The University of Saskatchewan

COLONY SITE SELECTION
IN BANK SWALLOWS

by

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ABSTRACT

Bank Swallow colony site selection was studied on a 6,129 hectare area in the Qu'Appelle Valley near Fort Qu'Appelle, Saskatchewan. Comparison of 60 banks used by Bank Swallows with the 349 unused sites showed that taller, vertical, more recently excavated sites with sand or fine gravel soils and no obstructions in front of the bank were selected. Colony size, which ranged from 1 to 48 pair with a mean of 7.7 pair, was not significantly correlated with any bank character.

Mean clutch size was 5.0. In successful nests 90.5% of eggs fledged. Probability of a nest surviving from laying through fledging was 63.4%. Nest success was only correlated with tunnel depth and date of initiation, although additional data suggest bank characters are also important.

Tunnel nesting gives Bank Swallows significant advantages and forces clustering on a restricted habitat base. Suitable habitat is left vacant, however, indicating that Bank Swallows probably derive additional advantages from associating with conspecifics.

ACKNOWLEDGEMENTS

A large number of people assisted with this study, some of whom I have undoubtedly forgotten to mention. Nonetheless the assistance of one person, my wife Paule, stands far above that of everyone else. Paule not only tolerated the time and money I spent on the project, but assisted at every stage. Her observations while we canoed on the Qu'Appelle River in 1979 gave me the idea for the project. She took part in all phases of the field work and in coding data for analysis. Without her physical and moral support this project would never have been completed.

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George Duff and John Hugel drafted some of the figures. Shirley Thomas word processed the manuscript and Sheila Flory repeatedly provided advice on data entry and analysis using the Dec 20.

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1. INTRODUCTION

1.1 Advantages and Disadvantages of Coloniality

Colonial nesting could only develop and persist if individuals nesting in colonies improve their fitness by this behaviour. Yet there are no automatic benefits to colonial nesting, while there are automatic disadvantages (Alexander 1974). Reported disadvantages of colonial nesting include increased parasitism (Feare 1976, Hoogland and Sherman 1976), increased competition for nest sites (Patterson 1965), and materials (Jenni 1969, Hoogland and Sherman 1976), and increased susceptibility to predation and kleptoporasitism (Anderson 1976, Hunter and Morris 1976). Concentrating in colonies also greatly increases the risk of cannibalism (Parsons 1976, Hunt and Hunt 1975) and misdirected parental investment (Hoogland and Sherman 1976). Perhaps the greatest disadvantage of colonial nesting is competition for food. This disadvantage may be so great that species only nest colonially when their food resource cannot be economically defended (Brown 1964).

Colonial nesting offers four possible advantages which could outweigh these disadvantages. Birds may nest in colonies due to extreme localization of a valuable resource such as nest sites (Alexander 1974). Nesting in colonies may reduce susceptibility to predation through predator swamping (Nisbet 1975) or group defence (Lack 1968) or provide advantages in obtaining food (Ward and Zahavi 1973, Emlen and Demong 1975). Birds nesting in colonies may also co-operate to modify the environment through construction of communal nests (White et al. 1975, Bartholomew et al. 1976) or other means. The relative importance of these advantages as causes of coloniality is not established and may well differ for different species.

1.2 The Bank Swallow

The Bank Swallow, Riparia riparia, has many attractions for students of coloniality. Most Bank Swallows nest in colonies (Hoogland and Sherman 1976). Nests are located in tunnels excavated into steep banks which are free of vegetation (Freer 1977). Such sites are conspicuous, allowing all potential nest sites to be located and studied. Finally the Bank Swallow is common in easily accessible areas allowing easy study of a large number of colonies.

Like all Hirundinidae the Bank Swallow is an aerial feeder. It is a generalized and opportunistic forager, concentrating its foraging effort wherever local concentrations of insects occur (Emlen and Demong 1975). In England prey items selected by the conspecific Sand Martin include 9 orders of insects (Waugh 1979).

Aerial insects are considered to be spatially and temporally variable in abundance and thus not economically defendable (Snapp 1976, Emlen & Demong 1975). Such a food source is a major prerequisite for evolution of coloniality.

Bank Swallow colonies are located in vertical banks which are nearly free from vegetation and face out into the open (Freer 1977). The soil must be suitable for excavation with sands and loamy sands being most commonly selected (Spencer 1962). Traditional colony sites include river banks and coastal cliffs, but sand and gravel quarries and other man made sites are now commonly used.

Bank Swallows incubate about 15 days and young fledge after 18-22 days (Bent 1942, Morgan 1979). Incubation normally starts with laying of the second last egg so the incubation period appears to be 14 days. After fledging young Bank Swallows return to the nesting tunnels for several days before moving to other areas in some regions, but in others leave almost immediately. This behavioural difference may be due to risk of predation by American Kestrels, Falco sparverius (Freer 1977).

Previous studies of the Bank Swallow have examined its homing ability (Mayhew 1963), sociobiology (Beecher & Beecher 1979), general nesting biology (Beyer 1938, Petersen 1955), the advantages and disadvantages of colonial nesting (Hoogland and Sherman 1976), importance of synchronized breeding (Emlen and Demong 1975), factors affecting site tenacity (Freer 1979) and physical characteristics of the sites (Freer 1977, Spencer 1962, Sieber 1980). In none of these studies have attempts been made to compare the selected habitat with unused sites in the area. Indeed such studies are very rare for all colonial species. Burger and Gochfeld's (1981) study of the Kelp Gull, *Larus dominicanus*, is a rare exception.

1.3 Scope and Purpose of the Study

My principal purpose in this study was to determine what habitat features Bank Swallows selected for nesting and to relate my findings to why Bank Swallows nest colonially. More specifically I established the following four hypotheses:

1) Bank Swallows select colony sites on the basis of certain recognizable environmental features.
2) The habitat features selected contribute to increased nest success by providing a superior microclimate or protection from predators.

3) Nest losses from predation and environmental hazards are lower for colonial species than for solitary nesters.

4) Nests are more clumped, spatially and temporally, than required by the habitat, leaving suitable habitats vacant.

As a secondary purpose I wished to collect basic information on the Bank Swallow, which has not been extensively studied in Western Canada.

2. STUDY AREA

2.1 Location

The study area was located along the Qu'Appelle Valley, 5 miles east of Fort Qu'Appelle and 8 miles north of Indian Head, Saskatchewan (Figure 1). The centre of the study area lies at 50°40' N. latitude and 103°38' W. longtitude. Katepwa Lake, the last of the four Fishing Lakes, is totally enclosed within the study area as is the village of Lebret (Figure 2).

2.2 Climate

The Katepwa Lake has a dry sub-humid continental climate characterized by warm summers, cold winters, and moderately low annual precipitation. Mean annual temperature is about 2°C. The growing season extends for 164 to 174 days from 20 or 30 April to 11 October and average frost free period exceeds 90 days (Hart and Stelfox 1981). July, with a mean of 18°C and extremes up to 43°C, is the warmest month.

Average annual precipitation is 44.5 cm with 60% of this total falling during the growing season. Evaporation from water bodies in spring and summer, 9.65 cm in May, 10.2 cm in June, 12.45 cm in July, 11.18 cm in August, and 7.37 cm in September, is almost double the average precipitation for each of those months (Christiansen 1960).

Prevailing winds in the study area are from the northwest in all seasons.

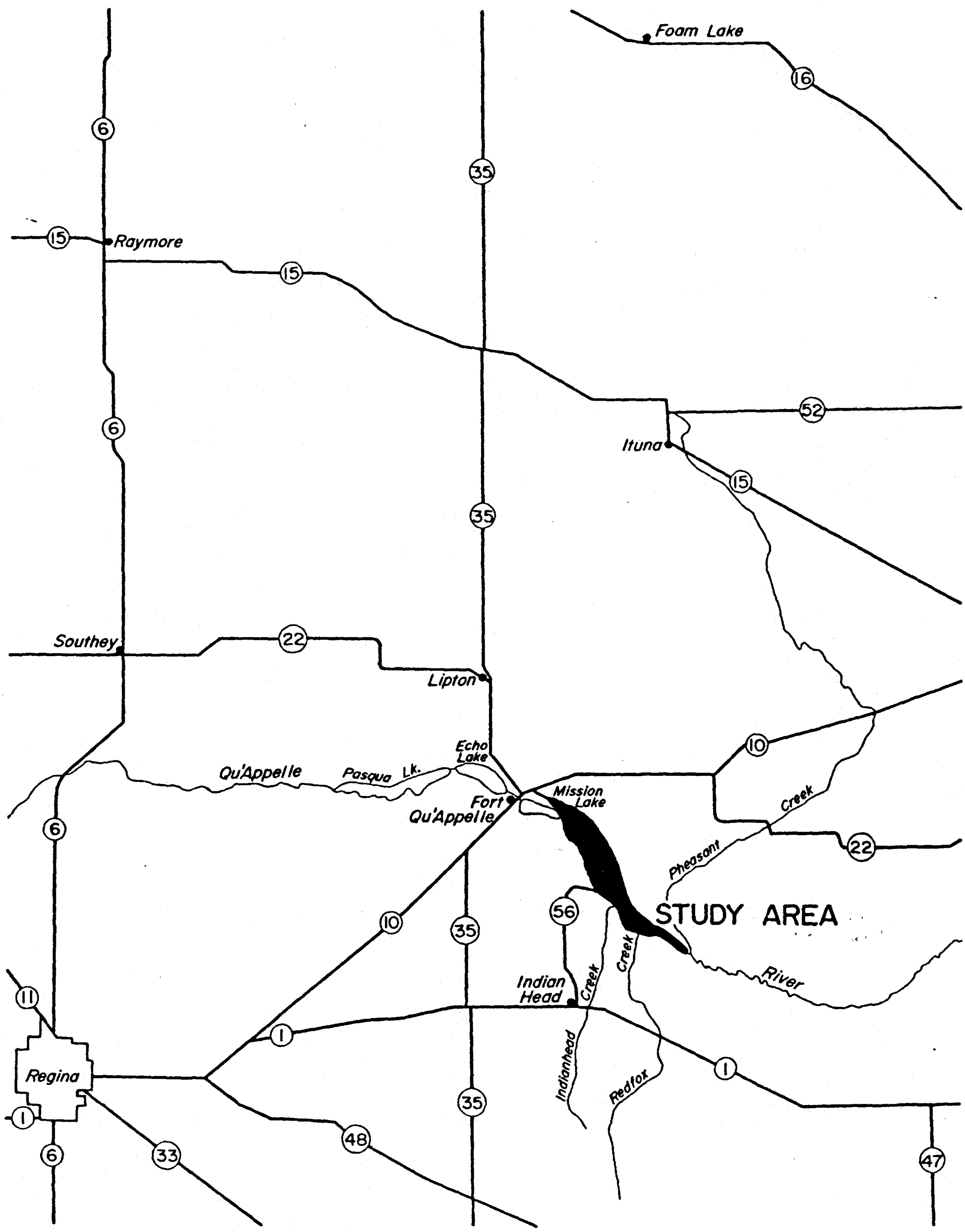


Figure 1: Location of the Study Area

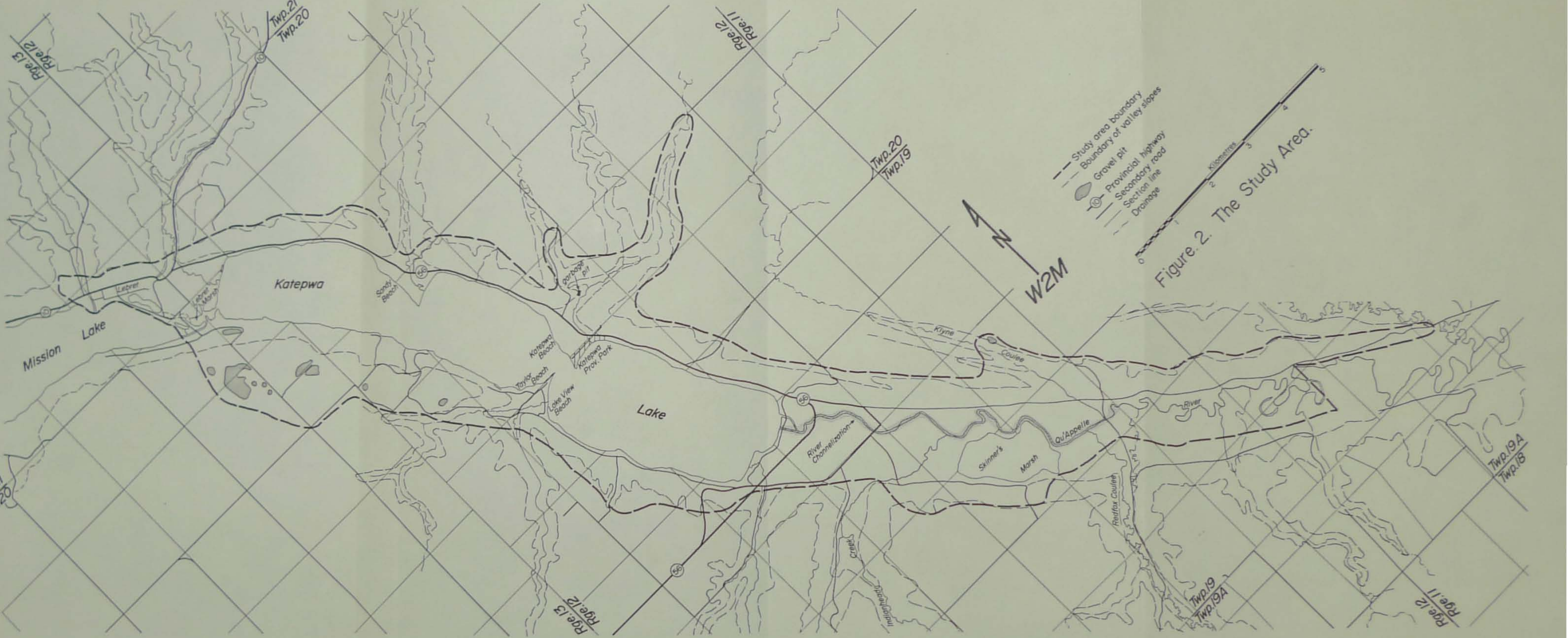


Figure. 2. The Study Area.

2.3 Landform

The dominant feature of the 6,129 hectare study area is the Qu'Appelle Valley (Figure 2). Most of the study area, 3,447 hectares, plus Katepwa Lake, lies on the valley floor. An additional 1,840 hectares lie on the valley slopes and 246 hectares along tributary coulees. The remaining 596 hectares of the study area lie on upland areas outside the valley.

The Qu'Appelle Valley is a glacial meltwater channel almost 2 kilometres wide at its bottom and 65 to 75 metres deep. The original meltwater channel has gradually filled with alluvial deposits from the eroding valley walls and uplands. These deposits, which range from fine silts to alluvial fans of sand and gravel, cover the original valley bottom to a depth of 25 to 48 metres (Hart and Stelfox 1981).

The valley bottom is dominated by water bodies. The Qu'Appelle River itself, a small misfit stream, meanders extensively back and forth across the valley. Katepwa Lake covers 1,607 hectares of the valley floor. Ducks Unlimited Canada and Saskatchewan Wildlife Branch manage 128 hectare Skinner's Marsh as a wildlife management area (Hjertaas 1980). Lebret marsh and several smaller Oxbow marshes add to the abundance of water on the valley floor. These water bodies ensure an abundant supply of aquatic insects, one food of the Bank Swallow. The study area was deliberately positioned along the Qu'Appelle Valley to ensure that all potential nest sites would be close to these wetlands and the food they supply, thus removing one potential inequality among sample sites.

The valley bottom is extensively developed. In addition to the village of Lebret, cottage developments line much of Katepwa Lake. Much of the valley bottom is cultivated or planted to tame hay crops. Areas which remain in native vegetation are dominated by wheat grass (*Agropyron* species), wild barley (*Hordeum jubatum*), and blue grass (*Poa* species). Marsh areas are dominated by bulrush (*Scirpus acutus*), cattail (*Typha latifolia*), and Whitetop (*Scolochloa festucacea*) (Lieffers 1977). Willow grows along less flood prone parts of the river while Manitoba maple (*Acer negundo*) and Green ash (*Fraxinus pennsylvanica*) grow on well drained sites. These occur principally along the lake edge and beside tributary creeks.

Potential colony sites are naturally created along the lake shore and by erosion of the river banks. Construction activities have created a small number of additional banks on the valley floor.

The slopes of the valley are modified by erosion, slumps and land slides. The valley walls are thus irregular, relatively steep, and almost totally covered with native vegetation. Porcupine grass, (*Stipa spartea*), green needle grass (*Stipa viridula*), blue grama (*Bouteloua gracilis*) and spear grass (*Stipa comata*) dominate the drier sun exposed areas. Areas shaded from the sun have a more favourable moisture regime and support shrubs and trees including snow berry (*Symphoricarpos occidentalis*), rose (*Rosa* species), saskatoon (*Amelanchier alnifolia*), chokecherry (*Prunus virginiana*), aspen (*Populus tremuloides*), Green ash and Manitoba maple (Lieffers 1977).

The valley slopes offer only the banks left by slumps as naturally occuring potential colony sites. However, man's activity building roads, buildings, and excavating material has provided a series of banks potentially attractive to the swallows.

The coulees formed where tributary creeks join the Qu'Appelle are V-shaped in cross section with narrow bottoms and steep sides. The steep slopes are totally covered with native vegetation similar to that of the main valley, although often with a greater proportion of woody cover due to shading from the sun in the narrow valley bottom.

Banks of the tributary creeks provide many potential colony sites. Other sites in the tributary creek valley are found along occasional road cuts or other excavations.

The 596 hectares of upland in the study area are principally located on fluvial deposits 3.2 kilometres south of Lebret. Sand and gravel were deposited here, producing soils of poor agricultural quality characterized by native grassland and aspen bluffs. Extensive gravel mining in this area has created many potential colony sites.

3. METHODS

3.1 Location of Banks and Colonies

During the spring and summer of 1980 and 1981 the entire study area was searched for cutbanks which offered potential Bank Swallow colony sites. Cutbanks are only created by certain natural and human processes. The search therefore required checking all lakeshore, river and tributary creek banks in the study area as well as checking the hills for slumps. All roads, gravel pits and piles, garbage pits, and construction sites in the study area were also visited each year.

Each site was inspected in 1980 and 1981 to determine if it was used by Bank Swallows. On the first visit all sites which had a cutbank, (i.e. an approximately vertical face) and exceeded one foot (35 centimetres) in height, plus several smaller banks, were plotted on a 1:50,000 map and numbered. Each site was referred to by the number of its 1:50,000 National Topographic sheet followed by a unique number for that sheet (e.g. 62L12-17). The physical parameters of these sites were also recorded on the first visit. Most bank measurements thus date to 1980. Only a small number of new sites were measured in 1981.

Fourty-four banks located along one ravine were not rechecked in 1981, but were checked in 1982. No sign of old nests from 1981 or nesting in 1982 was found.

3.2 Physical Parameters of Sites

When each bank was located and numbered the following twenty-two physical characteristics were recorded. Figure 3 illustrates many of these measurements.

Bank Height: The height of the bank at its highest point measured in metres from the top of the talus slope to the top of the bank.

Height of Talus Slope: The talus is the fallen material which accumulates at the base of almost all banks. Its height is the vertical distance from the top of the talus to the bank base. Maximum bank height and talus height usually occurred and were measured at the same point. On a few occasions they did not coincide and the talus height was taken at a more representative site.

Combined Height: The total vertical distance in meters from base ground level to the top of the bank. In most cases this equals the sum of bank height and height of talus slope.

Length: The distance in metres from the point at the right side of a bank where bank height dropped to 20 centimetres to the similar point at the left of the bank. If the bank curved distance was measured along the curve, not on a chord.

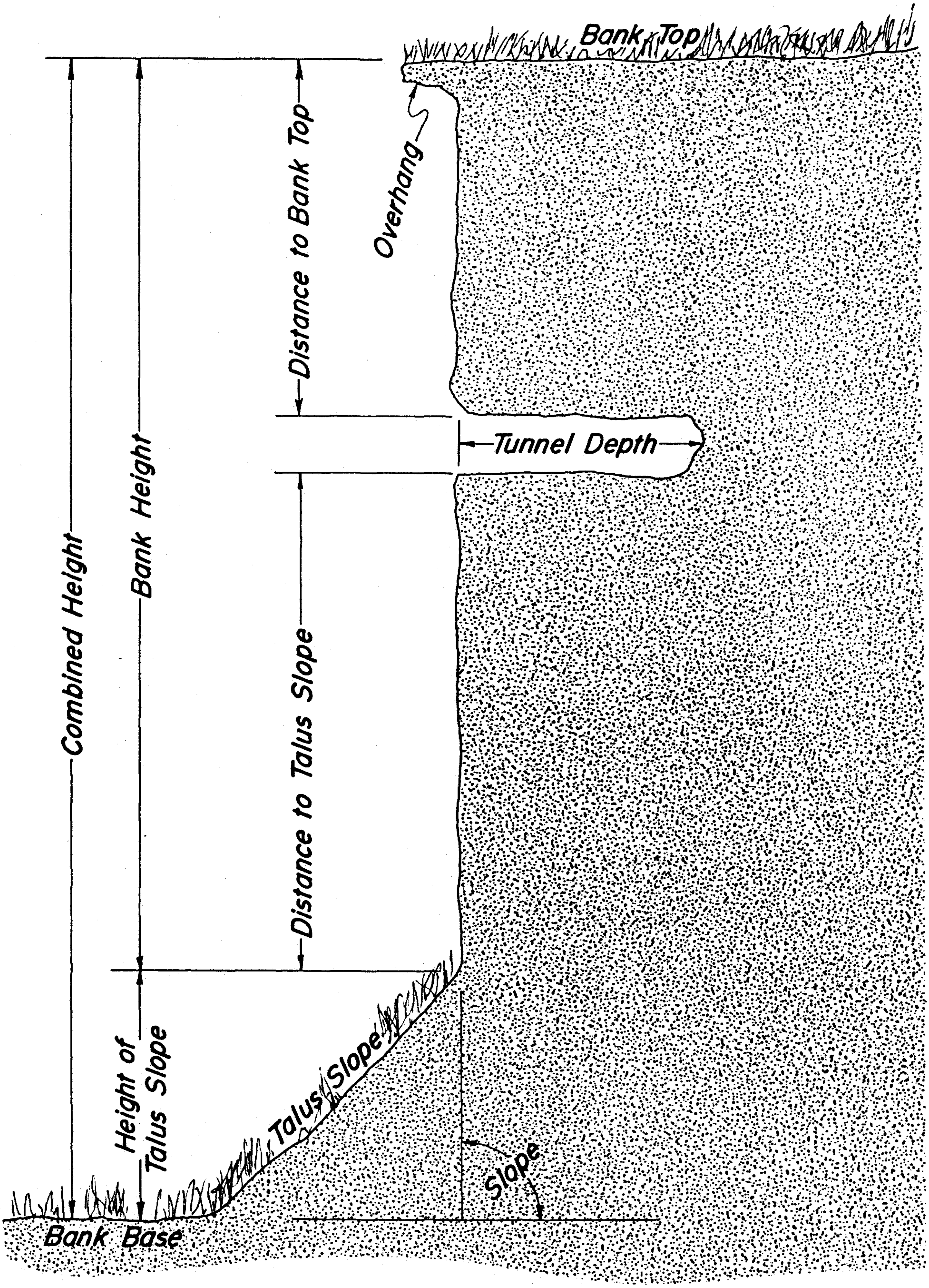


Figure 3: Physical Characters of the Bank and Nest

Area: Calculated in square metres by multiplying bank height by length and estimating the percentage of this imaginary rectangle actually covered by the bank face.

Orientation: The orientation indicates the compass direction a bank is facing. An orientation of 180° indicates a bank facing directly south and fully exposed to the noon hour sun. I used a Silva Type I5T compass corrected for local magnetic declineation of 14° to measure the orientation. If the bank curved, the orientation used was that of the dominant portion of the bank, except that on occupied banks, orientation was always that of the actual nesting area.

Slope: I measured the slope of the bank in degrees from horizontal by placing a straight edge on the bank and measuring the angle between the straight edge and a level. When slope varied from one part of the bank to another I tried to measure at the steepest area.

Overhang: On some banks an overhang of sod, roots or other material extended out 10 centimetres or more over all or part of the bank. The percentage of each bank sheltered under such an overhang was recorded.

Vertical Lift: An indication of the amount of flying space available in front of each bank was given by measuring how many metres above a potential nest site a Bank Swallow would have to be to clear obstacles 20 metres, 40 metres, and 60 metres from the nest. Because Swallows usually fly almost straight out from the bank, vertical lift at 20 metres was measured at the lowest point within 15° of a line perpendicular to the bank face. Swallows often turn after the initial direct flight and may follow the river or other path to gain altitude. Vertical lift at 40 and 60 metres were therefore measured as the minimum climb required to travel 40 or 60 metres in any straight line path from the bank.

Vegetation: The percentage of the ground covered by vegetation and the type of vegetation present (grass, forbes, shrubs, trees) was recorded for the bank top, bank base, and talus slope of each bank. Measurement of the percentage of ground covered by vegetation was somewhat inconsistent because measurement later in summer may show higher ground cover than measurement made early in the growing season.

Origin of Bank: Each bank was classified according to its origin as a river bank, road cut, gravel pit, building construction site, gravel stock pile, natural slump, tributary creek bank, lakeshore, garbage pit, or other.

Distance to Nearest Bank, Bank Swallow, and Cliff Swallow Colony: All banks, Bank Swallow colonies and Cliff Swallow, *Hirundo pyrrhonota*, colonies in the study area were plotted on 1:50,000 maps in 1980. The shortest distance from each bank to the nearest unoccupied bank,

Bank Swallow colony, and Cliff Swallow colony, was measured from the maps in 1980. The distance to nearest Bank Swallow colony was also measured in 1981. Some banks were so close to each other, often with as little as 1 metre separating 2 sites, that the distances were measured in the field.

Banks and Colonies Within 500 Metres: From the 1:50,000 maps the number of Bank Swallow colonies and unoccupied banks within 500 metres of each bank was determined.

3.3 Soil Analysis

A sample of approximately 500 mls of soil from each bank was placed in a paper bag, numbered, and stored for further analysis. If more than one soil layer was present, a sample was taken from each layer. The sample finally chosen to represent the bank was the one in which there were nests, if any were present, or the dominant soil type for the bank.

Soils were analysed using the facilities of the Saskatchewan Department of Highways Soil Laboratory in Saskatoon. A wet sieve analysis was used to determine the distribution of particle sizes in each soil sample.

Each sample was dried to a constant weight. A 100-200 gram sample was washed through a 75 micrometer sieve until all fine particles were washed out. Hydrogen peroxide was added to very plastic samples to break up lumps. All retained material was again dried and weighed, then placed in a set of standard sieves and shaken for 4 minutes. The soil retained by each sieve was weighed and percentage by weight in each particle size calculated. Weight lost during washing plus additional material passing the 75 micrometer sieve during shaking were added to give the smallest category, particles finer than 75 micrometers.

The wet sieve analysis separated the soil into 9 components referred to as SOL1 to SOL9. Table 1 shows particle size of each of these soil components.

Table 1: Particle Size of Soil Components

SOIL COMPONENT	PARTICLE DIAMERER
SOL1	Greater Than 19 Millimeters
SOL2	12.5 mm to 19 mm
SOL3	4.75 mm to 12.5 mm
SOL4	2.00 mm to 4.75 mm
SOL5	.850 mm to 2.00 mm
SOL6	.425 mm to .850 mm
SOL7	.150 mm to .425 mm
SOL8	.075 mm to .150 mm
SOL9	Smaller than .075 mm

3.4 Physical Characteristics of Nests

At each colony I endeavoured to locate all nests and record three physical characteristics. A small number of nests were missed because the young had fledged before the colony was located or nesting occurred after it had been visited. Figure 3 illustrates the three measurements made at each nest.

Tunnel Depth: The distance in centimetres from the mouth to the back of the tunnel was measured by inserting a calibrated rod into the tunnel.

Distance to Bank Top: The vertical distance, in centimetres, from the top of the bank to the top of the tunnel mouth.

Distance to Talus Slope or Bank Base: The vertical distance, in centimetres, from the bottom of the tunnel mouth to the top of the talus slope. If the talus slope was not present the measurement was taken to the bank base.

3.5 Observations of Nests

In order to study the nesting success of Bank Swallows a series of readily accessible colonies were visited at approximately 7 day intervals in 1980 and 1981. Each nest was inspected and its contents or other evidence of use recorded on a Prairie Nest Record card in 1980 and on specially designed forms in 1981.

Sketch maps were made of each colony when it was first visited. Nests were numbered on the map for identification on subsequent visits. Nest inspection was usually carried out by two people. The author worked along the bank inspecting each nest and reporting the contents to an assistant who recorded the data and kept track of nest locations from the map.

Difficulties were experienced identifying nests under this system if parts of the bank slumped or many new tunnels were started. Either occurrence altered the picture from that mapped on the previous visit and caused significant delays in locating nests. This problem was resolved in 1981 by noting more bank landmarks on the map and by placing numbered cardboard tags beside each nest tunnel. Hoogland and Sherman (1976) reported that similar use of tags had no noticeable effect on swallow behaviour.

In 1980, active nests were first located by placing toothpicks in tunnel mouths. Bank Swallows, at first, hovered in front of the bank but soon entered their tunnel, dislodging the toothpicks. Tunnels where toothpicks were dislodged after a one hour test were considered to be active provided further information confirmed nesting. Observations of swallows entering and leaving tunnels were also used as evidence of an active nest. For some inaccessible tunnels this was the only information available.

Wherever possible nest contents were observed using a wooden rod with a flashlight bulb at its end and a dental mirror attached beside the bulb with elastic bands. Similar in design to Ripariascopes described by Petersen (1955) and Hoogland and Sherman (1976), this light stick permitted inspection of nest contents except if the tunnel turned or exceeded 80 centimetres in depth. The former occurred most commonly when swallows encountered rocks or other obstacles while tunnelling.

Development of this light stick in 1980 required two weeks of false starts before obtaining a functional model. During this period toothpicks and observations of swallows entering nests were necessary. During the rest of 1980 and all of 1981 contents of almost all nests were checked directly using the light stick.

When using the light stick, nest contents were usually easily visible during egg laying and early incubation. Most measurements of clutch size come from this period. By late incubation the nests were surrounded with feathers making accurate counts of the eggs very difficult. During this period contents were usually recorded as 3+ or 4+.

While young in the nest were usually visible, their habit of huddling made exact counts of broods extremely difficult to obtain unless they could be counted as they left the nest. The young from many 1981 nests were captured by placing a cardboard tube with a nylon stocking over its end in the tunnel mouth. Ready to fledge young often responded to this disturbance, or that of examination with the light stick, by running out of the tunnel and falling in the trap. All captured young were held while the nest was inspected to count those remaining, then banded and returned to the nest. Most counts of number fledging were obtained by this method.

3.6 Analysis of Nest Success Using Mayfield's Index

The simple percentage of total nests which fledged successfully is a biased indicator of nest success because nests found later than the day of nest initiation have already survived part of the requisite term (Johnson 1979). As a result, nest success will be overestimated.

Mayfield's method allows comparison of all nests, regardless of when they are found, by comparing rates of loss for the period in which they are under observation (Mayfield 1961, Johnson 1979). The total number of days in which nests are observed, or at risk, are summed and divided into the number of nests which failed while under observation.

The result,

$$\text{daily mortality rate} = \frac{\#\text{ nests lost}}{\text{total days at risk}}$$

expressed as losses per nest day, is the estimated daily mortality rate of nests. From the daily mortality rate and the nest period one can calculate the probability of a nest hatching or failing.

Days at risk were calculated for each Bank Swallow nest. These days can be summed and Mayfield's index calculated for the entire study, any colony, or any group of colonies or nests in order to study the effects of habitat characteristics on nest success.

Calculation of days at risk for any nest started on the day that activity, either a swallow entering, a toothpick disturbed, or eggs or young in the nest, was first observed. The end of the observation period was taken as the last day that young were observed in the nest. In cases of nest failure, unless the failure could be dated exactly, the nest was assumed to have failed half way between the last observation and when the failure was discovered. This assumption produces a slight bias, but is reasonable for short observation periods such as the normal seven days in my study (Johnson 1979).

Many Bank Swallow tunnels are abandoned after being excavated for only a few centimetres. Perhaps these are initial excavations of unpaired males (Petersen 1955) or indicate where pairs found conditions unsuitable and resumed excavation at a new point. To remove possible bias caused by these false starts I included in calculation of nest success only those burrows which exceeded 50 centimetres in length or where I observed a nest or sustained activity by a pair.

Comparative nest success data were calculated for Tree Swallows, (*Tachycineta bicolor*), Barn Swallows, (*Hirundo rustica*), and Clay-colored Sparrows, (*Spizella pallida*), using data from the Prairie Nest Records Scheme. Clay-colored Sparrows introduced the added variable of Brown-headed Cowbird, (*Molothrus ater*), parasitism. Nests which retained only Cowbird eggs or young were considered to have failed at that point even if the Cowbird eventually fledged successfully.

To determine if observed differences in nest success were statistically significant I calculated the variance for each population:

$$\text{Variance} = s^2 = \frac{\dfrac{1}{(\text{exposure})^3}}{(\text{exposure} - \text{losses})(\text{losses})}$$

(Johnson 1979)

Then the ratio

$$\frac{(m_1 - m_2)}{(s_1^2 + s_2^2)}$$

is calculated where m = Mayfield's Index. This ratio is normally distributed. The probability of the observed difference occurring by chance can be determined from a table of the Cumulative Normal Frequency Distribution (Johnson 1979).

3.7 Data Handling and Analysis

All bank and nest data were transcribed from field sheets to summary forms. The data were then entered on the Decsystem 2060 at Academic Computing Services using OMB Data Coding Sheets and the optical mark reader (bank data) or direct keying (nest data). Printouts of both data files were checked and corrected against the summary forms.

All analyses were carried out using the Statistical Package for the Social Sciences (SPSS) (Nie et al. 1975) on the Decsystem 2060. Mean, standard deviation, and similar summary data were generated for all numeric variables using the subprogram condescriptive. Subprogram T-Test, which uses students t statistic was used to compare means. The distribution of classification variables was compared by Chi squared tests using the subprogram crosstabs. All data were summarized for presentation in Appendix A using the subprogram frequencies. Continuous variables were first recoded using the various recoding and variable transformation options available in SPSS (Nie et al. 1975). This option was also used to combine data, creating new variables for soil analysis.

The SPSS subprograms Pearson correlation and scattergram were used to look for correlations between colony size, nest success, bank characters, and other variables. Subprogram regression was used to do a multiple regression analysis of factors controlling colony size.

An effort to identify those factors which affect nest success was made by lumping all nest data except colony 62L12-09, which was destroyed by human activity. All data were categorized by bank height, colony size, slope, SOL13, SOL14, and percent bank base vegetated and Mayfield's index calculated for each category. I used a TI Programmable 58C to calculate regressions of Mayfield's index against these variables.

3.8 Discriminant Analysis

Discriminant analysis is a statistical technique designed to discriminate between two or more groups of discriminating variables. In this study I had only two groups, the used and unused banks. Bank characters were the discriminating variables.

Discriminant analysis attempts to group cases by forming one or more linear combinations of the discriminating variables. The discriminant functions take the form

$$D_i = d_{i1} Z_{i1} + d_{i2} Z_{i2} + \cdots d_{ip} Z_{ip}$$

where D_i is the score on the Discriminant function i, the d's are the weighted co-efficients and the Z's are the standardized values of the discriminating variables. The co-efficients are derived in such a way that the Discriminant scores produced (D's) are in standard form with a mean of 0 and S.D. of 1 (Nie et al. 1975).

The discriminant analysis subprogram is especially useful in that it can be used for both analysis and classification.

Use of the discriminant function for analysis in my case, where there are only two groups and thus only one discriminant function, is based on the weighting co-efficients. The absolute value of each co-efficient (d) represents the relative contribution of its associated variable to the discriminant function. If a function is derived which successfully discriminates between used and unused sites, the variables which are most important in the discriminant function should define the banks which Bank Swallows used.

The discriminating power of a discriminant function can be measured by the cannonical correlation or by Wilk's Lamda. A cannonical correlation is a measure of the association between the single discriminant function and the g-1 dummy variables representing the g groups. The cannonical correlation squared represents the proportion of the variance in the discriminant function explained by the groups (Nie et al. 1975).

Wilk's Lamda provides a measure of the discriminating power in the original variables which has not been removed by the discriminant function. The larger Wilk's Lamda, the less information remaining. Wilk's Lamda can be tested for significance using the Chi squared statistic (Nie et al. 1975).

Once a suitable discriminant function or set of functions has been derived, it may be used to classify unknown cases. I used this ability to classify the original cases and determine the success of the discrimination empirically by observing the proportion of cases classified correctly.

All discriminant analyses were run using SPSS subprogram Discriminant.

4. RESULTS

4.1 Origin and Location of Banks

During 1980, 397 banks were located inside the study area. Twelve new banks were created in 1981, mostly by gravel mining, for a total of 409. Figure 4 shows location of these banks. The clumped distribution is due to concentration at gravel pits and along the river, roads, and tributary creeks.

Sixty of these banks were used as nest sites by at least one pair of Bank Swallows in one or both years of the study. Location of these 60 colonies is shown in Figure 5. Most colonies were along the river or in gravel pits (Table 2).

A chi square analysis of the origin of banks and colonies shows that the swallows did not select colony sites randomly from among the total number of banks ($p < .001$). Instead the river bank, gravel pits, and building construction sites were selected for, while road cuts, natural slumps, tributary creek banks, and the lakeshore were selected against.

Fourty-seven of 60 colonies were located on man-made sites. The 13 natural sites, 21.6% of the total, account for 133 (17.4%) of the nests. This is a much lower use of natural sites than the 57% of all nests on the prairies and 40% of all nests in Canada shown by Erskine's (1979) review of nest record cards.

4.2 Physical Features of Banks and Colonies

Data from each of the numeric variables are presented in Appendix A, Tables 1 through 26. Results for each variable are discussed in the following subsections.

Bank Height

Bank Swallows tended to select higher banks for nesting although the highest banks are not necessarily used (Appendix A-1). The mean height of banks with colonies, 1.84 metres, is significantly higher than the mean height, 1.38 metres, of unused sites ($p = .002$). While the mean height of the talus slope was also slightly higher at used than unused sites (Appendix A-2) this difference was not statistically significant ($p = .203$). Mean combined height of occupied banks, 3.36 metres, is also significantly greater ($p = .004$) than that of the unused banks, 2.73 metres. As combined height is usually the sum of bank height and talus height, the indication is that Bank Swallows select for bank height rather than combined height.

Colonies in this study are generally on lower banks than those studied by Spencer (1962) in Pennsylvania and Vermont. His 25 colonies ranged from 1 to 7.6 metres and averaged 3.16 metres bank height. Minimum, maximum, and mean for 60 colonies in this study were all lower at 0.5, 6.6, and 1.84 metres.

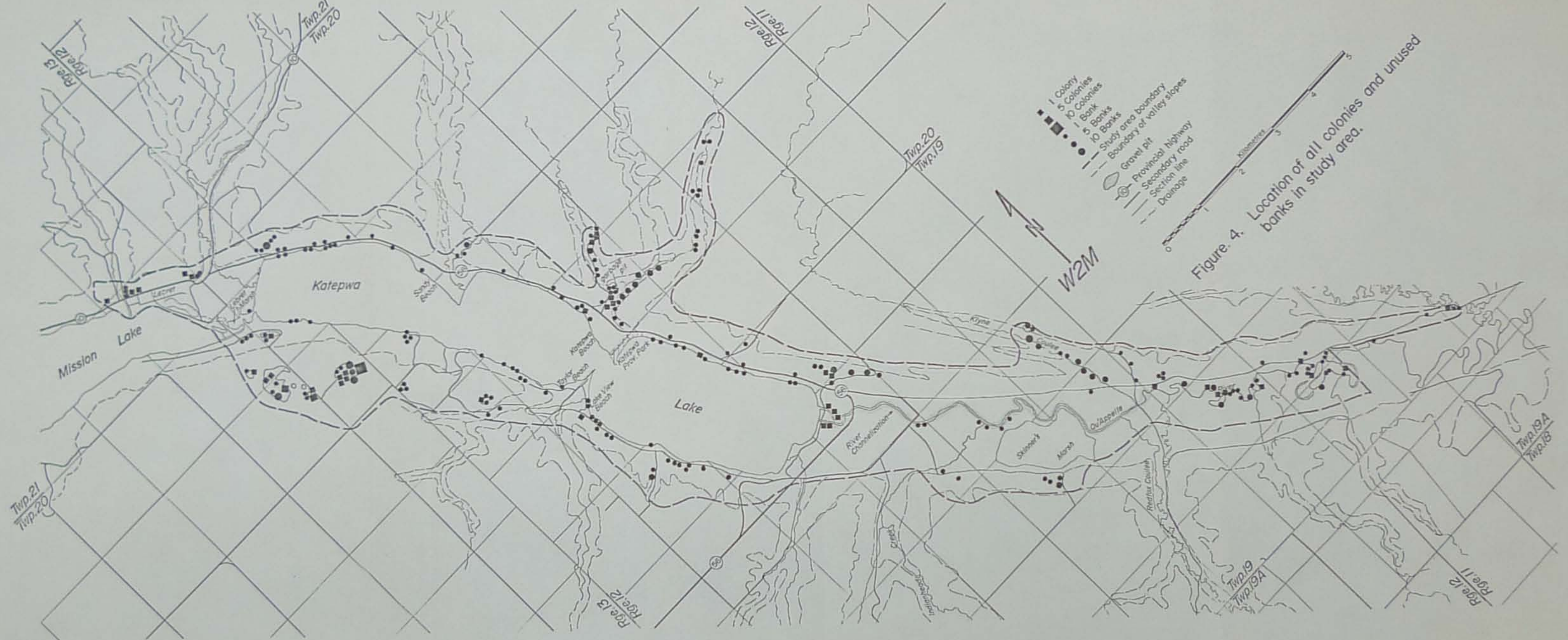


Figure. 4. Location of all colonies and unused banks in study area.

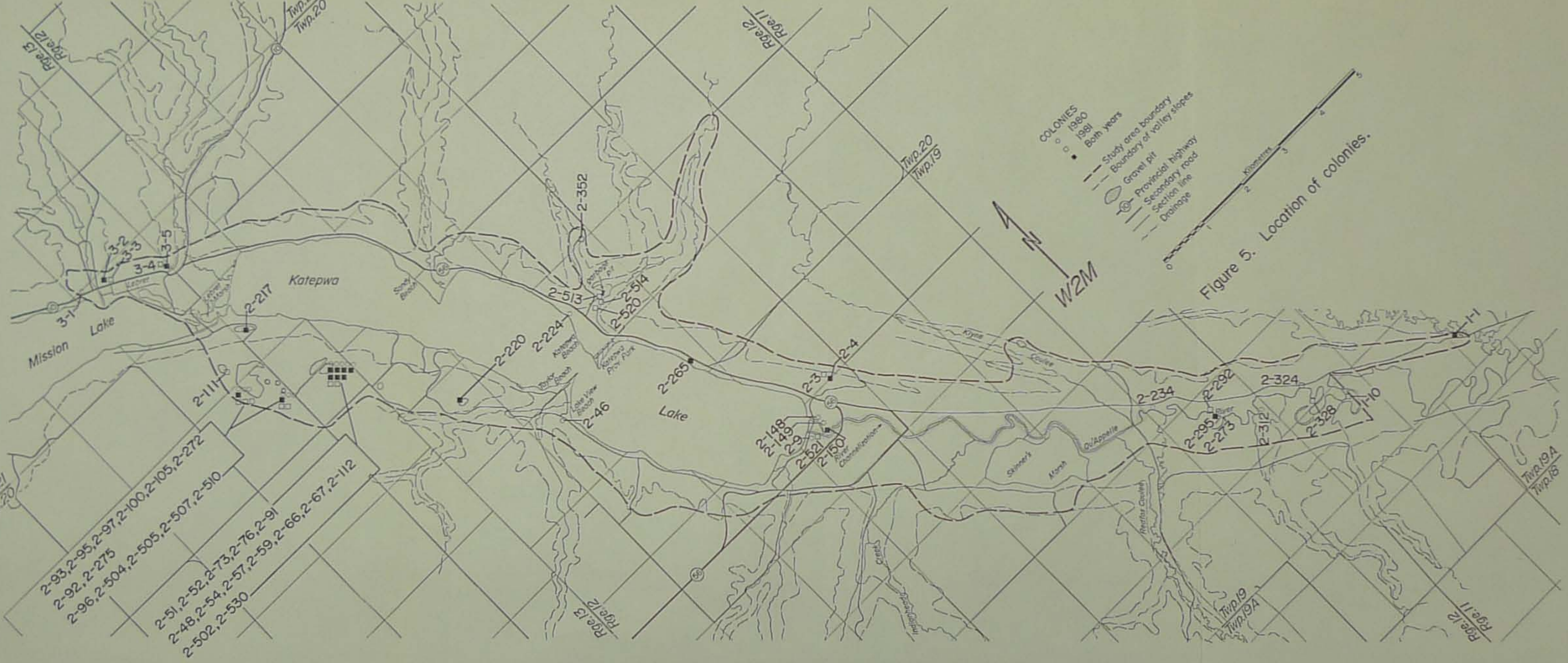


Figure 5. Location of colonies.

Combined height ranged from 2.1 metres to 7.6 metres in Spencer's study compared to 1.1 metres and 11.4 metres in this study. Mean combined height, 4.8 metres, is again greater than this study (3.4 metres).

As Spencer (1962) did not systematically locate all banks in his area, the greater height may be a facet of generally higher relief in Pennsylvania and Vermont or an artifact of observer bias towards spotting taller colony sites.

Length

Length of the used banks showed a great range from 4.2 to 221 metres while the unused sites ranged from 0.23 metres to 371 metres in length. The used sites averaged longer than unused sites (30.9 compared to 21.9 metres). This difference is barely significant (p = .044).

As with height, Spencer's (1962) colonies were on longer banks than those located in this study. Nest banks in his study ranged from 9.1 to 304.8 metres with a mean of 55.2 metres.

Area

The greater length and height of used banks produced a significantly greater bank area at used sites, mean 43.9 square metres (Appendix A-5), than unused sites, mean 24.7 square metres (p = .004). Nonetheless, the smallest used bank was only 3.1 square metres in area and 11 colonies were smaller than 10 square metres. Thus the Bank Swallow will accept relatively small banks.

Orientation

Although Spencer (1962) found 56% of his 25 colonies oriented either east, northeast, or southeast, and Freer (1977) reported 15 of 17 colonies faced east, south, or southwest and no colonies faced north in either sample, neither study proved selection for one orientation. Both lacked data on unused sites and did not systematically locate all colonies. In this study I found some tendency toward selection of south-facing banks (Table 3). Twenty-two percent of all colonies did face south while only 12% of all available sites faced south. However, a chi-squared analysis shows no significant difference in the distribution of used and unused sites among the eight major directions shown in Table 3 ($p = .36$).

Slope

Bank Swallows strongly selected for vertical banks. 47.5% of all colonies had slopes between 86° and 95° and another 45.8% were within 10° of this preferred area (Appendix A-6). Use of chi-squared analysis to compare used and unused banks shows that this selection for near vertical banks is highly significant ($p = .005$). Freer (1977) also reported selection for vertical banks.

Overhang

Freer (1977) reported an apparent preference of Bank Swallows for sites with sod or soil overhanging the banks. Sites with no overhang or a dense overhanging mass were avoided. Freer (1977) hypothesized that a small overhang protected the nest from storms and some types of predators.

This study does not support Freer's (1977) findings. Forty-seven of the 60 colonies (79.7%) had no overhang (Appendix A-7). The used banks had a mean of 4.5% of their length with an overhang compared to 20.2% for the unused sites. This difference is highly significant ($p < .001$).

Vertical Lift

Measurements of vertical lift required to reach 20 metres, 40 metres, and 60 metres from the bank when flying without striking an obstacle confirm Gaunt's (1965 cited in Freer 1977) conclusion that there must be no obstruction of any kind in front of a Bank Swallow colony. The mean lift required at 20 metres, (.12 metres), 40 metres (.05 metres), and 60 metres (.08 metres) from the colony was very significantly less than in front of the unused sites; 1.53, 1.64 and 1.72 metres respectively ($p < .001$ in each case).

Appendices A-8, A-9 and A-10 show that most colonies are located where Bank Swallows must climb less than 1 metre as they fly the first 60 metres out from the bank.

The only exceptions are colonies 62 L12-513 and 514. These colonies face each other across a narrow garbage pit. Because of the excavated dirt pile opposite 513, a Swallow would have to climb 3.5 metres to fly 20 metres directly out from the bank. In practice the Swallows turn sharply after leaving their burrows and fly down the length of the pit. By 40 metres they must climb 1 metre, by 60 metres, 2 metres.

These colonies indicate that an obstacle directly in front of a bank does not preclude its use as long as there is open flying space in one direction. Vertical lift at 40 metres provides an acceptable measurement of the availability of this open space.

It is interesting to note that the complete failure of Bank Swallows to nest in tributary creek banks can be explained by these variables. These tributary valleys are V-shaped and the actual creek banks are often lined with trees. As a result, flying space is severly restricted. The minimum measurement of vertical lift at 40 metres on these tributary creek banks was 1.0 metres. The mean of 6 metres indicates that most tributary creek banks had too little flying space for Bank Swallows.

Vegetation

Both type and the quantity of vegetation differed significantly between used and unused sites at the bank top, talus slope, and bank base. Tables 4, 5 and 6 show that in each case this selection is toward bare soil or early disturbance forbs and away from later successional species, especially trees and shrubs. Chi-squared analysis shows these differences to be highly significant ($p < .001$ in each case).

Appendices A-11, A-12 and A-13 show a strong tendency for less of the ground to be covered by vegetation at used than unused sites. The mean percent ground cover, 55.7% compared to 79.9% at the bank top ($p < .001$), 13.6% compared to 26.8% at the talus slope ($p < .001$) and 13.7% compared to 27.3% ($p = .003$) at the bank base is significantly lower at the used sites in each case.

The most probable explanation of this selection for early successional stages of vegetation and high proportion of bare soil is a preference for new banks. When first created most new banks will have no vegetation at their bases or on their talus. As time passes forbs will colonize, followed by grass, shrubs and trees. At the same time the percentage of the ground vegetated will increase. Thus the amount and type of vegetation at the bank is an indication of its age. Freer (1977) describes how, as banks age, the talus erodes and becomes covered with vegetation.

Eventually the eroded bank becomes too small and loses its attractiveness to Bank Swallows.

This explanation accounts for the selection for less vegetation on the bank base and talus, but the bank top should remain vegetated when the bank is created. However, 50% of all colonies were located in gravel pits in this study. The first step in gravel mining is removal of the top soil. As a result the vegetation had been removed from many of the gravel pit sites. If gravel pits are excluded from the analysis the percentage of the ground vegetated at the bank top is still lower at colonies, 74% compared to 83.7% at unused sites, but the difference is reduced and is no longer statistically significant ($p = .088$). If vegetation remained at these gravel pits, it was always grass and forbes, while trees were typical of the bank top in unused areas such as tributary creek banks. Thus the vegetation preferences at the bank are partly related to bank age and are partly an artifact of other preferences.

While I have argued that the preference for bare soil is related to a selection for young banks, it is possible that a vegetation free bank base and talus make the bank more visible and thus attract Bank Swallows.

Distance to Nearest Bank

The mean distance from a colony to an unoccupied bank, 104.5 metres, is significantly greater than the mean of 63.6 metres between unused banks ($p < .001$) (Appendix A-14). However, Appendix A-18 shows there are significantly more unused banks within 500 metres of a colony (mean = 15.2) than of an unused bank (mean = 11.6) ($p = .003$). This apparent contradiction is due to clustering of colonies in a large cluster of banks at the gravel pits. Removal of this cluster from the analysis leaves the average colony much further from the nearest unused bank than are other unused banks ($p < .001$). The number of unused banks within 500 metres is, however, no longer significantly different ($p = .327$).

Clustering of Colonies

Distance to nearest colony in 1980 and 1981 and the number of colonies within 500 metres (Appendices A-15 and A-17) each indicate a significant tendency ($p < .001$ in each case) for colonies to be clustered. This tendency is at least partly due to the clustering of 30 colonies in the gravel pits (Figure 4).

If the gravel pits are removed from the analysis the average of 1.6 colonies within 500 metres of a colony remains significantly greater than the average of .45 colonies within 500 metres of an average bank ($p < .001$).

Distance to the nearest colony in 1980 and 1981 also continue to show a tendency for colonies to be clustered although this tendency was not statistically significant in 1980 ($p = .102$).

Removal of the banks along tributary creeks, a large cluster of unused sites, reduces the difference between used and unused sites in distance to the nearest colony by 141 metres in 1980 and 156 metres in 1981, but these differences remain statistically significant ($p < .01$). The mean number of colonies within 500 metres of unused banks rises from 1.8 to 2.3, but remains significantly below the 5.3 colonies within 500 metres of used sites ($p < .01$).

Table 2: Origin of Bank for Used and Unused Sites

	USED		UNUSED		COMBINED	
ORIGIN	ABS	REL(%)	ABS	REL(%)	ABS	REL(%)
Other	4	6.7	23	6.6	27	6.7
Riverbank	12	20.0	50	14.3	62	15.2
Road Cut	4	6.7	100	28.7	104	25.4
Gravel Pit	30	50.0	54	15.5	84	20.5
Building Const	6	10.0	8	2.3	14	3.4
Gravel Stkpile	1	1.7	1	0.3	2	0.5
Natural Slump	0	0	10	2.9	10	2.4
Trib Crk Bank	0	0	82	23.5	82	20.0
Lakeshore	1	1.7	21	6.0	22	5.4
Garbage Pit	2	3.3	0	0	2	0.5
	60	100.0	349	100.0	409	100.0

Table 3: Frequency of Used and Unused Sites Oriented in Each Direction

	USED		UNUSED		COMBINED	
ORIENTATION	ABS	REL(%)	ABS	REL(%)	ABS	REL(%)
North	6	10.0	46	13.2	52	12.7
Northeast	6	10.0	38	10.9	44	10.8
East	8	13.3	47	13.5	55	13.4
Southeast	3	5.0	31	8.9	34	8.3
South	13	21.7	38	10.9	51	12.5
Southwest	7	11.7	62	17.8	69	16.9
West	9	15.0	51	14.6	60	14.7
Northwest	8	13.3	36	10.3	44	10.8
	60	100.0	349	100.0	409	100.0

Table 4: Frequency of Dominant Vegetation at Bank Top at Used and Unused Sites

	USED		UNUSED		COMBINED	
	ABS	REL(%)	ABS	REL(%)	ABS	REL(%)
Bare Soil	8	13.3	5	1.4	13	3.2
Forbes	13	21.7	8	2.3	21	5.1
Grass	27	45.0	136	39.0	163	39.9
Shrubs	11	18.3	154	44.1	165	40.3
Trees	1	1.7	46	13.2	47	11.5
	60	100.0	349	100.0	409	100.0

Table 5: Frequency of Dominant Vegetation Types on Talus Slope

	USED		UNUSED		COMBINED	
	ABS	REL(%)	ABS	REL(%)	ABS	REL(%)
Bare Soil	24	40.7	37	10.8	61	15.2
Forbes	14	23.7	78	22.8	92	22.9
Grass	17	28.8	127	37.1	144	35.9
Shrubs	4	6.8	93	27.2	97	24.3
Trees	0	0	7	2.1	7	1.7
	59	100.0	342	100.0	401	100.0

Table 6: Frequency of Dominant Vegetation Types at Bank Base

	USED		UNUSED		COMBINED	
	ABS	REL(%)	ABS	REL(%)	ABS	REL(%)
Water	9	15.0	36	10.3	45	11.0
Bare Soil	21	35.0	70	20.1	91	22.4
Forbes	14	23.3	41	11.8	55	13.5
Grass	13	21.7	143	40.1	156	38.2
Shrubs	3	5.0	57	16.4	60	14.7
Trees	0	0	1	0.3	1	0.2
	60	100.0	348	100.0	408	100.0

Cliff Swallow Colonies

The mean distance to the nearest Cliff Swallow colony from Bank Swallow colonies, 2448 metres, and unused sites, 2535 metres, were statistically indistinguishable ($p = .596$). My hypothesis that competition might prevent adjacent nesting is further disproved by perusal of Appendix A-16. All five sites within 100 metres of Cliff Swallow colonies were used by Bank Swallows.

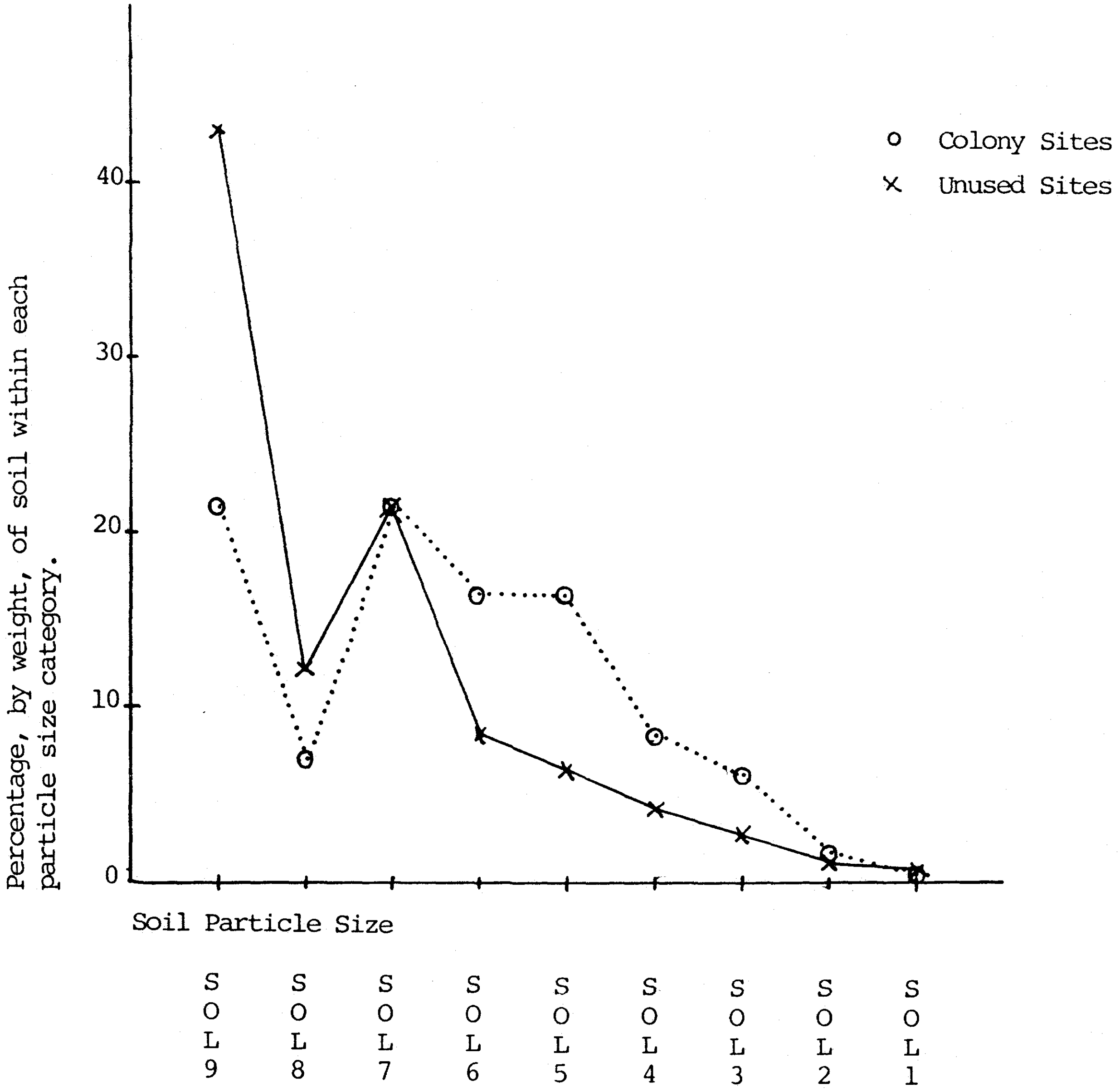
4.3 Soil Type Selected

Spencer (1962) found the soil of the 25 Bank Swallow colonies he studied to be composed of 50% or more of sand or fine gravel. Preference for this particle size is confirmed by the strong selection for fine gravels, SOL3 and SOL4, and sands, SOL5 and SOL6, shown in Figure 6 and Appendices A-21, A-22, A-23, and A-24. The differences in means between used and unused sites indicate strong selection for each of these soil variables ($p < .001$).

Figure 6 also shows that Bank Swallows select against the finer particles of SOL8 and SOL9 ($p < .001$), while SOL7 is a neutral point not selected for or against.

The largest soil particles represented by SOL1 and SOL2 were quite rare comprising less than 2% of most samples. Probably as a result of this rarity no selection for or against these particles could be identified.

Figure 6: Comparison of Soil Particle Size at Used and Unused Sites.



To simplify further analysis the soil variables selected for, SOL3, 4, 5, and 6, were grouped into a new variable SOL13. SOL8 and SOL9, the variables selected against, were also grouped as SOL14. Table 7 shows that while most colonies are in soils with less than 30% SOL14, two were 90 - 100% SOL14. SOL13 at colonies on average is 47.5% of the soil (S.D. = 28.5%) compared to 28.5% for SOL14 (S.D. = 29.8%). Bank Swallows thus clearly prefer sands and fine gravels, probably because they are easier to excavate, but will use some soils dominated by fine fractions.

Some soils dominated by SOL14 had dried to a brick like hardness that would almost certainly be beyond a Bank Swallows excavating abilities. The two colonies with the most fine particles, 62L12-2 and 3, were in the same excavation. Although the soil was 99% and 100% composed of SOL14, this soil contained a small portion of very fine sand. The result was a stable bank allowing holes to be reused for at least three years, and probably longer. Nonetheless presence of the very fine sand made the material relatively easy to excavate. I could easily scratch a number below a burrow using my finger. Presumably Bank Swallows also could scratch their holes without undue difficulty.

The greater use of fine particled soils in this area than observed by Spencer (1962) probably reflects the abundance of fine particles in the Qu'Appelle flood plain. For all sites combined, SOL14 comprises 51.2% of the soil (S.D. = 26.5) compared to 25.6% for SOL13 (S.D. = 24.1).

Table 7: Frequency of SOL13 and 14 at Colony Site

AS PERCENT OF TOTAL SOIL	SOL 13 NUMBER OF COLONIES	PERCENT OF COLONIES
0	1	1.7
1 - 10	7	11.8
11 - 20	6	10.2
21 - 30	5	8.5
31 - 40	7	11.8
41 - 50	4	6.8
51 - 60	9	15.3
61 - 70	4	6.8
71 - 80	3	5.1
81 - 90	10	16.9
91 - 100	3	5.1
	59	100.0

AS PERCENT OF TOTAL SOIL	SOL 14 NUMBER OF COLONIES	PERCENT OF COLONIES
0	0	0
1 - 10	21	35.6
11 - 20	9	15.2
21 - 30	8	13.5
31 - 40	4	6.8
41 - 50	3	5.1
51 - 60	4	6.8
61 - 70	3	5.1
71 - 80	5	8.5
81 - 90	0	0
91 - 100	2	3.4
	59	100.0

4.4 Identifying the Most Important Habitat Features

Cody (1978) used discriminant analysis to identify the habitat features which best separated niches of three British Warblers. My analysis of individual variables indicated significant differences between used and unused sites for 23 variables. I therefore followed Cody in selecting discriminant analysis to determine which of these variables are most important and to check for variables which may be important but were initially masked by the effects of other variables.

Subprogram Discriminant offers two methods of doing discriminant analysis. The direct method creates a discriminant function from the entire set of variables. The other option is a stepwise method which adds one variable at a time to the discriminant function. At each step the variable which makes the greatest contribution to the discriminant function is selected (Nie et al. 1975). Selection continues until further additions do not contribute significantly to discrimination between the groups.

Certain of my variables such as bank height and combined height or length and area are significantly correlated ($p < .001$). Test runs using the direct method identified bank height, talus height, and combined height as the three most important variables. In a stepwise run, once bank height is entered the high correlation with talus height and combined height makes the latter two variables redundant. They no longer contribute significantly to the discrimination. I, therefore, selected the stepwise method as most appropriate for this study.

The stepwise analyses were run using "method = Rao" which selects variables to maximize Rao's V, a measure of the separation between groups (Nie et al. 1975).

The initial discriminant analysis using all numeric bank variables clearly identified bank height and soil type as major factors influencing colony location (Table 8). Other variables making a significant contribution reflect bank age, e.g. overhang and percent bank base vegetated, or clustering.

As discussed in the previous section, the tendency for Bank Swallow colonies to be clustered in this study area appears to be, at least in part, due to the clustering of large numbers of suitable sites at gravel pits and, to a lesser extent, along the river. Similarly large clusters of unused sites are found along tributary creeks which do not offer adequate flying space for the swallows. Clustering, therefore, appears to be a result of, rather than a contributer to, habitat selection. Accordingly I removed distance to the nearest bank, nearest Bank Swallow colony in 1980 and 1981, nearest Cliff Swallow colony, and the number of banks and colonies within 500 metres, from further analysis so they would not obscure the physical features affecting colony site selection.

In the remaining analyses I further reduced the number of variables by using SOL13 and SOL14 instead of SOL1 - SOL9, and by dropping talus height and combined height.

Table 9 clearly shows that by order of selection and weighted co-efficients soil type (SOL13 and SOL14), bank height, bank age as indicated by overhang, percent bank base and bank top vegetated, slope, and vertical lift 40 metres from the bank are the factors which best differentiate between used and unused sites. This analysis successfully classified 81.5% of all cases, a very modest reduction from the 84% achieved with clustering variables included.

At least one group of variables, vertical lift at 20, 40 and 60 metres are not totally linear in relation to bank use. As shown in Appendices A-9 and A-10 vertical lift at 40 and 60 metres have a narrow acceptable range. Sites which require the Bank Swallow to climb more than 1 metre within 40 metres or 2 metres within 60 metres of the bank face are not acceptable. As the discriminant analysis is based on linear combinations of the discriminating variables, I attempted to improve the analysis by classifying some sites prior to the discriminant analysis. Analysis 3 is a repeat of analysis 2 except all sites where vertical lift at 40 metres is greater than 1 are classed as unused and removed before the discriminant analysis begins. This immediately classified 93 cases as unused, leaving only 300 with complete data for the discriminant analysis.

Table 10 shows that this analysis changed the apparent basis of colony site selection as the significance of percent bank top vegetated as a discriminating variable drops to .0525. The cannonical correlate dropped from .5300 to .5211 indicating some decline in discriminating power. However, when the 93 initially classified cases are included 82.6% of all cases, up slightly from 81.5%, were classified correctly. Nonetheless 14 used and 57 unused sites were incorrectly classified.

These data confirm that Bank Swallows selected taller, steeper, recently excavated banks with a sandy soil. Banks must have open flying space in front of the bank or they will not be selected. Bank Swallows may also be somewhat attracted by unvegetated areas.

Bank Swallows probably initially locate a nesting bank visually from the air, although subsequent birds may be attracted by the presence of other swallows at the site. A tall vertical bank would be easily visible from the air. Unvegetated areas at the talus slope and bank base might make a bank more conspicuous and therefore more likely to be used. As Swallows repeatedly fly in circles in front of their colony during the initial phases of burrow excavation (Hickling 1959), any bank with inadequate flying space would be immediately rejected.

Choosing a bank with a preferred soil may happen by trial and error. Observations at 62L12-111 support this view. On 29 May 1981 I observed activity by at least 20 pairs at this site. By 7 June I identified six holes which were active. Only one of these nests was still active on 26 June.

Bank 62L12-111 was created when topsoil was bulldozed off the gravel layer. As a result the soil was poorly structured and unstable. It also contained many small rocks. All of the original pairs but one appear to have abandoned this bank after experiencing difficulty excavating burrows. This suggests that Bank Swallows may sample banks which meet other requirements and move on if the soil is unsuitable for burrow excavation.

Table 8: Variables Selected
In First Discriminant Analysis

STEP	VARIABLE	CHANGE IN RAO'S V	SIGNIFICANCE	STANDARDIZED COEFFICIENT
1	SOL5	.4440D+02	.0000	.89839
2	Bank Height	.1750D+02	.0000	.52462
3	# of Colonies Within 500m	.1422D+02	.0002	.32548
4	Nearest Bank	.9428D+01	.0021	.25442
5	Overhang	.1045D+02	.0012	-.17811
6	% Bank Base Vegetated	.8243D+01	.0041	-.18885
7	Nearest Cliff Swallow Colony	.6960D+01	.0083	-.42316
8	SOL7	.7097D+01	.0077	.23598
9	Nearest 1981 Colony	.8277D+01	.0040	-.47656
10	Nearest 1980 Colony	.5622D+01	.0177	.31554
11	Slope	.3804D+01	.0511	.19629
12	% Bank Top Vegetated	.2907D+01	.0882	-.20225
13	Length	.2726D+01	.0988	.15371
14	SOL8	.2582D+01	.1081	.28587
15	SOL3	.2969D+01	.0849	.45738
16	SOL4	.1048D+01	.0012	-.59002
17	Vertical Lift at 40m	.2642D+01	.1040	-.17423
18	Cosine Orientation	.2693D+01	.1008	.14007
19	% Talus Vegetated	.2275D+01	.1330	-.13531

Table 9: Variable Selected In Second Discriminant Analysis

STEP	VARIABLE	CHANGE IN RAO'S V	SIGNIFICANCE	STANDARDIZED COEFFICIENT
1	SOL13	.6879D+02	.0000	-.29002
2	Bank Height	.1913D+02	.0000	-.48697
3	Overhang	.1549D+02	.0001	.26225
4	% Bank Base Vegetated	.1569D+02	.0001	.36613
5	Slope	.7310D+01	.0069	-.22665
6	% Bank Top Vegetated	.8520D+01	.0035	.25664
7	Vertical Lift at 40m	.5433D+01	.0198	.21317
8	SOL14	.6219D+01	.0126	.37545
9	Length	.3295D+01	.0695	-.15401
10	Cosine Orientation	.2908D+01	.0881	-.13928

Table 10: Variable Selected in Third Discriminant Analysis

STEP	VARIABLE	CHANGE IN RAO'S V	SIGNIFICANCE	STANDARDIZED COEFFICIENT
1	SOL13	.4329D+02	.0000	-.23078
2	Bank Height	.1831D+02	.0000	-.55393
3	% Bank Base Vegetated	.1843D+02	.0000	.41300
4	SOL14	.9781D+01	.0018	.42066
5	Overhang	.7649D+01	.0057	.27475
6	Slope	.6693D+01	.0097	-.28474
7	% Bank Top Vegetated	.3761D+01	.0525	.22937
8	Cosine Orientation	.3154D+01	.0757	-.16984

4.5 Colony Size

During 1980, 293 Bank Swallow nests were located in 40 colonies and in 1981, 318 nests were present in 39 colonies. Table 11 shows that the colonies ranged in size from 1 to 48 nests with a mean of 7.7 nests per colony. The smallest colonies of 1, 2, and 3 nests were most common, comprising almost 40% of all colonies. Most of the Bank Swallows, however, nested in larger colonies. Sixty-eight percent of all nests were in colonies of 10 or larger.

I attempted to determine what habitat features determined colony size by correlating each habitat variable with the total number of nests over two years and with colony size in 1980 and 1981. No correlations were significant over both years (Table 12). There was a trend toward larger colonies in sandier soils, but this trend was not significant in 1980. Freer (1977) reported a trend toward smaller colonies as banks age. The negative correlation between percent of talus vegetated and colony size supports this as does the positive correlation between overhang and colony size in 1980. However this trend was not significant in 1981.

Analysis of the 30 colonies in the gravel pits showed length (corr = .3736, p = .042) and area (corr = .3725, p = .043) were correlated with colony size. These colonies were similar, usually consisting of a single row of burrows. Bank length can determine colony size in this simplified situation.

Interaction of variables could hide the factors controlling colony size. I, therefore, tested the influence of bank height, slope, percent bank base vegetated, length, SOL14, and SOL13 on colony size in a multiple regression. No significant relationship was found with colony size in either year or for total nests.

This lack of a clear correlation between habitat and colony size is probably due to the generally small colonies. Table 11 shows that during the two years only 4 of 79 colonies had more than 20 nests while almost half of all colonies had less than 5 nests.

Colonies in this study were much smaller than reported from other areas. The 55 colonies studied by Hoogland and Sherman (1976) ranged from 1 to 451 nests in size. Forty percent of all colonies in their study were larger than 50 nests. Mean colony size in Britain is 37.6 nests (Morgan 1979) while Erskine's (1979) analysis of nest record schemes showed mean colony size in Canada is 42 nests. However, there is considerable variation across Canada. Colonies in the Maritimes, Quebec, Ontario and British Columbia averaged 56, 38, and 59 nests respectively. Colonies on the Canadian prairies averaged only 5 nests.

The small colony size in my study is thus typical of the prairies. This probably reflects the low relief and small banks available on the prairie. While comparative data on bank availability is not available from other areas, the colonies studied by Spencer (1962) were both taller and had more burrows than those present in this study.

Table 11: Colony Size

NESTS IN COLONY	NUMBER OF COLONIES 1980	1981	COMBINED	NUMBER OF NESTS
1	8	7	15	15
2	2	4	6	12
3	7	4	11	33
4	2	3	5	20
5	1	4	5	25
6	2	3	5	30
7	3	1	4	28
8	2	1	3	24
9	0	1	1	9
10	1	0	1	10
11	4	0	4	44
12	1	0	1	12
13	1	2	3	39
15	1	0	1	15
16	1	4	5	80
17	1	1	2	34
18	0	1	1	18
20	1	1	2	40
24	1	1	2	48
27	1	0	1	27
48	0	1	1	48
	40	39	79	611

Table 12: Bank Characters Correlated with Colony Size

VARIABLES	r	p
SOL6 with Total Nests	.38402	.003
% Talus Vegetated with Total Nests	-.25227	.054
% Talus Vegetated with Nests in 1980	-.3804	.007
Overhang with Nests in 1980	.3101	.030
SOL6 with Nests in 1980	.3123	.022

4.6 Physical Characteristics of the Nest

Tunnels were located an average of 111.2 cm above the bank base or talus slope with a range from 15 cm to 340 cm. The lowest measurements obtained included nests at colonies along the river with nests directly above water. These nests were 15 cm, 15 cm, 18 cm, 20 cm, 22 cm, 30 cm, and 32 cm, above the water at 62L12-328 in 1981. These colonies were along the river with nests directly above water. As the river had risen since the nest initiation period these nests were relatively higher than this when the swallows excavated their tunnels. Thus the closest to the bank base that tunnels were actually constructed was the 25 cm of two nests at 62L12-220 in 1981.

Tunnels were quite close to the ground compared to colonies in England where burrows averaged 290 cm above the base of the bank (Morgan 1979). The difference is probably due to generally smaller banks in my study area as Morgan (1979) noted a tendency for Bank Swallows to nest higher when higher sites were available. A highly significant correlation ($p < .001$) of .727 between bank height and height of the tunnel in this study confirms this relationship.

Nest tunnels were located an average of 64.5 cm (S.D. = 45.5 cm) below the top of the bank but ranged from 10 to 320 cm. Distance from the bank top shows a positive correlation of .671 ($p < .001$) with bank height.

The 545 tunnels measured in this study had been excavated to a mean depth of 63.6 cm (S.D. = 19.3) and ranged from 15 to 145 cm. Mean tunnel depth is similar to the 65.6 cm reported for 29 holes by Hickling (1959) and 71 cm reported for 89 holes by Stoner (1936). Beyer (1938) reported an average of 76 cm for tunnels in sand and 40 cm for those in clay, while Wickler and Marsh (1981) reported a mean of 90 cm for 34 burrows in sand. The range of tunnel depths in this study thus lies inside the range reported by other authors.

Earlier authors (Stoner 1936, Beyer 1938) reported that tunnels dug in sand were deeper than those in clay soils. However, initial analyses showed no significant correlation between SOL13 or SOL14 and depth in this study.

As discussed earlier the soil at 62L12-2 and 3 was 99 - 100% SOL14. Nonetheless the characteristics of these banks were more like a very fine sand than clay. Certainly they were more easily excavated than clay banks. I therefore excluded 62L12-2 and 3 and redid the analysis.

Correlation of the 488 burrows remaining shows a correlation of .076 between depth and SOL13 which is barely significant ($p = .047$). The correlation of -0.118 ($p = .005$) between depth and SOL14 appears much more important. Clearly the presence of fine particles normally impedes burrow excavation and produces shallower burrows. Colonies 62L12-2 and 3 are exceptions to this rule, probably due to soil differences not detectable by the particle separation done in this study.

4.7 Nest Chronology

The mean, mode, first, and latest days when incubation started, eggs hatched, and young fledged, shown in Table 13, were very similar in 1980 and 1981. Data from 1980 and 1981 were, therefore, combined in Figure 7 to show the number of nests starting incubation, hatching, and fledging in each 3 day period through the spring and summer.

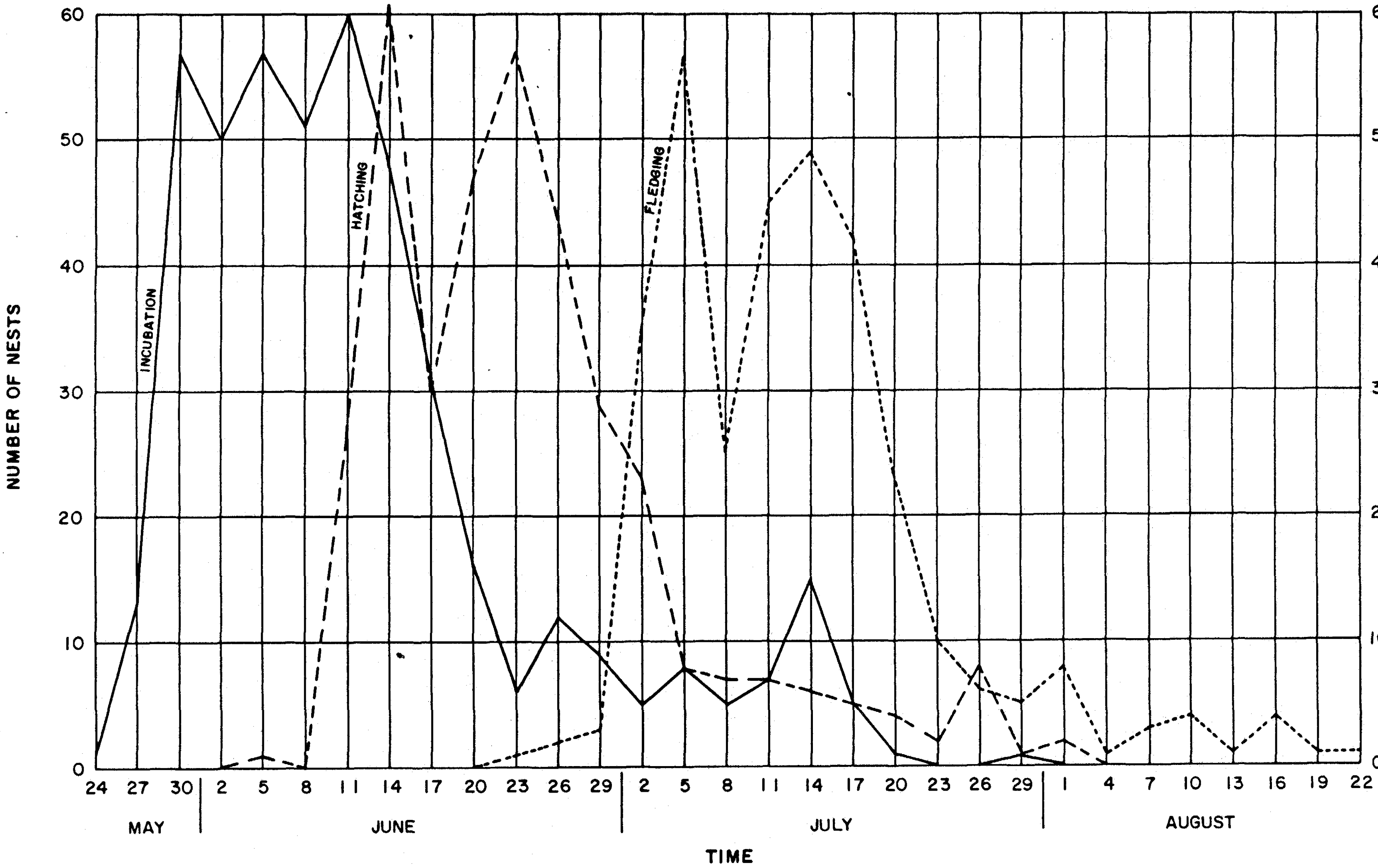


Figure 7 Chronology Of Bank Swallow Nesting Near Katepwa Lake In 1980 And 1981.

The first pairs began incubating during the last week of May in both years. Stoner (1936) reported the first eggs at Oneida Lake in New York on 19 May. Allowing five days to lay a clutch of five, the first New York Bank Swallows would have started incubating about 22 May, practically the same date as the earliest nest in this study. The peak of starting incubating in the Qu'Appelle extended from 29 May to 11 June. Nest initiation then declined with incubation of the latest clutch beginning 29 July 1981. Petersen (1955) reports the latest start of a clutch he observed in Wisconsin was 5 July, placing incubation at 10 July. In New York, Stoner (1936) reported fresh eggs as late as 13 July. Thus the last pair starting incubating on 29 July 1981 were sixteen days later than other reports.

Hatching and fledging follow, respectively, about fourteen and thirty-four days after incubation starts. The earliest young left the nest on 24 June 1980. A peak in fledging occurred around 4 July each year, with a high fledging rate continuing until 20 July. After this date the number of active nests at the colonies dropped rapidly with the latest nests fledging on 10 August 1980 and 21 August 1981.

Stoner (1926, and 1936) thought a small proportion of Bank Swallow pairs raised second broods. He based this on observation of incubating adults as late as 27 July. Petersen (1955) found no evidence of second nestings and pointed out that Stoner did not establish whether his late pairs were rearing second broods or were renests after failure of first nests.

Figure 7 shows significant overlap between fledging and start of incubation, leaving open the possibility that early nesters laid a second clutch. Additional evidence for this possibility is provided by five cases where two nestings occurred in the same tunnel. In each case the first nest was successful with young flying before 5 July. Incubation of the second clutch started 4, 7, 10, 17, and 18 days after the first young fledged. Only the nest in which incubation began four days after the first young fledged was successful.

The rapidity of the one renest suggests it was almost certainly a different pair moving into the tunnel, perhaps after their own nest was destroyed. The remaining cases may represent second clutches. Unfortunately my attempts to confirm this by banding failed.

Figures 8 and 9 show that early nests are more likely to be successful. The mean start of incubation for successful nests is 9 June compared to 19 June for unsuccessful nests. The difference is statistically significant ($p < .001$). Five of six nests initiated after 15 July failed in 1980, and all six nests initiated after this date in 1981 failed.

Figure 10 shows that later Bank Swallow nests had smaller clutches (corr = -0.547, $p < .001$). Reductions in clutch size by late nesting Bank Swallows were also reported by Stoner (1936) and Petersen (1955).

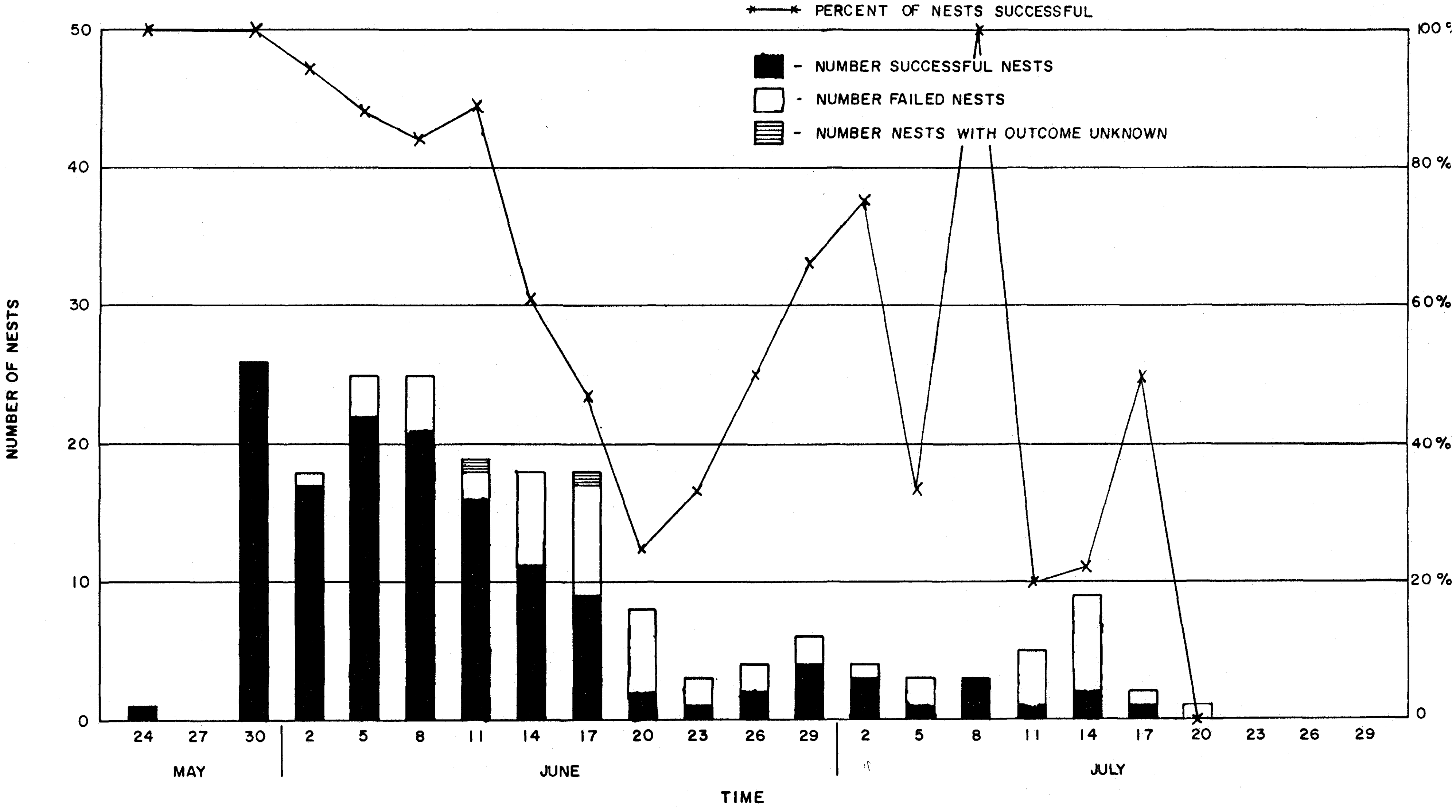


Figure 8 Chronology Of Start Of Incubation In 1980 Showing Success And Failures.

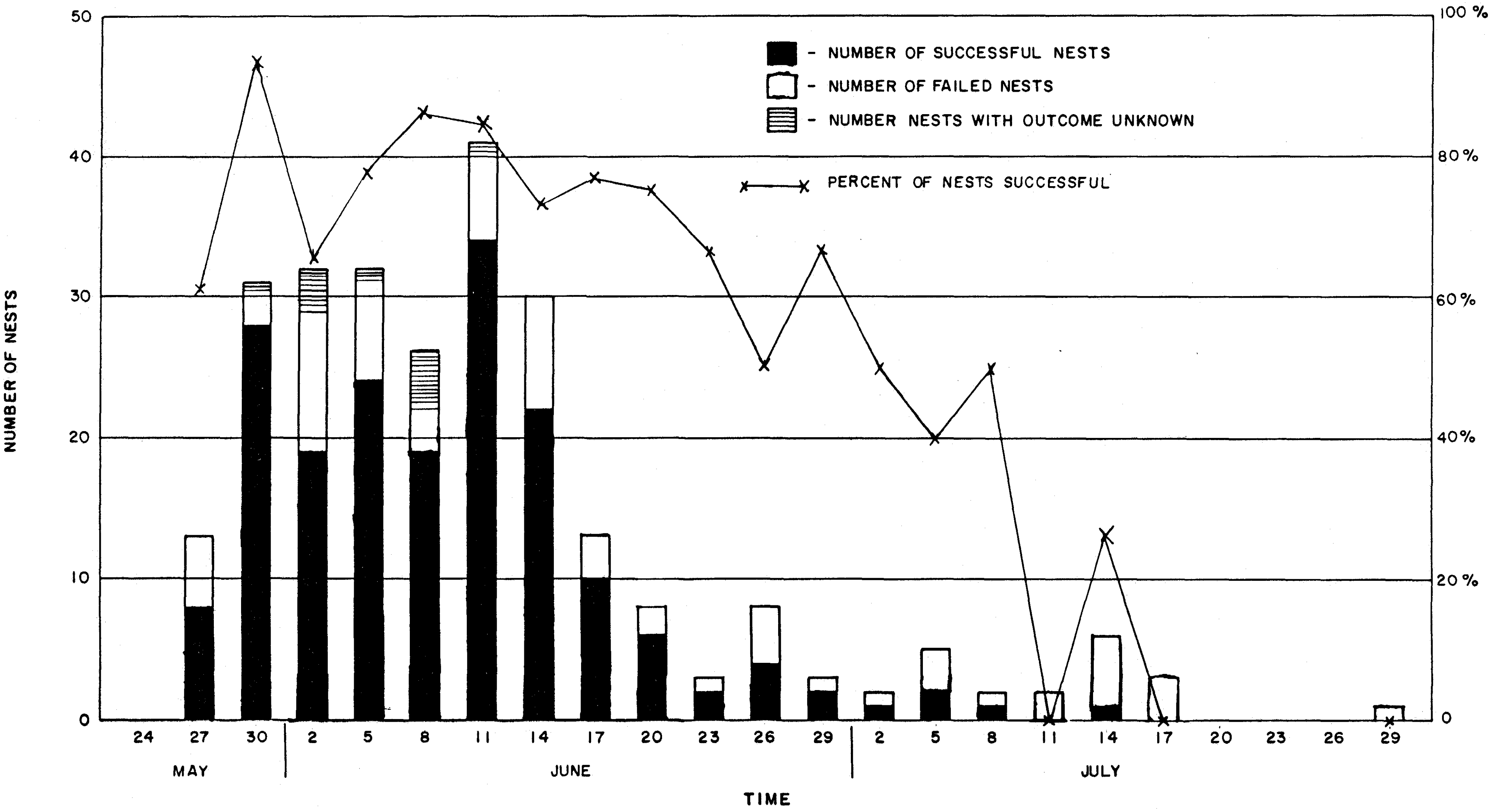


Figure 9 Chronology Of Start Of Incubation In 1981 Showing Success And Failure.

Table 13: Comparison of Nest Chronology In 1980 and 1981

		MEAN	MODE	FIRST	LAST
Start Incubation	- 1980	June 13	June 9	May 23	July 19
	- 1981	June 11	June 12	May 26	July 29
Hatch	- 1980	June 25	June 23	June 6	July 31
	- 1981	June 24	June 14	June 10	July 31
Fledge	- 1980	July 14	July 13	June 24	August 10
	- 1981	July 13	July 11	June 27	August 21

4.8 Reproductive Ecology

Complete clutches of 218 Bank Swallow nests averaged 4.87 (S.D. = 0.92) eggs. Clutches ranged from two to seven eggs but four, five and six eggs were most common (Table 14). Mean clutch size was 4.45 in 1980 compared to 5.0 in 1981. The difference is probably because only 51 nests were observed in 1980, all from the latter part of the breeding period when clutches are smaller. The 167 observations in 1981 covered the entire breeding season. Thus the mean clutch size of 5.0 eggs in 1981 is most representative of this area.

Clutch size in this study is similar to that reported for Michigan and slightly above levels reported for New York, Wisconsin, and Britain (Table 15).

Successful nests started with significantly larger average clutches than unsuccessful nests, 5.18 compared to 4.32 ($p < .001$). This difference is probably due, at least in part, to the smaller clutch size and higher failure rate of late nests.

Table 14: Clutch Size in 1980 and 1981

EGGS IN CLUTCH	NUMBER OF NESTS 1980	1981	TOTAL
2	2	1	3
3	7	5	12
4	17	36	53
5	16	77	93
6	9	47	56
7	0	1	1

Table 15: Bank Swallow Clutch Size Reported in Several Studies

MEAN CLUTCH	MOST COMMON CLUTCH	RANGE	STUDY AREA	AUTHOR
4.98	-	3 - 8	Michigan	Hoogland & Sherman (1976)
4.8	5	2 - 6	Wisconsin	Petersen (1955)
4.8	5	2 - 7	New York	Freer (1977)
4.78	5	2 - 6	Britain	Morgan (1979)
5.0	5	2 - 7	Saskatchewan	This Study (1981)

I made repeat observations on 498 of the 588 nests observed over two years . Data from these nests were used to calculate Mayfield's index (Table 18). These indices indicate significantly higher nest success in 1981 than 1980 ($p = .01$). The observed increase in nest success in 1981 is mostly due to greater construction and mining losses in 1980 (Table 17) but may, in part, be an artifact of the higher percentage of late nests observed in 1980 than in 1981.

The Bank Swallow nest must survive six days of egg laying, 14 of incubation and 20 with young, a total of 40 days. The probability of a nest surviving this period is calculated by taking the probability of surviving for one day (1 - Mayfield's Index) to the 40th power. This calculation indicates that a Bank Swallow starting egg laying in 1980 had a 43.5% chance of fledging young compared to a 63.4% chance in 1981.

An average of 4.4 (S.D. = 0.990) young fledged from each of the 91 successful nests at which I was able to count the total number of young fledging. Five was the most common number of fledglings (Table 16). These data are probably biased towards larger clutches as when only one or two young were observed in a nest I could not be certain if this represented the entire clutch or if several had already left the nest.

Table 16: Number of Young Fledged From Bank Swallow Nests

NUMBER OF YOUNG FLEDGING	NUMBER OF NESTS
2	4
3	12
4	26
5	40
6	9

At 46 nests the full clutch and number of young fledging were determined, allowing estimation of productivity. Of the 241 eggs in these nests, 218 or 90.5% fledged successfully.

During the study 329 nests were known to be successful. The mean clutch of 5.0 eggs and .905 probability of each egg fledging indicate production of 1,489 fledglings. Fifty-one of 80 nests whose outcome was not determined should also have succeeded and produced 230 young. Total production of Bank Swallows in the study area over a two year period was thus approximately 1,719 fledglings.

Of 183 nest failures, I could only determine the cause with certainty in 89 cases (Table 17). Forty-three of these failures were due to bank slumps and tunnel cave-ins, a problem which Stoner (1936) also reported as a major cause of nest failure. During 1981 a heavy rainstorm caused a series of slumps and cave-ins. One section of a bank moved as a block in a rotational slump. Two Swallow tunnels totally contained in the block survived at their new angle and were successful.

Thirty-seven nests failed due to human activities. Of these nests five were accidentally destroyed by the author, while 25 were destroyed by construction and gravel mining. Most construction or mining losses occurred in 1980 when one entire colony was destroyed as part of the Qu'Appelle conveyance construction. Cooperation of gravel pit operators also reduced nest losses from mining as the study progressed.

Predation was uncommon during the study. One Bank Swallow was taken by a Western Plains Garter Snake (Thamnophis radix) which entered a tunnel from above at 62L13-2. However, this predation did not cause a nest failure, as young were already flying from all nests in the colony.

Deer mice (Peromyscus maniculatus) nesting in a Bank Swallow tunnel at 62L12-217 in 1981 ate eggs of 9 nests. Only one nest, that furthest from the mouse nest, was successful at this colony. Stoner (1936) reported a deer mouse in a Bank Swallow colony but could see no evidence of it having damaged the eggs or young. Deer mice have been reported as a major predator of Spotted Sandpiper (*Actitis macularia*) eggs (Oring, Lank, and Maxson 1983).

Observed predation rates at Bank Swallow colonies in this study were probably lower than the population norm. Predation is likely irregular, depending on learned behaviour of individual predators. The 1982 predation by a mammal in four colonies, three of which were used successfully by Swallows in 1980 and 1981, is an example. A longer study or larger sample would, therefore, be expected to include more cases of predation and show a higher predation rate.

One probable source of nest failure not shown in Table 17 is flooding. In 1981 the Qu'Appelle river rose during the nesting season and some nests were observed only 15 cm above water level. The soil around these nests was wet, probably causing nest failure. However, these colonies were not monitored weekly, so the nest success is not known.

Table 17: Causes of Nest Failure

	1980	1981	TOTAL
DESTROYED BY AUTHOR	2	3	5
FAILURE DUE TO MAN:			
1) VANDALISM	3	1	4
2) DISTURBANCE BY CHILDREN PLAYING	2	0	2
3) MINING OR CONSTRUCTION	20	5	25
4) ADULTS SHOT	1	0	1
	26	6	32
NATURAL MORTALITY:			
1) PREDATION BY MOUSE	0	9	9
2) TUNNEL CAVE-IN	3	8	11
3) BANK SLUMP	16	16	32
	19	33	52
UNKNOWN CAUSE:			
1) NEST EMPTY EARLY	8	12	20
2) ABANDONED BEFORE EGGS LAID	4	5	9
3) EGGS ABANDONED OR FAILED TO HATCH	17	17	34
4) EGGS BROKEN	0	3	3
5) YOUNG DEAD	6	2	8
6) ADULT DEAD IN NEST	0	1	1
7) OTHER	13	6	19
	48	46	94
TOTAL	95	88	183

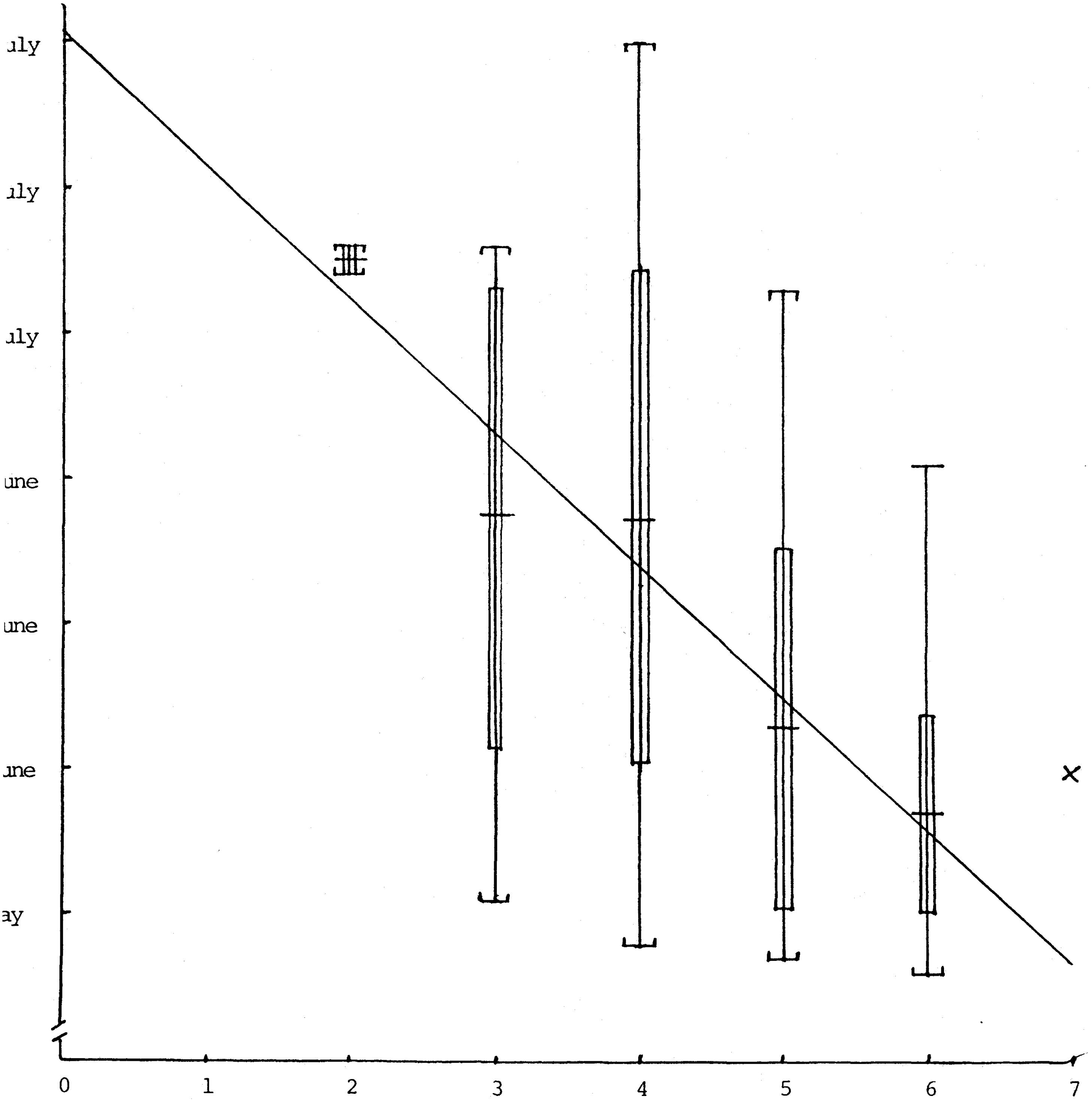


Figure 10: Relationship of Clutch Size to Date of Start of Incubation. Vertical line represents the range, horizontal line the arithmetic mean, with one standard deviation on each side of the mean represented by a vertical bar. The lone clutch of 7 is represented by an X. Diagonal line represents the linnear regression.

4.9 Habitat Features Affecting Nest Success

The mean height of successful nests was significantly lower (102.7 cm) than that of unsuccessful nests (127.0 cm) ($p < .001$). Unsuccessful nests were also on higher banks 2.39 metres compared to 2.08 metres ($p < .01$) than successful nests. This result was contrary to my expectations. Bank Swallows selected taller banks in this study and I had expected this selection to offer additional protection from predators and, at colonies along the river, from flooding. However, neither predation, nor flooding, was a major cause of nest failure at the colonies I monitored. The major identifiable causes of nest failure were bank slumps, mining or construction, and tunnel cave-ins. However, mean bank height at nests failing from these causes, 1.95 metres, 2.43 metres, and 2.32 metres, does not explain the greater losses at taller sites.

A potential source of error with this type of data is a single incident destroying all or part of a colony. Such an incident could bias nest data unless the sample is very large. I therefore removed 45 nests at 6 colonies which had been destroyed by single incidents such as slumps, mining, mouse predation, and soil unsuitability. This left mean bank height of unsuccessful nests at 2.22 metres, still greater than the 2.08 metres of successful nests.

I can not identify any selection force or source of error accounting for this difference. The selection against taller sites may be an accident of sampling without biological significance. Conversely further study may show that taller banks offer protection from predators but are more vulnerable to other causes of nest failure.

During 1980 and 1981 no significant difference in distance from the bank top was detected between successful and unsuccessful nests. Nonetheless a series of casual observations in 1982 indicate this distance is important. A mammal excavating down to the nest chamber destroyed a series of nests at 62L12-510, 500, 96 and 60 in 1982. All nests at the first three colonies were destroyed. These nests were from 42 cm to 11 cm below the bank top, all less than the average of the study. At 62L12-60 one nest was dug out and unsuccessful attempts made to reach three others. The soil sloped up behind the bank at this colony. As a result most nest chambers were 40 to 60 cm below ground and apparently beyond the reach of the predator.

Stoner (1936) reported a skunk (Mephitis mephitis) digging down to as many as five nests over a two night period. Nests lower than 60 cm were usually safe from this skunk.

These observations demonstrate the selective advantage of nesting far enough from the bank top. This advantage is real even though it did not operate during the two years of my study. The lone case of predation by a garter snake also demonstrates the disadvantage of nesting too close to the bank top.

During this study successful nests were slightly, but significantly, deeper than unsuccessful nests (65.6 cm to 58.9 cm, $p < .001$). This difference could be due to late nests being shallower and less successful. However, deeper nests may confer real advantages. One advantage would be increased probability of surviving a slump. During the study it was not uncommon to find a tunnel 10 or 15 cm less deep part way through the nesting cycle due to a bank slump. As bank slumps were responsible for 35 nest failures, deeper tunnels may confer an advantage.

As tunnel depth is correlated with soil type and distance to the bank base and bank top correlate with bank height, at least these bank characters should show correlations with nest success. However, regressions on grouped nest data from all colonies except 62L12-9, which was bulldozed, showed no significant correlations between Mayfield's index and colony size, bank height, slope, SOL13, SOL14, or percent bank base vegetated. Pearson's correlation between Mayfield's index for each colony and all variables revealed only one possibly meaningful correlation.

SOL3 and SOL4 show positive correlations with Mayfield's index (.2890 and .2600) indicating increased nest losses with increased amounts of fine gravels. This relationship is barely statistically significant for SOL3 ($p = .044$) and not statistically significant for SOL4 ($p = .071$). The relationship may reflect the vulnerability of gravel banks to tunnel cave-ins, slumps, and mining.

The lack of correlations is undoubtedly due in part to small sample size. Inclusion of data from 1982, for example, may have clarified the relationship between bank height and nest success.

4.10 Comparative Nest Success

Comparison of Bank Swallow nest success in this study with four other species (Table 18) shows both Tree and Barn Swallows have significantly higher nest success than the Bank Swallow ($p = .01$). However, all four sets of swallow data show significantly greater nest success ($p = .01$) than similarly sized territorial passerines, the Dickcissel (*Spiza americana*) and Clay-colored Sparrow.

Table 18: Comparative Nest Success of Five Species

SPECIES	MAYFIELD'S INDEX(m)	EXPOSURE (DAYS)	LOSSES (NESTS)	SOURCE OF DATA
BANK SWALLOW (1981)	.0113	7,816	88	This Study
BANK SWALLOW (1980)	.0206	4,612.5	95	This Study
TREE SWALLOW	.0036	27,677	101	P.N.R.S. [1]
BARN SWALLOW	.0073	9,216	67	P.N.R.S. [1]
CLAY-COLORED SP	.052	1,922	101	P.N.R.S. [1]
DICKCISSEL	.0706	5,025	355	(Zimmerman, 1982)

[1] Prairie Nest Records Scheme

4.11 Other Species Nesting at Bank Swallow Colonies

During the study five additional species, Belted Kingfisher (Megaceryle alcyon), House Wren (Troglodytes aedon), House Sparrow (Passer domesticus), Mountain Bluebird (Sialia currucoides), and Brewer's Blackbird (Euphagus cyanocephalus), were observed nesting in old Bank Swallow tunnels.

The Belted Kingfisher is quite capable of excavating its own tunnel. The one nest observed at colony 62L12-265 in 1980 may have been dug by the Kingfisher on the same bank as that used by Bank Swallows. However, two Belted Kingfisher pairs simply enlarged marked Bank Swallow tunnels from the previous year.

Two pairs of House Wrens nested in Bank Swallow tunnels in 1980. Both tunnels were filled with twigs in typical Wren fashion. Both banks had trees or shrubs at the bank top. As only 20% of colonies had woody vegetation at the bank top, this may have inhibited more extensive use by Wrens of the Bank Swallow tunnels.

Four of the five Mountain Bluebird nest attempts observed in Swallow tunnels were successful. One pair raised two broods in the same tunnel, another started a nest after Swallows left the tunnel 5 July. All Bluebird nests were in the gravel pits on the prairie area south of Lebret (Figure 2). The mix of native grass and aspen trees here apparently provided excellent Bluebird habitat.

With the exception of one possible nest at 62L12-265, all House Sparrow nestings were at 62L12-2 and 3 or 62L13-2. The last is an urban site in the town of Lebret, while the former are on a rural hillside 1/4 mile or more from buildings.

In 1980, I observed eight House Sparrow nests at 62L12-2, one at 62L12-3, and two at 62L13-2. House Sparrows nested at these colonies again in 1981, although they were not counted. They seemed to experience good nest success. The three colonies used by House Sparrows are similar in having a fine particle soil which is stable. Thus tunnels last for several years, perhaps allowing House Sparrows to establish a nesting tradition at the colony.

The lone Brewer's Blackbird nest was not really in a Swallow tunnel but in a niche made by erosion at the tunnel mouth. Nonetheless, the old Bank Swallow tunnel provided the base for this riverbank nest site. The nest failed due to human actions.

Each of these species appeared to interact little with the Bank Swallows. At 62L12-2 House Sparrows used many of the higher tunnels. Occupancy of old tunnels by House Sparrows may cause some Bank Swallows to move, gradually reducing colony size on a stable bank like 62L12-2. However this interaction was not studied.

The House Wren nesting at 62L12-3 may have helped the Bank Swallows by chasing rodents, including potential egg predators such as a chipmunk, off the bank. On 13 June 1980 I observed the Wren chase a Least Chipmunk (_Eutamias minimus_) and a Thirteen-lined Ground Squirrel (_Spermophilus tridecemlineatus_) off the bank. Both rodents were totally ignored by the Bank Swallows.

5. DISCUSSION

The principal purpose of this study was to determine what features Bank Swallows select for nesting habitat and to relate these findings to the broader question of why Bank Swallows nest in colonies. I hypothesized that Bank Swallows select colony sites on the basis of certain environmental features and that these features contribute to nest success.

Comparison of used and unused banks in the study confirm the first hypothesis - Bank Swallows selected taller, steeper, recently excavated banks with a sandy or gravelly soil and open flying space in front of the bank. While these features determined whether a site was used, colony size could not be consistently related to any variable.

Colony size was small in this study as is typical of the prairies. Absence of the large colonies of 400 or more nests reported from other regions (Hoogland and Sherman 1976) in the prairie provinces is undoubtedly related to habitat. An abundance of suitable sites in this region allowing Bank Swallows to disperse in small colonies or lack of the superior sites which would attract large colonies are possible explanations. The generally low relief on the prairie, greater bank height of colonies in Vermont (Spencer 1962) than this study, and observed vulnerability of many colonies to predators in 1982, indicate the latter is the true explanation. Banks in the study area mostly provide marginal habitats for Bank Swallows and so do not attract large colonies.

While analysis of 1980 and 1981 data showed no clear relationship between bank characters and nest success, this is probably due to small sample size and lack of predation during the study period. A larger sample or longer study would have included more nests on the poorer portions of the habitat and increased the probability of observing high rates of predation such as noted in 1982.

Selection of tall banks and vertical banks are complementary and act to reduce predation. Selection for younger banks is most likely an artifact of this selection as banks become shorter and less steep as they age (Freer 1977). Predation by digging mammals such as I observed is commonly reported in the literature (Stoner 1936, Freer 1977, Hoogland and Sherman 1976). Morlan (1972) even reported a Black Bear, Ursus americanus, digging out Bank Swallow nests. A Bank Swallow's best defence against such predators is to nest high enough to be out of reach and far enough below the bank top to be beyond economical digging range. Both tunnel distance to the bank base and the bank top are positively correlated with bank height, suggesting bank height will be a key factor influencing nest success.

Nesting on tall, steep banks will also provide protection from other reported nest predators including snakes (Blem 1979, Plummer 1977, Freer 1977, This Study), weasels, Mustela erminea, (Baudoin 1980), and chipmunks (Ginevan 1971, Freer 1977). Finally along water courses, taller banks provide protection from flooding. Some nests along the Qu'Appelle River were almost certainly destroyed in 1981 by rising waters.

Selection for sandy soil and fine gravels is probably due to ease of tunnel excavation. Clay soils dry to a brick like hardness and may be impossible for Bank Swallows to dig into. Tunnel depth is correlated with soil type with the deepest tunnels found in sands and fine gravels.

Tunnel nesting protects the nest from avian predators and brood parasites. It also provides the advantage of thermal stability. Ellis (1982) showed that cavity temperatures ranged from 15°C to 24.9°C while temperatures on the bank face varied between 2.4°C and 46.7°C. While the burrow temperature was always lower than the incubation temperature of 33 - 34°C, by nesting in tunnels Bank Swallows clearly avoid the temperature extremes which presumably would place the greatest stress on incubating adults and young birds. Unfortunately Ellis (1982) did not have adequate data to relate burrow temperature to tunnel depth or other features of the nest.

The deeper tunnels excavated by Bank Swallows in sandy soils may provide greater protection from predators and bank slumping, a major source of nest failure. Due to slumping Bank Swallow tunnels were often shortened by 10 cm or more during the nest period. However, this never affected nest success unless the nest chamber was exposed. While deeper tunnels in sand provide greater protection from slumping, sand and gravel also appeared more prone to slumps. Thus the greater depth may balance the greater risk in such sites.

It is clear that Bank Swallows gain significant advantages by tunnel nesting. Their apparent trial and error method of selecting a suitable nest site may indicate that any soil which allows construction of a stable tunnel is suitable. The preference for sands and gravels simply reflects ease of construction.

Selection for open flying space in front of the colony may provide some protection from raptors. American Kestrels (Freer 1973) and Hobbies, Falco subbuteo, (Edmandson 1983) have been reported preying on Bank Swallows at colonies. The Bank Swallows habit of diving out from its nest, losing altitude while rapidly gaining speed, requires open space. This habit may provide some defence against raptors by ensuring the swallow has space to maneuver and achieve flying speed.

My first two hypotheses are thus clearly correct. Bank Swallows select for tall, steep, sand or gravel banks with open flying space. These features do influence nest success. By a similar comparison of used and unused sites Burger and Gochfeld (1981) showed that Kelp Gulls also select colony sites which offer greater protection from predators than offered by unused sites.

The second purpose of this study was to relate the Bank Swallow's habitat selection to the reason why the species nests colonially. The disadvantages of coloniality will lower fitness sufficiently to prevent evolution of colonial nesting unless there are advantages which increase fitness. Two types of advantages are possible. First, the Bank Swallows may be concentrated on the best sites. Coloniality in that case would not be an advantage but a side effect of selecting a superior, restricted habitat. Alternatively, the Bank Swallows may derive some actual advantage from their association.

If Bank Swallows only nest colonially due to a habitat shortage, they should space themselves as much as possible over the available habitats. I, therefore, tested the hypothesis that nests are more clumped, physically and temporally, than required by the habitat, thus leaving suitable habitats vacant.

There were insufficient good sites available in the study area to allow each of the 293 pair in 1980 and 318 pair in 1981 their own bank. In the pre-settlement era there were even fewer sites. Excluding all man-made sites and the unsuitable tributary creek banks leaves only 121 potential colony sites. Many of these are very marginal habitats. Thus the Bank Swallows were forced to share their banks and nest in small, loose colonies, or to remain at lower population levels.

Discriminant analyses 2 and 3 indicate that Bank Swallows have clumped even more than required by the habitat. Figures 11 and 12 plot the distribution of colonies and unused sites along the discriminant function in these analyses. In both plots, moving toward the negatives indicates increases in bank height, steepness, and quantity of SOL13, declines in SOL14 and percentage of the bank base vegetated, and in Figure 11 only, declining vertical lift at 40 metres. The two analyses classified 62 and 57 unused sites as colonies. Overlap is even greater as 14 and 12 colonies are misclassified as unused sites. The actual overlap, shown in Figures 11 and 12, shows that more than half of all banks lie within the minimum range used by Bank Swallows.

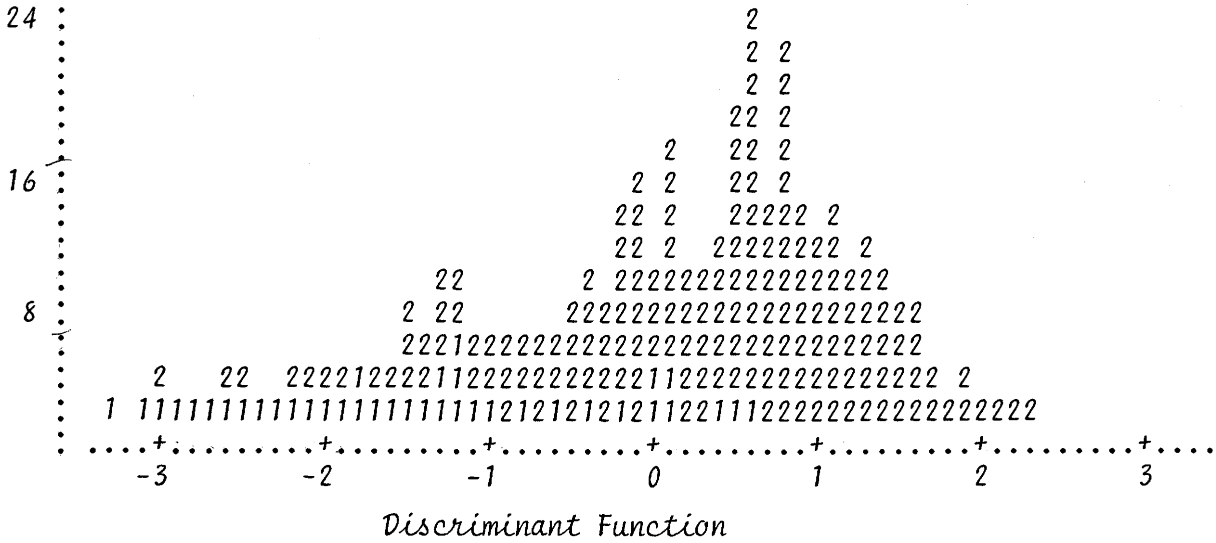


Figure 11:Distribution of used (1) and unused (2) sites along the discriminant function in the second discriminant analysis.

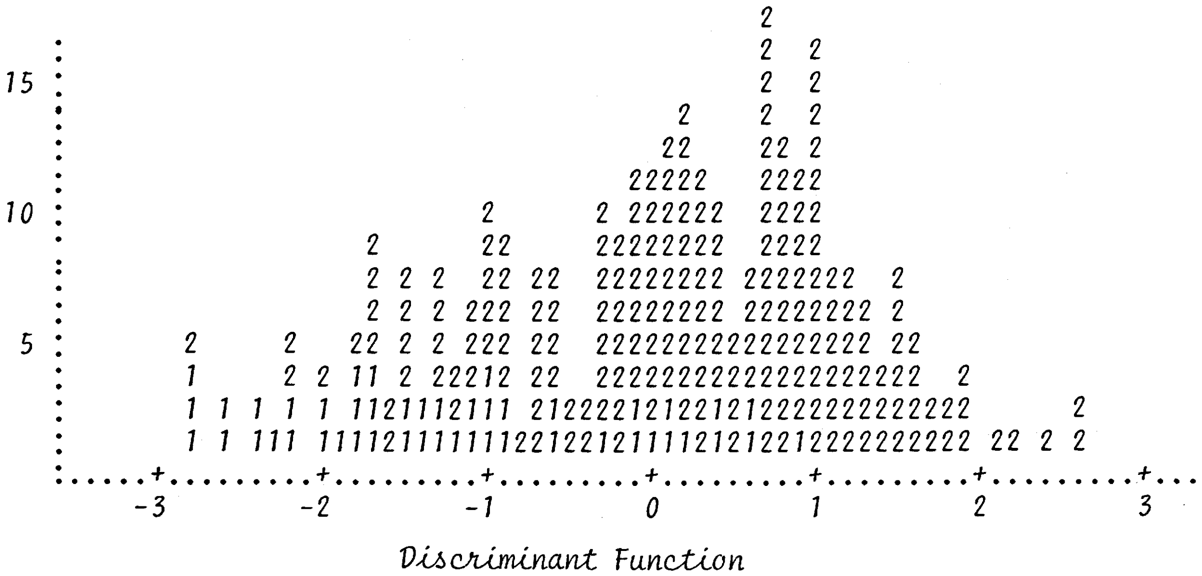


Figure 12: Distribution of used(1) and unused(2) sites along the discriminant function in the third discriminant analysis.

I checked this conclusion by selecting the best habitats in the study area. All banks with slopes between 75° and 105°, vertical lift at 40 metres of less than one metre, bank height greater than .75 metres, more than 30% SOL13 and less than 50% SOL14, and less than 50% of the bank base vegetated were examined. Of the 61 sites in this best group, 35 were colonies and 16 were not used. The only significant difference between the groups was slightly less SOL6, 16.25% compared to 21.0% ($p = .043$) at the unused sites. I doubt that this difference explains the lack of use. Thus Bank Swallows left 16 of the better sites in the study unused.

Further evidence of vacant habitat is failure of Bank Swallows to reuse 1980 sites in 1981. Site 62L12-224 was particularly striking as all 7 nests were successful in 1980 and the bank's condition did not appear to have changed. Hoogland and Sherman (1976) interpret similar fluctuations in bank use as evidence of clustering more than required by the habitat.

Observation of large colonies clustering on only part of the bank surface (Hoogland and Sherman 1976, Spencer 1962) high within colony synchrony (Hoogland and Sherman 1976, Emlen and Demong 1975) and reported rarity of solitary nesting (Hoogland and Sherman 1976) also support this conclusion. The hypothesis was correct. Bank Swallows do cluster more than required by the habitat alone.

Colonial nesting should only evolve if it increases nest success above that of solitary nesting conspecifics. I, therefore, tested the hypothesis that "nest losses from predation and environmental hazards are lower for colonial species than for solitary nesters". Working directly on Bank Swallows revealed no relationship between colony size and nest success. There were too few solitary nests to compare with all colonial nestings.

Comparing species (Table 18) does not support the hypothesis. While Bank Swallows do experience higher nest success than the Clay-colored Sparrow and Dickcissel which nest in grass and shrub habitats typical of the presettlement prairie, the noncolonial Barn and Tree Swallows achieve higher nest success than Bank Swallows. The difference may relate to territoriality.

Territoriality is thought to have evolved to defend a limited resource such as food, nest sites, or mates (Brown 1964). The Type A territoriality of the Dickcissel and Clay-colored Sparrow probably evolved to defend a food supply. Maintenance of this territory and time budget considerations (Horn 1968) usually force nesting inside the territory. This restricts choice of nest sites.

A swallow's food supply is not believed to be economically defensible (Snapp 1976, Emlen and Demong 1975). Swallows therefore do not maintain Type A territories and are free to select the most advantageous nest sites in the general area. Whether banks, cavities, or barn walls are selected, these advantageous sites offer greater security for the nest.

I, therefore, propose a new hypothesis, "That nest losses from predation and environmental hazards are lower for species which do not maintain Type A territories than for those which do". This hypothesis is supported by Table 18.

The preference of herons for nesting areas protected from racoons, Procyon lotor, (Jenni 1969) and the vulnerability of the Great Blue Heron, Ardea herodias, to racoons (Hjertaas 1982) indicate the value of protected nest sights. Island nesting is thought to protect sea birds from mammalian predators (Lack 1968). Occasional cases of mammal predation at seabird colonies (Kadlec 1971, Quinlan 1983) dramatize the value of these island nest sites.

The ability of species which do not maintain Type A territories to achieve lower rates of nest loss from predation and environmental hazards than Type A territorial species appears to be due to their freedom to select the most advantageous habitat. Bank Swallows also select the most advantageous habitat.

While concentration at superior sites could cause coloniality, the presence of vacant habitat shows that this is not the only reason Bank Swallows nest colonially. Other advantages, either co-operation for environmental enhancement, protection from predators through selfish herd effects or joint defense, or social facilitation of foraging, must have contributed to evolution of Bank Swallow coloniality.

There is no evidence that Bank Swallows improve their nest environment by colonial nesting. In fact presence of many pairs may cause slumps as the bank is weakened by many tunnels.

Clumping and synchronized nesting have been demonstrated to offer protection from predators if the predator is limited by food supplies at other times of the year and cannot increase its intake to take advantage of a sudden surplus. Nisbett (1975) demonstrated this benefit at a Common Tern, *Sterna hirundo*, colony preyed upon by Great-horned Owls, *Bubo virginianus*. Freer (1977) suggests nest synchrony in the Bank Swallow may offer this "selfish herd" advantage. Certainly some predators such as a skunk digging out two or three nests per night (Stoner 1936), a snake, Kestrels, or the deer mice observed in this study would be swamped by a large colony. The one nest which survived deer mouse predation at 62L12-217 in 1981 may be a case of predator swamping. The mouse was working down the row of nests taking eggs. The nest which survived was the last in line. However, colonies in this study were too small to swamp the mammal which dug up nests in 1982.

Colonial nesting has been demonstrated to reduce predation at seabird colonies through joint defence and intimidation of predators by numbers (Lack 1968, Patterson 1969, Buckley and Buckley 1977). Bank Swallows mob potential predators and this mobbing was sometimes effective in preventing predation by Blue Jays, Cyanocitta cristata, preying on young fallen below the nest. The effectiveness of this mobbing appears to increase with increasing colony size (Hoogland and Sherman 1968). Freer (1977) observed Bank Swallows mobbimg a snake and a chipmunk with little or no effect. I observed no attempted mobbing by Bank Swallows even though I saw a House Wren chase a chipmunk away from a Bank Swallow colony. Perhaps most colonies in my study were too small to mob effectively.

Emlen and Demong (1975) proposed that social foraging is a major advantage of and reason for the high degree of nest synchrony in Bank Swallow colonies. Ward and Zahavi (1973) have made similar proposals for many species. However the evidence necessary to prove this hypothesis, that unsuccessful foragers follow successful foragers and benefit from this action, is not available. This strategy should be particularly advantageous during periods of food stress (Emlen and Demong 1975). However, after a cold spell which produced such stress, Hoogland and Sherman (1976) observed juvenile survivorship to be negatively correlated with colony size, the opposite result to that predicted by the social facilitation of foraging hypothesis.

In conclusion, Bank Swallows appear to select nest habitat to provide protection from predators and a superior microclimate. The supply of superior sites is limited, forcing Bank Swallows to cluster. The benefits derived from nesting on these superior habitats exceed the costs of associating with conspecifics on the site.

The presence of vacant habitats indicates that Bank Swallows obtain additional benefits by nesting colonially. These may be reduced predation due to selfish herd effects and joint predator defence. However, it was beyond the scope of this study to determine the nature of these additional benefits.

Although Freer (1977) concluded that "the structure and synchrony of Bank Swallow colonies indicate that site shortage is neither the proximate nor the ultimate cause of colonial nesting in Bank Swallows", I disagree. Bayer (1982) argued that information exchange could only develop once birds were nesting in a group. The same is true for joint predator defence and synchronized nesting to reduce predation.

Bank Swallows most likely first nested in loose colonies due to a shortage of suitable sites. Defences against predators evolved later. Opportunity to nest at the superior habitat remains the primary benefit of colonial nesting in Bank Swallows.

6. SUMMARY

Most studies of nesting habitat selection by colonial species have concentrated on the used habitat and failed to make comparisons with unused sites. The Bank Swallow is ideal for this comparative approach. It is common in accessible areas and its potential colony sites can be easily identified. I compared 349 unused banks to 60 colony sites in a 6,129 hectare study area around Katepwa Lake.

The 409 potential colony sites included 176 natural sites along the lakeshore, banks of the Qu'Appelle River and tributaries, and created by natural slumps. The remaining 233 sites were manmade by road construction, gravel mining and stockpiling, building construction, excavation of garbage pits and other activities. Bank Swallows showed significant selection for gravel pits, building construction sites, and the riverbank.

Five physical features were most important in habitat selection. Colony sites were taller and closer to vertical than unused banks. Soil at colonies contained a higher proportion of sand and fine gravel and less clay than unused sites. Colony sites tended to be more recently excavated or were continually excavated by the river. Finally banks were only used if there was open flying space in front.

All available banks in the study area were small compared to nesting banks described in other areas. As a result colonies were small, ranging from 1 to 48 nests with a mean of 7.7. Colony size did not relate to any characteristic of the banks, probably due to the marginal nature of all sites.

I observed nests at selected colonies weekly in order to determine nest success. The earliest pairs started incubation in late May. The number of nests starting incubation peaked in early June and dropped off rapidly after 19 June. Mean clutch size was 5.0. Early clutches were larger and more likely to be successful than later nest attempts.

During 1981 Mayfield's Index (daily rate of nest loss) was .0113 indicating a nest had a 63.4% change of surviving from the start of laying to fledging. Major causes of nest failure during the study were destruction by mining or construction, slumping and tunnel cave-ins, and egg predation by deer mice. The only habitat features statistically correlated to nest success over the study were bank height, nest height, and tunnel depth. The relationship of bank height and nest height to nest success was the opposite of that expected and may not be biologically significant.

Predation was very low during the study. Observations by other authors and outside this study suggest that selection for features such as bank height does have adaptive value in providing protection from predators. This advantage would be apparent in a larger sample.

Tunnel nesting gives Bank Swallows a more stable microclimate and appears to offer protection from predators. Because they do not maintain Type A territories, Bank Swallows are free to concentrate on limited numbers of favourable nesting habitats. This selection of superior nest sites gives Bank Swallows significantly higher nest success than territorial species of similar size. This advantage is the primary cause of coloniality of Bank Swallows.

Bank Swallows concentrate more than required by habitat shortages alone. This concentration indicates that association with conspecifics at the colony is a second advantage of coloniality. However, it was beyond the scope of this study to determine the nature of this advantage.

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APPENDIX A

SUMMARIES OF RAW DATA

Appendix A-1: Data on Bank Height

	FREQUENCY OF EACH BANK HEIGHT					
	USED		UNUSED		COMBINED	
HEIGHT(m)	ABS	REL(%)	ABS	REL(%)	ABS	REL(%)
0 - .50	1	1.7	32	9.2	33	8.1
.50 - .75	4	6.7	61	17.5	65	15.9
.75 - 1.00	9	15.0	92	26.4	101	24.7
1.00 - 1.25	7	11.7	36	10.3	43	10.5
1.25 - 1.50	11	18.3	33	9.5	44	10.8
1.50 - 1.75	8	13.3	17	4.9	25	6.1
1.75 - 2.00	4	6.7	18	5.2	22	5.4
2.00 - 2.25	2	3.3	8	2.3	10	2.4
2.25 - 2.50	1	1.7	14	4.0	15	3.7
2.50 - 2.75	2	3.3	5	1.4	7	1.7
2.75 - 3.00	1	1.7	5	1.4	6	1.5
3.00 - 3.50	5	8.3	12	3.4	17	4.2
3.50 - 4.00	2	3.3	8	2.3	10	2.4
4.00 - 4.50	1	1.7	2	0.6	3	0.7
4.50 - 5.00	1	1.7	1	0.3	2	0.5
5.00 - 6.00	0	0	4	1.1	4	1.0
6.00 - 7.00	1	1.7	0	0	1	.2
7.00 - 8.00	0	0	0	0	0	0
8.00 - 9.00	0	0	1	0.3	1	.2
Total	60	100.0	349	100.0	409	100.0
Mean(m)	1.84		1.38		1.44	
S.D.	1.16		1.03		1.06	

Appendix A-2: Data on Height of Talus Slope

TALUS HEIGHT(m)	FREQUENCY OF EACH TALUS HEIGHT					
	USED		UNUSED		COMBINED	
	ABS	REL(%)	ABS	REL(%)	ABS	REL(%)
0	2	3.4	6	1.7	8	2.0
0 - .50	8	13.8	68	19.5	76	18.7
.50 - .75	2	3.4	38	10.9	40	9.9
.75 - 1.00	6	10.3	54	15.5	60	14.8
1.00 - 1.25	6	10.3	29	8.3	35	8.7
1.25 - 1.50	8	13.8	36	10.3	44	10.9
1.50 - 1.75	3	5.2	27	7.7	30	7.4
1.75 - 2.00	8	13.8	28	8.0	36	8.9
2.00 - 2.25	6	10.3	12	3.4	18	4.4
2.25 - 2.50	2	3.4	14	4.0	16	3.9
2.50 - 2.75	0	0	6	1.7	6	1.5
2.75 - 3.00	1	1.7	7	2.0	8	2.0
3.00 - 3.50	3	5.2	7	2.0	10	2.4
3.50 - 4.00	1	1.7	7	2.0	8	2.0
4.00 - 4.50	1	1.7	3	0.9	4	1.0
4.50 - 5.00	1	1.7	1	0.3	2	0.5
5.00 - 6.00	0	0	3	0.9	3	0.7
6.00 - 7.00	0	0	0	0	0	0
7.00 - 8.00	0	0	2	0.6	2	0.5
Total	58	100.0	348	100.0	406	100.0
Missing	2		1		3	
Mean(m)	1.55		1.35		1.38	
S.D.	1.03		1.11		1.10	

Appendix A-3: Data on Combined Height of Bank and Talus Slope

COMBINED HEIGHT (m)	FREQUENCY					
	USED		UNUSED		COMBINED	
	ABS	REL(%)	ABS	REL(%)	ABS	REL(%)
0 - .50	0	0	2	.6	2	.5
.50 - .75	0	0	5	1.4	5	1.2
.75 - 1.00	0	0	6	1.7	6	1.5
1.00 - 1.25	2	3.4	23	6.6	25	6.1
1.25 - 1.50	0	0	24	6.9	24	5.9
1.50 - 1.75	3	5.1	35	10.0	38	9.3
1.75 - 2.00	5	8.5	37	10.6	42	10.3
2.00 - 2.25	8	13.6	28	8.0	36	8.8
2.25 - 2.50	5	8.5	34	9.7	39	9.5
2.50 - 2.75	4	6.8	25	7.2	29	7.1
2.75 - 3.00	6	10.2	18	5.2	24	5.9
3.00 - 3.50	8	13.6	33	9.5	41	10.0
3.50 - 4.00	4	6.8	24	6.9	28	6.8
4.00 - 4.50	3	5.1	15	4.3	18	4.4
4.50 - 5.00	1	1.7	16	4.6	17	4.2
5.00 - 6.00	6	10.2	12	3.4	18	4.4
6.00 - 7.00	1	1.7	6	1.7	7	1.7
7.00 - 8.00	1	1.7	2	.6	3	.7
8.00 - 9.00	1	1.7	2	.6	3	.7
9.00	1	1.7	2	.6	3	.7
Total	59	100.0	349	100.0	408	100.0
Missing	1		0		1	
Mean(m)	3.36		2.73		2.82	
S.D.	1.03		1.50		1.57	

Appendix A-4: Data on Bank Length

	FREQUENCY OF EACH BANK LENGTH					
	USED		UNUSED		COMBINED	
LENGTH (m)	ABS	REL(%)	ABS	REL(%)	ABS	REL(%)
0 - 10	9	15.3	138	39.5	147	35.9
10 - 20	19	32.2	88	25.2	107	26.2
20 - 30	11	18.6	48	13.8	59	14.4
30 - 40	6	10.2	31	8.9	37	9.0
40 - 50	7	11.9	15	4.3	22	5.4
50 - 60	2	3.4	9	2.6	11	2.7
60 - 70	0	0	8	2.3	8	2.0
70 - 80	2	3.4	4	1.1	6	1.5
80 - 90	1	1.7	3	0.9	4	1.0
90 - 100	0	0	0	0	0	0
100 - 110	0	0	0	0	0	0
110 - 120	0	0	0	0	0	0
120 - 130	1	1.7	1	0.3	2	0.5
130 - 140	0	0	0	0	0	0
140 - 150	0	0	0	0	0	0
150 - 175	0	0	0	0	0	0
175 - 200	0	0	0	0	0	0
200 - 250	1	1.7	3	0.9	4	1.0
250 - 300	0	0	0	0	0	0
300 - 350	0	0	0	0	0	0
350 - 400	0	0	1	0.3	1	0.2
Total	59	100.0	349	100.0	408	100.0
Missing	1		0		1	
Mean(m)	30.92		21.93		23.23	
S.D.	33.23		31.38		31.76	

Appendix A-5: Data on Bank Area

AREA (m^2)	FREQUENCY OF EACH BANK AREA					
	USED		UNUSED		COMBINED	
	ABS	REL(%)	ABS	REL(%)	ABS	REL(%)
0 - 10	11	18.6	159	45.6	170	41.6
10 - 20	13	22.0	74	21.2	87	21.3
20 - 30	8	13.6	32	9.2	40	9.8
30 - 40	5	8.5	33	9.5	38	9.3
40 - 50	5	8.5	18	5.2	23	5.6
50 - 60	3	5.1	7	2.0	10	2.4
60 - 70	4	6.8	4	1.1	8	2.0
70 - 80	2	3.4	3	0.9	5	1.2
80 - 90	1	1.7	3	0.9	4	1.0
90 - 100	1	1.7	0	0	1	0.2
100 - 110	0	0	1	0.3	1	0.2
110 - 120	1	1.7	2	0.6	3	0.7
120 - 130	0	0	2	0.6	2	0.5
130 - 140	1	1.7	2	0.6	3	0.7
140 - 150	0	0	2	0.6	2	0.5
150 - 160	3	5.1	1	0.3	4	1.0
160 - 170	0	0	1	0.3	1	0.2
170 - 180	0	0	2	0.6	2	0.5
180 - 190	0	0	0	0	0	0
190 - 200	0	0	0	0	0	0
200 - 250	1	1.7	2	0.6	2	0.5
250 - 300	0	0	0	0	0	0
300 - 350	0	0	1	0.3	1	0.2
500 - 550	0	0	1	0.3	1	0.2
Total	59	100.0	349	100.0	408	100.0
Missing	1		0		1	
Mean(m^2)	43.9		24.7		27.5	
S.D.	47.1		46.6		47.1	

Appendix A-6: Data on Bank Slope

	FREQUENCY OF EACH SLOPE CATEGORY					
	USED SITES		UNUSED SITES		COMBINED	
SLOPE	ABS	REL(%)	ABS	REL(%)	ABS	REL(%)
0 - 53	0	0	2	0.6	2	.7
54 - 65	0	0	32	9.2	32	8.1
66 - 75	4	6.8	58	16.6	62	15.2
76 - 85	23	39.0	124	35.4	147	35.7
86 - 95	28	47.4	99	28.4	127	31.1
96 - 105	4	6.8	24	6.9	28	6.8
106 or More	0	0	10	2.9	10	2.4
Total	59	100.0	349	100.0	408	98.8
Missing	1		0		1	
Mean	87.0		83.0		83.6	
S.D.	6.6		11.6		11.1	

Appendix A-7: Data on Percent of Bank With Overhang

% OF BANK WITH OVERHANG	FREQUENCY OF EACH OVERHANG CATEGORY					
	USED		UNUSED		COMBINED	
	ABS	REL(%)	ABS	REL(%)	ABS	REL(%)
0	47	79.7	195	55.9	242	59.2
0 - 10	6	10.2	46	13.2	52	12.7
10 - 20	1	1.7	12	3.4	13	3.2
20 - 30	1	1.7	13	3.7	14	3.4
30 - 40	1	1.7	10	2.9	11	2.7
40 - 50	3	5.1	17	4.9	20	4.9
50 - 60	0	0	5	1.4	5	1.2
60 - 70	0	0	2	.6	2	0.5
70 - 80	0	0	14	4.0	14	3.4
80 - 90	0	0	9	2.6	9	2.2
90 - 100	0	0	26	7.4	26	6.4
Total	59	100.0	349	100.0	408	100.0
Missing	1		0		1	
Mean	4.5%		20.2%		18.0%	
S.D.	12.6%		32.7%		31.1%	

Appendix A-8: Data on Vertical Lift 20m From Bank

VERTICAL LIFT (m)	FREQUENCY OF EACH CATEGORY USED ABS	 REL(%)	 UNUSED ABS	 REL(%)	 COMBINED ABS	 REL(%)
0	54	90.0	222	64.5	276	68.3
.1 - 1.0	5	8.3	21	6.1	26	6.4
1.1 - 2.0	0	0	15	4.4	15	3.7
2.1 - 3.0	0	0	20	5.8	20	5.0
3.1 - 4.0	1	1.7	31	9.0	32	7.9
4.1 - 5.0	0	0	7	2.0	7	1.7
5.1 - 6.0	0	0	5	1.5	5	1.2
6.1 - 7.0	0	0	1	2.3	1	0.2
7.1 - 9.0	0	0	4	1.2	4	1.0
9.1 - 14.0	0	0	18	5.2	18	4.5
Total	60	100.0	344	100.0	404	100.0
Missing	0		5		5	
Mean(m)	0.12		1.53		1.32	
S.D.	0.49		2.75		2.59	

Appendix A-9: Data on Vertical Lift 40m From Bank

VERTICAL LIFT (m)	FREQUENCY OF EACH CATEGORY USED ABS	USED REL(%)	UNUSED ABS	UNUSED REL(%)	COMBINED ABS	COMBINED REL(%)
0	56	93.3	232	68.0	288	71.8
.1 - 1.0	4	6.7	16	4.7	20	5.0
1.1 - 2.0	0	0	8	2.3	8	2.0
2.1 - 3.0	0	0	19	5.6	19	4.7
3.1 - 4.0	0	0	21	6.2	21	5.2
4.1 - 5.0	0	0	6	1.8	6	1.5
5.1 - 7.0	0	0	10	2.9	10	2.5
7.1 - 9.0	0	0	6	1.8	6	1.5
9.1 - 14.0	0	0	23	6.7	23	5.8
Total	60	100.0	341	100.0	401	100.0
Missing	0		8		8	
Mean(m)	0.05		1.64		1.40	
S.D.	0.20		2.75		2.91	

Appendix A-10: Data on Vertical Lift 60m From Bank

VERTICAL LIFT (m)	FREQUENCY OF EACH CATEGORY					
	USED		UNUSED		COMBINED	
	ABS	REL(%)	ABS	REL(%)	ABS	REL(%)
0	56	93.4	230	67.4	286	71.4
.1 - 1.0	2	3.3	16	4.7	18	4.5
1.1 - 2.0	2	3.3	8	2.3	10	2.5
2.1 - 3.0	0	0	19	5.6	19	4.7
3.1 - 4.0	0	0	21	6.2	21	5.2
4.1 - 5.0	0	0	4	1.2	4	1.0
5.1 - 7.0	0	0	12	3.5	12	3.0
7.1 - 9.0	0	0	6	1.8	6	1.5
9.1 - 14.0	0	0	25	7.3	25	6.2
Total	60	100.0	341	100.0	401	100.0
Missing	0		8		8	
Mean(m)	0.08		1.72		1.48	
S.D.	0.37		3.22		3.03	

Appendix A-11: Data on Percent of Ground Vegetated at Bank Top

PERCENT VEGETATED	FREQUENCY OF EACH CATEGORY					
	USED		UNUSED		COMBINED	
	ABS	REL(%)	ABS	REL(%)	ABS	REL(%)
0	8	13.3	5	1.4	13	3.2
0 - 10	7	11.7	9	2.6	16	3.9
10 - 20	0	0	6	1.7	6	1.5
20 - 30	3	5.0	9	2.6	12	2.9
30 - 40	4	6.7	12	3.4	16	3.9
40 - 50	3	5.0	13	3.7	16	3.9
50 - 60	4	6.7	21	6.0	25	6.1
60 - 70	7	11.7	17	4.9	24	5.9
70 - 80	6	10.0	51	14.6	57	13.9
80 - 90	6	10.0	57	16.3	63	15.4
90 - 100	12	20.0	149	42.7	161	39.4
Total	60	100.0	349	100.0	409	100.0
Mean	55.7		79.9		76.4	
S.D.	36.9		25.7		28.9	

Appendix A-12: Data on Percent of Ground Vegetated at Talus Slope

	FREQUENCY OF EACH CATEGORY					
	USED		UNUSED		COMBINED	
PERCENT VEGETATED	ABS	REL(%)	ABS	REL(%)	ABS	REL(%)
0	24	40.7	39	11.3	63	15.6
0 - 10	13	22.0	122	35.4	135	33.6
10 - 20	2	3.4	31	9.0	33	8.2
20 - 30	11	18.6	33	9.6	44	10.9
30 - 40	6	10.2	29	8.4	35	8.7
40 - 50	2	3.4	30	8.7	32	7.9
50 - 60	1	1.7	16	4.7	17	4.2
60 - 70	0	0	16	4.7	16	4.0
70 - 80	0	0	16	4.7	16	4.0
80 - 90	0	0	9	2.6	9	2.2
90 - 100	0	0	3	.9	3	0.7
Total	59	100.0	344	100.0	403	100.0
Missing	1		5		6	
Mean	13.6		26.8		24.9	
S.D.	17.5		26.8		26.1	

Appendix A-13: Data on Percent of Soil Vegetated at Bank Base

PERCENT	FREQUENCY OF EACH PERCENTAGE CATEGORY					
	USED		UNUSED		COMBINED	
VEGETATED	ABS	REL(%)	ABS	REL(%)	ABS	REL(%)
0	30	50.0	105	30.3	135	33.4
0 - 10	15	25.0	89	25.6	104	25.5
10 - 20	2	3.3	21	6.0	23	5.6
20 - 30	3	5.0	20	5.7	23	5.6
30 - 40	0	6.7	14	4.0	14	3.4
40 - 50	4	3.3	14	4.0	18	4.4
50 - 60	2	5.0	10	2.9	12	2.9
60 - 70	0	0	11	3.2	11	2.7
70 - 80	3	5.0	29	8.3	32	7.8
80 - 90	0	0	24	6.9	24	5.9
90 - 100	1	1.7	11	3.2	12	2.9
Total	60	100.0	348	100.0	408	100.0
Missing	0		1		1	
Mean	13.7		27.3		25.3	
S.D.	25.0		33.6		32.8	

Appendix A-14: Data on Distance to Next Bank

	FREQUENCY OF EACH DISTANCE					
	USED		UNUSED		COMBINED	
DISTANCE (m)	ABS	REL(%)	ABS	REL(%)	ABS	REL(%)
0 - 100	47	78.3	302	86.5	349	85.3
101 - 200	6	10.0	18	5.2	24	5.9
201 - 300	3	5.0	18	5.2	21	5.1
301 - 400	0	0	3	0.9	3	0.7
401 - 500	0	0	5	1.4	5	1.2
501 - 600	0	0	1	0.3	1	0.2
601 - 800	3	5.0	2	0.6	5	1.2
801 - 1000	1	1.7	0	0	1	0.2
Total	60	100.0	349	100.0	409	100.0
Mean(m)	104.5		63.5		69.6	
S.D.	181.8		103.7		119.0	

Appendix A-15: Data on Distance to Nearest Bank Swallow Colony

1980

	FREQUENCY OF EACH DISTANCE CATEGORY					
	USED		UNUSED		COMBINED	
DISTANCE (m)	ABS	REL(%)	ABS	REL(%)	ABS	REL(%)
0 - 100	31	62	66	19.1	97	24.5
101 - 200	4	8	11	3.2	15	3.8
201 - 300	0	0	17	4.9	17	4.3
301 - 400	0	0	15	4.3	15	3.8
401 - 500	1	2	9	2.6	10	2.5
501 - 600	1	2	13	3.8	14	3.5
601 - 800	2	4	48	13.9	50	12.8
801 - 1000	0	0	18	5.2	18	4.5
1001 - 1500	3	6	51	14.7	54	13.6
1501 - 2000	5	10	47	13.6	52	13.1
2001 - 2500	2	4	37	10.7	39	9.8
2501 - 3000	0	0	7	2.0	7	1.8
3000	1	2	7	2.0	8	2.0
Total	50	100	346	100.0	396	100.0

1981

DISTANCE (m)	USED ABS	USED REL(%)	UNUSED ABS	UNUSED REL(%)	COMBINED ABS	COMBINED REL(%)
0 - 100	36	64.3	63	18.1	99	24.5
101 - 200	5	8.8	28	8.0	33	8.2
201 - 300	2	3.6	26	7.5	28	6.9
301 - 400	0	0	20	5.7	20	5.0
401 - 500	0	0	11	3.2	11	2.7
501 - 600	2	3.6	20	5.7	22	5.4
601 - 800	4	7.1	27	7.8	31	7.7
801 - 1000	2	3.6	15	4.3	17	4.2
1001 - 1500	1	1.8	22	6.3	23	5.7
1501 - 2000	2	3.6	28	8.1	30	7.4
2001 - 2500	2	3.6	46	13.2	48	11.9
2501 - 3000	0	0	29	8.3	29	7.2
3000	0	0	13	3.7	13	3.2
Total	56	100.0	348	100.0	404	100.0

Mean (1980)	516.7(m)	1044.2(m)	977.6(m)
S.D. (1980)	886.4	872.5	890.6
Mean (1981)	330.5(m)	1107.3(m)	999.7(m)
S.D. (1981)	584.4	1030.1	1016.1

Appendix A-16: Data on Distance to Nearest Cliff Swallow Colony

	FREQUENCY OF EACH DISTANCE CATEGORY					
	USED		UNUSED		COMBINED	
DISTANCE (m)	ABS	REL(%)	ABS	REL(%)	ABS	REL(%)
0 - 100	5	10	0	0	5	1.3
101 - 200	0	0	2	0.6	2	0.5
201 - 300	0	0	1	0.3	1	0.2
301 - 400	0	0	7	2.0	7	1.8
401 - 500	1	2	0	0	1	0.2
501 - 600	0	0	4	1.1	4	1.0
601 - 800	7	14	24	7.0	31	7.8
801 - 1000	0	0	29	8.4	29	7.3
1001 - 1500	2	4	23	6.6	25	6.3
1501 - 2000	1	2	31	9.0	32	8.1
2001 - 2500	1	2	8	2.3	9	2.3
2501 - 3000	2	4	9	2.6	11	2.8
3000	31	62	209	60.1	240	60.4
Total	50	100	347	100.0	397	100.0
Missing	10		2		12	
Mean(m)	2448		2535		2524	
S.D.	1261		1065		1090	

Appendix A-17: Data on Number of Colonies Within 500m

COLONIES WITHIN 500m	FREQUENCY OF EACH NUMBER USED ABS	USED REL(%)	UNUSED ABS	UNUSED REL(%)	COMBINED ABS	COMBINED REL(%)
0	12	20.0	228	65.5	240	58.7
1	6	10.0	38	10.9	44	10.8
2	7	11.7	36	10.4	43	10.5
3	7	11.7	4	1.1	11	2.7
4	2	3.3	1	0.3	3	0.7
5	2	3.3	4	1.1	6	1.5
8	8	13.3	0	0	8	2.0
9	0	0	9	2.6	9	2.2
10	3	5.0	0	0	3	0.7
11	0	0	1	0.3	1	0
13	13	21.7	0	0	13	3.2
14	0	0	27	7.8	27	6.6
Total	60	100.0	348	100.0	408	100.0
Missing	0		1		1	
Mean	5.4		1.8		2.3	
S.D.	5.0		3.9		4.3	

Appendix A-18: Data on Number of Banks Within 500m

NUMBER OF BANKS	FREQUENCY OF EACH NUMBER OF BANKS					
	USED		UNUSED		COMBINED	
	ABS	REL(%)	ABS	REL(%)	ABS	REL(%)
0	5	8.3	7	2.0	12	2.9
1	0	0	12	3.4	12	2.9
2	7	11.7	22	6.3	29	7.1
3	0	0	22	6.3	22	5.4
4	3	5.0	21	6.0	24	5.9
5	1	1.7	29	8.3	30	7.3
6	2	3.3	18	5.2	20	4.9
7	0	0	28	8.0	28	6.8
8	0	0	1	0.3	1	0.2
9	1	1.7	9	2.6	10	2.4
10	0	0	5	1.4	5	1.2
11	0	0	8	2.3	8	2.0
12	5	8.3	16	4.6	21	5.1
13	2	3.3	15	4.3	17	4.2
14	1	1.7	15	4.3	16	3.9
15	5	8.3	13	3.7	18	4.4
16	4	6.7	7	2.0	11	2.7
17	0	0	21	6.0	21	5.1
18	4	6.7	5	1.4	9	2.2
19	0	0	1	0.3	1	0.2
20	0	0	6	1.7	6	1.5
21	1	1.7	11	3.2	12	2.9
22	0	0	7	2.0	7	1.7
23	0	0	2	0.6	2	0.5
24	0	0	9	2.6	9	2.2
25	0	0	2	0.6	2	0.5
26	0	0	30	8.6	30	7.3
27	13	21.7	1	0.3	14	3.4
28	3	5.0	1	0.3	4	1.0
29	0	0	4	1.1	4	1.0
30	0	0	1	0.3	1	0.2
31	3	5.0	0	0	3	0.7
Total	60	100.0	349	100.0	409	100.0
Mean	15.2		11.6		12.1	
S.D.	10.3		8.2		8.6	

Appendix A-19: Data on SOL1

PERCENT OF TOTAL SOIL	NUMBER OF SAMPLES WITHIN EACH PERCENTAGE					
	USED		UNUSED		COMBINED	
	ABS	REL(%)	ABS	REL(%)	ABS	REL(%)
0	58	98.3	340	98.6	398	98.5
1 - 10	0	0	0	0	0	0
11 - 20	0	0	0	0	0	0
21 - 30	1	1.7	1	0.3	2	0.5
31 - 40	0	0	4	1.1	4	1.0
Total	59	100.0	345	100.0	404	100.0
Missing	1		4		5	
Mean(%)	.37		.45		.44	
S.D.	2.86		3.78		3.66	

Appendix A-20: Data on SOL2

PERCENT OF TOTAL SOIL	NUMBER OF SAMPLES WITH EACH PERCENTAGE					
	USED		UNUSED		COMBINED	
	ABS	REL(%)	ABS	REL(%)	ABS	REL(%)
0	44	74.6	301	87.2	345	85.5
1 - 10	12	20.3	31	9.0	43	10.6
11 - 20	3	5.1	12	3.5	15	3.7
21 - 30	0	0	0	0	0	0
31 - 40	0	0	1	0.3	1	0.2
41 - 50	0	0	0	0	0	0
Total	59	100.0	345	100.0	404	100.0
Missing	1		4		5	
Mean(%)	1.9		1.1		1.2	
S.D.	3.9		3.6		3.6	

Appendix A-21: Data on SOL3

PERCENT OF TOTAL SOIL	NUMBER OF SAMPLES WITHIN EACH PERCENTAGE USED ABS	 REL(%)	 UNUSED ABS	 REL(%)	 COMBINED ABS	 REL(%)
0	14	23.7	133	38.5	147	36.4
1 - 10	34	57.6	188	54.5	222	55.0
11 - 20	6	10.2	13	3.8	19	4.7
21 - 30	3	5.1	9	2.6	12	3.0
31 - 40	2	3.4	2	0.6	4	0.9
Total	59	100.0	345	100.0	404	100.0
Missing	1		4		5	
Mean(%)	6.1		2.9		3.4	
S.D.	8.7		5.3		6.0	

Appendix A-22: Data on SOL4

PERCENT OF TOTAL SOIL	NUMBER OF SAMPLES WITHIN EACH PERCENTAGE					
	USED		UNUSED		COMBINED	
	ABS	REL(%)	ABS	REL(%)	ABS	REL(%)
0	7	11.9	61	17.7	68	16.8
1 - 10	34	57.6	253	73.3	287	71.0
11 - 20	10	16.9	16	4.6	26	6.5
21 - 30	7	11.9	12	3.5	19	4.7
31 - 40	1	1.7	3	0.9	4	1.0
Total	59	100.0	345	100.0	404	100.0
Missing	1		4		5	
Mean(%)	8.4		4.1		4.7	
S.D.	8.1		6.1		6.6	

Appendix A-23: Data on SOL5

PERCENT OF TOTAL SOIL	NUMBER OF SAMPLES WITHIN EACH PERCENTAGE: USED ABS	USED REL(%)	UNUSED ABS	UNUSED REL(%)	COMBINED ABS	COMBINED REL(%)
0	3	5.1	15	4.3	18	4.4
1 - 10	22	37.3	271	78.6	293	72.5
11 - 20	18	30.4	35	10.1	53	13.2
21 - 30	5	8.5	17	4.9	22	5.4
31 - 40	7	11.9	6	1.8	13	3.2
41 - 50	2	3.4	0	0	2	0.5
51 - 60	2	3.4	0	0	2	0.5
61 - 70	0	0	0	0	0	0
71 - 80	0	0	1	0.3	1	0.3
Total	59	100.0	345	100.0	404	100.0
Missing	1		4		5	
Mean(%)	16.5		6.5		7.9	
S.D.	14.8		7.9		9.8	

Appendix A-24: Data on SOL6

PERCENT OF TOTAL SOIL	NUMBER OF SAMPLES WITHIN EACH PERCENTAGE					
	USED		UNUSED		COMBINED	
	ABS	REL(%)	ABS	REL(%)	ABS	REL(%)
0	1	1.7	4	1.2	5	1.2
1 - 10	19	32.2	243	70.4	262	64.9
11 - 20	17	28.8	70	20.3	87	21.6
21 - 30	19	32.2	23	6.7	42	10.4
31 - 40	2	3.4	5	1.4	7	1.7
41 - 50	1	1.7	0	0	1	0.2
Total	59	100.0	345	100.0	404	100.0
Missing	1		4		5	
Mean(%)	16.5		8.4		9.6	
S.D.	10.0		6.9		7.9	

Appendix A-25: Data on SOL7

	NUMBER OF SAMPLES WITHIN EACH PERCENTAGE					
PERCENT OF TOTAL SOIL	USED		UNUSED		COMBINED	
	ABS	REL(%)	ABS	REL(%)	ABS	REL(%)
0	1	1.7	0	0	1	0.2
1 - 10	16	27.1	51	14.8	67	16.6
11 - 20	12	20.3	137	39.7	149	36.9
21 - 30	15	25.4	89	25.7	104	25.7
31 - 40	6	10.2	39	11.3	45	11.2
41 - 50	7	11.9	22	6.4	29	7.2
51 - 60	2	3.4	4	1.2	6	1.5
61 - 70	0	0	2	0.6	2	0.5
71 - 80	0	0	1	0.3	1	0.2
Total	59	100.0	345	100.0	404	100.0
Missing	1		4		5	
Mean(%)	21.7		21.4		21.4	
S.D.	15.2		11.9		12.5	

Appendix A-26: Data on SOL8

PERCENT OF TOTAL SOIL	NUMBER OF SAMPLES WITHIN EACH PERCENTAGE USED ABS	 REL(%)	 UNUSED ABS	 REL(%)	 COMBINED ABS	 REL(%)
0	5	8.5	3	0.9	8	2.0
1 - 10	39	66.1	157	45.3	196	48.4
11 - 20	10	16.9	149	43.1	159	39.3
21 - 30	5	8.5	34	9.8	39	9.6
31 - 40	0	0	3	0.9	3	0.7
Total	59	100.0	346	100.0	405	100.0
Missing	1		3		4	
Mean(%)	7.1		12.1		11.4	
S.D.	7.8		6.8		7.1	

Appendix A-27: Data on SOL9

PERCENT OF TOTAL SOIL	NUMBER OF SAMPLES WITHIN EACH PERCENTAGE USED ABS	REL(%)	UNUSED ABS	REL(%)	COMBINED ABS	REL(%)
0	0	0	1	0.3	1	0.2
1 - 10	23	38.9	33	9.6	56	13.8
11 - 20	15	25.4	30	8.7	45	11.1
21 - 30	7	11.9	29	8.4	36	8.9
31 - 40	3	5.1	46	13.3	49	12.1
41 - 50	4	6.8	55	15.9	59	14.7
51 - 60	2	3.4	71	20.5	73	18.0
61 - 70	2	3.4	57	16.4	59	14.6
71 - 80	1	1.7	17	4.9	18	4.4
81 - 90	1	1.7	5	1.4	6	1.5
91 - 100	1	1.7	2	0.6	3	0.7
Total	59	100.0	346	100.0	405	100.0
Missing	1		3		4	
Mean(%)	21.4		43.0		39.8	
S.D.	22.3		21.3		22.8	