬

$$J = \begin{pmatrix} -\frac{r}{K}F - \mu_L - v_L & 0 & 0 & r \left(1 - \frac{L}{K}\right) \\ pv_L & -\mu_M & 0 & 0 \\ (1-p)v_L & 0 & -(v_F + \mu_F) & 0 \\ 0 & v_F \frac{M_s}{(M+M_s)^2} V & v_F \frac{M}{(M+M_s)} & -\mu_F \end{pmatrix}$$

- but with non-negative off-diagonal elements at equilibria 👍

$$J^* = \begin{pmatrix} \bullet & 0 & 0 & + \\ + & \bullet & 0 & 0 \\ + & 0 & \bullet & 0 \\ 0 & + & + & \bullet \end{pmatrix}$$

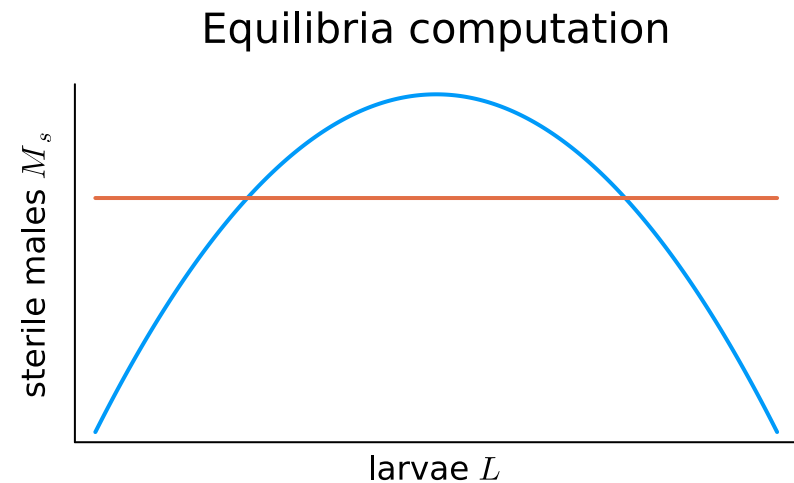


# Analysis: stability

- 0 equilibrium is always LAS, thanks to a nice block-triangular structure

$$J_0^* = \left( \begin{array}{ccc|c} -(\mu_L + v_L) & 0 & 0 & r \\ pv_L & -\mu_M & 0 & 0 \\ (1-p)v_L & 0 & -(v_F + \mu_F) & 0 \\ \hline 0 & 0 & 0 & -\mu_F \end{array} \right)$$

- for positive equilibria built on  $L_1^*$  and  $L_2^*$ 
  - strong clues for *fold bifurcation* at
 
$$M_s = \overline{M}_s = \frac{pv_L}{4\mu_M} \frac{(\eta_0 - 1)^2}{\eta_0} K$$
  - so that, given 0 is always LAS,  $E_1^*$  would be a saddle and  $E_2^*$  would be LAS



# Analysis: stability of $E_i^*$

- use the special structure of the Jacobian: a Metzler matrix

$$J = \begin{pmatrix} \ddots & \geq 0 \\ \geq 0 & \ddots \end{pmatrix}$$

- Bowong's lemma<sup>1</sup>

*Let  $J$  be a Metzler matrix that can be decomposed into blocks as*

$$J = \begin{pmatrix} A & B \\ C & D \end{pmatrix}$$

*Then  $J$  is stable if and only if  $A$  and  $D - CA^{-1}B$  are stable Metzler matrices*

# Analysis: stability of $E_i^*$

- express  $J$  in function of  $L^*$

$$J = \left( \begin{array}{cc|cc} \frac{-\eta_0(\mu_L + v_L) \frac{pvL}{\mu_M} L^*}{\frac{pvL}{\mu_M} L^* + M_s} & 0 & 0 & r \left(1 - \frac{L^*}{K}\right) \\ pvL & -\mu_M & 0 & 0 \\ \hline (1-p)vL & 0 & -(\mu_F + v_F) & 0 \\ 0 & \frac{\eta_0 \mu_F (\mu_L + v_L) M_s L^*}{r \left(\frac{pvL}{\mu_M} L^* + M_s\right)^2} & \frac{v_F \frac{pvL}{\mu_M} L^*}{\frac{pvL}{\mu_M} L^* + M_s} & -\mu_F \end{array} \right)$$

- so that

$$A = \left( \begin{array}{cc} \frac{-\eta_0(\mu_L + v_L) \frac{pvL}{\mu_M} L^*}{\frac{pvL}{\mu_M} L^* + M_s} & 0 \\ pvL & -\mu_M \end{array} \right) \text{ is Metzler stable}$$

- and

$$B = \begin{pmatrix} 0 & r \left(1 - \frac{L^*}{K}\right) \\ 0 & 0 \end{pmatrix}, C = \begin{pmatrix} (1-p)v_L & 0 \\ 0 & \frac{\eta_0 \mu_F (\mu_L + v_L) M_s L^*}{r \left(\frac{pv_L}{\mu_M} L^* + M_s\right)^2} \end{pmatrix}, \text{ and } D = \begin{pmatrix} -(\mu_F + v_F) & 0 \\ \frac{v_F \frac{pv_L}{\mu_M} L^*}{\frac{pv_L}{\mu_M} L^* + M_s} & -\mu_F \end{pmatrix}$$

# Stability of $E_i^*$

- further computations show

$$D - CA^{-1}B = \begin{pmatrix} -(\mu_F + v_F) & \frac{\mu_F(\mu_F + v_F)\left(1 - \frac{L^*}{K}\right)\left(\frac{pvL}{\mu_M}L^* + M_s\right)}{v_F \frac{pvL}{\mu_M}L^*} \\ \frac{v_F \frac{pvL}{\mu_M}L^*}{\frac{pvL}{\mu_M}L^* + M_s} & \mu_F \left( \frac{M_s\left(1 - \frac{L^*}{K}\right)}{\frac{pvL}{\mu_M}L^* + M_s} - 1 \right) \end{pmatrix} \text{ is Metzler}$$

- and

$$\begin{aligned} \det(D - CA^{-1}B) &= -\mu_F(\mu_F + v_F) \left[ \left(1 - \frac{L^*}{K}\right) \left(1 + \frac{M_s}{\frac{pvL}{\mu_M}L^* + M_s}\right) - 1 \right] \\ &= -\frac{\mu_F(\mu_F + v_F)}{\eta_0} \left( \eta_0 - 1 - \frac{2\eta_0 L^*}{K} \right) \end{aligned}$$

given that  $M_s = \frac{pvL}{\mu_M}L^* \left( \eta_0 - 1 - \frac{\eta_0 L^*}{K} \right)$  at equilibrium  $E_i^*$

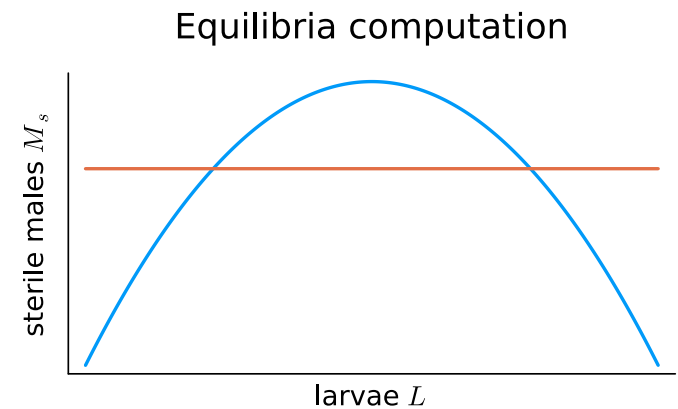
# Stability of $E_i^*$

- and this is it: the slope of the parabola at  $L_i^*$  is

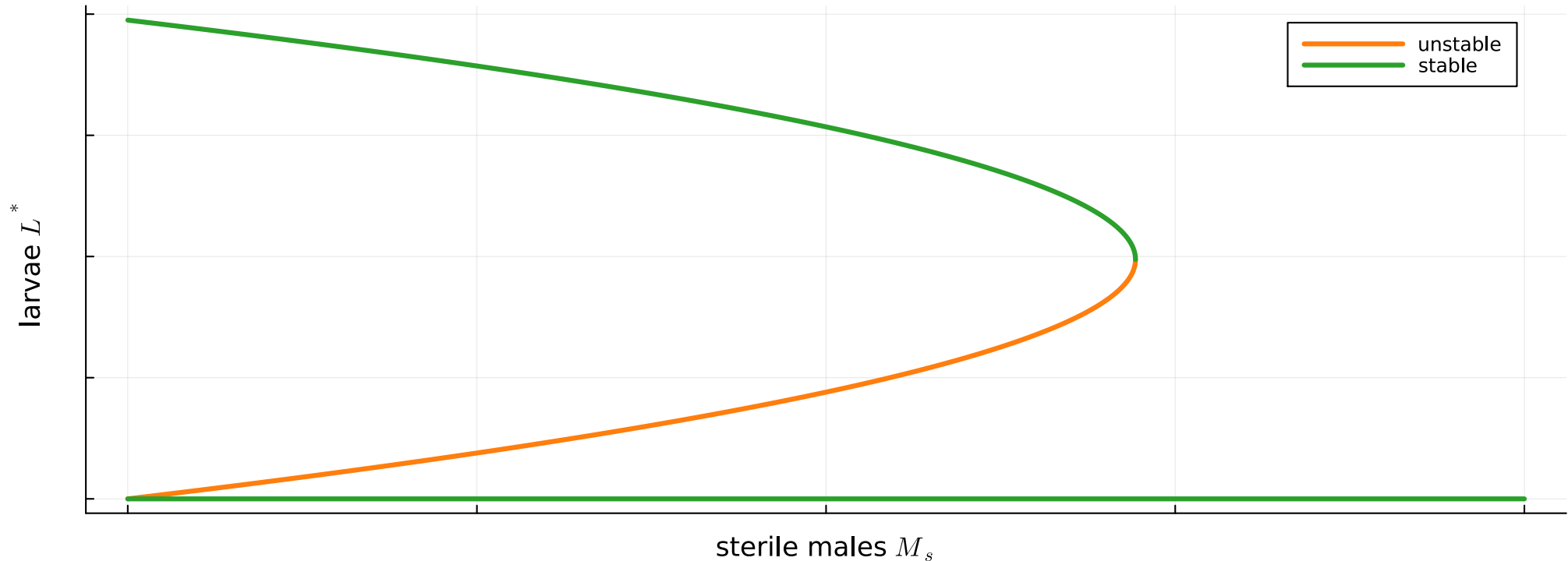
$$\frac{dM_s}{dL} = \frac{pv_L}{\mu_M} \left( \eta_0 - 1 - \frac{2\eta_0 L_i^*}{K} \right)$$

slope sign at  $L^*$  sets  $\det(D - CA^{-1}B)$  sign

- at  $E_2^*$ ,  $\frac{dM_s}{dL} < 0$  which implies:  $\det(D - CA^{-1}B) > 0$  and  $\text{tr}(D - CA^{-1}B) < 0^1$   
from Bowong's lemma,  $J(E_2^*)$  is thus stable and  $E_2^*$  is LAS
- at  $E_1^*$ ,  $\frac{dM_s}{dL} > 0$  which implies:  $\det(D - CA^{-1}B) < 0$   
from Bowong's lemma,  $E_1^*$  is unstable



# Bifurcation diagram

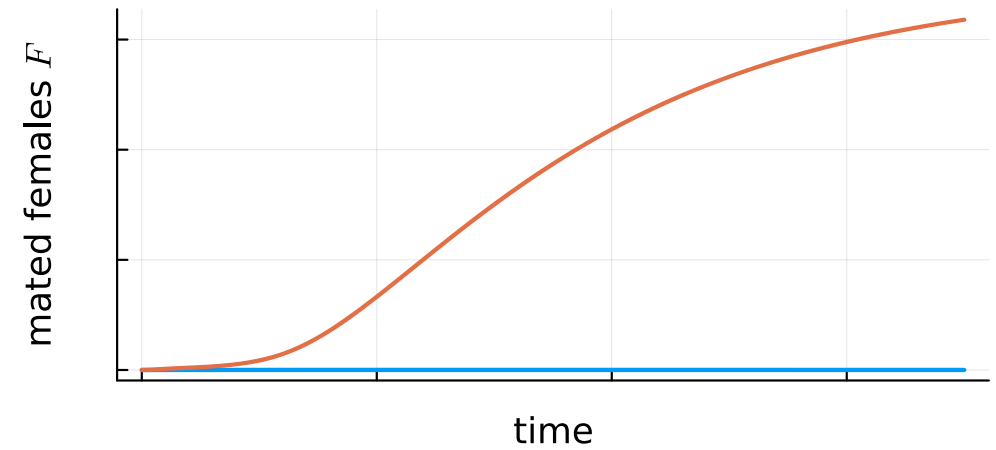
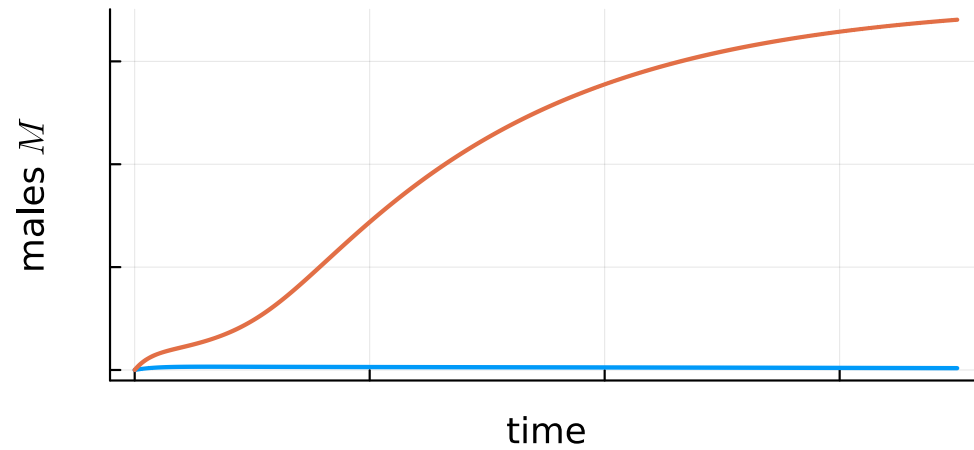
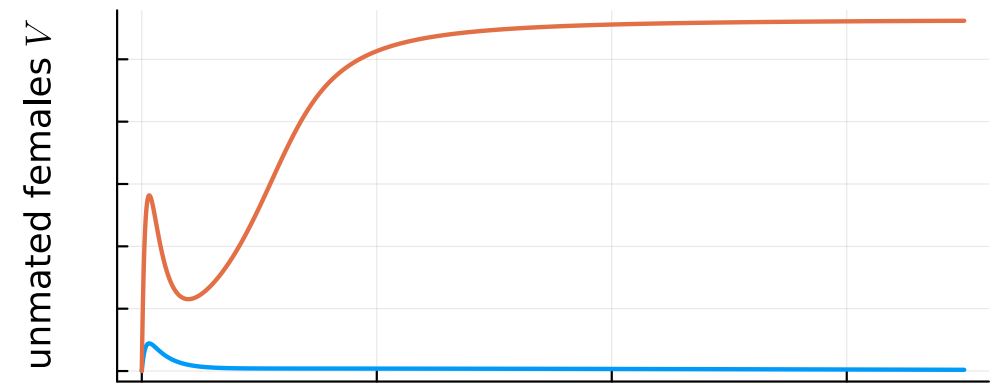
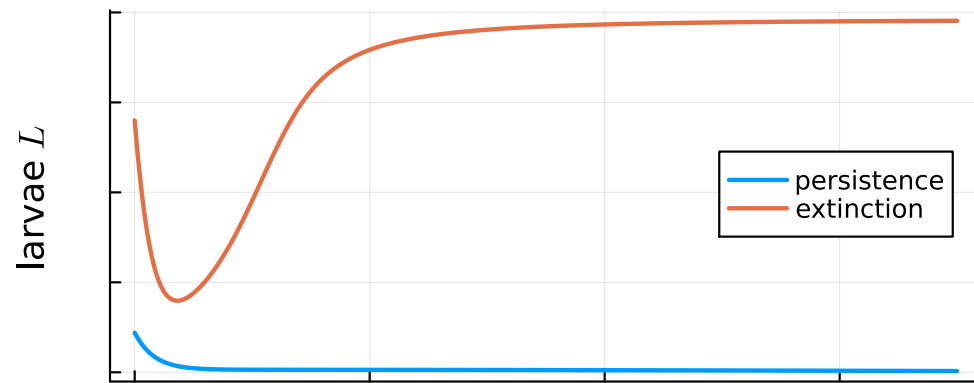


- thanks to the cooperativity of the model

- when  $M_S > \overline{M_S}$ , 0 equilibrium is GAS

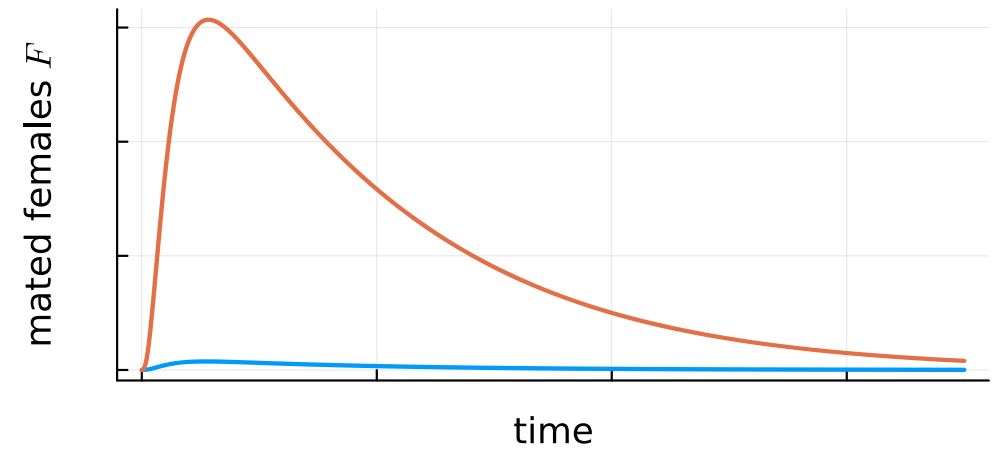
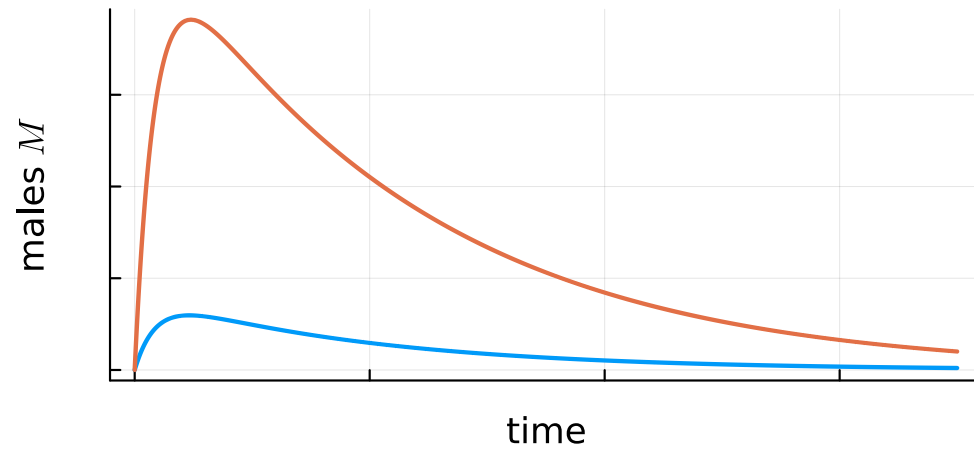
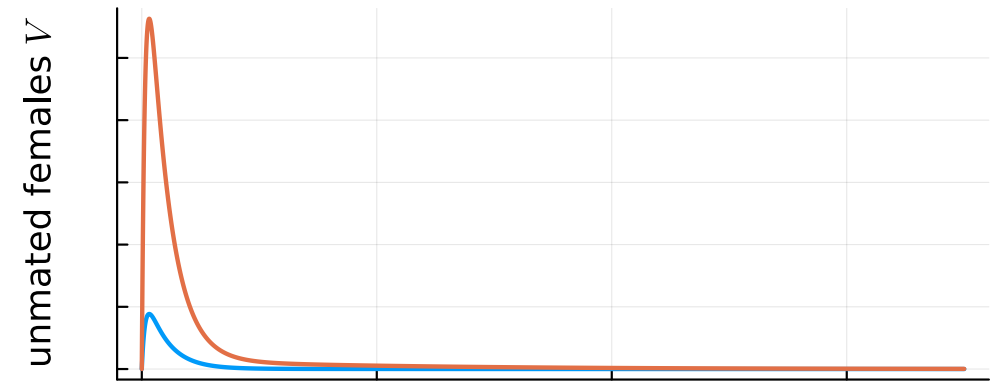
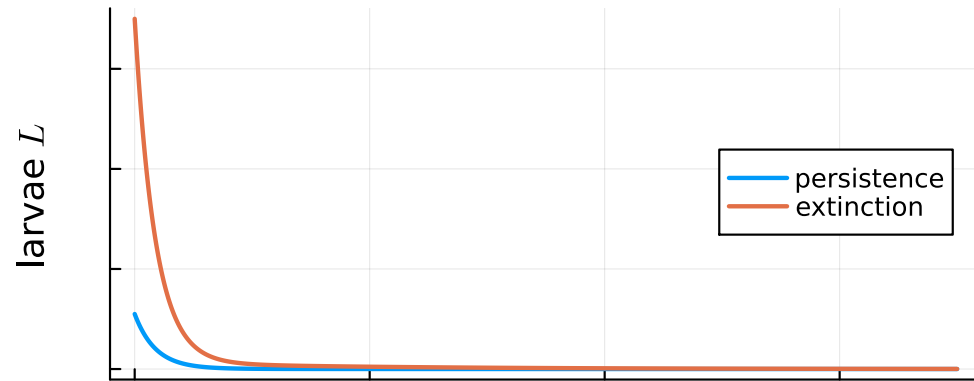
- when  $M_S < \overline{M_S}$  trajectories converge to either 0 or  $E_2^*$

# $M_S < \overline{M_S}$ : bi-stability



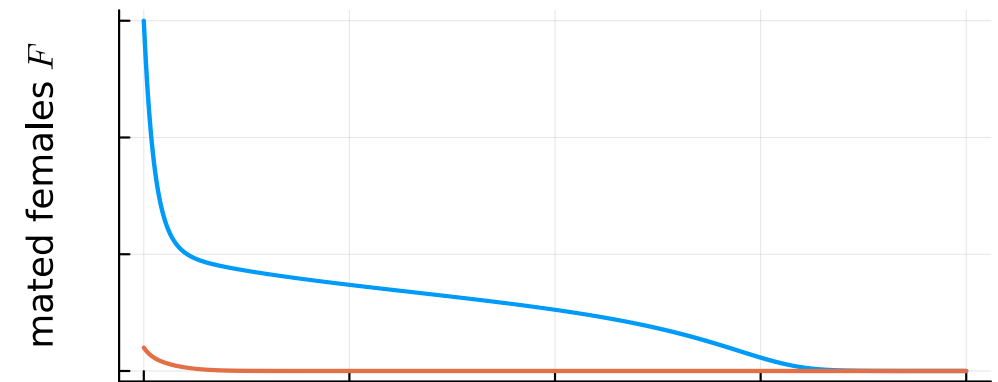
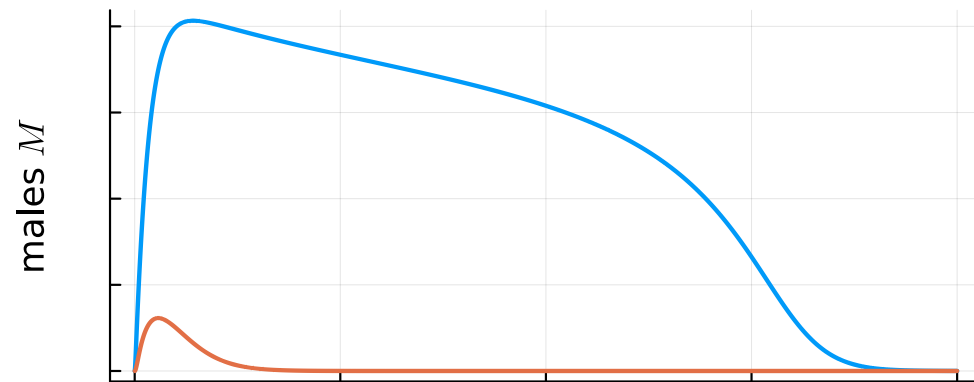
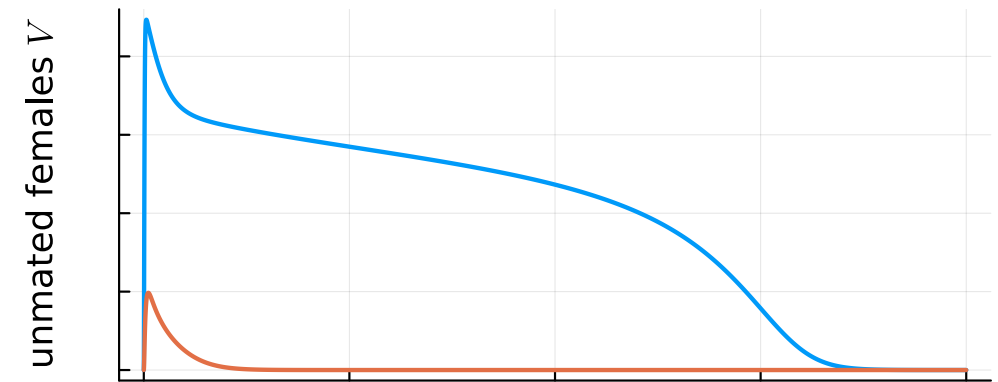
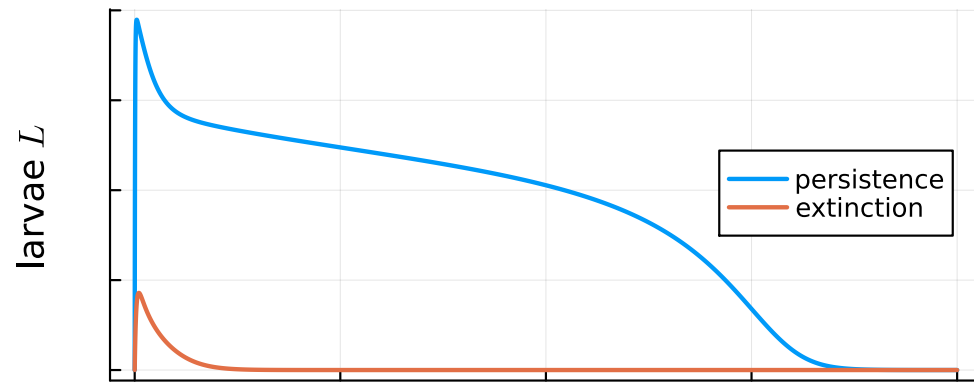


# $M_S > \overline{M_S} : 0 \text{ is GAS}$



# Mated females invade

- 0 is still GAS, but...

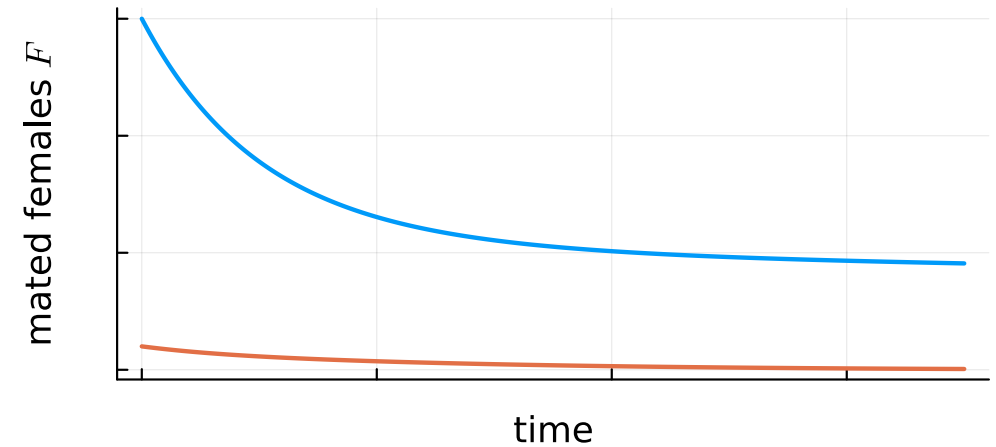
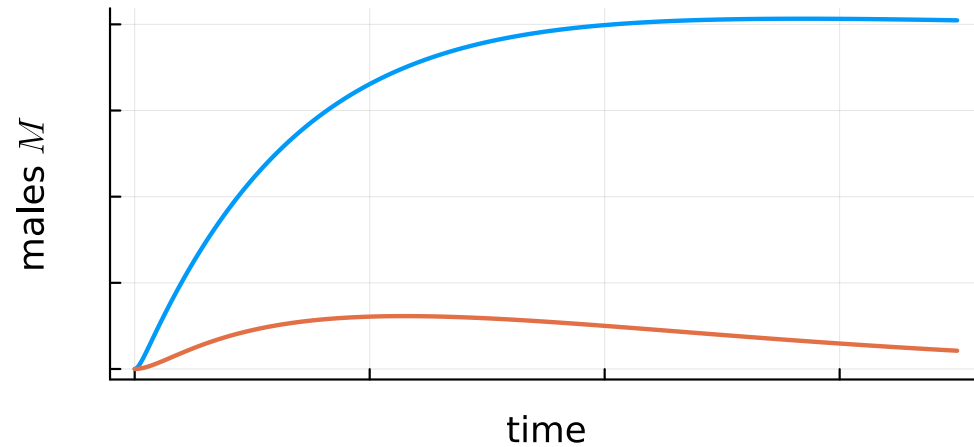
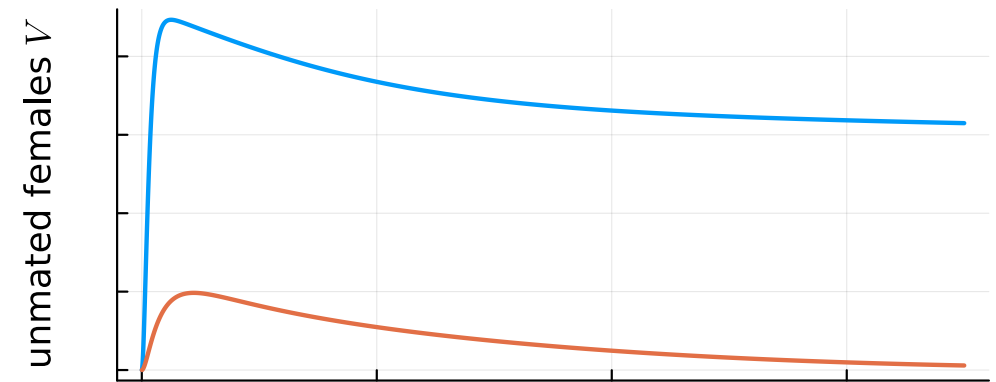
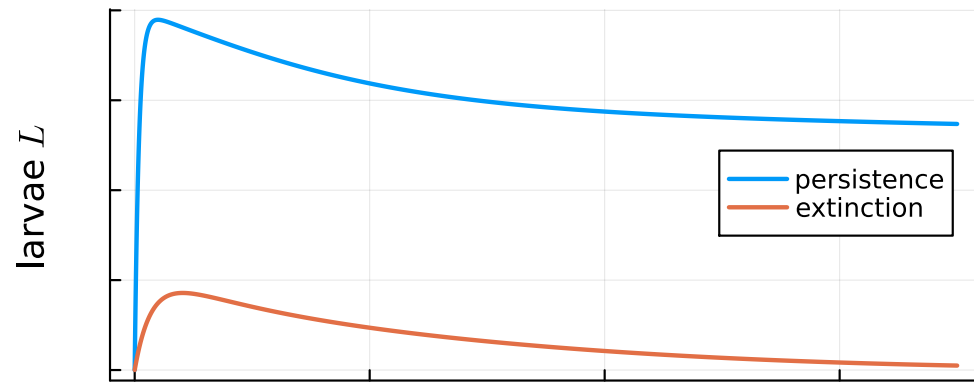


time

time

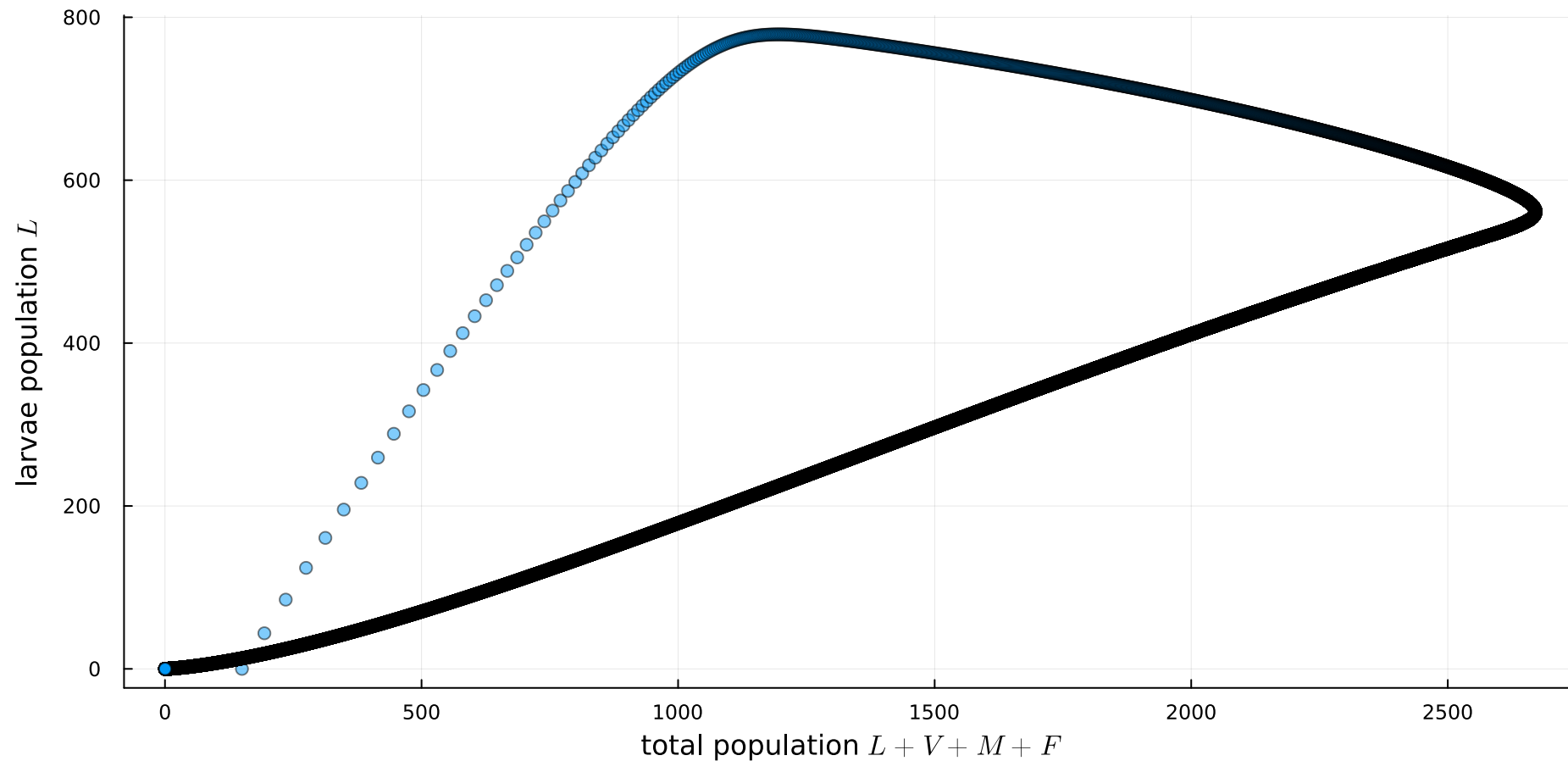
# Mated females invade

- but GAS is not always enough



# Larvae vs. population size

- total population not a very good proxy for larvae population / crop damage

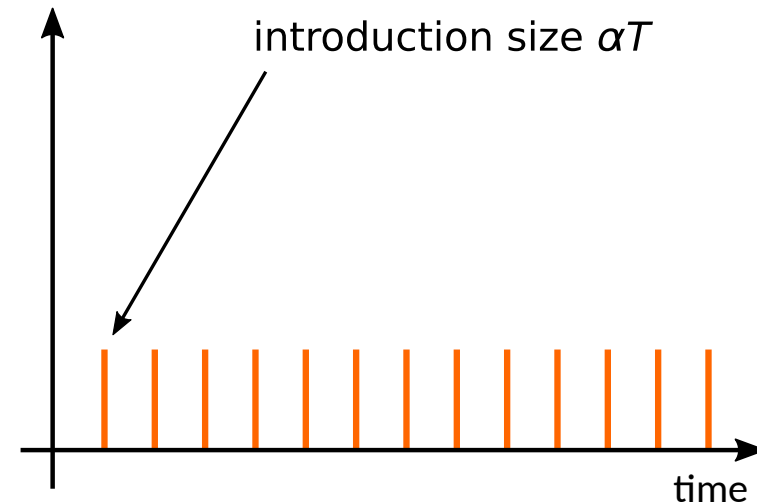
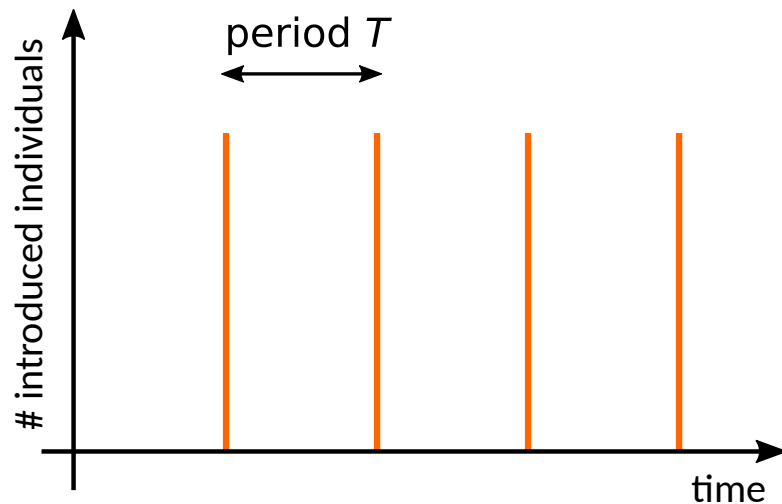


# Model with pulsed $M_s$ introductions

- same equations as before, but  $M_s$  is dynamic

$$\begin{cases} \dot{M}_s = -\mu_M M_s & \forall t \in (kT, (k+1)T) \\ M_s(kT^+) = M_s(kT) + \sigma T \end{cases}$$

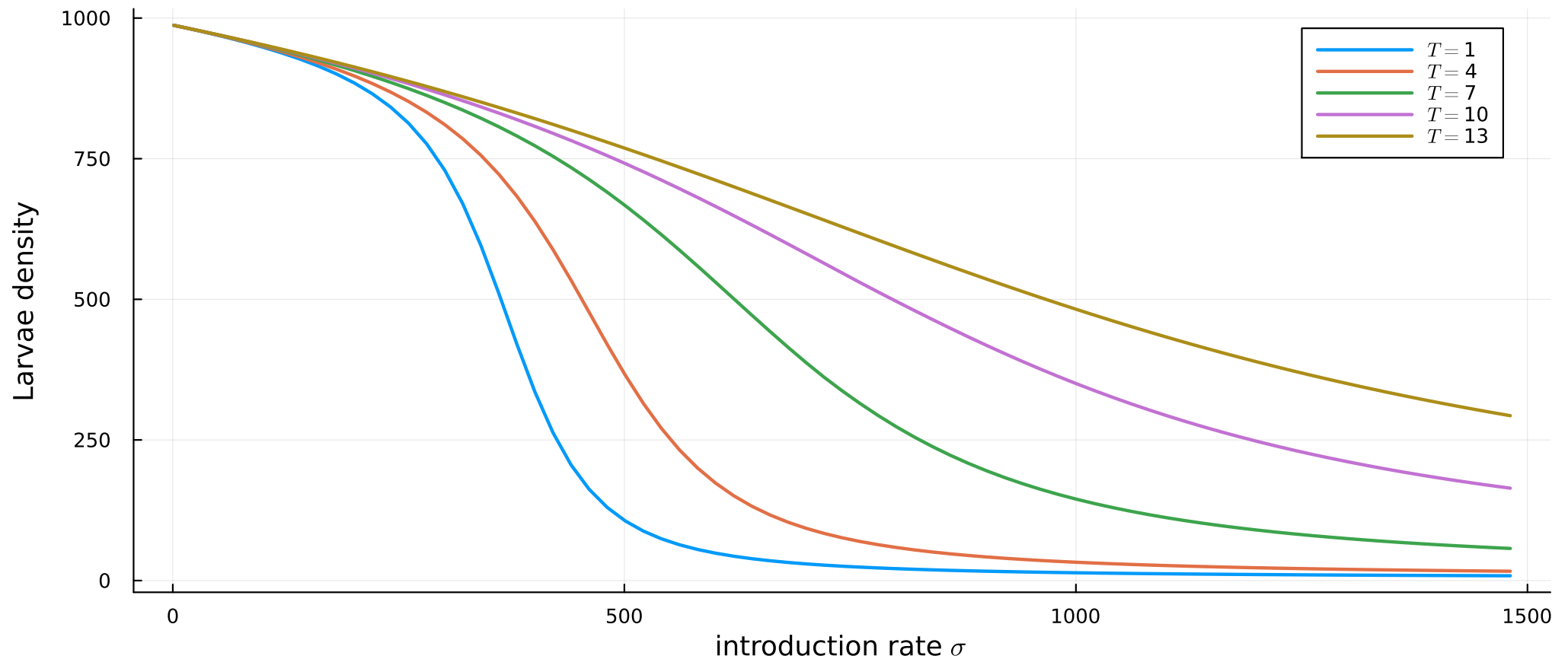
- classical trick to compare different introduction regimes for given introduction rate  $\sigma$ <sup>1</sup>



# Numerical experiments: pulses

- which introduction strategy works best: late introductions situation

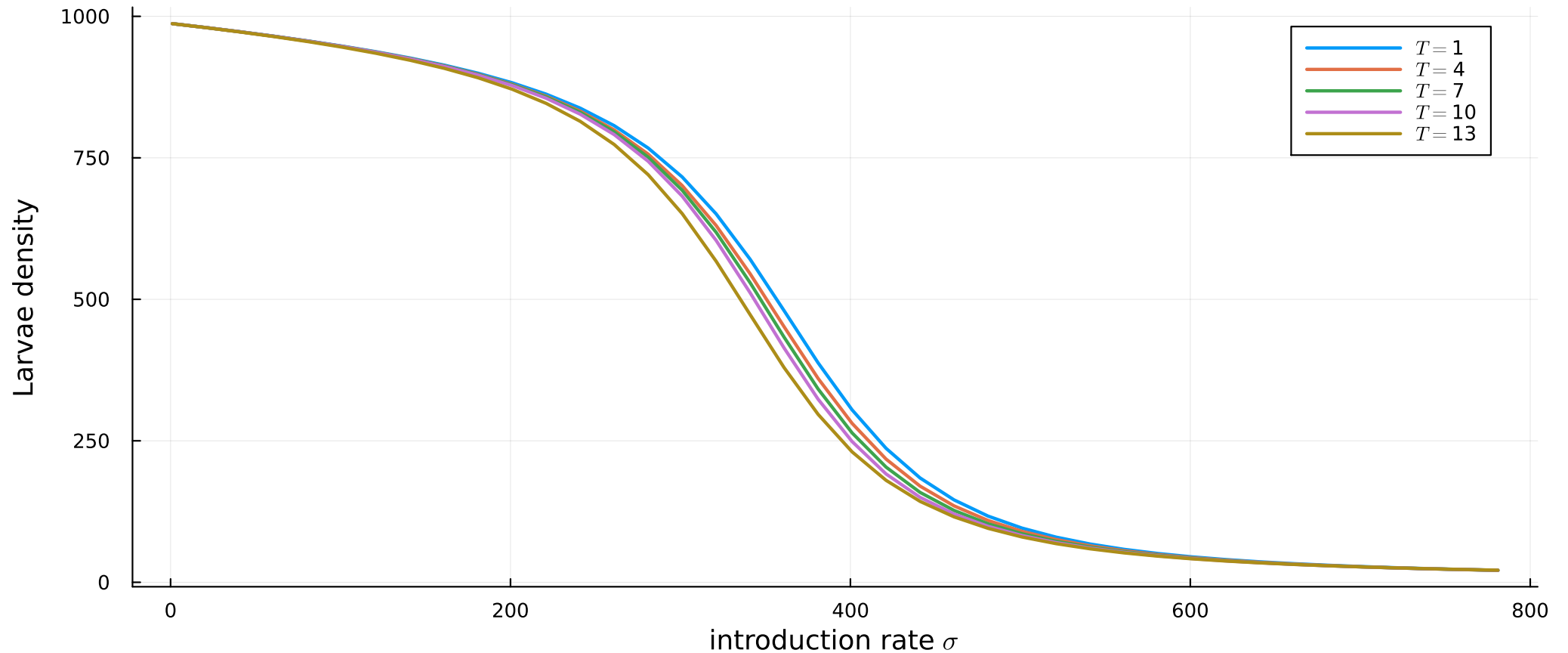
max. Larvae at end of program



# Numerical experiments: pulses

- which introduction strategy works best: early introduction situations

max. Larvae at end of program



# Conclusion

- sex- and stage- structured model of Anguelov *et alii* in a SIT context
  - quite thorough mathematical analysis
  - Metzler matrices and cooperativity tools
- showed importance of stage-structure consideration
  - dynamics are very different depending on initial condition
  - larvae density (damage) poorly correlates with total population size
- introduction strategy
  - timing is the essence
    - early, and not late introductions
    - if not possible, small and frequent introductions perform best by far
  - SIT most efficient in a preventive context



# Perspectives

- quantify basins of attraction in the bistable cases
- account for multiple female matings in the model
- provide mathematical grounds for the results on  $T$  / introduction strategies
- address complementary questions of biological interest, e.g.
  - what happens if *sterile* males are not *that sterile*?

Marine Courtois will give insights on this topic wednesday at 11 AM

# Thank you



## Acknowledgements

- Ecophyto Ceratis Corse
- ANR Suzukiiss:me



