ILLEGIBLE DOCUMENT

THE FOLLOWING DOCUMENT(S) IS OF POOR LEGIBILITY IN THE ORIGINAL

THIS IS THE BEST COPY AVAILABLE

IMPORTANCE OF SOCIAL AGGRESSION IN BOOMING GROUND HIERARCHY OF GREATER PRAIRIE CHICKEN (TYMPANUCHUS CUPIDO PINNATUS)

by

WARREN BAXTER BALLARD, JR.

B. S., New Mexico State University, 1969

A MASTER'S THESIS

submitted in partial fulfillment of the

requirements for the degree

MASTER OF SCIENCE

Division of Biology

KANSAS STATE UNIVERSITY

Manhattan, Kansas

1971

Approved by:

Major Professor

TABLE OF CONTENTS

INTRODUCTION

During the past 15 years a considerable amount of research has been devoted to the discovery and verification of various population regulatory mechanisms. For the most part, this research has evolved around the theories of Andrewartha and Birch (1954), Lack (1954), and Wynne-Edwards (1962). The theories of Lack and Wynne-Edwards involved birth or death rates in regulating the numbers in bird populations. Lack (1954) believed that the birth rate or clutch size of a bird is adjusted by natural selection to provide the maximum number of young that the parents, on the average, can raise. The birth rate does not vary with fluctuations in population size, and density regulation must be accomplished through mortality. In direct contrast was the theory of Wynne-Edwards (1962), which stated that population density was controlled by variations in the birth rate through self-regulatory mechanisms (territories, hierarchies, etc.).

Many researchers have partially verified the theories of Lack, but few experiments have been designed to test the theories of Wynne-Edwards. Wynne-Edwards postulated that the functional value of polygyny in avian species with equal sex ratios was to maintain a high level of competition among the males, thus perpetuating the most aggressive individuals through group selection. Wynne-Edwards' theory of group selection has been severely criticized as having

little genetic foundation (Lack, 1966; Brown, 1964 and 1969), but aggression or dominance ability could be transmitted through natural selection of the fittest. A genetic basis for inheritance of dominance ability was verified in the domestic fowl (Guhl et al., 1960; Craig et al., 1965; and others), thus inheritance of aggression in wild avian populations seems possible.

The present study was designed to test the theory that greater prairie chicken (Tympanuchus cupido pinnatus) booming grounds, or leks, are instrumental in perpetuating high aggressiveness in prairie chicken populations.

LITERATURE REVIEW

Introduction

Much research has been conducted on the behavior of birds. Only the literature pertaining to territorial behavior, mating success, and aggression will be presented here.

Wynne-Edwards (1962) was the first investigator to bring the theory of self regulation into modern view. He theorized that food ultimately determined the numbers in a population; but that some proximate factor, such as conventional behavior, was necessary to achieve a balance with the food supply. He theorized that all forms of property tenure provided conventional objects of competition which were contested as a prelude to reproduction and lead to a determinate pattern of dispersion. The objects were limited

in number, which placed a ceiling on breeding density and caused expulsion of surplus individuals. The indication was that the conventions governing social competition could only have evolved through group selection.

Wynne-Edwards' theory of group selection was criticized for its lack of genetic foundation (Brown, 1964). Lack (1966:304) stated that if behavior of this type occurred it was of such an obvious advantage to the individual that inheritance through natural selection of the fittest was the apparent means of transmission through the population.

A genetic basis for the inheritance of social dominance ability or aggressiveness was established in the domestic fowl (Guhl et al., 1960 and Craig et al., 1965). Studies of domestic chickens indicated sufficient additive genetic variation of social dominance ability to allow selection for the trait (Guhl et al., 1960 and Tindell and Craig, 1960). Five generations of bi-directional selection produced large differences in social dominance ability in chickens (Craig et al., 1965:130). Thus it appeared that selection for dominance ability could occur in wild avian populations, assuming there were no drastic differences in genetic makeup between wild and domestic populations.

General

Several studies have been conducted on various avian species

in order to ascertain the importance of territorial behavior in regulating bird populations. Some of the most noteworthy are those of Hensley and Cope (1951), Stewart and Aldrich (1951), and Kluyver and Tinbergen (1953).

Brown (1969), in his review of the literature on territorial behavior and population regulation in birds, concluded that there are three population levels at which territorial behavior might be hypothesized to regulate reproductive rates. Brown's (1969: 300) level three population considers surplus breeders which has been inferred to exist in several tetraonid populations. He concluded that at least four criteria must be met to conclude that territorial behavior limits breeding density. The four points are:

1. It must be demonstrated that some individuals are being deprived a chance to breed, and that they are part of a surplus.

2. It must be demonstrated that territory owners are preventing surplus birds from breeding.

3. It must be demonstrated that territoriality prevents some females from breeding.

4. The population studied must be representative for the species being studied.

All of the studies discussed have attempted to determine the role or importance of territorial behavior in population regulation, but none have attempted to test the theory that selection for aggression occurs in a natural, unconfined, avian population.

Grouse

Recently many researchers have been stimulated by the possibility of a behaviorally oriented, density dependent, population regulatory mechanism operating in the grouse family, Tetraonidae.

Grouse apparently originated in both eastern Siberia and the northwestern parts of North America (Hjorth, 1967:240). Several species of grouse exhibit behavior in which the males congregate on a traditional site (lek) for communal display. The females come to these sites for copulation. Lekking tetraonids exhibit both strong and weak breeding social hierarchies (Robel, personal communication). Strong social hierarchies are evident in three New World lekking tetraonids; the prairie chicken (Tympanuchus cupido), the sharptail grouse (Pedieciets phasianellus), and the sage grouse (Centrocercus urophasianus), while weak social hierarchies are evident in two Old World lekking tetraonids; the black grouse (Lyrusus tetrix) and the capercaillie (Tetrao urogallus) (Scott, 1950; Lumsden, 1968; and Robel, 1969b).

New World Lekking Grouse

Of the three New World lekking grouse which exhibit strong social hierarchies, the complexity of the hierarchy appears to increase in the following direction; the greater prairie chicken, the sharptail grouse, and the sage grouse (Scott; 1950:483).

Sage Grouse

Scott (1942;483) stated that dominance in sage grouse played an important role in the sexual life of the species. The male sage grouse hierarchy consisted of a mating spot occupied by master cocks, surrounded by sub cocks, who in turn were surrounded by guard cocks. Of the 154 matings which he observed, 74 percent were by master cocks, 13 percent were by sub cocks, 3 percent were by guard cocks, and 10 percent were by isolated cocks (Scott, 1942:483).

The achievement of dominance by the master cock was not simply a matter of location, because they were usually large, older birds, and apparently the most aggressive (Scott, 1942:483). Lumsden (1968:26) felt the function of the hierarchy was to concentrate mating among the most dominant males on the strutting ground. He concluded that the term lek was inappropriate for sage grouse because of the large number of cocks, which was due to a number of leks being grouped together in one place. Thus, he proposed the term conjunct lek for sage grouse.

Lumsden (1968:18) pointed out that Scott (1942) avoided the use of the word territory in his paper, but that he did acknowledge territorial behavior. Lumsden (1968:20) acknowledged the importance of what he termed the territory "place" in the absence of hens. He believed that sage grouse used landmarks for orientation

but that they did not appear to have territorial boundaries where rivals were met and defended against. Fighting when females were present was rare since the males spent most of the time strutting. Occasionally cocks moved considerable distances from their territories while chasing females, but more often kept their relative position to the other males.

Sharptail Grouse

Sharptail grouse exhibit territorial behavior similar to prairie chickens and other lek type grouse (Scott, 1950 and Lumsden, 1965). Each male had a territory nucleus which challenging males seldom penetrated (Lumsden, 1965:8). As the distance from the nucleus increased, challenging by neighboring males became more frequent until a "belt" was reached where no bird was intimidated, and at which "ritual fighting" took place. There was a hierarchy of dominance at least among neighbors. The most dominant and active cocks did not necessarily hold the largest territories. Yearling males normally did not hold territories, but on occasion were "vigorous" enough to claim an area.

Lumsden (1965:11) believed that dominance relationships in the sharptail grouse existed throughout the entire year and were important in determining the position and dominance hierarchy of neighbors on the strutting ground, thereby reducing the number of interrupted copulations. Of the 13 males he observed, the most

dominant cock completed or attempted 74 percent of the copulations (Lumsden, 1965:59).

Lumsden (1965:63) believed that the lek probably had a greater function than just to bring about matings. He concluded that the lek replaced territoriality in monogamous species and controlled dispersion of the population through suitable habitat. He thought it was unlikely that such birds were totally excluded from breeding.

Prairie Chicken

Of the lekking North American grouse, the prairie chicken apparently has the least complex of the breeding social hierarchies, although there are similarities to that of the sharptail grouse (Scott, 1950 and Robel, 1967).

The breeding display of the prairie chicken was described in several papers (Bent, 1932; Hamerstrom and Hamerstrom, 1960; and Robel, 1964). All of these authors have mentioned the importance of aggressive behavior during the display period.

Prairie chickens establish and defend their territories by fighting with neighbors (Schwartz, 1945:49). The prairie chicken territory has an area where the cock is dominant and where a majority of the booming takes place. Within a cock's own territory a male prairie chicken usually wins fights; in the territory of another he usually loses (Hamerstrom, 1941:39). Territory bound-

aries overlap so fighting is common on the booming ground. Territories dissolve when a hen appears, but the males usually maintain their relative positions to each other. Schwartz (1945:49) reported that the territories had no definite dimensions or exact positions, and when a male was removed by shooting or trapping the territory was quickly taken over by neighboring birds. He reported that at the height of the season the cocks stayed close to their territories with little or no fighting occurring during this time.

Hamerstrom (1941:42) believed that most copulations took place away from the booming grounds at isolated territories, because during 300 hours of observation on a booming ground only 19 or 20 copulations were recorded. During these observations Hamerstrom recorded many instances of males being knocked off females by neighboring males. In contrast are the findings of Robel (1970: 308), who during a 5-year study recorded 121 copulations on the booming ground. No copulations were observed away from the booming ground. Of the 121 copulations observed, 89 percent were performed by the two most aggressive males. Both males were at least 2½ years old and controlled the largest territory. Robel (1967: 113) had previously concluded that the mating success of an individual was correlated with social rank, and that social rank was reflected by aggressive defense of territory. He also determined

that the hierarchy was composed of alpha, beta, gamma, subordinate, and non-territorial males.

Females usually arrive on the booming grounds in late March or early April (Hamerstrom, 1941; Schwartz, 1945; and Robel, 1970). Schwartz (1945:52) reported competition among females on the booming ground when another hen would assume the copulation posture. Hamerstrom (1941:39) had reported similar interruptions between females due to what he felt was a general unreadiness by one female to mate. Robel (1970:308) reported that a definite dominance order existed among groups of three to six females on the booming ground. The dominant female of each group prevented the other females from breeding until after she was serviced.

Hamerstrom (1941:44) was uncertain about the function of the booming grounds because so few copulations were observed. Robel (1967:113) suggested that booming grounds serve two purposes: "rigorous natural selection for the fittest mating stock and the attraction and stimulation of females".

Old World Lekking Grouse

Old World lekking grouse have a less structured social hierarchy than those of the New World (Scott, 1950 and Robel, 1969b). Matings are spread out more evenly among participating males than those in the New World species.

Black Grouse

Several descriptions of black grouse behavior have been conducted by Selous (1909), Lack (1939), Hohn (1953), and Hjorth (1966). Selous (1909) first noted that each male had a territory on the lek. Size of territory varied considerably with the innermost male having the smallest, while those on the outer edge sometimes have enormous territories (Lack, 1939:292).

Hamerstrom and Hamerstrom (1960:280) reported that black grouse respected each others territories much more than prairie chickens. They agreed with Lack's (1939:295) conclusion that the function of the territory for the black grouse was to reduce interference from neighboring males during copulation.

Lack (1939:296) observed marked differences in the degree of aggressiveness of different black cock individuals. Hohn (1953: 54) indicated the same thought when he reported inferior birds being turned away from the lek unable to establish a territory. Robel (1969a:54) reported that during the spring the black cock population was stratified into two segments: "one a stable lekking flock and the other a less cohesive non-lekking group".

Kruijt and Hogan (1967) concluded that age and fighting ability were the primary factors determining a bird's location on the lek. They did not mention the existence of a social hierarchy, but observed that the birds in the center position of the lek

exhibited higher levels of aggression. Four of the birds occupying the center position performed more than 85 percent of the copulations. They also observed many instances of interruptions during copulation by neighboring males.

Capercaillie

The capercaillie uses the same display area each year (Lumsden, 1961:258). Capercaillie territories differ from other lekking grouse territories in that there is no overlap. Between each territory there is a void area which remains undefended. Territorial males paid no attention to non-territorial birds, most of which were juveniles. Due to these differences Lumsden (1961:261) felt the term lek was inappropriate for the capercaillie.

Fuschlberger (1956) believed that matings of capercaillie took place in the afternoon on what he termed "mating grounds", which may be removed from the display ground. Lumsden (1961:271) had no observations to substantiate Fuschlberger's findings. On the contrary, of three lekking males under observation, he recorded 13 copulations, 12 of which were performed by one cock. No interference from other cocks was recorded.

MATERIALS AND METHODS

Study Area

The study area was located 9 miles east of Junction City in T12S, R7E of Geary County, Kansas, and was enclosed almost entirely

by the 6000 acre Simpson Ranch. Vegetation was representative of the northern Flint Hills region being dominated primarily by big bluestem (Andropogon gerardi) and little bluestem (Andropogon scoparius). Detailed descriptions of vegetation and topography of the study area were presented by Briggs (1968) and Watt (19690.

Observations were conducted on two booming grounds: the north experimental ground and the south control ground. Both grounds have been active at least since 1964.

Trapping

Male prairie chickens were live trapped and marked with color leg bands and occasionally with plastic patagial tags to facilitate individual recognition. Cannon nets, Japanese mist nets, and bow traps were used to capture prairie chickens on booming grounds. Trapping techniques are described in detail by Viers (1967), Silvy and Robel (1967 and 1968), and Watt (1969).

Robel's (1966 and 1967) studies have shown that the dominant male on each booming ground conducts up to 95 percent of the copulations. Since this male is usually the most aggressive bird as indicated by territory size (Robel, 1966), it appeared that the booming ground regulated the number of birds which were allowed to breed and forced additional males to go elsewhere. An experiment was designed to test the hypothesis that the booming

ground hierarchy of the greater prairie chicken is instrumental in the natural selection of aggression.

Initially, the experiment was to involve the removal of dominant males and females from the experimental ground. However, removal of dominant females was not possible since they did not exhibit an observable social hierarchy while on the ground. The experiment was then modified and only dominant males were removed.

Removal of dominant males leads to the hyposthesis that there will be no change in the number of males on the ground. The alternate hypothesis would be that after removal new birds will come on the ground and establish territories.

Theoretically, the removal of dominant males would leave aggressive but socially equal individuals, which leads to the second hypothesis: removal of dominant males will cause no change in reproductive behavior. The alternate hypothesis being that removal will cause a change in reproductive behavior.

Behavioral Studies

Observations were made on two booming grounds during the spring of 1970 and 1971 from blinds constructed on the edge of the grounds. The two booming grounds were located on a ridge extending several kilometers northwest to southeast. The grounds were located approximately 2 kilometers apart. Approximately five mornings per week were spent between the two grounds. Ob-

servations usually began ½ hour before sunrise and lasted 2 to 3 hours, depending on booming ground activity. Removal experiments were conducted only on the north experimental ground. The south ground served as a control area.

Males were referred to as adult male (AM-No.), juvenile male (JM-No.) or just male (M-No.). Males referred to as M indicate that the bird was not handled by the author, therefore, no determination of age was possible.

Detailed notes were taken each morning describing behavior, aggressive encounters, female visits, copulations, and numbers of males present for each booming ground. Territoriality of males was determined by recording the exact location of each bird at 15 minute intervals. Locations were determined with the aid of a hand held compass mounted on an accurate range finder. Territories were plotted with the aid of a drafting machine. The area of each territory was determined with a compensating polar planimeter.

Territory sizes were used as an index of social standing in the dominance hierarchy. Robel (1964:705) divided territories into concentric rings to include approximately 50, 70, and 90 percent of the location records for each bird. He referred to these rings as primary, secondary, and tertiary territories. His territories showed little overlap, but only the locations of four

males were plotted. In this study territories were plotted using 70 percent of each bird's location record due to the large amount of overlap. Territories were originally plotted like those of Robel's, but due to the complexity involved in presenting such diagrams only the combined primary and secondary components were discussed in this report.

Bird location in reference to other males, number of aggressive encounters, and notes on individual behavior were also used as indices of social standing. Males were classified as alpha, beta, or tertiary depending on the above criteria. Alpha males have been shown to be the most aggressive bird controlling the largest territory (Robel, 1966 and 1967). Robel (1964) divided aggressive encounters into weak and strong social interactions. No such distinction was made in this study. An aggressive encounter occurred if two males met and exhibited aggressive tendencies.

An aggression index was calculated for the experimental ground by considering only those birds above the mean number of encounters per bird. The number of encounters for each bird was then divided by the number of males encountered. Birds with a higher index were generally considered to be more aggressive.

Beta males were subdominant to alpha males as determined by location of territory, aggressive encounters, territory size, and

individual behavior. Beta males were usually dominant to gamma males if their territories were adjoining. Gamma males usually held small territories on the periphery of the ground, spent most of their time fighting, and exhibited subdominance behavior to alpha and beta males.

The number of copulations per male was used as an index of mating success. Notes were taken on interruptions and disturbances by other displaying males and females. An interruption consisted of a bird being physically knocked off a female by another male, while a disturbance occurred when a copulation would have taken place if another male had not been present.

Procedure

Each spring of observation has been classified as a separate experiment (Experiment I for 1970 and Experiment II for 1971). Each experiment was then classified into separate phases.

Experiment I was stratified into four phases: Phase One consisted of the preremoval period. During this phase notes on the dominance hierarchy were obtained. Dominant individuals were determined and removed which initiated Phase Two. Phase Two included the first removal of dominant males and the time up to the second removal, which started Phase Three. Phase Three continued until a noticeable change in the dominance hierarchy was observed which initiated Phase Four. Phase Four lasted from the change in

dominance to the termination of Experiment I.

Experiment II was stratified into three phases: Phase One consisted of the preremoval period. During this phase notes on the dominance hierarchy were made. Dominant individuals were determined and removed which initiated Phase Two. Phase Two included the time up to the second removal which initiated Phase Three. Phase Three continued to the termination of Experiment II.

RESULTS

Banding and Trapping

Three adult males were captured with cannon nets between 23 February and 13 March 1970 on the control ground. Each male was aged and individually marked with colored leg bands and patagial tags before being released. Five adult males and one juvenile male were captured on the experimental ground between 14 March and 23 March 1970. Each male was aged and individually marked with colored leg bands. After termination of Experiment I another three adult males were captured on the experimental ground with cannon nets on 27 May 1970. Each male was aged and marked with colored leg bands prior to release.

Experiment I

Control Ground

Observations on the control ground were conducted from 21 April to 20 May 1970. A total of seven mornings were spent re-

cording behavioral data. No discernible changes in behavior were evident during that time period so the data were not stratified into phases. Observations consisted of notes concerning aggressive encounters, bird location sightings, female visits and behavior, and individual male behavior.

Attendance of males on the display area was classified as regular and irregular. Regular attendance occurred when a male established a territory and was present for at least three observation days. Irregular attendance occurred when an individual did not remain on the ground for at least three observation days. Seven regular males were in attendance throughout the observation period until 20 May 1970, when attendance for both regulars and irregulars started to decline (Figs. 1 and 2).

Two hundred and thirteen territory location sightings were recorded (Table 1). Bird M-2 had the largest territory (237.5 m^2). Bird M-3 had the second largest territory (157.5 m^2), while AM-1 had the fifth largest (62.5 m^2). Mean territory size was 98.73 m^2.

Birds on this ground appeared to have their territories established in primarily two clusters of individuals (Fig. 3). Bird M-2 had the largest area on the ground with very little overlap occurring except for the small amount with AM-1 and M-3. Bird M-3 and AM-1 had overlapping territories. In the other cluster M-4, M-5, and M-6 had considerable overlap of territorial boundaries

with M-5 having the largest non-overlapping portion.

A total of 487 aggressive encounters was recorded on the control ground (Table 2). Bird M-3 had the largest number of encounters (168), while AM-1 and M-6 rated second and third with 166 and 156 encounters, respectively. Bird M-2 had the fourth largest number of encounters (141). Bird M-2 interacted with more males (7) than did any of the other participants. Bird AM-1 interacted with six birds while M-3, M-5, and M-7 each interacted with five males.

Three female visits were recorded on the control ground (Fig. 4). Visits occurred on 28 April, 11 May, and 14 May 1970. Two successful copulations by M-2 were observed during the last two female visits. No interferences or disturbances were observed during any of the female visits.

Notes on individual female behavior were also recorded. Females did not wander from one side of the ground to the other, but went immediately to the alpha male's territory (M-2), where in two out of three instances they were mated shortly after arrival. Females left the ground within 5 minutes after copulation.

Males were not observed shifting territories with the appearance of females. Each male usually stayed within his own area, although disputes at territory boundaries were common.

The alpha and beta males on the control ground were easily

THIS BOOK CONTAINS NUMEROUS PAGES WITH DIAGRAMS THAT ARE CROOKED COMPARED TO THE REST OF THE INFORMATION ON THE PAGE.

THIS IS AS RECEIVED FROM CUSTOMER.

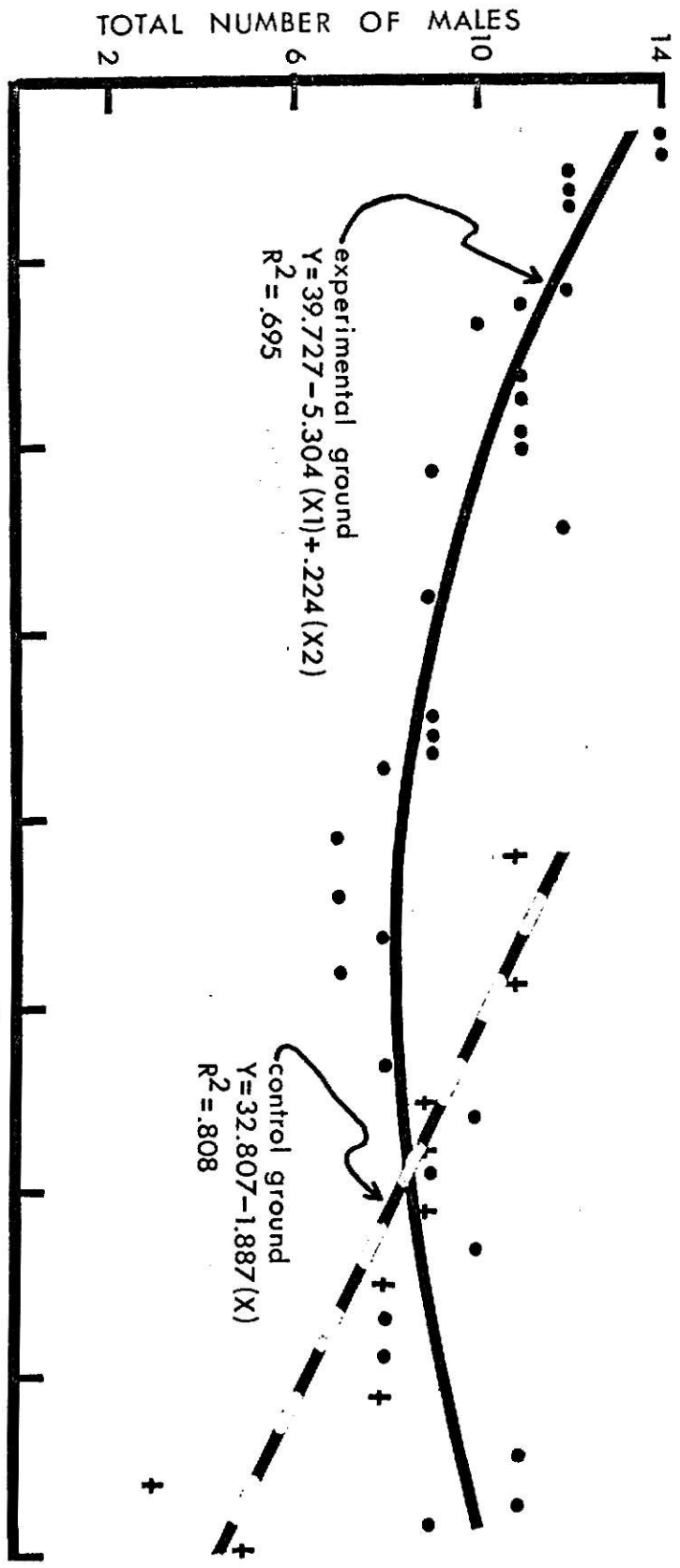

Fig. 1. Attendance of all males on the experimental and control booming grounds during the spring of 1970.

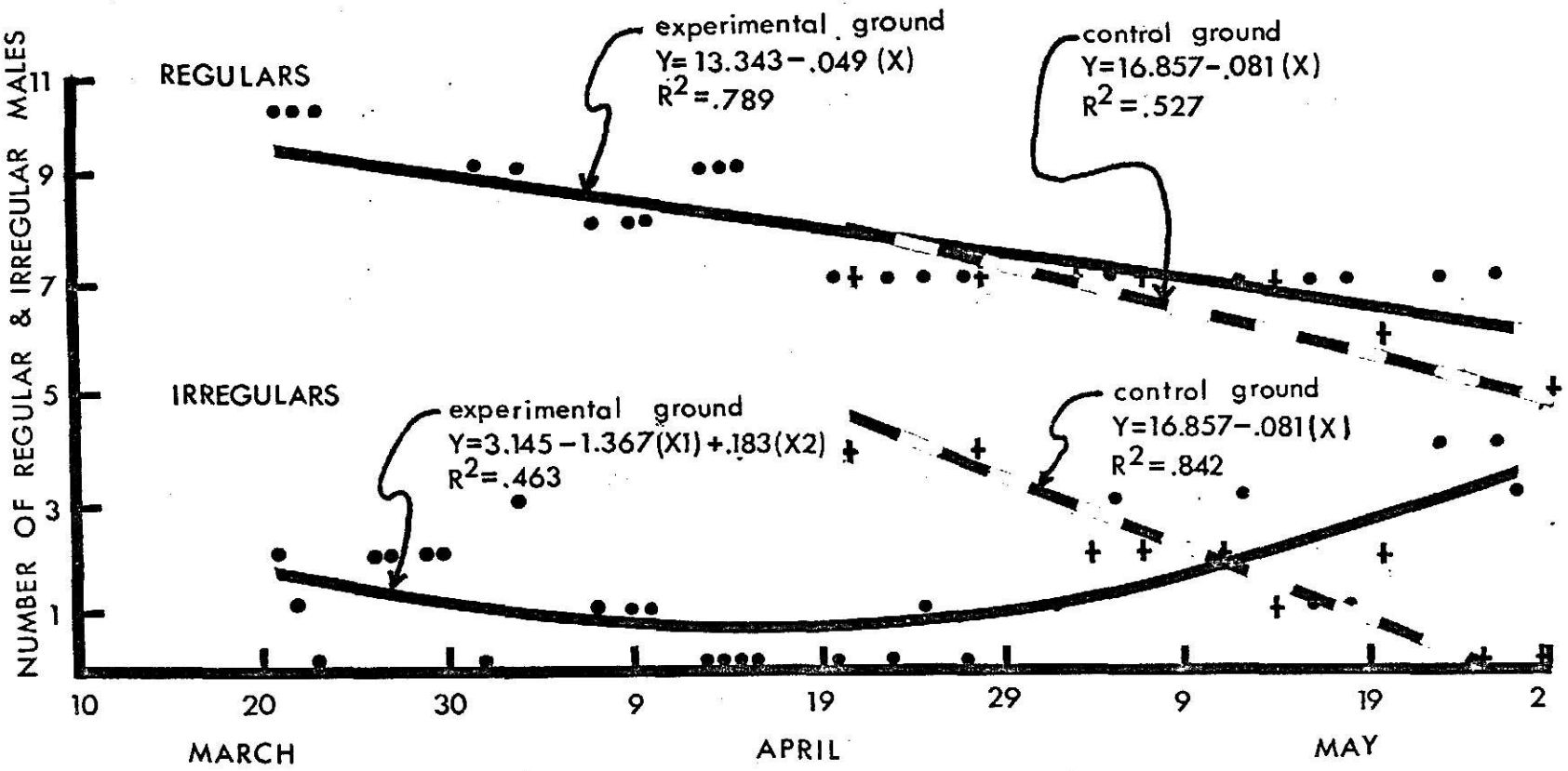

Fig. 2. Attendance of regular and irregular males on the experimental and control booming grounds during the spring of 1970.

Table 1. Area of territories (Fig. 3) and distribution of observed copulations for regular males present on the control ground during the spring of 1970.

Bird number	Total No. of sightings	No. of sightings used	Percent used	Territory area m^2	Observed copulations	
					No.	%
M-2	39	28	71.8	237.5	2	100
M-3	40	27	67.5	157.5		
M-7	15	10	66.7	100.0		
M-5	33	23	69.7	95.0		
AM-1	32	22	68.8	62.5		
M-4	26	18	69.2	20.0		
M-6	28	20	71.4	20.0		

Table 2. Distribution and numbers of observed aggressive encounters for each male on the control ground during the spring of 1970.

	M-2					
AM-1	70	AM-1				
M-3	25	92	M-3			
M-5		1	28	M-5		
M-7	23	1			M-7	
M-4			1	28		M-4
M-6			22	67		67
M-21	7	1			3	
M-22	3	1			3	
M-23	5			3		
M-24	8				1	
AM-16						27

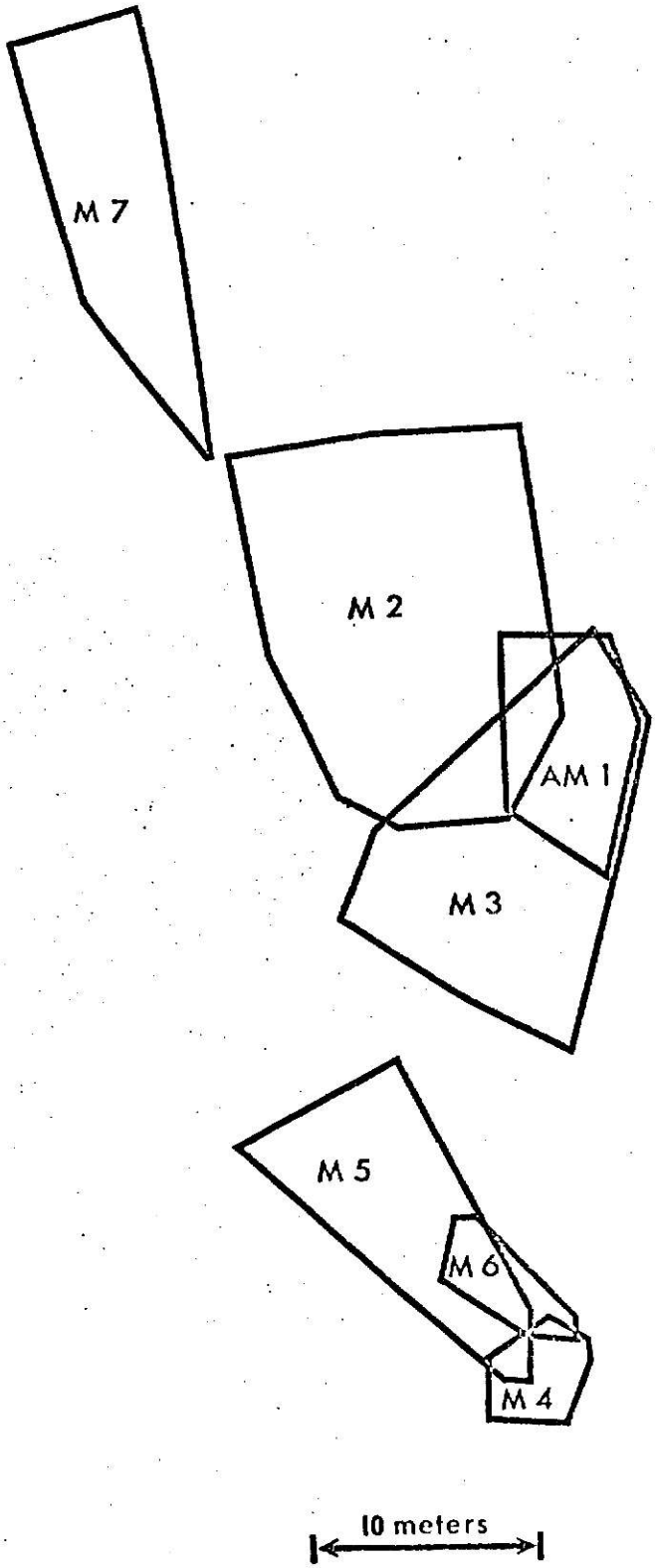

Fig. 3. Diagram of territories occupied by regular males on the control booming ground during the spring of 1970.

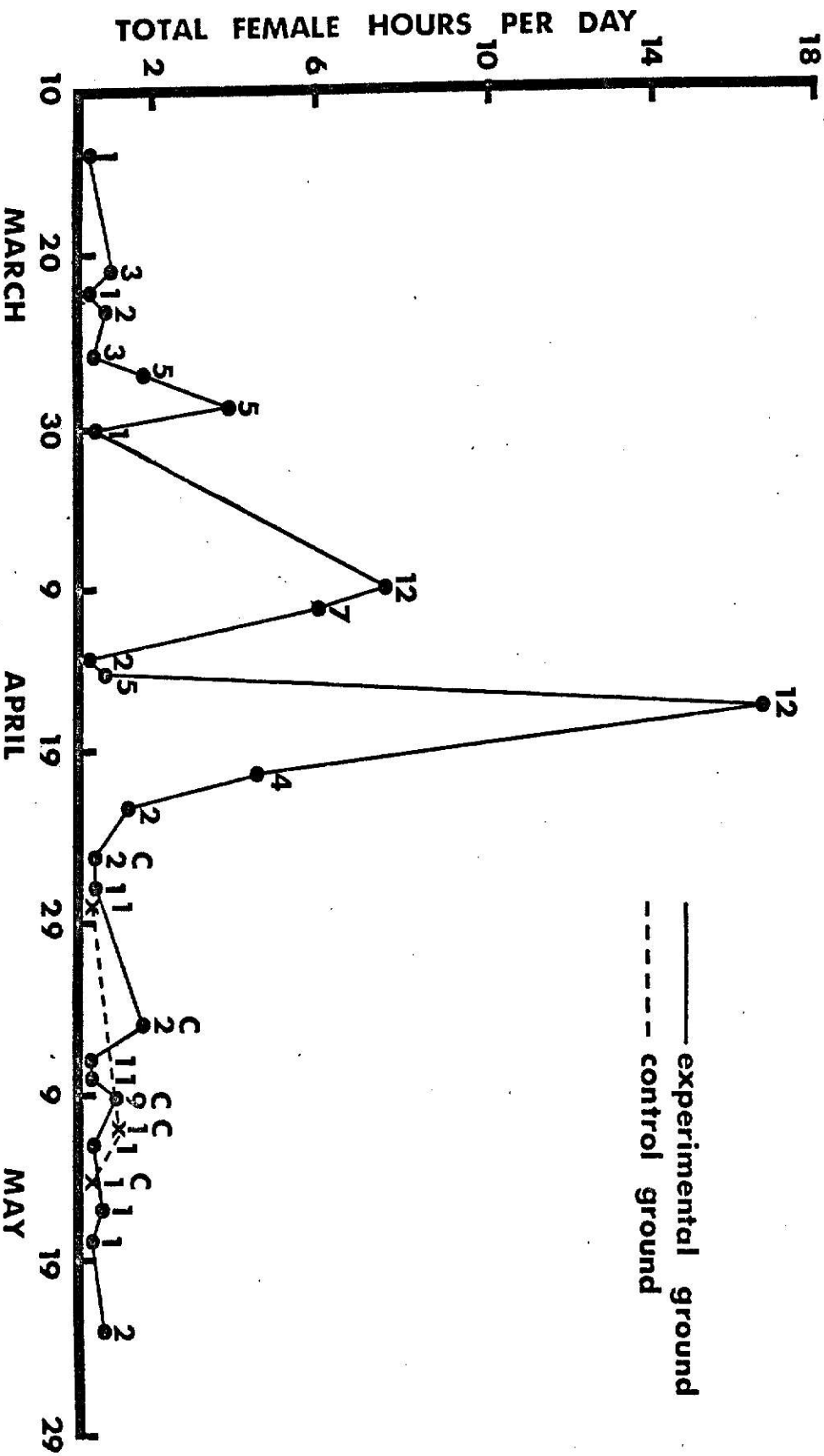

Fig. 4. Numbers of female visits and total time spent per day by females on the experimental and control booming grounds during the spring of 1970. Numbers above data points are the number of visits recorded on each day of observation. Letter C indicates dates of observed copulations.

determined after one morning of observation. The alpha male (M-2) interacted with the most males and had the largest territory. The beta male (M-3) had essentially the same characteristics, but interacted with fewer males and had a smaller territory.

Experimental Ground

Observations of behavior on the experimental ground were initiated on 26 March 1970. Twenty-two mornings were spent recording behavioral data. Observations consisted of notes concerning aggressive encounters, bird locations, female visits and behavior, and individual male behavior. The 22 days of observation were stratified into four distinct phases.

Phase One

Phase One included the period from 26 March to 30 March 1970. During this phase behavioral traits were recorded to ascertain dominant and subdominant individuals. Dominance was determined by considering each bird's territory size, position of territory in relation to other males, and number of aggressive encounters. Data were collected primarily on six individuals during Phase One. Nine regular males were present during Phase One, while numbers of irregulars varied from zero to three (Figs. 1 and 2).

One hundred and eighty-six territory location sightings were recorded during this time period (Table 3). Bird AM-17 had the largest territory (195.0 m^2), while AM-13 had the second largest

(130.0 m^2). Bird AM-10 had the third largest territory (122.5 m^2). Figure 5 shows the territory shape and position of each male. Bird AM-10 had the center position with the other males clustering around him. Bird AM-17, although having the largest territory, occupied a somewhat peripheral position in relation to AM-10.

A total of 161 aggressive encounters was recorded during Phase One (Table 4). Bird AM-10 had the largest number of encounters (65), while AM-11 and M-18 were tied for second at 55 encounters each. Bird AM-10 interacted with 5 other males, while AM-11 and M-18 interacted with six and five males each, respectively. Although AM-17 had only 35 encounters he interacted with eight males.

On the basis of position, interactions, and size of territory, AM-10 was determined to be the dominant male, AM-17 the second dominant or beta bird, and AM-12 the gamma bird.

Prior to and during Phase One, two of the marked bird (AM-8 and JM-9) attempted to establish territories but were repeatedly driven off primarily by AM-11 and M-18. These irregular males approached the ground and began to boom on the periphery, when one of the regulars chased them off. This occurred several times. Bird JM-9's last attempt to establish a territory was on 22 March, while AM-8 continued to attempt establishment daily throughout Phase One.

Table 3. Area of territories (Fig. 5) for regular males present on the experimental ground during Phase One from 26 March to 30 March 1970.

Bird number	Total No. of sightings	No. of sightings used	Percent used	Territory area m^2
AM-17	29	20	69.0	195.0
AM-13	32	21	65.6	130.0
AM-10	38	26	68.4	122.5
AM-12	31	22	71.0	105.0
AM-11	29	21	72.4	87.5
M-18	27	18	66.7	62.5

Table 4. Distribution and numbers of observed aggressive encounters for each male on the experimental ground during Phase One from 26 March to 30 March 1970.

	AM-17	AM-12	AM-11	AM-10	AM-13	M-18	M-19	AM-8	M-5
AM-12	1								
AM-11	1	1							
AM-10	16	20	16						
AM-13	9		8	9					
M-18		14	24	4	1				
M-19	4	2							
AM-8		1	5		1	12			
M-5	2						1		
M-31	1						3		2
M-32	1	1					1		

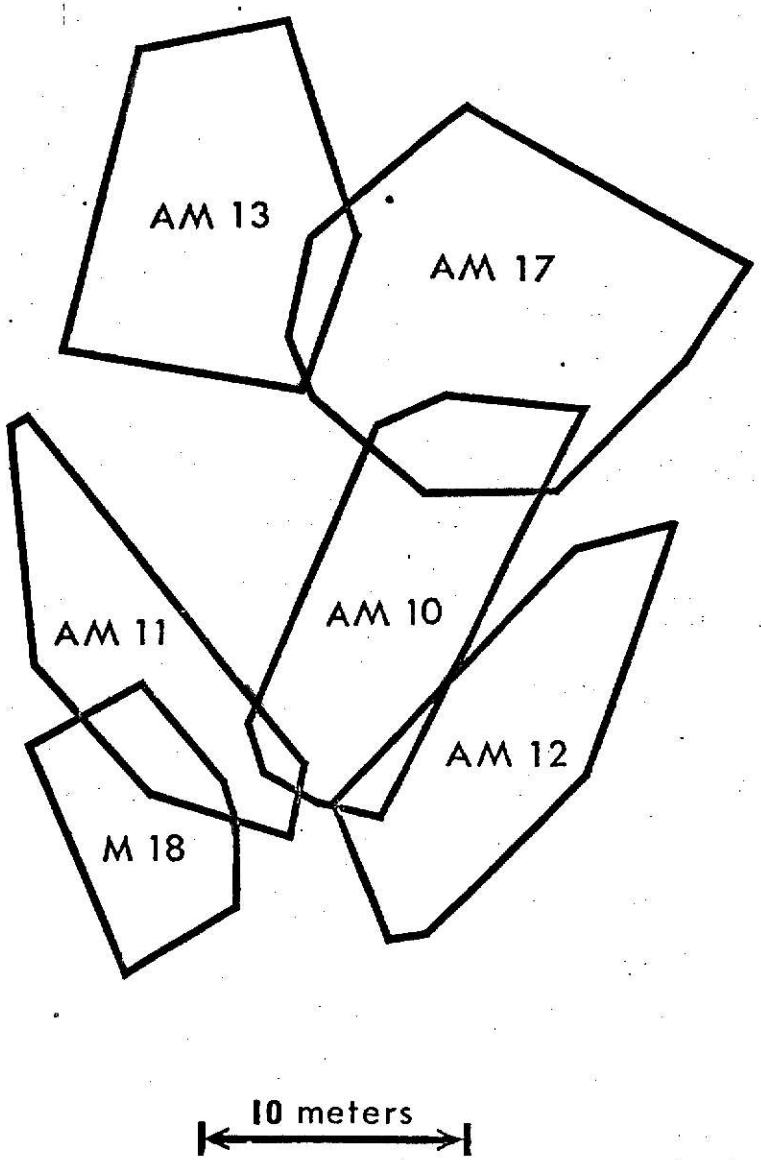

Fig. 5. Diagram of territories occupied by regular males on the experimental ground during Phase One of Experiment I, 1970.

Seven female visits occurred prior to Phase One, while 14 occurred during Phase One (Fig. 4). Females came to the display area singly but on occasion arrived in groups of two and three.

Only one interaction between females was observed: on 29 March a female was seen chasing and pecking another female. Females usually wandered from one side of the ground to the other, spending varying lengths of time with different males.

Males usually became quite active when a female appeared on the ground. "Hooting" became more pronounced upon the arrival of females. The frequency of hooting appeared to be almost proportional to the number of females approaching the ground. Males seemed to be more interested in attracting attention than fighting while females were present.

Territory location sightings were not taken when females were present. Territories generally shifted in the direction of female movement. Although territories shifted, each male kept its relative position to the other males.

No attempted copulations were observed prior to or during Phase One. Females appeared to be very unreceptive to courting males. The females walked through each territory, and ran away quickly when a courting male approached.

Courting males generally stayed within 3 meters of the visiting female unless it became necessary to chase out intruders.

Courtship consisted of males booming in a circular fashion around the hen.

Females ordinarily left the ground in a somewhat undeliberate fashion, usually walking off but on occasion flying from the ground. When a female walked off, one or more peripheral males accompanied her, returning to the display area 15 to 20 minutes later.

The alpha (AM-10) and beta (AM-17) males were removed on 3 April 1970.

Phase Two

On the morning following removal, a definite void area on the ground was evident. None of the other males encrouched into the old boundaries of the removed males. Bird AM-8, which had previously been attempting to establish a territory, appeared to be more tolerated since he was allowed to boom on the periphery of the ground. Observations were suspended for a few days following removal to keep human disturbance to a minimum.

Observations were again resumed on 7 April 1970. Nine males, consisting of seven old regulars, one new regular (AM-8), and one irregular were present (Figs. 1 and 2). The new regular (AM-8) had established himself in a portion of the void area created by the removal of AM-10 and AM-17. The gamma male (AM-12) from Phase One also appeared to have moved into the void area.

During this phase which lasted to 15 April, 178 territory

location sightings were recorded (Table 5). Bird AM-15 had the largest territory (185.0 m^2), while AM-13 had the second largest (125.0 m^2). Bird AM-11 and AM-12 had the third (107.5 m^2) and fourth (77.5 m^2) largest territories, respectively. Bird AM-8, which previously had been unable to establish a territory, had the sixth (27.5 m^2) largest territory.

Birds AM-12, M-19, and AM-8 shared a center position on the display area (Fig. 6). Peripheral males appeared to enlarge their territories toward the center of the ground. No territory readings were available for M-18 because of his inconsistent presence during the display period, although a territory was maintained.

A total of 239 aggressive encounters was observed during Phase Two (Table 6). Birds in Phase Two averaged 7.19 encounters per hour in contrast to the 3.60 encounters per hour in Phase One.

During Phase Two, birds AM-8 and M-19 had the largest number of encounters with 93 and 90, respectively; while AM-12 had the third largest number (71). Birds AM-12, M-19, and M-18 interacted with more birds than did any of the other males. Bird M-19 interacted with nine males while AM-12 and M-18 interacted with eight and seven males, respectively.

On the basis of territory size and location, bird AM-12 was determined to be the new alpha male. The decision was made primarily on the basis of territory size, since both AM-12 and M-19

Table 5. Area of territories (Fig. 6) for regular males present on the experimental ground during Phase Two from 7 April to 15 April 1970.

Bird number	Total No. of sightings	No. of sightings used	Percent used	Territory area m^2
AM-15	16	11	68.8	185.0
AM-13	26	18	69.2	125.0
AM-11	30	20	66.7	107.5
AM-12	36	25	69.4	77.5
M-19	31	22	71.0	40.0
AM-8	39	28	71.8	27.5

Table 6. Distribution and numbers of observed aggressive encounters for each male on the experimental ground during Phase Two from 7 April to 15 April 1970.

	M-19	M-18	AM-12	AM-15	AM-8	AM-13	AM-14	M-20	M-32
M-18	2								
AM-12	33	13							
AM-15	3	1	2						
AM-8	33	18	15						
AM-13	10	1			4				
AM-14	3		1	6		1			
M-20		1	6	11			1		
M-32	1		1						
AM-11		12			23	24			
M-33	2	1							3
M-34	3								4

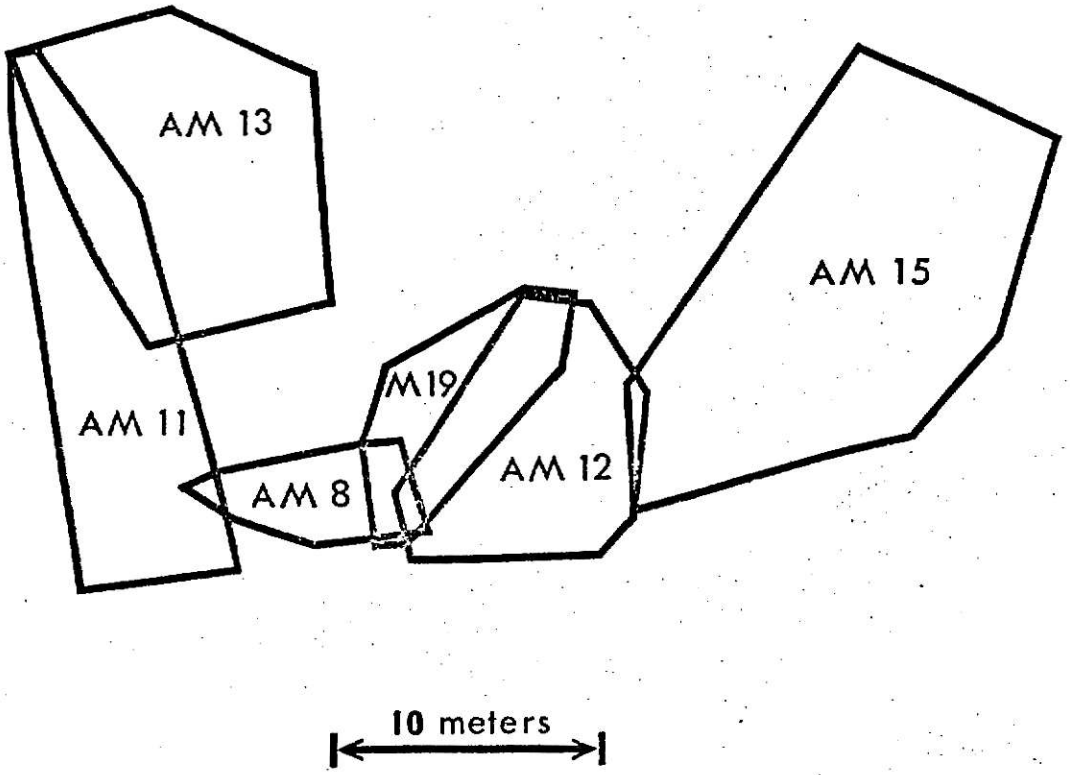

Fig. 6. Diagram of territories occupied by regular males on the experimental ground during Phase Two of Experiment I, 1970.

appeared to be equal with respect to position and numbers of aggressive encounters.

Twenty-one female visits occurred during Phase Two (Fig. 4). Females spent more time on the ground during this phase than they did during Phase One.

Some evidence of female aggression was recorded during Phase Two. On 10 April one hen was seen chasing five others in an attempt to peck them. On another occasion one female was observed chasing three others.

No attempted copulations were recorded during Phase Two, although the females did appear more receptive to courting males. On 14 April bird AM-12 was seen performing the "nuptial bow" to one of the less aggressive females. This was the first recording of such behavior.

Bird AM-12 was removed on 15 April 1970.

Phase Three

Phase Three consisted of observations from 16 April to 9 May 1970. Male attendance on the ground varied from seven to eight males (Fig. 1). Attendance of regulars dropped off after removal but gradually reached prior attendance by the end of Phase Three.

Attendance of regulars during this time period was more consistent allowing a larger number of territories to be plotted. Three hundred and ninety-four territory location sightings were

recorded (Table 7). During this phase AM-15 had the largest territory (258.8 m^2), while AM-14 had the second largest (157.5 m^2). Bird M-19, the beta male during Phase Two, had the sixth largest territory (86.3 m^2).

Figure 7 shows each bird's territory and location in relation to the other birds. Examination reveals that although M-19 retained a center position, both AM-14 and M-19 shared the removed bird's (AM-12) area.

A total of 870 aggressive encounters was recorded during Phase Three (Table 8). Mean number of encounters for each bird per hour increased to 9.33. Bird M-18 had the largest number of encounters (328) while M-19 had the second largest number (327). Birds AM-14 and AM-13 had 273 and 258 encounters, respectively. Birds AM-14 and M-18 each interacted with seven other males, while M-19 and AM-8 interacted with five and three males, respectively.

An aggression index was derived by considering only those birds above the mean number of encounters per bird, thereby eliminating the less aggressive birds from the analysis. The index was then computed by dividing the number of aggressive encounters for each bird by the number of other birds they encountered. Birds with a large index were considered more aggressive than those with a smaller index value.

A curvilinear relationship was found to exist during Phase

Table 7. Area of territories (Fig. 7) and distribution of observed copulations for regular males present on the experimental ground during Phase Three from 16 April to 9 May 1970.

Bird number	Total No. of sightings	No. of sightings used	Percent used	Terr. area m^2	Observed attempted copulations	
					No.	%
AM-15	52	36	69.2	258.8	1*	3.6
AM-14	59	42	71.2	157.5	0	0.0
M-18	56	40	71.4	147.5	6	21.4
M-20	52	35	67.3	133.8	0	0.0
AM-11	52	36	69.2	92.5	2	7.1
M-19	62	43	69.4	86.3	10**	35.7
AM-8	61	43	70.5	70.0	9	32.1

* one successful copulation
**two successful copulations

Table 8. Distribution and numbers of observed aggressive encounters for each male on the experimental ground during Phase Three from 16 April to 9 May 1970.

	M-18	AM-14	AM-11	AM-15	M-19	M-20
AM-14	74					
AM-11	1	1				
AM-15	34	54				
M-19	82	110	35			
M-20	84	6	1	56		
AM-13		3	3	15	1	
AM-8	52		107		99	
M-35		25	5	18		
M-36	1			2		1

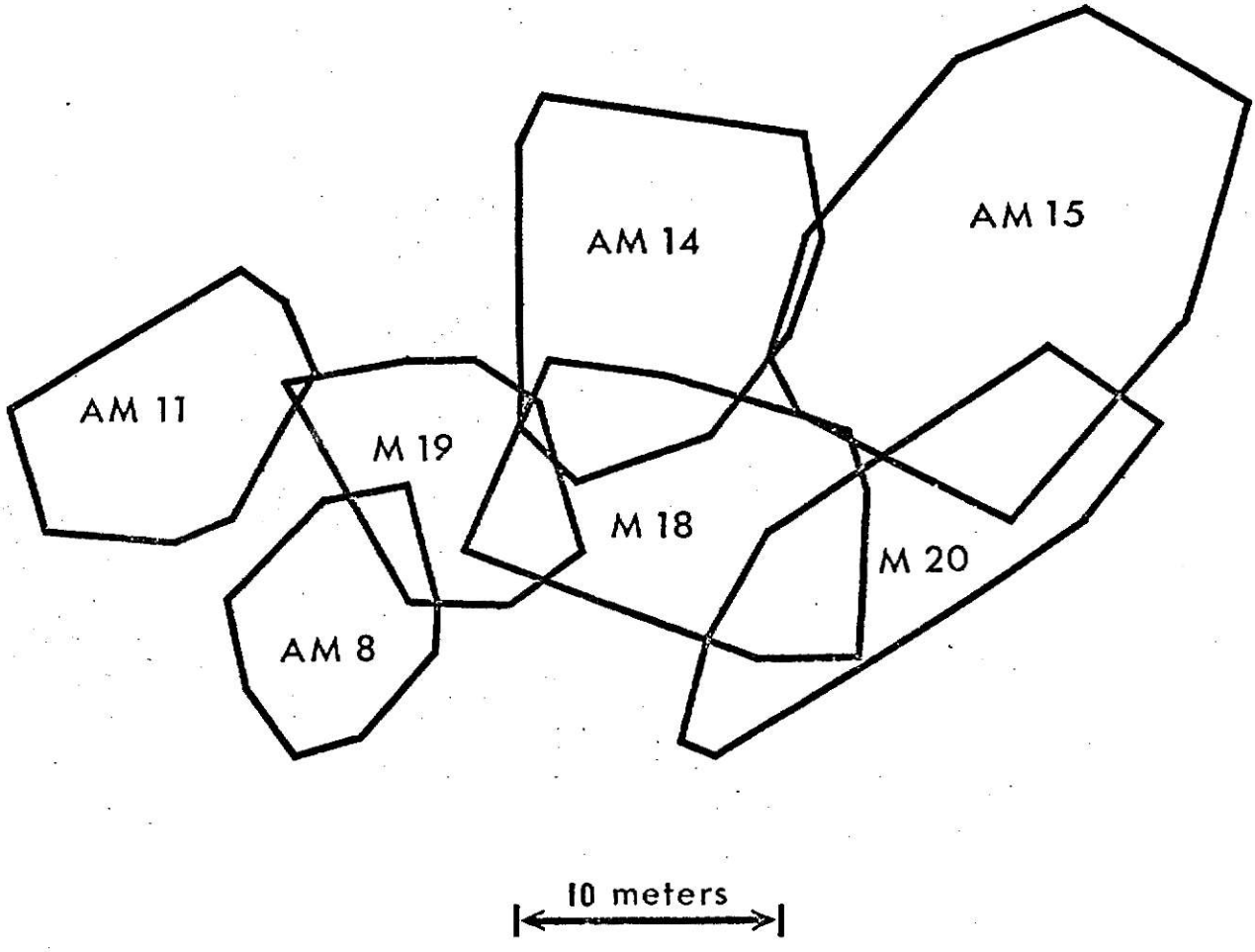

Fig. 7. Diagram of territories occupied by regular males on the experimental ground during Phase Three of Experiment I, 1970.

Three between territory size and the aggression index (Fig. 8). Birds with a larger index had smaller territories and a more central position than those which had a smaller index.

During Phase Three birds with smaller territories had more attempted copulations than did those with larger territories (Fig. 9). A curvilinear relationship existed between attempted copulations and the aggression index (Fig. 10). Individuals with larger indices attempted more copulations than those with smaller index values.

Since a relationship was found to exist between all three variables, the data were then fitted to a multiple linear regression analysis (Table 9). An attempt to fit the data to a multiple curvilinear regression analysis was made, but due to a complete loss of degrees of freedom, a linear regression analysis was used.

Thirty-five female visits were recorded during Phase Three (Fig. 4). The highest number of visits occurred during this phase on 16 April. Total time spent on the ground by females was also greatest during this phase.

Three successful copulations were recorded during Phase Three (Table 7). Bird M-19 accounted for two of the successful copulations, while AM-15 accounted for the other. Thirteen disturbances and 15 interruptions of attempted copulations were observed. Bird M-19 had the largest number of attempted copulations

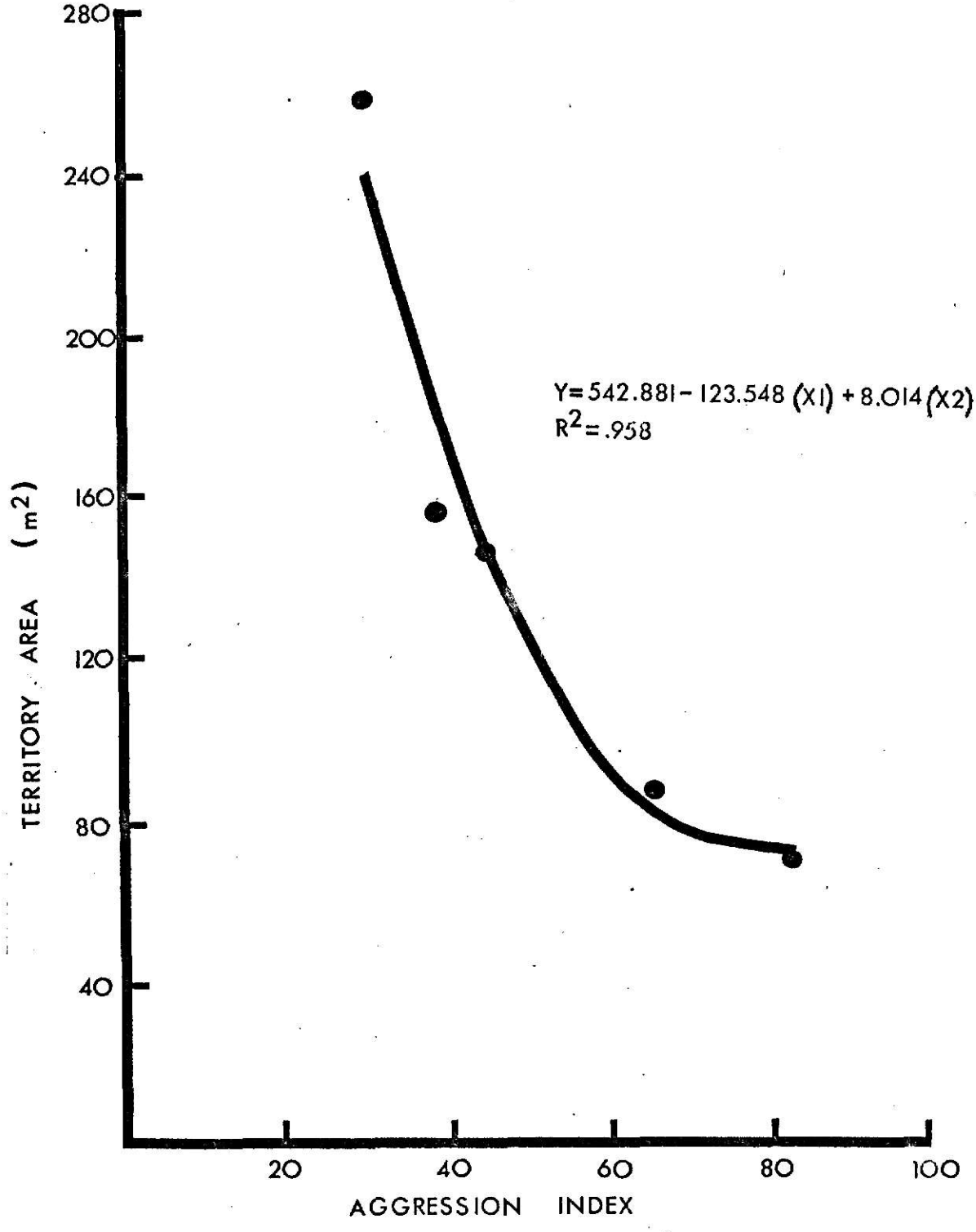

Fig. 8. Relationship between territory size (m^2) and the aggression index for regular males present on the experimental ground during Phase Three of Experiment I, 1970.

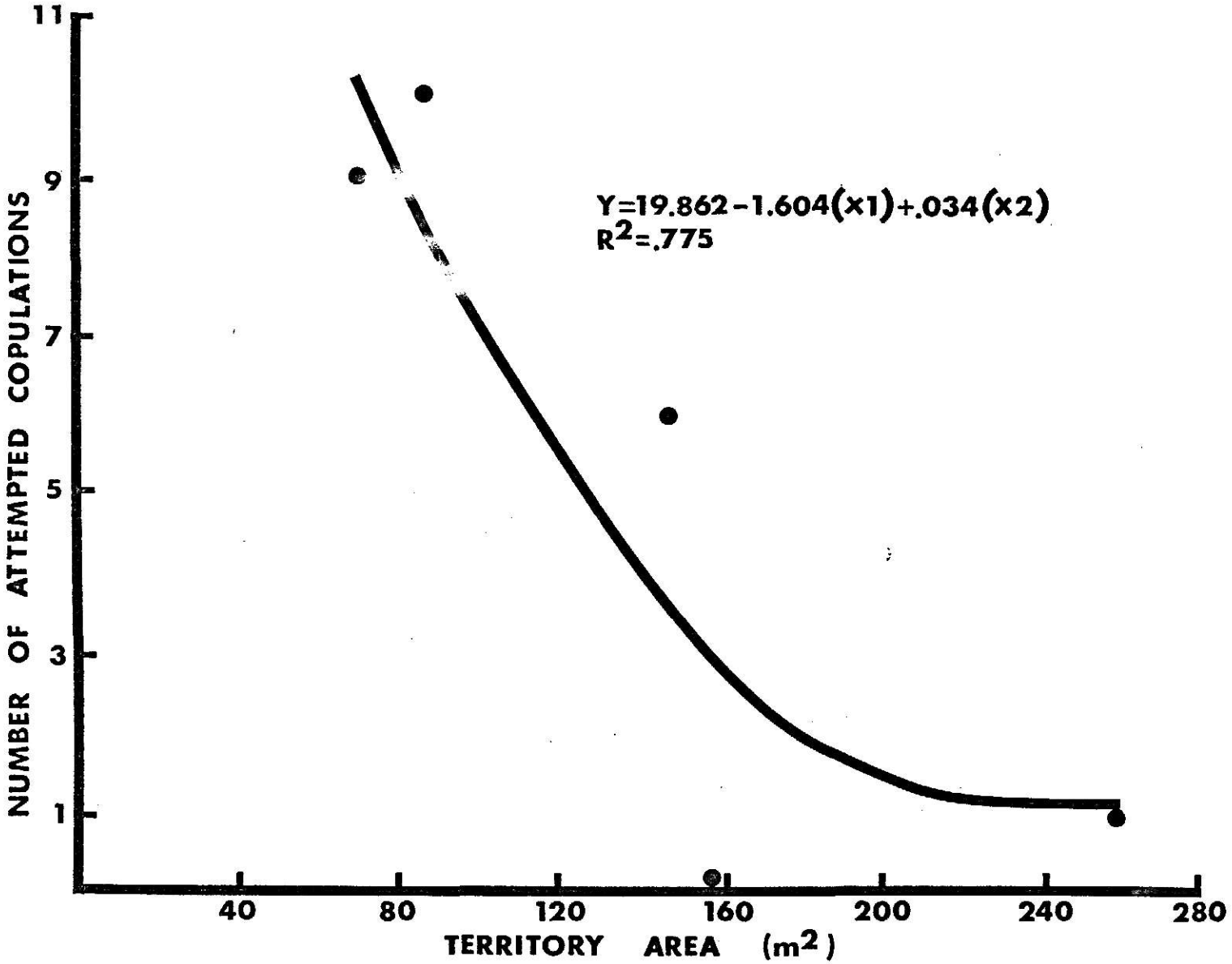

Fig. 9. Relationship between number of attempted copulations and territory area (m^2) for regular males present on the experimental ground during Phase Three of Experiment I, 1970.

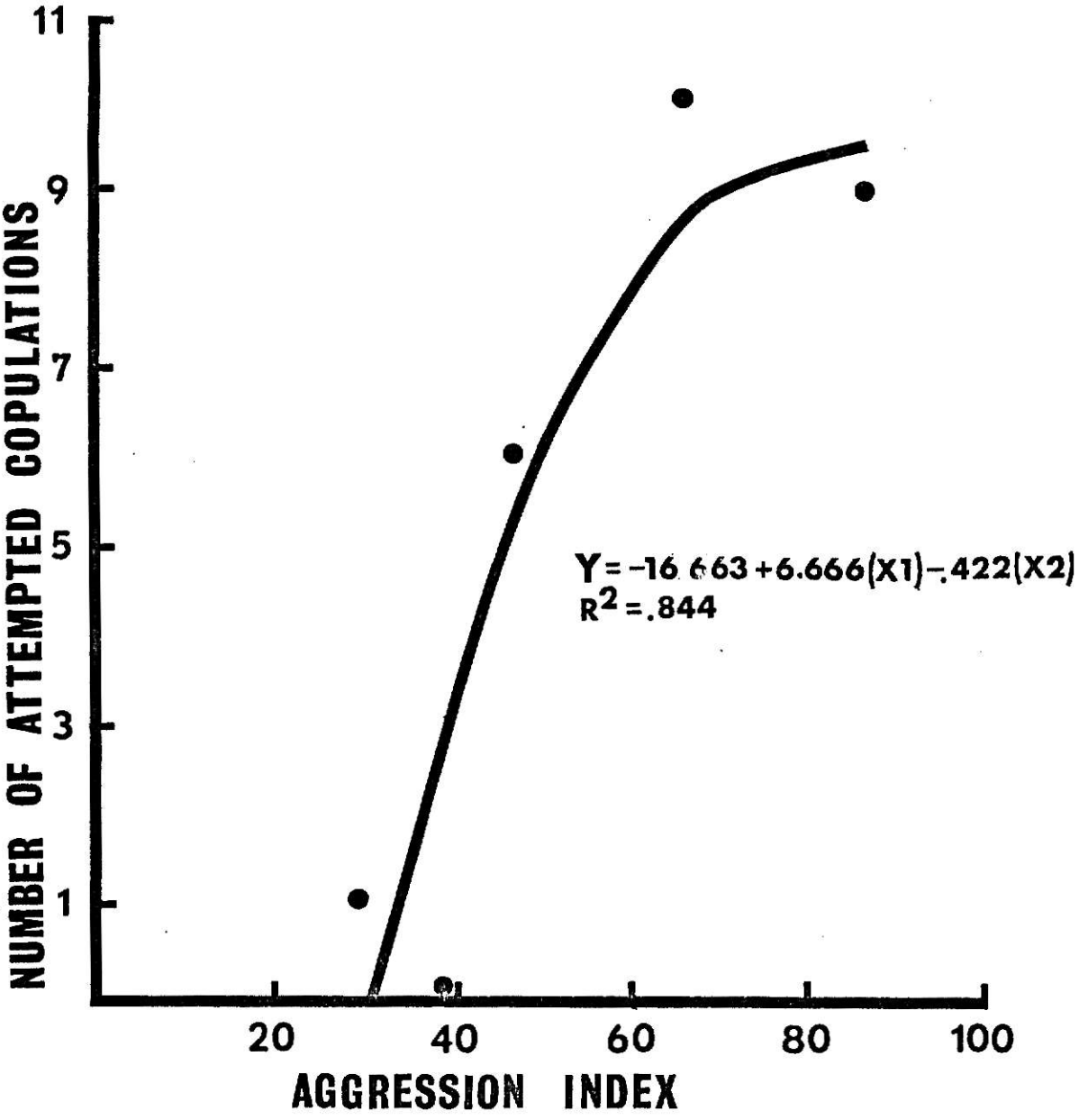

Fig. 10. Relationship between number of attempted copulations and the aggression index for regular males present on the experimental ground during Phase Three of Experiment I.

Table 9. Multiple linear regression using territory size and the aggression index to predict the number of attempted copulations for the more aggressive males present on the experimental ground from 16 April to 9 May 1970.

Bird number	X1 Territory size m^2	X2 Aggression index	Y Attempted copulations	$\hat{Y}$ Calculated copulations
M-19	86.3	65.40	10	7.61
AM-8	70.0	86.00	9	10.54
M-18	147.5	46.86	6	4.33
AM-15	258.8	29.83	1	.54
AM-14	157.5	39.00	0	3.16

$y=0.255-0.014(X1)+0.131(X2)$ $R^2=.746$ $(p<0.26)$

(10), while AM-8 had nine attempts. Bird AM-15 had only one attempt at copulation but it was a successful one. Bird M-19's two copulations were achieved under a great deal of harassment. In one attempt the male was actually knocked off the female following a successful service.

Successful copulations were easily discernible from unsuccessful attempts due to the amount of time the male spent on the female and by the female's behavior following copulation. During successful copulations the male usually spent 10 to 15 seconds on the female, whereas during interrupted attempts the male was knocked off immediately upon mounting the female.

Following successful copulations, females always spent some 20 to 30 seconds ruffling their feathers after which they would leave the ground within a 5 minute period. In contrast, following an unsuccessful attempt, the hen would not ruffle her feathers and would not leave the ground but would usually stay for more courting activity.

Female aggression was not noticeable during this phase except on 9 April when the largest number of visits occurred. On this date a flock of nine hens was observed pecking one another on several occasions. All of the attempted copulations except for one occurred when four or less visits were recorded. During those periods no female aggression was observed.

It was not possible to determine a definite alpha or beta male by behavioral observation during Phase Three. Four males (birds M-18, AM-14, AM-15, and M-19) appeared to be equally aggressive and shared a center position on the display area.

Phase Four

Previous phases consisted primarily of observations following removal of dominant males. Phase Four concerns a change in the hierarchy due to factors other than the removal of individuals.

Phase Four consisted of the period from 12 May to 23 May 1970. During this phase seven regular territory owners were present as in Phase Three (Fig. 2). Attendance of irregulars reached a peak of four males on 22 May.

Two hundred and seventy territory location sightings were recorded (Table 10). Bird AM-14 had the largest territory (310. m^2), while M-18 had the second largest (225.0 m^2). Bird AM-15, which had the largest territory in Phase Three, had only the fourth largest (152.5 m^2) during this phase.

Figure 11 shows each bird's territory and relative position to the other males during Phase Four. Bird AM-14 occupied the largest portion of the center position sharing it only with M-19 and M-18.

Four hundred and forty-four aggressive encounters were recorded (Table 11). Birds AM-14 and M-18 had the largest number

Table 10. Area of territories (Fig. 11) for regular males present on the experimental ground during Phase Four from 12 May to 23 May 1970.

Bird number	Total No. of sightings	No. of sightings used	Percent used	Territory area m^2
AM-14	51	35	68.6	310.0
M-18	39	28	71.8	225.0
M-20	29	21	72.4	180.0
AM-15	40	28	70.0	152.5
M-35	25	18	72.0	117.5
M-19	36	25	69.4	82.5
AM-11	22	16	72.7	80.0
AM-8	28	20	71.4	50.0

Table 11. Distribution and numbers of observed aggressive encounters for each male on the experimental ground during Phase Four from 12 May to 23 May 1970.

	M-18	AM-14	M-19	AM-15	AM-13	AM-11
AM-14	27					
M-19	33	25				
AM-15	28	56				
AM-13	16	9	1	3		
AM-11		2	9			
AM-8	18		57		1	23
M-35		38	15	9		1
M-37	2	2		1		1
M-20	33			34	1	
M-	2					

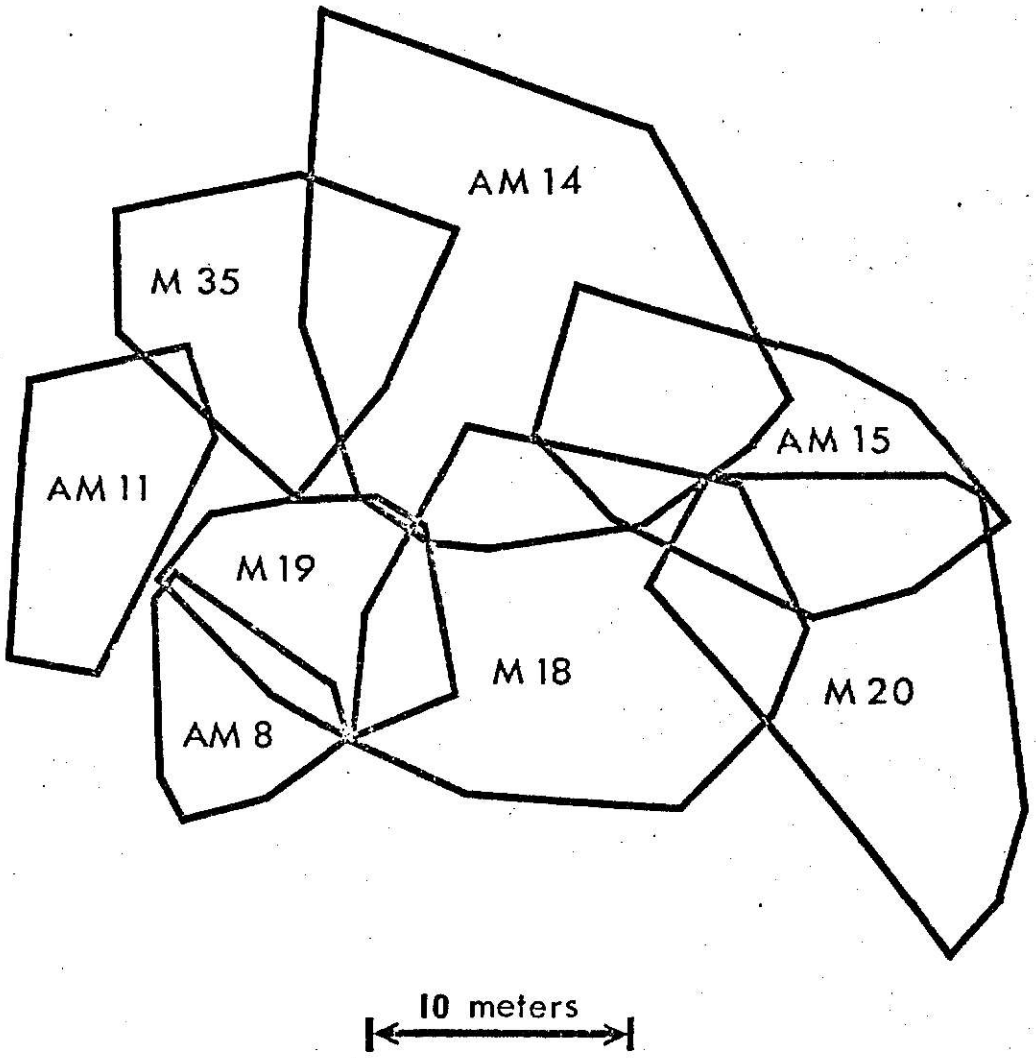

Fig. 11. Diagram of territories occupied by regular males on the experimental ground during Phase Four of Experiment I, 1970.

of encounters at 159 each. Bird M-19 had the second largest number (140), while AM-15 had the third largest number (131). Bird M-19 interacted with six other males, while AM-8 and M-20 interacted with four and three males, respectively. Mean number of encounters per bird per hour was 8.71 during Phase Four.

Five female visits were recorded during Phase Four (Fig. 4). Total time spent on the ground by females decreased to a level below that of Phase One. No attempted copulations were observed.

A few behavioral differences were detectible during Phase Four which had not been detectible during Phase Three. During Phase Four, AM-14 evolved as the new dominant male. Two factors may have explained this occurrence.

On 9 May a new male came on the ground and appeared to establish a territory between AM-11 and AM-14. This new bird (M-16) was considered an irregular, although it did patronize the same area. With the arrival of M-16 bird AM-14 shifted its territory to the left, causing him to interact with AM-11 and M-18. This caused an increase in the size of his territory.

The other factor which may have caused an enlargement of AM-14's territory was the cutting of the grass on 15 May. This was necessary to observe the birds on the ground. After this date AM-14 appeared to be more aggressive, at least more so than the remaining three co-dominants (M-18, M-19, and AM-15). Obser-

vations were curtailed on 26 May.

All Phases

A two way analysis of variance was conducted on aggressive encounters per hour per bird to test for differences between phases and between birds within phases. Phases, birds, and phase x bird interactions were all significant sources of variation (p 0.05). A Duncan's New Multiple Range Test was used to detect individual differences (Table 12). Mean numbers of encounters per hour for four (M-19, AM-8, AM-11, and M-20) of the seven regular males present were not significantly different.

Experiment II

Control Ground

Observations on the control ground were conducted from 17 March to 14 May 1971. Nineteen mornings were spent recording behavioral data. Observations consisted of the same type as those recorded during Experiment I.

Three regular males were in attendance up to 9 April when regular attendance dropped to two (Fig. 13). The highest number of males recorded was five on 1 April (Fig. 12). Numbers of irregulars fluctuated daily.

One hundred and thirty-nine territory location sightings were recorded during this time period (Table 13). No behavioral changes were observed so the territories were not stratified into

Table 12. Duncan's NMRT showing individual differences among mean aggressive encounters per hour per bird between phases and between birds within phases ($p<0.05$) for the experimental ground during Experiment I.*

Bird Number	Phase Two	Phase Three	Phase Four
AM-14	3.85	11.35	13.86
M-18	6.61	13.69	14.16
M-19	10.89	13.52	13.19
AM-8	10.59	10.73	8.90
AM-15	4.20	7.24	11.42
AM-11	6.52	6.13	3.18
M-20	3.22	5.60	5.96

Phase	Bird	Bird	Bird	Bird	Bird	Bird	Bird
	M-19	AM-8	M-18	AM-11	AM-15	AM-14	M-20
Two	10.89	10.59	6.61	6.52	4.20	3.85	3.22
	M-18	M-19	AM-14	AM-8	AM-15	AM-11	M-20
Three	13.69	13.52	11.35	10.73	7.24	6.13	5.60
	M-18	AM-14	M-19	AM-15	AM-8	M-20	AM-11
Four	14.16	13.86	13.19	11.42	8.90	5.96	3.18

* Birds underlined indicates that the means were not significantly different.

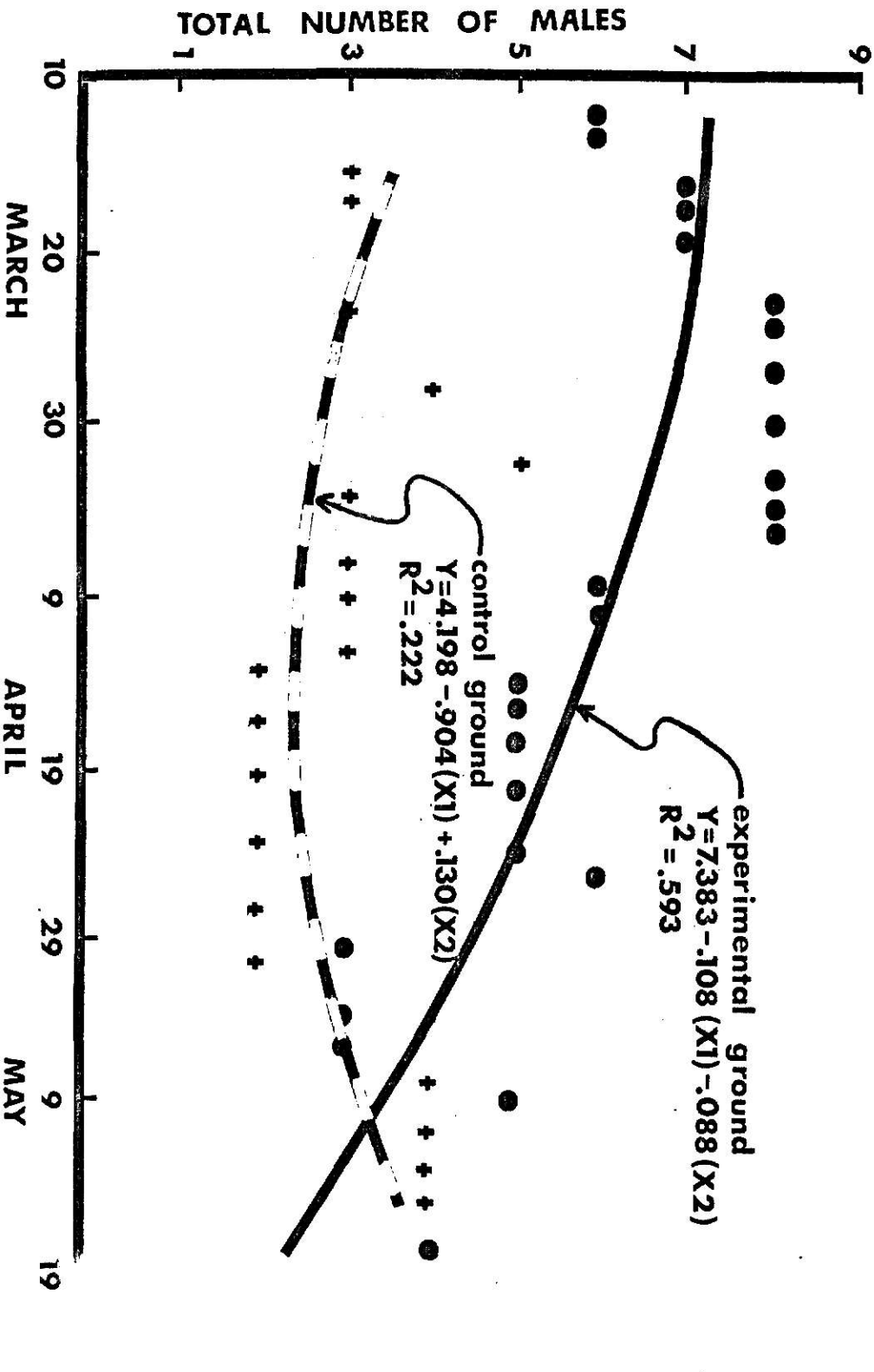

Fig. 12. Attendance of all males on the experimental and control booming grounds during the spring of 1971.

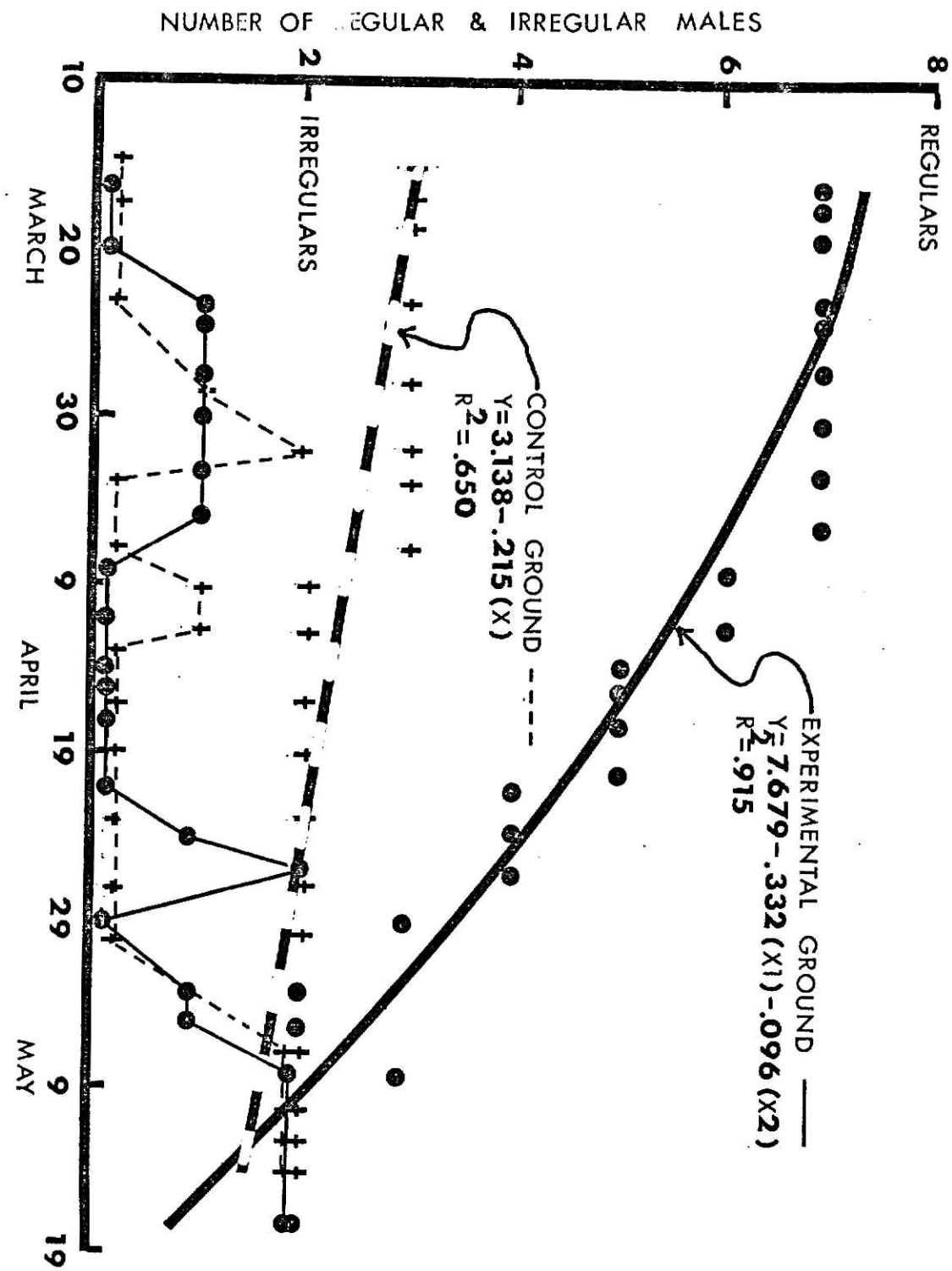

Fig. 13. Attendance of regular and irregular males on the experimental and control booming grounds during the spring of 1971.

Table 13. Territory sizes for regular males present on the control ground during the spring of 1971.

Bird number	Total Number of sightings	Number of sightings used	Percent used	Territory area m^2
M-26	68	48	70.6	165.0
M-25	51	36	70.6	135.0

Table 14. Distribution and numbers of observed aggressive encounters for each male present on the control ground during the spring of 1971.

	M-26	M-25	M-28	M-29
M-25	169			
M-28	9	11		
M-29	1	4		
AM-16	2	42		5
M-27	62	4	17	
M-30	1	1		

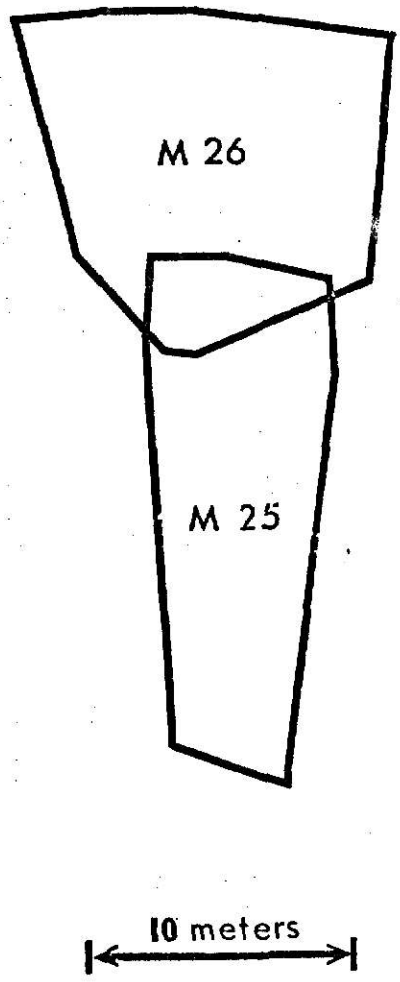

Fig. 14. Diagram of territories occupied by regular males on the control ground during the spring of 1971.

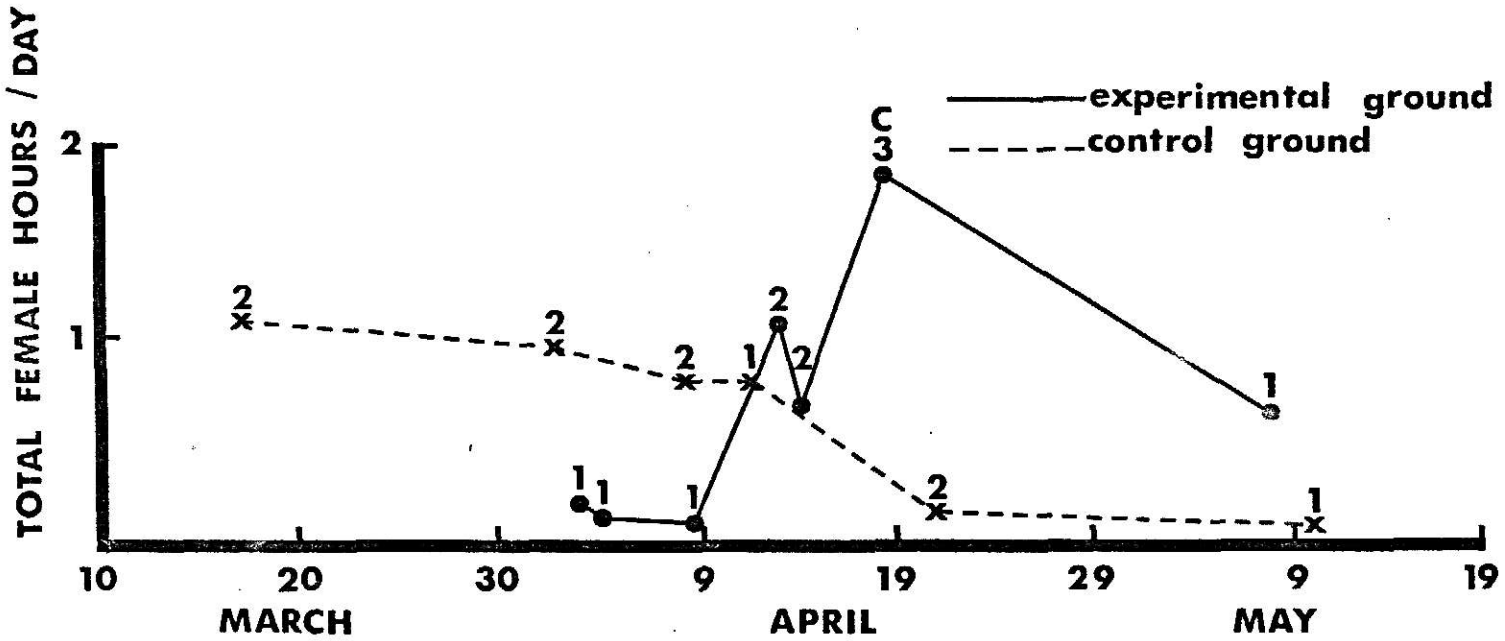

Fig. 15. Numbers of female visits and total time spent per day by females on the experimental and control booming grounds during the spring of 1971. Numbers above data points are the number of visits recorded on each day of observation. Letter C indicates dates of observed copulations.

phases. No statistical analysis was made due to the low number of males present. Bird M-26 had the highest number of encounters.

Ten female visits were recorded on the control ground (Fig. 15). No attempted copulations were observed. Females wandered on the periphery of the ground and paid little attention to displaying males. No aggression among females was observed. On two occasions two visiting females came on the ground with an irregular male. The irregular male followed the females both on and off the ground but was never observed entering into the alpha or beta male's territory. The alpha (M-26) and beta (M-25) male stayed in their territories during female visits.

Observations were suspended on 14 May 1971.

Experimental Ground

Observations on the experimental ground were begun on 19 March 1971. Twenty-five mornings were spent recording behavioral data. Observations were recorded in the same manner as those taken for Experiment I. Observations were stratified into three phases.

Phase One

Phase One included the period from 19 March to 4 April, 1971. Dominance was determined by considering territory size, position of territory, and number of aggressive encounters.

Attendance of males was classified as regular and irregular.

Seven regular males were present during Phase One, while the number of irregulars stayed constant at one (Fig. 14).

Two hundred and fifty territory location sightings were recorded during Phase One (Table 15). Bird M-39 had the largest territory (390.0 m^2), while M-41 had the second largest territory (212.5 m^2). Bird M-38 had the third largest territory (197.5 m^2). Figure 16 shows the shape and position of each territory. Arrangement of territories was similar to the control ground during Experiment I in that they had a linear appearance. Bird M-38 occupied a center position, while M-39 occupied a position near the end of the ground.

A total of 349 aggressive encounters was recorded during this phase (Table 16). Bird M-38 had the largest number of encounters (151). Birds AM-11 and AM-12 had the second (134) and third (102) largest numbers of encounters, respectively. Birds AM-15 and M-39 both had the fourth (89) largest number of encounters. Bird M-38 interacted with six males, while birds M-39, AM-11, and AM-15 each interacted with five males.

On the basis of territory position, numbers of aggressive encounters, and territory size, bird M-38 was determined to be the alpha male while M-39 was considered the beta male.

During Phase One an irregular male (M-42) was observed attempting to establish a territory between birds M-38 and M-39.

Table 15. Area of territories (Fig. 16) for regular males present on the experimental ground during Phase One from 19 March to 4 April 1971.

Bird number	Total No. of sightings	No. of sightings used	Percent used	Territory area m^2
M-39	40	28	70.0	390.0
M-41	23	17	73.9	212.5
M-39	51	37	72.5	197.5
AM-12	34	26	76.5	152.5
M-40	26	21	80.8	127.5
AM-11	42	29	69.0	112.5
AM-12	34	25	73.5	80.0

Table 16. Distribution and numbers of observed aggressive encounters for each male on the experimental ground during Phase One from 19 March to 4 April 1971.

	M-42	M-38	M-39	AM-11	AM-15	M-40	AM-12
M-38	17						
M-39	20	21					
AM-11	8	56	3				
AM-15	4	47	29	8			
M-40	3	1			1		
AM-12	8	9		59		26	
M-41	9		16				4

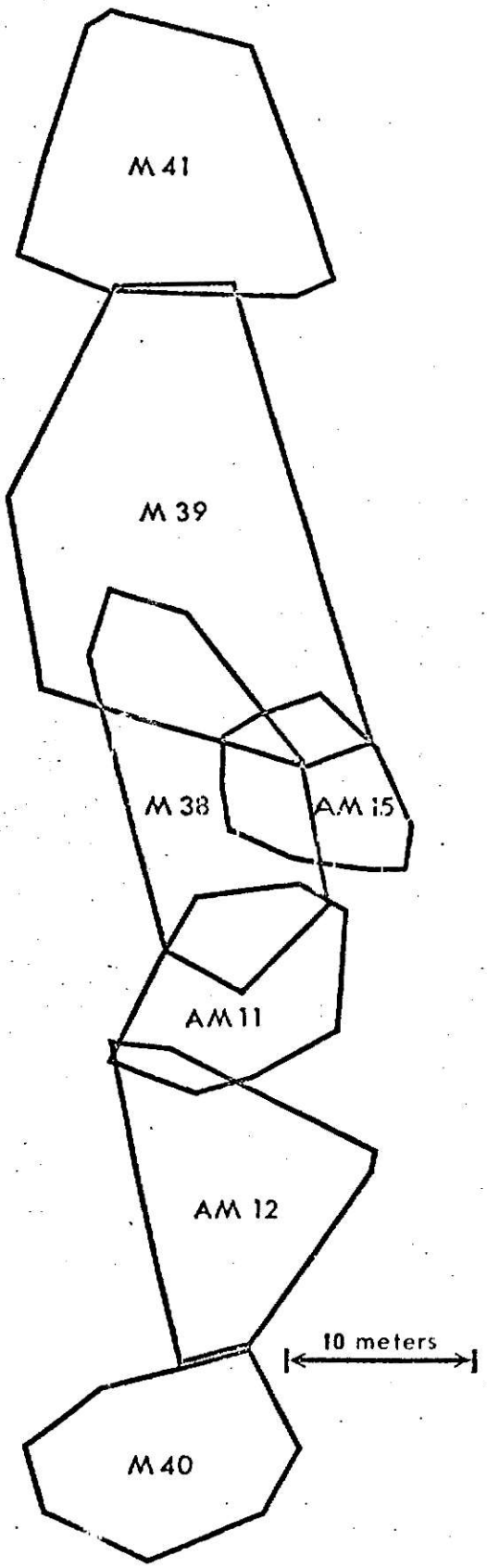

Fig. 16. Diagram of territories occupied by regular males on the experimental ground during Phase One of Experiment II, 1971.

Bird M-42 was repeatedly driven off during this period.

Two female visits were observed during Phase One (Fig. 15). Males behaved similarily to that described during Experiment I. Bird M-42 was observed following the females both on and off the ground. Bird M-42 frequently entruded into other territories which disrupted courting activities. When this occurred M-42 was vigourously chased from the ground.

The alpha male (M-38) was removed on 5 April 1971.

Phase Two

On the same day following the removal of M-38, bird M-42 was observed attempting to establish a territory in the vacated area. Bird M-42 was severely attacked by M-39 and AM-12. It was first thought that M-42 was killed by M-39 and AM-12, since it was knocked on its back and stayed in that position for some 15 minutes. Bird M-42 finally recovered and limped from the ground with one wing dragging behind. Bird M-42 was never seen on the ground again.

Regular observations were resumed on 8 April 1971. Six regular males were present (Fig. 14). Several instances of attempted coyote (Canis latrans) predation were observed during this phase. On 14 April it was noted that AM-15 was absent from the ground. Approximately one week later a dead prairie chicken, which was presumed to be AM-15 was found off the ground. The bird

had apparently been killed by a coyote.

One hundred and eighty-eight territory location sightings were recorded during Phase Two (Table 17). Bird M-39 had the largest territory (127.5 m^2), while AM-12 had the second largest (115.0 m^2). Bird M-40 replaced AM-15 and had the third largest territory (95.0 m^2).

Figure 17 shows each bird's territory and relative position during Phase Two. Following the removal of M-38, the remaining birds shifted their territories towards the center position. Birds M-39 and AM-12 shared the center area. Bird M-40 replaced AM-15 and also shared a center position.

A total of 246 aggressive encounters was observed during Phase Two (Table 18). Bird AM-12 had the largest number of encounters (134) and interacted with the second largest number of males (4). Bird M-39 had the second largest number of encounters (123) and interacted with the largest number of males (5). An aggression index was not calculated due to the low numbers of attempted copulations.

On the basis of territory size, position, numbers of aggressive encounters, and the numbers of males encountered, bird M-39 was determined to be the new alpha male. Bird AM-12 had comparable behavior but it was determined to be the beta male, although differences between the two were slight.

Table 17. Area of territories (Fig. 17) and distribution of observed copulations for regular males present on the experimental ground during Phase Two from 8 April to 17 April 1971.

Bird number	Total No. of sightings	No. of sightings used	Percent used	Territory area m^2	Observed attempted copulations	
					No.	%
M-39	46	32	69.6	127.5	4*	50.0
AM-12	50	34	68.0	115.0	4*	50.0
M-40	32	23	71.9	95.0		
M-41	24	17	70.8	80.0		
AM-11	36	26	72.2	72.5		

* one successful copulation

Table 18. Distribution and numbers of observed aggressive encounters for each male on the experimental ground during Phase Two from 8 April to 17 April 1971.

	M-39	AM-12	AM-11	AM-15
AM-12	68			
AM-11	2	20		
AM-15	10	11	15	
M-40	26	35	38	
M-41	17			4

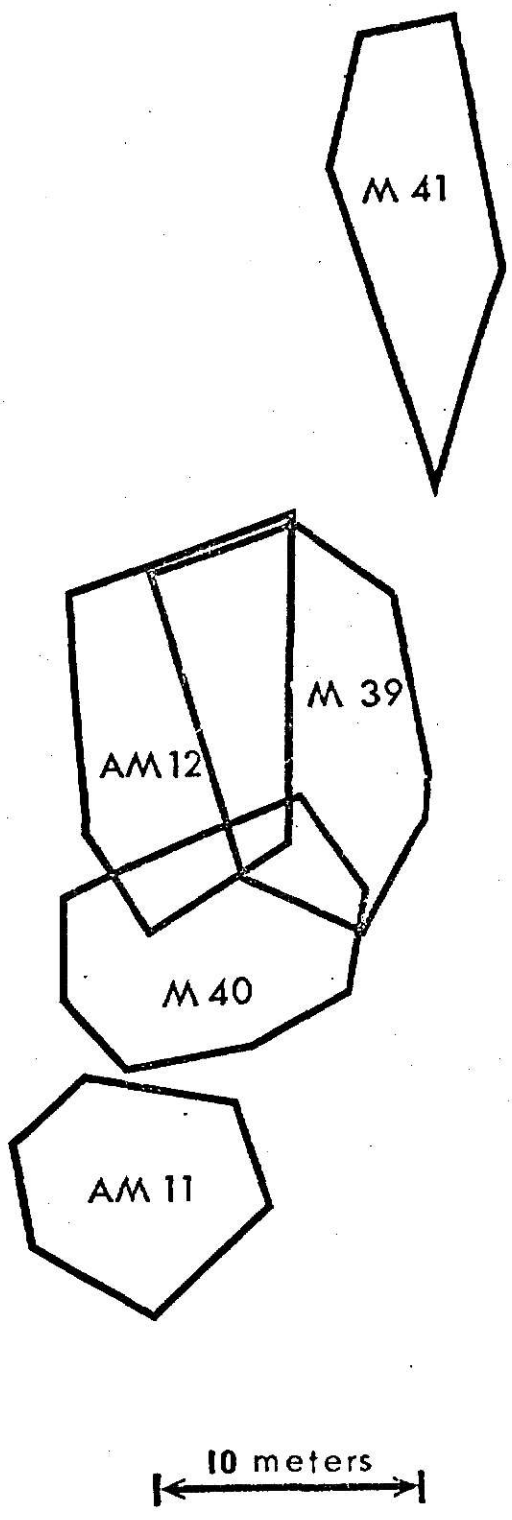

Fig. 17. Diagram of territories occupied by regular males on the experimental ground during Phase Two of Experiment II, 1971.

Eight female visits occurred during Phase Two (Fig. 15). Females spent more total time on the ground during this phase than in any other during Experiment II.

Several instances of female aggression were recorded during this phase. The most noteworthy occurred on 18 April when one female was seen chasing and pecking two other females about to accept a male. This occurred several times during the morning until the less aggressive hens were finally serviced. The aggressive female left the ground unserviced.

Two successful copulations were observed during Phase Two (Table 17). Birds M-39 and M-40 each accounted for one copulation. Three interruptions and three disturbances were also observed. Bird AM-12 was the aggressor in all three interruptions and in two of the disturbances. One of the disturbances was due to female aggression. Birds M-39 and M-40 each had four attempted copulations. Females behavior following successful copulations was the same as that described in Experiment I.

Bird M-39 was removed on 19 April.

Phase Three

Phase Three consisted of the period from 21 April to 17 May 1971. During this phase regular male attendance declined from four to two males (Fig. 14). Total male attendance increased but was very erratic during the late stages of Phase Three (Fig.

13).

One hundred and five territory location sightings were recorded during this phase (Table 19). Bird AM-12 had the largest territory (135.0 m^2), while M-41 had the second largest (130.0 m^2). Bird M-40, which had the third largest territory in Phase Two, had the fourth largest territory (40.0 m^2). Figure 18 shows that AM-12 retained its center position and extended its territory to the edge of M-41's territory. No other changes in position were evident.

One hundred and seventy-three aggressive encounters were observed (Table 20). Bird AM-12 had the largest number of encounters (110) and interacted with all three of the remaining regular males. Bird M-40 had the second largest number of encounters (64).

Only one female visit was recorded during Phase Three (Fig. 15). No attempted copulations were observed.

From 29 April through the remainder of the study, bird attendance on the booming ground became very erratic (Fig. 13). Regular males abandoned their territories with the appearance of two irregular males. Birds could be seen booming and fighting some three to four hundred meters off the ground.

Observations were curtailed on 17 May 1971.

Table 19. Area of territories (Fig. 18) for regular males present on the experimental ground during Phase Three from 21 April to 17 May 1971.

Bird number	Total No. of sightings	No. of sightings used	Percent used	Territory area m^2
AM-12	30	21	70.0	135.0
M-41	25	19	76.0	130.0
AM-11	22	16	72.7	87.5
M-40	28	20	71.4	40.0

Table 20. Distribution and numbers of observed aggressive encounters for each male on the experimental ground during Phase Three from 21 April to 17 May 1971.

	AM-12	AM-11	M-43
AM-11	18		
M-43	21	11	
M-41	32		20
M-40	39	25	
M-44		6	1

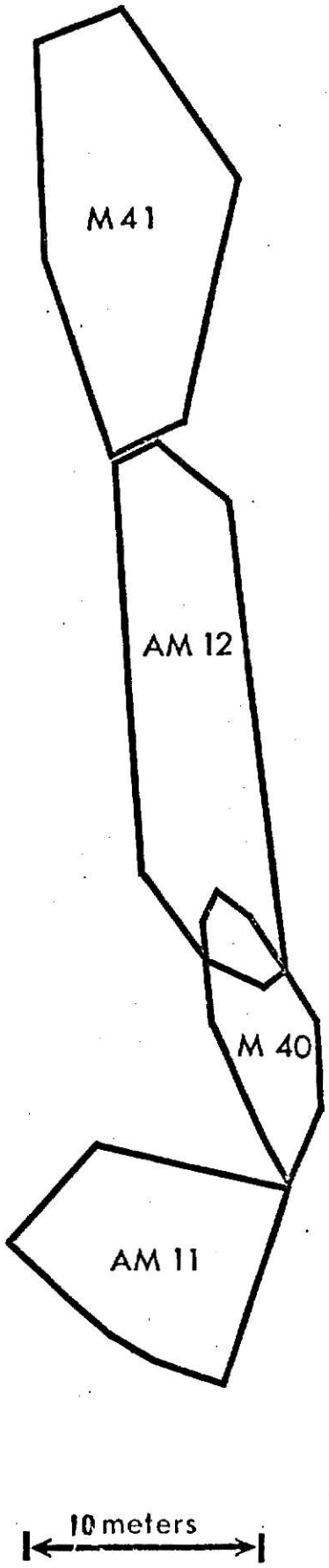

Fig. 18. Diagram of territories occupied by regular males on the experimental ground during Phase Three of Experiment II, 1971.

All Phases

A two way analysis of variance was conducted on aggressive encounters per hour per bird to test for differences between phases and between birds within phases. Phases, birds, and phase x bird interactions were all significant sources of variation ($p < 0.05$). A Duncan's New Multiple Range Test was used to detect individual differences (Table 21). Mean numbers of encounters per hour for birds AM-12, M-40, and M-41 were not significantly different during the three phases of Experiment II. Relative standing of each male varied during each phase. Bird AM-11 had the largest number of encounters per hour during Phase One, while AM-12 had the largest number during Phases Two and Three. No significant differences were detected among males during Phase Three.

DISCUSSION

Trapping and Banding

Advantages and disadvantages of using Japanese mist nets for capturing prairie chickens were thoroughly discussed by Silvy and Robel (1967) and Silvy (1968). One disadvantage not reported concerns the length of time necessary to trap. Viers (1967:18), Silvy (1968:37), and Watt (1969:44) captured one, seven, and seven males, respectively, during an entire display season of trapping. During this study mist nets were used for five days (15½ hours) prior to Phase One. No birds were captured during

Table 21. Duncan's NMRT showing individual differences among mean aggressive encounters per hour per bird between phases and between birds within phases (p 0.05) for the experimental ground during the spring of 1971.*

Bird Number	Phase One	Phase Two	Phase Three
AM-11	21.80	9.08	6.62
AM-12	15.19	15.59	12.88
M-40	4.98	9.93	7.62
M-41	2.78	1.78	6.92

Phase	Bird	Bird	Bird	Bird
	AM-11	AM-12	M-40	M-41
One	21.80	15.19	4.98	2.78
	AM-12	M-40	AM-11	M-41
Two	15.59	9.93	9.08	1.78
	AM-12	M-40	M-41	AM-11
Three	12.88	7.62	6.92	6.62

*Birds underlined indicates that the means were not significantly different.

the five mornings of effort using this technique. Therefore, it appears that mist nets are not suitable for capturing prairie chickens when it is necessary to capture several birds in a short period of time.

Experiments I and II

Examination of territorial maps indicate that alpha males select central positions on booming grounds. Alpha males occupied central positions on both the experimental and control lekking areas during Experiments I and II. Figures 5 and 16 are misleading in that alpha males were surrounded by irregular males at different time intervals. Males in central positions frequently interacted with a larger number of adjacent males than did peripheral birds, and usually had a large number of aggressive encounters.

Prior to removal on the experimental ground, alpha males occupied relatively large territories (third largest in both 1970 and 1971). Following removal territory sizes among remaining males appeared to maintain the same range of sizes. Changes in frequency and distribution of aggressive encounters were noted. The number of aggressive encounters increased progressively during the season.

Although a progressive increase in the frequency of aggressive encounters per bird was noted on the control ground, ter-

ritory positions and sizes remained constant throughout the observation period.

Distinct behavioral differences between the experimental and control grounds were evident during female visits. Following the removal of dominant males on the experimental ground, the remaining males paid no respect to either territory boundaries or positions. All males were seen shifting in the direction of female movement. Females appeared confused and wandered from one side of the ground to the other. In contrast males on the control ground stuck to a fairly rigid territorial system. Females usually stayed within the alpha male's territory.

Hypothetically, it would be to the alpha male's advantage to exert his dominance over as many males as possible before females arrive, thus reducing interference during courting activitities. Dominant individuals would then be in a position to interact with as many males as possible.

An aggression index was calculated for Phase Three of Experiment I by considering only those birds above the mean number of encounters per bird (Table 8). The number of encounters was then divided by the number of males encountered. Birds with a higher index were generally considered to be more aggressive. A correlation between the aggression index and territory size was

negatively correlated ($p<0.05$). More aggressive birds had smaller territories.

All attempts at copulation on the experimental ground during Experiment I were recorded during Phase Three. Birds with a higher aggression index and a smaller territory were responsible for the most attempts at copulation. In contrast, Robel (1967:112) in an earlier study on the same ground, determined that birds with larger territories had more attempts at copulation than did those with small territories. Observations on the control ground confirmed his findings (Table 1).

Since removal of dominant individuals would theoretically leave aggressive but socially equal males, it would be expected that a greater amount of competition between males would occur following removal. After removal it became impossible to detect an alpha or beta male, although broad differences in aggressiveness were noted (Table 12). On the basis of behavior birds M-19, AM-14, M-18, and AM-15 were thought to be equally aggressive. It appeared that the removal of the alpha and beta males caused the remaining birds to shift towards a center position, and due to the large amount of competition, the center birds had smaller territories. The favorable position might account for the large number of attempted copulations among center males although only three were successful.

Several authors have mentioned the importance of the center position in lekking grouse (Lack, 1939; Hamerstrom, 1941; Scott, 1942; Schwartz, 1945; Kruit and Hogan, 1945; and Lumsden, 1965). Birds in center positions have generally been described as being the most aggressive or "vigorous" males on the ground. Both age and fighting ability have been thought to be important factors in determining the social standing of lekking tetraonid males. Robel (1969:3) stated that all alpha and beta male prairie chickens during his 6 year study were at least 2 years of age. In this study all birds captured were at least 2 years old except for one juvenile male.

Thirty attempted copulations were recorded on the experimental lek during Experiments I and II. Of the attempted copulations recorded in 1970, bird M-19 accounted for 38 percent, bird AM-8 for 35 percent, bird M-18 for 23 percent, bird AM-11 for 8 percent, and bird AM-15 for 3 percent. In 1971 birds M-39 and M-40 each accounted for 50 percent of the attempted copulations. In contrast, Robel (1970:308) reported that in the springs of 1964 to 1967 the majority of copulations on the experimental ground were by the two most aggressive males. Of the 121 copulations observed, 108 (89 percent) were conducted by the alpha and beta males. Observations on the control ground showed a similar pattern of mating success. Thus it appears that removal of dom-

inant males reduces the differential mating success of participating males.

Wynne-Edwards (1962:215) postulated that the lek system regulates the number of breeding males in the population. Males which cannot establish a territory are "surplus" and are forced to disperse elsewhere. Wynne-Edwards also believed that as population density increased only a certain number of matings would be accomplished each year, thereby causing a decline in the reproductive rate.

During this study several males were observed being turned away from the ground by established territory holders. Only after the removal of dominant cocks were additional "surplus" males allowed to establish territories. Two males were allowed to establish territories after removal of dominant cocks in 1970, while no additional males were allowed to establish territories in 1971. One possible explanation for the difference between years could have been that the prairie chicken population was at a lower level in 1971, therefore, no "surplus" males were available for territory establishment.

Numbers of prairie chickens seen on the experimental ground have declined in the past few years; 21 in 1968, 14 in 1970, and 9 in 1971. Numbers of female visits for the last two years show similar trends (Figs. 4 and 15). Several environmental factors such as a decrease in winter food supply, range burning, or herb-

icide spraying may have operated together or individually to reduce spring populations. In any result it appeared that removal of dominant individuals allowed non-territorial males, which previously would have been excluded from breeding, to participate in breeding activities.

Prairie chicken copulations are usually conducted by one or two of the more aggressive cocks. Dominant cocks usually have the largest territory on the display area. Robel (1970:308) found that 89 percent of the attempted copulations were performed by two of the more aggressive cocks. Scott (1942:483) reported that of the 154 matings he observed in sage grouse 74 percent were conducted by the "master" cocks. Likewise in the sharptail grouse, Lumsden (1965:59) reported that 76 percent of 17 copulations were performed by the "most dominant cock". Lumsden (1961: 271) reported a similar mating differential in the capercaillie. Data collected on the control ground show a similar pattern in that 100 percent of the copulations were performed by the cock with the largest territory. It appears then there is strong selective pressure for dominance ability in most male lekking tetraonids.

Several instances of female aggression were observed on the experimental lek. Although individual recognition was not always possible, some individuals could be identified by plumage

characteristics. In two instances during 1971 an aggressive female was seen chasing and pecking other females about to accept a mate. Eventually both subdominant females were serviced, while the aggressive female left the ground unserviced. Hamerstrom and Hamerstrom (1960:280) noted aggressive tendencies among females about to accept a cock. Robel (1970:310) believed that the chances of a female being mated were correlated with the aggressiveness of the female (more aggressive females being more likely to be serviced than less aggressive females). The two instances of aggression among receptive females during this study indicated the opposite tendency (more aggressive females being less likely of success). Guhl (1950:5) found that in the domestic chicken the more aggressive females interrupted mating activities and usually were not serviced. Possibly this same mechanism is operating in prairie chicken populations. Craig et al.(1965:130) demonstrated that selection for aggressiveness occurred when both sexes were involved. Although Craig et al. (1965) used 85 to 90 percent selective pressures for social dominance ability, comparable selection occurs in prairie chickens; 85 to 100 percent. It appears that although evidence for selection of aggression is lacking in female prairie chickens, strong evidence of selection in males should override possible non-selection in the female portion of the population. Since aggressiveness is

additive, the level of aggression in the population can gradually increase. If this is true possible breakdowns in the mating system might be predicted after several generations of selection have produced birds of equal aggressive tendencies.

Comparisons of territory sizes and distributions of attempted copulations between years on the experimental ground reveals several differences. Alpha males on the experimental ground in 1964 and 1965 had larger territories (Table 22) than did those before or after removal in 1970 and 1971. As stated previously, removal of alpha males reduced the differential mating success of participating males, but the size ranges of territories remained approximately the same. These discrepancies in territory sizes might be explained on the basis of selection for aggression. Since alpha males accounted for most of the copulations in 1964, 1965, and 1966, it would seem possible that new males joining the population would be more aggressive than those preceeding them. Therefore, participating males in 1970 and 1971 may have had smaller differences in levels of aggression and thus account for the relatively smaller territories due to competition from equally aggressive males. If this be the case a reduction in differential mating success among males might have occurred without the removal of alpha males.

Behavioral comparisons between the experimental and control

Table 22. Area of territories for males present on the experimental ground during the springs of 1964 and 1965 (from Robel, 1966:329).

Spring, 1964 Bird number	Total number of sightings	Territory area m^2	Observed copulations No.	%
M-3	51	518.7	21	91.3
M-6	26	386.8		
M-8	22	327.6		
M-4	37	168.4	2	8.7
M-7	28	82.3		
Spring, 1965				
M-8	207	386.8	29	93.5
M-20	70	281.5	2	6.5
M-19	91	109.2		
M-7	174	63.7		

grounds revealed several significant differences. Males on the control ground stayed within territorial boundaries during female visits, while males on the experimental ground roamed over the entire area. During female visits males on the control ground interacted at territory boundaries, while birds on the experimental lek interacted at a variety of locations. As stated previously, it was to a bird's advantage to interact with as many males as possible before arrival of females. Since 25 of the 30 observed copulations on the experimental ground were interrupted or disturbed, and no interferences were observed on the control ground, the function of the hierarchy appeared to be one of reducing interference during courting activities.

The role of aggression in this hierarchy would appear to be one of utmost importance. Differential aggression would allow aggressive individuals to establish dominance over less aggressive individuals. Subdominant individuals would not enter into a dominant male's territory as was the case on the control ground. The hierarchy would then allow alpha males to court females within territory boundaries without interruptions from neighboring cocks since each bird's position was probably determined earlier in the season. It is concluded that removal of dominant cocks on the experimental ground disrupted the hierarchy and caused individuals to reevaluate their position. This reevaluation among

somewhat equally aggressive males during female visits caused a decline in reproductive success.

Aggressiveness may also have survival value for the more aggressive cocks. It was noted that aggressive cocks usually occupied center positions on the booming grounds. Prairie chickens were observed roosting in the vicinity of the ground each evening. If the birds keep their relative position off the ground, then center birds would be less susceptible to mammalian predation. Several instances of attempted coyote predation were observed during Experiments I and II. In 1971 a regular peripheral male did not return to his territory. Shortly thereafter, the remains of what was presumed to be the missing male were discovered some 60 meters southeast of the ground. Thus aggressive birds may have better survival than less aggressive individuals.

Since aggression is additive, aggressive levels in the population might be expected to increase to a point where several males are equally aggressive assuming there is an upper level of aggressiveness. If this be the case, disruptions in reproductive success might be expected to occur after several generations of selection. During this period females might be serviced by peripheral or non-territorial birds and thus cause a selection for non-aggressiveness. It is not intended to place aggression as the ultimate limiting factor, but it might well coincide with or

be related to changes in other environmental factors such as food, predation, etc.

Robel (1970:308) reported that male attendance decreased by about two birds per week after 1 March. The time of decrease coincided with the time of greatest inter-booming ground movements. A similar decline in regular male attendance occurred during this study. Numbers of total males increased toward the end of the season, especially on the experimental lek (Figs. 1 and 12). This might be explained by the presence of another booming ground just off the study area. This ground was plowed and planted to wheat (Triticum aestivum) in 1968. Toward the end of the season the wheat becomes so high that the birds cannot continue to display, thus an increase in attendance on the experimental lek probably reflects a drop in attendance on the wheat field booming ground.

Tables 12 and 21 show individual differences for numbers of aggressive encounters per hour for Experiments I and II on the experimental ground. Birds could generally be divided into two distinct groups based on differences between means. In Experiment I (Table 12) birds AM-14, AM-15, M-18, and M-19 all appeared to be equally aggressive during the latter phases. Birds with a higher frequency of encounters accounted for nearly all of the attempted copulation (93 percent). Birds in Experiment II ex-

hibited similar tendencies. Following the removal of the alpha male in Phase One, birds AM-12 and M-40 appeared to be equal (Table 21). Birds AM-12 and M-40 had the largest territories and accounted for the two successful copulations observed in 1971. Lumsden (1965:10) mentioned that a hierarchy of dominance existed at least among neighbors in the sharptail grouse. Tables 12 and 21 lend some support to the same situation in the prairie chicken. Birds with a higher frequency of encounters interacted predominantly among themselves, occupied central positions on the ground, and accounted for most of the copulations.

Brown (1969) reviewed the literature concerning the role of territorial behavior in population regulation, and concluded that little evidence existed for the sweeping generalizations found in textbooks and journal articles. Although speaking primarily about Nice's (1941 and 1943) Type A territories, he laid down four basic criteria which he felt would lend support to the hypothesis that territorial behavior limits breeding density. These criteria pertain to his (Brown, 1969:300) level three population which has been inferred to exist in tetraonid populations.

Brown's (1969:304) first criteria states that it must be demonstrated that some individuals are being deprived a chance to breed and that they are part of a surplus. This first point is well documented in lekking tetraonids. Peripheral and non-terri-

torial irregular prairie chickens would fall into this classification. During this study irregular males were never allowed to copulate with visiting females.

The second point is that it must be demonstrated that established territory holders are preventing surplus birds from breeding. If it is assumed that all copulations occur only on the leks then territory ownership is a necessity. Irregular or surplus males during this study were observed being constantly chased and harassed by established owners, thus for the most part preventing any kind of territory establishment. Even most territory owners were prevented from breeding by other more aggressive cocks. Removal of dominant cocks during this study demonstrates that surplus males will establish territories and participate in mating activities.

Brown's (1969:304) third criteria asks for demonstration that territoriality prevents some females from breeding. Female prairie chickens are not known to be territorial, therefore, this point can not be fully met. However, female prairie chickens are known to exhibit some type of dominance hierarchy on the lek which prevents or at least delays some females from breeding.

Brown's (1969:304) fourth point requires that the population be representative of the species being studied. There is no evidence that the prairie chicken population on the Simpson Ranch

in Kansas differs in any manner from other populations within its present range.

CONCLUSIONS

The following tentative conclusions appear to be justified from the data collected during this study.

1. Approximately 90 percent of the reproductive activity is conducted by less than 10 percent of the male population.
2. The booming ground mating system perpetuates high levels of aggression among participating males.
3. The hierarchy appears to act as a stablizing mechanism allowing successful reproduction by dominant males.
4. Removal of alpha males allows surplus males to participate in mating activities.
5. Removal of dominant males does not decrease the attractiveness of the lek to females.
6. Removal of dominant males reduces the differential mating success among males but causes a decline in overall reproductive success.
7. Alpha males usually occupy central positions on booming grounds and may have large or small territories depending on the aggressiveness of surrounding males.
8. Selection against aggression may occur in the female segment of the population.

ACKNOWLEDGEMENTS

I wish to express my gratitude to Dr. R. J. Robel for editing this manuscript. The cooperation of John Simpson, owner of the land on which the study was conducted, is appreciated. I also wish to thank Dan Bowen for his assistance with trapping operations. I also wish to thank my wife, Sheila, for her assistance in preparation and typing the manuscript.

Financial assistance and miscellaneous equipment were provided by the American Philosophical Society, the Kansas Agricultural Experiment Station, the Kansas Forestry, Fish and Game Commission, Kansas State University, the National Institute of Health, and the National Science Foundation.

LITERATURE CITED

Andrewartha, H. G., and L. C. Birch. 1954. The distribution and abundance of animals. Univ. Chicago Press. 782p.

Bent, A. C. 1932. Life histories of North American gallinaceous birds. U. S. Nat. Hist. Mus. Bull. No. 162:242-285.

Briggs. J. N. 1968. Vegetation and occurrence of greater prairie chickens (Tympanuchus cupido pinnatus) on three range sites in Geary County, Kansas. M. S. Thesis. Kansas State Univ., Manhattan. 59p.

Brown, J. L. 1964. The evolution of diversity in avian territorial systems. Wilson Bull., 6:160-169.

Brown, J. L. 1969. Territorial behavior and population regulation in birds. Wilson Bull., 81:293-329.

Craig, J. V., L. L. Ortman, and A. M. Guhl. 1965. Genetic selection for social dominance ability in chickens. Anim. Behav., 13:114-131.

Fuschlberger, R. H. 1956. Das Hahnenbuch. Hunchen-Solln. (in Lumsden, 1961).

Guhl, A. M. 1956. The social order of chickens. Sci. Amer., 194(2):42-46.

Guhl, A. M., J. V. Craig, and C. D. Muller. 1960. Selective breeding for aggressiveness in chickens. Poultry Sci., 39: 970-980.

Hamerstrom, F. N., Jr. 1941. A study of Wisconsin prairie grouse (breeding habits, winter foods, endoparasites, and movements). Ph.D. Thesis. Univ. of Wisconsin. 140p.

Hamerstrom, F. N., Jr., and F. Hamerstrom. 1960. Comparability of some social displays of grouse. Proc. Intern. Ornithol. Congr., 12:274-293.

Hensley, M. M., and J. B. Cope. 1951. Further data on removal and repopulation of the breeding birds in a spruce-fir forest community. Auk, 68:483-493.

Hjorth, I. 1966. Influence of abiotic factors upon the display of the black grouse (Lyrurus tetrix). Var Fagelvarld., 25: 289-314.

Hjorth, I. 1967. Reproductive behavior in male grouse (Tetraonidae). Var Fagelvarld., 26:193-243.

Hohn, E. O. 1953. Display and mating behavior of the black grouse (Lyrurus tetrix). Brit. J. Anim. Behav., 1:48-58.

Kluyver, H. N., and L. Tinbergen. 1953. Territory and the regulation of density in titmice. Arch. Neerlandaises Zool., 10:265-287.

Kruijt, J. P., and J. A. Hogan. 1967. Social behavior on the lek in black grouse (Lyrurus tetrix tetrix). Ardea., 55:203-240.

Lack, D. 1939. The display of the blackcock. Brit. Birds, 32: 290-303.

Lack, D. 1954. The natural regulation of animal numbers. Clarendon Press, Oxford. 343p.

Lack, D. 1966. Population studies of birds. Oxford Univ. Press. 341p.

Lumsden, H. G. 1961. The display of the capercaillie. Brit. Birds, 54:257-272.

Lumsden, H. G. 1965. Displays of the sharptail grouse. Ont. Dept. Lands and Forests Res. Rept. No. 66. 68p.

Lumsden, H. G. 1968. The displays of the sage grouse. Ont. Dept. Lands and Forests Res. Rept. No. 83. 94p.

Robel, R. J. 1964. Quantitative indices of booming Tympanuchus cupido pinnatus. Trans. Kansas Acad. Sci., 67:702-712.

Robel, R. J. 1966. Booming territory size and mating success of the greater prairie chicken (Tympanuchus cupido pinnatus). Anim. Behav., 14:328-331.

Robel, R. J. 1967. Significance of booming of greater prairie

chickens. Proc. Amer. Philosophical Soc., 111:109-114.

Robel, R. J. 1969a. Movements and flock stratification within a population of blackcocks in Scotland. J. Anim. Ecol., 38:755-763.

Robel, R. J. 1969b. Possible function of the lek in regulating tetraonid populations. Proc. XV Internat. Ornithol. Congress. 17p.

Robel, R. J. 1970. Possible role of behavior in regulating greater prairie chicken populations. J. Wildl. Mgmt., 34(2): 306-312.

Schwartz, C. W. 1945. The ecology of the prairie chicken in Missouri. Univ. of Missouri Studies. 99p.

Scott, J. W. 1942. Mating behavior of the sage grouse. Auk, 57:467-471.

Scott, J. W. 1950. A study of the phylogenetic or comparative behavior of three species of grouse. Ann. New York Acad. Sci., 51:1062-1073.

Selous, E. 1909. An observational diary on the nuptial habits of the blackcock (Tetrao tetrix) in Scandinavia and England. Part I, Scandinavia Acologist, 13:400-413.

Silvy, N. J. 1968. Movements, monthly ranges, reproductive behavior, and mortality of radio-tagged greater prairie chickens (Tympanuchus cupido pinnatus). M. S. Thesis. Kansas State Univ., Manhattan. 135p.

Silvy, N. J., and R. J. Robel. 1967. Recordings used to increase trapping success of booming greater prairie chickens. J. Wildl. Mgmt., 31:370-373.

Silvy, N. J. and R. J. Robel. 1968. Mist nets and cannon nets compared for capturing prairie chickens on booming grounds. J. Wildl. Mgmt. 32:175-178.

Tindell, D., and J. V. Craig. 1960. Genetic variability in social aggressiveness and competition effects between sire families in small flocks of chickens. Poultry Sci., 39:1318-1320.

Viers, C. E. 1967. Home range and movements of the greater prairie chicken (Tympanchus cupido pinnatus) with notes on activities. M.S. Thesis. Kansas State Univ., Manhattan. 78p.

Watt, P. G. 1969. Mobility patterns, habitat relationships, and reproductive success of greater prairie chickens (Tympanuchus cupido pinnatus) in northeastern Kansas. M.S. Thesis. Kansas State Univ., Manhattan. 146p.

Wynne-Edwards, V. C. 1962. Animal dispersion in relation to social behavior. Hafner, N. Y. 653p.

IMPORTANCE OF SOCIAL AGGRESSION IN BOOMING GROUND HIERARCHY OF GREATER PRAIRIE CHICKEN (*TYMPANUCHUS CUPIDO PINNATUS*)

by

WARREN BAXTER BALLARD, JR.

B. S., New Mexico State University, 1969

AN ABSTRACT OF A MASTER'S THESIS

submitted in partial fulfillment of the

requirements for the degree

MASTER OF SCIENCE

Division of Biology

KANSAS STATE UNIVERSITY
Manhattan, Kansas

1971

THIS BOOK CONTAINS NUMEROUS PAGES THAT ARE BLURRY DUE TO DOUBLE PRINTING IN THE TEXT.

THIS IS AS RECEIVED FROM THE CUSTOMER.

ABSTRACT

Wynne-Edwards postulated that the functional value of polygyny in avian species with equal sex ratios was to maintain a high level of competition among the males thus perpetuating the most aggressive individuals through group selection. Wynne-Edwards' theory of group selection has been criticized for having little genetic foundation. A genetic basis for inheritance of dominance ability has been verified in the domestic fowl. Therefore, social dominance could be transmitted through natural selection of the fittest. The present study concerns the role of social aggression in the booming ground hierarchy of the greater prairie chicken (Tympanuchus cupido pinnatus).

Previous research on prairie chickens has demonstrated that dominant males conduct approximately 90 percent of the copulations on the booming ground and that the size of territory was positively correlated with aggressiveness. Because aggressive birds conduct most of the copulations, it appears that there is natural selection for aggression on the booming ground. An experiment was designed to test the theory that prairie chicken booming grounds perpetuate high levels of aggression in the population.

Dominant males were removed from a booming ground, designated the experimental ground, during the springs of 1970 and 1971. Observations were conducted before and after the removal

of dominant males. During the same time periods observations were conducted on a control booming ground. Each year of observation was classified as a separate experiment (Experiment I for 1970 and Experiment II for 1971). Observations on the experimental ground were stratified into separate phases for each experiment; those on the control ground were not stratified.

Observations consisted of notes on female visits, numbers of males present, number of aggressive encounters, numbers of copulations, territory sightings, and individual male behavior. Dominance hierarchies were determined on both grounds by early spring.

Eleven male prairie chickens were trapped with cannon nets and individually marked on two booming grounds (experimental and control) during the spring of 1970.

Dominant males were removed from the experimental ground early in the breeding season for both Experiments I and II. Prior to removal dominant males had large territories (third largest in both 1970 and 1971) and occupied center positions on the booming ground. Following removal, aggressive males of equal social standing moved into central positions and occupied relatively small territories. In contrast dominant males on the control ground had the largest territories and occupied central positions throughout the breeding season. It was concluded that alpha

males usually occupy center positions on booming grounds and that their territory size depends upon the relative aggressiveness of surrounding males.

Surplus males established territories following removal of dominant males in 1970, while no territories were established following removal in 1971. Comparisons of numbers of booming males for the two years indicated that the 1971 male population was smaller than the population in 1970. Therefore, it was concluded that removal of dominant males allows surplus males to participate in mating activities.

Removal of dominant males on the experimental ground caused a complete breakdown of normal reproductive activities. Of the 97 female visits to the experimental ground during Experiments I and II, only five copulations of 36 attempts were successful. The 36 attempts were performed by seven different males. On the control ground no interruptions or disturbances were observed during courting activities. The removal of dominant males, therefore, reduced the differential mating success among males and caused a decline in overall reproductive success. The function of the hierarchy appeared to be one of stabilization during reproduction which allowed successful reproduction by dominant males.

On both the experimental and control grounds males in central

positions attempted most of the copulations. Males in central positions were more aggressive than those occupying peripheral positions. Because most reproductive attempts were conducted by the more aggressive individuals it was concluded that booming grounds perpetuate high levels of aggression in the males.

Several instances of female aggression were observed during the study. Two successful copulations by subordinate females on the experimental ground indicated that selection against aggressiveness may be occurring in the females.