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Mosquito Abundance is Correlated with Cliff Swallow (*Petrochelidon pyrrhonota*) Colony Size

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ABSTRACT   We measured the abundance of mosquitoes [primarily *Aedes vexans* (Meigen) and *Culex tarsalis* Coquillett] at cliff swallow (*Petrochelidon pyrrhonota* Vieillot) colonies of different sizes in southwestern Nebraska in 1999. Using CO_2 traps placed inside and outside of colonies, we found that total mosquito abundance increased significantly with the number of active cliff swallow nests at a colony site. We found no effect of date or weather conditions on the number of mosquitoes caught at the different sites. By classifying the landscape from aerial photographs within a 2-km-diameter circle centered on each colony site, we found no significant relationships between habitat type near a colony site and cliff swallow colony size or mosquito abundance. Proximity to livestock could not account for our results. *Culex tarsalis* was proportionately more likely to be caught inside a colony than at traps 30 m away, but the proportion of *C. tarsalis* inside a colony did not vary with colony size. Our results cannot be explained by date- or weather-related sampling artifacts or by differences in habitat between sites. Most likely, mosquitoes, especially *A. vexans*, are attracted to the vicinity of large cliff swallow colonies.

KEY WORDS   *Aedes vexans*, cliff swallow, *Petrochelidon pyrrhonota*, *Culex tarsalis*, coloniality, mosquito attraction

THE DISTRIBUTION AND abundance of mosquitoes tends to be patchy within most landscapes, apparently often in response to heterogeneity within the preferred habitat. The spatial distribution of many mosquito taxa is influenced by the availability of oviposition and resting sites (Wekesa et al. 1996), and correlations have often been established between habitat types and mosquito abundance. The effect of host (i.e., blood meal) availability on mosquito distributions independent of habitat is less clear. A few studies have suggested that mosquitoes may be more abundant near concentrations of potential hosts (Haddow 1942, Gillies 1955, Edman and Webber 1975), but relatively little attention has been paid to how the spatial distribution of hosts per se affects local abundance of mosquitoes. In many host–parasite systems, parasitism by blood-feeding arthropods increases in larger host groups, although whether this pattern applies in mosquitoes has rarely, if ever, been tested directly. Indirect evidence that mosquitoes are attracted to larger groups of hosts comes from an interspecific comparison in primates, in which malaria infection (transmitted by mosquitoes) increased with primate sleeping-group size (Davies et al. 1991). Establishing an effect of host population size on mosquito attraction is obviously important for maximizing mosquito surveillance and monitoring mosquito-borne diseases both in humans and livestock.

As part of a study on the population biology of a recombinant alphavirus associated with colonially nesting cliff swallows (*Petrochelidon pyrrhonota* Vieillot) in southwestern Nebraska, we surveyed mosquito abundance at cliff swallow colony sites that differed in the number of active nests. If mosquitoes are attracted to concentrations of potential hosts, we hypothesized that larger swallow colonies would be associated with larger local mosquito populations, possibly affecting transmission probabilities of the alphavirus. We sampled mosquitoes within each colony to learn which taxa were most likely using cliff swallows as food sources. In addition to measuring mosquito abundance, we quantified habitat features at swallow colonies to determine if landscape differences among sites might have explained any differences in mosquito abundance. This study is the first, to our knowledge, to measure abundance of free-flying hematophagous arthropods in relation to host colony size.

Materials and Methods

Study Animal and Study Site. Cliff swallows are highly colonial, insectivorous passerines that breed throughout most of western North America (Brown and Brown 1995). They build gourd-shaped mud nests and attach them to the vertical face of cliff walls, rock outcroppings, or artificial sites such as the eaves of buildings or bridges. Nests tend to be stacked together

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closely, often sharing walls. Cliff swallows are migratory, wintering in southern South America, and have a relatively short breeding season in North America. At our study site, they arrive beginning in late April or early May, and most depart by late July. They generally raise only one brood.

Our study site is centered near Ogallala, in Keith County, along the North and South Platte Rivers, and also includes portions of Deuel, Garden, and Lincoln counties, southwestern Nebraska. We have studied cliff swallows there since 1982. There are ≈160 cliff swallow colony sites in our 150 by 50-km study area, with about a third of these not used in a given year. Colony size at a site, defined as the number of active nests, varies widely, ranging from 2 to 3,700 nests, with some birds nesting solitarily. Over a 19-yr period, mean ($\pm$SE) colony size ($N = 1,282$) was 356.5 ($\pm$16.3) nests. Colony sites tend to be separated from the next nearest site by 1–10 km but in a few cases by $\geq$20 km. In our study area, the birds nest on both natural cliff faces along the south shore of Lake McConaughy and the North Platte River, and on artificial structures such as bridges, buildings, and highway culverts. The study site is described in detail by Brown and Brown (1996).

Mosquito Sampling. We selected six cliff swallow colonies ranging in size from 35 to 1,500 active nests for repeated mosquito sampling. Five of these were cement box-shaped culverts in which the birds placed their nests in tiers along the vertical walls near the ceiling, and the sixth was a metal cylindrical tube in which the birds affixed their nests in between the ridges of the corrugated metal, mostly near the top. These sites were all surrounded by pastures or agricultural fields and, thus, they occurred generally in the same habitat type. These sites were selected from among other cliff swallow colonies to maximize the range in colony sizes studied and because of similarity in substrate type and surrounding habitat.

We used CO_2 (dry ice)-baited CDC-survey traps (BioQuip, Gardena, CA) to collect adult mosquitoes. Samples were taken at one colony site per night. On each night, we set four identical traps, one at each entrance of the culvert or tube and the other two at 30 m from each end of the colony substrate. The former two traps ("within" the colony) collected mosquitoes that were presumably in the culvert with the birds, and the latter two ("outside" the colony) sampled those in the immediate vicinity of the colony. Traps were always set in open areas, at least 25 m and often much farther from the nearest trees or woody vegetation. Traps were hung on 2.5-m tall metal "T" hangers anchored in the ground and secured with ropes. Some of the culverts had exposed cement floors, and in these cases the "T" hangers were placed in sand-filled buckets. All traps were suspended from the hangers by 0.3-m ropes. Traps were set in place at least 0.5 h before sunset to allow the birds to habituate to them, ensuring that the presence of the traps did not affect bird behavior. The traps were run from 30 min before sunset to 1 h after sunrise. Mosquitoes were collected from the traps, frozen, and sorted by sex and species. Counts reported here are those of adult females only. Collections were made on three nights per site (except at one site which was sampled only once) between 8 June and 12 July 1999. Because a trap failed on three occasions, for most comparisons counts were expressed as the number of mosquitoes captured per trap per night.

Habitat Characterization. The habitat near each colony was quantified from aerial photographs supplied by the Aerial Photography Unit of the U.S. Department of Agriculture. These photos, taken in 1993, were overlaid with a transparent acreage grid centered on each colony site. We designated a circular region of 1-km radius, centered on the colony, in which to classify habitat. This area was chosen because cliff swallows generally forage within a 1-km radius of their colony site (Brown et al. 1992, Brown and Brown 1996), and these habitat classifications were originally done to characterize each colony's foraging range. Within the circular foraging range, we used the acreage grid to determine the total coverage in hectares of the following habitat types: flowing water (surface area of rivers and creeks), standing water (the surface area of lakes and ponds), roads and buildings (the surface area of asphalt roads and all artificial structures), bare earth (the surface area of dirt roads, sand pits, sand bars, plowed fields, or other unvegetated ground), trees (the surface area of deciduous and evergreen tree cover), marsh (the surface area of aquatic wetlands), grasses (the surface area of prairie vegetated with noncultivated grass, often grazing land), and crops (the surface area of cultivated fields, usually wheat or corn). Our qualitative observations showed that habitat acreage around colonies as shown by the 1993 photographs was almost identical to that in 1999.

Weather Data. Climatological data for the nights of sampling were taken from a long-term monitoring site at the Cedar Point Biological Station in Keith County, Nebraska, within the study area. This site is part of the University of Nebraska's Automated Weather Data Network and records hourly temperature, wind speed, and other climatological variables. We averaged the hourly values for temperature and wind speed (variables likely to affect mosquito activity) from 2100–0500 hours MDT on each night of sampling, and used the nightly means to examine the effect of weather on capture totals.

Statistical Analysis. We used univariate Spearman rank correlation tests to examine the relationship between mosquito abundance and colony size, mosquito abundance and habitat type, and habitat type and colony size. Because there were differences in mosquito abundance among different colonies, to examine the relative numbers of mosquitoes within versus outside a colony we used a univariate Wilcoxon matched-pairs signed-rank test, which allowed us to combine all colonies into a single analysis. Multivariate linear regression tests were used to examine the effect of temperature and nightly wind speed on mosquito abundance and to test for a colony size-by-date interaction. Statistical tests were done using SYSTAT (Wilkinson, 1989).
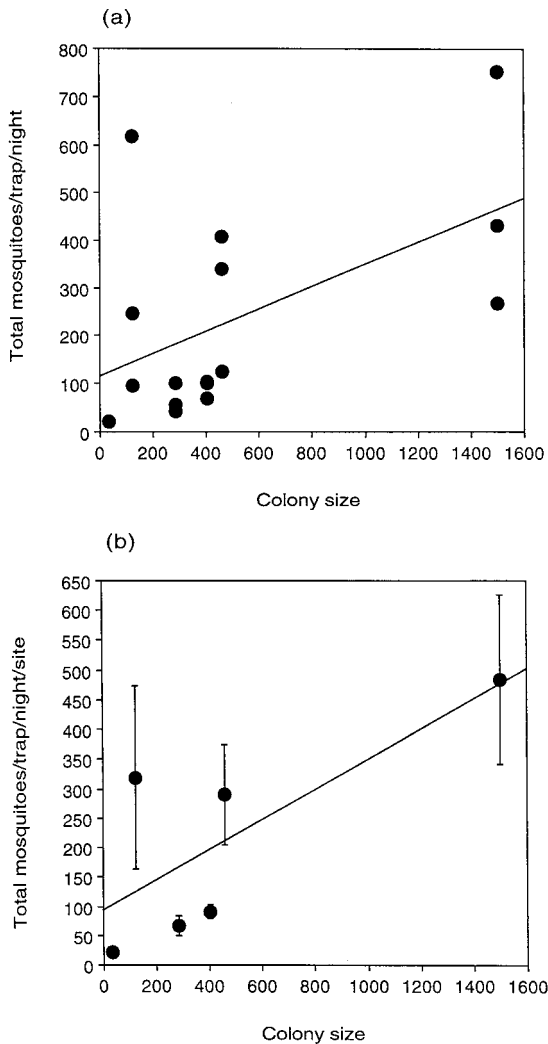
Fig. 1. Effect of cliff swallow colony size (number of active nests) on total mosquitoes caught per trap per night (a) when each sampling night was considered independent ($r_s = 0.58$, $P = 0.018$, $N = 16$ nights) and (b) when nightly means were averaged ($\pm$SE) for each colony site ($r_s = 0.94$, $P = 0.005$, $N = 6$ sites). In each case, the increase in mosquito abundance with colony size was highly significant. Lines indicate best-fit least-squares regression.

Results

Effect of Colony Size. We trapped a total of 14,215 adult female mosquitoes during 16 nights of trapping. Of these, 11,415 (80.3%) were identified as *Aedes vexans* (Meigen), 1,137 (8.0%) as *Culex tarsalis* Coquillett, and 1,663 (11.7%) as other species or unknown. The total number of mosquitoes per trap increased significantly with the size of the cliff swallow colony when each night of sampling was considered independent (Fig. 1a; in this case the average value for all traps run at a site on a given night was used). We found the same result when the nightly means at each site were

averaged (Fig. 1b). Thus, there was a higher adult-female mosquito abundance near larger cliff swallow colonies, both on a nightly basis and when averaged over all nights of sampling at a site.

This relationship (Fig. 1) might occur if there were systematic differences among the colony sites in dates of sampling or weather conditions, each of which might influence nightly mosquito abundance. However, a multiple regression analysis, using each night as an independent sample ($N = 16$), revealed no significant effect of date ($P = 0.41$), mean nightly temperature ($P = 0.31$), or mean nightly wind speed ($P = 0.88$) on total mosquitoes caught per trap. We also tested for a colony size-by-date interaction and found no evidence of one ($P = 0.79$). Thus, the finding of larger mosquito populations at larger cliff swallow colonies was not an artifact of hidden correlations with date of sampling or weather conditions on the nights chosen for sampling at the different sites.

This result (Fig. 1) might also be explained by relationships between colony size and habitat features, if larger cliff swallow colonies occurred in areas naturally preferred by mosquitoes. However, we found no significant associations between habitat types and colony size for the habitat classifications we used: Spearman rank correlations ($N = 16$) between colony size and acreage of flowing water, standing water, roads and buildings, bare earth, trees, marsh, grassland, and crops were all nonsignificant, varying from $r_s = -0.65$ ($P = 0.16$) for marsh to $r_s = -0.06$ ($P = 0.91$) for crops. Similarly, there were no significant associations between mosquito abundance (using nightly trap averages per site, $N = 16$) and acreage of these habitat types, with Spearman rank correlations varying from $r_s = -0.65$ ($P = 0.16$) for marsh to $r_s = -0.03$ ($P = 0.96$) for roads and buildings. Thus, we found no evidence that these colonies were situated in markedly different habitat or that any habitat differences among them influenced mosquito abundance in ways that could explain the increase in mosquitoes with colony size (Fig. 1).

Because *A. vexans* is often associated with livestock, we examined whether the proximity of cattle or horses to a site might have accounted for the apparent effect of cliff swallow colony size on mosquito abundance. The pastures surrounding all of the colony sites used in this analysis (Fig. 1) except one were used for winter grazing only and had no livestock use during the time of sampling. The exception was the smallest colony (35 nests) at which cattle routinely occurred $\approx$100 m from the site. At the other colonies, the nearest livestock (cattle, horses) were 0.8–3.5 km away. The largest colony (with the most mosquitoes) had no livestock within at least 3.0 km. There was thus no indication that larger colonies were situated in greater proximity to livestock than smaller colonies, and, if anything, the reverse was more likely.

The effect of colony size (Fig. 1) was generated by *A. vexans*. A separate analysis using only the number of *C. tarsalis* caught per trap revealed no significant correlation between mosquito abundance and cliff swallow colony size when using either nightly means

$(r_s = -0.11, P = 0.68, N = 16)$ or averages across nights per site $(r_s = 0.54, P = 0.26, N = 6)$.

Mosquitoes Within versus Outside Colony. Using our traps placed at the culverts versus 30 m away, we found a total of 1,827 *A. vexans* within the colonies and 9,588 outside the colonies. We found a total of 319 *C. tarsalis* within the colonies and 818 outside the colonies. The higher overall proportion of *C. tarsalis* within the colonies was significant (28.0% *C. tarsalis* versus 16.0% *A. vexans*; $\chi^2_1 = 105.9$, $P < 0.0001$). The mean ($\pm$SE) number of mosquitoes of all species per trap per night ($N = 16$) within a colony was 85.3 ($\pm$31.2), compared with 370.2 ($\pm$82.8) per trap per night outside a colony; the difference was highly significant (Wilcoxon matched-pairs signed-rank test; $P < 0.0001$). Most of the mosquitoes both inside and outside a colony were *A. vexans*; the mean ($\pm$SE) number of *C. tarsalis* per trap per night within a colony was only 11.2 ($\pm$3.5) and outside a colony 25.3 ($\pm$5.1). However, the percentage of *C. tarsalis* per trap per night among the mosquitoes found within the colony (mean 29.1%, SE = 7.8) was significantly higher than the percentage of *C. tarsalis* per trap per night among the mosquitoes found outside the colony (mean 11.9%, SE = 3.8; Wilcoxon matched-pairs signed-rank test, $P = 0.004$, $N = 16$). This suggests that, although *A. vexans* females were by far the most abundant mosquito in and around cliff swallow colonies, the *C. tarsalis* that were present were more likely to be found inside the colonies.

To determine if colony size affected the potential attraction of *C. tarsalis* to colony sites, we examined the difference in the percentage of *C. tarsalis* caught per trap per night within and outside a colony in relation to colony size (Fig. 2). A positive difference meant a greater fraction of the total mosquitoes caught within a colony than outside were *C. tarsalis*, whereas a negative difference reflected a greater fraction outside the colony. In 14 of 16 colonies we found a positive difference, and there was a suggestion that the difference declined with colony size—which would mean proportionately fewer *C. tarsalis* are attracted to larger colonies—but the correlation was not significant (Fig. 2).

Discussion

Our results indicate a positive correlation between local mosquito abundance and the size of a cliff swallow colony. We found no evidence that this relationship could be explained by date- or weather-related sampling artifacts or that it could have resulted from either differences in habitat between sites or the proximity to livestock. Although mosquitoes are attracted to CO_2 traps, our results cannot be explained by trap attraction per se because we used the same sampling protocol at each site. If trap attraction alone had accounted for our results, we should have seen similar mosquito abundance among all sites. Thus, it seems probable that the direct relationship between mosquito abundance and swallow colony size is real. This
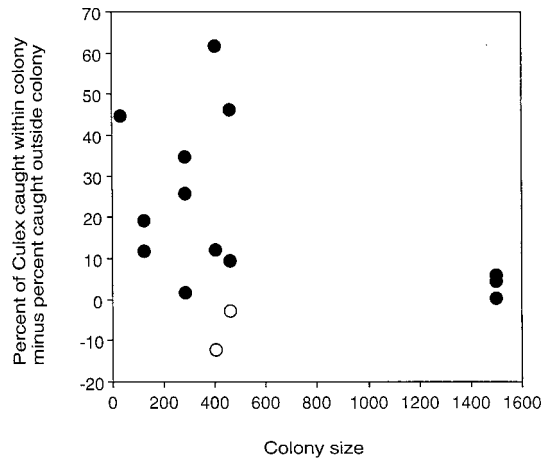

Fig. 2. Effect of cliff swallow colony size (number of active nests) on the difference in the percentage of *Culex tarsalis* among all mosquitoes caught within the colony versus outside (30 m away) per night ($r_s = -0.43$, $P = 0.10$, $N = 16$ nights). Black dots indicate nights when a higher percentage of *C. tarsalis* were caught within the colony and open dots nights when a higher percentage was caught outside the colony. There was no significant effect of colony size on the apparent attraction of *C. tarsalis* to colony sites.

pattern would seem most likely to be caused by attraction of mosquitoes to large concentrations of hosts.

Most mosquito survey work has sought to measure abundance in relation to habitat types or time of year, and relatively little is known in general about the degree to which localized concentrations of hosts attract mosquitoes independent of habitat. To our knowledge, the studies most closely similar to ours showing apparent attraction of mosquitoes to increase with the number of host individuals were ones done with *Anopheles* spp. in human huts in east Africa (Haddow 1942, Ribbands 1949, Gillies 1955). In these studies, the number of mosquitoes trapped in a hut was positively correlated with the number of human inhabitants, and Haddow (1942) demonstrated experimentally that changing the number of hosts per hut led to corresponding changes in mosquito abundance. The density of cattle in rice fields in Louisiana was positively correlated with larval density of *Psorophora* mosquitoes (McLaughlin and Vidrine 1987), suggesting that local food availability influenced mosquito reproductive rates and thus abundance of mosquitoes in different fields. Davies et al. (1991) hypothesized that larger primate sleeping groups attracted more mosquitoes based on malaria infection rates. Their results suggested that the number of mosquito bites per monkey increased at a rate greater than the linear increase in host number, but they had no direct data on mosquito abundance or behavior.

If large cliff swallow colonies attract mosquitoes and thus result in elevated local mosquito abundance near those sites, the mosquito taxa involved should include those that use cliff swallows as blood-meal sources.

The majority of the species in our samples were *A. vexans,* with lesser numbers of *C. tarsalis.* Known to commonly feed on mammals, *A. vexans* and other *Aedes/Ochlerotatus* species are opportunistic and have been recorded using birds as hosts, especially when birds are available in high densities (Shemanchuk et al. 1963, Corbet and Downe 1966, Shemanchuk 1969, Wright and DeFoliart 1970, Day and Edman 1984, Edman et al. 1984, Anderson and Fortner 1988). The fact that we caught more than 70 *A. vexans* per trap, on average, within the colonies suggests that they might have been using cliff swallows as hosts; in addition, we found some engorged *A. vexans* in the traps. The presence of *C. tarsalis* (including some that were engorged) at the colony sites is not unexpected, given this species' apparent preference for avian blood (Reeves and Hammon 1944, Tempelis et al. 1967, Hayes et al. 1973, Ritchie and Rowley 1981). Mosquitoes trapped 30 m outside the colony probably also had access to the birds at the site, as a dispersal study on *C. tarsalis* indicated that individuals could be commonly found up to 100 m or more from their feeding site (Tempelis et al. 1965).

Although total mosquito abundance increased with colony size, *A. vexans* was largely responsible for this result. The number of *C. tarsalis* did not vary significantly with colony size. This is consistent with the hypothesis of Wekesa et al. (1997) that generalist feeders such as *C. tarsalis* should be less sensitive to local abundance of a particular host taxon than more specialized feeders. Although our data for *C. tarsalis* support the hypothesis of Wekesa et al., the strong apparent response of *A. vexans* to cliff swallow colony size does not. Most *Aedes* species are also generalist feeders (e.g., Edman 1971, Tempelis 1975, Day and Edman 1984, Nasci 1984), and *A. vexans* is known to use many different host taxa.

There was a suggestion that apparent attraction of *C. tarsalis* to a colony site, as measured by the proportion of individuals caught within versus outside the colony, declined with colony size (Fig. 2), although the trend was nonsignificant. Such a decline might be expected if *C. tarsalis* exhibits a density-dependent switch away from hosts that are abundant. Because mosquitoes interfere with each other's feeding attempts and elicit greater behavioral defense responses from vertebrate hosts (Reeves 1971, Edman et al. 1972, Nelson et al. 1976), they often show negatively density-dependent feeding success. Consequently, we might expect mosquitoes at large swallow colonies to switch to other hosts if available. This would account for the fact that *C. tarsalis* populations in particular did not show an overall increase with cliff swallow colony size.

If some mosquitoes switch to other hosts when one becomes abundant, a benefit of living in a large group for cliff swallows could be reduced likelihood of mosquito attack, at least from taxa such as *C. tarsalis.* Our data suggest that this is not the case, however, for *A. vexans,* and coloniality might in fact increase the probability of attack by this species. Yet, whether the increase in mosquito abundance in larger colonies

translates into an actual cost for cliff swallows is unclear, given that grouping in some instances lowers the probability of attack by vagile hematophagous insects (Duncan and Vigne 1979, Rutberg 1987, Mooring and Hart 1992). This usually results from herding animals' clustering to reduce the amount of surface area (skin) exposed to attack. Although this mechanism is unlikely for cliff swallows that occupy nests of fixed positions in colonies, large colonies could numerically dilute the per capita mosquito attack rate by virtue of the many host individuals present, depending on whether mosquito abundance increases at a disproportionately faster rate than the increase in cliff swallow colony size. In addition, the fact that cliff swallows roost at night inside their enclosed mud nests may also reduce their likelihood of being fed on by swarms of mosquitoes in large colonies. Increased mosquito attack in subcolonies of albatrosses was thought to result in higher levels of nest failure, although whether attack rates were related to nest density was not reported (Anderson and Fortner 1988).

The most obvious alternative explanation for our results (Fig. 1) is that large cliff swallow colonies occur in places that also harbor large mosquito populations. If this was the case, attraction of mosquitoes to colonies might not occur or be important in generating the observed relationship between mosquito abundance and colony size. We detected no gross habitat differences among sites that would support such a scenario, and presence of livestock (an alternative host for mosquitoes) was not related to cliff swallow colony size. We recognize that our habitat classifications may have missed some salient landscape feature important to mosquitoes, although these colony sites were in such apparently similar habitat that we think this is unlikely. It is possible that the cliff swallows themselves may have cued on mosquito abundance as an index of local flying insect (food) availability, and large colonies formed in areas with many mosquitoes and other flying insects. We think this is also unlikely, however. Cliff swallows occasionally eat mosquitoes (Brown and Brown 1996), but they represent an insignificant part of the diet, mostly because they are active at night when cliff swallows do not feed. In addition, if cliff swallows were cueing on mosquito abundance at a site as an index of food availability, we should have seen this reflected to some degree in habitat differences between sites, and we found no evidence of any such differences.

The results presented here suggest that the patchy mosquito distributions observed in some areas may reflect local concentrations of hosts independent of habitat characteristics, and they provide one of the few demonstrations of this for nonhuman host taxa. At least in southwestern Nebraska, these results also make it possible to predict areas of highest mosquito abundance, providing useful information for mosquito/ encephalitis virus surveillance efforts or mosquito control.

Acknowledgments

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