SOCIAL ORGANIZATION IN THE JAPANESE QUAIL (COTURNIX COTURNIX JAPONICA): APPETITIVE AND CONSUMMATORY COMPONENTS

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ABSTRACT

SOCIAL ORGANIZATION IN THE JAPANESE QUAIL (*COTURNIX COTURNIX JAPONICA*): APPETITIVE AND CONSUMMATORY COMPONENTS

By

Robert Edward Otis

Studies of avian social organization have utilized the social dominance theory for 50 years despite the confusing array of data it has generated. Objections to this theory are twofold: First, linear hierarchies are infrequently found in avian societies and second, various definitions of dominance are frequently found to be unrelated.

Some of this confusion may be the result of measuring aggression without regard to its appetitive and consummatory aspects. Nine flocks of Japanese quail (*Coturnix coturnix japonica*) were used to test the following questions:

1. Can dominance behavior in quail be viewed as appetitive behavior for incentive-acquisition (food, water)? That is, are there differences in dominance relationships and aggressive behavior at different distances from incentives or between incentives?

2. What are the relationships between the appetitive and consummatory aspects of food- and water-getting sequences of behavior? More specifically, are measures of dominance at varying distances from the incentive good predictors of consummatory activity, such as latency and total amounts consummed?

3. Can a dominance hierarchy, when based on aggression at a food source, be modified by depriving individuals of food? Similarly, can a dominance hierarchy based on aggression at a water source be modified by depriving individuals of water?

The results of this experiment indicated the incentive-related (or appetitive) character of aggressive behavior. Japanese quail were found to have different aggressive-response profiles at different distances from food and water incentives. No differences in response profiles were observed when incentives were absent. Frequency of aggression increased as quail moved closer to the incentives while no differences in amounts of aggression were found across the cage when incentives were absent.

A trend towards unilateral aggressive interaction was found as incentive-distance increased, reflecting a change from a peck-dominance to a peck-order form of social organization. When incentives were absent social organization approximated a peck order.

Dominance hierarchies varied between different incentive-distances and between incentives. Dominance behavior in the appetitive phase could not be used to accurately predict measures of consummatory behavior (latency, total time and average time of incentive-access). However, when incentives were present, there were positive correlations between dominance hierarchies in the three incentive-distance sectors, indicating that the appetitive phase was a single component. Effects of incentive deprivation on dominance behavior could not be interpreted because of instability in dominance relationships among control groups.

The traditional view of aggression as a consummatory event was re-examined, particularly as it related to the measure of dominance in studies of avian social organization.

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By

Robert Edward Otis

A THESIS

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To my Wife

Barbara

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INTRODUCTION

Social dominance has been variously defined in terms of aggressive superiority of one individual over another and dominance relationships are known to exist in a stereotyped, predictable manner within social groups of many avian species. Social organization is frequently measured by allocating each individual to a rank order according to the number of flockmates dominated. This hierarchy reflects relative predictability of approach/retreat patterns of behavior when individuals meet in a competitive situation. A dominant bird is usually characterized by pecking or threatening behavior (approach) while the subordinate shows escape or avoidance behavior (retreat).

Dominance hierarchies were first described by the Norwegian Schjelderup-Ebbe (1922) in a flock of barnyard fowl. Nearly 10 years went past before the first extensive investigations of dominance hierarchies were begun in this country by W. C. Allee (1931). Allee's associates, Guhl and Collias, were preeminent in carrying this interest into the 1960's and today Allee's social dominance theory stands as the most widely used social-structuring mechanism for avian groups. Although the dominance theory was primarily developed from observations of captive domestic fowl researchers have felt free to utilize these theoretical constructs across a wide range of species, both in the field and in the laboratory (see reviews in Armstrong, 1965, and Noble, 1939).

The social dominance theory as developed by Allee and his associates is founded on two basic assumptions. First, a continuum of rank-order criteria is assumed to exist in all social groups of birds and second, dominance is assumed to be a cluster of interrelated behaviors which ramify into other social relationships. When irregularities have occurred in observations (ex. nonlinear hierarchies) researchers have tended to modify the theory _ad hoc_ rather than critically examine the theory's basic postulates (Gartlan, 1968). Recently, however, evidence has been gathered which renders both postulates invalid for primate societies (Gartlan, 1968; Bernstein and Sharpe, 1966; Rowell, 1966). The validity of these assumptions for avian societies has never been critically examined.

The first postulate assumes the dominance relationship to be transitive, allowing all individuals in a group to be ordered along on ordinal scale according to the number of flockmates dominated. Among avian groups, however, "triangular" (and "square") relationships are frequently reported where, for example, one bird is dominant to a second and the second is dominant to a third which, however, is dominant to the first (cf. Masure and Allee, 1934a). Researchers have generally explained intransitivity in any one of three ways: (1) as being caused by situational influences on aggression, or (2) because insufficient time was allowed for flock stabilization, or (3) because observational techniques were inadequate (cf. Guhl and Fischer, 1969; Masure and Allee, 1934a). Holabird (1955, p. 253). for example, suggested subordinate chickens to be "belligerent" when they pecked birds normally dominant to them and Armstrong (1965, p. 269) called such interactions "accidental."

Two forms of linear hierarchies were identified by Allee and his associates (Masure and Allee, 1934a). In the peck-right or peck order society aggression between dyadic members was unilateral with one bird always dominating the other. In the peck-dominance society aggression was bilateral, of the "now-one-wins-now-the-other" variety and dominance was assigned to the more frequent winner. Lack of a precise operational definition of these two hierarchy forms has led to arbitrary decisions as to which organization is being observed. Domestic fowl are always considered as fitting a peck order criteria yet, upon close examination, aggression between dyad members in flocks of fowl is frequently bilateral rather than unilateral (cf. Guhl, 1968; Masure and Allee, 1934a; Williams and McGibbon, 1956). Forcing data from a peck-dominance organization into a linear hierarchy model is obviously convenient for statistical analyses (e.g. rank order correlations) but it avoids a critical examination of the underlying theoretical assumptions.

The second postulate of the social dominance theory concerns the definition of dominance as a cluster of interrelated responses. Relationships between dominance hierarchies and other social interactions have produced a confusing array of correlational figures. The social dominance theory would predict highly significant correlations between dominance and other social behaviors which are essential for survival and reproduction. However, little or no relationship has been found between dominance and roosting priority or clumping organization (Andrew, 1957a; Guhl, 1953; Lill, 1968), approaching and consuming food (Guhl, 1953; Masure and Allee, 1934a), frequency of mating, including courting, crouching and treading (Guhl, 1953; Guhl and Warren, 1946; Guhl, Collias and Allee, 1945), number of eggs laid (Guhl, 1953), dusting and social preening (Lill, 1968), crowing (Allee, Collias and Lutherman, 1939), scratching and random walking (Banks, 1956), and approaching strange objects (Andrew, 1957; Ratner and Denburg, 1959).

Dominance hierarchies based on fighting often show little reliability across various localities (Masure and Allee, 1934b), between paired and flock situations (Guhl, 1953), and between seasons (Bennett, 1939; Coutlee, 1967; Masure and Allee, 1934a,b; Shoemaker, 1939). That is, a bird may be dominant in one part of the cage but not in another, in a paired contest but not in a flock situation, or he may be dominant to females during the winter but not during the breeding season. Furthermore, dominance hierarchies do not represent an accurate gradient of aggressiveness (Guhl, 1968; Lill, 1968). In fact, various components of fighting have been found not to correlate with each other (Williams and McGibbon, 1956).

Considering the foregoing evidence it is of interest that only a few researchers have spoken out against the unitary dimension model of social dominance and that the theory still remains essentially unchanged from its original conception. Scott (1956) long ago indicated that a description of any society solely in terms of dominance-subordination relationships was not enough.

Appetitive and Consummatory Aspects of Dominance

Some of the confusion that has arisen with regards to social dominance may be due to the wide variety of responses used in its measurement. Dominance has usually been defined in terms of aggressive responses observed during competitive situations where access to some incentive has been restricted. Aggression in these cases is appetitive or instrumental in incentive-getting. Since appetitive behaviors are specific to their consummatory stimuli, measures of aggression in various appetitive situations might not yield the same dominance orders. Even when the appetitive motor responses are similar in the different cases, they are directed toward different goals and involve responsiveness to different stimuli (Hinde, 1966). A bird will show one type of appetitive behavior when seeking food, another when selecting a perch or roost, and still another when attempting copulation. In group situations, aggressive responses are appetitive components of most of these behavior classes. In effect, dominance hierarchies can be conceptualized around different consummatory classes which have aggression-appetitive components. It is therefore not surprizing that researchers measuring dominance in group situations over long periods of time and without regard to consummatory classes often report fluctuating heirarchies (cf. Bennett, 1939).

Of 63 studies sampled where dominance was measured in birds (57% of which were domestic fowl), 22 recorded aggressive behavior at a food source, two measured aggression over food plus other incentives, one was in reference to perch attainment while 38 studies measured aggression during paired contests or in flock situations where the incentive conditions were difficult to define. Dominance hierarchies measured on the basis of these response classes would be expected to interrelate only to the extent that response components and motivational state (i.e. satiation or deprivation of consummatory stimulus) were similar. A food satiated bird, for example, might rank low in a hierarchy based on aggressive deference at a food source, but rank high, perhaps, in competition for a mate or for a perch or roost. Fighting over territory or in paired-contests is consummatory behavior since the response sequence terminates after the other member avoids or escapes. Aggression in these cases may not correlate highly with aggression which occurs as appetitive elements of other behavioral sequences.

Species in which males become dominant to females (or vice versa) during the breeding season may only reflect the fact that dominance hierarchies vary according to the consummatory class being measured. During the breeding season fighting may be appetitive to sexual behavior whereas fighting during other times of the year may be related to other goals. Likewise, territoriality in peck-dominance societies (e.g. pigeons) may often reflect differences in aggression around various incentives (e.g. territory, food, perch).

The relationship between dominance rank and consummatory behavior is not well understood. This relationship has often been found to be very unpredictable. For example, dominant birds, as measured by aggression around a food source, may or may not eat sooner or eat more food than subordinates (Marler, 1955a). When other consummatory classes are related to this dominance hierarchy, the correlations are frequently low and unreliable as was mentioned earlier.

Since consummatory behaviors are influenced by conditions of deprivation and satiation (Denny and Ratner, 1970) and since appetitive responses are functionally related to the consummatory act, modification of an individual's dominance status (e.g. upward mobility) would be a predictable consequence of food deprivation, given that the dominance hierarchy was based on aggression at the food source. This same individual would predictably rise in other dominance hierarchies to the extent that the consummatory classes were interrelated (e.g. thirst and hunger, Hinde, 1966, p. 150).

This hypothesis has not been tested and literature support is scattered. Collias (1950) noticed that subordinate chickens, which had been starved for two days, approached and ate from the food source despite the presence of dominant peers. No records of aggression were reported, but it was apparent that appetitive responses for food-attainment increased in strength following food deprivation. Many other studies have reported increased aggression at the food source when the flock as a whole was placed on food deprivation (Ellis, 1966; Marler, 1957) and in some cases dominance reversals have been observed (Guhl and Allee, 1944).

Specific Goals of this Experiment

The present experiment was designed to test the hypothesis that measures of dominance are, in effect, measures of appetitive behavior for incentive acquisition and that dominance status measured at varying distances from the incentive or between incentives might vary as a function of differing motivational conditions. This hypothesis will be referred to as the consummatory theory of social dominance. Japanese quail (*Coturnix coturnix japonica*) were used as subjects. Cages were constructed which allowed the measurement of aggression in quail at different distances from food and water cups. Incentive-distance was presumed to reflect different components of a consummatory sequence with consummatory and highly specific appetitive components occurring nearest the incentive while aggression which was less specific to or unrelated to incentive-acquisition was assumed to occur at the furthest distances from the incentives. Utilizing this operational definition of the consummatory sequence the present experiment sought to answer the following questions:

1. Can dominance behavior in quail be viewed as appetitive behavior for incentive-acquisition (food, water)? That is, are there differences

in dominance relationships and aggressive behavior at different distances from incentives or between incentives?

2. What are the relationships between the appetitive and consummatory aspects of food- and water-getting sequences of behavior? Are measures of dominance at varying distances from the incentive good predictors of consummatory activity, such as latency and total amounts consummed?

3. Can a dominance hierarchy, when based on aggression at a food source, be modified by depriving individuals of food? Similarly, can a dominance hierarchy based on aggression at a water source be modified by depriving individuals of water?

METHOD

Subject Population

The subjects used in this experiment were Japanese quail. In order to understand the ramifications of using the quail in a study of social organization, it is necessary to review its background information.

The Japanese quail is a small galliform which has been placed in the family PHASIANIDAE. It is apparently one of a number of subspecies of the European *Coturnix coturnix* although Vaurie (1965, p. 293) has listed it as a separate species *Coturnix japonica*. It is native to the Orient, particularly to the islands of Japan. Several attempts have been made since 1870 to introduce this bird to the United States as a game animal. These attempts have all failed, perhaps due to what Labiskey (1961) calls a genetic loss of wildness and vigor due to domestication. As a result of these conservation efforts, researchers at Auburn University and the University of California recognized the quail's value as a biomedical research animal (National Academy of Sciences, 1969), and today its popularity as a subject for behavioral research appears to be spreading (cf. Farris, 1967; Reese and Reese, 1962; Selinger and Bermant, 1967).

In its natural habitat the Japanese quail is highly solitary and territorial in its social behavior (Wetherbee, 1961). Stanford (1957) reports that quail roost separately in both cold and hot weather. There is no mention of the formation of winter covies. In the spring this bird migrates in large flocks but only at night (Meinertzhagen, 1954; Taka-Tsukasa, 1935). During daylight the birds separate. Groups of quail have also been noted around dusting areas, but, except for mating pairs, the quail does not form any permanent social bonds. This suggests the "unnaturalness" of housing quail in flocks in a laboratory setting.

Flocks of penned Japanese quail may form dominance hierarchies, but the exact nature of this organization and the factors that influence it are unknown. Only two researchers have investigated this behavioral process and their results, both unpublished, are conflicting. Preston (1961) studied the development of social behavior in Japanese quail up to the time that a dominance organization was recognizable (between 9 and 10 weeks). He found that "all of the quail in the flocks were controlled by a single dominant bird with little evidence occurring of a descending order among the subordinates" (p. 36). However, Preston reports little in the way of quantitative information regarding the nature of this social arrangement.

As a consequence his conclusions appear to be based more on anectodal observations than on carefully derived data.

This oligarchy organization was not seen by Eynon (1968) but rather a highly linear peck order. Eynon made an excellent ethological analysis of the quail's aggressive and sexual behavior and, apparently as a side interest, described the peck order in a small group (5 females, 1 male) of birds over a three-week period. Dominance was observed at the feed and watering troughs. The observed hierarchy did not remain stable over this period, and the factors controlling this fluctuation were not identified.

The reason why Eynon and Preston found different forms of social organization is not clear. Since neither research paper gives a detailed account of dominance relationships within the flock, it is difficult to obtain a precise understanding of the quail's social organization.

Three studies (1,2,3) were conducted with three groups of quail in each study. The mean body weights of all subjects (Ss) before and after each study are reported in Appendix A. Each group was composed of four males and four females. This was an arbitrary decision to use half males. Woodard and Abplanalp (1967) found highest fertility measures in flocks containing one male for every two females. However, in nature quail appear to be monogamous unless there are an excess of females (Wetherbee, 1961). Since little is known about sexual composition of quail flocks (e.g. during migration) and since intersex encounters are maximized when an equal number of each sex are present, it was decided to use a 1:1 sex ratio in the treatment groups.

The use of eight birds to a group was based on some observations made earlier by this researcher. The size of the apparatus apparently favors groups of ten or smaller. Flocks of 15 and 13 were placed in the cage on separate occasions and within one month their numbers had decreased to ten in both cases. No further reduction in flock size was ever observed. Since ten appeared to be the upper limit of flock size for the experimental cages, groups of eight were expected to further minimize any stress caused by population size.

The genetic origin of these birds is unknown. The original stock has been maintained by the Poultry Science Department here at Michigan State University since the mid 1950's. The birds in this experiment represent at least the 25th generation of interbreeding within this closed flock (Dennis Dodson, personal communication).

All Ss were transferred to the observation cages between 11 and 16 days prior to the beginning of a study in order that flock aggression might stabilize. As shown in Table 1 many birds had to be replaced to achieve this stability (ex. 14 in Group 1 of Study 3). Highly

TABLE 1.--The number of birds in each group and the amount of time required to achieve group stability, the time of year each Study was begun and the number of *S*s dying during this experiment.

Study	Group	Number of Birds Replaced	Time (days) in Cage Before Study Began	Date Study Began	Number Died During Study
1	1	1	11	December 23	3
	2	4	11		0
	3	0	11		1
2	1	6	12	February 3	0
	2	2	12		0
	3	10	12		1
3	1	14	16	March 22	0
	2	0	16		0
	3	2	16		0

aggressive individuals frequently caused fatal wounds on their flockmates, resulting in both the aggressor and the wounded being replaced. All birds were randomly assigned to treatment groups.

*S*s were 10, 14 and 11 weeks old when testing began for Studies 1, 2 and 3 respectively. Preston (1961) reported the appearance of a social organization in 10 week old quail, so these *S*s were of sufficient age.

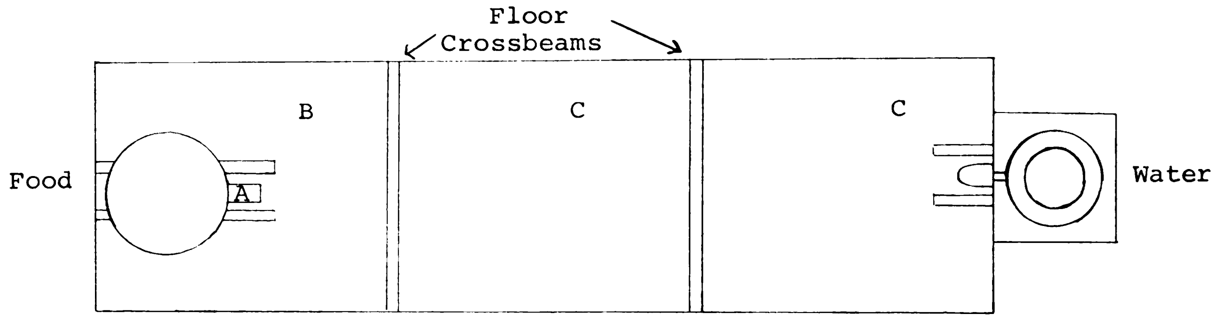
Dead birds were not replaced. Sickness, injury and death were recognized as a predictable occurrence in flocks of quail. Every effort was made to maintain healthy birds. Once each week *S*s were weighed and examined for ectoparasites and for other evidence of deterioration in general health.

Identification of Birds

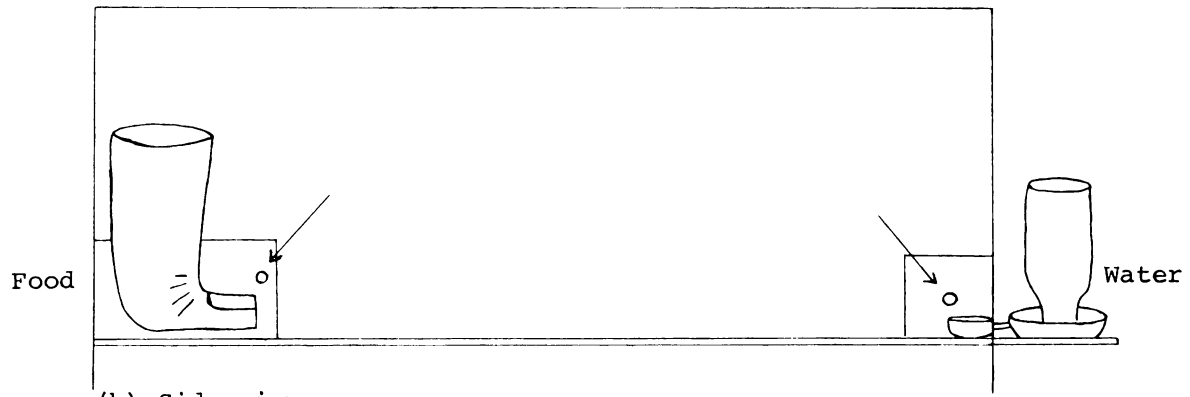
When studying the social organization of birds it is necessary to be able to recognize each individual in the flock under observation. Quail in this experiment were identified according to (1) their sex, and (2) according to a coded arrangement of metal bands on each leg. Since there were four of each sex in a cage, one of each sex had two leg bands on its left leg (referred to as MLL and FLL, where M means Male and F means Female); one had two leg bands on the right leg (MRR and FRR); one had one band on the left leg and one on the right leg (MLR and FLR); and the final two Ss had no bands at all (M and F). In addition, the male's leg bands were painted light blue during Studies 2 and 3 so as to facilitate identification. M had spots of blue paint on both legs. Since quail have a tendency to remain in crouched positions, particularly the females and subordinates, their fluffed feathers and drooping primaries retard observation of leg bands. The blue paint greatly facilitated identification in these situations, especially when the sex of a bird was not obvious due to its posture. The female is relatively larger than the male and has a "spreckled" breast caused by a dark and light feather arrangement. In most cases sexual differences were readily apparent.

Observation Cages and Room Conditions

Three observation cages were constructed so as to allow measurement of aggressive interactions at varying distances from a food and water cup. Each cage measured 17 inches high, 18 inches wide (or deep) and 63 inches long (see Figure 1). The front and back walls were built of 5/8 inch hardware cloth through which observations could be made. The floor was similarly constructed to allow fecal material to drop through to the table some 6 inches below the cage floor. The top or ceiling consisted of a sheet of 1/4 inch plywood. It could be removed to allow egg gathering and the giving of food.



(a) Top view



(b) Side view

Figure 1.--Top and side views of observation cages. Top view (a) shows location of food (left) and water cups (right). Sectors A, B and C are shown as if the food was being presented. Sector A is defined by the area within the walls immediately around the food cup. Sector B comprises the area outside Sector A but within the first floor crossbeam. Sector C consists of the rest of the cage beyond this first floor crossbeam. Sector identification reversed to the other end of the cage when water was presented, with Sector A being nearest the water cup and Sectors B and C were increasingly further away. In side view (b) one wall around the food and water cups has been removed to reveal each cup with its photocell placement (arrows).

Each cage had a water cup in the middle of one end-wall and a similarly placed food cup at the other end. The water cup consisted of a modified Hart cup (H. W. Hart Manufacturing Co., Glendale, California) with the operant lever removed and a plastic tubing coupled to a water container located outside the cage. The food cup was made from a sheet metal eaves trough. Four-inch high walls built up along the sides of both the water and food cups allowed a two-inch wide access to each cup. Only one quail could eat or drink at any one time. Photocell systems were situated at the top rim of each cup, allowing measurement of the duration of time any individual remained in this area. Interruption of this light beam did not constitute eating behavior but its relationship to eating was obviously very high.

The ceiling of each cage had two 25-watt light bulbs attached to it. Lights were on a fixed photoperiod of 10 hours dark, 14 hours light (8:00 AM to 10:00 PM).

Humidity and temperature were subject to variation in the experimental room. A 24-hour Bendix hygrothermograph was used to record this fluctuation. Temperature averaged 74° F during this experiment but slowly rose approximately 2° F (72° to 74°) with the presence of the experimentors in the room. A range of 23 to 35% relative humidity was recorded during the four months of this experiment.

Measures of Incentive-Distance

In order to answer the first two goals of this experiment, dominance behavior was measured at three distances from each incentive, defined as Sectors A, B and C. Cross-beams dividing the floor of the cage into three equal sectors were used to identify these three Sectors (see Figure 1). Dominance was always measured as to where the target bird was standing. Sector A was the area within the walls immediately surrounding the incentive cup, Sector B was the remaining area around the incentive walls defined by the nearest cross-beam in the floor, and Sector C was the rest of the cage beyond this cross-beam. Figure 1 shows these Sectors around the food cup only. When water was presented Sector identification reversed to the other end of the cage with Sector A being nearest to the water cup and Sectors B and C being increasingly further away.

During Study 3 Sector B for each incentive was made smaller in size by constructing an imaginary boundary line (in parallel to a cross-beam) 10 inches from each incentive cup. These lines were defined by placing tape on the side walls of the cage, making them visible to the observors but not to the quail inside the cage. Sector C was consequently made larger in this process for both incentives.

Measures of Dominance

It was pointed out earlier (Introduction) that definitions of dominance behavior have varied across species. In the present experiment dominance behavior was defined as the occurrence of supplanting or avoidance behavior. The specific agonistic responses involved are summarized below.

1. Peck--rapid thrusting of the beak, making contact with another bird usually on the head or shoulder region. Included in this category were pecks which resulted in grabs on the head, neck or back. Some grabs on the back or side region were oriented towards pulling out feathers and were not counted as aggressive pecks. The head or neck grab was also a component of the sexual response. Pecks to the beak, feet and leg region were frequently made in a slower, more deliberate manner, particularly when wounds were obvious in these regions. These pecks were not counted as aggressive pecks.

2. Push--causing another bird to be supplanted by a rapid thrust and contact with the breast or shoulder region.

3. Threat--rapid thrusting with beak, stopping short of contact with the target bird or the approach of one bird causing another to supplant. Situations where one quail suddenly moved while others around it remained stationary were not counted as avoidance responses since the stimulus was not apparent.

4. Kick--use of the feet to supplant another. Usually observed as a quick shuffling motion of legs and feet while the aggressor was on the back of his subordinate. Similar motions of feet seen when quail are dusting or scratching the floor.

5. Fight--aggressive interaction involving two individuals facing each other using any of the above aggressive responses.

Supplants involving birds engaged in the following behavior were not counted as aggressive supplants: resting, dusting, preening, defecating, pecking walls, pecking floor and eating feces. It was felt that these behaviors represented other consummatory sequences which, if counted, would constitute a source of variance in unilateral dominance relationships measured around food and water incentives.

Components of the male's courtship behavior frequently caused supplanting or avoidance responses in other males and females. These responses included Neck-and-Body-Tonus, Toe Walk and Churring (Otis, 1968). These responses were recorded but analyzed only in a sexual context.

Recording Techniques

Two observers were involved; one recorded agonistic and other social interactions, the other recorded sequential order of eating and drinking.

Two channels of a 10-pen Esterline Angus event recorder were wired into the photocell circuits at the food and water cups in each cage. Since observations could be made on only one cage at a time, these two channels were switched to the cage of interest, allowing the other eight pens to be free for recording each individual's behavior. These eight pens were, in turn, wired to a key board on one observor's chair, enabling her to record the sequential order of eating and drinking by each individual in the flock. Agonistic and other social behaviors were recorded by speaking into a tape recorder.

Procedure

Three studies were conducted (labeled 1, 2 and 3) with only slight differences in each. Each study involved three groups of quail (two experimental and one control) being observed over three phases of treatment. Each phase lasted for six days with a day of no observations interceding between phases. *S*s were weighed and feces were removed from beneath the cages on this day between phases.

Because of their overall similarity the procedure for Study 1 alone will be portrayed in detail followed by the changes which were made in the designs of Studies 2 and 3.

Procedure for Study 1

During each phase (labeled I, II and III) observations were made three times daily; during a nonincentive Morning session and during food and water sessions in the Evening.

Morning sessions.--Morning observations were concerned with social interactions which occurred following simultaneous access to both food and water. Both incentives were given between 9:00 and 9:45 a.m. (randomly staggered at 15 minute intervals to accommodate each of the three groups) and 15-minute observations of each group were made between 10:30 a.m. and 11:45 a.m. following removal of the food and water. Records were kept of aggressive interactions occurring throughout the cage.

Evening sessions.--Evening sessions began between 7:00 p.m. and 8:00 p.m. (randomly staggered at 30 minute intervals to accommodate each of the three groups) and involved the presentation of food and water during successive periods. Food always preceded water. While food was being offered, records were made of (1) the order and frequency with which individuals ate, (2) the amount of time each individual spent near the rim of the food cup, and (3) aggressive interactions occurring within the three Sectors of the cage. Food was presented for 15 minutes.

Water presentation followed the same format as food and involved similar measures being recorded. Water was also presented for 15 minutes.

In Phases I and III dominance was measured during identical conditions. Phase II was designed to answer the third goal of this experiment, namely what are the effects of food and water deprivation on dominance behavior. During Phase II one experimental group was examined for food deprivation effects while the second experimental group was examined for water deprivation effects. For the time-control group treatment conditions remained the same over all three phases, thus providing a measure of dominance stability over this period of time.

In Phase II, two mid-ranking Ss (one male, one female) in the food-deprived experimental group were selected as test Ss following the end of Phase I. Ninety minutes prior to the regular evening session, between 5:30 p.m. and 6:00 p.m. (staggered at thirty minute intervals to accommodate each of the experimental groups) these two test Ss were removed from the observation cage and placed singly in small wooden cages where water but not food was available for 30 minutes. During this time the remaining 6 Ss in the observation cage were allowed access to both food and water. Observations revealed that these 6 birds were always satiated on food and water (i.e. stopped eating and drinking) before 30 minutes had passed. After 30 minutes the two test Ss were returned to the observation cage where all food and water had been removed. One hour later the regular evening food session was begun, lasting for 15 minutes, followed by the regular 15 minute water session. The two test Ss were 7½ to 8½ hours food-deprived at the start of the evening food session while the others in the group were one hour deprived.

Similar procedures were followed for two midranking Ss (one male, one female) in the water-deprived group except that water, rather than food, was deprived from these test Ss during Phase II while their flockmates back in the observation cage were given access to both food and water.

Procedure for Study 2

Study 1 was essentially an exploratory attempt to define food and water deprivation parameters and to refine measures of dominance. As Table 1 shows four quail died during Study 1. In Study 2 quail were allowed longer access times to food and water. During the Morning sessions food and water were given between 9:00 a.m. and 9:45 a.m. They were removed 180 minutes later , between 12:00 noon and 12:45 p.m. During the evening sessions the regular food session lasted for 30 minutes rather than 15 minutes. All other experimental parameters were the same as in Study 1.

Only one quail died in Study 2 (see Table 1). In both Studies 1 and 2, however, the occurrence of dead quail raised questions about uncontrolled health-related variables operating (e.g. pathology). Since dead quail were not replaced and since space allotment per bird is different in flocks of seven or less than it is in flocks of eight, there arose questions as to what effects these two variables had on dominance expression. As a result of these questions statistical comparisons in Studies 1 and 2 were difficult to interpret.

Procedure for Study 3

In Study 3 an additional 15 minutes of simultaneous food and water was given to all groups following the evening sessions. None of the quail died during Study 3 (Table 1), apparently as a result of this increased food and water supply.

During Studies 1 and 2 it was felt that a small area around the incentive cups, extending approximately 8 to 10 inches into Sector B, yielded different forms of aggressive behavior from that seen in Sectors A and C alone. This effect was apparently being masked because Sector B, being as large as it was, encompassed both this suspected dominance form and dominance forms associated with areas further away. In an effort to delineate this apparent effect in Study 3 Sector B was reduced in size (see *Measures of Incentive-Distance*) for both incentives by moving the outer boundary toward the incentive to a point ten inches away from the incentive cups. Other than these changes in food and water access times and reduction in size of Sector B, the procedure for Study 3 was the same as for Study 2.

RESULTS AND DISCUSSION

Dominance Behavior as Appetitive Behavior

Aggressive Behavior at Different Incentive-Distances

Data from Study 3 alone provide a representative picture of aggressive interactions in quail in the present experiment. The measures reported in Table 2 are mean frequency of aggressive supplants (i.e. dominance) per every possible dyadic interaction. In a flock of eight birds there are 56 possible interactions with each bird being capable of dominating every other flockmate in an intransitive manner. The means reported in Table 2 were obtained by first combining all food and water sessions as well as all phases in each of the three groups in Study 3. The frequencies of aggressive responses used in all dominance displays were then summed for all 168 interactions (i.e. 56 in each of the three groups) for each response type and these totals were divided by 168 for each Sector during the Evening sessions and for all sectors combined in the Morning session. The averages reported in Table 2 provide a standard basis for comparison between response types within each incentive-distance as well as between the various incentive-distances and the

TABLE 2.--Mean frequency of response occurrence for every possible dyadic interaction in Study 3. All groups, phases and incentives have been combined as have all sectors during the Morning session.

	Evening Session			Morning Session
	Sector A	Sector B	Sector C	
Pecks	65.71	23.75	7.16	6.64
Push	33.55	10.86	.16	.02
Threat	1.30	24.46	10.82	7.91
Kick	1.84	.02	.04	.05
Total	102.40	59.09	18.18	14.63

nonincentive Morning session. For example, in Sector A for Evening sessions, quail used the Push response an average of 33.55 times whereas Threat responses were used an average of 1.30 times. Morning sectors were combined due to the small amounts of aggression occurring in each sector alone.

Comparisons within each incentive condition revealed differing response profiles at different distances from the incentive. In Sector A quail utilized the Peck and Push responses more than 97% of the time to supplant others from near the incentive cup. A Friedman x_r^2 test (Siegel, 1956) revealed significant differences ($p < .001$) between frequencies of different aggressive responses in this sector.[1]

Comparisons between specific response categories (Wilcoxin signed-ranks test) indicated Pecks to be significantly greater in frequency than each of the other response

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[1] Nonparametric analyses were necessitated because of heterogeneity of variance among several response classes. Although 10,881 aggressive responses were observed during Study 3, relatively few Kicks and Pushes were counted during this time. Unless otherwise indicated Kruskal-Wallis one-way analyses of variance were used to test for overall differences between independent samples. Where differences were found to occur beyond the .05 level of significance a Mann-Whitney U test for independent samples was used to detect differences between pairs of samples. Likewise the Friedman two-way analysis of variance and Wilcoxin signed-ranks tests were used to analyse differences among related samples (Siegel, 1956).

categories ($p<.01$) while the Push was used more frequently than the Threat and Kick ($p<.01$). Threats and Kicks were observed at the same frequency in Sector A.

In Sector B significant differences were again detected between aggressive responses (Friedman X_r^2 test, $p<.001$). Here, however, Pecks, Pushes and Threats accounted for 99% of the aggression. Subsequent comparisons of specific response categories (Wilcoxin signed-ranks test) revealed a different profile of behavior than that observed in Sector A. Threat responses were used as frequently as the Peck response in Sector B but whereas the Peck was significantly greater in frequency than the Push ($p<.001$), Threat responses were found not to differ in frequency from the Push. The Kick response was utilized less than each of the other aggressive responses in Sector B ($p<.001$).

Quail again showed a different pattern of aggressive behavior in Sector C, the furthest distance from the incentive cups. Overall differences in response categories were again highly significant (Friedman X_r^2 test, $p<.001$). Unlike Sectors A and B, the Peck and Threat responses in Sector C accounted for more than 98% of the aggression. Threats were used more often than Pecks ($p<.003$), Pushes and Kicks ($p<.001$), while Pecks in turn were observed more frequently than Pushes and Kicks ($p<.001$). Frequencies of Push and Kick behavior were found not to be different.

The profile of aggression observed throughout the cage during Morning sessions was most similar in appearance to the pattern observed in Sector C, with Pecks and Threats accounting for more than 99% of all aggression. Overall differences between response categories in the Morning session were found to be highly significant (Friedman X_r^2 test, $p<.001$). Threats were observed more frequently than each of the other response types ($p<.001$) while Pecks were used more frequently than Pushes and Kicks ($p<.001$). Pushes and Kicks were used equally often.

Patterns of aggressive activity in Study 3 were also analyzed according to the sex combination involved (Male-supplant-Male, labeled as Male-Male; Male-Female, Female-Male, and Female-Female) in each Sector of the Evening sessions and in all Sectors combined for the Morning session. The results of these analyses and a discussion of these findings in relation to what other researchers have reported for the quail are presented in Appendix B. In general these data reflect the overall data presented in Table 2. Both male and female quail used different aggressive responses depending upon how far from the food and water cups they were standing. So great was this effect that a description of male-female interactions was meaningless unless incentive-distance was taken into consideration. These data suggested that aggressive behavior was under the control of different stimuli in each Sector during the Evening session and in the Morning session when neither food nor water was present.

The Totals reported in Table 2 for each Sector and the Morning session indicate a trend of increasing amounts of aggressive behavior as incentive-distance decreased. This effect was tested by analysis of variance for each group separately and for each incentive separately. The results of these analyses are shown in Table 3. As Table 3 indicates, this trend was statistically significant for Food sessions but not for Water sessions. Although Sector A with Sector B (A,B) and Sector B with Sector C (B,C) comparisons revealed significant differences ($p<.01$, Newman-Keuls test, Winer, 1962) for only two of the three Groups during Food presentation (A,B, Groups 1 and 3; B,C, Groups 2 and 3) the probability of this occurring this many times by chance alone was .001 (Sakoda, Cohen and Beall, 1954). It was therefore concluded that frequencies in Sector A were greater than in Sector B and frequencies in Sector B were greater than in Sector C for Food sessions.

Water sessions revealed a different distribution of aggression. There were as many aggressive interactions in Sector A as there were in Sector B, while Sector C proved to have the fewest.

Morning sessions were analyzed somewhat differently. Since there were no incentives presented during the Morning session a Sector differentiation as used during the Evening

TABLE 3.--Results of analysis of variance for total amounts of aggression between Sectors in the Evening and Morning sessions of Study 3.

Group	Incentive	F(df = 2,54)	Sector Comparisons		
			A,B	B,C	A,C
1	Food	43.20**	**		**
	Water	7.09**		*	**
	None (Morning)	1.53			
2	Food	15.64**		**	**
	Water	18.20**		**	**
	None (Morning)	2.51			
3	Food	21.07**	**	**	**
	Water	5.26**		*	**
	None (Morning)	1.30			

*$p<.05$.

**$p<.01$.

sessions would be inappropriate. Consequently a Left and Right sector was defined by the area corresponding to Sector B at both ends of the cage as if both food and water were presented at the same time. The remaining middle section was defined as the Middle sector. During Study 3, the Middle sector was made larger with the reduction in size of Sector B. Aggressive interactions rarely occurred within the areas corresponding to Sector A during incentive presentation and they were not analyzed for the Morning session. Unless otherwise indicated all further analyses involving the Morning session will utilize this Left, Middle and Right classification. As Table 3 indicates no differences could be detected between these three Morning sectors for amount of aggressive behavior.

Intragroup response matrices for Study 3 are presented in Appendix D. These data reveal individual interactions among all _S_s in each group during Study 3 and serve to indicate absolute levels of activity in each incentive condition during each phase.

Unilateral Aggressive Interactions Measured at Different Incentive-Distances

Members of dyads may either show unilateral or bilateral aggression (or, of course, not respond at all) during any particular session. Avian societies characterized by unilateral aggressive interactions have been referred to as peck orders while societies characterized by bilateral aggression have been referred to as peck-dominance organizations. There was evidence in the present experiment suggesting that the form of social organization expressed by a flock of quail is a function of how close Ss are to the incentive when aggressive behavior is measured.

Table 4 presents the proportion of unilateral interactions within each Sector of the Evening session and within the Left, Middle and Right sectors of the Morning session. In most cases interactions become more bilateral as the quail approach the incentive. This is shown in Table 4 by the smaller proportion of unilateral interactions in Sector A. The Friedman X_r^2 test (Siegel, 1956) was used to evaluate overall differences in these proportions across the three Sectors. This nonparametric analysis was chosen because a predonderance of "zero" interactions occurred in Sector C, causing heterogeneity of variance and hence violating a basic assumption of the parametric analysis of variance model.

Results of analyses presented in Table 5 can best be understood by recalling the changes in Sector size that were made in Study 3. It was felt that by making Sector B smaller in size this would serve to delineate dominance behavior occurring in a small area around the incentive cup. It was suggested that dominance interactions in Sector B were different from those in Sectors A and B. Analyses of Study 3 subsequently revealed a different

TABLE 4.--Mean proportion of sessions per dyad in which unilateral aggressive interactions were observed.

		Food Session			Water Session		
Study	Group	Sect A	Sect B	Sect C	Sect A	Sect B	Sect C
Evening Sessions							
1	1	.69	.92	.90	.65	.87	.97
	2	.62	.94	.95	.76	.91	.94
	3	.53	.96	.93	.52	.92	.95
2	1	.58	.97	.85	.78	.96	.99
	2	.44	.94	.98	.79	.96	.98
	3	.49	.98	.96	.66	.99	.99
3	1	.42	.90	.92	.72	.89	.93
	2	.48	.86	.94	.69	.81	.97
	3	.45	.91	.93	.71	.76	.99

Morning Sessions

Study	Group	Left	Middle	Right
1	1	.96	1.00	.89
	2	.95	.96	.85
	3	.94	1.00	.94
2	1	.97	1.00	1.00
	2	1.00	1.00	1.00
	3	.95	1.00	1.00
3	1	.99	.97	.99
	2	1.00	1.00	1.00
	3	1.00	.83	1.00

TABLE 5.--Results of analyses of differences between amounts of unilateral and bilateral aggression occurring in different Sectors for each incentive.

Study	Group	Incentive	Friedman X_r^2	Sector Comparisons		
				A,B	B,C	A,C
1	1	Food	6.37*	***		*
1	1	Water	15.89***	**		***
1	1	Morning	1.08			
1	2	Food	20.43***	***		***
1	2	Water	12.08**	***		***
1	2	Morning	2.32			
1	3	Food	17.09***	***		***
1	3	Water	21.13***	***		***
1	3	Morning	1.25			
2	1	Food	38.99***	***		*
2	1	Water	13.68**	***		***
2	1	Morning	.26			
2	2	Food	9.45**	***		***
2	2	Water	7.63*	*		***
2	2	Morning	1.44			
2	3	Food	45.70***	***		***
2	3	Water	24.03***	***		***
2	3	Morning	.27			
3	1	Food	37.69***	***		***
3	1	Water	15.68***	***	*	***
3	1	Morning	.11			
3	2	Food	35.01***	***	***	***
3	2	Water	14.43***	***	***	***
3	2	Morning	.03			
3	3	Food	33.55***	***	**	***
3	3	Water	17.91***		***	***
3	3	Morning	.66			

*p<.05.

**p<.01.

***p<.005.

picture of dominance than that shown for Studies 1 and 2. Sector A for both food and water proved to contain more bilateral aggressive interactions than did the two Sectors further away from the incentive in all three Studies (see Table 4). Only in Study 3, however, were differences detected between Sectors B and C, suggesting that the hypothesis concerning different dominance forms existing near the incentive was correct.

When incentives were absent (Morning), social organization approximated a peck order arrangement characterized by unilateral aggressive interactions. Of particular interest was the absence of any gradient of dominance change over the three Sectors during Morning sessions. This is shown in Table 5 by the lack of significant effects for Morning sessions in all groups in all three Studies.

Dominance Status Related to Incentive-Distance

Aggressive behavior was initially examined in relation to the traditional model of the dominance hierarchy (Allee and Foreman, 1955, p. 93). However, this model created numerous statistical problems because of a high frequency of triangular and square relationships. A method initially developed by Butterfield and Crook (1968) was subsequently adopted allowing dominance to be measured along an interval scale rather than an ordinal scale. Crook referred to this measure as the Dominance Index (DI) and defined the DI for each S as

$$DI_i = \frac{\sum_{i=1}^{N} W_i/n_i}{N - 1}$$

where W is the number of wins and n the number of encounters with a particular flockmate, and N represents the number of birds in the flock. From this measure a linear hierarchy was constructed, with alpha and omega having the highest and lowest DI respectively.

Dominance indices (DI) were measured in Sectors A, B and C for both food and water and throughout all sectors combined in the Morning session. Therefore, each quail was given a dominance index (DI) on seven occassions each day. At the end of each Phase a mean DI was computed for each of these seven locations, reflecting the average performance throughout the week. These average DIs were then used in analyses of incentive-distance relationships and, unless otherwise indicated, a bird's DI will always refer to this averaged figure.

The relationship between a quail's dominance status at different incentive-distances is shown in Table 6 for the Food incentive. Correlations were not computed where dominance hierarchies were composed of four or more individuals whose DI was zero. This rule was followed in all

TABLE 6.--Correlations between dominance hierarchies measured in different Sectors during each phase of the Food session in Studies 2 and 3.

Group	Phase	Sector Comparisons A,B	B,C	A,C
Study 2				
1	I	.128	--	--
	II	.607	--	--
	III	.362	--	--
2	I	.524	--	--
	II	.437	.949***	.222
	III	.170	--	--
3	I	.472	--	--
	II	.305	.961***	.229
	III	.506	.851**	.635
Column Mean		.400	.933***	.382
Study 3				
1	I	.841**	.736*	.765*
	II	-.055	.838**	.354
	III	.591	.790*	.374
2	I	.761*	.738*	.308
	II	.654	.859**	.575
	III	.484	.359	-.462
3	I	.491	.914**	.414
	II	-.402	.944***	-.366
	III	-.281	--	--
Column Mean		.416	.770*	.280

*$p<.05$.

**$p<.01$.

***$p<.001$.

.707, .834 and .925 needed for the first correlation to be significant at the .05, .01 and .001 levels, respectively.

correlational analyses. Column means in Table 6 (and in all subsequent tables in which a series of correlations have been averaged) were computed by first transforming each r to a z score. The sum of these z scores was then divided by the number of scores involved. Finally this mean z score was transformed to r and listed as a column mean in Table 6.

A significant correlation was found between Sectors B and C for both Studies 2 ($p<.001$) and 3 ($p<.05$), indicating that stimulus control of dominance behavior in these two Sectors was highly similar. The lack of significant correlation between Sector A and the other Sectors suggests that a different set of causative factors were operating in Sector A. It is of interest that Sectors A and B had numerically higher correlations (.400 and .416) than Sectors A and C (.382 and .280), though none of these correlations were found to be significant.

Table 7 reports correlations between hierarchies measured in different Sectors during Water sessions. In Study 2 A,B and B,C comparisons were both significant ($p<.05$ and $p<.01$) while only B,C comparisons in Study 3 were significant ($p<.05$). Again, as with Food sessions (Table 6), comparisons of A with B and B with C yielded numerically higher correlations than did A,C comparisons.

TABLE 7.--Correlations between dominance hierarchies measured in different Sectors during each phase of the Water sessions in Studies 2 and 3.

		Sector Comparisons		
Group	Phase	A,B	B,C	A,C
		Study 2		
1	I	.750*	.881**	.809*
	II	--	--	--
	III	.810*	.959***	.795*
2	I	.829*	--	--
	II	.756*	.985***	.705
	III	.631	.875**	.688
3	I	.855**	--	--
	II	.752*	.824*	.596
	III	.746*	.800*	.361
Column Mean		.774*	.918**	.682
		(b) Study 3		
1	I	.587	.950***	.508
	II	.872**	.794*	.723*
	III	.720*	.659	.207
2	I	-.028	.538	.096
	II	.186	--	--
	III	.387	.716*	.085
3	I	.079	--	--
	II	.532	.945***	.477
	III	.693	.241	.531
Column Mean		.506	.776*	.401

$^{*}p<.05.$

$^{**}p<.01.$

$^{***}p<.001.$

.707, .834 and .925 needed for the first correlation to be significant at the .05, .01 and .001 levels, respectively.

Comparisons Between Morning and Evening Sessions

Correlations between Morning and Evening sessions are shown in Table 8. It is apparent that Morning hierarchies were more closely related to hierarchies in Sectors B and C than they were to hierarchies nearest the incentive. It is particularly interesting that Sector C in all but the Food session of Study 3 was most closely related to the nonincentive hierarchy derived during the Morning session.

Between-Incentive Comparisons of Dominance Hierarchies

Table 9 reports correlations between hierarchies measured at different incentives but in similar Sectors. For example hierarchies measured in Sector B for Food and later for Water during Phase II of Study 2 correlated .963 with each other.

Hierarchies measured in Sector A for each incentive were not closely related. Sectors B and C reflect similar hierarchies with an apparent trend in Study 3 towards greater similarity in Sector C. There were no apparent effects related to Phase.

Dominance Behavior Related to Consummatory Activity

Table 10 reports correlations between dominance status and latency for eating and drinking (i.e. initial photobeam interruption). Although photobeam interruption

TABLE 8.--Correlations between dominance hierarchies between Morning and Evening Sessions.

		Morning hierarchy with Evening Food Sectors			Morning hierarchy with Evening Water Sectors		
Group	Phase	A	B	C	A	B	C
				Study 2			
1	I	.175	.841**	-	.707*	-	.771*
	II	-.018	.478	-	.863**	-	-
	III	-	-	-	-	-	-
2	I	.278	.730*	-	.424	.770*	-
	II	.356	.990***	-	.729*	.959***	-
	III	.274	-	-	.542	.951***	.945***
3	I	.635	.472	-	.349	.360	-
	II	.291	.988***	.988***	.706*	.981***	.839**
	III	.819*	.679	.922**	.650	.811*	.860**
Column Mean		.391	.866**	.969***	.649	.893**	.869**
				Study 3			
1	I	.866**	.913**	.775*	.534	.772*	.835**
	II	.408	.812*	.497	.333	.193	.538
	III	.504	.948***	.760*	.107	.478	.674
2	I	-.075	.392	.791*	-.227	.762*	.011
	II	.650	.330	.455	.302	.180	-
	III	.229	.915**	.636	.327	.841**	.688
3	I	.410	.808*	.788*	-.214	.656	-
	II	-	-	-	-	-	-
	III	-.377	.965***	-	.051	-.106	.803*
Column Mean		.388	.846**	.691	.162	.540	.644

*$p<.05$.

**$p<.01$.

***$p<.001$.

.707, .834 and .925 needed for the first correlation to be significant at the .05, .01 and .001 levels, respectively.

TABLE 9.--Correlations between dominance hierarchies in similar Sectors during Food and Water sessions.

		Food and Water Comparisons		
Group	Phase	Sector A	Sector B	Sector C
		Study 2		
1	I	.026	-	-
	II	-.013	-	-
	III	.043	.626	-
2	I	.431	-	-
	II	.200	.963***	-
	III	.442	-	-
3	I	.312	.965***	-
	II	.225	.997***	.853**
	III	.522	.921**	.868**
Column Mean		.253	.958***	.861**
		Study 3		
1	I	.457	.863**	.971***
	II	.451	.504	.842**
	III	.160	.535	.828*
2	I	-.352	.600	.251
	II	.324	.770*	-
	III	.656	.882**	.840**
3	I	.452	.862**	-
	II	.464	.958***	.977***
	III	.498	-.080	.825*
Column Mean		.364	.747*	.932***

*p<.05.

**p<.01.

***p<.001.

.707, .834 and .925 needed for the first correlation to be significant at the .05, .01 and .001 levels, respectively.

TABLE 10.--Correlations between Dominance Index and latency for initial eating and drinking behavior.

		Food latencies with DI in			Water latencies with DI in		
Group	Phase	Sect A	Sect B	Sect C	Sect A	Sect B	Sect C
				Study 3			
1	I	.294	.083	.369	.434	.008	-.120
	II	.743*	.262	.426	.580	.680	.678
	III	-.607	-.421	-.292	.095	.563	.414
2	I	-.374	-.334	-.088	.064	.565	-.320
	II	.132	.125	.203	.357	.567	-
	III	.308	.222	-.058	.425	.059	-.183
3	I	.171	.044	-.214	-.443	-.048	-
	II	-.134	.000	-.142	.797*	.273	.175
	III	.401	-.382	-	.830*	.788*	.365
Column Mean		.118	-.050	.030	.409	.420	.168
				Study 2			
1	I	-.224	-.160	-	.563	-	.289
	II	.336	.464	-	.266	-	-
	III	-.207	.071	-	.555	.470	.405
2	I	-.507	-.093	-	-.613	-.229	-
	II	-.028	-.585	-	-.522	-.158	-.061
	III	-.230	-	-	.570	-.210	-.160
3	I	.053	-.163	-	.259	-.208	-
	II	.386	-.219	-.094	.002	-.036	.469
	III	-.354	-.300	-.261	.561	.196	.235
Column Mean		-.091	-.130	-.179	.196	-.021	.206

*p<.05

**p<.01

***p<.001

.707, .834 and .925 needed for the first correlation to be significant at the .05, .01 and .001 levels, respectively.

was not the same as eating or drinking it gave an extremely close approximation to this consummatory activity. Table 10 indicates that eating and drinking latencies were poor predictors of dominance status. In all three Sectors there were scattered negative correlations, although none were significant.

A second measure of consummatory behavior, total time spent eating or drinking, is shown in Table 11 in terms of its relationship to dominance status. This measure was also derived from photobeam interruption and does not directly provide a true measure of amounts consumed. It does give a good indication of time spent by each subject with head immediately above the food and water cups. Table 11 shows that this measure of eating, as it will be referred to here, was, like latency to consumption, a poor predictor of dominance behavior. Again a few negative correlations appeared in the analyses. It might be noted that the greatest number of significant correlations appeared in the Section A column.

A third measure of consummatory activity, average time spent at the incentive cup per visit, also showed a poor relationship with dominance status (Table 12). For both food and water a few negative correlations again appeared, albeit insignificant.

TABLE 11.--Correlations between Dominance Index and total time of eating and drinking behavior.

		Food total time with DI in			Water total time with DI in		
Group	Phase	Sect A	Sect B	Sect C	Sect A	Sect B	Sect C
				Study 2			
1	I	-.169	-.218	-	.499	-	.083
	II	-.037	.211	-	.749*	-	-
	III	-.801*	-.357	-	.521	.585	.704
2	I	.426	.086	-	.456	.382	-
	II	.217	-.340	-	.116	.277	.343
	III	.057	-	-	.552	.212	.239
3	I	.106	-.275	-	.470	.744*	-
	II	.721*	-.258	-.203	.750*	.680	.717*
	III	.080	-.510	-.411	.291	.299	.519
Column Mean		.058	-.216	-.311	.514	.481	.467
				Study 3			
1	I	.241	.249	-.269	.854**	.291	.152
	II	.835**	.302	.323	.313	.306	.063
	III	.474	.454	.532	.663	.481	.065
2	I	.845**	.742*	.342	.764*	.472	.340
	II	.672	.585	.370	.688	.320	-
	III	.536	.528	.019	.389	.721*	.168
3	I	.418	.102	-.261	.436	.004	-
	II	-.225	.008	-.189	-.027	-.198	-.059
	III	.248	-.277	-	.381	.828*	.007
Column Mean		.512	.331	.119	.544	.406	.107

*p<.05

**p<.01

.707 and .834 needed for the first correlation to be significant at the .05 and .01 levels, respectively.

TABLE 12.--Correlations between Dominance Index and average time spent at the food and water cups per visit.

		Average time per visit at Food with DI in			Average time per visit at Water with DI in		
Group	Phase	Sect A	Sect B	Sect C	Sect A	Sect B	Sect C
				Study 3			
1	I	-.385	-.299	-.418	.730*	.021	-.070
	II	.382	-.051	-.096	.033	-.127	-.233
	III	.270	.252	.368	.437	.189	-.171
2	I	.348	.245	-.118	.618	.206	.433
	II	.014	.231	-.006	.047	-.173	-
	III	.375	.401	.120	.486	.477	.047
3	I	.349	-.003	-.315	.495	-.282	-
	II	-.110	-.280	-.431	-.379	-.551	-.395
	III	.259	-.277	-	.222	.290	-.209
Column Mean		.172	.026	-.118	.331	-.008	-.085
				Study 2			
1	I	-.128	-.320	-	.031	-.029	-.280
	II	-.334	.056	-	.270	.356	-
	III	-.809*	-.404	-	.293	.514	.566
2	I	.506	.572	-	.329	-.000	-
	II	-.095	-.501	-	-.124	-.366	-.356
	III	-.101	-	-	-.228	-.062	-.220
3	I	.114	-.349	-	.259	-.208	-
	II	.558	-.461	-.439	.002	-.036	.469
	III	-.109	-.625	-.618	.561	.196	.235
Column Mean		-.067	-.268	-.534	.165	.046	.084

*$p<.05$.

.707 and .834 needed for the first correlation to be significant at the .05 and .01 levels, respectively.

Discussion of Dominance Behavior as Appetitive Behavior

Quail tended to use different types of aggressive behavior depending upon how far they were from the incentive. This effect would be expected if aggression were viewed as an instrumental response for incentive acquisition. Aggression observed at increasing distance from the food or water would have a decreasing relationship to food or water consumption and might consequently be expressed in a different manner.

In effect Sectors C through A might be thought of as an expression of a consummatory response sequence, reflecting a transition from unrelated (Sector C) to appetitive (Sectors B and A) to consummatory behavior (Sector A) for a particular incentive. The fact that greater amounts of aggression occurred nearer the incentive (Table 2) indicates the motivated character of this activity. This is further supported by the fact that Morning sectors (nonincentive conditions) could not be differentiated by amounts of aggression. This consummatory theory is a reasonable interpretation of the present data not only because it provides an explanatory framework for some of the findings of this experiment but it also generates testable questions with regards to the nature of consummatory behavior sequences (ex. do quail show greater variability in their behavior as incentive-distance increases?).

Alternate Explanations

There are alternative explanations for some of these findings which must be considered here. Perhaps different physical and social conditions present at different incentive-distances forced the forms of aggressive behavior that were observed. For example, the physical make-up of the incentive cup and walls around it forced the quail to bend over while eating (or drinking) and thereby face away from the other birds. Another bird attempting to supplant this "feeding" quail would be limited to Pecks on the back side, Kicks and Pushes. Threats would probably be ineffective as their effectiveness most likely lies with the visual features (i.e. conditioned aversive stimuli) of the attacking bird.

The presence of the incentive caused a greater number of birds to remain in Sector B than in Sector C during the evening sessions. Although this effect was not directly measured, there was clearly a greater amount of aggressive interaction in Sector B than in Sector C. The greater density of birds in Sector B may have forced the occurrence of Push responses in situations where space did not permit Pecks or Threats. Likewise Threats were more adaptive in Sector C because of the greater distance between birds.

The possible effects of physical and social factors on the form of aggressive behavior at different

incentive-distances cannot be disregarded. However, their role as causative factors does not rule out the appetitive nature of aggression.

A second alternative explanation based on frustration must also be considered here. The consummatory theory of social dominance assumes, perhaps naively, that the more victorious birds will reap the harvest of the incentive. That is, the dominant bird will eat first, eat more at each approach to the food cup and in the long run eat the most. This supposition follows from the argument being developed here that an appetitive sequence of behavior is reflected in Sectors C, B and A with the food and water incentives being the end goal of this instrumental activity. The data, however, show that a quail's dominance status has little relationship to his consummatory behavior. Perhaps fighting in Sectors A, B and C represents a reaction to frustration, that the high density of individuals crowded around the incentive cup act as barriers to incentive-acquisition, causing increased incidence of fighting, the goal of which is to remove these barriers to the incentive. In other words the goal or incentive to fighting is the removal of "blockading" individuals. The greatest influence of frustration would be expected nearest the incentive cup, in Sector A. Perhaps differences in aggression and dominance behavior in Sector A as compared with similar behavior in Sectors B and C reflect this influence of frustration.

Andrew (1957a) has shown that crowding rather than hunger or thirst causes a lowering of the threshold for aggression in yellowhammers. Studies by Duncan and Wood-Gush (1971) have recently shown that frustration causes an increase in levels of aggression in domestic fowl. However, these increases in aggression were specific to the dominant birds. Submissive fowl failed to fight more under frustrating conditions. In other words transitivity was maintained in dominance relationships during frustration.

In the present experiment frustration was probably a contributing factor to aggression in Sectors A and B. Unlike the domestic fowl in Duncan and Wood-Gush's study the Japanese quail here in this experiment showed greater levels of bilateral aggression as frustration presumably increased (i.e. nearer to the incentive). This may be a species-specific phenomenon. The specific role played by frustration in the present experimental condition needs to be defined.

Factor analytic studies of quail aggression in experimental conditions similar to those used here would be useful in the understanding of causative variables. There appear to be simple clusters around Sector A and Sectors B and C and a supercluster around the appetitive activity in Sectors A, B and C together. The consummatory activities (latency, total time and average time of incentive-consumption) may involve causative factors independent of those operating for the appetitive components.

Dominance Behavior and the Consummatory Theory

The consummatory theory of social dominance would predict differences in dominance hierarchies between Sectors A and C (or perhaps all three Sectors) because a good fighter in Sector A may be controlled by motivational factors related to incentive acquisition (e.g. deprivation) while a good fighter in Sector C might be fighting for some entirely different reason. Fighting in Sector C may reflect consummatory behavior, since the removal of the target bird results in termination of the behavioral sequence (Denny and Ratner, 1970). Aggression in Sectors B and A, however, was only secondary to incentive-acquisition (i.e. appetitive) and only food (or water) consumption, not removal of a target bird, could terminate the response sequence.

There is considerable support for this reasoning. The nature of aggressive interactions tended to change with decreasing incentive-distance (Table 4). Interactions close to the incentive were bilateral with members of each dyad supplanting each other during each session. If aggression in Sector A is being controlled by dynamic motivational variables (e.g. deprivation) than an ever-changing picture of dominance here in Sector A might be expected within each session. On many occasions dominant birds were observed to control access to the food cup at the beginning of a session but after several minutes of eating would easily be supplanted by presumably "hungrier" birds. Unilateral interactions recorded further away from each incentive may truly reflect "dominance" as a consummatory event, that event which the social dominance theory was designed to cover. That this gradient of dominance-form was related to the food and water incentives is supported by the lack of such a gradient across sectors during the nonincentive Morning session.

Bennett (1940) noted changes from a peck-right to a peck-dominance form of social organization in ring doves injected with testosterone propionate. Since this hormone is known to cause increases in aggressive behavior (Allee and Foreman, 1955; Selinger and Bermant, 1967), perhaps changes in organization-form in the present experiment are a function of the amount of aggression. It should be recalled that Sectors A, B and C reflected a gradient of decreasing amounts of aggression.

Dominance hierarchies were different in the different Sectors. The consummatory theory would specifically predict Sectors A and B and Sectors B and C to be more closely related to each other than Sectors A and C.

Because of their common borders these Sectors would reflect common segments of the consummatory sequence. Dominance hierarchies measured during Water sessions (Table 7) showed support for this hypothesis while Food session hierarchies (Table 6) did not. During Food sessions hierarchies in Sector A were unrelated to any of the other Sectors, indicating something entirely different was occurring in Sector A than in Sectors B and C.

Dominance hierarchies measured during the non-incentive Morning session would be expected to correlate most closely with hierarchies in Sector C of the incentive conditions, because aggression in Sector C, like in the Morning, would be unrelated to a specific incentive. Likewise the smallest correlations would be expected with Sector A hierarchies. Sector A did, in fact, show poor relationship to the Morning hierarchy (Table 8) but Sector B as well as Sector C were highly related to the Morning hierarchy. There was an apparent difference in Morning-Water correlations between Studies 2 and 3 which could not be explained with information available. Much higher correlations were found here with Study 2. Differences between Phases were not expected and no trends in this direction were detected.

An important test of the consummatory theory of social dominance came when hierarchies were correlated across incentives (Table 9). It was clear that Sector A dominance behaviors were not related while the appetitive components in Sectors B and C were. The consummatory theory would predict differences between dominance hierarchies in Sector A for food and hierarchies in Sector A for water and increasingly closer relationships between dominance hierarchies in Sectors B and C across food and water. Response components of a consummatory sequence are known to become more stereotyped as the sequence nears completion (Denny and Ratner, 1970). Since appetitive behaviors are specific to their consummatory stimuli (Hinde, 1966) Food and Water appetitive behaviors in Sector A would likely be different because a different consummatory stimulus was involved at the end of each sequence. Aggression in Sectors B and C would be increasingly nonspecific to a particular incentive (consummatory stimulus) and would in itself become a consummatory activity in Sector C. Therefore aggression in Sector C for food and water would be expected to be more closely related. The results lend some support for this interpretation. Both Sectors B and C were found to be highly correlated across incentives in both Studies 2 and 3.

Relationships between dominance behavior and consummatory activity related to eating and drinking did not support the consummatory theory. Sector A dominance behavior would be expected to relate highest with latency, total time and average time per visit measures. This was not found to happen! Appetitive behavior had no effect on consummatory activity.

Latency measures (i.e. the order of access to food or water) have been used as a measure of dominance activity in mammalian studies as has total time spent at a food or water source (cf. Baenninger, 1970; Bernstein, 1969; Collias, 1950). In this experiment neither were related to social dominance in other areas of the cage. The average time per visit was recorded because it was noticed that any quail could be supplanted from Sector A but the more dominant birds seemed to remain longer in Sector A on each visit to the incentive cup, at least initially during a session, than did other birds. The average time per visit measure was assumed to be a sensitive measure of this apparent affect, however it too proved to be a poor predictor of dominance status.

Bernstein (1969) found low correlation between dominance order and priority to incentives with pigtail monkeys. Bernstein reviews similar findings in other primate studies. Noble, Wurm and Schmidt (1938) found no correlation between eating behavior and dominance in the black-crowned night heron. This is not surprising since aggression was not observed as an appetitive component for food acquisition in this species. Among domestic fowl both good and poor correlations have been

reported (cf. Guhl, 1953; Masure and Allee, 1934a; Wood-Gush, 1955).

On several occasions during the present experiment it was noticed that an alpha quail would be easily supplanted from the incentive area and that it would spend a considerable amount of time aggressing against others who came near the incentive although not being able to prevent all others from eating (or drinking). Alpha's latency and total time scores were affected as a result of this apparent territorial behavior. In some cases alpha, who was usually a male (see Appendix C), would chase other males around the cage for several minutes at a time, thereby losing eating time. Otherwise he appeared capable of eating, or controlling the food cup, most of the 30-minute session.

Modification of Dominance Behavior

The effects of food and water deprivation on dominance behavior in Phase II were impossible to evaluate because the time-control groups did not provide a constant standard of control behavior upon which changes could be compared. Time-control groups in each Study showed continually changing patterns of dominance within each Sector indicating that any changes found during this time period in the experimental treatment groups could not be attributed to deprivation alone. Table 13 reflects this lack of concordance in Group 3 (the time-control group) of Study 3 by reporting the average Spearman rank-order correlation

TABLE 13.--Average correlation coefficients ($r_{S_{av}}$) for dominance hierarchies measured daily over each phase in the time-control group of Study 3.

	Food Sectors			Water Sectors			
Phase	Sect A	Sect B	Sect C	Sect A	Sect B	Sect C	Morning
I	.00	-.12	-.16	-.10	.17	-.01	-.15
II	-.02	-.10	-.09	-.03	-.14	.02	-.15
III	.08	-.14	-.16	.07	-.04	.20	-.02

coefficients (Siegel, 1956) between all daily sessions for each Phase of each incentive condition. As can be seen all correlations were extremely low and insignificant, indicating the ever changing dominance pattern in this control group.

Analyses of food and water deprived individuals in the experimental groups of both Study 2 and Study 3 showed no indicative changes in DI which might be related to experimental treatment. Likewise no changes in latency, total time or average time per visit measures were found for the experimental Ss to indicate changes in incentive-motivated behavior.

Discussion of Modification of Dominance Behavior

Japanese quail appear to be poor subjects for the study of dominance behavior. Stable dominance relationships are necessarily demanded in order that experimental treatment effects be clearly defined. It is for this reason that the domestic fowl has proven itself a useful experimental subject for the study of social dominance. The quail in this experiment demonstrated continually changing dominance relationships in control conditions.

There is some evidence that food deprivation does not cause greater aggressive activity but rather an increased tolerance for inflicted pain (Andrew, 1957; Collias, 1943, 1950). In other words deprivation may cause a "better" nonaggressive appetitive response, a stronger approach response. Aggression need not be an appetitive response for incentive-acquisition (even when crowded conditions prevail) and in some situations it has been shown to be nonadaptive or unrewarding (Marler, 1956).

In the present experiment food and water deprivation were expected to cause dominance changes in Sector A but not necessarily in Sectors B and C. Dominance in Sector A would be most closely related to the consummatory stimulus being deprived. No such changes were found.

Food and water deprived quail in Study 3 failed to show consequent changes in latency, total time and average time per visit measures. This would suggest that deprivation schedules were not stringent enough to induce behavior modification. However the more stringent deprivation conditions in Study 1 apparently caused a number of birds to die from wounds incurred during aggressive

interactions (Table 1). Perhaps a happy medium exists wherein stable dominance relationships can be maintained under controlled laboratory conditions but this does not seem likely with flocks of eight quail.

GENERAL DISCUSSION

The Stressful Nature of Dominance Studies

Aggression has generally been considered a consummatory response, void of any antecedant appetitive components, a response to "eliciting external stimuli and not (to) endogeneously triggered appetitive actions" (Marler and Hamilton, 1966). Rasa (1971) has recently pointed out that these ideas may be a function of the traditional laboratory experiment wherein aggression is measured in enclosed structures which prevent the subordinate from ever escaping the aggression of the dominant. This situation causes stress between the partners, resulting in the onset of "defence behaviour" which in turn may cause injury to the individuals and mask the appearance of any true appetitive behavior for aggression. Rasa experimentally controlled for these conditions and showed that damsel fish will learn mazes (appetitive behavior) in order to reach an environment where fighting is released.

In the present experiment it was suggested that aggression in Sector C and during the Morning session was void of appetitive features and therefore represented aggression as it has traditionally been defined in consummatory terms (i.e. Allee's social dominance theory).

Appetitive components would not be expected to appear, according to Rasa, since the enclosed environment of the test cages elicited considerable competing ("stress") behavior. However, it is not clear in what form appetitive responses would be expected to appear as in Sector C or in any other part of the cage.

Gartlan (1968) also considered the stressful nature of dominance studies and suggested that dominance hierarchies "may not therefore be a means of reducing aggression within the context of normal group structure, as much as a social artefact, symptomatic of social stress" (p. 102). Avian researchers have generally believed that dominance hierarchies reduce intragroup tension and aggression by allowing ritualized displays to become symbolic for actual aggression (Lorenz, 1963). The hypotheses of Rasa and Gartlan provide a reasonable (and testable) alternative to this traditional explanation. Aggression in flocks of quail in this experiment was clearly not retarded because of an established hierarchy. It was only during sessions when aggression was most abundant and injurious that dominance relationships were most clearly defined. This may reflect the unnatural condition of housing quail in social groups for they are asocial in their wild state (Wetherbee, 1961).

The Appetitive Nature of Aggression

The appetitive nature of aggression has been recognized by several investigators but never labeled as such. Tinbergen (1951) defined appetitive behavior to be variable and plastic as well as purposive whereas consummatory behavior was identified by its stereotyped topography and its "self-exhausting" effects. Tinbergen proposed that there were a number of different types of aggressive behavior, each type being subordinated to a major instinct (e.g. sex, food). Thus aggression was considered a sub-instinct or sub-consummatory response which in turn was an integral part of a larger consummatory class of behavior. Fighting was consummatory because it was characterized by stereotyped response patterns rather than the variable, purposive behavior of appetitive actions. Tinbergen's model of aggression, along with his theory of hierarchically organized neural centers, generated little interest among researchers. More recently, Dimond (1970) has considered the instrumental nature of aggression as being useful in the "service of any prevalent drive system" (e.g. food, sex, status).

Baenninger (1970), using rats, reported high correlations between appetitive food and water competition but she found poor relationships between food and water dominance and dominance measured in spontaneous group situations. In a similar study Ruskin, Thornton and

Corman (1971) found dominance hierarchies to correlate when based on two different measures of food acquisition but nonsignificant relationships were found between food dominance and dominance based on escape from the underwater "dominance tube." The situation specific character of dominance in these rat studies is apparent.

A few studies have reported fighting to have similar response characteristics in different incentive conditions. Hinde (1953) concluded that evidence of this sort in *Parus* preempted operation of different nervous centers for different fighting situations. Andrew likewise noted sexual-fighting and food-fighting in yellowhammers (1957b) and buntings (1957a) to be topographically similar. Andrew drew similar conclusions as Hinde, noting further that "attacks" did not always reduce aggression as a consummatory response would be expected to do. Marler (1955) observed topographically similar aggressive postures in chaffinches fighting over food and perches and concluded that fighting in these two situations was the same phenomenon. However, topographical similarity need not be an accurate reflection of similar causative factors.

In regard to the present experiment, aggression observed in Sectors A and B clearly fit into the appetitive classification since response profiles were not stereotyped across sectors and aggression did not terminate or "exhaust" the food- or water-getting behavior.

Measures of Social Dominance

Social dominance has been measured in several ways. The traditional method (Allee and Foreman, 1955, p. 93) has been to assign dominance to the individual who displaces another and a sociogram of all such displacements is utilized to allocate each flock-member to a rank order based on the number of flockmates dominated. This procedure of assigning ranks restricts differences between individuals and thereby masks the occurrence of oligarchical societies. Triangular and square relationships are also difficult to accommodate into this linear hierarchy.

A second procedure was used by Beilharz and Cox (1967) to characterize social organization in swine. Angular transformations were made on the proportion of animals that submitted to each individual under observation. This provided a quantitative score with an approximately normal distribution but this method suffered from the inconvenience of further statistical manipulations which are, as a rule, not well understood by behavioral scientists.

The dominance index (DI), first introduced by Butterfield and Crook (1968), provides a third and in some ways superior measure of dominance. A quantitative description of dominance should consider (1) whether an individual interacts aggressively with particular others or not, (2) how frequently this individual is dominant and (3) how much more dominant one individual is over another. The

DI satisfies all of these conditions by providing a dominance score along an interval scale.

Japanese quail display a high frequency of triangular and square dominance relationships. This preempted use of the more traditional ways of categorizing dominance (Allee and Foreman, 1955) and raised questions regarding the use of any method based on a linear model. A linear allocation of group members into a rank order assumes that an alpha bird who dominates most of his flockmates will also dominate others with whom he never interacted. Such assumptions may prove erroneous. The use of the dominance index suffers from this criticism as well. Nonlinear relationships in quail flocks were masked when individuals were allocated ranks according to their DI.

Nevertheless, the DI was valid for Sectors B and C during both food and water sessions for it was in these sectors that peck order arrangements were observed. The use of the DI for dominance behavior in Sector A is questionable.

SUMMARY

The present experiment was designed to test the hypothesis that measures of dominance are, in effect, measures of appetitive behavior for incentive acquisition and that dominance status measured at varying distances from the incentive or between incentives might vary as a function of differing motivational properties. It was predicted that incentive-deprivation would raise dominance status when dominance was measured in terms of the aggressive-appetitive component for that incentive.

Evidence which might be considered as negative to the consummatory theory of dominance was obtained during this experiment:

1. There were no apparent changes in dominance status in quail which had been experimentally deprived of food or water, although the experimental effects of food and water deprivation on dominance status were impossible to evaluate because of fluctuating hierarchies in control groups.

2. Dominance hierarchies measured nearest the incentive were expected to correlate highest with measures of consummatory activity (i.e. latency, total time and

average time measures of incentive-acquisition). This was not found.

The results of this experiment also provided considerable support for a naive interpretation of the consummatory theory:

1. Quail used different aggressive responses at different incentive-distances, indicating a changing set of causative factors as the bird moved closer to the food or water. When incentives were absent (Morning session), aggressive-response profiles were similar across these same sectors of the cage.

2. Number of aggressive interactions increased in relation to decreased incentive-distance, indicating the incentive-related character of the aggressive behavior. When incentives were absent (Morning session) amount of aggressive behavior was the same in all sectors of the cage.

3. A trend towards unilateral aggressive interactions was found as incentive-distance increased, reflecting a change from a peck-dominance to a peck order form of society. When incentives were absent (Morning session) unilateral interactions were observed in all sectors of the cage.

4. Dominance hierarchies varied between different incentive-distances and between incentives. Sectors which had common borders showed the most similar dominance

hierarchies, perhaps reflecting a common degree of incentive-related aggression. Hierarchies measured furthest from the incentive showed highest correlation with the nonincentive hierarchies observed during the Morning session.

The results showed that the appetitive and consummatory components of incentive-related aggression in quail are relatively independent of each other. The presence of incentives caused dominance hierarchies and their underlying aggressive responses to vary as a function of distance from the incentive. However, knowledge of dominance status did not allow accurate prediction of consummatory activity.

A naive interpretation of the consummatory theory was not adequate by itself to account for these findings. These data show that appetitive factors are involved but because of crowding around the incentive cups there was also a frustration factor superimposed. The results strongly suggest that the appetitive and consummatory components of quail social dominance behavior are relatively independent processes and that an awareness of these components and their relationships with each other must be carefully considered before a precise understanding of quail social organization in captivity is possible.

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APPENDICES

APPENDIX A

BODY WEIGHTS OF SUBJECTS

TABLE A1.--Mean body weights (grams) of subjects (± one SD) before and after each study and results of t-test for weight change.

Study	Sex	Before Study Began	After Study Ended	p Less than
1	male	110.30 (± 7.95)	108.64 (± 9.65)	ns
	female	117.98 (± 6.86)	115.33 (± 9.66)	ns
2	male	98.38 (±10.06)	108.88 (±12.23)	.01
	female	114.93 (±17.28)	113.24 (±11.88)	ns
3	male	88.97 (± 8.61)	102.62 (± 6.23)	.001
	female	100.25 (± 7.29)	107.97 (±14.99)	ns

ns - not significant ($P > .05$)

APPENDIX B

GENERAL CHARACTERISTICS OF AGGRESSIVE BEHAVIOR IN JAPANESE QUAIL

GENERAL CHARACTERISTICS OF AGGRESSIVE BEHAVIOR

Essentially every aggressive response observed in quail during these three studies caused an escape or avoidance response in the bird being attacked. Aggressive interactions which caused a retaliation by the attacked bird were called "fights." The frequency of fights and their sexual dynamics are shown in Table B1 for all three studies. Since more than 10,000 aggressive interactions were observed in each of the three studies the number of fights represents less than .4% of all aggressive interactions. There were no apparent trends in fights between male-female combinations although the low frequency of these data prevented statistical confirmation over the various phases, incentives and sectors. No changes in dominance were ever observed as a result of a fight!

During Study 3 records were made of supplants involving unknown supplanters or involving two, three or four birds taking part in supplanting another flockmate. These data are presented in Table B2 for each group. Since these data were only intended to reflect the extent of unaccountable supplants in this experiment, differences between groups, phases, sectors and incentives were not

TABLE B1.--Frequency of fights collated over all incentive conditions, phases and groups during each study.

Study	Two Males	Fights Involving Male and Female	Two Females	Total
1	5	13	11	29
2	1	9	18	28
3	33	3	1	37

TABLE B2.--Frequency of supplants involving unknown assailants in Study 3. Data was collated over all incentive conditions, phases, and groups.

Number of Unknown Assailants	Group		
	1	2	3
1	142	99	114
2	395	193	375
3	9	3	12
4	1	1	0
TOTAL	547	296	501

of interest. Table B2 indicates that 1344 supplants occurred where the assailant was unknown or part of a duo, trio or quartet of assailants. This represents about 11% of all aggression observed during Study 3. Only supplants involving a clear "winner" and "loser" in an aggressive interaction were utilized in the analysis of quail social organization.

The measures reported in Table B3 are mean frequency of supplants per dyadic interaction (see discussion of Table 2 for explanation). Since there were 12 dyadic combinations in each of the Male-supplant-Male (listed in Table B3 as Male-Male) and Female-Female classes and 16 in the Male-Female and Female-Male classes, the measure of mean number of supplants per dyadic interaction provides a standard basis for comparison. Food and water sessions were combined as were all phases in order that a general overall picture be provided in Table B3. Combining all sectors in the Morning session provided a "nonincentive" picture of aggressive interactions.

Male-Male Behavior

Incidence of Male-supplant-Male behavior accounted for 35%, 56% and 57% of all aggressive interactions in Sectors A, B and C respectively while in the morning this figure reached 61%. These overall Male-Male interactions proved to be more frequent than any other sex combination within the three Evening Sectors (see Table B4). During the Morning session, however, total Male-Male interactions were not differentiable from total Male-Female activity.

Overall differences in response-type related to incentive-distance were presented in the section on Dominance Behavior as Appetitive Behavior. It was pointed out that quail showed different response profiles in

TABLE B3.--Aggressive behavior displayed by quail over all groups and phases combined in Study 3. Data represent mean frequency of response occurrence per every possible dyadic interaction.

	Male-Male	Male-Female	Female-Male	Female-Female
(a) Evening, Sector A				
Peck	103.92	77.75	46.44	37.17
Push	36.08	30.06	42.88	23.25
Threat	2.67	1.81	.44	.42
Kick	2.50	2.88	.75	1.25
TOTAL	145.17	112.50	90.51	62.09
(b) Evening, Sector B				
Peck	58.17	26.56	5.88	9.42
Push	14.92	9.13	13.63	5.42
Threat	66.00	25.06	2.50	11.42
Kick	.08	.06	.00	.00
TOTAL	139.17	60.75	22.00	26.25
(c) Evening, Sector C				
Peck	13.75	7.19	3.19	5.83
Push	.25	.31	.06	.00
Threat	30.92	8.19	.94	7.42
Kick	.08	.06	.00	.00
TOTAL	45.00	15.75	4.19	13.25
(d) Morning				
Peck	15.00	7.94	2.00	2.75
Push	.08	.00	.00	.00
Threat	22.83	8.13	1.00	1.92
Kick	.08	.13	.00	.00
TOTAL	37.99	16.20	3.00	4.67

TABLE B4.--Results of analyses of aggressive response frequencies (shown in Table B3) between sex combinations within each incentive condition for food and water sessions combined (M = Male, F = Female).

Incentive Condition	Overall Comparisons; Kruskal-Wallis Test	Paired Comparisons, Mann-Whitney U Test					
		M-M vs M-F	M-M vs F-M	M-M vs F-F	M-F vs F-M	M-F vs F-F	F-M vs F-F
Sector A	H = 630.75***	*	***	***	***	***	***
Sector B	H = 30.07***	**	***	***	***	**	**
Sector C	H = 11.92**	**	***	***	ns	***	***
Morning	H = 247.19***	ns	***	**	***	***	ns

$^{*}p < .05$

$^{**}p < .02$

$^{***}p < .002$

ns - not significant

different parts of the cage (see Table 2). These effects are apparent in Table B3 as well. For Male-Male interactions a Friedman X_r^2 test revealed significant differences ($p < .001$) existing between response frequencies in every incentive condition. Subsequent paired-comparisons (Wilcoxin signed-ranks test) for all sex combinations in all incentive conditions produced the results shown in Table B5. In Sector A males tended to supplant other males more frequently with a Peck response than with any other type of aggressive response ($p < .01$).

In Sector B Pecks and Threats were used equally often and both were more frequently given ($p < .01$) than were Pushes. In the outer Sector C Threats were more frequent than all other responses ($P < .01$), with Pecks next in order ($p < .01$). The Morning session was most similar to Sector B in that frequencies of Pecks and Threats could not be differentiated though both were used more often than all other aggressive responses ($p < .01$).

Male-Female Behavior

Male-supplant-Female behavior ranked second to Male-Male behavior in total frequency of occurrence (see Tables B3 and B4), indicating the extensiveness of male-initiated aggressive activity in the Japanese quail. Male-Female aggression proved to occur more frequently than

TABLE B5.--Results of analyses of response frequencies (shown in Table B3) within each sex combination.

Incentive Condition	Sex Combination	Peck vs Push	Peck vs Threat	Peck vs Kick	Push vs Threat	Push vs Kick	Threat vs Kick
Sector A	Male-Male	**	**	**	**	**	ns
	Male-Female	**	**	**	**	**	**
	Female-Male	ns	**	**	**	**	ns
	Female-Female	ns	**	**	**	**	**
Sector B	Male-Male	*	ns	**	**	**	**
	Male-Female	**	ns	**	**	**	**
	Female-Male	**	**	**	**	**	**
	Female-Female	*	ns	**	ns	**	**
Sector C	Male-Male	**	*	**	**	ns	**
	Male-Female	**	ns	**	**	ns	**
	Female-Male	**	**	**	**	**	**
	Female-Female	**	ns	**	**	ns	**
Morning	Male-Male	**	ns	**	**	ns	**
	Male-Female	**	ns	**	**	ns	**
	Female-Male	ns	ns	ns	ns	ns	ns
	Female-Female	**	ns	**	*	ns	*

*p < .05

**p < .01

ns = not significant

all Female-initiated aggression in all three Evening Sectors as well as during the Morning ($p < .02$).

Response profiles for Male-Female behavior reflected those found for Male-Male interactions. Near the incentive cup (Sector A), the Peck was the most observed response ($p < .01$). As the male quail moved further from this area, to Sectors B and C, he gave both the Peck and Threat response to females with equal frequency to the exclusion of other behavior ($p < .01$). Morning sessions yielded this same heavy reliance on Pecks and Threats.

Female-Male Behavior

In Sector A females tended to supplant males more frequently on the average than they did other females ($p < .002$). This tendency reversed in the other two Sectors (B and C, $p < .02$), while in the morning no differences between male and female targets could be detected.

Response profiles shown by females on males were of considerable interest as they reflected marked differences from Male-initiated aggression. Whereas males supplanted females more frequently with Pecks in Sector A, females used Pecks and Pushes equally often to force males out of the incentive area. In Sector B the Push response was most frequently used ($p < .01$). No significant differences were found during the Morning session.

Female-Female Behavior

In Sector A Female-supplant-Female behavior was the least observed of the four sex combinations ($p < .002$). Again Female-Female response profiles are of particular interest for they reflect changes in stimulus control. Females used Pecks and Pushes equally often near the incentive cup (Sector A) followed in order of frequency by Kicks ($p < .01$), then Threats ($p < .01$). In Sector B, Pecks, Pushes and Threats were used with equal frequency while in the outer Sector C and in the Morning session Pecks and Threats were indistinguishable in frequency.

Discussion of General Characteristics of Aggressive Behavior

The aggressive behavior of Japanese Quail has been characterized by Farris (1964), Selinger and Bermant (1967), and Eynon (1968). Eynon's report gives the clearest picture of aggression in quail. He recorded responses emitted by pairs of quail placed together in neutral cages. The dominant bird was characterized by such behaviors as "attack, biting, bristle display, 'churring,' feeding, 'keking,' pecking, preening and strutting," whereas the subordinate more frequently showed such responses as "avoidance run, backward shuffle, crawling under the other, crouch, crowing, distress call and peering" (p. 67).

Aggression recorded in the flock situation of this experiment was considerably different from that described by Eynon for paired-contests. This is not particularly surprizing since different stimulus conditions were operating in the two conditions. A bird being attacked in a flock situation must respond not only to the "attacker" but also so as to avoid other potential attackers in the flock. Thus a full expression of some response categories might be prevented in the flock situation. This, in fact, was found to be the case.

The dominant quail in the present experiment (i.e., the aggressor in a particular dyadic interaction) corresponded to Eynon's in terms of "attack, biting (or head, shoulder grabs) and pecking" behavior. "Bristle displays, churring, keking and strutting" have also been observed by this researcher in paired contests but only rarely in the larger flock situation. If "bristle displays" occurred in the flock condition they were too rapid for precise identification. Eynon does not mention whether "feeding and preening" were performed before or after aggressive contact. "Churrs" consisted of low-frequency component tones which were difficult to localize in the flock condition. "Keks" had a number of behavioral accompaniments as well as higher frequency tones which made it more easily localized. A "keking" quail was usually in either an aggressive crouch ready to attack or actually

attacking other quail in the cage. There were also movements of the throat which accompanied the "kek." Except in sexual encounters, vocalizations are not reported in this paper because of the high probability of error in identifying the vocalizer. Nevertheless, "churrs" were rare during this experiment and their few occurrences were as components of the Threat sequence. "Keking" vocalization often characterized quail which appeared to go "crazy" during a session, running around the cage Pecking and Threatening essentially every flockmate. The stimulus for this sudden Pecking and Threatening behavior was never understood. Its effect was to cause many of the attacked birds to "pop" over and over again into the ceiling of the cage, resulting in numerous wounds. This frantic Pecking and Threatening behavior often ended in exhaustion.

Quail aggressive behavior in this experiment was primarily a male-initiated response. This effect was accentuated when the quail were further from the incentive, with males providing 81% and 78% of the aggression in Sectors B and C, respectively.

It was interesting to find that males in Sector B primarily used the Peck and Threat to supplant other females while females supplanted males primarily with the Push response. Some of the most ferocious aggression occurred here in Sector B and this tendency on the part

of females not to Peck other males was considered to be an avoidance of aggressive interaction. The relative effects of each type of aggressive response was not measured but it appeared that a Peck signified greater expression of dominance than a Push, causing greater degrees of avoidance behavior.

Again in Sector C males used both Pecks and Threats to supplant females while females either were unable to utilize the Threat or found it unrewarding to threaten other males. The effectiveness of a Threat lies most likely in the individual's conditioned aversive properties acquired during successful dominance behavior. Since it will later be shown that females ranked lower, on the average, than males (see Appendix C) it follows that their success as "threatening" stimuli would be lower.

APPENDIX C

DOMINANCE CORRELATED VARIABLES

DOMINANCE CORRELATED VARIABLES

Relationship Between Dominance Rank and Sex

Table C1 reports mean social ranks for all males combined and all females combined in Study 3. Results of the Mann-Whitney U test (Siegel, 1956) for differences between sexes showed that males were significantly higher in rank (lower numerically) in every case but one (Sector B during Water sessions). Similar analyses were not made on Study 2 because of unequal group sizes.

TABLE C1.--Mean dominance rank for males and females in Study 3. Means were computed from data collated over all phases and, for the morning session, overall sectors as well. Results of Mann-Whitney U test for differences between sexes in each incentive condition are also shown.

	Food Sectors			Water Sectors			
	Sect A	Sect B	Sect C	Sect A	Sect B	Sect C	Morning
Males	3.84*	3.46*	3.46*	3.86**	3.60	3.18	3.42**
Females	5.16	5.54	5.54	5.14	5.40	5.82	5.58

$^{*}p < .029$

$^{**}p < .014$

The percentage of sessions in which males assumed the alpha position in Study 3 is shown in Table C2. Sexual differences were detected by using the binomial test (Siegel, 1956). Males clearly held the number one rank more frequently than did females. However, no sexual differences were ever found in Sector A during water presentation or in any Water Sector for Group 2.

TABLE C2.--Percentage of sessions over all phases combined in Study 3 in which males were alpha. Results of binomial test of significance are also shown.

	Food Sectors			Water Sectors			
Group	A	B	C	A	B	C	Morning
1	.37	.88***	.77*	.55	.75*	.80**	.88***
2	.83**	.94***	.72*	.65	.67	.64	.73
3	.83**	.88***	1.00***	.68	.81**	.94***	.78**

*p < .05
**p < .01
***p < .001

Relationship Between Dominance Rank and Weight

Table C3 reports correlations between dominance index and weight for Studies 2 and 3. Although a tendency towards negative relationships was apparent, as would be expected since males were higher in rank and weighed less,

TABLE C3.--Correlations between Dominance Index and weight in each incentive condition for both Study 2 and Study 3.

		Food sessions			Water sessions			
Group	Phase	Sect A	Sect B	Sect C	Sect A	Sect B	Sect C	Morning
				Study 2				
1	I	.221	.787*	.082	.514	.659	.602	.770*
	II	.814*	.123	-.350	-.351	-.374	-	-.393
	II	.668	-.069	-.533	-.293	-.494	-.448	-
2	I	.133	-.174	-	-.251	-.304	-	-.303
	II	-.309	-.093	-	-.166	-.043	-.142	-.103
	III	.577	-	-	.511	-.063	.198	-.000
3	I	.671	.238	-	.054	.063	-	.640
	II	.483	.145	.030	.210	.094	.045	.132
	III	.116	-.189	.071	.354	.090	-.278	.086
Column Mean		.426	.130	-.154	.075	-.035	.005	.126
				Study 3				
1	I	-.325	-.709*	-.276	-.357	-.544	-.472	-.563
	II	.474	-.357	-.171	-.263	-.247	-.556	-.086
	III	.397	-.085	.038	.350	-.269	-.303	.029
2	I	.226	.223	-.151	-.609	-.111	.217	.017
	II	-.048	.222	.000	-.502	.271	-	.117
	III	.622	.485	-.416	.306	.343	-.356	.210
3	I	-.118	-.015	-.227	.040	-.062	-	-.163
	II	.152	-.270	-.353	-.667	-.498	-.424	-
	III	.377	-.367	-	-.475	-.263	-.603	-.441
Column Mean		.213	-.115	-.199	-.271	-.165	-.374	-.123

*p .05.

.707 and .834 needed for the first correlation to be significant at the .05 and .01 levels, respectively.

essentially all correlations were found to be nonsignificant. Overall mean correlations ranged from -.357 to .375 indicating weight to be a poor predictor of dominance status in all Sectors of all incentive conditions.

Relationship Between Dominance Rank and Sexual Behavior

There were 103 instances of heterosexual behavior in Study 3, only one instance in Study 2 and none in Study 1. The relationship between sexual behavior and dominance status was analyzed by first ranking males and females within their own sex groups (n=4) according to dominance status and then correlating ranks of each male with the rank of the female partner involved in the sexual relationship. Correlations of -.007, .344 and .106 were obtained for Groups 1, 2 and 3, respectively, during all sessions combined of Study 3.

The relationship between social rank and frequency of sexual behavior was determined by first ranking males and females within their own sex group (from one to four) according to their mean DI over all phases combined in Study 3. These dominance rank orders were then correlated with rank orderings of males and females based upon frequency of sexual behavior. Correlations obtained for males and females were -.986 and -.788, respectively. Only the males' correlation was significant ($p < .02$).

Sexual behavior in the male quail is characterized by a sequence of measurable components (Otis, 1968). The colorful courtship phase consists of Neck-and-Body-Tonus, Toe-Walk, and Churring (a vocalization) activity followed in order by Body-Orient, Neck-Grab, Mount and Tread. There may be chase components in the sexual sequence but these were not counted here because of their possible role in other behavior sequences (e.g., aggression). The question arose as to whether more dominant males were exhibiting more sexual-response components than others. In order to answer this question the sexual-response components were given values from 1 to 7 according to their sequential position in the chain, with Neck-and-Body-Tonus given the value of one. Dominance rank was then correlated with the observed sexual components during a particular sexual relationship. Correlations of .328, -.353 and .307 were obtained for Groups 1, 2 and 3 of Study 3.

It was of secondary interest that the 13 instances of courtship behavior never went beyond the Body Orient stage. That is, Mounting and Tread components of the sexual sequence were never preceded by these "courtship" responses. The role of the Neck-and-Body-Tonus and Toe Walk responses as sexual components should perhaps be questioned.

Discussion of Dominance-Correlated Variables

Male quail were clearly the more dominant sex during this experiment (Table C1). Male dominance is a well documented phenomenon in other gallinaceous species, particularly in the domestic fowl (Domm, 1939; Guhl, 1950; Masure and Allee, 1934a,b). Some avian researchers have felt this male dominance effect to be so phylogenetically widespread as to warrant the concept of "sexual dominance" apart from social dominance (Armstrong, 1965; Guhl, 1950; Noble, 1939; Wynne-Edwards, 1962). Since many species seem to require a dominating male for successful copulation with females, this widespread male dominance phenomenon is viewed as a highly adaptive feature (Armstrong, 1965).

Among captive Japanese quail the female is capable of assuming the alpha position (Table C2), though never to the same extent as the male quail. There was no evidence in this experiment that male and female quail had separate social orders as has been found in turkeys (Hale, Schleidt and Schein, 1969) and chickens (Guhl, 1953; Guhl and Fisher, 1969).

Since male quail held the more dominant ranks in the flock it is not surprising that body weight was negatively correlated with dominance rank albeit non-significantly so. Male quail ranged in average weight

from 88 to 108 grams while females ranged from about 100 to 117 grams (Table A1, Appendix A).

The relationship between weight and social status is not at all clear in the domestic fowl. Both a lack of correlation (Collias, 1943; Potter, 1949) and positive correlations (Craig, Ortman and Guhl, 1965) have been reported. Fennell found dominant game cocks to be the largest birds while Shoemaker (1939) found no relationship between dominance and weight in canaries.

There was no evidence that a dominating male quail was an essential factor for copulation. Female quail showed no preference for particularly ranked males. High ranking males showed the most sexual behavior while an apparent trend towards this relationship proved insignificant in females.

Among Gambel's quail it is known that the female will form an attachment to the more aggressive males (Gorsuch, 1934). Similar findings have been reported in other avian species (Heinroth, 1911, for ruddy shield-ducks; Murchison, 1935a,b for domestic fowl) although it is also known that a highly aggressive male may deter the female (see review in Armstrong, 1965). There was some suggestion of this latter finding in Study 1 where extent of aggression appeared to be higher throughout the day. There were no sexual responses observed during observation session of Study 1.

In domestic fowl it is known that dominant males will fight subordinates who are attempting to mate with hens. Guhl, Collias and Allee (1945) found the resulting suppression of sexual behavior to persist even when the dominants were removed from the group. They labeled this phenomenon "psychological castration." On many occasions subordinate quail were attacked by superiors while mating but these low ranking males were rarely, if ever, supplanted from their sexual activity. Though records of this event were never kept, it was apparent that these low ranking males (as based on aggression during food- or water-getting behavior) were "unsupplantable" while performing the consummatory sequence of sexual behavior.

It should be recalled that measures of sexual behavior during Study 3 were relatively few (103) due, perhaps, to the imposed food and water deprivation schedules. It was most interesting to find that courtship responses were never observed in sequence with copulatory behavior. This may reflect an artefact of the Study itself. An investigation of food deprivation effects on somponents of the male quail's sexual behavior would be of considerable interest.

APPENDIX D

INTRAGROUP RESPONSE MATRICES
FOR STUDY 3

INTRAGROUP RESPONSE MATRICES
FOR STUDY 3

Tables D1 through D21 show frequency of dyadic interactions in all groups during Study 3. Subjects are identified by sex (M means male, F means female) and placement of leg bands (MLL means two bands on left foot of male; MRR means two bands on right foot of male; M means a male with no leg bands; MLR means one band on each leg of a male). Subjects listed in the left column of each table represent aggressors and dominance interactions (i.e., where supplants occur by the aggressor) with each of the other seven flock members are found by reading across the row for each subject. All types of aggressive responses have been combined in these tables.

The mean DI for each subject is shown in the column to the right of each table. This mean DI was computed as an average of the DIs measured over the six days of each phase. It was <u>not</u> computed directly from the accumulated response frequencies shown in Tables D1 through D21.

TABLE D1.--Intragroup response matrices for Group 1 showing aggressive supplants (by Ss in left column) during Evening Food sessions in Sector A for Phases I(a), II(b) and III(c) of Study 3. Each S's mean DI, computed as an average of the six daily DIs measured during each phase in this incentive condition, is shown as well. Asterisks (*) denote those Ss Water-deprived during Phase II.

	M	MLL	MRR	MLR	F	FLL	FRR	FLR	Mean DI
(a) Phase I:									
M*	-	23	8	9	3	11	3	7	.31
MLL	23	-	24	92	4	35	15	12	.41
MRR	25	68	-	61	3	35	11	14	.62
MLR	14	83	34	-	3	31	7	12	.48
F	6	10	4	12	-		3	4	.28
FLL	10	39	7	26		-	2	3	.30
FRR*	1	9	6	3	1	5	-	1	.27
FLR	3	19	17	10	2	6	3	-	.40
(b) Phase II:									
M*	-		2			2	1	3	.10
MLL	2	-	1	19	14	15	3	20	.40
MRR		1	-	6	2	5	2	4	.20
MLR	6	11	13	-	8	6	1	50	.34
F		5	5	7	-	7		7	.25
FLL	3	15	4	15	12	-	3	9	.34
FRR*		1	1	2	1		-	2	.13
FLR	11	14	9	30	13	11	1	-	.47
(c) Phase III:									
M*	-	12	6	11	1	4		5	.27
MLL	12	-	14	28	34	16	5	28	.43
MRR	5	7	-	10	3	5		4	.27
MLR	19	33	23	-	7	8		32	.42
F	10	31	3	9	-	4	1	7	.30
FLL	12	17	7	12	12	-	3	15	.52
FRR*		2	3		1		-	2	.13
FLR	11	26	10	17	9	6	4	-	.42

TABLE D2.--Intragroup response matrices for Group 1 showing aggressive supplants (by Ss in left column) during Evening Food sessions in Sector B for Phases I(a), II(b) and III(c) of Study 3. Each S's mean DI, computed as an average of the six daily DIs measured during each phase in this incentive condition, is shown as well. Asterisks (*) denote those Ss Water-deprived during Phase II.

	M	MLL	MRR	MLR	F	FLL	FRR	FLR	Mean DI
(a) Phase I:									
M*	-			3		1	1	1	.10
MLL	4	-	9	1	1	4		3	.24
MRR	17	13	-	25	3	5	2	11	.61
MLR	2	7	5	-	4	2	2	10	.39
F	1	1	1	1	-	1		3	.15
FLL		1	6	3	3	-	2		.27
FRR*		1	3				-		.07
FLR		2	1	1				-	.05
(b) Phase II:									
M*	-				1			2	.07
MLL		-	1	1	3	2			.15
MRR	2		-	1	4	3	10	13	.34
MLR	4	4	85	-	5	2	3	3	.50
F	1		1	1	-	1	1		.09
FLL	2	5		1	2	-		1	.17
FRR*							-		.02
FLR	2		3	2	4	3		-	.20
(c) Phase III:									
M*	-		2		1	2		1	.11
MLL	2	-	1	6	3	2	1	1	.27
MRR	1	1	-		2	2	4	1	.20
MLR	2	6	53	-	6	2	4	3	.47
F	1				-			1	.05
FLL	2		2	1		-	1	3	.15
FRR*							-		.00
FLR	1	2	1	1	6	2	2	-	.22

TABLE D3.--Intragroup response matrices for Group 1 showing aggressive supplants (by Ss in left column) during Evening Food sessions in Sector C for Phases I(a), II(b) and III (c) of Study 3. Each S's mean DI, computed as an average of the six daily DIs measured during each phase in this incentive condition, is shown as well. Asterisks (*) denote those Ss Water-deprived during Phase II.

	M	MLL	MRR	MLR	F	FLL	FRR	FLR	Mean DI
(a) Phase I:									
M*	-			1			1	6	.07
MLL		-							.00
MRR	7	1	-	5	1	1	6		.28
MLR				-			1	1	.05
F					-		2		.05
FLL						-		1	.02
FRR*						1	-		.02
FLR	1					1		-	.05
(b) Phase II:									
M*	-	2			1	2			.08
MLL	3	-					2		.08
MRR	2	11	-		4	2	11	3	.28
MLR	3	1	43	-				1	.22
F	1				-	1	1		.07
FLL		9	1			-			.11
FRR*		1					-		.01
FLR	1				2	3	6	-	.21
(c) Phase III:									
M*	-				2	1			.07
MLL		-	3	4	1	1	2		.15
MRR		2	-			1	2	1	.14
MLR	1	5	11	-	1	1			.24
F	2	4	2	1	-	6		1	.16
FLL					5	-	2		.06
FRR*		1			2		-		.04
FLR	1	2		1	1	1	2	-	.16

TABLE D4.--Intragroup response matrices for Group 1 showing aggressive supplants (by Ss in left column) during Evening Water sessions in Sector $\bar{A}$ for Phases I(a), II(b) and III(c) of Study 3. Each S's mean DI, computed as an average of the six daily DIs measured during each phase in this incentive condition, is shown as well. Asterisks (*) denote those Ss Water-deprived during Phase II.

	M	MLL	MRR	MLR	F	FLL	FRR	FLR	Mean DI
(a) Phase I:									
M*	-	1	2	3		4	3	2	.23
MLL	1	-	2			2		2	.15
MRR	5		-	5		10	6	10	.30
MLR	5		11	-		5	5	7	.27
F					-	1	2		.07
FLL	8	1	6	1	3	-	6	4	.27
FRR*	2		7	4		4	-	4	.25
FLR	4		11	8		3	1	-	.23
(b) Phase II:									
M*	-	1	6		1	3	8	3	.21
MLL		-		1				1	.05
MRR	4		-	1	4	2	6	7	.32
MLR	2		3	-	1	2	4	9	.31
F	3	1	1		-	1	5	7	.26
FLL	5		2	2	4	-	4	2	.21
FRR*	5		4	1	1	1	-	5	.23
FLR	6		5	2			4	-	.16
(c) Phase III:									
M*	-		4	4	1		2	4	.19
MLL		-						1	.02
MRR	2	1	-	2	1	2	2	7	.18
MLR	3		5	-	2		1	20	.25
F	3		3	4	-	3	4	3	.30
FLL			1		1	-	1	7	.17
FRR*	1		1	2			-		.07
FLR	3		12	8	2	2	2	-	.26

TABLE D5.--Intragroup response matrices for Group 1 showing aggressive supplants (by *Ss* in left column) during Evening Water sessions in Sector B for Phases I(a), II(b) and III(c) of Study 3. Each *S*'s mean DI, computed as an average of the six daily DIs measured during each phase in this incentive condition, is shown as well. Asterisks (*) denote those *Ss* Water-deprived during Phase II.

	M	MLL	MRR	MLR	F	FLL	FRR	FLR	Mean DI
(a) Phase I:									
M*	-		2	1		3	2		.16
MLL		-	1	1			2		.10
MRR	16	1	0	25	6	19	7	9	.63
MLR	1	3	2	-	2	2		1	.18
F	2			1	-	2			.07
FLL	2	2	7	1	4	-	2	3	.29
FRR*		2	2			2	-		.06
FLR	2		2	1			2	-	.11
(b) Phase II:									
M*	-		3	1	2		1		.13
MLL		-		1					.02
MRR	4	1	-	1	11	10	1	9	.37
MLR	2		19	-	1		1		.23
F	4	1	4		-	2	1	2	.20
FLL	2			1	1	-	1	2	.14
FRR*	3		2		3	1	-	2	.18
FLR	2	1	4	3	2		2	-	.18
(c) Phase III:									
M*	-			2	2	3	1	2	.14
MLL	1	-				2			.07
MRR	1	1	-		3	6	1	3	.22
MLR	2	1	28	-	1			2	.25
F	3	3	3	1	-	3		1	.18
FLL			2			-		3	.10
FRR*	1	1					-	1	.06
FLR		1		5	1	2		-	.14

TABLE D6.--Intragroup response matrices for Group 1 showing aggressive supplants (by Ss in left column) during Evening Water sessions in Sector $\bar{C}$ for Phases I(a), II(b) and III(c) of Study 3. Each S's mean DI, computed as an average of the six daily $\overline{DI}$s measured during each phase in this incentive condition, is shown as well. Asterisks (*) denote those Ss Water-deprived during Phase II.

	M	MLL	MRR	MLR	F	FLL	FRR	FLR	Mean DI
(a) Phase I:									
M*	-	1		1				1	.07
MLL		-							.00
MRR	17	6	-	3	3	1	2		.38
MLR		2		-	1				.07
F				1	-				.02
FLL		1		1		-			.05
FRR*					1		-		.02
FLR								-	.00
(b) Phase II:									
M*	-	1			1			1	.07
MLL		-							.00
MRR	1	5	-		3		7	18	.27
MLR	3	1	22	-			1	1	.24
F					-		1		.02
FLL			1			-		1	.05
FRR*					1		-		.02
FLR	1	3					1	-	.06
(c) Phase III:									
M*	-				3	2			.07
MLL	2	-		5		1	1	2	.14
MRR	1	1	-		1		2	1	.14
MLR		6	10	-	1				.16
F	1	1		1	-		1		.10
FLL		1			4	-			.07
FRR*							-		.00
FLR		2			1		2	-	.08

TABLE D7.--Intragroup response matrices for Group 1 showing aggressive supplants (by Ss in left column) during Morning sessions (all sectors combined) for Phases I(a), II(b) and III(c) of Study 3. Each S's mean DI, computed as an average of the six daily DIs measured during each phase in this incentive condition, is shown as well. Asterisks (*) denote those Ss Water-deprived during Phase II in the Evening sessions.

	M	MLL	MRR	MLR	F	FLL	FRR	FLR	Mean DI
(a) Phase I:									
M*	-	1		2			1	1	.08
MLL		-	1		1			1	.07
MRR	33	7	-	5	14	6	6	9	.72
MLR	4	19	3	-	4	3	5	9	.55
F					-	1		1	.05
FLL		2				-		2	.07
FRR*		1			1	1	-		.07
FLR								-	.00
(b) Phase II:									
M*	-					2		1	.05
MLL	2	-			2		2		.08
MRR	7	9	-	2	11	3	6	17	.07
MLR	13	7	141	-	1	1	3	16	.53
F	2				-		2		.09
FLL		2			2	-		1	.07
FRR*		1			2		-	1	.04
FLR	1	1		2	2	2	4	-	.20
(c) Phase III:									
M*	-			1	7				.05
MLL	4	-	1	4	6	2		1	.24
MRR	1	3	-		1	2	2		.22
MLR	12	14	22	-	1	1	4	4	.44
F		1			-				.01
FLL		2		2	1	-			.12
FRR*				1		1	-		.05
FLR	2	4	3	3	1	1		-	.29

TABLE D8.--Intragroup response matrices for Group 2 showing aggressive supplants (by Ss in left column) during Evening Food sessions in Sector A for Phases I(a), II(b) and III(c) of Study 3. Each S's mean DI, computed as an average of the six daily DIs measured during each phvse in this incentive condition, is shown as well. Asterisks (*) denote those Ss Food-deprived during Phase II.

	M	MLL	MRR	MLR	F	FLL	FRR	FLR	Mean DI
(a) Phase I:									
M	-	24	11	18	25	12	31	27	.57
MLL*	17	-		2	1		1	6	.18
MRR	33	5	-	3	5	2	15	7	.41
MLR	6	4	4	-		3		4	.21
F	10	2	4		-		4	5	.23
FLL*	16	2	2		1	-			.18
FRR	37	2	14	5	4	3	-	7	.41
FLR	10	3	4	5		1	5	-	.21
(b) Phase II:									
M	-	31	41	9	17	24	22	24	.55
MLL*	22	-	12	7		6	3	2	.35
MRR	40	19	-	6	7	8	13	19	.54
MLR	8	4	8	-	1	12	3	5	.37
F	7	1	4	1	-	3		1	.16
FLL*	19	4	14	8	2	-	2	4	.35
FRR	16	6	7	2		7	-	6	.36
FLR	13	3	4	7	2	2	5	-	.33
(c) Phase III:									
M	-	10	42	7	1	5	14	14	.38
MLL*	16	-	9	3	7	1	6	2	.26
MRR	45	20	-	8	7	6	7	28	.49
MLR	3	5	11	-	1	2	2	2	.31
F	3	2	3		-		3		.11
FLL*	8	1	6	2	1	-	1	3	.27
FRR	5	5	7	5	2	2	-	3	.26
FLR	3	1	10	3		2	2	-	.16

TABLE D9.--Intragroup response matrices for Group 2 showing aggressive supplants (by Ss in left column) during Evening Food sessions in Sector B for Phases I(a), II(b) and III(c) of Study 3. Each S's mean DI, computed as an average of the six daily DIs measured during each phase in this incentive condition, is shown as well. Asterisks (*) denote those Ss Food-deprived during Phase II.

	M	MLL	MRR	MLR	F	FLL	FRR	FLR	Mean DI
(a) Phase I:									
M	-	38	49	52	32	28	22	28	.86
MLL*		-	1	2	2			1	.10
MRR	3	11	-	9	4	6	6	3	.42
MLR	35	9	15	-	16	12	4	30	.38
F	2	3		3	-	13	2	17	.22
FLL*						-		1	.02
FRR	1		2			3	-	1	.09
FLR	2			2	8	1		-	.13
(b) Phase II:									
M	-	41	29	3	5	13		2	.48
MLL*	1	-			2				.03
MRR	1	22	-	2	1	4	1	3	.29
MLR	32	11	3	-	3	2	2	7	.44
F	1				-	1		1	.07
FLL*				1		-			.02
FRR		1	1		4	2	-		.12
FLR	1		1	1	4		2	-	.12
(c) Phase III:									
M	-	8	13	1	3	5		4	.31
MLL*		-	1		1	1		1	.08
MRR	14	41	-	10	8	15	5	14	.47
MLR	5	3		-	1				.12
F	1	1	1		-	3	2	10	.12
FLL*					1	-			.02
FRR					1	1	-		.05
FLR	2	4	6	1	21	25	4	-	.36

TABLE D10.--Intragroup response matrices for Group 2 showing aggressive supplants (by Ss in left column) during Evening Food sessions in Sector C for Phases I(a), II(b) and III(c) of Study 3. Each S's mean DI, computed as an average of the six daily DIs measured during each phase in this incentive condition, is shown as well. Asterisks (*) denote those Ss Food-deprived during Phase II.

	M	MLL	MRR	MLR	F	FLL	FRR	FLR	Mean DI
(a) Phase I:									
M	-	2	5	2	2	1		3	.27
MLL*		-							.00
MRR	3		-	3	1	1			.09
MLR	2	2	4	-	4	7	2	6	.33
F					-			1	.02
FLL*						-			.00
FRR							-		.00
FLR			1		1	5	3	-	.12
(b) Phase II:									
M	-	1	9			1			.12
MLL*		-			1				.02
MRR		2	-		3	1			.12
MLR	4		3	-	2			1	.17
F					-				.00
FLL*						-			.00
FRR							-		.00
FLR					6	1	2	-	.10
(c) Phase III:									
M	-	1	1		1				.07
MLL*	1	-					1		.05
MRR		1	-						.02
MLR				-				1	.02
F					-			4	.05
FLL*					1	-			.02
FRR		1			2		-		.07
FLR		1	1		26	4	7	-	.24

TABLE D11.--Intragroup response matrices for Group 2 showing aggressive supplants (by Ss in left column) during Even Water sessions in Sector A for Phases I(a), II(b) and III(c) of Study 3. Each S's mean DI, computed as an average of the six daily DIs measured during each phase in this incentive condition, is shown as well. Asterisks (*) denote those Ss Food-deprived during Phase II.

	M	MLL	MRR	MLR	F	FLL	FRR	FLR	Mean DI
(a) Phase I:									
M	-	5	2		1	1	1	8	.22
MLL*	10	-	6	4	1	4	3	6	.35
MRR	3	5	-	4		2		8	.23
MLR	1	4	3	-	1	1		8	.20
F	3	2	1		-	1	2	2	.19
FLL*	2	4	2			-	3	2	.21
FRR		3	1	2		2	-	3	.17
FLR	5	1	5	9	4	2	2	-	.29
(b) Phase II:									
M	-	1	3			5		2	.12
MLL*	3	-	4		1	4	2	2	.27
MRR	6	1	-	1		3	1	8	.22
MLR		1	1	-	2	3	2	2	.18
F		1		1	-	1			.06
FLL*	6	2	7	3	1	-		2	.24
FRR	2	3		1			-		.11
FLR	1		8	1		2		-	.16
(c) Phase III:									
M	-	2	3	2			1	2	.11
MLL*	1	-	2	2					.06
MRR	9	3	-	4		1	1	5	.25
MLR	3		1	-	2			3	.12
F				1	-				.07
FLL*	2	2	3	1	1	-			.19
FRR	3			1		1	-		.11
FLR	7	1	2				1		.13

TABLE D12.--Intragroup response matrices for Group 2 showing aggressive supplants (by Ss in left column) during Evening Water sessions in Sector $\bar{B}$ for Phases I(a), II(b) and III(c) of Study 3. Each S's mean DI, computed as an average of the six daily DIs measured during each phase in this incentive condition, is shown as well. Asterisks (*) denote those Ss Food-deprived during Phase II.

	M	MLL	MRR	MLR	F	FLL	FRR	FLR	Mean DI
(a) Phase I:									
M	-	3	4	1		1	1	2	.20
MLL*	5	-	1				2		.09
MRR	5	6	-	6	4	3	1	5	.26
MLR	4	10	3	-		1	5	7	.34
F					-				.05
FLL*	1	2				-			.05
FRR		1		1			-		.04
FLR	1	1		5	1		1	-	.14
(b) Phase II:									
M	-	7	5	5	3	1		2	.32
MLL*	3	-	3	2	1	3			.15
MRR	5	13	-	2	1	3		5	.26
MLR	8	7	3	-		2		6	.34
F	3	2	1	1	-			3	.16
FLL*	2	2	10	1		-	1	2	.26
FRR	1	3		1			-		.10
FLR	4	1	3	3	3	1	1	-	.20
(c) Phase III:									
M	-	2	10	5	2	1	5	7	.32
MLL*	4	-	2		1	1	1		.11
MRR	15	14	-	4	2		3	2	.32
MLR	3	2	5	-	1	3	1	2	.22
F	2	1			-	2	1	5	.18
FLL*	2	3	1	1		-	3		.16
FRR			3	2		2	-		.12
FLR	7	2	3	9	1	2	5	-	.41

TABLE D13.--Intragroup response matrices for Group 2 showing aggressive supplants (by Ss in left column) during Evening Water sessions in Sector C̄ for Phases I(a), II(b) and II(c) of Study 3. Each S's mean DI, computed as an average of the six daily DIs measured during each phase in this incentive condition, is shown as well. Asterisks (*) denote those Ss Food-deprived during Phase II.

	M	MLL	MRR	MLR	F	FLL	FRR	FLR	Mean DI
(a) Phase I:									
M	-	1	5	1	1		2		.15
MLL*	1	-			2				.07
MRR	1	9	-	2	5	1	1	3	.25
MLR	1	1		-					.04
F					-			1	.02
FLL*						-			.00
FRR					1		-		.02
FLR					2			-	.02
(b) Phase II:									
M	-		2						.05
MLL*		-		2					.02
MRR	1	5	-	2	1	1			.12
MLR				-					.00
F			1	1	-			2	.09
FLL*						-			.00
FRR							-		.00
FLR								-	.00
(c) Phase III:									
M	-				1				.02
MLL*	7	-	1			3			.07
MRR	4	1	-						.09
MLR	1	1		-	1				.07
F					-	1			.02
FLL*						-			.00
FRR							-		.00
FLR	1	5	1	1	11	12	5	-	.29

TABLE D14.--Intragroup response matrices for Group 2 showing aggressive supplants (by Ss in left column) during Morning sessions (all sectors combined) for Phases I(a), II(b) and III(c) of Study 3. Each S's mean DI, computed as an average of the six daily DIs measured during each phase in this incentive condition, is shown as well. Asterisks (*) denote those Ss Food-deprived during Phase II during the Evening sessions.

	M	MLL	MRR	MLR	F	FLL	FRR	FLR	Mean DI
(a) Phase I:									
M	-		4	1				2	.10
MLL*	1	-			2				.05
MRR	1	1	-	1		1			.05
MLR	4	3	3	-	8	8	6	2	.35
F					-			1	.05
FLL*						-		1	.02
FRR					1		-		.02
FLR								-	.00
(b) Phase II:									
M	-					1			.02
MLL*		-				1			.02
MRR		2	-			2			.10
MLR				-				1	.02
F					-				.00
FLL*						-			.00
FRR						1	-		.02
FLR							1	-	.02
(c) Phase III:									
M	-	1		1					.05
MLL*	1	-							.02
MRR		3	-			1			.07
MLR				-					.00
F					-			1	.02
FLL*						-			.00
FRR				2			-		.02
FLR					2	4	3	-	.08

TABLE D15.--Intragroup response matrices for Group 3 (time controls) showing aggressive supplants (by Ss in left column) during Evening Food sessions in Sector A for Phases I(a), II(b) and III(c) of Study 3. Each S's mean DI, computed as an average of the six daily DIs measured during each phase in this incentive condition, is shown as well.

	M	MLL	MRR	MLR	F	FLL	FRR	FLR	Mean DI
(a) Phase I:									
M	-	7	9	2	14	6	13	9	.36
MLL	11	-	7	2	12	11	8	24	.54
MRR	9	3	-	15	13	16	41	29	.44
MLR	2		5	-	1	1		1	.11
F	13	6	11	1	-	2	4	15	.34
FLL	2	1	7			-	2		.11
FRR	9	9	16	2	15	2	-	21	.36
FLR	13	16	12	1	23	5	15	-	.44
(b) Phase II:									
M	-	3	11	23	17	9	17	12	.46
MLL	11	-	6	12	12	8	11	8	.62
MRR	7	1	-	14	6	5	8	7	.40
MLR	7	5	8	-	1	5	7	1	.22
F	13	7	7	9	-	16	7	7	.45
FLL	5	3		6	6	-		2	.24
FRR	12	13	10	18	7	7	-	7	.47
FLR	6	5	6	4	7	8	11	-	.39
(c) Phase III:									
M	-	6	13	18	17	11	14	27	.46
MLL	12	-	2	13	11	9	16	11	.50
MRR	4	6	-	8	11	12	12	4	.42
MLR	6			-			3	6	.08
F	12	7	8		-	13	2	15	.22
FLL	6	3	4	3	4	-	2	7	.28
FRR	6	8	7	13	4	12	-	18	.43
FLR	18	5	8	6	17	16	15	-	.45

TABLE D16.--Intragroup response matrices for Group 3 (time controls) showing aggressive supplants (by Ss in left column) during Evening Food sessions in Sector B for Phases I(a), II(b) and III(c) of Study 3. Each S's mean DI, computed as an average of the six daily DIs measured during each phase in this incentive condition, is shown as well.

	M	MLL	MRR	MLR	F	FLL	FRR	FLR	Mean DI
(a) Phase I:									
M	-		1					1	.03
MLL	3	-	2	5	1	1	1	2	.22
MRR	60	34	-	75	34	50	14	9	.78
MLR			1	-	1	2			.07
F	3			1	-	1	1		.11
FLL	1	1	1			-			.04
FRR	1		2		3	1	-	1	.15
FLR	8	5	3	3	16	6	1	-	.26
(b) Phase II:									
M	-				1				.02
MLL	1	-	3	2	1		2	1	.21
MRR	3		-	1		2			.09
MLR	59	23	89	-	32	38	2	6	.88
F	2				-	1			.07
FLL				1	1	-	1		.03
FRR		1	4		2	3	-		.22
FLR								-	.00
(c) Phase III:									
M	-	4	25	19	5	10	3	3	.34
MLL	2	-		1	1	2	4	4	.25
MRR	1		-		1		2		.10
MLR	12	14	26	-	2	13	5		.51
F				1	-	1			.05
FLL			2			-			.05
FRR	4		1	1		3	-	4	.16
FLR	1	1	1		5	2		-	.15

TABLE D17.--Intragroup response matrices for Group 3 (time controls) showing aggressive supplants (by Ss in left column) during Evening Food sessions in Sector C for Phases I(a), II(b) and III(c) of Study 3. Each S's mean DI, computed as an average of the six daily DIs measured during each phase in this incentive condition, is shown as well.

	M	MLL	MRR	MLR	F	FLL	FRR	FLR	Mean DI
(a) Phase I:									
M	-		1						.02
MLL	2	-	1		1		3	1	.14
MRR	5	12	-	10	1	5	1		.33
MLR				-			1	1	.04
F					-				.00
FLL					1	-			.02
FRR							-		.00
FLR						1		-	.02
(b) Phase II:									
M	-		1						.02
MLL	2	-	3		5	1	2		.19
MRR			-				1		.01
MLR	7	3	30	-		3		2	.43
F					-				.00
FLL	1	2	1		1	-			.09
FRR		1	1				-	2	.07
FLR								-	.00
(c) Phase III:									
M	-		7	8			1		.17
MLL		-	3		1		3	1	.14
MRR			-						.00
MLR		3	25	-	2	1	2	1	.34
F					-				.00
FLL									.00
FRR							-		.00
FLR		1			2			-	.05

TABLE D18.--Intragroup response matrices for Group 3 (time controls) showing aggressive supplants (by Ss in left column) during Evening Water sessions in Sector A for Phases I(a), II(b) and III(c) of Study 3. Each S's mean DI, computed as an average of the six daily DIs measured during each phase in this incentive condition, is shown as well.

	M	MLL	MRR	MLR	F	FLL	FRR	FLR	Mean DI
(a) Phase I:									
M	-	4			1	6	8	1	.23
MLL	6	-	6	1	5	10	4	3	.40
MRR	5	3	-	1	2	8	5	3	.26
MLR	1		2	-	1		1	1	.11
F	1	2	3	1	-	3	6	2	.28
FLL	1	3	6			-	5	1	.17
FRR	6	8	10	1	9	8	-	1	.37
FLR	1		1					-	.03
(b) Phase II:									
M	-	6	2		4	5	1		.26
MLL	2	-	17	1	6	14	7		.32
MRR	2	8	-		2	7	1	1	.22
MLR	2		2	-	3	2	2		.24
F	2	1	4		-	2	2		.17
FLL	1	4	4	1		-		1	.12
FRR		10	1	1	1	1	-		.15
FLR			1		1	2		-	.10
(c) Phase III:									
M	-	5	4	1	2	15	1		.36
MLL	2	-	2		2	4	2		.20
MRR	2		-		2	12	4	1	.25
MLR		1	2	-					.07
F				1	-	3	2		.12
FLL		1	3		2	-	1	1	.13
FRR			3		1	6	-		.13
FLR			2					-	.05

TABLE D19.--Intragroup response matrices for Group 3 (time controls) showing aggressive supplants (by Ss in left column) during Evening Water sessions in Sector B for Phases I(a), II(b) and III(c) of Study 3. Each S's mean DI, computed as an average of the six daily DIs measured during each phase in this incentive condition, is shown as well.

	M	MLL	MRR	MLR	F	FLL	FRR	FLR	Mean DI
(a) Phase I:									
M	-	1	1	1	2	1			.12
MLL	1	-	2	2	2	1	1		.11
MRR	8	11	-	15	3	9	6		.43
MLR	1	3	2	-			-		.11
F		1			-				.01
FLL	1	3	3	1		-	2		.15
FRR	3	2	1			5	-		.13
FLR			2		1	1	1		.09
(b) Phase II:									
M	-	2	4	2	2	2			.18
MLL	3	-	4	2	2	2	1	1	.21
MRR	4	2	-	1		4	2		.17
MLR	15	15	31	-	8	5	1		.58
F	1		1		-	1	1	1	.11
FLL		2	2		1	-			.06
FRR	2	5		1			-		.16
FLR				1				-	.02
(c) Phase III:									
M	-	6	4	8		2	1		.22
MLL	7	-	2			1	1	1	.10
MRR	2	3	-	1	1	2	3		.20
MLR	4	1	12	-					.10
F	1	1	1	1	-				.08
FLL	2	5	2	2		-		2	.22
FRR	2	2	2	1		1	-		.15
FLR		1						-	.02

TABLE D20.--Intragroup response matrices for Group 3 (time controls) showing aggressive supplants (by _S_s in left column) during Evening Water sessions in Sector C for Phases I(a), II(b) and III(c) of Study 3. Each _S_'s mean DI, computed as an average of the six daily DIs measured during each phase in this incentive condition, is shown as well.

	M	MLL	MRR	MLR	F	FLL	FRR	FLR	Mean DI
<u>(a) Phase I:</u>									
M	-	1	1		1	1			.09
MLL	3	-		3	1	2		7	.24
MRR	4	9	-	10		1			.19
MLR				-					.00
F	1				-				.02
FLL						-			.00
FRR						1	-		.00
FLR								-	.00
<u>(b) Phase II:</u>									
M	-						1		.02
MLL	4	-			2	1	2	1	.14
MRR			-					1	.02
MLR	7	2	40	-	1	1	1	1	.36
F					-	1			.02
FLL	1					-			.02
FRR						1	-		.02
FLR								-	.00
<u>(c) Phase III:</u>									
M	-	4	3	12	1		1	1	.19
MLL	1	-	1		3		2	2	.14
MRR	1		-		1	1	1		.10
MLR	1	1	9	-			1		.19
F					-				.00
FLL						-			.00
FRR		1					-		.02
FLR								-	.00

TABLE D21.--Intragroup response matrices for Group 3 (time controls) showing aggressive supplants (by Ss in left column) during Morning sessions (all Sectors combined) for Phases I(a), II(b) and III(c) of Study 3. Each S's mean DI, computed as an average of the six daily DIs measured during each phase in this incentive condition, is shown as well.

	M	MLL	MRR	MLR	F	FLL	FRR	FLR	Mean DI
(a) Phase I:									
M	-				2				.02
MLL	1	-		1		2	1	1	.14
MRR	9	3	-	22	8	6	2	4	.24
MLR	1	1		-		2	1	1	.12
F					-				.00
FLL						-	2		.02
FRR					1		-		.02
FLR	2	5	1	7	2		4	-	.17
(b) Phase II:									
M	-	1	1						.05
MLL		-			3			3	.14
MRR			-						.00
MLR	2	4	12	-	1	1		1	.31
F			1		-	1			.05
FLL						-			.00
FRR							-		.00
FLR								-	.00
(c) Phase III:									
M	-		6	13	2	2	4	4	.24
MLL		-	1		1	1		1	.10
MRR	1		-						.02
MLR	2	1	28	-	3	3	5	3	.38
F					-				.00
FLL						-			.00
FRR				1			-		.01
FLR					2	1	2	-	.10