

# Fitness components associated with alternative reproductive tactics in cliff swallows

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Two common alternative reproductive tactics are intraspecific brood parasitism and extrapair mating. Understanding the evolution of these traits requires estimation of fitness for individuals that do and do not exhibit them. We analyze fitness components associated with brood parasitism and extrapair mating in cliff swallows (*Petrochelidon pyrrhonota*). Annual survival probabilities for females known to be parasites, hosts, and nonparasites/nonhosts differed significantly, with highest survival (0.761) for parasites and lowest (0.289) for host females parasitized by egg laying. Survival probabilities did not differ among males paired to females of different status. First-year survival probabilities in the absence of ectoparasitic swallow bugs (*Oeciacus vicarius*) were 0.546 for young raised in the brood parasites' own nests versus 0.354 for young from all other nests; first-year survival probabilities in the presence of swallow bugs were 0.223 for young raised in host nests versus 0.132 for young from nests not brood parasitized. Males that engaged in extrapair copulation attempts had an annual survival probability of 0.413, significantly lower than the 0.614 estimated for males that were not seen engaging in extrapair mating. Annual reproductive success, measured as recruitment to breeding age, was greatest for brood parasites and similar among other classes of birds in the absence of swallow bugs and was greater for hosts than for birds not brood parasitized in the presence of swallow bugs, likely because hosts occupied less infested nests. Estimated lifetime reproductive success was highest for parasites and their mates. There were no apparent long-term effects of brood parasitism on survival of adult hosts or offspring from host nests, both because hosts did not have enlarged broods and because clutch and brood size did not affect cliff swallow survival. Brood parasites have greater fitness than hosts and nonparasitized birds, probably because parasites are superior individuals in good condition to start with. That males who participated in extrapair mating had lower expectation of survival suggests that extrapair copulations in cliff swallows are perpetrated by inferior males, and females should probably avoid them. **Key words:** alternative reproductive tactics, brood parasitism, cliff swallows, coloniality, extrapair copulation, fitness, life history, *Petrochelidon pyrrhonota*, reproductive success, social behavior, survival. [*Behav Ecol* 9:158–171 (1998)]

Some animal populations contain individuals that care for their own offspring and others that parasitize the parental care provided by conspecifics. Parasitic exploitation of others occurs through both extrapair mating and (in egg-laying species) intraspecific brood parasitism, each of which has been studied extensively in recent years (reviewed in Andersson, 1984; Birkhead and Møller, 1992; Brown and Brown, 1996; Field, 1992; Gladstone, 1979; Power et al., 1989; Rohwer and Freeman, 1989; Westneat et al., 1990; Yom-Tov, 1980). Most workers have been primarily interested in determining the frequency with which these parasitic tactics occur and identifying which individuals engage in them. Studies on intraspecific brood parasitism have commonly focused on the behavioral dynamics of parasitic laying, especially its timing, the host's responses to it, and the socioecological contexts promoting it.

The existing work has yielded much useful information, but it has been short-term in approach. There are few data on the long-term consequences for individuals that do or do not participate in extrapair mating and intraspecific brood parasitism (exceptions are Lank et al., 1990; Larsson et al., 1995). Knowing how these traits associate with fitness (reproductive success and survivorship) may shed light on both the characteristics of those animals that employ alternative tactics and their evolution within a population. For example, is brood parasitism a last-ditch tactic used by inferior individuals who cannot establish their own nest site or provide acceptable levels of parental care ("best of a bad job"), or is it an effective

supplemental reproductive strategy used by superior individuals to enhance their annual success? Single-season measures of nesting success cannot answer these sorts of questions because they do not address annual survival of individuals and potential life-history trade-offs between survivorship and annual reproductive output. More than a decade ago, Andersson (1984: 223) noted that the "data required for an appraisal of the fitness of hosts and parasites are offspring survival in relation to clutch size, relative success of parasitic and normal eggs, and the effect on adult mortality of parental care for different numbers of offspring." In instances where these data have been available, they have not been used to investigate the evolution of brood parasitism, and in some respects we do not understand intraspecific brood parasitism much better today than at the time of Andersson's review.

In this study we examined fitness components associated with extrapair mating and intraspecific brood parasitism in the cliff swallow (*Petrochelidon pyrrhonota*), a colonial passerine bird of western North America. Cliff swallows commonly engage in extrapair copulation, and parasitic laying among conspecifics occurs in up to 22% of nests and possibly more (Brown and Brown, 1996). Here we focus mostly on brood parasitism, which we have studied more extensively, but we also report data on annual survivorship for males that did and did not attempt extrapair matings. Because breeding life span is the major determinant of fitness in most small songbirds (Clutton-Brock, 1988; Newton, 1989), much of our emphasis in this paper is on estimating survival probabilities for different classes of birds. Our goals were to use information on annual survival and annual reproductive success (measured as recruitment to the next year's breeding population) to learn more about which individuals employ these tactics, the long-

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term costs and benefits associated with them, and their evolution. We relied on demographic data from a 15-year field study using mark-recapture, and our analysis of these data is based on the methods advocated by Lebreton et al. (1992).

## METHODS

### Study site and natural history

Our cliff swallow research is conducted along the North and South Platte rivers near Ogallala, primarily in Keith and Garden counties, southwestern Nebraska, USA. Our study area is approximately 150×50 km and contains about 150 separate colony sites where cliff swallows breed, 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).

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 the sides of steep 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 3700 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.

The close proximity of neighbors within a cliff swallow colony provides frequent opportunities for both intraspecific brood parasitism and extrapair copulation. The incidence of each increases with colony size (Brown and Brown, 1996). Cliff swallows parasitize nests in two ways: by laying eggs in nests during the host's laying period and by physically moving eggs from the parasite's nest to a host's. The transfer can occur at virtually any time before the host's eggs have hatched (Brown and Brown, 1988c, 1989). All birds directly observed parasitizing nests have been females resident within the colony. Most parasites parasitize nests near their own, usually within a five-nest radial distance (Brown and Brown, 1989, 1991). Parasites, especially those that transfer eggs, seem able to discriminate among potential host nests and often select those which are least infested with blood-sucking ectoparasitic insects—and are thus the most successful nests—as the hosts for their eggs (Brown and Brown, 1991). For additional information on the natural history of brood parasitism in cliff swallows, see Brown (1984) and Brown and Brown (1988c, 1989, 1991, 1996).

Extrapair copulation in cliff swallows occurs in two contexts: among birds away from nest sites while they gather mud for nest construction and among neighboring birds while at the nests. Neighbors engage in extrapair copulation when a male trespasses into a nearby nest during the male owner's absence. Other males regularly patrol the mud-gathering sites and attempt extrapair copulation with females who come there to collect nesting material. Most copulation attempts seem to be initiated by males, and females often (but not always) seem to resist. Extrapair copulation is attempted both by males who are resident in a colony and maintain a nest and mate of their own and by nonresidents who circulate among colony sites (Brown and Brown, 1996). The difficulty of catching and marking nonresidents meant that we could collect extrapair copulation data only on resident males.

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 are primarily nest-based ectoparasites, residing inside the cliff swallow nests or in the adjacent nesting substrate. They feed on blood of adult and nestling swallows, and swallow bugs have substantial effects on nestling survival and health (Brown and Brown, 1986, 1996). Infestations of both bugs and fleas increase with colony size and potentially confound any analysis involving nestling survivorship or reproductive success. For this reason and also because brood-parasitic swallows seem to use extent of ectoparasitism as a cue for host nest selection (Brown and Brown, 1991), where possible in this paper we present data for both ectoparasite-free (fumigated) nests and naturally infested nests.

### Field methods

#### Mark-recapture

We began marking (banding) adult and nestling cliff swallows when our project started in 1982, and through 1996 we had permanently marked 87,337 birds with numbered aluminum bands. Thousands of these birds have been recaptured in years after they were banded (see Brown and Brown, 1996); typically between 16,000 and 21,000 captures (counting within-season repeats) were processed each season. By rotating among different colony sites and systematically mist-netting at each, we monitored the presence of banded birds at 25–35 colony sites each summer. 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. The probability of recapture thus was a critical parameter in making meaningful estimates of survivorship, and we explored recapture probability thoroughly in assessing model fit (see below). Our capture effort increased each year of the study, and perhaps for this reason we often found significant yearly variation in recapture probabilities. 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 1995 for survival analyses involving birds that did and did not commit extrapair copulation and for those involving parasites, hosts, and non-parasites/nonhosts and their young. The most recent of these cohorts was that from 1987, and thus we had  $\geq 8$  years of recapture for them. 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). For analyses involving the effect of clutch and brood size on survival, in which our most recent cohort with relevant data was from 1992, we included recapture data from 1996 to give us  $\geq 3$  years of recapture for those cohorts.

#### Designating categories of birds

At certain colonies, birds were color marked on the forehead soon after arrival and intensively watched to document instances of brood parasitism (Brown and Brown, 1989). We assigned nest ownership by observing which marked birds were consistently associated with particular nests. Parasitic females were those seen laying or transferring eggs into a nest not their own. Host females were those whose nests were seen being parasitized by another bird or whose nests were found to be parasitized based on nest-check data. Daily or bi-daily

checks of nest contents allowed us to infer instances of parasitic laying as cases where two or more eggs appeared per 24-h period and egg transfer as cases where an egg appeared in a nest during the host's incubation period, yet hatched synchronously with the host's eggs (Brown and Brown, 1988c, 1989, 1996). Some parasitic females were also parasitized themselves, but they were not included in the host female category. Host females were those not known to also be parasites. Birds designated as neither hosts nor parasites were those in the color-marked sample who were not observed to be parasitized or to parasitize others and whose nests showed no evidence of brood parasitism in nest checks. For our fumigated sample, we included only nests with color-marked owners that we watched as the nonparasite/nonhost category. Using the nests we had watched decreased the likelihood that a nest in this category had in fact experienced a brood parasitism undetected by our nest checks and also made the nonparasite/nonhost nests more comparable to the other categories of nests within the fumigated class. Among nonfumigated nests, which did not contain any nests with color-marked owners that were watched, nonparasitized nests were designated as those with no evidence of either egg-laying or egg-transfer parasitism based on nest checks. No color-marked parasitic females were identified among nonfumigated nests, so we have no information on parasites' own nests in the non-fumigated class. Parasitized (host) nests were identified using the same nest-check criteria (above) in both nonfumigated and fumigated classes.

However, as in other field studies using observational criteria to infer parasitism or lack thereof (e.g., Lank et al., 1990), our categories of parasitized and nonparasitized nests unavoidably contained some undetected brood parasitism. When parasitic eggs are laid just before a host starts laying or just after a host ceases laying, nest checks will not detect the parasitism. Similarly, if either egg-laying or egg-transferring parasites remove host eggs (Brown and Brown, 1988a), we could not know that parasitism occurred. Even among the sample of color-marked birds watched, we could have overlooked some instances of parasitism because we did not observe these birds for 100% of daylight hours. Therefore, the potential pollution of our categories by undetected events reduces the power of our tests of differences among parasites, hosts, and nonparasites/nonhosts (Lank et al., 1990) and makes these tests conservative. Any differences we report are probably underestimated. The same situation applies to our analyses of extrapair copulation in males, in which we could not watch males for 100% of the time and thus could not know with certainty that "non-extrapair copulation" males never engaged in extrapair mating.

Any bird occupying a nest whose parasitic status was known, either from observations of color-marked birds or from capture of nest owners in nests at night for parentage studies (Brown and Brown, 1988b, 1996), was included in the cohorts for mark-recapture analysis involving adults. Because of the laborious nature of observing color-marked birds and catching owners in nests, our sample of adults of known parasitic status was a smaller subset of our overall sample of banded birds. Nestlings from nests whose parasitic status was known, and in some cases from a wider sample of all nests in which clutch size and surviving brood size were known, were included in mark-recapture analyses involving first-year birds. Clutch size of nests was monitored by daily or bi-daily nest checks throughout the egg-laying period. Our measure of fledging success was the number of young surviving to 10 days of age (Brown and Brown, 1996), which was the same as brood size in our analyses.

Observations of extrapair copulation attempts by males were made at colonies where we could get close enough to

the mud-gathering sites to identify color marks of resident males that perpetrated the copulation attempts (Brown and Brown, 1996). Only residents entered the colonies frequently enough to be caught in mist nets and color marked; many unmarked nonresidents also engaged in extrapair copulations. Other observations on extrapair copulation were collected while watching birds at their nests during the brood parasitism studies. Any color-marked male seen to engage in an extrapair copulation (EPC) attempt at least once, either at the nests or the mud-gathering sites, was designated an EPC male, whereas color-marked males that were part of our observation sample and not seen to perpetrate any extrapair copulation attempts were classified as non-EPC males.

#### Fumigation

We removed ectoparasites from nests by application of a short-lived acaricide, naled (also known as Dibrom), to the outsides 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 source of cliff swallow nestling mortality. For further details on fumigation procedures and the effects of swallow bugs on cliff swallows, see Brown and Brown (1996).

#### Statistical methods

##### Survival estimation

We estimated annual survival probabilities and tested for significant differences in survival between different classes of birds using the general methods of Lebreton et al. (1992). We used the program SURGE (Cooch et al., 1996; Pradel and Lebreton, 1993) to generate maximum-likelihood estimates of survival and recapture probabilities. SURGE is a commercially available software package that computes survival and recapture parameters using an information matrix derived from recapture histories. It provides a powerful way to test 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. (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.,  $\phi_{12}, p_{12}$ ), constancy over time (e.g.,  $\phi, p$ ), an effect of group classification (and if so, how many groups, e.g.,  $\phi_{g1}, p_{g1}$ ), an interaction between group and time (e.g.,  $\phi_{t \times g1}, p_{t \times g1}$ ), or a constrained model with parallelism in time for a group effect (e.g.,  $\phi_{1+g1}, p_{1+g1}$ ). 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). From this, we tested a variety of more general yet biologically relevant models incorporating various combinations of age, group, and time dependence. For cases where the CJS model provided the best fit, we assessed goodness-of-fit of the data to the CJS model's assumptions using the program RELEASE (Burnham et al., 1987). In all cases where we determined that the CJS model was the most parsimonious through use of likelihood ratio tests (LRT) or the Akaike Information Criterion (AIC), tests 2 and 3 of RELEASE also indicated no significant departure from the CJS model.

We tested among different models that were nested (e.g.,  $\phi, p$  versus  $\phi, p_t$ ) with an LRT. 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 equaling the difference in the number of estimable parameters ( $np$ ) between the two models (Lebreton et al., 1992). LRTs cannot be used for models that are not nested (e.g.,  $\phi_{12}, p_{12}$  versus  $\phi, p_{12}$ ), and for these use of the AIC

(Akaike, 1973) is recommended (review in Lebreton et al., 1992). AIC is computed as  $2np + DEV$ , and models with the lowest values of AIC are the most parsimonious. The AIC can often be used as a shortcut to select among different models. In general, we found models with age dependence to best fit the data involving nestlings; first-year survival of cliff swallows is considerably lower than that of older age classes (Brown and Brown, 1996). Models with age dependence tended not to fit the data involving only adult birds, in which all survival probabilities estimated were from the second year on. No systematic departures in test 3 of RELEASE for adults indicated that there were no trap-handling effects and no transients. Transients in particular were unlikely because our cohorts consisted only of known breeders.

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 and some that 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 do not present results of fits of all models tested; rather, in the tables we show only the three to five models with the lowest AICs.

#### Lifetime reproductive success

To estimate average lifetime reproductive success for different classes of birds, we used the method described in our book (Brown and Brown, 1996; and see Vehrencamp et al., 1988). We first determined average annual reproductive success for a category by multiplying the probability of first-year survival (from fledging until the next breeding season) by the average number of young fledged. Average annual reproductive success was then multiplied by average breeding life span for the category, yielding average lifetime reproductive success. Life span is estimated using the survival probability from the formula in Brownie et al. (1985: 206), as  $1/1 - 1 n\phi$ . Because this formula approximates expected subsequent life span, breeding life span for our purposes is that calculated from Brownie et al. plus 1, the current year. Brownie et al.'s formula assumes survival is constant over time, an assumption which was justified for data (Table 1) to which the formula was applied.

We earlier (Brown and Brown, 1989) presented measures of annual reproductive success for parasites, hosts, and nonparasites/nonhosts based only on the number of young that survived to fledging. We have reanalyzed those data for this paper, using slightly different and improved criteria for designating categories of birds (see above). Estimates of reproductive success given here should be considered more definitive than those in the earlier report.

#### Single-state assumption

Present capture-recapture methodology (e.g., SURGE) makes the implicit assumption that an individual's status does not change during the period in which its survival is estimated. If it changes from one group to another, perhaps from year to year, a multistate approach (Brownie et al., 1993; Nichols et al., 1992, 1993, 1994) is required. Although multistate theory is relatively well developed, no practical and widely available software exists that will readily estimate survival for animals exhibiting different transition probabilities between states (Lebreton JD and Pradel R, personal communication). Users of SURGE have assumed that status does not change, although in some cases this assumption may be problematic. This may be especially the case, for example, in studies of clutch size (e.g., Blondel et al., 1992; Clobert et al., 1987),

Table 1

Capture-recapture models and comparisons among models for adult cliff swallows in relation to nest status (see text for notation)

Model	$np$	DEV	AIC	Comparison
<b>Female nest owners</b>				
(1) $\phi_{F1}, \hat{p}_{F1}$	8	419.9	435.9	Best fit. Groups = parasites, hosts of each type, nonparasites/nonhosts.
(2) $\phi_{F2}, \hat{p}_{F2}$	6	426.6	438.6	Groups = hosts via laying, all other females. (2) vs. (1), $\chi^2_2 = 6.7, p = .035$
(3) $\phi, \hat{p}_{F1}$	5	428.1	438.1	Testing overall effect of female status. (3) vs. (1), $\chi^2_3 = 8.2, p = .042$
(4) $\phi, \hat{p}$	22	414.5	458.5	Full CJS model. Rejected by high AIC.
(5) $\phi_{F1}, \hat{p}_{F1}$	92	376.2	560.2	Full CJS model by group. (5) vs. (1), $\chi^2_{91} = 43.7, p = .99$
<b>Male nest owners</b>				
(6) $\phi, \hat{p}$	13	727.9	753.9	Best fit. No differences among males.
(7) $\phi_{M1}, \hat{p}$	16	725.9	757.9	Groups = mates of parasites, of hosts of each type, of nonparasites/nonhosts. (7) vs. (6), $\chi^2_3 = 2.0, p = .57$
(8) $\phi, \hat{p}$	22	722.6	766.6	Full CJS model. (8) vs. (6), $\chi^2_9 = 5.3, p = .81$

where females might produce different-sized clutches in different years.

To use SURGE, we make the assumption here that a bird maintains a fixed status (e.g., as host, parasite, or neither) in subsequent years. This assumption is key to our estimates of annual survival for breeding birds of different status and for estimating lifetime reproductive success, although it has no effect on estimates of first-year survival because natal nest characteristics cannot change. For the following reasons, this assumption seems justified for cliff swallows.

1. We could directly test this assumption in part for some birds: 78.7% of breeders of both sexes whose nest status was known in 2 years ( $n = 47$  birds) maintained the same status (nonparasitized) each season. Among the remaining 10 birds, 3 were hosts the first year and not known to be parasitized the next year (although undetected parasitism could have occurred), and 7 were not known to be parasitized the first year and were known to be hosts the second year. Two birds whose nest status was known for 3 years were nonparasitized all 3 years.

2. The capture history used in SURGE for each bird began in the year for which its status was known. Therefore, its status in a previous year (which may or may not have been different) had no statistical effect on its survival because the bird did not "exist" before we knew its status.

3. In small songbirds such as cliff swallows which show relatively low survival rates and short breeding life spans, a single year represents a substantial fraction of their life. Therefore, the known status in year 1 has a potentially much larger effect on eventual longevity than in longer-lived species where each season is proportionately less important. This makes determination of status in years 2 or 3 less critical in short-lived species such as swallows because fewer individuals can be expected to live that long.

4. If birds change status between years, this represents pol-

lution of our categories in the same way nest data were potentially polluted by undetected parasitism (Lank et al., 1990). Our tests for survival differences are thus conservative and mean that any differences we report may be underestimates. As we detected differences between categories (see Results), bird status either did not often change between years or the group effects were so great that they were still detectable with polluted data.

## RESULTS

### Survivorship

#### Adults in relation to nest status

Annual survival probabilities differed significantly among known parasitic females ( $n = 17$  birds), host females parasitized by egg laying ( $n = 32$ ), host females parasitized by egg transfer ( $n = 25$ ), and females not known to be parasites or hosts ( $n = 65$ ). A model with both survival and recapture probability dependent on nest status provided the best fit for females, significantly better than one without an effect of female status (Table 1). Survival did not vary significantly with time (Table 1). Annual survival probabilities ( $\pm$  SD) from model 1 were 0.761 ( $\pm$  0.0553) for parasitic females, 0.289 ( $\pm$  0.0820) for host females parasitized by laying, 0.595 ( $\pm$  0.0757) for host females parasitized by transfer, and 0.686 ( $\pm$  0.0451) for females that were neither parasites nor hosts. Given the low estimate for host females parasitized by laying, we tried another model with only two groups that treated all females except hosts by laying the same (model 2), but the model with the four groups provided a significantly better fit (Table 1).

We identified no phenotypic differences among these classes of females other than nest status (see discussion of effects of clutch and brood size under "Costs of brood parasitism"). Ages of these birds were unknown, but there were no significant differences among them in body mass, a variable that influences annual survival probability in cliff swallows (Brown and Brown, 1996). Mean body mass ( $\pm$  SE) taken during the nest-building and egg-laying period was 25.15 ( $\pm$  0.40) g for parasitic females, 24.72 ( $\pm$  0.64) g for host females parasitized by laying, 22.00 ( $\pm$  1.00) g for host females parasitized by egg transfer, and 24.56 ( $\pm$  0.22) g for females that were neither parasites nor hosts (Kruskal-Wallis ANOVA,  $p = .16$ ).

Annual survival probabilities of males attending nests of different status did not vary significantly (Table 1; sample sizes were 14, 46, 35, and 90 birds for the same 4 groups). A model with survival constant across both time and groups was the most parsimonious, and a model with a group-size effect did not provide a significantly better fit. According to model 6 (Table 1), survival of all males was 0.634 ( $\pm$  0.0230). As with females, body mass during nest building and egg laying did not vary significantly among these males: means were 24.50 ( $\pm$  1.09) g for males paired to parasitic females, 24.57 ( $\pm$  0.35) g for host males parasitized by laying, 24.58 ( $\pm$  0.87) g for host males parasitized by transfer, and 24.28 ( $\pm$  0.19) g for non-host males whose mates were not known to be parasites (Kruskal-Wallis ANOVA,  $p = .87$ ).

Annual survival probabilities of males and females reported in this section are for birds from fumigated nests. These estimates are presumably representative of survival probabilities among all nests, as nest fumigation has little apparent effect on survival of the occupying adults (Brown and Brown, 1996).

#### Nestlings in relation to nest status

Among fumigated nests, first-year survival probabilities (from fledging to the next breeding season) were significantly higher for birds raised in the parasitic females' own nests ( $n = 39$

Table 2

Capture-recapture models and comparisons among models for nestling cliff swallows in relation to natal nest status (see text for notation)

Model	$n\hat{p}$	DEV	AIC	Comparison
<b>Fumigated nests</b>				
(9) $\phi_{a2-g2}, \hat{p}$	17	3687.4	3721.4	Best fit. Groups = offspring of parasites, of all others combined.
(10) $\phi_{a2-g2}, \hat{p}$	19	3685.4	3723.4	Groups = offspring of parasites, of hosts of both types combined, of nonparasites/nonhosts. (10) vs. (9), $\chi^2_2 = 2.0$ , $p = .37$
(11) $\phi_{a2-g2}, \hat{p}$	21	3685.0	3727.0	Groups = offspring of parasites, of hosts of each type, of nonparasites/nonhosts. (11) vs. (10), $\chi^2_2 = 0.4$ , $p = .82$
(12) $\phi_{a2}, \hat{p}$	15	3698.2	3728.2	Testing overall effect of nest status. (12) vs. (9), $\chi^2_2 = 10.8$ , $p = .004$
(13) $\phi_{a2}, \hat{p}_{a2}$	48	3658.7	3754.7	Full CJS model. (13) vs. (12), $\chi^2_{23} = 39.5$ , $p = .018$
<b>Nonfumigated nests</b>				
(14) $\phi_{a2-g2}, \hat{p}$	17	2658.1	2692.1	Best fit. Groups = offspring of hosts of each type combined, of nonparasites/nonhosts.
(15) $\phi_{a2-g2}, \hat{p}$	19	2657.8	2695.8	Groups = offspring of hosts of each type, of nonparasites/nonhosts. (15) vs. (14), $\chi^2_2 = 0.3$ , $p = .86$
(16) $\phi_{a2}, \hat{p}$	15	2668.2	2698.2	Testing overall effect of nest status. (16) vs. (14), $\chi^2_2 = 10.1$ , $p = .006$
(17) $\phi_{a2}, \hat{p}_{a2}$	48	2609.9	2705.9	Full CJS model. (17) vs. (16), $\chi^2_{23} = 58.3$ , $p < .001$
(18) $\phi_{a2-g2}, \hat{p}$	63	2600.0	2726.0	Testing for CJS time dependence in survival. (18) vs. (14), $\chi^2_{46} = 58.1$ , $p = .11$

birds) than for birds raised in all other nest categories combined ( $n = 430, 487$ , and  $574$  for host nests by laying and transfer and nonparasites/nonhosts, respectively). Models that treated the other groups as separate did not provide significantly better fits (Table 2), indicating that there were no differences in survival among birds from the two kinds of host nests and those of nonparasites/nonhosts. A model with survival dependent solely on whether a bird was raised in a parasite's nest (model 9, Table 2) provided a significantly better fit than one with no group effect (model 12). First-year survival probability from model 9 yielded an estimate of 0.546 ( $\pm$  0.0850) for birds raised in the parasites' own nests and 0.354 ( $\pm$  0.0220) for birds raised in all other fumigated nests.

A different pattern emerged for birds from nonfumigated nests. First-year survival probabilities differed significantly between nestlings raised in the two kinds of host nests (laying,  $n = 134$  birds; transfer,  $n = 160$ ) and those raised in non-parasitized nests ( $n = 2687$ ; Table 2). A model that treated birds from laying and transfer host nests the same (model 14) provided a significantly better fit than a model that separated the two kinds of hosts (model 15, Table 2). Therefore, first-

Table 3

Capture-recapture models and comparisons among models for male cliff swallows in relation to whether they engaged in extrapair copulation (see text for notation)

Model	$n\phi$	DEV	AIC	Comparison
(19) $\phi_{gt}, \hat{A}$	13	608.8	634.8	Best fit. Groups = males engaging and not engaging in extrapair copulation.
(20) $\phi, \hat{A}$	12	618.8	642.8	Testing overall effect of male status. (20) vs. (19), $\chi^2_1 = 10.0, p = .002$
(21) $\phi_{gt}, \hat{A}$	33	582.1	648.1	(21) vs. (19), $\chi^2_{30} = 26.7, p = .14$

year survival probability did not differ for birds from host nests parasitized by laying and transfer, but the estimate for these two groups differed significantly from all other birds. Models without a group effect and with time dependence in survival did not provide a significantly better fit (Table 2). From model 14, estimated first-year survival probabilities were 0.223 ( $\pm 0.0518$ ) for birds reared in the two kinds of nonfumigated host nests and 0.132 ( $\pm 0.0222$ ) for birds reared in nonfumigated, nonparasitized nests.

#### Males in relation to extrapair copulation attempts

Annual survival probabilities for males that did ( $n = 76$  birds) and did not ( $n = 103$ ) engage in extrapair copulation attempts differed significantly (Table 3). A model with a group effect provided a significantly better fit than one without a group effect, and there was no evidence for time dependence in survival (Table 3). From model 19, annual survival probabilities were estimated to be 0.413 ( $\pm 0.0401$ ) for EPC males and 0.614 ( $\pm 0.0551$ ) for non-EPC males.

We found no other statistically significant phenotypic differences among the two classes of males. At each of the three colonies where we observed the color-marked males used in this analysis, average body mass taken during the nest-building and egg-laying period was larger for the EPC males than for the non-EPC males (Table 4). The lower survival for the EPC males was thus surprising given their slight weight advantage. However, none of the differences in body mass were significant within a colony (Table 4). Age of these males was unknown, and all maintained nests and mates of their own.

#### Annual reproductive success

##### Single-season measures

Clutch size varied significantly among nests of different status for both fumigated and nonfumigated classes (Table 5). Host nests averaged more total eggs than nests of parasites or of

nonparasites/nonhosts, and (among fumigated nests) the parasites tended the fewest eggs. Larger clutch sizes for hosts are not surprising given that eggs from other females were added to their nests. However, the hosts' clutches had on average less than one egg more than clutches of the other classes, meaning that the hosts probably compensated for being parasitized by reducing their own output of eggs (Brown and Brown, 1989). When one egg, representing the parasitic egg, was subtracted from the host clutch sizes (Table 5; and some hosts had more than one parasitic egg), hosts were at a disadvantage in producing fewer of their own eggs than either of the other classes of females.

The number of young surviving to day 10 varied significantly among fumigated nests of different status (Table 5). This was primarily because of larger brood sizes in the nonparasite/nonhost nests. Based on the number of young fledged, the nonparasites/nonhosts had a substantial advantage over the other classes. Their advantage was increased because often the surviving broods of hosts, and in some cases the parasites themselves, contained one or more parasitic offspring. This lowered realized reproductive success below that shown (Table 5) for hosts and some parasites, although the fraction of parasitic offspring that survived in these nests was unknown because we had no way to identify the offspring from parasitic eggs. There was no significant difference in the number of young surviving to day 10 for nonfumigated nests of different status (Table 5).

#### Recruitment to breeding age

The number of young surviving to their first breeding season, estimated as the number of young surviving to fledge times their first-year survival probability, revealed a reproductive advantage for parasites among the fumigated nests and for hosts among the nonfumigated nests (Table 5). This pattern resulted largely from the higher first-year survival probabilities for birds raised in the parasites' nests and, in the nonfumigated set, in the host nests. The results illustrate the importance of knowing first-year survival probabilities because in this case seasonal measures of the number of young fledged do not accurately reflect relative recruitment into the next year's breeding population (Table 5).

#### Costs of brood parasitism

##### Adult survival in relation to clutch and brood size

One interpretation for the survival differences among females of different status (Table 1) is that these reflect the long-term costs of caring for different numbers of eggs and young among parasites, hosts, and birds who are neither (Table 5). If survival of breeders varies with clutch or brood size, addition of parasitic eggs or young could impair host survival. We examined how cliff swallow annual survival varied with reproductive effort, using all birds irrespective of status for which

Table 4

Body mass (g) taken during the nest-building and egg-laying period for male cliff swallows that did (EPC males) and did not (non-EPC males) engage in extrapair copulation attempts

Colony		Mean mass	SE	n (birds)	$p^a$
A	EPC males	23.30	0.49	10	.09
	non-EPC males	22.34	0.39	13	
B	EPC males	25.22	0.45	9	.31
	non-EPC males	24.70	0.26	48	
C	EPC males	24.13	0.39	15	.53
	non-EPC males	23.85	0.27	38	

<sup>a</sup> Based on Mann-Whitney *U* test within each colony.

Table 5

Clutch size, number of young surviving to 10 days of age, and estimated annual reproductive success (ARS) as measured by recruitment to the next year for different classes of cliff swallows

Class of birds	Clutch size <sup>a</sup>			Surviving young <sup>b</sup>			ARS (no. of young)
	Mean	SE	n	Mean	SE	n	
<b>Fumigated nests</b>							
Parasites	3.48	0.16	25	2.76	0.21	21	1.51
Hosts via egg transfer	3.84	0.075	354	2.71	0.075	333	0.96
Hosts via egg laying	4.11	0.062	512	2.71	0.083	288	0.96
Nonparasites/nonhosts	3.68	0.046	279	2.97	0.077	267	1.05
<b>Nonfumigated nests</b>							
Hosts via egg transfer	3.89	0.11	108	1.89	0.18	104	0.42
Hosts via egg laying	3.91	0.090	88	1.70	0.21	81	0.38
Nonparasitized	3.43	0.022	1865	1.80	0.040	1775	0.24

<sup>a</sup> Clutch size varied significantly among classes for both fumigated (Kruskal-Wallis ANOVA,  $p < .001$ ) and nonfumigated nests ( $p < .001$ ).

<sup>b</sup> Number of surviving young varied significantly among classes for fumigated nests (Kruskal-Wallis ANOVA,  $p = .039$ ), but not for nonfumigated ones ( $p = .70$ ).

clutch and brood size were known. This analysis could not be done separately for nests of different parasitic status due to problems with estimating survival for small cohorts. Birds occupying fumigated and nonfumigated nests were combined because nest fumigation did not affect adult survival (Brown and Brown, 1996).

Annual survival probabilities did not vary among females attending clutches of one ( $n = 7$  birds), two ( $n = 31$ ), three ( $n = 187$ ), four ( $n = 298$ ), or five ( $n = 42$ ) eggs (Table 6). Models with group effects did not provide significantly better fits, when using either all 5 groups (Table 6) or fewer in exploratory analyses. Thus, survival of females attending large clutches was not significantly different from that of birds with

smaller clutches. The overall survival probability for females in this sample was 0.588 ( $\pm 0.0182$ ).

Annual survival probabilities did not vary among males attending clutches of one ( $n = 11$  birds), two ( $n = 32$ ), three ( $n = 187$ ), four ( $n = 323$ ), five ( $n = 54$ ), or six ( $n = 10$ ) eggs (Table 6). Unlike with females, a model with time-dependent survival provided a significantly better fit than one without time dependence, but there was no evidence of a significant group effect (Table 6). As with females, survival of males attending larger clutches was not significantly different from that of birds with smaller clutches. Overall annual survival probabilities for males in this sample ranged from 0.357 ( $\pm 0.154$ ) in 1992 to 0.833 ( $\pm 0.0730$ ) in 1989.

Annual survival probabilities differed significantly between females attending broods of zero young ( $n = 71$  birds) and those attending all other brood sizes combined (one,  $n = 35$ ; two,  $n = 93$ ; three,  $n = 189$ ; four,  $n = 146$ ; Table 7). A model with these two group classifications provided a significantly better fit than one with all 5 groups (brood sizes) separate (Table 7). As with female clutch size, models with time dependence did not provide significantly better fits for female brood size. From model 29 (Table 7), annual survival probabilities were estimated at 0.411 ( $\pm 0.0513$ ) for females with broods of zero (nests failing before hatching) and 0.602 ( $\pm 0.0170$ ) for females with broods of one to four combined. Survival of females attending larger broods (e.g., four young) was not significantly different from that of females attending smaller broods (i.e., one or two young).

The pattern in annual survival for males attending different brood sizes was similar to that seen for clutch size. Annual survival probabilities did not vary among males attending broods of zero ( $n = 86$  birds), one ( $n = 28$ ), two ( $n = 103$ ), three ( $n = 197$ ), four ( $n = 168$ ), or five ( $n = 15$ ) young. A model with time-dependent survival provided a significantly better fit than one without time dependence, but there was no evidence of a significant group effect (Table 7). Overall annual survival probabilities for males in this sample ranged from 0.280 ( $\pm 0.108$ ) in 1992 to 0.800 ( $\pm 0.0780$ ) in 1989. As with females, survival of males attending larger broods was not significantly different from that of birds attending smaller broods.

That we found no relationship between adult survival and clutch or brood size in successful nests suggests that differences in clutch or brood size per se (Table 5) had little impact

Table 6

Capture-recapture models and comparisons among models for adult cliff swallows in relation to their clutch size (see text for notation)

Model	np	DEV	AIC	Comparison
<b>Female nest owners</b>				
(22) $\phi, \hat{A}$	14	1784.7	1812.7	Best fit. No differences among females.
(23) $\phi_{ps}, \hat{A}$	18	1777.4	1813.4	Groups = birds laying clutch sizes 1-5. (23) vs. (22), $\chi^2_4 = 7.3$ , $p = .12$
(24) $\phi, \hat{A}$	25	1767.6	1817.6	Full CJS model. (24) vs. (22), $\chi^2_{11} = 17.1$ , $p = .11$
(25) $\phi_{1+ps}, \hat{A}$	30	1759.9	1819.9	Testing for parallelism over time for different groups. (25) vs. (23), $\chi^2_{12} = 17.5$ , $p = .13$
<b>Male nest owners</b>				
(26) $\phi, \hat{A}$	25	2453.3	2503.3	Best fit. Full CJS model. No differences among males.
(27) $\phi_{1+ps}, \hat{A}$	31	2452.0	2514.0	Testing for parallelism over time for different groups. Groups = birds paired to females laying clutch sizes 1-5. (27) vs. (26), $\chi^2_6 = 1.3$ , $p = .97$
(28) $\phi, \hat{A}$	14	2487.8	2515.8	(28) vs. (26), $\chi^2_{11} = 34.5$ , $p < .001$

Table 7

Capture–recapture models and comparisons among models for adult cliff swallows in relation to their brood size (see text for notation)

Model	$np$	DEV	AIC	Comparison
<b>Female nest owners</b>				
(29) $\phi_{gs}, \hat{A}$	15	1727.1	1757.1	Best fit. Groups = birds raising brood size 0, all other brood sizes combined.
(30) $\phi_{gs}, \hat{A}$	18	1722.1	1758.1	Groups = birds raising brood sizes 0–4. (30) vs. (29), $\chi^2_3 = 5.0$ , $p = .17$
(31) $\phi, \hat{A}$	14	1739.6	1767.6	Testing overall effect of brood size. (31) vs. (29), $\chi^2_1 = 12.5$ , $p < .001$
(32) $\phi_{gs}, \hat{A}$	25	1723.6	1773.6	Full CJS model. (32) vs. (31), $\chi^2_{11} = 16.0$ , $p = .14$
<b>Male nest owners</b>				
(33) $\phi_{gs}, \hat{A}$	25	2320.3	2370.3	Best fit. Full CJS model. No differences among males.
(34) $\phi_{gs}, \hat{A}$	31	2318.6	2380.6	Testing for parallelism over time for different groups. Groups = birds raising brood sizes 0–5. (34) vs. (33), $\chi^2_5 = 1.7$ , $p = .95$
(35) $\phi, \hat{A}$	14	2352.0	2380.0	(35) vs. (33), $\chi^2_{11} = 31.7$ , $p < .001$

on annual survival of birds occupying nests of different parasitic status. Clutch and/or brood size thus cannot explain the differences in survival among parasitic females, host females, and females who were neither hosts nor parasites. Adding an egg to a nest through parasitism would not appear to represent a long-term survival cost for the adult hosts.

#### Nesting survival in relation to clutch and brood size

Increases in clutch or brood size could reduce the fraction of parental resources allocated to each offspring, lowering the postfledging survival prospects for birds raised in nests with larger brood sizes. If so, brood parasitism could be costly to hosts in terms of expected recruitment into the next year's breeding population. We examined how first-year survival of cliff swallows varied with natal clutch and brood size, using all birds irrespective of status for which natal clutch and brood sizes were known. As with adults, we could not do this comparison separately for nests of different parasitic status due to problems with estimating survival for small cohorts. We analyzed birds from fumigated and nonfumigated nests separately, given the substantial effect of ectoparasites on first-year survival (Brown and Brown, 1996).

First-year survival probabilities did not differ significantly for birds reared in fumigated nests of different clutch sizes. A model with an age-dependent survival-by-group interaction, lowest in AIC among those that included a group effect, for natal clutch sizes one ( $n = 15$  birds), two ( $n = 207$ ), three ( $n = 2118$ ), four ( $n = 3966$ ), and five ( $n = 1183$ ) eggs did not provide a significantly better fit than a model without a group effect or one with time-dependent survival (Table 8). The overall first-year survival probability for fumigated birds irrespective of natal clutch size was 0.349 ( $\pm 0.00975$ ). A similar noneffect of clutch size was seen for birds from nonfumigated nests. An age-dependent survival-by-group model with clutch sizes two ( $n = 113$  birds), three ( $n = 695$ ), four ( $n = 2015$ ), and five ( $n = 516$ ) eggs (data were insufficient

Table 8

Capture–recapture models and comparisons among models for nesting cliff swallows in relation to natal clutch size (see text for notation)

Model	$np$	DEV	AIC	Comparison
<b>Fumigated nests</b>				
(36) $\phi_{gs}, \hat{A}$	16	1805.9	1837.9	Best fit. No differences among clutch sizes.
(37) $\phi_{gs}, \hat{A}$	24	1805.4	1853.4	Groups = birds from clutch sizes 1–5. (37) vs. (36), $\chi^2_5 = 0.5$ , $p = .99$
(38) $\phi_{gs}, \hat{A}$	41	1800.3	1882.3	CJS model. (38) vs. (36), $\chi^2_{25} = 5.6$ , $p = .99$
<b>Nonfumigated nests</b>				
(39) $\phi_{gs}, \hat{A}$	41	2987.2	3069.2	Best fit. CJS model. No differences among clutch sizes.
(40) $\phi_{gs}, \hat{A}$	22	3035.8	3079.8	Groups = birds from clutch sizes 2–5. Rejected by high AIC.
(41) $\phi_{gs}, \hat{A}$	16	3037.2	3069.2	(41) vs. (39), $\chi^2_{25} = 50.0$ , $p = .002$

to estimate survival for clutch size one) as the group effect (model 40) did not provide a better fit, as judged from the AIC (Table 8), than one with age- and time-dependent survival but no group effect (model 39; that these models were not nested precluded use of an LRT). The overall first-year survival probability for nonfumigated birds irrespective of natal clutch size varied from 0.0679 ( $\pm 0.0213$ ) in 1988 to 0.460 ( $\pm 0.244$ ) in 1985.

Analyses of how first-year survival probabilities varied with natal brood size were virtually identical to those for natal clutch size. For neither fumigated nests (brood size one,  $n = 132$  birds; two,  $n = 918$ ; three,  $n = 3173$ ; four,  $n = 3756$ ; five,  $n = 524$ ) nor nonfumigated nests (one,  $n = 60$ ; two,  $n = 554$ ; three,  $n = 1835$ ; four,  $n = 2275$ ; five,  $n = 385$ ) did a model with natal brood size as a group effect provide a significantly better fit than one without the group effect (Table 9). Among fumigated nests, a model with age-dependent survival but no time dependence provided the best fit, whereas for nonfumigated nests an age-dependent model with time dependence fit best. That survival of birds from nonfumigated nests, but not fumigated nests, showed time dependence for both natal clutch and brood size is probably attributable to a greater number of years with data for the nonfumigated cohorts. All cliff swallow survival probabilities likely vary with year, but large sample sizes are required to demonstrate time dependence statistically (Brown and Brown, 1996). The overall first-year survival probability for fumigated birds in this sample irrespective of natal brood size was 0.351 ( $\pm 0.00875$ ), and for nonfumigated birds it varied from 0.0761 ( $\pm 0.0265$ ) in 1988 to 0.372 ( $\pm 0.214$ ) in 1985.

That we found no relationship between first-year survival and natal clutch or brood size suggests that differences in clutch or brood size per se (Table 5) had little impact on postfledging survival of birds raised in nests of different parasitic status, and differences in natal clutch or brood size cannot explain the variation in first-year survival for birds from parasite, host, or nonparasitized natal nests. Adding a parasitic egg does not apparently represent a long-term cost to nestlings by increasing competition and thus reducing their first-year survival probabilities.



**Table 9**  
Capture-recapture models and comparisons among models for nestling cliff swallows in relation to natal brood size (see text for notation)

Model	np	DEV	AIC	Comparison
<b>Fumigated nests</b>				
(42) $\phi_{st}, \hat{p}_t$	16	2063.2	2095.2	Best fit. No differences among brood sizes.
(43) $\phi_{st-pst}, \hat{p}_t$	24	2062.7	2110.7	Groups = birds from brood sizes 1-5. (43) vs. (42), $\chi^2_3 = 0.5, p = .99$
(44) $\phi_{st}, \hat{p}_t$	41	2057.4	2139.4	CJS model. (44) vs. (42), $\chi^2_{25} = 5.8, p = .99$
<b>Nonfumigated nests</b>				
(45) $\phi_{st}, \hat{p}_{st}$	52	5220.4	5324.4	Best fit. CJS model. No differences among brood sizes.
(46) $\phi_{st-pst}, \hat{p}_{st}$	152	5104.0	5408.0	Groups = birds from brood sizes 1-5. (46) vs. (45), $\chi^2_{100} = 116.4, p = .13$
(47) $\phi_{st}, \hat{p}_t$	16	5316.9	5348.9	(47) vs. (45), $\chi^2_{25} = 96.5, p < .001$

#### Estimated lifetime reproductive success

The annual survival probabilities for adults generated estimates of life span, which when multiplied by the number of offspring recruited into the next year's breeding population each year, generated estimates of total offspring produced to breeding age for parasites, hosts, and nonparasites/nonhosts (Table 10). Parasitic females realized a lifetime advantage by almost 2:1 or better over all other classes of females. These estimates would also pertain to males to the extent that they pair consistently with females of the same status and assuming male reproductive success is not heavily skewed by extrapair fertilizations. The major difference between fumigated and nonfumigated estimates, aside from lower overall values for the nonfumigated nests attributable to the deleterious effects of swallow bugs (Brown and Brown, 1996), was a smaller estimate of LRS for the nonparasitized nests relative to host nests among the nonfumigated class (Table 10). These estimates of LRS should be regarded only as relative for comparison to each other. We emphasize that the estimated LRS values require that females do not alternate between being parasites, hosts, or neither from year to year (see Methods).

We had no data to estimate LRS for males that attempted and did not attempt extrapair copulations; knowing how often

these copulations result in fertilizations would be necessary. However, the survival probabilities of EPC males and non-EPC males led to estimates of 1.13 and 2.05 years in expected subsequent life span for the two classes of males, respectively.

#### DISCUSSION

Dozens of studies on intraspecific brood parasitism have been published over the last decade (partial listing in Brown and Brown, 1996), but to our knowledge only two have contained information on annual survival of parasitized and nonparasitized individuals and their offspring (Lank et al., 1990; Larson et al., 1995). Both were on precocial geese. Neither had survival measures for the parasites themselves, and neither found differences in first-year recruitment to the next year for different classes of birds. Our study of cliff swallows is the first to provide measures of annual survival for parasites, hosts, and birds who were neither; the first to demonstrate significant differences in first-year survival among birds reared in nests of parasites, hosts, and birds who were neither; and among the first to suggest a markedly higher fitness for parasites over all other classes of individuals. The main conclusion from our analyses is that, through their own higher survival and that of their offspring, parasitic female cliff swallows may realize a lifetime reproductive success at least double that of the next most successful class of birds (the nonparasites/nonhosts). The principal unresolved question, then, is why parasitism is not more common.

#### Survival as an index of individual quality

Various studies on other species have sought information on parasitic and host individuals, usually in the context of determining whether brood parasitism is a "best-of-a-bad-job" strategy by individuals incapable of or too inferior to provide parental care, or an obligate strategy by "professional" parasites who reproduce in no other way (Emlen and Wrege, 1986; Evans, 1988; Jackson, 1993; Lank et al., 1990; Lyon, 1993; Pinxten et al., 1991; Sorenson, 1991; Weigmann and Lamprecht, 1991; Yom-Tov, 1980). In cliff swallows, all parasitisms directly observed have been by females who maintained nests and mates of their own; no cases of parasitism by nestless birds or "professional" parasites have been seen or suspected (Brown and Brown, 1989). Parasitic laying is therefore a mixed strategy (*sensu* Trivers, 1972) in which females seek to place one or more eggs in a neighboring nest while at the same time raising some offspring in their own nests. Mixed strategies like this have also been reported in other species (Gibbons, 1986; Jackson, 1993; Lyon, 1993; Møller, 1987; Sorenson, 1991). Until now, we had no information on how, if

**Table 10**  
Estimates of breeding life span in years and lifetime reproductive success (LRS) in number of young recruited to the next year for female and male cliff swallows of different classes

Class of birds	Female life span	Male life span	Female LRS	Male LRS
<b>Fumigated nests</b>				
Parasites	4.66	3.19	7.04	4.82
Hosts via egg transfer	2.93	3.19	2.81	3.06
Hosts via egg laying	1.81	3.19	1.74	3.06
Nonparasites/nonhosts	3.65	3.19	3.83	3.35
<b>Nonfumigated nests</b>				
Hosts via egg transfer	2.93	3.19	1.23	1.34
Hosts via egg laying	1.81	3.19	0.69	1.21
Nonparasitized	3.65	3.19	0.88	0.77

at all, parasitic cliff swallows differed from nonparasites in phenotypic characteristics. It seemed that parasitism occurred unpredictably whenever a female happened to encounter an unattended nest at the appropriate time in the nesting cycle. Instead, the increased survival probabilities of parasitic females and of the offspring from their nests indicate that parasites are not a random collection of opportunistic individuals. Parasites more likely are high-quality individuals, reflected in their survivorship and that of their young, who for this reason may have the necessary resources (time, energy) to successfully parasitize neighbors at little cost to themselves. The higher survival of these females is not a consequence of their being parasites: parasitic females did not have substantially smaller broods of their own to care for as a result of being brood parasites (Table 5), and brood size had no apparent effect on adult survival anyway.

The lower survival probabilities of host females and the increased first-year survival probabilities of young reared in host nests in the presence of ectoparasites similarly suggest that hosts are not random collections of individuals who happened to have accidentally left their nests unguarded and thus vulnerable. Low survival, especially for females parasitized by egg laying, indicates that host females are probably ones in poorer condition than average or ones who invest more than average in offspring at a substantial cost to their own survival prospects. That egg-transferring parasites tend to select among nests and place their eggs in ones that are ultimately likely to successfully fledge young (Brown and Brown, 1991) means that hosts are not chosen randomly. The information on survival probabilities reported here confirms that conclusion and suggests that characteristics of the host females may influence their selection by the parasites in one of two ways. Either parasites somehow identify individuals who, at a long-term cost to themselves, lavish inordinate amounts of parental care on offspring, or individuals in relatively poor condition (reflected in their survival probabilities) are the ones most likely to leave their nests unattended (perhaps while away foraging) and are thus susceptible to brood parasitism in the first place. Given the constraints involved for egg-laying parasites who must find an unattended host nest in the narrow window of time within the nesting cycle when parasitic eggs can be laid, it seems more likely that parasites pick poorer condition birds who leave their nests unguarded. On the other hand, that offspring reared in host nests have higher first-year survival probabilities than birds from nonparasitized nests in the presence of ectoparasites suggests that host nests have advantageous characteristics. Most likely this is because parasites choose as hosts those nests that are relatively uninfested with ectoparasites (Brown and Brown, 1991).

Annual survival probabilities for males paired to females of different parasitic status showed no differences. This too suggests that the observed variation among females in survival probabilities reflected their inherent condition; had female survival instead reflected the costs or benefits of parasitism *per se*, males to whom the females were paired should have shown a similar pattern. Male quality seems unrelated to nest status. However, one might expect superior males to compete for parasitic females, given the reproductive advantages associated with this class of females (Table 5). If we had a larger sample of males of known status, especially of those paired to parasites, we might have demonstrated differences among male classes.

One of our more surprising findings was the significantly lower survival probability for EPC males compared to non-EPC males. This might mean that extrapair copulation is costly to male cliff swallows, although we cannot identify in what way. More likely, survival probability reflects male quality. If so, females who mated with these males did so with relatively

inferior partners. This result does not agree with the widely held view that extrapair copulation represents a way for females to achieve matings with males of high genetic quality (e.g., Birkhead and Møller, 1992; Wagner, 1993; Westneat et al., 1990) and field data on other species showing that longer-lived, more experienced males are more likely to achieve extrapair copulations or that they are preferred by females as mates (e.g., Alatalo et al., 1991; Andersson, 1994; Kempenaers et al., 1992; Morton et al., 1990; Wagner et al., 1996; Weatherhead and Boag, 1995). Our data suggest that female cliff swallows should resist extrapair copulation attempts, which they generally do, at least during the first half of the nesting season (Brown and Brown, 1996). If survival reflects in part male quality (which seems likely), female cliff swallows are unlikely to realize a genetic gain for their offspring from extrapair copulation. Extrapair mating may be a "best-of-a-bad-job" strategy for inferior males, with deleterious consequences for females who participate.

We detected significant differences in survival (Tables 1–3) despite our categories being polluted with undetected parasitisms or extrapair copulations and possibly with birds changing status between years (see Methods). This attests to the surprising strength of these patterns. The differences likely would have been greater had we had pure samples of birds of each status. We are confident, therefore, that the differences in survival probabilities reflect real differences among birds pursuing these alternative strategies.

#### Costs of brood parasitism

Brood parasitism is generally regarded as costly for hosts in altricial bird species (Nee and May, 1993; Yamauchi, 1993; Yom-Tov, 1980), in which brood sizes are limited by the extensive amount of care (incubation, feeding) that must be invested in each offspring. The nature of this cost is twofold: a host invests in at least one offspring to which it is unrelated, and addition of an extra egg(s) may reduce the survival of the parental host itself or its young by requiring increased parental care and reducing the fractional amount of care available to each offspring in the brood. By definition, all cliff swallow hosts pay the first cost, except for males in rare instances of quasi-parasitism (*sensu* Emlen and Wrege, 1986; Wrege and Emlen, 1987) in which a female parasitizes the nest of a male that fertilized her parasitic egg through extrapair mating. Quasi-parasitism may occur occasionally in cliff swallows and seems to be tolerated by "host" males (Brown and Brown, 1989).

Another potential cost of brood parasitism is its longer-term effect on hosts' expected reproductive success. Host nests contain more total eggs on average than nests of parasites or nonparasites/nonhosts (Table 5). Does the increased clutch size impair survival prospects of host parents through classic life-history trade-offs between survival and current reproductive effort (*sensu* Charnov and Krebs, 1974; reviewed in Linden and Møller, 1989; Stearns, 1992)? Lower survival probabilities for host females, especially for those parasitized by egg laying and who have the largest clutches, suggest that it might. However, we can reject brood parasitism as costly for adult host survival for three reasons. First, host brood sizes were not ultimately larger than those of other birds despite the host nests' beginning with more eggs; loss of eggs during incubation and loss of young during the early nestling stage produced little net change in the number of offspring cared for by hosts. These reductions may have occurred for the same reason that the host nests were parasitized in the first place: their owners left them unattended more often than other birds and thus they were susceptible to intruding conspecifics

that toss out eggs and small young (Brown and Brown, 1988a, 1996).

Second, even had the hosts cared for more young, we found no effect of either clutch or brood size on subsequent survival of adults attending successful nests. This, of course, came from birds under natural conditions in which clutch and brood sizes were not manipulated, and an alternative interpretation is that we saw no effect on survival due to positive phenotypic correlations between traits (Linden and Møller, 1989). For example, birds in better condition might naturally produce more eggs, and their superior condition might allow them to raise more young at no net cost relative to individuals in inferior condition who produced smaller clutches. However, brood parasitism itself represents a natural manipulation. That no effect of parasitism on male host survival was seen strengthens the case that brood parasitism is in general not costly to adult survival.

Third, parasitic eggs added to host nests during the 1-3 days immediately preceding the host's laying and during the first 1-2 days of the host's laying seem to cause hosts to reduce their own clutch sizes (Brown and Brown, 1989). This suggests that cliff swallows may be partially indeterminate layers and that addition of parasitic eggs does not always result in enlarged host clutches or broods. Even egg-transferring parasites, who frequently added eggs well after a host had ceased laying, often removed a host egg either during the transfer or at another time (Brown and Brown, 1988a, 1996), again resulting in no net change in host clutch size. For these reasons, host clutches were not markedly larger than those of parasites or nonhosts (Table 5), and any phenotypic correlation between host ability and clutch/brood size was maintained. Consequently, parasites gained by not having their young in an enlarged brood that the host was unable to care for, and hosts suffered no long-term costs.

The amount of parental care available for each offspring declines with increased brood size (reviewed in Clutton-Brock, 1991). Thus, another potential cost of brood parasitism, independent of adult survival, is that it may lower postfledging survivorship of host offspring. This is, of course, also costly for the parasites' young coming from host nests. But, as noted above, for several reasons host brood sizes were not larger than those of other birds. In addition, we found no effect of natal clutch or brood size on first-year survival probability in either the presence or absence of ectoparasites. Although this result might again reflect phenotypic correlations between brood size and parental ability to raise young, the absence of a negative association reinforces the conclusion that addition of parasitic young does not lower recruitment of offspring to breeding age from host nests.

We conclude that brood parasitism in cliff swallows may not be as costly to hosts as some have supposed (e.g., Nee and May, 1993; Yamauchi, 1993). There is the penalty of investing in an unrelated individual instead of one of the host's own, but there is no compelling evidence that hosts or their young suffer long-term survival-related costs due to being parasitized. This may be largely because parasites reduce the probability of these costs being expressed by laying eggs at a time when the host is likely to respond by reducing its own egg output and by removing host eggs before parasitizing nests by egg transfer. The loss of an egg when parasitized—either directly or indirectly—may be the most serious cost of brood parasitism in cliff swallows.

### Survival estimation

Until recently, the predominant approach to estimating survival probabilities in animal populations was to tabulate the percentages of marked animals resighted and equate this to

survival. This approach is still widely used, including in past studies of brood parasitism (Lank et al., 1990; Larsson et al., 1995), despite the development of sophisticated methodology to separate true survival from recapture/resighting probabilities (Lebreton et al., 1992). Maximum likelihood methods of survival estimation have many advantages, including more precise estimation of parameters and the ability to compare across groups (Lebreton et al., 1993). Our use of SURGE enabled us to test whether survival varied among classes of birds with far greater statistical rigor than would have been possible had we simply calculated survival separately for each group and qualitatively compared them post hoc.

Nevertheless, some caveats are in order. SURGE, and the body of mark-recapture theory on which it is based, cannot distinguish between permanent emigration and mortality. These parameters are confounded in virtually any field study with incomplete registration of deaths (Lebreton et al., 1993). Thus, the survival probabilities reported in this paper are not absolute and should be regarded as estimates of local or apparent survival only. They should be used as relative measures of survival among groups or classes, and to do so makes the explicit assumption that long-range dispersal and emigration out of the study area do not vary among the sets of birds being compared (see Brown and Brown, 1996). We see no reason to expect differential dispersal in the data sets presented in this paper, with two possible exceptions. The survival probability of females attending broods of zero, that is, whose nests failed before the nestlings reached 10 days of age, was only about two-thirds that of females that actually raised young. Because nest failure is often associated with short-range dispersal within the study area (Brown and Brown, 1996) and females relieved of parental duties might be expected to have the highest survival probability, we view this group of birds as a likely candidate for greater undetected dispersal and emigration. This potential bias would account for their lower apparent survival, although it has no effect on our conclusions about the costs and benefits of brood parasitism. Another, though less likely, possibility of differential dispersal is by males that engaged in extrapair copulations. Often, unpaired and unmarked males who are nonresident in a colony perpetrate extrapair copulation attempts (Brown and Brown, 1996), and these males might be more likely to disperse from an area in which they did not nest. However, our data on survival reported here all came from marked, resident males who maintained nests of their own. Dispersal biases seem unlikely among these males.

### Effects of ectoparasites

Nest fumigation allowed us to estimate fitness components in the absence of ectoparasitic swallow bugs, which, owing to their abundance and virulence, often overwhelm other reproductive effects in cliff swallows (Brown and Brown, 1996). In a sense, of course, this manipulation was unnatural, but it did reveal the potential fitnesses different classes of birds could achieve. In some cases, patterns among birds exposed and not exposed to ectoparasitism were qualitatively the same (e.g., effects of natal clutch and brood size on first-year survival). However, in other cases we detected a difference among fumigated and nonfumigated classes, and the most important of these concerned first-year survival of birds from host nests and those not parasitized. In the absence of swallow bugs, we found no significant differences in first-year survival for nestlings reared in host nests versus nests of nonparasites/nonhosts. In the presence of swallow bugs, though, we found first-year survival to be significantly higher for birds from host nests. This probably reflects the active selection by parasitic females of host nests relatively uninfested by ectoparasites

(Brown and Brown, 1991). Consequently, the young in those nests are in better fledging condition, likely leading to higher postfledging survival. Because of this, hosts under natural conditions have higher average annual reproductive success, as measured by recruitment to the next year, than birds who are not brood parasitized (Table 10). This advantage to hosts disappears when swallow bugs are removed, and in that case nonparasites/nonhosts have the highest success. Parasitic females might be those who occupy highly infested nests and resort to brood parasitism to place some of their offspring in nests less subject to the effects of swallow bugs. We cannot explore this fascinating possibility without information on parasite identities among nonfumigated nests, although the higher first-year survival probability for young reared in the parasites' own nests in the fumigated sample suggests that the brood parasites are superior parents at least in the absence of ectoparasites.

#### Fitness estimates

As a consequence of both their own greater probability of survival and that of the offspring reared in their nests, parasitic females had substantially greater fitness than the other three classes of birds. Although survival of males paired to different females did not vary, those paired with parasites also had higher fitness owing to the greater survival of offspring from their nests. To our knowledge, this is the first demonstration that females employing a mixed parasitic strategy have higher average lifetime fitness. In several other species, parasitic females were thought to have higher annual reproductive success based on numbers of eggs hatched or fledged (Lyon, 1993; Møller, 1987; Sorenson, 1991), but these studies had no long-term information on adult survival and first-year recruitment for different classes of birds. It does not necessarily follow that more young fledged by parasites means higher fitness because potential costs associated with larger host brood sizes or the time spent finding host nests may impose long-term survival costs (Jackson, 1993; Yamauchi, 1993).

The conclusion that parasitic cliff swallows and their mates do better than other birds seems solid, but the estimate of lifetime reproductive success for parasites is probably biased in two opposite ways. It does not contain a correction for instances in which the parasites themselves were parasitized and thus raised young to which they were unrelated. Over half of all known parasites were parasitized by other (in some cases unidentified) birds (Brown and Brown, 1989). We did not try to correct for this bias because we had no way to identify the eventual fates of individual parasitic eggs that appeared in nests, but the effect would be to lower the estimated fitness of parasites (Table 10). On the other hand, the fitness estimates for parasites do not include their young raised parasitically in host nests. Again, we did not try to estimate this increment because of difficulties with determining whether a given parasitic egg in a host nest survived to produce a fledgling; often we knew a parasitic egg appeared in a nest in a specified time period, but we could not know which of several eggs in the clutch was the parasite's. This bias increases the fitness estimates of parasites over those shown (Table 10). With two biases operating in opposite directions, the estimate shown in Table 10 is the best relative fitness measure we can be comfortable with. Also, our fitness estimate for parasites comes from fumigated nests. We see no reason why this estimate should not be an accurate relative measure of fitness, compared to other classes of birds. This is especially the case since the fitness differential for parasites is in large part a consequence of increased breeding life span, which is unaffected by nest fumigation.

Fitness of female hosts was lower than that of other classes

of birds in all comparisons except for females parasitized by egg transfer (Table 10). Hosts having nests less infested with swallow bugs and the greater postfledging survival of their young as a result was not enough to overcome the low adult survival for female hosts parasitized by laying. Males paired to host females in the presence of ectoparasites had higher apparent fitness than males occupying nests not brood parasitized, largely because first-year survival of young from host nests was enhanced. However, these estimates were biased by not being able to correct for the fate of parasitic eggs. Hosts clearly raised some parasitic young, lowering their fitness estimates (Table 10) by an unknown quantity. This does not change host fitness relative to other classes among fumigated nests, but in nonfumigated nests this bias could be enough to equalize host and nonhost fitness for all categories of males and females.

Our estimates of lifetime reproductive success rely on an expected breeding life span derived from the annual survival probabilities for different classes of birds. Life span as we calculate it assumes the same annual survival probability across years. The results of our model fitting suggested no time dependence in survival estimates for males and females of different status, supporting the assumption inherent in the expected life span. However, if status is directly associated with survival, we must assume that status remains unchanged across years; otherwise, survival probability (and hence expected life span) changes with annual status. This is not an issue if survival reflects overall bird quality or condition, which we argued earlier, and if that condition determines parasitic status (which would presumably be constant among years). Ideally, one would use multistate statistical models (Brownie et al., 1993; Nichols et al., 1992, 1993, 1994) to estimate survival conditional on annual status for birds exhibiting different status transitions from year to year, but the lack of tractable multistate software precludes such analyses at this time.

We emphasize that our fitness estimates (Table 10) are relative ones. They do not reflect absolute fitness because they do not contain a correction for long-range dispersers and permanent emigrants (Brown and Brown, 1996). If true lifetime reproductive success was as low as that estimated for the nonfumigated class, the population would be declining, which is not the case. However, our estimates are useful relative indices as long as we assume no differential dispersal among classes of birds (see above).

#### Evolution of brood parasitism

The laying of eggs in conspecifics' nests is a common alternative reproductive strategy in birds and insects, but we understand little about its evolution in any species. This is primarily because most workers have focused on the natural history of brood parasitism, and data to estimate fitness for parasites, hosts, and nonparticipants have been extremely limited. Several recent theoretical models have sought to identify conditions that allow parasitism to persist in populations (Eadie and Fryxell, 1992; Nee and May, 1993; Yamauchi, 1993, 1995), but the only previous data on long-term survival and recruitment with which to estimate fitness of brood parasites and their hosts are those of Lank et al. (1990) for snow geese (*Anser caerulescens*). Under various assumptions about fecundity, viability, and behavioral flexibility of parasites and nonparasites, Lank et al. concluded that parasitism, while less successful than nonparasitic nesting in their population, could persist as a conditional strategy used by females that are in too poor a condition to maintain nests.

Our data, however, show a clear reproductive advantage for brood parasites in cliff swallows. This is the first case documented in birds in which parasitic females achieve substan-

tially higher fitness returns than nonparasitic/nonhost females. With an estimated lifetime reproductive success almost twice that of the next most successful class of females, brood parasitism should spread in this population. Although parasitism is common (at least 22% of nests and possibly more receive a parasitic egg on average), most females are not parasitic. Why? One possibility is that the trait is a mixed evolutionarily stable strategy (ESS) under frequency-dependent selection, with parasites benefiting when rare and suffering when common. At equilibrium, parasitism and nonparasitic nesting should have equal fitness (Eadie and Fryxell, 1992). Either an equilibrium currently exists and our fitness estimates for parasites and nonparasites are functionally the same (which we doubt given the size of the apparent advantage for parasites), or no equilibrium exists and parasitism is increasing in the population at the present time. Assuming that equilibrium conditions exist can be risky in some situations (Ender, 1986). Perhaps the cliff swallow's recent conversion to nesting on artificial structures such as bridges and highway culverts (Brown and Brown, 1995) has provided more opportunities for parasitizing neighbors and is shifting the population toward a new equilibrium in these traits. However, we see no obvious reason why this should be so, as colonies on artificial sites are similar in many ways to those on natural cliffs (Brown and Brown, 1996).

The importance of density dependence in the evolution of brood parasitism was recently emphasized by Eadie and Fryxell (1992; see also Nee and May, 1993). Their simulation analyses suggested that when the frequency of brood parasitism is fixed, an increase in the total number of females increases the relative fitness of parasites because more potential hosts are available. The result is that there is no single ESS, and the equilibrium frequency of parasitism increases in a nonlinear fashion with the total density of females. We may be seeing a rise in the frequency of brood parasitism in response to an increased population density. Overall, cliff swallow population size has been increasing in Nebraska and adjacent Great Plains states since at least 1982 for unknown reasons (Brown and Brown, 1995). Until a new equilibrium is reached, we would expect parasites to have greater fitness than nonparasites, as we observed. If a single breeding colony constitutes a "population" in Eadie and Fryxell's (1992) sense, their simulations could explain why the apparent frequency of brood parasitism in cliff swallows varies widely among different colonies and generally increases in larger and more dense ones (Brown and Brown, 1996). Brood parasitism is infrequent in the Sierra Nevada (Smyth et al., 1993), perhaps because that population is smaller than the one we studied in Nebraska. If the Sierra population is below the density threshold required for parasite fitness to equal nonparasite fitness (Eadie and Fryxell, 1992), parasitism as a mixed ESS could be uncommon, explaining why few cases of parasitic laying were observed (Smyth et al., 1993).

We conclude that brood parasitism in cliff swallows is practiced by superior individuals who use it as part of a mixed reproductive strategy, analogous to extrapair mating in males, to supplement their reproductive success. Their inherent quality and ability to place their parasitic eggs in "good" host nests give them a substantial fitness advantage over other birds. The spread of parasitism is regulated by extensive nest guarding by nonparasitic individuals, and the high levels of guarding (Brown and Brown, 1996) may represent a constraint on parasitism's spread. No matter how much fitness gain parasitism may confer, it only does so if a parasite has the chance to enter a nest and lay or transfer an egg. Many cliff swallows never allow would-be parasites such an opportunity.

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