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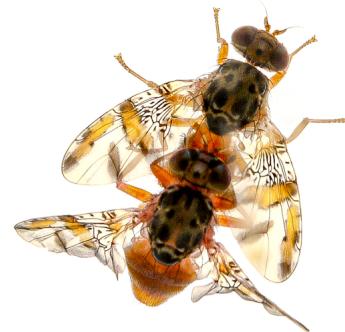
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A sex- and stage-structured model for pest control using the sterile insect technique



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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*

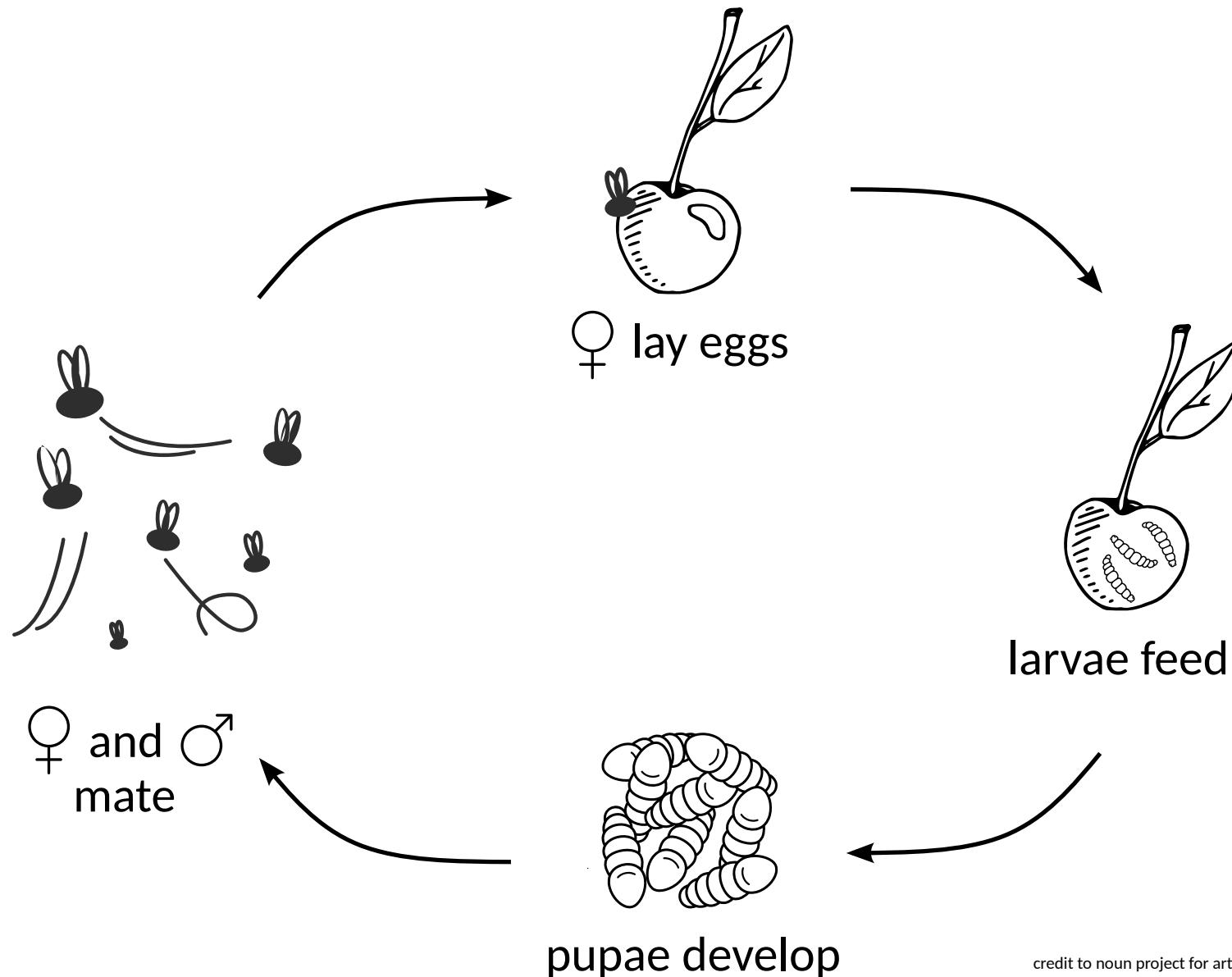


SIT is like a football game with so many people on the ground
you simply cannot find your teammates¹

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

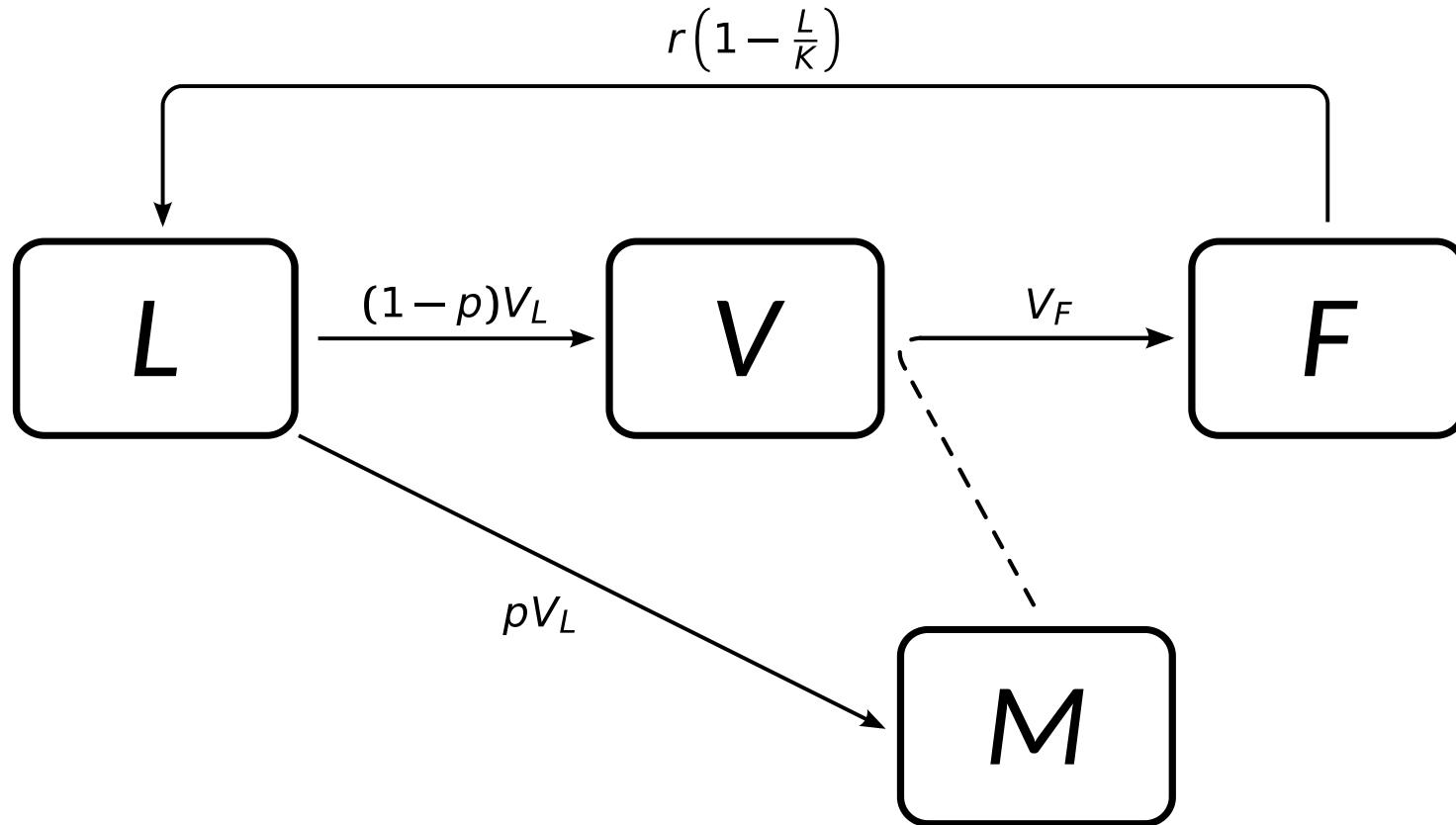


credit to noun project for art

Sex- and stage-structured SIT model - MPDEE 2023 Marseille

Model diagram

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



Mating model

- frequency dependent mating probability¹
 - # 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.

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

- 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

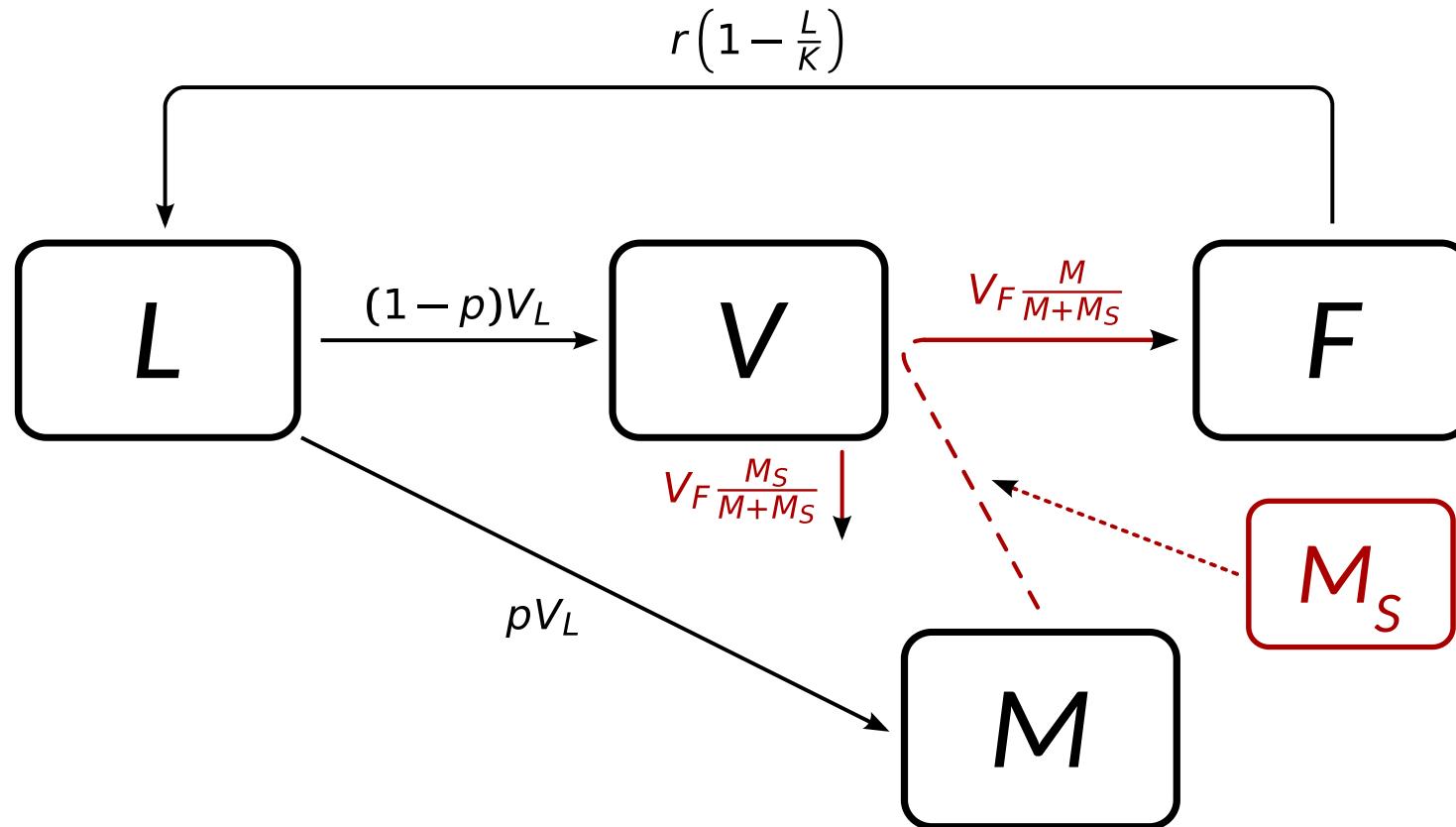
$$\begin{cases} \dot{L} = r \left(1 - \frac{L}{K}\right) F - v_L L - \mu_L L \\ \dot{M} = p v_L L - \mu_M M \\ \dot{V} = (1 - p)v_L L - v_F V - \mu_F V \\ \dot{F} = v_F V - \mu_F F \end{cases}$$

- 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

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

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

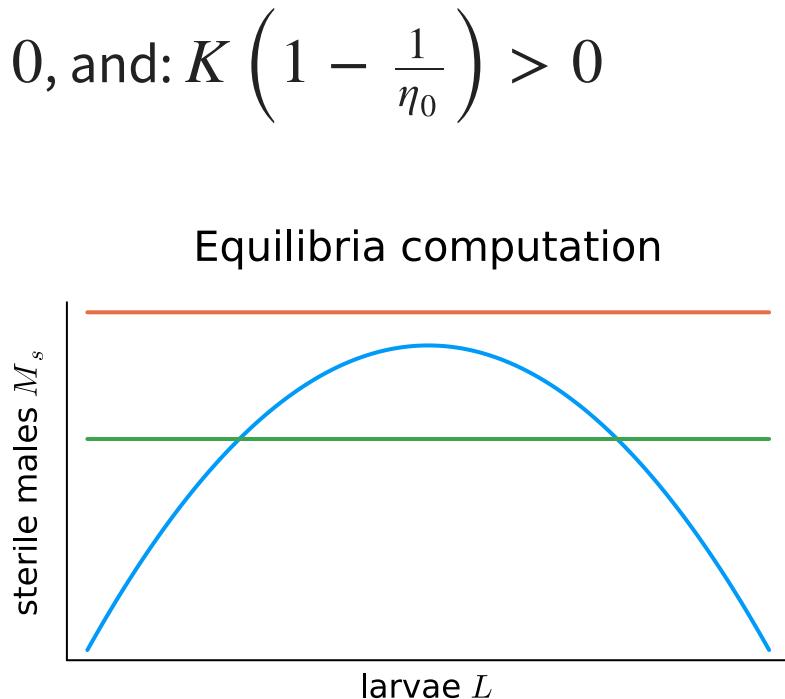
$$\frac{v_L + \mu_L}{r \left(1 - \frac{L}{K}\right)} = \frac{v_F}{\mu_F} \frac{\frac{pv_L}{\mu_M} L}{\frac{pv_L}{\mu_M} L + M_s} \frac{(1-p)v_L}{v_F + \mu_F}$$

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 😰

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

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

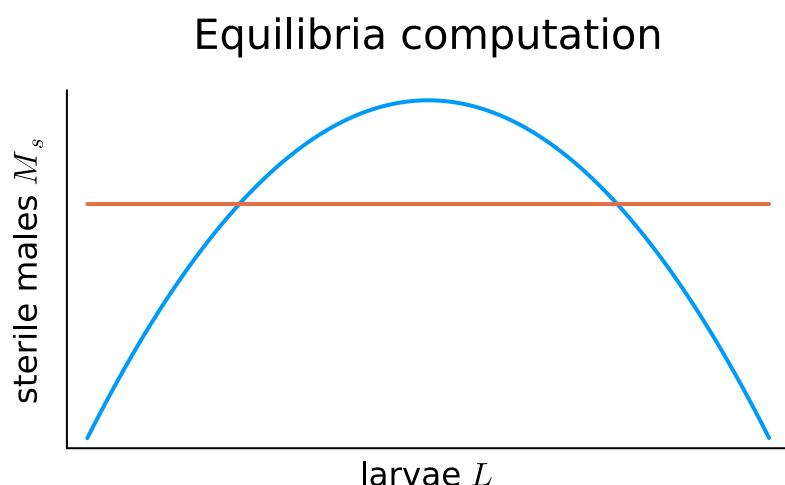
$$J^* = \begin{pmatrix} \bullet & 0 & 0 & + \\ + & \bullet & 0 & 0 \\ + & 0 & \bullet & 0 \\ 0 & + & + & \bullet \end{pmatrix}$$

Analysis: stability

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

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

- 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 ¹

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^*

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

- so that

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

is Metzler stable

- and

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

Stability of E_i^*

- further computations show

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

- and

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

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

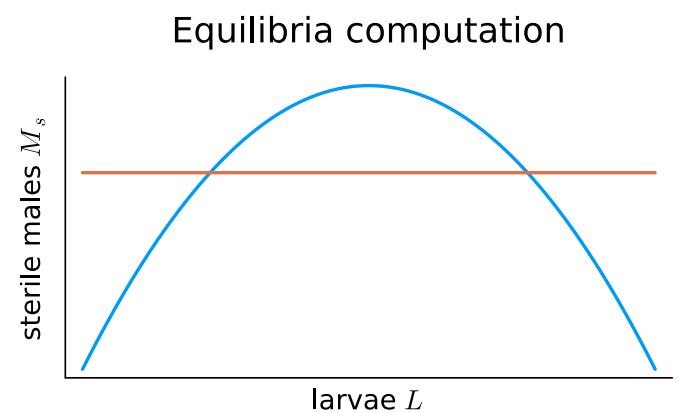
Stability of E_i^*

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

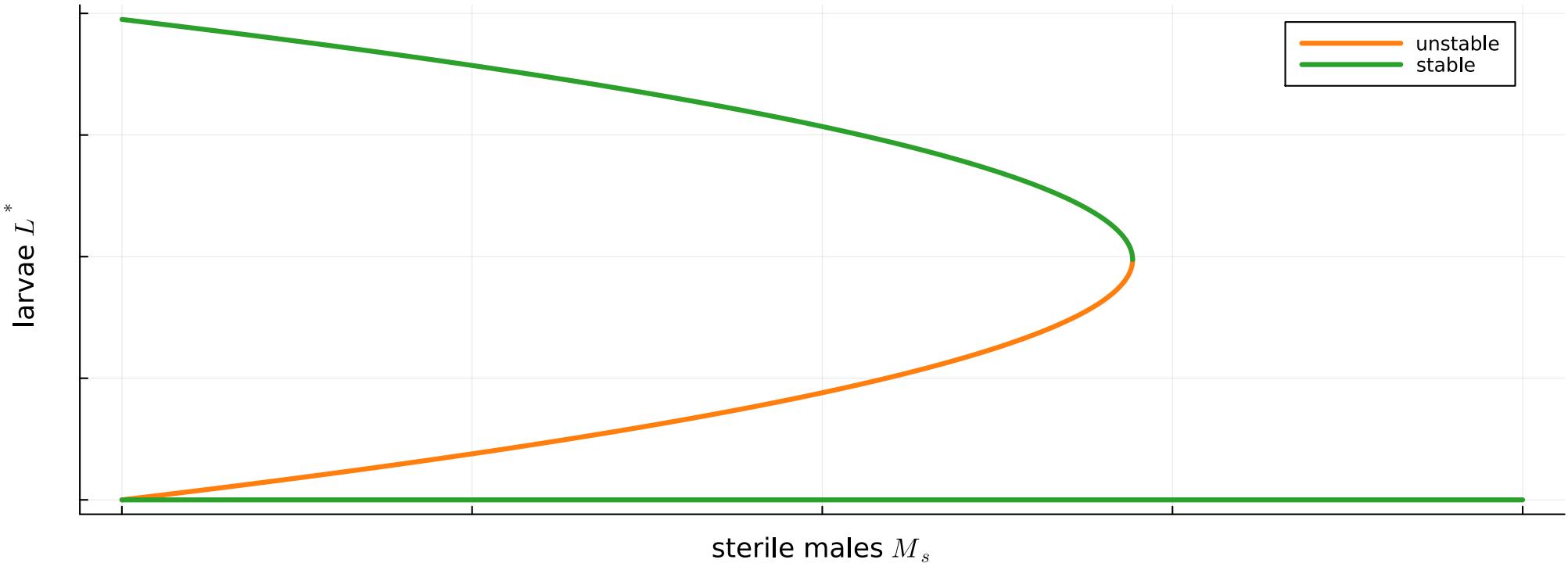
$$\frac{dM_s}{dL} = \frac{pv_L}{\mu_M} \left(\eta_0 - 1 - \frac{2\eta_0 L_i^*}{K} \right)$$

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

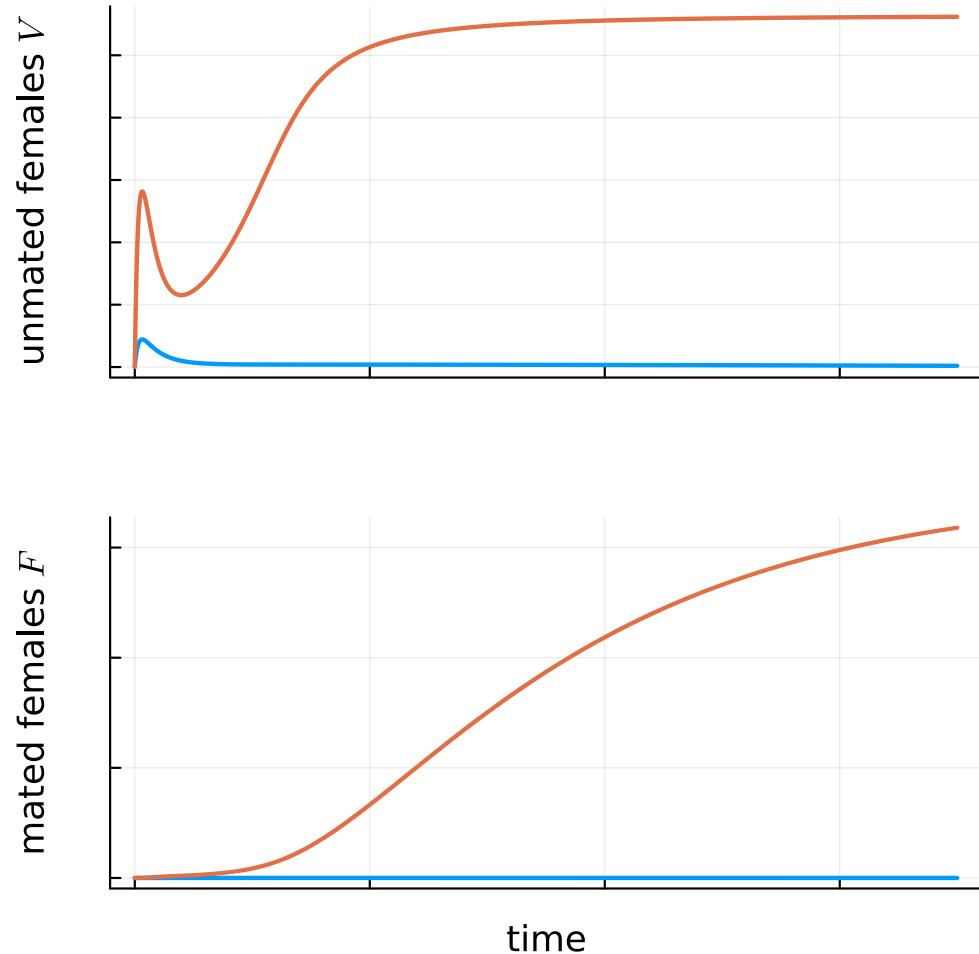
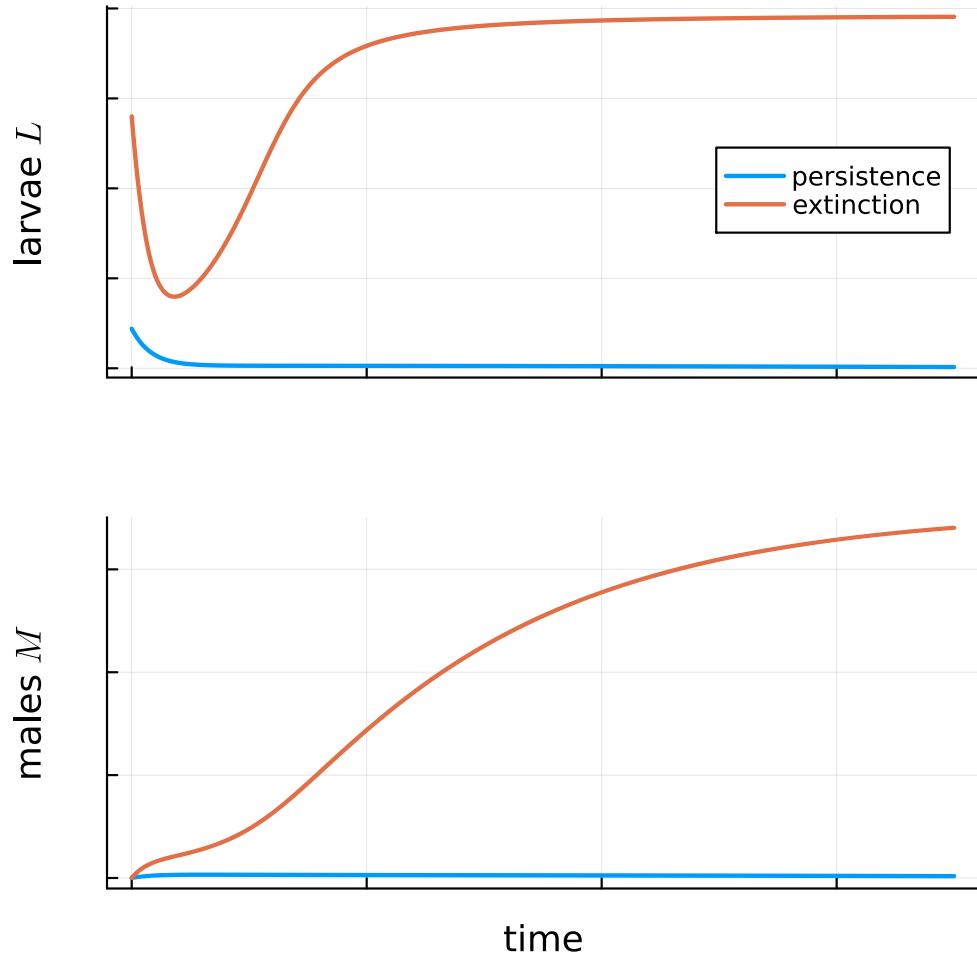


Bifurcation diagram

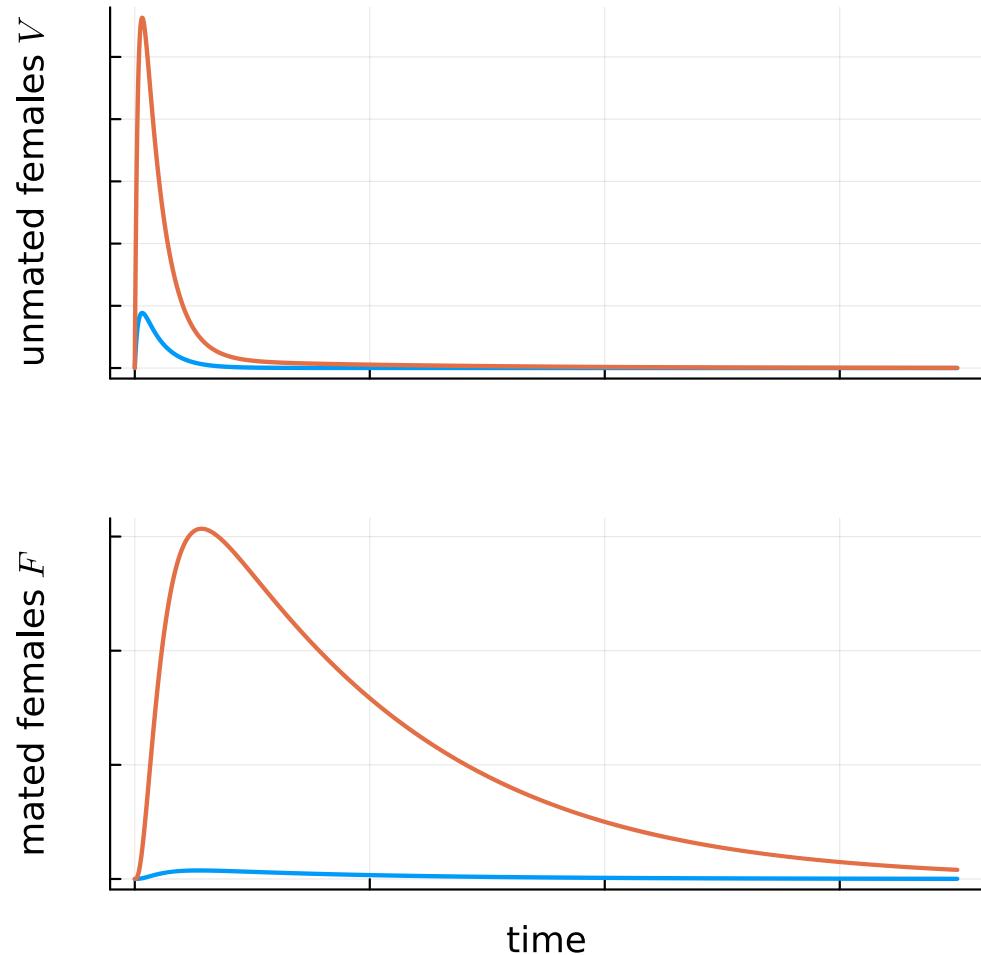
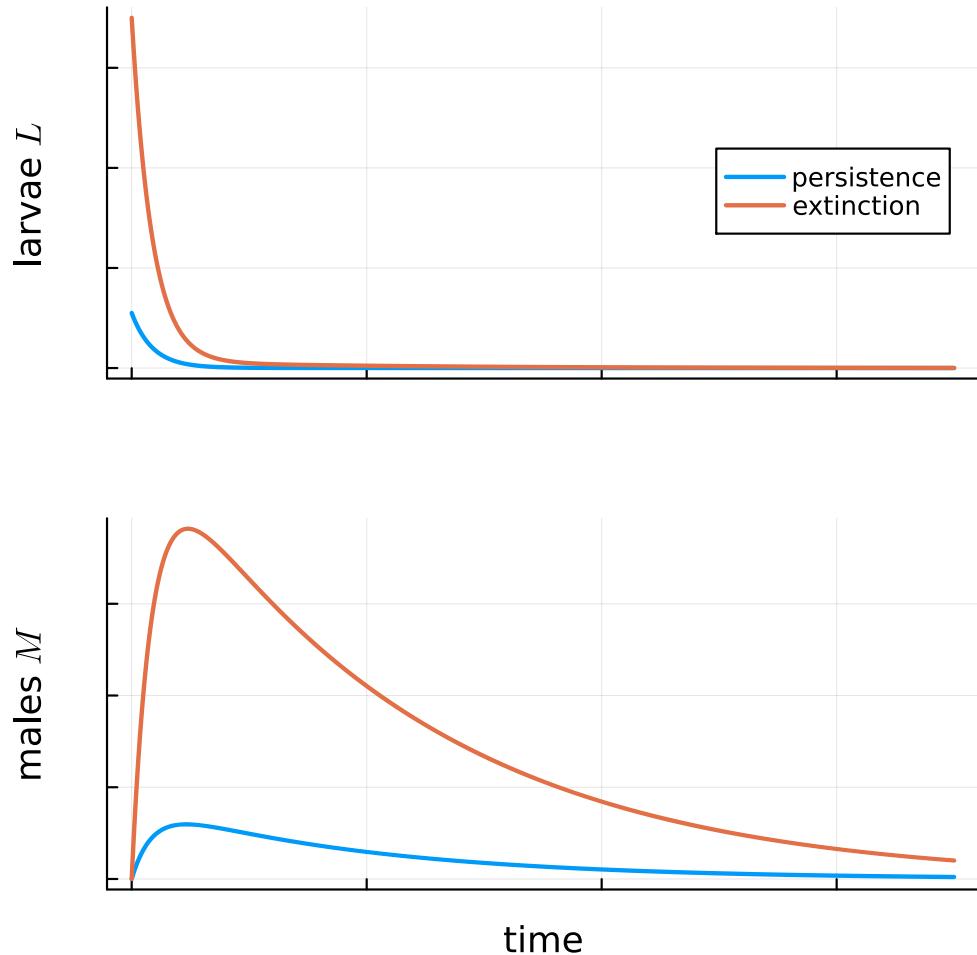


- thanks to the cooperativity of the model
 - when $M_S > \overline{M}_S$, 0 equilibrium is GAS
 - when $M_S < \overline{M}_S$ trajectories converge to either 0 or E_2^*

$M_s < \bar{M}_S$: bi-stability

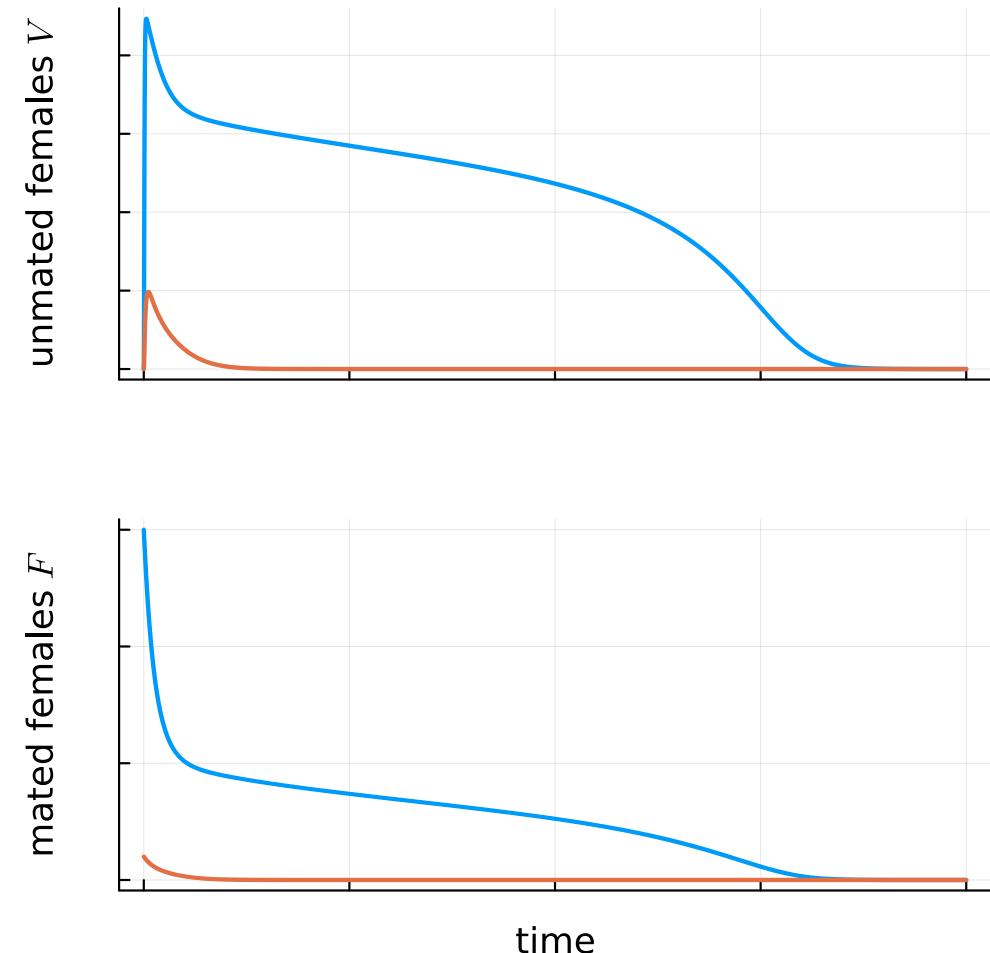
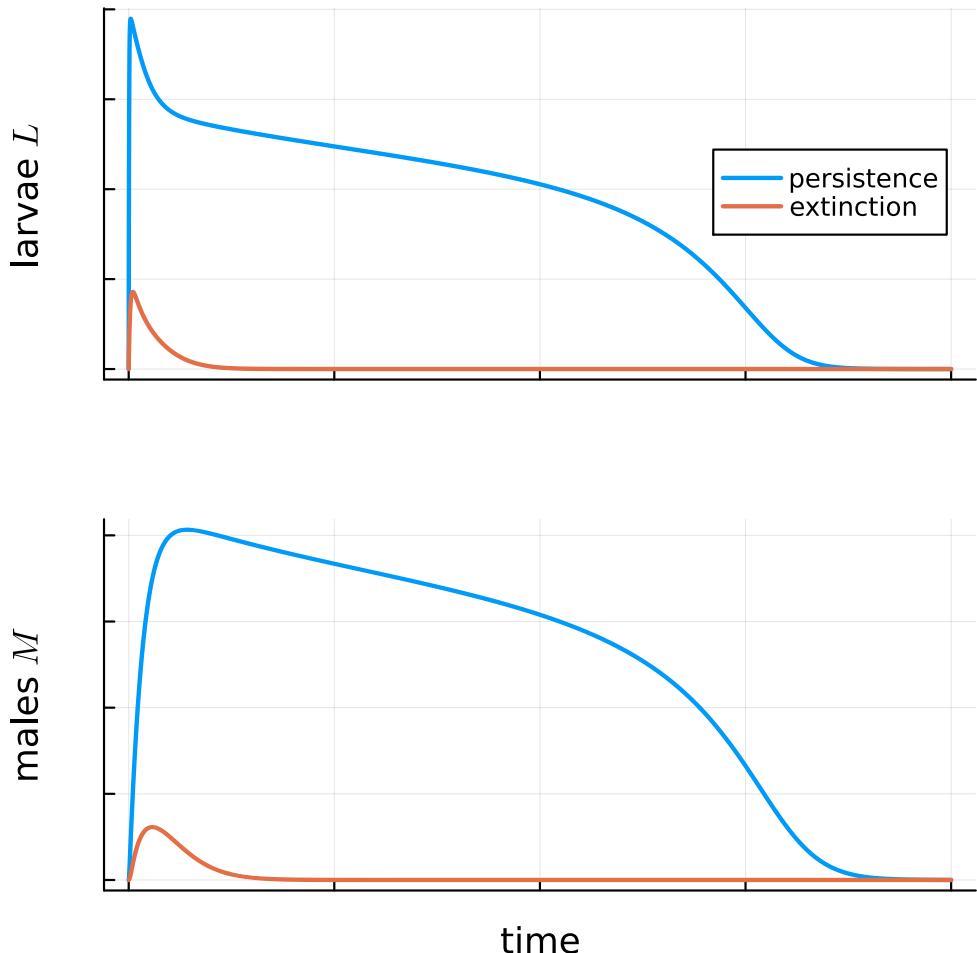


$M_s > \bar{M}_S : 0$ is GAS



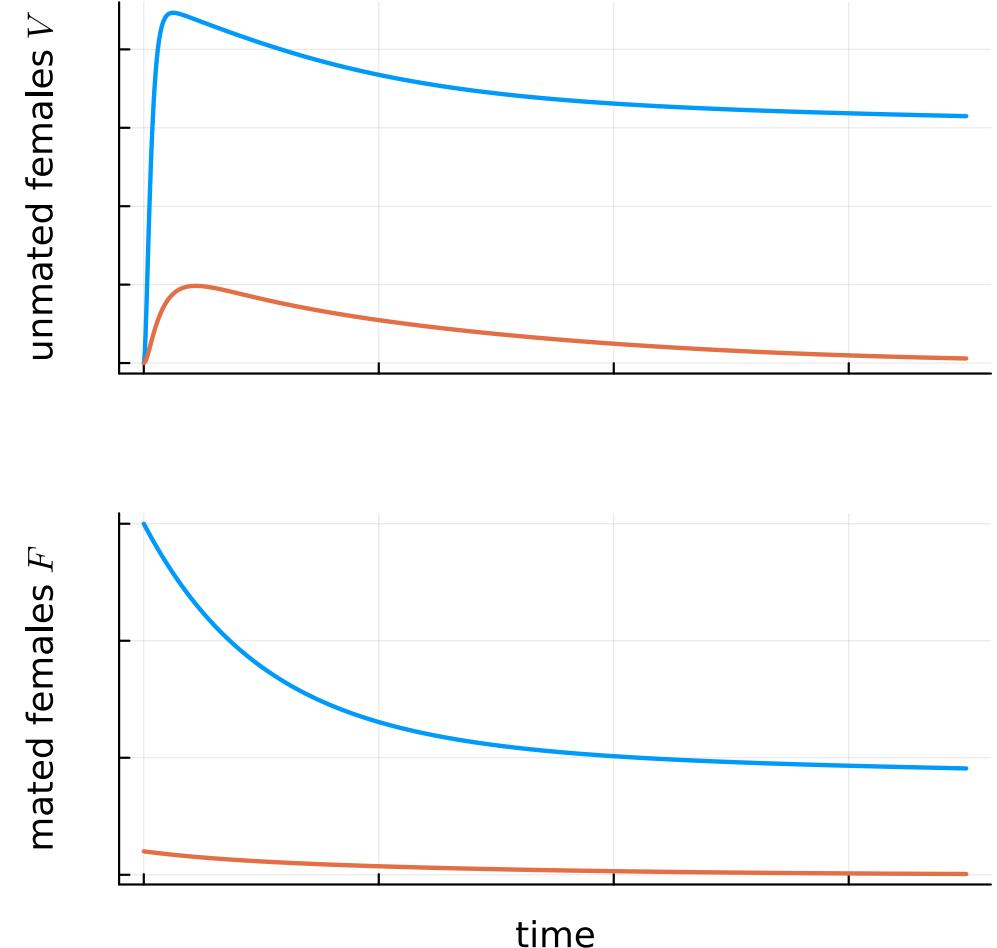
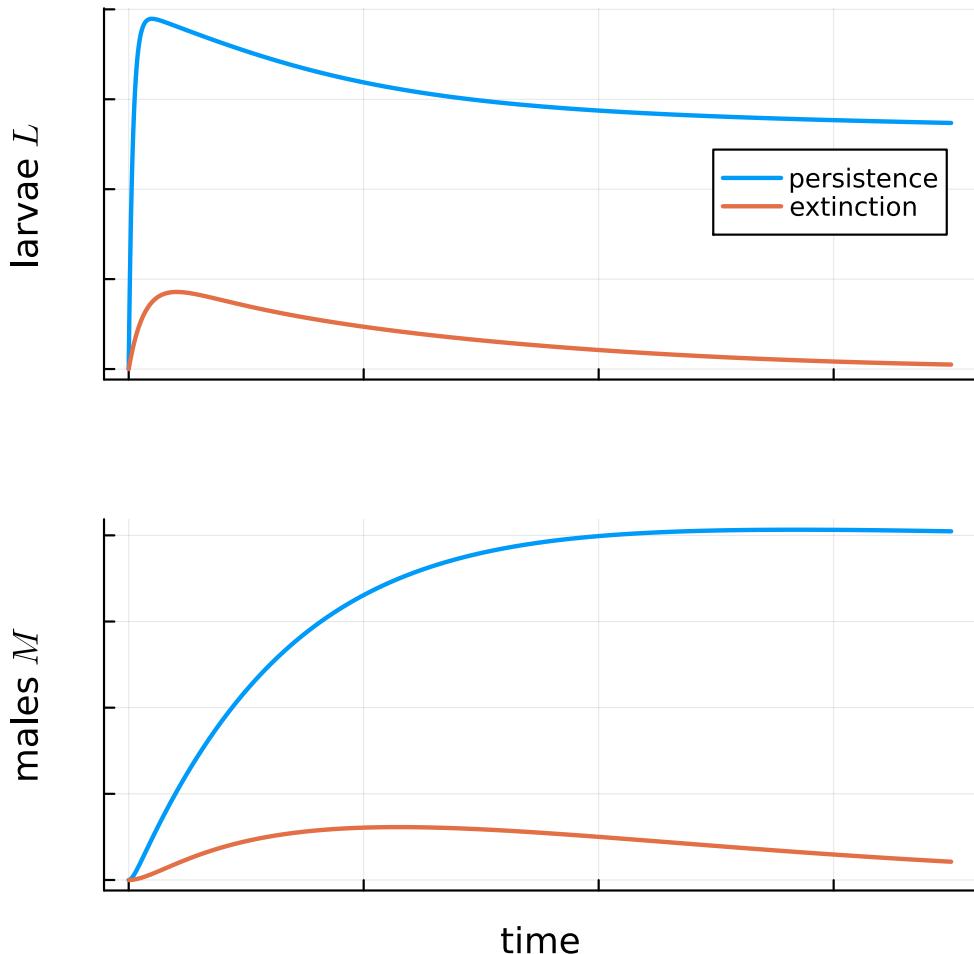
Mated females invade

- 0 is still GAS, but...



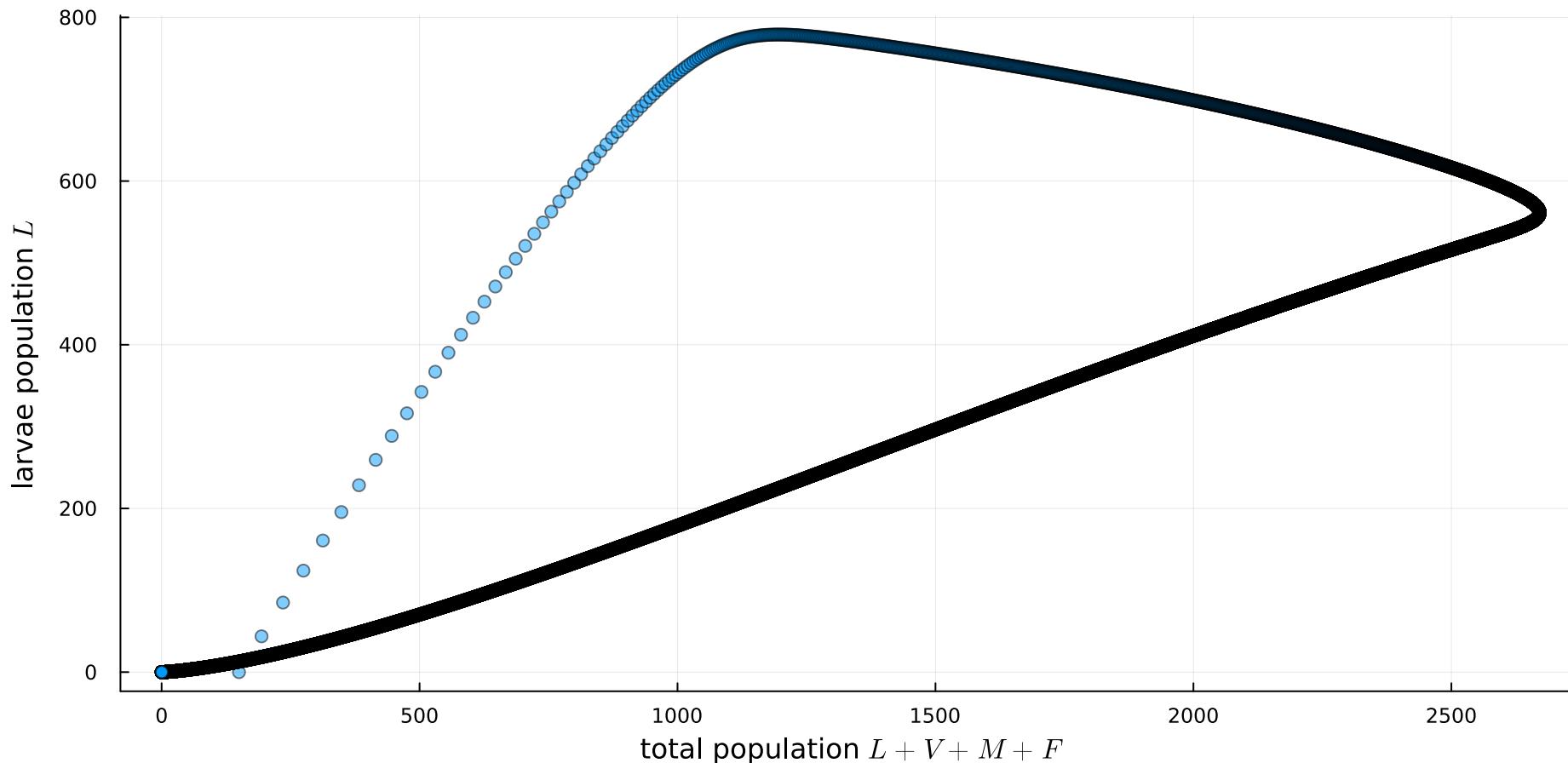
Mated females invade

- but GAS is not always enough



Larvae vs. population size

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

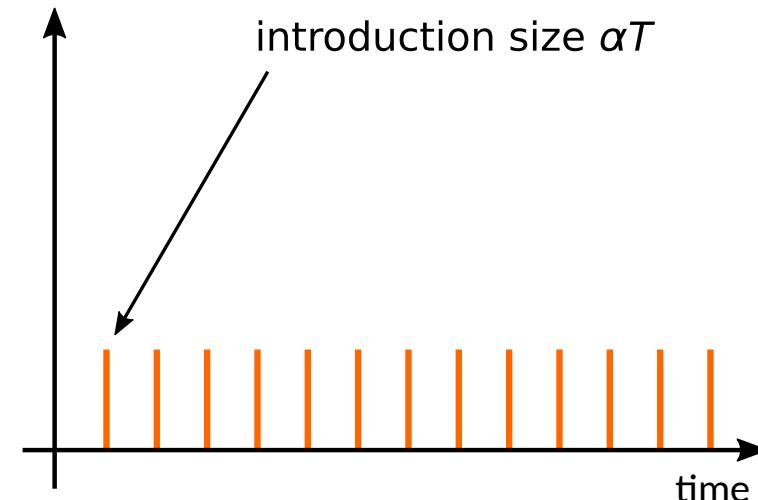
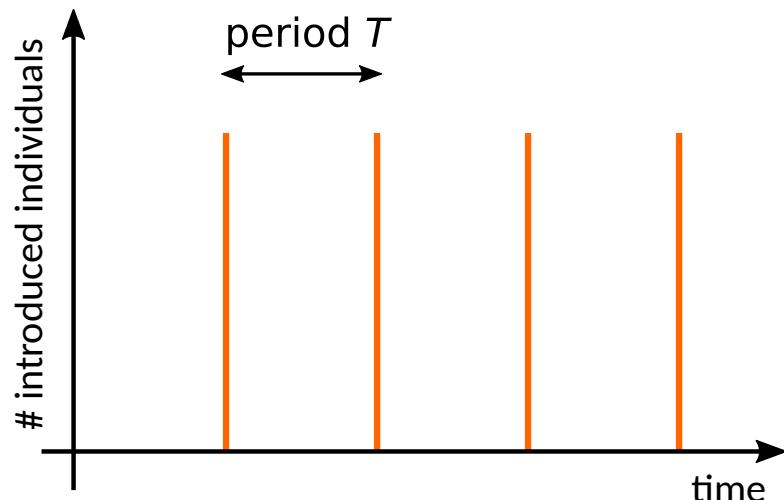


Model with pulsed M_s introductions

- same equations as before, but M_s is dynamic

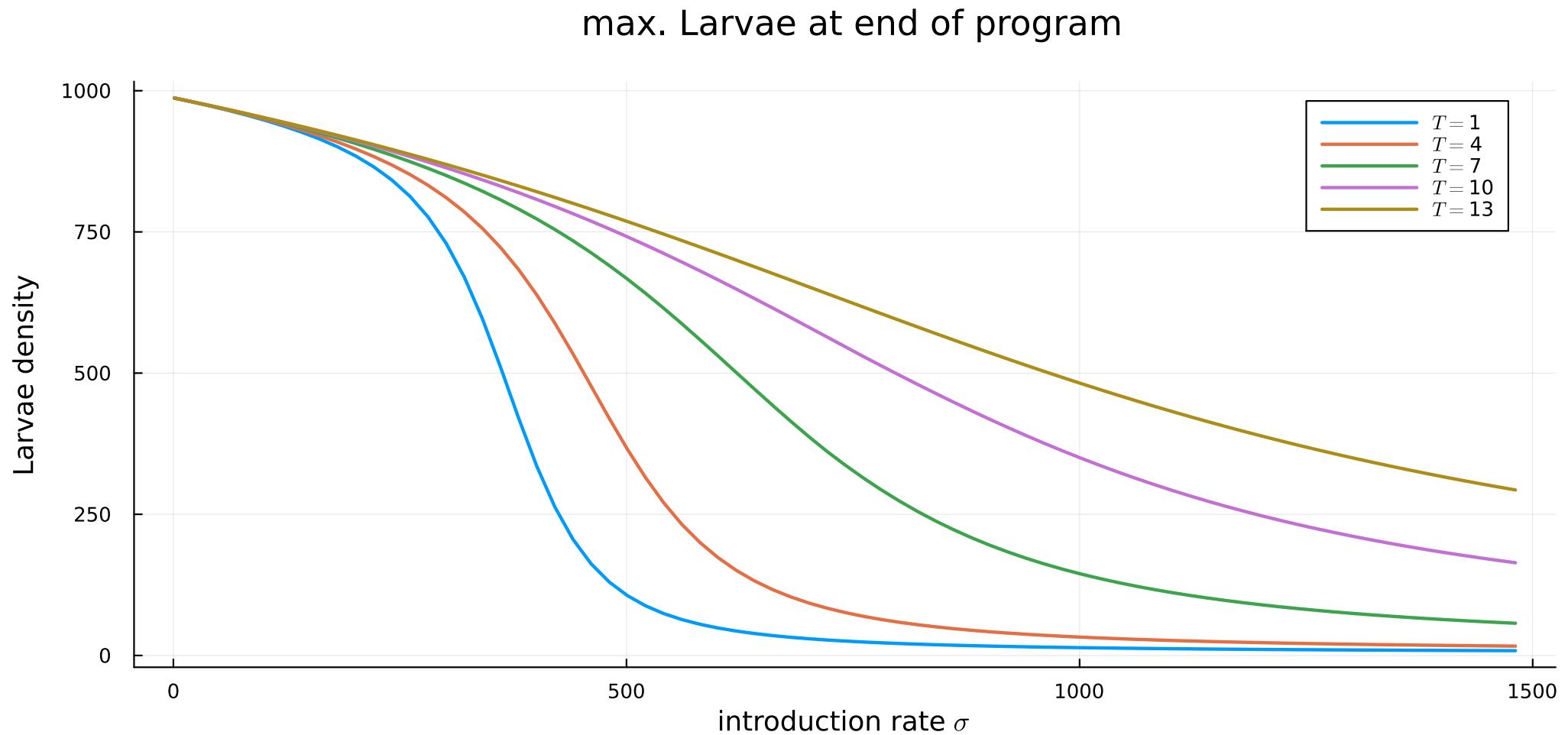
$$\begin{cases} \dot{M}_s = -\mu_M M_s & \forall t \in (kT, (k+1)T) \\ M_s(kT^+) = M_s(kT) + \sigma T \end{cases}$$

- classical trick to compare different introduction regimes for given introduction rate σ^{-1}



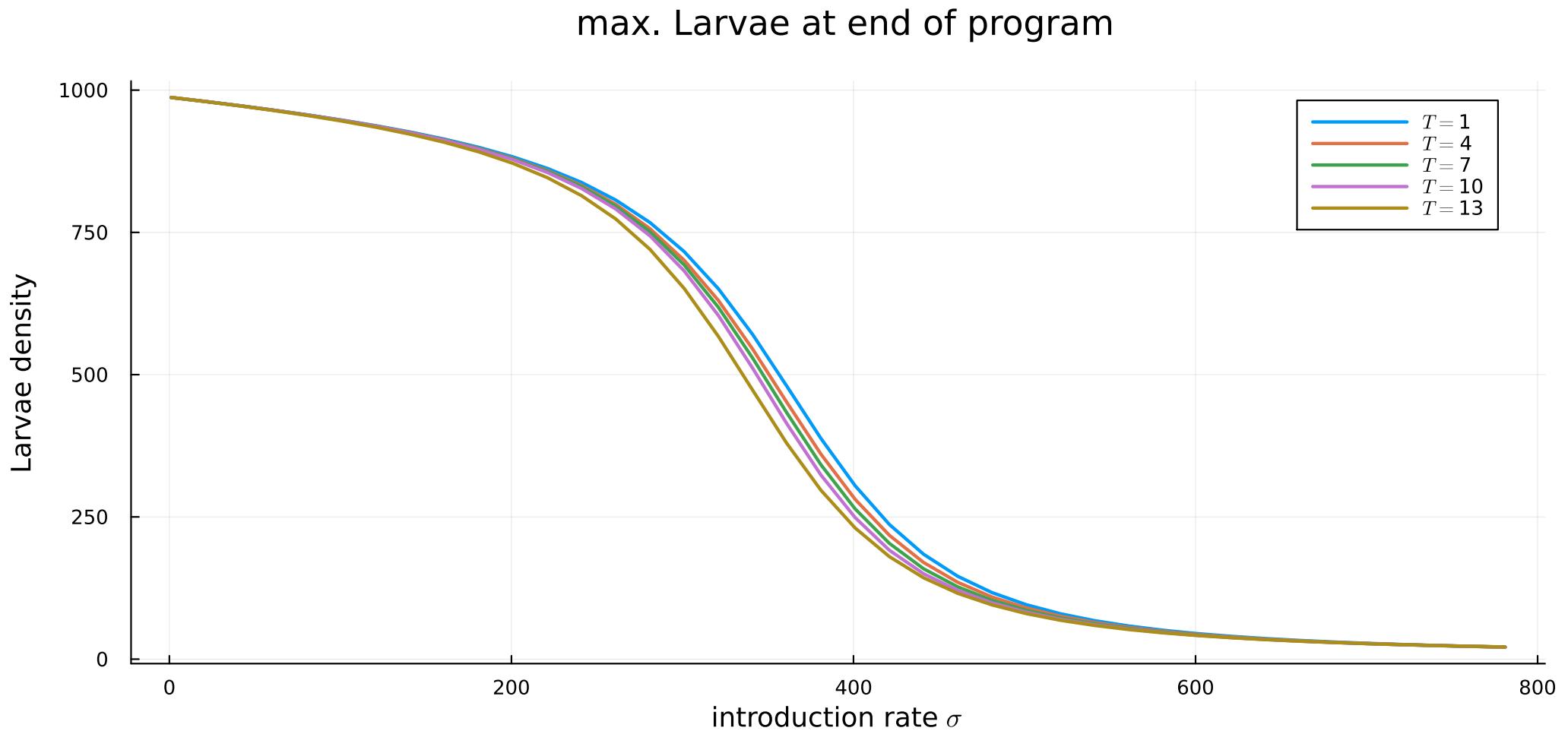
Numerical experiments: pulses

- which introduction strategy works best: late introductions situation



Numerical experiments: pulses

- which introduction strategy works best: early introduction situations



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



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- Ecophyto Ceratis Corse
- ANR Suzukiiss:me



