

POPULATION, TERRITORY AND SONG OF THE
LEAST FLYCATCHER (EMPIDONAX MINIMUS)

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A report of an original field study conducted
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Population, Territory and Song of the
Least Flycatcher (Empidonax minimus)

The nesting cycle of the Least Flycatcher was studied at the University of Michigan Biological Station, Douglas lake, Michigan, during the summers of 1942, 1944, and 1946. Information in the present paper is based on 33 nests (19 in 1942, 14 in 1944) confined to 7 acres of the Station grounds and 12 nests found in 1946 confined to 21 acres. The larger area contained the original 7 acres plus an additional 14 acres of woods continuous with it. This larger plot was studied to determine if the population density of the Least Flycatcher was as high in a continuous aspen associates as it had been in the original plot of broken woods. Within this area the territories of all of the Least Flycatchers were determined and morning and daytime song recorded in relation to them. This paper is a composite of work done over the three summers' study of this species.

Methods

All nests occurring within the area chosen were systematically located in 1942, 1944, and 1946. Each nest was numbered successively in the order found and its locations in the area indicated on a map. (See map 1) Each nest was carefully examined and watched by regular visits as long as it was occupied. A summarization of nesting data obtained is presented in Table 1.

Nests 1, 2, 3, 4, and 5 were selected for 165 hours of detailed observation on territorial and nesting activities between June 20 and August 3, 1942. For observation purposes, elevated platforms at nest level were set three feet from the base of the nesting trees. Nest 21 and 17 were chosen for 30 hours additional observation between June 27 and July 15, 1944. Territorial boundaries of the 15 pairs of

Table I

A Summarization of Nesting Data for the Least Flycatcher
at Douglas Lake, Michigan, 1942, 1944 and 1946

| Nests No. | Date found | Kind of tree | Position in tree | Height from ground | Contents when found | Total eggs laid | Date of hatching | Size of Brood | Date of leaving nest | Remarks |
|-----------|------------|--------------|------------------|--------------------|---------------------|-----------------|------------------|---------------|----------------------|------------------------------------|
| 1 | June 19 | Birch | v-fork | 15' | 2y | - | July 29 | 2 | July 29 | |
| 2 | June 19 | Maple | v-fork | 12' | 1e, 3y | 4 | June 19-20 | 4 | July 21 | |
| 3 | June 19 | Birch | h-fork | 9' | 1e, 2y | 3 | --- | 2 | July 26-27 | |
| 4 | June 23 | Birch | v-fork | 12' | 1e | 4 | July 10-11 | 3 | July 21-24 | 1e des |
| 5 | June 24 | Birch | v-fork | 13'7 | nest being built | 4 | --- | - | | Nest and eggs destroyed incubation |
| 6 | June 24 | Birch | v-fork | 12'7 | 4e | 4 | July 1 | 3 | July 11-12 | |
| 7 | June 20 | Birch | v-fork | 20' | --- | - | --- | - | --- | |
| 8 | June 28 | Birch | v-fork | 20' | --- | - | --- | - | --- | |
| 9 | June 26 | Birch | h-fork | 15' | 4y | 4 | --- | 4 | --- | |
| 10 | June 28 | Birch | v-fork | 10'7 | 1ce, 1e | ? | --- | 0 | --- | nest deserted |
| 11 | June 24 | Aspen | v-fork | 17'7 | 4y | 4 | --- | 4 | --- | |
| 12 | June 25 | Pine | h-fork | 15' | 4y | 4 | --- | 4 | --- | |
| 13 | June 23 | Aspen | v-fork | 30' | - | - | --- | - | --- | |
| 14 | June 26 | Aspen | v-fork | 17'9 | 3y 12' | - | --- | 3 | --- | |
| 15 | June 29 | Birch | v-fork | 18' | 4e | 4 | --- | 2 | --- | |
| 16 | June 17 | Maple | v-fork | 35' | - | - | --- | - | --- | |
| 17 | June 20 | Maple | v-fork | 25' | - | - | --- | - | --- | |
| 18 | June 25 | Aspen | v-fork | 17' | 1cy | - | --- | 1 | --- | |
| 19 | June 18 | Birch | v-fork | 15' | 2e | 4 | --- | 0 | | Nest destroyed June 20 |
| 20 | June 25 | Birch | v-fork | 10' | 2y | 3 | --- | 2 | June 28 | |
| 21 | June 27 | Maple | h-fork | 20 | 1e, 1ce, 1y | 3 | --- | 1 | July 10 | 1e inf. cy ? |
| 22 | June 27 | Aspen | v-fork | 26' | 3y 14' | - | --- | 3 | July 1 | |
| 23 | June 27 | Birch | v-fork | 25' | 2y | - | --- | 2 | | nest deserted |

e-eggs; y-young; ce-cowbird egg; cy-cowbird young; inf-infertile egg
v-vertical; h-horizontal

Table I Continued

| Nest No. | Date found | Kind of tree | Position in tree | Height from ground | Contents when found | Total eggs laid | Date of hatching | Size of brood | Date of leaving | Remarks |
|----------|------------|--------------|------------------|--------------------|---------------------|-----------------|------------------|---------------|-----------------|--------------------------------------|
| 24 | June 28 | Birch | v-fork | 30' | 4y | 4 | - | 4 | - | |
| 25 | June 28 | Birch | v-fork | 18' | 3y | - | - | 3 | July 1 | nest des. |
| 26 | June 29 | Birch | v-fork | 28' | 3e | - | - | 3 | July 14 | |
| 27 | June 28 | Birch | v-fork | 28' | 3y | - | - | 3 | July 15 | |
| 28 | June 28 | Birch | v-fork | 23' | 3y ¹⁴ | - | - | 3 | July 4 | |
| 29 | June 29 | Aspen | v-fork | 13' | 3y | - | - | 3 | July 4 | |
| 30 | June 29 | Birch | v-fork | 20' | 4y | 4 | - | 4 | July 12 | |
| 31 | July 5 | Birch | v-fork | 6' | 4y | 4 | - | 4 | July 6 | |
| 32 | July 6 | Birch | v-fork | 14' | - | - | - | - | - | nest partially torn apart when found |
| 33 | July 22 | Aspen | v-fork | 11' | 2y | - | - | - | July 31 | |
| 34 | July 5 | Aspen | v-fork | 13' | 4y ⁷⁹ | 4 | - | 4 | July 8 | |
| 35 | June 23 | Birch | v-fork | 15' | 4y | 4 | - | 4 | July 4 | |
| 36 | June 27 | Aspen | v-fork | 16' | e? | ? | July 11 | 2 | July 26 | |
| 37 | June 28 | Maple | v-fork | 9' | e | 4 | July 8 | 4 | July 23 | |
| 38 | June 28 | Birch | v-fork | 22' | 4y | 4 | - | 4 | July 1 | |
| 39 | June 28 | Birch | v-fork | 14' | - | - | - | - | July 10 | |
| 40 | July 3 | Maple | h-fork | 28ft | - | - | - | - | July 10 | |
| 41 | June 27 | Aspen | v-fork | 20' | e | - | July 3 | 2 | July 17 | |
| 42 | June 20 | Birch | v-fork | 20' | - | - | - | - | - | |
| 43 | July 5 | Birch | h-fork | 25' | being built | - | - | - | - | nest deserted |
| 44 | July 7 | Maple | v-fork | 15' | 4y | 4 | - | 4 | July 8 | |
| 45 | July 7 | Birch | v-fork | 25' | e | - | - | - | - | nest deserted |

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nesting flycatchers were determined during 40 hours of observation between June 24, and July 28 at which time both morning song^{perches} and intraspecific fighting were recorded by plotting their locations on a map taken into the field. Morning song was studied on 10 morning trips throughout the summer beginning about one hour and a half before sunrise and ending with the completion of the rhythmic song. (See map 2) All observations outside of the blind were made with 8x binoculars.

Special efforts were made to band or mark adult Least Flycatchers under observation in order that individuals might be distinguished and their respective activities followed with greater accuracy. Females from Nest 2,4, and 21 were banded with aluminum bands colored with nail polish while the female from Nest 21 was made even more identifiable by gluing a yellow feathers to the tail coverts.

Capturing the bird for the above purposes was accomplished by building a trap around the nest. It was made of quarter-inch mesh wire with a hinged top that could be left open for the bird to enter and released by a string from the blind when the bird had settled on the nest. When the birds were not banded or marked it was sometimes possible to recognize sexes by call notes and song and in a few cases individuals were recognized, though with less certainty, by peculiarities of mannerism or variations in plumage coloration.

Habitat and Population

The area of the Station grounds concerned with the study was largely the second-growth aspen associates which developed after 1901 when a fire destroyed the original forest. Aspen constituted the predominant tree growth with birch, maple, and a few relic pines sparsely intermingled. The crown of the Large-toothed aspen formed an

canopy about 35-40 feet high with a lower layer of birch maple and Trembling aspen saplings. Sample counts ^{1.} / revealed the following percentage of occurrence of tree species in Set 1, and Set 2. ^{2.}

| | <u>Set 1</u> | <u>Set 2</u> |
|--|--------------|--------------|
| Large-toothed aspen (<u>Populus grandidentata</u>) | 53 | 46 |
| Trembling aspen (<u>Populus tremuloides</u>) | - | 14 |
| Paper birch (<u>Betula papyrifera</u>) | 8 | 4 |
| Red maple (<u>Acer rubrum</u>) | 11 | 9 |
| Norway pine (<u>Pinus resinosa</u>) | 7 | 3 |
| Smooth sumack (<u>Rhus glabra</u>) | 11 | 6 |
| June berry (<u>Amelanchier canadensis</u>) | 4 | 5 |
| Red oak (<u>Quercus borealis</u>) | 4 | 4 |

The ground cover was primarily bracken under which grew a few tolerant plants. Listed below are the plants identified together with the percentage of occurrence per quadrat. ^{3.}

| | |
|--|-----|
| Bracken (<u>Pteris aquilina</u>) | 100 |
| Cow wheat (<u>Melanopyrum lineare</u>) | 56 |
| Wintergreen (<u>Gaultheria procumbens</u>) | 66 |
| Honeysuckle (<u>Diervilla lonicera</u>) | 48 |
| Bastard toad-flax (<u>Commandra umbellata</u>) | 30 |
| Mountain rice (<u>Oryzopsis asperifolia</u>) | 30 |
| Goldenrod (<u>Solidago luspida</u>) | 28 |

The vegetation complex of Set 1 was interrupted by sixteen buildings and four drives as well as by several areas where trees and ground cover had been cleared away (See map 1). Human activity along the drive and around the buildings was almost constant throughout the daylight hours. Set 2, rarely visited or disturbed, extended as continuous aspen woods bordered on each side by roads.

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1. Tree counts were taken by holding horizontally at waist level two meter sticks and counting every tree touched by the two sticks along the line traversed. **The strips were 600 ft. long.**
 2. Set 1 constituted the area of 7 acres first studied and in which the flycatcher population was concentrated. Set 2 constituted the adjoining 14 acres of continuous aspen added in 1946.
 3. Four quadrat counts were made in the area. In each quadrat (equal to one square meter of ground) all the plants were counted and their percentages tabulated. Two quadrat counts were made in each Set within the interior of the woods.

Breeding birds found in the area determined by plotting the singing males and locating nests totalled seiteen. (See Table 2)

The mammals of the area included several Thirteen-striped Gophers (Cittellus tridecemlineatus), Chipmunks (Tamias striatus), Flying Squirrels (Glaucomys volans), Woodchuck (Marmota monax) and one skunk (Mephitis mephitis).

Nineteen mated pairs of Least Flycatchers were counted in the study in 1942, 15 in 1944, thus giving a population of 2.6 and 2.0 pairs per acre, respectively. This population in 1942 and 1944 was noticeably restricted to the aspen associates of the Station grounds; farther away where the aspen associates continued without interruption the least was found sparingly. To test this observation an adjoining stand of unbroken aspen twice the size of the original plot was taken. IT was found that the Least Flycatcher did not extend its range of nesting beyond the original area and that the population dropped correspondingly to 0.7 pairs per acre.

Census counts of bird population found in aspen, beech-maple, and pine communities in Cheboygan county revealed that the Least Flycatcher occurred in only the beech-maple association¹. Hofslund found (1946) that the species nested primarily along the edges of paths and roads transecting his plot but did not invade the forest interior. Within the pine community Prescott (1946) found one Least Flycatcher but in this instance it SANG along the border

1. Plot censuses of bird populations were studied by members of the advanced Ornithology class in 1946 as special problems. They were as follows: aspen associates--29 acres, Ritsema and Vandegrift
beech-maple association--160 acres, Hofslund
pine associates--26 acres, Prescott

Table 2

Bird Population Found in 21 Acres of
Least Flycatcher Habitat

| No. of Pairs 1946 | Species | Breeding in | | |
|-------------------|--|-------------|------------|-------------|
| | | 1942 7 a | 1944 7a | 1946 2la |
| 15 | Least Flycatcher (<u>Empidonax minimus</u>) | n | n | n |
| 13 | Red-eyed Vireo (<u>Vireo olivaceus</u>) | n | n | n |
| 6 | Ovenbird (<u>Seiurus aurocapillus</u>) | s | s | s |
| 6 | Cedar Waxwing (<u>Bombycilla cedrorum</u>) | n | n | n |
| 6 | Chipping Sparrow (<u>Spizella passerina passerina</u>) | n | n | n |
| 3 | Tree Swallow (<u>Iridoprocne bicolor</u>) Eastern | - | n | n |
| 2 | Kingbird (<u>Tyrannus tyrannus</u>) | n | n | n |
| 2 | Purple Finch (<u>Carpodacus purpureus purpureus</u>) | n | n | n |
| 2 | Indigo Bunting (<u>Passerina cyanea</u>) | - | - | s |
| ? | Cowbird (<u>Molothrus ater ater</u>) | w | w | w |
| 1 | Crested Flycatcher (<u>Myiarchus cinerascens boreus</u>) Northern | n | n | n |
| 1 | Flicker (<u>Colaptes auratus auratus</u>) | n | n | n |
| 1 | Eastern Phoebe (<u>Sayornis phoebe</u>) | - | n | n |
| 1 | Baltimore Oriole (<u>Icterus galbula</u>) | n | n | n |
| 1 | Myrtle Warbler (<u>Dendroica coronata</u>) | - | w | s |
| | Purple Martin (<u>Progne subis subis</u>) | w | w | w |
| | Black-capped Chickadee (<u>Parus atricapillus atricapillus</u>) | w | w | w |
| | Blue Jay (<u>Cyanocitta cristata bromia</u>) | w | w | w |

a-acres; n-nest found; w-wandering individuals; s-singing males

of a small island of aspens within the pine forest.

Saunders (1936) noted the Least Flycatcher in four out of the nineteen habitats which he censused in the Quaker Run Valley, Allegany State Park, New York. One was characterized as of orchards and shade trees while the remaining three were of temporary (i.e., secondary) woods. Forbush (1927:361) has stated that the species "has become accustomed to man and his works and ^{pre}fers his neighborhood to more retired localities". A comparison of the above population studies are represented with mine in Table 3.

While Saunders' or Hofslund's censuses do not show the great density of population witnessed in the seven acres of the Station grounds, they are nevertheless significant in showing the least's preference for open woods. Saunders found that the greatest population of the birds in the Quaker Run Valley occurred among orchards and shade trees--decidedly the most open--while the smallest population occurred in the aspen-red maple thicket which was the least open. Hofslund, as well, found the species nesting along the edge of the woods. It thus appears without question that the preference of open areas in or adjoining a woods is a determinant of habitat, where as the type of trees and the nearness of human habitations would seem to be coincidental.

This preference for an edge was clearly shown by locations of 45 nest studied, 20 were located on the edge of clearings or roads, 18 were less than 10 feet from the edge, while only 6 were more than 20 feet away. If it is assumed that the niche requirement is the presence of an open areas in or adjoining woods the question arises as to what this niche provides that is essential for nesting.

Table 3
 A Comparison of Least Flycatcher
 Populations in Different Habitats

| Authority | Habitat type | Years censused | Number of acres | Total pairs counted | Average per 100 acres |
|-----------|--|----------------|-----------------|---------------------|-----------------------|
| Saunders | Orchard and Shade trees | 1930-31 | 50 | 6 | 12 |
| Saunders | Aspen-cherry forest, undisturbed | 1930-31 | 1166 | 43 | 3.7 |
| Saunders | Aspen-cherry forest cleared for camping | 1930-31 | 123 | 4 | 3.3 |
| Saunders | Aspen-red maple thicket | 1930-31 | 333 | 7 | 2.1 |
| Hofslund | Beech-maple forest | 1946 | 160 | 9 | 5.6 |
| Muirhead | Open aspen woods | 1942 | 7.3 | 19 | 260 |
| Muirhead | Open aspen woods | 1944 | 7.3 | 15 | 205 |
| Muirhead | Open aspen plus 14 acres of closed aspen | 1946 | 21 | 15 | 75 |

The combination of two factors, shade of a wooded area for the nest and yet the presence of an open edge effect for feeding and song posts seem to be the major requirements provided by this niche.

It was found in the study that the larger open areas surrounding in the woods (i.e. saw mill opening and dump area) were used as neutral feeding areas for all of the flycatchers nesting around them. The presence of such a neutral feeding area may be a factor in the density of population, not as a food factor, but because it would decrease intraspecific conflict and as well decrease the size of the territories.

No nest was found that was not bordered on at least one side by an opening in the woods and where ever a road or path was available it was used as a boundary for a territory. The song posts from which early morning song began were located on these edges and although the male moved about the boundaries of the territory the major portion of his song came from the edge. So that there seemed to be a definite correlation between morning song posts and the open edge requirement.

The density of population in the small ^{area?} ~~study~~ are might well be connected with the high nesting success since eighty-two percent of the pairs successfully raised broods. Over a period of years this nesting success might well compliment the niche requirement thereby creating a maximum population in the area. Whereas if another region were taken offering the same nesting conditions but with a higher nesting mortality the population would be smaller.

The niche requirement of this species does not depend upon the type of tree or woods in nesting as exhibited in the above studies

but does depend on the presence of an edge adjoining a woods. ^{deciduous or coniferous?}
This edge may provide song posts and feeding perches and also neutral feeding grounds thereby increasing the number of territories. High nesting success in the study area may also be an important factor in reaching a maximum nesting population. The abundance or existence of food does not appear to effect or control the population as there is always more food present than is needed.

Interspecific Habitat Relationships

The segregation of species into various niches within the area studied indicated that little interspecific competition existed. The Least Flycatcher tolerated the presence of other bird species within its nesting territory. At Nest 21, a Chipping Sparrow built its nest in the same tree, yet both species carried on their nesting activities with no evidence of fighting. Four flycatchers,--Eastern Phoebe, Eastern Kingbird, Wood Pewee, and Crested Flycatcher,---nested and fed in areas immediately adjoining Least Flycatcher territories and sometimes were seen to appear briefly on them but no instance of interspecific strife occurred. Williams (1936:66) , in his study of the beech-maple climax community, also noted the absence of strife between resident flycatchers (i.e. Acadian Flycatcher, Wood Pewee, Crested Flycatcher), although in this case the pairs were more widely spaced, thus eliminating opportunity.

Superficially it would appear that the Redstart and the Least Flycatcher's niche requirement would coincide because of the similarity in nest structure and location, yet in Hofslund's study (1946) both species nested side by side with no apparent

conflict in the beech-maple forest. It was found, however, that the Redstart (38 pairs per hundred acres) was the most abundant with nests located throughout the woods where as the least (6 pairs per hundred acres) nested only along the forest edge where paths and roads intersected. *Competition in remote part segregated two species in the manner?*

The only instance of interspecific conflict came when a pair of Cedar Waxwings raided a Least Flycatcher nest containing eggs to obtain nesting materials. This instance is recorded in the writer's notes taken on July 7,---

"Today, outside of the study area but on the Station grounds, several persons called my attention to a Least Flycatcher nest that was being dismantled by a pair of Cedar Waxwings. I watched the proceedings for a period of thirty-five minutes during which the Waxwings made three visits. Each time the waxwings appeared rapid chebec notes were uttered by the male perched fifty feet from the nest and the female on the nest. Neither the alarm notes or the presence of the female on the nest seemed to hinder the waxwings attacks. Even though the flycatchers sensed an oncoming danger which was apparent by their frequent calling, no move was made to initiate any direct defense until the waxwings were within three or four feet of the nest or had begun to actually tear at the nest. The female remained on the nest and the male continued to call from a distance until the nest had been reached then the male went into action, diving down at their heads and flying about at very close range. The female, at the same time, sitting on the nest called and pecked at the raiders. The tenacity of the female to remain on the nest when the whole structure was being rocked and torn to pieces amazed me. The waxwings seemed to show little concern for the noise

and commotion caused by the flycatchers; there was but one purpose in mind--nesting material. Finally on the third attack, as the nest began to tip over the female joined the male and both adults flew at the head of the waxwing and for the first time caused it to retreat still holding pieces of the nest in its beak.

Display here consisted of much the same kind seen in intra-specific disputes; the bird crouched slightly on its perch puffed out the breast feathers and with each call raised its crest and flicked its tail. As an actual attack was made the wings were vibrated in a fluttering manner as the bird hovered over the head of the waxwing uttering chebeé calls. //

It is evident from the above illustration that the male defended the nest against interspecific enemies and that the female joined in only under extreme conditions. Davis (1941:161) also found this in the Kingbird and he states, "the important characteristic of this interspecific fighting is that only the male fights".

This characteristic of only the male fighting did not hold true in cases involving mammals or anthropic disturbances. In these cases both sexes participated and did not lessen their attacks or calls until the nest or young were unmolested.

In summarizing interspecific behavior we may state that interspecific competition was not an important factor in the nesting of this bird. The only cases of conflict that were recorded in the study was one between the Cedar Waxwing. A characteristic of interspecific disputes was that the male did the fighting. Disturbances in which mammals or man were involved both sexes participated in the fighting. It was not uncommon to find other species nesting without competition in the same tree with the Least Flycatcher. Other flycatchers

nested within close range of the least without fighting indicating that the similarity of food habits was not a primary cause of interspecific competition.

Territory

Within its chosen habitat the Least Flycatcher selected a territory used for nesting purposes and for gathering food for itself and young. Beyond the borders of this territory the species enjoyed a neutral feeding ground where individuals of both sexes gathered without mutual protest. This kind of territory would appear to be a combination of types A and B described by Nice (1941: 457-462); in other words, a territory in which feeding was accomplished at times on the same area where nesting and mating took place (type A) and at other times away from the regular mating and nesting territory (type B).

Since the present study was not undertaken until late June, territories were already well established. Judging by the statement made by Barrow's (1912:406), the Least Flycatcher does not appear in northern Michigan until approximately May 20, hence the species may have been on its nesting grounds about a month.

Character of Territory

Each nesting pair of flycatchers was dominant in its own territory and the intrusion of neighboring pairs always brought the immediate reaction of defense. Actual boundaries of these territories fluctuated during the nesting season but locations changed only if the nests were destroyed and in these instances moved only a short distance from the original nest. The largest territory measured 0.3 acres (14,000 square feet), the smallest 0.1 acres

(5800 square feet), and the average 0.2 acres (9100 square feet). The average distance between nests was 175 feet. In 1946 territories were determined of all the nesting flycatchers through the study of morning song and intraspecific disputes and are shown on Map 2. The territories and territorial behavior of three nesting pairs⁽¹⁹⁴²⁻¹⁹⁴⁴⁾ were studied in detail and the description of each territory together with a history of the pairs in possession is given below.

Histories and descriptions of Territories

Territory of Nest 4.- When the nest was found on June 23 at 3:00 p.m. one egg was present. When examined at 8:00 a.m. on each of the following three days, one additional egg was found, thus making a clutch of four. The first two eggs hatched on July 10, the fourth on July 11. The first bird left the nest for the first time on July 21 but returned to the nest each night until July 25 when all three nestlings left the nest.

The territory was a small wooded area bounded on the north and south by two roads converging to a point which marked the western most extremity. The eastern boundary, approximately 100 feet from the nest, adjoined another Least Flycatchers's territory (Nest 11). The total area was estimated to be 4,000 square feet. The nest was located in the northeast fourth of the territory equidistant between two roads. (See map 1)

Neutral feeding extended beyond the boundaries of the territory for a radius averaging 100 feet except on the lakeside of the territory where it may have extended to the shore.

Territory of Nest 5.- The nest was found on June 24 during its second day of construction (estimated). IT was considered to be the second nesting of the pair occupying Nest 19 (65 feet away) that

had been destroyed seven days previously. It was completed on June 27. The first egg was laid before 9:00 a.m. on June 28 and one additional egg was found on each of the following three days until the clutch of four was completed. On July 11, the eggs were found destroyed and the nest severely damaged. Only one bird, presumably the female, was observed at the nest during the time that the nest was under observation. *in the reason for the small size of territory?*

The eastern boundary of the territory was bounded by the base line road and the remaining portion of the territory was determined by the borders of the territories of two adjoining nesting pairs of Least Flycatchers (Nest 14 and 15). These nests were approximately 36 feet from the boundary and approximately 65 feet from both Nests 14 and 15. (See map 1)

The neutral feeding area extended beyond the road to the east to include a section of wooded area (formerly incorporated in the territory of Nest 19) and a section of cleared land.

Territory of Nest 21.- The nest was found on June 27, and contained one nestling one-day- old (estimated), one egg, and one Cowbird egg. The Cowbird egg hatched on June 29 and developed normally in the nest until its disappearance during the morning of July 8. The flycatcher egg disappeared from the nest on on June 30. The nestling flycatcher developed normally, left the nest of its own accord on July 10, and was observed to remain in the vicinity of the nest until July 16.

The territory was bounded by three intersecting roadways. The territory covered nearly 13,000square feet, being the largest found in 1944. (See map 1)

The neutral feeding area extended beyond the territory to the east to include an open field designated as the saw mill clearing.

Maintenance of Territory

Since territories were already established when this study was undertaken, observations concerning territorial behavior have to do chiefly with maintenance. The ensuing information is based on above described unless otherwise indicated.

Territories were maintained by four methods, namely: pursuit, threat-posturing, fighting, and song.

Pursuit.-- The sequence of events which followed the entrance of a flycatcher into a neighboring territory was first the recognition of the bird as an intruder. There was never any hesitation of the male in this, nor was there any mistake observed of misidentifying the female as the intruder. A sharp note was given by the owner and an immediate chase began with both birds flying excitedly and swiftly about the territory. This ended with either the enemy being forced to the ground or his fleeing from the territory. If a fight ensued, both birds flew to the ground and a flash of feathers and tumbling struggle followed ending in the retreat of the defeated bird from the territory, the owner close behind. After following a few feet outside of the territory the males instinct to fight seemed to end and the bird returned to a singing perch to proclaim his victory. Pursuit maybe said to consist of two phases, one, before the fight and another following it. Pursuit seemed to imply, in itself, a fight was to follow so that often it was sufficient to force the intruder out of the territory.

Intruder ever successful?

The male was the first to recognize and fly to the defense of the territory and was the member of the pair that was most often seen chasing other flycatchers. The extent of defense on the part of the female was in some respects different from the male. First,

the female did not defend the entire boundaries of the territory but was primarily concerned with the twenty feet around the nest. She did not attack or pursue the intruder until it had come well within the territory, then if the male did not fly to the defense, the female flew off the nest in pursuit. In most instances in which the female flew toward the foreign flycatcher only a pursuit flight occurred and this was sufficient to force the bird out. If two birds entered the area at the same time, the female assisted the male in defense, however, in these cases, the male was always the first to fly toward the enemy with the female following a few seconds later.

Pursuit appeared to be a means of dominating another flycatcher that had entered the territory. The extent of chase was often determined by the intruder, for if it was forced out of the area before the actual fight the second chase did not take place. The female as well as the male took part in the pursuit if the male was absent or two birds entered to challenge the territory.

This type of defense seems to be especially aggressive in the tyrant-flycatchers as a group. Many examples of belligerency have been noted in the Kingbird, and Davis (41:158), especially, has observed the part taken by the female as well as the male in territorial maintenance.

Threat-posturing.- Display could be brought about by five different actions: the enlarging of the body size by fluffing out of the breast feathers, raising of the crest, extending, vibrating and bending the wings, spreading and flicking the tail up and down,

and crouching the body. All of these methods of posturing were used to intimidate the opponents in defense.

Upon the recognition of a foreign bird into the territory posturing occurred as the male flicked his tail, raised his crest and in a crouched position left the perch to pursue the bird. This took but a few seconds, then following the chase both birds flew to the ground and a more lengthened posturing performance took place. The movement on the ground took place so rapidly that all that was seen was a momentary stillness while both birds faced one another with outstretched wings and in a crouched position flew at one another. On the return to a singing perch, posturing again took place involving the quick movement of the tail and crest each time that a song was uttered.

Posturing on the part of the female did occur but only in a very limited sense. On meeting another bird another bird in defensive action, the tail was spread, and crest raised and in some instances the breast feathers fluffed out. In all cases of posturing the instances were of short duration and noted in most instances when defense involved predators rather than intraspecific fighting.

Posturing, as such, has been described in great detail by Nice (1943:255) in the Song Sparrow, by Tinberger (1939:13) in the Snow Bunting, and by Kendeigh (1941:21) in the House Wren. All of these studies deal with birds outside of the flycatcher group upon which little work has been done. Davis (158) does show much the same type of behavior in the Kingbird although there is exhibited a greater intensity. In all of the disputes described the role of the sexes is, in its essence, the same in both species.

Fighting.--Fighting was closely related to pursuit as it took place

in rapid sequence. Often during a chase the two birds would fly at one another in the air just before they dropped to the ground. Fighting took place so quickly that all that could be seen was the flash of feathers and the swirling movement of bodies. When the bird reached the ground the actual combat was but a very small part of the disputes for intimidation by posturing took up the greater part of the fight.

Fighting on the part of the female was rarely seen and then only in cases when two birds disputed the right of the territory. In these cases, both adults fought.

Defense of the territory was most intense at the beginning of the nesting season and as incubation, hatching, and feeding of the young progressed the adults became less attentive to the outer boundaries until after the dispersal of the fledglings the territory completely lapsed.

Territory in post-nesting

An interesting observation was made in the continuation of territory after the young were out of the nest in 1946 while studying song and territories of the 12 nesting pairs. Morning song was given at the same song posts and the male behaved much the same as if the young had been in the nest. Toward the end of two weeks when the fledglings were more active they often created territorial conflict by moving into adjoining territories. In one instance, a young cowbird being fed by the adults created constant disputes by moving across the road into the neighboring territory. Each time that the male or female came to feed they were immediately challenged and chased from the territory. Territory then continues as long as the young remain within its boundaries which is usually for two weeks after leaving the nest.

Song and other vocal notes

Song was one of the most important means of territorial maintenance. Its duration and intensity is greatest at the beginning of the egg-laying period and declines gradually until by the time the young leave the territory it has entirely ceased. A series of chebec notes uttered as a few single calls or as an extended series made up the complete song of the Least Flycatcher. Although the chebec note itself was subject to little deviation in tone, its rapidity of utterance in a series is subject to three major deviations resulting in distinct types of song: the morning song, the day time song, and the flight song.

The morning song is given for a period beginning before dawn and ending with sunrise. The exact time of beginning and length of time involved is subject to variations due to sky conditions, climatic factors, and most importantly stages in the nesting cycle. It is longest at the beginning of incubation, ending after an average lapse of 70-80 minutes, and decreases in length during the nesting cycle until, by the time the young have left the nest it lasts but 10-15 minutes and after they leave the territory it stops altogether. Morning song continues even though the young have left the nest as the young remain in family groups within the territory and morning song continues as long as they are present. The cessation of this song was a gradual process since the stages in the nesting cycle varied so that not all individuals were singing. The length of the song correspondingly decreases from the hour period in June to a ten minute song in the end of July. The incentive for morning song seemed to decrease with those individuals that are late in nesting so that

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even though they may still have young in the nest, their song is not as long or as intense as those males singing in the same stage in the nesting cycle, earlier in nesting, when all of the birds in the area are singing. The explanation for this would seem to be that a larger number of adults singing in adjoining territories would stimulate one another to sing with more intensity than would only one or two birds in scattered territories. Singing, then, would not depend entirely upon stages of the individual birds in nesting but also upon the number of individuals in adjoining territories that were present to stimulate song.

Regardless of the length of the period, the chebec notes are given almost continuously. The ^{singing} song begins slowly then increases in speed to an average of 60 chebec notes per minute gradually losing speed ^{towards} with the end of the ^{period} song. The tempo of singing decreases as well at the end of July to only 45 chebec ^{notes} per minute. The male gives the morning song within the confines of his territory, using a perch that is generally a foliated branch half to two-thirds of the way up a tree, usually a few feet above the level of the nest. He does not remain on one perch throughout the song as does the Wood Pewee but moves from tree to tree around the edges of the territory. In cases where the nests are concentrated in small areas as at Nests 34,38,44, singing occurred most often at the borders where the three adjoined. All of the males within the area gave their morning song at the same time and intensity often in unison. Each male jerked their heads and flicked the tail with each song. The female during this time remained silently on the nest.

There are, therefore, several reasons for believing that this morning singing functions as an advertizing song. First, the stimulation of

Is there an evening song?

of singing does not depend entirely upon the individual bird's stage in the nesting-cycle, but upon the number of individuals in adjoining territories that are present to stimulate song.

Second, the male ceases his singing only when the territorial relationships have been broken up. No evening song existed in this species.

The day time song is heard at irregular intervals during the day. It is rendered more slowly, usually at a speed averaging 50 chebec notes per minute. The notes are few and vary in number per song. It is given about the nest as a means of telling the female the male's location and also in protesting intrusions into the territory of birds of the same species and other species and predators jeopardizing the nest. When the male sings, following territorial disputes, the song averages from three to five minutes, and acts as an advertising song. In intraspecific fighting or threats, the singing continues as long as danger is impending, but as soon as the predator leaves, the adults give no extended song but go about their nesting activities.

An important difference was noted in the occurrence of the two types of song. Day time singing was unpredictable and varied depending upon intrusions, predators, or signals given by the male. Morning song, on the other hand, occurred spontaneously with no previous territorial disputes and was sung by all the Least Flycatchers in the area at the same time on their respective territories at a definite period before sunrise. (See table 4)

It is of interest to compare the twilight song of the Least Flycatcher with that of other flycatchers. In reviewing Craig's study (1943) of the Wood Pewee there seem to be several differences in the two songs. First, the song of the Least Flycatcher contained no multiplicity of phrases or extended prelude; second, the song of

the Pewee lasted beyond the nesting cycle and could be heard after the young had left the territory, as compared to the least that ceased singing with the dispersal of the young from the territory.

Both songs were similar in that they were rhythmical, came in the early hours before sunrise, and covered an extended singing period with all of the males in the vicinity singing at the same time.

Of the three other flycatchers, Eastern Kingbird, Phoebe, and Crested Flycatcher, nesting in the study area, all but the Crested were heard to give morning songs. This lack of song in the Crested was probably caused by the advanced stage in the nesting when the records were made, as Saunders (1935:82) states that the singing comes only irregularly and early in June. On June 25, the Phoebe began its song about an hour and a half before sunrise and ended it with sunrise. Records are meager for this species as it stopped singing by July so that no definite figures can be given. The Kingbird did however continue its singing through July, and was found to begin singing before the Wood Pewee and the least, at one hour and fifty minutes before sunrise with a song lasting one hour and forty minutes. This song was found to decrease in length and intensity as did the Least Flycatchers song as the nesting season progresses. (See table 4) The morning song of all the above flycatchers began during civil twilight and ended within a short time before sunrise.

Other writers have noted (Wright, 1913:585) that the least was one of the first of the early morning song birds but no indication was given as to the speed or length of the song.

A flight song distinct from other types of song was heard on July 3, 1945. I discovered it from the continuous chebecs songs heard high over my head. The flycatcher was spotted seventy five feet up exhibiting short dipping flights as it hovered over the forest. The song came in rapid succession and then suddenly the song and flight ended with a straight dive down into the woods below, effected by the closing of the wings, and the bird was out of sight.

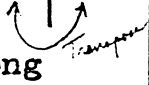
This song was noted by other observers, but is, in some cases, difficult to interpret. Forbush (1927:24) states that a flight song (?) "twittering warble", and Roberts (1936:24) states that a flight song uttered by the male at dawn and at dusk in which the call note whit and sebec are repeated many times. This song no doubt occurs most frequently when the birds are first setting up territories and mating and is probably a part of the courtship performance.

The variation of accents and additions to the chebec lead to many detailed differences in the song. The greatest question arises in reference to the lengthened song described by Chapman (1932:372) as the least giving "crescendo passages he literally rises to the occasion, and on trembling wing sings an absurd chebec tooral-ooral, chebec, ooral". On two occasions during the first four days of incubation I observed the male on his approach to the nest give a series of flight notes and chebec calls run together and at another time when the adults were warding off predators a series of jumbled mixed notes were heard but none of these possessed the quality described above. This song was not a part of the common song nor was it heard during the present study.

Table 4

Data on the Morning Twilight Song Records
 Made at the University of Michigan Biological Station

Song: Least Flycatcher

| Date | Time Sun's depression | | | First notes | Rhythmic song began | Rhythmic song ended | Number of males singing | Remarks |
|---|--------------------------|------|---------|----------------|---------------------------|---------------------------|-------------------------------|-----------------------------|
| | 6° | 12° | Sunrise | | | | | |
| June 29 | 3:49 | 3:29 | 4:56 | 3:45 | 4:00 | 5:10 | 15 | |
| July 4 | 3:49 | 3:27 | 4:59 | 3:50 | 4:07 | 5:05 | 14 | |
| July 12 | 3:48 | 3:25 | 5:05 | 4:10 | 4:20 | 4:50 | 10 | |
| July 15 | 3:48 | 3:23 | 5:07 | 4:25 | 4:30 | 5:05 | 11 | |
| July 18 | 3:48 | 3:21 | 5:10 | 4:30 | 4:40 | 5:05 | 10 | weather overcast |
| July 22 | 3:47 | 3:19 | 5:14 | 4:30 | 4:45 | 5:02 | 4 | |
| July 25 | 3:47 | 3:18 | 5:17 | 4:35 | 4:45 | 5:04 | 4 | |
| July 28 | 3:46 | 3:14 | 5:20 | 4:43 | 4:45 | 5:00 | 2 | speed song 49 per minute |
| Aug. 2 | 3:45 | 3:17 | 5:26 | 4:55 | -- | -- | 1 | |
| kingbird song  | | | | | | | | |
| June 29 | | | | | 3:20 | | | |
| July 4 | | | | | 3:30 | 4:05 | | |
| July 18 | | | | | 4:10 | 4:40 | | |
| July 22 | | | | | 4:12 | 4:50 | | |
| July 28 | | | | | 4:15 | 4:55 | | |
| Song: Wood Pewee | | | | | | | | |
| July 12 | | | | 4:14 | 4:18 | ? | | |
| July 18 | | | | 4:16 | 4:25 | 4:45 | | |
| July 25 | | | | | 4:40 | | | |

Sunrise determined for 85 longitude and 45 latitude on Eastern standard time. The duration of the three kinds of twilight—civil, nautical, and astronomical is the interval of time between sunset or sunrise and the instants when the center of the sun is, respectively, 6°, 12°, and 18° below the horizon.

The female on the whole did very little singing about the nest. Her movements about the nest were performed silently with only soft call notes occasionally given while moving about feeding. Most calls given were recognition signals to the male's coming and going at the nest. When the female was heard to give a song it consisted of only a short series in contrast to the extended singing of the males. The quality of the female's song, too, was different from the male's in that it did not end in a sharp accent but in a softer ending giving the effect of a chweep note. This difference in song was one of the primary methods used in distinguishing the sexes in the field.

The female's use of song seemed to be in response to disturbances of the nest and young and, in a few cases, to territorial maintenance when the male was absent from the territory. In those cases, in which the female did defend the territory, singing consisted only of a few short chweep notes given at the nesting tree before going back to the nest. The male, on the other hand, gave prolonged songs at the edge of the territory and rarely sang near the nest.

Song may be said to consist of three phases: morning, daytime, and a courtship flight song. It was closely associated with the male in his advertisement of territory and with the female, primarily in the protection of the young and nest. The types of song were greatest in length and intensity at the beginning of the nesting season, decreasing gradually as the season progressed and territories were abandoned, ending entirely with the dispersal of the young.

Call Notes

A common call given in flight consisted of guttural notes run together represented as spreet-spreet-reet-reet. Bent (1942: 221) gives a description of the notes taken from Minot as "querulous exclamations wheu, wheu, whey which are more or less guttural and subdued". The character of the notes are such as to lend themselves to many kinds of written interpretations but the calls are always as a series of notes run together in a guttural and rolling fashion. The male used these notes in his movements about the territory and on his approach to the nest. They were also often combined with the chebec in territorial chase and interspecific fighting. The female was only identified once giving these notes and that was while the nesting material was brought for building. This call was most closely associated with the male in his activity serving thereby to identify the bird in relation to the female.

A second call note identified with the female was the whit note softly uttered in her movements to and from the nest. The male was never heard to use this call as his call notes were louder and sharper in character. The use of these notes seemed to be one of the principal methods of sex recognition when combined with the characteristic behavior of the sexes. The female was usually inconspicuous in the territory while the male by song and conspicuous movements made himself obvious within the area.

Discussion and Summary

Population in relation to territory and song of the Least Flycatcher were studied during three summers 1942, 1944 and 1946 at the University of Michigan Biological Station for the purpose of analyzing the special niche requirement that existed to give the high density of population within the Station grounds as well as to study the breeding habits of the species.

It was found that the kind of tree and presence of food were second in importance to the arrangement of cover and the method of feeding. The presence of broken woods that provided shade for the nest as well as song and feeding posts along its edges, rather than a continuous wooded area that provided cover but only a few song and feeding posts along its fringes, was essential for nesting. Areas that afforded opportunities for neutral feeding grounds in small cleared islands within the woods probably created a larger population within the small area by decreasing intraspecific competition, thereby allowing for larger numbers of territories. The question arises as to why the species then is not found commonly along edges in all communities -- the answer here would seem to be that along edges adjoining large open area such as fields, light is too intense for this species and cover insufficient. The nesting success of 82 percent may also be a factor in population density within the small area around the Station grounds.

Interspecific competition between both birds and mammals was infrequent with only one instance observed of competition on the part of a Cedar Waxwing tearing apart the nest of the Least Flycatcher and Cowbird parasitism found in only ten percent of the nests. All of these factors contributed to the density of population present.

Competition did not exist among the members of the flycatcher group nesting side by side, a fact that further substantiates the theory that the competition for food is not as an important factor in nesting as nest sites and song posts.

Intraspecific fighting was participated in by both sexes. The female defense was limited to times in which the male was absent from the territory or when two birds challenged the territory.

Interspecific fighting differed from the above in that the male alone did the fighting with the female only participating under extreme conditions. In cases of predator or anthropic disturbances of the young and nest both sexes joined in the defense.

The common chebec song is divided into three uses: morning or twilight song, daytime song, and flight song.

Morning song was spontaneously given each morning throughout nesting at a period before sunrise in a rhythmical fashion by all of the Least Flycatchers in the area. Daytime song, on the other hand, was unpredictable depending upon territorial defense, disturbances at the nest, or signals given by the male to the female. Flight song was more limited and heard only once during the study as a rapid succession of songs given high in the air; probably closely associated with courtship in the early spring.

Song was most closely related to the male and territory since the female was heard to sing infrequently and with less intensity. Most of the notes of the female were call notes about the nest and territory, related to sex recognition.

Post-nesting, in connection with territory and song, were of especial interest as the young remained within the territory in family groups from 10 to 14 days during which time the territorial boundaries were maintained. Morning song continued, as well, over this period, ceasing as soon as the fledglings had dispersed. This song gains in importance when it is realized that little or no spontaneous singing occurs during the day, so that the morning ^{sings} serves as one of the chief means of advertising the territory.

Bibliography

- Barrows, W.B.
1912 Michigan Bird Life. Michigan Agricultural College, Lansing
- Bent, A.C.
1942 Life Histories of North American Flycatcher, Swallows, Larks, and Their Allies. U. S. Natl. Mus. Bull. 179
- Craig, W.
1943 The Song of the Wood Pewee (Myiochanes virens Linnaeus): A Study of Bird Music. New York State Museum Bull. No. 334 Albany
- Davis, D.E.
1941 The Belligerency of the Kinbird. Wilson Bull., 53:157-168
- Forbush, E.H.
1927 Birds of Massachusetts and Other New England States. Volume 2. Norwood Press, Norwood, Mass.
- Hofslund, P.B.
1946 A Study of the Breeding Bird Population of 160 Acres of Beech-Maple Hemlock Woods on Colonial Point, Burt Lake, Mich. Manuscript, Univ. Mich. Biol. St.
- Kendeigh, S.C.
1941 Territorial and Mating Behavior of the House Wren. Ill. Biol. Monogr. 18:1-120
- Nice, M.M.
1941 The Role of Territory in Bird Life. Amer. Midland. Nat., 26:441-487
1943 Studies in the Life History of the Song Sparrow, II. Trans. Linn. Soc. N.Y. 6:i-viii; 1-328
- Prescott, K.W.
1946 A Population Study of Birds of A Pine Community. Manuscript, Univ. Mich. Biol. St.
- Saunders, A.A.
1936 Ecology of the Birds of Quaker Run Valley, Allegany State Park, New York. New York State Museum Handbook., 16:1-164 Albany.
- Roberts, T.S.
1932 The Birds of Minnesota. Volume 2. University of Minnesota Press, Minneapolis.
- Tinberger, N.
1939 The Behavior of the Snow Bunting in Spring. Trans. Linn. Soc. N.Y., 5:1-94.
- Williams, A.B.
1936 The Composition and Dynamics of a Beech-maple Climax Community. Ecol. Monogr., 6:316-408
- Wright, H.W.
1913 Morning Awakening and Even. Song. Auk, 30:512-537