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Elevated Temperature Reduces Overwintering Survival of an Avian Ectoparasite, the Swallow Bug (Hemiptera: Cimicidae: *Cimex vicarius*)

Charles R. Brown,[1,3,] Stacey L. Hannebaum,[1] Andrew Eaton-Clark,[1] Warren Booth,[1,] and Valerie A. O'Brien[1,2]

[1]Department of Biological Sciences, University of Tulsa, Tulsa, OK 74104, USA, [2]School of Science and Mathematics, Tulsa Community College-Metro Campus, Tulsa, OK 74119, USA, and [3]Corresponding author, e-mail: charles-brown@utulsa.edu

Abstract

The survival of insects that are dormant in winter may either increase or decrease as a consequence of elevated winter temperatures under climate change. Warming can be deleterious when metabolism of the overwintering life stages increases to the point that energy reserves are exhausted before postoverwintering reemergence. We examined experimentally how overwintering survival of swallow bugs (Hemiptera: Cimicidae: *Cimex vicarius* Horvath), an ectoparasite primarily of cliff swallows (Passeriformes: Hirundinidae: *Petrochelidon pyrrhonota* Vieillot), was affected by a 3°C rise in mean daily temperature for populations in Oklahoma, Nebraska, and North Dakota. Adult and nymphal swallow bugs exposed to elevated temperature had an average reduction of approximately 31% in overwintering survival (from July/August to April/May), relative to controls exposed to current region-specific ambient-like conditions. Adult males in both groups survived less well in Nebraska and North Dakota than adult males in Oklahoma, but there was no consistent latitudinal effect of the elevated heat treatment. Our results indicate that projected increases in mean temperature in the Great Plains by 2050 could result in fewer swallow bugs surviving the winter and thus a reduced population size upon the arrival of their primary host in the spring, potentially affecting cliff swallow reproductive success, site use, and breeding phenology. Global climate change may alter the dynamics of host–parasite systems by reducing overall parasite abundance.

Key words: cliff swallow, climate change, ectoparasite, heat tolerance

The global rise in temperature is projected to have profound effects on insects, potentially altering distribution, life history, phenology, abundance, and community composition (Musolin 2007, Cornelissen 2011, Sangle et al. 2015, Harvey et al. 2020, Halsch et al. 2021). Insects that are dormant in winter in temperate latitudes may be especially sensitive to changes in temperature, given that thermal conditions often impose restrictions on where or how long insects can survive during the harsh winter months (Bale 1991, Lee and Denlinger 1991, Leather et al. 1993, Danks 2004, Sinclair 2015). Work on insect overwintering has often focused on adaptations by insects to survive cold temperatures (Danks 1991, Kukal 1991, Leather et al. 1993, Sinclair et al. 2003, Turnock and Fields 2005, Marshall et al. 2020), with suggestions that a warming climate may improve survival of insects in winter and/or allow some taxa to expand their range northward or to higher elevations (Bale and

Hayward 2010, Andrew and Terblank 2013, Kiritani 2013, Kutz et al. 2014).

Warmer winters, however, may also have deleterious consequences for those taxa that rely entirely on stored energy reserves to survive the dormancy period. When metabolism is temperature dependent, prolonged warm conditions can lead to elevated energy use and resulting mortality if reserves are exhausted before feeding resumes following the overwintering period (Hahn and Denlinger 2011; Adamo et al. 2012; Williams et al. 2012a, 2015; Sinclair 2015; Marshall et al. 2020). Studies that have examined the effect of warm temperatures have found both increases (Leather et al. 1993, Musolin 2007, Takeda et al. 2010, Mutshinda et al. 2011, Williams et al. 2012b, Fründ et al. 2013) and decreases (Irwin and Lee 2003, Williams et al. 2003, Xiao et al. 2017) in survival under warmer conditions.

The effect of climate change on overwintering survival could be especially important for obligate ectoparasites whose annual activity cycles are synchronized with those of their hosts (Merino 2019). For example, if warmer winters lead to parasitic insects ceasing dormancy before the hosts have returned in the spring, greater overwintering parasite mortality could occur. This scenario might apply to hematophagous ectoparasites that overwinter in or near the nests of their migratory bird hosts and cannot find food if they become metabolically active before the birds arrive. The situation is similar to that faced by migratory birds whose advancing spring arrival may sometimes be phenologically mismatched with their insect prey (Walther 2010), or insect herbivores that emerge before their food plants can support them (Singer and Parmesan 2010, Williams et al. 2015).

In this study, we examine experimentally how elevated temperature during dormancy affects overwintering survival of an ectoparasitic insect that is restricted to a relatively short reproductive season. The insect is the swallow bug (Hemiptera: Cimicidae: *Cimex vicarius* Horvath), an ectoparasite that feeds mostly on cliff swallows (Passeriformes: Hirundinidae: *Petrochelidon pyrrhonota* Vieillot). Swallow bugs reside primarily inside swallow nests or the adjacent nesting substrate and rarely travel on the adult birds (Brown and Brown 1996, 2004; Moore and Brown 2014). Large numbers of swallow bugs overwinter in cliff swallow nests and thus (unlike cave- or house-dwelling cimicids) are exposed to ambient temperatures in temperate latitudes that may be well below freezing during much of the winter (Brown et al. 2009).

Because of the importance of the swallow bug as a parasite of cliff swallows and its influence on the birds' reproductive success, site use, and breeding phenology (Brown and Brown 1986, 1996, 2002, 2015; Brown et al. 2013, 2021), we sought to determine if an increase in mean temperature may affect swallow bug overwinter survival, which ultimately may alter the cost of parasitism to cliff swallows. The study was done in the Great Plains, USA, where swallow bugs are often abundant at cliff swallow colonies; swallows are distributed almost continuously from south Texas north into Canada (Brown et al. 2020). The Great Plains are projected to warm by an average of 2–4°C by 2050 (Liu et al. 2012, Conant et al. 2018). Thus, in this study, we exposed swallow bugs in the laboratory to a 3°C increase in mean temperature between August and April, a time period when cliff swallows are absent from the nesting sites. Given the strong latitudinal temperature gradient in the Great Plains, especially in winter (Lavin et al. 2011), we assessed how the temperature increase affected overwintering survival of swallow bugs in three populations from Oklahoma, Nebraska, and North Dakota.

Materials and Methods

Study Animal and Study Site

The swallow bug is associated exclusively with colonially nesting cliff swallows or their colony sites throughout the bird's range in western and central North America (Brown et al. 2020); even the smaller swallow populations in eastern North America have swallow bugs (Usinger 1966, C. Brown, pers. obs.). Formerly in the genus *Oeciacus*, recent molecular evidence taxonomically reclassifies them as *Cimex* (Balvín et al. 2015). Swallow bugs are obligate ectoparasites, feeding on blood of adult and nestling birds, often at night, and rest in the nest or on the outside of the nest when not feeding. Cliff swallows are migratory and reside at their North American nesting colonies for only about 8–10 wk in the summer (Brown and Brown 1996), during which time all swallow bug reproduction

occurs. Swallow bugs undergo five developmental instar stages before becoming adults (Usinger 1966) and require a blood meal at each stage.

Once the birds finish breeding and desert a colony site in mid-summer, swallow bugs begin to aggregate at a subset of the gourd-shaped cliff swallow nests, wedging themselves between the mud nest and where the nest attaches to the nesting substrate. Such wintering aggregation may begin in July as cliff swallows depart, and continues until the first birds return in April or May, depending on latitude. Most cliff swallows now breed on artificial nesting sites such as concrete bridges or highway culverts (Brown et al. 2013), and swallow bugs harbor in concrete crevices over the winter, usually behind a nest wall. Both adults and nymphs (those of at least the third instar stage or older) overwinter, and nymphs resume development upon feeding again when their hosts return.

The Oklahoma study site was at the Tall Grass Prairie Preserve (36°50′38.87″N, 96°25′02.85″W) in Osage County (Fig. 1). In 2017, swallow bugs were collected from three cliff swallow colony sites in box-shaped culverts underneath gravel roads within the preserve boundaries. Cliff swallow nesting has increased in general in northeastern Oklahoma over the last 25 yr, with the birds (and presumably swallow bugs) present at the Tall Grass Prairie Preserve since at least 1984 (J. Hoffman, pers. comm.). The Oklahoma colony sites are active from late April to early July.

The Nebraska study site was centered at the Cedar Point Biological Station (41°12′34.74″N, 101°38′51.77″W) and included portions of Keith, Garden, Lincoln, and Morrill counties (Fig. 1; Brown et al. 2013). In 2020, swallow bugs were collected from four colony sites, three in culverts underneath railroad tracks and one on a highway bridge over the South Platte River. Cliff swallows and swallow bugs have been studied in this area since 1982 (Brown and Brown 1986, 1996, 2002, 2004, 2005, 2015), and cliff swallows have been nesting there since before European settlement (Brown and Brown 1996). The Nebraska colony sites are typically active from early May to late July.

The North Dakota study site was located near Bowman (46°10′49.88″N, 103°23′11.92″W) in Bowman and Adams counties (Fig. 1). In 2018, swallow bugs were collected from five colony sites in culverts underneath highways. The historical status of cliff swallows in this area is unknown, although they have been present since at least 2006 when we first visited the study area for other research. The North Dakota colonies are active from mid-May to early August.

Sample Collection

Swallow bugs were collected from all colony sites in mid and late July or early August after cliff swallows had finished nesting and vacated the nests. Swallow bugs were no longer active on the outsides of nests and at the time of collection had clustered behind the nests. Entire or partial nests were removed from the wall to expose swallow bugs, nests were placed in plastic bags, and any visible specimens on the wall were brushed into the bags. If swallow bugs were scarce at a site, specimens from multiple nests were combined. We collected 4–10 nests per colony site. Bags were held at room temperature until processed.

Processing of the bags was done 1–4 wk after collection. Contents were put into enamel pans and using forceps live swallow bugs were removed and placed into plastic jars (45 mm in diameter, 45 mm high, with a 35-mm hole in the lid covered by a fine mesh fabric). Care was taken to not injure swallow bugs during transfer, and any showing obvious injuries were discarded. Any undetected
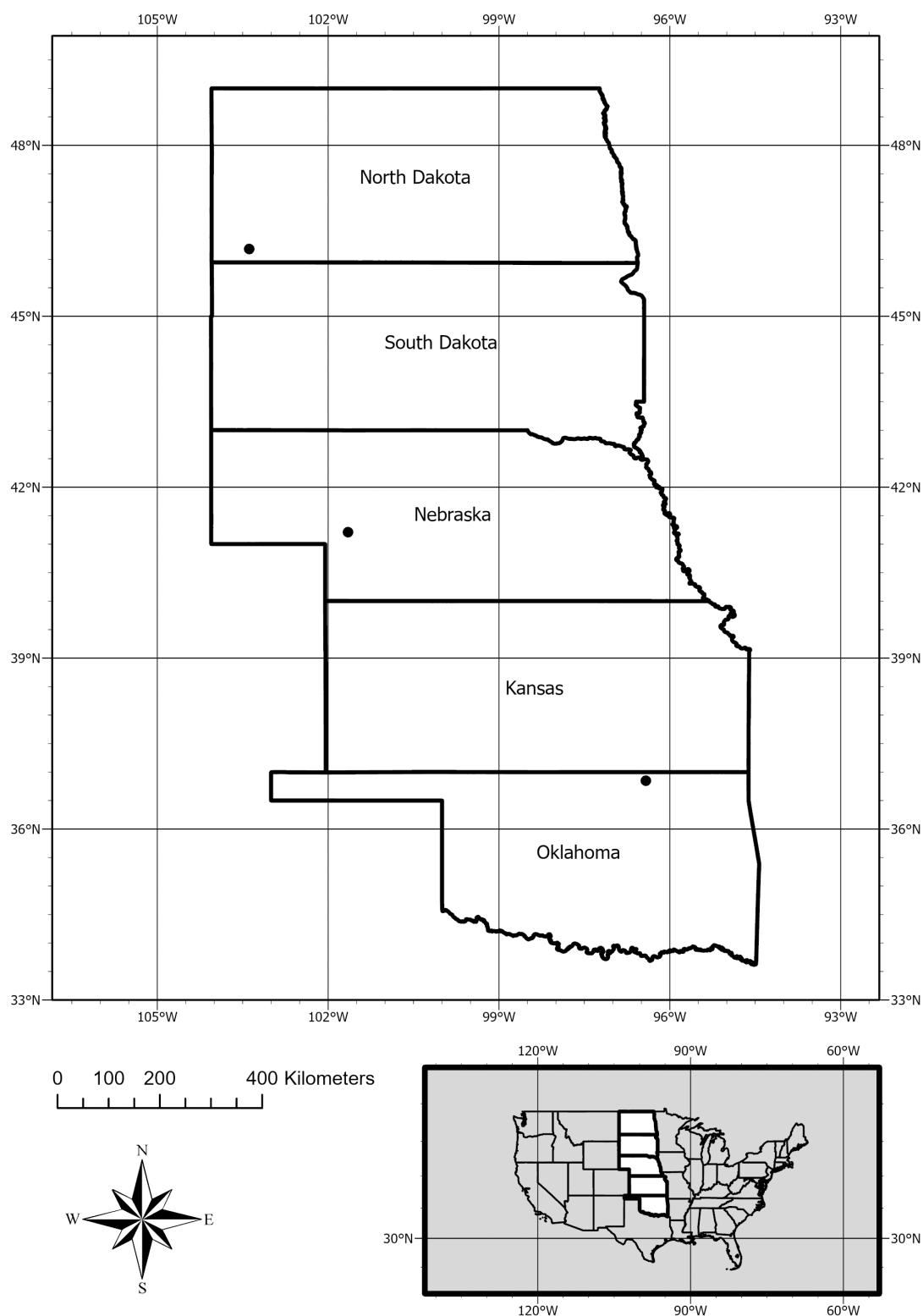
Fig. 1. Study areas (•) within the Great Plains, USA.

injury during transfer was presumably similar among experimental groups. Three pieces of brown paper folded in an accordion style to fill the space were placed in each jar, providing places for swallow bugs to cluster.

We put approximately 100 total swallow bugs in each jar, and recorded the number of adult males, adult females, and nymphs in each. Some samples contained all adults or nymphs, but most comprised a mix of ages. All sorting of swallow bugs was done under a dissecting microscope so that adults could be sexed by the presence of a paramere in males or an ectospermalage notch in females, and nymphs designated by their smaller size and/or their greater thorax to abdomen ratio (Usinger 1966). We did not distinguish instar

stages, but only ones of the third stage or above were large enough to sample without injury. Swallow bugs from multiple nests within a colony were sometimes combined to achieve 100 individuals per sample. There was little difference in the average number of swallow bugs of different ages or sexes between treatments within a population (Table 1), with the number of specimens not differing significantly between the treatment and control groups for any age or sex class in any of the states (Wilcoxon tests, $P \geq 0.24$ on all). We had a total 245 samples, representing ~24,500 swallow bugs, although not all samples had both sexes and age classes.

Experimental Procedures

Processing the swallow bugs into sampling jars took 3–7 d, and as each sequential sample was completed it was alternately assigned to either the control or the temperature-elevated treatment. Thus, there was no average difference in the time swallow bugs from either group spent in either the bags or environmental chamber. Sample jars were placed into a Percival model I36LLVLC8 environmental chamber as they were completed. Both control and temperature-elevated samples were initially held at the same temperature (close to the ambient expected at the collection site for that time of year) for ~14 d to allow specimens in both treatment groups to acclimate. Separate but identical environmental chambers were used for the elevated and control groups, with samples placed all on one shelf at the same height in each chamber.

We used the average daily temperature for each study site to establish a seasonal temperature profile from August until late April or early May (Fig. 2). The control group mimicked field temperatures and their seasonal rate of change as closely as possible; the elevated treatment had the same rate of change but was 3°C higher on each day. However, even in the control we kept the lowest temperatures slightly above 0°C because specimens were not provided the opportunity to select microhabitat sites in the jar that would be above freezing. The shape of the temperature regimen for the sites differed depending on ambient temperature variation at each over the 9 mo of the experiment (Fig. 2). Humidity in both experimental groups was held at 75–80% throughout the experiment. The environmental chambers were on a diesel generator circuit, so brief power interruptions resulted in no loss of chamber function or temperature regulation. Swallow bugs were not disturbed at any time during the experiment.

Experiments were concluded on 24–26 April (Oklahoma), 30 April–4 May (Nebraska), and 9–11 May (North Dakota). The differences in termination dates reflected when cliff swallows typically arrive in the different study areas and begin investigating nests, at which time postwinter swallow bug activity and feeding resumes. The contents of each jar were placed into a pan, and we determined the number of surviving and dead adult males, adult females, and nymphs in each sample. Individuals that still moved one or more legs were considered as surviving, because such individuals sometimes became active after being exposed to room temperature.

For the daily temperature means (Fig. 2), we accessed data from three state-wide automated weather networks: for Oklahoma from the Foraker site in Osage County on the Oklahoma Mesonet (mesonet.org/index.php/sites/site_description/fora); for Nebraska from the Keystone site in Keith County on the High Plains Regional Climate Center's Automated Weather Data Network (hprcc.unl.edu/awdn/); and for North Dakota from the Bowman site in Bowman County on the North Dakota Agriculture Weather Network (ndawn.ndsu.nodak.edu). We took the mean of the average daily temperature for each date over the last 5 yr to create our ambient temperature profiles (Fig. 2).

Statistical Analysis

For descriptive statistics, we expressed overwintering survival as the proportion of adult males, adult females, or nymphs that survived per sample. For each of the three populations (Oklahoma, Nebraska, and North Dakota) separately, we constructed a general linear model that contained both treatment (Elevated, Control) and age/sex (adult male, adult female, nymph) as independent predictor variables, with the number of surviving animals in each sample as the dependent variable. We used a Poisson regression in Proc GENMOD in SAS (SAS Institute 2004) to conduct our analyses. The Poisson option in GENMOD used the actual numbers of surviving and total animals in each sample and did not require transformation of proportions for analysis. We did not systematically record the colony sites from which swallow bugs were taken in each sample and thus could not model colony site as a random effect.

Results

Elevating temperature by 3°C led to a reduction in overwintering survival in adult males, adult females, and nymphs in all populations (Fig. 3). Overwintering survival varied significantly with treatment in Oklahoma ($\chi^2_1 = 104.9$, $P < 0.0001$, $N = 204$), Nebraska ($\chi^2_1 = 187.7$, $P < 0.0001$, $N = 264$), and North Dakota ($\chi^2_1 = 93.2$, $P < 0.0001$, $N = 261$); survival also varied significantly with swallow bug age/sex in Oklahoma ($\chi^2_2 = 20.4$, $P < 0.0001$),

Table 1. Number of swallow bugs in control and elevated-temperature treatment groups for the Oklahoma, Nebraska, and North Dakota populations

	Males			Females			Nymphs		
	Mean	SE	N^a	Mean	SE	N^a	Mean	SE	N^a
Oklahoma									
Control	10.8	1.08	31	16.6	1.8	35	72.3	2.6	35
Elevated	8.9	1.04	33	14.9	1.4	35	75.3	2.3	35
Nebraska									
Control	21.4	2.3	44	25.9	3.1	44	66.9	3.5	44
Elevated	21.9	2.4	44	24.8	3.1	44	68.1	3.9	44
North Dakota									
Control	15.8	1.5	43	18.0	1.6	43	64.6	2.5	43
Elevated	14.1	1.1	44	15.7	1.2	44	67.4	2.0	44

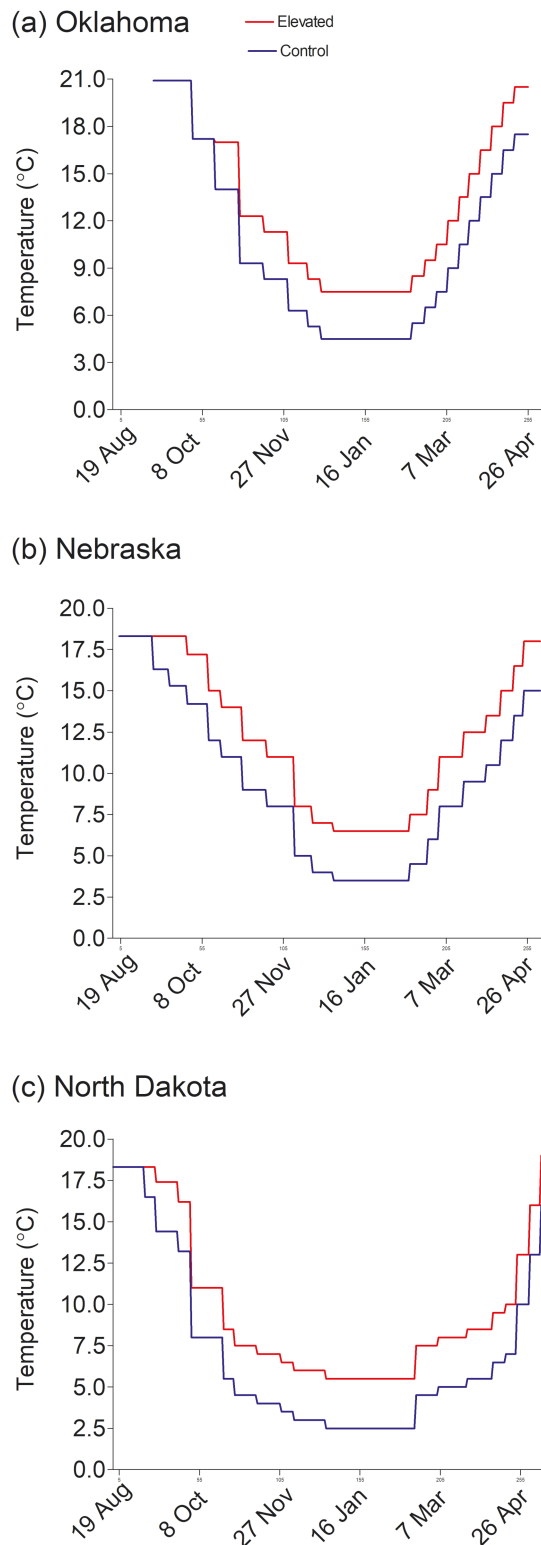[a]Number of samples containing at least one individual of that age or sex.

Fig. 2. Seasonal temperature profiles used in experimental studies of swallow bug overwintering survival based on daily mean temperatures at the study sites in (A) Oklahoma, (B) Nebraska, and (C) North Dakota. Lower line indicates temperatures used for the control group that mimicked ambient and upper line the experimental group elevated by 3°C. Duration of each experiment is indicated by the starting and ending dates.

Fig. 3. The proportion of (A) adult male, (B) adult female, and (C) nymphal swallow bugs surviving per sample at the end of the overwintering experiments for the control (ambient temperature) and heat-elevated treatment (increase of 3°C) for each state. Mean (±1 SE) is shown.

difference was a reduction of approximately 0.12 for males in Nebraska and nymphs in Oklahoma ([Fig. 3](#)). The average across the states, ages, and sexes was 0.20, which was an overall percentage reduction in survival of about 31%, relative to the average of the respective controls. Adult males in both groups seemed to have lower survival in Nebraska and North Dakota when compared to Oklahoma, but there were no other consistent latitudinal differences ([Fig. 3](#)).

Discussion

These findings reveal a consistent reduction in relative overwintering survival of swallow bugs when temperature was increased 3°C above that each population normally experienced. Although adult males in general did not survive as well as females over winter, the temperature effect applied across sexes and age classes. We recognize that the experiments may not have mimicked natural conditions and generalizing from laboratory experiments to field conditions can be difficult ([Pitts and Wall 2004](#)). For example, although we simulated the mean temperatures and rate of temperature change for each population

Nebraska ($\chi^2_2 = 328.3$, $P < 0.0001$), and North Dakota ($\chi^2_2 = 131.6$, $P < 0.0001$). The greatest difference was a reduction in proportion survived of about 0.27 for males in Oklahoma, and the least
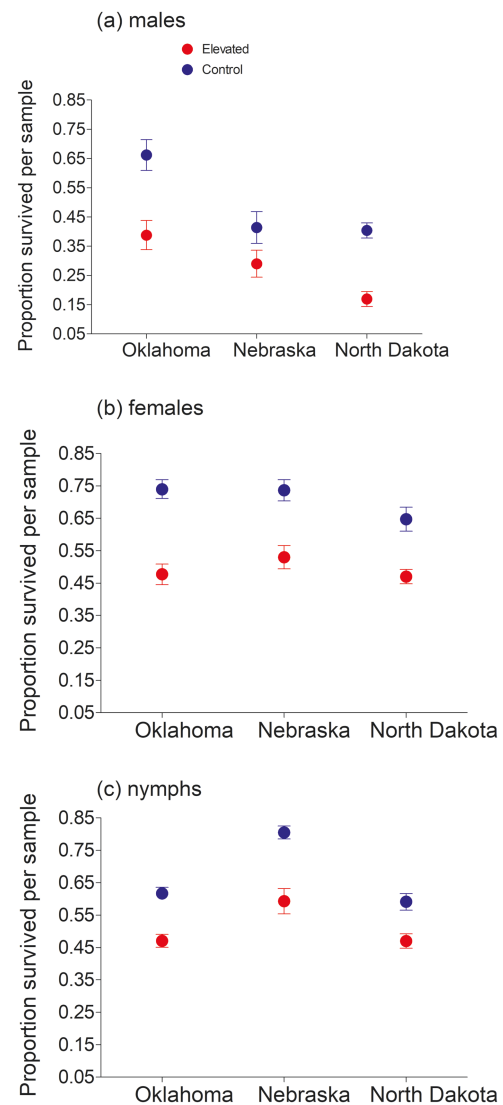
during the fall and spring, we were forced to keep our mid-winter temperatures slightly above freezing to avoid potentially killing swallow bugs that did not have the microhabitat in which to escape freezing temperatures within the jars. We also used 100 bugs in each sample, whereas swallow bugs in nature can be found overwintering in crevices that contain between 5–200 individuals (although the importance of population density during overwintering, if any, is unknown). Nevertheless, despite these limitations, we found a highly consistent relative survival difference for swallow bugs kept under identical conditions in which only the mean temperature varied.

We presume that the mortality we documented was caused by the warmer temperatures accelerating overwintering metabolism to the degree that some individuals deplete their energy reserves before spring when hosts would typically return. Energy depletion is supported by the finding in another cimicid species of a strong link between temperature and metabolic rate for all life stages (DeVries et al. 2013). Swallow bugs enter the overwintering period with large abdominal fat deposits, which are utilized over the course of overwintering before host return (Loye 1985). The swallow bugs not surviving in our experiments were usually shriveled and smaller in size than their counterparts still alive, suggesting exhaustion of all available fat.

If the mean temperature in the Great Plains increases by 3°C by 2050 (Liu et al. 2012, Conant et al. 2018), our results suggest that overwintering survival of swallow bugs could drop on average by about 30% by then. While we have not detected a change in swallow bug numbers per nest over the period 1984–2014 (Brown et al. 2021), it is possible that they are currently near the upper limit of their temperature tolerance during overwintering, and we will begin to see population declines in the coming years as the climate continues to warm. However, warmer summer temperatures may permit faster reproduction (Myers 1928) by the swallow bugs that do survive the winter, resulting in increased numbers of late-stage nymphs or adults later in the summer. A temperature effect on the rate of reproduction has been seen in other cimicids, with temperatures below 20°C resulting in development from hatching to adult taking one to two years, whereas under ideal conditions of 25–32°C, development is completed in approximately one month (Benoit 2011).

Whether swallow bugs in fact decrease over time due to higher overwintering mortality could also depend in part on how cliff swallows respond to climate change. While some evidence indicates that long-distance migratory species such as cliff swallows are less likely to change their arrival dates in response to warmer springs than short-distance migrant birds (Murphy-Klassen et al. 2005, Knudsen et al. 2011), we have detected an advancement of about 6–7 d in average colony initiation dates since 1982 in the Nebraska study area (Brown and Brown 2014). Earlier arrival would shave some time off the period that swallow bugs would typically overwinter in their hosts' absence and could partly ameliorate the elevated mortality that results. While 6–7 d is a relatively small percentage of the ~250-d overwintering period (Fig. 2), the fact that it comes at a time when swallow bugs are presumably most stressed could reduce mortality rates.

Although conceivably the most southerly population (Oklahoma) could be less affected by elevated temperatures because it routinely is exposed to warmer conditions in winter than farther north (Lavin et al. 2011), we found no evidence of a consistent latitudinal difference in the effect of elevated temperature on overwintering survival, at least across the 1,200-km distance in our study. The main difference among populations was that adult male survival in both the control and elevated treatments was lower at the two more northerly sites (Nebraska, North Dakota) than at the southernmost

(Oklahoma). Adult males consistently had lower overwintering survival than adult females in all populations and in all treatments, suggesting a female-biased sex ratio in spring should result. Field studies confirm such a sex ratio (Loye 1985), but it is unclear why males have lower survival than females or why males in northern populations survive less well than those in the more southerly population.

Global climate change is thought to drive changes in insect overwintering by altering snow cover, shifting mean temperature, and causing greater thermal variability (Williams et al. 2015). Snow cover is not relevant to swallow bugs because they overwinter well above ground. We addressed shifts in mean temperature in this study but did not explore how variability in temperature might affect swallow bugs, as demonstrated in other insects (Williams et al. 2012a, Paaijmans et al. 2013, Colinet et al. 2015, Halsch et al. 2021), partly because the number of experimental treatments possible under a fluctuating-temperature scenario is almost limitless. We recognize, however, that inherently greater variation in winter temperature may interact with changes in the mean to affect swallow bugs under climate change, and future work on this possibility is needed.

Our results indicate that projected warming in the Great Plains over the next 30 yr could reduce survival of an obligate ectoparasitic insect. Fewer swallow bugs in the next decades could possibly lead to large effects on cliff swallow social behavior (e.g., more frequent colony-site and nest reuse, more double brooding, higher nesting success; Brown and Brown 1996, 2015; Brown et al. 2013, 2021). Two studies on other avian ectoparasitic insects have also found decreases in parasitism under warmer conditions, although in these cases the warming was during the summer breeding season of the hosts (Dawson et al. 2005, Martínez et al. 2018). That climate change could reduce parasite load on hosts is a scenario not often considered in models of how global change will influence host–parasite dynamics (Brooks and Hoberg 2007, Lafferty 2009, Møller et al. 2013, Byers 2021), but our study suggests perhaps it should be, especially whenever dormancy during overwintering is a component of either host or parasite life history.

Acknowledgments

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