Jays of the Queen Charlotte Islands, British Columbia. Condor 60:38–49.

RIDDLE, O. 1963. Prolactin in vertebrates. Function and organization. J. Natl. Cancer Inst. 31: 1039–1110.

SCHALLER, G. B. 1964. Breeding behavior of the White Pelican at Yellowstone Lake, Wyoming. Condor 66:3–23.

SCHLEIDT, W. 1967. Turkey signals, p. 130–133. *In* D. Burkhardt, W. Schleidt, and H. Altner [eds.] Signals in the animal world. McGraw-Hill, New York.

VERBEEK, N. A. M. 1973. Pterylosis and timing of molt of the Water Pipit. Condor 75:287–292.

WILLIAMS, H. W. In press. Behavior and social organization, Chap. 3. *In* R. F. Labisky [ed.] Pheasant symposium. Proc. Midwest Fish and Wildl. Conf. (St. Louis) 2–5 Dec. 1973.

Accepted for publication 6 June 1974.

PREDATOR-PREY INTERACTIONS OF ADULT AND PREFLEDGLING BANK SWALLOWS AND AMERICAN KESTRELS

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Predation is believed to be an important selective pressure shaping the breeding biology of many avian species (Crook 1965, Tinbergen 1965, Lack 1968, Ricklefs 1969). For hole nesters, losses of eggs and nestlings to predators are greatly reduced and various changes in breeding behavior have been considered as resulting from the easing of this selective force (von Haartman 1957).

Many species of swallows increase the security of their nest locations by either building protective mud walls around the nest chamber or by digging nests deep into vertical cliffs of dirt or sand. Bank Swallows (*Riparia riparia*) use the second method. Studies show it to be quite effective; repeated observations on over 500 nests indicated that losses of eggs or nestlings to non-aerial predators amounted to less than 13% of the total eggs laid (Emlen and Demong, unpubl. data).

Young Bank Swallows are also subject to aerial predation. Freer (1973) recently documented that American Kestrels (*Falco sparverius*) will attack swallows both in flight and at their burrows. Observations that we have made at a number of colonies 50 miles N of Freer's colony support her contention that kestrels are frequent aerial predators on these birds. We describe below the hunting strategies of the kestrels and the "anti-predator" behavior of Bank Swallows, and discuss their possible adaptive significance.

We made observations at 16 colonies of Bank Swallows in sand and gravel pits within a 40 mile radius of Ithaca, New York, during May, June, and July 1969 through 1972. In the latter two seasons, observers were in the field almost continuously. Kestrels were seen 67 times; in 27 instances, the bird flew directly over the colonies without stopping, while on 40 occasions the kestrels perched on or near the edge of a colony. In these latter cases, kestrels flew to the burrow opening of swallow nests in pursuit of young on 25 instances and succeeded in capturing a total of 9 nestling swallows. Successful predation of this sort was observed at three different colonies. Additionally, one swallow (age unknown) was captured on the wing and a nestling was taken after it had fallen from its burrow. On several occasions, swallows in mist nets were also attacked.

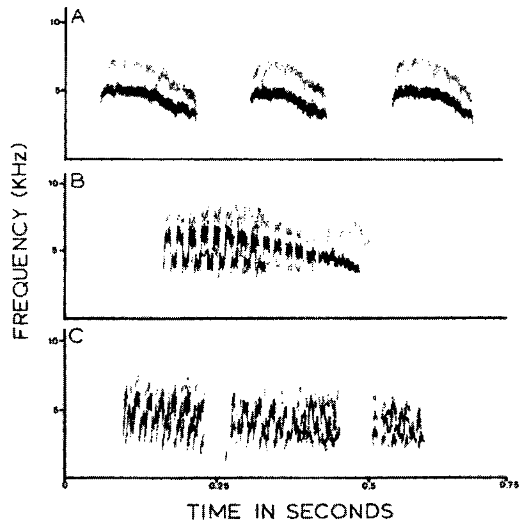

FIGURE 1. Spectrograms of Bank Swallow vocalizations. A. High intensity alarm call. B. Low intensity alarm call. C. "Social" (nonalarm) call notes.

Most predation attempts were seen in the middle and last weeks of June, when many colonies had broods near to or actually fledging. In fact, kestrels first appeared at colonies when the majority of the swallow young were approximately 14–16 days old. At the age of 14 days, swallows shift their diurnal position from the nest chamber—located at the rear of the 3-ft burrow—to a resting point at the burrow entrance. One of the presumed advantages of this shift is in decreasing the time needed for transferring food from adults to young. One of the disadvantages is an increased vulnerability to aerial predators.

We never observed more than two kestrels working a colony. In three instances where the kestrels were followed, their nests with young were found close to the swallow colony. We believe that the kestrels were opportunistically taking advantage of a food resource located within their normal feeding territories. We found no evidence that the kestrels increased their foraging range to concentrate at *Riparia* colonies, regardless of the size of the colony.

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The approach of a kestrel to a *Riparia* colony elicits a distinctive change in the call notes of the adult swallows. The low-frequency buzzing chatter of "social" notes changes to the high-pitched alarm calls given in triplets by the first swallows to respond to the predator. Normally, the initial alarm mobilizes other adults at the colony, causing them to leave the colony face, form a loosely organized flock, and utter a lower-pitched alarm call sounded singly. The spectral characteristics of these calls can be compared in figure 1. As the first alarm is sounded, the nestlings perched at the burrow entrances begin a tail-first retreat back into their tunnels. Hundreds of exposed prefledglings disappear within seconds.

A kestrel flying in the colony area is often harried by a loose, agitated flock of adult swallows who continue sounding alarm calls. While the swallows fly very close to the kestrel at times, they seem to be almost ignored. The kestrel flies through this ineffective mobbing to the perimeter of the colony where it perches. This behavior markedly dampens the alarm of the swallows; within a few minutes some adults disperse to forage and nestlings begin to reappear at their burrow entrances. It is at this moment that the kestrel flies directly from its perch to a burrow entrance, sometimes going from burrow to burrow, extending a foot into each for retreating young. This sudden action renews the colony alarm but its effectiveness in deterring the kestrel appears non-existent. If the kestrel has been unsuccessful, it may return to its perch, wait, and later launch another attack. If the attack was successful, the nestling prey is flown to a nearby perch where the head is crushed and body defeathered. These "plucking perches" commonly are located on top of the cliffs, directly above or slightly to one side of the swallow colony.

Freer (1973) observed five kills by a kestrel at a colony of Bank Swallows. In three instances, the kestrel captured a recently fledged bird in the air, while in a fourth a nestling was plucked from its hole in the manner described above. She also found several "plucking perches" near the colony. By analyzing the feather remains, she estimated that up to 21 additional young may have been captured there.

We were struck by the utter ineffectiveness of the "mobbing behavior" of these swallows in deterring the kestrels. Several authors have hypothesized that one advantage of colonial nesting lies in enabling individuals to pool their defensive responses. Hence, it is thought, they can detect, distract, or harass a predator more efficiently than would be possible if they nested alone. Among North American swallows, however, mobbing is most intense in solitarily nesting species; this behavior (measured either as strike rate, closeness of attack, or duration of attack) diminishes among the colonial nesters (Emlen, Demong, Snapp; pers. observs.). One possible explanation for this trend is that aggressive mobbing in swallows is more related to defense of a limited resource, namely a nesting cavity, than it is to anti-predator behavior. Solitary species often face severe intra- and interspecific competition for limited natural nest-sites. Colonial swallows, by contrast, construct their own nest "cavities." This behavior reduces the importance of aggressive nest defense and also serves as the necessary precondition for the evolution of truly colonial breeding.

A kestrel elicited alarm notes and organized group flying only when it was *moving*, particularly in flight. Shortly after it landed, regardless of its location within the colony, the alarm faded and birds resumed their normal behaviors. Nestling swallows returned to their burrow entrances even when a kestrel perched nearby would have been in direct view. This lack of response to a stationary predator seems to be crucially important to the hunting strategy of the kestrels.

TABLE 1. Summary of retreat responses of nestling Bank Swallows evoked by the playback of recorded alarm and social vocalizations.

Test	Intensity settings 1	2	3	4	5	Totals	
Alarm notes	2/15	15/29	13/14	17/18	31/41	78/117	(67%)
Social notes	6/46	6/83	0/42	10/62	26/126	48/359	(13%)

The denominator is the total number of nestlings observed before playbacks; the numerator is the number of nestlings retreating from sight during playback. Chi square of totals = 129 (df = 1); $P \ll 0.001$. Results are partitioned according to increasing loudspeaker intensity settings.

We suggest that the function of alarm flocking and mobbing in Bank Swallows may not be to drive away or to harass aerial predators as much as to warn the young in the nest. If true, then young at the entrance burrows should respond to alarm notes of a mobbing flock. In order to explore the function of vocalizations of Bank Swallows in this context, we recorded swallow calls at a colony during tranquil periods and periods of alarm (the latter both natural and induced artificially by the release of tethered kestrels). Recordings were made with a Uher 4000-report L tape recorder at 7½ ips, a 24-inch parabolic reflector, and Sennheiser NK 404 condenser microphone. Ten-second playbacks of the clearest alarm and social calls then were made using the same recorder and a Nagra DH portable amplifier and speaker. With binoculars, we watched a small section of the colony and its burrow inhabitants during the playbacks. We noted the number of nestlings in the field of view before and after the playback. Five-minute intervals between successive playbacks allowed the young to return to the burrow entrances. We conducted these tests at four colonies, and in different sections of each colony.

The results of these tests are presented in table 1. Under "alarm note" we have lumped the results from playbacks of the two forms of alarm calls shown in figures 1a and 1b. This was necessitated because the 10-sec playback segments all contained the calls of both forms as well as intermediates. Alarm notes of either form were excellent releasers of nestling retreat behavior. As many as 15 consequent replays of this same alarm tape did not noticeably lessen the retreat response in nestling swallows. In contrast, social notes (fig. 1c) had little effect in causing nestling retreat.

Alarm notes also stimulated adult swallows in the area or in burrows to take flight, occasionally to form a loose flock, and to propagate the alarm notes among themselves. This behavior was not elicited by playbacks of social vocalizations. The induced alarm quickly died out at the end of the playback and within 60 sec birds returned to their original positions.

Representative calls from the playback segments were analyzed on a Kay Model 6061-B Spectrum Analyzer. The first alarm note (fig. 1a) contains some of the design features suggested by Marler (1955) that may minimize the localizability of the caller—a relatively pure tone fading in and fading out and containing few discontinuities. The other form of the alarm call (fig. 1b), into which the first form rapidly shifts after the initial discovery of the predator, is distinctly different. Its discontinuities and frequency modulations suggest that it has functions in addition to those noticed during the playbacks. This call has similarities to the mobbing calls of other birds. It may enhance the localization of the sender, thereby distracting some predators from the brood to the adults buzzing around them. This call may also signal to nestlings in their burrows that the danger is not yet over.

The number of interactions observed by both Freer (1973) and us suggests that kestrels may frequently visit Bank Swallow colonies and prey on their nestlings. The impact of this predation appears to be minimized by (1) a vocal alarm system, which stimulates the retreat of young back into their burrows, and (2) a within-colony synchronization of reproductive efforts, which minimizes the period of vulnerability (Emlen 1971, Emlen and Demong 1975, and unpubl. data).

LITERATURE CITED

CROOK, J. H. 1965. The adaptive significance of avian social organizations. Symp. Zool. Soc. Lond. 14:181–218.

EMLEN, S. T. 1971. Adaptive aspects of coloniality in the Bank Swallow. Amer. Zool. 11:628 (abstr.).

EMLEN, S. T. AND N. J. DEMONG. 1975. Adaptive significance of synchronized breeding in a colonial bird: a new hypothesis. Science 188: 1029–1031.

FREER, V. M. 1973. Sparrow Hawk predation on Bank Swallows. Wilson Bull. 85:231–233.

VON HAARTMAN, L. 1957. Adaptation in hole-nesting birds. Evolution 11:339–347.

LACK, D. 1968. Ecological adaptations for breeding in birds. Methuen, London.

MARLER, P. 1955. Characteristics of some animal calls. Nature 176:6–8.

RICKLEFS, R. E. 1969. An analysis of nesting mortality in birds. Smithson. Contrib. Zool. 9:1–48.

TINBERGEN, N. 1965. *In* Moore, [ed.] Ideas in modern biology. Natural History Press.

Accepted for publication 23 April 1974.

POSSIBLE IMPAIRMENT OF NEST-BUILDING OF HUMMINGBIRDS BY ACETATE LEG TAGS

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Hummingbirds are difficult to color-mark for field study because color bands do not show on their short, retracted tarsi, and because they preen painted spots from their plumage. Stiles and Wolf (Condor 75: 244, 1973) reported a useful marking technique which employs acetate leg-tags. These did not seem to impede normal behavior including copulation. However, the authors did not use leg-tags on nesting females.

For the past three summers, we have been studying the nesting ecology of Broad-tailed Hummingbirds (*Selasphorus platycercus*) in Gothic, Colorado. The nest of this species is normally a tight, vertical-walled cup, with an inside diameter of approximately 2 cm, and is so maintained until after hatching, when the growing chicks cause stretching of the cup.

In 1973, 14 adult, female Broad-tailed Hummingbirds were leg-tagged according to the method of Stiles and Wolf. Only two nests were located which belonged to tagged females (out of 27 nests located). Confusion of a light orange and a dark yellow chosen for color-marking tags makes it ambiguous whether these nests were built by the same or by separate females ("red/orange" and "red/yellow"). Both nests were abnormally loose and flat during incubation (inside diameter approximately 3 cm), and daylight could be seen through holes in the walls, which were not repaired in either nest. It is possible that the female(s) involved were intrinsically poor nest-builders. Both nests were abandoned after disturbances in which the eggs were removed or knocked out of the nest. On the other hand, tags are relatively

FIGURE 1. A leg-tagged female on the nest.

large and extend conspicuously up the inside of the nest cup and forward out of the nest during incubation (fig. 1). In this position they may interfere with use of the legs in shaping the nest interior or with use of the wings and bill in forming or repairing the nest interior, behaviors we often observed in other females.

Two observations alone are not enough to condemn what is otherwise a very useful technique. The high visibility and good retention of leg-tags suggest that they be chosen for studies requiring intense or long-term observation of individuals. However, it seems necessary to caution that other marking techniques may be more appropriate for reproductive females. If acetate leg-tags do in fact impair nest construction and repair, they could lower breeding success, as well as disrupt normal nesting behavior, invalidating data and observations thereof.

Supported by grants from the Frank M. Chapman Memorial Fund, American Museum of Natural History (to NMW) and from the National Geographic Society (to WAC).

Accepted for publication 13 February 1974.