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American Robins as Reservoir Hosts for Lyme Disease Spirochetes

To the Editor: The article by Richter et al. (1) presents interesting results, not only on the ability of American robins to transmit Lyme disease spirochetes but also on the birds' tolerance to reinfection after the original infectivity has waned. Even more interestingly, spirochetes that had been transmitted by these avian hosts were then transmitted by laboratory mice. However, important research on wildlife hosts of the various genetic strains of Lyme spirochetes is not fully acknowledged. Therefore, the new results are not put into the context of existing information, missing the opportunity for much interesting comparison between the American N40 strain of *Borrelia burgdorferi* sensu stricto, the subject of this work, and European strains of this and other *Borrelia* genotypes.

Chipmunks (United States [2]), two species of squirrels (United Kingdom [3] and Switzerland [4]), and hedgehogs (5) are missing from the list of wildlife hosts, and the competence of sheep is denied despite evidence to the contrary (6). Moreover, European blackbirds, which have been shown to transmit spirochetes to xenodiagnostic larval ticks (7), are dismissed as transmission hosts on the basis of earlier negative transmission results from Matuschka (8), which came from two birds and pre-dated knowledge of the genetic diversity and apparent host specificity of *B. burgdorferi* sensu lato. Pheasants are also dismissed as not contributing to transmission because, according to the authors, larval ticks do not feed on them. Although significantly fewer larvae than nymphs feed on wild pheasants, in the summer similar numbers of larvae feed on pheasants (median 7, range 0-64 on cock birds; median 0, range 0-7 on hens) as on rodents (3,9,10). Laboratory and field data (9,11) analyzed within a general transmission framework (10) suggest that pheasants can act as a natural reservoir for spirochetes of some genotypes.

A growing body of evidence, both observational and experimental, suggests that certain *B. burgdorferi* s.l. genotypes (e.g., *B. afzelii*) are transmitted much more efficiently by mammals and that other genotypes (e.g., western European *B. garinii*) are transmitted more efficiently by birds (4,7,11-14). Given the apparent lack of host specificity of *B. burgdorferi* s.s. N40, the new results would add to recent advances in explaining Lyme spirochete ecology if they were put in the context of these consistent independent findings. It is now understood that Lyme spirochetes circulate through populations of mixed species of hosts, each species making different contributions to the overall persistence of the pathogen because of their differential transmission competence and infestations by each tick stage (11,15). Larval and nymphal ticks quest at different heights (16), and this behavior changes in response to microclimate, resulting in differential attachment rates to various vertebrate species (17). In such a population of hosts, any one species can contribute a basic reproduction number (R_0) of less than unity but still play an important role in maintaining enzootic cycles (10,18).

Finally, some aspects of Richter et al.'s experimental results need clarification. Was the laboratory colony of ticks screened regularly for infection? Given the very high transmission rates recorded in this study (86% transmission by robins and 97.5% by mice), reassurance that all infections were derived from the experimental procedure would be helpful. In addition, the tolerance of repeated tick feeding by robins is not as high as claimed; 82% of 32 nymphs at the third infestation is (not quite significantly) lower than 96% of 48 and 98% of 40 at the first two infestations (Yate's corrected $\chi^2 = 5.5$, 2df, $0.1 > p > 0.05$). Recent evidence suggests that

repeated infestations of ticks on mice, even without obvious reduced feeding success, result in reduced transmission of spirochetes between mice and ticks (19).

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Response to Dr. Randolph and Drs. Gern and Humair

To the Editor: We define reservoir competence of a host for a vector-borne pathogen in terms of three component questions: How susceptible is the putative reservoir host when the pathogen is delivered by the bite of an infected vector tick? How effectively does the pathogen proliferate and develop in this host? And how infective is the resulting infected host to vector ticks and for how long (1,2)? Drs. Gern and Humair insert the parenthesis (implied xenodiagnosis) into a citation of our text, thereby, equating reservoir competence with a simple xenodiagnostic test that partially addresses only the third component of this definition. At best, such a test records degree of infectivity to vector ticks at some arbitrary and often unknown point in time, a consideration that persuades us to limit our citations referring to reservoir competence. Conclusions derived from xenodiagnosis performed on field-derived animals differ from those that are obtained by an experimental study. With regard to acknowledging relevant research, we did cite the study on pheasants (3) in which these birds were infected in the laboratory by tick-borne spirochetes and subsequently infected only about a quarter of vector ticks. The cited study on blackbirds (4), on the other hand, used ticks solely to diagnose