

PREDATION AND COLONIALITY IN CLIFF SWALLOWS (*PETROCHELIDON PYRRHONOTA*)

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ABSTRACT.—The hypothesis that the time required to detect an approaching predator varies inversely with colony size was tested. Ninety-five attacks by Loggerhead Shrikes (*Lanius ludovicianus*) and American Kestrels (*Falco sparverius*) were simulated at six Cliff Swallow (*Petrochelidon pyrrhonota*) colonies. Colony size, which ranged from 18 to 320 nests, did not explain a significant portion of the variance in the time it took to detect approaching predator models, even when effects due to wind velocity, breeding stage, nest exposure, and air temperature were removed. Only air temperature proved to be a significant predictor of detection time. To determine whether or not large colonies might reduce the relative amount of predation more effectively than small colonies, we conducted periodic predator censuses around each colony and observed actual predator attacks. Relative predator density increased only five-fold, while colony size increased by a factor of 20. Further, we found no relationship between attack rate and colony size. Consequently, we suggest that larger colonies may dilute the effect of local predators and thereby suffer less nestling predation on a per nest basis. Received 24 April 1981, accepted 1 September 1981.

Most birds must detect and subsequently evade predators if they are to survive. Birds that live in groups may have an advantage over solitary individuals, because they can exchange information about a predator's location and thereby reduce the risk of predation on other group members. Although the evolutionary advantages of such alarm calling behavior are still in dispute (see Harvey and Greenwood 1978, for review), many workers believe that one major evolutionary advantage to being in a large group is early detection of approaching predators. In this paper we describe field experiments on the Cliff Swallow (*Petrochelidon pyrrhonota*) that test the effect of colony size on the time it takes to detect avian predators, and that demonstrate the ability of Cliff Swallows to discriminate predator from nonpredator models. In addition, we evaluate an alternative advantage to large colony size, that of diluting an individual's chances of being captured (Bertram 1978).

The dilution hypothesis states that any individual's probability of being captured by an attacking predator decreases as the number of his neighbors increases, assuming all have an equal chance of being captured. Obviously, this dilution effect will always occur unless predation increases with colony size in compensation. This may occur in two ways. Either the number of predators may increase, or the

attack rate of each predator may rise. If nestlings are being preyed upon, then the magnitude of the dilution effect will be greatest when the colony is highly synchronous. This idea is quite similar to the predator swamping or satiation hypothesis (Lloyd and Dybas 1966, Clark and Robertson 1979), which states that groups satiate predators by synchronizing vulnerability in time or space, thus decreasing the probability that any given individual will be preyed upon. Accordingly, we assess the validity of the dilution hypothesis by using predator censuses, direct observations of attempted predation on swallows, and breeding synchrony estimates at Cliff Swallow colonies of different sizes.

METHODS

Study subject.—Cliff Swallows were chosen as subjects of this investigation because they live in colonies of different sizes, emit high-pitched, single-note alarm calls (Samuel 1971a), and show a stereotyped display once an approaching predator is detected. They may build from 15 to several thousand of their gourd-shaped mud nests beneath a bridge, overhanging cliff, or building eave (Mayhew 1958, Samuel 1971b). Consequently, only avian predators can gain access to their nests easily. American Kestrels (*Falco sparverius*) often attack Cliff Swallow colonies (pers. obs.), as they do Bank Swallow (*Riparia riparia*) colonies (Freer 1973, Windsor and Emlen 1975). They attempt to grab perched adults (Bonnot

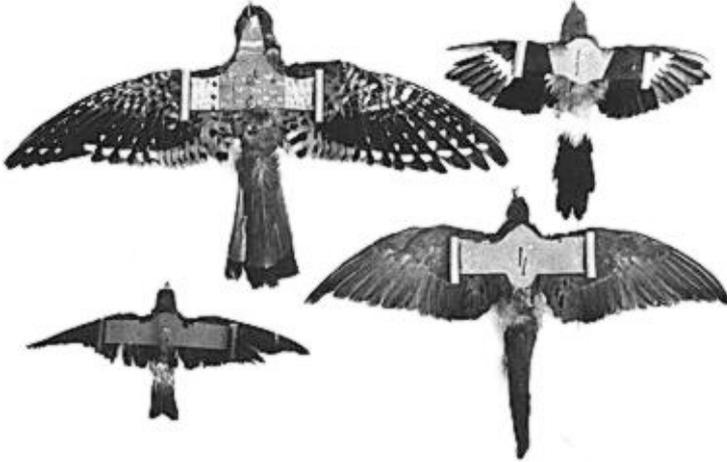


Fig. 1. The four models: American Kestrel, Loggerhead Shrike, Cliff Swallow, and Mourning Dove.

1921, this study) or flying swallows or to reach within nests for nestlings (this study). Loggerhead Shrikes (*Lanius ludovicianus*) capture most Cliff Swallows by pulling nestlings out of nests with their bills (this study).

Field experiment.—We simulated attacks of avian predators at six colonies in San Diego County, California between 6 April and 9 June 1978 to determine whether or not large colonies could detect approaching predator models faster than smaller colonies. We towed a stuffed predator, either a Loggerhead Shrike or American Kestrel, or a stuffed nonpredator control, either a Cliff Swallow or Mourning Dove (*Zenaidura macroura*), at the colonies (Fig. 1). The models emerged from a small blind, traveled along 30 m of horizontal guide lines, which were oriented perpendicular to the colony structure, and then entered another small blind beneath the center of the colony (Fig. 2). We designed the apparatus to mimic an actual attack; kestrels and shrikes, however, sometimes approached a colony from a greater distance or more laterally to the colony face. Due to differences in topography and the nesting structures, the geometry of the apparatus was similar but unique at each colony (Table 1).

We timed and tape-recorded the response using a stopwatch, Nagra IV-D tape recorder at 7½ ips, and a Sennheiser MKH 815T directional microphone and took a photograph of the colony at the end of the trial from within a blind adjacent to the starting pole. Written descriptions of the swallows' response were made after each trial, based on a mutual decision by the observers. We randomized the order in which we presented the models (except when testing for habituation and sensitization, in which case we presented the same model for many consecutive trials). The next model was not presented until the

colony had ceased giving a mobbing display and had resumed normal activity.

We presented between 2 and 12 models ($\bar{x} = 8.4$, $SE = 0.5$) every 9 min ($\bar{x} = 8.9$, $SE = 0.4$) at each colony. We began each of the 28 days of presentations at 0840 ($SE = 15$ min) Pacific Daylight Savings Time. Any trials in which the model stopped or otherwise was towed unusually were omitted from all analyses. Excluding those problem trials, the mean time, 7.0 s ($SE = 0.1$, $n = 161$), required to tow the models down the guide lines produced a flight speed of 4.3 m/s, which is about one-half our estimates of either a shrike or kestrel approaching a landing.

Using our recordings, written observations, and the photographs, we measured the response time and the intensity of the display for each trial. We used the elapsed time between when the model left the blind and when the first alarm call was given as the response time. We scored display intensity on a six-point scale: zero equals no detectable response

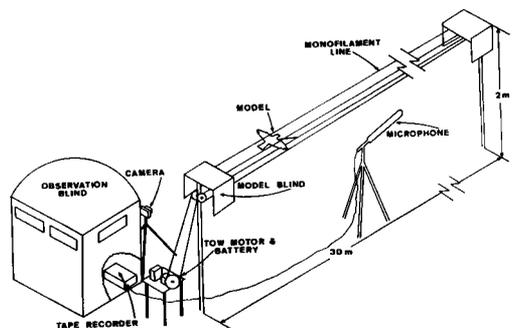


Fig. 2. Avian predator attack simulation apparatus.

TABLE 1. Summary of colony characteristics.

Name of colony	Number of active nests		Nesting structure	Direction model flown from	Deviation from perpendicular to structure (degrees)	Deviation from horizontal approach (degrees) ^b	Distance below (-) or above (+) nests (m)	Exposure (percentage nests facing out)
	1978	1979						
EC	320	674	Bridge	W	0	0	-2.5	90-95
DM	147	208	Bridge	W	35	0	-5.0	85-90
SF	96	100 ^a	Bridge	E	19	-5	-3.5	0
SP	92	100 ^a	Building	N	0	+8	-1.5	50
SV	76	92	Bridge	E	8	-2	+1.0	0
SM	18	35	Bridge	E	0	-2	-1.0	50

^a These are estimates based on a winter inventory of the nesting site.

^b Negative values refer to downward slope, positive values to upward slope.

and five indicates that the response was indistinguishable from that given to real predators during an actual attack. We based intermediate intensity scores on the proportion of birds in the colony that gave alarm calls and entered the mobbing flock. Alarm calls always preceded the formation of a mobbing flock. In an actual attack, once an alarm call was given, most birds vacated their nests and formed a coordinated flock that wheeled at the predator while individuals continually gave alarm calls. We compared median mobbing response intensities for each model to determine whether or not swallows could discriminate between models.

We measured exposure of the nest, air temperature, wind velocity, and breeding stage, in addition to colony size, for each trial, because each may have causal relationships with response time. If the first swallow to give the alarm tends to be sitting in the nest opening, then those colonies with greater nest exposure should have lower detection times. We arbitrarily divided nest exposure into three equal categories—more than two-thirds of the nests exposed, one to two-thirds exposed, or less than one-third exposed. If birds in flight tend to give the first alarm, then detection may be more rapid when insects are most available, such as periods of warm morning temperatures and low wind speeds (Johnson 1969). If predators concentrate their activities during one part of the breeding cycle, such as during the nesting period, then the swallows may become more vigilant and detect predators faster during that stage. Breeding stage was divided into two categories, before and after hatching. If cries of nestlings could be heard from at least half of the nests or at least half of the returning adults carried food rather than nest material, we scored the breeding stage as after hatching. We determined the synchrony of the breeding stage at two colonies by periodically examining most of the nests in the colony using a small flashlight and mirror and estimating the mean date of hatching for each nest. The standard deviation of the date of

hatching was used as a measure of colony synchrony (Emlen and Demong 1975).

Predator censuses.—We periodically censused American Kestrels and Loggerhead Shrikes in a 1-km circle around each colony during the 1979 breeding season. Five observation stations were established within each census area, one placed at the colony and the others distributed a mean distance of 0.6 km (SE = 0.1) around the colony. At each station an observer spent 5–15 min scanning the surrounding vegetation for perching kestrels or shrikes. Because both American Kestrels (Balgooyen 1976) and Loggerhead Shrikes (Craig 1978) typically sit on elevated perches, they are readily observed over long distances. At most of the colonies, the surrounding terrain was primarily level and covered with low vegetation. Both predator species nested within the census area of at least four of the colonies. The censuses included some of the nesting period of the predators and much of the first clutch of the swallows.

In addition to the experiments, in 1978 we conducted 20 h of observations within a blind at the two largest colonies after hatching to estimate predation rates. We observed colony DM, with 147 nests, for 490 min and colony EC, with 320 nests, for 795 min.

Statistical analyses.—We have used nonparametric statistics when the assumptions of normality or homogeneity of variances were obviously violated. To ascertain the relative importance of colony size and the other four factors in determining response time, a hierarchical analysis of covariance was performed. Because of the inherent lag time before response to any stimulus, we expected a skewed distribution toward short response times to the simulated attacks. Therefore, we transformed the dependent variable, response time, logarithmically. The log transformation removed heterogeneity among variances between colonies ($F_{6,12} = 4.94$, $P > 0.05$ for the log transformed data; $F_{6,12} = 19.68$, $P < 0.01$ for the untransformed data, F -max test, Sokal and Rohlf 1969).

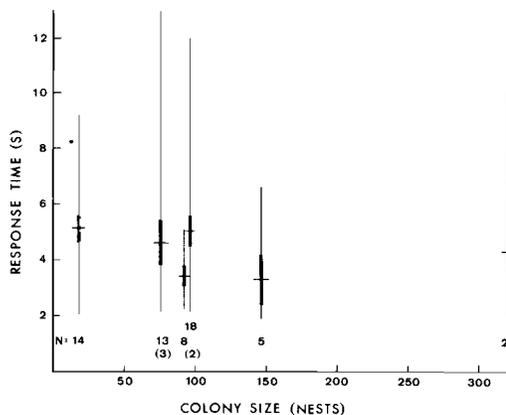


Fig. 3. Response time to the predator models as a function of colony size. The cross line shows the mean, the narrow line represents the range, and the wide line equals one standard error above and below the mean. N equals sample size, and the number of no responses at each colony is indicated in parentheses.

We used the regression method (Nie et al. 1975) and included only two-way interaction terms. The effects of colony size were evaluated independently, and then the factor or covariate that explained the greatest amount of the remaining variance was entered in subsequent steps. Interaction terms were evaluated after the main effects. All significance levels for this and other analyses are for two-tailed tests.

RESULTS

Predator detection.—Contrary to expectation, our results indicate that there is no trend between response time and colony size (Fig. 3). Furthermore, the analysis of covariance shows that colony size does not explain a significant portion of the variance when entered first (Table 2) or when entered after the other four main effects ($F_{1,86} = 0.52$, $P = 0.47$), nor do nest exposure, breeding stage, or wind velocity. Air temperature, however, explains a highly significant portion of the variance. Thus, if there is a correlation between swallow activity and temperature, this result implies that flying swallows are the first to detect an approaching predator. In support of this reasoning, we observed flying birds giving initial alarm calls on numerous occasions. These results indicate that for this range of colony sizes, large colonies detect predators no more quickly than do smaller colonies.

The swallows need not discriminate predator

TABLE 2. Summary of analysis of covariance for the determinants of response time.

Source	Squared multiple correlation coefficient (R^2)	df	F-ratio	P
Main effects	0.205	6	3.48	<0.005
Colony size	0.009	1	0.91	>0.25
Breeding stage	0.016	1	1.63	>0.10
Nest exposure	0.040	2	2.04	>0.10
Temperature	0.135	1	13.74	<0.001
Wind velocity	0.005	1	0.57	>0.50
Interactions	0.195	13	1.70	>0.05
Explained	0.400	19	2.39	<0.005
Residual	0.600	68		

from nonpredator models for us to measure detection time. If we are to extrapolate from our results to the natural situation, however, we must show that the Cliff Swallows recognize the predator models as potential predators. In addition, all trials must be statistically independent to justify an analysis of covariance. The following evidence supports these assumptions.

We believe that all trials, whether consecutive or not, can be treated as independent replicates for three reasons. First, we found no correlation (Spearman rank) between display intensity and the interval between consecutive trials ($r_s = 0.034$, $P > 0.05$, $n = 133$). We omitted cases in which there was no response from this correlation, because they corresponded to infinitely long response times. Second, the order of presentation did not significantly affect response time or display intensity (Table 3). Third, neither habituation nor sensitization occurred if the same model was towed repeatedly. We towed the kestrel on two series of consecutive trials (of 9 and 6 trials each) on 19 and 21 May at colony EC. The display intensities for all 15 trials were scored as four. The cumulative response times were not significantly different from a hypothetical cumulative distribution in which the response time was held constant ($P > 0.20$ for each sample, Kolmogorov-Smirnov one-sample test, Siegel 1956), even though the median response times were significantly different on the two days ($P < 0.02$, Mann-Whitney U -test).

The swallows did not discriminate (Mann-

TABLE 3. Effect of order of presentation on mobbing intensity and response time.

Model sequence	Mobbing			Response time		
	Intensity score ^a	<i>n</i>	<i>P</i> ^b	Time (s) ^a	<i>n</i>	<i>P</i> ^b
Predator after predator versus Predator after swallow or dove	3.5 ± 0.2 3.1 ± 0.2	42 43	0.152	4.35 ± 0.35 4.81 ± 0.36	40 41	0.301
Swallow after predator versus Swallow after swallow or dove	1.3 ± 0.4 1.4 ± 0.4	21 15	0.587	4.45 ± 0.69 4.56 ± 0.97	8 8	0.875
Dove after predator versus Dove after swallow or dove	2.0 ± 0.4 2.6 ± 0.4	20 13	0.277	4.65 ± 0.69 4.16 ± 0.46	14 11	0.935

^a Values are means ± SE.

^b Mann-Whitney *U*-test.

Whitney *U*-tests, Sokal and Rohlf 1969) between the two predator models or the two non-predator models in their mobbing responses. For the kestrel and shrike models $P = 0.35$ ($n = 64$ and 26), and for the dove and swallow models $P = 0.10$ ($n = 34$ and 37). They did, however, discriminate between predator (kestrel and shrike trials combined) and dove models ($P < 0.001$, $n = 90$ and 34) and predator and swallow models ($P < 0.001$, $n = 90$ and 37). The responses were directed only at the models, because we observed no response if the apparatus was operated without a model. Median responses for the models are listed in Table 3. Although the predator models elicited a significantly greater response than the non-predator models, the average response was noticeably less than that given to an actual predator (which, by definition, was always a five).

Our observations of the responses of Cliff Swallows to birds approaching the colony also suggested an ability to discriminate between predators and nonpredators. Like Bank Swallows (Hoogland and Sherman 1976), Cliff Swallows gave alarm calls when they encountered potential predators—Loggerhead Shrikes, American Kestrels, Roadrunners (*Geococcyx californianus*), Cooper's Hawks (*Accipiter cooperii*), Red-shouldered Hawks (*Buteo lineatus*), Red-tailed Hawks (*B. jamaicensis*), and Great Blue Herons (*Ardea herodias*). They ignored other birds of similar size and shape, however, that would or could not capture them—Swainson's Hawks (*B. swainsoni*), White-tailed Kites (*Elanus leucurus*), Forster's Terns (*Sterna forsteri*), Mourning Doves, Killdeer (*Charadrius vociferus*), and Starlings (*Sturnus vulgaris*).

Predator dilution.—As stated previously, the number of potential predators near a colony

should not increase linearly with colony size for the dilution effect to occur. Although there is a significant correlation between the estimated colony size in 1979 and the number of predators per census ($r_s = 0.597$, $P < 0.01$, $n = 27$, Spearman rank correlation), the relationship appears asymptotic, not linear (Fig. 4). That is, large colonies have proportionately fewer predators in their vicinity than do smaller colonies.

Even though the number of predators may not increase in proportion to colony size, the dilution effect could still be negated if each predator attacked more frequently. At the two colonies where we made observations, the mean attack rate per hour was very similar (0.70 at DM and 0.83 at EC). At colony DM we witnessed five predator attacks and at colony EC we observed 11 attacks. The daily rate at DM was not significantly different from the rate at EC ($P > 0.40$, $n = 7$ and 13 , Mann-Whitney *U*-test).

Breeding synchrony enhances the dilution of predation. If synchronized breeding were determined by other factors, however, such as the climate of a region, then dilution might be a result and not a cause of synchronous breeding. To determine the extent that regional effects have versus local colony effects, we compared within-colony synchrony to between-colony synchrony. Higher within- than between-colony synchrony implies that birds are synchronizing their breeding in response to some aspect of the local colony area. The two colonies for which we determined hatching dates, SM and SV, were asynchronous with respect to each other. That is, the colony means of the mean dates of hatching for each nest were significantly different ($P < 0.01$, $n = 54$

and 12). But both colonies had a high degree of within-colony synchrony. The standard deviation of the hatch dates was 5.15 for SV and 6.50 for SM, which is within the range (3–6.5) of synchrony estimates for Bank Swallows (Emlen and Demong 1975). Both Bank and Cliff swallows (Emlen 1952, 1954; Myres 1957; Emlen and Demong 1975; Hoogland and Sherman 1976) are considered to have high within-colony synchrony. We can conclude from these data that within-colony synchrony is greater than between-colony synchrony. Thus, Cliff Swallows may synchronize nesting to reduce predation via dilution. Alternative explanations for breeding synchrony and colony formation are discussed below.

DISCUSSION

Much of the work on predator detection by individuals in groups has been done with flocks of birds. Although colonies are different from flocks in that they are not mobile aggregations, individuals in both flocks and colonies are still faced with the problem of detecting predators. Several workers (Pulliam 1973, Treisman 1975, Caraco 1979a, Lazarus 1979) have argued from theoretical bases that the time required to spot an approaching predator should decrease with increasing flock size. This theoretical correlation has been supported in a number of laboratory and field studies of flocks of 50 or fewer birds (Lazarus 1972, Diamond and Lazarus 1974, Powell 1974, Siegfried and Underhill 1975, Kenward 1978) and contradicted in one (Lazarus 1979). Caraco (1979a), Hoogland (1981), and Lazarus (1979) suggest, however, that predator detection time should not continue to decrease with increases in group size. They predict that individuals will spend more time searching for food or interacting with other members of the group rather than continuing to scan for predators. Several studies (Lazarus 1972, Powell 1974, Abramson 1979, Caraco 1979b, Hoogland 1979, Bertram 1980) have documented a decrease in scanning rate and an increase in feeding rate per individual with increasing group sizes. Siegfried and Underhill (1975) and Hoogland and Sherman (1976) have found higher levels of aggression in larger groups. These data suggest that the time needed to detect an approaching predator may become asymptotic as group size increases and, therefore, that other hypotheses

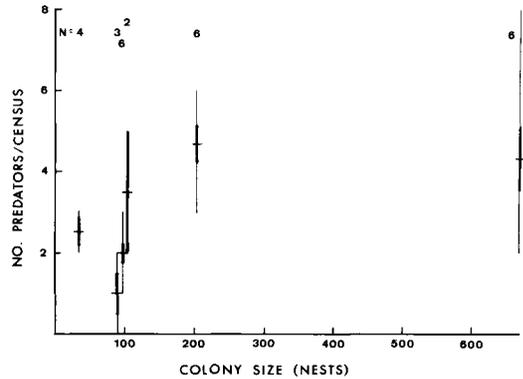


Fig. 4. Density of American Kestrels and Loggerhead Shrikes in a 1-km radius circle around each colony as a function of colony size. Range is given by a narrow line, one standard error by the wide line, and mean by the cross line. *N* equals the number of censuses at each colony.

are needed to explain group sizes that exceed that limit. Because we found no early detection effect, the Cliff Swallow colonies we studied may have exceeded this limit. Hoogland and Sherman (1976) showed that initiation of mobbing of a stuffed weasel placed in a Bank Swallow nest is more rapid for larger colonies of swallows. Their experiment was flawed, however, because they may have been measuring the time elapsed between a disturbance (caused by the experimenter placing the weasel in the burrow) and the first mobbing response by swallows that had subsequently returned to the nest site. This measure may or may not correlate with the time required to detect an approaching predator.

Although we have shown that large colonies do not detect predator models faster than do small colonies of Cliff Swallows, large colonies would still benefit if they detected predators at greater distances than did small colonies. If our apparatus had been set up within the zone of detection, that region in which predators are always detected by the smallest colony, then we would not have detected any distance effect if one existed. We observed that neither kestrels nor shrikes were mobbed, however, while perching in full view of colony EC, our largest colony, before attacking. Unfortunately, we could not estimate the detection distance for approaching predators. The zone of detection could be determined by varying the guide-line length at each colony.

Our results indicate that nesting Cliff Swallows discriminated between the predator and nonpredator models. Two aspects of their responses need discussion, however. First, the responses to the predator models were typically similar but less intense than the responses to actual predators. Part of this difference may be due to the blind at the end of the apparatus, which concealed the model after it had been towed. On those trials during which a predator model stopped half-way, the response was more intense and prolonged. It is not clear why the swallows apparently become neither habituated nor sensitized to the predator models nor why they will ignore a kestrel perched at 100 m but will mob an approaching or departing kestrel (pers. obs.). The swallows may be minimizing energy expenditure or maximizing feeding or nest-building time (see Withers 1977). If so, it is to be expected that the swallows will exhibit the response only when there is the genuine danger of an attacking kestrel rather than waste time or energy on a kestrel that may not be intending to attack.

Second, on some occasions the swallows did give alarm calls and the display to Cliff Swallow and Mourning Dove models. The responses to the swallow and dove models were not false alarms caused by some other stimulus, because the display was directed at the models. One explanation for the responses to the dove models is that the swallows gave the alarm before they had identified the approaching shape. The responses directed at the swallow model may be due to colony members recognizing the approaching model as a foreign swallow. On several occasions we observed colony members respond to approaching Cliff Swallows by attacking them and giving alarm calls. Eggs are commonly found beneath Cliff Swallow nests (Emlen 1954, this study), and Emlen (1954) suggested that this may result from foreign swallows rolling them out while attempting to usurp a nest.

The evidence in favor of the predator dilution hypothesis for other colonial nesting birds is inconclusive. For example, Nisbet (1975) showed that the number of tern chicks preyed upon was constant, although the number of susceptible chicks fluctuated during the nesting season. Because predation did not vary with prey availability, this supports a dilution effect. Some avian predators, though, adjust

their territory sizes to the density of their principal prey species (Maher 1970, Anderson 1976), which may reduce the dilution effect. Snapp (1976) reported that the fraction of both eggs and young lost to predators was constant for Barn Swallows (*Hirundo rustica*) in 47 colonies containing from 1 to 30 nests. Unfortunately, she did not report the losses on a per-nest basis. Furthermore, if predators are not territorial, colonies may suffer higher predation than solitary nesting birds (Burger 1974). Although our data are few, predator attack rate appears to be independent of colony size. In addition, the predator censuses indicate that predator densities increased at most five-fold, while swallow densities increased by a factor of 20. Since the American Kestrel and Loggerhead Shrike are territorial (Balgooyan 1976, Craig 1978, respectively), it is likely that dilution of these predators does occur. To test this idea more carefully, however, more extensive information is needed on predator encounter and attack rates.

From this study we cannot conclude that the dilution of predators is the only factor that currently favors Cliff Swallow coloniality, even though the data support this simple hypothesis. There are other alternative hypotheses that also explain how predation rates are decreased in group-living birds. Predation could be higher on peripheral nests, which would favor colonial nesting (Hamilton 1971); predators may be deterred by mobbing colony members (Hoogland and Sherman 1976); colonies may be cryptic and found less often by randomly searching predators than dispersed nests (Paloheimo 1971, Vine 1971, Treisman 1975); or the response displays of the swallows may confuse or distract attacking predators (Humphries and Driver 1967, Neill and Cullen 1974). In addition, group-living animals may benefit by increasing foraging efficiency, or groups may form as a result of a shortage of suitable breeding areas (Lack 1968, Alexander 1974). Whether or not any of these alternatives are plausible explanations for colony formation and maintenance must await further study. They could be tested by monitoring the dispersion of prey, manipulating prey dispersion and colony size, and following marked birds from the colony to the feeding areas. Only carefully designed field experiments will permit the exclusion of one or more of these hypotheses. The extensive

variation in Cliff Swallow colony size suggests that no single hypothesis will adequately explain group size in this species.

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