Questions, goals, suggestions

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1 Suggestions for our model

1. About the carrying capacity, is the normalization - done the way as it is in our model - legit? It probably should not affect both D and I compartments equally. For example in the Little paper they put its effect in the decline of reproduction. Maybe it could also be projected into the deathrate.
2. Should we stick with the environmental transmission or try the direct transmission model as well?
3. Should we study the effect of the age structure on the "infectivity" (or size of the burst)? It might be more depending on the age of the infection, should we structure our model with respect to the age of infection as well?
4. Possible thing we could check if it is consistent with our model: Paper [4] claims: "... The relationship between virulence and parasite transmission is believed to be a primary driver of the evolution of virulence, and it can be used to predict the optimal level of virulence [23]. Izhar and Ben-Ami [9] showed that this relationship is age-specific, because younger hosts produced more transmission stages than older ones even though parasite-induced **host mortality (virulence) did not vary with host age**..." We could try to check if we have a virulence which is constant with age.

2 Questions about the data

Is there some description of the experiment? I would be particulary interested in the following questions:

1. What is the chronology of the experiment? Was it one generation of peers observed over time? Or was there some non-trivial initial age distribution?
2. Was it all one population? Or were the populations somehow separated?
3. What was the process of the exposure to the pathogen? Were the death individuals removed from the population to avoid pathogen exposure outside of designeted time windows?

4. Is there some hypothesis concerning these data, which would be interesting to look at?

3 Review of the Little paper

Most of the useful information are mentioned in the appendix of the paper.

They observed in their experiment that older mothers give birth to less susceptible offsprings. Then they cited some papers [1],[2], [3] which showed that older individuals are less susceptible themself.

Then they build an epidemiological model, where they wanted to simulate the above mentioned age effects on the spread of epidemia (through R_0).

They used an age-structured SI model, but they also had a look at the environmental transmission for confirmation.

Their SI model has 4 age groups (Young individuals from young mothers, young individuals from old mothers, old individuals from young mothers and old individuals from old mothers). They include the effect of the finite carrying capacity into lowering of the reproduction rate.

Then they consider baseline susceptibility for the age group of young individuals from young mothers β_{YY} and then introduce the factors $M, V > 0$ which correspond to the lowering of the susceptibiblity due the age or due to the age of the mother, respectively. For the group of old individuals of old mothers they combine both effects first multiplicatively $\beta_{OO} = (1-M)(1-V)\beta_{YY}$ and then they confirm their claim even for additive combination of the effects with $\beta_{OO} = (1-M-V)\beta_{YY}$.

The above concerned the susceptibility, for the "infectivity" of the infector they did not explicitely consider the age effect. They only distinguised the cases when the infector died due to the infection and then it was transmiting and when it died due to natural causes and then it was transmitting only with some probability $p < 1$).

They assume constant virulence and death and reproduction rates accross all the age groups.

With the above model, they compute R_0 and find out that for some values of M and V (the proportional factors lowering the susceptibility due to the age effects) they can achieve R_0 to be decreasing with increasing death rate δ. Which opposes usual assumptions (and experience) and therefore claim to have found a new ecological context in which R_0 has a different behaviour.

They confirmed this for both multiplicative and additive model of the susceptibility $\beta_{OO} = (1 - M)(1 - V)\beta_{YY}$ and $\beta_{OO} = (1 - M - V)\beta_{YY}$.

Then they also took a look at the model with environmental transmission (basically the same as what we have now, they only added the consideration of pathogen being removed from the environment after infecting a new individual). This model also provided them with R_0 which had qualitatively the same behaviour as in the SI model without the environmental transmission.

4 Goals

What exactly should be our goal?

In the Little paper, they made their novel observation of the maternal age effect on the susceptibility, which they used to introduce a new parameter into the SI model, which produced unusual behaviour of R_0. Could we do something like this? Is there some potentially new information in the data we have?

Or should we try to confirm/disprove something which has been already demonstrated on a simpler model, using our more finely age structured model (with allowing age dependence of the parameters as well)?

References

[1] Rony Izhar and Frida Ben-Ami. Host age modulates parasite infectivity, virulence and reproduction. *Journal of Animal Ecology*, 84(4):1018–1028. doi: 10.1111/1365-2656.12352. URL `https://besjournals.onlinelibrary.wiley.com/doi/abs/10.1111/1365-2656.12352`.

[2] Jennie S. Garbutt, Anna J. P. O'Donoghue, Seanna J. McTaggart, Philip J. Wilson, and Tom J. Little. The development of pathogen resistance in daphnia magna: implications for disease spread in age-structured populations. *Journal of Experimental Biology*, 217(21):3929–3934, 2014. ISSN 0022-0949. doi: 10.1242/jeb.111260. URL `http://jeb.biologists.org/content/217/21/3929`.

[3] S. ALIZON, A. HURFORD, N. MIDEO, and M. VAN BAALEN. Virulence evolution and the trade-off hypothesis: history, current state of affairs and the future. *Journal of Evolutionary Biology*, 22(2):245–259. doi: 10.1111/j.1420-9101.2008.01658.x. URL `https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1420-9101.2008.01658.x`.

[4] Rony Izhar, Jarkko Routtu, and Frida Ben-Ami. Host age modulates within-host parasite competition. *Biology Letters*, 11(5), 2015. ISSN 1744-9561. doi: 10.1098/rsbl.2015.0131. URL `http://rsbl.royalsocietypublishing.org/content/11/5/20150131`.