

both females fed the young at the same time. The male visited the nest but was not observed feeding the young.

Unlike the nests studied by Wiley (1975), the rates of prey delivery were very similar between Nest 1 and Nest 2 during our four days of observation. The three adults tending Nest 1 made 23 visits to the nest and fed the nestling on 12 of those visits. The two adults at Nest 2 made 25 visits to their nest and fed the nestling on 14 of those visits. Adults at Nest 1 spent a total of 750 min at the nest (187.5 min/day) and those at Nest 2 spent 645 min (161.2 min/day). Adults at Nest 1 brooded the nestling eight times, and those at Nest 2 brooded the nestling five times. Preening of the young occurred during most brooding bouts. Although the number of brooding bouts were similar between the two nests, adults at Nest 2 spent 84% less time (51 min, 12.6 min/day) brooding than was spent by those at Nest 1 (365 min, 91.1 min/day). During a severe rainstorm on 6 June, the nestling at Nest 1 was brooded continuously for 79 min whereas the nestling at Nest 2 was brooded for only 5 min. Because we only observed one nest of each type and the sample of days was small, statistical tests are meaningless. However, the large difference in brooding time is substantial and might be attributed to the presence of the second female. We were unable to find studies that quantified the effect of "helpers" or of the number of mates in polygamous species on brooding, shading, or preening behavior.

Although the incidence of more than two adults at Red-tailed Hawk nests is undoubtedly rare, it may be more common than previously thought. It is difficult to detect more than two adults at a nest during short visits unless all adults defend together or unless prolonged observations of behavior are being made. Mader (1975) found a positive correlation between the number of times he visited Harris's Hawk (*Parabuteo unicinctus*) nests and the number of adults tending the nests. We discovered the three adults at Nest 1 during a detailed study on Red-tailed Hawk nest-defense behavior. After its discovery, Nest 1 was visited twice by other biologists who failed to detect that three

adults were defending the nest. In a study of nest-defense behavior in the United States and Canada, in which "extra" adults would have been detected if they were present, only one out of 105 Red-tailed Hawk nests had three adults defending (R. L. Knight et al., unpubl. data). More detailed observations of nest-defense behavior at raptor nests might increase the incidence of records of "helpers" or polygamous bonds.

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## RESPONSES OF BREEDING CLIFF SWALLOWS TO NIDICOLOUS PARASITE INFESTATIONS<sup>1</sup>

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*Key words:* Cliff Swallow; nidicolous parasites; nest desertions; colony abandonment; nesting response to parasite eradication.

Cavity- and burrow-nesting swallows are often plagued by vast numbers of bedbugs (*Cimicidae*), ticks (*Acarina*), and fleas (*Ceratophyllus*) swarming in the lining and walls of their nests (Knight 1908, Forbush 1929, Rothschild and Clay 1952, Loye and Hopla 1983). The principal direct victims of these parasites are the nestlings (Moss and Camin 1970). Equally and perhaps more important for the species, however, may be that infestations can induce mass colony desertions (Foster 1968) or prevent the repeated

use of otherwise favorable colony sites. Stoner (1936) was aware of these effects in the Bank Swallow (*Riparia riparia*), noting that colony sites were rarely reoccupied in successive years unless between-season erosion or excavation had sloughed off the old earth surface to create clean, parasite-free faces for fresh burrowing activities. Storer (1927) came to a similar conclusion for the Cliff Swallow (*Hirundo pyrrhonota*) after observing that a colony of long standing in a creek bed apparently depended for its annual occupancy on the regular flushing by spring floods of the rock surface on which it was built. Buss (1942) demonstrated that the usually shifting pattern of site selection in Wisconsin Cliff Swallow colonies could be stabilized, when he documented the history of a colony on a barn near Deerfield, Wisconsin, that had been "managed" by systematically scraping off the old nests each fall. With this treatment, plus a campaign of House Sparrow

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(*Passer domesticus*) shooting, the colony flourished without a break for five decades and grew to a spectacular metropolis of 4,000 pairs.

My first encounter with nest parasitism was in a small secondary colony in a road culvert near Moran, Wyoming, an area where I was conducting a two-year study of Cliff Swallow breeding behavior (Emlen 1952). On 13 June 1951 the nests in this culvert, then containing fresh eggs, were swarming with swallow bugs, ticks, and fleas. The colony, I was quite sure, had been free of parasites the preceding year; and, since swallow bugs and ticks overwinter in old nest shells and their underlying substrates (Loye and Hopla 1983), the infestations had presumably been established with the arrival of the birds a few weeks before. The nests in this colony were synchronous within a few days, and no new birds had appeared after laying in the colony had started. Thus, with the thought that parasitism might have played a part in an early termination of nest establishment, I scraped and brushed all parasite-infested nests (6) from the eastern end of the culvert, leaving the rest of the colony intact. When I returned a week later, two new nests had been established in the cleared area and none in the undisturbed area. The evidence that a release from parasite-related constraints was a factor is not clear, but it is suggestive.

In the spring of 1952 I visited the historic colony described by Buss (1942) near Deerfield, Wisconsin. Failing health in 1950 had prevented the resident farmer from scraping off all old nests, and in 1951 he was unable to remove any of them. The colony broke up early that year, the birds deserting their nests en masse and leaving many half grown young to starve. When I visited the site in mid-July the whole surface of the nesting area was swarming with bugs, ticks, and fleas. In the year 1952 the swallows arrived in early April and, after circling and making brief passes at the old, parasite-ridden nests which still lined the eaves of the barn, moved on to a neighboring farm. On 21 April, after several hundred nests were well under construction on this neighboring barn, I scraped off all the old nests on one side of the old barn and sprayed three-fourths of the scraped area with a DDT insecticide. On my return a week later the sprayed portion of the colony had been reoccupied and was densely covered with several hundred courting swallows while, in marked contrast, the unsprayed portion held no swallows at all. On 3 May I completed the demolition of the old nests on both sides of the barn and sprayed all but one 10-foot strip in the center of the second side. The swallows returned that same evening, and the next morning they were swarming on all parts of the barn. Nesting proceeded and success was good through hatching in all parts of the colony, as indicated by approximately equal densities of ejected (hatched) egg

shells beneath the sprayed and unsprayed portions of the colony on 14 June.

An interesting corollary to these 1951 and 1952 parasite episodes was the appearance of new nesting colonies in the Deerfield area. At least three such colonies were founded in 1951; in two, and possibly all three, the birds did not arrive until July (exact dates not known). Again in 1952 two new colonies were started about 2 km from the old barn before I had cleaned it. One of these was abandoned and the other partially abandoned after the cleaning and spraying at the old site. It seems likely that the birds in these colonies were refugees from the parasite invasions at the old barn.

More well-designed and controlled experiments are obviously needed to document and clarify the effects of nest parasitism on Cliff Swallow nesting behavior and colony stability. In the meantime the miscellaneous notes and observations described above lend support to the view that the presence of nest parasites often induces premature colony abandonment and discourages colony establishment in successive years at otherwise acceptable sites.

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