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THE COSTS AND BENEFITS OF EGG DESTRUCTION BY CONSPECIFICS IN COLONIAL CLIFF SWALLOWS

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ABSTRACT.—We studied egg destruction by conspecifics in colonial Cliff Swallows (*Hirundo pyrrhonota*) in southwestern Nebraska. Between 8.5% and 19.6% of all nests lost at least 1 egg to an intruding conspecific. Egg destruction occurred when nests were left momentarily unattended, often during colony alarm responses. Birds that destroyed eggs maintained nests of their own, and usually nested within 75 cm of their victims. Egg destruction was not related to attempts to usurp nests. Over a third of perpetrators of egg destruction lost eggs from their own nests to conspecifics. Egg destruction occurred more often in nests initiated early in the nesting season and in nests with large clutch sizes. Egg destruction usually occurred during a victim's egg-laying or early during incubation and declined in frequency as incubation proceeded. Breeding in a colony's peak period of nesting did not afford an advantage to potential victims by diluting their chances of being victimized. Cliff Swallows seldom destroyed all of the eggs in a neighbor's clutch, usually destroying only 1 egg at a time even though other eggs were present.

There was little direct evidence that egg destruction was associated with parasitic egg-laying by Cliff Swallows, but nests with egg destruction were over 3 times more likely than nests in general to have an egg physically transferred into them. The costs of egg destruction to victims were obvious, but the benefits to destroyers of eggs were not. Egg destruction is possibly a prelude to physical transfer of eggs, reducing host clutch sizes and ultimately within-brood competition among host and parasitic nestlings. Males may also benefit by destroying a female's eggs during laying, thereby causing her to continue laying and remain sexually receptive to forced extrapair copulations. Incidence of egg destruction by conspecifics increased with Cliff Swallow colony size and thus, for potential victims, represents a definite cost of coloniality. Received 22 January 1988, accepted 26 June 1988.

A POTENTIAL cost of colonial breeding is an increased number and proximity of neighbors that may interfere with one's attempt to reproduce. A dramatic form of reproductive interference is the destruction of eggs and chicks by conspecifics within the colony (Wittenberger and Hunt 1985). Potential destruction of eggs or chicks represents an enormous cost of coloniality. This cost is incurred routinely by some colonially nesting birds, especially skuas, gannets, and large gulls (Wittenberger and Hunt 1985, references therein). Conspecific interference centers on prefledged chicks, perhaps often to prevent giving care to unrelated offspring. Chicks can be attacked, killed, and eaten. Cannibalism is an important component of this form of reproductive interference (Wittenberger and Hunt 1985). A steady supply of available chicks presumably represents a major benefit of nesting in a colony for a cannibalistic individual.

Less attention has been paid to egg destruction and its effects in colonial birds. Lesser Black-backed Gulls (*Larus fuscus*; Harris 1964, Brown 1967, Davis and Dunn 1976), Herring Gulls (*L.*

argentatus; Paynter 1949, Harris 1964, Brown 1967), Arctic Terns (*Sterna paradisaea*; Pettingill 1939), Carrion Crows (*Corvus corone*; Yom-Tov 1974, 1975), and Marsh Wrens (*Cistothorus palustris*; Picman and Belles-Isles 1987) are reported to steal, puncture, or eat eggs from nests of neighboring conspecifics. Egg destruction in Cattle Egrets (*Bubulcus ibis*) occurs when nesting materials are stolen and during fights (Siegfried 1972). In communally nesting Ostriches (*Struthio camelus*), Groove-billed Anis (*Crotophaga sulcirostris*), and Acorn Woodpeckers (*Melanerpes formicivorus*), eggs in a clutch are removed and destroyed by later-laying females, a manifestation of reproductive competition among females (Vehrencamp 1977, Bertram 1979, Mumme et al. 1983). Egg destruction can have major effects on the fitness of both destroyer and victim (see Wittenberger and Hunt 1985). We must understand fully both egg destruction and chick-killing, because their costs and benefits must be measured if we are to construct a coherent general theory for the evolution of avian coloniality.

We discovered that colonial Cliff Swallows (*Hirundo pyrrhonota*) in southwestern Nebraska often destroy the eggs of conspecifics. Egg destruction varied with colony size and may affect the evolution of coloniality. Although the costs to a victim are clear, the benefits to an egg destroyer are not. We report on egg destruction in Cliff Swallows and examine the potential costs and benefits to both victims and perpetrators. Further, we investigated whether egg destruction was associated with alternate reproductive tactics such as intraspecific brood parasitism (Brown 1984, Brown and Brown 1988). Because Cliff Swallow nestlings are highly altricial and are very immobile prior to fledging, chick-killing of the kind described in colonial seabirds does not occur in this species. We therefore restrict our focus exclusively to consideration of egg destruction.

METHODS

Study site.—We studied Cliff Swallows in the vicinity of Ogallala, Nebraska, USA, near the University of Nebraska's Cedar Point Biological Station, from May to August, 1982–1987. Cliff Swallows are abundant in this area, and have likely increased in recent years with the construction of highway culverts and bridges upon which they nest. Before the appearance of artificial structures, the species probably occurred in southwestern Nebraska, nesting on bluffs and outcrops along the North Platte River and on cliffs in other parts of the state (Nichols, cited in Pearson 1917). We studied colonies that were located on artificial structures such as culverts and on natural cliff faces. During 1982–1987, there were 276 Cliff Swallow colonies totaling 97,980 nests in or near the study area in Keith, Garden, and Lincoln counties (Brown 1985). Colony size ranged from 2 to ca. 3,500 nests (\bar{x} = 355 nests, SD = 561). Birds also nested solitarily. The most common colony size was about 400 nests.

Checking nest contents.—Study colonies were named and, where possible, all nests were numbered and their progress followed throughout the nesting season. In large colonies, we sampled the nests, selecting nests from all accessible parts of the colony. We used aluminum ladders to reach Cliff Swallow nests. We also canoed, swam, or waded to the bases of cliff sites or into culverts. Nests were marked with chalk numbers on nearby concrete substrate (for colonies using bridges or culverts) or by driving nails with numbered heads into the cliff face. We checked nests each day or every other day, beginning as soon as nest construction began or as soon as fresh mud appeared on the nest's neck signaling that an existing nest was occupied. We observed nest contents with a dental

mirror and small flashlight inserted through each nest's mud neck. It was occasionally necessary to chip away pieces of dried mud to insert the mirror, but nests were not altered appreciably. Birds quickly repaired any damage. Cliff Swallows continually added fresh mud to all nests, which suggests that repair brought on by our activity did not lead to much additional energetic or time demands on the birds. Removal of small amounts of mud from the necks of nests had little adverse effect on reproductive success (Hamilton and Martin 1985, Brown pers. obs.). Once all eggs of a clutch hatched, we did not disturb that nest again until the 10th day after hatching, when we recorded the number of surviving nestlings. Because Cliff Swallows lay their eggs early each morning (Brown 1984), no nest checks were made prior to 0800 MDT to avoid possible disruption of natural egg-laying patterns. The criteria used to separate different groups of Cliff Swallow nests as different colonies are described in Brown and Brown (1986). "Colony size" refers to the number of active nests and does not include unused nests, which occurred commonly in many colonies.

Capturing, marking, and observing color-marked birds.—We captured Cliff Swallows in mist nets at selected culvert colonies. The birds' white forehead patches were colored in unique one-, two-, and three-color combinations with paint-marking pens. We used the colors light blue, light green, red, orange, pink, yellow, white (unpainted feathers), silver, black, and, to a lesser extent, gold. Except for black, the colors used were light and the shape of the birds' forehead patch remained unchanged. When birds were at their nests, usually only their heads were visible as they sat inside their nests. All color-marked birds also received standard U.S. Fish and Wildlife Service bands. Color-marked birds did not appear to behave differently from unmarked birds, nor did other birds seem to react to them in any unusual ways. Cliff Swallows were sexed by cloacal protuberance, which is about 90% accurate early in the season (Brown unpubl. data). Color-marking began at most colonies soon after the birds arrived in the spring and just prior to egg-laying. Paint remained fresh and visible on the feathers for 7–10 days, after which time birds were recaptured and the color marks refurbished. From 20–120 nests at each colony were selected as focal nests for observations. About 75% of the nest owners were color-marked (or individually recognizable by plumage irregularities).

Nest ownership by individuals was determined by observing which color-marked birds were routinely associated with a given nest. All observations of birds' behavior at their nests were made in culvert colonies. Our observations were confined to approximately the 20–60 nests closest to the colony's edge because the nests in the center or at the opposite ends of the culvert walls were difficult for us to see. Blinds were

unnecessary as Cliff Swallows habituated quickly to our presence and ignored us as long as we remained about 5 m outside of a culvert.

One or two observers, often working simultaneously, observed the focal nests for approximately 75% of daylight hours, beginning prior to or during egg-laying at each colony. Observations were continued until all egg-laying in the focal nests had stopped and all birds were incubating (about 2 weeks). All focal nests were observed during their egg-laying period but only the earlier-starting ones were watched for a major portion of their incubation period. All interactions among color-marked nest owners and unmarked non-owners at nests were recorded. Observations were conducted at 5 colonies of 125, 190, 345, 750, and 1,100 nests, respectively.

Our goal was to directly observe birds destroying eggs in other individuals' nests. It was often obvious when a Cliff Swallow entered a nest and tossed an egg out. Other times, however, the action happened so fast that it was impossible to be sure that the object tossed out of a nest was in fact an egg and not debris (such as chunks of dried mud). Therefore, we examined all nests at the start of each observation period and again after any suspicious interaction at a given nest to verify that any object removed was indeed an egg. Disturbances to the colony caused by checking nests seemed to be minimal. Often birds remained inside their nests during our examination of a nest and carried on seemingly normal activity less than a m away. All observations at colonies were conducted after 0800 MDT.

Inferring egg destruction through nest checks.—In colonies that we studied strictly by nest checks, a nest was scored as having lost eggs to conspecifics if part of the clutch disappeared between successive nest checks and if the nest was unaltered and still appeared active after the egg(s) disappeared. Some nests ultimately lost all of their eggs, but if these nests had lost part of their clutch prior to the total loss and met the above criteria, they were scored as having conspecific egg destruction. These criteria were conservative and probably caused us to overlook cases in which conspecifics destroyed entire clutches. Loss of entire clutches was also caused by snake predators and by House Sparrows (*Passer domesticus*; Brown and Brown 1987). There was no way to know accurately the cause of total clutch loss in some cases. There were, however, no known predators or nesting-site competitors in our study area that would destroy part of a clutch and otherwise leave the nest undisturbed. For this reason we are confident that partial clutch losses were caused by other Cliff Swallows. Another limitation of using nest checks to infer egg destruction is that only egg losses that happen after incubation starts can be detected. Losses during egg-laying, before clutch size was definitive, were masked by not knowing precisely when egg-laying began or

ended in a nest and by irregular laying caused by brood parasitism (Brown and Brown 1989). Thus, all inferred cases of egg destruction we report occurred during incubation and after egg laying presumably had ceased.

We are confident that nest checks revealed actual egg destruction by conspecifics and not observer error, irregular laying, or owners' removing damaged eggs. When checking a nest, we always had available the previous check. If fewer eggs were found than on the last check, the observer always double-checked the nest. Cliff Swallows are remarkably constant in their time of laying, virtually always laying the eggs in their own nests prior to 0800 (see Brown 1984). All of our nest checks occurred after 0800, which minimized any error caused by the timing of egg laying. We saw no instance of a nest owner removing a damaged egg from its nest, even when we accidentally damaged eggs in the process of marking them ($n = 10$). Thus, probably few "egg losses" represented owners' removing damaged eggs.

Detecting brood parasitism.—Instances of brood parasitism were detected by directly observing birds lay eggs in neighboring nests (Brown 1984, Brown and Brown 1989), and by checking the sequence in which eggs were laid. Any nest with more than 1 egg appearing/day was assumed to have been parasitized by a conspecific, since birds in general are not known to lay more than 1 egg/24-h period. Criteria used for inferring whether a nest was brood-parasitized via parasitic egg-laying are explained in Brown and Brown (1989). A novel form of brood parasitism practiced by Cliff Swallows is to physically transfer eggs to other nests. Nests were assumed to have had an egg added by transfer if eggs appeared in them more than 3 days after incubation started yet still hatched in synchrony with the rest of the clutch. Criteria used for inferring whether a nest was brood-parasitized via egg transfer are explained in detail in Brown and Brown (1988).

Measuring nesting synchrony.—The modal clutch initiation date (date first egg laid in a nest) was determined for each colony and the standard deviation (SD) of clutch initiation date calculated (Brown and Brown 1987). A single SD was 2–5 days for most colonies. Each nest was then assigned, based on its clutch initiation date, to the appropriate number of SDs on either side of the modal date. We thus compared relative intracolony synchrony of all nests which allowed us to pool data from different colonies.

Statistical analyses.—All statistical analyses were performed on an IBM XT computer, with PC Statistician software (Madigan 1983), or on a Texas Instruments 59 programmable calculator. All statistical tests were two-tailed. Because data were not normally distributed, we used nonparametric statistical tests (Siegel 1956). Sample sizes for different analyses often differed slightly because not all information was

available for every nesting attempt or observation. For Chi-square goodness-of-fit tests, categories were lumped when necessary to achieve expected frequencies of ≥ 5 .

RESULTS

Natural history of egg destruction.—We observed 23 instances of Cliff Swallows destroying eggs of conspecifics among the nests with color-marked owners. In 9 cases the identities of both the perpetrator and the victim were known. In 2 of these cases (22.2%) the perpetrator and victim lived in adjacent nests within the colony; in 6 cases (66.7%) their nests were separated by 2–5 nests (<75 cm separating them); and in only 1 case (11.1%) did more than 5 nests separate the perpetrator's and victim's nests. Color-marked perpetrators destroyed eggs by entering nests left momentarily unattended by their owners and tossing out single eggs. Cliff Swallows frequently tried to enter active neighboring nests within their colonies, but intrusions by neighbors were rarely successful since these birds guard their nests heavily. Egg destruction and attempted trespasses into neighboring nests were perpetrated by colony residents who maintained nests of their own. We had no evidence that egg destruction was caused by nonresidents who might have been trying to usurp a nest, although some unidentified birds did toss out eggs. Cliff Swallows entered neighboring nests and tossed out eggs at virtually all times of the day: 6 (28.5%) occurred between 0800 and 0959; 3 (14.2%) between 1000 and 1159; 3 between 1200 and 1359; 7 (33.3%) between 1400 and 1559; and 2 (9.5%) between 1600 and 1630, MDT.

Ten egg tossings were committed by birds of known sex. Nine were by males, and one was by a female. Among the males, 1 individual accounted for 2 separate cases of egg tossing and another individual accounted for 3. The female laid a parasitic egg at the same time she tossed an egg out of the nest (see later section). All egg tossings except 2 appeared to be deliberate. Birds rolled an egg up to the nest entrance by repeatedly flicking it with the bill and then either flicked it out the entrance or speared and punctured it with the mandibles and dropped it out of the nest. In 2 cases an egg was knocked out of a nest, perhaps inadvertently, during a fight inside the nest between the owner and an intruding neighbor.

We watched especially for egg tossings whenever large numbers of birds left their nests unattended in response to alarm calls. Upon hearing conspecific alarm calls stimulated by either observed predators or unidentified sources, many Cliff Swallows left their nests for 15–120 s. Not all individuals left the colony in these circumstances. Some birds used the opportunity to intrude into unattended neighboring nests. We observed 5 cases of egg tossing (of 23; 21.7%) during colony alarm responses when the victims had left their nests momentarily unattended. We were unable to determine which individuals actually gave the alarm calls.

Finding an unattended nest in which to destroy eggs might entail some cost. Trespassing elsewhere could require a perpetrator to leave its own nest unattended to the degree that it might also suffer egg destruction from a neighbor. Of eight different perpetrators for whom we had details of reproductive success, three (37.5%) had eggs destroyed in their own nest by other birds.

We observed 3 instances of owners tossing eggs from their own nests. In all 3 cases, an observed or inferred brood parasitism had occurred in the nest during the 3 h preceding the removal (Brown and Brown 1989). Cliff Swallows will remove parasitic eggs from their nests if these eggs are added more than about 3 days before the host begins laying. Details on egg tossings by nest owners in response to brood parasitism are given in Brown and Brown (1989). Here we address only egg destruction at nests caused by nonowners.

Chronology of egg destruction.—We combined all Cliff Swallow nests that were initiated during 5-day intervals. Nest initiation dates (date of first egg laid) ranged from 8 May to 28 July. The percentage distribution of nest initiation dates for all nests in all colonies differed significantly from that for all nests (inferred) that lost eggs to conspecifics during incubation (Fig. 1). Nests initiated prior to the seasonal peak of nesting tended to suffer disproportionately more egg destruction by conspecifics. A possible cost of early nesting thus is increased risk of losing eggs to conspecifics.

For 430 separate inferred egg losses in which time of egg loss could be assigned to within 4 days, 149 (34.7%) occurred during the first 4 days of incubation (days 1–4; day 1 = day incubation began); 126 (29.3%) occurred during

days 5-8; 102 (23.7%) occurred during days 9-12; and 53 (12.3%) occurred during day 13 or beyond.

Had nest checks been able to detect egg losses during egg laying, an even greater percentage of losses likely would have preceded days 1-4. We observed 14 egg tossings by color-marked birds in which we had exact information on when the toss-out occurred relative to the victim's egg-laying period. Thirteen of these occurred during the victim's laying period. Six of these egg losses (42.9%) occurred on the same day the victim began laying (i.e. the victim's first egg was lost to a conspecific). Three losses (21.4%) occurred 1 day after the victim began laying; 1 (7.1%) occurred 2 days after the victim began laying; and 3 occurred 3 days after the victim began laying. One egg tossing occurred 18 days after the victim began laying, nearly at the time of hatching. Only this latter egg tossing might have been detected by nest checks, but even its occurrence would have been potentially obscured by initiation of hatching in the nest. The combination of inferred data based on nest checks and our observations at focal nests suggests that egg destruction occurs most often during a victim's egg laying and early stages of incubation, and declines as incubation proceeds.

We had 9 different color-marked perpetrators for whom we knew the status of their own nest at the time they destroyed another bird's eggs. Two individuals (22.2%) destroyed eggs on the same day that laying began in their own nest; 2 destroyed eggs 2 days after laying began in their own nest; 1 (11.1%) destroyed eggs 4 days after; 1 destroyed eggs 5 days after; 1 destroyed eggs 1 day before laying began in its own nest; 1 destroyed eggs 4 days before; and 1 destroyed eggs 15 days before laying began in its own nest. There appeared to be little pattern in when Cliff Swallows destroyed others' eggs in relation to the perpetrators' own stage of nesting.

Egg destruction and colony synchrony.—Synchronous nesting within a colony could afford a benefit to a potential victim by diluting its chances of having an intruder enter and destroy eggs, analogous to avoiding predation. The distribution of synchrony categories for nests suffering inferred egg losses did not differ significantly from the distribution for all nests from all colonies (Fig. 2). Thus, nests initiated during a colony's peak of nesting did not suffer a dis-

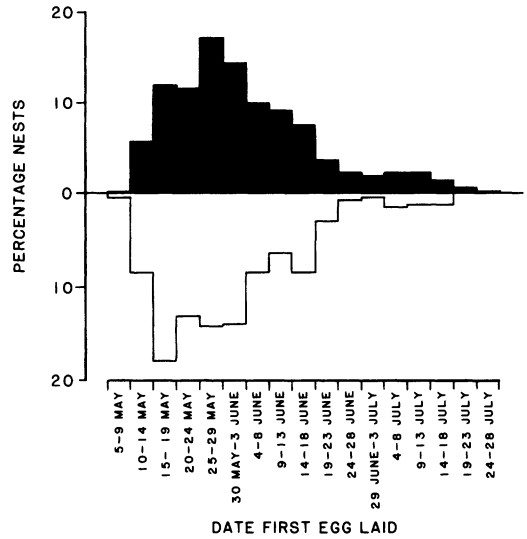


Fig. 1. Distributions of Cliff Swallow nests beginning egg-laying during 5-day intervals for all nests (upper; $n = 4,302$ nests) vs. for nests that lost at least 1 egg to conspecifics (lower; $n = 400$ nests). The distributions differed significantly ($\chi^2 = 35.4$, $df = 11$, $P < 0.001$).

proportionately lower incidence of egg destruction than ones initiated before or after the peak.

Clutch sizes of victimized nests.—The percentage distribution of clutch sizes in all nests in all colonies differed significantly from that of clutch sizes of all nests in which inferred egg destruction occurred (Fig. 3). In this analysis we used only nests which survived past the laying period (until laying stopped); i.e. only nests with definitive clutch sizes. Clutch size included all eggs ever known to be present in the nest including those destroyed. Nests with clutch sizes of ≥ 4 eggs suffered a disproportionately higher incidence of egg loss to conspecifics (Fig. 3). Nests with clutches of 1 egg could not suffer a "partial" clutch loss and thus could not meet our criteria for inferred egg loss due to conspecifics. Some losses of single-egg clutches were probably caused by conspecifics, although we had no way to estimate the extent of such losses.

Number of eggs destroyed/clutch.—Among the 479 nests with inferred egg losses in all colonies, there were 517 separate instances of partial clutch losses attributed to conspecifics in which 655 eggs were destroyed. In 407 instances (78.7%), a single egg was destroyed; in 83 instances (16.0%), 2 eggs were destroyed; in 26

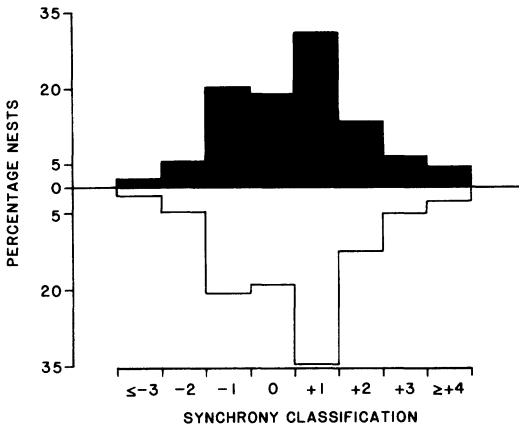


Fig. 2. Distributions of Cliff Swallow nests in each synchrony classification for all nests (upper; $n = 4,171$ nests) vs. for nests that lost at least 1 egg to conspecifics (lower; $n = 408$ nests). The distributions did not differ significantly ($\chi^2 = 6.06$, $df = 7$, $P = 0.53$).

instances (5.0%), 3 eggs were destroyed; and in 1 instance (0.2%), 4 eggs were destroyed. In all of these cases, other eggs remained in the nest after the egg losses. Mean number of eggs destroyed/egg-tossing event was 1.27 ($SD = 0.83$, $SE = 0.04$, $n = 517$). For all nests suffering losses, the mean number of eggs destroyed/nest was 1.37 ($SD = 0.60$, $SE = 0.03$, $n = 479$). There were 36 nests (7.5%, $n = 479$) that had >1 egg-loss event occurring at different times. Thirty-four of these nests had 2 separate egg tossings in which a mean of 2.3 eggs was lost ($SD = 0.65$, $SE = 0.11$). The remaining 2 nests had 3 separate egg tossings in which a mean of 3.5 eggs was lost ($SD = 0.71$, $SE = 0.50$). Thus, nests suffering multiple tossings lost 1.8–2.7 times as many eggs on average as did nests suffering only a single egg-loss event.

Among nests with color-marked owners, we directly observed 8 cases (47.1%, $n = 17$) in which an intruding Cliff Swallow tossed out a single egg but ignored additional eggs in the nest. In the remaining 9 cases (52.9%), the egg tossed out of the victim's nest was the only egg present in the nest at the time. Observations and nest-check data thus indicated that intruding Cliff Swallows often removed only part of a clutch even though apparent opportunity existed for removing additional eggs or even the entire clutch. Because some egg destruction occurred in nests with only a single egg present (usually

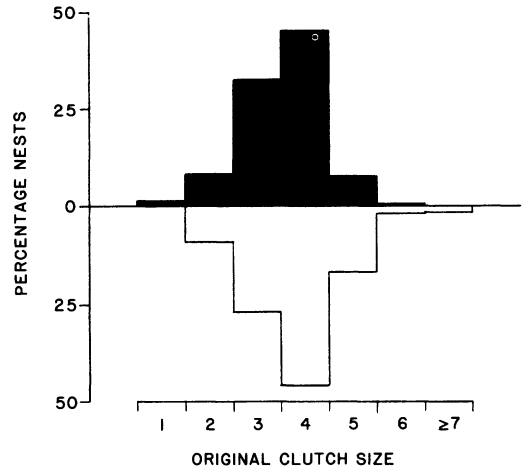


Fig. 3. Distributions of Cliff Swallow nests containing each clutch size for all nests (upper; $n = 4,942$ nests) vs. for nests that lost at least 1 egg to conspecifics (lower; $n = 479$ nests). The distributions differed significantly ($\chi^2 = 70.5$, $df = 5$, $P < 0.001$). Clutch size of 1 was excluded from the statistical analysis.

on the first day of the victim's egg-laying), instances of egg destruction inferred from partial clutch losses necessarily underestimated the frequency of this phenomenon.

Effects of egg destruction on reproductive success.—Color-marked victims of egg tossings laid a mean of 4.1 eggs ($SE = 0.26$, $n = 9$), compared to 3.5 eggs ($SE = 0.38$, $n = 8$) for color-marked perpetrators and 3.7 eggs ($SE = 0.05$, $n = 281$) for color-marked birds not known either to destroy others' eggs or to be victims. Victims had a mean of 3.1 eggs ($SE = 0.29$, $n = 9$) remaining after suffering egg losses. These results from our color-marked sample of individuals are consistent with data from inferred egg tossings in which individuals with larger clutch sizes tended to be victimized and the average egg loss was about 1 egg.

Color-marked victims fledged a mean of 3.0 offspring ($SE = 0.47$, $n = 9$), compared to 2.6 offspring ($SE = 0.53$, $n = 8$) for perpetrators and 2.9 offspring ($SE = 0.08$, $n = 264$) for nonvictims/nonperpetrators. Thus, there was a suggestion that victims had greater reproductive success despite suffering egg destruction than did perpetrators and that victims did at least as well as nonvictims/nonperpetrators. It was not possible to test whether statistically significant differences existed among the 3 classes of in-

dividuals because of small numbers of known color-marked victims and perpetrators for which nesting success data were known.

An analysis of overall nest survivorship, in which we examined only whether or not a nest produced at least 1 fledged offspring, led to a different conclusion. Any nest containing at least 1 nestling alive on the tenth day after hatching was considered a successful nest; and a nest without any nestlings alive, an unsuccessful nest. For all nests that suffered inferred egg losses, 34.7% (166 of 478) were eventually unsuccessful at fledging any young. This compares to 23.4% (1,102 of 4,708) for all nests in our population. Significantly more nests with egg losses ultimately failed than nests in general ($\chi^2 = 30.1$, $df = 1$, $P < 0.001$).

Egg destruction versus colony size.—A large colony might contain more potential destroyers of eggs and more potential victims than a small colony. This could increase the per capita probability of becoming a victim or finding a nest to raid. Percentage nests with at least 1 inferred egg loss increased significantly with colony size (Fig. 4). A significant correlation remained even when colonies ≤ 10 nests were excluded from the analysis (Fig. 4). This indicates that colony size affected the incidence of egg destruction across the entire colony size range (1–1,600 nests) observed.

Egg destruction and brood parasitism.—Destroying a neighbor's eggs could be associated with brood-parasitizing that same neighbor since some parasitic birds are known to remove some of their host's eggs. We observed only 1 instance in which a female Cliff Swallow entered an unattended neighboring nest, tossed out 1 egg, and then immediately laid an egg in the nest (Brown and Brown 1989).

Among nests known to have been parasitized via parasitic egg laying, 11.2% (37 of 330) suffered inferred egg losses. This compared with 9.0% nests (442 of 4,899) with inferred egg losses among all nests presumed not to have been parasitized. Egg removals did not occur disproportionately more often among parasitized nests ($\chi^2 = 1.78$, $P = 0.18$, NS; Brown and Brown 1989). The overall percentage of nests with inferred egg losses was 9.8%, (479 of 4,420), the same as the overall percentage of nests with at least 1 parasitic egg (487 of 4,455). If brood parasitism and egg destruction occurred independently at this frequency, we would expect 47 nests (0.0982;

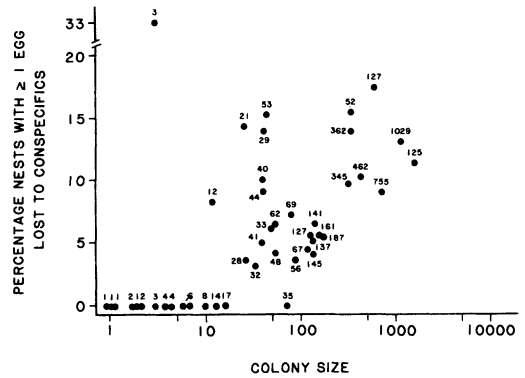


Fig. 4. Percentage of Cliff Swallow nests with at least 1 egg lost to conspecifics vs. colony size (no. of active nests). Sample size for each colony is shown. For all colonies combined, percentage of nests with egg losses increased significantly with colony size ($r_s = 0.65$, $P < 0.001$). The correlation was also significant when only colonies > 10 nests in size were considered ($r_s = 0.40$, $P = 0.02$).

$n = 4,899$) both to have parasitic eggs and to lose eggs to conspecifics. We detected 37 such nests, suggesting that parasitic egg laying and egg destruction occurred together only to (and perhaps less than) the degree expected by chance. These analyses and our observations thus do not suggest that parasitic Cliff Swallows routinely remove host eggs from nests in which they lay parasitic eggs.

Among our sample of color-marked individuals known to be parasites and hosts, however, more hosts (9 of 21; 42.8%) suffered egg losses than did parasitic individuals (5 of 24; 20.8%). The difference was not significant ($\chi^2 = 2.53$, $df = 1$, $P = 0.11$), but the trend suggests that at least when compared to parasites, hosts may be more likely to have their eggs destroyed by conspecifics. It is not clear whether this is because egg destruction is perhaps related to parasitic egg laying or because the same individuals who leave their nests unattended and consequently allow parasites entry also allow entry by destroyers of eggs.

A more convincing link between egg destruction and brood parasitism came from examining how often nests with eggs physically transferred into them (Brown and Brown 1988) suffered egg destruction. Over three times more nests with egg transfers had single eggs removed from them than did nests in general. These removals occurred prior to the time the

parasitic egg was carried in (Brown and Brown 1988). This suggests that egg destruction at a nest may at times be a prelude to physical transfer of eggs to that nest. Of the total nests with inferred egg destruction, 19.4% (93 of 479) had an extra egg or eggs added 1–4 days after the egg loss and during incubation, in all likelihood by physical transfer. The comparable overall percentage of nests with egg transfers for all nests from all colonies was 6.3% (306 of 4,821). The difference was significant ($\chi^2 = 106.8$, $df = 1$, $P < 0.001$), meaning that nests suffering egg destruction were more likely than nests in general to later have a parasitic egg added by transfer. Nests that suffered egg losses also had eggs transferred to them prior to the egg losses; 6.3% (30 of 479) had an extra egg or eggs added during incubation 1 or 2 days prior to the egg losses. These nests occurred at exactly the expected overall egg-transfer frequency, 6.3% (Brown and Brown 1988).

Estimated frequency of egg destruction.—We concluded from nest-check data (Fig. 4) that 0–33% of the nests in a given colony may lose eggs to conspecifics. The overall incidence of egg destruction in Nebraska Cliff Swallows can be estimated by nest checks and direct observation. Using nest-check data alone, we found that 9.8% of nests in all colonies combined had at least 1 inferred egg loss to conspecifics (479 of 4,899). In our sample of observed nests with color-marked owners ($n = 356$ nests), 35 separate egg-loss events in 32 nests were detected by daily nest checks; 17 egg-loss events in 16 nests were detected by direct observation. No egg-loss events were detected by both nest checks and direct observation. All 16 nests with egg losses detected by direct observation suffered these losses either during egg laying and thus would not have been detected by nest checks, or for other reasons which prevented detection during nest checks. Based on nest-check data, 324 of the focal nests had no evidence of egg loss at any time during laying or incubation. Thus, 4.9% of nests (16 of 324) that showed no evidence of egg loss based on nest checks in fact suffered egg losses. When we combine the estimated percentages from the two sampling techniques (9.8 and 4.9), we find that at least 14.7% of Cliff Swallow nests in our population might lose eggs to conspecifics. Combining these estimates is legitimate because each estimate is for a mutually exclusive subset of nests suffering egg losses.

DISCUSSION

We found that intruding conspecifics destroy eggs in nests relatively often among Cliff Swallows, and that this destruction may have an impact on individuals' fitness. Over 14% of all Cliff Swallow nests in southwestern Nebraska lost eggs as a direct result of neighbors' interference. The average egg loss/nest for those nests victimized was > 1 egg (1.37). Egg destruction by conspecifics is thus not a trivial phenomenon in Cliff Swallows, but its adaptive significance is unclear.

From the standpoint of a victim, egg loss to conspecifics represents a reduction in fitness. The loss amounts to a minimum of 1 egg and thus 1 potential offspring/victim. Individuals with larger clutches, however, tend to suffer most of the egg loss; and the net effect may be only to reduce their reproductive success closer to the population's mean. Color-marked victims tended to raise more offspring than perpetrators of egg tossings and as many offspring as non-victims.

Defensive measures against conspecific-caused egg destruction in Cliff Swallows are the same as those against brood parasitism: intensive nest-guarding (Brown and Brown 1989). Throughout egg laying and incubation, 1 or both members of a pair are usually at the nest. This generally prevents egg loss, because eggs are typically destroyed in unattended nests. Unlike in Carrion Crows (Yom-Tov 1975), synchronizing reproduction with other Cliff Swallows in a colony does not seem to afford protection in the form of diluting an individual's chances of being victimized. Potential victims show no other obvious adaptations to prevent egg loss, such as covering eggs with nest lining to hide them. A completely effective way to prevent egg loss from unattended Cliff Swallow nests may not be possible.

Egg cannibalism can be ruled out for insectivorous Cliff Swallows. No bird ever attempted to eat the yolk or shell of an egg it tossed, and Cliff Swallows, unlike Purple Martins (*Progne subis*; Bent 1942), have never been observed to eat their own eggshells after hatching occurs. That the behavior is spiteful is also unlikely. Destroying a neighbor's eggs results in reducing the neighbor's relative fitness while simultaneously representing a cost to the perpetrator (see below). These conditions theoretically promote spite. But, as noted by Pleasants and Pleas-

ants (1979) and Wittenberger and Hunt (1985), indiscriminate egg destruction cannot be explained by spite. There is no evidence that egg destruction reduces average fitness of all non perpetrators more than it reduces the fitness of perpetrators. Spite (*sensu* Pierotti 1980) could explain this phenomenon (Wittenberger and Hunt 1985) only if egg destruction were selectively directed at individuals who lacked the behavior themselves, and only if the cost to the perpetrator were very low. Neither of these conditions is definitely known to be met in Cliff Swallows or in any other colonial species so far studied. The only possible support for the notion that spite is important comes from our finding that nests with large clutches are disproportionately victimized. Spite could influence the behavior if egg destruction were selectively directed at individuals with large clutches by individuals with average to small sized clutches. The latter would thus be unlikely to suffer egg losses themselves. No support for this exists in Cliff Swallows at present, but it is possible. Although nests with large clutches are disproportionately victimized, we do not know to what degree these nests are disproportionately *sought out* by egg destroyers. Potential destroyers may seek to enter and destroy eggs at all nests, but simply succeed more often at nests where females have laid large clutches. These females must be gone more often to forage and to recoup the energetic costs associated with producing a large clutch.

A more likely benefit of destroying a neighbor's eggs is that it reduces a potential host's clutch size and enhances survivorship of eggs that the perpetrator later adds to the nest by physical transfer. Brood parasitism in Cliff Swallows is a sophisticated alternative strategy in which parasitism represents a definite cost to a host by reducing its annual reproductive output (Brown and Brown 1989). This reduction occurs in 2 ways. If a parasitic egg is laid in a host's nest while the host is still laying, the host responds by laying fewer of its own eggs (Brown 1984, Brown and Brown 1989). At times, a parasitic egg is added to a host's nest by physical transfer after the host has finished laying its own eggs (Brown and Brown 1988). The only way to reduce the host's clutch at that point is to toss out some of its eggs. We found that nests with egg losses are more than 3 times more likely to have eggs added by transfer than are nests in general. The egg losses came *prior* to

the egg transfers, consistent with the notion that birds are destroying eggs as a prelude to later adding eggs. Reduction of a host's clutch size presumably reduces within-brood competition, which is advantageous for the parasitic offspring. The link between egg destruction and later transfer of an egg implies that males may in fact engage in egg transfer, since among color-marked birds mostly males destroyed eggs. No instance of a male Cliff Swallow transferring an egg has been reported but the sample is quite small (Brown and Brown 1988).

Yet not all nests that lose eggs later have eggs added to them by physical transfer. Gaining access to an unattended nest is difficult and the odds of finding the same nest unattended twice—once to remove an egg and once to later add a parasitic egg—are small. As a result, some nests may lose eggs to conspecifics but, through nest-guarding, their owners prevent the perpetrators from returning with parasitic eggs.

The greater incidence of egg destruction from nests with large clutches is not consistent, however, with the hypothesis that perpetrators remove eggs as a prelude to adding eggs. Theoretically perpetrators should seek nests with small clutches in which within-brood competition among nestlings will be low. Although, as discussed above, for other reasons perpetrators may simply succeed more often at nests where owners have laid large clutches. An alternative hypothesis to explain some egg loss is that destruction of a neighboring female's eggs by a male may cause that female to continue to lay eggs and thus remain sexually receptive. Male Cliff Swallows often attempt forced copulations with neighboring females (Brown 1985, unpubl. data). Prolonging a female's egg-laying period could prolong the time that males could seek extrapair forced copulations. Cliff Swallows may be partially indeterminate layers because adding an egg during laying often causes a female to cease laying (Brown 1984). This interpretation could help explain why egg tossings most often occur among neighbors. Monitoring a female's activities and thus knowing when to seek forced copulations is probably most efficient when a male lives near a female.

The timing of egg loss, and the number of eggs lost from nests, is consistent with the interpretation that males destroy eggs to keep neighboring females sexually receptive. Losses often occurred during laying, the best time to destroy eggs from the standpoint of a male seek-

ing to keep an indeterminately laying female receptive. It is not surprising that egg destruction declines as incubation proceeds, because destroying a single egg once incubation begins will not cause a female to lay more and remain receptive. (Egg destruction during incubation may be mostly related to brood parasitism.) Egg losses tended to occur early in the season when females would be most likely to have the time and energetic reserves to replace lost eggs. We had no evidence that destroyers of eggs removed all of a victim's clutch, except during laying and only when there was just 1 egg in the nest. Full clutch loss usually causes Cliff Swallows to desert their nest and probably leave the colony. Thus, a male should not remove the entire clutch if it is in his interest to keep the neighboring female there to produce more eggs. Furthermore, Cliff Swallows benefit from socially foraging with their neighbors once eggs hatch (Brown 1986). Thus it is to an individual's advantage at that time to have neighbors. Causing neighbors to leave by destroying all of their eggs would be costly to a perpetrator later in the season.

These possible benefits of destroying neighbors' eggs may at times be balanced by the possible costs of being a perpetrator. Over a third of perpetrators also suffered losses from their own nests. Locating neighboring nests in which to destroy eggs requires that perpetrators leave their own nests unattended while they search for unattended victim nests. This potential cost is similar to one paid by parasitic individuals, who must leave their own nest unattended as they search for potential host nests. As a result they are parasitized themselves (Brown and Brown 1989). A greater than one-in-three chance of suffering an egg loss themselves could be an appreciable penalty for individuals who destroy others' eggs. Our sample of known perpetrators is too small to determine whether they consistently suffer greater egg loss than the population as a whole. If destroying others' eggs is in fact costly, this suggests that spite is unlikely (see above) and that whatever benefits are gained from destroying eggs must be important.

An intriguing observation was that nearly a quarter of observed egg tossings by color-marked Cliff Swallows occurred during colony alarm responses. The perpetrators of these tossings presumably incurred a risk of predation in remaining at the colony and destroying eggs at

these times. This also suggests that the benefits to a perpetrator must be great. Individuals who, for whatever reasons, are not of sufficient ability to gain access to unattended nests during normal colony activity may have to resort to remaining at the nests during alarm responses. Destroying eggs then is a definite high-risk tactic. Although we did not directly observe perpetrators give "false" alarm calls (*sensu* Munn 1986) to flush colony residents and then intrude into unattended nests to destroy eggs, the contexts in which alarm calls are used in Cliff Swallow colonies need to be studied. Often alarm calls were given by unknown individuals when no apparent predator was present, and only some colony residents would respond.

We estimate that 14.7% of all Cliff Swallow nests lost eggs to conspecifics. Nest checks are the only way to search efficiently for egg losses among large numbers of nests in many colonies, but nest checks can reliably detect only losses that occur after laying ceases and incubation begins. Egg losses during laying were estimated at 4.9% in the sample of focal nests. We think that this figure is an appreciable underestimate, because the efficiency of observing subtle, sneaky behavior such as egg tossings and brood parasitisms among color-marked individuals is not high (Brown and Brown 1989). If we assume that we observed half of the egg tossings that occurred among these nests (and we doubt that we saw that many), the frequency of nests with egg loss during laying would increase to 9.8%. The overall frequency of nests with egg loss (during laying plus during incubation) would increase to 19.6%.

The estimated frequency of nests with egg loss could be potentially inflated if some apparent instances of egg loss instead reflected owners' removing eggs from their own nests and physically transferring them elsewhere. Whenever an egg is transferred elsewhere during incubation, the nest from which it came would appear to have lost an egg. Since transfers of eggs generally occur among nests within the same colony, the frequency of nests that have an egg added during incubation (6.3%) should approximate the frequency of nests that have eggs removed by the owners and transferred elsewhere. The difference between the observed overall frequency of egg loss (14.7% of nests) and the 6.3% of nests with "losses" that are attributable to owners removing eggs is 8.4%. This percentage is a minimum estimate

frequency of nests with losses. This estimate does not take into account the probable increased frequency of egg loss during laying that we were unable to detect.

If some of the cases of presumed egg loss we reported are attributable to owners removing eggs and transferring them elsewhere, the increased "loss" of eggs from large clutches could instead reflect the more fecund individuals' tendency to transfer part of their large clutch elsewhere. It could also mean that the increased incidence of egg loss early in the season was caused partly by early nesting birds transferring their eggs elsewhere. Early in the season, before ectoparasite infestations become great, is the best time for a Cliff Swallow to breed, either by raising its own young or by parasitizing others (Brown and Brown 1986).

Regardless of the overall frequency of nests with egg losses, clearly there are large differences between different colony sites in the incidence of egg loss (Fig. 4). Incidence of egg loss increased with colony size across the whole range of colony sizes observed. Chance of egg loss rises per capita for individuals nesting in large colonies. Egg destruction by conspecifics is a cost paid by individual Cliff Swallows to live in colonies. Cliff Swallows that live solitarily or in extremely small colonies (≤ 10 nests in size) are seldom if ever victimized by egg-destroying neighbors. The significant increase in incidence of egg loss with colony size (Fig. 4) is interesting, because brood parasitism does not show a similar increase with colony size for colonies > 10 nests (Brown and Brown 1988, 1989). One would expect similar patterns for brood parasitism and egg loss because both phenomena are perpetrated by close neighbors and directed at close neighbors. Once colony size exceeds some relatively small size threshold in which each individual has roughly the same number of close neighbors, further increases in colony size should not affect per capita risk of being victimized. Why egg loss to neighboring conspecifics increases with colony size is not clear. A possible explanation is that egg losses are sometimes linked with colony alarms, and more colony alarm responses occur in large colonies where passing predators are more efficiently detected (see Brown and Brown 1987). For whatever reasons, the risk of losing part of one's clutch to conspecifics represents a definite cost of coloniality for Cliff Swallows. Cliff Swallows continue to nest in colonies, so the net cost

of egg destruction must be at least balanced by the benefits of colonial breeding.

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 ERRATUM

In Table 1 of "Polygyny in the Northern Shrike (*Lanius excubitor*)" by Reuven Yosef and Berry Pinshow (1988, *Auk* 105: 582), the territory sizes should read as follows: 76.0 ha, 71.2 ha, 78.8 ha, and 71.2 ha.