

Response to editor

Dear authors,

I have read with interest the detailed revisions of your manuscript and I think it is worth sending back to the reviewers. However, I noticed that the discussion of earlier results on modelling the evolution of virulence in host-parasitoid interactions (or "obligate killers") is still lacking. I believe this is an important issue since in simple parasitoid model will always select for higher virulences.

For instance, consider the following system of ODEs:

$$\frac{dS}{dt} = -\beta SV \quad (1)$$

$$\frac{dI}{dt} = \beta SV - (\mu + \alpha + \gamma)I \quad (2)$$

$$\frac{dV}{dt} = \sigma\alpha I - \delta V \quad (3)$$

where S are susceptible hosts, I are infected hosts, and V are free parasites (or viruses). β is the transmission rate, α is the virulence (disease-induced host mortality), μ is the natural mortality, γ is the recovery rate, δ is the clearance rate of free parasitoids, and σ is the number of parasitoids produced upon host death.

Following the next generation theory (Diekmann et al 1990), the invasion fitness of a mutant parasitoid in the system is given by

$$R(\alpha_m, \alpha) = \frac{\beta\sigma S(\alpha)}{\delta} \frac{\alpha_m}{\mu + \gamma + \alpha_m} \quad (4)$$

If we try to find the virulence that maximises this infection fitness, we get

$$\frac{\partial R(\alpha_m, \alpha)}{\partial \alpha_m} = \frac{\beta\sigma S(\alpha)}{\delta} \frac{\mu + \gamma}{(\mu + \gamma + \alpha_m)^2} \quad (5)$$

This partial derivative is always greater or equal than 0, meaning that in this simple model only parasitoids with greater virulence can invade.

In terms of references to mention but also, more importantly, to discuss and acknowledge, I can suggest the seminal article by Ebert Weisser (1997, Proc B), the model by Sasaki Godfray (1999) which includes coevolution, the study by Caraco Wang (2006, JTB) more focused on phages, and potentially Sofonea et al (2018) for an ebola model.

These are mainly suggestions and it is very possible I missed some relevant model so feel free to further investigate the literature.

Best regards,

- Samuel Alizon

Author response:

We thank the editor for this comment. We agree it is important to place our results in context with other studies on the evolution of virulence in obligate killer parasites and have added an explicit discussion starting on line 182.