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THE RELATIONSHIP OF FOOD SUPPLY TO THE TIMING OF BREEDING IN AERIAL FORAGERS

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The diets of many North American birds have been well documented but considerable study remains to determine the relationship between the availability of food and initiation of breeding, egg laying, molt, migration, etc. Largely because of the difficulties involved in obtaining quantitative samples of aerial arthropods, studies on birds that prey on them are few. This study examines the relationship between food supply and the breeding cycles of Kansas birds preying, at least in part, on aerial arthropods. The Mississippi Kite and Loggerhead Shrike with feeding habits intermediate between those of aerial foragers and raptors are included for the purpose of comparison.

Information on food supply (Figure 1) was derived from Johnston's study of Purple Martins in Douglas County, northeastern Kansas (1967, Figure 1). Data on the timing of arrival, egg laying, and departure were obtained from Johnston (1964, 1965) based on records obtained largely from northeastern Kansas. Information on the duration of incubation and nestling periods and molt was obtained largely from Bent (1937, 1940, 1942, 1950). Where data on breeding activities were limited (Figure 1), estimates were made by extrapolation of the data presented by Bailey and Niedrach (1965), Fitch (1963), Johnston (1964), Mengel (1965), Sutton (1967), and Wolfe (1967). Bird names follow the fifth edition of the American Ornithologists' Union's "Check-list of North American birds" (A.O.U. 1957).

Figure 1 indicates the density of diurnal flying arthropods from February through August. The number of arthropods in the air on any given day is highly dependent upon climatic conditions, especially temperature and wind speed. For example, using the same procedures as Johnston (1967) I collected three samples (0600, 1200, and 1800 hours) on 13 days between 15 April and 20 May 1968. Each sample was made with a 10 inch diameter insect net held out of an open car window while traversing a square course of one mile on each side, each side forming a cardinal compass direction, at 30 miles per hour. The route was covered twice during each sample period for a total of eight miles. Temperatures at the three sample times for each day were combined and a mean temperature calculated. In each case (six) where the mean temperature rose from one sample day to the next the number of arthropods caught also increased (Table 1). In all cases where the temperature fell from one sample day to the next (five) the number of arthropods caught decreased or, in one instance, remained the same.

Abundance of flying arthropods is largely dependent on and directly related to temperature (Roeder, 1953:686–690). Densities of diurnal aerial arthropods on any given day are probably directly related to densities of nocturnal arthropods owing to this temperature-density relationship. According to Williams (1940) on those nights when large numbers of insects were caught, the maximum temperatures

TABLE 1

ARTHROPODS CAUGHT ON 13 DAYS BETWEEN 15 APRIL AND 20 MAY 1968 AT LAWRENCE, KANSAS. SAMPLES WERE COLLECTED THREE TIMES EACH DAY (0600, 1200, AND 1800 HOURS.) TEMPERATURES ARE IN DEGREES FAHRENHEIT.

	April					May							
	15	17	21	24	26	3	6	8	11	13	15	17	20
Mean temperature	59.0	63.5	58.0	49.5	53.0	66.0	58.5	59.5	54.5	63.5	57.5	59.5	53.5
Total arthropods caught	47	119	17	17	115	156	16	68	35	187	53	246	85

of the previous day were higher than on nights with low catches. Breeding cycles of goatsuckers were assumed to be closely attuned to the abundance of diurnal flying arthropods because of this temperature-density relationship.

An analysis of breeding records over the entire breeding range of the Chuck-will's-widow (Rohwer, MS) suggests that the modal date of egg laying probably occurs somewhat later (about 20 May) than that given in Figure 1 (Johnston's (1964) data are limited to five breeding records). Additional study may also indicate a later modal egg laying date for the Mississippi Kite.

INITIATION OF EGG LAYING

The median arrival date in Kansas for the majority of aerial foragers examined here occurs in April (Figure 1); less than one-third arrive in May and only three species arrive in March. The two earliest arrivals, the Eastern Phoebe and Loggerhead Shrike, also initiate egg laying at an early date.

Egg laying by the majority of aerial foragers does not begin until late May or early June, although maximum values in the density of food change very little between mid-April and July. Prior to June, cold periods which would be unfavorable to arthropods would be expected to occur more frequently and be more prolonged. Hence, food supply could vary widely. Anderson (1965) reported a large die-off of four species of swallows and several species of flycatchers during a cold period from 26–29 May in Minnesota. Early breeders might then be selected against owing to occasional prolonged "cold snaps" which would severely limit food supply. Colder mean temperatures in April and May as compared with June (Johnston, 1964:591) may also act to delay egg laying by increasing the energy required for daily maintenance. Therefore, although the same maximum quantities of food are available to aerial foragers from mid-April through July, it is probably the minimum values that are most important in influencing egg laying. For example the Purple Martin arrives in March but delays egg laying until two months later, about the same time as the other swallows which arrive in late April and May. Johnston and Hardy (1962) thought that the very early arrival by martins, much earlier than the other swallows, may have arisen through intraspecific competition for nesting holes. House Sparrows and Starlings are permanent residents in Kansas and lay their first clutch at least one and one-half months before the martins (Johnston, 1964). Because all three species nest in man-made nest boxes in Kansas, some degree of interspecific competition for nest sites may also occur. Late-arriving martins probably find fewer and less suitable nest sites than do martins that arrive early.

Four species (Mississippi Kite, Chuck-will's-widow, Loggerhead Shrike, and Eastern Phoebe) concentrate egg laying in April and early May and are probably able to reduce the effects of prolonged cold periods by utilizing food sources other than aerial arthropods.

The diet of Mississippi Kites appears to be largely insects during the breeding season (Fitch, 1963) but some vertebrates (frogs, toads, lizards, snakes, bats,

rabbits, and small rodents) are taken (Bent, 1937; and Sutton, 1967:98). From a study of pellets collected in July and August by Fitch (1963) and of stomachs collected in the latter two-thirds of May and June by Sutton (1939), Fitch concluded that predation by kites on vertebrates was rare. Such predation may be important only in April and early May—a period, unfortunately, for which no records are available—when temperatures and insect populations are low.

The Chuck-will's-widow occasionally preys on birds. The remains of a flycatcher, a hummingbird, and various warblers have been recovered from their digestive tracts (Baird, Brewer, and Ridgway, 1874:413; Northrup, 1891; Gundlach, 1891; Stone, 1898; Owre, 1967;—as corrected, Wilson Bull., 79:458; and S. A. Rohwer, personal communication). It has been suggested that the taking of small birds by Chuck-will's-widows is accidental (see Bent, 1940); they are nocturnal feeders and could possibly confuse birds with large moths though Thayer (1899) reported seeing Chuck-will's-widows chasing and eating warblers in daylight. Dates of observation or collection are available for four of nine cases of predation on birds by Chuck-will's-widows reported in the literature. All four dates (13 and 19 April, 4 September, and 18 October) fall during a period when the population level of aerial arthropods could have been low or when the availability of small birds (due to migration) may have been high, or both.

Bent's (1950) list of vertebrates eaten by Loggerhead Shrikes is extensive. He noted a tendency toward heavier predation on mice and small birds in the winter than in the summer, presumably because of the low availability of insects (Bent, 1950:137). Considering the wide variety of food eaten and its high foraging flexibility, this species should be capable of initiating egg laying before all other aerial foragers and it does so (Figure 1).

Utilization of foods other than insects is limited in most flycatchers (Beal, 1912). However, the diet of Eastern Phoebes includes about 11 percent vegetable food. Feeding on berries and seeds occurs mainly in the fall, winter, and spring (Beal, 1912:35). Occasionally, vertebrates including fish (Binford, 1957) and frogs (Beal, 1912:30) are eaten by phoebes.

Ground-feeding by Eastern Phoebes may not be uncommon. Bailey (1905), Richard F. Johnston (personal communication) and Erwin Klaas (personal communication) have observed phoebes capturing insects on the ground. Klaas observed phoebes feeding in the litter in late March of 1961 and 1962. The 1962 observation was made on a cold but clear day (28 March). Significantly the birds had arrived on 14 March but their arrival was followed by cold weather, light snow, and freezing rain on 17 March. During the cold weather few birds were found in their usual places around bridges. It seems possible that on clear days localized areas protected from the wind may warm sufficiently to permit activity of terrestrial arthropods thereby creating a food source for ground-feeding birds. The Black Phoebe is also known to forage on the ground (Skutch, 1960:367) as well as eat small fish (Oberlander, 1939:139).

Unlike other flycatchers that breed in Kansas, Eastern Phoebes are found in considerable numbers in winter in the coastal states from Texas to Virginia (A.O.U. Check-list, 1957). The wintering of phoebes at these latitudes provides indirect evidence that they can survive under adverse climatic conditions. They might be expected, therefore, to be the first of their family to begin breeding.

Energy Requirements on the Breeding Grounds

Of all the species listed in Figure 1, it seems that only the Eastern Phoebe can complete three major energy-requiring activities on the breeding grounds, namely, raising two broods and undergoing a complete postnuptial molt. However, two additional species that molt on the breeding grounds may also raise two broods—Say's Phoebe (see Bailey and Niedrach, 1965:519) and Loggerhead Shrike (see Sutton, 1967:462). The only aerial forager other than the Eastern Phoebe known to be regularly double-brooded in Kansas is the Barn Swallow which is not known to molt on the breeding grounds.

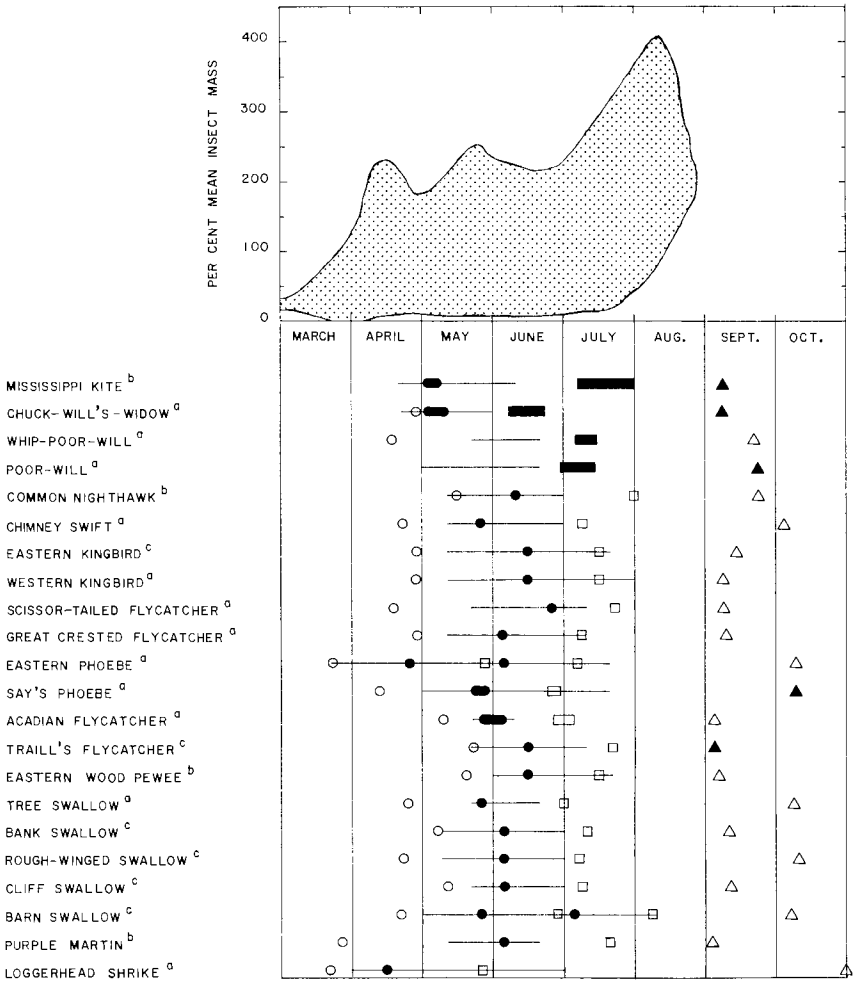

Figure 1. Nesting cycles of aerial foragers in Kansas compared with biomass of food (expressed as percentages of the average sample value). Maximum and minimum biomass values for any sample day are indicated by the upper and lower edges of the diagram. Symbols used: a, species undergoes a complete postnuptial molt on breeding grounds; b, postnuptial molt initiated on breeding grounds but completed on wintering grounds; c, species undergoes postnuptial molt on wintering grounds; (○), median arrival date; (●), modal date for completion of egg laying; (□), modal date for young leaving the nest; (■), estimated modal date for young leaving the nest; (△), median departure dates; and (▲), estimated median departure date.

All of the four goatsuckers and seven of the nine flycatchers that regularly breed in Kansas start or complete a postnuptial molt on the breeding grounds, whereas this is known for only two of the six swallows (Figure 1). This difference may be related to differences in feeding habits. The manner of feeding of swallows may be more demanding of energy than that of goatsuckers or flycatchers. While perched and waiting for suitable flying prey, flycatchers can rest, also, ground-feeding, especially in kingbirds and phoebes, and foraging on insects on trees and shrubs are more common among flycatchers than swallows. The larger size of

goatsuckers may increase their efficiency in feeding over that of swallows by permitting them to prey on arthropods of a greater range in size.

Of necessity, molt in aerial foragers must be protracted so as not to unduly impair flying ability and foraging efficiency. Flight feathers of swallows are less subject to the wear that affects many grassland and forest species. Thus, complete feather replacement prior to migration may not be necessary and molt may be delayed until winter when the energy demands of swallows may be lower or food supplies again more dependable. The Tree Swallow, the only swallow that is known to complete a postnuptial molt on the breeding grounds, and the Barn Swallow, which raises two broods per year, begin egg laying before all other swallows and migrate southward after most of the other aerial foragers have departed (Figure 1).

Abundance of Food and Biomass of Aerial Foragers

Food appears to be most abundant from mid-July to at least mid-September (Figure 1). This two-month period typically has the highest monthly mean temperature (about 80° F) and much rainfall (Johnston, 1964:591). Johnston (1967) suggested that August was three times better in quantity and quality of food than April. During late July and August the biomass of aerial foragers reaches its annual peak. The collective energy requirements of aerial foragers probably reach their maximum in late summer after the nestlings leave the nest in late July. The energy requirements of these active fledglings are probably much greater than those of the passive nestlings, even though there may be no difference in the size of the birds from both stages. Royama (1966) reported that the food intake of fledgling Great Tits was three or four times that of similar-sized nestlings owing largely to increased volume-surface ratio and increased activity.

A high density of available prey for aerial foragers is probably maintained through much of September. No samples were taken in September, but the mean temperature is about 70° F (Johnston, 1964:591); thus one might expect the arthropod density to be quite high. An abundance of food would be important to aerial foragers during September because many species (16 of the 22) initiate or undergo a complete molt prior to migration (Figure 1). A build-up of fat prior to migration would also be facilitated by ready availability of food. Earlier, Johnston (1967) showed that maximal energy requirements of Purple Martins coincided with the period of maximal availability of food.

Summary and Conclusions

The nesting cycles of 22 species of aerial foragers in Kansas are related to density of food in the breeding season. For a comparison of timing of breeding in birds with different foraging adaptations see Johnston (1964:590–595). The mode for completion of egg laying by most aerial foragers occurs in late May or early June. Maximum values in the density of available food change very little between mid-April and July, but the minima vary widely. Early breeding by most aerial foragers seems to be selectively disadvantageous because of occasional, sometimes prolonged cold periods early in the year which probably reduce the density of food to levels below those required for egg laying superimposed upon daily maintenance.

The Mississippi Kite, Chuck-will's-widow, Loggerhead Shrike, and Eastern Phoebe concentrate egg laying in April and early May. They probably seek out secondary food sources, and thus, are probably less specialized in the types of food eaten than most aerial foragers. This greater foraging flexibility seems to offset the effects of cold weather early in the spring, that is, reduced abundance of aerial arthropods and higher metabolic costs. The Eastern Phoebe seems to be the most efficient species examined, being capable of completing three major energy-requiring activities on the breeding grounds; raising two broods of young, and completing a postnuptial molt. Indirect evidence suggests that the phoebe is the least specialized feeder of the goatsuckers, flycatchers and swallows studied.

The timing of breeding of aerial foragers seems to be directly related to abundance

of prey. Prey density was greatest in August and September when the number of aerial foragers reached its annual maximum, when most species were in molt, and when fat accumulation and migration were under way. The swallows as a family completed fewer major energy-requiring activities on the breeding grounds than did the goatsuckers or flycatchers.

Acknowledgments

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NOTES

Black Skimmer in Douglas County, Kansas.—On 24 May 1968 at approximately 1500 hours a Black Skimmer (*Rynchops nigra*) was discovered by Allen C. Pursche, a student in my ornithology class. It was feeding in the characteristic "skimming" manner of the species in a series of shallow ponds maintained by the Kaw Valley Fish Farms Inc. for the purpose of raising golden shiners (*Notemigonus chrysoleucas*) as bait minnows. The locality is approximately two miles east and three miles north of Lawrence, Douglas County, Kansas.

After correctly identifying the skimmer, which was associating loosely with approximately 200 Black Terns (*Chlidonias niger*), Mr. Pursche called me. We watched the bird for a time before I succeeded in obtaining it for the University of Kansas Museum of Natural History, where it now bears number 59121. It was a female with the ovary measuring 15 × 8 mm (largest ovum 1 mm in diameter) and with the beginnings of a brood patch. It had little fat but was by no means emaciated and weighed 254.8 g. Its stomach contained partially digested remains of, apparently, golden shiners. The specimen has the pure white underwing linings and small size (flattened wing 344 mm) of the North American populations collectively known as *R. n. nigra*.

The North American populations of this strictly coastal species breed on the Atlantic and Gulf coasts from Massachusetts to Yucatan and on the Pacific coast of Mexico. According to the American Ornithologists' Union *Check-list of North American Birds* (1957), skimmers have wandered inland in Quebec, Texas, Georgia, New York, Massachusetts, and Tennessee. Interestingly, another was carefully observed by J. G. Newell (*Bull. Oklahoma Orn. Soc.*, 1, 1968:25; see also *Aud. Field Notes*, 21, 1967:518) and other observers at Lake Overholser, just east of Oklahoma City, Oklahoma, on 14 May 1967, just one year and 10 days prior to the present record. The Kansas record, the first for the state, appears also to represent the furthermost penetration inland thus far noted.

The Lawrence area experienced approximately 2.5 inches of rainfall from Tuesday, 21 May, through Thursday, 23 May 1968 (*Lawrence Daily Journal-World*, Friday, 24 May 1968). This precipitation and the very dark gloomy weather and poor visibility that accompanied much of it were associated with a slow-moving front which by Friday, 24 May, had become occluded and extended from Illinois and Missouri to the gulf coast of Texas (Associated Press wirephoto map; *op. cit.*). It appears entirely possible that a member of this non-migratory species, could be accidentally displaced inland in bad weather, and might then subsequently wander at random, particularly under conditions of continuous cloud cover and poor visibility, to such a degree that it could eventually appear as far inland as Kansas. —ROBERT M. MENGEL, *Museum of Natural History, The University of Kansas, Lawrence, Kansas* 66044.

Gray Flycatcher taken in southwestern Kansas.—Among a small series of *Empidonax* collected in southwestern Kansas in 1967 was one specimen (FHKSC 1555) which I could not identify satisfactorily. It was forwarded to Dr. Allan R. Phillips who identified it as *Empidonax wrightii*—a species new to Kansas. The specimen (male, left testis 4 × 2 mm, moderate fat) was taken in cottonwoods along the Cimarron River, 9 miles north and 4½ miles east of Elkhart, Morton County, on 29 April. *Empidonax minimus, E. traillí,* and *E. oberholseri* all were collected at the same locality during the 1967 spring migration.

The nearest breeding localities for the Gray Flycatcher are the pinyon-juniper areas of central New Mexico and western Colorado (Bailey and Niedrach, The Birds of Colorado, Denver, p. 529, 1965). During migration birds have been reported eastward to western Texas and central Colorado (Colorado Springs). The presence of *Empidonax wrightii* in Kansas is probably accidental but continued field work along the Arkansas and Cimarron rivers in western Kansas may show that it is of regular occurrence as is *E. oberholseri.* All but one of the North American Empidonaces (*E. fulvifrons*) have now been taken in Kansas.—CHARLES A. ELY, *Fort Hays Kansas State College, Hays, Kansas* 67601.

Cape May Warbler collected at Emporia, Kansas.—I observed a Cape May Warbler (*Dendroica tigrina*) on 10 May 1969 while accompanying the Kansas State Teachers College ornithology class on a field trip to the Emporia Country Club lake in Lyon County. I first noticed the bird in the upper part of a willow (*Salix* sp.) near the edge of the lake. It was a brightly plumaged male and appeared to be undisturbed by the class of about 20 students. It was observed by the class for nearly ten minutes before being collected by David F. Parmelee.

The bird (KSTC No. B1500) was prepared by Richard H. Schmidt. It weighed 13.1 g; the testes measured 4.5 × 5.0 mm (left) and 3.5 × 4.0 mm (right) and the skull was fully ossified. The Cape May Warbler has been previously reported from Kansas and is considered a rare transient but apparently the only previous Kansas specimen (KU 31644) is one taken in Lawrence, Douglas County on 6 December 1954 (Johnston, A directory to the birds of Kansas, Univ. Kansas Mus. Nat. Hist., Misc. Publ., 41:47, 1965).—WALTER E. BOLES, *Emporia, Kansas* 66801.

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