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**Temperature and breeding success for cliff swallows *Petrochelidon pyrrhonota*
nesting on man-made structures: ecological traps?**

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Temperature and breeding success for cliff swallows *Petrochelidon pyrrhonota* nesting on man-made structures: ecological traps?

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Abstract

When an environmental cue that previously signaled a suitable habitat leads an animal to use an unsuitable site, individual fitness can decrease, ultimately leading to population declines. Such “ecological traps” may be particularly likely for birds that use human infrastructure for nesting. Here we tested whether high nest temperatures and the physical properties of barns are associated with lower breeding success for a declining population of cliff swallows *Petrochelidon pyrrhonota* (Vieillot, 1817). We monitored nests under barn eaves below wood and metal roofs to determine nestling survival and mass, and recorded temperature under barn eaves, to relate ambient temperature to eave temperature. We found that eave temperature increased with ambient temperatures, and was higher at high temperatures and lower at cool temperatures under metal roofs than wood roofs. Nestling survival was lower during periods with higher ambient temperatures, and both survival and mass were lower under metal roofs. Our findings suggest that barn eaves, especially those with metal roofs, may be an ecological trap for cliff swallows, where a seemingly suitable nesting site early in the breeding season results in low breeding success. Furthermore, warming temperatures may lead to ecological traps for other bird species, particularly those nesting in man-made structures.

Keywords: breeding success, body condition, cliff swallow, climate change, ecological trap, mass, *Petrochelidon pyrrhonota*, survival

Introduction

Habitat selection can profoundly affect an individual's fitness. Habitats can vary in their suitability, and natural selection will favour individuals that use more suitable habitats over individuals that use less suitable habitats (Fretwell and Lucas 1969; Rosenzweig 1991; Morris 2003). One consequence of this selection is that animals have adaptations to respond to sensory or social cues that are associated with a suitable habitat (e.g., Mullineaux et al. 2000; Bernáth et al. 2002; Doligez et al. 2002; Fletcher 2007; Pupin et al. 2007; Martin et al. 2010; Kleist et al. 2017). However, when a habitat changes, either by anthropogenic or natural causes, the cues that previously signalled a suitable habitat may no longer result in the expected outcome (Gates and Gysel 1978; Hawlena et al. 2010; Anteau et al. 2012; Van Der Meer et al. 2014; Lamb et al. 2017). Instead, these cues may lead individuals to choose habitats that result in lower fitness, a situation known as an ecological trap (Schlaepfer et al. 2002; Robertson and Hutto 2006). Examples of ecological traps include the selection of foraging sites that lack sufficient food leading to lower survival (Sherley et al. 2017), and breeding sites that lead to lower breeding success (Gates and Gysel 1978; Kriska et al. 2004; Anteau et al. 2012; Frei et al. 2013) or lower survival for juveniles or adults (Reid et al. 2010; Ekroos et al. 2012; Jeffres and Moyle 2012). In some cases, the effects of these ecological traps are severe enough to cause or exacerbate population declines (Hawlena et al. 2010; Jeffres and Moyle 2012; Van Der Meer et al. 2014; Lamb et al. 2017; Sherley et al. 2017). Furthermore, if the traps persist for generations, they may lead to extirpation or extinction (Schlaepfer et al. 2002; Battin 2004; Robertson et al. 2013; but see Fletcher et al. 2012).

For birds, selecting a suitable nesting site is key for breeding successfully. One characteristic of a suitable nesting site, particularly for species that nest in cavities or other sites where the substrate and/or cover can affect nest microclimate (Maziarz et al. 2017), is temperature. Slight increases in nest temperature may have beneficial effects on nestling performance, such as increased nestling survival, higher body condition, and/or faster growth (Dawson et al. 2005b; Pérez et al. 2008; Salaberria et al. 2014; Larson et al. 2018b). However, for nestlings, warmer nest temperatures are also associated with higher corticosterone levels (Fairhurst et al. 2012), a component of the hypothalamic-pituitary-adrenal axis responsible for maintaining homeostasis (Sapolsky et al. 2000; Romero 2004). Furthermore, increasingly higher nest temperatures may lead to a multitude of detrimental effects on nestlings, including dehydration, slower growth, lower mass, and/or delayed fledging (Cunningham et al. 2013; Salaberria et al. 2014; Larson et al. 2015; Rodríguez and Barba 2016). Ultimately, these effects may lead to lower nestling or post-fledgling survival (Erbelding-Denk and Trillmich 1990; Lombardo 1994; Greño et al. 2008). As temperatures during the breeding season continue to rise as a result of climate change (Hansen et al. 2006; National Research Council 2007; Ji et al. 2014), selecting breeding sites that are too warm during the nestling period might lead to lower breeding success and, in turn, population declines (Larson et al. 2015; Rodríguez and Barba 2016).

The cliff swallow *Petrochelidon pyrrhonota* (Vieillot, 1817), as the name implies, historically nested on cliff faces throughout western North America. However, as Europeans colonized North America, the cliff swallow expanded its breeding range eastward over the last 150 years through the use of human infrastructure, such as barns, bridges and culverts, as nesting sites (Samuel 1971; Brown et al. 2017). In particular, barns provide the habitat characteristics

required for breeding birds: a large, open surrounding foraging area, a high vertical substrate with an overhang for nest attachment in the form of a barn eave, and a supply of nearby mud, the material used for nest construction (Emlen 1954; Brown et al. 2017). While these habitat characteristics allowed the population to expand its geographic range, they may now be acting as an ecological trap and contributing to population declines. More specifically, while the environmental cues provided by barns have likely stayed the same, the physical properties of barns have changed in ways that might yield poor breeding success. During colonization of North America, barns were exclusively made of wood (Visser 1997). However, since in the 1970s, it has become more common for farmers to install metal roofing on existing and newly-constructed barns (Visser 1997). When cliff swallow nests are built under barn eaves, the nest is often in direct contact with the roof, and the roof serves as the top of the nest (Fig. 1). This close proximity between nest and roof may yield higher than optimal temperatures for nests under metal-roofed barns. Indeed, barn swallow (*Hirundo rustica* L. 1758) nestlings in nests built close to roofs barns experience more heat-induced mortality than those built elsewhere (Mason 1953). In cliff swallows, higher nest temperatures may produce nestlings with lower nestling mass, which is a key predictor of first-year survival (Brown and Bomberger Brown 1996). Alternatively, increased temperature could have an overall positive effect on nestling survival and mass (Dawson et al. 2005b; Pérez et al. 2008; Salaberria et al. 2014; Larson et al. 2018b).

To determine whether barns are ecological traps for cliff swallows, we examined whether ambient temperatures predicted cliff swallow nestling survival and mass. We also determined if eave temperatures varied under roof materials (metal vs. wood), and examined the effects of roof material on nestling survival and mass; mass is an important predictor of post-fledging survival for other bird species (Naef-Daenzer and Gruebler 2016). Cliff swallows (*Petrochelidon*

pyrrhonota (Vieillot, 1817)) are declining in northeastern North America (annual rate of decline in New Brunswick, Canada: -5.31 [CI: -6.74, -3.77], Sauer et al. 2017), so determining if there is an ecological trap affecting cliff swallow reproductive success is imperative for conservation. If eaves are indeed ecological traps, then it may be possible to mitigate these effects with insulating materials (Maziarz et al. 2017; Larson et al. 2018a).

Materials and methods

Field methods

From May to August 2014-2016, we monitored 63 active cliff swallow nests at two colonies in New Brunswick, Canada: Wells (46.12, -64.24) and Wilz (45.93, -65.22). These colonies are 79 km apart from each other. Using the methods outlined in Imlay et al. (2017), we determined the hatching date, brood size, and nestling survival until day 12. We removed two nests from the analysis below where there was a 1) 6-day difference in the hatch dates of the oldest and youngest nestlings (likely from egg-dumping), and 2) complete nest failure after the nest was damaged by anthropogenic activities.

We also banded and weighed 157 nestlings on the tenth day post-hatch when nestling mass peaks (Stoner 1945). For cliff swallows, higher nestling mass at this age is related to higher fledgling mass and higher first-year survival for individuals with low numbers of ectoparasites (Brown and Bomberger Brown 1996). Given that reservoir populations of ectoparasites that overwinters in swallow nests (Brown et al. 2010) should be lost with the nests that are destroyed during the winter, and that ectoparasites were rarely observed during nest monitoring and banding activities (TLI pers. obs.), we assume that, for our study, nestling mass at 10 provides a suitable indicator of both post-fledging body condition and first-year survival.

For each nest, we also noted the type of roof directly above each nest (either metal or wood) and the cardinal direction of each eave. At Wells, the swallows nested under eaves with both metal and wood roofs ($n = 16$ and 11 , respectively) that faced either west or southwest (Fig. 1). At Wilz, cliff swallows nested under eaves with a wood roof ($n = 34$) that faced northeast or southeast. At both sites, the wood roof directly above the nest was often also covered with metal, however, the wood provided an insulating barrier between the nest and the metal roof (Fig. 1B). Therefore, in our analysis, we represent these different roof types as metal or wood. Also, to account for the differences in orientation of eaves between the two colonies, we included a variable for site, in our analysis below.

Finally, we retrieved data on ambient temperatures from Environment and Climate Change Canada: http://climate.weather.gc.ca/index_e.html (accessed 17 April 2018). We selected the closest weather station from each colony (26.4 or 35.2 km) with a complete record of daily temperatures during all years of this study. For each nest, we calculated the mean daily maximum temperature from hatching to day 12 (for the survival analysis) and from hatching to day 10 (for the nestling mass analysis). We have provided a summary of mean daily maximum temperatures during the period of peak cliff swallow breeding at our study sites (Supplementary Table S1).

In June 2017, we placed a Maxim Integrated (San Jose, California, USA) Thermochron iButton (DS1921G) temperature recording device under the eave of all barns (total: six eaves and six iButtons) where cliff swallows nested in any year from 2014-2016, except for one barn where the siding and roof had been replaced after the swallows had bred there. This included placing more than one iButton on a barn if eaves of different orientations were used by nesting cliff swallows. The iButtons were placed on small, wood ledges under the eaves, directly beside

active cliff swallow nests. We felt that this placement would provide us with temperature readings that were similar to the temperatures experienced by the nests. The iButtons recorded hourly temperature (to the nearest 0.5°C) for either 11 (Wilz) or 12 (Wells) days, during a period that largely coincided with the end of the incubation and the early nestling period. The iButton data, hereafter referred to as “eave temperature”, were paired with hourly ambient temperature data from the weather stations described above.

All field methods were approved by the Dalhousie University Animal Ethics Committee (protocol #'s 14-025, 15-103), with scientific and banding permits from the Canadian Wildlife Service (SC2788 and 10619 H, respectively).

Statistical analysis

First, to determine if ambient temperature was closely related to eave temperature, and whether eave temperatures varied with roof type and/or colony (to account for variation in orientation), we used the data collected in 2017 to relate eave temperature to ambient temperature. We used a linear mixed model that included ambient temperature, roof type, and colony as explanatory variables, with two interactions between ambient temperature and roof type or colony. This model also included random effect for the eave where temperature was recorded and an autocorrelation-moving average correlation structure to address temporal autocorrelation in the model.

Next, to determine the relationships between nestling survival or mass and ambient temperature, roof type, colony, and hatch date, we used a generalized linear model with a binomial distribution (nestling survival) or a general linear mixed model with nest ID as a random factor (nestling mass). In both models, we also included an interaction between ambient

temperature and colony. Since hatch date was strongly correlated with ambient temperature during the periods when we measured survival and mass (Pearson's $r = 0.68$ over 12 days and 0.65 over 10 days, respectively), we included the residuals from the relationship between ambient temperature and hatch date in the analysis, rather than hatch date itself (Dormann et al. 2013). Then, we modeled all possible combinations of these variables and a null model with no explanatory variables (total: 20 models). We determined that the best-fitting model was the model with the fewest number of parameters within ΔAIC_c of 2.0 of the top model (Arnold 2010).

For all models described above, we determined that explanatory variables had an effect on the response if the 95% confidence intervals did not span zero. All analyses were conducted in R version 3.4.3 (R Core Team 2017) with packages nlme (Pinheiro et al. 2018) and MuMIn (Barton 2016).

Results

Eave and ambient temperature

We found a positive relationship between hourly ambient temperatures and the corresponding temperature under the eaves of barns, with warmer ambient temperatures resulting in warmer eave temperatures (Table 1, Fig. 2). In addition, roof material and colony interacted with ambient temperature, resulting in warmer eave temperatures under metal, compared to wood roofs, and at Wilz, compared to Wells. At Wells, during periods of cooler ambient temperatures ($<11.7^\circ\text{C}$), eave temperatures under metal roofs were cooler than wood roofs, but, during periods of warmer ambient temperatures ($>16.5^\circ\text{C}$), eave temperatures under metal roofs were warmer. At the highest observed ambient temperatures (28.6°C), the disparity between eave

temperatures under metal and wood roofs was highest, with eave temperatures under metal roofs an estimated 6.4°C higher than wood roofs.

Nestling survival, mass and ambient temperature

Our best fitting model for nestling survival included ambient temperature and roof material (Supplementary Table S2). Nestling survival was negatively related to ambient temperature, with higher survival during cooler periods (Table 2, Fig. 3A). In general, nestling survival was higher under wood compared to metal roofs. Also, as ambient temperatures increased from the coolest to warmest temperatures observed in this study, nestling survival declined more slowly for nests under wood (46.7% decrease in the estimated proportion of surviving young) compared to metal roofs (59.7%).

Our best fitting model for nestling mass included ambient temperature, roof material, and colony (Supplementary Table S2). Nestling mass was negatively related to temperature, with higher nestling mass during cool periods (Table 2, Fig. 3B). However, the slope of this relationship varied between metal and wood roofs, with an estimated 1.7 g and 0.1 g decrease in nestling mass, respectively, for each 1°C increase in mean daily maximum temperature across the range of temperatures observed.

Discussion

The results of our study indicate that both nestling and post-fledging survival (as inferred by nestling mass) for cliff swallows nesting under barn eaves is reduced during periods of warmer ambient temperatures. These effects are particularly severe for cliff swallows nesting under eaves with metal roofs, as higher ambient temperatures result in even higher eave temperatures when compared to eaves under wood roofs. These findings are consistent with

other research demonstrating that high nest temperatures have detrimental effects on nestling survival and body condition (Erbelding-Denk and Trillmich 1990; Lombardo 1994; Greño et al. 2008; Cunningham et al. 2013; Larson et al. 2015; Rodríguez and Barba 2016), and that some nestlings may have limited options for mitigating the effects of high temperatures (Fairhurst et al. 2012; but see Andreasson et al. 2018).

Ecological traps can result through changes to habitats, their attractiveness and/or suitability (Robertson and Hutto 2006; Robertson et al. 2013). In this case, the ecological trap for cliff swallows is the result of changes to the nesting habitat, specifically newly constructed barns with metal roofs lacking insulation (Visser 1997), that reduce the suitability of these sites for breeding. In addition, warming temperatures in northeastern North America, as a result of global climate change (Vincent and Mekis 2006; Hayhoe et al. 2007; Vincent et al. 2012, 2015; Donat et al. 2013), may exacerbate the effects of temperature on breeding success, especially for metal roofs. Conceivably, these effects might impose selection on cliff swallows for greater sensitivity to cues that would steer their nest site preferences away from sites such as metal barns, provided there are cues available at settlement that correlate with temperature later in nesting. Our evidence so far, however, suggests that the cue signaling the attractiveness of these sites at the start of the breeding season has remained the same, despite changes to cliff swallow nesting habitats.

Ecological traps that result from habitat degradation, as we observed, typically have a greater effect on populations than ecological traps that result from the provision of novel habitats (Fletcher et al. 2012). This is largely due to habitat degradation changing the fitness of individuals using these habitats, rather than degradation resulting in changes to the habitat cues (Fletcher et al. 2012). Thus, the barns that once allowed cliff swallows to expand their breeding

range throughout eastern North America, now cause lower breeding success and may now be contributing to the observed population declines (Sauer et al. 2017).

It is also possible that our findings are the result of other seasonal factors, such as food availability, parasitism, or the pressure to migrate, that can affect breeding success and are correlated with ambient temperatures (Verhulst and Nilsson 2008), rather than an ecological trap. While we are unable to rule out all of these potential factors, previous work suggests that these seasonal factors have less of an effect on breeding success in our region. Firstly, a previous analysis of food availability and breeding success in our area (Imlay et al. 2017) suggested that although food availability declined during the breeding season, the decline was not enough to affect nestling survival or mass. Secondly, although previous work has shown that parasite loads increase during the breeding season for cliff swallows (Brown and Bomberger Brown 1996), at our sites, nests under wood roofs are more likely to persist across years, and thus likely to have higher parasite loads, than the newly constructed nests under metal roofs (T.L.I., pers. obs.). Furthermore, the high temperatures under metal roofs may have an adverse effect on parasite loads (Dawson et al. 2005a). Finally, Greño et al. (2008) demonstrated that temperature, rather than hatch date (as proxy for other seasonal factors), has a greater effect on post-fledgling survival than hatch date.

Global temperatures are rising and becoming increasingly variable with climate change (Hansen et al. 2006; Vincent and Mekis 2006; National Research Council 2007; Vincent et al. 2012, 2015; Donat et al. 2013; Ji et al. 2014). Thus the adverse effects of high temperatures temperature on breeding success for cliff swallows and other birds will likely increase as the warming trend continues (McKechnie and Wolf 2010; Larson et al. 2015; Rodríguez and Barba 2016). Furthermore, there may be additional carry-over effects of nest temperature on the survival

and recruitment of juveniles after leaving the nest (Greño et al. 2008), as we observed poorer body condition for young developing in warmer temperatures and, presumably, fledging with lower body condition. It is also likely that rising temperatures will result in additional species experiencing ecological traps as a result of climate change-related changes to their habitats, thus increasing a, presumably, already common issue (Battin 2004).

While some work has begun to consider and investigate possible ways to mitigate the effects of warming temperatures on breeding success for cavity nesters that use nest boxes, including insulation and reflective paint (Maziarz et al. 2017; Larson et al. 2018a), less thought has been given to other species that use human infrastructure for nesting, such as cliff swallows. One possibility to mitigate this effect in cliff swallows and other species with similar nesting sites, is to provide insulating material between metal roofs and nests that would minimize the transfer of heat from the roof to the nest. Attempts to mitigate the effects of nest temperature on cliff swallow breeding should be carefully monitored, to ensure that changes to the nest site do not prevent cliff swallows from using these sites and that they are effective in reducing the harmful effects of high temperatures. Also, comparisons in the temperatures under human infrastructure and natural cliff swallow nesting sites should be compared. Although it is possible that temperature at natural cliff swallows colonies is also being affected warmer global temperatures.

Finally, three listed Species at Risk in Canada, the barn swallow *Hirundo rustica* L. 1758, chimney swift *Chaetura pelagica* L. 1758 and common nighthawk *Chordeiles minor* J.R. Forster, 1771, all use human infrastructure for nesting in at least part of their breeding range (Brown and Bomberger Brown 1999; Brigham et al. 2011; Steeves et al. 2014). Ecological traps in the form of human infrastructure may help to explain population declines for these species

(Sauer et al. 2017) through reductions in their breeding success and should be investigated. If similar results are found for these species, then conservation efforts to mitigate these effects will be needed.

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Tables

Table 1. Parameter estimates and 95% confidence intervals (CI) for the relationship between ambient and eave temperature (°C) under metal or wood roofs at each colony.

Variable	Estimate	SE	Lower 95% CI	Upper 95% CI
intercept	0.17	1.98	-3.70	4.05
ambient temperature	1.33	0.05	1.22	1.43
roof (wood)	4.87	1.78	-0.79	10.53
site (Wells)	2.12	1.34	-2.14	6.39
ambient temperature : roof (wood)	-0.35	0.05	-0.44	-0.26
ambient temperature : site (Wells)	-0.37	0.04	-0.45	-0.29

Table 2: Parameter estimates and 95% confidence intervals (CI) for the best-fitting model describing the relationship between nestling survival or mass and ambient temperature (°C) and roof material.

Variable	Estimate	SE	Lower 95% CI	Upper 95% CI
<i>Nestling survival</i>				
intercept	9.02	2.38	4.51	13.92
ambient temperature	-0.40	0.10	-0.60	-0.22
roof (wood)	1.29	0.48	0.36	2.26
<i>Nestling mass</i>				
intercept	56.01	9.77	37.25	74.75
ambient temperature	-1.60	0.41	-2.38	-0.81
roof (wood)	-32.85	10.16	-52.33	-13.35
ambient temperature : roof (wood)	1.49	0.43	0.67	2.32

Figure captions

Fig. 1. Examples of cliff swallow *Petrochelidon pyrrhonota* nests under barn eaves in New Brunswick, Canada directly below an eave with either a A) metal or B) wood roof.

Fig. 2. Hourly ambient temperatures ($^{\circ}\text{C}$) were positively related to the corresponding temperature under barn eaves cliff swallows *Petrochelidon pyrrhonota* nested at A) Wells and B) Wilz. The slope of this relationship varied between metal (dashed) and wood (solid) roofs, with warmer and cooler eave temperatures under metal roofs, compared to metal roofs, when ambient temperatures were also warmer and cooler, respectively.

Fig. 3. Mean ambient temperature ($^{\circ}\text{C}$) was negatively related to A) nestling survival and B) mass, with higher survival and mass during periods of cooler temperatures. For nestling mass, this relationship varied with roof type with a greater decrease in mass for nestlings under metal roofs (dashed), compared to wood roofs (solid).

A)

B)

A)

B)

A)

B)