

Costs and benefits of late nesting in cliff swallows

Charles R. Brown · Erin A. Roche · Valerie A. O'Brien

Received: 26 March 2014 / Accepted: 15 September 2014 / Published online: 30 September 2014
© Springer-Verlag Berlin Heidelberg 2014

Abstract Many organisms of temperate latitudes exhibit declines in reproductive success as the breeding season advances. Experiments can delay the onset of reproduction for early breeders to investigate the consequences of late nesting, but it is rarely possible to observe a distinct second round of nesting in species that normally nest only once. The colonial cliff swallow (*Petrochelidon pyrrhonota*) is a migratory songbird that has a relatively short breeding season in the western Great Plains, USA, with birds rarely nesting late in the summer. Previous work suggested that ectoparasitism is a primary reason why reproductive success in this species declines over the summer. At colony sites where nests were fumigated to remove ectoparasitic swallow bugs (*Oeciacus vicarius*), cliff swallows frequently undertook a distinct round of late nesting after previously fledging young that year. Mark-recapture revealed that late-nesting pairs at these colonies produced fewer offspring that survived to the next breeding season, and that survival of late-nesting adults was lower during the next year, relative to pairs nesting earlier in the season. These reproductive costs applied in the absence of ectoparasites

and likely reflect other environmental costs of late nesting such as seasonal declines in food availability or a delayed start of fall migration. Despite the costs, the estimated fitness for perennial early-and-late nesters in the absence of ectoparasites was equivalent to that of birds that nested only early in the season. The collective disadvantages of late nesting likely constrain most cliff swallows to raising a single brood in the middle latitudes of North America.

Keywords Cliff swallow · Cost of reproduction · Ectoparasites · Fecundity · Life history · *Petrochelidon pyrrhonota* · Reproductive phenology · Survival · Time of breeding

Introduction

Studies in a variety of taxa have shown that annual reproductive success decreases as the breeding season progresses (Klomp 1970; Perrins 1970; Hochachka 1990; Rowe et al. 1994; Verhulst et al. 1995; Lapolla and Buckley 2005). The causes of this pattern have been extensively investigated (Price et al. 1988; Verhulst and Nilsson 2008) and have been hypothesized to involve either environmental conditions conducive to brood rearing (e.g., food availability) deteriorating over the summer, or lower-quality individuals nesting later and being unsuccessful because they are of lower quality (Brinkhof et al. 1997; Svensson 1997; Hansson et al. 2000; Wardrop and Ydenberg 2003).

Species in which individuals nest two or more times within a season offer opportunities to examine how changing environmental conditions potentially affect reproduction while controlling for the effect of individual quality (Verhulst et al. 1995; Verboven and Verhulst 1996; Husby et al. 2009). This approach is feasible when

Communicated by Oliver P. Love.

C. R. Brown (✉) · E. A. Roche · V. A. O'Brien
Department of Biological Sciences, University of Tulsa, 800 S.
Tucker Drive, Tulsa, OK 74104, USA
e-mail: charles-brown@utulsa.edu

E. A. Roche
USGS Northern Prairie Wildlife Research Center, Jamestown,
ND 58401, USA

V. A. O'Brien
Division of Science and Mathematics, Tulsa Community
College–Metro Campus, 909 S. Boston Avenue, Tulsa, OK
74119, USA

double-brooding is common, but at least among birds, there is extensive variation in the propensity to nest twice and many species rarely double-brood (Brown 1978; Nolan 1978; Geupel and DeSante 1990; Nagy and Holmes 2005; Mahony et al. 2001; Monroe et al. 2008; Jacobs et al. 2013). In these species, experimental manipulations have most often been done by delaying the reproductive attempts of individuals (usually by removing clutches) to examine how they perform later in the season (Verhulst and Nilsson 2008), while the opposite—forcing early nesters which have raised offspring to nest again later in the same year—has rarely been possible. Delaying first nesting by removing clutches only works within the seasonal window of time when single-brood reproduction naturally occurs. In contrast, forcing double broods greatly expands the length of the season over which reproductive success can be measured and can more feasibly investigate late-season environmental factors that may constrain breeding-season length.

In this study, we take advantage of a situation in which a normally single-brooded species, the colonially nesting cliff swallow (*Petrochelidon pyrrhonota*), nested much later in the season than is typical. Upon our removal of blood-feeding ectoparasites that affect these birds in a number of deleterious ways, cliff swallows apparently responded by undertaking a distinct second round of nesting at colony sites where many of the same individuals had earlier that season fledged offspring. That the birds would be sensitive to ectoparasite presence is not surprising. Ectoparasites often exert strong selective pressure on their avian hosts (Møller et al. 1990, 2001; Loye and Zuk 1991; Richner and Heeb 1995; Clayton and Moore 1997) and in a few species are known to influence the incidence or success of the hosts' late broods (Møller 1990; de Lope et al. 1993). An earlier study suggested that increasing numbers of ectoparasites during the summer could be a primary reason why reproductive success in cliff swallows declines seasonally among (single-brooded) birds in un-manipulated, natural conditions (Brown and Brown 1999).

Late nesting at fumigated colony sites afforded us the opportunity to observe the fecundity- and survival-related costs and benefits associated with late nesting among birds that might not otherwise have nested late, and at the same time to examine the contribution of ectoparasitism and other environmental factors to the seasonal decline in fitness of cliff swallows. We measured offspring fledging success, first-year survival of offspring, and subsequent annual survival of breeders for birds nesting in the two distinct times of the season (early and late). If ectoparasitism is the primary environmental constraint against late nesting, its removal should lead to late-nesting, double-brooding birds having higher annual fitness than those which nest only early in the season. We use the results to gain insight into how ectoparasites and other date-related costs of

reproduction potentially contribute to the seasonal decline in reproductive success in this species.

Materials and methods

Study site

We have studied cliff swallows since 1982 in the western Great Plains, USA, centered near the Cedar Point Biological Station (41°13'N, 101°39'W) in Keith County, southwestern Nebraska, along the North and South Platte rivers and including portions of Deuel, Garden, Lincoln, and Morrill counties (Brown and Brown 1996). Cliff swallows construct gourd-shaped mud nests, often in dense, synchronously breeding colonies. In our study area the birds nest mostly on the sides of bridges, in box-shaped road culverts, or underneath overhangs on the sides of cliffs (Brown et al. 2013). Colony size varies widely; in our study area it ranges from two to 6,000 nests (mean \pm SE, 404 \pm 13, $n = 2,318$ colonies), with some birds nesting solitarily. The typical phenology (in the absence of late nesting) is for cliff swallows to first arrive in southwestern Nebraska in mid-to late April, for most birds to have initiated egg laying by early June, and for nestlings to have mostly fledged by mid-July. Cliff swallows spend the winter in northeastern Argentina, Uruguay, and southwestern Brazil (Brown and Brown 1995), although the wintering range of our specific population is unknown.

Fumigation

The principal cliff swallow ectoparasite is the hematophagous swallow bug (Hemiptera: Cimicidae: *Oeciacus vicarius*), and bugs can have severe effects on nestling swallow growth and survival (Brown and Brown 1986, 1996, 2004b; Chapman and George 1991). Swallow bugs were removed from colonies by lightly misting the outside of all cliff swallow nests and adjacent nesting substrate with a dilute solution of the insecticide Dibrom. This chemical works largely as a contact pesticide, although we use the term “fumigation” to describe parasite removal. Nests were sprayed at 7- to 14-day intervals throughout the nesting season, typically beginning early in the season after birds had initially settled at sites. Dibrom is highly effective against swallow bugs; further details on fumigation procedures are given in Brown and Brown (1986, 1996, 2004a).

Breeding cliff swallows often responded to the removal of parasites by initiating second clutches at fumigated colonies, usually doing so 5–10 days after the nestlings from their first brood fledged. This led to a distinct second round of nesting and a breeding season that extended from mid-April to mid-August at some colony sites.

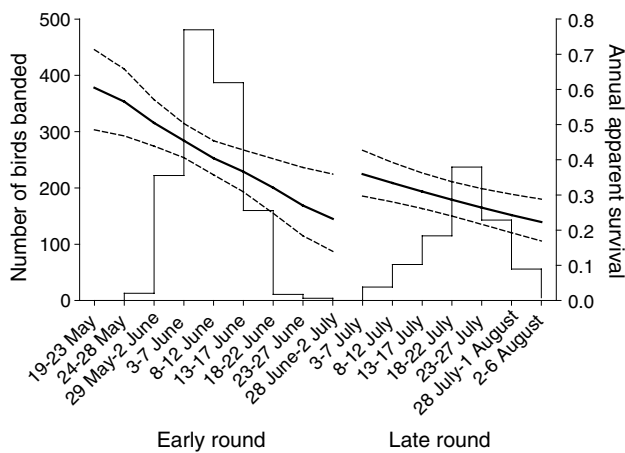


Fig. 1 Sample size (no. of 10- to 14-day-old nestlings banded) by date and associated first-year annual survival for cliff swallows hatched during the early and late rounds of nesting at two fumigated colonies during 2008. *Solid lines* represent survival probabilities and *dashed lines* the associated 95 % confidence intervals as generated from the top model (model 1; Table 1) and solved at the median banding date for each binned interval along the x-axis

Mark-recapture

This study was done at two colony sites, Whitetail and Junkyard, at which fumigation of all nests began in 1985 and 1998, respectively, and continued each year thereafter. Late nesting activity occurred at both sites in all years that they were fumigated, except for 5 years in which early nesting was delayed by cold weather and no late nesting happened anywhere. In 2008 we undertook a detailed study of Whitetail and Junkyard to estimate the annual apparent survival of nestlings hatched in first and second rounds and (at Junkyard) adults nesting at those times. These two sites were selected because both the early and late rounds of nesting at each site that year contained enough birds to achieve reasonable sample sizes for mark-recapture.

Nestlings were removed from their nests at 10–14 days of age, banded with United States Geological Survey numbered leg bands, and brood size recorded. Because all nestlings were at the same approximate age when banded, banding date is a relative index of hatching time. We banded 1,251 nestlings during the early round of nesting at the two colonies in 2008, with banding dates ranging from 10 June to 2 July and corresponding hatching dates from approximately 25 May to 23 June, and 644 nestlings during the late round of nesting, with banding dates ranging from 18 July to 14 August and corresponding hatching dates from approximately 8 July to 5 August (Fig. 1). Except for a few nests in which nestlings were inaccessible because of nest geometry, all nests with young in the late round were monitored and the nestlings there banded. In the early round, nests were too numerous to band all nestlings,

so we randomly selected nests in which to band nestlings in proportion to the number of active nests available at a given time. We also recorded the presence of runt nestlings in a brood, defined as a single bird that was an estimated ≥ 5 days earlier in development than the remaining brood members and in most cases obviously malnourished.

At Junkyard in 2008, we mist-netted adult cliff swallows at the colony site in both the early and late rounds of nesting to estimate subsequent survival of birds breeding at different times. Although netting was done at Junkyard on 18 days during 2008, we used only birds from the first four capture occasions (24 May, 1, 6, and 9 June) to represent a sample of early nesters, and used all birds caught during the late round of nesting (on 21, 23, 25, and 30 July) as our sample of late nesters. We confined the early-round sample to the time before 10 June to maximize the likelihood that birds designated as early nesters were among the first birds to have arrived in the study area and to have initiated nesting at the colony that year. Whitetail was not used for the adult analysis, as we did not sample there frequently enough during the late round to have three or more capture occasions.

Birds were always caught at the colony (culvert) entrance and well away from nests, meaning we could not assign adult owners to specific nests. Not all of the adults caught during the early and late rounds of nesting were residents of the colony. Junkyard, like other cliff swallow colony sites, attracted transient swallows that passed through each day (Brown and Brown 2004a; Brown et al. 2007; Roche et al. 2013). Because most of the transients were unbanded when first caught (and often never seen again), we investigated the potential effect of transients in the analyses by distinguishing birds first banded in 2008 from those (older) birds first banded in an earlier year (see below).

Mark-recapture efforts through mist-netting (Brown and Brown 2004b; Roche et al. 2013) continued in the study area from 2009 to 2011, affording opportunities to recapture nestlings and adults from the two focal colonies of 2008. We netted at both Whitetail and Junkyard each year, plus at an additional 21, 24, and 21 colony sites in our main study area in 2009–2011, respectively. Capture histories, beginning in 2008, were constructed for all nestlings and adults from each round of nesting, indicating whether an individual was subsequently encountered somewhere in the study area through 2011.

Statistical analysis of birds banded as nestlings

We used the recapture histories to build Cormack-Jolly-Seber models in program MARK (White and Burnham 1999) to estimate the first-year (FY) and after-first-year (AFY) apparent survival of two groups (g) of cliff swallows: those hatched in the early round of nesting and those in the late round. We built models for detection probability

Table 1 Set of models used in a Cormack-Jolly-Seber analysis of the influence of early- and late-round nesting on annual first-year (FY) and after-first-year (AFY) apparent survival (ϕ) of cliff swallows banded as nestlings

Model	ϕ	ΔAIC_c^a	w_i	k	Deviance	Description
1 ^a	$g + FY + AFY + g \times HATCHDT \times FY$	0.00	0.79	7	3,668.15	Survival of both ages varied by round of nesting and first-year survival varied by actual hatching date separately by round
2	$g + FY + AFY + HATCHDT \times FY$	3.19	0.16	6	3,673.35	Same as 1 except the effect of hatching date was modeled the same across both rounds
3	$g + FY + AFY$	6.89	0.03	5	3,679.07	Same as 1 except no effect of hatching date
4	$g \times FY + g \times AFY$	8.36	0.02	6	3,678.52	Survival varied by all age class and round combinations
5	$g + FY + AFY + BRDSZ \times FY$	8.60	0.01	6	3,678.77	Same as 3 except the effect of brood size was modeled the same across both rounds
6	$g \times FY + AFY$	9.55	0.01	5	3,681.72	Same as 3 except survival of the first age class varied only by round; after-first-year survival did not vary by round
7	$FY + AFY$	36.10	0.00	4	3,710.24	Same as 3 except no effect of round of nesting on survival of either age class

In all cases, detection probability (p) was parameterized as $[p(\text{age})]$

AIC_c corrected Akaike information criterion; g inclusion of early- or late-round group effects; FY , AFY age effects; $HATCHDT$ linear covariate for actual hatch date; $BRDSZ$ covariate for brood size; $+$ additive effects; \times interaction; w_i model weight; k no. of parameters. The change in AIC_c (ΔAIC_c) is that relative to the top model

^a $AIC_c = 3,682.19$

(p), ranked models using Akaike's information criterion values (AIC_c), and used the top-supported and most simplified parameterization for detection probability when constructing models for apparent survival (Lebreton et al. 1992). We assessed the goodness-of-fit of the fully parameterized model using the median \hat{c} -test, but found no evidence for over-dispersion ($\hat{c} = 1.01$) and thus did not correct AIC_c values for over-dispersion. The effective sample size was 2,514.

We assumed detection probabilities for birds marked as nestlings could be parameterized with two age classes (where p_1 = detection in the first year recaptured and p_{2+} = detection in the second or later recapture year). We assessed the fit of two parameterizations of detection probability where detection varied by: (1) two age classes and round of nesting [$p(\text{age} \times g)$], and (2) two age classes but no effect of round of nesting [$p(\text{age})$].

Models for apparent survival used two age classes and were ranked by AIC_c score (Table 1). We investigated an effect of natal brood size at banding by retaining this covariate in the top model if it resulted in a lower AIC_c score. Although we were interested primarily in whether the group of birds hatched during the early round of nesting differed from those hatched in the late round, we also tested whether a hatching date-related trend occurred within each of these rounds. We did this by building models for apparent survival that included a group-specific effect of actual nestling hatching date, modeled as a linear individual covariate ($HATCHDT$). Sex was not investigated, because sex cannot be determined for birds banded as nestlings.

Statistical analysis of adult breeders

Mark-recapture studies have been carried out in our study area since 1982, and provided information on whether the adults caught at Junkyard in 2008 had been captured in a previous year. This allowed us to correct, if necessary, for the presence of transient individuals during each round of nesting. We included eight groups (g) in this analysis based on whether: (1) a cliff swallow was caught during the early or late round of nesting, (2) a bird was male or female, and (3) a bird had been banded as an adult in a previous year (see Table 2 for groups and sample sizes). We assessed the goodness-of-fit of the fully parameterized model using the median \hat{c} -test ($\hat{c} = 1.29$) and used quasi- AIC_c values ($QAIC_c$) to rank models. The effective sample size was 2,613.

As all cliff swallows included in the analysis of breeders were adults older than 1 year of age, we had little reason to expect strong age-related differences in detection probabilities over the relatively short time frame we were studying this cohort. However, previous analyses of birds caught as adults have suggested sex-specific differences in detection probability and that detection probability can vary annually (Roche et al. 2013). Thus we built and compared models in which detection probability was parameterized as: (1) variable by year but not by group [$p(t)$], (2) variable by sex [$p(\text{sex})$], and (3) variable by year and sex [$p(\text{sex} + t)$].

Using the top model for detection probability, we built models to explore differences in cliff swallow apparent survival associated with whether a bird was caught during the early or late round of nesting during the 2008 breeding

Table 2 Sample sizes (no. of birds; *n*) in two Cormack-Jolly-Seber mark-recapture analyses of cliff swallows in early and late rounds of nesting in 2008

Analysis	Group	<i>n</i>
First-year survival (birds banded as nestlings)	Early round	1,251
	Late round	644
After-first-year survival (breeders banded as adults)	Early-round male, previously banded	367
	Early-round female, previously banded	366
	Early-round male, not previously banded	363
	Early-round female, not previously banded	293
	Late-round male, previously banded	68
	Late-round female, previously banded	54
	Late-round male, not previously banded	250
	Late-round female, not previously banded	186

Table 3 Set of models used in a Cormack-Jolly-Seber analysis of the influence of early- and late-round nesting on annual survival (ϕ) during the first year after breeding (FY) that adult cliff swallows were caught and during later years (AFY)

Model	ϕ	ΔQAICc	w_i	k	Qdeviance	Description
1 ^a	RN \times FY + BANDS \times SEX \times FY + SEX \times AFY	0.00	0.48	7	49.46	Survival varied by round of nesting in the first year but not in years beyond. The effect of round was consistent across sex and previous band status
2	RN + BANDS + SEX \times FY + SEX \times AFY	1.14	0.27	7	50.60	Same as 1 except round of nesting and previous band status had the same effect on sex-specific survival in the first and after first year
3	BANDS \times SEX \times RN \times FY + SEX \times AFY	2.13	0.17	8	49.57	Survival varied by round of nesting in the first year but not in years beyond. The effect of round was different for combinations of sex and previous band status
4	BANDS \times SEX \times FY + SEX \times AFY	4.05	0.06	6	55.52	Same as 1 except survival did not vary by round of nesting
5	BANDS \times SEX \times RN \times FY + RN \times SEX \times AFY	7.45	0.01	14	42.79	Survival varied by all group combinations except survival from 2008 to 2009 was based on whether a bird was previously banded in 2008
6	$g \times \text{FY} + g \times \text{AFY}$	15.77	0.01	22	34.88	Survival varied by all group and age combinations

In all cases, p was parameterized as $[p(\text{SEX})]$

g inclusion of all groups (Table 2); *RN* nesting group (early- or late-round) effects, *FY* or *AFY* year when survival estimated, *BANDS* bird banded in a year previous to 2008 (categorical), *SEX* sex (categorical); for other abbreviations, see Table 1. The change in QAICc (ΔQAICc) is relative to the top model

^a QAIC_c = 3,531.35

season (Table 3). We considered models with two “age classes” representing survival in the first year (FY) immediately following the 2008 nesting event and in all years after the first year (AFY).

Estimating fitness

Hypothetical average fitness for birds adopting either early-round nesting or an early-and-late-nesting strategy was estimated from brood sizes, first-year survival, and annual breeder survival by multiplying average brood sizes by first-year survival probability to determine annual recruitment. Annual recruitment was then summed over a breeder’s life based on its own annual survival and resulting

estimates of how long a breeder could expect to live, yielding total lifetime reproductive success. SEs of the sums or products of these calculations were derived using the δ -method (Powell 2007), and mean life span was calculated from annual survival probabilities using the formula in Brownie et al. (1985: 208).

Results

Survival of nestlings

In 2008, the mean (\pm SE) number of nestlings surviving to banding age was 3.23 (\pm 0.045) for early-round nests

($n = 397$) at Whitetail and Junkyard, and $2.54 (\pm 0.049)$ for late-round nests [$n = 264$; colonies combined because Whitetail did not differ from Junkyard (Wilcoxon tests, $p > 0.05$) in either round]. The number of nestlings surviving was significantly greater in early-round nests than in late-round nests (Wilcoxon test, $Z = -9.59$, $p < 0.0001$). This difference was brought about in part because of far more broods of four to six nestlings in the early round (42.1 %) than in the late (8.3 %) round. Runt nestlings were significantly more likely ($\chi^2_1 = 19.4$, $p < 0.0001$) in the late round: 20.4 % of all nests in the late round had a runt, vs. 8.6 % in the early round, including in 63.6 % of broods of four to six nestlings in the late round ($n = 22$), vs. 13.2 % of broods of four to six nestlings in the early round ($n = 167$).

The first-year and after-first-year apparent survival of cliff swallows hatched during the early round of nesting in 2008 at Junkyard and Whitetail was different from those of birds hatched in the late round of nesting (model 3 vs. 7; Table 1). First-year survival probability (\pm SE) of nestlings from the early round was $0.428 (\pm 0.043)$ vs. $0.298 (\pm 0.044)$ for those hatched during the late round. The magnitude of the effect on survival of being hatched in the early round [$\beta_{\text{Early}} = 0.57$; 95 % confidence interval (CI), 0.37 – 0.77] was the same for both the first year and subsequent (after-first) years (model 3 vs. 4; Table 1). Survival was higher in the subsequent years than during the first year for birds hatched in the early round (0.602 ± 0.09) and for those hatched in the late round (0.461 ± 0.096), but there was no difference between rounds in survival beyond the first year (95 % CI overlapped).

We found no support for an effect of brood size on first-year survival for birds hatched in either the early or late rounds of nesting (model 3 vs. 5; Table 1). However, we did find evidence for an effect of actual hatching date on first-year apparent survival (models 1–2; Table 1). In both the early and late rounds of nesting, first-year survival decreased as hatching dates became later (model 1 vs. 2; Table 1), with the magnitude of this effect more pronounced for birds hatched in the early round than for those hatched in the late round (Fig. 1). Depending on hatching date, first-year survival estimates ranged from 0.60 to 0.23 for chicks hatched during the early round and from 0.36 to 0.22 for chicks hatched during the late round (Fig. 1).

Survival of breeders

Although both sex and whether a bird had been banded in an earlier year (BANDS) were both included in the top model for breeding adults (model 1; Table 3), their β -estimates overlapped zero ($\beta_{\text{sex}} = 0.13$, 95 % CI -0.20 to 0.46 ; $\beta_{\text{BANDS}} = 0.24$, 95 % CI -0.13 to 0.61). This indicates that survival of males and females did not differ

strongly in this data set and that any presence of transients had little effect on survival estimates. Thus, we do not present results for breeders' survival divided by sex or previous band status.

Cliff swallows caught at Junkyard during the early round of nesting in 2008 were more likely to survive the subsequent year (2008–2009) than were those birds caught during the late round of nesting (Table 3). The annual apparent survival probability (\pm SE) of breeders in the late round, $0.481 (\pm 0.043)$, was approximately 22 % less than that of birds from the early round, $0.621 (\pm 0.039)$. However, we found little evidence to suggest that there were any differences in survival beyond that first year (model 1 vs. 2; Table 3). Annual survival probability for birds from both rounds beyond summer 2009 was $0.635 (\pm 0.024)$, similar to that of birds from the first round of 2008.

Estimated average fitness

Birds that nested in both the early and late rounds increased their annual reproductive success by about 55 % (~ 0.75 young) on average relative to early-round-only birds, as measured by offspring recruitment to the next year (Table 4). Perennial early-and-late nesters had a lifetime production about 20 % greater (0.86 young) than perennial early-round-only nesters (Table 4). Uncertainty in these estimates was high, owing to the fact that the estimates were derived from multiple mean values, each with its own error. The 95 % CI for these estimates, as inferred from the SEs (Table 4), overlapped, so the difference between the two groups was not statistically significant.

Discussion

Costs of late nesting

We found evidence that late nesting in cliff swallows had associated costs even in the absence of ectoparasites. Young raised during the late round of nesting at the fumigated colonies had lower probabilities of surviving to the next season than did birds raised during the early round of nesting, as determined by mark-recapture over the subsequent 3 years. A prior study of this population had identified ectoparasitism as a principal cause of the seasonal decline in reproductive success, largely because birds in non-fumigated sites exhibited the decline, whereas cliff swallows in fumigated sites did not (Brown and Brown 1999). This was interpreted to be because populations of swallow bugs increase over the summer, and their effects are worse on later nests (Brown and Brown 1996). A similar result was found for the congeneric fairy martin (*Petrochelidon ariel*), in which date negatively affected reproductive success

Table 4 Hypothetical fitness, as measured by total lifetime reproductive success, and methods of estimation for cliff swallows raising only early broods vs. those raising both early and late broods in southwestern Nebraska

Parameter	Early brood only	Early and late broods
Brood size in year _t (no. of nestlings)	3.23 _(0.045)	2.54 _(0.049)
First-year survival probability	0.428 _(0.044)	0.298 _(0.046)
Recruitment to year _{t+1} (no. of birds)	3.23 _(0.045) × 0.428 _(0.044) = 1.38 _(0.14)	1.38 _(0.14) + [2.54 _(0.049) × 0.298 _(0.046)] = 2.14 _(0.19)
Breeders' annual survival probability	0.621 _(0.076)	0.481 _(0.086)
Additional years lived as breeder	1/[−log(0.621 _(0.076))] = 2.1 _(0.54)	1/[−log(0.481 _(0.086))] = 1.4 _(0.33)
Subsequent lifetime production (no. of offspring) ^a	2.1 _(0.54) × 1.38 _(0.14) = 2.90 _(0.80)	1.4 _(0.33) × 2.14 _(0.19) = 3.00 _(0.76)
Total lifetime reproductive success (no. of offspring)	1.38 _(0.14) + 2.90 _(0.80) = 4.28 _(0.82)	2.14 _(0.19) + 3.00 _(0.76) = 5.14 _(0.78)

SEs of the estimates are shown *in parentheses*. For early-brood estimates, parameters for the early round of nesting were used, and for early-and-late estimates, parameters from both the early and late round of nesting

^a After year_t

more strongly in large colonies where parasites were more numerous (Magrath et al. 2009).

The previous cliff swallow study used only non-manipulated birds nesting during the early round at each site (Brown and Brown 1999) and thus did not measure date effects over the entire summer. In this study, with birds nesting much later than normal, we found that late-hatching birds were disadvantaged even without the cost of parasitism. Possible reasons could be: (1) that late-hatched birds are unable to start migration as early (Vega Rivera et al. 1998; Imlay et al. 2010) and are thus delayed in reaching optimal winter habitat; (2) that the delay in migration conflicts energetically with fall molt (Underhill et al. 1992; Nilsson and Svensson 1996; Sanz 1999; Dawson et al. 2000); or (3) that insect prey becomes more variable (Ramstack et al. 1998) and harder to find later in the summer or fall. Regardless, the pattern we document is consistent with that seen in many other species, and our results show that factors besides ectoparasitism cause some seasonal decline in offspring survival prospects. Although whether a bird was part of either of the two nesting groups (early or late) had the largest statistical effect on first-year survival, we found evidence of a seasonal decline in survival even within each group, suggesting a continuous effect of date throughout the summer.

Adult parents also incurred annual survival costs of nesting in the late round. Presumably the same date-related costs that applied to first-year birds (above) affected adults, although the wear and tear of raising a second brood may have also compromised their condition enough to affect survival. These results again contrast with those of Brown and Brown (1999), who found no effect of date on breeder survival. However, the previous study used a relatively small sample of adult breeders, included only early nesters, and did not do formal mark-recapture analyses.

The survival costs associated with late nesting happened only in the year immediately following a late brood. We found that survival in later years was unaffected by whether the birds had earlier shown late nesting. This suggests that there are no long-term consequences for either being hatched late or raising young late, once an individual survives the year that immediately follows.

As in most studies documenting declines in fitness with date (Verhulst and Nilsson 2008), distinguishing whether environmental effects or individual quality effects (or both) are causing date-related fitness variation is difficult. Could the cliff swallows nesting late relative to others (whether in either the early or late round) simply be inferior in quality and have lower personal and offspring survival for that reason?

Indirect evidence suggests that the date-related effect we documented is more likely of environmental origin. If a decline in success over the summer reflects birds of inferior quality nesting late, one would expect the birds involved in the late round of breeding to have been either those that failed during their first attempt or ones that had not nested at all earlier that year. If either scenario was true, we should have seen a more continuous distribution of nesting dates throughout the summer (as birds failed or arrived at various times and began nesting). Instead, we observed two distinct groups of nesting (Fig. 1). In addition, observations of color-marked birds show that when cliff swallows fail, they typically vacate the colony completely, so the birds during late-round nesting were not likely to have been low-quality ones which had failed earlier at the same site. Furthermore, the higher incidence of runt nestlings in general, and in the larger broods in particular, during the late round of nesting suggests that late-nesting adults had trouble finding enough food to sustain their nestlings (Emlen and Demong 1975) and thus that declines in food availability might be driving the environmental effect on survival.

Constraints on late nesting

From observations of color-marked birds at their nests in both time periods at different colonies throughout the study, and recaptures of birds at their nests, we verified that late nesting at the fumigated colonies was often by birds that had nested there earlier that season and that late nesters usually retained ownership of their nest and laid a second clutch in the same nest they had used earlier that year (C. Brown and E. Roche, personal observation). At Junkyard in 2008, we mist-netted 39 birds in the late round that had also been caught there in the early round. However, this number is hard to interpret quantitatively because cliff swallows increasingly exhibit net avoidance the more a site is netted during the summer (Roche et al. 2013), and by the late round of nesting, residents are wary of nets and by then very difficult to catch in a mist net.

Because at least some of the late nesters appeared to be double-brooders, we estimated the hypothetical fitness of birds adopting a strategy of either always nesting early and late or nesting only early. Double nesters had a lifetime production of about one more offspring on average, compared to the early breeders, although the difference was not significant (Table 4). While these are crude estimates, it seems that in the absence of ectoparasites, nesting during both rounds can potentially provide equivalent average fitness to that of only-early nesting despite the date-related declines in both breeder and offspring survival that result from late nesting. The advantage to late nesters is increased if they are primarily among the earliest of the first-round nesters, in that they would be fledging more young than the overall first-round average suggests. On the other hand, if only the highest quality birds nested late, we might be underestimating the costs of late nesting that would apply to the more “average” individuals should they attempt double broods.

Given the potential advantages of late nesting (Table 4) for certain individuals, why do not more individuals attempt second nestings? Only 10–15 % of nests were re-occupied for late nesting in the parasite-free colonies each year (although the percentage of late nesters has increased in recent years; C. Brown, unpublished data). That late nesting was most common at fumigated sites suggests that ectoparasites may be one constraint on late nesting and double-brooding in general. However, this study reveals that other costs of late nesting besides ectoparasitism apply, even when the same (high-quality?) individuals that bred earlier engaged in the late nesting. These disadvantages collectively probably prevent most cliff swallows in general from moving to unused and thus uninfested colony sites and undertaking second broods there later in a season. The fitness costs of late nesting documented here (along with ectoparasitism) may be responsible for the relatively short, synchronous breeding season observed in this species and

for its having few opportunities to raise multiple broods per season in middle latitude, temperate locations such as western Nebraska. In geographic areas where cliff swallows more often raise two broods per season (Weaver and Brown 2004), the costs of late nesting are likely reduced in magnitude.

Acknowledgments We thank Frank Axell, Alex Brazeal, Ananda Ellis, Emily Geary, Beate Hall, Bryce Hatfield, Jordan Herman, Allison Johnson, Kristen Lear, Nathan Miller, Catherine Page, Paul Smelcer, and Jessica Tipple for assistance with mark-recapture. Amy Moore managed the mark-recapture database. The Union Pacific Railroad provided access to land. The School of Biological Sciences at the University of Nebraska-Lincoln allowed us to use the Cedar Point Biological Station. We thank the National Science Foundation (DEB-0514824, DEB-1019423), the National Institutes of Health (AI057569), and the University of Tulsa’s Graduate School for financial support. This work was approved by the University of Tulsa’s Institutional Animal Care and Use Committee under protocol TU-0020 and was conducted in accordance with the laws of the United States of America.

References

- Brinkhof MWG, Cave AJ, Perdeck AC (1997) The seasonal decline in the first-year survival of juvenile coots: an experimental approach. *J Anim Ecol* 66:73–82
- Brown CR (1978) Double-broodedness in purple martins in Texas. *Wilson Bull* 90:239–247, 657
- Brown CR, Brown MB (1986) Ectoparasitism as a cost of coloniality in cliff swallows (*Hirundo pyrrhonota*). *Ecology* 67:1206–1218
- Brown CR, Brown MB (1995) Cliff swallow (*Hirundo pyrrhonota*). In: Poole A, Gill F (eds) *The birds of North America*. Academy of Natural Sciences, Philadelphia, PA, and American Ornithologists’ Union, Washington DC
- Brown CR, Brown MB (1996) Coloniality in the cliff swallow: the effect of group size on social behavior. University of Chicago Press, Chicago
- Brown CR, Brown MB (1999) Fitness components associated with laying date in the cliff swallow. *Condor* 101:230–245
- Brown CR, Brown MB (2004a) Empirical measurement of parasite transmission between groups in a colonial bird. *Ecology* 85:1619–1626
- Brown CR, Brown MB (2004b) Group size and ectoparasitism affect daily survival probability in a colonial bird. *Behav Ecol Sociobiol* 56:498–511
- Brown CR, Brown MB, Moore A, Komar N (2007) Bird movement predicts Buggy Creek virus infection in insect vectors. *Vector-Borne Zoonotic Dis* 7:304–314
- Brown CR, Brown MB, Roche EA (2013) Spatial and temporal unpredictability of colony size in cliff swallows across 30 years. *Ecol Monogr* 83:511–530
- Brownie C, Anderson DR, Burnham KP, Robson DS (1985) *Statistical inference from band recovery data—a handbook*, 2nd edn. Research publication 156. United States Department of the Interior, Washington DC
- Chapman BR, George JE (1991) The effects of ectoparasites on cliff swallow growth and survival. In: Loye JE, Zuk M (eds) *Bird-parasite interactions: ecology, evolution and behavior*. Oxford University Press, Oxford, pp 69–92
- Clayton DH, Moore J (1997) *Host-parasite evolution: general principles and avian models*. Oxford University Press, Oxford

- Dawson A, Hinsley SA, Ferns PN, Bonser RHC, Eccleston L (2000) Rate of moult affects feather quality: a mechanism linking current reproductive effort to future survival. *Proc R Soc Lond B* 267:2093–2098
- de Lope F, González G, Pérez JJ, Møller AP (1993) Increased detrimental effects of ectoparasites on their bird hosts during adverse environmental conditions. *Oecologia* 95:234–240
- Emlen ST, Demong NJ (1975) Adaptive significance of synchronized breeding in a colonial bird: a new hypothesis. *Science* 188:1029–1031
- Geupel GR, DeSante DF (1990) Incidence and determinants of double brooding in wrentits. *Condor* 92:67–75
- Hansson B, Bensch S, Hasselquist D (2000) The quality and the timing hypotheses evaluated using data on great reed warblers. *Oikos* 90:575–581
- Hochachka W (1990) Seasonal decline in reproductive performance of song sparrows. *Ecology* 71:1279–1288
- Husby A, Kruuk LEB, Visser ME (2009) Decline in the frequency and benefits of multiple brooding in great tits as a consequence of a changing environment. *Proc R Soc B* 276:1845–1854
- Imlay TJ, Crowley JF, Argue AM, Steiner JC, Norris DR, Stutchbury BJM (2010) Survival, dispersal and early migration movements of captive-bred juvenile eastern loggerhead shrikes (*Lanius ludovicianus migrans*). *Biol Conserv* 143:2578–2582
- Jacobs AC, Reader LL, Fair JM (2013) What determines the rates of double brooding in the western bluebird? *Condor* 115:386–393
- Klomp H (1970) The determinants of clutch size in birds: a review. *Ardea* 58:1–125
- Lapolla A, Buckley LJ (2005) Hatch date distributions of young-of-year haddock *Melanogrammus aeglefinus* in the Gulf of Maine/Georges Bank region: implications for recruitment. *Mar Ecol Prog Ser* 290:239–249
- Lebreton JD, Burnham KP, Clobert J, Anderson DR (1992) Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol Monogr* 62:67–118
- Loye JE, Zuk M (eds) (1991) Bird-parasite interactions: ecology, evolution and behaviour. Oxford University Press, Oxford
- Magrath MJL, Santema P, Bouwman KM, Brinkhuizen DM, Griffith SC, Langemore NE (2009) Seasonal decline in reproductive performance varies with colony size in the fairy martin, *Petrochelidon ariel*. *Behav Ecol Sociobiol* 63:661–672
- Mahony NA, Vander Haegen WM, Walker BL, Krannitz PG (2001) Male incubation and multiple brooding in sagebrush Brewer's sparrows. *Wilson Bull* 113:441–444
- Møller AP (1990) Effects of parasitism by a haematophagous mite on reproduction in the barn swallow. *Ecology* 71:2345–2357
- Møller AP, Allander K, Dufva R (1990) Fitness effects of parasites on passerine birds: a review. In: Blondel J, Gosler A, Lebreton JD, McCleery R (eds) Population biology of passerine birds. Springer, Berlin, pp 269–280
- Møller AP, Merino S, Brown CR, Robertson RJ (2001) Immune defense and host sociality: a comparative study of swallows and martins. *Am Nat* 158:136–145
- Monroe AP, Hallinger KK, Brasso RL, Cristol DA (2008) Occurrence and implications of double brooding in a southern population of tree swallows. *Condor* 110:382–386
- Nagy LR, Holmes RT (2005) To double-brood or not? Individual variation in the reproductive effort in black-throated blue warblers (*Dendroica caerulescens*). *Auk* 122:902–914
- Nilsson JA, Svensson E (1996) The cost of reproduction: a new link between current reproductive effort and future reproductive success. *Proc R Soc Lond B* 263:711–714
- Nolan V Jr (1978) The ecology and behavior of the prairie warbler *Dendroica discolor*. Ornithol Monogr 26. American Ornithologists' Union, Washington DC
- Perrins CM (1970) The timing of birds' breeding seasons. *Ibis* 112:242–255
- Powell LA (2007) Approximating variance of demographic parameters using the delta method: a reference for avian biologists. *Condor* 109:949–954
- Price T, Kirkpatrick M, Arnold SJ (1988) Directional selection and the evolution of breeding date in birds. *Science* 240:798–799
- Ramstack JM, Murphy MT, Palmer MR (1998) Comparative reproductive biology of three species of swallows in a common environment. *Wilson Bull* 110:233–243
- Richner H, Heeb P (1995) Are clutch and brood size patterns in birds shaped by ectoparasites? *Oikos* 73:435–441
- Roche EA, Brown CR, Brown MB, Lear KM (2013) Recapture heterogeneity in cliff swallows: increased exposure to mist nets leads to net avoidance. *PLoS One* 8:e58092
- Rowe L, Ludwig D, Schluter D (1994) Time, condition, and the seasonal decline of avian clutch size. *Am Nat* 143:698–722
- Sanz JJ (1999) Seasonal variation in reproductive success and post-nuptial moult of blue tits in southern Europe: an experimental study. *Oecologia* 121:377–382
- Svensson E (1997) Natural selection on avian breeding time: causality, fecundity-dependent, and fecundity-independent selection. *Evolution* 51:1276–1283
- Underhill LG, Prys-Jones RP, Dowsett RJ, Herroelen P, Johnson DN, Lawn MR, Norman SC, Pearson DJ, Tree AJ (1992) The biannual primary moult of willow warblers *Phylloscopus trochilus* in Europe and Africa. *Ibis* 134:286–297
- Vega Rivera JH, Rappole JH, McShea WJ, Haas CA (1998) Wood thrush postfledging movements and habitat use in northern Virginia. *Condor* 100:69–78
- Verboven N, Verhulst S (1996) Seasonal variation in the incidence of double broods: the date hypothesis fits better than the quality hypothesis. *J Anim Ecol* 65:264–273
- Verhulst S, Nilsson JA (2008) The timing of birds' breeding seasons: a review of experiments that manipulated timing of breeding. *Philos Trans R Soc B* 363:399–410
- Verhulst S, van Balen JH, Tinbergen JM (1995) Seasonal decline in reproductive success of the great tit: variation in time or quality? *Ecology* 76:2392–2403
- Wardrop SL, Ydenberg RC (2003) Date and parental quality effects in the seasonal decline in reproductive performance of the tree swallow *Tachycineta bicolor*: interpreting results in light of potential experimental bias. *Ibis* 145:439–447
- Weaver HB, Brown CR (2004) Brood parasitism and egg transfer in cave swallows (*Petrochelidon fulva*) and cliff swallows (*P. pyrrhonota*) in south Texas. *Auk* 121:1122–1129
- White GC, Burnham KP (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study* 46:S120–S139