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The City University of New York, Ph.D., 1974
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TRIGEMINAL DEAFFERENTATION AND FEEDING BEHAVIOR PATTERNS IN THE PIGEON (COLUMBA LIVIA)

by

MARIA G. MILLER

A dissertation submitted to the Graduate
Faculty in Biology in partial fulfillment of
the requirements for the degree of Doctor of
Philosophy, The City University of New York

1974

This manuscript has been read and accepted for the Executive Committee in Biology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

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Summary

The control of food intake and hence the regulation of body weight is mediated behaviorally by the pattern of feeding activity. In pigeons, even with continuous free access to food, feeding takes place in bouts of rapid ingestion followed by longer periods without eating. This is the case in most animals so far investigated and seems to represent an adaptive behavior pattern allowing the animal to take advantage of food opportunities when they occur without overeating when food is plentiful.

The features of the meal pattern such as bout frequency, duration, ingestion rate and temporal distribution of feeding are fairly stable over a period of time and rather characteristic for a given species or individual under the same circumstances. These characteristic features or parameters of the meal pattern presumably reflect the interplay between metabolic requirements, state of the ingestive and digestive system for handling food, sensory cues in regard to food and the environmental problems to be overcome in obtaining food as well as the previous experience and adjustment of the species and individual to these factors.

Influence of these factors on the feeding pattern is presumably mediated by neural mechanisms which finally control behavior. Changes in the metabolic state, ecological situation and the animals neural system all can lead to modification of pattern parameters. Therefore it was hoped that studying the pattern changes resulting from certain manipulations of the animal and its state would disclose information about the role of the various factors influencing the regulation of feeding.

It has recently been shown that sectioning the sensory branches of the trigeminal nerve leads to temporary aphagia, followed by hypophagia, and therefore to loss of body weight without loss of the bird's motor abilities for eating. It was therefore assumed that trigeminal sensation plays an important role in the control of feeding behavior. The objective of this thesis was to investigate the role of the trigeminal sensory system in influencing the pattern of feeding activity in such a way that food intake is adapted to metabolic requirements and body weight is kept relatively constant.

Pre- and post-manipulation feeding patterns were recorded in one experimental and two control groups of birds. The experimental group underwent bilateral triple branch trigeminal deafferentation. The control groups consisted of a sham deafferentation surgical control group and a deprivation control group for appraising the effect of food deprivation alone on feeding patterns. This made it possible to assess the influence of the post-operative aphagia and resulting weight loss in the experimental birds. Body weight, food intake and water intake were measured once a day for each bird. All feeding responses of each day were monitored continuously recording numbers and time of occurance. This allowed determination of the number of pecks per bout, bout duration and the interval between bouts. These data were analyzed with the aid of a digital computer. For characterizing the feeding pattern programs were developed that determined (a) the number of bouts per feeding period; (b) the mean bout size; (c) the frequency distribution of bout sizes; (d) the distribution of feeding activity by bout size; (e) the temporal distribution of feeding activity.

The major experimental results were as follows:

(1) The previous findings that trigeminal deafferentation leads to an immediate period of aphagia followed by a prolonged phase of hypophagia were confirmed.

(2) Although trigeminal deafferentation impaired the birds' pecking efficiency, it was found that the rate of ingestion was normal. Sensory motor deficits therefore could be excluded as the direct cause of the sub-normal food intake after resumption of feeding.

(3) The pattern of food intake was changed immediately when food intake was resumed after deafferentation. This change was permanent throughout the period of observation.

(a) There was a significant reduction of the bout frequency per feeding period.

(b) The size of a few bouts was greatly enlarged. They always exceeded the pre-operative largest bout size and comprised more than half of the daily food intake. The rest of the bouts were unchanged in size.

(c) The very large bouts occurred at the beginning of the feeding period and therefore more than half of the daily intake occurred during the first hours of feeding. Thereafter feeding activity tapered off more rapidly than before deafferentation and to such a degree that overall daily food intake remained below pre-operative levels.

(4) Food deprivation alone also influenced the feeding pattern. These changes however were only transient and led to an increase in daily food intake.

(a) There was a reduction in bout frequency per day - however this

was less than in deafferentation birds.

(b) The size of one bout per day was enlarged beyond pre-deprivation levels. The rest of the bouts were also increased although to a much lesser degree.

(c) The very large bout occurred at the beginning of the feeding period as in deafferentation birds. Thereafter feeding activity tapered off at the same rate as before deprivation with the result that the daily food intake exceeded the pre-deprivation levels.

Thus the food intake pattern after trigeminal deafferentation was greatly influenced by the state of deprivation resulting from the period of post-operative aphagia. However two effects could be identified going above and beyond that of deprivation and hence presumably are attributable to the neural deficit alone.

(a) The greater size and incidence of oversized meals in deafferentation birds suggested some deficiency in the mechanisms which tend to limit meal size.

(b) The more rapid falling off of ingestion per hour after the first hour, which led to the net reduction in daily food intake, suggested a deficiency in the mechanism that sustains the birds propensity to eat throughout the day.

Neither of these effects seemed adequately understandable in the framework of the homeostatic (cybernetic) model of feeding motivation usually employed to explain food intake regulation and feeding pattern changes. Therefore a new explanatory model was developed based on the adaptive learning theory of specific hunger researchers and the ecological constraint theory of Collier. In this framework it is postulated the trigeminal system normally transmits sensory cues with two kinds of functions:

(a) Some cues act as secondary reinforcement for sustaining feeding activity whenever the bird has learned to eat a diet appropriate for its metabolic requirements.

(b) Other cues are associated with the proper meal size learned as a compromise balance between metabolic requirements, gastro-intestinal tract loading and effort required to obtain meals from the environment.

Acknowledgements

Without the continuous encouragement and support of my thesis advisor, Professor Philip Zeigler, the completion of this dissertation would never have been possible. He provided scientific guidance, moral support and technical assistance far beyond the call of duty and made available generous financial support necessary to collect and analyze the data. In the difficult circumstances under which this research was completed, because of an allergy I acquired, his friendship, understanding and unstinting contribution of many hours of his own time were vital and are gratefully acknowledged.

I also wish to thank sincerely my thesis committee, Professors L. Aronson, G. Collier, E. Coons, J. Griswold, A. Sclafani and W. Tavolga, for their advice and patience in pouring through several voluminous drafts and for accepting seriously but in good humor the stubborn differences of opinion over theoretical interpretation.

Professor Harry Kissileff generously allowed me to use and modify his computer programs and techniques of data analysis which reduced considerably the amount of new programming required. The work was in part financed by a stipend for research training under an NIMH grant #5 T01 MH13051.

Mrs. Betty Michelman deserves special credit and thanks. Her complete cooperation and tender loving care of the animals and experiments made possible the continuation of the project - in the face of otherwise insurmountable difficulties. Many other regular and volunteer members of the laboratory staff were also extremely helpful in the course of the research.

Above all I am grateful to my husband without whose faith, encouragement, love and intellectual partnership this dissertation would never have been undertaken, let alone finished. His readiness to immerse himself in extended discussions of the work, his patience and support to the extent of often feeding me and sometimes the pigeons and his editorial assistance contributed to the form and substance of this dissertation in an inestimable way. To him this work is dedicated.

TABLE OF CONTENTS

TABLES

FIGURES

PART I: INTRODUCTION

1. Theoretical Background on the Control of Food Intake

The objective of this thesis is to investigate the role of the trigeminal sensory system in the adaptive regulation of the pattern of feeding activity in the pigeon. In its natural environment an animal must have two feeding behavior abilities if it is to meet its nutritional requirements and maintain a relatively constant body weight or growth rate. (1) It must select appropriate foods from those ecologically accessible. (2) It must control its intake of these foods in such a way that neither undereating nor overeating occurs. This thesis is primarily concerned with the second problem. However, as will be seen in the conclusions, the mechanisms of selection and intake control are interrelated in a manner that makes it impossible to separate the two problems completely.

There is extensive experimental evidence for several species that within a wide range of conditions body weight is regulated and food intake is quite accurately matched to metabolic requirements. Among mammals well researched examples are rats (Adolph, 1947 and many others), mice (Anliker and Mayer, 1957, Wiebkema, 1964),rabbits (Gasnier and Mayer, 1939), guinea pigs (Hirsch, 1973), dogs (Cowgill, 1928, Janowitz and Grossman, 1949). Among birds examples are pigeons (Cardini, 1971, Zeigler et al., 1972), cocks (Fisher and Weiss, 1956, Fisher et al., 1965), chicks (Reddy et al., 1962). Artifically imposed constraints on food intake are met differently and to varying degree, in general depending on how the experimental conditions differ from the species-typical and ecological situation of the animal under consideration (Fabry, 1967), By far the most thoroughly investigated animal in regard to feeding behavior is the rat, and most theoretical work on the control of food intake is based on this research. Possibly due to its omnivorous eating habits, the rat is able to adjust to quite different kinds of feeding regimens. If rats are deprived to a reduced body weight (Levitsky, 1970) or if their food is diluted by non-nutritive bulk (Adolph, 1947), or if their metabolic rate is raised through exposure to cold (Hamilton, 1967) they will eat more than normally and regain or maintain their weight. Under these circumstances of increased nutritional requirements rats also will work more (in form of bar-pressing) for food and recover their lost body weight (Marwine and Collier, 1971). If rats are artifically overfed (within certain limits) they adjust their daily food intake and compensate. If they are force-fed to obesity, they reduce their food intake until they again reach approximately their normal weight (Cohn and Joseph, 1962, Kissileff and Quartermain, 1973). Pigeons also have been found to overeat in response to food deprivation (Zeigler et al., 1972) in an even more immediate fashion than rats. Force-feeding reduces their intake very effectively (Cardini, 1971, personal observation). Thus there seem to be metabolic and physiological factors reflecting the nutritional state which influence feeding behavior in such a way that total intake is appropriate for metabolic requirements.

To accomplish this regulation of body weight in the natural environment the animal's feeding behavior must include two further abilities which allow it to adapt to ecological conditions. (1) To take advantage of food opportunities when they occur, it must be able to eat larger amounts of food in a shorter time than would be necessary if it could eat uniformly and continuously. Experiments show that animals can adapt to extremely non-uniform feeding circumstances. Rats can learn to eat almost their entire day's ration within one hour or so on a 23 hour deprivation schedule or under the constraint of having to bar-press in a very high ratio schedule for access to food (Ehrenfreund, 1959, Collier et al., 1972). Similar capabilities were found in chicks fed only for two hours per day (Leveille and Hanson, 1965). (2) On the other hand when food is abundant, the animal must limit food intake to below its ingestive capabilities if it is not to become obese. The usual behavioral "solution" to these two problems seems to be eating in rather discrete meals of limited duration at a moderately fast rate of ingestion followed by longer periods of no feeding activity until the next meal begins. The question of understanding the behavioral control of food intake can therefore be restated as the problem of discovering the mechanisms by which the meal pattern is controlled.

In recent years most experimental and theoretical work on the control of food intake has been based on a homeostatic or cybernetic model of feeding behavior control (Stellar, 1954), sometimes referred to as the depletion/repletion model (LeMagnen and Tallon, 1966). This postulates a thermostat-like mechanism with a predetermined "set-point" which monitors the nutritional state by means of some indicator(s) such as blood glucose and lipid levels or monitors the balance between nutritional state and fullness of the gastrointestinal tract as indicated by sensory inputs from it. When the balance of these factors falls below the set-point, activity is initiated which leads to feeding. Thus an animal is assumed to be "motivated" to eat by reaching a present level of nutritional deprivation. Since regulation of body weight depends on monitoring internal factors, most investigators believe the mechanisms which control feeding in relation to nutritional level (the so-called feeding centers) are located in the central nervous system. In fact because of considerable experimental evidence about aberrations of feeding behavior after lesions in the hypothalamus critical parts of the mechanisms are generally assumed to be situated there (Anand and Brobeck, 1951, Hetheringon and Ranson, 1942, and many others).

The model further postulates that as feeding takes place orogastric sensations (LeMagnen, 1969, 1971) and/or rapid systemic reactions such as elevation of blood sugar (Steffens, 1968,1969; Nicolaidis, 1969) build up inhibitory influences until they reach a level sufficient to stop the action of the feeding centers. When metabolic utilization again lowers the nutritional state to below the "set-point", the cycle starts over.

It is generally accepted that the digestion which takes place in the course of a single meal is not sufficient to determine its termination. For this reason most investigators assume that meal size is primarily under the control of orogastric events, while meal frequency, i.e. the initiation of meals is believed to depend critically on the changing level of metabolites.

2. Oral Sensation and the Control of Food Intake

In accord with this cybernetic model most previous work has emphasized the importance of central mechanisms for motivation in the regulation of body weight. More recently experimental evidence has accumulated that disturbances of peripheral sensory mechanisms alone lead to aberrations in feeding behavior and consequently in the level at which body weight is regulated. Substantial work on the role of orosensation in the regulation of body weight in the rat has been done by Epstein and Teitelbaum (1962, Epstein, 1967), and was extended by Snowdon (1969). These studies were explicitly concerned with taste and smell; but their experimental procedures actually manipulated oral tactile sensation as well. Generally the technique of intra-gastric feeding was used as a means of "eliminating" taste, oral tactile sensation and smell, which are usually connected with food intake. The animals fed themselves by bar-pressing which led to intra-gastric injection of a fluid nutriment by way of a nasopharyngeal catheter. With this technique orosensations were not really eliminated but only decoupled from the act of feeding. Feeding took place by instrumental response that no longer utilized the usual feeding activities such as gnawing, biting or swallowing. Snowdon found that the rats had to be retrained to feed themselves after the transition from oral to intra-gastric feeding. Furthermore intra-gastric food intake reached only 75% of the oral level due to a decrease in meal size without compensation by an increased meal frequency. Body weight therefore only remained stable instead of steadily increasing, as is usually the case in normally feeding rats. Snowdon concluded that oropharyngeal sensations are of great importance for motivating and sustaining feeding behavior. The complete elimination of the normal act of food intake, however, is a very gross interference, and it seems impossible from these experiments to assess the role of specific sensations .

in the control of feeding. Nevertheless these results are basically in agreement with the findings in trigeminally deafferented pigeons (see below).

The removal or reduction of olfactory input alone apparently has a less disturbing influence on overall food intake in the laboratory situation. LaRue and LeMagnen (1972) found that after olfactory bulbectomy in rats the fluctuation from day to day in the 24 hour intake was increased, while total intake over a longer period of time remained quite normal. Moreover the daily feeding pattern was greatly modified. The rats, which usually take a number of discrete meals, developed a nibbling pattern of feeding, eating over long periods of time but interrupted by many short pauses. LaRue and LeMagnen concluded that olfactory input provides an important cue for determining meal size.

For the pigeon Zeigler (1973) accumulated considerable evidence that oral tactile sensation is important not only for an efficient performance of the consummatory response of feeding but also for motivating mechanisms which underlie the regulation of body weight. Trigeminal deafferentation as well as lesions in the central projection system of the trigeminal nerve (Zeigler and Karten, 1973 a,b) produced a syndrome of feeding behavior deficits without affecting water intake directly. Lesions in the principal nucleus of the trigeminal nerve, the nucleus basalis or the quinto-frontal tract which connects the two brain structures or sectioning of the three sensory branches of the trigeminal nerve typically resulted in impairment of mandibulation of the kernel of food from the tip of the beak to the back of the mouth so that droppage occurred more often. (Zeigler, Miller, Levine, 1974). In addition interference with the trigeminal system seemed to result in orientation difficulty in the pecking act itself so that the birds succeeded less often in grasping a kernel of grain in its beak with each peck (Levine, 1974). However, the most obvious characteristic deficit was that lesioned and deafferented birds went through a period of aphagia lasting from several days to several weeks followed by a prolonged period of hypophagia. As a result the birds body weights remained abnormally low.

Zeigler et al. (1974) have recently shown that the importance of the trigeminal sensory system for regulation of feeding behavior is not limited to pigeons. By lesioning central trigeminal structures in rats, (trigeminal lemniscus, ventrobasal complex of the thalamus) as well as by lesioning the sensory branches of the trigeminal nerve they were able to produce aphagia and adipsia for several days followed by hypophagia and hypodipsia.

Because trigeminal deficits (unlike gustatory or olfactory deficits) affect sensory-motor feeding abilities it was necessary to develop a procedure to distinguish these defects from the effect of trigeminal deafferentation on readiness to eat. Using a photocell-feedometer (Zeigler and Feldstein, 1971) the birds' single feeding responses were monitored independently of their food intake. During aphagia feeding responses were not absent but their number was considerably under preoperative levels. This was interpreted as a sign of decreased responsiveness to food due to the deficit in trigeminal input. After resumption of food intake the birds remained hypophagic for many weeks and did not overeat in response to the loss of body weight as normal birds invariably do. In a time span of four weeks which is long enough for normal birds to gain back a body weight loss of 20%, deafferented birds recover only about 5% of their body weight.

However, Zeigler (1974) also found that deafferented pigeons resembled normal birds in their response to additional externally imposed food deprivation. In one-hour feeding tests after food deprivation the amount of food eaten increased in proportion to body weight loss in both groups and could reach four times the amount eaten in the same time interval in the free feeding situation.

These findings suggested that the sensory-motor deficit after deafferentation exhibited in the feeding response inefficiency was not sufficient in itself to account for the persistent hypophagia. This situation characteristically occurs after interference with central mechanisms of feeding behavior. Thus it was surprising to find it as a result of a peripheral nerve section alone. The objective of this research was therefore to investigate the mechanisms of this hypophagia after deafferentation and in so doing learn more about the normal role of the trigeminal sensory system in the control of feeding behavior.

3. Feeding Pattern Analysis as a Tool for Investigation of the Control of Food Intake

The choice of feeding pattern analysis as a method for studying this phenomenon deserves discussion in its own right since it is a relatively new technique and its potential analytic values is viewed quite differently by various workers (LeMagnen, 1971; Panksepp, 1973; Collier et al., 1972; Hirsch and Collier, 1974).

The study of feeding patterns provides several advantages.

(1) Because the recorded pattern and its analysis cover the entire 24 hour period of behavior, it is possible to evaluate the role of metabolic factors which act over longer intervals.

(2) Because it preserves a detailed record of the behavioral events over time, pattern analysis allows the study of the influence of neural mechanisms underlying feeding control.

(3) Because of the known influence of environmental factors pattern analysis offers the possibility of studying their interrelation with metabolic and neural factors.

The control of food intake and hence the regulation of body weight is mediated behaviorally by the pattern of feeding activity. The daily food intake is simply the product of the number and size of feeding bouts. However within the confines of the daily total intake there is considerable variation in the pattern and its parameters, e.g. in the temporal distribution of meals and the distribution of feeding activity among different sized bouts. This flexibility of the pattern seems to play an important role in allowing adaptation of the species and adjustment of the individual to changing metabolic needs and environmental conditions.

Different species have developed circadian feeding cycles and relations between meal size, frequency and ingestion rate which fit the ability of their gastrointestinal tracts and the requirements of their ecological situations. Among mammals herbivores tend to eat large, slow, low-caloric meals frequently and the restriction of the number of meals per day has rather adversive effects on the utilization of food in cattle and sheep (Mochrie, 1964). Carnivores tend to eat very large, rapid, high-caloric meals infrequently. In dogs fed usually once per day, frequent feeding induces disorders of gastric secretion (Putilin and Staritskaya. 1961, cited in Fabry, 1967). Omnivores like the rat are characterized by a relatively great adaptability to ingestion of food either in "loads" or in small and frequent portions.

Feeding patterns also provide the flexibility for the individual animal to adjust its food intake to meet changing metabolic requirements and environmental conditions. All factors that influence the control of food intake must do so in the final analysis by changing the feeding pattern. Reciprocally the feeding pattern must reflect the various influences as well as the neural mechanisms which underlie feeding behavior. If an animal's nutritional requirements are raised through deprivation or higher metabolism, the increased intake has to be accomplished behaviorally by more frequent and/or larger meals (Levitsky, 1970) i.e. by changing its feeding pattern. If environmental constraints make access to food more difficult the animal learns to eat larger meals less frequently (Collier et al., 1972). Therefore studying the changes in feeding patterns which occur in response to changes in food requirements or availability of food and to changes in neural factors participating in the feeding regulatory system can be a powerful tool for understanding the mechanisms of feeding control.

The problem is that there seems to be no one-to-one causal relationship between influencing factors and the obvious parameters of the meal pattern such as meal size and meal frequency. Each parameter is affected by multiple influences, and each causal factor has an effect on many pattern parameters. In some cases if environmental factors are held constant, nutritional states do seem to have selective influence predominately on certain parameters; e.g. Levitsky and Collier (1968) and Kissileff and Quartermain (1973), found that both food deprived and overfed animals compensate mainly by increasing or decreasing meal size, while meal frequency changed very little. However meal size is also affected by conditions such as palatability (LeMagnen, 1971; Levitsky 1970) or caloric density of diet available (Snowdon, 1969) and the amount of work (bar-pressing) required to obtain meals (Collier, et al., 1972). In animals so far investigated the size of the usual meal ingested comes nowhere near the capacity of the stomach or digestive tract as shown by the fact that under severe constraints they are able to eat many times the usual amount in a single bout of feeding. On the other hand in rats the meal size is clearly influenced by the state of the gastrointestinal tract. Thomas and Mayer (1968) and Quartermain et al. (1971) found that supplementary feeding by intra-gastric infusion resulted in decreased oral food intake as expected. However continuous infusion led to decrease in meal frequency without change in meal size, while larger shorter infusion during meals which were initiated by the animal itself led to decrease in oral meal size, the frequency remaining unaffected.

Similarly with meal initiation (and hence frequency) under certain constant conditions there is evidence that metabolic depletion can be a direct causal factor (LeMagnen and Tallon, 1966). On the other hand even overfed obese animals (Kissileff and Quartermain, 1973) and even animals with continuous intra-gastric nutritional supplementation equivalent to the usual food requirements (Quartermain et al., 1971) continue to display bouts of feeding activity. Moreover Collier et al, (1972) has shown that the amount of work required to obtain food has a marked diminishing effect on the frequency with which meals are taken and a reciprocal effect on meal size so that total intake remains constant. Thus depletion does not seem to be the only factor leading to bouts of eating. The problem therefore is to understand the interplay of the various factors and mechanisms and how they "converge" to determine the pattern of feeding activity.

Thus a large number of factors influence feeding behavior, and these factors do not seem to stand in any simple relationship either to the neural mechanisms through which they are mediated or to the most obvious parameters of the meal pattern (meal size and meal frequency). Why then, study feeding patterns as a way to learn about the neural mechanisms of feeding control? Even granted that patterns are the common behavioral medium through which all influence on feeding must act, is there any reason to assume that the study of patterns can tell us anything about these mechanisms?

Feeding patterns are extremely complex, but this complexity is made up of clearly definable and quantifiable parameters. There is no standardized method of analysis. However it is precisely this complexity which can make it possible to correlate specific manipulations with specific effects. For example in the case of the deafferented pigeon the increase in meal size and the reduction of the number of meals per day told us very little about the role of trigeminal sensation. It was the temporal distribution of meals and more exactly the temporal distribution of specific meal sizes which was found to be most crucial for describing and interpreting the effect of trigeminal deafferentation. Thus the task of pattern investigation depends critically on the discovery of analytic methods to find significant second order parameters i.e. parameters based on relationships between primary characteristics such as meal size and time of occurrance.

PART II: METHODS

Pre and post-operatively feeding patterns were recorded in one experimental and two control groups of birds. The experimental group underwent bilateral triple branch trigeminal deafferentation. The control groups consisted of a sham deafferentation surgical control group and a deprivation control group. Deprivation control birds were subjected to food deprivation sufficient to produce a body weight loss equivalent to that occurring during the post-operative aphagic period of experimental birds. This made it possible to assess the effect of food deprivation alone on the pattern of food intake.

Body weight, food intake and water intake were measured once a day for each bird. All feeding responses of each day were monitored continuously by recording their number and time of occurance. This allowed determination of the number of bouts per day, pecking rate, bout duration and temporal distribution. The average efficiency of the consummatory response was calculated from food weight consumed and total number of pecks per day.

1. Subjects and Maintenance

Eleven pigeons (White Carneaux) of both sexes and two to six years of age were obtained from a commercial supplier. Their body weights ranged from 443 to 619 gm. They were housed in individual cages in the colony room. The ambient temperature was maintained between 22° and 26°C. The light dark cycle approximated that during summer with 15 hours of light (8:00AM - 11:00PM) and nine hours of darkness (11:00PM - 8:00AM). Water was provided ad-lib in 250 ml graduated glass drinking tubes. The feed was milo, a single grain feed (in order to minimize grain selection by the birds) which is considered a palatable, nutritionally balanced diet for pigeons. It was available ad-lib except during a three and one-half hour period (1:00PM - 4:30PM) when general maintenance and data taking were carried out. This three and one-half hours without food fell in the middle of the day light period which is known to be an interval of low feeding activity (pilot work, Zeigler et al., 1971). Because pigeons eat only during the light hours, there were two feeding periods per day, the main feeding period from 4:30PM - 11:00PM during which the birds were undisturbed, and the morning feeding period from 8:00AM - 1:00PM when the normal laboratory activities were going on.

2. Experimental Procedures

After a period of adaptation to the laboratory and experimental feeding schedule conditions (at least four weeks), body weight, intake (food and water) and pattern data of each bird were recorded for at least seven days pre-operatively. This provided the base line data and the "normal" feeding pattern of each bird. After surgery the same data were taken as continuously as possible for ten to fourteen days. Starting with the third post-operative week the number of days on which feeding patterns were recorded was gradually decreased. Body weight, food intake and total number of responses were monitored daily for the whole post-operative period of six to twelve weeks (in most cases eight weeks). The post-operative period was extended until body weight, intake and pattern had stabilized.

3. Surgical Procedures

All birds were food deprived on the day before surgery. Equi-Thesin (0.25ml per 100gm body weight) was used for anesthesia.

Experimental group: Deafferentation group (N=6). The ophthalmic, maxillary and sensory division of the mandibular branch of the Vth nerve were sectioned bilaterally using a dissection microscope. Approximately 10 - 15mm of the ophthalmic and of the mandibular branch were removed, while the sections of the maxillary branch removed were somewhat less extensive. The branching and distribution of the trigeminal nerve in the pigeon is such that the motor part can be spared. The mandibular and the maxillary branch were sectioned distally enough to leave proprioception of the jaw musculature intact (FIG.1).

Control group I: Deafferentation control group (N=2). Except for actual nerve section, the surgical procedure was identical to that of the experimental group.

4. Deprivation Procedure

Control group II: (N=3). The birds were subjected to total food deprivation until their body weight decreased to 88 to 90% of the normal level which approximated the reduction of body weight in the experimental birds due to aphagia after surgery.

FIG. 1
PERIPHERAL DISTRIBUTION OF THE TRIGEMINAL SENSORY BRANCHES

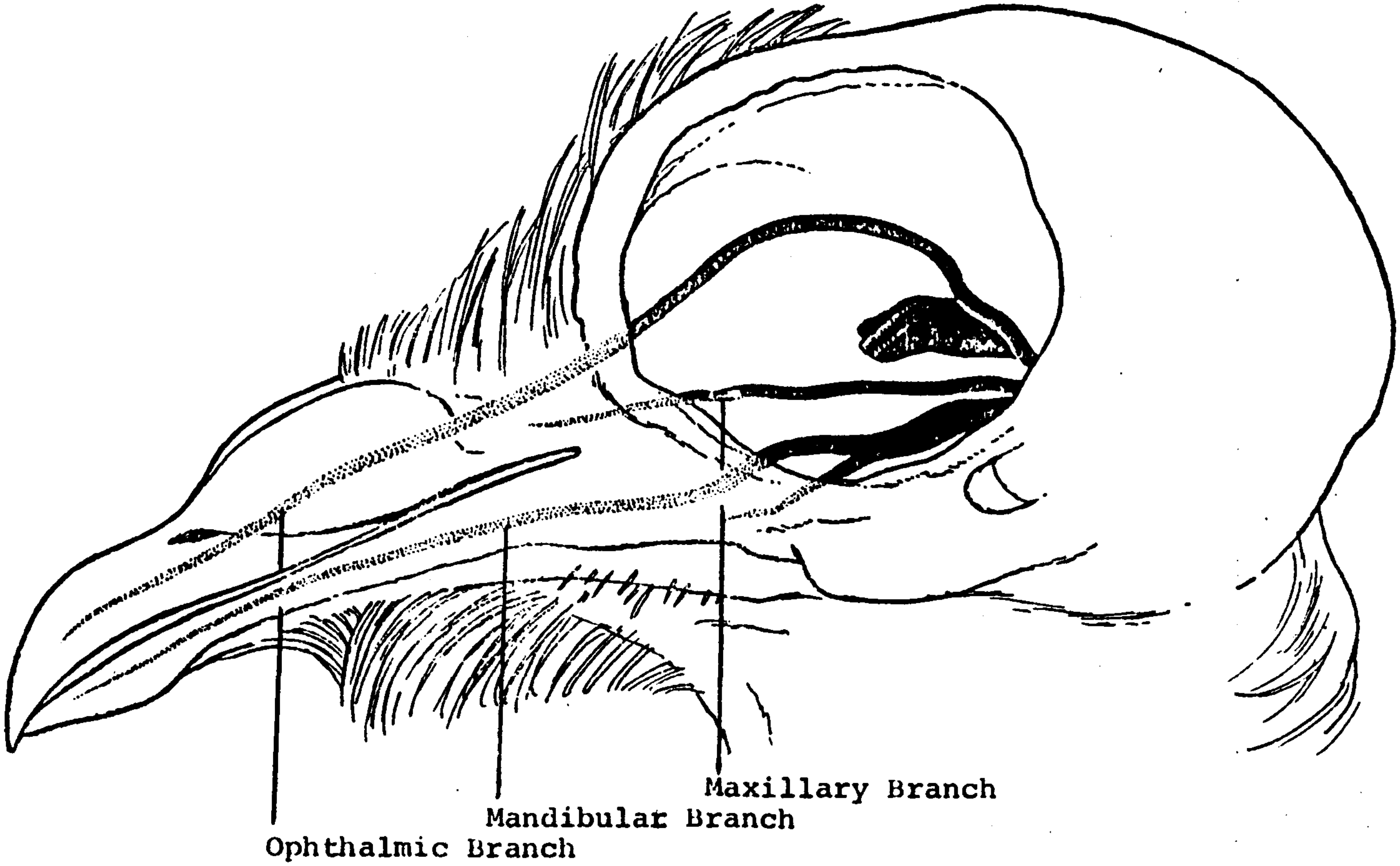


TABLE 1: SUBJECTS

DEAFFERENTATION BIRDS (DF)	373	349	435	
	441	412	367	N = 6
DEAFFERENTATION CONTROL BIRDS (DC)	348	362		N = 2
DEPRIVATION BIRDS (DP)	339	374	360	N = 3

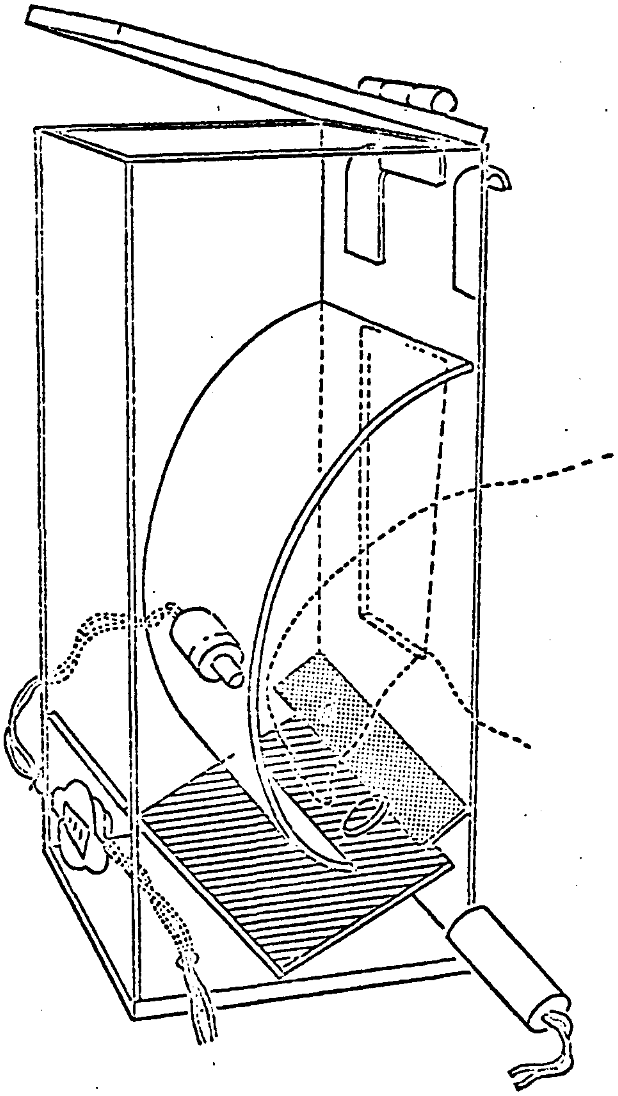
5. Apparatus

Food was provided in feedometers (FIG.2), food magazines especially designed for pigeons (Zeigler and Feldstein, 1971). They had a capacity of 500gm and allowed recording of single feeding responses. Pecks into the food magazine interrupted a light beam across the food which triggered a photo cell circuit and provided a recorded output pulse. Three different arrangements of recording equipment were used to monitor the number and temporal distribution of the output pulses from the feedometers. They provided equivalent information but differed in ease of data analysis.

In the first arrangement the individual responses were recorded on an Esterline Angus event recorder which provided data on the temporal distribution of the feeding bouts. The number of responses per bout was recovered from the same recording simply by counting the pen marks (every tenth response was specially marked). The total number of daily responses, as a cross check, was cumulated by electronic counters.

In the second set up the response number per bout was obtained from print-out counters (modified Sodecos) which were connected in parallel with the Esterline Angus event recorder. These counters cumulated the feeding responses until an interval of one minute

FIG. 2 FEEDOMETER



occurred without a response. At this point the bout was considered as ended (one-minute bout criterion). The number of responses was then printed out and the counters reset.

A third (more complex) type of recording equipment was developed in the course of the experiment. Feedometer output pulses simultaneously triggered an electronic cumulative counter and a digital clock, both of which were connected to a modified print out calculator. Thus a record was obtained of the real time when each feeding bout started, the number of feeding responses in each ten second period within one feeding bout (defined again by a one-minute criterion), the total number of responses per bout, the duration of the feeding bout and the time interval between bouts (FIG.3). This kind of equipment also provided data on the temporal distribution of feeding responses within feeding bouts (not used for analysis in this research project).

6. Efficiency of the Feeding Response

The equipment used in recording feeding activity depended on the bird's head breaking a light beam in the act of pecking and thereby counting the number of feeding responses. However the pigeon did not always succeed in grasping a grain with its beak, mandibulating it to the back of its mouth and consummating the response by swallowing a grain. In order to calculate the grams of food intake during any bout it was therefore necessary to know not only the number of feeding responses which occurred but also the efficiency of those responses in grams consumed per peck. Since food consumption could only be measured directly once a day when the

FIG. 3 EXAMPLE OF PRINT-OUT FROM RECORDING EQUIPMENT

```
163438· #          Starting Time of Bout (4.34.38 PM)

     7· +          Number of Responses in consecutive
     9· +          10 sec Periods
    15· +
    14· +
    10· +
    12· +
    13· +
    13· +
    12· +
     2· +
     0· +
     0· +
   107· *          Total Number of Responses
                   (Printed after 30 sec of not responding)
   100· #          Duration of Bout in sec

   219· #          Interval in sec until Next Bout

163957· #          Starting Time of Bout

     6· +          etc.
    12· +
    12· +
    13· +
    13· +
    11· +
    12· +
    13· +
    13· +
     8· +
     8· +
    10· +
     9· +
    12· +
     6· +
     7· +
     2· +
     0· +
     0· +
   167· *

   170· #

   293· #

164740· #
```

food magazine was weighed, it was only possible to calculate the average efficiency for the day.

In the normal birds the efficiency was fairly constant from day to day. Pre-operative means for the ten birds ranged from 0.60 to 1.4gms/100 pecks with an average of 0.89. Since there are approximately forty grains of milo per gram, this means a grain was successfully swallowed in about 36% of the feeding responses. In order to appraise the stability of the efficiency during the day the food of a normal and a deafferented bird was weighed two or three times during the morning feeding period. The number of pecks during each time period was compared with the amount of food consumed in the same interval. No evidence was found of marked variation in efficiency expressed in grams of food per 100 responses (APP. TABLE 2). Therefore the daily average efficiency was used as the basis for calculating the food ingested in the single feeding bouts.

7. Bout Characteristics of Feeding Pattern

Nearly 100% of the food intake occurred in discrete bouts (meals) of fast pecking (at 0.8 to 1.2 responses/sec on the average). A bout was considered as ended if one minute had gone by, without a response (one-minute criterion). In order to exclude occasional pecks into the food magazine only bouts were counted of at least 7 pecks within 30 seconds. These criteria for distinguishing bouts were arrived at pragmatically in view of the following: 1) The low number of pecks taken as a criterion for constituting a bout led to exclusion of very few feeding responses (less than 1%) and allowed recognition of possible dispersed pecking after neural manipulation. 2) The cut-off of feeding bouts was quite sharp and was followed by a longer period during which there was a very low probability that feeding activity would resume. Therefore if the bird had not responded for one minute the meal could be considered clearly ended.

Because of the clear structure of feeding activity into bouts in the pigeon the feeding pattern can be characterized in terms of:

1) number of bouts per day (frequency),
2) size of each bout (measured in number of feeding responses, duration of feeding and grams of food intake),
3) hourly distribution of bouts,
4) feeding rate during each bout (measured in number of responses per 100 sec).

8. Quantitative Analysis of Data

Data on number of responses per bout, bout duration, and interbout intervals, as well as the general information on daily body weight, water and food intake were punched onto Hollerith cards and analysed by a digital computer. Programs were developed for the following analyses:

1. Comparison of pre- and post-operative data:

   The mean and the standard deviation of seven pre-operative days (base line data) were calculated for each bird singly for a series of parameters. The post-operative daily data and weekly averages were compared with the corresponding base line mean and expressed as a percentage of it. The parameters included:

a) Daily body weight and
   daily total food and water intake

b) Daily total number of responses and their distribution between main feeding and morning feeding period

c) Feeding efficiency expressed as $\frac{\text{grams of food}}{\text{100 responses}}$

d) Daily total feeding duration and its distribution between main feeding period and morning feeding period.

e) Ingestion rate expressed as $\frac{\text{grams of food}}{\text{100 seconds}}$

f) Feeding pattern parameters (separately for main and morning feeding period), such as number of bouts, mean bout size (measured in number of responses and in duration).

2. Frequency distribution of bout sizes (adaptation of a program developed by Kissileff, 1970). Three different measurements for bout size were used: number of responses, duration (both recorded directly) and grams of intake (calculated).

   a) Bout size in responses reflects the actual feeding activity of the bird including successful and unsuccessful pecks.

   b) Bout size in duration is a comparable measurement (assuming a constant pecking rate) and was introduced for some birds that developed an unusual pecking technique post-operatively which no longer allowed recording of the number of responses exactly.*

---

* During some post-operative weeks a few birds exhibited a technique of pecking that apparently compensated for their grasping difficulties but diminished the recording accuracy in regard to the single pecks. These birds produced a burst of very rapid responses (about 5-8) before raising their head above the light beam of the magazine photocell, as the pigeons normally did. The recording equipment then indicated too low a number of responses - only showing that the light beam was interrupted an unusually long time (about 10 sec.) for "each" recorded peck. The bout duration was however recorded correctly.

c) Bout size in grams expresses the amount of food actually ingested in the single feeding bouts and adjusts, therefore, for the decreased pecking efficiency after deafferentation. It was not recorded directly in this experiment but calculated from the daily average feeding efficiency (grams of food per 100 responses) and the recorded number of responses per bout. Although this did not correct for the minor differences in pecking efficiency in different bouts of the day, the difference in meal size before and after deafferentation was so dramatic that this inaccuracy was negligible for the purpose of this study.

3. Distribution of feeding activity by bout size. As in point 2 above bout size was measured in responses, duration and grams of intake. The total number of responses, total duration and total intake (grams) occuring in each bout size category was tabulated for every day and weekly averages were calculated.

4. Distribution of feeding activity over time (adaptation of a program developed by Kissileff, 1970). The hourly distribution was calculated for:
   a) number of responses
   b) duration of feeding activity
   c) grams of food ingested
   d) number of bouts
   e) mean bout size

   All distribution parameters were also expressed as percentage of the total of the feeding period under consideration.

PART III: EXPERIMENTAL FINDINGS*

1. Total Food Intake and Body Weight

Three groups of birds were studied after manipulation as described in PART II: (a) The deafferentation group, 6 pigeons subjected to bilateral triple branch deafferentation. (b) The surgical control group, 2 pigeons subjected to bilateral sham deafferentation surgery without nerve section. (c) The deprivation group, 3 pigeons subjected to total food withdrawal until body weight fell to 88-90% of the stable pre-deprivation norm. As exhibited in TABLE 1 each group of birds showed a rather characteristic set of changes in food intake and body weight.

(a) Deafferentation group. In spite of basically similar characteristics in feeding activity there was considerable variation in the response to deafferentation in the six experimental birds. Four of the birds were aphagic for four to six days following surgery and then began to eat spontaneously. The other two birds were aphagic for three and seven weeks respectively and tube feeding or hand feeding was initiated when the body weight fell to about 77% of the pre-operative value nine to eleven days after surgery. One of these birds (#367) died twenty-one days after deafferentation without recovering the ability to feed by itself. The other (#412) began to feed itself spontaneously, though not very effectively, in the eighth post-operative week.

During the pre-operative period the body weight of each bird varied only slightly with extremes ranging from 99% to 102% of the mean. The rate of weight loss during aphagia showed no sign of abnormality.
11 to 15% of the ad-lib body weight was lost in five to seven days, while neurally normal birds on total food deprivation lost 10 to

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* Findings are summarized on page 76 in tabular form.

TABLE 1
BODY WEIGHT AND FOOD INTAKE AFTER MANIPULATION AS PERCENTAGE OF THE PRE-MANIPULATION MEAN

	Bird	Aphagia		Week 1		Week 3		Week 5		Week 7		Week 9		Week 11	
		# of Days	Minim. BW	Maxim. BW	Mean Food	Mean BW	Mean Food	Mean BW	Mean Food	Mean BW	Mean Food	Mean BW	Mean Food	Mean BW	Mean Food
Deafferentation Group	373	4+1	87	90	90	92	98	91	91	90	106	94	129		
	349	6+1	85	87	63	88	73	88	81	96	91	97	86		
	435	4+1	86	88	74	87	87	83	83	81	100	84	113	86	120
	441	4+1	89	93	129	96	128	94	99	94	142	93	166		
	412	52+1	82*	84**	77**	85	68	86	61	88	68	88	59	90	76
Control Group	348	0+1	97	100	105	101	108	100	117						
	362	1+1	96	98	134	99	112	99	109						
Deprivation Group	339	3	90	96	134	99	108	98	109	100	122				
	374	5	88	95	103	99	103	100	104	104	106	103	96	102	91
	360	6	90	95	94	99	84	100	94	-	-	102	80	102	77

---

* Body Weight Maintained by Hand Feeding   ** 9th Post-operative Week, 1st Week of Feeding

12% in three to six days. When feeding was resumed spontaneously, food intake remained significantly under pre-operative levels for a minimum of five weeks (#435) and did not reach pre-operative levels during the whole observation period of nine to eleven weeks in two of the birds (#349, 412).

One of the birds (#441) overate from the very beginning after an aphagia of four days, however not enough to raise its body weight permanently beyond 93 to 94%. This could suggest that the week selected as pre-operative control week had an abnormally low food intake although the mean daily intake of a total of twenty-seven days preceding surgery was only slightly higher (i.e. 21.2gm instead of 20.3gm with a mean body weight of 566gm instead of 561gm. Several months earlier however, when data were taken for a period of five weeks, the bird ate 23.1gm on the average but maintaining a body weight of only 562gm).

The body weight did not recover completely in the observation period of nine to thirteen weeks in any of the birds. The resumption of feeding resulted generally in a small increase in weight (average 2.6% in the first seven days). On this level body weight was then maintained for several weeks and showed only slight but persistent increases later in the sixth to ninth weeks. Only one bird (#435) kept losing weight during the period of hypophagia. This was gained back later when food intake increased above pre-operative levels. However, in general the fluctuations in body weight from day to day and week to week were so small (about 1%) that body weight regulation clearly remained possible in spite of the loss of some control mechanism(s) which resulted in the lower levels of food intake and weight.

It seems reasonable that sensory-motor deficits might result in behavioral incapacities accounting for at least part of the hypophagia after deafferentation. The efficiency of the consummatory feeding response was in fact affected after surgery in all birds. Observation of the birds confirmed the findings of Zeigler (1973) and Levine (1974) that the act of mandibulation as well as pecking accuracy was affected so that droppage of the grain occured more frequently and grasping of the kernels was less often successful than in the normal bird. This decreased efficiency of the feeding response had several effects on the birds' behavior in their apparent attempt to compensate, which led to paradoxical results. Some birds (e.g. #349) especially in the early period after deafferentation increased the pecking rate going through the typical pecking movements each time although not always succeeding with mandibulation and thus with swallowing a grain. In this way the daily total number of responses increased although total food intake was decreased. Bird #412 showed these problems in an exaggerated form. In the face of extraordinarily high numbers of feeding responses (306% of the pre-operative level) it accomplished only 67% of its pre-operative intake. Some birds (e.g. #435) attempted to overcome the pecking deficit in a quite different way. Bursts of very rapid responses (about 5 to 8) were emitted during which the head was raised very little so that the beak almost stayed in contact with the grain. Only between these bursts, did the bird go completely through the usual pecking movements - raising its beak far enough to trigger the recording equipment with the following pecking response. This resulted in paradoxically low numbers of daily feeding responses and a seemingly high pecking efficiency. Data collected under such conditions were clearly recognized on the pattern records and in the analysis were labelled as such or replaced by data on feeding duration which was recorded accurately at all times.

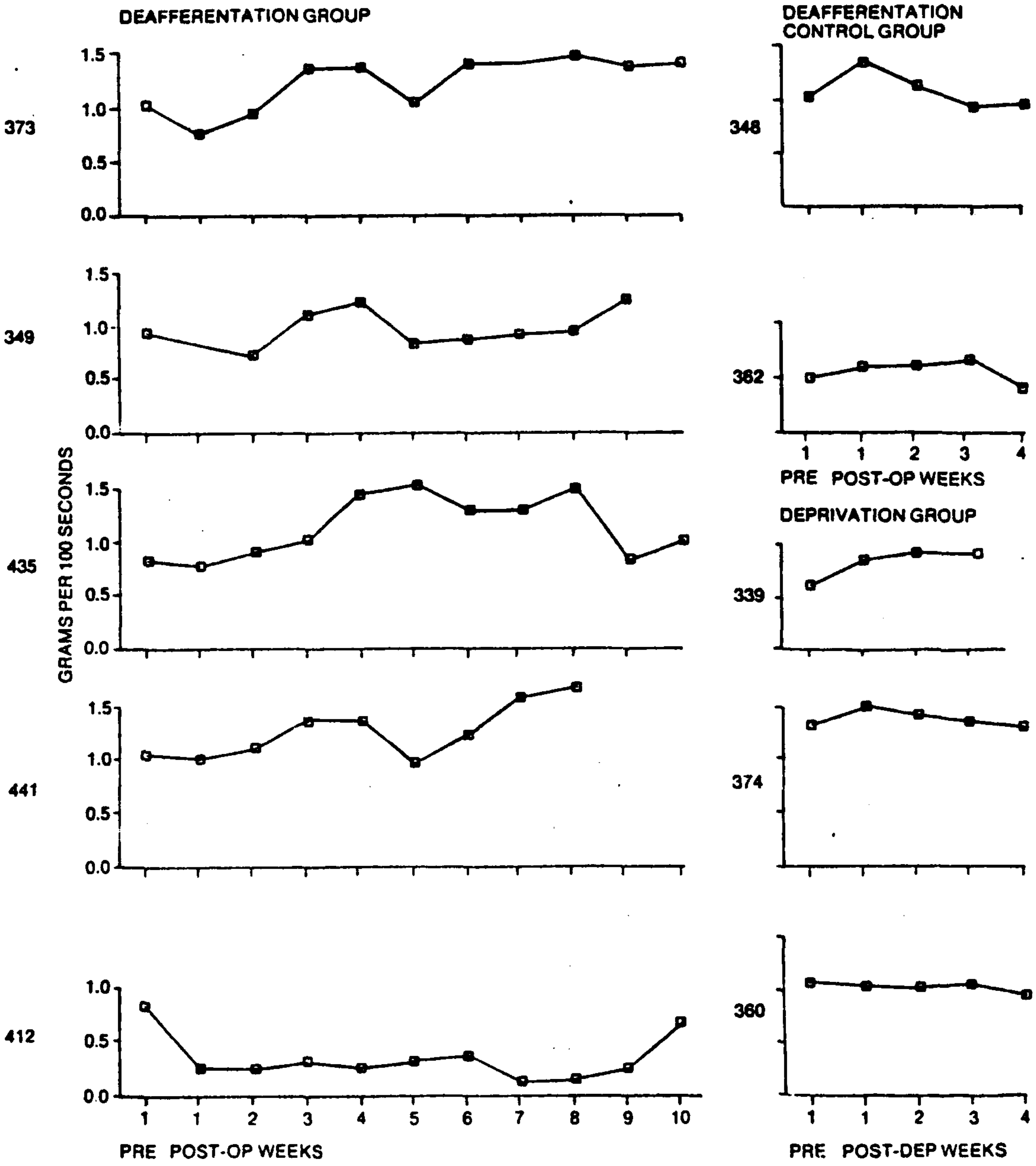
In order to assess the effect of decreased feeding efficiency after deafferentation on actual food intake per time unit, the mean rate of food ingestion was calculated by dividing the total daily food intake by the total time spent feeding during the day (FIG.4, APP. TABLE 3). In normal birds the ingestion rate was on the average 0.94 grams per 100 seconds. After deafferentation the ingestion rate in the first and sometimes also in the second post-operative week was decreased on the average by 17% (with the exception of bird #412). However, thereafter the ingestion rate was raised above the pre-operative level for practically the whole period of observation. Thus most deafferented birds obviously manage to feed themselves as rapidly as before. Therefore we cannot assume that decreased feeding efficiency is the direct cause for decreased food intake post-operatively.

Bird #412 was the only bird whose feeding efficiency was affected to a degree that clearly limited the rate of food ingestion. With a virtually unchanged mean pecking rate its ingestion rate fell to 33% of its pre-operative level when the bird resumed feeding in the eighth post-operative week. Only in the eighteenth post-operative week did the ingestion rate increase suddenly to 87% concommitantly with an increase in pecking rate (which was of a comparable magnitude).

(b) Surgical control group. The surgical control birds resumed spontaneous feeding within twenty-four hours following the sham surgery and lost on the average only 3.5% of their body weight due to the one day of pre-anesthetic food deprivation. The normal body weight was regained in the first week in one case (#348) and in the second week by bird #362

FIG. 4

MEAN INGESTION RATE (GRAMS/100 SEC)



which actually had been without food for two days because surgery was performed late in the day. That the birds continued to overeat somewhat beyond this point without increasing their weight further is consistent with the known anabolic and water retention effects of surgery due to adrenal activity requiring increased food intake as recovery occurs (Moore, 1952). No change was observed in the efficiency of the feeding response. But a transient raise in ingestion rate was observed immediately after surgery, probably an effect of deprivation.

(c) Deprivation group. Deprivation birds required three to six days of total food withdrawal to lose 10-12% of their body weight. The same range of weight loss incurred by deafferented birds during their period of aphagia. However as soon as food was restored, the deprived birds overate significantly (30-50%) and regained their normal body weight within a few weeks, about half of the loss being made up in the first week.

A raised ingestion rate was also observed in deprivation birds. As in surgical control birds it occurred immediately after manipulation and was generally of short duration. This suggests that the increase in ingestion rate was a response to food deprivation in deafferented birds as well. This assumption is supported by the finding of Zeigler, Green and Lehrer (1971) that the initial rate of feeding in a one hour feeding test increased with increasing food deprivation.

Water intake was not included in TABLE 1 because there was no characteristic difference between the three groups. None of the birds was adipsic at any time. Water intake was initiated spontaneously on the day of surgery in all cases. The daily water intake during aphagia was lower than during the pre-operative control period, as is generally the case during total food deprivation, and the reduction was of the same order of magnitude. Water intake during the hypophagia following recovery from aphagia also remained lower than pre-operatively but not as low as during the aphagic phase. (For detailed data compare APP. TABLES 1/a through 1/j).

In summary the general results on changes in body weight and food intake confirm the findings of Zeigler (1973) that trigeminal deafferentation in pigeons leads to aphagia followed by prolonged hypophagia and loss of body weight. Equivalent reduction of body weight due to simple food withdrawal in neurally normal birds was quickly corrected by overeating.

Beyond this in the present thesis research it was clearly demonstrated that the hypophagia cannot be attributed directly to sensory-motor deficits. With the exception of one bird (#412), where the inefficiency became extreme after deafferentation, the birds were capable of ingesting food at rates as great or greater than pre-operatively. Therefore the reduction in food intake cannot be explained simply by inability to eat sufficient amounts, but rather as a result specifically of the loss of trigeminal sensation. In order to determine the characteristics of the feeding behavior deficits after trigeminal deafferentation it was necessary to turn to the analysis of the changes in the feeding pattern.

2. Diurnal Distribution of Feeding

Unlike rats and many other species pigeons eat only during the hours of light. A maximum of 26% of the daily feeding activity took place in the five hours of morning feeding period while from 74% to 100%

took place in the $6\frac{1}{2}$ hours of the main feeding period (APP. TABLE 4). During the main feeding period the animals were not disturbed by any laboratory activities, while during the morning feeding period disturbance frequently occurred in the colony room. Therefore no attempt was made at detailed analysis of the morning feeding pattern. However the following general statements can be made about the feeding pattern during the morning period:

1) Feeding occurs in discrete bouts, just as during the main feeding period but the single bouts are generally much smaller and their frequency is much lower.

2) The first feeding bouts usually occur within a few minutes after the light goes on. However, there is no obvious concentration of feeding activity in any particular time interval of the morning period. (One might have expected feeding to be concentrated in the first light hour because of the preceding nine hours dark period without feeding and because there is no laboratory activity going on in the colony room during this hour).

Post-operatively the diurnal feeding rhythm was retained by all birds: feeding occurred only during the light hours, with the major food intake in the afternoon (termed main feeding period). Three deafferented birds (#373, #349, #441) were as consistent in their percentage-wise distribution of feeding responses between the two daily feeding periods pre- and post-operatively as the control birds were (surgical and deprivation controls). Only bird #349 ate appreciable amounts in the morning (23% of the daily total). The two other deafferented birds (#435, #412) with the most severe pecking efficiency deficits, shifted their feeding activity almost totally to the main feeding period (APP. TABLE 4).

3. Overview of the Daily Food Intake Pattern and Its Changes

The pattern of distribution of feeding activity and food intake which leads to the daily total and its variation is neither random, nor uniform, nor does it simply change proportionately as the total intake varies. There is a typical definable recurring pattern in normal birds, and there are characteristic changes which accompany the different metabolic and neurological manipulations. These changes give clues about the possible mechanisms involved in the control of the normal feeding pattern and hence regulation of food intake as well as the role and relation of different factors in bringing about the changes.

Although the patterns between birds can vary considerably there are certain characteristic features that are quite stable for each bird. These are:

(1) the number of bouts per feeding period.

(2) the range of bout sizes.

(3) a more or less even temporal distribution of feeding over the feeding period, often with some concentration at the beginning and rarely extending beyond 5½ hours of the 6½ hour period.

(a) Deafferentation Group

The reduction of food intake after deafferentation was accompanied by several significant changes in the characteristic parameters of feeding bouts:

1) The mean meal size was increased but the daily number of meals was decreased even more to give the net decrease in total intake.

2) The increase in mean meal size was not due merely to a proportional enlargement of all feeding bouts but rather to a marked increase in the size of only a few meals each day. As a result the major portion of food intake was in these few large meals.

3) There was a concomitant decrease in the number of smaller meals (leading to the overall reduction in total number of meals).

4) The large meals tended to occur immediately after food was made available at the beginning of the main feeding period, leading to a marked concentration of feeding activity in the first hour.

5) In most normal birds there was a gradual decrease (attenuation) in feeding per hour (size and/or frequency of meals) from the beginning to the end of the main feeding period. In deafferented birds this attenuation was much more rapid so that feeding activity (as well as pecking rate in the bouts) declines significantly after the first hour, and the intake during the rest of the day was much less than in normal birds leading to a net decrease in food intake in spite of the high ingestion rate during the first hour.

These changes are illustrated graphically in the computerized plots of meal patterns over time produced by a program adapted from Kissileff (1970). The meal plots give a qualitative visual impression of general characteristics of the feeding pattern and its changes. FIG. 5 includes plots of four representative pre-operative days and selected days of ten post-operative weeks. For comparison the meal patterns of a surgical control bird (#348) should be viewed in FIG. 6. Additional meal plots of deafferented, surgical control and deprivation control birds are included in APP. FIG. 1-3.

FIG. 5a TEMPORAL DISTRIBUTION OF FEEDING— DEAFFERENTATION (BIRD 373)

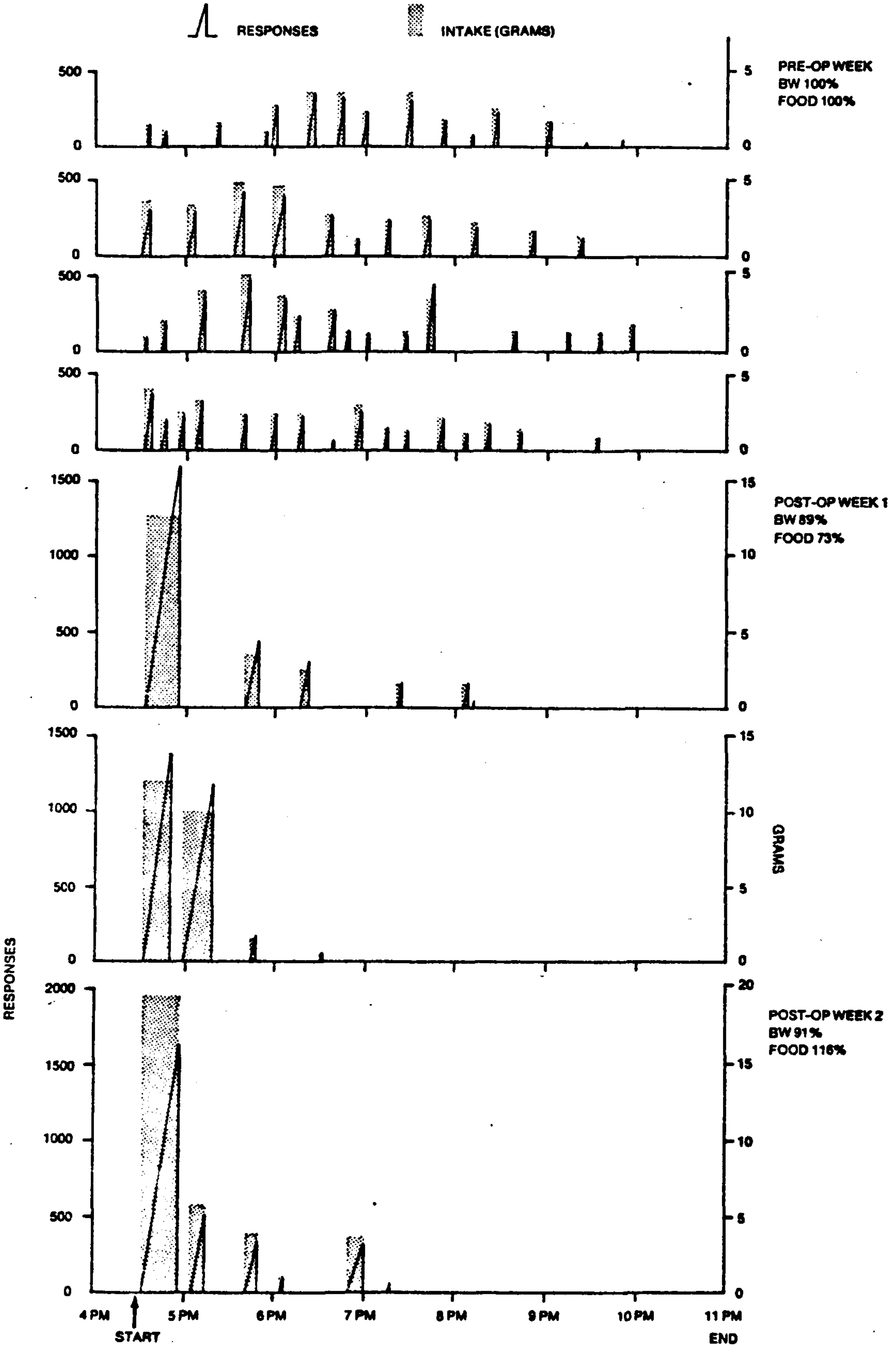


FIG. 5b

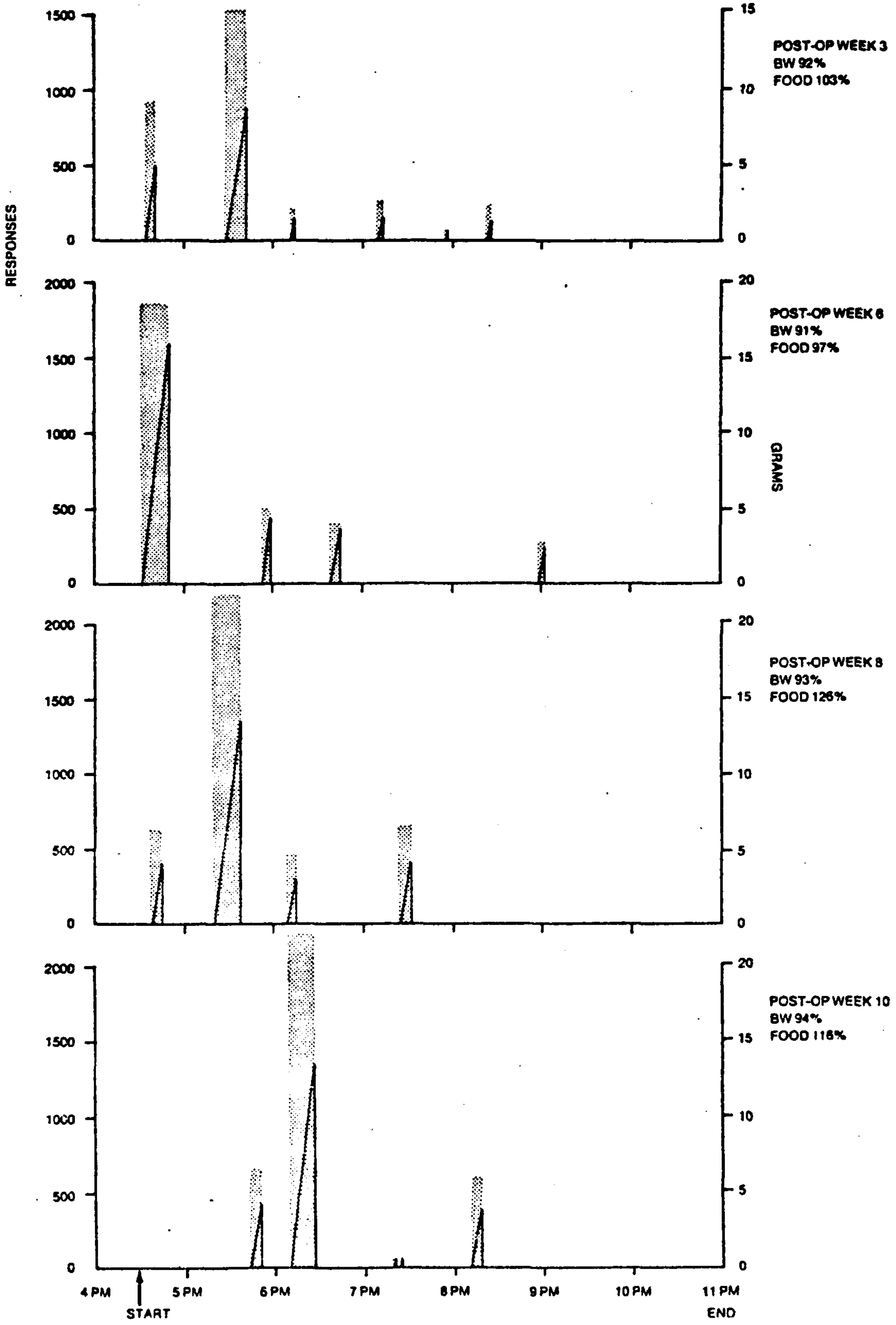
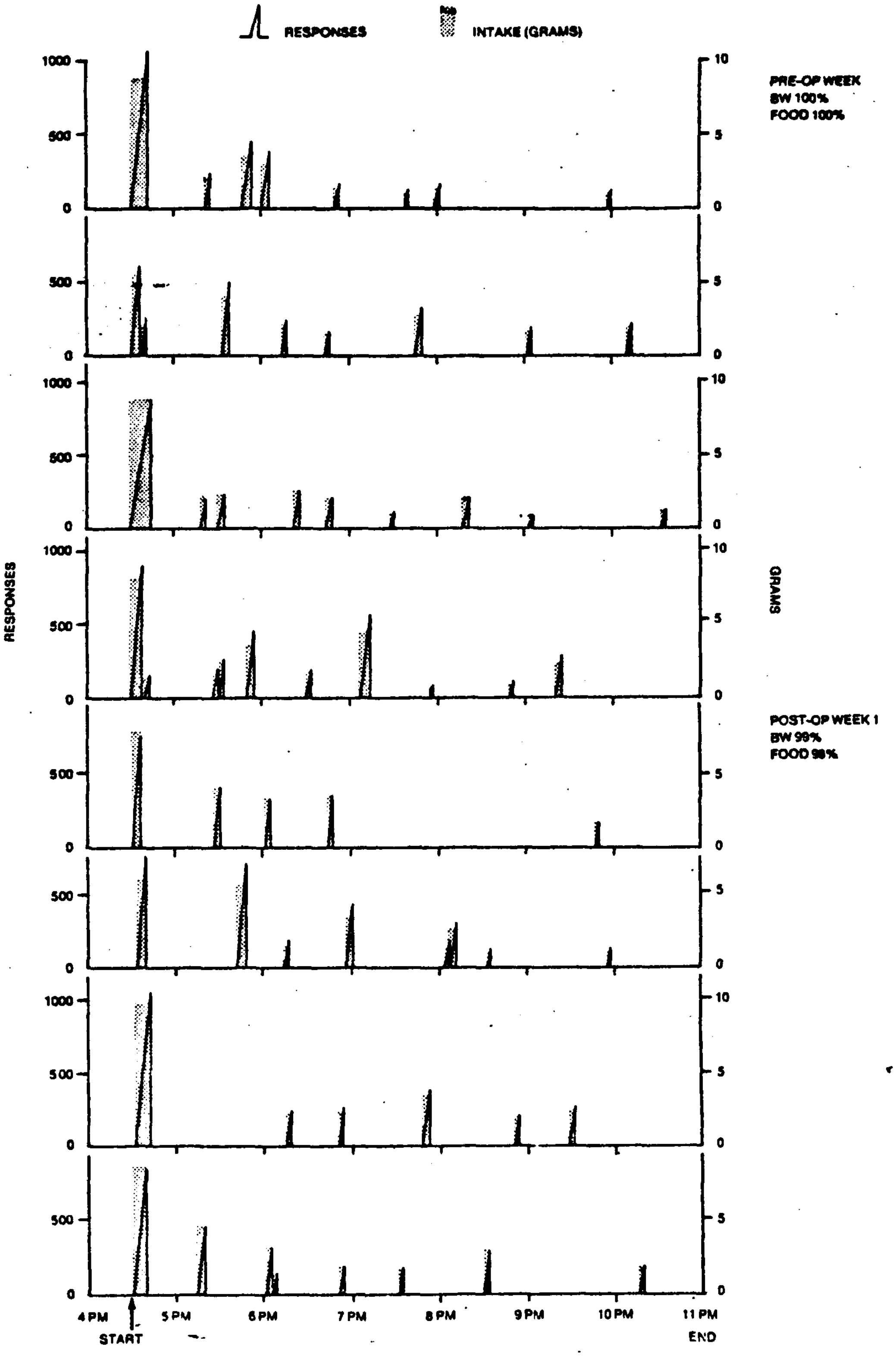

RESPONSES
GRAMS
1500
1000
500
0
15
10
5
0
POST-OP WEEK 3
BW 92%
FOOD 103%
2000
1500
1000
500
0
20
15
10
5
0
POST-OP WEEK 6
BW 91%
FOOD 97%
2000
1500
1000
500
0
20
15
10
5
0
POST-OP WEEK 8
BW 93%
FOOD 126%
2000
1500
1000
500
0
20
15
10
5
0
POST-OP WEEK 10
BW 94%
FOOD 118%
4 PM
5 PM
6 PM
7 PM
8 PM
9 PM
10 PM
11 PM
START
END

FIG. 6 TEMPORAL DISTRIBUTION OF FEEDING— DEAFFERENTATION CONTROL (BIRD 346)



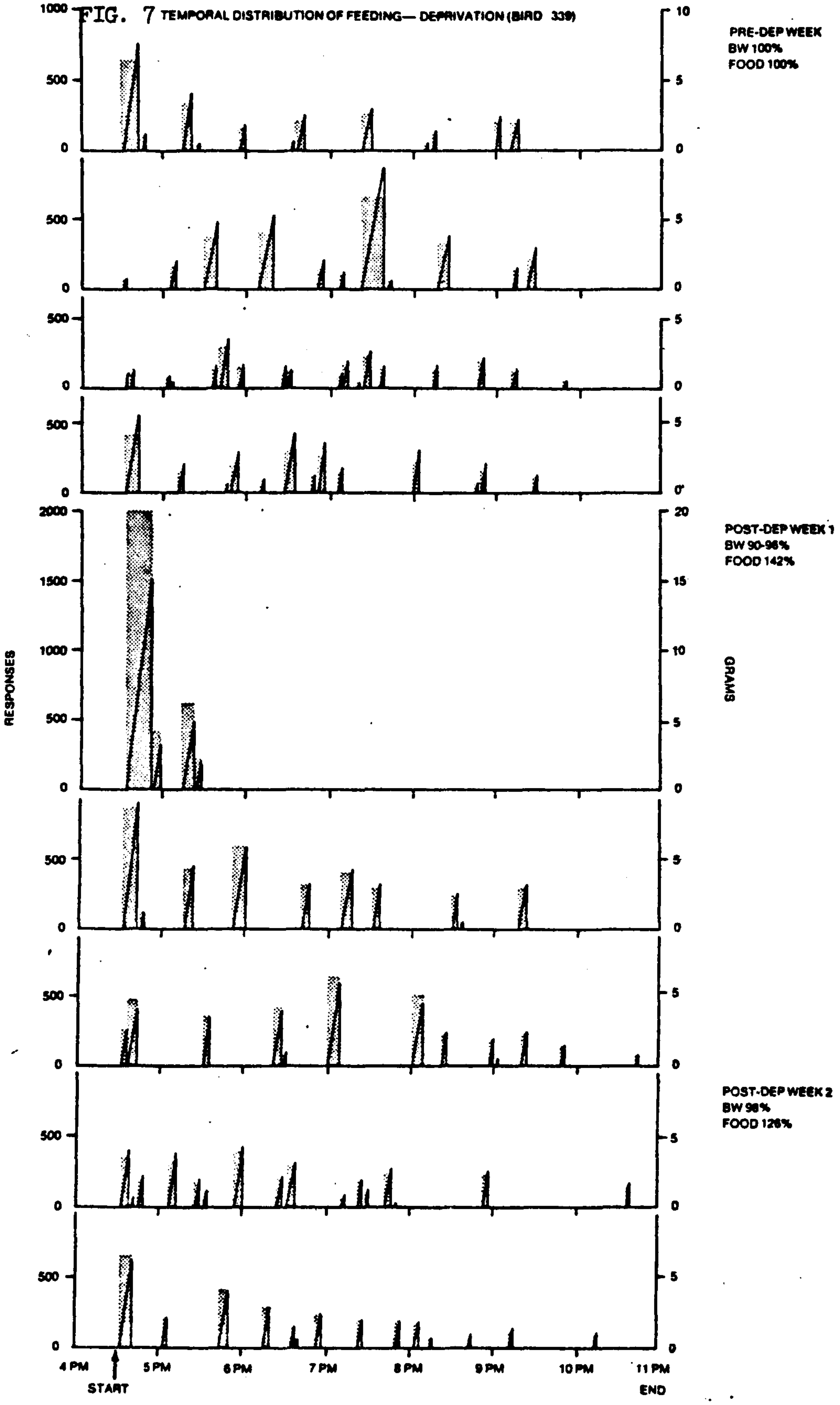


FIG. 7 TEMPORAL DISTRIBUTION OF FEEDING— DEPRIVATION (BIRD 339)

This constellation of changes seen in deafferented birds can be tentatively "dissected" into two parts:

1) Those due to the state of nutritional deprivation resulting from the lack of food intake;

2) Those above and beyond the deprivation effect which can therefore be attributed to the neurological deficity per se. These in turn must be sufficient to account for the maintenance of the deprivation state through lack of adequate intake and the failure to correct it by compensatory increased intake.

(b) Deprivation Group

Birds that were deprived to the same level of body weight simply by withdrawal of food for several days exhibited many of the same characteristic changes in the feeding pattern during the initial days or week after food is again made available. During the phase of transient (accumulated) nutritional deficit in deprivation control birds the following major changes were found:

1) The mean meal size was increased to about the same degree as in deafferented birds, but the daily number of bouts was not decreased as much so that the total day's food intake was increased.

2) The increase in mean meal size was due primarily (but not only) to the presence of one or more very large feeding bouts with the result that a large portion of feeding activity occurred in these large meals just as in deafferented birds. However this shift was not as marked as in deafferented birds (with the possible exception of the first day after food was restored), and the number of smaller bouts did not diminish to the same degree.

3) The very large meals also tended to occur as soon as food was available at the beginning of each main feeding period.

4) The deprivation control birds did not attenuate their rate of feeding (response rate, bout size and frequency) in the course of the main feeding period as rapidly as the deafferented birds. In fact after the increased activity in the first hour, the feeding during the rest of the day remained at about the same level as it was prior to deprivation with the result that the total food intake for the day was greater than before.

Again these changes are roughly discernable in the computerized meal plots of FIG. 7. However accurate comparison and differentiation of the effects due to deprivation and those due solely to the neural deficit of deafferentation require more precise quantitative measures of the pattern changes. For this reason the series of parameters and analyses was developed and applied to the detailed feeding pattern data. These demonstrated that the net effects attributable to the neural deficit alone (above and beyond the superimposed changes of deprivation) can be reduced to two:

1) greater size and/or incidence of the larger meals in which the major part of feeding occurred (and greater overall variability in the size of meals) suggesting some deficiency in the mechanisms which tend to limit the size of meals - above and beyond the "pressure" for larger meals resulting from the deprived state alone;

2) decrease in the number of smaller meals which in turn can be mainly ascribed to the rapid attenuation of feeding activity in the course of the main feeding period after the initial hour of

intensive eating. The attenuation rate was not only more rapid than in the normal bird but also more rapid than in the deprived bird which likewise overeats during the first hour. As a result the deafferented bird undereats in total for the day, which accounts for its failure to regain weight in spite of its strong first hour propensity to eat. Since there is also a rapid attenuation over the day in the pecking rate (in most deafferented birds) which neither occurs in normal birds nor in deprivation controls, this suggests that there is some deficiency in the mechanisms for sustaining propensity to eat.

In itself this cannot account for the initial aphagia since there is by definition no rapid feeding activity from which attenuation can occur. Nevertheless lack of trigeminal input obviously plays a key role in the aphagia since surgical control birds do not exhibit it. Investigation of the aphagic phase and the development of pattern changes lies outside the scope of this study. However because of the important interrelationship, implications of findings here for the explanation of the aphagia are discussed in Part IV.

4. Detailed Analysis of the Pattern Parameters

In the following pages the individual meal pattern parameters and their changes are discussed and compared for the three groups of birds. These parameters are the basis in terms of which quantitative analyses of manipulation effects were carried out. They are the key to any demonstration of causal relationships in the control of feeding patterns.

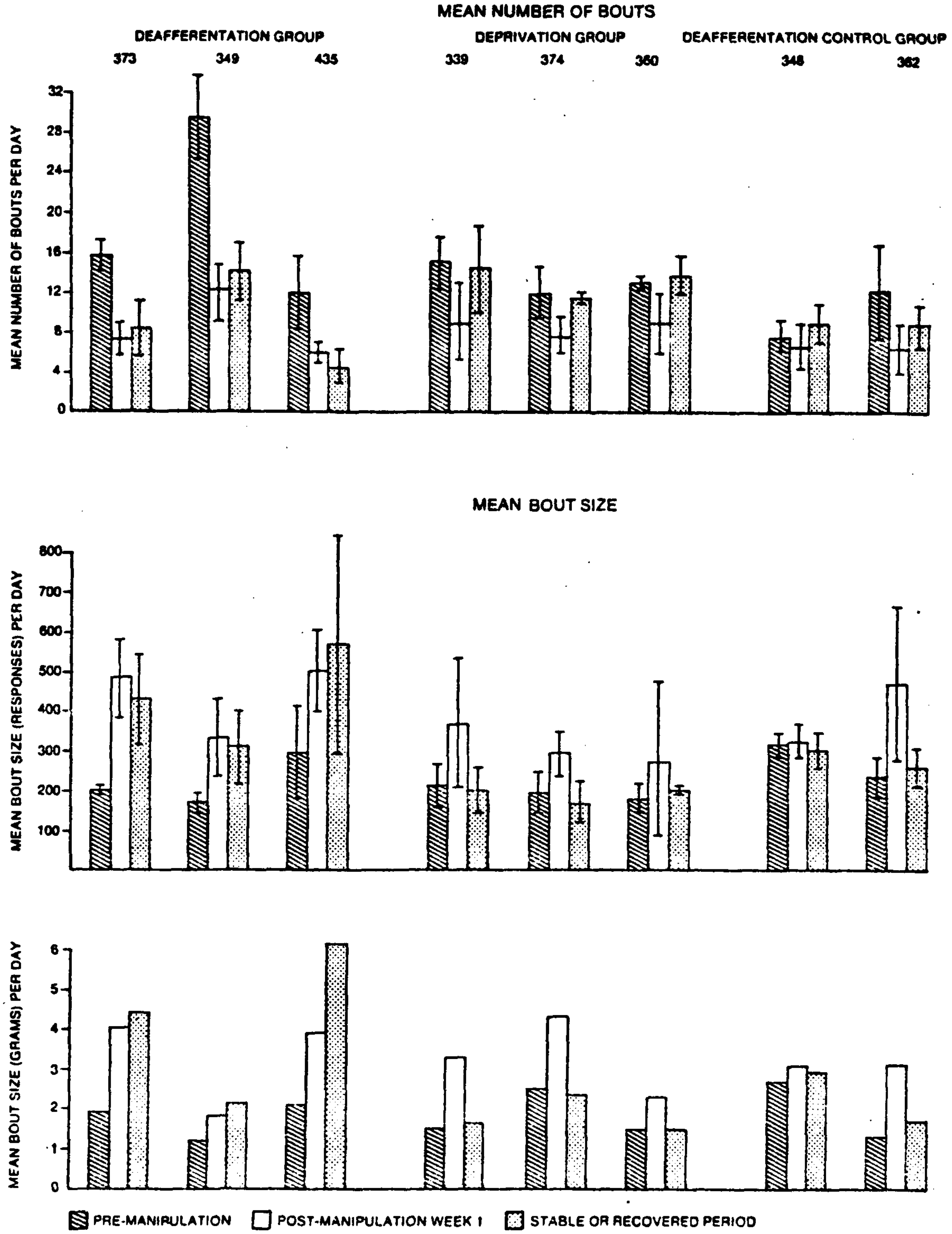
Throughout the discussion the effects of deafferentation are primarily based on analysis of three birds (#373, 349, 435) which were strikingly uniform. Two other deafferentation birds (#441 and 412) generally support the basic findings. However they are discussed separately under point 4.6. because the typical changes in their meal parameters were modified in one case by a lesser degree of the deafferentation effect and in the other by an especially marked effect on sensory-motor ability.

4.1. Mean Number of Bouts (FIG. 8; APP. TABLE 5)

(a) A pronounced decrease in number of feeding bouts during the main feeding period occurred in the deafferented birds - although the distribution of feeding activity between the morning and the main feeding period remained unchanged or was shifted more into the main feeding period. The post-operative overall mean daily bout frequency lay between 38% and 53% of the pre-operative level. The mean of single weeks ranged between 25% and 80% of the pre-operative mean; but there was no trend of development observed towards higher or lower bout numbers during the post-operative observation period.

(b) The bout frequency in surgical control birds was reduced only for a short period. During the first post-operative week the mean number of daily bouts was reduced to 87% (#348) and 53% (#362). Comparable data in the deafferented birds showed a reduction to 44%. By the second week one of the control bird's bout frequency (#348) had recovered, while the other control bird (#362) took four weeks to reach the pre-operative level. (This latter bird had gone

FIG. 8



MEAN NUMBER OF BOUTS

MEAN BOUT SIZE

two days without food during the surgical period, and resembled, therefore, somewhat more the deprivation birds).

(c) The deprivation control birds were similar to the surgical controls in regard to bout frequency. After an initial decrease to about 64% of the pre-operative value (which also is appreciably smaller than in deafferented birds) recovery of the normal bout frequency occurred fairly rapidly in the following weeks.

4.2. Mean Bout Size(FIG. 8; APP. TABLE 6)

(a) The mean bout size as measured in number of responses was increased dramatically in deafferented birds in the first post-operative week and remained above the pre-operative level throughout the observation period. The overall mean of the post-operative period of observation ranged from 166% to 221% of the pre-operative mean. It is not surprising that a decreased pecking efficiency after trigeminal deafferentation led to an increased number of responses per feeding bout and consequently to an increase in bout duration. However, post-operatively the mean bout size was also consistently larger when measured in grams of food ingested. Its weekly mean ranged between 172% and 291% of the pre-operative level.

(b) Mean bout size was practically unchanged in one of the surgical control birds (4% when measured in responses, 15% when measured in grams of food). This bird had initiated feeding on the day of surgery so food deprivation was minimal. The second control bird (#362) showed a considerably increased mean bout size in the first post-operative week of feeding (97% for responses and 138%

for gram food) and a slow tapering off in the following three weeks. This resembled closely the behavior of food deprived birds and was in agreement with the fact that this bird was operated late in the day and initiated feeding only on the day following surgery, thus undergoing two full days of food deprivation.

(c) The mean bout size of deprivation control birds was always raised significantly in the first week of free feeding. Measured in responses the mean bout size ranged between 152% and 175% of the pre-deprivation mean. For the same time period after deafferentation typically the mean bout size was increased from 179% to 253% (APP. TABLE 7). Measured in grams of food, however, the increase of deafferented and deprived birds was roughly the same. Mean size for four deafferented birds ranged between 149% and 218% for simply deprived birds between 147% and 220%. The relatively higher number of responses per bout in deafferented birds can be accounted for by the decreased feeding efficiency after surgery. Thus on the basis of mean bout size alone one might be tempted to conclude that the feeding pattern of deafferented birds is merely a pattern of food deprived birds. However in deprived birds mean meal size recovered to baseline levels within three weeks in two birds (#339 and #360). The third bird required more than four weeks.

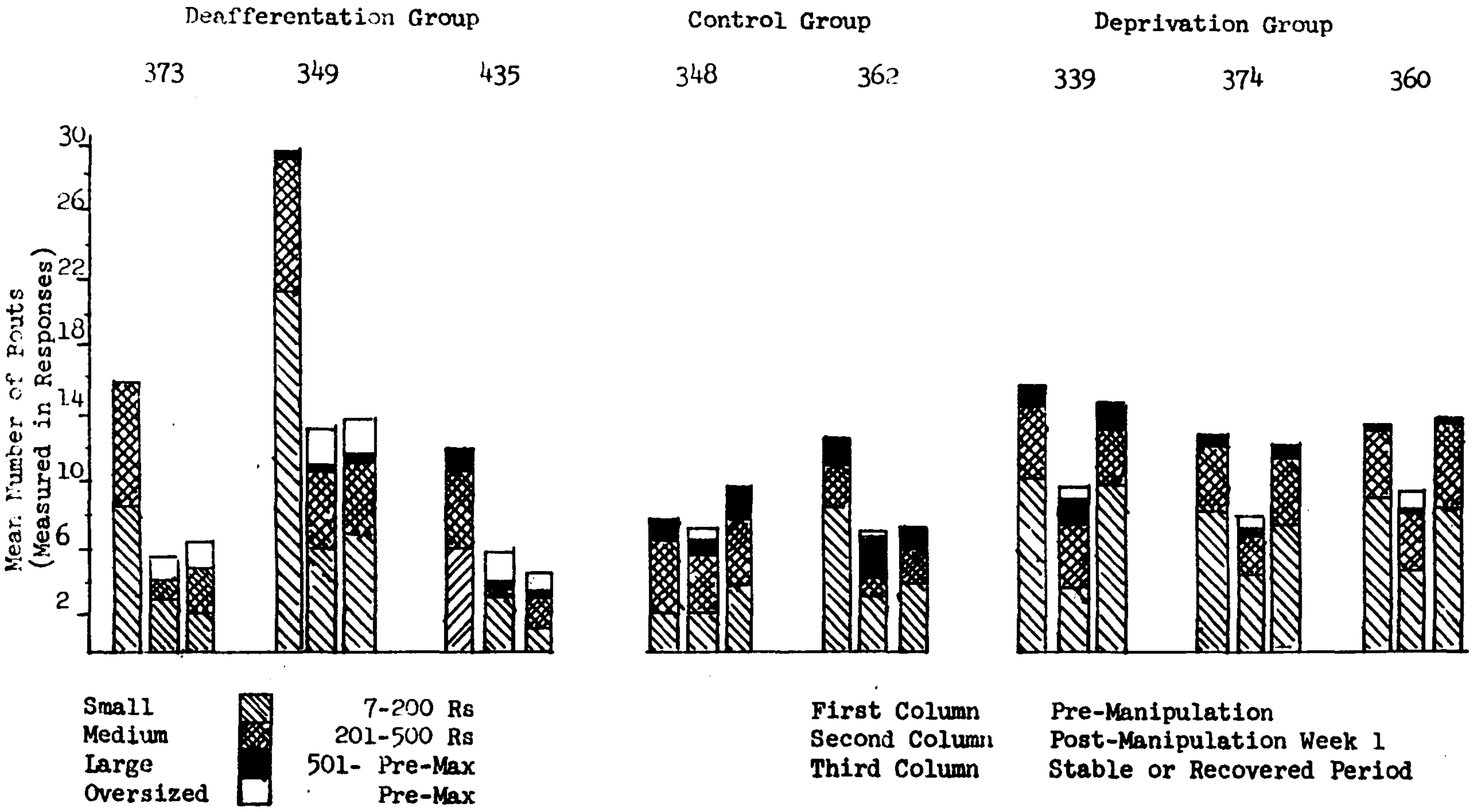
The question arises then, why deafferented birds do not also regain their pre-operative body weight level. This can be answered by the finding that daily bout <u>frequency</u> after deafferentation was more reduced than after food deprivation. Moreover simply comparing the <u>means</u> of bout size and bout frequency conceals characteristic changes in the distribution of intake among the bouts of different sizes.

4.3. Frequency Distribution of Bout Sizes (FIG. 9; APP. TABLES 8, 9)

The results of this and the next sub-chapter are based on detailed computer analyses of the frequency distribution of bout sizes and the distribution of feeding activity by bout size. Examples of frequency distribution of bout sizes are given in APP. FIGS. 4, 5. The daily and weekly averages of number of bouts were calculated and plotted for bout size categories of less than 100 responses or one gram, 100-200 responses or 1-2 grams, and so on up to 2400 responses or 16 grams. (The last category also includes all bouts larger than the indicated size). The bout frequency distributions show the tremendous dispersion of bout sizes after deafferentation compared to pre-operatively. Post-operatively, bouts occurred in all the pre-operative bout sizes, but in addition very large feeding bouts were exhibited. Post-operatively maximum bout size occurred in the first week after food intake was resumed and reached as much as 540% of the pre-operative maximum bout size measured in responses, 460% measured in grams. Post-operatively the largest number of bouts still fell within the pre-operative range: However, they no longer accounted for the major part of the food intake, as they did pre-operatively, since the bulk of the food intake after deafferentation took place in a few very large meals (compare next sub-chapter).

Four bout size categories were used for secondary analysis of distribution of bout sizes and the distribution of feeding activity

FIG. 9
MEAN FREQUENCY DISTRIBUTION OF FOUR BOUT SIZE CATEGORIES



among bout sizes in the normal bird. These were selected and based on the frequency of occurrence.

Small bouts: up to 200 responses or 2 grams. This category usually includes a high number of meals and comprises about half of the daily intake in the normal bird.

Medium sized bouts: between 200 and 500 responses or 2 and 5 grams. This category usually includes a smaller number of meals but also usually comprises about half of the daily intake.

Large bouts: bigger than 500 responses or 5 grams. They are very few in number (usually only 0-1 per day) and comprise relatively little of the pre-operative daily intake.

Oversized bouts: bouts, larger than the biggest bout of the period before the experimental manipulation occurred (surgery or deprivation).

The value of this classification of bout sizes is three-fold: (1) It allows a more easily comprehensible comparison of bout size frequencies between birds. (2) It pinpoints the post-operative effect on meal size to specific size categories. (3) It helps distinguish the effect of deprivation on meal size from that of deafferentation.

(a) FIG. 9 shows that the decrease in number of bouts after deafferentation was primarily due to a reduction in the number of small bouts (to 26-37% of the pre-operative value) and to a somewhat lesser degree to the reduction of medium sized bouts (to 31-50% of the pre-operative value) (APP. TABLE 8a). If large meals were taken pre-operatively, they occurred infrequently and their number did not change much post-operatively (although percentage-wise this can appear as a large increase). Post-operatively one to two oversized meals per day always occurred. If we compensate the apparent bout sizes for the changing feeding efficiency by expressing them in grams of food intake, the same trends are observed.

(b) The surgical control birds did not show drastic changes. In one of the birds (#348) the post-operative changes deviated very little from its pre-operative mean. The second bird's (#362) bout size distribution showed features that resembled to some degree the characteristics of deprivation controls (as previously mentioned this bird had actually been without food for two days).

(c) The discussion of food deprived birds (FIG. 9; APP. TABLE 8b) has to be based on the first post-deprivation week during which the body weight had not yet recovered in order to be comparable with deafferented birds. During this first phase all deprivation controls showed, like deafferented birds, an impressive decrease in the number of small bouts (to 37-53% measured in responses) and a more moderate reduction (to 60-79%) or no change in the number of medium sized bouts. The large bouts did not change appreciably in number, but there were always some oversized feeding bouts, though fewer than were typical for deafferented birds. Thus the same type of frequency changes in the different bout sizes occurred in deprived and deafferented birds. The only difference seems to be one of degree. The lower reduction of small and medium sized bouts was responsible for the smaller reduction of total daily bouts after simple food deprivation than after deafferentation. As we will see, this is a significant difference with important consequences for understanding the regulation of body weight.

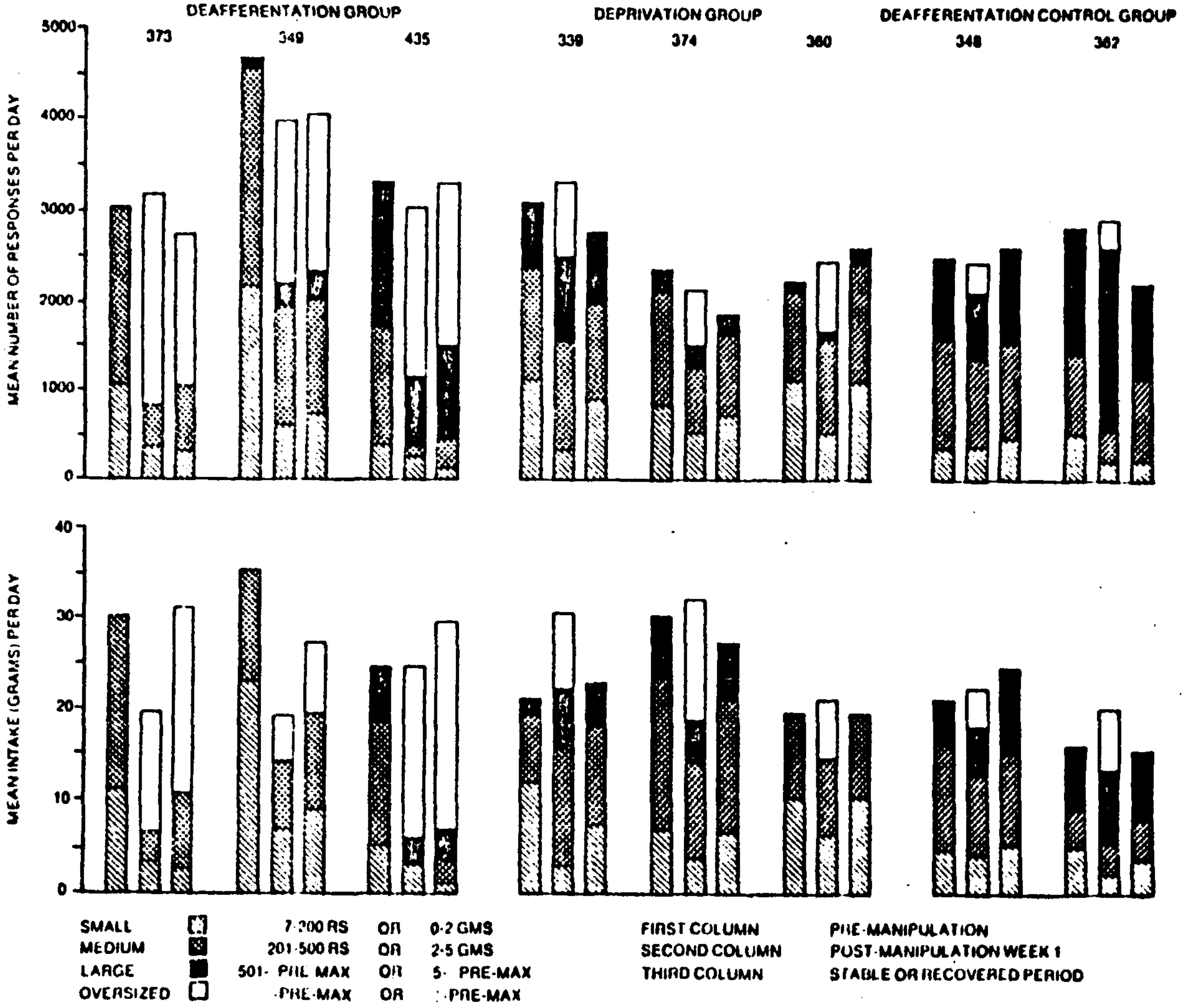
A week-by-week comparison of the described effects showed no recovery of total number of bouts nor of the bout size frequency distribution in deafferented birds in the post-operative observation period of up to 12 weeks. (Some indication of recovery in weeks 6, 7, 8 in bird #349 will be discussed below). The surgical and the deprivation control birds, however, showed recovery of the pre-operative frequency distribution of bout sizes (as well as total number of bouts).

4.4. Distribution of Feeding Activity by Bout Size (FIG. 10; APP. TABLES 10,11

These changes in the frequencies of different bout sizes entailed a qualitatively new distribution of feeding activity and food intake, which was persistent in deafferented birds, while it was transient and less pronounced in simply deprived birds. Any bout size frequency distribution necessarily gives the same weight to each bout, no matter whether it consists of 7 or 2,000 responses. It demonstrates in which way the bird grouped its feeding activity into bouts but reflects only indirectly in which bout size the major part of the daily food intake was consumed, i.e. whether the major intake was accomplished in many small, or a few large meals or was more evenly distributed among many bout sizes. Therefore, the total number of responses and the total grams of intake have been calculated for each bout size for each day and week. An example of the computerized analysis on which the following discussion is

FIG. 10

MEAN FEEDING ACTIVITY IN FOUR BOUT SIZE CATEGORIES



based is given in APP. FIGS. 6,7 for a deafferented bird. It is obvious that the distribution curve is not just displaced or flattened or more spread (as it would have been if all bouts were merely proportionately increased in size), but that a completely different curve shape arose after deafferentation.

(a) To quantify these results feeding activity was compared in the four already described bout size categories (FIG. 10; APP. TABLES 10a,11a). The most conspicuous characteristic of the post-operative pattern was that on the average more than 50% of the food intake occurred in oversized bouts, i.e. in bouts larger than the pre-operative maximum bout size (APP. TABLE 11a). However this size category makes up only 19% of the daily total number of bouts (or 23% if bouts are measured in grams) (APP. TABLE 10a). Thus more than half of the daily intake occurred post-operatively in very few large bouts.

Before deafferentation almost the total food intake (about 90%) occurred in small and medium sized bouts, i.e. in bouts smaller or equal to 500 responses (or 5 grams). A large number of small bouts ($\leq$ 200 responses, or 2 grams) comprised about 40% of the daily food intake, and fewer medium sized bouts (200-500 responses or 2-5 grams) comprised 50% of the daily intake. After deafferentation food intake in small bouts played only a minor role, barely including 10% of the daily intake (although about 40% of all bouts were still small). Post-operatively medium sized bouts comprised about 25% of the daily intake (in about 25% of the total bouts). Large (but not oversized) bouts showed practically no difference from their pre-operative level.

These drastic changes in intake distribution were apparently permanent in deafferented birds. Only bird #349 developed an interesting inclination toward partial recovery in weeks 6, 7, and 8. In week six its food intake rose by 19% (of pre-operative intake level) reaching the mean pre-operative food intake. Body weight increased to 93% of its pre-operative value. During this week the largest amount ever was eaten in oversized meals. In the 7th and 8th week, however, when its body weight reached 96% and 97% and food intake was again down to 91% and 79%, there was a conspicuous decrease of the role of oversized meals. This clearly resembles the recovery of feeding distribution in food deprived birds, although in the deafferented bird this process was not completed.

(b) Changes in food intake distribution in surgical control birds were conspicuously smaller than in deafferented birds. Bird #348 recovered in one to two weeks. Bird #362 showed larger changes presumably due to its longer food deprivation, but also recovered.

(c) Deprivation controls exhibited interesting findings during the first week of resumption of feeding (FIG. 10; APP. TABLES 10b, 11b). At first glance distribution of feeding activity after food deprivation alone may look quite similar to that after deafferentation. However on the average only 30% of the food intake occurred in oversized meals.

The pre-deprivation distribution of feeding activity was quite similar to that described for the pre-deafferentation birds, also with about 40% of the food intake occurring in small bouts, and about

50% occurring in medium-sized bouts. In the first week of feeding after deprivation small bouts included an average of 18% of the daily intake, medium-sized bouts an average of 40%. Large (but not oversized) bouts showed no change or minor increase. However if we exclude the first day with the extreme feeding pattern from the mean of the first week, large bouts and/or medium-sized bouts clearly played a more important role in food intake than before deprivation. This is also indicated during the later weeks of recovery. Rather than talking of a new distribution of feeding activity it seems, therefore, more appropriate to describe the feeding pattern of the deprived bird as characterized by a general increase in bout size upon which only one very large (oversized) bout per day has been superimposed. (Compare APP. FIG. 3)

Thus clearly the food intake pattern after trigeminal deafferentation was greatly influenced by the state of deprivation resulting from the period of aphagia following surgery. However the described intake pattern led to overeating in the deprived bird and to body weight recovery while the deafferented birds remained hypophagic for many weeks and maintained body weights only slightly above the level to which they fell during aphagia. The described quantitative differences in intake distribution must account for the impairment of body weight regulation after deafferentation.
In order to learn more about the relationship between meal taking as described above and overall food intake, the temporal distribution of feeding activity was investigated.

4.5. The Hourly Distribution of Feeding Activity*(FIG. 11-13; APP. TABLES 12-14)

Most of the normal birds (8 out of 10) exhibited the peak of their feeding activity at the beginning of the main feeding period. Food intake was highest during the first hour, tapered off very slowly during the second and third hour in some birds (#373, #435, #339, #374), fell then more rapidly during the next two hours and was generally insignificant during the last 1½ hours of the light period. Other birds (#349, #348, #412) already showed a sharper decline of food intake in the second hour. Only two birds (#441 and #360) had their peak of feeding activity in the middle of the feeding period.

(a) After deafferentation (FIG. 11; APP. TABLE 12) the food intake in the first hour was increased by about 100% in two birds (#373, #435) while bird #349 with the consistently lowest intake did not even reach its pre-operative mean intake of the first hour. In the second hour however, food intake fell off sharply in all three birds to below pre-operative levels and kept falling more rapidly than before surgery. From the second hour onward only an average of 51-67% of the pre-operative mean food intake of the same period was consumed.

(b) The surgical control birds (FIG. 11; APP. TABLE 13) did not deviate significantly from their pre-operative temporal feeding

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* To make the presented data directly comparable between birds feeding activity is based on grams of food eaten. Thus we eliminate the differences in pecking efficiency between birds and between pre- and post-operative conditions.

FIG. 11

HOURLY MEAN FOOD INTAKE

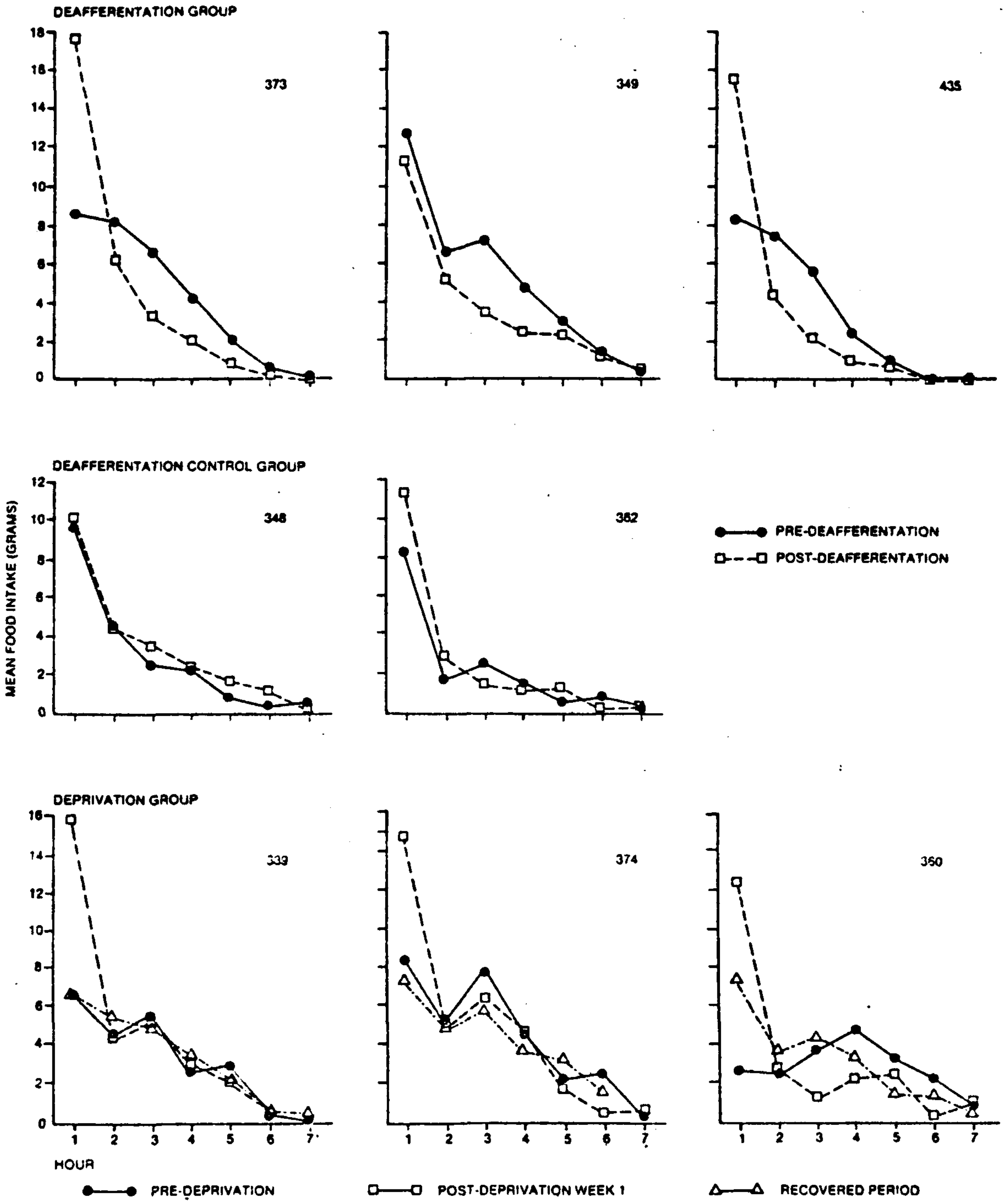
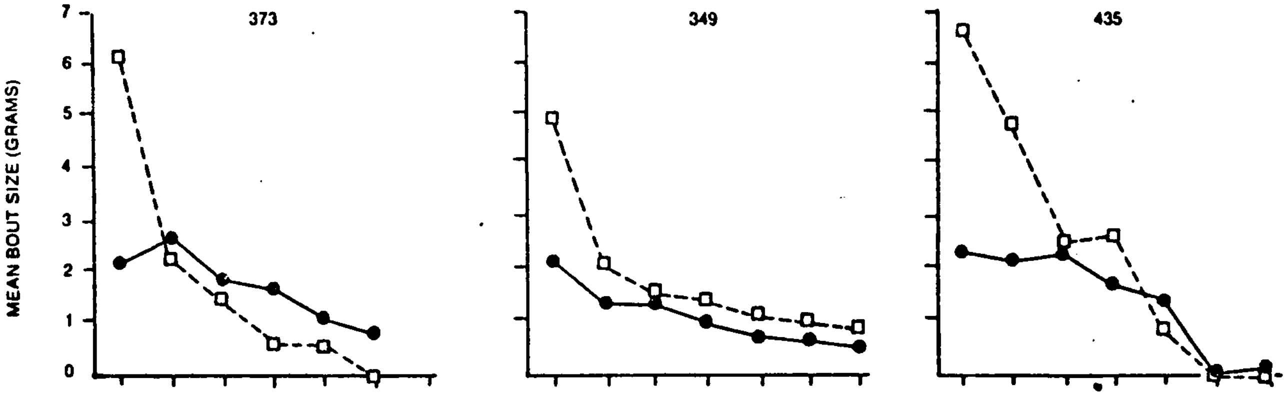


FIG. 12

HOURLY MEAN BOUT SIZE—DEAFFERENTATION GROUP



HOURLY MEAN NUMBER OF BOUTS—DEAFFERENTATION GROUP

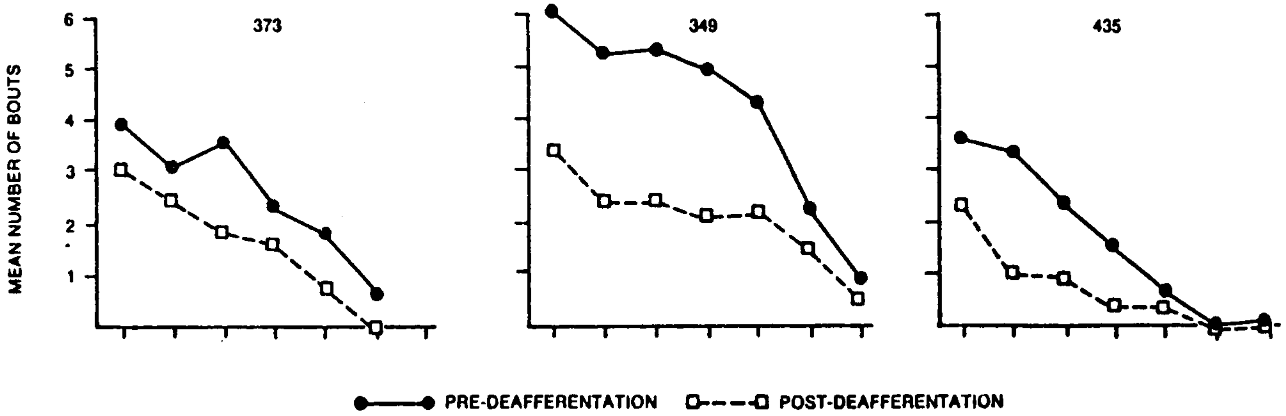
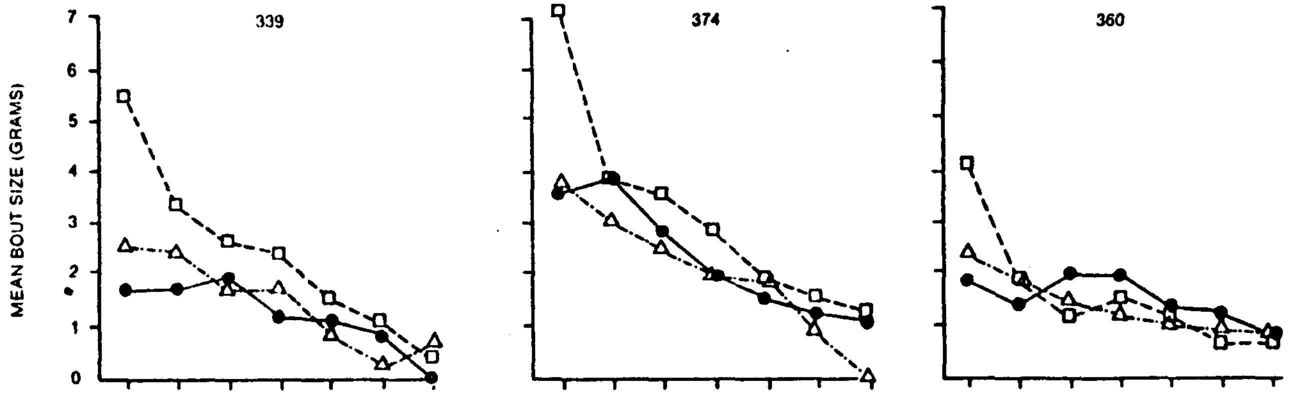
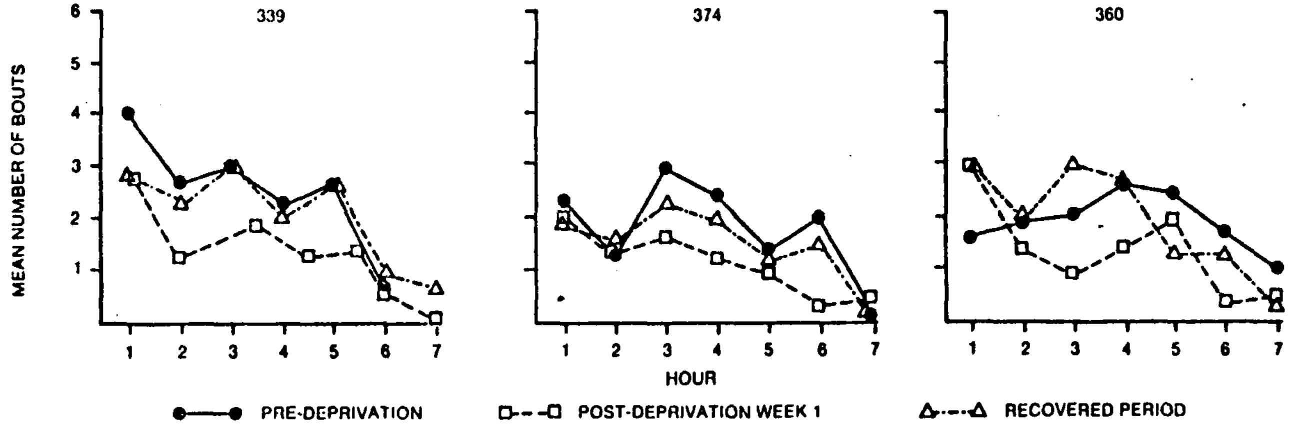


FIG. 13

HOURLY MEAN BOUT SIZE—DEPRIVATION GROUP



HOURLY MEAN NUMBER OF BOUTS—DEPRIVATION GROUP



distribution. One of the birds (#348) showed practically no change. It regained its small weight loss (3%) by eating slightly more throughout the day. The other bird (#362), probably due to its more food deprived state, increased its food intake in the first hour by 37%; but the feeding activity during the following hours was clearly normal (99% of the pre-operative intake level).

(c) The deprivation control birds (FIG. 11; APP. TABLE 14) differed from deafferented birds in a very interesting way. While they also increased food intake during the first hour by about 100% (birds #374, #339), they exhibited only about the same rate of feeding attenuation during the following hours as they did before deprivation, eating 84% to 91% of the pre-operative intake of this period. It is this difference in the level at which food intake was maintained, after the initial burst of intense feeding activity, that seems to be responsible for the inability of deafferented birds to regain their normal body weight.

Deprivation bird #360 is not directly comparable with the other deprived birds in this regard, because of its different intake curve before deprivation with the peak in the middle of the feeding period. It followed, however, the same trend. In the first hour its intake was increased to more than 400% of the pre-deprivation level. This was then compensated for by eating only 63% of the pre-operative intake for the rest of the feeding period.

After regaining their body weight, the deprivation birds also recovered their normal temporal distribution of intake completely. Only bird #360 continued to have its highest intake in the first hour of feeding, but showed no appreciable deviation in the later hours of the feeding period. Thus its "recovered" intake curve very much resembled the normal intake curve of the other two deprivation birds.

The hourly distribution of meal sizes and of the number of meals sheds light on the behavioral mechanisms that lead to undereating by deafferented birds (FIG. 12; APP. TABLE 15,17) and to overeating by deprived birds (FIG. 13; APP. TABLE 16). Both deafferented and deprived birds ate their exceptionally big meals during the first hour of the feeding period. Both groups ate consistently fewer meals than pre-operatively during all hours of the feeding period. In two points, however, deafferented and deprived birds differed. (1) Deafferented birds (especially #349) showed a higher reduction of number of meals after the first hour of feeding than simply deprived birds. (2) While deprived birds compensated for this reduction in number of meals by an increase in meal size, deafferented birds failed to do so (the mean meal size was even slightly decreased in bird #373). Thus it becomes clear that simply food deprived birds made up for their lost body weight by increasing the amount of intake at the beginning of the feeding period in very large feeding bouts. During the rest of the day their intake was normal, though accomplished in somewhat fewer but therefore somewhat larger bouts. Deafferented birds overate in the first hour too, but they failed to maintain a normal level of feeding activity during the rest of the day eating fewer bouts without compensating by a significant increase in bout size.

4.6. Discussion of Special Features in Two Deafferented Birds (#441, #412)

Although all birds in the experimental deafferentation group exhibited the same general tendencies in regard to the changes of most feeding pattern parameters, two of the birds require special discussion because of certain anomalies which occurred in their behavior after surgery.

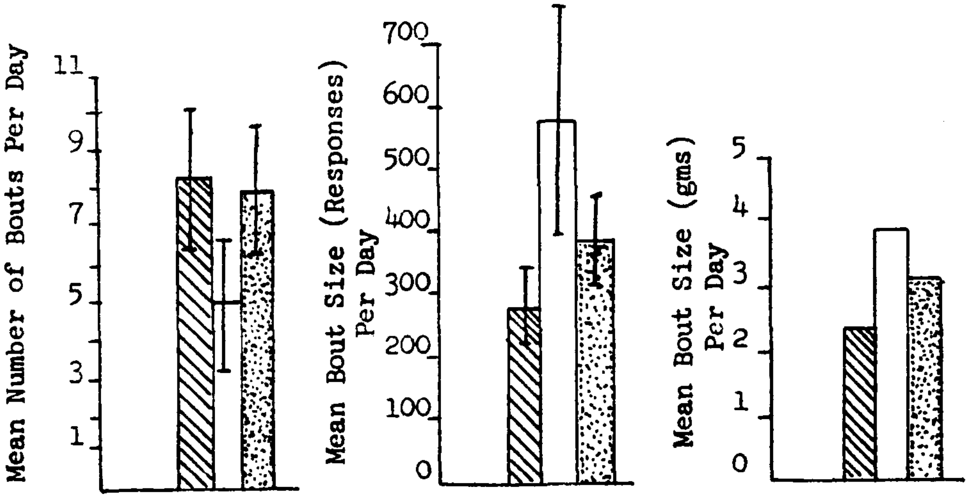
As already described, bird #441 after four days of aphagia exhibited a higher food intake than pre-operatively during most of the post-operative period of nine weeks, but only high enough to maintain a body weight of 93-94% (TABLE 1; APP. TABLE 1). The mean bout size in the first post-operative week was increased (193% of the pre-operative level) and compared well with deafferented and simply deprived birds (FIG. 14; APP. TABLE 7). The mean number of bouts in the same period was reduced less than in other deafferented birds (to 69% of the pre-operative level). This is in accord with the fact that the bird's food intake was 129% of the pre-operative intake.

During the first week of feeding the frequency distribution of bout sizes and the distribution of feeding activity by these bout sizes (FIG. 15) showed the extensive changes that are typical for the other deafferented birds. The feeding pattern was dominated by bouts larger than the biggest pre-operative bouts, i.e. more than 50% of the intake occurred in very few oversized bouts. The reduction of the total number of bouts was mainly due to the reduction of medium sized bouts by 95%. Feeding in this bout size category comprised 64% of the daily total

FIG. 14

MEAN NUMBER OF BOUTS MEAN BOUT SIZE

DEAFFERENTATION BIRD 441



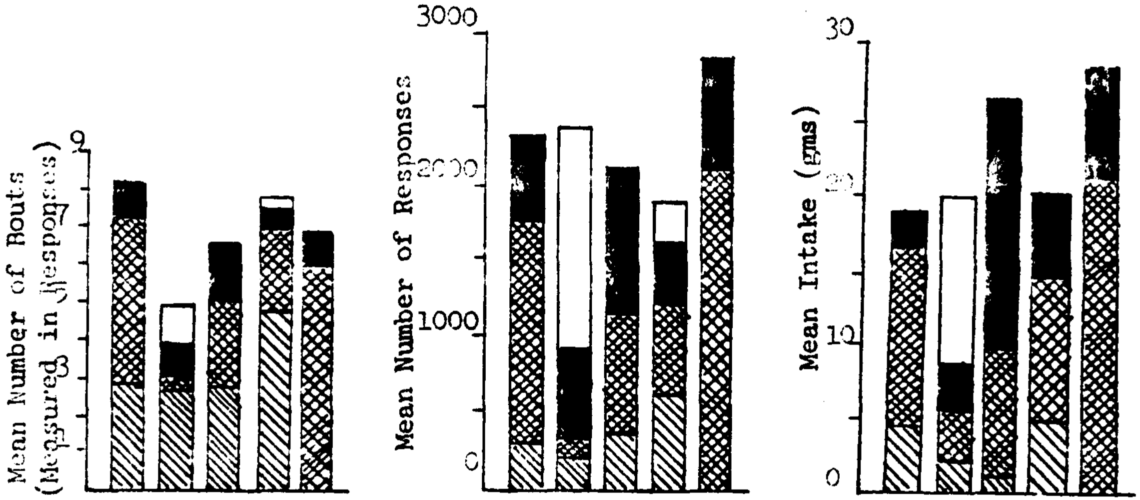
▨ Pre-operative Week ☐ Post-operative Week 1 ▩ Post-operative Weeks 2-7

FIG. 15

MEAN FREQUENCY DISTRIBUTION OF FOUR BOUT SIZE CATEGORIES

MEAN FEEDING ACTIVITY IN FOUR BOUT SIZE CATEGORIES

DEAFFERENTATION BIRD 441



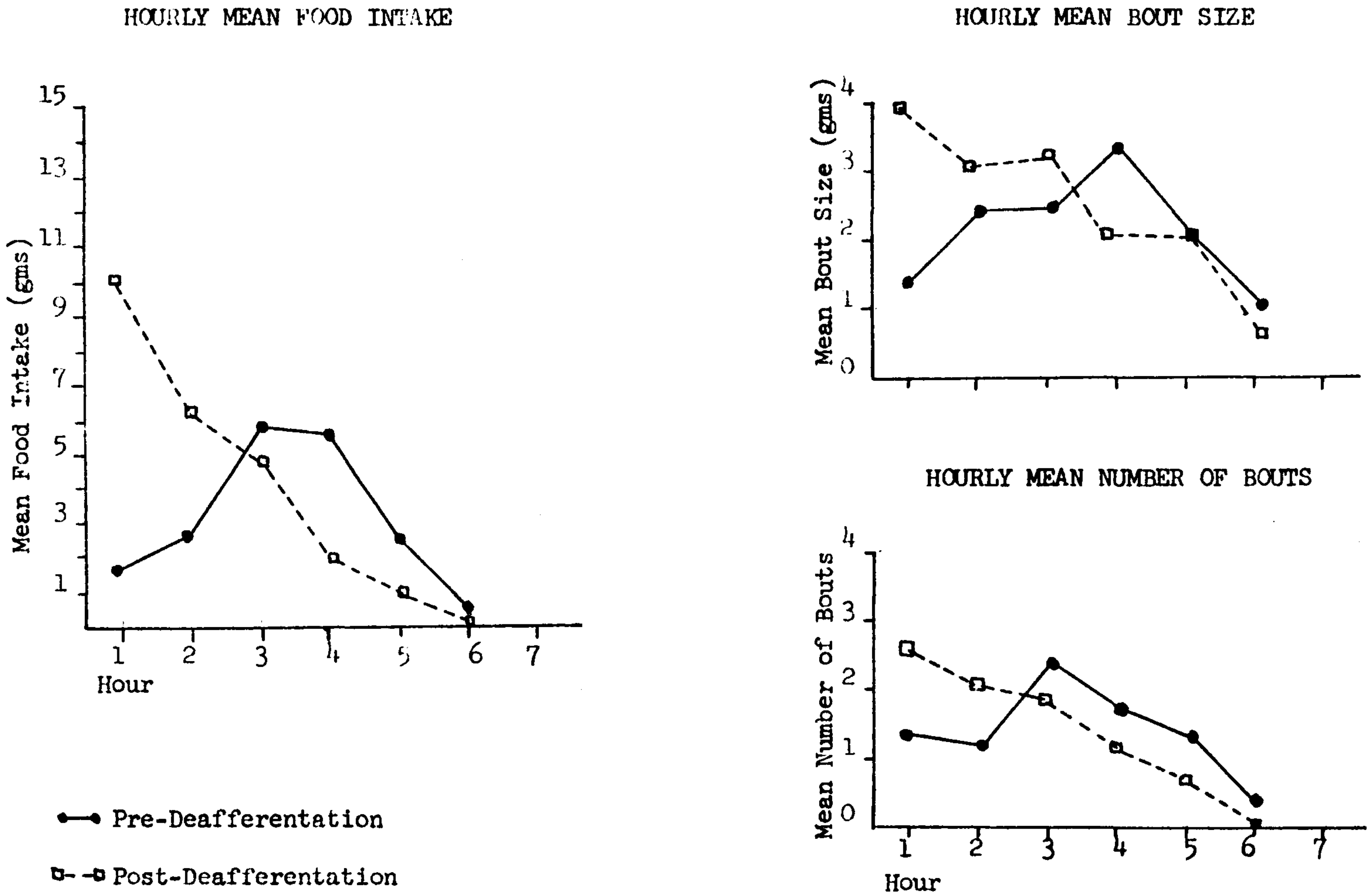
Small	▨	7-200 Rs or 0-2 gms	
Medium	▩	201-500 Rs or 2-5 gms	First Column - Pre-op Week
Large	■	501- Pre-Max or 5- Pre-Max	Second to Fifth Column -
Oversized	☐	Pre-Max or Pre-Max.	Post-op Week 1,2,4,7

intake before surgery and was reduced to 3% if bout size is measured in responses, and to 19% if measured in grams. However, this pattern of feeding activity was not maintained in the later weeks, as was typical for the other deafferented birds. Nor did bird 441 return to a stable feeding pattern in the way deprivation birds did. The daily feeding pattern remained highly variable during the whole post-operative observation period. For example in post-operative week 2 "large" bouts contributed a major part to food intake (64% compared to 13% preoperatively). Oversized bouts were exhibited again in the fourth postoperative week. However actual food intake per bout did not exceed pre-operative bout sizes due to the persistently decreased pecking efficiency. This seems to indicate that in bird 441 deafferentation also led to disturbance of meal size control, although the shift in intake to oversized bouts was not as marked and persistent as in the other experimental birds.

The hourly distribution of feeding was permanently changed after deafferentation (FIG. 16; APP. TABLE 12). Bird 441 was one of the two cases with the peak of food intake in the middle of the feeding period rather than at the beginning. This makes a direct comparison with the other deafferented birds more difficult. However, as soon as food intake was resumed feeding was concentrated in a one to two hour interval starting in the second hour of the main feeding period. Beginning with the fourth day of feeding the peak activity and the largest bouts shifted permanently to the first hour of the feeding period followed by a continuous attenuation throughout the rest of the day. Thus after the third day the hourly feeding activity distribution closely resembled

FIG. 16

HOURLY MEAN FEEDING ACTIVITY -- DEAFFERENTATION BIRD 441



HOURLY MEAN FOOD INTAKE

HOURLY MEAN BOUT SIZE

HOURLY MEAN NUMBER OF BOUTS

that of other deafferented birds, although the attenuation was slower. This is in accord with the relatively large amount of intake. Food intake in the first hour amounted to 571% of the pre-operative intake during the same period, in the second hour to 222%. Only thereafter was food intake lowered to 57% of the comparable pre-operative level.

Thus bird 441 exhibited the typical feeding pattern characteristics of a deafferented bird but to a lesser degree than the other birds, possibly due to a less extensive deafferentation. This is paralleled by a comparatively high daily food intake - though not high enough to regain the pre-operative levels of body weight in nine weeks of post-operative observation. (Compare also APP. TABLE 15D)

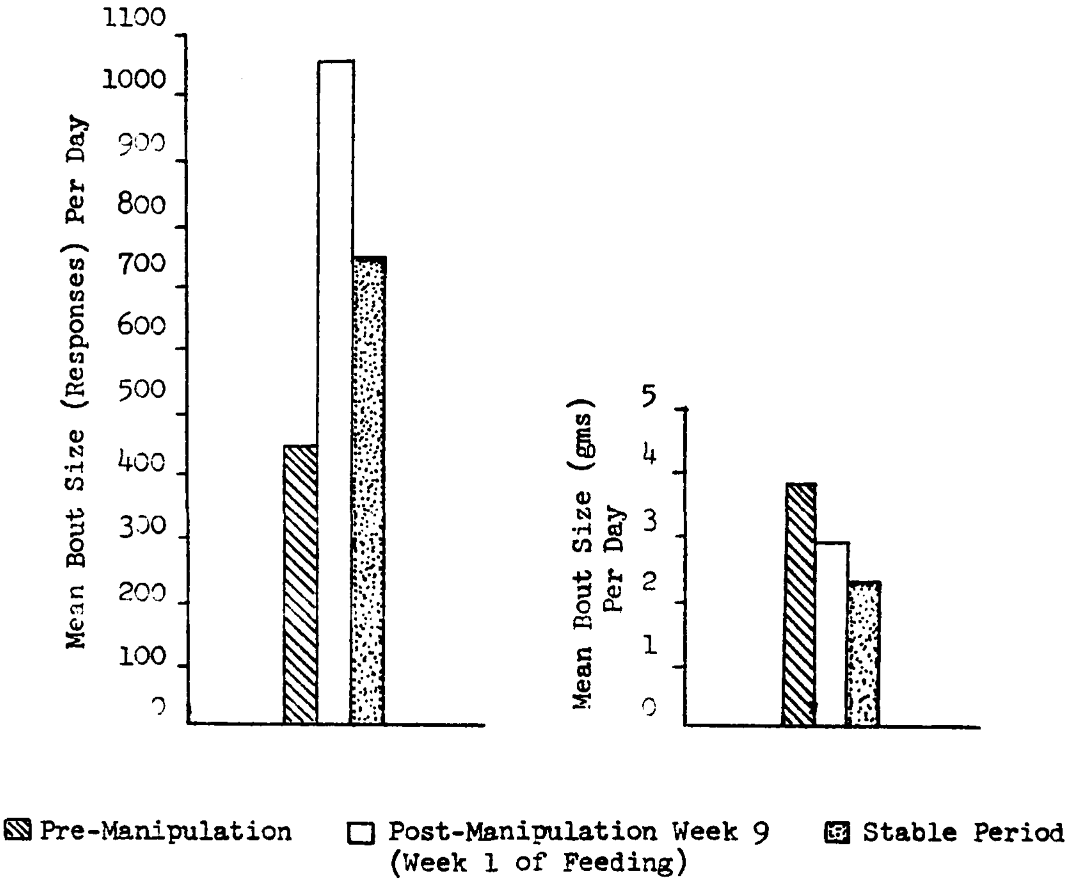
Bird #412 displayed much more marked effect from the deafferentation procedure than other birds (suggesting that perhaps the surgery was inadvertently more extensive). It was totally aphagic for 52 days. However on the fifth day after surgery, approximately the time when the other deafferentation birds began to feed themselves, bird 412 started to make substantial numbers of feeding responses. On some later days the number of responses was within the pre-operative range (APP. TABLE 15). Clearly the bird was motivated to eat and was able to perform the pecking movements completely enough to break the light beam about $\frac{1}{2}$ inch above the feed. However, even with more than 4500 pecks per day it obtained no food. When the body weight had fallen to 77% of the pre-operative level, tube and/or hand feeding was initiated, maintaining the body weight at 80-84% in order to prevent demise. During this phase the bird ceased responding entirely. Later observations disclosed that the bird had great difficulties in orienting itself correctly to food and that its droppage rate during mandibulation was very high. Spontaneous self-feeding began only after the bird was "retrained" to eat by allowing access to an open dish.

In the period of eleven weeks after resumption of self-feeding food intake did not exceed 77% of the pre-operative level and body weight was raised only from 82% to 90% (TABLE 1). The feeding pattern was dominated by two factors that tended to obscure somewhat the general trends which were similar to other deafferented birds. Most important was the exceptionally low pecking efficiency in bird 412 (27% of its pre-operative level) which reduced the ingestion rate to 26%, i.e. from 0.82 grams/sec to 0.21 grams/sec. This tremendous inefficiency made it very difficult to directly compare the feeding pattern with that of other deafferented birds which maintained a normal ingestion rate (FIG. 4; APP. TABLE 3). As a result the <u>mean bout size</u> measured in grams was consistently lower than pre-operatively (74% in the first week, 56% on the average in the total post-operative period) in spite of the fact that the mean bout size measured in responses was markedly increased (234% in the first week. 161% on the average in the post-operative week) (FIG. 17; APP. TABLE 6,7).

Besides the inefficiency, the lower mean food intake per bout was partly a result of the second pattern anomaly. Perhaps simply due to the sheer amount of time spent feeding, perhaps due to other factors, bird 412 tended to interrupt feeding activity for intervals of a few minutes. Though much shorter than interbout intervals in most birds, these periods of non-feeding were longer than the one-minute

FIG. 17

MEAN BOUT SIZE -- DEAFFERENTATION BIRD 412



criterion by which bouts were delimited by definition. As a result the bird exhibited a persistently higher daily number of bouts than pre-operatively unlike other deafferented birds (APP. TABLE 5). However, using a 2-3 minute criterion would have combined many bouts into one meal; while in the other deafferented birds this would not have changed the number of meals appreciably (FIG. 19; the width of the pen lines corresponds to one-two minutes).

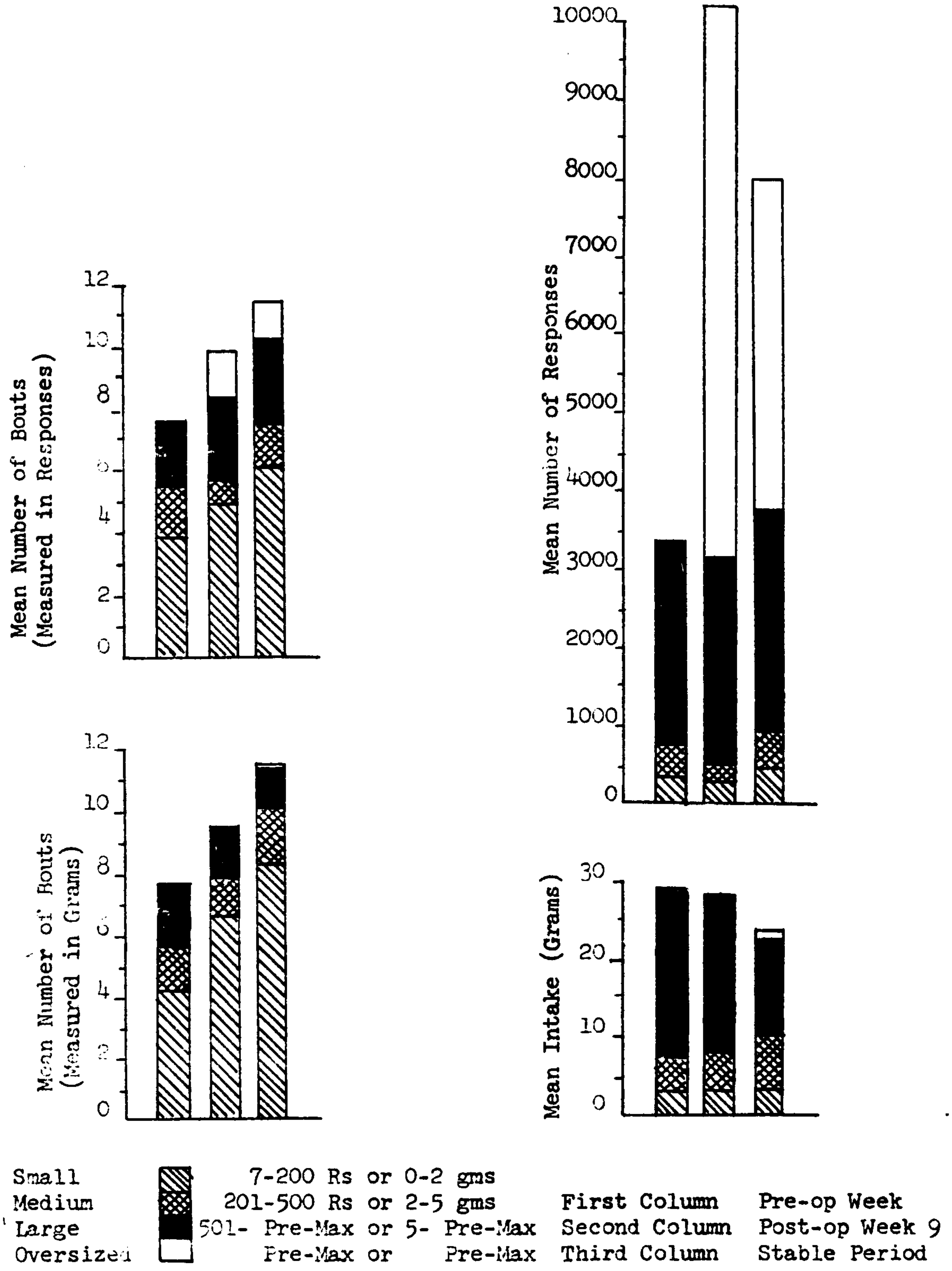
The frequency distribution of bout sizes (FIG. 18; APP. TABLE 8a) shows that the high daily number of meals in bird 412 was mainly due to an increase of small meals. In fact the exclusion of meals smaller than 0.5 gm would reduce the pre-operative mean number of bouts by 1.7 but the post-operative mean number of bouts, e.g. of the first week of eating by 4.3. By comparison in deafferentation bird 373 the reduction would amount only to 0.7 and 1.14 meals respectively. The very small size of "small" bouts is indicated by the distribution of feeding activity by bout size (FIG. 18; APP. TABLE 10a,11a). Bird 412 did not make appreciably more feeding responses in small bouts than pre-operatively (increase 11%) although the number of small bouts was increased by 57%. However, as was typical for the other deafferented birds, more than 50% of the post-operative feeding activity (69% in the first week of feeding, 54% on the average in the total post-operative period) consistently occurred in bouts bigger than the largest pre-operative bout. The maximum daily bout size on the average was 5355 responses post-operatively compared with 2345 responses pre-operatively. But the bird's feeding efficiency was so low that even bouts with up to 8200 responses did not lead to food intake that exceeded the largest pre-

FIG. 18

MEAN FREQUENCY DISTRIBUTION OF FOUR BOUT SIZE CATEGORIES

MEAN FEEDING ACTIVITY IN FOUR BOUT SIZE CATEGORIES

DEAFFERENTATION BIRD 412



operative bout sizes (FIG. 18). Again as seen in the other deafferented birds there was not a proportionate increase of all bout sizes but rather an asymmetrical new distribution of feeding activity.

That the pecking deficits alone could not account for the persistent hypophagia was clarified in the temporal distribution of feeding activity. Even before surgery bird 412 exhibited a very high attenuation rate of feeding activity, eating 74% of the total food intake of the main feeding period in the first hour. After deafferentation the intensification of food intake in the first hour could not occur because of the low feeding efficiency although the bird was pecking at a high rate almost without interruption (FIG. 19; APP. TABLE 12E). During the first hours of the main feeding period its feeding activity was rarely interrupted by longer intervals of non-feeding and essentially filled the time completely. However, when bird 412 had stopped its initial intensive feeding usually in the fourth hour of the period it did not initiate further feeding until the main (afternoon) feeding period again started about 20 hours later. Before surgery bird 412 ate about 26% of its daily intake in the morning period, but after surgery only 7% on the average. In fact there were many days where not a single peck occurred during the morning period. (The same observation was also made in deafferentation bird 435.) Thus in spite of much unused potential feeding time during the whole 24 hour period bird 412 compressed all of its feeding activity into the first hours of the period and failed to initiate an adequate amount of feeding later on to reach pre-operative levels of intake. This and the marked pecking inefficiency which prevented an increase in food intake at the beginning of the feeding period when the bird was eating led to the lowest level of intake of all experimental birds.

FIG. 19 TEMPORAL DISTRIBUTION OF FEEDING ACTIVITY OF BIRD 412 (DEAFFERENTATION) (* percentage of total daily intake; ** percentage of preoperative mean body weight)
TWO PREOPERATIVE DAYS

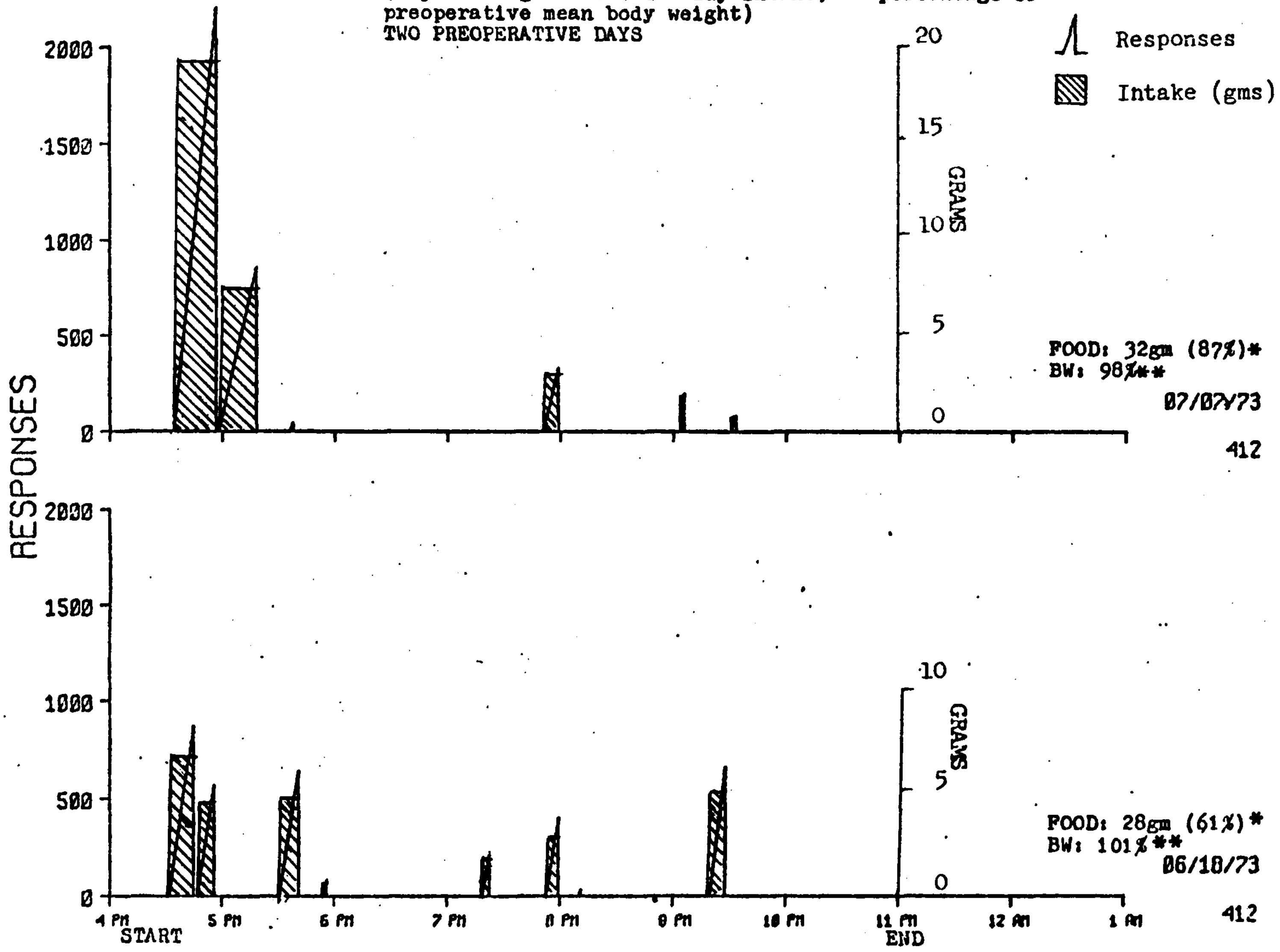
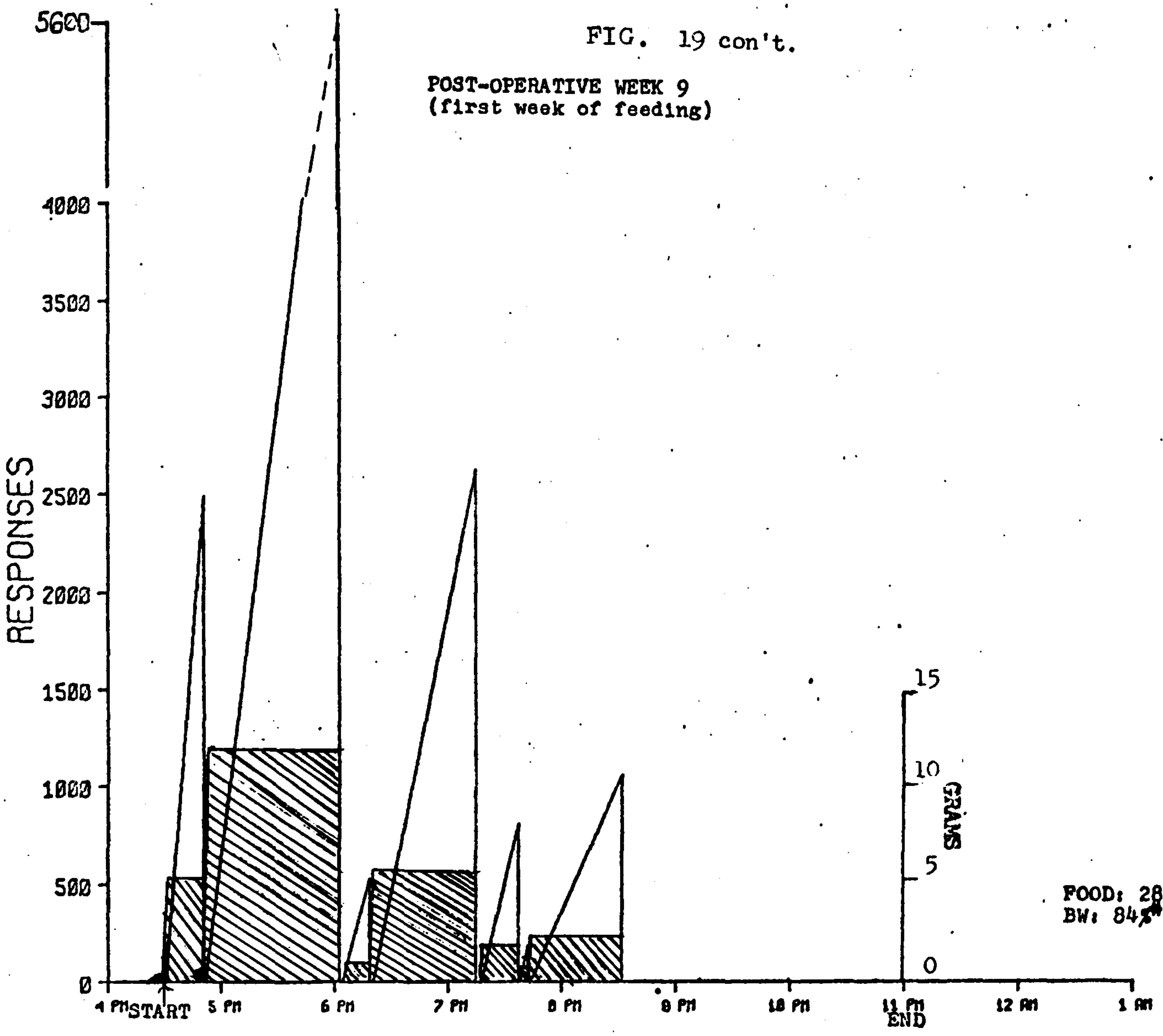


FIG. 19 con't.



POST-OPERATIVE WEEK 9
(first week of feeding)

FOOD: 28gm (98%)*
BW: 84%**

08/05/73

412

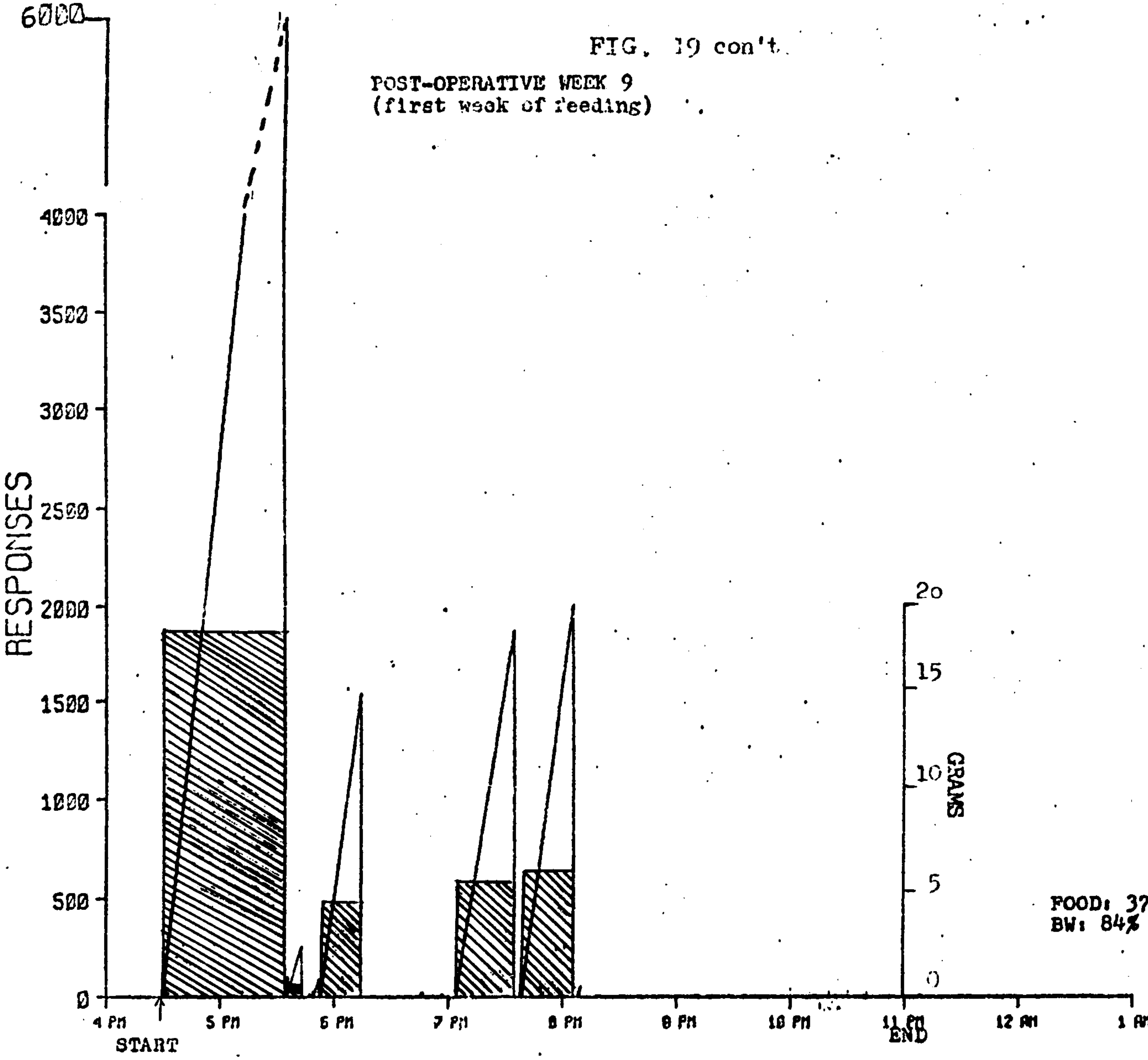


FIG. 19 con't.

POST-OPERATIVE WEEK 9
(first week of feeding)

FOOD: 37 gm (94%)*
BW: 84% **

08/06/73

412

TABLE 2 SUMMARY OF FINDINGS

Condition	Bird	# Days No Food	Body Weight	Food	# Bouts Total	Bout Size	# Bouts in 4 Bout Sizes				Food Intake in 4 Bout Sizes				Feeding Attenuation	Bout Size		# Bouts	
							Small	Medium	Large	Over-Sized	Small	Medium	Large	Over-Sized		Hour 1	Hour 2 - 7	Hour 1	Hour 2 - 7
Deafferentation	373	4	<	<	≪	>	≪	<	=	>	≪	≪	=	≫	>	≫	<	<	<
	349	6	<	<	≪	>	≪	=	=	>	≪	≪	=	≫	>	≫	=	≪	<
	435	4	<	<	≪	>	≪	≪	=	>	≪	≪	=	≫	>	≫	=	<	<
	441	4	<	>	< rec	> rec	=	unstable	=	> rec	<	≪ unstable	=	> rec	>	>	<	>	<
	412	54	<	<	Gross Pecking Inefficiency Requires Special Discussion (pg. 67) Major Findings Agree with Other Deafferented Birds														
	367	21	<	Died															
Deaff. Control	348	0	=	> rec	=	> rec	< rec	=	=	> rec	< rec	=	=	> rec	=	> rec	=	=	=
	362	1	=	> rec	< rec	> rec	< rec	=	> rec	> rec	< rec	< rec	> rec	> rec	=	=	> rec	=	rec
Deprivation	339	3	< rec	> rec	< rec	> rec	< rec	=	=	> rec	< rec	=	=	> rec	=	≫ rec	> rec	< rec	< rec
	374	5	< rec	> rec	< rec	> rec	< rec	=	> rec	> rec	< rec	< rec	=	> rec	=	≫ rec	> rec	=	< rec
	360	6	< rec	> rec	< rec	> rec	< rec	=	=	> rec	< rec	=	=	> rec		≫ rec	=	> rec	< rec

= No or Little Change	> Increase
rec Recovered	< Decrease

PART IV. DISCUSSION AND THEORETICAL IMPLICATIONS

As concluded above (see p. 62, or pp. 35 to 43 for overview) two primary effects emerged after deafferentation. These underlay the complex set of changes in the feeding pattern and accounted for the hypophagia and failure to recover body weight for several weeks. (1) There was a marked shift in meal size due to the occurrence of a few very large meals, especially in the first hour of the main feeding period, which comprised the major part of the day's food intake. This seems in part attributable to the ("self-imposed") deprivation resulting from the aphagia and hypophagia, in part to the neural (sensory) deficit itself. Therefore a complete understanding of the finding requires explanation of both factors. (2) There was an abnormally rapid attenuation of feeding activity after the first hour of the main feeding period exhibited in the decreased number of (smaller) meals occurring in the later hours. This led to the net hypophagia and accentuated the shift of feeding activity from smaller to larger meals.

1. The Cybernetic Model

As noted in the introduction in recent years nearly all work on the regulation of food intake has been interpreted by theories using the homeostatic or cybernetic model. Therefore it seems appropriate to attempt an explanation of our findings by means of one or another variation of this conceptual framework. The cybernetic model postulates mechanisms of regulation based entirely on homeostatically corrective negative feedback actions. These mechanisms tend to keep the nutritional state within a normal range. If it falls below the "optimum level" (set-point), feeding activity is initiated to correct it. As feeding continues toward an amount which would lead to overnutrition, this in turn is corrected by inhibitory mechanisms. There are numerous modifications of this model with varying assumptions about the precise role of different factors and neural mediators in the instigating and inhibiting mechanisms. However they all use the basic idea of stabilization of the nutritional level by means of negative feedback actions which correct deviations in either direction from the set-point.

(1) The cybernetic model seems to allow explanation of the increase in meal size after deprivation in neurally normal birds if the set-point itself is assumed to arise from a <u>balance</u> of facilitory and inhibitory influences rather than being an absolute level against which a particular metabolic factor is measured. It could be expected that because of the abnormally large metabolic depletion supranormal inhibitory influences from ingestion would be required to terminate a meal.* The concomitant reduction in number of meals (not observed in the rat, Levitsky 1970) could be a consequence of the huge size of the meals. The tapering off of meal size and frequency after the first hour of the main feeding period in deprived birds could probably be attributed to filling of the crop and gastrointestinal tract.

In deafferented birds the increased meal size cannot so easily

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* The extraordinarily large meals observed in the pigeon give an impression of the relatively massive storage capacity of its gastrointestinal tract compared to the rat.

be accounted for by the cybernetic model. The concomitant deprivation resulting from aphagia and hypophagia does not adequately explain the skewed nature of the increased size in meals. (a) The percentage shift of feeding activity into the largest bout size categories was much greater in deafferented birds than in equivalently deprived birds. (b) Moreover the effect persisted even in later weeks when food intake approached or, as in bird #373, even exceeded the pre-operative mean (See Fig. 5a,b) and when body weight has also increased to nearly the normal range. Interestingly in these later weeks of the observation period there was a shift of the intense feeding activity from the first hour of the feeding period to the second and third hour. This also indicates that the bird was reacting less like a simply food deprived bird.

On the other hand within the framework of the cybernetic model it would seem that oral sensory deficits might account for the increase in meal size because part of the inhibitory influence, which normally leads to bout termination, has been removed. If trigeminal input contributes inhibitory influences to feeding centers in relation to the amount eaten, elimination of such input, however, should lead to a proportional enlargement of all bouts and not just of the one or two first meals of the feeding period. In point of fact the few meals taken in later hours of the day are approximately the same size as the meals before surgery taken in the same hours while those taken in the first hour are greatly enlarged. Since deprived birds eat about the same amount in the first hour as deafferented birds, the gastrointestinal tract of both should be filled to approximately the same degree. Therefore negative feedback from this source should have a comparable effect. This would suggest that bouts in later hours should be larger in deafferented birds (due to loss of inhibitory influences from orosensory feedback) than in deprived birds. However, the reverse is true, leading to the disproportional enlargement of meal sizes in deafferented compared to simply deprived birds. Thus deafferentation has produced an influence on meal size which seems partly, but not entirely, explainable within the cybernetic model.

(2) On the other hand the second major finding, viz. the more rapid tapering off (attenuation) of feeding activity during the feeding period after deafferentation, is much more difficult to explain in the cybernetic model. Crop filling and negative feedback from the gastrointestinal tract may account for the gradual decrease in feeding activity in normal and in deprived birds. However these factors cannot explain the high degree of attenuation after deafferentation, which leads to a net hypophagia. This is also supported by the fact that after deafferentation virtually no food intake occurred in the 5 hour morning feeding period (except bird #349 which ate about 23% of its daily intake in the morning, but did not reach pre-operative intake levels in 9 post-operative weeks).

Hypophagia after a purely peripheral deafferentation poses a serious problem for an explanation within the cybernetic model of feeding control because this model generally assumes that central mechanisms are the primary force for initiation of feeding and overall regulation of total food intake (LeMagnen, 1969, and many others).

Zeigler (personal communication) therefore postulates that trigeminal input must be assumed to contribute a constant "tonic" excitatory component to the "set-point" equilibrium of the homeostatic mechanisms. If such an input were removed by deafferentation, the set-point in effect would fall so that only lower than normal metabolic levels would lead to initiation of feeding. This would be comparable to set-point lowering after lateral hypothalamic lesions as suggested by Powley and Keesey (1970). Such a hypothesis can account for the effect of deafferentation on total food intake. However the changes in feeding pattern cannot be explained by this hypothesis. If the effect of deafferentation were merely to lower the set-point, feeding should be decreased uniformly or proportionally over the day. The combination of deprivation and set-point lowering in deafferented birds should produce an hourly feeding activity proportionally less than in the deprived bird in every hour, rather than being the same in the first hour and then much less later in the day as was actually the case. The rapid tapering off of feeding activity, which was found to be the basis of the hypophagia, would therefore not be expected and remains unaccounted for in the cybernetic model.

Finally a number of investigators working on feeding behavior have invoked the concept of "palatability" to explain the differences in total intake and/or bout size which occur when diets are changed in taste (LeMagnen, 1969, 1971; Sclafani and Kluge, 1974). This concept has been broadened to include all factors acting by way of oronasal sensation (including texture) which seem to influence an animal's food preference or differential readiness to eat certain foods. It has been suggested that the aphagia and hypophagia following trigeminal deafferentation might be due to the aberration of sensation acting like changes in palatability.

In the literature the concept of palatability seems to be used in at least two ways. In one sense it apparently refers to a kind of factor influencing upward (or downward) the amount of a certain food consumed at any given nutritional level in relation to a set-point (Sclafani and Kluge,1974). A factor working in synergy with the "motivation" occurring from the given level of nutritional deprivation would have a uniform or proportional influence on all meal sizes throughout the day. Therefore it could not account for the differential effect noted in the changed bout size distribution or the attenuation of feeding in the course of the day.

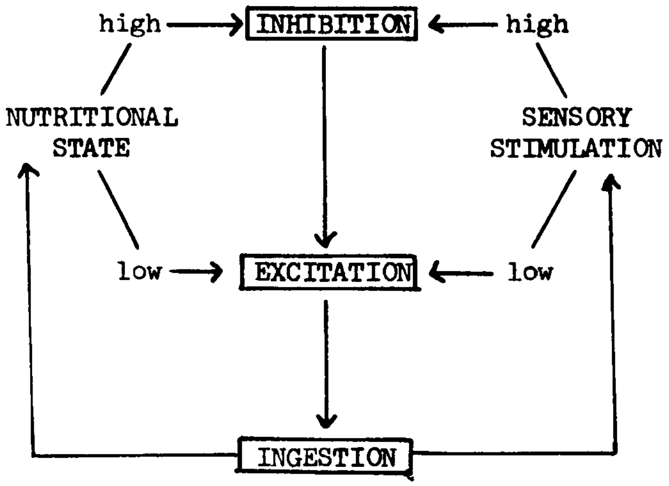
Apparently using the concept in a different sense, LeMagnen refers to the palatability of food as acting by way of "secondary reinforcement". This sense may be close to the way in which the concept of "conditioned oral sensory cues" will be used below (See pp. 82ff). However, LeMagnen continues to emphasize the importance of metabolic levels for initiation of meals and hence control of total food intake (LeMagnen, 1971). Thus change of palatability in this sense if due to loss of oral sensation would merely influence meal size and could not account for the overall hypophagia.

2. The Adaptive Learning Model

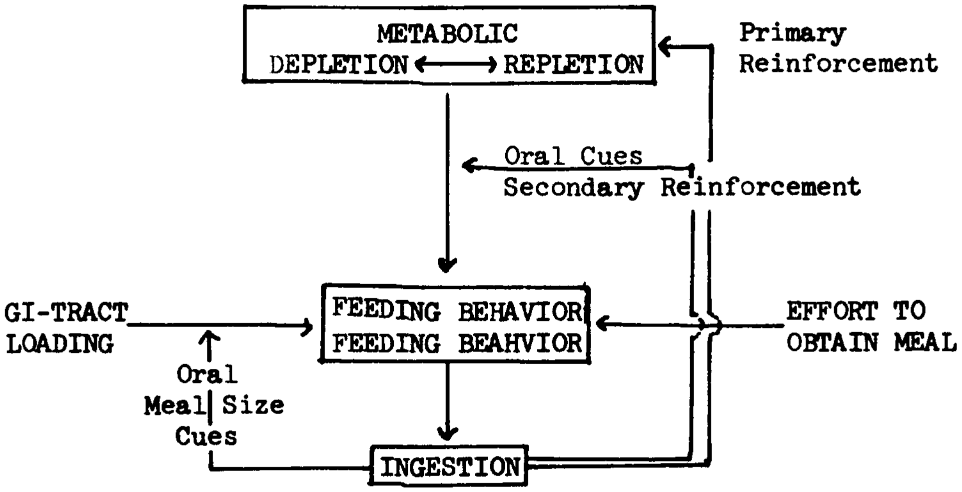
The cybernetic model seems unable to explain satisfactorily the changes in feeding patterns found after deafferentation -

FIG. 20

CYBERNETIC MODEL



ADAPTIVE LEARNING MODEL



especially the rate of attenuation of feeding activity in the course of the day. Therefore it seems necessary to explore alternative theoretical models which have been used in the explanation of feeding behavior. The adaptive learning model which grew out of work on specific hungers seems to offer an interesting potential for expansion to account for sensory control of food intake in general. This theory originally centered around the problem of learned aversions to toxic and deficient diets (Rozin, 1967; Rozin and Kalat, 1971). However Garcia et al. (1967) have shown rats can also learn positive preferences for diets that correct deficiencies or that have relatively neutral consequences (Revusky, 1967). It was postulated that the rat "selects" its diet by <u>increasing</u> the intake of the learned appropriate diet due to the <u>positive</u> <u>feedback</u> of the conditioned cues. The problem in both cases was to understand the relationship between metabolic and oral sensory factors which made it possible for the animals (in both cases rats) to select the appropriate diet. Their explanations were based on the (classical) conditioning model, and assumed that late metabolic reinforcement led to linkage of certain sensory cues to the act of eating so that these cues in turn determined the choice of the proper diet. Garcia et al. (1967) demonstrated that the necessary conditioning could be established even when the reinforcement occurred as late as 30 minutes after ingestion.

An extension of this hypothesis is that the same mechanisms of reinforcement and conditioning, which act in the selection of diets for specific needs, are also at work in regard to <u>all</u> dietary selection including the meeting of general caloric requirements. Thus the animal learns to eat diets appropriate for all its metabolic needs by linking feeding behavior to oral sensory cues under the influence of late reinforcement from the products of digestion. It is assumed that not only taste and smell but also the texture of the food (conveyed by trigeminal sensation) is important at least in the pigeon for forming this association. Loss of these cues thus accounts for the failure to sustain adequate feeding and hence for the rapid attenuation after trigeminal deafferentation.

Specific-hunger researchers generally have assumed a classical conditioning paradigm in their theories of adaptive learning for food selection. Because this dissertation research centers around the problem of determining the amount of feeding and the shaping of the feeding activity into a meal pattern, the <u>operant</u> conditioning paradigm seems more adequate as a basis of explanation. Feeding activity itself is considered to be the operant - corresponding to the key-pecking or bar-pressing in the usual experimental design for operant conditioning research. The late metabolic consequences of this feeding are the primary reinforcement of the activity analogous to the food rewards which are the primary reinforcement of the usual key-pecking. Just as the key-pecking can be conditioned to an originally unrelated stimulus or cue, which then calls forth the operant activity, so too the feeding activity is conditioned to sensory cues such as visual, olfactory, gustatory and oral tactile sensation. Although originally unrelated to metabolic events, these cues now call forth and sustain the feeding activity in relation to the proper diet. Thus once established the sensory cues act as secondary reinforcements which determine not only the kind of diet eaten (by positive selection) but also participate in controlling the amount.

The amount of feeding activity having been established as the circadian feeding rhythm, the feeding behavior (operant) is further shaped into the actual meal pattern.* This takes place under the reinforcing influence of opposing factors which act on meal size such as "environmental barriers" and response of the gastrointestinal tract to loading. On the one hand if the bird eats very large meals, the overfilling of the crop, stomach and intestinal tract creates aversive stimuli which negatively reinforce this feeding pattern. On the other hand if the animal eats smaller meals more frequently, it expends more effort to obtain an adequate amount of food - especially in the natural environment. This expenditure of effort can also be considered aversive, hence negatively reinforcing meals which are too small. Collier et al. (1972) have shown that this effect is an important factor in determining meal size. Under these opposing influences the feeding activity operant is therefore shaped into an "optimal compromise" and linked by conditioning to oropharyngeal sensory cues. These cues in turn serve as immediate determinants of meal size by in effect monitoring meal intake during the act of feeding as opposed to the reinforcement from the gastrointestinal tract which is necessarily delayed.

With this model it seems possible to account for the dual role

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* This conceptual distinction between shaping the circadian rhythm or daily amount of intake and shaping the meal pattern does not necessarily imply a temporal sequence. It is assumed in fact that both processes occur simultaneously.

of the trigeminal sensory system disclosed by the findings of this dissertation. (1) One function of oral sensation is to mediate the cues which come to be associated with the circadian feeding pattern leading to the appropriate total intake. These cues act in effect as secondary reinforcement to sustain feeding activity during the day although primary reinforcement comes only later. If this mechanism is destroyed by trigeminal deafferentation, the bird is less able to control its feeding accurately until it can learn to use new cues. The immediate result however is the loss of the usual secondary reinforcement of the meal pattern operant so that the bird tends to extinguish its feeding activity (attenuate more rapidly than normally) in the course of each day. The circadian feeding rhythm is maintained but the amount ingested is diminished because of the daily extinction of feeding activity. The feeding activity as a whole does not disappear because late primary reinforcement from the ingested food still occurs and because metabolic depletion is relatively high due to the hypophagia (and initial aphagia). (2) The meal pattern consisting of fewer very large bouts of activity concentrated at the beginning of the main feeding period is explained by the combination of several factors: (a) Loss of cues which monitor meal size lead to a general (proportional) tendency toward larger meals. (b) The chronic (and $3\frac{1}{2}$ hour acute) state of deprivation leads to larger meals especially at the beginning of the feeding period when the nutritional state is lowest just as in the deprived neurally normal bird. (c) The attenuation discussed above leads to a diminution not only of total feeding activity in later hours but also to a diminution of bout size in the corresponding hours. The attenuation of feeding more than overbalances the meal enlarging tendencies resulting from loss of monitoring cues and deprivation. Thus the net effect is a very disproportionate enlargement of first-hour meals and decrease in size of later-hour meals with a marked shift of the percentage of feeding activity into the larger bout sizes.

The adaptive learning model should not be understood as standing in opposition to the cybernetic model. The latter deals primarily with the regulation of body weight in response to metabolic factors while the former deals with the flexibility and adaptability of feeding patterns. Thus each explains a different level of behavioral control. Obviously the two must fit together in any overall theory. It seems possible that the homeostatic influence of the nutritional requirement instead of acting directly in regard to a set-point to initiate meals serves as the "motivational framework" within which the operant learning takes place.

3. The Aphagic Period

The experimental design and procedures used in this research were not intended to investigate the behavior of the birds during the period of post-operative aphagia. To do this would require different observation techniques and methods for testing the birds' capability and readiness for various aspects of feeding behavior short of actual feeding. Therefore it is only possible to speculate about the factors involved in producing the transient total aphagia after deafferentation. Nevertheless the problem of aphagia is so closely related to the general question of disturbed control of food intake after deafferentation that it seems important to discuss some of the possible causes. One at least seems justified in assuming that the mechanisms underlying the aphagia should not be inconsistent with those used in explaining the subsequent hypophagia. Records of pecking responses during the period of aphagia show that this first post-operative phase is not homogeneous. Several stages may be distinguished, characterized by an increasing number of responses per day (APP. TABLE 18).

(1) A period where no feeding responses could be recorded.

(2) A period where few feeding responses were recorded, but no food intake was accomplished.

(3) A period where a considerable number of responses was recorded, however significantly below the pre-operative mean number of responses per day (only bird #412 which was aphagic for 52 days, reached the level of pre-operative daily responses), but again without accomplishing food intake.

Just as with the hypophagia there are two major aspects to be considered in attempting to understand or explain the aphagia, viz. (1) Sensory-motor deficits and (2) interference with the responsiveness of food. If the aphagia were completely the result of pecking inefficiency one would expect the daily number of responses to be highest immediately after deafferentation (surgical control birds resumed feeding within 24 hours after surgery). Absence of the primary reinforcement normally provided by food intake might then lead to extinction of the feeding responses. This hypothesis is contradicted by the response records. It also would be incompatible with the fact that during the period of hypophagia in spite of a normal ingestion rate the birds did not reach normal levels of food intake.

The abrupt change in efficiency from zero to a level that allowed almost a normal rate of ingestion which occurs from one day to the next, certainly does not suggest a neural recovery. This would obviously be impossible in five to seven days, if at all, after nerve section of this kind. Instead it seems more probable that a relearning process was involved. This would be consistent with our assumption that both the reduced ability to monitor and limit meal size and the reduced ability to sustain feeding activity (or originate more meals) in the course of the day was due to the loss of trigeminal sensory cues.

Limited observation of trigeminally deafferented birds (mainly bird #412) during the aphagic period suggested that they were having great difficulty in properly orienting their pecking to the grain. The beak often stopped as much as 2 cm short of the kernels. Thus it seems likely that sensory-motor factors were important in the aphagic period not only as an exaggeration of the later persisting inefficiency but also as a superimposed disruption of orientation and coordination of the feeding response which was overcome by learning to use other sensory cues.

It has been repeatedly suggested that trigeminal deafferentation produces painful sensations in the oral region which make pecking aversive in the immediate post-operative period but which diminish during recovery. This explanation is unlikely in view of the persistence of drinking and the finding that deafferentation does not impair the performance of an operant key-pecking response (Zeigler and Feldstein, 1971).

The second aspect to be considered in the control of feeding behavior, the degree of responsiveness to food, seems to play an important role in the aphagic as well as the hypophagic period after deafferentation. The number of feeding responses during aphagia is drastically reduced from the very beginning so that extinction can be excluded as an explanation. Furthermore Zeigler et al. (1974) have shown that the length of the aphagic period after deafferentation can be shortened by depriving the birds to 85% body weight prior to surgery. This would indicate that an increased nutritional depletion makes the deafferented bird more likely to initiate feeding.

Zeigler therefore hypothesized the aphagia could be explained by assuming that trigeminal sensation provides a "tonic" input to the set-point equilibrium in the mechanism for metabolic motivation. When this is removed by deafferentation, the set-point is in effect lowered so that the nutritional level has to fall lower for initiation of feeding to occur than in the normal bird. Aphagia therefore ensues after surgery until the nutritional state drops below this new level. However as discussed above (p. 81) this explanation does not seem to be supported by the pattern data during the hypophagic period.

Within the framework of the adaptive learning model the shorter period of aphagia in deafferented birds which are previously food deprived might be accounted for by the greater motivational pressure to learn new cues for orienting and coordinating the consummatory feeding response. However, since our research was not really designed to investigate the aphagic period directly, no definitive explanation can be given as to its cause. The answer to this and other related questions will have to await further investigations where they are specifically addressed.

4. Implications for Further Research

As with most research the findings of this dissertation raise more new questions for investigation than they answer. The adaptive learning model leads to many further hypotheses about the relationships between oral sensation, gastrointestinal tract factors, metabolic levels and environmental conditions. These need testing by further experiments.

If oral sensation mediates essential cues which act as secondary reinforcement, one would expect not only a decreased total food intake after deafferentation but also a decreased ability to compensate for further challenges to the metabolic state. Analysis of feeding patterns at different forced nutritional levels (deprived and overfed animals) after deafferentation should reveal less corrective response to these imposed changes than before.

A second way to explore the relationship between metabolic, gastrointestinal and oral factors would be by creating esophageal and gastric fistulas. This would completely decouple nutrition from oral feeding so that the consequences of the pattern and amount of food arriving in the stomach could be varied independently of the oral feeding pattern and its effects.

The influence on meal size of effort required to obtain food should be investigated after deafferentation. Again it is presumed that birds or rats would be less capable of adapting their meal pattern to environmental change after deafferentation than before.

The effect of the inefficiency of the response should be explored independently of sensory loss by creating motor lesions which produce a comparable impairment of efficiency. Furthermore the aphagic period also needs to be investigated to determine the nature of the behavioral deficits during this phase.

Finally the techniques developed for quantitative analysis of feeding patterns in relation to the multiple factors influencing them promise to open up many new possibilities for investigation of *interrelationships* between causal factors. This could serve as a general paradigm for methods to deal with the ever present problem of multicausation in behavioral studies.

APPENDIX

APPENDIX TABLES

APPENDIX FIGURES

APP. TABLE 1A

MEAN BODY WEIGHT AND MEAN INTAKE --DEAFFERENTATION BIRD 373

Condition	Body Weight	%	Food (gm)	%	Water (ml)	%	Food / Water	Food / BW	Water / BW
Pre	559	100	31.6	100	54	100	0.59	0.06	0.10
Post Week 1 4 Days	504	90 87*	0.0	0.0	18	33	0.00	0.00	0.04
1 3Days	493	88	24.2	76	39	72	0.62	0.05	0.08
2	506	91	33.2	105	40	73	0.84	0.07	0.08
3	516	92	30.9	98	37	68	0.89	0.06	0.07
4	515	92	30.5	96	44	82	0.71	0.06	0.09
5	508	91	28.8	91	53	97	0.55	0.06	0.10
6	507	91	29.3	93	38	70	0.78	0.06	0.08
7	501	90	33.4	106	51	94	0.67	0.07	0.10
8	519	93	37.6	119	66	121	0.60	0.07	0.13
9	526	94	40.7	129	100	183	0.42	0.08	0.19
10	524	94	36.9	117	98	180	0.40	0.07	0.14

---

* lowest body weight

APP. TABLE 1B

MEAN BODY WEIGHT AND MEAN INTAKE -- DEAFFERENTATION BIRD 349

Condition	Body Weight	%	Food (gm)	%	Water (ml)	%	Food/Water	Food/BW	Water/BW
Pre	570	100	43.1	100	119	100	0.36	0.08	0.21
Post Week 1	511	90 85*	0.0	0	19	16	0.00	0.00	0.04
2	480	84	28.0	65	29	24	0.93	0.06	0.06
3	503	88	31.6	73	42	35	0.79	0.06	0.08
4	499	87	33.6	78	113	95	0.32	0.07	0.22
5	503	88	34.8	81	155	130	0.23	0.07	0.31
6	530	93	43.1	100	81	69	0.55	0.08	0.15
7	548	96	39.4	91	98	82	0.40	0.07	0.18
8	552	97	42.0	97	95	80	0.44	0.08	0.17
9	553	97	37.0	86	87	73	0.44	0.07	0.16

---

* lowest body weight

APP. TABLE 1C

MEAN BODY WEIGHT AND MEAN INTAKE -- DEAFFERENTATION BIRD 435

Condition	Body Weight	%	Food (gm)	%	Water (ml)	%	Food / Water	Food / BW	Water / BW
Pre	612	100	33.1	100	75	100	0.47	0.05	0.12
Post Week 1 4 Days	560	91 86*	0.0	0	27	36	0.00	0.00	0.05
1 3 Days	533	87	17.7	53	53	71	0.30	0.03	0.10
2	537	88	30.0	91	57	76	0.53	0.06	0.11
3	532	87	28.7	87	75	100	0.39	0.05	0.14
4	519	85	26.4	80	90	121	0.30	0.05	0.17
5	509	83	27.5	83	96	129	0.29	0.05	0.19
6	502	82	33.4	101	106	142	0.33	0.07	0.21
7	497	81	33.0	100	129	172	0.26	0.07	0.26
8	499	82	36.0	109	128	172	0.28	0.07	0.26
9	515	84	37.3	113	120	160	0.32	0.07	0.23
10	523	85	35.1	106	99	132	0.36	0.07	0.19
11	527	86	39.7	120	107	143	0.38	0.08	0.20
12	532	87	47.6	144	107	143	0.45	0.09	0.20
13	544	89	41.7	126	100	134	0.41	0.08	0.18

APP. TABLE 1D

MEAN BODY WEIGHT AND MEAN INTAKE -- DEAFFERENTATION BIRD 441

Condi-	Body	%	Food (gm)	%	Water (ml)	%	Food / Water	Food / BW	Water / BW
Pre	561	100	20.3	100	67	100	0.31	0.04	0.12
Post Week 1 4 Days	522	93 89*	0.0	0	22	32	0.00	0.00	0.04
1 3 Days	515	92	21.0	104	61	90	0.34	0.04	0.12
2	526	94	30.4	152	71	105	0.45	0.06	0.13
3	539	96	26.0	128	89	133	0.30	0.05	0.17
4	533	95	19.0	94	84	125	0.25	0.04	0.16
5	525	94	20.0	99	80	119	0.26	0.04	0.15
6	526	94	27.6	136	84	125	0.33	0.05	0.16
7	529	94	28.8	142	75	111	0.39	0.05	0.14
8	525	94	27.5	136	95	141	0.29	0.05	0.18
9	522	93	33.6	166	100	149	0.34	0.06	0.19

---

* lowest body weight

APP. TABLE 1E

MEAN BODY WEIGHT AND MEAN INTAKE -- DEAFFERENTATION BIRD 412

Condition	Body Weight	%	Food (gm)	%	Water (ml)	%	Food/Water	Food/BW	Water/BW
Pre	601	100	39.4	100	115	100	0.35	0.07	0.19
Post Week 1	524	87	0.0	0	29	25	0.00	0.00	0.06
2	465	77	0.0	0	25	22	0.00	0.00	0.05
3 - 7	Bird was maintained by hand feeding								
8 4 Days	502	84	28.8	73	53	46	0.45	0.05	0.11
9	511	85	29.8	76	59	51	0.53	0.06	0.11
10	514	85	26.6	68	72	63	0.50	0.05	0.14
11	514	86	24.6	62	77	67	0.33	0.05	0.15
12	518	86	24.1	61	68	59	0.37	0.05	0.13
13	527	88	25.0	64	68	59	0.39	0.05	0.13
14	528	88	26.6	68	57	50	0.49	0.05	0.11
15	534	89	24.0	61	83	72	0.30	0.04	0.16
16	529	88	23.3	59	106	92	0.23	0.04	0.20
17	533	89	26.3	67	76	66	0.36	0.05	0.14
18	539	90	29.8	76	81	71	0.37	0.06	0.15

APP. TABLE 1F

MEAN BODY WEIGHT AND MEAN INTAKE -- CONTROL BIRD 348

Condition	Body Weight	%	Food (gm)	%	Water (ml)	%	Food/Water	Food/BW	Water/BW
Pre	596	100	28.4	100	65	100	0.44	0.05	0.11
Post Week 1 2 Days	581	97 97*	12.0	42	40	61	0.29	0.02	0.07
1 5 Days	589	99	36.8	130	60	91	0.62	0.06	0.10
2	604	101	36.6	129	67	102	0.55	0.06	0.11
3	604	101	30.6	108	59	90	0.54	0.05	0.10
4	596	100	33.3	117	65	100	0.52	0.06	0.11

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* lowest body weight

APP. TABLE 1G

MEAN BODY WEIGHT AND MEAN INTAKE --CONTROL BIRD 362

Condition	Body Weight	%	Food (gm)	%	Water (ml)	%	Food/Water	Food/BW	Water/BW
Pre	491	100	20.4	100	25	100	0.85	0.04	0.05
Post Week 1 1 Day	473	96 96*	0.0	0	14	57	0.00	0.00	0.03
1	476	97	27.2	133	30	121	0.92	0.06	0.06
2	486	99	25	123	26	106	0.97	0.05	0.05
3	485	99	22.9	112	23	95	1.00	0.05	0.05
4	484	99	22.2	109	20	81	1.10	0.05	0.04

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* lowest body weight

APP. TABLE 1H

MEAN BODY WEIGHT AND MEAN INTAKE -- DEPRIVATION BIRD 339

Condition	Body Weight	%	Food (gm)	%	Water (ml)	%	Food/Water	Food/BW	Water/BW
Pre	619	100	31.9	100	98	100	0.34	0.05	0.16
Deprivation	593	96 90*	0.0	0	48	49	0.00	0.00	0.08
Post Week 1	587	95	42.8	134	132	135	0.33	0.07	0.22
2	604	98	42.1	132	138	141	0.31	0.07	0.23
3	611	99	34.4	108	131	133	0.27	0.06	0.21
4	612	99	31.1	98	128	131	0.24	0.05	0.21
5	605	98	34.8	109	133	136	0.26	0.06	0.22
6	617	100	39.1	122	125	127	0.32	0.06	0.20

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* lowest body weight

APP. TABLE 11

MEAN BODY WEIGHT AND MEAN INTAKE --DEPRIVATION BIRD 374

Condition	Body Weight	%	Food (gm)	%	Water (ml)	%	Food / Water	Food / BW	Water / BW
Pre	557	100	36.6	100	78	100	0.49	0.07	0.14
Deprivation	532	96 88*	0.0	0	41	53	0.00	0.00	0.08
Post Week 1	523	94	37.5	103	72	93	0.56	0.07	0.14
2	541	97	39.9	109	89	111	0.47	0.07	0.16
3	553	99	37.7	103	88	113	0.43	0.07	0.16
4	557	100	38.0	104	81	104	0.47	0.07	0.14
5 - 7									
8	578	104	38.8	106	96	123	0.42	0.07	0.17
9	575	103	35.3	96	95	122	0.37	0.06	0.17
10	572	103	30.5	83	56	73	0.54	0.05	0.10
11	567	102	33.1	91	60	77	0.56	0.06	0.10

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* lowest body weight

APP. TABLE 1J

MEAN BODY WEIGHT AND MEAN INTAKE --DEPRIVATION BIRD 360

Condition	Body Weight	%	Food (gm)	%	Water (ml)	%	Food/Water	Food/BW	Water/BW
Pre	448	100	27.1	100	65	100	0.42	0.06	0.14
Deprivation	425	95 90*	0.0	0	24	36	0.00	0.00	0.06
Post Week 1	422	94	25.4	94	28	43	0.92	0.06	0.07
2	439	98	22.7	84	29	45	0.81	0.05	0.07
3	443	99	22.8	84	36	55	0.64	0.05	0.08
4	448	100	25.4	94	34	53	0.77	0.06	0.08
5 - 9									
10	456	102	21.7	80	31	47	0.71	0.05	0.07
11	455	102	20.9	77	27	42	0.79	0.05	0.06
12	465	104	26.3	97	41	63	0.66	0.06	0.09

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* lowest body weight

APP. TABLE 2

PECKING EFFICIENCY DURING DIFFERENT INTERVALS OF THE DAY OF A NORMAL AND A DEAFFERENTED BIRD
(IN GRAMS/ 100 RESPONSES)

	Interval	Day 1	Day 2	Day 3	Day 4	Day 5	Day 6
Deafferented Bird	7½h	0.9	0.8	1.0	0.7	0.9	0.4
	2 h	0.7	0.8	0.9	0.5	0.8	0.6
	2 h	0.5	-	-	0.5	0.8	0.4
	11½h*	0.8	0.8	1.0	0.6	0.9	0.5
Normal Bird	7½h	1.5	1.4	1.7	1.9	1.5	1.4
	2 h	1.4	1.7	1.9	1.5	1.7	1.6
	2 h	-	-	-	1.8	-	1.5
	11½h*	1.4	1.5	1.7	1.8	1.5	1.4

* represents the total daily feeding time. This is the value on which the calculation of grams of food intake per bout was based.

APP. TABLE 3

MEAN INGESTION RATE BEFORE AND AFTER MANIPULATION [IN: GRAMS OF FOOD PER 100 SEC]

Condition	Bird	Pre-op	Post-operative Weeks:											
		Week	1	2	3	4	5	6	7	8	9	10	11	12
Deafferentation Group	373	1.08	0.74	0.93	1.35	1.33	1.06	1.32	1.39	1.49	1.33	1.43		
	349	0.97	0.00	0.75	1.18	1.22	0.85	0.88	0.93	0.99	1.25			
	435	0.82	0.77	0.91	1.08	1.47	1.61	1.30	1.34	1.53	0.86	1.09	–	0.89
	441	1.07	1.00	1.16	1.37	1.37	0.97	1.23	1.67	1.70				
	412	0.82	0.27*	0.25	0.30	0.25	0.31	0.37	0.17	0.19	0.25	0.71	0.61	
Control Group	348	1.09	1.33	1.16	0.92	0.99	-	1.24						
	362	0.51	0.65	0.65	0.72	0.40	-	0.57						
	339	0.65	0.87	0.91	0.91	1.14								
Deprivation Group	374	1.30	1.50	1.42	1.37	1.31	-	-	-	1.33	1.28	1.42	1.37	
	360	1.11	1.06	1.04	1.13	0.94	-	-	-	-	-	0.84	0.83	0.89

* 9th post-operative week, 1st week of feeding

APP. TABLE 4

MEAN PERCENTAGE OF TOTAL DAILY FEEDING ACTIVITY TAKING PLACE IN THE MAIN FEEDING PERIOD - BEFORE AND AFTER MANIPULATION

Condition	Bird	Pre-op Week	Post-operative Weeks 1	2	3	4	5	6	7	8	9	10	11	12
Deafferentation Group	373	95	97	100	100	99	100	100	100	100	88	99		
	349	84	93	74	82	74	76	72	78	80	82			
	435	75	89	76	92	99	94	95	99	99	89	97		93
	441	93	93	88	96	97	97	84	99	100				
	412	76	96	89	92	91	92	95	83	96	100	99		
Control Group	348	74	64	68	76									
	362	79	75	76	84	79								
Deprivation Group	339	74	73	74	69									
	374	84	87	86	92	89				82	84	89	88	
	360	74	82	81	79	78								

APP. TABLE 5

MEAN NUMBER OF BOUTS BEFORE AND AFTER MANIPULATION

	Bird	Pre-	Post-Manipulation Weeks													Post Mean	Post/Pre %
			1**	1	2	3	4	5	6	7	8	9	10	11	12		
Deafferentation Group	373	15.7	9,5	5.7	8.6	12.8	12.0	10.5	4.0	6.5	7.5	7.0				8.3	5.3
	349	29.4	12.3	0.0	12.3	9.7	11.0	16.2	15.3	19.0	19.0	10.0				14.1	48
	435	11.9	2.0	4.0	5.3	5.0	4.3	5.3	2.7	4.0	3.5	6.0	4.0	0.0	5.0	4.5	38
	441	8.1	0.0	5.0	6.7	11.0	7.8	8.5	-	7.0						7.7	95
	412	7.7	8.5	9.8*	11.7	12.0	13.0	14.7	12.3	11.3	11.3	9.0	8.5			11.4	148
Control Group	348	7.9	-	6.9	8.4	10.0										8.4	107
	362	12.3	-	6.5	9.3	9.0										8.7	70
Deprivation Group	339	15.4	-	9.4	14.7	14.3	12.0									12.4	81
	374	12.4	-	7.7	9.0	11.0	10.7				13.0	12.5	11.7	10.5		10.7	87
	360	13.1	-	9.0	10.5	11.5	13.7									12.3	94

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* Post-operative Week 9, etc.

** No Food Intake, but Bouts of Responses

APP. TABLE 6A
MEAN BOUT SIZE BEFORE AND AFTER MANIPULATION
MEASURED IN RESPONSES, DURATION AND GRAMS OF FOOD

	Bird		Pre-	Post-Manipulation Weeks													Post Mean	Post/Pre %
				1	1	2	3	4	5	6	7	8	9	10	11	12		
Deafferentation Group	373	Rs/Bout	192	103	561	358	150*	159*	232	659	395	343	419				424	221
		Min/Bout	3.0	2.0	8.9	7.0	3.2	3.4	4.4	9.5	6.4	5.8	6.3					
		Gms/Bout	1.9	0.0	4.1	3.9	2.5	2.5	2.7	7.5	5.3	5.1	5.1				4.3	226
	349	Rs/Bout	159	81		332	312	316	324	323	246	216	287				295	185
		Min/Bout	2.1	1.7		3.6	3.0	3.3	3.1	3.9	2.9	2.7	4.0					
		Gms/Bout	1.2	0.0		1.7	2.6	2.3	1.6	2.0	1.6	1.7	3.0				2.1	172
	435	Rs/Bout	282	80	511	278*	245*	278*	185*	566	427	519	480	525	-	870	557	197
		Min/Bout	4.2	1.9	9.0	8.5	7.1	7.4	4.9	14.8	9.3	9.6	9.3	11.6	-	13.6		
		Gms/Bout	2.1	0.0	4.2	4.3	5.2	5.1	4.8	11.7	5.7	5.3	5.3	8.0	-	7.7	6.1	291
	441	Rs/Bout	285	64	576	323	128*	238	391	-	408						387	136
		Min/Bout	3.7	0.8	6.5	5.5	2.8	3.2	3.8	-	4.0							
		Gms/Bout	2.3	0.0	3.9	4.0	2.3	2.6	2.2	-	4.0						3.2	138
	412	Rs/Bout	447	136	1035**	650	535	526	478	715	946	934	943	555	862		744	166
		Min/Bout	6.9	7.7	18.7	13.3	9.7	10.6	8.1	9.3	16.4	14.8	14.0	7.1	11.7			
		Gms/Bout	3.8	0.0	2.9	2.0	1.8	1.5	1.5	2.0	1.8	1.8	2.1	2.7	3.5		2.2	56
Control Group	348	Rs/Bout	315		329	260	264										284	90
		Min/Bout	3.9		3.9	3.8	4.2											
		Gms/Bout	2.7		3.1	2.9	2.5										2.8	104
	362	Rs/Bout	228		450	334	249										344	151
		Min/Bout	4.6		7.8	5.2	4.5											
		Gms/Bout	1.3		3.1	2.1	1.7										2.3	177

APP. TABLE 6B

MEAN BOUT SIZE BEFORE AND AFTER MANIPULATION MEASURED IN RESPONSES, DURATION AND GRAMS OF FOOD

Bird			Pre-	Post-Manipulation Weeks 1	2	3	4	5	6	7	8	9	10	11	12	Post Mean	Post/Pre %
Deprivation Group	339	Rs/ Bout	204	357	216	192	231									249	122
		Min/Bout	3.9	6.3	3.8	3.0	3.2										
		Gms/Bout	1.5	3.3	2.1	1.7	2.2									2.3	155
	347	Rs/Bout	189	287	470	378	280				240	247	160	247		289	153
		Min/Bout	3.1	4.6	4.3	3.8	3.8				2.9	2.9	2.7	3.2			
		Gms/Bout	2.5	4.3	3.9	3.1	3.1				2.4	2.4	2.3	2.8		3.0	122
	360	Rs/Bout	171	263	213	189	191									214	125
		Min/Bout	2.4	3.6	2.9	2.4	2.8										
		Gms/Bout	1.5	2.2	1.8	1.6	1.5									1.8	118

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* Low Number is an Artifact Due to Pecking Deficits

** Post-operative Week 9. etc.

APP. TABLE 7

MEAN BOUT SIZE AND MEAN NUMBER OF BOUTS IN THE 7-DAY PERIOD AFTER RESUMPTION OF FEEDING

Condition	Bird	Bout Size in Responses			Bout Size in Grams			Number of Bouts		
		Pre-op Mean	Post-op Mean	%	Pre-op Mean	Post-op Mean	%	Pre-op Mean	Post-op Mean	%
Deafferentation Group	373	192	485	253	1.9	4.1	218	15.7	7.3	46
	349	158	335	212	1.2	1.8	149	29.4	12.4	42
	435	282	501	179	2.1	3.9	183	11.9	6.0	50
	441	285	481	169	2.3	4.4	193	8.1	5.6	69
	412	447	1048	234	3.8	2.9	77	7.7	9.8	127
Control Group	348	315	329	104	2.7	3.1	115	7.9	7.3	92
	362	228	450	197	1.3	3.1	238	12.3	6.7	54
Deprivation Group	339	204	357	175	1.5	3.3	220	15.5	9.4	61
	374	189	287	152	2.5	4.3	172	12.4	7.6	61
	360	171	263	154	1.5	2.2	147	13.1	4.3	71

APP. TABLE 8A
MEAN NUMBER OF BOUTS IN FOUR BOUT SIZE CATEGORIES BEFORE AND AFTER DEAFFERENTATION AND THEIR PERCENTAGE OF THE PRE-OPERATIVE MEAN NUMBER

			Bout Size in Responses							Bout Size in Grams of Food						
	Bird	Condition	Small Mean		Medium Mean		Large Mean		Oversized Mean	Small Mean		Medium Mean		Large Mean		Oversized Mean
			#	%	#	%	#	%	#	#	%	#	%	#	%	#
Deafferentation Group	373	Pre	8.6	100	7.1	100	0.0	0	0.0	9.1	100	6.6	100	0.0	0	0.0
		Post	2.4	28	2.3	32	0.0	0	1.6	2.6	29	2.3	25	0.0	0	2.0
	349	Pre	21.0	100	8.3	100	0.1	100	0.0	24.7	100	4.7	100	0.0	0	0.0
		Post	7.1	37	4.2	50	0.5	366	1.8	9.6	39	3.4	73	0.0	0	1.2
	435	Pre	6.4	100	4.4	100	1.0	100	0.0	6.6	100	4.3	100	1.0	100	0.0
		Post	1.7	26	1.4	31	0.5	50	0.9	1.8	27	0.9	21	0.6	55	1.6
	441	Pre	2.9	100	4.4	100	0.9	100	0.0	4.0	100	3.9	100	0.3	100	0.0
		Post	2.9	100	4.2	95	1.0	112	0.2	3.4	85	4.5	115	0.7	225	0.1
	412	Pre	3.9	100	1.6	100	2.3	100	0.0	4.3	100	1.3	100	2.2	100	0.0
		Post	6.1	157	1.6	100	2.6	113	1.1	8.3	193	1.8	138	1.3	59	0.1
Control Group	348	Pre	2.6	100	4.1	100	1.2	100	0.0	3.3	100	3.9	100	0.7	100	0.0
		Post	3.1	119	3.6	88	1.0	83	0.1	3.2	97	3.5	90	0.8	114	0.4
	362	Pre	8.6	100	2.4	100	1.3	100	0.0	9.9	100	1.4	100	1.0	100	0.0
		Post	4.3	50	1.7	71	1.6	123	0.1	5.2	52	1.3	93	0.9	90	0.4

APP. TABLE 8B
MEAN NUMBER OF BOUTS IN FOUR BOUT SIZE CATEGORIES BEFORE AND AFTER DEPRIVATION AND THEIR PERCENTAGE OF THE PRE-DEPRIVATION MEAN NUMBER

			Bout Size in Responses							Bout Size in Grams of Food						
	Bird	Condition	Small Mean #	%	Medium Mean #	%	Large Mean #	%	Oversized Mean #	Small Mean #	%	Medium Mean #	%	Large Mean #	%	Oversized Mean #
Deprivation Group	339	Pre	10.0	100	4.3	100	1.1	100	0.0	11.9	100	3.3	100	0.3	100	0.0
		Post 1	3.7	37	3.4	79	1.6	145	0.7	3.7	31	3.9	118	1.2	400	0.7
		Rec	9.7	97	3.3	77	1.3	118	0.0	10.0	84	3.3	100	1.0	333	0.0
	374	Pre	8.1	100	4.0	100	0.4	100	0.0	6.4	100	5.0	100	1.0	100	0.0
		Post 1	4.3	53	2.4	60	0.4	100	0.4	2.4	38	3.6	72	0.9	90	0.7
		Rec	7.7	95	3.7	93	0.3	75	0.0	5.7	89	5.0	100	1.0	100	0.0
	360	Pre	9.3	100	3.7	100	0.14	100	0.0	9.7	100	3.4	100	0.0	0	0.0
		Post 1	4.6	49	3.9	105	0.14	100	0.7	6.0	62	2.7	79	0.0	0	0.4
		Rec	8.7	94	4.7	127	0.3	214	0.0	10.0	103	3.3	97	0.0	0	0.3

Pre: Mean of pre-manipulation period
Post 1: Mean of post-manipulation week 1
Rec: Mean of recovered period

APP. TABLE 9A
MEAN NUMBER OF BOUTS IN FOUR BOUT SIZE CATEGORIES BEFORE AND AFTER DEAFFERENTATION AND THEIR PERCENTAGE OF THE TOTAL NUMBER OF BOUTS

			Bout Size in Responses								Bout Size in Grams of Food							
	Bird	Condition	Small Mean #	%	Medium Mean #	%	Large Mean #	%	Oversized Mean #	%	Small Mean #	%	Medium Mean #	%	Large Mean #	%	Oversized Mean #	%
Deafferentation Group	373	Pre	8.6	55	7.1	45	0.0	0	0.0	0	9.1	58	6.6	42	0.0	0	0.0	0
		Post	2.4	38	2.3	37	0.0	0	1.6	25	2.6	38	2.3	33	0.0	0	2.0	29
	349	Pre	21.0	71	8.3	28	0.1	1	0.0	0	24.7	84	4.7	16	0.0	0	0.0	0
		Post	7.1	52	4.2	31	0.5	4	1.8	13	9.6	68	3.4	24	0.0	0	1.2	8
	435	Pre	6.4	54	4.4	37	1.0	9	0.0	0	6.6	56	4.3	36	1.0	8	0.0	0
		Post	1.7	38	1.4	31	0.5	11	0.9	20	1.8	37	0.9	18	0.6	12	1.6	33
	441	Pre	2.9	36	4.4	54	0.9	10	0.0	0	4.0	49	3.9	48	0.3	3	0.0	0
		Post	2.9	35	4.2	51	1.0	12	0.2	2	3.4	39	4.5	52	0.7	8	0.1	1
	412	Pre	3.9	50	1.6	20	2.3	30	0.0	0	4.3	55	1.3	17	2.2	28	0.0	0
		Post	6.1	53	1.6	14	2.6	23	1.1	10	8.3	73	1.8	16	1.3	11	0.1	0
Control Group	348	Pre	2.6	33	4.1	53	1.2	14	0.0	0	3.3	42	3.9	49	0.7	9	0.0	0
		Post	3.1	40	3.6	47	1.0	13	0.1	0	3.2	41	3.5	44	0.8	10	0.4	5
	362	Pre	8.6	70	2.4	20	1.3	10	0.0	0	9.9	81	1.4	11	1.0	8	0.0	0
		Post	4.3	56	1.7	22	1.6	21	0.1	1	5.2	67	1.3	17	0.9	11	0.4	5

APP. TABLE 9B

MEAN NUMBER OF BOUTS IN FOUR BOUT SIZE CATEGORIES BEFORE AND AFTER DEPRIVATION AND THEIR PERCENTAGE OF THE TOTAL NUMBER OF BOUTS

			Bout Size in Responses								Bout Size in Grams of Food							
	Bird	Condition	Small Mean #	Small %	Medium Mean #	Medium %	Large Mean #	Large %	Oversized Mean #	Oversized %	Small Mean #	Small %	Medium Mean #	Medium %	Large Mean #	Large %	Oversized Mean #	Oversized %
Deprivation Group	339	Pre	10.0	65	4.3	28	1.1	7	0.0	0	11.9	77	3.3	21	0.3	2	0.3	0
		Post 1	3.7	39	3.4	36	1.6	17	0.7	8	3.7	39	3.9	41	1.2	12	0.7	8
		Rec	9.7	68	3.3	23	1.3	9	0.0	0	10.0	70	3.3	23	1.0	7	0.0	0
	374	Pre	8.1	65	4.0	32	0.4	3	0.0	0	6.4	53	5.0	41	1.0	8	0.0	0
		Post 1	4.3	56	2.4	32	0.4	6	0.4	6	2.4	32	3.6	47	0.9	12	0.7	9
		Rec	7.7	66	3.7	31	0.3	3	0.0	0	5.7	44	5.0	43	1.0	8	0.0	0
	360	Pre	9.3	71	3.7	28	0.14	11	0.0	0	9.7	74	3.4	26	0.0	0	0.0	0
		Post 1	4.6	49	3.9	41	0.14	2	0.7	8	6.0	65	2.7	30	0.0	0	0.4	5
		Rec	8.7	64	4.7	34	0.3	2	0.0	0	10.0	73	3.3	24	0.0	0	0.3	3

Pre: Mean of pre-manipulation period
Post 1: Mean of post-manipulation week 1
Rec: Mean of recovered period

APP. TABLE 10A
MEAN FEEDING ACTIVITY IN FOUR BOUT SIZE CATEGORIES BEFORE AND AFTER DEAFFERENTATION AND ITS PERCENTAGE OF THE PRE-OPERATIVE MEAN FEEDING ACTIVITY

	Bird	Condi- tion	Bout Size in Responses							Bout Size in Grams of Food						
			Small Mean		Medium Mean		Large Mean		Oversized Mean	Small Mean		Medium Mean		Large Mean		Oversized Mean
			#	%	#	%	#	%	#	#	%	#	%	#	%	#
Deafferentation Group	373	Pre	1020	100	2005	100	0	0	0	11.1	100	18.9	100	0.0	0	0.0
		Post	275	27	734	37	0	0	1773	3.3	30	8.0	42	0.0	0	20.7
	349	Pre	2176	100	2414	100	77	100	0	23.5	100	12.7	100	0.0	0	0.0
		Post	773	36	1287	53	246	319	1735	8.1	34	10.6	83	0.0	0	8.8
	435	Pre	10.8*	100	26.7*	100	12.6*	100	0	5.2	100	14.1	100	5.8	100	0.0
		Post	2.6*	24	9.1*	34	8.8*	70	28.8*	1.2	23	2.9	21	3.7	64	21.7
	441	Pre	310	100	1459	100	552	100	0	4.3	100	12.1	100	2.4	100	0.0
		Post	310	100	1479	101	630	114	314	3.4	80	14.4	120	4.8	202	1.4
	412	Pre	309	100	445	100	2695	100	0	3.3	100	4.1	100	21.9	100	0.0
		Post	343	111	511	115	2898	108	4295	3.5	106	5.9	144	13.3	61	1.2
Control Group	348	Pre	337	100	1230	100	906	100	0	4.2	100	11.4	100	5.7	100	0
		Post	345	102	999	81	708	78	70	3.7	88	10.1	88	5.7	100	1.7
	362	Pre	528	100	865	100	1418	100	0	4.8	100	4.2	100	6.9	100	0
		Post	286	54	555	64	1734	122	223	3.2	67	4.0	95	6.5	94	5.3

APP. TABLE 10B
MEAN FEEDING ACTIVITY IN FOUR BOUT SIZE CATEGORIES BEFORE AND AFTER DEPRIVATION AND ITS PERCENTAGE OF THE PRE-DEPRIVATION MEAN

			*		Bout Size in Responses					Bout Size in Grams of Food						
	Bird	Condition	Small Mean		Medium Mean		Large Mean		Oversized Mean	Small Mean		Medium Mean		Large Mean		Oversized Mean
			#	%	#	%	#	%	#	#	%	#	%	#	%	#
Deprivation Group	339	Pre	1154	100	1255	100	743	100	0	12.0	100	9.7	100	1.8	100	0.0
		Post 1	347	30	1188	95	975	131	853	3.5	29	12.4	128	6.8	378	8.3
		Rec	885	77	1075	86	796	107	0	8.3	69	10.3	106	5.4	200	0.0
	374	Pre	849	100	1299	100	204	100	0	7.3	100	16.3	100	6.9	100	0.0
		Post 1	537	63	713	55	304	149	620	3.2	44	10.6	65	5.1	74	13.3
		Rec	721	85	966	74	174	85	0	6.6	90	14.8	91	5.9	86	0.0
	360	Pre	1124	100	1050	100	76	100	0	10.8	100	9.1	100	0.0	0	0.0
		Post 1	489	44	1080	103	78	103	794	6.7	62	7.5	82	0.0	0	6.8
		Rec	1022	91	1386	132	199	132	0	10.4	96	9.0	99	0.0	0	1.7

Pre: Mean of pre-manipulation period
Post 1: Mean of post-manipulation week 1
Rec: Mean of recovered period

* Feeding activity measured in minutes

APP. TABLE 11A
MEAN FEEDING ACTIVITY IN FOUR BOUT SIZE CATEGORIES BEFORE AND AFTER DEAFFERENTATION AND ITS PERCENTAGE OF THE TOTAL FEEDING ACTIVITY

			Bout Size in Responses								Bout Size in Grams of Food							
	Bird	Condition	Small Mean		Medium Mean		Large Mean		Oversized Mean		Small Mean		Medium Mean		Large Mean		Oversized Mean	
			#	%	#	%	#	%	#	%	#	%	#	%	#	%	#	%
Deafferentation Group	373	Pre	1020	34	2005	66	0	0	0	0	11.1	37	18.9	63	0.0	0	0.0	0
		Post	275	10	734	26	0	0	1773	64	3.3	10	8.0	25	0.0	0	20.7	65
	349	Pre	2176	47	2414	52	77	1	0	0	23.5	65	12.7	35	0.0	0	0.0	0
		Post	773	19	1287	32	246	6	1735	43	8.1	29	10.6	39	0.0	0	8.8	32
	435	Pre	10.8*	22	26.7*	53	12.6*	25	0.0	0	5.2	21	14.1	56	5.8	23	0.0	0
		Post	2.6*	5	9.1*	18	8.8*	19	28.8*	58	1.2	4	2.9	10	3.7	13	21.7	73
	441	Pre	310	13	1459	63	552	24	0	0	4.3	23	12.1	64	2.4	13	0.0	0
		Post	310	11	1479	54	630	23	314	12	3.4	14	14.4	60	4.8	20	1.4	6
	412	Pre	309	9	445	13	2695	78	0	0	3.3	11	4.1	14	21.9	75	0.0	0
		Post	343	4	511	6	2898	36	4295	54	3.5	15	5.9	25	13.3	55	1.2	5
Control Group	348	Pre	337	13	1230	53	906	34	0	0	4.2	20	11.4	55	5.7	25	0.0	0
		Post	345	16	999	47	708	34	70	3	3.7	17	10.1	48	5.7	27	1.7	8
	362	Pre	528	19	865	31	1418	50	0	0	4.8	30	4.2	26	6.9	44	0.0	0
		Post	286	10	555	20	1734	62	223	8	3.2	17	4.0	21	6.5	34	5.3	28

APP. TABLE 11B

MEAN FEEDING ACTIVITY IN FOUR BOUT SIZE CATEGORIES BEFORE AND AFTER DEPRIVATION AND ITS PERCENTAGE OF THE TOTAL FEEDING ACTIVITY

			Bout Size in Responses								Bout Size in Grams of Food							
	Bird	Condition	Small		Medium		Large		Oversized		Small		Medium		Large		Oversized	
			Mean #	%	Mean #	%	Mean #	%	Mean #	%	Mean #	%	Mean #	%	Mean #	%	Mean #	%
Deprivation Group	339	Pre	1154	36	1255	40	743	24	0	0	12.0	51	9.7	41	1.8	8	0.0	0
		Post 1	347	11	1188	35	975	29	853	25	3.5	11	12.4	40	6.8	22	8.3	27
		Rec	885	32	1075	39	796	29	0	0	8.3	34	10.3	43	5.4	23	0.0	0
	374	Pre	849	39	1299	56	204	5	0	0	7.3	24	16.3	54	6.9	22	0.0	0
		Post 1	537	24	713	35	304	15	620	26	3.2	10	10.6	33	5.1	16	13.3	41
		Rec	721	42	966	51	174	7	0	0	6.6	24	14.8	54	5.9	22	0.0	0
	360	Pre	1124	50	1050	47	76	3	0	0	10.8	54	9.1	46	0.0	0	0.0	0
		Post 1	489	20	1080	44	78	3	794	33	6.7	32	7.5	36	0.0	0	6.8	32
		Rec	1022	38	1386	54	199	8	0	0	10.4	49	9.0	43	0.0	0	1.7	8

Pre: Mean of pre-manipulation period
Post 1: Mean of post-manipulation week 1
Rec: Mean of recovered period

* Feeding activity measured in minutes

APP. TABLE 12A

MEAN HOURLY DISTRIBUTION OF FEEDING ACTIVITY --DEAFFERENTATION BIRD 373

	Hour	1		2		3		4		5		6		7
Pre	# Responses	859	28%	822	27%	667	22%	425	14%	202	7%	59	2%	
	Food (gms)	8.5		8.2		6.6		4.1		2.0		0.6		
Post Week 1 3 Days	# Responses	2338	74%	643	20%	114	4%	77	2%	5	0%			
	Food (gms)	17.4		4.5		0.8		0.6		0.0				
2	# Responses	2303	75%	424	14%	301	10%	31	1%	14	1%			
	Food (gms)	24.9		4.5		3.4		0.3		0.1				
3	# Responses	1083	57%	397	21%	159	8%	198	10%	78	4%			
	Food (gms)	18.5		6.7		2.6		3.4		1.3				
4	# Responses	978	51%	391	21%	279	15%	205	11%	53	3%			
	Food (gms)	15.5		5.8		4.5		2.9		0.9				
5	# Responses	1159	47%	638	26%	345	14%	260	11%	45	2%			
	Food (gms)	13.4		7.5		4.0		3.1		0.5				

APP. TABLE 12 B

MEAN HOURLY DISTRIBUTION OF FEEDING ACTIVITY -- DEAFFERENTATION BIRD 349

	Hour	1		2		3		4		5		6		7	
Pre	# Responses	1642	35%	854	18%	928	20%	624	13%	382	8%	174	4%	57	1%
	Food (gms)	12.9		6.7		7.1		4.8		3.0		1.4		0.4	
Post Week 1	No Food Intake														
2	# Responses	1759	43%	528	13%	697	18%	497	13%	387	9%	139	3%	180	2%
	Food (gms)	9.6		2.9		2.8		2.1		1.9		0.8		0.5	
3	# Responses	1484	50%	455	15%	287	9%	296	9%	333	11%	161	5%	17	1%
	Food (gms)	12.5		3.7		2.3		2.3		2.7		1.3		0.1	
4	# Responses	1753	50%	529	16%	565	16%	259	8%	187	5%	149	4%	35	1%
	Food (gms)	12.5		4.0		3.9		2.0		1.3		0.9		0.3	
5	# Responses	1897	36%	1054	20%	659	13%	669	13%	539	10%	224	4%	220	4%
	Food (gms)	9.3		5.0		3.1		3.1		2.6		1.1		1.0	
6	# Responses	1170	24%	2033	41%	574	12%	355	7%	542	11%	263	5%	28	1%
	Food (gms)	7.5		12.9		3.6		2.2		3.0		1.9		0.2	
7	# Responses	1835	38%	648	14%	797	17%	596	12%	460	10%	277	6%	179	4%
	Food (gms)	12.0		4.0		5.4		3.9		3.0		1.8		1.2	
8	# Responses	1916	47%	496	12%	721	18%	323	8%	378	9%	207	5%	142	2%
	Food (gms)	14.5		4.0		5.6		2.4		3.0		1.5		0.6	
9	# Responses	1366	47%	637	22%	304	11%	315	11%	152	5%	126	4%		
	Food (gms)	13.9		6.7		3.5		3.3		1.7		1.4			

APP. TABLE 12C

MEAN HOURLY DISTRIBUTION OF FEEDING ACTIVITY --DEAFFERENTATION BIRD 435

	Hour	1		2		3		4		5		6		7	
Pre	**# Responses**	1101	33%	1004	30%	768	23%	338	10%	127	4%	0	0%	1	0%
	Food (gms)	8.2		7.5		5.6		2.6		1.0		0.0		0.01	
Post **Week 1** 3 Days	**# Responses**	605	20%	89	3%	2375	77%								
	Food(gms)	5.0		0.7		19.3									
2	**# Responses**	736	50%	357	24%	311	21%	62	4%	0	0%	0	0%	4	0%
	Food (gms)	12.5		5.5		3.4		1.4		0.0		0.0		0.1	
3	**# Responses**	724	59%	310	25%	90	7%	46	4%	60	5%				
	FOOd (gms)	15.2		6.5		2.0		1.0		1.4					
4	**# Responses**	815	69%	213	18%	93	8%	0	0%	64	5%				
	Food (gms)	14.8		4.7		1.0		0.0		1.4					
5	**# Responses**	783	79%	63	6%	74	8%	56	6%	9	1%				
	Food (gms)	20.1		1.7		2.0		1.4		0.2					

APP. TABLE 12D

MEAN HOURLY DISTRIBUTION OF FEEDING ACTIVITY --DEAFFERENTATION BIRD 441

	Hours	1		2		3		4		5		6		7
Pre	# Responses	204	9%	314	14%	715	31%	696	30%	343	15%	49	2%	
	Food (gms)	1.7		2.7		5.9		5.6		2.6		0.3		
Post Week 1 3 Days	# Responses	139	5%	530	18%	2019	70%	0	0%	191	7%			
	Food (gms)	0.8		3.2		14.3		0.0		1.1				
2	# Responses	1012	47%	524	24%	352	16%	183	8%	85	4%			
	Food (gms)	13.1		6.6		4.1		2.1		0.9				
3	# Responses	376	27%	424	30%	272	19%	159	11%	143	10%	34	2%	
	Food (gms)	7.2		7.4		4.7		2.8		2.5		0.8		
4	# Responses	554	30%	526	28%	438	24%	263	14%	73	4%			
	Food (gms)	6.1		5.7		4.7		2.8		0.6				
5	# Responses	1763	53%	239	7%	967	29%	199	6%	153	5%			
	Food (gms)	10.0		1.4		5.5		1.1		0.9				
6														
7	# Responses	1219	43%	881	31%	509	18%	118	4%	129	5%			
	Food (gms)	12.0		8.7		5.1		1.1		1.3				

APP. TABLE 12E

MEAN HOURLY DISTRIBUTION OF FEEDING ACTIVITY -- DEAFFERENTATION BIRD 412

	Hour	1		2		3		4		5		6		7	
Pre	# Responses	2543	74%	244	7%	163	5%	299	9%	184	5%	15	1%		
	Food (gms)	21.7		2.2		1.5		2.3		1.5		0.1			
Post* Week 9	# Responses			7536	74%			2610	26%			29	0%	2	0%
	Food (gms)			21.2				7.6				0.1		0.0	
10	# Responses			6062	80%			1493	20%			34	1%		
	Food (gms)			19.0				4.5				0.1			
11	# Responses			4722	74%			1498	23%			207	3%		
	Food (gms)			16.4				4.9				0.7			
12	# Responses			4827	71%			2005	29%			8	0%		
	Food (gms)			13.9				6.0				0.0			
13	# Responses			4771	68%			1976	28%			265	4%		
	Food (gms)			14.7				5.9				0.8			
14	# Responses			5230	60%			2789	32%			567	7%	226	3%
	Food (gms)			14.8				8.0				1.4		0.8	
15	# Responses			7460	71%			3051	29%			29	0%	45	0%
	Food (gms)			14.0				5.7				0.1		0.1	
16	# Responses			7792	73%			2314	23%			344	3%		
	Food (gms)			17.0				5.9				0.7			

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* Post-operatively data are calculated on the basis of 2-hour intervals because of the extreme duration of bouts resulting from marked feeding inefficiency.

APP. TABLE 12E Cont.

	Hour	1	2	3	4	5	6	7
Post 17	# Responses		4166 83%		713 14%		98 2%	24 1%
	Food (gms)		21.0		4.5		0.4	0.2
18	# Responses		5436 75%		1894 26%			
	Food (gms)		22.7		6.8			

APP. TABLE 13A

MEAN HOURLY DISTRIBUTION OF FEEDING ACTIVITY -- DEPRIVATION BIRD 339

	Hour	1		2		3		4		5		6		7	
Pre	# Responses	910	29%	640	20%	742	24%	388	12%	399	13%	72	2%		
	Food (gms)	6.8		4.7		5.6		2.8		3.0		0.5			
Post Week 1	# Responses	1626	48%	524	15%	568	17%	317	9%	258	7%	74	2%	5	0%
	Food (gms)	15.8		4.3		5.1		3.0		2.1		0.6		0.1	
2	# Responses	1115	35%	551	17%	757	24%	364	11%	226	7%	125	4%	34	1%
	Food (gms)	10.8		5.4		7.4		3.6		2.2		1.2		0.3	
3	# Responses	783	28%	655	24%	581	21%	396	14%	252	9%	35	1%	54	2%
	Food (gms)	6.8		5.7		5.0		3.5		2.2		0.3		0.5	

APP. TABLE 13B

MEAN HOURLY DISTRIBUTION OF FEEDING ACTIVITY -- DEPRIVATION BIRD 374

	Hour	1		2		3		4		5		6		7	
Pre	# Responses	666	28%	316	13%	624	27%	360	15%	178	8 %	201	9 %	8	0.5%
	Food (gms)	8.3		4.9		7.9		4.6		2.1		2.6		0.2	
Post Week 1	# Responses	1287	59%	363	17%	260	12%	172	8 %	63	3 %	22	1 %	7	0.3%
	Food (gms)	19.3		5.2		4.0		2.5		0.8		0.3		0.2	
2	# Responses	1213	29%	559	13%	1059	25%	868	21%	306	7 %	67	2 %	158	4%
	Food (gms)	10.3		4.4		8.6		7.1		2.5		0.6		1.2	
3	# Responses	1069	26%	597	14%	1165	28%	644	15%	479	12%	146	4 %	56	1%
	Food (gms)	8.7		4.8		9.7		5.3		3.8		1.2		0.5	
4	# Responses	799	27%	637	21%	743	25%	318	11%	255	9 %	142	5 %	96	3%
	Food (gms)	8.9		7.4		8.0		3.6		2.9		1.4		1.1	
5-7	# Responses														
	Food (gms)														
8	# Responses	946	30%	557	18%	670	22%	637	20%	186	6 %	62	2 %	58	2%
	Food (gms)	9.8		5.3		7.4		6.8		1.7		0.5		0.8	
9	# Responses	580	19%	707	23%	764	25%	541	18%	201	6 %	227	7 %	70	2%
	Food (gms)	5.6		6.8		7.2		5.2		1.9		2.2		0.7	
10	# Responses	554	30%	358	19%	341	18%	273	15%	234	13%	102	5 %		
	Food (gms)	7.5		5.0		5.8		3.9		3.2		1.7			
11	# Responses	912	35%	500	19%	436	17%	295	11%	306	12%	81	3 %	64	2%
	Food (gms)	10.5		5.3		4.9		3.2		3.3		1.1		0.6	

APP. TABLE 13C

MEAN HOURLY DISTRIBUTION OF FEEDING ACTIVITY -- DEPRIVATION BIRD 360

	Hour	1		2		3		4		5		6		7	
Pre	# Responses	303	13%	294	13%	408	18%	559	25%	354	16%	249	11%	85	4%
	Food (gms)	2.8		2.5		3.8		4.9		3.1		2.1		0.8	
Post	# Responses	1391	57%	331	14%	146	6%	252	10%	265	11%	19	1%	37	2%
Week 1	Food (gms)	12.3		2.7		1.1		2.1		2.3		0.2		1.0	
2	# Responses	922	41%	333	15%	291	13%	271	12%	225	10%	195	9%		
	Food (gms)	7.8		2.8		2.3		2.3		1.9		1.6			
3	# Responses	774	36%	305	14%	434	20%	398	18%	148	7%	119	5%		
	Food (gms)	6.4		2.6		3.6		3.3		1.2		1.0			
4	# Responses	884	34%	463	18%	505	19%	396	15%	181	7%	140	5%	39	2%
	Food (gms)	7.2		3.8		4.2		3.2		1.4		1.2		0.3	

APP. TABLE 14A

MEAN HOURLY DISTRIBUTION OF FEEFING ACTIVITY -- CONTROL BIRD 348

	Hour	1		2		3		4		5		6		7	
Pre	# Responses	1138	46%	553	22%	304	12%	269	11%	111	4%	47	2%	51	2%
	Food (gms)	9.9		4.7		2.4		2.3		0.9		0.4		0.5	
Post Week 1	# Responses	1042	47%	363	17%	289	12%	276	11%	191	9%	118	4%		
	Food (gms)	9.8		3.2		2.7		2.5		1.8		1.2			
2	# Responses	924	42%	382	17%	358	16%	226	10%	202	9%	50	2%	44	2%
	Food (gms)	10.3		4.4		4.0		2.5		2.2		1.4		0.5	
3	# Responses	1065	40%	634	24%	429	16%	232	9%	179	7%	93	4%	5	0%
	Food (gms)	10.1		6.4		3.8		2.3		1.5		1.0		0.0	

APP. TABLE 14B

MEAN HOURLY DISTRIBUTION OF FEEDING ACTIVITY — CONTROL BIRD 362

	Hour	1		2		3		4		5		6		7	
Pre	# Responses	1446	52%	381	14%	462	16%	241	9 %	80	3 %	140	5 %	60	2%
	Food (gms)	8.3		1.8		2.7		1.5		0.5		0.9		0.3	
Post Week 1	# Responses	1555	53%	339	11%	475	16%	42	1 %	434	15%	52	2 %	40	1%
	Food (gms)	10.9		2.3		3.2		0.4		2.9		0.3		0.3	
2	# Responses	2023	65%	462	15%	170	5 %	298	10%	43	1 %	89	3 %	38	1%
	Food (gms)	12.7		3.0		1.0		2.0		0.2		0.6		0.3	
3	# Responses	1421	61%	529	23%	89	4 %	162	7 %	61	3 %	0	0 %	20	1%
	Food (gms)	10.5		3.8		0.6		1.2		0.9		0.0	0 %	0.1	

APP. TABLE 15A

MEAN HOURLY BOUT SIZE AND MEAN HOURLY NUMBER OF BOUTS -- DEAFFERENTATION BIRD 373

	Hour	1	2	3	4	5	6	7
Pre	Bout Size (gms)	2.1	2.6	1.8	1.7	1.1	0.8	
	Number of Bouts	4.0	3.1	3.6	2.4	1.9	0.7	
Post	Bout Size (gms)	8.7	2.7	0.8	0.9	0.1		
Week 1	Number of Bouts	2.0	1.7	1.0	0.7	0.3		
3 Days								
2	Bout Size (gms)	8.7	1.8	1.6	0.4	0.4		
	Number of Bouts	2.9	2.4	2.1	0.9	0.3		
3	Bout Size (gms)	5.4	1.9	1.2	1.4	1.1		
	Number of Bouts	3.4	3.6	2.2	2.4	1.2		
4	Bout Size (gms)	3.9	2.3	1.9	1.5	0.8		
	Number of Bouts	4.0	2.5	2.3	2.0	1.2		
5	Bout Size (gms)	4.5	3.0	2.0	1.5	0.5		
	Number of Bouts	3.0	2.5	2.0	2.0	1.0		

APP. TABLE 15B

MEAN HOURLY BOUT SIZE AND MEAN HOURLY NUMBER OF BOUTS -- DEAFFERENTATION BIRD 349

	Hour	1	2	3	4	5	6	7
Pre	Bout Size (gms)	2.1	1.3	1.3	1.0	0.7	0.6	0.5
	Number of Bouts	6.1	5.3	5.4	5.0	4.4	2.3	0.9
Post Week 1		No Food Intake						
2	Bout Size (gms)	3.2	1.9	1.4	1.1	0.7	1.2	1.5
	Number of Bouts	3.0	1.5	2.0	1.8	3.0	0.7	0.4
3	Bout Size (gms)	5.1	2.1	1.5	1.8	1.7	1.3	1.0
	Number of Bouts	2.4	1.7	1.6	1.3	1.6	1.0	0.1
4	Bout Size (gms)	5.3	2.4	1.9	1.0	0.8	0.9	0.9
	Number of Bouts	2.3	1.7	2.0	2.0	1.7	1.0	0.3
5	Bout Size (gms)	3.3	1.9	1.2	1.3	0.9	0.5	1.0
	Number of Bouts	2.8	2.6	2.6	2.4	2.8	2.0	1.0
6	Bout Size (gms)	4.5	3.9	1.2	0.8	1.3	1.0	0.5
	Number of Bouts	1.7	3.3	3.0	2.7	2.3	2.0	0.3
7	Bout Size (gms)	3.4	1.3	1.6	1.2	1.2	0.7	1.0
	Number of Bouts	3.5	3.0	3.5	3.3	2.5	2.5	1.3
8	Bout Sizd (gms)	2.8	1.4	1.5	1.1	1.0	1.0	1.1
	Number of Bouts	5.3	2.8	3.8	2.3	3.0	1.5	0.5
9	Bout Size (gms)	5.6	2.4	2.0	3.3	1.7	1.4	
	Number of Bouts	2.5	2.8	1.8	1.0	1.0	1.0	

APP. TABLE 15C

MEAN HOURLY BOUT SIZE AND MEAN HOURLY NUMBER OF BOUTS -- DEAFFERENTATION BIRD 435

	Hour	1	2	3	4	5	6	7
Pre	Bout Size (gms)	2.3	2.2	2.3	1.7	1.4	0.0	0.1
	Number of Bouts	3.6	3.4	2.4	1.6	0.7	0.0	0.1
Post Week 1 3 Days	Bout Size (gms)	2.5	0.5	7.7				
	Number of Bouts	2.0	1.5	2.5				
2	Bout Size (gms)	5.1	3.9	4.0	3.3	0.0	0.0	0.5
	Number of Bouts	2.4	1.4	0.9	0.4	0.0	0.0	0.1
3	Bout Size (gms)	6.0	0.5	2.5	2.6	3.4		
	Number of Bouts	2.4	1.0	0.8	0.4	0.4		
4	Bout Size (gms)	6.6	6.2	1.3	0.0	2.8		
	Number of Bouts	2.3	0.8	0.8	0.0	0.5		
5	Bout Size (gms)	8.6	2.5	2.0	2.1	0.3		
	Number of Bouts	2.3	0.7	1.0	0.7	0.7		

APP. TABLE 15D

MEAN HOURLY BOUT SIZE AND MEAN HOURLY NUMBER OF BOUTS -- DEAFFERENTATION BIRD 441

	Hour	1	2	3	4	5	6	7
Pre	Bout Size (gms)	1.3	2.4	2.4	3.3	2.0	1.1	
	Number of Bouts	1.3	1.1	2.4	1.7	1.3	0.3	
Post Week 1 3 Days	Bout Size (gms)	0.6	3.2	6.1	0.0	3.4		
	Number of Bouts	1.3	1.0	2.3	0.0	0.3		
2	Bout Size (gms)	4.9	3.9	4.9	2.5	1.3		
	Number of Bouts	2.7	1.7	0.8	0.8	0.7		
3	Bout Size (gms)	3.1	2.3	1.9	1.6	2.5	3.0	
	Number of Bouts	2.3	3.3	2.5	1.8	1.0	0.3	
4	Bout Size (gms)	3.4	2.4	3.0	1.8	1.6		
	Number of Bouts	1.8	2.4	1.6	1.6	0.4		
5	Bout Size (gms)	2.9	1.4	2.2	1.1	1.7		
	Number of Bouts	3.5	1.0	2.5	1.0	o.5		
6								
7	Bout Size (gms)	4.8	4.4	3.4	2.2	2.6		
	Number of Bouts	2.5	2.0	1.5	0.5	0.5		

APP. TABLE 16A

MEAN HOURLY BOUT SIZE AND MEAN HOURLY NUMBER OF BOUTS -- DEPRIVATION BIRD 339

	Hour	1	2	3	4	5	6	7
Pre	Bout Size (gms)	1.7	1.7	1.9	1.2	1.1	0.8	
	Number of Bouts	4.0	2.7	3.0	2.3	2.7	0.7	
Post	Bout Size (gms)	5.5	3.4	2.7	2.4	1.5	1.1	0.4
Week 1	Number of Bouts	2.9	1.3	1.9	1.3	1.4	0.6	0.1
2	Bout Size (gms)	3.2	2.3	2.3	1.4	1.3	0.9	0.9
	Number of Bouts	3.3	2.3	3.2	2.5	1.7	1.3	0.3
3	Bout Size (gms)	2.6	2.4	1.7	1.7	0.8	0.3	0.7
	Number of Bouts	2.7	2.3	3.0	3.0	2.0	2.7	1.0

APP. TABLE 16B

MEAN HOURLY BOUT SIZE AND MEAN HOURLY NUMBER OF BOUTS -- DEPRIVATION BIRD 374

	Hour	1	2	3	4	5	6	7
Pre	Bout Size (gms)	3.6	3.8	2.8	1.9	1.5	1.3	1.1
	Number of Bouts	2.3	1.3	2.9	2.4	1.4	2.0	0.1
Post	Bout Size (gms)	8.5	3.3	2.8	1.9	1.4	1.2	0.7
Week 1	Number of Bouts	2.3	1.6	1.4	1.3	0.6	0.3	0.1
2	Bout Size (gms)	5.6	4.4	4.3	3.6	2.1	1.8	1.8
	Number of Bouts	1.8	1.0	2.0	2.0	1.2	0.3	0.7
3	Bout Size (gms)	4.4	4.8	3.7	2.3	1.9	1.8	1.6
	Number of Bouts	2.0	1.0	2.7	2.3	2.0	0.7	0.3
4	Bout Size (gms)	5.3	4.4	4.0	1.8	1.8	1.4	1.6
	Number of Bouts	1.7	1.7	2.0	2.0	1.7	1.0	0.7
5 - 7								
8	Bout Size (gms)	4.5	2.1	2.5	2.3	1.7	1.1	0.8
	Number of Bouts	2.0	2.5	3.0	3.0	1.0	0.5	1.0
9	Bout Size (gms)	3.7	2.7	2.9	2.1	1.3	1.4	1.4
	Number of Bouts	1,5	2.5	2.5	2.5	1.5	1.5	0.5
10	Bout Size (gms)	3.8	3.0	2.5	2.0	1.9	0.9	
	Number of Bouts	2.0	1.7	2.3	2.0	1.7	2.0	
11	Bout Size (gms)	4.7	3.5	2.5	1.8	1.9	1.5	1.2
	Number of Bouts	2.3	1.5	2.0	1.8	1.8	0.8	0.5

APP. TABLE 16C

MEAN HOURLY BOUT SIZE AND MEAN HOURLY NUMBER OF BOUTS --DEPRIVATION BIRD 360

	Hour	1	2	3	4	5	6	7
Pre	Bout Size (gms)	1.8	1.4	1.9	1.9	1.3	1.2	0.8
	Number of Bouts	1.6	1.9	2.0	1.6	1.4	1.7	1.0
Post	Bout Size (gms)	4.1	1.9	1.2	1.5	1.2	0.6	0.7
Week 1	Number of Bouts	3.0	1.4	0.9	1.4	1.9	0.3	0.4
2	Bout Size (gms)	3.1	1.7	1.4	1.1	1.1	1.6	
	Number of Bouts	2.5	1.7	1.7	2.0	1.7	1.0	
3	Bout Size (gms)	2.6	1.3	1.8	1.3	1.2	0.7	
	Number of Bouts	2.5	2.0	2.0	2.5	1.0	1.5	
4	Bout Size (gms)	2.4	1.9	1.4	1.2	1.0	0.9	0.8
	Number of Bouts	3.0	2.0	3.0	2.7	1.3	1.3	0.3

APP. TABLE 17A

MEAN HOURLY BOUT SIZE AND MEAN HOURLY NUMBER OF BOUTS -- CONTROL BIRD 348

	Hour	1	2	3	4	5	6	7
Pre	Bout Size (gms)	4.3	3.0	2.0	1.6	1.3	1.3	1.6
	Number of Bouts	2.3	1.6	1.3	1.4	0.7	0.3	0.3
Post Week 1	Bout Size (gms)	6.9	2.0	2.7	1.9	2.1	1.1	
	Number of Bouts	1.5	1.3	1.0	1.3	0.8	0.8	
2	Bout Size (gms)	6.4	3.1	2.2	1.5	1.4	0.9	1.2
	Number of Bouts	1.6	1.4	1.8	1.0	1.6	0.6	0.4
3	Bout Size (gms)	4.3	2.1	2.3	1.7	1.5	1.5	0.1
	Number of Bouts	2.3	2.7	1.7	1.3	1.0	0.7	0.3

APP. TABLE 17B

MEAN HOURLY BOUT SIZE AND MEAN HOURLY NUMBER OF BOUTS -- CONTROL BIRD 362

	Hour	1	2	3	4	5	6	7
Pre	Bout Size (gms)	2.5	0.7	1.1	0.9	0.7	0.9	0.5
	Number of Bouts	3.3	2.6	2.6	1.6	0.7	1.0	0.6
Post	Bout Size (gms)	4.4	2.8	4.9	0.7	2.9	0.5	0.8
Week 1	Number of Bouts	2.5	0.8	0.7	0.5	1.0	0.7	0.3
2	Bout Size (gms)	3.8	1.2	1.2	1.7	0.7	0.7	0.8
	Number of Bouts	3.3	2.5	0.8	1.2	0.3	0.8	0.3
3	Bout Size (gms)	3.1	2.3	1.7	3.5	0.7	0.0	0.4
	Number of Bouts	3.3	1.7	0.3	0.3	1.3	0.0	0.3

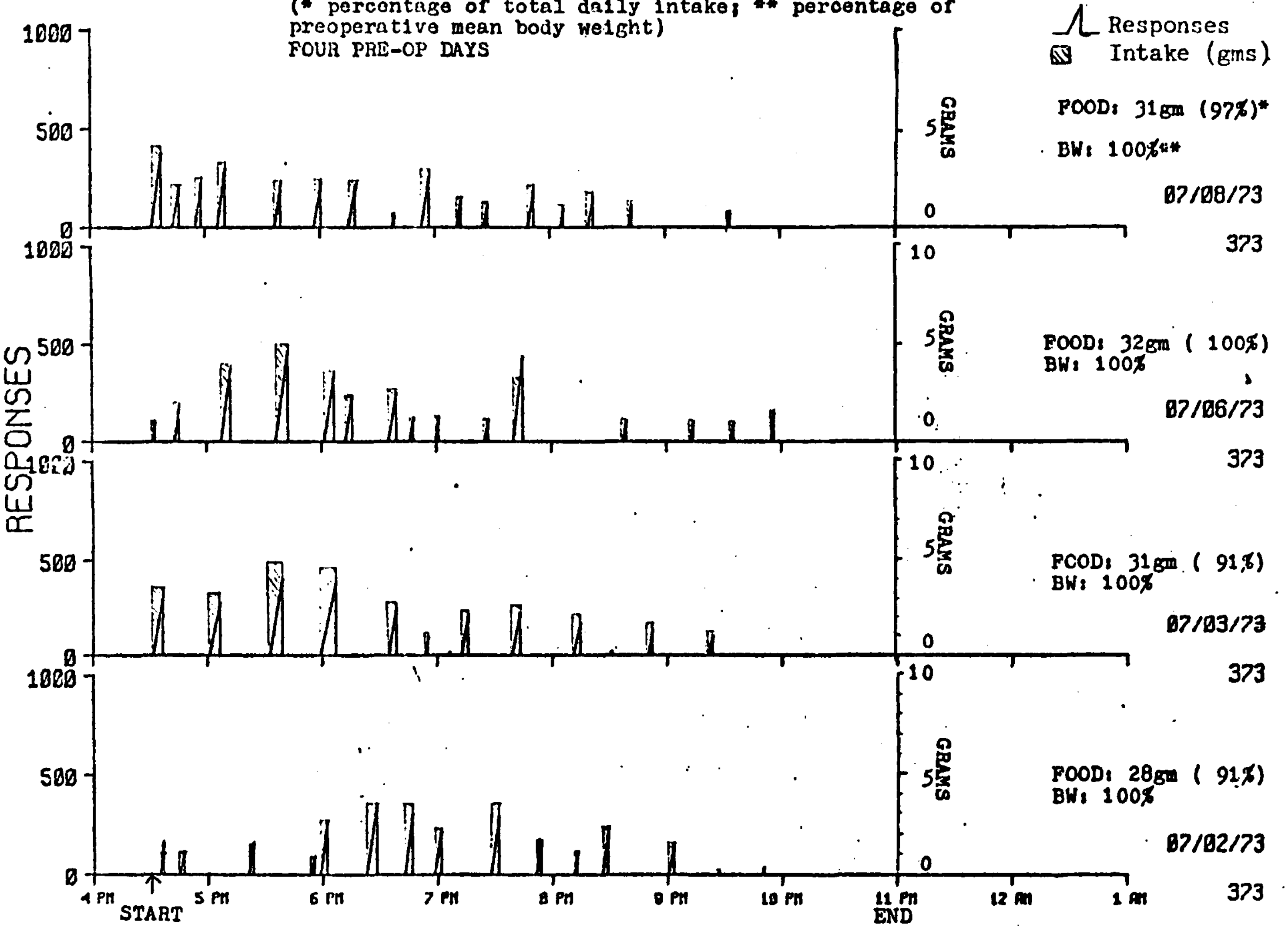
APP. TABLE 18

NUMBER OF DAILY FEEDING RESPONSES DURING THE PERIOD OF APHAGIA

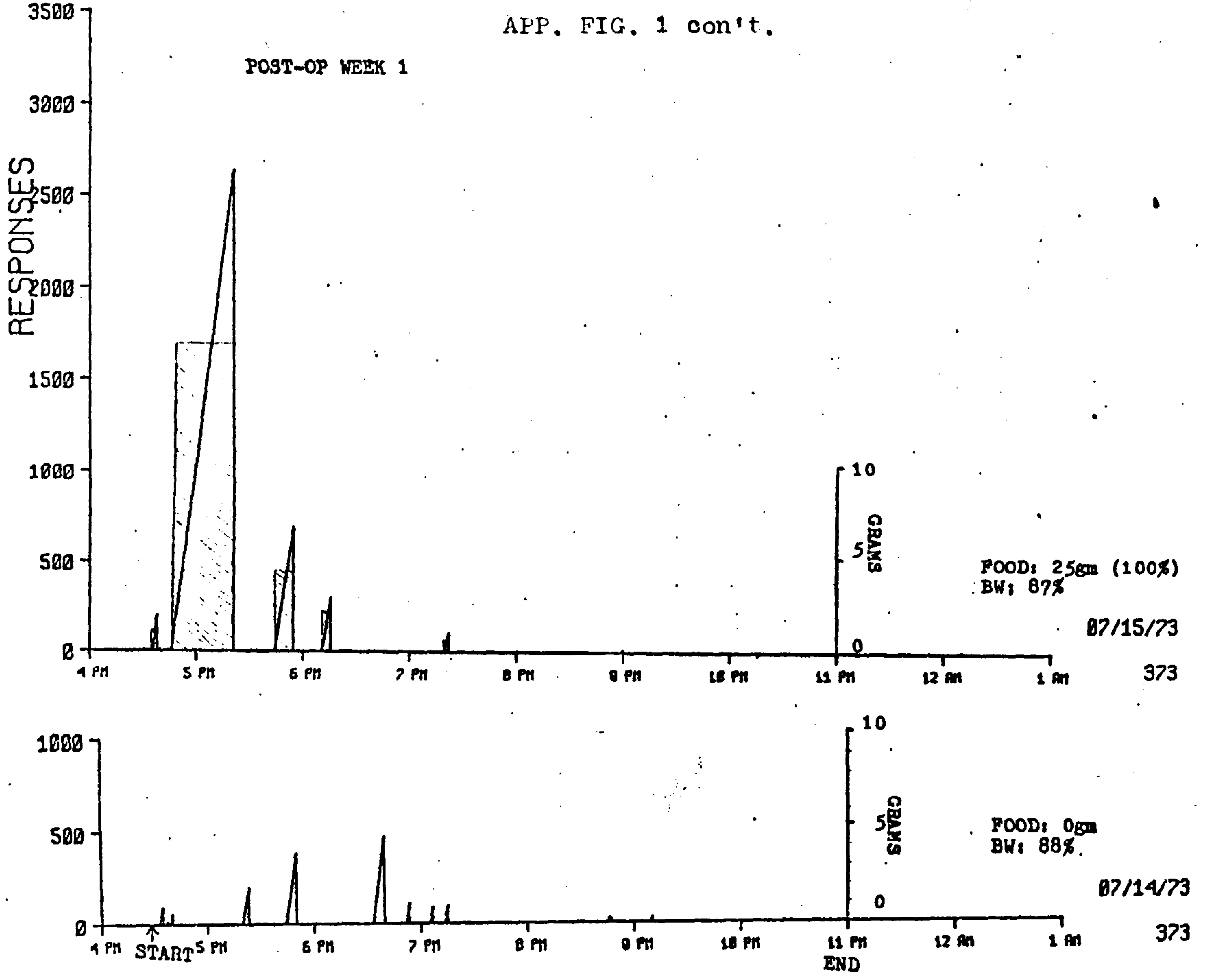
	Day of Aphagia	1	2	3	4	5	6	7	Post-op. Day 1 of Ingestion	Pre-op. Daily Mean
Deafferentation Birds	373	0	0	401	1596				3925	3158
	349	87	0	0	731	1323	1213		3566	5550
	435	0	25	41	649				3155	4438
	441	0	12	35	262				3951	2521
	412	0	0	412	130	1531	1656	4584		
	Day 8-14	3105	221	-	2097	399	3921	1479	9161	4652
	367	0	0	0	0	323	24	11		
	Day 8-20	0	0	0	0	0	0	1060	Died	3403

APP. FIG. 1

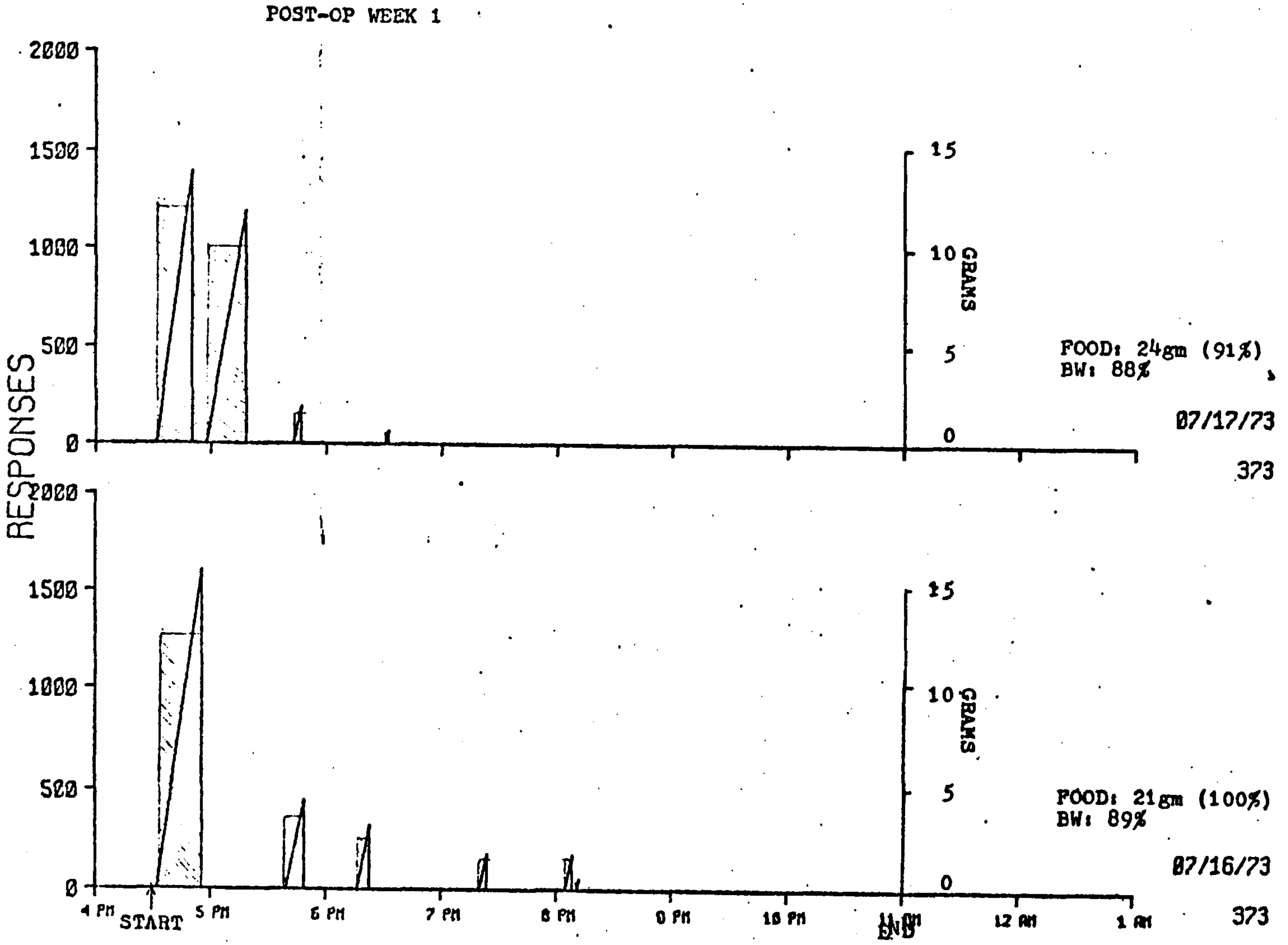
TEMPORAL DISTRIBUTION OF FEEDING ACTIVITY OF BIRD 373 (DEAFFERENTATION)
(* percentage of total daily intake; ** percentage of preoperative mean body weight)
FOUR PRE-OP DAYS



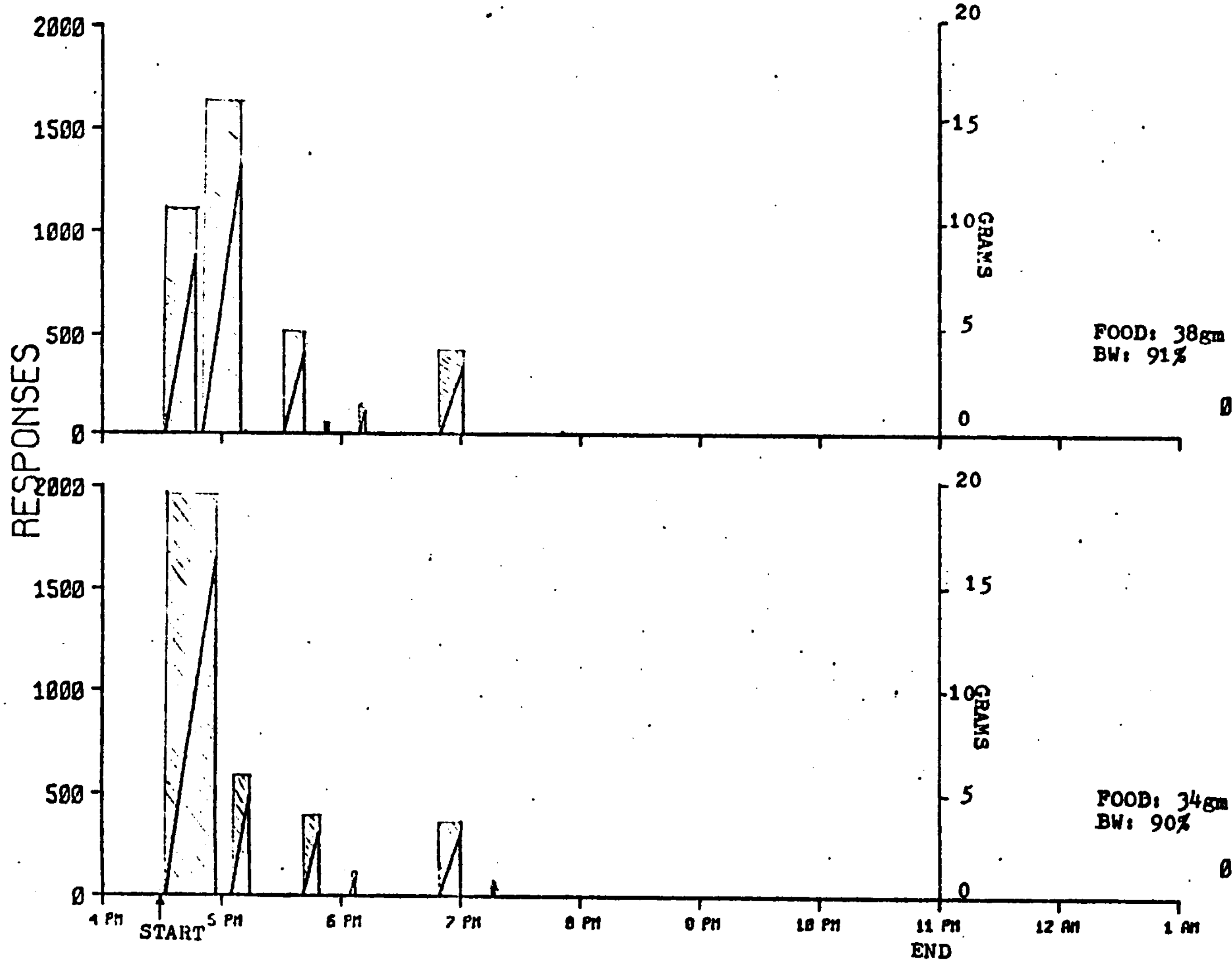
APP. FIG. 1 con't.



APP. FIG. 1 con't.



APP. FIG. 1 con't



POST-OP WEEK 2

FOOD: 38gm (100%)
BW: 91%

07/23/73

373

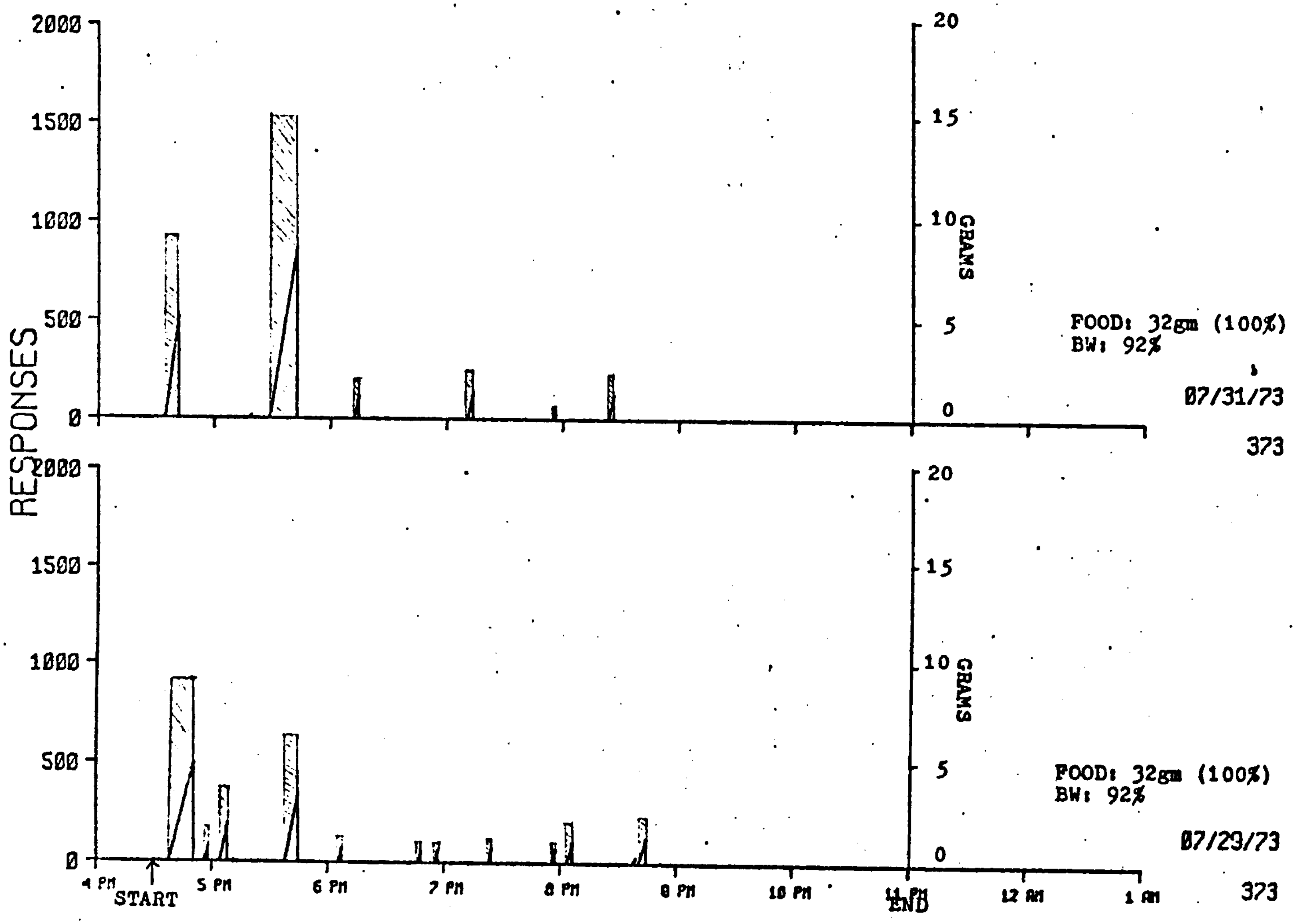
FOOD: 34gm (100%)
BW: 90%

07/21/73

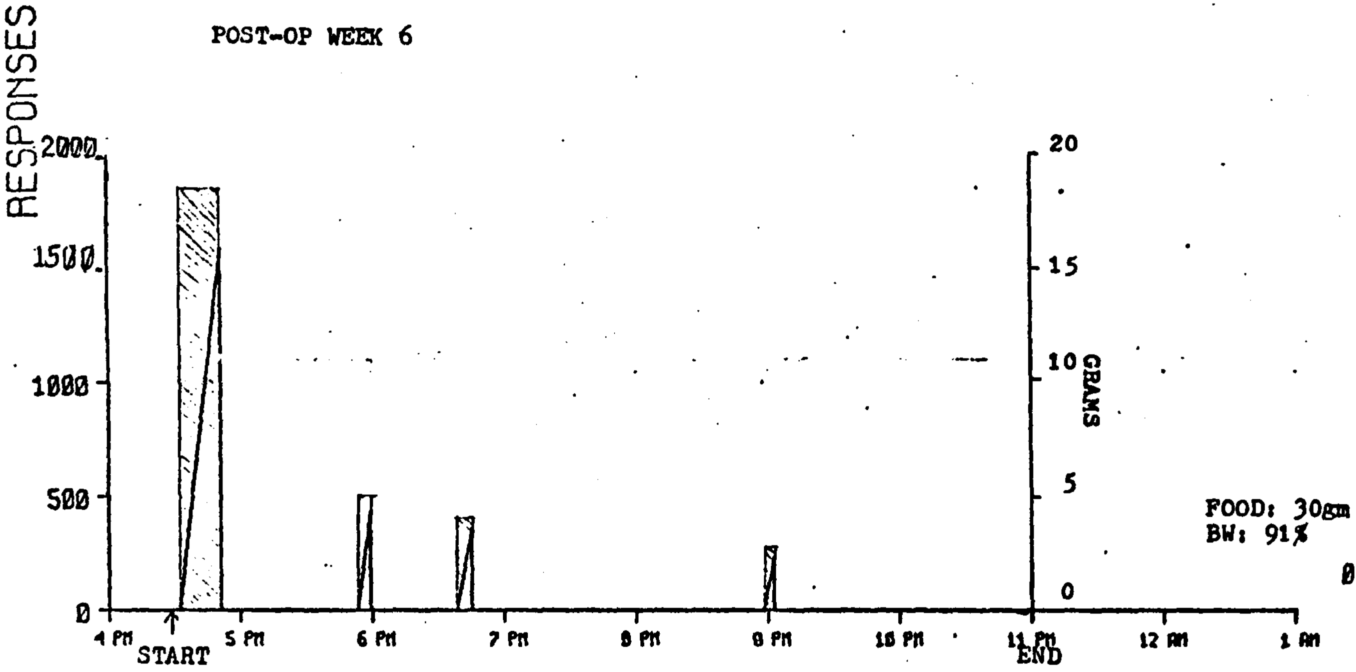
373

APP. FIG. 1 con't.

POST-OP WEEK 3



APP. FIG. 1 con't.

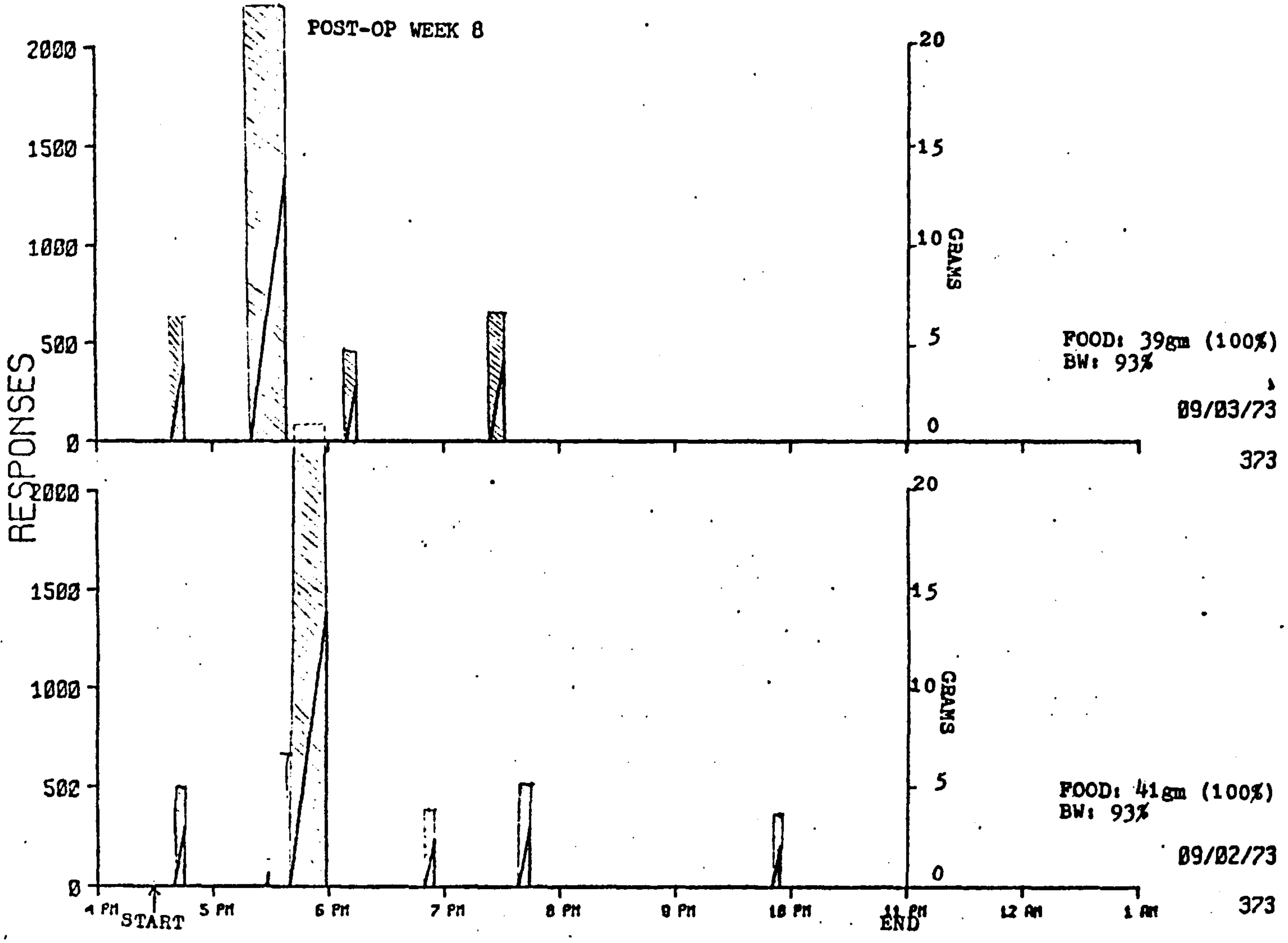


FOOD: 30gm (100%)
BW: 91%

08/15/73

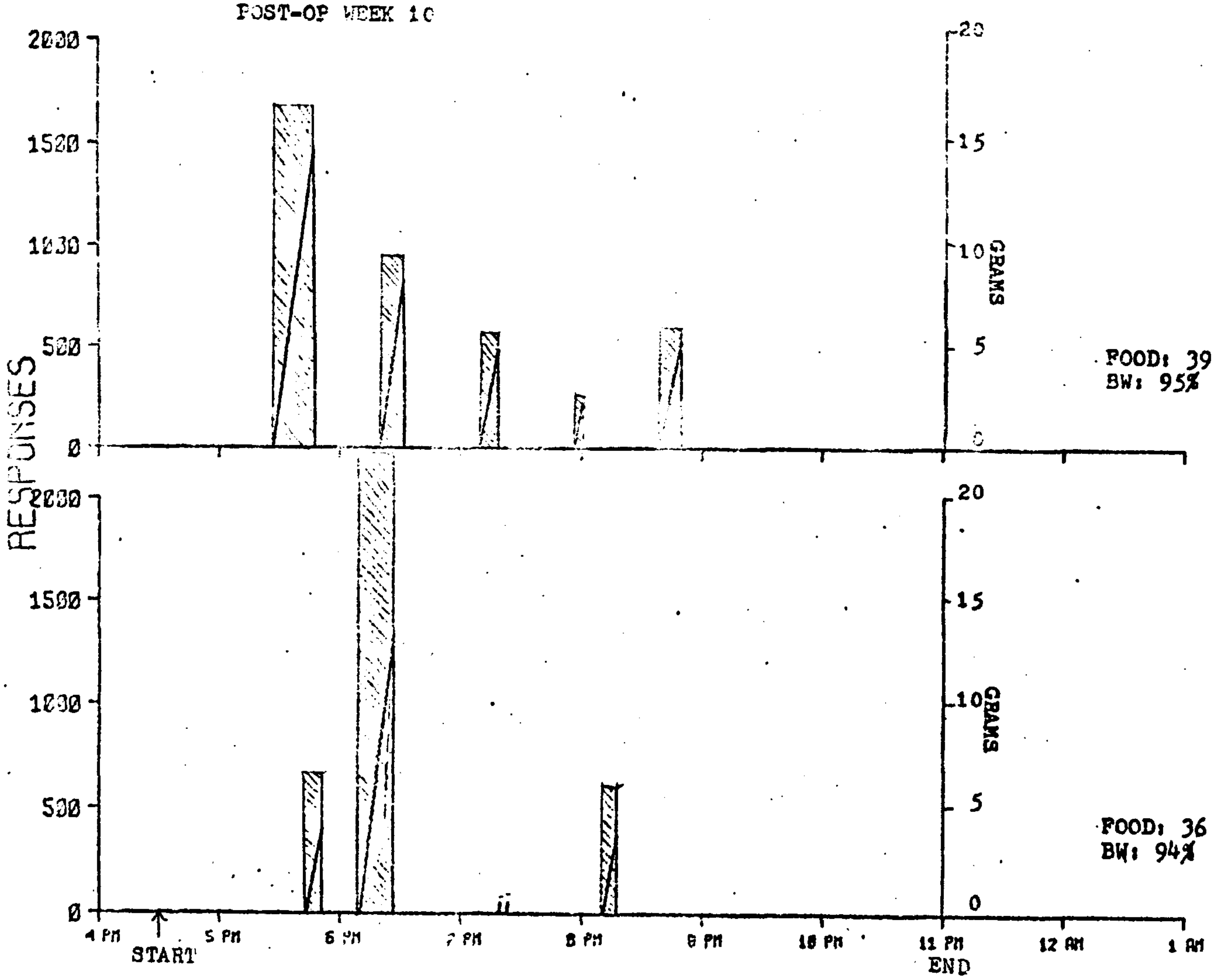
373

APP. FIG. 1 con't.



APP. FIG. 1 con't.

POST-OP WEEK 10

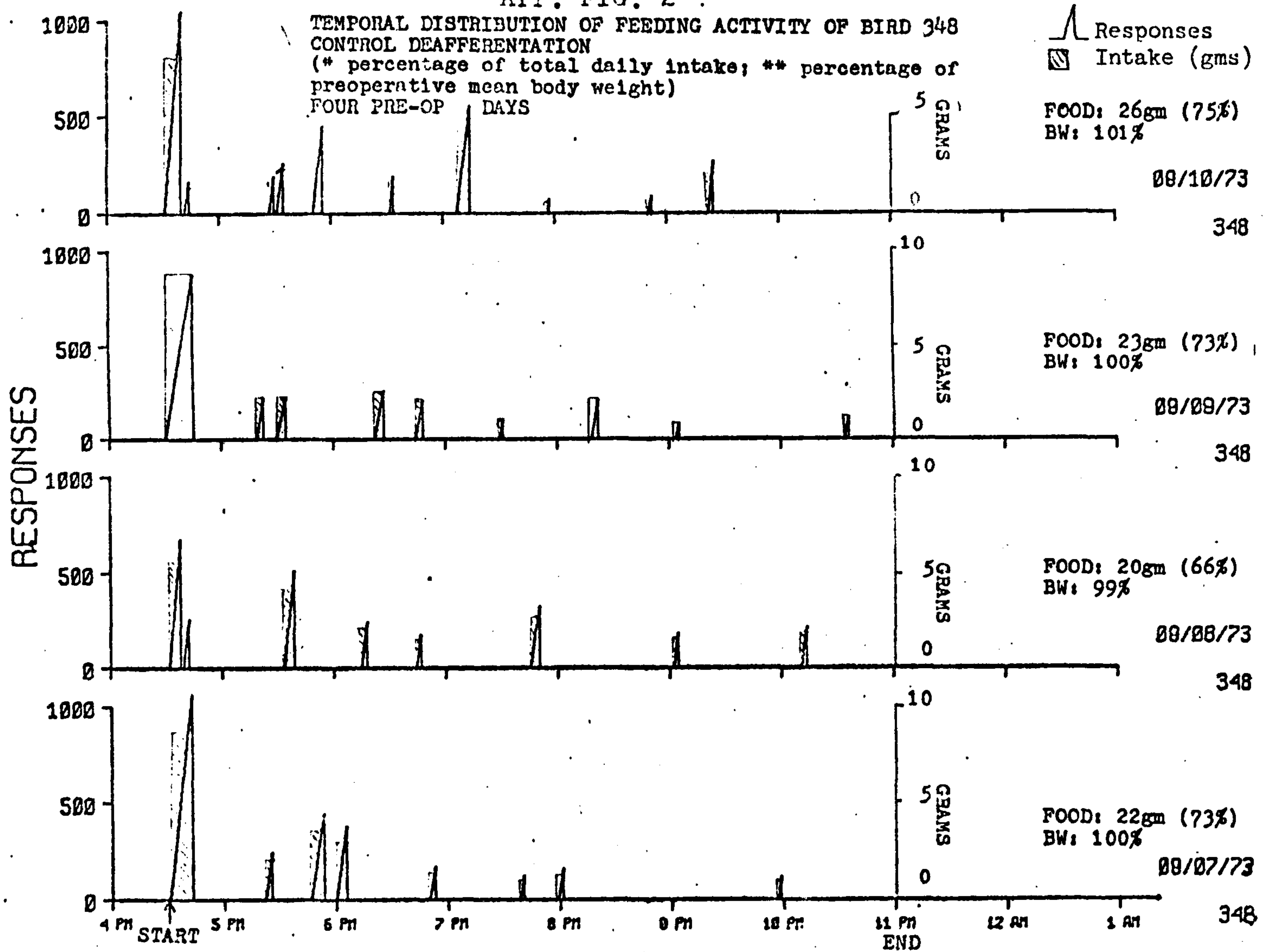


FOOD: 39gm (99%)
BW: 95%
09/14/73.
373

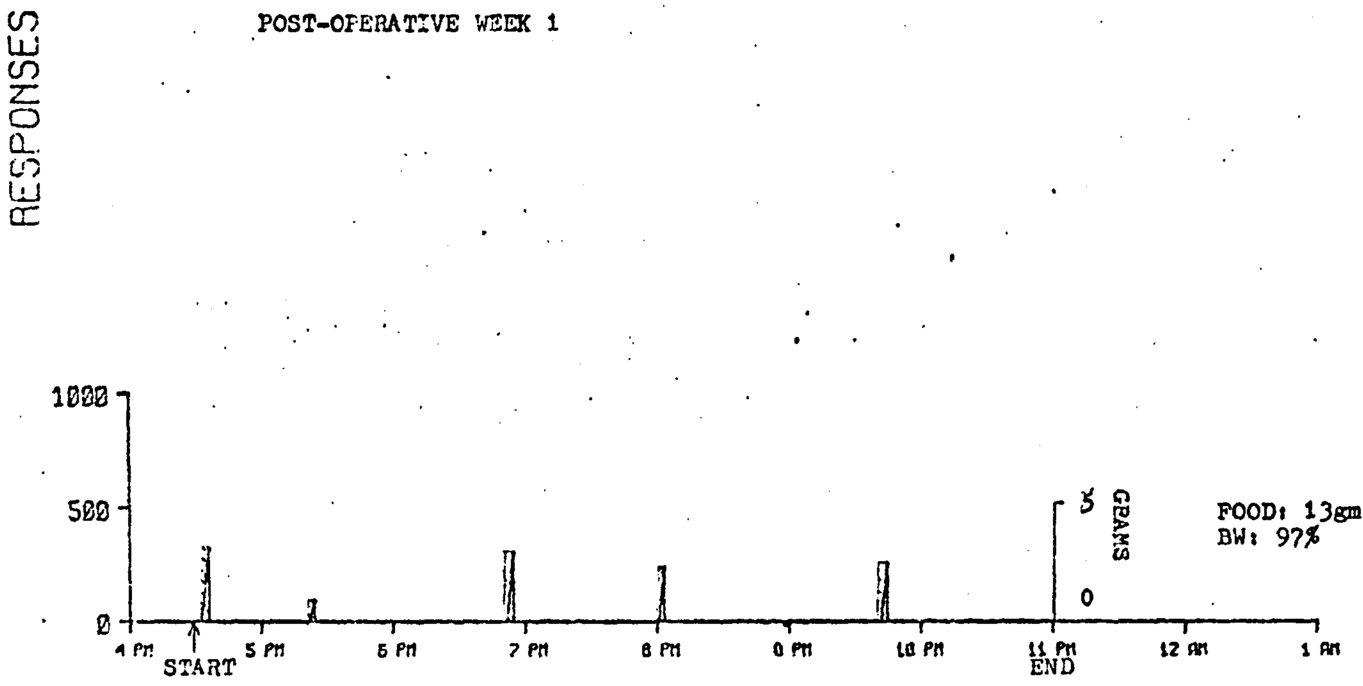
FOOD: 36 gm (100%)
BW: 94%
09/12/73
373

APP. FIG. 2

TEMPORAL DISTRIBUTION OF FEEDING ACTIVITY OF BIRD 348
CONTROL DEAFFERENTATION
(* percentage of total daily intake; ** percentage of
preoperative mean body weight)
FOUR PRE-OP DAYS



APP. FIG. 2 con't.

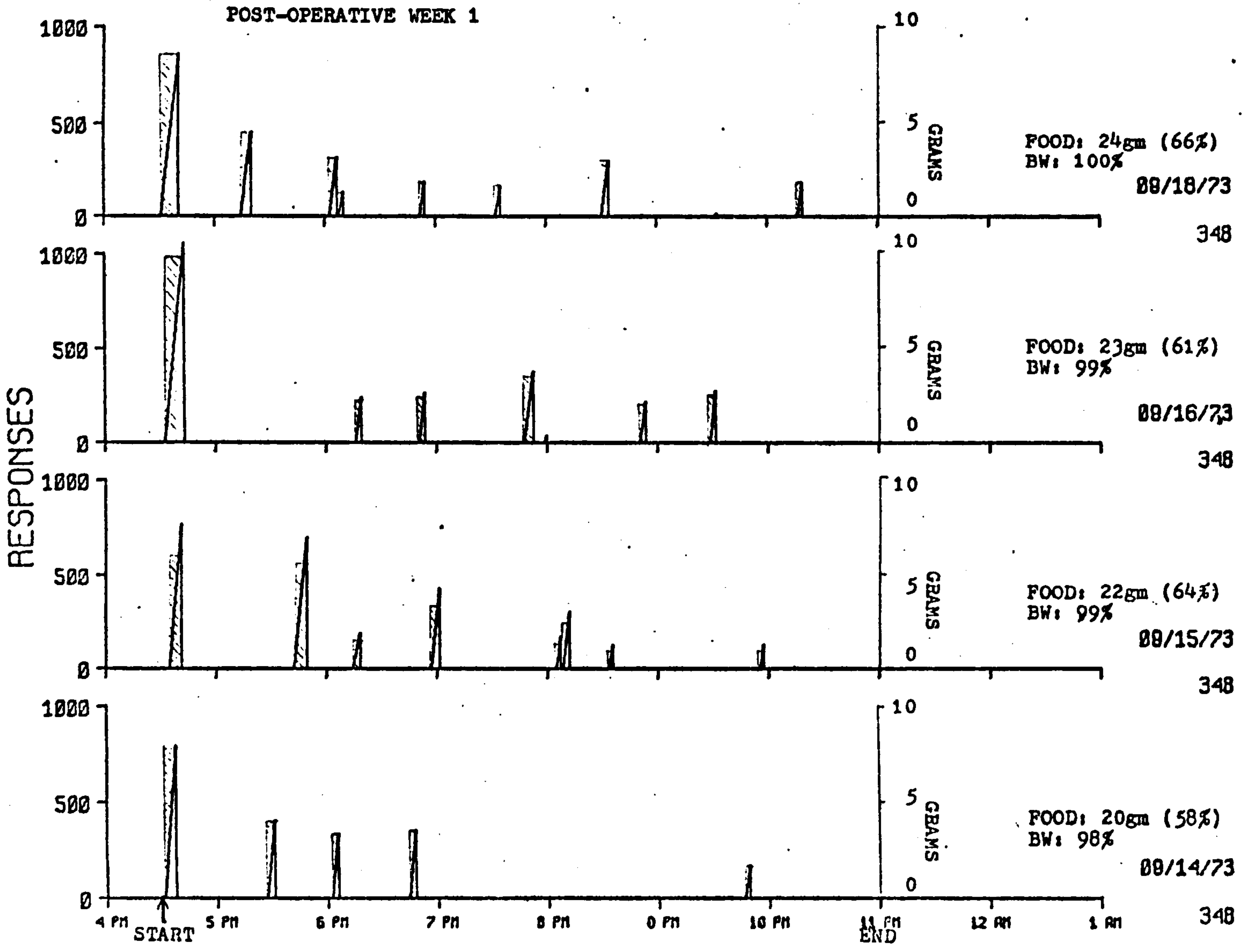


FOOD: 13gm (74%)
BW: 97%

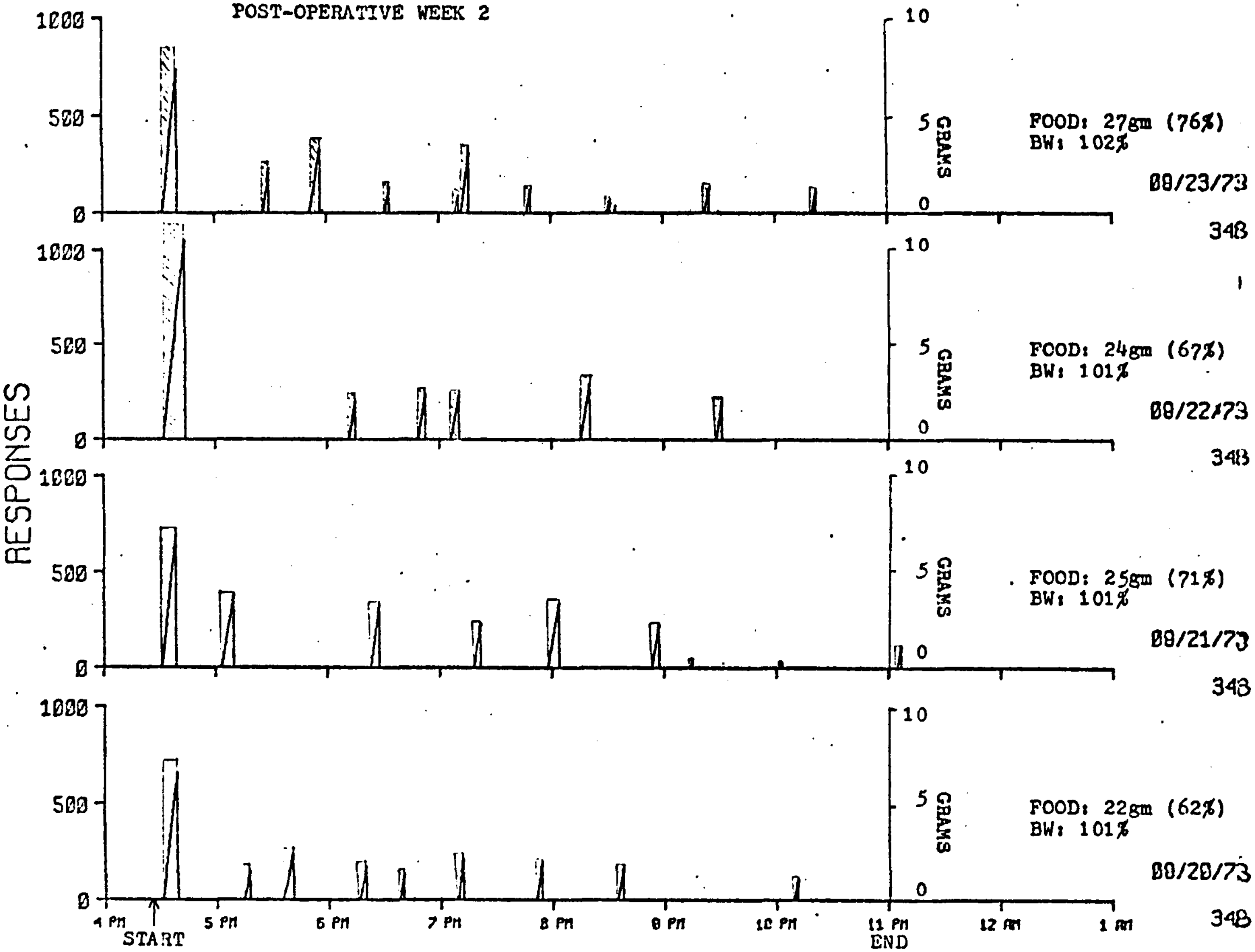
08/13/73

348

APP. FIG. 2 con't.

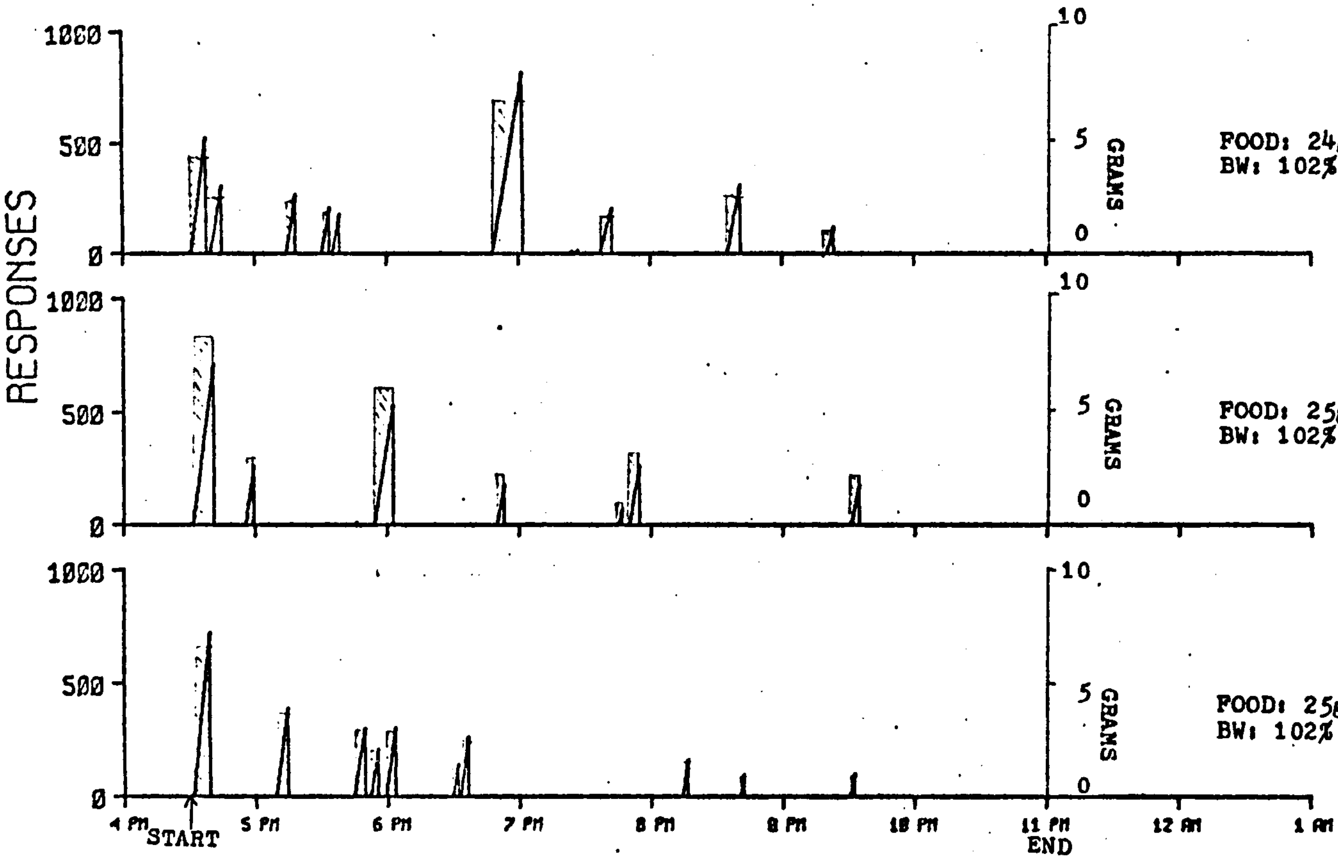


APP. FIG. 2 con't.



APP. FIG. 2 con't.

POST-OPERATIVE WEEK 3



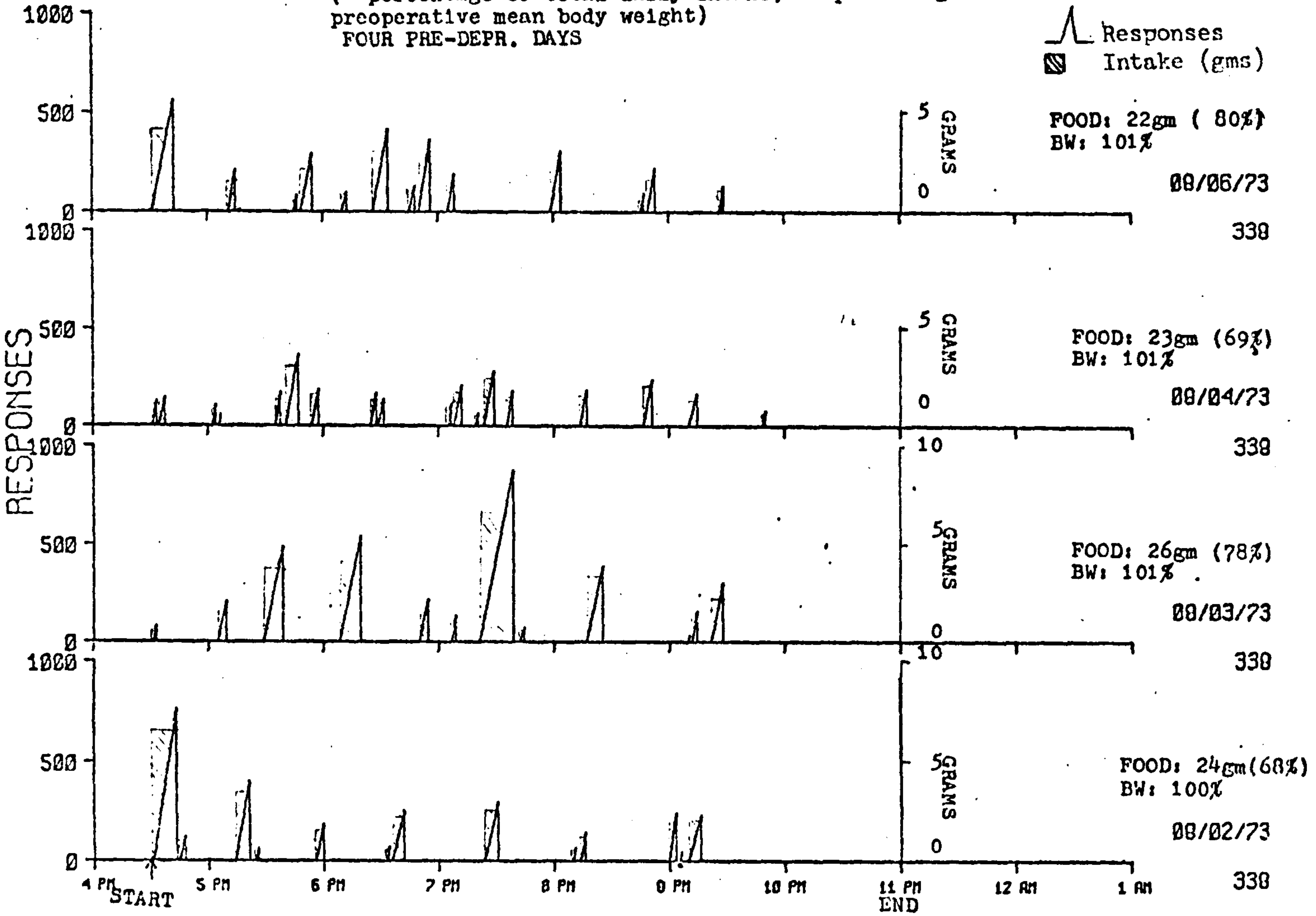
FOOD: 24gm (87%)
BW: 102%
08/28/73
348

FOOD: 25gm (69%)
BW: 102%
08/27/73
348

FOOD: 25gm (71%)
BW: 102%
08/26/73
348

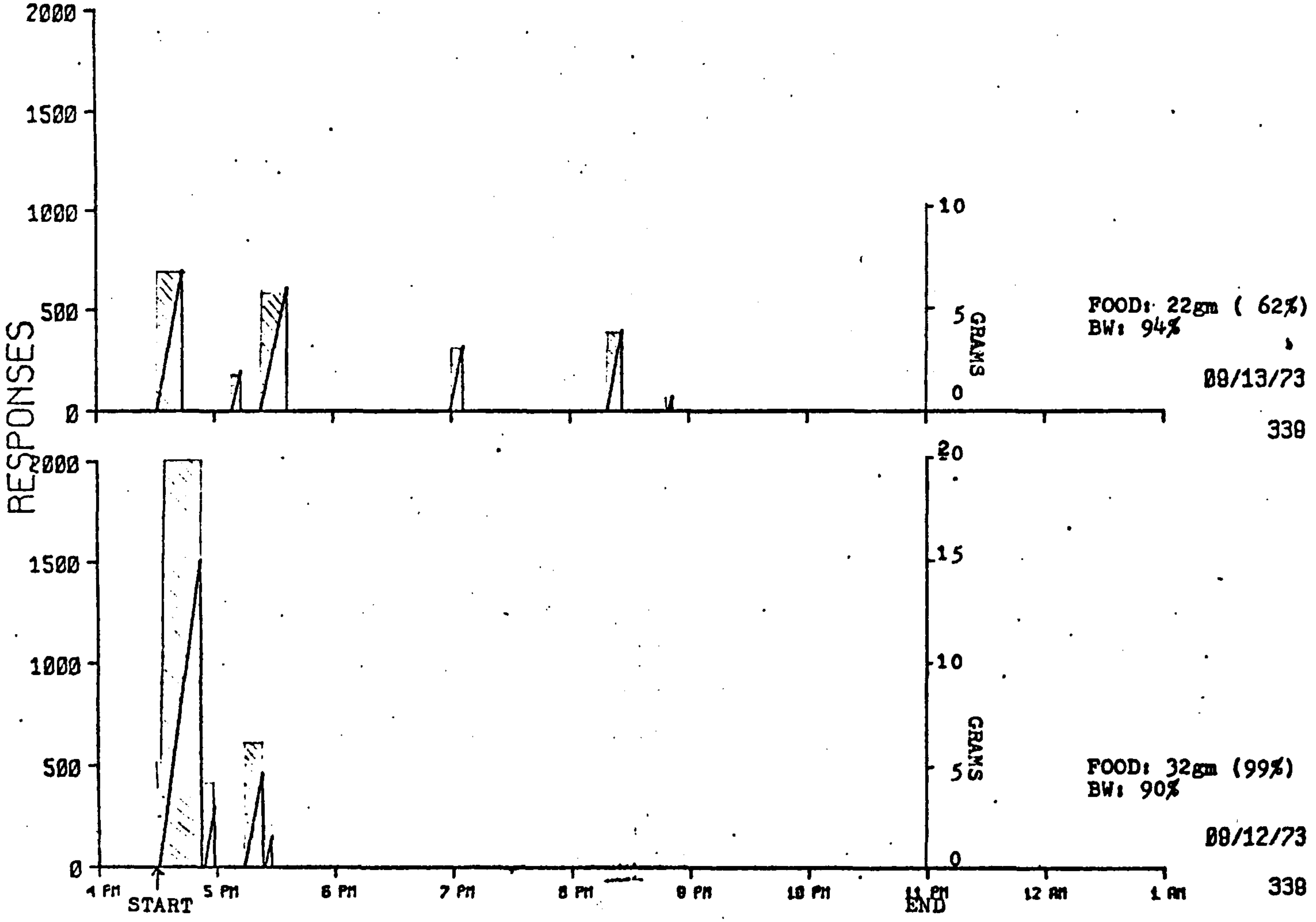
APP. FIG. 3

TEMPORAL DISTRIBUTION OF FEEDING ACTIVITY OF BIRD 339
BEFORE AND AFTER FOOD DEPRIVATION
(* percentage of total daily intake; ** percentage of preoperative mean body weight)
FOUR PRE-DEPR. DAYS

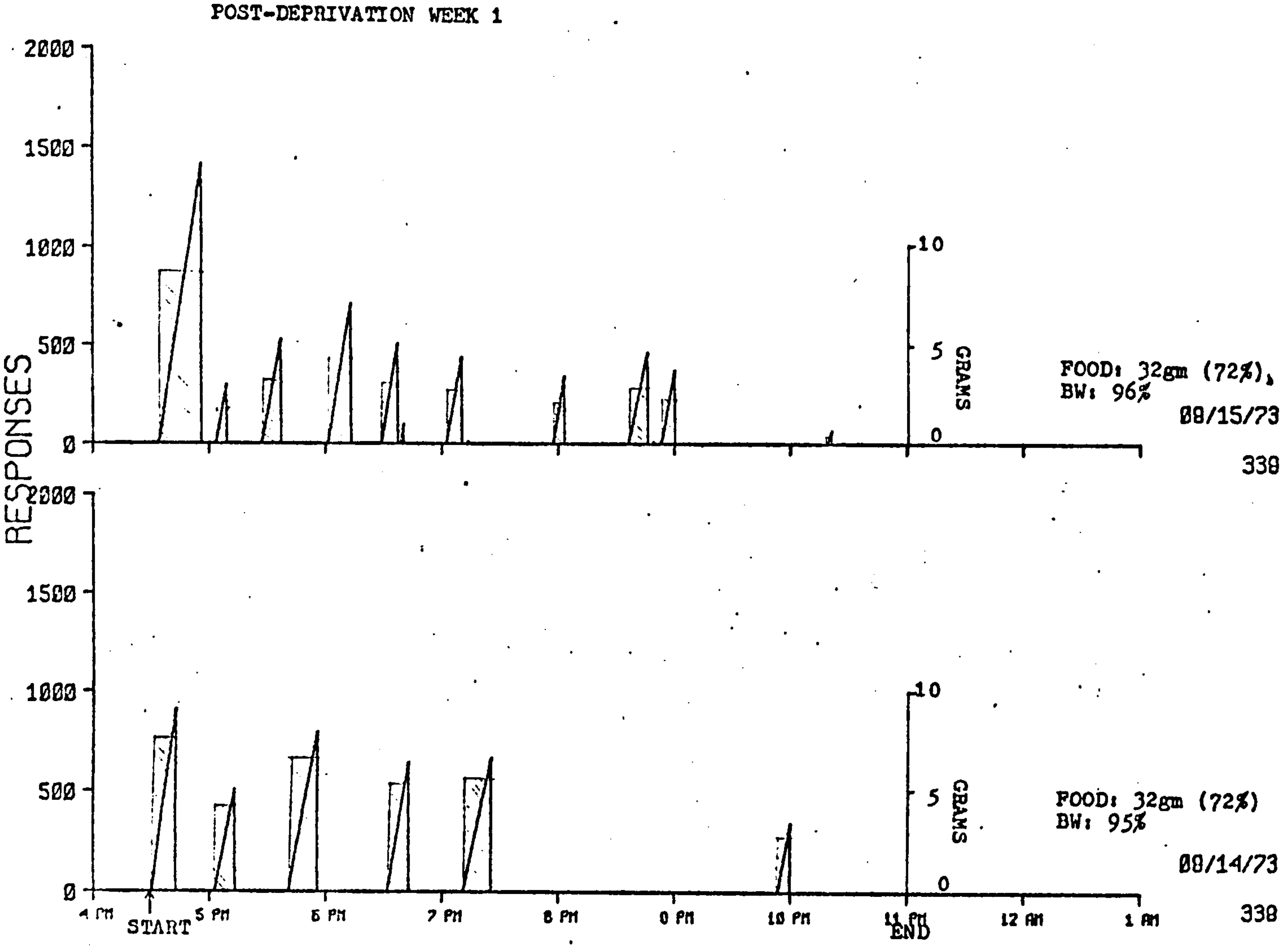


APP. FIG. 3 con't.

POST-DEPRIVATION WEEK 1

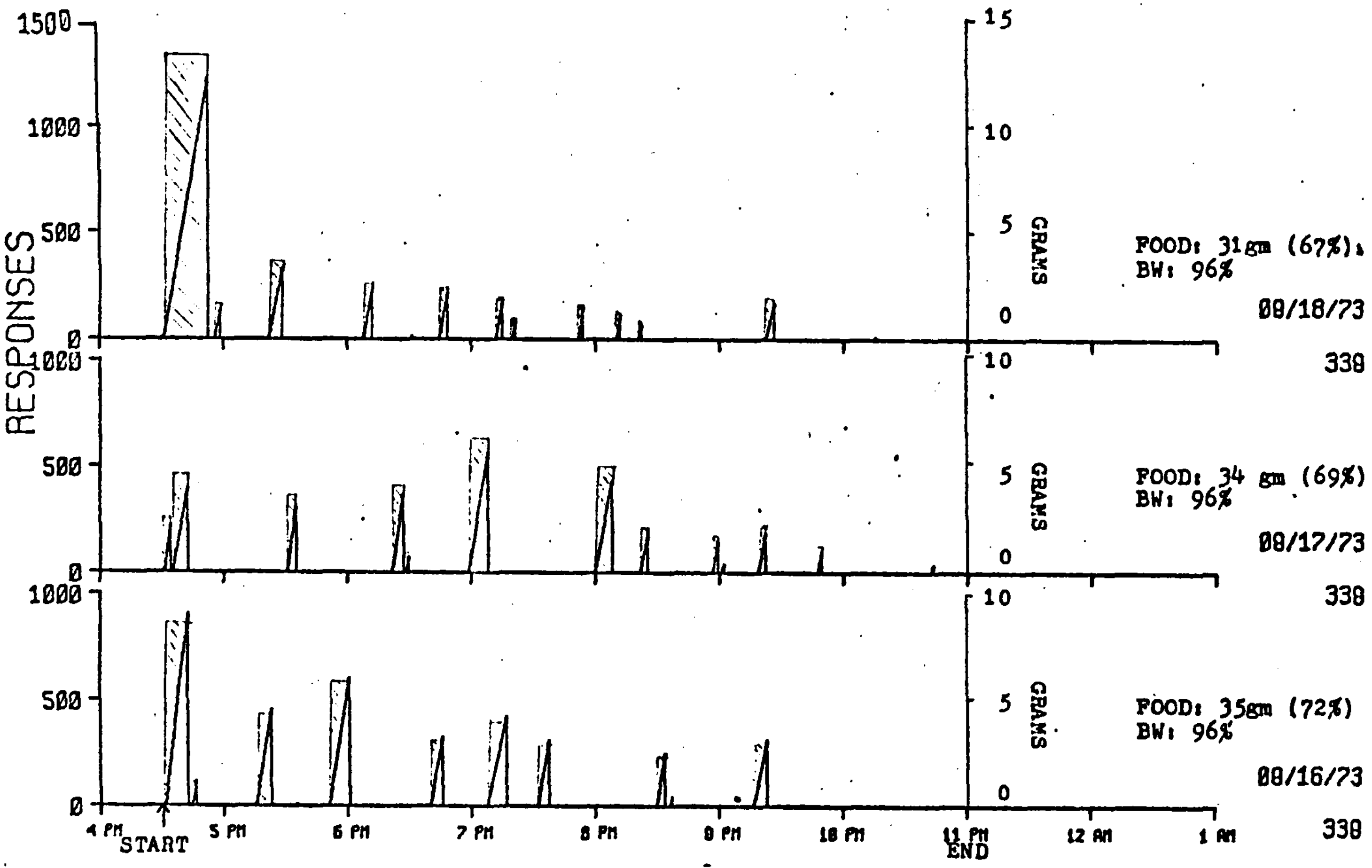


APP. FIG. 3 con't.



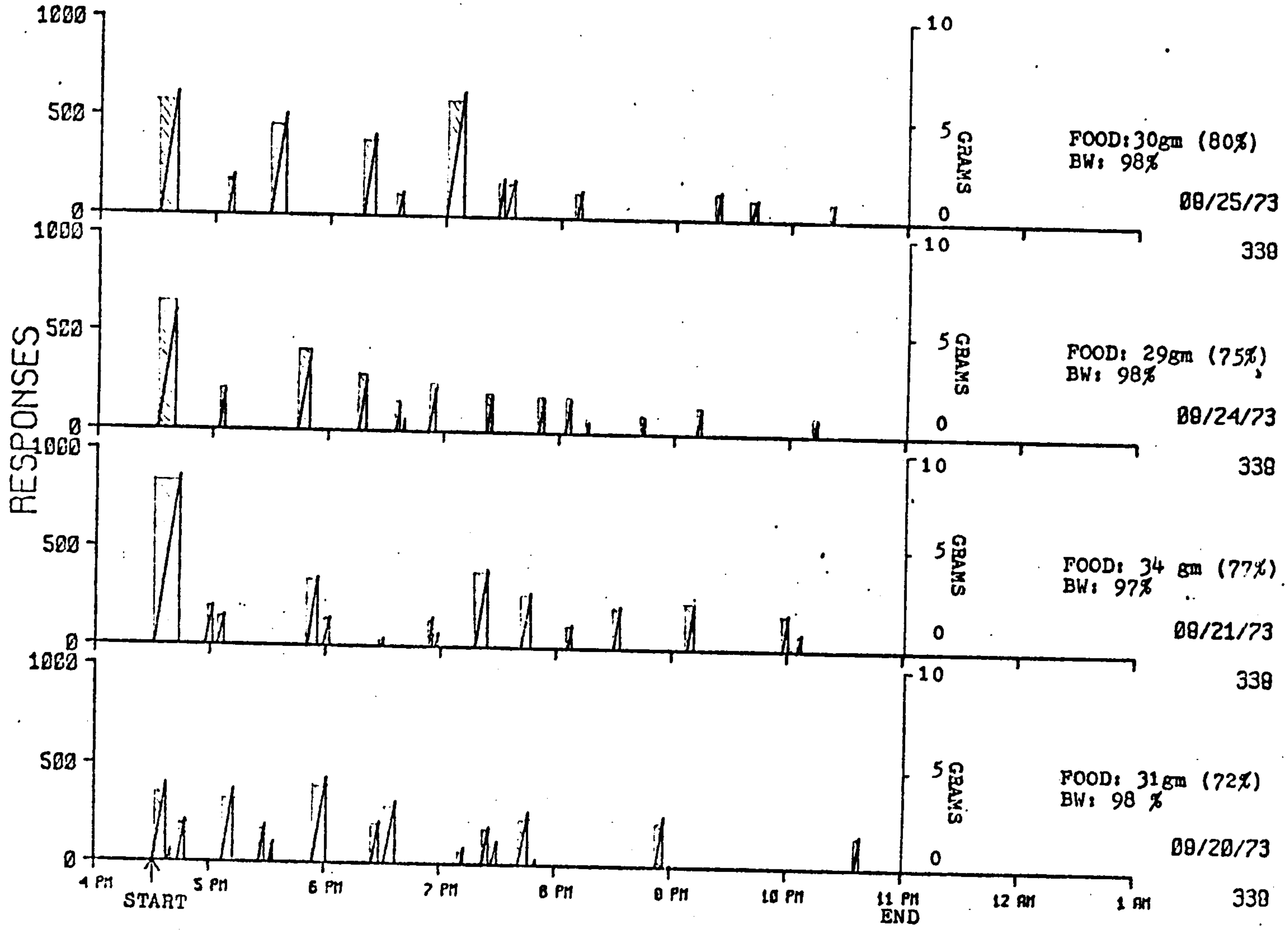
APP. FIG. 3 con't.

POST-DEPRIVATION WEEK 1



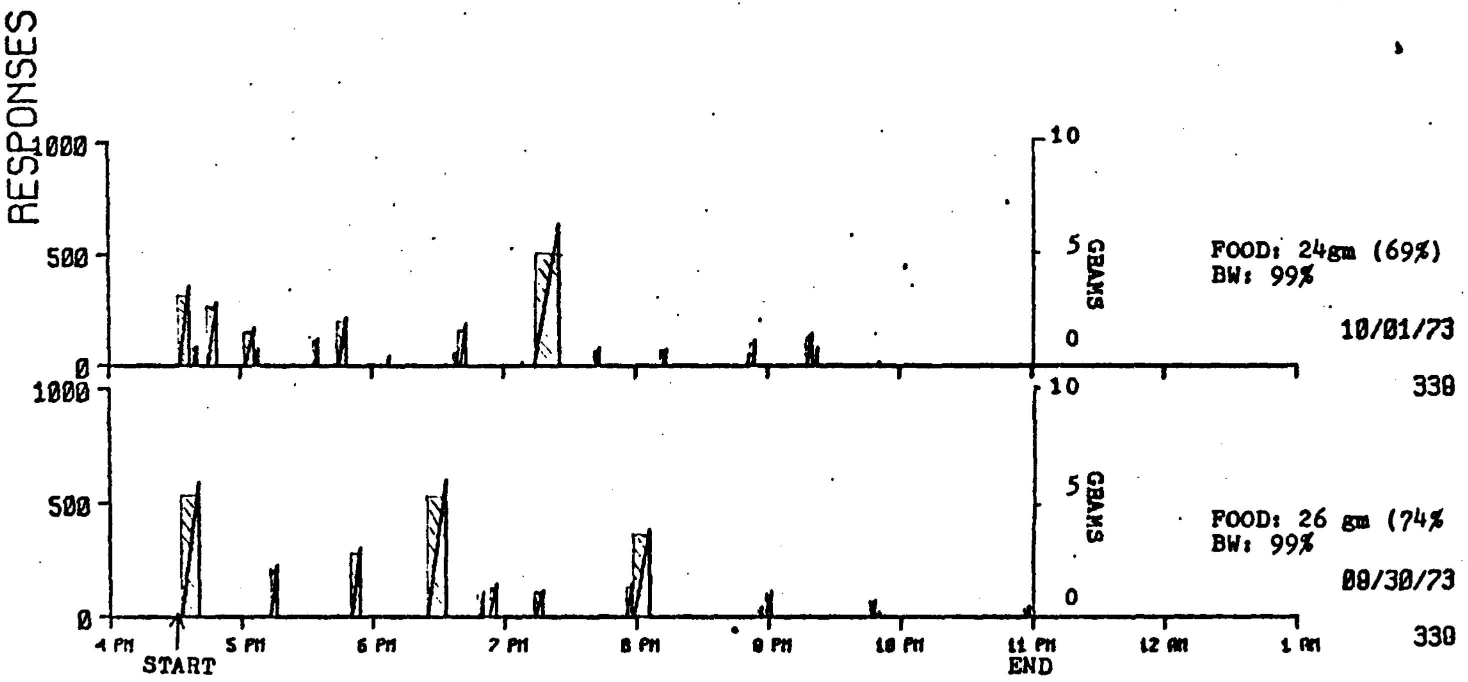
APP. FIG. 3 con't.

POST-DEPRIVATION WEEK 2



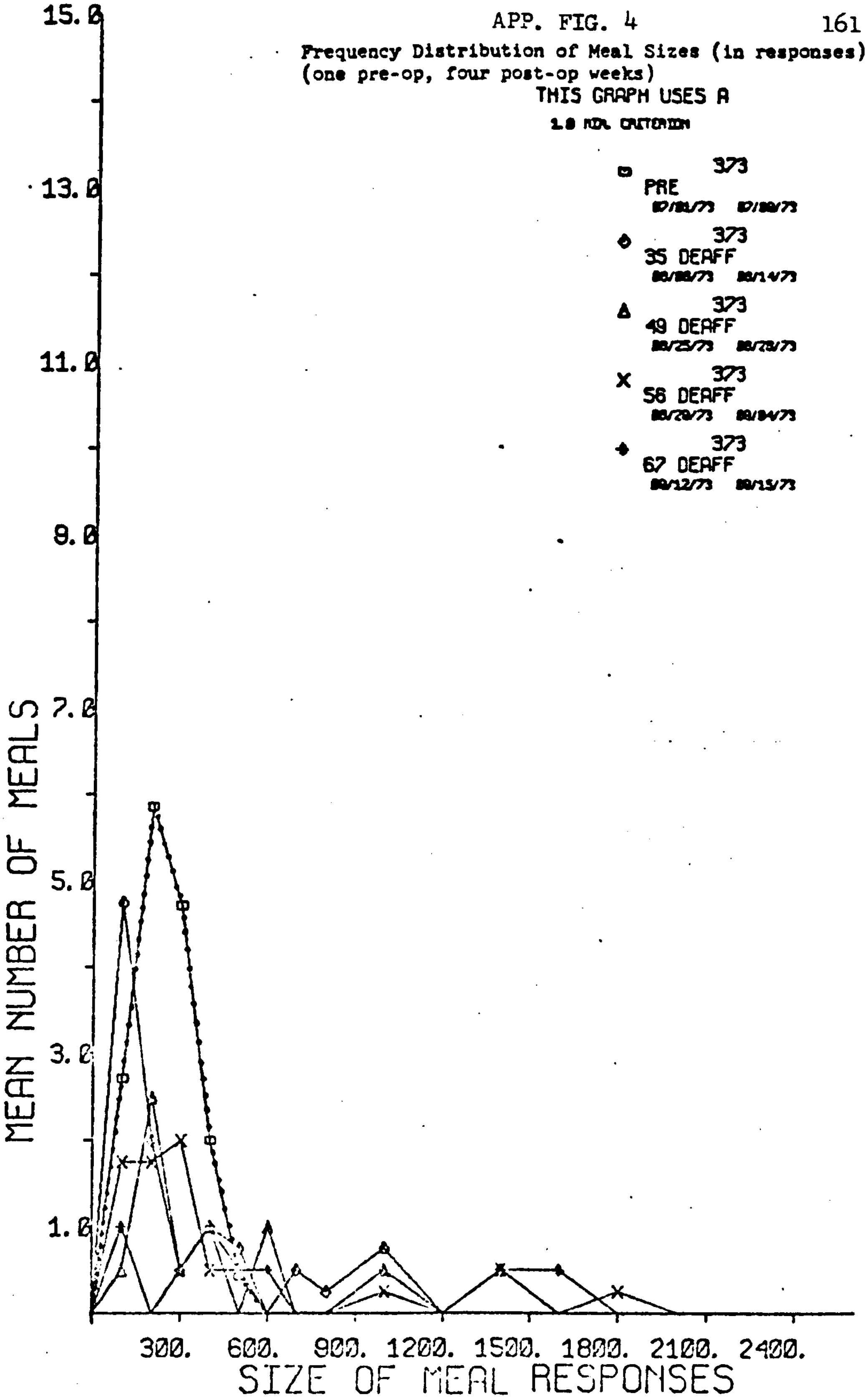
APP. FIG. 3 con't.

POST-DEPRIVATION WEEK 3

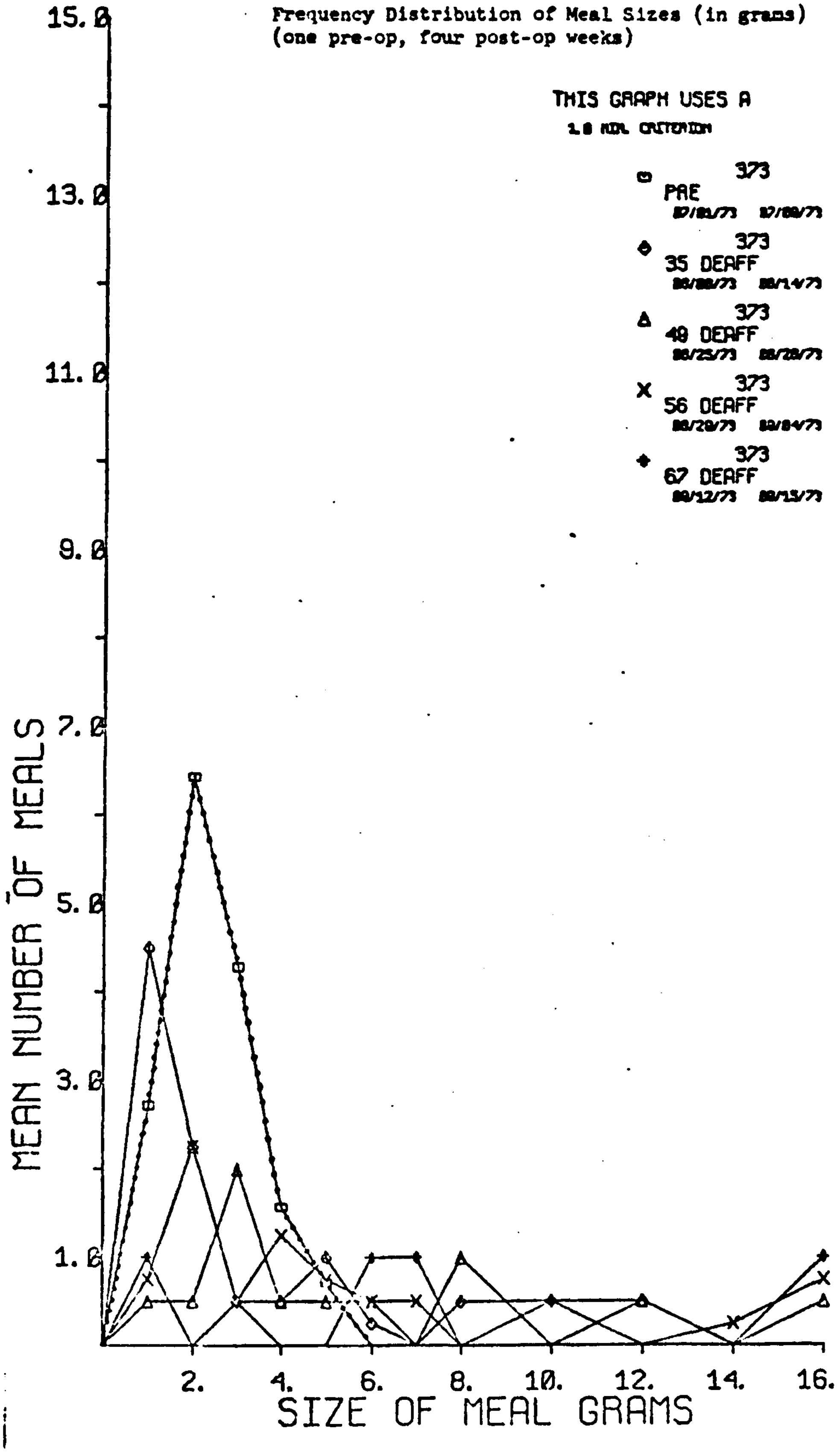


APP. FIG. 4

Frequency Distribution of Meal Sizes (in responses)
(one pre-op, four post-op weeks)



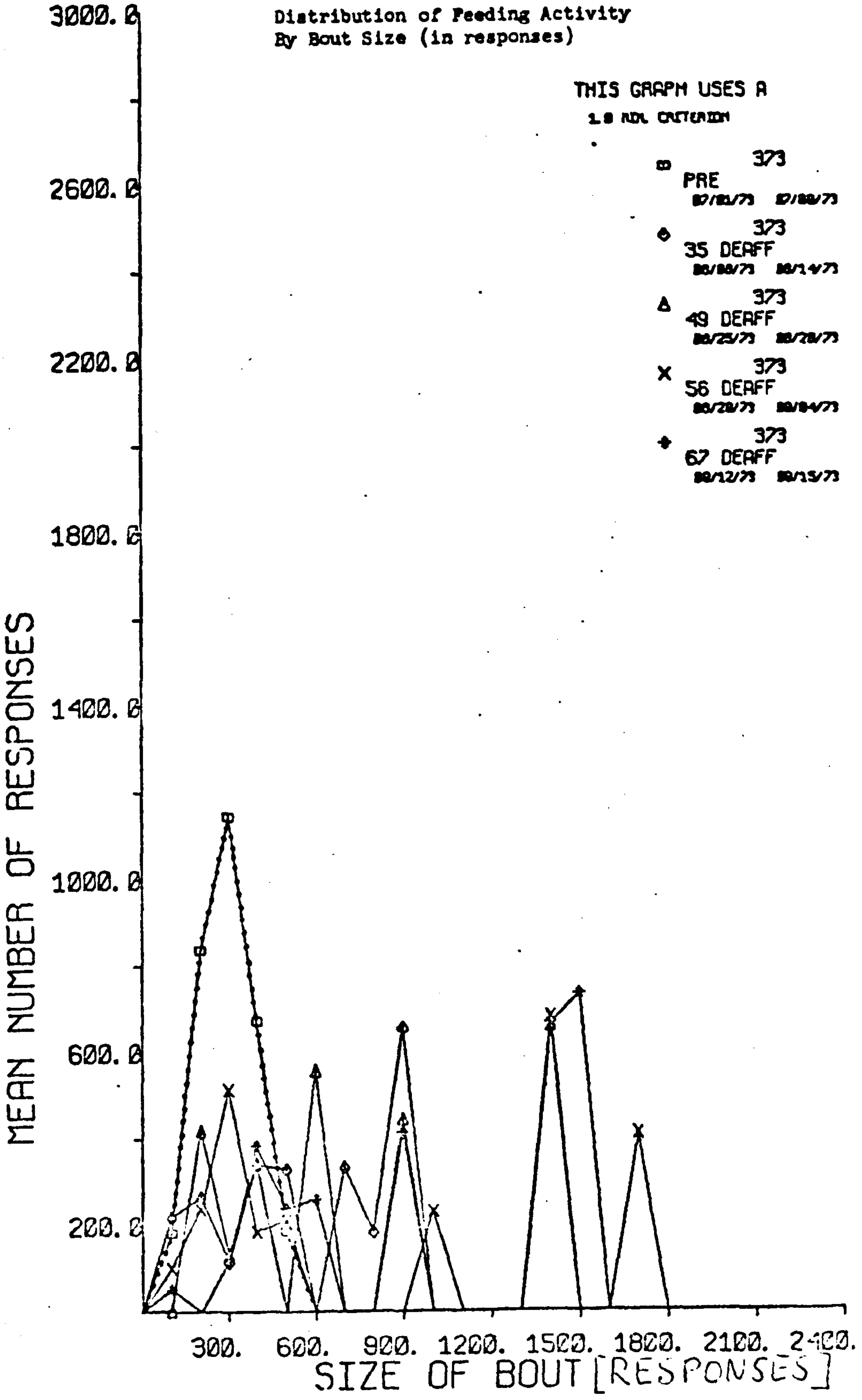
APP. FIG. 5



Frequency Distribution of Meal Sizes (in grams)
(one pre-op, four post-op weeks)

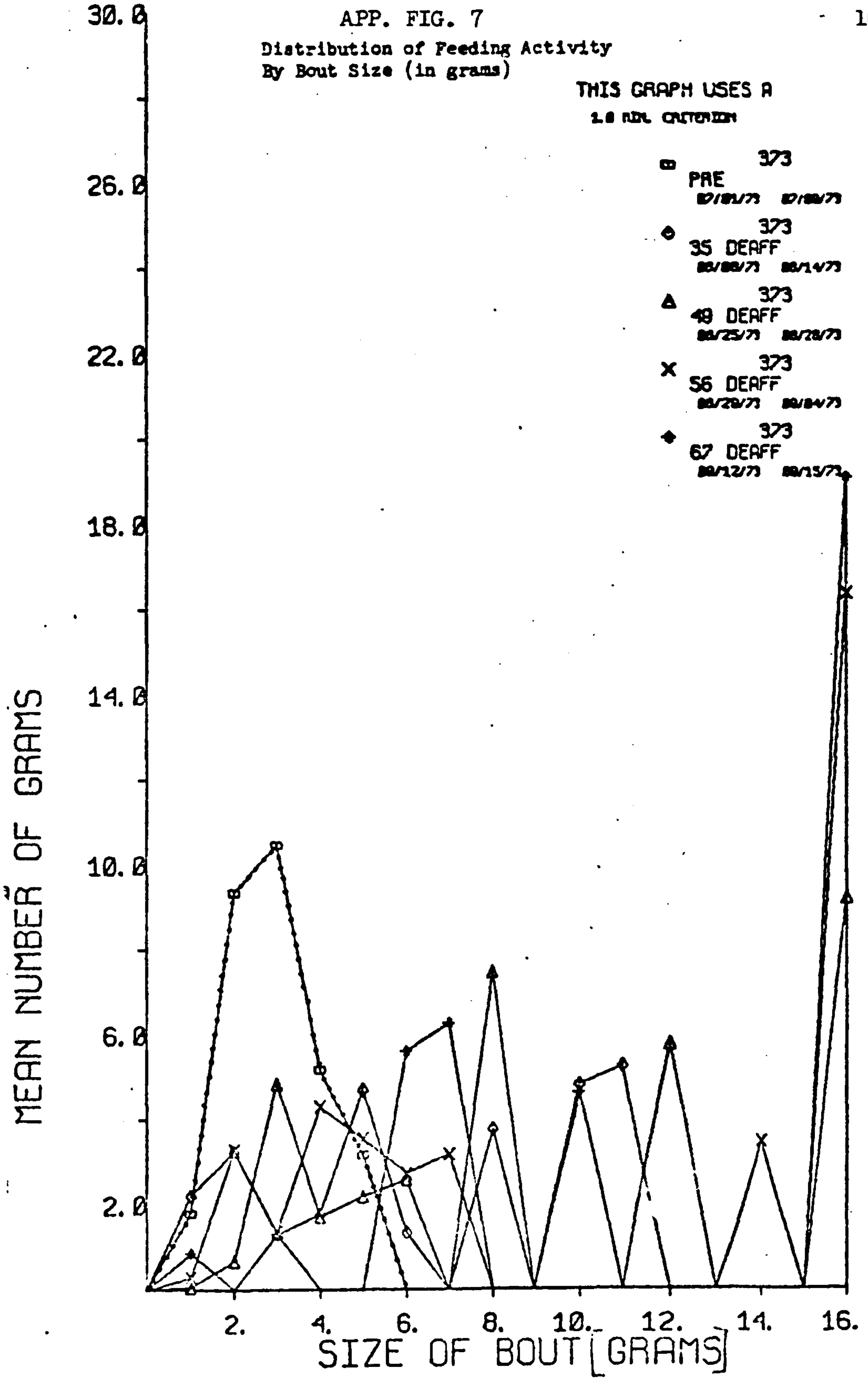
APP. FIG.6

Distribution of Feeding Activity
By Bout Size (in responses)



APP. FIG. 7

Distribution of Feeding Activity
By Bout Size (in grams)



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