CONTROL OF FEEDING PATTERNS IN THE BARBARY DOVE (STREPTOPELIA RISORIA)

Hamish Alexander Macleod

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The research which is presented in this thesis was carried out by myself, with the exception of the work discussed in Chapter 10 which was an experiment carried out jointly with Mr. David Flitton.

Hamish Macleod.

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ABSTRACT

This thesis reports a study of the temporal patterns of feeding behaviour in the Barbary dove or Blonde Ring dove, Streptopelia risoria. The normal diurnal distribution of feeding in the intact, freely feeding bird is described, as is the way in which this pattern may be altered by a surgical manipulation which removes much of the sensory inflow from the trigeminal nerve.

On the basis of the observation of the effect of this sensory trigeminal nerve section in the doves, an alternative interpretion of the role of this nerve in the control of feeding behaviour and food intake in birds to that presented in the literature, is offered. In line with this interpretation, it is shown that a manipulation of the physical nature of an offered food material will produce a change in the temporal patterning of food intake in a way similar to that brought about by trigeminal nerve section, and that the past feeding experience of a bird has an effect on the probability that nerve section will produce a noticeable disruption in gross food intake.

The fine structure of feeding behaviour is described to demonstrate the principle that the feeding control system of these birds acts so that future needs are anticipated, and it is shown that environmental cues giving information about future deprivation are used by them to feed in advance of such deprivation.

In addition, the feeding behaviour of the birds in a continuous, fixed ratio operant situation is described, to show how the means of observing a behaviour can alter the pattern of that behaviour, and also how this alteration can give information about the operation of the underlying control system.

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Introduction

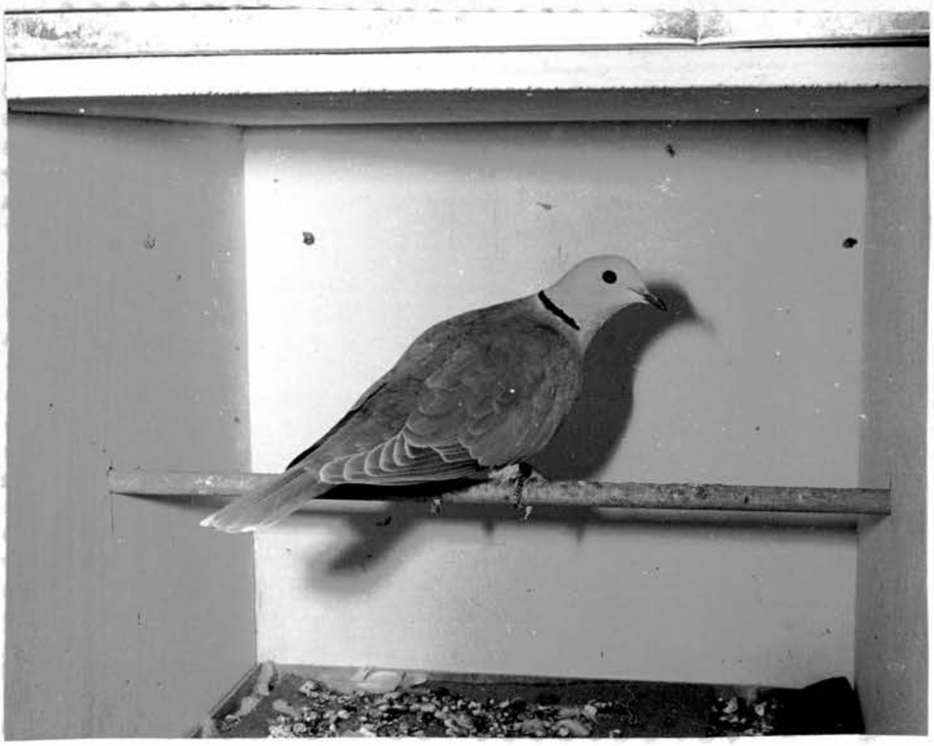
The subject animal used for all of the original experimental work to be disucssed in this thesis was the Barbary Dove or Blonde Ring Dove, Streptopelia Risoria (Figure A). The Ring dove is very similar in appearance to the Collared dove (Staeptopelia Decaocto) which is now commonly found in Britain, having spread north-west across Europe and arrived on the British mainland about 25 years ago, but is slightly lighter in colour. The adult birds are about 28 cm in length and range from about 140 - 180 grams in weight.

The streptopelia doves are similar to the Columbiforme pigeons (e.g. the Wood pigeon, Columba Palumbus) in being essentially sexually monomorphic and in forming monogamous pairs. Indeed the only means of determining the sex of an individual Ring dove (apart from a surgical exploration) is to observe the behaviour. Each member of the pair takes an equal part in the parental responsibilities of nest construction and feeding of the young. Murton (1965) notes that as early as Aristotle men were aware of the division of labour in incubation duties on the nest between the male and female pigeon.

Pigeons and doves are unique among birds in that they feed their young immediately after hatching from their own body substance. They secrete a curd-like substance into the lumen of the crop which is formed by the shedding of proliferating crop epithelial tissue. This mechanism obviates the necessity, encountered by most other birds, to supplement the food intake of the growing young with some animal protein. This substance (called "crop milk") is regurgitated and constitutes the whole of the food intake of the squabs for the first one or two days

FIGURE A

The Barbary dove or Blonde Ring dove, Streptopelia risoria.



after hatching. Thereafter the crop milk is fed to the young mixed with regurgitated seed material from the crop, and thus the young are weaned onto the adult grameniverous diet.

The crop (a diverticulum of the oesophagus) is well developed in Columbiformes and is used as a storage organ for food. This is important not only from the point of view of feeding the young before fledging, but also because it allows the birds to eat at a rate in excess of that at which the food is processed in the digestive track during the day, and to go to roost at night while that extra is dealt with. This is particularly significant when the birds are feeding on a diet of very low nutritive density which other herbivores would have to deal with by well nigh continuous feeding. Even from the first days of life the crop seems to be important for the feeding behaviour of the squabs. Intake of crop milk from the parents seems always to be in great excess of the stomach volume, with the volume of the crop and contents in the one or two day old squab often greater than one quarter of the body size. The squab thus always carries a reservoir of food. Perhaps this feeding in very large meals is the most efficient way to encourage the milk production of the adult.

Columbiformes, although basically grameniverous, are relatively unspecialised feeders. One of the reasons for the success of the Wood pigeon in this country has been its ability to make use of the various extra sources of food provided by man's agricultural efforts. Similarly, the feral, or street pigeon (descended from the wild Rock dove, Columba Livia) of our towns and cities might reasonably be regarded as the avian equivalent of the rat, their numbers being supported largely on food provided by man (either intentionally (Figure B) or unintentionally in the form of refuse). Pigeons have also been encouraged

FIGURE B

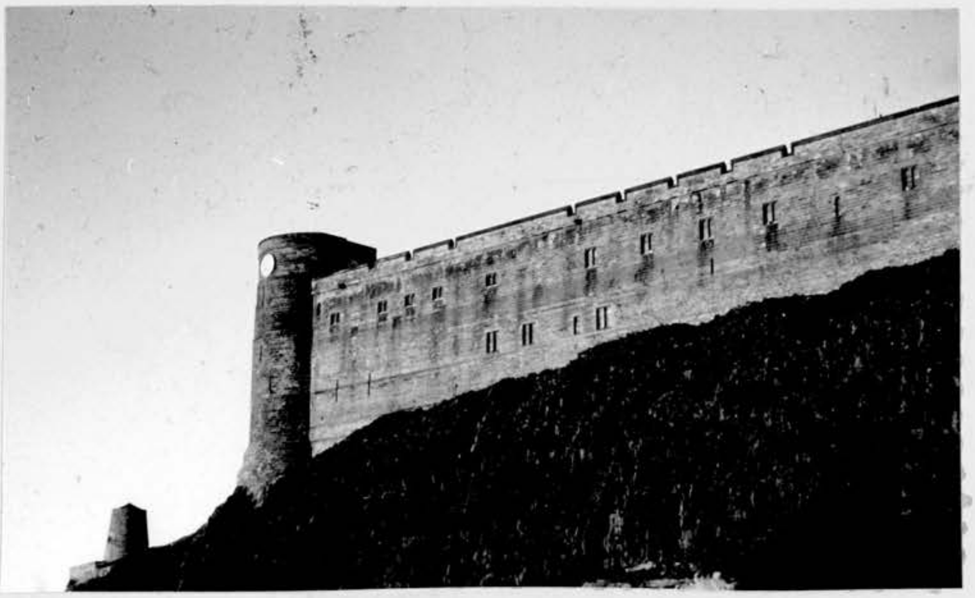
Pigeons in Princes St. Gardens, Edinburgh.

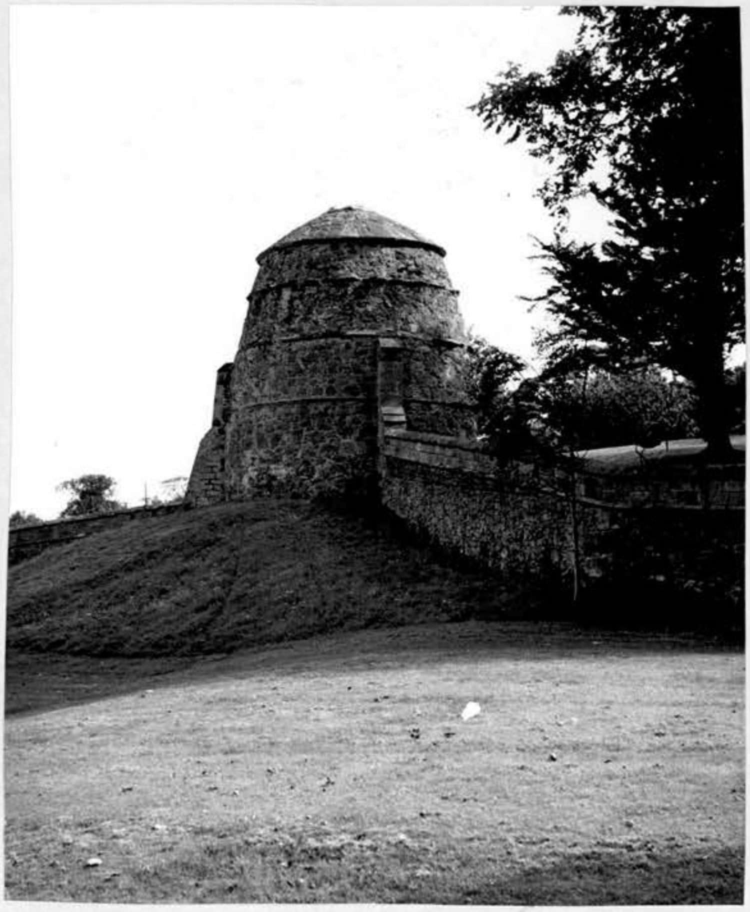
in the past to breed and roost around human habitation so that they could be culled for food. The dove-cots often seem associated with castles or manor houses (Figure C) provided a steady supply of meat in time of seige. They also represented a symbol of the dominance of the feudal landowner over the surrounding agricultural community whose crops provided the food for these birds, but often were forbidden to catch or shoot them. The nagivational and homing abilities of pigeons have also been utilized by man for the purposes of communication and navigation at sea, and more recently in the sport of pigeon racing. This long established relationship of commensalism with man has been possible because of, but has also contributed to the birds fairly catholic tastes in food. In addition to the above examples of essentially voluntary co-operation, pigeons have, in more recent times, been intensively bred for human food production. This is particularly found on the European continent and in North America.

Columbiformes are characteristically flock feeders, this being particularly the case in seasons of low food availability. Flying birds will be highly likely to respond to the sight of a feeding flock by descending to join them. Many of the pigeon and dove species have neck flashes or rings which may serve to attract the attention of a flying conspecific to a feeding site. There has been much debate on the significance of flock feeding in birds (Murton, 1971; Lazarus, 1972; Siegfried and Underhill, 1975) the animals probably gaining individual advantages in terms of food searching efficiency and reduction of the risk of predation. The organization of the flock, with the fit, dominant animals towards the centre and the weak subordinates towards the periphery probably also serves to extenuate the existing likelihood

FIGURE C

Dove-cots at Bamburgh Castle, Northumberland and Dirleton Castle, East Lothian.





that predation loss will be greater among the less fit animals, thus conferring an overall advantage on the population. The flock feeding habit of the Columbiformes indicates the sensitivity of the animals to external environmental stimuli for the initiation of feeding.

The Use of the Ring Dove in Psychological Research

Dating perhaps from the pioneering work of the late Professor Daniel Lehrman on the interaction of hormones and reproductive behaviour (Lehrman, 1958 ; Lehrman, 1959; Lehrman, 1961; Lehrman, 1964), the Ring dove has been a favourite subject of study for a number of groups working on the area of brain mechanisms and behaviour in birds (Vowles, 1975).

There are four main centres in which the physiological basis of behaviour in Streptopelia risoria is now actively studied. First of all is Rutgers University in the United States where Lehrman's work was carried out and where the present tradition is very much a continuation of his original interest in reproductive behaviour (Cheng and Follett, 1976; Buntin, 1977). Also actively involved in the analysis of the hormonal basis of reproductive behaviour in the dove is a group working at Madingly in Cambridge (Hutchison 1975; Hutchison, 1976). The work of the Oxford group (McFarland, 1971; Sibly, 1975; Sibly and McCleary, 1976) has been particularly concerned with the study of feeding and drinking behaviour, and with the development of precise mathematical descriptions of motivational processes. The offshoot of the Oxford dove tradition which now exists at Edinburgh has been involved in the study of feeding behaviour (Wright, 1975) and affective behaviour

(Wright and Spence, 1976) and has produced a stereotaxic atlas of the dove brain (Vowles, Beazley and Harwood, 1975).

The subject of the present research has been a study of the diurnal pattern of feeding behaviour in the Ring dove and of the way in which this is influenced by external, environmental constraints to bring about an appropriate day to day regulation of food intake.

VCHAPTER 1

1.1 BEHAVIOUR AND THE ENVIRONMENT

Particular organisms exist in close interrelationship with particular environments. The organism possesses certain capacities and abilities, derived from its evolutionary history, which fit it to cope with the vagaries of its own environment and to capitalize on its resources. The concept of an organism or animal must carry with it the concept of an environment in which it has been designed to live, or it would be impossible for us to understand most aspects of its physiology and behaviour (Reed and Jones, 1977). Indeed the concept of environment envolves the concept of organism, suggesting as it does, surrounding and containment. The two ideas are inextricably linked. Lorenz (1969) talks of the organism developing a 'mould' or an 'image' of the natural environment so that by examination of any animal we can make suggestions as to the nature of the environment from which it was drawn.

It often is the case however, that the Comparative Psychologist tends to miss the significance of this interrelationship in his attempt to formulate general principals about behaviour and its control. Zeigler (1973(a)) suggests that there are two rationales which may be adopted for the comparative study of animal behaviour. The first approach is to concentrate on that which is common across species, ignoring the differences and assuming that the similarities provide information about the more fundamental rules. For this approach, cross-species variability must be seen as something of an embarrassment and source of undesirable and unfortunate error variance. That which constitutes an embarrassment for some however, is the very substance of study for others. Diversity across the Animal Kingdom may be seen as illustrating a range of possible solutions to the problems of survival posed by vastly differing environments. Zeigler describes this diversity as providing a wide range of 'natural preparations' (as the physiologist might use the term) for the study of the general problems and principals for which they represent the specific answers and adaptations of individual animals.

1.1(a) The Example of Avoidance Learning and the Species-Specific Defence Reaction

An example of an ecological approach to the study of behaviour would be the idea of the Species-specific defence reaction (SSDR) and the laboratory study of avoidance responding as reviewed by Bolles (1970). Rather than describing the performance of the animal in the wild, whereby it is able to escape from and avoid predation, in terms of the classical ideas of laboratory acquired avoidance, Bolles sought to account for some of the paradoxical findings in the laboratory by consideration of the innate defence mechanisms which the animal obviously possesses. He showed quite clearly that it was not possible for all behaviours to be used as operants in a learned avoidance experiment, even although the operant level of the behaviour was quite high. For example, a bar-press response, although easily learned by a rat for a food or water reward, is particularly difficult for it to associate with avoidance of electric shock (Bolles and McGilles, 1968). When such an association is made the structure of the response is very unlike that of the food reinforced bar press, but looks much more like the animal 'freezing' on the bar, as it might freeze in response to a startling external stimulus. Bolles suggests that a bar-press lies at one end of a 'continium of difficulty' of learning with reference to avoidance of shock. Other behaviours which could be placed on such a continium would be 'Shuttle-box' avoidance responding which has been reported to require about 100 trials to acquire, wheel-running which can be learned in about 40 trials, and the other extreme of alley-running which can be learned with only about 6 trials. The degree to which, or the ease with which a behaviour will be learned as an avoidance response then, will depend on the similarity which that behaviour has to a functionally successful, natural avoidance behaviour which Bolles terms the Species-specific Defence Reaction. Thus alley-running is seen as being an appropriate response by a rat to avoid a noxious external stimulus (like an electric shock) as it serves to quickly remove the animal from the area of danger. A shuttle-box situation involves the animal in quickly returning to the physical site which it has previously found to be dangerous, and is thus not so easily learned. A bar-press response, which would seem to the animal like doing nothing, will only be learned if it becomes fortuitously linked to the species-specific behaviour of freezing in response to threat.

The important point then, is that it is not the actual physical characteristics of the behaviour which determine how easily it is acquired, but the significance of that behaviour for the animal in the context of its own ecological niche. Bolles suggests that the continuum of difficulty in learning a behaviour as an avoidance response would differ between animals as a function of the animals natural behaviour. He notes that Solomon and Wynne (1953) apparently found it quite easy to train a dog to perform a shttle-box avoidance. The response of a dog to danger or attack is not to flee as far as possible, as would be that of a rat, but to withdraw and stand off waiting for the possibility of striking back. Thus the shuttle-box behaviour would be closer to the SSDR repertoire of the dog than that of the rat.

What is general and significant then, is not the individual performance of the dog or the rat in a given situation, but the performance seen in the context of the animal's ecology and life style. We do not conclude from the fact that a dog can learn easily something that a rat finds difficult to learn that the dog is more intelligent ;than the rat. We conclude that animals differ in the degree to which they are genetically set to make certain associations. The true comparative approach in Zeigler's terms then, takes the anomalies and, on the basis of them, constructs an overview which can better describe and predict the behaviour of widely differing animals from different environmental backgrounds.

This view was seen as being a novel insight in the face of a Behaviourist tradition which suggested that all stimulus-response connections could be made, Bolles specifically attrributing this error with respect to avoidance learning to Hull (1929). However it would be more correct to say that these ideas were contrary to the pervading view, rather than being novel. For example, Verplank (1955) emphasized that 'the laws of learning operate within limits determined by the genetic characteristics of the animal'. This has often been taken to mean that an animal cannot learn to perform a behaviour which its physical structure would make impossible, thus rendering it something of a truism, but the original statement was meant to convey more. Indeed Thorndike (1911) was under no illusion that his cats would be able to learn to associate any arbitrary behaviour with escape from a 'Puzzle-box.'

1.1(b) The 'Visual Cliff'

Just as there are 'constraints' on the learned associations which can be made by an animal (Shettleworth, 1972) so are there constraints on cognitive ability which can be understood only in terms of ecological niche. An example of this would be the 'Visual Cliff' described by Walk and Gibson (1961) in which visual information about a discontinuity in a surface and a risk of a fall, is set in conflict with touch information (a solid, plate-glass sheet) indicating adequate support. Most infants (humans, cats, goats, chicks and so on) show a marked confidence in the visual information in preference to the tactile information and, when placed on the slightly elevated platform at the edge of the 'cliff' will, without fail, move off the platform towards the 'shallow' side. Rats however will be perfectly satisfied with the information from their vibrissae that the glass surface 'affords' support (Gibson, 1976) and show no preference. The reason is not simply that they cannot see well enough to use the visual information as can be demonstrated by raising the platform slightly so that vibrissae contact is possible on neither side. In this case 95 - 100% of the rats accept the visual information and descend on the shallow side. The nocturnal habit of the rat would obviously be aided by tendencies to allow tactile information to dominate visual information when a conflict occurred.

A similar observation on the significance of depth perception information was made by Yerkes (1904) who studied the behaviour of three species of turtle presented with a physical drop into a net from an elevated platform. One of the species was largely aquatic, another was terrestrial and the third was both aquatic and terrestrial. Each of the species showed increased latency to leave the platform as the height above the net was increased. When the platform was at a height of 180 cm. above the net, the majority of terrestrial and amphibious habit animals refused to leave it during the hour long observation period, while all but one of the 40 aquatic turtles jumped. Yerkes suggested that the height indicated a particularly dangerous fall to the land turtles, but might be associated with water and safety for the aquatic turtles. The three species appeared equally able to detect the differences in height as indicated by the increased latency to leave the platform with increased height. However the significance of that perception appeared to differ as a function of ecology.

1.2 Feeding Behaviour and the Environment

Similar connections have begun to be seen between ecology and the regulatory capacities of animals.

1.2(a) Control of Energy Intake

The laboratory rat seems remarkably able to maintain its body weight within very strict limits (Adolph, 1947; Strominger, Brobeck and Cort, 1953), and can respond appropriately to challenge to its energy regulation by dilution of its food by non-nutritive bulk (Carlisle and Stellar, 1969). This observation has led to the conclusion that the normal intact rat eats in order to take in a certain daily caloric requirement, and will stop eating when this requirement is met (Jacobs and Sharma, 1969). It is clear that the termination of feeding in the minute by minute control of meal taking cannot be brought about by an exact metering of the caloric intake leading to a negative feedback which would terminate the meal, as such information could not be gathered quickly enough. Booth et al. (1976) have shown that a prior knowledge of the satiating power of a certain foodstuff can be learned and become associated with its taste, thus an accurate estimate of the caloric worth of a meal can be made as the meal progresses by metering the gross amount of food ingested and associating this with the predicted caloric density per unit volume. Familiar foods then, have associated with them 'metabolic expectancies' as to their energy content.

The rat has for long been the favoured animal of those who study the physiological control of feeding behaviour, and it often appears that many researchers consider the regulatory abilities of the rat to be the sine qua non of adequate food intake regulation in all other species as well. Some recent research, notably by Collier and his co-workers, has attempted to show that capacities which the rat seems to possess are not part of (and hence are presumably not required for) the normal regulation of food intake in other species which occupy different ecological niches. For example, Hirsch (1973) found that calocir dilution of a powdered diet with cellulose led to a reduction in caloric intake and body weight in Guinea pigs. It was argued that these animals did not appear to have the rat's ability to respond to caloric content, but were regulating their food intake simply in terms of bulk. This finding is possibly confounded by the relative palitability of a normal and cellulose diluted diet, the animals failing to increase their food intake because of the unpleasant taste and texture of the dilute material (Corbit and Stellar, 1964). However it was found that the food intake, after a brief depression, was held relatively constant by gross weight as level of dilution was increased, whereas a palatability hypothesis would predict a reduction in intake. Kanarek (1975) found a similar failure to regulate body weight and appropriately increase food intake in response to calor dilution in cats, and Hirsch, Dubose and Jacobs (1978) confirmed and extended these findings with cats by obtaining data from a wider range of dilutions, and also by using kaolin as the dilutant to take account of the possibility that cellulose might be digested to a certain extent by animals not normally thought to be able to do so. In addition to this failure to respond to calor dilution, Skultety (1969) has reported that cats will similarly fail to reduce food intake in response to increased caloric density. It has been argued that these species, in view of the nature of their normal diet, might be expected to be able to adequately regulate food intake and control body weight within reasonable limits without any mechanism which could take account of changes in caloric density. The Guinea pig (a herbivore) and the cat (a carnivore) would be adapted and designed to eat material or respectively low and high, but both fairly constant caloric density. They would thus have no need of a mechanism for caloric regulation. The rat on the other hand is an opportunistically feeding omnivore which would have to cope with great varieties of food material (mostly supplied by man) which would differ greatly in their energy value. To make full use of the available food sources, the rat would require a means of assessing its intake in terms of calories so that dangerous deficits or surpluses were not accumulated.

One would expect the above analysis to predict a similar failure of caloric regulation in the dog, being also naturally a carnivore. Janowitz and Grossman (1949) found that caloric regulation in dogs was far inferior to that shown in rats. Where compensation did seem to be occurring it was incomplete and slow to show itself. The results of this study were questioned by Jacobs and Sharma (1969) who suggested that the procedure of feeding the dogs only once per day meant that they were in a chronic state of food deprivation which was likely to result in changes in the animals responsiveness to the palitability of the food. They presented data from three dogs fed ad libitum to suggest that, under these circumstances, compensation did take place. However this data has been questioned by Hirsch, Dubose and Jacobs (1978) who point out that only one animal showed a sustained increase in food intake on the low-calorie diet, and even this variation did not seem to be beyond the range of the fluctuations seen on the undiluted diet.

Returning to herbivores, failures of caloric compensation have also been reported for the rabbit (Hoover and Heitman, 1972) and the opossum (Maller, Clark and Kane, 1965). Considering those cases in which caloric compensation is reported to occur (Dalton (1965) with mice; Hill and Dorsky (1954) with chickens; Van Hemel and Myer (1969);

Savory and Gentle (1976) with quail; Rozin and Mayer (1961) with goldfish) we can see that the animals involved are similar to the rat in being fairly unspecialized in their feeding, and perhaps thus having greater need of such a mechanism. As pointed out by Savory and Gentle (1976) seasonal changes in diet fibre content may be associated with changes in the gut dimensions in some birds (Lewin, 1963; Prendergast and Boag, 1973) which would clearly be a different order of effect from the day to day changes which a rat might be required to deal with. Further, they note that the regulation which was taking place in their quail was to hold constant the amount of nutrient digested and not the body weight as is normally reported in laboratory rats (Adolph, 1947). A larger amount of energy was expended in feeding on the dilute diet and hence constant nutrient intake was associated with slight body weight loss. Thus they suggest it would be possible for this sort of regulation to be taking place on the basis of holding constant some dietry component other than energy.

1.2(b) Response to Food Deprivation

A further response of the rate feeding control system to external challenge can be seen in the fact that deprivation of food for a certain length of time will result in a restorative hyperphagia when food is again made available such that the deficit incurred will be made good (Bolles, 1962). The relative abilities of the rat and the golden hamster to respond to periods of deprivation were assessed by Silverman and Zucker (1976). They observed the response of both of these animals to a regime of feeding in which food was available only every second day (and in which food hoarding was, of course, prevented). Rats subjected to this intermittent starvation regime settled their food intake to a level of about 162% of their previous daily intake on the one day out of two on which food was given. Hamsters on the other hand maintained an intake of about 99% of the previous daily level (that is, they were eating about half as much overall) and rapidly lost weight. Extremes of body weight loss did not seem to overcome this deficit, as some of the animals actually starved to death. A similar pattern was seen in a 12 hour deprivation schedule in which the animals were fed either in the dark or the light phase of a 12 hour light cycle. Rats increased their intake when food was available but the hamsters ate only as much as they normally would have done in the time limit. Further, it was found that when hamster survivors of the deprivation experiment were allowed continuous access to food they were slow to regain lost weight and apparently settled at a level of about 85% of the pre-deprivation weight. It has been shown that some other animals, for example the mouse (Nelson et al., 1973) and the guinea pig (Kutscher, 1969) appear to have difficulty in adapting to periods of deprivation by increasing intake when food is available. This might be explained in terms of the small size and consequent high metabolic rate of the former and the naturally low calorific value and hence high bulk of the preferred diet of the latter, leading to a need for a very high rate of food intake relative to gut size in both of these animals. However the hamster appears to be unique in its complete lack of any tendency to respond to deprivation by increased food intake.

The fundamental significance of this remarkable lack of regulatory ability on the part of the hamster is discussed by Silverman and Zucker (1976) in terms of the animals tendency to hoard or to hibernate in response to low food availability, which might remove, or at least greatly reduce the need for a system producing compensatory hyperphagia. The surprising nature of this anomaly is emphasised by the fact that hamsters appear to be perfectly able to alter their food intake in response to calorie dilution, thus this aspect of regulatory ability seems just like that of the rat. They are not deficient in energy regulation per se, but in one particular expression of it.

1.2(c) Effect of Exercise

A further peculiarity of the food intake and weight regulatory mechanisms of the hamster was demonstrated by Borer (1974). She found a marked increase in body weight as a result of voluntary exercise on a running disc, which was most marked and consistent in the case of the females. The weight gain could be divided into two phases, the first of which was actually during the period of daily exercise and appeared to be independant of the type of food offered. The second phase was a rapid spurt in body weight gain which occurred when the animals were 'retired' from the exercise condition, and was clearly seen to be greater when a more preferred food (Sunflower seeds) was available in addition to the normal laboratory diet. A study of body structure at the end of the experiment indicated that the exercise phase of weight gain was due to an increase in body size, whereas the additional post-exercise 'retirement' effect was produced by an increase in the amount of body fat. The weight gained under these exercise conditions appeared to be maintained, the animals continuing to hold their body weights at the new elevated levels after removal from the experimental situation. This is again in marked contrast to the effect of exercise on the rat (Collier, 1970) which seems to be to increase food intake to an extent which takes account of the amount of exercise involved and which lasts only as long as the exercise condition is in force, normal regulation and food intake returning after the manipulation has ended. Nance et al. (1977) found a sexually dimorphic effect of forced exercise on body weight in rats. Male animals were found to choose a drop in body weight and food intake while the experimental condition lasted, whereas the females increased their intake to hold the weight constant.

A further series of anomalous effects of the interaction of work and food intake have been discussed by Mrosovsky (1964). He has found that a group of animals (Dormice (Glis glis), Golden mantled squirrel (Citellus lateralis) and Golden Hamsters (Mesocricetus auratus)) which can be classified as hibernators, differ very markedly in their response to certain classic measures of feeding motivation from the normal findings with rats. Of particular interest is the response of the Dormouse (Mrosovsky, 1964) and the Golden mantled squirrel (Mrosovsky, 1971) to a fixed ratio requirement for a food reward in an operant situation. A rat will normally increase its work output as the ratio of work to return increases, so that a constant amount of food is gained. This will be true in the case of a food deprived animal working in a learning experiment (Ferster and Skinner, 1957) and also for undeprived animals working in a free operant situation for all of their food (Collier, Hirsch and Hamlin, 1972). Very large ratios can be tolerated (several hundreds of responses for one reinforcement) before the animals show any marked evidence of failure to compensate. Mrosovsky's dormice and Squirrels however, will give up responding when the ratio increases beyond about 10 responses. The similarity between these findings and those obtained using rats with lesions in the ventromedial nucleus of the hypothalamus (VMH) (Miller, Bailey and Stevenson, 1950) have been offered as evidence to suggest that the VMH is concerned with long-term control of food intake rather than being a 'satiety centre' controlling hour by hour meal taking, and that the anomalous behaviour of the hibernating animals can be attributed to a state a hypothalamic quiesence associated with the pre-hibernation weight gain (Mrosovsky, 1971). Here again then we find an example of what would seem at first sight to be a very significant failure of food intake regulation occurring in a group of animals occupying a distinct and specialised ecological niche. This failure to compensate in the operant situation is perhaps similar to the absence of post-deprivation hyperphagia found by Silverman and Zucker (1976) in the hamster. However, the differences in the procedures used by Mrozovsky and those used in most other cases makes comparisons impossible. The animals were not deprived of food to encourage them to perform in the half-hour test period, but were offered a highly preferred food (Sunflower Seeds) in the test and fed ad libitum on the normal laboratory diet at other times. Thus, what was being measured was the degree to which the animals would work to obtain a preferred 'tit-bit' in the absence of deprivation. The motive force for such responding was the incentive provided by the type of food rather than any deficit which would exist as a consequence of the failure to respond (Sibly, 1975).

1.2(d) Feeding and Sexual Behaviour

It is a very well established finding that female rats show a reduction in food intake at the time of sexual receptivity in the oestrus cycle (Slonaker, 1925; Tartellin and Gorski, 1971; Ter Haar, 1972; Drewitt, 1973). The reduction has also been found in mice (Petersen, 1975; 1975), hamsters (Petersen, 1975; Morin and Flemming, 1978) and in the Guinea pig and Rhesus monkey (Czaj and Goy, 1975). The usual interpretation of this effect is that oestrogens, of which circulating levels are high at this time, have a depressant effect on hunger motivation. The importance of oestrogens in producing these effects has been established by the appropriate procedures of gonadal removal and exogenous hormone treatment. However, Petersen (1975) has shown that this effect only appears to hold good in his mice when they are feeding on the normal laboratory diet. If the animals are given a highly preferred sweet diet their food intake at the time of sexual receptivity is increased rather than decreased. This paradoxical finding is interpreted by Petersen to indicate that the effect of reproductive condition on food intake is a secondary effect of a change in the tendency of the animal to respond to external, environmental influences. It is important for a sexually receptive female to give priority to responding to external information which would lead to successful mating and pregnancy. A secondary result of this 'externalized' mode of behaviour is to increase the salience of sensory food related cues leading to overeating of a preferred diet and hypophagia on the normal, less preferred diet. Again, this is a hypothesis which generates predictions about species differences in the original effect as described. Maass and Wade (1977) have reported a study of the effect of gonadal hormones on feeding behaviour and body weight in the Mongolian gerbil (Meriones unguiculatus). The picture in this animal appears to be completely different from that which is found in the rat. Just as changes in natural levels of oestrogens lead to a depression of feeding at pro-oestrus, so exogenous treatment after ovariectomy similarly reduces eating in the rat (Wade, 1975). However, similar oestrogen treatment after ovariectomy in the gerbil leads to increased food intake and body weight. Progesterone was found to have no effect on the feeding behaviour of the gerbil, but to synergize with oestrogen to produce larger increases in both measures than did oestrogen alone. Again, this is in marked contrast to the rat in which progesterone is found to consistently inhibit effects of oestrogen on feeding behaviour (Wade, 1975) and on sexual behaviour (Morin, 1977).

It would be pure speculation to suggest that these differences in the effects of gonadal hormones on non-sexual behaviour might be related to the differences between the opportunistic nature of sexual contact in rats, mice or hamsters and the pair-bonded, monogamous habit of the gerbil. The hypothesis would be worth testing however, by repeating observations on a number of species about which specific predictions could be made.

1.2(e) Summary

The above examples serve to illustrate the importance of consideration of the particular ecological background of animals in feeding behaviour studies and also the need to understand the way in which feeding behaviour interacts with other behaviours, both regulatory (Kutscher, 1969; McFarland, 1964; Wright, 1976) and social (Petersen, 1975, 1976). The accurate control of intake to meet energy and nutrient needs which we see in the normal, free living animal can be brought about predominantly by internal regulatory and homeostatic mechanisms as is the case in the rat, or by the interaction of such internal mechanisms with the external, environmental constraints as we see in the specialist feeders (Collier et al., 1976) or other ecological specialists (Mrosovsky, 1971; Silverman and Zucker, 1976).

It is hoped that a systemic study of other specialist groups and the regulatory capacities and strategies which they uniquely possess (or lack) will similarly contribute to our understanding of the general principals of the behavioural control of food intake.

1.3 Feeding Adaptations in Birds

The class Aves contains a wide variety of individual evolutionary specializations, and indeed one of the classic examples of influences contributing to Darwin's ideas comes from anatomical and behavioural adaptations for feeding in finches (Lack, 1947). There are a number of capacities and characteristics which are common to the class as a whole however, and it is these which will be considered here.

The first obvious characteristic of birds which distinguishes them from most mannals is that they fly. This is going to be of vital importance from the food intake and energy regulation point of view. Just as the skeletal structure of the bird is clearly designed to minimize weight, we may expect to find a feeding control system marked by contra-preparedness to allow the accumulation of excess body weight (Cardini, 1971). On the other hand, flying is a very energy demanding mode of locomotion. This can be seen in the relative metabolic rates of birds and mammals, and the size of heart tissue compared with body weight in birds. A very fine line might be expected between what was excess dead weight and vital energy reserve.

A further general characteristic of the bird is that it is strongly dominated by its visual system as compared with many mammals and particularly rodents. This can be seen in the relative unimportance of the chemical senses of smell and taste in most birds, with the possible exception of fruit eaters (Gentle, 1975), the large size of areas in the avian brain (e.g. the optic tectum) receiving visual projections, and also the nature of avian social communication which involves a large amount of visual display (Armstrong, 1965; Tinbergen, 1953). This reliance on visual information has meant that most birds confine their activities to the daylight hours and remain relatively inactive during the night. This can be seen in a total confinement of feeding to the daytime in most birds not specially adapted to nocturnal hunting (Van Hemel and Myer, 1969; Zeigler, Green and Lehrer, 1971).

Some specific anatomical peculiarities of birds, with reference to food intake, are also found. They lack teeth for the tearing and grinding of their food. Those birds which are carnivores have powerful tallons and beak with which to tear their prey, but the main grinding role of the teeth to aid and speed digestion is filled in most birds by the muscular stomach. In this second chamber (immediately next to, and lower down the alimentary canal from the glandular stomach) the partly digested food is churned along with small pieces of stone and grit which are eaten by the bird and retained to serve this abrasive function. Many birds have a crop (a diverticulum of the oesophagus) which is sufficiently well developed to act as a storage organ. Food which is eaten may lodge in the crop before being passed downwards to the proventriculus for digestion. The crop may also be used for the storage of food which will subsequently be regurgitated to feed the young.

The peculiarities of avian physiology and behaviour, and the way in which these will interact with the normal feeding ecology of the animals should provide further 'natural preparations' to contribute to the comparative analysis of food intake regulation which was discussed above.

1.4 Chapter Summary

The behaviour of an animal cannot be adequately understood without reference to the nature of its normal environment. Several examples were presented to indicate the importance of this principal.

The importance of ecological factors in the study of feeding behaviour was illustrated with reference to several examples of rather paradoxical results obtained using (for the physiological Psychologist) relatively unusual animals. It was seen that over the past decade more effort is being directed to this comparative approach to the study of feeding.

Some of the particular characteristics of birds were noted to indicate that the "ecological" approach applied here might be expected to be fruitful.

CHAPTER 2

2.1 Brain Mechanisms and Feeding Behaviour in Birds

A great deal of early neuro-anatomical research was carried out using birds (Flourens, 1824). However, compared with the vast number of studies reported on the neural substrate of feeding behaviour in the rodent, there has been relatively little work on such brain/behaviour relations in birds. The position is further complicated by the fact that the bulk of the avian literature which does exist comes from a completely different tradition from that which has supported the rodent work, making comparisons and analogies difficult. It would be a reasonable generalization to say that the physiological psychology of the rodent owes most (in terms of volume of research) to the American Behaviourist tradition, whereas the foundations of avian work rests firmly in the European Ethological tradition (Caryl and Wright, 1975). There are many reasons why this should be so. On the one hand the rat has always been the subject of choice of the operant researcher simply because of its availability and convenience as a laboratory animal. Although not denying the importance of species differences, it was held as dogma that the way to achieve most rapid progress in the study of behaviour was to concentrate one's efforts on a single, or a small number of 'representative' species (Skinner, 1938). Although the the whole idea of a 'representative Species', and the suitability and qualifications of the Norway rat to hold this position were questioned (Beach, 1950) a situation analogous to industrial inertia existed whereby the ubiquity of the rat as a laboratory animal in all other areas of research guaranteed its future in psychology.

The ethologists on the other hand, were traditionally wont to study behaviour in the field rather than the laboratory. The criterion of choice of ones subject matter then, was the ease of finding and observing it in the wild rather than the ease of feeding and maintaining it artificially. Further, if the ethological approach is one of observing and describing, it is clear that the predominantly visual and auditory nature of bird behaviour will be more amenable to human study than the behaviour of rodents which relies so heavily on channels of communication, like ultra-sound and smell, closed to us without relatively sophisticated equipment.

When the study of behaviour moved to the neuro-biological level, clear differences in approach can be seen between the ethological and behaviourist derived research (which we can label comparative psychology). Much of the rodent work was directed by the 'drive-reduction' theories of behaviour and reinforcement (notably the ideas of Neal Miller) and sought to identify the actual physical locus in the brain of mechanisms which these theories required. Emphasis was given to the exact anatomical description of brain areas under examination (whether stimulation or lesion investigations) and yet the behavioural measures and descriptions used tended to be gross and imprecise. A good example of this would be the account of the aphagic syndrome which followed bilateral lesions of the lateral hypothalamic area. Many of the early accounts of the effect of such lesions (Anand and Brobeck, 1951; Teitelbaum and Stellar, 1954; Teitelbaum and Epstein, 1962) tend to convey the idea that the animals are normal apart from their failure to eat and drink.

> 'The researchers outside this field could easily form the impression from reading the literature that the LH lesioned rats differ only from intact animals in their pathological aversion to laboratory chow.'
>
> Wright (1975)

Of profound importance however, in the interpretation of the significance of this effect, is the fact that the lesioned animals are also suffering from very marked disturbances of orientation and attention to external stimuli (Marshal et al., 1971; Marshal and Teitelbaum, 1974).

At the other extreme, some of the early avian work which was behaviourly very explicit, tended to neglect the anatomical considerations. A particular example of this is the work of Von Holst and Von St. Paul (1963) on electrically elicited behaviour in chickens. They presented only the most gross information about sites of electrode placement, stating that they felt premature emphasis on anatomical details would detract from the description of the functional organization of the behaviours themselves.

Coming from these antecedents then, it can be seen that much of the rodent work would be directed towards an analysis of the homeostatic drive systems like hunger and thirst, whereas the avian work would concern itself more with social behaviour and display in the 'Fixed Action Pattern' tradition of Tinbergen and Lorenz.

There is another good reason for the dearth of investigations into the brain mechanisms underlying control of feeding behaviour in birds, which is the fact that there is an almost qualitative difference between the sorts of effects which can be produced by surgical intervention or stimulation in rodents and those which can be produced in birds. People continue to debate the meaning and significance of the hyperphagia resulting from lesions of the ventromedial hypothalamus which was first reported by Hetherington and Ransom (1942) or the aphagia described by Anand and Brobeck (1951) after lesions of the lateral hypothalamic area, and the assessments may range from the early dual excitation/inhibition models (Stellar, 1954) which held that these two centres were just about all we needed to account for the control of normal feeding behaviour, to the recent radical reanalyses (e.g. Friedman and Stricker, 1976; Mrosovsky, 1971) which hold that such phenomena have little to say about the animal's day-to-day behaviour. What is not in question however are the phenomena themselves. Although facts like pre-operative body weight (Powley and Keesey, 1970), diet palitability (Carlisle and Stellar, 1969), and the sex of the animals (Valenstein et al., 1969; Wright and Turner, 1973) have been shown to be important variables in the experimental situation for the production of lesion effects, and although distinctions must be made between motor reflex behaviours and motivated behaviours when considering electrical brain stimulation effects (Morgane, 1961; Morgane and Jacobs, 1969), all these effects do seem to be reasonably repeatable. The picture in the avian literature is not so clear.

2.2 'Stimulus Bound' Behaviour in Birds

Both electrical stimulation (Coons et al., 1965; Miller, 1964) and chemical stimulation (Grossman, 1960, 1962; Miller, 1964) applied to certain areas of the rat brain have been shown to elicit feeding behaviour which is very closely dependant on the stimulus. That is, the behaviour can be switched on and off by the electrical current or the infusion of chemical. Morgane (1961) was able to show that there were two distinct populations of stimulation sites in the lateral hypothalamus of the rat, one of which produced reflex eating and licking responses while the other was able to produce integrated sequences of food searching and feeding behaviour.

Åkerman et al. (1960) was able to produce feeding, drinking and panting behaviour by electrical stimulation of the hypothalamus in pigeons. From this they concluded that the hypothalamic organization of food and water intake and of temperature regulation were similar for birds and mammals. Using the Ring dove, Harwood and Vowles (1966) were able to demonstrate some influences of electrical stimulation on feeding, but the effects observed were very different from the compulsive eating produced in rats. They found forebrain stimulation (in the area of the paleostriatum and the ventral and posterior neostriatum) to be ineffective in actually eliciting feeding, but that it would have a facilitatory effect on any feeding behaviour which was going on at the time when the stimulation occurred. They also found an after effect of stimulation which lasted for about 10 minutes after the offset. Wright (1969) also working with Ring doves, found great difficulty in producing stimulus bound feeding. Only very few of the total number of diencephalic sites (14 out of 100 electrodes in 37 animals) were found to 'produce' feeding behaviour, and stimulation of those sites which were associated with feeding led to very variable results. Any one electrode found to produce marked and obvious responses on one day, might produce very little or indeed no effect at all the next, and there was apparently no external cues which could be used to predict when an effect was likely to occur.

Phillips (1964) using Mallard ducks did not report any stimulus bound feeding as such, but did observe movements of the bill, head and neck which he felt looked rather like food searching behaviour.

Delius (1967, 1971) found no feeding behaviour after electrical stimulation in Herring, and Lesser Black-backed gulls, but found that stimulation (in some sites in the neostriatum) le~~a~~d to a pattern of behaviour characterised by paddling of the feet and looking downwards. This behaviour appears similar to that which can be seen in many gull species while feeding in the shallows, the function of which is assumed to be the stirring up of the sand under the water so that small animals are uncovered and can be caught. Putkonen (1967) found sites in the forebrain and diencephalon of the chicken in which electrical stimulation produced bill movements, salivation and disjoint pecking responses, but no clear feeding behaviour. Tweeton et al. (1973) in a study of electrical stimulation in the chicken diencephalon found only 12% of over 600 sites sampled to produce clear feeding behaviour. When repeated tests were made only 10 sites continued to give positive results, and indeed only 4 on the final testing. In addition to the above rather inconclusive results, Phillips and Youngren (1971) were unable to find any evidence of electrically stimulated feeding in an extensive study of the forebrain and diencephalon in chickens and ducks.

In short then, it would appear that, of all the studies mentioned, only that of Åkerman et al. (1960) can really be said to show any clear-cut stimulus bound feeding effects. And indeed the generality of this study itself must really be questioned because, as pointed out by Wright (1975), as the whole procedure from the implantation of the electrodes to the testing and subsequent sacrifice of the animals was carried out within one day, the work might be seen as being semi-acute and thus not easily comparable with the bulk of the rodent literature. Their conclusion too, that the anatomical organization of the avian brain was similar to that of the rodent is highly questionable in view of the fact that many of the brain regions which classically support self-stimulation in the rat, and are believed to be involved in the reward and reinforcement system (e.g. the septal regions) in this animal, are associated with escape and aversion in the bird (Macphail, 1967; for review see Wright, 1975).

Thus, although the conclusions which we might draw about the specificity of anatomical localizations of the underlying motivational processes may be questioned (Valenstein et al., 1968; Wise, 1969; Valenstein, 1970), electrically stimulated behaviour and self-stimulation (Olds and Milner, 1954) seem to be relatively easily repeatable phenomena in the rat as compared with the rather inconclusive picture in the bird.

2.3 Brain Lesions and Feeding in Birds

As might be expected, lesion studies of feeding behaviour in birds show a similar pattern of difficulty encountered in the actual production of the effects. Lepkovsky and Yasuda (1966) reported hyperphagia as a result of hypothalamic lesions in chickens, but although these animals did appear to gain weight, this gain was not associated with increased food intake (Wright, 1975) and therefore must be assumed to be a result of some non-specific effect on the animals metabolism or general activity rather than an enhancement of their responsivness to food. In fact the only really reliable report of true hyperphagia in birds comes from a study of the White-throated sparrow (Kuenzel and Helms, 1967, 1970; Kuenzel, 1972) in which destruction of certain areas of the ventromedial hypothalamic area was found to produce significant weight gains and increased food intake. Of particular interest however, is the fact that these weight gains were in the same order of magnitude as those which occurred naturally in the animals in advance of winter migration, or which could be artificially stimulated by appropriate alterations in the diurnal light cycle. This would suggest that this particular area of the hypothalamus is related to anticipatory hyperphagia and weight gain in preparation for migration,rather than being a short-term satiety system involved in the day to day control of eating (c.f. Mrosovsky, 1971). The failure to find any obvious hyperphagia in most birds has been accounted for by the suggestion that a satiety system would be of less importance to the bird which has a significant capacity for food storage in the crop and might thus be seen as an opportunistic feeder tending to eat whenever food was present (Harwood and Vowles, 1966). However, the opposite argument has been offered by Cardini (1971) to explain the accuracy with which the pigeon can reduce its food intake in response to artificial loading of the crop. A flying animal, goes the argument, would be expected to be designed so that it avoids the carrying of excess weight, and would thus have a very sensitive satiety system. It is not necessary however, to invoke such teleological arguments to explain a paradox which may only be so because of our previous expectations derived from the rodent literature. Our search for feeding and satiety systems in the hypothalamus probably owes more to early two-process models of feeding control (e.g. Stellar, 1954), than to any observationally derived theory of feeding motivation.

2.3(a) Lesions Producing Aphagia

Total decerebration in the pigeon (Flourens, 1824) was found to produce a permanent abolition of feeding behaviour although the animals could still groom, walk about and swallow food placed in the mouth. Aphagia has also been reported to result from lesions of the basal forebrain in pigeons (Rogers, 1922), and the diencephalon in Ring doves (Wright, 1968) and chickens (Feldman et al. 1957), and in various parts of a complex circuit of neural structures from the sensory trigeminal nucleus and the quinto-frontal tract to the archistriatum in the pigeon (see Zeigler, (1976) for review; to be discussed in greater detail below). Aphagic effects are always difficult to interpret as very non-specific, gross disturbances can reduce or abolish feeding behaviour. It is rare to find reductions in intake which can be unequivocally seen to be disruptions of motivational processes without there being associated motor deficit, or problems of general arousal or responsiveness.

Brain lesions and electrical or chemical stimulation studies of feeding behaviour in birds then, can be seen to be still, for the most part, at the stage or determining whether or not any usable effects are there at all. Conversely, the early findings of hypothalamic hyperphagia or aphagia in rodents have produced a proliferation of confusing and often contradictory findings for the simple reason that the basic phenomena themselves are easy to reproduce.

2.4 The Avian Brain

In addition to the frequent differences of approach to the study of brain/behaviour relations in birds and mammals, and the problems presented by difficulties in repeating early mammal observations with similar procedures in birds, there is the basic stumbling block created by the neuro-anatomical divergence between the two groups of animals. This diversity is particularly marked in the organization of the diencephalon and the cerebral hemispheres of birds and mammals, with the lower regions (mesencephalon, rhombencephalon and spinal chord) having a much more similar functional organization across vertebrate classes (Nauta and Karten, 1970). Unique to mammals is the highly developed neo-cortex which forms the greater part of the cerebral hemispheres. The forebrain structure in birds on the other hand, appears to be more like that of the reptiles assumed to be the common ancestral stock, with no neo-cortex, but enlargement of the striatal regions. It was often suggested that the mammal, because of its neo-cortical areas, would possess unique abilities and capacities which would be denied to the 'lower' animals which had no neo-cortex. Birds then, would differ from mammals by lacking those cognitive abilities which the developed neo-cortex made possible. It has recently been realized however, that the avian and mammalian forebrains simply show two developmental and structural 'strategies' for the provision of increased processing capacity. It is not the case then, that the striatal regions of the avian brain are homologues of the corpus striatum (caudate nucleus, putamen and globus pallidus) of the mammal, but is a massive elaboration of that same ancestral 'theme'. To illustrate this, we will consider the anatomy of the mammalian and avian visual systems, as this is one area in which the comparisons have been most fully described.

2.5 The Comparative Anatomy of the Visual System

> 'The traditional view of the comparative anatomy of the visual system of vertebrates has been that certain unique developments, not present in other vertebrates, can be seen in mammals.'
>
> Hodos, Karten and Bombright (1973)

The geniculo-striate visual pathway of the mammal (for long thought to be 'the' mammalian visual system) was considered until quite recently to be something unique. The visual projection of the mammal was thought to be the visual cortex, while that of the bird was the optic tectum. In line with this view, the mammalian optic tectum or superior colliculus was seen as being little more than a vestigial remnant of the 'original' retino-tectal visual system used by the early reptilian ancestors of the modern mammal. This position can now be seen to be an oversimplification from two points of view. First of all, particularly as a result of Schneider (for example the 1969 paper on the 'Two Visual Systems') it has come to be recognised that the ascending tectofugal system in mammals has a function in its own right which is quite distinct from that of the geniculo-striate system. Schneider (1967) described the deficits produced by experimental lesions in the colliculus and the visual cortex in hamsters. These animals are particularly suitable for such study as the fibres of the optic nerve divide approximately equally between the visual cortex and the superior colliculus. If the colliculus alone is lesioned the animals appear to be blind, showing no responsiveness to peripheral visual stimuli. They will however, take and eat food items which are presented immediately in front of their noses and can discriminate between food and non-food. Lesions of the cortex produce completely different patterns of behaviour. The animals do respond to stimuli presented in the periferal visual field and will orient towards such stimuli. They appear however, to be unable to discriminate objects by sight. The colliculus then, may be described as a 'where' system and the visual cortex as a 'what' system (Blakemore, 1973).

In addition to the very real importance of the ascending tectofugal system in mammals, a visual system which is considered in some way homologous with or analogous to the mammalian geniculo-striate system has been studied in birds and other non-mammalian vertebrates (Karten, Hodos, Nauta and Revzin, 1973; Hodos, Karten and Bombright, 1973).

2.5(a) Tectofugal Visual Pathway

The point to point topographical representation of the retina on the optic tectum was first demonstrated by Hamdi and Whittridge (1954) working with pigeons. They found units of small receptive field (about 5^{o}) in the superficial layers, noting that the area of the receptive field from which responses could be obtained was constant as the electrode was passed through the whole thickness of these layers. It was in these superficial layers of small receptive field that the clear retinotopic mapping was most easily demonstrated, similar to the pattern seen in the mammalian superior colliculus. They discuss the function of the optic tectum in terms of what they call the "visual grasp reflex", noting that stimulation (electrical or chemical) applied to the upper surface of the tectum leads to opening of the opposite eye and to orienting head and eye movements. Similar studies have been carried out recently on the mammalian superior colliculus (Gordon, 1972);

showing that electrical stimulation of a part of this structure causes eye movements of the animal in such a direction and to such a degree as to bring the fovea to bear on that region of the optic array to which the colliculus cell was responsive.

The next stage of this tectofugal pathway in the bird brain was demonstrated by Karten and Revzin (1966) in a systematic study of the afferent connections of the Nucleus Rotundus. They placed lesions in 9 different regions of the pigeon central nervous system from the spinal cord to the retina and found evidence of degeneration in the nucleus rotundus only after damage in the optic tectum. From the consideration of several cases of tectal lesions in different areas, it was possible to suggest that the tecto-rotundal projections were topographically arranged. In view of the vast amount of organized visual input, it is interesting to note that lesions of the retina do not result in degeneration in the rotundus. This fact rules out the possibility of the rotundus being compared with the mammalian lateral geniculate body which receives a large amount of direct retinal input.

The further progress of the avian tectofugal pathway was followed in a study by Karten and Hodos (1970). Lesions were placed in the nucleus rotundus of a number of pigeons and the pattern of axonal and terminal degeneration was followed. Fibres from the rotundus join the lateral portion of the lateral forebrain bundle and pass ventral to the anterior commissure through the nucleus interpeduncularis and the paleostriatum primitivum without any points of termination. As the fibres pass upwards through the paleostriatum augmentatum they begin to divide (yet with no sign of termination in the paleostriatum itself) and finally reach the core region of the ectostriatum. No other terminal degeneration was found, so it can be assumed that the nucleus rotundus receives connections only from the optic tectum and projects only to the ectostriatum.

2.5(b) The Thalamofugal Visual Pathway

As mentioned above, the tectofugal system was, for long, considered to be 'the' visual system of the non-mammalian vertebrates while other visual connections were thought to be secondary aspects of this system, or possibly visual projections onto other brain mechanisms. A completely separate ascending pathway in the avian brain however, has been traced by Karten, Hodos, Nauta and Revzin (1973) which might be compared, in terms of pattern of connectivity and receptive fields, to the mammalian geniculo-striate system. The existence of this additional visual circuit was previously suggested by electrophysiological recording techniques in a study of Revzin (1969) using pigeons. Karten and Nauta (1968) were also able to trace the retinal projections of this system in the pigeon and the Burrowing owl to the diencephalon using degeneration techniques, and found connections to the group of nuclei which they have designated the nucleus opticus principalis thalami (OPT). Karten et al. (1973), again using degeneration techniques attempted to look for the telecephalic projections from the OPT in pigeon and owl. Fibres from the OPT pass inwards and upwards to join the lateral margin of the lateral forebrain bundle. In addition to this ipsi-lateral projection, a smaller bundle of fibres extend inwards and cross to the contralateral side of the brain as an element of the dorsal supraoptic decausation where they join themselves to the lateral forebrain bundle and pass upwards into the telencephalon with the ipsilateral OPT projections of that side. The fibres of both sides pass upwards with no sign of termination until they reach the region known as the 'Visual Wulst' with some termination in the hyperstriatum dorsale (both controlateral and ipsilateral). No evidence of termination was seen however in the ectostriatum which was shown to be the end point of the tectofugal visual projections.

In two papers Revzin (1969, 1970) has produced interesting information on the receptive field characteristics of these two avian visual systems. It would appear that the thalamofugal system (recording at the level of the 'Wulst') is characterised by exceptionally small receptive fields, being in the range of 0.5° to 4° and only rarely exceeding 10^6. On the other hand the tectofugal system is dominated by cells having particularly large receptive fields which were designated by Revzin W.F.s (wide fields). This comparison would suggest that the two distinct visual systems carry information for quite different purposes which might seem analogous to the foveal and peripheral systems of the mammal (or the geniculostriate pathway and the retino-tectal pathway of Schneider).

2.5(c) Summary

Using the organization of the avian and mammalian visual systems as an example then, we can see that birds appear to perform functions with the striatal regions of the brain which the mammal performs with the neocortex. Structures in the two brains which appear to be anatomically and histologically similar may be found, on closer examination to be quite distinct and unrelated from a functional point of view. Analogous or even homologous functions on the other hand, may be found to be performed by very different pieces of 'hardware.'

2.6 The Neuro-anatomy of Feeding in Birds

Because of these clear anatomical differences then, it is essential that an approach to the study of brain mechanisms controlling feeding behaviour in birds should not be guided by naive assumptions of homology with mammalian mechanisms. It is to be hoped on the other hand, that new insights gained from anatomically and behaviourally sophisticated studies of the avian brain will lead to fresh light being cast on mammalian feeding control. A good example of a program of investigation of bird feeding behaviour which has not sought to give undue emphasis to models or mechanisms derived from the mammalian literature is that of Philip Zeigler and his co-workers, which has been progressing for the last decade. An advantage which this group has enjoyed has been a close association with the excellent neuro-anatomical studies of Karten (see for example, Zeigler and Karten, 1973(a) and (b)).

From these studies has been built up a picture of an avian 'Feeding System' (Zeigler, 1974) of connected anatomical structures, damage to any part of which can lead to a disruption of feeding control. This circuit originates in the principal sensory trigeminal nucleus (the main point of input of sensory information from the beak and mouth region) which is connected via the quinto-frontal tract to the nucleus basalis of the basolateral forebrain. The nucleus basalis gives rise to ascending fibres (the tractus frontoarchistriaticus) which projects to the caudal neostriatum overlying the dorsolateral nucleus of the archistriatum. The archistriatum has been considered to be the homologue of the avian amygdala, but there is now strong anatomical and behavioural evidence (Zeier and Karten, 1971; Zeier, 1971; Wright and Spence, 1976) to suggest a division of the archistriatum into a 'limbic' region (archistriatum posterior and mediale) and somaticmotor region (archistriatum anterior and intermedium). The 'limbic' region then, is seen as being the true homologue of the amygdaloid nuclei of the mammalian brain, whereas the 'somaticmotor' region is probably more closely related to the sensory motor cortex of the mammal. The division is based largely on study of the efferent projections of the archistriatal nuclei. The tractus occipitomesencephalicus (TOM) which originates exclusively in the archistriatum and passes downwards into the brain, can be divided, on the basis of points of termination, into a hypothalamic component which projects from the limbic region of the archistriatum to the medial and lateral hypotalamic areas, and projections arising from the anterior and intermediate regions of the archistriatum passing, without termination in the hypothalamus, to the thalamic nuclei, optic tectum and brian stem sensory nuclei, and to a lesser degree to the spinal cord. This second group of fibres is considered to be similar in its course and distribution to the pyramidal tract of the mammal. It should be noted that the anterior region of the archistriatum (part of the somaticmotor region) is the only area receiving afferent connections, via the tractus frontoarchistriaticus, from the nucleus basalis (Zeier and Karten, 1971) which indicates that the earlier suggestion of Zeigler, Green and Karten (1969) that the nucleus basalis projects to the amygdala and from thence to the hypothalamus, was not strictly accurate. It would appear then that the 'Feeding System' circuit is connected rather to the motor than the 'hypothalamic' and limbic archistriatal regions. Figure 2.1 presents a schematic representation of this circuit redrawn from the accounts given in several of Zeigler's papers. (See particularly Zeigler, Green and Karten, 1969; Zeigler, 1974).

2.7 Experimental Investigations of Zeigler's Feeding System

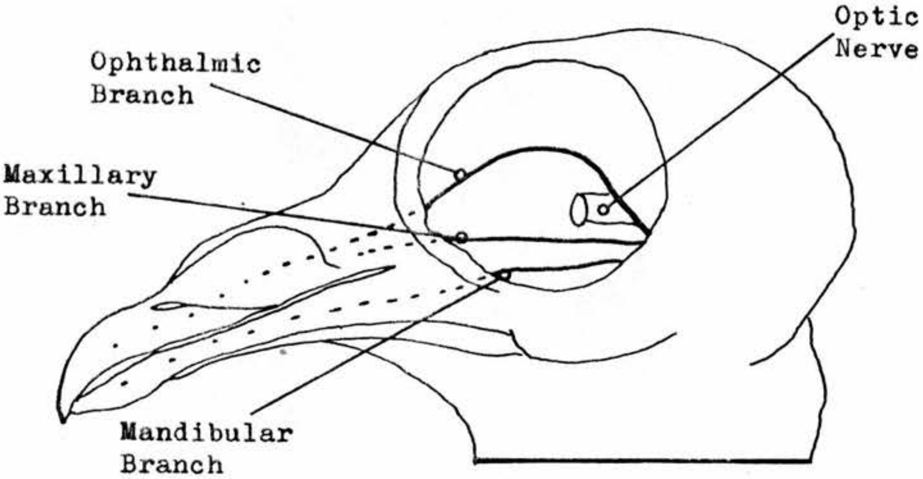
Zeigler, Green and Karten (1969) found that bilateral eletrolytic lesions placed in all of the above mentioned structures lead to periods of aphagia and hypophagia the severity of which appeared to be related to the size of the area of damage produced. They also found evidence of disruption of drinking behaviour, but it did seem likely that those effects were secondary to the disruption of food intake regulation leading to an effect on water balance (McFarland, 1964) as the extent of the reduction of water intake was no greater than would be expected in intact animals deprived of food. No indication is given in the paper (Zeigler et al. 1969) of the nature of the feeding deficits, but it would seem reasonable to suggest, in view of the structures which were being lesioned, that aphagia might be due to a simple mechanical problem, either of sensory information or of motor output, leading to a physical inability to feed. This interpretation would be supported by the study of Zeier (1971) on operant responding after archistriatal lesions in pigeons. He found, after lesions of the somaticmotor archistriatum which he considered to be the area referred to as the

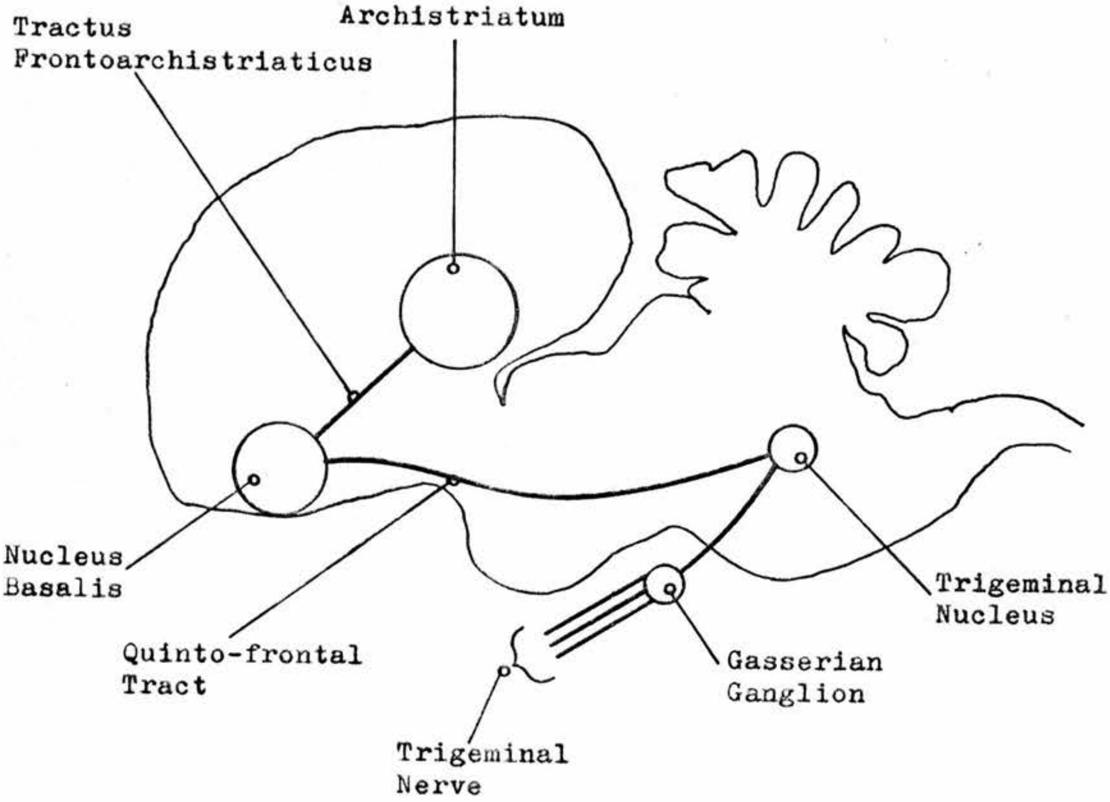
FIGURE 2.2

Passage of the three branches of the trigeminal nerve (Redrawn from Zeigler et al, 1975).

FIGURE 2.1

Schematic diagram of Zeigler's "Feeding system" in the avian brain.


Optic
Nerve
Ophthalmic
Branch
Maxillary
Branch
Mandibular
Branch


Tractus
Frontoarchistriaticus
Archistriatum
Nucleus
Basalis
Quinto-frontal
Tract
Trigeminal
Nerve
Gasserian
Ganglion
Trigeminal
Nucleus

dorso-lateral archistriatum by Zeigler et al., that the birds showed disturbances of pecking and feeding whereby they were unable to keep the grains of food within their mouths to be swallowed. The birds had to be fed by hand for the week which was required for recovery, but it was also noted that they would perform in the operant situation and attempt to eat the grain earned during the 'aphagic' period. It is clear then, that if this is the sort of deficit which was encountered by Zeigler at al. after archistriatal and other lesions, this would not be what we would normally describe as 'aphagia' as the term would be applied to the deficits produced by lateral hypothalamic lesions in rodents. That is, the deficit would seem to be purely mechanical rather than motivotional if the animals would still work for food.

The findings of Zeigler et al. (1969) were repeated and extended by Zeigler and Karten (1973(a)). They found that lesions of the trigeminal nucleus, quinto-frontal tract and the nucleus basalis led to marked aphagia and adipsia, but again the conclusion was that the adipsia was a secondary effect of reduced food intake, being no more marked than that seen during equivalent food deprivation in intact birds. On recovery of feeding behaviour they noted that the normal restorative hyperphagia which would result from body weight loss due to food deprivation in an intact bird was not seen. Birds thus maintained a reduced body weight for prolonged periods after the operation. Zeigler and Karten (1973(b)) extended the above observations to attempt to describe the nature of these feeding disturbances. First of all, two pieces of evidence show that part of the story may indeed be a reduction in the animal's feeding efficiency due to mechanical inability to eat. Lesioned birds showed problems of sensory control of what is described as mandibulation. That is, they appear to be able to peck normally and also to swallow food, but the behavioural act which transfers the food item from the tip of the beak to the back of the mouth for swallowing is disrupted. One measure of feeding efficiency comes from tests in which the bird (deprived of food to a certain standard level of weight loss relative to the previous baseline level, so that motivation due to deprivation was equated) were observed pecking at a quantity of food material in a test cage. The other measure of efficiency came from a computation of the ratio of number of feeding responses made as measured by a photocell monitor device described by Zeigler and Feldstein (1971) to amount of food consumed in the home cage.

The photocell feeding monitor device was also used to give some additional information about the nature and basis of the initial aphagia of the birds. It was realized that the mechanical disruption might be all that was needed to explain the changes in food intake after the lesion. However, if this was the case one would expect to find many feeding responses but little or no food consumed, whereas a true motivational disturbance leading to a reduction in the responsiveness of the animal to the food offered would show the low or zero intake to be associated with little attempt to feed. The latter appeared to be the case. Immediately after the operation the birds showed little or no food intake and also little sign of any attempt to approach and peck at the food.

In addition to this, it was found that the lesions of these quintofrontal structures (trigeminal nucleus, quintofrontal tract and nucleus basalis) led to the abolition of operant responses for food reinforcement which could not be attributed to the motor deficit as water reinforced responding was little affected. Not only did the birds not perform the learned response for food, but they also failed to respond when the food hopper was presented non-contingently. However, the birds would attempt to eat a supplementary food ration offered in the home cage or in the operant chamber. It is difficult to know exactly what is meant by 'aphagia' therefore, and it is possible that the absence of responding in the operant task might be due to the availability of this supplement (Wright, 1975). It has also been shown recently (Mitchell et al., 1973; Mitchell and White, 1977) that all food sources are not regarded as being equal by animals, but that past experience and familiarity with a particular source is a factor of greater importance than a work requirement in determining which food source or sources would be made use of.

Essentially similar effects are found as a result of lesions of the archistriatum. Zeigler, Silver and Karten (1969) (cited in Zeigler, 1976) reported effects of archistriatal lesions in a small group of pigeons to be again initial aphagia, reduction in feeding efficiency and reduction in responsiveness to food. Results were reported to be difficult to interpret as the exact extent of the lesion was difficult to control. Effects therefore might be due to damage done to distinct nuclear groups or to efferent fibre tracts or to both. One of the birds was apparently aphagic for sixteen days (data is presented for two birds with archistriatal lesions in Zeigler (1976)) and did not recover. The other was aphagic for about 9 days and then showed a fairly rapid restoration of pre-operative body weight as a result of a very marked degree of compensatory hyperphagia. Feeding efficiency was obviously greatly reduced in the second animal after recovery of spontaneous food intake, as evidenced by a high ratio of pecks recorded to food consumed, but the normal level had returned by about the third post-operative week (within about 10 days of the return of feeding). In view of the absence of any published clear anatomical data to confirm that the lesions were indeed in the dorsolateral (somaticmotor) archistriatum, and the lack of actual behavioural information on more than 2 birds showing vastly different effects, conclusions would be difficult. It is possible that the bird which did not recover might have suffered damage to the lateral lumbic region of the archistriatum reported by Zeier (1971) to produce marked effects on food intake and arousal.

Investigations of the effects of damage to the descending projections of the archistriatum in the pigeon have been carried out by Levine (1976) (cited by Zeigler, 1976). There does seem to be some discrepancy however between the description of these data and the tabulated data themselves. These data are described as again showing a picture of reduced responsiveness to food resulting in aphagia, followed by marked reduction in efficiency of feeding as indicated by observations of birds feeding in a test situation after return of voluntary intake.

Tables 2.1 and 2.2 show a summary of these data as presented by Zeigler (1976). It should be noted first of all that although the data collected from observations of birds feeding does show a marked reduction in efficiency as indicated by the ratio of pecks to grains obtained, the picture shown by the home cage feeding records is quite different. From the information given on food intake and pecking

TABLE 2.1

OBSERVATIONAL TESTS OF FEEDING EFFICIENCY AFTER TOM LESIONS IN PIGEONS

(Modified from Table VII, Zeigler, 1976)

BIRDS	Pre-operative			Post-operative		
	No.of Pecking Responses	Grains Obtained (%)	Pecks/ Grain	No.of Pecking Responses	Grains Obtained (%)	Pecks/ Grains
188	1583	99	1.8	7411	45	18.2
321	1162	99	1.5	4701	97	8.1
337	763	100	1.3	3463	51	13.6
436	1084	80	1.5	2731	52	7.5
535	932	99	1.3	3035	99	5.1
Mean:			1.48			10.50
S.D.:			0.205			5.311

TABLE 2.2

PHOTOCELL MONITORED FEEDING EFFICIENCY AFTER TOM LESIONS IN PIGEONS

(Modified from Table VI, Zeigler, 1976)

BIRDS	Pre-operative			Post-operative (Feeding)		
	Total Food Intake (grams)	Total Pecking Responses	Pecks/ Grain	Total Food Intake (Grams)	Total Pecking Responses	Pecks/ Grain
524	242	13656	56	85	3885	45
541	145	15420	106	144	52755	366
543	187	10437	56	99	3831	39
545	178	17065	96	81	4272	52
559	235	19689	84	88	5778	65
562	219	15599	71	167	9383	56
565	212	34667	163	164	18851	114
568	138	9405	68	161	8822	55
Mean:			87.5			99.0
S.D.:			35.38			110.31

responses for the pre-operative 7 days and the 7 days after recovery of feeding we can compute the ratio of number of pecks to grams of food ingested. Discarding two animals which did not recover from the lesions we see that the mean number of pecks per gram was 87.5 before the surgery and 99 after. However the larger mean in the post-operative case is due to the score of only one bird, the other seven actually showing lower ratios after surgery than before. The two measures of feeding efficiency come from two different groups of birds so that cross comparisons cannot be made but, if it is assumed that the variance shown by the two groups is similar, one of two conclusions must be made. Either the effect of the lesion is to enhance the feeding efficiency of the animals or (more likely) the scores derived from the photocell feeding monitor do not provide a reliable measure of feeding efficiency. It is quite probable that the animals suffering from some mandibulation deficit might adopt a different strategy from the intact birds. For example, Wright (1969) often observed his aphagic birds (aphagia produced by diencephalic lesions) to feed by pushing the whole open beak into the grain and allowing food to fall into the back of the mouth from whence it could be swallowed. As the output from Zeigler's feeding monitor devices was the number of pecks, we must assume that the system operates by counting the number of times the photocell beam is broken. Thus a count of one would be produced by one single discrete peck or by the bird holding its head in the box for any prolonged period. It is noted (Zeigler, 1976) that the efficiency deficit produced by lesions of this descending tract (the tractus oclipitomesencephalicus - TOM) is a result of the mandibulation problem, but also of a failure to set the beak open to the correct amount when a peck is made. Thus the animal may peck with the beak completely shut or unsufficiently open for the size of the grain. It is not clear however that this could account for the differences between the observational and photocell monitored measures of efficiency.

Wright and Spence (1976) reported the effect of section of the TOM in the Ring dove using a blade inserted into the brain rather than an electrolytic lesion technique. Both the hypothalamic and non-hypothalamic components of the tract were cut as was unavoidably the anterior commissure. Mid-line section of the anterior commissure in a second group of birds was therefore also required to control for the effects of this damage. The bulk of the discussion in this paper refers to the effects of this procedure on emotional behaviour and responsiveness, but observations of feeding behaviour were also reported. There was no sign of aphagia or feeding difficulties in any of the animals and indeed a pronounced though transient hyperphagia was observed in some immediately after the surgery. That the tract had indeed been cut was later confirmed histologically. These findings seem to be in conflict with the reported effects of lesion of the TOM described above. The reason for the use of the knife cut technique rather than a lesion technique in the study of Wright and Spence (1976) was that it was found that the insertion of an electrode served to physically depress the fibre tract and thus a lesion aimed to destroy the tract almost always resulted in damage to the surrounding tissue leaving the fibres of passage intact. No histological data was presented by Zeigler to indicate the success of Levine's procedures, so the possibility exists that the aphagia and other effects reported to be a result of TOM damage may well be due to disruption of some surrounding nuclear group at the point of lesion placement.

2.8 The Sensory Trigeminal Nerve

The final item of Zeigler's trigeminal feeding system to be considered here is the sensory trigeminal nerve itself. All of the above mentioned effects of damage to the central trigeminal system can be divided into those which could be described as motivational and others which are sensorimotor (Lashley, 1938). Thus deficits of feeding efficiency are clearly caused by some effect on the sensory or motor control of the feeding act, whereas a reduction in the tendency to approach and peck at food or a reduced level of operant responding seem more likely to be caused by a motivotional deficit. Unfortunately both motivational and sensory motor disturbances appear to be inextricably associated with damage in each of the brain regions making up the feeding system, according to Zeigler's findings. Zeigler suggests that this is either due to the fact that the fundamental distinction between sensorimotor and motivotional is not a real distinction, in the sense of being part of the actual neural organization of the behaviour, or that the neural system subserving the two aspects of feeding are so completely anatomically overlapping and interconnected that the crude techniques of brain lesion placement cannot investigate one without disturbing the other. It was hoped therefore that section of the peripheral sensory nerve would produce a deficit in feeding behaviour which was only sensory, and thus the first step towards the dissociation of sensory and motivational effects might be achieved (Zeigler, 1976; 1977).

2.8(a) Anatomy of the Trigeminal Nerve

Figure 2.2 redrawn from Zeigler, Miller and Levine (1975) shows the gross anatomy of ;the trigeminal nerve and the regions which are innervated by it. Branches of the nerve carry sensory information about touch, pressure and joint articulation from the upper and lower mandibles (Zeigler and Witkovsky, 1968; Zeigler, Miller and Levine, 1975). There does not appear to be any trigeminal innervation of the tongue. It can be seen from the nature of the trigeminal projections that the loss of sensory information from this nerve could have a profound effect on the control of feeding behaviour. Of importance however is the fact that the sensory elements of the nerve can be readily cut in the bird without loss of trigeminal motor innervation, thus making the bird a particularly useful subject for such denervation studies.

2.8(b) Effects of Trigeminal Section

Accounts of the effect of trigeminal nerve section on feeding behaviour in the pigeon have been given by Zeigler and Feldstein (1971), Zeigler (1973, 1975(a) and (b)) and by Zeigler, Miller and Levine (1975) and the experiments and conclusions have been reviewed in several places (Zeigler, 1974, 1976, 1977). The following account therefore will be presented in an order which will not necessarily always be the chronological order in which the findings appeared, in an attempt to summarize the nature of the deficits reported and the conclusions which have been drawn by Zeigler and his co-workers as to the significance of these effects.

2.8(c) Trigeminal Section and Food Intake

The first and most obvious effect of trigeminal nerve section was to produce periods of aphagia in the birds which were reported to be every bit as profound and lasting as those which were produced by central lesions (as discussed above). Bilateral section of all of the three branches of the nerve has been variously reported to produce periods of aphagia from 1-6 weeks (Zeigler, 1974) and from 1-8 weeks (Zeigler, 1976) but the original data first published in 1973 and then reproduced in 1975 indicate that the most marked example of aphagia persisted for 40 days. When this animal is excluded from the group, which would seem reasonable as it was clearly a very extreme case requiring to be maintained by intubation of a liquid diet, we find that the mean is 7 days of aphagia with standard deviation of 2.4 (Zeigler, 1973 Table I; Zeigler, 1975 Table II). Bilateral section of two branches of the nerve was found to produce aphagic effects ranging from 2-4 days.

The only data on food intake and body weight presented for an individual animal are those of this above mentioned extreme case (first presented in Zeigler (1973) fig. 2, and reproduced four times since then). On the first occasion on which the figure appears it is referred to as the "case showing the greatest deficit". Elsewhere the figure is described as referring to "a single bird" (1974) and to "a case typical of those showing pronounced disruption of food intake." The effect of the procedure is very variable then, and indeed much more variable than would be indicated by a casual reading of some of Zeigler's more recent reviews. This variability is remarkable in that we are not dealing with a lesion procedure of uncertain size and location, but with a highly defined loss of sensory information.

The magnitude of the effect appears to be a function of the number of branches which are bilaterally sectioned, damage to all three producing the greatest deficit. Unilateral nerve section on the other hand appears to have very little effect. Of interest too is the fact that the effect of nerve section appears to be cumulative and that this cumulation will be seen even if the bird is allowed to recover from the effects of the first section before the second is carried out and so on. That is, if one branch of the nerve is sectioned bilaterally and the animal allowed to recover, the effect of cutting a further branch will be that which would normally be encountered after one stage section of two branches.

Aphagia is followed by prolonged periods of hypo-phagia. Thus the birds are slow to recover their pre-operative weight and fail to show the degree of restorative hyperphagia which one would expect to find in intact birds deprived of food to the same degree of body weight loss.

There is some evidence of reduction in drinking, but it can be shown that this reduction is no greater than that which would occur as a result of food deprivation in intact animals. Indeed some birds show increases in water intake immediately after surgery. Thus here, as with the central lesions, the disruption of water intake can be seen as a secondary consequence of the absence or reduction in food intake (Zeigler et al., 1972; McFarland, 1964).

2.8(d) Feeding Efficiency after Trigeminal Section

As might be expected the section of the trigeminal nerve leads to gross disruption of the sensory control of the consummatory act of feeding. As with lesions of the trigeminal nucleus and the nucleus basalis, the major deficit appears to be associated with mandibulation. The birds can swallow grains normally and can also peck normally, but the transfer of the grain from the front to the back of the mouth is rendered difficult due, presumably, to the lack of sensory feedback. In addition to the mandibulation problem there was also some evidence (reported in the papers from 1975 but not reported in Zeigler (1973) that the ballistic control of pecking was also affected. There was a slight tendency, most marked in the three branch condition, for the birds to peck slightly to the side of the grain. However, this disturbance was not nearly as marked as that of mandibulation.

As noted above, these deafferentiation experiments were performed with the expectation that the sensorimotor deficit would be all that would be found, in contrast to the central lesions which also appeared to lead to some loss of motivational arousal or responsiveness to food. Thus when the feeding behaviour of the post-operative aphagic animals was monitored in the home cage using the photocell device, one would expect to find a large number of feeding responses as the animal repeatedly tried to consume the food but failed because of its sensorimotor disability. However, post-operative aphagia was associated with a marked reduction in the number of feeding responses attempted, as was found in the case of lesions to the central trigeminal structures discussed above. Zeigler therefore concluded that even at the level of the peripheral nerve it was not possible to dissociate the sensory and motor deficits from that of motivation. The aphagia is not a simple result of the reduction in the feeding efficiency, but has also to do with a reduction in the animals level of responsiveness to food.

As discussed above, the photocell device also possibly gives information on the post-recovery feeding efficiency of the animals which can be compared with the estimates derived from the feeding tests in the observational situation. From the data of Zeigler (1975) it can be seen that the mean number of responses per gram before the operation is 123 and after is 264.1. Again however, we find that the bulk of this difference between the means comes from one animal (No.61 which we have previously suggested to be too extreme a case to be reasonably considered with the others). If that one animal is removed the mean ratios become 119 pre-operatively and 136.7 post operatively. Further, two of the animals show a decreased ratio of pecks to grains of food consumed after the operation, so it can be seen (as with Levine's study of the effect of lesions of the TOM described above) that the photocell monitors data ~~does~~ not give a reliable impression of feeding efficiency if the animals behaviour in the observational "pick-up" tests are to be taken as the standard. However, it is also possible that the very gross effects seen in the observational study might be less obvious in animals feeding from large quantities of grain in the home cage. The difficulty encountered in trying to swallow one grain out of a full food box may be much less than that of picking up single grains spread out over the floor of a test cage. The lack of correspondence however does cast doubt on the use of the photocell device.

2.8(e) Effect of Food Deprivation on Trigeminal Sectioned Animals

Section of the trigeminal nerve was also shown to affect the way in which birds responded to enforced food deprivation and body weight loss. Two situations were used by Zeigler to investigate this relationship. Birds which had received bilateral section of the trigeminal nerve were exposed to various levels of food deprivation and weight loss and the way in which this influenced their subsequent feeding behaviour was observed. It was found that the denervated birds responded to deprivation in essentially the same way as did intact birds by decreasing their latency to approach food and to start feeding and by increasing their food intake when food became available so as to tend to restore the pre-deprivation body weight. This facilitatory effect of food deprivation on feeding response however was only obvious at the higher levels of deprivation (i.e. reductions of 20% and 30% on the ad libitum weight). At the level of 10% of ad libitum weight however the birds seemed to show much less response to deprivation than did the control (intact) animals.

Similarly birds which were reduced to 80% of their ad libitum weight and then subjected to bilateral trigeminal section showed less effect of the surgery (i.e. shorter periods of aphagia), but they were still slower to regain the pre-deprivation body weight than were controls, and would remain with a chronically lowered body weight for long periods. Thus it would appear that the short term responsiveness to deprivation in the deafferentiated birds is much like that of the intact or surgical control birds, but the long term control of body weight does seem to be lacking. The response of the animals to food appears to be reduced by the effect of the nerve section, but this effect can be overcome by other stimuli to feed, like level of deprivation. As those other stimuli become less important however (return of body weight) the overall reduction in feeding motivation becomes evident.

2.8(f) Operant Responding after Trigeminal Section

A further investigation was designed to see whether or not the nerve sectioned animals would perform an operant response which was previously learned for a food reward. Indeed if the nerve section serves to reduce the bird's feeding motivation we would expect a clear effect on operant responding. What is apparently found however, is that the birds, immediately after the operation will respond in the operant situation for food at approximately the pre-operative level, but will not consume or attempt to consume the reinforcement when it is earned. (Zeigler and Feldstein, 1971; Zeigler, 1975(b)). This is clearly a very paradoxical finding which is difficult to account for on the basis of a theory of the effect of trigeminal nerve section which involves a reduction in feeding motivation. The results are discussed by Zeigler (1975(b) in terms of a dissociation between operant and consummatory responding in a motivational sense.

> "These results suggest that the mechanisms underlying operant key pecking involves different neural structures than those involved in the performance of the consummatory response."

and

> "the neural processes underlying consummatory responding to food and those controlling food reinforced instrumental responses may be experimentally dissociated."
>
> Zeigler (1975(b)

2.8(g) Zeigler's Proposed Model of the Effect of Trigeminal Section

The reduced responsiveness to food as evidenced by the reduced number of approach responses recorded by the photocell feeding monitor devices during the aphagic period, taken along with the reduced effectiveness of food deprivation to facilitate feeding behaviour after nerve section cannot easily be explained, Zeigler argues, simply in terms of the obvious effects of nerve section on sensory and motor control of mandibulation. The reduced food intake of the nerve sectioned animals is due, not only to the mechanical difficulties experienced as a result of the lack of trigeminal feedback, but also to a markedly reduced tendency for the animals to approach and attempt to eat the food offered. Zeigler (1975(a)) offers three possible hypotheses to account for the reduced approach tendency after nerve section.

1) That nerve section leads to painful peripheral sensations associated with pecking which serve to inhibit the attempts. This seems unlikely in view of the fact that the animals will perform a key peck operant immediately after surgery (Zeigler and Feldstein, 1971; Zeigler, 1975(b)) and also the fact that the consummatory response of drinking might also be expected to be inhibited by such painful sensations, but is in fact well nigh unaffected by nerve section. The latter point is perhaps less convincing in view of the fact that the consummatory response of feeding and drinking are so distinct.

2) That the lack of success in feeding as a result of the mechanical inability to mandibulate the grains, leads to a reduction in attempts to feed which is analogous to extinction due to non-reward in an operant situation. However, animals which are maintained at 80% of their ad libitum body weight will persist, making hundreds of unsuccessful attempts, in trying to feed on a grain material although their success rate is low, which would tend to make an extinction hypothesis less likely.

3) That, in addition to the obvious phasic trigeminal feedback which is associated with the consummatory act of feeding, the trigeminal nerve also gives rise to a tonic level of input to the feeding system which contributes to the overall level of feeding tendency of the birds. This third hypothesis is the one which Zeigler espouses (Zeigler, 1977).

2.8(h) Phasic and Tonic Components of Trigeminal Input

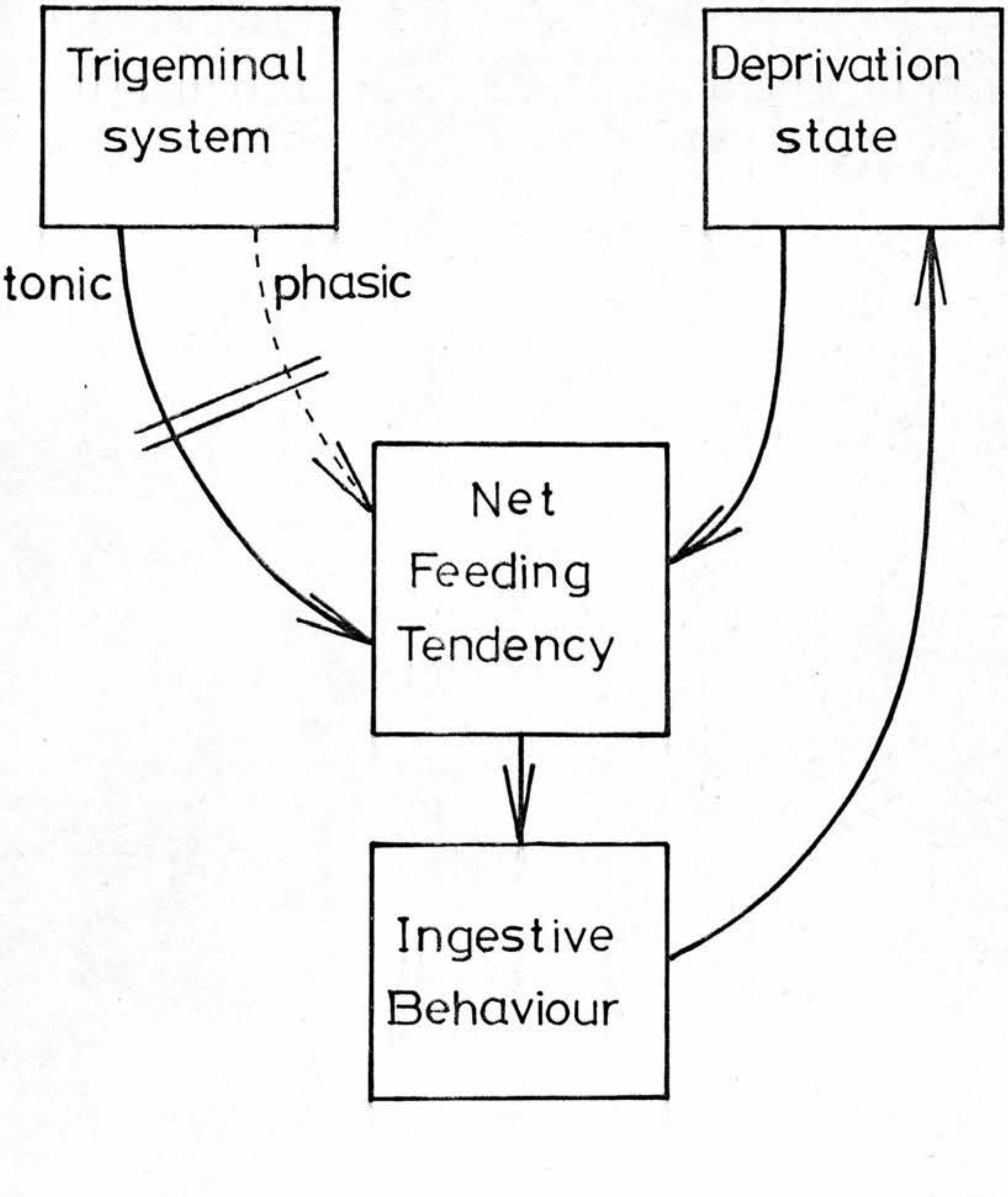
Part of the role of the trigeminal nerve then, will be to provide the sensory feedback which is associated with the act of feeding. This feedback provides information by which the bird mechanically controls its feeding behaviour (e.g. mandibulation) and selects appropriate food material and also serves to maintain ongoing feeding by way of a positive feedback loop (McFarland and McFarland, 1968; Wiepkema, 1971). Another role of the trigeminal system however, is to contribute a certain tonic level of neural excitation which is part of the net feeding tendency of the animal. Thus the aphagia and hypophagia which are found as a result of section of the trigeminal nerve can be seen as being a result of these tonic and phasic feedbacks respectively.

Cutting the nerve leads to a reduction of the animals net feeding tendency to a point below that at which feeding will be initiated. This aphagia results in a loss of body weight which has the effect of increasing the net feeding tendency. Thus, after a certain degree of deprivation has occurred, the effect of this deprivation will be to goad the animal into beginning to eat again. However the phasic trigeminal excitation which normally accompanies feeding behaviour and serves to cause feeding to continue and to give it momentum (Toates and Archer, 1978) will be absent. Feeding may be stimulated to start by deprivation then, but will not continue as it should and a period of hyp6phagia will result.

Figure 2.3 provides a summary of Zeigler's model as it can be understood from Zeigler (1975(a)). This model apparently accounts for the gross aphagia and hypophagia which are found after the section

FIGURE 2.3

Summary of Zeigler's proposed model of trigeminal aphagia (see text).


Trigeminal system
Deprivation state
tonic
phasic
Net Feeding Tendency
Ingestive Behaviour

of the trigeminal nerve and are associated with a reduced tendency to approach food. It also accounts for the way in which level of deprivation interacts with the effect of nerve section such that a reduction in body weight will overcome the effect of the surgery, but as normal body weight is approached the hypophagia returned leading to a slower final return to the pre-deprivation weight.

It does not account for the fact that an aphagic bird will continue to perform an operant for food, the use of terms like "dissociation" (Zeigler, 1975(b)) serving only to describe the effect and not to explain it. Neither does the model account for the fact that the effect of sequestial surgical procedures, cutting one branch of the nerve at a time, should lead to a cumulative effect even when the animal has recovered from the first operation before the next is performed. Table 2.3 presents a summary of the trigeminal section research along with Zeigler's conclusions from it.

Chapters 4 of the present study will describe some attempts to repeat Zeigler's procedures using the Ring dove. Chapter 5 will present some additional information from studies of the Ring dove which suggest a possible alternative interpretation of the effects of sensory nerve section which, it is felt, better accounts for the results reported both here and by Zeigler, and also accounts for some of the more paradoxical effects (e.g. operant responding in the apparent absence of feeding motivation) which Zeigler's model does not deal with.

TABLE 2.3

SUMMARY OF TRIGEMINAL SECTION EFFECTS IN THE PIGEON

	Observations	Results	Conclusions	Sources
1	**Effect of nerve section on food intake and body weight.**	Aphagia and weight loss followed by hypophagia. Absence of compensatory overeating to return body weight to normal after return of feeding behaviour.	Gross disruption of food intake control (similar to aphagia produced by central lesions).	Zeigler (1973) Zeigler (1974) (R) Zeigler (1975 (a))(R) Zeigler (1976) (R) Zeigler (1977) (R)
2	**Observational tests of feeding efficiency.**	Marked decrease in feeding efficiency produced by mechanical failures of mandibulation, and also balistic errors of pecking. No effect on swalling. No change in frequency of pecking in test session.	Nerve section disrupts the sensorimotor co-ordination of feeding.	Zeigler (1973) Zeigler (1974) (R) Zeigler, Miller & Levine (1975) Zeigler (1976) (R) Zeigler (1977)
3	**Monitoring of feeding behaviour in home cage using photocell "feedometer".**	Reduction in number of pecks directed at food in the post-operative aphagic period. Increase in the ratio of pecks at food to amount of food consumed in the period after return of voluntary food intake.	Fewer approach responses to food hopper suggests reduction in feeding motivation or "responsiveness" to food, in addition to the sensorimotor disturbance. Increase in pecks/food ratio suggests reduction in efficiency of feeding (agreeing with (2) above).	Zeigler (1975(a)) Zeigler (1976)(R) Zeigler (1977)(R)
	Effect of food deprivation on feeding behaviour after nerve section.	Deprivation produces enhancement of responsiveness to food in nerve section as in normal birds. The compensation is not as great in the nerve sectioned birds at the lower levels of deprivation, but appears to be the same at the higher levels.	Gross response to food deprivation is present after nerve section. Thus, deprivation contributes, as it did, to the animal's net feeding tendency, but the overall long term responsiveness to food is reduced.	Zeigler (1975(a)) Zeigler (1976) (R) Zeigler (1977) (R)

	Observations	Results	Conclusions	Sources
5	Effect of nerve section after enforced body weight loss.	Degree of aphagia and hypophagia is greatly reduced. Effect still present in the long term in that sectioned birds are slower to regain weight than controls deprived to equivalent body weight and then allowed to refeed.	Again, implies that facilitatory effect of body weight loss is present only in the short term. Reduction in overall feeding tendency.	Zeigler (1975) Zeigler (1976) (R) Zeigler (1977) (R)
6	Performance of pre-operatively acquired operant for a food reward after nerve section.	Immediately after surgery birds will continue to perform a key pecking response previously associated with food reward, but will not consume the food which is earned. This responding decays with time after the surgery if no food is consumed, the decay looking identical to that seen during extinction by non-reward.	As the animals will peck at the key, the absence of feeding is not a result of pain due to pecking per se. The fact that the animal performs the operant but does not eat the food reward, implies an experimental dissociation of operant and consummatory responses as a result of nerve section.	Zeigler and Feldstein(1971) Zeigler (1975(b)) Zeigler (1976) (R) Zeigler (1977) (R)
7	Observations of feeding patterns after nerve section.	Reduction in meal frequency and alteration in diurnal distribution of feeding towards greater morning intake. This pattern may persist for several weeks.	The pattern of feeding behaviour shown by the nerve section animals is similar to that observed in animals deprived of food. However, body weight loss is not recovered and the pattern persists for a prolonged period. Again, disruption of restorative feeding.	Miller (1974) (U) Miller & Zeigler (1974)(U) Zeigler (1975(a) (R) Zeigler (1976) (R)

U: Unpublished R: Review

2.9 Chapter Summary

Brain mechanisms and feeding behaviour in birds was discussed with particular reference to the difficulty encountered in the replication of early rodent observations using birds. The vast differences in the anatomy of the mammalian and avian brain were illustrated by the example of the visual system to indicate that homologous functions in the two groups can be dealt with by different structural organization.

The work of Zeigler and his co-workers was discussed as being an example of a research program not guided by preconceptions derived by the mammalian literature. Particular attention was given to the studies of the importance of the trigeminal sensory nerve in the control of feeding as being an area in which more study was required to clarify some anomalies.

CHAPTER 3

3.1 The Study of Feeding Behaviour Patterns

The experimental study of animal feeding patterns by automatic recording techniques has a long history dating back to the work of Richter (1927) on rats, who used a device which recorded the presence of the whole animal in a feeding chamber. With this system Richter was able to show the characteristic periodicity of feeding behaviour and showed how this was associated both with gross body activity and with stomach contractions. Since then, a great variety of different means of transducing feeding behaviour has been devised which can broadly be divided into three types.

1) Perhaps the most obvious is the use of some operant technique. "Skinner Boxes" were first devised so that small quantities of food reward could be offered to an animal for the performance of a particular task. It would be easy then, to record the occurence of a response for food, or to note the time at which a reinforcement is delivered and thus to follow the animal's pattern of feeding (Teitelbaum and Campbell, 1958; Balagura and Coscina, 1968; Duncan et al., 1970; Duncan and Hughes, 1972; Kenny and Mook, 1974).

2) The second method is to continuously monitor the amount of material in a food hopper or to record the removal of discrete amounts of food (usually standard food pellets) from the hopper (Kissileff, 1970; Panksepp, 1973; Decastro, 1974; Davies, 1977).

3) Finally, the presence of the animal at the feeding cup or box can be sensed in some way and the feeding behaviour recorded in terms of time spent feeding rather than amount ingested. An example of

this method would obviously include the early work of Richter, although there are others (Richter, 1927; Fitzsimons, 1958; Van Hemel and Myer, 1968; Levitsky and Collier, 1968; Zeigler and Feldstein, 1971; Slater, 1974; Petersen, 1975, 1976).

It should be noted that the system which is used to measure feeding behaviour may have an effect on the results which are obtained. That is, the above distinctions are made on the basis of the experimenter's idea of the system, and may not reflect the way in which the animal sees or responds to the particular situation of food availability. For example, the systems used by Kissileff (1970) and Davies (1977) appear to be similar in that they both measure the number of food pellets consumed by the animal and note the time at which a pellet is taken. Kissileff's system involves the sensing of the presence of a food pellet in a tray using a photocell. When the pellet is removed by the animal, another is immediately dropped into its place. Davies' system involves the detection of an approach to the food box by the animal and the dispensing of a pellet each time the animal puts its head into the box. Similarly, the system used by Panksepp (1973) detects the approach of the animal to the food box (by sensing a touch on a brass plate above the opening to the box) and dispensing a pellet of food.

The Systems of Davies (1977) and Panksepp (1973) do not appear to be classical operant situations at first inspection then, but it is clear that both involve the performance of a certain behaviour in order to abtain food. It might be suggested that the approach to the food cup is hardly an arbitrary behaviour when it is feeding that is being measured, yet the animals will have to learn the necessary responses none the less. The main difference between these systems and that of Kissileff (1970) is that in the former cases food is not present until the animals make an approach to it, whereas in the latter case food is continuously present in the food cup.

It is clear that part of the stimulation to feed in laboratory animals is the presence of food. It will often be noted by those studying feeding behaviour in animals, that the daily filling of the food hopper or the removal of the hopper to be weighed and subsequent return to the cage, will stimulate a bout of feeding activity in the animals. The environmental prominance of food in the home cage then, may have a strong effect on the distribution of feeding behaviour.

Despite the early work of Richter (1927) and a few other studies which looked at temporal distribution of feeding in various conditions, it does seem to have been the case that the study of the mechanisms of feeding motivation up until the last decade, have involved the measurements of gross daily amounts of food eaten by animals in various experimental conditions. They have also tended to centre on the concept of "hunger" as being the motive force of feeding behaviour and have sought to produce it experimentally by regimes of food deprivation (Bolles, 1962; 1965; Megibow and Zeigler, 1968). The systematic study of the temporal distribution of feeding behaviour in free feeding, undeprived animals is best traced to the work of Le Magnen (Le Magnen and Tallon, 1966; Le Magnen and Devos, 1970) using rats. As a result of this early work it has been realized that a great deal of information can be gained about the operation of the mechanisms which underly feeding behaviour by studies of the way in which this behaviour is aggregated and distributed in the normal, freely feeding animal.

This chapter will describe the system which was developed to monitor the feeding behaviour of the Ring dove and discuss the basic organization and structure of that behaviour.

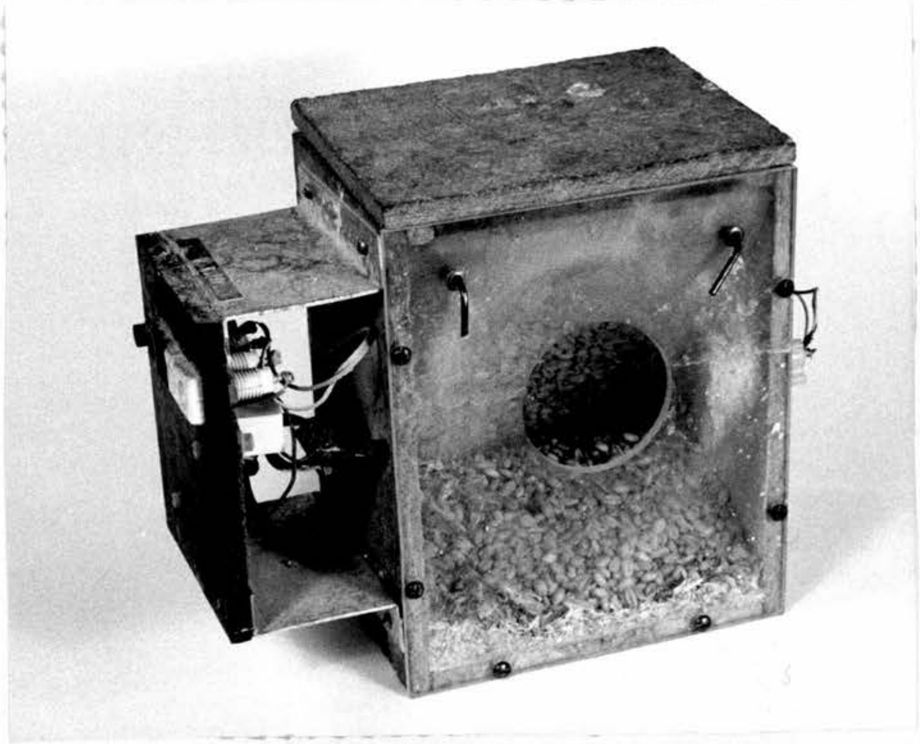
3.2 A System for the Recording of Feeding Behaviour

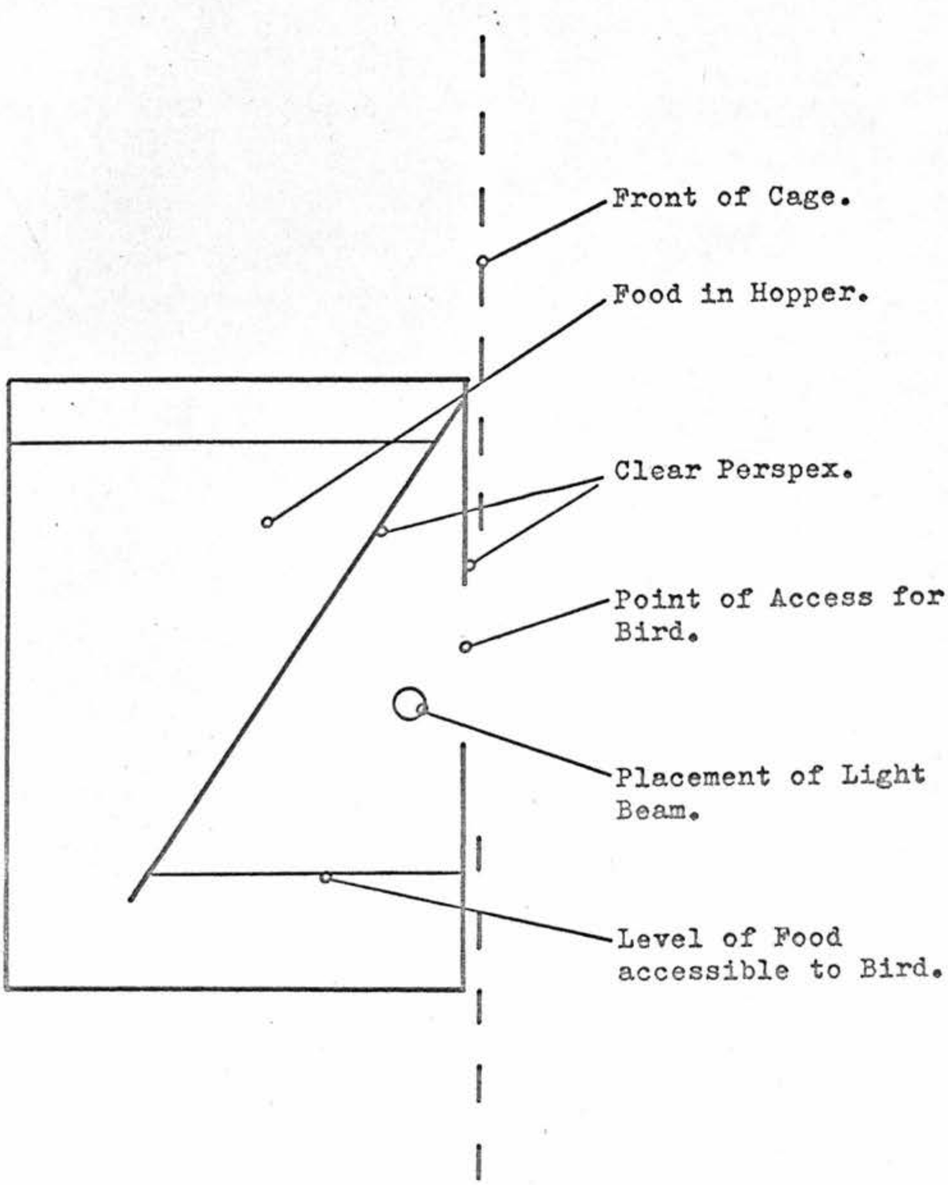
After experimentation with several other methods (for example, a capacitance proximity detector and a microswitch and door system) a simple photocell device, similar in conception to that described by Zeigler and Feldstein (1971), was finally used. The photoswitch circuit (Appendix I) was attached to the side of a standard food box and the lamp and photocell were positioned on either side of the entrance to the box so that the light beam was broken whenever the bird inserted its head to feed (Figure 3.1).

In the system developed by Zeigler and Feldstein (1971) the photobeam was so positioned that it was broken only by a downward peck into the food. Zeigler therefore hoped that the number of pecks could be counted and a fairly accurate measure of food intake could be made. However, observation of the feeding behaviour of doves in this laboratory indicated that many of the 'pecking' responses were not pecks but downward sweeps of the beak into the food which looked as if they were designed to scatter the food and search for preferred items. This behaviour was particularly obvious if a mixed grain diet was given to the birds rather than a single grain. As discussed above there is

FIGURE 3.1

Photograph and line drawing to illustrate photocell monitored food hoppers.




Front of Cage.
Food in Hopper.
Clear Perspex.
Point of Access for Bird.
Placement of Light Beam.
Level of Food accessible to Bird.

reason to be suspicious of the validity of a system designed to measure the number of pecks, as certain surgical manipulations which were otherwise shown to greatly reduce feeding efficiency did not vary obviously affect the ratio of pecks to food obtained as measured by this system. It was argued above that differences in strategy of feeding might differentially interact with the recording system to confuse the interpretation. Because of these difficulties it was felt better to simply use the photocell to register the time spent feeding by the animal.

The only other modification to the food box was the insertion of a sloping perspex panel to produce a gravity fed hopper system. This meant that a constant amount of food was continuously available for the birds and also that the level of food in the box was kept low so that the bird had to put its head fully in to reach the food.

Some means had now to be found of recording the output of the photoswitch circuit.

3.3 Recording of the Data

There was available in the Department an event recording system which comprised a keyboard attached to a data-logger and a "Facit" computer tape punch. The function of the system was to respond to the pressing of ony one key by printing, in ISO code, the time (in hours, minutes, seconds and tenths of seconds) at which the key press occurred, along with a label (an alphabetic character) to identify the key. As an event recorder this system had proved to be rather unsuitable for various reasons. When used independently however, the data-logger and tape punch appeared to be perfectly reliable. It was decided to use this unit as the basis of the feeding behaviour recording system.

An interface was built between the data-logger and photoswitch circuits by using modular solid state logic (Behavioural Research and Development Ltd.). Connection was made in such a way that the breaking of the light beam caused one channel of the logger to be activated and the time printed out, and remaking of the beam caused a second channel to respond. That is, a time on channel 'A' would indicate the start of a feeding period and the next time recorded on channel 'B' would indicate the end of that feeding period.

The logger had 16 input channels and thus could potentially record data from eight photoswitches connected in the above manner. A major drawback of the logger however, was the fact that it did not reliably handle inputs which occurred concurrently or very close in time. If a system was going to be developed then, to monitor the feeding behaviour of more than one animal it would always be possible that several channels might be active at the same moment and thus data might be lost or confused. Some means had to be derived to take account of the possibility that a number of animals would eat at once. This was done by elaboration of the solid state interface circuit. A time sampling circuit was added so that inputs to the logger would not arrive at a rate (determined empirically to be about 3 per second) greater than that at which the inputs were recognised.

3.4 The Basic Circuit

Sufficient logic equipment was available to build a four channel time sampling circuit, using 8 channels of the data-logger (four for "on" signals and four for "off" signals). In preliminary tests it was found that this system produced not so much a vast amount of data, but a vast amount of paper tape! The feeding behaviour of the bird was such that very short breaks in feeding (which were probably pauses between pecks, or movements of the bird's head) were recorded by the system. It was felt that this was not only a waste of computer tape but also made the data rather cumbersome. Much of this data would probably be discarded when some preliminary analysis could be carried out, so it would be better not recorded. The simplest way to get around the problem would be to interpose a delay in the recording circuit so that breaks in feeding behaviour which were shorter than a certain critical length would not be recognised by the data-logger. This was done by the addition of a timer and a sequence counter into each channel of the time sampling circuit. The final version of the circuit is presented in figure 3.2. Input to the system caused a change in state of a bistable and remaking of the beam caused the bistable to be reset. In the normal "off" state of the circuit the counter in the "smoothing" element of the system (that which caused the delay to be interposed) was held under inhibition and the sequence counter rested at a certain non-zero value. Change to the "on" state in the first bistable caused the sequence counter to be reset to zero and the timer to be released from inhibition, while the first bistable remained in the "on" condition on input to the sequence counter held it reset to zero. When the bistable changed back to the

FIGURE 3.2

Schematic diagram of logic circuit of feeding behaviour monitoring system.

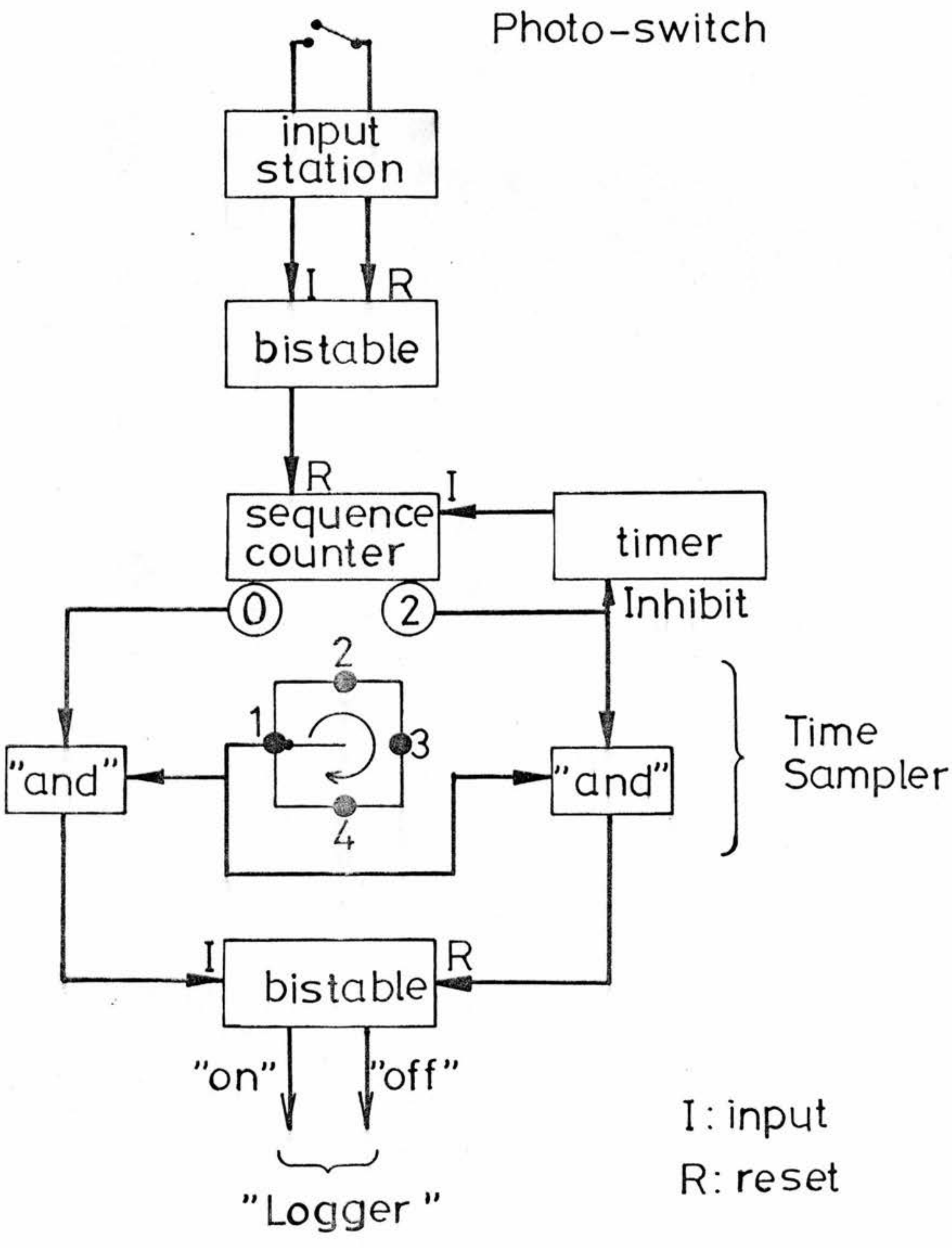


Photo-switch
input station
I
R
bistable
R
I
sequence counter
timer
0
2
Inhibit
2
1
3
4
"and"
"and"
Time Sampler
I
R
bistable
"on"
"off"
"Logger"
I: input
R: reset

"off" condition as the photobeam was remade, the reset signal to the sequence counter was removed and a "countdown" was started, the duration of which determined the duration of breaks which would be ignored. A signal from the time sampling counter while the sequence counter was in the "countdown" a "reset" condition would lead to a change in state of a second bistable and the output of a "start of feeding" signal to the data-logger. A second pulse from the time sampling counter when the sequence counter of the "smoothing" element had completed its "countdown" would cause the second bistable to be reset and an "end of feeding" signal to be recorded. If the animal returned to feed within the time of the pre-set delay however, the sequence counter would be reset to zero and the "countdown" would begin again at the next break. Thus short breaks in the feeding which were

attributable to the recording of inter-peck-intervals were "smoothed out" by this procedure.

It remained to determine however what would be an appropriate "smoothing interval" at which to set the system.

3.5 Estimation of an Appropriate "Smoothing Interval"

To determine such an estimate the continuous feeding data for one animal was recorded with the photoswitch connected as directly as possible to the data logger so that all breaks and pauses were noted.

3.5(a) Method

The subject bird (an adult female dove) was housed in one of the normal individual cages (40x35x45 cm) in a temperature regulated room designed for the housing of the birds. A 9 hour light cycle was in operation (9 am to 6 pm) and the temperature was held constant at about 70°F. The light cycle was kept to this short length as experience in this laboratory indicated that this served to keep the birds out of reproductive condition and thus prevent any problems which might otherwise have been caused for the measurement of feeding behaviour and food intake by spontaneous ovalation in the females or by the development of the reproductive apparatus in males or females, which can be brought about by the sounds of other birds.

The bird was visually isolated from other animals, but the normal colony sounds could be heard. Food was continuously available (from the modified photocell feeder) as was water and grit. The animal was allowed a few days to settle into the new cage (which was very similar to the individual cage in which it had previously been housed) and then continuous 24 hour records of feeding behaviour were collected for 4 days.

3.5(b) Analysis of Data

The data so collected was input to the Edinburgh Regional Computing Centre's multi-access computer (EMAS) and was ordered into a series of "on" times and "off" times. The "on" periods will be referred to as "bouts" of feeding and the "off" periods will be called inter-bout

-intervals (IBI). The data were then arranged into "meals" or groups of bouts on thekbasis that any interval of non-feeding which was longer than 5 minutes would be counted as an inter-meal-interval (IMI). This criterion of 5 minutes was chosen quite arbitrarily. A program was then written to simulate the effect on the data of the imposition of a series of "smoothing intervals" from 0 to 10 seconds in units of 0.2 of a second. That is, the data was modified so that certain short intervals were disregarded and the length of the "off" period was added to the bout length.

Figure 3.3 shows a plot of the number of bouts of feeding which would have been recorded if certain "smoothing intervals" had been set on the recording system. It can be seen that the number falls off very rapidly up to about 2 seconds at which point the rate of fall decreases and continues in a relatively linear way. Thus it would be the case that small variations in the "smoothing interval" below about 2 seconds would have a greater effect on the recorded bout frequency than would variations above two seconds. It might be suggested that the shape of the curve indicates the presence of two populations of inter-feeding intervals. The very short intervals (less than 2 seconds) of which there are a large number are probably inter-peck-intervals which we might do well to discard, the intervals of greater than 2 seconds then, being true inter-bout-intervals.

Figure 3.4 shows the mean inter-bout-interval as a function of the "smoothing interval." Again the curve is fairly linear for the higher values of "smoothing interval" but changes more rapidly over values from 0 to 2 or 3 seconds. Similarly, the curves of mean bout length (Figure 3.5) and mean meal size (Figure 3.6) show changes of

<u>FIGURE 3.3</u>

Number of bouts of feeding recorded as a function of the Smoothing Interval.

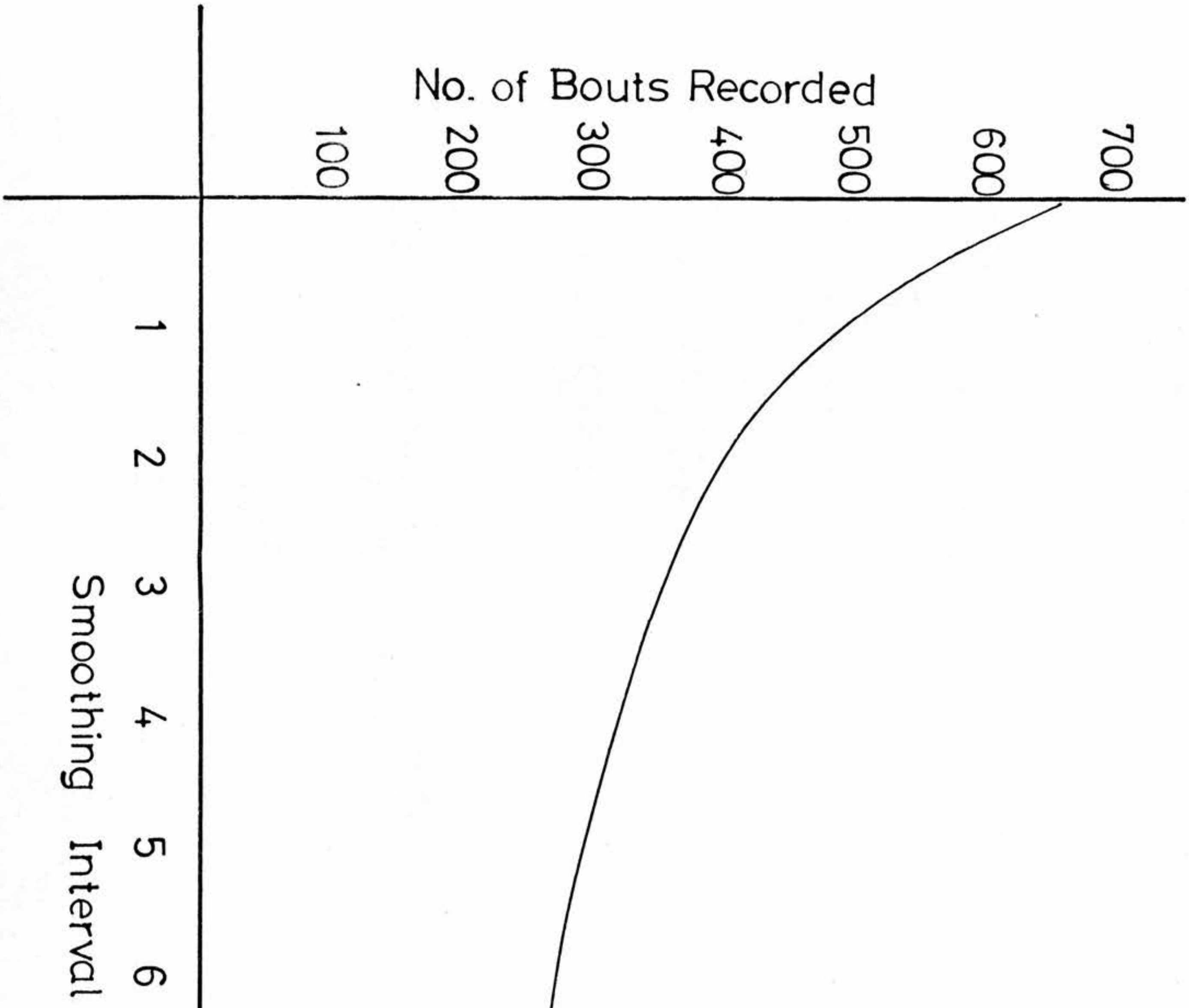

No. of Bouts Recorded
100
200
300
400
500
600
700
Smoothing Interval (secs)
1
2
3
4
5
6
7
8
9
10

FIGURE 3.4

Mean interval between bouts of feeding as a function of the Smoothing Interval.

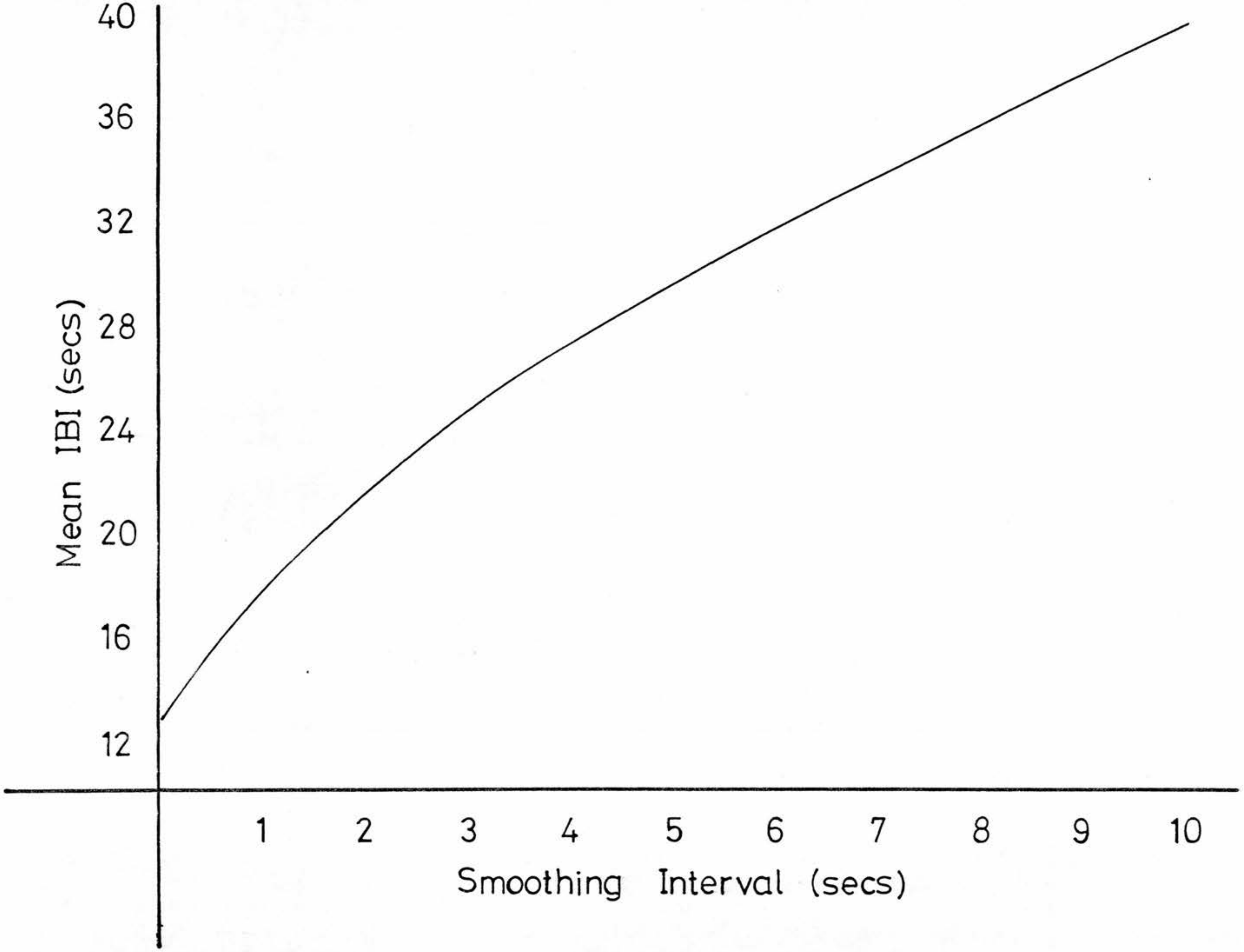

40
36
32
28
24
20
16
12
Mean IBI (secs)
1
2
3
4
5
6
7
8
9
10
Smoothing Interval (secs)

FIGURE 3.5

Mean length of feeding bouts as a function of the Smoothing Interval.

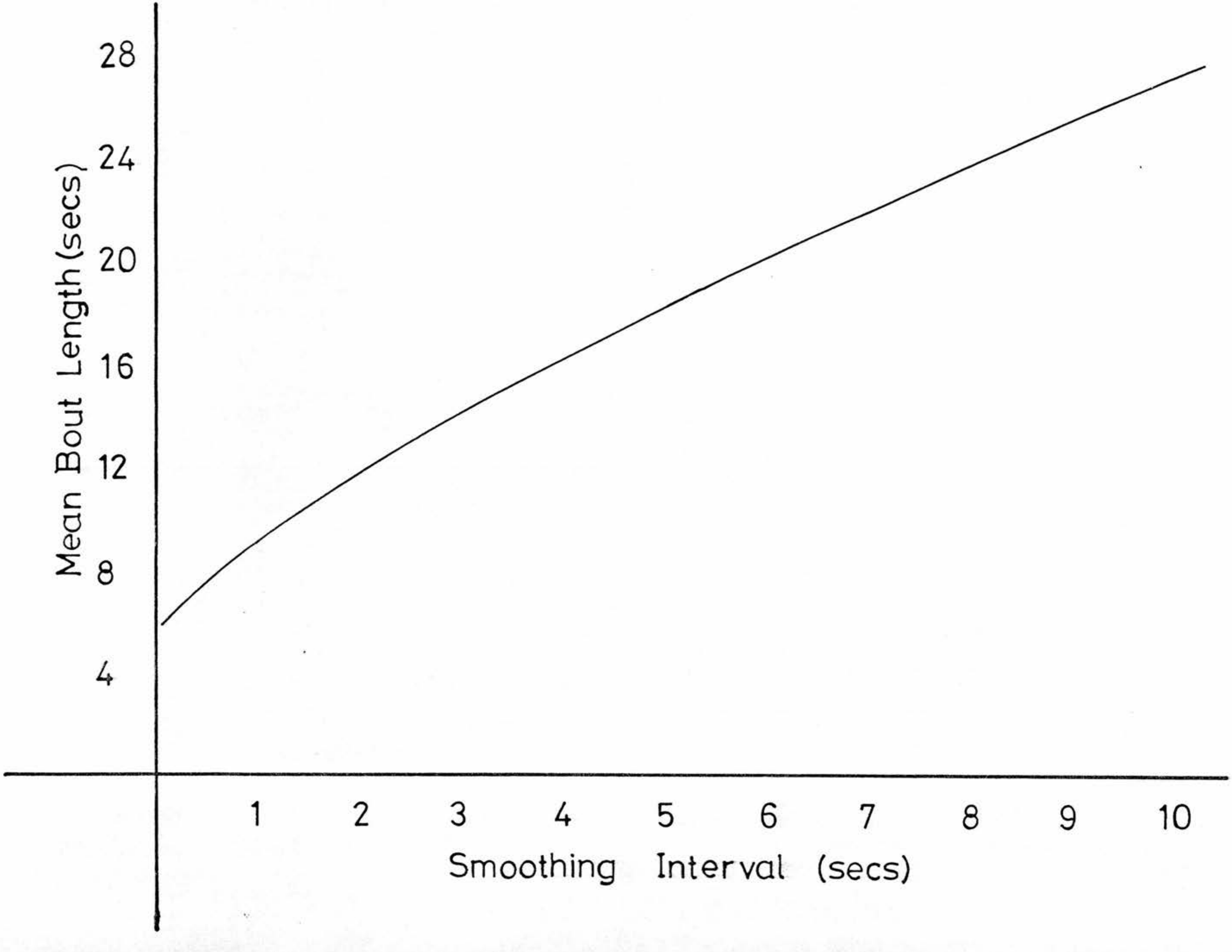
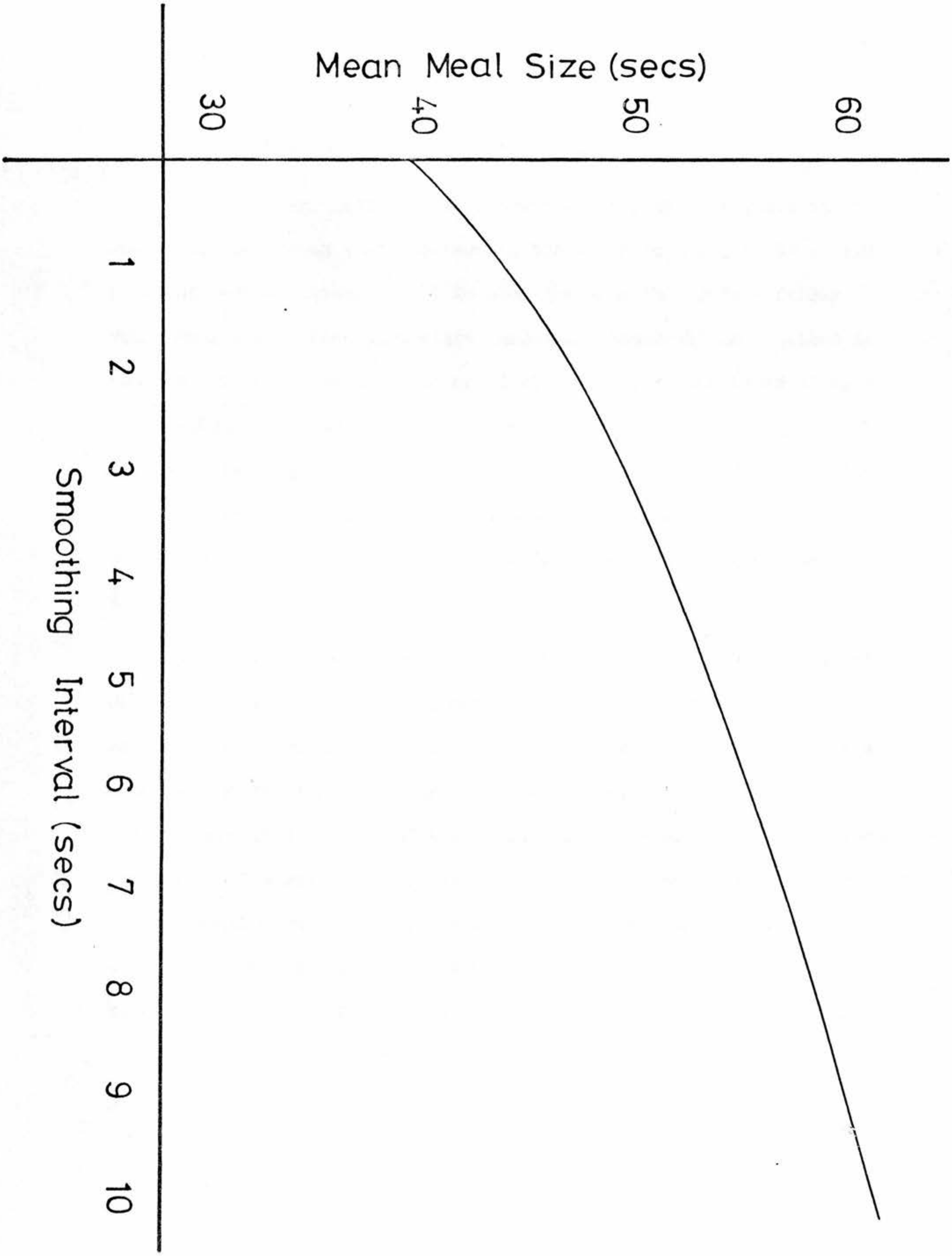

Mean Bout Length (secs)
4
8
12
16
20
24
28
1
2
3
4
5
6
7
8
9
10
Smoothing Interval (secs)

FIGURE 3.6

Mean size of meals as a function of the Smoothing Interval.


Mean Meal Size (secs)
30
40
50
60
Smoothing Interval (secs)
1
2
3
4
5
6
7
8
9
10

shape at the short smoothing interval lengths.

These data are derived from a study of only one bird, but it is reasonable to assume that thehpecking behaviour is going to be fairly constant between animals. It is also the case that only a fairly rough estimate of the appropriate "smoothing interval" is required to set the recording system. It was decided then, on the basis of this information, that the recording system should be set to disregard all breaks in feeding activity which were shorter than 2 seconds. This criterion was set on all of the channels and was in force in the collection of all of the feeding behaviour records to be discussed below.

The recording system has thus a certain inaccuracy built into it. The exact time which will be recorded for any make or break sequence will depend on the interaction of the behaviour of the animal and the behaviour of the time sampling circuit. On average, the circuit would be expected to respond about 0.6 seconds after the animal inserts its head. The circuit will also add about 2 seconds (depending on the interaction of the delay element and the time sampling element) onto the end of each recorded period. These would not seem to be unreasonable distortions of the feeding record and there is no reason to suppose that any systematic artefacts would be generated.

3.6 Validation of the Recording Procedure

When one uses a measure of time spent feeding in a study of this sort, the implication is always that the measured time spent feeding will actually correlate with the amount of food which the animal eats.

It is necessary first of all however, to make some estimate of the degree of correlation.

3.6(a) Method

Four adult female doves were used for this study. The birds were housed as described above and were allowed 3 days to settle into the cages with the photocell feeding devices attached. Until the start of the data collection the animals were fed ad libitum on a standard mixed grain diet, and had water and grit continuously available. For 3 days then, data was collected on feeding behaviour (as measured by the photocell device) and on amount of food eaten. The birds were given access to the food hopper for 15 minutes in each hour of the day from 9 am to 5 pm. At the end of each of the 9 feeding periods in each of the three days, the photocell feeders were removed from the cages and weighed to determine the amount of food consumed in that period. The records from the feeding monitor system were input to the computer and the time spent feeding and the number of bouts of feeding in each of the 27 periods was calculated.

3.6(b) Results

The correlation between the amount eaten and the time spent feeding, and also the amount eaten and the number of bouts of feeding recorded were calculated. The data are summarised in Table 3.1 and the raw data included in Appendix II. In all cases the correlations were high and positive, so the use of the time spent feeding measure is to some

TABLE 3.1

VALIDATION OF RECORDING SYSTEM

(see Appendix II; Tables 1 (a) to (d))

BIRDS	1	2	3	4
Correlation of Time Feeding with Amount Eaten	0.8504	0.8512	0.8810	0.7380
Correlation of No. of Bouts with Amount Eaten	0.8632	0.8644	0.8537	0.8930
Mean Rate of Food Intake (Grams/Minute)	0.31	1.80	1.65	0.69

degree validated.

It should be noted however that this procedure may have involved a mild degree of food deprivation, as theebirds might have normally eaten more frequently than once in every hour. (Indeed data to be presented below would indicate that this was most certainly the case). If this is the case then, one might expect to find a higher correlation between food intake and time spent feeding than would have been obtained with a freely feeding animal. It is also the case that this procedure of feeding for only 15 minutes in every hour would have upset the birds to a certain extent. In some instances little or no feeding was observed in an hour period which may have contributed to an even higher level of deprivation when the bird finally came to feed. An evidence of this disruption and effect of the limited availability of the food can be seen in the ratio of the time spent feeding to the number of bouts recorded. It seemed that the mean bout length which was found in this validation trial was characteristically longer than that normally found in the records of free feeding animals. This might suggest that they were persisting in feeding to a greater degree when food was available.

It is reasonable to assume however that even if the correlations obtained are somewhat inflated by the procedures used, they are sufficiently strong to indicate that the correlation would also hold good in the free feeding situation. What should be noted however is that although the correlation between time spent feeding and the amount of food consumed is reasonably strong within one animal, it can be seen that the ratio of grains consumed per unit of time spent feeding varies greatly from animal to animal (Table 3.1). Thus it would clearly not be reasonable to make comparisons of meal size or time spent feeding between animals as the significance of a time measure in terms of amount ingested would be very uncertain.

3.7 Collection of Feeding Pattern Data

As described above, the cages in which the animals were housed while records of feeding behaviour were collected were standard individual dove cages (40x35x45 cm) in one of the rooms within the dove colony at the Department of Psychology (Figure 3.7). In most cases the animals were maintained on a 9 hour light cycle with light onset at 9 am and offset at 6 pm. The short day length avoids the problems of birds in reproductive condition as noted above. The temperature in the room was held at about 70°F and the birds were visually isolated but able to hear the sounds of the activity of other birds in the surrounding cages.

As the photocell feeding monitor devices were normal feeding boxes with only slight modification, there was no special training involved for the birds in feeding from them. There was no indication that the coloured plugs and leads running from the boxes in any way disturbed the birds. In all cases however (even when the birds were moved into the recording cages from other identical cages in the same room) the birds were allowed at least 3 days to settle into the cages and become accustomed to the feeder, before the data collection was begun.

At all times the food was continuously available for the animals (in the photocell feeders) as was grit and water. The feeders contained quite enough food to last for the whole of the normal period of data

FIGURE 3.7

Dove in standard individual cage (approximately 40 x 35 x 45 cms.).

collection (usually at least seven days) and so there would be no question of the hoppers having to be topped up in the middle of a period of recording. To ensure that the food was flowing freely however, it was a daily practice to enter the room in which the animals were housed before the onset of the light phase of the cycle, and shake the food down.

3.8 Analysis of the data

Seven or eight days of data were normally recorded for each of the animals or for each animal in each experimental condition. The data on paper tape was then input to the computer and ordered into files of standard format for further analysis. The crude data file included the records taken from all of the animals which were being monitored at the same time (up to four) in the format shown by the example in figure 3.8. The format in which the data was stored for further analysis is shown in figure 3.9.

3.8(a) Screening for Errors

After the data had been ordered into the standard format, the first task was to look for any blatant errors in the record. These took the form of negative times (which were presumably a result of a printing error by the data logger) and exceptionally long bouts of "feeding" which could be identified as being a result of a failure of the logger to recognise an "off" signal and responding to the next "off" signal which came many minutes later. In the later case it was

FIGURE 3.8

```
C0902474
D0902500
C0902564
D0903036
C0903054
D0903079
C0903097
D0903123
C0903125
D0903181
C0903214
D0903225
C0903243
D0903254
C0903319
D0903376
C0903409
D0903467
C0903484
D0903556
C0904054
D0904217
```

FIGURE 3.9

```
T  9  1 21.9 F  3.3 I   8.6
T  9  1 33.8 F  5.1 I   1.4
T  9  1 40.3 F  8.7 I    .6
T  9  1 50.6 F  5.1 I   5.2
T  9  2  0.9 F 10.2 I 3264.0
T  9 56 35.1 F  4.8 I   1.6
T  9 56 41.5 F 12.2 I   6.9
T  9 57  0.6 F  5.5 I   1.5
T  9 57  7.6 F  6.8 I  17.5
T  9 57 31.9 F  8.7 I 1366.1
T 10 20 26.7 F  1.7 I   1.5
T 10 20 29.9 F  5.1 I 1207.0
T 10 40 42.0 F  1.8 I 1540.4
T 11  6 24.2 F  3.7 I  89.7
T 11  7 57.6 F  1.7 I   1.6
T 11  8  0.9 F  1.6 I   6.9
T 11  8  9.4 F  1.6 I   3.4
T 11  8 14.4 F  1.9 I 324.1
T 11 13 40.4 F  3.0 I   5.1
T 11 13 48.5 F 10.5 I   1.6
T 11 14  0.6 F 14.0 I   5.5
```

felt to be reasonable to simply delete the item from the data and to save the rest. In the former case however, it was felt that the safest procedure would be to discard the whole day. The errors were not sufficiently frequent to make a systematic record of them necessary, but it might be estimated that one such error would occur in every 8 seven day records (that is, once in every second set of four records).

In addition, data was sometimes lost due to failure of the photocell apparatus which was usually due to a fused bulb or to bad or broken connections at the output leads. On one or two occasions remarkable "feeding patterns" were generated by feathers becoming lodged beside the lamp or photocell and moving with currents of air!

3.8(b) Patterns of Feeding Behaviour

A predominant characteristic of the feeding behaviour of almost all animals is that it is not randomly distributed throughout the day, but is aggregated into distinct periods of activity, separated by prolonged periods of inattention to food (Richter, 1927).

There is however obviously going to be some degree of uncertainty associated with the termination of feeding behaviour. The animal may break off from a bout of feeding but return to the food after a short time. In the analysis of the preliminary data from which the estimate of an appropriate "smoothing interval" was derived, a criterion of 5 minutes was used (quite arbitrarily) to be the length of break which would constitute an inter-meal-interval (IMI). We would want to have some objective means of deciding whether a break in feeding activity is a pause which is within a period of ongoing feeding (which we have called a "meal") or whether it is sufficiently long to constitute an interval between meals.

Kissileff (1970) draws attention to the vast range of inter-feeding-interval criteria which have been used by others studying animal feeding patterns and uses his own data to illustrate how the choice of the criterion can markedly affect the analysis and hence the conclusions drawn from the data. Thus the conclusions taken from the experiment, or the way in which the author chooses to describe the effects may be due to the particular criterion chosen. Indeed the choice of the criterion may be affected by some of the conclusions or predictions made about the data. The solution which he offers to the problem is to present the data analysed in terms of several widely different criteria in order to demonstrate that the effect under discussion still holds good. This might be described as a conservative approach to the analysis. If an effect is still present in the worst possible conditions, then it can be considered to be sufficiently robust to be of importance. However it does seem reasonable to talk in terms of an appropriate criterion inter-feeding-interval length; appropriate not in terms of the data analysis but in terms of the behaviour of the animal. It can thus be seen that information would be discarded if an inappropriate (in this behavioural sense) criterion was used, and thus Kissileff's procedure would seem to be too strict.

However, this commits us to finding some means of objectively determining what is an appropriate criterion. A method which has been successfully employed in the last few years (Nelson, 1964; Wiepkema, 1968; Allison and Castellan, 1970; Slater, 1974; 1975; Petersen, 1975; 1976) is the Cumulative Logarithmic Survivorship Plot (Cox and Lewis, 1966).

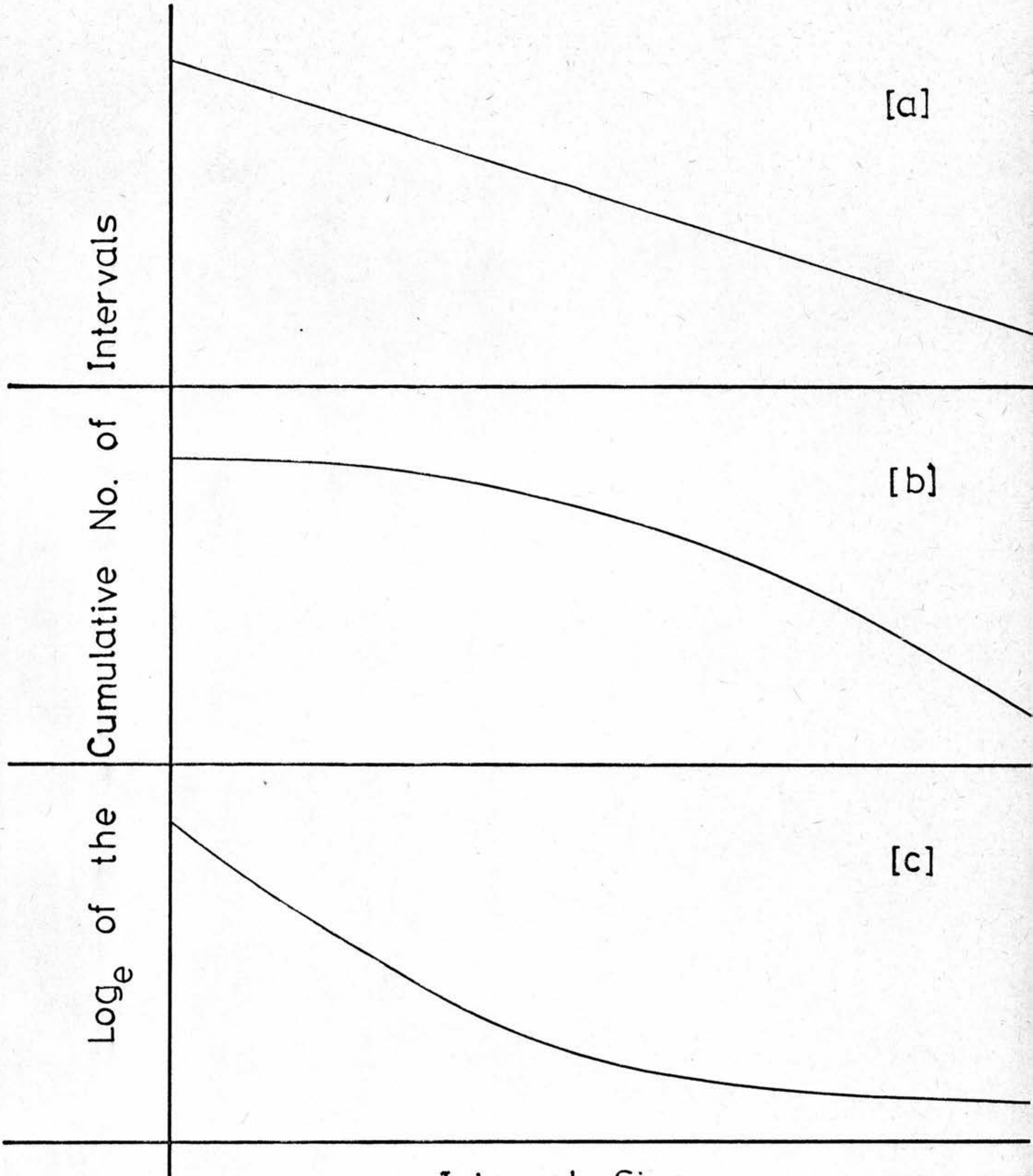
3.8(c) The Logarithmic Survivorship Plot

The procedure for the generation of such a plot is to consider all of the intervals of non-feeding from a continuous record and to divide the potential range of interval lengths into a number of equal parts. The frequency of occurrence of intervals less than or equal to the upper limit of part of the range is then computed, and the logarithm of the frequency (in this case the natural logarithm) plotted against the interval length range.

The slope of the plot so constructed can be seen as providing an estimate of the probability of feeding occurring at any time since the last occurrence of feeding. The interpretation of the curve will be explained with reference to the idealised examples presented in figure 3.10. A straight line derived from this procedure would indicate that the probability of feeding was not a function of the time since the animal last fed, and that the occurrence of feeding behaviour was essentially randomly distributed over the available range. A convex curve (b) would indicate that the probability was low immediately after a feeding occurrence and that there was a certain minimum time involved before the next feeding could take place. (A distribution of this sort will be encountered in chapter 10) The concave curve (c) would be the pattern we would expect to find for normal feeding behaviour. The probability of feeding is high immediately after feeding has just taken place and thus the occurrences are aggregated into groups. Thus the origin of the term "survivorship" plot can be seen. We are interested in the chance which a period of non-feeding has of "surviving", uninterrupted by feeding, from one range to the next. Short intervals

FIGURE 3.10

Idealized logarithmic survivorship curves.


[a]
[b]
[c]
Log$_e$ of the Cumulative No. of Intervals
Interval Size

have a very low chance of surviving to be longer ones. Long intervals have a fairly good chance of surviving to be still longer.

Figure 3.11 shows the curves so produced from 4 sample animals. It should be noted that the verticle axes are not immediately comparable from one graph to the next as the program used to generate the graphs involved automatic scaling. However, as the orders of magnitude are similar and as it is the shape of the graph with which we are concerned, no attempt was made to modify this.

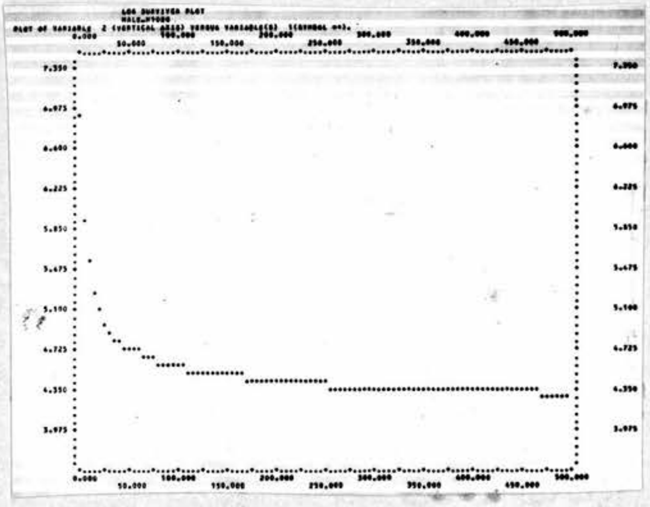
It can be seen that the slope and sharpness of the curve does vary between animals, but even in the more shallow cases they look less like the smooth curve of figure 3.10(c) and more like two intersecting straight lines. It is argued therefore that the group of interval lengths can be broken down clearly into two populations; very frequent, short intervals (below about 100 seconds) which should be considered to be pauses within a meal, and infrequent, long intervals which are pauses in feeding between meals. Arguing again in terms of probabilities, it can be seen that there is a certain pause length below which the animal has a very high probability of returning to feeding. Any given interval however which continues and exceeds the criterial length is likely to be an inter-meal-interval. That is, after a certain time of non=feeding the animal is very unlikely to return to feed.

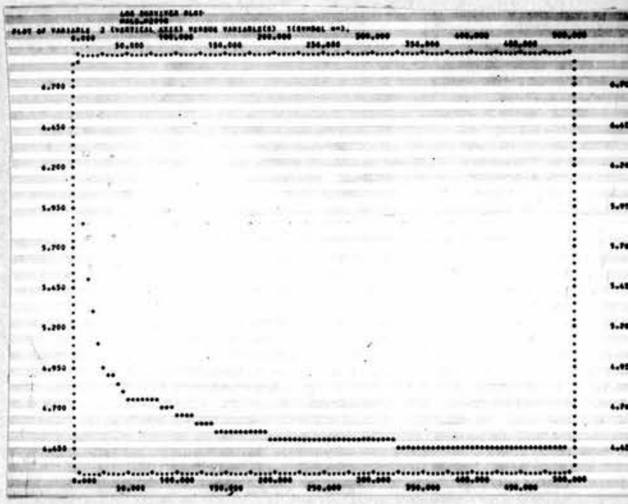
3.8(d) Meals and Inter-Meal-Intervals

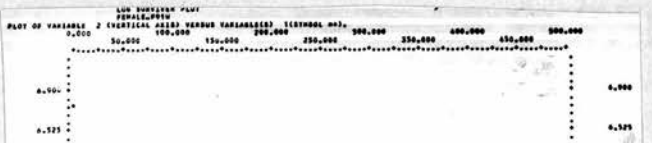
On the basis of the logarithmic Survivorship Plot the continuous record of feeding can be structured into a discontinuous series of

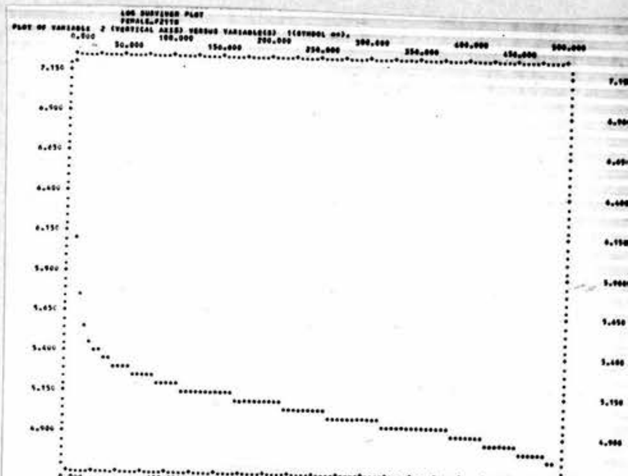
FIGURE 3.11

Examples of logarithmic survivorship plots of inter-feeding interval generated for four animals. Data analysed in terms of 100 five second interval units and output on a line-printer formatted by a BMD Biomedical Computer Programs routine.


LOG SURVIVOR PLOT
MALE,M7000
PLOT OF VARIABLE 2 (VERTICAL AXIS) VERSUS VARIABLE(S) 1(SYMBOL =*).
0.000
50.000
100.000
150.000
200.000
250.000
300.000
350.000
400.000
450.000
500.000
7.350
6.975
6.600
6.225
5.850
5.475
5.100
4.725
4.350
3.975


LOG SURVIVOR PLOT
PLOT OF VARIABLE 2 (VERTICAL AXIS) VERSUS VARIABLE(S) 1(SYMBOL =*).
0.000
50.000
100.000
150.000
200.000
250.000
300.000
350.000
400.000
450.000
500.000
6.700
6.450
6.200
5.950
5.700
5.450
5.200
4.950
4.700
4.450


LOG SURVIVOR PLOT
FEMALE,F91W
PLOT OF VARIABLE 2 (VERTICAL AXIS) VERSUS VARIABLE(S) 1(SYMBOL =*).
0.000
50.000
100.000
150.000
200.000
250.000
300.000
350.000
400.000
450.000
500.000
6.900
6.525
6.150
5.775
5.400
5.025
4.650
4.275
3.900
3.525


LOG SURVIVOR PLOT
FEMALE,F2T18
PLOT OF VARIABLE 2 (VERTICAL AXIS) VERSUS VARIABLE(S) 1(SYMBOL =*).
0.000
50.000
100.000
150.000
200.000
250.000
300.000
350.000
400.000
450.000
500.000
7.150
6.900
6.650
6.400
6.150
5.900
5.650
5.400
5.150
4.900

meals separated by inter-meal-intervals. The bouts of feeding within a meal stand as individual units of analysis. The procedure adopted then, was to generate a survivorship plot for each individual record of feeding behaviour and to base all further analyses on a criterion derived from that plot. If the point of discontinuity was very sharp the criterion could be easily chosen. If the decision was less clear than the criterion would be set at the point at which the most "horizontal" portion of the curve first began to deviate noticably from a straight line.

3.9 Description of Dove Feeding Patterns

This preliminary description will be based on data collected from seven male and seven female doves, analysed over seven days for each bird. Using the logarithmic survivorship technique described above, the continuous records were structured into meals and inter-meal-intervals. Table 3.2 presents a summary of the basic parameters of the animal feeding patterns.

Two measures of size of a meal are given. The first (meal size) is the total time within a meal for which the data-logger recorded the animal's head to be in the feeding box (i.e. the total of all the bout lengths within the meal). The second (meal duration) includes the inter-bout-intervals also, and is thus a measure of the total time during which the animal is engaged in approach to food.

TABLE 3.2

FEEDING BEHAVIOUR IN DOVES - SUMMARY

		MEAL FREQUENCY	MEAL SIZE (SECONDS)	MEAL DURATION (SECONDS)	TIME SPENT FEEDING DAY (MINUTES)
MALES	MEAN	20.5	60.0	101.2	20.5
	S.D.	7.028	23.654	26.455	9.329
FEMALES	MEAN	23.7	43.5	103.9	15.5
	S.D.	9.343	19.969	56.794	4.553

3.9(a) Diurnal Distribution of Feeding Behaviour

It soon becomes obvious that such measures as mean meal size and frequency taken from data collected from all times of the day are not very useful or meaningful. What does appear strikingly about the feeding behaviour of the birds is that it is ordered into a very particular diurnal pattern which is fairly similar across animals.

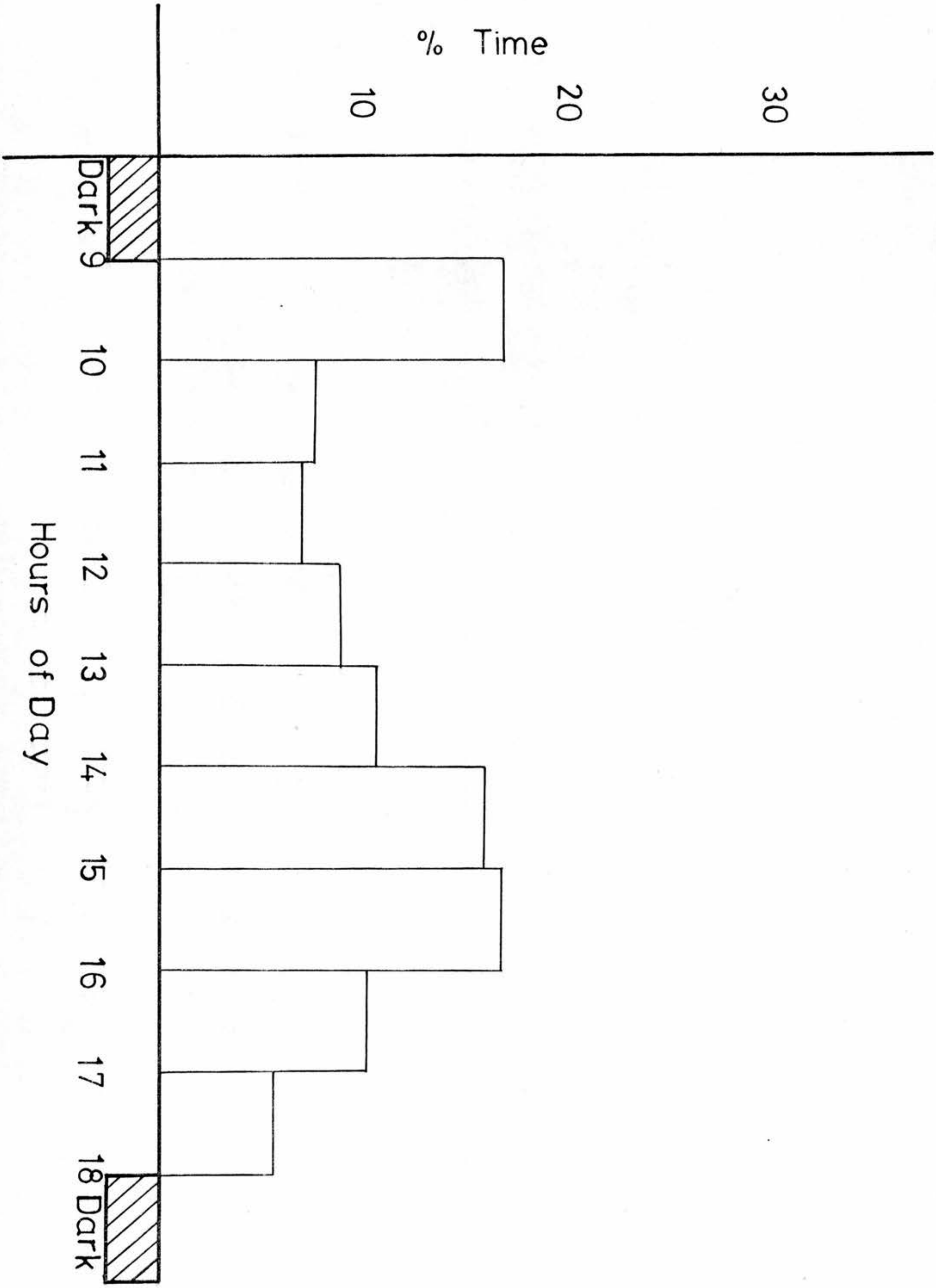
An estimate of this diurnal pattern was made by arranging the feeding data into meals as described above, and then computing the total time spent feeding in each hour of the day. (For the purposes of this analysis a meal is assigned to the hour in which it starts.) As noted above, time spent feeding can vary greatly from animal to animal, so these totals were expressed as percentages of the daily total time spent feeding. The mean pattern taken from all of the animals is presented in figure 3.12. It can clearly be seen that the diurnal pattern is characterised by two main peaks of feeding activity, one at the start of the day and the other in the middle of the afternoon. This appears to be similar to the pattern seen in wild populations of birds (Murton, 1965; Schmid, 1965) and also in laboratory studies of feeding (Van Hemel and Myer, 1969; Zeigler, Green and Lehrer, 1971; Slater, 1974). Feeding is not found during the hours of darkness.

It would appear from the picture shown by figure 3.12 that the peak at the time of light onset is of the same order of magnitude as that in the middle of the afternoon. However, consideration of the data for individual animals shows that the afternoon peak is characteristically larger than the morning peak, and that the smooth curve shown in figure 3.12 is a result of this afternoon peak falling

FIGURE 3.12

Percentage of daily total time spent feeding in each hour of the day (Means of 14 birds).

Data for individual birds given in Table 3(a) (Appendix II).
Results of hour by hour comparisons using Wilcoxon matched pairs test given in Table 3(b) (Appendix II).


% Time
10
20
30
Dark 9
10
11
12
13
14
15
16
17
18 Dark
Hours of Day

at different times in different birds. The morning peak on the other hand is synchronised by the light onset and so the mean taken across animals more accurately represents its size. By way of illustration then, figure 3.13 has been produced by artifically synchronising the hours in which the afternoon peak occurs in all of the birds. In this figure the predominance of the afternoon peak can be clearly seen. In addition, the data shown for each animal represent~~s~~ a mean taken over several days and it is also the case that the time at which the afternoon peak occurs will vary from day to day within one animal, which will further serve to "dilute" the prominance of this peak.

The changes in the amount of feeding activity across the day must be brought about by changes in the patterns of meal size and inter-meal-interval. Figure 3.14 shows the mean meal size for each hour of the day and figure 3.15 the mean inter-meal-interval. Again, for the purposes of this analysis, the meal is assigned to the hour of the day in which it began and the interval is assigned to the hour of the day in which the preceding meal began. It should be noted that the overnight intervals of non-feeding are not included in the analysis. That is, if a meal occurs in the last hour of the day, that meal will be counted towards the mean meal size, but the succeeding interval will not contribute to the calculation of mean interval length. If no feeding activity is recorded in any one hour the mean meal size will be counted as zero and the mean interval length will be counted as a full hour (3600 seconds). It should also be noted that the computations of % time spent feeding have been rounded up or down to the nearest whole number so that any given hour may have a mean and size associated with it, but the total feeding time in that hour is not

FIGURE 3.13

Percentage of daily total time spent feeding in each hour of the day, synchronized so that the peak of feeding by each bird contributes to the same mean (indicated [p]). Figure represents data from 14 birds, and numbers associated with some of the bars indicate the number of individual items contributing to these particular means.

Results of hour by hour comparisons using Wilcoxon matched pairs test given in Table 3(g) (Appendix II).

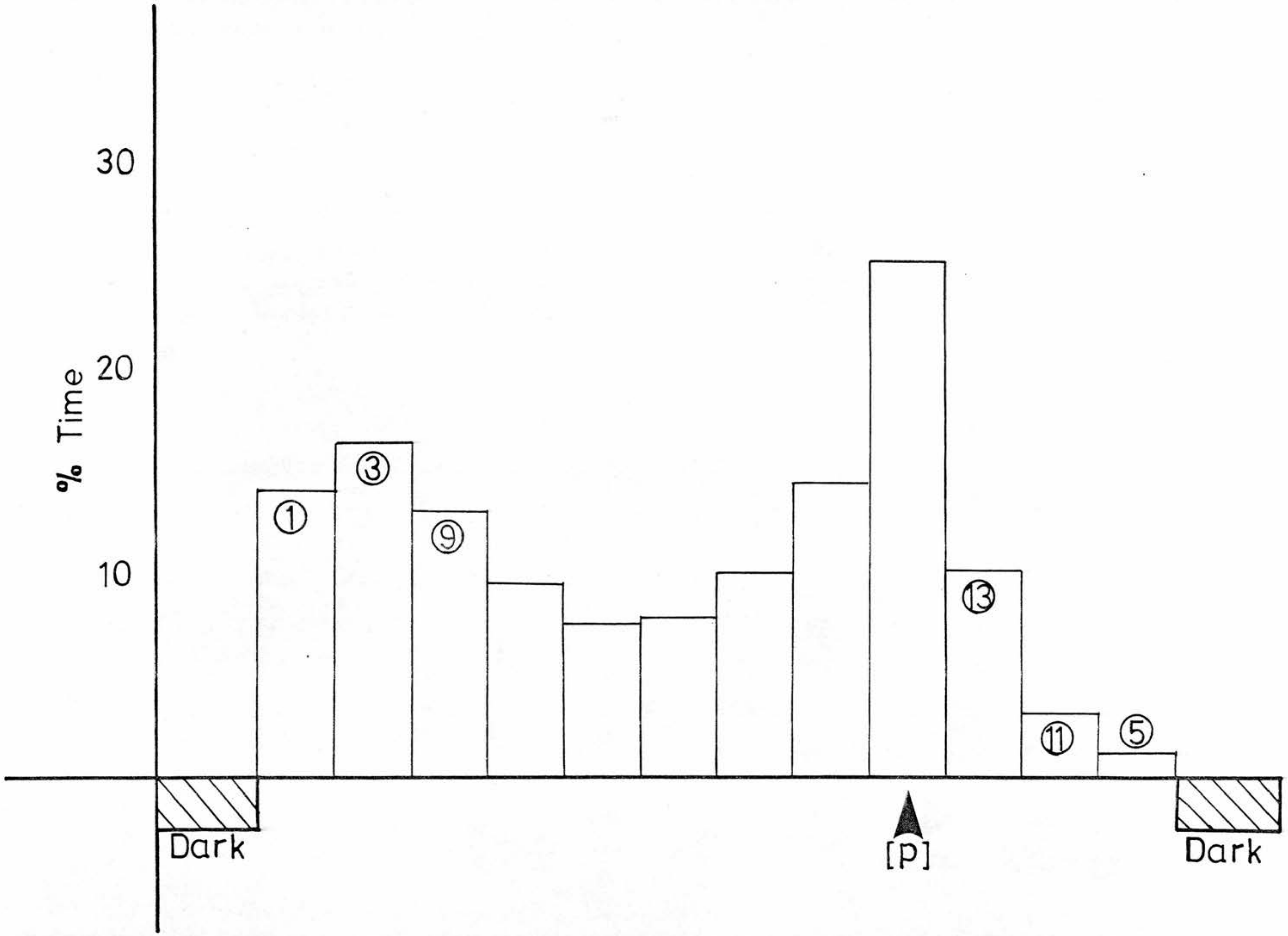

% Time
30
20
10
①
③
⑨
⑬
⑪
⑤
Dark
[p]
Dark

FIGURE 3.14

Grand means of mean meal size in each hour of the day from 14 birds. Error bars indicate one standard error.

Data for individual birds given in Table 3(c) (Appendix II). Results of hour by hour comparisons using Wilcoxon matched pairs test given in Table 3(d) (Appendix II).

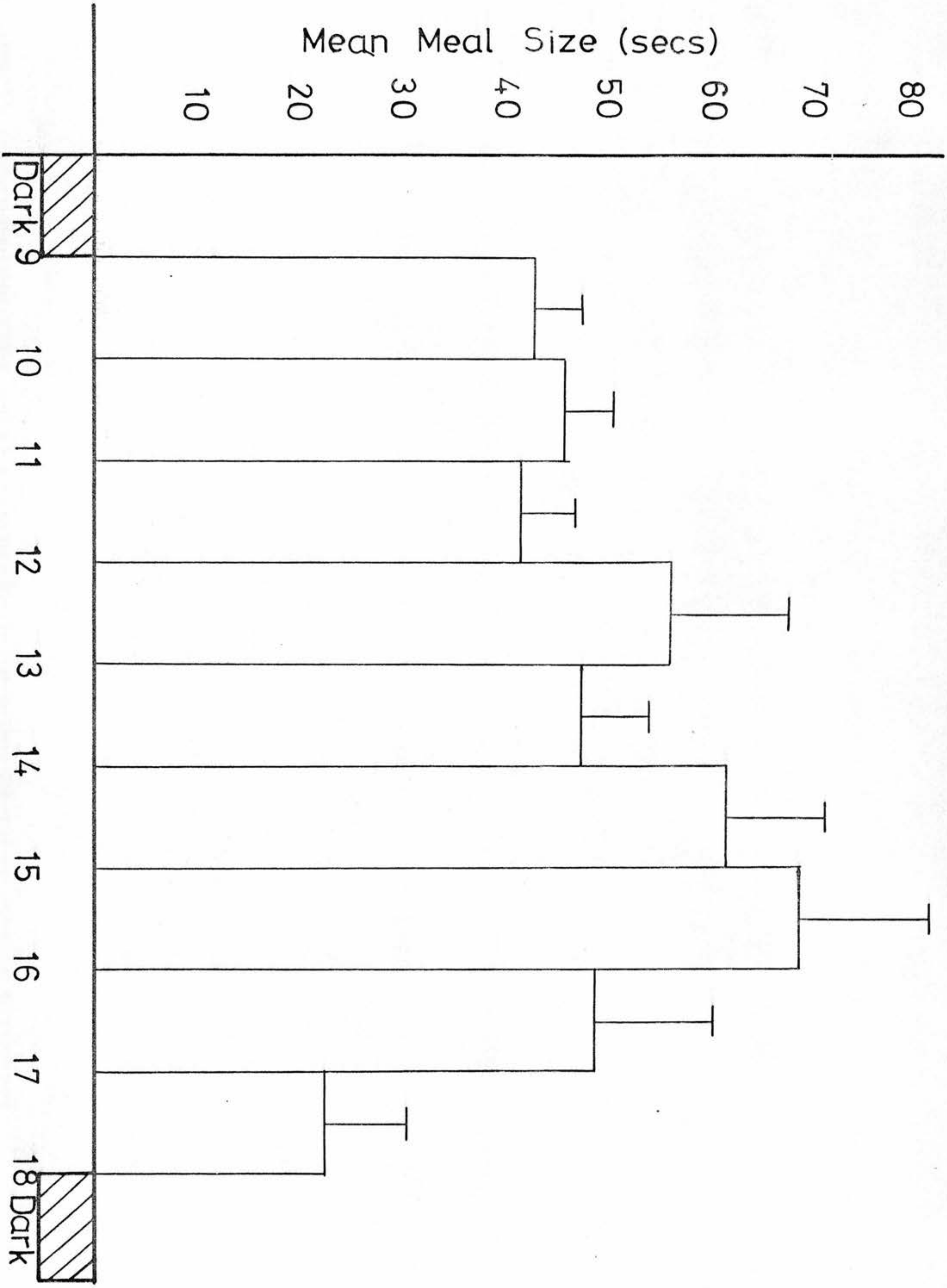
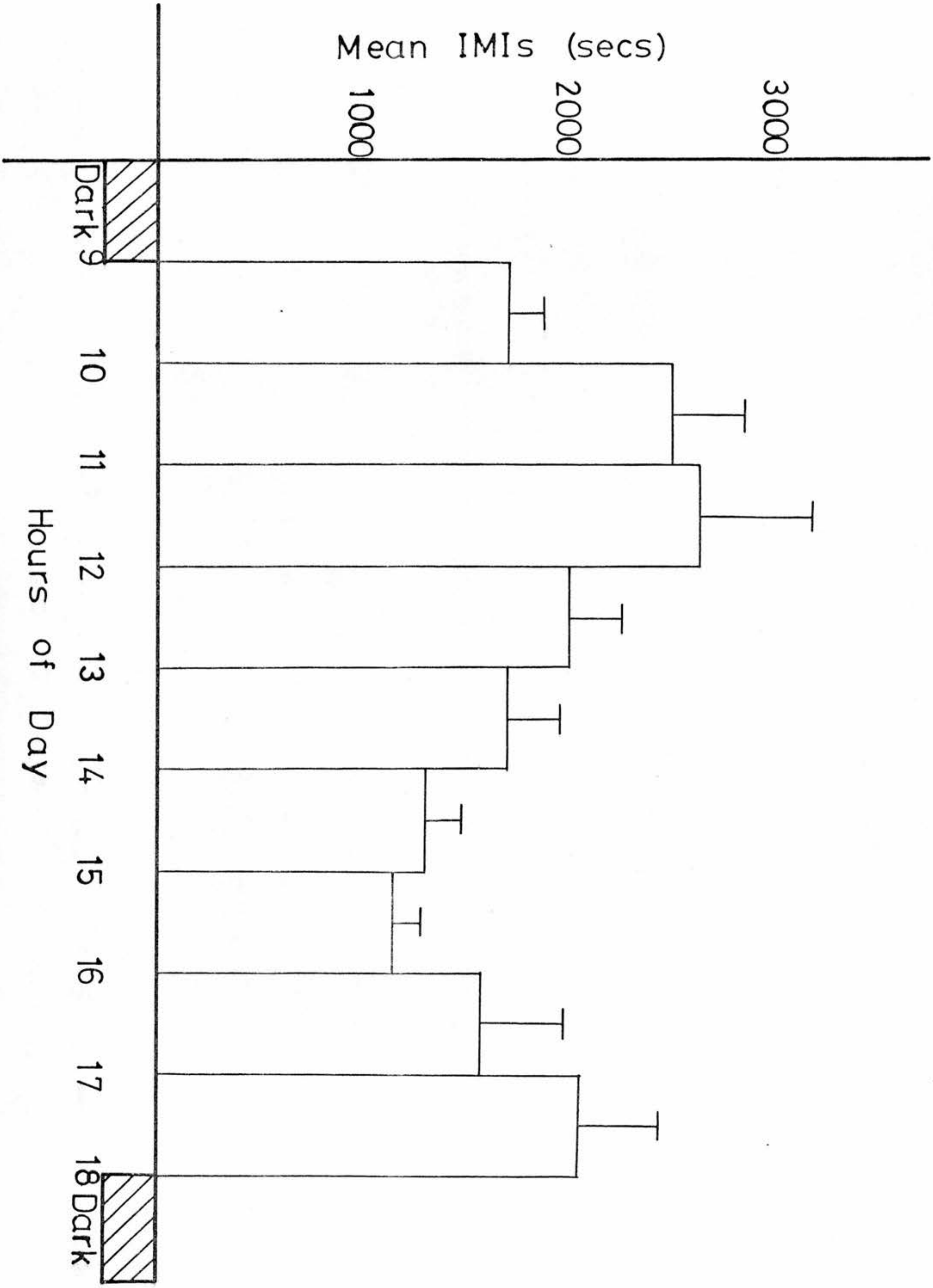

Mean Meal Size (secs)
10
20
30
40
50
60
70
80
Dark 9
10
11
12
13
14
15
16
17
18 Dark

FIGURE 3.15

Grand means of mean inter-meal interval in each hour of the day from 14 birds. Error bars indicate one standard error.

Data for individual birds given in Table 3(e) (Appendix II). Results of hour by hour comparisons using Wilcoxon matched pairs test given in Table 3(f) (Appendix II).


Mean IMIs (secs)
1000
2000
3000
Dark
9
10
11
12
13
14
15
16
17
18
Dark
Hours of Day

great enough to be noted.

It can be seen then that the peak in feeding activity at the start of the day is associated with an increase in the frequency of meal taking as compared with the rest of the day, as shown by a decrease in the mean inter-meal-interval at this time. There is little evidence of a change in meal size however. The afternoon peak in feeding is brought about by both an increase in the size and frequency of meals.

3.10 Chapter Summary

A brief introduction to the sorts of techniques used for the study of animal feeding patterns was given and a description of the system devised for use with the doves in the present study was presented.

Data were presented to indicate that the measure of time spent feeding does correlate to a reasonable degree with the amount of food ingested. It was noted that, although the correlations were strong within any one animal, large differences existed between animals in the rate of time spent feeding to grams of food consumed (i.e. the rate of food ingestion).

The form of the data collected was described and the use of the logarithmic survivorship plot to derive appropriate criteria for the ordering of continuous feeding records into series of meals and inter-meal-intervals was discussed.

Some of the basic characteristics of the feeding behaviour of the Ring dove were described.

CHAPTER 4

4.1 Effect of Trigeminal Nerve Section on Feeding Behaviour in the Ring Dove

Anyone working in the area of physiological psychology is aware of the difficulty encountered in the interpretation of the effects produced by experimental brain lesions. Many indeed consider it naive to suppose that anything of worth can be learned from such gross and crude procedures. This attitude might be expressed in Gandalf's response to Saruman's comment about the nature of white light.

> "He who breaks a thing to find out what
> it is has left the path of wisdom."
>
> Tolkien "The Fellowship of the Ring"
> (19)

However, the analysis of the effects of surgical intervention remains one of the few sources of information available to those who wish to study the biological and physiological bases of behaviour, and as such its crude nature must be excused by those working outside the field, but constantly borne in mind by those within.

It might be hoped that peripheral nerve section would present a less problematical picture however, than that found in studies of central lesions, as the actual damage being produced is fairly easy to define. As indicated in the preceding chapter this does not seem to be the case for the section of the sensory trigeminal nerve as reported by Zeigler (1975(a)). Far from producing only the sensory and motor disturbances which might be expected, this procedure also alters the birds motivation to feed and responsiveness to food.

If such crude physical and anatomical procedures must be excused, what cannot be excused are behaviourally crude or unsophisticated means of investigating the deficits produced. It should be the case then, that a closer study of the actual feeding behaviour of birds after trigeminal section in addition to the basic information provided by Zeigler, would contribute to an understanding of the nature of the feeding deficits produced. The present chapter describes attempts to repeat Zeigler's experiments on the effects of trigeminal section on feeding in the pigeon, using the Ring dove. The following chapter describes extention of this investigation in doves to look at the changes which surgical denervation cause in the patterns of feeding behaviour.

The two species are so anatomically and behaviourally similar that the nerve section effects reported by Zeigler should be identical. However, it was reliably difficult to produce anything like the very pronounced effects on feeding and food related behaviour by this procedure in the dove.

4.2 Surgical Procedures

The birds are anaesthetised with Equi-Thesin (2.44 ml/Kg of body weight) injected intra-muscularly. 30 minutes were allowed for the anaesthetic to take effect before preparation for surgery began, and the injection was supplemented with an inhalation anaesthetic (Penthrane) if at any time the birds showed signs of responsiveness. The inhalation anaesthetic was administered by holding a tube containing a small amount of the liquid on a piece of cotton over the beak and nares for a few seconds. Care had to be taken to deprive the birds of food before the anaesthetic so that they were not sick (continuation of surgery in that event being almost inevitably fatal). Complete deprivation of food on the day before surgery however, also seemed to increase the probability that the birds would not survive. The most successful procedure was to remove the food before the onset of the light phase of the cycle on the day of surgery thus ensuring that the bird had not eaten for at least 15 hours.

The anatomical background and general surgical procedures came from Zeigler and Witowsky (1968) and Zeigler, Miller and Levine (1975). It was found however that the techniques required much development and modification and that the surgery was apparently more difficult in the dove than the pigeon, presumably due to the smaller size of the animal. All surgery was performed under direct observation using a Wild binocular microscope. For approach to the Ophthalmic and Maxillary branches of the nerve the birds were held in a slightly modified Trent Wells Stereotaxic instrument mounted on a plinthe, the angle of which could be altered and set by a lockable ball and socket joint. It was found that slight alterations in the angle of the stereotaxic instrument made it much easier to see and approach the site of operation, and this was particularly so in the case of the ophthalmic branch where it was necessary to look into the back of the orbit behind the retracted eyeball.

4.2(a) Preparation for Surgery

Feathers were removed from the skin overlying the top of the head, nares and ears in the anaesthetised bird. When the stereotaxic instrument was being used the body of the animal was supported in a metal cage which was attached to the instrument by a powerful magnet. The bird's head was supported by the beak and ear bars of the instrument with the beak set approximately horizontal. The skin surfaces were then swabbed with antiseptic (Figure 4.1).

The letters given in brackets in the following descriptions of surgical procedures refer to the lists of instruments used (Appendix III). These are noted only where necessary for complete clarity.

4.2(b) Ophthalmic Branch Section

With the animal held in the stereotaxic instrument a midline incision was made in the top of the head with a scalpel and enlarged to about 2 cm with a pair of fine scissors. The skin was retracted to expose the upper part of the orbital region and held in place with two artery clips (d) (See Figure 4.2). The skin over the eyeball could then be cut around the line of the ridge of the orbit without damage to the eye itself. The preceding parts of the operation could be carried out with the naked eye but the following procedures required the binocular microscope. The angle of the stereotaxic instrument was set so that the body of the bird was leaning slightly away from the experimenter and the microscope (held above the animal on a rod attached to the nearby bench) was pointed directly into the eye. The eyeball was then retracted by sliding a fine metal spatula (f) over the top and pressing downwards. It was found that the most successful way of holding the eyeball under retraction was by an elastic band tied around the stem of the spatula and attached to the support rod of the ear bars

(Figure 4.3). The orbital cavity could then be explored by teasing away the membranes around the eye using fine forceps (g) until the point of passage of the nerve could be seen (Figure 4.4).

Actually detaching the nerve from the groove at the back of the orbit in which it ran was found to be the most difficult part of the surgery as the nerve ran in close association with a fairly large blood vessel. This blood vessel was almost always ruptured and the time for the whole procedure was greatly increased by the need to pause and stem this bleeding. The technique adopted was to tease away the membranes which held the nerve in the groove until it was detached and to pull the nerve out of the groove, sometimes with the help of a fine hook (h). Once this had been done the nerve could then be easily cut with microscissors and a fairly large section (about 3 mm) removed.

After a piece of nerve had been removed the retraction of the eyeball was released and the overlying skin was replaced. The whole procedure was then repeated on the other side of the head. It was found in some cases that the groove in which the nerve ran was continuous with the groove at the other side of the head at some points. This presented the additional problem that bleeding resulting from damage done by the intervention on the first side would lead to immediate difficulties when approach was attempted to the second side.

The whole procedure (involving section of the nerve on both sides usually took about 30 minutes, but could take as long as 45 minutes, the difference usually being due to the need to pause and deal with bleeding. When the procedure was complete on both sides the wound on the top of the head was closed with three or four stitches.

FIGURE 4.1

Dove held in stereotoxic instrument immediately prior to start of operation on maxillary or ophthalmic branch of trigeminal nerve.

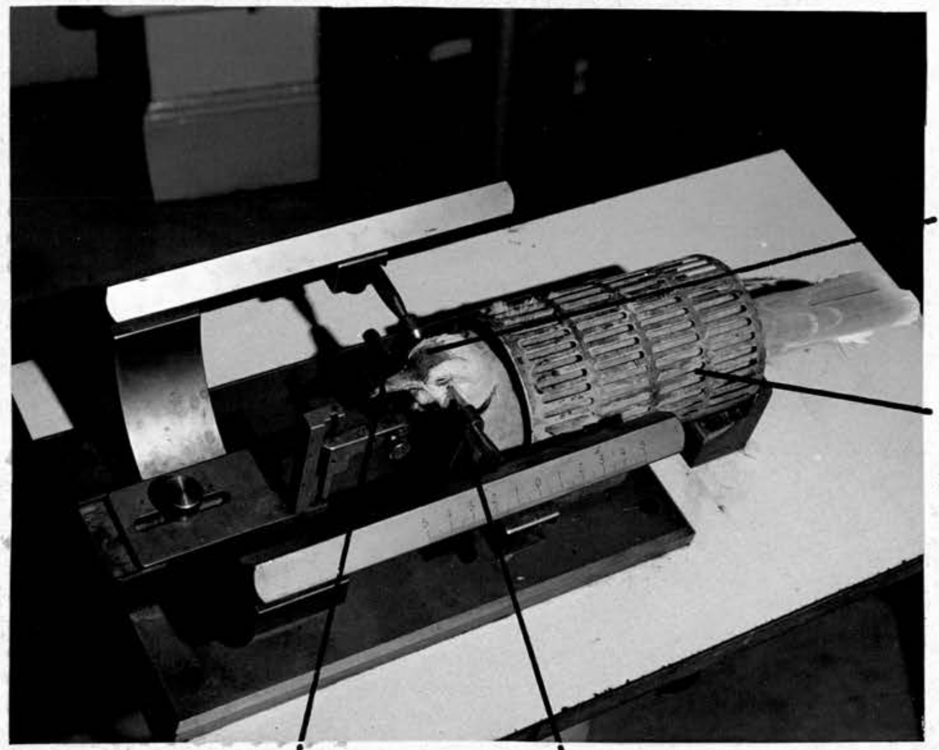
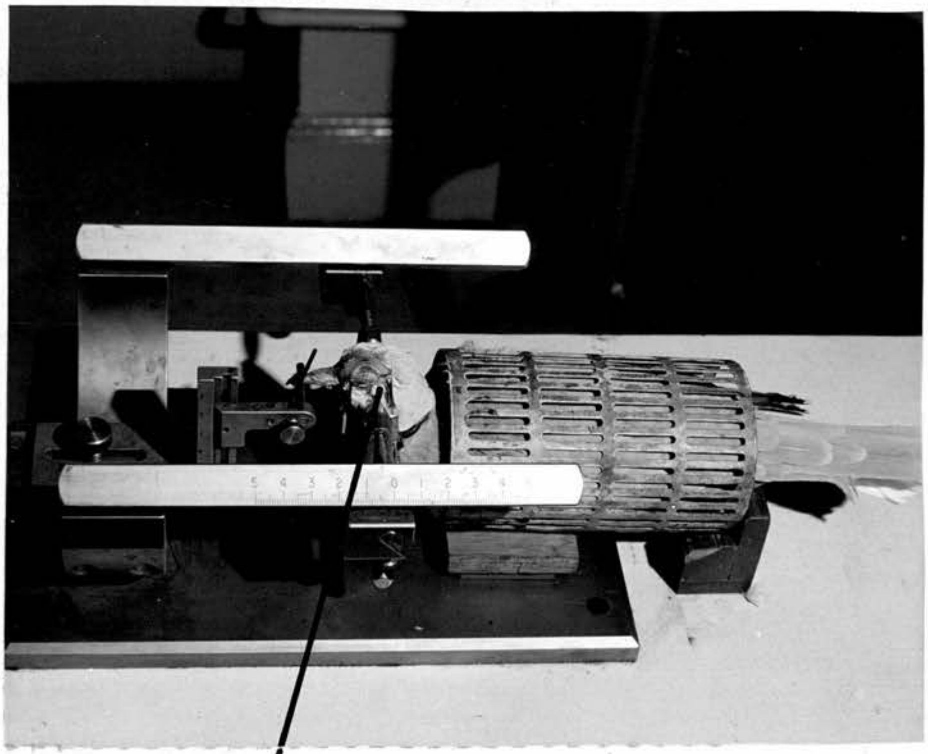

Feathers removed from appropriate skin regions.
Body of bird supported in metal cage.
Beak support bars.
Ear bars.

FIGURE 4.2

First stage of approach to ophthalmic branch of trigeminal nerve, showing incision above orbit and skin retracted to allow access to eyeball.

FIGURE 4.3

Eyeball held retracted to allow ophthalmic branch of nerve to be visualized at the back of the orbit. The stereotoxic instrument is tilted away from the experimenter, so that the microscope can be used more easily to see the site of the operation.



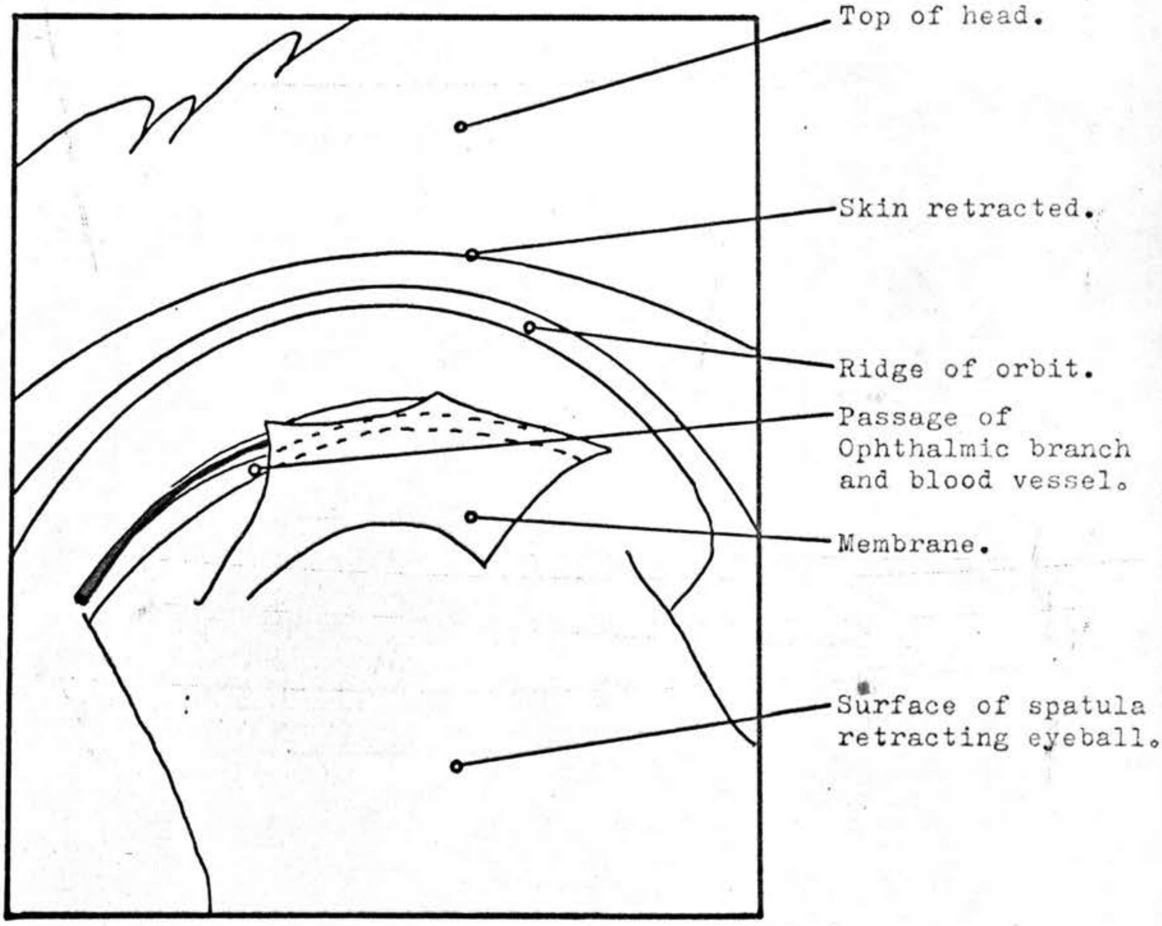
Skin retracted from
eye with artery clips.

Dissecting microscope.

Eyeball retracted
with spatula.

FIGURE 4.4

High magnification photograph of the region of passage of the ophthalmic branch of the trigeminal nerve, with a line drawing to illustrate the main anatomical features.


Top of head.
Skin retracted.
Ridge of orbit.
Passage of Ophthalmic branch and blood vessel.
Membrane.
Surface of spatula retracting eyeball.

4.2(c) Maxillary Branch Section

The stereotaxic instrument was positioned such that the head of the bird was towards the experimenter and tilted slightly upwards. An incision was made using scissors on one side of the head immediately above the beak and the skin was retracted using forceps (a). When the area of the nerve had been exposed the skin over the area was held retracted with two pairs of artery forceps (c) (Figure 4.5). The whole of this procedure was performed using the microscope. The region of passage of the nerve was then explored with the fine forceps (d) by teasing away the tissue to expose the nerve which, at this point, is extensively branched (Figure 4.7). Wherever possible pieces of nerve were fully cut away using microscissors (e), but where this was not possible attempt was made to damage the nerve by tearing pieces with the forceps. Because of the degree of branching of the nerve it was difficult to know the extent of denervation which had been achieved. Zeigler also reports that surgery and damage to the maxillary branch of the nerve was always less extensive than in the cases of the ophthalmic and mandibular branches.

The wound was closed with one stitch and the procedure was repeated on the other side. Maxillary denervation usually took from 20 to 30 minutes.

4.2(d) Mandibular Branch Section

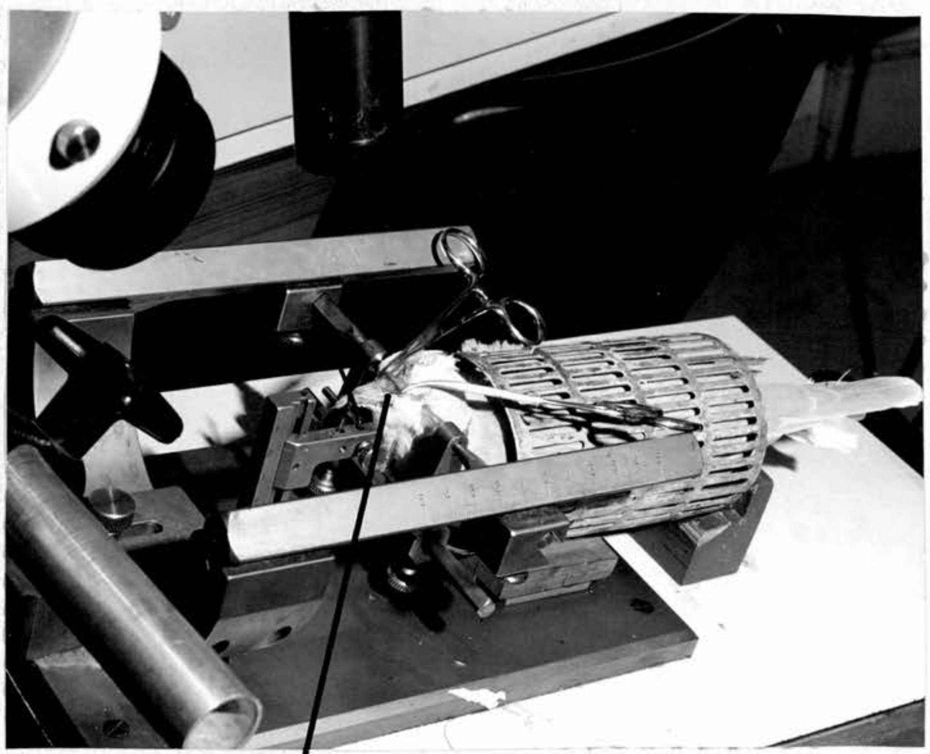
This was undoubtedly the most straight forward of the three surgical procedures. The bird was laid on its back with the head slightly raised and to one side. An incision was made in the skin

FIGURE 4.5

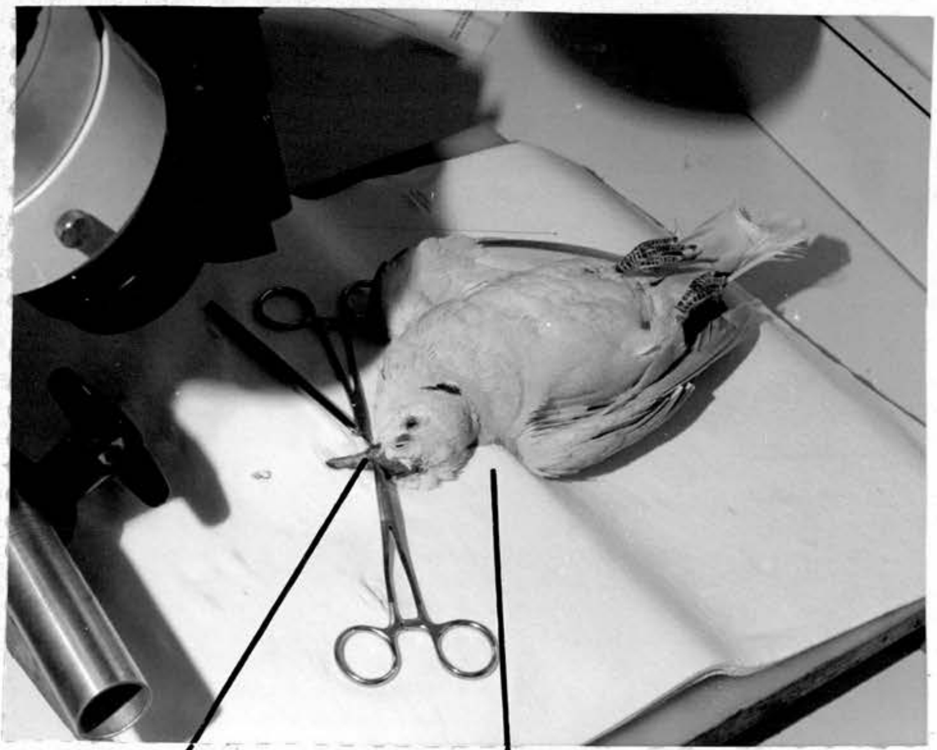
First stages of approach to the maxillary branch of the nerve. The front of the stereotaxic instrument is angled slightly upwards so that the region of passage of the nerve can be better visualized.

FIGURE 4.6

Bird undergoing section of the mandibular branch of the trigeminal nerve.



Skin over area of nerve held retracted by artery forceps.

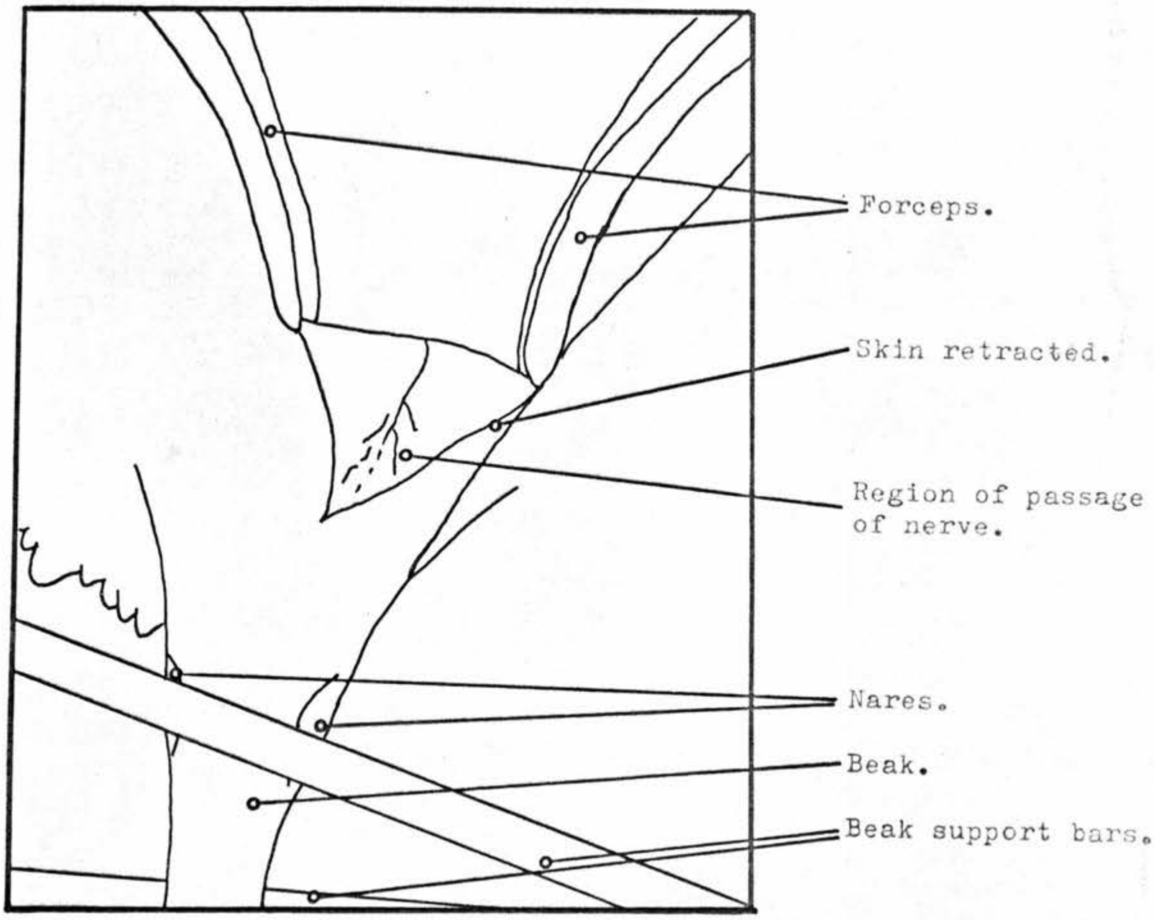


Block to raise bird's head.

Skin of mandible held retracted by forceps.

FIGURE 4.7

High magnification photograph of the region of passage of the maxillary branch of the trigeminal nerve, with line drawing to illustrate the main anatomical features.


Forceps.
Skin retracted.
Region of passage of nerve.
Nares.
Beak.
Beak support bars.

over the lower mandible by catching the skin with forceps (a) and cutting with fine scissors. This was the most difficult part of the procedure as no easy way was found to hold the animal still and, even under deep anaesthesia the touching of this skin region with the forceps often resulted in scratching movements of the ipsilateral foot and leg.

The incision, made adjacent to the corner of the mouth, was enlarged in both directions to about 1.5 cm and the skin opened and held back with two pairs of artery forceps (c) (Figure 4.6). When the bone of the mandible was exposed the nerve could be clearly seen running inside the bone and its point of entry could be found. The nerve was exposed by first making a cut with a microscalpel (d) starting at the point of entry of the nerve and following the nerve for 3-4 mm towards the tip of the beak, and then removing the piece of bone which lay over the nerve with fine curved forceps (e). The more proximal piece of nerve was then exposed by teasing away the surrounding membranes with the fine forceps. A large section (about 4-5 mm) could then be removed and the skin replaced and closed with one stitch (Figure 4.8).

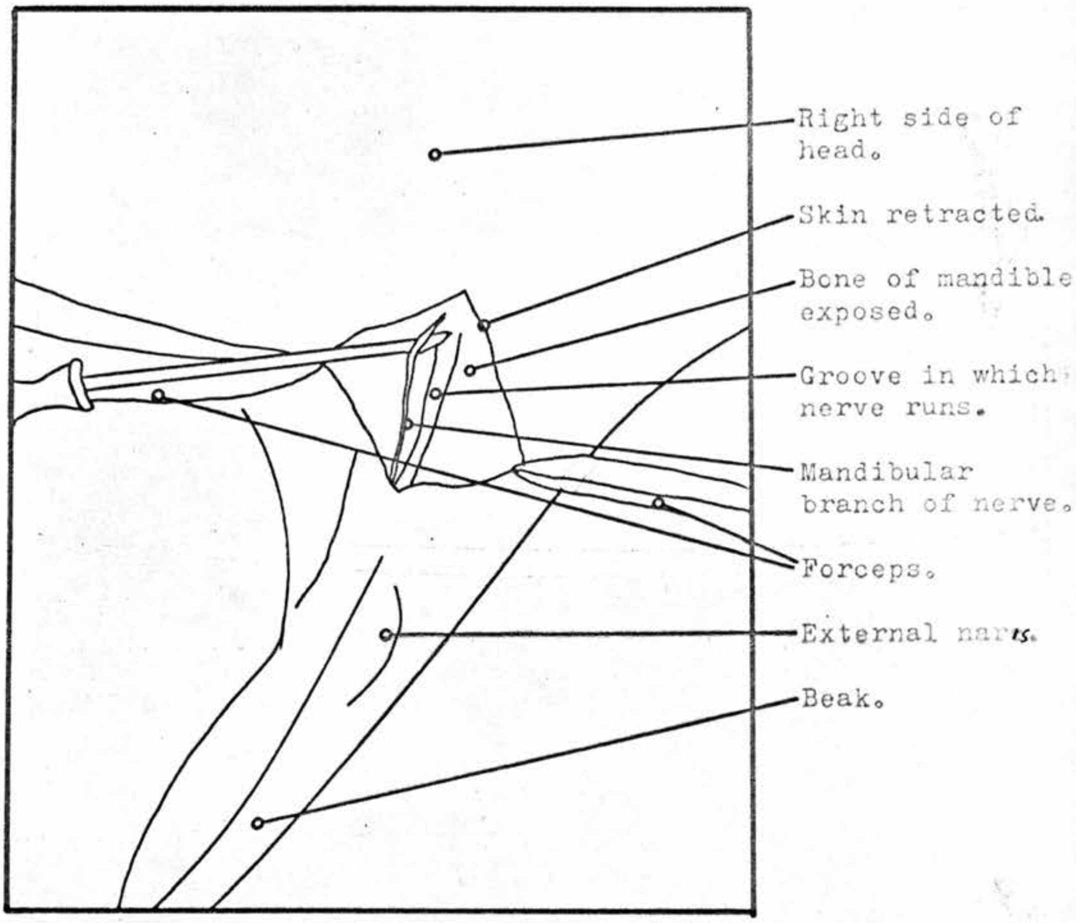
Bleeding was also found to be a problem here as the tissue over the mandible was highly vascularized. The blood was kept away from the area of the nerve by swabbing with cotton tipped sticks (g). This whole procedure also took about 30 minutes.

4.2(e) Control Surgical Procedures

It would be reasonable to expect that the trauma involved in such

FIGURE 4.8

High magnification photograph of the region of passage of the mandibular branch of the trigeminal nerve, with line drawing to illustrate main anatomical features.


Right side of head.
Skin retracted.
Bone of mandible exposed.
Groove in which nerve runs.
Mandibular branch of nerve.
Forceps.
External naris.
Beak.

physically extensive surgery might disturb food intake in a completely non-specific way. Because of this the control surgical procedures needed to be very rigorous. In each case, a control procedure involved the identical degree of surgical intervention as in the actual deafferentation surgery without section of the nerve. That is the nerve would be located detached from the surrounding tissue and then re-placed rather than cut. Note was taken of the time involved in the control procedures, that they should be comparable with the complete experimental procedures.

4.3 Effects on Food Intake and Feeding Behaviour

4.3(a) Experiment 1

In the first experiment on the effect of trigeminal deafferentiation it was decided to attempt to look at both the effect on food intake and body weight regulation of the birds, and on the efficiency of feeding. To gather information about both of these in the same group of animals the birds were first trained to consume their whole daily food requirement in one hour per day. It was then possible to administer tests of the animal's feeding efficiency at a point in the day before food was available in the home cage, so that one could know that the birds would be sufficiently hungry to respond in the test situation. If the time of day at which the animals were tested was constant before and after the operation (as near as was possible) then that level of hunger would be equated in the pre- and post- operative tests.

4.3(b) Method

24 female Ring doves were housed in individual cages (40x35x45 cm) in a room with a 9 hour light cycle (lights on at 9 am and off at 6 pm)and a temperature of about 70°C. Water and grit were continuously available to the birds, but the availability of food (a mixture of wheat, millet and corn) was restricted to one hour every day (3-4 pm). The body weights and food intakes of the birds were noted daily until they stabilized on the schedule of restricted availability. When this had taken place (after about 3 weeks) it could be seen that the birds were eating just as much and defending approximately the same body weight as they had done before the restricted availability schedule was imposed. It can be seen from the data presented in chapter 2 (See also Appendix II, Table 2) that the birds spend relatively little time out of the whole day actually eating although the intake is normally spread over the whole day. Presumably the presence of the crop, used as a storage reservoir, enables the birds to concentrate their feeding activity into one short period, and to slowly pass the food material from the crop to the lower gastro-intestinal tract for digestion during the rest of the day. It may also be the case that the fact that the period of access to food (3-4 pm) coincides with the normal peak of the birds' daily feeding activity made it easier for the birds to settle onto this regime.

4.3(c) Test of Feeding Efficiency

Birds were removed from their home cages and placed singly in a slightly larger (45x45x45 cm) perspex observation cage. The floor of the cage was covered with sandpaper and in the middle of the floor was a small, clear plastic petri dish (9 cm diameter) which contained 20 grains of wheat. It had previously been found that intact animals made practically no errors in pecking at grain material on a sandpaper surface, thus the smooth surface of the petri dish made the scoring of feeding efficiency slightly easier by making the task a little more difficult for the birds. In some cases errors in pecking would cause the grain to be displaced to the side rather than grasped. Even in this situation the feeding efficiency of the intact birds was very high, most requiring not more than 25 pecks to consume the 20 grains. The birds were given three days trial experience in the test situation to ensure that they would reliably perform in it. They soon realized that food was available in the test cage and would quickly approach and consume it. Testing was carried out in a darkened room with the test cage lit from above with a 100w lamp, so that the birds are as little disturbed as possible by the presence of the experimenter.

The time taken to consume the food was noted and also the number of pecks directed at the food. Any other pecking behaviour, directed towards the floor or the sides of the cage, was not recorded. The time taken was recorded from the first peck at the food and if no approach was made within 5 minutes the test was terminated. 5 minutes was allowed after the approach to the food. This was normally more than enough time for the birds to eat the 20 grains but, if all were not taken before this time, the test was again terminated. In all cases after the bird had become used to the experimental situation the food was approached and some (usually all) was eaten. As noted above, the restricted feeding regime was in force so that the birds would be maximally likely to approach the food in the test situation.

4.3(d) **Results**

A summary of the pre-operative data and for the first 6 days after surgery is given in Table 4.1. Table 4.2 shows the same data for a group of animals receiving control surgical procedures. The surgery and the data collection was carried out in two groups of 12 animals. The pre-operative data is presented here only for those animals (9 in the surgical condition and 8 in the control surgical condition) which survived the operation.

In the test situation the birds rapidly approached and consumed the food with a very low ratio of pecks to grains. Post-operatively the pattern was quite different. It should be noted that the feeding efficiency test on day one after the operation was the first contact which these animals had with food, as the tests were carried out on the morning before the animals were fed. They showed no reluctance to approach and attempt to consume the food offered in the test situation, although the effect of the nerve section would be expected, from Zeigler's reports, to reduce feeding motivation. However the birds were in a greater state of food deprivation than normal as they had not eaten on the day of surgery and had not been fed on the last pre-operative day.

In most cases the effect of surgery was such that they were unable to consume any food, but made repeated unsuccessful attempts to eat. This is not the sort of behaviour which one would expect from animals with a tonic reduction in feeding motivation.

TABLE 4.1

FEEDING EFFICIENCY - TRIGEMINAL SECTION

BIRDS		PRE-OPERATIVE MEANS(4 DAYS)	SURGICAL PROCEDURE	POST-OPERATIVE DAYS					
				1	2	3	4	5	6
	TOTAL No. OF PECKS	25.7	OPHTHALMIC	56	73	24	2	0	0
1	PECKS/GRAIN TIME	1.29	+MAXILLARY	-	-	-	-	-	-
	FOR 20 GRAINS(SECS)	31.2		300	300	300	300	-	-
		20.7	OPHTHALMIC	221	15	75	33	39	36
2		1.30	+MANDIBULAR	-	-	3.75	1.65	1.95	1.80
		117.5		300	300	105	100	55	45
		20.2	ALL	73	6	0	0	0	0
3		1.18		-	-	-	-	-	-
		198.7		300	300	-	-	-	-
		26.7	MAXILLARY	64	26	26	24	30	26
4		1.34	+MANDIBULAR	3.2	1.3	1.3	1.2	1.5	1.3
		33.7		100	15	60	85	60	27
		20.0	ALL	114	3	7	5	2	0
5		-1.50		-	-	-	-	-	-
		188.7		300	300	300	300	300	-
		23.0	OPHTHALMIC	20	87	12	0	0	0
6		1.15	+MANDIBULAR	-	-	-	-	-	-
		46.7		300	300	300	-	-	-
		25.7	OPHTHALMIC	49	87	12	0	0	0
7		1.29	+MAXILLARY	-	-	-	-	-	-
		85.7		300	300	300	-	-	-
		23.5	OPHTHALMIC	175	70	288	0	13	0
8		1.17	+MANDIBULAR	-	-	-	-	-	-
		121.2		300	300	300	-	300	-
		24.0	MAXILLARY	39	38	37	34	41	40
9		1.39	+MANDIBULAR	1.95	1.9	1.85	1.9	2.16	2.0
		151.2		40	220	35	95	300	300

TABLE 4.2

FEEDING EFFICIENCY - TRIGEMINAL CONTROL

BIRDS		PRE-OPERATIVE MEANS(4 DAYS)	SURGICAL PROCEDURES	POST-OPERATIVE DAYS					
				1	2	3	4	5	6
	TOTAL No.OF PECKS	25.2	OPHTHALMIC	129	83	52	10	0	0
1	PECKS/GRAIN	1.26	+MAXILLARY	-	-	-	-	-	-
	TIME FOR 20 PECKS(SECS)	47.5		300	300	300	300	-	—
		22.5	OPHTHALMIC	85	43	28	29	27	29
2		1.15	+MANDIBULAR	21.25	2.87	1.4	1.45	1.35	1.45
		35.0		300	300	85	100	60	75
		22.0	ALL	137	58	26	29	31	26
3		1.27		-	2.9	1.3	1.45	1.55	1.3
		138.7		300	240	85	125	75	100
		25.5	MAXILLARY	33	26	28	24	25	30
4		1.27	+MANDIBULAR	1.65	1.3	1.4	1.2	1.25	1.5
		67.5		105	80	95	40	65	110
		22.0	MAXILLARY	28	32	24	24	23	27
5		1.30	+MANDIBULAR	1.4	1.6	1.2	1.2	1.15	1.35
		150		60	35	35	40	80	75
		24.5	OPHTHALMIC	92	127	63	38	29	31
6		1.22	+MANDIBULAR	5.41	6.35	3.15	1.9	1.45	1.55
		38.7		300	140	165	85	230	80
		25.0	OPHTHALMIC	225	123	21	0	0	0
7		1.25	+MANDIBULAR	-	-	-	-	-	-
		97.5		300	300	300	-	-	-
		19.2	OPHTHALMIC	74	133	21	3	0	0
		1.25	+MAXILLARY	-	-	-	-	-	-
		220		300	300	300	0	-	-

4.3(e) Nature of Feeding Efficency Deficits Produced

We clearly require to attribute some of the problems in feeding to the surgery per se and not to the effect of nerve transection, as the feeding efficiency is seen to be reduced in the control as well as the experimental group (Tables 4.1 and 4.2).

There were two sorts of error which were observed in the post-operative birds.

1) Clear faults in the mechanism of mandibulation (as described by Zeigler). On some occasions the birds would be able to catch hold of a grain, but would be unable to execute the motor behaviour necessary to get the grain from the tip of the beak to the back of the mouth to be swallowed. The typical pattern would be that the bird would peck downwards and grasp the grain; the head would then rise but at the point where the grain would normally be flicked to the back of the mouth by the action of the tongue together with the motion of the head, the grain would fall from the beak. This was observed repeatedly in the experimental group but, although their ratio of pecks to grain eaten was slightly higher immediately after the operation, was rarely seen in the control group.

2) Ballistic errors

The birds would direct a peck at a grain but strike to one side rather than making contact. This type of error was encountered in the control surgical birds as well as the experimental birds and thus is most likely attributable to some artefact of the surgery. Ballistic errors were found only in the cases of the birds which had received control or actual ophthalmic branch surgery. The point of approach to the ophthalmic branch (see above and Figure 4.3) involves retraction of the eyeball. It seems likely that the ballistic pecking errors are a direct result of this mechanical displacement of the eyeball resulting in a displacement of vision which persists for some time after the surgery. The degree of actual displacement and the persistance of the effect would be related to the amount of damage done to the eye musclature or to membranous material around the orbit. Also, as some degree of bleeding (often severe) was always associated with the surgery in the ophthalmic region due to the close proximity of the nerve to a blood vessel, it is likely that the formation of small clots could also help to displace the eye to some extent.

A further contribution to the ballistic problems of pecking after intervention in the ophthalmic region was noted by Dr. Deitrich Meyer in a reported discussion of a paper presented by Zeigler at the New York Academy of Sciences (1977). Meyer pointed out that pigeons and some other birds have musclature inside the retina which has been thought to contribute to some fine tuning system of visual control. Some evidence suggests that this musclature receives connections from the ophthalmic brands of the trigeminal nerve, thus section of this branch would lead to a disruption of the muscle system and associated problems of visual control. Apart from the fact that this would be likely to be a rather subtle effect rather than the gross mispecking observed with the doves, this could not explain the occurrence of the effect after the control surgical procedures (unless some unrealized damage was being done).

It is strange that these very marked ballistic errors do not seem to be present in the post-operative nerve sectioned pigeon. Zeigler, Miller and Levine (1975) note a slight reduction in the probability of contact with the grains associated with a slight displacement of the beak. This amounts to a reduction from 99% in the intact bird to 87% in the one and two branch sectioned animals and to 73% in the three branch sectioned animals. This is relatively small as compared with the deficits found here, and the suggestion that it is not related to eyeball displacement comes from two cases of serial section in which the deficit did not show itself until the third stage of the operation and this third stage was not the ophthalmic branch. As mentioned in the above section on surgical procedures however, the surgery does seem to be more difficult to perform in the doves than the pigeon, probably due to the smaller size of the animal. Zeigler, Miller and Levine (1975) report that the bilateral section of the ophthalmic branch of the nerve could be carried out in 15 minutes with little or no blood loss. In the present study it was found to take up to three times as long with some degree of blood loss being inevitable. Thus the greater physical trauma associated with the surgery in the doves may account for the greater mechanical deficit.

4.3(f) Recovery of Feeding Efficiency

Tables 4.1 and 4.2 summarise the behaviour of the birds in the test situation over several days following the surgery. It can be seen that they fall into one of two different categories. Either 1) attempts to eat persist and the birds eventually return to some degree of success in feeding from the dish, or 2) they completely give up, showing little or no tendency to approach after several days.

In the birds which do return to feeding, some degree of reduction of efficiency can be seen in the increased ratio of pecks to grains eaten in the experimental group. The most obvious effect however is the complete absence of any attempt to eat in many of the birds. It is felt that this very gross effect is quite likely to be due to the visual disturbance of pecking as it occurs in all but one of the experimental group after ophthalmic section and in three of the control group all of which had received surgery involving eyeball retraction.

If this deficit is due to visual displacement, then it is important to note that birds appear to be characteristically poor at visual adaptation and recovery after visual displacement produced by wedge prisms (Hess, 1956; Gregory, 1966). Although ways in which experiments might be designed to demonstrate adaptation in birds have been suggested by Arlinsky (1967), the basic finding does seem to stand (Moray and Jordan, 1967). It might be the case then, that such visual displacement would be particularly disruptive to birds and might not be overcome until the physical cause had healed and passed away.

It should be noted (see below and Table 4.3) that the birds which showed little or no approach to food in the test situation, showed a virtually normal pattern of food intake in the home cage. Thus it could be that the birds were finding it quite easy to catch hold of and eat single grains in the home cage where food was available in large quantities, but had learned that the pecking of single grains from the smooth dish in the test cage was beyond them and had given up attempting to feed in that particular situation. We should not conclude a reduced motivation then, from the absence of approach to food (especially as this also occurs in the control animals) but to an extinction of responding in a particular situation due to lack of success.

4.3(g) Food Intake and Body Weight Regulation

If the effect of visual displacement is excluded, it is still the case that the section of the trigeminal nerve did lead to very obvious disturbances in the sensory motor control of feeding behaviour. The birds found it difficult to grasp grains in the beak and, if a grain could be caught, to control the movements necessary to get the grain from the tip of the beak to the back of the throat to swallow. In fact, it is difficult to imagine that such effects would not be produced by this sensory denervation. However, it is by no means clear from the present data that there was any associated deficit which could be described as "motivational."

Tables 4.3 and 4.4 summarize the findings on food intake and body weight loss in the experimental and surgical control groups of birds, While the animals were trying unsuccessfully and subsequently refusing to feed in the test situation, they semmed to be quite able to eat, and to regain the weight loss due to pre-operative deprivation. Two animals did show a transient effect, being aphagic for one day after the operation, but these animals both showed clear approach to food on the first day of the test situation.

The immediate approach and consumption of food by the experimental birds might be attributable to the loss of body weight due to the necessary pre-operative deprivation of food, were it not for the fact that there is no sign that the experimental group take a longer time to recover body weight after surgery than do the control group.

TABLE 4.3

FOOD INTAKE AND BODY WEIGHT - TRIGEMINAL SECTION

(BIRDS FED 1 HOUR PER DAY - 3 pm to 4 pm)

BIRDS	1	2	3	4	5	6	7	8	9
DAYS OF APHAGIA	0	0	0	0	0	0	1	1	0
DAYS TO BASELINE WEIGHT	6	5	3	7	4	5	5	4	5
DAYS OF 0 OR NEGATIVE WEIGHT GAIN	0	0	0	0	0	0	1	1	0
BASELINE WEIGHT	153	138	149	158	159	155	173	160	154

Mean Body Weight = 155.4 (S.D. = 9.369)

TABLE 4.4

FOOD INTAKE AND BODY WWEIGHT - TRIGEMINAL CONTROL

(BIRDS FED 1 HOUR PER DAY - 3 pm to 4 pm)

BIRDS	1	2	3	4	5	6	7	8
Days of Aphagia	0	0	0	0	0	0	0	0
Days to Baseline Weight	7	3	5	5	4	3	4	6
Days of 0 or Negative Weight Gain	0	0	1	0	0	0	0	0
Baseline Weight	139	148	143	152	157	135	160	151

Mean Body Weight = 148.1 (S.D. = 8.659)

4.3(h) Conclusions

The above experiment supports previous reports that trigeminal nerve section leads to a disturbance of the sensory and motor control of feeding, but they provide no evidence of an associated "motivational" disturbance or a reduction in responsiveness to food. In addition mandibulation deficits, although present immediately after surgery, do not persist in the doves as long as Zeigler's data would indicate them to persist in pigeons, but can be overcome by experience.

The first obvious problem with this present study is the fact that the animals were on a restricted food availability schedule, and thus might be seen as being in a chronic state of food deprivation. Zeigler (1975) has demonstrated that the response of animals to food deprivation is essentially the same before and after the trigeminal nerve section. That is, even in the hypothesised state of tonic reduction in feeding motivation produced by nerve section, the energizing effect of food deprivation can still be seen. In fact, if nerve section is carried out after the animals have been reduced to 80% of their normal resting body weight then the effect of the surgery is markedly reduced. This is analogous to the experiments carried out to study the changing "set point" hypothesis about the effect of lateral hypothalamic lesions in rats (Powley and Keesey, 1970). It was found that a lesion which would lead to aphagia in a normal weight animal would be followed by a greatly reduced effect (or even a mild post-operative hyperphagia) if the animal's body weight was reduced prior to the operation being carried out. Aphagia after LH lesion then, was seen as a perfectly adaptive attempt (in the abnormal context) to reduce body weight to a new, lower baseline level. It is perhaps the case then, that the failure to find an effect in this study was due to the abnormal regime of food availability. Although the animals were eating just as much as they had previously done they were probably spending part of the day in some degree of food deprivation. Perhaps this was enough to goad the birds into eating when they otherwise would not have done.

4.4 Experiment 2

To test this hypothesis, the surgery was repeated on a second group of birds which were maintained on an ad libitum food regime.

4.4(a) Method

There were 18 female birds used in this study of which 14 survived the surgery. They were housed in identical conditions to the first group, but had continuous availability of food for the whole of the 9 hour (9 am to 6 pm) light cycle. In each case bilateral section of the ophthalmic and mandibular branches of the trigeminal nerve were made. On the basis of experience with the first group and with preliminary trials of the surgical procedure, it was decided that the amount of damage which could be done to the maxillary branch of the nerve probably did not merit the extra time taken to perform the surgery and the consequent added risk that the animal would not survive. Zeigler too notes that the section of the maxillary branch was meritably less extensive in his procedures because of the degree of branding at the only point of access. As it was nearly always possible to remove large sections of both the mandibular and the ophthalmic branches, one could be completely confident about the success of the surgery in these cases, but this was never so of the maxillary branch.

In addition to the experimental group, 6 animals (of which 5 survived) were given the control surgical treatment in which all of the preliminary approaches were made without cutting the nerve.

4.4(b) Results

The effects of trigeminal section on food intake were again minimal. Tables 4.5 and 4.6 summarize the data for the experimental and control groups respectively. In this case two of the experimental birds showed a mild aphagia but no more. With conditions as close to those used by Zeigler as possible, the effect of trigeminal section cannot be reproduced in the Ring dove.

4.5 Interpretation of the Differences between the Pigeon and Dove Findings

Why should an effect reported to be as pronounced as that found after trigeminal section in the pigeon be impossible to replicate with similar procedures in such a closely related species as the Ring dove? A number of possible explanations must be discussed.

4.5(a) Reliability of Surgical Procedures

One is always open to the fear that there might be something

TABLE 4.5

FOOD INTAKE AND BODY WEIGHT - TRIGEMINAL SECTION

(BIRDS FED AD LIBITUM)

BIRDS	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Days of Aphagia	0	0	2	0	0	0	0	0	0	0	0	1	0	0
Days to Baseline Weight	10	6	8	7	3	4	4	9	6	12	4	9	16	5
Days of 0 or Negative Weight Gain	0	0	2	0	0	0	0	0	0	0	0	2	0	0
Baseline Weight	139	141	146	127	134	147	142	145	141	153	148	151	160	141

Mean Body Weight - 143.9 (S.D. = 8.138)

TABLE 4.6

FOOD INTAKE AND BODY WEIGHT - TRIGEMINAL CONTROL

(BIRDS FED AD LIBITUM)

BIRDS	1	2	3	4	5
Days of Aphagia	0	0	0	0	0
Days to Baseline weight	8	3	7	5	5
Days of 0 or Negative weight gain	0	0	0	0	0
Baseline weight	130	135	145	141	153

Mean Body Weight = 140.8 (S.D. = 8.898)

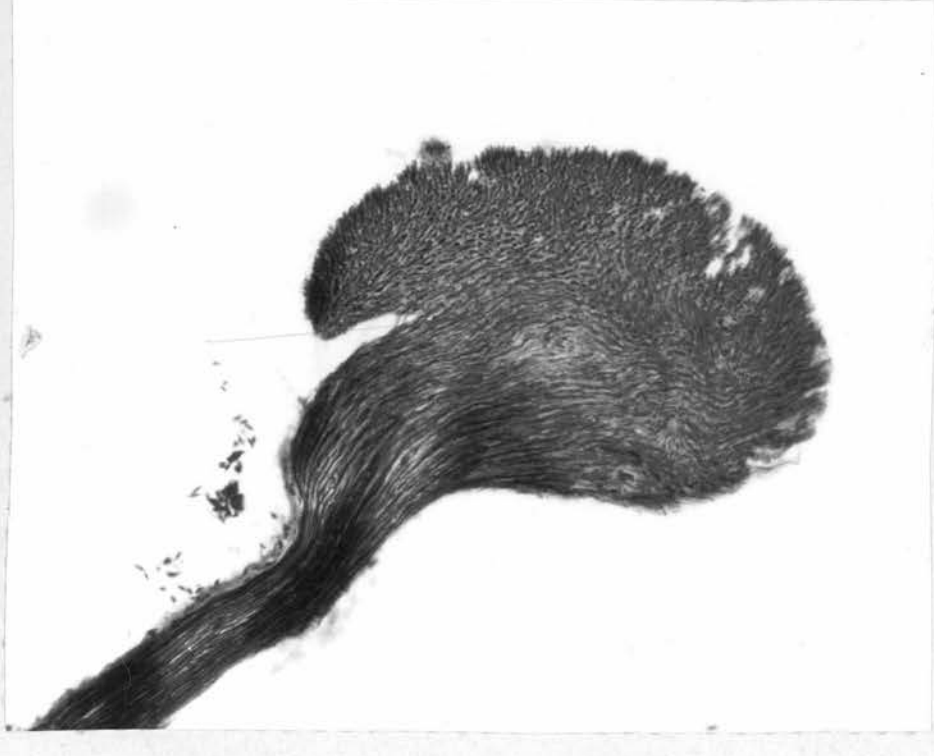
profoundly wrong with one's experimental procedures when such a large discrepancy exists between results reported by another and one's own experimental findings. As was mentioned above, the procedure adopted for the second experiment was to perform section on only the mandibular and ophthalmic branches of the nerve, and to abandon attempts to cut the maxillary branch. Although examinations of Zeigler's reported work indicates a high degree of variability of effects produced, he does report very striking effects after only one or two branch surgery, so it is unlikely that the fact that damage in this case was confined to two sensory branches can account for the present findings.

It is possible that the surgery performed on the two branches which were cut was incomplete in some way. This is highly unlikely for several reasons. First of all, the sensory-motor disturbance of mandibulation was found after the surgery in the doves. This does suggest that the surgery was adequate if any of the associated effects are found. However, the strongest piece of evidence to suggest that the surgical procedures were being performed fully and correctly is the fact that the procedures are so gross that one can be immediately certain of success. In the cases of the mandibular and ophthalmic branches no mistakes can be made.

In order to dispel any doubts however, surgery was performed on a further 2 birds and pieces of the tissue removed were fixed, sectioned and stained to confirm that the material was actually nerve (Figure 4.9). After establishing that no marked effect of nerve section followed, the birds were immediately sacrificed and dissected to check that the nerve had indeed been removed. This too confirmed that the surgery itself was not the root of the problem.

FIGURE 4.9

Sections of tissue removed during surgery, and stained to verify that it was nerve material.



4.5(b) Differences between the Two Species

As noted above the Ring dove (Streptopelia Risoria) and the pigeon (Columba Livia) are very similar animals as far as anatomy and feeding behaviour are concerned. It seems therefore highly unlikely that the interruption of what is a very basic sensory system in both birds would have such a profound effect in one and little or no effect in the other. This is particularly so as Zeigler has reported analogous effects (although not immediately comparable effects because of the differences in procedure) to those found in the pigeon, by electrolytic lesions of the trigeminal sensory roots in the rat (Zeigler et al., 1974; Marwine and Zeigler, 1975; both cited in Zeigler 1976) and also by central trigeminal lesions (Zeigler and Karten, 1974). Although the exact interpretation of these effects is open to question, the work does indicate that Zeigler considers the importance of the trigeminal system to extend beyond the pigeon or even the avian case.

It may be possible however to find reasons related to the two species past breeding history which would contribute to the differences in effect. Of particular importance might be the fact that the White Carnaeux or Silver King pigeons (used by Zeigler) have been selectively bred for the table. For almost 100 years strains of pigeons have been systematically produced with the objective of rapid and high weight gain in mind. Indeed the name "Carnaeux" indicates the preoccupation with commercial meat production. Although the weight range reported by Zeigler (1975) of 400 to 800 grams for 2 to 6 year old birds is not high compared with the breed standard weights of about 680 to 850 grams for a cock and 625 to 795 for a hen (Levi, 1957) it seems likely that the "standard" bird bred for meat production is carrying a fair amount of extra flesh. Just as it was earlier suggested that the effects of both trigeminal section (Zeigler, 1975) and LH lesion (Powley and Keesey, 1970) can be decreased by enforced body weight loss, so it may be the case that the extra body weight carried by the pigeon stock used by Zeigler (which were obtained from a commercial breeder whose normal market would be for food) would lead to an increased probability of producing aphagia (whatever the mechanism). The Ring doves used in the present study however have certainly never been systematically selected for high body weight. Neither is there any evidence however to suggest that they would be chronically under weight in any way analogous to the enforced body weight loss used in the above mentioned studies, making such an explanation unlikely.

4.6 Summary

Using laboratory conditions and surgical techniques which appear to be similar to those described by Zeigler, it has proved to be impossible to reproduce with doves the findings on food intake and body weight regulation of the trigeminal section which he has reported with pigeons.

The following chapter will show that, although the very gross effects on food intake after sensory deafferentiation cannot be found, the pattern of feeding behaviourhis clearly altered by the surgical intervention. Chapter 6 will attempt to present a reformulation of the significance of trigeminal section effects.

4.7 Chapter Summary

The surgical procedures and techniques used in the present study for the bilateral section of the Ophthalmic, maxillary and mandibular branches of the trigeminal nerve of the Ring dove were described. Data were then presented on the effects of such nerve section on:

1) The sensory control of feeding behaviour, and
2) Food intake and body weight regulation.

It was found that the effect of the surgery on the sensory-motor control of feeding was twofold; the first disruption was that of the directional control of the pecking response and the second was that of mandibulation of food items in the beak. Surgical control procedures suggested that the former effect was an artefact of one of the surgical procedures which involved the retraction of the eyeball to gain access to the ophthalmic branch of the nerve, thus causing a temporary displacement of vision. The latter deficit did seem to be attributable to the cutting of the sensory nerve per se.

Although the motor control of feeding was affected, there appeared to be little effect of nerve section on food intake and body weight regulation. This lack of effect was found both in birds maintained on a restricted availability of food (1 hour per day) and in birds maintained on ad libitum food availability.

Possible reasons for the discrepancy between these findings and those previously reported by Zeigler using pigeons were discussed, but no convincing explanation was found.

CHAPTER 5

5.1 Patterns of Feeding in Birds after Trigeminal Section

In the previous chapter, the effects of trigeminal section in the Ring dove on gross measures of body weight and food intake were shown to be minimal. It was felt that a study of temporal distribution of feeding behaviour in operated birds on recovery of their pre-operative body weights might show some more subtle changes in alementary behaviour and responsiveness.

5.2 Experiment 1

Data were collected from a group of birds which had received bilateral section of two branches of the trigeminal nerve as described in the previous chapter, and also from a group which had received control surgery, at least one month but not more than two months after the date of the surgery. All of the birds used had, by this time, "recovered" from any effects of the surgical procedure in that they had at least regained and often exceeded their pre-operative weights, and showed no sign of any disturbance of the sensory control of feeding as determined by informal observations in the home cage.

5.2(a) Method

Birds were transferred to the room in which the photocell feeding devices were used and allowed at least three days to settle in the cages with the feeders attached. The light cycle (9 hours of light from 9 am to 6 pm) was the same as that in force in the room in which they had previously been housed, so no time was needed for them to become accustomed to the change. The birds had constant, free availability of water and grit, and also of the normal mixed grain feed in the photocell feeders. Data was collected for each animal for at least seven days.

5.2(b) Results

The most obvious effect of nerve section was observed in one bird (T131G) which repeatedly showed some feeding activity in the early hours of the morning before the house lights were switched on. This was particularly interesting as such behaviour had never been observed in the intact birds, neither was it seen in the control surgical animals. Van Hemmel and Myer (1969) report "almost" no occurences of nocturnal feeding in their quail. Zeigler (1976) reports "no evidence of eating during the dark phase of the cycle", although the diagrams which he presents (reprinted from Zeigler, Green and Lehrer, 1971) clearly show a large amount of feeding to be occurring outside the 6 am to 6 pm period of light. Reference to the original paper indicates however that the occurrences of feeding behaviour during the "dark" were probably due to the fact that the laboratory was not fully light tight and thus there would be some degree of illumination before and after the artificial "day". As the cubicles in which the doves were housed and in which the feeding pattern data were collected were almost completely light tight and are notadjacent to rooms which receive illumination from outside, the only illumination in the room at the times at which this bird (T131G) was feeding during the night would have been coming from the very weak lamp used to provide the beam for the photocell.

In addition to feeding activity occurring at 3 and 4 in the morning, the records show that periods of feeding also often occurred immediately before the onset of the light cycle at 9 am. As mentioned in the section on feeding patterns in Chapter 3, the normal procedure was to check the hoppers daily at this time to ensure that the food was properly shaken down. It would appear that this brief period of intervention (in which the lights were not switched on) was enough to arouse the bird's interest in the food and to start a bout of feeding.

Several of the other birds showed occasional small amounts of feeding at the point immediately before light onset which again was presumably due to experimenter intervention. That this is so is suggested by the fact that such early meals were often seen to coincide in cases in which data from two or three birds were collected at the same time. That the coincidence is not due to some obscure mechanical fault in the recording equipment on the other hand, is suggested by the fact that the onset may be coincident but the time spent feeding is variable. Again, these brief periods of approach to food stimulated by experimenter intervention are not seen in the feeding behaviour of intact birds.

It was argued by Zeigler that the birds whichhhad received section of the trigeminal nerve were in a state of chronically reduced responsiveness to food. These present data support the opposite conclusion that the trigeminal sectioned doves are more rather than less motivated to approach food, if feeding behaviour can be so easily stimulated out of the normal context.

Such observations, along with the cases of birds T325G and T480G which showed very marked morning peaks of feeding activity as opposed to the usual afternoon peak, suggested that a significant switch in the diurnal distribution of feeding behaviour would be found to have taken place after trigeminal section. However, figure 5.1 (which should be compared with figure 3.12 in chapter 3) shows that the pattern exhibited by the trigeminal group as a whole is not obviously different from that previously found in the normal intact birds. And there are always intact birds which tend to show pronounced morning pecking. It should be noted that for the purpose of this analysis (Figure 5.1), any of the above mentioned occurrences of feeding immediately prior to light onset were included in the 9 am to 10 am hour. Even when this was done no significant effect was found.

When the data is presented synchronized for the peak hour (Figure 5.2; compare with figure 3.13) as described previously, it can be seen that the activity in the peak hour is still very great. The large size of the morning peak is due however, to the over-representation of some of the animals when the numbers from which the means are computed are very small.

5.2(c) Frequency of Meal Taking

Logarithmic survivorship plots were again used to determine the appropriate inter-feeding-interval criterion for each bird, and the frequency of meal taking was then computed. Comparing the meal frequency of the trigeminal animals with that of the control surgical

FIGURE 5.1

Mean percentage of daily total time spent feeding in each hour of the day by birds after bilateral section of the trigeminal nerve (means of 11 birds).

Data for individual birds given in Table 6 (Appendix II).

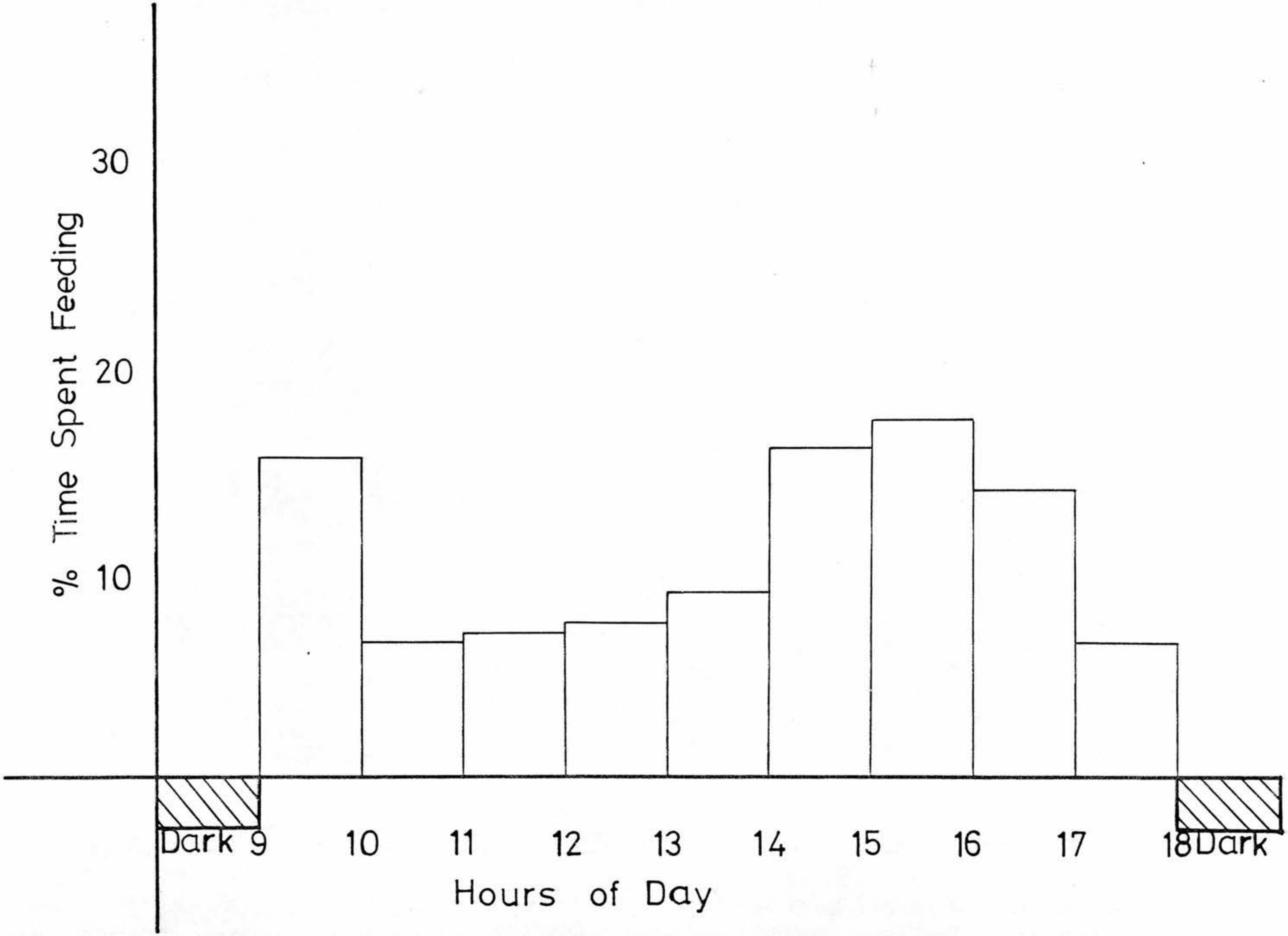
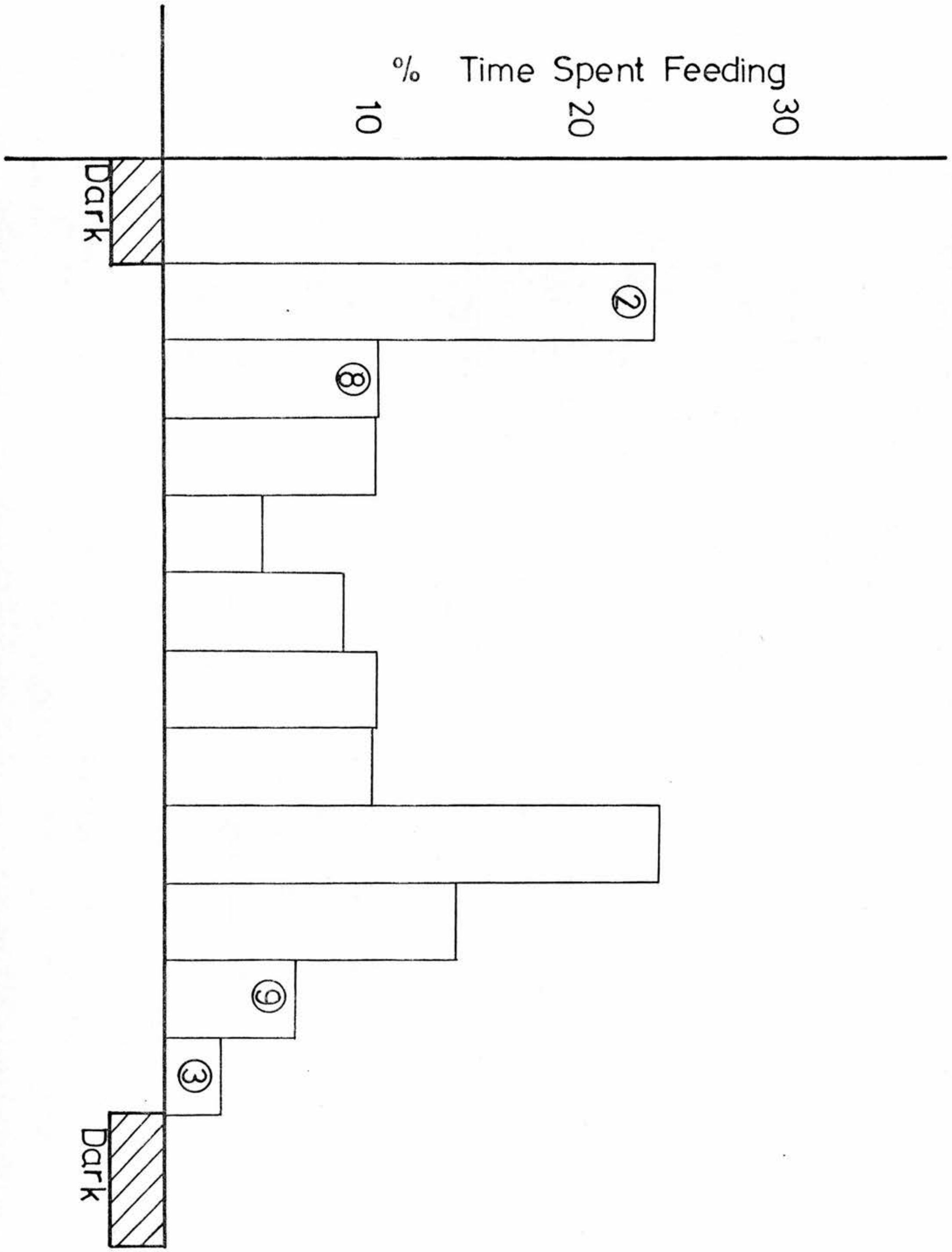

% Time Spent Feeding
30
20
10
Dark 9
10
11
12
13
14
15
16
17
18Dark
Hours of Day

FIGURE 5.2

Percentage of daily total time spent feeding in each hour of the day by birds after bilateral section of the trigeminal nerve, synchronized so that the peak of feeding by each bird contributes to the same mean (indicated [p]). Figure represents data from 11 birds, and numbers associated with some of the bars indicate the number of individual items contributing to those particular means.


% Time Spent Feeding
10
20
30
Dark
②
⑧
⑨
③
Dark

animals we find that the trigeminal animals are taking significantly fewer meals (Mann-Whitney "U"=7.5; $p < 0.002$, two-tailed test). They are also taking significantly fewer meals than the previously discussed intact animals ("U" = 17.0; $p < 0.002$, two-tailed test). As the animals had regained any weight which was lost in association with the surgical procedures, it must be the case that they are eating the same amount of food but are doing so in fewer meals. Although comparison of meal size is not meaningful when only a time spent feeding measure is available and there is such obvious variability present between animals in the mean daily time spent feeding, we must conclude that a reduced meal frequency associated with a normal pre-operative level of food intake and body weight is a result of the birds feeding in fewer, larger meals.

At this point however, it was realized that one could not reasonably compare meal frequencies between groups without establishing that the derived logarithmic survivorship criteria of inter-meal-interval are equivalent. Figure 5.3 shows the distribution of the derived criteria for the three groups of birds. It can be seen that there is something distinctive about the temporal patterning of feeding of the trigeminal sectioned animals which is evidenced by longer appropriate inter-feeding-interval criteria to define meals. That is, the trigeminal birds appear to break off for longer periods within an ongoing meal. Can we now say that there is a true difference between trigeminal and control birds in their frequency of meal taking?

It was argued in Chapter 3 that the procedure of Kissileff (1970) of presenting analysis of feeding patterns in his rats derived from data ordered by several widely separated inter-feeding-interval criteria to

FIGURE 5.3

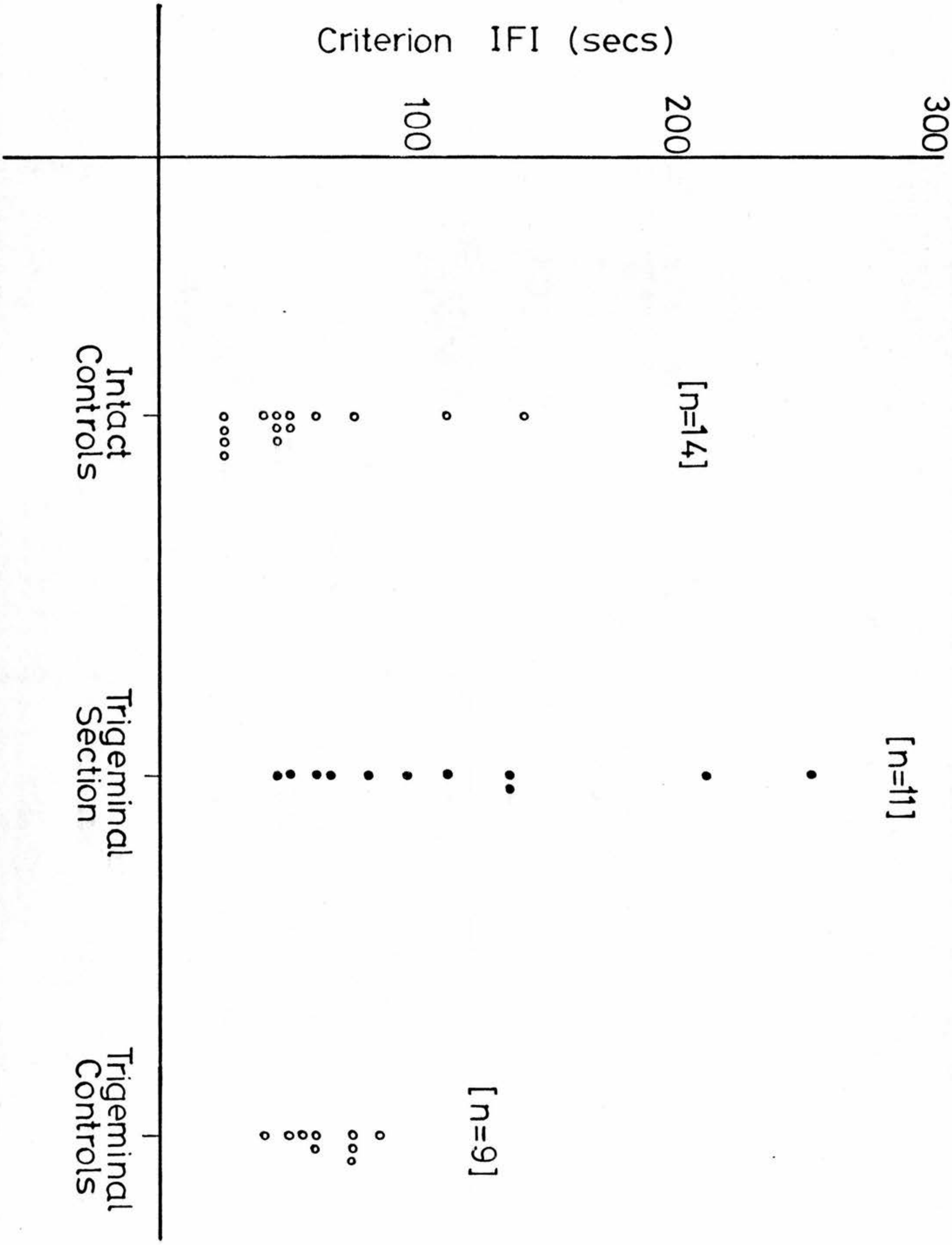
Criterion inter-feeding interval (IFI) derived from individual logarithmic survivorship plots for birds in Intact Control (Table 2; Appendix II), Trigeminal Control (Table 5; Appendix II) and Trigeminal Section (Table 4(a); Appendix II) groups.

Significance of comparisons tested with a Student's "t" test.

	"t"	"F"	Significance (p < ; two tailed)
Intact vs. Trigeminal	2.8389	3.8772	0.01
Control Trigeminal vs. Trigeminal	2.1304	20.9692	0.05

Also a Mann-Whitney "U" Test.

	"U"	Significance (p < ; two tailed)
Intact vs. Trigeminal	26.5	0.02
Control Trigeminal vs. Trigeminal	25.5	0.05


Criterion IFI (secs)
100
200
300
Intact Controls
[n=14]
Trigeminal Section
[n=11]
Trigeminal Controls
[n=9]

confirm the reality of efferts discussed, was potentially throwing away information as there could be no way of knowing that any of the criteria used were meaningful. For this reason the logarithmic survivorship technique was used to obtain an objective estimate of the appropriate interval length. It would seem now however, that there is no way of confidently talking about meal frequency or changes in meal frequency across groups without adopting Kissileff's procedure. The meal frequencies were therefore recompared using a blanket criterion of 250 seconds. This was chosen as it was equal to the highest criterion derived from the logarithmic survivorship plots. Figure 5.4 shows the meal frequencies of the three groups using the originally derived criteria and the 250 second criterion. The larger the criterion used, the smaller will be the computed meal frequency. Further, the larger the difference between the criterion used previously and derived from the logarithmic survivorship plot and the blanket criterion of 250 seconds, the larger will be the potential reduction in computed meal frequency. However, the validity of the use of the survivorship technique rests on the fact that changes in chosen criterion below that which are predicted by the plot should have more effect than changes above that predicted.

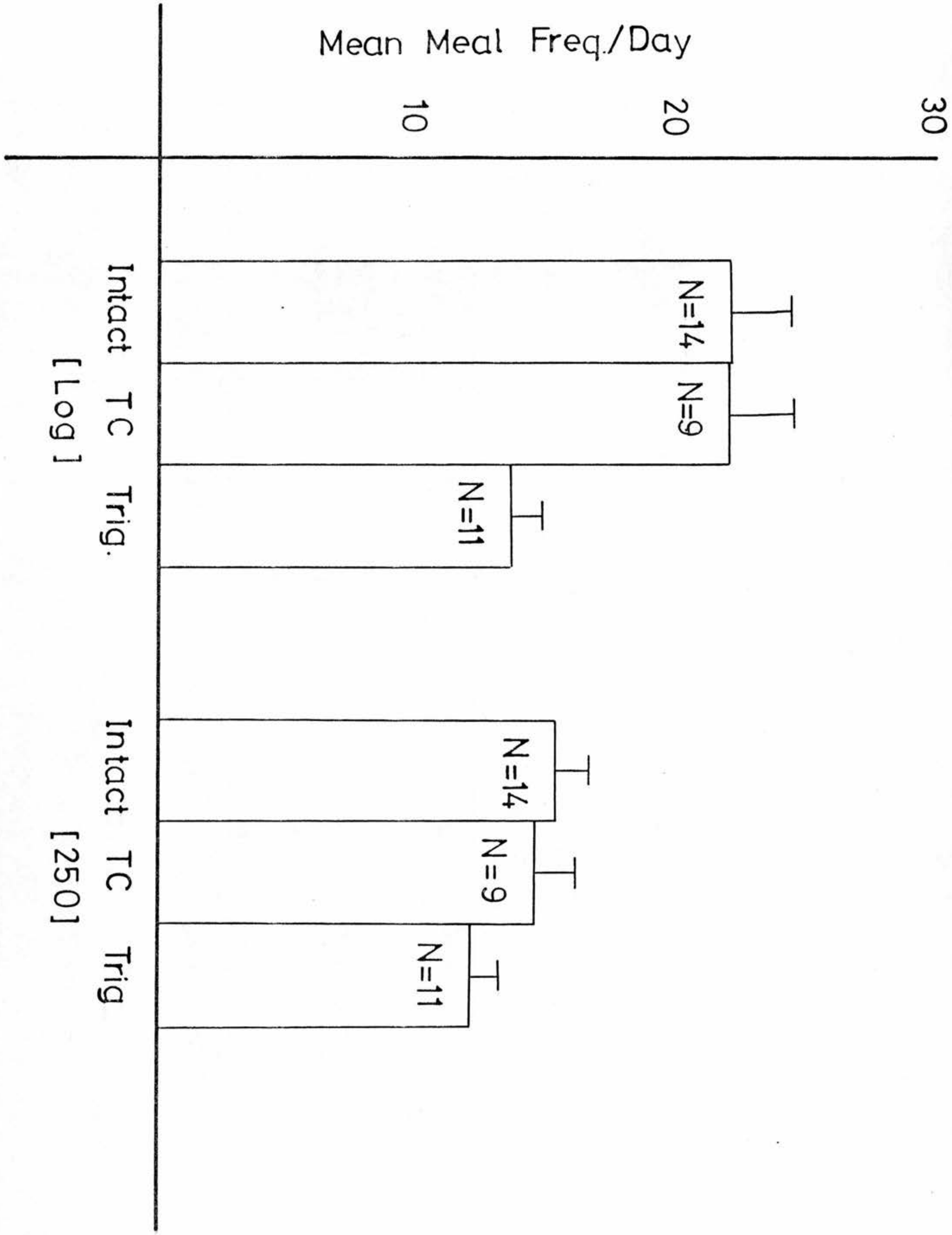
It can be seen from figure 5.4 that the differences are still present when the 250 second criterion is used, but are somewhat reduced and not significant using a Mann-Whitney "U" test. Although non-parametric statistics were normally used, a parametric test would seem to be acceptable. The comparison between the trigeminal animals and the intact controls is significant then, if a Student's "t" statistic is used ($t = 2.1468$; $F = 2.2631$; $p < 0.05$, two-tailed test).

FIGURE 5.4

Mean frequency of meal taking of birds in Intact Control (Table 2; Appendix II), Trigeminal Control (Table 5; Appendix II) and Trigeminal Section (Table 4(a); Appendix II) groups, with continuous record ordered on the basis of criteria derived from logarthmic survivorship plots (log) or on the basis of a "blanket" criterion of 250 seconds (250).

Significance of comparisons tested with a Mann-Whitney "U" Test:

	"U"	Significance (p < ; two tailed)
Log. Criterion		
Intact vs. Trigeminal	17.0	0.002
Control Trigeminal vs. Trigeminal	7.5	0.002
"Blanket" Criterion		
Intact vs. Trigeminal	42.0	N.S.
Control Trigeminal vs. Trigeminal	35.5	N.S.


Mean Meal Freq./Day
10
20
30
N=14
N=9
N=11
Intact
TC
Trig.
[Log]
N=14
N=9
N=11
Intact
TC
Trig
[250]

5.2(d) Conclusion

There is some evidence to suggest that the temporal patterning of feeding behaviour is changed as a result of trigeminal section. Birds seem to break off for longer within an on-going meal as a result of the surgery, as evidenced by the shapes of the logarithmic survivorship curves. Some evidence exists that the frequency of meal taking is reduced by the operation, but the fact that this effect can be markedly reduced by changing the inter-meal-interval criterion makes conclusions a little difficult.

5.2(e) Time of Feeding Onset

As mentioned above, some birds showed feeding behaviour outside the period of the light phase of the cycle as a result of the nerve section. It was suggested that this indicated them to be more rather than less motivated to approach food than were the intact and surgical control animals. As body weight was being regulated normally, this change in feeding tendency might be associated with a change in the overall diurnal pattern of food intake towards a situation in which the birds are more hungry at the start of the day. An examination of this overall diurnal pattern however showed no change in most of the birds, with only a few showing very marked morning peaking of feeding. It was hoped that as the cues to think along these lines came from indications that some birds were approaching and starting to feed with very little encouragement, the latency to onset of feeding first thing in the morning might be a reasonable measure in which to predict a change which would show itself in the whole group.

The mean time at which each animal began feeding after light onset was computed for the trigeminal and trigeminal control groups. Unfortunately it was felt that the use of the original group of birds as intact controls would not be reasonable in this case as the exact time of light onset was not known. Dawn was normally timed to occur at 9 am on the hour, but as the time switch had been adjusted for other reasons since the original data were collected and before the trigeminal data were collected one could not be confident that the time of light onset was the same, except to within the accuracy with which it can be set (which would be several minutes). It was not realized that to know the exact time of "dawn", when the prelminary data were collected, would be quite so important.

Once set however, the time switch was relatively accurate and constant. As a test of this carried out later, a fifth photocell switch was set in the room in which the birds were housed and attached to the data logger, so that an exact estimate of the variance in the time of light onset could be made. The mean time of onset was 3.71 minutes after 9 am with a standard deviation of 0.62 from 12 days of observation.

For the purposes of this analysis, a second intact control group has been used. This data was collected as part of a study of the effects of food type on feeding patterns which will be considered in a later chapter. We can be confident that the time of light onset is the same for this group within the limits of the above noted variance as the time switch was not adjusted between the collection of the trigeminal data and these data.

As predicted, the time of onset of feeding in the trigeminal animals is earlier than that of the control surgical group (t = 3.1322;

$F = 1.0407$; $p < 0.005$, two-tailed test) and that of the intact control group ($t = 2.1151$; $F = 5.4859$; $p < 0.05$, two-tailed test). The comparison between the trigeminal group and both of the control groups is significant at the level of $p < 0.01$ ($t = 2.5389$; $F = 3.4433$) (Figure 5.5).

5.2(f) Conclusions

Although the animals in the group had recovered from any obvious effects of the surgical procedures, they can be seen to be starting the day hungrier than the control groups and with a stronger rather than a weaker tendency to approach food and initiate feeding.

5.2(g) Time Spent Feeding After Trigeminal Section

If there are any effects of the operation performed on those animals on their efficiency of feeding, we might expect to find an increase in the mean daily total time which they need to spend feeding in order to obtain enough food. Thess does not appear to be any evidence of this (Figure 5.6) and indeed the comparisons are all non significant.

This might be due to the fact that the time between surgery and the recording of these feeding opatterns was sufficient for any recovery of efficiency due to learning and experience to take place. It is also obvious however that, as noted in the previous chapter, the reduction of efficiency seen clearly in the feeding test situation did not produce any very marked effect on food intake in the home cage as indicated by

FIGURE 5.5

Mean time of onset of feeding in minutes after "dawn", in birds in Intact Control (Table 8; Appendix II), Trigeminal Control (Table 5; Appendix II) and Trigeminal Section (Table 4(a); Appendix II) groups.

Significance of comparison tested with a Student's "t" test.

	"t"	"F"	Significance (p < ; two tailed)
Intact vs. Trigeminal	2.1151	5.4859	0.05
Control Trigeminal vs. Trigeminal	3.1322	1.0407	0.005
Both Controls vs. Trigeminal	2.5389	3.4433	0.01

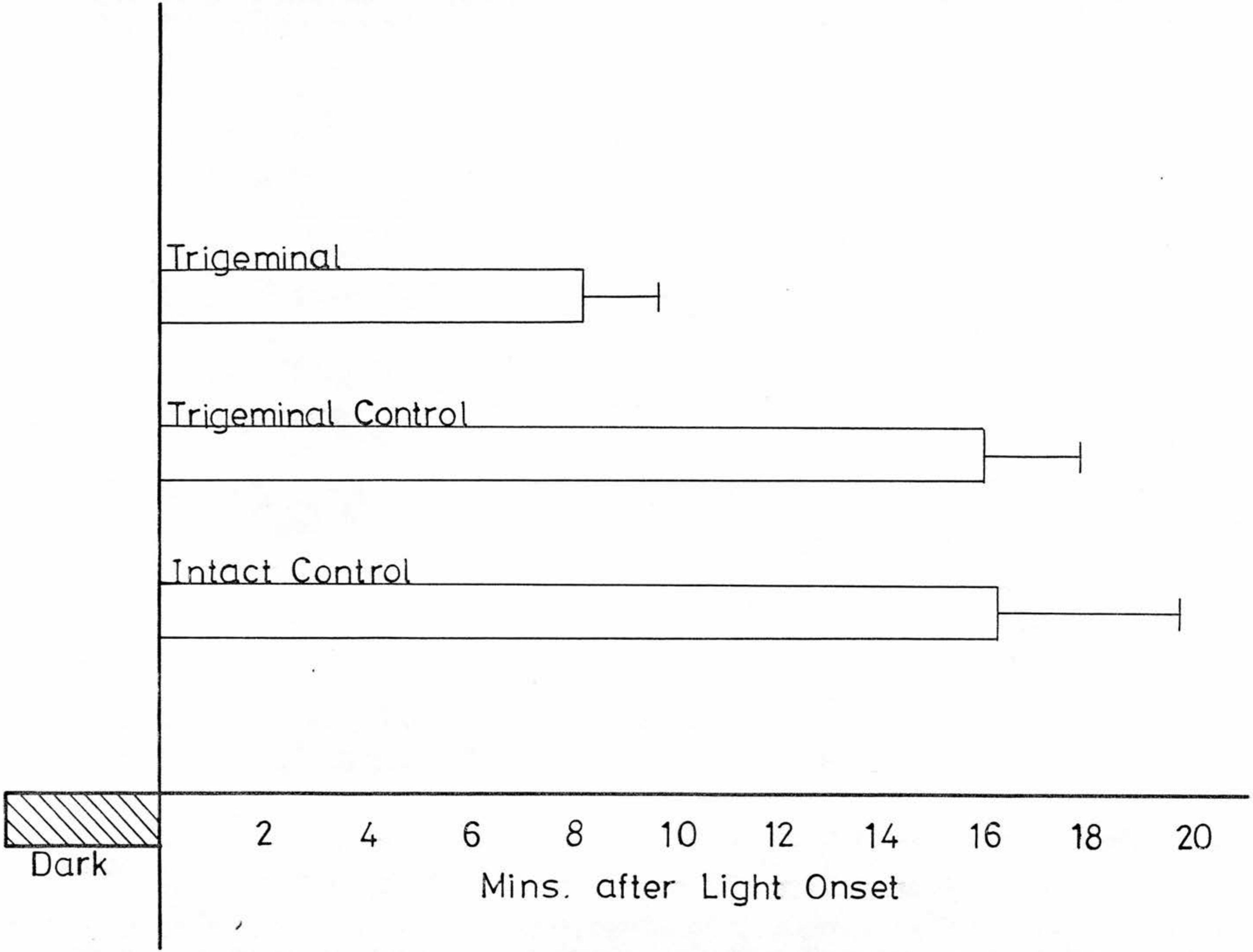
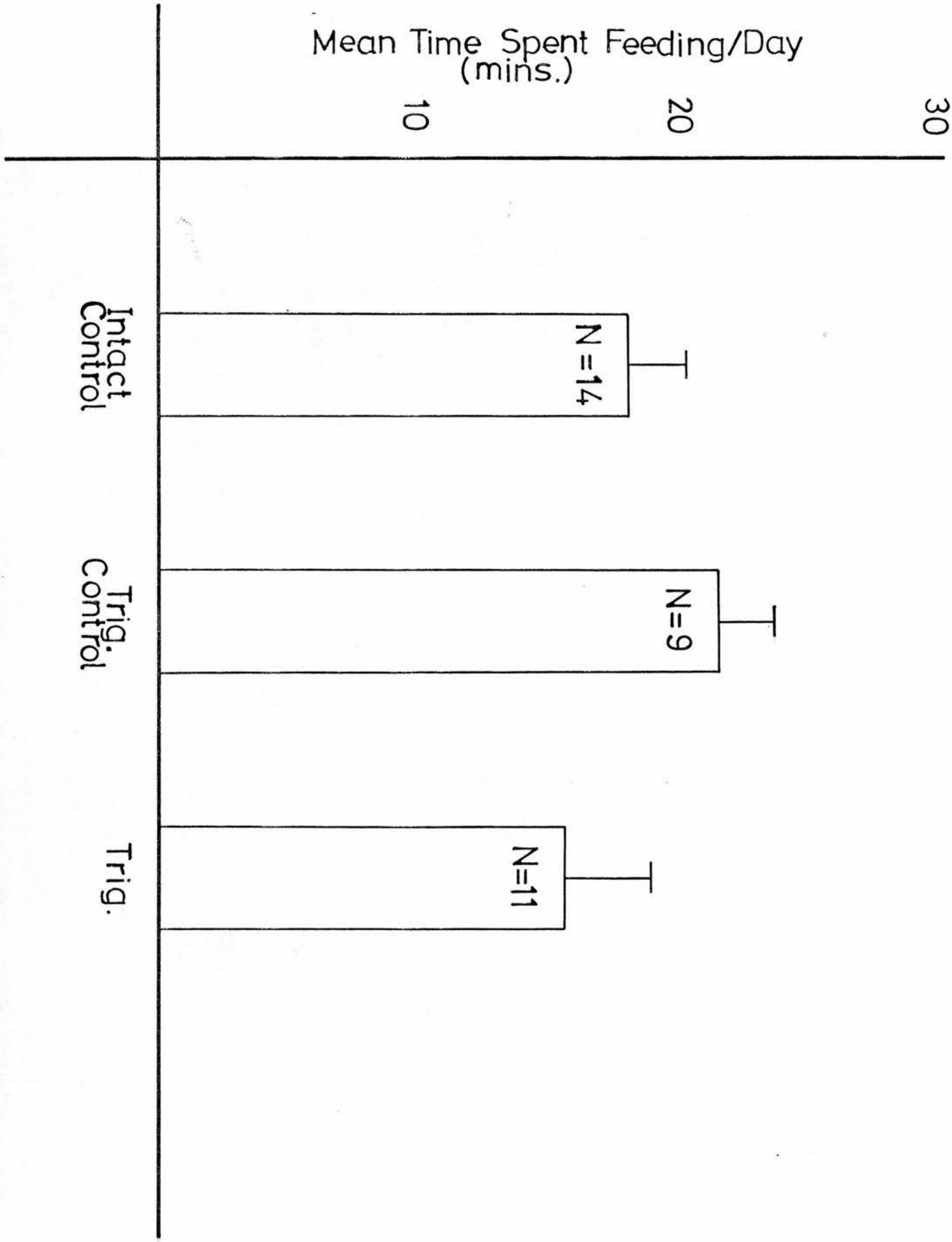

Trigeminal
Trigeminal Control
Intact Control
Dark
2
4
6
8
10
12
14
16
18
20
Mins. after Light Onset

FIGURE 5.6

Mean time spent feeding in each day by birds in Intact Control (Table 2; Appendix II), Trigeminal Control (Table 5; Appendix II) and Triegeminal Section (Table 4(a); Appendix II) groups.

Significance of comparison tested with a Mann-Whitney "U" test.

	"U"	Significance (p < ; two tailed)
Intact vs. Trigeminal	58.5	N.S.
Control Trigeminal vs. Trigeminal	28.0	N.S.
Both Controls vs. Trigeminal	86.5	N.S.


Mean Time Spent Feeding/Day (mins.)
10
20
30
Intact Control
N=14
Trig. Control
N=9
Trig.
N=11

a fairly rapid return to the pre-operative baseline weight. The task of picking up single grains from a slippery surface is obviously going to be more difficult than simply managing to swallow one grain from a whole hopper full of food. It should also be noted that the ratio of pecks to food consumed in Zeigler's birds after nerve section (Zeigler, 1975) was not obviously greater (if the one extreme case was removed) than before the operations (see chapter 2, section 2.8(d)), thus it would be difficult to conclude that the feeding behaviour and rate of food intake in the home cage is being very markedly affected by the deficits observed in the test situation, even very soon after the operation.

5.2(h) Summary

On recovery of body weight after section of the trigeminal nerve then, birds can be seen to differ in two ways from intact and surgical controls.

1) There is a tendency in some animals to show a peak in feeding behaviour at the start of the day rather than in the afternoon. In the group as a whole, this trend is evidenced by a more rapid onset of feeding at dawn.

2) There is a change in the fine structure of feeding behaviour with birds tending to show longer pauses within on-going meals. This may also be associated with an increased persistance in feeding leading to feeding in fewer, larger meals.

It was felt that more information might be gained on the above differences in feeding pattern by studying the behaviour of a group of animals before and after surgery.

5.3 Experiment 2

A group of 8 female birds was chosen and pre-operative data on feeding patterns were collected in the normal way as described above. When these data had been gathered on all of the animals, a week of baseline food intake and body weight data was collected so that the effect of the surgery could be assessed. Bilateral section of the mandibular and ophthalmic branches of the nerve was then carried out in two groups of four birds (all of which survived the surgery). After surgery was performed on the first group of animals, the body weight and food intake was recorded until they had returned to and remained at, or above, the pre-operative baseline levels for at least seven days. The birds were then returned to the room in which the photocell feeders were and, after 3 days was allowed for them to settle, another seven days of data were collected. At the end of this time the surgery was performed on the Second group of animals.

Two of the second group of birds however were completely aphagic after the first post-operative day, so it was decided to obtain data from them immediately after surgery. They were therefore transferred to the cages with the photocell feeders on the second day after surgery and data collection was begun immediately.

5.3(a) Results

The data collected from the six animals serve to support the findings with the previous group of operate animals. The data collected from the other two animals also support an idea of increased rather than decreased tendency to approach food after surgery and will be discussed as individual cases.

5.3(b) Meal Frequency

Here again we see a reduction in the meal frequency after return to normal body weight after surgery (Figure 5.7) and a systematic difference in the size of the appropriate criterion derived from the logarithmic survivorship plots (Figure 5.8).

This meal frequency reduction holds good for all of the birds when the data and analyses on the basis of the logarithmic survivorship derived criterion, but is lost in one case when the blanket criterion of 250 seconds is used. This reduction is significant using the log. criterion (Wilcoxon matched pairs test, $T = 0.0$; $p < 0.05$) but is lost when the 250 second criterion is used ($T = 1.0$). However, it would seem to be acceptable to combine the two trigeminal sectioned groups and to compare the meal frequency of the whole group with that of the original intact control group. We then find a significant reduction in meal frequency even when the 250 second criterion is used (Mann-Whitney "U" = 55.0; $p < 0.02$, two-tailed test). Reduction in meal frequency is more therefore, than simply on artefact of the different criterion used for the analysis.

5.3(c) Time of Onset of Feeding

The birds start feeding significantly earlier in the morning after section of the nerve than they did before the surgery (Figure

FIGURE 5.7

Mean frequency of meal taking in a group of birds before and after section of the trigeminal nerve, calculated with criteria of inter-meal interval derived from individual logarithmic survivorship plots and with a "blanket" criterion of 250 seconds (Table 4(b); Appendix II).

Significance of comparison tested with a Wilcoxon matched pairs test.

Log. Criterion "T" = 0.0; $p < 0.05$, two tailed

"Blanket" Criterion "T" = 1.0; N.S.

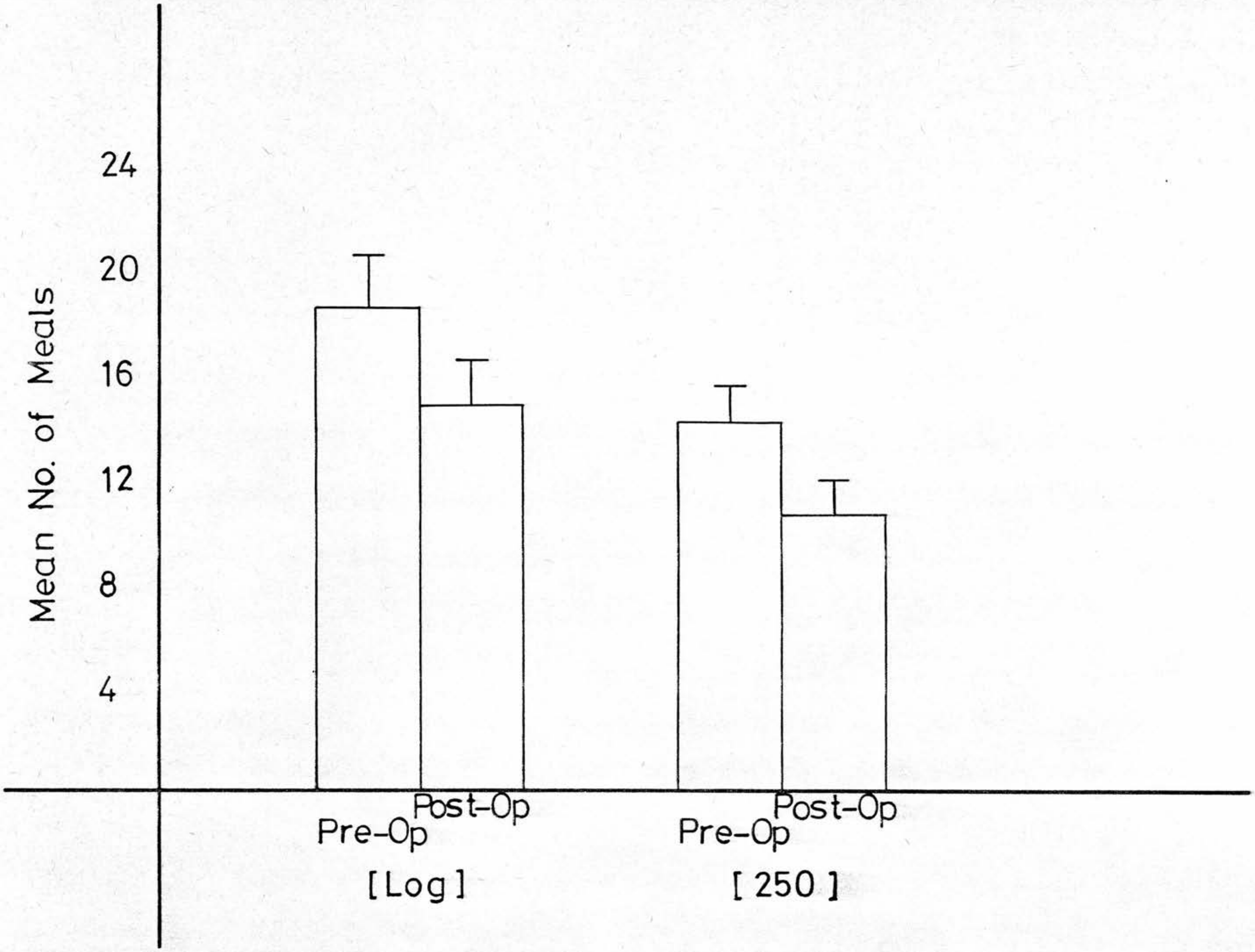
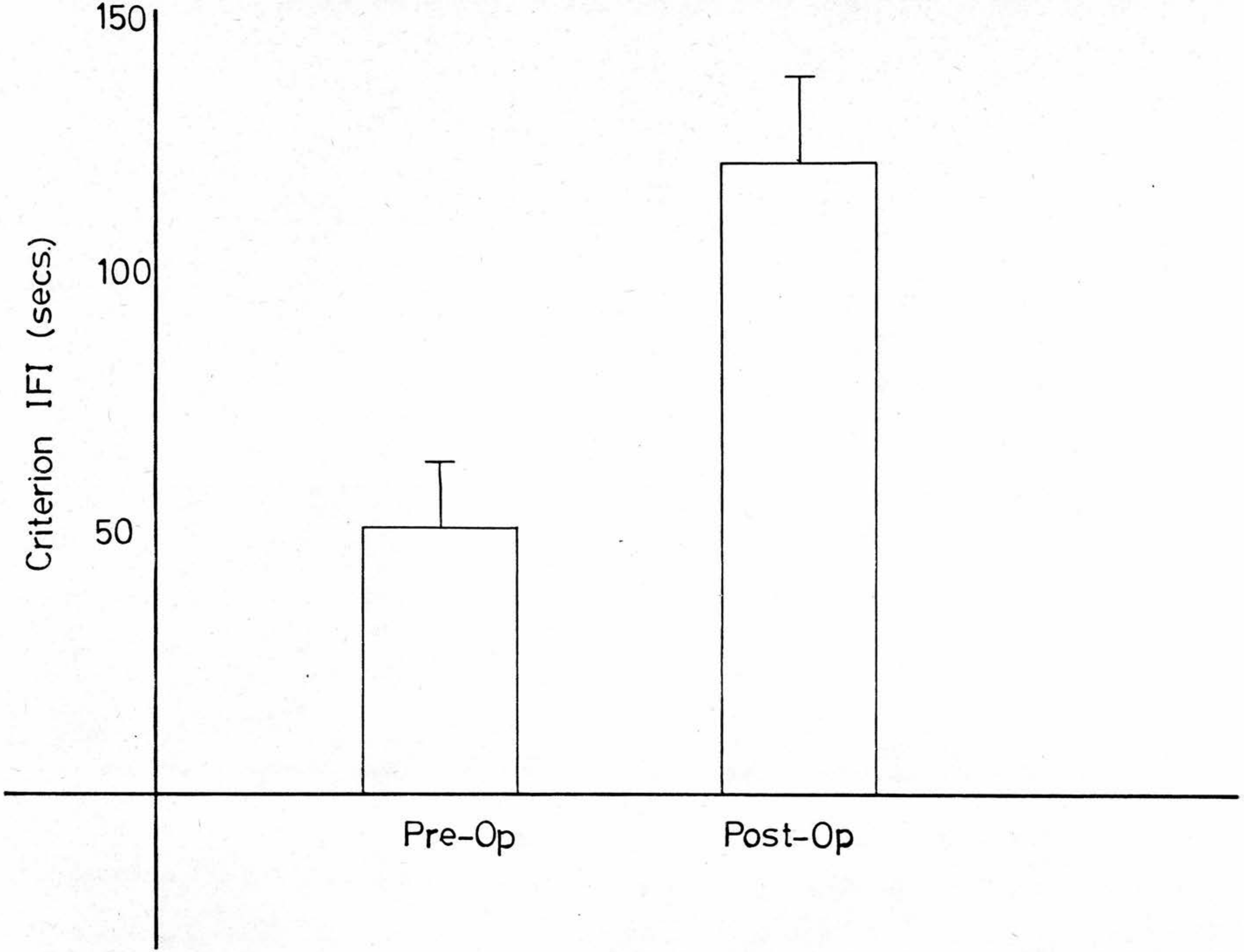

Mean No. of Meals
24
20
16
12
8
4
Pre-Op
Post-Op
[Log]
Pre-Op
Post-Op
[250]

FIGURE 5.8

Criterion inter-feeding interval (IFI) to define meal size, as derived from individual logarithmic survivorship plots for birds before and after section of the trigeminal nerve (Table 4(b); Appendix II).

Significance of comparison tested with "t" test for correlated samples.

"t" = 3.8865; $p < 0.02$, two tailed.


Criterion IFI (secs.)
150
100
50
Pre-Op
Post-Op

5.9). Again one bird fails to show the effect and the bird which showed no change in meal frequency showed only a small change in time of onset. The other four animals however show very marked decreases in latency to start feeding after dawn.

5.3(d) Time Spent Feeding

The mean time spent feeding in each day by the animals after section of the nerve is slightly less than before surgery, but the difference is not significant being attributable for the most part to two animals, with another two showing slightly more time feeding after section (Figure 5.10).

5.3(e) Feeding Patterns of Animals Showing Marked Aphagia

Tables 5.1 and 5.2 give a summary of the diurnal distribution of feeding behaviour shown by these two birds recorded for two weeks immediately after surgery. The first day of the data recorded is the second day after surgery as noted above. The tables also show the 9 am body weights of the animals on each day of the record. The data was ordered into meals and inter-meal-intervals using a criterion interval size of 100 seconds arbitrarily chosen. It is obvious that the pattern of feeding and food intake distribution is changing over the time for which the record was collected and thus a logarithmic survivorship plot computed on pooled data would not be legitimate.

The disturbance shown by bird 15G can be seen to be very marked and prolonged. The effect was so persistent, in fact, that the bird

FIGURE 5.9

Mean time of onset of feeding in minutes after "dawn" in birds before and after section of the trigeminal nerve (Table 4(b); Appendix II).

Significance of comparisons tested with "t" test for correlated samples.

"t" = 3.8865; $p < 0.02$, two tailed.

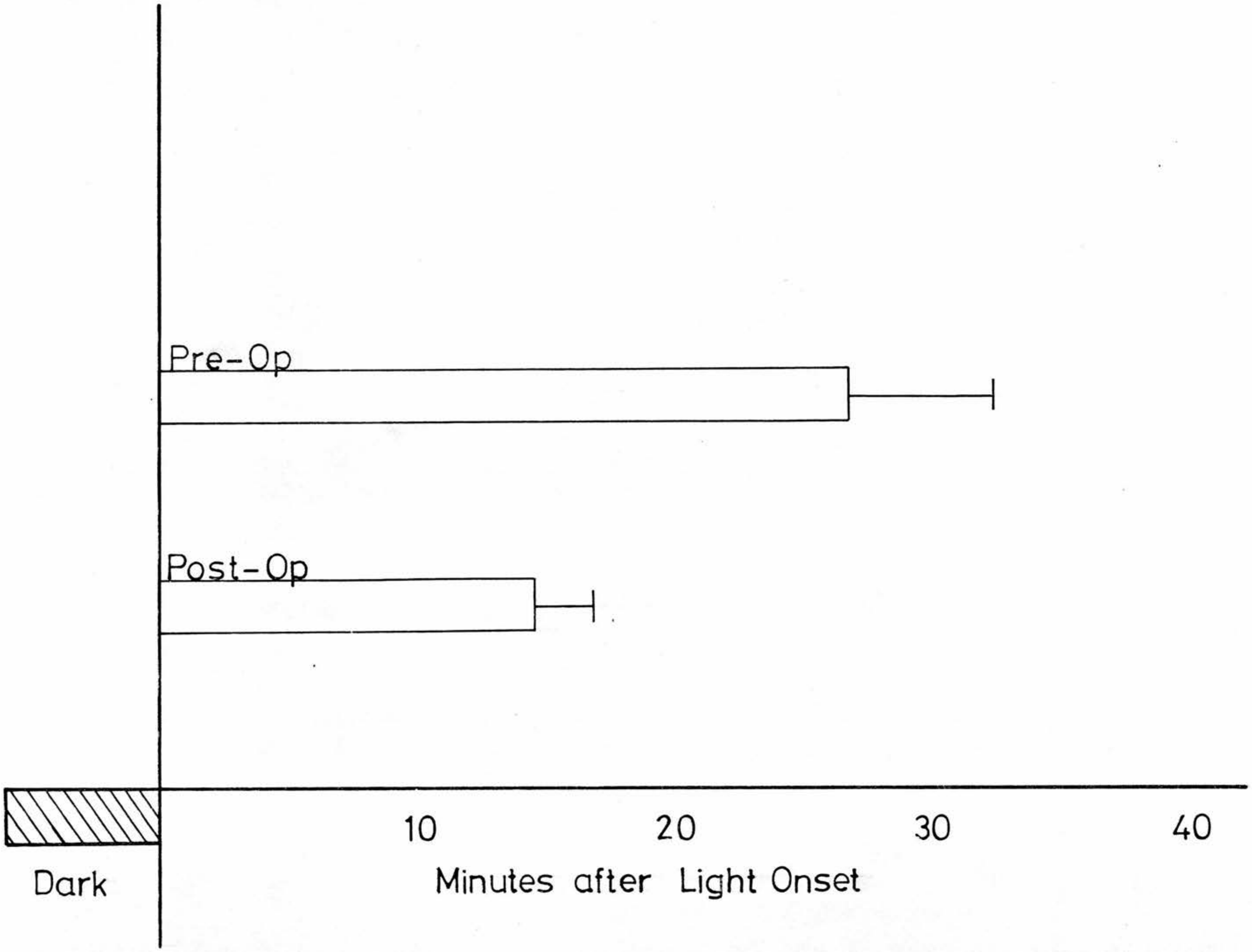

Pre-Op
Post-Op
10
20
30
40
Dark
Minutes after Light Onset

FIGURE 5.10

Mean time spent feeding in each day by birds before and after section of the trigeminal nerve (Table 4(b); Appendix II).

Significance of comparison tested with Wilcoxon matched pairs test.

"T" = 3.0 N.S.

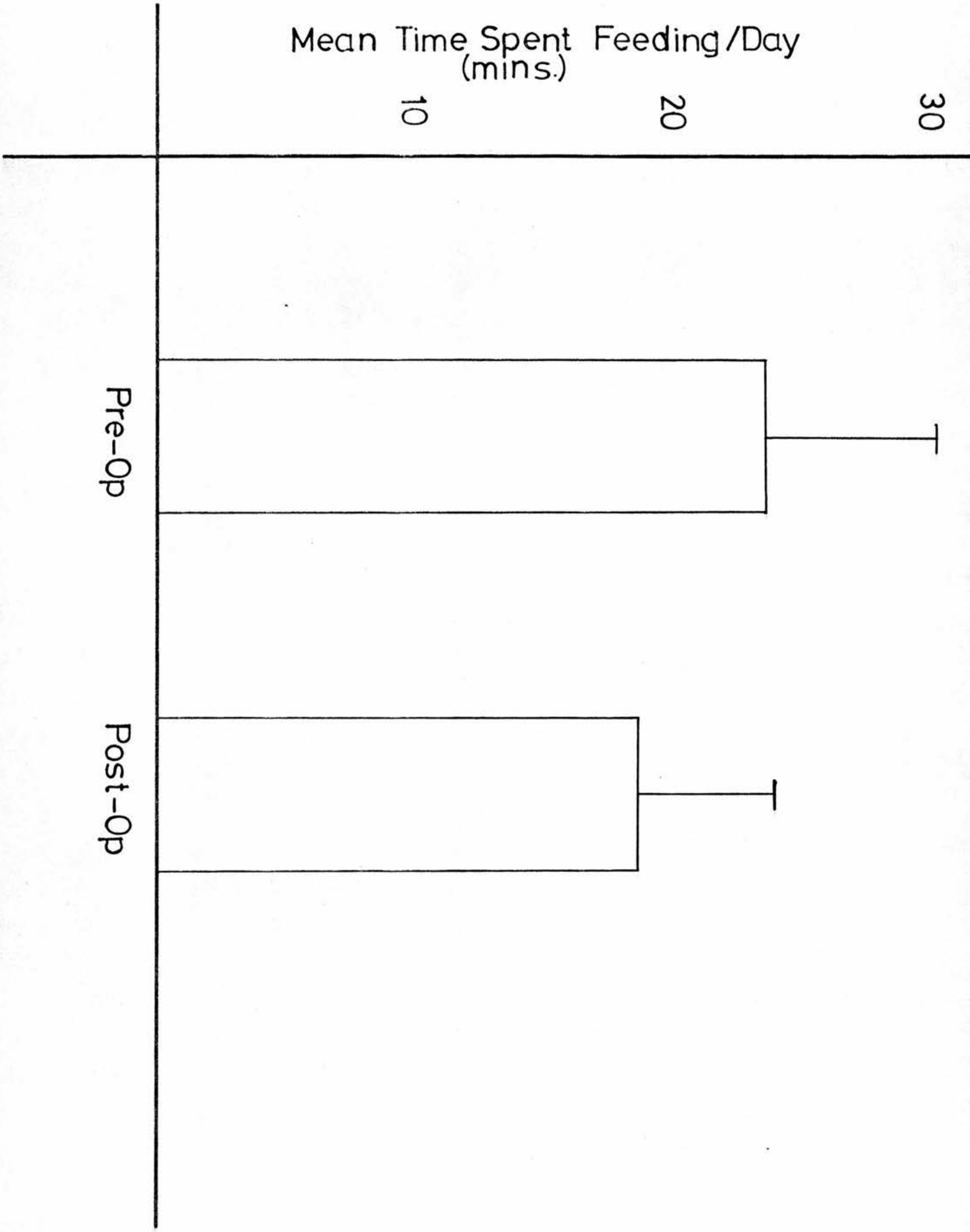

Mean Time Spent Feeding/Day
(mins.)
10
20
30
Pre-Op
Post-Op

TABLE 5.1

FEEDING PATTERNS IMMEDIATELY AFTER TRIGEMINAL SECTION
INDIVIDUAL CASE - BIRD 15G
(TIME SPENT FEEDING IN EACH HOUR OF DAY (SECS))

HOURS DAYS	BEFORE DAWN	9	10	11	12	13	14	15	16	17	TOTAL DAILY TIME	BODY WEIGHT (GRAMS)
1									31.7		31.7	154
2								2.6	66.5		69.1	148
3							45.1	7.3	232.8		285.2	141
4							113.0		40.7	363.1	516.8	136
5		71.9				36.2		196.1	48.3	21.8	374.3	131
6	44.5		2.6	76.6		233.1	103.1		6.5	43.4	509.8	135
7	100.0	124.5	4.5	132.4	18.6		88.0	5.9	48.3	9.6	532.8	133
8	68.4	7.4				20.3	55.2	49.1			200.4	128
9	34.5	9.8				147.4	62.6		9.5		263.8	125
10	83.3	12.1				2.6	54.5		173.3		325.8	123
11			27.7				216.4	27.0			271.1	124
12						19.2		63.1	300.7		383.0	120
13		1674.0	622.0	550.9	379.8	261.8	302.3		174.0	2.5	3967.7	122
14		541.2	469.1	136.8	248.4	102.6	146.2	12.6	12.6		1655.9	125
15		1567.6	481.8	13.5	524.2	134.1	469.7	318.0	541.4	19.8	4070.1	125

NOTE: Baseline body weight = 164 grams

Force fed from day 9 to day 13

TABLE 5.2

FEEDING PATTERNS IMMEDIATELY AFTER TRIGEMINAL SECTION
INDIVIDUAL CASE - BIRD 253G

(Time spent feeding in each hour of the day (secs))

HOURS DAYS	BEFORE DAWN	9	10	11	12	13	14	15	16	17	TOTAL DAILY TIME	BODY WEIGHT (GRAMS)
1			1.2							3.1	14.3	142
2								117.7	4.9		122.6	138
3		1.8				3.4	3.4	443.9			452.5	140
4		289.8	5.1	5.1			116.6	111.3	132.4		660.3	142
5		361.5	50.6			5.5		127.1	59.0		603.7	145
6		194.2	15.3	21.5	88.8		147.8	133.7	18.2		619.5	145
7		314.5	18.7	279.2			38.5	15.8	148.8		815.5	146
8		445.9		50.4		144.2	132.1	199.3	63.7		1035.6	145
9		314.1			115.5	16.2	38.3	43.8	81.5		609.4	146
10		273.1			134.5	26.2	183.5	138.3	109.5		865.1	146
11		266.4	3.4	111.1	15.4		107.4	9.9	1.9		515.5	147
12		374.2		17.7	95.2	18.1	123.2				628.4	150
13		222.2		93.5	30.5	97.6	17.7	126.8		3.4	591.7	153
14		194.2	142.6			43.2	223.2	76.4	148.8		828.4	154
15		225.0	103.7	49.4	52.7	24.7	25.6	28.5	129.5		639.1	155

NOTE: Baseline body weight - 155 grams

had to be force fed to prevent body weight falling to a dangerous level. This force feeding obviously leads to confusion in the data, but certain patterns can be seen, which appear to be similar to those shown by bird 253G which was aphagic (or markedly hypophagic as far as can be determined from only body weight records) for only three days . Immediately after surgery in both birds we can see very little approach to the food and a fall in the body weights. At this time, the greatest amount of approach behaviour is being recorded in the afternoon at the time at which the intact animal characteristically does most of its feeding. In the case of bird 253G there is a rapid transition to a pattern of feeding most first thing in the morning, which is associated with a restoration of a reasonable food intake as indicated by a stabilization and subsequent increase in body weight, and by an increased time spent feeding. Bird 15G shows this pattern of afternoon feeding activity changing to morning peaking, but there is an intermediate stage during which there are fairly frequent occurrences of feeding during the dark phase of the cycle which was not observed at any time in bird 253G. There is a slight peak in the body weight record of bird 15G at the start of this intermediate stage, which falls off again leading to force feeding being needed to keep the bird alive. It should be noted that the body weights were measured at 9 am just before the onset of the light phase of the cycle, so that the occurrence of early morning feeding behaviour would lead to a peak in the body weight record without the animal making a net gain in body weight overall. The feeding activity occurring during the night at this time is shown as one total figure for each day for simplicity, although it characteristically occurred in 2 or 3 short bouts between 3 am and 9 am. The bird then shows two days of a return to the afternoon peaking of feeding behaviour and then a very rapid transition to large amounts of feeding activity with marked morning peaking and a restoration of reliable voluntary food intake. Judging by the amount of food directed activity and the body weight however, this animal was obviously having very great physical difficulties with feeding, but is clearly motivated to approach and attempt to eat.

Recording was terminated at this point, but bird 15G took a very long time to return to its pre-operative body weight. This bird is obviously an example of an extreme case of disruption of feeding after nerve section. It can be seen therefore, that the overall picture of the effects resulting from nerve section as reported by Zeigler and those found here is very similar (although the interpretation is different). That is, the majority of animals show little effect of the surgery (although most of Zeigler's pigeons showed more effect than found here with doves), yet some can be very profoundly affected showing persistent changes in behaviour (like bird 15G here and Zeigler's No.61; see Zeigler (1975)).

The case of bird 15G was inevitably confused by the need to force feed the animal. There are however, some characteristics which its recovery shares with that of 253G and which do give information about the less extreme effects of nerve section normally found. The recovery of food intake may be summarized by indicating two distinct stages:

1) Absence of food intake, and peaking in approach to food taking place in the afternoon where the largest amount of feeding behaviour might be expected to be found in the intact bird.

2) Return of voluntary food intake associated with a morning peak in feeding behaviour. Along with this, some birds may show the nocturnal feeding found in 15G and also reported earlier in T131G.

There is presumably a third stage of recovery which is characterised by a return to the normal afternoon peaking in food intake.

It might be suggested that the predominance of afternoon peaking in the approach tendency shown by these two birds during the initial aphagic stage gives support to Zeigler's model of the effect of nerve section in terms of a reduction in the net feeding tendency of the animal which can be overcome by other inputs to the system. He showed that food deprivation was one possible input which could serve to overcome the effect of nerve section. Perhaps there exist variations in this net feeding tendency which will also help to overcome the depressing effects of nerve section at certain times of the day.

5.4 Return to Pre-Operative Body Weight

Knowing that the birds do not normally eat during the night, body weights are measured immediately before light onset in all cases, as this was a constant point of reference which would not be affected by hour to hour fluctuations in food intake as would a measure taken at any point during the light phase of the cycle. When food intake records were being kept, that also was noted at 9 am.

The fact that nocturnal feeding has been observed after nerve section however, would mean that when it was stated that body weight had returned to their pre-operative levels, this could only mean that they had returned to these levels as measured at a particular time of day. That, of course, was always really true, but did not matter as the diurnal distribution of intake could be assumed to be fairly constant. For example then, bird T131G was monitored and feeding patterns collected at a time when the 9 am weight was back to its previous level. It would have reached or exceeded that level however, only by virtue of the fact that a certain amount of feeding was going on before 9 am. The time of day at which the body weight was measured was constant, but its relative position in the diurnal cycle had changed.

Although it cannot be confirmed, it is highly probable that this complication existed in the cases of other animals for which no feeding pattern records exist. If this were true, it would suggest an explanation for a particular observation made in the body weight records of some of the previously mentioned experimental groups. The curve of the return of body weight to the normal level from the deprivation level associated with the surgical procedures often contained a step or steps of more rapid weight gain occurring over one day. Often too, this was not associated with any similar step in the food intake record. It was assumed at the time that these weight increases might be due to rehydration after blood loss, or to the intale of a large amount of grit. However, they would certainly be better explained by a reorganization of the time at which food was eaten in the absence of any net increase in intake. Thus birds might be deemed to have returned to pre-operative weight before the feeding behaviour had completely returned to normal, and thus the duration of post-operative effects might be underestimated.

5.5 Feeding Patterns and Trigeminal Section in the Pigeon

Zeigler (1975) does not indicate the time of day at which body weight and food intake records were collected. If the accounts given by Zeigler, Green and Seigel (1972) can be taken to indicate standard laboratory procedures which might be expected to be in force at the time at which the trigeminal section data was collected, then records were taken at noon in a 12 hour (7 am to 7 pm) light cycle.

No full published account yet exists of systematic studies of feeding patterns after trigeminal section carried out by Zeigler's laboratory. Miller and Zeigler (1974) (cited in Zeigler, 1975 and 1976) do appear to have found similar effects to those reported above. No data are presented but certain qualitative statements are made. The feeding patterns of the trigeminal sectioned animals are compared with those of animals deprived of food to equivalent levels of body weight loss and it is found that the deafferentiated birds appear, on return of voluntary food intake, to behave exactly like food deprived animals. There is an increase in the amount of feeding behaviour in the early stages of the daily cycle and a reduction in the number of meals taken in the subsequent stages of the day. They also found an increase in the rate of food ingestion in both groups (which, if occurring in the trigeminal sectioned doves, would account for any tendency to reduce time spent feeding). The difference however was that this pattern of behaviour served to return the intact, food deprived animal to its normal weight whereupon the normal pattern of ingestion returned, whereas the pattern persisted in the deafferentiated animals without the long term restoration of body weight.

The effect of two days of food deprivation on the diurnal pattern of feeding behaviour was observed in two doves. Figure 5.11 shows the normal baseline distribution of feeding behaviour and the pattern seen after food deprivation in one of these birds. The second animal showed essentially the same effect of increased feeding at the start of the day, but did not settle back to the predeprivation level as quickly and obviously.

Zeigler (1975) also reports that this study found a reduction in the frequency of meal taking as a result of nerve section, but it is not clear if this referred to a long term change which persisted after recovery of body weight, or was only found immediately after the operation when net food intake was reduced, therefore it is not known if this can be compared with the reduction in meal frequency reported above in the post-operative doves.

There is no report of nocturnal feeding in the pigeon even after nerve section, but as noted above in the section on normal feeding patterns, feeding activity was clearly seen in the intact pigeons outside the period of the light phase of the cycle (Zeigler, 1976) but was attributed to light from outside being able to penetrate into the laboratory (Zeigler, Green and Lehrer, 1971). Thus with no clear demarcation between light and dark an increased tendency towards early morning feeding might go unnoticed. With a similar tendency towards morning feeding in Zeigler's pigeons, it is likely that the recording of body weight at noon would also be confused by such a switch in diurnal pattern. In this case too one would expect that the noon body weights would be over estimates of the net state of weight gain in the birds, so that it is unlikely that recording of weights at 9 am lead to a particular systematic bias which would not also have occurred in Zeigler's procedure.

No data are given either, about the immediate post-operative distribution of the few feeding responses which did occur in the pigeons, so there is no confirmation from Zeigler's work that the maintenance of the normal pre-operative distribution of feeding activity during the aphagic period reported above in two doves, was found in the more prolonged aphagia in the pigeons.

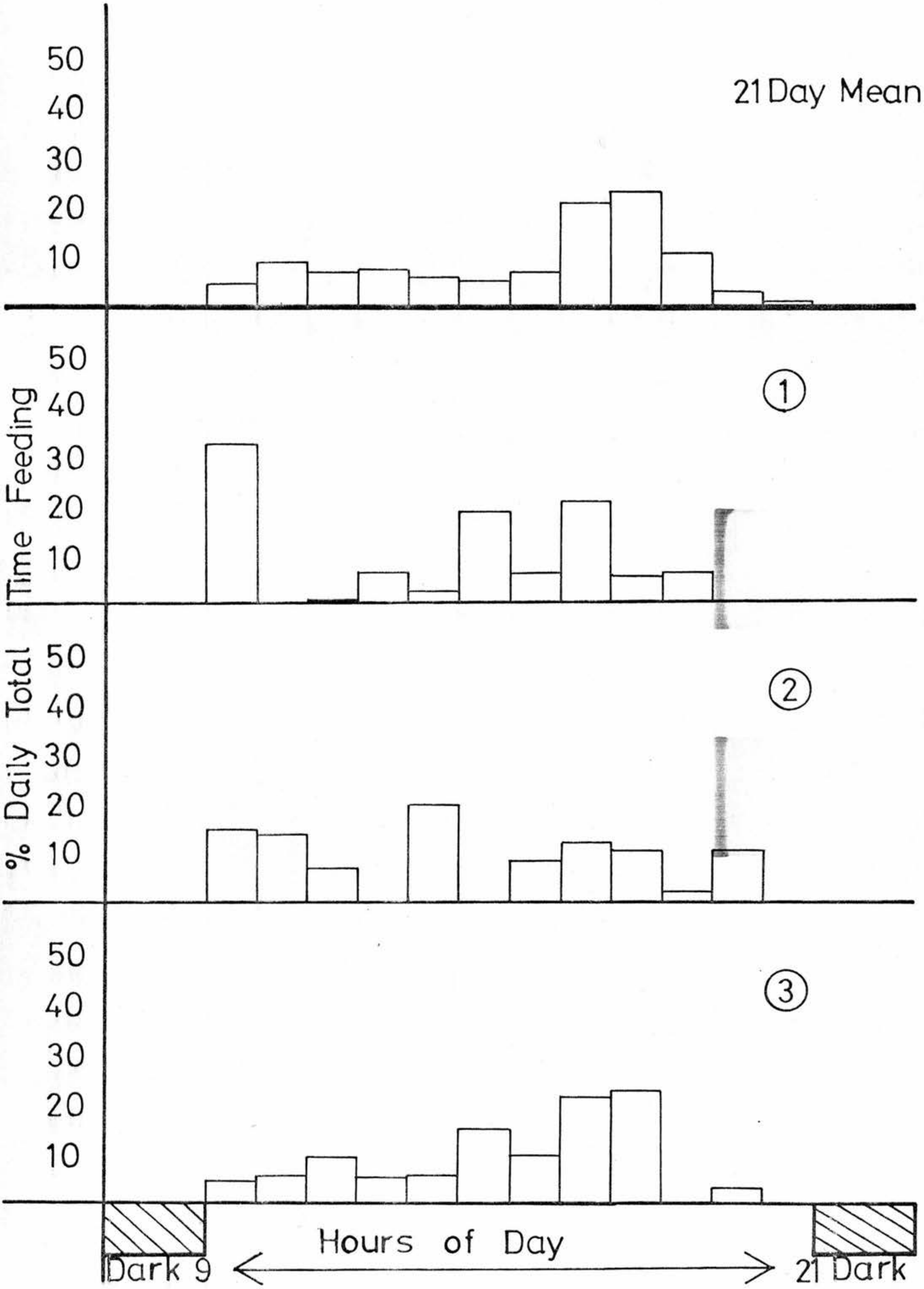
5.6 Interpretation of Effects on Temporal Distribution of Feeding

Central lesions leading to aphagia in pigeons (Zeier, 1971) and doves (Wright, 1975) have also been found to be associated with problems of arousal. Wright for example reports that his aphagic birds could often be encouraged to eat by any non-specific external stimulation which would arouse them out of their somnolent state. Perhaps the effects of the loss of trigeminal sensory input is to lower the general state of arousal of the birds (quite possible as it is such an important sensory system). The alteration in diurnal pattern could then be seen as being caused by the animals response to external stimuli. Perhaps the most arousing event for the caged laboratory birds is the sudden onset of light at the start of the day. Thus a great deal of feeding takes place at this time, but decreases as the general arousal decays across the day. This might be a plausible explanation but for the occurrences of nocturnal feeding at times of the night when external arousal would be very unlikely to take place. It seems still more likely that the trigeminal sectioned animals are indeed (at least in some sense) hungrier than the intact birds. This is particularly the case in view of the fact that they show temporal distributions of feeding behaviour like those seen in animals deprived of food (Figure 5.11). The obvious question is, why should animals choose to remain in a state of deprivation (as indicated by the diurnal pattern) when food is freely available to them?

Another interesting question raised (particularly by the data from bird 15G) is why should there be such a variation in the effects produced by constant surgical procedures? It seems likely that an explanation for the effect of nerve section in terms of physiological, excitatory processes is less probable than one in terms of the individual responses of animals to alterations of sensory information. The following chapter will attempt to present such an explanation.

FIGURE 5.11

Percentage of the daily total time spent feeding by one bird, showing the mean pattern over a 21 day period prior to 48 hours of food deprivation, followed by the pattern shown on the first three days of recovery after the deprivation.


50
40
30
20
10
21 Day Mean
% Daily Total Time Feeding
①
②
③
Hours of Day
Dark 9
21 Dark

5.7 Chapter Summary

Patterns of feeding behaviour were recorded in a group of birds which had received bilateral section of the trigeminal nerve and, in a second group of birds, pre-operative and post-operative data were collected to determine the effects of surgery.

Although the overall diurnal pattern was found to be similar in the operate animals to that observed in intact animals, certain more subtle features were found to differ.

1) Post-operative birds show an earlier onset of feeding behaviour than do intact animals.

2) Deafferentiated birds consume the daily food requirement in fewer, larger meals than the normal birds.

3) The fine structure of the meal seems to differ before and after surgery, so that the operate birds show longer within meal intervals than normals as indicated by the shapes of the logarithmic survivorship plots.

The immediately post-operative feeding patterns of two birds which showed some degree of aphagia were discussed at length and certain stages of recovery from the aphagia were noted.

The above data were compared with some previously reported observations of Zeigler's laboratory on feeding patterns in pigeons.

CHAPTER 6

6.1 An Alternative Hypothesis Concerning the Effect of Trigeminal Section

The data presented in the preceding two chapters indicated that, although very clear motor effects were produced and also subtle changes in the pattern of feeding behaviour existed as a result of section of the trigeminal nerve in doves, these effects were not nearly as marked and obvious as those which Zeigler has reported after essentially similar procedures in pigeons.

In all his discussions of the nature of the deficits produced by trigeminal section, Zeigler has argued strongly that, although sensory and motor disturbances must obviously be present, the major part of the effect is attributable to a motivational disturbance. It is felt however, and will be argued here, that there is a third possibility which is not incompatible with Zeigler's interpretation or data, but which can handle some of the more paradoxical findings associated with trigeminal surgery and also might serve to cast some light on the reason why extreme effects are found in Zeigler's pigeons (and also a few birds in this study) but not in the vast majority of Ring doves used.

6.2 Motivation and Goal

Pfaffman, Norgren and Grill (1977) suggest that on animal's behavioural response to sensory stimulation will fall into one of three broad categories: (1) Approach and acceptance; (2) Rejection and withdrawal; and (3) Neutrality. For the purposes of their argument these categories were defined to be mutually exclusive. It is argued here however, that categories (1) and (2) must be allowed to overlap, or that a fourth exclusive category is required to account for the behaviour of the animals which have undergone trigeminal section, and also the behaviour of animals in certain other feeding situations which will be defined below. That is, it would seem perfectly possible to conceive of a situation in which an animal would approach a goal object but then, on making contact, would reject and withdraw.

Associated with any concept of motivation is the concept of an appropriate goal object. If we say that the goal of the motivational system which we label "hunger" is "food", we still require to define what is food, and the definition which we may derive from first principles of biochemistry and anatomy may be very different from that which the animal will carry around to control its behaviour. A particular material may contain all of the nutrients and minerals which an animal requires and in addition be quite physically appropriate for the animal's digestive tract, and yet still not be eaten. For example a survey of the feeding habits of deer (Quinton and Horejsi, 1977) showed that animals consistently selected 10 out of the possible range of about 250 items which the researchers identified as being quite appropriate by all objective criteria other than the behaviour of the animal. On the other hand, many experimental studies have been able to show that a material which has no nutritional value (Sheffield and Roby, 1950; Taylor, 1969) will be eaten by animals because of particular sensory qualities it may possess. There are a great many pieces of anecdoted evidence which come from stories about the maintenance of exotic animals in captivity (for example, the writings of Gerald Durrel) and which indicate how difficult it can often be to persuade these animals to accept readily available alternatives to their normal diet. In humans too there are vast cultural differences in the things which may or may not be eaten, which are not a function of nutritional value and, as pointed out by Yudkin (1963), advances in food processing technology have meant that the factors (like taste and texture) which are the basis on which one makes decisions about palàtability can often be dissociated from the nutritive value of the foodstuff.

This would lead then, for the purposes of the present discussion to an operational definition of food which would simply be that which the animal in question is prepared to eat. The animal's preparedness to accept a particular material as food will be a function of its past experience associated with certain innate predispositions which, under normal and natural circumstances, would lead to the animal consuming only that which was nutritionally valuable in sufficient quantity to meet its needs.

The corrolary of this of course, is that if we find that an animal does not eat, in fact does not even approach the food we offer, we can not immediately conclude that the animal is in some way lacking in normal feeding motivation. The correct conclusion may simply be that it does not consider the material which is available to be a legitimate food.

Similarly, it is possible that the reason that an animal will refuse to feed immediately after section of the trigeminal nerve is not that its overall level of feeding motivation has been reduced, but rather that the effect of the surgery is to alter the animal's perception of the food material to such an extent that it is no longer regarded as being within the category "food." Aphagia as a result of sensory deafferentation is seen as being analogous to food neophobia rather than the result of the disruption of the physiological substrate of motivation itself. The nerve sectioned bird will approach and attempt to eat a material that looks like food, but will reject if on the basis of its altered sensory feedback.

6.3 Reanalyses of the Effects of Trigeminal Deafferentation on Feeding Behaviour

Table 2.3 presented above gives a summary of the main findings reported by Zeigler and his co-workers along with the conclusions which they draw from these findings. The present discussion will follow the order of the account provided by the table and will show that the findings can be better understood with reference to the above mentioned neophobia hypothesis.

6.4 Trigeminal Aphagia

Zeigler has argued that pigeons stop eating after section of the trigeminal nerve because the surgery leads to the removal of a tonic component of trigeminal feedback which contributes to the overall level of feeding motivation of the animal (see Figure 2.3). The alternative interpretation to be considered here is that the change in sensory feedback from the oral region after nerve section is such that the bird no longer recognises the food which it is offered after the surgery as being the same as that which it was used to eating before the operation. The material may look similar to the bird, but it certainly would not feel the same in the mouth. Sensory feedback will be used for motor control of feeding, but will also obviously be used for food selection or rejection.

6.5 Response to a Novel Diet

Neophobia (Barnett, 1958) is a term used to describe the tendency of certain animals (usually rats in the experimental situation) to avoid novel stimuli of various sorts. Of interest to the present argument is the more particular form of neophobia sometimes referred to as "Bait shyness" (Rzoska, 1953). This refers to the finding that rats will avoid eating large amounts of a new diet which they may come across, but will rather "sample" the material to ensure that it is safe to eat. This behaviour pattern means that rats can be particularly difficult to kill by the laying of poisoned bait as they soon learn to leave untouched foods which they have sampled and found to cause illness (Garcia and Koelling, 1966; Garcia, Ervin and Koelling, 1966). This behaviour can obviously be seen to be adaptive and to have developed in the context of omnivorous feeding habits in an animal which has existed in close commensalism with man for thousands of years.

Associated with the idea that novelty often leads to initial rejection of food is the fact that experience (particularly in the early stages of life) can lead to the establishment of strong preferences for certain foods. A situation analagous to imprinting appears to exist (Immelman, 1972; Hess, 1964) whereby the animal's early contact with a particular food item will result in an enduring preference for that item when a choice is available.

Rabinowitch (1968) showed that the types of food selected by gull chicks (Larus Argentatus and Larus Delawarensis) was strongly determined by their feeding experience for the first five days of life. If a choice situation was presented in which the familiar food was paired with a novel food the chicks almost always selected the familiar food. When a choice of two unfamiliar foods was offered, 3 out of 24 L. argentatus and 10 out of 24 L. delawarensis refused to eat either. It should be noted that the test trials were observations on the same situation as the normal feeding procedures, so that the birds would rapidly approach the familiar food cup and yet, in some cases, refuse to accept the food offered. Rabinowitch summarized these findings by suggesting that "lack of familiarity with a particular food material may be equivalent to non-recognition of the material as food at all." In a similar study of early experience on food selection in domestic chicks (Rabinowitch, 1961; cited by Rabinowitch, 1968) on group of birds was raised for 8 days on a diet of milo and another group on a wheat diet. At the end of this time the available foods were reversed and it was found that 2 of the six milo trained birds and 5 of the 8 wheat trained birds starved to death because they refused to accept the novel food. This finding is similar to the observation of Hogan (1977) that chickens which are allowed to feed for a period on a highly preferred food material (meal worms) sometimes subsequently starve to death when returned to the less preferred grain diet.

Rabinowitch (1969) reported similar although less extreme effects of early experience on food preferences in Zebra finches. He showed also that early experience would interact with immediate past experience and innate predispositions and preferences to produce the overall choice response. Hess (1950) found that when chickens were allowed to feed on grain which was lit from below (a translucent floor to the cage) or above, there subsequent pecking towards a photograph of grain in a test situation would be directed to the photograph taken in the lighting conditions with which they were familiar. Such effects have been found in rodents (Rozin, 1976; Soane and Clarke, 1973) and reptiles (Burghardt, 1967; Arnold, 1978). There is also a large amount of information about the food selection habits of wild populations (Cushing, 1944; Coppinger, 1969).

6.5(a) Response to a Novel Food by Ring Doves

Some of the above examples suggest that the response of animals to changes in their diet can be extreme to the point of severe aphagia and starvation. All the very extreme examples of this however come from young animals. It was decided therefore to study the effect of a novel food on the food intake and body weight of the adult Ring dove to see if this sort of hypothesis would provide an adequate model for the effects of trigeminal deafferentiation.

6.5(b) Method

18 female birds were used for the study. They were housed individually in cages 40 x 35 x 45 cm) in a room with a 9 hour (9 am to 6 pm) light cycle and constant, free availability of water, food and

grit. Baseline body weight and food intake records were collected while the animals were feeding on the normal laboratory mixed grain diet and then a novel food (long grain rice in 12 of the cases and split peas in 6 others) was introduced. The novel grains were chosen to vary as much as possible in appearance and other sensory qualities from the normal diet and also so that one could be quite confident that the birds had had no previous experience of them. Food intake and body weight information was collected from the animals for three weeks after the change of diet at which point the animals were returned to familiar food. A summary of the data is presented in Table 6.1.

6.5(c) Results

It is clear that some of the birds showed a very marked aphagia in response to the novel food and indeed one animal (11) could not be persuaded to accept it at all, and had to be returned to the normal mixed grain diet. As many however were completely unaffected by the change, accepting the novel food completely and maintaining body weight without any sign of disturbance. As well as highlighting the extreme variability of the response of these birds to a novel diet, these animals serve as very vital "controls" to indicate that the failure of the others to accept the new diet cannot be attributed to nutritional inadequacy of the unusual food, or to a mechanical inability on the part of the birds to grasp or mandibulate the unusually sized or shaped grains. This is also suggested by the fact that most of the other animals which did show some initial reluctance to feed on the novel material did finally accept it.

TABLE 6.1

EFFECT OF THE INTRODUCTION OF A NOVEL FOOD

BIRDS	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
	(Rice)												(Split Peas)					
DAYS OF APHAGIA	0	0	9	0	4	5	0	0	0	3	*	0	8	0	0	3	1	0
DAYS TO BASELINE WEIGHT	0	0	**	0	10	14	0	1	2	7		0	16	0	0	8	2	0
DAYS OF 0 OR NEGATIVE WEIGHT GAIN	0	0	8(f)	0	4	6	0	1	1	3		0	9(f)	0	0	3	1	0
BASELINE WEIGHT	151	135	166	155	134	151	142	158	134	161	149	140	149	142	139	137	158	147

* Totally refused to accept novel food, therefore returned to normal diet.

** Had not returned to baseline weight before end of observation.

(f) Systematic force feeding.

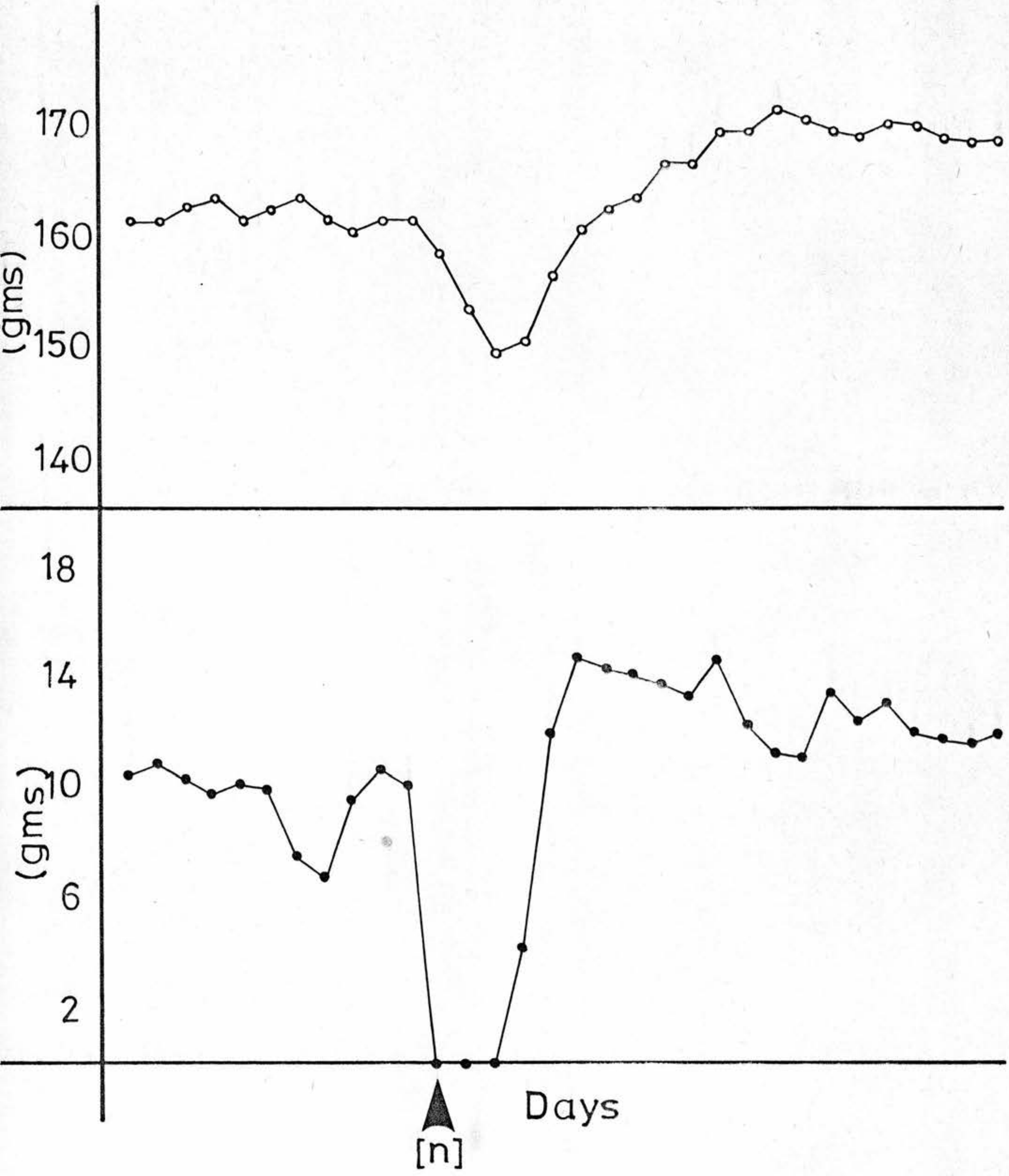
The procedure which was adopted when the animals had not shown any food intake for several days was to attempt to force them to recognize that the new material was really food, by force feeding of a small amount of the new food. If the aphagia persisted to an extreme level, then animals were force fed the amount needed to prevent any further weight loss. This was done by dropping small quantities of moistened food into the back of the mouth. The food would normally then be swallowed immediately.

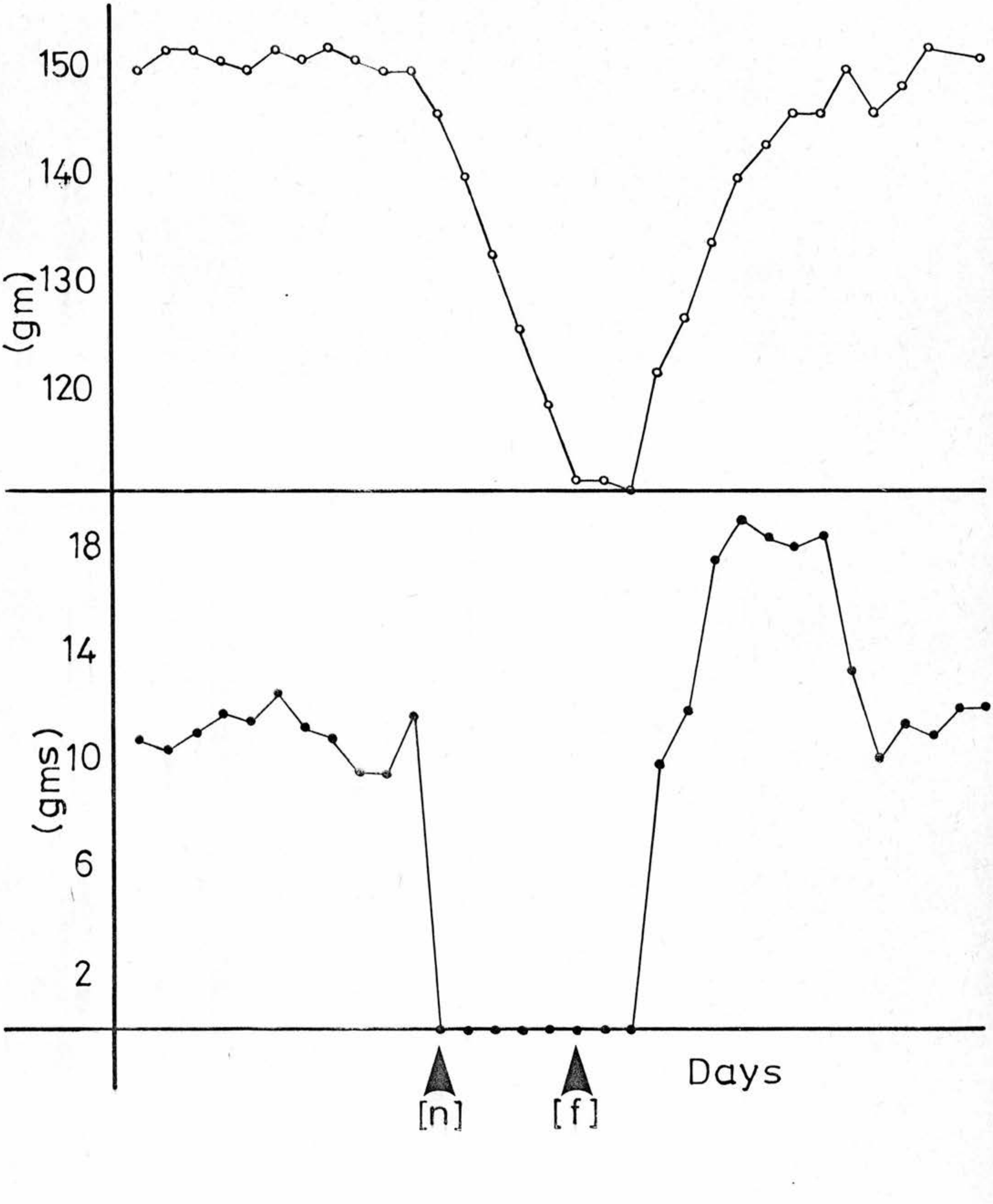
The records of two animals showing fairly marked effects of the manipulation are presented in figures 6.1(a) and (b). There are several points of interest illustrated by these two records which were also observed with some of the other birds. First, on return of voluntary food intake there was usually a day or two in which the birds showed a lower than normal food intake. This may be analogous to the hypophagia and lack of post-deprivation compensatory hyperphagia which is reported by Zeigler after the return of voluntary feeding following trigeminal aphagia. However, far from being a prolonged hypophagia after recovery of intake, the birds often showed a slight hyperphagia and increase in body weight on the new diet. This is possibly due to the fact that after the animals overcome the initial novelty of the food and accept and eat it, they find this novelty a pleasant change from the laboratory diet and thus are stimulated to overeat.

Finally, there is every evidence of compensatory overeating directed initially to the restoring of the pre-manipulation body weight after the first one or two days of lower intake.

FIGURE 6.1 (a) and (b)

Examples of the effect of the introduction of a novel food (indicated [n]) on the body weight (upper panel) and food intake (lower panel) of doves. Point [f] in Figure 6.1 (b) indicates systematic force feeding to prevent starvation.


170
160
150
140
(gms)
18
14
10
6
2
(gms)
Days
[n]


150
140
(gm) 130
120
18
14
(gms) 10
6
2
Days
[n]
[f]

6.5(d) Conclusion

Some Ring doves display a very obvious neophobic response when presented with an unfamiliar diet, this phenomenon being more marked and reliable than the aphagia produced by sensory trigeminal deafferentiation in doves. It is therefore suggested that the aphagia as a result of nerve section may simply be a result of the post-operative animals failure to recognize the food material as being the same as it was before the operation. The neophobic effect differs from nerve section in that there is no accompanying prolonged period of reduced food intake.

6.6 Lingual Nerve Section

Some support for the analysis of trigeminal aphagia as being a problem of food recognition comes from the work of Gentle (1971) on the effect of section of the Lingual nerve (carrying taste information from the tongue) in domestic chickens. Gentle found that chickens with lingual nerve section showed periods of aphagia ranging from 1-14 days after surgery. This aphagia was not complicated, as was the effect of trigeminal section, by any motor disturbances as could be seen by the fact that the reduced food intake was associated with reduced pecking rather than any inability to eat. The first conclusion from this aphagic effect then, is that it calls into question the central role of the trigeminal system in the control of feeding behaviour, suggesting that both examples of aphagia are due to some more general effect of the loss of sensory information.

A second important aspect of Gentle's work is the effect of novelty of diet on the food intake of intact and lingual denervated birds. The novelty was only in the visual quality of the food as it was produced by colouring the normal mash diet with tasteless dyes. Birds which had received only control surgery showed no response to this minor alteration in their food. Lingual nerve sectioned animals however showed a significantly lower tendency to approach and eat the coloured mash as compared with the normal mash in an eight hour test situation. That is, the intake in the first hour of the period was depressed as compared with the normal diet, after which time there was a tendency for increased intake to compensate. In short then, the birds would not be disturbed by the change in colour of the diet if they had taste information to confirm that it was suitable. If taste information was denied, they were wary of the additional change.

The original lingual nerve aphagia can, of course, be explained as a neophobic response as in the case of trigeminal section.

6.7 Post-Recovery Hypophagia after Trigeminal Section

If the aphagia shown after nerve section was due to the loss of tonic excitatory input from the trigeminal nerve, the hypophagia which persisted after the return of some feeding activity was held by Zeigler (1975, 1976) to be a result of the loss of phasic input which was normally associated with feeding behaviour. That is, the feedback obtained via the trigeminal nerve acted as a positive feedback system to keep the animal eating once it had started to eat. When the nerve was cut, the animal might be goaded into feeding by its state of body weight loss, but when feeding was initiated it did not persist as it should. Thus complete return to the pre-operative body weight level might take a very long time, or indeed might not occur at all.

The present argument however, suggests that one need only assume that one of the lasting effects of the loss of trigeminal sensory feedback is the reduction in the perceived palatability of all food materials.

Wirtshafter and Davis (1977) have produced a mathematical model of the control of body weight in animals which they offer as an alternative to any idea of a "set point" of body weight. The model is a system with no built in set point, but which will "settle" at a certain level of body weight which can be predicted by an input parameter which embodies an estimate of the perceived palatability of the diet for the animal. Thus changes in the diet which the animal is offered (or by the present argument, changes in the animal's ability to sense and perceive correctly) will lead to changes in the point at which the body weight would settle. This model would clearly predict a lowered level of body weight after loss of trigeminal feedback if, as would be reasonable, one of the effects of such a loss is to reduce the perceived pleasantness of eating.

In addition to the model (which embodies an intuitively very reasonable suggestion) there is a great deal of experimental evidence to suggest that the perceived palatability of food offered can indeed determine the body weight of the animal. Keesey and Boyle (1973) showed that reduction in diet palatability lead to a reduction in the maintained level of body weight in both normal intact rats and also recovered lateral hypothalamic lesioned rats. Similarly, increases in diet palatability (Powley and Keesey, 1970) lead to higher maintained body weights in both recovered aphagic and control rats. Indeed Mufson and Wampler (1972) found that the effect of lateral hypothalamic lesions on body weight could be eliminated by keeping the animals on a highly palatable diet. Hamilton (1964) found that the food intake of animals on high fat diets was significantly increased when the fat was in the form of nutritive lard or non-nutritive mineral oil. There was however no indication of the effect on body weight, as it is possible that the fat content lead to changes in the rale of gut clearance which confused the effect of higher caloric intake. Cabanac and Rabe (1976) were able to demonstrate a similar dependence of body weight on diet palitability in humans.

It should be noted however, that it is by no means clear that this interpretation of trigeminal hypophagia in terms of diet palatability actually differs from the interpretation of Zeigler, on the basis of phasic sensory feedback. That is, it must be assumed that judgements about pleasantness and palatability of a food are made on the basis of just such sensory information. However, in the context of Zeigler's overall model of tonic sensory processes which is being questioned here, it seems safer not to talk as yet about the exact nature of the mechanisms responsible for making the palatability judgements, but to assume that the effect of deafferentiation would be to alter these judgements in a certain way. After nerve section the birds enjoyed eating less.

6.8 Decrease in Responsiveness to Food after Trigeminal Section

The weight of Zeigler's case that the effect of trigeminal section on food intake is a motivational one rather than a purely motor one comes from the observation that the reduction or absence of food intake after surgery is associated with a reduction in the amount of feeding behaviour as monitored by the photocell feeder devices. The conclusion that this is indicative of a disturbance in the motivation to eat may be legitimate when the only other hypothesis is that of a disturbance of mechanical ability to feed. However, the suggestion that the animals do not eat because they judge the offered material not to be food also carries the prediction that the reduction in food intake will be associated with a reduced likelihood of approach to the food.

What is required by the food recognition hypotheses however is that the animals make at least sufficient approaches to the food in the initial stages of aphagia for them to come to their decision to reject it. This hypothesis would also suggest that some degree of food searching behaviour might be found in which approaches to the food box would be made (perhaps with decreasing frequency as time goes on) in the hope that the place which was previously associated with food would again reward the effort.

It can be seen from the data presented (Zeigler, 1975) that the birds were at least making some attempt to approach the food even immediately after the operation. The mean number of responses per day by the 8 post-operative birds for which data was available was 159 (S.D. of 74.7) (Table III, Zeigler, 1975). As data are presented in terms of total number of pecking responses over the aphagic period it is impossible to make any comment about the time course of the effect. Where data are presented grouped over days (Figure 3, Zeigler, 1975;

only one case is ever presented) the scale is such that a very few approach responses would not make an impression. It is quite possible that the low level of feeding responses to the food box represents an extinction of approach due to the absence of reward. That is, the box no longer contains what the animal considers to be food.

Informal observations in the above described neophobia experiment with Ring doves indicated that where aphagia was found it was also associated with lack of approach to the food box. On the first day of the availability of the novel food it was clear that the animals had been pecking in the food material (perhaps trying to find some "real" food) yet without consuming any. As time progressed however (this was particularly obvious in the extreme cases of aphagia), indication of any approach to the food became very much less frequent. In this case, where we can be perfectly sure that the animals were motivated to feed, they showed little indication of the motivation by attempting to approach that which they did not consider to be food.

In the two doves in which feeding behaviour records were collected almost immediately after the surgery it was found (chapter 5) that they showed signs of feeding approach most obviously during the afternoon, over the aphagic period. It was suggested that this might indicate a diurnal cycle superimposed on the reduced net feeding tendency which led to some evidence of motivation at the normally peak feeding time. It might also be interpreted to mean that the normal diurnal peak in food searching tendency led to the animal "trying again" to find food in the old source. In the case of a bird individually housed in a very small cage with only one possible source of food, this would not lead to much activity before the bird again gave up the search. Although no evidence is available to confirm this, one might expect that the provision of several food sources would lead to the animal making approach to all of them in search of recognizable food, and thus to evidence of a greater feeding motivation.

6.9 Response to Food Deprivation after Trigeminal Section

Zeigler observed that the facilitatory effect of body weight loss on feeding tendency appeared to be similar in deafferentiated and control animals at the high levels of deprivation, but that the nerve sectioned birds showed much less response than the controls at the lower levels of body weight loss. He also found that birds deprived to 80% of their normal, ad libitum baseline of weight showed less effect of trigeminal section in terms of days of aphagia, but that the return to the original pre-manipulation body weight was every bit as slow as in those operated on at normal body weight. His conclusion was that the effect of deprivation is to contribute an input to the animal's feeding motivation system which can serve to override the depressant effect of section of the nerve, but that the long term regulation of body weight is effected so that the animals are slow to regain their normal weights (if they ever do).

Again, these findings would seem to be perfectly easily accounted for by a palatability hypothesis which suggests that the effect of the surgery was a reduction in the "set point" of body weight in the sense of "settling point" as described by Wirtshafter and Davis (1977).

This is analogous to the findings of Powley and Keesey (1970) that the effects of lateral hypothalamic lesions can be reduced by the reduction in the pre-operative body weight by enforced deprivation. In fact the usual post-operative aphagia may be replaced by a hyperphagia if the body weight loss is sufficiently great.

That is, the response to deprivation in the animals, shown at high levels of weight loss are normal. Low levels of weight loss however, do not represent reductions very much below the new, reduced level of stable body weight as determined by the diet palatability.

6.10 Operant Performance after Trigeminal Section

It was found (Zeigler and Feldstein, 1971; Zeigler, 1975(b)) that pigeons would continue to perform an operant for food, which had been acquired before the operation, at a point in time immediately after trigeminal section at which they were aphagic and unresponsive to food by all other measures. This is in marked contrast to the effect seen after central lesions, which usually result in an absence of operant performance as long as the food intake deficit lasts, then a return with the return of voluntary food intake (Wright, 1975; Zeigler, 1976). Although the animals would perform the response at approximately the pre-operative level they would not consume the food reward obtained. As the aphagia continued, the performance of the operant would decrease, and be reinstated when voluntary food intake returned. It was shown (Zeigler, 1975(b) that the decrease in responding with time after the surgery appeared to be identical to extinction due to non-reward.

This is the most unaccountable finding as far as Zeigler's motivational hypothesis is concerned. It is quite contrary to so many of the assumptions underlying animal research in motivation that an animal will work to gain access to a goal which it does not want, and thus this finding alone should lead to the rejection of the original hypothesis. However, Zeigler's conclusion is that a dissociation is possible between the performance of the consumatory act of feeding and the operant response previously learned for food reward. This word "Dissociation" (Zeigler, 1975(b)) serves only to describe what is observed in the context of his existing theory, but does not explain why it should be.

Teitelbaum (1966, 1967) has suggested that when an operant response can be interposed between the animal and the goal object we can truly infer that the animal is motivated towards that goal object. This suggestion was particularly important for the analysis of the effects of electrical stimulation of the brain on feeding behaviour as it could be shown that stimulation of some areas would lead to true motivated feeding behaviour in which the animals would perform an operant to obtain food, whereas stimulation in other areas produced feeding which was only reflexive in nature. It was also an important distinction in the study of the apparently increased "feeding motivation" as a result of ventro-medial hypothalamic lesions. Although eating more when food was available, the lesioned animals were less motivated as measured by their tendency to work to obtain food (Miller, Bailey and Stevenson, 1950). Teitelbaum's generalization that "if an operant occurs motivation exists" has been widely accepted with the qualifications which are always necessary to handle such statements.

Zeigler (1976) however, requiring to get around this problem, quotes Campbell and Misanin (1969) as questioning the validity of Teitelbaum's position on theoretical grounds and thus appears to feel that he needs to say no more in answer to the paradox. The real objection which is raised by Campbell and Misanin (1969) is not however that the presence of an operant cannot, or should not be taken to indicate the presence of motivation, but that the absence of an operant cannot be taken to indicate its absence. They indicate that the main objection to Teitelbaum's idea came from Dethier (1964, 1966) and his work on feeding behaviour in the blowfly. It would be strange to be forced to conclude that a fly is not motivated to feed simply because it could not be trained to perform an operant in order to gain access to food. Thus an operant should certainly be taken as an indication of motivation but should not, in Dethier's view, be regarded as a sine qua non.

What Zeigler would require to do then, if he wished to hold to the view that the aphagic bird which is performing an operant at the normal level is not motivated to feed, would be to show that operant performance occurs in a situation where motivation is clearly absent (if that is not blatantly circular). One possible source of such evidence would come from the oft repeated observation that animals which are working in an operant situation for food will continue to work when free food is also available (Neuringer, 1970; Mitchell and White, 1977; Osborne, 1977). This would seem to indicate that the animal somehow "prefers" to earn its food by the operant response in the absence of any real need to do so. However, Mitchell and White (1977) have shown that this paradoxical responding in the presence of free food does not take place if the animals are equally familiar with the different sources of food. That is, the presence of responding when free food is available is understood not in terms of the animal's preference for the performing of the operant per se, but in its preference for the source from which the earned food comes. Thus it is neophobic of the free food and the food container in which the free food is presented, and prefers to continue to work to obtain food from the source it trusts.

Further, it is difficult to accept the idea of "dissociation" of operant and consummatory behaviour in view of the fact that there is a lot of evidence to suggest that the actual appearance of the water reinforced key peck differs from the food reinforced key peck in birds (Jenkins and Moore, 1973; Wolen, 1968). When the pigeon is pecking a key for a food reward the beak is slightly open, just as it would be if it were normally pecking at food. The water response however, is with a closed beak which corresponds to the fact that Columbiformes uniquely among birds drink by inserting the beak into the water and "pumping" the water up into the mouth using the tongue, rather than the behaviour of other birds which involves taking a mouthful of water and throwing the head back to swallow. It was a familiar idea to the Gestalt psychologists that every stimulus in the environment told the perceiver what to do with it.

> "a fruit says "Eat me"; water says "Drink me" "
>
> Koffka (1935)

Gibson (1976) in his "Theory of Affordances" argues that an operant panel which a monkey presses to obtain a banana could only say "Push me" and no more. However, the fact of the different appearance of the operants for food and water in the pigeon clearly indicate that the key says to the bird "Push me in order to obtain ....." whatever the reinforcement is.

Again however, if we assume that the trigeminal sectioned animal is normally motivated to feed but does not recognise the food, we would predict that it would initially respond at the normal level but would show a simple extinction over time. That is, it would treat the hopper as if it were empty to all intents and purposes and would not show any attempt to consume the reward. This hypothesis would predict that some approach to the food hopper would need to be made in order for the animal to try and reject the unrecognised food. Zeigler's data are here a little difficult to interpret. Zeigler (1975(b)) presents data in full for only one animal for one session (graphically) which shows food intake and pecking responses to the food hopper to be zero. However, the text indicates that in the first 5 post operative sessions in the operant chamber the reduction in approaches to the food ranged from 31 to 100% with a mean of 67%. Data presented by Zeigler and Feldstein (1971) for one representative animal shows a peak in the ratio of approach responses to food consumed immediately after the nerve section in the operant test. As the graph indicates that the food intake was well nigh zero at this point it is difficult to be sure exactly what this would mean. We can however quote the text here which indicates that "while the pigeon is making a <u>great many feeding responses</u> it is getting no food."

Thus it does seem possible that the animals in Zeigler's operant test situation could have sufficient contact with the food to sample and reject it as here it is suggested they do in the home cage.

6.11 Operant Performance and Novel Food

As an illustration of the operant behaviour of birds suddenly presented with a novel food, 4 Ring doves were used which had previously become accustomed to living and obtaining all of their food requirement in operant cages in a study of feeding patterns and fixed ratio work load to be discussed in chapter 10.

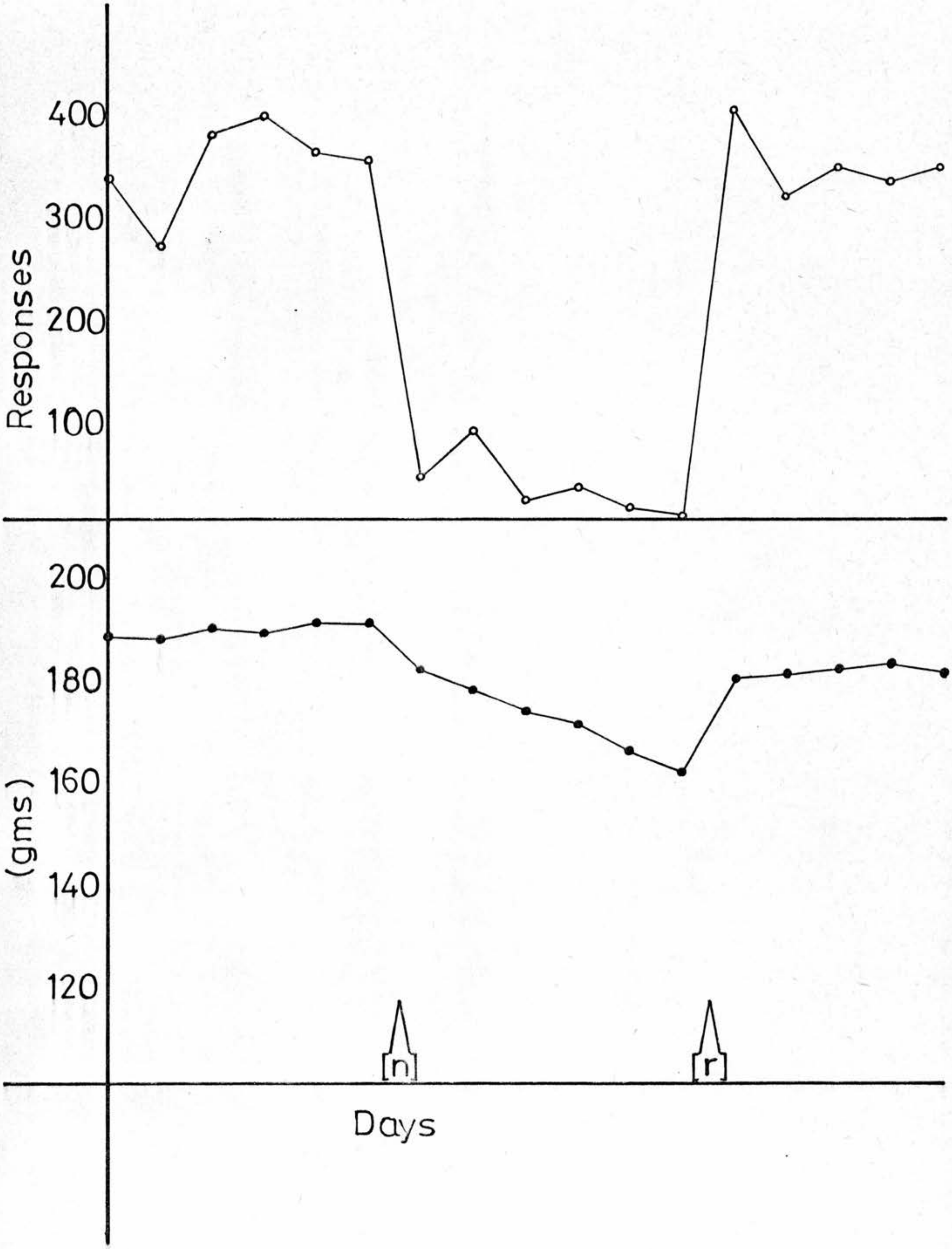
6.11(a) Method

At the end of a prolonged series of operant observations in which the birds had been required to perform for food on ratios ranging from continuous reinforcement to a fixed ratio of 160 responses to one short (7 second) period of access to the food hopper, the birds were returned to the continuous reinforcement and some additional baseline data were collected. The animals had been fed on single grain millet diet for the whole of the time which they had been housed in the operant cages (about 6 months at this time). They were housed in a room away from the main colony on a 12 hour light cycle (see chapter 10 for details).

The millet was removed from the food hoppers and was replaced by long grain rice and the responses of the animals was observed. Two showed no effect, accepting the new food and maintaining body weight. A third showed a slight dip in body weight on the first day of the novel diet, but apparently overcome any initial reluctance to feed quite quickly. The other bird however refused to eat the rice and lost weight. The record of body weight and operant responses for this bird is summarized in Figure 6.2. Some attempt was made to wean the bird onto the novel food by force feeding small quantities,

FIGURE 6.2

Response of one bird living and earning all its food requirement in an operant cage on continuous reinforcement, to the introduction of a novel food (indicated [n]). The upper panel shows the number of operant responses for food each day and the lower panel shows the body weight of the bird. Point [r] indicates the return of the normal diet.


400
300
Responses
200
100
200
180
160
(gms)
140
120
n
r
Days

but this was finally abandoned and the familiar millet diet was returned.

It was not possible to record the actual amount of food consumed in this situation, but it could be seen by simply examining the hopper that little or no food material was being removed during the period of body weight loss indicated on the graph. On the first day or two after the introduction of the novel food a small amount of material was seen to have been removed, but an approximately equivalent quantity was found to have been spilt below the hopper.

Again we can assume that the success in persuading the other three animals to accept the diet indicates that there is no physical or nutritional reason why the fourth should hot have. What was also found however, was that although the bird was actually eating no food, it was still producing a fairly large number of operant responses. Zeigler's birds were working on a variable interval (60 second) schedule in short sessions and the doves were working for continuous reinforcement in a continuous, free operant situation, so it would be difficult to make any very close comparisons. But there is clear evidence of a continuation of the tendency to approach the operant key which had previously been associated with food, and to peck in an attempt to produce food. The failure of the animal to consume the reinforcement however, simply indicates that it is not accepted as food. Over days the number of responses decays as one would expect to find during extinction.

6.12 Differences between Pigeons and Doves

Is there any way in which this "neophobia" hypothesis about the effect of the trigeminal section could shed light on the differences between the effects reported by Zeigler using pigeons and those reported here with the doves?

Zeigler (1975) indicates that the pigeons were fed on single grain milo diet. The birds in the dove colony at Edinburgh are normally maintained on a diet which is a mixture of approximately two parts of wheat to one part of both millet and corn. Zeigler's pigeons were obtained from a commercial breeder and no information is given about the diets which the birds would have been used to before they arrived at the laboratory. It can be assumed however that at least for the period of the pre-operative observations and the time for which they were kept in the laboratory, Zeigler's pigeons had had the experience of a much more homogeneous diet than the doves. It might be suggested then that familiarity with a number of different food types might make an animal less likely to show reluctance to try and accept a further diet. Following the present analogy, the pigeons, with their rather homogeneous past experience of food might be more disturbed by the effect of nerve section on the sensory quality of their food than the doves which were accustomed to a mixed diet of fairly variable composition. If that were true, one would expect to be able to enhance the effect of trigeminal section on the doves by a pre-treatment involving maintaining the animals for a period on a diet of only one grain type.

6.13 Trigeminal Section and Post Feeding Experience (1)

A group of 12 adult female Ring doves (of which 9 survived the surgery) were kept for two months on a single grain wheat diet with all other conditions of housing being identical to those described for the second group (ad libitum food availability) of trigeminal sectioned animals described in chapter 4. At the end of this time a week of baseline food intake and body weight data were collected before the birds were subjected to bilateral section of both the ophthalmic and the mandibular branches of the trigeminal nerve.

6.13(a) Results

A summary of the data is presented in Table 6.2. It can be seen that no very obvious effect of the nerve section was found in this group either, although two of the 9 surviving birds showed fairly marked aphagic effects (three and four days). However, there did appear to be more evidence of post-operative hypophagia in this group than in the original series (chapter 4). If we take a very broad definition of an "effect" of nerve section being found in any one animal as being evidenced by either a continued drop in body weight after the surgery or no body weight increase towards the baseline for at least one post-operative day (that is, zero or negative weight gain for at least one day after surgery), it is possible to compare the frequency of occurrence of "an affect" of the surgery in the original and the present single grain group. A "Chi-squared" statistic was used to test the null hypothesis that there would be no difference in the frequency of occurrence of the effect in the two groups. Thus

TABLE 6.2

EFFECT OF TRIGEMINAL SECTION

(Adult birds maintained on wheat)

BIRDS	1	2	3	4	5	6	7	8	9
DAYS OF APHAGIA	0	3	0	0	0	4	0	0	0
DAYS TO BASELINE WEIGHT	5	14	18	5	17	25	5	18	6
DAYS OF 0 OR NEGATIVE WEIGHT GAIN	0	3	0	0	3	4	2	3	1
BASELINE WEIGHT	151	160	149	138	154	154	137	139	141

Mean body weight = 147.0

S.D. = 8.4261

the expected frequency is taken as the overall proportion of effect to no effect multiplied by the number in the group. We find then (Chi-squared = 6.87; $p < 0.01$) that an effect of trigeminal section on food intake is more likely to be observed when the animals have had a period of rather homogeneous feeding experience.

6.14 Trigeminal Section and Post Feeding Experience (2) - The Effect of Early Experience

Encouraged by this agreement with the hypothesis, it was hoped that birds which had had this constant and homogeneous feeding experience from weaning might be expected to show an even greater effect.

6.14(a) Method

A group of 12 weanling doves were taken from the parental cages and placed first of all in a group cage and then later (when fully fledged) into individual cages in preparation for surgery. From the time at which the birds were removed from the parents they were fed only on wheat and were kept on this diet until the age of three months. At this time, baseline data were collected on food intake and body weight. Bilateral section of the ophthalmic and mandibular branches of the trigeminal nerve was then attempted in all cases. However, of the 12 birds available the surgery was only successfully completed in 7 (Table 6.3). 2 of the other animals died and the remaining 3 were sick under the anaesthetic on two occasions and so no surgery was actually performed. The reason for this difficulty was presumably the age and the low body weights of the animals.

TABLE 6.3

EFFECT OF TRIGEMINAL SECTION

(Weanling birds maintained from weaning on wheat)

BIRDS	1	2	3	4	5	6	7
DAYS OF APHAGIA	0	0	0	0	0	1	0
DAYS TO BASELINE WEIGHT	6	8	7	16	11	16	9
DAYS OF 0 OR NEGATIVE WEIGHT GAIN	1	2	0	3	0	1	0
BASELINE WEIGHT	132	145	139	135	146	133	144

Mean body weight = 139.1

S.D. = 5.9283

6.14(b) Results

Table 6.3 shows a similar tendency towards a greater effect of the surgery than was found in the original group (Chi-squared = 3.20; not significant).

However, there is another possible reason for the enhancement of the effect of nerve section in these groups which is related to wheat grains per se and not to the past experience. If the nerve section is associated with a sensory and motor disturbance, perhaps the normal diet allows the animals to select smaller pieces of food (for example, the small millet grains) which can be more easily handled. The single grain wheat diet thus produces a larger deficit not because of the effect of pre-operative homogeneity, but because of greater physical difficulty in eating after the surgery. In order to test this, the above procedure (with adult animals) was repeated using millet rather than wheat.

6.15 Trigeminal Section and Past Feeding Experience (3)

12 adult female doves were maintained on a diet of single grain millet for a period (in this case 3 months) before surgery, in conditions as described above. At the end of the period baseline data on body weight and food intake were kept for a week before bilateral section of the ophthalmic and mandibular sensory trigeminal branches was carried out.

6.15(a) Results

The effect of nerve section in these animals (10 survived the operation) is summarized in Table 6.4. The fact that in this group also, the frequency of accurrence of an effect of surgery is greater than the original group (Chi-squared = 5.63; $p < 0.02$) indicates that the hypothesis about greater mechanical problems with the single grain wheat is largely disconfirmed.

6.16 Conclusions

The greater overall effect of trigeminal section in the pigeon as reported by Zeigler may have been due, in part, to the more homogeneous pre-operative feeding experience of these birds. This is indicated by the fact that the effect is more likely to occur in the doves when a pre-operative period of constant, homogeneous diet is given (Figure 6.3). (Chi-squared for all of the above groups compared with the original 14 animals is 8.20; $p < 0.01$). This is in line with the present reinterpretation of the effect of trigeminal section in terms of altered sensory feedback leading to food neophobia.

We might expect to find the effect of this manipulation on the probability of trigeminal section producing a noticeable disruption of food intake regulation would be enhanced by the period of homogeneous gustatory experience extending to the time of hatching. Perhaps the reason that the disruption was not more marked in the weanling group was that a certain critical period had passed, before the animals left the parental cages, during which firm food habits are acquired.

TABLE 6.4

EFFECT OF TRIGEMINAL SECTION

BIRDS	1	2	3	4	5	6	7	8	9	10
DAYS OF APHAGIA	0	1	0	2	1	0	1	0	1	0
DAYS TO BASELINE WEIGHT	11	10	4	9	5	10	13	10	10	8
DAYS OF 0 OR NEGATIVE WEIGHT GAIN	2	1	0	2	2	0	3	0	1	0
BASELINE WEIGHT	144	146	146	156	146	150	140	147	162	141

Mean body weight = 147.8

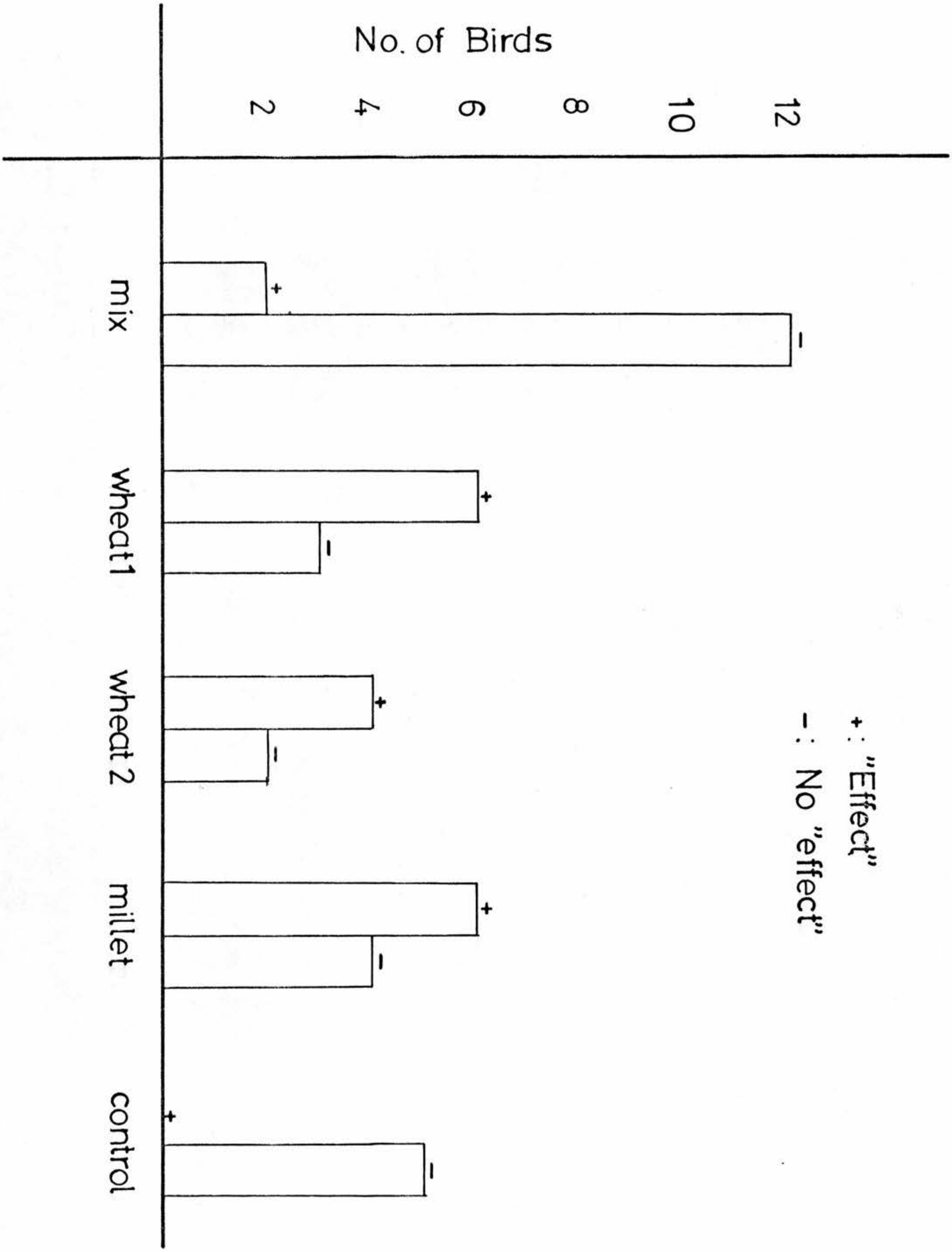
S.D. = 6.7132

FIGURE 6.3

Summary of the effect of trigeminal section on birds maintained on different types of food. ("Wheat 1" indicates the adult group maintained on single grain wheat, and "Wheat 2" indicates the group maintained on wheat from weaning.) The figure shows the number of birds in each group in which an "effect" (see text) of surgery was observed.

Differences between frequencies was tested with a Chi-squared test.

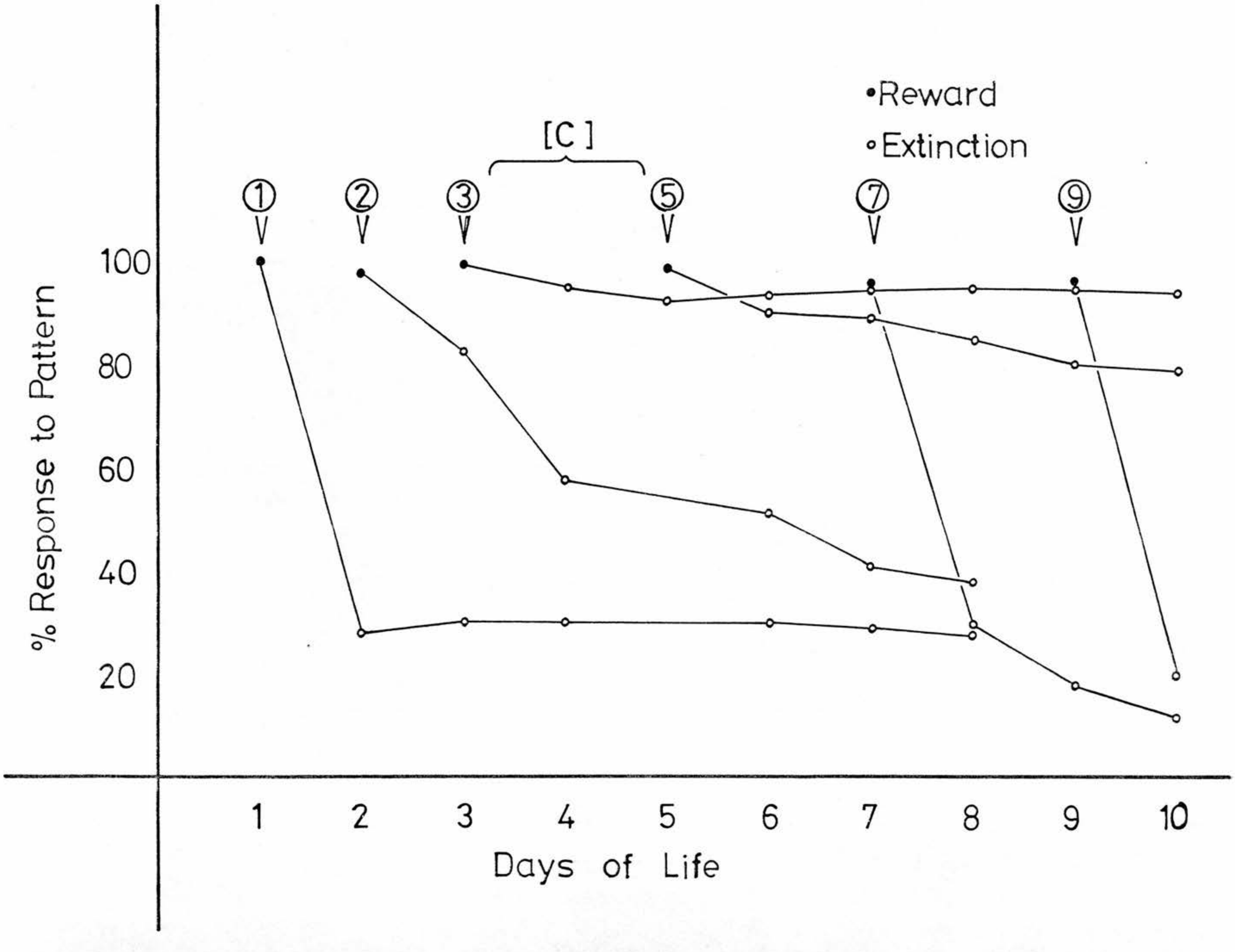
	Chi-squared	Significance ($p <$)
Mix vs. Wheat 1	6.87	0.01
Mix vs. Wheat 2	3.20	N.S.
Mix vs. Millet	5.63	0.02
Mix vs. All others	8.20	0.01


No. of Birds
2
4
6
8
10
12
mix
wheat1
wheat 2
millet
control
+
-
+: "Effect"
-: No "effect"

That this might be so is suggested by Hess (1964) in some work on feeding behaviour and food imprinting in newly hatched chicks. The chicks were trained to peck at a certain patterned stimulus in order to gain access to food material. The training trials took place on one day and the extinction trials were given over several subsequent days to determine the tendency of the birds to persist in pecking at the previously rewarded pattern. The independent variable was the day of life on which the training experience was given. Figure 6.4 is redrawn from Hess's data to summarize the findings. It can be seen that training on the first two days of life and on days seven and nine are followed by very rapid extinction in the absence of reward. When the training experience is given on days three or five however, the response to the pattern stimulus is remarkably resistant to extinction. It would be concluded from this that days 3 to 5 or 6 in the life of the chick include a sensitive period for the acquisition of food preferences and feeding habits. It is likely that, if such a sensitive period exists in the early life of the dove or pigeon, it will be later than that seen in the precocious chicken, but that it will be before the squabs are sufficiently weaned to leave the parents. Young are removed from the parents in the breeding colony here before they would normally leave the nest in the wild and long before they would leave the parental influence. However, it is possible that the appropriate procedure in the above mentioned weanling experiment would have been to raise a population of birds whose parents were being fed on a homogeneous diet, so that all of the early experience was the same.

<u>FIGURE 6.4</u>

Redrawn from data given by Hess (1964) to show a critical period (⌈o⌋) in domestic chicks for the imprinting of an association between a visual pattern stimulus and a food reward.


•Reward
∘Extinction
[C]
①
②
③
⑤
⑦
⑨
% Response to Pattern
100
80
60
40
20
1
2
3
4
5
6
7
8
9
10
Days of Life

6.17 Results of Breeding for Weight Gain

As discussed above, the pigeons used by Zeigler for his studies of the trigeminal section had come from a commercial breeder and were varieties which have been selected specifically for meat production for many years. Although we have no external evidence to support this suggestion, it is possible that an animal which has been selected for weight gain may be more "finicky" or sensitive about the sensory quality of its food, in a way rather analogous to Schachter's (1971) discussion of over-weight in humans, and sensitivity to external sensory information. If this were the case, this would also be expected to lead to an enhancement of the effect of trigeminal nerve section, if this is seen as being due to neophobic avoidance. The pigeon would also show a more prolonged after-effect of surgery resulting from a reduction in the perceived pleasantness of the diet with the reduced sensory feedback.

6.18 Effects of Serial Surgical Procedures

Zeigler (1975) reported that if section of the branches of the trigeminal nerve were carried out serially rather than in one complete procedure, and the animals allowed to recover as far as possible from the effects of the first surgery before the next is performed and so on, then the effect of the surgery appeared to be cumulative. No attempt was made to account for this in terms of the reduction of motivation hypothesis, and indeed it is difficult to see how such an account could be given.

If the data are interpreted in terms of food neophobia however, it can be seen that serial surgery would result in a series of percepts of food novelty, each of which would be compared with the original pre-operatively experienced "norm." Even if the animal was allowed to recover voluntary intake after each procedure, the deviation of the "perceived food" from the animal's previous normal food experience would be greater in each case. Thus a hypothesis in terms of the animal's response to a new food as compared with its previous normal experience, accounts for these serial surgery effects better than Zeigler's own interpretation.

6.19 Chapter Summary

An alternative hypothesis is presented to account for the behaviour of birds after section of the trigeminal nerve. It is suggested that nerve section leads to an altered perception of the animal's normal, familiar diet to being novel and unpalatable, due to the altered sensory feedback.

A discussion of all of the effects of the surgery as reported by Zeigler was offered to argue that this alternative interpretation can handle the experimental evidence better than that of Zeigler, and data were presented on the effect of food novelty in the Ring dove to show that such a manipulation can produce aphagia quite as marked as those seen after trigeminal section.

A prediction of the food neophobia hypothesis, that homogeneous past experience of food material would tend to enhance the very gross effects of the trigeminal section, was tested and confirmed.

CHAPTER 7

7.1 Effect of Food Type on Feeding Pattern

It was argued in the preceding chapter that all of the more obvious effects of section of the trigeminal nerve on food intake and body weight could be explained in terms of a failure of the post-operative birds to recognize their food as being edible. Similarly, the prolonged hypophagic effects which lasted even after recovery from the first aphagic stage might be seen as being analogous to reduced body weight as a result of a reduction in diet palatability.

It is suggested here then, that the more subtle effects of trigeminal section on meal taking and patterns of feeding behaviour in the Ring dove, which were discussed in chapter 5, may also be due to the change in perceived diet palatability. It should be possible theh, to mimic these effects by feeding the animals on a less preferred diet than the normal mixed grain material.

It was decided therefore to look at the feeding behaviour in a group of animals when feeding on their familiar mixed grain diet and also on a single grain diet of the grain material which the animals preferred least. It was assumed that a mixed grain material would be more pleasant for the birds to feed on than any single grain diet, simply because it was varied, and also because birds appeared to spend a lot of time in food searching behaviour when provided with a mixed diet, which they seemed to enjoy (Zeigler and Feldstein, 1971).

7.2 Choice of the Least Preferred Grain

The first thing which had to be done was to determine which, of

TABLE 7.1

Food Preference Experiment

Two Choice Preference Tests - Design

	Wheat	Millet	Corn	Hemp
Wheat	1	+	+	+
Millet		1	+	+
Corn			1	+
Hemp				1

i.e. 6 by 2 way comparisons

all of the food materials available, the birds liked the least. This was achieved by a series of two choice preference tests as illustrated in Table 7.1.

7.2(a) Method

12 adult female Ring doves were observed in order to obtain some overall estimate of the food preferences of the birds in the Colony. The birds were maintained in the usual individual cages (40 x 35 x 45 cm) and were given free access to water and to grit, and also two types of grain in separate hoppers set side by side on the fronts of the cages. The animals were kept on a 9 hour light cycle with lights on at 9 am and off at 6 pm. Food intake was measured at 9 am before the onset of the light phase of the cycle. The animals were allowed two days to become accustomed to feeding from the hoppers on each of the 6 pairs of food materials and the data for the next 5 days were used to compute a mean intake of each of the pair. The next pair of foods was then offered and the procedure repeated. The

food hoppers were reversed each day to avoid any error which might arise if the animals had a preferred side from which to feed, although no indication was ever seen that this might be the case.

7.2(b) Results

Figure 7.1 summarizes the results from these 6 two choice comparisons. It would seem that hemp and millet were preferred approximately equally, and preferred more than both corn and wheat which was also almost equal. The overall preference is for corn over wheat however when a comparison is made. On the basis of these tests it was decided to use wheat as the low preference food material.

7.3 Collection of Feeding Pattern Data

12 adult female doves were used for this study. The animals were housed in individual cages (40x35x45 cm) with continuous availability of water and of grit, and with the food material available in the photocell feeding monitor devices. The light cycle in the room in which the birds were was 9 hours (9am to 6pm) and the room was kept at a constant temperature of about 70°F.

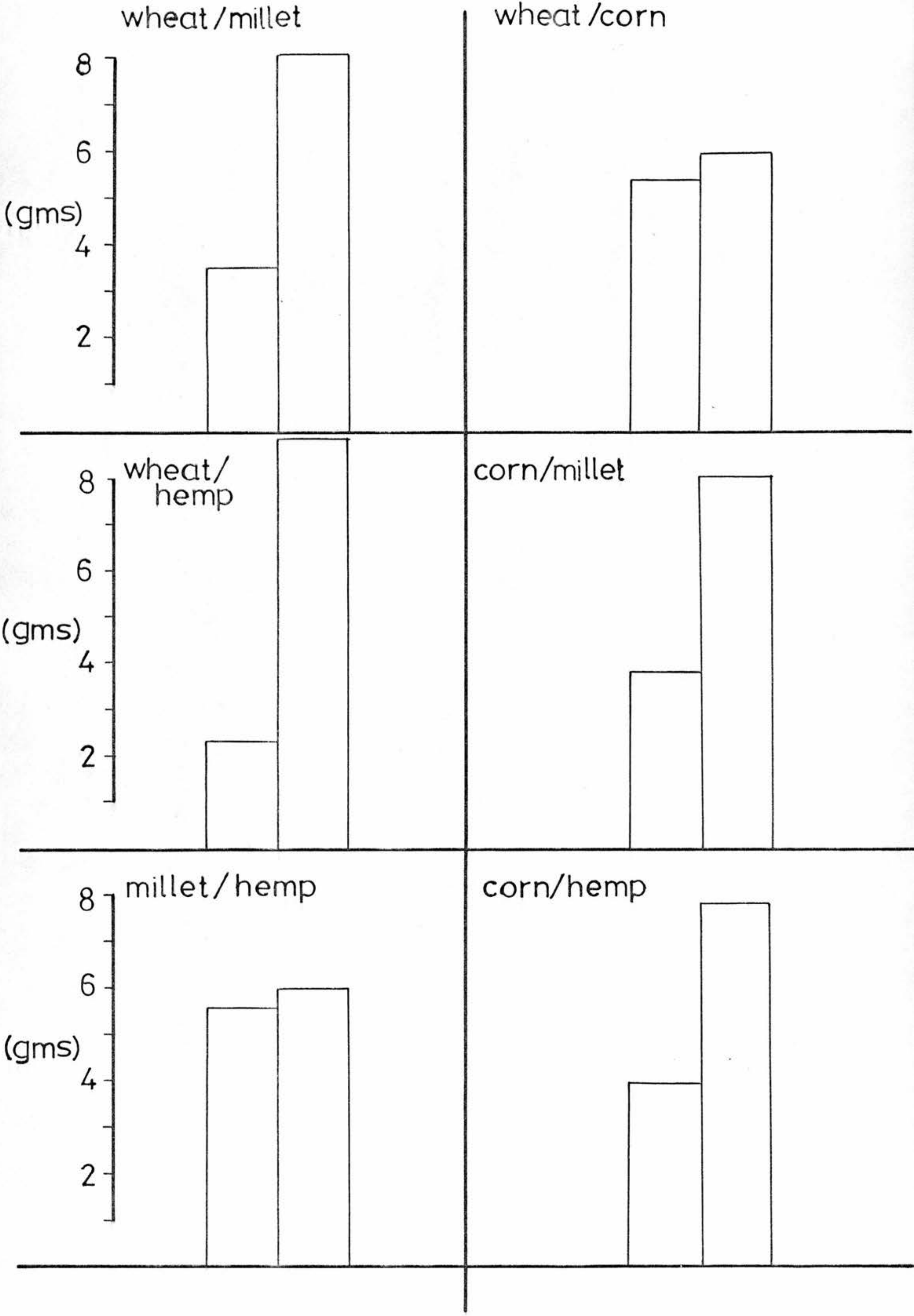
Feeding pattern data were collected for each bird for seven days feeding on the mixed grain diet and then this diet was removed and the hoppers filled with the single grain wheat diet. After a period of three days to settle on to feeding on the new material a further seven days of data were collected.

FIGURE 7.1

Summary of two choice preference tests (Table 7 (a) to (f); Appendix II).

Significance of comparisons tested with a "t" test for correlated samples.

	"t"	Significance ($p <$)
Wheat/Millet	10.821	0.001
Wheat/Corn	3.473	0.01
Wheat/Hemp	14.886	0.001
Corn/Millet	15.767	0.001
Millet/Hemp	0.528	N.S.
Corn/Hemp	11.800	0.001


wheat / millet
wheat / corn
8
6
(gms)
4
2
wheat / hemp
corn/millet
8
6
(gms)
4
2
millet / hemp
corn/hemp
8
6
(gms)
4
2

It was predicted that some of the subtle changes in feeding pattern which were found as a result of the trigeminal nerve section would also be found to follow from the transfer to the less preferred diet.

7.4 Logarithmic Survivorship Plots

Cumulative logarithmic survivorship plots were generated as described in chapter 3 for each of the animals on each of the two food types. It was expected that the shape of the curves produced as a function of food type would vary in a similar direction to the variations observed after nerve section. That is, the behaviour of the animals feeding on the less preferred (wheat) diet would produce "shallower" curves with higher values for the criterion inter-feeding intervals than those produced from the feeding patterns on the mixed grain diet.

As there is always a certain degree of individual judgement involved in the derivation of the criteria from the survivorship plots, it was decided that these should be scored blind by another researcher who was familiar with the theory and use of the technique, but who was unaware of the present hypothesis. The results are summarized in figure 7.2.

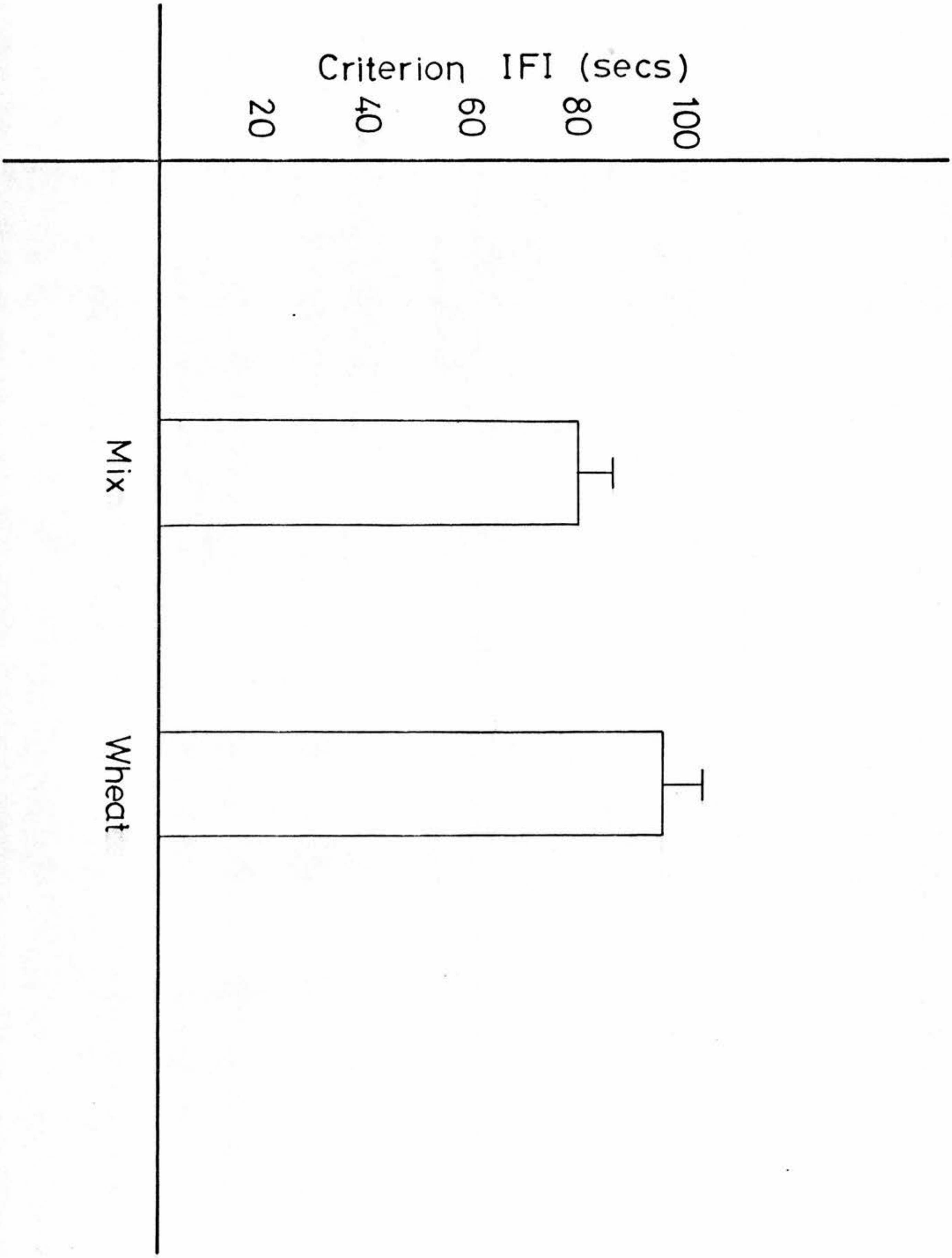
The feeding behaviour of the animals on the low preference food can, like the post-operative behaviour, be seen to involve longer pauses within ongoing meals.

FIGURE 7.2

Mean size of criterion inter-feeding interval (IFI) for birds feeding on a mixed grain diet and a single grain wheat diet (Table 8; Appendix II).

Significance of comparison tested with "t" test for correlated samples.

"t" = 1.8258; N.S.


Criterion IFI (secs)
20
40
60
80
100
Mix
Wheat

7.5 Frequency of Meal Taking

To look at the effect on meal frequency of the change in foods, it is obvious that the choice of an inter-meal interval criterion from the logarithmic survivorship plots is going to have a similar confusing influence. For this analysis then, as with the analysis of meal frequency after trigeminal section, it was felt necessary to compute the meal frequencies using a "blanket" criterion in addition to those derived from the survivorship curves. A summary is given in figure 7.3. The birds got their total daily requirement in fewer meals, and this is seen to be a significant difference when the data are ordered on the basis of the derived criteria (Wilcoxon "T" = 6.0; $p < 0.05$ one tailed) and using a blanket criterion of 250 seconds (Wilcoxen "T" = 7.5; $p < 0.01$ one tailed).

7.6 Problems of Interpretation

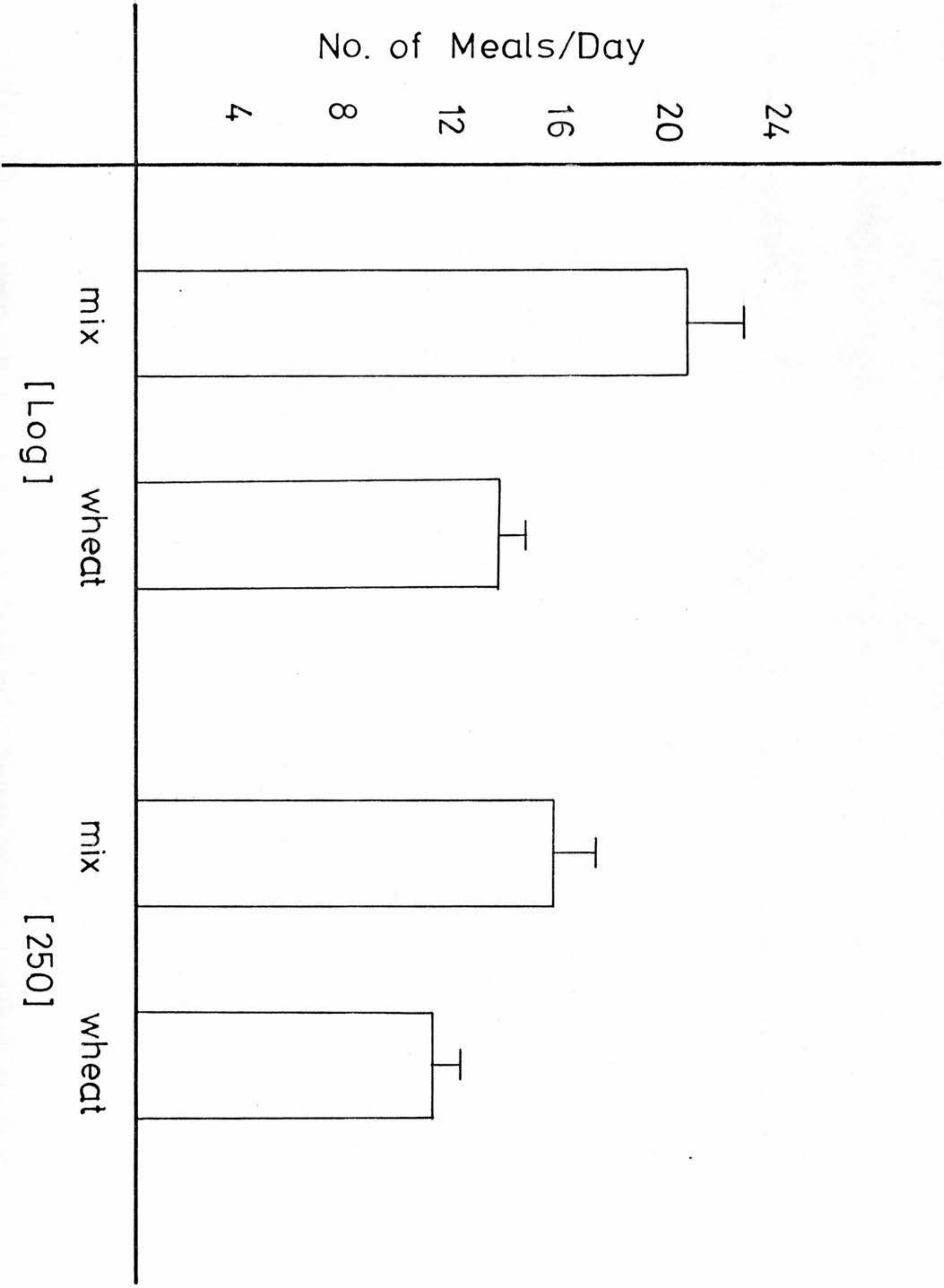
It has been reported elsewhere (Keesey and Boyle, 1973) that animals may show lowered body weights on less preferred, unpalatable diets. These experiments, performed using rats, usually involve some extreme manipulation of food palatability like adulteration of the food with an unpleasant testing substance. It seems unlikely that the very minor reduction in diet palatability used in the present experiment would result in a reduction in gross daily food intake, such that the reduction in meal frequency could be explained in these terms. However, in order to establish that the reduction in mean daily meal frequency is not associated with a tendency to drop body weight, but is truly an indication of the tendency of the animal to eat the same amount

FIGURE 7.3

Mean frequency of meal taking by birds feeding on a mixed grain diet and on a single grain wheat diet, computed using criteria derived from individual logarithmic survivorship plots (Log) and using a "blanket" criterion of 250 seconds (250) (Table 8; Appendix II).

Significance of comparisons tested with a Wilcoxon matched pairs test.

	"T"	Significance ($p <$; one tailed)
Log	6.0	0.005
250	7.5	0.01


No. of Meals/Day
4
8
12
16
20
24
mix
wheat
[Log]
mix
wheat
[250]

of food in fewer, longer meals, it was decided to look at the body weights of a group of animals feeding on the mixed grain diet and on single grain wheat.

7.6(a) Method

A group of 12 adult female Ring doves was used. These animals were housed in single cages in the main colony room on a light cycle of 10 hours (8am to 6pm). Body weights and food intakes were measured at 9 am approximately.

The birds were normally maintained on the mixed grain diet. Body weight and food intake information was collected for one week to get them used to the disturbance involved in making the measures. At the end of this time, 6 of the birds were transfered to the single grain wheat diet, and the other 6 were left with the mix diet. After 3 days to settle to the change the body weight and food intake measures were kept for one week. At the end of that time the foods were switched around so that the birds which had previously fed on the wheat were given the mixed grain, and those on the mix were given the wheat. A further 3 day period was allowed and another 7 days of information was collected.

7.6(b) Results

There is no sign that the animal's body weight is affected by the change of diet. Neither can any significant change in food intake be seen (Appendix II; Table 9). It was therefore assumed that the change in meal frequency noted above represents a behavioural change which has no obvious metabolic cause.

7.6(c) Other Problems

The above two food materials obviously differ in ways other than palatability. For example, the fact that one food is a mixture of grains and the other is a single grain means that the birds spend a great deal more time feeding on one than on the other (Figure 7.4). Perhaps this indicates that they spend time sorting through the mixture to find preferred items of food.

Although there is very little difference in the calorific value of the different grains used there could be other problems relating to the rate of passage of the material through the gut or to the ease of digestion which could account for the changes in meal frequency. Perhaps the mixture, which would contain smaller items of grain, would be digested more quickly resulting in a pattern of more frequent meal taking.

It is possible too that some factor such as the salt content of the diets produced a change in the interaction of food and water intake leading to a change in meal frequency analagous to that seen after desalivation in rats (Kissileff, 1970).

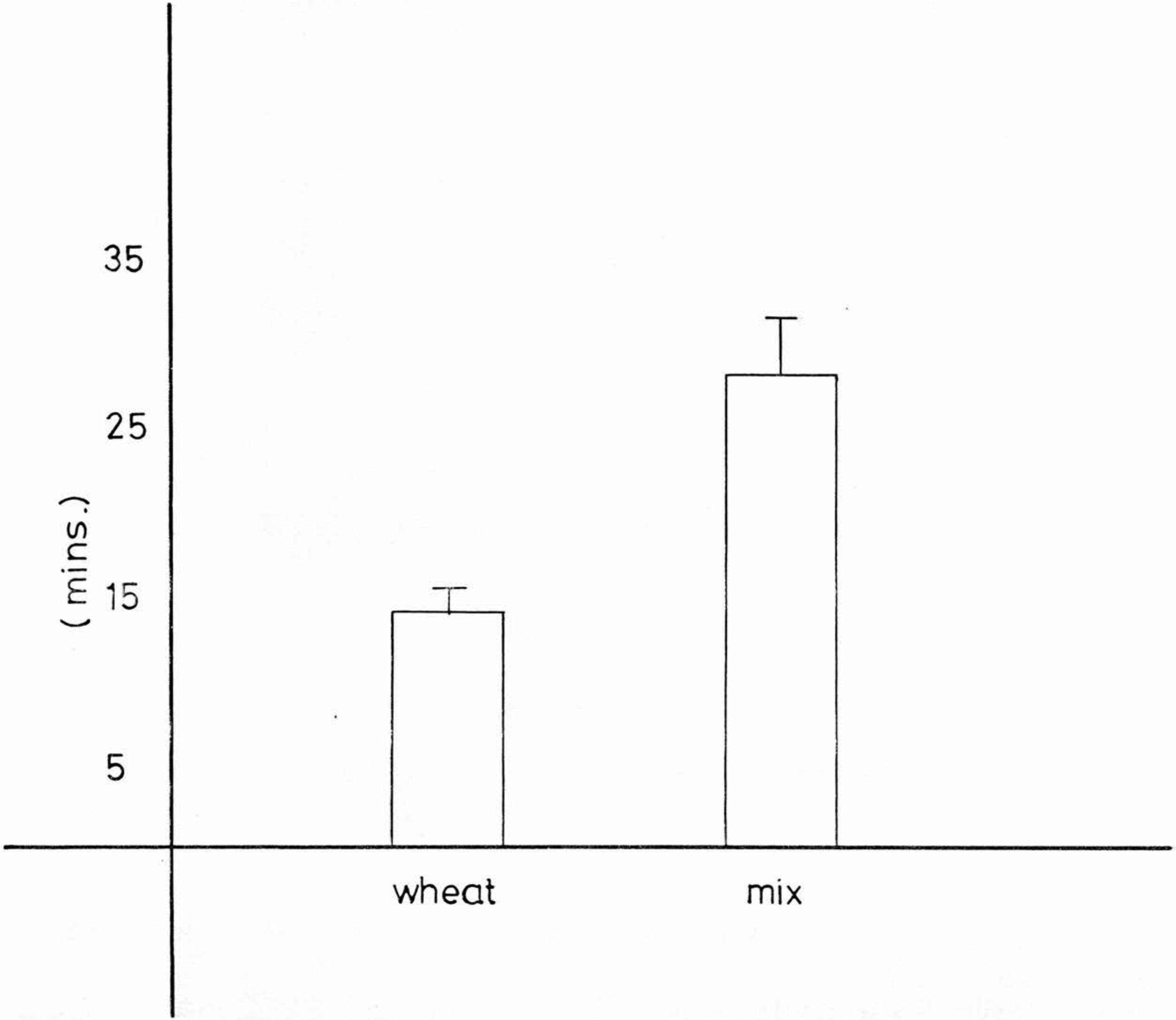
Clearly this study could have been better carried out using artificially prepared food materials rather than grain, and using a procedure of systematic adulteration of the food with quinine or some such substance, but this too might have been problematic as the doves,

FIGURE 7.4

Mean time spent feeding each day by birds feeding on a mixed grain diet and a single grain wheat diet (Table 8; Appendix II).

Significance of comparison tested with a Wilcoxon Matched Pairs test.

"T" = 4.0; $p < 0.01$, two tailed.


35
25
15
5
(mins.)
wheat
mix

like all graminivorous birds, are relatively insensitive to taste and smell (Gentle, 1975).

7.7 Time of Onset of Feeding Behaviour

It was found that there was a very marked tendency in the case of some of the post-operative trigeminal sectioned animals to show peaking of feeding activity during the initial stages of the day to a greater extent than would be normal with intact birds. Although this tendency was not seen in all of the birds, it was possible to suggest that some facilitatory effect of feeding motivation was present first thing in the morning as indicated by a significantly earlier onset of feeding behaviour after dawn in the operate birds.

Figure 7.5 shows that a similar trend was evident in the birds feeding on the less preferred diet. This effect however is not significant (Wilcoxon "T" = 25.0). From consideration of the overall diurnal pattern of the feeding behaviour of the birds it could be seen that several animals showed particularly large peaks in morning activity in the mixed grain group. It was noted above (chapter 5; Figure 5.11) that a period of deprivation or body weight loss can lead to pronounced patterns of morning peaking. Perhaps the act of moving these birds from one room to another before the collection of the feeding behaviour data caused an upset or disturbance which had not settled before the data was collected. The fact that this might be so is indicated by the absence of the morning peak, and a more normal pattern of behaviour in the data collected later on the wheat diet.

FIGURE 7.5

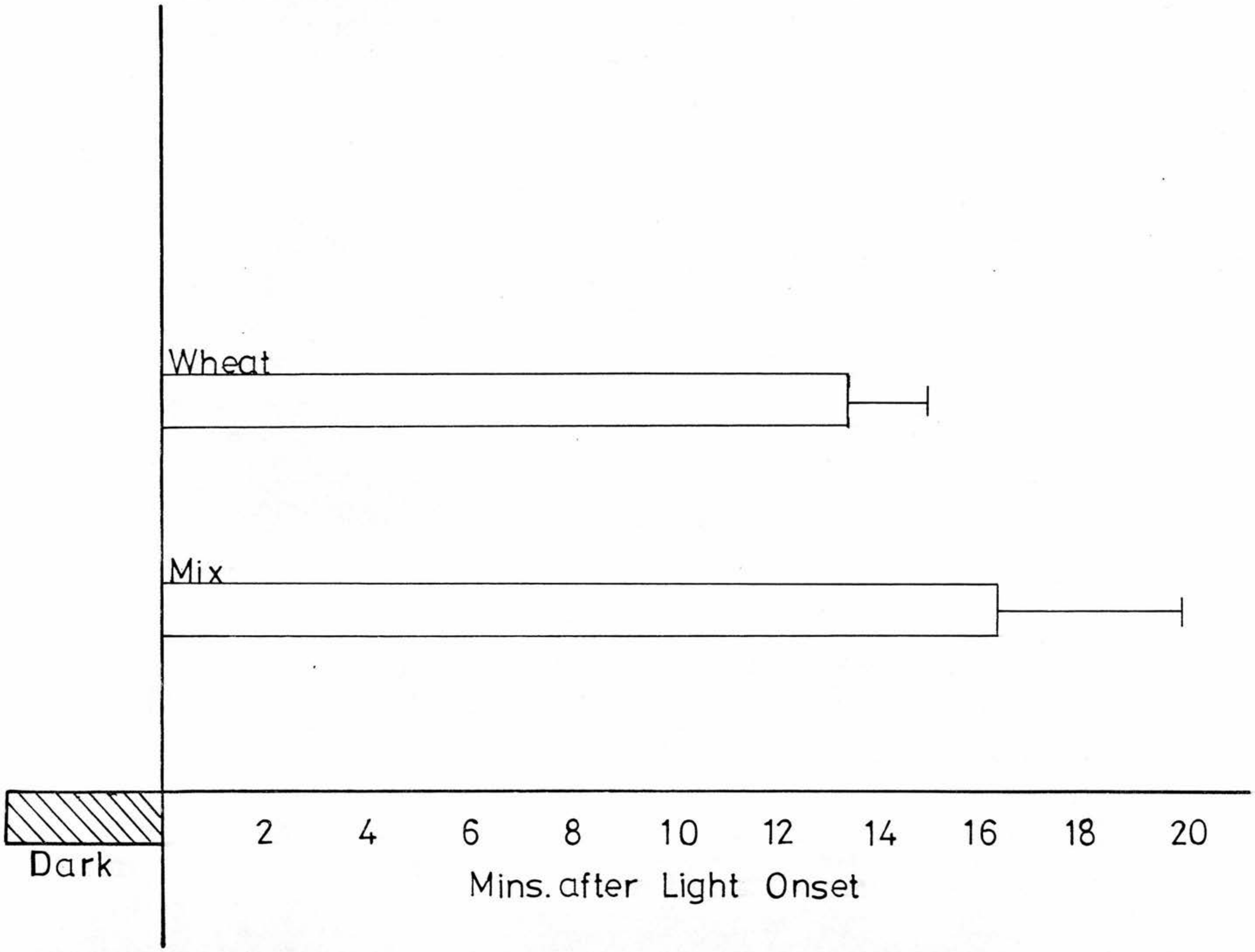
Mean time of onset of feeding in minutes after "dawn" in birds feeding on a mixed grain diet and on a single grain wheat diet (Table 8: Appendix II).

Significance of comparison tested with Wilcoxon Matched Pairs test.

"T" = 25.0; N.S.

Also, a "t" test for correlated samples,

"t" = 0.9194; N.S.


Wheat
Mix
Dark
2
4
6
8
10
12
14
16
18
20
Mins. after Light Onset

If the animals (F206G, F471G and F655S) are excluded from the analysis then the comparison does become significant. (Wilcoxen "T" = 6.0; $p < 0.025$ one tailed).

7.8 Summary - Diet Palatability and Food Intake Distribution

It would seem that all of the effects of trigeminal section on the temporal patterning of feeding behaviour can also be produced by a manipulation of the food offered to the animals, which has been described as a change in palatability. It is also unfortunately clear that the two diets used in this experiment differ in ways other than simply palatability. It would therefore be desirable to repeat this experiment in a more controlled way.

7.9 Discussion

7.9(a) The By-Passing of Sensory Feedback by Direct Intra-gastric Feeding

The lack of sensory feedback produced by the section of sensory nerves might be analagous to experiments which have been carried out to study the importance of such feedback by removing this stage of the ingestion process altogether, by the use of techniques of direct, intra-gastric delivery of food.

Berkun, Kessen and Miller (1952) found that milk injected directly into the stomach of rats served to inhibit feeding in a subsequent 10 minute test trial to a greater extent than an injection of the same volume of saline. They found however that milk injected into the stomach did not inhibit feeding in the test as much as did the same amount of milk ingested in the normal way. Food which the rat actually consumed itself was more satisfying than an equal amount of food injected directly. Miller and Kessen (1952) and Kohn (1951), using operant measures of hunger motivation found essentially similar effects. Kohn concluded that "drive reduction can occur in the absence of need reduction." This referred to theories of motivation and reinforcement (e.g. Hull, 1943) which attempted to view all motives in terms of biological, homeostatic needs. It seemed to be the case that the performance of the ingestive behaviour and the associated oro-sensory feedback was rewarding in itself and contributed to the reduction of drive.

The by-passing of oropharyngeol feedback in the above experiments could be seen as analagous to the reduction in such feedback by sensory nerve section. Thus some of the satiating power of the food is lost due to this reduction, causing a meal to continue longer than it normally would have done. The oropharyngeol sensory information has a "metering" function. With absence or reduction in this feedback the rate on amount of food ingested is underestimated. Blass et al. (1976) demonstrated that some regulatory information was provided by the performance of the consumatory act of drinking. They found that "sham drinking" (ingestion of water which did not reach the stomach due to an oesophageal fistula) in rats, was always in proportion to the state of deprivation. The ratio of "sham" intake to normal intake was about 4:1, this ratio holding constant over a large range of deprivation levels. It might be argued that the increased meal size found after the reduction of orosensory feedback by trigeminal section, was due to the reduction in the satiating consequences of the meal. The decrease in meal frequency would then be seen as a compensatory reduction secondary to the effect on meal size. This argument however, would predict an initial increase in food intake after nerve section rather than a decrease or even an aphagia.

Epstein and Teitelbaum (1962), using a technique of direct injection of food into the stomachs of animals controlled by a bar press response of the animals themselves, found that body weight and food intake regulation were essentially normal in the absence of orosensory feedback. Those results, in keeping with a biological need-reduction view of motivation and reinforcement, were taken to show that it was the metabolic and not the sensory consequences of food intake which were important. However, as pointed out by Snowdon (1969) the amount of food which was injected into the rats stomach for one press of the operant bar in the procedure of Epstein and Teitelbaum approximated to a whole meal. When Snowdon himself attempted to repeat the procedure with much lower rates of injection (rates which were more nearly equivalent to the normal rate of ingestion of the animal) he found it very difficult to train the animals to perform the operant at all for food only delivered directly into the stomach. When an animal which had previously learned to press the bar to deliver injections of liquid diet into the mouth to be swallowed in the normal way was transferred onto direct intra-gastric injection, the bar press behaviour was extinguished. In order to train the animals to respond for direct injection it was necessary to vastly increase the rate of delivery of the food (by about 32 times) so that very few presses were needed to obtain the daily food requirements, and then to slowly reduce the rate until the animals increased their responding to compensate. In some cases the direct intra-gastric food was supplemented by oral food to encourage the animals to continue to respond. The whole training procedure took about 2-3 weeks, so it is clear that, in Seligman's (1970) terms the rat is "contra-prepared" to learn the task.

A further objection to Epstein and Teitelbaum's claim of normal regulation in the absence of oropharyngeal sensations comes from Holman (1968) who suggested that the animals used were not really deprived of oro-sensory feedback. The region of passage of the tube through which the food was delivered was such that the passage of the food down the tube would give a crude approximation to normal sensory feedback. This was shown to be important as the temperature of the liquid diet which was injected had an effect on the probability that the rats would acquire the response. If the food was kept cool, as was done by Epstein and Teitelbaum to prevent it from going bad, then the rats learned the response more easily than if the injected diet was warm. Presumably the passage of the cool liquid through the tube caused cooling of the nasopharynx and oesophagus which was detected by the animals. When the material was closer to the body temperature of the rat (40°C) there would be less change and sensory feedback associated with its passage.

That is, when all of the available sources of oropharynageol feedback were eliminated (Holman, 1968), or the rate of injection of food more closely approximated the normal rate of ingestion (Snowdon, 1969) the rats did not regulate or "feed" normally.

Sterrit and Smith (1965) found that the opportunity to peck at food, when combined with food intake (either directly into the gut or by the normal route) was reinforcing for their chickens, but that pecking without ingestion, or ingestion without normal feeding behaviour was not. McFarland (1969) found that water injected directly into the crops of his Ring doves would not reinforce an operant response, but that if the directly injected water was supplemented with water to be swallowed in the normal way, the response could be learned. On the other hand, the degree of satiation of thirst was a function of the total intake by both routes.

The act of feeding and the associated oropharyngeal feedback seem to have two main roles in the regulation of food intake. First of all, without it the rewarding or reinforcing aspects of feeding are lost so that food intake does not occur normally. Secondly, the sensory feedback gives information about how much of the activity has been performed and thus contributes to satiety. The pattern of food intake after trigeminal section may be seen as an interaction of the effect of the surgery with these two factors.

7.9(b) Feeding Patterns after Surgical Intervention in Rodents

Further information about the nature of the trigeminal section on patterning of food intake in the doves may come from consideration of surgical manipulation effects on feeding patterns in other species.

The "lateral hypothalamic area" in which the placement of lesions can lead to profound disturbances of eating and drinking in rats, is by no means a homogeneous nuclear mass. It has been suggested (Gold, 1967; Grossman, 1971; Marshall et al., 1974) that the effects on feeding after such lesions are a result of damage done to fibres passing through the area rather than damage to the area itself. (Gold (1973) has also made a similar suggestion about the effects of lesions in the hypothalamic ventro-medial area). Zeigler and Karten (1974) showed that lesions in some of the central trigeminal structures at several levels of the rat brain led to aphagic effects without the other gross disturbances of posture, locomotion and sensory attention which have been reported after lateral hypothalamic lesions (Marshall et al., 1971; Marshall and Teitelbaum, 1974). They therefore suggest that the feeding deficits observed in the classical lateral hypothalamic syndrome are due to damage to trigeminal system fibres passing through the hypothalamics and are therefore homologous with the feeding deficits observed in birds with trigeminal lesions at various levels (Zeigler, 1976). Kissileff (1970) has presented data to suggest that the pattern of feeding in animals after recovery from lateral hypothalamic lesions is one of frequent, small bouts of activity; the opposite of the fewer, longer meals pattern reported by Miller and Zeigler (1974) and also in the present study, as a result of trigeminal nerve section.

Similarly, considering the relative importance of the two sensory systems for the animals, one might suggest that olfactory sensory denervation in the rat would have analogous effects to those of trigeminal denervation in birds. Larue and Le Magnen (1972) found that the loss of olfactory information turned the normal, discrete meal pattern of the rat into one of continuous "nibbling". Again, quite different from the effect reported here to follow trigeminal section.

However, there is some indication that this increase in meal frequency might be a function of the criterion of inter-meal interval size which was chosen, a short criterion giving a high meal frequency and low meal size with a large criterion giving a pattern of low meal frequency and increased size. The criteria used by Kissileff (1970) were in the range of 10 to 20 minutes which is obviously a different order of magnitude from the 1 to 5 minutes employed for the present analysis. Yet it might be that this rat data indicate a similar change in appropriate inter-meal interval as a result of the surgical intervention.

7.9(c) Feeding Patterns and Food Palatability

Pursuing the analogy between sensory denervation and food palatability, it was reported in this chapter that animals feeding on a less preferred diet showed a lower frequancy of meal taking. A similar manipulation of food palatability in rats (Levitsky, 1974) again showed the opposite effect. When the diet of the animals was adulterated with quinine, or was diluted with a non-nutritive substance to reduce caloric density (which would also presumably reduce palatability) it was found that the meal frequency increased and the meal size decreased. Kenny and Mook (1974) using free feeding, operant and liquid diet techniques to monitor feeding patterns in rats, found that the animals fed in a small number of large meals when on the liquid diet as compared with free feeding on a solid diet. As the body weight of the animals declined slightly on the liquid diet it might be inferred that this was less palatable for them. However, this decline in body weight and change in pattern of intake was associated with a net increase in caloric intake, so there were obviously problems of the efficiency of utilization of the liquid food, making interpretation difficult.

Spiegel and Jordan (1978) in a study of simultaneous oral and intra-gastric feeding in humans found that the meal size (these meals being taken at socially conventional times) were longer in the case of simultaneous intake by both mouth and stomach tube, than in either the oral or intra-gastric alone cases, and that these increases lead to the reduction in snacks or breakfast intake to compensate. Campbell et al. (1977) compared the meal taking behaviour of humans fed on a liquid diet when this diet was either consumed orally or was directly injected into the stomach. In both cases, meal taking was not constrained by convention but was free to vary as the subjects desired, and thus the situation is more analogous to most of the free feeding animal studies than the experiments of Spiegel and Jordan. The mean size of meals in the oral feeding condition was found to be 272 Kcals. with an average of 6.8 meals being taken each day. When all of the food was obtained by direct injection into the stomach however, the meal size dramatically increased to 877 Kcals. and the frequency of meal taking declined to 2.7 per day. No information is provided about the subjective responses of the people involved in this study to the procedures used. It might be initially assumed that a situation involving all food intake being directly into the stomach would be unpleasant, but it might be less unpleasant than feeding orally for prolonged periods on a homogeneous liquid diet. The experiment does clearly involve loss of oropharyngeal feedback (and provides similar results to the present study) but it may be that the loss is of unpleasant rather than pleasant sensory stimulation.

7.10 Conclusion

It is proposed that if an animal finds the act of feeding less pleasant, either as a result of a change in the food material, or as a result of loss of sensory feedback for one reason or another, then it will continue to feed for longer at any one meal and take fewer meals. This suggestion does seem to be slightly paradoxical. One would expect an animal to persist in feeding to a greater extent on a preferred food material and to only eat a small amount of a non-preferred material. This is the sort of argument which is advanced by Cabanac (1971) in his discussion of the ecological and physiological role of "pleasure" for an organism. In the context of a natural environment (although the picture can be confused in captivity), animals which are designed to select the sorts of foods which smell and taste pleasant to them will not go far wrong. The environment can be manipulated so that errors are made (Yudkin , 1963) but this does not invalidate the principle. Animals should then eat a lot of what they find pleasant, but little of less palatable alternatives.

The key word is, of course, "alternative". When an animal has a choice, it would be expected to eat more of the more highly preferred food. Indeed we infer an animals preference from the choice it makes when more than one food material is present (Figure 7.1 above). When the animal has no choice however, what would we expect to be the effect of only a highly preferred or only a less preferred food being available at any one time? Panksepp and Krost (1975) showed that rats, whose normal pattern of feeding is predominantly nocturnal, could be induced into a cycle of feeding most during the daylight hours if a particularly palatable food material was offered only at this time.

That is, if the alternation of the availability of the high and low palatability foods is fairly rapid, then the animal will inhibit feeding on the low palatability material and wait until it can gain access to the preferred material. Possibly the main effect of palatability when a choice is present is to determine the degree of persistance of feeding on any one material, but when no choice is possible the animals knowledge about the palatability of the available food affects the probability of initiation of feeding. Thus in the normal free feeding situation in which feeding pattern data were collected in this study, a decrease in actual palatability or in perceived palatability as a result of sensory deafferentiation, would lead to a decrease in the probability of the initiation of feeding at any one time. Associated with this would be a compensatory increase in meal size. This does seem to be in conflict with the data of Levitsky (1974) who found an increase in meal frequency on a diet adulterated with quinine. However, the mean meal size of his animals free feeding on the normal diet was 11.2 calories with a mean inter-meal interval of 2.77 hours, while feeding on the adulterated diet the mean meal size was 2.86 calories with a mean inter-meal interval of 1.59 hours. That is, the reduction in palatability was clearly such that the food intake on the adulterated diet was markedly reduced. A higher frequency of initiation of feeding would be due to the animal's state of deprivation, thus this effect is probably qualitatively different from the reduction of meal frequency with slight reduction in palatability observed here.

On the other hand, a lowered tendency to initiate feeding does not seem to be in keeping with an earlier onset of feeding at the start of the day as was found in the trigeminal animals and also indicated although not significantly present in the case of the less preferred diet. The start of feeding at the beginning of the day however is obviously a special case of initiation of feeding. Part of the feeding activity at dawn would be due to the food deprivation as a result of the nocturnal fast. Although the peak in feeding at the end of the day seems to prepare the bird for this fast, it is likely to start the day with some degree of deficit. The deficit with which the bird starts the day then, is greater if the food is less palatable. Thus we can infer that another effect of feeding on a less preferred diet is to reduce the significance of the afternoon feeding peak. It is possible that the feeding going on at this point in the afternoon is more susceptible to influences of palatability than the hour by hour feeding during the rest of the day.

7.11 Chapter Summary

It was hypothesised that some of the effects of trigeminal section on patterning of feeding in birds are due to a reduction in the effective palatability of the diet. The effect of an actual reduction in palatability on feeding pattern was therefore studied.

The effect of a reduction in diet palatability was indeed similar to that of trigeminal section, namely a reduction in the frequency of meal taking, and some indication that feeding began earlier after the onset of the light phase of the cycle.

Attempt was made to account for these effects in terms of a reduction in the probability of the initiation of a meal on a less preferred diet when no alternative was available.

CHAPTER 8

8.1 Feeding Patterns and Ambient Temperature

8.1(a) Metabolic and Non-metabolic Influences on Feeding

In chapter 5 it was reported that the effect of section of the trigeminal nerve on food intake distribution was to reduce the frequency of meal taking and (implied by the fact that this reduction was associated with a return to pre-operative weights and food intake) to increase meal size. In chapter 7 it was shown that a change in the type of food offered to the animals, in the direction of lowering the animals' preference for the food, resulted in a similar reduction in meal frequency. Both of these effects were discussed in terms of a reduction of the perceived palatability of the food.

Consideration of the animal and human literature on the effect of manipulations which might be thought to modify diet palatability or oropharyngeal feedback, it was found that in most cases this was associated with an increase in meal frequency and decrease in meal size, with one or two possible exceptions.

If sensory nerve section can be taken to be truly analogous to change in diet palatability and these effects can be seen as non-metabolic influences on the parameters of meal taking control (although changes in food type might be better seen as having some metabolic effects) it might be suggested that an investigation of a manipulation of metabolic demands on feeding pattern in the doves might contribute to the understanding of these non-metabolic effects.

8.2 Effect of Temperature on Food Intake

Decreased ambient temperature leads to an increase in the energy requirements of homeotherms to maintain their body temperature, which is responded to by an increase in food intake. This can readily be demonstrated in the doves.

8.2(a) Method

8 adult female Ring doves were housed in individual cages (40x35x45 cm) in a temperature controlled cubicle. The birds had continuous availability of food, water and grit and the light cycle was 9 hours (from 9am to 6pm).

The normal ambient temperature in the rooms in which the birds were housed is 70°F. Measures of food intake were collected for 7 days at that temperature and then the temperature in the room was reduced to 50°F. The birds were left at the reduced temperature for one week at the end of which a further week of data were collected.

8.2(b) Results

Figure 8.1 shows the mean daily intake of food by the birds. Clearly reduction in ambient temperature leads to a significant increase in the food intake of the birds.

8.3 Changes in Pattern of Feeding

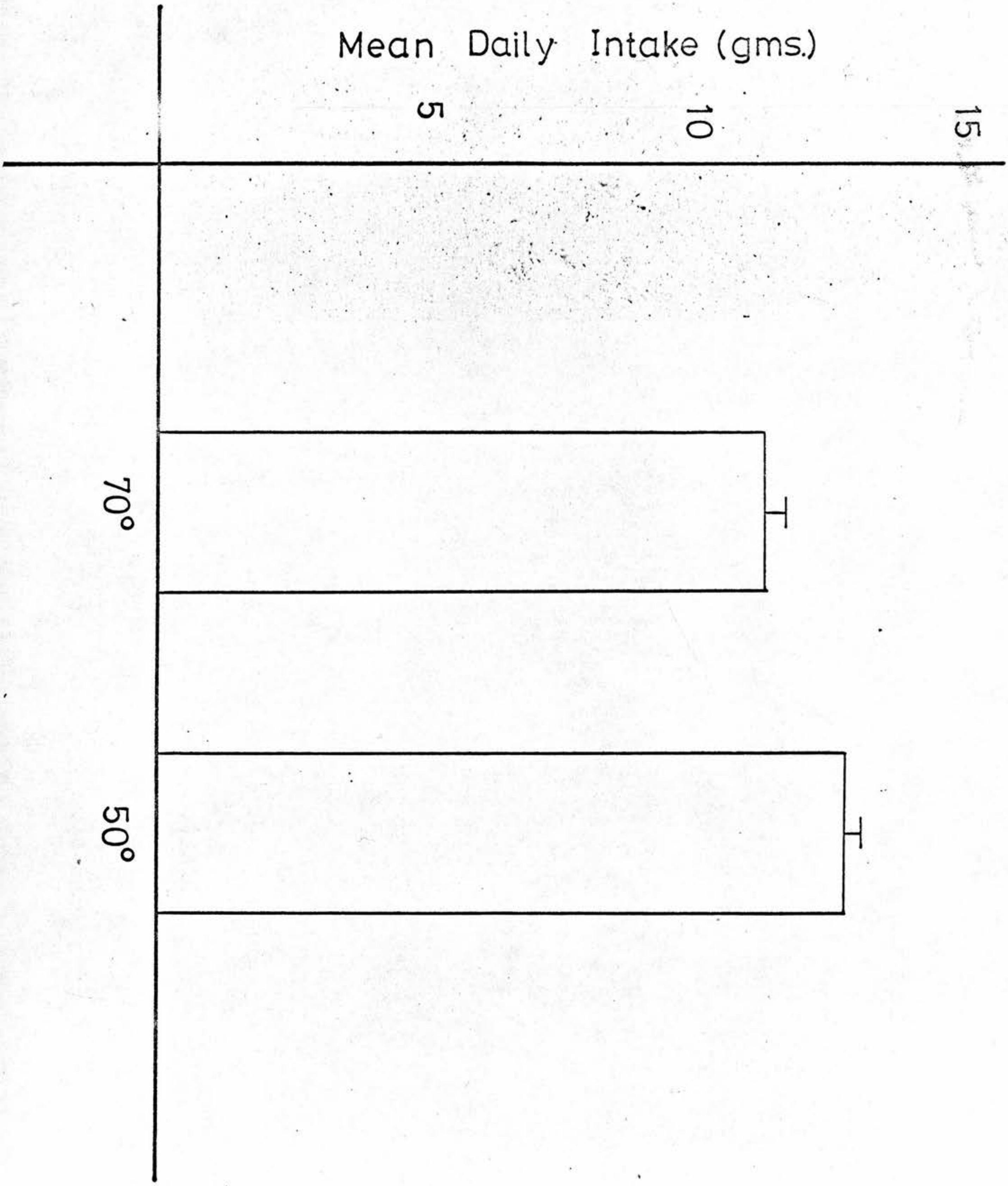
This change in food intake with ambient temperature must be brought

FIGURE 8.1

Mean daily food intake of birds feeding at a high (70°F) and a low (50°F) ambient temperature.

Significance of comparison tested with "t" test for correlated samples.

"t" = 4.6064; $p < 0.01$, two tailed.


Mean Daily Intake (gms.)
5
10
15
70°
50°

about by changes in the frequency of meal taking or the size of the meals eaten. In order to investigate this, records of feeding behaviour were collected from a group of birds housed at low and high ambient temperatures.

8.3(a) Method

12 adult female doves were housed in individual cages (40x35x45 cm) with continuous availability of water and grit and also of food (single grain wheat) in the photocell feeding monitor devices. The birds were maintained on a 12 hour light cycle (9am to 9pm) rather than 9 hours as in most other cases. This was done so that the data collected could be compared with earlier data to look for specific effects of day length. This will be discussed in chapter 9.

Seven days of feeding behaviour data were collected for each animal at an ambient temperature of 70°F and then the temperature was reduced to 50°F and a further seven days of behaviour was recorded. Birds which were used for this experiment were kept in another cubicle at normal ambient temperature while the low temperature data were collected for the others, in groups of 4 birds at a time. This was done so that some of the animals did not have more experience of the low temperature than others.

8.3(b) Results

The data were again first analysed using the above described logarithmic survivorship technique in order to derive appropriate criteria of inter-meal interval lengths. Criteria were established from the plots by another researcher, who was given no information as to the experimental groups. Unlike the trigeminal section case, there did not seem to be any systematic effect of temperature on the shape of the curves (Figure 8.2). All that was observed was that the appropriate criteria did seem to be fairly reliable within any one animal across the two conditions (Pearson Product Moment correlation coefficient of 0.67; $p < 0.02$). The derived criteria were not always equal however, so the procedure of using a blanket criterion of 250 seconds was again followed for some of the analyses.

As would be expected, the time spent feeding by the birds was greater in the low temperature condition than the high temperature condition. This is true if a feeding time (time spent by the animal with its head in the food box) or a "Foraging" time (total time spent in approach to food) measure was used (Figure 8.3). In neither case was the difference significant. This again clearly indicates the inadequacy of a method of monitoring feeding patterns which does not take account of actual amount eaten, but only time spent feeding. It must be assumed then, that part of the response of the birds to reduction in ambient temperature is an increase in the rate of food intake. It should be noted that what effect there was on time spent feeding is largely attributable to a few animals showing very marked increases in feeding time at low temperatures. It is possible that this indicates different modes of responding to low temperature in different animals.

A measure of the mean number of bouts per meal (Figure 8.4(a)) however did prove to be a significant indicator of increased meal size.

FIGURE 8.2

Mean criterion inter-feeding interval (IFI) for definition of meal size in animals feeding at an ambient temperature of 70°F and an ambient temperature of 50°F (Table 10(b); Appendix II).

Significance of comparison tested with "t" test for correlated samples.

"t" = 0.4410; N.S.

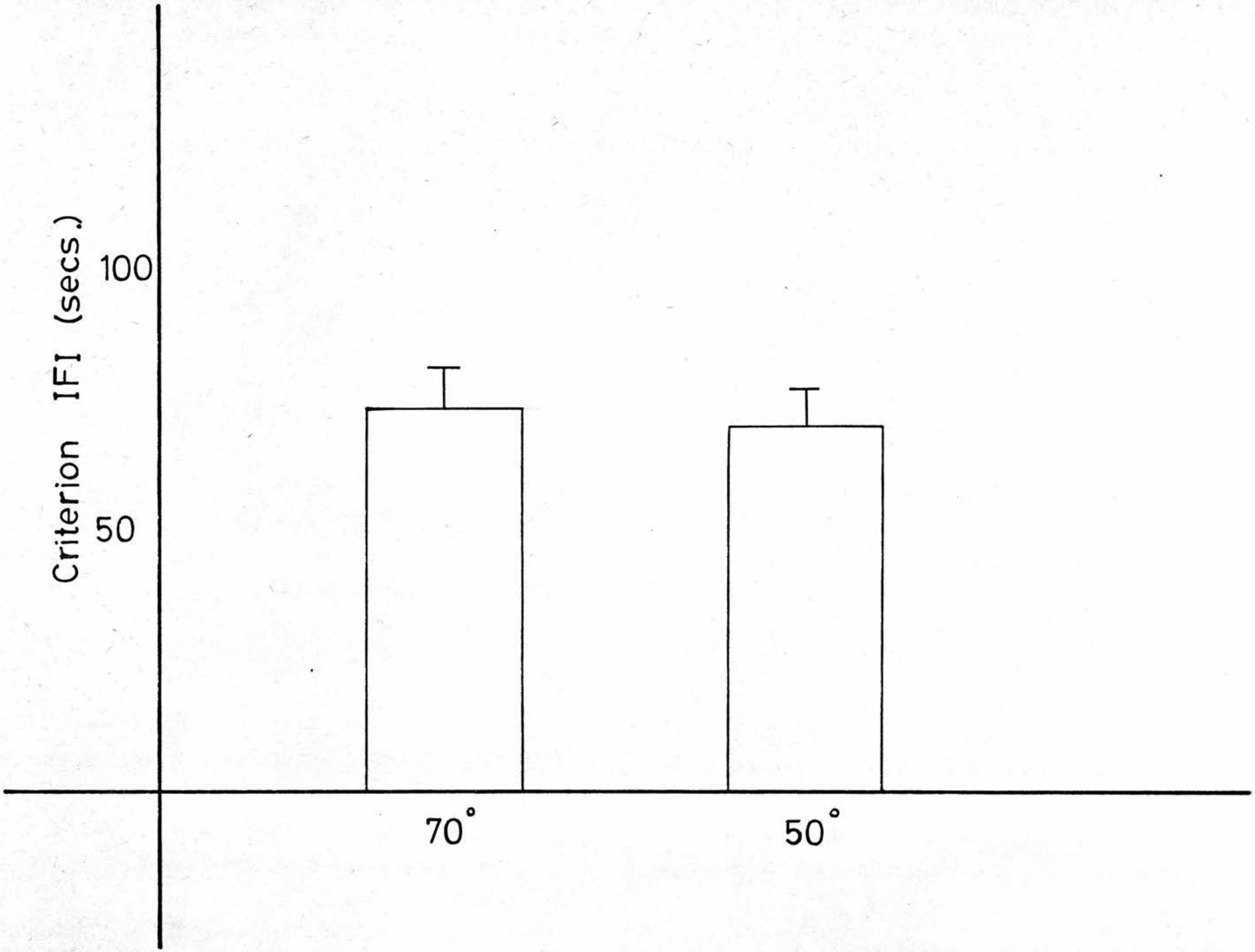

Criterion IFI (secs.)
100
50
70°
50°

FIGURE 8.3

Mean time spent feeding in each day by birds feeding at an ambient temperature of 70°F and an ambient temperature of 50°F. The "Feeding" means indicate the time which the birds actually spent with their heads in the food box. "Foraging" means are computed to include the inter-bout intervals within meals and thus indicate the daily total time spent by the birds in approach to food (Table 10(b); Appendix II). Bars indicate one standard error.

Significance of comparisons tested using a Wilcoxon Matched Pairs test.

	"T"	Significance ($p <$)
Foraging	24.0	N.S.
Feeding	28.0	N.S.

(Data analysed using a "blanket" criterion of 250 seconds for meal size definition.)

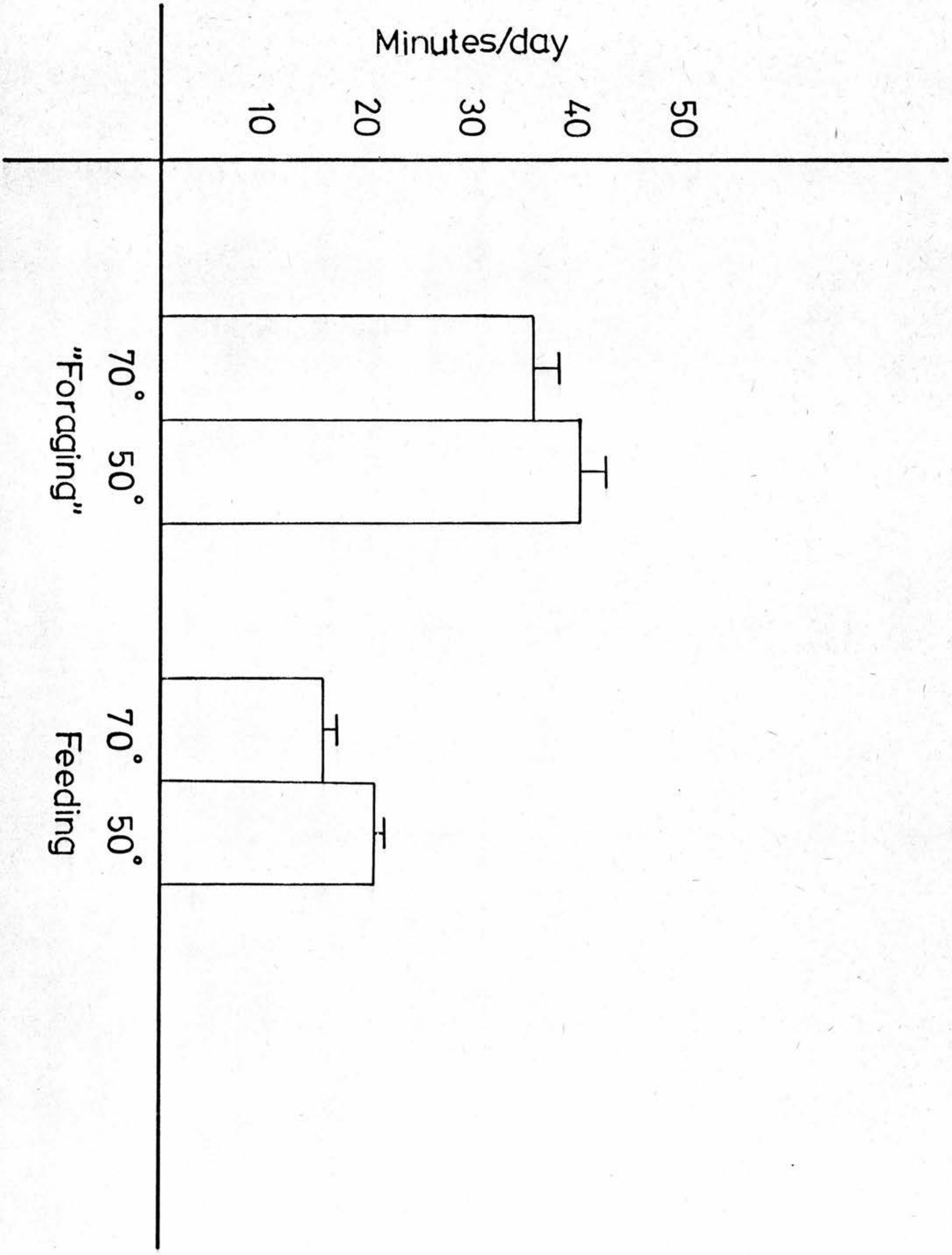

Minutes/day
10
20
30
40
50
70°
50°
"Foraging"
70°
50°
Feeding

FIGURE 8.4(a)

Mean number of feeding bouts in each meal in birds feeding at an ambient temperature of $70^{\circ}F$ and at an ambient temperature of $50^{\circ}F$ (Table 10(b); Appendix II). Bars indicate one standard error.

Significance of comparison tested with a Wilcoxon Matched Pairs test.

"T" = 4.5; $p < 0.01$, two tailed.

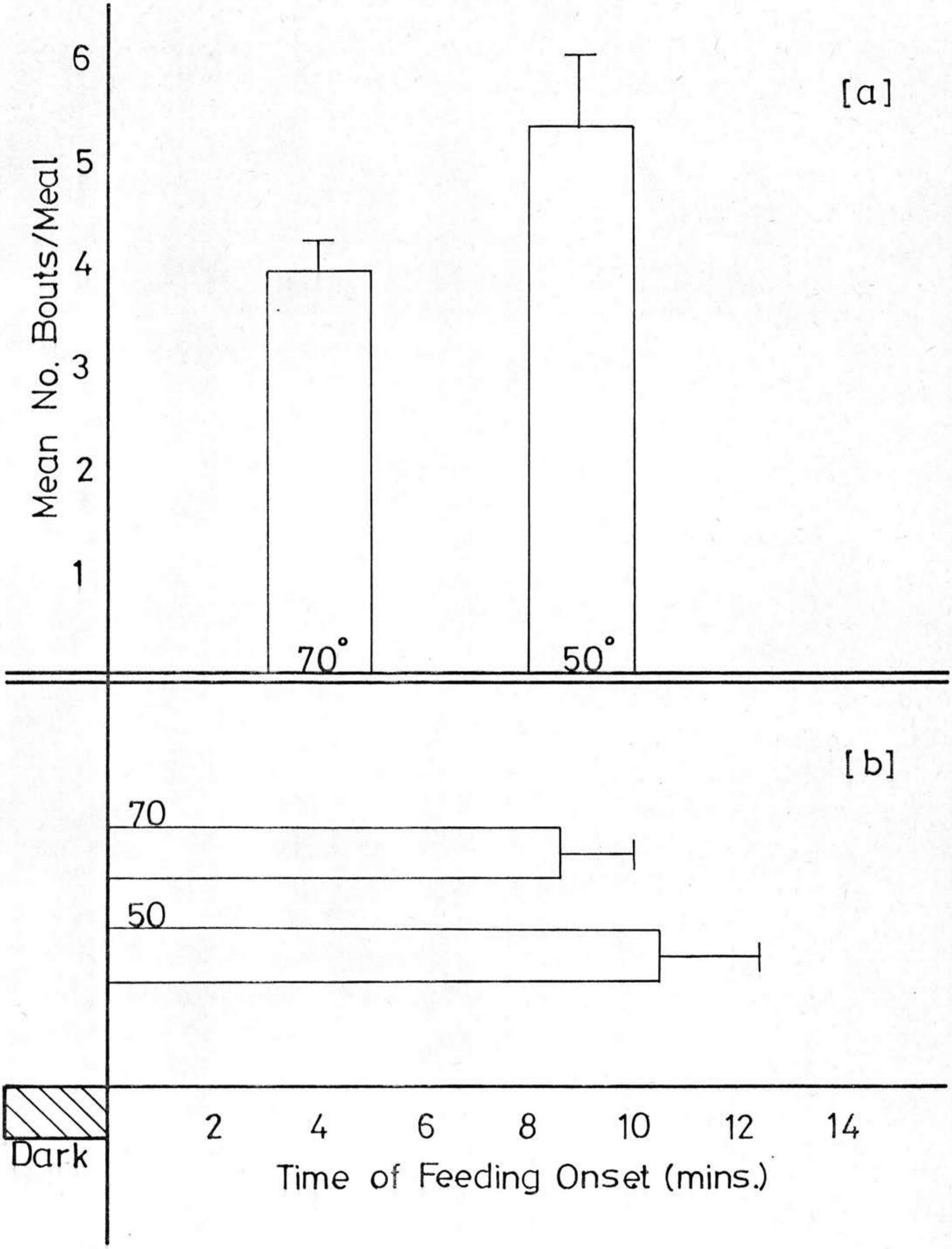
(Data analysed using a "blanket" criterion of 250 seconds for meal size definition.)

FIGURE 8.4(b)

Mean time of onset of feeding in minutes after "dawn" in birds feeding at an ambient temperature of $70^{\circ}F$ and at an ambient temperature of $50^{\circ}F$ (Table 10(b); Appendix II). Bars indicate one standard error.

Significance of comparison tested with "t" test for correlated samples.

"t" = 2.2095; $p < 0.05$, two tailed.


[a]
Mean No. Bouts/Meal
1
2
3
4
5
6
70°
50°
[b]
70
50
Dark
2
4
6
8
10
12
14
Time of Feeding Onset (mins.)

A result which was certainly not expected was that there was a significant reduction in meal frequency with decreased temperature (Figure 8.5). Further, the animals do not seem to be starting the day hungrier as a result of the overnight cold stress as evidenced by the time of onset of feeding in the two conditions (Figure 8.4(b)). The effect that there is, is in the direction of slightly later onset in the cold condition.

8.4 Discussion

Le Magnen (1971) in a review of studies of the physiological control of food intake argues that the main means of control is response to increased metabolic demands is by increased meal frequency with meal size being held constant. With specific reference to the effect of temperature on feeding patterns, he quotes a personal communication with Kissileff which would seem to agree with the generalization. Davies (1977) however, in a systematic study of long- and short-term components of food intake regulation in rats showed that the response of his animals to cold stress was to increase meal size keeping meal frequency constant. This, along with other data, was generalized to argue that short-term, meal to meal control was brought about by variations in meal frequency (or inter-meal interval) whereas long term control was achieved by changes in the mean meal size.

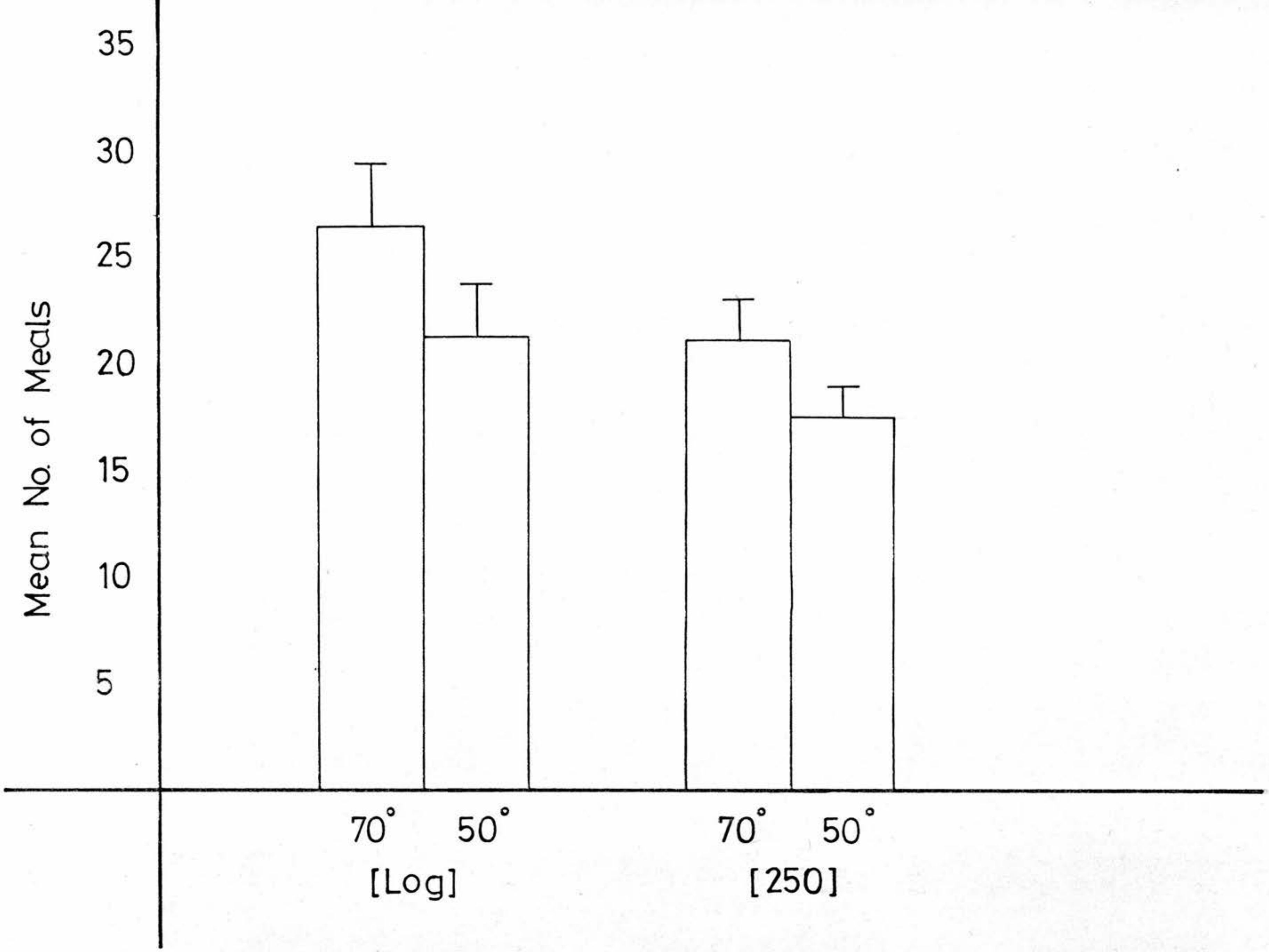
It should be assumed then, that the pattern of response to cold stress in the doves is similar to that reported by Davies with rats. The meal size is increased with a compensatory decrease in meal frequency to maintain an overall level of intake appropriate to needs.

FIGURE 8.5

Mean frequency of meal taking of birds at a high (70°F) and a low(50°F) ambient temperature (Table 10(b); Appendix II), with the continious records ordered on the basis of criteria derived from logarithmic survivorship plots(log) or on the basis of a "blanket" criterion of 250 seconds(250).

Significance of comparison tested with Wilcoxon "T" test:

	"T"	Significance (p <; two tailed)
Log. Criterion	0.0	0.01
"Blanket"Criterion	2.0	0.01


35
30
25
20
15
10
5
Mean No. of Meals
70°
50°
[Log]
70°
50°
[250]

Panksepp and Ritter (1975) found a similar effect of experimental diabetes in rats. Meal size was increased with some evidence of a compensatory decrease in meal frequency. It is possibly the case too however, that the reduction in meal frequency is in some sense an "active" response of the animal to decreased temperature. If one considers a bird in the natural situation which might have to expend a large amount of energy flying to its feeding grounds for each foraging bout, decrease in temperature might cause it to attempt to reduce energy expenditure by making fewer trips to the food and eating more at each trip.

8.5 Chapter Summary

Decrease in ambient temperature was shown to lead to an increase in food intake in the dove.

When the pattern of feeding behaviour was recorded at high and low ambient temperatures, it was seen that the increase in food intake was associated with a slight increase in time spent feeding (which was probably confounded by an increase in the rate of ingestion) and also a decrease in meal frequency.

This pattern is similar to that seen in rodents in response to cold or other metabolic demands. Perhaps the marked reduction in meal frequency could be seen as a strategy to conserve energy by going on fewer foraging expeditions.

CHAPTER 9

9.1 The Role of Anticipation in Feeding

As mentioned earlier, one of the most characteristic features of the feeding behaviour of most birds as compared with that of most laboratory rodents, is that they show no feeding (or any other) activity during the hours of darkness. In the present study, no occurrance of nocturnal feeding behaviour was recorded in intact doves under normal circumstances. Similarly, Van Hemel and Myer (1969) found that "feeding and drinking was almost never initiated during the hours of darkness " in their Japanese quail, and for this reason they felt justified in confining the analysis of their data to the light phase of the daily cycle. Zeigler, Green and Lehrer (1971) note that where feeding behaviour was recorded in their pigeons outwith the time at which the laboratory house lights were on, it was probably due to the fact that the room was not entirely sealed, and the animals were responding to the changes in external illumination.

Thus most birds are adapted to survive fairly long periods of daily fast. Feeding in anticipation of that fast rather than restoring the deficit incurred seems to be the normal mode of operation of the feeding control system. That is, the diurnal distribution of feeding activity seems to be characterised by a small peak in feeding at the start of the day, but a much larger one in the middle of the afternoon. This is true of the Ring dove (Figure 3.12), the laboratory pigeon (Zeigler, Green and Lehrer, 1971), the domestic fowl (Savory, 1976(a)) and also of free feeding animals in the wild (Murton et al., 1963; Irving et al., 1967; Savory, 1974; Schmid, 1965). Some cases have been reported however in which the birds were found to show the greatest peaking of food intake at the start of the day (Duncan et al., 1970; Wood-Gush and Horne, 1970; Hughes, 1972). It has been found in the present study (chapter 10; Figure 10.2) that the diurnal pattern was much less marked when recorded with an operant technique, with a tendency towards morning peaking. Although these birds were housed on a reversed light cycle leading to potentially maximal disturbance of the daily pattern in the first instance, they had fully 6 months to settle to this regime, but showed no signs of producing the more characteristic afternoon peak shown by the free feeding birds. It could be therefore, that there is something particular about the different recording situations used (as discussed in chapter 3) and about the operant situation in particular which leads to a modification of the otherwise normal pattern.

9.2 The Diurnal Distribution of Feeding in Rodents

Although the rat or mouse does engage in some feeding activity at all times of the day, most of its intake is during the hours of dark (Le Magnen, 1971). Nocturnal feeding can be seen as an attempt to reduce the risk of predation by staying concealed for the most part during the day. Although intuitively reasonable, one does have to be careful abaut such interpretations. The hamster for example shows no clear difference in the amount of food eaten during the dark and during the light (Zucker and Stephen, 1973), but it does appear that most of the food consumed during the day comes from the hoard and does not involve trips away from the nest (Toates, 1978). On its own, this might suggest that the hamster's behaviour was in keeping with the predation risk idea, but as Toates (1978) also points out, the animals are making regular daylight trips to a water source so net removal of food from the hoard cannot be explained by a disinclination to leave the nest during the day.

Whatever the underlying reason for the confinement of the bulk of feeding activity to the night time, this diurnal pattern in intake has associated with it a diurnal variation in lipid metabolism (Le Magnen and Devos, 1970), whereby there is a net lipogenesis during periods of high food intake with net lipolysis during the daylight time of lower feeding activity. There is then, a building up of energy reserves to be used to carry the animal over the period of low feeding activity. The animal always has stores of food to cushion it against any short term interruption of supply and to ensure that normal body functioning can go on during such interruptions. The interaction of feeding and food storage can perhaps be illustrated by the effects of brain stimulation on liver metabolism (see Shimazu et al., 1976 for review). Stimulation of the lateral hypothalamus in rabbits and rats, which might be expected to start feeding behaviour, can produce Glycogenesis and inhibit gluconeogenesis in the liver. Ventro-medial hypothalamic stimulation, which would be expected to inhibit or switch off feeding, is associated with Glycogenolysis and gluconeogenesis. In short, activity in brain regions associated with the starting of feeding is also associated with energy storage. Activity in the region which is traditionally supposed to mediate satiety leads to release of energy from the liver store. Feeding is in advance of the immediate need for the energy or nutrient being ingested.

9.3 Diurnal Distribution of Feeding in Birds

Although metabolic cycles of energy storage are present in birds, an additional mechanical possibility is available. Many birds have a crop which is sufficiently developed to act as a storage organ. They are thus able to fill the crop before going to roost and the material stored can be passed through the digestive system during the night. Murton (1965) points out that during the winter months when food availability is low and only very poor food is available, the Wood pigeon can increase its effective day length by 10-14% by eating during the day at a rate in advance of that which can be dealt with by the digestive system. The excess is then stored in the crop to pass through the rest of the digestive tract while the bird roosts. Indeed this mechanism has enabled the Wood pigeon to take advantage of the large winter food supply created by man in the form of clover leys. Although abundant, this material is very low in usable energy and must be ingested in great bulk; greater bulk than could be passed through the digestive tract on the short winter days. Short days obviously imply long nights, so the afternoon peak in feeding has been observed to be larger in free feeding birds during the winter than the summer (Irving et al., 1967; Savory, 1974) so that a larger preparatory load is accumulated.

9.4 Feeding and Environmental Change

Kendeigh et al. (1969) studied the effects of varying the day time and night time ambient temperatures on the body weight of the House sparrow (Passer domesticus). It was found that when the birds had to tolerate lower night time temperatures they adjusted to the situation by increasing the weight level which was recorded at the end of the day before going to roost, rather than tolerating a greater weight loss over the night to be made up in the morning. This is similar to the effect reported in chapter 8 whereby the doves showed no indication of starting the day hungrier at the low ambient temperature as evidenced by the time of feeding onset.

A similar study of the effect of temperature on food intake in rats was carried out by Kraly and Blass (1976). Their procedure was to subject their animals to periods of food deprivation in either a high (22°C) or a low (5°C) ambient temperature and then to measure the subsequent food intake during a 6 hour period again in either a high or a low temperature. The argument was that if increases in food intake in response to cold stress were a result of increased energy depletion and subsequent restoration, then the intake would depend on the ambient temperature at the time of deprivation. They found however, that increased food intake was a response to the immediate ambient temperature and not a result of the prevailing temperature during the time of food deprivation. The conclusion then is that environmental cold per se enhances the motivation to feed rather than doing so indirectly by an effect on energy depletion.

9.4 Longer Term Anticipation in Food Related Behaviour

Anticipation of future needs also takes place on a longer term basis. Animals which hibernate (see Mrosovsky, (1971) for review) will increase their body weight and prepare a hoard of food in advance of going to sleep for the winter. Hibernation is not simply an inevitable result of lowered ambient temperature, but will be inhibited if the animal is not allowed to gather a food hoard. Similarly migrating birds will increase body weight by fat deposition prior to the migratory flight (King and Farner, 1965; Kuenzel and Helms, 1967).

The anticipation of future deficit by the preparation of a hoard of food can be seen in a number of animals (for example, the rat (Wolfe, 1939; Lowney, 1958), the golden hamster (Waddell, 1951; Beron and Grodsky, 1958)). Evidence also exists, although it is often only anecdoted, of surplus killing of prey by predatory birds and the preparation of hoards of food material which are then visited at a later date (Smith, 1972, 1973; Nunn et al., 1976; Stendell and Waian, 1968).

9.5 Nature of the Anticipatory Peak of Feeding in the Ring Dove

The diurnal distribution of feeding in the Ring dove (Figure 3.12) is clearly one in which the onset of the dark phase of the cycle, and the associated enforced fast, is behaviourally anticipated by the birds so that crop filling takes place which, at least in part, provides a reserve of food to carry the birds over the night. The changes in meal size (Figure 3.15) which occur across the day would seem to be all that is needed to account for such a diurnal pattern. That is, the peak in feeding activity which occurs in the afternoon is a product of a combination of gradually increasing meal size and decreasing inter-meal interval.

One has the feeling however, looking at the original data that these means serve to obscure what is "really" going on. As illustrated earlier (Figure 3.13), if the hourly means of feeding activity are computed after the data has been synchronized in terms of occurrence of the peak of activity for each bird, there is a much sharper transition evident between the level of feeding behaviour at this point and that level over the rest of the day. That is, the original impression of gradual change is a product of the combination of data across birds with slightly different cycles. Indeed slight variations in the day to day cycles of individual birds would add to this illusion.

The impression which is in fact given by the examination of the daily feeding records is that the peak of feeding activity is a product of one very large meal, or perhaps two large meals separated by a short interval which, although longer than the derived inter-meal interval criterion, would perhaps be better considered to be a break within a meal. That is, the peak in feeding activity should not be seen as a gradual filling of the crop across the afternoon, but as a quantal shift in the animal's feeding tendency from a mode in which it is content to supply the needs of the lower regions of the gastro-intestinal tract, to one in which the crop also demands to be filled. Although that might describe the actual motivational tendency of the animal, this sort of behaviour would only be possible in a situation of very high food availability as experienced by animals in the laboratory. Such high availability is not unknown in free living populations however. For example, Murton (1965) suggests that the daily food requirement of the Wood pigeon (about 50 grams weight of grains) could be obtained in one to two hours of total foraging time during the abundance of food during springtime grain sowings. It is proposed here, that this quantal shift in behavioural feeding tendency is an evolutionary result of the balance between the pressure not to carry excess weight which would increase the risk of predation by making flight more difficult, and the need to prepare as fully as possible for the overnight fast so that the next day was not begun with an energy deficit.

This argument requires that the peak in feeding activity which is found before nightfall would be contributed to, to a greater extent, by increases in meal size than by increases in meal frequency. This cannot be seen to be the case if the data on mean meal size and mean inter-meal interval (presented in chapter 3) are considered. Neither is it the case if the data are synchronized by the hour at which the peak of feeding activity is shown (Figures 9.1 and 9.2). This procedure does show the transitions to be more rapid however, but there is still clear indication of a peak in meal frequency at the point of maximum feeding activity. It is also interesting to note that the main dip in the inter-meal interval histogram (Figure 9.2) begins in the hour before the peak feeding hour. That is, if there are characteristically short intervals at the time of the afternoon peak feeding they are coming before as well as after the peak meal. This can be seen as indicating that the preceding normal sized meal no longer has the same satiating effect, leading to the need by the animal to restart feeding again soon after. The animal would feed to satiation by one criterion (i.e. the filling of the lower gastro-intestinal tract to a certain degree) and a meal would be terminated. Before the spontaneous initiation of the next meal however, the criterion changes (filling of

FIGURE 9.1

Grand means of mean meal size in each hour of the day from 14 birds (Table 3(c); Appendix II), synchronized so that the mean meal sizes in the peak feeding hour for each bird contribute to the same grand mean (indicated [p]). Figure represents data from 14 birds, and numbers associated with some of the bars indicate the number of individual items contributing to these particular means.

Results of hour by hour comparisons using Wilcoxon Matched Pairs test given in Table 3(h) (Appendix II).

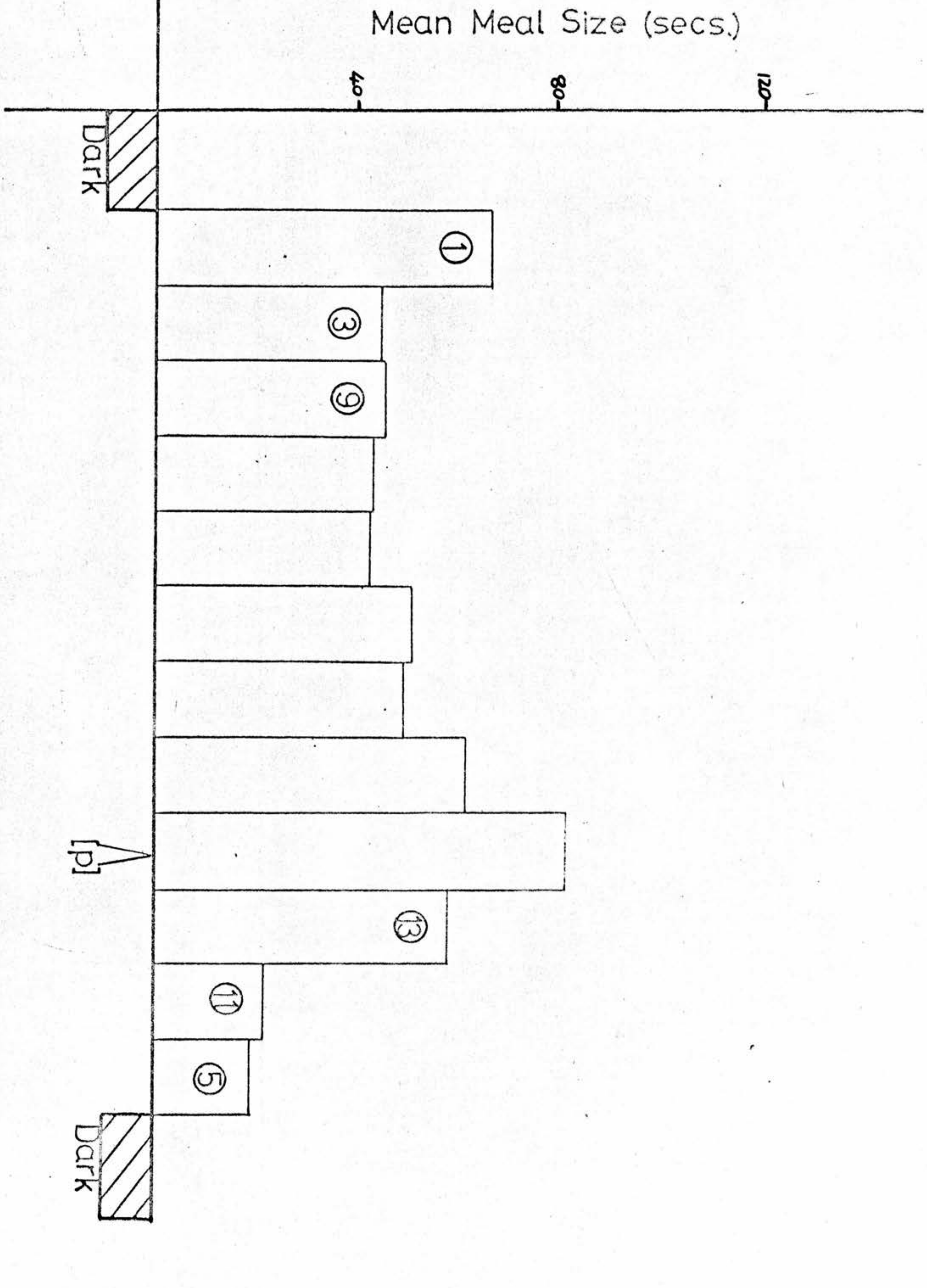
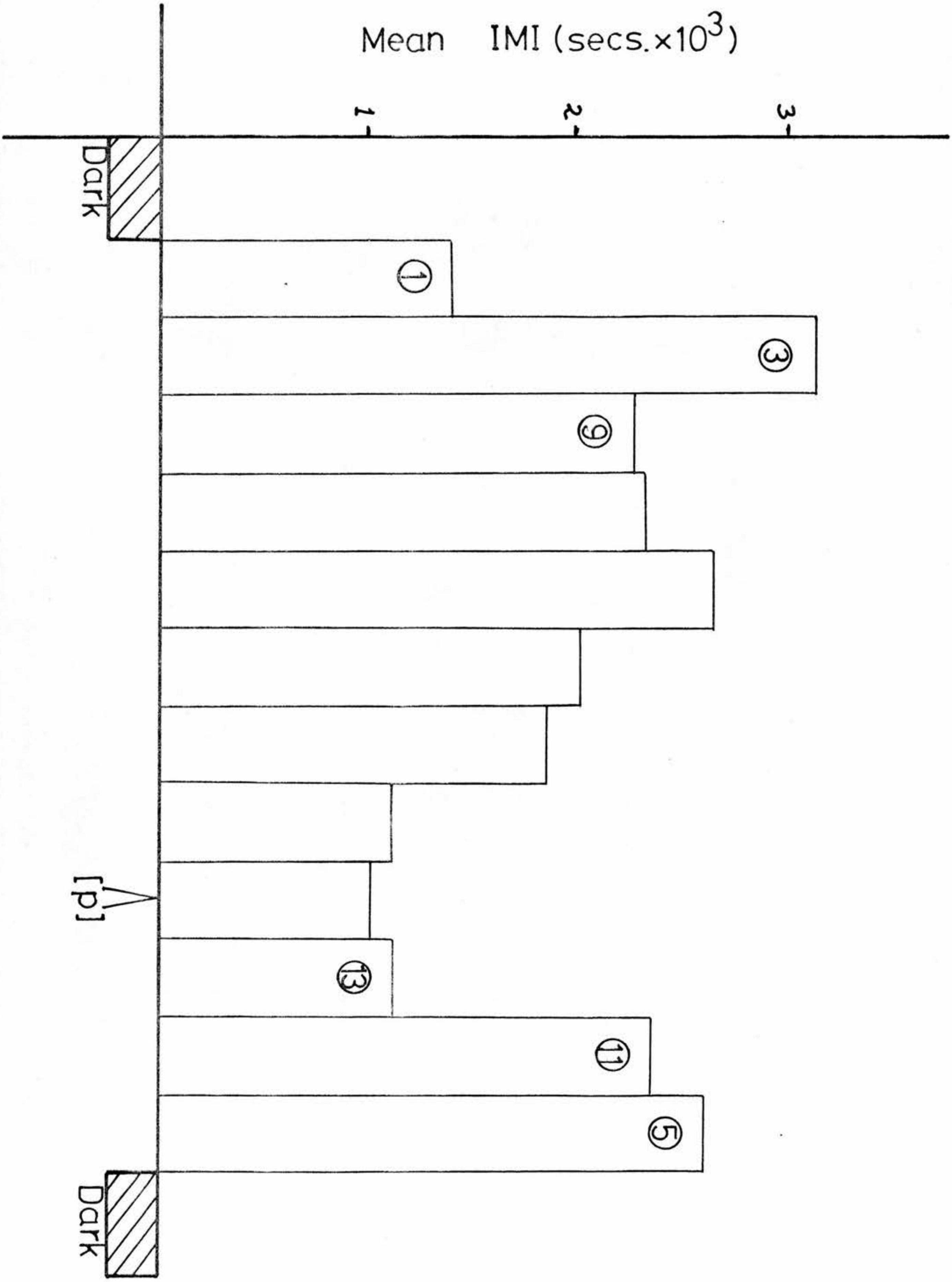

Mean Meal Size (secs.)
40
80
120
Dark
①
③
⑨
[p]
⑬
⑪
⑤
Dark

FIGURE 9.2

Grand means of mean inter-meal interval (IMI) in each hour of the day from 14 birds (Table 3(e); Appendix II), synchronized so that the mean IMIs in the peak feeding hour for each bird contribute to the same grand mean (indicated ⌊p⌋). Figure represents data from 14 birds, and numbers associated with some of the bars indicate the number of individual items contributing to these particular means.

Results of hour by hour comparisons using Wilcoxon Matched Pairs test given in Table 3(i) (Appendix II).


Mean IMI (secs.×10^3)
1
2
3
Dark
①
③
⑨
[p]
⑬
⑪
⑤
Dark

the crop also) and so feeding is stimulated to occur almost immediately.

As mentioned above, the presence of short intervals at the time of the peak in feeding activity might be due to particularly short breaks which would be better seen as within meal, rather than between meal pauses. It would be reasonable to suggest for example, that the use of one set inter-meal interval criterion might be only a first approximation to an analysis of meals and inter-meal intervals. Any one criterion might only indicate a mean, but might not be appropriate for all meals. That is, it might be the case that the appropriate interval criterion was a function of the size of the ongoing meal, birds breaking off for longer within meal pauses at points when the amount or rate of feeding was higher. This might be one possible interpretation of the longer criterion found with birds feeding on a single grain diet. In these cases the rate of ingestion is obviously higher as the same amount of food is being ingested in about half of the time. In this case the birds might be expected to pause longer to "let the food go down" within an ongoing meal. More data would be required on individual animals however before logarithmic survivorship plots could be generated for different times of the day.

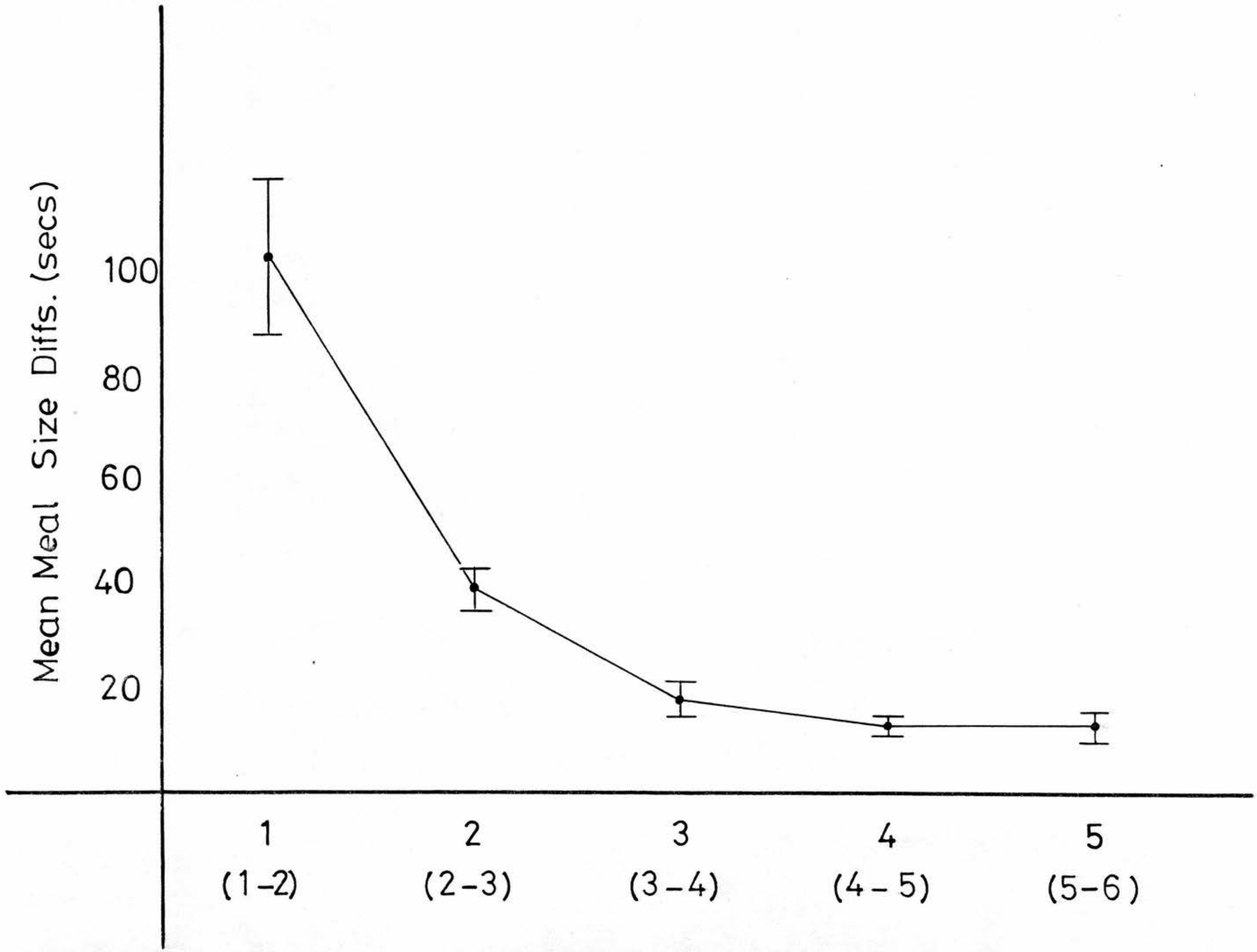
9.5(a) The Size of the Largest Meal of the Day

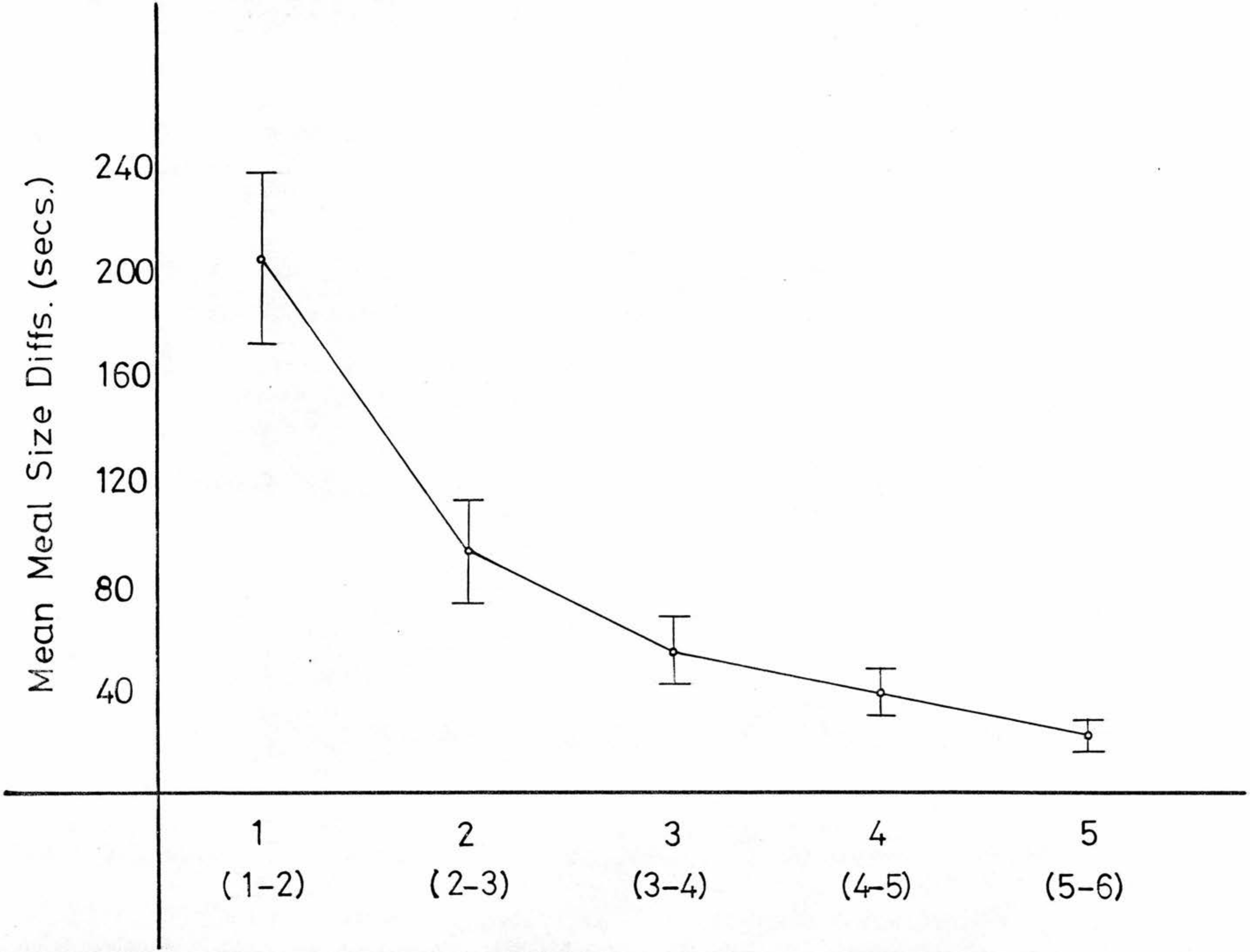
The hypothesis that crop filling takes place in one very large meal would also suggest that the longest meal of the day would be very much longer than the other meals. In order to investigate this, an analysis was carried out on some of the feeding records in which the meals for each day were arranged in decreasing order of size and the mean difference in length between the first and second, second and third and so on, were computed. This analysis is shown in Figure 9.3 for birds when fed on a single grain diet (chapter 7) and in Figure 9.4 for the same animals fed on the mixed grain diet. Comparison between the two shows that the picture appears to be clearer in the case of the single grain diet. This is probably due to the mixed grain diet inducing a large amount of searching and sorting behaviour in the food box by the birds, so that feeding time on the mixed grain diet is, on average, double that of time on the single grain diet. In addition, the ratio of time spent feeding to grains consumed may vary across the day. For example, Murton et al (1963) showed that the rate of feeding behaviour in Wood pigeons as measured in peaks per distance moved, increased during the afternoon peak, which suggested a decrease in selectivity. Savory (1974) showed that the distribution of food items in the digestive tracts of grouse shot in the afternoon was closer to the actual distribution of food items in the environment, than it was in birds shot in the morning, implying that birds were being more selective in their feeding at the start of the day than at the end. If a similar tendency existed with the doves feeding on the mixed grain diet, it would mean that the ratio of time spent feeding to food consumed would be smaller at the peak feeding times thus serving to de-emphasise the peak when a time measure was being used.

It can be seen then, that the difference in size between the largest meal and the second largest is very much greater than the difference between the second and the third largest. The difference between the second and third and third and fourth is small, and by the third meal the meal size differences down the series are approximately

FIGURES 9.3 and 9.4 (Two pages)

Grand means of mean differences between largest and second largest meal, second largest and third largest meal, etc., from 12 birds feeding on a single grain diet (Figure 9.3) and a mixed grain diet (Figure 9.4) (Table 11; Appendix II). Bars indicate two standard errors.


Mean Meal Size Diffs. (secs)
100
80
60
40
20
1
(1-2)
2
(2-3)
3
(3-4)
4
(4-5)
5
(5-6)


Mean Meal Size Diffs. (secs.)
240
200
160
120
80
40
1
(1-2)
2
(2-3)
3
(3-4)
4
(4-5)
5
(5-6)

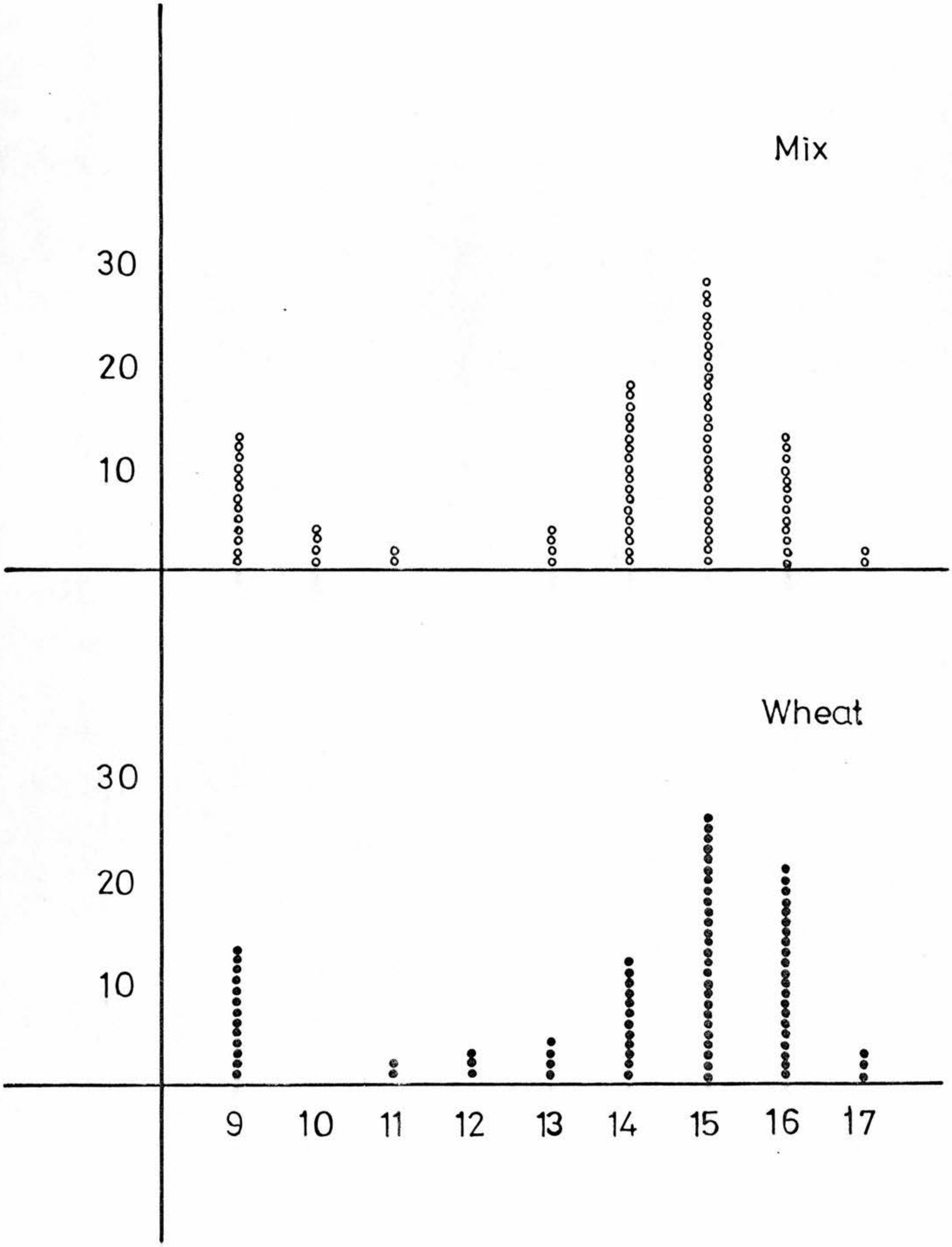
equal. This latter point is particularly so for the wheat grain diet (Figure 9.3) but less clear in the case of the mixed grain diet. This analysis illustrates that there is a population of meals which is very much longer than the rest. Figure 9.5 shows the hours of the day in which each of these largest meals falls. It can be seen that, for the most part, these long meals coincide with the afternoon peak feeding time and the hypothesised point of rapid crop filling. Those that appear at the start of the day are actually due to a small number of animals which showed a tendency towards morning peaking of food intake, rather than being randomly distributed throughout all of the birds observed.

9.5(b) The Filling of the Crop

The preceding analysis and discussion does suggest that, for the most part, the peak of feeding is relatively abrupt rather than gradual, and that this peak is contributed to by one very large meal. To suggest that this discontinuity is brought about by a transition from a mode of feeding controlled by the filling of the lower gastro-intestinal tract to one involving the filling of the crop also, it would be necessary to show that crop contents also vary in a sharply non-linear way. It is true of the free feeding Wood pigeon (Murton, 1965) and the Red grouse (Savory, 1974) that animals shot in the morning are carrying little or no food in the crop, but the crop contents begin to increase as the afternoon progresses. That is, the rate of feeding is related to immediate needs for the most part of the day, but is increased towards the end of the day to establish a stock for the

FIGURE 9.5

Hour of occurrance of day's longest meal in 12 birds feeding on a mixed grain diet and a single grain wheat diet.


Mix
30
20
10
Wheat
30
20
10
9
10
11
12
13
14
15
16
17

night. Schmid (1965) however, found two peaks in crop weight in the Mourning dove in North Dakota, U.S.A. associated with the morning and afternoon peaks in feeding activity. There appeared to be a regular cycle of crop filling and passage of food through the digestive tract and this cycle was repeated twice each day centred around two trips to a water hole. Digestion did not start until food was wetted. It seems likely that this pattern would only be associated with low availability of water and particularly dary food.

9.5(c) Observations of Crop Filling in the Ring Dove

To obtain some idea of the way in which crop filling takes place in Ring doves, a group of birds were observed hourly during the light phase of the daily cycle and some estimate of crop contents made.

9.5(d) Method

Six adult female ring doves were housed in individual cages (40x 35x45 cm) with continuous availability of food, water and grit in a room with a nine hour light cycle (8am to 5pm). Immediately before the onset of the light phase of the cycle and at every hour of the day until light offset the birds were removed from their cages and their crops palpated to detect any food present. This procedure was carried out for two weeks (Monday to Friday) to get the animals used to the interference and then for a further two weeks over which time note was taken of the observations.

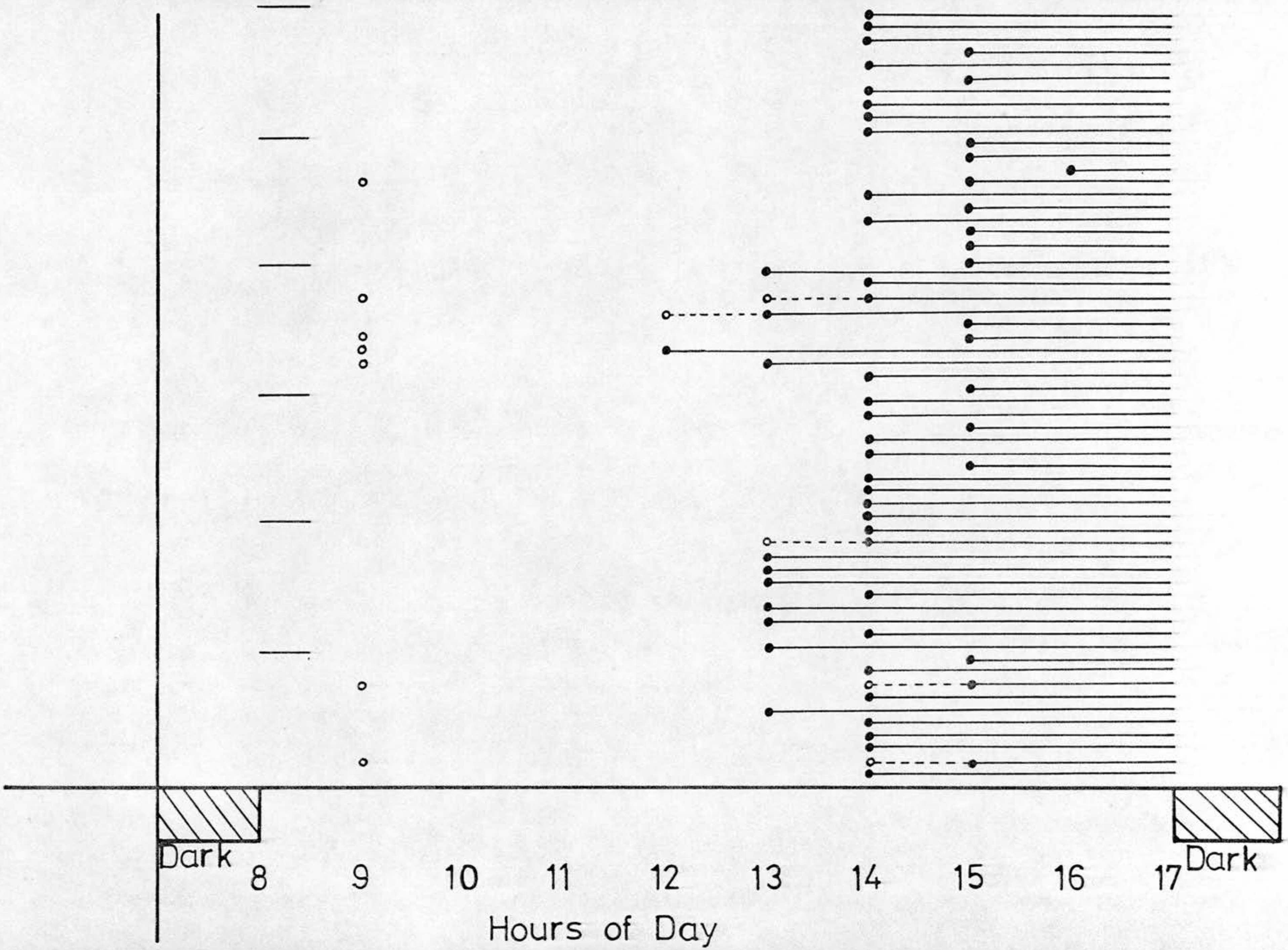
7.5(e) Results

It would obviously be difficult to obtain any very accurate quantitative information on crop contents from such a procedure, but the present hypothesis would suggest, and indeed the observations confirmed, that in most cases the crop could be described as being either completely empty or very full. Figure 9.6 summarizes the observations for each of the six birds for the 10 days on which data were collected. Filled circles indicate the time at which the birds were found to have (as near as could be determined) "full" crops. Open circles indicate that a small amount of food was present in the crop. In most cases when food was detected in the crop (that is, all except those cases indicated by open circles) no discernable change (increase or decrease) was observed in any hour until the end of the day. As predicted then, the crop did seem to be filled in a once and for all manner, any feeding which occurred after this time serving to top up the crop contents rather than increase it. On a few occasions there was evidence of a small amount of material in the crop after the first hour of the day. This was very rare however, so it would be concluded that the peak in feeding occurring at the start of the day (present in most birds) is a result of feeding to fill up the lower gastro-intestinal tract which would have emptied over the night. In the few cases where food was found in the crop after the morning feeding period, this may have been due to a larger deficit being incurred during the nocturnal fast than can be restored by a meal which fills only the lower tract, and thus would be seen as being due to a failure of anticipatory feeding on the previous day.

As noted earlier, it was found in the analysis of diurnal

FIGURE 9.6

Summary of observation of crop contents across the day of 6 birds for 10 days for each bird. Open circles indicate some food detected in the crop and filled circles indicate points at which the crop was found to be full. Dashed lines indicate that the crop contents were detected to increase from one hour to the next, while continuous lines indicate no detectable change in crop contents.


Dark
8
9
10
11
12
13
14
15
16
17
Dark
Hours of Day

distribution of feeding that the significant peak in % time spent feeding in the first hour of the day seemed to be due to an increase in meal frequency rather than an increase in meal size, as compared with the afternoon peak which was more obviously a result of a change in meal size. It is suggested then, that these two patterns are a result of increased feeding at the start of the day being a response to mild deprivation, and feeding in the afternoon being motivated by the need to anticipate the fast to come.

The above observations indicate that the crop filling does not take place gradually over the day but is usually well nigh completed within one hour. Feeding occurring later in the day appears to be at a "baseline" level which serves to keep the crop "topped up" as food is passed into the gizzard and proventriculus. Although small amounts of food may lodge in the crop before passing down the alimentary canal after meals occurring during the rest of the day, this was not noted in this brief observation. It is suggested that the animal's normal meal size in the laboratory situation of continuous free availability is never sufficiently large for the crop to be needed save at the time of the afternoon peak.

9.6 Postponement of Feeding before Dusk

It was suggested above that the shape of the diurnal pattern of feeding was a compromise between ensuring an adequate reserve to carry the animal over the night, and the need to avoid holding this reserve in the crop for too long and thus increasing the risk of predation due to the added dead weight. If this were so it is surprising that the

crop is filled quite so early in the afternoon. However, it should be noted that the laboratory lighting regime does not give the animal very much information to enable it to predict when night is going to fall. The filling of the crop would be expected to occur at a sufficient time before the offset of the room lighting so as to prevent errors being made. It would also be predicted that if the birds were allowed to have some more information about the time of offset of the lights, they would tend to move the peak of feeding activity further towards the end of the day. This is exactly the effect reported by Savory (1976(a)) in a study of diurnal pattern of feeding behaviour in domestic fowl. He found that the daily distribution of feeding in his birds on a 12 hour light/dark cycle showed the same small morning and larger afternoon peaks in activity observed in this study with the doves. When simulated two hour "dawn" and "dusk" periods were added to the basic 12 hour cycle (that is, the overall day length was still 12 hours but the first two hours were of gradually increasing light levels and the last two gradually decreasing) the effect was to move the peak of feeding activity towards the end of the day and to abolish the dawn peak altogether. It should be noted too that these data indicate a smooth increase in food intake from the middle to the end of the day rather than an abrupt peak as the present argument would demand. As no information was presented on individual animals however, it is possible that this can also be attributed to the averaging of data for a number of animals with slightly different cycles.
Savory (1976(b)) showed an increased rate of weight gain and food intake on the lighting regime with the dawn and dusk periods included. It seems likely that the additional information provided allowed the

animals to more efficiently administer their food intake.

The period of changing illumination then, was able to act as a cue which signalled to the birds that dusk was approaching, and allowed them to postpone further the point in time at which crop filling took place. The reason for the presence of some variability in the behaviour of Savory's birds and the doves in the present study would be that there are other factors which contribute uncertainty to the choice of the appropriate time to fill the crop. One factor would be the presence of a flock feeding mode meaning that when the bulk of the flock went to roost any individual animal would have to follow suit, as remaining at the feeding site alone or in smaller numbers would increase the predation risk. Thus a need to feed in advance of the actual fall of darkness would be associated with a need to feed in advance of the "effective" end of the foraging day, as defined by the behaviour of the whole flock.

9.6(a) Information about Light Offset

An attempt was made to perform a crude repetition of what was believe to be the essence of Savory's (1976(a)) experiment. That is, it was suggested that the presence of information about the time of onset of the overnight fast period would allow the anticipatory food intake of the birds to occur later in the day.

9.6(b) Method

The cue to light offset was given by arranging for the timer controlling the room lights to switch the lights off for about 5 minutes (as short a period as could actually be manufactured by the setting of the mechanism) at one hour before the lights finally went off for the night. The dependant measure which was taken was the difference between the gross food intake for the first half of the day and the last half of the day. It was predicted that the intake pattern would switch towards more food being consumed in the last half of the day when the light offset cue was available.

Six female birds were maintained on a 12 hour light cycle with lights coming on at 4 am and going off at 4 pm. In the experimental condition the room lights were switched off for 5 minutes at 3 pm approximately. Body weights and food intake were recorded for the 6 animals at 10 am (their "noon") and 4 pm. The birds had been kept on this particular lighting schedule for at least 2 months while other observations were being made, so it is hoped that the diurnal pattern would have been quite stable on the altered light cycle.

Food (single grain wheat) was continuously available as was water and grit. Records were kept for 3 weeks (Monday to Friday) and the data for the final ten days were used in the analysis. The experimental condition (cue present) was then introduced and a further 3 weeks data recorded. Again the final ten days were used for the analysis thus allowing the animals 9 days to establish the connection between the cue and the end of the day.

9.6(c) Results

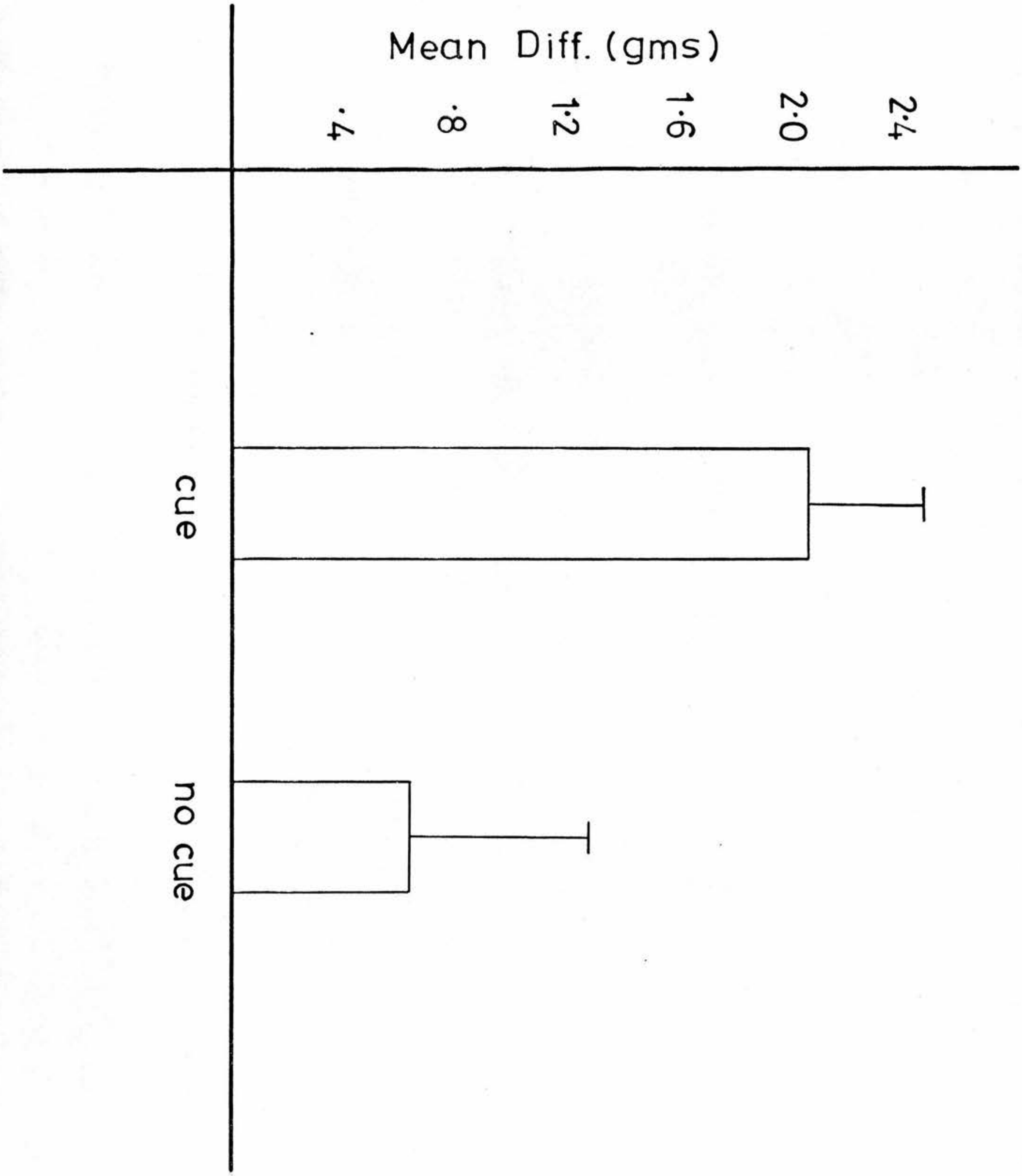
Figure 9.7 shows that when the cue was present the animals showed more of their daily food intake in the final 6 hours of the day. The

FIGURE 9.7

Mean difference between gross morning and afternoon food intake in a group of birds when they were, or were not, given a cue to signal impending light offset. Bars indicate one standard error. (Table 12; Appendix II).

Significance of comparison tested with a "t" test for correlated samples.

"t" = 2.8048; $p < 0.05$, two tailed.


Mean Diff. (gms)
·4
·8
1·2
1·6
2·0
2·4
cue
no cue

fact that this rather crude experiment produced an observable effect suggested that it might be possible to devise a more structured experiment to test whether this particular case of anticipatory feeding in advance of a nocturnal fast might not simply be an example of a more general mechanism to deal with periods of predictable food deprivation.

9.6(d) <u>Method</u>

12 adult female doves were maintained on continuous light for 4 weeks to allow the previously entrained diurnal pattern to decay. Whether of not the birds' feeding behaviour was randomly distributed across the full 24 hour period however, was not important. It was simply the case that no time during the day existed when they did not have access to food or could not eat.

Food intake between the hours of 9 am and 10 am and between 4 pm and 5 pm was measured for a further two weeks (Monday to Friday) to allow the birds to become accustomed to the intervention. Following this, on randomly allocated days, a period of fast was imposed on the birds by switching the room lights off between the hours of 10 am and 4 pm. The impending occurrence of the fast period was signalled to the birds by the lights being switched off (again for about 5 minutes) at 9 am. The number of days between each fast day was not less than 3 and not more than 6, and was randomly determined save that weekends (Saturday and Sunday) were not included.

9.6(a) <u>Results</u>

Figures 9.8 and 9.9 show the intake of food in the hours before and after the fast period in each successive experience of the fast. Figures 9.10 and 9.11 show the intake in the pre- and post-fast hours on the days immediately preceding the fast days to serve as a control for diurnal variation. The picture is very clear. The first few occasions of the 6 hour fast period lead to a restorative increase in feeding in the hour following the fast as compared with the control day. In addition, it can be seen that there is less feeding occurring in the hour preceding the fast on the days on which the cue and fast occur than at the same time on the control days. The depression of feeding is presumably explained by the upsetting effect of the brief period of dark which the animals have not been used to. As time passed however, the birds came to recognize that the brief light offset always predicts a prolonged fast, and respond by increasing their food intake in advance of that fast, so that the food intake in the post-fast hour can return to normal. Friedmann analyses of variance show that the increase of intake in the pre-fast hour, and the decrease in the post-fast hour with repeated experience of the relationship between the cue and the fast , are significant. There is no significant change over time in the control days however.

9.6(f) Discussion

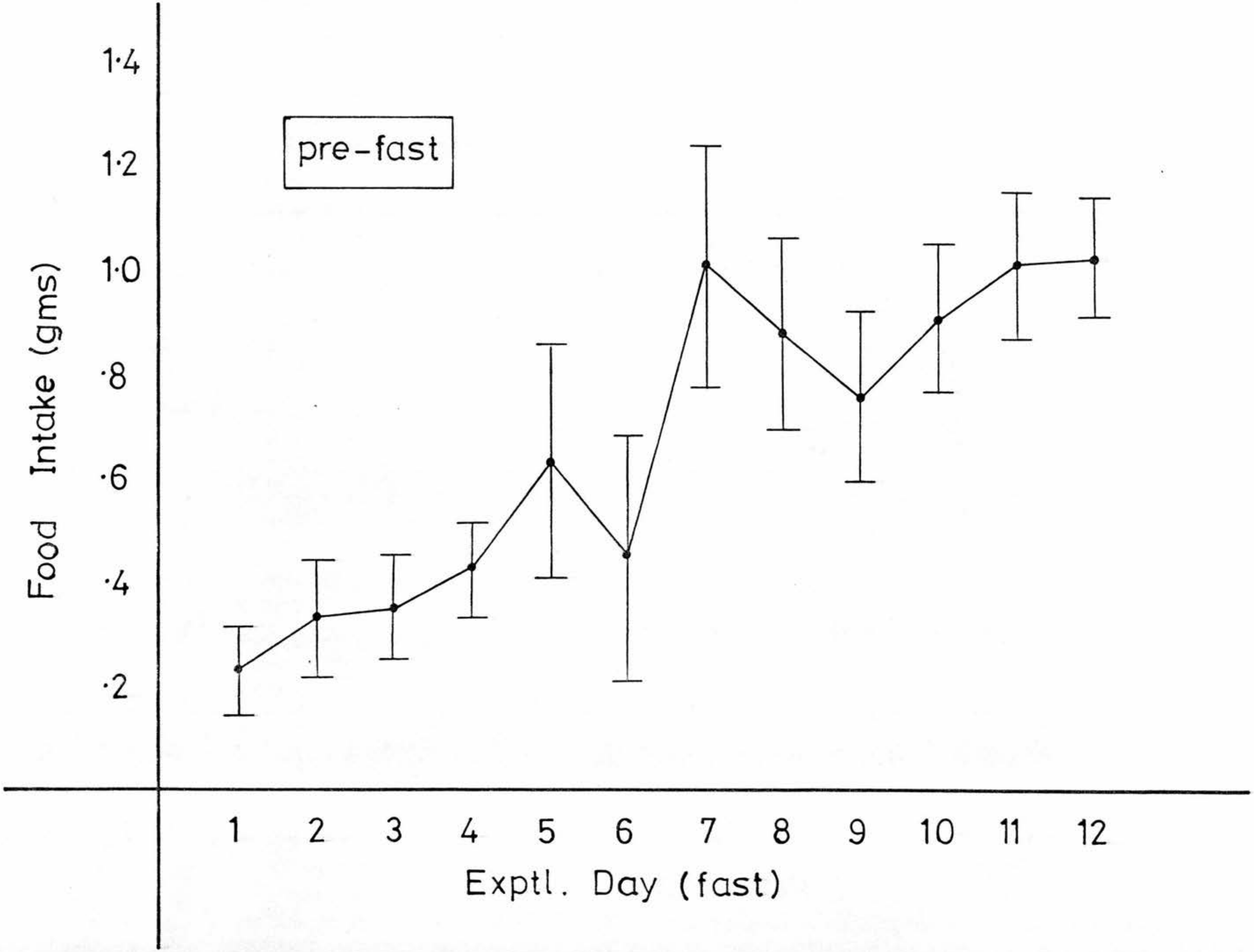
In short then, when the possibility of prediction exists, the birds prefer not to allow themselves to incur a deficit, but avoid doing so by increasing their food intake so as to anticipate the deficit. In the context of the preceding discussion one would easily

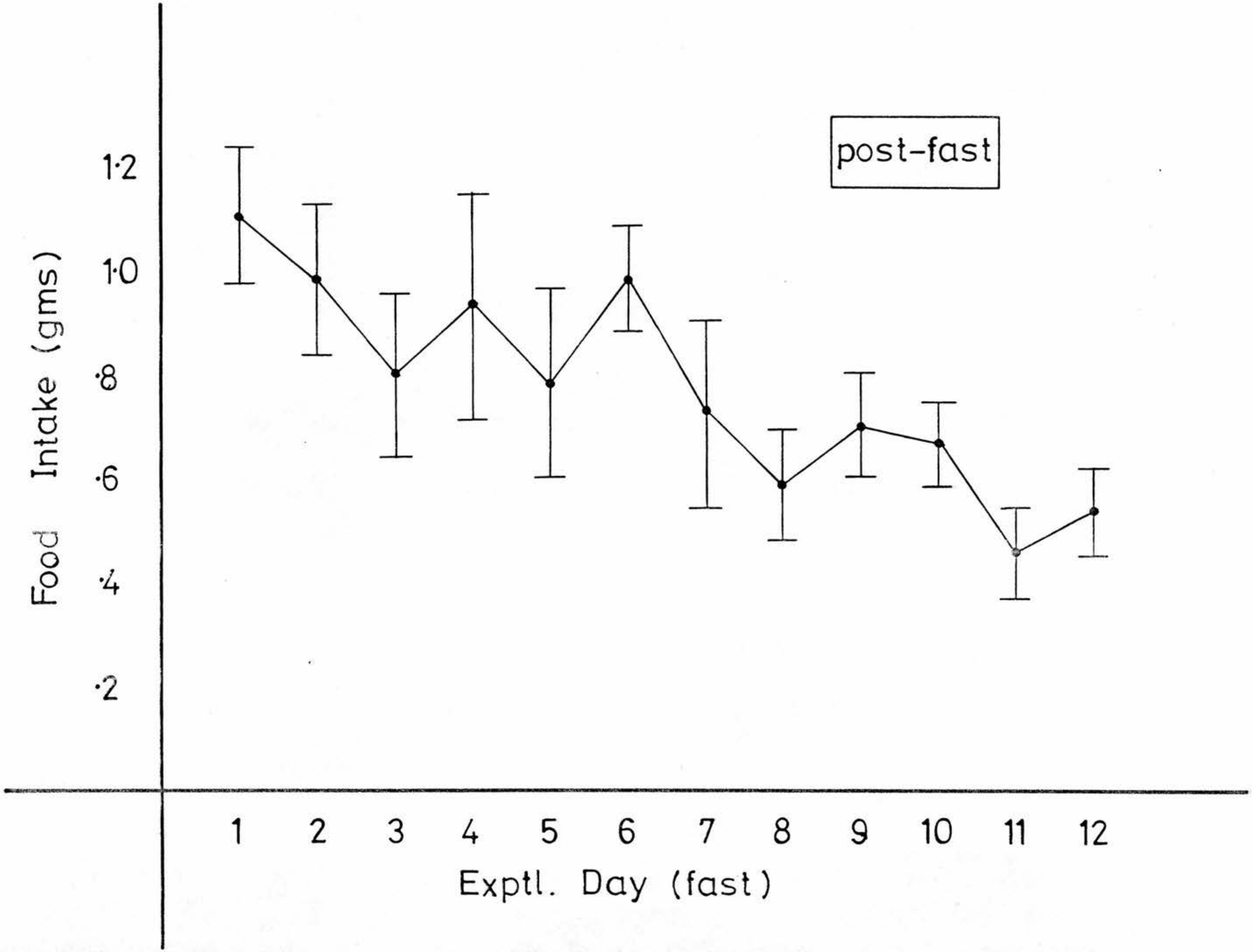
FIGURES 9.8 to 9.11 (Four pages)

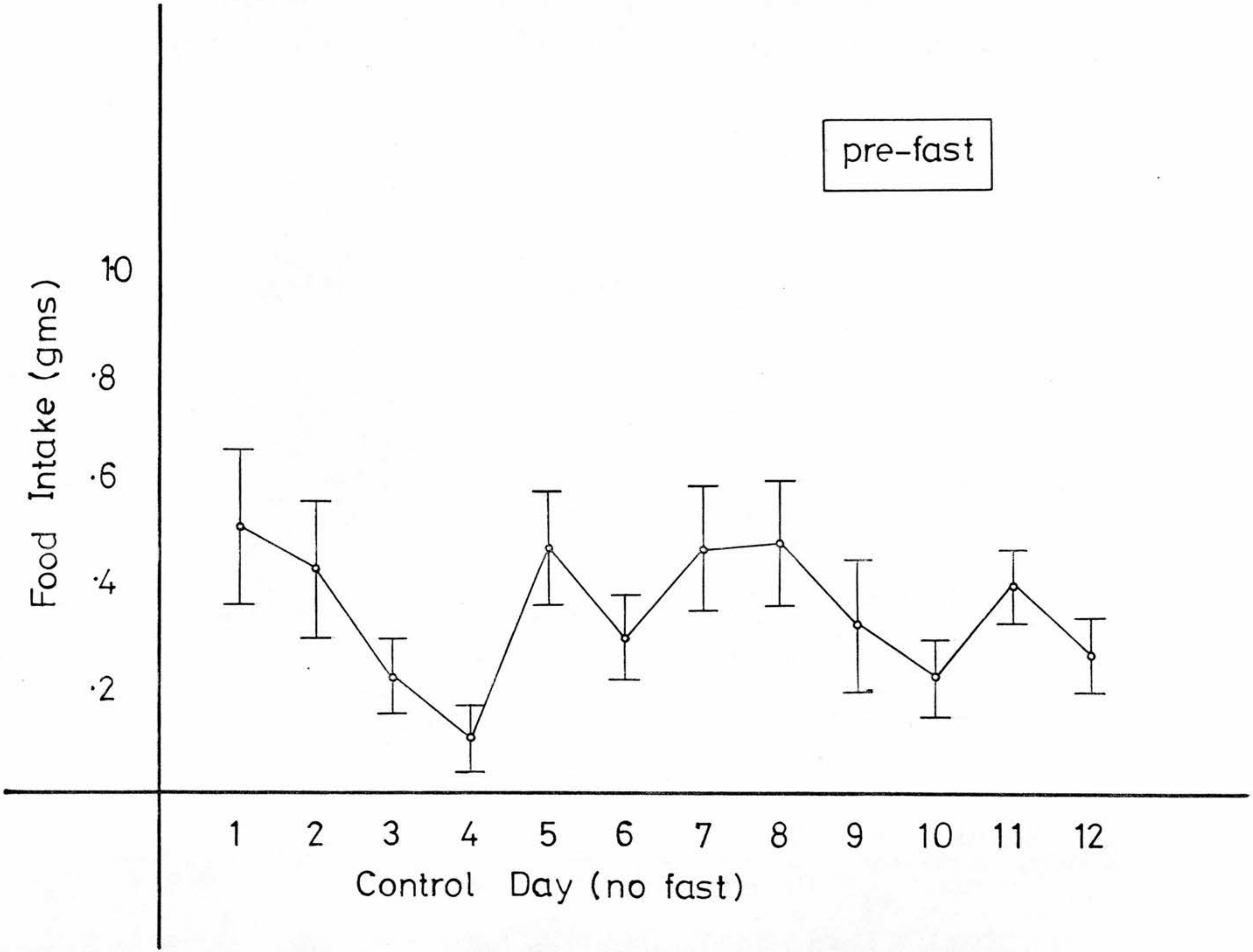
Mean food intake by 12 birds in the pre- and post-fast hour on fast and control days (see text) with repeated experience of a fast period, predictable on the basis of an available cue (Tables 13(a) to (d); Appendix II). Bars indicate two standard errors.

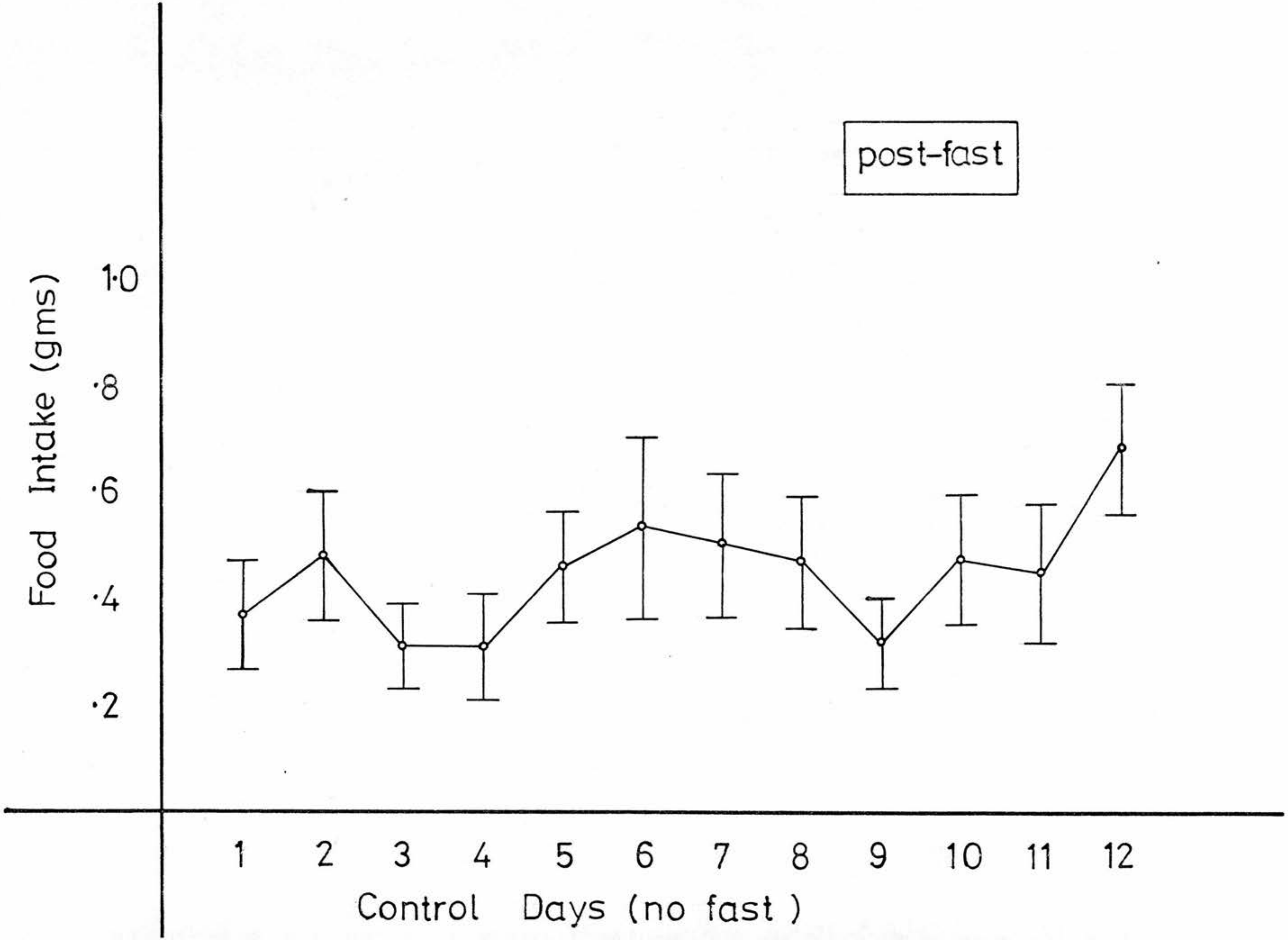
A Friedmann analysis of variance was used to show a significant change in hourly food intake with experience on the days when the cue signalled the deprivation period (Figures 9.8 and 9.9), with no change in the equivalent hours on the control days when no fast was experienced (Figures 9.10 and 9.11).

	Friedmann's Chi	Significance ($p <$)
Experimental Day; Pre-fast	37.22	0.001
Experimental Day; Post-fast	20.78	0.05
Control Day; Pre-fast	15.81	N.S.
Control Day; Post-fast	11.18	N.S.


Food Intake (gms)
1·4
1·2
1·0
·8
·6
·4
·2
pre-fast
1
2
3
4
5
6
7
8
9
10
11
12
Exptl. Day (fast)


post-fast
Food Intake (gms)
1·2
1·0
·8
·6
·4
·2
1
2
3
4
5
6
7
8
9
10
11
12
Exptl. Day (fast)


pre-fast
Food Intake (gms)
1·0
·8
·6
·4
·2
1
2
3
4
5
6
7
8
9
10
11
12
Control Day (no fast)


post-fast
Food Intake (gms)
1·0
·8
·6
·4
·2
1
2
3
4
5
6
7
8
9
10
11
12
Control Days (no fast)

have predicted this result. Under normal circumstances the way in which an animal will respond to its needs for food will be anticipatory rather than restorative.

There is another theoretical context into which this experiment could be fitted however, and that is the question as to the possibility of conditioning hunger and thirst drives. In this present experiment, a certain arbitrary environmental stimulus comes to elicit an increase in feeding behaviour in the absence of any manipulation of the animal's physiological state. Thus we can say, in a very real sense, that hunger has been conditioned, and that very easily.

It has been traditionally regarded possible to condition withdrawal and escape behaviour in response to a noxious stimulus (Miller, 1948), but difficult or impossible to condition eating or drinking. Some experiments have produced positive results (Calvin et al., 1953; Wright, 1965; Trost and Hamzie, 1966) while others have been unable to produce the effect (Novin and Miller, 1962; Siegel and MacDowell, 1954) or have attempted to account for the positive experimental findings in terms of secondary reinforcement (Howard and Young, 1962) or the reward value of "exploratory" behaviour (Myers and Miller, 1954). The experimental paradigm which has been used has been to pair an environmental situation (normally a very distinctively coloured holding box or the like) with different levels of food deprivation and to show that after a certain amount of exposure to this pairing, the environmental situation itself will (or will not) lead to an increase in the subsequent food intake. This experimental procedure is held to be analogous to the conditioned avoidance situation in which an arbitrary environmental stimulus, when paired for a time with a noxious stimulus (like electric shock) comes to elicit the avoidance and escape responses previously produced by the noxious stimulus itself.

It is now recognized that no stimulus or response can be truly arbitrary (Bolles, 1970; Seligman, 1970; Shettleworth, 1972; Hinde and Stevenson-Hinde, 1973). In the area of avoidance responding for example it has been shown that certain responses can be easily learned by a rat in order to avoid electric shock, but that others are almost impossible to learn. Seligman (1970) has suggested a continium of "preparedness" to make associations. Those which can be most easily made are those which make most ecological sense. In the area of conditioned aversion to gustatory stimuli, Garcia (Garcia et al. 1966; Garcia and Koelling, 1966; Garcia et al., 1968) has shown that animals do not connect external environmental stimuli with the onset of illness, but will readily learn to avoid interceptive stimuli like taste which are associated with illness, and that this learning can take place after surprisingly long delays in time. Such effects have also been demonstrated in birds (Wilcoxon et al., 1971) where visual information was shown to be more salient.

An organism is designed to learn, not all connections, but ones which seem to be of ecological importance. For example, Bolles and Grossen (1969) showed that the ease with which an animal would acquire an avoidance response could be seen to be related to the degree to which the response brought about change in environmental stimuli which would indicate to the animal that its efforts to escape were successful. The termination of the conditioned stimulus, known to be important in conditioned avoidance learning, could be seen as being one special case of stimulus change. With particular reference to the attempts to condition eating we can say that the sorts of cues which the animal will pay attention to and learn about will be those which actually provide information to help the feeding control system to operate. If the normal mode of operation of that system is one of anticipatory rather than restorative feeding we would not expect it to learn anything about an environmental cue which is associated with deprivation induced hunger. That would be of no use to the system at all. The animal does not need environmental information to tell it that it is hungry in the deprivation sense, as it would be perfectly capable of judging its own state. What it would be expected to remember however, would be any cue which tells it that if no action is taken now a state of deficit will exist in the future. The behaviour which the animal engages in can be seen as a type of avoidance response; avoidance of deficit. It is clear from the preceding experiment that even a few hours of deprivation must be unpleasant for the animal, as it will learn to use environmental information to forestall that deprivation.

Perhaps an interpretation in terms of the salience of the information to the feeding control system might help to account for the fact that some experiments did find a positive result in the conditioned hunger situation and others did not. For example, Wright (1965) used three conditions for the testing of the animal's responsiveness to food after the experience of the conditioned stimulus (being placed in the holding box). The animal's food intake was measured either in the holding box, in the home cage with the food immediately available, or in the home cage with food available after a short delay. This should be compared with most of the earlier experiments in which food intake was measured in the holding box (a situation in which the animals were not accustomed to feeding). Effects were found in all cases, but by far the greatest effect was shown in the home cage/delay condition. The interpretation of the greater effect in the delay condition was in terms of frustration, but it might be suggested that the absence of food in the home cage (where food was normally always available) served to indicate to the animal that another period of the deprivation condition should be anticipated, thus leading to the greater intake.

9.7 Anticipatory Feeding in the Short Term

It has long been known that a period of food deprivation will produce a facilitation in subsequent feeding behaviour in that the latency to approach and consume food will be reduced and the amount eaten will be increased when food is again made available (Bolles 1962; Bolles, 1965; Megibow and Zeigler, 1968; Collier, 1969). This effect of deprivation can readily be demonstrated in the doves.

9.7(a) Method

6 femalesRing doves were housed in individual cages (40x35x45 cm) on a 9 hour light cycle (9am to 6pm) with continuous availability of water and grit, but subjected to different periods of food deprivation.

The animals were observed for 5 weeks and on each day of the week (Monday to Saturday) the food boxes were removed from the cages just before the onset of the light cycle and returned to the cages after a period of one to six hours. For each of the 5 weeks the birds were subjected to the 6 different deprivation times presented in pseudorandom order (the deprivation time which the animals experienced on any day being largely a matter of convenience for the experimenter). Each bird then experienced each of the 6 different lengths of deprivation on 5 occasions. It should be noted that as the food boxes were removed just before the onset of light at the start of the day, the total length of deprivation was the overnight period of 15 hours plus the one to six hour additional period. The food intake of the birds in the half hour after the return of the food was measured.

9.7(b) Results

Figure 9.12 shows that the amount of food eaten by the doves is clearly a function of the time since the animals last fed.

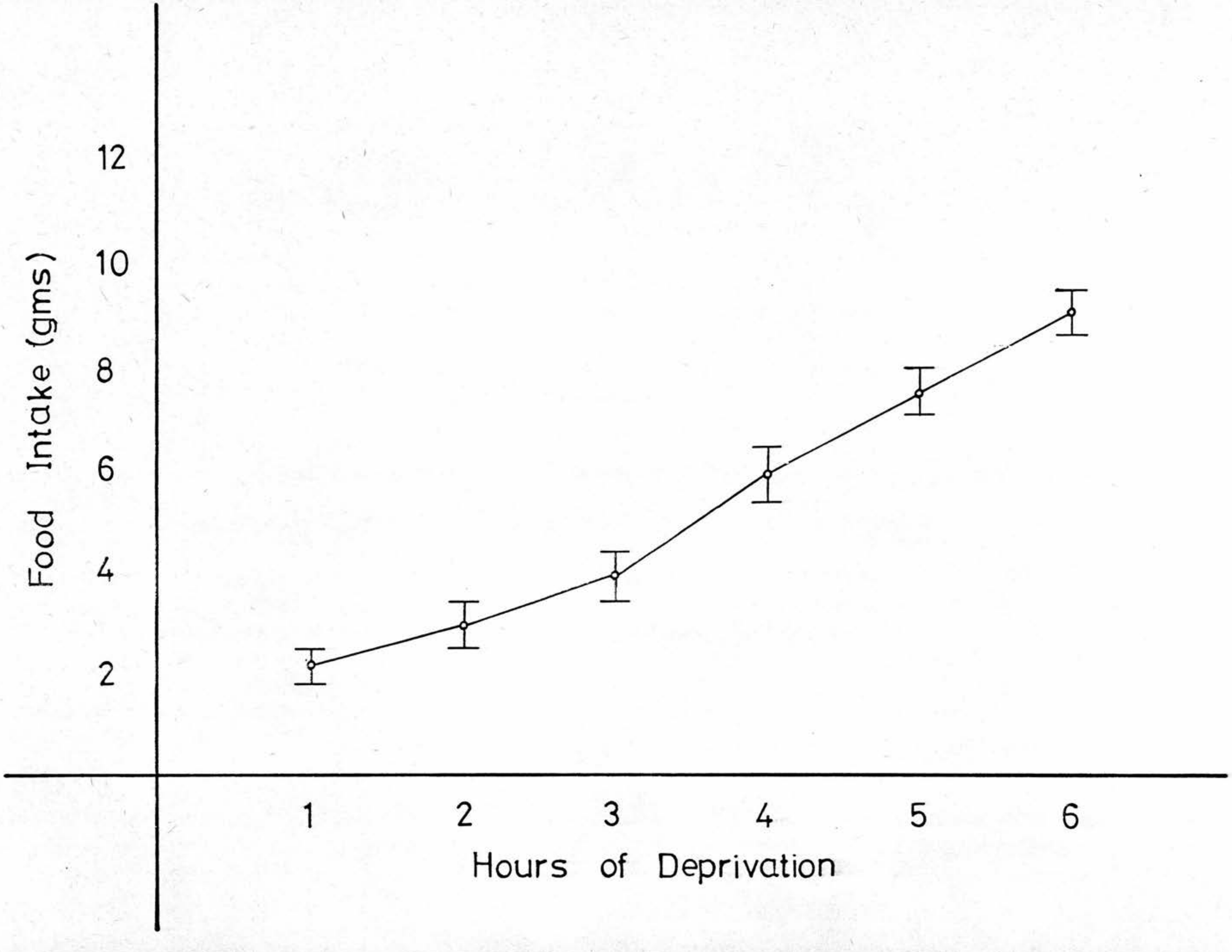
9.7(c) Free Feeding Animals

It has frequently been pointed out however (e.g. Collier et al., 1976) that the frequency of feeding in animals is usually such that the inter-meal interval is always shorter than the time required to show any facilitatory effect of deprivation on food intake in an experiment like the one described above. That is, eating would not normally be in response to hunger in the deprivation sense. Would there be any relationship between meal size and the time since the animal last fed if the animal itself were controlling the length of deprivation experienced?

A way of studying this question is to look at the correlations

FIGURE 9.12

Effect of different lengths of food deprivation on subsequent food intake (Table 14; Appendix II).


Food Intake (gms)
2
4
6
8
10
12
1
2
3
4
5
6
Hours of Deprivation

between meal size and inter-meal interval in the normal, free feeding animal. If meal size is controlled by the same sort of mechanism that produces a compensatory increase in intake after an enforced fast, then one would expect to find a correlation between the size of meals and the intervals of non-feeding which precede those meals. This is not the usual finding however, When correlations have appeared they have not been between meals and preceding intervals (the so-called pre-prandial correlation) but between meals and succeeding intervals (the post-prandial correlation).

Such post-prandial correlations have been reported by a large number of researchers studying vastly different animals (Balagura and Coscina, 1965; Thomas and Mayer, 1968; Balagura and Coscina, 1969; Snowdon, 1969; Balagura and Devenport, 1970; Le Magnen and Devos, 1970; Larue and Le Magnen, 1972; Lavitsky, 1974; Slater, 1974; Snowdon and Wampler, 1974; Decastro, 1975; De Castro and Balagura, 1975; Bernstein, 1975; Petersen, 1975; Bernstein, 1976; Davies, 1977; Wolf and Hainsworth, 1977). Others have completely failed to find a significant relationship (Zeigler, Green and Lehrer, 1971; Panksepp, 1973; Kenny and Mook, 1974). Panksepp (1973) has suggested that the presence of the correlation might be due, in some of the earlier studies, to the use of questionable statistical procedures involving the grouping of data. This objection cannot be made about most of the more recent studies however as correlations are presented for individual animals on ungrouped data.

(9.7(d) Feeding Pattern Correlations in Doves

Tables 9.1 to 9.7 represent summaries of the Pearson Produce Moment

TABLE 9.1

MEAL PATTERN CORRELATIONS - INTACT GROUP

BIRDS	POST-	SIGNIFICANCE ($p <$)	PRE-	SIGNIFICANCE ($p <$)
M108G	0.22	0.0134*	- 0.05	0.5785
M201G	0.13	0.1216	- 0.02	0.8130
M211G	0.05	0.6460	0.32	0.0028*
M284G	0.15	0.0211*	- 0.05	0.4450
M339B	0.19	0.0433*	- 0.06	0.5284
M574S	0.35	0.0000*	0.18	0.0248*
M76G	- 0.03	0.7640	- 0.07	0.4831
F196W	0.09	0.2861	- 0.00	1.0000
F211B	0.02	0.7345	0.16	0.0067*
F252G	0.03	0.6724	- 0.04	0.5729
F36G	0.37	0.0000*	- 0.09	0.2931
F479S	0.00	1.0000	0.05	0.6402
F687S	0.32	0.0010*	- 0.11	0.2559
F91W	0.07	0.3876	- 0.08	0.3234

(* indicates $p < 0.05$)

POST- / PRE- comparison: Wilcoxen 'T' = 19; p 0.05
two tailed

TABLE 9.2

POST-PRANDIAL CORRELATION - MOVING AVERAGE

BIRDS	CORRELATION	SIGNIFICANCE ($p <$)
M108G	0.33	0.0012^{*}
M201G	0.10	0.2888
M211G	- 0.16	0.1595
M284G	0.17	0.9142^{*}
M339B	0.37	0.0007^{*}
M574S	0.29	0.0012^{*}
M76C	- 0.05	0.6707
F196W	0.06	0.5247
F211B	0.05	0.4207
F252G	0.22	0.0040^{*}
F36G	0.31	0.0012^{*}
F479S	0.01	0.9392
F687S	0.28	0.0114^{*}
F91W	0.14	0.1163

(* indicates $p < 0.05$)

TABLE 9.3

FEEDING PATTERN CORRELATIONS - TRIGEMINAL SECTION

BIRDS	POST-	SIGNIFICANCE ($p <$)	PRE-	SIGNIFICANCE ($p <$)
T1	0.14	0.2166	0.00	1.0000
T131G	0.05	0.5959	0.02	0.8610
T133B	0.02	0.8465	- 0.05	0.6271
T198G	0.29	0.0034*	- 0.15	0.1325
T252G	0.01	0.9216	0.12	0.2330
T3	0.05	0.5635	- 0.02	0.8177
T325G	0.00	1.0000	0.12	0.2842
T357G	0.36	0.0012*	0.07	0.5354
T4	0.32	0.0112*	0.08	0.5377
T482G	- 0.10	0.3610	- 0.18	0.0969
T490G	0.26	0.1062	0.00	1.0000

(* indicates $p < 0.05$)

Post-/Pre- comparison: Wilcoxen "T" = 11; $p < 0.05$ two tailed

TABLE 9.4

FEEDING PATTERN CORRELATIONS - CONTROL TRIGEMINAL SECTION

BIRDS	POST-	SIGNIFICANCE ($p <$)	PRE-	SIGNIFICANCE ($p <$)
C112G	0.17	0.0058*	0.13	0.0337*
C116G	0.09	0.2793	0.04	0.6306
C332G	0.44	0.0000*	- 0.08	0.3922
C411G	- 0.02	0.8130	0.12	0.1536
C421S	0.02	0.8144	0.04	0.6378
C474G	- 0.02	0.8371	- 0.09	0.3532
C476G	0.15	0.1345	- 0.03	0.7663
C82W	- 0.00	1.0000	- 0.11	0.2387
C480G	0.11	0.1237	0.08	0.2646

(* indicates $p < 0.05$)

Post-/Pre- comparison: Wilcoxen "T" = 8; Not significant

TABLE 9.5

FEEDING PATTERN CORRELATIONS BEFORE AND AFTER TRIGEMINAL SECTION

	PRE-OPERATIVE				POST-OPERATIVE			
BIRDS	POST-	SIGNIFICANCE ($p <$)	PRE-	SIGNIFICANCE ($p <$)	POST-	SIGNIFICANCE ($p <$)	PRE-	SIGNIFICANCE ($p <$)
F19G	0.13	0.0878	- 0.00	1.0000	- 0.04	0.6946	- 0.02	0.8449
F215G	0.08	0.3723	0.14	0.1163	0.12	0.2126	0.16	0.0946
B245G	0.28	0.0009^*	0.02	0.8117	0.11	0.2065	0.02	0.8191
B289Y	0.19	0.0540^*	- 0.13	0.1913	0.19	0.1237	0.34	0.0051^*
B337G	0.13	0.2427	- 0.01	0.9292	0.03	0.8322	0.22	0.1135
B387G	0.10	0.3043	0.06	0.5379	0.28	0.0246^*	0.15	0.2382

(* indicates $p < 0.05$)

Post-/Pre-comparison:

Pre-operative - Wilcoxon "T" = 2; not significant

Post-operative - Wilcoxon "T" = 7; not significant

TABLE 9.6

FEEDING PATTERN CORRELATIONS AND FOOD TYPE

	MIXED GRAIN DIET				WHEAT GRAIN DIET			
BIRDS	POST-	SIGNIFICANCE (p <)	PRE-	SIGNIFICANCE (p <)	POST-	SIGNIFICANCE (p <)	PRE-	SIGNIFICANCE (p <)
F138	0.06	0.6024	- 0.03	0.7950	0.02	0.8402	- 0.02	0.8402
F17G	0.12	0.1370	0.00	1.0000	0.27	0.0244*	- 0.14	0.2527
F206G	0.24	0.0003*	0.02	0.7521	0.14	0.3449	0.12	0.4187
F226B	0.07	0.4661	0.11	0.2515	- 0.08	0.4370	0.11	0.2847
F248B	- 0.03	0.7628	0.19	0.0528	0.28	0.0026*	0.04	0.6687
F298W	0.19	0.0341*	0.01	0.9129	0.02	0.8575	- 0.08	0.4705
F446G	0.03	0.8018	0.02	0.8675	0.22	0.0778	0.10	0.4296
F471G	- 0.06	0.4390	- 0.01	0.8979	0.07	0.4387	0.01	0.9125
F479S	0.02	0.8104	0.01	0.9049	0.15	0.1999	0.13	0.2677
F485G	- 0.00	1.0000	- 0.03	0.6868	- 0.01	0.9185	- 0.10	0.3021
F655S	0.09	0.3400	- 0.10	0.2888	0.18	0.1486	0.02	0.8742
F999G	0.07	0.4036	0.06	0.4740	0.10	0.3114	0.01	0.9200

(* inidcates p; 0.05)

Post-/Pre-comparisons:

Mixed Grain - Wilcoxon "T" = 23; Not significant

Wheat Grain - Wilcoxon "T" = 10; p 0.02 two tailed

TABLE 9.7

FEEDING PATTERN CORRELATIONS AND TEMPERATURE

	70°F				50°F			
BIRDS	POST-	SIGNIFICANCE ($p <$)	PRE-	SIGNIFICANCE ($p <$)	POST-	SIGNIFICANCE ($p <$)	PRE-	SIGNIFICANCE ($p <$)
F126Y	0.15	0.0360*	0.12	0.0944	0.22	0.0033*	0.02	0.7896
F147Y	0.20	0.0019*	- 0.07	0.2729	0.02	0.8053	0.00	1.0000
F153Y	0.09	0.1463	0.05	0.4207	0.23	0.0011*	- 0.04	0.5929
F164Y	- 0.03	0.5886	0.07	0.2072	0.01	0.8806	0.01	0.8806
F203Y	0.14	0.1105	0.10	0.2567	0.12	0.2126	0.10	0.2998
F22Y	0.43	0.0000*	0.04	0.6201	0.00	1.0000	- 0.01	0.9111
F229G	0.37	0.0000*	0.14	0.0904	0.48	0.0000*	0.31	0.0006*
F235B	0.02	0.8124	- 0.03	0.7213	0.02	0.8348	- 0.05	0.6009
F344B	0.17	0.0269*	- 0.09	0.2454	0.36	0.0001*	0.04	0.6580
F359G	0.35	0.0021*	0.22	0.0539	0.34	0.0040*	0.02	0.8694
F301G	0.21	0.0059*	- 0.05	0.5138	0.03	0.7204	0.09	0.2827
F388C	0.19	0.0415*	- 0.26	0.0053*	0.20	0.0423*	- 0.11	0.2698

(* **indicates** $p < 0.05$)

Post-/Pre- comparison:

70°F - **Wilcoxon "T" = 5;** $p < 0.01$ **two tailed**

50°F - **Wilcoxon "T" = 4;** $p < 0.01$ **two tailed**

Correlation coefficients for the relationship between meal size and pre- and post-meal intervals in all of the groups of data discussed in the previous chapters. Considering first Tables 9.1, 9.3, 9.4 9.5 and 9.6 which are the data gathered from animals on a 9 hour light cycle, it can be seen that there are very few significant correlations and that the significances present are such by virtue of the large number of meals considered rather than the strength of the correlations themselves. If overall group effects are considered, as advocated by Decastro (1975), we find that in most cases a comparison between th4 derived post- and pre-prandial correlations indicates that the post-prandial relationship, although not individually significant in many animals, is more positive than the pre-prandial relationship.

9.7(e) Diurnal Variation

There is an obvious problem in the computation of correlations between meal size and inter-meal interval using data pooled across the whole day. It has been shown earlier that the peak in feeding activity at the end of the day is associated with an increase in meal sizes and a decrease in inter-meal interval lengths. This diurnal variation would tend to obscure the presence of any correlation which did exist in the meal to meal control of intake.

It might be expected then, that the shorter the day length, the more would the feeding activity going on during the day be directed towards coping with the overnight fast. As noted above, the day length was normally kept short so as to prevent the problem of animals being in reproductive condition and perhaps showing spontaneous ovulation and broody behaviour. The data gathered for the study of ambient temperature effects on feeding however were collected from birds which were kept on a 12 hour light cycle, so that comparison could be made with data from birds on the shorter cycle. It can be seen from Table 9.7 that there do seem to be many more significant correlations in this data than in the original data.

It might also be possible to remove the effect of diurnal variation by statistical manipulation of the data. In an attempt to do this, some of the correlations were recomputed on the basis, not of the originally recorded meals and intervals, but on the basis of the differences between each individual value and the mean value at that time of the day. The mean was computed around each individual meal size and interval length by taking the average of the meal or interval along with the two items which preceded it and the two items which followed it. This procedure reduced the degrees of freedom by 4 for each day (as an average could not be computed for the frist 2 or last 2 items of each day), but it can be seen from the correlations presented in Table 9.2 that this procedure did serve to enhance the effect in some cases.

9.8 The Ontogeny of Anticipatory Feeding

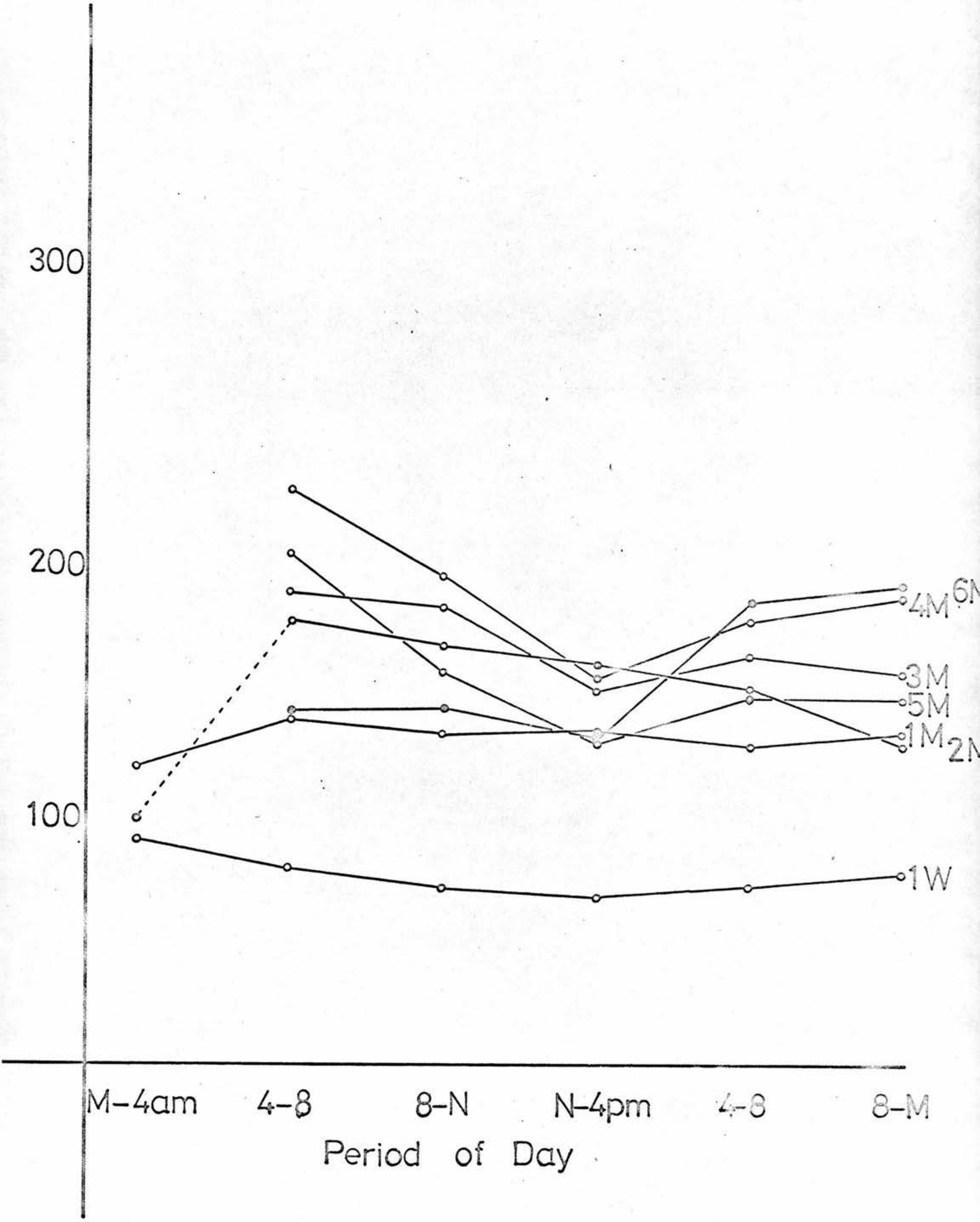
The importance of anticipatory feeding will be a function of the probability of periods of deprivation occurring and this will be true on the long-term, diurnal and meal to meal levels.

For example, it might be suggested that food availability was continuous for young, suckling mammals in the early days of life. Anticipatory feeding implies anticipation of fast and if no periods of fast were experienced, then a mode of regulation by restoration would be perfectly adequate. Decastro and Balangura (1975) reported finding predominantly pre-prandial correlations in the suckling behaviour of young rat pups. As the animal got older, the relationship changed to being post-prandial rather than pre-prandial, but there could be no way of deciding between an explanation in terms of the learning of environmental contingencies and one involving some developmental change. Although this finding was questioned by Bernstein (1976), who suggested that the pre-prandial correlations found might be artefacts of the relatively low temperature at which the young rats were maintained in the previous study, she too failed to find any very marked post-prandial relationship in the feeding behaviour of her animals before the age of 4 to 5 weeks. After this time, relatively strong correlations (0.4) began to appear.

A further interesting example of anticipatory feeding emerging at a certain developmental stage is given by Wright (1978) in a study of the diurnal pattern of food intake by human infants over the first few months of life. It was found that as nocturnal feeds were dropped, the infants responded initially by increasing their intake of food at the start of the following day, but gradually changed to showing a peak in intake at the end of the day (Figure 9.13). Again it is not possible to say that this is a spontaneous developmental change or is one which comes by learning. It should be noted too, that the food intake of young mammals is controlled by an interaction of the infant and the maternal behaviour such that it is difficult to assign the dominant regulatory rote to one or other of the pair, and might even be wrong to attempt to do so. These findings do make certain points about

FIGURE 9.13

Data from Wright (1978) on the mean food intake in a group of human infants during 6 periods of the day, broken down by developmental stages from one week (1W) to six months (6M). The figure shows that the gradual loss of a meal between midnight and 4 a.m. results initially in an increase in food intake at the start of the day, which has changed, by the six month stage (highlighted with filled circles), to an increase in intake at the end of the day.


300
200
100
M-4am
4-8
8-N
N-4pm
4-8
8-M
Period of Day
4M
6M
3M
5M
1M
2M
1W

infant feeding practice however. It is common for mothers to try to help their infants sleep longer by encouraging them to eat a larger amount at a certain meal; that is, to assume that the infant is regulating intake post-prandially. If the system is operating in a pre-prandial, restorative mode however, not only will the procedure not be effective, but it could result in a net overeating on the part of the infant.

As suggested earlier, food hoarding and caching in animals can be seen as behavioural anticipatory food regulation. Although rats are not natural hoarders of food, a great deal of study has been carried out on this behaviour which can be induced in the laboratory. Wolf (1939) found that animals which had early experience of "hoardable" foods (pelleted rather than powdered diet) tended to hoard more in later life when such a hoardable food material was available. He also found that animals experiencing food deprivation pre-pubertally tended to show more hoarding behaviour, indicating that animals with prior experience of food shortage and hunger might be more likely to attempt to behaviourally forestall such shortage. Similarly Mandler (1958) found that early deprivation in rats led to increased responsiveness to food either on an operant or a consummatory measure. Seitz (1954) reported that hoarding behaviour was more frequent in large as compared with small litter sizes in rats, perhaps related to early competition and deprivation.

From these examples it might be argued that certain sorts of early experience of a group of animals, which the experimenter felt to be irrelevant, or indeed was not aware of, might contribute to the variability in the probability of obtaining a significant meal size/inter-meal interval relationship. For example, it might be predicted that animals on a regime of intermittent feeding or low food availability would be subsequently more likely to show post-prandial feeding pattern correlations than those reared without any experience of food deprivation. Collier (personal communication cited by Zeigler, Green and Lehrer, 1971) has made the observation that most of the studies (at that time) reporting significant post prandial relationships involve methods of behavioural transduction (for example, the use of an operant) which demands a certain degree of work on the part of the animal. It is possible that animals perceive a work requirement as a situation of low food availability, and thus may learn in the short term to take account of the perceived unreliability of the source.

9.9 The Continuation of Ongoing Feeding

Wiepkema (1971) in an observational study of free feeding mice, reported that there is a progressive lengthening of the bouts of feeding over the initial stages of a meal. Petersen (1975, 1976) demonstrated the same lengthening effect in his mice using an automatic recording technique.

Some of the free feeding dove records were analysed to determine if a similar relationship could be obtained. The data gathered from the original group of animals (chapter 3) will be considered. All meals of six bouts or greater were included and the mean lengths of the first, second, up to the fifth bout and inter-bout interval were computed. Looking too at the last five bouts, all meals having 8 or more bouts were considered and the means of the last five bouts and inter-bout intervals were computed. The number 8 was chosen so that at least the initial bouts of the start of a meal would not be included in means looking at the end of the meal, yet two many meals would not be excluded from the analysis. Figure 9.14 shows the mean bout lengths for the first five and last five bouts of meals included in the analysis for all of the 14 birds considered. Figure 9.15 shows the corresponding inter-bout intervals.

Wiepkema argued that if longer periods of uninterrupted feeding were indicative of a higher feeding tendency (demonstrating that this was a reasonable assumption by showing that food deprivation increased the animals' persistance at feeding) then the animals were becoming more rather than less likely to continue feeding as the meal progressed. Initial contact with the food, far from having any satiating effects, served to increase the animals' appetites. He argued further, that as there was no associated decrease in the length of the inter-bout intervals, the change which was taking place was a change in the probability of the transition from feeding to non-feeding rather than a change in the probability of the transition from non-feeding to feeding. This was taken to suggest that it was the sensory contact with the food which was having the effect, as this would act to increase the animals' persistance at ongoing feeding, but would not affect the chance of initiation of feeding.

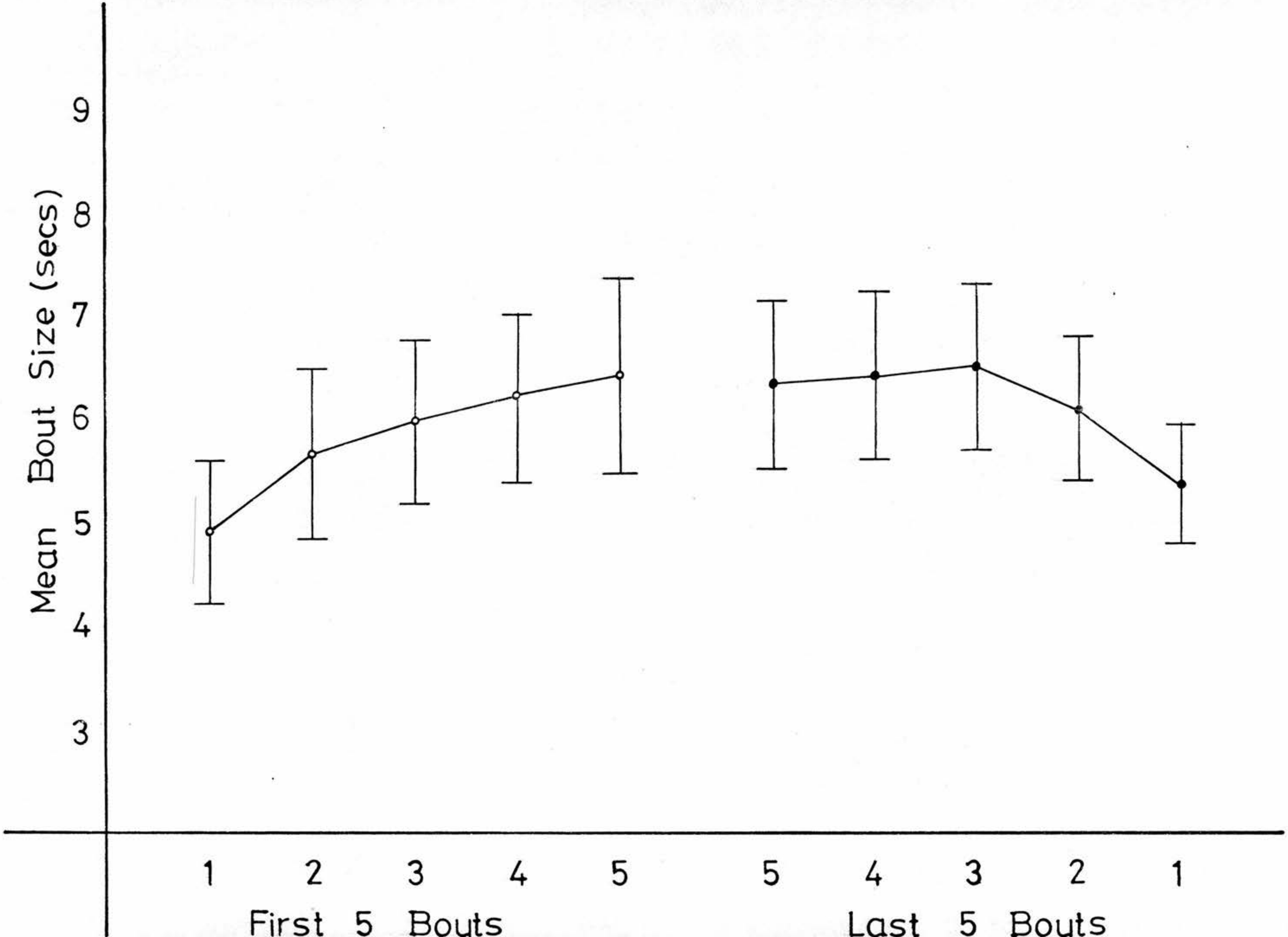
Immediately before the animal started to eat then, its feeding tendency would be some function of its physiological state. Upon making contact with the food a "positive feedback" would contribute to this base level so that feeding would continue to an extent which exceeded the immediate need of the animal. Considering the meal size/inter-meal interval relationship discussed above, it would be suggested that

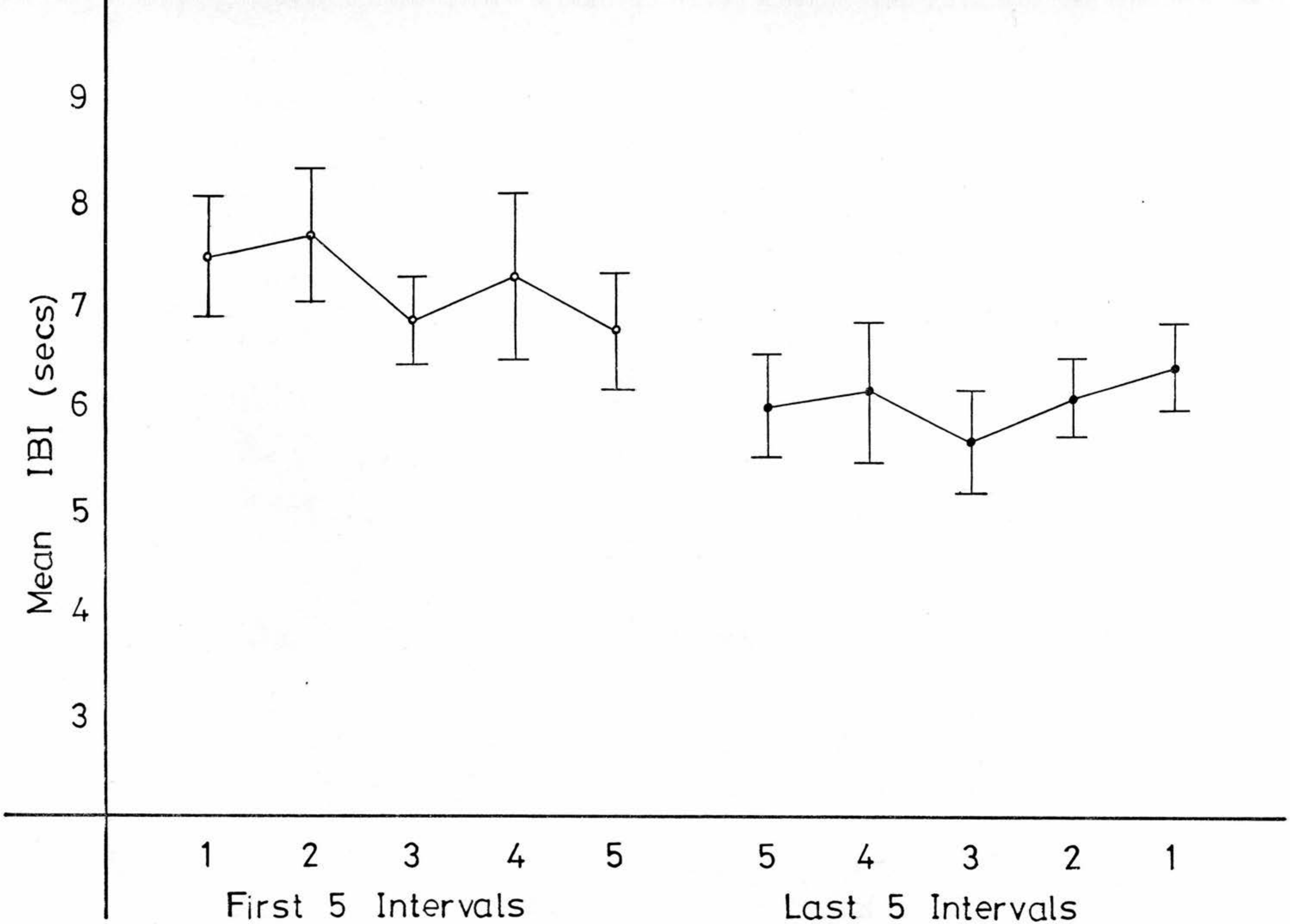
FIGURES 9.14 and 9.15 (Two pages)

Grand means of the mean bout length (9.14) and mean inter-bout interval (9.15) of the first five and last five bouts of meals (see text for description of analysis) taken from 14 birds (Tables 15(a) and (b); Appendix II). Bars indicate two standard errors.

Friedmann analysis of variance was used to test significance of change in length of bouts and intervals with Serial Order.

	Friedmann's Chi	Significance ($p <$)
First Bouts	17.7	0.01
First Intervals	5.02	N.S.
Last Bouts	17.15	0.01
Last Bouts (excluding last item)	0.20	N.S.
Last Intervals	0.82	N.S.


Mean Bout Size (secs)
3
4
5
6
7
8
9
1
2
3
4
5
First 5 Bouts
5
4
3
2
1
Last 5 Bouts


Mean IBI (secs)
3
4
5
6
7
8
9
1
2
3
4
5
First 5 Intervals
5
4
3
2
1
Last 5 Intervals

the animal would then break off from feeding for a time which would be proportional to the size of the meal it had just eaten.

Considering the ending stages of the meal (Figure 9.15) it can be seen that there is again no effect shown in the interval lengths but there does seem to be a tailing off in bout lengths (Figure 9.14). The Friedmann analysis of variance indicates a significant shortening of bout length at the end of the meal, but this is contributed to only by the very last bout as can be seen by the fact the analysis recomputed on the data excluding the last item shows no significant effect. Thus it can not be really said that the bout length shows a tailing off in feeding tendency, but rather a continuation to the end of the meal with a truncation of the last bout.

9.9(a) The Role of Positive Feedback in Feeding

Wiepkema (1971) saw the function of this facilitation of ongoing feeding by sensory feedback from contact with food as serving to convert a pattern of continuous "nibbling" at food (which one might expect to be produced by a homeostatic system controlled only by negative feedback) into a pattern of food intake in meals with prolonged intervals between. This can be seen as being important in ecological terms for several reasons. Feeding in discrete meals and then concealing oneself between meals would reduce the animal's risk of predation. It would also mean that the feeding behaviour of the animal was in closer correspondence with the pattern of food availability in the environment. Food is rarely (except perhaps for the herbivore) evenly distributed about the environment but is concentrated in certain places or at certain times. It would thus be an advantage to the animal if its feeding control system was designed to take account of food where and when it occurred and to eat in the anticipation of not coming accross another source for some time. Further, in a natural environment in which an animal is designed to live, the sensory quality of food carries implicit information about its nutritive worth (Cabanac, 1971). A "pleasant" food, in terms of smell, taste and texture is likely to be a nutritive food; an "unpleasant" food may be poisonous or decaying.

However change in the environment can lead to the system being confused. Yudkin (1963) has suggested that the over abundance of highly palatable foods (particularly material containing refined sugar) is one important causal factor in the development of certain sorts of obesity in Western man. Not only is palatability dissociated from nutritive value a problem, but also the variety in which food is available. It is the case (Yudkin, 1956) that animals may be satiated for one food but not another. If animals are given access to various sorts of highly palatable foods they will over-eat and quickly become obese (Sclafani and Springer, 1976). This point is underlined by Wirtshafter and Davis (1977) who note that the largest rat which they were able to find in the literature (1445 grams) was a product, not of hypothalamic damage, but of maintenance on an extremely palatable high fat diet. Rowe and Rolls (1977) have recently suggested that such changes produced in animals as a result of highly palatable diets result in permanent changes in body weight.

9.9(b) Further Evidence of Feeding Motivated by the Presence of Food

Landless (1974) showed an increase in the rate of feeding as a feeding period progressed in a study of demand feeding in Rainbow trout. This facilitation in feeding behaviour however, was occurring over hours rather than minutes or seconds, so it would be a little difficult to suggest that the effect was comparable with those of Wiepkema. He was also able to show however (Landless, 1974, 1975) that a single presentation of food to the fish at a time before a feeding period might be expected to begin spontaneously, had the effect of stimulating such a period, which was identical in every respect to that which would occur normally; clear and reliable evidence of a "priming" effect in feeding behaviour.

There are a number of studies reporting a facilitatory effect of contact with food on feeding tendency, without specifically discussing the significance of this. Allison (1971) for example, found that the rate of ingestion of nutritive and non-nutritive sweet solutions by rats showed an acceleration at the start of the period of drinking. DeNoble and Caplan (1977) and Deluty (1976) both showed that the presentation of a response independent food reward in an operant situation led to a short lived increase in the rate of responding. Hunsicker and Reid (1974) found a rather similar effect of one reward carrying over to the next performance, in a water reinforced maze running task. They observed that their rats would run faster when the trials were separated by 7 rather than 95 seconds.

It has been shown (Campbell and Sheffield, 1953) that deprivation of food causes an increase in the random activity of rats. Increased activity presumably has the effect of increasing the probability of a contact with food. Gilbert and Sturdivant (1958) found that the locomotor activity of ad libitum fed rats in a maze would be similarly increased by the presence in the situation of food related smells. Bruce (1938) and Anderson (1941) found that pre-feeding of a small amount of food before placing deprived rats in a maze test situation led to an improvement in performance and more rapid learning. This was discussed for the most part in terms of reducing the level of drive to some optimum for performance, but could be equally easily interpreted as indicating an increase in motivation due to the "priming" effect of the free food. Solomon (1946) found a similar improvement in the rate of acquisition of a jumping stand discrimination using a pre-feeding procedure.

Harwood and Vowles (1966) provided information as to a possible physiological and anatomical mechanism for the facilitatory influences of sensory feedback on feeding behaviour in birds. They found that electrical stimulation in certain sites in the dove brain which would not actually produce feeding behaviour, did seem to enhance any ongoing feeding at the time of stimulation. These sites lay mostly in the paleostriatum and posterior neostriatum. Similarly, Ritter and Epstein (1975) found that infusions of nor-adrenalin, into the brains of rats, which were not themselves large enough to produce stimulus bound feeding, had the effect of prolonging ongoing meals if infusion was timed to coincide with food ingestion. Thus electrical or chemical stimulation of the brain can be seen as acting directly on the anatomical structures which normally cause the continuation of ongoing behaviour (Trowell, Panksepp and Gandelman, 1969).

Much evidence exists then to indicate an "appetizer" effect of the sensory contact with food.

9.10 Chapter Summary

Evidence was presented from the literature to support the suggestion that, in most cases, animals feed in advance of their immediate needs.

An example of this is the diurnal distribution of food intake in the Ring dove. As no feeding goes on during the hours of darkness, each day involves a fairly long but predictable period of fast. The major peak in feeding activity of the birds is seen to be at the end of the day in advance of the nocturnal fast, rather than at the beginning of the day to make up for the previous night's fasts.

It was suggested that the afternoon peak in intake was a result of a rather abrupt change in feeding tendency rather than a slow increase in the rate of food intake over the day. This suggestion was found to be in keeping with observations made as to the use of the crop for food storage by the bird. The crop was found to be empty for the greater part of the day but to be filled in a very short time during the afternoon feeding peak. It was argued that this mode of feeding behaviour seen in the laboratory with high availability of food was the result of a balance between pressures to carry sufficient stores of food to last the animal over the night, but to postpone carrying such reserves for as long as possible towards nightfall, as added weight would increase risk of predation. Evidence was presented that such diurnal anticipatory feeding was simply a special case of feeding in advance of any period of predictable fast.

Analysis of feeding pattern records also show4d a tendency towards a correlation between the size of a meal and the succeeding rather than the preceding interval of non-feeding. Again this is seen as being a mode of control by feeding in advance of future needs.

Evidence of a facilitatory effect of contact with food on feeding behaviour was presented, which may be part of the mechanism for the maintenance of ongoing meals.

CHAPTER 10

10.1 Operant Study of Feeding Patterns

Operant techniques have been used in the study of feeding motivation in two main ways.

1) Short operant sessions for food reward have been used to measure the effects of various manipulations (like experimental brain lesions or food deprivation) on the animal's immediate level of feeding motivation (Teitelbaum, 1966).

2) The performance of an operant response has been used as a convenient method of transducing feeding behaviour so that records of feeding patterns can be kept. (see chapter 3 for review).

In the former situation, the amount of work which the animal is prepared to carry out in order to obtain food (usually in the form of a fixed ratio schedule) is taken as a measure of how hungry it is. Thus Teitelbaum (1957) argued that although rats with lesions in the Ventromedial nucleus of the hypothalamus showed an increase in food intake and body weight they were less prepared to tolerate high ratios of work to reward than were intact rats of normal body weight. In the latter situation however, the schedule of reinforcement is rarely considered to be important as the operant response is simply an event, indicating approach to food, which can be easily recorded electically. In some cases (e.g. Collier et al., 1972) to be considered below, a ratio of responses to food reward is used as a model of food availability in a continuous, free feeding situation.

10.2 Ratio Responding as a Model of Trigeminal Section Deficits

Section of the trigeminal nerve in the dove was shown to reduce the efficiency of feeding as measured in observational tests (Table 4.1). A method of experimentally reducing the efficiency of feeding in intact birds would be to increase the ratio of pecks at an operant key to food reinforcements earned. In addition to the effect of fixed ratio on feeding efficiency, Kissileff (1970) argued that the imposition of a work requirement would add an aversive component to the food getting sequence. As suggested in chapter 6, trigeminal section would reduce the perceived pleasantness of feeding, so this aspect of the effect of surgery would also be modelled by an operant ratio requirement.

It was therefore predicted that the reduction in meal frequency which was found as a result of trigeminal deafferentiation and also as a result of feeding a less preferred food, would be found when the birds were required to perform a number of pecks at a key to obtain food.

10.3 Method

Six birds were used for this study, but repeated mechanical faults in one of the operant mechanisms meant that data for only 5 birds was finally collected. Adult female doves were used, each being housed continuously for the duration of the experiment in a cage (35x35x35 cm) with constant, free availability of water and grit. On one side of the cage was mounted a large panel key (8 x 8cm), pecks at which activated a reed switch. On the same wall and to the right of the key was a food hopper which could be raised into a position allowing the animal access to the food. The food used here was single grain millet, the smaller grains allowing smoother flow in the hopper. Above the point of access to the hopper was a green pannel lamp which was used as a cue signalling the presence of food.

The cages were arranged in the room so that the animals were usually isolated and partitions between the cages were of one inch expanded polystyrene in an attempt to provide sound attenuation. It was obvious however that the animals would be able to hear not only the vocaligations of the others, but also the sounds associated with the key pecking and food hopper presentation.

Key pecking was recorded and access to the food hopper controlled by a PDP 11/34 computer. The machine was programmed to simultaneously control six cages and to record, on magnetic disc, the time of occurrence of each response made by the animal and the time at which a food reinforcement (a certain time of access to the food hopper) was delivered. The animals were maintained on a 12 hour light cycle with the room lights coming on at 9 pm and going off at 9 am. The reverse of the cycle was simply in order that the computer could be used when there was no other user demand.

10.3(a) Pretraining of the Birds

At the start of the experiment the birds were placed in the operant cages and allowed to feed from the hoppers which were left continuously in the up position. The body weights of the birds were noted daily to ensure that they were indeed finding the food and eating it. After a few days the hoppers were lowered and one or two grains of millet attached to the operant key with clear adhesive tape. The computer was set to reward each peck to the key with a seven second period of access to the food hopper. Seven seconds was chosen simply because it was the shortest period which could be programmed due to limitations of the electronic logic controlling the operant chambers. The birds quickly approached and pecked at the grains taped to the key and, in most cases, this was all that was required to allow them to learn the association between the key and the food. In some, additional manual "shaping" of the response was required. After the response had been acquired by all of the animals, they were allowed fully two weeks to settle to a stable level of performance and constant body weight.

10.3(b) Reward Schedule

Reinforcements were delivered by the computer on a simple fixed ratio schedule (FR). For a certain number of key pecks the bird would earn one seven second period of access to the food hopper. No time limit was imposed within which the animals had to complete a run of responses in order to gain the reinforcement as it was felt that this would differentially reinforce continuation of pecking. The bird could, for example, perform half of the required number of responses towards a reinforcement and then break off and return an hour later to complete the run of responding.

10.3(c) Data Collection

Data were collected for at least seven stable days at each of seven ratios of response to reinforcement from one to one hundred and sixty. At the end of this series the animals were returned from FR160 to FR10 so that the effect of the transition from a high to a low ratio could be seen. At each change of ratio the animals normally settled (body weight and level of responding) quickly, with only two or three days data having to be discarded.

During the initial stages of the experiment the rate of data collection was low as failures of the electronic logic circuits controlling the mechanisms of the hoppers were frequent, and it was always necessary to allow the animals two or three days to settle after such failures. It was decided to make a minor modification of the apparatus so that the computer not only sent instructions to the logic circuits but also received feedback as to whether or not the instructions had been correctly obeyed. This was done by attaching mercury tilt switches to the food hoppers so that the computer could sense if the hopper was up or down. This simple modification allowed the computer to correct any logic failures when they occurred, and thus vastly improved the rate of data collection.

Another problem encountered was the fact that at the higher ratios the amounts of data generated became unmanagably large, and a day to day storage problem existed. Response time data therefore was discarded and only reinforcement time data kept.

10.4 Results

The first point to note is that the birds are perfectly capable of supporting fairly high ratios of work to reward without any sign of loss of body weight (Figure 10.1). It should be emphasised here that these animals were continuously free feeding and were in no way actively deprived of food as is the case in most operant studies, yet the size of ratio tolerated without any sign of failure to compensate, compares with those which have been reported in earlier rodent work (Teitelbaum, 1957).

10.4(a) Diurnal Pattern of Food Intake in Operant Situation

As noted in chapter 3 and also chapter 9, the characteristic diurnal pattern of feeding behaviour in the free feeding doves involves a small peak in activity at the start of the day with a much larger peak at the end of the afternoon. Some cases were found to show more marked morning peaking of food intake, but the vast majority show the afternoon peaking pattern.

In the operant study however (Figure 10.2) the predominant pattern found at all ratios in all animals involves obvious morning peaking in feeding activity with a smaller afternoon peak. The data presented in figure 10.2 are those found in animals responding at FR10 at the end of the experiment. Thus it cannot be suggested, as might possibly be the case with the earlier data, that the abnormal pattern was simply attributable to the fact that the animals had not adapted to the reversed light cycle. By the time these data were collected, the birds had been kept on the reversed cycle for fully six months, so

FIGURE 10.1

Mean body weight of birds as a function of fixed ratio size (Table 23; Appendix II).

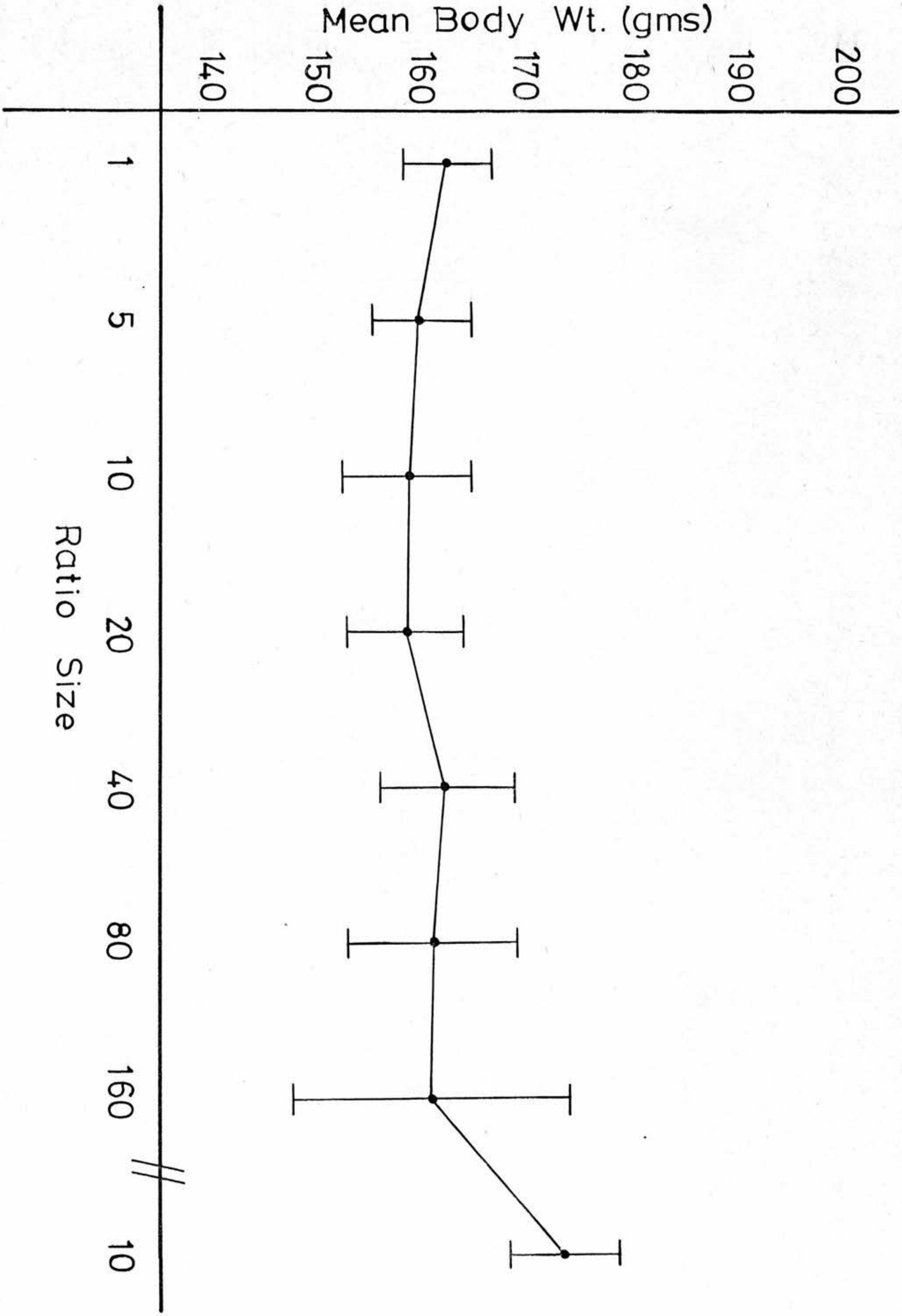
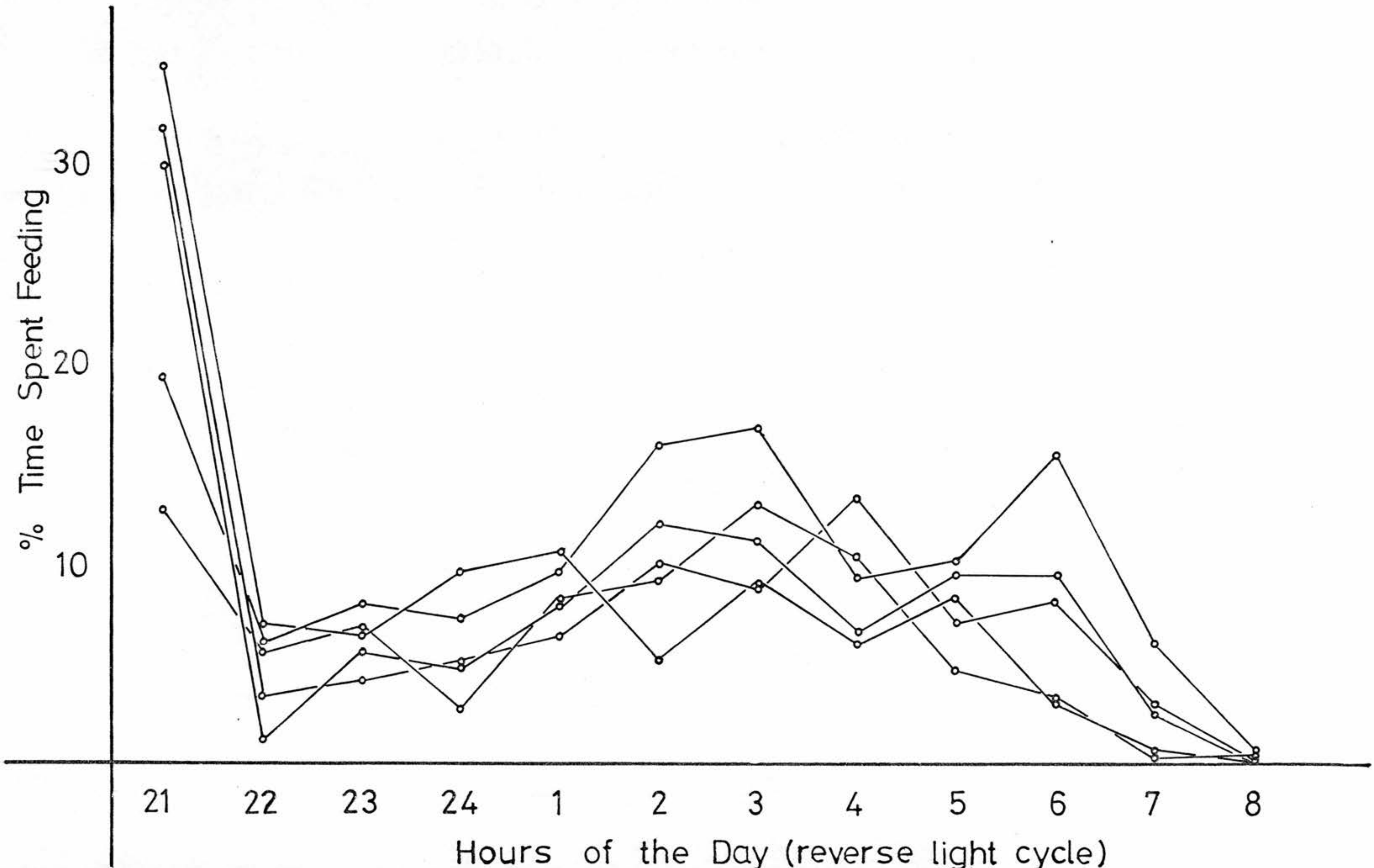

Mean Body Wt. (gms)
140
150
160
170
180
190
200
1
5
10
20
40
80
160
10
Ratio Size

FIGURE 10.2

Percentage of daily total time spent feeding in each hour of the day for each of the five birds in the operant study. Data was collected at FR 10 at the end of the study.


% Time Spent Feeding
10
20
30
21
22
23
24
1
2
3
4
5
6
7
8
Hours of the Day (reverse light cycle)

that a failure to adapt explanation becomes very unlikely.

As discussed earlier (chapter 9) other studies which have used an operant technique to transduce feeding activity for recording (for example, Duncan et al., 1970; see section 9.1) have found patterns of diurnal distribution of feeding behaviour with predominant morning peaking in birds. There would seem to be something particular about the operant situation which leads to a disruption of what must be considered to be the normal diurnal distribution of feeding behaviour. This lends weight to the argument in chapter 3 that the exact nature of the situation in which the animal finds itself (with reference to things like food availability and prominence of food related cues in the environment) will affect the recorded pattern in ways which may not be predictable.

It should be noted however, that when body weights were recorded at the end of the day (at 9 am) the crops of the birds were normally found to be full. That is, the very obvious change in the distribution of feeding activity might not indicate an equally large change in the distribution of food intake. Here again we see the problem of using any measure of feeding behaviour which does not provide a direct measure of amount of food ingested.

10.4(b) The Frequency of Meal Taking

A logarithmic survivorship plot (chapter 3, section 3.8(c)) was again used to provide a definition of a meal for this study. Plots of inter-reinforcement-intervals were generated so that a decision could be made as to whether a given interval length was within a meal or between meals. The feeding behaviour of the animals as recorded in the operant situation is clearly also very markedly bouted. Using separate logarithmic survivorship plots for each animal at each ratio the effect of the fixed ratio size on meal frequency was calculated (Figure 10.3). It can be seen that meal frequency decreases over the lower ratios and then begins to increase again as the fixed ratio size continues to increase. The graph of meal size (Figure 10.4) by fixed ratio shows the complementary picture, with mean meal size increasing slightly at the low ratios and then decreasing.

It should be noted however that the mean number of reinforcements earned each day goes down as the ratio increases (Figure 10.5) although the body weight is remaining fairly constant (Figure 10.1). This is presumably a result of the fact that the reinforcement is by a certain time of access to the food rather than a certain amount, and thus the response to increased ratio requirement can come both by increase in the work output (that is, the number of responses emitted; Figure 10.6) and by increase in the rate and efficiency of feeding during any one period of access. Thus as the total number of reinforcements earned per day changes with ratio, it would be more appropriate to compute meal size as a percentage of the daily total number of reinforcements (Figure 10.7).

10.5 Discussion

It can be seen therefore, that the degree to which feeding behaviour is bouted varies as an inverted U-shaped function of fixed ratio size. In all cases, at the low ratios as compared with

FIGURE 10.3

Mean frequency of meal taking as a function of fixed ratio size (Table 19; Appendix II). Bars indicate two standard errors.

Friedmann analysis of variance was used to test significance of change in meal frequency with ratio size.

	Friedmann's Chi	Significance (p <)
All ratios (1 to 160)	18.34	0.01
1 to 10	5.2	N.S.
10 to 160	16.16	0.01

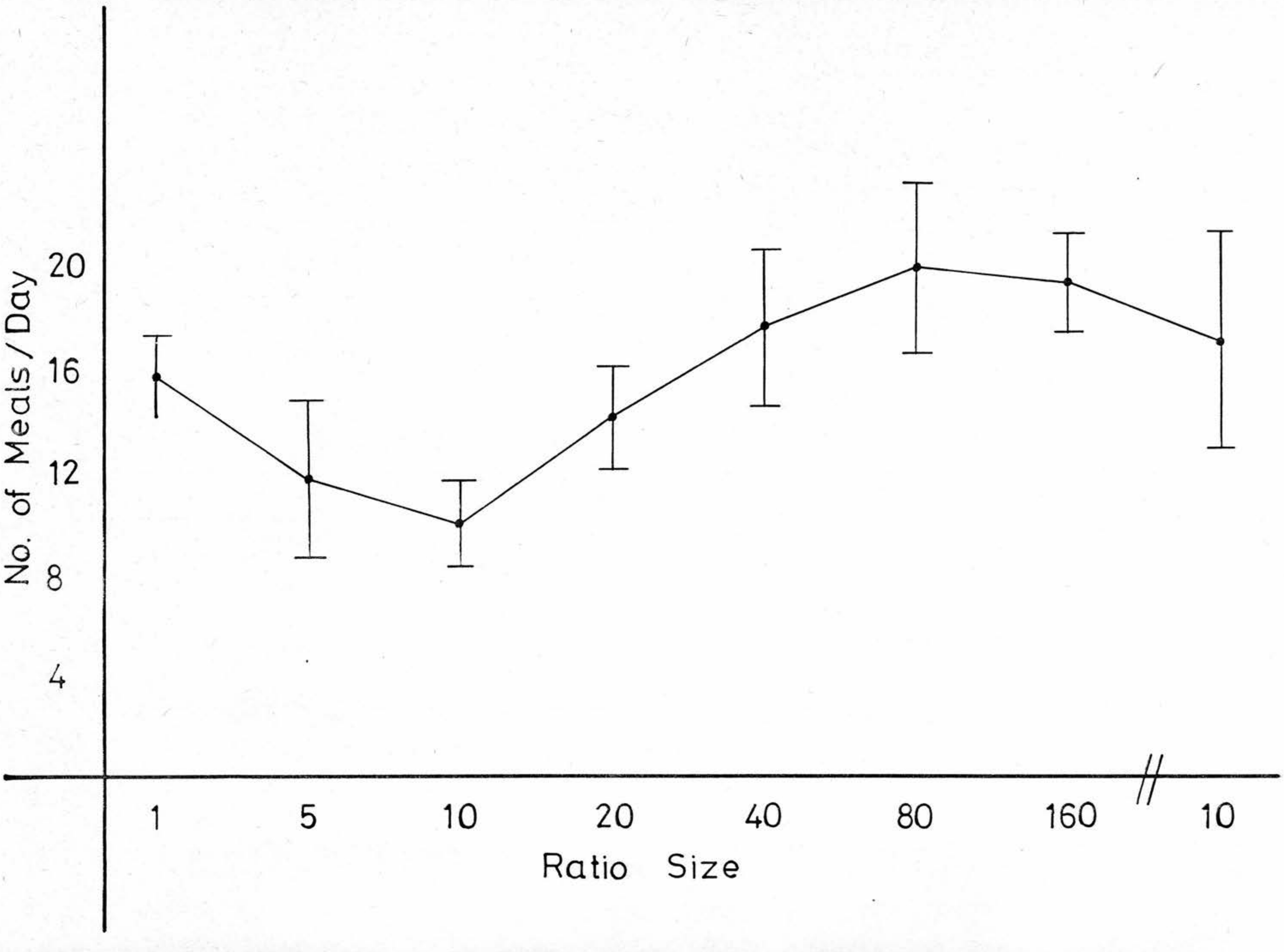

No. of Meals / Day
20
16
12
8
4
1
5
10
20
40
80
160
10
Ratio Size

FIGURE 10.4

Mean meal size as a function of fixed ratio size (Table 20; Appendix II). Bars indicate two standard errors.

Friedmann analysis of variance was used to test the significance of change in meal size with ratio size.

	Friedmann's Chi	Significance ($p <$)
All Ratios (1 to 160)	26.31	0.001
1 to 10	2.8	N.S.
5 to 160	22.14	0.001

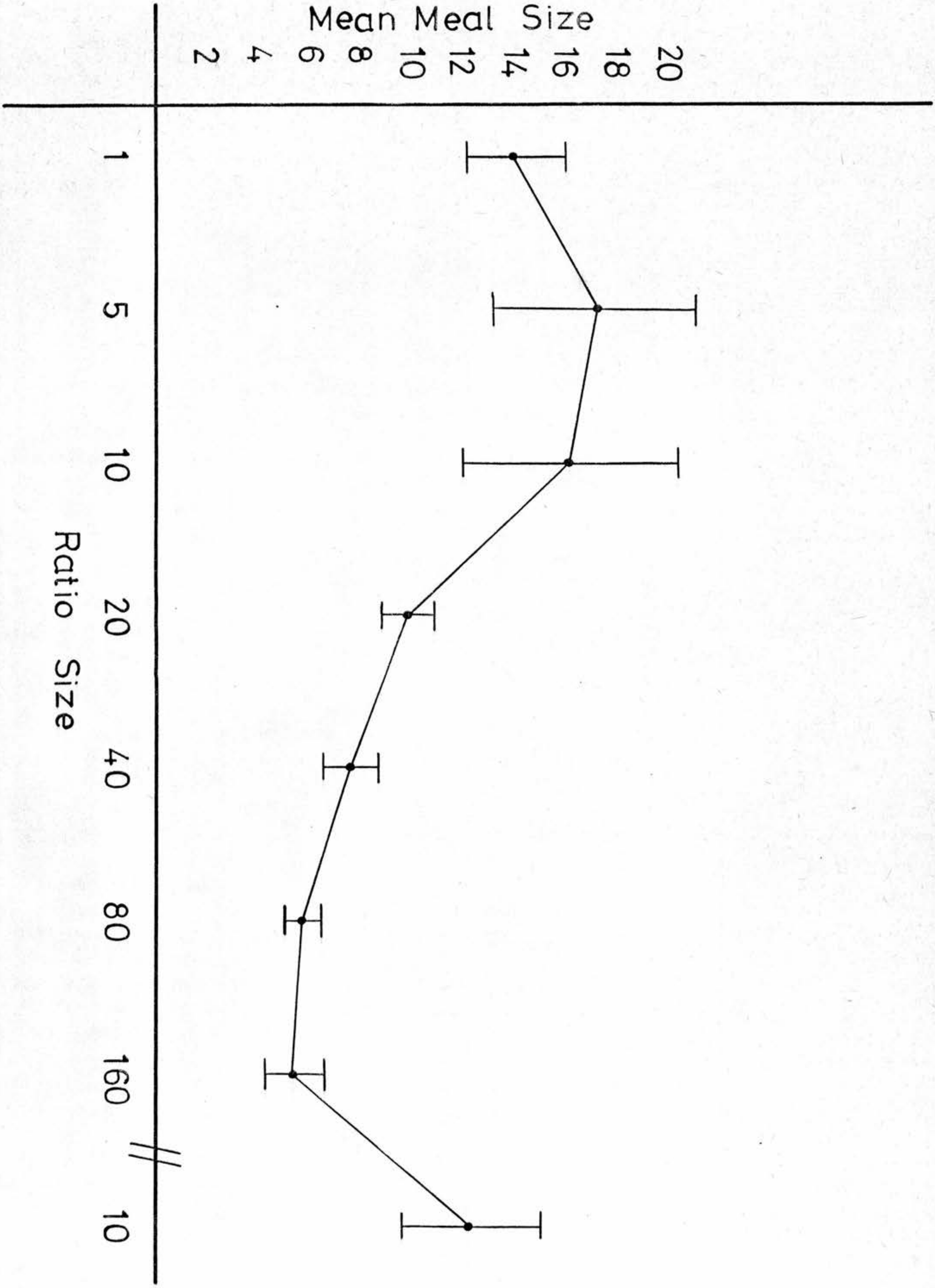

Mean Meal Size
2
4
6
8
10
12
14
16
18
20
Ratio Size
1
5
10
20
40
80
160
10

FIGURE 10.5

Mean number of reinforcements earned each day as a function of fixed ratio size (Table 17; Appendix II). Bars indicate two standard errors.

Friedmann analysis of variance was used to test the significance of the change (from 1 to 160).

Friedmann's Chi = 23.31; $p < 0.001$.

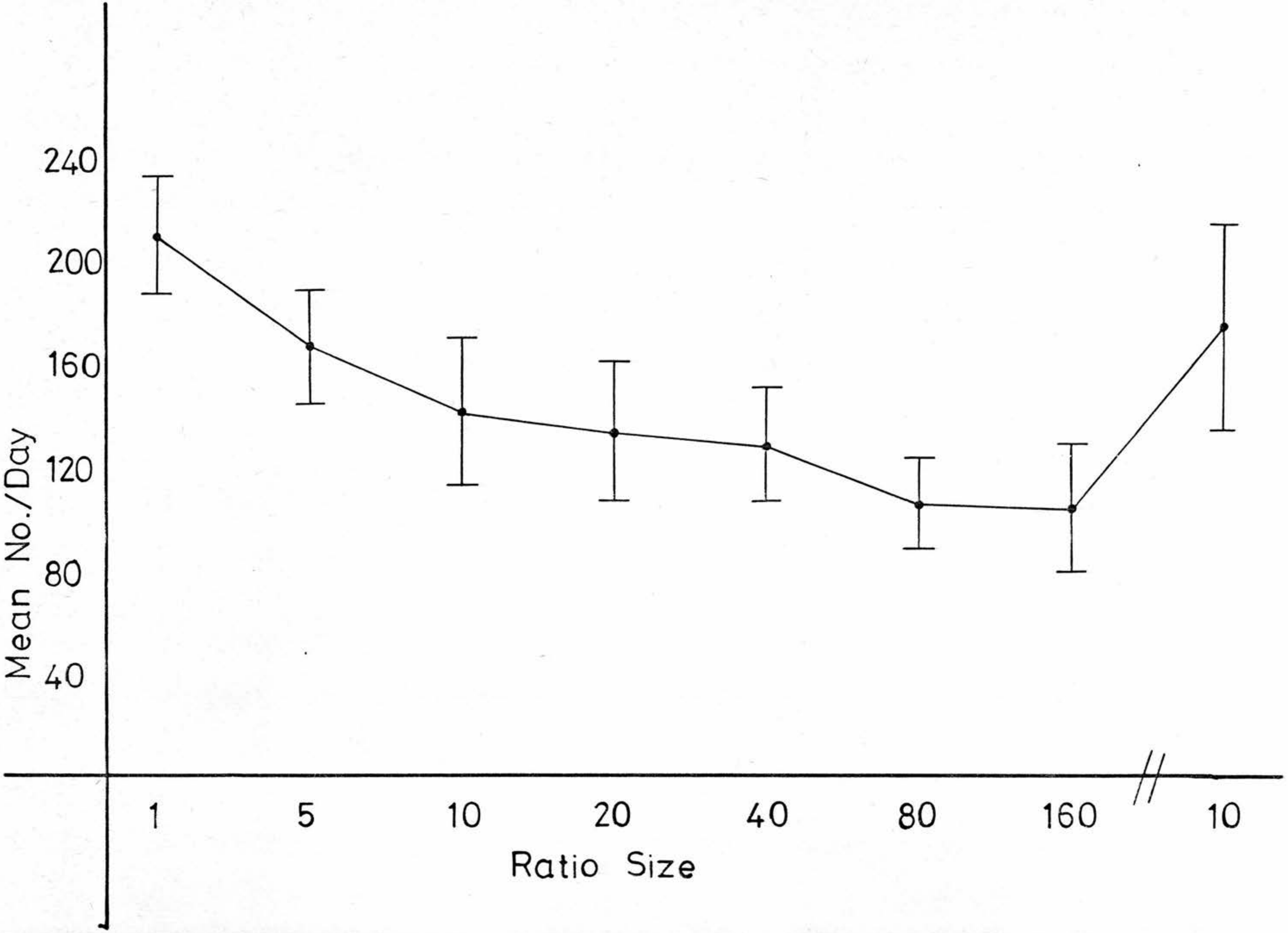

Mean No./Day
240
200
160
120
80
40
1
5
10
20
40
80
160
10
Ratio Size

FIGURE 10.6

Mean number of responses emitted per day as a function of fixed ratio size (Table 18; Appendix II).

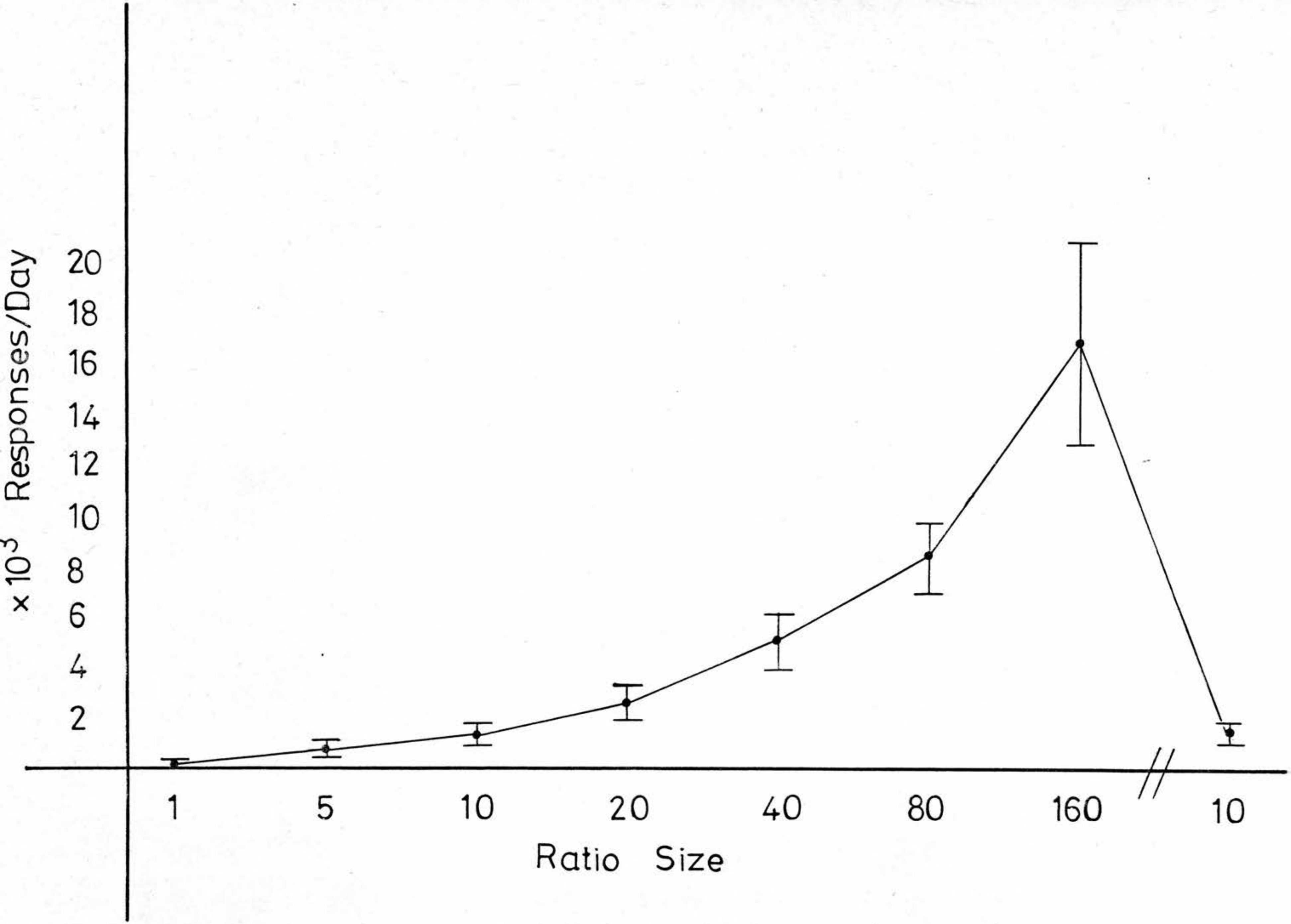
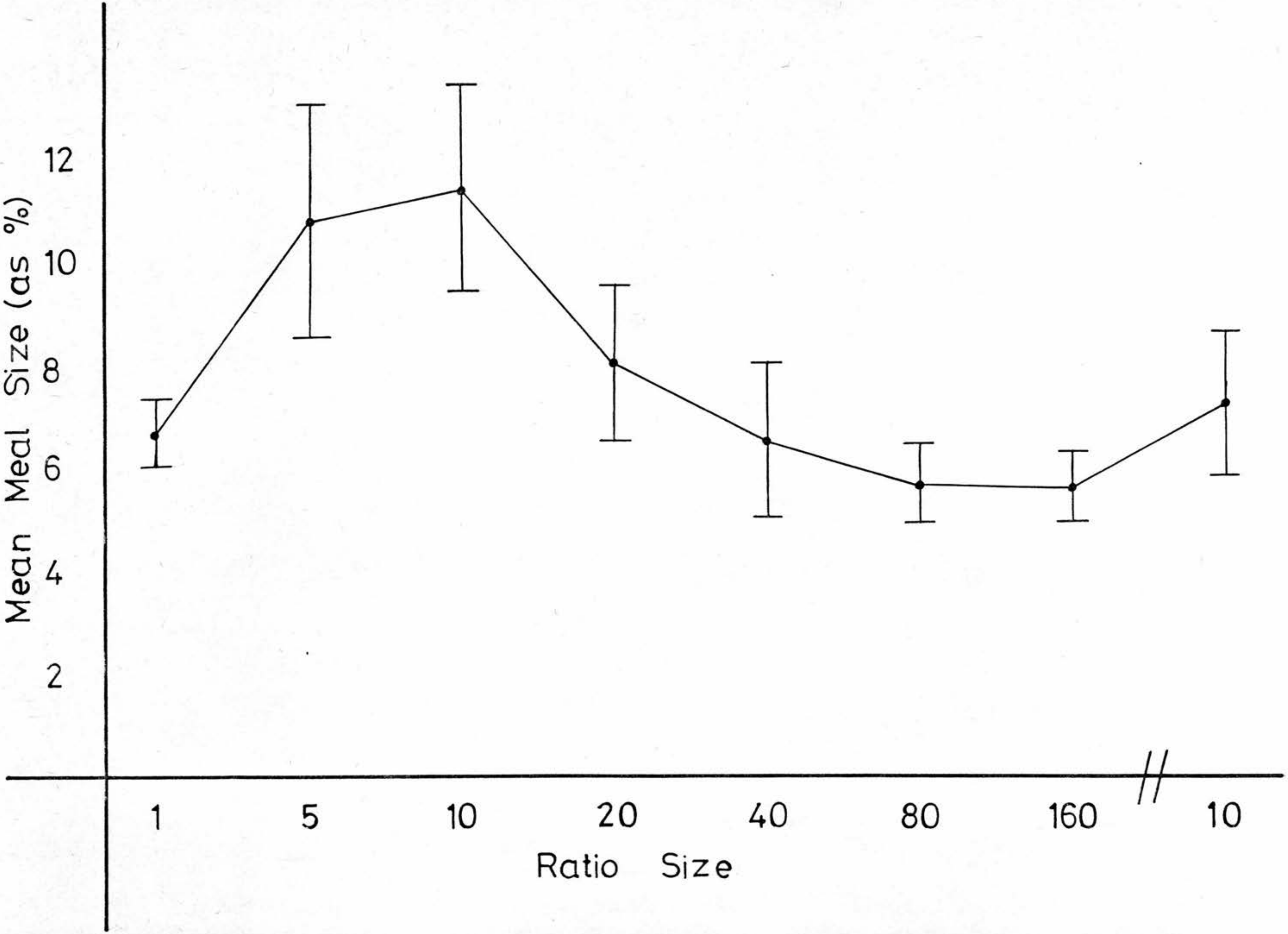

× 10^3 Responses/Day
2
4
6
8
10
12
14
16
18
20
1
5
10
20
40
80
160
10
Ratio Size

FIGURE 10.7

Mean meal size (as percentage of daily total number of reinforcements earned) as a function of fixed ratio size (Table 21; Appendix II). Bars indicate two standard errors.

Friedmann's analysis of variance was used to test significance of change in meal size with ratio size.

	Friedmann's Chi	Significance ($p <$)
All ratios (1 to 160)	17.57	0.01
1 to 10	5.20	N.S.
10 to 160	16.16	0.01


Mean Meal Size (as %)
2
4
6
8
10
12
1
5
10
20
40
80
160
10
Ratio Size

continuous reinforcement (CRF), the birds feed in larger meals which occur less frequently. As the ratio of responses to food reinforcements increases over about 10 or 20 (the exact point of the meal size peak varies across animals), the opposite occurs. The frequency of discrete approaches to the food increases with an associated decrease in meal size.

It is first necessary to emphasise why such an effect is unexpected. The ratio of the work output of the animal to the amount of food earned is always constant for any given fixed ratio size. That is exactly what the term "fixed ratio" means. The way in which the animal aggregates its feeding activity does not affect this. There is no straight forward"energetic" explanation. Perhaps this can be illustrated by comparison with the experimental procedure used by Collier et al (Collier, Hirsch and Hamlin, 1972; Hirsch and Collier, 1974; Kanerek, 1975) in studies of the effect of different work requirements (described as differences in food availability) on patterning of food intake in various animals. Their subjects were required to perform a certain number of operant responses in order to gain access to a food hopper. Once the food hopper had been produced, the animal could keep it there by remaining in a feeding chamber next to the food. If the animal left the chamber for more than a certain length of time the hopper was removed, a repeat of the work requirement being needed to bring it back. That is, the animal was required to do a certain amount of work to get at the food, but once access had been gained it could eat as much as it liked. In such a situation one would easily predict that animals would increase their meal size and decrease their meal frequency for, by so doing, it would tend to decrease the amount of work required. And indeed this is exactly what does happen. The limiting factor on this effect would be the maximum time for which the animal could survive without feeding, which would be a function of such things as caloric concentration of the normal diet, and size and efficiency of the digestive tract. In the present situation however, one would make no such predictions.

Collier, Hirsch and Hamlin (1972) also studied the effect of a normal fixed ratio schedule on meal taking in freely feeding rats. The results are difficult to interpret as the observation was made on young animals whose baseline body weights were increasing over the duration of the experiment. Increased ratio lead to an obvious decrease in the rate of body weight increase after about FR20. A pattern of increasing meal size and decreasing meal frequency could be seen however up to this point. After this point, the decrease in meal frequency continued but the increase in meal size was less clear, and there was also an overall decrease in the number of reinforcements (single food pellets) which were being earned. This effect then is clearly similar to that found in the doves at the low fixed ratios, but there was no evidence of the pattern of increasing meal frequency at the higher ratios in the Collier et al. study.

An analysis of the present experiment, and also the Collier et al. fixed ratio experiment, simply in terms of the energy efficiency for the animal would predict no change in the aggregation of feeding activity. As a very obvious change does take place it must be attributed to some non-metabolic effect. Some aspect of the external situation is interacting with the animal's food intake control system to produce a spurious output.

There are two effects to explain then.

1) A moderate amount of work causes an increase in the animal's tendency to persist in feeding as indicated by a pattern of fewer, longer meals.
2) Further increases in fixed ratio size lead to a decrease in feeding persistance and increase in meal frequency.

10.5(a) Decrease in Meal Frequency at Low Ratios

It is felt that this effect lends weight to the interpretation prescribed earlier (chapter 6) of the reduction of meal frequency after trigeminal section and (chapter 7) as a result of feeding a less preferred food material. It was suggested quite plausibly (Kissileff, 1970) that there was an aversive component associated with work requirement, which is analogous to the reduction in perceived "pleasantness" of food as a result of trigeminal section. As argued earlier, when an animal finds itself in an ongoing situation in which feeding is perceived to be less pleasant, the energising effect of contact with food will result in an overall pattern characterised by an increased tendency to continue to feed once feeding has started, but a decreased tendency to initiate meals.

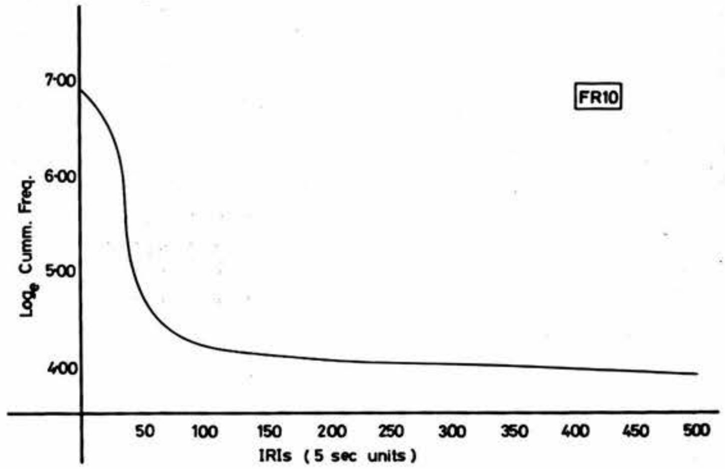
10.5(b) Increase in Meal Frequency at Higher Ratios

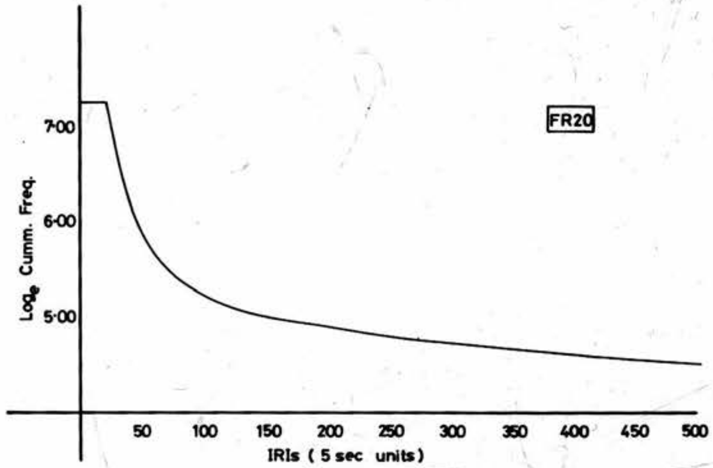
The interpretation of the increase in meal frequency at the higher ratios is also in terms of excitatory feedback and follows from the preceding discussion. It should be noted that the decrease in meal frequency at the low fixed ratios has been discussed in terms of the aversive nature of the work requirement, but that the effect of increasing meal frequency has been referred to as being associated with increase in "fixed ratio size." The reason for this can be explained by reference to the series of logarithmic survivorship plots showing the data from one animal collected at various different ratios (Figure 10.8). It can be seen that there is a certain minimum time after each reinforcement before which a further reinforcement cannot occur. This time is the sum of the reinforcement duration (7 seconds) and the time required by the animal to complete its run of responses. As the ratio size increases, the ratio of effort to return increases, but so does this minimum inter-reinforcement-interval (Figure 10.9). If it is argued that the sensory contact with food is the source of a positive feedback to the feeding motivation system which keeps the animal feeding in advance of its immediate needs, it will also be the case that this positive feedback will decay with a certain time course. An imposed delay in an on-going meal will thus allow time for this decay of excitation to take place and decrease the probability that the meal will continue to the next reinforcement. The result will be that the animal will break off from feeding sooner than it normally would and will require to re-initiate feeding behaviour more often.

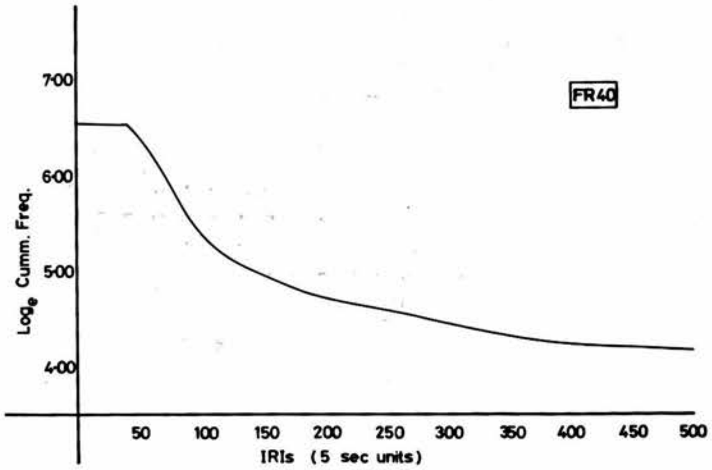
It is clear therefore that this particular experiment confounds the effects of work requirement and those of an enforced time out during a meal on the frequency and patterning of meal taking, and this suggests which should be done to isolate these effects.

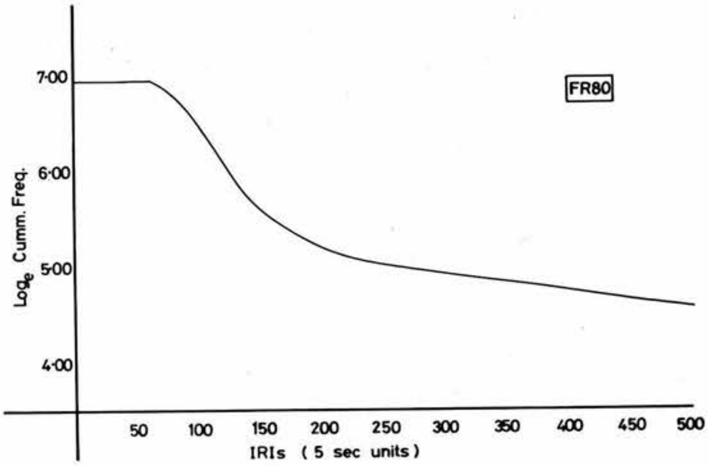
<u>FIGURE 10.8</u> (Two pages)

Example series of logarithmic survivorship plots of inter-reinforcement interval (IRI) from one of the birds, to show change in shape of curve and change in size of criterion IRI with ratio size.


FR10
Log$_e$ Cumm. Freq.
7·00
6·00
5·00
4·00
50
100
150
200
250
300
350
400
450
500
IRIs (5 sec units)


FR20
Log$_e$ Cumm. Freq.
7·00
6·00
5·00
50
100
150
200
250
300
350
400
450
500
IRIs (5 sec units)


FR40
Log$_e$ Cumm. Freq.
7·00
6·00
5·00
4·00
50
100
150
200
250
300
350
400
450
500
IRIs (5 sec units)


FR80
7·00
6·00
5·00
4·00
Log$_e$ Cumm. Freq.
50
100
150
200
250
300
350
400
450
500
IRIs (5 sec units)

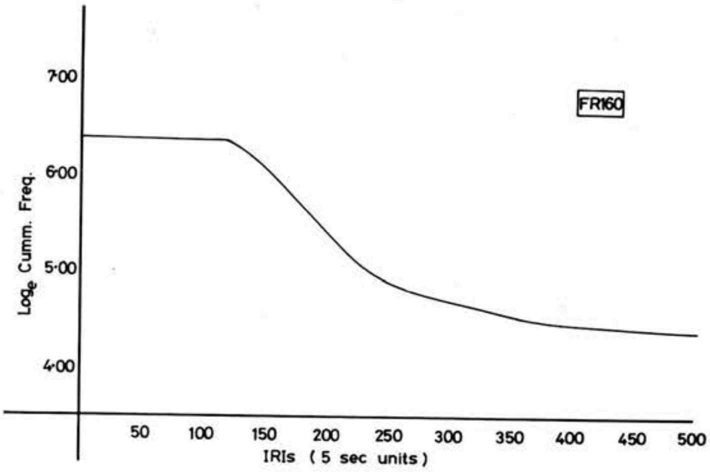
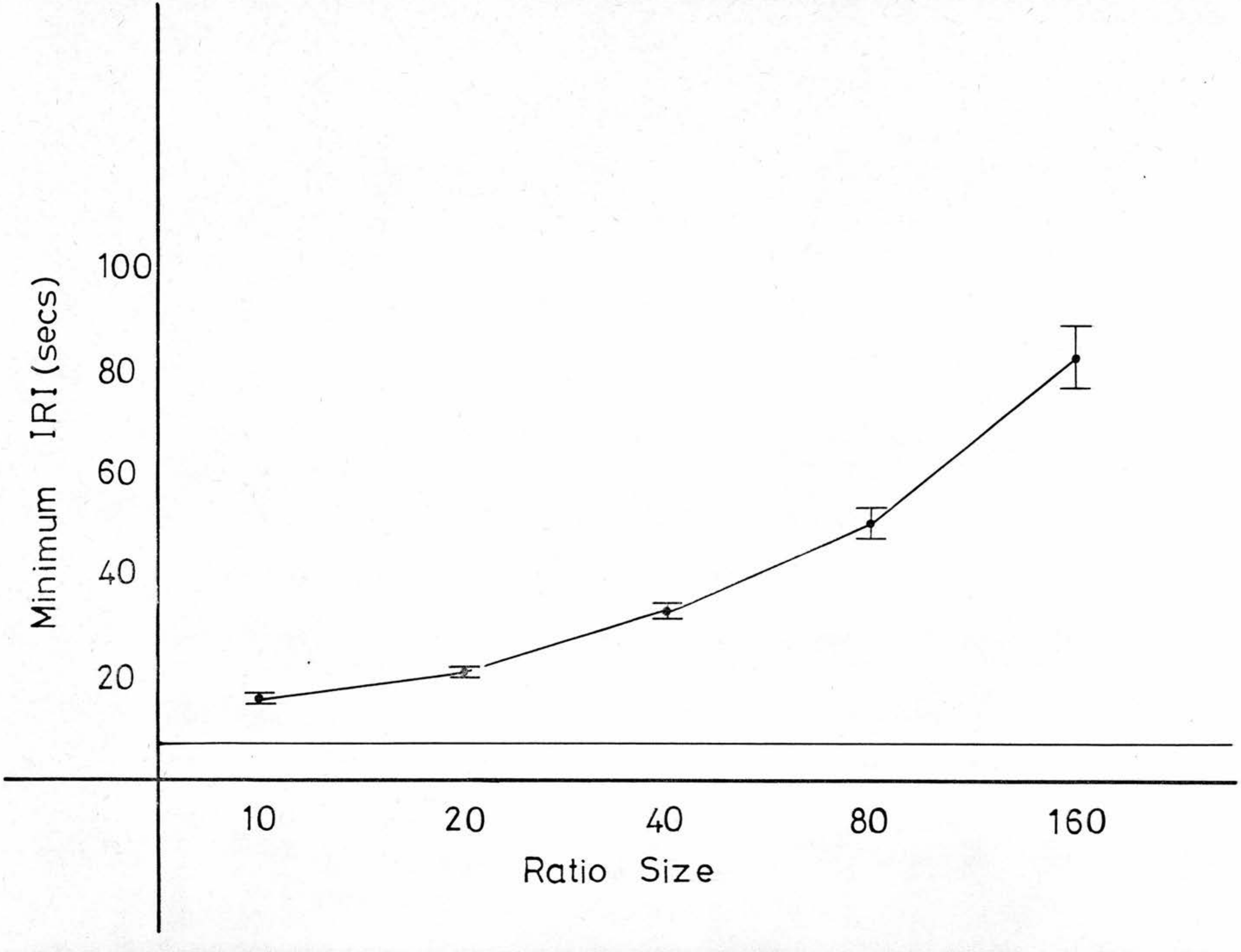

FR160
7·00
6·00
5·00
4·00
Log$_e$ Cumm. Freq.
50
100
150
200
250
300
350
400
450
500
IRIs (5 sec units)

FIGURE 10.9

Mean minimum inter-reinforcement interval (IRI) as a function of fixed ratio size (Table 22; Appendix II). Horizontal line (at 7 seconds) indicates duration of reinforcement for comparison. Bars indicate two standard errors.


Minimum IRI (secs)
100
80
60
40
20
10
20
40
80
160
Ratio Size

10.6(a) Changes in Rate of Feeding within a Meal

It was demonstrated earlier (chapter 9) that some effect of contact with food in the initial stages of a meal carries over from one bout to the next, so that there is a facilitation of the feeding tendency resulting in a progressive lengthening of feeding bouts. A possible point of comparison in the present operant study would be the rate of responding for successive reinforcements as a meal progresses.

Figure 10.10 shows the mean inter-reinforcement interval following the first five and preceding the last five reinforcements in all recorded meals of greater than 11 reinforcements at FR1. Several points are of interest. First, it is clearly the case that there is an acceleration in the rate of responding for food over the opening stages of the meal as indicated by a decrease in the inter-reinforcement interval. It can be seen too, that this acceleration is apparently continuing into the later stages of the meal with the first point of the "last" group being below the last point of the "first" group. Of particular interest is the fact that there is no sign of a deceleration in response rate at the end of the meal. Indeed the rate of pecking at the end is greater than at any time over the first five reinforcements and there is no significant downward trend over the last five. There is evidence then of a positive facilitatory effect on feeding behaviour as a meal begins but no behavioural evidence of any gradual build up of a negative, satiation effect.

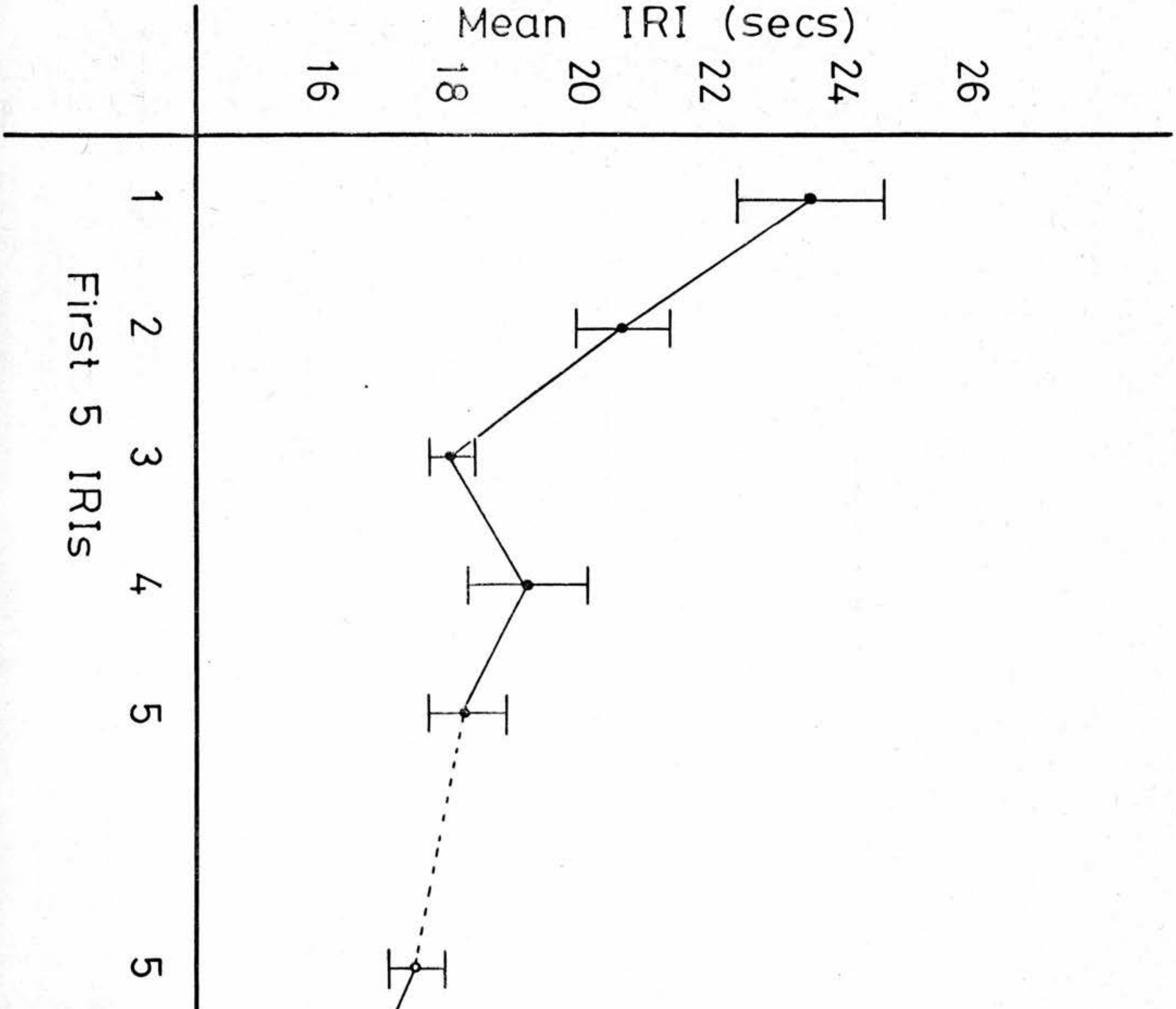
One would expect this pattern to be increasingly difficult to find however at the higher fixed ratios where it is suggested that

FIGURE 10.10

Grand means of the means for each bird, of the first five and last five inter-reinforcement intervals (IRI) in all meals of greater than 10 reinforcements recorded at fixed ratio of 1 (Table 26(a); Appendix II). Bars indicate two standard errors.

Friedmann's analysis of variance was used to test the significance of the change in IRI length with serial order in the meal.

	Friedmann's Chi	Significance ($p <$)
First 5	13.92	0.01
Last 5	7.55	N.S.


Mean IRI (secs)
16
18
20
22
24
26
1
2
3
4
5
First 5 IRIs
5
4
3
2
1
Last 5 IRIs

positive feedback effects are being allowed to decay because of the enforced time delay. Figure 10.11 shows the same data plotted out for each ratio, and this does seem to be the case. It should be noted however that as the ratio size increases, meals of greater than 10 reinforcements become more difficult to find. Absence of a significant facilitation then, could be due to increase in the variance of each data item. The data were reanalysed to look at the first five inter-reinforcement intervals in all meals of greater than five reinforcements. This obviously increases the number of data items, but does not change the overall picture (Figure 10.12). At the higher ratios we see that the decrease in inter-reinforcement interval is lost, and indeed there is a slight though non-significant trend towards a deceleration across the meal at FR160. Also, at the higher ratios we see that the inter-reinforcement intervals at the end of the meal are no longer obviously shorter than those at the start. This suggests again the overall deceleration taking place in the rate of responding for food across the meal at the higher ratios.

10.6(b) Feeding Pattern Correlation and Ratio

It was suggested earlier that animals characteristically feed in what might be described as an anticipatory mode. That is, food intake occurs in advance of immediate needs (chapter 9). This mode of feeding is brought about to a certain extent by the system which allows contact with food to enhance immediate, ongoing feeding tendency (chapter 9 and section 10.6(a)).

FIGURE 10.11

Inter-reinforcement interval serial order effect as a function of ratio size (Tables 26(a) to (h); Appendix II).

Friedmann analysis of variance was used to test the significance of the effect at the various ratios.

Fixed Ratio Size	First 5 Friedmann's Chi ($p <$)	Last 5 Friedmann's Chi ($p <$)
1	13.92 (0.01)	7.55 (N.S.)
5	16.16 (0.01)	7.88 (N.S.)
10	13.60 (0.01)	10.88 (0.05)
20	6.56 (N.S.)	7.04 (N.S.)
40	8.32 (N.S.)	2.88 (N.S.)
80	14.72 (0.01)	4.32 (N.S.)
160	4.64 (N.S.)	7.20 (N.S.)

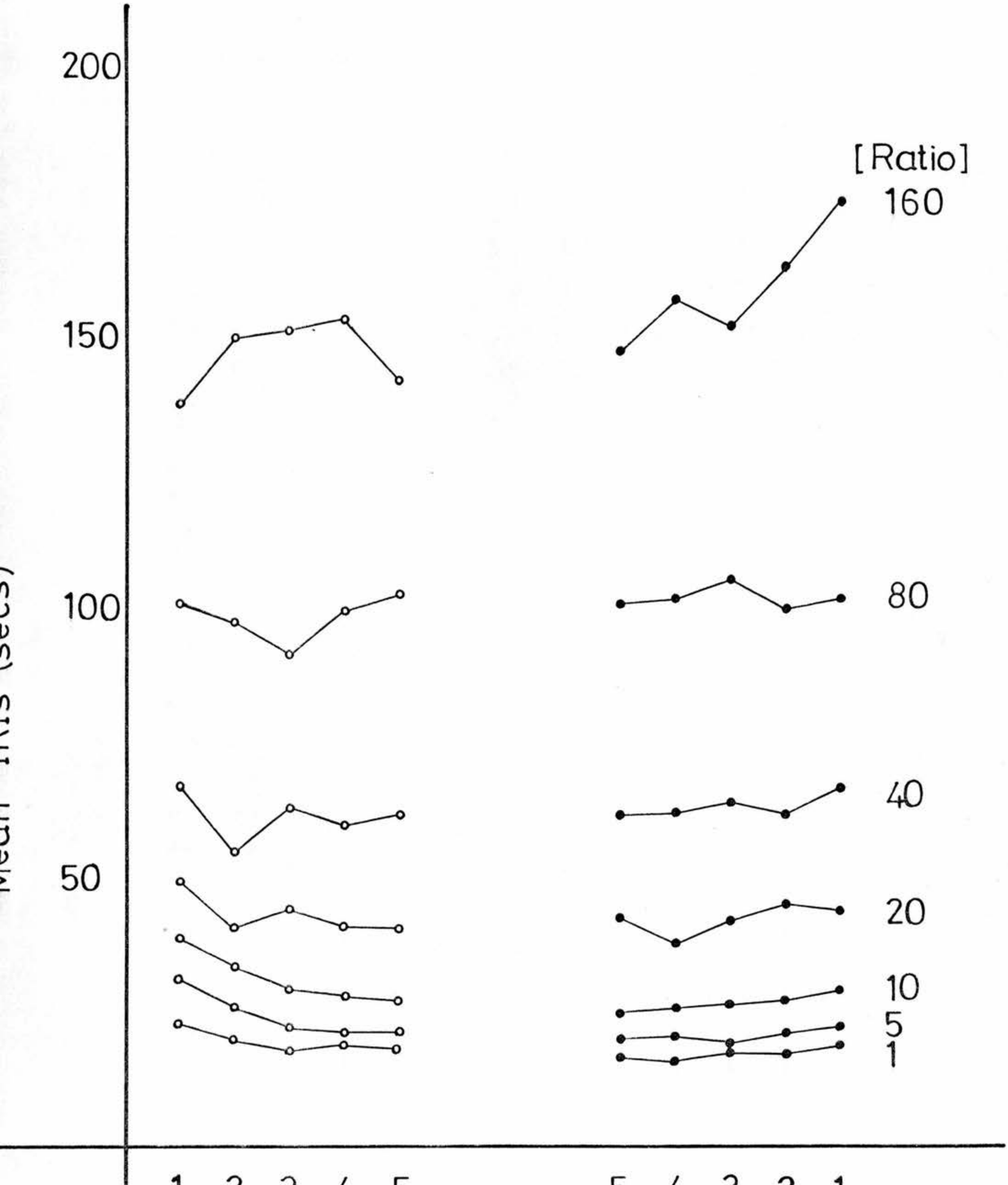
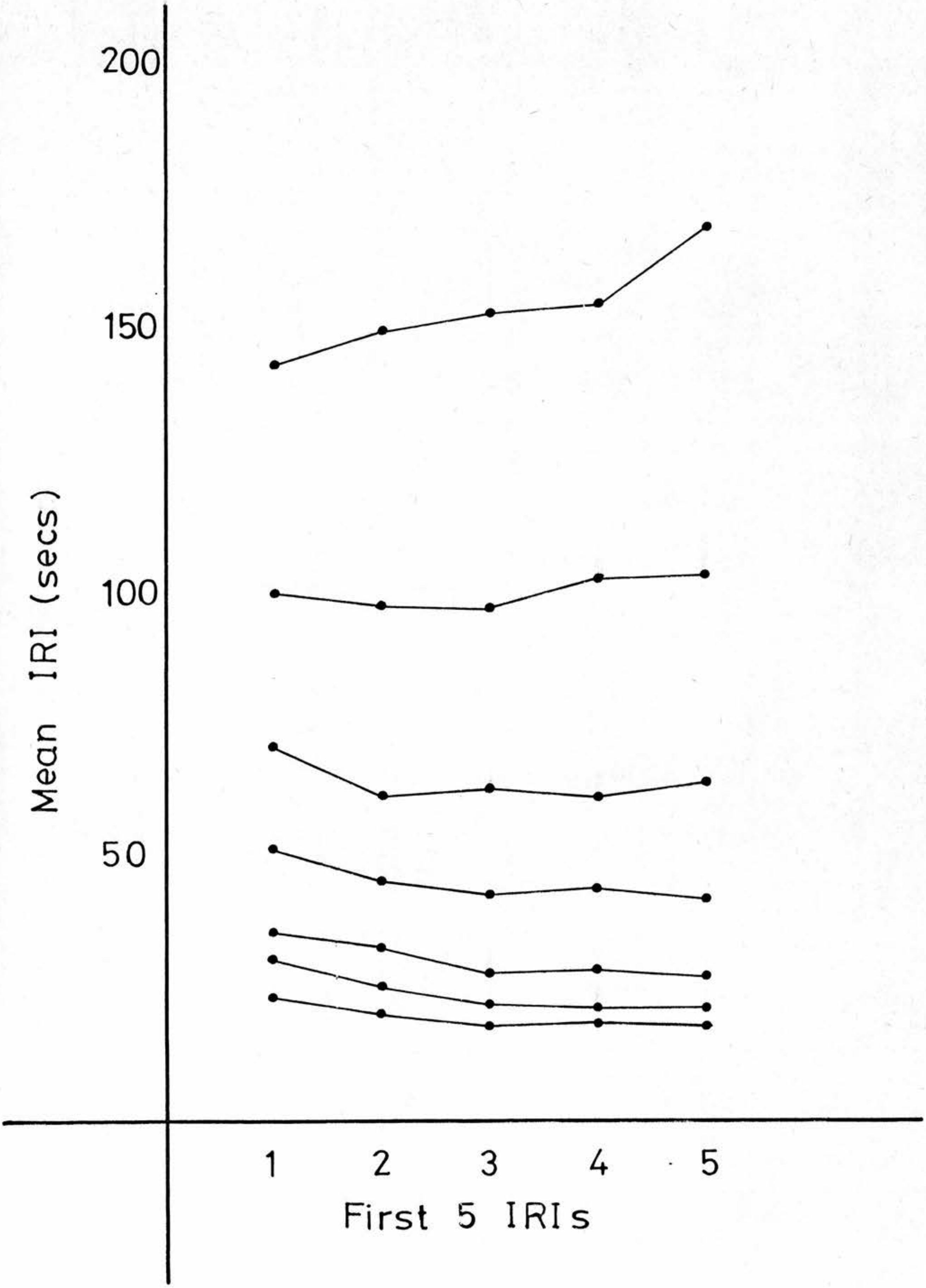

Mean IRIs (secs)
200
150
100
50
[Ratio]
160
80
40
20
10
5
1
1 2 3 4 5
First 5 IRIs
5 4 3 2 1
Last 5 IRIs

FIGURE 10.12

Inter-reinforcement interval serial order effect as a function of ratio size. Analysis as figure 10.11 but considering only first five inter-reinforcement intervals in all meals of greater than five reinforcements.

Friedmann analysis of variance was used to test the significance of the effect at the various ratios.

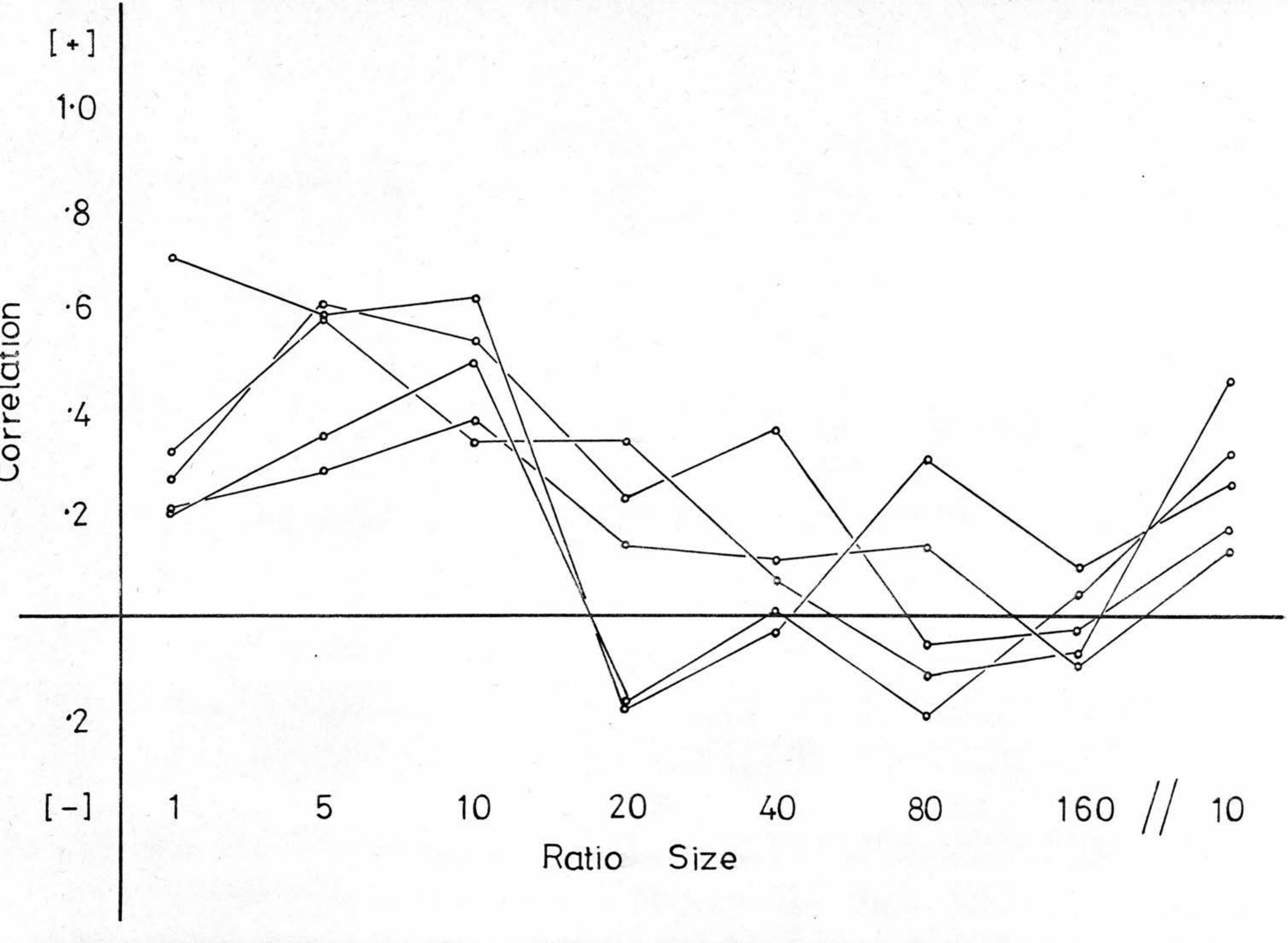
Fixed Ratio Size	Friedmann's Chi	Significance ($p <$)
1	12.32	0.02
5	16.28	0.01
10	13.05	0.02
20	10.40	0.05
40	10.24	0.05
80	8.80	N.S.
160	7.84	N.S.


200
150
100
50
Mean IRI (secs)
1
2
3
4
5
First 5 IRIs

The operation of this positive feedback system could be seen in the predominance of a post-prandial over a pre-prandial feeding pattern correlation in the normal, free-feeding behaviour of most animals. Implied then in the suggestion that an enforced "time out" is disrupting the normal operation of the positive feedback system is the prediction that the normal post-prandial meal taking pattern will also be disrupted. Figure 10.13 shows the post-prandial correlations computed for each animal at each of the ratios. These correlations, which were so elusive when the free feeding data were considered, appear to be very easy to find in the operant situation, and particularly when the data for FR5 and FR10 are considered. This might simply be due to the relative validity of the two methods of recording food intake; that a number of reinforcements earned is a better measure than time spent feeding. However, as a reinforcement is a certain time of access to the food, the food intake in the operant situation translates to a time spent feeding measure also, making this interpretation less likely. It has been suggested elsewhere (Zeigler, Green and Lehrer (1971) citing a personal communication with Collier) that post-prandial feeding pattern correlations are only found in recording situations which require the animal to engage in a certain amount of work. In view of Collier's emphasis on control of food intake by ecological factors (Collier et al., 1976), we might interpret this as indicating that the presence of a significant correlation is in some sense an "artefact" of the work, and therefore less interesting. However, it would be equally reasonable to suggest that the constraint imposed on the system by the work requirement interacts with the system to cause what is a basic underlying principle to show itself.

FIGURE 10.13

Post-prandial correlation as a function of fixed ratio size (Table 25; Appendix II).


Correlation
[+]
1·0
·8
·6
·4
·2
·2
[-]
1
5
10
20
40
80
160
//
10
Ratio Size

Although a moderate work requirement serves to excentuate the probability of obtaining a significant post-prandial correlation, the correlations disappear at the higher ratios. If the graph in figure 10.13 is compared with figure 10.4, it can be seen that the post-prandial correlations are appearing most clearly at the point where the feeding behaviour is most bouted. As discussed above, this reduction in meal frequency and associated increase in the size of the post-prandial correlations is slightly paradoxical in that it is suggested that the decrease in meal frequency is a result of there being aversive components associated with feeding when a work requirement is imposed. That is, the animal seems to persist longer in an activity which it finds to be less pleasant, and indded (as indicated by the large post-prandial correlations) persists in advance of immediate needs. This can be compared with the finding of Richter (1927) that rats will decrease their frequency of meal taking (and therefore presumably increase the meal size, as there is no reason to expect a decrease in overall intake) if housed in cages allowing them to engage in a large variety of other behaviours like gnawing, climbing, wheel running and sexual behaviour. These animals, with other alternative activities to be envolved with, might be seen as attributing less overall "hedonic weight" to feeding activity. The response to this is to persist in feeding to a greater degree than before rather than (as would be equally plausible) to break off more often to attend to these other possibilities (Petersen, 1975). If such a reduction in meal frequency is associated not only with an increase in meal size, but also a post-prandial correlation, the animal has obviously recalibrated its feeding control system to anticipate longer inter-feeding intervals rather than eating larger amounts in response to longer periods of non-feeding.

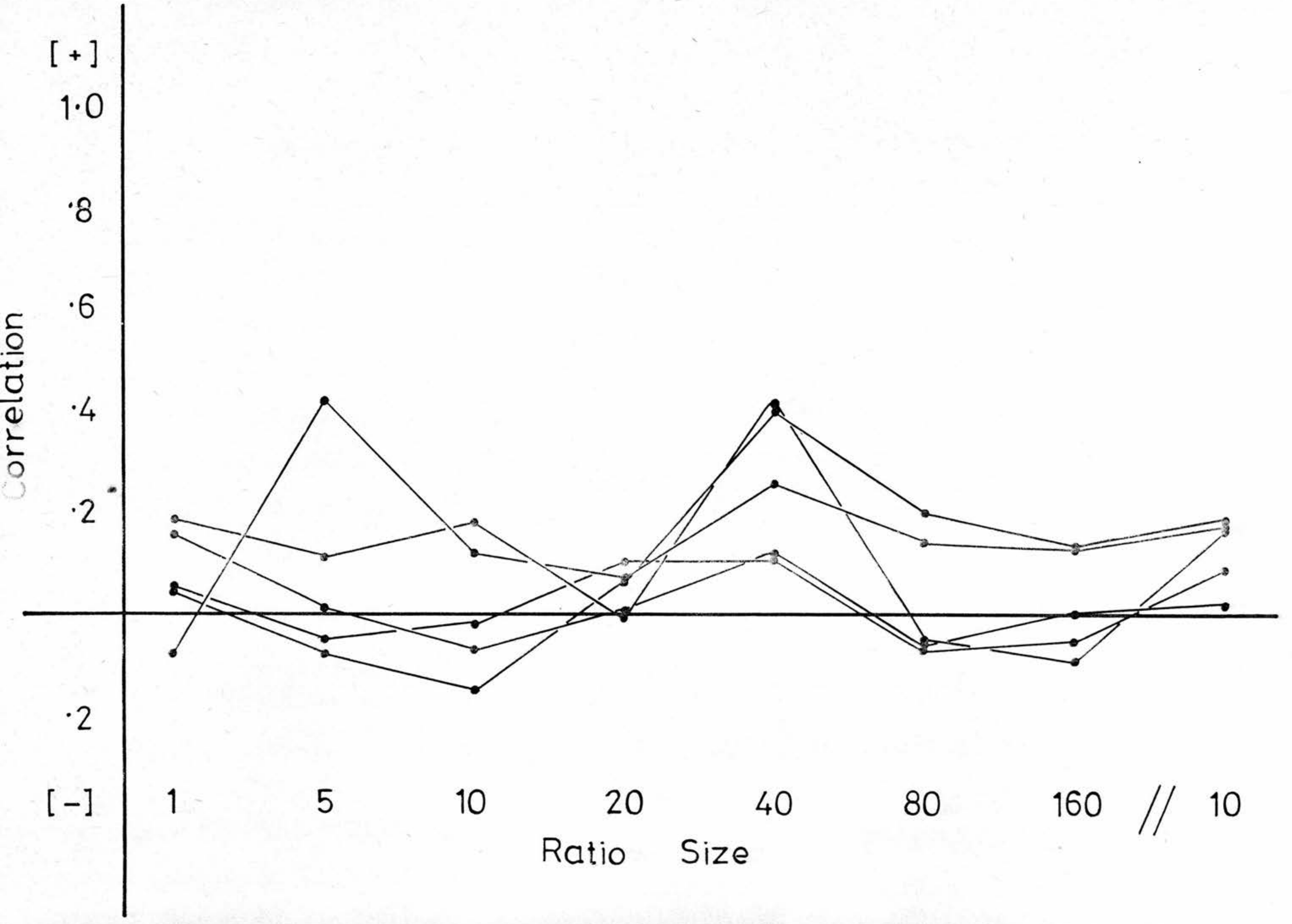
As the ratios increase on the other hand, the correlations decrease, so that over the range where it was argued that positive feedback processes were contributing less and less to the continuation of the meal, the animals show less tendency towards anticipatory feeding (in the sense of significant post-prandial correlations). Force to this argument is given by the fact that the pre-prandial correlations (Figure 10.14) not normally found in the free feeding animals or at the lower ratios in this study, begin to appear at the higher ratios. Evidence suggests then, that the animals are feeding not in anticipation of needs at the higher ratios, but in restoration of deficit.

10.6(c) Logarithmic Survivorship Plots

Another interesting piece of evidence comes from the examination of the shapes of the logarithmic survivorship plots of inter-reinforcement interval at various ratios (Figure 10.8). At the lower ratios the plots are basically two intersecting straight lines which may be described as indicating the presence of two distinct populations of intervals; those between groups of reinforcements which we have called meals, and those which are pauses within meals. At the higher ratios however the plot divides into three distinctly straight portions indicating that another "class" of intervals is present. It becomes a matter of definition as to whether one describes this third class of intervals as indicating that individual meals are grouped,

FIGURE 10.14

Pre-prandial correlation as a function of fixed ratio size (Table 24; Appendix II).


Correlation
[+]
1·0
·8
·6
·4
·2
·2
[−]
1
5
10
20
40
80
160
//
10
Ratio Size

or that there exists a population of unusually large pauses within ongoing meals. The later definition was used here as it was intended to show that even using this all inclusive criterion, meal frequency could still be seen to increase with increasing ratio. On the basis of this description then, there appears to be two classes of within meal interval. Talking again in terms of probabilities, we can see that immediately after a reinforcement has been consumed there is a high probability that the bird will continue to respond and earn a further reinforcement. If a pause lasts for a certain length of time however, the bird passes into a state of intermediate probability of reinitiation of feeding. This can be seen as the operation of the two mechanisms of incentive and deficit (Sibly, 1975) controlling the initiation of a feeding bout. The shorter class of within meal intervals (as found in the normal low ratio or free availability case) indicate an immediate continuation of feeding motivated by after-effects or positive feedback from consumption of the last reinforcement earned. The class of larger within meal intervals are occasions on which the animal is not immediately stimulated to return to feed, but is goaded to do so by accumulated deficit. That is, these intervals represent not the continuation of feeding but the reinitiation of feeding after a brief pause, resulting from the "realization" by the animal that the meal has terminated too soon.

A similar tight grouping of short feeding periods was described by Kissileff (1970) in an operant study of feeding patterns in rats. This pattern appeared even with continuous reinforcement, and was described in terms of breaking off from feeding too soon as a result of the aversive nature of the work requirement, and being forced to reinitiate feeding immediately to ensure that sufficient food was eaten to meet the animal's needs. As noted above, it is a matter of definition whether Kissileff's data indicates a pattern of very frequent, small meals or one of large pauses within meals.

Another study should be mentioned as appearing to be in conflict with the present data and the decay of excitation hypothesis discussed above. Levitsky (1974) required rats to hold down an operant bar for certain times ranging from 0 to 50 seconds in order to obtain a food reward. This was seen as being a manipulation of food availability. A delay then, was interposed in the ongoing meal in a more direct way than in the present study. Levitsky found an increase in meal size and a decrease in meal frequency with increasing delay. Reference to figure 10.9 will indicate that the delays involved in the present study could be as long as about 95 seconds, so that a 50 second delay would certainly be within the range which a decay of excitation idea would predict an increase in meal frequency. Two points should be made however about Levitsky's results.

1) This decrease in meal frequency with increasing delay may be analogous to the decrease in meal frequency found at the low fixed ratios in the present study. That is, even at the low fixed ratios the delay rather than the work may be the important factor. Perhaps both are perceived by the animal as indicating a low availability of food thus encouraging the animals to persist in feeding to a greater degree.

2) It should be noted that the significance of a certain time delay

may differ for the dove or the rat, so that a delay of 50 seconds may not be "as long" for a rat as for a dove with reference to meal taking behaviour. Levitsky's criterial inter-meal interval was 15 minutes, whereas the average interval size used to define dove meals in the present study was about 1 minute. Thus the data collected by Levitsky probably only covers the range of relative time over which a decrease in meal frequency was found in the present study.

10.7 Chapter Summary

The patterns of feeding behaviour shown by doves at various fixed ratio sizes in a continuous, free operant situation were observed.

As the fixed ratio size increased, two distinct patterns were seen.

1) At the low ratios, there was an increase in meal size and a decrease in meal frequency with increased ratio. This was associated with an increase in the size of the post-prandial feeding correlation.

2) As the ratio increased above about FR10 or 20, the increases lead to decreased meal size and increased meal frequency. Post-prandial correlation size decreased and some evidence was seen of significant pre-prandial relationships.

The decreased meal frequency (1) was explained in terms of the aversive nature of the work requirement, and was seen as analogous to the decrease in meal frequency as a result of trigeminal nerve section or of feeding a less preferred food. The increased meal frequency (2) was seen as being a result of the pre-mature termination of meals due to a decay, with time, of the positive feedback which normally leads to their continuation.

Some aspects of the changes in the pattern of within meal inter-reinforcement intervals with ratio size were shown to be in line with this decay of excitation hypothesis.

SUMMARY

11.1 Feeding and External Information

Ross, Goldstein and Koppel (1962) showed that the amount of food which would be eaten by domestic chickens in a test situation was proportional to the total amount offered where the latter was always big enough to place no constraints on the former. That is, external sensory information about the nature and availability of food can greatly influence feeding behaviour and food intake. Another example of external stimulation of food intake comes from the phenomenon of social facilitation (Zajonc, 1965). This is a vast topic of social psychology involving the effects, on various behaviours, of the presence of an audience or a co-acting individual. With particular reference to feeding behaviour, intake of a satiated subject can be stimulated by the presence of an actively feeding companion. This has been demonstrated in chickens (Tolman, 1964, 1965; Rajecki et al., 1976), Ring doves (Wright, 1975), dogs (Ross and Ross, 1949(a), (b); James, 1953, 1960; James and Gilbert, 1955; James and Cannon, 1956), rodents (Harlow, 1932; Drew, 1932; Liebelt, 1963) and primates (Harlow and Yudkin, 1933). Feeding in response to others feeding can be seen to be an important behavioural mechanism for flocking birds (Murton, 1965, 1971; Murton et al., 1971), again concerned with appropriate responding to the immediate availability of food.

The theme of the present study has been the way in which the perceived nature of the food material offered to birds contributes to the organisation of the pattern of food intake. In particular three manipulations (the reduction in sensory feedback by section of the trigeminal nerve known to mediate what Edinger (1908) termed "oral sense" in birds, the provision of a less preferred food and the imposition of a minimal work requirement), which might all be considered as changes which would reduce the perceived "Pleasantness" of the feeding situation for the animal, were investigated. In all of these three cases (considering for the present the low ratios of work requirement, the higher ratios having a different interpretation, as described in chapter 10) the most obvious effect of the change in the perceived nature of the feeding situation was that the birds fed in fewer, larger meals over the day than in the corresponding control condition.

This change in meal frequency is seen as being brought about by changes in the probability of initiation or continuation of feeding. In the natural, free foraging situation where a number of different foods are available, it would be expected that the continuation of a feeding bout which was initiated by the animal coming upon food (Landless, 1975) would be determined by the perceived pleasantness of the food material. That is, a large amount of a highly preferred, pleasant food material would be consumed, whereas the animal would not persist in feeding for long on an unpleasant material. With a sensory system evolved in a particular natural environment, such a hedonistic mode of operation of the feeding control system would make perfect sense. What an animal perceives as being pleasurable can be defined as that which is physiologically appropriate. What is "good" in the sense of survival is perceived by the animal to be "good" in the hedonic sense.

In the laboratory situation however, where only one food material is available to the animal or only one fixed regime of availability is in force, the animal is able to predict the sensory "return" to be expected from a meal. The perceived (or predicted) quality of the food then becomes more important for decisions about initiation of feeding behaviour. Thus decreases in the predicted pleasantness of the feeding situation would lead to a reduced probability of initiation of a meal.

11.2 Long- and Short-term Control

The short-term control of feeding behaviour (the response to immediately available food) is controlled chiefly by this sensory information. For example, satiation is not an absolute thing, but is with reference to one particular food material. We may be quite "full" at the end of the main course of a meal, and yet able to consume a sweet course also. The availability of a large number of highly palatable foods for a rat may lead to obesity (Sclafani, 1976; Sclafani and Springer, 1976).

Long-term control mechanisms on the other hand, require to ensure an adequate supply of energy and nutrients for the animal to survive. Thus a decrease in the probability of the initiation of a meal brought about by considerations of diet palatability, must be associated with an increase in meal size brought about by considerations of energy need. This distinction is similar to that made by Sclafani (1976) between "hunger" and "appetite." Hunger is defined as the motivation to feed aroused by internal, physiological state, whereas appetite is that motivation which results from external sensory information.

Thus changes in feeding pattern in response to sensory quality of the feeding situation are brought about by an interaction of these two considerations. Also included in the "calculation" will be the need to feed in advance or anticipation of future requirements. Thus an increase in meal size on a less preferred food would be in anticipation of the predicted reduction in the probability of feeding initiation. The correct pattern would, of course, take a certain amount of time to become established. This can be seen in the inevitable, brief drop in food intake and body weight on the introduction of a novel food or an increase in work requirement.

11.3 The Breakdown of the System

This mechanism obviously begins to break down when the degree of reduction in palatability of a diet is so great that the overall body weight of the animal is no longer maintained (Keesey and Boyle, 1973; Levitsky, 1974). Another interesting example of the breakdown of this control system comes from the operant study of feeding behaviour reported in chapter 10. At the low ratios of operant responses to food reward the meal size of the birds increases and the meal frequency decreases, as compared with the continuous reinforcement situation. As the ratio continues to increase however, there is an increase in meal frequency and a decrease in meal size. It was argued that the important factor was the time delay between reinforcements at the high ratios. A positive feedback (Wiepkema, 1971) associated with the contact with the food helps to maintain ongoing feeding from one bout (or reinforcement) to the next. A delay interposed between reinforcements (by the time taken to complete the necessary number of responses) allows this excitation to decay. Thus meals terminate prematurely and have to be reinitiated more frequently so that the overall amount of food ingested is maintained. Associated with this increase in meal frequency is the disappearance of the anticipatory (post-prandial) relationship between meal size and intermeal interval, and there is also some evidence that regulation may be taking place pre-prandially. The facilitation in the rate of responding for food into a meal (argued to be evidence of this positive feedback meahanism) also becomes more difficult to find as the ratio size increases. It was further argued that there was evidence in the feeding behaviour of the animals at high ratios for two distinct populations of within meal interval, which were indicative of the existence of two mechanisms controlling food intake. The shorter intervals represented the reinitiation of feeding within a meal in response to the incentive (Sibly, 1975) or appetite (Sclafani, 1976) factors determined by the sensory feedback from the food or overall feeding situation. The larger pauses indicated reinitiation of feeding goaded by deficit (Sibly, 1975) or hunger (Sclafani, 1976). It seems likely that such deficit mechanisms play little part in the short-term control of feeding in the freely feeding animal.

11.4 Sensory Stimulation and Motivation

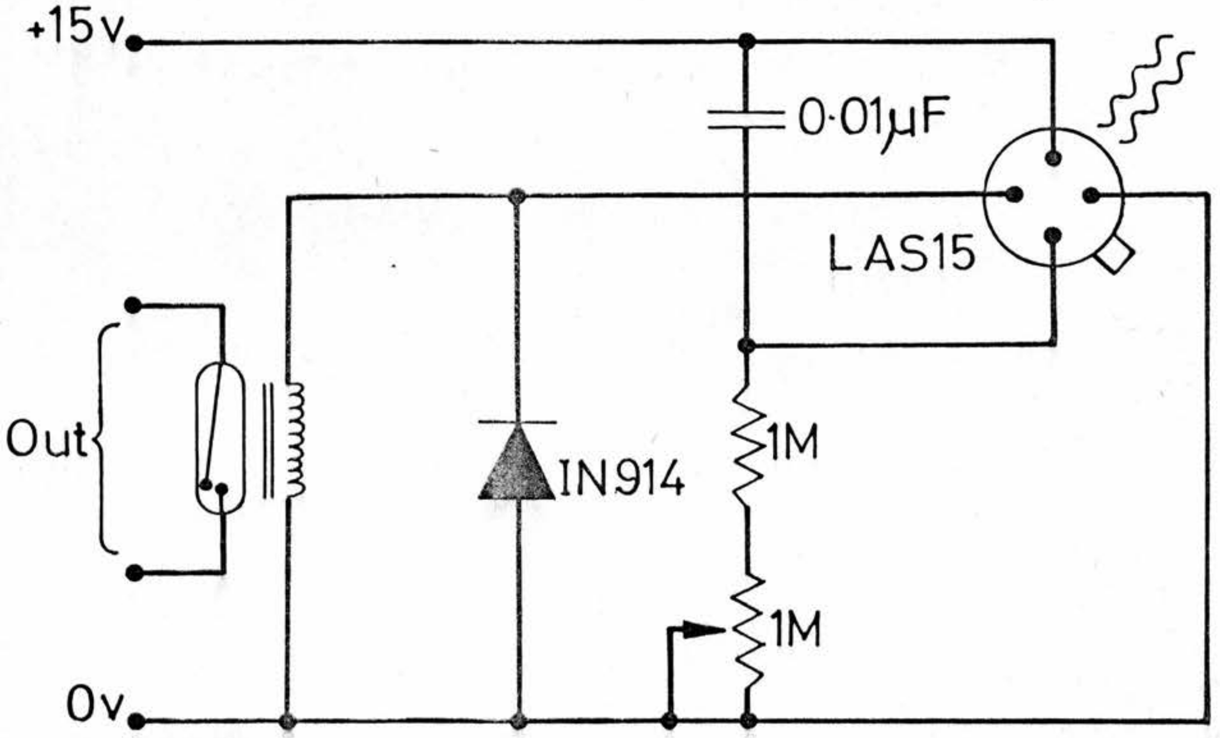
The observations which were formalized by Wiepkema (1971) appear to have been around for quite some time. Indeed Shufford (1959) showed the same increase in the rate of feeding at the initiation of a meal as was taken by Wiepkema to provide important insight into the underlying motivational processes. Pfaffman (1960) discussed the role of sensation in the controlling, but also the motivating of behaviour.

> My basic theme has been that sensory stimulation "qua stimulation" plays a significant role in the motivation as well as guidance of behaviour - euphemistically we might say, in controlling behaviour for the "Pleasures of Sensation."
>
> Pfaffman (1960)

Yet it is only in recent years that the importance of sensory information has been generally recognized in the control of feeding motivation. The serving of the homeostatic needs of the organism has always been seen as the one factor of overriding importance. This can perhaps be explained in terms of the words and concepts used to convey these ideas. Words like "pleasure" and "hedonism" must have been regarded with great suspicion by people attempting to formulate models of mechanisms controlling behaviour. Yet when those ideas gained the respectability, which description in terms of modern control theory allowed (McFarland, 1971; Toates, 1975; Toates and Archer, 1978), without actually changing in form they become acceptable and began to be incorporated within the physiological theories of motivation (Carlson, 1977).

APPENDIX I

Circuit diagam of photoswitch device used to monitor feeding behaviour. The sensitivity of the circuit can be controlled by the setting of the 1M variable resister. The light beam was provided by a 24 volt pannel lamp running at 15 volts.
(My thanks to Mr. D. Wight.)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APPENDIX II

Tables of Data

Appendix II - TABLES of DATA

Table

TABLE 1 (a)

Feeding Monitor Validation

(a) **Bird 1**	Amount Eaten (Grams)	Time Spent Feeding(Secs.)	No.of Bouts
Day 1	1.4	172.1	4
	0.0	0.0	0
	1.2	377.6	12
	0.9	230.4	5
	1.1	360.3	10
	0.0	22.0	1
	0.9	173.4	7
	2.1	383.1	10
	1.0	153.4	6
Day 2	0.7	158.2	5
	0.0	10.4	2
	1.1	298.4	8
	0.9	199.3	6
	1.2	274.6	6
	0.0	0.0	0
	3.0	366.5	12
	1.0	176.2	5
	0.0	12.8	1
Day 3	1.2	99.6	6
	0.5	73.3	3
	0.0	0.0	0
	1,6	342.8	10
	1.1	295.1	7
	0.3	85.7	5
	2.6	353.2	11
	0.9	178.6	6
	0.2	28.7	3

Correlations: Amount and Time - Pearson Product Moment
Correlation Coefficient
0.8504 ($p < 0.01$)

Amount and Bouts - Spearman Rank Order
Correlation Coefficient
0.8632 ($p < 0.01$)

Mean rate of Food Intake: 0.31 Grams/min.

TABLE 1 (b)

(b) Bird 2	Amount Eaten (Grams)	Time Spent Feeding(Secs.)	No.of Bouts
Day 1	3.0	71.2	12
	1.1	51.0	3
	1.0	52.4	5
	0.0	4.2	1
	0.0	0.0	0
	0.9	21.5	1
	2.3	49.4	4
	1.6	46.7	4
	0.2	18.8	2
Day 2	1.4	59.7	6
	1.1	44.3	4
	0.9	60.5	8
	0.0	1.8	1
	0.7	27.5	3
	0.0	0.0	0
	3.2	68.2	10
	1.5	42.9	3
	0.8	29.1	2
Day 3	1.6	63.7	7
	0.0	7.8	1
	1.7	58.1	6
	0.8	20.2	1
	0.8	47.4	3
	0.2	12.2	1
	2.7	58.6	8
	1.6	47.9	9
	0.6	31.8	3

Correlations: Amount and Time - 0.8512 ($p < 0.01$)

Amount and Bouts - 0.8644 ($p < 0.01$)

Mean Rate of Fodd Intake: 1.80 Grams/min.

TABLE 1 (c)

(c) Bird 3	Amount Eaten (Grams)	Time Spent Feeding(Secs.)	No.of Bouts
Day 1	1.4	32.8	7
	1.9	59.6	6
	1.0	62.1	7
	0.2	9.7	1
	0.8	13.8	1
	0.0	0.0	0
	1.2	40.4	4
	0.9	27.4	3
	1.0	45.7	4
Day 2	0.5	21.2	3
	1.5	47.2	5
	0.0	3.4	1
	1.8	65.2	8
	0.7	20.6	3
	0.0	0.0	0
	2.1	57.7	6
	1.1	35.7	5
	0.2	12.8	1
Day 3	1.2	67.2	10
	0.0	0.0	0
	0.8	25.2	3
	1.0	44.9	7
	1.1	34.4	8
	0.5	18.7	3
	1.8	53.2	5
	1.0	48.9	5
	0.7	26.8	3

Correlations: Amount and Time - 0.8810 ($p < 0.01$)

Amount and Bouts - 0.8537 ($p < 0.01$)

Mean Rate of Food Intake: 1.65 Grams/min.

TABLE 1 (d)

(d) **Bird 4**	Amount Eaten (Grams)	Time Spent Feeding (Secs.)	No.of Bouts
Day 1	1.4	99.2	5
	0.2	10.8	1
	0.5	31.4	2
	0.2	7.7	1
	1.6	390.0	24
	0.0	0.0	0
	0.0	3.1	1
	1.3	63.9	6
	0.3	21.6	2
Day 2	0.7	42.1	6
	1.1	85.9	8
	0.5	29.9	8
	0.0	6.1	1
	1.3	104.8	11
	0.8	66.3	5
	2.2	196.4	13
	0.0	0.0	0
	0.2	15.8	1
Day 3	1.0	167.2	14
	1.0	71.4	8
	0.3	19.2	3
	0.0	5.7	1
	0.6	22.8	2
	1.4	78.3	5
	1.8	74.3	6
	0.7	41.2	6
	0.0	0.0	0

Correlations: Amount and Time - 0.7380 ($p < 0.01$)

Amount and Bouts - 0.8930 ($p < 0.01$)

Mean Rate of Food Intake: 0.69 Grams/min.

TABLE 2

Feeding Behaviour in Intact Birds - Summary Table

	Meal Frequency		IFI Criterion (Secs.)	Time Spent Feeding (Mins.)	Mean Meal Size(Secs)	Mean Meal Duration (Secs.)
	Log	250				
M108G	18.9	12.6	45	32.0	101.5	145.1
M201G	21.3	16.6	50	23.7	66.8	102.8
M211G	13.3	11.0	25	9.3	41.9	102.1
M284G	34.6	19.9	40	23.4	40.6	62.3
M339B	17.0	12.3	25	12.7	44.8	78.3
M574S	23.0	17.7	45	30.7	80.1	101.2
M76G	15.6	11.6	50	11.5	44.2	116.4
F196W	21.3	15.3	45	23.2	65.3	94.3
F211B	41.6	27.6	25	18.4	26.6	45.3
F252G	29.6	15.3	25	12.5	25.4	51.1
F36G	20.7	17.6	110	13.7	39.6	120.8
F479S	13.7	11.0	140	17.7	77.4	216.2
F687S	16.4	13.9	60	9.5	34.8	92.4
F91W	23.0	13.0	75	13.6	35.5	107.1
Means:	22.14	15.38	54.3	18.0	51.75	102.5
S.D.	8.117	4.445	33.790	7.507	22.701	42.588
S.E.	2.251	1.233	9.372	2.082	6.296	11.812

TABLE 3 (a)

Time Spent Feeding as % of Daily Total

Hours of Day Bird	9	10	11	12	13	14	15	16	17
M108G	16	7	8	13	11	28	7	1	6
M201G	17	6	6	4	9	3	14	29	12
M211G	17	4	7	4	12	6	26	13	9
M284G	7	7	5	17	14	25	21	4	0
M339B	21	7	12	16	16	22	4	2	0
M574S	16	7	7	10	8	9	22	13	5
M76G	14	12	7	4	18	33	12	0	0
F196W	15	6	5	5	9	19	30	9	2
F211B	25	9	10	11	9	11	13	6	6
F252G	26	2	7	7	5	6	9	26	12
F360	13	10	5	9	15	19	24	5	0
F4795	19	5	5	7	3	21	30	8	0
F6875	16	18	11	12	14	15	9	6	0
F91W	14	6	3	4	6	5	13	20	28
Mean	16.8	7.6	7.0	8.8	10.6	15.8	16.7	10.1	5.7
S.D.	4.849	3.877	2.542	4.526	4.413	9.437	8.641	9.105	7.829
S.E.	1.345	1.075	0.705	1.255	1.224	2.617	2.396	2.525	2.171

TABLE 3 (b)

% Time Spent Feeding - Hour by Hour Comparisons

Hours of Day	N	Wilcoxen 'T' (two-tailed)	Significance (p <)
9			
	13.0	1.5	0.01
10			
	11.0	33.5	N.S.
11			
	12.0	21.5	N.S.
12			
	13.0	43.5	N.S.
13			
	14.0	21.5	N.S.
14			
	14.0	47.0	N.S.
15			
	14.0	24.0	N.S.
16			
	12.0	14.5	0.02
17			

TABLE 3 (c)

Mean Meal Size in Each Hour of the Day

(Size in Seconds)

Hours of Day	9	10	11	12	13	14	15	16	17
Birds									
M108G	85	67	68	138	106	136	102	31	94
M201G	61	66	95	28	72	34	76	144	37
M211G	22	38	37	144	23	61	78	77	49
M284G	18	38	20	49	56	60	50	18	0
M339B	37	33	43	70	59	46	27	22	0
M594S	53	62	48	91	49	100	162	101	46
M76G	31	76	32	31	47	63	33	0	0
F196W	75	47	33	37	53	99	101	47	38
F211B	36	25	33	34	20	27	32	21	12
F252G	35	14	23	23	20	32	14	31	19
F36G	39	41	36	24	46	33	67	34	0
F479S	72	39	44	43	49	98	148	88	0
F687S	31	56	35	46	29	33	30	20	0
F91W	66	36	27	26	35	39	41	46	22
Means	47.2	45.6	41.0	56.0	47.4	61.5	68.0	48.6	22.6
S.D.	21.217	17.610	19.521	40.643	22.997	33.927	45.788	39.839	27.703
S.E.	5.885	4.884	5.414	11.272	6.375	9.409	12.699	11.049	7.683

TABLE 3 (d)

Mean Meal Size - Hour by Hour Comparisons

Hours of Day	N	Wilcoxen 'T'	Significance (p <)
9			
	14.0	46.0	N.S.
10			
	14.0	39.5	N.S.
11			
	13.0	29.5	N.S.
12			
	14.0	48.0	N.S.
13			
	14.0	25.5	N.S.
14			
	14.0	35.5	N.S.
15			
	14.0	21.5	N.S.
16			
	13.0	11.0	0.01
17			

TABLE 3 (e)

Mean Interval Length in Each Hour of the Day

(Length in Seconds)

Hours of Day	9	10	11	12	13	14	15	16	17
M108G	1373	1496	1416	2362	793	1015	2217	4067	77
M201G	2054	3160	3811	1945	3222	1649	1203	1039	636
M211G	2787	5160	9272	2975	3508	1452	1404	1763	1397
M284G	735	1477	908	814	908	423	487	786	3600
M339B	1564	1749	1816	1360	1594	1637	1024	4717	3600
M574S	1246	2647	1670	1851	1348	1601	1702	1486	1087
M76G	1893	4025	2635	2370	1141	590	1593	3600	3600
F196W	1435	2784	1329	2740	1183	1821	792	969	1479
F211B	921	726	1193	768	994	616	805	959	970
F252G	2761	1484	2247	2300	1027	2180	638	502	812
F360	2071	2504	2484	1276	1535	745	1029	431	3600
F479S	1989	1465	4005	2173	3316	555	989	499	3600
F687S	1738	1959	2087	2680	1033	1317	1755	275	3600
F91W	1388	4535	3749	3242	2243	2640	552	963	714
Means	1711.1	2512.2	2759.7	2061.0	1703.2	1302.9	1156.4	1575.4	2055.1
S.D.	603.064	1307.960	2124.320	778.877	963.958	672.312	514.045	1456.150	1426.950
S.E.	167.260	362.763	589.180	216.022	267.354	186.466	142.570	403.863	395.765

TABLE 3 (f)

Mean Interval Length - Hour by Hour Comparisons

Hours of Day	N	Wilcoxen 'T' (two-tailed)	Significance (p <)
9			
	14.0	18.0	0.05
10			
	14.0	52.0	N.S.
11			
	14.0	32.0	N.S.
12			
	14.0	35.0	N.S.
13			
	14.0	36.0	N.S.
14			
	14.0	49.0	N.S.
15			
	14.0	39.0	N.S.
16			
	13.0	38.0	N.S.
17			

TABLE 3 (g)

% Time Spent Feeding - Hour by Hour Comparisons

Data synchronised by 'Peak' Hour

Hours of Day (Relative to 'Peak')	N	Wilcoxen 'T' (two-tailed)	Significance (p <)
- 5			
	9.0	11.5	N.S.
- 4			
	12.0	45.5	N.S.
- 3			
	13.0	31.5	N.S.
- 2			
	12.0	19.5	N.S.
- 1			
	13.0	0.0	0.01
'Peak'			
	13.0	0.0	0.01
+ 1			

Note: Item F91W was excluded as it contained no post-peak datum.

TABLE 3 (h)

Mean Meal Size - Hour by Hour Comparisons

Data Synchronised by 'Peak' Hour

Hours of Day (Relative to 'Peak' Hour)	N	Wilcoxen 'T' (two-tailed)	Significance (p <)
- 5			
	12.0	38.5	N.S.
- 4			
	13.0	41.5	N.S.
- 3			
	13.0	40.0	N.S.
- 2			
	13.0	28.0	N.S.
- 1			
	13.0	5.0	0.01
'Peak'			
	13.0	0.0	0.01
+ 1			

TABLE 3 (i)

Mean Interval Length - Hour by Hour Comparisons

Data Synchronised by 'Peak' Hour

Hours of Day (Relative to 'Peak' Hour)	N	Wilcoxen 'T'	Significance ($p <$)
- 5			
	13.0	33.0	N.S.
- 4			
	13.0	33.0	N.S.
- 3			
	13.0	44.0	N.S.
- 2			
	13.0	16.0	0.05
- 1			
	13.0	36.0	N.S.
'Peak'			
	13.0	41.0	N.S.
+ 1			

TABLE 4 (a)

Feeding Behaviour in Trigeminal Sectioned Animals - Summary Table

Bird	Meal Frequency		IFI Criterion (Secs.)	Time of Feeding Onset (Mins.)	Time Spent Feeding (Mins.)
	log.	250			
T1	12.3	12.0	210	7.0	8.2
T131G	17.3	15.9	135	0*	22.3
T133B	14.7	13.6	135	2.9	30.1
T198G	15.4	12.1	65	8.7	16.5
T252G	15.3	12.9	45	10.1	15.0
T3	20.3	16.3	60	5.4	10.0
T325G	12.6	12.6	250	12.4	11.5
T357G	12.4	10.7	95	18.8	18.0
T4	9.7	8.6	80	7.6	11.1
T482G	13.1	11.6	110	10.6	20.0
T490G	6.6	5.9	50	6.1	5.9
Means:	13.61	12.02	112.3	8.1	15.3
S.D.	3.667	2.967	66.534	4.990	7.061
S.E.	1.160	0.938	21.040	1.578	2.231

* Night feeding

TABLE 4 (b)

Feeding Behaviour and Trigeminal Section - Pre-Operative/Post-Operative Date

	Meal Frequency(Log)		Meal Frequency(250)		Time of Onset(Mins.)		Criterion IFI (Secs.)		Time Spent Feeding (Mins.)	
Bird	Pre-Op	Post-Op	Pre-Op	Post-Op	Pre-Op	Post-Op	Pre-Op	Post-Op	Pre-Op	Post-Op
F19G	25.6	15.0	16.7	11.7	25.7	10.4	60	180	49.6	40.9
F215G	19.0	16.6	14.7	11.0	22.7	9.0	40	75	18.9	23.9
F245G	21.6	20.0	13.7	15.6	18.7	13.4	40	80	16.7	11.2
F289Y	15.6	10.4	11.6	9.4	11.0	15.0	100	120	12.8	6.9
F337G	12.7	8.4	9.6	6.4	47.8	22.1	55	145	32.1	15.1
F387G	16.3	11.4	12.0	9.3	34.3	17.0	75	130	10.5	12.8
Means	18.5	13.6	13.0	10.6	27.7	14.5	61.7	121.7	23.4	18.5
S.D.	4.629	4.337	2.513	3.070	12.888	4.744	22.949	39.833	14.859	12.352
S.E.	2.070	1.939	1.124	1.373	5.763	2.122	10.263	17.814	6.645	5.524

TABLE 5

Feeding Behaviour in Trigeminal Control Animals - Summary Table

Bird	Meal Frequency		IFI Criterion (Secs.)	Time of Feeding Onset (Mins.)	Time Spent Feeding (Mins.)
	log.	250			
C112G	38.9	23.0	40	9.6	22.9
C116G	21.9	15.9	60	23.7	25.8
C332G	17.6	8.6	55	17.5	9.3
C411G	21.3	12.0	75	9.7	13.9
C421S	21.0	15.7	75	18.0	22.7
C474G	16.4	13.7	50	8.2	24.7
C476G	15.3	9.7	75	8.2	10.9
C480G	29.0	19.4	85	18.3	40.3
C82W	17.6	12.7	60	15.7	22.5
Means:	22.11	14.52	63.9	15.2	21.4
S.D.	7.508	4.578	14.530	5.090	9.391
S.E.	2.654	1.618	5.137	1.800	3.320

TABLE 6

Trigeminal Section - Diurnal Distribution of Feeding

(Time spent feeding as % of daily total.)

Hours of Day	9	10	11	12	13	14	15	16	17
Birds (Trigeminal Section)									
T1	19	10	6	9	8	27	11	9	2
T131G*	7	6	3	7	18	8	23	15	2
T133B	18	1	7	11	8	37	11	5	0
T198G	19	5	5	5	4	10	29	11	12
T252G	2	9	3	10	13	18	26	17	2
T3	12	6	6	6	8	15	24	17	5
T325G	31	12	7	6	6	7	14	12	4
T357G	4	13	4	9	10	9	20	20	12
T4	12	4	24	9	7	21	12	6	6
T482G	25	7	10	1	7	7	13	15	15
T490G	22	0	1	8	8	17	7	25	12
Means:	15.5	6.6	6.9	7.4	8.8	16.0	17.3	13.8	6.5

(* Night Feeding)

TABLE 7 (a)

Food Prōference Tests

(Mean daily intake in grams)

(a) Wheat/Millet

Bird	Wheat	Millet
1	5.4	7.4
2	4.1	8.6
3	3.3	7.1
4	3.4	7.4
5	2.7	8.1
6	2.1	10.0
7	3.1	7.6
8	4.7	8.0
9	2.2	7.7
10	3.5	8.1
11	4.5	8.6
12	2.9	9.0
Means:	3.5	8.1
S.D.	1.012	0.815
S.E.	0.305	0.246

$t = 10.821$ $(p < 0.001)$

TABLE 7 (b)

(b) Wheat/Corn

Bird	Wheat	Corn
1	5.9	6.8
2	6.1	6.9
3	4.9	5.5
4	5.7	5.0
5	3.9	5.7
6	5.2	6.0
7	5.0	5.7
8	5.9	6.5
9	4.3	5.2
10	5.9	5.7
11	5.9	6.4
12	5.5	6.1
Means:	5.3	5.9
S.D.	0.705	0.604
S.E.	0.213	0.182

$t = 3.473$ $(p < 0.01)$

TABLE 7 (c)

(c) Wheat/Hemp

Bird	Wheat	Hemp
1	3.7	8.5
2	2.5	11.4
3	3.4	8.4
4	1.3	7.3
5	1.7	9.5
6	1.8	9.5
7	2.0	7.7
8	3.5	8.1
9	1.2	8.6
10	2.1	8.6
11	3.0	9.7
12	1.2	10.5
Means:	2.3	9.0
S.D.	0.919	1.180
S.E.	0.277	0.356

$t = 14.886$ ($p < 0.001$)

TABLE 7 (d)

(d) Millet/Corn

Bird	Millet	Corn
11	7.9	4.9
2	8.4	4.7
3	8.1	3.3
4	7.5	3.3
5	7.2	3.0
6	8.4	2.5
7	7.9	2.7
8	7.9	5.2
9	7.7	3.1
10	8.4	4.6
11	9.0	5.2
12	8.6	3.4
Means:	3.8	8.1
S.D.	1.012	0.502
S.E.	0.305	0.151

$t - 15.767$ ($p < 0.001$)

TABLE 7 (e)

(e) Millet/Hemp

Bird	Millet	Hemp
11	6.6	6.8
2	5.1	6.7
3	6.5	4.3
4	5.2	6.5
5	5.7	5.3
6	3.3	7.9
7	5.2	6.8
8	8.3	3.4
9	4.3	5.7
10	6.1	6.6
11	5.8	6.1
12	6.1	6.3
Means:	5.4	6.0
S.D.	0.937	1.217
S.E.	0.283	0.367

$t = 0.528$ (n.s.)

TABLE 7 (f)

(f) Corn/Hemp

Bird	Corn	Hemp
1	4.9	7.5
2	5.0	5.3
3	3.7	6.9
4	2.7	8.0
5	3.1	8.2
6	3.5	8.5
7	3.4	7.1
8	4.7	7.7
9	3.1	6.7
10	3.3	9.1
11	5.3	8.6
12	4.2	7.9
Means:	3.9	7.8
S.D.	0.875	0.733
S.E.	0.264	0.221

$t = 11.800$ ($p < 0.001$)

TABLE 8

Feeding Behaviour and Food Type - Summary Table

BIRD	MEAL FREQUENCY(LOG)		MEAL FREQUENCY(250)		TIME SPENT FEEDING(MINS)		CRITERION IFI (SECS)		TIME OF ONSET (MINS)	
	MIX	WHEAT	MIX	WHEAT	MIX	WHEAT	MIX	WHEAT	MIX	WHEAT
F13B	12.0	15.9	10.6	12.6	47.2	15.7	90.7	95	21.0	5.3
F17G	23.0	10.7	16.7	7.7	38.1	6.4	90	110	5.7	13.3
F206G	36.9	7.7	24.6	5.9	19.5	25.1	80	85	6.7	18.3
F226B	16.7	14.7	14.7	12.0	18.9	9.9	60	75	2.7	4.1
F248B	15.7	17.6	11.1	14.1	41.5	10.7	90	80	26.3	16.8
F298W	18.6	12.9	15.1	10.3	20.4	13.8	100	60	38.8	20.0
F446G	11.3	10.1	10.7	8.7	23.6	11.7	100	110	13.9	11.7
F471G	25.0	18.7	20.3	17.7	20.2	15.0	60	150	14.4	14.3
F479S	21.9	11.6	13.6	10.0	39.0	15.7	50	95	31.9	13.2
F485G	27.0	16.4	20.3	12.6	27.8	19.3	75	95	20.0	16.6
F655S	17.3	10.3	11.7	7.6	11.3	10.8	55	75	2.8	17.0
F999G	21.6	17.3	17.7	13.7	20.7	18.4	100	115	10.3	8.6
MEANS	20.6	13.7	15.6	11.1	27.3	14.4	79.2	95.4	16.2	13.3
S.D.	7.065	3.578	4.475	3.345	11.258	5.016	18.688	23.785	11.688	55.054
S.E.	2.130	1.079	1.349	1.009	3.394	1.512	5.635	7.171	3.524	1.524

TABLE 9

Food Type and Daily Food Intake

(Mean daily food intake and body weight in grams.)

Bird	Mixed Grain		Wheat	
	Body Wt.	Food Intake	Body Wt.	Food Intake
1	159.6	11.6	150.2	10.3
2	140.1	11.1	141.2	11.7
3	159.4	11.3	159.4	10.7
4	158.8	11.4	158.0	12.3
5	153.1	11.2	157.6	12.6
6	156.6	12.8	155.7	12.0
7	167.4	12.7	168.3	13.2
8	146.1	11.8	147.7	11.6
9	146.7	11.5	152.3	10.4
10	144.0	11.4	143.0	10.9
11	136.6	10.5	137.0	10.4
12	153.4	11.5	153.1	10.5
Means:	151.8	11.6	151.9	11.4
S.D.	9.173	0.639	8.776	0.988
S.E.	2.766	0.193	2.646	0.298

TABLE 10(a)

TEMPERATURE AND FOOD INTAKE

(Mean daily food intake in grams)

Temperature:	70°F	50°F
Birds		
1	11.5	13.0
2	12.4	12.2
3	11.6	12.2
4	11.5	14.0
5	12.0	13.5
6	10.7	13.3
7	10.2	12.0
8	9.5	11.5
Mean	11.2	12.7
S.D.	0.9677	0.8626
S.E.	0.3657	0.3260

$t = 4.6064$; $p < 0.005$, two tailed.

TABLE 10(b)

Feeding Behaviour and Temperature - Summary Table

BIRD	MEAL FREQ.(LOG)		MEAL FREQ.(250)		TIME SPENT FEEDING(MINS)		TIME SPENT "FORAGING"(MINS)		NO. OF BOUTS PER MEAL		TIME OF ONSET(MINS)		CRITERION IFI (SECONDS)	
	70°F	50°F	70°F	50°F	70°F	50°F	70°F	50°F	70°F	50°F	70°F	50°F	70°F	50°F
F126Y	28.7	19.7	26.7	17.9	11.1	5.8	27.1	13.5	2.7	2.7	1.4	3.3	125	100
F147Y	36.3	27.6	23.0	21.9	17.8	30.2	49.4	49.0	3.7	4.9	12.1	16.7	40	40
F153Y	38.3	35.3	30.9	25.9	33.3	19.2	61.7	53.3	5.6	6.1	4.3	3.0	45	60
F164Y	47.6	37.1	33.7	26.1	19.5	15.3	60.9	66.5	2.4	3.9	4.7	4.3	70	100
F203Y	19.6	16.9	16.6	13.9	7.8	30.3	19.0	46.6	3.6	4.0	8.3	10.3	65	85
F22Y	23.1	20.1	19.3	15.7	6.9	28.3	18.6	42.0	3.3	4.1	9.8	6.7	50	50
F229G	21.9	19.4	19.1	17.6	10.1	9.4	22.9	18.4	3.9	4.3	11.7	12.9	75	50
F235B	21.4	21.1	16.9	18.1	13.2	31.9	31.4	43.7	2.9	3.9	10.4	13.0	90	55
F344B	23.6	18.9	18.7	14.0	27.6	24.8	46.8	49.6	6.0	11.5	4.4	8.0	50	50
F359G	11.9	9.4	11.0	8.9	7.2	7.6	11.4	12.5	4.4	5.7	19.3	25.0	45	40
F361G	25.6	13.6	21.6	15.4	20.3	20.3	46.1	50.7	4.8	7.1	8.4	7.7	100	125
F388G	17.3	15.4	15.6	13.6	24.7	23.7	36.3	38.2	3.5	5.9	8.9	15.4	115	80
MEAN	26.3	21.2	21.1	17.4	16.6	20.6	36.0	40.3	3.9	5.3	8.6	10.5	72.5	69.6
S.D.	9.991	8.278	6.559	5.102	8.702	9.264	16.916	16.936	1.116	2.348	4.716	6.465	29.037	27.754
S.E.	3.012	2.496	1.977	1.538	2.624	2.973	5.100	5.106	0.336	0.708	1.422	1.949	8.755	8.368

TABLE 11 (a)

Meal Size Distribution - Meal Size Differences

(Means in seconds for each bird)

(a) Mixed Grain Diet

Birds	1 (1st-2nd)	2 (2nd-3rd)	3 (3rd-4th)	4 (4th-5th)	5 (5th-6th)
F13B	225.2	71.4	98.6	103.5	44.6
F17G	377.2	142.9	34.1	19.0	8.9
F206G	230.3	212.1	141.9	70.6	41.9
F226B	37.4	37.6	12.4	11.9	9.4
F248B	313.7	204.3	87.6	66.4	38.5
F298W	83.2	79.4	21.6	20.2	10.5
F446G	257.4	53.1	87.3	40.3	30.6
F471G	86.4	66.2	14.7	45.1	7.1
F479S	363.4	114.4	87.4	35.8	33.6
F485G	209.3	95.5	26.6	13.7	28.0
F655S	146.0	19.0	29.1	16.9	10.3
F999G	120.7	19.7	20.5	23.2	18.4
Means:	204.2	93.8	55.1	38.9	23.5
S.D.	111.983	66.555	42.930	28.324	14.270
S.E.	33.764	20.067	12.944	8.540	4.303

TABLE 11 (b)

(b) Wheat Grain Diet

Birds	1	2	3	4	5
F13B	159.7	55.9	13.5	12.9	8.6
F17G	40.4	47.3	10.1	13.9	6.7
F206G	103.0	48.0	12.1	21.9	17.1
F226B	40.8	20.7	10.4	6.4	4.1
F248B	63.6	28.0	21.8	6.1	7.5
F298W	193.2	32.7	19.0	24.4	8.2
F446G	88.0	27.7	19.2	16.7	15.0
F471G	132.5	32.7	17.2	8.2	12.4
F479S	132.0	68.3	31.7	10.2	21.4
F485G	148.2	40.2	12.9	14.5	15.5
F655S	83.2	54.3	43.0	12.0	28.5
F999G	44.7	15.1	9.0	10.9	15.2
Means:	102.4	39.2	18.3	13.2	13.3
S.D.	50.863	15.859	10.051	5.665	6.962
S.E.	15.336	4.778	3.030	1.708	2.009

TABLE 12

Light Offset Cue Effect

(Mean difference between afternoon and morning intake in grams.)

Birds	No Cue	Cue
1	- 2.7	1.2
2	2.1	3.1
3	2.6	2.7
4	1.9	2.8
5	- 0.7	0.5
6	- 0.5	1.4
Means:	0.42	1.95
S.D.	2.051	1.056
S.E.	0.917	0.472

TABLE 13 (a)

Pre-fast Cue Effect

Fast Day - Pre-fast Hour
(Hourly intake in grams.)

Days -	1	2	3	4	5	6	7	8	9	10	11	12
Birds												
1	0.3	0.1	0.7	0.4	0.6	0.0	1.4	0.0	1.0	0.8	0.8	1.0
2	0.4	0.5	0.8	0.0	0.8	2.1	0.2	1.6	0.8	0.3	1.7	1.5
3	0.5	1.1	0.7	0.0	0.2	1.8	0.0	2.1	0.8	0.9	0.4	1.3
4	0.0	0.2	0.5	0.0	0.0	0.0	1.2	1.2	0.2	1.0	0.6	0.9
5	0.7	0.1	0.0	0.3	0.8	0.0	0.6	0.0	0.0	0.8	0.5	0.6
6	0.1	0.0	0.1	3.0	0.8	0.1	1.2	1.0	0.3	0.9	1.6	1.1
7	0.0	0.2	0.6	0.0	0.3	0.0	1.3	1.0	0.9	0.5	1.1	1.5
8	0.0	1.0	0.0	0.0	0.0	0.2	0.5	0.7	1.3	1.6	1.1	0.7
9	0.0	0.5	0.1	0.0	1.5	1.2	1.4	1.0	0.4	0.7	1.3	0.8
10	0.7	0.1	0.1	0.6	0.0	0.0	2.1	0.6	1.0	0.7	0.6	0.8
11	0.1	0.2	0.6	0.8	0.8	0.0	0.0	1.0	1.9	0.6	0.8	1.8
12	0.0	0.0	0.0	0.0	2.8	0.0	2.4	0.3	0.0	2.0	1.8	1.1
Means:	0.2	0.3	0.3	0.4	0.6	0.4	1.0	0.8	0.7	0.9	1.0	1.1
S.D.	.227	.372	.323	.857	.758	.781	.781	.615	.559	.469	.486	.368
S.E.	.084	.112	.097	.258	.229	.234	.235	.185	.169	.141	.147	.111

TABLE 13 (b)

Fast Day - Post-fast Hour

(Hourly intake in grams.)

Days -	1	2	3	4	5	6	7	8	9	10	11	12
Birds												
1	0.9	1.4	0.3	1.0	1.1	1.5	0.6	0.7	0.6	0.8	1.0	1.0
2	1.4	1.1	0.1	1.2	0.8	0.4	1.4	0.6	0.9	1.3	0.6	0.4
3	0.3	0.8	0.1	0.9	0.8	0.6	0.3	0.7	1.0	0.3	0.7	0.4
4	1.0	0.5	0.4	0.1	0.8	0.9	0.7	0.2	1.0	0.4	0.1	0.4
5	1.2	1.3	1.3	0.5	0.9	0.3	1.2	1.4	1.0	0.5	0.7	0.7
6	0.6	1.5	1.5	0.2	0.4	1.3	0.5	0.7	0.9	0.6	0.3	0.4
7	1.8	0.9	1.3	1.1	0.7	1.7	0.6	0.4	0.7	1.0	0.3	0.4
8	0.7	0.3	1.4	1.1	0.5	0.9	0.9	0.5	0.4	0.6	0.3	0.7
9	1.8	0.3	0.8	1.3	0.4	0.1	0.5	0.3	0.8	0.5	0.7	0.3
10	1.2	1.7	1.0	0.7	1.4	0.4	0.9	0.3	0.5	0.7	0.1	0.8
11	1.0	0.8	0.4	0.3	1.3	1.6	1.0	0.5	0.4	0.7	0.4	0.1
12	1.4	1.2	1.0	2.8	0.3	1.8	0.2	0.8	0.2	0.6	0.3	0.9
Means:	1.1	1.0	0.8	0.9	0.8	1.0	0.7	0.6	0.7	0.7	0.5	0.5
S.D.	.455	.463	.520	.715	.354	.694	.358	.317	.276	.271	.278	.271
S.E.	.137	.140	.157	.216	.107	.182	.108	.096	.083	.082	.084	.082

TABLE 13 (c)

Pre-fast Cue Effect

Non-fast (Control) Day - Pre-fast Hour

(Hourly intake in grams)

Days -	1	2	3	4	5	6	7	8	9	10	11	12
Birds												
1	0.3	0.1	0.1	0.8	0.5	0.7	0.0	0.8	0.0	0.0	0.2	0.1
2	1.0	0.7	0.7	0.1	0.2	0.0	0.4	0.7	1.0	0.4	0.4	0.6
3	0.3	1.4	0.0	0.0	0.7	0.5	0.2	0.3	0.0	0.0	0.7	0.2
4	0.9	0.4	0.1	0.1	0.7	0.7	0.0	0.7	0.1	0.0	0.6	0.4
5	0.8	0.0	0.4	0.0	0.5	0.0	0.1	0.0	0.3	0.6	0.3	0.5
6	0.0	0.3	0.0	0.0	1.0	0.1	0.6	0.1	0.6	0.3	0.5	0.7
7	0.0	0.0	0.4	0.2	0.0	0.4	1.2	0.9	0.0	0.0	0.5	0.3
8	0.0	0.1	0.0	0.0	0.0	0.0	0.9	0.0	0.8	0.2	0.0	0.1
9	0.0	0.9	0.0	0.0	0.3	0.2	0.9	0.0	1.1	0.2	0.5	0.2
10	1.5	0.7	0.0	0.0	0.0	0.4	0.9	1.1	0.0	0.6	0.7	0.0
11	0.8	0.6	0.3	0.1	0.8	0.6	0.4	0.3	0.0	0.3	0.1	0.0
12	0.5	0.0	1.6	0.0	0.1	0.0	0.0	0.9	0.0	0.0	0.3	0.1
Means:	0.5	0.4	0.2	0.1	0.5	0.3	0.5	0.5	0.3	0.2	0.4	0.3
S.D.	.493	.440	.255	.227	.374	.283	.425	.409	.431	.229	.226	.235
S.E.	.148	.133	.077	.069	.113	.085	.128	.123	.130.	.069	.068	.071

TABLE 13 (d)

Non-fast (Control) Day - Post-fast Hour

(Hourly intake in grams.)

Days -	1	2	3	4	5	6	7	8	9	10	11	12
Birds												
1	0.3	0.4	0.0	0.0	0.3	0.0	0.0	0.5	0.3	0.0	0.0	0.1
2	0.0	1.1	0.4	0.3	0.7	0.4	0.0	0.0	0.6	0.2	0.0	0.6
3	0.0	1.3	0.0	0.0	0.2	0.3	0.6	0.0	0.0	0.4	0.2	1.5
4	1.0	0.9	0.5	0.1	0.5	0.3	0.6	1.1	0.6	0.9	1.2	0.7
5	0.0	0.2	0.3	0.7	0.4	1.5	0.4	1.0	0.0	0.7	0.5	0.9
6	0.3	0.5	0.7	0.2	0.9	0.2	0.7	0.5	0.3	0.6	1.0	0.4
7	0.1	0.4	0.6	0.5	0.8	1.0	0.9	0.6	0.9	1.1	0.3	0.7
8	0.5	0.0	0.0	0.3	0.0	0.1	0.0	0.5	0.1	0.0	0.0	0.2
9	0.9	0.3	0.6	0.0	0.9	1.7	0.9	1.1	0.5	0.7	1.0	0.8
10	0.4	0.1	0.0	1.1	0.1	0.0	1.4	0.3	0.1	0.9	0.9	1.2
11	0.7	0.6	0.6	0.5	0.7	0.3	0.0	0.0	0.4	0.1	0.3	0.8
12	0.2	0.0	0.0	0.0	0.0	0.6	0.5	0.0	0.1	0.0	0.0	0.3
Means:	0.4	0.5	0.3	0.3	0.5	0.5	0.5	0.5	0.3	0.5	0.4	0.7
S.D.	.347	.424	.291	.342	.340	.569	.447	.427	..283	.401	.456	.406
S.E.	.105	.128	.088	.103	.102	.172	.135.	.129	.085	.121	.138	.122

TABLE 14

Effect of Food Deprivation on Food Intake

(Mean Intake in grams.)

Hours of Deprivation - 1		2	3	4	5	6
Birds						
1	2.9	3.1	3.9	5.8	7.2	9.5
2	1.3	2.1	3.5	5.2	6.6	7.2
3	1.6	2.5	3.0	6.1	7.3	8.2
4	2.4	2.9	3.6	5.1	6.8	8.9
5	3.0	4.8	6.1	8.2	9.6	11.1
6	1.7	2.2	3.4	4.8	7.3	9.3
Means:	2.1	2.9	3.9	5.9	7.5	9.0
S.D.	0.718	0.993	1.109	1.239	1.084	1.314
S.E.	0.321	0.444	0.496	0.554	0.485	0.588

TABLE 15 (a)

Bout Length Serial Order Effect (Time in Seconds)

First 5 Bouts	(1)	(2)	(3)	(4)	(5)
Birds					
M108G	6.6	9.5	8.8	9.1	8.1
M201G	3.8	4.7	7.2	7.6	7.1
M211G	3.5	4.4	4.8	3.8	4.2
M284G	11.0	8.4	12.4	11.6	14.0
M339B	3.6	4.6	3.7	4.5	5.2
M574S	7.9	7.1	8.5	8.8	8.9
M76G	3.2	2.4	2.9	3.2	3.0
F196W	8.1	13.9	9.2	10.4	11.4
F211B	2.9	3.8	4.5	3.9	4.2
F252G	4.4	5.2	3.9	4.0	4.5
F36G	2.7	3.2	3.6	3.9	4.0
F479S	4.3	4.9	6.4	7.5	6.6
F687S	2.6	3.1	3.1	4.1	2.8
F91W	4.3	4.2	4.9	4.6	5.8
Mean:	4.9	5.7	6.0	6.2	6.4
S.D.	2.514	3.107	2.846	2.851	3.256
S.E.	0.697	0.862	0.789	0.701	0.903

First 5 Intervals	(1)	(2)	(3)	(4)	(5)
Birds					
M108G	8.0	7.6	5.7	5.5	5.9
M201G	7.9	7.5	6.9	6.7	5.1
M211G	4.1	5.0	6.1	5.0	5.9
M284G	9.0	7.7	6.2	4.6	6.6
M339B	6.0	9.0	6.0	3.5	4.4
M574S	8.4	8.8	8.4	7.0	7.0
M76G	7.0	5.4	5.4	5.6	7.3
F196W	4.3	9.1	8.9	12.9	12.0
F211B	6.7	5.5	3.9	4.7	3.7
F252G	5.6	5.4	6.4	6.9	8.0
F36G	9.4	8.5	7.9	6.6	7.6
F479S	11.5	14.5	9.7	13.5	7.4
F687S	6.6	5.3	6.9	10.1	5.0
F91W	9.7	7.8	6.9	8.9	8.4
Mean:	7.4	7.6	6.8	7.2	6.7
S.D.	2.098	2.484	1.515	3.053	2.065
S.E.	0.582	0.689	0.420	0.847	0.573

TABLE 15 (b)

Bout Length Serial Order Effect (Times in Seconds)

Last 5 Bouts	(5)	(4)	(3)	(2)	(1)
Birds					
M108G	10.5	9.6	10.5	9.6	8.8
M201G	8.4	7.3	7.1	6.8	6.8
M211G	4.0	4.1	3.9	5.1	3.1
M284G	10.5	12.0	11.9	10.3	6.6
M339B	4.1	4.7	3.9	4.2	4.0
M574S	8.4	8.8	7.9	6.4	6.3
M76GG	3.9	3.3	4.1	3.7	3.3
F196W	11.0	10.8	10.3	11.0	9.9
F211B	4.7	5.0	4.1	4.0	3.2
F252G	3.9	3.9	4.1	4.3	3.6
F36G	3.9	3.3	5.4	4.7	4.2
F479S	7.2	7.2	8.5	6.3	6.8
F687S	3.2	3.9	3.7	4.0	3.5
F91W	5.5	5.0	5.8	6.2	5.3
Mean:	6.3	6.4	6.5	6.2	5.4
S.D.	2.899	2.872	2.859	2.462	2.197
S.E.	0.804	0.796	0.793	0.683	0.609

Last 5 Intervals	(5)	(4)	(3)	(2)	(1)
Birds					
M108G	6.3	3.8	4.9	4.5	5.2
M201G	4.7	6.5	8.5	5.2	7.1
M211G	5.6	5.3	7.0	4.4	5.3
M284G	7.4	4.3	4.8	6.2	7.2
M339B	4.0	4.5	2.8	3.7	4.3
M574S	6.9	5.9	7.0	5.7	6.5
M76G	4.1	3.7	4.0	5.9	6.9
F196W	6.6	11.5	8.9	7.8	6.4
F211B	4.9	4.3	3.0	5.7	6.7
F252G	7.7	5.7	6.3	7.5	6.2
F36G	5.4	5.6	4.4	6.5	8.4
F479S	10.7	11.1	5.7	8.5	9.7
F687S	4.6	6.7	6.1	7.2	4.8
F91W	5.0	7.2	5.8	6.4	4.7
Mean:	6.0	6.1	5.7	6.1	6.4
S.D.	1.801	2.434	1.833	1.372	1.491
S.E.	0.500	0.675	0.508	0.380	0.414

TABLE 16

Chosen Inter-feeding Interval Criterion (Seconds)

Ratio -	(1)	(5)	(10)	(20)	(40)	(80)	(160)	(10)
Birds								
Blank	100	135	140	180	220	280	340	70
F355G	125	115	150	200	220	260	360	110
F67G	100	120	140	180	200	240	380	120
F206G	140	120	120	160	180	200	280	110
F687S	100	75	100	120	180	300	320	110
Mean:	113	113	130	168	200	256	336	104
S.D.	18.574	22.528	20.000	30.331	20.000	38.471	38.471	19.494
S.E.	9.287	11.264	10.000	15.166	10.000	19.235	19.235	9.747

TABLE 17

No. of Reinforcements Earned

Ratio -	(1)	(5)	(10)	(20)	(40)	(80)	(160)	(10)
Birds								
Blank	225	177	192	144	142	125	148	249
F355G	185	146	96	87	88	59	46	107
F67G	169	133	109	111	88	87	75	113
F206G	174	127	85	103	107	105	82	115
F687S	295	255	227	223	215	157	177	296
Mean:	209.5	167.6	141.8	133.6	128.0	106.6	105.6	176.0
S.D.	52.562	52.534	63.598	54.128	53.399	37.186	54.638	89.694
S.E.	26.281	26.267	31.799	27.064	26.700	18.593	27.319	89.694

TABLE 18

No. of Responses

Ratio -	(1)	(5)	(10)	(20)	(40)	(80)	(160)	(10)
Birds								
Blank	225	885	1920	2880	5680	10000	23680	2490
F355G	185	730	960	1740	3520	4720	7360	1070
F67G	169	665	1090	2220	3520	6960	12000	1130
F206G	174	635	850	2060	4280	8400	13120	1150
F687S	295	1275	2270	4460	8600	12560	28320	2960
Mean:	209.6	838.0	1418.0	2672.0	5120.0	8528.0	16896.0	1760.0
S.D.	52.562	262.669	635.979	1082.552	2135.977	2974.881	8742.064	869.939
S.E.	26.281	131.330	317.990	541.276	1067.989	1487.441	4371.441	448.470

TABLE 19

No. of Meals/Day

Ratio -	(1)	(5)	(10)	(20)	(40)	(80)	(160)	(10)
Birds								
Blank	11.6	5.4	6.1	15.9	16.7	20.6	22.4	11.9
F355G	15.7	9.0	6.4	7.6	9.4	14.7	17.7	12.0
F67G	13.3	8.0	9.4	10.4	12.9	11.7	11.9	8.7
F206G	20.7	13.6	13.4	17.9	26.7	31.9	22.9	31.9
F687S	17.3	22.1	14.1	18.6	22.4	20.6	21.9	20.7
Mean:	15.7	11.6	9.9	14.1	17.6	19.9	19.4	17.0
S.D.	3.540	6.565	3.769	4.844	6.996	7.734	4.654	9.429
S.E.	1.776	3.283	1.885	2.422	3.500	3.867	2.327	4.714

TABLE 20

Mean Meal Size (No. of Reinforcements)

Ratio -	(1)	(5)	(10)	(20)	(40)	(80)	(160)	(10)
Birds								
Blank	19.4	32.8	31.5	9.1	8.5	6.1	6.6	20.9
F355G	11.8	16.3	15.0	11.4	9.4	4.0	2.6	8.9
F67G	12.7	16.7	11.6	10.7	6.8	7.4	6.3	13.0
F206G	8.4	9.3	6.3	5.7	4.0	3.3	3.6	3.6
F687S	17.0	11.5	16.1	12.0	9.6	7.6	8.1	14.3
Mean:	13.9	17.3	16.1	9.8	7.7	5.7	5.4	12.1
S.D.	4.357	9.209	9.416	2.525	2.325	1.956	2.270	6.434
S.E.	2.179	4.605	4.704	1.263	1.163	0.978	1.135	3.217

TABLE 21

Mean Meal Size as % of Daily Total

Ratio -	(1)	(5)	(10)	(20)	(40)	(80)	(160)	(10)
Birds								
Blank	8.6	18.5	16.4	6.3	6.0	4.9	4.5	8.4
F355G	6.4	11.2	15.6	13.1	10.7	6.8	5.6	8.3
F67G	7.5	12.6	10.6	9.6	7.7	8.5	8.4	11.5
F206G	4.8	7.3	7.4	5.5	3.7	3.1	4.8	3.1
F687S	5.8	4.5	7.1	5.4	4.5	4.8	4.6	4.8
Mean:	5.5	10.8	11.4	8.0	6.5	5.6	5.6	7.2
S.D.	1.493	5.352	4.409	3.334	2.791	2.075	1.635	3.306
S.E.	0.746	2.677	2.205	1.667	1.396	1.038	0.8173	1.653

TABLE 22

Minimum Inter-reinforcement (Seconds)

Ratio -	(1)	(5)	(10)	(20)	(40)	(80)	(160)
Birds							
Blank	-	-	20	25	30	50	80
F355G	-	-	15	20	35	55	95
F67G	-	-	15	20	35	55	95
F206G	-	-	15	20	35	40	60
F687S	-	-	15	20	30	50	80
Mean:			16	21	33	50	82
S.D.			2.236	2.236	2.739	6.124	14.405
S.E.			1.118	1.118	1.369	3.062	7.202

TABLE 23

Mean Body Weights (gms)

Ratio -	(1)	(5)	(10)	(20)	(40)	(80)	(160)	(10)
Birds								
Blank	161.1	157.9	151.3	151.0	157.7	151.6	145.7	162.1
F355G	160.0	157.9	158.3	154.7	164.2	163.9	161.6	176.1
F67G	152.71	145.9	142.6	143.3	140.1	136.8	136.0	159.4
F206G	177.2	175.1	175.5	172.9	176.5	183.5	190.1	187.7
F687S	159.5	161.1	166.4	171.0	172.0	170.0	170.5	182.3
Mean:	162.1	159.6	158.2	158.6	162.1	161.2	160.8	173.5
S.D.	9.063	10.440	12.802	12.897	14.258	17.815	29.191	12.396
S.E.	4.531	5.220	6.401	6.448	7.129	8.908	14.597	6.198

TABLE 24

Pre-prandial Correlation and Ratio

Ratio -	(1)	(5)	(10)	(20)	(40)	(80)	(160)	(10)
Bird								
Blank	- 0.0892 (0.4417)	0.4274 (0.4567)	0.1248 (0.4516)	0.0747 (0.4454)	0.2599 (0.0057)	0.1412 (0.0958)	0.1316 (0.1046)	0.1771 (0.1184)
F355G	0.1949 (0.0447)	0.0655 (0.6231)	0.1837 (0.2522)	-0.0100 (0.9463)	0.4186 (0.0009)	-0.0508 (0.6179)	0.09931 (0.2817)	0.1762 (0.1179)
F67G	0.1646 (0.1232)	0.0146 (0.9191)	-0.0760 (0.5582)	-0.0086 (0.9447)	0.1224 (0.2629)	-0.0692 (0.5480)	0.0092 (0.9365)	0.0263 (0.8470)
F206G	0.0541 (0.5244)	-0.0553 (0.6031)	-0.0286 (0.7896)	0.1039 (0.2578)	0.1156 (0.1200)	-0.0789 (0.2457)	0.0564 (0.4848)	0.0920 (0.1752)
F687S	0.0431 (0.6447)	-0.0832 (0.3108)	-0.1513 (0.1435)	0.0641 (0.4764)	0.4039 (0.0000)	0.2026 (0.0163)	0.1332 (0.1039)	0.1999 (0.0174)

(Figures in brackets indicate significance levels)

TABLE 25

Post-prandial Correlation and Ratio

Ratio -	(1)	(5)	(10)	(20)	(40)	(80)	(160)	(10)
Bird								
Blank	0.7024 (0.0000)	0.5805 (0.0004)	0.3465 (0.0299)	0.3478 (0.0004)	0.0752 (0.4295)	-0.1137 (0.1815)	-0.0653 (0.4233)	0.4764 (0.0000)
F355G	0.3230 (0.0010)	0.5819 (0.0000)	0.6205 (0.0000)	-0.1808 (0.2153)	-0.0248 (0.8492)	0.3151 (0.0018)	0.1035 (0.2617)	0.2631 (0.0182)
F67G	0.2041 (0.0545)	0.3518 (0.0104)	0.4999 (0.001)	-0.1788 (0.1419)	0.0180 (0.9801)	-0.1989 (0.0804)	0.0573 (0.6166)	0.3258 (0.0132)
F206G	0.2720 (0.0014)	0.6092 (0.0000)	0.5435 (0.0000)	0.2330 (0.0130)	0.3708 (0.0000)	-0.0573 (0.3994)	-0.0200 (0.8047)	0.1778 (0.0085)
F687S	0.2061 (0.0255)	0.2844 (0.0006)	0.3860 (0.0002)	0.1410 (0.1152)	0.1178 (0.1471)	0.1421 (0.0936)	-0.0917 (0.2653)	0.1357 (0.1084)

(Figures in brackets indicate significance levels)

TABLE 26 (a)

Inter-reinforcement Interval Serial Order Effect (FR1) (Times in Seconds)

First 5 - Birds	(1)	(2)	(3)	(4)	(5)	No.of Items
Blank	22.4	20.3	16.7	18.3	20.2	69
F355G	26.0	21.5	18.9	22.3	16.6	73
F67G	22.5	20.1	18.2	20.4	18.7	89
F206G	26.1	22.8	18.3	17.3	18.5	87
F687S	20.3	18.5	17.8	17.3	16.9	49
Mean;	23.5	20.6	18.0	19.1	18.2	73.4
S.D.	2.523	1.612	0.817	2.182	1.465	
S.E.	1.261	0.806	0.408	1.091	0.733	

Last 5 - Birds	(5)	(4)	(3)	(2)	(1)
Blank	17.4	16.5	17.8	18.2	17.4
F355G	17.6	17.1	18.1	18.0	26.0
F67G	16.6	17.0	16.1	17.0	18.1
F206G	18.8	16.5	19.0	17.2	18.8
F687S	16.6	15.7	18.5	17.0	16.3
Mean:	17.4	16.6	17.9	17.5	19.3
S.D.	0.906	0.555	1.102	0.576	3.847
S.E.	0.453	0.277	0.551	0.288	1.923

First 5 - (All Greater Than 5) Birds	(1)	(2)	(3)	(4)	(5)	
Blank	21.9	20.1	16.7	18.1	19.8	75
F355G	26.7	27.5	19.0	21.2	18.1	82
F67G	22.1	19.6	18.7	20.2	18.5	108
F206G	26.8	23.6	18.0	18.4	18.7	107
F687S	21.3	17.9	18.9	17.2	18.4	67
Means:	23.8	20.7	18.3	19.0	18.7	87.8
S.D.	2.746	2.294	0.956	1.635	0.676	
S.E.	1.373	1.147	0.478	0.817	0.338	

TABLE 26 (b)

Inter-reinforcement Interval Serial Order Effect (FR5)

(Times in Seconds)

First 5 - Birds	(1)	(2)	(3)	(4)	(5)	No.of Items
Blank	38.3	31.3	25.1	27.4	26.5	51
F355G	34.9	25.9	20.6	22.2	21.3	23
F67G	31.2	24.9	23.0	21.4	21.6	45
F206G	31.5	28.0	24.3	20.5	20.3	42
F687S	19.6	19.5	18.8	16.3	17.5	77
Mean:	31.1	25.9	22.4	21.6	21.4	47.6
S.D.	7.048	4.345	2.620	3.979	3.258	
S.E.	3.524	2.173	1.310	1.989	1.629	

Last 5 - Birds	(5)	(4)	(3)	(2)	(1)
Blank	24.8	25.4	22.7	23.7	27.7
F355G	20.9	21.6	20.1	28.1	23.5
F67G	20.2	19.7	20.0	19.8	23.1
F206G	19.1	21.1	18.5	19.6	19.6
F687S	15.4	16.6	16.7	16.7	18.8
Mean:	20.1	20.9	19.6	21.6	22.5
S.D.	3.385	3.190	2.216	4.413	3.553
S.E.	1.692	1.595	1.106	2.207	1.776

First 5- (All Greater than 5) Birds	(1)	(2)	(3)	(4)	(5)	
Blank	39.4	31.1	25.1	27.2	27.5	56
F355G	33.8	25.4	20.6	22.3	21.1	25
F67G	31.2	24.8	22.8	21.7	21.7	47
F206G	30.9	26.6	24.8	21.3	21.1	61
F687S	19.4	18.9	18.4	17.5	18.1	103
Mean:	30.9	25.7	22.3	22.0	21.9	58.4
S.D.	7.297	4.374	2.847	3.463	3.432	
S.E.	3.648	2.187	1.424	1.731	1.716	

TABLE 26 (c)

Inter-reinforcement Interval Serial Order Effect (FR10)

(Times in Seconds)

First 5 - Birds	(1)	(2)	(3)	(4)	(5)	No.of Items
Blank	44.7	37.8	32.1	31.5	33.6	33
F355G	31.7	28.6	29.4	27.3	28.3	38
F67G	39.9	30.7	22.1	25.7	24.0	20
F206G	49.8	44.6	37.9	30.9	25.4	10
F687S	27.8	25.1	24.9	25.3	23.9	56
Mean:	38.8	33.4	29.3	28.1	27.0	31.4
S.D.	9.061	7.810	6.185	2.900	4.075	
S.E.	4.531	3.905	3.092	1.450	2.037	

Last 5 - Birds	(5)	(4)	(3)	(2)	(1)
Blank	29.9	27.3	31.4	30.1	31.3
F355G	28.8	29.3	29.8	30.8	33.5
F67G	22.5	24.4	23.6	28.5	30.0
F206G	23.1	23.3	24.3	23.2	26.5
F687S	24.61	25.9	24.9	25.7	25.2
Mean:	25.8	26.0	26.8	27.7	29.3
S.D.	3.370	2.368	3.545	3.172	3.420
S.E.	1.685	1.184	1.772	1.586	1.710

First 5 - (All greater than 5) Birds	(1)	(2)	(3)	(4)	(5)	
Blank	44.6	37.4	32.1	31.5	34.4	39
F355G	32.2	29.0	29.8	29.9	28.8	52
F67G	37.5	34.8	22.4	25.9	25.9	26
F206G	36.5	37.1	30.4	32.7	26.3	29
F687S	28.6	26.7	25.6	25.3	23.8	72
Mean:	35.9	33.0	28.1	29.1	27.8	43.6
S.D.	6.033	4.876	3.965	3.318	4.075	
S.E.	3.016	2.438	1.983	1.659	2.037	

TABLE 26 (d)

Inter-reinforcement Interval Serial Order Effect (FR20)

(Times in Seconds)

First 5 - Birds	(1)	(2)	(3)	(4)	(5)	No.of Items
Blank	56.8	51.0	53.2	47.5	45.7	31
F355G	54.9	42.3	37.9	40.7	40.9	30
F67G	44.7	43.8	38.5	43.2	49.5	28
F206G	52.9	32.6	60.4	38.9	35.8	11
F687S	36.4	32.7	30.1	34.2	30.6	41
Mean:	49.1	40.5	44.0	40.9	40.5	28.2
S.D.	8.485	7.868	12.392	4.944	7.555	
S.E.	4.243	3.934	6.196	2.472	3.777	

Last 5 - Birds	(5)	(4)	(3)	(2)	(1)
Blank	43.9	38.5	44.9	50.6	49.7
F355G	41.5	44.1	46.1	43.9	51.5
F67G	37.7	34.0	38.2	34.2	41.5
F206G	53.9	41.0	47.6	62.5	38.1
F687S	35.2	31.5	33.2	35.8	36.1
Means:	42.4	37.8	42.0	45.4	43.4
S.D.	7.232	5.112	6.092	11.611	6.897
S.E.	3.616	2.556	3.046	5.806	3.449

First 5 - (All greater than 5) Bird	(1)	(2)	(3)	(4)	(5)	
Blank	55.5	52.0	52.3	51.9	49.9	48
F355G	59.9	48.7	42.3	46.6	43.6	46
F67G	45.9	45.6	42.2	45.0	46.1	37
F206G	57.5	50.3	48.5	44.8	41.2	27
F687S	37.6	31.5	29.7	33.1	30.8	66
Mean:	51.3	45.6	43.0	44.3	42.3	44.8
S.D.	9.312	8.238	8.584	6.878	7.200	
S.E.	4.656	4.119	4.292	3.439	3.600	

TABLE 26 (e)

Inter-reinforcement Interval Serial Order Effect (FR40)

(Times in Seconds)

First 5 - Birds	(1)	(2)	(3)	(4)	(5)	No.of Items
Blank	71.4	60.9	63.1	58.9	60.6	48
F355G	75.2	59.4	76.7	67.9	70.7	26
F67G	83.5	68.3	69.6	74.0	66.5	24
F206G	52.8	40.3	55.3	47.5	56.0	6
F687S	50.7	44.3	48.5	48.9	53.5	48
Mean:	66.7	54.6	62.6	59.4	61.5	30.4
S.D.	14.368	11.843	11.182	11.592	7.153	
S.E.	7.184	5.921	5.591	5.796	3.577	

Last 5 - Birds	(5)	(4)	(3)	(2)	(1)
Blank	58.1	57.6	63.9	62.8	63.2
F355G	60.2	67.9	86.6	65.1	77.1
F67G	86.5	71.2	63.7	76.2	88.9
F206G	49.5	59.6	49.8	48.9	44.2
F687S	53.9	53.5	55.5	59.1	58.4
Mean:	61.6	62.0	63.9	61.7	66.4
S.D.	14.491	7.362	14.006	10.311	17.232
S.E.	7.245	3.681	7.003	5.156	8.616

First 5- (All Greater than 5) Birds	(1)	(2)	(3)	(4)	(5)	
Blank	72.1	66.0	64.2	64.5	59.2	74
F355G	78.5	65.0	76.4	69.0	71.3	32
F67G	85.2	72.8	74.3	71.7	75.4	44
F206G	64.3	55.1	52.7	48.7	59.0	33
F687S	53.1	48.5	48.2	52.9	55.2	83
Mean:	70.6	61.5	63.2	61.4	64.0	53.2
S.D.	12.488	9.620	12.587	10.087	8.785	
S.E.	6.244	4.810	6.293	5.044	4.393	

TABLE 26 (f)

Inter-reinforcement Interval Serial Order Effect (FR80)

(Times in Seconds)

First 5 - Birds	(1)	(2)	(3)	(4)	(5)	No.of Items
Blank	98.4	98.6	81.4	95.4	102.4	28
F355G	106.5	98.8	96.2	114.5	106.8	11
F67G2	111.4	106.9	105.9	109.1	111.9	23
F206G	86.2	84.3	76.0	80.2	91.0	25
F687S	100.2	97.6	95.7	98.8	99.5	54
Mean:	100.5	97.2	91.0	99.6	102.3	28.2
S.D.	9.537	8.142	12.127	13.294	7.873	
S.E.	4.768	4.071	6.064	6.647	3.937	

Last 5 - Birds	(5)	(4)	(3)	(2)	(1)
Blank	101.4	95.6	104.6	96.7	108.8
F355G	95.0	126.3	125.3	110.3	103.1
F67G	126.7	95.7	96.1	104.4	101.0
F206G	77.2	82.8	85.1	83.7	83.3
F687S	100.8	106.7	113.6	102.5	110.7
Mean:	100.2	101.4	104.9	99.5	101.4
S.D.	17.749	16.280	15.503	10.089	10.862
S.E.	8.874	8.140	7.752	5.044	5.431

First 5 - (All greater than 5) Birds	(1)	(2)	(3)	(4)	(5)	
Blank	96.8	94.5	86.9	96.1	100.9	47
F355G	95.8	106.2	108.5	110.5	112.6	38
F67G	120.0	108.0	105.9	118.0	110.0	66
F206G	85.3	80.5	79.1	89.2	85.2	88
F687S	100.3	97.6	104.8	98.2	107.1	97
Mean:	99.6	97.4	97.0	102.4	103.2	67.2
S.D.	12.683	10.998	13.179	11.625	10.944	
S.E.	6.341	5.499	6.589	5.812	5.472	

TABLE 26 (g)

Inter-reinforcement Interval Serial Order Effect (FR160)

(Times in Seconds)

First 5 -	(1)	(2)	(3)	(4)	(5)	No. of Items
Birds						
Blank	128.4	140.5	132.5	152.8	151.5	47
F355G	149.3	181.4	191.0	171.6	124.4	3
F67G	175.3	159.0	162.3	182.6	186.7	14
F206G	106.1	113.4	112.7	115.4	100.6	13
F687S	129.5	153.3	154.2	141.3	144.0	49
Mean:	137.7	149.5	150.5	152.7	141.4	25.2
S.D.	25.984	25.032	29.774	26.327	32.072	
S.E.	12.992	12.516	14.887	13.164	16.036	

Last 5 -	(5)	(4)	(3)	(2)	(1)
Birds					
Blank	156.9	155.2	162.0	165.6	161.9
F355G	127.1	176.2	158.9	187.3	222.6
F67G	175.3	182.5	163.8	188.6	179.2
F206G	126.2	112.1	127.0	128.8	143.9
F687S	150.6	156.3	146.9	142.1	166.2
Mean:	147.2	156.5	151.7	162.5	174.8
S.D.	20.858	27.555	15.309	26.729	29.578
S.E.	10.429	13.778	7.654	13.364	14.789

First 5 - (All greater than 5)	(1)	(2)	(3)	(4)	(5)	
Birds						
Blank	129.1	147.6	140.5	160.1	158.0	123
F355G	158.8	159.3	170.2	156.8	197.8	13
F67G	173.1	168.7	172.9	185.0	206.6	33
F206G	115.2	112.0	120.5	119.0	125.7	48
F687S	136.0	157.3	157.6	150.0	155.6	116
Mean:	142.4	149.0	152.3	154.2	168.7	66.6
S.D.	23.287	21.989	21.928	23.701	33.235	
S.E.	11.643	10.994	10.964	11.850	16.618	

TABLE 26 (h)

Inter-reinforcement Interval Serial Order Effect (FR10 - Return)

(Times in Seconds)

First 5 -	(1)	(2)	(3)	(4)	(5)	No.of Items
Birds						
Blank	21.9	21.9	22.1	23.8	21.9	44
F355G	32.3	29.7	27.6	26.7	28.5	66
F67G	35.1	33.0	30.4	33.8	29.8	61
F206G	32.9	20.4	22.0	19.8	18.5	20
F687S	26.7	24.2	21.8	23.4	22.5	97
Mean:	29.8	25.8	24.8	25.5	24.2	57.6
S.D.	5.384	5.414	3.979	5.247	4.757	
S½E.	2.692	2.707	1.989	2.623	1.064	

Last 5 -	(5)	(4)	(3)	(2)	(1)
Birds					
Blank	21.8	22.5	20.8	21.7	22.2
F355G	27.5	28.9	27.7	30.0	28.6
F67G	31.1	27.9	26.9	26.2	28.0
F206G	19.4	23.1	21.6	19.0	17.8
F687S	23.7	24.7	25.5	27.5	28.2
Mean:	24.7	25.4	24.5	24.9	25.0
S.D.	4.645	2.859	3.126	4.458	4.792
S.E.	2.322	1.429	1.563	2.229	2.396

First 5 - (All greater than 5)	(1)	(2)	(3)	(4)	(5)	
Birds						
Blank	22.3	21.5	21.9	23.4	22.3	56
F355G	32.4	31.8	28.8	27.9	29.3	107
F67G	34.9	32.6	30.7	34.7	30.1	78
F206G	26.1	19.9	20.4	21.2	19.1	73
F687S	25.6	26.1	24.0	23.8	23.5	142
Mean:	28.3	26.4	25.2	26.2	24.9	91.2
S.D.	5.208	5.787	4.432	5.332	4.710	
S.E.	2.604	2.893	2.216	2.666	2.355	

APPENDIX III

Illustrations of Surgical Instruments Used.

Ophthalmic Branch Section

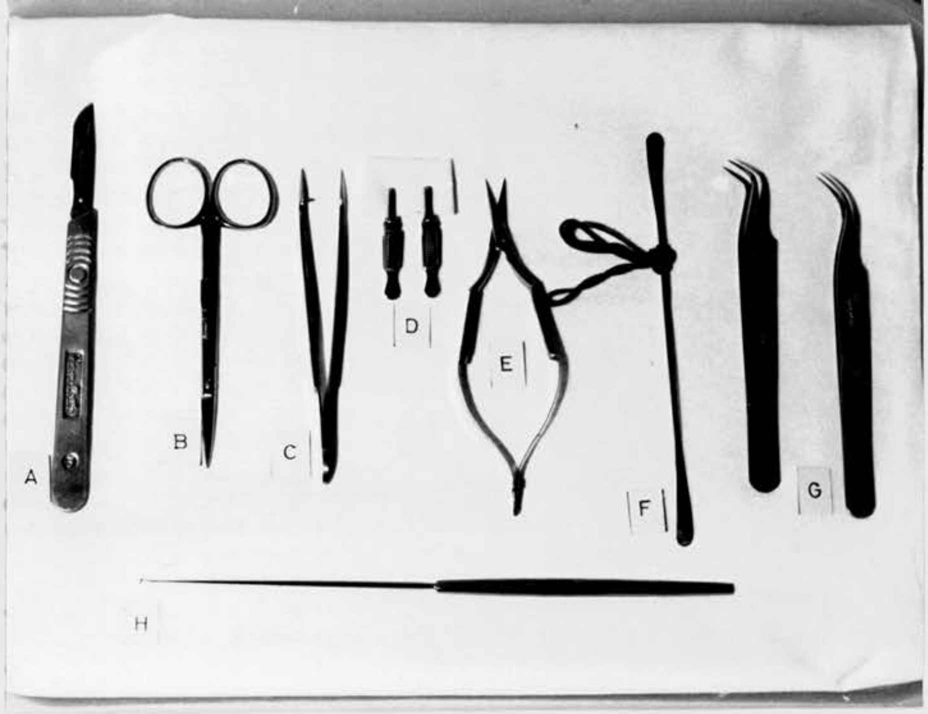
A Scalpel.
B Fine scissors.
C Forceps.
D Artery clips.
E Microscissors.
F Fine spatula (attached to stereotaxic instrument with rubber band).
G Curved watchmaker's forceps.
H Hooked probe.

Maxillary Branch Section

A Forceps.
B Fine scissors.
C Artery forceps.
D Watchmaker's forceps.
E Microscissors.

Mandibular Branch Section

A Forceps.
B Fine scissors.
C Artery forceps.
D Microscalpel.
E Curved watchmaker's forceps.
F Microscissors.
G Cotton "bud" swabs.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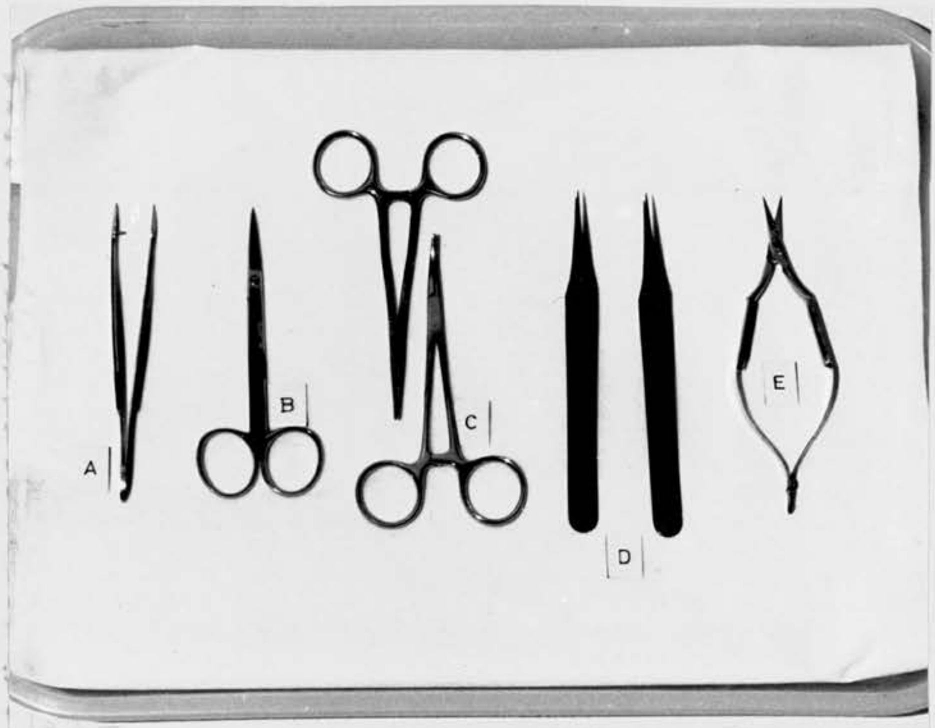
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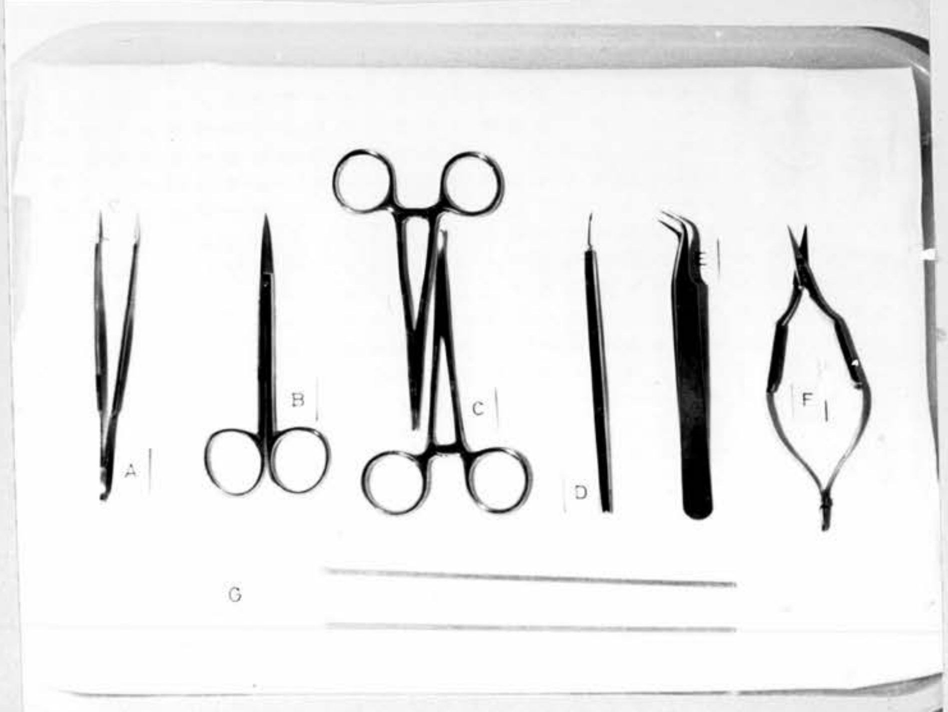
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