Tick-borne Diseases Transmission Research: Co-Feeding in Ticks

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Systemic vs co-feeding transmission

Ixodidae ticks are vectors responsible for the spread of a variety of pathogens including viruses, bacteria and parasites. After hatching from eggs, larvae, nymphs and adults need to complete a series of questing, feeding and engorging activities to progress from one stage to the next.

Tick-borne diseases such as Lyme disease and tick-borne encephalitis are primarily transmitted during the blood feeding process, through systemic and co-feeding horizontal transmission routes.

Systemic transmission involves the transmission of the pathogen from infectious ticks to susceptible hosts, and the transmission of pathogen from infectious hosts back to susceptible feeding ticks. Co-feeding transmission provides an exchange of tick-borne pathogens between co-feeding infected and susceptible ticks (perhaps at different stages) directly even though pathogens have not been established within the reservoir host.

Co-feeding in ticks facilitates pathogen transmission

The 1987 Science paper by Jones et al. (1) considered the mode of co-feeding transmission, although qualitative analysis on how co-feeding transmission contributes to the complexity of pathogen spread patterns is still an infancy. The modeling studies by Rosa et al. (2, 3) incorporated both systemic and co-feeding transmission routes to understand conditions for infection persistence of tick-borne pathogens.

Hartemink et al. (4) showed that the basic reproduction number (R_0)-a summative index that can be used to show that the tick-borne disease transmission cannot be maintained in a region where $R_0 < 1$-could be underestimated to such an extent that in many tick-borne disease endemic areas, $R_0 > 1$ would be impossible without co-feeding transmission included. It was until the study of Nah et al. (5) in 2019 that the contribution of co-feeding transmission towards tick-borne encephalitis infection spread in an epidemic area is quantified.

A sequel by Nah et al. (6) evaluated the impact of climate change on co- feeding transmission and concluded that the transmission potential and the risk in a tick-borne encephalitis endemic area in Europe are expected to increase along with the increase of the temperature in 2021-2050 and 2071-2100. This increase will be facilitated by the expected extension of the tick questing season and the increase of the numbers of susceptible ticks (larval and nymphal) and the number of infected nymphal ticks co-feeding on the same hosts, leading to com- pounded increase of infections through the non-systemic transmission.

These studies (5, 6) call for further development of mathematical tools to integrate climate projection with emerging knowledge about the region-specific tick ecological and pathogen enzootic processes in order to provide long-range forecast of the contribution of co-feeding transmission to the prevalence of tick-borne disease.

Multi-scale modeling to evaluate co-feeding transmission efficacy

Since co-feeding depends on local infection under the skin of the host rather than widespread distribution of the pathogen within the host, the vector aggregation patterns are important for the efficacy of co-feeding transmission. The success of disease transmission through the co- feeding transmission route requires the co-feeding of susceptible ticks in the close proximity to infected ticks on the same host.

The co-feeding transmission probability is increased when the density of infected ticks in the neighbourhood of the co-feeding susceptible tick increases. It is therefore critical to understand the (nymphal) tick-on- host distribution, and how it is influenced by such factors as, the questing rate and duration, the tick attaching and engorging behaviour, and the host grooming behaviour in a relatively shorter time scale, and the tick population dynamics (reproduction, development and death) in a relatively longer time scale.

In Zhang and Wu (7), we started to develop a general mathematical framework that integrates vector-host population dynamics with vector-on- host (infestation) distribution dynamics in order to answer the question “how patterns of pathogen transmission in the zoonotic cycle are formed from the interactions of vector attaching and host grooming behaviour”. We stratified the tick population according to a particular stage (nymph) of the tick population, for which the tick-on-host distribution is important for the co-feeding pathogen transmission.

We also stratified the host population according to the nymphal tick loads and investigated how the membership dynamics of the host subpopulations (indexed by their tick loads) is governed by the tick attaching preference and the host grooming behaviour. We showed that these individual tick and host behaviour have strong influence on the long-term tick-on-host distribution and the tick population dynamics.

Multi-stability due to co-feeding

Since tick loads on the host is determined by the interplay between tick questing and tick attaching to hosts and the host grooming behaviour, the tick-borne disease transmission model developed Zhang and Wu (8) assumed the probability of a susceptible larval tick to get infected by co-feeding with multiple infected nymphal ticks on the same host is assumed to be a uni-modal function reaching the peak at the intermediate nymphal tick loads on the host.

This is to account for the lower co- feeding probability due to host grooming when there are too many nymphal ticks on the host, and the lower co-feeding transmission probability when there are too few infected nymphal ticks on the host. We proved that the co-feeding transmission, with the uni-modal co-feeding transmission probability, leads naturally to the bi-stability of the tick-borne disease transmission dynamics.

The finding has significant implications for future studies of tick-borne disease transmission modelling, as the co-feeding transmission coupled with the seasonality of tick-host interaction in the natural environment, and the spatial movement of ticks along with their hosts can produce rich dynamics to enrich the theory of vector borne disease transmission, and potentially provide better understanding of the complicated disease patterns observed in the surveillance system.

References

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