



Human presence outweighs non-anthropogenic factors as a driver of avian nest parasite loads

Lauryn Benedict^{1,2} · Nora E. Covy¹ · Paul A. Love¹ · Steven T. Stier²

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Abstract

Human presence and landscape change can alter many aspects of ecological communities and can interact with natural factors to change host–parasite dynamics. In the study reported here, we tested whether an anthropogenic factor, urbanization, affected the abundance and size of hematophagous ectoparasites (swallow bugs: *Oeciacus vicarius*) found in the nests of cliff swallows (*Petrochelidon pyrrhonota*). We also examined how swallow bug infestations might be affected by multiple non-anthropogenic biotic and abiotic factors, including season, nest mass, nest colony size, the history of colony occupation, and the presence of other parasitic and non-parasitic arthropods in cliff swallow nests. Our sample included 73 nests collected from 18 cliff swallow colonies in Northern Colorado, USA. Results indicated that swallow bug loads were most strongly predicted by human land use and density, with urban colonies having much heavier infestations than rural colonies. Swallow bugs were more numerous in colonies that were known to have been recently occupied by cliff swallows, and in nests that contained high numbers of other parasitic arthropods, including fleas and ticks. Swallow bug population size did not vary with season, nest mass, or nest colony size, and none of our measured factors predicted swallow bug body length. Results suggest that cities may exacerbate harmful effects of avian ectoparasites by promoting large population sizes, and that these effects may be compounded by the presence of multiple parasitic species in heavily infested nests.

Keywords Cliff swallow · Human impacts · *Oeciacus vicarius* · *Petrochelidon pyrrhonota* · Swallow bug

Zusammenfassung

Die Gegenwart von Menschen überwiegt nicht-anthropogene Faktoren bei der Erklärung der Parasitenbelastung in Vogelnestern

Gegenwart von Menschen und Landschaftswandel können viele Aspekte ökologischer Gemeinschaften beeinflussen und mit natürlichen Faktoren interagieren, was Wirt-Parasit-Dynamik verändert. In der hier beschriebenen Studie untersuchten wir, ob die Urbanisierung als anthropogener Faktor die Häufigkeit und Größe hämatophager Ektoparasiten (Amerikanische Schwalbenwanzen: *Oeciacus vicarius*) beeinflusst, die in den Nestern von Fahlstirnschwalben (*Petrochelidon pyrrhonota*) vorkommen. Weiterhin untersuchten wir, wie der Befall mit Schwalbenwanzen durch mehrere nicht-anthropogene biotische und abiotische Faktoren wie Jahreszeit, Nestmasse, Größe der Nestkolonie, die Geschichte der Kolonieentstehung und das Vorkommen anderer parasitärer und nichtparasitärer Arthropoden in Fahlstirnschwalbennestern beeinträchtigt wird. Unsere Stichprobe umfasste 73 Nester aus 18 verschiedenen Fahlstirnschwalbenkolonien im nördlichen Colorado, USA. Unsere Ergebnisse deuteten darauf hin, dass die Belastung durch Schwalbenwanzen am stärksten durch die Bevölkerungsdichte

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✉ Lauryn Benedict
lauryn.benedict@unco.edu

¹ School of Biological Sciences, University of Northern Colorado, 501 20th St. CB 92, Greeley, CO, USA

² Department of Applied Statistics and Research Methods, University of Northern Colorado, 501 20th St. CB 92, Greeley, CO, USA

und deren Landnutzung bestimmt wurde. Dabei hatten städtische Schwalbenkolonien einen stärkeren Parasitenbefall als ländliche Kolonien. Schwalbenwanzen waren zahlreicher in Kolonien, von denen bekannt war, dass sie kürzlich durch Fahlstirnschwalben besetzt wurden, sowie in Nestern, die eine hohe Anzahl anderer parasitärer Arthropoden wie Fliegen und Zecken enthielten. Die Populationsgröße der Schwalbenwanzen variierte nicht mit der Jahreszeit, Nestmasse oder Größe der Nestkolonie, und keiner unserer gemessenen Faktoren bestimmte die Körperlänge der Schwalbenwanzen. Unsere Ergebnisse lassen vermuten, dass Städte möglicherweise schädliche Auswirkungen von Vogelektoparasiten durch die Förderung großer Populationsgrößen verstärken und dass diese Auswirkungen womöglich durch das Vorkommen mehrerer Parasitenarten zusammen in starkbefallenen Nestern verschlimmert werden.

Introduction

Much evidence suggests that urbanization has negative impacts on organisms, including birds (Marzluff 2001; La Sorte et al. 2018). These negative consequences may manifest in varied ways, including via altering host–parasite dynamics (Bradley and Altizer 2007; Murray et al. 2019). Such changes, in turn, can have large-scale impacts on ecosystem function, making them an important subject for study (Marcogliese 2004). In multiple avian systems, urban and rural birds are differentially affected by parasites (Reviewed in Delgado-V and French 2012). For example, urbanization increased the prevalence of both a viral and gastrointestinal parasite in house finches (*Haemorhous mexicanus*) and changed the epigenetics of Darwin’s finches (*Geospiza fortis* and *G. fuliginosa*) (Giraudeau et al. 2014; McNew et al. 2017). This trend is not universal, however, because some species have reduced ecto- and endoparasite loads in urban areas (Evans et al. 2009; Calegario-Marques and Amato 2014). The factors driving parasite presence can be variable, and therefore focused studies of multiple systems will help us to make universal predictions regarding parasitism in undeveloped versus human-altered landscapes (Schmid Hempel 2011; Delgado-V and French 2012; Leung and Koprivnikar 2016).

One well-studied avian host–parasite system is that of the migratory cliff swallow (*Petrochelidon pyrrhonota*) and its hematophagous North American parasite, the swallow bug (*Oeciacus vicarius*) (Myers 1928; Smith and Eads 1978; Brown and Brown 1996). The movement of cliff swallows into cities, and the wealth of historical data on these species make them valuable subjects for studies of urbanization. Cliff swallows build enclosed mud nests within colonies on vertical substrates (Brown et al. 2020). Colonies, which vary widely in size and location, are often inhabited by birds across years with individual nests being reused (Brown et al. 2020). Cliff swallows return to summer breeding grounds in the central USA in April and pairs rear a single brood each year (Brown et al. 2020). Clutch initiation dates peak in late May and June in the central plains and Rocky Mountains, young generally fledge by the end of July, and all individuals depart on fall migration in July, August and September (Brown et al. 2020). Swallow bugs feed on the seasonally

breeding birds during the spring and summer, and then overwinter in the nests, surviving for a year or more without food (Loye 1985). Heavy infestation by swallow bugs decreases cliff swallow nesting success; these parasites are the primary source of nestling mortality and can prevent second breeding attempts within a season (Brown and Brown 1986, 2015). Swallow bugs shorten host life spans and are vectors for multiple viruses with negative impacts on birds, including buggy creek virus and other *Alphaviruses* (Brown et al. 1995; Padhi et al. 2008; Allison et al. 2015). Hosts of this parasite include the house sparrow (*Passer domesticus*), as well as the cliff swallow (Fassbinder-Orth et al. 2018).

Many factors are likely to impact ectoparasite prevalence in this system. Swallow bug population sizes within nests are known to fluctuate throughout the year, increasing dramatically during the birds’ breeding season and then shrinking when the birds depart on migration (Loye and Hopla 1983). Overwintering mortality of swallow bugs was high in one population in Oklahoma, USA, with only 1–5% of the fall population surviving to the following spring (Loye 1985). Despite this, swallow bugs regularly persist in nests across years, as do the viruses that they host, and high swallow bug populations in old nests deter cliff swallows from recolonizing those nests in the spring (Brown and Brown 1996; Brown et al. 2010). Swallow bug population sizes are known to increase with colony size and recent nest use by cliff swallows (Brown and Brown 1986; Brown et al. 2020). Nest size also has the potential to impact parasite populations, with larger nests potentially offering increased space and nesting material to support more individuals (Reynolds et al. 2016). Further, cliff swallow nests house a variety of other ectoparasites and arthropods, creating an invertebrate community within the nest (Hopla and Loye 1983; López-Rull and Macías Garcia 2015). The negative effects of swallow bugs may be amplified if they are often accompanied by other parasites, such as ticks and fleas, but the interactions between these invertebrates are currently not well understood, particularly during the non-breeding season (Thompson et al. 1997). Conversely, swallow bug populations may be reduced by the presence of predatory arthropods, such as spiders or ants (Reinhardt and Siva-Jothy 2007; Brown et al. 2015).

With human population growth and urban sprawl, more cliff swallows are being affected by anthropogenic factors.

Cliff swallows have long been considered “suburban adaptable” (Blair 1996) and known to use man-made structures for nesting within cities. Bridges and underpasses provide ideal vertical substrates for their nests, particularly when they are located over water, which offers building material (mud) and prey (insects) (Brown et al. 2020). A study from Denver, Colorado, USA, found multiple colonies located in a major metropolitan area (Sowa et al. 2014). Colonies were typically located under bridges, and urban nest colonies were larger than suburban colonies (Sowa et al. 2014). Additionally, resident house sparrows, an alternative swallow bug host, have been observed to roost in cliff swallow nests throughout the year in urban areas where they have the potential to maintain parasite loads through the non-breeding season (Brown et al. 2020). These findings raise the possibility that cliff swallows living in human-dominated environments may experience high swallow bug parasitism. It is currently unknown whether urban cliff swallow colonies suffer from parasite infestations that may be heightened due to increased numbers of swallow bugs, increased swallow bug size, or the presence of other parasitic species.

Our goal with this study was to assess which factors, including human land use and density, have the greatest impact on swallow bug population sizes and body sizes in cliff swallow nests. Although results from other systems are mixed, we predicted that urbanization would increase swallow bug loads. Following theory and the results of previous studies on this species, we predicted that swallow bug populations would be highest in large nests within recently occupied and large colonies. We expected to find more swallow bugs in nests during the fall (soon after the swallows have departed) than in the following spring, due to overwinter mortality. We also sought to test whether swallow bug populations vary in tandem with the presence of other arthropods in the nest. We predicted that swallow bug populations would decrease in the presence of arthropods that could act as predators or competitors. To evaluate patterns of parasite size, we measured swallow bug body length. We tested for effects of human presence, nest size, nest colony size, colony occupation, season, and competitor presence on swallow bug body size. We predicted that individuals surviving to the spring would be larger, following previous studies (Loye 1985). We did not have a priori predictions about the effects of other factors on swallow bug body size, as there is little literature examining size variation in this species.

Methods

We collected 73 nests from 18 cliff swallow colonies during the fall of 2014 and the spring of 2015. Colonies were located at 11 different sites on public land in and around the city of Fort Collins, Larimer County, Colorado, USA (Lat:

40.46903–40.95935 N, – 105.22475 to – 105.035667 W) (Fig. 1). All sites were separated by at least 1 km. At each site, we collected nests from one to three colonies, choosing colonies of different sizes. Colonies were identified as contiguous groups of cliff swallow nests, and distinct colonies were located at least 75 m away from each other, far enough that swallow bugs could only disperse between them by attaching to an avian host, and not by independent movement (Brown et al. 2020).

We sampled 22 nests from five “urban” colonies in the city of Fort Collins. Following the literature, we classified these as urban sites because they were within city limits, were within 100 m of industrial and high-density housing areas, and had a human population density greater than 1000 people/km² (MacGregor-Fors 2011; Dmowska and Stepinski 2017) (Fig. 1). Population density data were obtained from http://sil.uc.edu/webapps/socscape_usa/ and is based on 2010 US census data (Dmowska and Stepinski 2017; Space Informatics Lab 2017). All urban colonies were located on the undersides of bridges. We sampled 51 nests from 13 “rural” colonies located in areas of predominantly undisturbed ground cover with human population densities ranging from 0 to 50 people/km² (Fig. 1). All rural sites were on publicly protected land. Twelve of these colonies were located on cliffs and one was located on the underside of a bridge. We further confirmed our urban and rural classifications using national MRLC land cover data for 2013 and 2016 (<https://www.mrlc.gov/>, Jin et al. 2019) imported into ArcGIS Desktop 10.7.1. These data have a 30 m resolution and provide land cover classifications including a range of “developed” and undeveloped designations (<https://www.mrlc.gov/>). All of our urban sites were on developed land, confirming anthropogenic impacts. Rural sites were classified predominately as shrub/scrub, but also included herbaceous, open space, and evergreen forest. There was no change in land cover classification for any of our sites from 2013 to 2016.

Samples included 39 nests (29 rural, 10 urban) collected from 14 colonies between 8-Nov-2014 and 26-Nov-2014 (“fall”), and 34 nests (22 rural, 12 urban) collected from 13 colonies between 16-Mar-2015 and 23-Apr-2015 (“spring”). For all colonies, we noted their history of use by cliff swallows in spring/summer 2014. Forty-four nests were from colonies that we observed to be “active”, and 29 were from colonies that we did not observe in 2014 (“unknown”). Nests were collected by covering them with a gallon-sized Ziploc bag and using a knife to scrape them from the substrate to which they were attached. We collected nests from both the edges and the centers of colonies, as location can affect swallow bug load (Brown and Brown 1986). Collected nests were weighed on a digital scale and then stored in plastic bags at 4 °C for up to 3 days (mean = 0.97 days). Arthropods were extracted

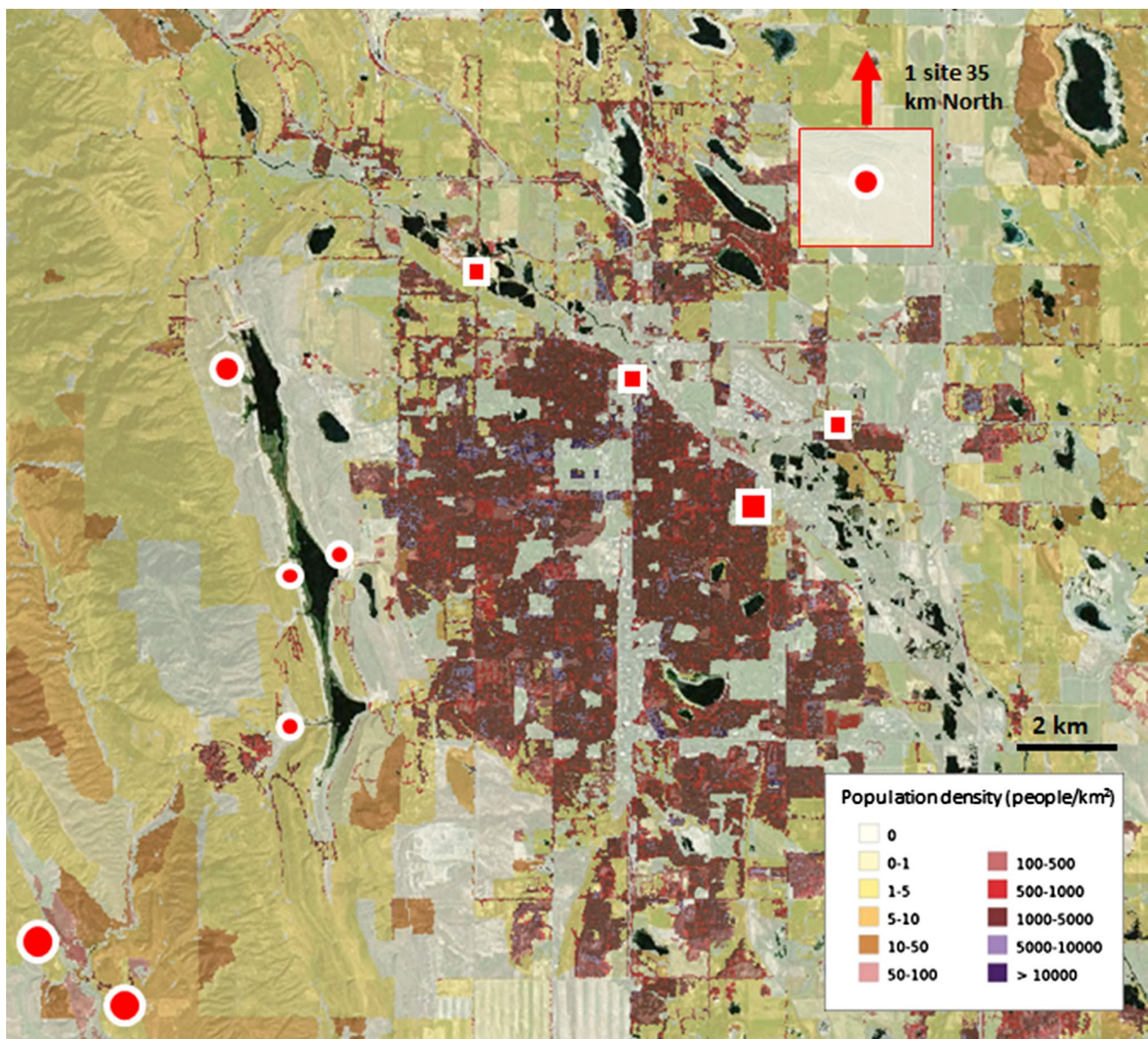


Fig. 1 Urban (squares) and rural (circles) cliff swallow (*Petrochelidon pyrrhonota*) nest collection sites overlaid on a map showing population density in and around Fort Collins, CO, USA. Population

density was obtained from http://sil.uc.edu/webapps/socscscape_usa/ and is based on 2010 census data. Markers are scaled to reflect the number of colonies (1–3) sampled at each site

from nests using Berlese funnels, a method verified for this system by other researchers, and preserved in 70% ethanol (Brown et al. 2001). Nests were left on the Berlese funnels for 24 h. Arthropods were counted by a single observer and identified under a dissecting microscope. Common parasites of cliff swallows, including the swallow bug *O. vicarius*, the tick *Argas cooleyi*, and the flea *Ceratophyllus celsus*, were identified to species. All other arthropods were identified to order. Ten swallow bugs were selected randomly per nest and measured for body length (mm) by one observer using digital calipers. When fewer than ten swallow bugs were available for a single nest, all

individuals were measured. Length was measured from the front of the head to the end of the abdomen along the central body axis. We did not sex individual swallow bugs.

We built a generalized linear mixed model (GLMM) with a log link function to assess the potential effects of human presence (urban versus rural), season (fall versus spring), history (known-active in 2014 or unknown), colony size (number of nests), nest size (mass in grams), parasitic competitors (number of ectoparasitic ticks and fleas), and other arthropods (number of non-parasitic arthropods) on swallow bug population size per nest. These seven variables were included as fixed factors in the model. Colony

identity nested within site was included as a random factor. Model sample sizes were 73 nests, 11 sites, and 18 colonies. Multicollinearity was assessed using VIF values and condition indexes. We fit our model using a negative binomial distribution. For comparison, we fit a similar Poisson GLMM to assess fit. The AIC and BIC values for the Poisson model were 1525.69 and 1548.59, respectively. The AIC and BIC values for negative binomial GLMM were 651.44 and 676.63, respectively. We also assessed residuals for each model across the different sites. The AIC, BIC, and residual plots suggested the negative binomial model was a good fit for the data.

We ran a second model to assess the potential effects of our measured factors on swallow bug body length. This model included 465 individual swallow bugs from 64 nests and 16 colonies. We used human presence, season, history, colony size, nest size and parasitic competitors as fixed factors, and nest identity nested within colony as a random factor. Because swallow bug length data were normally distributed, we ran this model as a linear mixed model (LMM) using the standard least squares method. The LMM was run in JMP 13.0 (JMP® 2020)). The GLMM were run in R Version 3.4.0 (R Development Core Team 2016) using package glmmadmb (Skaug et al. 2013; <http://glmmadmb.r-forge.r-project.org/>). Figures 2 and 3 and the descriptive statistics within them were also generated in R Version 3.4.0. Values are reported as means plus standard deviations unless otherwise noted.

Results

Swallow bug infestation rates were highly variable, ranging from 0 to 1,138 swallow bugs per cliff swallow nest (mean: 100.14 ± 212.42). Other arthropods common in our samples included the ectoparasitic tick *A. cooleyi* (4.63 ± 8.55 per nest), the flea *C. celsus* (19.23 ± 44.95 per nest), and a variety of millipedes (Diplopoda) (9.11 ± 24.37 per nest). Spiders were relatively rare (0.63 ± 1.11 per nest), and ants were extremely rare, with only two individuals found among all nests.

We found differences in swallow bug population size in relation to some of our measured variables, but not others (Figs. 2 and 3). Our GLMM had a negative binomial dispersion parameter of 0.85 (std. err.: 0.16784). When testing for multicollinearity, all of the VIF values were close to one and the condition indexes were less than 20, indicating no collinearity for the fixed effects in the model. Random factors site and colony nested within site had variances of 1.61 and 0.61, respectively. Model results (Table 1) indicated that swallow bug population size was most strongly predicted by human presence, with colony activity history in the previous season, and high competitor (tick and flea) populations also having

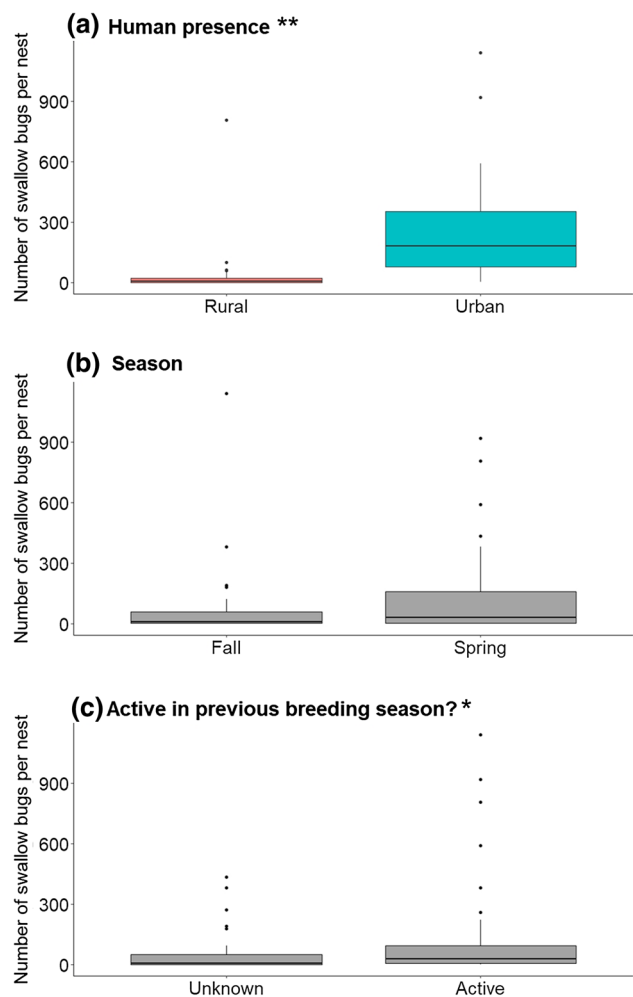


Fig. 2 Mean number of Swallow Bugs (*Oeciacus vicarius*) per cliff swallow nest ($n=73$) at **a** rural versus urban sites colored as in Fig. 3, **b** nests collected in the fall versus spring, and **c** nests known to be occupied by cliff swallows in the previous breeding season versus those not known to be occupied. $N=73$ nests. Box plots show medians, quartiles and potential outliers. Asterisks indicate significant differences obtained from the GLMM: **significant at $P<0.01$, *significant at $P<0.05$

significant effects (Figs. 2 and 3). Model output indicated that nests at urban sites had expected swallow bug loads more than 20 times larger than those at rural sites (Table 1). This pattern coincided with human development more than nest substrate; the four nests collected from the one rural bridge contained a mean of only 31 ± 16.43 swallow bugs. A history of colony occupation increased expected swallow bug loads approximately fivefold, while the presence of parasitic ticks and fleas predicted only a 1% increase in swallow bug load (Table 1). Season, colony size, nest size, and the number of other (non-parasitic) arthropods within the nest did not predict swallow bug load per nest (Table 1).

The 465 swallow bugs that we measured had a mean body length of 2.91 ± 0.78 mm. Our LMM assessing the

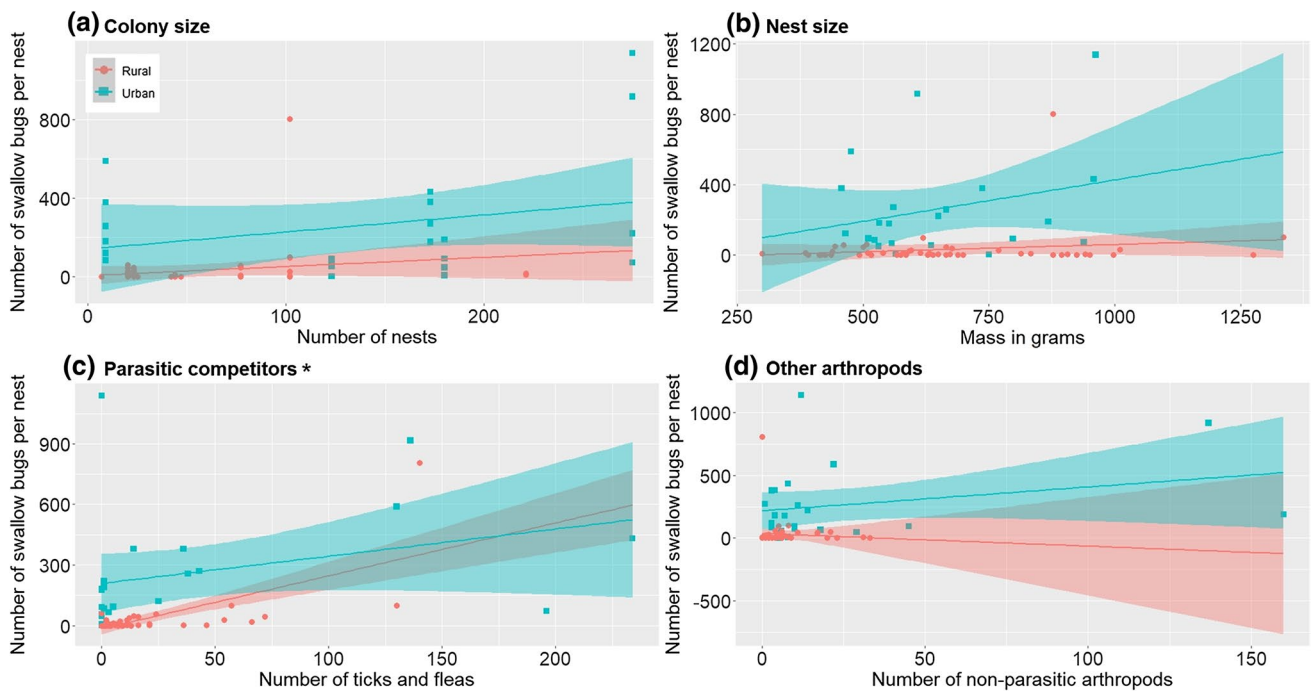


Fig. 3 Number of swallow bugs per cliff swallow nest ($n = 73$) in relation to **a** nest colony size, **b** nest size, **c** parasitic competitors, and **d** the number of other (non-parasitic) arthropods per nest. Circles indicate rural colonies and squares indicate urban colonies with lin-

ear regression lines and 95% confidence intervals. Asterisks indicate significant differences obtained from the GLMM: **significant at $P < 0.01$, *significant at $P < 0.05$

Table 1 Output of a generalized linear mixed model testing whether seven fixed factors predict swallow bug population size in cliff swallow nests in Northern Colorado

| Factors | β | Exp(β)—expected effect ^a | Standard error | z value | P |
|--|---------|---|----------------|-----------|----------|
| Human presence (urban/ rural ^b) | 3.016 | 20.41 | 1.13 | 2.68 | 0.0074** |
| Season (fall /spring) | 0.097 | 1.10 | 0.42 | 0.23 | 0.82 |
| History (active/ unknown in previous breeding season) | 1.72 | 5.58 | 0.71 | 2.42 | 0.015* |
| Colony size (number of nests) | 0.0058 | 1.01 | 0.0058 | 1.00 | 0.32 |
| Nest size (grams) | 0.00075 | 1.01 | 0.00096 | 0.78 | 0.43 |
| Parasitic competitors (number of ticks and fleas) | 0.014 | 1.01 | 0.0057 | 2.46 | 0.014* |
| Other arthropods (number of non-parasitic arthropods) | 0.0061 | 1.01 | 0.0078 | 0.79 | 0.43 |

Negative binomial distribution, log link, model dispersion parameter: 0.85 ± 0.17 (SE)

**Significant at $P < 0.01$, *significant at $P < 0.05$

^aInterpretable as the expected change in swallow bug population size per unit increase of the fixed factor

^bBolded levels are the reference for each factor

effects of six fixed factors and one random factor on the body length of swallow bugs in all nests had an R^2 value of 0.33 (RMSE 0.68). The random factor had a variance of 0.17. None of the colony or arthropod community fixed factors significantly predicted swallow bug body length (Table 2).

We made opportunistic observations of avian presence and activity during colony observations and nest collection

events. We did not quantify the full avian community composition at urban versus rural sites, but we did note several differences. Canyon wrens, a species known to forage and nest in cliff swallow nests (Warning et al. 2015), were present at all rural sites but no urban sites. We regularly observed house sparrows within and around cliff swallow nests at the urban colonies. During many hours of field work at the rural sites included in this study, we have never

Table 2 Output of a linear mixed model testing whether six fixed factors predict swallow bug body length in cliff swallow nests in Northern Colorado

| Factor | β | Standard error | F ratio | P |
|--|---------|----------------|---------|------|
| Human presence (urban/ rural ^a) | 0.050 | 0.076 | 0.43 | 0.52 |
| Season (fall /spring) | 0.013 | 0.069 | 0.037 | 0.85 |
| History (active/ unknown in previous breeding season) | 0.039 | 0.071 | 0.30 | 0.59 |
| Colony size (number of nests) | 0.0011 | 0.00089 | 1.52 | 0.22 |
| Nest size (grams) | 0.00036 | 0.00035 | 1.035 | 0.31 |
| Parasitic competitors (number of ticks and fleas) | -0.0011 | 0.0014 | 0.65 | 0.43 |

*Significant at $P < 0.05$ ^aBolded levels are the reference for each factor

observed house sparrows at cliff swallow nests (Warning et al. 2015; Benedict and Warning 2017).

Discussion

Cliff swallow nests in Northern Colorado house multiple species of ectoparasites, including highly variable numbers of swallow bugs. We found more than 1000 swallow bugs in some individual nests, a number that fits with known parasite loads in this system in other locations (Brown et al. 2001, 2020). Perhaps more surprisingly, we found that some nests did not house any swallow bugs, despite existing estimates suggesting that most cliff swallow nests harbor these hematophagous parasites (Brown et al. 2001). What drives such variability in parasite load? The strongest local predictors of high swallow bug populations per nest were (1) human presence and landscape alteration, (2) nest use by cliff swallows in the previous breeding season, and (3) the presence of other ectoparasites, including ticks and fleas.

Although previous studies have shown that swallow bug loads correlate with cliff swallow nest colony size (Brown and Brown 1986), our data did not support that pattern. This may represent a regional difference, it may be a sampling effect, or it might result from the inclusion of multiple variables in the model that were not measured by other researchers. In particular, studies have shown that urban colonies are often large (Sowa et al. 2014). Among our samples, the primary driver of high parasite loads in large urban colonies appears to be human density rather than colony size. We also failed to support our prediction that swallow bug population sizes would be higher in larger nests. Large nests support more parasites in other avian systems, but we know of no evidence to this effect among cliff swallows (Reynolds et al. 2016). In a previous study, nest diameter did not correlate with swallow bug immigration; this study suggests that nest mass also does not correlate with swallow bug population size or persistence (Brown and Brown 2005). Because swallow bugs depend on the hosts much more than the nest material for subsistence, nest size may be unimportant in determining their presence and prevalence (Loye 1985). In

accordance with this idea and with previous studies, historic host presence had an effect in this system; nests known to be more recently occupied by cliff swallows housed higher numbers of swallow bugs (Brown and Brown 1986).

Our sampled nests did not contain significantly different swallow bug population sizes in the fall versus spring. Despite the well-documented ability of swallow bugs to survive for multiple years without a host, previous studies suggested that numbers would be fewer following the winter (Loye 1985). We, however, found no significant difference in swallow bug population sizes in nests collected during the spring versus the fall, and not even a trend in the predicted direction. This result argues strongly against a reduction in parasite population sizes due to overwinter mortality. Our results may differ from those of other researchers because we sampled fall nests in November, several months after swallow departure, rather than immediately following the swallow breeding season (Loye 1985).

Across all conditions, swallow bug size did not vary predictably. Little is known about the growth rates and sizes of swallow bugs, but at a minimum we recognize that females are larger than males and that as they develop through successive instars they achieve larger body sizes (Loye 1985; Reinhardt and Siva-Jothy 2007). The consistency we observed in body sizes across seasons and sites suggests that the sex ratios and developmental stages of swallow bugs did not differ due to any of our measured variables. We expect that most individuals were adults, as they typically reach that stage soon after swallows depart on fall migration, and then overwinter in that state (Loye 1985). Adult developmental stages improve survivability in close relatives of swallow bugs (bedbugs: *Cimex lectularius*), and it is possible that larger body sizes further enhance that effect, but we did not find that swallow bugs surviving to the spring were on average larger than individuals alive in the fall. Bedbugs, close relatives of swallow bugs, survive better and develop faster when in groups than when alone, but we did not find larger body sizes among swallow bugs living within larger populations (Benoit et al. 2007; Saenz et al. 2014).

The strongest non-anthropogenic correlate of swallow bug population size that we measured was the number of

ticks and fleas in the nest. Throughout their range, cliff swallows are frequent hosts of multiple ectoparasites (Hopla and Loyer 1983; Brown et al. 2020). Flea population sizes, like those of swallow bugs, have been shown to increase with increasing nest colony size (Brown and Brown 1986). Ticks also frequently coexist with swallow bugs in nests and can have negative fitness consequences for their hosts (Larimore 1987; Brown et al. 2020). The pattern of coexistence that we measured here suggests that competition among ectoparasites does not limit their population sizes. Instead, multiple parasites appear to have parallel patterns of abundance and survivorship across seasons, with frequent overwinter survival. Because all three of these groups are hematophagous, their effects on cliff swallow nesting success and survivorship are likely to be synergistic, although specific impacts may vary (Brown and Brown 1986). Furthermore, the factors promoting parasite presence appear to differ from those controlling the presence of other arthropods in the nest, as the abundance of non-parasitic species did not correlate with swallow bug abundance. Interestingly, we found very few spiders or ants in the collected nests, suggesting that arthropod predators are rare in this system and may not represent a significant check on swallow bug population (Reinhardt and Siva-Jothy 2007; Brown et al. 2015). We did not test for viral load in the swallow bugs we collected, but interactions with this class of pathogen are likely to further alter the community dynamics and represent an important avenue for further investigation (Brown et al. 2001, 2010).

As predicted, we found that cliff swallow nests at urban sites housed many more ectoparasites than those at rural sites. Urbanization is known to pose threats to native bird species, and host–parasite relationships represent one avenue for detrimental effects (Bradley and Altizer 2007; Delgado-V and French 2012). Our results suggest that cliff swallows living in urban colonies could receive negative impacts from inflated swallow bug populations, plus the “double-whammy” of inflated tick and flea populations. This result matches patterns seen across all animals, for which urban environments increase both the number and diversity of parasites in a range of host species (Murray et al. 2019). We did not fully investigate what proximate factors generate these patterns, but a likely driver is the presence of an alternate host, house sparrows, at urban sites throughout the year. House sparrows are permanent residents throughout the cliff swallow breeding range, with a distribution restricted to human-dominated habitats (Lowther and Cink 2006). We regularly observed them at our urban sites, but never at our rural sites, a pattern confirmed during other work in similar local habitats (Covy et al. 2019). House sparrow presence would maintain near-permanent host availability in cities, which could keep swallow bug populations high (Fassbinder-Orth et al. 2018). Furthermore, house sparrow presence in cliff

swallow colonies increases the prevalence of buggy creek virus in hosts and vectors (Brown et al. 2012). Thus, invasive species can harm natives in multiple ways—not only do invaders compete for resources, but they also induce higher parasite loads in human-altered landscapes. Community structure among avian species may also impact arthropod populations in cliff swallow nests via other mechanisms. In particular, canyon wrens (*Catherpes mexicanus*) are closely associated with cliff swallow colonies at rural sites in our study area (Warning et al. 2015). Canyon wrens frequently forage in cliff swallow nests, and are known to eat a diverse diet of arthropods (Warning et al. 2015, Warning and Leatherman 2016). If canyon wrens prey on swallow bugs, fleas, or ticks, the coexistence of canyon wrens and cliff swallows could represent a mutualistic heterospecific relationship.

Given the higher parasite loads in human-altered areas (Sowa et al. 2014), why do cliff swallows form large urban colonies? Urban sites may be more consistently occupied if they offer benefits that outweigh the cost of parasites (Brown and Brown 1996). Anthropogenic lights located on roads above urban nest colonies can act as attractants for flying insects, creating rich foraging grounds for aerial insectivores (Rydell 1992). Concrete bridges provide excellent substrates for nest adhesion and are often located over water where swallows prefer to forage (Sowa et al. 2014, Brown et al. 2002). Nests on bridges may also have favorable microclimates relative to other nest types, although the specific benefits of this for cliff swallows are unknown (Withers 1977; Amat-Valero et al. 2014). Finally, high nest density on bridges and underpasses near humans could provide predator protection to the nesting birds (Berger 2007). Given the low numbers of swallow bugs at our one colony on a rural bridge, we think it unlikely that substrate alone drive swallow bug presence. Rather, a combination of the factors discussed above most likely support parasite persistence. These (and other) factors deserve more study to help explain why cliff swallows regularly nest in large, heavily parasitized urban colonies.

As in other avian systems, we found that multiple kinds of ectoparasites increased with urban living (Giraudeau et al. 2014; Murray et al. 2019). Our results add to the extensive body of knowledge about avian host–parasite dynamics, as well as to the growing body of knowledge about how urbanization impacts native wildlife (Brown and Brown 1996; Marzluff 2001). Animals in cities respond to parasites in varied ways, and recent research reveals much about the interplay between parasite presence and host response (Fokidis et al. 2008; McNew et al. 2017). Future work evaluating cliff swallow reproductive success at urban versus rural sites will be important in testing the specific fitness outcomes of the patterns described here. Overall, these patterns suggest that differences in

urban and rural avian community structure alter ectoparasite presence and abundance. Outcomes add to the growing body of research aimed at understanding and preserving biodiversity in human-dominated landscapes.

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Author contributions LB and NEC conceived and designed the experiments. NEC conducted all field research and nest processing. PAL identified and measured all arthropods. LB, NEC, and PAL conceived the hypotheses and predictions. LB and STS conducted statistical analyses, and STS created Figs. 2 and 3. LB wrote the manuscript with input from NEC, PAL, and STS.

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