COMPARATIVE BREEDING ECOLOGY OF PHOEBES IN TRANS-PECOS TEXAS

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The Black Phoebe (*Sayornis nigricans*) and Say's Phoebe (*S. saya*) occur sympatrically in an area from western Texas and north-central Mexico to California. In addition, each of the species is found over a relatively wide range; Black Phoebes occur as far south as Argentina and Say's Phoebes nest in northern Alaska.

I conducted a field study to quantify the phoebes' use of resources in the area of overlapping occurrence. My approach was to consider the use of different resources, of the same resources at different places, and of the same resource in different ways. The objective was to determine which of these factors facilitate the sympatric occurrence of Black and Say's phoebes in the Trans-Pecos region.

METHODS AND STUDY AREA

Methods.—I conducted field work from June through August 1969 and May through August 1970, with supplemental observations in November 1970 and May 1971. I travelled throughout the Trans-Pecos area to determine the geographical and ecological distribution, nesting habits, and food consumption of the phoebes, as well as to study the habitat types of the area. Detailed studies were carried out at selected sites. Literature and museum locality records supplement my distributional data.

Phoebes were banded with colored plastic, and aluminum Fish and Wildlife Service, leg bands to learn about daily activities of individuals, including behavior toward other flycatchers. I caught adults with an insect net at their roost sites after dark; others were banded as nestlings.

Specimens for food analysis were shot. Food items were identified, counted, and then measured by volumetric displacement. The material contained in the stomach (proventriculus and ventriculus) of an individual bird is defined here as a sample. I also collected samples of food delivered to nestlings using the pipe-cleaner collar devised by Orians (1966) and Willson (1966).

Habitat data were analyzed by appropriate methods presented in Snedecor and Cochran (1967). Means and 95% confidence intervals were calculated for measurement data, and chi-square and t-test analyses were generally used to determine statistical significance. Additional details concerning methods have been described previously (Ohlendorf 1974).

Study area.—The Trans-Pecos, an area of some 83,000 km^2, encompasses a variety of habitat types, including the most arid and the highest areas of the state. It is situated west of the Pecos River, north of the Rio Grande, and south of New Mexico.

Most of the region is drained by the Rio Grande, the Pecos River, and their tributaries. Several perennial streams, although small, provide water at isolated spots throughout the region. Rainfall for the Trans-Pecos region averages 30.5 cm

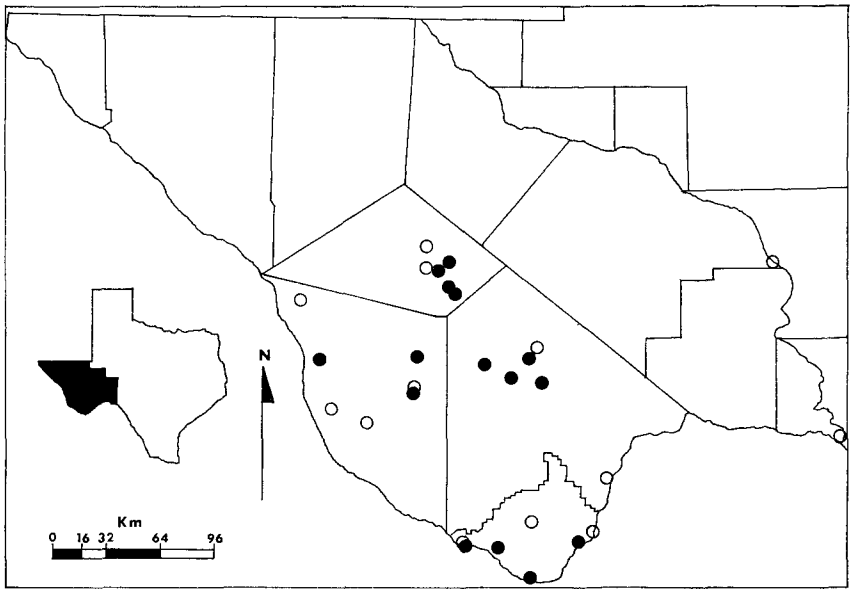

FIG. 1. Breeding distribution of Black Phoebes in the Trans-Pecos region. Filled circles represent nesting localities. Open circles represent locality records during the breeding season (10 April to 10 August) without observed nesting.

per year. Amounts are generally less at lower and greater at higher elevations, with a maximum of 45.7 cm in the Davis Mountains (Orton 1969).

The biota is typical of the Chihuahuan Desert (Blair 1950), and most of the area remains natural, but modified by grazing of livestock. Considerable vertical zonation exists in vegetative types. Desert shrub predominates up to 1200–1500 m; grassland and pine-oak-juniper types occur above this elevation. Cultivated areas are generally confined to irrigated valleys, e.g. at El Paso, Presidio, Balmorhea, and near Pecos.

DISTRIBUTION AND HABITAT

Both species of phoebes are near the margins of their distributions in the Trans-Pecos region. The area represents the northeastern limit for the Black and the eastern limit for Say's phoebe (A.O.U. 1957 and other sources). Farther north, the Eastern Phoebe (*S. phoebe*) occurs sympatrically with Say's Phoebe during the breeding season, but within my study area it occurs only as a winter resident (Wauer 1973).

The breeding distributions of the Black and Say's phoebes in the area were quite different (Figs. 1 and 2). Both species are resident, with individuals of the more northern populations (particularly Say's) also over-wintering in the Trans-Pecos region. Nest construction frequently

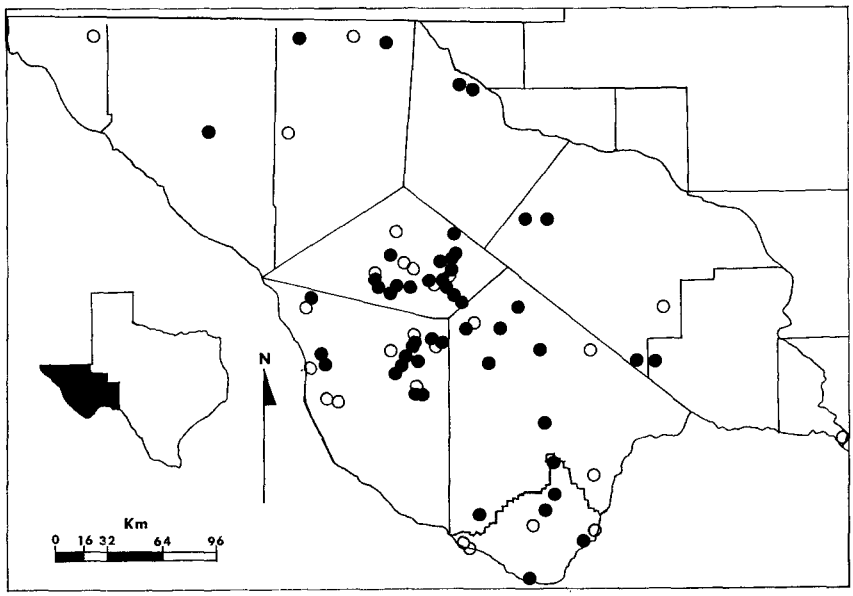

FIG. 2. Breeding distribution of Say's Phoebes in the Trans-Pecos region. Filled circles represent nesting localities. Open circles represent locality records during the breeding season (10 May to 10 August) without observed nesting.

begins in March, although it was observed at Fort Davis in February 1969 (Say's) by Pansy Espy (pers. comm.). Some migrant Black Phoebes are in the region until early April, and some Say's pass through until early May (Wauer 1973). Post-nesting dispersal from typical nesting situations occurs late in the summer, especially after early August. Therefore, I considered only localities at which the Black Phoebe was recorded from 10 April to 10 August, or at which Say's was recorded from 10 May to 10 August, as breeding localities. Nesting localities referred to in this paper are those at which nests, or fledglings incapable of extended flight, were found.

Nest data are based on the total number of nest constructions. Nests were frequently re-lined with fresh material and used for subsequent clutches, or new nests were sometimes constructed at a previously used locality. Counting each of these nest uses at a locality tends to reflect more nearly the relative importance of various habitat types than if the data were based merely on nesting localities.

Location of nests differed somewhat in respect to elevation, but the differences were not significant (χ^2, $P > 0.1$), based on 36 nestings of Black

and 115 of Say's phoebes. The mean elevation for Black Phoebe nests was 1232 ± 86 m; Say's, 1297 ± 47 m.

Distributional differences in these species are due primarily to their differing habitat requirements, based on 35 nestings of Black Phoebes and 115 of Say's. The pine-oak-juniper and grassland types, in which 45.2% (52) of the Say's Phoebe nests occurred, were occupied primarily by this species. Distributional differences between the phoebes in the shared habitat types (i.e. desert shrub and riparian) are highly significant (χ^2, $P < 0.01$).

The Black Phoebe was restricted in nesting to areas with mud and suitable nesting substrate such as overhanging boulders, bridges, or culverts. The paucity of nesting records for this species reflects the scarcity of such habitat in the region. However, a nest may be constructed during one wet breeding season and then used again in subsequent dry ones. In one instance a pair of Black Phoebes began construction after a shower, but mud became too dry for completion. Construction resumed several days later when there was another shower, and the birds nested successfully.

One Jeff Davis Co. sight record for Black Phoebes was at 1737 m in the pine-oak-juniper type. Although nesting was not observed, I consider it probable that nesting does occur at these higher elevations where mud and nest substrate are available. The other breeding season locality in the county was in the riparian type flanked by grassland-oak. All of the nests recorded for the county were under bridges or in culverts in the grassland-oak type.

The occurrence of Say's Phoebe in all habitat types except farmland reflects its less restrictive requirements.

NESTING

Phoebes have benefited from man's construction of bridges, culverts, and buildings by having available an increased number of suitable nesting sites. I found many nests in habitat types that would otherwise have been unsuitable for phoebe nesting. Before man-made structures, both species probably nested only where there were vertical surfaces such as cliffs, rimrocks, steep creek banks, and caverns. Such substrates are rare over a great portion of the Trans-Pecos.

Black Phoebes build mud nests on vertical or near-vertical surfaces which are protected from rain. These sites must be within carrying distance of a source of mud. I did not find nests more than 15 m from mud. Say's Phoebes nest in holes, crevices, and on ledges and other protected horizontal surfaces of cliffs, rimrocks, steep creek banks, and caverns. They also use nests previously constructed by Cliff Swallows (*Petrochelidon pyrrhonota*),

TABLE 1

NEST SUBSTRATE USED BY PHOEBES

Substrate	Black	Say's
"NATURAL"	5 (13.9%)	9 (8.0%)
Boulder	3	1
Rimrock	1	1
Cavern	1	–
Gravel bank	–	6
Cliff	–	1
MAN-MADE STRUCTURES	31 (86.1%)	103 (92.0%)
Bridges	24	42
Structural	24	21
Cliff Swallow nests	–	18
Black Phoebe nests	–	3
Culverts	2	30
Structural	2	–
Cliff Swallow nests	–	22
Barn Swallow nests	–	5
Black Phoebe nests	–	3
Buildings	4	31
Unoccupied	4	25
Occupied	–	6
Well	1	–
TOTAL	36 (100.0%)	112 (100.0%)

Barn Swallows (*Hirundo rustica*) and Black Phoebes. Only when the Cliff Swallow nests had been broken into the form of a shelf were they used by Say's Phoebes. I do not know whether these nests were appropriated by the phoebes while still in use by the swallows. In this study I found 3 instances of nest reclamation by Cliff Swallows and Barn Swallows after use by Say's Phoebes. In each case the phoebes nested again in a similar nest at the same locality. In 2 cases, nests known to have been abandoned by Black Phoebes (but for unknown reasons) were used by Say's Phoebes.

Only 5 of 36 Black Phoebe nestings (13.9%) and 9 of 112 Say's Phoebe nestings (8.0%) occurred on "natural" substrates (Table 1). Nests of Black Phoebes on bridges and culverts were on vertical surfaces of structural elements. Those of Say's Phoebes were on guard rail supports or on other horizontal surfaces such as pillars and beams under the bridges. Culverts were composed of smooth vertical and horizontal surfaces devoid of structural features suitable for Say's nesting.

The relative use of natural, bridge, culvert, and building nest sites by the 2 species was significantly different (χ^2, $P < 0.01$).

Nests of both species were re-used for successive clutches in the same year, and in subsequent years. Many nest sites used in 1969 were also used in 1970, sometimes by the same birds. One Black Phoebe banded at Capote Canyon, northeast of Candelaria, in 1969 laid 2 clutches of eggs in that year and nested there again (same nest) in 1970. A similar observation was made in the case of Say's Phoebe at Plata.

Other data indicate a rapid replacement of birds at favored nest sites. Such replacement occurred in the case of a Black Phoebe at Plata after it was injured in a mist net. A nest in Capote Canyon that was used by Say's Phoebes in 1967 was used again in 1969 and 1970. Both adults of the pair were collected on 12 June 1969. Another pair of Say's was feeding nestlings in the same nest on 21 July. Southeast of Fort Davis, I collected an adult female and single nestling on 15 June 1969. An adult was carrying nesting material on 18 June and "improving" the same nest. On 22 June an adult was incubating 3 eggs and on 27 and 28 June 4 eggs were in the nest.

A pair of Say's Phoebes began construction about 6 March 1971 at a ranch house where nesting was recorded during previous seasons (Pansy Espy, pers. comm.). Eggs were laid from 20–24 March and the young were fledged on 29–30 April. At least one individual of this pair was replaced and 5 eggs had been laid in the same nest by 23 May. The replacement individual had been banded at this locality on 29 November 1970.

The mean height of Black Phoebe nests above ground or water (3.1 ± 0.7 m, range 0.3–10.7 m) was not significantly different from that of Say's (2.8 ± 0.3 m, range 1.2–12.2 m).

Nests of Black Phoebes were generally so widely separated that measurement was not meaningful, but in one case nests were separated by only 160 m. These 2 nests were under bridges located northeast of Fort Davis.

I recorded separation of Say's Phoebe nests by as little as 410 m at Capote Canyon. In 2 instances they were as near as 480 m at localities northeast of Fort Davis and north of Plata.

Only one nest of a particular species was ever located under a bridge or culvert, or at an isolated locality such as Plata, but there were 7 instances where the 2 species occurred relatively close to each other. At Capote Canyon, nests of Say's and Black phoebes were located as near as 390 m during both breeding seasons. The phoebes also nested close to each other at Plata (76 m), and under bridges north of Plata (56 and 61 m) and northeast of Fort Davis (23, 27, and 38 m). The species have nested within 15 m of each other in an abandoned building (Wauer 1973).

TABLE 2

FATE OF 66 PHOEBE CLUTCHES

	Black	Say's
Number of clutches[1]	21	45
Eggs laid	75	169
Eggs per nest	3.57	3.76
Eggs hatched	69 (92.0%)	124 (73.4%)
Eggs hatched per nest	3.29	2.76
Eggs infertile	1 (1.3%)	12 (7.1%)
Eggs lost	5 (6.7%)	33 (19.5%)
Young fledged	53	96
Fledged per nest	2.52	2.13
Fledged of eggs laid	53/75 (70.7%)	96/169 (56.8%)
Fledged of eggs hatched	53/69 (76.8%)	96/124 (77.4%)
Young lost before fledging	16 (23.2%)	28 (22.6%)
Successful nestings[2]	15 (71.4%)	30 (66.7%)

[1] Excluding abandoned nests.
[2] At least one young fledged.

Young-of-the-year Black Phoebes that had attained adult size were observed at Plata on 11 May 1970; this indicates hatching about 19–20 April. A brood of Say's Phoebes at Plata fledged on 11 May, indicating hatching about 24–25 April. A pair of Say's Phoebes at Fort Davis hatched its first clutch of eggs 12 April 1969; nest construction had begun in February (Pansy Espy, pers. comm.). The latest recorded dates of hatching were 10 July for Black Phoebes and 27 July for Say's.

Clutch size ranged from 1 to 4 (mean = 3.42 ± 0.30) for 26 clutches of Black Phoebe and from 1 to 6 (mean = 3.77 ± 0.30) for 69 clutches of Say's. I was able to determine the fate of 21 Black (mean clutch size 3.57 ± 0.23) and 45 Say's (3.76 ± 0.29) clutches (Table 2). The primary differences noted were in the number of infertile eggs (1.3% for *S. nigricans*, 7.1% for *S. saya*) and eggs lost prior to hatching (6.7% for *S. nigricans*, 19.5% for *S. saya*). I attributed almost half (44.7%) of the egg loss before hatching to human destruction of nests located under culverts and bridges. Heavy infestation by argasid tick larvae (*Argas cooleyi*) and dermanyssid mites (*Ornithonyssus sylviarum*) resulted in loss of 6 Black and 5 Say's nestlings. All of the Black and 3 of the Say's lost to these ectoparasites were in nests constructed above or within a few meters of Cliff Swallow nests. The other 2 Say's were in a nest constructed over one used previously that season by a House Finch (*Carpodacus mexicanus*). Eggs of Brown-headed Cowbirds (*Molothrus ater*) were never found in phoebe nests, although cowbirds do occur in the area.

Ten broods of Black Phoebes were raised near 8 broods of Say's. The average clutch size for such nests (3.7 and 3.5) was not significantly different (t-test, $P > 0.75$) from those for other nestings.

An insufficient number of adult birds was banded to determine the number of clutches laid per pair. At least 2 pairs of Black Phoebes still fed earlier broods of young while the female of each pair began laying the second clutch and sat on the eggs at night. One Say's Phoebe nest used in 1969 was used again for 3 clutches in 1970. Another nest in which well-feathered young were banded on 10 May 1970 had been used for 3 broods in 1968 (Roland Wauer, pers. comm.). There is an indication that 3 broods are produced by some birds, but 2 are clearly more frequent. Furthermore, when 3 broods are produced in some nests, they may be progeny of different adults.

FEEDING

An analysis of 14 Black and 23 Say's phoebe stomach samples taken during the study illustrates similarities and differences in the diets of the birds.

Most food items could be identified to family. Percent occurrence, percent individuals, and percent volume were considered in analyzing the samples. For each prey taxon of each phoebe species, the "% occurrence" represents its frequency in the occurrence of different prey taxa in the diet; "% individuals" represents its frequency in the total number of individual prey items; and "% volume" is its portion of the volume for all food. The relative importance of these parameters was described previously (Ohlendorf 1974).

Both phoebes fed primarily on insects (96.4% in Black, 98.1% in Say's). Spiders (Arachnida) were taken by both species, and Black Phoebes consumed fruits of buckthorn (Rhamnaceae) on one occasion. Black had a mean of 3.93 ± 1.43 prey taxa per sample and Say's a mean of 4.78 ± 0.33. This difference is not significant (t-test, $P > 0.2$).

The relative occurrence of various food types is different in the 2 species (Fig. 3). Extent of overlap (see Ohlendorf 1974) in diet is 77.7% on the basis of major food types (Fig. 3), but only 42.9% when based on families. Although many of the food items for both species were beetles (Coleoptera), the diets were still quite different because of the families that were represented.

The great number of termites (Isoptera) which had been consumed by 2 of the Black Phoebes was among the factors contributing to differences in the consumption of individual prey items (Fig. 4). I noted, however, that more swarming termites were seen in the habitat types in which

FIG. 3. Relative frequency, expressed as percent total taxon occurrences, of major prey types in Black (n = 14) and Say's phoebe (n = 23) samples. Asymmetry indicates different diets of these birds.

Black Phoebes occurred than in the more xeric types where Say's Phoebe predominated. Thus, Black Phoebes were more likely to capitalize on this resource when it became available.

Some prey taxa are of greater importance in the diet because of their larger size (Fig. 5). Dragonflies and damselflies (Odonata) seem to be most important for Black Phoebes, whereas grasshoppers (Orthoptera) seem to be most important for Say's. There was no overlap in the occurrence of these taxa in the samples.

Although they do not represent a large portion of the diet, other water-related insects (i.e. Corixidae, Notonectidae, Naucoridae, Omophronidae, and Hydrophilidae) were taken exclusively or more frequently by Black Phoebes. Other beetles, flies (Diptera), and bees (Apoidea; Hymenoptera) were taken principally by Say's.

Differences in composition of diets are illustrated by 2 groups of specimens. At Capote Canyon, I collected 5 Black Phoebes on 11 June 1969,

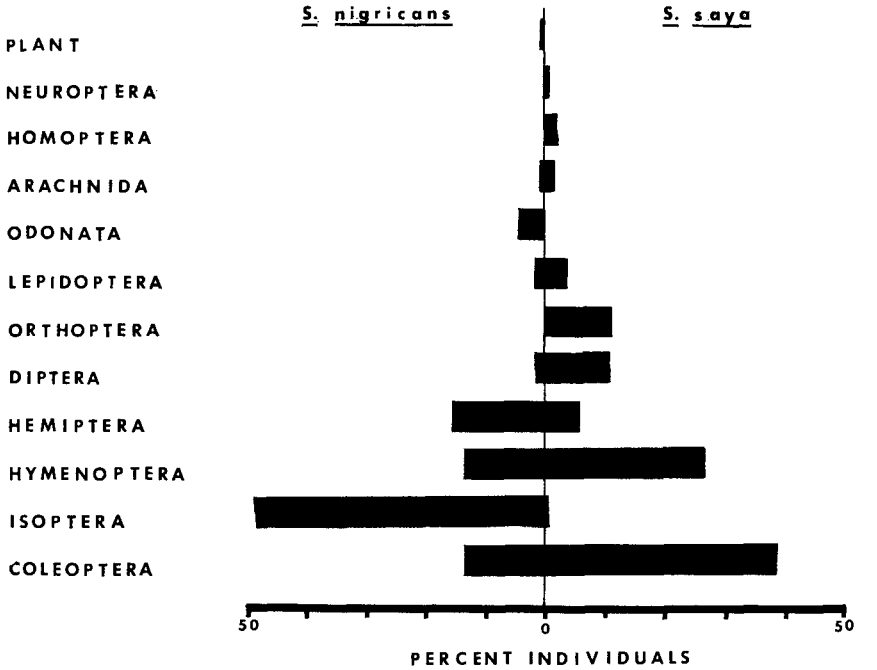

FIG. 4. Relative number of individuals, expressed as percent total individuals, of major prey types in Black (n = 14) and Say's phoebe (n = 23) samples. Asymmetry indicates different diets of these birds.

and 3 Say's Phoebes on the following day. The prey taxa in Black Phoebe samples consisted entirely of damselflies, termites, assassin bugs (Reduviidae), stink bugs (Pentatomidae), tiger beetles (Cicindelidae), round sand beetles (Omophronidae), water scavenger beetles (Hydrophilidae), and wasps (Vespidae). Prey in Say's Phoebe samples were grasshoppers (Acrididae), bugs (Lygaeidae), and bees.

A Black Phoebe sample from south of Marfa contained damselflies, assassin bugs, creeping water bugs (Naucoridae), leaf beetles (Chrysomelidae), and spiders (Lycosidae), whereas a Say's Phoebe sample from near this location on the same day had grasshoppers and robber flies (Asilidae). The Black Phoebe had been feeding in the riparian habitat type and the Say's was in the nearby desert shrub, similar to their typical occurrence in the region.

The intimate association of the Black Phoebe with water is demonstrated in its feeding behavior. Aquatic insects are sometimes picked from the water as the bird hovers near the surface. I never saw this species feeding

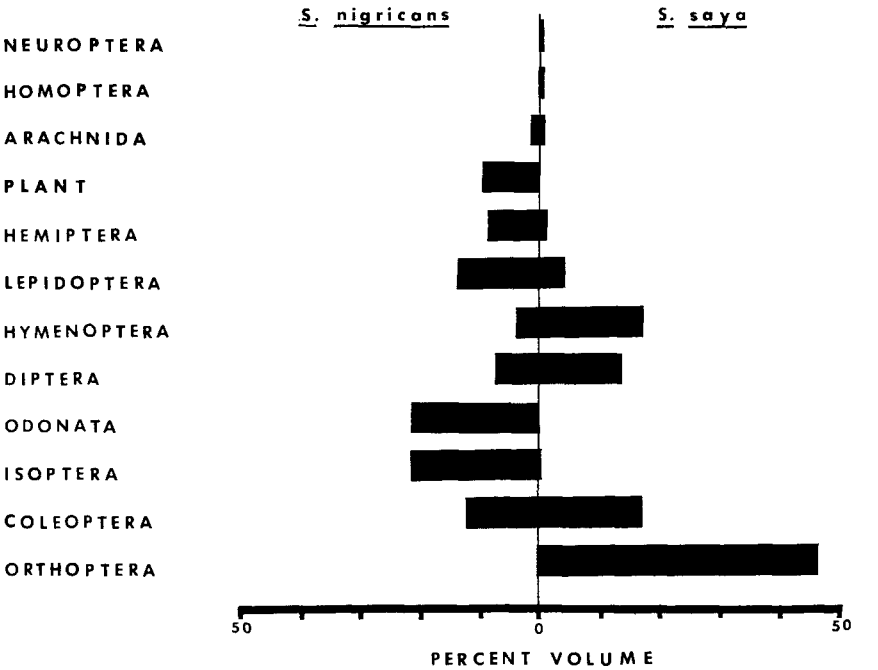

FIG. 5. Relative importance, expressed as percent total volume, of major prey types in Black (n = 14) and Say's phoebe (n = 23) samples. Asymmetry indicates different diets of these birds.

more than a few meters from water. On the other hand, I never saw Say's Phoebe feeding in such a manner, and aquatic insects were absent in the samples. Both species took spiders from the ground.

The perches used by Black Phoebes were shaded lower branches (less than 2 m) of willows (*Salix* spp.) and baccharis (*Baccharis* spp.). Mesquite (*Prosopis* sp.) was also used at Plata where it bordered the marshy sedge (*Eleochris* sp.) field in which the birds fed. Say's fed from perches exposed to full sunlight; these were generally using the tops of mesquite, acacias (*Acacia* spp.), yuccas (*Yucca* spp.), and fences. Differences in coloration of these 2 birds may be adaptations to this difference in feeding perches. The back of Black Phoebes is black; it is predominately pale gray in Say's.

In addition to items found in the samples, Black Phoebes caught other dragonflies, moths (Lepidoptera), and butterflies (Nymphalidae). Items of food recovered from 3 nestlings by use of pipe-cleaner collars were a

TABLE 3

FOOD ITEMS CARRIED BY SAY'S PHOEBES TO NESTLINGS AT DAVIS MOUNTAINS STATE PARK[1]

Prey taxa	Number	Percent
ORTHOPTERA	**14**	**35.0**
Acrididae	14	35.0
COLEOPTERA	**1**	**2.5**
Cicindelidae	1	2.5
LEPIDOPTERA	**7**	**17.5**
Papilionoidea	3	7.5
Lycaenidae	1	2.5
Hesperiidae	3	7.5
DIPTERA	**4**	**10.0**
Tabanidae	1	2.5
Asilidae	2	5.0
Undetermined	1	2.5
HYMENOPTERA	**3**	**7.5**
Formicidae	1	2.5
Apoidea	2	5.0
CHILOPODA	**1**	**2.5**
UNDETERMINED	**10**	**25.0**
TOTAL	**40**	**100.0**

[1] Observations made at one nest.

dragonfly nymph, cicada (Cicadidae), long-horned wood borer (Cerambycidae), skipper (Hesperiidae), and soldier fly (Stratiomyidae).

More extensive sampling of Say's Phoebe nestling food was possible. At a nest in Davis Mountains State Park, I made intermittent observations during the last 3 days before the young fledged. It was usually possible (30 of the 40 items) to determine what the adults were carrying as they made their final pre-nest stop (Table 3).

I used pipe cleaners to prevent other Say's nestlings from swallowing food, and obtained 57 items from 17 July to 6 August 1970, near Fort Davis. Such sampling involved 9 nestlings in 5 nests (Table 4). Some smaller food items may have been swallowed in spite of the collars. Nevertheless, the items give a representation of nestling food which indicates that the diet of nestlings is similar (73.7% overlap) to that of the adults. Most interesting was the large size of grasshoppers (up to 0.9 ml displacement) given to nestlings weighing as little as 14 g.

TABLE 4

COMPOSITION OF SAY'S PHOEBE NESTLING FOOD
(9 NESTLINGS IN 5 NESTS) NEAR FORT DAVIS

Prey taxa	% Individuals (n = 57)	% Volume[1] (12.625 ml)
ISOPODA	**1.7**	**0.6**
ORTHOPTERA	**35.1**	**60.8**
Acrididae	(35.1)	(60.8)
Acridinae	3.5	4.6
Oedipodinae	31.6	56.2
HEMIPTERA	**1.7**	**0.6**
Reduviidae	1.7	0.6
HOMOPTERA	**3.5**	**5.5**
Cicadidae	3.5	5.5
COLEOPTERA	**14.0**	**9.2**
Cicindelidae	5.3	1.4
Meloidae	3.5	4.4
Tenebrionidae	3.5	2.2
Scarabaeidae (Cetoniinae)	1.7	1.2
LEPIDOPTERA	**13.9**	**9.2**
Pieridae	1.7	0.8
Hesperiidae	3.5	3.2
Noctuidae	7.0	3.2
Aegeriidae	1.7	2.0
DIPTERA	**19.5**	**11.5**
Asilidae	12.5	6.3
Bombyliidae	3.5	2.8
Tachinidae	3.5	2.4
HYMENOPTERA	**3.5**	**T**
Formicidae	3.5	T
TOTAL INSECTA	**92.7**	**97.4**
ARACHNIDA	**7.0**	**2.8**
Lycosidae	5.3	2.4
Oxyopidae	1.7	0.4
TOTAL	**99.7**	**100.2**

[1] T — Indicates trace value, less than 0.4 percent.

AGONISTIC BEHAVIOR

A Black Phoebe was seen on 24 April 1970, by Charles Crabtree (pers. comm.) as it apparently defended its territory repeatedly and successfully against a Say's Phoebe at a small pond. This indicates that early in the

breeding season there is some interspecific territoriality in this species pair, but I never observed such aggression later in the breeding season. On one occasion both species fed from perches in the same tree at Capote Canyon. The adult Black there also passed with its 4 fledglings within 10 m of a Say's and its nest without either bird reacting.

This same Black Phoebe chased an Ash-throated Flycatcher (*Myiarchus cinerascens*) which entered its feeding territory, but the phoebe was in turn chased away by a Pyrrhuloxia (*Pyrrhuloxia sinuata*) a few minutes later.

I saw a Cassin's Kingbird (*Tyrannus vociferans*) and a Black Phoebe feeding about 40 m from the phoebe's nest. There was no aggression in this instance.

Where Vermilion Flycatchers (*Pyrocephalus rubinus*) were feeding over dried mud and Black Phoebes were feeding over the mud and water, the phoebes defended their feeding perches intraspecifically without responding to the Vermilions.

An Ash-throated Flycatcher was sitting quietly within 3 m of a pair of Say's Phoebes whose nest (with nestlings) was only 5 m away. Likewise, at another Say's nest site an Ash-throated Flycatcher and the phoebe were perched in the same shrub about 11 m from the phoebe's nest.

When one of the banded Say's Phoebes (thought to have been the female) at Plata disappeared, 2 unbanded birds entered the area. One of these subsequently nested there with the remaining banded bird, but only after a period of intense aggression (chasing) between the banded resident and one of the unbanded birds.

I banded one brood of Say's Phoebes that was near fledging. When I returned the birds to their nest, some of them flew a short distance and were attacked by a pair of Cassin's Kingbirds, but the attack did not persist.

COMPARISONS BETWEEN PHOEBES AND KINGBIRDS

In addition to the observations that are reported in this paper, I studied the Western Kingbird (*Tyrannus verticalis*) and Cassin's Kingbird (Ohlendorf 1974). There were considerable differences in the 2 pairs of species.

There was distinct altitudinal segregation (and consequently also in habitat type) of the kingbirds throughout most of the region. This was not the case with the phoebes, but they did differ in respect to habitat type.

Although there was no indication of interspecific defense of feeding areas in either pair of species, such behavior was exhibited by kingbirds in relation to nesting sites. For kingbirds, I considered nesting sites to be the resource most limited in supply and therefore worthy of inter-

specific defense. Wherever substrate suitable for phoebe nesting occurred it was almost invariably used, but in several instances pairs of opposite species nested close together without apparent interaction. Interspecific phoebe nesting compatibility may be related to their dietary differences, which are much greater than I observed in the kingbirds.

On one occasion a Say's Phoebe began nesting within a few days after nesting substrate was provided. The rapid replacement of lost nesting birds, particularly evident in Say's Phoebe but also observed in Black Phoebes, is also an indication of the shortage of suitable nesting substrate.

I found great differences in selection of nest sites and food, as well as in feeding behavior, between the genera. The kingbirds are principally tree-nesting species, but the phoebes nest in sheltered locations on cliffs, bridges, culverts, and buildings. Differences in food and feeding behavior are particularly evident in comparing Black Phoebes with the other 3 species. As a result, there was considerably less overlap in the diets of the 2 phoebes than there was in the diets of the 2 kingbirds.

These 4 species of flycatchers occurred together only at Plata, where the presence of kingbirds apparently had no effect on phoebes, and the converse was also true. Only one pair of each phoebe species nested there. This limitation in phoebe numbers was not caused by the presence of kingbirds, but rather was the result of intraspecific territoriality of the phoebes and the scarcity of nesting substrate for them. Three pairs of Western Kingbirds and 2 pairs of Cassin's Kingbirds remained there with such intense intraspecific aggression in the Western Kingbirds that nesting by one pair was prevented. I attributed the nesting failure of the Cassin's Kingbirds to other environmental factors.

Essentially, the kingbird species occupied different habitat types but exploited the resources in a similar manner and seldom occurred together. The phoebe species were frequently found together but were dependent on different resources. Hence, different strategies may serve to reduce competition in the 2 species pairs.

DISCUSSION AND CONCLUSIONS

Ecologically diverse areas favor sympatry and less interspecific territoriality than do uniform areas (Orians and Willson 1964). The selective pressure for ecological divergence in areas of sympatry favors selection of different habitats, different ways of exploiting the same habitat, and reduction of the area of interspecific aggression. Orians and Willson consider the main function of territorial behavior to be to allow more effective exploitation of food resources.

One instance of interspecific (i.e. Black and Say's phoebes) aggression

was reported to me, but the cause for this behavior was unknown. It appears unlikely that it was related to a feeding territory, for the diets of these birds are quite different.

Effects on reproductive success may be an indication of competition (Elton and Miller 1954), but I observed no effect of this nature during my study. There were instances of both phoebe species nesting at the same locality and the success of these pairs was not different from the success of those nesting away from each other.

Location of nests by the 2 species was not significantly different in respect to elevation, but the species differed in respect to habitat type. The presence of mud plus suitable substrate was required for the presence of Black Phoebes. Such conditions are not widespread in the region; consequently the less restricted tolerances of Say's Phoebe contribute to greater relative abundance and more widespread distribution.

Both species have responded favorably to man's construction of buildings, bridges, and culverts by nesting on them in habitat types that were otherwise favorable, but lacked nesting substrate. The presence of only one pair of either species is an indication of their intraspecific exclusion. However, interspecific tolerance is indicated by the presence of pairs of both species in several instances. Separation of the nesting pairs of any one species was always greater than their separation from nesting pairs of the other species.

The overlap in diets of phoebes was 77.7% on the basis of major taxa (i.e. insect orders) and 42.9% when minor taxa (families) were compared. The use of damselflies and dragonflies by the Black Phoebe as a major food resource and of grasshoppers by Say's Phoebe contributes to their ecological compatibility.

SUMMARY

Some aspects of the breeding ecology of Black and Say's phoebes were studied in the Trans-Pecos region of Texas. The geographical and ecological distribution, nesting habits, food composition, and behavioral interactions were determined for each species.

There was no apparent elevational difference between the phoebes, but differences were noted in habitat types. Black Phoebes nested only where mud was available in the immediate vicinity of suitable nest substrate, i.e. a vertical surface protected from rain. Nesting requirements of Say's Phoebes were less restrictive and account for that species' wider distribution within the study area. Rapid replacement of lost breeding birds indicated a shortage of nesting sites. On several occasions the birds were not separated interspecifically, but intraspecific separation was maintained. The clutch size for nests in close proximity (interspecifically) was similar to that of the species means for other nests in the area.

Differences in feeding behavior of the phoebes were reflected in the composition of the diets.

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