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Group-living in cliff swallows as an advantage in avoiding predators

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Summary. Cliff swallows (*Hirundo pyrrhonota*) in SW Nebraska, USA, nest in colonies and associate in groups away from their colonies. The degree to which group-living in this species affords advantages in the avoiding of predators was examined. The distance from the colony at which a snake predator was detected increased with colony size. In flocks away from the colonies, group vigilance increased, but the time that each individual spent vigilant decreased, with flock size. As a result, birds in large flocks had more time for preening and mud-gathering. Cliff swallows did not effectively mob predators and thus were unable to deter predators regardless of group size. Nesting within each colony was highly synchronous, but when the effects of ectoparasites on nesting success were removed, individuals nesting during the peak breeding period were no more successful than those nesting before or after the peak. This suggests that swamping of predators is unlikely in cliff swallow colonies. Nests at the edges of colonies were more likely to be preyed upon than nests nearer the center, suggesting that colonial nesting conferred some selfish herd benefits. Overall reproductive success did not vary with colony size. While cliff swallows receive some anti-predator benefits by living in groups, the avoidance of predators is probably not a major selective force for the evolution of coloniality in this species.

Introduction

Animals living in groups may reduce their risk of predation in several ways. Predators may be *detected* sooner if group vigilance increases with the number of individuals present. Many studies, primarily on noncolonial species that flock when feeding, have shown that vigilance increases with flock size (reviewed by Bertram 1980; Pulliam and Caraco 1984). Individuals in large flocks reduce the amount of time spent vigilant and devote more time to feeding or other activities, but flock vigilance remains high because many individuals are present. The same benefits might accrue to individuals nesting together. With more "eyes" present, colonies also might detect approaching predators at greater distances than would individuals nesting alone. Hoogland (1981) showed that individual alertness in prairie dogs (*Cynomys* spp.) declined, but colony vigilance increased, with colony size.

Predators, once detected, may be effectively *deterred* through group mobbing and defense. Mobbing has been observed in many colonial animals (e.g., Burton and Thurston 1959; Kruuk 1964; Horn 1968; Hoogland and Sherman 1976; Andersson and Wiklund 1978; Dominey 1981; Rood 1983). The effectiveness of mobbing is presumably increased (Hoogland and Sherman 1976; Robinson 1985), and an individual's risk of falling victim during mobbing decreased (Brown and Hoogland 1986), as the number of mobbers increases. Thus an important benefit of coloniality could be an increased number of potential mobbers.

Theoretically, individuals living in colonies can synchronize their reproduction and *swamp* the ability of predators to exploit them. In large colonies the probability that an individual's nest will be attacked could be reduced during the peak reproductive period. Synchrony affords a benefit if predators are relatively rare or territorial and do not recruit to colonies of their prey. There is evidence that the percentage of successful nests and individual survival rises during periods of synchrony (Darling 1938; Patterson 1965; Veen 1977; Emlen and Demong 1975; Estes 1976; Arnold and Wasserug 1978; Gochfeld 1980; Gross and MacMillan 1981).

A fourth way predators may be avoided is by clustering nests or bodies in space to create the *selfish herd* effect. Hamilton (1971) pointed out that animals may group to increase the probability that predators will attack other group members. This probability can be increased if individuals position themselves in such a way as to maximize the number of conspecifics between them and the predator's approach. In nesting colonies (Tenaza 1971), the selfish herd is achieved by positioning nests as close as possible to the geometric center of each colony, assuming that predators are equally likely to approach from any side. Terrestrial predators encounter edge nests first, resulting in greater reproductive success of individuals breeding toward the center. Numerous studies have examined position effects on reproductive success, and many have concluded that edge nests do suffer increased predation (e.g., Taylor 1962; Siegfried 1972; Coulson 1968; Feare 1976; Gross and MacMillan 1981).

In this study we examined whether group-living in cliff swallows (*Hirundo pyrrhonota*) affords these birds any anti-predator advantages. We examined whether any relationships existed between group size and individual alertness, group vigilance, and the detection of predators, and evaluated the importance of mobbing. We also investigated whether intracolonial synchrony was related to nest success and whether synchrony affords benefits to cliff swallows by swamping predators. Finally we examined whether there were intracolonial effects of nest position on reproductive success.

The cliff swallow is a small migratory passerine that nests in colonies throughout much of western North America from the Lower Sonoran through the Transition zones to about 3000 m (Grinnell and Miller 1944). Its general biology has been well studied (Emlen 1941, 1952, 1954; Mayhew 1958; Samuel 1971; Grant and Quay 1977; Withers 1977; Brown 1985). Cliff swallows build gourd-shaped nests out of mud pellets that are attached underneath overhanging rock ledges on the sides of cliffs and canyons. They feed exclusively on insects caught in flight, and colonies serve as centers in which individuals aquire information from other individuals on the location of food sources (Brown 1986). The birds are highly social in all of their activities, feeding, preening, mud-gathering, and loafing in large groups (Emlen 1952; Brown 1985). The species is usually single-brooded, and hematophagous ectoparasites are responsible for much of the observed nestling mortality (Brown and Brown 1986).

Methods

Study site

This study was done primarily in Keith and Garden cos., Nebraska, USA, near the University of Nebraska's Cedar Point Biological Station, from May to August, 1982–86. Cliff swallows are abundant in Nebraska and have probably always occurred there (Nichols, cited in Pearson 1917). We studied colonies that were located on artificial structures such as bridges and culverts and on natural cliff sites along the south shore of Lake McConaughy. During 1982–86, we studied 218 cliff swallow colonies totalling 70,545 nests (Brown 1985). Colony size ranged from 1 to 3000 nests ($\bar{x} = 324$, SD = 510).

General procedures and definitions

Study colonies were named and, where possible, all nests were numbered and their progress followed throughout the nesting season. In large colonies, we could study only a sample of the nests, and in these cases we selected nests from all accessible parts of the colony. Nests were marked by writing chalk numbers on the nearby substrate or by driving nails with numbered heads into the cliff face. All nests were checked each day or every 2–3 days until hatching in a colony started; we then began checking them every day or every other day. We observed nest contents with a dental mirror and a small flashlight inserted through each nest's mud neck. It was occasionally necessary to chip away pieces of dried mud from the neck to insert the mirror, but it was not necessary to alter the nest in any appreciable way, and birds quickly repaired any damage (see Brown 1985). Once all eggs of a cliff swallow clutch hatched, we did not disturb that nest again until the 10th day after all eggs had hatched, at which time we recorded the number of nestlings present as a measure of nestling survivorship and reproductive success.

"Colony size" in this paper refers to the number of active nests. For most colonies, size remained largely constant throughout the nesting season, but whenever appreciable numbers of pairs lost their clutches and deserted the colony, we estimated smaller colony sizes later in the season for those colonies. In most cases neighboring colony sites were separated by at least 1 km, and often >15 km. For colonies located on artificial structures, nests were considered to represent a separate colony if the nest substrate upon which they were located was not physically connected to another nest-group's substrate or if at least 25 m separated them from the nearest group of nests; and if nest owners used approaches (to and from nests) that were predominantly different from that of neighboring nests. For colonies located on cliff sites, groups of nests were treated as separate colonies if separated by at least 75 m of substrate obviously unsuitable for nest attachment. Owners of nests distinguished by these criteria seldom, if ever, interacted with each other and thus probably belonged to separate colonies.

Parts of some colonies were fumigated with an insecticide to kill ectoparasitic swallow bugs (Hemiptera: Cimicidae: *Oeciacus vicarius*) (see Brown and Brown 1986). These fumigated nests were either excluded from analyses for this paper or, if included, were analyzed separately. Fumigated nests represented samples in which the confounding effects of ectoparasite-induced nestling mortality were removed.

Statistical analyses were performed on the Princeton University IBM 3081 computer, using the Statistical Package for the Social Sciences (Nie et al. 1975), and on an IBM XT personal computer, using the PC Statistician (Madigan 1983). All statistical tests were two-tailed. Since data were not normally distributed in most cases, nonparametric statistical tests were used (Siegel 1956). Significance was set at $P<0.050$.

Model predator presentation procedures

A model predator was used to measure the effect of colony size on distance at which predators were detected. The model was a life-like rubber snake that closely resembled a real bullsnake (Colubridae: *Pituophis melanoleucus*). We placed the rubber snake in a small wooden box (snake blind) 100 m from each colony. This distance was well beyond the normal distance at which real predators were detected in even the largest colonies (pers. obs.). An observer's blind was placed approximately 10 m from an edgemost nest in each colony. Because predators presumably approach from the edge of a colony, we made our predator presentations on the edge, rather than at the center, of each colony (cf. Wilkinson and English-Loeb 1982). The snake was towed by monofilament fishing line from the snake blind to the observer's blind at about 0.1 m/s across sand or dirt, and it was continually in full view for the birds and not obstructed by weeds or debris. Tow rate was fixed by the spool diameter of the tow line take-up reel, and our estimates indicated that 0.1 m/s was a good approximation to the velocity of an undisturbed, foraging bullsnake. Presentations were always done when at least half of the active nests in a cliff swallow colony contained eggs or nestlings.

Birds habituated quickly to the presence of our blinds and ceased responding to us immediately after we entered the observer blind. No more than three presentations on which the snake was detected, or a total of six, were done on the same day at a colony, to avoid habituation to the snake model, and we did not present it on consecutive days at the same colony. Between successive presentations, we waited at least 10 min after the last alarm call (whether elicited by us or not) before starting the next presentation, to insure that the swallows were not already in a state of alarm when the presentation began.

Cliff swallows responded to the snake by alarm-calling, hovering above the snake, and occasionally diving at it. Either a single swallow or up to 10 or more would detect the snake and respond. We were interested in *initial* detection distance at each colony, so as soon as one bird detected it, we stopped the tow and measured the snake's distance from the colony.

We often observed bullsnakes near colonies, and the swallows' responses to the rubber snake were similar to their behavior when real snakes appeared. Six times we towed a stick of size similar to the snake at the colony where responses were most pronounced, but the birds always ignored the stick. This further suggests that the cliff swallows were perceiving our model as a predator.

Measuring individual alertness and group vigilance

We measured individual alertness of cliff swallows in loafing flocks indirectly by examining the percentage of time spent preening and sun-bathing by individuals. We selected focal birds as randomly as possible from a flock, noted flock size, and with stopwatches recorded the total time the bird was observed and the total time it spent preening or sun-bathing. We watched focal birds for as long a time as possible, usually between 1 and 8 min. An observation was terminated if the flock was disturbed by either apparent or observed predators or if the flock size changed. Because flock size and composition were constantly changing, each observation was treated independently. These data were taken from the start of the nesting season until fledglings appeared in the loafing flocks. For flocks containing at least 15 birds, where possible we distinguished focal birds in the *center* of the flock, defined as individuals with at least five (and usually many more) other birds surrounding them, and ones on the *edge* of the flock, defined as ones with no other birds adjacent on at least one side. If a focal bird's position changed, the observation was terminated. Using the same procedures and criteria, we also quantified the percentage of time focal individuals spent gathering mud at a mud hole.

We measured group vigilance in loafing flocks by scan-sampling each flock, recording at that instant the number of alert individuals, defined as birds with their "heads up" who were not preening or sun-bathing. Scan samples were done at 5-min intervals if flock size persisted unchanged or more often if flock size changed in the interim. After each scan, we recorded flock size.

Measuring nesting synchrony

We investigated the relationship between reproductive success and the degree to which each nest was synchronized with each colony's peak period of nesting. For each colony the modal clutch initiation date (i.e., date of first laying in a nest) was determined and the standard deviation of clutch initiation date calculated. For most colonies a single standard deviation was 2–5 days. Each nest was then assigned, based on its clutch initiation date, to the appropriate number of standard deviations on either side of the modal date. We thus compared *relative* intracolonial synchrony of all colonies, allowing us to pool data from different colonies. For each nest we measured nestling survival when nestlings were 10 days old. Each nest containing at least one nestling alive was scored as a successful nest and one without any nestlings alive as an unsuccessful nest.

Measuring nest positions

The positions of all active nests in each colony were mapped at the end of the nesting season. Relative nest locations were drawn on paper, and overlapping series of photographs at some colonies provided further documentation of nest positions. Distances between all active nests were measured (in cm) in the field. Since colonies were usually roughly linear in shape, i.e., single rows of nests with little vertical stacking, it was easy to designate a centermost nest, one with an equal number of neighbors on either side. For the few colonies that were less linear in shape and more "honeycombed", the nest with an equal number of nests on all respective sides (regardless of its position with respect to the geometrical center of the colony's substrate) was considered the centermost nest. Each nest's linear distance from the centermost nest was determined.

In comparison of center versus edge nests, edge nests were considered to be the 10 sequentially placed active nests, beginning with the edgemost nest and moving inward (see Results for rationale for using 10). Center nests were the 10 sequentially placed active nests, beginning with the centermost nest and moving outward. In linearly shaped colonies (such as in culverts), center nests included the 10 nests on either side of the centermost nest; edge nests included the 10 nests closest to the colony's edge on either side. This analysis was done only in colonies where nest array and colony size would yield an equal number of edge and center nests on all sides of the colony's geometric center. For culvert colonies that were split in half for fumigation, the center nest was considered to be the innermost fumigated nest, i.e., the nest closest to the dividing line between fumigated and nonfumigated nests. The only edge nests in these colonies were considered to be the fumigated edgemost ones at the opposite end of the colony from the dividing line.

Results

Predators of cliff swallows

Bullsnakes were the principal predators of cliff swallows in SW Nebraska. During 1982–86 we observed 15 bullsnake predation attempts in swallow colonies. Eight of these attempts were successful. These snakes seemed equally capable of reaching nests on natural cliff sites and ones on artificial structures such as metal bridges and concrete highway culverts. Bullsnakes and rat snakes (*Elaphe obsoleta*) also are known to be predators of cliff swallows in other parts of the bird's range (Bent 1942; Ganier 1962; Sutton 1967; Thompson and Turner 1980; Hopla and Loye 1983; W. Pulich pers. comm.). During 1982–86, we observed five cases of predation by avian predators: an American kestrel (*Falco sparverius*) took a juvenile cliff swallow that had recently fledged; a black-billed magpie (*Pica pica*) was seen eating a juvenile swallow that had probably fallen out of a nest; a loggerhead shrike (*Lanius ludovicianus*) took one adult swallow at a colony; and common grackles (*Quiscalus quiscula*) twice killed and ate adult swallows that were gathering mud. Cliff swallow remains also were found in a great horned owl (*Bubo virginianus*) pellet (Brown and Hoogland 1986), but it was unknown where or how the owl captured the swallow. Thus, while avian predation on cliff swallows in Nebraska occurred, it happened less often than snake predation at the actual colony sites. Mice (*Peromyscus* sp.) nested in unused swallow nests, but neither they nor any other mammals were known to prey on cliff swallows in Nebraska.

Introduced European house sparrows (*Passer domesticus*) and rarely native house wrens (*Troglodytes aedon*) in Nebraska competed with cliff swallows for existing nests and at times ousted the swallow owners. Swallow eggs were sometimes destroyed in nest takeover attempts, and these instances resembled predation. However, wrens were seen in a cliff swallow nest only once, and most of our data on presumed nest predation came from colonies that contained few to no sparrows. Known cases in which sparrows were responsible for apparent "predation" events were excluded from our analyses since interaction between swallows and non-native sparrows is a relatively recent, human-caused artifact of having introduced these sparrows to North America.

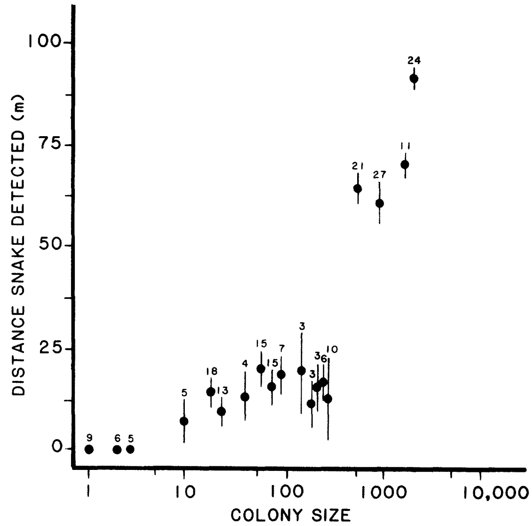

Fig. 1. Distance in meters at which the model snake predator was first detected by cliff swallows versus colony size (no. of active nests). Mean ± 1 SE and total number of snake presentations for each colony are shown. Distance from the colony at which the snake was detected increased significantly with colony size ($r_s = 0.84$, $P < 0.001$)

Detection of predators versus colony size

We presented model snake predators to cliff swallows 205 times at 19 colonies. Based on detection distances, three classes of cliff swallow colonies can be distinguished (Fig. 1): small colonies containing less than 10 nests which never detected the approaching predator; colonies containing between 10 and 275 nests which detected the predator on average at about the same distance; and large colonies containing over 500 nests which detected the predator at great distances. Distance at which the approaching predator was detected increased significantly with colony size (Fig. 1). These data clearly show that swallows nesting in large colonies detect snake predators at greater distances than do birds nesting in small colonies.

Individual alertness and group vigilance versus group size

The model snake presentations suggested that overall colony vigilance was increased when more individuals were present (Fig. 1). We attempted to learn if time individuals spent alert at colonies declined with colony size, thereby freeing individuals to engage in other (i.e., nesting) activities. Measur-

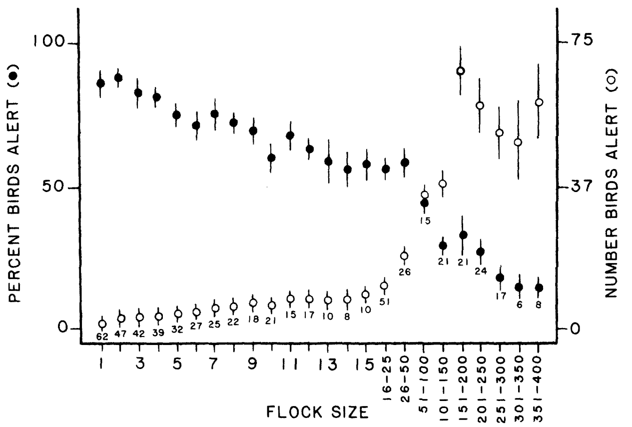

Fig. 2. Percentage of cliff swallows in a flock that were alert (*closed circles*) and number of cliff swallows in a flock that were alert (*open circles*) versus flock size (no. of birds in flock). Mean ± 1 SE and total number of observations for each flock size are shown. Percentage of birds that were alert declined significantly with flock size ($r_s = -0.60$, $P < 0.001$), whereas the number of birds that were alert increased significantly with flock size ($r_s = 0.68$, $P < 0.001$)

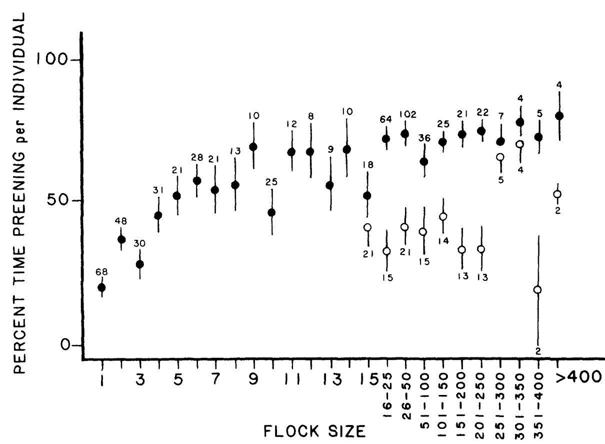

Fig. 3. Percentage of time that individual cliff swallows spent preening (and sun-bathing) versus flock size (no. of birds in flock) for all individuals except edge birds in large flocks (*closed circles*), and for edge birds in large flocks (*open circles*). Mean ± 1 SE and total number of observations for each flock size are shown. For all individuals excluding edge birds, percentage of time spent preening or sun-bathing increased significantly with flock size ($r_s = 0.51$, $P < 0.001$). For edge birds only, there was no significant correlation between time spent preening or sun-bathing and flock size ($r_s = 0.09$, $P = 0.152$)

ing individual alertness at colonies proved difficult, because often the birds were not readily visible to us as they sat inside their nests. Furthermore, since there is considerable interaction between birds in adjacent nests (Brown 1985), it was often impossible to know if "alert" individuals were scanning for predators or were engaged in other activities such as monitoring conspecific foraging success at adjacent nests (see Brown 1986).

However, cliff swallows also associate in large groups away from colonies. Throughout the nesting season in Nebraska, the birds assemble in loafing flocks, sometimes up to 2 km away from the nearest colony site, where they preen and sun-bathe. By studying these groups in which few or no intraspecific interactions (e.g., fights) occurred, we were more likely to measure individual alertness truly directed towards predators. Loafing flocks assemble on wires, rock ledges, trees, and the ground. The number of birds with their heads up was used to examine group vigilance, and percent time preening and sun-bathing was used to examine individual vigilance because whenever birds do not preen or sun-bathe, they alertly look around. Thus, time spent preening and sun-bathing is an inverse measure of how much time cliff swallows spend scanning, presumably for predators such as American kestrels.

The percentage of birds that were alert at any instant declined significantly with flock size, but the absolute number of alert birds at any instant increased significantly with flock size (Fig. 2). These data show that overall group vigilance increases with group size simply because more birds are present to be alert at any one time.

Since percentage of birds that were alert declined with flock size, individuals in large flocks spent less time alert and presumably were freed to engage in other activities such as preening and sun-bathing. When all individuals (except edge birds in flocks larger than 15) were considered, percentage of time spent preening and sun-bathing per individual increased significantly with flock size (Fig. 3) with a corresponding decrease in time spent alert. These individuals probably benefitted from flocking because, with decreased individual alertness, time available for preening and sun-bathing increased. However, edge birds probably realized no benefit from flocking, because preening by them did not increase with flock size (Fig. 3). Instead, they spent much of their time scanning. Since individuals at the edges of a flock presumably are potentially closest to a predator's approach, their increased amount of scanning supports our assumption that alertness in these flocks is indeed directed towards predators.

Similar results were obtained for mud-gathering flocks of cliff swallows. Swallows assemble at mud holes where they gather mud in their bills and then transport it back to their nests (Emlen 1954). Mud is gathered throughout the nesting season because nests often require repair. Mud-gath-

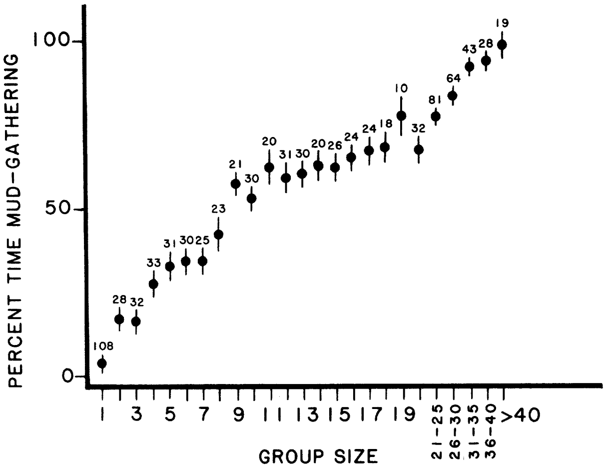

Fig. 4. Percentage of time that individual cliff swallows gathered mud versus group size (no. of birds in mud-gathering group). Mean ± 1 SE and total number of observations for each group size are shown. Percentage of time spent mud-gathering increased significantly with group size ($r_s = 0.88$, $P < 0.001$)

ering is a highly social activity, especially early in the season when many colony members gather mud simultaneously. When individuals alight to gather mud, they either alertly scan, presumably for both aerial and terrestrial predators, or actively gather mud. When gathering mud, their heads are bent close to the ground and they are then probably vulnerable to predators. In observed predation attempts, common grackles would slowly stroll toward a mud-gathering flock and suddenly pounce on a swallow, kill it, and eat it.

Individuals who gathered mud in large flocks did so more efficiently than individuals in small flocks or alone (Fig. 4). Cliff swallows in large flocks spent almost the entire time at a mud hole actually gathering mud and virtually no time alert. Individuals in small flocks spent most of their time scanning for predators. Efficient mud-gathering in large flocks likely reduced the cumulative time birds were vulnerable to predation, and over the course of the season might have sped up the building of nests.

Mobbing and the deterrence of predators

Predator attacks against cliff swallows were uncommon, so we could not measure the effectiveness of mobbing in deterring predators (cf. Robinson 1985). On 8 occasions bullsnakes successfully preyed on eggs, nestlings, or adult cliff swallows. In these cases the adult swallows' mobbing responses were slight with only three to six individuals (in colonies of 85–750 nests) hovering near the predator. After a snake entered a nest and disappeared from view, the birds resumed normal activity. Even neighboring birds of the nest containing a snake seemed to ignore the reptile when it was out of sight in the nest. Snakes captured adult cliff swallows by coiling inside a nest, out of sight, and waiting for the owner(s) to return. Upon detecting our model snake, cliff swallows alarm-called and one to 10 birds circled above the predator. When black-billed magpies appeared near colonies or when model great horned owls were presented near colonies, cliff swallows milled overhead in disorganized fashion (Brown and Hoogland 1986). Responses were more marked when American kestrels passed near colonies. Swallows left the colony in a tight cluster, gained altitude while flying as a highly coordinated unit, and, when reaching the same altitude as the kestrel, spread out in loose groups and appeared to start foraging. There was never a group effort to chase a kestrel, although sometimes two or three swallows would swoop close to the back of the kestrel. Loggerhead shrikes and common grackles were ignored when they approached colonies. None of these qualitative observations suggested that cliff swallows were able to effectively deter an approaching predator through mobbing or group defense of nests.

Nesting synchrony and the swamping of predators

If synchronizing reproduction within colonies swamps the ability of predators to exploit their prey, per capita risk of predation is reduced for individuals nesting during the peak period of reproduction. We examined whether the proportion of successful nests varied with the degree of nesting synchrony.

Most cliff swallow clutches were started during a period of 15–20 days or less (Fig. 5; only colonies for which we knew exact clutch initiation dates for at least 95% of the nests are shown). This high degree of synchrony suggests that cliff swallows might theoretically escape predation by nesting near or within the peak breeding period. For *nonfumigated* nests, i.e., unaltered ones exposed to natural levels of ectoparasites, reproductive success varied significantly with degree of nesting synchrony (Fig. 6). The percentage of nests containing at least one nestling alive at day 10 was significantly greater for nests started during the peak breeding period than for nests started before and after the peak (Fig. 6). These results suggest that clutches begun during the peak breeding period have a greater probability of escaping predation than clutches begun earlier or later in the year.

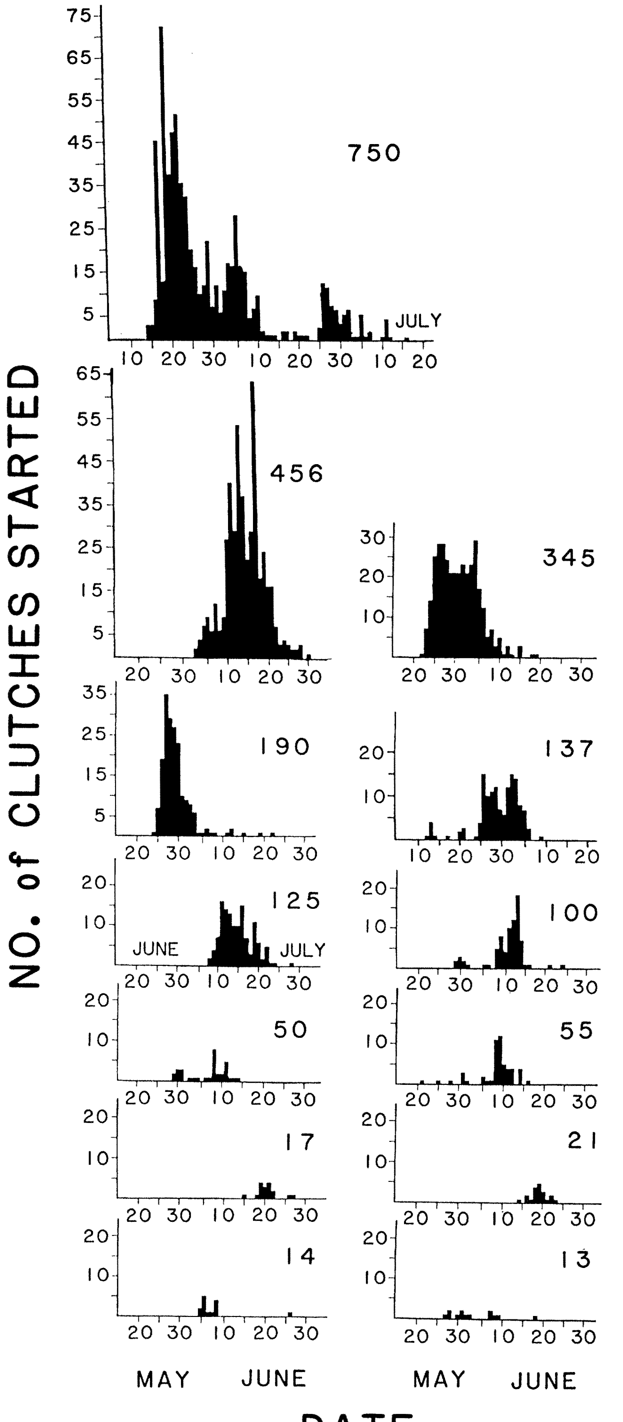

Fig. 5. Number of clutches started per day in 13 Nebraska cliff swallow colonies. Colony size (no. of active nests) is shown in the *upper right corner* of each graph. Unless noted, all dates refer to May and June

However, ectoparasites were responsible for many nesting failures by cliff swallows, through killing of nestlings and causing adult birds to abandon nests containing eggs and nestlings (Brown and Brown 1986). Nesting failures caused by ectoparasites often resembled predation events, and therefore we examined reproductive success versus degree of nesting synchrony for *fumigated* nests. For these nests the confounding effects of ectoparasites were removed, and thus we were more likely to measure the effects of predation on reproductive success. For fumigated nests degree of synchrony had little effect on reproductive success (Fig. 6; results approached significance only because of slightly lower success of nests in the −2 SD category). This means that fumigated nests started during the peak breeding period were no more successful than asynchronous nests started earlier or later in the year. This also means that the effects of synchrony documented in the nonfumigated nests (Fig. 6) were probably not caused by predators but were probably instead related to patterns of ectoparasitism. There was no evidence that fumigation caused nests to be less likely to be preyed upon by snakes or other potential predators.

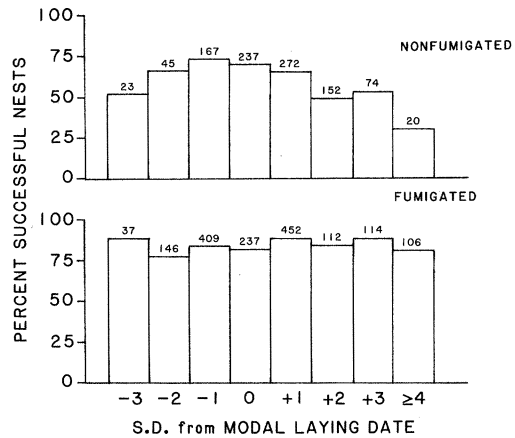

Fig. 6. Percentage of successful cliff swallow nests (ones containing at least one nestling alive on the 10th day after hatching) versus degree of intracolonial synchrony (see text). Total number of nests in each category is shown. Fumigated nests were ones in which the effects of ectoparasites were removed; nonfumigated nests were unaltered ones with natural levels of ectoparasites. Percentage of successful nests varied significantly with degree of nesting synchrony for nonfumigated nests ($\chi^2 = 39.63$, $P < 0.001$, $df = 7$) but only approached significance for fumigated nests ($\chi^2 = 14.15$, $P = 0.050$, $df = 7$)

The selfish herd and the avoiding of predators

In colonies nests located closest to a predator's potential approach, i.e., edge nests, are theoretically more likely to be preyed upon than ones located farther from the predator's approach, i.e., center nests. Bullsnakes entered cliff swallow colonies on the edges and moved inward, progressively visiting each nest they encountered. We therefore predicted

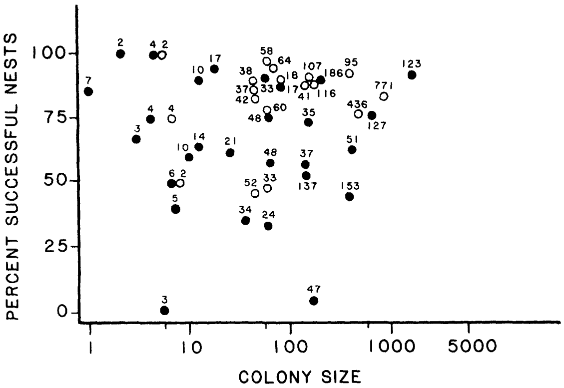

Fig. 7. Percentage of successful cliff swallow nests (ones containing at least one nestling alive on the 10th day after hatching) versus colony size (no. of active nests). Total number of nests examined for each colony is shown. Fumigated Colonies (ones in which the effects of ectoparasites were removed) are shown with *open circles* and nonfumigated Colonies with *closed circles*. There was no significant correlation between percentage of successful nests and colony size for either fumigated Colonies ($r_s = 0.14$, $P = 0.57$) or nonfumigated Colonies ($r_s = -0.11$, $P = 0.58$)

a negative correlation between nesting success and a nest's distance from the center if selfish herd effects are important. We examined this prediction in two ways.

For *all* nests (fumigated and nonfumigated), there was no significant correlation between nestling survival to day 10 and a nest's linear distance from the centermost nest (data from 1982–84: $r_s = 0.05$, $N = 894$ nests, $P = 0.067$). This suggests that there are virtually no selfish herd advantages for cliff swallows. However, because predation attempts occurred fairly rarely, perhaps only the extreme edge nests in a colony are likely to suffer predation attempts. Therefore we examined reproductive success for the 10 edgemost nests on all sides per colony and for the 10 centermost nests on all sides per colony. We selected 10 nests because in observed predation attempts, bullsnakes usually visited a maximum of about 10 nests, beginning at the colony's edge, on a single visit. Ten center nests were selected to give a roughly balanced comparison for statistical purposes. Since ectoparasites tend to concentrate toward the centers of colonies (Brown and Brown 1986) and would thus complicate measuring position effects on likelihood of predation, for this analysis we used only fumigated nests. Data for colonies ranging in size from 61 to 750 nests were combined.

Edge nests were significantly more likely to be preyed upon than center nests, as measured by whether at least one nestling was alive at day 10 (total edge nests = 254, edge nests unsuccessful = 57 (22.4%); total center nests = 225, center nests unsuccessful = 17 (7.5%; $X^2 = 20.23$, $P < 0.001$).

These results suggest that cliff swallow nests located at the extreme edges of colonies are more likely to be preyed upon than nests located closer to the colony's center. There are probably no nest position advantages (with respect to avoiding predation) once past the 10 nests closest to the colony's edge.

Nesting success versus colony size

If coloniality affords any major anti-predator advantages for cliff swallows, nesting success should increase with colony size (Hoogland and Sherman 1976). We examined the percentage of successful nests (ones with nestlings alive at day 10) in colonies ranging in size from 1 to 1600 nests. For neither fumigated nor nonfumigated colonies did the percentage of successful nests increase with colony size (Fig. 7).

Discussion

Our results show that the principal anti-predator benefits of group-living in cliff swallows are enhanced detection of approaching predators at colony sites and increased group vigilance with decreased individual vigilance in groups away from the colony sites. There are advantages to nesting toward the centers of colonies because extreme edgemost nests are more likely to be preyed upon. There is little evidence that cliff swallow groups effectively deter predators through mobbing or that synchronous nesting swamps the ability of predators to exploit these birds.

In a similar study, Wilkinson and English-Loeb (1982) presented stuffed predator models to cliff swallows in California. Surprisingly, they found no difference in time of detection or distance of detection of the model predators among colonies of different sizes. However, their methodology was flawed in that they presented their conspicuous avian predator models at distances of only 30 m from each colony. Their predators thus "attacked" from so close a distance that birds in even the smallest colonies probably detected the predators immediately. Our results differed from Wilkinson and English-Loeb's (1982) because we used a much less conspicuous snake predator and began our presentations much farther from each colony (100 m).

The importance of enhanced detection of predators by cliff swallows at colony sites is unclear. Early detection of predators may serve to warn one's mate inside the nest, giving it time to escape, but since cliff swallows do not mob effectively, there would seem to be few other benefits of early predator detection. Alarm calls might also warn nearly fledged offspring who could then escape a predator by fledging early. Early fledging was observed in one case of actual snake predation in a colony. However, early warning in big colonies may not be important because, at least in the case of snakes, only after the predator enters the colony and is poised to enter a nest does early fledging at that nest occur. We are uncertain whether cliff swallows detecting a slow-moving snake predator at, for instance, 75 m benefit appreciably over swallows detecting it at, for instance, 15 m. Early detection of fast-moving avian predators such as kestrels could be more important, but we have no data to evaluate whether that is so.

There is unambiguous evidence for the importance of enhanced group vigilance in loafing and mud-gathering cliff swallow flocks *away from colonies*. Flock vigilance was clearly enhanced (Fig. 2), and an individual's time devoted to other activities correspondingly increased (Figs. 3 and 4), with increasing flock size. Though we have no direct evidence that increased time for preening and mud-gathering is translated into increased fitness, it seems likely that this is the case. Enhanced group vigilance and decreased individual alertness are the classical benefits of flocking (reviewed in Pulliam and Caraco 1984), although direct field evidence for increased group vigilance (e.g., Fig. 2) is rare. But whether these benefits apply to cliff swallows when *at* their nesting colonies (as in prairie dogs; Hoogland 1981) is not known.

Our finding little evidence for swamping of predators in cliff swallow colonies (Fig. 6; fumigated nests) is surprising given the relatively high degree of synchrony exhibited by colonies (Fig. 5) and the fact that the birds' principal predators – snakes – are clearly satiable predators. Although one bullsnake consumed 35 eggs from 10 nests on one visit to a colony while another killed and ate three adult birds and 8 eggs on a single visit, snakes are satiable because they eat infrequently (e.g., Shaw and Campbell 1974). Each cliff swallow colony might have only to contend with three or four attacks from a bullsnake during the entire time it contains eggs and nestlings, and per capita probability of being preyed upon should decline for nests active in the most synchronous periods. However, perhaps swamping of predators is not important for cliff swallows simply because predation attempts are relatively rare, and a high degree of synchronous nesting could be a response to seasonal peaks in local food resources or to enhance the efficiency of colonies as information centers for food-finding (Brown 1985, 1986). Interestingly, if we had considered only nonfumigated nests and had not removed the confounding effects of ectoparasites through fumigation, we might have concluded that synchronous nesting does afford benefits in swamping of predators (Fig. 6; nonfumigated nests). This illustrates the difficulty in disentangling potential causes of synchronous nesting if relevant manipulations are not performed.

Cliff swallows did not effectively mob approaching predators or attempt to deter them from attacking in any way. This is not surprising given these birds' small size and their lack of weapons in the form of strong beaks or talons. Predators such as bullsnakes are unlikely to be deterred by any bird as small as a cliff swallow regardless of mob size. Colonial species such as cliff swallows instead seem to rely on a large group's physical and vocal conspicuousness to perhaps bewilder or confuse an approaching predator and in the process greatly reduce their risk of falling victim to the predator during these mobbing displays (Brown and Hoogland 1986).

Cliff swallows nesting on the extreme edges of colonies were clearly less successful than ones nesting nearer to the center. Predation probably accounted for these results since any potential effects of ectoparasites were removed. In some species individuals nesting on the edges of colonies are young and inexperienced and this accounts for reduced success (e.g., Coulson 1968). Research on how age and experience might affect settlement patterns within cliff swallow colonies is still in progress. Because ectoparasites are more numerous towards the center of colonies (Brown and Brown 1986), nest positioning within the colony may be a trade-off between the risks of predation which are higher toward the colony's edges and the effects of ectoparasites which are greater toward the colony's center.

Although this study demonstrated that cliff swallows receive some anti-predator benefits by living in groups and nesting in colonies, reproductive success did not vary with colony size (Fig. 7). Birds nesting solitarily or in small colonies were as successful, on average, as birds nesting in large colonies. The anti-predator benefits afforded to cliff swallows therefore are probably not major ones and are probably not responsible for the evolution of colonial nesting in this species. Other selective factors are likely to be primarily responsible for group-living in cliff swallows, in part because coloniality may at times even *increase* cliff swallow vulnerability to predators. For instance, in observed predation attempts by snakes, a snake always hung onto a neighboring nest in order to enter another one. Tight clumping of nests within colonies therefore enhances a snake's access to all nests. Cliff swallow nests usually touch two or more neighboring nests, and birds in large colonies pack their nests more densely than do birds in small colonies (Brown 1985). Solitary cliff swallow nests often appeared more difficult for snakes to reach because they had no neighboring nests nearby to serve as a "toehold" for the predator.

In a similar study on another colonial swallow, the bank swallow (*Riparia riparia*), Hoogland and Sherman (1976) also found no correlation between reproductive success and colony size. However, in the absence of other clear benefits of group-living in that species, they concluded that avoidance of predators was the major advantage of coloniality in bank swallows. Hoogland and Sherman (1976) reasoned that although coloniality might be advantageous for bank swallows in avoiding diurnal predators, living in colonies might make these birds more vulnerable to predation by nocturnal digging predators. This argument is unlikely to apply to cliff swallows in Nebraska because, with the possible exception of great horned owls, there were no known nocturnal predators in our study area.

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