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Understanding the influence of tick co-aggregation on R0 for tick-borne pathogens

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Tick-borne pathogens are transmitted when ticks take blood meals from vertebrate hosts. Ticks need to take blood meals to progress through immature life-stages and reach adulthood. For the most important zoonotic pathogens, including *Borrelia burgdorferi* (the causative agent of Lyme disease), two immature life-stages of the tick vector, termed larvae and nymphs, maintain the pathogens. Key features of tick feeding behaviour, and therefore of tick-host contact patterns, include the aggregation of ticks on hosts (whereby most ticks of a given life-stage feed on only a small minority of the hosts) and the co-aggregation of larval and nymphal ticks on the same minority of hosts.

A mechanistic network model is presented for tick-borne pathogen transmission that explicitly accounts for larval and nymphal tick co-aggregation and coincident coaggregation, also known as co-feeding. Co-feeding of nymphs and larvae allows transmission from an infected nymph to susceptible larvae feeding in close proximity and at the same time, but without the involvement of a systemic infection in the vertebrate host. By relating the next generation matrix epidemic threshold parameter R_0 to the in- and out-degrees of vertebrate host nodes in the mechanistic network model, a simple analytic expression for R_0 that accounts for the co-aggregation and coincident coaggregation of ticks is derived. Simulations of Lyme disease transmission on finite realizations of tick-mouse contact networks are used to visualize the relationship between R_0 and the extent of tick co-aggregation.

The derived analytic equation explicitly describes the relationship between R_0 and the strength of dependence between counts of larvae and counts of nymphs on vertebrate hosts. Tick co-aggregation always leads to greater values for R_0, whereas higher levels of tick aggregation only increases the value of R_0 when larvae and nymphs also co-aggregate. Aggregation and co-aggregation have a synergistic effect on R_0 such that their combined effect is greater than the sum of their individual effects. Co-aggregation has the greatest effect on R_0 when the mean larval burden of hosts is high and also has a larger relative effect on the magnitude of R_0 for pathogens sustained by co-feeding transmission (e.g. TBE virus in Europe) compared with those predominantly spread by systemic infection of the vertebrate host (e.g. Lyme disease).

Co-aggregation increases R_0, particularly in geographic regions and seasons where larval burden is high and for pathogens that are mainly transmitted during co-feeding. For all tick-borne pathogens though, the effect of co-aggregation can be to lift R_0 above the threshold value of 1 and so lead to persistence.

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