




The cost of ectoparasitism in Cliff Swallows declines over 35 years

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Abstract. Host–parasite dynamics often vary over time, brought about by changes in the parasite's virulence or the host's ability to resist or tolerate the parasite. Although virulence evolution in microparasites is well studied, we know little about temporal change in the pathogenicity of macroparasites such as blood-feeding insects. Using data collected over 35 yr, we report a reduction in pathogenicity of the hematophagous swallow bug (*Cimex vicarius*) on its Cliff Swallow (*Petrochelidon pyrrhonota*) host. Relative to experimentally fumigated, parasite-free nests, the negative effects of bugs on nestling swallow body mass and survival were less in the later years of the study than in the earlier years, and the negative relationship between nestling body mass and bug abundance became weaker over time. The survival of adult birds exposed to swallow bugs increased throughout the study, while survival of birds from parasite-free nests decreased over time. Swallow bug abundance per nest, bug body size, and bug age ratios did not change during the study. Between-colony transmission of bugs showed less immigration into larger colonies than in earlier studies, but there was no net change in transmission. Cliff Swallows did not reduce their exposure to bugs over time by being more likely to avoid infested nest or colony sites. Parents increased the number of food deliveries to their offspring over time in the presence of parasites, but the total amount of food delivered was unchanged. The reduced cost of swallow bug ectoparasitism does not seem related to changes in parasite narrow-sense virulence, the host's avoidance of parasites, the presence of alternative hosts for bugs, or climate-driven phenological mismatches. The results probably reflect the Cliff Swallow's evolving of greater tolerance to swallow bugs, brought about by the bird's shift from natural cliff nesting sites to artificial structures that may harbor more bugs than natural cliffs. This study shows that hosts can respond relatively rapidly to high levels of parasitism, and provides support for models that suggest the evolution of tolerance should be expected in some host–parasite systems.

Key words: *Cimex* (= *Oeciacus*) *vicarius*; coloniality; group living; host–parasite coevolution; parasite tolerance; parasitism; *Petrochelidon pyrrhonota*; social behavior; swallow bug; virulence.

INTRODUCTION

The ecological and evolutionary dynamics of host–parasite systems often change over time, typified in many cases by systematic temporal variation in the

parasite's virulence (Ewald 1995, Poulin 1998, Gandon and Michalakis 2000, Poulin and Forbes 2012). Definitions of virulence vary; it is most commonly defined by the extent of host pathogenicity attributable to the parasite (Bull 1994), but because pathogenicity also reflects host biology to various degrees, some have argued that virulence is better measured instead by ease of host-to-host transmission or by parasite fitness independent of the parasite's pathogenic effects on a host (Poulin 1998, Pfenning 2001, Ebert and Bull 2008). Regardless of definition, empirical studies have documented both reductions and increases in a parasite's virulence over time (Ebert and Mangin 1997, Ebert 1998, Gandon et al. 2001, Stewart et al. 2005, Ebert and Bull 2008).

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When measured as an effect on a host, virulence may change for three reasons. One reason is that the parasite is selected to alter its transmission or life history to accommodate changes in host biology or environmental conditions (Poulin 1998, Poulin and Combes 1999, Kleindorfer et al. 2014), and these changes may alter the parasite's pathogenicity. A second reason is that hosts evolve better resistance by minimizing damage caused by the parasite and reducing parasite fitness (Hart 1997, Clayton et al. 2010), although heightened resistance by hosts is likely also to counter-select for parasites' ability to overcome that resistance (Price 1980, Richner 1998, Read et al. 2008). Finally, pathogenicity of the parasite can decline when the host reduces the costs of resisting the parasite (such as mounting physiologically demanding immune responses that themselves may cause pathogenicity; Råberg et al. 2009, Medzhitov et al. 2012, Kutzer and Armitage 2016, Adelman and Hawley 2017), which can be a viable strategy even when parasite numbers are unchanged or increase (Roy and Kirchner 2000, Baucom and de Roode 2011). Net changes in pathogenicity may reflect the host's ability to increasingly tolerate the parasite's effects at lower cost, rather than changes in transmission dynamics of parasites or parasite life history per se. Theoretical models show that host tolerance (i.e., reducing parasite damage without reducing parasite fitness) can be advantageous to hosts by removing countervailing selection on parasites to overcome host defenses, and that tolerance is especially likely when high levels of parasitism affect the host's reproductive success (Roy and Kirchner 2000, Restif and Koella 2004, Best et al. 2008, 2009). In general, studies on the evolution of tolerance and virulence have proceeded on parallel tracks, and rarely have the two been integrated either empirically or theoretically even though both can explain temporal changes in parasite pathogenicity (Little et al. 2010).

Most of the work on changes in parasite virulence (as defined by pathogenicity) has involved microparasites such as viruses or bacteria (e.g., Ebert 1998, Ebert et al. 2004, Stewart et al. 2005). Rarely have long-term temporal changes in virulence or pathogenicity of macroparasites such as blood-feeding ectoparasites been studied: the one example we are aware of is Kleindorfer et al. (2014), who reported that pathogenic effects on avian hosts increased over a 10-yr period for an invasive fly in a new environment. Hematophagous ectoparasites such as flies, which often affect host reproductive success (Møller et al. 2009), might be particularly likely to drive the evolution of host tolerance.

In our study, we examine 35-yr changes in pathogenicity of an ectoparasite, and evaluate whether those changes can be attributed primarily to (1) temporal variation in parasite transmission or parasite fitness (virulence in the narrow sense), (2) increased ability of the host to resist the parasite by avoiding exposure to it, or (3) changes in the host's tolerating of the parasite's effects. We use a definition of virulence independent of

pathogenicity per se (Poulin 1998, Pfenning 2001) that includes measures of between-group parasite transmission, parasite fitness as reflected in parasite abundance, and parasite body size (viewed as one measure of narrow-sense virulence for blood-feeding parasites; Ewald 1995). We also evaluate other potential explanations for changes in pathogenicity, such as host switching and phenological mismatches between host and parasite brought about by climate change.

The colonial Cliff Swallow (*Petrochelidon pyrrhonota*) of North America is parasitized by a blood-feeding ectoparasitic insect, the swallow bug (Hemiptera: Cimicidae; *Cimex* [formerly *Oeciacus*] *vicarius*). Studies in the 1980s showed that bug infestations led to severe reductions in nestling swallow body mass and survival (Brown and Brown 1986, 1996) in the larger Cliff Swallow breeding colonies, becoming a textbook example of the cost of parasitism in large social groups (Alcock 1989–2013, Davies et al. 2012, Rubenstein and Alcock 2018). By repeating the same field experiments in the same western Nebraska, USA study area in 2015–2019, in which Cliff Swallow nests were fumigated to remove parasites and others left untreated in the same colonies, we found temporal changes in the cost of parasitism on a scale not previously reported in any host–ectoparasite system.

Using long-term data from our Cliff Swallow population, we examine changes in host traits such as nestling body mass and nestling and adult survival that are negatively affected by ectoparasites (Brown and Brown 1986, 1996). We evaluate changes in transmission of swallow bugs between colonies (Brown and Brown 2004) and body size of bugs (Ewald 1995) as measures of narrow-sense virulence, and whether pathogenicity may have changed due to temporal increases or decreases in Cliff Swallows' exposure to bugs, as reflected in parasite load (Brown and Brown 1996) and the birds' reuse of the same nesting sites in successive years (Brown et al. 2013). Because tolerance of parasites can be achieved in part by parental compensation via increased provisioning rates (Knutie et al. 2016, Grab et al. 2019), we also evaluate how Cliff Swallow food deliveries to nestlings may have changed over time. To some degree, we must rely on retrospective analyses of data collected in earlier years originally for other purposes but, in all cases, we collected the more recent data using the same protocols as in the earlier years to allow direct comparisons. Parasite-free (i.e., fumigated) nests served as a control for temporal changes in the environment (e.g., changes in food abundance or climatic variation) that might have also affected the parasite's pathogenicity.

METHODS

Study animals and study site

The Cliff Swallow is a migratory, sparrow-sized passerine bird found commonly throughout the Great Plains and westward to the Pacific coast of North

America (Brown et al. 2020a). In its ancestral habitat, the species built its gourd-shaped mud nests underneath horizontal overhangs on the sides of steep cliffs, but now many Cliff Swallows nest under the sides of bridges and buildings or inside concrete culverts underneath roads (Brown et al. 2013). The birds arrive in our study area beginning in late April, with most colony sites being occupied in May and early June, but colonies can begin as late as early July. Most colonies have completed nesting by late July. The species winters in southern South America, primarily Argentina (Brown et al. 2020a).

Swallow bugs are nest-based ectoparasites that spend most of their time in cracks and crevices of the nesting substrate or in the Cliff Swallows' nests. They move on to birds to feed mostly at night and relatively rarely travel on the adult birds. Bugs can endure long periods of host absence (>12 months). They seemingly prefer to parasitize Cliff Swallows, but they will also take blood meals from Barn Swallows (*Hirundo rustica*) and invasive House Sparrows (*Passer domesticus*) that nest at Cliff Swallow colony sites (Kopachena et al. 2007, O'Brien et al. 2011). Bugs undergo five instar stages before becoming adults, and temperature affects bug development time (Loye 1985). Up to 3,000 bugs have been found in a single Cliff Swallow nest in our study area. Bugs affect their swallow hosts through blood loss and anemia, slower feather growth, reduced body mass, changes in blood immunochemistry, and increased daily energy expenditure (Brown and Brown 1986, Chapman and George 1991, Møller et al. 1994).

We studied Cliff Swallows near the Cedar Point Biological Station (41.2097° N, 101.6480° W) in western Nebraska, USA, along the North and South Platte rivers. The study area includes portions of Keith, Garden, Deuel, Lincoln, and Morrill counties. Our work was done primarily at Cliff Swallow colonies on highway bridges and box-shaped culverts underneath roads or railroad tracks (Brown et al. 2013). Colonies were defined as birds from groups of nests that interacted at least occasionally in defense against predators or by sharing information on the whereabouts of food (Brown and Brown 1996). Typically, all the nests on a given bridge or culvert constituted a colony. Colony size varied widely, ranging from 1 (solitary nests) to 6,000 nests (mean \pm SD: 404 \pm 631, $n = 3277$ colonies). Colony size in all cases refers to the maximum number of active nests at a site in a season, with an active nest defined as one in which one or more eggs were laid. We use the term "colony" to refer to the collection of birds occupying a structure in a given year, whereas "colony site" refers to the physical substrate.

Climate data

Climatic comparisons among the earlier and later periods of the study used the Palmer Drought Severity Index (PDSI), an integrative measure of temperature and rainfall that predicts Cliff Swallow breeding time

and annual survival (Brown and Brown 2014, Brown et al. 2016). PDSI metrics were retrieved from the National Climate Data Center of the National Oceanic and Atmospheric Administration (data *available online*).⁹ We used PDSI calculated for Nebraska's Climate Division 7 (southwest Nebraska), corresponding to the location of our study area (Brown and Brown 2014). NOAA currently provides PDSI for 1-month intervals, and we averaged these for May, June, and July (the Cliff Swallow's breeding season) each year, 1984–1988 and 2015–2019, and used the average yearly values in analyses.

We included hourly weather covariates in our analyses of food deliveries. These variables as recorded to the nearest hour of when we watched a given nest were extracted from the High Plains Regional Climate Center's Automated Weather Data Network (data *available online*).¹⁰ The nearest recording station for observations in the 1980s was at Arthur (41.39° N, 101.31° W), whereas in the 2010s, we used the Keystone (BETA) station (41.12° N, 101.39° W) except for 2018 on dates prior to 13 June when this station was offline and Big Springs (41.09° N, 101.60° W) was used.

Fumigation experiments

Portions of colonies were fumigated, with colony sites typically divided in half so that both fumigated and non-fumigated sections contained nests of similar spatial orientation with respect to the center or edge of the site. The two sections were divided by a sticky insect barrier (Tree Tanglefoot, The Tanglefoot Company, Grand Rapids, Michigan) applied to the substrate to prevent bugs from crawling between the sections. Nests were lightly misted with a dilute solution (1:170 parts water) of naled (Dibrom 8), an organophosphate insecticide shown to be highly effective in eliminating swallow bugs from Cliff Swallow nests (Brown and Brown 2004, Runjaic et al. 2017). Nests were sprayed 10–13 times at 4–8 d intervals to remove any bugs immigrating into the nests on birds over the season. Naled works primarily as a contact insecticide, although for semantic convenience we use the term "fumigation." There was no experimental evidence that bugs at the fumigated sites had developed any resistance to naled over the course of the study (Runjaic et al. 2017).

Nests were numbered and their contents monitored by periodic checks using a dental mirror and flashlight inserted through the nest's entrance hole. This technique allowed us to determine laying date, clutch size, hatching date, and nestling survival for all nests. The actual number of nestlings reaching 10 d of age in each nest was a relative index of nestling survival to fledging (Brown and Brown 1986, 1996). Survival was measured only for nests followed from the time of egg laying, and nests failing before 10 d were treated as having 0 nestlings surviving.

⁹ <https://www.ncdc.noaa.gov/cag>

¹⁰ <http://awdn.unl.edu/classic/home.cgi>

For nests with nestlings surviving to day 10, we weighed each nestling with a Pesola scale (to the nearest 0.5 g) to determine body mass and counted the number of visible swallow bugs on a nestling's body during a relatively fixed search time of about 30 s per bird (Brown and Brown 1996). Nestlings were banded with U.S. Geological Survey bands at that time. Nests were checked and nestlings processed in the same way throughout the study, with the same person (C. R. Brown) doing or supervising data collection in all years.

We performed the split fumigated/non-fumigated design at 11 colonies in 1984, 1 in 1985, 2 in 1986, 1 in 1987, 2 in 1988, 2 in 2015, 4 in 2016, 5 in 2017, 7 in 2018, and 3 in 2019 (Appendix S1: Table S1). In some years at some sites, two distinct colonies formed, one early and one late in the season, with almost no temporal overlap in nesting between the two groups of birds. These were treated as separate colonies that in all cases differed in colony size (Appendix S1: Table S1). Analyses of nestling body mass and survival to fledging were confined to birds from the split colonies. Because of temporal changes in site suitability and the distribution of birds among colony sites in the study area across years, only one split site was used in both decades (1984–1988, 2016–2019; Appendix S1: Table S1). Sample sizes for analyses of nestling survival were 744 and 1,759 non-fumigated nests in 1984–1988 and 2015–2019, respectively, and 1,027 and 1,357 fumigated nests in 1984–1988 and 2015–2019, respectively. Sample sizes for analyses of nestling body mass were 621 and 1,414 nestlings from non-fumigated nests in 1984–1988 and 2015–2018, respectively, and 1,114 and 1,193 nestlings from fumigated nests in 1984–1988 and 2015–2018, respectively. How these sample sizes were distributed by year and colony is shown in Appendix S1: Table S1. Analysis of nestling body mass in relation to the number of swallow bugs counted on the nestlings used all birds ($n = 4,453$) from non-fumigated colonies (including ones not part of the split design), with sample sizes distributed among years and colonies as shown in Appendix S1: Table S2.

Mark-recapture

We used mark-recapture data collected over a 30-yr period, 1984–2013, in which we banded ~229,000 Cliff Swallows with United States Geological Survey bands and had ~405,000 total bird captures in mist nets during that time at up to 40 different colony sites each year (Brown et al. 2016, Hannebaum et al. 2019). As swallows exited their nests, they were captured by putting nets across the entrance of highway culverts or along the sides of bridges that contained swallow colonies. In order to achieve roughly equal recapture probability across the study area, we shifted our recapture efforts among accessible colony sites, netting at each several times each season (Brown 1998, Roche et al. 2013, Brown et al. 2016). Over the summer, we typically

captured 10–60% of the residents at a colony, as inferred from a colony's capture total and the colony size.

Annual survival was estimated for all known-age birds in the dataset from all years. Known-age birds included nestlings from the split colonies (see Methods: Fumigation experiments) and from other colonies that were either entirely fumigated or entirely non-fumigated as part of other research (Brown and Brown 2000, Brown et al. 2015). In addition, juvenile birds first caught soon after fledging, presumably at their birth colony, were included as known-age individuals, and we used only juveniles from sites where all nests were either fumigated or non-fumigated. The mark-recapture data set for these analyses contained 60,989 birds of known age, distributed among years and colony sizes as given in Brown et al. (2016).

Bug nest counts

Entire nests were collected from active Cliff Swallow colonies in July, placed into plastic trash bags, and kept at room temperature for 3–21 d before processing. Only nests that had been active that season were collected, and all collections were made after nestlings had fledged from the nests, typically 1–2 weeks earlier. Sampled nests were selected as randomly as possible from among the formerly active nests at a site. Each nest was placed into a pan, nest chunks broken apart, and all swallow bugs present counted as they were removed by forceps from the pan. At the time of collection, if bugs remained on the concrete wall behind the nest after the nest was removed, those that could not be collected were estimated (all by C. R. Brown), and that number added to the nest count. We saw no bug mortality in the bags resulting from holding before processing. Nests were collected from entirely non-fumigated colonies, or in three cases, from non-fumigated sections of colonies that had been split for fumigation (see Methods: Fumigation experiments). Bug counts came from 15 colonies in 1983–1984 (ranging in size from 2 to 345 nests) and 13 colonies in 2014–2016 (ranging in size from 19 to 356 nests).

Measuring bug size and age ratios

As one measure of parasite virulence (Ewald 1995), we used the dry mass of swallow bugs as an index of body size. Bugs that had been collected in the study area in summer 1993 and kept stored frozen and in alcohol were compared with ones collected 21 yr later in summer 2014. Bugs were collected in both years by brushing them off the outsides of nests. We used bugs taken from 19 colony sites in 1993 and 16 in 2014, with 10 of these sites used in both years. Bugs from both years were processed at the same time by first drying them at 37°C for 50 minutes in a drying oven. By drying bugs for different time intervals up to 120 minutes, we established that bug dry mass stabilized after 40 minutes of drying. Bugs were sexed using a dissecting microscope, and only adults (no instars) were used. We did not include

blood-engorged bugs. After drying, bugs were weighed to the nearest 0.0001 g in pools of five randomly chosen bugs of the same sex and from the same site and year. A single dried bug weighed so little that we deemed masses more accurate by using pools of five. The collections had been made both early in the nesting season (in May) and late in the season (in July) in both years, so month of collection was used as a covariate in analyses.

To examine whether swallow bug age ratios at the beginning of the nesting season changed over time, we used the collections from 1993 and 2014 described, and sorted each sample into adults and instars. Since bugs in both years were collected the same way, the ages represented a random sample that presumably reflected the relative age ratio of the bugs in a nest. Only samples taken in May were used, with data from 14 colony sites and 6,651 total bugs in 1993 and 18 colony sites and 1,864 total bugs in 2014, and of those, 7 colony sites were sampled in both years. Samples in which some bugs had been removed for use in genetic analyses were excluded.

Between-colony transmission experiments

At some colonies where weekly fumigation occurred, we periodically counted all swallow bugs on selected nests prior to each week's fumigation (Brown and Brown 2004). This method gave the number of bugs introduced into that nest since the previous fumigation. Nests were first fumigated in early to mid-May, with fumigation continuing each week throughout the season (until mid to late July). The outsides of the nests in each sample were visually examined for parasites during the day using a flashlight. Any parasites seen anywhere on the nest or wedged between the nest and the substrate were counted. The number of visible bugs on the outsides of nests was highly correlated with the total number of bugs present in a nest, based on nests that were collected (Rannala 1995). Because of the effectiveness of the fumigant (Runjaic et al. 2017), the number of bugs visible on the outside of a nest prior to the weekly spraying was a relative index of the bugs that had immigrated into the site on Cliff Swallows that week (Brown and Brown 2004).

The first set of experiments was done in 1999–2002 at 12 active colonies in Keith and Garden Counties. We repeated those at 8 colonies in 2015–2016, using the same colony sites in both decades. Because parasite immigration depends on colony size mediated by the extent of site visitation by transient Cliff Swallows (Rannala 1995, Brown and Brown 2004), we selected 8 colonies from 1999–2002 that were closest in size to the 8 from 2015–2016, and confined our analyses to those 16 colonies. The two late-starting colonies from 1999–2002 (Brown and Brown 2004) were not used, as there were no late colonies in the 2015–2016 set. Because bug activity at a nest depends on the host's phenological stage, for analysis each nest was assigned a status at the time

of a bug count: (1) before eggs were laid, (2) eggs present, (3) nestlings present, and (4) nestlings fledged or nest had failed. Earlier analyses (Brown and Brown 2004) had not explicitly accounted for the phenological stage of nests. Analyses were based on a total of 5,439 nest counts across all years and colony sites.

Scoring bugs on birds' feet

As a relative index of the extent of swallow bugs being moved between colonies by Cliff Swallows, during mark-recapture efforts (see Methods: Mark-recapture) we recorded whenever a bird was captured in a mist net with bugs clinging to its toes or tarsus (see photo in Brown and Brown 2004). Such bugs are ones typically picked up by transient birds that visit the entrances of unoccupied nests where bugs cluster in apparent attempts to disperse (Moore and Brown 2014). While some dispersing bugs fell off birds when they collided with a mist net, those remaining should give a relative index of the rate at which bugs dispersed and were potentially transmitted among colonies each year. Bugs on birds' feet were not systematically recorded prior to 1993. The number of Cliff Swallows carrying bugs each year, 1993–2013, was expressed as a percentage of the total number of times Cliff Swallows were captured in mist nets that year. Individual birds caught multiple times in a season counted multiple times, as they presumably had a chance to be carrying bugs on each capture. Bug presence or absence was scored on 294,165 bird captures across 19 yr.

Determining annual colony site and nest reuse

Cliff swallow exposure to swallow bugs can be measured by both (1) the reuse of a colony site the next year, given that bugs remain at the site in cracks and crevices of the substrate over the winter and move into nests as soon as birds arrive (Brown and Brown 1996, Brown et al. 2010a), and (2) the birds' reuse of old nests that may contain bugs from the previous summer. We scored colony-site reuse (yes/no) in the successive year for a total 248 colony sites during the study, yielding 3,190 site-years for analysis. We visited each site usually in late June (occasionally in early July in years when nesting was delayed), after eggs had been laid and before fledging had started, and always in sunny weather when birds would be at the site if nesting there (Brown et al. 2013). At that time, we also estimated colony size. Colony sizes were determined by direct counts of all active nests (from inspecting nest contents) or by estimation based both on nest counts of portions of a colony site and on the number of birds present at a site (Brown and Brown 1996, Brown et al. 2013). Sites were classified into one of four substrate types: (1) bridge, overpass-like structure typically spanning a river or road; (2) culvert, a box-shaped concrete structure underneath a road or railway, often used for drainage; (3) building, a human habitation (often a house or barn), and (4) natural cliff face. For

more details and photos of the substrate types, see Brown et al. (2013). Prior to 1990, we did not comprehensively survey all sites in the study area, instead focusing on a smaller subset where we were doing other research. From 1990 to 2020, all known Cliff Swallow colony sites between Maxwell, Nebraska, and Broadwater, Nebraska, were surveyed each year.

We studied nest reuse by scoring whether an active nest had been used the previous season. Nests were numbered with chalk on the substrate and the same numbers used each year, allowing us to know the usage history of each nest. A nest not previously used could have been an inactive intact one from the previous year or one built anew in the current year. If a new nest was built at the same place on the substrate where an active one had existed the previous year (but perhaps had fallen), it was classified as not previously used if less than half of it remained from the previous year. The percentage of previously used nests at a colony site in a given year was the metric used in analyses. We used data from 151 colonies for which we had nest reuse data. No colony sites that were fumigated in whole or in part were used in analyses of site and nest reuse.

Cliff Swallows will sometimes initiate second nesting at a colony site, with these late nesting attempts by both birds that had nested earlier that season and ones not having nested previously (Brown and Brown 2015, Brown et al. 2015). Second nesting was considered to have occurred at a site when we observed birds engaged in nesting activities (e.g., nest-building) there after the early round of nesting had been completed (known by fledging of young from most nests). For many colonies, we ruled out any second nesting whenever all birds had vacated the site by 25 July (by which time most Cliff Swallows had migrated from the study area). Our definition of second nesting as a temporally distinct round of breeding at a site meant that all colonies included in our analysis were ones that were active during May and June (the typical time when Cliff Swallows nest in the study area). There was generally about a 45–50 d difference between the mean egg-laying date for the early round at a site and the mean egg-laying date for the second round (Brown and Brown 2015). Some sites were not visited again late enough in the season to know whether second nesting occurred. Only non-fumigated colonies were included in analysis of second nesting, which spanned the years 1982–2020.

Measuring food deliveries and bolus mass

Parental food deliveries by Cliff Swallows were recorded as the number of times either parent entered a nest that contained nestlings. Often they could be seen feeding the nestlings by their characteristic tail-pumping as they placed food in the nestlings' mouths or when nestlings sat at the entrance of nests. Visits in which no food was brought were not counted. We sat under the nests and at a distance at which the birds were not

disturbed by our presence and recorded visits typically at 5–20 nests during an hour. We observed nests where the brood size and age of nestlings were known, given the effects of these variables on feeding rates (Brown and Brown 1996). Because Cliff Swallow foraging is strongly dependent on local weather conditions, we included hourly weather covariates (temperature, wind speed, and extent of sunshine, measured as solar radiation in watts/m²) in our analyses of food deliveries. We used these variables as recorded by the High Plains Regional Climate Center (see footnote 10) to the nearest hour of when we watched a given nest.

Cliff Swallows typically deliver a tightly compressed mass (bolus) of insects to a nestling per visit. We used pipe cleaners loosely fitted around a nestling's neck to prevent it from swallowing the bolus (Orians and Horn 1969). Ring-collaring does not harm nestlings if collars are adjusted correctly, and it does not normally affect their growth (Henry 1982). Nestlings were left ring-collared for 40–60 minutes, after which we removed any boluses from the nestlings with forceps and placed the boluses in 70% alcohol. The wet mass of each bolus provided a relative index of the amount of food delivered per trip (Brown and Brown 1996). We typically ring-collared nestlings that were 10–12 d old, as ring-collaring was ineffective on younger or older nestlings. Ring-collaring was never done on nestlings at nests where food deliveries were recorded. Data on food deliveries and bolus mass were taken from both fumigated and non-fumigated nests. In some cases, we used the split colonies (see Methods: Fumigation experiments), and in other cases we used entirely fumigated or entirely non-fumigated sites, depending on nest availability, accessibility, or visibility (Appendix S1: Table S3).

Scoring alternative hosts

During the course of research activities at colonies, we noted whether an active Cliff Swallow colony site also contained at least one active nest of either Barn Swallows or House Sparrows. The presence or absence of Barn Swallows was recorded at each site each year of the study, but we only included culvert and building colony sites in analyses, because Barn Swallows avoided sites on highway bridges and natural cliffs, and their near-complete aversion to these sites did not change over time. This yielded a total of 712 site-years for Barn Swallows. House Sparrows occupied nests on all substrate types except cliffs, so analyses for them excluded only cliff sites. We had 373 site-years for House Sparrows, less than for Barn Swallows in part because we did not systematically record the presence of House Sparrows in all years. In addition, because House Sparrows in our study area shun people, they were less obvious to us unless we visited a colony frequently, and thus most of the presence/absence data for sparrows came from colonies where we checked nests or otherwise did intensive

research there and were sure of the sites' status. The analyses of alternative hosts spanned the years 1982–2020.

Statistical analyses

Analyses of nestling body mass, nestling survival, bugs per nest, bug mass, bug age ratios, bug transmission, colony-site reuse, food deliveries, bolus mass, and presence of alternative hosts used mixed-model regression implemented with Proc MIXED (for quantitative response variables) or Proc GLIMMIX (for categorical response variables) in SAS (SAS Institute 2004). Independent covariates (fixed effects) were identified a priori based on past work and are presented for each analysis (Appendix S1), along with (in most cases) a relevant interaction term describing how the dependent variable changed across years in relation to fumigation status or parasite load. All models with interactions contained the same variables as main effects, but in those cases, the main effects were not interpreted. Any nonsignificant interactions were removed in preliminary analyses. We treated year as a categorical predictor variable (e.g., two categories, 1984–1988 and 2015–2019), designated as decade, whenever multiyear (e.g., 20-yr) gaps existed in when data were collected. Other analyses, when data were collected more continuously across the years of the study, treated year as a continuous predictor variable. Because we had a biological rationale for all of the independent predictor variables used (Grueber et al. 2011), we did no stepwise model selection for these analyses. Dependent variables expressed as proportions (e.g., age ratios, probabilities that a colony site was reused the next year or that an active nest had been active the previous year) were logit transformed for analysis.

To account for non-independence of observations (and potential pseudoreplication) in our data sets, we used the following random intercept variables: colony site, coded as the same site designation across years, to account for potential spatial dependence of a colony site's physical location in different years; colony-site-by-year, coded the same for all nests at a colony site in the same year but different between years, to account for dependence of observations among the nests at a single colony within a year; nest identity, coded the same for all nestlings within the same nest in a given year but different among years, to account for potential dependence among nestlings from the same nest; and year, coded the same for all nests in a given year, to account for year-specific variation (only in cases where a categorical fixed effect of decade was used). For sites divided for fumigation, the colony-site-by-year random variable was further split by fumigation status to code all fumigated nests at that site that year as different from all non-fumigated nests at that site that year (colony-site-by-year-by-fumigation-status). Some analyses did not contain all four random effects, depending on the data structure and the analysis employed (Appendix S1).

When means and standard errors (SE) are presented for analyses involving interactions between fumigation status and decade, we used estimates of the means and SEs based on the relevant mixed model with an interaction term, generated from Proc PLM in SAS. In these cases, if means are presented by year, we substituted year for decade in the model to generate the appropriate yearly estimates in Proc PLM, but we based statistical inference on the model containing an effect of decade. In some analyses, Proc PLM was used to generate predicted regression lines (which held other fixed effects in the mixed model at their average values).

For annual survival analyses, we used a multistate recaptures-only model in Program MARK (Lebreton et al. 2009), in which state was coded as F or N, depending on whether the nest or colony the bird occupied was fumigated or non-fumigated. This enabled us to estimate survival, recapture, and transitions between states for each year in relation to a bird's fumigation status. Because we used only known-age birds, the survival estimates were age-specific. We used a fully age- and time-dependent model for survival and recapture (Brown et al. 2016), but to simplify computations and prevent parameter proliferation, we treated transition probability as age and time constant. Survival of first-year birds was estimated in relation to the fumigation state of their natal colony (or nest), and for second-year birds in relation to the fumigation state of their breeding colony. Survival estimates accounted for instances of a bird switching from a fumigated to a non-fumigated colony (and vice versa) by our including state transition probabilities in modelling survival. Significance of survival trends over time was judged by whether 95% confidence intervals of regression coefficients overlapped 0.

RESULTS

Changes in host body mass

The body mass of nestling Cliff Swallows serves as a proxy for the effects of swallow bugs (Fig. 1A). As parasite abundance per bird increased, nestling mass at day 10 was reduced, but this negative effect of parasites (the reaction norm) was weaker in the 2010s than in the 1980s (Fig. 2). While controlling for the effects of brood size and date in the season when weighed, there was a significant interaction between decade and number of bugs per nestling in predicting nestling body mass; the random effects of colony-site-by-year and nest identity also were significant (Appendix S1: Table S4).

Relative to fumigated nests in the same colony, the average (\pm SE) percentage reduction in body mass for nestlings at day 10 exposed to swallow bugs per year was 8.9 ± 0.3 in the 1980s ($n = 3$ yr) and 3.4 ± 0.6 in the 2010s ($n = 4$ yr; Fig. 3). While controlling for the effects of brood size, date when weighed, and colony size, there was a significant interaction between decade and nest fumigation status in predicting nestling body mass



FIG. 1. Changing cost of swallow bug parasitism in Cliff Swallows. Examples of the range in development of 10-d-old nestlings from non-fumigated nests exposed to parasites (left) and from fumigated nests where parasites had been removed (right) at the beginning of the study (1984) and 30 yr later (2015) from the largest colony studied in each year. Upper photo from Brown and Brown (1986).

(Appendix S1: Table S5). The random effects of colony site, colony-site-by-year-by-fumigation, and nest identity were also significant (Appendix S1: Table S5). The quantitative disparity in nestling body mass at day 10 had lessened in the 2010s, relative to the 1980s (Fig. 3), and in the 2010s 10-d-old nestlings in non-fumigated nests differed less in size and feather development from their fumigated counterparts than in the 1980s. For example, the range in development of parasitized vs. non-parasitized nestlings in the largest colony, where swallow bugs tend to be the most abundant (Brown and Brown 1986), was much greater in 1984 than in 2015 (Fig. 1).

Changes in host survival

The average percentage (\pm SE) reduction in nestling Cliff Swallow survival to day 10 for non-fumigated nests relative to fumigated nests in the same colony per year was $59.1\% \pm 12.5\%$ in the 1980s ($n = 5$ yr) and $13.4\% \pm 5.1\%$ in the 2010s ($n = 5$ yr; Fig. 4). While controlling for the effects of laying date (when the first egg in the

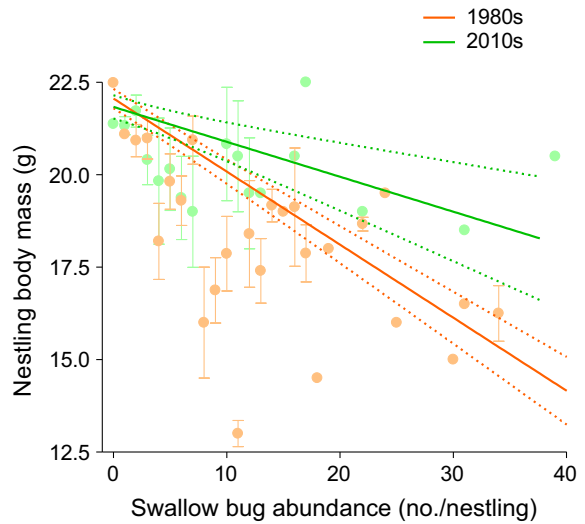


FIG. 2. Reaction norms across two decades for nestling Cliff Swallow body mass (g) in relation to the number of swallow bugs counted on a nestling at day 10 for non-fumigated nests. Regression lines (and 95% CI [dashed lines]) give predicted values from a model containing effects of date weighed, brood size, and a decade \times number of bugs interaction (Appendix S1: Table S4). Circles indicate actual data, with body mass averaged (\pm SE) for each number of swallow bugs. Analysis was based on 4453 nestlings from 58 colonies (Appendix S1: Table S2).

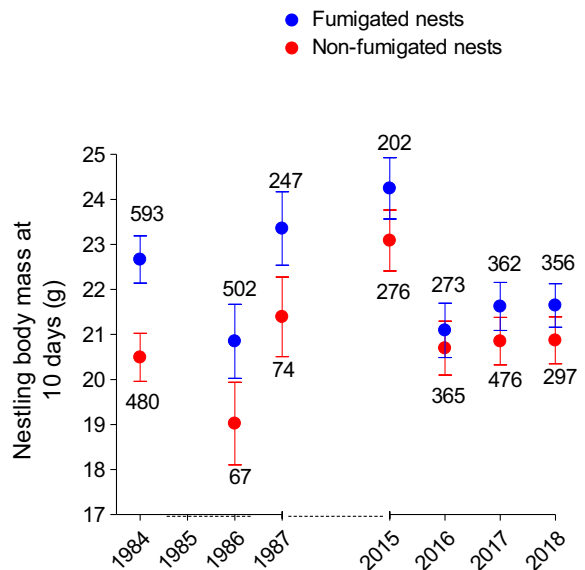


FIG. 3. Estimated mean (\pm SE) nestling Cliff Swallow body mass (g) at 10 d of age for birds from non-fumigated and fumigated nests in each year of the study. Estimated body mass was derived from a model containing brood size, date weighed, colony size, and a significant year \times fumigation status interaction (Appendix S1: Table S5). Numbers show sample sizes (number of nestlings weighed) and were distributed among colonies as shown in Appendix S1: Table S1.

nest was laid), clutch size, and colony size, there was a significant interaction between decade and nest fumigation status in predicting nestling survival (Appendix S1: Table S6). The random effects of colony site and colony-site-by-year-by-fumigation were also significant (Appendix S1: Table S6). Nestling survival in non-fumigated nests increased over time, in contrast to that for nestlings in fumigated nests (Fig. 4).

The mark–recapture analysis showed that annual survival of first-year birds from non-fumigated colonies increased significantly over time ($\beta = 0.0385$, $SE = 0.0190$), whereas that for birds from fumigated colonies did not change ($\beta = 0.0086$, $SE = 0.0076$; Fig. 5A). For second-year adults, annual survival increased significantly over time for those from non-fumigated breeding colonies ($\beta = 0.0203$, $SE = 0.0053$) and decreased significantly for those from fumigated sites ($\beta = -0.0142$, $SE = 0.0050$; Fig. 5B).

Changes in climate and host phenology

In the decades of the fumigation experiment, the mean Palmer Drought Severity Index (PDSI) did not differ significantly between 1984 and 1988 (mean annual PDSI, 0.258) and 2015–2019 (mean annual PDSI, 0.942; Wilcoxon test, $Z = -0.627$, $P = 0.47$). There was no significant relationship between the mean annual difference in nestlings survived between non-fumigated and fumigated nests and the mean PDSI for May–July each year over the years of the study ($r = -0.53$, $P = 0.11$, $n = 10$ yr).

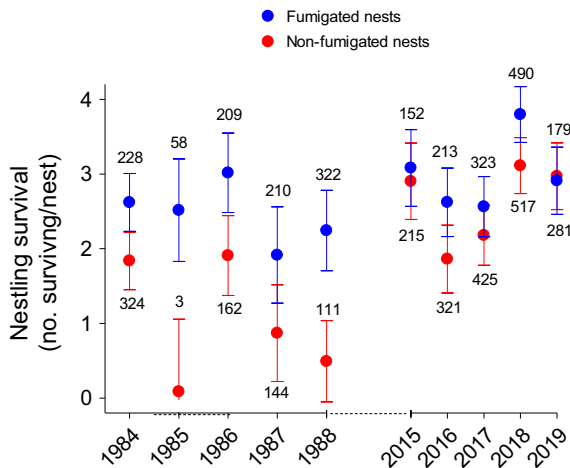


Fig. 4. Estimated mean (\pm SE) number of nestling Cliff Swallows surviving to 10 d of age from non-fumigated and fumigated nests in each year of the study. Estimated survival was derived from a model containing nest initiation date, clutch size, colony size, and a significant year \times fumigation status interaction (Appendix S1: Table S6). Numbers show sample sizes (number of nests monitored) and were distributed among colonies as shown in Appendix S1: Table S1. Values for 2019 were jittered slightly to avoid almost complete overlap.

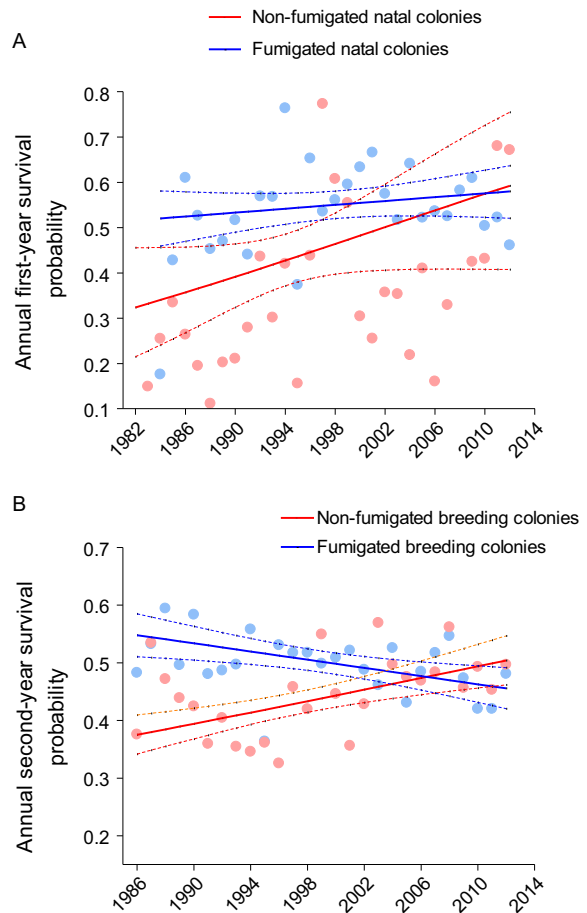


Fig. 5. Annual survival probability for Cliff Swallows (A) in their first year in relation to fumigation status of their natal colony and (B) for birds in their second year in relation to fumigation status of their first year’s breeding colony. Solid lines indicate predicted values from a trend model in Program MARK, dot-dashed lines indicate 95% CI, and circles show yearly survival estimates.

Cliff Swallows’ laying dates (when the first egg was laid in a nest) were earlier in 2015–2019 (31.45 ± 0.17 , where 1 = 1 May, $n = 3,431$ nests) than in 1984–1988 (36.42 ± 0.44 , $n = 1,954$ nests), but decade was not a significant predictor of laying date after controlling for the effect of colony size (larger colonies laid earlier; Appendix S1: Table S7). The random effects of colony site and colony-site-by-year were significant, but year was not (Appendix S1: Table S7).

Changes in parasite abundance, body size, and age ratios

Based on the total number of swallow bugs in collected nests from non-fumigated colonies, there was no change in parasite abundance over time: mean (\pm SE) bugs per nest in 1983–1984 was 487.7 ± 32.8 ($n = 135$ nests) vs. 574.2 ± 43.5 ($n = 120$ nests) in 2014–2016.

There was no significant effect of decade on the number of bugs per nest (Fig. 6A, Appendix S1: Table S8). Although the number of bugs per nest was found to increase with colony size in the 1980s (Brown and Brown 1986, 1996), this effect was less pronounced in the 2010s (Fig. 6A), leading to a marginally nonsignificant effect of colony size and no significant interaction between decade and colony size for this data set (Appendix S1: Table S8). The number of bugs was higher in the smaller colonies in 2014–2016 than in 1983–1984 (Fig. 6A). Only the random effect of colony site was significant in this analysis (Appendix S1: Table S8).

Swallow bug body size, as measured by dry mass, varied significantly with sex and month (May, July) of

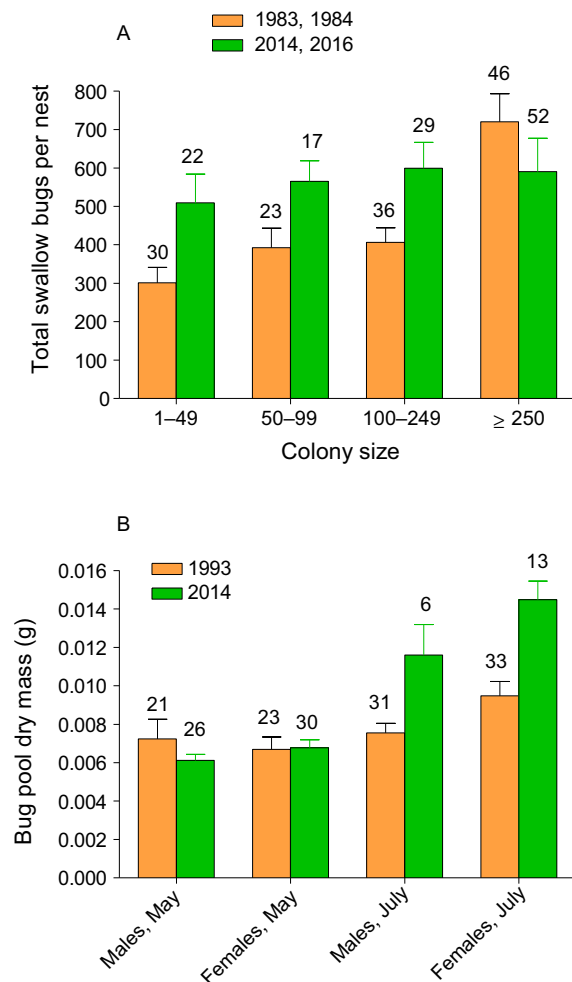


FIG. 6. (A) Number (mean \pm SE) of swallow bugs counted per nest in colonies of different sizes in 1983–1984 and 2014–2016. Number of bugs per nest did not vary with decade or colony size (Appendix S1: Table S8). (B) Swallow bug dry mass (mean \pm SE) for pools of five individuals collected in May and July in 1993 and 2014. Mass varied significantly with sex and month of collection but not with year (Appendix S1: Table S9). Numbers show sample sizes (number of nest counts or number of bug pools).

collection, but did not vary with decade (1993 vs. 2014) when collected (Fig. 6B; Appendix S1: Table S9). The random effect of colony site was significant (Appendix S1: Table S9).

Swallow bug age ratios (expressed as the proportion of adults per colony sample) in May averaged 0.495 ± 0.058 per colony in 1993 and 0.582 ± 0.057 per colony in 2014. There was no significant effect of decade, colony size, or date in May when collected (Appendix S1: Table S10) on the proportion of adult bugs per sample. There were no random effects in this analysis.

Changes in parasite transmission

Across all years, nests, and colonies, the mean (\pm SE) number of immigrant bugs introduced per Cliff Swallow nest per week was highest when nests contained nestlings (1.363 ± 0.105 , $n = 1,988$ nest counts), followed by fledged or failed nests (0.753 ± 0.097 , $n = 738$), nests prior to egg-laying (0.571 ± 0.0674 , $n = 1,049$), and nests with eggs (0.477 ± 0.0452 , $n = 1,664$). The same trends were apparent in both 1999–2002 and 2015–2016. Averaged over all nests of all statuses, the mean (\pm SE) number of immigrant bugs introduced per nest in 1999–2002, 0.951 ± 0.0690 , was not significantly different from that in 2015–2016, 0.772 ± 0.0588 , as judged from their overlapping 95% confidence intervals.

After controlling for the effect of nest status, we did not find a significant interaction between colony size and decade in predicting the number of immigrant bugs introduced to a nest (Fig. 7, Appendix S1: Table S11). Only the random effect of nest identity was significant in this analysis (Appendix S1: Table S11). However, when the same analysis was done for each decade separately, colony size was a significant predictor of bug immigration in 1999–2002 ($F_{1,2322} = 42.82$, $P < 0.0001$) but not in 2015–2016 ($F_{1,2217} = 1.62$, $P = 0.20$). This seemed to be largely due to lower immigration into the larger colonies by 2015–2016 (Fig. 7).

Parasite dispersal, as measured by the percentage of Cliff Swallows carrying swallow bugs on their feet when captured during mist netting, showed a significant decline over time ($r = -0.61$, $P = 0.0056$, $n = 19$ years; Fig. 8). The annual percentage of birds with bugs fell by about 70% from 1993 to 2013 (Fig. 8).

Changes in hosts' exposure to parasites

Cliff Swallows became more likely over time to reuse colony sites in successive years (Fig. 9A). This result was especially apparent when using only the comprehensive site surveys that began in the study area in 1990 ($r = 0.58$, $P = 0.0008$, $n = 30$ yr; Fig. 9A). However, the same result remained even when including the subset of colony sites studied prior to 1990 ($r = 0.33$, $P = 0.042$, $n = 38$ yr). When analyzing the probability that any given site was reused the next year (response variable yes/no) and controlling for the effects of colony size,

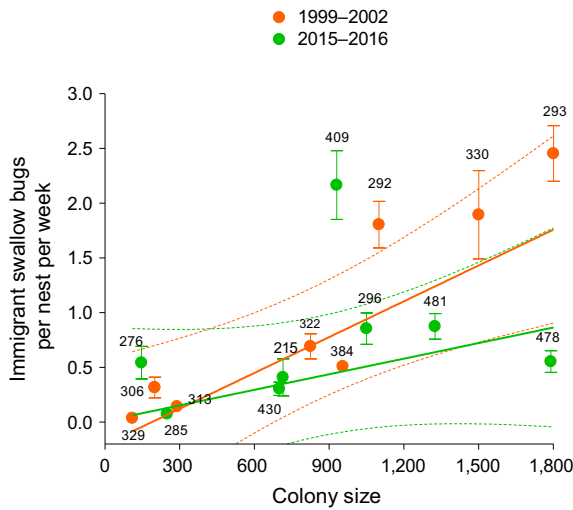


FIG. 7. Number of immigrant swallow bugs introduced into a Cliff Swallow nest per week in relation to colony size in 1999–2002 and 2015–2016. Circles indicate mean (\pm SE) of all weekly nest counts at a colony in a given year, solid lines give predicted values from a model containing nest status and a non-significant decade \times colony-size interaction, and dashed lines show 95% CI (Appendix S1: Table S11). Immigrant bugs per nest increased with colony size in 1999–2002 but not in 2015–2016 (see Results: Changes in parasite transmission). Numbers by circles indicate total weekly nest counts from each colony.

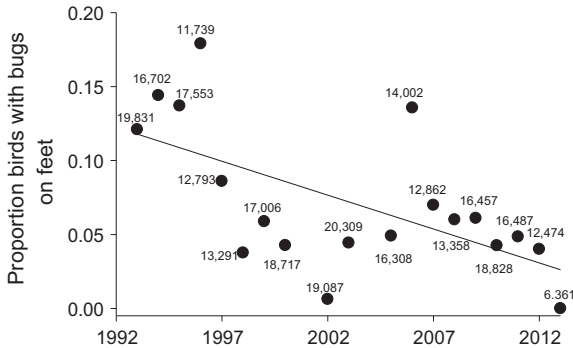


FIG. 8. Proportion of Cliff Swallows mist-netted each year that were carrying swallow bugs on their feet when caught. The total number of captures each year is given. The proportion of birds with bugs declined significantly over time (see Results: Changes in parasite transmission). Line indicates best-fit least-squares regression.

there was a significant interaction between year and substrate type (Fig. 9B, Appendix S1: Table S12) in predicting whether a site was reused. Natural cliff colony sites were less likely to be reused over time, while those on buildings tended to be more likely to be reoccupied the next year in the latter part of the study; sites on bridges and culverts showed little change over time (Fig. 9B).

Combining all non-fumigated colonies and years, the percentage of active Cliff Swallow nests that had also been active the preceding year was 20.8% in 1983–1993

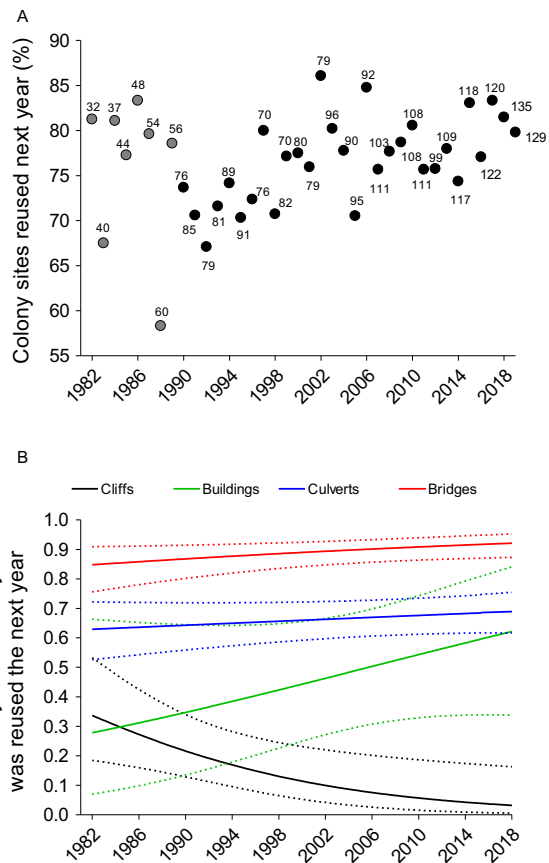


FIG. 9. (A) Percentage of Cliff Swallow colony sites reused the next season in relation to year. Gray circles indicate those years before all colony sites in the study area were surveyed; black circles represent years with comprehensive site surveys. The number of colony sites for each year is given. The percentage of sites reused increased over time (see Results: Changes in hosts' exposure to parasites). (B) Predicted probability (dashed lines show 95% CI) that a given Cliff Swallow colony site was reused the next season over time for sites on natural cliffs, buildings, highway culverts, and bridges. Predicted values came from a model containing colony size and a significant year \times substrate-type interaction (Appendix S1: Table S12).

($n = 1,718$ nests) and 22.3% in 2013–2019 ($n = 9,995$ nests); the difference was not significant ($\chi^2_1 = 1.87$, $P = 0.17$). Treating each colony separately and using the percentage of active nests at the site that had also been active the preceding year, we found that neither colony size nor decade (1983–1993 treated as one) significantly predicted whether an active nest had been used the past year, and a decade by colony size interaction was not significant (Appendix S1: Table S13). No random effects were significant in this analysis (Appendix S1: Table S13).

Reoccupancy of a non-fumigated colony site for a second round of nesting in the same season was not detected at all in the 1980s (Fig. 10). It had become relatively regular by the 2010s, with over 20% of sites having a second round of nesting in 2020 (Fig. 10). While

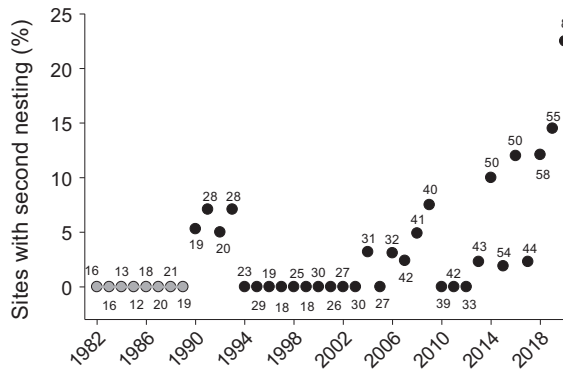


FIG. 10. Percentage of active Cliff Swallow colony sites reused later in the same season for a second round of nesting in relation to year. Gray circles indicate those years when relatively few colony sites in the study area were surveyed for second nesting; black circles represent years with more comprehensive site surveys. The number of colony sites for each year is given. The percentage of sites reused increased over time (Appendix S1: Table S14).

controlling for colony size, second nesting at a site within the season increased significantly with year across the entire study (Appendix S1: Table S14). The random effect of colony site was significant (Appendix S1: Table S14), reflecting that some sites generally seemed to be more likely to have second nesting than others for unknown reasons.

Changes in parental provisioning by hosts

In the 1980s, parental Cliff Swallows at non-fumigated nests fed their nestlings less often than parents at fumigated nests, but by the 2010s the pattern had reversed (Fig. 11A). The average number of food deliveries per hour to non-fumigated nests increased by 3.3 from the 1980s to the 2010s, while those at fumigated nests declined by 0.4. While controlling for date, brood size, nestling age, and weather variables that influence foraging, there was a significant decade by nest fumigation status interaction (Appendix S1: Table S15) in predicting parental food deliveries. Nest identity was the only significant random effect (Appendix S1: Table S15). Over a period when food deliveries to nestlings in parasite-free nests declined or stayed the same, those to nestlings in parasitized nests increased.

The amount of food delivered to nestlings per visit (the bolus mass) declined over time for birds at both fumigated and non-fumigated nests, but the decline was less for birds at non-fumigated nests (Fig. 11B). However, the interaction between decade and a nest's fumigation status was not significant, and only the random effect of colony-site-by-year was significant in this analysis (Appendix S1: Table S16).

Multiplying the average number of food deliveries per nest per hour times the average bolus mass for each delivery, the average (\pm SE) amount of food delivered

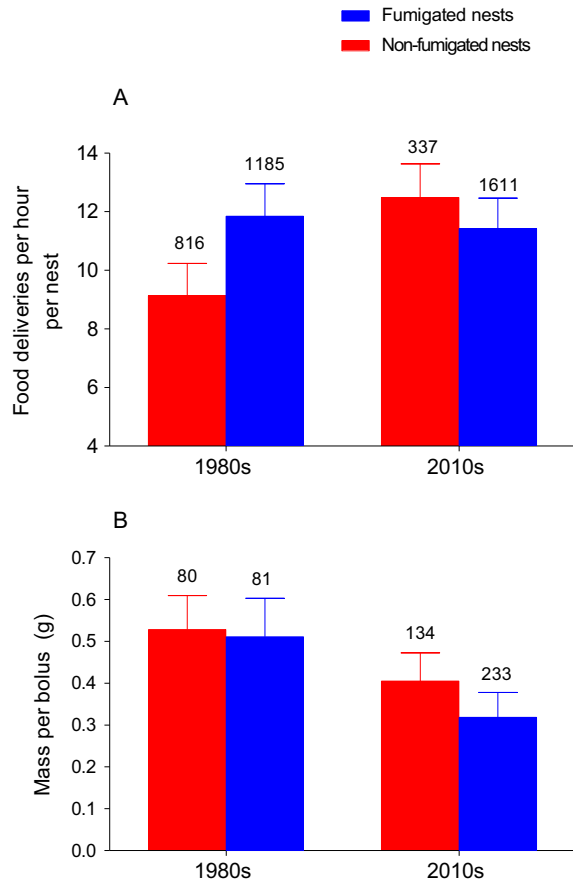


FIG. 11. (A) Estimated number of food deliveries by parental Cliff Swallows to a nest per hour (mean and SE) at non-fumigated and fumigated nests in the 1980s (1982–1989) and the 2010s (2016–2018). Food deliveries were predicted by a model containing a significant decade \times nest-fumigation status interaction (Appendix S1: Table S15). Numbers above bars indicate total hourly watches for each category, distributed among years and colonies as shown in Appendix S1: Table S3. (B) Estimated mean bolus mass (mean and SE) delivered per visit by parental Cliff Swallows at non-fumigated and fumigated nests in the 1980s (1983–1987) and the 2010s (2016–2018). Bolus mass was explained by a model containing colony size and a decade \times nest-fumigation status interaction, neither of which was significant (Appendix S1: Table S16). Numbers above bars indicate number of boluses collected for each category, distributed among years and colonies as shown in Appendix S1: Table S3.

per nest per hour for non-fumigated nests was 4.82 ± 0.94 g in the 1980s and 5.06 ± 1.03 g in the 2010s; for fumigated nests, 6.05 ± 1.16 g in the 1980s and 3.63 ± 0.76 g in the 2010s. Although this suggested that birds in fumigated nests were bringing back less food now than in the 1980s, the total amount of food delivered per hour did not vary significantly between the decades for either class of nests or between non-fumigated and fumigated nests within decades, based on overlap of the 95% confidence intervals.

Changes in presence of alternative hosts

The percentage of active Cliff Swallow colonies (in culverts) containing Barn Swallows each year exhibited a significant decline over time ($r = -0.69$, $P < 0.0001$, $n = 39$ yr; Fig. 12A). The relationship between whether a site had Barn Swallows (yes/no) and year was significant while controlling for the fact that Barn Swallows were more likely to occur in smaller Cliff Swallow colonies (Appendix S1: Table S17). The opposite pattern held for House Sparrows: the percentage of active Cliff Swallow colonies with sparrows increased significantly over time ($r = 0.77$, $P = 0.0002$, $n = 18$ yr; Fig. 12B). Whether an active site had sparrows varied with year but

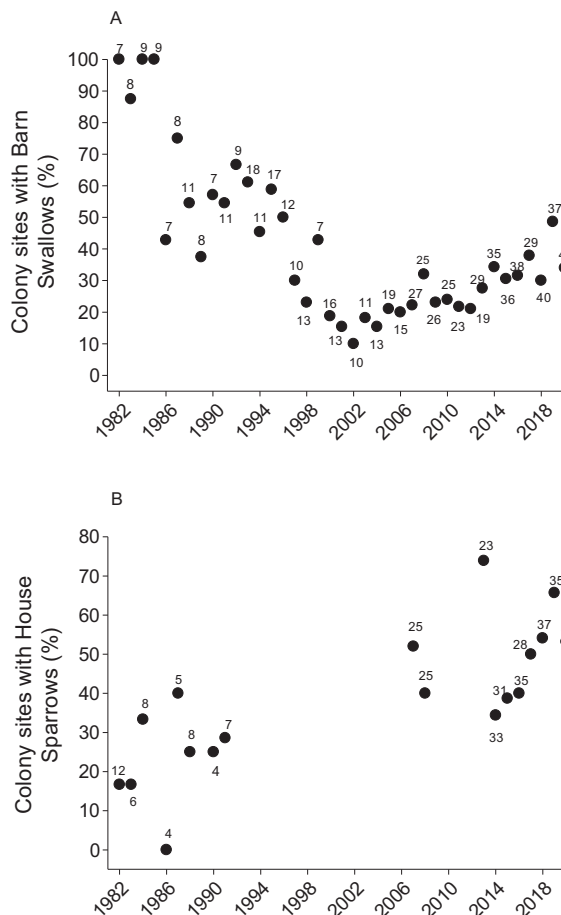


FIG. 12. (A) Percentage of active Cliff Swallow colonies also occupied by Barn Swallows (at least one active nest) in each year of the study. Only colonies on culverts and buildings were included. The percentage of colonies with Barn Swallows decreased over time (Appendix S1: Table S17). (B) Percentage of active Cliff Swallow colonies also occupied by House Sparrows (at least one active nest) in each year of the study. The percentage of colonies with House Sparrows increased over time (Appendix S1: Table S18). In both panels A and B, the numbers by circles indicate the number of colony sites monitored for Barn Swallows or House Sparrows each year.

not with Cliff Swallow colony size (Appendix S1: Table S18).

DISCUSSION

Over the approximately 35-yr period of this study, pathogenicity of swallow bugs to Cliff Swallows declined as measured by nestling body mass and the survival of nestlings, first-year birds, and older adults. These patterns could not be interpreted as due to changes in environmental conditions (e.g., climate change) independent of parasitism, as in all cases, the opposite trend or no temporal change was observed among birds occupying parasite-free nests. The results could not be explained by a reduction in parasite abundance over time and thus a net change in levels of parasitism. To our knowledge this is the first reported case of a temporal decline of this magnitude in the cost of ectoparasitism.

Has parasite virulence changed?

A parasite's virulence can be measured (independently of its pathogenic effects on a host) by its ease of transmission, its fitness, and its body size (Clayton and Tompkins 1994, Ewald 1995, Poulin 1998, Pfennig 2001). Below we address each of these indices of virulence.

Changes in transmission.—Swallow bug transmission occurs both between colonies as transient Cliff Swallows transport bugs on their feet from one site to another (Brown and Brown 2004, Moore and Brown 2014) and within colonies as bugs crawl on the substrate from nest to nest. We know little about within-colony transmission, other than that marked bugs can move up to 65 m from where they were marked but that most movement occurs to nests within about a 1-m radius of the marking site (Rannala 1995, Brown and Brown 1996; V. O'Brien, unpublished data).

Between-colony transmission has been better studied (Brown and Brown 2004). Our results here do suggest some potential change in bug transmission patterns, mostly a declining frequency of Cliff Swallows carrying bugs between colonies (Fig. 8). Over a 15-yr period, we also documented a weakening colony-size effect, in which there was little difference in transmission among colonies by 2015–2016 (Fig. 7). Because bugs are moved between colonies by transient Cliff Swallows that circulate among colonies and in 1999–2002 were attracted to larger colonies (Brown and Brown 2004), our results could indicate that larger colonies are attracting fewer transients now than in the early 2000s. If the net fitness advantages for Cliff Swallows in larger colonies are now lower, owing to a trend toward warmer climate that favors survival of birds in smaller colonies (Brown et al. 2016), the consequence could be transient birds having less interest in larger colonies and leading to lower net introduction of bugs into those sites. If transient

swallows are not visiting large colonies with heavier bug infestations as often, this could also explain the declining numbers of birds with bugs on their feet.

However, there was little net change over time in the average number of immigrant bugs introduced into Cliff Swallow colonies overall. Thus, it seems unlikely that changes in between-colony transmission have been drastic enough to drive lowered parasite pathogenicity to Cliff Swallows. This conclusion is further supported by no net change in total bug abundance per nest from 1983–1984 to 2014–2016 (Fig. 6A).

Bug abundance (fitness) and body size.—That bug abundance per nest is not lower now than in the early 1980s also argues against changes in parasite fitness, at least as measured by population growth. We do not have comparative data on bug reproductive success across time, but any such changes in reproductive success should result in total bug abundance either increasing or decreasing.

In the absence of a change in bug abundance, virulence could still be lower if bugs have evolved smaller body size (Ewald 1995). Smaller body size could result in smaller blood meals now than 35 yr ago and consequently might cause lower pathogenicity to the hosts. This explanation for our results seems unlikely, given that we found no evidence for a change in bug body size as measured in dry mass over the period 1993 to 2014. If anything, we found a trend toward larger bugs over time (Fig. 6B). When considering collectively the three components of virulence studied here, parasite transmission, parasite fitness, and parasite body size, there is no strong evidence that swallow bug virulence in the narrow sense has changed to an extent that could account for the temporal reduction in the bugs' pathogenicity to Cliff Swallows.

Has hosts' exposure to parasites changed?

Because the flightless swallow bugs are not well adapted to long-distance dispersal (Moore and Brown 2014) and remain in nests during the hosts' non-breeding period (Brown et al. 2010a), Cliff Swallows encounter bugs primarily when the birds re-occupy nest or colony sites where bugs have overwintered. Female swallow bugs store sperm from the previous summer (Loye 1985), enabling them to begin reproducing in the spring as soon as birds occupy a nest and the bugs get a blood meal (Brown and Brown 1996). Bugs can undergo long periods without blood meals, and bug numbers typically remain high into the next summer after a colony site is used (Brown et al. 2010a,b). Numbers begin to decrease, presumably mostly through mortality, only by the second winter at vacated sites. The legacy of parasites from the previous year thus determines both how many bugs Cliff Swallows encounter at a site and how rapidly in the spring bug reproduction begins. Previous work has hypothesized that Cliff Swallows' reuse of nest and

colony sites in successive years represents a trade-off between the costs of new nest construction vs. taking over an intact nest but inheriting a higher initial parasite load as a consequence (Brown et al. 2013).

One strategy that Cliff Swallows could potentially use to avoid bugs would be to shun nests and colony sites that were active the previous year and wait until at least one more year has elapsed before reoccupying them (Emlen 1986, Loye and Carroll 1991, Brown et al. 2013). Avoidance could occur through the birds' memory of active sites they visited the previous year during late-season prospecting (Brown 1998), or by observing directly the bugs clustering at the entrances of unused nests at the start of the nesting season (Moore and Brown 2014). Not only would avoidance lead to lower parasite load but it might also create a delay in bug reproduction in a host's nest, a consequence of it taking longer for immigrant bugs to initially colonize an un-infested nest or colony site. This delay could change the phenology of bug population increase relative to when the birds have nestlings present and result in lower pathogenicity if Cliff Swallows got a temporal head start on the bugs.

Colony and nest avoidance.—We found no evidence to indicate that Cliff Swallows were more effectively avoiding bugs by being less likely to choose sites infested from the previous year. The colony sites in the study area showed a significant increase over time in their tendency to be occupied in successive years (Fig. 9A). This indicates that Cliff Swallows in the latter years of the study were not increasingly likely to avoid colony sites that had been previously infested, and if anything, more often successive-year use of colony sites may be increasing the birds' exposure to bugs, possibly accounting in part for the apparent increases in parasite load during the study (Fig. 6A).

In addition, the temporal increase (Fig. 10) in the frequency of birds reusing the same site within the same season for a second round of nesting (either re-nesting or late nesting by birds that had previously not bred) suggests that Cliff Swallows are not avoiding sites with high parasite load within the same season to the extent that they did formerly. Conventional wisdom has been that late nesting does not occur at colony sites previously active that same season because such sites typically have many swallow bugs from the earlier nesting attempts (Brown and Brown 1996, 2015). The greater frequency with which a second round of nesting now occurs at a previously used site suggests that the parasite-related cost of reuse of a site from the same summer has lessened in recent years.

Even if a colony site itself is reused in successive years, bug exposure could still be reduced if Cliff Swallows were more likely not to reuse nests there that were occupied the year before. Many existing unused nests remain each year at active colony sites, so it is conceivable birds that are more discriminating in avoiding nests used the past year could be favored through reductions in

parasite load. However, the percentage of nests being used that were active the previous year was consistent throughout the 35-yr study. Thus, Cliff Swallows' exposure to bugs from the previous year has not changed in ways that could account for our finding of reduced pathogenicity.

Has tolerance of parasites changed?

Another explanation for our results is that Cliff Swallows have evolved greater tolerance of their parasites within the last 35 yr. Although tolerance has attracted considerable theoretical interest (Boots and Bowers 1999, Roy and Kirchner 2000, Best et al. 2009), empirical tests are difficult (Baucom and de Roode 2011) and thus few, and mostly center on interspecific comparisons in how different taxa cope with parasites (Rohr et al. 2010, Sears et al. 2015, Knutie et al. 2016, Grab et al. 2019). We know little about the proximate mechanisms by which tolerance is achieved in animals or its capacity to evolve as rapidly as we witnessed in this study. Cliff swallows seem likely candidates for tolerance, in that the evolution of tolerance is predicted to be especially effective when the parasite has strong effects on the host's fecundity (Roy and Kirchner 2000, Best et al. 2009), which is clearly the case in Cliff Swallows (Brown and Brown 1986, 1996).

Parasite abundance.—Tolerance by a host should lead to no changes or even an increase in parasite load over time (Roy and Kirchner 2000, Read et al. 2008, Baucom and de Roode 2011), which we did find in Cliff Swallows. On the other hand, some have suggested that tolerance should impose selection on parasites to become more virulent (Råberg et al. 2009, Little et al. 2010; cf. Miller et al. 2006), which we found not to be the case in Cliff Swallows.

Parental provisioning by hosts.—One way that parasites may be tolerated is through increased effort by parents in provisioning offspring to compensate for blood loss, mass reduction, and other physiological consequences of parasitism (Knutie et al. 2017). Several studies have shown that birds increase provisioning rates in the presence of parasites (Tripet and Richner 1997, Hurtrez-Boussès et al. 1998, Bouslama et al. 2002, Tripet et al. 2002, Avilés et al. 2009, Hund et al. 2015; cf. Møller 1994, DeSimone et al. 2017), although none have interpreted their results in the context of parasite tolerance.

We found that parental Cliff Swallows have increased their relative rate of nestling provisioning over time. Relative to birds occupying parasite-free nests, parents now make more food deliveries to their offspring than they did in the 1980s (Fig. 11A), and this increase in feeding effort might suggest that parents are now better compensating their nestlings for the effects of parasites. The temporal increase has occurred even though levels of parental provisioning have declined over time in the

absence of parasites. However, despite the increased rate of provisioning by parents in the presence of parasites today, the net amount of food delivered at non-fumigated nests is unchanged from that of the 1980s, largely because of a temporal decline in the amount of food collected on each trip (Fig. 11B). We do not know if the increased rate of food delivery alone compensates enough for the effects of swallow bugs to allow greater tolerance of parasites and to reduce their pathogenicity. This might be the case if more frequent, smaller meals somehow result in greater energetic gain to nestlings than larger, less frequent meals, but nothing is known about how or if this might occur in Cliff Swallows or other species.

Cellular mechanisms of tolerance.—In addition to changes in parental provisioning, several cellular mechanisms can confer greater tolerance of parasites (Ayres and Schneider 2012, Jackson et al. 2014, Ademolue et al. 2017), none of which we could investigate without physiological assays of birds from the 1980s. The birds could have evolved more effective tissue repair mechanisms after being bitten by the parasite, which might reduce blood loss or the likelihood of secondary infections (Raberg et al. 2009, Medzhitov et al. 2012). Additionally, the immune inflammatory response can be energetically costly or damaging to host tissue, resulting in immunopathy (Sears et al. 2011, Medzhitov et al. 2012). Perhaps across the past 35 yr, swallows have developed reduced immune responses to the bugs or higher tolerance to immunopathy (Adelman et al. 2013, Adelman and Hawley 2017) and/or modulated production of swallow bug-specific IgY antibodies (Fassbinder-Orth et al. 2013). If the cost of the immune response is high, then down-regulating the response could help the birds reallocate energy to other processes, such as provisioning or begging. Given that adults are also fed upon by bugs, changes in inflammatory responses or production of bug-specific antigen could allow parental birds to reallocate energetic investment in the immune system to provisioning (i.e., making more foraging trips), and this could reduce the costs of mounting immune responses in both adults and nestlings. Interestingly, increased provisioning did not seem to be costly to parents, given the long-term increase in adult survival for birds from non-fumigated colonies (Fig. 5B).

Changes in parasites under tolerance.—Host tolerance can sometimes favor parasites with higher growth rates and transmission because of the reduced chance of killing the host (Miller et al. 2006, Little et al. 2010). Although we found no changes in overall bug abundance or body size, we did document increases in bug numbers and lessened between-colony transmission at larger Cliff Swallow colonies. This could indicate some selection on bugs for avoiding transmission into or within larger colonies as a possible response to host tolerance (for unknown reasons), and is consistent with the prediction

that tolerance can lead to changes in the adaptive landscape for parasites (Little et al. 2010). Further study of this possibility is needed. Further work is also needed to determine whether the Cliff Swallow colony network in the study area represents enough spatial genetic structure in both hosts and parasites to drive the evolution of either resistance or tolerance to parasites in different colony populations (Horns and Hood 2012).

Shifts in performance of birds exposed and not exposed to parasites

Most analyses of pathogenicity reported here that use fumigated nests as controls show that birds from fumigated nests are performing worse now than they did 35 yr ago. For example, birds in parasite-free nests had declines in nestling body mass (Fig. 3), no change or a reduction in adult survival (Fig. 5), and nonsignificant declines in parental provisioning (Fig. 11). In each case, birds from non-fumigated nests showed the opposite pattern. Cliff swallows in general are faced with widespread environmental change, such as reductions in flying insect populations (Hallmann et al. 2017, Sánchez-Bayo and Wyckhuys 2019), changes in land use within the study area (e.g., conversion of pastures to corn) that might alter insect distribution and/or abundance, and a population size of Cliff Swallows that has increased by more than 50% in the study area since 1990 (C. R. Brown, *unpublished data*). These changes may have led to shifts in foraging behavior: Cliff Swallows now feed in smaller groups than in the 1980s and seem to rely on information transfer less (C. R. Brown, *unpublished data*). A decline in flying insects would reduce food availability relative to the 1980s and explain the possible decline in the amount of food brought back per delivery (Fig. 11B).

These food limitations (and their consequences) seem to be expressed more strongly in birds not subject to bug parasitism for unknown reasons. Nevertheless, that parasitized Cliff Swallows forage more efficiently and survive better than non-parasitized ones under current conditions underscores the ability of these birds to modulate their response to parasites. The reduced pathogenicity documented here probably reflects not only a gain in performance for birds exposed to parasites but also their ability to “catch up” with non-parasitized birds whose performance is now lower. Long-term removal of parasites at some sites may have relaxed parasite-driven selection on birds perennially occupying those colonies and led to our finding of birds at fumigated sites doing less well now than in the 1980s.

Another possibility is that long-term exposure to the naled insecticide caused undetected toxicity effects on hosts, expressed in reduced performance of birds in fumigated nests over time. Such effects have been seen with pyrethroid insecticides in short-term studies of birds (López-Arrabé et al. 2014), but have not been documented with organophosphates such as naled. Toxicity

effects might be more likely to explain the temporal trend in performance if the same individuals were exposed to the insecticide repeatedly, but this generally was not the case, with different colony sites (and thus different subsets of the population) subjected to the fumigation treatments in different and sometimes widely spaced years (Appendix S1: Table S1).

Changes in alternative hosts

In some cases, new hosts may reduce the parasite’s presence in the original host through the “dilution effect” (Ostfeld and Keesing 2000, Holt et al. 2003, Keesing et al. 2006), while in others a new host that is better than the original may lead to higher parasitism throughout the system through parasite “spillback” (Kelly et al. 2009). Could reduced parasite pathogenicity to Cliff Swallows have resulted from swallow bugs’ shifting to Barn Swallows or House Sparrows as alternative hosts, at least for part of their life cycle? Evaluating these possibilities is difficult in the absence of good data on the extent to which Barn Swallows and House Sparrows serve as hosts for bugs and at what times of the year. However, Barn Swallow use of Cliff Swallow colonies has declined over time, and this disappearance of Barn Swallows would suggest neither dilution nor spillback is likely for them.

The increase in House Sparrow usage of sites could be important if bugs prefer sparrows as hosts and have moved off Cliff Swallows. Yet, counts of bugs on the outsides of nests at sites where nests of both Cliff Swallows and House Sparrows were active simultaneously suggest that bugs currently strongly prefer Cliff Swallows when nests of both species are available (O’Brien et al. 2011). Furthermore, if House Sparrows acting as alternative hosts served to dilute the effects of bugs on Cliff Swallows by drawing them off swallows, we should have seen a reduction in bugs per nest, which was not evident in our data. For these reasons, a host shift is unlikely to explain our results, although the presence of House Sparrows at the colonies year-round (where they roost) may eventually alter dynamics of bug populations in the non-breeding season. The temporal increase in colonies with sparrows bears watching in the future.

Changes in host and parasite phenology?

Global climate change is known to affect host–parasite dynamics in various (and often poorly understood) ways (Poulin 2006, Rohr et al. 2011, Musgrave et al. 2019). A long-term advancement in Cliff Swallow breeding date has occurred during this study, attributable to warmer and drier conditions (Brown and Brown 2014). Nests in 2015–2019 were initiated about 5 d earlier, on average, than in 1984–1988. If Cliff Swallows can advance their phenology but bugs cannot, a phenological mismatch as documented in predator–prey systems (Stenseth et al. 2002, Burgess et al. 2018) could result. A

few days head start for the birds could lessen the parasites' effects if nestling swallows hatch and achieve a larger body size before bugs hatch or before bug instars grow large enough to take the larger blood meals. Yet if this scenario were to occur, presumably it would be reflected in a smaller bug population size per nest by the end of the season, which we did not observe.

Another way Cliff Swallows could get a head start on swallow bugs would be if a warming climate affects the age distribution of bugs at the start of the nesting season and especially if there are now fewer adult bugs in reproductive condition at that time of year. Warmer and more variable weather in late summer and during the winter can affect diapause in insects (Musolin 2007, Paaijmans et al. 2013) and thus their overwinter survival. Ongoing experiments with swallow bugs show that adults do not survive over the winter as well as instars when subjected to warmer conditions in the laboratory (C. Brown *unpublished data*). However, here we found no significant temporal change in the early-season age ratios of bugs, suggesting that so far global climate change has not affected swallow bug overwintering dynamics in ways that could account for the reduction in observed bug pathogenicity.

A role for Buggy Creek virus?

Another potential explanation for our results could be that Cliff Swallows are now better tolerating a swallow bug-borne pathogen, Buggy Creek virus (BCRV) known to infect Cliff Swallows, rather than the bugs themselves. BCRV is an alphavirus confined to the Cliff-Swallow—swallow-bug ecosystem (O'Brien et al. 2011, Brown et al. 2009, 2010a, 2012). Bugs serve as vectors for the virus, which has been found only in Cliff Swallows, swallow bugs, and House Sparrows that nest in Cliff Swallow colonies. As of 2006–2009, BCRV had no detectable effects on Cliff Swallows, and few birds were found with either active virus or antibodies to it (O'Brien et al. 2011). BCRV now seems to circulate mostly among bugs and House Sparrows (Brown et al. 2012). Unfortunately, we do not have data on BCRV prevalence or its effects on Cliff Swallows from the earlier years of the study. However, work in the 1970s in eastern Colorado about 215 km from our study area found little nestling swallow mortality attributable to BCRV (Scott et al. 1984). For this reason it seems unlikely that temporal changes in BCRV's impacts could contribute to the reduced pathogenicity we observed.

Changes in colony-size effects

Along with the changes in swallow bug pathogenicity over the last 35 yr, we also observed a diminution of colony-size effects of parasitism. In the 1980s, larger colonies had significantly more bugs per nest, and likely as a result the effects of bugs on Cliff Swallow nestling survival were more pronounced in the larger colonies

(Brown and Brown 1986, 1996). By the 2010s, we found no significant effect of colony size on bugs per nest (Fig. 6A) or on nestling survival. That bugs no longer apparently represent a cost of coloniality in Cliff Swallows is a major ecological change, potentially profoundly affecting the fitness payoffs associated with different colony sizes and requiring exploration of its consequences beyond the scope of this study. The reduction of the colony-size effect may have been brought about partly by increased between-group bug transmission into smaller colonies, but there is likely more than this going on that requires further investigation.

Rapid evolution of parasite defense

Rapid evolution of effective parasite defense, as documented here in the temporal decline in pathogenicity observed, was presumably driven by the substantial fitness effects of parasites in the 1980s (Brown and Brown 1986), costs so severe it seemed perplexing then that the birds could persist, especially in the larger colonies (Fig. 1A). Rapid evolution of host defenses against swallow bugs (whether tolerance or some other unidentified mechanism) over 35 yr is consistent with rapid development of both resistance and tolerance by House Finches (*Haemorrhous mexicanus*) to a bacterial pathogen over a period as short as 12 yr (Bonneaud et al. 2011, Adelman et al. 2013) and experiments showing additive genetic variation for tolerance in lab mice (Råberg et al. 2007).

That we could observe such rapid evolution of parasite defense may have been because the earlier work documenting the severe cost of swallow bug parasitism to Cliff Swallows (Brown and Brown 1986; Fig. 1A) was done in nonequilibrium conditions that reflected the relatively early stages of the birds' exposure to large numbers of parasites brought about by a shift in nesting-site use. Although Cliff Swallows began moving off natural cliff nesting sites onto artificial structures in our study area as early as 1942 (Brown and Brown 1996), the birds did not adopt bridge and culvert sites in large numbers until the early 1980s (Brown and Brown 2013). Cliff Swallows at the beginning of this study were thus in the early phases of a nesting-site and population expansion induced by an increase in numbers of suitable artificial nesting structures. Because swallow bugs are more abundant on concrete structures than on natural cliffs (Benedict et al. 2021; C. Hopla, *personal communication*), the nesting-site shift exposed them to parasite loads that were historically higher than they had ever experienced, a situation we were unaware of at the time of the original experiments (Brown and Brown 1986, 1996). Relative to cliff nesting sites, nests on culverts and bridges are more stable and more likely to remain intact between years, undergo less dramatic daily and annual temperature fluctuations, and are more likely to be reoccupied by Cliff Swallows in successive years. These factors all promote larger bug population sizes on concrete structures. Cliff Swallows' near-exclusive preference for bug-

infested artificial sites in the study area at present (Brown et al. 2013; Fig. 9B) is probably only possible because the costs of ectoparasitism are now less than in the 1980s.

Our not finding evidence of changes in parasite narrow-sense virulence or host avoidance suggests that rapid evolution of host tolerance best explains the reduced cost of parasites documented in this study, although the tolerance mechanisms are unclear and we reach this conclusion partly by default. Nevertheless, our results demonstrate the capacity of a host to relatively rapidly respond to high levels of parasitism and lend empirical support to theoretical predictions that parasites, especially those that negatively affect host reproduction, should drive selection for host tolerance (Best et al. 2009). As animals encounter novel parasites or altered abundance of parasites because of anthropogenic habitat modifications or global climate change, greater tolerance may be an increasingly common response in host species.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecm.1446/full>

DATA AVAILABILITY

Data sets used in this paper are available in the Dryad Digital Repository (Brown et al. 2020b): <https://doi.10.5061/dryad.15dv41nw7>.