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SPATIAL RELATIONSHIPS IN PERCHING BARN AND CLIFF SWALLOWS

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Many investigators (e.g. Marler 1956, Crook 1961, Sparks 1964) have conducted quantitative investigations of spatial relationships among captive birds. Although there have been observations of spacing in free-ranging birds (Burckhardt 1944, Condor 1949, Emlen 1952, Hediger 1955, Swinebroad 1964), few quantitative studies have been done in the field. Miller and Stephen (1966) used the nearest-neighbor model of spatial distribution proposed by Clark and Evans (1954) to analyze distances between foraging Sandhill Cranes (*Grus canadensis*). Grubb (1974) investigated the individual distance (i.e., the closest distance an individual can approach another without resulting avoidance or aggression, Hediger 1950) of Herring Gulls (*Larus argentatus*) by marking intervals on a plank where they commonly perched.

The spatial regularity of Barn and Cliff swallow (*Hirundo rustica* and *Petrochelidon pyrrhonota*) flocks has been reported by Condor (1949), Emlen (1952), and Hediger (1955). I investigated quantitatively the spatial relationships within flocks of these species and studied behavioral mechanisms which maintain or modify spatial relationships.

METHODS AND MATERIALS

Field methods.—Observations of Barn and Cliff swallows were made from 14 July to 19 September 1975 near Saffordville, Chase County, Kansas, where both species flocked together on barbed wire fences. Barn Swallows nested in a culvert there; 15 to 50 birds were present until 12 September. From 22 to 1000 Cliff Swallows (mostly immatures) gathered there, possibly as a pre-migratory flock, from 14 July to 21 August.

Sections of the fence most frequently used by both species were marked at 13 cm intervals with yellow paint. Birds flocked along these fences from sunrise until late morning, and then again in the evening. Observations were made from a parked vehicle from 05:30 to 09:30, and twice from 18:00 to 20:00. Perched flocks flew as cars passed and then reassembled immediately; a parked car did not seem to modify the birds' behavior.

Photographs, motion pictures, and field notes were used to record interactions and the distribution of birds on the marked fence. Observations and estimates of distances between birds were made from 5 to 15 m away using 7 × 35 binoculars. For 46 field estimates, there was an average difference of 3.0% when compared to corresponding 35 mm slide measurements.

Film analysis.—Slides were projected from a distance of 3 m (the projected image was 70 × 32 cm). The outline of each bird, the location of its feet, and the marked

fence were traced onto paper. Motion pictures were viewed in slow motion, and stopped periodically to make tracings. Distances from the midpoint between one bird's feet to the midpoint between the adjacent bird's feet, and the distances between marks on the fence were measured from the tracings. To reduce error due to parallax, the closest visible marks to the birds were used for calibration. Actual distances between birds on the wire (hereafter referred to as "perch intervals") were calculated using a ratio of the true and measured distances between fence marks.

Individual distance analysis.—I assumed that all interactions between swallows were due to spatial violations, although dominance, age, activity, sex, and other factors were probably sometimes involved (Marler 1956, McBride 1964). Three possible results of interactions were recorded: (1) the incumbent flew or retreated, (2) the approaching bird flew or retreated after the incumbent gave a threat display, or (3) the approaching bird discontinued its advances, but remained where it was when the incumbent displayed. Individual distance was considered to be violated in the first 2 cases because the incumbent either retreated or its display effectively removed the aggressor from within its individual distance. In the third case, the approaching bird was assumed to have stopped at the incumbent's individual distance; no further aggression was demonstrated. In all 3 cases, the closest distance between birds was recorded. Perch intervals were not recorded if the approaching bird retreated when the incumbent gave no display. Encroachment of individual distance in this instance was not evident, although unrecognized signs of communication may have resulted in the approacher's retreat.

RESULTS

Spatial distribution.—Frequency distribution curves of perch intervals were significantly skewed to the right for both species (Fig. 1A and B; g_1 test, Sokal and Rohlf 1969, $P < 0.001$), and for interspecific spacing between individuals in mixed-species flocks (Fig. 1C; g_1 test, $P < 0.01$). There was an abrupt drop in percentages at the shorter perch intervals and a gradual decline at the larger intervals. The 3 distribution curves differed significantly (log transformation and analysis of variance, Sokal and Rohlf 1969, $P < 0.001$). Interspecific spacing was more irregular and perch intervals were at larger distances than in intraspecific spacing; the mean (48.6 ± 25.5 cm) and the mode (35–39 cm) of the former were larger than for either species (Barn Swallow, $\bar{x} = 28.2 \pm 17.5$ SD; Cliff Swallow, $\bar{x} = 34.5 \pm 20.5$ cm).

The mean individual distances of Barn and Cliff swallows were significantly different (t-test, $P < 0.005$). Both species exhibited narrow ranges and prominent peaks (Fig. 2). The mode occurred at 12 to 13 cm for the Barn Swallow, and at 10 to 11 cm for the Cliff Swallow (Barn: $\bar{x} = 11.7 \pm 3.9$ cm; Cliff: $\bar{x} = 9.3 \pm 3.1$ cm). Although the individual distance appears to be fairly well defined for these species, it is not absolute since conflicts occurred outside these intervals.

Eight interspecific interaction distances were recorded; Barn Swallows

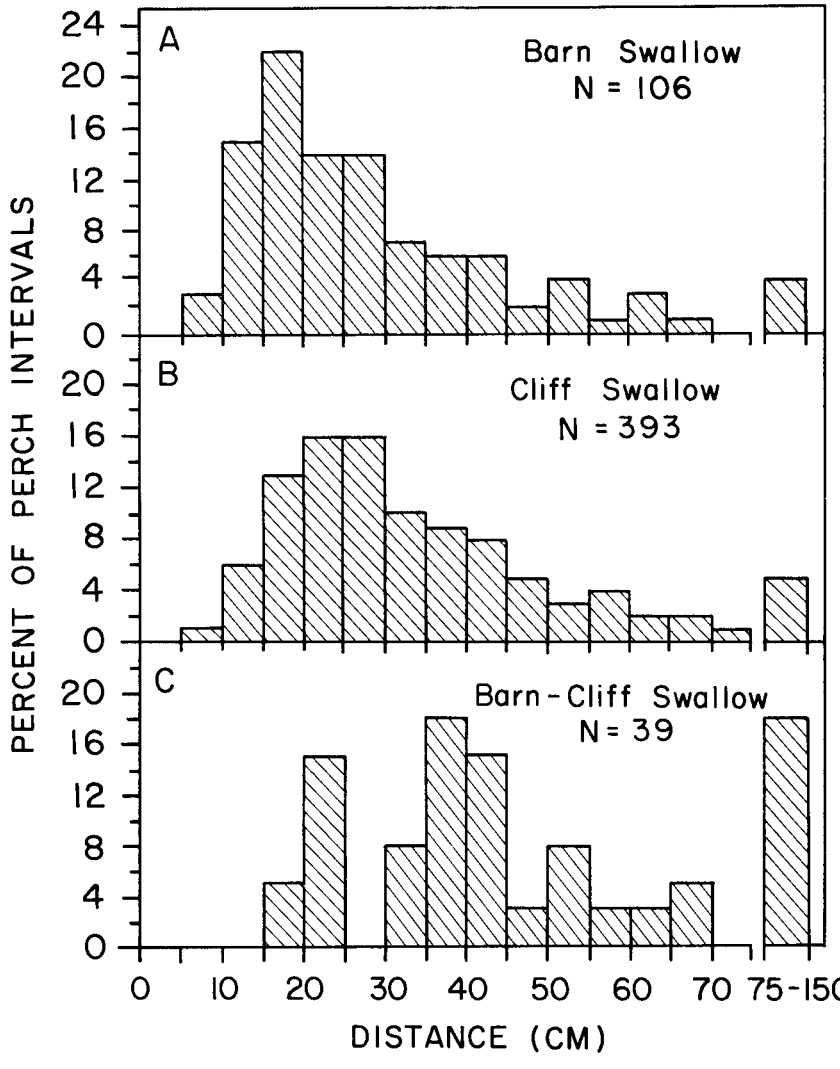

FIG. 1. Frequency distribution of perch intervals for the Barn and Cliff swallows. Abscissa numerals indicate the beginning of an interval.

were the incumbent in all 8 interactions. The interspecific interactions occurred at the shorter perch intervals ($\bar{x} = 14.1 \pm 3.4$ cm), as did the individual distance interactions. The incumbent Barn Swallows appeared to defend their individual distance against Cliff Swallows as well as conspecifics; there

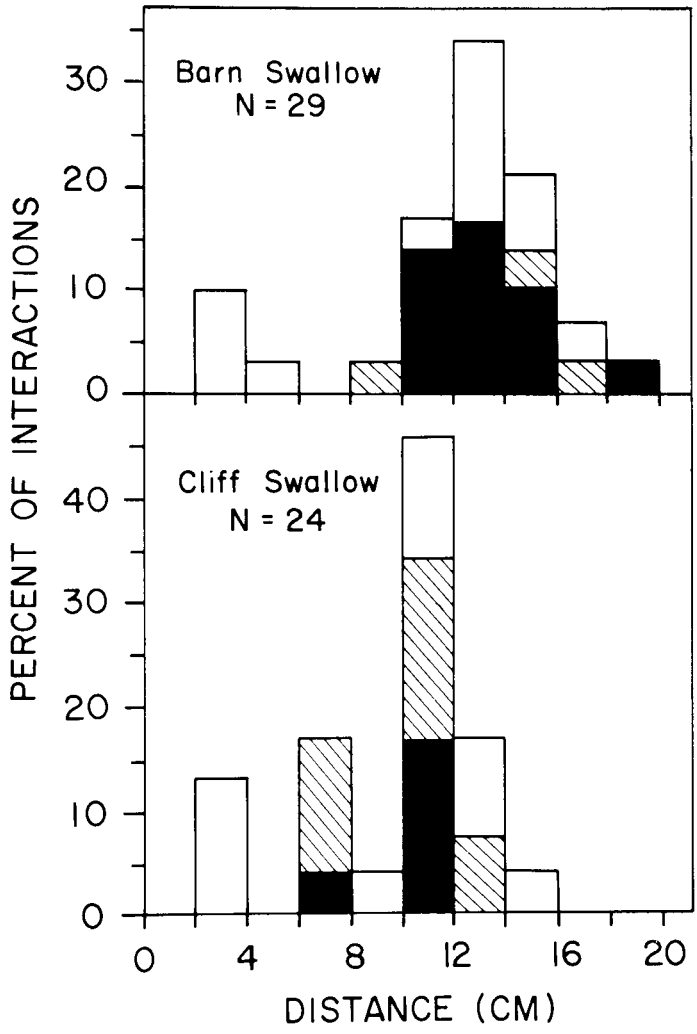

FIG. 2. Distribution of interactions in maintenance of individual distance. Black: approaching bird remained after the incumbent displayed. Shaded: approachng bird retreated. White: incumbent retreated.

was no significant difference between these interspecific distances and the Barn Swallow's individual distance (t-test, $P > 0.10$). The former were significantly different from the Cliff Swallow's individual distance (t-test, $P < 0.001$).

Behavior related to spacing.—Spacing between swallows was established

by direct flight approaches, hovering, and displacement of perched birds; subsequent spatial adjustments were made by sidling, which sometimes involved agonistic interactions. Agonistic displays were similar for both species and were exhibited during establishment and adjustment of spacing. Since birds sometimes landed at locations previously rejected by others, spacing may not be the only factor involved in perch selection. Most new arrivals remained motionless for several seconds before initiating preening, or aggression toward adjacent birds, and they displayed a submissive posture if neighboring birds were close.

Head orientation was important in setting up and maintaining distances between birds. On one occasion, a preening bird intermittently pecked at another whenever the adjacent bird's head turned toward it. Although a gaping mouth was directed toward opponents during threat displays, it was turned away during "yawning" movements in preening. Submissive birds directed their bills outward.

Maintenance of distances between birds was dependent on the birds' attentiveness. Conflicts within the individual distance that resulted in the incumbent's retreat (Fig. 2) occurred when an approaching bird was able to sidle unusually close to an incumbent preoccupied with preening or "sleeping." These birds often sidled to within a body's width of the preoccupied bird. When the approaching bird's presence was noticed, the incumbent flew; if unnoticed, it seemed to advertise its presence by pecking at the incumbent. If the preoccupied bird noticed the approach before the intruder was close, an aggressive response usually caused the approacher's retreat.

Swallows commonly moved apart prior to, or during preening; this probably lessened conflicts and interference from adjacent birds. Only 2 cases of contact during preening were observed; both resulted in avoidance (1 after a brief conflict).

Adult birds in a submissive posture and young birds sometimes perched within the individual distance without being attacked. Fledgling Barn Swallows sidled over and directed a food begging display (similar to adults' agonistic gaping) toward any bird perched nearby, or pecked a neighbor's wing or tail. Adults were very tolerant of young birds and usually retreated or ignored their approaches and displays.

DISCUSSION

The similarities of interaction distances and approach and agonistic behaviors make possible the formation of mixed-species flocks, and account for their apparent spatial regularity. The skewed perch interval distributions indicate that within a species, swallows, like Sandhill Cranes (Miller and Stephen 1966), tend to perch at or near the minimum approachable distance.

Barn and Cliff swallows did not tend to perch at the minimum distance from each other, as indicated from the interaction distance and the distribution curve.

Hediger (1955) estimated the Barn Swallow's individual distance to be 15 cm, whereas I found it to be 12 to 13 cm. The Cliff Swallow's 10–11 cm individual distance and their large percentage of interactions where the aggressor retreated, correspond well with Emlen's (1952) observations.

Interactions where the aggressor remained were mostly restricted to the individual distance interval in the Cliff Swallow, but ranged more widely in the Barn Swallow. This and the Cliff Swallow's more prominent peak interval indicate greater rigidity of individual distance than for the Barn Swallow. Barn Swallow flocks and colonies are often smaller than those of the Cliff Swallow; individual recognition within a Barn Swallow flock would be more likely, resulting in more complex social relationships and more variable spatial patterns. Vocalizations of these species, with the Cliff Swallow's repertoire being smaller than that of the Barn Swallow (Samuel 1971), tend to confirm the Cliff Swallow's less complex social structure. Greater spatial homogeneity might also occur within pre-migratory Cliff Swallow flocks in correlation with increased flock integration.

Individual distance can be a sharp threshold as Grubb (1974) and I found, or a zone of intolerance as determined by Marler (1956) and Dilger (1960). These differences in individual distance values may be due to differences in experimental approach and the birds' activities. Marler and Dilger used 2 movable feeding hoppers to bring captive Chaffinches (*Fringilla coelebs*) and Common Redpolls (*Acanthis flammea*) respectively into close proximity. The perching swallows' major activities were resting and preening, as is likely for Grubb's perched Herring Gulls. McBride (1971) suggested that individual distance be measured at rest when it is constant; Crook (1961) reported that individual distance varies with food dispersion. Determination of individual distance may be more distinct and comparable for perched birds than for feeding birds.

Swallows often took advantage of another's preoccupation to approach closely—a phenomenon also recognized by Emlen (1952), Crook (1961), and McBride (1964). Such approaches always resulted in displacement of the incumbent, and unnoticed intruders pecked preoccupied birds, indicating the approaches were of aggressive intent rather than contact seeking behavior.

Inter- and intraspecific spacing in swallows may decrease, or contact be tolerated, during unusually cold weather (Grubb 1973, Meservey and Kraus 1976). During adverse weather it may be more advantageous to conserve energy by bodily contact than to maintain individual distance.

The toleration of young birds within the individual distance may be

adaptive for colonial life because of the close association of adults and young swallows.

SUMMARY

Field observations and still and motion pictures were used to analyze the spatial patterns of perched Barn and Cliff swallows in Chase County, Kansas from 23 June to 19 September 1975. Individual distance was determined from analysis of spatial interactions between approaching and incumbent birds.

Both species perched near the individual distance; both species had greater interthan intraspecific spacing; and interspecifics did not tend to perch at the minimum approachable distance. A similarity of swallows' interaction distances and spatial behavior may help explain the apparent spatial regularity of mixed-species flocks. Individual distances of Barn and Cliff swallows differed significantly. The Cliff Swallow's individual distance appears to be more rigidly maintained, possibly because of a simpler social organization or increased integration of their pre-migratory flocks.

The maintenance of spacing was dependent on head orientation and attentiveness. Distances increased during preening activities, which lessened interference and potential conflicts between adjacent birds. Adults tolerated young birds and adults in a submissive posture within their individual distance.

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