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Social Relationships Among Captive Tufted Titmice (*Parus bicolor* linnaeus) and Carolina Chickadees (*Parus carolinensis* audubon)

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To the Graduate Council:

I am submitting herewith a thesis written by Larry M. Stearns entitled "Social Relationships Among Captive Tufted Titmice (*Parus bicolor* linnaeus) and Carolina Chickadees (*Parus carolinensis* audubon)." I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Animal Science.

J. C. Howell, Major Professor

We have read this thesis and recommend its acceptance:

Arthur C. Cole, Edward E. C. Clebsch

Accepted for the Council:
Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

February 22, 1965

To the Graduate Council:

I am submitting herewith a thesis written by Larry M. Stearns entitled "Social Relationships Among Captive Tufted Titmice (Parus bicolor linnaeus) and Carolina Chickadees (Parus carolinensis audubon)." I recommend that it be accepted for fifteen quarter hours of credit in partial fulfillment of the requirements for the degree of Master of Science, with a major in Zoology.

J. C. Howell
Major Professor

We have read this thesis and recommend its acceptance:

Arthur C. Cole

Edward S.C. Deboch

Accepted for the Council:

Hilton A. Smith
Dean of the Graduate School

SOCIAL RELATIONSHIPS AMONG CAPTIVE TUFTED TITMICE (*PARUS BICOLOR* LINNAEUS) AND CAROLINA CHICKADEES (*PARUS CAROLINENSIS* AUDUBON)

A Thesis

Presented to

the Graduate Council of

The University of Tennessee

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

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by

Larry M. Stearns

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TABLE OF CONTENTS

LIST OF TABLES

TABLE PAGE

LIST OF FIGURES

FIGURE PAGE

CHAPTER I

INTRODUCTION

Some time ago as a result of study in ornithology and perusal of literature in the University of Tennessee libraries, I became interested in observing behavior of birds closely, i.e., particularly captive birds. In the literature I found no mention of the use of feeding behavior as a focal point for observations concerning species interaction and dominance relationships. Therefore, after consultation with Professor Howell, approval of plans, and receipt of funds from the University of Tennessee, I built an aviary. We decided to build the aviary on the roof of the east wing of Hesler Biology Building, University of Tennessee campus because of the secluded nature of the site. It was an outdoor site easily and conveniently reached by myself and Professor Howell and was not subject to visits by unauthorized personnel.

Since Gibb (1957) had stated that his birds fought little when given plenty of cage space, we decided to make the aviary large enough for twelve birds without placing too large a demand on the zoology department budget. I built the cage forty feet long, twelve feet wide, and eight feet high on a redwood foundation which was treated with two coats of redwood sealer. The floor was built of five-eighths inch exterior plywood sheets treated with two coats of sealer on each side, four coats of marine varnish on the top, and two coats of marine

varnish underneath. Square, hollow, one-inch steel tubing and one and one-half inch steel angle-bar were used for the uprights or superstructure. All steel was painted with metal primer. The covering used was one-half inch standard hardware cloth joined along the seams by shoat rings. The whole superstructure was steadied by one-eighth inch steel cable anchored to the lower floor railing on the southwest side and to the roof on the northeast side. One large door was provided at the west end of the cage so that the observation booth could be removed if necessary. Another smaller door was built into the east end of the cage and was the one primarily used for entrance and exit throughout the study. The cage was sloped to the east end a total of four inches in the forty feet, and, as a result of this, absolutely no drainage problems arose, and the floor dried exceptionally fast after rains.

The observation booth was made five and one-half feet high, three feet in length, and three feet wide. A small door was cut in one side, and in the opposite side a one by two feet section of one-way glass was placed at eye level, sitting position. The booth was built of three-quarter inch exterior plywood and finished with one coat of sealer and one coat of red barn paint. It was furnished with a shelf at standard table height, or thirty inches, for writing. It was reinforced at the corners with two-inch steel L-bars and wood screws. Since the cage had a good floor, the booth was not provided with one.

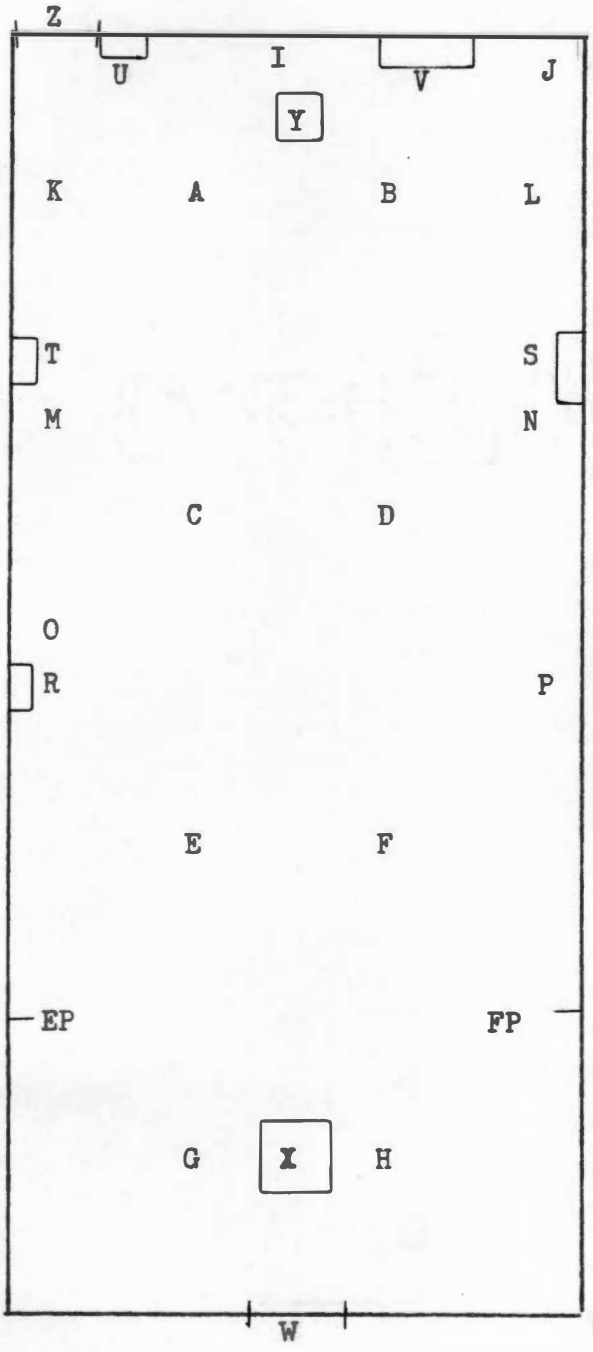
Provisions were made for occupation by birds by supplying shelter boxes, feeding stations, trees, perches, and two canvas tarpaulins for shade and shelter. Shelter boxes with small holes were

provided for chickadees, and boxes with larger holes for titmice. Titmice were thereby prevented from entering chickadee shelters. One shelter box for shelter and feeding was used by both species. There were four feeding stations, eight trees, and four small dowel perches.

The wooden boxes, feeding stations, dowel perches, and east and west doors were painted with one coat of sealer and one coat of red barn paint. The movable feeding station was painted with black enamel. Boxes and feeding stations placed on uprights were sixty-four inches from the floor. The feeding station on the booth was thirty-six inches from the floor, and the movable feeding station was fifty-four inches high. Water was provided in an aluminum pan on the floor and in a small shallow glass container on the movable feeding station.

The cage was divided into eight areas designated A through H. All trees, perches, feeding stations, shelter boxes, etc. were designated as shown in Figure 1, page 4. This designation of areas and objects in the cage made the collection of data simpler and faster. The observation booth was in Position GH throughout the course of this study.

We obtained from the Department of the Interior, Fish and Wildlife Service permits to hold in captivity protected species, i.e., Carolina Chickadees and Tufted Titmice, not more than six of each. The birds were captured in the areas shown in Figure 2, page 5, and Figure 3, page 6. These areas are part of the University of Tennessee Cherokee Farm woodland property. The area shown in Figure 2 is woodland composed mostly of oak, ash, maple, and elm with very little



A through H--Cage Areas

I--Deciduous Tree

J--Evergreen Tree

K--Deciduous Tree

L--Deciduous Tree

M--Privet

N--Privet

O--Evergreen Tree

P--Deciduous Tree

R--Shelter, Feeding Station

S--Titmouse Shelter

T--Shelter, Feeding Station

U--Chickadee Shelter

V--Chickadee Shelter

W--West Door

X--Observation Booth

Y--Movable Feeding Station

Z--East Door

EP--Dowel Perches

FP--Dowel Perches

Figure 1. Cage Layout

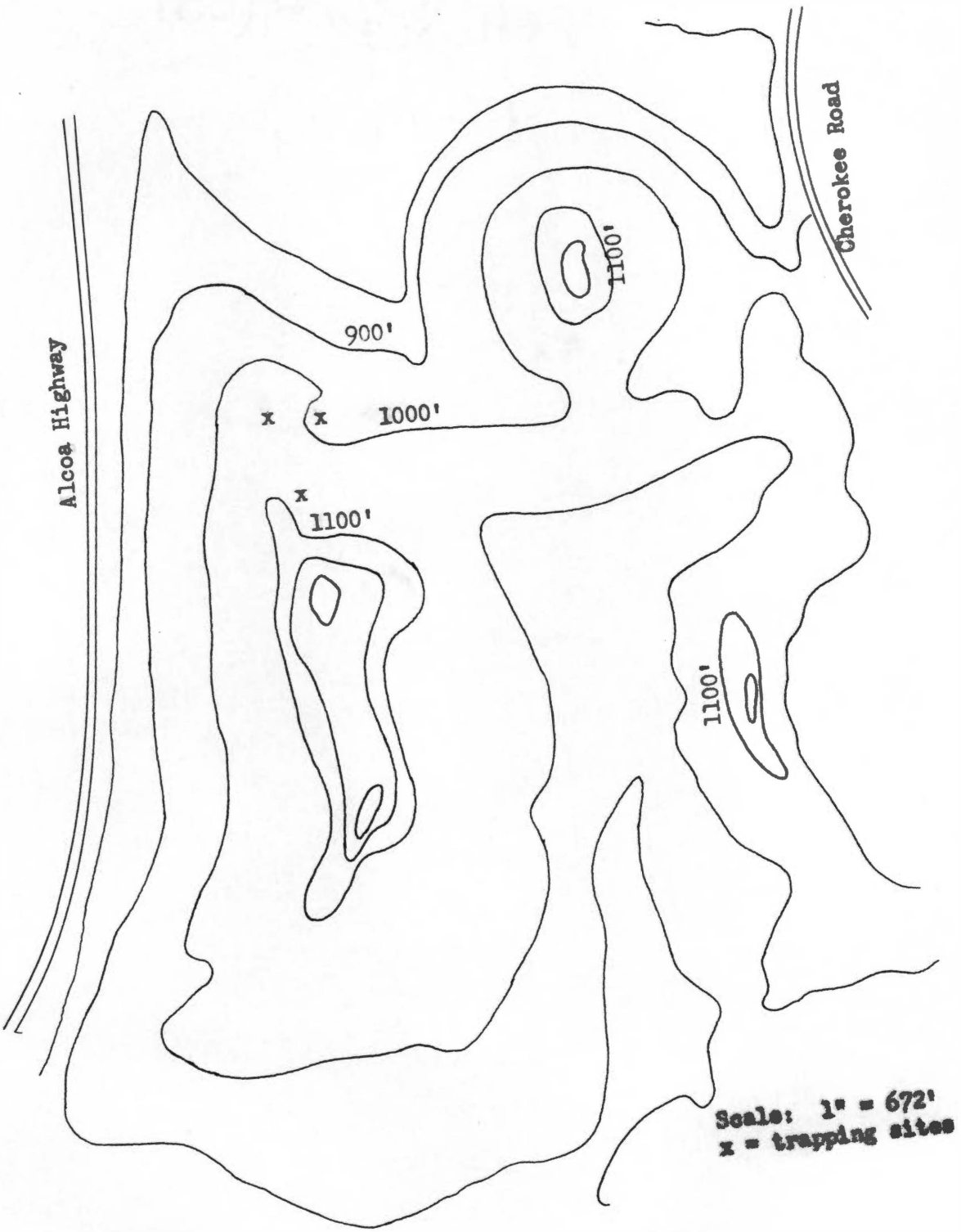


Figure 2. Contour map of capture area 1.

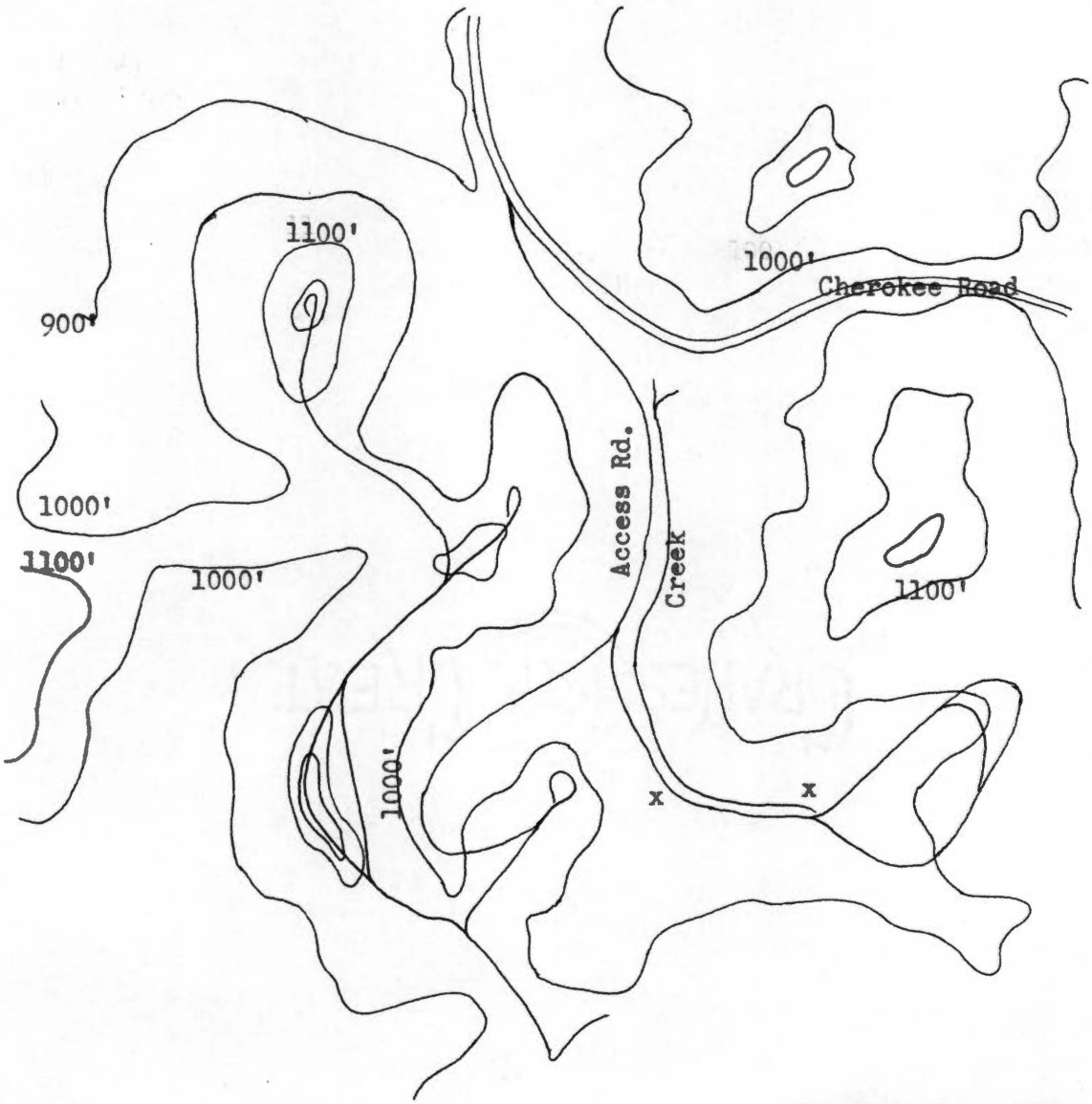


Figure 3. Contour map of capture area 2.

evergreen. The understory is mostly herbaceous because of ground fire in recent years. The area shown in Figure 3 is mixed forest, composed mostly of oak, ash, maple, cedar, and pine. The birds were captured in mist nets after several weeks of supplying food at the designated feeding stations set up nearby. The birds were weighed, measured, banded, and color banded before being released into the cage. Pertinent information about each bird is contained in Table I, pages 8 and 9.

At introduction into the cage, some problems arose with birds flying into the wire in their attempts to escape. Few chickadees were adversely affected in this manner, but titmice were slow to learn that they could not fly through it. I believe this to be the direct reason for most of the deaths of titmice and indirectly the reason for the deaths of a few others which apparently were so unable to adjust that they refused to eat. Their state of alarm was probably initiated by their collisions with the wire. Most of the chickadees, after one trial, never flew into the wire again. Always the titmice were slower to adjust.

A review of literature indicated that chickadees and titmice eat mostly seeds, nuts, and insects, so I decided to provide a variety of food, i.e., a self-choice diet, offered either on the feeding station shelf or in Petri dish halves. The foods offered were unsalted, chopped, roasted peanuts; mixed small seeds, sold commercially as wild bird food; sunflower seeds; suet; live mixed insects; and frozen mixed insects. At the beginning of the study, a mixture of

TABLE I

DATA ON CAGED BIRDS AT DATE OF CAPTURE

Supposed Rank	Species	Age	Sex	Size	Date Captured	Leg Bands Left Prox.	Left Dist.	Right Prox.	Right Dist.	Band Numbers
1	Tufted Titmouse	I.	F	W. 73 mm. T. 64 mm. Wt. 20.2 g.	8/10/64	R	LP	DB	AL	33-196384
2	Tufted Titmouse	U.	F	W.76 mm. T. Molt. Wt. 21.9 g.	9/25/64	DG	LP	DB	AL	33-196386
3	Tufted Titmouse	I.?	M	W. 78 mm. T. 67 mm. Wt. 20.5 g.	7/14/64	LG	H	DB	AL	33-196363
4	Tufted Titmouse	I.	F	W. 73 mm. T. * Wt. 21 g.	6/30/64	W	Y	DB	AL	33-196343
5	Tufted Titmouse	A.	F	W. 73 mm. T. * Wt. 18.5 g.	7/15/64	LG	Bk	DB	AL	33-196364
6	Tufted Titmouse	A.	M	W. * T. * Wt. 22.2 g.	6/30/64	W	LB	DB	AL	33-196349
7	Carolina Chickadee	A.	M	W. 57 mm. T. 49 mm. Wt. 9.5 g.	7/30/64	LP	W	DB	AL	32-00887

TABLE I (continued)

Supposed Bank	Species	Age	Sex	Size	Date Captured	Leg Bands Left Prox.	Left Dist.	Right Prox.	Right Dist.	Band Numbers
8	Carolina Chickadee	A.	M	W. 61 mm. T. 50 mm. Wt. 8.8 g.	7/27/64	Bk	W	DB	AL	32-00884
9	Carolina Chickadee	A.	F	W. 58 mm. T. 48 mm. Wt. 8.9 g.	7/27/64	DG	W	DB	AL	32-00882
10	Carolina Chickadee	U.	F	W. 58 mm. T. 51 mm. Wt. 9 g.	9/25/64	W	R	DB	AL	32-00885
11	Carolina Chickadee	A.	M	W. 62 mm. T. 58 mm. Wt. 9.4 g.	7/30/64	LG	Y	DB	AL	32-00881
12	Carolina Chickadee	A.	F	W. 58 mm. T. 45 mm. Wt. 9.9 g.	8/18/64	R	W	DB	AL	32-00892

*Not taken
I. Immature
A. Adult
U. Unknown
F Female
M Male
W. Wing length in millimeters
T. Tail length in millimeters
Wt. Weight in grams
DB Dark blue
DG Dark green
LP Light pink
LG Light green
LB Light blue
AL Aluminum
Bk Black
W White
Y Yellow
H Heliotrope
R Red

milk and egg yolk was supplied, especially for sick birds, until, for some unexplained reason, they ceased drinking it. Insects were trapped in a black light funnel trap and were mostly of the following families: Coleoptera--Dytiscidae, Carabidae, Scarabaeidae, Histeridae, Hydrophilidae, Staphylinidae, Lampyridae, Silphidae, Elateridae, Tenebrionidae; Hemiptera--Pentatomidae, Reduviidae, Miridae, Coreidae; Lepidoptera--Cossidae, Sphingidae, Tortricidae, Notodontidae, Geometridae, Lasiocampidae, Arctiidae, Noctuidae; Diptera--Tabanidae, Tachinidae, Muscidae; Hymenoptera--Ichneumonidae. During the summer they were given live insects and during fall and winter were fed mostly frozen insects.

I found stressed throughout the literature the importance of feeding substantial amounts of a variety of insects to insectivorous birds. There are many methods of obtaining insects for birds. The more common methods are insect culture, using crickets, houseflies, honeybee larvae, etc. and insect capture with sweep nets, light traps, or baited traps. Trapping insects is an excellent way of supplementing the diet of birds since it yields a wide variety and involves a minimum of time and effort. Of night light traps, black light or filtered ultraviolet is very effective in bringing in large numbers of a variety of insects (Ficken and Dilger, 1961).

Studies with birds in captivity have been handicapped by the problem of supplying adequate diets. Behavioral studies are especially dependent on the health of the birds. Although birds in the wild feed on a variety of insects, their nutritional requirements in

captivity may be satisfied with only a few species. Insectiverous birds are adapted physiologically to the nutritional constituents of insects. There are probably trace elements, certain amino acids, vitamins, and other factors which make insects more desirable nutritionally than elaborate laboratory preparations (Gary, Ficken, and Stein, 1961). Ficken and Dilger (1961) froze insects and earthworms for use in the winter.

Ordinarily vitamin supplements are not necessary if the animal is fed a diet scientifically determined to be perfect, but, since such information is not available for so many birds, it is best to add vitamins to the diet. Ficken and Dilger (1961) used Zymadrops because they contain Vitamin D_3, which is the most active form of the vitamin in chickens. For birds the size of a canary, two drops per day per bird are recommended in addition to insects. It is convenient to supply vitamins in drinking water for seed-eating birds. Since they usually discard the seed coat, mixing vitamins with seed would be quite ineffective (Ficken and Dilger, 1961).

Morris and Scott suggest powdered milk as a useful addition to diets of some birds (Ficken and Dilger (1961). Self-choice diets are suggested by Ficken and Dilger (1961). A variety of foods should be supplied, i.e., a variety of seeds, insects, etc. To maximize self-choice, food should be presented in flat shallow containers.

I could not find any information about the importance of grit to small passerines. Nevertheless, I supplied a quantity of very small limestone gravel for grit, but it was rarely used. The following

is a list of birds which used grit. Each is followed by the number of times it was observed consuming grit: Procedure 1a--Titmouse R/LP, 5; Chickadee LP/W, 3; Chickadee R/W, 4; Procedure 1b--Titmouse R/LP, 1; Titmouse LG/B, 1; Chickadee Bk/W, 2; Chickadee LG/Y, 1; Chickadee R/W, 1. No consumption of grit was observed during Procedure 2.

Between October 3, 1964 and October 12, 1964, I spent some time in observation attempting to discover a plan or procedural technique which would be best for the information I was seeking. The plan was to use only the large movable feeding station and to place it in each of four different areas of the cage for six hours of observation in each area. I listed observations in the following manner: time, bird observed, food eaten or taken, where food was taken or where bird flew after eating, miscellaneous pertinent information, such as encounters, fights, bathing, etc. This information was later analyzed with respect to interaction, both interspecific and intraspecific, and to dominance relationships. Because Procedure 2 was begun before Procedure 1a was completed, only the first eighteen hours of observation for Procedure 1a and 1b were considered comparable.

I have three major sets of observations. The first covered October 12 through October 24, 1964, involved eighteen hours of observation, and will be designated Procedure 1a.

The second set of observations, designated Procedure 1b (November 11 through 18), was a follow-up repeat of Procedure 1a to determine any changes caused by a reduction in population. Four

birds were found dead after completion of Procedure 2 and were presumed to have been killed by others in the cage. No bird was ever observed actually killing another, but on November 22, 1964, Titmouse R/LP was observed to jump upon the back of Titmouse W/Y and peck the latter twice on the back of the skull. This attack took place on the cage floor, Area AB, and was apparently unprovoked. Only one other attack resulting in a fight was observed. The fight involved Chickadees R/W and Bk/W. The latter initiated the attack on the cage floor, Area AB, and the fight lasted about fifteen seconds with Chickadee R/W on its back for the duration.

The third set of observations was a food deprivation experiment to determine the effects of a stress-inducing procedure upon interactions. The procedure was to supply one small container two and one-half inches in diameter containing a mixture of all foods previously offered for one hour (9:00 a.m. to 10:00 a.m.) on each of four mornings (October 25 through October 28), followed on two afternoons (October 25 and October 28) at the regular observation time (11:00 a.m. to 2:00 p.m.) by a return to normal observational procedure, i.e., with a large supply of food in several small containers on the feeding station (an area of four or five square feet). Thus, Procedure 2 consists of four one-hour periods of observation in the morning on October 25 through October 28 and two three-hour periods of observation at the regular time (11:00 a.m. to 2:00 p.m.) on October 25 and October 28 for a total of ten hours of observation. The amount of food supplied during Procedure 2 was sufficient, but placing it in the

small container had the effect of limiting feeding choice and availability of food. This procedure was apparently responsible for the increased aggressiveness of Titmouse R/LP, not only during the morning hour on each of the four days observations were conducted, but also during the regular 11:00 a.m. to 2:00 p.m. observation period when the normal food complement was restored. This bird may have been the killer of four birds (three chickadees and one titmouse) found dead with apparent peck wounds on their skulls. After this, it was decided to proceed along the lines of Procedure 1a and assess any differences that may have arisen as a result of the reduction in population level.

The statistical tests used in analysing the data were a standard t test, a two-way test of Chi square, and a two-way analysis of variance. The latter was especially valuable for analysis of interspecific and intraspecific interaction (Bailey, 1959, Kurnow, et al., 1959, Snedecor, 1934, and Steel and Torrie, 1960).

Mortality of birds in captivity is of prime concern because of the disruption of experimental procedures it may cause. For this reason, each bird, when found dead, was autopsied, re-weighed, if this was appropriate, re-measured when possible, and sexed. As far as possible, the cause of death was ascertained. Table II, page 15, is a presentation of pertinent information for each fatality.

During the period of October 3, 1964 to October 12, 1964, I also tried to obtain a mental impression of the dominance order and planned to refer to my assessment after I had thoroughly analyzed the data and formulated a more scientifically exact report. This order

TABLE II

BIRD MORTALITY

Date of Death	Species	Sex	Age	Weight at Death	Probable Cause of Death	Band Number
6/30/64	Tufted Titmouse	F	A.	14.7 g.	Dehydration; failed to eat or drink.	28-152834
6/30/64	Tufted Titmouse	M	A.?	16.8 g.	Dehydration; failed to eat, lost 3.5 g. weight in 5 hours.	33-196338
7/1/64	Tufted Titmouse	M	I.	20.8 g.	Unknown. Possibly shock.	33-196347
7/2/64	Tufted Titmouse	M	I.	*	Unknown	33-196351
7/15/64	Tufted Titmouse	F	I.	*	Unknown	33-196362
8/1/64	Tufted Titmouse	U	I.	*	Unknown	33-196379
9/21/64	Carolina Chickadee	M	A.	10.0 g.	Probably due to blow on skull (inflicted by another bird?)	32-00868
9/24/64	Tufted Titmouse	U	A.	19.8 g.	Brain hemorrhage and muscle hemorrhage above left leg. Cause unknown.	33-196378
10/28/64	Carolina Chickadee	F	A.	8.6 g.	Blows on skull, probably peck wounds	32-00882
10/28/64	Carolina Chickadee	M	A.	9.0 g.	Blows on skull, probably peck wounds	32-00887

TABLE II (continued)

Date of Death	Species	Sex	Age	Weight at Death	Probable Cause of Death	Band Number
10/28/64	Carolina Chickadee	F	A.	8.5 g.	Blows on skull, probably peck wounds	32-00885
10/31/64	Tufted Titmouse	F	A.	*	Blows on skull, probably peck wounds	33-196386
11/22/64	Tufted Titmouse	F	A.	19.3 g.	Bird apparently froze. Found on exposed perch which was not its regular roosting place.	33-196384
11/22/64	Carolina Chickadee	F	A.	8.4 g.	Blows to skull, probably peck wounds	32-00892
12/11/64	Tufted Titmouse	F	A.	*	Blows to skull. Possibly the bird was dead or dying when the wounds were inflicted. Apparently had been excluded from shelter once before and was sick three days but recovered.	33-196343
12/21/64	Carolina Chickadee	M	A.	8.7 g.	No brain damage. Possibly froze to death.	32-00884

* Not taken
F Female
M Male
U Unknown
I. Immature
A. Adult

was as follows: Tufted Titmice: (1) Alpha, R/LP, (2) DG/LP, (3) LG/R, (4) W/Y, (5) LG/Bk, (6) W/LB; Carolina Chickadees: (1) Alpha, LP/W, (2) Bk/W, (3) DG/W, (4) W/R, (5) LG/Y, (6) R/W. Alpha designates the dominant bird in each group. The birds are designated by their left leg color bands. The color code is given in Table I, page 9. This assessment of dominance relationships was made on October 10, 1964.

Table III, page 18, is a presentation of information on birds sacrificed at the end of the study. These were etherized, autopsied, and preserved in formalin along with all of the other birds which died in the course of this study.

Hereafter in this paper, abbreviations will be used which are consistent with those given in the cage layout drawing (Figure 1, page 4) and the dominance order list. This should greatly facilitate brevity, clarity, and understanding. Birds will be referred to by their color band designations, procedures by their number, i.e., 1a, 1b, or 2; and cage areas, objects, etc. will be referred to by their letter designations. Photographs of the cage may be found in Appendix A.

TABLE III

BIRDS SACRIFICED FOR POSITIVE SEXING

Date of Death	Species	Sex	Age	Size	Band Number
12/23/64	Tufted Titmouse	F	A.	W. 72 mm. T. 64 mm. Wt. 19.3 g.	33-196364
12/23/64	Tufted Titmouse	M	A.	W. 78 mm. T. 70 mm. Wt. 20.3 g.	33-196349
12/23/64	Tufted Titmouse	M	A.	W. 77 mm. T. 66 mm. Wt. 21.7 g.	33-196363
12/23/64	Carolina Chickadee	M	A.	W. 62 mm. T. 50 mm. Wt. 10.7 g.	32-00881

CHAPTER II

DOMINANCE AND SPATIAL RELATIONSHIPS

I. DOMINANCE

The following is a review of literature pertinent to a study of dominance:

Schjeldrup-Ebbe (Van Tyne and Berger, 1959) first used the word dominance in describing his observations of social hierarchies in birds. Within any flock and between any two individuals, one bird invariably has precedence.

An individual is said to be dominant over another when it has priority in feeding, sexual and locomotor behavior, and when it is superior in aggressive encounters with other birds. In foraging flocks of mixed species, interspecific dominance relationships arise. For example (Armstrong, 1947), in feeding flocks of nuthatches and titmice in England, nuthatches usually dominate Great Tits; Great Tits dominate Blue Tits; and Blue Tits dominate Marsh Tits. The most definite type of dominance relationship in a group of birds is known as peck-right and involves a straight line order of dominance. Peck-right as opposed to peck-dominance has been noted in various passerine species in captivity.

Etkin (1964) and Allee (1951) say that dominance in chickens and other birds is often clear cut, vigorous, and uniform in expres-

sion. Such invariable dominance might be described as complete dominance or peck-right. In other species, however (i.e., pigeons), dominance may be of a partial and relative character called peck-dominance. For example, among pigeons, there is no complete dominance of one animal by another but rather the greater number of successful attacks determines the dominant bird, i.e., a dominant bird delivers more pecks than he receives and wins more encounters than he loses.

Dixon (1962) found that Carolina Chickadees in the wild were organized in a peck-right hierarchy. In general the dominant birds fed first and returned more frequently to a food source. Order of precedence at a food source was used as one criterion of social ranking, and the structure of flocks was determined by observation at feeding stations. Tordoff (Dixon, 1962) found no difference in rank determined by fighting and that determined by order of feeding in the Red Crossbill.

Dixon (1962) found that some individuals avoided the feeding station when the dominants were present. He also observed that Tufted Titmice dominate Carolina Chickadees. In many cases there was an avoidance of contact by closely ranked individuals. The mate of the Alpha male had precedence over other males when her mate was present.

Armstrong (1947) observed that dominant birds do not consistently have things their own way, and subordinate birds have peck-right when on perches or resting places where they feel particularly at home. It is not necessarily the strongest bird which becomes the top

ranking one. If a dominant bird is confronted by another when it is feeling badly, it may become subordinate to it although the newcomer is a weaker bird. Thus, psychological factors as well as physical strength play their part in determining a bird's status. The bird lowest in the social scale is liable to decline in health. The social subjugation of some birds when artificially crowded together may result in death due to severe mental shock, loss of appetite, and possible starvation. If there is a shortage of food, subordinate birds suffer most. Newcomers introduced into a cage with established inmates almost always assume a low social rank. Nice (Armstrong, 1947) found that Song Sparrows in captivity were organized unilaterally by peck-right, which she thought was partly caused by lack of adequate territorial facilities.

Birds such as parids, which form flocks, are less likely to become involved in recurrent fights when in cramped quarters if organized according to peck-right rather than peck-dominance. Supercedence enables food to be obtained by all members of a flock without wasting too much time in disputes (Armstrong, 1947). Threats, gestures, and avoidance serve as substitutes for fighting (Dixon, 1962). Nice (Armstrong, 1947) found that in captivity a subordinate Song Sparrow was not allowed to use the bathing place. According to Odum (Armstrong, 1947), chickadees maintain peck-right at the top and bottom of the order and peck-dominance among intermediates.

In a study by Gibb (1957), Great, Blue, and Coal Tits were trapped wild, and as many as six at a time were confined in an aviary

eighteen feet long, fifteen feet wide, and eight feet high. They were given two weeks to become adjusted to their new surroundings. They did not fight, probably because they were not unduly crowded. There was a rigid order of peck-right both between and within the species. In general, the bolder, dominant, and more inquisitive individuals (which were the first to find freshly introduced foods) adjusted more readily than more submissive birds. Almost anything new placed for the first time in the aviary was thoroughly inspected by the birds. They were fed on mixed seeds and mealworms supplemented regularly by dead insects and ground nuts. They removed their food from the containers and ate it elsewhere. Coal Tits stored food in substantial amounts. Blue and Great Tits did not store as much.

Some birds, such as nuthatches, titmice, owls, etc., store some of the food they find in times of plenty to use when supplies are scarce (Van Tyne and Berger, 1959). Gibb (1957) found that Blue, Great, and Coal Tits in captivity also stored food.

Many birds in flock conditions attack male and female indiscriminately. Dominance may be exercised regardless of sex. It cannot be assumed that it is by virtue of sex alone that a male or female is dominant. Also, there may be reversals of precedence between paired birds. In captivity the dominant among Blackbirds (Turdidae) or tits may kill those of its own species or others confined with it. Low ranking birds in captivity undergo more suffering than those in the wild through being kept close to their tormentors without the buffering protection of territory. In captivity weakly or deformed birds

are commonly persecuted by their fellows. The social order becomes more rigid and aggression more severe as space or food supply is reduced (Armstrong, 1947).

There is usually little competition between species for food. When food is scarce, the various species of Parus feed in different places in trees. The external stimulus for aggression is usually certain stimuli from a fellow member of the species. Sometimes it is elicited by members of other species (Hinde, 1961).

Marler and Andrew (Hinde, 1961) found that a period of food deprivation did not affect the threshold for aggression of chaffinches and buntings at a feeding place in the wild.

One of the most important projects of the present study was to assess dominance relationships among the birds. The criteria decided upon were these: number of trips to the feeding stand; number of successful, as opposed to unsuccessful, encounters; amount of spatial restriction; successful encounters with the bird judged to be next lowest in the social order; and precedence at the feeding station.

Etkin (1964) reported that when two strange hens are brought together, they immediately approach and watch one another carefully. If there is a difference in size or vigor that is obvious enough to be detected by the human observer, the chickens may be counted on to see it at a distance. In this case, one will, by lowering its head and avoiding the other, show that it accepts the subordinate position. If the birds are closely matched, each may try to lift its head higher than the other. If one's head should be lowered, the issue is decided.

Usually, though, closely matched animals will approach close enough to fight. The fight is usually a matter of a few seconds and a few swift pecks, and one leaves defeated.

The above discussion suggests that there is a size and vigor factor involved in determinations of dominance. This is true of many species of birds. Of course, size may enter into the picture as a function of maturity. With chickadees and titmice, size, weight, and age should be important considerations in establishment of a hierarchy among such active and aggressive birds. Hereafter, where sex and age of a bird is of interest, the information will follow mention of the bird in parentheses using abbreviations found in Table IV, page 25, such as (A., F.) for adult female. It would be expected that since males tend to be more aggressive and dominant year round that they should dominate females. Titmice, because of their larger size and greater strength, should dominate chickadees. Under ideal conditions we should expect that larger male birds should dominate the rest. This was not entierly true as shown in Table IV, page 25. It would seem more appropriate among titmice for the male W/LB to dominate. At first, in fact, this bird did seem to be dominant but declined in status as more birds were introduced into the cage. It is strange indeed that two females should be found at the top of the titmouse order and especially for Titmouse R/LP to be so aggressive, since she was immature when captured. This ranking of titmice may be a measure of relative adaptability, because titmice were more adversely affected by caged living, i.e., they reacted more violently and adapted much

TABLE IV

COMPARISON OF BIRDS BY SEX, WEIGHT, AND AGE

Supposed Rank	Color Bands of Bird	Date Captured	Age	Sex	Weight at Capture	Band Number
Titmice						
1	R/LP	8/10/64	I.	F	20.2 g.	33-196384
2	DO/LP	9/25/64	U.*	F	21.9 g.	33-196386
3	LG/R	7/14/64	A.	M	20.5 g.	33-196363
4	W/Y	6/30/64	I.	F	21.0 g.	33-196343
5	LG/Bk	7/15/64	A.	F	18.5 g.	33-196364
6	W/LB	6/30/64	A.	M	22.2 g.	33-196349
Chickadees						
7	LP/W	7/30/64	A.	M	9.5 g.	32-00887
8	Bk/W	7/27/64	A.	M	8.8 g.	32-00884
9	DO/W	7/27/64	A.	F	8.9 g.	32-00882
10	W/R	9/25/64	U.	F	9.0 g.	32-00885
11	LG/Y	7/30/64	A.	M	9.4 g.	32-00881
12	R/W	8/18/64	A.	F	9.9 g.	32-00892

*Unknown

more slowly than chickadees. Judging from encounters and aggressive behavior, I would conclude that the birds were probably overcrowded and lacked sufficient cover for escape from dominant birds.

The ranking for chickadees shows a more "normal" arrangement with only one adult male superceded by females. It can be seen with titmice that the two most recently introduced birds became dominant. This may mean there was a decline in vigor among birds already present, and the new arrivals took precedence by virtue of strength.

Among chickadees the two most dominant birds were first and third to be introduced into the cage. This also is more nearly a normal situation.

It was assumed beforehand that titmice would be dominant, and this was soon confirmed. Very rarely was a titmouse dominated by a chickadee in the course of this study. Table V, page 27, illustrates the dominance structure of these birds. The following comments define the headings and explain the figures found in this table. The total number of trips means the total number of trips made to the feeding stand in the course of sets of observation periods totaling eighteen hours for each of the two procedures. Number of successful encounters means the total number of successful encounters with birds of both species. Number of unsuccessful encounters means the number of unsuccessful encounters each bird had with members of its species. Dominance over the next bird involved two figures. The first figure is the number of successful encounters with the bird judged to be next lowest in rank. The second figure is the number of unsuccessful

TABLE V

ANALYSIS OF DOMINANCE

Supposed Rank	Color Bands of Bird	No. Trips	No. Successful Encounters	No. Unsuccessful Encounters	Dominance Over Next Bird	Total Sites	No. Sites Visited More Than Five Times	Precedence
				Procedure 1a				
Titmice								
1	R/LP	272	66	6	17—3	38	33	2.87
2	DG/LP	247	14	17	7—0	32	28	3.97
3	LG/B	203	9	17	7—0	30	26	5.64
4	W/Y	169	9	13	6—1	25	23	5.43
5	LG/Bk	105	3	15	2—3	25	24	7.98
6	W/LB	112	8	9		14	12	9.33
Chickadees								
7	LP/W	220	19	1	8—0	38	32	5.08
8	Bk/W	271	14	9	5—0	44	38	6.94
9	DG/W	223	7	6	8—0	35	30	6.27
10	W/R	125	10	9	6—1	36	31	7.73
11	LG/Y	137	3	20	0—2	31	28	8.25
12	R/W	117	2	10		27	24	8.30
				Procedure 1b				
Titmice								
1	R/LP	133	11	5	0—2	31	13	4.27
2	LG/B	95	10	0	1—0	40	2	3.55
3	W/Y	103	1	5	0—0	33	6	4.94
4	LG/Bk	56	2	3	0—0	17	3	6.27
5	W/LB	53	1	0		12	4	6.85
Chickadees								
6	Bk/W	201	34	0	22—0	32	13	2.99
7	LG/Y	198	1	22	4—0	44	12	3.99
8	R/W	105	0	15		27	6	4.88

encounters with the bird judged to be next lowest in rank. Total sites is the number of different cage sites visited in three six-hour periods. The figure is the sum of the number of different sites visited in each period. Sites visited more than five times means the number of cage sites visited (to feed or after feeding) more than five times. The figure is a sum of three six-hour totals. The figure for precedence was obtained by scoring a bird's arrival at the feeding station as first, second, third, or whatever, in each hour period. The figures for a six-hour period were averaged, and the three six-hour averages were averaged. A low figure thus indicated a greater precedence than a high figure. The table compares results obtained with Procedures 1a and 1b, the first eighteen hours of each procedure being comparable. Hereafter, some statistical values will be included in the text. Chi square, f, or t values will be given followed by the corresponding probability figure (P).

Birds were compared with regard to successful and unsuccessful encounters. Comparing 1 and 2, 2 and 3, etc., and using a Chi square test, it was found that the following relationships were statistically significant as regards encounters between individual birds. Titmouse R/LP was dominant over Titmouse DG/LP ($X^2 = 26.9$, $P = <.001$); Chickadee LP/W over Chickadee Bk/W ($X^2 = 8.69$, $P = <.05$); Chickadee W/R over Chickadee LG/Y ($X^2 = 7.82$, $P = .05$). It can be readily seen that the loss by death of three chickadees and one titmouse did not alter the dominance ranking in Procedure 1b.

It is clear that dominant birds visited the feeding station

more often. These data treated by analysis of variance are highly significant for intraspecific variation ($f = 31.17$, $P = .01$). Thus it may be concluded that visits to the feeding station may be used as a reliable estimate of dominance. Birds which visited the feeding stand less often were more often relegated to feed from food discarded or dropped to the cage floor. There was no significant difference between the number of trips by chickadees and by titmice ($f = .99$, $P = >.10$).

Analysis of variance showed that there was a significant difference intraspecifically in the number of successful encounters between individuals for chickadees and titmice ($f = 5.42$, $P = .05$), but there were no significant interspecific differences ($f = 1.37$, $P = >.10$). Thus the number of successful encounters can be reliably used as a tool for assessing intraspecific dominance. Also titmice had significantly more successful encounters with chickadees than vice versa ($P = <.001$). Of the few times when a chickadee had a successful encounter with a titmouse, most were not connected with feeding or the feeding station.

Of interest is a drop in the number of successful encounters for titmice and chickadees in Procedure 1b. This probably reflects a decrease in interaction brought on by a lessening of population pressure. There are less occasions for assertions of dominance when the number of birds is reduced.

The number of unsuccessful encounters within each species offers some interesting information. In Procedure 1a the dominant

bird in each species had fewest unsuccessful encounters as expected. Birds lowest in the order also had relatively few unsuccessful encounters, probably because their greater relative restriction resulted in fewer encounters. In other words, a bird restricted because of its low status has less chance for contact with dominant birds. The high figure (20) for Chickadee LG/Y (A., M.) in Procedure 1a is due to persecution of this bird by Chickadee Bk/W (A., M.) and Chickadee W/R (U., F.). For some unknown reason, Chickadee LG/Y (A., M.) was particularly singled out for attacks by Chickadee Bk/W (A., M.). Exceptions to the above are the apparent reversal between Titmouse R/LP (I., F.) and Titmouse LG/R (A., M.) and the high number of unsuccessful encounters for Chickadee R/W (A., F.) in Procedure 1b.

In the column labeled Dominance Over Next Bird, the figures show successful encounters by individual birds with the bird ranked just below it. This analysis also supports the order of rank given in Table V, page 27. It shows reduced interaction among titmice in Procedure 1b, which is probably a result of reduction of the two populations. Statistical figures may be found in Table XIII of Appendix B. The increased interaction among chickadees in Procedure 1b is apparently due to persecution of Chickadee R/W (A., F.) by Chickadee Bk/W (A., M.) and Chickadee LG/Y (A., M.).

The two columns headed Total Sites and Number Sites Visited More Than Five Times were included as a measure of the relative spatial restriction of each bird. It was assumed that the lower a bird's station, the more restricted it would be in its movements connected

with feeding, feeding sites, and favorite perches, i.e., a dominant bird would have precedence in a greater number of cage sites than a bird of low social rank.

These data, treated by analysis of variance, supported the above assumption by attributing to it significance both between and among the two species as follows: total sites, interspecific difference--$f = 14.37$, $P = <.05$; total sites, intraspecific difference--$f = 6.85$, $P = <.05$; sites visited more than five times, interspecific difference--$f = 10.17$, $P = <.05$; sites visited more than five times, intraspecific difference--$f = 5.30$, $P = <.05$. There was less variation among chickadees with regard to relative restriction. This may mean that chickadees were more active spatially, i.e., besides being generally more active, they also spent less time on the feeding station and very rarely fed there, preferring to take their food and eat it elsewhere. Titmice often spent some time eating on the stand. These data also suggest that the ranking according to relative restriction is correct.

The fact that the figures shown for precedence at the feeding station follow the order suggested by the rest of the data further confirms the ranking given in Table V, page 27 (significance intraspecifically by analysis of variance--$f = 5.72$, $P = <.05$). There are only three reversals here. The reversal between Titmouse LG/H (A., M.) and Titmouse W/Y (I., F.) in Procedure 1a may not be too important since it is much more difficult to accurately rank birds intermediate in the social structure than it is to rank the top and bottom of the

order. This may be readily explained if there is peck-right at the top and bottom of the scale and peck-dominance among intermediate birds as found by Odum (Armstrong, 1947) with chickadees. The reversal of precedence figures between Chickadees Bk/W (A., M.) and DG/W (A., F.) concerns two birds which avoided one another spatially, as will be shown later. This would explain this reversal. The reversal of precedence figures between Titmice R/LP (I., F.) and LG/H (A., M.) in Procedure 1b is also a case of closely ranked birds which tended to avoid one another.

The most consistent differences between the two procedures are that there was less interaction between chickadees and titmice ($t = 2.36$, $P = .05$) and less interaction among titmice, though not significantly less ($t = 1.32$, $P = .10$) in Procedure 1b. The number of feeding trips dropped significantly for titmice ($t = 3.12$, $P = .02$) but did not significantly change with chickadees ($t = .37$, $P = >.60$). These changes were probably caused by reduction of the population.

The following two tables--Table VI, page 33, and Table VII, page 34--are included to illustrate the nature of the dominance expressed by titmice and chickadees used in this study. It can be seen that the ranking is not rigid but suggests "peck-dominance" rather than "peck-right." The chart form is that used by Etkin (1964) to illustrate the peck order among chickens. These charts combine figures obtained in Procedures 1a and 1b.

The average number of visits per hour for water for each species as well as the average number of feeding trips without eating,

TABLE VI

ILLUSTRATION OF DOMINANCE ORDER AS ESTABLISHED BY AGGRESSIVE ENCOUNTERS (TITMICE)

	R/LP	DG/LP	LG/H	W/Y	LG/Bk	W/LB
R/LP		3*	3	1	1	2
DG/LP	17		0	0	0	0
LG/H	15	1		0	0	0
W/Y	5	0	9		1	1
LG/Bk	6	4	3	3		3
W/LB	5	0	0	2	2	

*The number of successful encounters a given bird had with other members of the population is given in the vertical columns. The number of unsuccessful encounters for each bird may be read in the horizontal columns.

TABLE VII

ILLUSTRATION OF DOMINANCE ORDER
AS ESTABLISHED BY AGGRESSIVE
ENCOUNTERS (CHICKADEES)

	LP/W	Bk/W	DG/W	W/R	LG/Y	R/W
LP/W		1*	0	0	2	0
Bk/W	10		0	1	0	0
DG/W	1	5		0	3	1
W/R	5	2	3		1	1
LG/Y	4	27	3	6		3
R/W	3	13	1	6	4	

*The number of successful encounters a given bird had with other members of the population (chickadees) is given in the vertical columns. The number of unsuccessful encounters for each bird may be read in the horizontal columns.

and food items stored per hour can be used as reasonably good indicators of increased competition and interaction. This is shown in Table VIII, page 36, which compares the figures obtained from Procedures 1a and 1b with Procedure 2. The table seems to indicate that caged birds, under greater than normal stress, tend to store more food, consume more water, make fewer feeding trips to the feeding station, and visit the feeding station more often without eating. This is caused not only by increased interaction but also by stress brought about by uncertainty and disruption of normal routine. When competition is abruptly increased, stress may reduce the desire for food by occupying them with other matters such as assertions of dominance and precedence. This may be the reason for increased water consumption. Dominance is expressed much more strongly when food is involved. Not once did I observe a bird actively chase another from water while drinking. Under increased stress, average storage per hour increases significantly ($t = 14.07$, $P = <.001$) and may be a mechanism by which feeding competition is reduced.

Figure 4, page 37, is a graph contrasting the number of trips to the feeding station in which no food was eaten or taken with the number of trips in which food was taken. The solid line designates titmouse trips, and the dotted line designates chickadee trips. The scale on the right is for feeding trips, and the scale on the left for non-feeding trips.

The movable feeding station (Y, page 4) was left in Area AB when observations were not being made. Since the observation time for

TABLE VIII

AVERAGE TRIPS FOR WATER, FEEDING AND NON-FEEDING TRIPS, AND ITEMS STORED PER HOUR

	Procedure 1a		Procedure 2		Procedure 1b		Average Excluding Procedure 2	
	C.*	T.**	C.	T.	C.	T.	C.	T.
Average Number Trips per Hour For Water	2.05	1.82	2.33	2.33	1.82	1.32	1.98	1.63
Average Number Feeding Trips per Hour	5.03	5.16	2.91	2.66	3.50	3.06	4.27	4.11
Average Number Non-Feeding Trips per Hour	1.33	2.28	3.21	1.71	1.57	.42	1.49	1.57
Average Number Food Items Stored per Hour	1.45	.13	4.25	3.75	.29	.63	.87	.38

* Chickadees
**Titmice

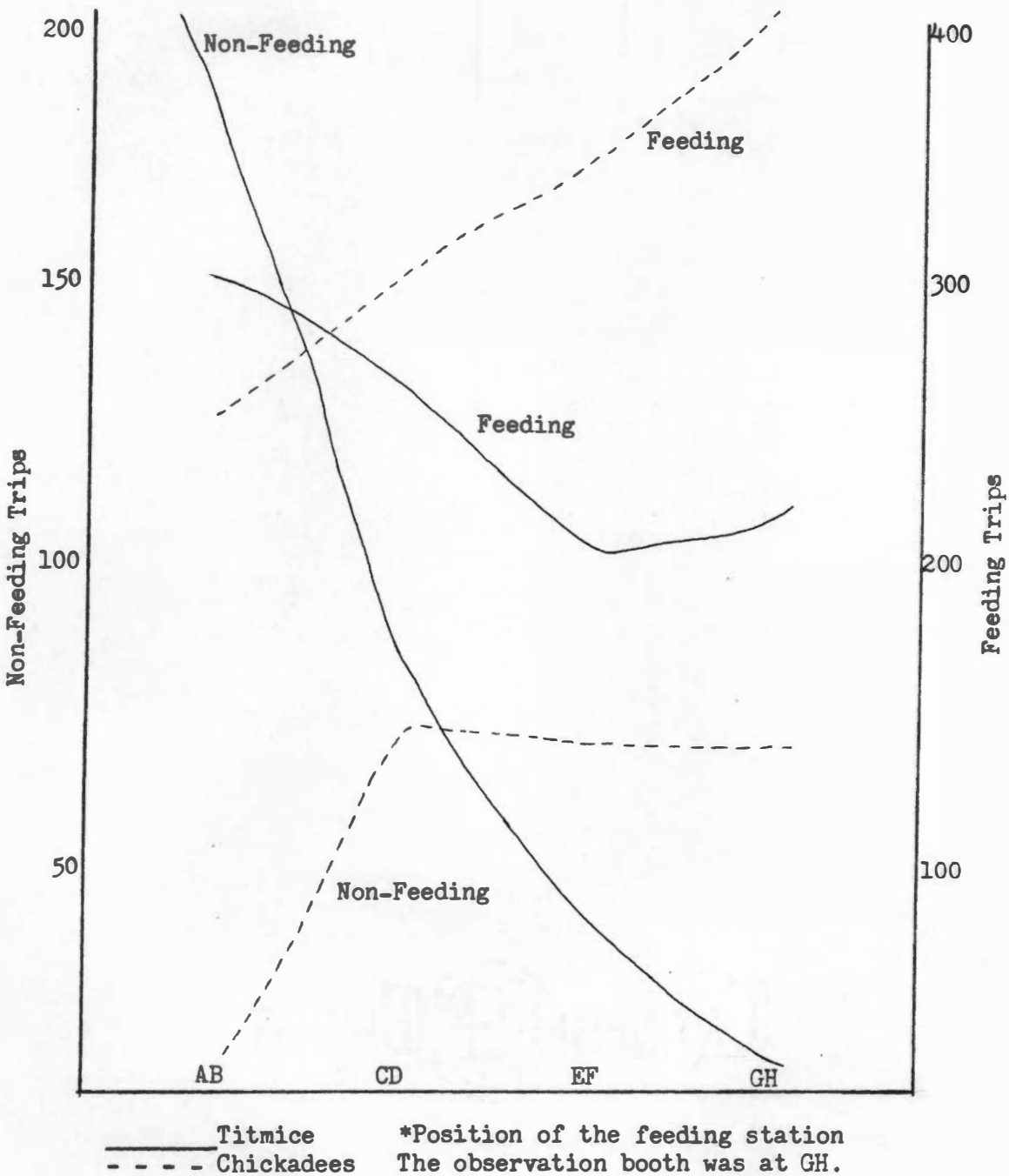


Figure 4. Number of feeding and non-feeding trips for chickadees and titmice, Procedure 1a.

a single day rarely exceeded six hours, it is obvious that the feeding station was in Area AB for a much greater period of time than in any other area (CD, EF, or GH). The titmice, being the dominant species, would tend to have their maximum precedence in the area which contained the feeding station for the longest period of time. This assumption seems to be substantiated by data shown in Figure 4, page 37. This figure shows that titmice had their greatest number of both feeding and non-feeding trips to the feeding station when it was located in Area AB. If this assumption is correct, then the chickadees would be expected to have more relative freedom with regard to visits to the feeding station with the feeding station farthest removed from the area where titmice had their greatest precedence. This too seems to be borne out by the data in Figure 4, page 37, which shows that chickadees had their greatest number of both feeding and non-feeding trips when the feeding station was placed in Area GH.

I have assumed that a bird would have its greatest amount of excess activity with regard to feeding in areas where it had most freedom of movement, i.e., greater precedence. This also is reflected in Figure 4, page 37. Each species had its maximum number of non-feeding trips when the feeding station was located in the area of its greatest precedence, Area AB for titmice and Area GH for chickadees. Significant differences in feeding and non-feeding trips between chickadees and titmice were determined by t tests. Chickadees had significantly more non-feeding trips to the feeding station when it was moved from Area AB to Area CD ($t = 6.58$, $P = <.001$). Chickadees

also had significantly more non-feeding trips with the feeding station in Area GH than in Area AB ($t = 9.79$, $P = <.001$). There was a nearly significant difference for chickadee feeding trips comparing feeding station positions AB and GH ($t = 2.00$, $P = .06$).

Titmice had significantly fewer non-feeding trips with the feeding station in Area GH as compared with position AB ($t = 7.94$, $P = <.001$). There were, however, no significant differences for titmouse feeding trips comparing feeding station positions EF and GH ($t = .26$, $P = >.50$) or positions AB and GH ($t = .98$, $P = .30$).

Table IX, page 40, shows data gathered in each of the two time periods used for Procedure 2. Table XIV (Appendix B) shows that there are no significant differences between data of the two time slots, so all data was grouped for computations in other tables.

It was thought that reduction of availability of food would cause increased interaction and aggressiveness in a population of caged birds. Since only one food source was available during observation periods, it was supposed that this would increase competition for food.

Table X, page 41, shows that this, in fact, was not true. By comparing figures as follows: Procedure 1a with Procedure 2, Procedure 2 with Procedure 1b, and Procedure 1a with Procedure 1b, Chi square tests were run to check for significant differences. (Results of Chi square tests of the data in Table X, page 41; Table XI, page 43; and Table XII, page 45, may be found in Appendix B, Tables XV and XVI.) Five significant differences and four nearly significant

TABLE IX

COMPARISON OF DATA FOR BOTH TIME PERIODS
COMPRISING PROCEDURE 2

	Feeding Trips		Non-Feeding Trips		Titmouse-Titmouse Encounters	Titmouse-Chickadee Encounters	Chickadee-Chickadee Encounters	Total Encounters
	C.*	T.**	C.	T.				
9:00 a.m. to 10:00 a.m. Observation Period (4 hours)	183	130	78	41	10	39	16	65
11:00 a.m. to 2:00 p.m. Observation Period (6 hours)	321	203	58	34	1	32	14	47

* Chickadees
**Titmice

TABLE X

INFLUENCE OF POPULATION PRESSURE AND REDUCTION OF AVAILABILITY OF FOOD ON AGGRESSIVE ENCOUNTERS

	Procedures		
	1a	2	1b
Number of Chickadee-Chickadee Encounters	56	30	33
Number of Titmouse-Titmouse Encounters	74	11	10
Number of Titmouse-Titmouse Encounters Excluding Titmouse R/LP	24	9	2
Number of Titmouse-Chickadee Encounters	44	71	16
Number of Titmouse-Chickadee Encounters Excluding Titmouse R/LP	19	13	8
Total Number of Encounters	174	112	59
Total Number of Encounters Excluding Titmouse R/LP	99	52	43

differences were noted. These are: significant reductions in titmouse-titmouse encounters (1a and 1b); titmouse-titmouse encounters excluding encounters involving Titmouse R/LP (1a and 1b); chickadee-titmouse encounters (2 and 1b); and total encounters (1a and 1b, 2 and 1b). The four nearly significant differences are: reductions in titmouse-titmouse encounters (1a and 2); titmouse-titmouse encounters excluding those involving Titmouse R/LP (2 and 1b); and total encounters excluding those involving Titmouse R/LP (1a and 1b). There was also a nearly significant increase in titmouse-chickadee encounters (1a and 2). Most of these changes and reductions came about as a result of the smaller population present during Procedure 1b (eight instead of twelve birds). Also it can be seen that in many cases, differences are reduced by deleting encounters involving Titmouse R/LP.

Table XI, page 43, shows the generally high percentage of encounters involving Titmouse R/LP. There were two significant differences in figures here. They are reductions in encounters involving Titmouse R/LP (1a and 1b, 1b and 2). This was probably due to the fact that the birds which stimulated its aggressive tendencies were not present.

Titmouse R/LP was by far the most aggressive and dominant in the population and was suspected of killing most, if not all, of the three chickadees and one titmouse, which evidently died from peck injuries to the skull.

Apparently R/LP was the only one affected by a reduction

TABLE XI

ENCOUNTERS INVOLVING TITMOUSE R/LP AS A MEASURE OF AGGRESSIVENESS

	Treatments		
	1a	2	1b
Number of Titmouse-Titmouse Encounters	74	11	10
Number of Titmouse-Chickadee Encounters	44	71	16
Number of Encounters Involving Titmouse R/LP	75	60	16
Percent of Total Encounters Involving Titmouse R/LP	43%	54%	27%
Percent of Titmouse-Titmouse Encounters Involving Titmouse R/LP	68%	18%	80%
Percent of Titmouse-Chickadee Encounters Involving Titmouse R/LP	57%	82%	50%

in availability of food and its greatly increased aggressive behavior might well be termed aberrant. It can be seen in Table XI, page 43, and Table XII, page 45, that this bird shifted its interest almost completely to chickadees and to Chickadees LP/W, DO/W, and W/R in particular. These three birds were found dead on the morning of October 29, 1964. (Ten hours of observation with Procedure 2 were conducted on the four days immediately preceding October 29.) Titmouse R/LP was aggressive toward titmice in particular during the period of October 12 to October 21, 1964, and ignored or rarely bothered titmice after October 22, 1964. Titmouse R/LP was significantly more active and aggressive than any other bird during the period of Procedure 1a and 2, yet showed few aggressive tendencies in Procedure 1b. This was apparently due to the fact that the number of birds was reduced, or that the particular birds which had stimulated its aggressive tendencies were not present.

Table XII, page 45, shows data illustrating the somewhat aberrant aggressive behavior of Titmouse R/LP. There was a significant rise in encounters between Titmouse R/LP and chickadees for Procedure 2, a significant drop in encounters between Titmouse R/LP and chickadees for Procedure 1b, and a nearly significant drop in encounters between R/LP and chickadees comparing Procedures 1a and 1b. Along with the rise in number of encounters between R/LP and chickadees came a drop in the number of encounters involving this bird and titmice. Titmouse R/LP significantly increased its aggressiveness toward Chickadees LP/W and W/R, and there was a nearly significant

TABLE XII

ENCOUNTERS INVOLVING TITMOUSE R/LP

	Procedures		
	1a (18 hours)	2 (10 hours)	1b (18 hours)
R/LP Encounters With Chickadees	25	58	8
R/LP Encounters With Titmice	50	2	8
R/LP Encounters With Chickadee LP/W	6	21	*
R/LP Encounters With Chickadee DG/W	11	23	*
R/LP Encounters With Chickadee W/R	1	12	*

*Bird not present

increase in its aggressiveness toward Chickadee DG/W.

It must be concluded, then, that the reduction in availability of food employed in Procedure 2 had no significant effect upon the number of aggressive encounters between birds in a caged situation, excepting Titmouse R/LP whose aggressiveness was significantly increased. However, the behavior of this bird must be judged to be the exception, rather than the rule. Thus, the finding of Marler and Andrew (Hinde, 1961) that a period of food deprivation did not increase aggressiveness among birds in the wild seems to be the case with caged chickadees and titmice.

II. SPATIAL RELATIONSHIPS

Spatial relationships showed up clearly in this study. Dominant birds had much greater precedence over most of the cage space than did lower ranking birds. Birds lowest in the order were restricted as to where they ate and what sites they might safely occupy.

Low-ranking birds are relegated to feeding more from the floor than birds of higher station. They fed more often on discarded food and on food accidentally dropped by other birds.

In several cases, closely ranked birds, whether high or low ranking, tended to avoid one another spatially. Chickadees and titmice lowest in the order were at times greatly restricted and failed to visit the feeding station for long periods of time. They were most restricted in the number of cage sites where they might

feed. These birds also occupied good cover such as a shelter box or the two evergreens in the cage much more than did the other birds.

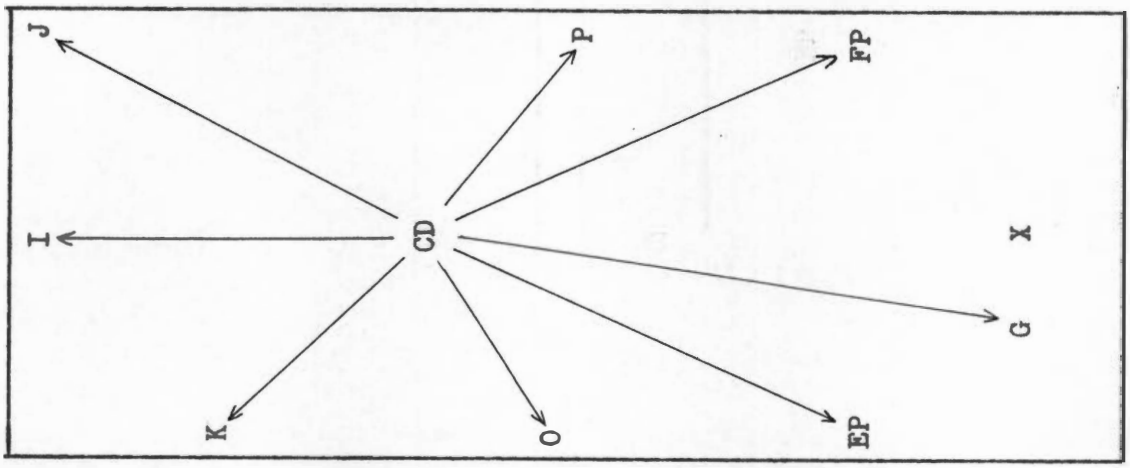
In Figure 5, page 48, on the cage layout are marked arrows signifying cage sites used more than five times for feeding. The two birds compared are R/LP (I., F.) and W/LB (A., M.), the Alpha and lowest ranking titmice. It can be seen that R/LP had much more freedom of movement about the cage. This illustrates the general finding that dominant birds had more freedom of movement and precedence in a greater number of cage sites.

In Figure 6, page 49, the two birds compared are LP/W (A., M.) and R/W (A., F.), the Alpha and lowest ranking chickadees. This comparison demonstrates that the principles of restriction mentioned above are the same for chickadees.

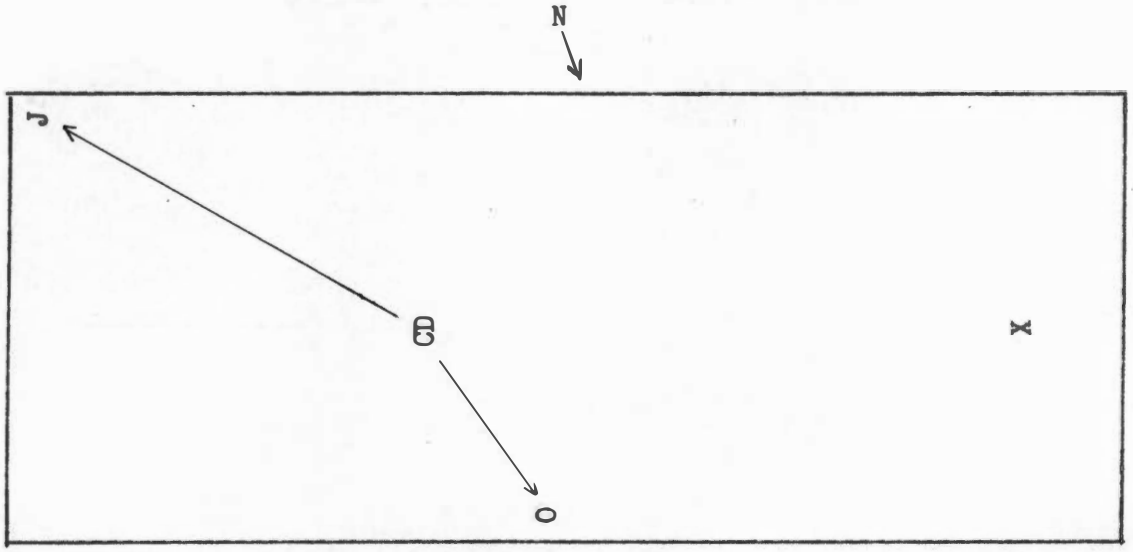
The fact that closely ranked birds often avoided one another spatially presented problems when the birds were ranked. Figure 7, page 50; Figure 8, page 51; and Figure 9, page 52, illustrate this phenomenon and thereby explain why some of the figures in Table V, page 27, do not follow perfectly the expected trend.

In Figure 7, page 50, the birds compared are Titmice DG/LP (U., F.) and LG/H (A., M.). These birds avoided one another consistently with respect to feeding sites chosen during the period of Procedure 1a.

In Figure 8, page 51, the birds compared are Titmice W/Y (I., F.) and LG/Bk (A., F.). These birds also consistently avoided one another with respect to feeding sites chosen.



R/LP

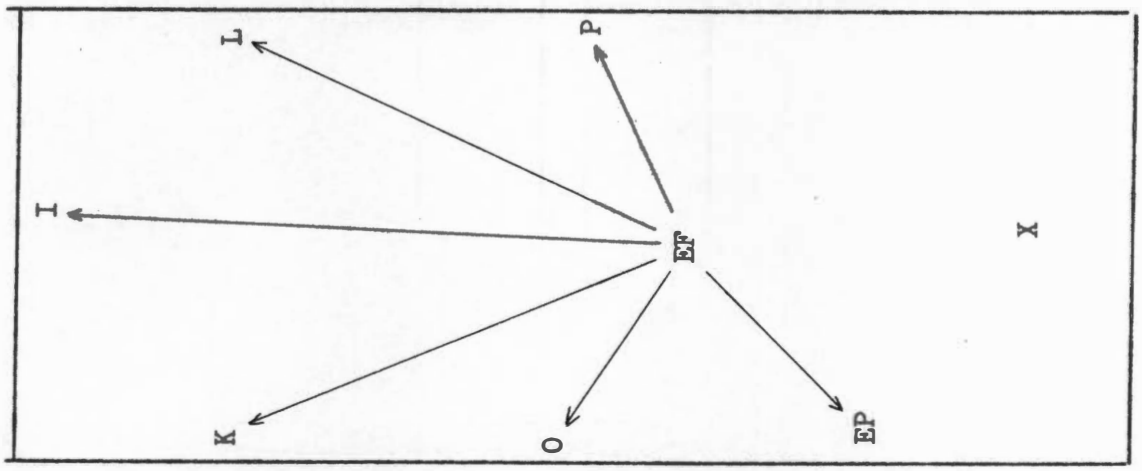


W/LB

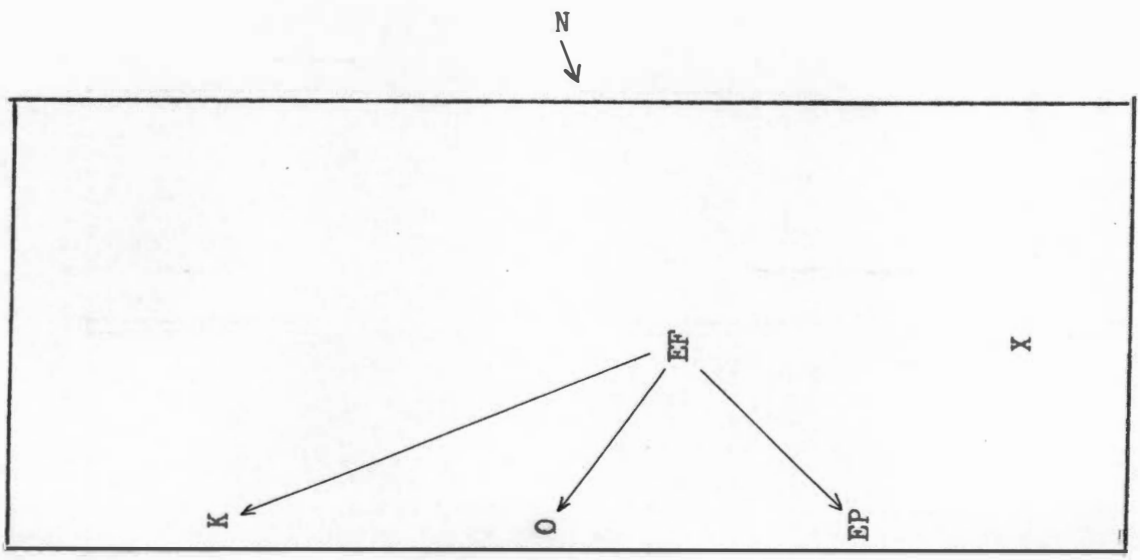
October 18 and 21

CD = Position of Feeder
X = Observation Booth

Figure 5. Comparison of relative restriction between Titmice R/LP (I., F.) and W/LB (A., M.).



LP/W

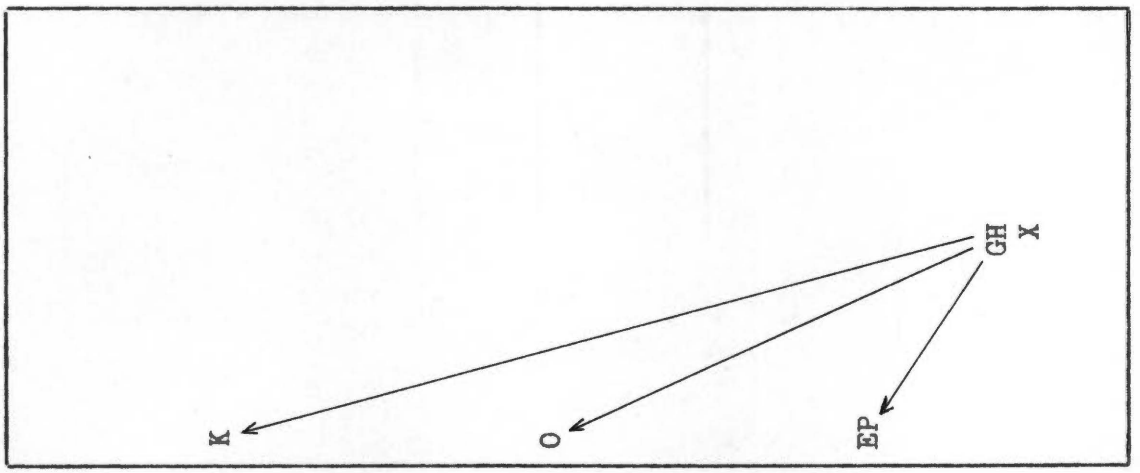


R/W

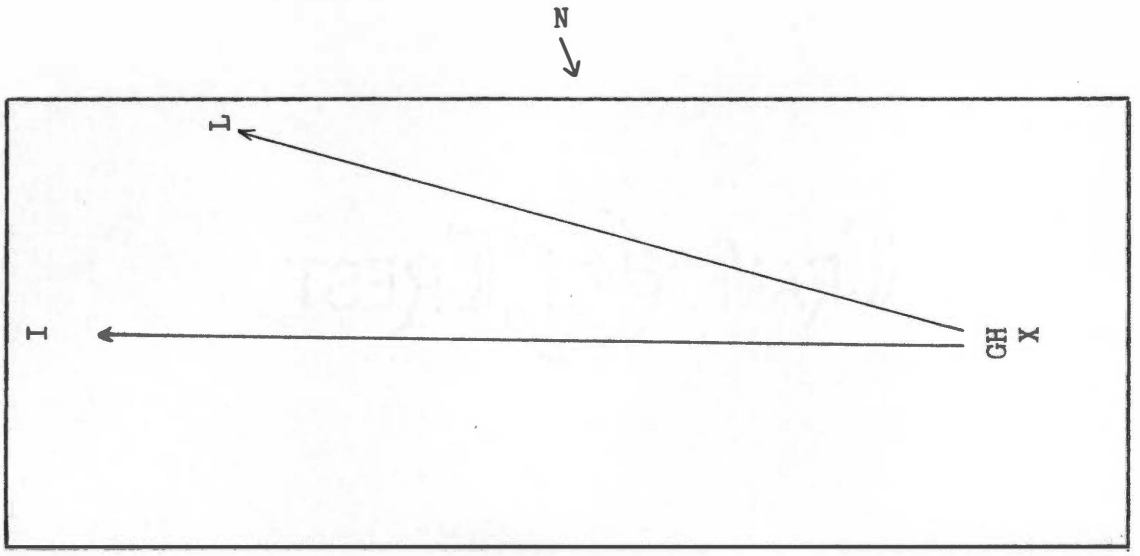
October 27 and 28

EF = Position of Feeder
X = Observation Booth

Figure 6. Comparison of relative restriction between Chickadees LP/W (A., M.) and R/W (A., F.).



DG/LP

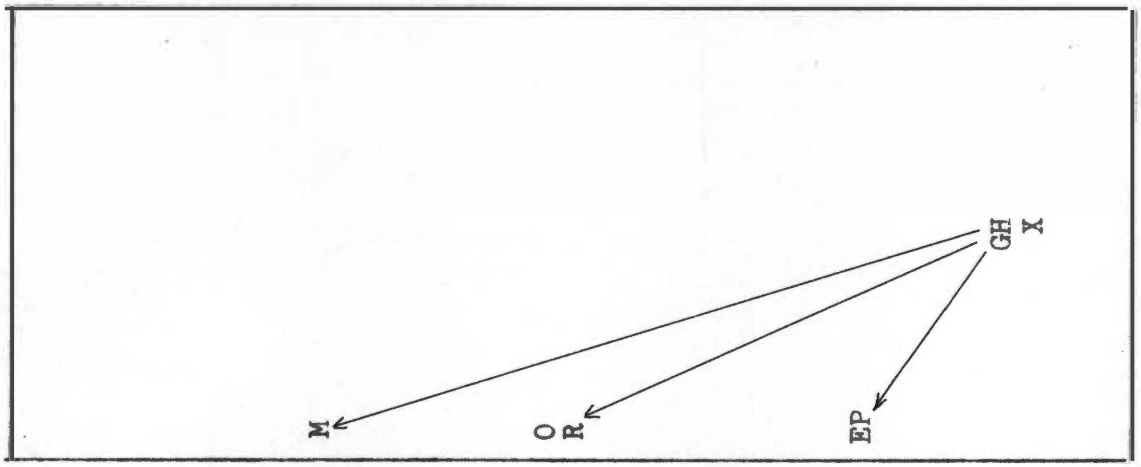


LG/H

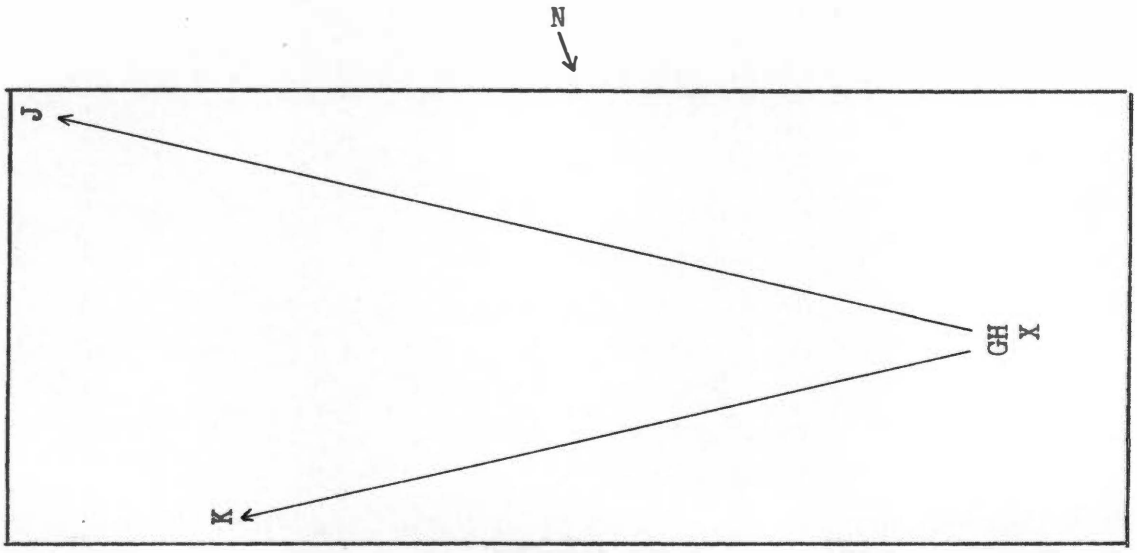
October 23 and 24

GH = Position of Feeder
X = Observation Booth

Figure 7. Avoidance between Titmice DG/LP (U., F.) and LG/H (A., M.).



W/Y

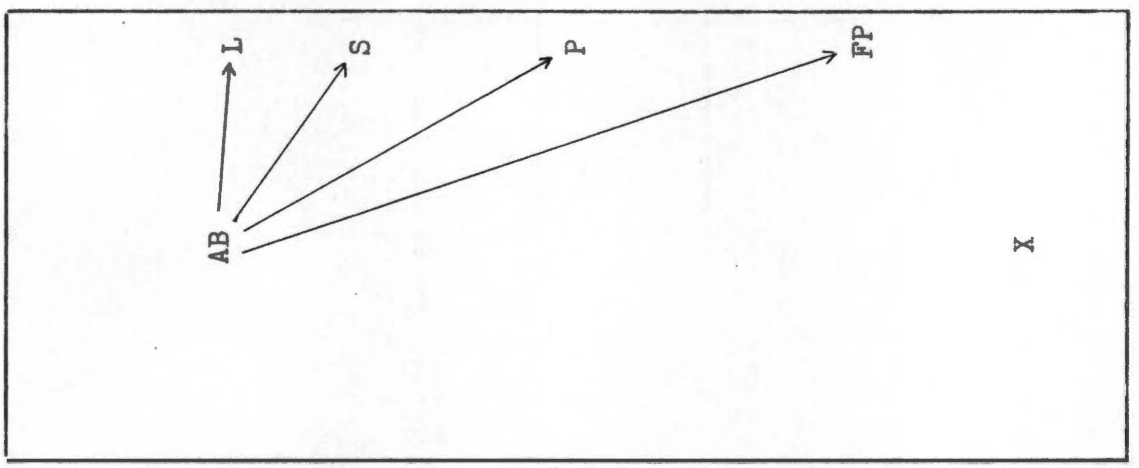


LG/Bk

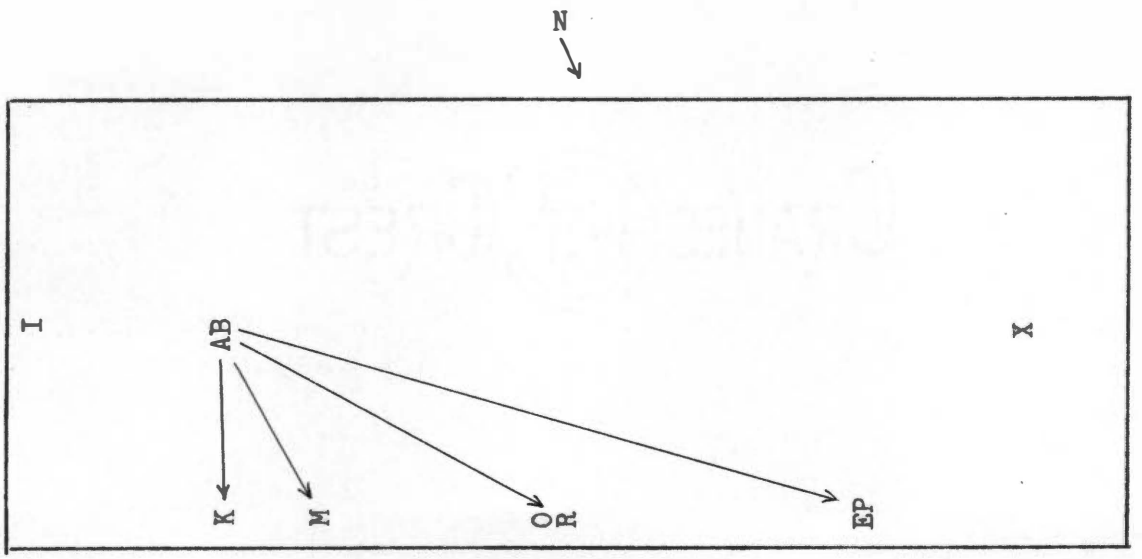
October 23 and 24

GH = Position of Feeder
X = Observation Booth

Figure 8. Avoidance between Titmice W/Y (I., F.) and LG/Bk (A., F.).



Bk/W



DG/W

October 12 and 17

AB = Position of Feeder
X = Observation Booth

Figure 9. Avoidance between Chickadees Bk/W (A., M.) and DG/W (A., F.).

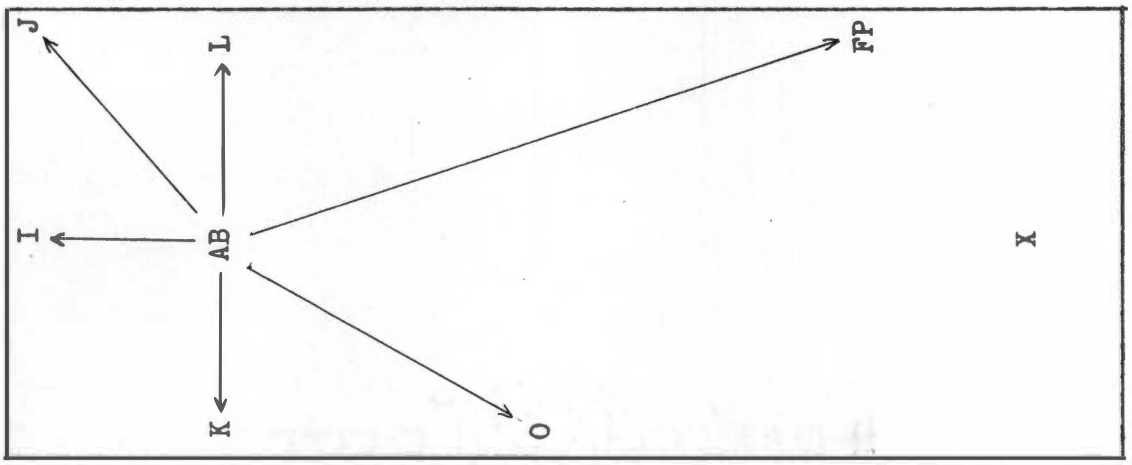
In Figure 9, page 52, the birds compared are Chickadees Bk/W (A., M.) and DG/W (A., F.). These birds demonstrate the clearest and most consistent case of avoidance by closely ranked birds in this study.

Avoidance of one another by closely ranked birds seems to be a mechanism by which encounters and fighting are reduced, allowing the birds more time free from strife for more important activities such as feeding.

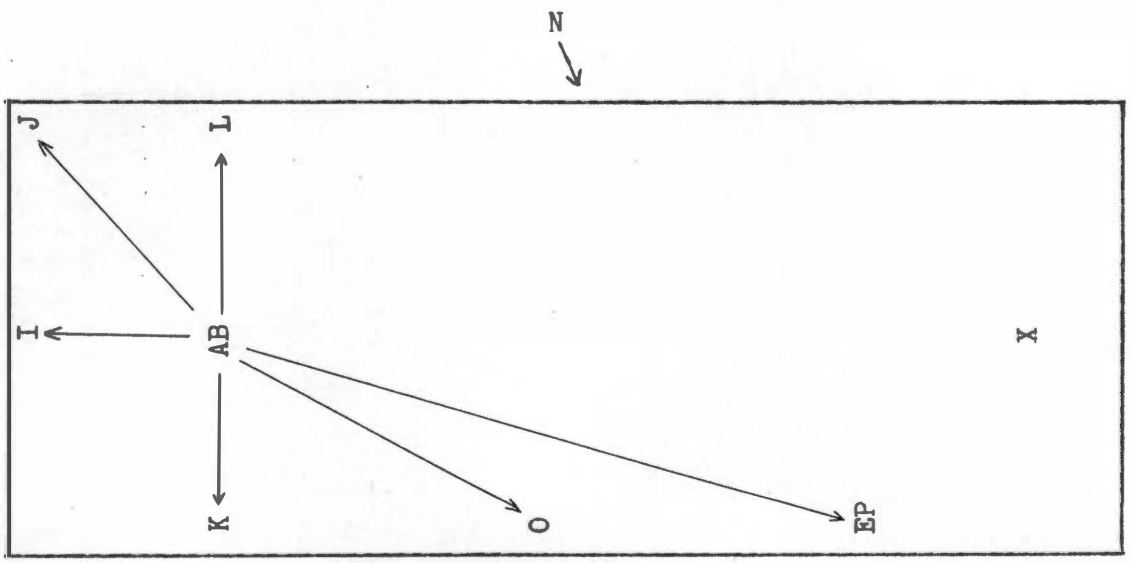
Chickadees Bk/W (Ad., M.) and DG/W (Ad., F.) were captured on the same morning in the same mist net. They apparently entered the net at approximately the same instant. These two birds avoided one another so consistently in the cage that they were not thought to be mated. However, it may have been that they were mated and captivity broke the mating bond by increasing competition.

Titmouse W/Y (I., F.) and Titmouse W/LB (A., M.) were caught on the same morning in the same net at an interval of about thirty minutes. They were probably not paired, because the female was immature and because W/LB seemed to be paired with LG/Bk (A., F.).

In Figure 10, page 54, the birds compared are Titmice LG/Bk (A., F.) and W/LB (A., M.). The exact rank of these birds was hard to determine, because they consistently used the same feeding sites, especially sites O and J, which were the two evergreens and offered good cover. This may be the most important cause of the slightly uncertain status of these two birds with respect to each other. On the other hand, these two birds may have been mated. LG/Bk was



LG/Bk



W/LB

October 12 and 17

AB = Position of Feeder
X = Observation Booth

Figure 10. Utilization of the same sites by Titmice LB/Bk (A., F.) and W/LB (A., M.).

captured fifteen days after the capture of W/LB at the same location. This could be the reason for their use of the same cage sites so consistently. Also, dominance relationships between two possibly paired birds probably would not show significant differences. There were no other two birds of opposite sex whose activities indicated a pair relationship.

CHAPTER III

SUMMARY

A study of dominance and competitive behavior related to feeding among caged Carolina Chickadees and Tufted Titmice was made during October and November, 1964. Study facilities were first planned during the fall quarter, 1963, and a cage was built for the study during the period of February to May, 1964. Birds were captured with mist nets at locations on the University of Tennessee Cherokee farm woodland property during June, July, August, and September, 1964. Also from June through September, diet, shade, shelter, and other needs of the birds were carefully studied and worked out.

A permit from the Department of the Interior, Fish and Wildlife Service, allowed capture and caging of six birds of each species. The birds were banded and color banded for easy and positive identification.

Data were gathered by periods of observation from a booth with a window of one-way glass so that the birds were not aware of the presence of the observer. The more important data were tested for significance by t tests, two-way Chi square tests, and analysis of variance (Bailey, 1959; Kurnow, et. al., 1959; Shedecor, 1934; Steel and Torrie, 1960).

Three observational procedures were used. The first was to observe by use of one large feeding station (Y, page 4) behavior with

regard to feeding, i.e., precedence, number of feeding and non-feeding trips to the station, aggressive encounters, etc. This feeding station was placed in three different locations in the cage, and six hours of observations were made at each location. The observation booth remained stationary. This was designated as Procedure 1a.

The second procedure was to limit the availability of food by placing it in a single small container on the feeding station (Y) for one hour (9:00 to 10:00 a.m.) on each of four mornings followed on two of these mornings by an observation period following the time schedule (11:00 a.m. to 2:00 p.m.) and plan of Procedure 1a. A study of dominance and spatial relationships were the two most important aspects of this procedure.

After Procedure 1a was completed, four birds (three chickadees and one titmouse) were killed, probably by an aggressive titmouse. Then the plan of Procedure 1a was repeated to ascertain differences, if any, arising from the reduction of the population. This was designated Procedure 1b.

The criteria used for assessing dominance were the following: number of feeding and non-feeding trips to the feeding station (Y), number of successful as opposed to unsuccessful encounters with the bird judged to be next lowest in the social order and precedence at the feeding station.

Size, sex, and maturity were considered to be important determining factors in the establishment of a dominance hierarchy. This was well borne out by the fact that titmice were the dominant species and

that two of three adult males were ranked first and second among chickadees.

The ranking of titmice, however, was somewhat aberrant with two females ranked first and second. The Alpha bird was immature at capture and the second bird was probably immature or subadult at capture. The two adult males were ranked third and sixth. This odd situation was probably due to the poor adaptability of titmice to a caged environment, thereby leading to reduced vitality. Thus when two strong females were introduced into the cage as the fifth and sixth titmice, they took precedence over the others because they were more vigorous.

Dominant birds visited the feeding station more often. Lower ranking birds were more often relegated to feed on food discarded or dropped to the cage floor.

There was a general drop in the number of aggressive encounters for chickadees and titmice in Procedure 1b. This decrease in interaction was probably brought on by the reduction of population pressure.

In Procedure 1a both the dominant and lowest ranking birds had fewer unsuccessful encounters than those of intermediate rank--the dominant birds because they were stronger and more vigorous, and the low ranking birds because their greater relative restriction prevented too much contact with higher ranking birds.

Birds of low rank were more restricted in their movements and sites used about the cage, while dominant birds had precedence practically over the entire cage.

The most consistent differences between Procedures 1a and 1b are that there was less interaction between chickadees and titmice and less interaction among titmice in Procedure 1b.

With regard to the increased stress caused by limited access to food in Procedure 2, it was found that caged birds, under greater than normal stress tend to make fewer feeding trips to the feeding station, store more food, and consume more water. They also visited the feeding station more often without eating. The increased storage may have been a mechanism naturally employed to reduce feeding competition.

Titmice had their greatest precedence at the feeding station when it was located in Area AB of the cage. This was probably because the feeding station (Y) was left in Area AB most of the time. It was always left there when observations were not being made. On the other hand, chickadees had their greatest precedence at the feeding station when it was located in Area GH at the opposite end of the cage from Area AB. This was probably because it was far removed from the area in which titmice had most precedence.

Aggressive encounters per hour increased markedly during Procedure 2. Aggressive encounters between birds increase as stress and competition increase. However, it was found that, except for one bird (Titmouse R/LP), reduction in availability of food does not significantly affect aggressiveness.

The Alpha titmouse, R/LP (I., F.), was a very aggressive and highly dominant bird during the periods of Procedures 1a and 2. This bird, in fact, accounted for fifty-four percent of the total

encounters and eighty-two percent of titmouse-chickadee encounters during Procedure 2. After the population had been reduced by four birds, Titmouse R/LP accounted for only twenty-seven percent of the total encounters (Procedure 1b). This bird shifted its interest almost completely to chickadees during Procedure 2 and was especially aggressive toward three chickadees in particular (DO/W, LP/W, and W/R, the Alpha, third, and fourth ranked chickadees). These three birds were found dead of peck wounds on the morning of October 29, 1964, and it was suspected that Titmouse R/LP had killed them. Armstrong (1947) noted that in captivity tits may slaughter birds of their own species or others confined with them. This bird (R/LP) showed few aggressive tendencies in Procedure 1b. This was apparently due to the fact that the birds which stimulated its aggressive tendencies were no longer present.

With regard to spatial relationships, it was noted that dominant birds had much greater precedence over most of the cage space than did lower ranking birds. Low ranking birds were restricted as to where they ate and what sites they might safely occupy. The lowest ranking birds preferred good cover such as a shelter box or an evergreen much more than did the other birds.

Closely ranked birds in several cases tended to avoid one another spatially, especially with regard to sites for eating food obtained at the feeding station. Avoidance of one another by closely ranked birds was noted by Dixon (1963), and it seems to be a mechanism by which encounters and fighting among birds are reduced, allowing

more time free from strife for more fruitful pursuits.

One pair of titmice were hard to rank accurately because they consistently used the same feeding and roosting sites. One was an adult male, and the other an adult female captured at the same location, so it could have been that they were paired. Other evidence which might support this idea is that there was no significant difference between the very few encounters between the two birds.

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APPENDIX A

Photographs

Figure 11. View of the cage looking toward the west end showing entrance (right) with chickadee shelter box above it; movable feeding station (center) in normal position (Area AB), above which is the larger chickadee shelter; a large tarpaulin on the cage roof placed there primarily for shade; and six trees, five of which were planted in large cans of soil.

Figure 12. View of cage interior looking toward west end showing observation booth (center), tarpaulin on cage roof above, evergreen (O) on right, and small tree (P) at far left.

Figure 13. View of cage interior looking toward east end showing two dowel perches (EP) on left.

Figure 14. Movable feeding station (Y), containers of water and suet (left) used for Procedure 2, evergreen (J) on the right.

Figure 15. Shelter-feeding station (T), wire joint and rings used to join wire sections on the left.

Figure 16. Chickadee shelter (V), east end of cage.

Figure 17. Portable observation booth with window of one-way glass and feeding shelf under the window.

APPENDIX B

Statistical Tables

TABLE XIII

STATISTICAL VALUES FOR ENCOUNTERS
BETWEEN INDIVIDUAL BIRDS

Color Bands of Bird	Dominant Over	Chi Square Value*	Approximate Probability
		Procedure 1a	
Titmice			
R/LP	DG/LP	13.09	.01
DG/LP	LG/H	14.00	.01
LG/H	W/Y	14.00	.01
W/Y	LG/Bk	7.14	.05
LG/Bk	W/LB	No significant difference	
Chickadees			
LP/W	Bk/W	16.39	.001
Bk/W	DG/W	10.00	.01
DG/W	W/R	16.00	.001
W/R	LG/Y	7.14	.05
LG/Y	R/W	No significant difference	
		Procedure 1b	
Chickadees			
LG/Y	R/W	8.00	.02

*Two-way Chi square test (Steel and Torrie, 1960). Degrees of freedom is 3 in each case.

TABLE XIV

RESULTS OF CHI SQUARE TESTS OF DATA
IN TABLE IX, PAGE 40

Feeding Trips		Non-Feeding Trips		Titmouse-Titmouse Encounters	Titmouse-Chickadee Encounters	Chickadee-Chickadee Encounters	Total Encounters
C.*	T.**	C.	T.				
$X^2 = .05$	$X^2 = .003$	$X^2 = 1.13$	$X^2 = .76$	$X^2 = 6.10$	$X^2 = .78$	$X^2 = .53$	$X^2 = 1.21$
$P = >.99$	$P = >.99$	$P = >.70$	$P = >.90$	$P = .10$	$P = >.90$	$P = >.80$	$P = >.70$

* Chickadees
**Titmice

TABLE XV

RESULTS OF CHI SQUARE TESTS OF DATA IN TABLE X, PAGE 41, AND TABLE XI, PAGE 43

	Comparisons		
	Procedures 1a and 2	Procedures 2 and 1b	Procedures 1a and 1b
Number of Chickadee-Chickadee Encounters	$X^2 = .006$ $P = >.99$	$X^2 = 1.12$ $P = >.80$	$X^2 = 1.77$ $P = >.80$
Number of Titmouse-Titmouse Encounters	$X^2 = 7.22$ $P = .07$	$X^2 = 1.36$ $P = >.70$	$X^2 = 20.44$ $P = <.001$
Number of Titmouse-Titmouse Encounters Excluding Titmouse R/LP	$X^2 = .50$ $P = .90$	$X^2 = 6.71$ $P = .08$	$X^2 = 12.37$ $P = <.01$
Number of Titmouse-Chickadee Encounters	$X^2 = 6.20$ $P = .10$	$X^2 = 21.4$ $P = <.001$	$X^2 = 5.35$ $P = >.10$
Number of Titmouse-Chickadee Encounters Excluding Titmouse R/LP	$X^2 = .28$ $P = >.90$	$X^2 = 3.84$ $P = >.30$	$X^2 = 2.64$ $P = >.30$
Total Number of Encounters	$X^2 = .12$ $P = >.90$	$X^2 = 8.90$ $P = <.05$	$X^2 = 9.29$ $P = <.05$
Total Number of Encounters Excluding Titmouse R/LP	$X^2 = .01$ $P = >.99$	$X^2 = .34$ $P = >.90$	$X^2 = 4.90$ $P = >.10$
Number of Encounters Involving Titmouse R/LP	$X^2 = .65$ $P = >.80$	$X^2 = 17.00$ $P = <.001$	$X^2 = 13.82$ $P = <.01$

TABLE XVI

RESULTS OF CHI SQUARE TESTS OF DATA
IN TABLE XII, PAGE 45

	Comparisons		
	Procedures 1a and 2	Procedures 2 and 1b	Procedures 1a and 1b
Number of Encounters Between Titmouse R/LP and Chickadees	$X^2 = 10.29$ $P = <.02$	$X^2 = 26.73$ $P = <.001$	$X^2 = 4.86$ $P = >.10$
Number of Encounters Between Titmouse R/LP and Titmice	$X^2 = 14.49$ $P = <.01$	$X^2 = .84$ $P = >.80$	$X^2 = 14.55$ $P = <.01$
Number of Encounters Between Titmouse R/LP and Chickadee LP/W	$X^2 = 10.13$ $P = <.02$		
Number of Encounters Between Titmouse R/LP and Chickadee DG/W	$X^2 = 6.28$ $P = .10$		
Number of Encounters Between Titmouse R/LP and Chickadee W/R	$X^2 = 11.43$ $P = <.01$		