

Feather mites are positively associated with daily survival in cliff swallows

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Abstract: Feather mites (Acari: Astigmata) have been reported to be parasitic, commensal, and even mutualistic on the birds that serve as their hosts. We investigated whether there was a relationship between number of feather mites (*Pteronyssoides obscurus* (Berlese, 1885)) on the wing and daily survival of cliff swallows (*Petrochelidon pyrrhonota* (Vieillot, 1817)) during the breeding season at 12 nesting colonies in Nebraska in 2005. Survival of birds with known mite loads was monitored by mark-recapture, and survival models with and without a linear effect of mites were compared with the program MARK. For adult swallows, mites were positively associated with daily survival at six colonies, negatively associated at two colonies, and there was no relationship at four colonies. For recently fledged juveniles studied at two colonies, survival varied positively with mite load at one, while the other showed no relationship. Feather mites may provide direct benefits to cliff swallows by consuming old oil, pollen, fungi, and harmful bacteria on the feathers or by pre-empting resources used by deleterious fungi or bacteria. The data do not support a truly parasitic relationship in which mites are costly to cliff swallows; these particular feather mites may be beneficial mutualists.

Résumé : Les acariens des plumes (Acari : Astigmata) sont connus pour être des parasites, des commensaux et même des symbiotes des oiseaux qui leur servent d'hôtes. Nous avons vérifié s'il existe une relation entre le nombre d'acariens des plumes (*Pteronyssoides obscurus* (Berlese, 1885)) sur les ailes et la survie journalière des hirondelles à front blanc (*Petrochelidon pyrrhonota* (Vieillot, 1817)) durant la saison de reproduction dans 12 colonies de nidification au Nebraska en 2005. Nous avons suivi la survie d'oiseaux avec une charge d'acariens connue par marquage et recapture; nous avons comparé au moyen du programme MARK les modèles de survie avec et sans effet linéaire des acariens. Chez les hirondelles adultes, il y a une association positive entre les acariens et la survie journalière à six des colonies, une association négative à deux colonies et aucune association aux quatre colonies. Chez les jeunes qui viennent de prendre leur envol étudiés à deux colonies, la survie varie positivement en fonction de la charge d'acariens dans une colonie, mais à l'autre il n'y a pas de relation. Les acariens des plumes fournissent peut-être des bénéfices directs aux hirondelles à front blanc en consommant le vieux mazout, le pollen, les champignons et les bactéries nuisibles sur les plumes ou alors en accaparant les ressources utilisées par les champignons et bactéries délétères. Nos données n'appuient pas l'existence d'une relation vraiment parasitaire qui pourrait être coûteuse aux hirondelles à front blanc; dans ce cas-ci, les acariens des plumes sont vraisemblablement des symbiotes bénéfiques.

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Introduction

Parasitism can often have strong effects on fitness that influence many aspects of an organism's behavior and life history, and many putative parasites have been described from most species (Price 1980; Møller et al. 1990; Loye and Zuk 1991; Clayton and Moore 1997; Janovy 1997). However, not all symbiotic organisms associated with a host species are truly parasitic; in some cases, the relationship may be commensal or even mutualistic. The feather mites (Acari: Astigmata) represent a highly specialized but relatively poorly known group of symbionts that have been reported at various times to affect their hosts in negative ways (Thompson et al. 1997; Harper 1999; Proctor and Owens 2000; Figueroa et al. 2003; Bueter 2005), or not at all (Blanco et al.

1999; Dowling et al. 2001; Pap et al. 2005), and possibly to be advantageous to their hosts in some circumstances (Blanco et al. 1997, 2001). Residing entirely on or inside the wing and tail feathers of many bird species, some groups of feather mites are thought to feed on feather pulp, while others apparently feed on excess oil, detritus, or microorganisms present on feathers (O'Connor 1982; Blanco et al. 2001; Proctor 2003).

Like other ectoparasites that reside more or less permanently on their hosts (e.g., chewing lice; Brown et al. 1995), feather mites could potentially affect survival of hosts. Ectoparasites may negatively affect host survival by serving as vectors for deleterious pathogens such as bacteria and viruses, by requiring hosts to spend more time in self maintenance (preening, grooming), or by directly consuming

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host resources (blood, feathers). Because ectoparasites present on the bodies of adult hosts can be difficult to quantify and monitor regularly, and because of the need for large sample sizes to document potentially subtle effects of parasites, we know little about how ectoparasites in general affect survival of adult hosts. Effects on survival are likely to be important especially for relatively short-lived hosts, such as small songbirds (Brown et al. 1995).

In this study, we examined how daily survival probabilities of cliff swallows (*Petrochelidon pyrrhonota* (Vieillot, 1817)) during the nesting season are related to the extent of feather mite infestation found on the birds' flight feathers. Using mark–recapture, we monitored the presence of banded birds at different nesting colonies throughout the breeding season. Cliff swallows are well suited for such a study because individuals vary in the number of feather mites that they have, large numbers of birds can be caught and recaptured, and patterns of within-season survival in this species have been previously explored (Brown and Brown 2004b). By fitting models with and without feather mite load as a covariate, we investigated whether daily survival was related to the number of feather mites and the direction of the relationship, if any.

Daily survival probability within the season was an especially appropriate index of fitness because it was estimated specifically for the time of the birds' annual cycle when no molt was occurring and thus when mite loads were not potentially changing independently in response to feather loss. Consequently, during this time of year we were more likely to measure effects associated with mite infrapopulations. In addition, although survival estimation is confounded by dispersal away from a study site in many animals (e.g., Cilimburg et al. 2002; Altwegg et al. 2003; Marshall et al. 2004), survival within the breeding season is less sensitive to dispersal biases because it does not include the phase of the life cycle when many individuals travel long distances away from their nesting sites. Our study is the first to formally model host survival in relation to the number of feather mites. Furthermore, our results are based on over 2000 individuals scored for mites and survival estimated, representing the largest sample size we are aware of for any single species of how feather mites might affect their hosts' survival. We use the findings (*i*) to explore whether mites represent a parasitic, commensal, or mutualistic relationship with cliff swallows and (*ii*) how any effect on survival might also vary with swallow colony size.

Methods

Study animals and study site

Cliff swallows are highly colonial passerines that breed throughout most of western North America (Brown and Brown 1995). They build gourd-shaped mud nests and attach them to the vertical faces of cliff walls, rock outcrops, or artificial sites such as the eaves of buildings or bridges. Their nests tend to be stacked closely together, often sharing walls. Cliff swallows are migratory, wintering in southern South America, and have a relatively short breeding season in North America. They begin to arrive at our study site in late April or early May and depart by late July. Cliff swallows are associated with a variety of ectoparasites, endopar-

asites, and viruses throughout their range (Monath et al. 1980; Scott et al. 1984; Brown and Brown 1995; Brown et al. 2001). The ectoparasites, in particular the hematophagous swallow bug (*Oeciacus vicarius* Horvath, 1912 (Hemiptera: Cimicidae)), are responsible for most of the nestling mortality and nest failures that occur in Nebraska (Brown and Brown 1986, 1996).

Cliff swallows in our study area are associated with a plumicolous feather mite, *Pteronyssoides obscurus* (Berlese, 1885) (Acari: Astigmata, Avenzoariidae). This mite appears confined mostly to the wing (largely the primary) feathers, where they cluster between the barbs and the barbules along the vane. Occasionally mites are found on the tail, primarily the middle feathers. In this group of mites, transmission occurs vertically, from parents to offspring, and possibly also among adult birds when in close physical contact (Blanco et al. 1997; Blanco and Frias 2001). Little is known about the ecology and population biology of feather mites (Proctor 2003).

Our study sites are centered primarily around the Cedar Point Biological Station (41°13'N, 101°39'W), near Ogallala, in Keith County, along the North and South Platte rivers, with a few sites in portions of adjacent Deuel, Garden, and Lincoln counties, southwestern Nebraska, USA. We have studied cliff swallows there since 1982. Approximately 160 cliff swallow colony sites are in our 150 km × 50 km study area, and about a third are not used in a given year. Colony size varies widely; in our study area, it ranges from 2 to 3700 nests, with some birds nesting solitarily. Over a 20-year period, mean (±SE) colony size ($N = 1363$) was 363 ± 16 nests. Each colony site tends to be separated from the next nearest by 1–10 km, but in a few cases by ≥ 20 km. The study sites are described in detail in Brown and Brown (1996).

Cliff swallow colony size was defined as the maximum number of nests at a site to have contained one or more eggs. Active nests were counted at some sites by periodically checking the nest contents with a dental mirror and flashlight, whereas the colony size at other sites was estimated by counting the total number of nests in sections of the colony known to be active. Full details on these methods of determining colony sizes are given in Brown and Brown (1996).

Mist-netting and capture of birds

We mist-netted cliff swallows at the study colonies at intervals throughout the nesting season and used the resulting captures and recaptures to estimate daily survival probability. Colonies were chosen for study based on their accessibility to us, ease of netting, and colony size. In 2005, there were 12 colony sites where we both had mite data for individuals and netted frequently enough to estimate daily survival (see below).

We used two principal methods for mist-netting cliff swallows (Brown 1998). One was to set a net across one end of a culvert, usually the upwind side, and catch birds as they exited the tunnel. Because cliff swallows enter and exit culverts into the wind, they usually enter the downwind side and exit the opening into the wind. The other method, employed at sites where deep water prevented our access to the nests from below, was to briefly drop a net attached to

Table 1. The six models fit to mark–recapture data at each cliff swallow (*Petrochelidon pyrrhonota*) colony, used to estimate daily survival (ϕ) and daily recapture probabilities (p).

Model No.	Variable
1	ϕ (time-dependent 1st-year age class, time-constant > 1-year age class), P (time-dependent, no age dependence)
2	ϕ (time-constant 1st-year age class, time-constant > 1-year age class), P (time-dependent, no age dependence)
3	ϕ (time-dependent 1st-year age class, time-constant > 1-year age class), P (time-constant, no age dependence)
4	ϕ (time-constant 1st-year age class, time-constant > 1-year age class), P (time-constant, no age dependence)
5	ϕ (time-constant, no age dependence), P (time-dependent, no age dependence)
6	ϕ (time-constant, no age dependence), P (time-constant, no age dependence)

Note: “Age” classes do not represent real age but only model structure used to test for the presence of transients (see Pradel et al. 1997).

poles over the side of a bridge containing nests. As the net dropped over and below the bridge, birds in their nests flushed out into the net. The net was then raised and carried away from the bridge for processing. Additional details on netting are provided in Brown and Brown (2004b).

Birds were captured at each colony on 3–15 days during the season. Three capture occasions were the minimum necessary for estimating survival and recapture probabilities (Lebreton et al. 1992). An occasion equated to a single day, with netting usually done for 3–3.5 h·day⁻¹·site⁻¹, although in some cases netting extended for up to 7 h·day⁻¹ at a site. The occasions on which adult birds were caught extended over total time periods ranging from 4 to 62 days within the season at a site. The different time intervals in between daily capture occasions were accounted for in statistically estimating survival probability (below).

All birds caught received a numbered US Fish and Wildlife Service band, gender determined by presence or absence of a brood patch or cloacal protuberance, and mass taken. The total sample size of birds in this study was 2146 adults and 339 recently fledged juveniles with mite loads scored, and ranged from 82 to 433 birds per colony. All recaptures of banded birds were recorded. If a bird was found at two (or more) different colonies in the same year, it was treated as an initial capture at each colony but as a recapture only if it reappeared on a subsequent day at one of the same sites and as a recapture only for that site. Thus, survival was estimated only for presumed resident birds at a site (see below), and individuals moving to a different colony in a season were treated as permanent emigrants even if we knew of their survival in the study area at large. The majority of such individuals were transients at any site where they might have been captured only once.

Scoring mite loads

We used a method slightly modified from Blanco et al. (1999) and Behnke et al. (1999) to score feather mites on each bird. The left wing was extended and held up to ambient light. All nine primaries were examined, and each given a score of 0–5 based on the relative numbers of mites present: 0, no mites visible; 1, 1–10 mites; 2, 11–20 mites; 3, 21–30 mites; 4, 31–40 mites; and 5, >40 mites. This method gives an accurate relative index of infestation, based on removal of feathers and microscopical examination (from similar species; Behnke et al. 1999). Based on Behnke et al.’s (1999) results from seven other passerine bird species in which scores from a single wing provided as good a relative index as both wings, and the tail and other feathers

proved unnecessary to score, we chose not to do the right wing or tail of cliff swallows, in part to minimize handling time per bird. Scores for all nine primaries were added to give an overall mite index per bird (maximum score per bird, 45). We scored a random sample of individuals twice on a single day and another sample on different days within the season (always blind with respect to previous scores). The repeatability of the mite index on a given bird was high and significant: within a day, $r_1 = 0.90$ ($P < 0.0001$); between days, $r_1 = 0.71$ ($P < 0.0001$). All mite scoring was done by a single person (K.R.B.).

Statistical estimation of survival

We estimated survival probabilities using the general methods of Lebreton et al. (1992) and Burnham and Anderson (2002). Program MARK (White and Burnham 1999) was used to assess the fit of different models to a given data set and to generate maximum-likelihood estimates of survival and recapture probability. Encounter histories were constructed for all birds caught at least once at each colony. Daily survival was estimated for each colony separately because the number of capture occasions, dates of sampling, and intervals between the occasions were different for each site. Each colony represented a single population and thus an independent data set.

We identified a priori six different survival and recapture models that were fitted to the data at each colony (Table 1). These models incorporated different degrees of time-dependence in both the survival (ϕ) and recapture (p) parameters. We knew from previous work (Brown and Brown 2004a, 2004b) that recapture probability often varies with time, owing to daily differences in weather and hours netted that affect capture success. We used age-dependent survival models to control for the presence of transients at a site and to estimate survival of the residents (Pradel et al. 1997). Briefly, by fitting an age-dependent model (with two “age” classes) to the capture data at a site, the “1st-year age” class can be used to approximate the transients, who, by virtue of not reappearing at a site, have much lower apparent survival than the residents who tend to be caught multiple times. If an age-dependent model fit better than one without age-dependence, it indicated the presence of transients, and we used estimates of ϕ for the “age 2 and older” class as our estimate of within-season survival probability of residents (see Pradel et al. 1997). If an age-dependent model did not provide a better fit, transients were not a factor, and we used constant ϕ (without age-dependence) for survival estimation.

Table 2. Model-fitting results, colony size (number of nests), sample size (N , number of birds), and daily recapture probabilities (p) for birds at 12 cliff swallow colonies for which a linear effect of feather mite load on daily survival was investigated.

Colony*	ΔAIC_c^\dagger	Regression coefficient [‡]	Colony size	N	p^\S ($\pm SE$)
Adults					
A	2.167		80	121	0.8870 (± 0.1402)
B	0.000	0.537	125	124	0.2848 (± 0.0924)
C	0.000	1.800	200	129	0.2492 (± 0.0606)
D	0.576	0.532	325	82	0.9999 (± 0.0002)
E	1.881	0.120	350	106	0.5393 (± 0.1487)
F	0.000	-0.117	375	85	0.1736 (± 0.0985) - 0.6150 (± 0.1477)
G	0.000	0.440	385	170	0.4604 (± 0.1172)
H	2.097		425	184	0.0546 (± 0.0168) - 0.2308 (± 0.0584)
I	3.642		600	156	0.1876 (± 0.0475) - 0.3401 (± 0.0645)
J	0.513	-0.326	1150	265	0.0519 (± 0.0310) - 0.3369 (± 0.2111)
K	2.135		1460	433	0.0173 (± 0.0089) - 0.2954 (± 0.0422)
L	0.000	47.808	1810	415	0.0251 (± 0.0128) - 0.3508 (± 0.0844)
Juveniles					
K	2.181		1460	190	0.0072 (± 0.0072) - 0.1177 (± 0.0781)
L	1.072	0.682	1810	149	0.1707 (± 0.0884) - 0.2250 (± 0.0965)

Note: Change in Akaike's information criterion corrected for sample size (ΔAIC_c) and regression coefficient values pertain to the model with an effect of mites.

*Colony designations are the same as in Fig. 1.

[†]Change in AIC_c relative to best-fitting model.

[‡]Regression coefficients are not presented for sites without an effect of mites (when $\Delta AIC_c > 2.00$ from best-fitting model).

[§]Daily recapture probability from the best-fitting model. A single recapture probability is shown for those sites for which a model with constant (time-independent) recapture was the best fit, and the range of recapture probabilities observed at a site is shown for those with time-dependent recapture in the best-fitting model.

Because our models also specifically estimated daily recapture probability, any differences in the likelihood of recatching birds at a site (owing to colony size or daily differences in weather conditions or hours netted) were accounted for in estimating daily survival probability. Across all colonies, the daily recapture probability varied from 0.2492 to 0.9999 per site for colonies with constant (time-invariant) recapture, and from 0.0072 to 0.6150 at sites with time-dependent recapture probabilities (Table 2).

Model fit was assessed by Akaike's information criterion (Burnham and Anderson 2002) corrected for sample sizes (AIC_c) as provided by MARK. In theory, the model with the lowest AIC_c is the so-called best model. The currently accepted convention (Burnham and Anderson 2002) is that models with AIC_c values that differ by 2.00 or less are indistinguishable statistically.

Before comparing the fit of the candidate set of models, we performed a goodness-of-fit test for each colony's data set using the program RELEASE (Burnham et al. 1987). This test evaluated how well the data met the variance assumptions inherent in the binomial distribution used in mark-recapture analysis. When a data set does not meet the assumptions, it is usually because the data are overdispersed, reflecting a lack of independence or some heterogeneity among observations after accounting for relevant covariates, and is usually brought about by the presence of transients or trap-dependence. We assessed the goodness-of-fit of model 1 (Table 1), the most highly parameterized one in our candidate set, by calculating a combined χ^2 value based on tests 3m, 2ct, and 2cl in RELEASE. This subset of tests can incorporate age-dependence in determining goodness-of-fit

(Pradel et al. 2005). The total χ^2 value allows estimation of a variance inflation factor, \hat{c} , as χ^2/df . The \hat{c} value is used in MARK to adjust the AIC_c through quasi-likelihood, resulting in a QAIC_c when \hat{c} departs from 1.0.

Although we often found time-dependence for the "1st-year age" class in age-dependent models (e.g., model 1, Table 1), reflecting differing numbers of transients versus residents caught on different days, we did not use models with full time-dependence for the "older age" classes, that is, for resident survival. Such heavily parameterized models (especially for sites with many capture occasions) would seldom reach convergence in exploratory analyses.

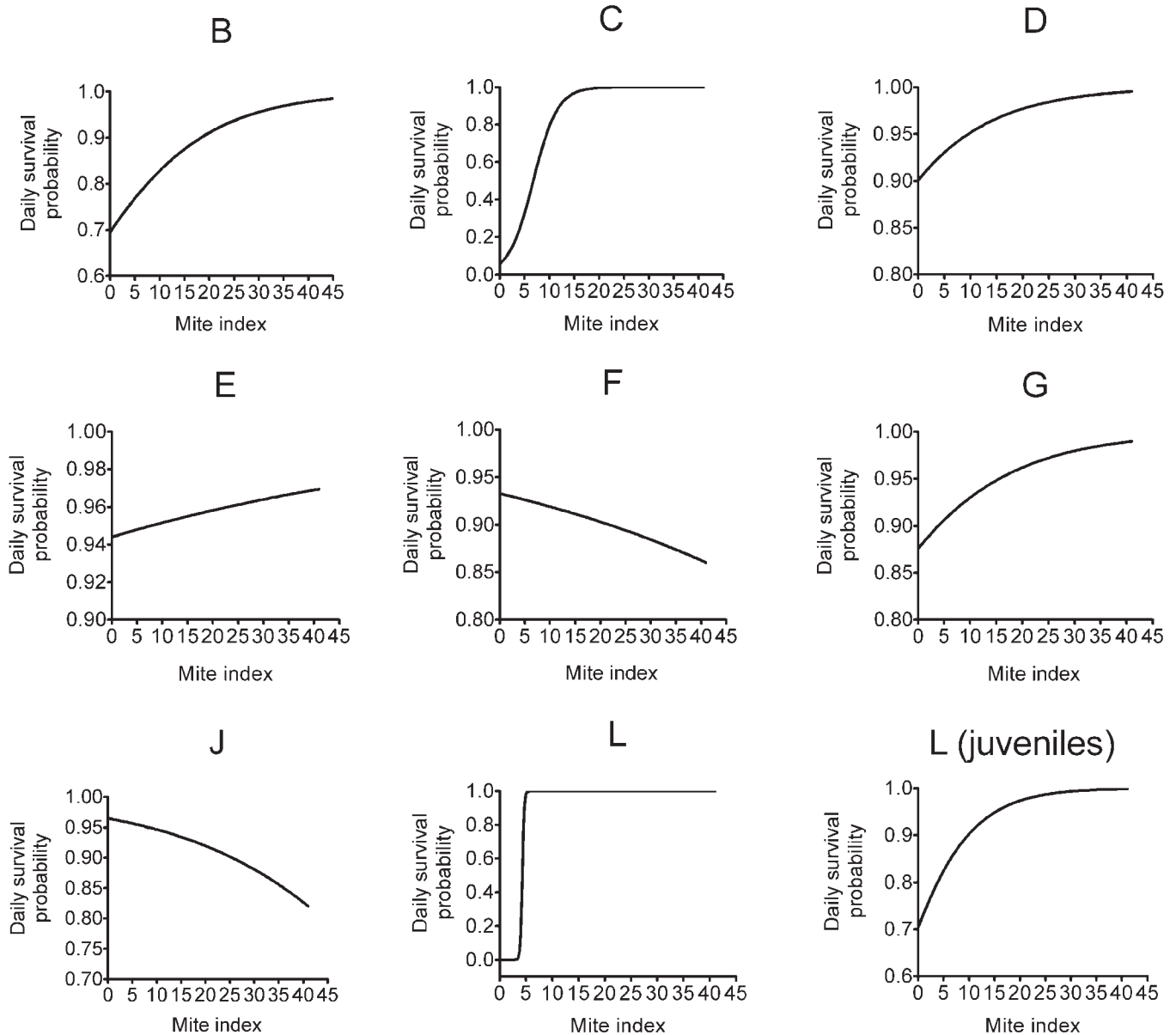
Some colonies were sampled on back-to-back days, but usually several days separated capture occasions at a given site. We standardized survival estimates to intervals of 1 day, however, using the Set Time Intervals utility in MARK. This made all survival probabilities comparable, being estimated for a period of the same length (1 day). MARK uses the actual time interval as an exponent of the estimated survival probability to correct for the length of the time interval.

The effect of feather mites on survival was modeled by using an individual's mite index as a linear covariate incorporated into the best-fitting model at each site (Table 1). Models with mite index as a covariate used the log-link function in MARK to generate the survival function, and ϕ was back-transformed from the logit scale using the expression

$$\phi = \frac{e^{\text{logit}\phi}}{1 + e^{\text{logit}\phi}}$$

MARK automatically standardized all covariates by sub-

Fig. 1. Estimated within-season (daily) survival function for the observed feather mite indices in cliff swallows (*Petrochelidon pyrrhonota*) shown for adults at eight colonies and for recently fledged juveniles at one colony (lower right corner). Colony designations (letters) refer to colonies shown in Table 2. Survival curves were generated from the best-fitting model at each site that contained mite index as a covariate.



tracting the mean from each and dividing by the standard deviation. Models with a mite effect were compared with equivalent ones without an effect of mites. When models with and without a mite effect were within 2.00 in AIC_c , we considered both to have support and treated those colonies as ones exhibiting possible evidence of a relationship between mite load and within-season survival. We used this more liberal criterion for inferring a possible effect because small apparent differences in survival are often difficult to detect statistically, as sampling error and daily variability can hamper our ability to “prove” differences among individuals (Brown et al. 2003).

In preliminary analyses, we also explored whether survival might vary with mite load in a curvilinear fashion, by using both the mite index and its square as covariates. In all cases, however, these models would either not reach conver-

gence or had AIC_c values greater than 2.00 from that of the best-fitting model, so quadratic survival functions were not considered further.

Results

For the 12 colonies studied in 2005, we found evidence in 8 for a relationship between mite load and daily survival of adult cliff swallows (Table 2). The model with an effect of mites was the best fitting at five of the eight colonies, and in the remaining three, the model with a mite effect was within 2.00 in AIC_c of the (best fitting) one without a mite effect (Table 2). The relationship between mite index and survival was positive for six of the eight colonies, although its shape varied among sites (Fig. 1). For some, there was evidence of a sharp threshold effect, with birds having few mites show-

ing very low survival and all other birds with very high survival (Fig. 1). For others, the relationship was more linear (although relatively weak in some cases). The two colonies with a negative relationship between mite index and survival expressed the effect over a relatively narrow range of survival probabilities (Fig. 1). For recently fledged juvenile cliff swallows at two colonies, birds at one showed a positive relationship between mite load and daily survival (Table 2), broadly similar to the patterns for adults (Fig. 1).

Colony sizes of the sites studied ranged from 80 to 1810 nests. There was no strong effect of colony size on the survival patterns, although the larger colonies appeared perhaps to have been more likely to either have no mite effect or a negative one (Table 2).

Discussion

We found little evidence that plumicolous feather mites have any consistently negative effects on survival of their cliff swallow hosts. The positive relationships between mite index and within-season survival probability suggest instead that feather mites might benefit the birds and that having large numbers is associated with a higher likelihood of surviving from day to day. This result is in contrast to those for other ectoparasites found on adult cliff swallows, such as fleas and lice, which have strongly negative effects on annual survival (Brown et al. 1995). The shapes of the survival curves (Fig. 1) show a large survival difference between birds with few versus many feather mites. The survival probabilities reported are daily ones, and even small differences in daily survival can translate into huge effects on annual survival (Brown and Brown 2004b). Based on the survival probabilities we estimated (Fig. 1), at most colonies birds with the fewest number of mites had daily survival so low that they would not have survived the breeding season.

Plumicolous feather mites, such as the *P. obscurus* that we studied, feed primarily on uropygial-gland oil (waxes and fatty acids) and pollen and fungi that adhere to feather barbs (O'Connor 1982; Proctor and Owens 2000; Proctor 2003). Removal of these materials from feathers presumably improves feather condition and performance, which would be especially important for wing feathers in aerial-foraging birds such as cliff swallows. In addition, some evidence indicates that feather mites may compete for food with bacteria that also reside on feathers, or possibly feed on bacteria and fungi (Blanco et al. 1997, 2001; Walter and Proctor 1999; Blanco and Frias 2001; Proctor 2003). Because some feather-dwelling bacteria may be deleterious (Burt and Ichida 1999), the degree to which feather mites indirectly keep numbers of harmful bacteria low may be advantageous to a bird. Removal of old oil may also benefit an avian host by removing microhabitat for fungi and bacteria (Blanco et al. 2001). The positive effects of mites applied to both adult cliff swallows and recently fledged juveniles, despite the lower average mite loads of juveniles (K.R. Brazeal and C.R. Brown, unpublished data). These possibly beneficial effects of feather mites have led to suggestions that they may be mutualists (Blanco et al. 1997; Proctor and Owens 2000), although there is little empirical evidence showing strongly positive correlations between mite intensity and measures of host fitness. In the barn swallow (*Hirundo rustica* L., 1758),

birds with more mites tend to arrive earlier in the spring, suggesting a positive correlation between individual quality and ability to support feather mites (Møller et al. 2004). The only previous studies of survival in relation to feather mite load found no significant associations (Dowling et al. 2001; Pap et al. 2005).

While our data suggest that having feather mites might directly benefit cliff swallows, it is equally possible that the patterns we observed reflect mite load being correlated with some other attribute of the birds that in turn affects fitness (survival). An interspecific study of 17 passerine species in Portugal showed that heavier birds had more feather mites, possibly because bigger birds present more habitat for the mites (Rózsa 1997; cf. Poulin 1991). If the same relationship applies within species, perhaps heavier cliff swallows had more mites and survived better because their greater mass allowed them to store more fat, that in turn helped them survive periodic spells of cold weather which reduce the birds' flying-insect food supply (Brown and Brown 1996, 1998). Heavier birds might also be in better condition and consequently able to produce more uropygial-gland oil, providing more food resources for mites and thus supporting larger in-frapopulations (Blanco et al. 1999; Blanco and Frias 2001; Proctor 2003). However, we found little evidence that mite load in cliff swallows varied with a bird's mass. Using all birds scored, there was no significant correlation between mite index and body mass for either adults ($r_S = 0.01$, $P = 0.31$, $N = 3062$ birds) or juveniles ($r_S = -0.01$, $P = 0.83$, $N = 370$ birds). This result tends to reinforce the conclusion that mites provide active benefits to these birds.

Although the predominant pattern across all analyses was for cliff swallow survival to increase with mite load (e.g., Fig. 1), there was variation among colonies. Two showed a negative relationship and four had no significant association between mite load and survival. The finding of no significant effect could not be explained by low power owing to sample size, as three of the four colonies with no effect were ones with the larger sample sizes (Table 2). There was some evidence, however, that colony size might have influenced our results. With the exception of the colony with 1810 nests that showed a strong threshold relationship between mite load and survival (site L in Fig. 1), none of the colonies greater than 400 nests in size showed a positive effect of mites. Perhaps birds in larger colonies, where foraging efficiency is greater owing to information transfer among colony residents (Brown 1986; Brown et al. 1991; Brown and Brown 1996), are in such uniformly good condition that any direct or correlated effects of mites cannot be detected.

Experimental manipulations of feather mite loads are needed to establish definitively that these organisms represent a beneficial mutualism to cliff swallows and other birds (Walter and Proctor 1999). However, the results reported here show a relatively strong positive relationship between the number of mites on a bird and the daily survival at some colonies, and represent one of the clearest cases yet reported for a positive association between a feather mite and its host. Unlike most ectoparasites of cliff swallows, plumicolous mites are apparently not costly and, on balance, do not negatively affect fitness of birds in different-sized colonies.

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