

## NEWS AND VIEWS

## PERSPECTIVE

## Host–parasite determinants of parasite population structure: lessons from bats and mites on the importance of time

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By definition, parasitic organisms are strongly dependant on their hosts, and for a great majority, this dependence includes host-to-host transmission. Constraints imposed by the host's spatial distribution and demography, in combination with those of the parasite, can lead to a metapopulation structure, where parasite populations are highly stochastic (i.e. prone to frequent extinctions and re-colonizations) and where drift becomes a major force shaping standing genetic variation. This, in turn, will directly affect the observed population structure, along with the ability of the parasite to adapt (or co-adapt) to its host. However, only a specific consideration of temporal dynamics can reveal the extent to which drift shapes parasite population structure; this is rarely taken into account in population genetic studies of parasitic organisms. The study by Bruyndonckx *et al.* in this issue of *Molecular Ecology* does just this and, in doing so, illustrates how a comparison of host–parasite co-structures in light of temporal dynamics can be particularly informative for understanding the ecological and evolutionary constraints imposed by the host. More specifically, the authors examine spatial and temporal population genetic data of a parasitic mite *Spinturnix bechsteini* that exclusively exploits the Bechstein's bat *Myotis bechsteinii* and consider these data in relation to host–parasite life histories and the population structure of the host.

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*Myotis bechsteinii* is a small bat found in mature deciduous forests in Europe. In the summer months, females form isolated nursery colonies of 10–50 individuals where they raise their offspring communally (Fig. 1a). The members of



Fig. 1 Female Bechstein's bats *Myotis bechsteinii* (a) are frequently infested by the mite *Spinturnix bechsteini* (b). The close association among female bats in nursery colonies favours within-colony transmission of the mite. However, limited social interactions among bats outside the nursery colony, combined with strong parasite demographic variability, results in significant spatio-temporal structure in this system. Photos courtesy of G. Kerth and N. Bruyndonckx.

these colonies are highly interactive and the reproducing females are closely related due to strong natal philopatry (Kerth *et al.* 2008). In contrast, males are solitary, moving freely throughout the home ranges of different female colonies and rarely roosting with females. The major period of contact between males and females therefore occurs during mating in late summer and early fall when bats from up to 100 km apart interact at swarming sites. Some interactions may also occur at winter hibernacula, but little information is currently available on the nature and composition of overwintering groups.

*Myotis bechsteinii* is frequently parasitized by *Spinturnix bechsteini*, a Spinturnicid mite that lives exclusively on the wing and tail membranes of its host (Fig. 1b). Female mites are nymphiparous, giving birth to live adult-like protonymphs (eggs and larval develop within the mother) (Reckardt & Kerth 2009). All active stages require host blood/lymph meals and cannot survive off the host for more than a few hours (Giorgi *et al.* 2004). Between-host transmission is therefore almost exclusively restricted to direct contact among hosts and thus is conditioned by host movements and social behaviour. Female bats are much more heavily exploited by mites than males and, due to their solitary behaviour, male bats may only represent a temporary habitat patch for the parasite (Reckardt & Kerth 2009).

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Based on current knowledge of the host–parasite system and mite mitochondrial sequence data (513 bp of the cytochrome *b* gene) collected from 24 nursery colonies in two different regions of Germany, Bruyndonckx *et al.* (2009) test specific predictions concerning mite population genetic structure. They predict that parasite transmission should occur freely among female bats within nursery colonies (see Fig. 1a), but infrequently at the among-colony level. These predictions are validated by results; whereas no difference was found among mites from different individuals within colonies, colonies within and between regions were strongly structured. An experimental field study on individual re-infestation rates confirmed the within-colony results. Indeed, only a few days after removal, no significant difference in mite abundance could be detected among treated (i.e. all mites removed) and control bats, indicating frequent among-host dispersal within colonies. The authors also predict significant patterns of isolation by distance (IBD) within regions, if mites disperse between neighbouring colonies (via contact with roaming males, for example). Similarly, if these interactions lead to mite transmission but not gene flow in the host, they predict an absence of co-structure between mite and bat populations. As expected, there was no significant pattern of IBD in their data suggesting that mite dispersal is probably restricted to bat swarming and/or hibernation. Although both host and parasite populations were strongly structured among colonies (host data based on mitochondrial and nuclear microsatellites; Kerth *et al.* 2008), no correlation between host and parasite population structures were evident, indicating that gene flow in the mite is indeed decoupled from that of the bat.

These results are all very well, but they must be considered in light of temporal structure. Indeed, the authors also analyse parasite DNA samples collected from a subset of nursery colonies in two different years. Surprisingly, there was strong temporal structure found in four of the five colonies examined ( $\Phi_{2002-2007}$  ranging from 0.10 to 1.0). The degree of pairwise differentiation among colonies was uncorrelated in the 2 years suggesting that changes in parasite structure were not predictable. In the resampled colonies, haplotype frequencies changed dramatically in the 5-year period with the appearance of new variants. These patterns in the parasite are mostly likely explained by the occurrence of strong winter bottlenecks due to high mortality and an absence of reproduction and suggest that, despite some dispersal, drift is the dominant force shaping among-colony structure in this mite.

These results call for caution in the interpretation of gene flow inferences based on spatial structure alone. Most population genetic analyses assume an equilibrium between the forces of drift and migration. Frequent extinction and recolonization events and strong bottlenecks may mean that parasite populations never reach equilibrium and thus may show high among-population genetic variance due to founding events and drift alone (Whitlock & McCauley 1990). In the case of *S. bechsteini*, strong among-colony structure does not likely reflect an absence of dispersal, but rather that signatures of dispersal are erased by high

winter mortality followed by seasonal population expansion. Likewise, an absence of IBD may not be due to a lack of mite dispersal between neighbouring colonies *per se*, but rather to yearly bottlenecks that overwhelm the pattern of these dispersal events.

In this way, the results of the Bruyndonckx *et al.* (2009) study highlight several important issues and open numerous avenues for future research. For example, for the biological system in question, what is the extent of mite dispersal at swarming vs. hibernation sites, how might dispersal at hibernation sites alter the spatial scale of dispersal and what factors (host or environmental) act on the severity of winter bottlenecks? New technologies for tracking individuals may allow us to gain some insight into the composition and behaviour of overwintering groups, their parasite loads before and after hibernation, and thus, the nature of parasite exchange during this period of the host's life cycle. Further information on these issues and on the constraints imposed by the host's ecology can also be obtained via co-structure studies with other parasites infesting these bats (Criscione 2008). Parasites with contrasting transmission modes, reproductive systems and life-history traits can differ in their response to host life-history constraints (Gomez-Diaz *et al.* 2007; Whiteman *et al.* 2007; Reckardt & Kerth 2009), but may reveal key information on host behaviours that favour transmission (Nieberding & Olivieri 2007). Finally, the outcome of co-evolutionary interactions depends on the structure and ecological dynamics of the interacting populations (Gandon & Michalakis 2002). However, causal links between parasite spatial structure, life history and evolutionary dynamics in relation to the host have received relatively little attention (Barrett *et al.* 2008). Here, Bruyndonckx *et al.* (2009) show that a combination of parasite demographic constraints and host-associated behaviours may largely shape parasite genetic variation within colonies over time. The strong temporal variability shown in this study should lower the probability of mite adaptation and thus is an essential factor to consider for predicting the outcome of the co-evolutionary interaction. Such temporal patterns may be frequent in parasite organisms given their life cycles and reproductive systems. In this way, focusing on parasite spatial structure alone may mislead us on the nature of gene flow and thus, on the evolutionary potential of these biologically significant organisms.

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