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

Crésus Kounoudji, Suzanne Touzeau, Frédéric Grognard, Louise van Oudenhove, Ludovic Mailleret

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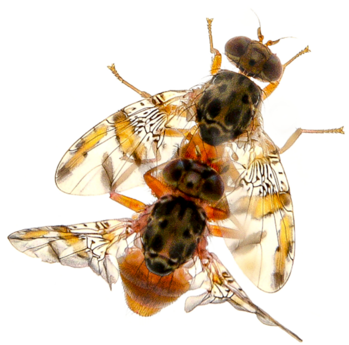

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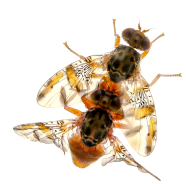
1: M2P2, ISA (INRAE, CNRS, Univ. Côte d'Azur)

2: MACBES (Inria, INRAE, CNRS Univ. Côte d'Azur)

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*

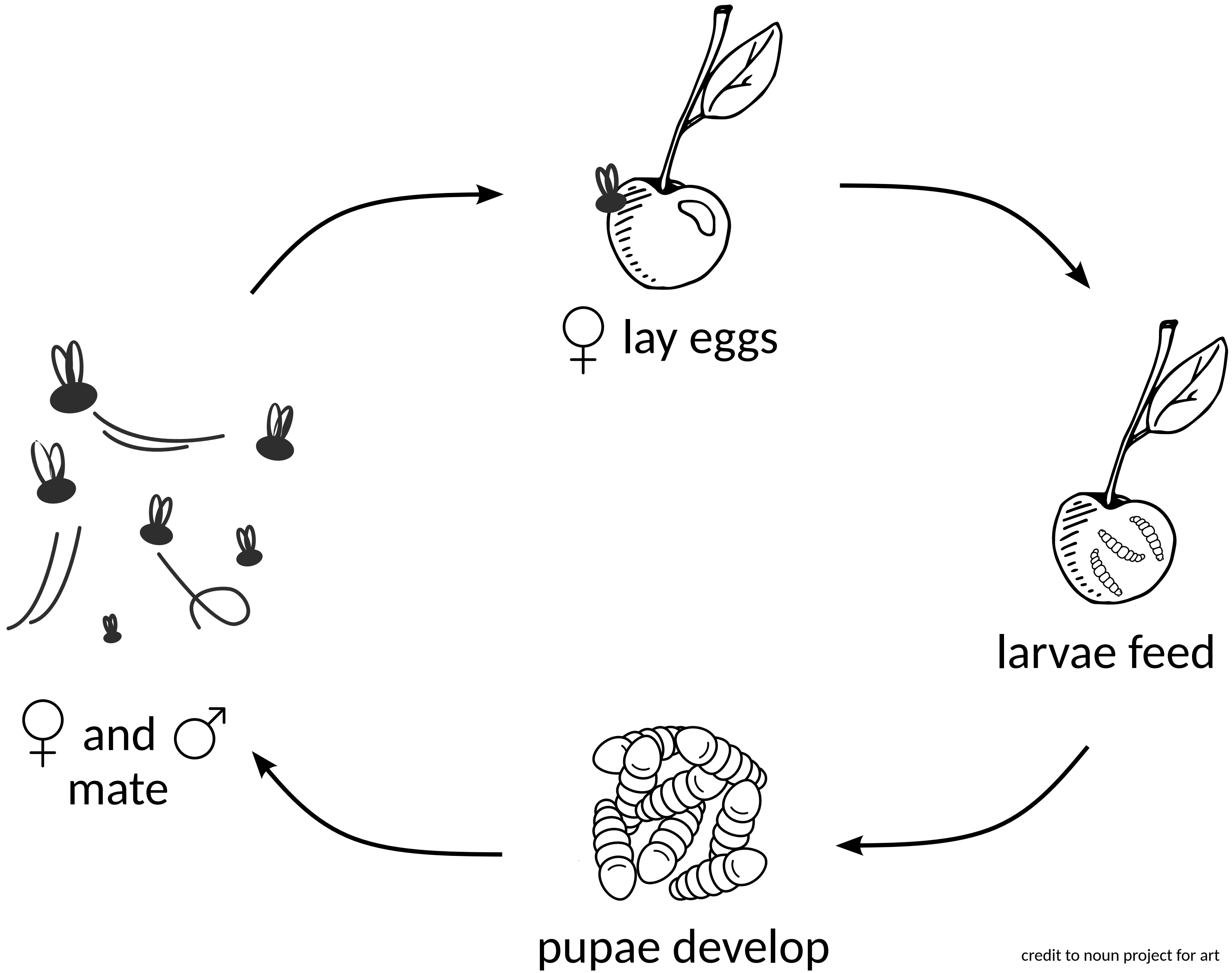
SIT is like a football game with so many people on the ground you simply cannot find your teammates [1]

1. Nick Secomb, General Manager of the Fruit Fly Response Program in Australia

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

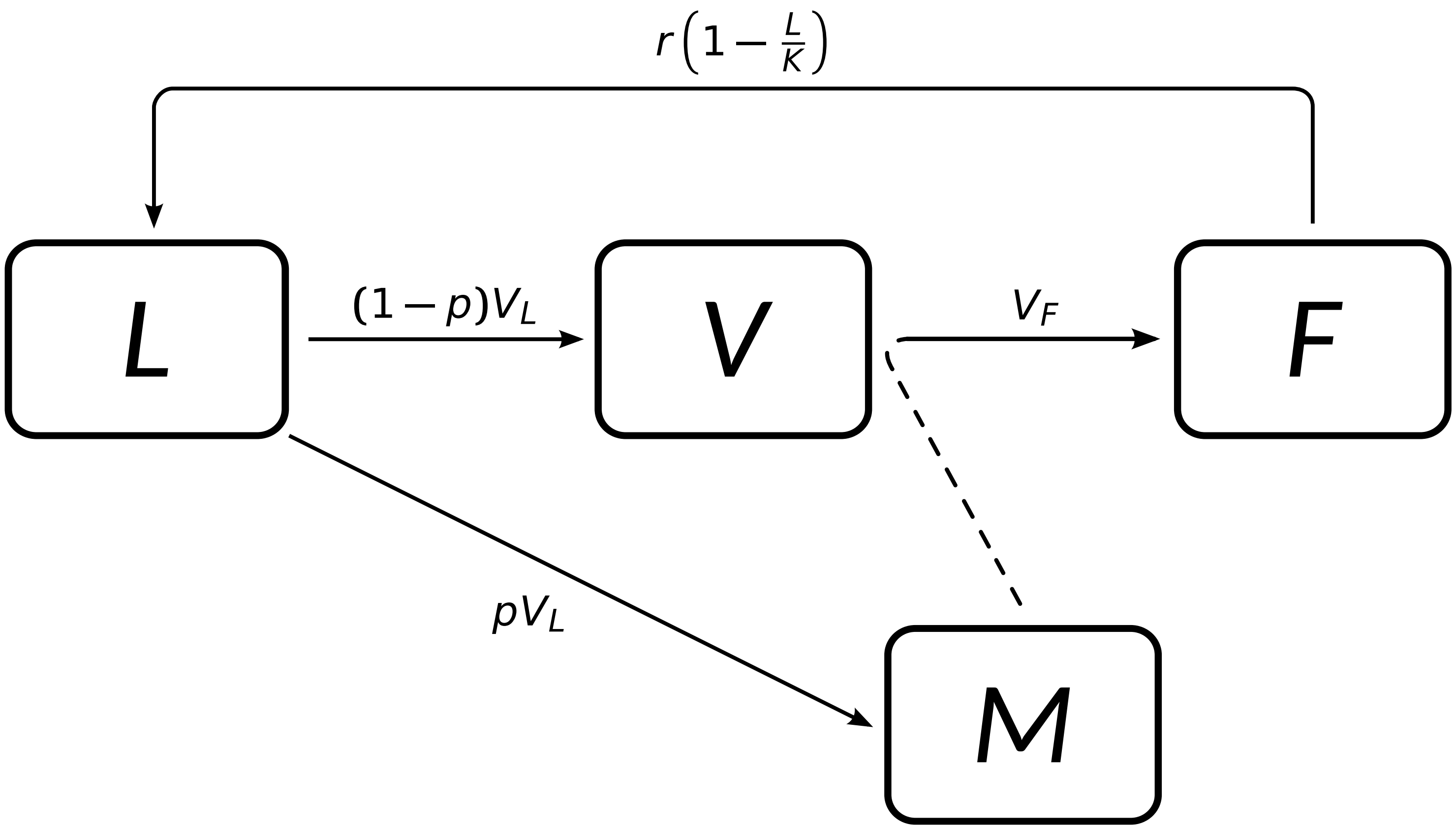
Fruit flies life cycle



credit to noun project for art

Model diagram

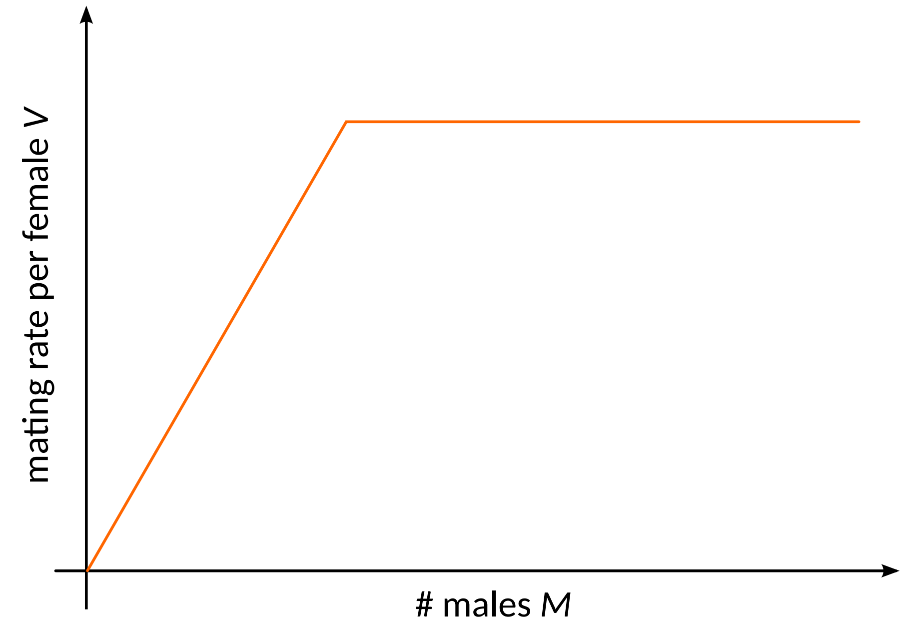
- 4 stages: eggs/larvae L, unmated females V, males M, mated females F [1]



1. based on the model proposed, in a different context, by: Anguelov, Dufourd and Dumont, *Ann. Math. Mod.*, 2017

Mating model

- frequency dependent mating probability [1]
  - \# 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

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

1. Anguelov *et alii*, 2017

Population dynamics model

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

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

$$\eta_0 = \frac{r\,(1-p)\nu_L \nu_F}{\mu_F(\mu_F + \nu_F)(\mu_L + \nu_L)} > 1$$

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

Reduced model

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

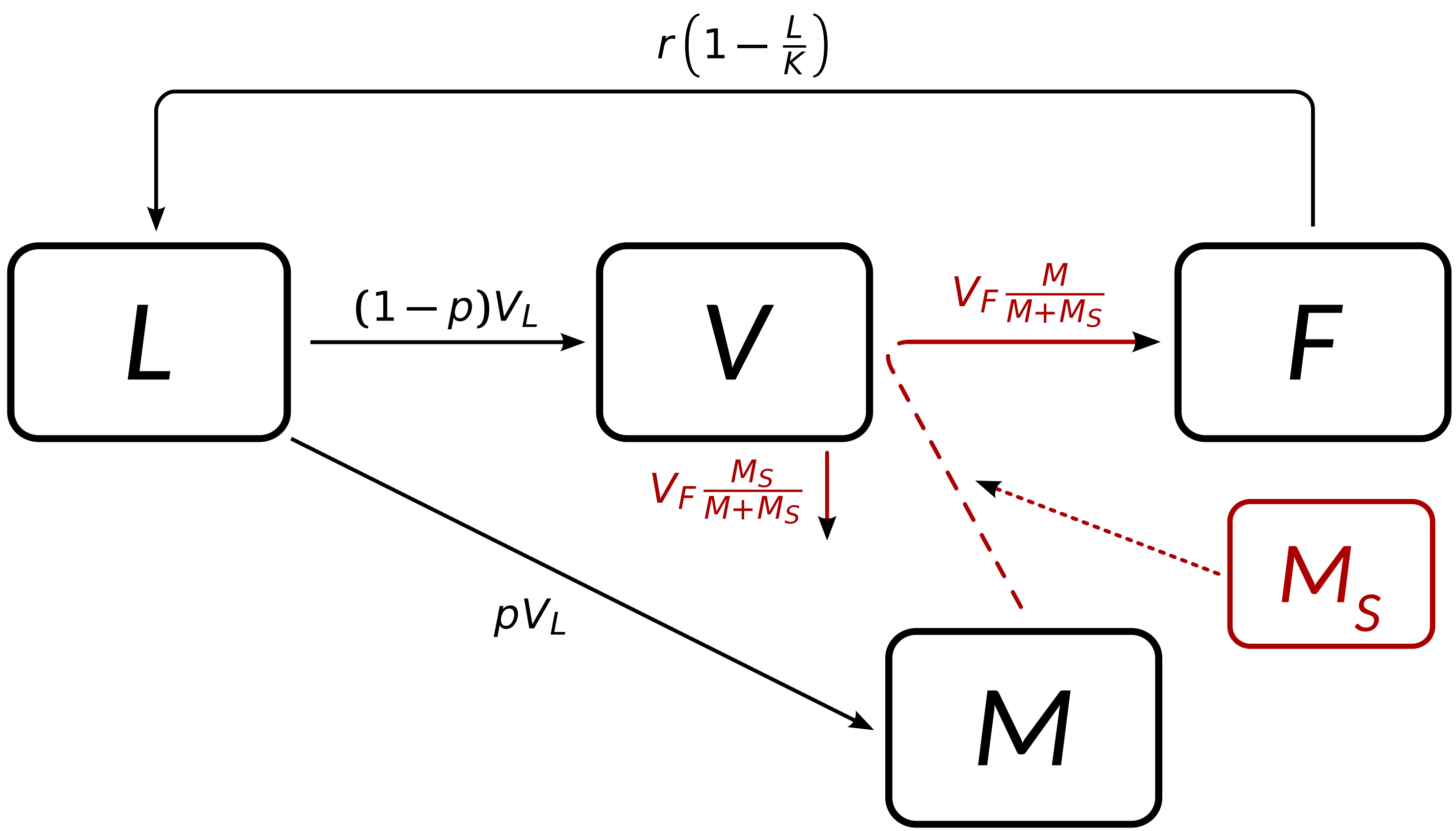
$$\begin{cases} \dot{L} = r\left(1 - \frac{L}{K}\right)F - \nu_L L - \mu_L L \\ \dot{M} = p\nu_L L - \mu_M M \\ \dot{V} = (1-p)\nu_L L - \nu_F V - \mu_F V \\ \dot{F} = \nu_F V - \mu_F F \end{cases}$$

- assuming that the basic reproduction number

$$\eta_0 = \frac{r\,(1-p)\nu_L \nu_F}{\mu_F(\mu_F + \nu_F)(\mu_L + \nu_L)} > 1$$

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

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

Analysis: equilibria

- equilibria are solutions of

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

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

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

Analysis: equilibria

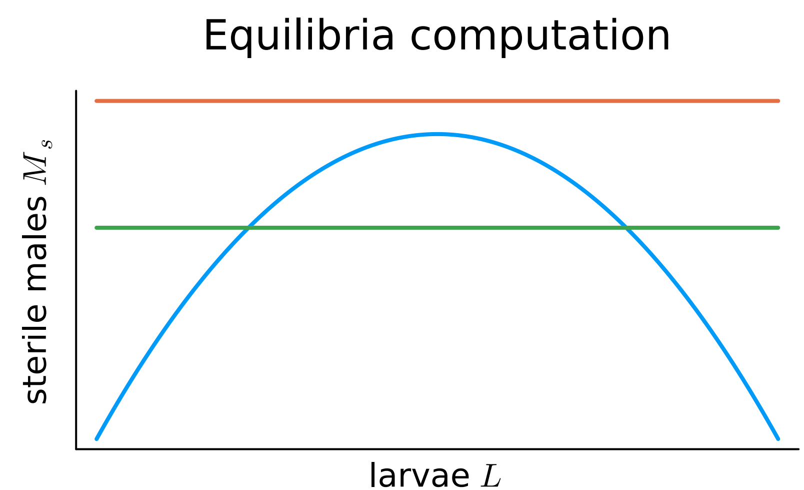
- rearranging, other equilibria must verify

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

- 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 😨

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

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

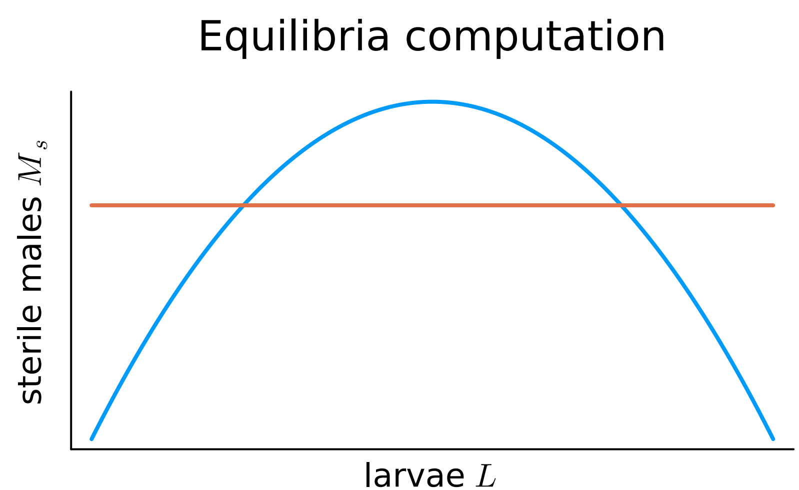
$$J^* = \begin{pmatrix} \bullet & 0 & 0 & + \\ + & \bullet & 0 & 0 \\ + & 0 & \bullet & 0 \\ 0 & + & + & \bullet \end{pmatrix}$$

Analysis: stability

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

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

- for positive equilibria built on L_1^* and L_2^*
  - strong clues for *fold bifurcation* at $M_s = \overline{M_s} = \frac{p\nu_L}{4\mu_M}\frac{(\eta_0-1)^2}{\eta_0}K$
  - 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 Meztler 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

1. S. Bowong, *PhD Thesis*, 2003

Analysis: stability of E_i^*

- express J in function of L^*

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

- so that

$$
A = \begin{pmatrix}
\frac{-\eta_0(\mu_L+\nu_L)\frac{p\nu_L}{\mu_M}L^*}{\frac{p\nu_L}{\mu_M}L^*+M_s} & 0 \\
p\nu_L & -\mu_M
\end{pmatrix} \quad \text{is Metzler stable}
$$

- and

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

Stability of E_i^*

- further computations show

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

- and

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

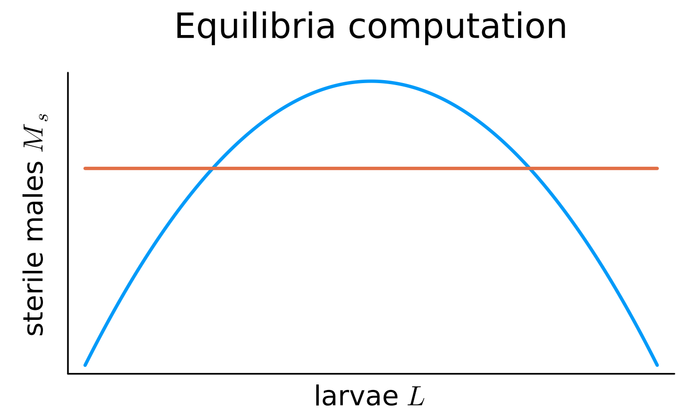
given that $M_s = \frac{p\nu_L}{\mu_M}L^*\left(\eta_0 - 1 - \frac{\eta_0 L^*}{K}\right)$ at equilibrium E_i^*

Stability of E_i^*

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

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

  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 $\mathrm{tr}(D - CA^{-1}B) < 0$[1]

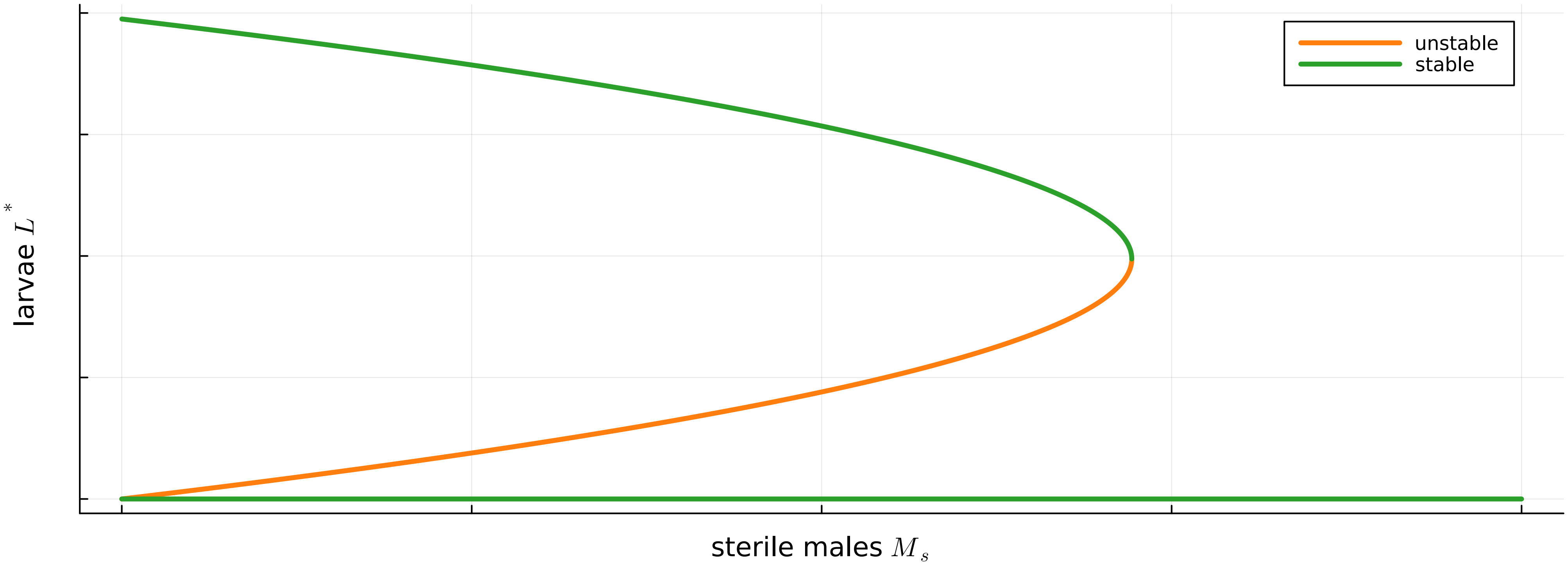
  from Bowong's lemma, $J(E_2^*)$ is thus stable and E_2^* is LAS

- at E_1^*, $\frac{dM_s}{dL} > 0$ which implies: $\det(D - CA^{-1}B) < 0$

  from Bowong's lemma, E_1^* is unstable

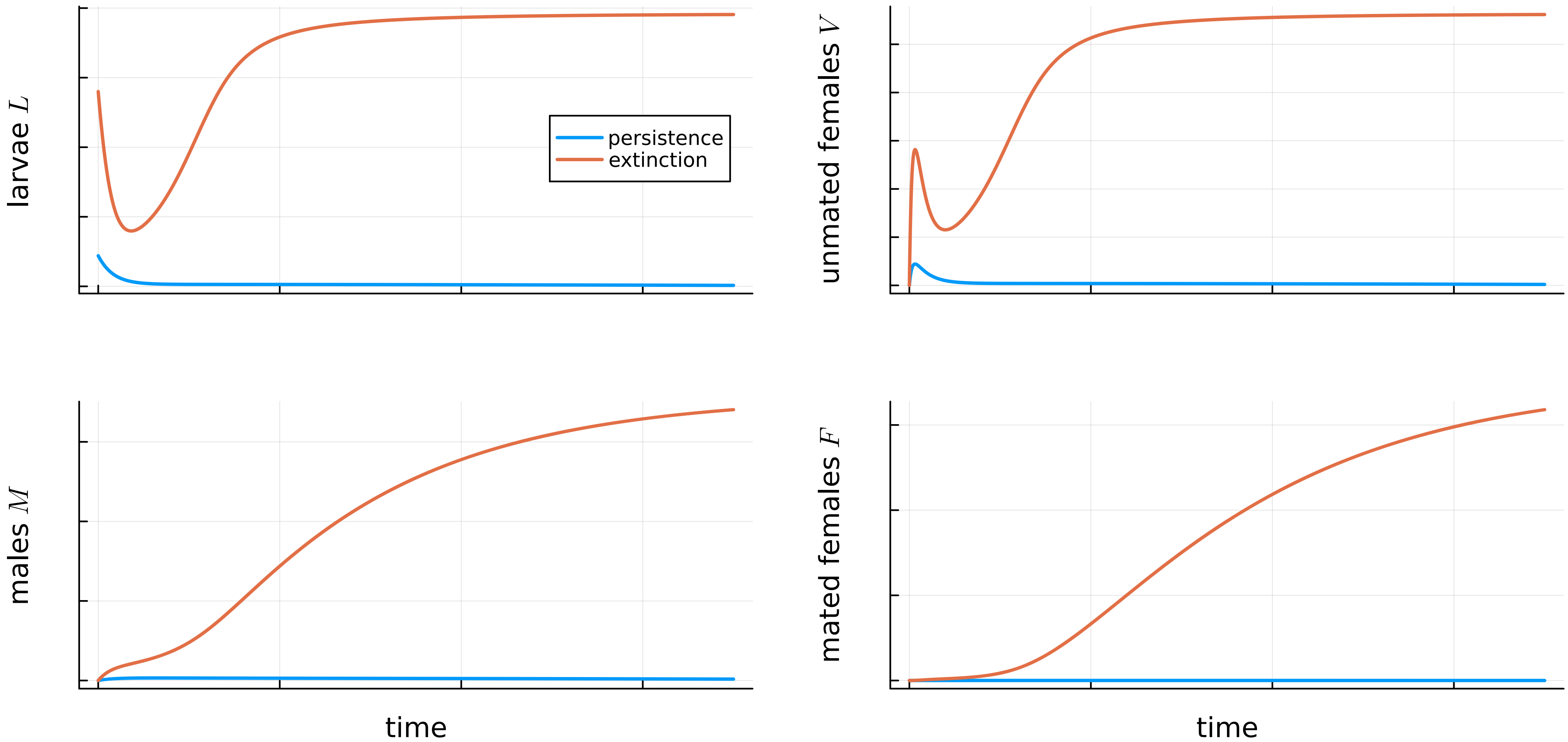
1. follows from $\det(D - CA^{-1}B) > 0$

Bifurcation diagram

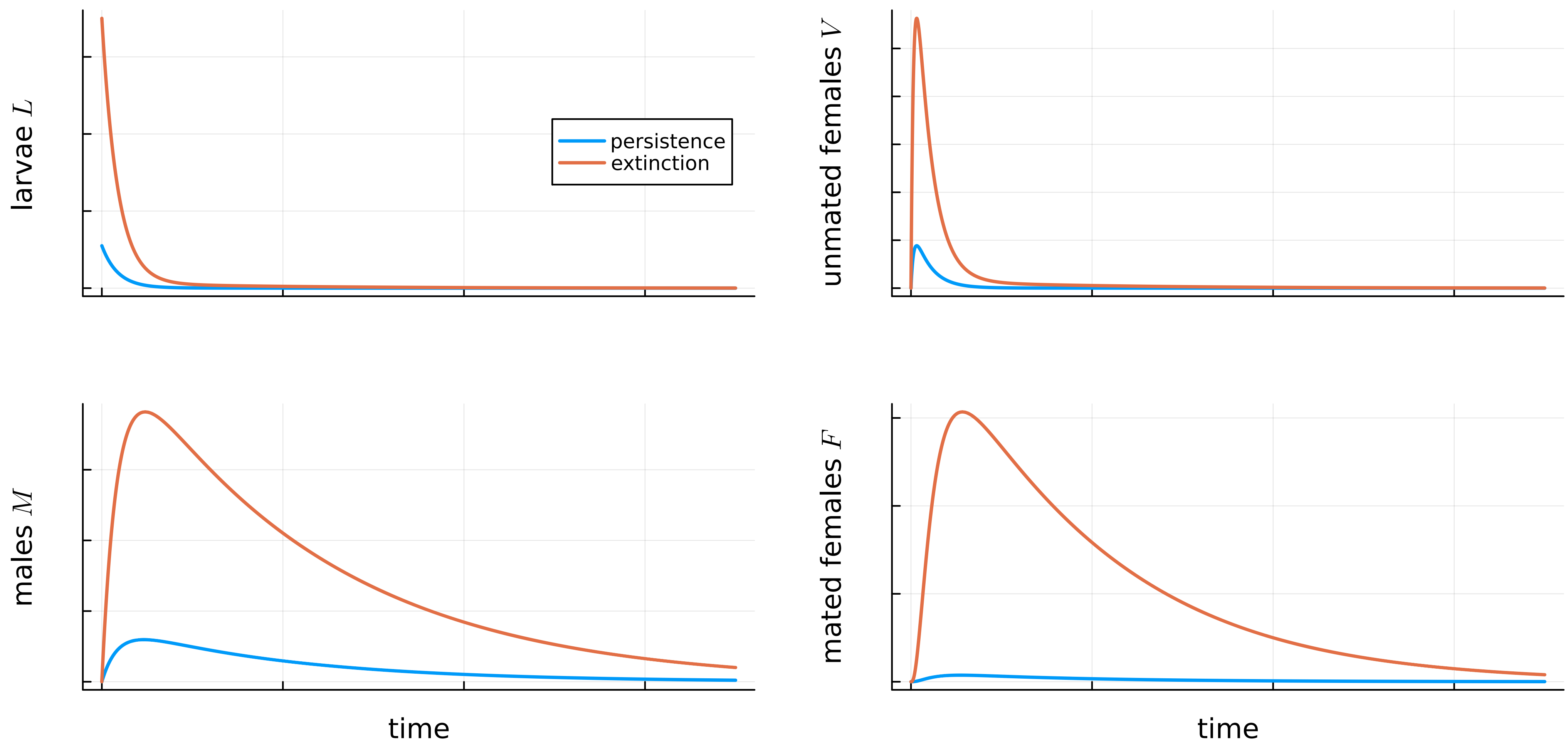


- thanks to the cooperativity of the model
  - when $M_S > \overline{M_S}$, 0 equilibrium is GAS
  - when $M_S < \overline{M_S}$ trajectories converge to either 0 or E_2^*

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

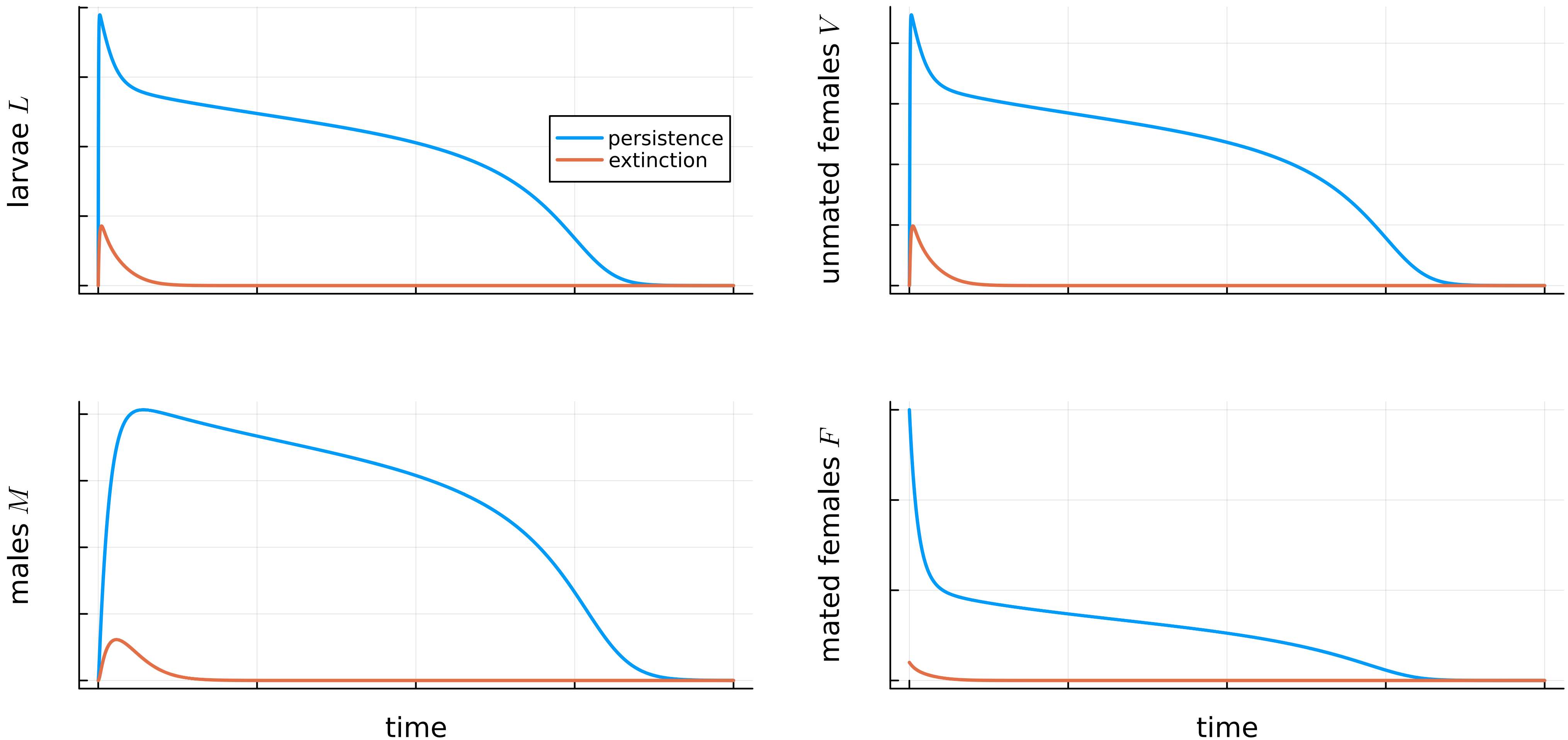


$M_s > \overline{M_S}$: 0 is GAS



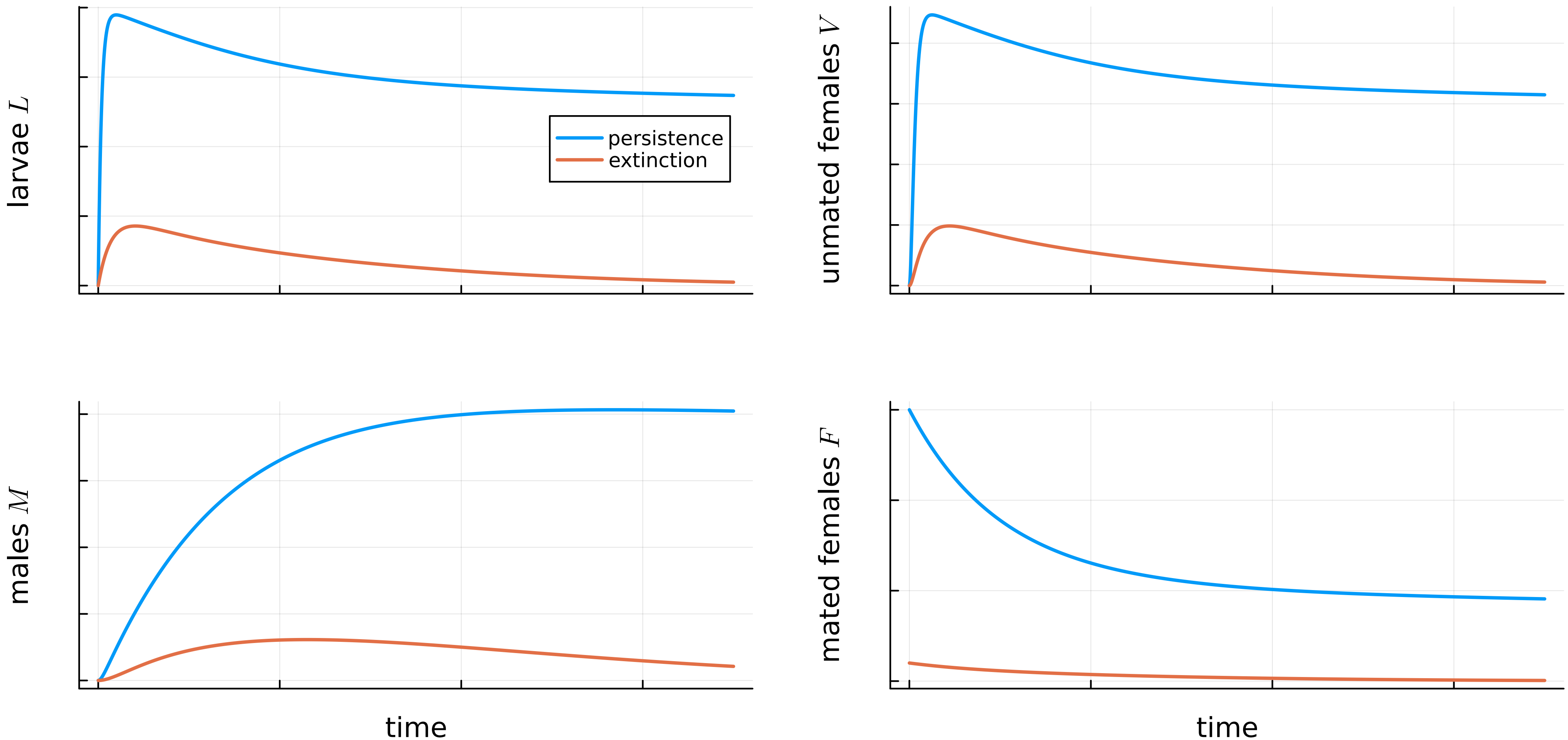
Mated females invade

- 0 is still GAS, but…



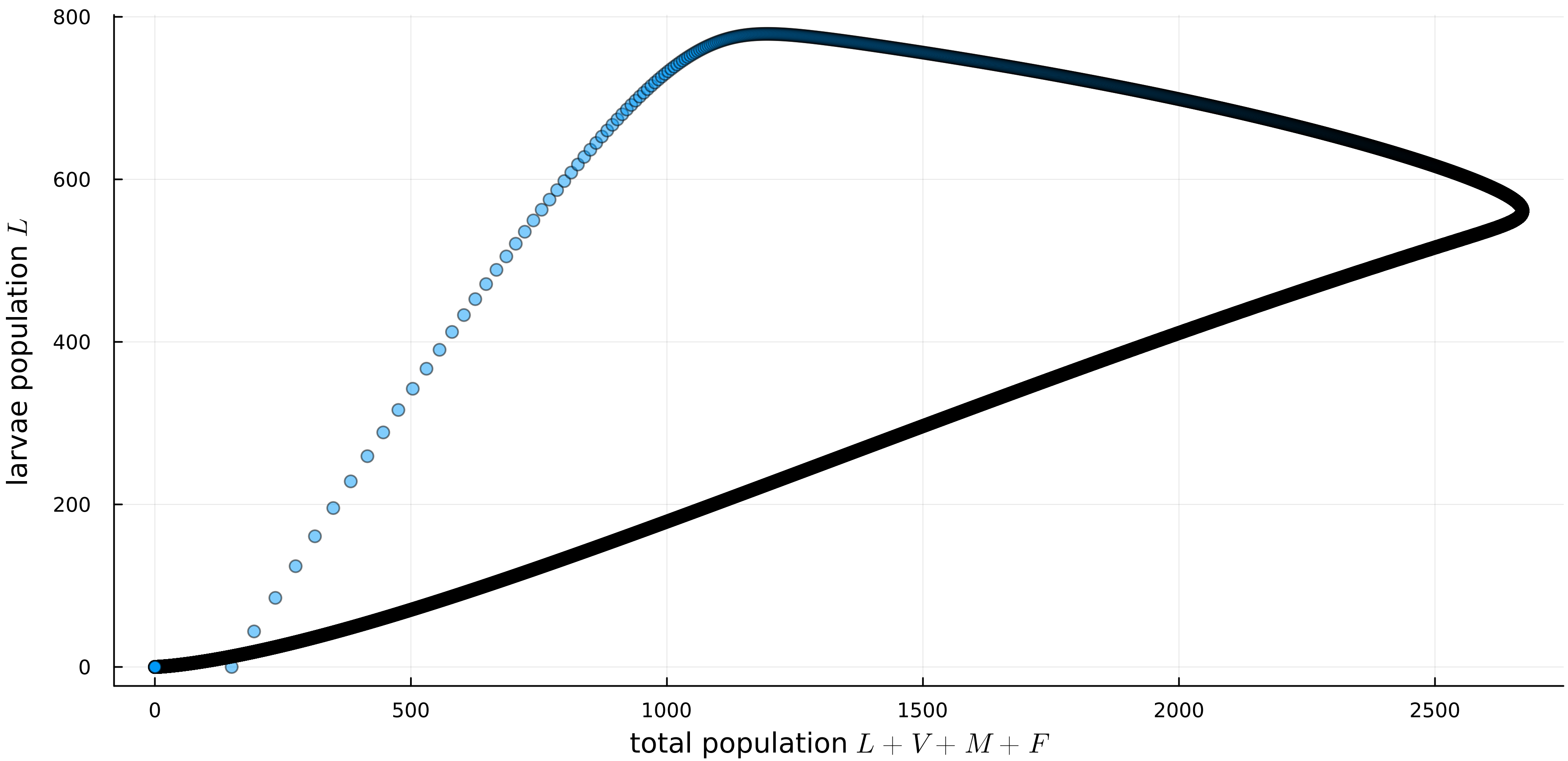
Mated females invade

- but GAS is not always enough



Larvae vs. population size

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

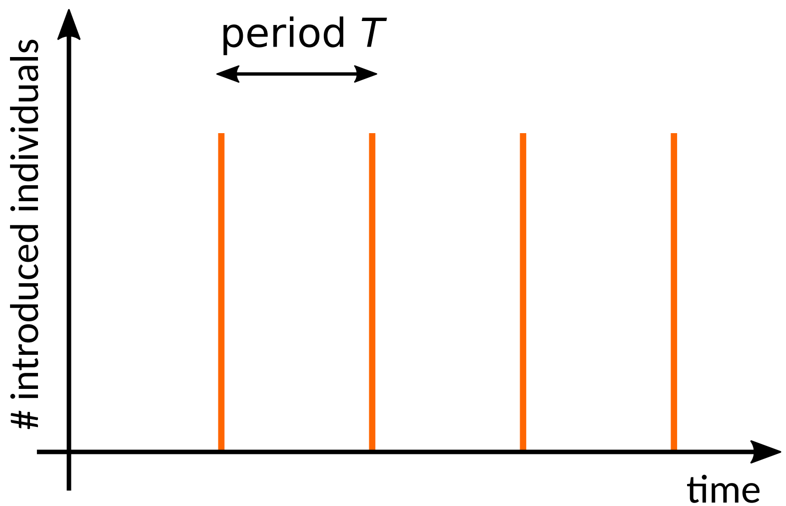


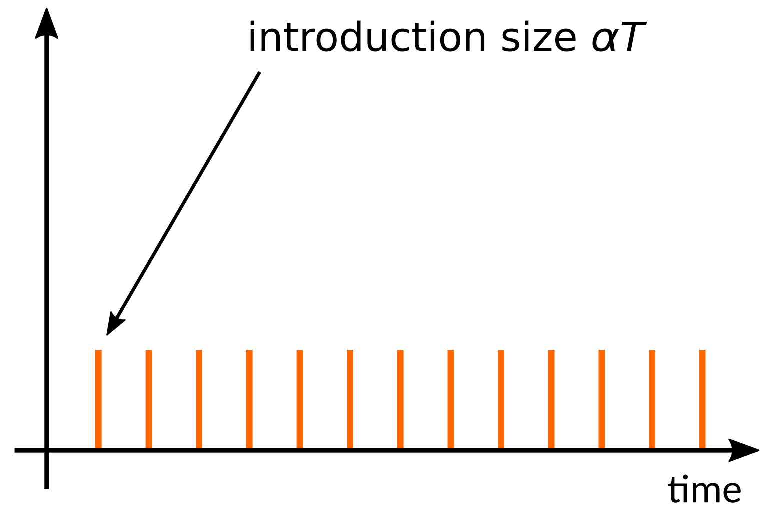
Model with pulsed M_s introductions

- 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]

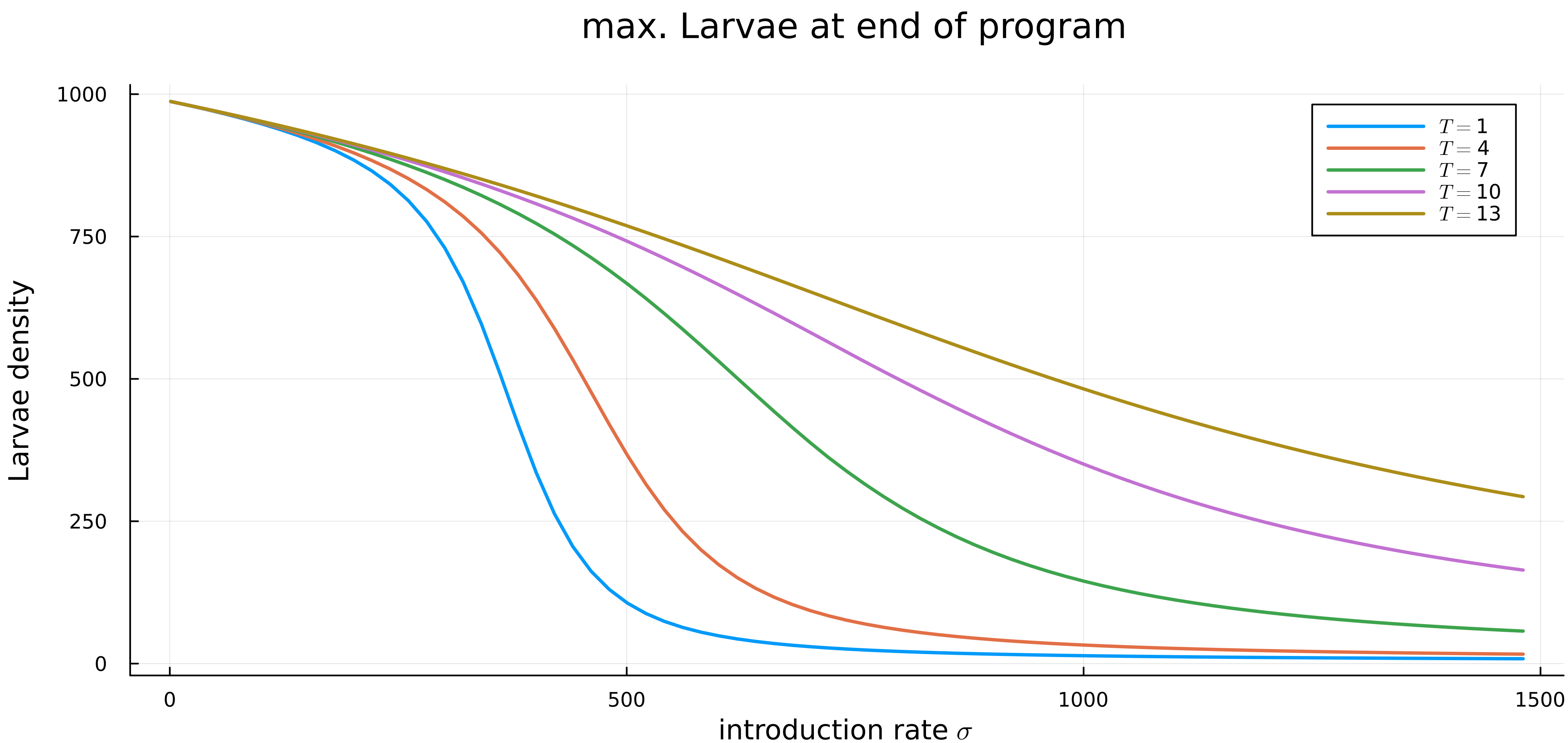




1. Mailleret & Grognard, 2009

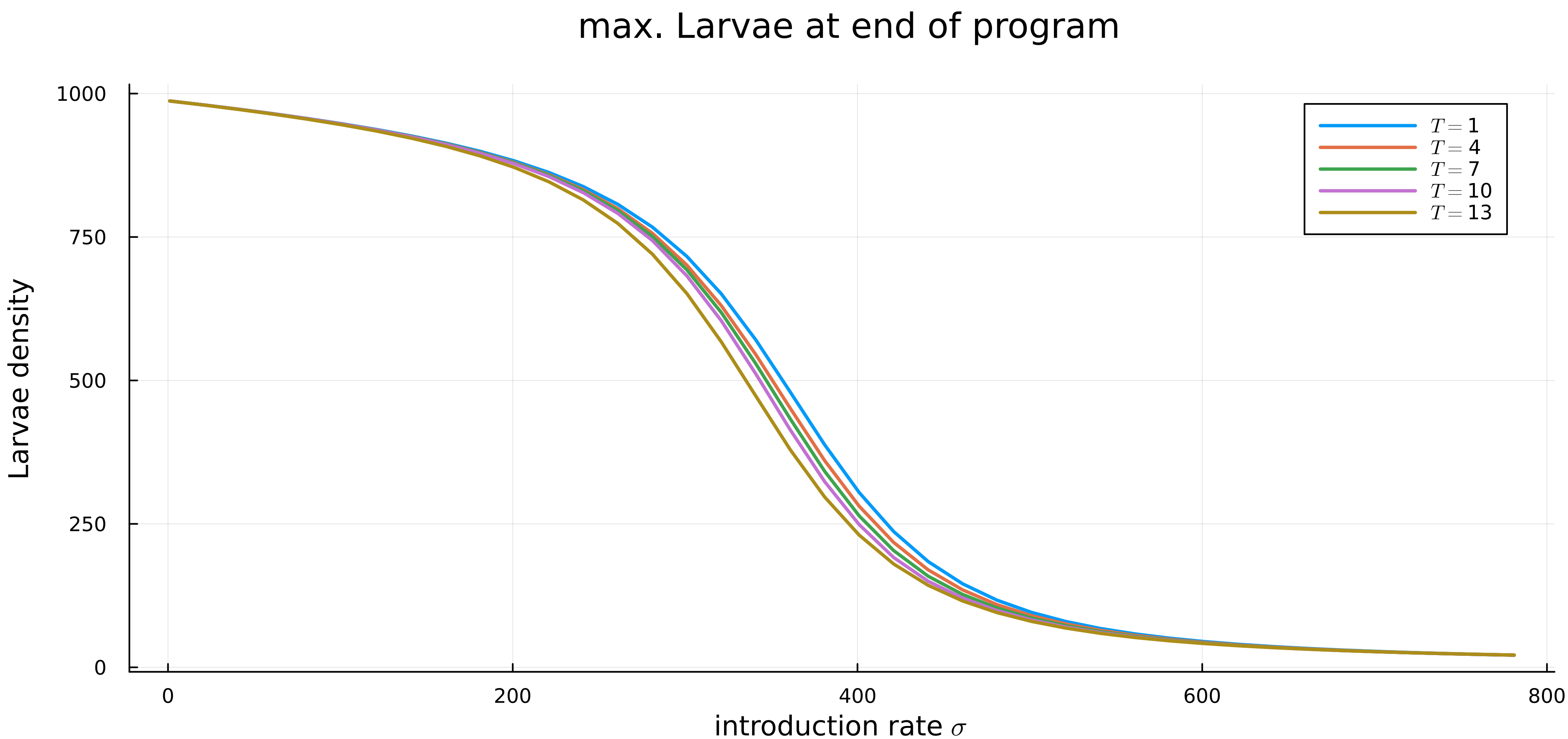
Numerical experiments: pulses

- 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

Where is
Waldo?

Acknowledgements

- Ecophyto Ceratis Corse
- ANR Suzukiiss:me