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Niche Differentiating Mechanisms in Two Sympatric Species of Swallows

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NICHE DIFFERENTIATING MECHANISMS

IN TWO SYMPATRIC SPECIES

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INTRODUCTION

When two closely related species exploit the same habitat, it can reasonably be expected that competition between the species will occur. The Volterra-Gause concept of competitive exclusion proposes that two species with similar habitat requirements cannot exist in an area of ecological overlap without one of the species being eliminated from the zone of sympatry (Smith, 1966). Brewer (1963) stipulated two conditions for populations to exist sympatrically: (1) the populations must be reproductively isolated and (2) they must avoid continued competition.

A common method of avoiding competition is reduction in niche overlap. According to Dilger (1956), "differences in feeding niches involve both height and location. By a simple alternation of these places of foraging a maximum amount of ecological diversification is accomplished, with a minimum amount of biological effort". Dilger found in his study of the thrush genera, Catharus and Hylocichla, that adaptive modifications of the wing, bill, and hind limb enable each species to occupy its specific feeding niche. Avian ecological studies by MacArthur (1958), Gibb (1953), Grant (1954), Root (1964), and many others have demonstrated differences in food preference and in the method of feeding. In his study of the foraging behavior of two species of ant-tanagers, Willis (1960) mentions vertical height as the main isolating mechanism with some horizontal zonation occurring.

Hamilton (1962) in his study of adaptations for sympatry in the genus, Vireo, found differences in foraging levels and habitat preference. In some areas as many as five species of the genus, Vireo, were sympatric during the breeding season. The species were usually separated "spatially" by thicket or arboreal foraging at various levels.

The chestnut-backed chickadee (Parus rufescens) recently invaded the East Bay region of San Francisco, California, and came into contact with a population of the plain titmouse (Parus inornatus). Root (1964) discovered a difference in the type of food and in the method of feeding between the two sympatric species. He maintained that dissimilarities in body and bill size between the species were adaptations for feeding in different places thus making it possible for each species to exploit different food sources. The plain titmouse has a larger body and beak enabling it to feed better on surfaces covered with bark. The chestnut-backed chickadee, on the other hand, is a smaller bird found feeding more frequently in small foliage surrounding terminal twigs. By feeding at different levels, the sympatric chickadee and titmouse minimize competition for food and hence reduce niche overlap.

Gibb (1954), in his study of sympatric species of tits, mentioned structural variations in the bills of the different species which permitted them to feed on specific food sources more effectively than the other species of tits. He further theorized that differences in foraging behavior among the six species of the family Paridae allow them to exist in the same habitat without competing for food.

In MacArthur's (1958) study of warblers, species specific differences in feeding positions, behavior and nesting dates reduce interspecific competition. Behavioral adaptations, such as feeding in different positions, hawking, and hovering with different frequencies, expose the warblers to different foods. According to MacArthur, the warblers further avoid competition for food by nesting on different dates, hence isolating the species during their period of increased biological stress.

Grant (1966) made preliminary investigations of the foraging behavior of three species of sparrows, stating that interspecific differences in foraging are adaptations for avoiding competition.

Upon reading the literature, it becomes evident that many niche differentiating mechanisms in birds reduce competition by varying the method of acquisition or the type of food consumed. Apparently, food is a significant limiting factor in the determination of the ecological niche of sympatric birds. Of course, it would be naive to assume that food is the only limiting factor. As the environment is constantly fluctuating, limiting factors change. In areas where food is abundant, competition may occur for other critical factors, such as nesting space or the availability of nesting materials.

The present study considers certain aspects of the ecologies of cliff swallows (Petrochelidon pyrrhonota) and barn swallows (Hirundo rustica) in an area of overlap, where both species are found nesting together and foraging over the same fields. Careful attention was given to foraging flight patterns, foraging elevations, and food consumed by each species in an effort to determine whether or not there is any evidence of competition for food resources. Aggressive interactions between the species were recorded, and the general timing of their nesting cycles was noted.

THE BARN SWALLOW AND CLIFF SWALLOW

The cliff swallow is a sparrow-sized bird possessing a square tail, rusty-colored rump and a dark throat patch. This species of swallow is truly colonial, nesting in large aggregations throughout the state, mainly "on the cliffs in the upper Sonoran and Transition zones" (Jewett, et. al., 1953). The cliff swallow forages on the wing and possess a short bill with a large gape, which facilitates their capturing flying insects.

This species winters in South America, returning to Washington in early April and remaining until late September (Jewett, et. al., 1953). These authors list two subspecies in the state of Washington, *P. p. pyrrhonota*, a form found west of the Cascade Mountains, and *P. p. hypopolia* (*P. p. aprophata*) a form found east of the Cascade Mountains. The colony sites are located along bodies of water where the birds attach their gourd-like nests of mud to the sides of available man-made structures such as bridges or culverts.

The barn swallow is similar in size to the cliff swallow. A very distinctive characteristic is its deeply forked tail. This species' plumage coloration is quite striking with its dark blue back and orange or buffy tinge below. The barn swallow also forages on the wing, catching flying insects.

The single subspecies in the state of Washington, *H. r. erythrogaster*, is found from late April to late October throughout the State at "moderate altitudes in Upper Sonoran and Transition zones" (Jewett, et. al., 1953).

After completing its nesting cycle, the barn swallow migrates to its winter range in South America (A.O.U. Checklist of North American Birds, 1957). The barn swallow is usually found in association with man, quickly taking advantage of shelter offered by man-made structures. It constructs open, cup-shaped nests, lined with feathers, under bridges, in barns or buildings. Barn swallows prefer a mesoseric environment consisting of irrigated farmlands, ranches, and fields.

STUDY AREA

The study area was located approximately six miles south of Ellensburg, Kittitas County, Washington (Township 17 North, Range 19 East). A government benchmark at the study bridge (number 8, see figure 1) records an elevation of 1,425 feet. About 600 feet to the south of bridges 7 and 8, the irrigated terrain rises abruptly into rolling, sagebrush-covered hills. The farmland in the study area has only recently (1910) come under irrigation and consists mostly of alfalfa and pastureland.

The main study bridge (Kittitas County bridge number 79302) is located at the intersection of Wilson Creek and Thrall Road. This particular bridge was selected for a study site because of the large swallow populations and easy accessibility under the bridge for checking nests and conducting observations. The bridge was built of wood in 1948 and later rebuilt of concrete in 1955. The overall dimensions of the bridge are: length--89 feet, width--27 feet, 9 inches. Underneath the bridge are four spans running lengthwise with six spans spread across the width of the bridge, forming 15 parallelograms with inside lengths of 14 feet, 4 inches and widths of 7 feet, 8 inches.

At its passage under the bridge, Wilson Creek measures a width of 36 feet and exhibits a 4 to 5 foot variation in water level, dependent upon the amount of farmland irrigation.

METHODS

Visitations to the nesting area were mainly made in the morning, but observations were occasionally varied by making afternoon and evening visitations.

Four steel poles were constructed to fit over the bridge railing and extend down to the surface of the water. Mist nets were suspended between the poles on both sides of the bridge to capture the birds alive. Upon capture, the birds were marked with various combinations of Tester's dope paint. Initially, the ninth primary was marked and the seventh and eighth were clipped to expose the ninth for easy recognition of the colors in flight (Peterson, 1955). This technique was later abandoned and the wingtips and tail feathers were painted. A sample was obtained from the digestive tract of each captured swallow and preserved in an alcohol solution for later identification. A total of 72 stomach samples was collected, including samples from adults and nestlings of both species.

Both populations of swallows were small, which precluded the normal procedure of sacrificing individuals to obtain stomach samples. As a result, a flushing technique was developed to obtain food samples without decimating the study population.

The flushing technique required two men in the field. A 10cc disposable, plastic syringe was filled with warm saline solution and an attached plastic tube (16 mm long with 4 mm outside diameter) was coated with vasoline and gently inserted into the esophagus. Insertion was continued until the tube rested against the proventriculus. A receptacle, such as glass jar, was then held under the cloaca of the bird. The saline solution was gently forced into the digestive tract until it began to flow from the cloaca into the receptacle. Pressure was then increased on the plunger of the syringe and the water forcibly flowed through the digestive tract and out the cloaca, carrying whole and particulate insects which were collected in the glass receptacle. The bird was held with its head downward to prevent excess water from flowing back into the oral cavity and to prevent the bird's feathers from becoming wet.

The technique worked well on adults and nestlings; however, the nestlings presented a special problem. Their fecal sac obstructed the passage of the saline solution, and unless the sac was first removed, the flush could not be completed. The fecal sac was sometimes defecated by the nestlings during handling. If not, it could be removed by rubbing the abdomen in a posterior direction.

An occasional death was recorded but could be attributed to the capture procedure. Two of the cliff swallows that died were dissected and found to contain only a few particles at the cloaca, thus confirming the effectiveness of the technique in evacuating the digestive tract.

The insect samples were distributed and dried on circular filter paper. The filter paper was divided into quadrants to facilitate orientation during microscopic observations. Certain insect particles, such as elytra, hemilytra, wings, and head, withstood digestion quite well, and insect counts were based on these particles. For example, elytra were counted and divided by two to give an estimate of the frequency of Coleopterans in the sample.

Flight patterns of the barn and cliff swallows were observed and described on a tape recorder. Horizontal zonation, vertical stratification, and gliding and flapping patterns were described. The tapes were later replayed, and a stop watch was used to determine the amount of time spent flapping and gliding. A limit of twenty seconds was placed on each observation of the flight patterns. However, the barn swallow's style of flight, close to the ground and in among vegetation, made it impossible to always adhere to the twenty second limit. Therefore, all observations were utilized, regardless of their length, and percentages were computed from the total time of the observations.

A rubber raft was used to investigate nests and to remove captured birds from the mist nets. Ropes were strung at strategic locations under the bridge for easier maneuvering and to keep the raft from drifting in the swift current. A large inner tube was used, with a rope attached, for investigating smaller bridges.

RESULTS

ZONE OF SYMPATRY

Eleven bridges (Figure 1) in the general study area were investigated to determine which species of swallows nested at the colony sites. The map indicates bridges 6, 7, and 8 (within red triangle) where both species of swallows were found nesting. To the northward, bridges 1-5, 9, and 10 were found to be occupied solely by barn swallows. Toward the south, from the 3 bridges in the red triangle, bridge 11 had only cliff swallows nesting beneath it. More pure colonies of cliff swallows were located further down the Yakima Canyon.

ARRIVAL DATES AND POPULATION SIZES

The cliff swallows arrived at the colony site on 11 April 1967. The barn swallows appeared 17 days later, on 28 April. Individual barn swallows were sighted at the colony on 12 and 21 April; they flocked with the cliff swallows but had left the colony by the following day.

The population of cliff swallows at bridge 8 consisted of approximately 240 breeding individuals. The barn swallow population was smaller, totaling about 60 breeding individuals.

NESTING CYCLE

The barn and cliff swallow reproductive cycles occurred during different periods of time (Figure 2). The cliff swallow began nest construction on 24 April under and on the sides of bridge 8. A few cliff swallow nests were constructed by adding mud to existing barn swallow

FIGURE 1

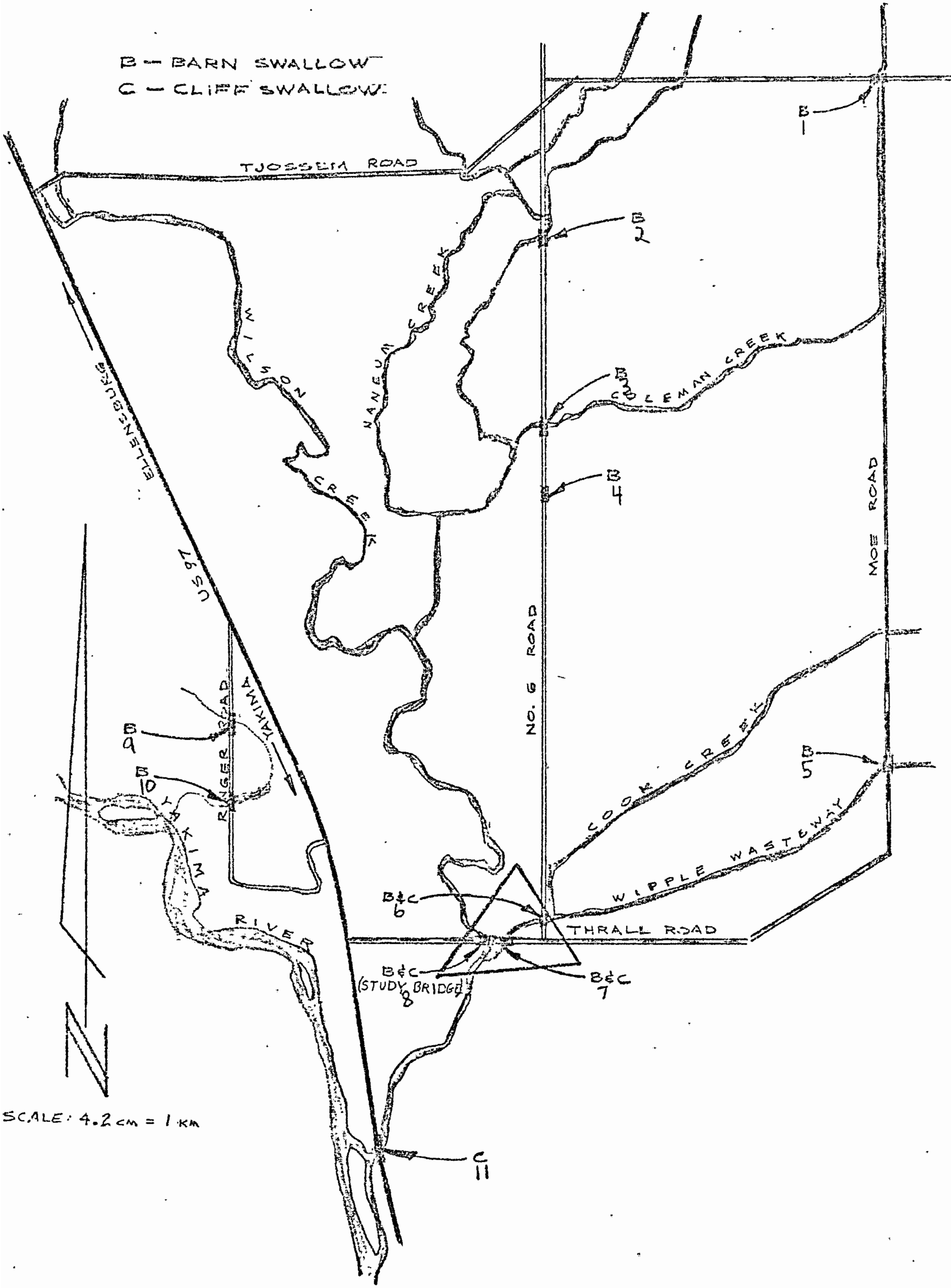
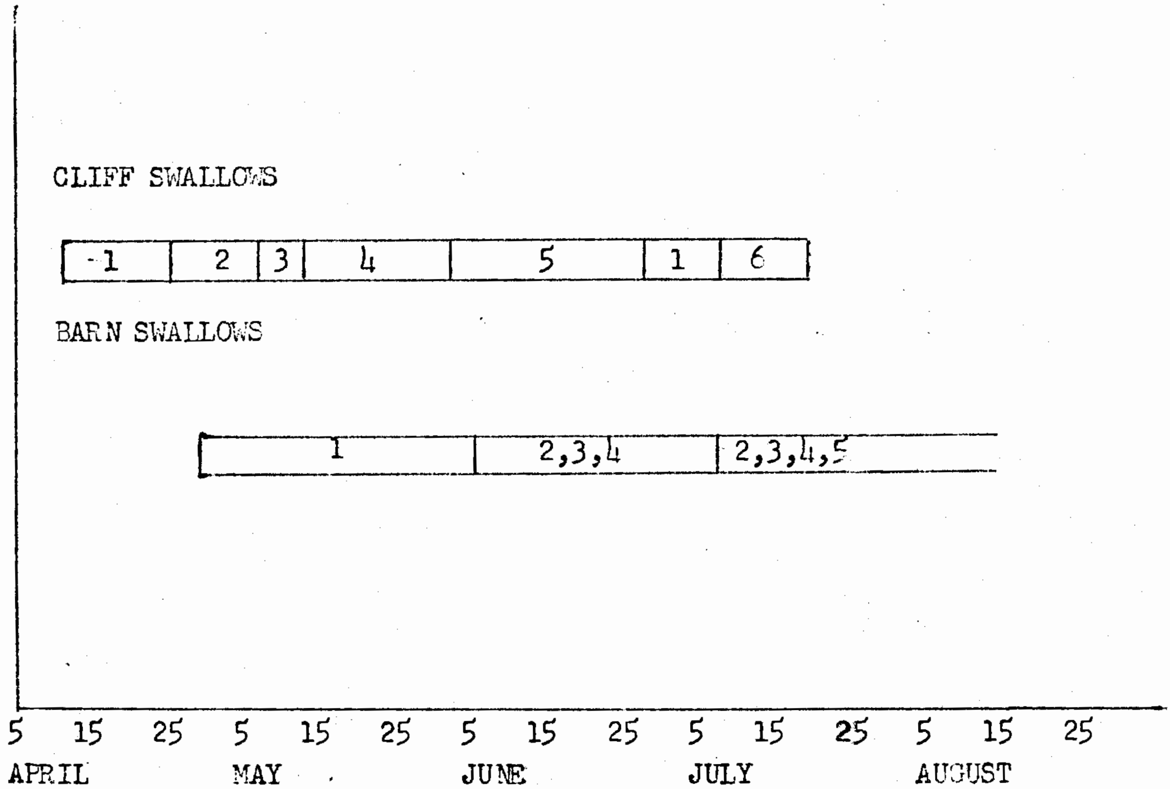

B — BARN SWALLOW
C — CLIFF SWALLOW
TJOSSEM ROAD
WILSON CREEK
NANEUM CREEK
COLEMAN CREEK
ELLENSBURG
US 97
YAKIMA
NO. 6 ROAD
MOE ROAD
RINGER ROAD
COOK CREEK
WIPPLE WASTEWAY
THRALL ROAD
YAKIMA RIVER
B 1
B 2
B 3
B 4
B 5
B&C 6
B&C 7
B&C (STUDY BRIDGE) 8
B 9
B 10
C 11
N
SCALE: 4.2 cm = 1 km

FIGURE 2

Comparative Reproductive Periods of Both Species of Swallows



1- FLOCKING ACTIVITY

2- NEST BUILDING

3- EGG LAYING

4- INCUBATION

5- FEEDING NESTLINGS

6- WINTER MIGRATION

FIGURE 3

Monthly Percentages of Identifiable Food Material

in Cliff Swallow Stomach Samples

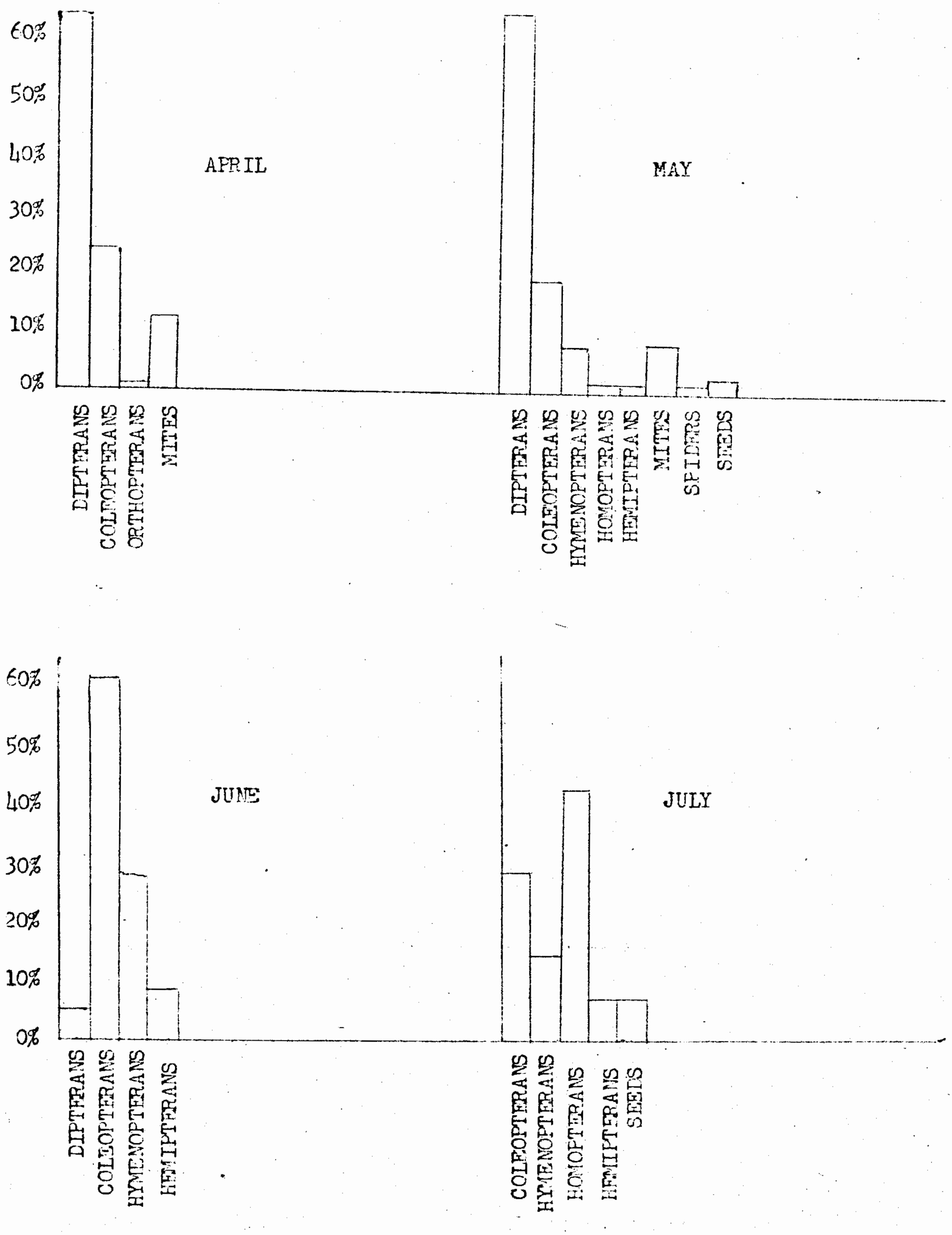


FIGURE 4

Monthly Percentages of Identifiable Food Material

in Barn Swallow Stomach Samples

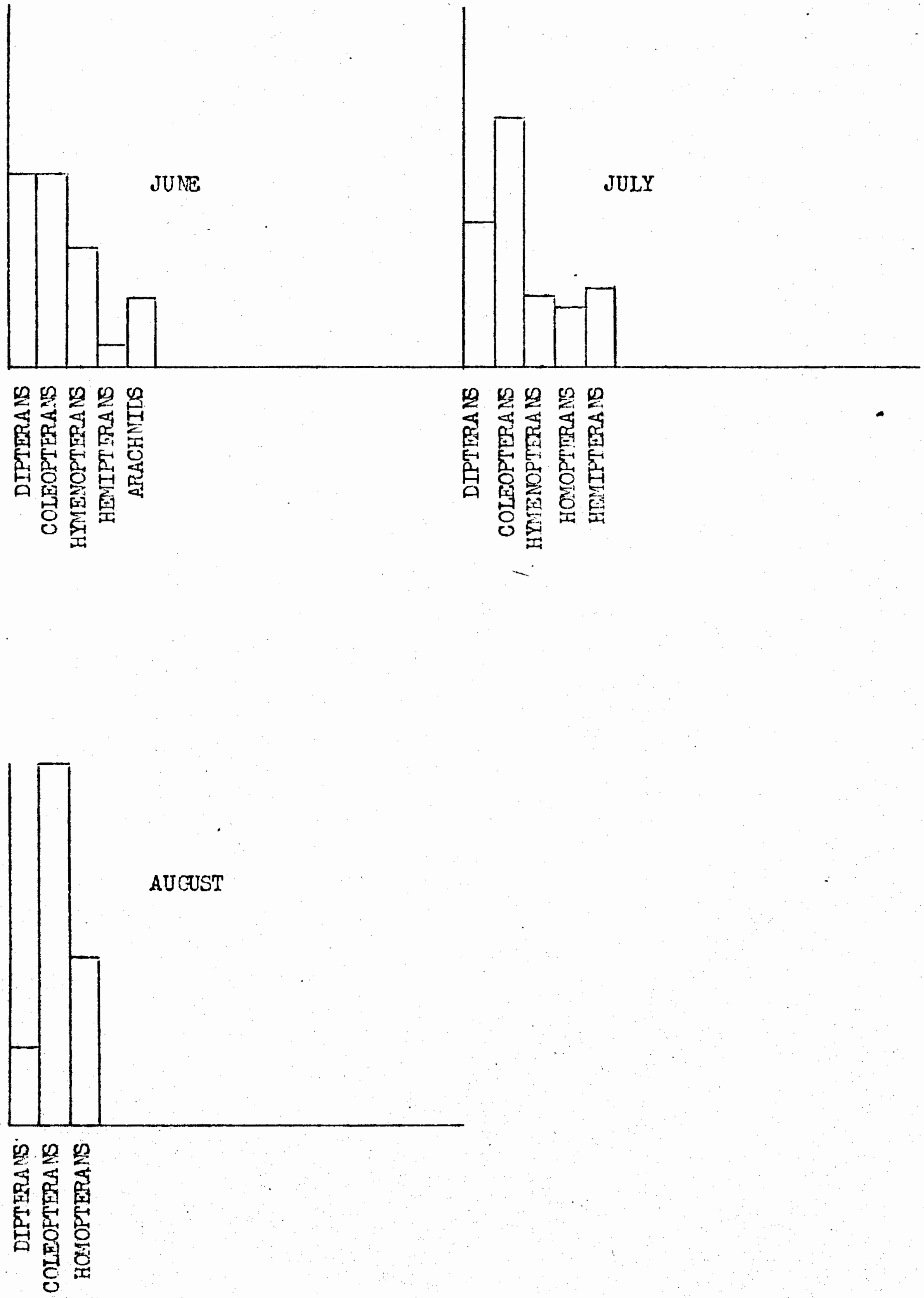


FIGURE 5

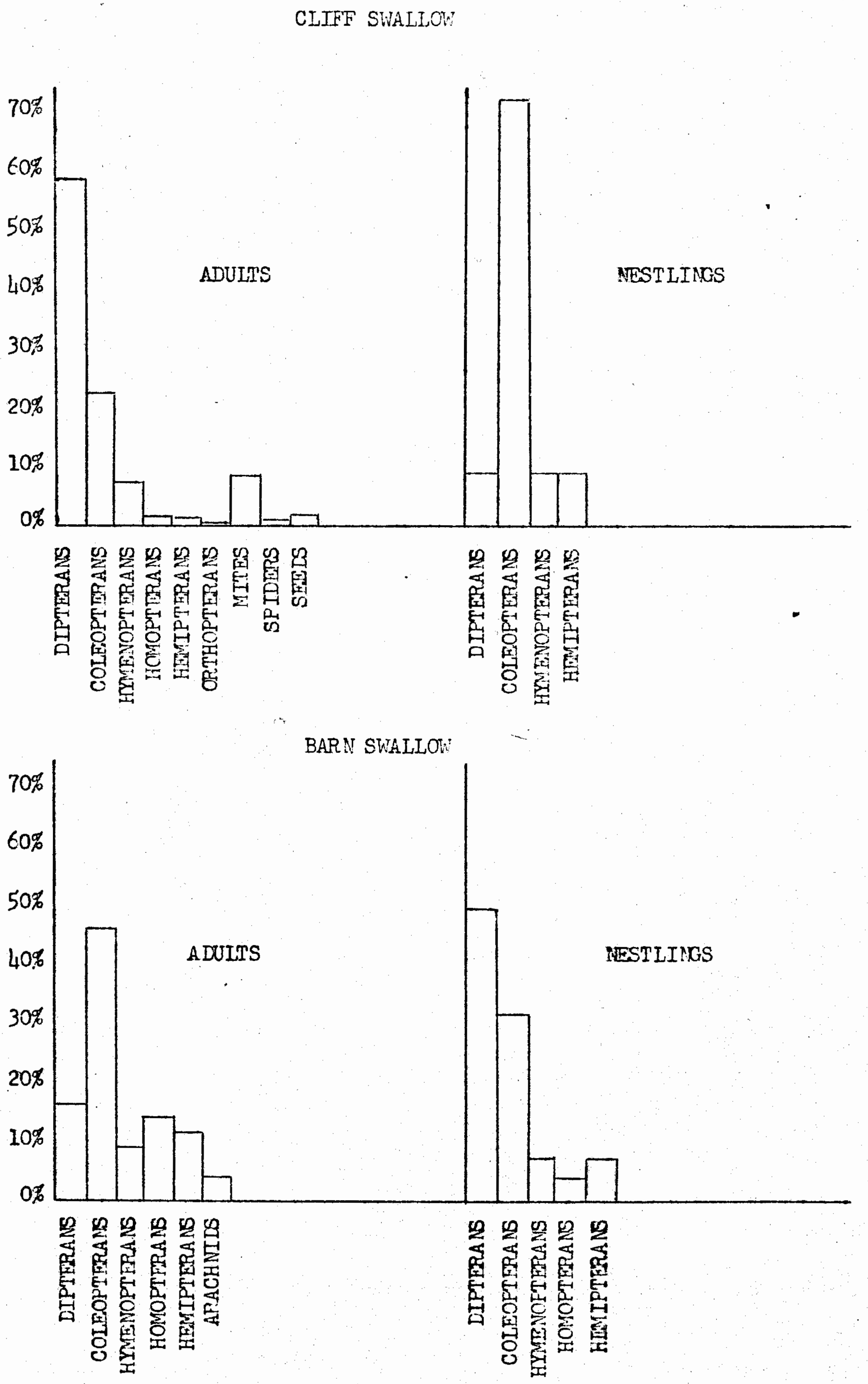
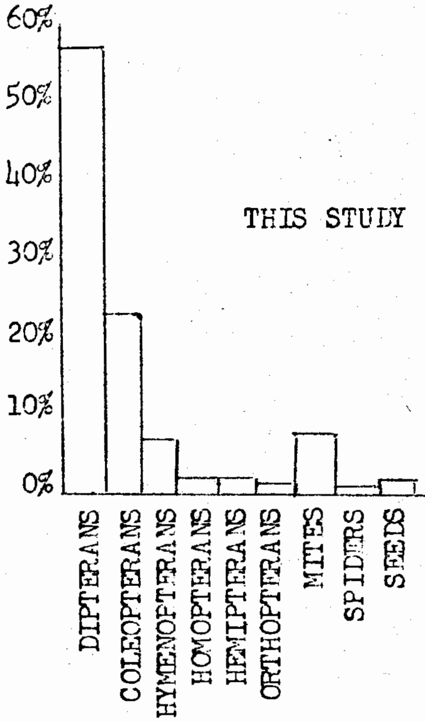
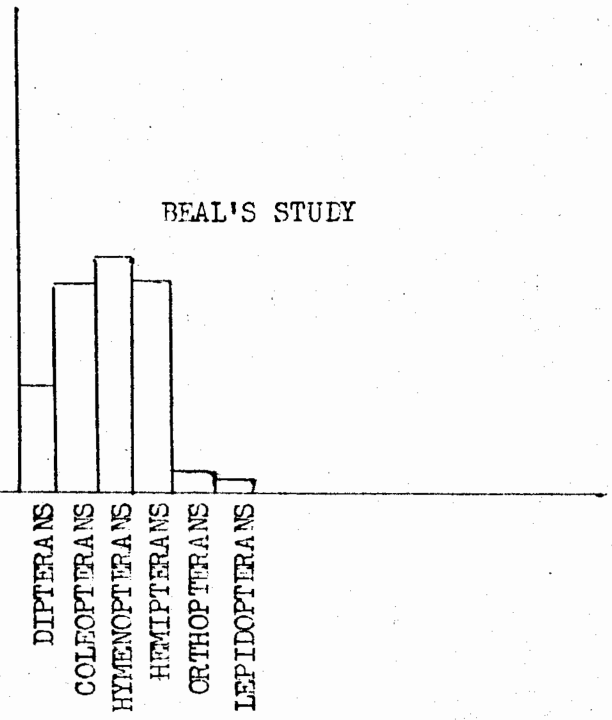

CLIFF SWALLOW
70%
60%
50%
40%
30%
20%
10%
0%
ADULTS
NESTLINGS
DIPTERANS
COLEOPTERANS
HYMENOPTERANS
HOMOPTERANS
HEMIPTERANS
ORTHOPTERANS
MITES
SPIDERS
SEEDS
DIPTERANS
COLEOPTERANS
HYMENOPTERANS
HEMIPTERANS
BARN SWALLOW
70%
60%
50%
40%
30%
20%
10%
0%
ADULTS
NESTLINGS
DIPTERANS
COLEOPTERANS
HYMENOPTERANS
HOMOPTERANS
HEMIPTERANS
ARACHNIDS
DIPTERANS
COLEOPTERANS
HYMENOPTERANS
HOMOPTERANS
HEMIPTERANS

FIGURE 6

Percentage of Identifiable Food Materials

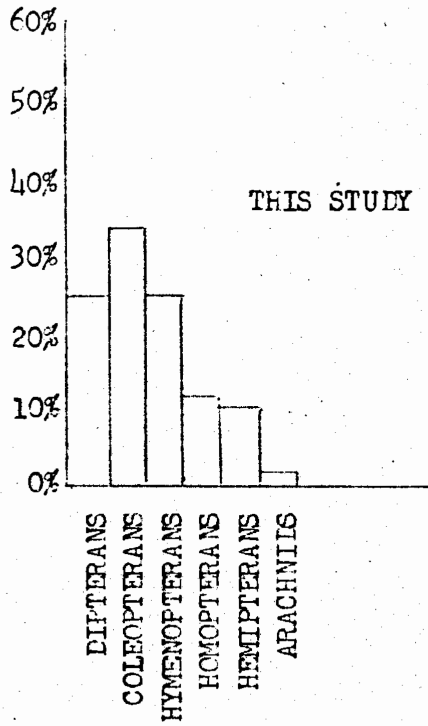
in Cliff Swallow Stomach Samples

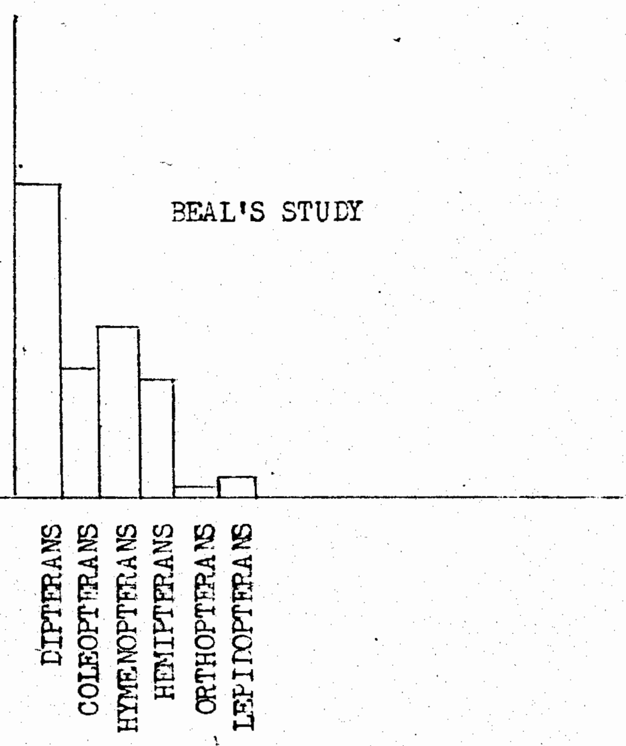




Percentage of Identifiable Food Materials

in Barn Swallow Stomach Samples





nests from previous seasons. At a wooden bridge (number 7), every cliff swallow nest under the bridge was built onto a barn swallow nest, with some barn swallow nests remaining separate and available for barn swallow nesting.

Although some cliff swallows constructed their nests under the bridges, most of them placed them on the sides of the bridges. Barn swallows, on the other hand, always constructed their nests under the bridges. Neither of the two species seems capable of destroying or removing the nests under the bridges and the nests seem to hold up quite well, being protected from weather and man.

The cliff swallows arrived first and began nest construction first. If the population is large, there may not be enough of the preferred nesting space on the sides of the bridges, so some cliff swallows construct nests under the bridge, consuming free nesting space or building on top of already-present barn swallow nests. Nelson (1955) mentioned a pair of barn swallows attempting to build on to a cliff swallow nest only to have the nest fall to the floor.

Not all cliff swallows initiated nest construction at the same time, but by 15 May most nests contained eggs (Figure 2). By early June, nestlings were present in the cliff swallow nests. The cliff swallows finished their nesting cycle in late June and were observed flocking on wires to the south of the study area over a high hill. After 18 July the cliff swallows were not seen around the colony site except for an occasional individual or pair circling the study area.

The barn swallows arrived on 28 April and flocked and foraged around the colony until they began nest construction. Three pairs of barn swallows began nesting early, occupying old nests, and by 12 June there were eggs in three nests. Unfortunately, the nests were accessible to fishermen and were destroyed. By 10 July, after the cliff swallows had finished their reproductive phase, two barn swallow nests contained nestlings and other barn swallow nests contained eggs. Some barn swallows were beginning nest construction at this time. Barn swallows were not synchronized in their nesting activity as was the case with the cliff swallows. From July through August, barn swallows could be found in various stages of their reproductive cycle (Figure 2).

Investigations of bridges 1-5, 9, 10, and 11 revealed that the reproductive phases of the isolated populations of barn and cliff swallows corresponded with those of the swallows at bridges 6, 7, and 8. Cliff swallows at bridge 11 had completed their nesting cycle by 10 July. Barn swallows at bridges 1-5, 9 and 10 were found in the same phases of nesting as the barn swallows at bridge 8.

FORAGING BEHAVIOR

Both species of swallows fed over the same area, for the most part restricting their foraging to an alfalfa field north of bridge 8. Twenty-one separate observations of barn and cliff swallow flight patterns were made totaling 827.5 and 824.8 seconds, respectively. The barn swallows performed a cursorial style of flight spending 76% of their flight time flapping and 24% of their flight time gliding. Cliff swallows foraged with a rollercoaster style of flight, flapping upward, then gliding downward and spending 60% of its time gliding and 40% flapping.

When both species first returned to the colony site, they did not adhere to any particular stratification. Both species foraged side by side at various altitudes, ranging from a few feet above the ground to over 300 feet. Until 12 June, both species varied their feeding elevations and were observed foraging together close to the ground and at higher altitudes. Observations after 12 June indicate that the species began to stratify, exhibiting the typical barn and cliff swallow style of flight. This stratification occurred during the cliff swallow nesting period (Figure 2).

Blake (1948) previously described the flight behavior of both species. His investigations revealed that the barn swallow's preferred flight style is to course close to the ground or water in long straight runs, with glides being rare and brief. Blake described the cliff swallow flight as a series of long ellipses, with frequent glides, stratifying between 15 feet and 30 feet above the ground. Results of the present study thus confirm those of Blake.

FOOD HABITS

Food samples taken from adults, juveniles, and nestlings of both species revealed the occurrence of spiders, mites, seeds and six orders of insects. Percentages based on the number of insects and other materials in the stomach samples were determined for both species.

A total of 35 cliff swallows--26 adults and 9 nestlings--was sampled during the period of 26 April to 10 July. From 26 June to 21 August, 14 adult and 23 nestling barn swallows were sampled.

Monthly percentages of identifiable food material in cliff swallow stomach samples (Figure 3) demonstrate a heavy reliance on dipterans during April and May. A shift of their diet to coleopterans occurs in June, with an increase in homopteran consumption in July. A striking decrease occurs in dipteran consumption in June with a total absence of dipterans in the cliff swallow stomach samples in July.

During June and July, the barn swallows relied essentially on three insect orders (Figure 4). However, the monthly percentages do indicate an increase in coleoptera consumption during the months of July and August.

Figure 5 offers a comparison of the respective diets of adults and nestlings of both species. The adult cliff swallows feed mainly on Dipterans but their young a high percentage of coleopterans. Adult barn swallows consume a high percentage of coleopterans, but feed their young a larger proportion of Dipterans.

The graphs in Figure 6 provide a relative comparison of the total food sources of the two species. It is evident that the barn swallows rely heavily on three insect orders--Coleoptera, Diptera, and Hymenoptera, which comprise 78% of their diet.

The cliff swallow consumes coleopterans and dipterans with a greater frequency. These two orders make up 81% of their diet.

Beal (1918) conducted food habit studies of barn and cliff swallows. Stomach samples were collected from both species in 27 states, the District of Columbia, and Canada. Three hundred and seventy-five cliff swallow stomachs and four hundred and sixty-seven barn swallow stomachs were examined and the percentages of insect orders computed.

Upon comparison of the graphs of Beal's percentages with those of this study (Figure 6) it immediately becomes apparent that there are differences in the proportions of insect orders consumed by populations of barn and cliff swallows (Beal's data) and the proportion of insect orders consumed by both species in the area of overlap in the Kittitas Valley. Beal's data show that the cliff swallow relys heavily on three insect orders: coleopterans, hymenopterans, and hemipterans. According to Beal, the barn swallows consume a large proportion of dipterans also relying rather equally on coleopterans, hymenopterans, and hemipterans.

AGGRESSIVE BEHAVIOR

During the course of this study, two aggressive incidents were recorded between barn and cliff swallows, and both occurred during the cliff swallow nesting period. The cliff swallow dominated in each case, chasing the barn swallow away from the bridge and pursuing it out over the field where the chase terminated. During the early part of the breeding season, both species foraged side by side and flocked on the same telephone wires, staying four inches apart (which agrees with Emlen's (1952) observations of cliff swallows) without any aggressive behavior.

Rough-winged swallows were observed feeding and roosting with both barn and cliff swallows with no antagonistic behavior recorded. On the other hand, the cliff swallows were aggressive towards violet-green swallows during roosting and foraging activity, not allowing them to roost closer than four feet on the same telephone wire and commonly interrupting foraging behavior to drive away violet-green swallows that were apparently foraging too near.

NESTING SPARROWS

English sparrows were found occupying cliff swallow nests of previous years under the study bridge before the arrival of the swallows. Although English sparrows occupied cliff swallow nests, they did not utilize barn swallow nests. When the cliff swallows began their nesting activity, they also occupied some intact cliff swallow nests remaining under the bridge. They did not, however, occupy any cliff swallow nests from earlier seasons that had been previously utilized for nesting by English sparrows. The sparrows lined the nest to overflowing with nesting materials and defecated freely in and on the nest, turning the entrance white with fecal material. At no time during this study were cliff swallows replaced in a nest by English sparrows.

DISCUSSION

The data clearly indicate differences in food preferences between the cliff and barn swallow in the area of overlap. Apparently correlated with this were differences in foraging flight patterns as well as flight elevations, at least during the period when the cliff swallows were feeding their young. Finally, the separation in time of the nestling and fledgling periods of the two species would serve to minimize competition for resources during those periods of increased demand. There seems to be little room for doubt that competition, at least for food was at a minimum between these two species. The results, however, give rise to a number of other problems that warrant discussion.

First of all, two possible explanations may be offered as to how these niche differentiating mechanisms were developed: (1) they could have been developed in isolation prior to any contact or (2) these differences may have evolved as a result of competitive interaction.

The foraging data (Blake's data) and the food preference data collected by Beal indicate that the barn and cliff swallows may have been isolated prior to any competitive association. These adaptations could have been developed for exploiting different niches in isolated habitats. When these species came into contact in the Kittitas County, these adaptations could effectively function as niche differentiating mechanisms.

Two other differences between the species can perhaps be better explained resulting from a competitive association. Jewett, et al., (1953) list the mean nesting date for barn swallows (full sets of fresh eggs) as 25 May, with nesting activity in its height in May, June, and July. The barn swallows in the study area reached their peak during July and August. Only one sound explanation can be offered for the delay in the nesting activity of the barn swallows. The barn swallows could not successfully rear their young when their nesting cycle coincided with the cliff swallow nesting cycle and were forced to delay their nesting activity until the cliff swallows had finished in order to achieve reproductive success.

The timing of barn and cliff swallow stratification also may have developed because of interspecific competition. The fact that the species stratify during the time when the cliff swallows are feeding their young, seems to indicate that food is a critical factor during the nesting cycle requiring the species to forage at different levels. This functionally reduces competition for food by placing the sympatric species at different places, hence varying food sources during foraging.

Competition may be occurring for nesting space. English sparrows contribute to the loss of nesting space. Once the English sparrows have occupied a cliff swallow nest, the cliff swallows will no longer lay eggs in the nest and the nestling space is essentially removed from use by the swallows until the nest is destroyed.

If cliff swallows continue to arrive first and construct their nests under the bridges, the barn swallows may eventually be replaced at the colony site. If, indeed, this is occurring, it should be possible to demonstrate numerically, over a period of years, changes in the breeding populations at the various bridges in favor of the cliff swallows. Interspecific competition for nesting space would then be definitely indicated.

As previously mentioned, cliff swallows are colonial, constructing their nests side by side or partially on other cliff swallow nests.

They are normally found in large numbers, tolerating close association with other individuals in the population. On the other hand, it is not uncommon to find isolated pairs of nesting barn swallows. Davis (1937) stated that the barn swallows had definite territories two to five feet around the nest and extending out in the form of a cylinder to the perch, which may be ten or more feet away. Aggressive behavior resulted whenever other barn swallows entered their territory.

If the barn swallows are territorial and cannot tolerate close association during nesting, they may be facing another limiting factor at the study bridge. The cliff swallows, by sheer numbers, may be forcing the barn swallows to seek new nesting sites.

SUMMARY

Breeding populations of cliff and barn swallows were investigated near Ellensburg, Washington, during the spring and summer of 1967. The study site was a concrete bridge spanning Wilson Creek. The bridge was located near an interface consisting of the meeting of an arid sage brush environment and irrigated farmlands.

Barn and cliff swallow breeding populations were estimated to be 60 and 240 respectively.

A total of 72 stomach samples were taken from barn and cliff swallows and percentages determined based on the number of insects consumed by each species. The stomach samples indicate that both species feed on the same insect orders but with different frequencies.

Foraging styles were determined and differences in elevations during foraging were noted. Until 12 June, both species foraged side by side from ground level to over 300 feet. After 12 June, at the time cliff swallows young hatched, the two species exhibited vertical stratification.

The cliff swallows arrived first and began nesting, terminating their reproductive phase by late June. The barn swallows arrived 17 days later and flocked around the colony, with the majority of barn swallows starting their nesting cycle in early July.

Interspecific competition for nesting space may be occurring between the species, with the cliff swallows seeming to have a definite advantage because of (1) their early arrival and (2) their building on top of existing barn swallow nests.

Only two incidents of aggressive behavior were recorded during the course of the study with the cliff swallow dominating and chasing the barn swallow away from the colony site. If aggressive interaction is a measure of competition, it may be postulated that interspecific competition between the species is at a minimum.

Explanations were offered concerning the evolution of differences displayed by the species. It would appear that foraging and feeding behavior developed in allopatry prior to any competitive association. The timing of the stratification during foraging behavior of both species and the delay in the time of the barn swallow nesting cycle indicate that these mechanisms evolved as a result of interspecific competition.

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