Predation by ants controls swallow bug (Hemiptera: Cimicidae: *Oeciacus vicarius*) infestations

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Received 15 October 2014; Accepted 12 December 2014

ABSTRACT: The swallow bug (*Oeciacus vicarius*) is the only known vector for Buggy Creek virus (BCRV), an alphavirus that circulates in cliff swallows (*Petrochelidon pyrrhonota*) and house sparrows (*Passer domesticus*) in North America. We discovered ants (*Crematogaster lineolata* and *Formica* spp.) preying on swallow bugs at cliff swallow colonies in western Nebraska, U.S.A. Ants reduced the numbers of visible bugs on active swallow nests by 74-90%, relative to nests in the same colony without ants. Ant predation on bugs had no effect on the reproductive success of cliff swallows inhabiting the nests where ants foraged. Ants represent an effective and presumably benign way of controlling swallow bugs at nests in some colonies. They may constitute an alternative to insecticide use at sites where ecologists wish to remove the effects of swallow bugs on cliff swallows or house sparrows. By reducing bug numbers, ant presence may also lessen BCRV transmission at the spatial foci (bird colony sites) where epizootics occur. The effect of ants on swallow bugs should be accounted for in studying variation among sites in vector abundance. ***Journal of Vector Ecology* 40 (1): 152-157. 2015**.

Keyword Index: Biological control, Buggy Creek virus, cliff swallow, *Crematogaster lineolata*, *Formica*, *Oeciacus vicarius*, swallow bug.

INTRODUCTION

The swallow bug (Hemiptera: Cimicidae: *Oeciacus vicarius*) is a vector of Buggy Creek virus (BCRV; Togaviridae, *Alphavirus*), an arbovirus within the western equine encephalomyelitis virus complex that circulates in colonially nesting cliff swallows (*Petrochelidon pyrrhonota*) and introduced house sparrows (*Passer domesticus*) occupying swallow nests (Hopla 1993, O'Brien et al. 2011, Padhi et al. 2011). Swallow bugs increase in larger cliff swallow colonies (Brown and Brown 1986, 1996), and this leads to higher BCRV prevalence at sites with more cliff swallows and/or house sparrows (Brown et al. 2001, Moore et al. 2007, O'Brien and Brown 2011). House sparrows are particularly effective amplifiers of BCRV, and cliff swallow colony sites with many house sparrows represent spatially predictable foci for BCRV epizootics (O'Brien et al. 2011, O'Brien and Brown 2012).

Swallow bugs can be quite abundant at some cliff swallow colony sites, with as many as 2,600 found in a single swallow nest (Brown and Brown 1996). Bugs are sometimes so numerous that they lead to cliff swallow nestling mortality and site abandonment by swallows (Brown and Brown 1986, Loye and Carroll 1991). Reducing infestations of swallow bugs is the primary way to maintain cliff swallows at a site (Brown and Brown 1996) and thus to reduce the transmission of BCRV, through, in part, the dilution effect. When swallows are present, fewer house sparrows are infected by BCRV because bugs prefer swallows as hosts, and swallows are less effective amplifiers for the virus than are sparrows (O'Brien et al. 2011). However, swallow bugs (and other cimicids) have few natural predators, being commonly depredated only by spiders (Reinhardt and Siva-Jothy 2007, C. Brown, pers. obs.). Predation of *Cimex hemipterus* eggs by larvae of the painted meal moth, *Pyralis pictalis,* has also been documented, although this sort of predation is unlikely to be widespread (Wattal and Kalra 1960).

Ants are known to control populations of many insects (González-Hernández et al. 1999, Eubanks 2001, Vandermeer et al. 2002) and also have been shown to decrease tick abundance in some areas (Harris and Burns 1972, Samish and Rehacek 1999). Colonially breeding seabirds were found to suffer less tick parasitism in habitats with large populations of ants, although in some cases the ants were also detrimental to nesting birds (Duffy 1991). The role of ants in controlling arthropod disease vectors in general has not been systematically studied.

During the course of studies on cliff swallows, swallow bugs, and BCRV in western Nebraska, we observed ants preying on swallow bugs at active cliff swallow nests. Here we document ant predation, assess its efficacy in controlling swallow bugs, and evaluate whether foraging ants negatively affect cliff swallows. We use the results to better understand factors potentially regulating swallow bug populations and generating the variability in the numbers of this disease vector among different bird colony sites.

MATERIALS AND METHODS

Study site

Our study site is centered at the Cedar Point Biological Station (41° 12.591' N, 101° 38.969' W) near Ogallala, in Keith County, NE, and also includes portions of Lincoln, Garden, Deuel, and Morrill counties. Cliff swallow nesting activities in the study area generally span the period from late April to early August. This region of the western Great Plains exhibits extensive temperature variability across the year: seasonal mean high temperatures are 15-25° C, 19-30° C, and 25-34° C for May, June, and July, respectively (Brown and Brown 1996), and the three coldest months of the winter (December, January, and February) average low temperatures of -11.5° C, -13° C, and -9.8° C, respectively (Brown et al. 2010). The study area, located principally within the North and South Platte River valleys, is characterized by riparian forest along the rivers, with land adjacent to the floodplain being primarily shortgrass and mixed-grass prairie used mostly for farming and ranching.

Within the study area, cliff swallows nest on highway bridges, box-shaped culverts underneath roads or railroad tracks, and buildings, with most colonies associated with human structures in some way, although small numbers of birds still nest on natural overhangs of cliffs (Brown et al. 2013). The birds' gourd-shaped mud nests tend to be built in clusters, often sharing walls with adjacent ones, and nesting activities within a colony are highly synchronous (Brown and Brown 1996). Colonies vary widely in size among sites, with some cliff swallows nesting solitarily and other colonies as large as 6,000 nests (mean ± SE, 404 ± 13, *n* = 2,318 colonies). House sparrows usurp swallow nests at some sites and will remain there as long as the mud nests remain intact.

Field methods

During our 33-year research on cliff swallows, beginning in 1982, we annually visited 20-40 cliff swallow colony sites at intervals throughout the nesting season, where we checked the contents of nests, temporarily removed nestling birds for banding, surveyed the number of swallow bugs present on nestlings or on the outsides of nests, or collected swallow bugs from nests. We routinely looked for any arthropods present in or on the nests (e.g., spiders, ticks, fleas) during visits that involved contact with nests.

In 2013-2014, the effects of ant predation were studied at one colony site, Poison Ivy, in Morrill Co. (Table 1), where we collected systematic information on cliff swallow nesting success and swallow bug presence. At this site, ant activity was confined to the north end of the culvert, and for comparison to nests without ants we selected a similar number of active nests at the opposite (south) end of the culvert (positioned identically with respect to the culvert entrance) where no ants were ever seen. Nests with ants were separated from those without ants by approximately 29 m at this site.

We counted all visible swallow bugs present on the outside of each cliff swallow nest at Poison Ivy at ~four-day intervals during the period the swallow colony was active (approximately 10 May to 12 July) each year. One person did all bug counts, and thus these counts represent an index of the relative abundance of swallow bugs among nests. No bugs were removed from the nests during counting. The number of cliff swallow nestlings alive at day 10 was our measure of bird reproductive success (Brown and Brown 1996). Nests failing before hatching were not included in this comparison, as most of these losses were attributable to other swallows tossing out eggs or house sparrows destroying eggs during nest takeover attempts.

Ant identification

Ant specimens were collected directly off cliff swallow nests and stored in 95% ethanol until later genetic analysis. Genomic DNA was extracted using the GeneJET Genomic DNA Purification Kit (Thermo Scientific Inc.). A 658-bp fragment of the cytochrome oxidase I (COI) gene, commonly used in "DNA barcoding", was amplified using primers LepF1 (5'-ATTCAACCAATCATAAAGATATTGG-3') and LepR1 (5'-TAAACTTCTGGATGTCCAAAAAATCA-3') (Hebert et al. 2004, Hajibabaei et al. 2006), following the methods of Menke et al. (2012). PCR products were visualized on a 2.5% agarose gel to confirm samples contained a single band, purified using ExoSAP-IT (Affymetrix Inc.), and bi-directionally sequenced on an ABI PRISM 3100xl Genetic Analyzer (Applied Biosystems) using the BigDye® Terminator v3.1 cycle sequencing kit (Applied Biosystems). Sequences were visualized and edited in CLC Main Workbench (CLC bio). Ants were identified based on morphology at two sites (Table 1) where we did not have molecular data.

RESULTS

Ant identity

The principal ant preying on swallow bugs had greatest genetic similarity to *Crematogaster lineolata* (91%), and was found to occur at five of seven cliff swallow colonies (Table 1). Ants collected during 2013 at the Arroyo site were identified as belonging to the genus *Formica*. Multiple *Formica* species shared equal genetic identity (95%) to this sample, although it likely belonged to one of two Nearctic members of the *F. fusca* complex. We were unsuccessful in amplifying a PCR product for the species collected at Conoco South and did not have specimens for Dust Bowl House (Table 1), but they had close morphological affinity with *Formica* and *C. lineolata*, respectively.

Table 1. Cliff swallow colony sites in western Nebraska with ant predation on swallow bugs.

Site	Location	Year	Ant species (GenBank accession #)	Time of ant activity[a]	Colony size[b]
Conoco South	Keith Co., 41° 07.159′ N, 101° 34.514′ W	2007	*Formica* sp.	19-30 July	70
Arroyo	Morrill Co., 41° 32.384′ N, 102° 42.216′ W	2013	*Formica* sp. (KP252162)	11 July	13
Narcissa Whitman	Morrill Co., 41° 33.507′ N, 102° 44.150′ W	2013	*Crematogaster lineolata* (KP252161)	11 July	4
Wildflower	Morrill Co., 41° 33.552′ N, 102° 44.336′ W	2013	*C. lineolata* (KP252163)	29 June - 11 July	146
Poison Ivy	Morrill Co., 41° 33.004′ N, 102° 43.188′ W	2013	*C. lineolata* (KP252160)	21 June – 11 July	47
Poison Ivy	Morrill Co., 41° 33.004′ N, 102° 43.188′ W	2014	*C. lineolata*	4 June – 12 July	61
Dust Bowl House	Garden Co., 41° 27.385′ N, 102° 29.538′ W	2014	*C. lineolata*	31 May – 10 June	12

[a]Period when ants were observed to be present.
[b]Number of active cliff swallow nests at the site.

Observations across sites

Ants were not detected on any cliff swallow nests in 1982-2006 and 2008-2012. In 2007 and 2013-2014, ant predation on swallow bugs was observed at a total of seven cliff swallow colonies in Keith, Garden, and Morrill counties (Table 1). The sites with ants represented 4.0, 16.0, and 5.5% of the colonies monitored ($n = 25$, $n = 25$, and $n = 36$) in those three years, respectively. Ants were most active at these sites in June and early July (the period when most cliff swallows are nesting), with ant activity extending throughout July at the late-starting swallow colony at Conoco South (Table 1). All colonies where ants preyed on swallow bugs were in concrete culverts underneath roads and were relatively small cliff swallow colonies (Table 1). Each colony site was situated in the highway right-of-way with grassland immediately surrounding it.

At all sites with ant predation, ants foraged on the outsides of the birds' mud nests, finding swallow bugs that were clustered or wedged in the crevices of the nests. The ants preyed on eggs, nymphs, and adults. Bugs were carried by ants away from the nests, and it appeared the ant colony was outside the culvert, with ants disappearing into the crack between the culvert's outside flared concrete edge and the ground. All ants seemed to be using the same subterranean entry. Single ants carried single bugs, including some bugs fully engorged with bird blood. Ant foraging at most sites was restricted to the edge-most 2.5-5 m of culvert wall on a side, with the span of wall usually containing 5-15 active cliff swallow nests.

Effects of ants

We documented effects of *C. lineolata* on both swallow bugs and cliff swallows at the Poison Ivy colony site in 2013-2014. There, ants were primarily concentrated on the east wall at the north end of the culvert. Ants extended into the culvert about 7.7 m, with all 14-16 nests in that span used for foraging. The next nest beyond this point was 8.5 m away in the interior of the culvert, and ants were not observed to go that far in. No ants were ever seen on the south end of the culvert.

Ant presence was associated with a dramatic per-nest reduction in swallow bugs throughout the season in both years at Poison Ivy (Figure 1), with the reduction most obvious during the period when ant activity peaked. Averaged over the 15 surveys during the 2013 season, north-end nests with ants had a mean (± SE) 40.5 (± 9.2) bugs per nest, compared to 155.2 (± 24.7) for south-end nests without ants. Over the 14 surveys in 2014, nests with ants had a mean 13.1 (± 2.1) bugs per nest, vs 136.1 (± 21.1) for those without ants. Swallow bugs were significantly less numerous at nests with ants than at nests without ants in both years (Wilcoxon matched-pairs signed-rank test, $P > 0.0001$ each year). Swallow nests with ants exhibited an average 74% reduction in 2013 and a 90% reduction in 2014, relative to nests without ants at that site. Nests with ants showed no late-season spike in bug numbers, unlike at ant-free nests (Figure 1) where bug abundance rose as both nestling birds and instar bugs hatched.

The number of cliff swallow nestlings surviving to ten days of age did not differ significantly between nests with and without *C. lineolata* in either 2013 (Wilcoxon signed-rank test, $Z = -0.67$, $P = 0.50$) or 2014 ($Z = -0.15$, $P = 0.88$; Figure 2).

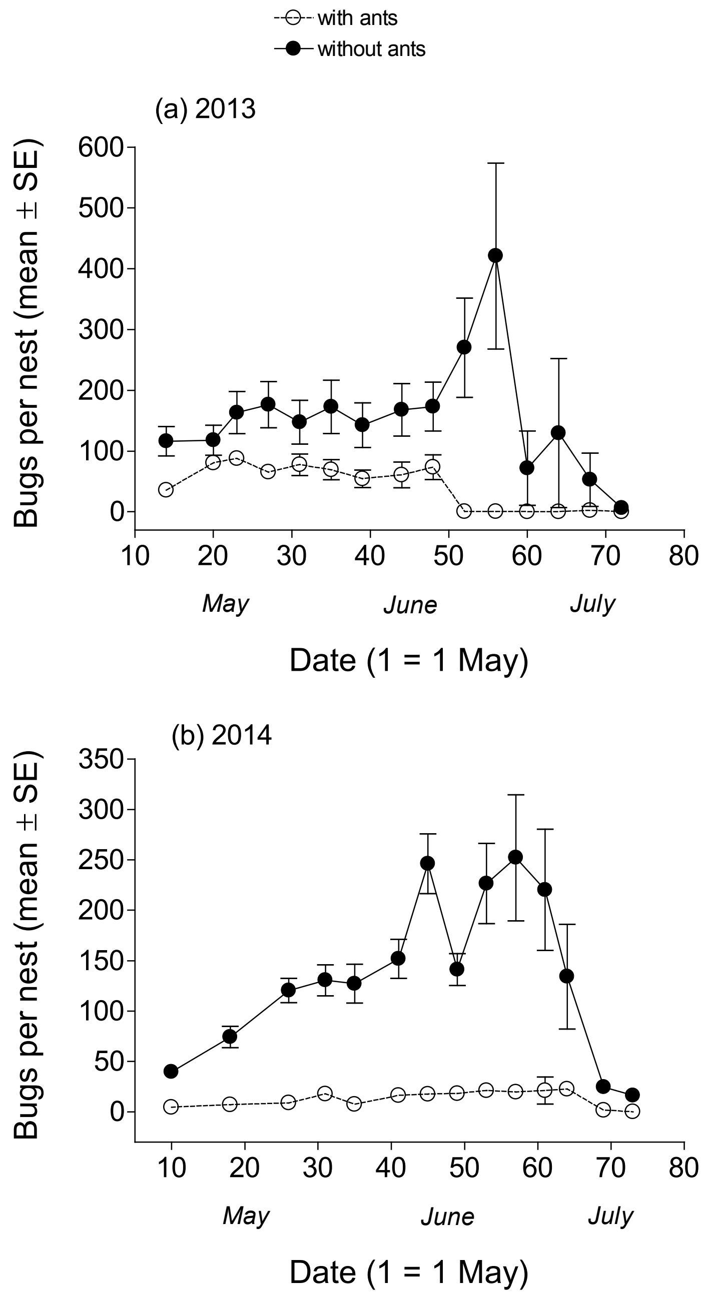

Figure 1. Mean (± SE) number of swallow bugs counted on cliff swallow nests at an active colony site in Morrill County, NE, in relation to date for nests with ants (○) and without ants (●) in (a) 2013 and (b) 2014. Sample sizes were 14 nests for each in 2013 and 16 nests for each in 2014.

DISCUSSION

While there are anecdotal reports of ants occasionally preying on human bed bugs (*Cimex lectularius*; Usinger 1966, Reinhardt and Siva-Jothy 2007), our study is the first to document widespread predation on a cimicid species. Ants were particularly effective at controlling bugs. There was no evidence that ants negatively affected reproductive success of cliff swallows occupying the nests from which bugs had been removed by ants. These ants were the only predator we witnessed in the course of the study to obviously

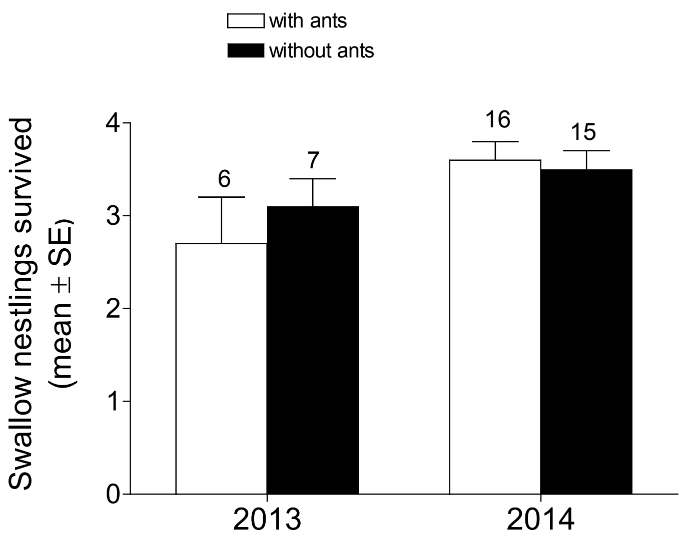

Figure 2. Mean (± SE) number of cliff swallow nestlings surviving to ten days of age at nests with ants (light bars) and without ants (dark bars) in 2013 and 2014 at the colony shown in Figure 1. Sample size (number of nests that did not fail prior to hatching) is shown above each bar.

reduce swallow bug numbers on nests. Spiders of unknown species were frequently present in swallow colonies, but massive bug infestations often occurred in colonies with spiders, so their impact on bug populations appeared negligible.

Relatively little is known about the typical diets of *Crematogaster* and *Formica* ants. There are anecdotal accounts of *Crematogaster* species tending aphids (Enzmann 1946), harvesting honeydew from scale insects (Buren 1958), and scavenging from *Anelosimas eximius* spider webs (Fowler and Venticinque 1996). Bait tests using termites and orthopterans have proven effective for *Crematogaster* (Oliveira et al. 1987, Richard et al. 2001). *Formica fusca* has been recorded consuming honeydew from aphids, scavenging other insects, and feeding on fruit (Pickles 1935). Both ant taxa apparently are generalists in foraging, and thus their preying on swallow bugs is perhaps not surprising.

All ant activity observed in cliff swallow colonies was since 2007, and most was since 2013. Why this is apparently a recent phenomenon is unclear but may reflect a general trend of summers in the study area becoming warmer and drier over time (Brown and Brown 2014). Climatic changes could promote earlier onset of seasonal activity in ants that allows a greater temporal overlap with the relatively short period of time in summer that cliff swallow colonies are active. Changing climatic conditions might also increase ant colony size, daily foraging range, or overall abundance, increasing the likelihood of their contacting cliff swallow colonies. Another possibility is that these ant taxa have recently expanded their range into western Nebraska, although this seems less likely because *C. lineolata* and the Nearctic members of the *F. fusca* complex are widespread species throughout much of the United States and use a diversity of habitats (Gregg 1945, Buren 1958, Antweb 2014) that include grasslands.

Ant predation on swallow bugs can reduce bug population sizes (e.g., at Poison Ivy in 2014) to a level near that achieved by application of insecticide to cliff swallow nests (Brown and Brown 2004). That ant presence does not harm cliff swallows suggests that, in certain contexts, these ants can exert relatively benign biological control of swallow bugs. By reducing the birds' hematophagous parasite load, nestlings in nests with ants might even be in better condition at the time of fledging than those in ant-free nests (Brown and Brown 1986, Chapman and George 1991). Our results contrast with work in other locations that showed different species of ants preying on cliff swallow nestlings, and thus reducing the birds' nesting success (Sikes and Arnold 1986, Chaya and Channaveerappa 2012).

Ants in this study appeared to restrict their foraging activities to only the nests relatively near the culvert entrances. Their apparent reluctance to traverse long sections of culvert wall without cliff swallow nests may restrict their impact on swallow bugs throughout entire colonies. Whether they would be similarly reluctant to venture farther into culverts if nests were distributed contiguously across the substrate is unknown, as all sites where ants were observed were relatively small cliff swallow colonies (Table 1) with variable-sized gaps between nests in places. To date, no ants have been observed at sites in the study area where cliff swallow nests are stacked in high density throughout a culvert.

The prevalence of BCRV varies among bird colony sites, affected by the number of cliff swallows, house sparrows, and swallow bugs resident there and history of the site (Brown et al. 2001, Moore et al. 2007, O'Brien and Brown 2011, Moore and Brown 2014). BCRV has not been systematically studied at swallow colonies with ants. However, such colonies may potentially lessen local BCRV transmission by simply reducing the population size of the virus's vector. In addition, because cliff swallows are more likely to perennially use sites where reproductive success is high (Brown and Brown 1996) and are the preferred hosts of bugs, by indirectly promoting cliff swallow presence at a site, ant activity may divert the remaining bug vectors away from the better BCRV-amplifying house sparrows. Thus, ant presence is another variable that may influence the local emergence and severity of BCRV epizootics. The ability of ants to reduce swallow bug numbers at select nests may also be useful to behavioral ecologists interested in studying the effects of swallow bugs on cliff swallows (Brown and Brown 1996) without application of insecticide, or if the bugs eventually evolved resistance to it. Perhaps farmed ants could be considered as control agents for swallow bugs and thus BCRV in certain circumstances.

Acknowledgments

We thank the University of Nebraska-Lincoln's Cedar Point Biological Station for use of their facilities, Richard Grantham for identifying ants, and three anonymous reviewers for comments on the manuscript. The National Science Foundation (DEB-0514824, DEB-1019423), the National Institutes of Health (AI057569), the Oklahoma Center for the Advancement of Science and Technology (HR13-211), and the University of Tulsa provided financial support.

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