EFFECTS OF SPRING LEAF-FALL ON COMPOSITION AND DENSITY OF BREEDING BIRDS IN TWO SOUTHERN ARIZONA WOODLANDS

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Nesting bird composition and population densities reflect the suitability of a given plant community for providing the requisites for survival and reproduction, and also, the selection of these suitable habitats by the birds. Two important features in habitat selection are availability of food and nest-sites (Hilden 1965). Open-nesting species depend on foliage for concealment and protection of the nest from harsh weather and predators (Nice 1957). More than ample foliage for nest-sites is usually available to these species, whereas a major problem confronting hole-nesting species is locating suitable sites (von Haartman 1957). Tree-foliage nesting birds of the oak woodlands in southeastern Arizona may be limited in the same manner as hole-nesters because a portion of the tree foliage is absent during a period in spring and summer when most birds initiate nesting.

These woodlands of the desert mountains can be subdivided into two plant associations: evergreen or live oak woodland, and pine-oak woodland. The oak woodland lies on gentle slopes and flat sandy plains below the pine-oak woodland. The lower limit of oak woodland is partly dependent on slope exposure and soil type but it is generally at about 4500 ft, where this woodland merges with grassland, forming a savanna. The upper limit of the pine-oak woodland occurs at about 7800 ft, where ponderosa pine (*Pinus ponderosa*) becomes the dominant and predominant tree. These, or very similar woodlands, extend well into México (Leopold 1950). In the Chiricahua Mountains, Cochise County, Arizona, Emory oak (*Quercus emoryi*) and Arizona oak (*Q. arizonica*) predominate. The pines of the higher woodland are Chihuahua pine (*Pinus leiophylla*) and Apache pine (*Pinus engelmannii*), with a scattering of ponderosa pine. The woodlands also contain relatively high densities of various shrubs and succulents. Alligator juniper (*Juniperus deppeana*) varies in abundance in the two woodlands. More detailed information on these plant associations in southern Arizona may be found in Shreve (1915), Wallmo (1955), Marshall (1957), and Lowe (1961, 1964).

The oaks mentioned above are often referred to as "live" oaks because they retain their leaves throughout the winter months. Marshall (1957) noted that oak leaves turned brown and/or were dropped during drought conditions, and that new leaves appeared when more mesic conditions followed. Shreve (1915) mentioned that these oaks shed most, if not all, leaves in late April or May. A biseasonal rainfall pattern exists in this area. Heavy leaf-fall occurs during a spring drought period which follows the winter rainy season. Summer rains usually begin in late June or early July.

Few observations have been made on the birds of these woodlands except by Marshall (1957), who analyzed the pine-oak avifauna, and Balda (1969), who studied foliage use by birds. Marshall concluded that both oak woodland and pine-oak woodland are climax communities, but that the avifauna of the pine-oak woodland is a unique mixture of bird species from the oak woodland below and ponderosa pine forest above. He did not comment on the effects of spring leaf-fall of the oaks on the breeding birds of either woodland.

The pattern of leaf-fall, flowering, and appearance of new oak leaves exerts two principal effects on the diversity and density of breeding birds in these two woodlands in the Chiricahua Mountains of Arizona. First, the loss of oak leaves may result in a loss of potential nest-sites for birds that nest in tree foliage. Second, the flowering and growth of new leaves attracts large numbers of insects that serve as an abundant source of food for birds that nest in other sites.

METHODS AND MATERIALS

Observations were made in two woodlands of the Chiricahua Mountains in June 1964 and February–August 1965. Detailed plant sampling in each woodland was done in conjunction with a bird censusing program to obtain an understanding of some of the basic plant-bird relationships that exist in these wood-

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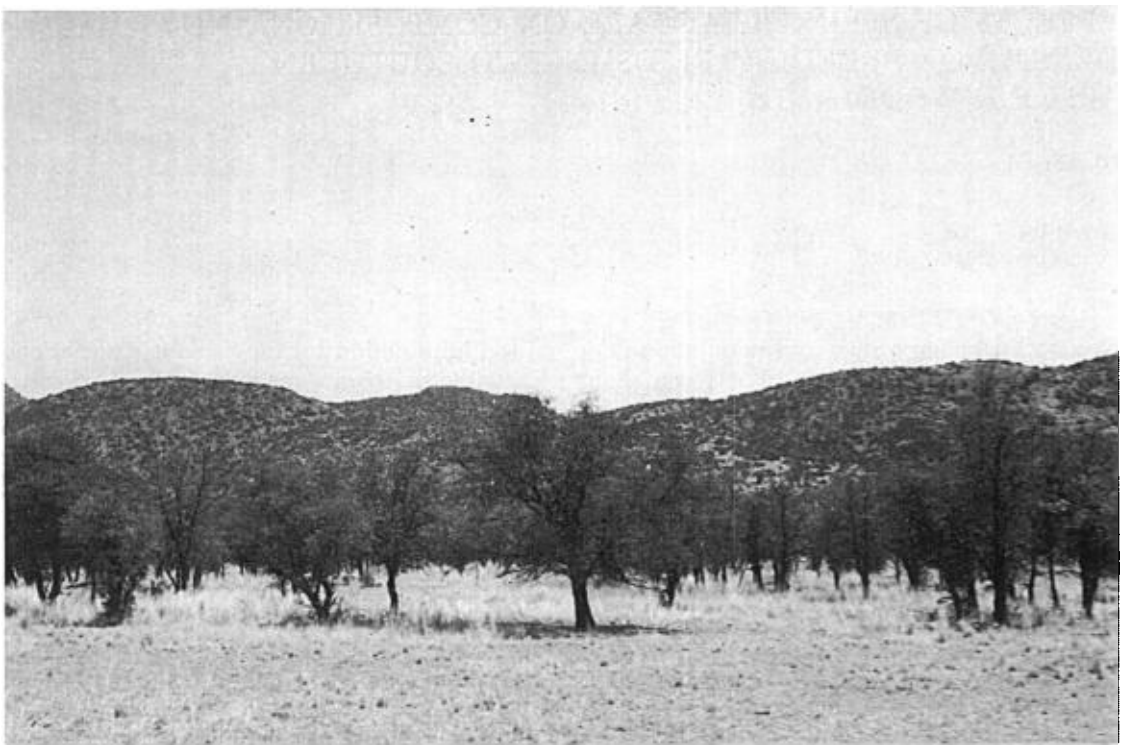

FIGURE 1. The oak woodland study area showing well scattered *Quercus emoryi* in full leaf during the month of February.

lands. Trees three or more inches in DBH were sampled with the point-quarter method (Cottam and Curtis 1956). A total of 30 points (120 trees) was sampled in both woodlands. Detailed notes were kept on the growth and flowering of all predominant plants. Birds were censused with the spot-map method (Kendeigh 1944) to obtain an estimate of the absolute breeding population of each species. Densities of birds are expressed as numbers of breeding pairs per 100 acres. Non-territorial species were censused on the basis of average number seen. The areas were thoroughly searched for nests, and details such as nest location, time of egg laying, etc., were recorded. Eleven complete daylight counts and four night counts were taken in the oak-juniper-pine woodland study plot, and 10 daylight and three night counts were made in the oak woodland. Data presented herein were analyzed primarily with reference to the numbers of pairs and species that place their nests in various locations.

RESULTS AND DISCUSSION

OAK WOODLAND

This 36-acre study area was within the Chiricahua National Forest and was used for grazing by the local rancher. The plot was 9 mi. SW of Apache, New Mexico and 0.8 mi. NW of the Glass Ranch on an unpaved road leading into Price Canyon.

Vegetation. The vegetation was park-like in appearance, with scattered trees of almost uniform height (fig. 1). There were 68 trees per acre, with *Quercus emoryi* predominant (table 1). The absolute density of oaks was 66 individuals per acre. The shrubby and succulent understory of this area contained predomi-

TABLE 1. Tree species composition, density, and dominance of the two woodlands in the Chiricahua Mountains.

Species	Oak woodland		Oak-juniper-pine woodland	
	Relative density	Relative dominance[a]	Relative density	Relative dominance
Quercus emoryi	95.0	96.5	20.8	10.7
Quercus arizonica	2.9	2.7	17.4	11.0
Juniperus deppeana	1.4	0.5	38.3	60.1
Juniperus monosperma	0.7	0.2	—	—
Pinus leiophylla	—	—	21.7	17.9
Pinus cembroides	—	—	1.8	0.3

[a] Relative dominance = $\frac{\text{basal area of a species}}{\text{basal area of all species}}$

nately the following: *Fallugia paradoxa*, *Brickellia* sp., *Rhus microphylla*, *Calliandra* sp., and *Nolina microcarpa*. Total shrub and succulent density was 308 individuals per acre. The phenology of oak leaf-fall, and replacement is shown in figure 2. The two species of oaks which contribute 99 per cent of the foliage (see dominance figures, table 1) in this community were in the process of replacing their leaves during most of the spring and early summer. It is of interest to note that *Quercus emoryi* did not complete new leaf growth until the advent of the summer rains in July.

Breeding birds. This plant community supported 36 species of nesting birds, with a total density of 224 pairs per 100 acres (table 2). The four most abundant species (Bewick's Wren, Ash-throated Flycatcher, Bridled Titmouse, Lark Sparrow) nested either in natural cavities, old woodpecker holes, or on the ground.

In most areas where cavity nesting species are common, the holes are provided by woodpeckers. In this area, however, woodpeckers and old woodpecker holes were noticeably rare. Most cavities were located at decayed places on oaks where large branches had broken off the trunk. Some of the oaks sampled in this area had hollow trunks because of heartwood rot. Thus, after the branch stub rotted away, potential nest-sites became available but certainly not plentiful or obvious. Of the 24 apparently suitable cavities located in the study plot and permanently marked and inspected throughout the nesting season, 10 (42 per cent) contained active nests. The total nesting density of cavity nesters was 76 pairs per 100 acres and made up almost 34 per cent of the total breeding bird population (table 2).

Four species nested on the ground, with a total nesting density of 24 pairs per 100 acres. These totals are low for a number of reasons. The topography of the area varied little, with few rocky outcroppings, washes, or slopes to add habitat diversity. Also, few fallen logs or branches added debris to the woodland floor. The area was heavily grazed by cattle, leaving little standing grass, and new growth was not forthcoming until the advent of the summer rains in July. There was, therefore, little diversity of habitat and only limited area suitable for ground nest-sites.

All 24 foliage-nesting species had relatively low densities, totaling 121 pairs per 100 acres. Of these 24 species, 10 nested in the shrubs and succulents and contributed 36 per cent of the foliage nests. Of the four most abundant foliage nesters, two nested in trees and two in shrubs and succulents.

Three important tree-foliage nesters (contributing 41 per cent of nests in tree foliage) apparently were able to nest successfully in the area because of their ability to use the dense foliage of *Juniperus deppeana* for at least a portion of their nest-sites. The Chipping Sparrow had three of five nests in juniper. Five of six nests of the Black-throated Gray Warbler were located in juniper. The sixth nest was built in *Quercus emoryi*, but the incubating female deserted shortly after the leaves fell. Three of seven nests of the Black-chinned Hummingbird were in juniper. A female Mexican Jay whose nest was located in an oak also deserted after incubating for three days, during which time the nest was completely exposed as leaf-fall was complete. Thus, some species attempted to nest in oak at the very time leaf-fall was underway, and there were strong indications that many failed.

It is also of interest to note that the number of singing male Chipping Sparrows on the area until the second week in April indicated a nesting density of 16 pairs per 100 acres, or six more than actually nested there. One male Western Wood Pewee and one Gray Vireo also appeared to leave established territories about mid-April. It is possible that these birds deserted their territories when oak leaf-fall occurred. Thus, some individuals may leave their territories without attempting to nest once leaf-fall is underway.

Breeding commenced in this area about the first week in April but some species were still initiating nesting through the first week in June (fig. 2). The first species observed to begin nesting were the Black-chinned and Broad-tailed Hummingbirds, which were observed gathering nest material from 1 April on. At this time *Quercus emoryi* was still in full leaf. Other early nesters include the Common Bushtit, Plain Titmouse, Scott's Oriole, and Mexican Jay.

OAK-JUNIPER-PINE WOODLAND

This study area consisted of 36 acres of undisturbed woodland located within a relatively homogeneous tract extending along the south side of Cave Creek about 0.10 mi. S of the Southwestern Research Station of the American Museum of Natural History.

Vegetation. Juniperus deppeana, a densely foliated evergreen, is the most abundant tree species (table 1). Oaks, with an absolute density of 46 individuals per acre, contributed only 22 per cent of the foliage present in this area, (as compared with 99 per cent in oak

TABLE 2. Densities of breeding birds and nest-sites in two Arizona woodlands.

Species	Nest site[a]	Oak woodland		Oak-juniper-pine woodland	
		pairs per 100 acres			
Foliage nesters					
Black-throated Gray Warbler (*Dendroica nigrescens*)	T		14		24
Mockingbird (*Mimus polyglottos*)	S		12		—
Chipping Sparrow (*Spizella passerina*)	T		10		30
Scott's Oriole (*Icterus parisorum*)	S		10		2
Black-chinned Hummingbird (*Archilochus alexandri*)	T		8		21
Mexican Jay (*Aphelocoma ultramarina*)	T		8		6
Common Bushtit (*Psaltriparus minimus*)	T		8		10
Gray Vireo (*Vireo vicinior*)	T		8		—
House Finch (*Carpodacus mexicanus*)	S		8		—
Black-headed Grosbeak (*Pheucticus melanocephalus*)	T		6		6
Brown-headed Cowbird (*Molothrus ater*)	T, S		4		6
Western Kingbird (*Tyrannus verticalis*)	S		3		—
Cassin's Kingbird (*Tyrannus vociferans*)	T		3		—
Broad-tailed Hummingbird (*Selasphorus platycercus*)	T		3		6
Western Wood Pewee (*Contopus sordidulus*)	T		3		5
Bell's Vireo (*Vireo bellii*)	S		3		—
Rufous-sided Towhee (*Pipilo erythrophthalmus*)	S		3		—
Mourning Dove (*Zenaidura macroura*)	S		1		—
Rivoli's Hummingbird (*Eugenes fulgens*)	T		1		6
Scrub Jay (*Aphelocoma coerulescens*)	S		1		—
Hooded Oriole (*Icterus cucullatus*)	T		1		—
Hepatic Tanager (*Piranga flava*)	T		1		3
Crissal Thrasher (*Toxostoma dorsale*)	S		1		—
Brown Towhee (*Pipilo fuscus*)	S		1		—
Robin (*Turdus migratorius*)	T		—		7
Solitary Vireo (*Vireo solitarius*)	T		—		5
Blue-throated Hummingbird (*Lampornis clemenciae*)	T		—		3
Blue-gray Gnatcatcher (*Polioptila caerulea*)	S		—		3
Grace's Warbler (*Dendroica graciae*)	T		—		3
Buff-breasted Flycatcher (*Empidonax fulvifrons*)	T		—		3
Hutton's Vireo (*Vireo huttoni*)	T		—		2
Total foliage nesting species and pairs[b]		(24)	121	(19)	151
Tree nesters		(14)	78	(17)	146
Shrub and succulent nesters		(10)	43	(2)	5
Cavity nesters					
Bewick's Wren (*Thryomanes bewickii*)			27		9
Ash-throated Flycatcher (*Myiarchus cinerascens*)			18		12
Bridled Titmouse (*Parus wollweberi*)			15		18
Plain Titmouse (*Parus inornatus*)			13		10
Screech Owl (*Otus asio*)			3		—
White-breasted Nuthatch (*Sitta carolinensis*)			—		7
Eastern Bluebird (*Sialia sialis*)			—		7
Olivaceous Flycatcher (*Myiarchus tuberculifer*)			—		3
Elf Owl (*Micrathene whitneyi*)			—		3
Pygmy Nuthatch (*Sitta pygmaea*)			—		2
Total cavity nesting species and pairs[b]		(5)	76	(9)	71
Ground Nesters					
Lark Sparrow (*Chondestes grammacus*)			15		—
Rufous-crowned Sparrow (*Aimophila ruficeps*)			6		11
Harlequin Quail (*Cyrtonyx montezumae*)			2		—
Poor-will (*Phalaenoptilus nuttallii*)			1		1
Painted Redstart (*Setophaga picta*)			—		6
Whip-poor-will (*Caprimulgus vociferus*)			—		4
Turkey (*Meleagris gallopavo*)			—		3
Total ground nesting species and pairs[b]		(4)	24	(5)	25

TABLE 2. *Continued*

Species	Nest site[a]	Oak woodland		Oak-juniper-pine woodland	
		pairs per 100 acres			
Cavity Excavators					
Red-shafted Flicker (*Colaptes cafer*)			1		8
Acorn Woodpecker (*Melanerpes formicivorus*)			1		8
Arizona Woodpecker (*Dendrocopos arizonae*)			1		4
Total cavity excavating species and pairs[b]		(3)	3	(3)	20
Grand totals		(36)	224	(36)	267

[a] T = tree nesters; S = shrub and succulent nesters.
[b] Number of species in parentheses.

woodland). They also dropped their leaves in the spring (fig. 2). The shrub and succulent understory contained 13 species contributing a total of 478 individuals per acre. The most abundant species were in the genera *Mimosa*, *Chrysothamnus*, *Opuntia*, and *Agave*. This study area is described in greater detail elsewhere (Balda 1969).

Breeding birds. This plant community supported 36 species of nesting birds with a total density of 267 pairs per 100 acres (table 2). The three most abundant species, comprising 28 per cent of the total breeding pairs, were tree foliage nesters. Woodpeckers and, consequently, old woodpecker holes were common in the live and dead pines found in the area. Heartwood rot and natural cavities were not common. A total of 32 potential nest-site cavities were located, but only six (19 per cent) contained active nests. Cavity nesting pairs made up 27 per cent of the total nesting pairs.

The five species nesting on the ground had a total nesting density of 25 pairs per 100 acres (table 2). This area, which was not grazed, provided a good cover of tall grass and had a relatively rugged topography containing numerous rocky outcroppings, dry washes, and scattered boulders. These features, plus dead branches and fallen trees, contributed to the diversity of the woodland floor, and provided diverse and ample nest-sites.

A total of 19 species nested in the foliage, of which 17 nested in trees and only two in shrubs and succulents. The latter contributed only three per cent of the foliage nests.

Breeding was initiated in the first week of April, when the Bewick's Wren began nesting. During the second week the Common Bushtit, Broad-tailed and Black-chinned Hummingbirds commenced nesting. Initiation of nesting reached a peak in the third week of May, when oak leaves were missing or very small, but most birds nested in either juniper or pine.

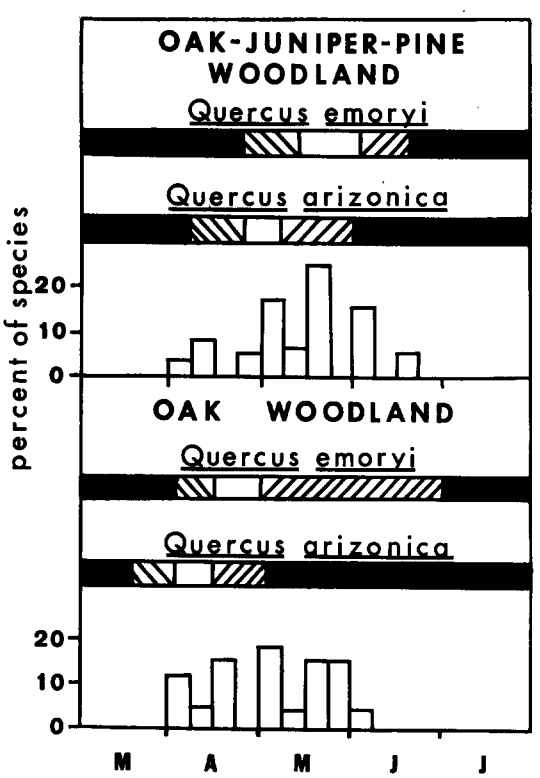

FIGURE 2. Leaf-fall and nesting in two woodlands. Black portions of horizontal bars indicate full leaf, hatched sections indicate leaf-fall and replacement, open sections indicate trees bare. Oaks contributed 99 per cent of all tree foliage in the oak woodland and 22 per cent in the oak-juniper-pine woodland. Histograms indicate per cent of species initiating nesting by weekly periods.

CONCLUSIONS AND SUMMARY

The sequence of leaf-fall by the two species of oaks followed the same pattern. *Quercus arizonica* dropped its leaves two weeks before *Q. emoryi* on both plots. Leaf-fall started three weeks earlier in the oak woodland than in the oak-juniper-pine woodland. During the time of leaf-fall and new growth, almost all species of birds in both areas began nesting. Since oaks predominate in the oak woodland

but not in the oak-juniper-pine woodland, the loss of oak foliage should be of greater consequence to the foliage nesting birds of the former area.

Comparison of nest-site utilization in the two woodlands yields some striking differences. In the oak woodland plot there were 24 foliage-nesting species with a total density of 121 pairs per 100 acres, whereas 19 foliage-nesting species with 151 pairs per 100 acres nested in the oak-juniper-pine study area. Of the 24 oak woodland foliage nesters, 12 also occurred in the oak-juniper-pine woodland. The other 12 show a stronger preference, based on densities elsewhere, for either desert or riparian habitats. Of the 12 species common to both areas, nine had lower densities in the oak woodland. The Wilcoxon matched-pairs signed-ranks test indicates this difference as significant at the 0.025 level. Among these nine species there were 59 fewer pairs per 100 acres in the oak woodland. The biggest difference in density between the two areas was found for the Chipping Sparrow, Black-throated Gray Warbler, and Black-chinned Hummingbird, all of which are known to use both oak and juniper for nest-sites. The low density of juniper, combined with the loss of oak foliage, apparently restricted their abundance in the oak woodland (cf. Balda 1969). Tree-foliage nesters averaged 5.6 pairs per species in the oak woodland and 8.6 pairs per species in the oak-juniper-pine woodland. Five of the seven tree-foliage nesters found exclusively in the oak-juniper-pine woodland are known to select conifers for nest-sites and would therefore avoid pure stands of oaks. These five species (Robin, Solitary Vireo, Grace's Warbler, Blue-throated Hummingbird, and Buff-breasted Flycatcher) all had relatively low densities in oak-juniper-pine woodland.

Ten species in the oak woodland nested in shrubs and succulents where they were unaffected by oak leaf-fall. These 10 species averaged 4.3 pairs per 100 acres, whereas only two species, with an average of 2.5 pairs per 100 acres, selected nest-sites in the understory in the oak-juniper-pine woodland. The low densities of species nesting in shrubs and succulents in the latter area do not reflect a lack of nest-sites, as there were more shrubs and succulents present in the oak-juniper-pine community.

Although there were four more species of cavity nesters present in the oak-juniper-pine woodland, their total nesting density was less than that of the cavity nesters in the oak woodland, even though more holes were present in the former area. Each of the five species averaged 15.2 pairs per 100 acres, whereas the oak-juniper-pine cavity nesters averaged only 7.9 pairs per 100 acres. Three of the four species of cavity nesters (excluding woodpeckers) found in both study areas had higher populations in the oak woodland and contributed 27 more pairs there.

In the oak woodland 19 species used nest-sites other than tree foliage, as did 16 species in the oak-juniper-pine woodland. The 19 oak woodland species had 42 pairs more per 100 acres than their counterparts in the oak-juniper-pine woodland.

The number of pairs expected to nest in each type of site was calculated for the oak woodland by using the oak-juniper-pine woodland percentages. On the basis of Chi-square, the utilization of the various types was significantly different for the two areas.

It appears that the lower density of tree-foliage nesters in the oak woodland is partially offset by higher densities of birds nesting in sites other than tree foliage. This is supported by the fact that a much higher percentage of cavities was occupied in the oak woodland; also, more species with higher densities nested in shrubs and succulents.

The almost total absence of tree foliage in the oak woodland during the start of the nesting season may be an important limiting factor for species which normally place their nests in tree foliage. However, their resulting low densities may reduce demands for food, so that species which can procure nest-sites, such as cavity nesters or species which nest in shrubs, succulents, evergreens or on the ground, may be able to procure ample food to maintain relatively higher populations. The oaks of both woodlands, when in flower, attracted large numbers of insects and consequently large numbers of foraging birds, but of course provided little foliage for nest concealment. In the oak-juniper-pine woodland, oak flowers also attracted insects (Balda 1969), but there were considerably fewer oaks present and ample tree-foliage nest-sites were available in the pines and juniper. Von Haartman (1957) emphasizes that the benefits derived from nesting in tree cavities may be partly offset by severe competition resulting from lack of suitable holes. The present study suggests that in the oak woodland, a unique and geographically limited plant association, a lack of suitable tree foliage sites may limit the density of tree-foliage nesting birds.

It appears that ample insect food, associated

with the flowers and new oak leaves, is available to satisfy reproductive demands. The usual consumers, tree foliage nesters, however, are limited in density by a factor other than interspecific competition with birds that nest elsewhere, i.e., the untimely loss of tree foliage.

The question arises as to whether the difference in density of tree foliage nesters is a result of increased predation, or simply a failure of some individuals to establish and maintain territories in the oak woodland. My meager data show no difference in intensity of nest predation between woodlands, nor between different nest-sites within either woodland.

The lower densities of species nesting in tree foliage in the oak woodland may be due, in part, to a lack of initial selection of territories and/or a desertion of territories or nests when an important sign stimulus, foliage, is removed. Individual nests started in trees before leaf-fall may be deserted because of lack of concealment and protection, or because the microhabitats surrounding these nests have been seriously altered by the loss of foliage. One important factor in this regard may be an increase in solar radiation.

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