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BIRDS OF A PRAIRIE COMMUNITY

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With white man rapidly penetrating and disturbing the last remnants of pristine plant and animal communities on the North American continent, it is desirable to record the biological composition and dynamics of such communities before further modification takes place. Even now such studies often must be made, if at all, on areas where the plants and animals, formerly disturbed, have been allowed to return and re-establish somewhat limited natural relations. The present report concerns such a restored prairie community (fig. 40) of approximately fifty acres situated next to the Iowa Lakeside Laboratory, near Milford, in northwestern Iowa, on the west shore of Lake Okoboji. The study covered the period from early June to mid-August, 1940.

Vegetation.—The area is not entirely typical prairie. Formerly it was pastured, but parts of it were never plowed. For about the last twelve years it has been left alone, and two or three inches of dead grass debris have accumulated over the ground. As evidence of former disturbance, the Kentucky blue grass (*Poa pratensis*) is by far the most important species, constituting 25 to 100 per cent of the vegetation in various parts of the area. On the higher knolls, the vegetation approaches more nearly that of true prairie and consists of the grasses, *Poa pratensis*, *Andropogon furcatus*, *A. scoparius*, *Sporobolus heterolepas*, and *Stipa spartea*. Over sixty-five species of plants occur on the area, the principle forbs being an aster (*Aster multiflora*), a golden-rod (*Solidago rigida*), a lead plant (*Amorpha canescens*), a ragweed (*Ambrosia artemisiifolia*), and a vervain (*Verbena stricta*). I am indebted to W. A. Anderson, State University of Iowa, for help with the plant taxonomy of the area. The vegetation is not entirely stabilized, although little yearly fluctuation is evident. The annual weeds have been largely eliminated by the *Poa*, and there is some evidence that the prairie grasses are expanding at the expense of *Poa*. There appears to be some invasion of box elder (*Acer negundo*) into the *Poa* grass along the south side. Small bogs and a kettle hole occur with aquatic vegetation, and in some of the ravines and along the shore of Millers Bay occur willows (*Salix* spp.) and cottonwood (*Populus balsamifera*). There are a few scattered clumps of buckbrush (*Cephalanthus occidentalis*) and weed patches with grape (*Vitis* sp.) along the boundary fence.

This area is near the center of the True Prairie Association in the Stipa-Antilocapra Biome described by Clements and Shelford (Bio-ecology, 1939, John Wiley and Sons). It is surrounded by pasture and cultivated farmland, except on the south where it contacts a forest-edge of box elder, green ash (*Fraxinus pennsylvanica lanceolata*), wild plum (*Prunus nigra*), and, farther back, bur oak (*Quercus macrocarpa*). This oak is the outermost representative of the Deciduous Forest Biome that covers the eastern part of the country.

Climate.—The only climatic data available for the vicinity are from Lake Park, ten miles to the northwest, and information is available only for temperature and pre-



Fig. 40. View looking north over the prairie near Milford, Iowa. The light-colored grass in the foreground is Kentucky blue grass; the darker grasses on the distant hills are true prairie grasses.

precipitation (table 1). These data were kindly furnished me by Charles D. Reed, Senior Meteorologist, Des Moines, Iowa.

TABLE 1.
Climatic data for summer months at Lake Park, Iowa

Month	Record	Mean Monthly	Temperature		Total Precipitation
			Mean Minimum	Mean Maximum	
May	Normal	57.6° F.	45.4° F.	69.8° F.	4.02 in.
	1940	56.8	43.7	69.8	1.46
June	Normal	66.6	55.0	78.2	3.93
	1940	68.2	57.0	79.4	5.57
July	Normal	72.1	60.5	83.7	3.32
	1940	75.0	62.5	87.6	0.52
August	Normal	69.4	57.5	81.3	3.68
	1940	68.4	59.0	77.7	4.00

During the nesting season of 1940, it is evident, temperatures were approximately normal, but the precipitation fluctuated, being far above normal in June and August and well below normal in May and July.

Bird Population.—Group A in table 2 lists the population of strictly prairie species, that is, those species that passed practically all their breeding season in the prairie itself and depended on it for nest sites, food, and shelter. It may be a surprise to see the Ring-necked Pheasant included here, but it appeared to have some of the habits of a prairie bird and may be thought to occupy now the niche formerly taken by the Prairie Chicken (*Tympanuchus cupido*). However, after the young hatched they were usually conducted into the wooded ravines and forest-edges.

In addition to those species that both nested and fed in the prairie there are those that nested in the near-by forest-edge or marsh but did most of their feeding in or over the prairie (group B). All species listed, except the Kingbird, ranged over an area larger

than these fifty acres. Mention might be made here also of a single female Mallard (*Anas platyrhynchos*) with a newly-hatched brood of young that was found in a nest in the middle of the area. Probably its presence depended on the near-by lake and marshes.

A third group of species includes those that occurred in the forest-edge and along stream and lake margins (group C). The forest-edge is formed by the inter-penetration of forest and prairie. These birds commonly both nested and fed in this transition area or at least did not penetrate into either the prairie or forest to any great extent, although they occurred elsewhere in more open seral stages leading up to a climax forest. The Crow's habits were somewhat different from those of the other species listed, in that it

TABLE 2.
POPULATION OF PRAIRIE BIRDS ON FIFTY ACRES
Group A. Species that both nested and fed on the prairie

	NUMBER OF BIRDS
Bobolink, <i>Dolichonyx oryzivorus</i>	16
Grasshopper Sparrow, <i>Ammodramus savaannarum</i>	16
Ring-necked Pheasant, <i>Phasianus colchicus</i>	14±
Western Meadowlark, <i>Sturnella neglecta</i>	6
Group B. Species that nested elsewhere but fed on the prairie	
Barn Swallow, <i>Hirundo erythrogaster</i>	5±
Purple Martin, <i>Progne subis</i>	5±
Kingbird, <i>Tyrannus tyrannus</i>	2
Sparrow Hawk, <i>Falco sparverius</i>	2
Marsh Hawk, <i>Circus hudsonius</i>	2
Short-eared Owl, <i>Asio flammeus</i>	1
Group C. Species confined chiefly to the forest-edge	
Yellow Warbler, <i>Dendroica aestiva</i>	18
Alder Flycatcher, <i>Empidonax traillii</i>	4
Crow, <i>Corvus brachyrhynchos</i>	2
House Wren, <i>Troglodytes aëdon</i>	2
Catbird, <i>Dumetella carolinensis</i>	2
Song Sparrow, <i>Melospiza melodia</i>	1
Group D. Species confined chiefly to seral communities	
Yellow-throat, <i>Geothlypis trichas</i>	8
Red-winged Blackbird, <i>Agelaius phoeniceus</i>	2

commonly fed in the surrounding farmland. Additional species occurred in seral stages of the prairie and confined both their nesting and feeding to these communities (group D).

Of strictly prairie species (group A) the average population amounted to only 1.0 bird per acre. If all species are included that use the prairie either for nesting or feeding, the population is raised to about 1.4 birds per acre. If the population is based on species found in all habitats associated with the prairie, the average population is increased to 2.2 birds per acre.

Undoubtedly if a much larger area could have been included in this study a somewhat greater variety of species would have been listed. Burrowing Owls (*Speotyto cunicularia*) are reported to have occurred formerly in this area but are now absent. In the near-by Montgomery prairie, a brief half-day census of about 150 acres of an unplowed area that is annually cut for hay and is dominated almost exclusively by *Stipa spartea* revealed the Bobolink as the most numerous species; pheasants, Western Meadowlarks, Grasshopper Sparrows, three Upland Plovers (*Bartramia longicauda*) and a pair of Savannah Sparrows (*Passerculus sandwichensis*), the latter near the margin of a slough, also were noted.

Clements and Shelford (*loc. cit.*) list as strictly prairie birds of this association the Prairie Chicken, Eastern Meadowlark (*Sturnella magna*), Dickcissel (*Spiza americana*), Field Sparrow (*Spizella pusilla*), and Horned Lark (*Otocoris alpestris*). Inclusion of the last four species needs qualification. The transition from the range of the Eastern to the Western Meadowlark is somewhat gradual. The eastern species predominates east of the Mississippi River where it appears in the tall grass prairie and in grassy seral stages of the deciduous forest. West of the Mississippi River the Western Meadowlark assumes a more important role and at least in the northern part of the True Prairie is almost exclusively the species present. Dickcissels were common in the general area, but none occurred in the prairie under study. The impression gained was that this species belonged not to climax prairie but to seral stages with sparser vegetation and to disturbed areas resulting from agricultural practices. No Field Sparrows were observed except one pair several miles away that had a nest in a low bush. It is a forest-edge species and is not typical of climax conditions in the True Prairie. Horned Larks were observed in the neighborhood but not on the study area. Their breeding season begins early in the spring, and no nests were found in this summer study. Observations of their occurrences indicated that their habitat relations may be similar to those of the Dickcissel. Studies in several areas of course are desirable before a list of typical species in this prairie community can be drawn up with any degree of certainty.

Territorial Relations.—Some attempt was made to study the territorial interrelations of these birds even though mating was already nearly complete and nesting well begun by the time the study was started. Maps were prepared showing the location of nests or territories of each species.

Two nests of the Western Meadowlark were found (fig. 41), both with eggs at the time. The first nest with six eggs was well concealed in *Poa pratensis* under a clump of *Solidago rigida*. The eggs hatched June 20 but the young were gone on June 29, and probably had been destroyed. The second nest was under a tuft of *Andropogon* and had a tunnel a foot long, slightly curved, leading to it. The eggs hatched July 4, and two of the four young successfully left on July 15 or 16. Possibly there were earlier nesting attempts than these reported.

Territorial behavior is well established in this species, although only the male defends the territory. At least two variations of song were given from singing posts, and a song was given occasionally while flying. Flight songs were not so frequent as one might expect. Possibly they were given more often during the earlier mating season. Most of the singing was from fence or telephone poles or from tall weeds or small trees. The song served as an advertisement to other males that the area was occupied. When another meadowlark encroached on the area or simply flew high over it, the male met the challenge and gave chase until the intruder passed the limits of the owner's jurisdiction. The females, on the other hand, were at no time observed to be concerned about territorial boundaries.

As soon as nesting was over, the meadowlark territories were no longer defended, and singing ceased except for occasional outbursts. Through July six to a dozen or more meadowlarks were seen frequently in the evenings as they went to roost in the grass within the former territory of the male of nest No. 1 or in other parts of the area. Male No. 1 was not a member of this group; his tail had been clipped for recognition purposes. These birds did not roost on any perch above the grass cover. Although they could not be observed at very close range, it appeared that they passed the night on the ground under some clump of grass, where they were relatively well protected. During the day they fed in the near-by prairie or more frequently in areas outside of the tract under study.

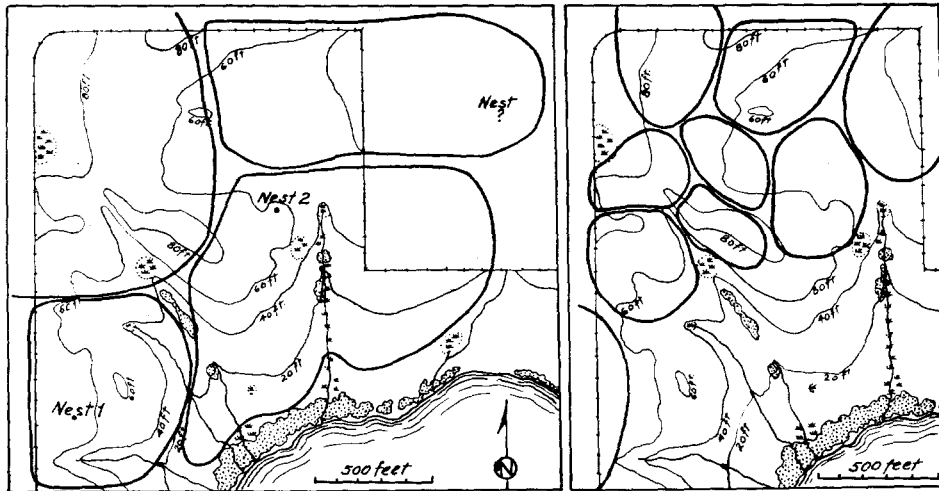


Fig. 41. Territories of the Western Meadowlark.

Fig. 42. Territories of the Grasshopper Sparrow.

In computing the bird population only three pairs of meadowlarks were counted for the area although four territories were represented. Three of the four territories extended well outside the area under study. The male at nest No. 1 had the smallest territory of approximately 10 acres. The male at nest No. 2 at various times maintained rights over about 24 acres. The other two territories were about 21 and 32 acres, respectively, as near as could be estimated.

As is evident in figure 42, Grasshopper Sparrows were largely confined to the northern part of the area where the prairie grasses were better developed. None was observed at the lower elevations nearer the lake where blue grass predominated. Less time was given to work with Grasshopper Sparrows. No nests were found, although adult males were seen defending territories, heard singing their inconspicuous song from the top of weed stalks, and adults were seen carrying food presumably to young. The approximate territories were marked out on the basis of repeatedly observing birds in the same places on different days. The average size of the six territories shown is 3.4 acres.

Ten nests of Bobolinks were found, all containing young birds at the time and probably representing all the nests of this species in the area. Five of the nests were well concealed in the base or under clumps of *Andropogon* grass, four nests were in *Poa pratensis* and were not so well concealed or protected from the sun, and one nest was under *Stipa spartea*. Of seven nests not unduly disturbed by human interference, four had their young leave successfully after ten or eleven days in the nest. There were ten females here, but evidence for no more than six males, with polygyny strongly indicated. The male at nest No. 1 (fig. 43) was frequently present also at nest No. 7 about 200 feet away, although he was only seen to feed the young at No. 1. He was recognized by the characteristically clipped tail given him when caught at nest No. 1; no other male was seen around nest No. 7. Nests number 9 and 10 were separated by only 44 feet and the male appeared equally concerned for both nests, although he was observed feeding young only at number 9. No other male was seen here. When nest number 4 was found, one male and three females became excited; possibly the females were those from this nest and from 5 and 3. It was also characteristic at both 1 and 9 that both females responded to the alarm call of their common mate. When the female was captured at nest 4, she

deserted, and the male attempted to raise the young in this nest alone, devoting all his attention to them, but he failed. During this period no other male was observed at nest 5 or at nest 3. Nest 5 was roughly 150 feet from nest 4 and 470 feet from nest 3. Nest 3 seemed rather far removed to belong to the same male as nests 4 and 5. However, mere nearness of nests to each other is not evidence that they belong to the same male, as

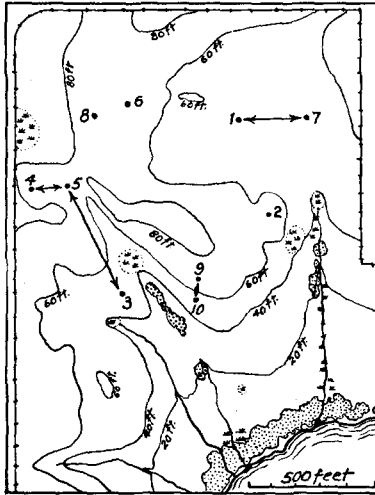


Fig. 43. Locations of nests of the Bobolink. Arrows join nests belonging to the same male.

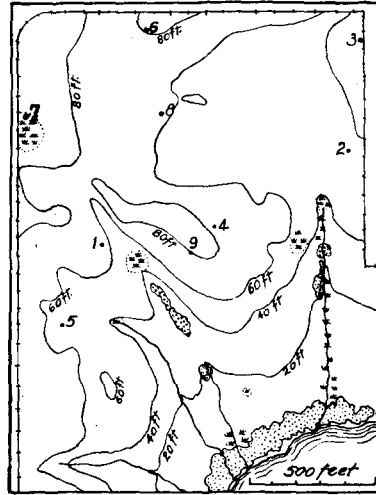


Fig. 44. Locations of nests of the Ring-necked Pheasant.

nests 6 and 8, which were only 180 feet apart, certainly belonged to different males. All attempts to prove that the same male was simultaneously associated with two or more nests by capturing them at each nest were unsuccessful. Failure resulted because the young were fed regularly by a male at only one nest and because of the high nest mortality. Polygyny is well known among some other members of the Icteridae, but to prove it definitely for the Bobolink would require study during the actual mating period.

Notable in this species was the lack of territorial defense by either the adult male or female. If these birds establish a territory at all, it must be only for the mating and early nesting period. The fairly good spacing of the nests over the area would indicate that they may establish territories during the period when nests are started, but certainly after the young are hatched there is very little evidence for their continued maintenance. Although the males sang from tall stalks of grass or forbs while aiding the female in feeding the young and also sang during flight, the singing was neither frequent nor vigorous except when the bird became excited or alarmed as, for instance, when I approached the nest. Furthermore, the males were by no means confined to the neighborhood of their nests. On several occasions different males were observed to rise high into the air and fly straight away for a half mile or a mile, well beyond the range of 8x glasses. Then after a time the birds would be found back at their nests. Lack of territory was also manifested by the tolerance of other males close to the nest. This was often noticed; once two foreign males were observed near the nest with the male who owned it disregarding them. Frequently when a male from a neighboring nest left to procure food, he would stop temporarily near the nest of the male under observation before proceeding onward. These males usually did not sing or call during their visits.

Nine nests of the Ring-necked Pheasant (fig. 44) were found on the area. Each was possessed, no doubt, by a different female, but the number of males could only be guessed. Males were frequently heard or seen; certainly there were less than nine. Excrement was commonly seen all over the area, and isolated eggs were frequently found. Nothing could be ascertained concerning territorial relations in this species, although the regular spacing of the nests suggests a possibility that territorial relations of some sort exist at an earlier period.

Although only nine pairs of Yellow Warblers can be counted for the prairie area under study, a total of 34 nests were seen around the laboratory grounds, and certainly not all the nests were found. In figure 45 certain nests and territories to the east of the prairie area are also shown, as they were subject to special study. Of 21 nests, 2 had three eggs or newly hatched young birds, 12 had four eggs or young, and 7 had five eggs

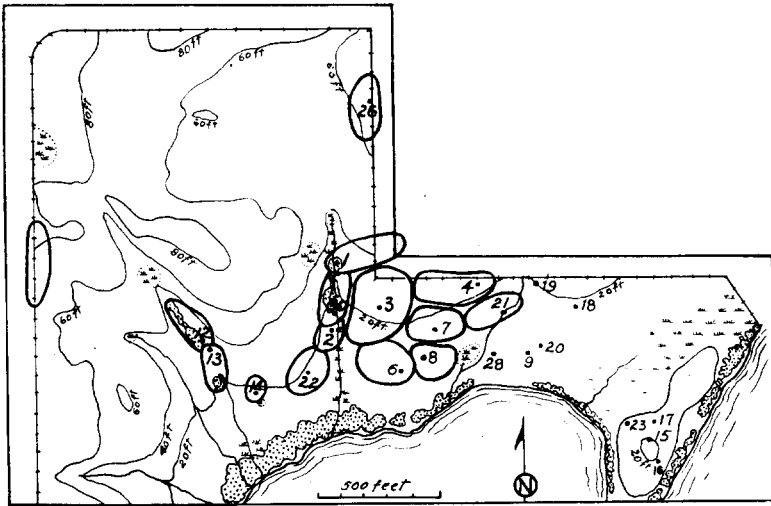


Fig. 45. Locations of territories and nests of the Yellow Warbler.

or young. Three nests were double in that a second nest was built over the first one which contained a Cowbird egg as well as the warbler eggs. In no instance did the warbler lay another set of eggs in the upper nest. Yellow Warblers here do not have a second brood, and there is some question whether the female will lay again in event the first egg-laying cycle is interrupted or the first nest destroyed. An adult, in some cases certainly the male, was observed a number of times to persist in the vicinity of the nest for several days and even to defend the territory, although no progress was made in re-nesting. When nesting was over, the birds disappeared rapidly, and only a few scattered birds remained after the end of July. The nests were made in large part of the dry and shredded outer fibers of previous year's stalks of milkweed (*Asclepias* sp.), and probably also Indian hemp (*Apocynum* sp.), which plants were readily available in the vicinity. Twelve out of sixteen nests, where data were reasonably satisfactory, had at least some of the young leave the nest.

Twenty out of twenty-nine nests were placed in buckbrush, with the rest in box elder, lilac, willow, or currant. The buckbrush is a low bush usually three to four feet high, growing in rather dense thickets in the open, especially in grassy areas of *Poa* and *Agropyron* (fig. 46). Nests placed here varied between two and three feet above the

ground. The nest found closest to the ground (18 inches) was, however, in a small box elder. In taller shrubs and trees, the nests were found up to about seven feet above the ground. Strangely, no nests were located in willows on the shore of the lake. Some nests were found in isolated buckbrush thickets only a few feet square, while in one large thicket, 180 by 120 feet, two nests were situated in opposite corners. Size of the thicket seemed not to be a limiting factor in the selection of a nest-site. Many thickets both smaller and larger than ones with nests did not contain any. The age of the bush did seem to make a difference. During the first year or two the plant shoots straight up, but in later years numerous side branches develop which later also turn upwards so that vertical crotches between the branches make secure nest-sites. With one or two exceptions, brush less than five or six years old was not used. Furthermore, the density of the thicket was important, but this was a function not so much of its size as of its age. Thickets that were open, with the individual shrubs widely spaced, only rarely contained nests. Cover for concealing the nest was therefore a factor.

These warblers possessed territories that averaged about 150 feet in diameter, or approximately two-fifths of an acre. Even in locations where trees were included, the territories appeared to be of about the same size. The limits of the territory often did not coincide with the boundaries of the thicket in which the nest was located but extended over the neighboring grassland and often included parts of neighboring thickets. These territories were defended by the males partly by singing, although in shrubby areas lacking trees (fig. 46) they were handicapped by lack of singing posts from which to proclaim their ownership and to advertise themselves. A few made use of fences from



Fig. 46. Nesting area of the Yellow Warbler east of the prairie and looking south across Little Millers and Millers bays. Note patches of buckbrush in foreground in which birds nested and forests in background where they frequently went to procure food.

which to sing and also of tall posts and wire from an abandoned electric line that extended through this area. The role of the female in defense of territory was not determined.

Probably due to this lack of singing posts and to the unusual abundance of birds, chasing was also extensively used as a defense measure, and during the height of the nesting season squabbling birds were a common sight all over the area. At times it was suspected that much of the chasing was after the bird's own mate, although this could

not often be verified as the individual identity of the shifting birds was very difficult to ascertain. Neighboring males seemed to lack any conception of the limits of each other's territories and moved about indiscriminately until chased out. No actual fighting was observed. The resulting confusion may be laid to the inability of the birds clearly to define the limits of their territories by singing, which was not possible for lack of singing posts of suitable height. In other parts of the area where trees were available, the males commonly sang at a height of 18 feet, often up to a height of 45 feet, and chasing was not often observed.

Another cause for confusion was the lack of typical areas for feeding within the territorial boundaries. This species ordinarily gets most of its food in trees and taller shrubs similar to those from which it sings. Since such shrubs and trees were lacking in their territories, the birds regularly left for feeding. Occasionally they were seen to dart down into the grass, and they obtained some food from the buckbrush, yet this was not sufficient. Commonly they went to the willows, 400 to 600 feet away at the edge of the lake. The birds from nest 26 (fig. 45) were observed going in that direction, 1200 feet away. Sometimes birds did not stop at the lake margin but went on, flying across Millers Bay, to a bur oak forest on the opposite shore. This was regularly observed; it involved a round trip of at least 3200 feet, three-fifths of a mile. Certainly they did not go so far for every morsel they fed the young, but the male at nest No. 4 was seen to do so twice in fifteen minutes of observation, making each round trip in about five minutes. Frequently, although not invariably, these birds on their outward journeys mounted high into the air to fly over the intervening territories of other birds. Even then they were often chased, but less frequently than on their return trips, when laden with food and at the end of the long flight they passed low over neighboring territories to reach their own. This behavior added to the confusion of territorial relations and explained much of the chasing and competition so frequently observed. In adjacent areas where a sufficient number of trees or tall shrubs were available the birds were more nearly confined to their territories, and these long journeys were not observed. Where all requirements for nesting are not found in any one area, this species appears capable of modifying its behavior to make the best of conditions available.

Discussion.—This report cannot be considered to give a true picture of bird conditions in the pristine prairie until similar studies can be carried out in other relic areas, preferably of larger size. The great abundance of *Poa pratensis* in this area introduced a modifying factor. True prairie species of grasses were not present in their proper abundance, proportions, and position. Some of the ground, now covered by *Poa pratensis*, may originally have been bare space between the prairie bunch-grasses. Likewise the thick layer of dried grass covering the ground is probably not normal for primitive conditions. The Dickcissel, Horned Lark, Lark Sparrow (*Chondestes grammacus*), and other species might have occurred if the grass cover had not been so dense and continuous. Likewise the pristine modifying influences exerted by trampling bison and antelope, and the burrowing of pocket gophers and badgers, may have produced conditions favorable for other species to nest. Such habitats are now better found in certain farmland and on roadsides. Since they result from human influence, they are difficult to fit into the picture of what original prairie looked like.

When the exact habitats of different species are found and their abundance in each determined, the next question that arises is why each species is restricted to particular places. How the prairie is used by strictly prairie species has been indicated. These uses seemed easier to determine than in the case of such forest-edge birds as the Yellow Warbler. When analysis of special features required in the habitat is carried back far enough,

it leads into the physiology of the bird and to questions of innate behavior. For example, the young of Bobolinks and meadowlarks occur in grass nests on the ground and are not attacked by the abundant biting ant (*Formica cinerea neocinerea*) until they die or become weakened as by lack of food. However, when nestling Yellow Warblers were placed in a trap on the ground for short periods of fifteen to thirty minutes, they were quickly attacked. Is this one reason the Yellow Warbler does not nest on the ground? What gives the active young of ground-nesting species protection? Many prairie species have flight songs which compensate for lack of singing posts, and they commonly sing from low perches close to the ground. Why does the Yellow Warbler require a song post eighteen feet or more above the ground? The simplest explanation and perhaps a proper one is that it is due to behavior patterns inherited from the past and developed through evolution; but this only begs the question, since it leaves unexplained why and how the peculiar behavior patterns were evolved.

SUMMARY

The size and territorial relations of a bird population was studied on a fifty-acre tract of True Prairie in northwestern Iowa belonging to the *Stipa-Antilocapra* Biome.

Four species were mostly confined to the prairie for all their activities, six species nested in the forest-edge or marsh but fed largely in the prairie, six species were largely confined to the forest-edge, and two species occurred only in seral stages of the prairie.

The four most typical prairie species averaged 1.0 bird per acre in abundance, but if all species that used the prairie to at least some extent be included, the population is raised to 2.2 birds per acre.

The Western Meadowlark and Grasshopper Sparrow had well-defined territories, averaging in size about 22 and 3.4 acres, respectively. The Bobolink and Ring-necked Pheasant appeared not to possess territories after mating had been completed, and there is evidence that both species were polygynous.

A special study of the Yellow Warbler indicated that territorial requirements included suitable nest-sites, concealing cover, tall singing posts, feeding areas in trees, and space, and that when certain of these factors were lacking, territorial relations became confused and the behavior of the birds was modified.

University of Illinois, Urbana, Illinois, March 29, 1941.