

Charles R. Brown · Mary Bomberger Brown

Group size and ectoparasitism affect daily survival probability in a colonial bird

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Abstract Little is known in general about how group size or ectoparasitism affect survival in colonial animals. We estimated daily within-season survival probabilities for nesting adult and recently fledged juvenile cliff swallows (*Petrochelidon pyrrhonota*) at 239 colonies from 1983 to 2003 in southwestern Nebraska, USA. Some colonies had been fumigated to remove ectoparasites. We conducted mark-recapture at each colony site to estimate daily survival. There were no systematic differences between males and females in daily survival. Adults and juveniles occupying parasite-free colonies had, on average, 4.4% and 62.2% greater daily survival, respectively, than their counterparts in naturally infested colonies. Daily survival of all birds increased with colony size for both parasite-free colonies and those under natural conditions, although the effect was stronger for adults at fumigated sites and for juveniles. Average daily survival probability for adults tended to increase during warmer and drier summers. Although daily survival varied at some sites over the course of the nesting cycle, there were no strongly consistent within-year temporal effects on survival. Even small differences in daily survival probability can translate into large effects on mean lifespan. The deleterious effects of ectoparasites on daily survival within the season represent a previously unknown cost of ectoparasitism. The increase in within-season survival with colony size reflects the net effects of many costs and benefits associated with colony size. Ectoparasitism is probably the most important cost that tends to partly balance the positive effects of large colonies. The greater survival of cliff swallows in the larger colonies is a previously unknown advantage of colonial nesting.

Keywords Cliff swallow · Coloniality · *Oeciacus vicarius* · *Petrochelidon pyrrhonota* · Swallow bug

Introduction

Many animals live in groups for part or all of their lives, yet the ecological and social factors causing group-living are unknown for many species. This is especially true for colonially nesting birds, many of which nest in groups of widely different sizes even within a single population (Brown et al. 1990). For most, we do not know either why colonies form to begin with or why they vary so much in size. Advantages of forming groups, such as better avoidance of predators or enhanced food-finding, have been identified and well studied in some species, and we also know that there can be serious disadvantages of group-living, such as increased exposure to pathogens or parasites and increased competition for local resources (e.g., Alexander 1974; Hoogland and Sherman 1976; Snapp 1976; Hoogland 1979, 1995; Wiklund and Andersson 1994; Brown and Brown 1996, 2001). However, few studies have looked at both costs and benefits in the same species or been able to measure them in the same currency. For example, predator-related advantages of group-living are often expressed in terms of the likelihood of a group detecting a predator, while parasite-related costs are measured in terms of per capita parasite load. Consequently, it has been difficult to estimate either the net fitness associated with groups of different sizes or the relative contributions of the component costs and benefits.

An alternative approach is to use reproductive success and survival as an integrative index of the positive and negative effects on fitness associated with group-living (Brown and Brown 1996, 2001; Danchin and Wagner 1997; Brown et al. 2003). Being two major components of fitness, survival and fecundity should reflect the net selective pressures for or against group-living. It has also been argued that animals themselves use reproductive success as a reliable cue to select breeding sites, precisely

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C. R. Brown (✉) · M. B. Brown
Department of Biological Sciences,
University of Tulsa,
Tulsa, OK 74104, USA
e-mail: charles-brown@utulsa.edu

because it represents a single index of the many positive and negative factors associated with a particular habitat (e.g., Danchin and Wagner 1997; Danchin et al. 1998; Doligez et al. 2002, 2003).

Despite the potential insight provided by patterns of survival and fecundity, rarely has either been measured with respect to group size. In birds, for example, most work on reproductive success in relation to colony size was done with other objectives and/or is plagued by small sample sizes and confounding yearly effects (Brown and Brown 2001). Survival has attracted even less attention: we are aware of only two studies to date in any taxa that have specifically measured survival in relation to colony size (Brown and Brown 1996; Brown et al. 2003), and those studies examined survival between years.

In this paper, we investigate within-season survival of breeding and fledgling cliff swallows (*Petrochelidon pyrrhonota*) in relation to colony size using mark-recapture data from over 160,000 marked birds in 239 colonies of different sizes over a 21-year period. Our primary objective is to determine how daily survival probability within the breeding season varies with colony size as an index of the costs and benefits associated with living in groups of different sizes. Among the advantages of studying within-year survival in colonial birds is that it should directly reflect any group-size effects, because it is specifically for the time of year when the migratory cliff swallows are resident in the breeding colonies. 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. 2005), survival within a breeding season is much less sensitive to dispersal biases because it does not include the phase of the life cycle when many individuals travel (often long distances) away from their nesting sites.

By experimentally removing ectoparasites at some of our sites, we also investigated the contribution of ectoparasitism to variation in within-season survival probabilities. The few previous studies on the effects of ectoparasites on survival in birds measured only between-year survival (e.g., Brown et al. 1995; Fitze et al. 2004). As far as we know, our work represents the first study of within-season survival in relation to colony size or levels of parasitism in any species, and we use the results to gain insight into the evolution of coloniality in cliff swallows. Colony size in cliff swallows varies widely, from less than 10 to over 3,000 nests, and thus the species is especially suitable for studying the effects of group size. A number of separate costs and benefits of coloniality have been identified in cliff swallows (e.g., Brown and Brown 1996; Brown et al. 2001), and other work has focused on how these birds choose colonies (Brown and Brown 2000; Brown et al. 2000, 2002), but to date little has been known about within-season survival or how it varies with colony size.

Methods

Study animal 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. Most birds raise only one brood; in rare instances, up to 10% of the pairs at a colony may attempt a second brood there later in the summer, primarily at parasite-free sites. Cliff swallows are associated with a variety of ectoparasites, endoparasites, 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 (Hemiptera: Cimicidae: *Oeciacus vicarius*), are responsible for much of the nestling mortality and nest failures that occur in our study area (Brown and Brown 1986, 1996). The main predators of adult and recently fledged juvenile cliff swallows in southwestern Nebraska are American kestrels (*Falco sparverius*), great horned owls (*Bubo virginianus*), black-billed magpies (*Pica hudsonia*), and common grackles (*Quiscalus quiscula*). Bull snakes (*Pituophis catenifer*) attack nests in colonies, usually preying on eggs or nestlings, but sometimes catching adults inside their nests (Brown and Brown 1996).

Our study site is centered at the Cedar Point Biological Station (41°13'N, 101°39'W) near Ogallala, in Keith County, along the North and South Platte Rivers, and also includes portions of Deuel, Garden, and Lincoln counties, southwestern Nebraska, USA. We have studied cliff swallows there since 1982. There are approximately 160 cliff swallow colony sites in our 150×50 km study area, with about a third of these not used in a given year. Colony size varies widely; in our study area, it ranges from 2 to 3,700 nests, with some birds nesting solitarily. Over a 20-year period, mean (\pm SE) colony size ($n=1,363$) 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. In our study area, the birds nest on both natural cliff faces and artificial structures such as bridges, buildings, and highway culverts. The study site is described in detail by Brown and Brown (1996).

Climatological data were taken each year from an automated weather-reporting station in Arthur, Arthur County, just north of the study area, and part of the Automated Weather Data Network administered by the University of Nebraska.

Fumigation

Beginning in 1984, we fumigated selected colonies each year to remove swallow bugs. Nests within colonies were sprayed with a dilute solution of an insecticide, Dibrom, that was highly effective in killing swallow bugs (Brown and Brown 1986, 1996, 2004). Nests were fumigated weekly to remove any bugs brought into the colony by transient birds. In the earlier years of the study, 1984–1988, some colonies were divided in two with some nests fumigated and others left untreated. These sites were considered as fumigated colonies in the analyses presented here because most birds in these colonies tended to occupy the fumigated sections. After 1988, all fumigated sites were sprayed in their entirety. Because fumigation disrupts, perhaps permanently, natural patterns of ectoparasitism at colony sites and would thus affect the birds' use of those sites, we restricted fumigation to a relatively few colony sites and fumigated the same ones perennially.

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. We chose colonies to include based on their accessibility to us, ease of netting, and colony size. We tried to maximize the range of colony sizes studied each season. From 1983 to 1987, mark-recapture occurred at a relatively few sites as part of other objectives (e.g., Brown 1984, 1986; Brown and Brown 1988, 1989); from 1988 to 2003, mark-recapture was a primary focus of our research, and we captured birds at 20–35 colonies annually. All of the colony sites included here were in the center of our study area within a 35-km radius of the Cedar Point Biological Station.

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. This method of setting a net and waiting for birds to encounter it was also used for a relatively few colonies on tall bridges where a moveable net rigged on pulleys was used to span sections of the bridge containing nests, and birds flew into the net when both entering and exiting their nests. 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 poles over the side of a bridge (or cliff) containing nests. This worked whenever it was possible for two people carrying the net to walk out onto the bridge above the nests undetected by the birds. 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.

The two netting methods differed in two important ways. Drop-netting tended to catch almost exclusively birds at or inside their nests at the moment the net was dropped over. Consequently, birds caught by drop-netting tended to be largely residents of the colony. In contrast, set nets that were left in place for an extended period (usually several hours at a time) also tended to catch transient birds which briefly passed through the colonies, but did not own nests to flush out of (Brown and Brown 2004). Thus, captures at set-net sites included a fraction of transient birds, whereas those at drop-net sites did not. The presence or absence of transients was accounted for in modeling survival probabilities (below).

The other difference between the two netting methods was that set-netting could be employed the entire nesting season since it relied on birds' natural comings and goings to and from their nests. Set-net sites were the only places that recently fledged juveniles could be caught. Drop-netting, however, that relied on birds' flushing out of their nests, could only be used effectively early in the season and throughout the incubation period, when birds were almost constantly at or inside their nests. Once nestlings hatched, parents were usually away from the nests foraging, and any given flush would yield very few birds. We terminated drop-netting once eggs began hatching at a colony. Thus, estimated daily survival probabilities tended to be based on a longer span of the season at set-net sites than at drop-net sites. Despite these methodological differences, survival estimation was unaffected by the type of netting method (see Table 2).

Adult birds were captured at each colony on 3–37 days during a season (mean: 7). Three capture occasions were the minimum necessary for estimating survival and recapture probabilities (Lebreton et al. 1992), and thus any site for which we had only one or two capture occasions in a season was excluded. An occasion equated to a single day, with netting usually done for 3–3.5 h per day per site, although in some cases netting extended for up to 7 h per day at a site. The occasions on which adult birds were caught extended over total time periods ranging from 3 to 82 days within the season at a site (mean: 31.9). The different time intervals in-between daily capture occasions were accounted for in statistically estimating survival probability (below). Recently fledged juvenile birds were captured during a shorter time span in the latter half of the season, beginning once fledging started at a site. We used only

colonies for which we had at least three capture occasions (range: 5–25) after fledging began for estimating juvenile survival probability.

All birds caught received a numbered U.S. Fish and Wildlife Service band, gender determined by presence or absence of a brood patch or cloacal protuberance, mass taken, and, for some, additional procedures done (e.g., color-marking, morphological measurements taken, blood sampled). Juveniles were birds recently fledged, easily known by their variable mottled color patterns on the throat and forehead (see Stoddard and Beecher 1983). The total sample size of birds banded and used in this study, over all years and colonies, was 144,349 adults and 22,709 juveniles distributed among 239 colonies from 1983 to 2003, and ranged from 11 to 5,174 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. Most such individuals were transients at any site where they might have been captured only once.

Determining colony size

Cliff swallow colony size was defined as the maximum number of nests at a site known 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 active sections of the colony. Full details on these methods of determining colony sizes are given in Brown and Brown (1996).

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, with the resulting survival estimates for each colony independent of each other, and therefore subject to standard statistical testing in aggregate. Because we were interested in within-season survival only, each encounter history automatically ended at the conclusion of each breeding season (after the last day of netting at each site).

We identified a priori six different survival and recapture models that were fit 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 2004) that recapture probability often varies with time, owing to daily differences in weather and hours netted that affect capture success. We also knew that the presence of transients varies among days, requiring us to test for time-dependence in survival parameters. 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 "first-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, that indicated the presence of transients (usually the case for the set-net sites, as described above),

Table 1 The six models fit to mark-recapture data at each cliff swallow (*Petrochelidon pyrrhonota*) colony, used to estimate daily survival (ϕ) and recapture (p) probabilities. “Age” classes did not represent real age, but only model structure used to test for the presence of transients (see Pradel et al. 1997)

Model	Structure
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)

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 (in most cases) constant ϕ (without age-dependence) for survival estimation. This was often the case for drop-netting sites. Adults and juveniles were treated separately at each colony, but the same candidate set of models (Table 1) and the same procedures (below) for assessing model fit and estimating daily survival were used for both. Especially among juveniles, we usually found evidence for transients, as even ones recently fledged move between colonies (Brown and Brown 1996).

Model fit was assessed by the Akaike Information Criterion (Burnham and Anderson 2002), corrected for sample size (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 2.0 or less are indistinguishable statistically. For each colony, we used the model with the lowest AIC_c for parameter estimation unless there were two or more models whose AIC_c values differed by ≤ 2.0 . In those cases, we used the “ AIC_c weight” for each model, a measure of a model’s relative probability of being the best model for the data compared to the others tested, provided by MARK to average the survival parameter estimates among those models. Because our models also specifically estimated daily recapture probability, any differences in likelihood of recatching birds at a site (due to colony size or daily differences in weather conditions or hours netted) were accounted for in estimating daily survival probability.

Before comparing the fit of the candidate set of models, we performed a goodness-of-fit test for each colony’s data set using program RELEASE (Burnham et al. 1987). This 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 lack of independence or some heterogeneity among observations after accounting for relevant covariates, and 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. Whenever we used $QAIC_c$, model selection and parameter estimation was based on models with the lowest $QAIC_c$ values as described above for AIC_c . This variance inflation adjustment allowed use of data sets that departed from the assumptions of the binomial distribution (usually due to the presence of transients). In such cases, after adjustment maximum likelihood can still provide optimal point estimators of model parameters (Wedderburn 1974; Burnham and Anderson 2002).

Although we often found time-dependence for the “first-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. This was

because (1) there was no a priori reason to expect survival probability to vary from day to day among resident birds, and (2) such heavily parameterized models (especially for sites with many capture occasions) would seldom reach convergence (despite our large sample sizes) in exploratory analyses. However, we did examine resident survival for three distinct time periods for each colony. These were designated as the “early” stage, defined as when over half of the colony was nest-building and egg-laying; “mid” stage, when over half of the colony was incubating; and “late” stage, when over half of the colony was feeding nestlings. These periods were designated separately for each colony, and different colonies active at the same time may have been at different stages depending on when they started and how synchronous they were. These three periods, however, corresponded broadly to the early, middle, and latter parts of the breeding season and allowed us to test for temporal variation within a season in daily survival. The exact nesting stage was not known for most of the adult birds captured, as relatively few were caught at their nests. However, the high degree of synchrony within cliff swallow colonies (Brown and Brown 1996) ensured that most individuals could be classified accurately based on the status of the colony as a whole.

After assessing the fit of the six models (Table 1) described above and generating a global estimate of residents’ survival for each colony without time-dependence, we added a model of structure similar to the best-fitting one but that had three different survival parameters for the “older age” class (i.e., for resident survival) that corresponded to the early, mid, and late stages. Each capture occasion was assigned to early, mid, or late based on its date and the colony’s stage at that time, and this model was fit to the data. When an interval between two capture occasions spanned two stages, that interval (and its associated survival parameter) was assigned to the stage of the second capture occasion. Not all colonies were sampled at all stages; some were sampled at only two stages, and for those sampled at only one, the colony’s global survival estimate derived from the original model fitting (Table 1) was assigned to the appropriate stage based on when the sampling was done. In comparing relative daily survival between the time periods, we used separate parameter estimates for the early, mid, and late periods at each colony (when available) even if the $QAIC_c$ suggested no difference between the periods (that is, when the model with no effect of time period was a better fit).

The effect of sex on daily survival probability was evaluated for a subset of 22 colonies. These were both fumigated and nonfumigated and represented those with the largest sample sizes (from 710 to 5,174 total birds marked per colony). Thus, if an effect of sex existed, these colonies gave us the greatest power to detect it. For each of these colonies, we fit a model equivalent to the best-fitting one in the original candidate set (Table 1), but with two groups (males and females). If the model with the group (sex) effect fit better, as determined from $QAIC_c$, we inferred a difference in survival among the sexes.

Although some colonies were sampled on back-to-back days, 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.

Once generating point-estimates of survival probabilities for all colonies, we found that the distribution was not normal, and no transformations successfully normalized it. We thus used non-parametric statistical tests for most of our analyses. In order to assess the separate effects of several independent variables on average survival probability per colony, we ranked all variables and used the rank-transformed values in an analysis of covariance (ANCOVA) (Montgomery 2001). Statistical analysis of the per-colony survival probabilities was done with SAS (SAS Institute 1990). Survival probabilities (± 1 SE) are reported.

Results

Effects of sex

For the subset of 22 colonies for which an effect of sex was examined, in only 2 (9.1%) was the model with separate survival probabilities for the sexes the best fit. In these two cases, the QAIC_c for the model with a sex effect was 2.51 and 3.39 less, respectively, than the next best-fitting candidate model without a sex effect. For these two colonies, daily survival probability for males was 0.982 (± 0.012) and 0.998 (± 0.002), respectively, compared to 0.995 (± 0.011) and 0.994 (± 0.002) for females. In the other cases, models without an effect of sex were either clearly the best fit, or models with and without a sex effect had QAIC_c values within 2.0 of each other, suggesting no strong difference between the groups (sexes). These 22 colonies, with the largest sample sizes, were ones where a detectable effect of sex on survival should have been most likely. Given the absence of a strong effect for most colonies, we conclude that daily survival within the season does not vary systematically by sex in cliff swallows, and the sexes were combined for all further analyses.

Effects of ectoparasitism

Across all colonies and years, the daily within-season survival probability per colony for adult cliff swallows was 0.985 (± 0.002) for fumigated sites ($n=36$) and 0.943 (± 0.005) for nonfumigated sites ($n=203$); the difference was significant (Wilcoxon test, $Z=5.73$, $P<0.0001$). Average colony size for the fumigated colonies (955.5 ± 111.4 nests) was significantly different from that for the non-fumigated ones (430.1 ± 38.4 nests; $Z=4.50$, $P<0.0001$). For this reason, and because of the separate effect of colony size on survival probability (below), we divided the colony sizes into two classes, and compared survival probabilities for birds in fumigated and nonfumigated colonies within each class. For colonies $\geq 1,000$ nests, daily within-season survival probability per colony was 0.992 (± 0.001) for fumigated sites ($n=18$) versus 0.956 (± 0.006) for nonfumigated sites ($n=19$); the difference was significant (Wilcoxon test, $Z=3.66$, $P<0.001$). For colonies 100–999 nests in size, daily within-season survival probability per colony was 0.978 (± 0.004) for fu-

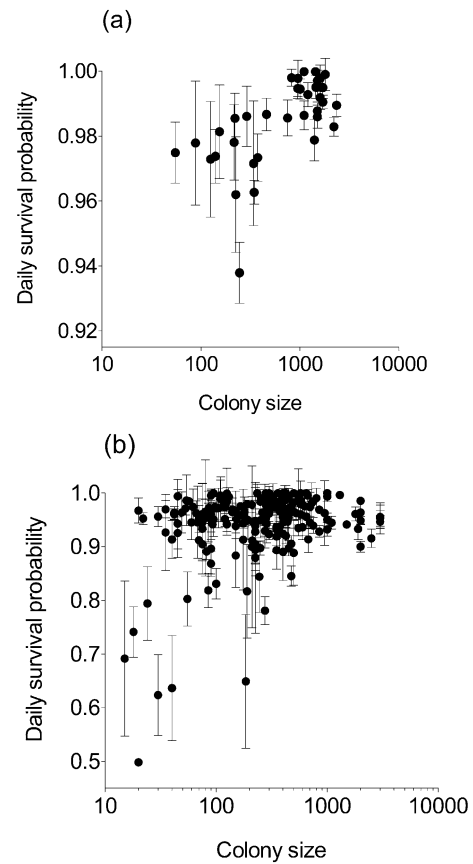


Fig. 1 Daily survival probability (\pm SE) for adult cliff swallows (*Petrochelidon pyrrhonota*) in relation to colony size (number of nests) for fumigated (parasite-free) colonies (a) and nonfumigated colonies (b). Daily survival probability increased significantly with colony size for both fumigated ($r_s=0.66$, $P<0.0001$, $n=36$ colonies) and nonfumigated colonies ($r_s=0.19$, $P=0.006$, $n=203$ colonies). Note different scales of Y-axes

migated sites ($n=16$) versus 0.953 (± 0.004) for nonfumigated sites ($n=136$); this difference was also significant ($Z=2.28$, $P=0.022$). Finer size-class categories were not possible given the number and size distribution of fumigated colonies (see Fig. 1a). Whether a colony was fumigated or not remained a significant effect on daily survival when the potential effects of other variables were controlled in an ANCOVA (Table 2).

Effects of colony size

Among fumigated colonies across all years, daily survival probability per colony for adult cliff swallows varied from 0.934 to 0.999 (Fig. 1a), and among nonfumigated colonies, from 0.498 to 0.999 (Fig. 1b). Daily survival probability increased significantly with colony size for both categories, although the pattern was stronger for fumigated sites (Fig. 1). Among nonfumigated colonies under natural conditions, most of the sites with low adult survival probability were relatively small colonies, <100 nests (Fig. 1b). Colony size remained a significant effect

Table 2 Analysis of covariance to detect effects of variables potentially affecting estimation of daily survival probability per colony for adult cliff swallows, 1983–2003. All colonies were combined for the analysis ($n=239$). The effect of colony size was nested within colony site

Variable	<i>F</i>	<i>df</i>	<i>P</i>
Fumigated or not	18.16	1	<0.0001
Year	1.15	19	0.31
Colony site	3.24	46	<0.0001
Colony size (site)	1.79	32	0.012
Sample size ^a	0.10	1	0.75
Span of days ^b	2.02	1	0.16
Number of capture occasions ^c	0.33	1	0.57
Capture method ^d	1.61	1	0.21

^a Number of adults marked per colony

^b Total number of days over which survival was estimated (first capture occasion to last) at a colony

^c Number of days on which adults were captured at a colony

^d Whether a colony site was netted using drop or set nets

Table 3 Spearman rank correlations (r_s) between daily survival probability of adult cliff swallows per colony and colony size for each year with $n \geq 8$ colonies sampled

Year	r_s	<i>P</i>	<i>n</i>
1988	−0.06	0.85	11
1989	−0.62	0.03	12
1990	0.03	0.94	11
1991	−0.07	0.80	14
1992	0.15	0.58	15
1993	0.00	0.99	17
1994	0.02	0.96	11
1995	0.51	0.03	18
1996	0.19	0.65	8
1997	0.53	0.12	10
1998	0.43	0.14	13
1999	0.24	0.48	11
2000	0.42	0.23	10
2001	0.51	0.16	9
2002	0.43	0.29	8
2003	0.22	0.37	19

on daily survival probability when the potential effects of other variables were controlled in an ANCOVA (Table 2). Colony site itself was a significant effect (Table 2), but colony size remained significant after controlling for covariation between site and size by nesting the effect of colony size within site (Table 2).

In case combining years might obscure patterns, we examined the effect of colony size on survival for each season individually, using only years with data for at least 8 colonies (Table 3). This was for nonfumigated sites only, because we had only 1–3 fumigated colonies per season. For the 16 years included, the correlation coefficient was positive in 12 cases, negative in 3, and zero in 1 (Table 3). Although most of these were not significant individually and some were very small (Table 3), the preponderance of years with positive correlations was significant (binomial test, $P=0.04$). All years with the stronger positive colony-size effects were since 1995; prior to that time, there was little evidence for even weak positive relationships, and in one year (1989) daily sur-

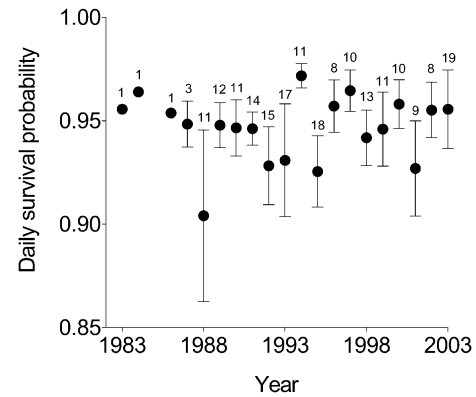


Fig. 2 Daily survival probability (\pm SE) per colony for adult cliff swallows in each year of the study. Numbers above error bars indicate number of colonies sampled each year. Only nonfumigated colonies are included

vival probability per colony declined significantly with colony size (Table 3).

Yearly effects

Average daily survival probability of adult cliff swallows varied among the 20 years for which we had data (Fig. 2). To investigate whether any of this variation reflected yearly differences in weather during the breeding season (which often varies in the study area and to which cliff swallows are sensitive; Brown and Brown 1998), we selected a subset of 13 years (Fig. 2) for which we had survival estimated for at least 10 colonies per year, potentially providing a relatively robust index of overall survival for those seasons. This analysis used only nonfumigated colonies. We compared average daily survival per colony with the average high temperature for June and the total precipitation for June in each year (Fig. 3). June was chosen because the cliff swallow's breeding season at our study site spans that entire month each year, regardless of whether the season is an early- or late-starting one, and because the period when survival was estimated included much of June at almost all sites. When all 13 years were included, average daily survival probability per colony did not vary significantly with either temperature or rainfall during the breeding season (Fig. 3). However, one season, 1988, was very unusual, being the fourth warmest June on record for the state of Nebraska (Brown and Brown 1996). When it was excluded from the correlation, average daily survival increased significantly with June high temperature and decreased almost significantly with total June precipitation (Fig. 3).

Within-season variation

For nonfumigated sites, the model with survival estimated separately for the early, mid, and late periods within the season was the best fit at 41 colonies, was not the best fit

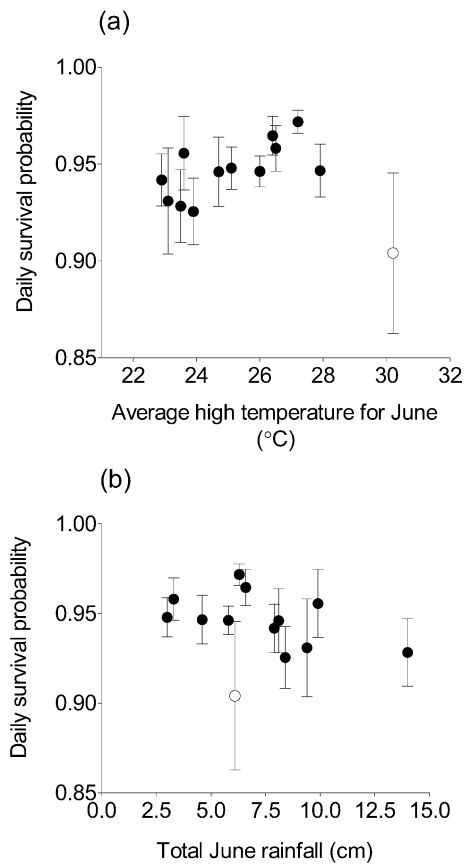


Fig. 3 Daily survival probability (\pm SE) per colony for adult cliff swallows in relation to the average June high temperature ($^{\circ}$ C) each year (a) and the total June precipitation (cm) each year (b) in the study area. *Open circle* denotes 1988, a climatologically anomalous year. Daily survival probability increased significantly with June high temperature when 1988 was excluded ($r_s=0.69$, $P=0.02$, $n=12$ years) but not when it was included ($r_s=0.33$, $P=0.27$, $n=13$). Daily survival probability tended to decrease with June rainfall when 1988 was excluded ($r_s=-0.55$, $P=0.07$, $n=12$ years) but not when it was included ($r_s=-0.38$, $P=0.19$, $n=13$). Only nonfumigated colonies were used

but was within 2.0 in AIC_c or $QAIC_c$ at 37 colonies, and clearly did not fit at 33 colonies (the AIC_c or $QAIC_c$ differing by >2.0 from the best-fitting model). At the remaining 92 nonfumigated colonies, survival was estimated only within a single period. Thus, 36.9% of nonfumigated colonies ($n=111$) showed within-year variation in daily adult survival probability, whereas 29.7% did not, and the evidence was equivocal at 33.3%. For fumigated sites, the model with period-dependent survival fit best at 16 colonies, was not the best fit but was within 2.0 in AIC_c or $QAIC_c$ at 8 colonies, and clearly did not fit at 10 colonies (AIC_c or $QAIC_c$ differing by >2.0 from the best-fitting model). Thus, 47.1% of fumigated colonies ($N=34$) showed within-year variation in daily adult survival probability, whereas 29.4% did not, with equivocal evidence for 23.5%. These proportions did not differ significantly between fumigated and nonfumigated colonies ($\chi^2_2=1.48$, $P=0.48$).

Using data for all colonies, the average daily survival probability per colony for adult cliff swallows at non-

fumigated sites was 0.900 (± 0.021) for the early period ($n=47$ colonies), 0.944 (± 0.007) for the mid period ($n=165$), and 0.937 (± 0.006) for the late period ($n=127$). The average daily survival probability per colony at fumigated sites was 0.990 (± 0.005) for the early period ($n=17$ colonies), 0.985 (± 0.004) for the mid period ($n=34$), and 0.978 (± 0.003) for the late period ($n=36$). Average survival per colony did not differ significantly among the three periods for nonfumigated colonies (Kruskal-Wallis ANOVA, $\chi^2_2=3.21$, $P=0.20$) but did differ significantly among the three periods for fumigated colonies ($\chi^2_2=13.9$, $P<0.001$). In case using all colonies might have biased our results by the inclusion of sites that had no survival estimates for particular time periods, we also analyzed only the colonies for which survival in all three time periods was estimated in a given season. For these, we found the same overall pattern as in the more global analysis: for nonfumigated sites ($n=23$), average daily survival per colony was 0.923 (± 0.025), 0.973 (± 0.006), and 0.918 (± 0.015) for the early, mid, and late periods, respectively; and for fumigated sites ($n=17$), 0.990 (± 0.005), 0.991 (± 0.003), and 0.975 (± 0.005) for the early, mid, and late periods, respectively.

For each time period across all colonies, daily survival per colony at fumigated sites was significantly different from that at nonfumigated sites in the same period (Wilcoxon tests, $P\leq 0.004$ for all). When divided into two colony-size classes to partly control for a colony-size effect, at colonies $\geq 1,000$ nests in size, average daily survival probability per colony during the early period was 0.866 (± 0.079) and 0.991 (± 0.005) for nonfumigated ($n=6$) and fumigated ($n=11$) sites, respectively; during the mid period, 0.963 (± 0.007) and 0.998 (± 0.001) for nonfumigated ($n=15$) and fumigated ($n=18$) sites, respectively; and during the late period, 0.911 (± 0.022) and 0.980 (± 0.005) for nonfumigated ($n=15$) and fumigated ($n=18$) sites, respectively. For all three periods, daily survival was significantly higher in fumigated colonies than in nonfumigated ones (Wilcoxon tests, $P<0.01$ for all). At colonies 100–999 nests in size, average daily survival probability per colony during the early period was 0.930 (± 0.019) and 0.988 (± 0.011) for nonfumigated ($n=33$) and fumigated ($n=6$) sites, respectively; during the mid period, 0.946 (± 0.009) and 0.972 (± 0.008) for nonfumigated ($n=118$) and fumigated ($n=14$) sites, respectively; and 0.943 (± 0.008) and 0.974 (± 0.004) for nonfumigated ($n=82$) and fumigated ($n=16$) sites, respectively. For colonies 100–999 nests in size, daily survival per colony did not differ significantly between fumigated and nonfumigated colonies in any of the three time periods (Wilcoxon tests, $P>0.09$ for all).

When the effect of colony size on daily survival probability was analyzed for each time period separately, we found similar patterns for nonfumigated (Fig. 4) and fumigated colonies (Fig. 5). For this we used all survival estimates, including sites that may have had only one time period represented. There was markedly more variation in survival probabilities during the early period for nonfumigated colonies, and this period in-

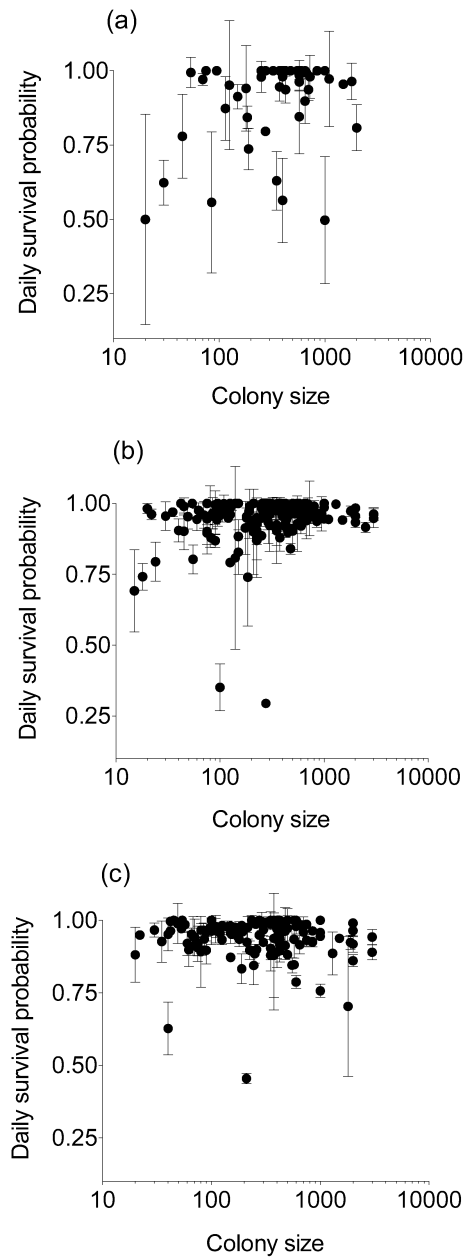


Fig. 4 Daily survival probability (\pm SE) for adult cliff swallows in relation to colony size (number of nests) for the periods of nest-building and egg-laying (early period; **a**), incubation (mid period; **b**), and feeding of nestlings (late period; **c**) at nonfumigated colonies. Daily survival probability did not vary significantly with colony size in the early period ($r_s=0.19$, $P=0.19$, $n=47$ colonies) or late period ($r_s=-0.02$, $P=0.85$, $n=127$) but increased significantly with colony size in the mid period ($r_s=0.18$, $P=0.02$, $n=165$)

cluded many of the sites with low survival (Fig. 4a). The effect of colony size was significant only for the mid period for both fumigated and nonfumigated sites (Figs. 4, 5) with the pattern during the mid period reflecting the overall one (Fig. 1) for both kinds of colonies. There was a suggestion of a decline in daily survival for adults in the largest colonies during the late period, especially at fumigated sites (Fig. 5c).

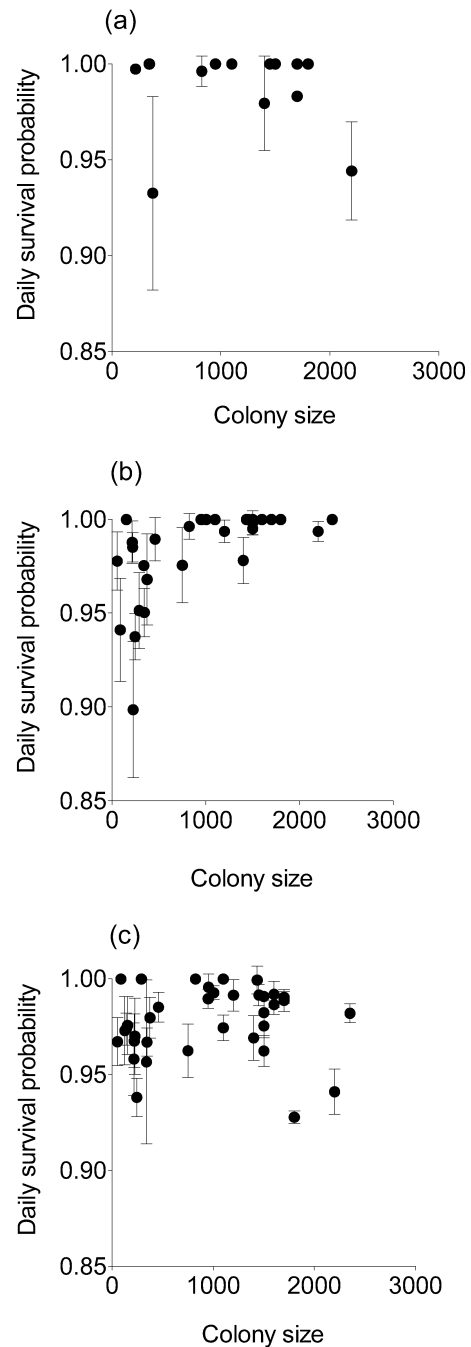


Fig. 5 Daily survival probability (\pm SE) for adult cliff swallows in relation to colony size (number of nests) for the periods of nest-building and egg-laying (early period; **a**), incubation (mid period; **b**), and feeding of nestlings (late period; **c**) at fumigated (parasite-free) colonies. Daily survival probability did not vary significantly with colony size in the early period ($r_s=0.02$, $P=0.94$, $n=17$ colonies) or late period ($r_s=0.13$, $P=0.46$, $n=36$) but increased significantly with colony size in the mid period ($r_s=0.66$, $P<0.0001$, $n=34$)

Daily survival of juveniles

The daily within-season survival probability for recently fledged juvenile cliff swallows per colony varied from

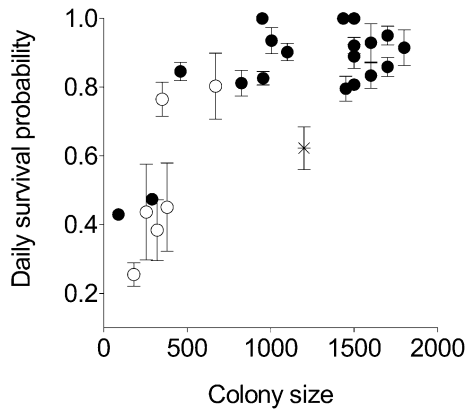


Fig. 6 Daily survival probability (\pm SE) per colony for recently fledged juvenile cliff swallows in relation to colony size for non-fumigated colonies (open circles), fumigated (parasite-free) colonies (closed circles), and a fumigated colony in 1996 (asterisk), a year in which extensive adult mortality had occurred (see text). For all colonies combined, daily survival probability increased significantly with colony size ($r_s=0.69$, $P<0.0001$, $n=26$ colonies). Daily survival probability also increased significantly with colony size for nonfumigated sites ($r_s=0.86$, $P=0.02$, $n=6$)

Table 4 Analysis of covariance to detect effects of variables potentially affecting estimation of daily survival probability per colony for recently fledged juvenile cliff swallows, 1983–2003. All colonies were combined for the analysis ($n=26$). The effect of colony size was nested within colony site

Variable	<i>F</i>	<i>df</i>	<i>P</i>
Fumigated or not	213.39	1	0.004
Year	29.66	12	0.033
Colony site	53.34	3	0.018
Colony size (site)	19.66	4	0.049
Sample size ^a	0.00	1	0.95
Span of days ^b	1.65	1	0.33
Number of capture occasions ^c	0.02	1	0.91

^a Number of juveniles marked per colony

^b Total number of days over which survival was estimated (first capture occasion to last) at a colony

^c Number of days on which juveniles were captured at a colony

0.255 to 0.999. The average daily survival probability per colony for nonfumigated colonies ($n=6$) was 0.516 (± 0.089), compared to 0.837 (± 0.035) for fumigated colonies ($n=20$). Survival at fumigated colonies was significantly different from that at nonfumigated colonies (Wilcoxon test, $Z=-3.07$, $P=0.002$). The average daily survival probability per colony for juveniles increased with colony size (Fig. 6). The small number of nonfumigated colonies for which we had data on juveniles limited our analysis, but the effect of colony size appeared stronger for juveniles (Fig. 6) among nonfumigated colonies (correlation coefficient much larger) than for adults (Fig. 1b). The one fumigated site with a daily survival probability much lower than that of other colonies of similar size was the single colony sampled for juveniles in 1996 (Fig. 6). That year was unusual in that a massive adult mortality event had occurred earlier that season (Brown and Brown 1998). The significant effect of colony size on daily survival probability remained after control-

ling for the effects of other variables, including colony site (Table 4). Sample size, span of time over which survival was estimated, and the number of sampling occasions all had no significant effect on average daily survival probability per colony (Table 4). Because juveniles were only present for a part of the nesting season (the late period), we did not attempt to analyze temporal variation in survival within a season, and our total sample sizes per year (especially for nonfumigated colonies) were too small to investigate yearly variation.

Discussion

This study is the first to estimate daily survival probabilities within the breeding season for birds occupying colonies of different sizes and exposed to varying levels of parasitism by hematophagous arthropods. Daily survival per colony over the range of colony sizes studied varied by a factor of 2 for breeding adults and by a factor of 4 for recently fledged juvenile cliff swallows. In the absence of ectoparasites, average daily survival increased by 4.4% for breeding adults and 62.2% for recently fledged juveniles. These effects could not be explained by differences in sampling effort, span of time over which survival was estimated, or sample size at the different colonies. Our results reveal a previously unknown cost of ectoparasitism in this species and underscore the importance of colony size in the evolutionary ecology of cliff swallows.

We should emphasize that even small apparent differences in daily survival probability can translate into potentially major effects on fitness. For example, assuming the same daily survival probability throughout the year and using the formula of Brownie et al. (1985, p. 208) to convert annual survival probability into mean lifespan, daily survival probabilities of 0.999 versus 0.998 result in a 1.37-year difference in mean lifespan. Probabilities of 0.999 versus 0.949 result in an even greater difference of 2.69 years in mean lifespan. Although these examples are oversimplifications because daily survival probability almost certainly varies at different times of the year (e.g., summer versus winter) and changes between years (and may not account for emigration; see below), they do illustrate the potential importance of even small variation in daily survival probability, especially for relatively short-lived songbirds such as cliff swallows.

As in virtually any study of survival in open populations, our results cannot distinguish mortality from permanent emigration. Although emigration within the nesting season is likely to be less than that occurring between seasons, cliff swallows that permanently left a colony site during the season would be treated as dead in our statistical estimation of survival. We addressed this in part by specifically testing for the presence of, and if necessary excluding, transient individuals in our analyses and thus deriving survival estimates only for resident birds in each colony (see Pradel et al. 1997). However, this still does not account for birds that may have been resident at a

colony for part of a season but emigrated from the site before the season ended. We know that this occurs occasionally, especially when a nest fails and owners abandon that colony completely (Brown and Brown 1996). Thus, our daily survival probabilities are underestimates to some degree. Yet they still provide relative indices of survival, so long as emigration does not co-vary with, for example, colony size. Because the probability of total nest failure is unrelated to colony size in cliff swallows (e.g., Brown and Brown 1987), emigration of residents (when it occurs) is unlikely to vary in ways that could bias our primary results or cause the observed effects on apparent survival.

Ectoparasitism and survival

The blood-sucking swallow bugs that infest cliff swallow nests have various negative effects on the birds, including reduced nestling survivorship and body condition, increased wing-feather asymmetry in juveniles, and the probable transmission of an alphavirus to individuals of all ages (Brown and Brown 1986, 1996, 2002; Brown et al. 2001). In addition, other ectoparasites, primarily fleas and lice, reduce annual (between-year) survival of adults (Brown et al. 1995). Because nest fumigation is effective primarily at eliminating the nest-based swallow bugs, the effects of ectoparasites shown in this paper are attributable mostly to the bugs. The reduction in daily survival probabilities for adults and juveniles in the presence of parasites (relative to fumigated colonies) illustrates a surprisingly strong short-term effect of ectoparasites on cliff swallows. This effect held when the comparison was done among parasitized and parasite-free colonies of similar size and during all three of the principal periods of the birds' nesting cycle (nest-building, incubation, and feeding of nestlings). Ectoparasitism apparently had a greater effect on survival of recently fledged juveniles than on adults.

How might the effects of parasites on survival be brought about? Although the precise ways that the alphavirus transmitted by swallow bugs, known as Buggy Creek virus, affects cliff swallows is unknown (Brown et al. 2001), the virus does infect them, as determined from serological antibody tests of adults. Any negative effect of the virus could be expressed in survival probability. Ecologically similar viruses are known to reduce survival in other birds (Nuttall 1997; Komar et al. 2003). It is also likely that bug infestations, because of their consequences for nestling growth and survival, may require adults to invest more in parental care as compensation (e.g., Fitze et al. 2004). An increased parental work load (e.g., more and/or longer foraging trips) may be reflected in adult survival through greater exposure to predation or increased energetic needs. Besides the direct physiological costs of being parasitized, such as lowered hemoglobin levels and elevated white blood cell counts (Chapman and George 1991), swallow bugs also cause increased levels of bilateral asymmetry in wing length of juveniles (Brown

and Brown 2002). Because the extent of bilateral symmetry is positively correlated with survival of adult cliff swallows when food is scarce (Brown and Brown 1998), possibly because high symmetry confers aerodynamic advantages during foraging, the higher asymmetry among heavily parasitized juveniles is probably costly in the period immediately after fledging when they are learning to forage for themselves and routinely undergo food deprivation.

Although we argued earlier that undetected emigration probably did not bias our results for adults, we suspect that the juvenile survival estimated in fumigated versus nonfumigated colonies may be one instance where within-season emigration did account for some of the difference between the groups being compared. Juvenile survival was estimated for the period immediately after fledging when juveniles are still coming and going to and from their natal colony site, often returning to their own nest in the company of their parents or entering other nests to steal food intended for smaller nestlings (Brown and Brown 1996). At highly infested colonies, both juveniles and their parents depart permanently almost immediately after fledging and do not return. Although juveniles doing this would be, statistically, transients in our models and not figure into our survival estimates (often unlikely to have even been banded), and we did not estimate juvenile survival at any large, highly infested colonies, it remains likely that in general recently fledged juveniles spend less time around the nests at nonfumigated sites, thereby avoiding more exposure to bugs in the nests. Consequently they would be less likely to be recaptured by us. How much this might have contributed to the observed difference between fumigated and nonfumigated colonies in juvenile survival is unknown.

Colony size and survival

Daily survival probability within the breeding season reflects many of the costs and benefits associated with colonial nesting. In cliff swallows, at least 26 different costs and benefits that vary to some degree with group size have been identified (Brown and Brown 1996). The most important benefit of coloniality in cliff swallows is increased success at food-finding. The swarming insects on which cliff swallows feed are spatiotemporally variable even over a single morning, and the birds often rely on information provided by other foragers to find the food sources (Brown 1986; Stoddard 1988; Brown et al. 1991; Brown and Brown 1996). Foraging efficiency increases with colony size, with birds not wasting as much time searching for swarms when many foragers are present. The net result may be that adult swallows in larger colonies are in better condition and/or that their young fledge in better condition, contributing to the increase in daily survival with colony size for both adults and juveniles. This may be especially important during times of food scarcity, such as periods of cool and rainy weather in which insect activity is reduced and cliff swallows have

trouble finding food. Such spells of bad weather occur regularly in most years at our study site (below), particularly during the first half of the nesting season (May through mid-June; Brown et al. 1991).

In addition, the better detection of avian and snake predators in larger cliff swallow colonies (Brown and Brown 1987, 1996) may contribute to increased survival of adults and juveniles at those sites. Increased avoidance of predators in larger colonies may be especially important for juveniles (e.g., Fig. 6). American kestrels and common grackles attack crèches of recently fledged juveniles that form near colonies. The very large number of juveniles present at the larger sites (up to 1,000 juveniles at times) probably confers dilution of personal risk and enhanced predator detection that both increase with colony size.

A third advantage of larger colonies is reduced rates of fighting for nest sites. Cliff swallows fight more in smaller colonies, probably because there are higher numbers of nonresidents searching for nesting sites, per capita, than in larger colonies. Fights can result in drowning or injury (Brown and Brown 1996).

However, the relatively constant daily survival probabilities across much of the colony-size range under natural conditions, especially for adults (Fig. 1b), suggest that there are other factors that affect daily survival in opposite ways, and in some cases these may represent costs of larger groups. Although overall vigilance and the detection of predators increase with cliff swallow colony size, avian and snake predators direct far more attacks at the larger colonies (Brown and Brown 1996). There is increased personal risk of being a victim, particularly for adults, in larger colonies. The negative effects of ectoparasitism are likely to vary with colony size. With more parasites in larger colonies (Brown and Brown 1986, 1996), parasite-related effects on survival (above) increase with colony size. Other costs of cliff swallow coloniality include the difficulty in locating one's own still-dependent offspring in crèches near the colony to feed them, having unrelated fledged juveniles steal food from one's own offspring while still in the nest, being entombed alive in one's own nest by a neighbor, and the depletion of food near the colony and resulting need to travel farther during foraging (Brown and Brown 1996). All of these are likely to negatively affect daily survival probabilities of adults and/or fledged juveniles, and their effects will be potentially greater in larger colonies.

The comparison of how daily survival varies with colony size in fumigated colonies (Fig. 1a) allows one to infer the relative effect of ectoparasitism on survival under natural conditions (Fig. 1b). In the absence of parasites that represent the most important cost of coloniality for cliff swallows, daily survival increased with colony size, and the effect was relatively strong, statistically (Fig. 1a). This suggests that the other costs of coloniality probably have relatively little impact, certainly not enough to depress survival in the larger groups. That we did not see as strong an effect of colony size in the presence of parasites (Fig. 1b) suggests that any given cliff swallow

colony size reflects a trade-off between the advantages and disadvantages of coloniality, and that ectoparasitism is likely the main disadvantage.

Phenotypic differences among birds in different colonies

Survival differences among cliff swallows in colonies of different sizes could also reflect the inherent quality of birds occupying the different sites. In some colonial species, for example, younger birds and ones in poorer condition settle in smaller colonies (Brown and Brown 2001). If this occurs in cliff swallows, age-dependent or condition-dependent survival could account for our results independent of any colony-size effects. However, cliff swallows apparently show genetically based preferences for certain colony sizes (Brown and Brown 2000), and there is no evidence that inferior individuals prefer one colony size over another. Younger birds, if anything, settle more often in larger colonies (Brown and Brown 1996). This would lead to more experienced individuals in smaller colonies and yield a pattern opposite that we observed if individuals' phenotypic characteristics were primary determinants of daily survival. It seems more likely that within-year survival in this species reflects the costs and benefits associated with the different group sizes. We acknowledge, however, that the return of many of the same individuals to colonies of similar size between years (Brown and Brown 2000) means that some marked birds were used in survival estimation at more than one site in different years. If individual quality affects survival in any way, this could make within-season survival estimates among colonies of similar size in different years more alike than might be the case if all birds were newly marked at each colony each year.

Temporal variation in survival

We detected between-year variation in daily survival probabilities of adult cliff swallows. The effects of colony size discussed above showed a peculiar pattern in which daily survival seemed to either vary inversely with colony size or showed no discernable pattern in the first half of the study (the 7 years prior to 1995), in contrast to the last 9 years in which the correlation between daily survival probability and colony size was positive (Table 3). Although most of the correlation coefficients were not statistically significant, probably because of the much smaller sample sizes within years, several of them were relatively large, and the preponderance of positive ones since 1995 was striking. This did not seem to be a sample-size effect, as sample sizes were roughly equivalent across years of the study (partly because we used only years with $n \geq 8$ for this analysis). While the reasons for the difference between 1988–1994 and 1995–2003 are not clear, it suggests that (1) in some years larger colonies do not confer a survival advantage for adults and nesting in them occasionally may even be costly, and (2) because the an-

nual variation apparently occurs on multiyear scales (seven consecutive years of one pattern, nine consecutive years of another), short-term or even moderate-term studies would not detect it.

The differences among years in average adult daily survival probability per colony appeared to generally correlate with climatic factors. Survival tended to be higher in warmer and drier years. Cliff swallows are sensitive to periods of cold, rainy weather in late spring that reduce availability of flying insects, and if spells of bad weather last for four or more consecutive days, extensive mortality can result (Brown and Brown 1998). Prolonged rain is especially bad, as the birds do not forage at all during rainy conditions. Even when major mortality events do not occur in a season, periodic short-lasting cold and rainy conditions require the birds to work harder to find food. Our analyses indicate that cool and wet years may take some toll on survival, and this is consistent with the argument above that daily survival reflects in large part an individual's foraging success.

The 1988 season, however, was an anomaly. This was an unusually warm year, among the hottest on record for Nebraska, and average daily survival probability that year was unusually low (and varied among colony sites more than in other years; Fig. 3). Although warm years are on average advantageous for adult survival, extremely warm conditions apparently are stressful. During that summer, for example, adult cliff swallows at many colonies seemed to have trouble finding the swarming insects that they typically feed their young and resorted to feeding on less preferred grasshoppers.

The generally positive effect of warm years on adult survival contrasts with that of juveniles, whose post-fledging survival (as measured to the next season) tends to be higher in cooler years (Brown and Brown 1999). This seems to be because swallow bug infestations are worse in warm years, and the bugs affect nestlings more than they do adult cliff swallows. In cooler years, nestlings survive better even though their parents may have more trouble finding food and may not survive as well.

The most unusual climatic event during the study occurred in 1996, when in late May a 6-day period of cold and rainy weather resulted in the starvation of thousands of cliff swallows in the study area (Brown and Brown 1998). Climate records showed that only two such events have occurred there in the last 130 years, and we estimated that the population was reduced by over 50%. This event was not explicitly included in any of our daily survival estimates for 1996, as all survival probabilities that year were estimated for birds after the event (that is, for survivors). For adults, average daily survival probability per colony that year, 0.957 (± 0.013), was not unusually low or high, as compared, for example, to survival probabilities of 0.925 (± 0.017) the year before and 0.965 (± 0.010) the year after. For juveniles, however, daily survival that year was unusually low (Fig. 6). The most likely explanation is that the surviving adults, following that period of intense stress, invested less in offspring that season, resulting in their young fledging in unusually poor

condition and being less likely to survive in the period immediately after fledging. There was no reason to believe that the single colony studied in 1996 was in any way anomalous, as the same site was also studied in all other years when juvenile survival there was much higher.

We had expected greater evidence for within-season variation in daily survival probability. Over the course of the approximately 8-week nesting season for any individual bird, cliff swallows engage in a predictable series of very different activities that potentially could affect daily survival differently. Upon arrival at colony sites, the birds immediately begin building or refurbishing their mud nests, requiring frequent trips to collect mud and in the process are exposed to predators at the mud holes such as common grackles. Nest-building requires substantial energy expenditure (Withers 1977) at a time when spells of bad weather that restrict foraging opportunities occur regularly in most years. Cliff swallows in California spent more time foraging during nest-building than at any other time (Withers 1977). After eggs are laid, daily activity is reduced, with members of a pair alternating between incubation and foraging throughout most of each day. Once eggs hatch, both parents continually forage to collect food for their young, another period of heavy energy expenditure (Withers 1977). Yet we found that adults' average daily survival probability, combined across all colonies, was not significantly different among these three distinct phases of the annual cycle under natural (nonfumigated) conditions.

Perhaps surprisingly, gender had no consistent effect on survival across colonies, suggesting, for example, that producing eggs is not so costly for females that it lowers their survivorship relative to males, or that males' prospecting for and defense of nest sites early in the year before females settle with them has little long-term survival cost. Our results suggest that the positive and negative effects on daily survival discussed earlier either are constant throughout the breeding cycle and for the two sexes, on average, or that different factors acting at different times of the season have the same net effect on daily survival. Average daily survival at fumigated colonies, in contrast, varied significantly among the three periods, being lowest during the time when birds were feeding nestlings. While one should probably not make too much of the difference between fumigated and non-fumigated colonies in this case, it does suggest that the presence of parasites and their effects may obscure any temporal variation in daily survival under natural conditions.

The effect of colony size on daily survival was most apparent during the middle part of the nesting season (incubation) for both nonfumigated and fumigated colonies (Figs. 4, 5). Why this pattern was not stronger during the other times of the nesting cycle is unclear, although the early (nest-building and egg-laying) period had less data available. Thus, any conclusions for the early period should be made cautiously, especially for fumigated colonies (Fig. 5). We suspect that the greater variation among nonfumigated colonies in daily survival

probability during the early period, and the low survival probabilities registered during that time (Fig. 4), reflect in some cases predation by great horned owls. Owls tend to kill many adult swallows during nocturnal raids, but their attacks are unpredictable and do not occur every year. Owl predation generally happens early in the cliff swallow's nesting season, probably reflecting when the early-nesting owls themselves have young to feed.

Fitness and the evolution of coloniality

Daily survival probability provides an integrative measure of the many different costs and benefits associated with group size in cliff swallows. It thus provides an index of the average fitness that can be expected for birds in a given colony size. The survival results reported here are consistent with earlier evidence based mostly on reproductive success (Brown and Brown 1996) that individuals in colonies of different sizes often have similar fitness although they experience very different costs and benefits. While we did find an increase in daily survival with colony size under natural conditions, this was driven mostly by all the sites with low survival being relatively small ones. There were many small colonies that had daily adult survival probabilities as high as the largest colonies, often near 0.999. This pattern is also similar to that seen for reproductive success, in which between-site variance is much greater for small colonies even though birds in some small colonies can do quite well. Nesting in small colonies appears riskier, on average, than in large colonies.

The much stronger positive effect of colony size on daily survival of adult cliff swallows in parasite-free colonies establishes ectoparasitism as a major cost of coloniality that influences survival probability. The difference in patterns between fumigated and nonfumigated colonies (Fig. 1) alone suggests that colony size represents a trade-off between the costs of (especially) ectoparasitism and the advantages of large groups. The foraging benefits of large colonies are apparently partly balanced by the greater costs of ectoparasitism there, and these survival results provide the best evidence yet consistent with this trade-off.

In conclusion, there was a detectable advantage for adult cliff swallows that used large colonies, if anything just in avoiding the risk associated with small colonies, and there was an apparently substantial advantage for juveniles in the period just after fledging. Despite the trade-offs in the costs and benefits of different colony sizes, cliff swallows nesting in large colonies can expect slightly better odds of surviving the nesting season and thus potentially of having higher lifetime reproductive success. This represents a previously unknown benefit of colonial nesting and suggests a net benefit to large colonies in cliff swallows.

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