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NON-BREEDING SURPLUS AND POPULATION STRUCTURE OF THE RED-WINGED BLACKBIRD (*Agelaius phoeniceus*)

by

Louis Joseph Laux, Jr.

A dissertation submitted in partial fulfillment
of the requirements for the degree of
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ABSTRACT

NON-BREEDING SURPLUS AND POPULATION STRUCTURE OF THE RED-WINGED BLACKBIRD (Agelaius phoeniceus)

by

Louis Joseph Laux, Jr.

Co-Chairmen: Frederick E. Smith and Francis C. Evans

Non-breeding surplus in a territorial passerine was investigated by selectively removing territorial adult male Red-winged Blackbrids from several small marshes during several nesting seasons. A large number of the population, both within the removal marshes and in the surrounding marshes, were individually marked by color-banding, and included both sexes and all age classes. Observation of replacement of removed males and of the individually marked birds yielded data on density, survivorship, age specific production, nestling sex ratio, breeding sex ratio, male age class ratios, and dispersion. The data are discussed and formulated into a proposed hypothesis for the population structure of this species during nesting as follows: 1) Males select a breeding home range during the subadult year, possibly earlier, to which they return as adults and within which they seek territory. 2) Subadult males are for the most part behaviorally incapable of breeding regardless of availability of habitat. 3) All yearling females probably do breed, but may lay fewer eggs on the average. 4) During breeding season approximately 1/2 of the adult males are territorial and breeding and 1/2 are non-breeding. 5) Subadult males occur in numbers approximating 1/2 - 2/3 the total adult male population. 6) At nesting the total of females, all of which nest, equals the total of males, which includes the breeding males, the excluded adult males and the subadult males, thus accounting for the degree of polygyny

in the nesting population. The study suggests but does not directly document the inferences that 1) the non-breeding males, including subadults, are organized within the territorial structure of the nesting population, and that 2) the exclusion of potentially breeding males is probably not a major factor in regulating the population size of this species.

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INTRODUCTION

Studies of territorial species of birds, especially those of passerine birds, suggest that not all adult members of the population have access to the breeding habitat during the breeding season. The life of these individuals is generally unknown but their existence is most strongly indicated by the recurring observation that vacancies created by mortality of breeding individuals are frequently filled. Probably the most dramatic demonstration of replacement was recorded when an attempt was made to remove by shooting all birds from two small areas of coniferous forest as a means of assessing the role of bird predation upon a spruce-budworm outbreak (Stewart and Aldrich, 1951; Hensley and Cope, 1951). Replacement of all of the original 27 territorial species removed, some of them several times over, assured failure of the experiment, but provided convincing evidence for the probable existence of non-breeding surplus adult birds. Likewise, many investigators working with breeding bird populations, particularly when banding was done, become aware of apparently surplus adults which appear when breeding individuals are either lost or temporarily displaced, i.e. banding, etc. (Moffat, 1903; Michener and Michener, 1935; Nice, 1937; Erickson, 1938; Kendeigh, 1941; Lack, 1946; Southern, 1950; Nero, 1956; Snow, 1956). Orians (1961) discovered available replacement adult male Red-winged Blackbirds (Agelaius phoeniceus) when he removed territorial males from two small marsh areas. In this case replacement spanned a two month period, and the adult replacements numbered several times the original territorial populations.

The evidence that replacement individuals actually are non-breeding surplus remains inferential, though several authors have cited the phenomenon as evidence for territory functioning as a density limiting factor (Orians, 1961; Wynne-Edwards, 1962). Though it seems unlikely, even the dramatic demonstrations involving the spruce-budworm outbreak

and Orian's removal experiments could not preclude the possibility that the replacements merely represent shifting territorial individuals. Moreover, for most breeding bird studies territory is the primary basis for recognizing and marking individuals. Individuals not on territory generally go unnoticed. Therefore, a conservative view regarding the existence of surplus potentially breeding individuals as an expected component of territorial populations has prevailed (Nice, 1941; Lack, 1954; Hinde, 1956; Lack, 1966).

Two patterns have emerged from the replacement phenomenon. First, if replacement is to occur, it does so rapidly. This has been specifically noted by Southern (1950), Shannon (1958), and Orians (1961). Orians stated that several times he observed "a replacement to occur within an hour" and on one occasion within fifteen minutes. In fact, the rapid replacement of lost territorial individuals is one of the best reasons for believing the replacements to be surplus, and literally "waiting in the wings". Second, males seem to be replaced more readily than females. In the study done by Stewart, et al. (1951), a total of 295 males of the 27 territorial species were removed and they were replaced by approximately 310 males. All of the species were represented in the replacements in at least one of the two years of the study. However, most species were not replaced by a number equal to their original territorial density, while some species were replaced several times over. By contrast for the 138 females removed only 43 replacements were subsequently removed. About one-half of the species were not replaced at all, and only two species were replaced in excess of the initial population of females. From the single species studies a similar but far less extensive pattern emerged. Males were mostly replaced whereas females were often not replaced. Orians' experiment involving removal of males only also suggested a large reserve for male replacement. However, the Red-winged Blackbird is polygynous, and an excess of males might be expected.

Another observation which may support the suggestion of excess males over females is the frequent occurrence of unmated males holding territories. Most studies report their presence. Some authors had reason to specifically discuss the phenomenon (Erickson, 1938; Haartman, 1956; Kendeigh, 1941; Mayfield, 1960; Verner, 1964), and in the Partridge (Perdix p. perdix) unmated males directly interfere with the territorial pairs and become a special feature of the breeding population (Black and Ash, 1956).

THE PROBLEM

The data suggesting that replacements are non-breeding surplus were obtained incidentally during studies of breeding populations. This study sought to make the replacement population the object of study. The purpose was to 1) affirm the existence of such a population under conditions which would preclude the possibility of territorial individuals expanding or changing territory, and 2) discover information regarding the dynamics of the replacement population prior to becoming replacements. The strategy was essentially an elaboration of the accidental procedures which suggested the existence of the surplus in the first place. Territorial individuals are selectively removed from relatively small and discrete subpopulations within a larger nesting population; but, in addition, sufficient numbers of birds are individually marked in the larger population to detect patterns of movement resulting from the removal experiments. The strategy required an abundant species, relatively easy to trap, and somewhat discontinuously dispersed during nesting by its habitat. For these reasons the Red-winged Blackbird was chosen.

Though the primary purpose of this study was to focus upon the replacement population, observations of an increasing number of marked individuals within the study area provided a basis for enlarging the objectives of the study.

Later analysis of the observational and recapture data, particularly those obtained for subadult males, when considered with the results of the removal experiments, suggested a hypothesis for the population structure of the Red-winged Blackbird. However, the results of the removal experiments are presented separately and first, followed by the results and analysis of the observational data. The observational data are presented by sex and age-class.

As might be expected no species is without its special features. The Red-winged Blackbird poses two problems requiring modification of the strategy of removal. The species does have a recognizable yearling (subadult) male, which does not ordinarily participate in nesting. However, subadult males have been reported as capable of spermatogenesis (Wright and Wright, 1944), and in rare instances nesting (Beer and Tibbits, 1950; Nero, 1956). Are the subadult males potential replacements, and therefore, part of the non-breeding surplus? To investigate this possibility removal of males was done until only subadult males remained, but the subadult males were not removed in order to discover their capabilities at maintaining a breeding stance in the absence of adult males. The second problem is that of polygyny. Surplus females would not be expected. Removal, therefore, was initially of males only with female removal deferred. One attempt was made to remove females. For purely logistical reasons it proved impossible to remove all the nesting females at one time, and further attempts were abandoned. This study is limited to male removal only.

THE SPECIES

The Red-winged Blackbird is one of the most abundant native North American species, and probably one of the best studied. Its life-history is well known (Allen, 1914; Mayr, 1941; Wright and Wright, 1944; Campbell, 1948; Mehner, 1950; Bent, 1958; Macklin, 1958; Orians, 1961;

Frankhauser, 1964), and it has been specifically studied with respect to passerine behavior (Beer and Tibbits, 1950; Nero and Emlen, Jr., 1951; Nero, 1956; Orians and Collier, 1963; Orians, 1968), population dynamics (Smith, 1943; Meanley, 1961; Case and Hewitt, 1963; Meanley and Webb, 1963), sex ratio (Herman, 1938; McIlhenny, 1940; Williams, 1940), growth and development (Nice, 1950; Selander and Giller, 1960; Strosnider and Gleason, 1960), nestling survival (Young, 1963), and energetics (Brenner, 1966; 1968). A brief resume of the life-history is given here to acquaint the general reader with the species as well as to point up information relevant to this study.

The Red-winged Blackbird is a strikingly dimorphic, strongly territorial, polygynous migratory icterid whose ancestral nesting habitat appears to have been marshes of all kinds (Bent, 1958). In recent years the species has been found in increasing numbers nesting extensively in agricultural hay fields throughout its range and, presumably as a result of this addition to its nesting habitat, has reached pest proportions in some parts, particularly in the midwest. In addition to sexual dimorphism there is also the recognizable yearling male, as noted earlier. The yearling female, which is not known to be morphologically distinguishable from the older females, probably does nest.

The species winters mostly in the southern United States and in Mexico, and begins its northern migration in early February. The males precede the females, and in southern Michigan the males begin arriving at the nesting areas toward the end of February and into early March. By late March into early April territories are generally established and the first females are on territory. The arrival of the females, however, is spread over several weeks with new females still appearing in territories as late as early May. A male may have from one to eight females, and in this study the most common ratio recorded was three females to one male (31%). Nesting within a territory is usually asynchronous, with the

first nests started as early as the middle of April. Nest building to fledging usually spans just over a month and the first fledglings may be found as early as the third week in May. Though some females are probably double-brooded (Frankhauser, 1964), the species appears to be characteristically single-brooded with fledgling production usually peaking toward the end of May and into the first week of June. Nesting may continue into early August, largely by females renesting after the loss of an early nest or nests, and probably to a limited extent by females raising a second brood. By the middle of August virtually all nesting activity is finished. Beginning in early July flocking gradually replaces nesting until all the birds are associated in large flocks by late August. Migration, however, does not begin until late October and early November. During the interim the birds feed by day in flocks, and return nightly to very large regional roosts.

The Red-winged Blackbird appears to be colonial. Polygyny and the marsh habitat tend to create relatively dense and somewhat discrete subpopulations dispersed over the landscape. Within these marsh groups there is a very strong territorial structure as well as cooperative behavior involving warning calls and ganging when danger threatens. In the hay field habitat the birds tend to saturate the habitat, thus dispersing more widely and more continuously, suggesting that the apparent colonial behavior may be more a by-product of habitat and polygyny. Advantage, however, was taken of the apparent colonial nature of the species in the establishment of areas from which individuals would be removed.

STUDY AREAS

The wetlands of Michigan have been inventoried and divided into five zones based upon vegetation, topography, soil, climate, and land use (Panzner, 1955). This study was

done within the region designated zone A (Fig. 1), the southern half of the lower peninsula excluding the eastern lake bed plain. The landscape of this zone is described as running "from smooth and rolling plains to morainic highlands characterized by rounded hills, short drainage hollows, basin depressions, lakes, and swamps" (ibid.). The drainage hollows, basin depressions, and swamps are common and support a full complement of emergent vegetation from sedges to deciduous and coniferous trees (Tamarack and some Arborvitae).

The first study area (Study Area I), abandoned after the first year because of farm activities, was located on a farm about three miles northeast of Ann Arbor, Michigan. Marshy areas were scattered throughout the farm, typically drainage hollows and basin depressions. All but one of the areas was characterized by dense stands of cattails with a border of willows (mostly small) and deciduous shrubs. Within this complex of marshes a small marsh of approximately one acre was selected for removal experiments and designated Experimental Marsh A. (Fig. 2).

After the first year Study Area II (Fig. 3) became the location for the remainder of this study. The area is located about 25 miles northwest of Ann Arbor within the Pinckney Recreation Area (Livingston County). This second study area included a section of the E. S. George Reserve, a wildlife reserve managed by the University of Michigan. Again many marshes are scattered throughout the area but there is much less agriculture, and the marshes have a more diversified vegetation, including most of the types of marsh and swamp habitats possible in southern Michigan. Two marshes, one about an acre and very similar to Experimental Marsh A and the other about two acres, were utilized for removal experiments and designated Experimental Marshes B and C respectively (Fig. 2). Both marshes were characterized by a dense stand of cattails, and among the surrounding trees and shrubs were some large deciduous trees.

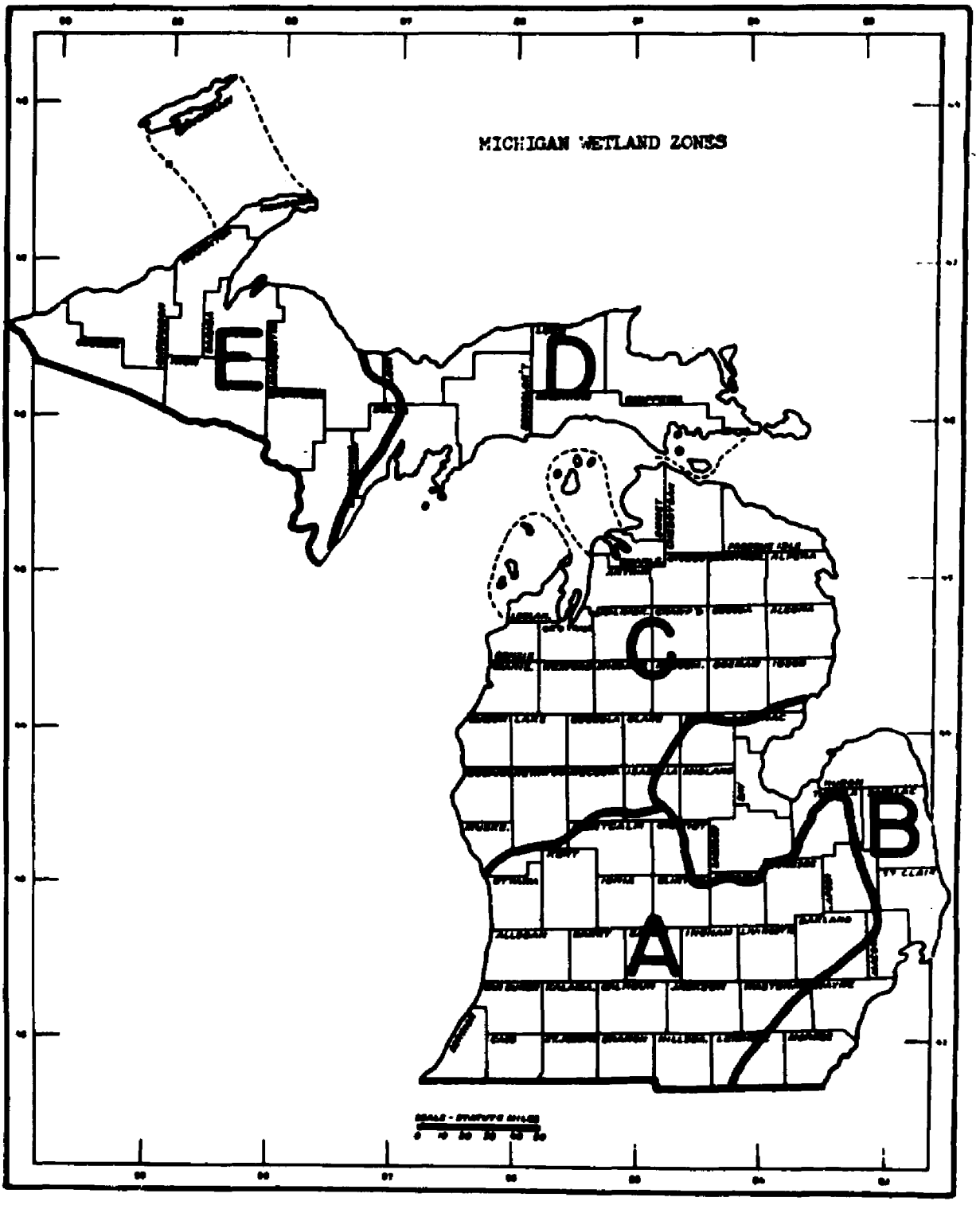

Fig. 1 MICHIGAN WETLAND ZONES (from Panzner, 1955)

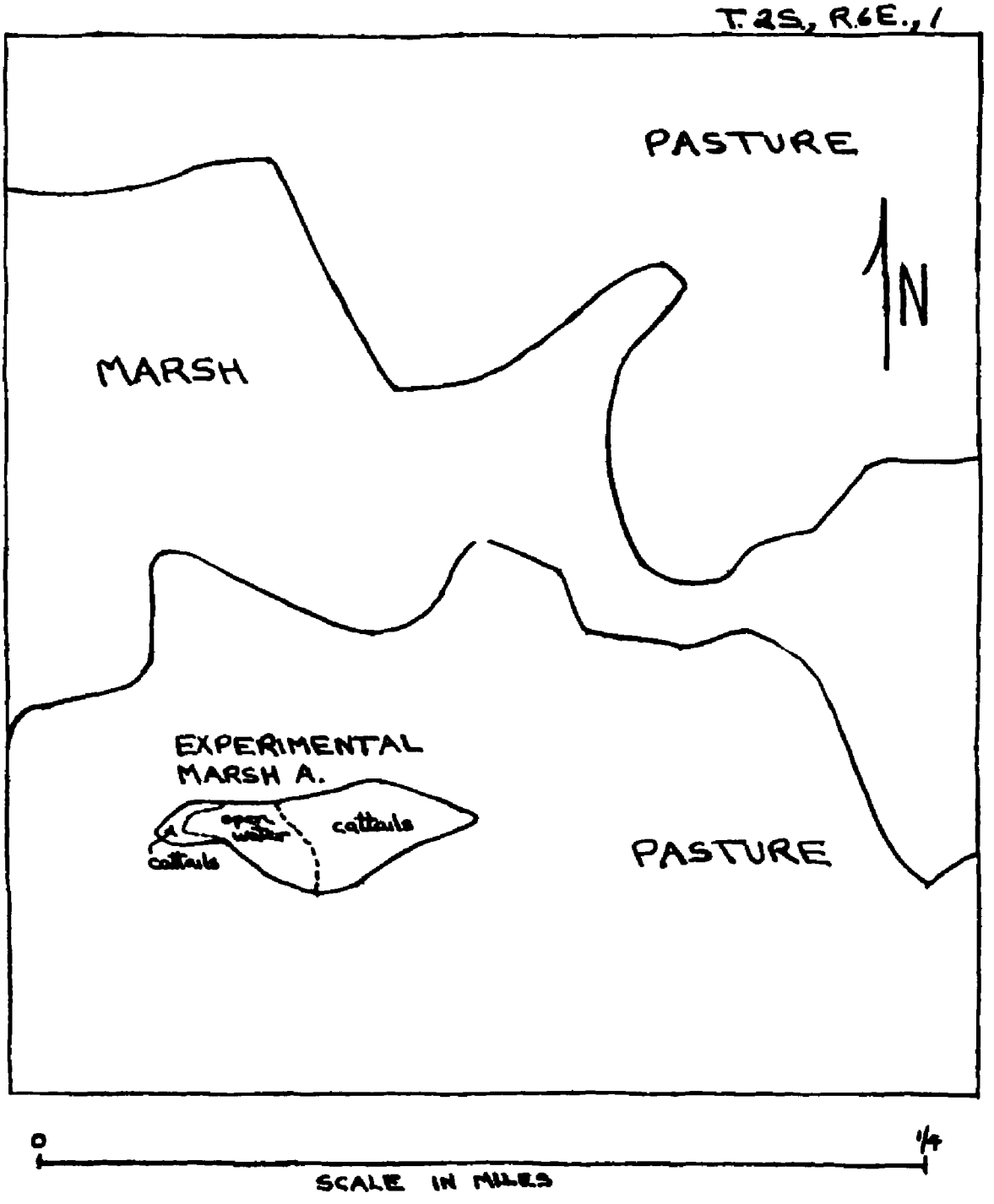

Fig. 2 STUDY AREA I

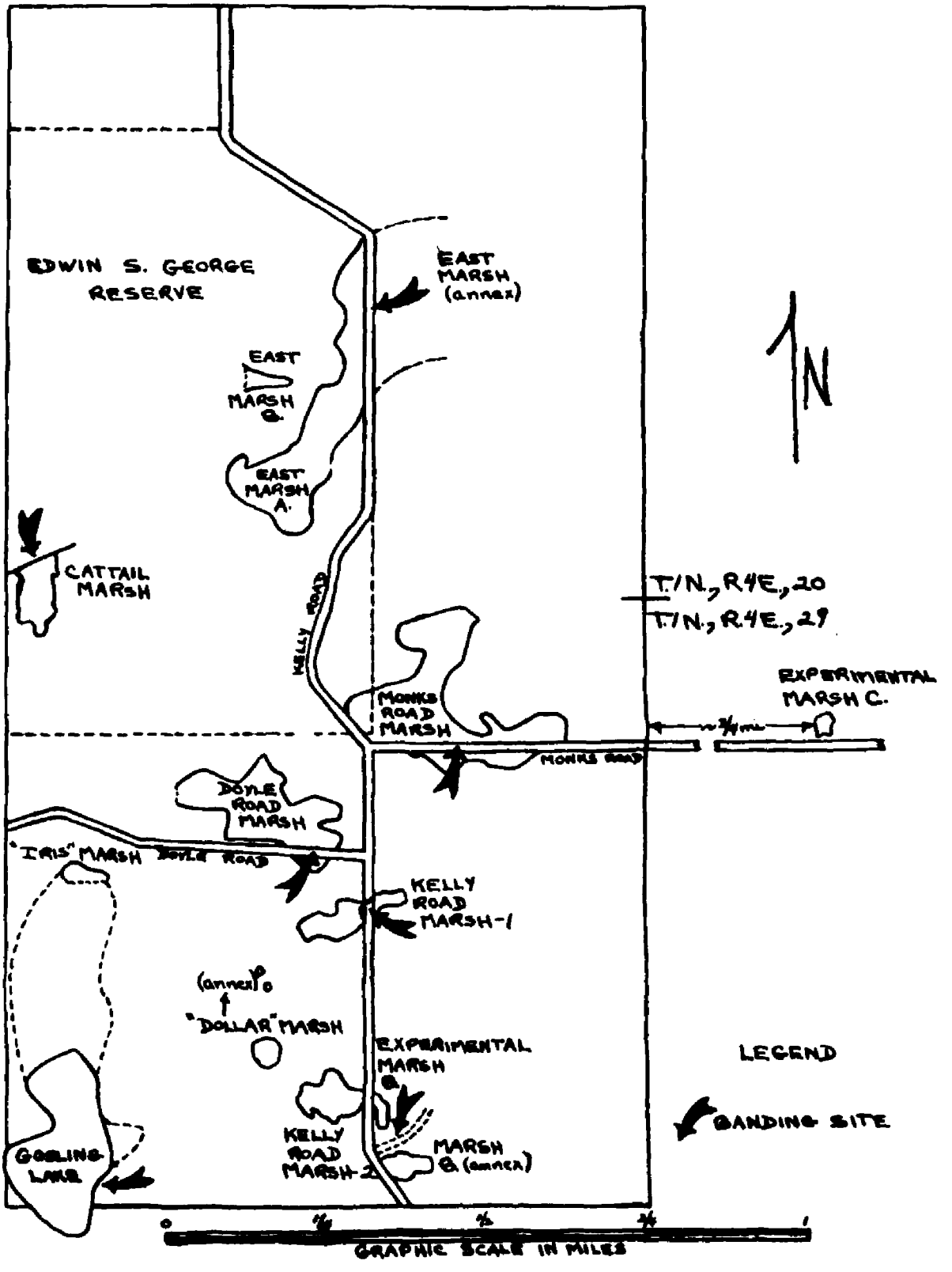

Fig. 3 STUDY AREA II

METHODS AND MATERIALS

General: The field schedule for this study required three major activities: trapping and banding; observation; and removal of adults and other manipulations with the experimental marshes. A typical day's schedule was as follows:

Dawn to mid-morning:

1) trapping and banding or
2) removal followed by observation of the experimental marsh or
3) observation of an experimental marsh on subsequent days or
4) observation to locate nests, confirm territorial males in marshes near the experimental marshes, and study flocks for marked individuals and patterns of movement.

Mid-day:

1) nest hunting,
2) banding of nestlings,
3) trapping of especially sought individuals,
4) and observation of experimental marshes.

Late afternoon to dusk: the morning schedule repeated. The data were collected during the years 1958-62. The field work for 1958-61 spanned the entire nesting season; in 1962 only a couple of week of field work during May and June were possible, thus effectively terminating the study.

Each of the three major field activities, trapping and banding, observation, and removal of adults, are described separately. The removal procedures constitute a somewhat novel approach to collecting field data. Also, because the approach was unorthodox, the removal procedures were usually modified in successive removal experiments; thus, some discussion of results is included in the description of methodology.

Trapping and Banding: For this study recognition by sight of individual members of the population was crucial.

This was achieved through color-banding. In addition to the U. S. Fish and Wildlife Service aluminum band, each adult male, female, and subadult male carried two or three coiled plastic color-bands. A system of color combinations was designed based upon the availability of eight different colors and the government band, which actually served as a ninth color. No more than two bands were placed on a leg. Juveniles, mostly captured from flocks in the late summer to early fall, carried but one color-band and the government band, and large numbers of individuals banded over a period of several days at one banding station carried the same combination. However, because of an on-going trapping program, juveniles were retrapped in subsequent years and were rebanded with individual combinations. Nestlings were only government banded. If captured subsequently, either as juveniles or older, they were color-banded according to their age. Loss of color-bands was minimized by laminating with acetone the free end of the plastic coil to the rest of the band. This proved very effective, except in cold weather. When lost color bands were suspected, or no color bands observed, three methods of confirmation were employed. Only rarely did an individual lose all its color bands; therefore, a history of observation of the individual coupled with some attempt to have similar combinations dispersed throughout the study area, usually precluded a replacement with so similar a combination. It was then merely noted that the individual had lost a color band, and, when in the course of normal trapping operations that bird was recaptured, its combination was restored. If a bird had no color bands, then recapture of the specific individual was sought, usually successfully. Most frequently, these birds were banded as nestlings. If recapture failed, then as a last resort, the bird was collected by shooting. Fortunately, this was not often necessary.

The capture of other than nestlings was accomplished by several trapping techniques. The most common method was to set Potter-type and/or funnel traps over previously established

feeding areas baited with corn. Such areas were established both on land near the marshes, and on wooden platforms floated in the marshes (Nero, 1956). During the early spring and late summer to fall, a large number of individuals from the flocks, i.e. up to 50-75 during a single trapping period of approximately three hours, were caught by this method. Particularly sought males were occasionally trapped with an automatic bow net trap "baited" with a dummy female or male in a response eliciting position: the female in a pre-copulatory display and the male in song-spread display (Nero, 1956). Particularly sought females were frequently trapped with a Potter-type trap "baited" with their nestlings or with nylon snares placed upon their nests. Nestlings were banded from the sixth day of nest life up to fledging (eleventh day), usually between the eighth and tenth day.

It was not possible to trap all individuals within the study areas. The intensity of trapping was greatest in the experimental marshes. All males were usually banded, and, though it was not usually possible to capture all the females, all male territories were represented by banded females. Beyond the experimental marshes only part of the total population was banded. This was not a statistical sample, but reflected a) more intensive trapping, the closer the neighboring marsh to the experimental marsh; b) relative ease of capturing one individual over another, i.e. in the larger marshes birds occupying territories in the center of the marsh were less apt to be caught than those nesting along the edge of the marsh; and c) trapping in easily accessible staging areas, i.e. roadways, which were frequented by the large flocks during early spring, late summer, and early fall. Many of the adult males captured in the latter group were subsequently discovered on territory within the study area. It was assumed that should none of these marked males that were territorial in nearby marshes act as replacements for removed birds, then the replacements were other than nearby

territorial males. Many females were also trapped making it possible to also check the over-all tendency of females to move from one marsh to another.

Observation: Observations were made with both binoculars (8 X 40) and a spotting scope (20 X 60). The importance of these observations cannot be over-emphasized, particularly in Study Area II, where approximately 700 birds one year and older were individually marked during the four year period, 1958-61. To a large extent it was the analysis of these observations, particularly those of the subadult males, which expanded the objective of this study.

Removal of Adults: Since most of the territorial males to be removed were trapped and banded before their removal, trapping could not be relied upon as a method of removal. Therefore, removal of the males was accomplished with a .410 shotgun, and, in most cases, was done at dawn. Occasionally, removal was done at dusk, and observation begun the next day at dawn. All adult male replacements were removed as quickly as possible after it was ascertained, either by banding or behavior, that the replacements had become territorial. Subadult males were not removed, thus assuring that the experimental marshes were available to them.

During the removal of the adult males, both the initial territorial males and their replacements, the females were left relatively undisturbed, i.e. effort was made to avoid entering the marsh except for essential nest checking. Since all of the incubation is done by the female, who also provides virtually all of the nestlings' food, loss of the adult male appeared to have little immediate effect upon the completion of the nesting cycle by the female. By the time the marsh was available to only subadult males, most of the females were at some stage of either egg incubation or nestling care, and, therefore, generally non-receptive to copulation. In order to provide subadult males with potentially receptive resident females, then, some nests were deliberately destroyed by removing their contents. However,

observations made early in the study also suggested that the presence of nesting females was at least one of the important factors in attracting subadult males to the marsh. Because of this some females were allowed to remain undisturbed, usually females with advanced nests, and/or unmarked females. The remaining nests were destroyed both at the egg and nestling stage. In addition some nests were usually destroyed by other causes during the removal experiments. Thus, the stage was set for sexual interaction between subadult males and marked females known to have been nesting in the experimental marsh.

The three marshes chosen for the removal experiments were primarily selected because they were small (three to six territories per marsh). Small marshes offered three important advantages: a) removal of individuals was accomplished quickly (usually in less than two hours) and with relatively little disturbance to the remainder of the population, b) recovery of removed individuals was usually easy, as in most cases the bird could be collected outside of the marsh proper, and c) observation of the entire marsh was possible from at least one vantage point. In an experimental marsh, then, all the males could be removed at the same time, thus creating a vacated marsh within the larger population of marshes.

As previously indicated the initial removal procedures required modification in response to unanticipated results. Because of these modifications the first two removal experiments are designated as pilot experiments, and the last three removal experiments as removal experiments. Each experiment is numbered chronologically and detailed below, but they are arranged according to the experimental marsh in which they were done. This arrangement is chosen because after the first pilot experiment which was done in Marsh A, the entire study had to be moved to Study Area II; also, the physiognomy of the marshes was in part responsible for the order of the experiments.

Study Area I, Experimental Marsh A (Fig. 1). This marsh was initially divided among three territorial males in the spring of 1958. It was to have been the principal experimental marsh, but the change to pasturing the surrounding land coupled with a dry spring virtually destroyed this marsh during the summer of 1958. However, the first removal experiment was done in this marsh, and the results obtained guided the subsequent experiments done in Study Area II. Therefore, this first removal experiment is designated Pilot Experiment #1. It differed significantly from subsequent removal experiments in that the initial territorial males were removed in early April (April 8th). The number of replacements obtained seemed inordinately high. Since migration was still in progress in early April, it was feared that migrants were participating as replacements. Therefore, this possible variable was eliminated in future experiments by waiting until May to remove the initial territorial males.

Study Area II, Experimental Marsh B (Fig. 2). This marsh was initially divided among four territorial males in the spring of 1959. It possessed a large willow which divided the marsh into portions approximately two-thirds and one-third in area. The stand of cattails in the larger, north end was more dense. This detail of vegetational topography appeared to influence the territorial divisions within the marsh with one territory in the smaller, south end distinctly separated from the three territories in the larger, north end by the large willow. To simplify removal and observation it was decided to take advantage of the vegetational topography and remove the single territorial male in the south end of the marsh and leave the remaining three males in the north end undisturbed. This, then, became Pilot Experiment #2 and was done in the spring of 1959.

In the breeding season of 1961 this marsh was again used, this time for Removal Experiment #2, in which all four initially territorial males were removed in late May.

Study Area II, Experimental Marsh C (Fig. 2). This marsh was initially divided among six territorial males, and became the principal experimental marsh. Based upon results from the pilot experiments all the initially territorial males were removed from this marsh in both 1960 (six males) and 1961 (five males). These last two experiments are designated Removal Experiments #1 and #3.

A total, then, of five experiments involving removal were done, the last three following a similar pattern of removing all the initially territorial males after spring migration. In addition, by the spring of 1961 the fact of replacement seemed reasonably well established; therefore, the possibility that replacements may be closely attached to a particular marsh was checked by removing the males from Marshes B and C, i.e. Removal Experiments #2 and #3, consecutively, and within the same breeding season.

Even though a major part of this study was experimental, a field study of this kind does not readily lend itself to setting up controls. However, the more normal pattern of events occurring outside of the experimental marshes and detected by observation alone acted as a general control for the experiments. These events will be compared to the results of the experiments where appropriate.

RESULTS

The results will be presented under three major headings: 1) those of the pilot and removal experiments, 2) those of the observations of banded adults and subadults, and 3) those based upon the study of banded nestlings. The results of the pilot experiments are presented separately and in considerable detail as they established the procedures for the removal experiments. The results of the removal experiments are then presented as a group and in less detail.

Though the removal experiments were to have been the substance of this study, the large number of individually

banded birds provided much observational data of equal, if not greater, significance. The results of these observations are presented in three subsections: a) adult territorial males, b) subadult males, and c) nesting females.

Finally, limited results are presented from the subsequent recapture of banded nestlings, as well as some data regarding the nesting sex ratio.

Pilot and Removal Experiments:

A. Pilot Experiments: By April 8, 1958, observation had established that Experimental Marsh A was divided among three territorial males. During the last preliminary observation period (dawn to 9:00 A.M.) of these males on April 8th, at least three additional adult males were observed attempting to enter the marsh, but all were chased, usually quickly, from the marsh by one or more of the established males. Pilot Experiment #1 (Table 1) was begun by removing all three territorial males between 9:00 and 9:30 A.M., April 9th. The marsh was observed until 11:00 A.M., but no adult males appeared in the marsh. Observation was resumed at 4:45 P.M. until dusk. During this period only one adult male entered the marsh. He remained in the marsh throughout most of the observation period, singing periodically, and staying within an area approximating the territory of one of the previously established males.

Observation was resumed the following morning at 6:00 A.M. Upon arrival three adult males were in the marsh, two of which were contesting for one end of the marsh. By 6:30 A.M. at least seven males were contesting for territories in the marsh, from which two were succeeding, one at each end of the marsh. These two males were challenged by one or more males continuously throughout the morning, but it always appeared as if the same two males remained after each encounter. However, by 9:00 A.M. one of the two males did yield part of his territory, which was then contested by three adult males, one of which emerged with a territory. By 9:30 A.M. three adult males were established. After 9:30 A.M. until observations

TABLE 1. REMOVAL OF TERRITORIAL ADULT MALE REDWINGED BLACKBIRDS

PILOT EXPERIMENT # 1, EXPERIMENTAL MARSH A, 1958

Date	Days elapsed from initial removal	Adult males removed (cumulative total)	+Adult males available	Total adult males observed (cols.2+3)	Subadult males observed	Subadult male replace-ments	‡Receptive resident females	‡Remaining resident females
4-9	0	3	7	10	-	0	3	-
4-16	7	- (3)	11	14	1	0	3	-
4-19	10	4 (7)	7	14	1	0	7	-
4-23	14	3 (10)	6	16	1	0	7	-
5-1	23	2 (12)	4	16	2	1	2	2
5-2	24	1 (13)	3	16	2	1	2	2
5-5	27	1 (14)	2	16	2	(d)	2	2
5-5	27	1 (15)	1	16	4	2	2	2
5-9	31	- (15)	-	15	6	3	1	1
5-14	*36	- (15)	-	15	0	1	0	0

+Any male observed contesting for a place in the marsh was considered "available": for marked males those actually trapped within the marsh; for unmarked males, the total number observed at any one time.

‡"Receptive" females were those resident females either without a nest, or with a nest, but before the completion of the clutch.

‡"Remaining" females were those resident females with a completed clutch, nestlings, or fledglings.

(d) - displaced by adult male(s)

*see text

were discontinued at 11:00 A.M., contesting among males was mostly among the newly established males to determine territorial boundaries. Observation was resumed at 5:15 P.M., and, though challenging of the territorial males by intruders was still evident, territories in the marsh appeared decided as left in the morning.

The following morning, April 10th, traps were opened and the territorial males banded. However, trapping territorial males permits intruders into the marsh and may result in resumption of territorial contesting (Nero, 1956; Orians, 1961). Intensive contesting for territories did resume in Marsh A and by trapping again on the 12th and 15th, nine adult males contesting for territories within the marsh were banded. By the 16th, four of these adult males emerged holding territory: the first bird captured on the 10th, the two captured on the 15th, and one from those captured on the 12th. Three days were allowed to elapse to confirm the territoriality of these males. Little challenging was observed by intruders, and none of the challengers was banded, even though five banded males were presumably available. At dusk on April 19th, ten days after the initial removal, the four banded territorial males were removed.

The following morning five adult males contested for territories in the marsh, three of which were banded: one a territorial bird of April 10th, the other two from those captured on the 12th. By 7:00 A.M. the latter two held territories in the marsh, and by late morning the third banded male was also territorial. Subsequent removal of these males four days later was followed by contesting among four unmarked adult males, with two emerging as territorial. One of these males was trapped and banded, but retained his territory with no difficulty. However, during the following six days while I confirmed the territoriality of the above males, a subadult male was permitted sufficient time within the marsh to be trapped.

At dusk on May 1st, twenty-three days after the initial removal, the two territorial males were removed. Over the next four days three adult males established territory in the marsh, each one holding the entire marsh until removed. Two of these permitted a subadult male to occupy a small piece of the marsh, and the last adult male to hold the entire marsh was the first bird banded in the marsh on April 12th. This male was removed at 8:45 A.M. on May 5th, twenty-seven days after the initial removal.

Within fifteen minutes after the removal of the adult territorial male at least four subadult males entered the marsh, but only two persisted, the one banded during the six day confirmation period between April 24th and May 1st, and the other banded from a flock in the study area on April 23rd. Over the next two days these males were challenged by other subadult males. Contesting among the subadult males was similar to, but less intense than, that of the adults, with much less singing and displaying, but more direct chasing and actual combat. By May 7th, moreover, the first of the above subadult males to persist was displaced by another subadult male banded on May 2nd from a flock in the study area. On May 9th this latter lost most, but not all, of his territory to another subadult, thus dividing the marsh into three territories. This change corresponded with the loss of the only two active nests in this end of the marsh. The other subadult male which had become established on May 5th lost territory temporarily to an unmarked subadult male on being retrapped, but regained his territory. However, by May 14th both active nests in his territory were also destroyed, probably including both females. The marsh subsequently became dry, and during the third week in May no nesting or territorial activity was observed in the marsh. Pasturing of the field in which the marsh was located was begun this year; so, observation of this marsh was discontinued.

At the time of the initial removal, three females appeared to be resident in the marsh; one of these was trapped and

banded. By the time of the second removal seven females appeared to be resident, and during this period a second female was trapped and banded. However, on May 5th, the day the subadult males became established in the marsh, only four females were nesting in the marsh, including one banded female at each end of the marsh. On this day one of the banded females had only a lined nest; she was left undisturbed, and completed a clutch of three eggs over the next three days, May 6th, 7th, and 8th. On the morning of May 9th the nest was destroyed, as was also the nest of the unmarked female in this end of the marsh. The banded female failed to reappear. The second banded female, located at the opposite end of the marsh, had a clutch of three eggs on May 5th. The nest was purposefully destroyed that evening. This female renested in the marsh and completed a clutch of three eggs. This nest was destroyed naturally on May 13th along with the other nest in this end of the marsh. Adult female feathers were found at the base of both nests, and the banded female was not observed again. However, both the clutches of the banded females were laid when only subadult males were territorial in the marsh.

At the end of twenty-seven days, then, the supply of adult males was apparently exhausted, no new adult males appearing in the marsh over a ten day period. Subadult males held territories in the marsh during this period. During this same period only two banded females were receptive, one completing a clutch in a nest begun while adult males were present, the other renesting with only subadult males present. Destruction of the marsh by drought and pasturing terminated the experiment. In fact, the destruction of Experimental Marsh A was sufficiently great to render the marsh unsuitable for further experiments.

The first removal experiment suggested three guidelines for subsequent experiments. First, the physiognomy of the marsh appeared to play an important role in determining the boundaries of some territories. In Marsh A (Fig. 1), for

instance, the border stand of cattails, distinctly separated from the remaining cattails by open water, always constituted one territory throughout the experiment even for the subadult males. The large willow in Experimental Marsh B divided the cattails in this marsh into a large north section and a small south section, and appeared to be a deciding feature in the territorial boundaries of the male blackbirds in this marsh. Second, the successful replacements were always established during the morning of the first day after removal; therefore, removal of the adult replacement males could be done more rapidly. Finally, the high number of replacements during the time of migration left open the possibility that migrants were dissuaded from continuing on by the availability of a territory; therefore, removal should be delayed until migration was over. In pilot Experiment #1 all the initial territorial males were removed at one time, but with the above as guidelines advantage was taken in Marsh B of the dividing willow and only the single territorial male south of the willow was removed in Pilot Experiment #2; successive removals of replacements for this male were done quickly; and the experiment delayed until the middle of May. Table 2 summarizes the results of this experiment.

In this experiment all but the last removal was done at dusk, and observation begun at dawn. Only following the first removal was there contesting among replacement males. Two adult males contested for about an hour during the morning with one of these emerging as territorial. Subsequent removals were followed by a single adult male appearing and becoming territorial. In each case the adjacent territorial male to the south of the willow set the boundary between him and the new male. This primarily involved perches in the willow and an arbitrary dividing line on a utility wire above the willow. The third replacement was trapped and banded, and while in the trap, another adult appeared in the territory. Presumably, this latter male became the fourth replacement, and was removed late in the morning of May 24th. No adult male replacements

TABLE 2. REMOVAL OF TERRITORIAL ADULT MALE REDWINGED BLACKBIRDS

PILOT EXPERIMENT # 2, EXPERIMENTAL MARSH B, 1958

Date	Days elapsed from initial removal	Adult males removed (cumulative total)	+Adult males available	Total adult males observed (cols.2+3)	Subadult males observed	Subadult male replacements	‡Receptive resident females	‡Remaining resident females
5-18	0	1	2	3	-	0	1	1
5-19	1	1 (2)	1	3	-	0	1	1
5-20	2	1 (3)	1	4	-	0	1	1
5-23	5	1 (4)	2	6	1	0	1	1
5-24	6	1 (5)	1	6	-	3	1	1
5-28	*10	- (5)	1	6	-	(d)	0	1

+Ibid, Table 1.

‡Ibid, Table 1.

‡Ibid, Table 1.

(d) - displaced by adult male(s)

*see text

appeared following this removal, and during the remainder of the day no subadult males entered the territory. However, from dawn until about 6:00 A.M. the next morning, three subadult males appeared around the marsh, but before they could (or would) enter the vacant territory, the adjacent territorial male incorporated the territory, and chased any subadult males that finally did attempt to enter the territory. On the evening of May 28th, an adult male appeared and unsuccessfully challenged the above-mentioned male, thus confirming the incorporation of the territory.

At the beginning of the experiment there were two females in the territory: an unbanded bird with four eggs, and a banded female whose nest had been naturally destroyed on May 17th. The unbanded female was allowed to continue nesting, and fledged four young on May 28th. The banded female completed a clutch of three eggs by May 27th, and disappeared in early June.

This experiment confirmed the rapid establishment of replacement males, and also supported the possibility that removal during migration might yield a higher than expected number of replacements. However, this experiment also suggested that whatever role physiognomy may play in setting territorial boundaries within a marsh, conterminous vacated habitat is likely to be incorporated by adjacent adult males in the absence of adult male replacements, whereas vacated habitat separated by unsuitable habitat will probably remain vacated even though within sight of nearby males. Marsh A was within sight of a very large marsh but separated from it by a strip of pasture; no adult male from the larger marsh incorporated Marsh A.

B. Removal Experiments: Based upon the experience of the pilot experiments, the design of each of the three removal experiments was as follows: Removal was done well after the spring migration; <u>all</u> of the initially territorial males were removed at one time and replacements were removed as quickly as it was feasible. Marsh C, discovered in 1959, was used as

the principal removal marsh in 1960 and 1961. In 1960 Marsh B was left undisturbed but observed frequently. However, by 1961 observations of banded males in other parts of the study area suggested the possibility that each marsh possessed its own local supply of replacements. In order to check this possibility, the territorial males of Marsh C were removed after all the adult males, including replacements, had been removed from Marsh B. The results of the final three experiments are individually summarized in Table 3.

Although the pilot experiments established the pattern for the removal of the territorial adult males, each pilot experiment was terminated prematurely, the first because Marsh A was destroyed by grazing, and the second because all the initial territorial males in Marsh B were not removed thus permitting an adjacent territorial male to eventually incorporate the vacated territory. The possibility of extended occupancy by subadult males and resident females was precluded in the pilot experiments. Because all the adult males, both those initially territorial and their replacements, were removed rapidly in the removal experiments, these experiments did permit the possibility of subadult males becoming territorial and pairing with the receptive resident females. However, this did not materialize as expected. Adult replacement males actually appeared in three separate groups: a relatively rapid influx of presumably very nearby non-territorial birds (observed in the pilot experiments); a delayed appearance of birds whose previous movements are completely unknown (not readily detected in the pilot experiments); and, finally, individuals who had already completed a nesting cycle in some other part of the study area (not observed in the pilot experiments). It was the erratic but periodic appearance of the middle group of adult male replacements which made it virtually impossible to maintain conditions where subadult males and adult females could remain uninterrupted long enough to determine if genuine territorality and pairing were established. Subadult males who appeared to be establishing

TABLE 3. REMOVAL OF TERRITORIAL ADULT MALE REDWINGED BLACKBIRDS

Date	Days elapsed from initial removal	Adult males removed (cumulative total)	+Adult males available	Total adult males observed (cols.2+3)	Subadult males observed	Subadult male replacements	‡Receptive resident females	‡Remaining resident females
REMOVAL EXPERIMENT # 1, EXPERIMENTAL MARSH C, 1960								
5-22	0	6	1	7	4	-	13-14	8
5-22	0	1 (7)	3	10	4	-	13-14	8
5-31	9	3 (10)	0	10	3	3	8	7
6-1	10	- (10)	3	13	3	(d)	8	7
6-6	15	1 (11)	2	13	2	-	5	7
6-7	16	1 (12)	0	12	2	1	3	7
6-19	28	- (12)	1	13	2	(d)	0	4
6-25	*34	1 (13)	2	15	2	(d)	2	2
REMOVAL EXPERIMENT # 2, EXPERIMENTAL MARSH B, 1961								
5-26	0	4	2	6	2	-	1	8
5-26	0	1 (5)	2	7	2	-	1	8
5-27	1	1 (6)	0	6	4	1	1	8
5-28	2	- (6)	3	9	4	(d)	1	8
5-28	2	1 (7)	2	9	3	-	1	8
6-3	8	2 (9)	1	10	8	-	0	9
6-4	9	1 (10)	0	10	8	2	0	9
6-11	16	- (10)	0	10	6	2	3	6
6-28	*33	- (10)	1	11	2	(d)	2	6

TABLE 3. (CONTINUED)

REMOVAL EXPERIMENT # 3, EXPERIMENTAL MARSH C, 1961								
6-7	0	5	2	7	12	-	9	19
6-10	3	1 (6)	0	6	12	5	7	21
6-15	8	-	3	9	12	(d)	4	24
6-25	18	1 (7)	2	9	19	4	2	20
6-26	19	1 (8)	1	9	19	(d)	2	20
6-29	22	1 (9)	-	9	20	4	9	13
7-1	*24	- (9)	1	10	4	(d)	9	13

+Ibid, Table 1.

‡Ibid, Table 1.

‡Ibid, Table 1.

(d) - displaced by adult male(s)

*see text

territory or apparently had established territory would invariably yield to an adult male intruder upon just his appearance in the marsh. The subadult males usually left the marsh completely, not returning until the adult male was removed. Within minutes a single adult male could hold the entire marsh and would vigorously begin courting receptive females present. Because of these interruptions it was not possible to determine clearly the relationship between the subadult males and the resident females. However, as a matter of record and probably suggestive, of the females receptive while subadults occupied a marsh, 27 probably interacted long enough with the subadult males for their actions to be considered a result of the contact with the subadult males. Seventeen of these females responded by leaving the marsh and presumably nesting elsewhere. (In 1960 five of these females from Marsh C were found nesting in nearby marshes.) Of the ten remaining females, four abandoned their nests which had been completed but in which the clutch was incomplete during the period when the subadults were in control. Six females completed clutches of three eggs in the presence of subadults: three of these nests were destroyed at the egg stage; of the remaining three, one clutch failed to hatch, and of the six remaining eggs, five hatched. The last two nests were subsequently destroyed.

In addition the 1961 experimental data lent support to the possibility that each marsh possessed a local supply of replacement males. During the remainder of June after the fourth no additional adult male replacements were observed at Marsh B, but during approximately the same period four replacement males were removed from Marsh C, approximately two and one half miles away. Though the number is admittedly small, had the source of replacement males been a group of generally distributed and relatively mobile individuals, a more even distribution of replacement at the two marshes would certainly have been the greater expectation. Further evidence for the probability of a local supply of replacements will be cited later in the paper.

Each experiment was terminated by the arrival of an adult male late in June. That these late replacements were previously territorial adults was confirmed in 1961, when the final replacements in experiments #2 and #3 were males banded as territorial adults in other parts of the study area, in the first instance in a marsh about 300 yards from Marsh B where he had but one female, and in the second instance in a marsh about one mile from Marsh C. However, even before these last adult males appeared, the intensity of territorial and courtship behavior on the part of the subadult males was diminishing rapidly. Also by early July small flocks of subadults and some adults, presumably previously territorial males whose duties as father were finished, began using Marsh C as a roost. For the subadult males the breeding season was over.

A significant difference between the 1960 data and the 1961 data was the apparently larger number of subadults present in the vicinity of the experimental marshes in 1961. By 1961 trapping and banding in the experimental marshes had been perfected; also, subadult males banded as nestlings were observed in greater numbers throughout the entire study area in 1961 as a result of the increased banding of nestlings in 1960. Specifically, trapping around Marsh C during times when subadults were in control resulted in fifteen different individuals being banded. Just as in the case of adult males, trapping of territorial subadults resulted in a resumption of territorial contesting, thus permitting successive waves to be trapped. In addition two subadults observed at Marsh C were banded as nestlings. At Marsh B six of the eight subadults seen there were also banded; three of these were banded as nestlings in 1960. Had these birds been unmarked, observation alone would have suggested a much lower number.

Observations of Banded Adults and Subadults:

A. Adult territorial males: Within the Study Area II, fifteen relatively discrete marshy areas were observed (Fig. 2)

and ultimately censused for territorial males. Only within the dense tamarack stands did the habitat appear unsuitable for nesting. Table 4 summarizes the yearly censuses of adult territorial males within Study Area II. Though the data are incomplete, the overall picture is one of relative stability in number of territories. In the cases where a change in density did occur, it appeared to coincide with a change in the habitat. For instance, the cattails in the Kelly Road marsh were extensively destroyed during the spring of 1960, whereas in 1961 the Monks Road marsh was partially drained. The accuracy of the censuses was greatly enhanced by the fact that each year more territories were represented by banded males and by 1961, 143 territories were represented by individually banded males. Within the area studied, then, some 200+ territories were established each year.

Ninety-seven of these territorial males, banded as adults, were observed enough to determine their yearly status within the study area. Table 5 summarizes the year to year return of these 97 banded males. In all cases when the male was observed in a subsequent year, he was found in the marsh in which he was first observed as a territorial bird, and most often occupying an area overlapping his previous year's territory.

B. Subadult Males: In study Area II no detectable subadult male was observed defending a territory, other than in the experimental marshes. Therefore, subadult males could not be trapped, observed, or censused as was done with most adult males. However, two techniques emerged during this study which ultimately made possible a crude estimate of subadult males within the study area.

By the end of the 1959 season feeding areas were established within the study area at which good numbers of subadult males were banded during the nesting season and between the spring and fall migrations. In 1959, 44 such subadults were banded; in 1960, 56; and in 1961, 69. Of these 169 subadult males banded as subadults 41 were discovered subsequently.

TABLE 4. NUMBER OF TERRITORIAL MALES WITHIN STUDY AREA II BY YEAR AND MARSH

Marsh	*Approx. size (in acres)	1958	1959	1960	1961	1962
East Marsh (annex)	27	-	14	16	14	-
East Marsh (A),+ESGR	21	-	10	10	10	-
East Marsh (B), ESGR	1½	3	3	3	3	3
Cattail Marsh, ESGR	4	-	18	17	17	-
Monks Road Marsh	25	-	~45	~60	~45	-
Doyle Road Marsh	15	-	~25	~30	~30	-
"Iris" Marsh	1½	-	4	6	6	-
Gosling Lake Marshes	20	-	-	~40	~40	-
Kelly Road Marsh - 1	4	11	10	8	8	-
Kelly Road Marsh - 2	3	-	6	6	6	-
"Dollar" Marsh	1½	-	5	5	5	9
"Dollar" Marsh annexes	-	-	3	3	3	3
Marsh B	½	4	5	3	4	3
Marsh B annex	2	3	3	2	3	3
Marsh C	½	-	-	6	5	5
		Total		~215	~199	

*Estimated from an aerial photograph

+ESGR: Edwin S. George Reserve

TABLE 5. YEARLY RETURN OF TERRITORIAL MALES BANDED AS ADULTS

The top number in each vertical column is the number of new residents banded that year. Reading down each column gives the subsequent return of each year's population.

Year	1958	1959	1960	1961
1958	17			
1959	10	46		
1960	5	34	28	
1961	3	18	18	6
1962	1	-	-	4

Second, it was not uncommon to have a subadult male or a group of 2-10 of them appear along the edge of a marsh, or pass through quickly, sometimes perching momentarily in trees and shrubs, as I was nest checking or censusing territorial males. When they did stop, they usually elicited, almost instantly, an aggressive response, usually a direct intimidatory flight (Nero, 1956) toward the subadults, from one or more of the territorial males. The subadults retreated, usually quickly, before such threats.

These small groups of subadult males persisted throughout the nesting season (middle April to early August in southern Michigan), and they were relatively independent of the large spring and fall flocks which waxed and waned with migration. There is no question that they did mix with these large flocks, but unlike the large flocks, they would attempt, even toward mid-day, to enter the breeding areas including even the smaller marshes. The large migratory flocks usually descended upon the larger marshes, mostly at dusk for roosting, and left at dawn.

Observing one of these groups was a matter of chance. They could not really be sought out, but were seen during the day's routine of censusing, banding, and nest checking. Attention to these small groups revealed that members of these groups were banded, some as subadults, and others as nestlings and juveniles. This strongly suggested the possibility of a relatively stable local population and by 1960 a concerted effort to census these groups was begun. Not all groups seen were censused, but when a group came close enough and remained long enough, a census could be done quickly and accurately. Tables 6 and 7 summarize the data for 1960 and 1961.

TABLE 6. SUBADULT MALE GROUPS OBSERVED DURING THE BREEDING SEASON OF 1960

Date	(N) Number marked	Date	*(k) Number of groups observed	Subadults *(n) marked as *(m) sub-adults	juveniles	nest-lings	Unmarked sub-adults
5-30	4						
5-31	4						
6-1	5						
		6-9	2	2	0	1	1
		6-10	1	0	0	0	2
6-13	1						
6-16	2						
		6-17	1	1	1	1	1
6-18	1	6-18	3	1	0	0	6
		6-19	1	2	0	0	0
6-21	2	6-21	3	2	3	1	8
6-22	2						
		6-23	1	0	0	1	5
6-24	2	6-24	1	1	0	0	0
6-25	2	6-25	1	0	0	0	2
6-28	1	6-28	1	0	1	0	0
6-29	1	6-29	1	0	1	0	1
6-30	18						
		7-1	1	1	0	0	0
		7-2	2	1	1	1	2
7-4	2						
		7-6	1	0	0	0	1
7-8	4						
7-9	5	7-9	1	0	0	2	1
		7-17	1	1	0	0	0
		7-20	1	1	0	0	0
		7-29	1	0	0	1	2

*Refers to formulae used to calculate subadult population size; see text, page 37.

TABLE 7. SUBADULT MALE GROUPS OBSERVED DURING THE BREEDING SEASON OF 1961

Date	(N) Number marked	Date	*(k) Number of groups observed	Subadults *(n) marked as *(m) sub-adults	juveniles	nest-lings	Unmarked sub-adults
6-4	1						
6-5	3	6-5	1	0	0	0	2
6-6	2						
		6-8	1	0	1	0	0
		6-10	1	0	1	1	0
		6-12	1	0	0	1	0
6-13	1	6-13	1	1	0	1	5
		6-14	1	0	0	1	2
6-15	2	6-15	1	0	0	2	1
6-16	2						
6-17	1	6-17	2	0	0	2	2
6-19	5	6-19	1	0	0	1	1
6-21	5						
6-22	4	6-22	2	1	2	6	11
6-23	3						
6-24	7	6-24	1	1	0	2	0
6-25	8						
6-27	8	6-27	1	0	0	2	2
6-28	3	6-28	1	0	0	1	0
		6-29	1	0	2	1	0
6-30	9	6-30	1	0	0	1	2
7-1	2	7-1	1	0	1	0	3
7-3	2	7-3	1	2	2	0	3
		7-4	1	1	1	1	1
		7-5	1	0	0	0	2
7-6	1	7-6	1	0	0	0	2
		7-10	1	0	0	0	1
		7-11	1	2	0	1	3

*Ibid, Table 6.

From these data a crude estimate of the local subadult population can be made with a modification of the Lincoln Index:

$$P = \frac{Mn}{m}$$

where M = number of marked individuals in the area
m = number of recaptured individuals in each sample
n = number of individuals in each sample (Mosby, 1963)

For m and n the censused groups are substituted and each group treated as a sample. Only males marked as subadults are considered "recaptures"; all others are "unmarked". The "recapture" ratio, therefore, is an observed ratio. For M the subadults banded as subadults are used but weighted by the number of samples observed for a given value of M. To compensate for the accumulation of marked individuals summation and averaging are used resulting in the following formula:

$$P = \frac{\left(\frac{\Sigma kM}{\Sigma k}\right)\left(\Sigma n\right)}{\Sigma m}$$

where k is the number of samples for a given value of M. The actual calculations are given in Appendix A.

For 1960 the value of P was 132 and for 1961 P was 356 with an average for the two years of 215.

The technique of modifying the Lincoln Index by summation to compensate for M accumulating over an extended length of time is also used in the Schumacher-Eschmeyer (1943) procedure:

$$P = \frac{\Sigma M^2 n}{\Sigma Mn}$$

In this procedure it is intended that m be recaptures, but if observation of marked individuals is substituted for

actual recapture, this formula may also be applied. Again the calculations are shown in Appendix B. Using this procedure, then, the value of P for 1960 was 140 and for 1961 P was 302 with an average for the two years of 222.

Though both of these procedures are related modifications of the Lincoln Index, it is noteworthy that in the first procedure both m and n are observational whereas in the Schumacher-Eschmeyer procedure only m is observational. In the first procedure an observational ratio is used to calculate P whereas in the second procedure the observational recaptures are incorporated into an essentially capture procedure. These comparable results then from two related procedures suggest a subadult male population oriented to the study area, averaging about 200+ individuals but relatively variable in number from year to year.

As indicated earlier 41 of 169 subadult males banded as subadults (approximately 24%) returned as territorial males within the study area. Once discovered they were censused in subsequent years as adult males. The yearly status of these males is summarized in Table 8. By contrast with the yearly return of males banded as adults these males are of known age.

Of the 41 subadults that returned as territorial adult males, 40 had been banded at the summer feeding areas described earlier. Even though these areas were "neutral" ground, each was adjacent to a particular marsh as shown in Fig. 2. Therefore, it was possible to determine the relationship between the banding site of a subadult male and his subsequent territory the following year. A look at Fig. 2 quickly reveals that each subadult male could return to the marsh at which he was banded. Failing to do this his opportunity to return near his banding site varied according to where the individual was banded. In some cases a marsh as close as several hundred yards was available, i.e. the Kelly Road site to the Doyle Road marsh, or in other cases the next nearest marsh was a mile away, i.e. the roadway adjacent to

TABLE 8. YEARLY RETURN OF TERRITORIAL MALES BANDED AS SUBADULTS

The top number in each vertical column is the number of subadults banded as subadults during the nesting season. Reading down each column gives the subsequent return of each year's population.

Age / Year	1959	1960	1961
1	44	56	69
2	10	17	14
3	8	10	-
4	5	-	
5	-		

Cattail Marsh in relationship to East Marsh. At a distance of a mile or more away from any of the banding sites several marshes become available relative to the banding site. Table 9 summarizes the relationship of banding site to subsequent territory for the 40 subadults returning as adults. The first two columns reflect the availability of nearby habitat, the remaining columns relfect distances as such. Three fourths of the subadults occupied territories the following year no more than a mile away and half of these individuals were in the marsh adjacent to their banding site.

Of special interest are the subadult males banded within and around the experimental marshes during 1961 and returning to the study area in 1962 as territorial males. At Marsh B which was within the main study area, six of the eight subadults observed following the removal experiment were marked. Two of these, the first two, incidentally, to occupy Marsh B after adult male removal, were banded as subadults within the marsh. One of these returned to Marsh B in 1962 as a territorial male. The remaining two territorial males in Marsh B in 1962 were also banded as subadults but approximately a mile away, one in 1959, the other in 1961.

At Marsh C, just outside of the main study area, 15 of the 20 subadults observed following the removal experiment were banded as subadults in and around this marsh. Three of these, all of which were among the first six banded following adult removal, returned as territorial males to Marsh C in 1962. Two others of these six became territorial in marshes within the study area approximately two miles away. In addition a fourth territorial male in Marsh C in 1962 had been banded as a subadult within the main study area in 1961 from a late summer flock. The remaining two territorial males in Marsh C in 1962 were unmarked.

Therefore, of 17 subadult males banded within the experimental marshes in 1961, six returned the following year as territorial males, four of these returning to the

TABLE 9. LOCATION OF TERRITORIAL MALES RELATIVE TO THEIR BANDING SITE AS SUBADULTS

Banding site	Same marsh	Next nearest marsh	Approximately 1 mi.	Approximately 1½ mi.	Approximately 2 mi.	Beyond the study area
Monks Road	8	4	2	1	1	2
Doyle Road	4	2	2	0	0	1
Kelly Road	0	1	1	1	0	0
Cattail Marsh	0	1	0	1	1	0
East Marsh	1	0	0	0	0	0
Marsh B roadway	0	0	1	0	0	1
Gosling Lake	2	0	1	1	0	0
Totals	15	8	7	4	2	4

marsh in which they were banded. Also, of the nine territories in the experimental marshes in 1962, seven were occupied by males banded as subadults within the general study area.

C. Nesting Females: Because of polygyny the density of nesting females was greater than that of territorial males, and given more secretive behavior of females, observing and identifying a previously marked individual was very time consuming by comparison to male observations. Furthermore, the variation in the number of females per male made a female census comparable to the male census impossible, and also reduced the opportunity for associating a particular female with her own nest especially in the large marshes. The observational data, then, for nesting females are the least complete for individually marked birds.

To compensate for the inability to accurately census the entire nesting female population in the study area advantage was taken of the variation in polygyny. Over the four year period of 1958-61 some of the smaller marshes were studied intensively enough for there to be a good percentage of individually marked females, and in which nest checks could be correlated with the females present. In these marshes a female to male ratio was obtained for each male present. Table 10 summarizes the data for each marsh by year, but a single ratio for all years taken together is calculated. Therefore, within the time span of this study each 100 territorial males averaged 327 females.

Year to year territorial fidelity in the adult males warranted tabulating their year to year return. However, females were much less faithful about returning to the previous year's territory. Of 64 females banded as nesting females and who were found and identified within the study area in a subsequent year, 17 were found in a marsh other than the one in which they were banded initially. And among those that returned to the same marsh most showed a tendency to shift their nesting location within the marsh, some to the extent of changing mates (Nero, 1956). By contrast

TABLE 10. FEMALE TO MALE RATIO FOR SELECTED MARSHES BY YEAR

Marsh	Year	Number of males with 1	2	3	4	5	6	7	8	Total females	Total males
East (B),	1958	0	1	2	0	0	0	0	0		3
Kelly,	1958	1	4	3	1	1	1	0	0		11
East (B),	1959	0	1	1	1	0	0	0	0		3
Cattail,	1959	1	3	4	4	1	0	0	0		13
Marsh B,	1959	0	1	3	0	1	0	0	0		5
East,	1960	0	0	1	1	0	0	0	0		2
Kelly,	1960	2	4	3	0	0	0	0	0		9
Dollar,	1960	0	0	0	3	0	1	1	0		5
Marsh B,	1960	0	0	1	3	0	0	0	0		4
Marsh C,	1960	0	2	2	0	1	1	0	0		6
Marsh B,	1961	0	3	1	0	0	0	0	0		4
Marsh C,	1961	0	1	1	0	0	0	2	1		5
	Total females	4	40	66	52	20	18	4	8	229	
	Total males	4	20	22	13	4	3	3	1	70	= 3.27

females renesting following nest destruction within a given breeding season showed virtually complete fidelity to a territorial male, usually renesting within a small area within the male's territory (Nero, 1956; Case, 1963; Frankenhauser, 1964). Therefore, territorial fidelity in females is strong within a breeding season, but significantly weaker on a year to year basis.

The relatively large number of individually marked females returning annually also provided data on a possible relationship between age and clutch size. A nesting female returning the year after the one in which she was banded would be at least two years old or older. To reduce bias as much as possible only the first clutches of females in their first returning year were tabulated. Twenty-six females laid a clutch of 4 eggs; 2 females, a clutch of 3 eggs; and one female, a clutch of 2 eggs. The 2 egg clutch resulted in 2 fledged young. One 3 egg clutch was destroyed, the other resulted in 3 fledged young. Table 11 summarizes the fate of the 4 egg clutches. Fledging was not especially checked, and, therefore, some uncertainty exists for this event. The most doubtful nests are listed under "fate unknown". However, destroyed nests were usually detectable, i.e. tipped nest, nest torn apart, nestling remains nearby, failure of female to defend nest area, etc. Fledging was assumed if there was no evidence of disturbance, and if the young were old enough to fledge. Of primary interest, though, was the high number of 4 egg clutches among the older females.

Study of Banded Nestlings

A. Observations of Returning Individuals. Very surprisingly, birds banded as nestlings within the study area were both observed (Tables 6 and 7) and trapped as juveniles, subadults in the case of the males, and adults within the area. However, nestlings were not individually banded; so, until they were actually captured or became territorial, they could not be individually identified. Therefore, the data are incomplete, but they do suggest some continuity between nestlings and territorial adults. For example,

TABLE 11. FATE OF INITIAL FOUR EGG CLUTCHES OF FEMALES TWO YEARS AND OLDER

Number of nests	Young fledged from	Eggs hatched
4	0	0
1	1	1
2	2	2
3	3	3
1	2	4
1	3	4
9	4	4
4	fate unknown	4
1		fate unknown
Total 26		

from the 487 nestlings banded in 1960, 22 males and 8 females were recaptured as juveniles. Three of the males were recaptured as subadults, and at least two others were observed (Table 7). One of the males recaptured as a juvenile became territorial within the study area. None of the females captured as juveniles were either observed or recaptured as adults. Three other females, though, banded as nestlings in 1960 were captured as nesting females; a fourth female was collected.

Eleven additional males were captured as subadults in 1961; some of these were undoubtedly observed as part of the subadult census of 1961 (Table 7). Two of these became territorial the following year. Finally, in 1962 eight additional males banded as nestlings in 1960 were collected on territory, thus making a total of 11 nestling males which ultimately became territorial with the study area.

Finding older individuals, particularly females, banded as nestlings was mostly a matter of luck; the data are probably conservative.

The limited survival data from nestling males banded in 1958 and 1959 and becoming territorial in 1960 and 1961, respectively, are summarized in Table 12. Like the subadults of Table 5 these are known-age individuals.

Four first nests of year-old females were also recorded. Three laid clutches of 3 eggs and one, a clutch of 4 eggs. All the eggs hatched, and all but one nestling probably fledged. These results contrast with the results recorded for the older females as to clutch size, but, unfortunately, the sample is too small to be any more than interesting.

B. Nestling Sex Ratio: Nestling Red-winged Blackbirds may be sexed by measuring the length of the tarsus from the ninth day at which time the tarsus of the male is diagnostically longer than that of the female (Williams, 1940). Sexing by measuring tarsal length was done whenever time permitted, and when the age of the nestlings was known to be nine or ten days. The results are divided between two

TABLE 12. YEARLY RETURN OF TERRITORIAL MALES BANDED AS NESTLINGS

The top number in each vertical column is the total number of birds banded as nestlings during that nesting season. Reading down each column gives the subsequent return of each year's male population.

Age / Year	1958	1959
0	47	139
1	-	-
2	5	13
3	3	9
4	1	-
5	-	

tables and sample nestlings from three breeding seasons, 1959-61. Table 13 summarizes the sex ratio of nestlings from nests in which there were complete clutches of 3 to 4 eggs, in which all the eggs hatched, and in which all the nestlings survived to be measured at an age of nine days or older. Table 14 summarizes the sex ratio of the remaining nestlings from nests in which either some eggs failed to hatch and/or nestlings failed to reach nine days of age, as well as nests in which the initial clutch size was unknown. The sex ratio for all nestlings taken together, then, was 162 males to 166 females for individuals just prior to fledging. This evidence conforms well with the findings of Williams (1940) in suggesting that the sex-ratio at hatching in the Red-winged Blackbird is 1:1.

As a matter of record the mean tarsal length of each sex is given for the nestlings tabulated in Table 13. Unlike Williams' results these means were derived from birds spanning a forty-eight hour age period and including nine and ten day old nestlings. The mean for the males was 27.73 ± 0.84 mm. with a measured range of 26.2 - 30.0 mm., and for the females, 24.66 ± 0.74 with a measured range of 23.0 - 25.9 mm. Williams' means were 29.15 ± 0.51 mm. for males with a range of 27.95 - 30.15 mm., and 25.68 ± 0.66 mm. for females with a range of 24.35 - 27.35 mm. All of Williams' birds were ten days old.

A few nestlings banded and measured were captured as juveniles. In all cases the sexing by tarsal length was verified.

DISCUSSION

The results of this study must be considered from two points of view: 1) as confirming and elaborating upon previously recorded features of the ecology of the Red-winged Blackbird, and 2) as contributing to a hypothesis for the population structure of this species, support for which

TABLE 13. SEX RATIO OF NESTLINGS FROM COMPLETE CLUTCHES

Male:female ratio	Frequency	Males	Females
4:0	2	8	0
3:0	1	3	0
3:1	6	18	6
2:1	9	18	9
2:2	7	14	14
1:2	10	10	20
1:3	11	11	33
0:3	2	0	6
0:4	1	0	4
Total	50	82	92

TABLE 14. SEX RATIO OF NESTLINGS FROM OTHER THAN KNOWN COMPLETE CLUTCHES

Male:female ratio	Frequency	Males	Females
3:0	2	6	0
2:0	9	18	0
1:0	7	7	0
2:1	13	26	13
1:1	15	15	15
1:2	8	8	16
0:1	12	0	12
0:2	6	0	12
0:3	2	0	6
Total	74	80	74

to an important degree is the evidence for a non-breeding population of adult males. In fact, the latter evidence, which was a primary objective of this study, is best discussed within the larger framework of supporting the hypothesis for population structure. Before setting forth this hypothesis, however, three features of Red-winged Blackbird ecology, which appear to be confirmed by this study, will be discussed. First, the sex ratio at fledging is most likely unity; second, subadult males are generally incapable of successful reproduction, but yearling females most likely breed; and finally, the breeding sex ratio averages about three females to one male.

Sex Ratio: One possible explanation for the unbalanced sex ratio at nesting would be an unbalanced sex ratio at or after conception, possibly during nest life. The attempt by Williams (1940) to determine an early sex ratio rested upon the assumption, suggested by Mayr (1939), that a fledgling sex ratio derived from complete clutches would reflect the sex ratio at fertilization or "primary" sex ratio of Mayr. Variation in clutch size complicates the determination of complete clutches, but the evidence does suggest that in the Red-winged Blackbird both 3 and 4 egg clutches represent complete clutches. The sex ratio obatined by Williams (1940) were derived from complete 3 and 4 egg clutches, and his procedure was followed in the present study. My findings basically confirm the findings of Williams. My ratio derived from 3 and 4 egg clutches of 82 males to 92 females is comparable to Williams' ratio of 57 males to 62 females. The unbalanced ratios found by McIlhenny (1940) and Herman (1938), both of which heavily favored males, remain unexplained. Neither used Williams' method of sexing, and Herman's method of sexing appears open to question (Williams, 1940). Be that as it may, no results to date support a "primary" sex ratio suggesting the one male to three females found at nesting.

However, when polygyny is found in a species, it is common to seek an explanation in the primary sex ratio. For instance, recent theoretical discussions of the primary sex ratio (Fisher, 1958; Kolman, 1960) suggest that any sex ratio must meet the requirement of equality for total energy expenditure per sex by the parents, but it is not necessary for the average energy per male to equal the average energy per female. For instance, should sexual dimorphism start developing early in the nest life, then the number of each sex could vary from equality and the total energy expenditure per sex remain equal (Willson and Pianka, 1963). Sexual dimorphism in the Red-winged Blackbird does begin in the nest at about the eighth day when the males begin growing larger than the females. Unfortunately, the sexing data from this study cannot be directly checked for its relationship with the early sexual dimorphism. However, at fledging there did not appear to be a significant change in the primary sex ratio. Williams' ratio of 47 males to 47 females best approaches a fledging ratio. My ratio of 80 males to 84 females is somewhat comparable except that I did not especially check that each nestling measured successfully fledged. Actually, the combined ratio of 162 males to 166 females from this study probably represents a good fledging ratio; it samples both complete clutches and clutches suffering mortality before fledging. Based, then, upon the limited data available, I believe that neither the "primary" sex ratio nor the sex ratio at fledging will depart significantly from equality.

Observation and trapping of juveniles have on occasion been used as a means of assessing the primary sex ratio. Invariably these data suggest a ratio heavily in favor of males. For instance, many times while checking nests, I would come upon a recently fledged nest and find a single fledgling perched nearby. Twenty-four such fledglings were captured and sexed. Eighteen were males and 6 were females! Also, during late summer and early fall trapping many more juvenile males than females were captured. The 22 male and

8 female juveniles banded in 1960 as nestlings and then captured as juveniles were typical of the ratio. The sex ratio found by Herman (1939) was determined from the subsequent capture as juveniles of banding nestlings, and showed a similar pattern. I cannot believe these results reflect a primary sex ratio. A more likely explanation for this apparent discrepancy would be the early development of the behavioral and anatomical differences related to sex which ultimately result in the more retiring and inconspicuous female and the more aggressive and conspicuous male. Females of all ages were always in the minority of captured individuals particularly at the feeding areas where most of the juveniles were trapped. Other sources of error are also possible (Selander, 1960), and hopefully, further studies will resolve the apparent paradox between the nestling sex ratio and the post-nestling observations.

Yearling Age Class: In a species as well understood as the Red-winged Blackbird the role of the subadult male remains singularly little known. One suggestion which has been proposed (Williams, 1952; Case, 1963) is that given a primary sex ratio of unity, polygyny is balanced by a non-breeding subadult male population. Before assessing this suggestion, two questions must be resolved: 1) are subadult males completely incapable of maintaining the conditions necessary for nesting; and 2) do yearling females nest? This study strongly suggests affirmative answers to these questions.

Though many subadult males apparently have testes which produce active sperm, the removal experiments indicated that they are generally incapable behaviorally of maintaining the social structure necessary for nesting. Instances of individuals holding territory (Beer and Tibbets, 1950) and breeding (Wright and Wright, 1944; Nero, 1956) are apparently exceptional. In the present study subadult males which were finally permitted access to a marsh by removal of the adult males could be displaced from territory by any adult

male, even previously non-breeding adult males. Whatever the shortcomings of these latter males, they had no difficulty in displacing territorial subadult males. Usually the adult male had only to appear, and all the subadults left the marsh. If a subadult did remain, the adult male would merely approach the subadult, singing and displaying, and the subadult yielded, usually quickly, occasionally by a gradual retreat. Never did an adult become extremely aggressive, either by ritual or attack, to have a subadult leave the marsh. The encounters were strictly "no contest".

The response and results of nesting of females available to territorial subadult males also suggests behavioral shorcomings on the part of the subadult males. Most of the females (21 out of 27) abandoned their marsh when only subadult males were in control, and probably nested elsewhere. In those cases where the females remained, though some produced viable eggs, none suceeded in fledging young. Because of the adult male interruptions, it is not even possible to suggest that sperm from the subadult males fertilized the eggs of those females which remained and nested. The evidence, though not definitive, appears to rule out subadult males as potentially breeding individuals.

The question of whether all yearling females nest must yet be verified. However, some did in the present study, and I believe that most if not all reproduce in their first year. The probability, though, that yearling females have a lower reproductive rate than older females is very significant, affecting profoundly as it would the population growth. The difference between the initial clutch size of yearling females (Page 46) and the clutch size for the older females (Table 11) is probably not accidental, but further study is needed.

Breeding Sex Ratio: Beginning with Allen's classic work (1914), polygyny in the Red-winged Blackbird has been well established. However, accurate ratios of breeding female to breeding male are very difficult to obtain.

Counts based upon active nests are probably conservative. Nests within a territory tend to be asynchronous (Nero, 1956). Nero recorded a maximum spread of twenty-five days between two females, and in marshes where I color-banded females intensively, it was not uncommon for new nests to appear belonging to unmarked females after the earliest nesting female(s), now marked, had fledged young. The asynchronous nestling is further complicated by nest destruction and renesting. On one occasion a color-banded female remained away three weeks before returning and renesting after her first nest was destroyed. Counts based upon unmarked females present would also be conservative. Not only might the females not all be present at one time, but, especially, in the large nesting areas many females can pass unnoticed. It was rare that I would find all the color-marked females present and/or visible for a particular territory at one time. Table 15 summarizes the available data from the literature including the present study and gives the census method where known. Though the variation in polygyny recorded appears to lack consistency, I believe most of the ratios must be considered conservative. Until more counts are available based upon color-marked females, I suggest two females per male is probably a minimal ratio, and ratios approaching 4:1 are exceptional. I expect average ratios approximating 3:1 will be encountered most frequently.

The discussion to this point introduces the framework within which a hypothesis for population structure during nesting is proposed; namely, that the unbalanced sex ratio at nesting, probably around 3:1 in favor of females, must be balanced in the population as a whole, assuming that the fledgling sex ratio is unity, and that the yearling age class is composed of nesting females and non-breeding males which are potentially incapable of breeding. The remainder of the discussion will seek to support the hypothesis that the unbalanced sex ratio during nesting is balanced by a non-breeding male population consisting of approximately equal

TABLE 15. SEX RATIOS OF NESTING ADULT REDWINGED BLACKBIRDS

Source	Geographic region	Habitat	Nesting seasons	Method	Av. no. females per male	Female range	Most freq. ratio	% of total
Smith, 1943	Illinois	mixed marshes	1	count of unmarked females and nest counts	2.00-2.20	-	-	-
Smith, 1943	Illinois	cattail marsh	1		2.75	-	-	-
Smith, 1943	Illinois	mixed marshes	1		2.67-3.06	-	-	-
Nero, 1956	Wisconsin	cattail marsh	5-7	color-marked females	1.96	1-3	2:1	64
Orians, 1961	California	cattail marsh	1	-	3.72	1-6	-	-
Orians, 1961	California	cattail marsh	1	-	2.84			
Case, 1963	New York	cattail marsh	2	maximum daily nest count	2.17	1-3	2:1	50
Case, 1963	New York	cattail marsh	2		2.30	-	-	-
Case, 1963	New York	upland fields	1	count of unmarked females	1.85	1-2	2:1	85
Meanley, 1963	Maryland	tidal marshes	4	-	1.9	-	-	-
Giltz, 1967	Ohio	alfalfa field	1	alarm cry playback followed by count of unmarked females	3.26	-	-	-
Giltz, 1967	Ohio	clover field	1		3.10	-	-	-
Giltz, 1967	Ohio	old field	1		1.81	-	-	-
Giltz, 1967	Ohio	cattail marsh	1		1.51	-	-	-
Giltz, 1967	Ohio	timothy hay	1		2.32	-	-	-
this study	Michigan	cattail marsh	4	color-marked females	3.27	1-8	3:1	31

number of subadult males and adult males the total of which is approximately two-thirds the entire male population, when the nesting ratio is approximately 3:1. This hypothesis is chosen as reasonable and consistent with the limited data available. It is also a hypothesis which does not require differential mortality after fledging between the sexes. Analysis of the results of the removal experiments and those of the observations of banded males provide the relevant ratios. These are the ratio of replacement males to territorial males, the ratio of subadult males to territorial males, and the ratio of subadult males to all adult males.

Replacement Male Ratio: The present study confirmed all previous observations regarding available adult males for replacement of lost territorial males (Nero, 1956; Orians, 1961). Many of the replacements in this study appeared within an hour of removal, and further evidence for these males being non-breeding surplus individuals was obtained when males banded early in the removal experiments later returned for territories as the removal process proceded (Table 1). It seems unlikely that these males would persist at establishing a territory in the experimental marsh if territorial elsewhere, even in marginal habitat.

But what of the status of the surplus males before they become territorial should the opportunity arise? At least one aspect of their previous status was discovered by the removal experiments: a surplus male probably limits its interest if not its activity to a particular area, possibly a single marsh, even though a territory is unavailable to it within that area, but is available outside of the area. Or, as previously stated, each marsh may actually possess a local replacement population of adult males. Evidence supporting this idea is derived from the total pattern of the removal experiments. First, the removal experiments of 1961 at Marshes B and C, which were approximately $2\frac{1}{2}$ miles apart and at which replacement of the territorial males was sequential and non-overlapping, suggest this probability.

Second, the number of replacements for the experiments begun in May and June were relatively small (Table 16), and curiously enough approximated the number of males originally on territory in the experimental marsh. I have no explanation at this time for the delayed response of the "middle" group of males. However, because of the non-overlapping replacement at Marshes B and C in 1961, I feel they were not far away. Had birds been coming in from a distance, not only would overlapping in replacement been expected, but the number of replacements should have been higher. Not infrequently extra males appeared when a territorial male was trapped most anywhere in the study area even while vacancies existed in the experimental marshes. Both Nero and Orians reported this experience with the Red-winged Blackbird. It seems reasonable, therefore, to combine the delayed replacements with the rapid replacements. For this admittedly small sample, then, the ratio of replacement males to territorial males is 20/19 or 1.05.

Additional support for a local replacement population is also suggested by the pattern of return of the subadult males when they become territorial adults both at the experimental marshes and elsewhere in the study area. For the experimental marshes in 1961 when many subadults were banded and actually held territory for brief periods of time, 4 of the 9 territorial males in 1962 were known to be from the subadult males banded within the same marsh and 3 others were banded within 2 miles of the marsh in which it became territorial. In addition Table 9 shows 36 of 40 subadults returning as territorial males within 2 miles of their banding site, and 15 of these returned to the same marsh. Not only do these returns suggest that the site of capture for these subadult males was not random, but I believe they strongly suggest that these males had selected their potential territorial area as subadults. An extension of this possibility would be to suppose that the selection is a preferential one and that the individual retains this

TABLE 16. SUMMARY OF ADULT MALE REPLACEMENTS

Marsh	Year	Initial territories	Rapid replace-ments	Delayed replace-ments	Total
Marsh B	1959	4	4	-	4
Marsh C	1960	6	4	2	6
Marsh B	1961	4	3	3	6
Marsh C	1961	5	1	3	4

preference as an adult even if a territory is unavailable when he first becomes an adult. In effect, then, I believe the data suggest that a male recognizes a "home range" as a subadult in which it will become territorial as an adult if possible, but which it will not leave if unable to become territorial.

Subadult Male Ratios: There is little question that there were shortcomings in the collection of the census data for the subadult male population. Apart from the usual problems inherent in the Lincoln Index analysis, observational errors might have occurred when attempting to quickly identify by sight color-banded birds. However, I have accepted the data at face value for purposes of calculating the ratio of subadult males to territorial males because they can be supported independently by other data of the study which will be discussed later. Either of the average yearly subadult census values calculated could be used, but because they are so close a value between them will be used, 219, simply as a matter of convenience. The census of territorial males is probably quite accurate and gives an average of 207 for the two years when all the marshes in Study Area II were successfully censused. Therefore, the ratio of subadult males to territorial males is approximately 219/207 or 1.06.

It is now possible to derive the third ratio of subadult males to all adult males as follows: a population value of unity is given to the territorial males, and the total male population becomes 1.00 (territorial adult males) + 1.05 (non-breeding surplus adult males) + 1.06 (subadult males)=3.11. Considering the relative independence of each of these values as well as the data collection problems, this value compares favorably with the breeding ratio of 3.27 females per male, and strongly suggests that the unbalanced sex ratio at nesting is balanced in the population as a whole. The third ratio, then, is 1.06/2.05 or approximately 1 subadult male to every 2 adult males in the whole population.

The subadult male population might be expected to vary considerably from year to year, as it did in this study, since they represent a single age class resulting from a particular year's reproduction. Likewise, the degree of polygyny might also vary for the same reason, the yearling females paralleling the subadult males on a year to year basis. However, since the breeding population is ultimately composed of a number of age classes, the effect upon the breeding population would be averaged and somewhat stabilized. Only the subadult male population would clearly indicate a given year's productivity.

Survival Rates: The discussion thus far has organized the evidence sufficient to propose a hypothesis for population structure, and has considered the problem of non-breeding males in support of this hypothesis. An additional line of evidence derived from survival rates will now be discussed as it too provides support for the proposed hypothesis. Assuming an age independent survival rate, i.e. an average annual survival rate, after the first year, and setting the subadult population equal to 1, the sum of S (survival rate of the adults) + S^2 + S^3 + S^4 ..... S^n is $\frac{S}{1-S}$. To obtain, then, the proportion of subadults to adults necessary to balance the sex ratio at nesting, a ratio (R) of subadults to adults is calculated as follows:

$$R = \frac{\text{subadults}}{\text{adults}} = \frac{1}{\frac{S}{1-S}} = \frac{1-S}{S}$$

Substituting values of S will give a table of ratios for each survival rate (Table 17). Conversely, a given ratio of subadult males to adult males requires a particular survival rate. Assuming the breeding male to breeding female ratio of 3:1, the 2:1 adult male to subadult male ratio suggested to balance the sex ratio would require an annual average survival rate of 67% after the first year. This rate can now be compared with the actual survival rate derived from the annual return of the adult males in this study.

TABLE 17. CALCULATED MALE RATIOS FOR DIFFERENT SURVIVAL RATES

Survival Rate	Ratio: $\frac{\text{Subadult male}}{\text{Adult male}}$
.33	2/1
.40	3/2
.50	1/1
.60	2/3
.67	1/2
.75	1/3

Eighteen nestling males and 27 subadult males returned as breeding adults, were color-marked, and followed for more than one year as territorial adults. If the usual assumption is made that a surviving territorial male will return to approximately his previous year's territory and failure to reappear, therefore, constitutes death; then, for these males, age specific survival can be determined. However, because the samples are small (Tables 8 and 12) and the follow-up limited to two years, only the average annual survival rate is calculated (Husting, 1965). The number of males returning each year are summed and divided by the sum of the males of the previous year. The quotient of the first sum divided by the second sum represents the fraction of surviving territorial males returning as territorial males. The average annual survival rate, then, for young (four years or less) territorial males was 65% (Appendix C).

Applying this same method to the returning territorial males banded as adults (Table 5), where all age classes are probably represented, gives an annual average survival rate of 62% (Appendix D). Nero (1956) also color-banded adult males and recorded their subsequent return. A total of 51 males were banded over a six year period and checked each year for seven years. The average annual survival rate was 62%! For these results to be mere coincidence seems unlikely. Nero's population represents all of the males from a single marsh observed for a sufficient number of years to have all of the first two groups banded decline to zero; whereas, my results included more individuals scattered over a wider area, but observed for fewer years. The results, then, suggest that the survival rate may be slightly higher for younger males, but in all probability this species will follow the general trend for passerine birds (Deevey, 1947) of basically a constant survival rate with age.

The survival rates for the territorial males, then, places the subadult male to adult male ratio between 1/2

and 2/3, in quite good agreement with the ratio derived earlier from census data. All the evidence, therefore, argues against the subadult male population alone balancing polygyny at nesting, and supports the hypothesis of a non-breeding male population which could equal in number the territorial males.

It is reasonable to expect the survival rate for females and non-breeding males, both subadult and adult, to be like that of the territorial males, though it would be desirable to have an independent check on this assumption. Determining the survival rate for females was seriously handicapped by their year to year mobility. However, I applied the method used for calculating the male survival rates to Nero's 1956 data for color-marked females returning to his study marsh over a five year period. The average annual survival rate obtained was 56%. Applying a correction factor based upon my findings for mobility raised this rate to 70% (Appendix E). The promise of a rate comparable to the male survival rate appears good. The survival rate for other than territorial males may be impossible to obtain. However, their survival rate may very well depend upon their role within the total population. Being just "surplus" is one thing; being integrated into the social structure of the species is quite another matter. In the last section of this report I will speculate upon the probability that these males are integrated into the total social structure. As such I would expect their survival rate to be like that of their territorial colleagues.

CONCLUDING REMARKS

The most important conclusion from this study has to be the hypothesis for population structure discussed in the previous section. As regards the existence of surplus there seems no reason to doubt the existence during the breeding season of surplus non-breeding males, both adult and

subadult, in the Red-winged Blackbird. However, since the total number of males involved approaches balancing the sex ratio at nesting, the more general problem of surplus individuals as members of excluded potential pairs remains. What is suggested by this study is that a species with an unbalanced sex ratio on the nesting grounds is probably balanced in the population as a whole. This possibility appears more likely than, say, differential mortality prior to nesting.

The dynamics of the replacement population prior to replacement can only be inferred. It is probably safe to assume that their life as surplus is similar whether they represent the sex, in this case male, of lower number on the nesting grounds or represent members of a balanced surplus population. Be that as it may the data I collected regarding their ecology are more tantalizing than tangible, and my remaining remarks more speculative than substantiated.

In his classic study of the House Wren (Trogodytes aedon), Kendeigh (1941) detected a non-breeding surplus as well as polygyny. As a result he proposed a hierarchy in the males involving a scale of breeding intensity ranging from no attempt to nest through territorial bachelors, a single female nesting once, two successive nests usually by the same female, to ultimately polygyny. In his report on the Long-billed Marsh Wren (Telmatodytes polustris), Verner (1964) discussed only territorial males but he also supported a heirarchy of bachelor, monogamous and bigamous males which correlated primarily with territory size and total amount of emergent vegetation within the territory. He judged bachelor males to occupy inferior territories. I believe the surplus males revealed in this study likewise are part of a hierarchy related to territory in which the non-territorial males in the strict sense share a home range associated with a particular marsh or possibly a cluster of marshes. The evidence for "local" adult male replacement populations, and the evidence from subadults returning as

territorial adults suggests this view, even to the extent that the home range is established in the subadult year. It is this latter aspect that raises an interesting problem regarding a hierarchal territorial relationship. Subadult males with an established home range as subadults may find themselves without territory as adults even when space is available elsewhere. The compensation for such a future risk would appear to be in the similar and immediate reduced risk of mortality offered by territoriality; namely, familiarity with a relatively small area thus providing quick access to escape from predators (Hinde, 1956 and others). Since survival and not reproduction would appear to be the immediate concern facing a subadult, natural selection could very well favor subadults establishing a home range even at the risk of being excluded from reproduction at a future time. A subadult male must survive that first year for it to have a future! It may even be that selection of a home range begins when the males are juvenile as indicated by the very limited return data for nestling males.

Early fidelity on the part of males to a specific area within the nesting grounds would also permit year to year recognition of individuals, and suggests the possibility of a relationship between territoriality and social hierarchy. This possibility is also suggested by the trapping data which revealed that most of the subadults becoming territorial as adults in the removal marshes were among the first trapped following adult male removal the previous year. The implications of such a relationship are beyond the scope of this study, but it does seem apparent that greater attention to the social organization of the total population during breeding must replace intensive study of territorial pairs if territoriality is to be completely understood.

As indicated in the beginning of this report, the presence of excluded potentially breeding individuals has been cited (Orians, 1961; Wynne-Edwards, 1962) as evidence

supporting the notion that territoriality limits population size in birds. For the Red-winged Blackbird the most obvious objection to this idea is the apparent fact that all the adult females nest. Unless there is some limitation placed upon the reproduction of the individual female correlated with polygyny, then, the fact that all the adult males do not participate in nesting should have no effect upon the productivity of the population. As a check upon this possibility, I tabulated the average egg production and the number of young fledged relative to the number of eggs laid in accordance with the number of females nesting with a single male. I used only data from territories for which I had recorded the outcome of either all the nests or all but one of the nests. Table 18 summarizes this analysis. The data are insufficient to be conclusive but they appear to indicate that polygyny will have little effect upon the reproduction per female by lowering the average egg production. Except for monogamy there seems to be little effect of polygyny upon fledging success. Complicating the matter, though, is the possible lower egg production in yearling females. Their distribution among the territorial males, therefore, must also be determined before any definite conclusions regarding the effect of polygyny upon reproduction can be stated. In addition to my observations there is also the evidence (Brenner, 1968) linking energy supply to the size of the breeding population in this species. It certainly appears as if the interaction of factors regulating the population size is complex with no factor demonstrated as primary. However, the presence of excluded adult males I suspect is the least influential.

TABLE 18. PRODUCTION OF REDWINGED BLACKBIRDS AS RELATED TO POLYGYNY

Number of females per male	No. of territories	Total nests recorded	Eggs laid	No. of nests per clutch size 1	2	3	4	5	Av. no. eggs laid per nest	Eggs hatched	Nestlings fledged	% of eggs laid
1	4	4	16				4		4.00	14	11	69
2	10	20	68	2		6	12		3.40	53	31	46
3	8	23	90			2	21		3.91	51	36	40
4	7	24	88	1		6	16	1	3.66	50	31	35
5	3	14	48		2	5	6	1	3.43	27	19	40
6	2	11	37		2	3	6		3.36	21	15	41

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APPENDIX A

Calculation of Subadult Male Population Estimates
Using Data from Tables 6 and 7

1960 Date	*N	k	M	kM	n	m
5-30	4					
5-31	4					
6-1	5					
6-9	0	2	13	26	4	2
6-10	0	1	13	13	2	0
6-13	1					
6-16	2					
6-17	0	1	16	16	4	1
6-18	1	3	16	48	7	1
6-19	0	1	17	17	2	2
6-21	2	3	17	51	14	2
6-22	2					
6-23	0	1	21	21	6	0
6-24	2	1	21	21	1	1
6-25	2	1	23	23	2	0
6-28	1	1	25	25	1	0
6-29	1	1	26	26	2	0
6-30	18					
7-1	0	1	45	45	1	1
7-2	0	2	45	90	5	1
7-4	2					
7-6	0	1	47	47	1	0
7-8	4					
7-9	5	1	51	51	3	0
7-17	0	1	56	56	1	1
7-20	0	1	56	56	1	1
7-29	0	1	56	56	3	0
Totals		24		688	60	13

*N = Number of subadults banded as subadults

$$P = \frac{(\Sigma kM / \Sigma k)(\Sigma n)}{\Sigma m} = \frac{(688 / 24)(60)}{13} = 132$$

APPENDIX A (CONTINUED)

1961 Date	*N	k	M	kM	n	m
6-4	1					
6-5	3	1	1	1	2	0
6-6	2					
6-8	0	1	6	6	1	0
6-10	0	1	6	6	2	0
6-12	0	1	6	6	1	0
6-13	1	1	6	6	7	1
6-14	0	1	7	7	3	0
6-15	2	1	7	7	3	0
6-16	2					
6-17	1	2	9	18	4	0
6-19	5	1	9	9	2	0
6-21	5					
6-22	4	2	19	38	20	1
6-23	3					
6-24	7	1	26	26	3	1
6-25	8					
6-27	8	1	41	41	4	0
6-28	3	1	52	52	1	0
6-29	0	1	55	55	3	0
6-30	9	1	55	55	3	0
7-1	2	1	64	64	4	0
7-3	2	1	66	66	7	2
7-4	0	1	68	68	4	1
7-5	0	1	68	68	2	0
7-6	1	1	68	68	2	0
7-10	0	1	69	69	1	0
7-11	0	1	69	69	6	2
Totals		24		805	85	8

*N = Number of subadults banded as subadults

$$P = \frac{(805 / 24)(85)}{8} = 356$$

APPENDIX B

Calculation of Subadult Male Population Estimates by the Schumacher-Eschmeyer Procedure

1960 Date	k	M	M^2	m	n	M^2n	Mm
5-30	0	0	0	0	4	0	0
5-31	1	4	16	0	4	64	0
6-1	2	8	64	0	5	320	40
6-9	3	13	169	2	2	338	26
6-13	4	13	169	0	1	169	0
6-16	5	14	196	0	2	392	0
6-17	6	16	256	1	1	256	16
6-18	7	16	256	1	2	512	16
6-19	8	17	289	2	2	578	34
6-21	9	17	289	2	4	1156	34
6-22	10	19	361	0	2	722	0
6-24	11	21	441	1	3	1323	21
6-25	12	23	529	0	2	1058	0
6-28	13	25	625	0	1	625	0
6-29	14	26	676	0	1	676	0
6-30	15	27	729	0	18	13122	0
7-1	16	45	2025	1	1	2025	45
7-2	17	45	2025	1	1	2025	45
7-4	18	45	2025	0	2	4050	0
7-8	19	47	2209	0	4	8836	0
7-9	20	51	2601	0	5	13005	0
7-17	21	56	3136	1	1	3136	56
7-20	22	56	3136	1	0	0	56
Totals				13		54388	389

$$P = \frac{\sum M^2 n}{\sum Mm} = \frac{54388}{389} = 140$$

APPENDIX B (CONTINUED)

1961 Date	k	M	M^2	m	n	M^2n	Mm
6-4	0	0	0	0	1	0	0
6-5	1	1	1	0	3	3	0
6-6	2	4	16	0	2	32	0
6-13	3	6	36	1	2	72	6
6-15	4	7	49	0	2	98	0
6-16	5	9	81	0	2	162	0
6-17	6	11	121	0	1	121	0
6-19	7	12	144	0	5	720	0
6-21	8	17	289	0	5	1445	0
6-22	9	22	484	1	5	2420	22
6-23	10	26	676	0	3	2028	0
6-24	11	29	841	1	8	6728	29
6-25	12	36	1296	0	8	10368	0
6-27	13	44	1936	0	8	15488	0
6-28	14	52	2704	0	3	8112	0
6-30	15	55	3025	0	9	27225	0
7-1	16	64	4096	0	2	8192	0
7-3	17	66	4356	2	4	17424	132
7-4	18	68	4624	1	1	4624	68
7-6	19	68	4624	0	1	4624	0
7-11	20	69	4761	2	2	9522	138
Totals				8		119408	395

$$P = \frac{119408}{395} = 302$$

APPENDIX C

Calculation of Survival Rate Using Data from Tables 8 and 12
Average Annual Survival Among Known Age Breeding Males

Age	Number banded	Age	Number returning
2	10 + 17 + 5 + 13 = 45	3	8 + 10 + 3 + 9 = 30
3	8 + 3 = 11	4	5 + 1 = 6

$$\text{Survival} = \frac{30 + 6}{45 + 11} = 0.65$$

APPENDIX D

Calculation of Survival Rate Using Data from Table 5
Average Annual Survival Among Adult Breeding Males

Year	Number banded	Year	Number returning
1958	17 = 17	1959	10 = 10
1959	10 + 46 = 56	1960	5 + 34 = 39
1960	5 + 34 + 28 = 67	1961	3 + 18 + 18 = 39
1961	3 + 6 = 9	1962	1 + 4 = 5

$$\text{Survival} = \frac{10 + 39 + 39 + 5}{17 + 56 + 67 + 9} = 0.62$$

APPENDIX E

Calculation of Survival Rate Using Data from Nero, 1956:p. 7
Adjusted for Yearly Female Dispersion from this Study, p. 42
Adjusted Average Annual Survival Among Breeding Females

Year	Number banded	Year	Number returning
1949	15 = 15	1950	12 = 12
1950	12 + 32 = 44	1951	5 + 14 = 19
1951	5 + 14 + 2 = 21	1952	2 + 9 + 0 = 11
1952	2 + 9 + 0 + 0 = 11	1953	0 + 9 + 0 + 0 = 9

$$\text{Dispersion (D) (this study)} = \frac{\text{No. returning to new marsh}}{\text{No. returning and breeding}} = \frac{17}{64} = 0.27$$

$$\text{Survival (adjusted)} = \frac{(51) + (51)(D)}{91} = \frac{(51) + (51)(0.27)}{91} = 0.70$$