SHORT COMMUNICATIONS

Wing Fluttering by Mud-Gathering Cliff Swallows: Avoidance of "Rape" Attempts?

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Beecher and Beecher (1979) suggested that colonially nesting male Bank Swallows (*Riparia riparia*) escorted their mates 7 to 8 days following pair formation to guard against "promiscuous copulations." They observed that unguarded females were frequently chased by males, and, although chases ended in copulation on only three occasions, the authors interpreted female-escorting behavior by their mates as "mate guarding."

The Cliff Swallow (*Petrochelidon pyrrhonota*) also is a colonial nester, but I saw no indication of nor can I find any reference to mate guarding. Here, I present data that suggest that Cliff Swallows flutter their wings above their backs while gathering mud for their nests primarily to reduce rape attempts and secondarily to reduce the theft of mud pellets used in nest construction.

My study was conducted April–July 1980–1981 at the Creston Valley Wildlife Interpretation Centre, 10 km west of Creston, British Columbia (49°10′N, 116°36′W). The Cliff Swallow colony had been established in the past 6 yr. A maximum of about 200 completed nests was counted in 1980 and 1981. Another Cliff Swallow colony numbering over 500 nests was located about 1 km away, although those birds were not observed gathering nest material with the swallows in my study. The colony in my study built their nests on floor beams supported about 2 m above water by vertical pilings. During my study about 40 Barn Swallows (*Hirundo rustica*) also nested in the Cliff Swallow colony. The colony is located on a 616-ha marsh that is dominated by *Equisetum* sp., *Carex* sp., and *Myriophyllum* sp. The Cliff Swallows gathered mud from the exposed banks of a dyke located within 50 m of their nests.

In 1981 Cliff Swallows were first seen at the study area on 13 April. Nest building began by about 25 April, and clutches were initiated 5–28 May. Cliff Swallows gather mud by alighting on the ground in flocks of up to 20 or more birds, raising the tail about 15° above the horizontal and fluttering the extended wings above the back while pecking mud into a pellet. That pellet is then flown back to the nest, and the partners exchange places (Emlen 1954, pers. obs.).

Brown (1910) said that wing fluttering prevented Cliff Swallows from sticking in the mud and soiling their feathers. I noticed, however, that individual Cliff Swallows fluttered their wings more vigorously when other Cliff Swallows were present than when they were alone. To quantify the effect of various-sized flocks on the wing-fluttering behavior of individual swallows, I randomly chose a bird as it arrived at the mud source and recorded whether it fully extended, partially extended, or folded the wings over the back when it began to gather mud. I then counted or estimated the size of the flock. In addition, I cut a small hole in the side of 27 nests and examined the contents to determine clutch-initiation dates. I found that before egg laying (28 April–4 May) and during egg laying (5–28 May) swallows fully extended or partially extended their fluttering wings significantly more often in flocks of greater than two birds than in smaller groups ($\chi^2 = 9.2$, $P < 0.001$). During incubation and the nestling stage (29 May–17 June), however, there was no significant difference in wing fluttering behavior with increasing flock size (1–2 birds, 3–5 birds, >5 birds). Furthermore, swallows fluttered rather than folded their wings significantly more often during egg laying than either before or after egg laying ($\chi^2 = 15.76$, $P < 0.001$) (Fig. 1). Clearly, wing fluttering increased in frequency with flock size and the onset of egg laying.

Cliff Swallows that folded their wings appeared to be attacked by other Cliff Swallows more often than those that fluttered their wings, although the attacks happened too quickly to be quantified. To test the hypothesis that wing fluttering reduced the frequency of attacks, I recorded the number of attacks directed at a stuffed, female Cliff Swallow when her wings were wired motionless in the folded and fluttering positions. On 19 May 1980 I placed the model with its wings in the folded position at a mud-gathering site where swallows gathered in flocks of 10–15 individuals. The model was vigorously attacked 18 times in 300 s of observation. Attacks resembled the copulation attempts described for many other birds, including swallows, although semen was never deposited on the model. Typically the attacking bird alighted on the model's back and grasped the nape with its mandibles. The attacker then moved its tail in a lateral motion, as if searching for the model's cloaca, while it vigorously fluttered its wings above its back. Those attacks lasted about 5–15 s, although in four cases the attacker remained mounted for 45 s until it drooped its wings on either side of the model and the tips touched the ground. Within a few seconds a second bird attacked the first attacker and both birds departed after a brief skirmish. Some swallows ignored the model at the mud source and gathered mud around and under it. Others ig-

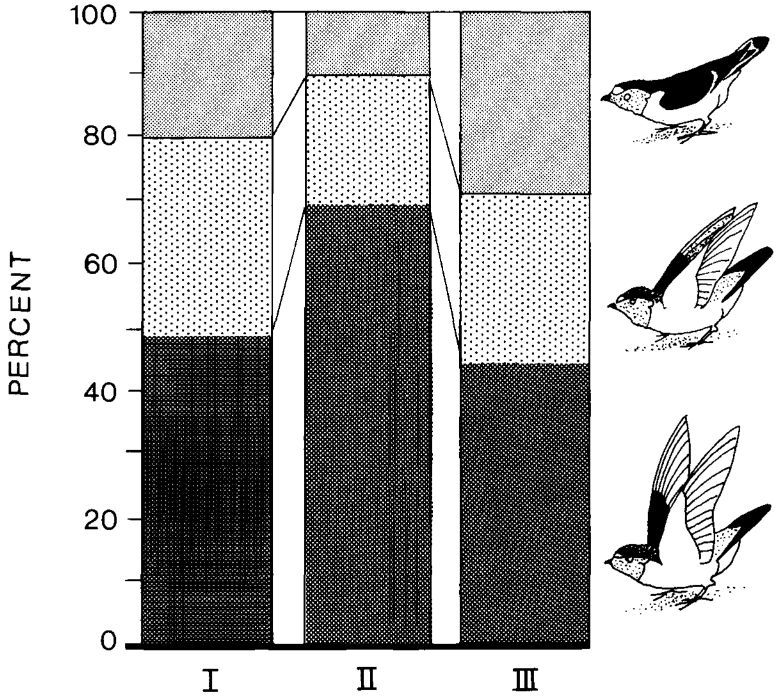

Fig. 1. Percentage of Cliff Swallows in various-sized flocks that folded, partially fluttered, and fully fluttered their wings before (I, $n = 78$), during (II, $n = 103$), and after egg laying (III, $n = 216$).

nored attackers on the model and continued gathering mud. In attacks involving live swallows the victim always struggled vigorously and usually escaped within a few seconds.

I repeated the above experiment on the same day using the model, but this time I extended the wired wings. There were no attacks during 355 s of observation. To test that habituation toward the model had not occurred, I repeated the first experiment for 210 s, which resulted in seven attacks. Admittedly, the length of time that the model was not attacked would have been a better measure of attack frequency than the number of attacks, but the results still indicate that wing fluttering reduces attacks by other Cliff Swallows.

In one instance when no model was present, I witnessed a Cliff Swallow attack three mud-gathering Cliff Swallows in about 15 s. It appeared that the sole intention of the attacker was to pounce on the three swallows, because it never gathered mud, although there was plenty of room to do so. Each time, the victim departed following a brief skirmish. I also saw a Cliff Swallow attack a live Tree Swallow and a dead Barn Swallow at the mud source in May 1980.

In 1981, I used the folded-wing model to examine the seasonal frequency of attacks from 28 April–16 June and compared those results with the number of attacks on live swallows from 2 May–15 June, all at the mud source. Results did not differ significantly between the model tests and actual attacks, indicating that habituation to the model had not occurred (Fig. 2). Those results also suggest that the behavior of live swallows towards the model accurately represents the behavior between live swallows. There also were significantly more attacks during egg laying than preceding or following that stage in both tests (one-sided Proportion Test; Z *pre-egg/egg* $= 3.16$, Z *egg/post-egg* $= 4.47$, $P < 0.001$).

In a few instances, an attacking swallow stole mud from the attacked bird, while in others the attacks appeared to be of a sexual nature. To test whether Cliff Swallows were stealing mud from one another, I placed a pellet between the folded-wing model's mandibles and placed the model on the mud source for about 300 s during the late egg-laying stage. The model was mounted several times, but no attempt was made to steal the mud. That suggests that the motive for the attacks was not to steal mud pellets, although mud stealing might be more prevalent during the early nest-building stage.

The reason for wing fluttering by mud-gathering Cliff Swallows remains uncertain. I have shown that wing fluttering is most frequent during the egg-laying stage. In addition, the attacks on the model resembled copulations and were most frequent during the egg-laying stage. I also witnessed Cliff Swallows

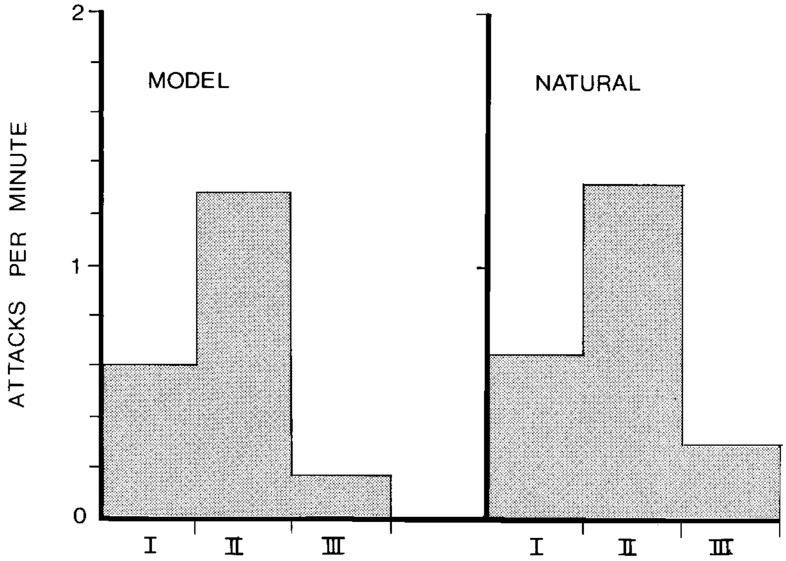

Fig. 2. The number of attacks per minute directed by Cliff Swallows toward a stuffed, folded-wing model and toward live Cliff Swallows before (I), during (II), and after egg laying (III).

stealing mud from one another at the mud source, however. To confuse the issue further, Cliff Swallows begin egg laying before the nest is complete, so that a mud-gathering swallow could be building a nest, laying eggs, or both.

One possible explanation for the evolution of wing-fluttering behavior of mud-gathering Cliff Swallows is as follows. Cliff Swallows invest large amounts of time and energy in building the nest. Withers (1977) showed that the daily energy expenditure of Cliff Swallows was greater during nest construction than during incubation or nestling periods. At the end of the 1981 nesting season, only 36% (n = 139) of the Cliff Swallow nests in this study could support eggs, so most swallows must build nests at the start of a new season. That implies that there might be strong competition for old nests and nest material. I found that nests from previous years were occupied about 10 days before the swallows began construction of new nests. In addition, Cliff Swallows steal mud from one another's nests (Emlen 1954) and from one another (this study). The loss of a nest by a pair of Cliff Swallows would mean a loss of a large investment of time and energy and would favor the evolution of nest guarding. Cliff Swallows appear to guard their nests (Emlen 1954, Mayhew 1958). Emlen (1954) has shown that one member of a mated pair remains in the nest while the other is at the mud source. After collecting a pellet of mud, the swallow returns to the nest and exchanges places with its mate. Nest guarding precludes mate guarding and thus frees the male to seek opportunities for extra-pair copulations with unguarded females. That implies that females are vulnerable to extra-pair copulations while guarding the nest. I made few observations of pairs at the nest. Emlen (1954), however, mentioned forced-copulation attempts toward females in their nests. Another interpretation is that the energetic costs of building the nest require sharing the duties between both members of the pair.

Cliff Swallows presumably are very susceptible to rape attempts while gathering mud in a tight flock. Hoogland and Sherman (1976) found that extra-pair copulations in Bank Swallows were attempted on the ground. Furthermore, the Cliff Swallow tail-up posture may solicit rape attempts, because it resembles the female's copulatory posture at the nest. There is strong competition within the flock for sites at which to gather mud, and alighting Cliff Swallows could presumably settle more easily on the back of a swallow with folded wings than on one with fluttering wings. Barlow et al. (1963) found that sunning Cliff Swallows raised their wings to prevent others from settling on their backs. Any swallow that settled on the back of another could steal its mud or usurp its spot at the mud source regardless of sex. The same would hold true whether a female alighted on a male or a female. If a male swallow alighted on a female, he could copulate with her, steal her mud pellet, or usurp her spot at the mud source. Any swallow that fluttered its wings, however, would reduce the chance of being settled upon. All of this suggests that natural selection has favored nest guarding over mate guarding in Cliff Swallows. Males could be cuckolded, but they also have opportunities to cuckold other males. I never witnessed a rape that appeared to be successful, however, and I believe that successful rapes ending in sperm transfer are rare. I never found semen deposition on the Cliff Swallow model, although similar studies by other investigators have found semen near the cloacal region of model Bank Swallows (Hoogland and Sherman 1976) and Savannah Sparrows (*Passerculus sandwichensis*) (Weatherhead and Robertson 1980).

Females might increase or decrease their fitness by participating in extra-pair copulations with males of unknown fitness. Presumably, it is to the female's advantage to copulate conservatively with males of known fitness (i.e. their mates) and not to risk decreased fitness by mating with other males.

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Effect of Intrusion Pressure on Territory Size in Black-chinned Hummingbirds (*Archilochus alexandri*)

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Within many avian species, territory size is inversely correlated with food abundance (Pitelka et al. 1955, Gass et al., 1976, Myers et al. 1979). Two hypotheses have been proposed to explain these correlations: (1) animals may assess resource availability directly and defend areas that contain sufficient amounts of food, or (2) animals may adjust territory size in response to an intermediate variable, intrusion pressure. By the second hypothesis, areas of greater food abundance are more costly to defend because they attract more competitors, the result being smaller territories.

Myers et al. (1979) tested these hypotheses in studies of wintering Sanderlings (*Calidris alba*). Their results supported the second hypothesis: when the interaction of prey density and intrusion pressure was controlled statistically, the effect of food density on territory size was no longer significant, yet the correlation between intrusion pressure and territory size was highly significant. Furthermore, when intrusion pressure declined seasonally while prey densities remained constant or increased, territory size doubled. This increase in territory size was attributed to the decreased intrusion pressure. Similarly, Ewald et al. (1980) documented an inverse correlation between intrusion pressure and territory size in a colony of Western Gulls (*Larus occidentalis*). Because gulls do not forage on their territories, variations in food abundance could not have caused the variation in territory size in this colony.

These two hypotheses, however, need not be mutually exclusive. Hixon (1980) developed a model of optimal territory size in which he dealt with both food availability and intruder density. Integral to his model is the assumption that these two factors can vary independently of each other, but he points out that disproportionately high food production in a given territory in comparison with surrounding territories might cause a concurrent increase in intrusion pressure. Thus, theoretically, these two factors can act together and have the same effect on territory size.

Ewald et al. (1980), Myers et al. (1979) and Hixon (1980) all suggest that further studies are needed on species in which intrusion pressure and food abun-

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