1968

The Social Organization Of Breeding Brown-headed Cowbirds

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THE SOCIAL ORGANIZATION OF BREEDING BROWN-HEADED COWBIRDS

by

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Submitted in partial fulfillment

of the requirements for the degree of

Doctor of Philosophy

Faculty of Graduate Studies

The University of Western Ontario

London, Canada

August 1968

ABSTRACT

The social behavior of 256 banded Brown-headed Cowbirds (Molothrus ater) was studied at London Ontario in 1966 and 1967. The functions of various behavior patterns observed in Cowbirds were determined so the status of individuals could be ascertained. The Cowbirds arrived in the study area during the last week of March and the first two weeks of April and left by the end of July. Adult birds arrived about two weeks before the appearance of yearlings. A surplus of males was observed, the sex ratio being 1.5:1. A high mortality rate (55%) in adult females compared to that of adult males (38%) appeared to be the cause of the different proportions in the sex ratio. Forty-six resident and 56 non-resident females were observed in the study area; these non-residents appeared to use the area for feeding. The breeding resident females established territories mainly through the performance of threat displays. Thirty-nine breeding resident females, 17 yearlings and 22 adults, held territories ranging from 0.9 to 13.4 ha. (average 4.5 $\pm$ 0.4 ha.). Since Cowbirds appeared to be monogamous, unmated males were present in the population. The 154 banded males observed in the study area were assigned to three groups: mated males (44), unmated residents (35) and non-resident males (75). Males using mainly threat displays

appeared to establish hierarchies among other males in the area; mated males were dominant over unmated males. Although males were found in certain ranges, these were not defended; mated males defended their mates. Pair formation appeared to take place in about 2 weeks. The proportions of mated yearling (11) and adult males (21) did not differ significantly from the proportions of these age groups in the population (58 and 96). Thus, yearling males seemed to participate in reproduction to the same extent as older males. An experiment with captive birds indicated no differences in the ability of yearling and adult males to procure mates although numbers were small. In this experiment dominant males mated with the females which was consistent with observations of males in the wild.

ACKNOWLEDGEMENTS

The present work has incurred many debts of gratitude from people too numerous to mention. This work was supported primarily through grants from the National Research Council to D.M. Scott. In addition, some financial support was given by The Society of Sigma Xi. I am especially indebted to D.M. Scott, my supervisor, who suggested the problem, constructively criticized my work and was helpful at all times.

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INTRODUCTION

In spite of many studies of the Eastern Brown-headed Cowbird (Molothrus ater), hereafter called the Cowbird, the social behavior of Cowbirds within the breeding season is not clearly understood. Observations of territorial behavior are contradictory. Friedmann (1929) considered the Cowbird to be territorial whereas Laskey (1950) and Nice (1937) reported that Cowbirds did not defend territories. Friedmann (1929) and Laskey (1950) believed the Cowbird to be monogamous but both reported suspected cases of polygamy. Nice (1937) felt that Cowbirds were promiscuous.

Several possible mating arrangements, dependent on the sex ratio, may be found in Cowbirds. Friedmann (1929) at Ithaca, New York and McIlhenney (1940) at Avery Island, Louisiana reported a surplus of males. Assuming that all adult and yearling females attain breeding condition, as seems to be the case locally (Scott, 1963; Kennedy, personal communication), and assuming an excess of males over females, then the mating arrangements depend upon the number of males that breed. If all males breed there may be promiscuity or polyandry; monogamy and polygyny are unlikely. If equal numbers of males and females breed, promiscuity and monogamy are possible and polyandry and polygyny are unlikely. The third alternative, fewer breeding males than females, presents the possibilities of promiscuity and polygyny. Thus,

the ratio of males to females and the breeding behavior of males in the population are factors to consider in determining the sexual relationships in Cowbirds.

Observations by other workers indicated differences in reproduction in yearling and adult males. Some data collected at London, Ontario in 1962 and 1963 by Bowen (personal communication), concerning the breeding roles of one-year old (yearling) and older (adult) males, indicated a difference in the behavior of the two age groups. He reported significantly fewer observations of yearling than adult males. An influx of yearling males noted in the first week of June coincided with the time of maximum development of testes in yearling Cowbirds as reported by Scott and Middleton (1968). Because these yearling males appeared to be residents in the area from mid-June to mid-July, the end of the breeding season, Bowen thought that yearling males possibly did not breed. Scott and Middleton (1968) observed that the development of testes in yearling males lagged behind that of adults. Wright and Wright (1944) in a study of Red-winged Blackbirds (Agelaius phoeniceus) and Selander and Hauser (1965) in a study of the Great-tailed Grackle (Quiscalus mexicanus), two species in which yearling males do not normally breed, observed that testes in yearling males did not develop as early and did not attain the size of those in adult males. These observations suggested possible differences in reproduction of yearling and adult male Cowbirds.

The present study was designed to determine 1) if territorial behavior is exhibited by Cowbirds, 2) if Cowbirds are monogamous,

polygamous, or promiscuous, and 3) if yearling males participate in reproduction to the same extent as older males.

METHODS

This study was conducted on the campus of the University of Western Ontario. The campus is covered mainly by lawn interspersed with areas of trees and shrubs. The Cowbird, normally absent from November to late March, breeds on campus. The breeding season, judged from egg-laying dates, begins in the third week of April and ends about mid-July (Scott, 1963).

Two hundred and fifty-six Cowbirds studied in 1966 and 1967 were caught in baited potter-traps and banded with numbered service bands of the United States Fish and Wildlife Service and unique combinations of colored plastic bands. Because bands were difficult to see when birds walked in the grass, wing tags were used in 1967; colored 1/4 inch wide pieces of 3M Scotch Brand tape of the same color combination as the colored bands were placed around the base of the outer two primary feathers with a one inch leader projecting down. This tape did not appear to affect the flight or the behavior patterns of the birds. The colors of the tape were usually visible using binoculars. In 1966 banding began 16 April and continued on week days for 3 weeks after which sporadic banding was continued up to 24 June. In 1967 banding was conducted on week days from 11 April until 19 June. In 1967 the study area of 1966 was expanded to include a region south of the original area. Three main banding areas were

used in 1966 and 1967; one in the central portion, one at the northern and the third in the southern region of the study area.

Observations of the behavior of Cowbirds were recorded on a portable Philips recorder using a microphone attached to binoculars A map of the study area made from an aerial photograph was divided into a grid composed of 100 m. squares. When birds were observed, the date, time, period of observation, participants, behavior (32 patterns described later) and the grid locations to the nearest 25 m. were recorded. The behavior patterns were recorded in the sequence in which they occurred. The data collected were: the actor, the bird which performed a behavior pattern, the behavior, and the reactor, the bird towards which the behavior was directed, if it was directed at another bird, were noted. If behavior patterns of different birds or the same bird occurred simultaneously, these were also recorded. Since there were often 3, 4 or more birds exhibiting different behavior almost simultaneously, this method of recording data was not always adequate to describe all of the interrelated behavior which occurred. The data were transferred to IBM data cards and sorted and partially analysed by computer. After every fifteen minutes of observation time in the field, I recorded my location. Daily tallies of these data were made so equal coverage of all parts of the study area was maintained.

Previous observations of Cowbirds by Bowen (personal communication) on campus indicated that resident and non-resident birds were present in the area. It was, therefore, necessary to distinguish between these birds; separation was based on two factors: 1) frequency of

observations and 2) difference in behavior. Resident females were composed of 1) breeding birds, i.e. those that defended territories and exhibited breeding behavior and 2) females that showed little or no breeding behavior. The latter females were observed relatively frequently, they did not defend territories but ranged throughout the study area. Females observed infrequently which did not defend territories within the study area were assumed to be non-resident females. Two groups of resident males were recognized: 1) mated males i.e. those mated to the breeding resident females and observed frequently in the study area and 2) unmated males, those observed frequently but not associated with particular breeding resident females. Mated males displayed courtship behavior and almost constant attention to particular breeding females whereas unmated males were not attached to particular females and were usually prevented from displaying to females by mated males. Non-resident males were considered to be those observed infrequently in the study area which were not mated to resident breeding females.

The non-feeding ranges of males and females were plotted on a map made from an aerial photograph. The areas were determined by joining the outermost points of the observations of individual birds and measuring the area with a planimeter; observations in which any of the participants were observed feeding were not included in the determination of this range.

Yearlings were distinguished from adults by the presence of some juvenal feathers in an apparent adult plumage (Baird, 1958; Selander and Giller, 1960). These authors noted that the age of males was easily determined but the age of females was more difficult to estimate

because of the similarity in the color of juvenal and new first-winter feathers. Selander and Giller (1960) point out that "Compared with first-year females, adult females are generally darker, are less mottled dorsally, show less conspicuous striping ventrally, and tend to have the light brown edgings of the remiges less conspicuous because they are darker and contrast less with other parts of these feathers." The new first-winter under wing coverts, unlike the corresponding juvenal feathers, are darker with a dark brown edge, the vane is compact with barbs generally remaining parallel to each other. These feathers also show less wear than the juvenal feathers. The reliability of using these feather differences was tested on 68 pairs of wings from females of known age (42 adults, 26 yearlings) obtained from A. Kennedy. The age of 91% (39 adults and 23 yearlings) was correctly determined. Thus, the use of this aging technique probably results in a few females being placed in the incorrect group. In addition Selander and Giller (1960) observed that 2% of juvenal males had a complete post-juvenal molt and were indistinguishable from adults. Some females probably have a complete post-juvenal molt as well, hence, a few birds of both sexes regarded as adults by me were probably yearlings.

The gonads of the following groups of birds were examined to determine their reproductive condition: unbanded males and females, mated males and banded males and females. The gonads were removed within 10 minutes of death and fixed for 24 hours in Bouin's solution and then embedded in paraffin. Representative 10 micron sections were cut and stained with Ehrlich's haematoxylin and eosin. The

stained sections were examined and classified according to stages described in Scott and Middleton (1968). In the females, macroscopic observations were made to determine the number of post-ovulatory follicles present and measurements were made to the nearest 0.5 mm. of all ova 2 mm. or greater in width.

In 1967 an experiment, consisting of eight parts, was conducted from 30 January to 24 March to 1) determine if adult males mated more frequently than yearling males and 2) see if dominant males mated more frequently than subordinant males. Twenty-five males and 15 females were captured in Japanese mist nets in September 1966 at a blackbird roost 12 miles northeast of London. These birds were placed randomly in 8 outside cages, 4 x 16 x 8 ft., and provided with water and a mixture of weed and millet seed, scratch grain, and waste seeds from threshing millet. On 18 December 1966 after the refractory period, the birds were brought inside and exposed to long photoperiod to bring them into breeding condition. Each bird was placed in a separate cage, 12 x 12 x 10 in., at 22 $\pm$ 2 C. degrees and subjected daily to 16 hours of fluorescent light of an average intensity of 32 ft. candles. The cages were arranged in two banks 2 m. apart. Five sides of the cage were opaque with the open side facing the other bank of cages. Thus the birds were visually isolated from adjacent neighbours but could see birds 2 m. away. In order to study the effect of dominance and age on ability to procure mates, various combinations of males and females were introduced into an observation room in a greenhouse and behavior patterns during two 15 minute periods each morning were recorded in the

same fashion as the field observations. The observation room was 12 x 15 ft. with a roof which sloped from 12 to 6 ft. Incandescent light with an average intensity of 20 ft. candles was on for 16 hours per day and temperature was maintained at 22 ± 2 C. degrees. One male and three female canaries under the same photoperiod and temperature conditions as the Cowbirds were placed in the observation room 17 December 1966 to simulate the presence of host species during the breeding period. Eight wire nesting cups lined with burlap string were placed about the room. Two female canaries exhibited nesting behavior throughout the experiment. During part 1 of the experiment the two canaries each laid 1 egg; one 31 January and the other 1 February. Both eggs were broken; one on 2 February and the other on 4 February. During the rest of the experiment a dummy egg was placed in each of 2 nests the day after the Cowbirds were introduced and a second dummy egg was placed in the same 2 nests on the following day.

The statistical tests used in the thesis were found in Snedecor (1956): chi-square, p. 18, Student's (t), p. 45, chi-square 2 x 2, p. 219, and chi-square R x 2, p. 227. The exact probabilities for 2 x 2 chi-square tables were calculated using the method described by Steel and Torrie (1960), p. 379.

COWBIRD BEHAVIOR PATTERNS

The Cowbird is a difficult bird to study under natural conditions, partially because of the parasitic nature of the female. The female does not spend long periods of time at a nest, as many other species do, and thus cannot be located easily by an observer. Also, Cowbirds move around in mixed groups. A female and 2 males or 2 females and 3, 4 or more males are often observed flying about displaying to one another. The social and sexual relationships between various members of these groups are seldom clear to an observer. Bowen (personal communication) recorded the individual birds found associated with one another during the breeding season. This method was not satisfactory to establish the structure of social relationships between birds because of the number of different individuals found with particular males and females. Laskey (1950), however, was able to determine some of the relationships between Cowbirds observed at a feeding station. She maintained records of the displays and other behavior observed between particular Cowbirds, and knowing the functions of the displays, the relationships between the birds were ascertained.

Analysis of behavior patterns

To determine the roles of individual Cowbirds in the social structure during the breeding season, Cowbird activities were divided into 32 discrete behavior patterns. The function and causation of these behavior patterns were then assessed so that individual relationships could be ascertained. The methods used for the analysis have been described by Tinbergen (1965) and Hinde (1966).

a) Some evidence arises from the conditions in which the behavior pattern occurs. If the behavior usually occurs at territorial boundaries, it may be agonistic behavior. If the behavior is seen only between rival males it is probably aggressive in nature whereas behavior seen only between males and females may have a sexual function.

b) Sometimes accompanying behavior indicates the purpose of the display. For instance, if the actor approaches the reactor at the same time as the behavior pattern is given, it may be an aggressive or sexual pattern depending on the sex of the reactor, but if it moves away it may be a submissive behavior.

c) Another method of analysis is the examination of behavior shown by the actor immediately before and after it performs the particular behavior pattern. It is generally accepted by ethologists that a series of behavior patterns which occur over a short period of time usually have related causes or motivations.

Tinbergen (1965) states "When therefore, in an undisturbed environment, a certain display alternates consistently in a matter of seconds with other movements, we must conclude that the displays and these movements betray roughly the same motivational state." If the behavior of the actor preceding and following the exhibition of a particular behavior pattern of unknown cause is aggressive, the behavior pattern in question is probably aggressive as well.

d) Patterns can sometimes be divided into distinct components. The form and context of these components can be examined. If the function of components are known, some understanding of the complete behavior pattern can be obtained. Various sources of evidence can be used to determine the motivation associated with particular components.

1) If a particular pattern includes components observed in overt aggressive behavior, the pattern probably has an aggressive function. If a pattern includes components from overt aggressive and submissive behavior, its function is presumably a combination of the two tendencies. Hence, it may be classified as a threat behavior pattern.

2) If the components are observed in displays of known function they presumably have a similar function.

3) Circumstances in which components occur can also be considered. If they are seen at territory boundaries consistently they probably have a threat or aggressive function.

4) The associated components of known motivation also provide information on cause of particular components. The component

presumably has a similar motivation.

The causation of particular displays in Cowbirds was determined by examining the "adjacent" behavior patterns of the actor (Table 1). Adjacent patterns refer to the behavior pattern performed by the same bird immediately before and the pattern performed immediately after the particular display being examined.

The number of observations analysed to determine causation (Table 1) varied considerably. In order to determine the causation of a particular display, as many as possible different adjacent behavior patterns performed by the same actor are required for analysis. But some displays were often repeated (e.g. male-male bowing, Table 1) and in others the actor performed very few adjacent patterns (e.g. flight bill-pointing, Table 1). These factors restricted the data used in the analysis, so that some interpretations of causation of displays are necessarily based on few data.

Similar problems arose in the analysis of the function of displays (Table 2). In this analysis, only behavior patterns that were 1) different from the display being studied and 2) performed by the reactor immediately following the display, were used to determine function. Patterns performed by birds other than the reactor, responses with the same display, and displays observed infrequently restricted data available for analysis. The relative numbers of males and females used in the analysis of displays do not reflect the proportions observed because particular displays by one sex were sometimes observed frequently and all of the data were not required for analysis. Also displays that occurred at the

TABLE 1. COWBIRD DISPLAYS AND BHEAVIOR PATTERNS PERFORMED BY BIRDS IMMEDIATELY BEFORE AND AFTER THE DISPLAY.

DISPLAYS OF ACTORS	NO. OF BIRDS	NO. OF OBSERVATIONS	SEX ACTOR	SEX REACTOR	NON-ACTOR %	ADJACENT BEHAVIOR PATTERNS PERFORMED BY: ACTOR — PERCENTAGE OF DIFFERENT BEHAVIOR PATTERNS																										
						FEEDING	PREENING	SCRATCHING	STRETCHING	BILL-WIPING-1	PECKING	FIGHTING	SUPPLANTING	RETREATING	BILL-POINTING	FLIGHT BILL-POINTING	BILL-WIPING-2	BOWING ♂-♂	COPULATION	GUARDING	BOWING ♂-♀	SONG 1	SONG 2	SONG 3	SONG 6-2	SITTING	FLYING	ARRIVING	FOLLOWING	APPROACHING
BILL-POINT	37	329	♀	♀	70	7	1			1	1	1	1	3	(18)	(2)	(10)							6		22	1	12	42
BILL-POINT	42	244	♂	♂	65	9	9								(5)			(46)							3	26	6	9	38
FLIGHT BILL-POINT	9	23	♀	♀	70	40				20						(2)										20		20	
FLIGHT BILL-POINT	21	54	♂	♂	70	21												(2)				7	7			65			
BILL-WIPE-2	15	110	♀	♀	27	5								4	63		(32)							2		4		6	21
BOW	40	527	♂	♂	69		5	3	3				2		43	3	2	(103)				2				14	2	2	14
BOW	38	607	♂	♀	56	12	7		4					1					2	25	(161)	2	3	3		1	8	10	10	12

THE VALUES IN BRACKETS ARE THE NUMBER OF OBSERVATIONS OF ADJACENT BEHAVIOR PATTERNS OF THIS TYPE. THEY WERE NOT INCLUDED IN CALCULATION OF PERCENTAGES BECAUSE THE FUNCTIONS OF THESE PARTICULAR PATTERNS WERE NOT KNOWN AT THIS POINT.

TABLE 2. COWBIRD DISPLAYS AND THE BEHAVIOR DISPLAYS PERFORMED BY BIRDS IMMEDIATELY FOLLOWING THE DISPLAY.

DISPLAYS OF ACTORS	NO. OF BIRDS	NO. OF OBSERVATIONS	SEX ACTOR	SEX REACTOR	ACTOR OR NON-REACTOR (%)	FOLLOWING BEHAVIOR PERFORMED BY: REACTOR — PERCENTAGE OF DIFFERENT BEHAVIOR PATTERNS															
						FEEDING	PREENING	SCRATCHING	STRETCHING	BILL-WIPING-1	CHASING	RETREATING	BILL-POINTING	BILL-WIPING-2	BOWING ♂-♂	SONG 6-1	SONG 2	SONG 6-2	SITTING	FLYING	APPROACHING
BILL-POINT	36	162	♀	♀	50			3		3		31	(60)	(7)				3	3	48	9
BILL-POINT	47	125	♂	♂	52		12			4		35	(17)		(17)				4	41	4
FLIGHT BILL-POINT	9	12	♀	♀	42	14				14		29	14							29	
FLIGHT BILL-POINT	12	27	♂	♂	44	12							63		(7)					25	
BILL-WIPE-2	18	56	♀	♀	57					8		21	46							17	8
BOW	42	254	♂	♂	63	2	7		2			5	20		(51)		2	2		58	2
BOW	31	324	♂	♀	49	3	1	1	1	1	2	21	7			20		35		28	

THE VALUES IN BRACKETS ARE THE NUMBERS OF OBSERVATIONS OF PATTERNS OF THIS TYPE GIVEN IMMEDIATELY FOLLOWING THE DISPLAY. THEY WERE NOT INCLUDED IN CALCULATION OF PERCENTAGES BECAUSE THE FUNCTIONS OF THESE PARTICULAR PATTERNS WERE NOT KNOWN AT THIS POINT.

end of a bout of activity (e.g. observed birds, flew away) were not used in Table 2 since I could not record any response by a reactor.

The behavior of Cowbirds was recorded in sequence with time, and most patterns recorded were separated from adjacent patterns by a few seconds. However, data were not collected in such a manner that the exact period between adjacent patterns was known, the time between such patterns ranged from a second to a few minutes. These widely spaced patterns probably did not have related motivations but since situations in which adjacent patterns were separated by several minutes seldom occurred, the bias in the determination of causation and function was small.

Only displays with obscure causes and functions were examined in detail. Patterns, such as feeding, scratching, fighting, pecking and copulation, with readily apparent motivations were not analysed.

The 32 behavior patterns of Cowbirds were grouped into 5 categories: maintenance, agonistic, courtship, vocal and a fifth group including behavior that did not fall in the other categories. Each of the first three categories was composed of behavior with functions which were presumed to be similar. Vocalizations were grouped because of the similarity of form.

Sequences of postures (Fig. 1) were made from 16 mm film of the various Cowbird behavior patterns photographed with a Bolex H16 movie camera. Songs and call notes were recorded on a Uher 4000 tape recorder and analysed on a Kay Electric Sonograph.

I. Maintenance behavior.

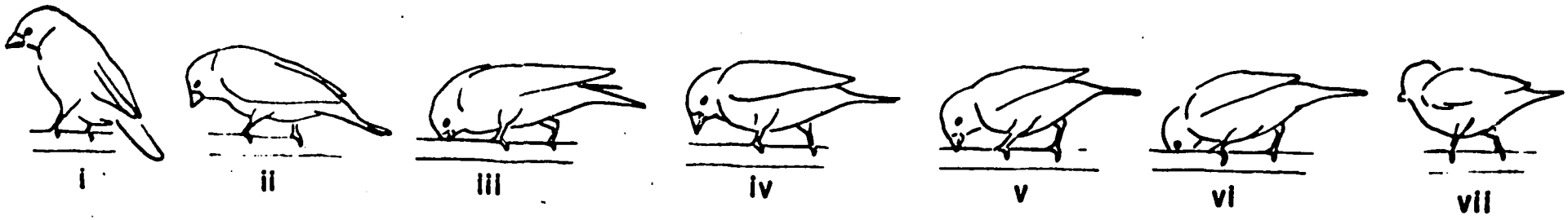
The maintenance activities observed in both sexes were feeding,

Figure 1. Some displays of the Cowbird.

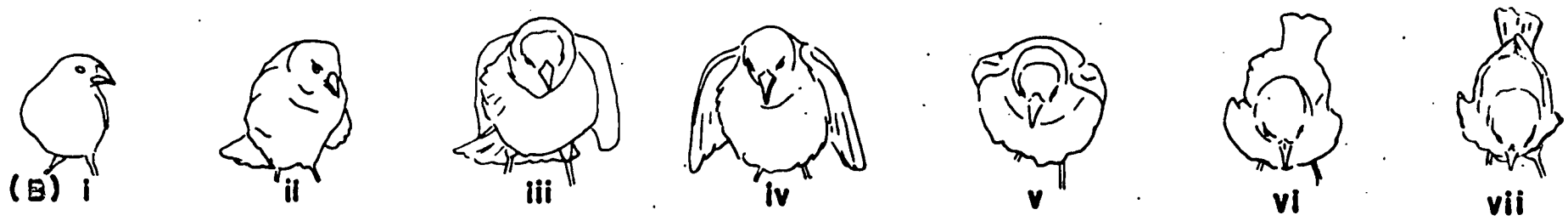
Bill-wipe-1: the interval between each successive figures is 0.0625 seconds

Bow: the interval between each successive figure is 0.3125 seconds

BILL-WIPE

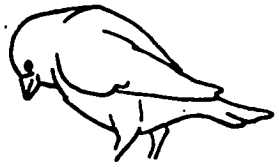


BOW



BILL-POINT

HEAD-DOWN



preening, scratching, stretching and bill-wiping-1.

Feeding. This behavior consists of foraging for food. Rarely a bird was observed feeding along a branch of a tree. The Cowbird normally fed in groups of varying sex ratios in open areas in the study area, the individuals walked along slowly feeding on seeds or insects on the ground or grass as they moved. Often a bird ran for short distances after an insect, then resumed walking. All of the individuals moved in roughly the same direction and at the same speed; thus the group remained relatively cohesive as the birds fed.

Preening. This behavior is similar to preening observed in most passerines. The bill is used for general maintenance, cleaning, and arranging of the feathers. Feathers are sometimes grasped in the top of the bill and drawn through the mandibles in one movement or there may be nibbling along the feather with the mandibles. Another form, using the closed bill, consists of moving the bill along the shaft of the feather to arrange the feathers properly. The contour feathers are ruffed during preening to make them more accessible and the bird bends its head and body to reach the areas to be preened.

Scratching. This pattern includes the motor patterns the bird makes to preen feathers on the head, and presumably to relieve irritation on the head. The bird supports itself on one foot and scratches the head parts with the other foot, which is lifted straight up to the head, extending between the primaries of the slightly lowered wing.

Stretching. Two forms of stretching behavior were observed. In one, the bird balances on one leg and extends the other laterally and posteriorly accompanied by the full extension of the corresponding wing and the fanning of the tail. In the other form the legs are

stretched both at once by straightening the tarsal joints followed by an upward extension of both wings with only the primaries spread.

Bill-wiping-1. This is a characteristic behavior pattern (Fig. 1) in which the bill is wiped from the base to the top on alternate sides of the bill on a branch or some other firm object. Bill-wipe-1, unlike bill-wipe-2, is not directed towards another bird. It was also observed in association with other maintenance activities, thus, it was considered to be maintenance behavior as well.

II. Agonistic behavior.

Ten behavior patterns were considered agonistic. The agonistic function of 5 patterns, pecking, fighting, supplanting, chasing and retreating, was evident from the form of the behavior patterns, the effect they had on reactors and the situations in which they were observed. The other five patterns, bill-pointing, flight bill-pointing, bill-wiping-2, male-male bowing, and song 6-1, were displays, movements that had become specialised in the course of evolution to serve as "signals" in social communication. Since displays, unlike overt behavior patterns such as pecking or fleeing, are usually associated with tendencies to behave in ambivalent ways, (e.g. threat display with tendencies of attacking and fleeing), the circumstances of the displays had to be examined in more detail before their function can be determined.

Pecking. The pecking behavior was described by Laskey (1950): "the plumage was usually puffed, the wings spread horizontally or raised vertically, and the head thrust forward. Sometimes there were a few running steps or a flight toward the other bird." It

was hard to determine if actual contact was made since the reactor avoided the attack.

In 49 observations of pecking, 94% were female-male encounters, 4% were male-male, and 2% were female-female. The male reactor bowed towards the female immediately before the attack by the female in 67% of the observations. The male reactor sometimes continued to court the female or frequently he retreated by flying away. Pecking was considered to be an aggressive behavior used primarily by the female towards courting males. Laskey (1950) considered this pattern a "threat" behavior.

Fighting. In this behavior the birds strike each other with outspread wings, pecking and scratching at one another while tumbling around on the ground. Sometimes they become locked together, pushing against one another with their feet while holding onto the opponent's feathers with their bill. Fighting was usually observed on the ground but one fight began in the air. The two males started to fight during a courtship flight. They both fell to the ground and continued to fight for several seconds then rejoined the female. Fighting was only observed 7 times; 2 were female-female and 5 were male-male encounters.

Supplanting. This behavior consists of the approach of an actor, flying, walking, or hopping to a reactor until it moves, then the actor occupies the reactor's former position.

This pattern was recorded 22 times in 4 female-female, 5 female-male, 12 male-male and 1 male-female encounters. The actions of the reactor were interpreted as retreating behavior since the reactor

vacated the position it held. Thus, supplanting was considered to be an aggressive behavior pattern.

Chasing. This describes the behavior in which the actor actively follows a fleeing bird. Aggressive behavior occurs before the chase and may continue throughout it.

In 38 chasing patterns, 24 were female-male, 7 female-female, 1 male-male and 6 male-female encounters. In 15 of the 24 female-male encounters the male bowed to the female immediately before being chased. In the male-female chases the male was guarding another female. Chasing was considered as aggression since by definition it was associated only with aggressive behavior.

Retreating. This behavior includes any pattern, walking, hopping, or flying, used by a submissive bird to leave an aggressive encounter in which the actor performed an overt aggressive act such as fighting, pecking, supplanting or chasing.

Displays.

Bill-pointing. This behavior ranges in intensity from a form in which the bird is crouched with legs bent and the head withdrawn with the bill pointed vertical, to the form in which the legs are straight, the head, neck, bill and body being held in a vertical position with the feathers sleek (Fig. 1). The actor often approaches the reactor while the bill-point posture is held.

Bill-pointing was observed in both sexes and was directed only to birds of the same sex. In 247 observations of bill-pointing, 65% were female-female and 35% were male-male encounters.

Examination of the female-female encounters revealed the agonistic

nature of this display. The adjacent behavior of the actor (Table 1) consisted mainly of approaching, flying and following. Since the reactors were the same sex, approaching and following were probably aggressive behavior. This behavior in addition to the pecking, fighting, supplanting and retreating behavior indicated agonistic motivations in the female actor. The response of the female reactor to bill-point (Table 2) was predominantly flying or retreating. If flying was also considered retreat behavior in this context, bill-pointing seems to be an agonistic display, since the reactor's main response was retreat. Most of the bill-point displays occurred at territory boundaries (Table 3) where aggression generally occurs in many species. Thus, the bill-pointing display performed by females to other females was considered to be an aggressive display.

Bill-pointing observed between males also seemed to be a threat display. Adjacent behavior of the actor (Table 1) consisted mainly of approaching, flying and following. These patterns were considered agonistic since the actor and reactor are males. The reactors' predominant responses to male bill-pointing were flying and retreating (Table 2). Flying was assessed as retreating behavior in this context. Thus, bill-pointing appears to be a threat display in males since the reactors responded most often with retreat behavior. Friedmann (1929) and Laskey (1950) considered this display in both males and females to be an "intimidation" display.

Flight bill-pointing. This display appears to be the same posture as bill-point except that it is given in flight just before landing. The actor may fly from another area or may fly just a few

Table 3. Location of female actors and reactors, in relation to territory boundary when displays are performed.

	Displays	Number of observations	Number of birds	Percentage of displays occurring: At territory boundary	Outside territory boundary	Within boundary of territory
Actors	Bill-point	71	21	60	20	20
	Flight bill-point	7	6	86	0	14
	Bill-wipe-2	16	11	52	16	32
Reactors	Bill-point	65	22	62	23	15
	Flight bill-point	3	3	100	0	0
	Bill-wipe-2	14	13	59	6	35

feet to approach particular birds. It was sometimes hard to determine any particular reactor since the display was often given when landing in a group of birds. The reactors were males in 72% and females in 28% of the 39 observations of this display.

Observations of adjacent behavior of the female actor (Table 1) were too few to indicate the nature of the motivations for flight bill-point. Female reactors responded mainly to this display (Table 2) with agonistic behavior: retreating, flying and bill-pointing, and most observations of the display occurred at territory boundaries (Table 3). Thus, flight bill-point between females was considered a threat display because of the conditions in which it was observed and its similarity in form to bill-pointing.

Flight bill-point with male participants was also considered to be a threat display because of the similar posture to bill-pointing and the predominant agonistic response of reactors (Table 2) to the display.

Bill-wiping-2. The motor patterns of bill-wiping-2 are the same as those of bill-wiping-1 but they are directed towards another bird. No other differences were observed in the forms of these two patterns. The actor was female in 88% of 67 observations of this display. In 59 bill-wipes by 15 females the reactor was female 93% of the time.

The adjacent behavior of the female actor giving a bill-wipe-2 display (Table 1) consisted mainly of bill-pointing and approaching. Approaching was considered to be agonistic since the reactor was female. Hence, most associated behavior was agonistic in nature. Most reactors responded with agonistic behavior, namely

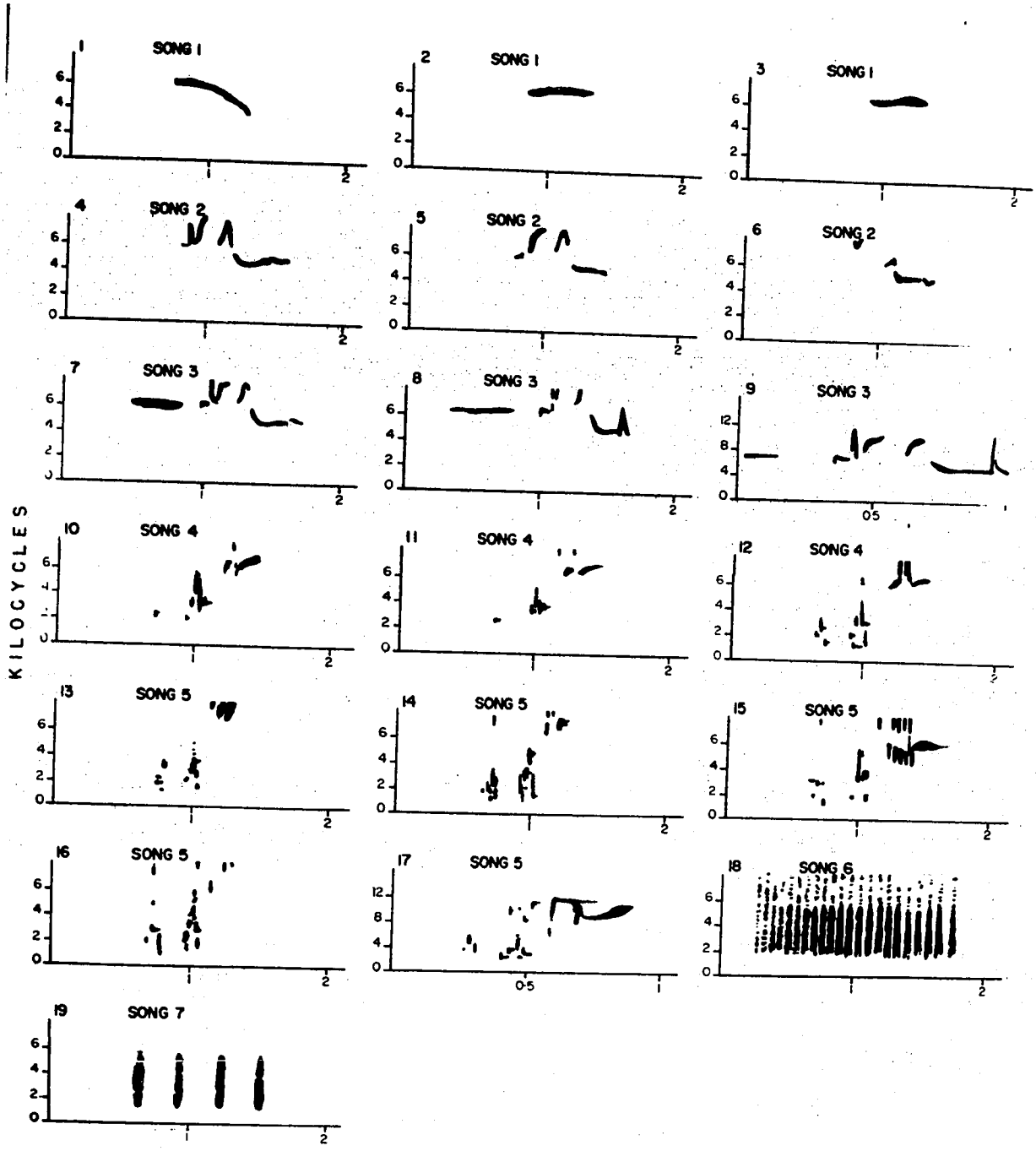
bill-pointing and retreating (Table 2). The displays were observed predominantly at territory boundaries (Table 3). Because bill-wiping was usually associated with agonistic conditions and was often observed at territory boundaries it was considered to be a threat display used most often between females.

Bowing. This display consists of raising the feathers on the back and chest, extending and spreading the wings, spreading the tail and bowing forward followed by a single bill-wipe on each side of the bill. Song 5 (Fig. 2) was given simultaneously with the bow. The completion point of bowing varies considerably, ranging from a slight bow with ruffled feathers (Fig. 1, (A)ii) to the full elaborate bow and bill-wipe. A particular form of bowing, involving males only, was called group bowing. Laskey (1950) called this behavior "triangle and quadrangle ceremonies". A number of males (3 to 6) form a circle on the ground or in trees and proceed to give elaborate bows, usually one after another to the other males. The bows are directed to the adjacent male or apparently to the group.

The bow, with a single exception, was given by males. Laskey (1950) stated that the female bows "very rarely". The bows vary in intensity with the less elaborate bows usually directed towards the female and complete bows to the males. In 460 observations of this display (group bowing excluded), 56% of the reactors were males and 44% were females.

In the male-male bowing displays most adjacent behavior (Table 1) was agonistic in nature: bill-pointing, approaching, supplanting and flight bill-pointing. Most male reactors responded to this

Figure 2. Sonograms of the vocalizations of the Cowbird.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13 SONG 5
14 SONG 5
15 SONG 5
16 SONG 5
17 SONG 5
18 SONG 6
19 SONG 7
KILOCYCLES
SECONDS

display (Table 2) with agonistic behavior: flying, bill-pointing and retreating. Flying was considered as retreat behavior in this context. Since the bowing display was usually observed associated with agonistic behavior of both actor and reactor, it was considered to be a threat display. Laskey (1950) considered male-male bowing pattern to be an "intimidation" display.

Song 6-1. The nature of the song portion of this display is discussed in section IV (Vocal behavior). The song and accompanying display is given by a female to a male; the postures and motor patterns of the display are the same as those described for pecking except the movement of the bill to strike the reactor is replaced by the vocalization. Song 6-1 was preceded by bowing by a male in 88% of 104 observations of the display. Since the display associated with this song was the same as the pecking behavior pattern (minus the peck) and the display was observed most often following bowing of a male, the same situation in which pecking was frequently observed, it was concluded that song 6-1 and accompanying posture was a threat display.

III. Courtship behavior.

Five behavior patterns were assumed to be courtship behavior. Four patterns, pre-coition, copulation, guarding and courtship flight, were placed in this category on the basis of the circumstances in which the behavior was observed and the form of the pattern. The fifth, bowing, required more detailed analysis.

Pre-coition. This behavior, performed by females, is characterized by the posture of the actor. The body of the female is tipped

forward, the bill is held upward at a slight angle, the wings are held motionless somewhat out from the body and the tail is elevated and the body rigid. The male reactor copulates with the female immediately after this posture is assumed.

Copulation. When the female assumes the pre-coital position the male mounts her, the tail of each bird is laterally displaced, and the male attempts to make cloacal contact with the female.

Guarding. This behavior was described by Laskey (1950) "the male ran quickly between a female and one or more males, and attempted to remain between them while the group was feeding or otherwise engaged. While guarding, a male sometimes bowed low to another male, then turned to extend a shallow bow to the female." The male uses threat displays during the performance of guarding to prevent other birds from approaching the female. Also during guarding, as Laskey pointed out, the males display courtship behavior (bowing) towards the female.

When guarding by the male was observed the female was recorded as the reactor which is not correct by definition since the behavior was not directed at the female. But, because this behavior indicates which birds were mated, it was collected in this manner. Only data of guarding with male actors were recorded. Laskey (1950) noted "The dominant female occasionally guarded her mate from another female." Guarding by females was observed on occasion by me but was not recorded. Since guarding was observed between sexes and the circumstances of the behavior included courtship behavior and the driving away of potential rivals by the actor, the pattern was considered to be courtship behavior.

Courtship flight. The courtship flight behavior had a relatively characteristic pattern shown in this example. On 8 April 1967 a flying female, followed by 2 males continuously and a third male occasionally, was observed for 40 minutes. In this period the group made 26 circles ranging in altitude from about 10 to 50 ft. without stopping to rest. The female was always in the lead looping and diving through trees with the same male remaining closest to her at all times. This behavior by the male may be interpreted as aerial guarding. During the flight all members were heard giving song 6, and the males were observed attempting to give the bow and song 5 in flight. In one of the 6 observations of courtship flight there was a fight between two males in mid air. They both fell to the ground then separated and flew to the female which had meanwhile landed in a tree. Sometimes another female and other males joined the flight. Friedmann (1929) described similar behavior while discussing aerial bowing by the male.

Since the behavior was observed only with both sexes present and the males were observed giving courtship displays (bowing) during the flight as well as showing rivalry with males present, it was assumed this pattern was courtship behavior.

Display.

Bowing. This display (Fig. 1) given by the male to the female appears to be the same bowing pattern described earlier in section II (Agonistic behavior).

Most of the adjacent behavior of the actor (Table 1) consisted

of courtship behavior: guarding, copulation, approaching, following and arriving. The last three patterns were assessed as courtship in this situation because the male was moving towards or attempting to remain with a potential sex partner. The main responses of females to bowing (Table 2) were song 6-2, flying, song 6-1 and bill-pointing. Flying in this context was considered as retreat behavior. Since song 6-2 is so closely associated with flying, it was not considered to have any separate significance in relation to the bowing. Song 6-1 and bill-pointing are agonistic patterns; thus, the main response of females to bowing was agonistic behavior. This response is probably due to the relatively short period during which females are receptive to advances by the male. Since the display was observed between the sexes and adjacent behavior of the male was predominantly courtship, bowing was assumed to be a courtship display when directed towards a female. Laskey (1950) considered this display to be a "greeting or courtship" pattern when directed towards a female.

IV. Vocal behavior.

Seven types of song were recognized in the Cowbird (Fig. 2). The males gave all seven but females gave only songs 6 and 7. Since it was hard to determine if vocalizations were directed at particular individuals, any individual that appeared or was present and exhibited a behavior pattern immediately following a song was considered to be a reactor and the behavior exhibited was assumed to be in response to the song.

Song 1. This is the whistle given by males (Fig. 2). It was often given when an observer approached a group of birds; then the birds paused, looked around and frequently flew away.

In 547 observations, 45 patterns immediately following song 1 were performed by other birds (42 females, 3 males). The response by females to song 1 was mainly song 6-2 and flying. Most adjacent behavior of the actor was singing. The circumstances in which this song was uttered and the response of the females seemed to indicate that the song served to alert females to possible danger.

Song 2. This song (Fig. 2) was called the flight whistle by Friedmann (1929). He describes it as "a thin wheezy, inhaling squeak, whsse, and then an equally thin, but not so wheezy, exhaling whistle, pseeee." The form and some variations of this song can be observed in Fig. 2, sonograms 4, 5, 6.

This song was given by males often while flying (48% of 124 records) and was sometimes given prior to flying (12%). Other birds (25 females, 3 males) performed the behavior pattern immediately following song 2 in 12% of 239 observations. The main response to song 2 by females was flying. Adjacent behavior of the actor was predominantly song 1. Since the reactor was usually female, the actor was frequently flying when song 2 was uttered and adjacent behavior of the actor was song 1, it was assumed that song 2 was directed towards females to indicate the actor was flying or intending to fly.

Song 3. Song 3 (Fig. 2) appears to be a combination of song 1 and song 2. Fig. 2-9 is the same recording as Fig. 2-8 at half speed to show the high notes above the ordinate limits of Fig. 2-8. This is probably the song which Friedmann (1929) referred to as a variation of the flight whistle (song 2) with a few notes added.

It was not given as often as song 2 while flying, 20% of 238, but was heard more often (16%) prior to flying. Eleven percent of

238 song 3 vocalizations were followed by behavior patterns by other birds (23 females, 3 males). The main patterns exhibited by females in response were song 6-2 and flying. The behavior of the actor associated with song 3 was song 1, song 4 and flying. Since song 3 appears to be a composite of song 1 and 2 (Fig. 2), it is possible that it has a function intermediate to that of song 1 and 2. Song 1 was given while flying in 2% of 176 observations, and was followed by flying in 11% of the observations. Hence, song 3 was intermediate in terms of the number of times it was uttered while flying (20%). Also it was followed most often by flying (16%) which indicates it was intermediate to song 1 which normally was not given in flight and song 2 which was often given in flight. Thus, song 3 appeared to indicate to females incipient flight by the male actor.

Song 4. Songs 4 and 5 are almost identical (Fig. 2) and were called the "true song" by Friedmann (1929) and have been described by Wetmore (Friedmann, 1929 p. 166) as "bub ko lum tsee". Song 4 was separated from song 5 on the basis of sound, the accompanying display and conditions in which it was given. The first component of song 4 is reduced relative to the comparable component in song 5 (Fig. 2) and is seldom heard in the field. The bow behavior accompanying song 4 is never completed, ending with the ruffling of the breast and back feathers and slight spreading of the wings (Fig. 1, bow A(iii)), and song 4 is usually given when the male is alone.

The behavior pattern following song 4 was given by another actor in 16 (2%) of the 1050 observations of song 4. Thirteen of the 16 behavior patterns were performed by females. Adjacent behavior of

the actor was flying and singing. Song 4 was the only song which was given repeatedly in bouts of singing. Seventy percent of 325 adjacent patterns of song 4 by the actor were also song 4. This song was given by males from particular branches of particular trees of "singing trees" as Friedmann (1929) called them, the characteristic perch being an uppermost branch of high trees. Since song 4 was repeated so often in a conspicuous position and there was relatively no response by other birds, it was assumed that the probable function of this song was to advertise the actor's presence in the area to its mate and other birds.

Song 5. Song 5 (Fig. 2) is an integral part of the bow behavior (Fig. 1). Fig. 2-17 is the same recording as Fig. 2-16 at half speed to show the high notes in the last component of song 5. Unlike song 4 the first component of the song is heard in the field, the song is accompanied by the complete bow and it is normally directed at another bird. Since song 5 is a component of bowing, the function of the song was assumed to be similar to the function of bowing.

Song 6. Fig. 2-18, song 6, is a recording of the female rattle. Males, however, infrequently give song 6 which is similar but appears to have a harsher quality than that of the female. Friedmann (1929) calls this male song "the call to the flock". Two forms of song 6 are observed in females, an aggressive form (song 6-1), described elsewhere, and a non aggressive form (song 6-2). Since the female gives song 6-2 so frequently it was impossible to collect accurate data on frequency and context of male song 6 in order to determine its function. I have heard caged males give song 6 and have also heard males utter

it while following females during a courtship flight.

In females song 6-2 was given in flight in 30% of 347 observations and in 18% of the cases the actor flew immediately after uttering the song. The behavior pattern following song 6-2 was performed by another bird in 46% of the observations. A male was the actor in 147 of 159 patterns following the song. The response of males was mainly following and courtship behavior. Adjacent behavior of the female was mainly flying. Thus, song 6-2 appeared to be directed towards males to indicate flight or incipient flight by the actor and the males usually responded by following the actor.

Song 7. This song (Fig. 2) was called the "feeding note" by Friedmann (1929) and was termed a "chuck" or "kuk". Laskey (1950) stated that the female gave these notes as she fed alone. However, the same sound by males was interpreted as scolding or alarm notes. I collected no data on this song.

V. Other behavior.

This group is composed of behavior patterns which do not fit in the other groups. They are sitting, walking, flying, arriving, following, approaching, searching and head-down behavior. The purpose of the behavior patterns describing the position of birds, such as sitting, walking, flying, arriving, following and approaching do not require any explanation since they depend on the associated behavior and the situation.

Sitting. This behavior describes the state of a bird that remains motionless in one position.

Walking. This is the movement brought about by advancing the feet in turn along the ground or a branch.

Flying. This behavior is any movement through the air.

Arriving. Arriving is used to describe the behavior of a bird when it first appears or joins a group of birds being watched.

Following. This is any movement made to go after another bird on the ground or in the air, but not associated with other behavior (e.g. overt aggressive behavior or courtship flight).

Approaching. This term is used to describe any movement of one bird towards another.

Searching. This term describes the behavior the female uses for location and examination of host nests. When observing a possible host or host nest the female often takes up a particular stance. Facing the host, she crouches down resting her horizontally oriented body against the perch with her head pulled close to the body. Another form of search behavior is described in the following example: a female was observed for 7 minutes moving back and forth on the ground through thick vegetation. The activity was terminated when a song sparrow, on a ground nest with four young in the area of activity, chased the female away. Females were also observed examining nests, sometimes just peering into the nest and other times climbing into the nest crouching down and then flying away.

The adjacent behavior of searching was flying and sitting behavior. The function of searching was to locate potential nests in which eggs could be laid.

Head-down. The head-down display (Fig. 1) was described by

Selander and La Rue (1961) "the head is bowed to a point at which the bill is directed either vertically downward or in toward the Cowbird's body. The feathers of the head and nape are conspicuously ruffed, but other body plumage is generally slightly compressed or sleeked. The wings and tail are held in normal resting position, and the Cowbird is often slightly crouched." This display is usually directed towards other species.

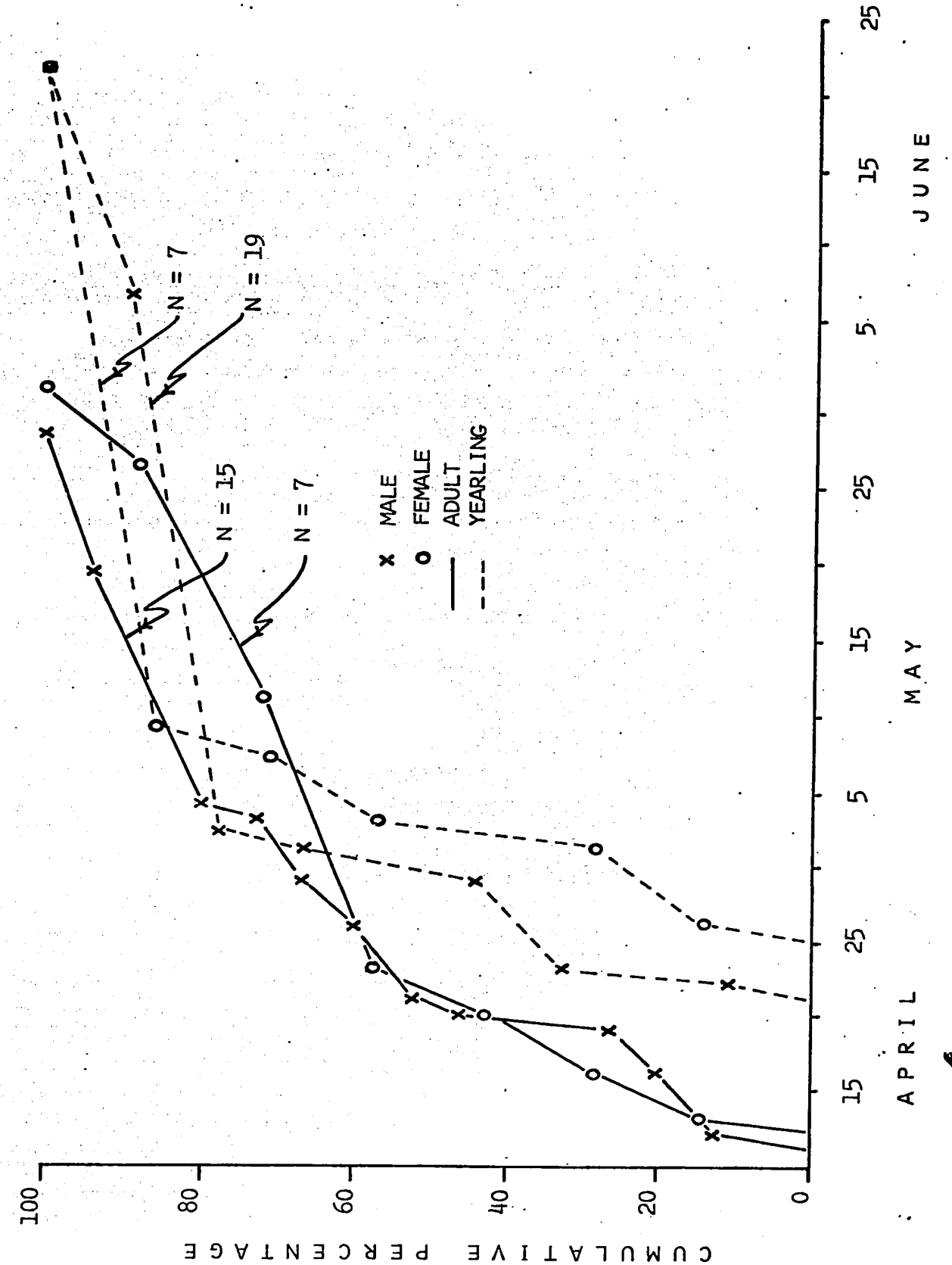
Selander and La Rue (1961) suggest that the display is "an adaptation for parasitism, functioning to decrease the probability of attack by individuals of host species by decreasing their aggressive tendencies." I observed the head-down display often given by caged birds to Cowbirds and Canaries but saw it only once in approximately 325 hours of observations in the field.

FIRST APPEARANCE OF RESIDENT COWBIRDS

The times of arrival of resident adult and yearling males and females on the breeding grounds were examined to see if there were any differences in the first appearance of various groups (Figs. 3, 4). The resident birds included in Figs. 3 and 4 were birds that returned to specific areas examined daily for several days prior to their appearance in the area.

Adults arrived before yearlings in 1966 (Fig. 3). However, since a number of Cowbirds (3 males, 1 female) were observed 8 April before fieldwork began (12 April), the exact time between the arrival of adults and yearlings could not be determined. Adults arrived back at the end of March in 1967 (Fig. 4). The yearlings arrived 2 and 3 weeks after their adult counterparts. The first observations of yearling males may be biased since the age of unbanded males could not be determined until banding began 13 April. However, a maximum of only 2 unbanded males per day was observed before banding began, so few yearling males could have been present and any bias in Fig. 4 would be small. Migration of the adult group was completed 2 to 3 weeks before that of the yearling group.

Figure 3. Dates of first appearance of resident adult and yearling males and females on campus in 1966.


CUMULATIVE PERCENTAGE
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MALE
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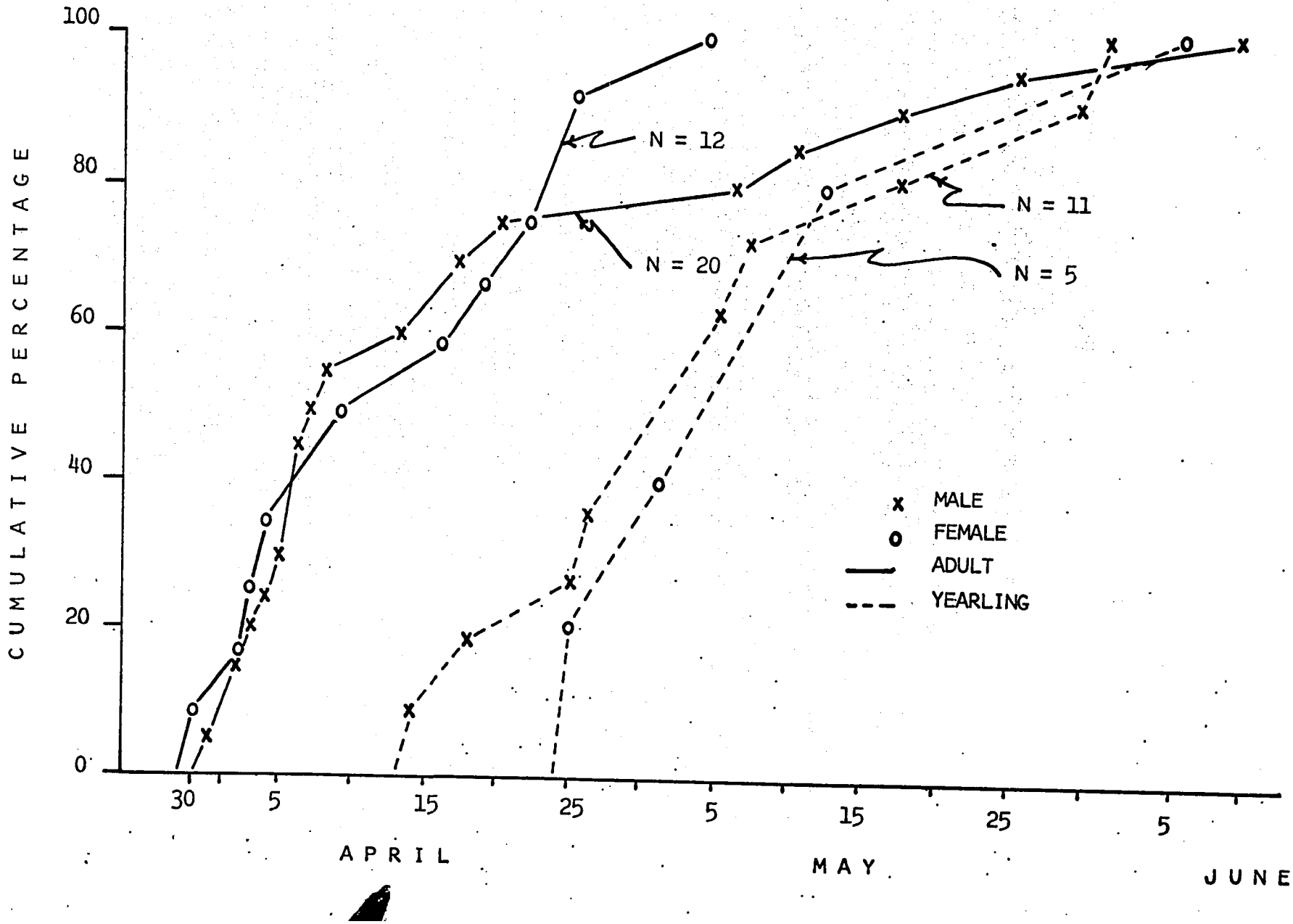
ADULT
YEARLING

Figure 4. Dates of first appearance of resident yearling and adult males and females on campus in 1967.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MALE
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ADULT
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POPULATION STRUCTURE

The sex-ratio, i.e. the ratio of banded males to females observed in the study area, was 1.5:1 (Table 4). The numbers of yearling males and females observed were similar but significantly more adult males than adult females were observed (chi-square, $P < 0.005$). To determine if the proportions of males and females observed were due to differences in actual numbers or due to differences in the movements of sexes (i.e. if males ranged farther than females more males than females would be observed in an area), the feeding behavior of the birds was examined. Feeding behavior was chosen because a Cowbird's feeding range is larger than its non-feeding range. Some of the resident cowbirds were observed feeding 1000 m. or more from their non-feeding range. Since the birds were caught by baiting, recapture data of the 1967 trapping period were examined to ascertain the feeding behavior of both sexes. The 1967 trapping continued throughout the breeding season at three trapping areas that were arranged in a line; the second was 1100 m. from the first, the third was 600 m. from the second and 1700 m. from the first. Individual birds were recaptured at a single trapping station or sometimes at two or three trapping stations (Table 5). If birds of one sex habitually range farther to feed than those of the other, the former birds should be

Table 4. Numbers of banded adult and yearling males and females observed in the study area in 1966 and 1967

Year	Percent Adults		Percent Yearlings	
	Male	Female	Male	Female
1966	37 (31)*	18 (15)	23 (19)	22 (18)
1967	37 (65)	18 (32)	23 (39)	22 (37)
Totals	37 (96)	18 (47)	23 (58)	22 (55)
Sex Ratio	2:1		1:1	

*actual numbers in brackets.

Table 5. Number of Cowbirds recaptured at primary and secondary trapping stations in 1967.

	Number of birds recaptured		
	One trapping station only	More than one trapping station	Probability determined from chi-square analysis
Adult females	10	11	$0.9 > P > 0.75$
Yearling females	13	13	$0.9 > P > 0.75$
Adult males	17	14	$0.75 > P > 0.5$
Yearling males	18	12	$0.75 > P > 0.5$

$0.75 > P > 0.5$

recaptured more often at more than one trapping station. There was no significant difference, within the sexes, in the numbers of adult and yearling birds recaptured at more than one trapping station (Table 5). Similarly, there was no difference between the sexes. Thus, the feeding range of adult and yearling males and females are similar so the apparent excess of males is not due to larger feeding ranges in males.

Another factor which might bias the relative numbers of each sex observed is the difference in their behavior. Males are usually conspicuous and easily observed whereas females are often secretive. Hence, the recapture data, which were not affected by the conspicuous or secretive nature of either sex, were examined to see if there were any differences between age groups or sexes (Table 6). To eliminate migrants this table included only birds which were recaptured two or more times. The number of recapture days was determined by including all trapping days between the first and last recapture of all birds examined. There was no significant difference in the number of recaptures in the two age groups in females or males. Females were, however, captured significantly more frequently than males. Thus, recapture data may indicate a smaller ratio of males to females than actually exists in the population.

The numbers of adult and yearling males and females captured at the 3 trapping stations (Table 7) were analysed to determine the sex ratio. Particular birds were usually caught at one station, the "primary station" but sometimes were recaptured at other stations, the "secondary stations". Thus, there was overlap in the areas

Table 6. Recapture rate in adult and yearling males and females in 1967.

	Number of recapture days	Number of days birds were recaptured	Probability determined by chi-square analysis
Adult females	564	310	0.25>P>0.1
Yearling females	480	241	
Adult males	758	268	0.25>P>0.1
Yearling males	579	184	

P<0.001

Table 7. Adult and yearling males and females recaptured two or more times at trapping stations at London, Ontario in 1967.

Station	Number of birds recaptured									
	Adult females		Yearling females		Adult males		Yearling males		Total	
	P*	S**	P	S	P	S	P	S	P	S
1	13	3	13	6	16	2	12	6	54	17
2	5	8	6	5	9	9	4	6	24	28
3	3	2	7	6	8	5	14	2	32	15
Total	21	13	26	17	33	16	30	14		

*P - primary trapping station

**S - secondary trapping station

served by each baiting station. The sex ratio of birds caught at primary stations was 1.3:1. Station 2 was a secondary trapping station for significantly more birds than station 1 (chi-square 2 x 2 test, $P < 0.005$) or station 3 (chi-square 2 x 2 test, $0.05 > P > 0.025$). There was no significant difference in the numbers of birds recaptured at secondary trapping stations 1 and 3 (chi-square 2 x 2 test, $0.5 > P > 0.025$). The difference in numbers was probably due to the position of station 2 between stations 1 and 3. Birds caught at primary stations 1 and 3 were also attracted to station 2. Thus, the numbers of birds recaptured at primary stations 1 and 3 were probably high since these stations would attract birds from outside the range of the other baiting stations. Because females were captured more frequently than males (Table 6) the values probably favored the females, making the sex ratio of 1.3:1 a minimum value.

Since males are more conspicuous than females, the ratio of 1.5:1, based on observations of birds, is probably a maximum value. Because the ratio of 1.3:1 attained from recapture data, is probably a minimum value, the actual sex ratio probably lies between these two ratios.

The presence of an excess of males was established directly when mated males were removed from the population in 1967. Fifteen of 20 males mated to breeding resident females were removed during the last week of May and the first week in June. These males could not be removed before this time because of the long observation period

required to establish their status. Nine males, that had been observed but had not been mated to females prior to this time, became mates of 9 females and 3 mated males established bigamous relationships with 3 females. Data were insufficient to determine if the other 3 females got new mates. If one assumes that all excess males became mated which was probably the case since 3 mated males became bigamists, then 9 males represents the unmated segment of the male population. Thus, the ratio of males and females in the population would be 29:20 or 1.5:1.

The difference in the numbers of males and females present indicates a difference in mortality rates if one assumes the sex ratio in eggs to be 1:1. The numbers of yearling males and females present in the population were similar (Table 4). Thus, differential mortality does not appear to be operating within the first year of the Cowbird's life. The difference in sex ratio appears to be in the adult birds (Table 4). Since yearlings and adults from one year comprise the adult population in the following year and, assuming a stable population, the mortality rate in adult males would be 23/60 or 38%. Similarly, the mortality rate in adult females would be 22/40 or 55%. Hence the difference in numbers of birds in each sex appears to be due to higher mortality in adult females.

RESIDENT AND NON-RESIDENT FEMALES

Differences in the frequency of observations of particular birds, but primarily differences in observed behavior formed the basis for distinguishing resident from non-resident females. Observations of 102 banded females were made in the study area in 1966 and 1967. The number of observations per bird in the breeding season ranged from 1 to 103 (Fig. 4) with breeding resident females being observed most frequently. Since the first observation was considered to be the first sighting of a bird after it was banded most migrants were probably excluded from the records.

The non-feeding ranges of the females were considered to be territories because females defended them. Females which held territories were considered to be breeding residents. When they arrived on the breeding grounds they established territories with overlapping boundaries (Figs. 5, 6). Females were observed in virtually all areas where trees and shrubs, providing potential host nesting sites, occurred. However, territories and their resident breeding females could not be ascertained for certain areas because of insufficient data. Females established territories using mainly threatening displays and little fighting and most aggressive encounters occurred at the boundaries (Table 3). One of the two records of female-female fighting was observed at the boundary of the actor's

Figure 5. Territories of breeding resident female Cowbirds on campus in 1966.

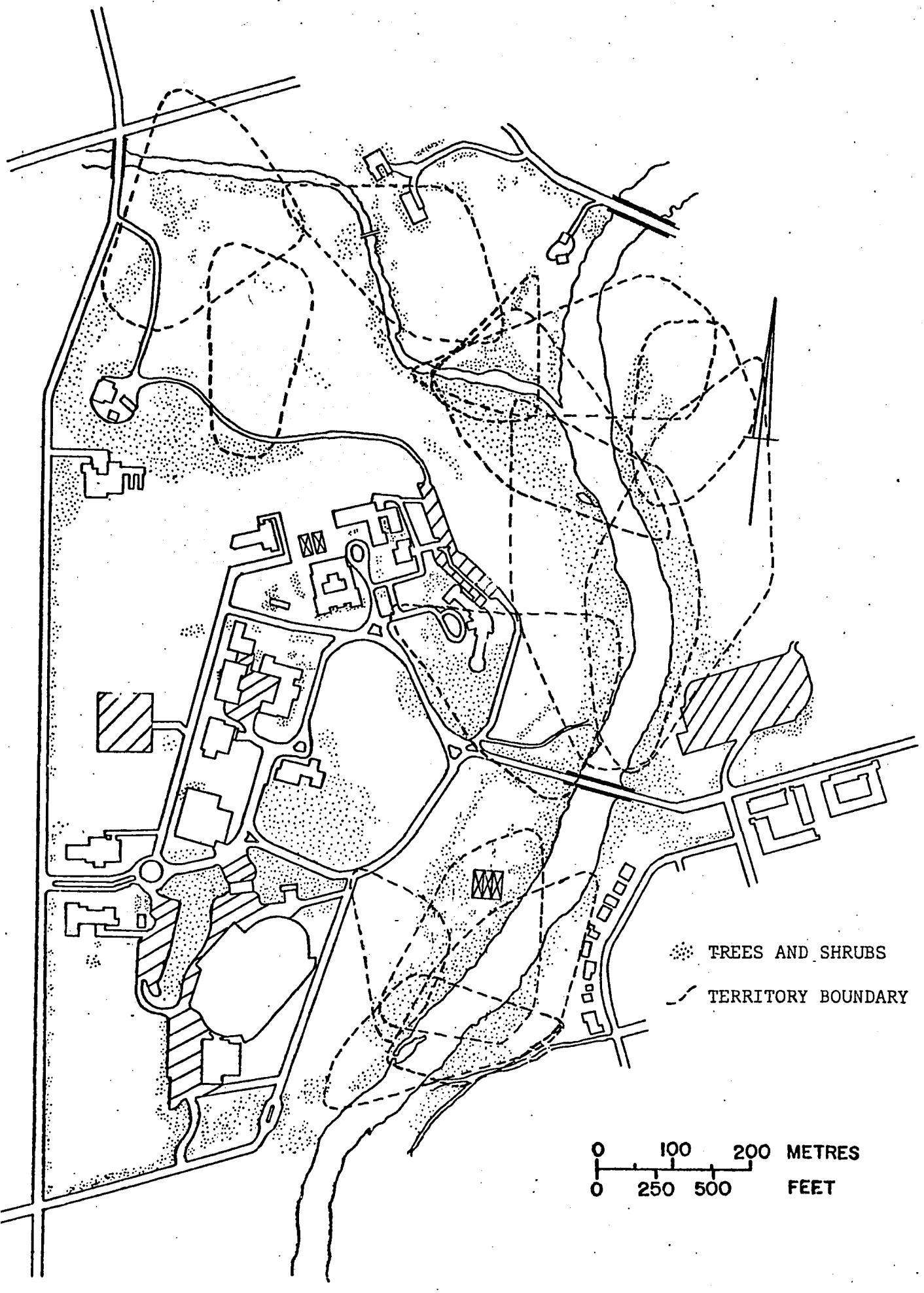

TREES AND SHRUBS
TERRITORY BOUNDARY
0 100 200 METRES
0 250 500 FEET

Figure 6. Territories of breeding resident female Cowbirds on campus in 1967.

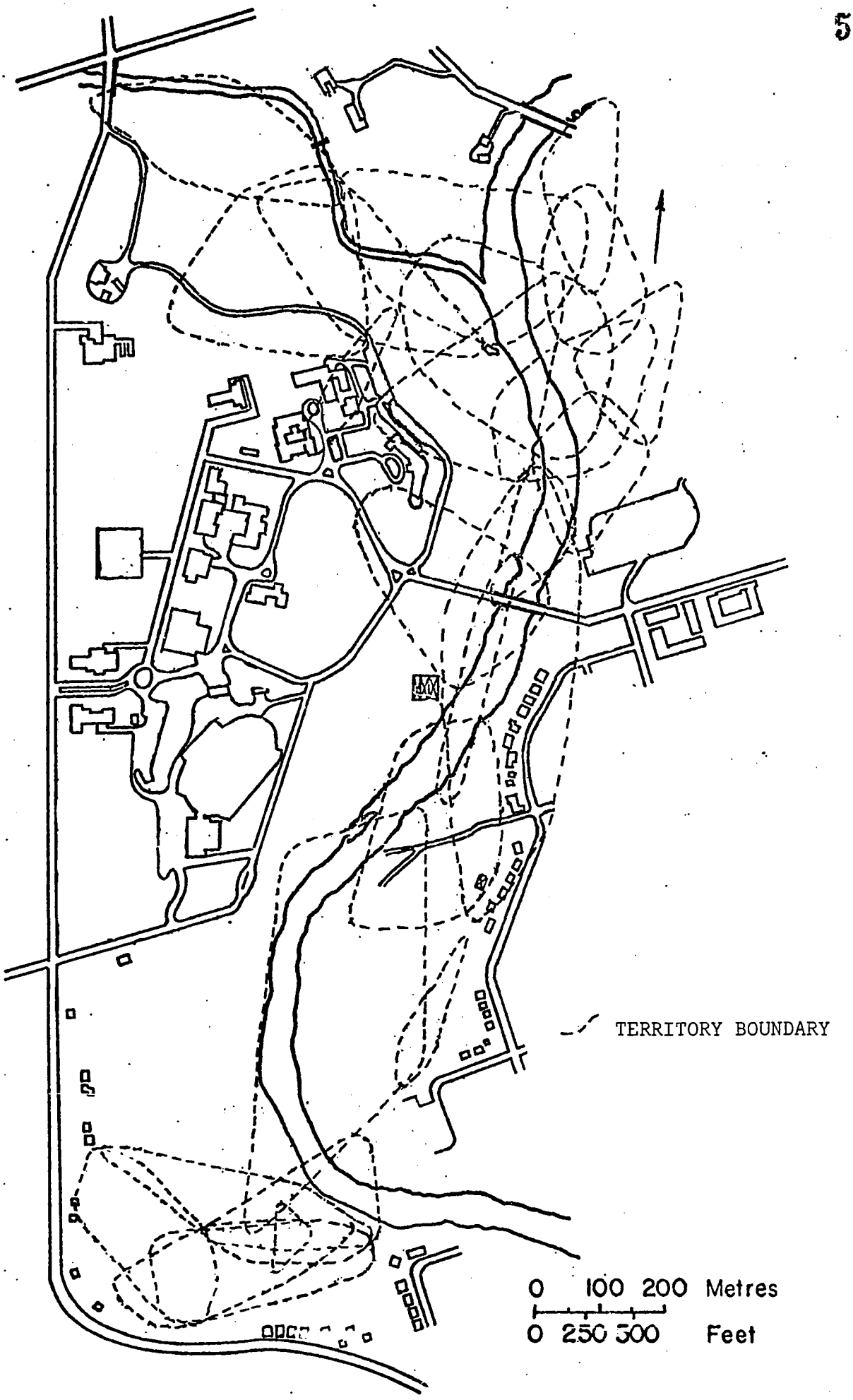
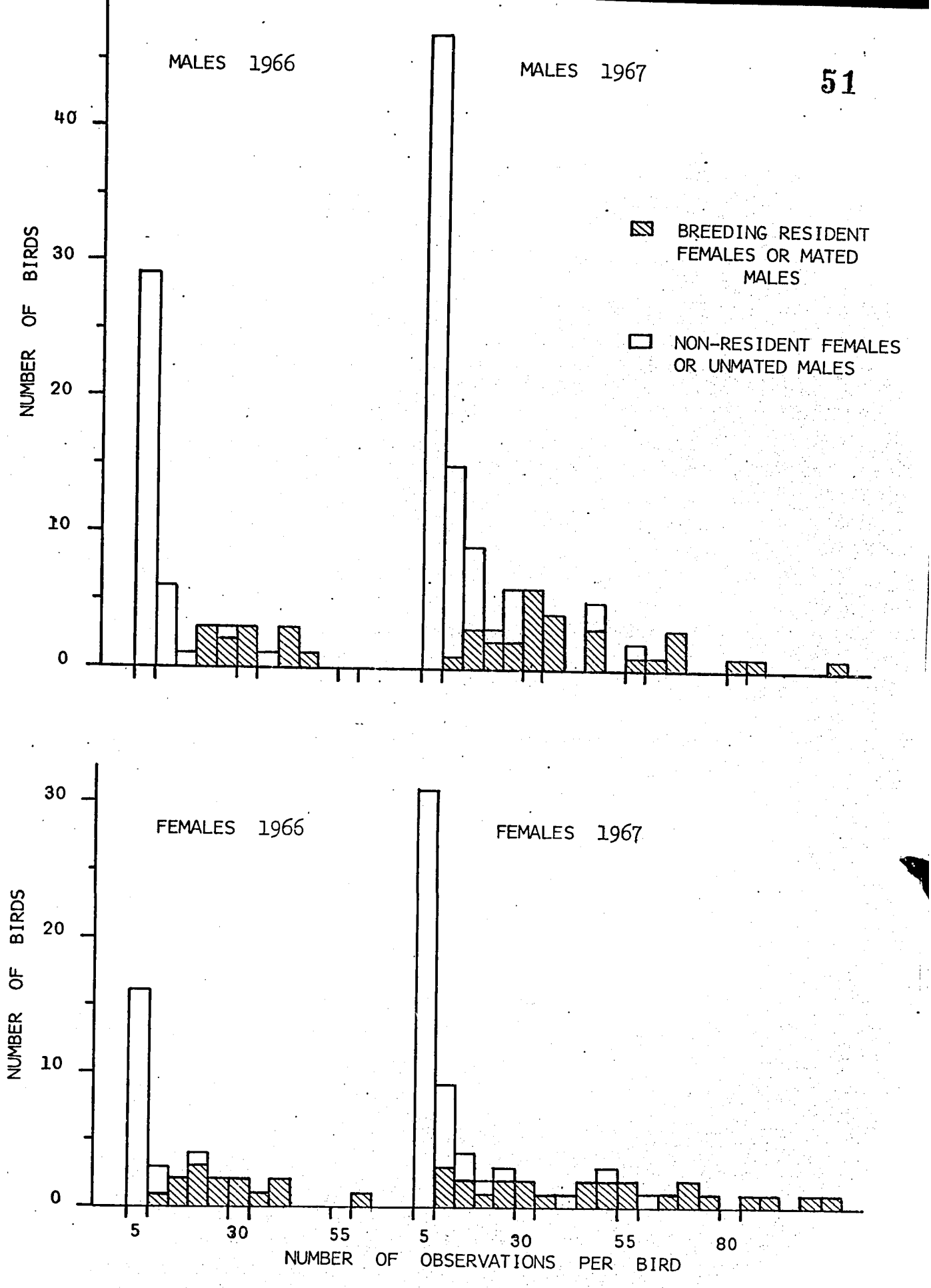

TERRITORY BOUNDARY
0 100 200 Metres
0 250 500 Feet

Figure 7. Number of observations of banded male and female Cowbirds at London Ontario in 1966 and 1967 breeding seasons.


MALES 1966
MALES 1967
NUMBER OF BIRDS
40
30
20
10
0
BREEDING RESIDENT FEMALES OR MATED MALES
NON-RESIDENT FEMALES OR UNMATED MALES
FEMALES 1966
FEMALES 1967
NUMBER OF BIRDS
30
20
10
0
5
30
55
5
30
55
80
NUMBER OF OBSERVATIONS PER BIRD

territory and the other was inside the boundary; one of the reactors was unbanded and the other was not identified. Females used a number of threatening behavior patterns (Table 3), predominantly bill-pointing, to intimidate other females. Females established territories immediately on arrival in the study area. The first observations of all resident females in Fig. 4 were in their eventual territories. Although agonistic behavior between females was observed infrequently, it occurred throughout the season. No significant differences were observed in the number of days agonistic behavior was recorded for 17 resident females in April, May or June in 1967 (Table 8). I assume that the female lays her eggs in host nests within her territory since all 16 observations of searching behavior given by 11 females occurred within their territories.

Some of the resident females returned to the study area in the following year. Six of 14 females that had bred in 1966 (3 adults, 3 yearlings), were observed in 1967. One was observed once and the others established territories that overlapped varying amounts of their 1966 territories.

Thirty-nine breeding resident females (17 yearlings and 22 adults) held territories that ranged from 0.9 to 13.4 ha. (average 4.5 $\pm$ 0.4 ha.) in the study area in 1966 and 1967. There was no significant difference ($P > 0.5$, Student's (t) test) between the areas of territories of yearling (4.4 $\pm$ 0.7 ha.) and adult females (4.8 $\pm$ 0.5 ha.).

Most of the females that did not defend territories in the study area were observed infrequently (Fig. 7), but several were seen as often or more often than many breeding resident females. To determine

Table 8. Number of days agonistic behavior between females was performed by 17 resident females in April, May and June of 1967.

	Number of days agonistic behavior was:		
Month	observed	not observed	Probability
April	14	198	$0.9 > P > 0.75$
May	27	424	$0.25 > P > 0.10$
June	14	331	$.25 > P > 0.1$

the status of these females, their behavior was examined. Since no breeding resident females were observed less than 6 times (Fig. 7), females observed less frequently were examined together. This group probably included some migrants which were observed a few times before they continued migration.

Seventy-nine percent of 86 observations of 47 females were of feeding, 5% of courtship, 3% of agonistic behavior, and 13% were of other activities (sitting, flying, and song 6-2). The reasons for the presence of the 16 females observed more than 5 times (Fig. 7) were also examined. Five, on the basis of scanty data on agonistic behavior, appeared to be breeding residents in the study area. Five were observed feeding only and the remaining 6 females were engaged in several activities. In the 74 observations of these 6 females 84% were of feeding, 4% of agonistic behavior, 1% of courtship and 11% of other activities (sitting, preening, flying, and song 6-2). Two of these 6 (observed 6 and 17 times), unlike other females, ranged widely in the study area; this behavior might indicate they were non-breeding residents. Thus, 56 females were considered non-residents since they did not defend territories and restricted their behavior primarily to feeding; two were deemed non-breeding residents and 44 were regarded as breeding resident females.

No differences were apparent between the breeding condition of resident and non-resident females (Table 9). Fourteen residents (9 adults, 15 yearlings) and 15 non-residents (1 adult, 14 yearlings) were killed between 20 June and 30 June (24 on 26, 27, 28 June) in 1967. All birds except for 6 were banded; these were considered to be non-residents since residents were banded. Two birds, both yearling

Table 9. Reproductive condition of resident and non-resident females collected on University of Western Ontario campus in 1967.

	No. Birds	Birds with no ova 2(mm) or greater	Birds with egg in oviduct	Number and size of ova				Number of post-ovulatory follicles
				2-3(mm)	4-5(mm)	6-7(mm)	8-9(mm)	
Resident	14	0	9	11	13	11	13	28
Non-resident	15	2	6	15	9	6	11	22

non-residents, appeared to be non-breeding birds; their ovaries had no ova 2 mm. wide or greater and no post-ovulatory follicles. Two other non-residents, an adult and a yearling, had one 2 mm. ovum and one post-ovulatory follicle each. The remaining 11 ovaries from non-residents were indistinguishable from those of resident females. One of the 2 non-breeding females was banded 13 April in the northern region of the study area; she was observed sitting in the southwest region a month later and on 4 other occasions was observed feeding in the northern part of the study area. The other non-breeding female, banded 17 May, was observed on 4 occasions feeding in the northern, central and southern parts of the study area. The 2 non-residents each with one post-ovulatory follicle and one 2 mm. ovum were observed feeding in the study area on one occasion each, after banding.

A few of the 42 non-residents were observed outside the study area in 1967. Five were observed 650, 650, 550, 350, and 350 m. beyond the nearest edge of the study area. None of the resident females was observed outside the study area.

Since non-residents used the study area primarily for feeding, appeared to be in breeding condition, and were observed outside the study area, they were probably breeding on territories outside the study area.

That 2 females were not in breeding condition and two were considered to be non-breeding residents probably indicates the presence of a small non-breeding segment of the population. Thus, 44 of 46 resident females and 54 of 56 non-resident females were assumed to be breeding.

RESIDENT AND NON-RESIDENT MALES

In 1966 and 1967, 154 banded males were observed in the study area. They were assigned to three groups based on frequency of observation and behavior: 1) mated and 2) unmated resident males and 3) non-resident males.

Male Cowbirds did not defend specific areas. Aggressive encounters of mated males (Table 10), unlike those of females (Table 3), were observed mainly inside the non-feeding range. A chi-square analysis of the locations of agonistic encounters in males (Table 10) and females (Table 3) showed a significant difference ($P < 0.001$). Thus, males do not defend their non-feeding ranges.

Forty-one males were mates of breeding resident females and were considered resident males. Mated males were observed more frequently than most other males (Fig. 7). Their non-feeding range usually overlapped most or all of their mate's territory and was usually larger. In 41 mated males (including 9 replacement males) it ranged from 0.4 to 25.0 ha. (average 7.9 ± 1.0 ha.) (Fig. 8, 9). When alone within his range the male often gave song 4 from a high perch. This behavior was observed from the time of arrival in the area up to the end of the breeding season. He was frequently observed with the resident female and if other males were present, he guarded

Table 10. Locations of 106 male-male aggressive encounters of 1966 mated males in relation to their non-feeding range in the study area in a total of 76 bouts.

	Location of Encounters relative to Non-feeding Range			
	Boundary (%)	Outside Boundary (%)	Inside Boundary (%)	Unknown
Actor	26(28)	18(19)	56(59)	
Reactor	35(15)	21(9)	44(19)	(43)

Numbers in brackets are actual numbers of male-male encounters.

Figure 8. The non-feeding range of mated resident male Cowbirds at London Ontario in 1966.

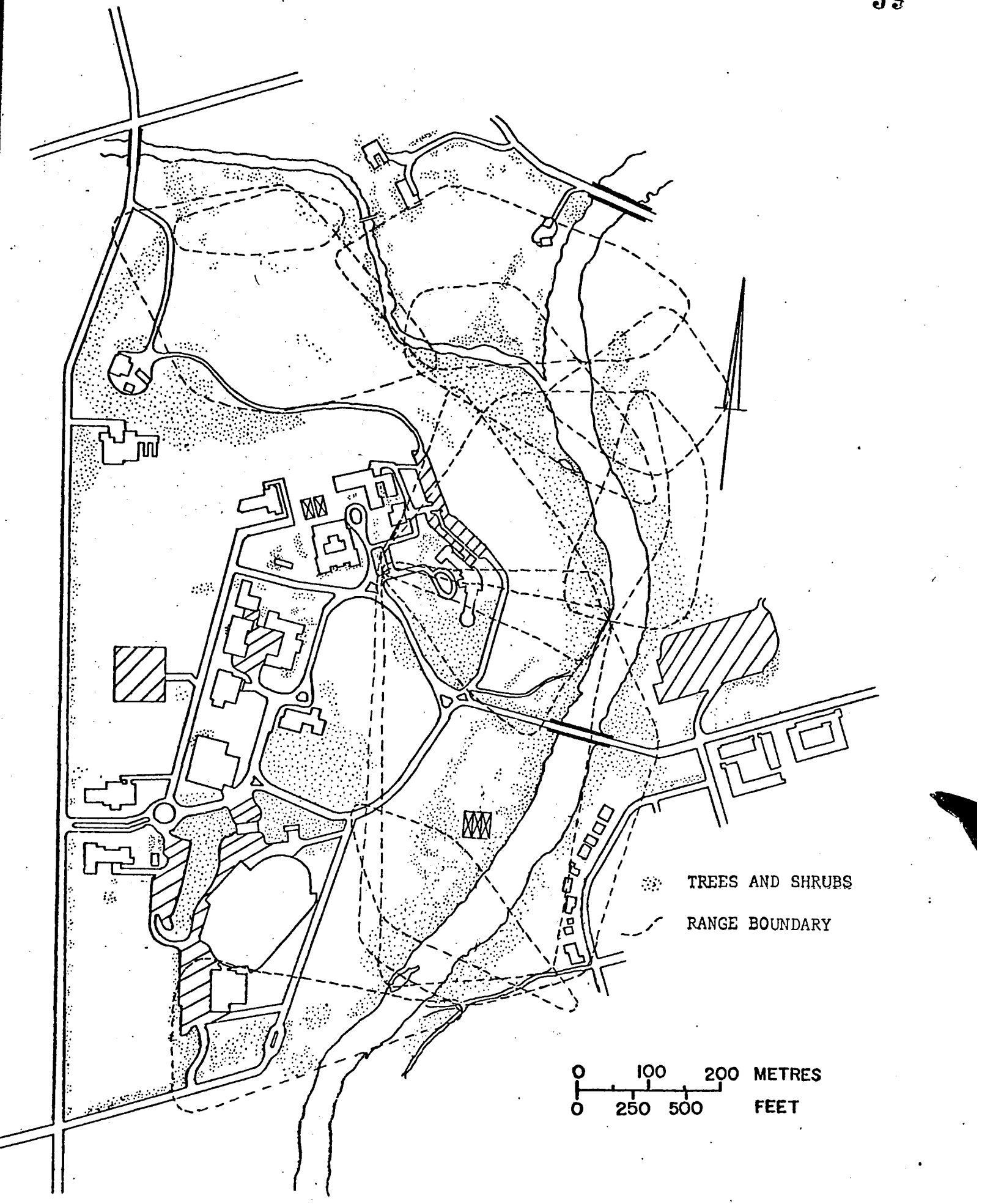
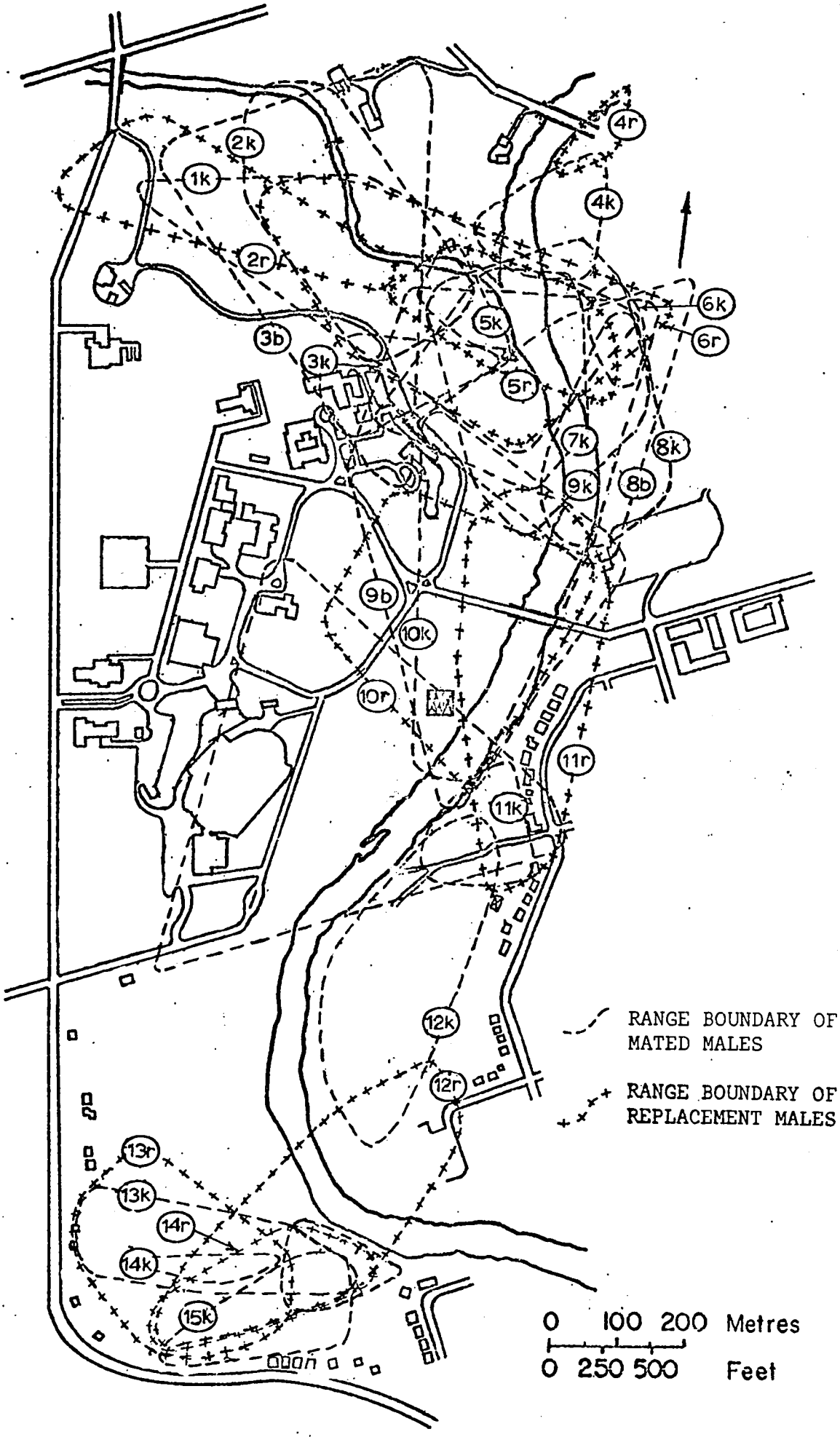

TREES AND SHRUBS
RANGE BOUNDARY
0 100 200 METRES
0 250 500 FEET

Figure 9. The non-feeding range of mated resident male Cowbirds and replacement males at London Ontario during the breeding season in 1967.

k - mated male killed

r - replacement male

b - bigamist male


2k
1k
4r
4k
2r
6k
6r
5k
3b
3k
5r
7k
8k
9k
8b
9b
10k
10r
11r
11k
12k
12r
13r
13k
14r
14k
15k
RANGE BOUNDARY OF MATED MALES
RANGE BOUNDARY OF REPLACEMENT MALES
0 100 200 Metres
0 250 500 Feet

his mate. Guarding was first observed about 2 weeks after the birds' arrival and continued throughout the season. This behavior was particularly evident if two pairs were feeding together; they often moved in a line with the two males on the inside and the two females on the ends, each male preventing the other from approaching his mate. The mated male gave many courtship bows to the female while accompanying her about. In 4 of 7 observations of copulation the participants were resident breeding females and their mates. Three of the females in these observations had been on their territories for several weeks, the other was observed on her territory only a week before the copulation occurred. The participants in the other three copulations were a resident breeding female and an unbanded male and in 2 cases a resident breeding female and a male observed one day after being banded. All three copulations occurred within a week of the females' appearance on their territories. Pair formation may not have taken place by this time.

Although males did not defend areas, their non-feeding activities were restricted to certain ranges (Fig. 8, 9). Some degree of attachment to an area must be present since males from outside did not move into the study area when 15 mated males were removed in 1967. But 4 of 9 replacement males and the 3 bigamists shifted their ranges when the 15 males were removed. The new ranges of these males incorporated the territories of their new mates, so the amount of shift in range depended on the distance from the male's former range to the female's territory. These males continued to be found in the area of their former range as well as their expanded new range. Thus, the non-feeding range of

replacement males was partially dependent on the location of his mate's territory.

The returns in 1967 of males observed in the study area in 1966 (Table 12) gave some indications of the attachment of different males in the population to the study area. Most of the mated males returned, indicating strong attachments, but only half were mated to females in the study area in 1967. The 1967 non-feeding range of 8 of the mated males that returned overlapped varying proportions of their 1966 ranges. One male was observed once, 4 April 1967, on his 1966 range and the other male was observed twice in the study area 200 m. and 700 m. from his 1966 range on 7th and 16th of June 1967.

The behavior of the apparently unmated males observed in the study area was examined to assess the reasons for their presence in the area. Since none of the mated males was observed less than 6 times (Fig. 7) it was assumed that males observed less frequently were probably not residents and these were examined as a group. Similarly males observed more than 5 times were examined as a group because the frequency of their sighting in the study area indicated they were probably residents.

Seventy-six of the 154 males were observed less than 6 times. Some of these males were likely migrants that stopped for a short period then continued. The 179 functions attributed to 167 observations of their behavior were feeding (51%), agonistic encounters (13%), courtship (17%) and other functions (19%) consisting of flying, sitting, preening, songs 1 and 4.

Examination of the reactors in courtship and agonistic behavior

was made to determine the associates of these 76 males. The courtship behavior included bowing, guarding, copulation and following (Table 10). Three of the 8 observations of bowing towards resident females (Table 11) involved the same pair of birds; they appeared to be mated because they were frequently seen together and courtship occurred between them, but observations were too few to verify this. In the other 5 bowing displays to resident females the mates of these females were not present although in one case the female's mate arrived immediately after the display and chased the other male away. Both observations of guarding a resident female (Table 11) involved the same pair, mentioned above, that appeared to be mated. The copulation (Table 11) occurred 5 May 1966 in the female's territory one week after she first appeared in the territory. This female became mated to another male. In the 3 cases in which males followed resident females (Table 11) the mates of these females also accompanied them.

All but one of the agonistic encounters occurred between males. In the male-female agonistic pattern the male chased a non-resident female away from a resident female. The resident female had given a number of threat displays to the non-resident female just prior to the chase by the male. In 36 agonistic patterns, including bowing, group bowing, bill-pointing, flight bill-pointing and chasing, 12 of the reactors were mated males.

All but 1 of the 76 males observed less than 6 times were considered to be non-residents. The status of the single male was not certain; this male exhibited guarding and bowing behavior with a resident female and appeared to be mated to this female. The other

Table 11. Female reactors to courtship patterns performed by 1) males observed less than 6 times in the study area and 2) males observed more than 5 times in the area.

Number of observations of males in study area	Courtship behavior patterns	Number of behavior patterns	Female reactors			
			Breeding residents	Non-residents	Unbanded birds	Unknown birds
<6	a) Bowing	13	8	5		
	b) Guarding	8	2	5	1	
	c) Copulation	1	1			
	d) Following	14	3	1	5	5
>5	a) Bowing	52	25	4	19	4
	b) Guarding	26	14	4	8	
	c) Following	65	29	12	12	12

Table 12. Status of males in 1966 and of those which returned to the study area in 1967

	Number of males observed in 1966	1967 status of males that returned to study area			
		Total mated males		Unmated residents	Non-residents
Mated	12	10	5	3	2
Unmated residents	9	2	0	2	0
Non-residents	29	15	4	4	7

75 males exhibited little agonistic behavior towards mated males or courtship behavior towards breeding resident females. The courtship behavior with resident females that did occur was observed when their mates were not present. Surprisingly a large proportion of males observed less than 6 times were seen again in 1967 (Table 12) indicating strong attachments to the study area. In addition, much of the courtship and agonistic behavior by these birds was observed with non-resident reactors indicating that these males were probably residents immediately outside the study area.

The behavior of the 37 unmated males observed more than 5 times was examined to determine why they were in the study area. The 624 functions of the 543 observations in the area were feeding (41%), agonistic encounters (17%), courtship (20%), and other functions (22%) including these patterns: sitting, flying, stretching preening and songs 1 and 4.

The reactors in the courtship and agonistic behavior were examined to determine the associates of the 37 males. The courtship behavior included bowing, guarding and following (Table 11). In 24 of the 25 observations of bowing to resident females (Table 11), the mate of the female reactor was not present. Similarly, in 13 of the 14 observations of guarding behavior with resident females (Table 11) the mates of the females were not present, but one female's mate arrived just after the display and displaced the male which exhibited the guarding behavior. Forty-nine percent of the bowing and guarding behavior patterns were performed by 3 of the 37 males. One gave 9 of 10 behavior patterns to unbanded female(s) (probably a single unbanded female) and a second male directed 7 patterns to unbanded

female(s) (probably a single female). These unbanded females may have been residents and the 2 males their mates. The third male gave 21 patterns: 7 to unbanded females, 2 to a non-resident and 12 to 2 resident females. This male appeared to be an unmated resident of the study area. In 45% of the following of females, the bird followed was a resident. In 55% of these cases the mate of the resident female also followed the female. None of the 37 males consistantly followed any particular female indicating that the males were probably not mated to any of these females. In 136 male-male agonistic encounters, including bowing, group bowing, bill-pointing, flight bill-pointing, supplanting and retreating, 55% of the 179 reactors were mated to resident breeding females.

Some males frequently were observed feeding in the study area. Eight of the 37 males accounted for 50% of the 258 feeding observations; these males were probably unmated residents.

Of the 37 males observed more than 5 times, 2 males appeared to be mated to unbanded females. A third male courted a number of females. The remaining 34 males did not court any particular females. The few courtship displays directed to resident females usually occurred when their mates were not present. Only 2 of 9 males observed more than 5 times in 1966 returned to the study area in 1967 indicating relatively weak attachments to the area. One of the two was observed once in 1967 300 m. from his former range. The other was observed 4 times in 1967, 600 m. from his 1966 range. Most of these males appeared to be unmated, although some may have had mates outside the study area. The number of agonistic encounters of these males with

mated males was significantly higher (chi-square, $0.025 > P > 0.01$) than the number of agonistic encounters of males observed less than 6 times with mated males. This may indicate that many of the males observed more than 5 times were unmated residents and were considered rivals by mated males.

The areas of the non-feeding range of unmated males (8.7 ± 2.2 ha.) were greater than those of mated males (6.6 ± 1.4 ha.) observed in the study area in 1967. For this comparison the ranges of 17 unmated males observed 10 or more times in the study area were compared to the ranges of 17 mated males (the 9 replacement males and 3 bigamous males were excluded from this analysis). The values, although not significant at the 0.05 level, suggested a difference in the ranges of these two groups of males ($0.10 > P > 0.05$), Student's (t) Test). The movements of mated males may be restricted by their attendance to the females, which have smaller non-feeding ranges than males. Unmated males, not limited by the movements of particular females, are free to range more widely.

On 5 occasions between 27 June and 6 July 1967 a total of 8 hours were spent searching outside the study area for birds which had been observed in the area. Eight of 83 unmated males were found; two were observed 300 m., three 400 m., two 450 m., and one 900 m. from the nearest edge of the study area. Five of these males were observed more than 5 times in the study area and 3 were observed less than 6 times. In addition to these unmated males 1 mated male was observed 300 m. from the study area. The preponderance of apparently unmated males found outside the area may have been due to weak

attachments they had to specific areas or they may have been mated to females outside the study area.

Unbanded males were captured at the banding station throughout the breeding season in 1967. In order to determine if there were any differences in the breeding condition of unbanded and banded birds as well as mated and unmated adult and yearling males, 53 males were killed in 1967 and their testes were examined. Nineteen adult and 16 yearling banded males were killed between 26 June and 30 June; sections of the testes of 16 adult and 15 yearling males contained mature sperm (stages 5, 6, 7, Scott and Middleton, 1968) and the testes of 3 adults and 1 yearling male were in the regressed condition (stage 9, ibid). Eleven of the 35 males (7 adults and 4 yearlings) were mated to resident females. The testes of the mated males were indistinguishable from those of other males. Eighteen new unbanded males (11 yearlings and 7 adults) were killed from 20 June to 30 June. Except for a yearling with regressed testes, all had mature sperm present in their testes. Thus all males were in breeding condition or had recently been in breeding condition.

BREEDING MALES AND FEMALES

In 1966 and 1967, 22 adult and 17 yearling females were considered to be breeding residents. The mates of 32 of these females were determined; 21 were adult and 11 were yearling males.

There were no significant differences (chi-square 2 x 2 test, $P > 0.9$) between the total number of adult and yearling males observed in the study area (96 and 58) and the numbers of mated adult and yearling males (21 and 11). Also when 15 mated males were removed from the population in 1967 the replacements, 8 adults and 4 yearlings, reflected the relative numbers of adult and yearling males present in the population. The numbers of adult and yearling females (47 and 55) observed in the study area were not significantly different (chi-square 2 x 2 test, $0.5 > P > 0.25$) from the numbers of their resident counterparts (22 and 17). Thus, the age of the birds did not appear to affect their breeding activities.

Monogamous pair bonds were established with males by 32 of the 39 breeding resident females. For 6 of the other 7 females there were insufficient observations of courtship behavior to determine whether they had mated with particular males. In the 7th female, courtship behavior was observed with 4 different males. This particular female was breeding, as an egg was in her oviduct when she was killed 28 June 1968. The evidence indicated that females usually had only

one mate as only one case was seen in which a female might have had more than one.

Formation of the pair bond in the 32 mated pairs usually began immediately after they were observed together. The male accompanied the female and began courtship. Bowing, the courtship behavior usually seen first, was observed an average of 4 days after the first observation in which a pair was seen together. Guarding, which probably signifies completion of pair formation, was observed an average of 12 days after a pair was first observed together indicating that pair formation takes about 2 weeks to complete.

MALE-MALE RELATIONSHIPS

Male Cowbirds appear to establish a hierarchy among themselves with dominant males being mated to the resident breeding females. Dominance was determined in 22 observations of male-male encounters (retreat, supplant and chase behavior). Mated males were dominant in 17 and unmated males were dominant in 5 observations (Table 13). Unmated males were subordinate in 19 and mated males were subordinate in 3 cases. Dominance was observed in significantly more mated than unmated males and subordination was observed in significantly more unmated males than mated males ($P < 0.005$, chi-square test). On the occasion in which a mated male dominated another mated male the subordinate male was with the other male's mate. This male arrived and immediately established dominance over the other male. This encounter occurred within the territory of the dominant male's female; the territory of the mate of the subordinate male did not overlap this position. The observations of dominance of mated males over the unmated males occurred in a number of different situations. In 7 cases the dominant males were guarding their mate within her territory. Dominance was observed on 2 other occasions inside the territory of the female of the dominant male and 7 times outside the female's territory. Dominance was established after group bowing in 2 of the 7 cases observed outside the female's territory. All 16 of the

Table 13. Dominance and subordinance in mated and non-mated male Cowbirds.

Dominant males	Subordinate males	
	Mated	Unmated
Mated	1	16
Unmated	2	3

observations occurred within the non-feeding range of the dominant male. In both cases in which an unmated male dominated a mated male their mates were not present. One case was observed outside the territory of the male's mate and outside of his non-feeding range. The other was observed at the edge of the female's territory and within his non-feeding range. The maintenance or establishment of dominance does not appear to be related to the presence of his mate or to the proximity of the male to the territory of his mate. Mated males seem to be dominant in their non-feeding range. Dominance probably would be maintained outside the non-feeding range of the male if his mate were present since the male guards his female everywhere, but data were inadequate to prove this.

Insufficient data were available to determine if hierarchies were present within groups of mated males or unmated males, but some information was collected that suggested a form of hierarchy. Males usually remained mated to the same female for the whole breeding season. On one occasion a mated male was last seen with its mate 16 May 1967; another male apparently took over this male's female 19 May and the first male was observed with another male's female which became its new mate. This third male did not get another female. These observations may indicate the presence of a hierarchy within mated males.

Because of the difference in arrival times of adults and yearlings (Fig. 3, 4) one might expect non-random mating, with adult males mated to adult females and yearling males mated to yearling females. In 32 mated pairs, adult males were mated to 13 adult and 8 yearling

females; yearling males were mated to 3 adult and 8 yearling females. Although the difference between the numbers of adult and yearling females mated to adult and yearling males was not significant (Fisher exact chi-square test, $P = 0.07$) the values suggest that adult males mated more often with adult females than yearling males did. The yearling males mated to adult females arrived in the study area earlier than most of the yearling males mated to yearling females. Similarily, the adult males mated to adult females arrived before most adult males mated to yearling females.

BREEDING EXPERIMENT

In 1966-67, an experiment consisting of 8 parts was conducted to determine whether dominant or subordinate males mated with available females. The age of males was also examined to see if adult rather than yearling males became mated to the females.

In all 8 parts of the experiment the dominant males mated with the females (Table 14) i.e. they guarded the females and bowed to them frequently. This is consistent with observations of mated males in the wild.

Although the numbers of yearlings and adults in the experiment were small, the data indicated no differences in the ability of yearling and adult males to procure mates (Table 14). Similar observations were made in the wild, and the proportions of yearling and adult males mated to females were similar to proportions of each age group in the population.

Table 14. Results of an experiment conducted to compare the mating ability of yearling vs. adult males, and dominant vs. subordinate males.

Part	Duration	Birds Present		Dominance hierarchy		Mated pair	
		Males	Females	Males	Females	Male	Female
1	30 Jan-13 Feb	A1,2,Y1,2	A1,Y1	A1>Y2>A2>Y1	Y1>A1	A1 - Y1	
						Y2 - A1	
2	15 Feb-27 Feb	A3,Y3	Y2	A3>Y2		A3 - Y2	
3	28 Feb-3 Mar	A4,Y4	A2	Y4>A4		Y4 - A2	
4	4 Mar-7 Mar	A5,Y5	Y3	A5>Y5		A5 - Y3	
5	8 Mar-11 Mar	A6,Y6	A3	A6>Y6		A6 - A3	
6	12 Mar-15 Mar	A7,A8	A4	A7>A8		A7 - A4	
7	16 Mar-19 Mar	A9,A10	A5	A9>A10		A9 - A5	
8	20 Mar-24 Mar	A11,A12	A6	A11>A12		A11 - A6	

A = adult bird

Y = yearling bird

DISCUSSION

Territorial Behavior

The Cowbird appears to be a territorial species. In the various definitions of territory, defence of an object or an area is the fundamental concept involved. The female Cowbird defends an area and the male defends a female. If egg-laying is considered "nesting", the female territories could be classified as type B of Nice (1943, p. 163), i.e. areas for mating and nesting but not feeding.

Some aspects of Cowbird territoriality as described by Friedmann (1929), Nice (1937) and Laskey (1950) are consistent with my findings. Friedmann (1929) believed that Cowbirds have definite territories. He said "Not only has the female a definitely marked-off breeding area, but the male has a definite post, entirely comparable to the 'singing tree' that Mousley described." He concluded that the male was territorial because it could be found almost constantly on the same perch in the same tree. He also felt that females seemed to have certain definite territories. At Ithaca the territories of 3 pairs appeared to be distinct from one another, but at Cayuga Lake the extremities of territories were found to merge with neighboring ones. He also stated that "the Cowbirds do not make any very spirited attempts to defend their territories and consequently in regions of unusual abundance the territorial factor is much less noticeable." Nice (1937) noted

that her banded Cowbirds had definite ranges but showed no territory defence. In a study of banded Cowbirds attracted to a baited area Laskey (1950) observed many threats and fights but they did not appear to be in defence of territory. She stated "I witnessed no sustained effort to keep males or females out of a pre-empted area." One pair seemed to be dominant over other Cowbirds which feed in the area. She stated "I believe the dominant pair showed vestigial territory behavior in intimidating others and keeping the domain for their own in pair formation and mating."

Friedmann considered the Cowbirds to be territorial because they restricted their movements to certain areas not because they defended particular areas or things. I observed defence of territory by the females whereas Laskey and Nice did not. This discrepancy probably arises from the fact that the areas I designated as territories did not encompass the feeding areas. I found that feeding females would defend their mates against other females but otherwise made no attempt to restrict the movements of other females. Laskey made her observations at a feeding station which probably was part of a particular female's territory and this would account for one pair's dominance in the area. Since it was also a feeding area the other female Cowbirds were not excluded. The territories of the females as noted by Friedmann overlapped adjacent territories. Further evidence of this overlap was recorded by D.M. Scott (personal communication) who found 2 Cowbird eggs laid on the same day in each of 10 nests of the Cardinal (Richmondena cardinalis) at London Ontario. He also observed 4 Cowbird eggs laid in a Cardinal nest and 4 eggs laid in a Yellow Warbler

(Dendroica aestiva) nest in one day.

A number of female Icterids defend the nest or nest area: Common Grackle (Quiscalus quiscula), (Ficken, 1963); Brewer Blackbird (Euphagus cyanocephalus), (Williams, 1952); Yellow-headed Blackbird (Xanthocephalus xanthocephalus), (Fautin, 1940); and the Red-winged Blackbird (Agelaius phoeniceus), (Nero, 1956). The defence of an area which contains host nests by the female Cowbird may be an extension of nest defence found in other female Icterids.

The males in the study area restricted their movements to specific ranges and were often found in particular trees. However, there was no defence of these ranges or trees and different males were often observed in the same "singing trees". Friedmann could not be certain of the identity of males in the "singing trees" since his birds were not banded. Mated males defended their females from other males. These mated males were dominant over other males even when their females were not present. Laskey (1950) also noted indications of dominance: "There was much evidence of what I came to regard as sexual jealousy, however, and, particularly early in the season, of strife for dominance". She also stated "There was no indication of a peck-order similar to that described by Allee for domestic chickens (Nice, 1943: 92) nor of a society comparable to that of the Jackdaw (Corvus monedula)". I was not able to establish the exact relationships between each male in the hierarchy other than noting that mated males were dominant over non-mated males. There were indications of a more complex hierarchy then simply mated males being dominant over unmated males. In the experiment with captive birds the 4 males with 2 females

present had a straight-line hierarchy. In the field one male usurped the female of a second male which in turn took the mate from a third male and the third male was unable to procure another mate.

A dominance hierarchy in the males is probably established and maintained by the group bowing behavior observed frequently in the field. It appears that dominance is established by a male in an area and this male then mates with the female in the area. This interpretation is supported by the fact that 3 of the males which replaced 15 mated males removed from the population already had mates, that is, they were dominant over unmated males still present in the population and thus obtained second females. Laskey (1950) also reported "To me it appeared that the female which was successful in gaining dominance among females in an area of her own choosing accepted the dominant male of the same area as her mate." The dominant male would guard its female from the advances of other males for the remainder of the season. The guarding of the female rather than a territory is observed also in the Brewer Blackbird (Williams, 1952). Ficken (1963) reports that the male Common Grackle guards its mate and a small area around the nest site.

Population structure

The Cowbirds were all monogamous except for 3 bigamous relationships which developed only after 15 mated males were removed from the population. Williams (1952) noted in the Brewer Blackbird there were more cases of monogamy than polygyny. He also states that polygyny usually occurs when the first female is incubating. The male does not guard this female as assiduously as before and may acquire a second

female. The female Cowbird is not restricted by nesting and the male must devote his full time to guarding one female. Friedmann (1929), Wetmore (Friedmann, 1929, p. 171) and Laskey's (1950) observations also indicated monogamous mating in Cowbirds. Nice (1937), however, stated "...here on Interpont, with an abundance of Cowbirds promiscuity prevails just as the older writers maintained." Nice bases this assumption on observations of particular males with different females and particular females with varying numbers of males. Also she observed different combinations of males and females accompanying each other. In this study observations similar to those of Nice were recorded. However, when one or more females were accompanied by a number of males their mates were usually present and if present were guarding them from other males. If a female's mate was not present another male would often guard her. If her mate returned, he would drive away the other male. The different males were attracted to the female(s) when song 6 was given i.e. any male within auditory range of song 6 would usually join the female or females which uttered the song. Females often would drive away any males including her mate and fly off without uttering song 6. The behavior was probably conducted prior to the searching behavior by the female since the female was normally along when searching for nests. During this period her mate would usually be found on a prominant perch or "singing tree" uttering song 4 repeatedly. When the female returns from searching she would fly by uttering song 6 and her mate would rejoin her. Thus there are periods when the female is separated from her mate and a temporary relationship with other males could develop.

This is supported by the observation that 3 of 7 copulations were between unmated birds.

Icterids show interesting differences in sex ratios. Mayr (1939) writes of the group that "... it contains some genera with an equal sex ratio, some with a surplus of males and some with a surplus of females. An equal sex ratio probably occurs in the majority of the species; there is evidence to support it in the case of the Bronzed Grackle (Quiscalus aeneas)". He also notes that a surplus of males occurs rarely and cites the Cowbird as an example.

More males than females, 1.5:1, were observed in the study area. The apparent surplus of male Cowbirds has been reported by Friedmann (1929), Norris (1947) and Laskey (1950). Norris stated "During the breeding season in the Firth the male Cowbirds probably outnumbered the females but not by a large margin." Friedmann observed the ratio to be about 1.5 males to each female and Laskey's notes indicated that it was 1.6:1.

This ratio indicates a higher mortality in females. Since the proportions of yearling males and females are the same the excessive mortality must occur after the first spring migration. I have no data indicating that females were disappearing on the breeding grounds so that most mortality must occur after the breeding season. Perhaps the physiological strain of egg laying in the breeding season affects the chances of females surviving during the migration at the end of the season.

Almost all females examined were in breeding condition. This is supported by the more extensive observations of A.V. Kennedy

(personal communication) who observed in 1965 that only 3 of 149 female Cowbirds collected from 7 May to 25 June in the London area lacked ova greater than 2 mm and post-ovulatory follicles. Observations on the behavior of females seem to indicate that most non-residents observed in the study area were using it as a feeding area and that most probably held territories outside the study area.

Yearling female Cowbirds were assumed to breed since there was no significant difference in the proportions observed in the population and those breeding. Other Icterid yearling females also breed. Wright and Wright (1944) state "There seems to be no doubt but that the yearling females of Agelaius phoeniceus breed." Linsdale (1938) noted that the female Yellow-headed Blackbird breeds in the first year.

Breeding activities of adult and yearling males

There was no difference between the proportions of yearling and adult males breeding and those present in the population. This is surprising since many male yearling Icterids do not breed in their first year. This has been recorded for the Red-winged Blackbird (Wright and Wright, 1944), Tricolored Red-wing (Lack and Emlen, 1939), Yellow-headed Blackbird (Fautin, 1940), and the Boat-tailed Grackle (McIlhenney, 1937). But in the Brewer Blackbird (Williams, 1952), which is similar to the Cowbird in that the male defends the female rather than a territory, it was observed that 4 first year males bred in the study colony and one outside the colony. Williams could not distinguish yearling from adult males on the basis of plumage and

and therefore he noted that there was a possibility that there may have been more yearling males in the group of males of unknown age.

Bowen's (personal communication) observations that yearling males were late residents in the study area may be due in part to the yearling males late arrival back from the wintering grounds. Bowen's observations of fewer yearling resident males than adults was probably due to the small proportion of yearling males present in the population. I also had similar observations for yearling males in 1966, as reported by Scott and Middleton (1968, p. 85). Few yearling males appeared to be breeding in 1966. When the sample size was increased in 1967 the relative numbers of yearling and adult mated males reflected their proportions in the total population.

In conclusion, this study indicated that female Cowbirds defend territories and males defend females. Cowbirds appear to be monogamous and yearling males seem to participate in reproduction to the same extent as older males.

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