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Dispersing hemipteran vectors have reduced arbovirus prevalence

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A challenge in managing vector-borne zoonotic diseases in human and wildlife populations is predicting where epidemics or epizootics are likely to occur, and this requires knowing in part the likelihood of infected insect vectors dispersing pathogens from existing infection foci to novel areas. We measured prevalence of an arbovirus, Buggy Creek virus, in dispersing and resident individuals of its exclusive vector, the ectoparasitic swallow bug (*Oeciacus vicarius*), that occupies cliff swallow (*Petrochelidon pyrrhonota*) colonies in western Nebraska. Bugs colonizing new colony sites and immigrating into established colonies by clinging to the swallows' legs and feet had significantly lower virus prevalence than bugs in established colonies and those that were clustering in established colonies before dispersing. The reduced likelihood of infected bugs dispersing to new colony sites indicates that even heavily infected sites may not always export virus to nearby foci at a high rate. Infected arthropods should not be assumed to exhibit the same dispersal or movement behaviour as uninfected individuals, and these differences in dispersal should perhaps be considered in the epidemiology of vector-borne pathogens such as arboviruses.

1. Introduction

Predicting the spread of vector-borne zoonotic pathogens is necessary for effective management of health threats to humans and wildlife, especially in an era of changing climate and potentially shifting ranges of pathogens, vectors and vertebrate host species [1,2]. The regular movement of infected vertebrate hosts through migration or dispersal is a widely recognized mechanism by which pathogens may be introduced or re-introduced between geographical regions [3,4]. Far less attention, however, has been paid to the extent to which dispersal by the vectors themselves serves to move pathogens between infection foci [5]. This is surprising, given that infected vectors (e.g. mosquitoes) are known to passively transport pathogens such as arthropod-borne viruses (arboviruses) over long distances by wind [6,7], and that parasitic infection has been found to directly affect the feeding and locomotory behaviour of other insect vectors [8–10], a potential manipulation (in some cases) by the pathogen to increase its own dispersal and/or transmission [11–13].

Here, we report the first field study to examine whether ectoparasitic insect vectors infected with an arbovirus differ from uninfected animals in their likelihood of successfully dispersing between geographically discrete infection foci. The swallow bug (Hemiptera: Cimicidae: *Oeciacus vicarius*) is an ectoparasite of primarily colonially nesting cliff swallows (*Petrochelidon pyrrhonota*), residing in the birds' mud nests or cracks in the substrate throughout the year and taking blood meals from the birds when the nests are occupied in summer [14]. An alphavirus, Buggy Creek virus (BCRV; Togaviridae, *Alphavirus*), circulates in bugs that serve as its only vector and in cliff swallows and invasive house sparrows (*Passer domesticus*) as its only vertebrate hosts [15,16]. When cliff swallows and/or house sparrows occupy a nesting colony, bugs reproduce rapidly, but if birds do not use a nesting site in a given year, the bugs have no host resource

Figure 1. (*a*) Swallow bugs clustering at the entrance of an unused cliff swallow nest before dispersing by crawling onto the legs or feet of a transient cliff swallow investigating the nest. (*b*) A swallow bug dispersing by clinging to the foot of a transient cliff swallow captured in a mist net at an established colony site. Part (*a*) courtesy of Art Gingert.

and mortality can be high. Thus, if a colony site is unused by birds in a given summer, some of the bugs there will disperse in attempts to find an active colony that can support their reproduction that season. When the wingless bugs disperse from an inactive colony site, they do so by first clustering at nest entrances (figure 1*a*). They then climb onto the legs and feet of transient cliff swallows (figure 1*b*) that investigate nests at inactive sites before flying to an active colony, where the bugs crawl off onto nests that the birds visit [17]. Birds are not known to pick bugs off their feet, probably deterred by the noxious scent glands present in cimicids [18].

2. Material and methods

We compared BCRV prevalence in three classes of dispersing bugs with those resident in established colonies and bugs clustering at established colony sites before dispersing. The dispersers were (i) bugs found in or on nests in new colonies, defined as sites never before occupied by cliff swallows or ones last used more than or equal to four years ago; as bugs apparently cannot survive without a blood meal for more than four years [19], any bug at a new site had to have been introduced that year; (ii) bugs collected off nests at weekly intervals at fumigated, parasite-free colonies, where the weekly application of insecticide insured that any bug appearing in the interval between fumigations was an immigrant from elsewhere [17]; and (iii) dispersing bugs directly collected off the legs and feet of cliff swallows (figure 1*b*) caught in mist nets at colony sites during the course of a mark–recapture study [17]. As bugs on feet were deemed to be dispersers, those found on feet at both established and new colony sites were considered to be equivalent. Established colonies were those that had been used by cliff swallows at least twice and in more than or equal to one year out of the previous four years, where bugs were collected from the outer underside of the nests or from inside the nests. Clustering bugs were ones aggregating at the lip of unused nests at established colony sites (figure 1*a*).

Swallow bugs were sampled in May–August from 2004 to 2008 at bird colony sites in our long-term study area in western Nebraska [20]. Bugs were sorted into pools of 100 (if numbers permitted) while alive, frozen at −70°C and tested for BCRV with a BCRV-specific RT-PCR [21]. Prevalence was expressed as the number of virus-positive pools/total pools at a given colony site in a given year. Prevalence per colony site per year was examined in a mixed model, using colony site and year as random effects, and bug status, colony size (number of cliff swallow nests), sample size (total pools tested) and presence/absence of house sparrows at a site as fixed effects. A description of the study area and additional methodological details are contained in the electronic supplementary material.

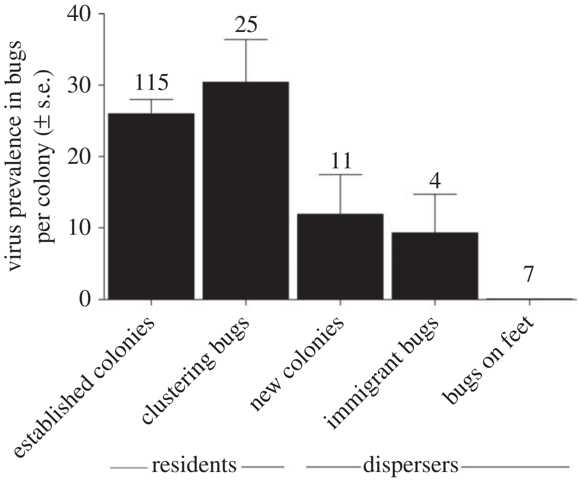

Figure 2. BCRV prevalence in swallow bugs (per cent pools positive for virus) per cliff swallow colony site per year for two categories of resident bugs at established colony sites and three categories of dispersing bugs. The number of colony sites sampled for each category is shown above the bars. Total bug pools screened was 4528 from 162 colonies over five years.

3. Results

The mean (±s.e.) BCRV prevalence for the three classes of dispersing bugs combined was 7.7 (±3.1)% per colony site, and the three classes (figure 2) did not differ significantly from each other (mixed model, $p = 0.85$; other fixed effects, $p \geq 0.26$; see the electronic supplementary material, table S1). These classes were combined and, collectively, differed significantly from the BCRV prevalence per site for resident bugs at established colony sites ($p = 0.003$; other fixed effects, $p \geq 0.11$; electronic supplementary material, table S2) and from that of clustering bugs ($p = 0.005$; other fixed effects, $p \geq 0.10$; figure 2; electronic supplementary material, table S3). BCRV prevalence among dispersing bugs was only about 26% of that of bugs at established colony sites.

4. Discussion

Although dispersing bugs are predominately adults, and those resident at established colonies represent a mix of adults and instars, there was no difference in virus prevalence between adults and instars [22], so differing age composition cannot explain our results. Prevalence of BCRV in bugs can also vary with cliff swallow colony size and with the presence of house sparrows as alternative hosts [22,23], but neither factor was a significant predictor of BCRV prevalence in these analyses and can be ruled out as confounding effects.

Infected bugs were either less likely to get on a bird that travels to a new site, less likely to survive the ride on the bird's legs or feet or less likely to disembark at a new site. We cannot distinguish among these alternatives, but the relatively high prevalence of BCRV among unfed clustering bugs suggests that virus infection did not affect the movement (at least within nests) of bugs to their dispersal point within established colonies. Perhaps infected bugs were less active while clustering and thus less likely to crawl onto a visiting cliff swallow. Other analyses have shown that BCRV infection (among house sparrows) is concentrated at particular spatial hotspots within a colony [24], so infected bugs may also move relatively little along the nesting substrate between nests. Another possibility is that the infected bugs (e.g. among those clustering) were ones that had fed more recently, and the more starved individuals were simply more likely to crawl onto a dispersing swallow. However, among the clustering bugs and those from birds' feet, none appeared to have recently fed.

The more perennially used cliff swallow colony sites maintain a relatively high prevalence of BCRV among bugs [21,22], but these results suggest that immigration of virus is not a major way that infection is maintained in these foci. Apparently, higher BCRV prevalence in bugs at established colonies only happens after repeated years of bird presence, allowing time for the relatively rare virus introductions to accumulate [23] and/or bug-to-bug transmission to occur [25].

The limited previous work on how arboviruses affect insect vectors, focused on mosquitoes in the laboratory, has shown that some arboviruses decrease vector flight activity [26] and others do not affect flight [27]. No study on mosquitoes has measured whether arbovirus-infected individuals in the field have the same rate of active dispersal between infection foci as uninfected ones. Our study reveals that a hemipteran vector infected by an arbovirus has reduced movement to a new locale, and consequently BCRV is dispersed between bird nesting colonies by infected vectors at a relatively low level. While the ecology of swallow bugs and BCRV clearly differs from that of mosquito-borne viruses in a number of ways, the results do suggest that we must not always assume that infected animals show the same pattern of dispersal as the population at large [4], or that pathogens always alter the locomotory behaviour of vectors in ways that maximize their own movement in space.

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Data accessibility. Original data deposited in Dryad: doi:10.5061/dryad.07551.

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