ECOLOGY OF CULVERT-NESTING OKLAHOMA BARN SWALLOWS (*HIRUNDO RUSTICA*)

By

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ECOLOGY OF CULVERT-NESTING

OKLAHOMA BARN SWALLOWS

(*HIRUNDO RUSTICA*)

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INTRODUCTION

This thesis is comprised of 2 manuscipts written in formats suitable for submission to selected scientific journals. Each manuscript is complete without supporting materials. The manuscipt, "Site Tenacity in Culvert-Nesting Oklahoma Barn Swallows (*Hirundo rustica*)" (Chapter II), was written in the format of the JOURNAL OF FIELD ORNITHOLOGY. Chapter III, "Breeding Ecology in Culvert-Nesting Oklahoma Barn Swallows (*Hirundo rustica*)", was written for submission to the WILSON BULLETIN and is the principal paper of this thesis.

CHAPTER II

SITE TENACITY IN CULVERT-NESTING OKLAHOMA BARN SWALLOWS (*HIRUNDO RUSTICA*)

BY SARAH STILES IVERSON

Site tenacity, the return to a former nesting location and geographical locality, has been demonstated in many swallows (Boyd and Thomson 1937, Allen and Nice 1952, Mason 1953, Chapman 1955, Davis 1965, Samuel 1971b, Stamm and Stamm 1975, and Freer 1979). Chapman (1955) reported that 40% of breeding adult Tree Swallows returned the following year. Of 79 breeding adult Purple Martins banded, 77 were recovered in later years at the colony where originally banded (Allen and Nice 1952). Twenty-eight of 183 Purple Martins banded as nestlings were recovered within one mile of the banding locality during subsequent years. Freer (1979) showed an overall return rate of 13% for Bank Swallows banded as adults and 8.1% for the young.

In Barn Swallows, Boyd and Thomson (1937) concluded that in England, yearlings seldom returned to the exact nesting location where hatched, recovering 0.79% nestlings and 9.5% adults of 13,105 total birds banded. Many were recovered in the same sheds as banded but no data were given. Davis (1965) reported 144 adult Barn Swallows recovered at or near the banding locality and 226 nestlings within five miles of birthplace of 73,000 birds banded in England and Ireland, based on B.T.O. files between 1909 and 1963.

In West Virginia, seven Barn Swallows banded as adults returned the following year to the same barn and two yearlings returned the next year to a nearby barn (Samuel 1971b). In 30 barns in Massachusetts, Mason (1953) recovered 654 Barn Swallows of 2469 birds banded in a thirteen year period, an overall return rate of 34% for adults and 2% for nestlings. Stamm and Stamm (1975) recovered 1.24% nestlings and 29.7% adults of 475 Barn Swallows banded in Kentucky during an eight year period.

In North America, Barn Swallows primitively nested in rocky caves, crevices, and rock walls (Bent 1942) and later adapted to new nesting sites in man-made structures such as barns and bridges (Parnell et al. 1963, Goertz 1970, Jackson and Burchfield 1975, Erskine 1979). Within the last decade, Barn Swallows have expanded their nesting activities to highway culverts (Martin 1974, Wall 1982). Site tenacity modifies the habitat selection mechanism leading to the occupation of new kinds of environment (Hilden 1965). The purpose of this study was to determine how intensely Barn Swallows demonstrate fidelity to subterranean cement structures.

MATERIALS AND METHODS

The study area was located in Payne County, Oklahoma, along state highway 51, between Stillwater and the intersection with interstate highway 35. The study area was characterized by deciduous forest-grassland ecotone (Odum 1971) and rangeland is the dominant land use (United States Department of Agriculture land use maps of Payne Co.). Twenty-three rectangular cement culverts ranging in size from 0.9 m (height) X 0.9 m (width) X 55.5 m (length) to 2.1 m X 1.5 m X 108.5 m were located within a 25.7 km transect.

Culverts were visited weekly at night between May and August, 1980 and 1981, and once (June 12) in 1982. Headlamps covered with red cellophane provided sufficient illumination and rarely disturbed the birds. Swallows are less sensitive to red light than white, a phenomenon also observed in hawks (Lish, pers. comm.). Adult birds were removed from nests and nest stage (eggs, young, or no contents) and nest location identified. Sex was determined by the presence or absence of a brood patch and tail length (Samuel 1971a). Nestlings were banded in 1980 only. They were banded between post-hatching days seven and twelve (Samuel 1969) during daytime nest data collection. All birds were banded using U.S. Fish and Wildlife Service bands according to regulations (U.S. Fish and Wildlife Service 1976).

On some occasions, a cloth was used to cover one end of the culvert to hold birds that flushed until their identity could be determined. Use of a cloth was preferred to a mist net because birds did not become entangled for long periods of time nor did birds become net shy as described by Stamm and Stamm (1975).

Birds caught during the same breeding season were classified as recaptures while swallows captured in subsequent breeding seasons were classified as returns. Statistical analyses included comparisons of proportional returns of nestlings, adults, and sexes and comparison of the sex ratio at different nest stages (Snedecor and Cochran 1980).

RESULTS

The total number of Barn Swallows banded in 1980 was 159 adults and 592 nestlings in 15 culverts. In 1981, 81 adults were banded in 11 of the 15 (1980) culverts. Fifteen nestlings and one adult were found dead during the 1980 season and numbers were adjusted accordingly for calculations (Table 1).

The overall return rate to the study area for adults for both years was 15.35%. No significant difference in return rate was found between 1981 (19.6%) and 1982 (11.1%) ($Z = -1.7$, $P > 0.10$). Adult (19.6%) and nestling returns (0.52%) differed significantly ($Z = -10.12$, $P < 0.01$), whereas the rate of female (22.9%) versus male (12.2%) returns did not differ significantly ($Z = -1.09$, $P < 0.28$). In addition, one female banded in 1980 returned in 1982 and not in 1981. The age (adult or nestling) of returning individuals significantly affected their return rate to the same or different culverts ($X2 = 12.67$, $N = 34$, $P < 0.005$, $df = 1$) (Table 2). Nestlings returned to culverts other than their natal culverts. Adults in this analysis returned to the same and different culverts in expected frequencies based on sample size. In addition, one 1980 nestling returned in 1982 to a different culvert than where it was banded.

No significant difference ($P > 0.25$) was found between the sexes for returns to culverts in 1981 ($X^2 = 1.195$, N = 31, df = 1) or 1982 ($X^2 = 0.62$, N = 9, df = 1) (Table 2). However, no adult males returned to different culverts either year. Those adult females that returned to different culverts moved an average distance of 1.6 km, all moving to the nearest active culvert with at least ten breeding pairs (Iverson, in preparation). Three adults (two females and one male) nested in the same culvert for three consecutive years. Percent returns of adult Barn Swallows to the culverts where banded tended to decrease with increasing distance from I-35 (Fig. 1). In simple linear regression (using all culverts with banded birds whether they returned or not) as distance from I-35 increased, the proportion of returning adults decreased in 1981 ($r = -0.83$, $P < 0.01$) and 1982 ($r = -0.77$, $P < 0.01$).

Female adults identified to nest site during consecutive years tended to change nest sites more than males (Table 3). Individuals that did change sites tended to stay within the same half of the culvert. Two males and nine females returned to nests within the culvert half where banded and one female returned to nest in a different culvert half. Birds moved a mean distance of 12.1 m from the original nest site.

Males and females captured at different nest stages differed significantly (X^2 = 16.39, P < 0.0005, N = 225, df = 2) (Table 4). More males and fewer females than expected were observed on empty nests. Of the 28 males caught on active nests, six were with second clutches and only two of these had previously fledged nestlings. One female banded in 1980 on an inactive nest was recaptured the following year on an adjacent inactive nest and again in 1982 in the same culvert.

Approximately 90 banded adults recaptured within the same nesting season yielded the following information about bird movements. Three females initially caught on nests with no contents were later recaptured on active nests at different locations, two in the same culverts and one in a different culvert. Three females were captured four times during the same breeding season. One female was captured twice in 1980, three times in 1981, and once in 1982. Of 16 birds (all females) recaptured during subsequent clutch attempts, 13 (81.3%) were at the same nest sites. Of the three (18.7%) females recaptured on different sites during successive clutches, two had previously fledged young from the first clutch. One nest was occupied by House Sparrows within a week of Barn Swallows fledging. The female swallow was recaptured on a nest 5.0 m from the site of the first clutch. The other successful female was recaptured on a nest 1.6 m from the original fledging site which was not occupied later. The unsuccessful female whose first-clutch eggs did not hatch, was recaptured on a new nest built 0.8 m from the previous site. Near the end of the breeding season several birds, including first-clutch young, were found roosting on nests.

DISCUSSION

Nestling returns to the study area. Other studies have shown that yearling Barn Swallows have low return rates to their natal area (Boyd and Thomson 1937, Mason 1953, Davis 1965, Stamm and Stamm 1975, and Barrentine 1978). The first-year return rate (0.52%) in this study was even lower than these studies. One contributing factor may be the short duration (2 years) of this banding project compared with the above studies (8 - 54 years). In these longer banding projects, additional birds banded as nestlings were recovered during nonconsecutive years, a phenomenon which was also observed in one instance during this study. Also, one first-year bird was recovered 3.2 km outside the study area indicating that first-year breeders may disperse, as suggested by Davis' (1965) recoveries up to 225 miles from their birthplace. Barrentine (1978) and Moller (1982) found that older Barn Swallows arrive on the breeding grounds first and establish themselves on the "best" nests. Hilden (1965) attributed the dispersal of first-year birds to their inability to displace older birds in the more suitable nesting habitat.

Adult returns to the study area. The overall return rate for adults in this study (15.35%) was considerably lower than other North American Barn Swallow studies with 34% (Mason 1953) and 29.7% (Stamm and Stamm 1975) return rates. Both of these studies were conducted at buildings. Barn Swallows have nested in buildings over many generations and perhaps are more adapted to this nesting habitat than their relatively recent occupancy of cement highway culverts. The return rates to culverts for the population may be lower as Barn Swallows adapt to new nesting habitat. As Cliff Swallows occupy culverts as well (Martin 1974), their return rate could be compared with that of Barn Swallows, revealing differences in the adaptability of these two species.

Although not statistically different, the return rate for 1982 was lower, probably due to only one night of trapping effort. Of particular interest were the additional adult birds banded (81) in 1981. If Barn Swallow colonies are passive aggregations and do not recruit additional pairs (Snapp 1976), then perhaps the new birds were first-year birds dispersing from distant colonies or adults moving from other nesting locations. It seems unlikely that so many birds could have survived and remained unbanded during the 1980 breeding season.

Limited knowledge of the navigational mechanisms used by swallows during their annual migration from South America make speculation difficult about their homing ability to culverts used the previous summer. Although Barn Swallows have shown homing ability from 96 km (Nastase 1982) and orient to nest site even with nests removed (Grzybowski 1981), these responses may be due to their parental investment and nesting behaviors during the reproductive process rather than clues to long-range migration.

Mortality. Annual mortality for adults has been estimated at 73% (Mason 1953), 60-72% (Medway 1973), and 63% (Lack 1954). Using a conservative 60% estimate, my overall return rate for adults would be 41% and 1.7% for nestlings. Juvenile mortality would likely exceed that of adults. Freer (1979) estimated postfledgling mortality in Bank Swallows at 80%.

Returns to culvert, entrance, nest site. Although no significant differences in return rate due to sex were found, no males changed culverts, indicating site tenacity. All nestlings that returned to the study area were males and all returned to culverts different from their natal culverts. This observation is similar to one made in barns (Mason 1953). Males may select nest sites and have a greater affinity to them. Other studies have shown several pairs mated for two (Boyd and Thomson 1937) and three years (Mason 1953). Future studies could relate mating-pair duration and selection of nest sites.

An overall tendency for birds to return to culverts nearest interstate highway 35 and, conversely, further from the town of Stillwater, may indicate Barn Swallow ability to locate culverts near large highway systems more easily. As other birds navigate using rivers and coastlines which serve as guiding lines from the air (Welty 1962), the adaptability of Barn Swallows may enable them to navigate using highways. However, the larger colonies found nearer I-35 (Iverson, in preparation) may somehow enhance the return rate of adults.

Barn Swallows showed a stronger fidelity to culvert halves than to nest sites. Only one bird of 12 that changed sites moved to a different half of the culvert. They likely entered via the same culvert entrance as the previous year. Prior reproductive success (Freer 1979) did not seem to be the reason birds returned to the same nest site. Of the two birds which returned to their previous nest site, neither was successful in two attempts each during the 1980 breeding season. This does not exclude the possibility of nesting success in previous years.

Nesting stage. Mated pairs were more easily captured on first clutches because the male perches beside the incubating female at night as reported by Samuel (1971b) and Smith (1933). Males were often not present at subsequent clutches after fledging young previously, perhaps because they were tending young elsewhere (Smith 1937). Males probably select and defend nest sites since a higher proportion of males (33%) than females (9%) were captured on nests with no contents. It might be helpful in future banding projects if banding were done when most nests are being incubated, especially first clutches, because of the increased likelihood of capturing both adults on the nest. Birds show a greater attachment to the nest during incubation, compared with periods of defense at an empty nest or egg-laying.

Banding effects. The banding activities in this study did not appear to significantly reduce reproductive success by causing desertion as discussed by Burtt and Tuttle (1983) in Tree Swallows. The proportion of abandoned nests would have been comparably high both years, if banding activities were a significant factor causing nest abandonment. However, the proportion of abandoned nests in 1981 (3.4%) was nearly half the rate observed in 1980 (6.7%) with comparable disturbance levels (Iverson, in preparation). Several other factors may lead to desertion including death, competition, and severe environmental conditions.

SUMMARY

The overall return rate the following breeding season for banded Barn Swallows was higher for adults than nestlings. Birds returned most frequently to culvert, to culvert half, and, finally, to nest site. Adults tended to return to culverts nearest interstate highway 35 suggesting a migratory guideline. Males tended to be captured more frequently on empty nests while females were caught on nests containing young or eggs.

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Table 1. Barn Swallows banded (1980 and 1981) and returned (1981 and 1982) to the study area by age and sex.

	Number banded		Returns in 1981		Returns in 1982 banded in		Percent returns in 1982
	1980	1981	No.	Percent	1980	1981	(banded in 1981)
Nestlings	577	0	3	0.52	1	---	---
Adult males	49	26	6	12.2	1	3	11.5
Adult females	109	55	25	22.9	3	6	10.9
Total adults	158	81	31	19.6	4	9	11.1
Total for all classes	735	81	34	4.6	5	9	11.1

Table 2. Barn Swallows banded (1980), returned (1981), and banded (1981), returned (1982) to culverts by age and sex.

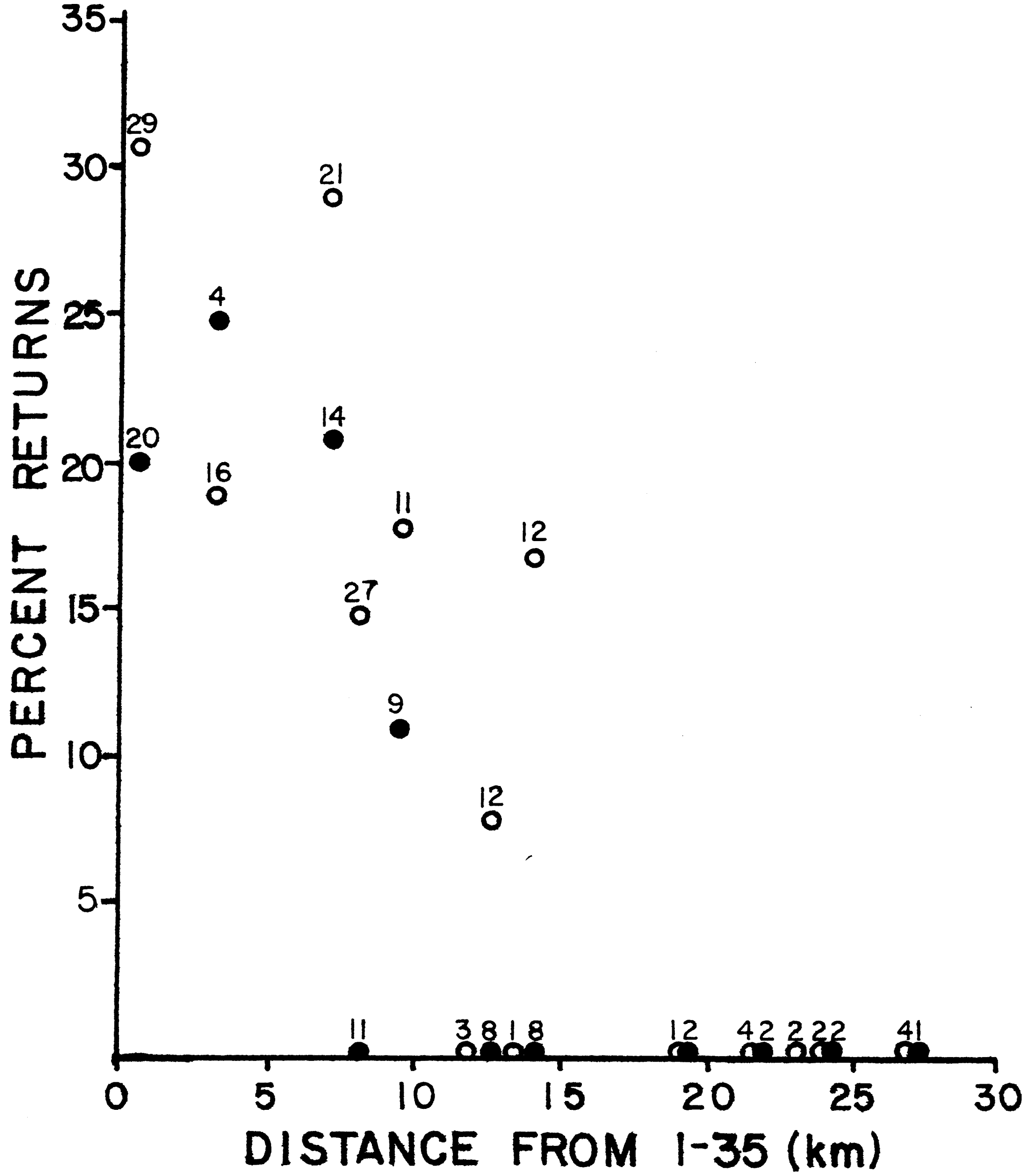
	1981 Returns		1982 Returns	
	To same culverts as banded	To different culverts than banded	To same culverts as banded	To different culverts than banded
Nestlings	0	3	---	---
Adult males	6	0	3	0
Adult females	21	4	5	1

Table 3. Barn Swallow adults banded (1980 and 1981) and returns (1981 and 1982) to nest site by sex.

	Same nest site as banded	Different nest site than banded
Adult males	1	2
Adult females	1	10

Table 4. Barn Swallows, in 1980 and 1981, identified to nest site and nest stage by sex.

	Nest stage			Total
	Eggs	Young	No contents	
Females	125	41	17	183
Males	24	4	14	42
Total	149	44	31	225


PERCENT RETURNS
35
30
25
20
15
10
5
29
21
4
14
20
16
11
12
27
9
12
11
3
8
1
8
12
4
2
2
2
2
4
1
0
5
10
15
20
25
30
DISTANCE FROM I-35 (km)

CHAPTER III

BREEDING ECOLOGY OF CULVERT-NESTING OKLAHOMA BARN SWALLOWS (*HIRUNDO RUSTICA*)

SARAH STILES IVERSON

Several bird species have successfully adapted to nesting in man-made habitats (Welty 1962 and Hilden 1965). In North America, Barn Swallows primitively nested in rocky caves, crevices, and rock walls (Bent 1942) and later adapted to new nesting sites in man-made structures such as barns and bridges (Parnell et al. 1963, Goertz 1970, Jackson and Burchfield 1975, and Erskine 1979). Within the last decade, Barn Swallows have expanded their nesting activities to highway culverts (Martin 1974 and Wall 1982). Limited knowledge exists of their nesting ecology and success in this recently-adopted habitat.

Numerous studies have investigated the breeding biology of Barn Swallows nesting in barns (Bent 1942, Mason 1953, Adams 1957, Parnell et at. 1963, Samuel 1971, Snapp 1976, McGinn and Clark 1978, Goodman 1982, and Moller 1982) and beneath highway bridges (Jackson and Burchfield 1975 and Barrentine 1978). Reproductive success (number of young fledged / number of eggs laid) ranged from 85.1% in barns (Goodman 1982) to 62.6% below bridges (Barrentine 1978). One objective of this study was to determine the reproductive success and factors influencing Barn Swallow productivity within culverts.

Barn Swallow nest-site selection in barns involved several environmental requisites; an open foraging area, a vertical substrate with an overhang for nest attachment, an adequate supply of mud, and any entrance to their breeding area, large or small (Samuel 1971). Additionally, nest-site availability and spacing of at least 3 m between active nests influenced nest-site selection (Snapp 1976). Jackson and Burchfield (1975) concluded that Barn Swallows nesting beneath bridges preferred to nest under structures open to the north and south (providing protection against prevailing winds and inclement weather) which were near water and utility wires (for perching). Inter-specific competition with sparrows and phoebes for old nests may also affect selection (Bent 1942 and Weeks 1977). Selection variables have not been investigated for culvert-nesting Barn Swallows nor compared with their other nesting habitats. A second objective of this study was to identify environmental variables, both intra- and inter-culvert, that influenced nest-site selection and reproductive success of culvert-nesting Barn Swallows.

MATERIALS AND METHODS

The study area was located in north central Oklahoma in Payne County along state highway 51, between Stillwater and the intersection with interstate highway 35 (Fig. 1). The study area was characterized by deciduous forest-grassland ecotone (Odum 1971) and rangeland is the dominant land use (United States Department of Agriculture land use maps of Payne Co.). Twenty-three rectangular cement culverts ranging in size from 0.9 - 3.0 m (height), 0.9 - 3.7 m (width), to 55.5 - 108.5 m (length) were located within a 25.7 km transect along state highway 51. Two additional culverts on the west side of Stillwater were located 0.8 km north of highway 51.

All culverts were checked approximately every five days from May through September, 1980 and 1981 for active nests (with contents), nest stage (number of eggs or young), and nest outcome (failures or number of young fledged). Climatological data during the breeding seasons were obtained from the Oklahoma State University Agricultural Experiment Station. Presence and nest success of Eastern Phoebes and House Sparrows in swallow nests were also recorded. Nesting success of Barn Swallows was calculated for each nest, pair, and culvert. Statistical analyses of basic nesting data included a chi-square goodness of fit comparison of productivity within all culverts, a simple correlation of productivity in culverts across both years, Student's t-test comparison of the overall mean number of young fledged per clutch each year, and a one-way-analysis of variance of mean number of young fledged and eggs produced from successive clutches (Snedecor and Cochran 1980).

Conditions of existing nests were determined before the 1980 breeding season only. Depending on the amount of nest remaining on the culvert wall, nests were catagorized as good (a complete nest), fair (half to almost complete), poor (less than half), or an old site (only outline of nest remained) and their occupancy frequencies compared using a Chi-square analysis. Each nest occupied during the breeding seasons originated as either a refurbished, a new (on new nest site), or a new nest built on an old site. Means of number of young fledged and number of eggs produced from refurbished, new, and new nests on old sites were analyzed using one-way analysis of variance (Snedecor and Cochran 1980). Distances between nest sites and the culvert entrances were determined using a meter tape. The number of nest attempts, nest failures, and young fledged were compared to distance into the culverts by simple linear regression (Snedecor and Cochran 1980).

Culverts with a minimum of 15 nest sites started by June 7, 1980, were compared for synchronous initiation date (laying of first egg). Dates from observations of nests were extrapolated back to first-egg-laying dates and converted to Julian dates. Mean initiation dates per culvert were analyzed using one-way analysis of variance and compared using least significant difference.

Physical characteristics of culverts including height, width, length, number of shared walls, directional orientation, number of wires available for perching (utility lines and fences), and distance from the city of Stillwater, or inversely, distance from I-35 were recorded. Additional, dynamic intra-culvert variables were measured each week during 1981 at each culvert entrance and their mean values calculated. These included water depth, temperature, wind speed and direction, light intensity (using a DeJur Dual Professional Light Meter), and humidity (using a Bacharach Sling Psychrometer). Light intensity readings were also indicative of the amount of vegetation blocking culvert entrances. Water depth at each nest site was measured and mean number of young fledged and eggs produced over various amounts of water were analyzed using one-way analysis of variance (Snedecor and Cochran 1980).

Land use data within one square mile (2.59 km^2) centered over each culvert were obtained from aerial photographs available from the USDA Agriculture Stabilization and Conservation County Committee. One square mile of land area was selected because Barn Swallows foraged within one-half mile of nests (Samuel 1971). For each culvert, the number of acres of cropland, woods, pasture, and water were quantified using a planimeter. Crop type was determined from ground observation.

Ten habitat variables (including physical characteristics of the culverts, intra-culvert variables, and land use data) were not found to be significantly intercorrelated ($P > 0.01$) using Pearson product-moment correlations. Five variables which did intercorrelate (P <

0.01) were not included in further analysis. Independent variables were analyzed against the dependent variable, number of nest sites used per culvert (indicative of colony size), using stepwise multiple regression, and minimum R square improvement via SAS computer language (Barr et al. 1979).

RESULTS

A total of 384 nest sites were utilized by Barn Swallows during this study, 229 in 1980 and 155 in 1981. Active nests were located in 22 culverts in 1980 and 21 in 1981. The mean number of nest sites used per culvert was 8.3, ranging from one to 45. The number of nest sites in a culvert which were occupied both years increased with distance towards I-35 (7, 15, 18, and 24 nest sites).

Initiation dates. The majority of nests (63.9%) were started the month of May and the first two weeks of June for both years (Table 1). In culverts with a minimum of 15 active nests initiated by June 7, 1980, a significant difference was found in mean date of nest initiation among culverts ($F = 7.28$, 2 and 72 df, $P < 0.01$) (Fig. 2). The mean dates of initiation were May 12, May 22, and May 18 for Culverts A, B, and C, respectively. Culvert A, nearest I-35 (Fig. 1), was significantly earlier than B ($LSD = 6.59$, $P < 0.01$) and C ($LSD = 4.96$, $P < 0.05$).

Nest origins. Rather than construct new nests, Barn Swallows tended to refurbish old structures. There were 324 nest sites used in 1980; 257 (79.3%) refurbished, 49 (15.1) new nests, and 18 (5.6%) new nests built on old sites. Of the new nests built, 48.7% were constructed during the first two weeks of June near the time of heavy rainfall. Refurbished nest occupancy of available nests from the previous year was significantly (X^2 = 45.1, N = 367, P < 0.0005, df = 3) affected by the quality of the nest (amount of nest from the previous year remaining on the culvert wall and available only for 1980). Nests classified as "good" were occupied more than expected based on sample size. In 1981, 172 (84.3%) were refurbished, 20 (9.8%) new nests built, and 12 (5.8%) built on an old site. No significant difference was found in number of young fledged or number of eggs produced either year on a refurbished, new, or new nest built on an old site.

Reproductive success. Although 18% more nests were initiated in 1980 than in 1981, the total number of young fledged between years differed by only 23 birds (Table 2). The mean number of eggs laid per clutch both years was 4.18, and the most young fledged per nest (3.2 young) were from clutches of six eggs. A significant difference in the mean number of young fledged per clutch, 1.83 (44.3% of eggs laid) in 1980 and 2.78 (66.5%) of eggs laid in 1981, was observed between years (t = -5.31, 525 df, P < 0.0001). The mean number of young fledged per successful clutch for both years was 3.58 (Table 3).

The greatest cause of nest failure was attributed to the fall of nests from the culvert wall (Table 4). Of the 12 nest failures containing entire clutches of dead young, one failure occurred on June 2, another on July 1, and the remainder after July 25. Partial clutch mortality was also observed; in 11 nests, single young were found dead after their siblings had fledged. The low rate of young fledging (44.3%) in 1980, was attributed to unusually heavy rainfall, (5.93 inches above the 1893-1975 average) during the months of May and June, 1980, which caused 55 nests to fall due to condensation or flooding within culverts. Following the heavy rainfall dates, two culverts were abandoned for data collection because of excessive flooding. Their nesting data are included in some statistical analyses of number fledged and number of eggs produced in comparing clutch attempts, sequential clutches, refurbished versus new nests, and amount of water in culverts.

In 1980, 25.8% (59/229) of the assumed population raised second broods compared with 31% (48/155) in 1981. In 1980, 4.4% (10/229) of the assumed population attempted third broods compared with only 0.6% (1/155) in 1981. The mean numbers of eggs produced in 1980 for clutches 1, 2, and 3 were 4.19, 3.92, and 3.72. Subsequent mean egg numbers in 1981 for clutches 1, 2, and 3 were 4.22, 4.04, and 4.00. No significant difference was found between successive clutches and number of eggs produced or number of young fledged (one-way analysis of variance).

<u>Nest distance</u>. The number of active nests less than 3

m apart was 171, representing 54% of the total nests used in culverts where less than 3 m spacing was observed (culverts = 12 in 1980, culverts = 7 in 1981). Sixty-four of the nests were on the same culvert walls, and 107 were on the opposite walls. Through the breeding season, the number of active nests less than 3 m apart declined: 66 (May), 58 (June), and 46 (July). However, the proportion of active nests less than 3 m apart increased during the breeding months: 30% (May), 34% (June), and 50% (July).

Barn Swallows preferred to select nest sites near the culvert entrance. The number of nest attempts (and failures) decreased with distance into the culvert ($r = -0.98$ and -0.98, respectively, $P < 0.01$) (Fig. 3). Although the total number of young fledged also decreased with distance into the culvert ($r = -0.98$, $P < 0.01$), the mean number of young fledged per clutch was not higher nearer the culvert entrance (Table 5). During 1980, all nests which were rebuilt on an old site after the previous nest had fallen due to moisture, were within the first 15 m of the culvert.

Other species present in Barn Swallow nests. House Sparrows occupied 25 nests in 1980 and 21 in 1981 at an average distance of 6.3 m from the culvert entrance. Eastern Phoebes occupied 11 nests in 1980 and eight in 1981 at an average distance of 2.1 m from the entrance. Several deer mice (*Peromyscus maniculatus*) nested in empty Barn Swallow nests.

Culvert productivity and habitat variables. Productivity was not equal in all culverts either year. The number of eggs produced in 1980 ($X^2 = 1930.9$, $N = 1227$, $df = 22$) and in 1981 ($X^2 = 1208.4$, $N = 852$, $df = 22$) varied significantly ($P < 0.0001$). Also, the number of young fledged in 1980 ($X^2 = 897.2$, $N = 544$, $df = 22$) and in 1981 ($X^2 = 856.2$, $N = 567$, $df = 22$) varied significantly ($P < 0.0001$). Productivity for individual culverts was comparable between years; culverts producing many young ($r = 0.95$, $N = 23$, $P < 0.01$) and eggs ($r = 0.98$, $N = 23$, $P < 0.01$) in certain culverts in 1980, did so in 1981, while culverts producing low numbers of eggs and young in 1980, also yielded low numbers in 1981 (Fig. 4).

Several physical culvert characteristics and environmental variables were found to correlate with the colony size of Barn Swallows (Table 6). The most significant variable measured was the amount of water within a culvert. This variable explained over 57% of the variation of colony size between culverts. In general, the more water present in a culvert, the larger the colony size. Three additional variables were found to influence colony size: the distance of a culvert from the town of Stillwater, height of the culvert, and amount of woods surrounding the culvert. As height of the culvert and distance from Stillwater increased, so did colony size. As the acreage of woods declined around a culvert, the colony size increased. Collectively, these four variables explained 87% of the variation in colony size between culverts ($P < 0.0001$, $df = 22$) in a stepwise regression procedure.

Variables explaining the least variation (lowest R^2) in colony size between culverts were temperature (0.4%), amount of water acreage around the culvert (1.0%), and light intensity (3.0%) using minimum R-square improvement. The amount of water in culverts did not have a significant effect on the mean number of young fledged or eggs produced.

DISCUSSION

Nesting success. Reproductive success of Barn Swallows in this study was somewhat less than that reported in other studies of swallows nesting in barns and below bridges. The mean clutch size was within the range reported in other studies and nearest the 4.2 found in 200 nests in Louisiana culverts (Wall 1982). The percent fledged in 1981 resembled culvert-nesters (63%; Wall 1982) and bridge-nesters (63%; Barrentine 1978). In comparison with other open-nesting passerines, Barn Swallows during a normal breeding year, such as 1981, fledged a higher percent of eggs laid than was typical according to a review of past studies (Nice 1957).

Barns and buildings probably provide a more sheltered environment free of flood water and condensation. However, nesting space is limited, especially with the replacement of wooden buildings by metal ones. As Barn Swallows adapt to man-made structures, with less limited nest space (especially culverts), they may have an increased likelihood of securing nest space and perhaps fledging more young.

Overall, my presence did not increase natural predation by leading predators to the nests (Bart 1977). This was probably due to the inaccessability of Barn Swallow nests. Only four nests were known or suspected as losses to predators. Indirect evidence of predators in this study included two nests knocked down in a short culvert (0.9 m) and racoon (*Procyon lotor*) tracks seen on the culvert wall. Black rat snakes (*Elaphe obsoleta*) were seen twice on the culvert walls and once on the culvert floor. Following one sighting, the next culvert visit revealed two nests whose entire clutches of eggs had disappeared. On several occasions Barn Swallow eggs were seen below the nest or with peck holes within the nest. Several nests contained old eggs covered with new lining. Two nests contained multiple clutches, one with nine eggs and the other with eight. Egg covering and multiple clutches probably occurred in abandoned nests, most likely attributable to death of the adults. Four young in one nest were found dead due to ectoparasites of the Order Mallophaga.

Nests and nest sites. Different localities and, likewise, different soil types may partially explain the greater use of refurbished nests (82%) in Oklahoma compared to Louisiana (47%; Wall 1982) and Massachusetts (57%; Samuel 1971). The clay content of soils increases the strength of Cliff Swallow nests (Welty 1962) and the cohesion of Barn Swallow nests (Kilgore and Knudsen 1977). In the present study area, the soil consists of a high percent of clay and a low percent of sand particles (Aandahl 1982) which may result in more intact nests remaining from year to year. The greater utilization of refurbished nests in this study than in past studies was probably due to this higher nest availability. Future research could include the comparison of soil types used in nests at different locales.

Although no differences were found in the number of young fledged from refurbished, new, or new nests rebuilt, one behaviorial explanation for the high utilization of refurbished nests might be that less time and energy is required in nest construction, enabling a nesting pair to initiate nesting earlier and fledge young before the food supply diminished. On August 15, 1980, the probable cause of death for three entire clutches of nestlings from a total of six active nests was food shortage. Limited food supply may also be a factor in the low percent of second clutches attempted. In comparison with the incidence of second broods in other studies (50%; Bent 1942, Moller 1982, and Wall 1982) (65%; Snapp 1976) (35%; Samuel 1971), the occurrence of second broods (28%) in this study was the lowest ever reported. Past studies assumed that the same birds attempt second clutches at the same nest. However, 19% of the banded Barn Swallows were found to change nest sites within culverts for second broods (Iverson, in preparation).

Barn Swallows showed affinity within the same breeding season to previously used nest sites, especially within 15 m of the culvert entrance. They tended to rebuild on the same sites if the original nests were destroyed. Grzybowski (1981) observed females locating nest sites after the nests had been removed. However, the tenacity to nest site does not exist strongly from year to year (Iverson, in preparation).

Barn Swallows preferred to nest within the first 15 m of the culvert entrance yet nesting in this area did not increase the probability of successfully fledging more young. A possible explanation is less expenditure of energy in foraging for the young, i.e. less distance involved in flying in and out of the culvert. Also, birds could escape more rapidly from culverts in case of predators. Mason (1953) showed that Barn Swallows selected nest sites in barns with more light. In the present study, however, light intensity was found to be an unimportant factor influencing colony size. Light intensity was also indicative of the amount of vegetation blocking a culvert entrance. Therefore, birds utilizing culverts were not influenced by the size of the culvert entrance, similar to Samuel's (1971) findings in barns.

Environmental variables. This study has demonstrated that Barn Swallow colonies were larger in taller culverts with more water inside, which were further from town, and with less wooded area within a square-mile of the culvert. Nesting pairs using culverts further from town tended to refurbish the same nests both years, and were more likely to return to the same culverts the following years (Iverson, in preparation). The acreage of wooded habitat declined farther west, providing more open habitat for foraging. The preference for taller culverts may be partially attributed to the unlikelihood of flooding and also as a deterrent against predators such as racoons. Water within the culvert may increase predator detection. Barn Swallows in culverts with more water appeared to flush sooner, especially during nighttime banding activities (Iverson, pers. obser.).

Coloniality. Snapp (1976) described Barn Swallows nesting in buildings as aggregations lacking synchronous within-colony breeding and with distances between active nests no less than 3 m. However, in another Oklahoma study of culverts, 60% of the Barn Swallow nests were less than 3 m apart with a mean distance of 2.79 m (Grzybowski 1981). The present study indicated crowding of active nests (79%) within 15 m of the culvert entrance, suggesting less intense territorial spacing. Differences in nesting habitats may account for more Barn Swallows crowding within culverts than those nesting in other structures. A greater variation in nest initiation dates between culverts than within culverts among those culverts with at least 15 active nests further suggests synchronous nesting. The largest colony (located nearest I-35) had the earliest nesting date which was significantly different from the other two large colonies. Synchronous nesting may perhaps be related to colony size. Possible mechanisms explaining 'how' birds synchronize their breeding activities have not been investigated.

Physiologically "holding back" to initiate nesting at the same time as neighbors seems unlikely. An ethological explanation, such as arrival time on the breeding grounds, seems the most likely. If Barn Swallows were to migrate using I-35 as a guiding line (Iverson, in preparation), then first-arrivals, generally older birds which select choice sites (Barrentine 1978, Moller 1982, and Turner 1982), would initiate nesting earlier while late-arrivals would disperse to other culverts.

In Bank Swallows, synchronous breeding was suggested as a response to a limited resource (food, nesting habitat) or predators (Hoogland and Sherman 1976). In this study, nesting space did not appear to be limiting, nor were predators a major factor. The availability of open foraging area may be the limiting factor in nesting habitat. Food is the most likely limiting factor in culvert-nesting Barn Swallows. Bank Swallows begin incubation before the last egg is laid, resulting in asynchronous hatching over a period of 2 or 3 days. If food supply is abundant, the most recently hatched Bank Swallow nestling becomes indistinguishable in development; but that individual will be the most likely to perish during a food shortage (Emlen and Demong 1975). In this study, asynchronous hatching of Barn Swallows was observed. The partial clutch mortality (nestlings) also observed was probably due to starvation (Lack 1954). The entire clutches of dead young late in the season and the low percentage of second clutches attempted probably indicate a food shortage as well. Twenty-four percent of the total second-clutch attempts which occurred during the 1980 breeding season were in Culvert A. This could be related to the earlier dates of nest initiation, a more abundant food supply, or an enhanced ability to locate food supplies due to larger colony size. Barn Swallows have been observed foraging in groups of two or more (Snapp 1973). Future research is needed to investigate the possible occurrence of synchronous breeding and its relation to colony size in culvert-nesting Barn Swallows, particularly in Oklahoma.

SUMMARY

Barn Swallows preferred nest sites within 15 m of the culvert entrance and to refurbish old nests. The variation in colony size was influenced positively by 1) water depth within the culvert, 2) distance from the town of Stillwater, 3) height of the culvert; and negatively by 4) amount of wooded acreage. Active nests were often less than 3 m apart. One large culvert exhibited synchronous date of nest initiation.

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Table 1. Barn Swallow nests initiated each 2-week interval.

Year	Apr 1-15	Apr 16-31	May 1-15	May 16-31	June 1-15	June 16-31	July 1-15	July 16-31	Aug 1-15	Total
1980	1	10	65	70	65	34	48	5	0	298
1981	0	7	41	44	36	36	38	1	1	204
Total	1	17	106	114	101	70	86	6	1	502
%	0.2	3.4	21.1	22.7	20.1	13.9	17.1	1.2	0.2	

Table 2. Overall reproductive success of all nests attempted by clutch size.

Clutch size	No. of nests		No. of eggs		No. of fledglings		% success	
	1980	1981	1980	1981	1980	1981	1980	1981
1	11	10	11	10	0	0	0	0
2	24	9	48	18	17	2	35.4	11.1
3	49	21	147	63	53	38	36.1	60.3
4	73	69	294	276	135	174	46.2	63.0
5	117	85	585	425	283	300	48.4	70.6
6	24	10	144	60	56	53	38.9	88.3
Total	298	204	1227	852	544	567	44.3	66.6

Table 3. Overall reproductive success of Barn Swallow nests fledging at least one young by clutch size.

	No. of nests		No. of eggs		No. of fledglings		% success	
Clutch size	1980	1981	1980	1981	1980	1981	1980	1981
2	9	1	18	2	17	2	94.4	100.0
3	20	16	60	48	53	38	88.3	79.2
4	42	52	168	208	135	174	80.4	83.7
5	69	67	345	335	283	300	82.0	89.6
6	12	10	72	60	56	53	77.8	88.3
Total	152	146	663	653	544	567	82.1	86.8

Table 4. Barn Swallow nest outcome in 1980 and 1981. Percentages are given in parentheses.

Year	Fledged	Nests fall	Contents disappear	Abandoned	Young died	Total
1980	151 (50.7)	64 (21.5)	58 (19.5)	20 (6.7)	5 (1.7)	298
1981	146 (71.6)	32 (15.7)	32 (15.7)	7 (3.4)	7 (3.4)	204
Total	297 (59.2)	96 (19.1)	90 (17.9)	27 (5.4)	12 (2.4)	502

Table 5. Number of Barn Swallow nestlings fledged by distance from the culvert entrance. The mean number of young fledged per nest attempt within each distance category was calculated for both years combined.

Year	0.1-5.0	5.1-10.0	10.1-15.0	15.1-20.0	20.1-25.0	25.1-30.0	30.1-35.0	35.1-40.0
1980	144	137	108	78	23	38	16	0
1981	133	121	140	78	50	39	6	0
Total	277	258	248	156	73	77	22	0
Mean	2.18	2.17	2.36	2.33	1.92	2.26	2.44	0

Table 6. The four most significant physical culvert characteristics and environmental variables identified in a stepwise multiple regression analysis using the number of nest sites used per culvert (colony size) as the dependent variable in each of the 23 culverts studied.

Variables in model	R^2	df	F	*P*
Water depth[a]	0.57	22	28.14	< 0.0001
Water depth, Distance[b]	0.69	22	21.79	< 0.0001
Water depth, Distance, Height[c]	0.78	22	22.09	< 0.0001
Water depth, Distance, Height, Woodland[d]	0.87	22	30.59	< 0.0001

[a]Water depth within each culvert (cm)

[b]Distance from Stillwater, Oklahoma (km)

[c]Height of each culvert (m)

[d]Woodland within 2.59 km^2 of each culvert (ha)

FIG. 1. Relative location of culverts (black rectangles) within the study area. Letters A, B, and C represent culverts with a minimum of 15 nests initiated by June 7, 1980.

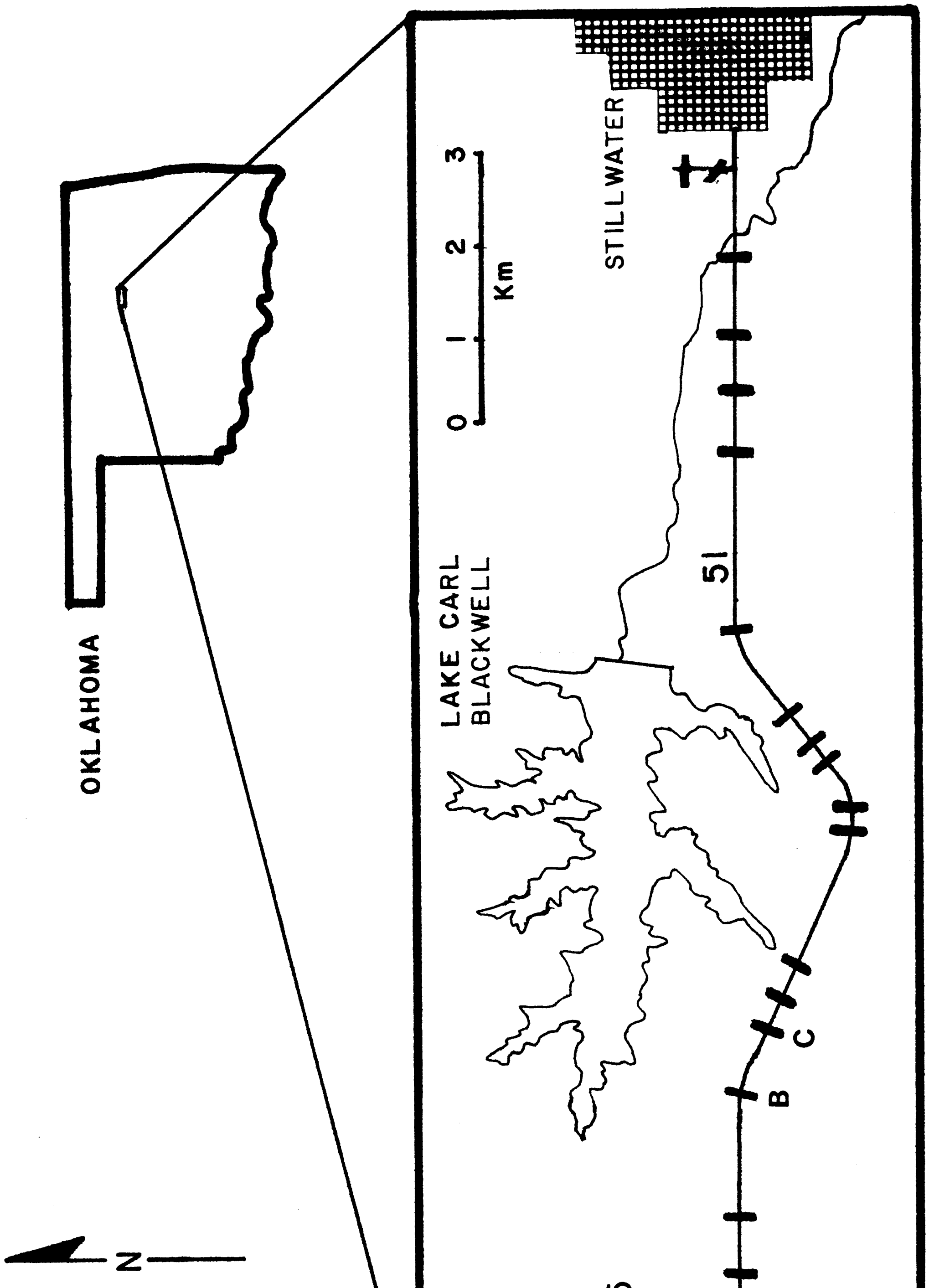

OKLAHOMA
LAKE CARL
BLACKWELL
STILLWATER
0 1 2 3
Km
51
I-35
A
B
C
N

FIG. 2. Number of nests initiated in culverts with a minimum of 15 active nests by June 7, 1980. Culvert A, 0.5 km from interstate highway 35, is represented by barred rectangles. White rectangles designate Culvert B, 7.2 km from I-35. Culvert C, 8.2 km from I-35, is indicated by dark rectangles. Week 1 = April 25 - May 1, Week 2 = May 2 - May 8, Week 3 = May 9 - May 15, Week 4 = May 16 - May 22, Week 5 = May 23 - May 29, Week 6 = May 30 - June 5.

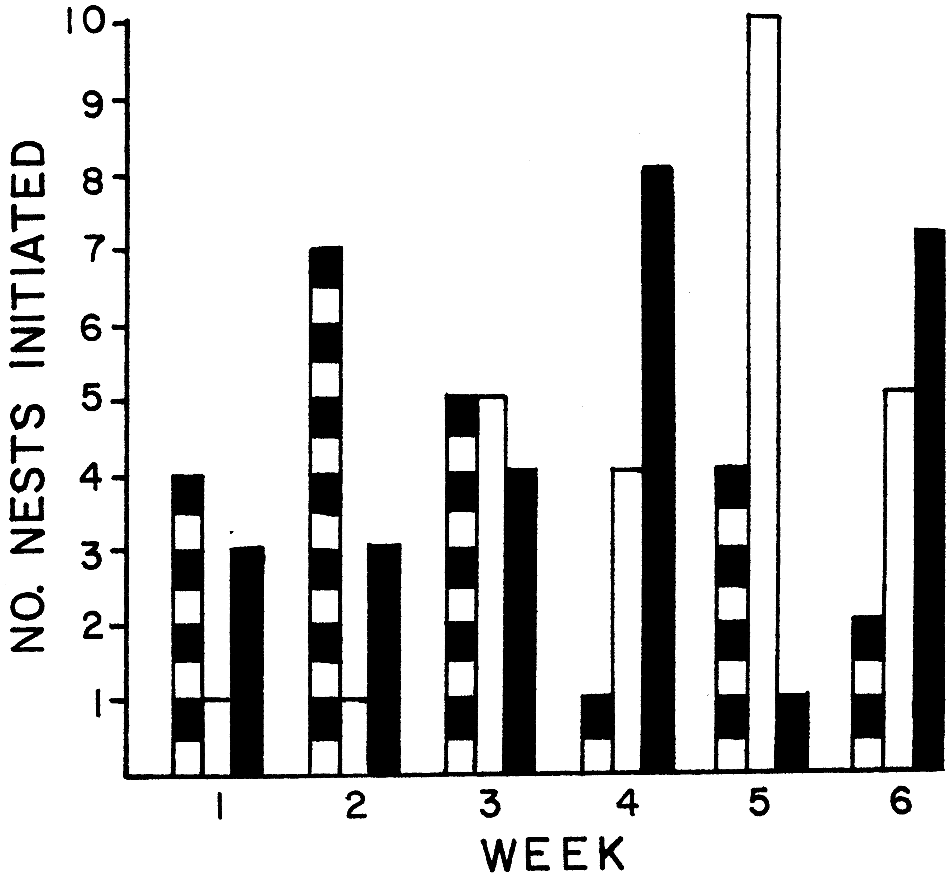

NO. NESTS INITIATED
10
9
8
7
6
5
4
3
2
1
1
2
3
4
5
6
WEEK

FIG. 3. Number of nest attempts and failures by distance from the culvert entrance. Distance 1 = 0.1 - 5.0 m, Distance 2 = 5.1 - 10.0 m, Distance 3 = 10.1 - 15.0 m, Distance 4 = 15.1 - 20.0 m, Distance 5 = 20.1 - 25.0 m, Distance 6 = 25.1 - 30.0 m, Distance 7 = 30.1 - 35.0 m. Distance 8 = 35.1 - 40.0 m.

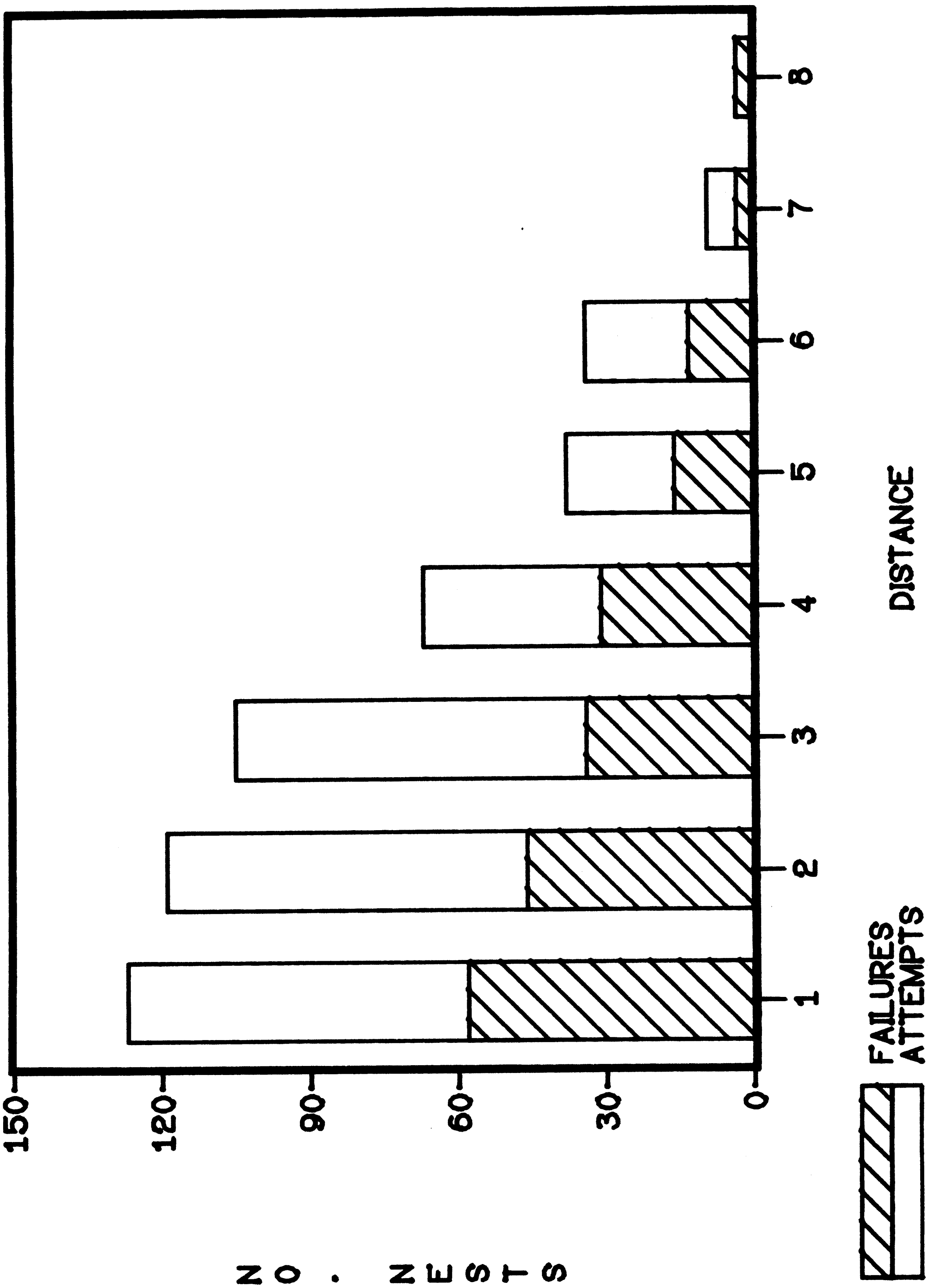
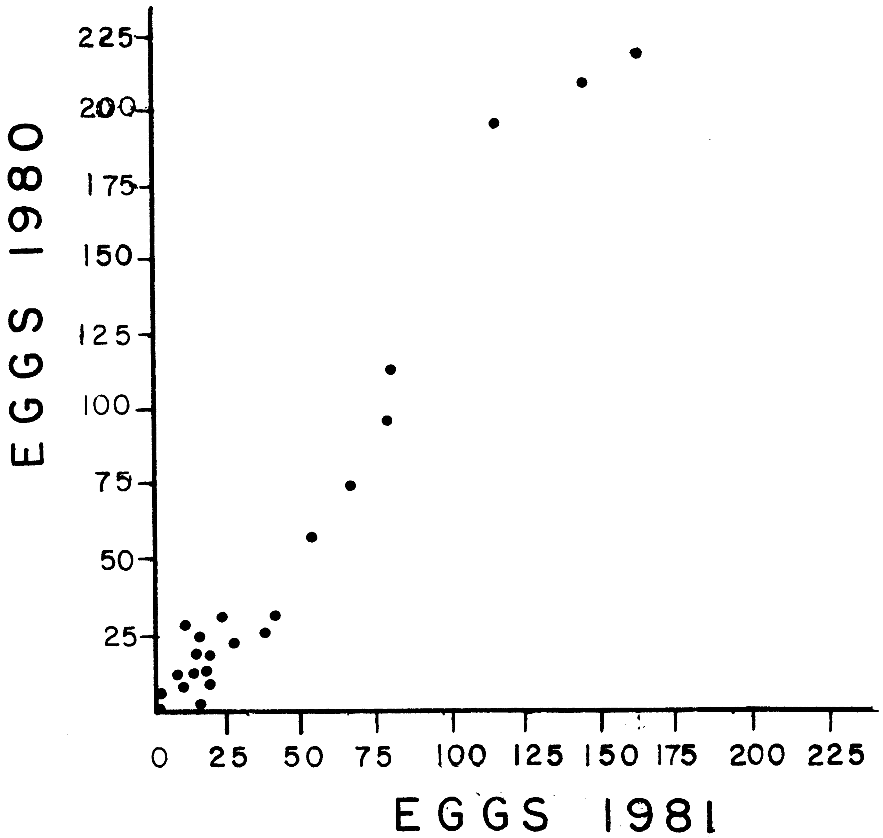
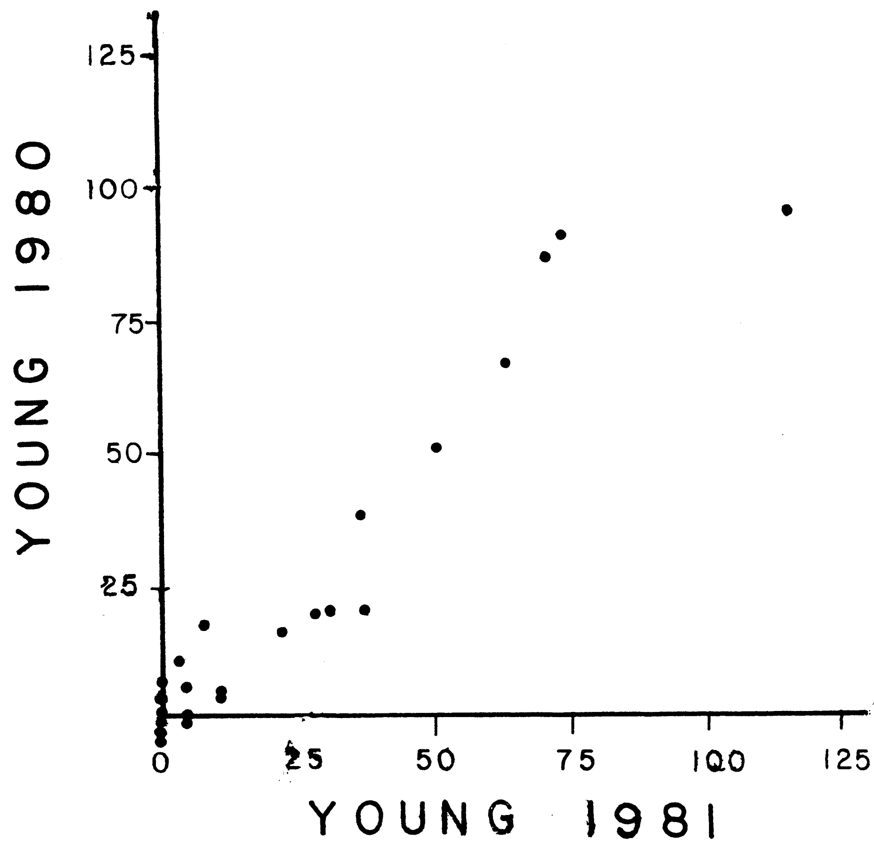

NO. NESTS
150
120
90
60
30
0
1
2
3
4
5
6
7
8
DISTANCE
FAILURES
ATTEMPTS

FIG. 4. Relationship of egg and young productivity between years by culvert.


EGGS 1980
225
200
175
150
125
100
75
50
25
0
25
50
75
100
125
150
175
200
225
EGGS 1981


YOUNG 1980
125
100
75
50
25
0
25
50
75
100
125
YOUNG 1981

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