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Charles R. Brown

University of Tulsa, charles-brown@utulsa.edu

Mary Bomberger Brown

University of Tulsa, mbrown9@unl.edu

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Between-Group Transmission Dynamics of the Swallow Bug, *Oeciacus vicarius*

Charles R. Brown and Mary Bomberger Brown

Department of Biological Sciences, University of Tulsa, Tulsa, Oklahoma, USA

Abstract

The parasitic cimicid swallow bug, *Oeciacus vicarius*, is the principal invertebrate vector for Buggy Creek virus (BCRV) and has also been associated with Venezuelan equine encephalitis virus. To help understand the spread of this vector, we experimentally measured the transmission of *O. vicarius* between groups (colonies) of its main host, the cliff swallow (*Petrochelidon pyrrhonota*), in the field. Transmission of bugs between colonies varied significantly with year, size of the colony, and week within the season. Bug immigration into sites tended to peak in mid-summer. Swallow nests in larger colonies had more consistent rates of bug introduction than did nests in small colonies, but within a colony a given nest's weekly immigrant-bug count varied widely across the season. Transmission of *O. vicarius* between host social groups follows broadly predictable seasonal patterns, but there is nevertheless temporal and spatial heterogeneity in bug transmission. By understanding how long-distance movement by this vector varies in time and space, we can better predict where and when BCRV epizootics may occur.

Keywords: Buggy Creek virus, cliff swallow, coloniality, parasite transmission, *Petrochelidon pyrrhonota*

Introduction

Buggy Creek virus (BCRV) is a recombinant alphavirus related to western equine encephalitis virus (Hayes et al. 1977, Calisher et al. 1980, 1988). The principal known invertebrate vector for BCRV is the blood-feeding swallow bug (Hemiptera: Cimicidae: *Oeciacus vicarius*), an ectoparasite of the colonially nesting cliff swallow (*Petrochelidon pyrrhonota*; Rush et al. 1980, 1981, Hopla et al. 1993, Brown et al. 2001). Little is known about how BCRV is spread or maintained in natural populations, although apparently both swallow bugs and cliff swallows play major roles in both its enzootic and epizootic stages. Unlike many

highly vagile arthropods that vector alphaviruses, such as mosquitoes, the wingless swallow bugs are relatively sedentary and are confined during much of the year to occupied and unoccupied cliff swallow nests. Consequently, the spatial foci for BCRV infections are predictable, and vector-infection rate can be related to site characteristics such as swallow colony size or bug population size (Brown et al. 2001). Some evidence indicates that *O. vicarius* can also serve as a vector for Venezuelan equine encephalitis virus (Monath et al. 1980).

Swallow bugs move between colony sites during the summer months, when they attach themselves to cliff swallows and thereby can be transmitted over wide geographical areas. By understanding the seasonal dynamics of bug transmission between groups of cliff swallows, we hope to better understand variation in the patterns of BCRV infection among sites. In this study we used an experimental approach to determine the frequency with which swallow bugs were introduced into colonies of cliff swallows from outside the group. We fumigated colony sites at weekly intervals and recorded the number and distribution of swallow bugs appearing at the sites in the intervals between fumigations. This yielded information on whether bug transmission varied between years, between colony sites, between nests within a colony site, and within a season. To our knowledge, this study is the first to measure experimentally the transmission of a macroparasite vector between social groups in a natural population.

Materials and Methods

Study animals and study site

Cliff swallows build gourd-shaped mud nests underneath overhangs on the sides of steep cliffs and canyons, or under the eaves of bridges and buildings, throughout much of western North America (Brown and Brown 1995, 1996). Nests are stacked together closely at a site, often sharing walls. Cliff swallows are migratory, wintering in southern South America, and have a relatively short breeding season in North America. They begin to arrive at our study site in late April or early May, and most depart by late July. Cliff swallows usually raise only one brood.

The principal ectoparasite of cliff swallows is *O. vicarius*, a hematophagous cimicid bug that commonly vectors BCRV (Hayes et al. 1977, Rush et al. 1980, 1981, Scott et al. 1984, Hopla et al. 1993, Brown et al. 2001). Infestations can reach 2,600 bugs in a single cliff swallow nest. The swallow bugs typically inhabit the outsides of nests during the day and move inside nests at night, crawling onto the birds primarily to feed. The wingless bugs can disperse between colony sites only by clinging to the legs and feet of a swallow that moves between colonies (Brown and Brown 2004). When a transient bird briefly perches on a nest, the bugs crawl off and thus reach new sites. There is some evidence that female bugs are more likely than males to be moved by birds (Loye 1985). The swallow bug is a long-lived parasite that begins to reproduce as soon as it feeds in the spring. Eggs are laid in and on swallow nests in several clutches that hatch over variable lengths of time, ranging from 3–5 days (Loye 1985) to 12–20 days (Myers 1928). Nymphs undergo five instars before maturing, and they feed on birds' blood at each instar stage.

Our study area was near the Cedar Point Biological Station (41°13'N, 101°39'W) in southwestern Nebraska. It was approximately 150 × 50 km and included portions of Keith, Garden, Deuel, and Lincoln counties, primarily along the North and South Platte Rivers. In this area, cliff swallows nested on both natural cliffs and artificial structures such as bridges.

Colony size was the number of active nests at a site. Mean (\pm SE) colony size ($N = 1,629$ colonies) was 385 nests, and ranged from 2 to 6,000 nests with some birds nesting solitarily. All nests at a given bridge or cliff represented a nesting colony (Brown and Brown 1996). Each colony site tended to be separated from the next nearest by 1–10 km although in some cases by as much as 20 km or more. In 1999–2002, we monitored 14 experimental colonies in concrete culverts underneath roads or railroad tracks. These sites were 3.1–44.7 km from each other, and each had 18–28 neighboring colony sites within 10 km.

Fumigation and parasite counts

Experimental colonies were first fumigated on about 10 May each year and weekly thereafter for 10–11 weeks, at which time most cliff swallows had migrated from the study area. Nests were fumigated by spraying them with a dilute solution of an insecticide, Dibrom®, that was highly effective in killing swallow bugs in previous work with no negative effects on cliff swallows (Brown and Brown 1986, 1996, 2004). The active ingredient in Dibrom (also known as naled) is 1,2-dibromo-2,2-dichloroethyl dimethyl phosphate, which acts as a cholinesterase inhibitor. We diluted the insecticide 1:150 parts water and applied it as a light mist directly to the outsides of nests and the adjacent substrate. It served primarily as a contact insecticide. The effectiveness of Dibrom against swallow bugs has been verified experimentally (Brown and Brown 2004).

Weekly counts of parasites at 30 randomly selected nests per site began a week after the first fumigation. We used the same 30 nests each week unless colony size was too small to allow a full 30 (in addition, some nests that we selected were later excluded because they fell or were abandoned by the birds using them during the season). The outsides of all nests in the sample at a site were visually examined for parasites during the day using a flashlight. Any seen anywhere on the nest or wedged between the nest and the substrate were counted. The number of visible bugs on the outsides of nests is highly correlated with the total number of bugs present in a nest (r^2 , 0.68 to 0.92, depending on nest status), as determined from nests that were collected (Rannala¹). Thus, even if a few bugs inside the nest were missed on a given week, our counts still provided reliable relative indices of bug presence. Age of the bugs (adult or instar) was also recorded; age can be told by the instars' smaller size and lesser difference in width of the head versus the abdomen (Usinger 1966). The same observer (CRB) made all counts at all sites in all years. Fumigation of the entire colony (all nests and surrounding substrate) was done immediately after each count, ensuring that any bug counted each week was one introduced from elsewhere since the previous week's fumigation.

Because a nest's physical characteristics might have affected its immigrant-bug count, for each nest in our samples we measured: its diameter, defined as its widest point along the base and determined by holding a meter stick across the front of the nest; how many adjacent nests were touching, defined as those making physical contact at any point; and

the nearest neighbor distance, the straight-line distance to the nearest nest, measured from the center of the nests' entrances.

Statistical analysis

Statistical analyses were performed with SAS (SAS Institute 1990). To correct for differences among sites in the mean number of bugs introduced, we used the coefficient of variation to describe the extent of between-site variability in the average number of bugs detected per nest at a site. To assess the repeatability of a nest's immigrant-bug count from week to week, we used the intra-class correlation coefficient (r_i ; Zar 1999).

Results

Factors affecting transmission

The average number of immigrant *O. vicarius* introduced per colony per week varied significantly with year, size of the cliff swallow colony, and week within the season (Table 1). Sample size (the number of nests studied per colony) and the temperature and time of day when counts were conducted had no effect on the number of immigrant bugs detected (Table 1).

Table 1. Analysis of covariance to detect effects of variables potentially affecting the mean number of immigrant *O. vicarius* counted per cliff swallow nest per week per colony, 1999–2002 ($N = 129^*$)

Variable	<i>F</i>	df	<i>P</i>
year	5.39	3	0.0017
colony size	37.09	1	< 0.0001
sample size	0.53	1	0.47
air temperature**	1.51	1	0.22
time of day**	0.15	1	0.70
week***	2.61	12	0.004

*Sample size lower than in Figure 3 because some colonies did not have immigrant bugs censused in the first two weeks of the season.

**When samples were taken.

***Week since beginning of fumigation; week 1 began on about 19 May each year.

A nest's physical characteristics had no influence on the number of immigrant bugs detected at it. A repeated-measures ANOVA of between-subject effects showed no significant effect of nest diameter ($F_{1, 172} = 0.10$, $P = 0.76$), number of nests that were close enough to be touching ($F_{1, 172} = 1.19$, $P = 0.28$), or nearest neighbor distance ($F_{1, 172} = 3.08$, $P = 0.08$) on a nest's weekly bug count.

Seasonal pattern of transmission

The mean number of immigrant bugs (\pm SE, range) counted per nest per week over all colonies was 0.99 (\pm 0.37, 0.00 to 6.40) in 1999, 1.06 (\pm 0.17, 0.03 to 3.53) in 2000, 0.41 (\pm 0.06, 0.00 to 1.23) in 2001, and 1.51 (\pm 0.30, 0.00 to 7.20) in 2002. These differences were significant (Table 1). The seasonal pattern in bug immigration across all colonies tended to peak in

mid-summer, although there were yearly differences in the magnitude and shape of this peak (Figure 1). Introduction of *O. vicarius* into new colonies was limited both early in the summer (May through mid-June) and later in the summer (mid-July onward; Figure 1). The patterns for adults and instars were similar in most years, with instars also peaking in mid-summer; very few were transmitted between colonies prior to early June (Figure 1). Overall, relatively few instars were detected in our counts. Of 3,446 total immigrant bugs counted across all years and colonies, only 468 (13.6%) were instars, mostly the fourth or fifth stage.

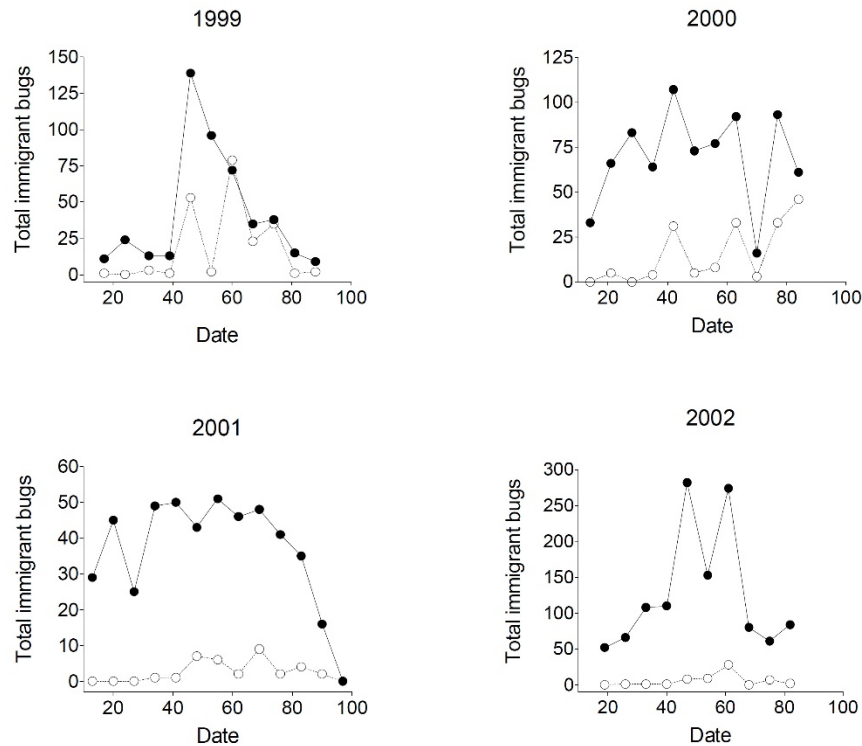


Figure 1. Total immigrant *O. vicarius* introduced across all cliff swallow colonies in relation to date (20 = 20 May, 40 = 9 June, 60 = 29 June, 80 = 19 July, 100 = 8 August) within the season for the years 1999-2002. Immigrant bugs were counted at all sites on the same day at weekly intervals. Total adult bugs are denoted by closed circles, instars by open circles. Note different scales of y-axes.

Variation between and within colonies

The coefficient of variation in the mean number of immigrant bugs per nest per week at a colony was significantly inversely related to colony size (Figure 2). Small colonies exhibited more nest-to-nest variation in the number of bugs introduced than did the larger sites. The percentage distribution of nests with different mean numbers of bugs counted per week, combined across colonies, showed the overdispersion typical of most parasite distributions (Figure 3). Almost a quarter of all nests ($N = 358$) had no bugs introduced at any

time within the season, 55% had a mean number of bugs per week less than 0.50, and 71% had less than 1.0 per week (Figure 3). A few nests attracted relatively large numbers of bugs, up to a mean of 14.5 per week (Figure 3). Intra-class correlation coefficients for the number of bugs introduced per week at a nest showed that bug immigration per nest was significantly repeatable at four of 13 colonies (Table 2). These tended to be the larger ones where overall rates of bug introduction were higher. Most correlation coefficients were quite low in magnitude (Table 2), suggesting little between-week consistency in a nest's having immigrant bugs introduced into it.

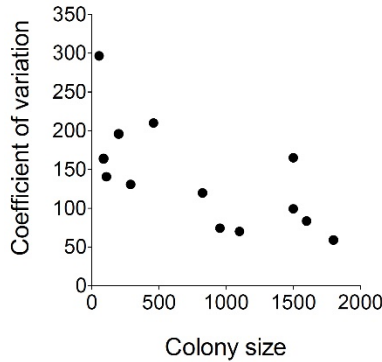


Figure 2. Coefficient of variation in the mean number of immigrant *O. vicarius* introduced per nest per week in relation to cliff swallow colony size (number of nests) at a site. The coefficient of variation declined significantly with increasing colony size ($r_s = -0.71$, $P = 0.007$, $N = 13$ colonies).

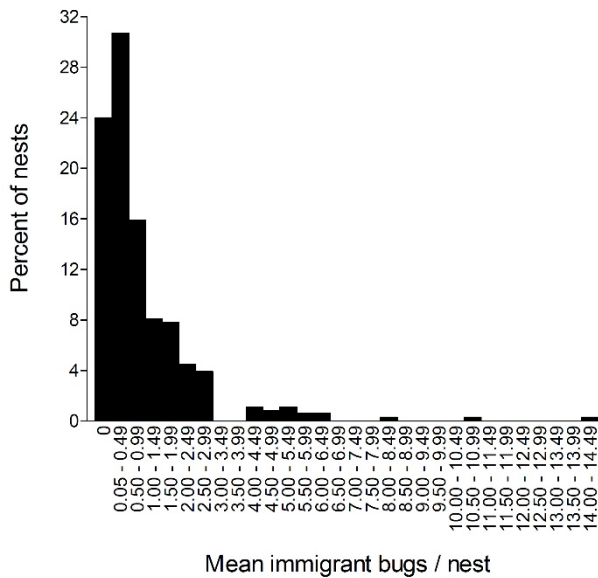


Figure 3. Percentage distribution of the mean number of immigrant *O. vicarius* introduced per nest per week across all colonies ($N = 358$ nests).

Table 2. Repeatability, as indicated by the intra-class correlation coefficient (r_1), in a nest's weekly count of immigrant *O. vicarius* at 13 cliff swallow colonies of different sizes, 1999–2002. Those in boldface were significant at $P \leq 0.05$ after applying a sequential table-wide Bonferroni correction for multiple comparisons (Rice 1989).

Colony	Colony size (number of nests)	r_1	P
1	55	-0.02	0.68
2	88	0.06	0.06
3	110	-0.02	0.77
4	200	0.07	0.12
5	290	0.04	0.04
6	460	0.00	0.47
7	825	0.07	0.005
8	955	0.10	< 0.0001
9	1100	0.02	0.25
10	1500	0.10	0.0003
11	1500	0.04	0.06
12	1600	0.11	< 0.0001
13	1800	0.01	0.30

Discussion

These analyses illustrate that the transmission of *O. vicarius* between colonies of cliff swallows varies among years, among weeks within the season, and among nests within colonies, and that smaller colonies have less consistent rates of bug introduction among nests than do larger colonies. Previous analyses have also shown that the total bugs introduced per nest increases with cliff swallow colony size (Brown and Brown 2004). The results indicate that between-group transmission of swallow bugs follows broadly predictable patterns over the course of the cliff swallow's summer nesting season, although there is substantial temporal and spatial heterogeneity in transmission likelihood.

In most years, bugs were most likely to move between colonies on birds during a relatively brief time period in midsummer. We hypothesize that bugs more readily disperse between sites at this time because by then, colony sites unoccupied by birds are likely to remain so for the rest of that season (C. and M. Brown, unpublished data) yet enough of the summer remains that reproduction may still be possible for a bug reaching an occupied swallow colony elsewhere. Earlier in the summer, *O. vicarius* may be less likely to move because the current colony site may still become occupied by birds that season. Late in the summer dispersal is unlikely to result in successful reproduction because the birds' imminent migration does not leave enough time to reproduce at another site even if dispersal is successful. A bug presumably increases its chances of finding a bird on which to disperse long distances by sitting on the outer edge of an unoccupied nest's entrance; if a swallow investigates that nest by attempting to enter it, the bug crawls on to it. The consequence can be clusters of 100 or more bugs at the entrances of some nests. However, long-distance dispersal between sites is apparently risky for *O. vicarius*, as they can become dislodged

relatively easily from a swallow's feet or legs (e.g., when a bird makes contact with a mist net). Adult bugs are more likely to be moved between colonies than instars, perhaps because the non-reproductive instars have less reason to disperse until they mature. Swallow bugs do not reproduce at sites unused by cliff swallows.

Although the seasonal pattern of between-group bug transmission was similar across years, there were significant differences among years in the magnitude of transmission. The average immigrant bugs counted per nest per week per colony varied by as much as 3.5× from year to year (e.g., 2001 to 2002). Colonies of similar size were studied each year, so the yearly differences are not sampling artifacts. This seems to indicate annual variation in the likelihood of bug dispersal, but the reasons are unclear. Since bugs disperse primarily from unoccupied cliff swallow colonies, the annual variation in dispersal may possibly reflect the number of unoccupied sites in a local area in a given year or the abundance of bugs at those unused sites. Bug introduction to active colony sites will be more frequent in years when there are more potential dispersal sources or when sources have more potential dispersers.

The spatial heterogeneity in bug transmission (at the landscape level) seems to be related in large part to colony size (Brown and Brown 2004). Sites with larger cliff swallow colonies have higher rates of bug immigration to them, likely because more transient swallows pass through them. The transient birds visiting large colonies also are more likely to have visited other large colonies that are more likely to be infested (Brown and Brown 2004). Analyses here reveal that introduction of *O. vicarius* is more uniform among the nests within a colony at sites that have larger swallow colonies. With more transients attracted to and visiting the larger colonies, perhaps each nest is more likely to be visited by a nonresident bird, receiving bugs in the process. In smaller colonies with fewer transients, some nests may not be visited by transients at all. The consequence is increased total numbers of bugs in larger colonies and (with more immigration) decreased likelihood of a bug population decline or total bug extinction at those sites (Brown and Brown 1996).

Within colonies, the likelihood of a nest receiving immigrant bugs seemed to be largely independent from week to week. At only four of 13 colonies was a nest's bug count significantly repeatable across weeks. This is consistent with bug introduction being by transient birds that, while investigating sites and assessing reproductive success of residents (Brown et al. 2000), visit existing nests largely randomly and usually without respect to nests that other transients may have visited recently. In a few cases, however, certain nests seemed to attract large numbers of immigrant bugs (the rightmost nests in Figure 3). We did not detect any obvious correlates that could explain the bug loads of these nests (e.g., nesting stage, nest contents, spatial position in the colony), but the implication is that they were more likely to have been visited by transients, perhaps because they were more often left unattended by their owners. We found no evidence that a nest's size or proximity to others within a colony affected the number of immigrant bugs it attracted.

These results have several implications for the epidemiology of BCRV. First, the marked annual variation in the magnitude (and to a lesser extent, the timing) of bug immigration to sites may be a cause of any annual variation in BCRV prevalence. Presence of BCRV tracks directly the population size of *O. vicarius* (Brown et al. 2001), and in years with less

bug dispersal between sites, BCRV epizootics may be less likely simply because bug populations are lower, on average, and less virus is spread to potentially susceptible hosts. Second, the more consistent introduction of bugs into larger colonies than into smaller ones means that, potentially, BCRV will be more continually reintroduced into larger cliff swallow colonies, both promoting local maintenance of the virus and potentially increasing the number of genetic variants of the virus at those sites. Third, the greater likelihood of bugs being introduced into larger colonies (Brown and Brown 2004) may mean that cliff swallows resident in those colonies are more likely to be infected initially with BCRV or reinfected with a different strain that may have come from a distant site. To the degree that infected cliff swallows spread the virus through their own movements, this will serve to further distribute virus strains over relatively long distances and potentially to new sites. BCRV exhibits genetic differences among different colony sites, as determined from sequencing a region of the subgenomic 26S RNA (M. Pfeffer et al., unpublished data). Understanding the movement patterns of both infected bugs and birds between colony sites may help us to predict what subtypes of the virus should occur where.

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Note

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