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## FITNESS COMPONENTS ASSOCIATED WITH CLUTCH SIZE IN CLIFF SWALLOWS

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**ABSTRACT.**—We report measures of annual reproductive success and survival probabilities of adult and offspring Cliff Swallows (*Petrochelidon pyrrhonota*) associated with clutches of different sizes in southwestern Nebraska from 1982 to 1997. Clutch size 4 was the most common (47.6% of nests). Mean clutch size varied among years, mostly through differences in the proportions of clutch sizes 3 and 4. Temperature and rainfall during egg laying were unrelated to mean annual clutch size. Incubation period declined slightly with clutch size, suggesting no incubation costs associated with larger clutches. Fledging success increased with clutch size. Ectoparasites lowered fledging success significantly in clutch sizes 3 and 4 but not in smaller or larger clutch sizes. First-year survival probability was unaffected by clutch or brood size when ectoparasites were removed, but under natural conditions survival probabilities varied among years and differed significantly among birds reared in brood sizes 1 to 2, 3 to 4, and 5. Birds tending clutch size 4 produced the highest number of young recruited as breeders in four of eight years; in the remaining years, birds tending clutch size 5 apparently did best. Fitness associated with clutch size 5 varied significantly with temperature during brood rearing, being lowest in warm years. Averaged over all years, the highest fitness was conferred at clutch size 5. Parental survival did not differ among clutch or brood sizes for birds under natural levels of ectoparasitism. Body mass of nestlings at 10 days did not vary among clutch sizes in nonfumigated nests and was significantly higher for nestlings in fumigated nests only for the intermediate clutch sizes (2 to 4). Classical life-history tradeoffs probably cannot account for the observed distribution of clutch sizes in Cliff Swallows. Climate and ectoparasite load vary enough annually and are unpredictable enough that Cliff Swallows apparently pursue the risk-averse strategy of laying smaller clutches on average than they can sometimes raise. Ectoparasitism accounted for much of the risk associated with producing clutch size 5, but Cliff Swallows did not adjust their clutch sizes in response to levels of ectoparasitism. Clutch size in aerial insectivores such as swallows may also reflect energetic constraints associated with egg production early in the breeding season when food is often reduced by cold weather. Received 12 January 1998, accepted 21 September 1998.

THE STUDY OF AVIAN LIFE HISTORIES has been influenced heavily by David Lack's (1947, 1954) view that selection should favor birds that lay a clutch size that yields the most surviving offspring. However, many species produce clutches smaller than the most productive size (Klomp 1970, Stearns 1992, VanderWerf 1992). Numerous hypotheses have been proposed to explain this paradox. That clutch size represents a tradeoff between current and future reproduction, with birds producing fewer, higher-quality offspring in the present year while increasing their chances of surviving to reproduce the next year, has been the most popular explanation for deviations from Lack's prediction. Survival studies show conflicting results, however, some demonstrating a cost of large

clutch size to parents or offspring (supporting Lack) and others revealing no detrimental effect of increased clutch size (Murphy and Haukioja 1986, Nur 1988a, Stearns 1992, VanderWerf 1992). The early emphasis in studies of clutch size was to examine potential costs associated with brood rearing, but the energetic costs of egg production and incubation are now recognized as additional factors that may lead to smaller clutch sizes than predicted by Lack (Monaghan et al. 1995, Monaghan and Nager 1997).

Another explanation for the discrepancy between the most common and the most productive clutch sizes centers on environmental uncertainty and the risk it causes for individuals that rear larger clutches (Mountford 1973, Boyce and Perrins 1987, Nur 1987, Yoshimura and Shields 1992). When fitness tends to vary

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more for birds tending large clutches, selection generally will favor a smaller clutch as the best risk-averse strategy. This assumes that environmental conditions are sufficiently uncertain to prevent birds from predicting them at the time of laying and facultatively adjusting their clutch sizes in response. Testing for environmental uncertainty requires data on clutch size and fitness over multiple years from the same population; thus, only long-term studies can address this hypothesis. Despite the plethora of clutch-size studies (see Stearns 1992), few have lasted long enough to provide sufficient information on temporal variability. An exception was Boyce and Perrins (1987), who found that reduced fitness for Great Tits (*Parus major*) rearing large clutches in the occasional bad years was enough to select for smaller average clutch sizes than could be produced in good or average years.

A more recent hypothesis has provided another explanation for deviations from the "Lack" clutch size (Richner and Heeb 1995). When nests are infested by ectoparasites with short life cycles, which permits rapid parasite buildup during the period of nestling growth, larger broods will support more total parasites, and the condition of fledglings will be impaired. Birds may reduce their clutch size in response (Richner and Heeb 1995). The potential effect of ectoparasitism on clutch size has not been widely appreciated (Møller 1991), perhaps because many studies of clutch size have been on hole-nesting species that occupy nest boxes with unnaturally low levels of ectoparasitism (Møller 1989).

In this paper, we examine measures of reproductive success and annual survival of adults and offspring associated with clutches of different sizes in colonial Cliff Swallows (*Petrochelidon pyrrhonota*). We use these fitness components to estimate the success of different clutch sizes, assess the degree to which the most common clutch size differs from the most productive, and examine potential life-history tradeoffs between clutch size and survival. Throughout, we investigate yearly differences in fitness components, specifically to examine whether environmental uncertainty and higher annual variance in reproductive success associated with larger clutches can account for discrepancies between the most common and the most productive clutch sizes (see Boyce and

Perrins 1987). We experimentally removed nest ectoparasites to assess their potential effect on clutch-size evolution and address Richner and Heeb's (1995) generation-time hypothesis. Our study differs from many previous ones on clutch size because of its long-term approach (up to 11 years of data in some analyses), use of modern statistical methods (Lebreton et al. 1992) to estimate annual survivorship for first-year birds, explicit focus on the role of ectoparasitism, and large sample sizes (more than 8,800 nests in total).

#### METHODS

*Study site and study animals.*—Our research is conducted along the North and South Platte Rivers near Ogallala, primarily in Keith and Garden counties, southwestern Nebraska. Our study area is approximately 150 × 50 km and contains about 160 colony sites where Cliff Swallows breed. The study site is described in detail by Brown and Brown (1996). Cliff Swallows (body mass 20 to 28 g) are Neotropical migrants that breed throughout most of western North America and winter in South America. They build gourd-shaped mud nests beneath overhanging rock ledges on the sides of steep cliffs or underneath the protected eaves of artificial structures. Cliff Swallows often breed in dense colonies. In southwestern Nebraska, mean colony size is  $393.0 \pm \text{SE of } 24.3$  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 per year (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 hematophagous ectoparasites. In southwestern Nebraska, the two most common ones are the swallow bug (Hemiptera: Cimicidae: *Oeciacus vicarius*) and a bird flea (Siphonaptera: Ceratophyllidae: *Ceratophyllus celsus*). These insects reside primarily in Cliff Swallow nests or the adjacent nesting substrate. They feed on blood of adults and nestlings, and in the case of swallow bugs, they have substantial effects on nestling survival and health (Brown and Brown 1986, 1996).

*Nest checks.*—We checked nests at intervals of one to three days from shortly before egg laying until eggs hatched or the nest failed. Nest contents were observed with the aid of a dental mirror and flashlight. Clutch size was the maximum number of eggs appearing in a nest. In some cases, clutch size included eggs laid or transferred by conspecific brood parasites. Cliff Swallows often parasitize neighboring nests within a colony (Brown and Brown 1988a,

1989, 1998a). We did not attempt to correct for known cases of parasitism because parasitic eggs were not marked, preventing us from knowing the exact fate of many of them (especially when eggs were tossed from a nest by a conspecific; Brown and Brown 1988b). Once hatching date was determined, we did not check a nest again until the nestlings were 10 days old. At that time, nestlings were banded, weighed, and examined for ectoparasites. All swallow bugs and fleas anywhere on a nestling's body were counted. Parasite counts and 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." Unhatched eggs were those that remained when nestlings were processed at 10 days. Nestling survival was based on young surviving to 10 days, which is an accurate relative index of survival to fledging in Cliff Swallows. All years for which we had relevant data are included in each analysis; missing years reflect our not collecting that type of data in that season.

*Fumigation.*—To test the possible relationship between ectoparasitism and clutch size, we fumigated nests by application of a short-lived acaricide called Naled (also known as Dibrom) to the outside of nests and the surrounding substrate every 2 to 7 days throughout the nesting season. This fumigant was highly effective against swallow bugs, which were the principal cause of nestling mortality (see 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. This site, part of the University of Nebraska'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 associated with a given clutch or brood size. We banded 87,337 adults and nestlings from 1982 through 1996 and typically obtained 16,000 to 21,000 recaptures each season (see Brown and Brown 1996). We monitored the presence of banded birds at 25 to 35 colony sites each summer by systematically mist netting at each site. 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. Birds were assigned as owners of nests based on observations of color-marked individuals (white forehead patches painted in unique three-color stripes) or from capture of individuals inside nests. Body mass of adults was recorded each time a bird was captured, and measures were assigned to the time periods of nest building and egg laying or feeding of nestlings, depending on when the bird was encountered.

We used all cohorts recaptured through 1996 for survival analyses. Because our most recent cohort with clutch- or brood-size data was from 1993, this gave us at least three years of recapture for all cohorts. After three 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 different clutch and brood sizes using the 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. We use the notation of Lebreton et al. (1992) in which annual survival probability is denoted  $\phi$  and recapture probability  $p$ . Subscripts indicate whether a model incorporates time dependence in a parameter estimate (e.g.  $\phi_t, p_t$ ), an effect of age (and if so, how many age classes; e.g.  $\phi_{a2}, p_{a2}$ ), constancy over time (e.g.  $\phi, p$ ), an effect of group classification (if so, how many groups; e.g.  $\phi_{gs}, p_{gs}$ ), or an interaction between group and time (e.g.  $\phi_{tgs}, p_t$ ). 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 a variety of more general yet biologically relevant models incorporating various combinations of age, group, and time dependence (see Brown and Brown 1998a).

We compared models that were nested (e.g.  $\phi_t, p_t$  vs.  $\phi, p_t$ ) with a likelihood-ratio test. SURGE provides a relative deviance (DEV),  $-2 \ln L(\theta)$ , for each model fitted, and the difference among DEVs is the  $\chi^2$  statistic with degrees of freedom equal to the difference in the number of estimable parameters between the two models (Lebreton et al. 1992). To compare models that were not nested (e.g.  $\phi_{a2}, p_t$  vs.  $\phi_t, p_{g2}$ ), we used Akaike's Information Criterion (AIC; Akaike 1973) and selected those with the lowest AICs as the best-fitting models.

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 a group-effect model did not provide a significantly better fit, the more parsimonious model without a group effect was accepted, and we inferred no difference among the groups. We show only the fits of the three to six models with the lowest AICs. Because SURGE estimates local survival only and cannot distinguish between permanent emigration and mortality, our survival estimates are relative ones

that are useful in comparing among different classes of birds, but they do not represent absolute survival.

For a given model, the number of estimable parameters reported may differ slightly from those in Brown and Brown (1998a) because here we used a new version of SURGE with automatic parameter counting (E. Cooch pers. comm.). These discrepancies had no effect on the results of the model fitting for either the analyses reported here or those of Brown and Brown (1998a).

SURGE and the capture-recapture methodology on which it is based make the implicit assumption that an individual's status does not change during the period in which its survival is estimated. This assumption is met for analyses of first-year survival in relation to natal clutch or brood size because these characteristics of an individual are fixed. However, the status of adults with regard to annual clutch size or brood size is not fixed because birds can lay clutches of different sizes in different years. Thus, SURGE is not appropriate for estimating annual survival of breeding adults in relation to clutch size or brood size. 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 used observed recapture probabilities to infer relative survival among adults associated with different clutch and brood sizes. We tabulated the percentage of adults recaptured the next season in relation to their clutch and brood size the previous year; individuals "missed" in the next year but recaptured in a later year did not figure in our recapture analysis because their presence could have been affected by their tending a different clutch or brood size in the intervening year(s).

## RESULTS

*Clutch-size distribution.*—The distributions of clutch sizes for 10 years between 1982 and 1997 (Fig. 1) show that clutch size 4 is the most common in Cliff Swallows (47.6% of 8,835 nests). Clutch size 3 is the next most common (32.7%), followed by clutch sizes 2 (8.4%) and 5 (6.8%). Clutches  $\geq 6$  eggs are unusual (0.8%). These distributions combine clutch sizes from fumigated and nonfumigated nests because average clutch size was unaffected by parasite removal (Table 1). Only in 1988 did average clutch size differ between fumigated and nonfumigated

nests, with larger clutches produced in parasite-free nests (Table 1). The distribution of clutch sizes varied little among years (Fig. 1) even though average clutch size differed significantly among years for both nonfumigated (Kruskal-Wallis test,  $\chi^2 = 30.7$ ,  $df = 9$ ,  $P < 0.001$ ) and fumigated ( $\chi^2 = 19.2$ ,  $df = 5$ ,  $P = 0.002$ ) nests. The principal differences among years were the relative proportions of clutch sizes 3 and 4 (Fig. 1).

*Clutch size relative to weather.*—Yearly variation in clutch size could be caused by seasonal differences in weather patterns, especially for insectivorous birds such as Cliff Swallows that depend on a food supply that is highly sensitive to temperature and rainfall (Brown and Brown 1996, 1998b). Seasonal climatic conditions vary markedly among years in our central Great Plains study area. For example, 1988 was one of the warmest summers during the last 100 years and was followed by one of the coldest in 1992 (Brown and Brown 1996). Mean clutch size per year did not vary significantly with average daily high temperature (nonfumigated nests,  $r_s = -0.15$ ,  $P = 0.70$ ,  $n = 9$ ; fumigated nests,  $r_s = -0.39$ ,  $P = 0.39$ ,  $n = 7$ ) or total precipitation (nonfumigated nests,  $r_s = 0.38$ ,  $P = 0.31$ ,  $n = 9$ ; fumigated nests,  $r_s = 0.56$ ,  $P = 0.19$ ,  $n = 7$ ) recorded between 1 May and 15 June each year. This period was likely to have the greatest weather-related influence on clutch size because 85.9% of clutches ( $n = 6,996$ ) were initiated during this 46-day span. We explored other time intervals (e.g. prior to 1 May, subsets of 1 May to 15 June) in our analyses and also found no effect of weather on clutch size.

*Incubation period relative to clutch size.*—One measure of the production costs of different clutch sizes is the time taken to incubate them. Incubation period, measured from the laying of the last egg to the hatching of the first nestling, was shortest for clutch sizes 4 and 5 (Fig. 2). For clutch sizes 3, 4, and 5, incubation periods were significantly shorter in the absence of ectoparasites (Wilcoxon tests,  $P \leq 0.02$ ; for clutch sizes 1 and 2,  $P \geq 0.28$ ), although all differences in incubation period among clutch sizes were rel-

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FIG. 1. Distribution of clutch sizes by year in Cliff Swallows in southwestern Nebraska. Data from nonfumigated and fumigated nests are combined.

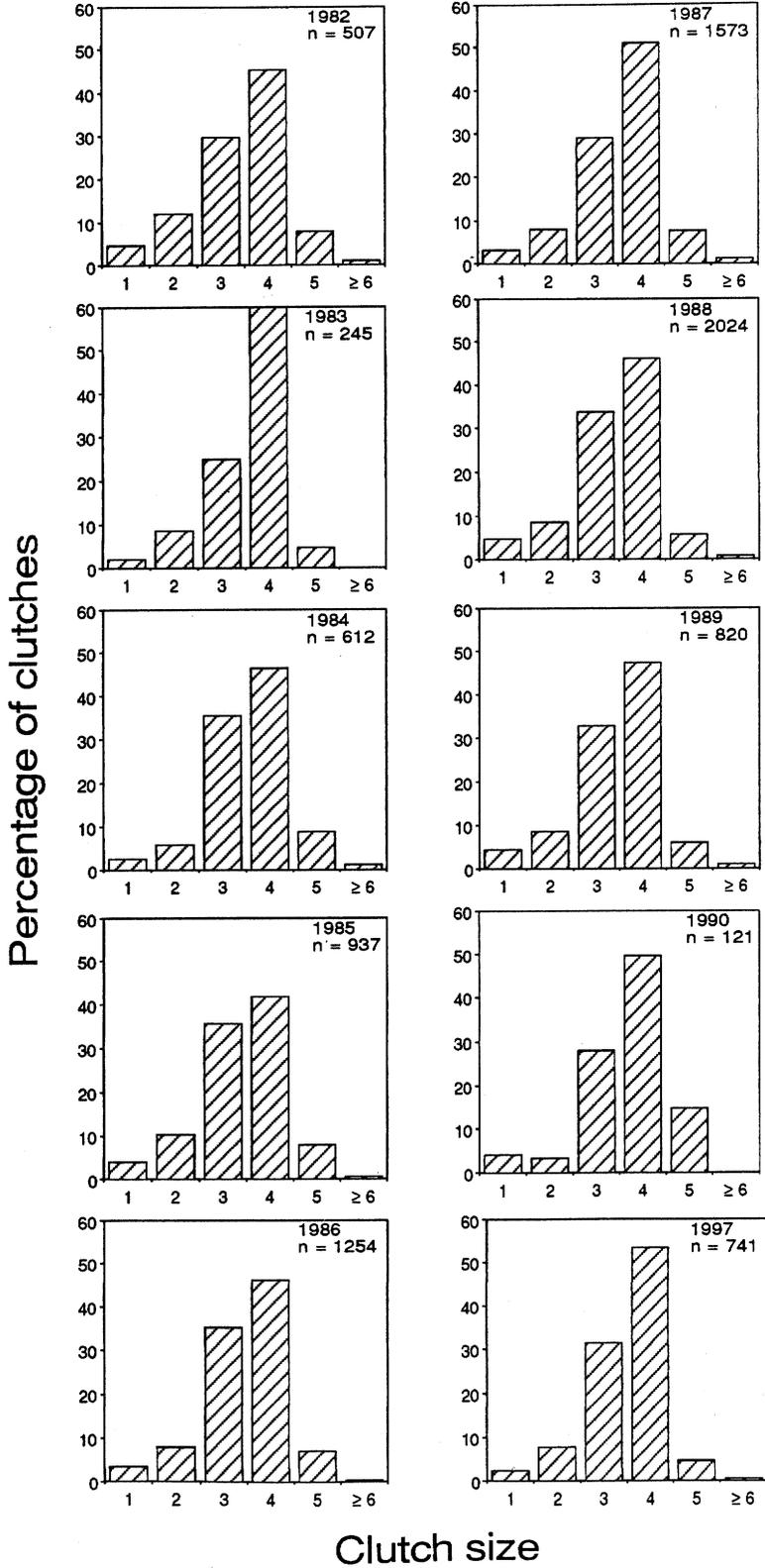


TABLE 1. Clutch size of Cliff Swallows ( $\bar{x} \pm SE$ , with  $n$  in parentheses) occupying nests that had been fumigated to remove ectoparasites, and those not fumigated, during six years in southwestern Nebraska.

Year	Fumigated nests	Nonfumigated nests	$P^a$
1984	3.57 $\pm$ 0.05 (236)	3.57 $\pm$ 0.04 (376)	0.96
1986	3.50 $\pm$ 0.03 (991)	3.39 $\pm$ 0.06 (263)	0.41
1987	3.57 $\pm$ 0.03 (1,250)	3.54 $\pm$ 0.05 (323)	0.46
1988	3.45 $\pm$ 0.02 (1,748)	3.28 $\pm$ 0.06 (276)	0.02
1989	3.46 $\pm$ 0.04 (689)	3.49 $\pm$ 0.08 (131)	0.47
1997	3.49 $\pm$ 0.07 (161)	3.53 $\pm$ 0.04 (580)	0.76
All	3.48 $\pm$ 0.01 (6,008)	3.49 $\pm$ 0.02 (2,827)	0.11

<sup>a</sup> Based on Wilcoxon test within years.

atively small. We found a similar result when each year was analyzed separately.

**Fledging success relative to clutch size.**—Fledging success, as measured by the number of nestlings surviving to 10 days, generally increased with clutch size (Fig. 3A). This also held when fledging success was expressed as the percentage of clutches producing at least one surviving nestling (Fig. 3B), averaged over all years. Success peaked at clutch size 5 and appeared to decline slightly for clutch sizes  $\geq 6$ . The pattern was similar among nonfumigated and fumigated nests (Fig. 3). Nestling survival was higher in fumigated nests, reflecting the deleterious effects of swallow bugs. The effects

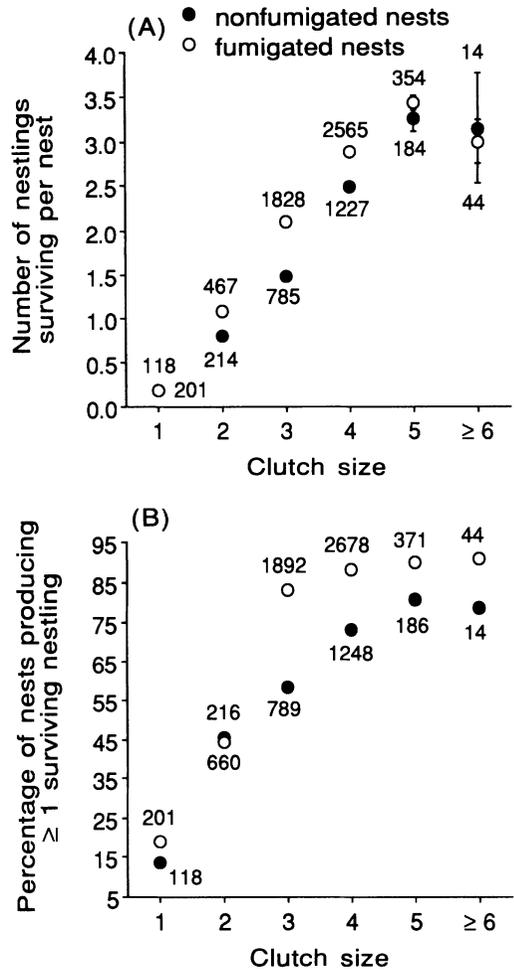


FIG. 3. Mean ( $\pm SE$ ) number of Cliff Swallow nestlings surviving per nest (A) and percentage of nests producing at least one surviving nestling (B) relative to clutch size. Sample sizes (number of nests) shown above or below error bars. The number of nestlings surviving varied significantly with both clutch size and fumigation treatment (two-way ANOVA,  $P < 0.0001$ ). The proportion of nests that was successful varied significantly with both clutch size and fumigation treatment ( $\chi^2$  tests,  $P < 0.0001$ ).

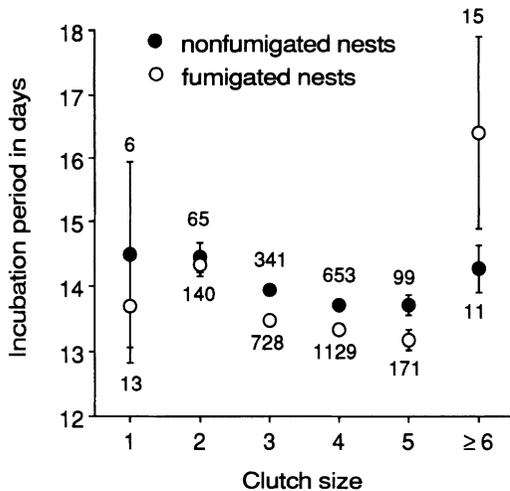


FIG. 2. Mean ( $\pm SE$ ) incubation period of Cliff Swallows relative to clutch size. Sample sizes (number of nests) shown above or below error bars. Incubation period varied significantly with both clutch size and fumigation treatment (two-way ANOVA,  $P < 0.0001$ ).

of bugs were greatest in clutches of 3 and 4 eggs, the two most common clutch sizes (Fig. 3). Fledging success expressed as the mean number of surviving young did not differ significantly between fumigated and nonfumigated nests for the smallest (1) or the two largest (5 and  $\geq 6$ ) clutch sizes (Wilcoxon tests,  $P \geq 0.41$ ); success differed significantly between fumigated and nonfumigated nests for clutch sizes 2, 3, and 4 ( $P < 0.001$ ; Fig. 3A).

Fledging success showed similar patterns among years for both nonfumigated and fumigated nests (Fig. 4). Clutch size 5 was consistently as productive (usually more so) than the smaller clutches in both the presence and absence of ectoparasites. Conclusions about clutch size 6 are risky owing to small sample sizes; in some years, fledging success for clutch size 6 was higher than that of clutch size 5, whereas in other years it was much lower (Fig. 4).

Fledging success is determined by how many eggs are lost before hatching, how many nestlings are lost before fledging, and how many eggs fail to hatch. Egg loss was lowest for the more common clutch sizes 3 and 4 (Fig. 5A), whereas loss of nestlings (Fig. 5B) and the number of unhatched eggs (Fig. 5C) tended to increase with clutch size. Patterns were similar for nonfumigated and fumigated nests, although in general the biggest differences between nests with and without parasites again were at clutch sizes 3 and 4 (Figs. 5B, C). In comparing fumigated and nonfumigated nests, significant differences in the number of eggs lost occurred only for clutch sizes 2 and 3 (Wilcoxon tests,  $P \leq 0.03$ ; for other clutches,  $P \geq 0.11$ ); significant differences in the number of nestlings lost occurred only for clutch sizes 3 and 4 ( $P \leq 0.008$ ; for other clutches,  $P \geq 0.17$ ); and significant differences in unhatched eggs occurred for clutches 3, 4, and 5 ( $P \leq 0.03$ ; for other clutches,  $P \geq 0.23$ ).

*First-year survival relative to clutch size and weather.*—Model fitting revealed no significant differences among natal clutch sizes in probability of first-year survival for nestlings from either nonfumigated or fumigated nests (Table 2). However, natal clutch size does not necessarily reflect the brood size a bird is reared in, given the loss of eggs and nestlings and the fact that some eggs do not hatch (Fig. 5). Brood size, measured as the number of young surviving to day 10, better reflects actual rearing conditions and the potential for nestling competition. For fumigated nests, brood size had no apparent influence on first-year survival; a model without brood size as a group effect (model 9; Table 3) provided a significantly better fit than ones that modeled either each brood separately or fewer brood-size classes. For birds from nests exposed to natural levels of ectoparasites, however, first-year survival differed significantly

among natal brood sizes. An age-stratified CJS model with brood sizes 1 and 2 combined, brood sizes 3 and 4 combined, and brood size 5 (no data were available for brood size  $\geq 6$ ) provided the best fit (model 13; Table 3). First-year survival estimates (from model 13) varied significantly among years (Fig. 6). In three years (1984, 1990, 1993), birds from brood sizes 1 or 2 had the highest survival; in four years (1983, 1986, 1987, 1988), birds from brood sizes 3 or 4 had the highest survival; and in four years (1982, 1989, 1991, 1992), birds from brood size 5 had the highest survival. Averaged over all years, first-year survival probabilities for birds from brood sizes 1 to 2, 3 to 4, and 5 were 0.153, 0.210, and 0.267, respectively.

Given these yearly differences, we examined whether annual variation in climatic conditions during the breeding season potentially influenced first-year survival. We used weather data for the month of June because most Cliff Swallows in our study area hatch and are raised during that month (Brown and Brown 1996). Total precipitation during June ( $n = 11$  years) had no effect on first-year survival probability (brood sizes 1 to 2,  $r_s = 0.32$ ,  $P = 0.34$ ; brood sizes 3 to 4,  $r_s = 0.17$ ,  $P = 0.61$ ; brood size 5,  $r_s = -0.18$ ,  $P = 0.59$ ). However, average daily high temperature for June was significantly associated with first-year survival of birds from brood size 5, with survival declining in warmer years ( $r_s = -0.77$ ,  $P = 0.005$ ,  $n = 11$ ). There was no significant correlation between temperature and survival for birds from brood sizes 1 to 2 ( $r_s = -0.36$ ,  $P = 0.27$ ,  $n = 11$ ) or 3 to 4 ( $r_s = -0.06$ ,  $P = 0.85$ ,  $n = 11$ ).

*Annual reproductive success relative to clutch size.*—The number of nestlings that survive to fledge (Fig. 4) is one measure of annual reproductive success (ARS). A better measure is the number of nestlings that enter the breeding population the next season. For nonfumigated nests, we estimated ARS (Fig. 7) by multiplying the number of young fledged (Fig. 4) by the probability of first-year survival for birds from broods of different sizes (Fig. 6). For fumigated nests, measures of ARS based on fledging success (Fig. 4) reflected relative recruitment the next year because first-year survival was not associated with clutch size or brood size in parasite-free nests.

When ARS was estimated using average yearly values for fledging success and first-year

survival, reproductive success generally increased with clutch size (Fig. 7). However, results varied among years. Considering only the mean values, in four of eight years the most common clutch size, 4 eggs, was the most productive; in the remaining four years, productivity was highest for clutch size 5 (Fig. 7). The superiority of clutch size 4 occurred in warm years when first-year survival of birds from broods of 5 was low. The error (standard deviation) associated with each ARS estimate was relatively high because we were estimating the variance of a product (Fig. 7).

*Parental survival relative to clutch size.*—The percentage of breeders recaptured the next year did not vary significantly among clutch sizes for either sex in the presence (males,  $\chi^2 = 3.84$ ,  $df = 3$ ,  $P = 0.28$ ; females,  $\chi^2 = 0.14$ ,  $df = 3$ ,  $P = 0.99$ ) or absence (males,  $\chi^2 = 0.95$ ,  $df = 4$ ,  $P = 0.92$ ; females,  $\chi^2 = 0.87$ ,  $df = 4$ ,  $P = 0.93$ ) of ectoparasites. The percentage of breeders recaptured the next year did not vary significantly with brood size for either sex in nonfumigated nests (males,  $\chi^2 = 3.78$ ,  $df = 3$ ,  $P = 0.29$ ; females,  $\chi^2 = 1.74$ ,  $df = 3$ ,  $P = 0.63$ ) but varied significantly with brood size for females in parasite-free nests (males,  $\chi^2 = 6.29$ ,  $df = 5$ ,  $P = 0.28$ ; females,  $\chi^2 = 20.2$ ,  $df = 5$ ,  $P = 0.001$ ).

*Ectoparasitism relative to clutch size.*—Clutch sizes 1 and  $\geq 6$  showed a marked difference in total swallow bugs per nest (those counted on all nestlings), but bug loads exhibited relatively little variation for clutch sizes 2 to 5 (Fig. 8A). Bugs per nestling declined from clutch size 2 to 5, with the lowest per capita bug loads in clutch size 5 (Fig. 8B). Except for an increase in clutch size  $\geq 6$ , flea numbers were similar among clutch sizes (Fig. 8).

*Nestling body mass relative to clutch size.*—Nestling body mass is a useful measure of the effects of ectoparasites and the potential rearing costs of different clutch sizes (Brown and Brown 1996). Mean body mass per nestling did not vary significantly with clutch size among nonfumigated nests; in the absence of ectoparasites, body mass varied significantly with

clutch size (Fig. 9). The difference in body mass between fumigated and nonfumigated nests was significant for clutch sizes 2, 3, and 4 (Wilcoxon tests,  $P \leq 0.0001$ ) but not for the other clutch sizes ( $P \geq 0.17$ ). As clutch size increased, the removal of ectoparasites had markedly less effect on nestling body mass (Fig. 9). In the presence of ectoparasites, only clutch size  $\geq 6$  resulted in nestlings of low body mass.

*Adult body mass relative to clutch size.*—Body mass of breeding females during egg laying varied significantly with clutch size (Fig. 10A); body mass was higher among females that laid larger clutches. In contrast, body mass of females during brood rearing did not vary significantly with clutch size, although mass tended to decline with clutch size for clutches 2 to 5 (Fig. 10A). Among breeding males, body mass during egg laying did not vary significantly with clutch size, but the overall pattern was similar to females in that heavier males were associated with larger clutches (Fig. 10B). Body mass during brood rearing declined significantly with clutch size for breeding males (Fig. 10B). Most of these clutch-size comparisons came from birds occupying nonfumigated nests; combining fumigated and nonfumigated nests for this analysis was warranted because adult body mass was unaffected by nest fumigation (Brown and Brown 1996).

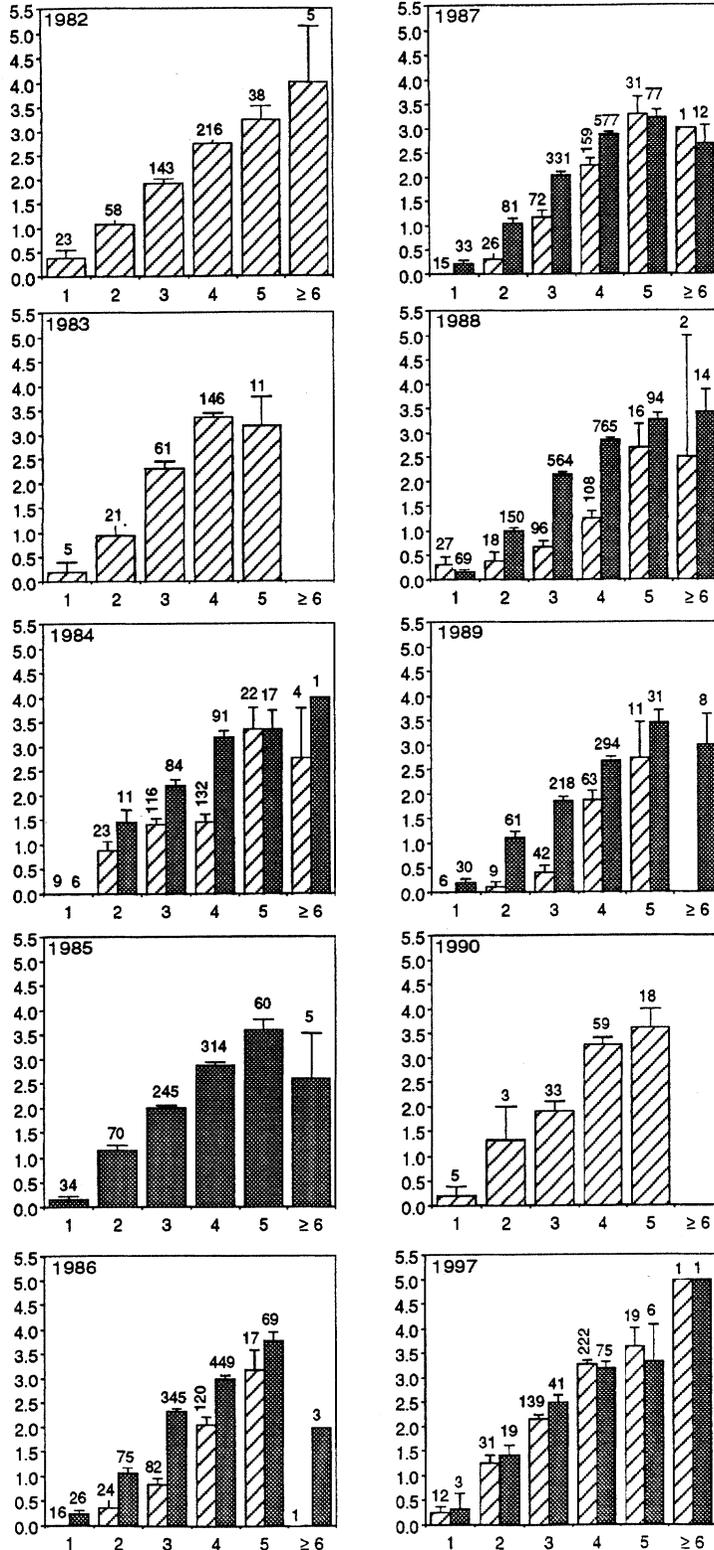
## DISCUSSION

Our results for Cliff Swallows are similar to those for many other species in that the most common clutch size (4 eggs) does not seem to be the most productive (5 eggs). However, we found substantial yearly variation, and the most common clutch size was the most productive in some years. This provides partial support for the contention that selection favors clutch sizes that produce the most young (Lack 1947, 1954). Ectoparasites seemed to inflict a serious cost for birds that raised the most common clutch sizes (3 and 4 eggs). The effect of ectoparasites on first-year survival also led to

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FIG. 4. Mean ( $\pm$ SE) number of Cliff Swallow nestlings surviving per nest relative to clutch size each year for nonfumigated nests (hatched bars) and fumigated nests (stippled bars). Sample sizes (number of nests) shown above error bars. The number of nestlings surviving varied significantly with both clutch size and year for nonfumigated and fumigated nests (two-way ANOVA,  $P < 0.0001$  for each comparison).

Number of nestlings surviving per nest



Clutch size

lower success of clutch size 5 in some years and was the principal reason that the most common clutch size, 4 eggs, was the most productive in those years.

*Tradeoffs in clutch size.*—The view that clutch size represents a tradeoff between current and future reproduction has a long history (Williams 1966, Charnov and Krebs 1974) and has been perhaps the most popular explanation for the observed discrepancy between the modal and the most productive clutch sizes (see Nur 1987, 1988a; Linden and Møller 1989; Dijkstra et al. 1990; Stearns 1992). This tradeoff may take a variety of forms: (1) offspring quality may be compromised by raising a larger clutch, especially when food is limiting, resulting in reduced offspring survival either before or after fledging (e.g. Perrins 1965; van Noordwijk et al. 1981; Nur 1984a, 1988b; Gustafsson and Sutherland 1988; Wiggins 1990); (2) parental survival may be reduced by the costs associated with producing, incubating, or provisioning a large clutch (e.g. Bryant 1979, Nur 1984b, Martin 1987, Dijkstra et al. 1990, Daan et al. 1996, Heaney and Monaghan 1996, Monaghan and Nager 1997); or (3) parental resistance to parasites and pathogens may be compromised by investing in a large clutch (Gustafsson et al. 1994, Oppliger et al. 1997). Experiments on many species show that investing heavily in a current clutch reduces a parent's future reproductive success (Stearns 1992). However, this cost of reproduction is often obscured by phenotypic correlations between clutch size and individual ability (Nur 1987, 1988a; Pettifor et al. 1988; Linden and Møller 1989).

The evidence from Cliff Swallows that clutches above the modal size are costly under

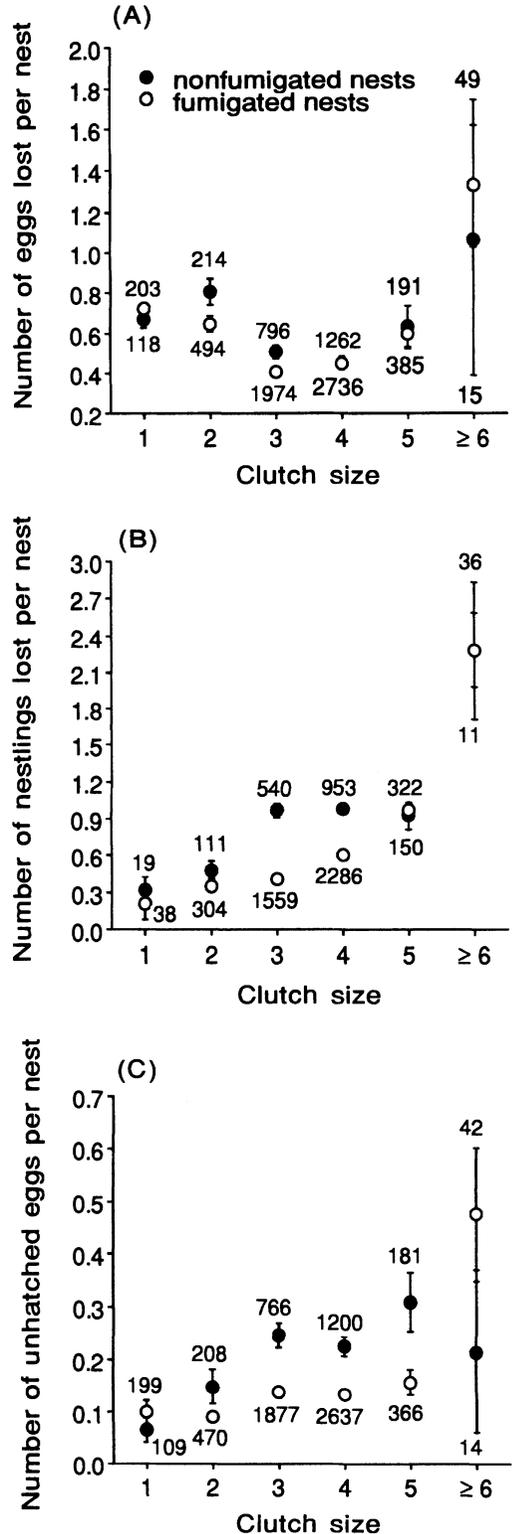


FIG. 5. Mean ( $\pm$ SE) number of Cliff Swallow eggs lost per nest (A), mean number of nestlings lost per nest (B), and mean number of unhatched eggs per nest (C) relative to clutch size. Sample sizes (number of nests) shown above error bars. The number of eggs lost varied significantly with clutch size (two-way ANOVA,  $P < 0.0001$ ) but not with fumigation treatment ( $P = 0.09$ ). The number of nestlings lost varied significantly with clutch size and fumigation treatment (two-way ANOVA,  $P < 0.0001$ ). The number of unhatched eggs varied significantly with both clutch size and fumigation treatment (two-way ANOVA,  $P < 0.0001$ ).

TABLE 2. Capture-recapture models and comparisons among models for Cliff Swallows banded as nestlings in relation to natal clutch size (see text for model notation).

Model	No. parameters <sup>a</sup>	DEV <sup>b</sup>	AIC <sup>c</sup>	Comparison <sup>d</sup>
<b>Fumigated nests</b>				
(1) $\phi_{a21r} p_{a21}$	34	17,972.0	18,040.0	Best fit; no differences among clutch sizes
(2) $\phi_{a21r_{g2r}} p_{a21}$	42	17,959.6	18,043.6	Groups = birds from clutch sizes 1 to 3, 4 to 5; (2) vs. (1), $\chi^2 = 12.4$ , $df = 8$ , $P = 0.13$
(3) $\phi_{a21r_{g2r}} p_{a21}$	40	17,970.7	18,050.7	Groups = birds from clutch sizes 1 to 2, 3 to 5; (3) vs. (1), $\chi^2 = 1.3$ , $df = 6$ , $P = 0.97$
(4) $\phi_{a21r_{g2r}} p_{a21}$	42	17,975.4	18,059.4	Groups = birds from clutch sizes 1 to 4, 5; (4) vs. (1), $\chi^2 = 3.4$ , $df = 8$ , $P = 0.91$
(5) $\phi_{a21r_{g5r}} p_{a21}$	110	17,888.0	18,080.0	Groups = birds from clutch sizes 1, 2, 3, 4, 5; (5) vs. (1), $\chi^2 = 84.0$ , $df = 76$ , $P = 0.25$
<b>Nonfumigated nests</b>				
(6) $\phi_{a21r} p_{a21}$	43	2,969.0	3,055.0	Best fit; no differences among clutch sizes
(7) $\phi_{a21r_{g2r}} p_{a21}$	56	2,950.3	3,062.3	Groups = birds from clutch sizes 2 to 3, 4 to 5; (7) vs. (6), $\chi^2 = 9.7$ , $df = 13$ , $P = 0.72$
(8) $\phi_{a21r_{g4r}} p_{a21}$	102	2,917.5	3,121.5	Groups = birds from clutch sizes 2, 3, 4, 5; (8) vs. (6), $\chi^2 = 51.5$ , $df = 59$ , $P = 0.74$

<sup>a</sup> Number of estimable parameters.

<sup>b</sup> Relative deviance.

<sup>c</sup> Akaike's Information Criterion.

<sup>d</sup> Respective sample sizes were 15, 207, 2,118, 3,966, and 1,183 for clutch sizes 1 to 5 in fumigated nests and 113, 695, 2,015, and 516 for clutch sizes 2 to 5 in nonfumigated nests.

natural conditions was mixed. Here, we contrast clutch size 5 with the smaller clutches because clutch size  $\geq 6$  occurred so rarely. Parental survival did not seem to be compromised by raising larger clutches, body mass of nestlings under natural conditions did not vary with clutch size, and clutch size 5 resulted in more total offspring surviving to fledging than did smaller clutch sizes. We found no evidence that clutch size 5 took longer (and thus was more costly) to incubate, a potential cost often neglected in considerations of clutch-size evolution (Ankney and MacInnes 1978, Smith 1989, Siikamaki 1995, Heaney and Monaghan 1996, Monaghan and Nager 1997). These results would be predicted if clutch size in Cliff Swallows reflects nonheritable variation in individual quality (see Price and Liou 1989), and they are consistent with results from long-term studies of other species (e.g. van Noordwijk et al. 1981, Boyce and Perrins 1987, Rockwell et al. 1987).

Body mass of males and females while feeding young tended to decline for the larger clutch sizes, suggesting that Cliff Swallows raising larger clutches were in poorer condition at the end of the breeding season than those raising smaller clutches. More important, first-year survival of birds from brood size 5 was re-

duced such that local recruitment of offspring in the next season was higher for broods of 4 in half of the eight years for which we had estimates. Ours is one of the few studies to demonstrate an offspring survival cost of larger broods under natural conditions. We may have been able to show this in part because we used modern statistical methods to estimate first-year survival. Thus, birds raising clutch size 5 in some years are at a disadvantage by presumably expending more effort per successful recruit. In other years, however, we found no evidence of a cost associated with clutch size 5. Why, then, are clutches of 5 eggs so comparatively rare (6.8%) in Cliff Swallows?

*Environmental uncertainty and "bad" years.*—When environmental conditions vary from year to year, individuals may have little difficulty raising large clutches in favorable years. In other years, the same individuals may be unable to raise similarly large clutches without incurring substantial costs. Food availability is often thought to vary with environmental conditions and thus to directly affect prospects of success for different clutch sizes (Perrins 1965, Cody 1966, Murphy 1986, Hussell and Quinney 1987, Martin 1987, Forbes and Mock 1996). Parasite load may be another important component of environmental variability (see below).

TABLE 3. Capture-recapture models and comparisons among models for Cliff Swallows banded as nestlings in relation to natal brood size (see text for model notation).

Model	No. parameters <sup>a</sup>	DEV <sup>b</sup>	AIC <sup>c</sup>	Comparison <sup>d</sup>
<b>Fumigated nests</b>				
(9) $\phi_{a2v} P_{a2v}$	41	20,537.3	20,619.3	Best fit; no differences among clutch sizes Groups = birds from brood sizes 1 to 3, 4 to 5; (10) vs. (9), $\chi^2 = 17.9$ , $df = 17$ , $P = 0.39$ Groups = birds from brood sizes 1 to 4, 5; (11) vs. (9), $\chi^2 = 4.9$ , $df = 16$ , $P = 0.99$ Groups = birds from brood sizes 1, 2, 3, 4, 5; (12) vs. (9), $\chi^2 = 93.6$ , $df = 78$ , $P = 0.11$
(10) $\phi_{a2v} \phi_{g2v} P_{a2v}$	58	20,519.4	20,635.4	
(11) $\phi_{a2v} \phi_{g2v} P_{a2v}$	57	20,532.4	20,646.4	
(12) $\phi_{a2v} \phi_{g2v} P_{a2v}$	119	20,443.7	20,681.7	
<b>Nonfumigated nests</b>				
(13) $\phi_{a2v} \phi_{g2v} P_{a2v}$	97	5,119.2	5,313.2	Best fit; groups = birds from brood sizes 1 to 2, 3 to 4, 5 Groups = birds from brood sizes 1 to 2, 3 to 5; (14) vs. (13), $\chi^2 = 43.5$ , $df = 25$ , $P = 0.012$ ; although higher AIC, (13) considered better by likelihood-ratio test. Testing effect of brood size; (15) vs. (13), $\chi^2 = 101.2$ , $df = 46$ , $P < 0.0001$ Groups = birds from brood sizes 1 to 4, 5; (16) vs. (13), $\chi^2 = 55.7$ , $df = 21$ , $P = 0.0001$ Groups = birds from brood sizes 1 to 2 and 5 combined, 3 to 4; (17) vs. (13), $\chi^2 = 34.4$ , $df = 19$ , $P = 0.016$ Groups = birds from brood sizes 1, 2, 3, 4, 5; (18) vs. (13), $\chi^2 = 15.1$ , $df = 46$ , $P = 0.99$
(14) $\phi_{a2v} \phi_{g2v} P_{a2v}$	72	5,162.7	5,306.7	
(15) $\phi_{a2v} P_{a2v}$	51	5,220.4	5,322.4	
(16) $\phi_{a2v} \phi_{g2v} P_{a2v}$	76	5,174.9	5,326.9	
(17) $\phi_{a2v} \phi_{g2v} P_{a2v}$	78	5,153.6	5,309.6	
(18) $\phi_{a2v} \phi_{g2v} P_{a2v}$	143	5,104.1	5,390.1	

<sup>a</sup> Number of estimable parameters.

<sup>b</sup> Relative deviance.

<sup>c</sup> Akaike's Information Criterion.

<sup>d</sup> Respective sample sizes were 132, 918, 3,173, 3,756, and 524 for brood sizes 1 to 5 in fumigated nests and 60, 554, 1,835, 2,275, and 385 for brood sizes 1 to 5 in nonfumigated nests.

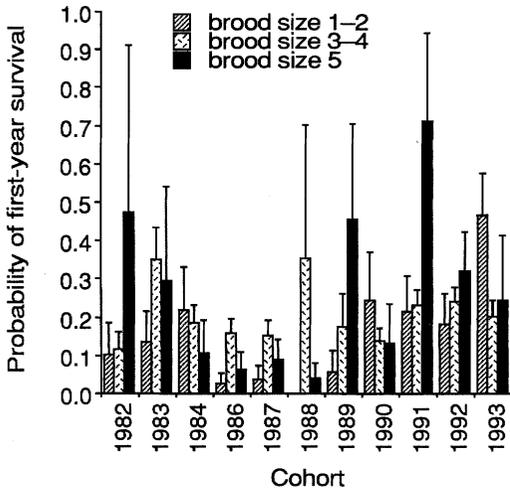


FIG. 6. Probability of first-year survival (from fledging to first breeding season) for Cliff Swallows from different brood sizes by year for nonfumigated nests. Cohort refers to natal year. Survival probabilities ( $\pm$  SD) were estimated with SURGE using model  $\Phi_{a2t} \gamma_{3a} p_{a2t}$  (see Table 3). Total sample sizes are given in Table 3.

Uncertainty causes greater variance in reproductive success (risk) associated with the larger clutch sizes (Boyce and Perrins 1987, Stearns 1992, Yoshimura and Shields 1992). If environmental conditions cannot be predicted, a risk-averse strategy of laying a smaller clutch size would be best (Mountford 1973, Bulmer 1985, Yoshimura and Shields 1992). Environmental variation can select for smaller clutch sizes on average and potentially can explain the Lack paradox (Boyce and Perrins 1987).

Environmental uncertainty can be addressed empirically only with long-term studies, and ours is similar to Boyce and Perrins' (1987) on Great Tits in demonstrating the importance of annual variation. In "good" years (e.g. 1982), clutch size 5 yielded a higher number of recruits than did all other clutch sizes, but in "bad" years (e.g. 1988), birds raising clutch sizes 3 or 4 did better than those raising clutch size 5. Cliff Swallows, like Great Tits, periodically encounter bad years for raising large clutches. These fitness differences (Fig. 7) may have been magnified by undetected clutch-size differences in parental survival. The reduction in body mass for females tending larger clutches suggests that parents of larger clutches have lower annual survival, because late-season body mass is directly associated with survival

of adult Cliff Swallows in general (Brown and Brown 1996).

The higher variance associated with clutch size 5 is illustrated by a comparison of the geometric means in estimated fitness across years. The geometric mean is regarded as the best measure of fitness for different clutch sizes in temporally variable environments (Bulmer 1985, Boyce and Perrins 1987, Boyce 1988, Stearns 1992). Arithmetic means for clutch sizes 1 to 5 were 0.014, 0.098, 0.272, 0.458 and 0.644 young recruited, respectively, compared with geometric means of 0.000, 0.000, 0.217, 0.407, and 0.458. Success of birds with clutch sizes 4 and 5 was more similar than arithmetic means might suggest. However, we still found the rarer clutch size 5 to have a higher estimated fitness.

If Cliff Swallows can predict environmental conditions at the time of laying, the frequency of clutch size 5 should have been higher in good years and lower in bad years. We found no evidence for this sort of facultative adjustment among years. Although overall clutch size differed among years, mostly due to different proportions of clutch sizes 3 and 4, yearly variation in clutch size was largely independent of fitness expectations. For example, the relative frequency of clutch size 5 in 1982, a "good" year for survival of offspring, did not differ from that in 1988, a "bad" year for clutch size 5 ( $\chi^2 = 2.42$ ,  $df = 1$ ,  $P = 0.12$ ). Furthermore, clutch size did not seem to be sensitive to weather conditions in the early phases of the breeding cycle.

Selection for smaller clutches is also expected whenever the clutch-size fitness function is asymmetrical (Mountford 1968), as it usually seems to be (Mountford 1973, Boyce and Perrins 1987, Yoshimura and Shields 1992, DeWitt 1997). If the distribution of fitness is severely truncated to the right (at larger clutch sizes) and clutch size is distributed normally, there will be a negative (to the left) skew in fitness as a function of clutch size. This can also result in selection for clutches smaller than the most productive. Although our data for clutch size  $\geq 6$  are limited, fitness is probably truncated to the right in Cliff Swallows. Clutches of  $\geq 6$  eggs were associated with substantially lower fledging success in some years, higher levels of ectoparasitism, lower nestling body mass, and lower adult body mass. On average, however, clutch size  $\geq 6$  fledged as many young, and was

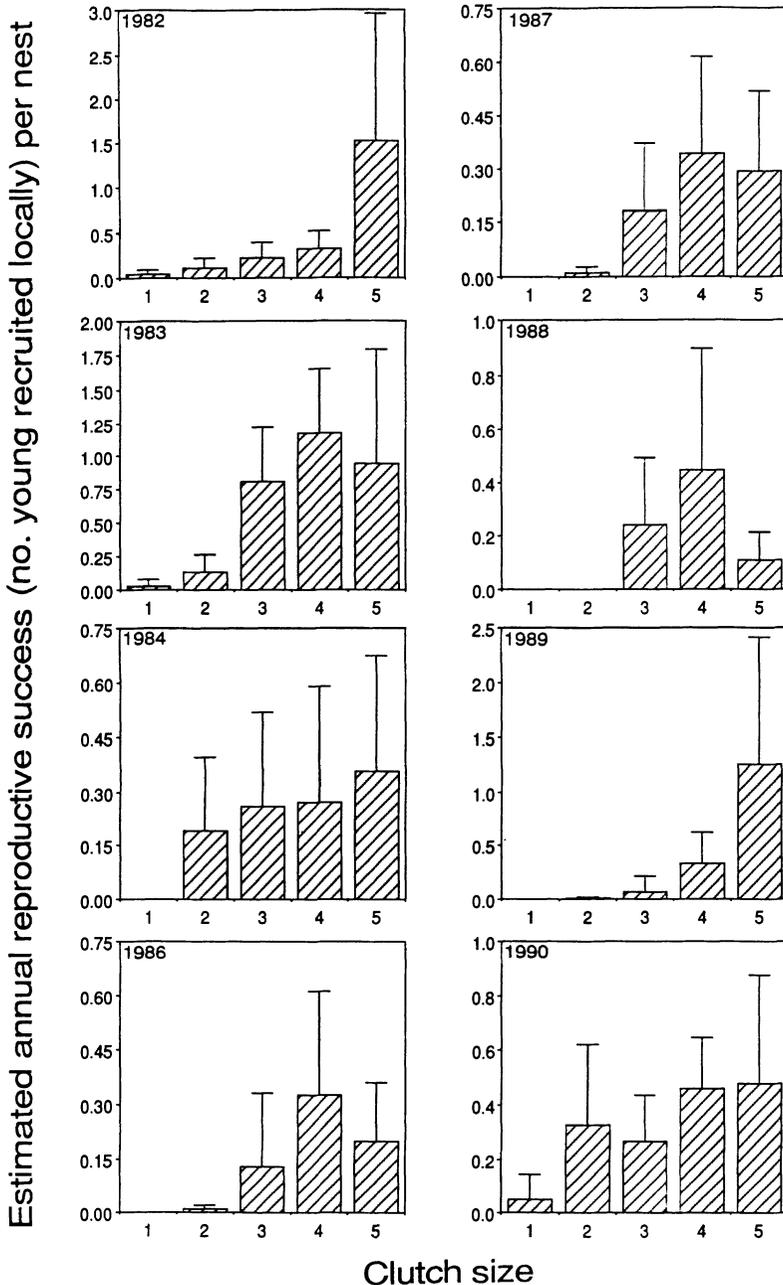


FIG. 7. Estimated annual reproductive success (number of young recruited to breeding) for Cliff Swallows tending clutches of different sizes for nonfumigated nests. Estimates were generated by multiplying the number of nestlings surviving to fledge (Fig. 4) by the first-year survival probability (Fig. 6) for each year. Error bars show SD for a product calculated from Goodman (1960).

no more likely to experience total failure, than did clutch sizes 4 and 5.

*Effects of ectoparasites.*—The potential effect of ectoparasitism on avian clutch size has received much recent attention (Møller 1991,

1994; Richner et al. 1993; Richner and Heeb 1995), although this relationship has been known since at least Moss and Camin's (1970) study of Purple Martins (*Progne subis*). Richner and Heeb (1995) hypothesized that the life-cy-

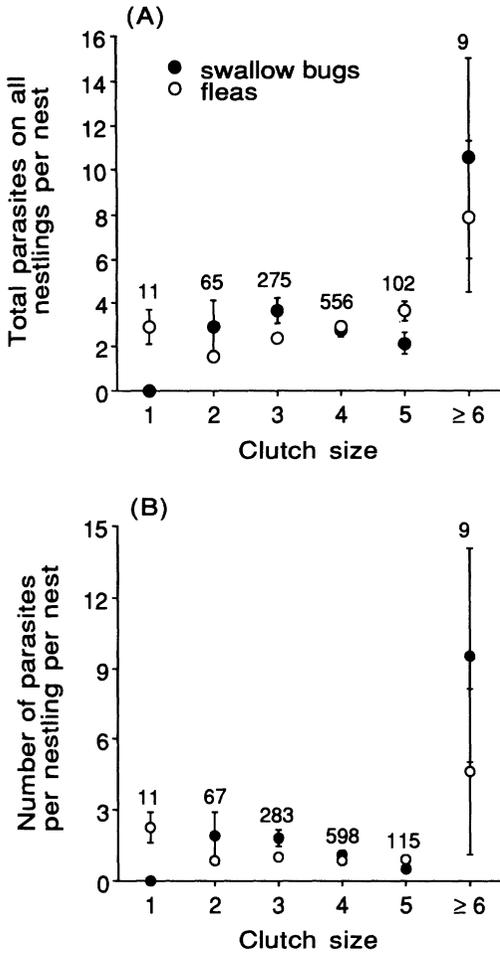


FIG. 8. Total ectoparasites (swallow bugs and fleas) on all Cliff Swallow nestlings (A) and mean number per nestling (B) relative to clutch size for nonfumigated nests. Sample sizes (number of nests) are shown above error bars; discrepancies between (A) and (B) resulted when not all nestlings in a nest were examined. In (A), total bugs per nest did not vary significantly with clutch size (Kruskal-Wallis test,  $P = 0.09$ ); total fleas per nest varied significantly with clutch size ( $P = 0.002$ ). In (B), both bugs per nestling and fleas per nestling varied significantly with clutch size (bugs,  $P = 0.048$ ; fleas,  $P = 0.037$ ).

cle length of the most common ectoparasite(s) of a species will determine whether the host should raise a large or a small brood. Ectoparasites that have long life cycles relative to the host's nestling period generally 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

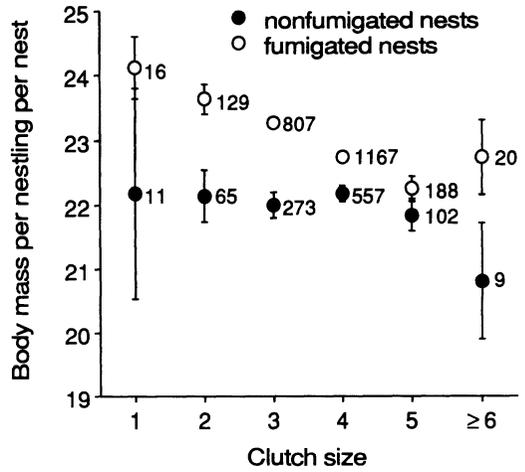


FIG. 9. Mean ( $\pm$ SE) body mass (g) per 10-day old Cliff Swallow nestling per nest relative to clutch size. Sample size (number of nests) shown by error bars. Body mass varied significantly with both clutch size and fumigation treatment (two-way ANOVA,  $P < 0.0001$ ).

broods can be advantageous because they dilute the parasite load per individual nestling. But 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. Parasitism by short-cycled ectoparasites potentially can lead to truncated clutch-size fitness functions, but in hosts with long-cycled ectoparasites, other environmental factors presumably constrain clutch size.

Fleas that parasitize Cliff Swallows are clearly long-cycled, producing one generation per year, and much of their development occurs in the nest during the swallows' nonbreeding season (Brown and Brown 1996). Thus, fleas should show no correlation between total parasite load per nest and brood size, and a negative correlation between parasite load per nestling and brood size (Richner and Heeb 1995). For the most part, this prediction was supported: the number of fleas per nestling declined noticeably in clutch sizes 3, 4, and 5 before rising in clutch size  $\geq 6$ , although the sample size for the latter clutch size was small.

Swallow bugs, on the other hand, exhibit characteristics of both long- and short-cycled ectoparasites. Generation time is influenced heavily by temperature, but 30 days seems to be

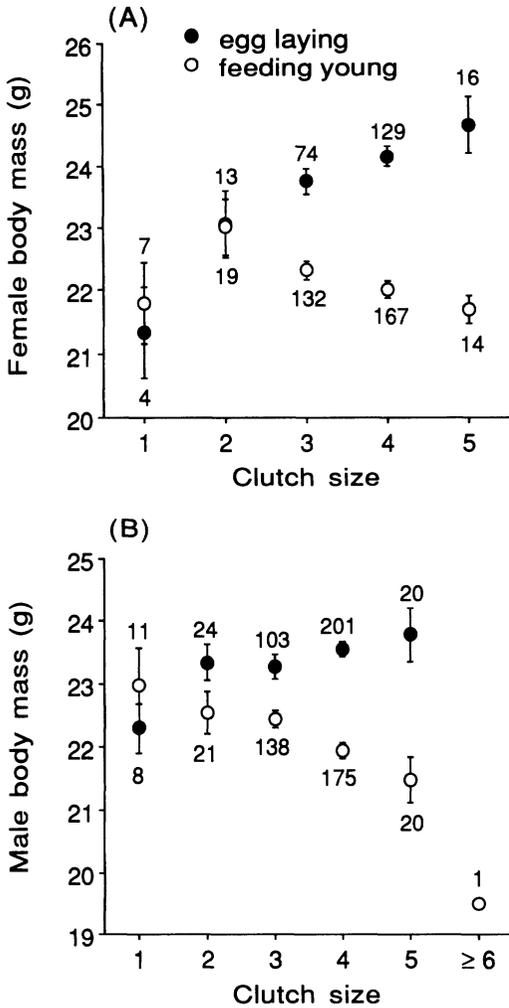


FIG. 10. Mean ( $\pm$ SE) body mass (g) for breeding female (A) and male (B) Cliff Swallows relative to clutch size during egg laying and brood rearing. Sample size (number of birds) shown by error bars. Body mass of females varied significantly with clutch size during egg laying (Kruskal-Wallis test,  $P = 0.011$ ) but not during brood rearing ( $P = 0.08$ ); male body mass did not vary significantly with clutch size during egg laying ( $P = 0.20$ ) but varied significantly during brood rearing ( $P = 0.013$ ).

about average (Usinger 1966). This means that swallow bugs are long-cycled relative to the Cliff Swallow's nestling period of 24 to 26 days. However, swallow bugs are extremely mobile, crawling on the substrate between nests and often moving from one nest to another. As nestlings within a colony fledge, bugs move out of vacated nests and aggregate at the active nests

that remain (Brown and Brown 1996). Thus, at least for the later nests in a colony, bug loads potentially can be determined by brood size, with larger broods supporting more bugs that arrive via immigration. Although the overall pattern for bugs is similar to that for fleas and matches that predicted for a long-cycled ectoparasite, the marked seasonal decline in Cliff Swallow clutch size (Brown and Brown 1999) could reflect the later birds' reducing their clutch sizes at a time when swallow bugs start moving among nests and become essentially short-cycled parasites.

Mean clutch sizes differed significantly between fumigated and nonfumigated nests in only one year out of six (Table 1). This agrees generally with Møller's (1991) result for Barn Swallows (*Hirundo rustica*) and might suggest that parasite load cannot be predicted early enough to adjust clutch size if warranted. However, the one year in which average clutch size differed between fumigated and nonfumigated nests was 1988. This was an unusually warm summer, the fourth hottest on record for Nebraska (Brown and Brown 1996) and the season when clutch size 5 was the least productive. Parasites in the nests (especially swallow bugs) possibly were sufficiently numerous early enough in the year to cause the swallows to adjust their clutch sizes.

We detected an apparently large effect of ectoparasites at clutch sizes 3 and 4, the two most common clutch sizes, but parasites had relatively little effect on larger or smaller clutches. Fledging success did not differ between fumigated and nonfumigated nests for clutch sizes 1, 5, and  $\geq 6$ ; in contrast, parasite-free nests fledged more young than did infested nests for clutch sizes 2, 3, and 4. Perhaps clutches of 5 and  $\geq 6$  dilute per capita parasite load of long-cycled fleas and bugs (*sensu* Richner and Heeb 1995) to the point that they were not deleterious to prefledging survival. Another potential explanation is that larger clutches were produced by high-quality individuals who were inherently resistant to parasites, and fumigation had less effect for them than for lower-quality individuals who produced intermediate-sized clutches.

Our fumigation experiment demonstrated that ectoparasitism was probably directly responsible for brood-size differences in first-year survival and thus may have caused the

lower annual success for clutch size 5 in some years. Presumably, parasites exerted long-term effects on birds after fledging (Brown and Brown 1996). The strong correlation between first-year survival of birds from broods of 5 and temperature during the time a young bird was raised suggests that the negative effects bugs have on subsequent survival are manifested during warm summers. Assuming that swallows cannot predict in advance whether the brood-rearing period will be hot or cold, the best risk-averse strategy presumably is to lay 4 eggs, which was the most common clutch size. Møller (1991) also found a greater effect of ectoparasites in larger broods of Barn Swallows, and he suggested that ectoparasitism limits clutch size in that species.

Removal of ectoparasites led to higher body mass of nestling Cliff Swallows in small broods than in large ones, but in the presence of parasites, nestling body mass did not vary among brood sizes. A similar pattern was found for Great Tits (Richner et al. 1993). This suggests that under natural ectoparasite loads, fitness gains can come only through offspring quantity and that a tradeoff between offspring quantity and quality can occur only if parasites are absent (Richner et al. 1993, Brown and Brown 1996). Paradoxically, we might therefore expect selection for larger clutch sizes when ectoparasites are common (Richner et al. 1993).

Ectoparasite loads in Cliff Swallows are strongly affected by colony size (Brown and Brown 1996). We have not, however, analyzed fitness components of clutch size separately by colony size, principally because clutch size shows no relationship with colony size (Brown and Brown 1996). Furthermore, had we subdivided our mark-recapture samples by colony size, we would not have had large enough data sets to test different survival models with any degree of sophistication (Tables 2, 3). Parasite-mediated effects on clutch size possibly vary with colony size and might be greatest in larger colonies where parasites are the most numerous.

*Energetic constraints on clutch size.*—Cliff Swallows are unusually sensitive to cold weather in spring that can reduce their insect food for prolonged periods, sometimes causing mortality (Brown and Brown 1998b). Harsh conditions early in the nesting season could prevent many females from producing clutches

of 5 or 6 eggs, even though later in the summer when the weather is better they can raise those clutches without added costs. Unfortunately, little is known about the costs of egg production in altricial birds (Carey 1996). Some female passerines use reserves of fat and protein that may be depleted significantly during laying even when food is abundant. In the Red-billed Quelea (*Quelea quelea*), some females deplete their fat reserves so seriously during laying that mortality may result the night following the laying of the last egg (Jones and Ward 1976).

We do not know if fat or protein reserves represent a constraint on egg production in Cliff Swallows, but clutch size could be related to a female's condition and to her energy reserves early in the season. Heavier females laid larger clutches (Fig. 10A). A similar pattern between body mass and clutch size was found for House Martins (*Delichon urbica*) in Great Britain (Bryant 1979). Positive correlations between food abundance and mean clutch size in House Martins, Tree Swallows (*Tachycineta bicolor*), and other species (Bryant 1975, Hussell and Quinney 1987, Nager et al. 1997) further indicate that clutch size in Cliff Swallows may be regulated in part by food availability during laying. In Barn Swallows, females expend as much energy per day during egg formation and incubation as they do during brood rearing (Ward 1996, Monaghan and Nager 1997).

Cliff Swallows lay smaller clutches than all other North American swallows except the congeneric Cave Swallow (*P. fulva*; Petersen 1955, Lunk 1962, Shields and Crook 1987, Brown et al. 1992, Robertson et al. 1992, West 1995, Brown 1997). Ramstack et al. (1998) suggested that clutch sizes are smaller in Cliff Swallows because these swallows exploit a more spatio-temporally variable insect food supply. If their food is also scarce at times, then the ability of parents to produce or feed large clutches will be limited (Murphy 1986). Whether the food supply of Cliff Swallows is sufficiently variable to create a food shortage independent of unusual weather events is unclear. Behavioral adaptations to overcome periods of food scarcity exist in Cliff Swallows (Brown et al. 1991, Brown and Brown 1996); thus, these birds may compensate for short-term interruptions in food supply. Another suggestion is that smaller clutches in Cliff Swallows reflect the relative abundance of breeding opportunities afforded

to them (Ramstack et al. 1998). When nesting sites are limited, reproductive effort may be increased (i.e. larger clutch sizes) to take advantage of the current breeding opportunity (Martin 1993). Cliff Swallows have unlimited nesting substrates (Brown and Brown 1996), in contrast to other swallows such as secondary cavity nesters that produce larger clutches (Brown et al. 1992, Roberston et al. 1992, Brown 1997).

Energetic constraints on egg production probably increase the costs of larger clutches for Cliff Swallows. If these costs exacerbate the risk associated with larger clutches in some years, stabilizing selection should produce the observed clutch-size distribution. We urge that more attention be paid to the effects of ectoparasitism on clutch size and to the energetic constraints on egg production. Long-term studies of clutch-size evolution are also essential, because if other species are like Cliff Swallows, fitness may change markedly among years.

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