

FITNESS COMPONENTS ASSOCIATED WITH LAYING DATE IN THE CLIFF SWALLOW¹

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Abstract. We report how clutch size, annual reproductive success, and annual survival of breeders and offspring vary with laying date in Cliff Swallows (*Petrochelidon pyrrhonota*) in southwestern Nebraska, from 1982–1993. Clutch size declined significantly across the season for both parasite-free (fumigated) and naturally infested nests. Larger clutches of 4 and 5 eggs were initiated significantly earlier in warm and dry seasons; laying dates for smaller clutches showed no relationship with weather. Incubation period declined significantly with laying date and was shorter in the absence of ectoparasites. Fledging success declined significantly with laying date in nonfumigated nests, primarily through greater loss of nestlings to parasitic swallow bugs (*Oeciacus vicarius*). First-year survival probabilities of nestlings varied significantly with date among nonfumigated nests but not among fumigated nests; earlier-hatched young survived best in some years, and in other years intermediate- or late-hatched young had highest survival. Number of young locally recruited was highest for early nesters in 5 of 7 years with intermediate nesters doing best in the remaining years. Annual survival of female breeders increased with laying date, suggesting a benefit to late nesting and a potential life history trade-off between reproduction and adult survival. Nestling body mass did not vary with laying date, suggesting no decline in food availability over the summer. Female body mass prior to and during laying declined significantly with laying date but during brood rearing increased significantly with laying date. Female body mass had no significant effect on clutch size independent of laying date. The primary environmental factor causing the seasonal decline in reproductive success is ectoparasitism. A seasonal decline in clutch size may be a strategic adjustment to reduce ectoparasitism by lowering the parasite carrying capacity per nest. Greater apparent survival of late-nesting females may prevent directional selection for earlier breeding times in Cliff Swallows.

Key words: Cliff Swallow, ectoparasitism, fitness, laying date, *Petrochelidon pyrrhonota*, reproductive success, survival.

INTRODUCTION

Why birds show declining prospects of reproductive success as the breeding season advances is a still unresolved question in the study of avian life histories. This seasonal decline is perplexing because natural selection should remove the less successful late breeders and lead to earlier breeding times. Two general hypotheses have been proposed to explain the negative correlation between reproductive success and breeding date. One is that breeding date reflects nonheritable variation in parental condition (nutrition): good-condition birds lay first and lay more eggs as a result of their condition, whereas others can get into sufficient nutritional shape to lay fewer eggs only later in the season (Perrins 1970, Price et al. 1988). The alternative is that the seasonal decline in reproductive success is an adaptive response by birds to environmental

conditions for brood rearing which deteriorate during the nesting season and preclude the raising of larger broods (Winkler and Allen 1996, Daan and Tinbergen 1997). This “environment” hypothesis requires that each individual regardless of its condition or quality be affected by the extrinsic factors that cause seasonal declines in reproductive success. These hypotheses are not mutually exclusive, however, and combinations of them (Rowe et al. 1994, Verhulst et al. 1995) are possible. For example, environmental factors such as food supply may limit reproduction later in the season, and female condition dictates whether laying can be initiated before or after the environmental constraints become important (Verhulst et al. 1995, Winkler and Allen 1996, Daan and Tinbergen 1997).

The relatively few studies that have tested the condition vs. environment hypotheses in natural populations have yielded mixed results. Using multivariate statistical analyses, Winkler and Allen (1996) concluded that measures of body con-

¹ Received 12 January 1998. Accepted 28 December 1998.

dition in Tree Swallows (*Tachycineta bicolor*) had no detectable effect on clutch size when laying date was held constant. This appeared to refute the condition hypothesis and supported the notion that the seasonal decline in reproductive success is a strategic adjustment to deteriorating environmental conditions during the nesting season. The condition hypothesis also was rejected in a study of Blue Tits (*Parus caeruleus*) in which laying dates were experimentally advanced or delayed (Svensson and Nilsson 1995, Svensson 1997). In contrast, a nonmanipulative study of Song Sparrows (*Melospiza melodia*) found support for the condition hypothesis, with variation among birds or the territories they held accounting for most of the seasonal decline in clutch size (Hochachka 1990). Support for both hypotheses was found in experimental studies of Great Tits (*P. major*) and European Coots (*Fulica atra*). In tits, 87% of the seasonal decline in reproductive success was attributed to an environmental effect per se and 13% to condition of breeders (Verhulst et al. 1995). In coots, chick survival to independence suggested a mostly environmental influence on the seasonal decline in reproductive success, growth rates of young suggested both environmental and parental-condition effects, and first-year survival of chicks was consistent with the condition hypothesis (Brinkhof et al. 1993, 1997).

As part of a larger study of clutch size in the colonial Cliff Swallow (*Petrochelidon pyrrhonota*; Brown and Brown 1999), in this paper we investigate fitness components associated with breeding time. We estimate annual reproductive success and annual survival of breeders and offspring associated with different laying dates. We use these fitness components to examine potential life-history tradeoffs associated with different breeding times and adopt the multivariate statistical approach of Winkler and Allen (1996) to test the condition vs. environment hypotheses for the seasonal decline in clutch size in Cliff Swallows. We experimentally removed nest ectoparasites to assess their potential effect on laying date and associated fitness components. Ectoparasites affect avian clutch size (Møller 1991, Richner and Heeb 1995, Brown and Brown 1999) and reproduction in general (Loye and Zuk 1991, Møller 1994, Brown and Brown 1996). As we show here, parasites can be an important cause of the seasonal decline in reproductive success. Our study differs from previous

ones on laying date by its use of modern statistical methods (Lebreton et al. 1992) to estimate annual survivorship of first-year birds, explicit focus on the role of ectoparasitism, and a total sample size of nearly 7,000 nests.

METHODS

STUDY SITE

Our Cliff Swallow research is conducted along the North and South Platte Rivers near Ogallala in primarily Keith and Garden Counties, southwestern Nebraska. Our study area is approximately 150 × 50 km and contains approximately 160 separate colony sites, about 100 of which are active in any given year. These colony sites consist of both natural cliffs along the south shore of Lake McConaughy and artificial sites such as bridges, buildings, and highway culverts on which the birds now commonly nest. The study site is described in detail by Brown and Brown (1996).

STUDY ANIMALS

The Cliff Swallow is a 20–28 g Neotropical migrant that breeds throughout most of western North America and winters in southern South America. These insectivorous birds build gourd-shaped mud nests and place them beneath overhanging rock ledges on cliffs or underneath the protected eaves of artificial structures. Cliff Swallows often breed in dense colonies, with nests stacked together closely, although colony size within a single population varies widely. In southwestern Nebraska, mean (\pm SE) colony size is 393.0 \pm 24.3 nests, ranging from birds that nest solitarily to colonies of 3,700 nests (Brown and Brown 1996). Cliff Swallows typically have a short breeding season, 10 weeks or less in our study area, and raise only one brood (Brown and Brown 1995). In southwestern Nebraska, most birds arrive in May, and breeding is largely completed by the end of July.

Cliff Swallows are associated with a variety of ectoparasites throughout their range, and in southwestern Nebraska the two most common ones are the hematophagous swallow bug (Hemiptera: Cimicidae: *Oeciacus vicarius*) and a bird flea (Siphonaptera: Ceratophyllidae: *Ceratophyllus celsus*). These insects primarily reside inside the Cliff Swallow nests or in the adjacent nesting substrate. They feed on blood of adult and nestling swallows and have substantial ef-

fects on nestling survival and health (Brown and Brown 1986, 1996).

NEST CHECKS

Nests were checked at 1–3 day intervals from shortly before egg laying was expected to begin until either the eggs hatched or the nest failed. Nest contents were observed with a dental mirror and flashlight inserted through a nest's mud neck (see Brown and Brown 1996). Laying date for each nest was determined directly by observing when the first egg appeared. We did not "back-date" from hatching to infer laying times for any nest, and for this reason sample sizes in this paper are slightly different than in analyses of clutch size (Brown and Brown 1999). Clutch size was the maximum number of eggs appearing in a nest, which in some cases included eggs laid or transferred by brood-parasitic females (see Brown and Brown 1989, 1996). Once hatching date was determined, we did not check a nest again until the nestlings were 10 days old. At that time, nestlings were removed, banded, and weighed. Body masses were averaged for all nestlings within a nest, and these average values were used in statistical analyses. Eggs disappearing during incubation and nestlings known to have hatched but absent at 10 days were scored as lost. Nestling survival was that measured at 10 days, which is an accurate relative index of survival to fledging for Cliff Swallows. Most of our nests with data on laying date came from 1982–1989, although we used recaptures through 1996 to estimate first-year survival probabilities (see below). For clarity of presentation, we combined data on clutch size and fledging success into 5-day intervals (Brown and Brown 1996) and calculated mean values per interval for analyses of seasonal patterns. Because egg laying was not distributed equally across dates, using mean values ensured that each date was represented equally in our statistical tests, thus avoiding pseudoreplication. Changing the intervals had no effect on the results.

FUMIGATION

To test the effect of ectoparasites on fitness components associated with laying date, we fumigated nests by application of a short-lived acaricide, Naled (also known as Dibrom), to the outside of nests and surrounding substrate at intervals of 2–7 days throughout the nesting

season. This fumigant was highly effective against swallow bugs, the principal cause of Cliff Swallow nestling mortality. We generally fumigated entire colonies, beginning as or just after birds established nest ownership at a colony site. In some cases, principally in 1984 and 1986, we fumigated half of a colony, dividing it into two blocks and spraying all the nests in one half. Further details on fumigation procedures are provided in Brown and Brown (1996).

WEATHER DATA

Climatological data were taken from a long-term monitoring site in Arthur County, Nebraska, about 48 km north of the center of the study area. Weather conditions in Arthur County reflect those in the study area (Brown and Brown 1996). This site, part of the University of Nebraska–Lincoln's Automated Weather Data Network, recorded daily high and low temperatures and amount of precipitation.

MARK-RECAPTURE

Annual survival estimates were based on mark-recapture of birds from nests with a given laying date. From 1982–1996, we banded 87,337 adult and nestling Cliff Swallows, with typically 16,000–21,000 recaptures each season. We rotated among 25–35 colony sites and systematically netted birds at each. This enabled us to build a capture history for each individual, indicating if the bird was encountered each season and, if not, whether it was known to be alive by virtue of its being caught in a later year. Individuals often escaped detection in a given season, due to the large population size in the study area which could not be completely censused. Our capture effort increased each year of the study, and perhaps for this reason we often found significant yearly variation in recapture probabilities. Birds were assigned as owners of nests based on observations of color-marked birds (their white forehead patches were painted in unique 3-color stripes) or from capture of individuals inside nests. Body mass of adults was recorded each time a bird was captured, and assigned to the time periods of nest building and egg laying or feeding of nestlings depending upon when the bird was encountered. See Brown and Brown (1996) for further details on mark-recapture and field methods of capturing and processing birds.

We used all cohorts recaptured through 1996

for survival analyses. Our most recent cohort with laying-date data was from 1993, and thus we had at least 3 years of recapture for all cohorts. After 3 years of recapture, Cliff Swallow survival estimates for a cohort cease to change with the addition of more years of data (Brown and Brown 1996).

SURVIVAL ESTIMATION

We estimated annual survival probabilities for first-year Cliff Swallows and tested for significant differences in survival between birds from nests of different laying dates using the general methods of Lebreton et al. (1992). We used program SURGE (Pradel and Lebreton 1993, Cooch et al. 1996) to generate maximum-likelihood estimates of survival and recapture probabilities. SURGE provides a powerful way of testing the fit of different survival and recapture models and thus tests different biological hypotheses (Lebreton et al. 1992). We use the general notation of Lebreton et al., in which annual survival probability is denoted ϕ and recapture probability p . Subscripts indicate whether a model incorporates time-dependence in a parameter estimate (e.g., ϕ_t, p_t), an effect of age (and if so, how many age classes, e.g., ϕ_{a2}, p_{a2t}), constancy over time (e.g., ϕ, p), an effect of group classification (and if so, how many groups, e.g., ϕ_{g5}, p_{g5}), an interaction between group and time (e.g., $\phi_{t \times g5}, p_t$), or a constrained model with parallelism in time for a group effect (e.g., $\phi_{t \times g5}, p_t$). In testing different models for a given data set, we began with the Cormack-Jolly-Seber (CJS) model with time-dependent survival and recapture probabilities (Lebreton et al. 1992). We then tested more general yet biologically relevant models incorporating various combinations of age-, group-, and time-dependence (see Brown and Brown 1998a for further details).

We compared different models that were nested (e.g., ϕ_t, p_t vs. ϕ, p_t) with a likelihood ratio test (LRT). SURGE provides a relative deviance (DEV), $-2\ln L(\theta)$, for each model fitted, and the difference among DEVs is the χ^2 statistic with degrees of freedom equaling the difference in the number of estimable parameters (np) between the two models (Lebreton et al. 1992). LRTs cannot be used for models which are not nested (e.g., ϕ_{a2}, p_t vs. ϕ_t, p_{g2}), and for these, use of the Akaike Information Criterion (AIC; Akaike 1973) is recommended (Lebreton et al. 1992). AIC is computed as $2np + \text{DEV}$, and

models with the lowest values of AIC are the most parsimonious. We found models with age dependence to provide the best fits; first-year survival of Cliff Swallows is considerably lower than that of older age classes (Brown and Brown 1996).

Potential differences in survival among different groups of birds were assessed by comparing different models, some of which modeled the effect of the separate groups whereas others considered the groups identical. If a model with a group effect provided a significantly better fit than one without it, we concluded that survival differed among the groups. If, however, a group-effect model did not provide a significantly better fit, the more parsimonious model without a group-effect (with fewer parameters) was accepted, and we inferred no difference among the groups. We show the results of only the 4–5 models with the lowest AICs. Because SURGE estimates only local survival and cannot distinguish between permanent emigration and mortality, our survival estimates are relative ones, useful in comparing among different classes of birds, but do not represent absolute survival. We assume no relationship between the explanatory factors we investigate and dispersal beyond the study area.

SURGE and the capture-recapture methodology on which it is based makes the implicit assumption that an individual's status does not change during the period in which its survival is estimated. This assumption is fully met for analyses of first-year survival in relation to natal laying date. However, laying dates for adults are not fixed because birds may change laying dates between years. Thus, SURGE is not appropriate for estimating annual survival of breeding adults in relation to laying date. Theoretically, a multistate approach (Brownie et al. 1993, Nichols and Kendall 1995) could be applied when individuals change status and when transition probabilities are known, but there is no tractable or widely available software to do this. We instead used observed recapture probabilities to infer relative survival among adults associated with different laying dates. We tabulated the percentage of adults recaptured the next season in relation to their laying dates the previous year; individuals "missed" the next year but recaptured in a later year were not used in our recapture analysis because their presence could have been affected

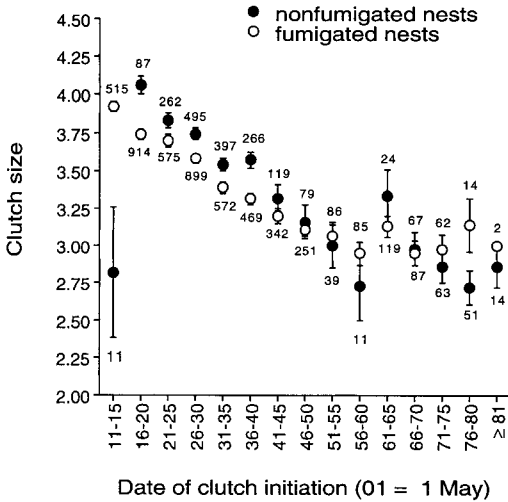


FIGURE 1. Mean (\pm SE) Cliff Swallow clutch size in relation to date of clutch initiation. Sample sizes (number of nests) are shown above or below error bars. Clutch size did not vary significantly with fumigation treatment (two-way ANOVA, $F_{1,14} = 0.52$, $P = 0.47$) but varied significantly with laying date ($F_{1,14} = 30.84$, $P < 0.001$). Mean clutch size declined significantly with date for both nonfumigated ($r_s = -0.62$, $P = 0.013$, $n = 15$ date intervals) and fumigated nests ($r_s = -0.85$, $P < 0.001$, $n = 15$).

by their laying on a different date in the intervening year(s).

RESULTS

CLUTCH SIZE IN RELATION TO DATE

Cliff Swallow clutch size declined significantly with laying date (Fig. 1; all years combined). There was an overall reduction of about 1 egg in mean clutch size over the course of the approximately 70-day nesting season in southwestern Nebraska. The seasonal decline was the same among parasite-free nests and ones subject to natural levels of ectoparasitism: linear regressions of clutch size on laying date produced identical regression coefficients (slopes) for fumigated and nonfumigated nests ($\beta = -0.013$ in each case).

LAYING DATE IN RELATION TO WEATHER

Egg-laying times in Cliff Swallows might vary with seasonal weather conditions, given these birds' exclusive reliance on flying insects for food and their sensitivity to periods of cold weather that reduce the availability of their food (Brown and Brown 1998b). Annual climatic

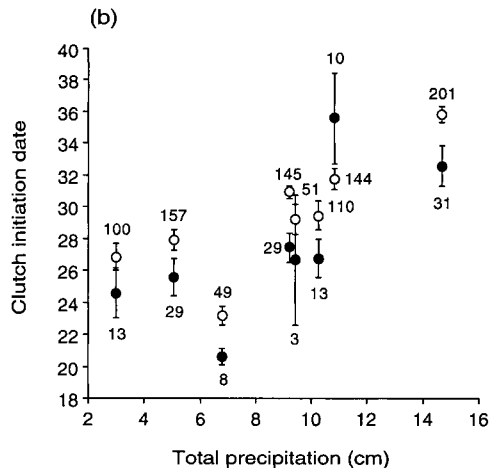
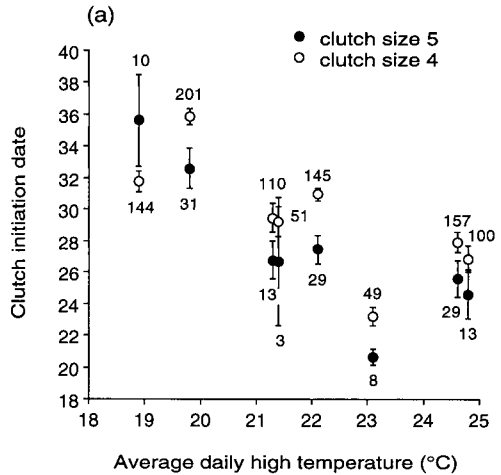


FIGURE 2. Mean (\pm SE) Cliff Swallow clutch initiation date per year for clutch sizes 4 and 5 in relation to (a) average daily high temperature and (b) total precipitation for the interval 1 May to 15 June (nonfumigated nests only). Sample sizes (number of nests) are shown above or below error bars. Mean clutch initiation date declined significantly with temperature for clutch size 4 ($r_s = -0.83$, $P = 0.011$, $n = 8$ years) and 5 ($r_s = -0.85$, $P < 0.01$, $n = 8$) and increased significantly with total precipitation for clutch size 4 ($r_s = 0.86$, $P < 0.01$, $n = 8$) and 5 ($r_s = 0.83$, $P = 0.01$, $n = 8$).

conditions in our central Great Plains study area vary considerably; for example, 1988 was one of the warmest summers during the last 100 years, followed in 1992 by one of the coldest (Brown and Brown 1996). Mean laying date for nonfumigated clutch sizes 4 and 5 declined significantly with average temperature during the period 1 May to 15 June each year (Fig. 2a) and

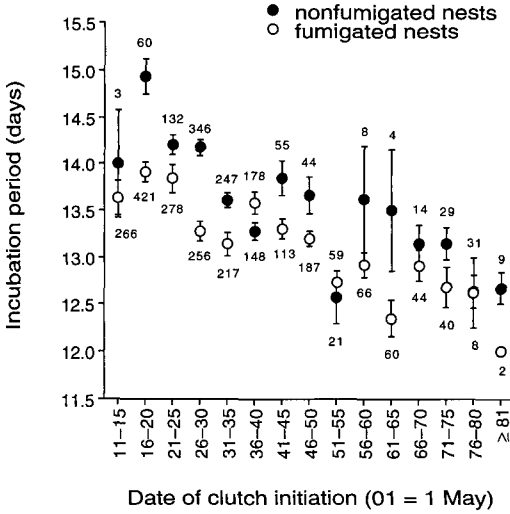


FIGURE 3. Mean (\pm SE) Cliff Swallow incubation period in days in relation to date of clutch initiation. Sample sizes (number of nests) are shown above and below error bars. Incubation period varied significantly with both fumigation treatment (two-way ANOVA, $F_{1,14} = 7.89, P < 0.01$) and laying date ($F_{1,14} = 8.76, P < 0.001$). Mean incubation period declined significantly with laying date for both nonfumigated ($r_s = -0.82, P < 0.001, n = 15$ date intervals) and fumigated nests ($r_s = -0.91, P < 0.001, n = 15$).

increased significantly with amount of precipitation during that period (Fig. 2b). This date interval likely reflected overall weather conditions during laying; 85.9% of clutches ($n = 6,996$) were initiated during this time. Mean laying dates for nonfumigated clutch sizes 2 and 3 were unaffected by either temperature (clutch size 2: $r_s = -0.19, P = 0.65, n = 8$ years; clutch size 3: $r_s = -0.28, P = 0.46, n = 9$) or rainfall (2: $r_s = 0.24, P = 0.57, n = 8$; 3: $r_s = -0.12, P = 0.76, n = 9$).

INCUBATION PERIOD IN RELATION TO LAYING DATE

Incubation period, measured in days from the laying of the last egg to the hatching of the first nestling, varied significantly with laying date, declining in later nests, and was significantly shorter in the absence of ectoparasites (Fig. 3). Mean incubation period declined by about 2 days over the course of the season, possibly due in part to increasing ambient temperatures. To the degree that incubation period represents a clutch production cost, later clutches were thus less costly for Cliff Swallows to produce.

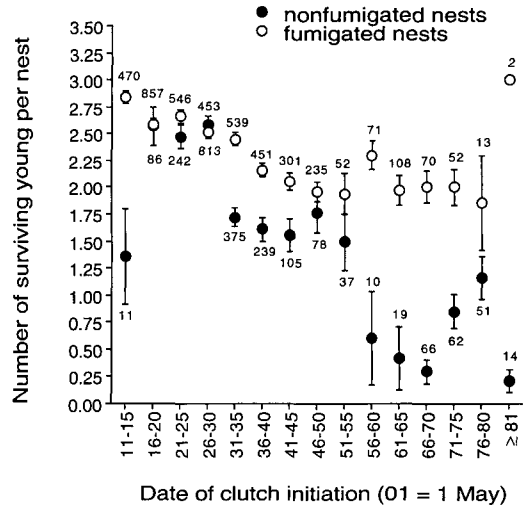


FIGURE 4. Mean (\pm SE) number of Cliff Swallow nestlings surviving per nest in relation to date of clutch initiation. Sample sizes (number of nests) are shown above and below error bars. Number of surviving nestlings varied significantly with both fumigation treatment (two-way ANOVA, $F_{1,14} = 77.51, P < 0.001$) and laying date ($F_{1,14} = 25.38, P < 0.001$). Mean number of surviving nestlings declined significantly with laying date for nonfumigated nests ($r_s = -0.78, P = 0.001, n = 15$ date intervals) but not for fumigated nests ($r_s = -0.50, P = 0.06, n = 15$).

FLEDGING SUCCESS IN RELATION TO LAYING DATE

The number of nestlings surviving to day 10 varied significantly with laying date and fumigation treatment (Fig. 4). Fledging success in nonfumigated nests declined significantly with laying date, with the latest nests showing a marked reduction in success. The seasonal decline for fumigated nests was less pronounced (Fig. 4). The slopes of the declines for nonfumigated (linear regression, $\beta = -0.029$) and fumigated nests ($\beta = -0.008$) were significantly different ($t_{13} = 2.16, P = 0.05$). Among nonfumigated nests, 25 June seemed to represent a threshold, after which expected fledging success fell to less than 1 nestling per nest. This comparison (Fig. 4) reveals that ectoparasites are responsible for most of the seasonal decline in Cliff Swallow reproductive success. All years were combined here (Fig. 4), but a similar pattern held for each year separately.

Fledging success in Cliff Swallows is determined mostly by how many eggs are lost before hatching and by how many nestlings are lost be-

TABLE 1. Capture-recapture models and comparisons among models for Cliff Swallows banded as nestlings in relation to hatching date (see text for model notation).

Model	np^a	DEV ^b	AIC ^c	Comparison ^d
Fumigated Nests				
(1) ϕ_{a2t}, p_{a2t}	37	20,606.6	20,680.6	Best fit. No differences among hatching dates.
(2) $\phi_{a2t;g2}, p_t$	43	20,620.8	20,706.8	Groups = birds from hatching dates $\leq 43, \geq 44$. (2) vs (1), $\chi^2_6 = 14.2, P = 0.03$
(3) $\phi_{a2t;g2}, p_t$	42	20,627.8	20,711.8	Groups = birds from hatching dates $\leq 55, \geq 56$. (3) vs (1), $\chi^2_5 = 21.2, P < 0.001$
(4) $\phi_{a2t;g3}, p_t$	56	20,600.8	20,712.8	Groups = birds from hatching dates $\leq 40, 41-43, \geq 44$. (4) vs (1), $\chi^2_{19} = 5.8, P = 0.99$
(5) $\phi_{a2t;g4}, p_t$	70	20,580.0	20,720.0	Groups = birds from hatching dates $\leq 40, 41-43, 44-49, \geq 50$. (5) vs (1), $\chi^2_{33} = 26.6, P = 0.78$
Nonfumigated Nests				
(6) $\phi_{a2t;g3}, p_t$	73	5,149.4	5,295.4	Best fit. Groups = birds from hatching dates $\leq 40, 41-49, \geq 50$.
(7) ϕ_{a2t}, p_{a2t}	47	5,216.2	5,310.2	Testing effect of hatching date. (7) vs (6), $\chi^2_{26} = 66.8, P < 0.001$
(8) $\phi_{a2t;g2}, p_t$	52	5,198.8	5,302.8	Groups = birds from hatching dates $\leq 40, \geq 41$. (8) vs (6), $\chi^2_{21} = 49.4, P < 0.001$
(9) $\phi_{a2t;g4}, p_{a2t}$	90	5,128.2	5,308.2	Groups = birds from hatching dates $\leq 40, 41-49, 50-55, \geq 56$. (9) vs (6), $\chi^2_{17} = 21.1, P = 0.22$

^a np = number of estimable parameters.

^b DEV = model deviance from SURGE.

^c AIC = Akaike Information Criterion.

^d Sample sizes for hatching dates $\leq 37, 38-40, 41-43, 44-46, 47-49, 50-52, 53-55$, and ≥ 56 in fumigated nests were 2,806, 690, 649, 678, 726, 502, 526, and 1,955 birds, respectively; in nonfumigated nests, 263, 522, 614, 935, 802, 787, 247, and 952 birds, respectively. SURGE allows a maximum of 8 groups per model.

fore fledging. The mean number of eggs lost, while differing significantly between fumigated and nonfumigated nests (two-way ANOVA, $F_{1,14} = 6.85, P < 0.01$), did not vary significantly with laying date for either parasite-free ($r_s = -0.46, P = 0.09, n = 15$ date intervals) or naturally infested nests ($r_s = -0.14, P = 0.62, n = 15$). Nestling loss appeared to be the primary cause of the seasonal decline in reproductive success. The number of nestlings lost per nest differed significantly between fumigated and nonfumigated nests ($F_{1,14} = 96.61, P < 0.001$); mean nestlings lost increased significantly with laying date among nests infested with ectoparasites ($r_s = 0.62, P < 0.02, n = 15$) and decreased significantly with laying date among parasite-free nests ($r_s = -0.89, P < 0.001, n = 15$). Increased loss of nestlings to ectoparasites appears to represent a serious cost of late nesting for Cliff Swallows.

FIRST-YEAR SURVIVAL IN RELATION TO LAYING DATE

A series of model fittings in SURGE revealed a significant effect of breeding time on first-year survival probabilities for nestlings reared in nonfumigated nests, but no effect of breeding time for those raised in fumigated nests (Table 1). The model that best fit for nonfumigated nests showed significant differences in first-year survival for three groups of birds: those from nests with hatching dates of 9 June or earlier, those between 10-18 June, and those of 19 June or later (Table 1). Changing these categories did not improve model fit and usually worsened it. The best fitting model (model 6, Table 1) also indicated significant annual variation in first-year survival probabilities among these categories. From model 6, we estimated first-year survival (from fledging to the first breeding season) in nonfumigated nests in relation to hatching

date for 11 years between 1982 and 1993 (Fig. 5). Annual variation in breeding times meant that in some years certain hatching-date categories contained either no birds or not enough to yield SURGE estimates. There was no consistent pattern in first-year survival: in some years, birds hatched earliest had the highest survival, and in other years birds hatched later appeared to do best (Fig. 5). Averaged over all years, birds hatched on 9 June or earlier had a mean first-year survival probability of 0.246, compared to 0.159 for birds hatched 10–18 June, and 0.180 for birds hatched on 19 June or later. This indicates an overall advantage to earlier breeding times. That hatching date had no significant effect on first-year survival in the absence of ectoparasites (Table 1) indicates that swallow bugs and fleas apparently cause the survival differences between Cliff Swallows hatching at different times (Fig. 5).

ANNUAL REPRODUCTIVE SUCCESS IN RELATION TO LAYING DATE

We estimated annual reproductive success (ARS) by multiplying the average number of young fledging (Fig. 4) during each of the three date categories by the probability of first-year survival for birds from those dates as estimated by SURGE (Fig. 5). This relative index of ARS took into account both fledging success and first-year survival (Fig. 6). Our analysis was confined to nonfumigated nests, because first-year survival was unaffected by breeding time for fumigated nests (Table 1).

Estimated ARS revealed an apparent reproductive advantage to early nesting in 5 of 7 years (Fig. 6). In the two remaining years, mid-season birds seemed to do best. Advantages occurred mostly through differences in the number of young fledged (Fig. 4) and not through recruitment patterns which varied considerably and were not consistently greater for early-hatched young (Fig. 5). The error (standard deviation) associated with each ARS estimate was relatively high because we were estimating the variance of a multiplication product (Fig. 6).

PARENTAL SURVIVAL IN RELATION TO LAYING DATE

The percentage of females recaptured the next year increased significantly with laying date the previous year; the percentage of males recaptured

did not vary significantly with laying date (Fig. 7).

NESTLING BODY MASS IN RELATION TO LAYING DATE

Nestling body mass is directly associated with first-year survival and also reflects patterns of food availability and ectoparasitism (Brown and Brown 1996) that potentially vary with breeding time. Although body mass of 10-day-old Cliff Swallows varied significantly with fumigation treatment and overall date, there was no significant trend for mean body mass to change systematically over the season for either nonfumigated or fumigated nests (Fig. 8). The results for fumigated nests—with the confounding effects of ectoparasites removed—suggest little evidence for a strong seasonal decline in food availability. This analysis (Fig. 8) is unlikely to be affected by date-related differences in average clutch or brood size, because nestling mass is unaffected by clutch or brood size under natural conditions (Brown and Brown 1999).

FEMALE BODY MASS IN RELATION TO LAYING DATE

Body mass of breeding females prior to and during egg-laying declined significantly with laying date (Fig. 9a). Heavier females were likely to lay earlier. The opposite pattern was observed for females weighed while feeding nestlings: later-nesting birds had significantly greater mass (Fig. 9b). This positive correlation is consistent with the greater survival of late-nesting females (Fig. 7); heavier birds late in the season seem to show higher annual survival probabilities in Cliff Swallows.

MULTIPLE REGRESSION OF LAYING DATE, CLUTCH SIZE, AND CONDITION

We used multiple regression to determine whether condition affected the seasonal decline in clutch size once variation in laying date was controlled statistically (Winkler and Allen 1996). Condition, as measured by body mass taken prior to and during egg-laying, had no significant effect on clutch size independent of laying date (Table 2). The only significant predictors of clutch size were laying date and colony size, and mass for laying date. These are consistent with earlier analyses, although the significant effect of colony size was surprising. No reason for an effect of colony size is obvious;

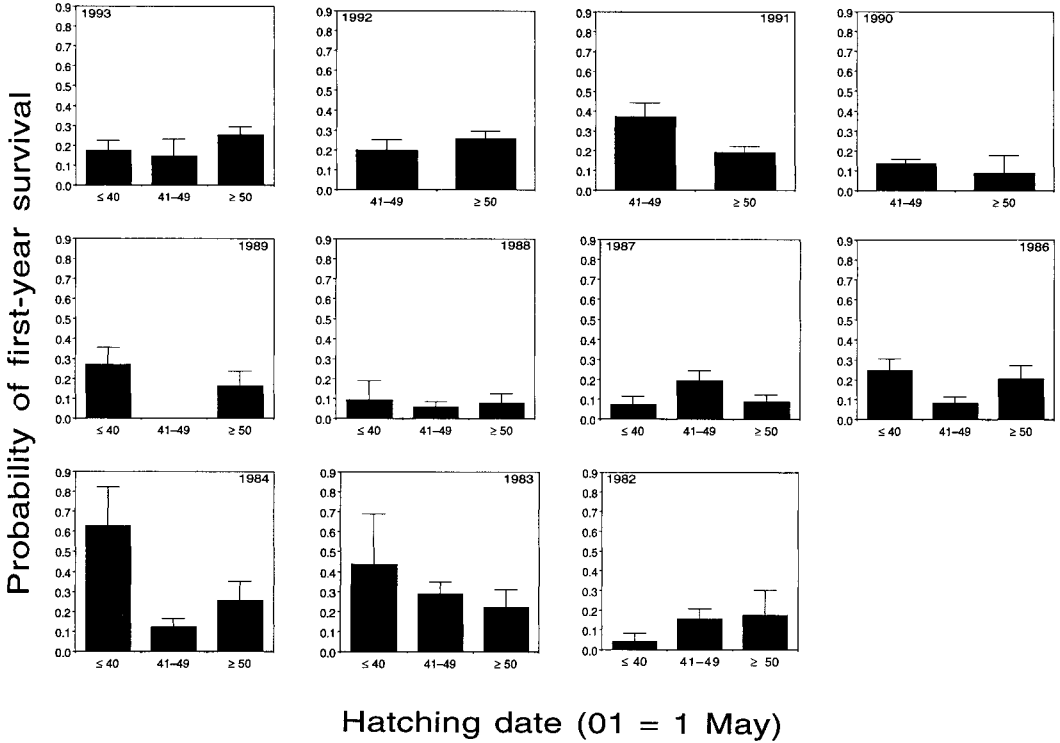


FIGURE 5. Probabilities of first-year survival (from fledging to first breeding season) for Cliff Swallows in relation to hatching date in different years for nonfumigated nests. Survival probabilities (\pm SD) were estimated with SURGE using model ϕ_{a2t-g3} , p_1 (see Table 1). Total sample sizes are given in Table 1.

other analyses (Brown and Brown 1996) suggested no relationships between clutch size and Cliff Swallow colony size.

DISCUSSION

Cliff Swallows exhibit the typical pattern among birds with reproductive success declining during the breeding season. Part of this decline can be attributed to a decline in clutch size, but much of the reduction in success is caused by increased loss of nestlings in later nests. Our fumigation experiment revealed that ectoparasitic swallow bugs and fleas are largely responsible for the loss of young among late nesters. These reductions in fledging success usually lead to an overall decline in annual reproductive success as measured by recruitment of young into the next year's breeding population, even though first-year survival probability in some years is higher for mid- or late-hatched young. Later-nesting females appear to show higher annual survival, and this life-history tradeoff may prevent directional selection on laying date in Cliff Swallows.

THE CONDITION HYPOTHESIS

One of the more popular explanations for the decline in avian clutch size during the breeding season is that laying date reflects a female's non-heritable physiological or nutritional condition (Perrins 1970, Price and Liou 1989, Rowe et al. 1994). There is relatively little empirical support for the condition hypothesis, however, especially among small passerines (Winkler and Allen 1996). This is in part because measures of condition are often confounded by environmental effects (e.g., food supply, ectoparasitism) which may vary with laying date and themselves lead to seasonal declines in reproductive success. Winkler and Allen's (1996) multivariate statistical analyses suggested little effect of female condition on clutch size in Tree Swallows when laying date was controlled statistically. We found a similar result for Cliff Swallows: condition, as measured by body mass prior to and during egg-laying, had no significant effect on clutch size independent of laying date (Table 2).

Although condition seemed unrelated to the

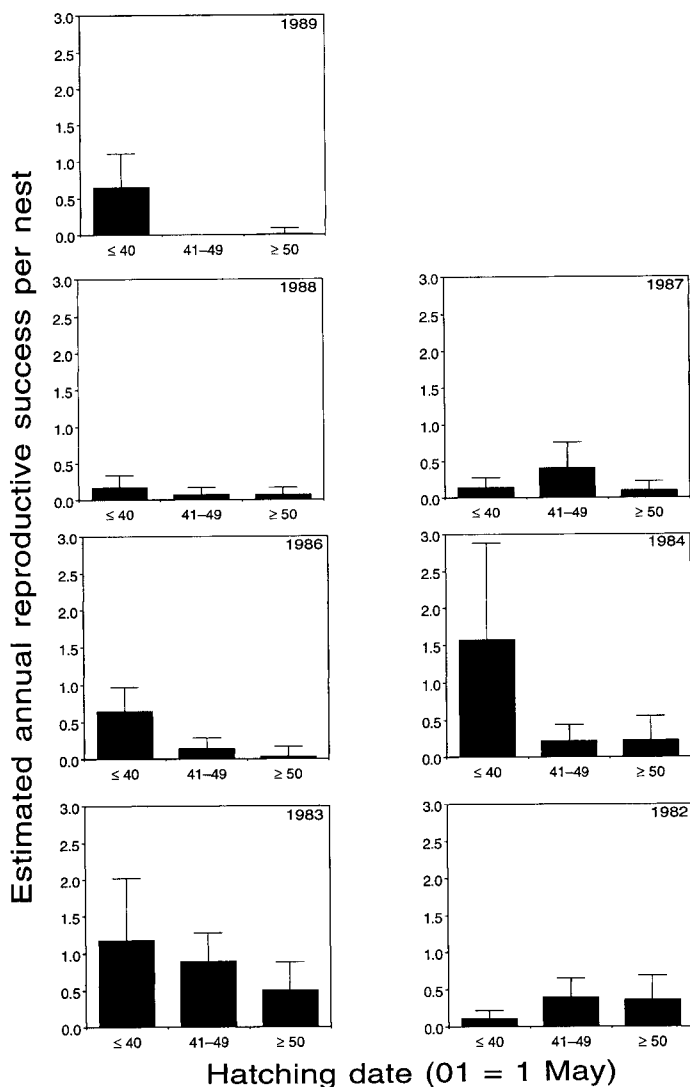


FIGURE 6. Estimated annual reproductive success (number of young locally recruited to breeding) per nest for Cliff Swallows in relation to their clutch's hatching date in different years for nonfumigated nests. Estimates were generated by multiplying the average number of young surviving to fledge per nest in each date interval times the first-year survival probability (Fig. 5) for that interval. Error bars show SD for a multiplication product calculated from Goodman (1960).

seasonal decline in clutch size, condition was related to laying date in Cliff Swallows. Lighter females laid later (Fig. 9a, Table 2). This may have been a noncausal relationship that reflected seasonal variation in body mass. Cliff Swallows typically arrive on the breeding grounds with relatively high levels of body fat and use these reserves to survive periodic bouts of cold weather that reduce flying insect availability (Brown and Brown 1996, 1998b). Birds laying later in

the season have probably experienced more bouts of weather-related food deprivation and thus have lower fat stores. On the other hand, an effect of condition on laying date was suggested by the inverse relationship between laying date for clutch sizes 4 and 5 and weather conditions early in the nesting season (Fig. 2). The time taken to produce larger clutches declined in warm and dry years, seasons in which food availability was greater and female condi-

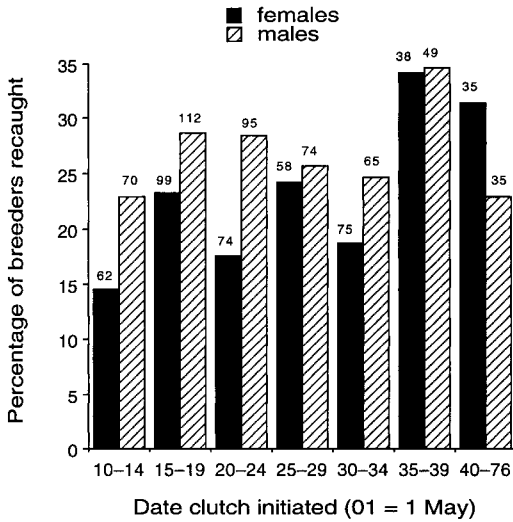


FIGURE 7. Percentage of breeding Cliff Swallows recaptured the next year in relation to the date that they initiated laying during the first year. Sample sizes (number of birds) are shown for each date interval. The percentage of females recaptured the next year increased significantly with laying date the first year ($r_s = 0.78, P = 0.04, n = 7$ date intervals), whereas the percentage of males recaptured did not vary significantly with laying date ($r_s = 0.15, P = 0.74, n = 7$).

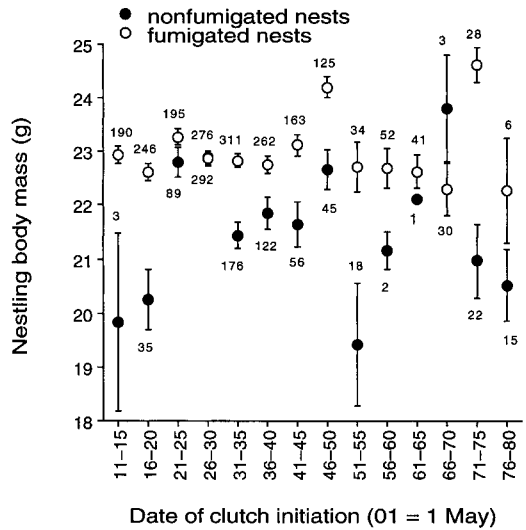


FIGURE 8. Mean (\pm SE) body mass per 10-day-old Cliff Swallow nestling per nest in relation to date of clutch initiation. Sample sizes (number of nests) are shown above and below error bars. Nestling body mass varied significantly with both fumigation treatment (two-way ANOVA, $F_{1,14} = 23.79, P < 0.001$) and laying date ($F_{1,14} = 7.56, P < 0.001$). Mean nestling body mass did not vary significantly with laying date for either nonfumigated ($r_s = 0.04, P = 0.89, n = 14$ date intervals) or fumigated nests ($r_s = -0.30, P = 0.30, n = 14$).

tion probably better because of fewer weather-related foraging interruptions. However, average annual clutch size was unrelated to weather conditions and thus food availability (Brown and Brown 1999). Other birds show similar patterns in which increased food availability leads to earlier breeding but no change in clutch size (Davies and Lundberg 1985, Murphy 1986, Winkler and Allen 1996).

STRATEGIC ADJUSTMENT TO ENVIRONMENTAL CONDITIONS

An alternative to the condition hypothesis is that changing environmental factors over a season may select for smaller clutches among late nesters, leading to individual optimization of clutch size with respect to date. However, empirical support for the strategic adjustment hypothesis also is limited.

Food supply is the most commonly invoked environmental factor that may regulate clutch size (Lack 1947, Hussell and Quinney 1987, Martin 1987) and lead to a seasonal decline in the number of eggs laid (Perrins 1965, Drent and Daan 1980, Murphy 1986). If food declines in absolute abundance or is more costly to find and

collect later in the season, birds laying smaller clutches will be favored by ultimately producing more or higher-quality offspring per unit of parental resource expended (Lack 1954, Williams 1966, Trivers 1972). Although food may decline in availability for some species (Klomp 1970, Perrins 1970, Brinkhof and Cave 1997), it seems unlikely for Cliff Swallows that food is less available later in the breeding season. The opposite is more probable in our Nebraska study area: cold weather and resulting food deprivation are less frequent later in the season, and many insects on which Cliff Swallows feed (e.g., grasshoppers) become more abundant later in the summer (pers. observ.). That food availability does not decline with date is suggested by the positive correlation between late-season female body mass and laying date (Fig. 9b). Furthermore, a seasonal decline in food availability might result in lower weight nestlings in late nests, especially when the confounding effects of ectoparasites are removed (Brown and Brown 1996). However, we saw no such pattern in fumigated nests (Fig. 8). No decline in food avail-

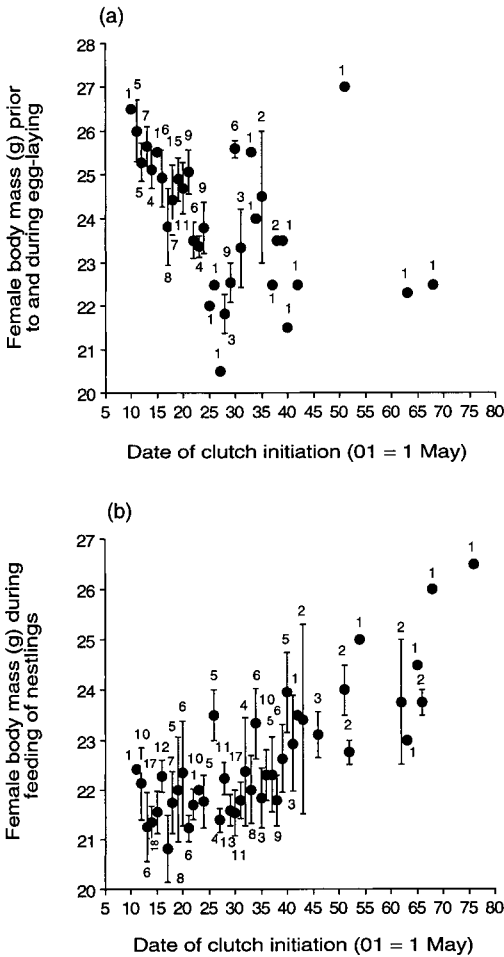


FIGURE 9. Mean (\pm SE) body mass per breeding female Cliff Swallow taken (a) prior to and during egg-laying and (b) during feeding of nestlings in relation to date of clutch initiation. Sample sizes (number of birds) are shown above or below error bars. In (a), mean body mass declined significantly with laying date ($r_s = -0.34$, $P = 0.03$, $n = 44$ laying dates); in (b), mean body mass increased significantly with laying date ($r_s = 0.59$, $P = 0.001$, $n = 31$).

ability over the breeding season was found for British House Martins (*Delichon urbica*; Bryant 1975) or Purple Martins (*Progne subis*; Johnston 1967) in Kansas when insect abundance was sampled with suction traps and sweep nets.

A more likely environmental factor leading to the seasonal decline in clutch size and resulting reproductive success in Cliff Swallows is ectoparasitism. Our fumigation treatment revealed that later nests had substantially reduced fledging success because of increased loss of young

to ectoparasitic bugs and fleas. Our study and that of Brinkhof and Cave (1997) on coots are the only experimental ones we are aware of that have shown a cause of the seasonal decline in reproductive success.

Ectoparasites, especially swallow bugs, have severe effects on Cliff Swallows (Brown and Brown 1986, 1996, Chapman and George 1991, Brown et al. 1995). Among nestlings, parasites cause reduced weight, slower feather growth, lower levels of hemoglobin and hematocrit, elevated levels of leucocytes and lymphocytes, higher mortality both before and after fledging, and greater natal dispersal. Among adults, ectoparasites cause reduced annual survival and influence reuse of colony sites and nest sites within colonies. Swallow bugs, which have greater effects on Cliff Swallows than do fleas, increase in colonies over the summer (Brown and Brown 1996). The increase is caused both by reproduction of bugs in colonies over the summer and immigration of bugs transported on birds from unoccupied sites into active colonies. The consequence is that later-nesting birds experience increased ectoparasite loads and their associated costs.

Why might a seasonal decline in clutch size (Fig. 1) be a strategic response to ectoparasitism? Recently, Richner and Heeb (1995) hypothesized that the life-cycle length of a species' most common ectoparasite(s) will directly affect whether the host should lay a large or small clutch. In their model, ectoparasites which have long life cycles relative to the host's nestling period will not produce multiple generations while the nestlings are present, and therefore the parasite load per nest will be largely fixed. In this case, larger broods can be advantageous because they dilute the parasite load per individual nestling. On the other hand, if ectoparasites have short life cycles relative to the host's nestling period, multiple generations of parasites may be produced quickly and parasite load will be set by brood size. In this case, hosts should reduce their brood size. Comparisons across species tend to support these predictions in general, and Richner and Heeb (1995) suggest that ectoparasitism is a major determinant of clutch size in birds.

The generation times of Cliff Swallow ectoparasites suggest that they are long-cycled relative to the nestling period (Brown and Brown 1996, 1999). However, due to substantial move-

TABLE 2. Multiple regression of female body mass (condition), laying date, and clutch size to test the condition vs. environment hypotheses for the seasonal decline in Cliff Swallow clutch size.

Variable	Laying-date model			Clutch-size model		
	Regression coefficient	SE	$P \leq$	Regression coefficient	SE	$P \leq$
constant	-67.787	88.947	0.45	16.645	7.486	0.03
year	1.490	1.017	0.14	-0.153	0.086	0.08
colony size	-0.002	0.002	0.27	0.001	0.000	0.01
body mass	-1.535	0.416	0.001	0.016	0.037	0.66
laying date				-0.021	0.007	0.006
overall model P value	<0.001			0.001		
multiple r^2	0.12			0.13		
n	134			134		

ment of swallow bugs among nests, this ectoparasite can show population increases within nests characteristic of short-cycled parasites. As Cliff Swallow nestlings within a colony fledge, bugs move out of vacated nests and aggregate at the active nests that remain (Brown and Brown 1996). For the later nests in a colony, bug load can potentially be determined by brood size, with larger broods supporting more bugs that arrive via immigration. By reducing clutch sizes, later-nesting Cliff Swallows can lower the swallow bug carrying capacity in their broods and may consequently reduce per-capita parasite load. Thus, the seasonal decline in clutch size can be seen as a strategic adjustment to increasing ectoparasitism.

If extent of ectoparasitism is used as a cue for strategically adjusting the number of eggs laid, clutch size should decline less over the season among fumigated nests. However, clutch size in fumigated nests declined in a pattern similar to that for nonfumigated nests (Fig. 1). Cliff Swallows occupying parasite-free vs. infested nests show no differences in average clutch size (Brown and Brown 1999). There are at least two possible reasons for the similarities between fumigated and nonfumigated nests (Fig. 1). One is that we usually began fumigation at a colony during egg-laying (Brown and Brown 1996), meaning birds from both fumigated and nonfumigated nests may have experienced similar levels of ectoparasitism in the colony prior to egg-laying. A second is that fumigation at a site had no effect on the extent of ectoparasitism a female may have experienced elsewhere prior to settling, and females visit several colonies before choosing one (Brown and Brown 1996). Many late-nesters in Cliff Swallows are birds

whose nests failed at other sites, often in response to heavy ectoparasitism (Brown and Brown 1996). Thus, if clutch size reflects a bird's recent history of ectoparasitism, that history was unlikely to have been changed to any degree by our nest fumigation.

In their study of Tree Swallows, Winkler and Allen (1996) emphasized the importance of age and thus experience in analyzing the seasonal decline in reproductive success. First-year Tree Swallows lay smaller clutches and are generally less successful than older birds (Stutchbury and Robertson 1988). Much of the seasonal decline in Tree Swallow clutch size can be explained by younger females laying fewer eggs later in response to their lack of experience as foragers (Winkler and Allen 1996). Unfortunately, unlike Tree Swallows, Cliff Swallows cannot be aged by plumage characteristics, and we could not rigorously analyze age effects in our study. Based on banding data, we know that yearling Cliff Swallows do lay slightly smaller clutches than older birds (Brown and Brown 1996), but we have no good information on age-related laying times. Again unlike Tree Swallows, in which adults often arrive on the breeding grounds well in advance of yearlings (Cohen 1978, Stutchbury and Robertson 1985), Cliff Swallows exhibit relatively few age-related differences in arrival times (Brown and Brown 1996). This alone would suggest that age and experience in Cliff Swallows are less likely to explain the seasonal decline in clutch size, unless yearlings take longer than adults to secure breeding sites or initiate laying after arrival.

With no evidence for a seasonal decline in food availability or age-related foraging differences or laying times, we conclude that the sea-

sonal decline in clutch size among Cliff Swallows is most likely a strategic response to increasing levels of ectoparasitism (Richner and Heeb 1995). The lack of attention to the effect of ectoparasites on clutch size may be due in part to the fact that most studies have been on hole-nesters occupying nesting boxes where the effects of ectoparasites are often artificially minimized by nest-box cleaning (Møller 1989).

DIRECTIONAL SELECTION ON LAYING DATE?

The seasonal decline in reproductive success seen in most birds should lead to strong directional selection for earlier breeding times, especially because laying date has moderately high heritability in some species (van Noordwijk et al. 1981, Cooke and Findlay 1982, Gustafsson 1986). That laying date apparently has not undergone widespread directional selection has perplexed ornithologists, and led to suggestions that high-quality females are constrained to breed earlier than is optimal (Price et al. 1988) or that there is no additive genetic variance for breeding time (Winkler and Allen 1996). Neither of these seem likely in general or for Cliff Swallows in particular. A more likely possibility is that there are life-history tradeoffs associated with laying date, and unidentified costs of early nesting or benefits of late nesting prevent directional selection on breeding time and may lead to stabilizing selection on laying date. That earlier birds fledge more young in Cliff Swallows (Fig. 4) and other species is indisputable and suggests that any life-history tradeoffs must involve either first-year survival of young (recruitment) or parental survival.

Among birds in general, first-year survival (recruitment) tends to parallel the pattern seen for fledging success, with later-hatched young less likely to survive their first year (Hochachka 1990, Harris et al. 1992, Verhulst et al. 1995), although a caveat must be that appropriate statistical techniques (Lebreton et al. 1992) have seldom been used to analyze seasonal patterns in recruitment. We found yearly variation in recruitment of Cliff Swallows (Fig. 5), and in some years later-hatched young had higher first-year survival probabilities. This suggests that later-hatched young in Cliff Swallows do not necessarily have lower reproductive value than birds born earlier, in contrast to the prevailing assumption in discussions of breeding-time evolution (Drent and Daan 1980, Daan et al. 1990,

Rowe et al. 1994). Still, the earlier breeders had higher annual reproductive success in most years (Fig. 6). This would suggest directional selection on Cliff Swallow breeding time.

Largely ignored in studies of breeding-time evolution, however, is the effect of laying date on parental survival. In Cliff Swallows, parental survival was apparently greater for later-nesting females, with the latest breeders showing recapture percentages twice that of the earliest breeders (Fig. 7). Only our study and that of Nilsson (1994) on Blue Tits have shown an advantage to late nesting. Our data suggest a major cost to early nesting, at least for females. Selection need operate only on females because laying date is under their control. Given the dangers associated with bouts of cold weather in late spring that reduce food availability (Brown and Brown 1996, 1998b), survival costs of early nesting for adults—especially females—seem likely and could be enough to prevent directional selection on breeding time (Svensson and Nilsson 1995). Later-nesting Cliff Swallows also invest less time in incubation (Fig. 3), an activity that may be more costly than often assumed (Heaney and Monaghan 1996), and late-nesting females have greater body mass (are in better condition) during nestling rearing (Fig. 9b).

Our study emphasizes the importance of annual variation in fitness components associated with laying date: in only 6 of 11 years was offspring recruitment highest for the earliest nesters, and in 2 of 7 years annual reproductive success was highest for intermediate-date breeders. Annual variation in ectoparasite load, perhaps mediated by weather conditions (Brown and Brown 1996), may account for these differences. Our results illustrate the danger of making conclusions from 1–2 year studies, which are common especially among those that manipulate clutch size or laying date. Svensson (1997) also found yearly variation in Blue Tits, detecting directional selection on breeding date in 2 of 3 years and stabilizing selection in the third season. In a 25-year study of Great Tits, early nesting was selected for in some years, yet in other seasons intermediate- or late-nesting was apparently favored (van Noordwijk et al. 1981). As illustrated by Cliff Swallows, long-term studies, coupled with experiments such as fumigation, may provide insights into the seasonal decline in reproductive success and the evolution of laying date.

ACKNOWLEDGMENTS

For field assistance, we thank Cathy Boersma Anderson, Carol Brashears, Karen Brown, Rachel Budelsky, Barbara Calnan, Sasha Carlisle, Beth Chasnoff, Miyoko Chu, Zina Deretsky, Laurie Doss, Kristen Edelmann, Jessica Thomson Fiorillo, Ellen Flescher, Jennifer Grant, Winnie Hahn, Leila Hatch, Audrey Hing, Jerri Hoskyn, Sarah Huhta, Laura Jackson, Deborah Johnson, Veronica Johnson, Mike Kostal, Josef Kren, Lorky Libaridian, Bara MacNeill, Kathi Miller, Christine Mirzayan, Laura Molles, Laura Monti, Cecily Natunewicz, Charlene Patenaude, Bruce Rannala, Barbara Raulston, Gabriela Redwine, Craig Richman, Kara Rodgers, Sarah Rosenberg, Annemarie Rundquist, Todd Scarlett, Martin Shaffer, Lora Sherman, Karen Van Blarcum, and Zoe Williams. The School of Biological Sciences at the University of Nebraska-Lincoln (UNL) allowed use of the facilities at the Cedar Point Biological Station. Mathew Werner at the UNL Department of Agricultural Meteorology provided climatological data. For financial support, we thank the National Science Foundation (grants BSR-8407329, BSR-8600608, BSR-9001294, BSR-9015734, DEB-9224949, DEB-9496113, DEB-9613638), the Erna and Victor Hasselblad Foundation, the National Geographic Society (grants 3244-85, 3996-89, 4545-91, 5469-95), the American Philosophical Society, Princeton University, the University of Tulsa, Yale University, the Cedar Point Biological Station, the Chapman Fund of the American Museum of Natural History, the National Academy of Sciences, Sigma Xi, and Alpha Chi.

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