THE FEEDING ECOLOGY AND BEHAVIOUR OF WIGEON (ANAS PENELOPE)

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by

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CONTENTS

CHAPTER 4. THE SELECTION OF FEEDING SITES BY WIGEON

CHAPTER 5. THE EFFECT OF GRASSLAND TYPE ON WIGEON FEEDING BEHAVIOUR

5.4 DISCUSSION

CHAPTER 6. THE EFFECTS OF WIGEON GRAZING ON GRASSLAND

6.2 METHODS

6.3 RESULTS

6.4 DISCUSSION

CHAPTER 7. THE FUNCTIONS OF FLOCK FEEDING BY WIGEON

7.2 METHODS

7.3 RESULTS

7.4 DISCUSSION

CHAPTER 8. THE DIGESTIVE PHYSIOLOGY OF WIGEON

8.1 THE THROUGHPUT TIME OF FOOD IN THE WIGEON GUT

8.2 THE DIGESTIVE EFFICIENCY OF WIGEON

8.3 GUT MORPHOLOGY ALTERATION IN WIGEON

APPENDICES

SUMMARY

The aim of the project was to investigate the behavioural and physiological strategies used by wigeon to maximise their nutrient intake during winter. The reasons for selecting this species were its totally herbivorous diet, its simple digestive physiology and its small body size, all of which should lead to problems in gaining sufficient nutrition during the winter.

The daily energy expenditure of this species was estimated from faecal output studies to be 150 kcal bird^{-1} day^{-1}. This figure was compared with estimates for the larger grazing geese in order to assess the effect of body size on energy intake. The strategy of feeding for long periods (as much as 17 hours per day) to increase food intake seems to be very important in this species.

Feeding site selection was investigated as this is an obvious way to increase nutrient intake. Wigeon show clear preference for particular feeding sites both in terms of amount and timing of use. Grass biomass, grass protein content and proximity to water are all important factors in site selection, reflecting the requirements for efficient feeding and safety from predators. Fertilization of a site increased its use by a factor of 2.5 A spectrophotometer for grass biomass assessment was designed and built for this part of the work.

The behavioural changes resulting from differences in grassland type were studied. An increased biomass (and protein content) of grass on a site resulted in higher peck rates, slower walking rates and increased defaecation rates. These changes increased the efficiency of food intake on high biomass areas and allowed birds to exploit optimally a patchy food resource. The effect of grass height on peck rate was also investigated.

Wigeon grazing has a great effect on the biomass, height and spring production of grass on their feeding sites. Of more importance is the fact that winter grazing can signficantly affect the protein content of grass in the spring. This effect is caused by the increased turnover rate of leaf material on grazed sites.

The pressures leading to the tight feeding flocks, characteristic of this species, were studied. The flock-feeding strategy is likely to be important for nutrient intake since it leads to an increased protein intake in spring, and may also allow information regarding good feeding sites to be exchanged. Studies on vigilance activity showed that a decrease in vigilance time is important in small flock formation. This would have advantages for both feeding efficiency and safety from predators. The reduced likelihood of individual predation is also important in producing larger flocks.

Finally, the physiology of wigeon digestion was studied. Wigeon have a very rapid throughput time and a low digestive efficiency. The storage of protein in the form of gut tissue may also be important for breeding reserves in female birds.

CHAPTER 1

INTRODUCTION

It is an assumption of evolutionary biology that organisms are adapted to their environment through natural selection. Thus, studies of adaptation do not test whether or not a particular species is adapted, but ask how it is adapted to its particular ecological situation, ie. food supply, predation pressure, etc. (Krebs & Davies 1981). One of the most useful methods of studying adaptation in animals is to attempt to understand the adaptiveness of different behavioural strategies in terms of the ecology of the animal: this is where the selection pressures producing the varied evolutionary solutions present in the animal kingdom are found. The rationale of this project is based on the reverse of this approach. The ecology of a particular bird species is known in terms of its diet and energetic constraints. From this standpoint, this study attempts to elucidate the adaptive strategies used by this bird to meet these ecological constraints. It is thus a study of adaptation from the ecologist's, rather than ethologist's, point of view.

The problem of nutrient intake can, in fact, be 'tackled' by organisms on three separate fronts - anatomical, physiological and behavioural. While any rigid categorisation of adaptive strategies into these groupings is rather artificial, they do help to identify the main emphasis of each solution. Thus anatomical adaptations concern mainly head and gut morphology, physiological ones deal with the actual digestion of food in the gut and behavioural ones concern foraging methods. This project deals primarily with the latter two types of strategy in wigeon.

Studies of feeding biology have always had a central place in research into adaptation. The reason is obvious: acquiring sufficient nutrient intake is essential for an organism's survival. Much work, therefore, has looked at food type, quantity and quality in a large number of different species and for most animals a catalogue of food species can be found in the literature.

In the last 15 or so years, however, not only has the type or sufficiency of food intake been the object of research, but also the efficiency of nutrient intake. Basically, since an animal's time is limited it should harvest its food as efficiently as possible. Inefficient feeders are less fit than efficient ones since they have less time to watch out for predators, build up reserves for breeding, find mates and so on (Krebs 1978). The main hypothesis in this approach to feeding ecology (optimal foraging) is that natural selection acts to maximise the capture rate of some particular nutrient (Westoby 1974). In most studies energy is the nutrient considered but it could be protein, calcium or any other limiting nutrient. The type of question addressed in these studies is what size of prey should be taken, how long should an animal spend in areas of differing food density or what is the best search path to use in order to locate good feeding areas (Krebs 1978). These predictive and quantitative models have been very successful in elucidating the relationships between predators and their food supply ('predator' is used here in the sense of a feeding strategy and includes carnivores, granivores, insectivores, frugivores and nectarivores) which depend on discrete food items with high nutrient content and short handling time.

Grazers (ie. folivores and browsers) are not so easily studied by these methods. They differ fundamentally from predators in that they are surrounded by an apparent surfeit of potential food items, the nutrient content of which is generally low. Their diet is often highly indigestible and they therefore have to spend a large part of their time in handling and digesting a very bulky food supply (Harwood 1975, Owen-Smith and Novellie 1982). This means that their problems arise not so much in finding their food supply or in deciding when to move onto a better feeding site, but in optimising the quality of their diet, its processing time and its digestion. Some authors have claimed therefore that the most important objective for grazing animals should be the achievement of the best mix of nutrients within a fixed total food intake (Westoby 1974, Belovsky 1978). Others have questioned this view and suggested that energy intake remains most important, as in most predators (Owen-Smith and Novellie 1982).

Because of the problems of plant digestion, most mammalian herbivores possess complex guts compared to the predators. Gut expansions accommodate symbiotic microbial populations (McBee 1971), because vertebrates do not possess enzymes of their own which can break down the tough cellulose cell walls of their plant food (Bell 1971, Janis 1976). This strategy is most highly developed in the ruminants with their complex of 'stomachs' including the large fermentative rumen. However, fermentative forestomachs are also found in kangaroos, whales, dugongs, the hippopotamus, sloths and colobid monkeys. Other non-ruminants, such as the horses, the rodents and the lagomorphs are usually endowed with enlarged caecae and possibly other hindgut modifications eg. the horse colon (McBee 1971). Moreover, some rodents and the lagomorphs are copraphagous - the practice of ingesting soft faecal pellets in order to pass them through the gut a second time. This system is essential for the adequate nutrition of these species as they will die if they are prevented from carrying out this procedure (Young 1962).

Avian grazers are largely restricted to the Anseriformes and Galliformes. The browsing Galliformes (ie. the Tetraonids) have been intensively studied over the last 30 years (see, for example, Hudson and Watson 1985) and have been shown to possess some of the morphological and physiological adaptations to grazing found in the mammals, ie. caecal fermentation allowing the digestion of cellulose (McBee and West 1969, Moss 1977). The Anseriformes, however, have less well developed caeca and do not seem to be able to digest cellulose to any great extent (Marriot and Forbes 1970, Mattocks 1971). This results in significantly lower digestive efficiences when compared to the Tetraonids (Sibly 1981). One suggested reason for the simplicity of the wildfowl gut is that intestinal elaboration is incompatible with the long migratory flights of ducks and geese - weight must be kept to a minimum (Harwood 1975). Grazing Anseriformes therefore rely on ingesting very large quantities of food, which they pass through the gut rapidly and digest inefficiently (Owen 1972b). Thus, they have to use behavioural strategies rather than physiological/ morphological ones to optimise their nutrient intake (Harwood 1975).

When comparing the nutrient requirements and feeding strategies of different animals, one other factor which must be taken into account is the body size of the species concerned. Since basal metabolic rate increases to the 0.75 exponent of body mass (Peters 1983) the cost per gram of body tissue of maintaining a given biomass declines with increasing body size. This relationship is of particular importance to grazing species, feeding on an abundant but low quality food source, since energetic intake is limited by gut size (which increases linearly with body size). In effect this means that a large grazer can more easily meet its energetic requirements than a small one (Robbins 1983).

The wigeon (*Anas penelope*) is one of the smallest folivorous bird species. In winter it feeds entirely on coarse vegetable matter, mainly grasses. It is the smallest grazing anseriform - around half the size of the brent goose (*Branta bernicla*) (one of the smallest geese) and under three-quarters of the size of a mallard (*Anas platyrhynchos*). Although some grouse species are smaller, the wigeon is probably close to the smallest size a totally folivorous bird can become without major gut adaptations (the two members of the genus *Anas* which are smaller than wigeon, teal (*A. crecca*) and garganey (*A. querquedula*), both extensively supplement their diets with seed or animal material). For these two reasons therefore (diet and body size) the wigeon should theoretically face major problems in meeting its nutritional requirements. It thus provides an excellent subject to study how behavioural and physiological strategies used by a grazing animal can maximise its nutritional intake, ie. how is the behaviour and physiology of the wigeon adapted to its ecology.

In the last 15 years much work has been carried out on grazing wildfowl - in Britain (eg. Owen 1971, 1972a, 1972b, 1976), in America and Canada (eg. Harwood 1975, 1977, McLandress and Raveling 1981) and in the Netherlands (eg. Drent et al 1979, Ydenberg and Prins 1981). This research has, however, been carried out entirely on geese. Anecdotal accounts of wigeon feeding behaviour date back to the turn of the century. Most of these observations were made by wildfowlers, whose knowledge of their quarry species was often quite considerable. The majority of these authors (eg. Millais 1902) reported that this species fed primarily on coastal mudflats, its diet consisting mainly of eelgrass (*Zostera* spp.). However, many authors also reported regular inland feeding, mainly on saltmarshes but also on flooded inland pastures (eg. Cornish 1903, review in Glegg 1943).

The decline in *Zostera* stocks during the 1930s (probably caused by a fungal infection) raised fears that wigeon (and brent goose) numbers would also decline (Berry 1939). However, Glegg (1943) suggested that the wigeon's diet was sufficiently varied to allow them to adapt to changing circumstances. Analysis of data on the distribution of wigeon in Britain today (Owen and Williams 1976) suggests that this prediction has, in fact, been realised. There has been a large increase in the use of inland sites, although this is probably due not only to the Zostera decline, but also to the increase in inland reservoirs and the establishment of unshot refuges.

Detailed studies of the diet of wigeon date back to the 1930s (Campbell 1936, 1946). These data, although biased towards coastal sites, suggested that in winter the diet was purely vegetarian and that any animal material was ingested accidentally. This result was confirmed by Olney (1965, 1970) during a study of the diet of several duck species on the north Kent marshes. In coastal situations he found that they fed primarily on Zostera and Enteromorpha or the saltmarsh grass Puccinellia. Inland, their guts contained a variety of grasses, eg. Glyceria, Festuca, Poa and Agrostis.

More recent studies of wigeon feeding ecology (Owen 1973b, Owen and Thomas 1979, Williams & Forbes 1980) have again dealt primarily with diet selection. However, Owen (1973b) did also look at feeding site selection on saltmarsh at Bridgwater Bay, Somerset. This study constituted the first detailed research into wigeon feeding ecology outside diet analysis. The management implications of this work were also studied in some detail (Cadwalladr et al 1972, Cadwalladr and Morley 1974). Finally, Kanel (1981), whose main research looked at numbers, distribution and feeding activity of wigeon in the Ouse Washes over a single season, also carried out a few experiments on food availability for wigeon and the effects of this on their grazing. In general then, wigeon feeding ecology and behaviour has received little attention apart from diet analyses, not only in its own right but also in relation to herbivory in small animals.

This thesis is divided into six main sections dealing with the behavioural (Chapters 3-7) and the physiological (Chapter 8) strategies used by wigeon to maximise nutrient intake. Chapter 3 introduces the theoretical problems faced by wigeon in obtaining enough energy by attempting to estimate the daily energy expenditure of the bird. The simple behavioural strategy of feeding for long periods to increase food intake is discussed. Chapter 4 looks at feeding site selection in wigeon and the factors which influence where they feed. The ways in which wigeon feeding behaviour is adapted to different grassland types is studied in Chapter 5, with emphasis being placed on the methods by which wigeon capitalise on good feeding areas. Chapter 6 deals with the effects of wigeon grazing on the grassland, concentrating on the importance of protein intake to these birds. Chapter 7 is a study of the benefits of, and reasons for, the characteristic tight feeding flocks found in wigeon. Finally, Chapter 8 examines some of the physiological adaptations to herbivory found in this species.

CHAPTER 2

STUDY SITE AND GENERAL METHODS

2.1 STUDY SITE

Virtually all of the work reported in this thesis was carried out at Eastpark Farm, a Wildfowl Trust refuge at Caerlaverock, approximately 7 miles south of Dumfries on the Solway coast (Grid Ref. NY 051656). This reserve was established in the early '70s, primarily to provide undisturbed winter feeding grounds for the flock of barnacle geese (Branta leucopsis) which traditionally winters in this area. However, many other species of British wildfowl winter here, primarily wigeon, teal and mallard.

The fairly large population of wigeon (up to 800, normally around 450 - see Figure 2.1) which remains at Caerlaverock for most of the winter (late October - early April), along with the ease with which wildfowl can be observed, made Eastpark Farm an excellent site for this study.

The reserve comprises 235 acres of grass and arable fields and 600 acres of tidal merse (saltmarsh). The grass fields are grazed by cattle or sheep during the summer to provide a nutritious sward for the geese during winter. They are regularly re-sown (approximately every 5 years) with grass mixtures which are attractive to geese. The reserve adjoins the Caerlaverock National Nature Reserve which comprises 13,500 acres of foreshore and grazed merse. Thus, virtually the whole of the Caerlaverock 'peninsula' ie. Eastpark Farm and the saltmarsh running east to the Lochar River, is unshot and disturbance effects from this source are negligible. A little shooting can and does take place on foreshore in the Lochar River to the north-east of the reserve, but this is well removed from the main wigeon sites.

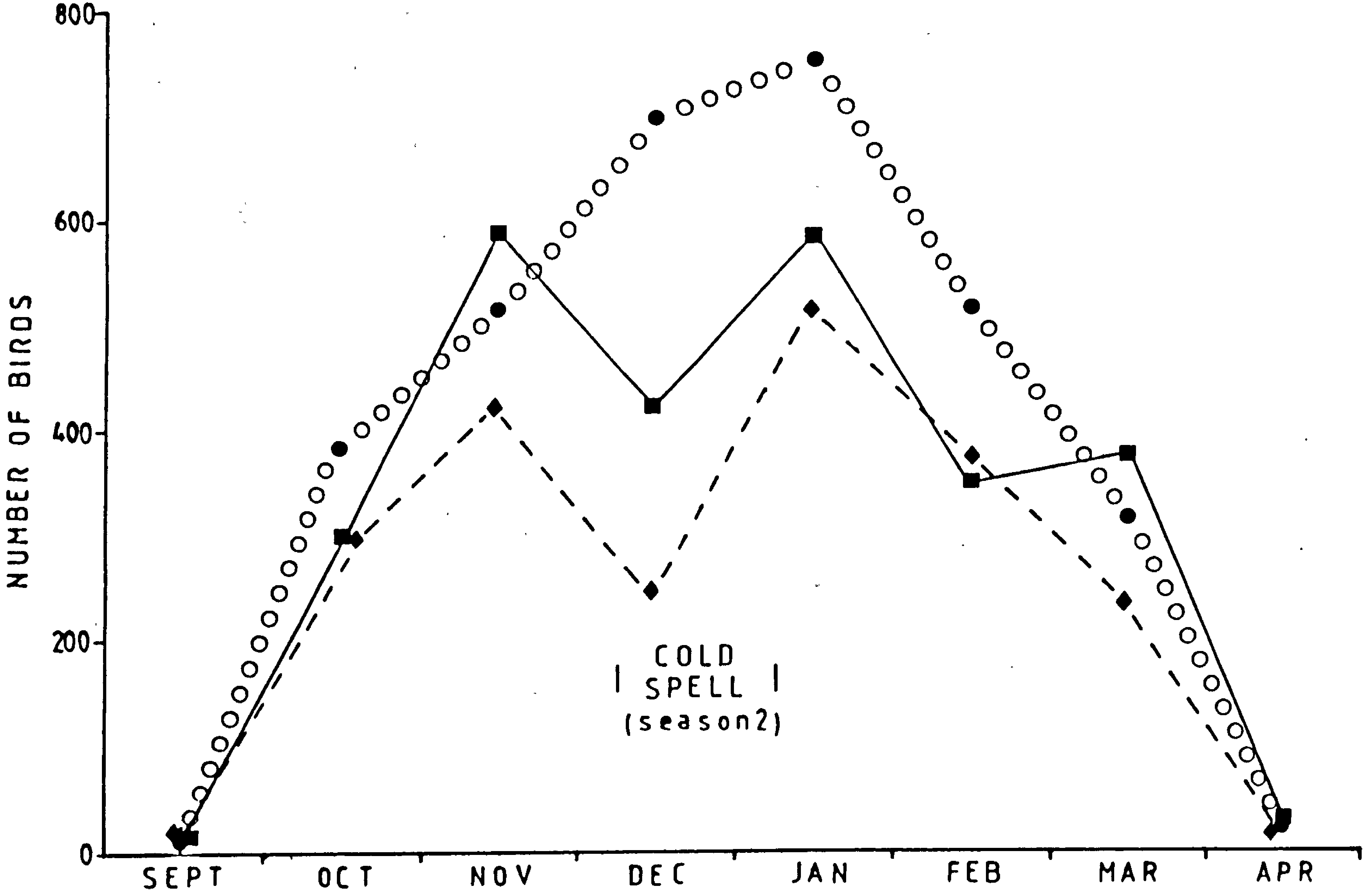
The area of importance for this study was confined to the ponds and field edges on either side of the two main roadways, which dissect the main 'inland' part of the refuge (see Fig. 2.2). In order to allow undisturbed viewing of the wildfowl and waders on the reserve, eight foot high earth embankments were constructed during the creation of the reserve to screen visitors walking on the roadways. Within these embankments, small fibreglass hides were positioned, allowing very close observation of feeding wildfowl in all weather conditions. The earth used to construct these banks was taken from the adjoining fields, thus creating borrow-pits along the edge of the fields. The design of these ponds are especially attractive to wigeon, since they have gently sloping edges leading to open grass fields - excellent for wigeon grazing.

Wigeon are, in fact, very dependent on water at their feeding sites (see Chapter 4), so that for the purposes of this study a 'wigeon feeding site' comprised a water body (whether a single pond, part of a pond or several ponds) plus an area of grassland extending to approximately 30m from the outer edge of the ponds(s). Although suitable feeding sites (according to the above definition) existed along the field edges adjoining the

Figure 2.1

Number of wigeon on the Caerlaverock Wildfowl Trust Reserve during the three study seasons. Data from single count in middle of month.

○ ○ ○ ○	Season 1
- - - - - -	Season 2
———————	Season 3


800
600
400
200
0
NUMBER OF BIRDS
SEPT
OCT
NOV
DEC
JAN
FEB
MAR
APR
COLD SPELL (season2)

embankments throughout the reserve, the wigeon concentrated their feeding on the sites nearest to the enclosure, possibly because they used this field as a resting area (see Chapter 4). Thus, ten sites were identified as being the main feeding sites for wigeon at Caerlaverock, labelled A to I excluding the enclosure (see Fig. 2.2). All these sites were virtually identical in their proximity to the roadways and their general pond design, eg. the slope of the pond edge. However, water depth did vary between ponds so that some were more likely to become very shallow in dry weather. All were overlooked by hides, whether tower hides (of which there were two) or fibreglass ones set into the banks.

The enclosure differed in several respects from areas A to I. Firstly the whole 20 acre field was surrounded by a fox-proof fence. Secondly, this field contained the main observatory pond which was fed with barley - once a day at about 0900 hours during the first winter, and twice a day (at 0900 and 1400 hours) during the second and third winters. Wigeon did come and take the grain on this pond, but this was not considered to influence this study, for two reasons. Firstly, most of the grain was in fact taken by the large numbers of swans (around 2-300 during mid-winter) which stayed on this pond and were dominant to the wigeon when feeding. Secondly, general observation of wigeon movement on the reserve, plus results from a few ringed birds, suggested that the wigeon which did take grain were a group of about 50-80 birds which stayed on the main pond for most of the day. Thus, although some 'wild' wigeon did occasionally supplement their diet with barley, this grain was not a regular or important part of their diet and the birds used for this study usually grazed throughout the whole of the day.

The section of the enclosure which was included as one of the feeding sites in this study was the 'teal pond' area (Fig. 2.2) which extended from the eastern side of this field to a line down the centre of the field. Birds which were grazing on this feeding site were included in the inter-site comparisons and other feeding studies, while birds which were using the observatory pond area were excluded.

2.2 GENERAL METHODS

Methods which are relevant to several chapters are included in this section, while all other methods pertaining to particular chapters are described in those chapters.

The study lasted for three winter seasons, from October 1980 to April 1983. Throughout this thesis, season 1 refers to October 1980 to April 1981, season 2 refers to October 1981 to April 1982, and season 3 refers to October 1982 to April 1983.

Adverse weather did occasionally hinder or terminate field work. Season 1 was a typical mild damp season and no problems were encountered apart from a few days of frost when ponds were frozen over. From the middle of December to mid January of season 2, one of the coldest spells recorded this century occurred. Temperatures regularly dropped to -17°C or below at night. After

Figure 2.2

Map of the 10 main wigeon feeding sites on the Caerlaverock Wildfowl Trust Reserve.

▨ Main buildings/observation towers


ENCL
Teal pond
H
I
A
B
C
D
E
F
G
N
Approx scale:
100 m

a few days most birds left Caerlaverock and so fieldwork ceased. Season 3 was extremely wet initially, but no great problems were encountered. However, during February frosts occurred most nights and some of the ponds were regularly frozen.

All observations were carried out from the nearest hide to the observation site. This was usually one of the small fibreglass hides set into the embankments, or the large observation tower overlooking site I (Fig. 2.2). Observations on site A were made from the house tower which was attached to the main farmhouse building. This tower, about 35 ft high, also gave excellent views of all the main wigeon feeding sites, so that overall counts could be made and the best flocks for observation pinpointed each day.

All observations were made using a pair of 8 x 40 binoculars and a 25-40x prismatic zoom telescope. A large pair of naval binoculars (22-32x) were available in the house tower.

The total number of wigeon on the reserve (see Figure 2.1) was assessed once a month on the most convenient day nearest the middle of the month. A general count was carried out from the main observation tower, but more detailed counts of each area, eg. the observatory pond (see Figure 2.2) were carried out if necessary.

Throughout this project, if it was necessary to select an individual bird for a particular study, the focal bird was selected at random by 'unconsciously' choosing a bird and moving three birds left or right. If the sex of the bird was important for the observation, then the nearest bird to this random one of correct sex was chosen.

All statistical tests and methods were used as in Siegel (1956), Bailey (1959), and Nie et al (1975).

2.3 GRASS AND FAECAL MEASUREMENTS AND ANALYSES

Since data derived from these analyses are used in several chapters, all methods relating to this subject are described here.

2.3.1 Collection and storage of samples

All grass samples, whether collected from exclosures or the field, or whether they were for grass quality or digestive efficiency analyses, were collected by hand grazing rather than clipping. This involved grasping the grass blades between the thumb and first finger and plucking. This was done for two main reasons. Firstly it was extremely difficult to clip and collect the short grass swards at Caerlaverock. Secondly this method more closely simulated the method of grazing used by wigeon (Owen 1976a) which was very important in, for example, digestive efficiency samples (see Chapter 8.2).

Wigeon produce easily identifiable solid faeces, which are very simple to collect. Only fresh droppings were collected - these could be identified by the fresh colour of the uric acid crystals which are deposited on the outside of the dropping.

Both grass and faecal samples were collected in plastic bags which were labelled, sealed and frozen (within 15-30 mins) in a deep freeze at Eastpark Farm. At the end of the season samples were transported to the Zoology Department at Glasgow University and frozen again. MacRae et al (1975) have shown that freezing and thawing have no effect on total nitrogen or fibre levels in grasses.

When required for analysis, grass samples were thawed and dried at about 30-40°C for a few hours in order to remove excess moisture and were then sorted into green and dead portions. Only completely green material was used in the analyses. Although grazing wildfowl almost certainly do take in some dead material in winter the actual amounts are low eg. 15% in a sward of 50% dead material (Owen 1971). Moreover the selection of green material alone allowed standardisation of samples. All samples were dried at 80°C for at least 15 hours (normally longer) in a drying oven. They were then ground to a powder with a pestel and mortar before weighing and analysis.

2.3.2 Grass quality analyses

The crude protein content of grass samples was assessed using a Kjel-Foss 16200 Automatic Kjeldahl Analyser at the Department of Animal Husbandry, Veterinary School, Glasgow University. This machine automatically performs a standard Kjeldahl digestion in sulphuric acid, and then measures ammonia production by titration. Grass samples were dried at the Zoology department, transported in a dessicator to the Veterinary school and then weighed there. Two replicates of each sample (of between 0.2 and 0.6g dry weight) were analysed. Crude protein content was estimated by multiplying the total nitrogen figure by 6.25.

Fibre levels were measured using the acid-detergent fibre method of van Soest (1963). The method used was exactly as described in the paper except that it was scaled down by a factor of ten, ie. 0.2g of sample was added to 100ml of the CTAB solution. The analysis was carried out at Strathclyde University, Glasgow, where suitable equipment was available.

2.3.3 Calorific content of grass and faeces

This analysis was again carried out at the Department of Animal Husbandry at the Veterinary school using a Gallenkamp automatic adiabatic bomb calorimeter. Two replicates (0.5 - 1g dry weight) of each sample were analysed.

2.3.4 Silica-free ash content

The silica-free ash content of grass and faecal samples was assessed using the methods described by Allen et al (1974).

2.3.5 Biomass estimation

Because of the amount of time required to clip, sort, dry and weigh samples for repeated biomass measurement, it was decided to attempt to build a portable spectrophotometer for biomass assessment. This project was started during the summer following season 1 and the instrument was tested and ready for use by January, season 2. The details of the design, calibration and accuracy of the spectrophotometer were published in Oikos 43: 62-67 (see Appendix 1). This instrument was in fact found to be indispensable to the project, since it allowed biomass measurements to be taken on a large number of sites each month. The actual process of biomass estimation took only a few seconds.

2.3.6 Grass height estimation

This variable was measured using a ruler to which was riveted a flat metal spike. This spike could be pushed into the ground and the ruler left in an upright position. The observer then moved approximately ten metres away from the ruler and viewed it using a pair of binoculars. The 'average' sward height could be assessed fairly accurately as the point below which the ruler could not be seen. The height was taken to the nearest 0.5 cm.

2.3.7 Grass species abundance

This was assessed using a point-quadrat method (Goldsmith and Harrison 1976). This method basically measures plant abundance by percentage cover, ie. the proportion of the ground occupied by each species. A plastic frame was constructed from which ten knitting needles could be suspended - in a straight line with a 1 cm gap between each needle. The frame was then placed on the randomly chosen sampling point (see page 24) and the needles were lowered one at a time. The species of the first leaf touched was recorded. In this way, 10 'hits' were recorded from each sampling position, and 100 'hits' from each feeding site (10 sampling positions).

CHAPTER 3

THE DAILY FOOD INTAKE OF WIGEON

3.1 INTRODUCTION

This chapter aims to establish the daily energy requirements of wigeon. In so doing, it also aims to quantify the theoretical problems faced by wigeon in obtaining enough energy. This is done primarily by comparing this bird's energetic requirements with similar estimates for the larger grazing geese in order to consider the effect of the wigeon's small body size on their daily food requirements. From this standpoint, the strategies used to overcome these problems are investigated in this and the following chapters. In particular, the strategy of feeding for long periods is discussed here in detail.

Daily food intake is an extremely difficult variable to quantify in wild animals. With a captive animal it is a fairly simple operation to feed it so that it does not gain or lose weight, calculate the total food intake and total faecal output over a period of several days, and then work out its energetic intake from the difference. However, the relationship between this "existence metabolism" of a caged bird and a wild animal's "daily energy expenditure" (D.E.E.) is a matter of some dispute (Kendeigh et al 1977).

In most animals, to assess D.E.E. directly, one has to quantify the total weight of all food eaten throughout the day and, knowing its calorific digestibility, calculate its energetic intake. Alternatively, one can carry out a detailed time-budget analysis for the wild animal, calculate the energy required for each activity, and simply sum the increments to arrive at a figure for its total energy requirements. Both of these methods face problems in terms of accuracy or technique. Finally, a more recent method involves the use of doubly labelled water (D_2 O^{18}), injected into the blood-stream to assess metabolic rate (eg. Bryant and Westerterp 1980). However, the expense of this technique and its methodological problems (eg. recapture of the animal) make its use somewhat limited.

There is, however, a method of assessing D.E.E. in grazing wildfowl, which, to some extent, presents no major methodological problems and should give a reasonably accurate result. This is based on the fact that these birds defaecate very regularly and produce discrete, easily collected faeces. Thus data on dropping weight, defaecation rate and total time over which this rate is maintained allows an estimate of total faecal output per day. This can be converted to food intake from digestive efficiency studies. Finally the calorific value of food and faeces can be measured, to give an estimate of D.E.E. The simplicity of this method has resulted in its use in several studies on grazing geese, eg. white-fronted geese (*Anser albifrons*) (Owen 1972b), barnacle geese (Ebbinge et al 1975), upland geese (*Chloephaga picta*) and ruddy-headed geese (*C. rubidiceps*) (Summers and Grieve 1982). However, it has never been used to assess D.E.E. in wigeon.

3.2 METHODS

3.2.1 Measurement of foraging time

The proportion of the day spent grazing by wigeon was estimated by instantaneous sampling procedures (Altmann 1974). Flocks of between 35 and 350 (normally about 70-150) birds were observed from dawn to dusk on five separate days, approximately one each month from the end of October to March, season 3. The actual dates were 28/10/82, 30/12/82, 21/1/83, 21/2/83, 16/3/83. Normally the main flock stayed in the same field for the whole day and was observed from the nearest hide. However, on one of the observation days the flock moved to another field and so the observation hide was changed. Birds regularly joined or left the flock throughout the day so that the total sample size varied not only between days but also within days. Every 15 minutes the flock was counted and the number of birds actively foraging (ie. head down and feeding) was recorded. No other activities were recorded.

An attempt was also made to assess nocturnal foraging which could obviously be of great importance in terms of total food intake, but which has been the subject of rather contradictory reports (Owen and Thomas 1979, Kanel 1981). Night observations were carried out using an image-intensifier. It proved possible to get accurate observations on feeding/ non-feeding birds only on brightly moonlit nights. Even on these nights it was often impossible to locate or get near to actively grazing flocks. Thus, only two full (or almost full) nights' observations were carried out, one in November (28/11/82) and the other in February (23/2/83), season 3. During the section of the night when the birds were actively grazing, the flock was counted and the number foraging recorded (as above) every 15 or 30 minutes. When the flock finally stopped grazing, observations were carried out once each hour. The flock size varied from 30 to 130 birds. On eight other nights in season 3, observations were made (though not throughout the night) in an attempt to ascertain whether wigeon grazed nocturnally in all phases of the moon.

3.2.2 Other measurements

Average dropping weight was calculated from a total sample of 149 fresh droppings, collected from five different grazing sites throughout the year during season 3. There was no seasonal effect on dropping weight. The droppings were dried overnight at 80°C and individually weighed. Average defaecation interval was calculated from the mean of 274 timed intervals carried out during all times of the year, on all sites and at all times of the day (see p.51).

The calorific content of grass and faeces was calculated from the mean of 12 grass samples and 9 faecal samples (collected from wigeon-grazed areas on several sites, throughout seasons 2 and 3) according to the method outlined on p. 8.

3.3 RESULTS

3.3.1 Foraging time

Figure 3.1 shows the mean percentage of birds actively foraging for each hour of daylight. This data is based on the five full observation days - a total of 180 individual observations. On average the wigeon at Caerlaverock spent 74.0% of the daylight hours actively foraging. The most intense foraging periods are clearly at dawn and dusk. There is also a tendency for foraging to decline during the middle part of the day, as has been reported in several other studies (Owen 1972b, Ebbinge et al 1975, Owen and Thomas 1979). Table 3.1 shows the average proportion of birds foraging for each individual observation day through the winter.

TABLE 3.1

Mean % birds foraging on each observation day in relation to lunar cycle.

DATE	AVERAGE PROPORTION OF BIRDS FORAGING	LUNAR CYCLE AT TIME OF OBSERVATION
28/10	74.2	1/2 - 3/4 moon
30/12	53.9	Full moon
21/1	68.5	1/2 moon
21/2	78.8	1/4 - 1/2 moon
16/3	91.3	New moon (ie. none)

Foraging intensity was not related to daylength, since the shortest day (30/12) was also the day of least intense foraging, nor air temperature, since the coldest day (22/2) was not the most intense foraging day. However, it may have been related to the lunar cycle, since there was a good negative correlation ($r_s = -0.9$, $n=5$, $P<0.05$) between foraging intensity during the day and lunar brightness (see Figure 3.2).

Figure 3.3 shows the mean percentage time spent foraging, for each hour of the night, based on the two full nights' observations. Unfortunately there is a gap in the data of 2 hours after dusk and one hour before dawn. However, for the total observation period ie. 1900-0630 hours (a total of 41 individual observations) an average of 39.0% of the wigeon were actively foraging. It should be emphasized that both of these nights were well lit by a full or three quarter moon.

Other, more casual, moonlit night observations (on 5 separate nights) gave similar results with a high percentage of birds grazing until around 0200 hours, but very few grazing after this

Figure 3.1

Mean percentage of birds actively foraging (± 1 s.e.) for each hour of daylight.

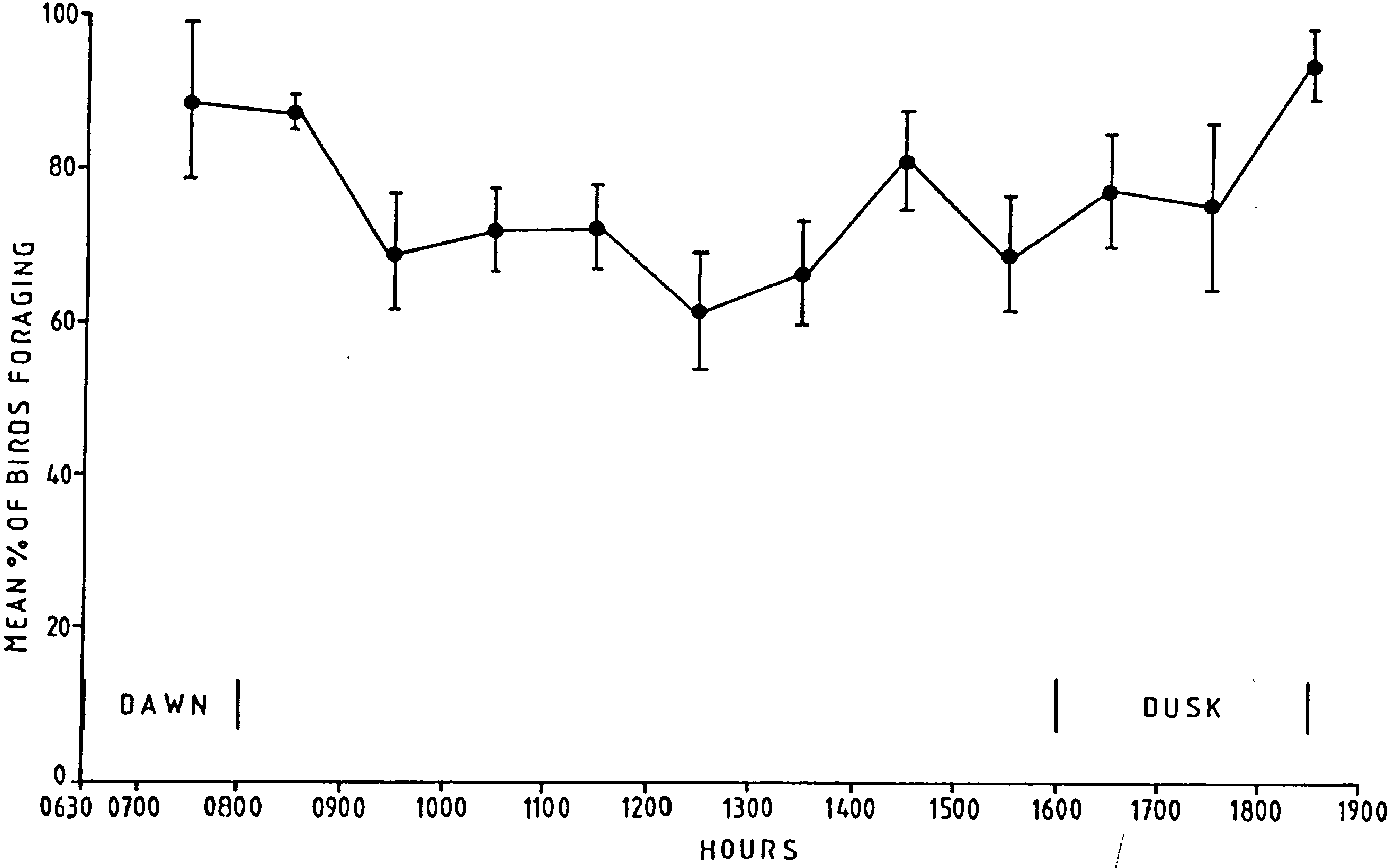

100
80
60
40
20
0
MEAN % OF BIRDS FORAGING
DAWN
DUSK
0630
0700
0800
0900
1000
1100
1200
1300
1400
1500
1600
1700
1800
1900
HOURS

Figure 3.2

Correlation between lunar phase and mean percentage of birds foraging for each feeding day (see Table 3.1).

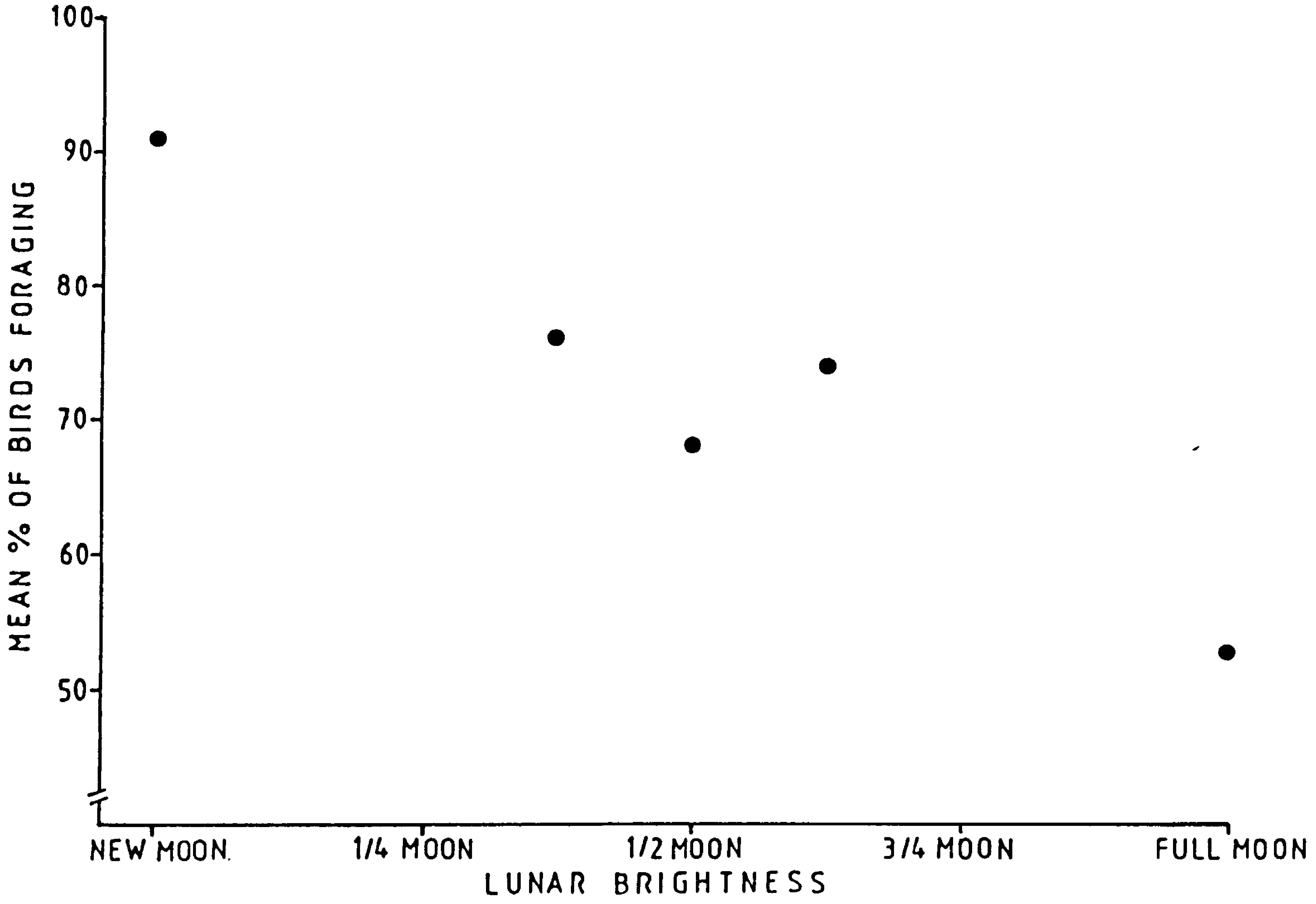
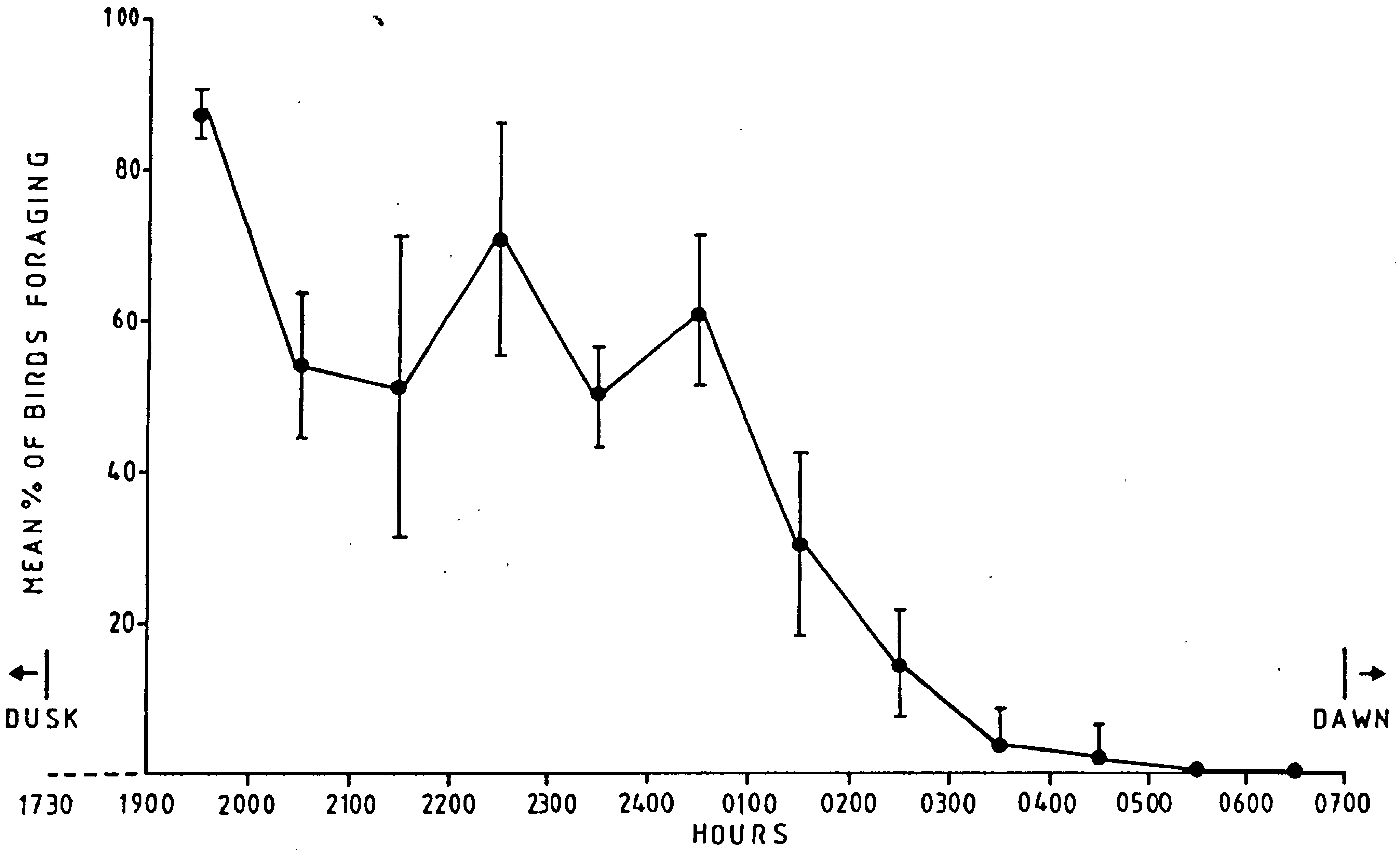

100
90
80
70
60
50
MEAN % OF BIRDS FORAGING
NEW MOON.
1/4 MOON
1/2 MOON
3/4 MOON
FULL MOON
LUNAR BRIGHTNESS

Figure 3.3

Mean percentage of birds actively foraging (± 1 s.e.) for each hour of the night.


MEAN % OF BIRDS FORAGING
100
80
60
40
20
DUSK
DAWN
1730
1900
2000
2100
2200
2300
2400
0100
0200
0300
0400
0500
0600
0700
HOURS

time. Cessation of feeding at this hour was not due to moonset, since on both full nights' observations, moonset occurred several hours after the birds had stopped grazing. Whether birds graze on dark nights is obviously very difficult to assess accurately. On one clear but moonless night, wigeon were observed moving about a great deal on the flashes in the centre of a field. This certainly suggested some active grazing even on dark nights, but this could not be confirmed, even using the image intensifier.

3.3.2 Other results

The mean defaecation interval of wigeon at Caerlaverock was 3.12 ± 0.15 mins. (n=274). The mean dry weight of a wigeon dropping was 0.193 ± 0.007g (n=149). The mean calorific content of the grass samples was 4.40 ± 0.06 Kcal (18.41 KJ)g^{-1} dry weight. The mean calorific content of the faecal samples was 3.87 ± 0.07 Kcal (16.22 KJ)g^{-1} dry weight.

3.4 DISCUSSION

3.4.1 Daily energy intake of wigeon

To calculate total daily faecal output of a wigeon, one must ascertain the length of time over which a measured defaecation rate is maintained. In two studies of geese (Ebbinge et al 1975, Summers and Grieve 1982), the authors simply measured the total time the geese spent on the feeding grounds and the average defaecation interval during this period, subtracted one hour for the inital time lag to defaecation at the start of the day, and added on an approximate figure for the number of faeces produced during the night (from food stored in the oesophagus: geese rarely feed at night except during the full moon). However, defaecation rate may alter with foraging intensity. Ebbinge et al (1975) found that barnacle geese foraged for 75-86% of the day, but assumed that defaecation rate remained constant, and cited some work on captive birds to back up their case. Summers and Grieve (1982) showed that in summer, when upland geese forage for only 69% of the day, there was a significant difference in defaecation rate between feeding and non-feeding birds. In winter, however, when 90% of the day is spent feeding, foraging intensity had little effect on defaecation interval.

Studies on throughput rate in captive wigeon (Chapter 8.1) suggested that intake rate may significantly affect throughput rate; but free-living birds forage more intensely than captive ones and defaecation rate in these birds may not be limited by intake rate but by the rate of passage of food through the gut (Drent et al 1979). Thus, a reduced intake for a short period may easily be made up by intensive foraging when feeding is resumed, and thus the effect on defaecation rate would be minimal. Moreover, any differences in defaecation interval would have been accounted for to some extent by the randomised method of choosing a focal bird (see p.7) since the intensity with which a wigeon had been feeding before the observation did not affect its inclusion in the sample. There are, however, still problems with using a single defaecation rate figure, most important of which is that no figure for defaecation interval during night feeding was obtained (since foraging intensity at night was lower than during the day, it is likely that defaecation rate was similarly lower). The approach taken here was therefore to calculate an approximate figure for the maximum intake rate of a wigeon ie. a bird which grazes all day and half the night (which is certainly the case on a moonlit night and may be so on a dark night) and maintains a steady defaecation rate throughout this period.

The length of the foraging period is not nearly so clearly defined as in the grazing geese, since wigeon at Caerlaverock do not move from feeding ground to roost en mass. However, each 24 hours, the foraging period is approximately 0730 hours to 0100 hours (see Figures 3.1 and 3.3). This assumes that birds continue actively foraging between dusk and 1930 hours (a fairly sound assumption) and that the foraging day includes only that period when 50% or more of birds were grazing. This would mean that the length of time during which the measured defaecation rate is maintained is 17.5 hours. No initial time lag to first defaecation needs to be taken into account in this analysis (as was done in the above goose studies) since it can be assumed that there will be a corresponding extension of the time during which defaecation occurs at the end of the active period - this is equivalent to the figure for faeces produced at night on the roost in the goose studies.

With a mean defaecation interval of 3.12 minutes a wigeon will produce approximately 338 droppings in 17.5 hours. Since the mean dry weight of a wigeon dropping is 0.193g, in a 24 hour period a single bird will produce 65.2g dry weight of faeces. The average digestive efficiency of wild wigeon is 28.8% (dry weight calculation) - see Chapter 8.2. A wigeon will therefore take in a maximum of 91.6g dry weight of grass, each day.

Since the mean calorific content of the grass at Caerlaverock was 4.40 kcal (18.41 kJ) g^{-1} dry weight and that of wigeon faeces was 3.87 kcal (16.22 kJ) g^{-1} dry weight, in a single 24 hour period, a wigeon would assimilate a maximum of about 150.7 kcal (631.1 kJ) of energy.

3.4.2 The foraging activity of wigeon

The most obvious method by which an animal can increase its energy intake is simply by increasing the amount of time it spends actively feeding. Barnacle geese for instance increase their feeding time from around 8 hours/day in mid-winter, when they only require to meet their immediate energetic demands, to virtually feeding around the clock on their staging islands off Norway, when they are building up reserves for breeding (M. Nugent, pers. comm.). This effect is also found when comparing species with different diets. For example, in a study of the feeding ecology of waterfowl on the Ouse Washes, England, Thomas (1982) found that the herbivorous species (eg. wigeon, gadwall (*Anas strepera*), coot (*fulica atra*)) spent a much greater part of the daylight hours feeding compared to the carnivorous or seed-eating species (eg. shoveler (*Anas clyeata*), teal, mallard). The most likely explanation of this is that the low energy value and low digestibility of the herbivore's diet necessitates a high gross food intake and consequent increased foraging time (Owen and Thomas 1979).

The results from this study (eg. 74% of the daylight hours spent foraging) show that the energetic problems faced by wigeon necessitate long, intensive feeding periods each day. This result compares well with Kanel's (1981) study of wigeon on the Ouse Washes in which she found that the birds spent 70-80% of the day actively foraging. Owen and Thomas (1979) however, found that wigeon spent slightly longer grazing (91.2% of the day) even though their study was carried out in the same area as Kanel's.

Grazing geese spend a similarly large part of the day grazing: white-fronted geese - about 90% (Owen 1972b), barnacle geese - 75 to 85% (Ebbinge et al 1975), upland geese and ruddy-headed geese - 90% (Summers and Grieve 1982). Another primarily folivorous duck, the gadwall, also spends most of the day feeding - 60% of daylight hours (Paulus 1984).

Night activity of wigeon is, as expected, less well studied. It is generally accepted that wigeon can and will feed both by day and night (Owen and Williams 1976). The deciding factor is thought to be disturbance ie. birds are primarily diurnal in undisturbed areas and nocturnal in disturbed ones. However, reports such as these do not necessarily mean that no feeding takes place outside of 'normal' hours: nocturnal birds could be feeding on less disturbed sites during the day and, as shown in this study, primarily diurnal birds do feed at night in many situations. This was also shown by Kanel (1981), who reported that wigeon spent 48% of one night in March foraging, which is close to the figure reported here (39%). However, Owen and Thomas (1979), working on this same site, suggested that little nocturnal feeding took place. This was based on the quantity of food found in the gut of birds shot during morning and evening flight. They did, however, report that diurnal feeding was more intense than in Kanel's study and this may explain the discrepancy. Finally, Owen (1973b) found that wigeon feeding at Bridgewater Bay, Somerset, were mainly nocturnal feeders, again based on quantity of food in the gut at different times of the day.

Other wildfowl vary in the amount they feed at night. Some are almost purely nocturnal eg. teal and pintail (Anas acuta), possibly as an anti-predator response, since most predation takes place during the day (Tamisier 1970, 1976). Ducks will also feed intensively at night during the summer on emerging insects (Swanson and Sargeant 1972). Geese are primarily diurnal but do feed at night during the full moon period (Ebbinge et al 1975, Ydenberg et al 1984), if badly disturbed during the day (Owen 1972a), or if dependent on tidal fluctuations for exposing their food supply (Lebret 1970, Burton and Hudson 1978).

The fact that grazing geese are not reported as being completely nocturnal in highly disturbed sites suggests that wigeon (which do seem to become mainly nocturnal) are preadapted to nocturnal feeding ie. they would feed at night as well as during the day without any human interference. Possible reasons for this are discussed in Section 3.4.4, but it is interesting to note that the only other primarily folivorous duck, the gadwall, also feeds extensively by night and day - 70% of the night is spent feeding (Paulus 1984).

Wigeon at Caerlaverock spend around 13 hours per 24 hours actively grazing when the nights are moonlit (ie. 74% of the daylight hours (approx. 10 hours) and 39% of the night - see 3.3.1). It is also likely that they spend some time grazing when there is no moon, since birds were observed moving about even on these nights. In this context it is interesting that the intensity of diurnal foraging was closely related to the lunar cycle - the fuller the moon, the less intense the grazing during the day (Figure 3.2). This suggests that nocturnal foraging time/ intensity may be reduced on dark nights so that wigeon need to feed more during the daylight hours. However, it is also likely that other variables, such as temperature, are also important in determining foraging intensity. Kanel (1981) suggests that wigeon spend around 15.5 hours actively grazing on the Ouse Washes and quotes another study, in France, in which wigeon were found to graze for 13-15 hours per 24 hours. This can be compared with the grazing geese which spend around 7-9 hours grazing per 24 hour period (Owen 1972b, Ebbinge et al 1975, Summers and Grieve 1982) and with another folivorous duck - the gadwall - 15.4 hours per 24 hours (Paulus 1984).

3.4.3 The effect of body size on energetic requirements

As was discussed in Chapter 1, wigeon feed on a diet which is poor in nutrients and not easily digested. They are of small body size and so require more energy (and protein) per unit body weight than larger birds. The ecological implications of size relationships will vary with the feeding habits of the species concerned. In a situation where there is a limited amount of a certain high quality food type available, eg. seeds or fruits, a smaller animal may be at an advantage to a larger one, since its absolute intake will be less and it will be able to meet its requirements more easily (Bell 1971). However, if there is an abundant low quality food source available, as is the case for most folivores, then energetic intake will be limited by the passage rate of food through the gut which in its turn is limited by the size of the gastro-intestinal tract (Robbins 1983). Since gut capacity varies linearly with body weight (ie. body weight to the power 1) in most species (Calder 1974, Robbins 1983) larger species will be in a more favourable energetic state compared to smaller species since more food can be gathered, transported and processed relative to energy requirements (Robbins 1983). Another effect is that smaller animals will lose weight more rapidly during periods of reduced intake ie. they are more susceptible to starvation (Bell 1971, Peters 1983). Wigeon should therefore face more difficulty in meeting their daily energetic demands than the larger grazing geese.

This problem is best illustrated by comparing some figures on energetic requirements and food intake. The barnacle goose has a body weight of 1900g (Drent et al 1979) and a standard metabolic rate (SMR) of 134 kcals bird^{-1} day^{-1} (based on the non-passerine equation of Kendeigh et al 1977). The wigeon has a body weight of 720g and an SMR of 61.7 Kcal b^{-1} d^{-1}. Thus, with a body size over 2.5 times that of a wigeon, the goose requires only twice as much energy for standard metabolism. The goose produces a dropping weighing 0.66g every 3.5 minutes and has a digestive efficiency of about 27.5% dry weight (Ebbinge et al 1975). Thus, using the figures for calorific content of grass and faeces in Section 3.3, a barnacle goose should assimilate 24.9 kcals hr^{-1} and thus meet its standard metabolic requirements in 5.4 hours. A wigeon, on the other hand, with a dropping weight of 0.193g, a defaecation interval of 3.12 minutes and a digestive efficiency of 28.8% (Section 3.3) would assimilate 8.5 kcals hr^{-1} of grazing and require 7.3 hours to meet its standard metabolic requirements. A scan of the figures will show that the main cause of this difference in intake is the small dropping size of a wigeon compared to that of the goose (a wigeon dropping weighs less than one-third that of the goose). The slightly higher defaecation rate in the wigeon is not sufficient to make up the difference in intake (8.6 kcals h^{-1} compared to 24.9 kcals h^{-1}). This reduced rate of food passage will be caused primarily by the wigeon's smaller gut size. Thus it can be seen that, even though its absolute energetic requirements are lower than those of the goose, the wigeon's low rate of food passage means that it must feed for longer to meet those energetic requirements.

3.4.4 Comparison of energy intake with theoretical estimates

In recent years, a number of attempts have been made to estimate the energy requirements of free-living birds - their daily energy expenditure (DEE) - from their body weight, in a similar way to SMR estimations. These have ranged from Kendeigh et al's (1977) equation based on sparrow energetics, to Drent et al's (1979) estimate of DEE approximating to 2.6 BMR. Recently two further allometric equations have been published based on large literature surveys (Robbins 1983, Walsberg 1983) the latter based on DEE estimates from 42 birds.

When applied to wigeon (body weight of 720.1g) all of these estimates lie in the region of 155-170 kcals $bird^{-1}$ day^{-1}. It is interesting to compare these theoretical estimates with the 'observed' maximum estimate of 150.7 kcals b^{-1} d^{-1} for wigeon at Caerlaverock with an active period of about 17.5 hours per day. While this 'observed' estimate is certainly as close to the theoretical requirements as most other species in the published graphs (Drent et al 1979, Walsberg 1983) it is, if anything, an over-estimate (see Section 3.4.1). Based on the data collected at Caerlaverock, a bird grazing purely on grass would need to feed for 19 hours per day to meet the above theoretical requirement. While no great weight can be put on the detailed accuracy of these estimates, this type of data would suggest that nocturnal foraging is an essential part of the wigeon's normal feeding strategy and not just an artifact of human disturbance.

Thus, in a totally natural situation, wigeon may have evolved to feed around the clock in order to meet their relatively high energetic demands. In disturbed areas, they shift the balance of their feeding to nocturnal grazing. In mid-winter purely nocturnal grazing (of over 16 hours) should meet their requirements. However, in autumn and spring, unless birds have access to alternative foods of higher energy content than grass, eg. grain, they should require to feed at night as well as during the daylight hours. It would be interesting to investigate whether the reports of wigeon populations which spend all day on the roost (Owen & Williams 1976) are from areas where birds have access to, for example, spilt grain, or whether they are based primarily on mid-winter observations. These results can be compared with Dugan's (1981) research of nocturnal foraging in grey plovers. He found that diurnal feeding in winter would only rarely meet BMR requirements in this species, and that the major part of the plover's energetic requirements must be met at night.

In general then, once the rate of energetic intake is set, there are only two strategies open to a small animal for achieving energetic balance (Storer 1971). One is to reduce metabolic requirements as in the bats and humming birds. The other is to feed day and night as in shrews. Wigeon have opted for the latter strategy.

CHAPTER 4

THE SELECTION OF FEEDING SITES BY WIGEON

4.1 INTRODUCTION

This chapter considers the factors which influence where wigeon feed. It comprises the most detailed study of the project, since the selection of suitable feeding sites was considered to be one of the most important ways in which wigeon could enhance their nutrient intake.

Animals should select habitats that maximise their fitness (Kaminski and Prince 1981a). In most species, the two most important factors which affect fitness are food and predation. Thus, an animal should select an area which allows maximal foraging efficiency and maximal safety. There is, however, a strong possibility that these requirements will lead to conflict.

The importance of foraging efficiency to fitness has led to a vast literature on optimality in animal feeding (see Krebs 1978). Unfortunately, many of the ideas used to describe the optimal foraging of 'predators' feeding on discreet prey items are not applicable to herbivores (Owen-Smith and Novellie 1982). Nevertheless the concept of maximisation of nutrient intake per unit time (nutrient here includes energy yield) is as relevant to herbivore as carnivore. One of the simplest methods an animal can use to maximise its rate of nutrient intake is to select an area (or 'patch') which contains a high food density. This has been shown to be the case for a wide variety of species from redshank (Tringa totanus) feeding on amphipods to coccinellid larvae preying on aphids (Krebs 1978).

The literature on feeding site selection in wildfowl is large and varied. The hypothesised reasons for site selection include:

a) Factors affecting foraging efficiency

These are primarily the biomass, height, primary production, nutrient composition, and species composition of the food. The first three should generally increase energy, ie. calorific intake, the last two nutrient, eg. protein intake. It is, however, recognised that many of these factors will interact. Thus, selection for primary producton may well be the best way to maximise protein intake, and selection for protein may well increase digestive efficiency and thus calorific intake of the food (Owen et al 1977). All of these factors have been claimed as the basis for selection in some species of wildfowl at some time of the year. The biomass of food on a site was found to be important in some of Owen's (1972a) work on white-fronted geese at Slimbridge, in Drent et al's (1979) study of barnacle and brent geese in the Netherlands, in Buxton's (1981) and Bryant and Leng's (1975) studies on shelduck (Tadorna tadorna), in Eriksson's (1978) work on goldeneye (Bucephala clangula) ducklings and in Kaminski and Prince's (1981b) research on dabbling duck foraging in artifically created habitats.

The height and rankness of the vegetation was considered to play a leading role in the site selection of wigeon at Bridgewater Bay (Cadwalladr et al 1972, Owen 1973b, Cadwalladr and Morley 1974) and also in white-fronted goose foraging (Owen 1975b). The primary production on each site was found to be the major determinant in barnacle goose site selection during spring in the Netherlands (Ydenberg and Prins 1981).

Possibly the best studied aspect of wildfowl feeding biology is that of food species selection. From studies carried out in Britain and especially North America detailed accounts exist of the food species taken by almost every species of wildfowl at all times of the year, using the techniques of gut analysis (eg. Owen and Thomas 1979) and faecal analysis (Owen 1975a). This aspect of the wigeon's feeding biology has been the subject of several studies, the most recent being: Owen (1973b), Owen and Thomas (1979), Williams and Forbes (1980). However, in only a few projects have the food species on a site been related to the site selection of wildfowl (eg. Owen 1971, Owen 1973b). In some cases Owen attempted to relate these species preferences to food quality differences (Owen 1973a,b). The food species (possibly related to food quality) available on each site were also found to be influential in feeding site selection by brent geese in Norfolk (Ranwell and Downing 1959).

b) Factors affecting the liklihood of predation

Sites which render a bird more vulnerable to predators may be less favoured, regardless of food availability. For instance, many authors have found disturbance to be the over-riding factor in site selection eg. in Owen's work on white-fronted geese (1972a, 1973a) and Newton and Campbell's (1973) study of greylag and pink-footed geese feeding in east Scotland.

The work described in this chapter was designed to investigate feeding site selection in wigeon. The layout of the study site lent itself to this type of research, since the reserve consists of several discreet feeding areas, all next to ponds and all equally available to wigeon (see Chapter 2). As mentioned above, disturbance has often been found to be the major factor determining site selection, and in some studies it has been necessary to correct for this variable in order to examine the effect of other factors (Owen 1972a). However, at Caerlaverock, disturbance is at a minimum, and it was therefore possible to examine the other factors affecting site use more easily.

In the first place, observations were made to see if site selection was actually taking place, and if so, how this was exhibited by the birds. Data was also collected on the number of sites used per day through the season. Next, based on the above results, the factors affecting this site selecton were examined. These were a) grass biomass, quality, species, height and primary production, and b) proximity to water.

The normal methodology employed in this part of the study was to record data on wigeon use plus all of the above factors for each site, and then look at the relationships between the levels of site use and the corresponding levels of each of the factors (normally using regression techniques). This is an 'a posteriori' approach to functional ecology (Calow and Townsend 1981) and suffers from the inherent problems of this methodology eg. the confusion of cause and effect and the tendency to see all traits as adaptive. Therefore, to study in more detail the most important factors affecting foraging site selection, an experimental approach was used. Areas of grassland were artificially fertilized and the effect on site use studied. This is a commonly used and very successful technique in herbivore studies (eg. Thomas et al 1964, Miller 1968, Harwood 1975, Owen 1975b). Artificially increasing food supply has also been used in invertebrate feeding studies, eg. starlings (Sturnus vulgaris) feeding on leatherjackets (Tinbergen 1976).

Finally, as part of an investigation into the importance of open water proximity to wigeon feeding site selection, some studies on vigilance rates were carried out. While being relevant to this section, they are discussed more fully in Chapter 7.

4.2 METHODS

4.2.1 Assessment of site use

The amount of use wigeon make of a particular site is a combination of two variables: the number of birds using the site and the amount of time spent on the site. Two different methods were used to measure site use, one direct but subject to some inaccuracy, the other indirect but more accurate.

a) Observational method

In season 1, site use was assessed by observation. Three times each day - dawn, midday (approx. 1200-1300 hours) and dusk - the position of, and number of birds in, all wigeon feeding flocks on the 10 study sites was recorded. Thus, birds which were resting on feeding sites were not counted. This was carried out from the main observation tower which provided good views of all sites (see p.7). All observations were recorded on a plan of the refuge, colour coded according to the time of observation. From these records a 'wigeon hours' figure was calculated for each site from the following approximations: each dawn observation was equivalent to 4 hours grazing (0700-1100 hours), based on the observation that most flocks grazing in the morning would stay till that time; each midday observation was equivalent to 3 hours (1230-1530 hours); each dusk observation was equivalent to 3 hours (1530-1830 hours). Thus a site which had 20 birds grazing at dawn, 10 at midday and 30 at dusk would be given a wigeon hours figure for that day of 200: (20x4) + (10x3) + (30x3). This method was obviously an approximation since birds would move to and from sites between observations, and dawn and dusk observation times would alter according to day length during the season. However, it was considered to give the most accurate measure of site use from the available data. It should also be recognised that observations only took place on about 5 days/ week through the season. These figures do not therefore give total wigeon hours for each site, but can be used for comparisons between sites.

From the daily wigeon hours figures, monthly or seasonal figures were calculated for most site use analyses.

b) <u>Droppings density method</u>

The inaccuracies of the previous method were two-fold: firstly it was not possible to be present at Caerlaverock every day to observe wigeon and secondly birds were feeding at night, which obviously excluded accurate observational techniques. In seasons 2 and 3 therefore droppings densities on each of the sites were used to assess site usage, after the method of Owen (1971). This technique is very sensitive since wigeon defaecate approximately every 3 minutes (see Chapter 3). It also gives an indication of total use of a site.

On each study site, droppings quadrats (marked at each corner by bamboo posts which protruded approximately 4cm out of the ground) were marked out. Because of the considerable time input (in terms of field data collection and lab analysis) required to sample each site, the least used site (G) from the season 1 data was not marked out with quadrats. Also, since it was not possible to obtain access to the enclosure site, no quadrats were marked out on this feeding area either (see p.27 for more details).

Owen (1971) found that this form of quadrat marking had no effect on goose usage. Since the pegs used in this study were much smaller than Owen's (4cm as opposed to 25cm) it was considered safe to assume that wigeon usage would be likewise unaffected. Furthermore, general observation suggested that wigeon completely ignored the bamboo posts when grazing.

All quadrats were counted every two weeks. This operation was carried out when no wigeon were grazing on the study sites, so as not to disturb the birds. Since droppings persist for at least a month, this frequency of counting was sufficient. A piece of string was stretched round the quadrat corners in order to accurately define the quadrat and all droppings lying wholly within the quadrat were counted. Droppings were removed from the quadrat as they were counted, so as to prevent recounting. On the occasions when a quadrat was partly flooded an approximation was used. If the flooding covered up to two thirds of the quadrat, the dry area was counted and the extent of flooding estimated. The dry area count was then multiplied up to give a figure for the whole quadrat. If the flooding covered more than two thirds, the quadrat was ignored for that fortnight's count. However, heavy flooding was rare and excluded counting on only about one quadrat once per season.

In season 2 quadrats were made 3m x 2m in size. They were laid out fairly regularly over each study site in lines following the edge of the ponds (see Figure 4.1). The first quadrat line was laid out at the pond edge, the next line 10m beyond, and the final line 10m beyond that. Thus the centre point of each quadrat line was approximately 2m, 12m, and 22m from the water

Figure 4.1

Map of the ten study sites showing the positions of droppings quadrats in season 2. Circled quadrats are ones which were used in inter-site comparisons (see p.28).


N
Approx scale:
1
100 m

edge. All quadrats (total number = 61) were individually numbered during data collection to allow accurate analysis of results. It will be seen from Figure 4.1 that the number of quadrats on each site altered according to the size of the site and the amount of use wigeon had made of the site.

In season 3 a different method was used, since the season 2 method had resulted in uneven sampling of all sites. Six quadrats were placed on all sites in season 3 (see Figure 4.2), two next to water, two 10m beyond and a final two 10m beyond that, as in season 2. The distance between quadrats along the pond edge was fixed by random numbers. However, once the position of these first two was decided, the others were placed in line behind them.

In season 2 it was found that a quadrat size of 3m x 2m was too large, since the density of droppings meant that it was taking too long to count each quadrat. The quadrats were therefore reduced to 2m x 2m in season 3. They were counted in exactly the same way as in season 2. A total of 48 quadrats were marked out in this season.

While the droppings density method of assessing site use was clearly more useful and accurate than the observational method, it is theoretically subject to error, when used to compare between feeding sites of variable biomass (as in this study). This is because birds which feed in high biomass areas should theoretically have higher intake rates and thus might have higher output, ie. defaecation rates (see Chapter 5). This would mean that a similar number of wigeon using two sites, one high and one low biomass, for a similar time period would deposit more droppings/ m^2 on the high biomass site than the low biomass site. The difference in droppings density would not reflect site use but would be an artifact of the biomass on the site. This possible source of error was checked by recording the defaecation rate on five of the main feeding sites (A,B,D,H,I) during season 2 (see Chapter 5.2 for methods used). The results are shown in Table 4.1. An analysis of varience test was carried out on the data and was found to be not significant (F = 0.8714 with 4 + 104 d.f.). Thus the variability of biomass on these sites did not result in a significant difference in defaecation rate. The use of droppings density to assess site use is, therefore, valid in these situations.

Figure 4.2

Map of the ten study sites showing the positions of droppings quadrats in season 3.


N
Approx scale:
1 100 m

TABLE 4.1

Defaecation intervals on five feeding sites, season 2.

Feeding Site	Mean Defaecation Interval (±1s.e.)	n
A	2.93 ± 0.17	38
B	2.73 ± 0.15	8
D	3.00 ± 0.28	19
H	2.47 ± 0.17	17
I	2.96 ± 0.17	28

The implications of this result for the function of feeding in high biomass sites is discussed in Chapter 5.

4.2.2 Assessment of other site variables

(See Chapter 2 for accounts of methods used for grass and faecal analyses).

Biomass was measured on all droppings quadrats once a month during seasons 2 and 3 using the spectrophotometer. However measurements did not begin until January season 2, since the instrument was not ready before then.

Protein was measured from the 'wigeon grazed' samples (see p.66) which were collected once a month during seasons 2 and 3. Fibre was measured from these same samples. However not all samples were analysed for fibre so that only start of season (November) and end of season (March) results were used in the site use analyses.

The primary production of ungrazed grass was assessed (using the spectrophotometer) on those sites with an ungrazed exclosure (see Chapter 6.2), ie. A,B,D,H,I. The data used was for late winter only (January-March) and was collected in season 2.

Grass height was assessed on all droppings quadrats once a month. Again this was measured in season 2 only.

Food species was examined by point-quadrat on all sites in September/October of season 3, ie. before the birds were regularly grazing the sites. Ten sampling points were chosen in each area using random co-ordinates obtained from a random numbers table. The position of each sampling site was found by pacing out these co-ordinates.

4.2.3 Fertilizer experiment methods

In season 3, two separate field experiments were conducted, one on site A and the other on site I, using fertilized vegetation. The rationale behind this work was to compare the site use of (Chapter 4) and the behavioural changes on (Chapter 5) fertilized and unfertilized vegetation.

In late September, 10 vegetation strips (3m wide) were marked out on site A with coloured bamboo posts. These strips were clearly visible from the main observation tower, so that a bird could be easily assigned to a particular vegetation strip. Alternate strips were fertilized using a standard agricultural fertilizer (22N:11K:11P) applied at the rate of $20gm^{-2}$. A warm damp autumn resulted in very obvious differences in biomass within a month. Due to the varied strip lengths, 14 droppings quadrats (1m x 1m) were set out on the strips: ie. 7 fertilized and 7 unfertilized. All quadrats were less than 5m from water.

Droppings counts were carried out every two weeks through the season. Biomass on the quadrats was measured once per month using the spectrophotometer and averaged for the fertilized and unfertilized strips. Protein content of the green grass was assessed (once per month) by hand-grazing grass from an approximate 15 x 15cm plot, chosen at random, on each strip. Samples from each treatment (ie. fertilized/ unfertilized) were pooled, thoroughly mixed, and the protein content analysed in the usual way.

The use of fertiliser in the autumn led to changes in both biomass and protein content of the grassland. To separate these effects a second experiment was run in Season 3 on site 1 in which fertiliser was applied in spring (9/3/83). This led to an initial increase in protein content without a change in biomass, and the wigeon use of these experimental plots was studied. Again 10 strips (3m wide) were fertilized, as before. 10 quadrats (1m x 1m) were marked out, ie. 5 fertilized and 5 unfertilized. Three droppings counts were carried out on separate days over a 4 day period at the end of March. Biomass was measured this time by clipping for reasons discussed in the results (p.38). Protein was assessed (again during this 4 day period) in the same way as in the site A fertilizer experiment.

4.3 RESULTS

4.3.1 Feeding Site Selection

Before reporting the detailed results from the site selection studies, two general points on the way in which wigeon used their feeding sites during the daytime should be noted. Firstly, wigeon site use was, in many ways, based around the enclosure site (Figure 2.2). A great deal of feeding did occur here, but birds also rested around the teal pond to a far greater extent than the other sites. Moreover some observations suggested that this pond was regularly used as an overnight roost. Secondly, there was a distinct periodicity in the use made of other feeding sites (ie. A-G). On most days wigeon fed on these outlying sites from before dawn to around 1100 hours. They then moved to the enclosure where they remained for most of the rest of the day. This periodicity was not so apparent at the end of the season when birds regularly fed on outlying sites in the afternoon (possibly on account of the reduced food availability in the enclosure). Birds also tended to use the outlying sites throughout the day in very wet weather. The use of the enclosure as a "home base" by the wigeon was almost certainly because of the extra safety afforded by the fox-proof fence which enclosed this site.

In this first section of the results the question of whether wigeon were being selective in their choice of feeding site or were simply using sites at random, is investigated. Due to the larger number of sites which were studied and the measurement of site use employed (observation of wigeon hours/ day) all of this data refers to season 1.

Figure 4.3 shows that wigeon were highly selective in their choice of feeding site. Similar results were found in seasons 2 and 3 using droppings counts /m^2. The data from season 1 was tested for deviation from uniformity by a X^2 test and found to be very significantly different from a random distribution (X^2=105806; df=9; $p<0.001$). As discussed above, the amount of use made of the enclosure was well above that of the other sites. It should be remembered that this data refers only to feeding birds.

This preference for certain sites was not solely exhibited in the total amount of use (ie. total wigeon hours through the season) but also in the timing of site use. This can be seen in Figure 4.4, in which the percentage of the total wigeon hours (ie. sum of all sites) which was spent on each site has been calculated for each month. In this figure, sites have been arranged in order of decreasing preference (see Figure 4.3) with the most frequented sites at the top. If one considers the November to March period alone (for reasons discussed below) one finds that the most frequented sites tend to peak early in the season and the least used peak at the end of the season (the arrows, which mark the peaks for each site, move from left to right as one moves down the figure). This suggests that the attractiveness of a site (in relation to the other sites) varies through the season. In fact, if the peak month of attraction is plotted against the rank of the number of wigeon grazing hours (the larger the wigeon hours figure the higher the rank) one finds a significant negative correlation (Figure 4.5 - $r_s = 0.875$, $n = 10$, $P < 0.01$). Thus the most frequented sites are most attractive early in the season. Preference is being shown by both amount of grazing and time of grazing. There are obviously some sites which do not exactly fit this picture eg. site I, but the general trend is fairly clear. The reason for excluding April from this analysis is that by March wigeon have 'spread out' as far as they are going to and, as numbers fall to only a handful in April, the remaining birds move back to a few sites, primarily those which were most frequented early in the season eg. the enclosure and site H. This effect can also be seen by studying the mean number of sites used per day by the wigeon (ie. the number of sites on which birds were observed grazing) as the season progresses (Figure 4.6). This number tends to increase

Figure 4.3

Total wigeon hours spent on each feeding site throughout season 1.

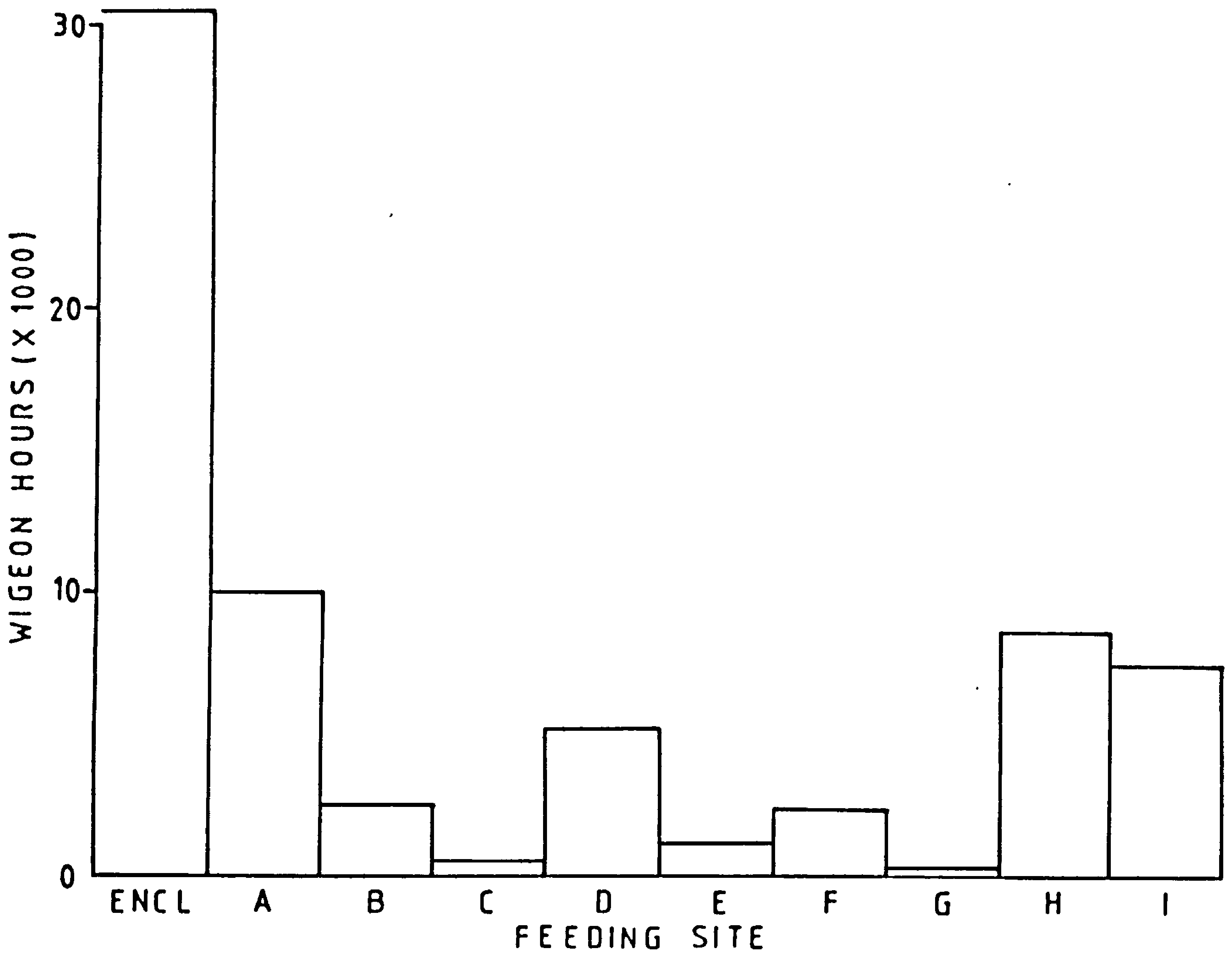

WIGEON HOURS (X 1000)
30
20
10
0
ENCL
A
B
C
D
E
F
G
H
I
FEEDING SITE

Figure 4.4

The percentage of the total wigeon hours (sum of all sites) which was spent on each site during each month of season 1. Sites arranged in order of decreasing frequency of use (see Figure 4.3). Arrows indicate the peak month of 'attraction' for each site.

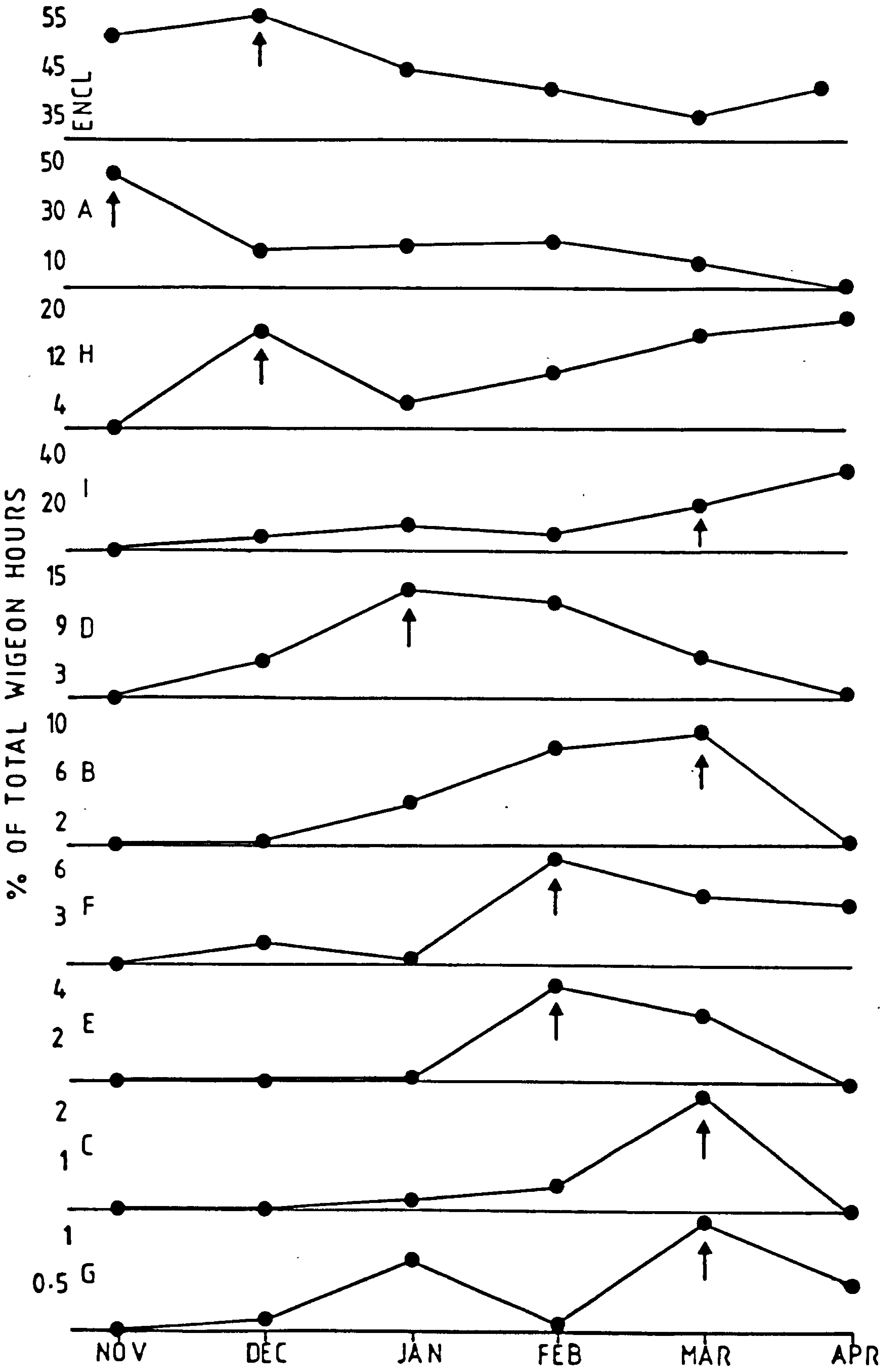

55
45
35
ENCL
50
30
A
10
20
12
H
4
40
I
20
15
9
D
3
10
6
B
2
6
F
3
4
E
2
2
C
1
1
0.5
G
% OF TOTAL WIGEON HOURS
NOV
DEC
JAN
FEB
MAR
APR

Figure 4.5

Peak month of attraction (see Figure 4.4) plotted against rank of wigeon hours (the larger the wigeon hours, the higher the rank) for each site.

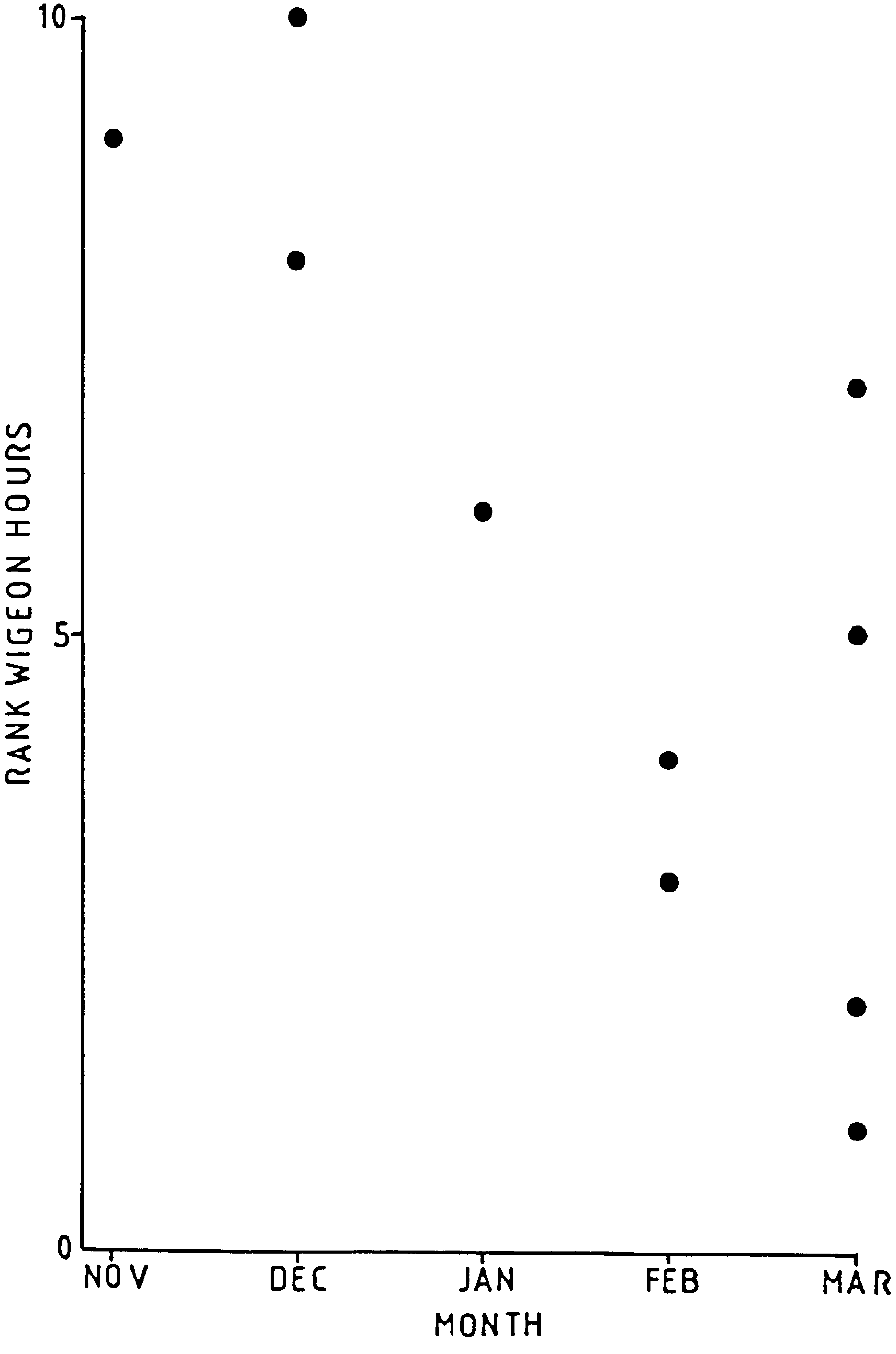
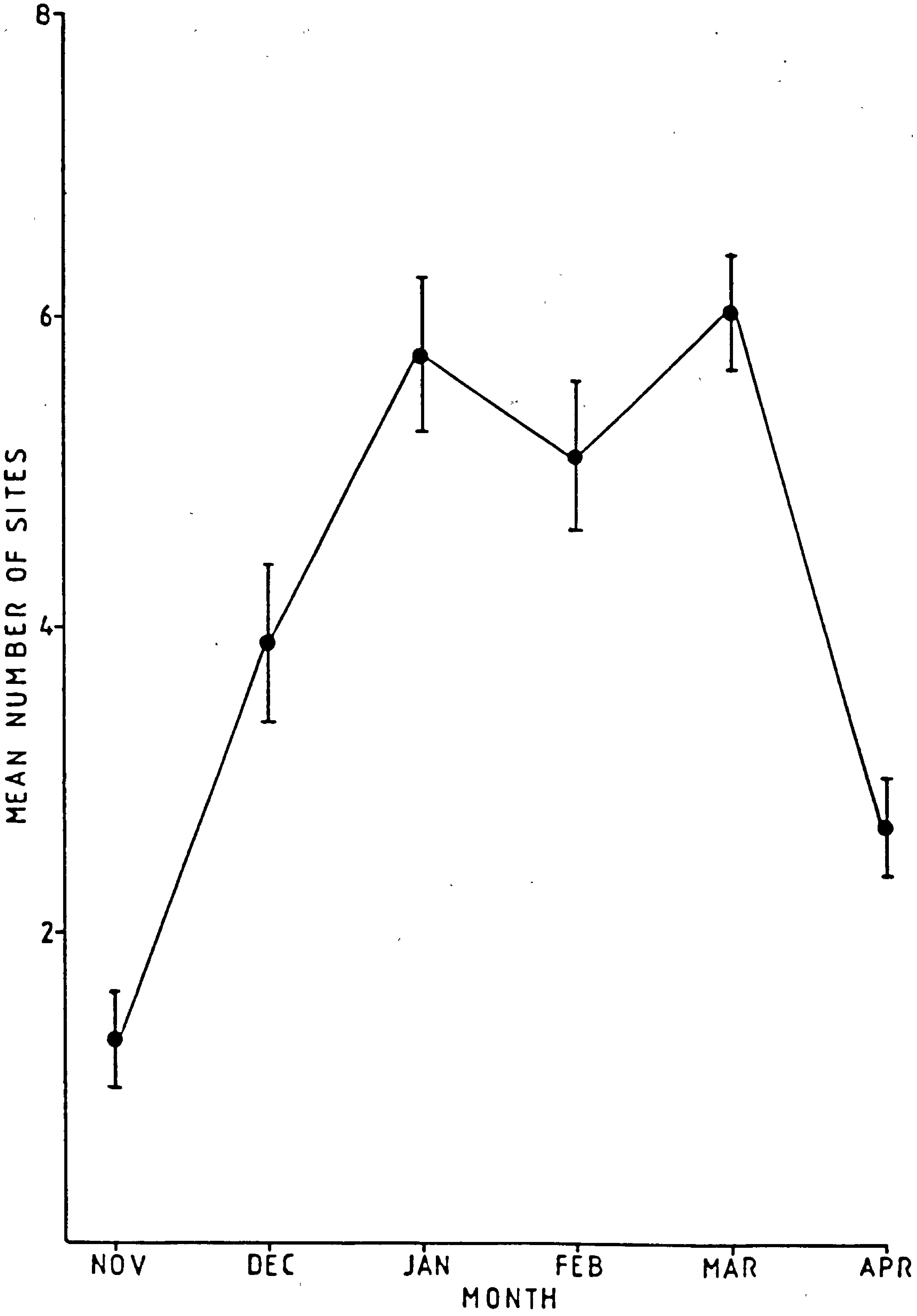

10
5
0
RANK WIGEON HOURS
NOV
DEC
JAN
FEB
MAR
MONTH

Figure 4.6

Mean number of sites used per day (± 1 s.e.) for each month of season 1.


8
6
4
2
MEAN NUMBER OF SITES
NOV
DEC
JAN
FEB
MAR
APR
MONTH

from November to March and then decreases in April. Thus, in the middle of winter, birds are using more, presumably less preferred, feeding sites. The relation of these results to seasonal food availability and the ideal free distribution is discussed later.

4.3.2 Reasons for feeding site selection

Having established that wigeon were being selective in their use of feeding sites in season 1, a study of the basis on which sites were being selected was undertaken in seasons 2 and 3. This study included work on selection between sites (inter-site selection) and on selection of feeding areas within sites (intra-site selection).

As was stated in the methods, droppings quadrats were set up on only 8 of the 10 feeding sites in these seasons since no access could be gained to the enclosure and because site G was virtually unused in season 1. The exclusion of the enclosure from these studies of inter-site selection was not, however, considered to be a major loss, since birds were using this site in a different way from the other sites (see above). Thus, while data from this site was considered to be valid in the season 1 inter-site preference studies (since the reasons for site preference were not considered) it was not included in the more detailed inter-site comparisons in the next two seasons. Site G was excluded in the later seasons because so little use had been made of it in season 1 (see Figure 4.3). It had been grazed by only a handful of birds for a few hours per day at the end of the season. The reason for this under-use was most likely due to the fact that the pond area on this site was shallow and sometimes dried out. Since wigeon require a good sized pond on their feeding site (see section 4.3.2 B) this lack of water would have made the site unattractive. There were in fact several other potential feeding sites beside shallow ponds on the reserve which were occasionally used by the birds but which were excluded from the study since time was limited.

This meant that quadrats were marked out on sites A,B,C,D,E,F,H and I (Figure 4.1). However, sites E and F, which had been among the least used by the wigeon in season 1, were virtually unused in seasons 2 and 3. Plant biomass on these sites was high and the reason why wigeon did not feed there was again probably because the ponds were shallow and sometimes dried up: grazing tended to take place on these sites only in wet weather.

The results presented in the following sections therefore refer to only six sites: A,B,C,D,H and I. All were grazed to a greater or lesser extent right through the season and all contained deep ponds. In relation to the results from season 1 this study refers only to sites used in the earlier part of the season, ie. the more preferred ones (except the enclosure field).

The decision to include data from only particular situation~~s~~ must be done carefully and with good reason in any study of this sort. The justification is thus: in field observations, controlled conditions are difficult, if not impossible, to obtain. Thus, instead of controlling conditions and collecting data from only those conditions (as in the laboratory) the problem must be approached from the other direction and data used only if it comes from strictly defined conditions. It is not abnormal data which is discarded but data from abnormal conditions. The conditions necessary for inclusion of a site in this study were that the site was used for most of the season, whether to a greater or lesser extent, and that the pond on the site was permanently filled. Within these conditions, the reason for differential use of sites was examined. A very large number of potential feeding sites were therefore not studied at all, eg. the middle of the fields, but the reason for their under-use was not the subject of this particular study. These results are however relevant to the studies in section 3.3.2 B which suggest that wigeon require feeding sites to be in close proximity to substantial and deep bodies of water. This hypothesis is in fact substantiated by the fact that, in very wet weather, birds not only grazed on sites E and F and other shallow pond areas like them, but also grazed well out into the centre of the fields.

The data relating to site use (ie. droppings density) biomass and grass height were analyzed as follows. In season 2 the number of quadrats on each site was different (see methods and Figure 4.1). In order to allow statistically acceptable inter-site comparisons it is best if sites are equally sampled. For this reason only 4 quadrats per site were used in these results (4 being the number of quadrats marked out on the least sampled site - site C). On each site, therefore, 4 quadrats which gave a representative coverage of the site were selected, two by the water's edge and two directly behind. The quadrats selected for this analysis are marked on Figure 4.1. Biomass and grass height data were also taken from these quadrats alone for inter-site comparisons.

In season 3, all sites had six quadrats marked out in similar positions on each site and all six were used in the inter-site comparisons (Figure 4.2).

In the intra-site selection study and also the distance from water study, data from all quadrats (except for those on sites E and F) were used.

4.3.2 A) Factors affecting foraging efficiency

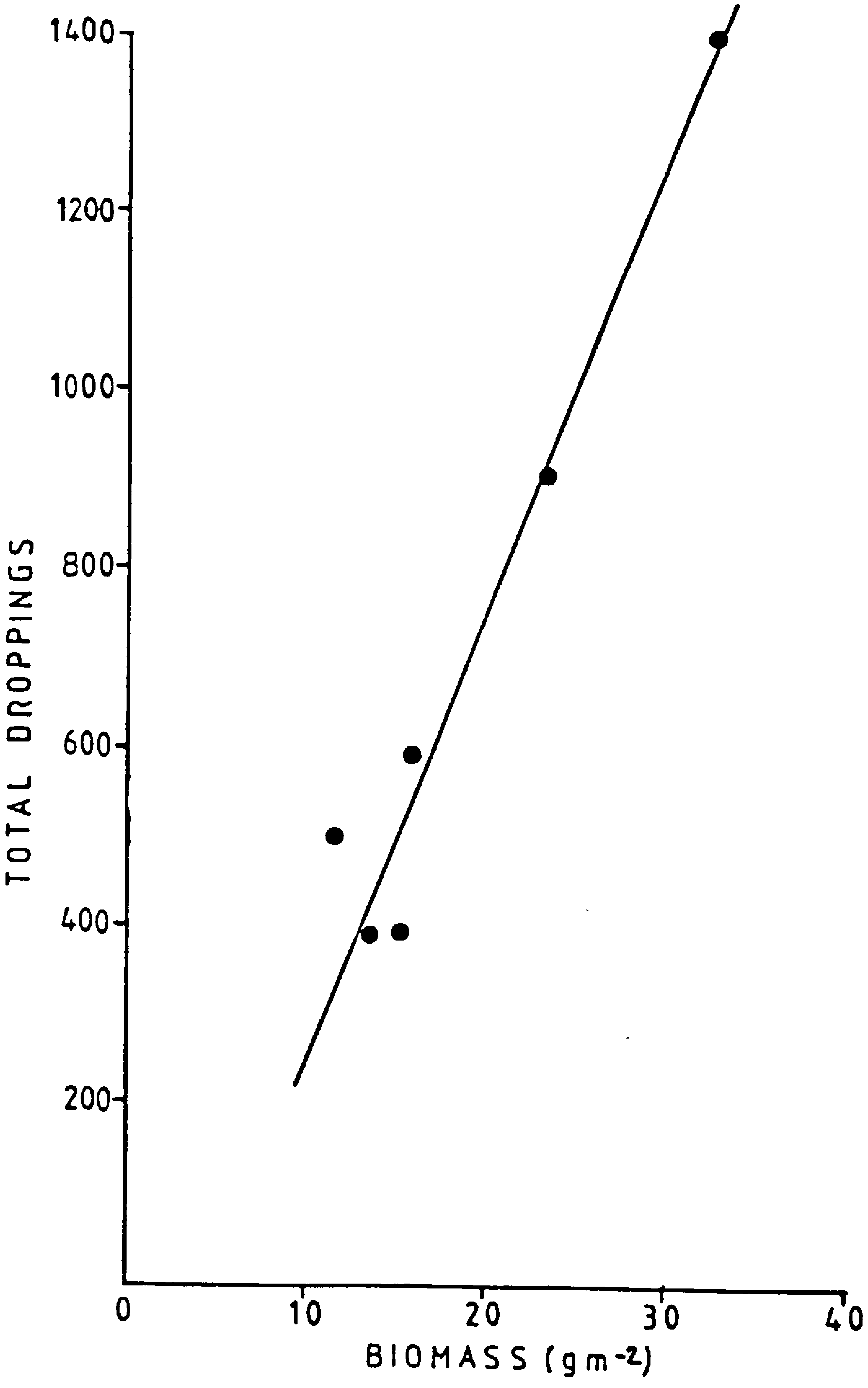
a) Biomass on the site

Figure 4.7 shows the relationship between the average biomass of grass over the whole season on the six study sites (A,B,C,D,H and I) and site use in season 2. Biomass was measured from January to the end of the season (average of 3 monthly measurements on the 4 study quadrats) since the spectrophotometer was only available from January. Site use was measured by the total number of droppings deposited on all 4 study quadrats through the season. The relationship is very close ($r=0.973$, $d.f.=4$, $P<0.002$). However, when this analysis was carried out on the season 3 data for the same six sites, the relationship was not so clear-cut (Figure 4.8) ($r=0.09$, $d.f.=4$, n.s.). While some form of positive relationship does seem to be evident, the data from one site in particular (with the highest biomass) resulted in a non-significant relationship.

Figure 4.7

Total droppings deposited on each site in season 2 (4 quadrats) regressed against average biomass on that site.

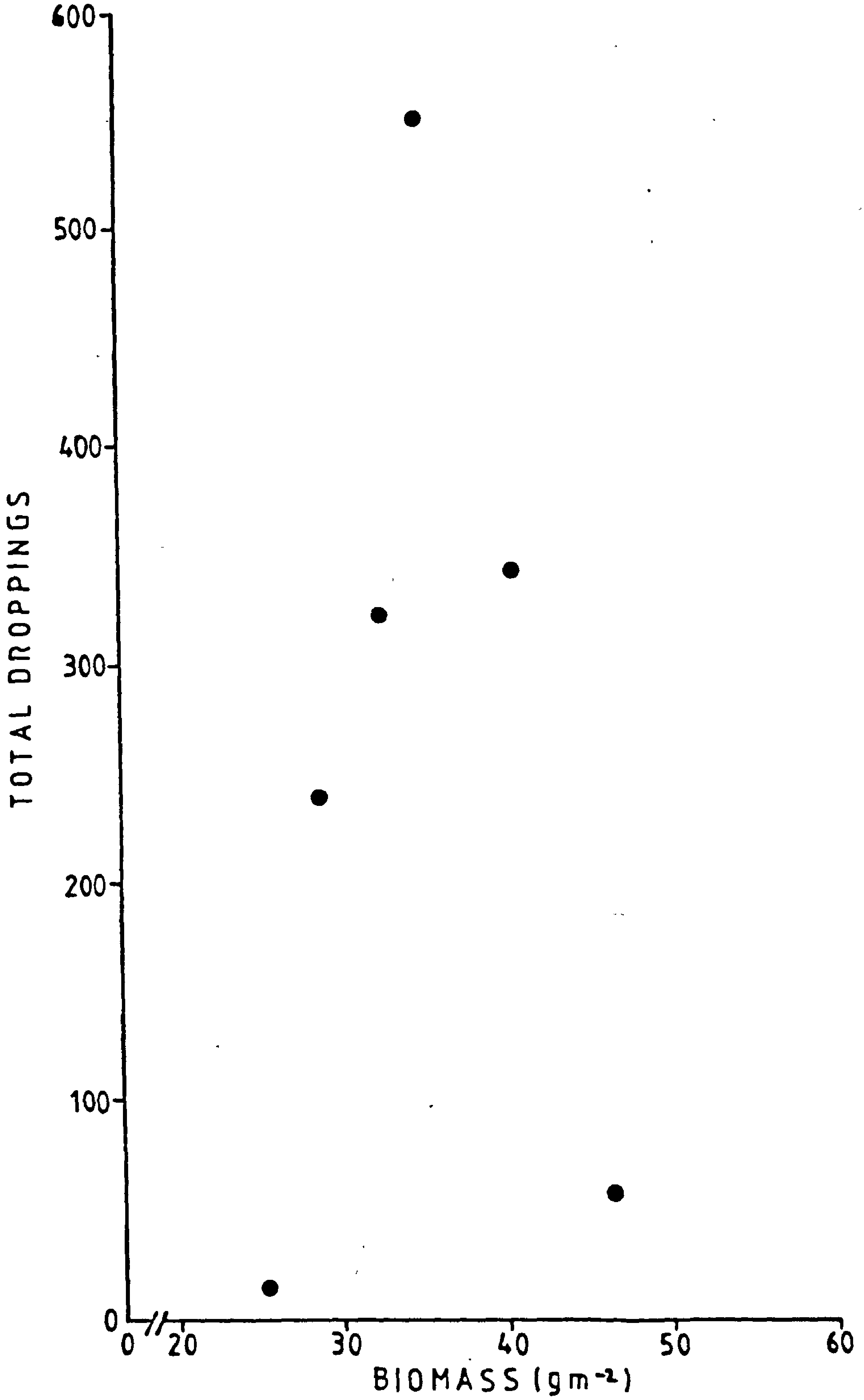
The equation of the line is $y = 47.6x - 200.0$.



TOTAL DROPPINGS
1400
1200
1000
800
600
400
200
0
10
20
30
40
BIOMASS (gm-2)

Figure 4.8

Total droppings deposited on each site in season 3 (6 quadrats) regressed against average biomass on that site.


600
500
400
300
200
100
0
TOTAL DROPPINGS
0
20
30
40
50
60
BIOMASS (gm⁻²)

The hypothesis that wigeon were, at certain times, selecting feeding sites on the basis of biomass availability was investigated further by studying the relationship between biomass and site use on the individual quadrats. The quadrats used in this analysis were only those greater than 10m from water (sites A,B,C,D,H and I) since distance from water had a significant effect on area use (see 4.3.2 B). This gave a sample size of 31 in season 2 and 24 in season 3. Table 4.2 shows the level of correlation between the biomass on each quadrat (measured once per month) and the total number of droppings deposited on that quadrat in the subsequent month, ie. 2 counts during seasons 2 and 3. This table does, of course, reflect the levels of correlation for the whole season (Figures 4.7 and 4.8). Thus, season 3 is seen to very rarely show any significant correlation. However, the analysis does show that site selection can occur over short time periods as well as over the whole year.

TABLE 4.2

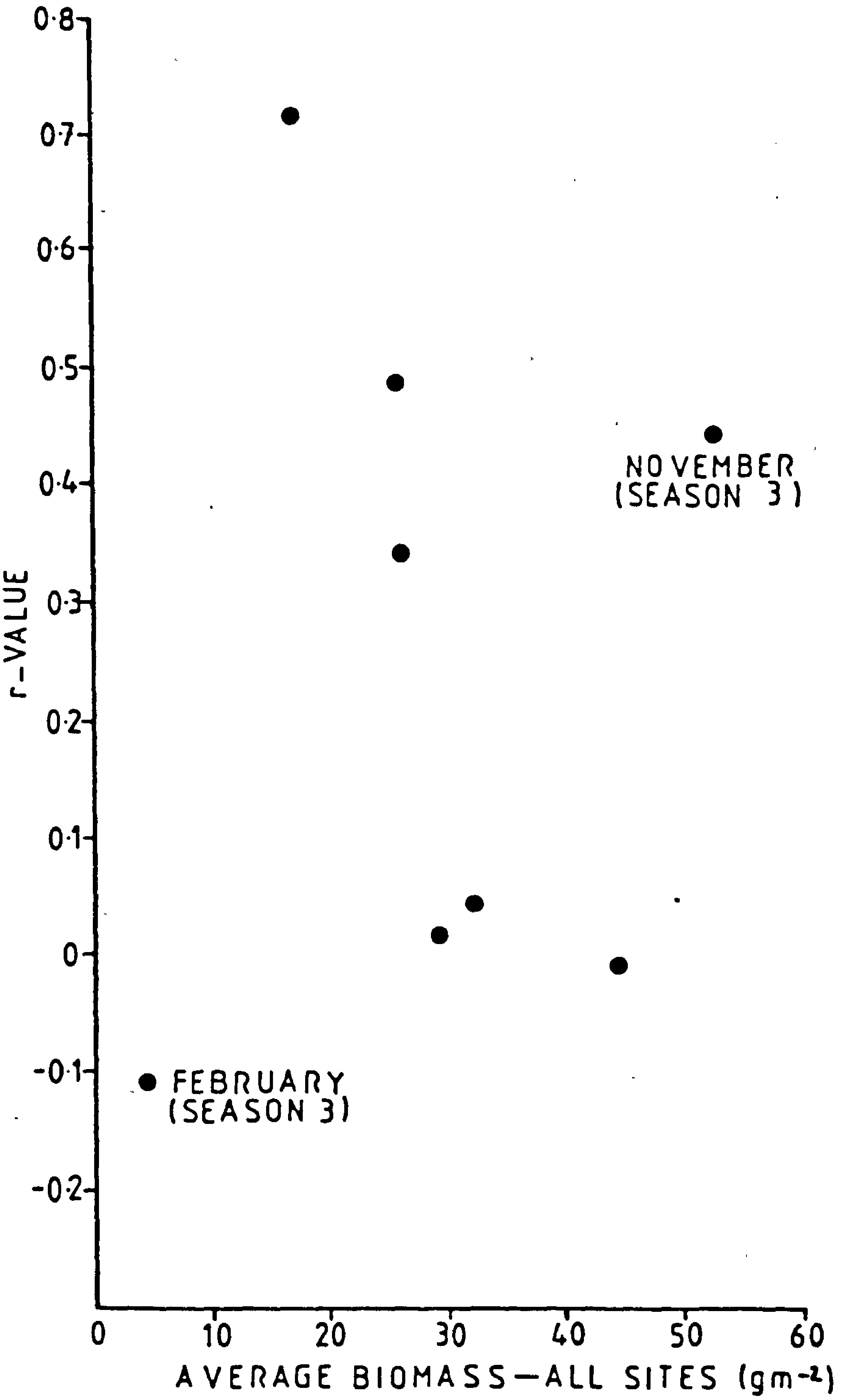
Correlations between biomass and droppings counts (in the subsequent month) for individual quadrats > 10m from water.

SEASON	2			3				
MONTH	JAN	FEB	MAR	NOV	DEC	JAN	FEB	MAR
CORRELATION (r-value)	.486	.717	.044	.437	-.008	.017	-.108	.338
SIGNIFICANCE	P<0.01	P<0.0001	n.s.	P<0.05	n.s.	n.s.	n.s.	n.s.
n	31	31	31	24	24	24	24	24

The reason for these seasonal changes in how closely wigeon track the available biomass was investigated by studying how the biomass/ droppings correlations in Table 4.2 (r-values) varied with the total amount of food on the reserve. The hypothesis was that when food is in short supply birds may track it more closely than when there is an abundance of food available. Figure 4.9 shows how the r-values vary with average biomass on the reserve. There is no significant correlation, the negative relationship being spoiled by the November and February points from season 3. Interestingly, these are the times of highest and lowest biomass. Also, November was an extremely wet period and February a very frosty one, when many ponds were frozen for several weeks. Thus, it is possible that other factors were coming into play in these two unusual months, since the relationship is significant at P<0.05 if these points are left out. It must be stressed that this discussion is not an attempt to justify poor data, or to claim a significant relationship where none exists, but to

Figure 4.9

Relationship between the average biomass on all sites for each month and the corresponding correlation (r-value) between biomass and droppings counts (see Table 4.2).


0·8
0·7
0·6
0·5
0·4
0·3
0·2
0·1
0
-0·1
-0·2
r–VALUE
NOVEMBER (SEASON 3)
FEBRUARY (SEASON 3)
0
10
20
30
40
50
60
AVERAGE BIOMASS—ALL SITES (gm⁻²)

present some possible explanations as to why an effect, which is extremely obvious at certain times of the year, should disappear at other times.

The increase in the number of sample points resulting from the individual quadrat data (as opposed to using the mean biomass for each site) allowed an analysis of the exact nature of the relationship between biomass availability and area use to be undertaken. The two months for which highly significant correlations existed, ie. January and February (season 2) were studied. Figures 4.10 and 4.11 show that while significant linear correlations exist, the relationships tend more towards exponential curves. Thus, birds tend to spend almost all of their time in high biomass areas and seldom visit medium to low areas. This type of resource exploitation approximates far more to the optimal solution for a non exhaustable resource (Krebs 1978) than a simple linear distribution down the resource gradient, since it will allow a maximisation of energy intake/ unit time. From a comparison of the two graphs it can be seen that the main inflection in the site use curve comes higher up the resource gradient when overall biomass availability is higher. Thus, the curve for January, with a maximum biomass of 50 gm^{-2}, steepens at around 20-40 gm^{-2}, while that for February (maximum of 36 gm^{-2}) steepens around 10-20 gm^{-2}. The level of resource which the birds exploit seems to be dependent on the overall availability of that resource. Finally, it will be seen that in the February graph an asymptote is reached at a site use level of about 75 droppings/ quadrat. In January this level of site use is only just reached at the last point. Possibly this is the point at which site use becomes independent of resource availability, as other factors, eg. feeding interference, come into play.

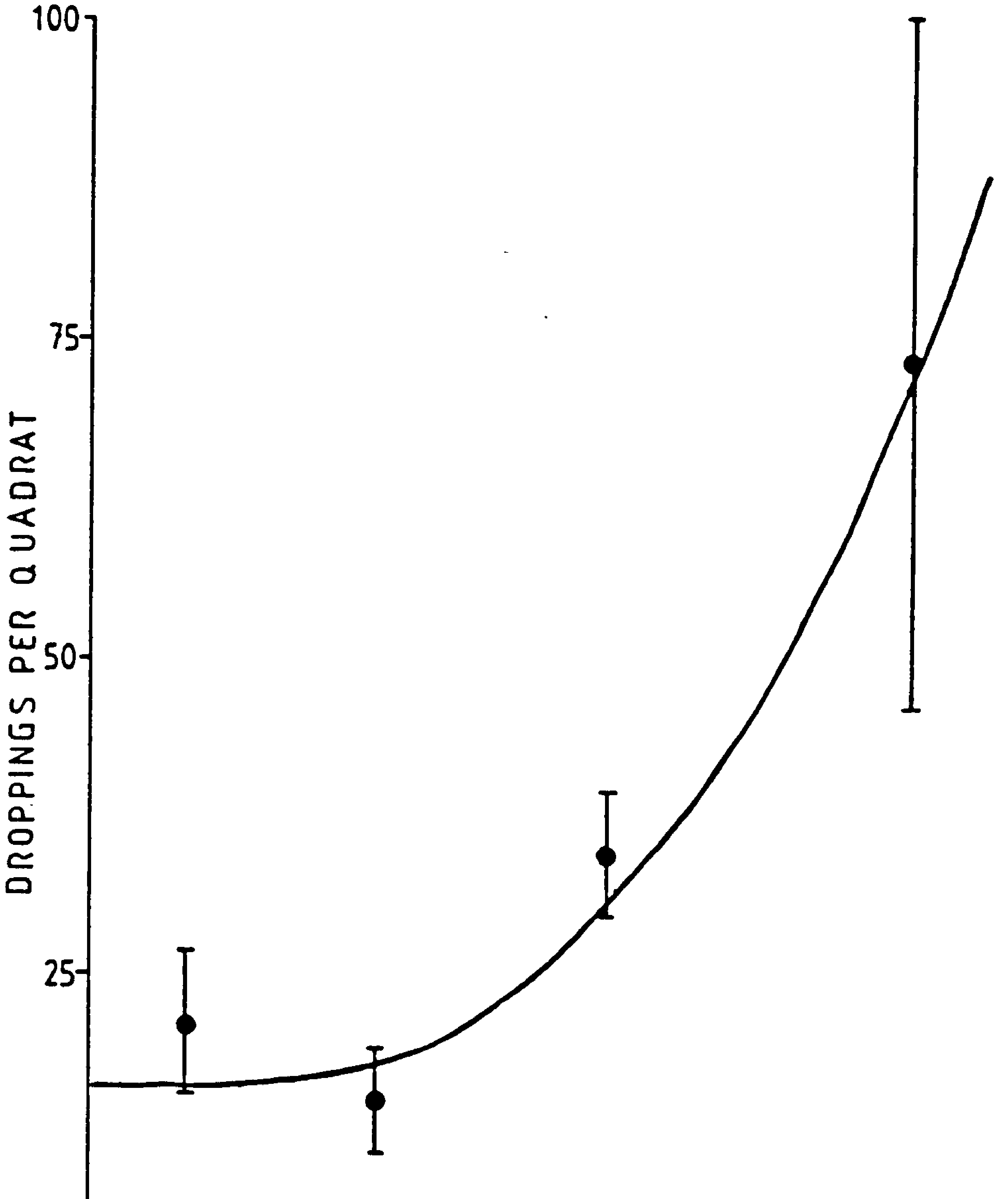
b) Food quality on the site

The quality of forage on the site was defined as the ratio of protein/ fibre. Several authors have used this type of quality measurement, eg. Owen (1973a) used protein x soluble carbohydrate/ fibre, to assess the quality of white-fronted goose forage. This ratio should result in a measure of two separate components of the food a) the level of an important limiting nutrient (see Chapter 6) b) the digestibility of the food, since fibre level is negatively correlated with digestive efficiency (Chapter 8 and Drent et al 1979).

The hypothesis that birds may be selecting feeding sites on the basis of food quality was examined by comparing the site use data with the grass quality on that site. Since fibre analyses were only carried out on some of the grass samples, grass quality was calculated from the average of the protein/ fibre ratios for November and March for each site. Data was available for 8 points in seasons 2 and 3. Site use is the total droppings deposited on the 4 quadrats on each site through the season. No correction was made for quadrat size (which differed between seasons) since the total area covered was the same in both seasons ($24m^2$).

Figure 4.10

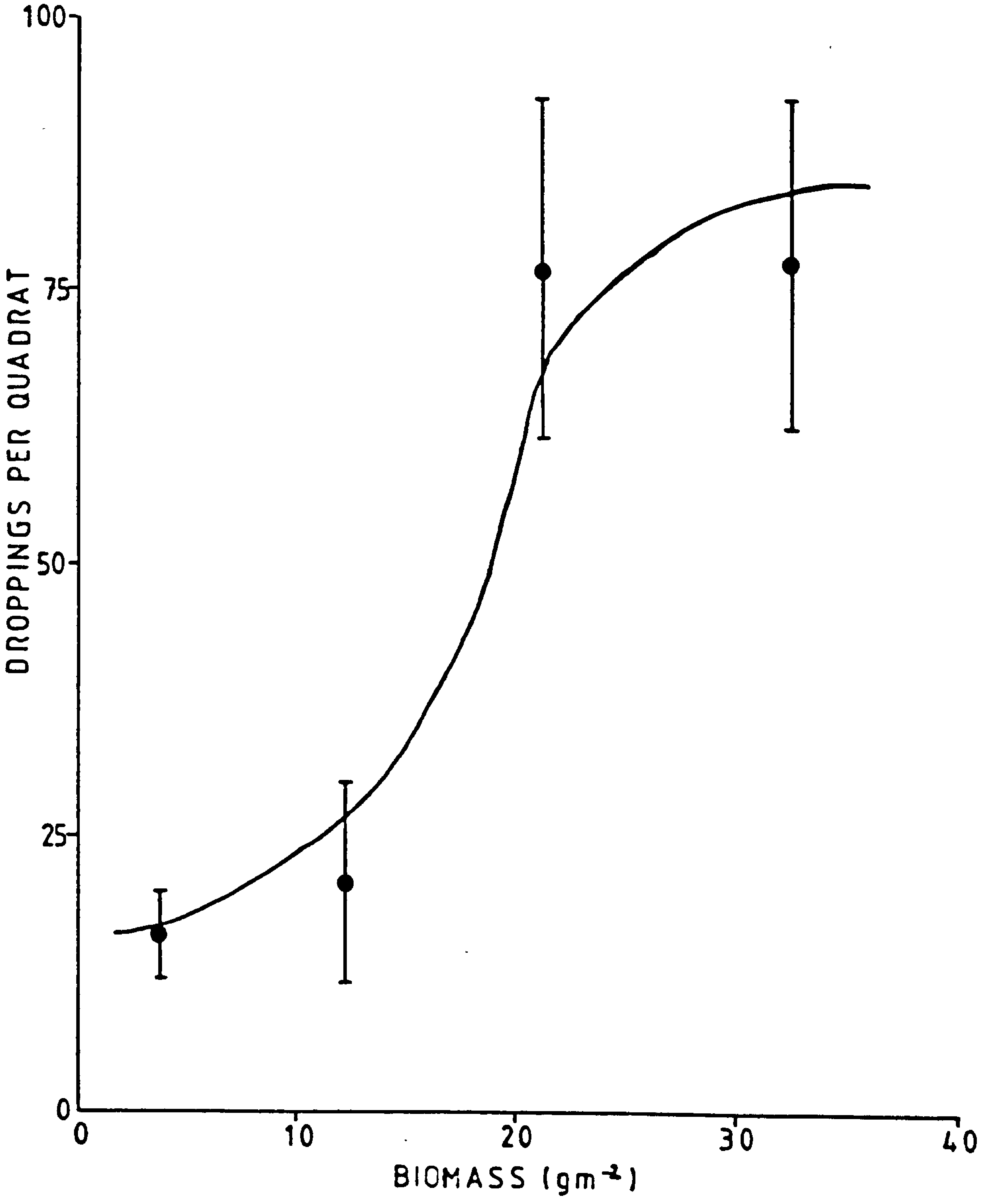
The relationship between biomass and droppings counts (in the subsequent month) on individual quadrats (> 10m from water) in January, season 2. Curve fitted by eye.



100
75
50
25
0
DROPPINGS PER QUADRAT
0
10
20
30
40
50
BIOMASS (gm-2)

Figure 4.11

The relationship between biomass and droppings counts (in the subsequent month) on individual quadrats (> 10m from water) in February, season 2. Curve fitted by eye.


DROPPINGS PER QUADRAT
100
75
50
25
0
0
10
20
30
40
BIOMASS (gm⁻²)

From Figure 4.12 it can be seen that, at an inter-site level at least, high quality forage on a site does not lead to increased site use. Indeed, in season 2, there is a negative relationship (not significant), the most used sites tending to have the poorest quality forage.

c) Food species on each site

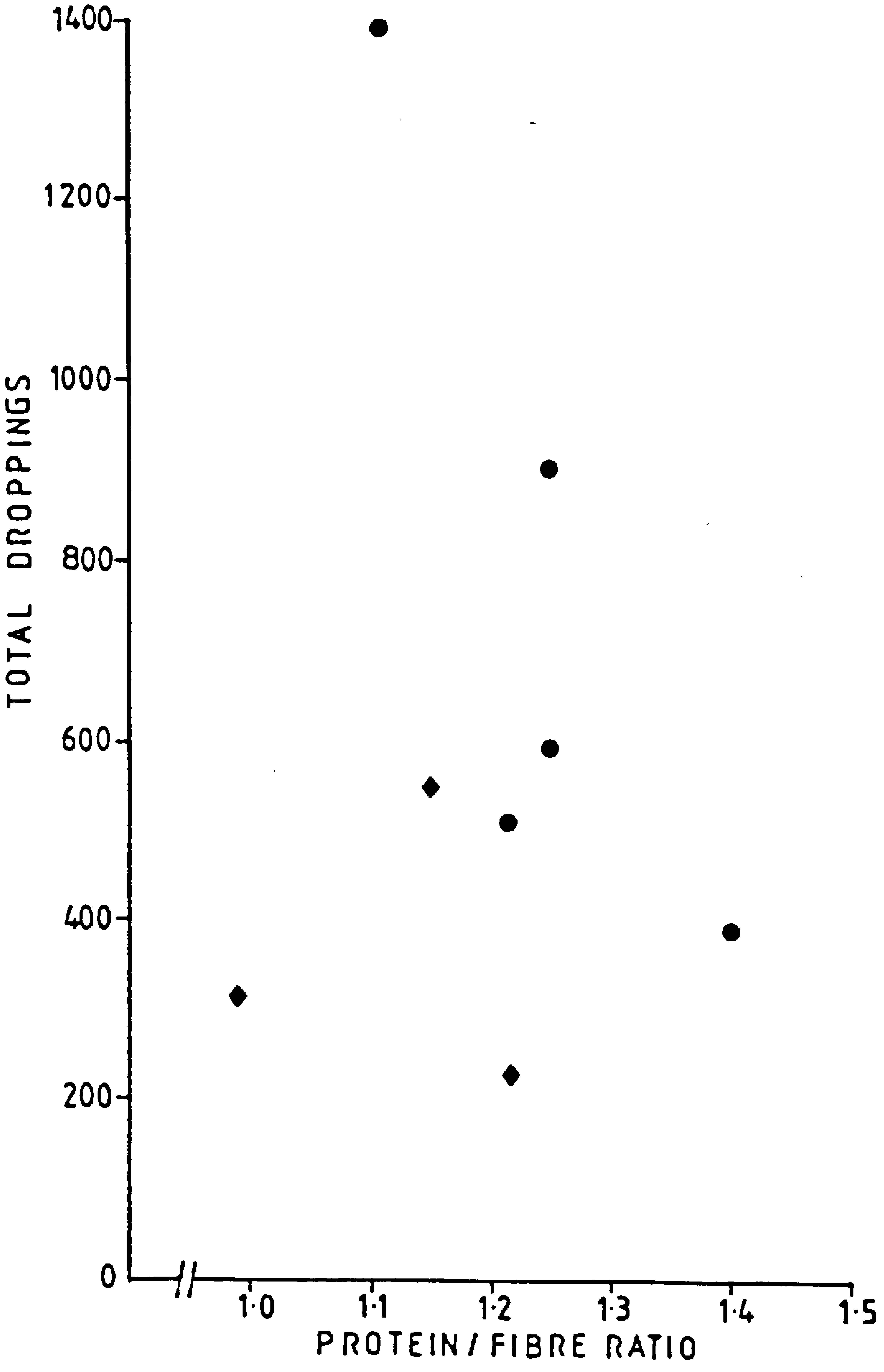
While birds did not seem to be choosing feeding areas (on an inter-site level) for food quality, they may have been responding to the grass species on a site. To study this, two methods were used. Firstly, an accurate assessment of the species composition of each site was undertaken. Table 4.3 shows the results of this study. It can be seen that, while some variation does exist, eg. in the *Lolium*/ *Agrostis*/ *Poa* ratios, the sites are in fact very similar in their general composition. It was therefore felt unlikely that this factor was playing a major role in site selection.

Figure 4.12

Relationship between food quality (protein/ fibre ratio) on a site and total droppings deposited on it during seasons 2 and 3.

● Season 2

◆ Season 3



1400
1200
1000
800
600
400
200
0
TOTAL DROPPINGS
1·0
1·1
1·2
1·3
1·4
1·5
PROTEIN / FIBRE RATIO

TABLE 4.3

Relative abundance of grass and forb species on each site. Numbers refer to the number of hits (out of a total of 100 on each site) recorded for each species (m = mainly).

	GRASSES								FORBS			
SITE	Lolium perenne	Agrostis (m.stolonifera)	Poa (m.pratensis)	Holcus lanatus	Phleum pratense	Festuca pratensis	Cynosurus cristatus	Dactylis glomerata	Ranunculus spp.	Trifolium repens	Bellis perennis	Plantago major
A	19	44	4	2					20	5	2	3
B	43	37						2	4	8	5	
C	52	16	6				6	4		10	4	
D	63	17	4		7	9						
H	49	20	10	6					9	3	2	
I	30	22	15		2	4			8	9	6	

However, to check on this further, a second method was employed. Basically, this was to initially ascertain the species selection of the birds and then look at the levels of preferred species on each site.

To examine species selection by the birds an exclosure method was used - this was considered more useful than gut or faecal analysis, since an in-depth study was not desired. Two 1 x 1m plots, one exclosed and one not, were set up in two areas which in past seasons had been grazed (but not excessively) by wigeon. Unfortunately, the birds did not sufficiently graze one of the areas, so data was collected from one site only. One hundred blades were examined by the point quadrat method in each plot. This was carried out in October and then in March of season 3. From the exclosure results, species differences due to natural die-back can be examined, while the grazed plot results give some indication of species composition changes brought about by wigeon grazing. The obvious disadvantage of the method is the possibility of grazing by other animals in the plot, eg. geese and rabbits. For this reason, the plots were sited beside the water edge - the geese only very rarely grazed at the edge of the field (Owen 1972a and Chapter 6). No goose droppings were ever found in these plots. Rabbits, though not common, could however have grazed in the plots. Therefore, since the data are based on only one site, the following results are not presented as a definitive study. They do, however, provide some interesting results as to: a) possible species selection by wigeon, b) the accuracy of the point quadrat technique.

Table 4.4 shows the changes in species composition in the ungrazed exclosure and the wigeon grazed plot. The ungrazed area remains almost identical in major species composition, while the wigeon grazed area changes a great deal between October and March, but in the relative proportions of the two major species only, ie. Lolium and Agrostis. A X^2 test on the proportions of these species reveals a highly significant difference between October and March ($X^2=12.881$; 1 d.f.; $P<0.001$). Wigeon seem to be selecting Agrostis over Lolium. While not wishing to put too much emphasis on this in relation to species selection by wigeon, an attempt was made to see if this could have affected inter-site use. Thus, the Agrostis abundance for each site was regressed against the site use data for seasons 2 and 3. No significant relationships were found (season 2: $r=-0.519$; season 3: $r=0.303$).

Thus, on this rather crude level at least, birds do not seem to be responding to the food species availability on each site.

TABLE 4.4

Effect of grazing on relative species abundance. Recording method as in Table 4.3.

UNGRAZED EXCLOSURE

	Lolium perenne	Agrostis stolonifera	Holcus lanatus	Dactylis glomerata	Festuca pratensis?	Poa spp.	Agropyron repens	Phleum pratense	Bellis perennis	Trifolium repens
OCTOBER	47	26	3			2	4	3	4	11
MARCH	46	25	3	1	5	2			9	9

GRAZED PLOT

	Lolium perenne	Agrostis stolonifera	Dactylis glomerata	Poa spp.	Agropyron repens	Bellis perennis	Trifolium repens	Ranunculus spp.
OCTOBER	48	47			1	2	1	1
MARCH	57	28	2	9		3		

d) Grass height

From an experiment with captive birds (Chapter 5) it was thought that the height of grass on a site could affect the ease of feeding and therefore intake rates of wigeon. Tall grass could also affect the risk of predation due to reduced field of view. In season 2, therefore, data on the height of grass on all sites was collected. It was found that grass height (average of the 4 quadrats through the season) was positively correlated with site use (total droppings on 4 quadrats) ($r=.888$; d.f.=4, $P<0.02$). However, it also correlated positively with biomass ($r=.911$; d.f.=4, $P<0.01$). This was almost certainly because high biomass was the result of the grazing regime (see also Owen 1972a): heavy grazing during autumn resulted in sites with short grass and low biomasses. The confusion of these two variables will be dealt with in more detail in section (f).

e) Primary production

From the outset, it was thought unlikely that this factor would be important, since production is very low or non-existant during the winter months. However, its effect on site use was checked in season 2. The primary productivity of a site was defined as the difference between grass biomass in the ungrazed exclosure (see Chapter 6) between the January and March biomass measurements. The correlation between this and site use was not significant ($r=-0.760$, d.f.=3, n.s.).

f) What factors are important to wigeon?

From the results presented above, it seems that the factor which is most important to wigeon when selecting feeding sites is the biomass on that site. The importance of this factor does, however, seem to vary with the overall biomass conditions prevailing at the time. None of the other factors (except grass height) showed a significant correlation with site use. The significant relationship between grass height and site use is best understood by comparing the r-values of site use, biomass and grass height. All these results refer to season 2. The correlation (r) between site use and biomass is 0.973, between site use and grass height, 0.888, and between biomass and grass height 0.911. Thus, since site use follows biomass more closely than grass height, and also since grass height follows biomass more closely than site use, it seems evident that the relationship between grass height and site use is merely due to the confounding correlation between grass height and biomass.

g) Fertilizer experiment

The fertilizer experiment allowed this hypothesised effect of biomass to be examined in a more rigorous way, since any pond depth or disturbance factors were controlled for in this approach. Table 4.5a shows the mean and s.e. of droppings/quadrat for the fertilized and control plots. In November and December significant differences between the two were found, fertilized sites being used almost 2.5 times as much as unfertilized. However, the effect reduced through the rest of the season, so that, while the use of fertilized sites was always greater from January to March, the difference was never significant. The effect of time was taken into account in an analysis of variance (Table 4.5b). The effect of fertilization on site use over the year was significant at $P<0.001$.

TABLE 4.5a

Number of droppings/quadrat (mean ±1s.e.) on fertilized/control strips - Area A (season 3).

MONTH	FERTILIZED STRIPS	CONTROL STRIPS	T-TEST SIGNIFICANCE
NOV	23.6 ± 4.1	10.3 ± 2.7	$P < 0.02$
DEC	9.07 ± 1.1	4.0 ± 0.7	$P < 0.001$
JAN	10.3 ± 1.9	6.5 ± 1.5	N.S.
FEB	14.6 ± 2.1	10.8 ± 1.5	N.S.
MAR	7.5 ± 1.7	5.3 ± 2.3	N.S.

TABLE 4.5b

Results of an analysis of variance carried out on the droppings counts data for the fertilizer experiment (Site A).

MAIN EFFECTS	F VALUE	SIGNIF. OF F
FERTILIZER	20.096	< 0.001
TIME	6.319	< 0.001

Fertilisation can have many varied effects on grassland, increasing standing crop, primary production, protein content, etc. In an attempt to discover just which factors the birds were responding to, the biomass and protein content of grass on the site were measured each month (Table 4.6). The biomass was higher on fertilized plots throughout the season (the difference was significant from November to January only). Protein content was again always higher on the fertilized plots.

TABLE 4.6

Biomass, protein, site use differences between fertilized and control plots - Site A (season 3).

	BIOMASS (gm^{-2})				PROTEIN (%)			DROPPINGS COUNTS
MONTH	FERTILIZED (± 1 s.e.)	CONTROL (± 1 s.e.)	T-TEST SIGNIF.	DIFF. (BETWEEN MEANS)	FERTILIZED	CONTROL	DIFFERENCE	DIFFERENCE (expressed as % of mean for all plots)
NOV	84.4 ± 4.8	62.0 ± 3.1	$P < 0.01$	22.4	24.37	18.32	6.05	78.7
DEC	63.1 ± 3.3	51.7 ± 1.1	$P < 0.01$	11.4	22.10	19.16	2.94	77.6
JAN	61.2 ± 3.1	50.5 ± 3.2	$P < 0.05$	10.7	28.61	22.99	5.62	45.2
FEB	18.3 ± 3.8	14.3 ± 4.5	N.S.	4.0	22.37	20.56	1.81	29.4
MAR	49.8 ± 2.9	43.2 ± 3.5	N.S.	6.6	26.51	24.76	1.75	35.3

Figure 4.13 shows how site use differences (between fertilized and control plots) changed over the year, along with the biomass and protein differences. (The difference in droppings number was expressed as a percentage of the mean of all plots for that month). As can be seen from the graph, site use follows biomass more closely than protein, the correlation coefficients being 0.830 (biomass) and 0.545 (protein). Neither was significant. However, in this experiment, the wigeon seemed to be responding to biomass rather than protein.

To investigate whether wigeon could respond to protein alone, a second experiment was set up in March in Area I. The rationale behind this was to see if one could alter the protein content of the grassland, without altering the biomass, and then observe the response of the wigeon. If there was differential use of the experimental and control areas, the wigeon must be responding to protein. The idea was to fertilize the strips and then observe site use in the time period when protein content of the grass would be increased, but biomass would not be significantly changed.

Initially, the biomass of the two areas was measured with the spectrophotometer. However, it was soon realised that this instrument was responding to the higher production rates of the fertilized grass, since the instrument, to some extent, measures the 'greenness' of the grass (Curran 1982). No significant difference was found, but the fertilized vegetation tended to give a higher reading than the unfertilized. This problem was not encountered during routine biomass estimation, since during the winter months and on unfertilized vegetation, production was very low/ non-existant. In the other fertilizer experiment, after an initial rapid growth phase, no growth took place, so that grass production did not affect biomass estimation during the period when results were collected.

It was therefore decided to assess the biomass by clipping. This was carried out once, in the middle of the four days of site use data collection. A 15 x 15cm plot was clipped in each strip and the clippings pooled for fertilized and control areas. They were then sorted into live and dead material and dried at 60°C. Unfortunately, the vegetation on this site, at this time of year, does not lend itself to clipping, since it rarely exceeds about 0.5 cm in height. Also, on the clipping day, the vegetation was very damp. Both of these factors lead to a significant underestimation of the absolute biomass present. However, the above problems related equally to both fertilized and control strips. Since the desire was simply to provide a check on biomass - it was considered extremely unlikely that the prevailing weather conditions (low temperatures) and the time period since fertilization (about 2.5 weeks) could have resulted in any biomass changes - the technique was considered to give a reliable estimate of the relative levels of biomass on fertilized and control strips. As can be seen from Table 4.7 the control areas tended to contain more grass.

The clippings were analysed for protein (Table 4.7) and an 8.5% difference was found between the fertilized and control strips.

Figure 4.13

Site use, biomass and droppings differences between fertilized and control strips (Site A experiment) for each month. Site use difference is expressed as % of the average number of droppings on the experimental area for each month.

————	Droppings
– – – – –	Biomass
○○○○○	Protein

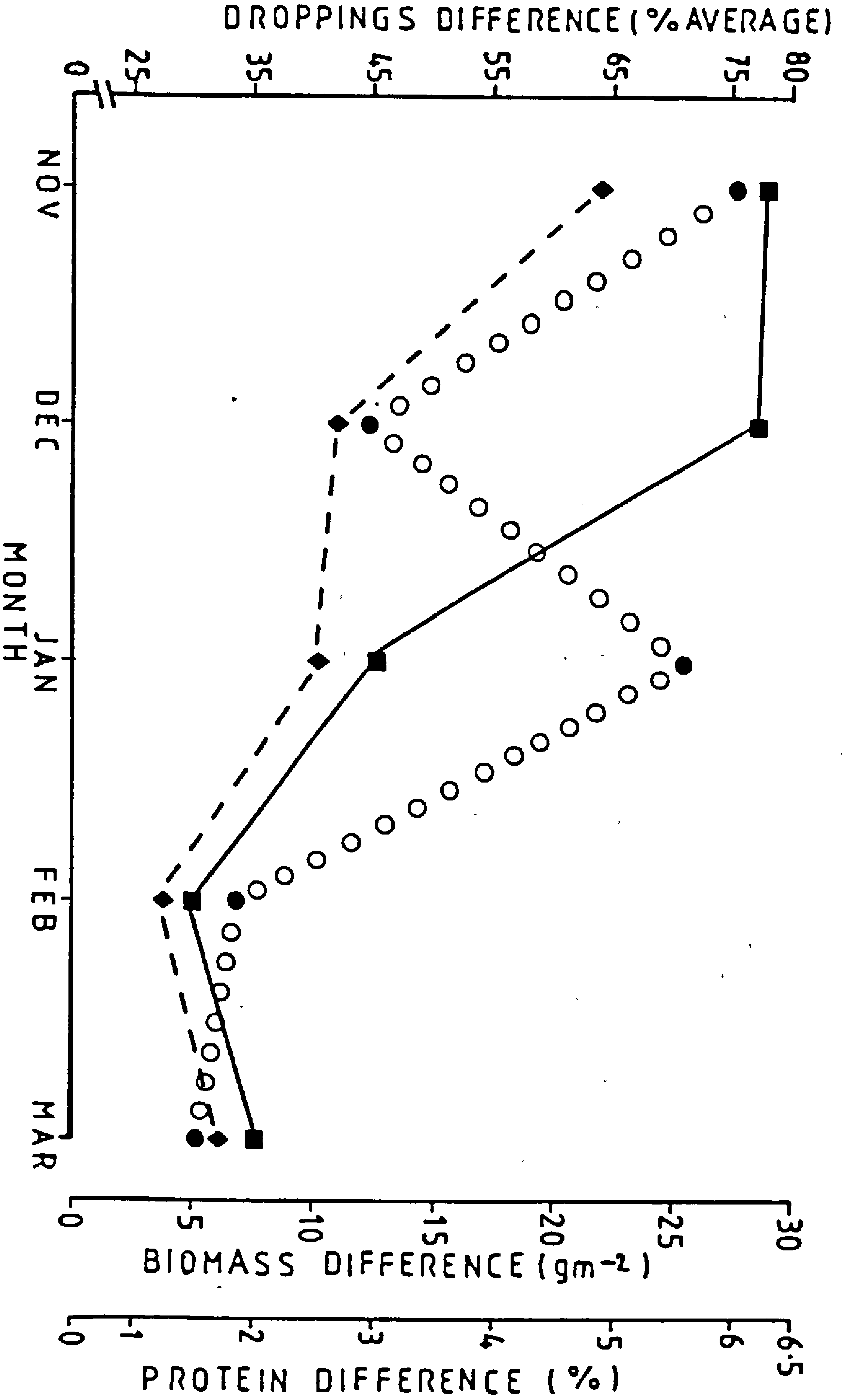

DROPPINGS DIFFERENCE (% AVERAGE)
0
25
35
45
55
65
75
80
NOV
DEC
JAN
FEB
MAR
MONTH
BIOMASS DIFFERENCE (gm⁻²)
0
5
10
15
20
25
30
PROTEIN DIFFERENCE (%)
0
1
2
3
4
5
6
6.5

TABLE 4.7

Droppings, biomass and protein analysis for the fertilizer experiment on Site I (March, season 3)

	BIOMASS (gm^{-2}) (from clippings)	PROTEIN (%)	DROPPINGS/QUADRAT (± 1 s.e.)
FERTILIZED	8.3	30.97	16.0 ± 1.9
CONTROL	11.6	22.56	6.2 ± 1.3

The site use data is presented in Table 4.7. A very clear and significant difference was found between fertilized and control plots (t=4.24, d.f.=8; P<0.01) with wigeon using fertilized plots over 2.5 times as much as unfertilized. In this experiment, wigeon must have been responding to protein levels.

4.3.2 B) Factors Affecting Predation

There are many other factors, outside foraging efficiency, which can influence an animal in its choice of habitat. Probably the most important of these is predation. It was not possible to study site selection in relation to disturbance due to the nature of the Caerlaverock reserve. However, it was possible to investigate wigeon feeding in relation to water, since quadrats were positioned at known distances from the water edge. Wigeon always fed in close proximity to a pond, and so each feeding site had a pond within its boundary. The birds would fly into a pond and then gradually graze towards the centre of the field for anything from 30 secs. to 30 mins. before moving back to the pond again. Thus, grazing tended to be concentrated at the pond edges.

The use of the areas near to and away from water was studied by comparing the number of droppings per quadrat in these two 'sectors' for each date on which a droppings count was carried out. A paired t-test analysis for the 17 count days (seasons 2 and 3) showed a statistically significant bias towards feeding at the pond edge; inner plots (<10m from water): 20.7 droppings/quadrat; outer plots (>10m from water): 8.9 droppings/ quadrat. (t=3.394; d.f.=16; P<0.001).

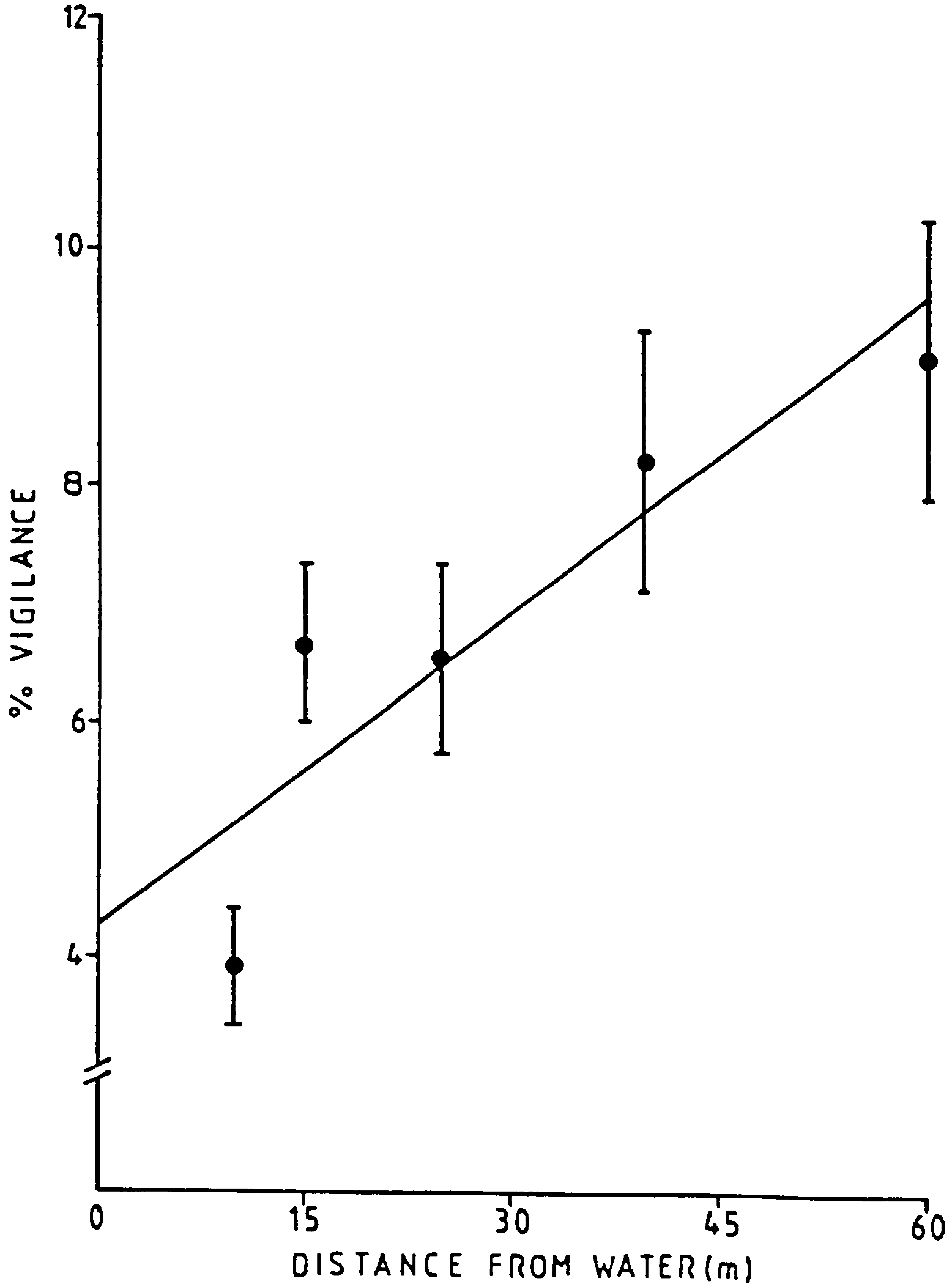
Why should wigeon tend to feed close to water? The normal explanation for the requirement of water by wildfowl is to provide areas for bathing and drinking (Owen 1972a, 1973a). While this requirement also applied to wigeon, the reason for feeding in such close proximity to water was thought to be due to other considerations. From many hours of observation it was thought likely that these considerations had something to do with predation, since wigeon tended to walk, run or fly back to water if any danger was evident and would remain in the water till the danger (eg. a raptor) had passed. To test this hypothesis a study of the effect of distance from water on vigilance was carried out in season 3 (see p.81 for the methods used in this study). Figure 4.14 shows that distance from water had a highly significant effect on vigilance ($t=57.2$; d.f.=156; $P<0.0001$). It is hypothesised that since birds become more 'wary' as they move away from water, they must be at greater risk further from water. Thus, feeding close to water functions as an anti-predator strategy. The results from this study are discussed further in Chapter 6.

The effect of season on proximity to water was also studied. In season 2 it was found that feeding in areas away from ponds increased greatly at certain times of the year (Figure 4.15). It was thought that this could be due to the reduction in biomass on the reserve, since the dates when birds spent most time well out from water were also the dates of lowest biomass on the reserve. However, in season 3, even though there was again a large variation in feeding proximity to water through the season (Figure 4.16) the changes did not seem to be related to the biomass level on the reserve (eg. in February, biomass was very low and yet birds remained close to water). To investigate the cause of these relaxations in an important anti-predator strategy, the difference between the average biomass in the outer and inner sectors was calculated for each site for each month (over both seasons). Next, the difference in site use was calculated for each site and month. The droppings/ quadrat figures were standardised by dividing the average number of droppings for each sector (ie. inner or outer) by the average number for the whole site for each count date. Then the biomass difference was plotted against sector use difference. As can be seen from Figure 4.17 a significant regression resulted ($t=2.94$; d.f.=30, $p<0.01$). Thus, birds tend to feed further out from the water when the biomass further out, *compared to the biomass further in*, is high. This makes much more sense than simply moving out if biomass on the reserve is low, since a bird could simply be moving into an even poorer feeding area.

However, it had been noted in the graphs of feeding proximity to water through the season that the birds also tended to feed well out after the shooting season had finished (at the end of February). Movements in response to the end of the shooting season are well documented in wildfowl (eg. at Caerlaverock barnacle geese move to the normally shot Rockcliffe marsh at the end of February). Today, man is a very important 'predator' on wildfowl and birds have obviously learnt to respond to his fixed 'predation' periods. It was therefore suspected that wigeon could also be responding to the greater safety after shooting had ceased, and possibly moving further away from the water. To study this, the data on sector use against biomass difference was divided into two: during the shooting season (ie. November-February) and after the shooting season (ie. March/ early April). When a covariance analysis was run on the two regression lines (see Figure 4.17) it was found that the upper line (after shooting season) was significantly different ($P<0.01$) from the lower line (during shooting season) in elevation but *not* in slope (Table 4.8). Thus, after the shooting season, even though wigeon

Figure 4.14

Regression of % time vigilant (mean ± 1 s.e.) on distance from water. The equation of the line is $y = 0.087x + 4.29$. Data only from flock sizes greater than 20.



12
10
8
6
4
% VIGILANCE
0
15
30
45
60
DISTANCE FROM WATER(m)

Figure 4.15

Changes in relative use of inner (< 10m from water) and outer (> 10m from water) sectors through season 2. The percentage figure was calculated as follows: the average number of droppings/ quadrat was calculated for all inner sector quadrats and all outer sector quadrats (irrespective of site) for each count date. Average values were used since there were fewer inner quadrats than outer (22 as opposed to 31). The average number for each sector was then expressed as a percentage of the sum of average droppings (inner) plus average droppings (outer). This procedure standardised the figures between count dates.

↑ indicates end of foreshore shooting season.

▨ quadrats < 10m from water

□ quadrats > 10m from water

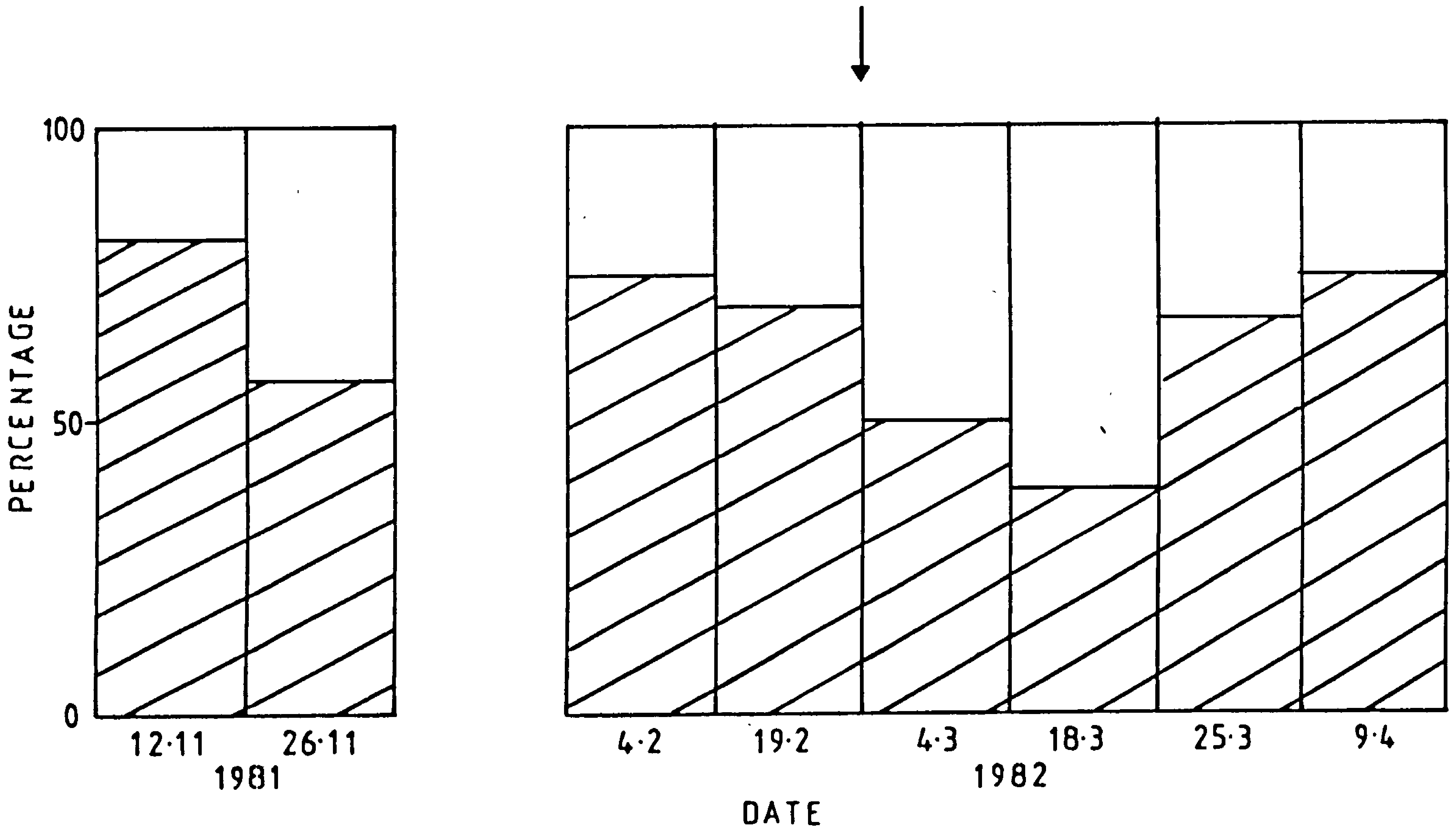

100
50
0
PERCENTAGE
12·11
26·11
1981
4·2
19·2
4·3
18·3
25·3
9·4
1982
DATE

Figure 4.16

Changes in relative use of inner and outer sectors through season 3. Percentage figure calculation and key as in Figure 4.15.

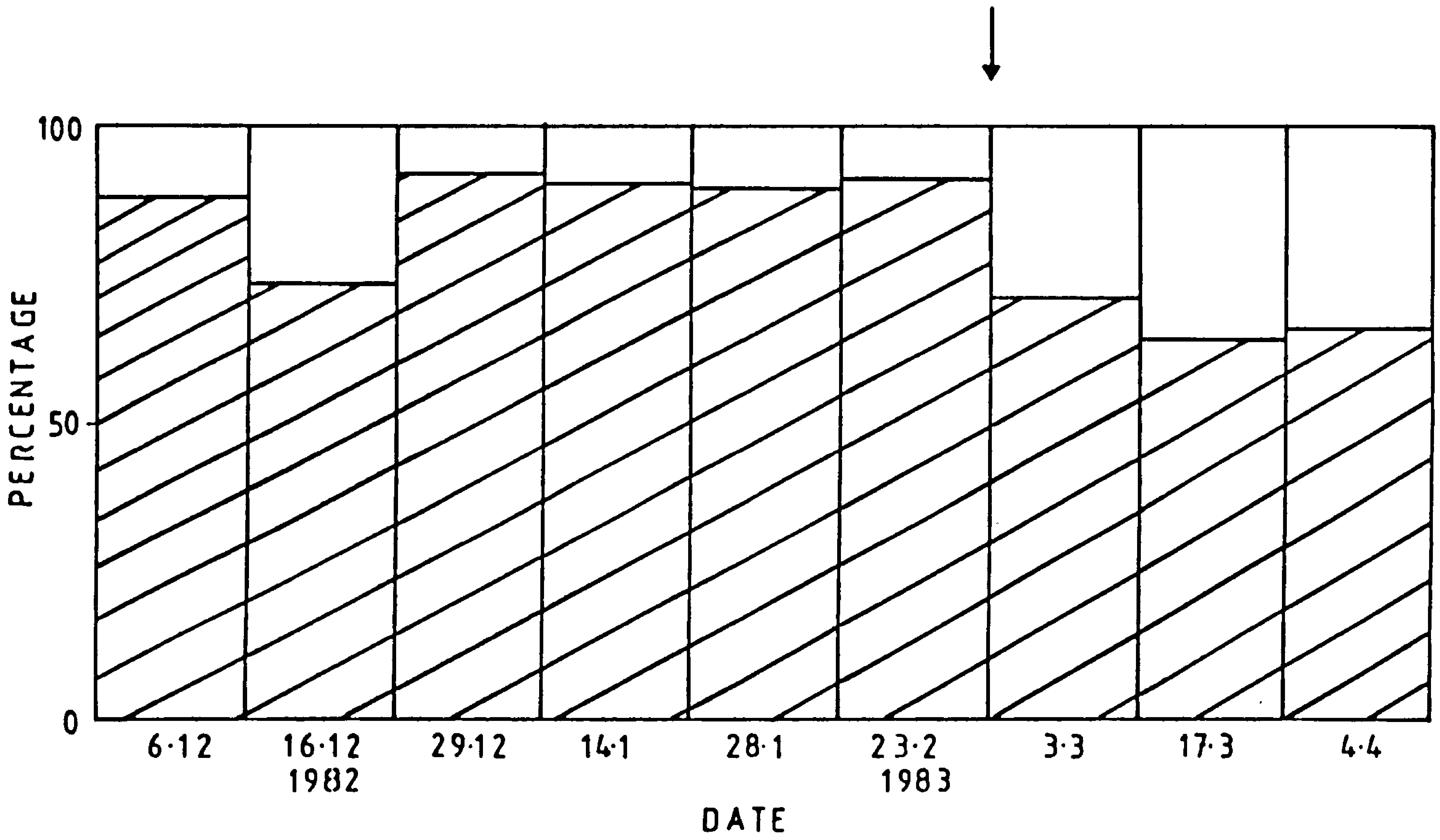
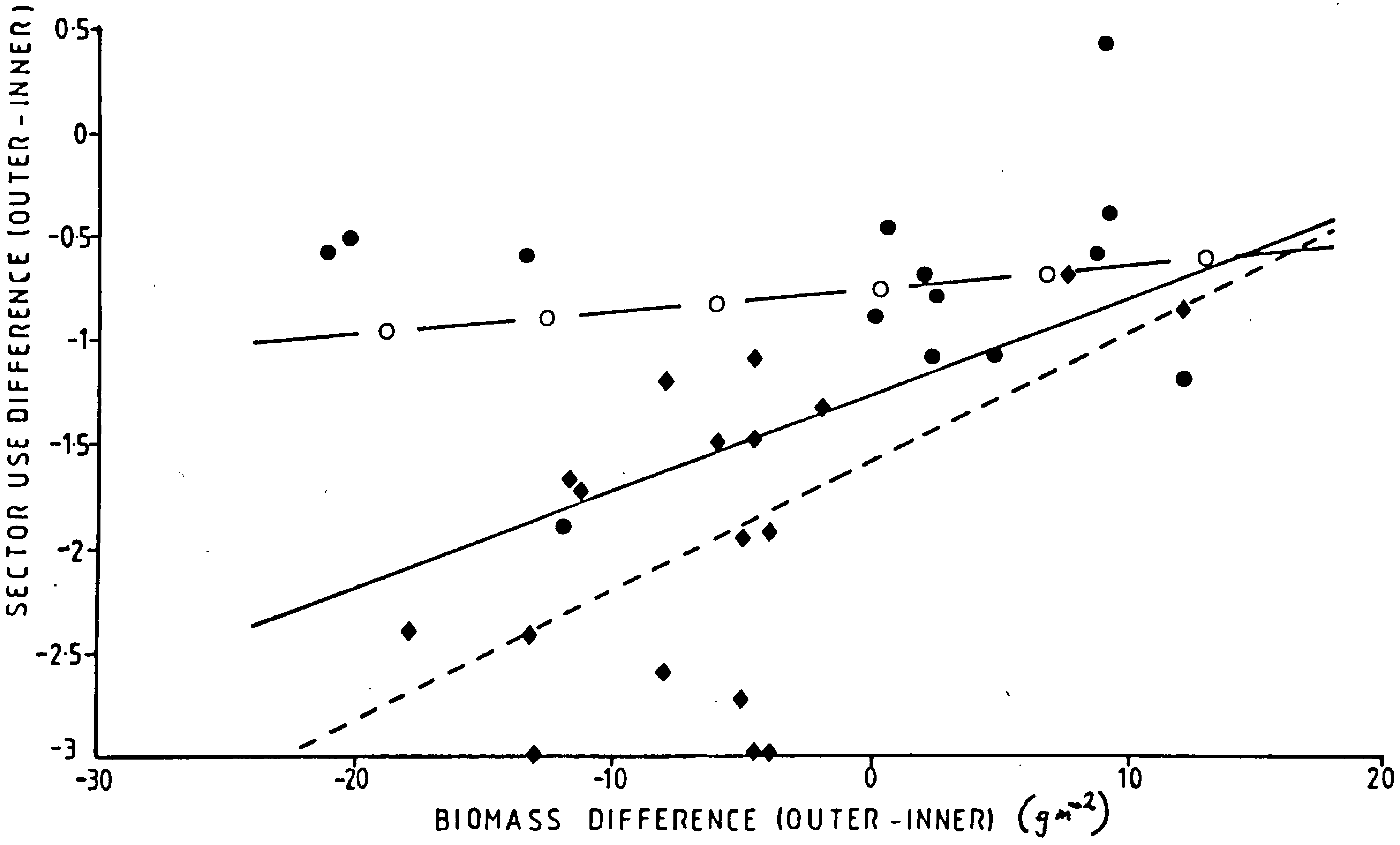

100
50
0
PERCENTAGE
6·12
16·12
1982
29·12
14·1
28·1
23·2
1983
3·3
17·3
4·4
DATE

Figure 4.17

Regression of sector use difference (outer minus inner) on biomass difference (outer minus inner). Each point is the result for one site for one month during seasons 2 and 3. The sector use difference figure was calculated as follows: the average number of droppings/ quadrat was calculated for each sector and for each site for each count date. This figure was then divided by the average droppings/ quadrat for each site for each count date to standardise the results. Since count dates occurred once every two weeks, the two results for each month were averaged to allow comparison with biomass data, which was collected monthly.

◆	during shooting season
●	after shooting season
———	regression line for all data
- - - -	regression line for during shooting season data
—○—	regression line for after shooting season data

The equation for the all data line is
$y = 0.046x - 1.27$.


0·5
0
-0·5
-1
-1·5
-2
-2·5
-3
SECTOR USE DIFFERENCE (OUTER - INNER)
-30
-20
-10
0
10
20
BIOMASS DIFFERENCE (OUTER - INNER) ($g\,m^{-2}$)

still tend to respond to biomass differences in their use of the inner and outer sectors, they also tend to feed further out than expected during the shooting season.

TABLE 4.8

Covariance analysis comparing "during shooting season" and "after shooting season" regression lines (see fig. 4.17).

Variance	F value	d.f.	Significance
Slope	4.174	1,28	n.s.
Elevation	21.273	1,29	P <0.01

4.4 DISCUSSION

4.4.1 The choice between food quantity and quality

All the factors investigated in this study (relating to food intake) can be divided into two main types: those affecting forage quantity, ie. biomass, height, primary production and those affecting forage quality, ie. species and nutrient composition. The results presented in this chapter suggest that, while wigeon are able to select feeding sites on the basis of both quantity and quality, if the two conflict, they tend to choose quantity. This preference may, of course, change with time of year (eg. protein may be more important in early spring) but over most of the winter, biomass tends to be most important. Thus, the physiological method of digestion in wildfowl - requiring large quantities of poorly digested food (Owen 1972b) - seems to be the major factor determining the site on which a wigeon should feed.

As mentioned in the introduction, a large number of studies have found food biomass to be most important in wildfowl feeding site selection. However, others have found quality to be the major determinant. For example, Owen (1973b) found that wigeon at Bridgewater Bay selected feeding areas on the basis of the rankness of the vegetation, probably because the quality of grass on the preferred Puccinellia/ Agrostis zones was higher than on the less used Festuca zones. Again, in white-fronted geese, the preferred foraging zones contained the highest quality forage but had the shortest grass and probably lowest biomass (Owen 1973a). Finally, in a fertilizer experiment with geese, Owen (1975b) found that the birds selected cut/ fertilized vegetation over uncut/ unfertilized areas on which biomass was higher.

Why should grazing wildfowl sometimes select sites on the basis of vegetation quantity (eg. wigeon at Caerlaverock) and at other times select for grass quality as in the above studies? Possibly the fact that preferred zones contained less dead material in Owen's (1973a) white-fronted goose study meant that energy intake rates were in fact higher on low biomass areas due to the need for less selection. Possibly, lower gross intake rates were offset by higher digestibilities of good quality grasses (Harwood 1975, Owen et al 1977, Boudewijn 1984). Finally, the selection of high biomass sites by wigeon at Caerlaverock may reflect the fact that species composition was very similar between sites and food quality differences were therefore only slight. Wigeon were not having to select between rank Festuca and easily digestable Puccinellia/ Agrostis zones (Owen 1973b), but between several Lolium/ Agrostis/ Poa swards of similar composition. In this situation, biomass may become more important because the costs of discrimination and increased searching and handling time would far outweigh the rewards (Crawley 1983).

The second fertilizer experiment provided evidence that wigeon in late winter do select for protein content alone, because biomass was roughly similar on both experimental sites. However, this may be because protein content is more important before migration/ nesting, and that feeding priorities may change at this time of year. This idea will be discussed more fully in Chapter 6.

The (hypothesised) relationship between how closely wigeon track the available food biomass and overall food abundance (Figure 4.9) has been found in other studies. Eriksson (1978) reports that in three out of four years goldeneye duckling lake selection was positively correlated with invertebrate food abundance. However, in one year, when food abundance was very high, the ducklings fed on the lake nearest their nesting grounds. Eriksson hypothesised that the ducklings would only undertake risky journeys to good lakes if the pay-offs were high. Charman (1979) found that dispersion of brent geese in certain areas was related to Zostera density only below 15% leaf cover. Dugan (1982) found a similar situation in the site use of a single territorial grey plover, foraging on inter-tidal mudflats. He found that the relationship between site use and prey abundance/ intake rates was closest on days with temperatures of $1^{o}C$ or less when energy requirements would be greatest. Finally, Murton et al (1966) suggested that woodpigeons were only distributed according to food density when food supplies were poor. Thus, it is certainly possible that at high food densities, when birds find it easier to meet their energy requirements, other factors governing site selection may come into play, eg. food quality, proximity to water (see next section). Furthermore, if food intake in wigeon follows the functional response ie. intake increases with food density to a certain point and then asymptotes (see Section 4.4.3 and Chapter 5) then, above a certain biomass density, there would be no point in wigeon selecting high biomass sites since food intake would not be improved.

4.4.2 The choice between food intake and safety

The possible conflict between food quantity and quality is not the only problem facing wigeon when deciding where to feed. The trade-off between foraging efficiency and anti-predator behaviour may also influence choice of feeding sites. It has long been recognised that efficient anti-predator responses can conflict with vital functions such as reproduction and feeding (eg. Edmunds 1974). However, only recently have quantitative studies relating to this problem been carried out (eg. Milinski and Heller 1979, Sih 1980, Grub and Greenwald 1982). The major problem faced by studies of this subject is the precise measurement of predation pressure. The difficulty of obtaining data on actual predatory attacks in the field often means that less satisfactory, indirect methods have to be used (as in this study). However, the observation that wigeon become more vigilant the further they are from water (Figure 4.14) is not necessarily sufficient evidence that the probability of predation increases as a bird moves further away from water. (This relationship between vigiliance and distance to cover was also found by Barnard (1980), Caraco et al (1980a) and Lendrem (1983a)).

However, several other observations support this hypothesis. Firstly, some studies have shown that there is a relationship between vigilance rates and predator avoidance (see Bertram 1978). For example Barnard (1980) not only found a positive correlation between distance from a hedge and looking rates in house sparrows (Passer domesticus) but also that flight distance at the approach of a predator increased with increasing looking rate. Secondly, it is unlikely that vigilance behaviour for, say, food assessment (Drent and Swierstra 1977) would vary with distance from water, or that a well-adapted animal would indulge in spurious behaviour, which would have a significant effect on the efficiency of food intake. Lastly, several studies have shown the importance of cover to bird anti-predator strategies (eg. Barnard 1979, 1980; Caraco et al 1980a; Grub and Greenwald 1982).

However, this last point raises another question. Is open water to a wigeon the equivalent of a hedge or woodland to a passerine? Only anecdotal evidence is available here. As reported in the results section, wigeon tend to move into water if disturbed. This disturbance could be due to noise (eg. visitors or aircraft); aerial predators (eg. peregrines or harriers); land predators (eg. foxes, which were seen on several occasions during night watches). Kruuk (1972) reports how several large herbivore species flee to water when attempting to escape from land predators. With respect to birds, Goethe (1956) documents how 60 gulls were killed by a single fox when roosting on mudflats rather than water, and Sharp (1951) reports how a golden eagle was unable to pick a duck off the water. Thus, from several lines of evidence, it does seem that the proximity of wigeon feeding sites to water is primarily an anti-predator strategy.

Several studies have shown that animals tend to feed in the safest places. Barnard (1979, 1980) showed that house sparrows feeding in open fields, tended to feed close to a hedge at the edge of the field (mean of 18-20m from the hedge) even though food was more plentiful toward the centre of the field. Grub and Greenwald (1982) found that white-throated sparrows always fed closest to cover if this entailed no reduction in energy return. Grant (1972) reports how arctic hares in Newfoundland are only found in areas with ample cover, allowing escape from its main predator, the lynx. Sih (1980) found that the lower instars of Notonecta hoffmanii preferred to feed in low prey density areas with no predation risk, rather than high food density sites with adult conspecifics - their main predators. This preference for safe feeding is not only shown in space but also in time, eg. Tamisier (1970, 1976) suggests that the reason why teal feed nocturnally is to avoid predation by harriers and gulls.

A few studies have also looked at the effect of changing circumstances on this, often delicate, balance. Milinski and Heller (1978) found that sticklebacks tended to attack the densest daphnia swarms, in line with optimal foraging theory. However, after exposure to a model kingfisher, they went for the least dense swarms. They hypothesised that this behaviour gave the fish more time for vigilance activities when a predator was in the vicinity. Grub and Greenwald (1982) found that, if given a choice of a safe, cold feeder or a risky, warm one, sparrows tended to choose the risky feeder in high winds or low temperatures. In other words, their choice was dependent upon risk of starvation.

The results reported here, while being similar to the last study, examine the reaction of wigeon to an increasing difference in food availability on a safe and risky site (ie. close to and away from water). Moreover net energy intake is assessed in terms of food availability rather than weather variables. They suggest that the risks a wigeon will take are dependent upon the relative rewards of safe and risky sites. Birds stay in safe/ low food sites if the alternative risky food site is little better in terms of food availability. However, as the food difference increases, the birds are prepared to take greater risks. This situation would lend itself to a more detailed experimental study.

Finally, it is interesting to note how far-reaching are the consequences of man's predation on wildfowl. Even in the absence of direct predation (there is no shooting on the reserve) the results from Figure 4.17 suggest that birds are responding quite significantly to the periodicity of his hunting season.

The effects of anti-predator behaviour on site selection is not only evident in intra-site selection, but also in inter-site selection. Thus, the enclosure received a high level of use primarily on account of its fox-proof fence while some sites, eg. G, were hardly used on account of their lack of water. The relationship between site biomass, safety and use by wigeon is developed more fully in the next section.

4.4.3 The choice between aggregation and ideal-free distribution

How should a population of animals distribute themselves over a resource gradient so as to obtain optimal food intake? If one is considering a species in which there is no active defence of the resource - this applies to most over-wintering avian feeding flocks - then there are two fairly simple models which the birds should theoretically obey. If there is no social interference, animals should aggregate in the areas where resource intake is highest (eg. Hassell and May 1974, Pyke et al 1977). If there is interference, which affects resource intake, they should initially aggregate on the best areas, but as density increases, should spread out onto poorer areas, so as to always obtain the maximum possible resource intake - which will now be dependent upon a combination of resource density and interference level. This type of distribution is termed the ideal-free (Fretwell 1972).

Predictions from the two models are fairly simple. If animals are conforming to an aggregative distribution, one would expect an exponential or sigmoid relationship between resource level and animal density, ie. all animals would be crowded into the best areas. This sigmoid relationship initially seems sub-optimal since animals do not spend all their time in the best areas. However, Hassel and May (1974), using simple predator searching rules, eg. increased turning and slower walking in good areas, show how a sigmoid curve could result from this type of area-restricted search. Also, many foragers obey Holling's (1965) functional response curve type 2, ie. food intake increases rapidly with food density until it reaches an asymptote. This saturation effect is due to limited time for food handling or limited gut capacity (Kenward and Sibly 1978, Crawley 1983). This would result in there being no clear advantage to an animal in selecting higher food densities, once the food density at which its functional response curve asymptoted had been reached.

If animals are conforming to the ideal-free distribution, the predictions are slightly more complex. Firstly, at high densities there should be some evidence of feeding interference (Sutherland and Koene 1982). Secondly, one would expect good sites to be filled initially and then, as numbers increase, animals should gradually spread to poorer sites (Crawley 1983). Conversely, as numbers decline animals should initially vacate the poorer areas. Lastly, due to the optimum density of animals being dependent upon the food density in the patch, there should be a linear correlation between resource density and site use.

These two models are not mutually exclusive in that the ideal-free merges into aggregation as interference declines, and vice versa. Indeed, Sutherland (1983) has published a model relating the two, using a measure of interference (m) derived from the slope of log feeding rate against log animal density. As m increases the prey density/ predator density graph moves closer to a linear correlation.

Animals which obey the aggregative model are many, including redshank feeding on corophium (Goss-Custard 1970) and many insect predators (Hassel and May 1974).

Although the ideal-free distribution has only been formulated fairly recently, several studies have shown that, given the right conditions, it provides a good description of animal distribution and behaviour. For example, Goss-Custard et al (1981) found that oystercatchers feeding on mussels initially occupied the most favourable beds, but gradually moved to poorer ones as the population increased. Milinski (1979) found that sticklebacks feeding on daphnia distribute themselves according to food availability. Harper (1982) found that mallard feeding on bread in a public park do the same. Hunter (1964) found that the best grazing areas were first to be occupied and carried the highest densities of hill sheep.

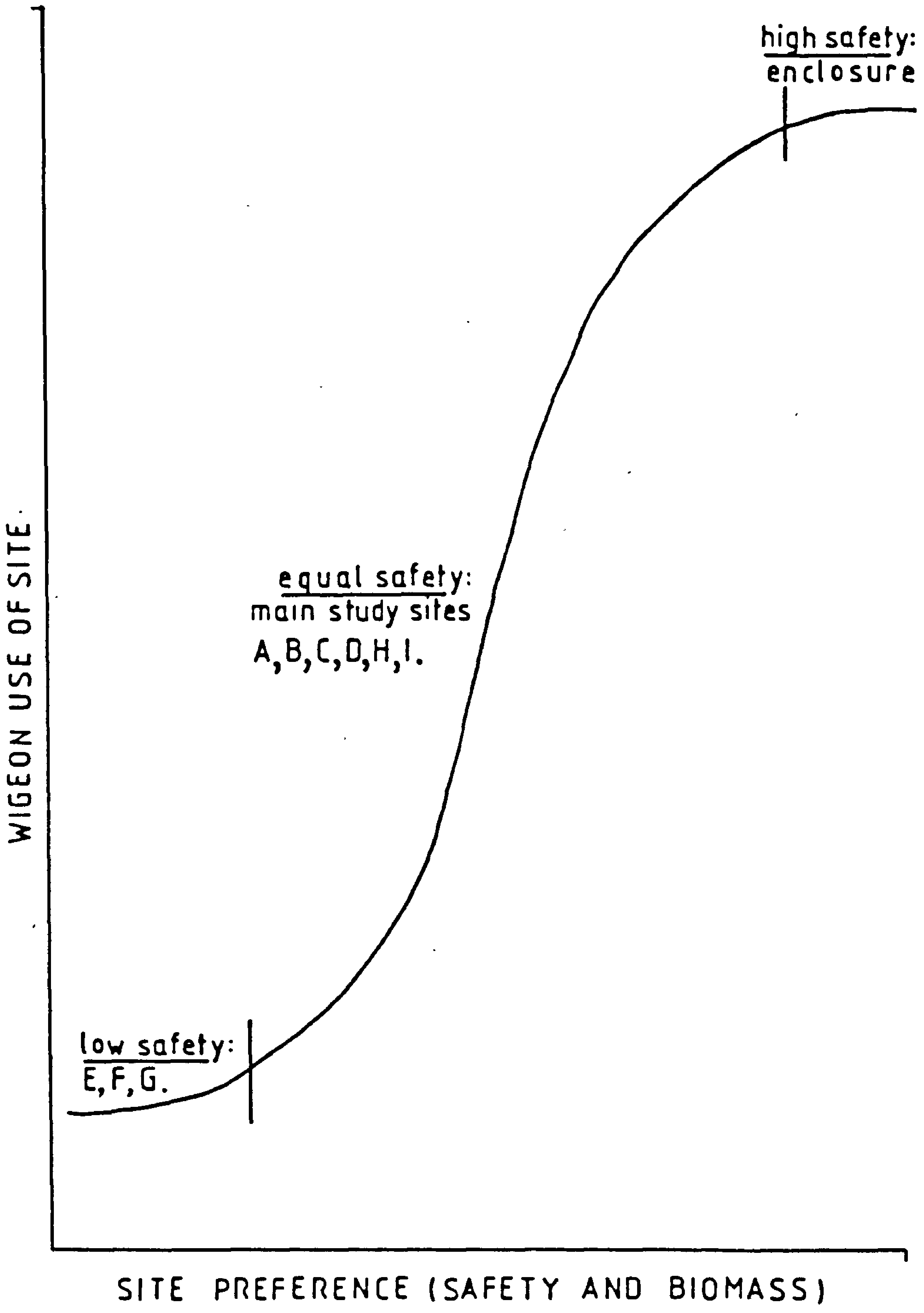
Before discussing the application of these models to the results presented here, one point should be noted. The quality of a site in terms of wigeon usage relates not only to its food biomass but also its safety (whether due to fox-proof enclosure or large deep pond). The data for the six sites studied in Section 4.3.2 A did, of course, relate only to biomass. However, in terms of all 10 study sites both safety and biomass were involved in their selection. A site with an average level of biomass but high safety may receive a very high level of wigeon use (eg. the enclosure, although biomass level was never measured). Conversely, a site with fairly high biomass but low safety (eg. sites E,F,G) will be rarely used (see Figure 4.18). The 'spreading out' of birds over the reserve will therefore be dependent on both biomass level and safety on the site.

The results from this study are at first rather confusing. From Figures 4.4 and 4.6 it seems that wigeon initially occupy the best sites (in terms of wigeon hours through the season) and then, as the season progresses, spread out to forage on other sites with increasing regularity. This increase in the number of sites used coincides with increasing number of birds on the reserve from November to January (Figure 2.1). This pattern of site use exhibits some of the characteristics of the ideal-free distribution - all birds initially use the best sites but, as bird density increases, some birds find it more profitable to move to new areas. After January, however, the number of birds on the reserve decreases and yet the number of sites used remains the same and even increases slightly. This apparent anomaly could be due to the fact that grazing wigeon have a great effect on the biomass of food on their feeding sites reducing it by up to 75% compared to ungrazed sites by the end of the year (Chapter 6). Thus, even though bird numbers are decreasing, the biomass of food on the best sites is also decreasing and at a greater rate than that on the poorer sites, since by definition the best sites are grazed more heavily. The remaining birds will therefore tend to use the poorer sites more often, since feeding profitability is dependent on both bird density and food density.

In effect then, decreasing biomass would have the same effect on bird distribution as increasing bird numbers. Birds are not simply depleting the biomass on the best area to the level of the

Figure 4.18

A simple model to explain how safety and food biomass are both involved in the selection of feeding sites by wigeon, and how the 10 main feeding sites fit into this safety/ biomass requirement.


high safety:
enclosure
equal safety:
main study sites
A,B,C,D,H,I.
low safety:
E,F,G.
WIGEON USE OF SITE
SITE PREFERENCE (SAFETY AND BIOMASS)

next best and then using both (a form of aggregation (Sutherland 1983)) since there were still major differences in biomass (even though reduced) between feeding sites at the end of season 2. The enclosure was certainly grazed down to a level below that of other sites (see Chapter 5) but this was because of its use as a 'home base' by the birds.

Finally, when numbers of birds on the reserve dropped to a very low level in April all the birds moved back to occupy a few sites only (Figure 4.6). In the classical ideal-free model, these sites would be the same ones that were occupied at the start of the season. Figure 4.4 shows that this was the case for two sites, H and the enclosure, but that site A was "replaced by" site I, which had been little used at the start of the season. It is difficult to explain the change of "attractiveness" of these sites. The biomass, and thus profitability of site A, should theoretically have been higher than site I at the end of the season. Possibly factors other than feeding efficiency became more important at the end of the season, at least in relation to site I.

The ideal-free distribution model depends on there being density-dependent feeding interference between foraging birds. Unfortunately this subject was not examined in depth. However, aggression (without any clear sexual reasons such as mate stealing) was frequently observed in feeding flocks. When two birds of either sex became too close together one would commonly threaten the other (using a characteristic threat posture (Cramp and Simmons 1977)). This would normally result in the two individuals moving further apart. There are, of course, two contradictory requirements here. Firstly, the need to flock for various reasons (Chapter 7), secondly the requirement of sufficient feeding space to maintain intake rates. However, since wigeon only use a narrow strip of grassland next to the water, the potential for feeding interference is probably quite large.

One observation, however, seems to go against the hypothesis that birds use sites according to the ideal-free distribution. This is that the detailed graphs of site use against biomass (Figures 4·10 and 4·11) suggest an aggregative response - they are either sigmoid or exponential. The answer to this dilemma is possibly found in Sutherland (1983). He shows that different levels of interference result in a continuum between aggregation and ideal-free. While interference does seem to be taking place in wigeon, the level of interference should not be great since it is a herbivore feeding on a 'super-abundant' food supply - food stealing, as found in oystercatchers (Goss-Custard 1980), does not take place. This could explain why the site use/ biomass graphs tend more towards the exponential. One interesting observation from these graphs, which supports this idea of a balance between the ideal-free and aggregation models, is that the asymptote in Figure 4.11 is not due to the wigeon reaching their maximum food density at 20 g/m^2 (as predicted by the functional response theory) since Figure 4.10 shows that wigeon do distinguish between biomass levels above this. However, the asymptote could be the result of feeding interference coming into play at a wigeon density of about 75 droppings/ quadrat, as the droppings density in Figure 4.10 does not go above this level.

It is recognised that this discussion of wigeon distribution over feeding sites is rather speculative, and does not explain all the results reported in this chapter, especially since the data on the 'spreading out' of wigeon over the reserve were collected in season 1 and those on site use/ biomass levels were collected in season 2: the two are not directly comparable. However, what this discussion does do is to put forward suggestions which help to explain why wigeon do not all congregate on the few best sites throughout the season but tend to spread out over the reserve.

4.4.4 Proximate factors in feeding site selection

The above discusion raises a further question. How are birds assessing the biomass on a site? For instance, the ideal-free model assumes perfect knowledge of the resource density on a site.

There are two main ways that herbivores are attracted to the best habitat: a) at long range by sight or smell (taxis), or b) by certain simple decision rules when in the habitat (kinesis), which would result in area-restricted searching (Crawley 1983).

In the case of wigeon both possibly play a part. Many wildfowl species, including wigeon, have been shown to be strongly attracted to green (Kear 1964a) and it is possible that wigeon could use the greenness of a field to assess the amount of forage available (Owen 1976a).

Rabe et al (1983) found that woodcock used soil colour as an important proximal cue for selecting good feeding sites. Wigeon could also possibly use the height of grass on a site as an indication of biomass, due to the high level of correlation between these two variables (see 4.3.2 a).

Once grazing on a site, birds would require further methods to select good areas within the site as it is unlikely that colour could be used at such close range, eg. in the fertilizer experiments. Birds could employ simple kinetic responses such as slower walking (Chapter 5) and higher turning rates (Owen 1976a) to keep them in good areas (Hassel and May 1974). (This aspect of site selection is dealt with in more detail in Chapter 5). However, in order to accomplish this area-restricted searching they would still require a method of assessing food intake. There are two main possibilities for wigeon. Firstly, a bird could assess the food density on a patch by intake rates (Royama 1970). If intake rates are high, stay in the patch. Secondly, if selecting for food quality, this could be assessed by the tensile strength of the grass: high protein grass tends to have a high water content which reduces tensile strength (Owen et al 1977, Owen 1980). Again, if the grass breaks easily, stay in the patch.

4.4.5 Grass species selection by wigeon

The result that wigeon seem to be selecting for *Agrostis stolonifera*, even though based on little data, was compared with the three most recently published analyses of wigeon diet. Owen (1973b) reporting on wigeon feeding at Bridgewater Bay, Somerset, found that *Agrostis* species are the third commonest item in the diet, while *Lolium perenne* comes ninth. However, he did not compare this with the species frequencies in the sward, so just how this relates to selection is unknown. Owen and Thomas (1979) studying wigeon in the Washes found the same sort of result: *A. stolonifera* was the second commonest item, *L. perenne* the seventh. However, again they did not compare this in a detailed way with species availability. Finally, Williams and Forbes (1980), working on marshland in Kent, found that on improved swards wigeon positively selected for *A. Stolonifera* but not for *Cynosurus/ Lolium* (they could not distinguish between the two). However, on unimproved grassland they positively selected for *Cynos/ Lol.* and rejected *A. stolonifera*. While this last study is rather confusing, the results most applicable to this work would be those from the improved grassland. Thus, the general concensus would seem to be that, in certain circumstances at least, *A. stolonifera* is positively selected by wigeon.

4.4.6 The reasons for site selection by wigeon

In the introduction to this chapter, it was stated that animals are most likely to select sites in terms of foraging efficiency or safety. The results presented here would suggest that these factors are indeed the most important for wigeon feeding at Caerlaverock. Thus, while anti-predator behaviour does seem to affect the amount and timing of selection between sites, biomass levels seem to be important in selecting between sites of equal safety (Figure 4.18). Within a site, birds tend to feed in high biomass areas, but always constrained by the need to feed in safety ie. close to water (Figure 4.17).

CHAPTER 5

THE EFFECT OF GRASSLAND TYPE ON WIGEON FEEDING BEHAVIOUR

5.1 INTRODUCTION

It was shown in Chapter 4 that, at certain times, wigeon respond very significantly to the quantity and/or quality of grass on their feeding areas. In order to understand in more detail this bird's behavioural response to varying grassland types, a number of studies on several different aspects of its feeding behaviour such as pecking rates, walking rates and defaecation rates were undertaken. These studies included work on wild birds (carried out during all three field seasons) and on a captive flock of wigeon (during the spring of 1981). This type of observation is essential in answering several important questions about how this species is adapted to maximising its energetic and nutrient input during the winter.

Firstly, in this study it has been more or less assumed that grazing in high biomass areas is selectively advantageous to the birds (Chapter 4). This assumption has been made in a number of similar studies, eg. Kaminski and Prince (1981b), Eriksson (1978), the idea being that the higher the food availability the higher the food intake per unit time, ie. feeding efficiency (E/T) is maximised (Goss-Custard 1970). In those studies, however, where the effect of food abundance on food intake has actually been measured (either by assessing prey removal rate or, less directly, by observing feeding rates) the relationship has been found to be positive and linear at low food levels, but normally asymptoting once a particular rate of food intake has been achieved (see p.45). This relationship has been termed the functional response, and functionl response curves have now been determined for a large number of herbivores ranging from lemmings to wood-pigeons (Crawley 1983), but not wigeon. Observations were made therefore on peck and defaecation (and thus throughput) rates on sites of varying biomass to consider if wigeon show a functional response and therefore if there is a selection advantage to feeding in high biomass areas.

Secondly, behavioural observations can investigate how wigeon manage to exploit successfully their heterogenous grassland habitat. Patches of high grass biomass or high quality grass may alternate with low biomass/quality areas. To forage optimally birds need to concentrate their grazing time on the best areas and the mechanisms by which they do this can be elucidated by studies of walking rates and turning rates on different quality patches.

Finally, these studies can give insights into how the wigeon's grazing behaviour adapts to possibly unfavourable grass types, eg. very long or short grass, or, alternatively, for which sward types this species is best adapted. Owen (1973b), for instance, suggested that one of the reasons why wigeon concentrated their grazing on particular sward types was that the grass on the preferred feeding areas was short, and the birds could graze this type of sward more efficiently. Drent and Swierstra (1977), on the other hand, considered short grass to reduce grazing efficiency in barnacle geese.

In summary, this chapter includes results from observations on a range of wigeon feeding behaviours, with the emphasis placed on the methods used by wigeon to successfully exploit the varied nature of their feeding habitat.

5.2 METHODS

5.2.1 Field observations

a) Peck rate.

The method used to measure peck rate was that of Owen (1972b). The time taken to perform 50 pecks by a focal bird was recorded on a stop-watch and the data expressed as pecks min^{-1}. Thus every peck is assumed to be 'successful' which is a reasonable assumption for herbivorous wildfowl. Wigeon tend to be very wary birds, and look up more often than geese. Thus, birds which looked up for a short time were still included in the analysis - Owen (1972b) discarded results from birds which stopped grazing. However, the watch was stopped when the bird looked up so that the time recorded was for 50 pecks when in the head down position only. If a bird looked up for a long time (> c.5s) or walked off without grazing, the result was discarded.

b) Step rate.

This was measured by recording the time taken for 20 steps. The data were expressed as steps min^{-1}. As with peck rate, if a bird looked up, the watch was stopped, so that the steps min^{-1} figures refer to birds in the grazing position only.

c) Defaecation rate.

This was measured after the method of Ebbinge et al (1975) by keeping an individual wigeon in view for as long as possible and timing the interval between successive droppings. Two stop-watches were used so that, at the end of one defaecation interval, one watch was stopped and the other started. The bird was observed for a few seconds and then the time of the previous defaecation interval recorded. Even though the bird was unobserved for approximately 5 seconds, the technique was considered valid since the liklihood of a defaecation occurring within the first 10 seconds of a previous defaecation was very remote. The advantage of this technique was that the sample size was doubled.

Owen (1971) and Cargill (1981) used a different method whereby total observation time was divided by the number of defaecations observed in order to derive an estimate of defaecation interval. While this method is obviously an indirect measure of the interval, Cargill (1981) claimed it was more accurate since the observation of complete intervals introduced a bias towards short intervals: the liklihood of the cloaca being obscured increases with time. While this assumption is questionable (the cloaca will be obscured at random with respect to time) it was not considered to be a problem with wigeon observation since normal flock size was small compared to geese and defaecation interval much shorter (Cargill's (1981) estimate for snow geese was 5.2 mins.). Defaecation interval was, for some analyses, converted to defaecation rate, ie. defaecations min^{-1}.

5.2.2 Captive flock observations

A small flock of 11 pinioned wigeon, which had been bred in captivity, were obtained from the Wildfowl Trust reserve at Martin Mere, Lancashire, Great Britain. All were first year birds - 6 males and 5 females. During the first winter, one of the female birds died, so that the observations and experiments (reported here and in Chapter 8) were carried out on ten birds.

In the spring (April and May) of 1981 two observational experiments were carried out on these birds. They were housed overnight in a fox and mink proof enclosure. A small pond was dug to provide water. During the experiments the birds were fed solely on grass - either grazed naturally in the experimental enclosure or cut grass which was provided for the birds in the overnight pen.

The experiments were carried out in a small grazing enclosure, approximately 6m x 2.5m. Each morning the height of grass in the enclosure was estimated by randomly placing a ruler in the enclosure, its based pushed down to ground level, and measuring the height of the longest blade touching the ruler. This process was repeated 35 times, and the mean grass height calculated for each day.

At 0830 hours the birds were let into the enclosure and allowed to settle down for about 1 - 1.5 hours (the wigeon were herded into the enclosure, so that no handling was necessary).

Observations were carried out for several hours from approximately 1000 hours. The observer watched from a "fensman" hide situated approximately 10m from the enclosure. Peck rate and defaecation rate were measured by the same methods as for wild birds. However, since feeding bout length was shorter in the captive birds, the time for 25 pecks (as opposed to 50) was recorded. About 30 peck rates were recorded each day, and as many defaecation intervals as possible (normally about 10). After the observation period the birds were allowed to graze in the experimental enclosure until sunset. They were then put back in the overnight enclosure. By this method, the grass in the experimental enclosure was gradually grazed down, so that data was collected from birds grazing a different grass height each day. The enclosure was cleared of droppings at the end of the day so that it did not become fouled.

Data were collected in two main experiments - the first lasting for 16 days (11 to 26 April) and the second lasting 6 days (29 April to 4 May). The position of the grazing enclosure was changed between experiments so that birds were once again grazing on long grass for the second experiment. Observations were carried out on 11 days in the first experiment and all 6 days in the second.

5.2.3 The relevance of captive bird results for studies on wild birds

It is useful at this point to consider in more detail just what relevance studies on captive birds have for research in field ecology. The main thrust of this project has related to feeding in wild birds. This is in line with traditional ecological/ ethological thinking, which recognises that to understand an animal in relation to its environment you must study it in that context. Results from studies on captive birds are often as artificial as the environment in which they are kept and bear very little relationship to the 'real' world. It may be suggested that studies on captive birds are useful purely from the point of view of understanding how captive animals work and behave. This may be true, but is more relevant to zoo-keepers than ecologists. However, the ease of working in 'lab' conditions, as opposed to the field, does mean that it is sensible to thoroughly investigate the relationships between these two methods of study, and to attempt to define the areas of research in which captive studies are a help and those in which they are a hindrance.

With respect to work on feeding ecology, there are two main effects of captivity which must be taken into account. Firstly the bird may be under a great deal of stress. This can be caused either by the surroundings in which it is kept or by contact (especially handling) with researchers. It is obvious that heavily stressed birds will not behave as normal, whether the behaviour concerned is feeding, mating or whatever. Stress can, to some extent, be overcome by using birds which have been imprinted on the researcher. However, while stress may be reduced, it is a matter of debate as to how much of the behaviour of imprinted birds can be regarded as normal.

Despite these problems, feeding behaviours are mostly simple motor activities and can reasonably be assumed to be little affected in captive birds which are not subjected to stressful living or experimental regimes. The digestive physiology of birds on the other hand can be profoundly affected by stressful living or handling. Throughput time, and thus digestive efficiency, is likely to be significantly altered, either because the bird does not feed normally or because normal gut movements are affected.

The second relevant effect of captivity on birds is its effect on gut size. Several authors have reported that gut size (especially gizzard, small intestine and caecum) was found to be significantly reduced (by anything up to 30% of the normal size) in captive-reared birds (Moss 1972, Owen 1975a). Furthermore, Pendergast and Boag (1971) found that spruce grouse that had been fed on a captive diet for six months lost more than three times more weight in feeding trials on their natural foods than birds which had been on the captive diet for only two weeks. Clearly captivity can have a major effect on gut morphology and digestive physiology (eg. digestive efficiency and throughput time). This effect is almost certainly due to the altered diets which are fed to captive birds (Moss 1972). This suggests that captive birds, maintained on natural diets, may retain a similar gut morphology and thus digestive physiology to wild birds. However, the feasibility of exactly matching a wild diet is questionable. Certainly in this research, while birds were kept on natural diets as much as possible, some grain (barley) was provided during periods when natural food was difficult to obtain (ie. late winter).

In summary, then, captive birds which are kept totally on natural diets and subjected to little experimental stress could possibly make good models for application to the wild situation. Since these requirements are rarely met, results confined to simple feeding behaviours in little stressed birds are most useful. Results on digestive physiology must always be treated very carefully when applying them to the wild situation, since both stress and captive diets can radically affect a bird's digestion.

5.3 RESULTS

5.3.1 Field observation results

5.3.1 A) Season 1 studies

During the early part of the first season, birds grazed solely on the enclosure field and only later moved out to any great extent onto the other feeding areas, ie. sites A,B,D,H and I. Even then the enclosure tended to receive much more grazing than the other sites, so that by the end of the year the enclosure had received a total of 30,835 wigeon hours of grazing, while the other five areas mentioned above averaged 6,702 wigeon hours (see Figure 4.3). Even though the area of the enclosure is slightly greater than that of the other sites, the intensity of grazing per m^2 of grass on the enclosure would still be approximately four times that of the other areas.

One result of this was that by February the biomass of grass on the enclosure was greatly reduced in comparison with that on the other sites. This could not be determined by accurate measurement since the spectrophotometer was not available. In addition, no access could be gained to the enclosure field to carry out any other form of accurate measurement. However, a subjective assessment of grass biomass was undertaken using visual estimates: scored on a scale of 0-4 (0=all dead vegetation; 1=mostly dead; 2=half dead/ half green; 3=mostly green; 4=all green).

This survey was carried out on 13 February 1981 during the early part of the behavioural study reported here. The score for the enclosure area averaged 1.25, while the average score for the five other sites was 2.6. While no claims can be made for the detailed accuracy of this method, it is reasonable to assume that it gave some indication of gross biomass levels.

This situation allowed the possibility of conducting a large-scale 'natural' experiment. Behavioural data was recorded from these two areas, ie. enclosure versus other sites between 1 February and 14 April of the first field season. The primary aim was to compare wigeon feeding behaviour on high biomass (ie. sites A,B,D,H,I) and low biomass (ie. enclosure field) feeding areas. Data on peck, step and defaecation intervals was recorded in this study.

The results from this work are shown in Figure 5.1. All data sets were very large ($80 < n < 266$), therefore d-tests were used to compare the high and low biomass sites. As can be seen from the figure, peck rate was significantly higher on the high biomass area ($d=10.99$; $P < 0.001$); step rate was significantly lower ($d=6.90$; $P < 0.001$); and defaecation interval was shorter, ie. birds produced more droppings per unit time ($d= 5.41$; $P < 0.01$). Thus, in this set of observations, biomass had a very significant effect on feeding behaviour: birds peck faster, walk more slowly and defaecate more often on high biomass areas.

This same data set was used to look at the relationship between peck rate and defaecation rate - the hypothesis being that the higher the peck rate, the higher the food intake and thus defaecation rate. In other words, if a negative relationship was found between peck rate and defaecation interval, this would show that peck rate was a good measure of rate of food intake: the amount of food taken per peck was not affected by the rate of pecking.

Due to the difficulty of accurately observing each defaecation event only one behaviour was observed at one time. Because of this, data on defaecation and peck rates for individual birds were not available. Another method was therefore chosen to study the peck/ defaecation relationship. This was to calculate an average peck rate for each site and then compare this with defaecation data collected on five of the six sites. The resulting regression is shown in Figure 5.2. The relationship is a good one ($t=5.57$, d.f.=166, $P <0.001$) showing that increasing peck rate does tend to result in higher throughput rates.

Finally, the peck rate data was examined for sex differences. In this analysis all data from all sites was lumped together since more or less equal numbers of male/ female observations had been made during each observation period. Thus date or site would not influence the results. In all 266 male and 215 female pecking rate observations had been recorded. The average rate for males was 115.3 ± 1.3 pecks min^{-1}, and for females 111.9 ± 1.4 pecks min^{-1}. The difference was not significant ($d=1.79$, $0.1 > P > 0.05$).

This result may at first seem to be at odds with the finding that male wigeon tend to be more vigilant than females (Chapter 7). The explanation for this is that peck rates were recorded only when birds were in the head-down position (see Methods) and thus were not affected by vigilance rates.

Figure 5.1

Peck rate, step rate and defaecation interval (mean ± 1 s.e.) comparisons between low biomass (enclosure) and high biomass (sites A,B,D,H,I) feeding sites - season 1.

☐ low biomass

▨ high biomass

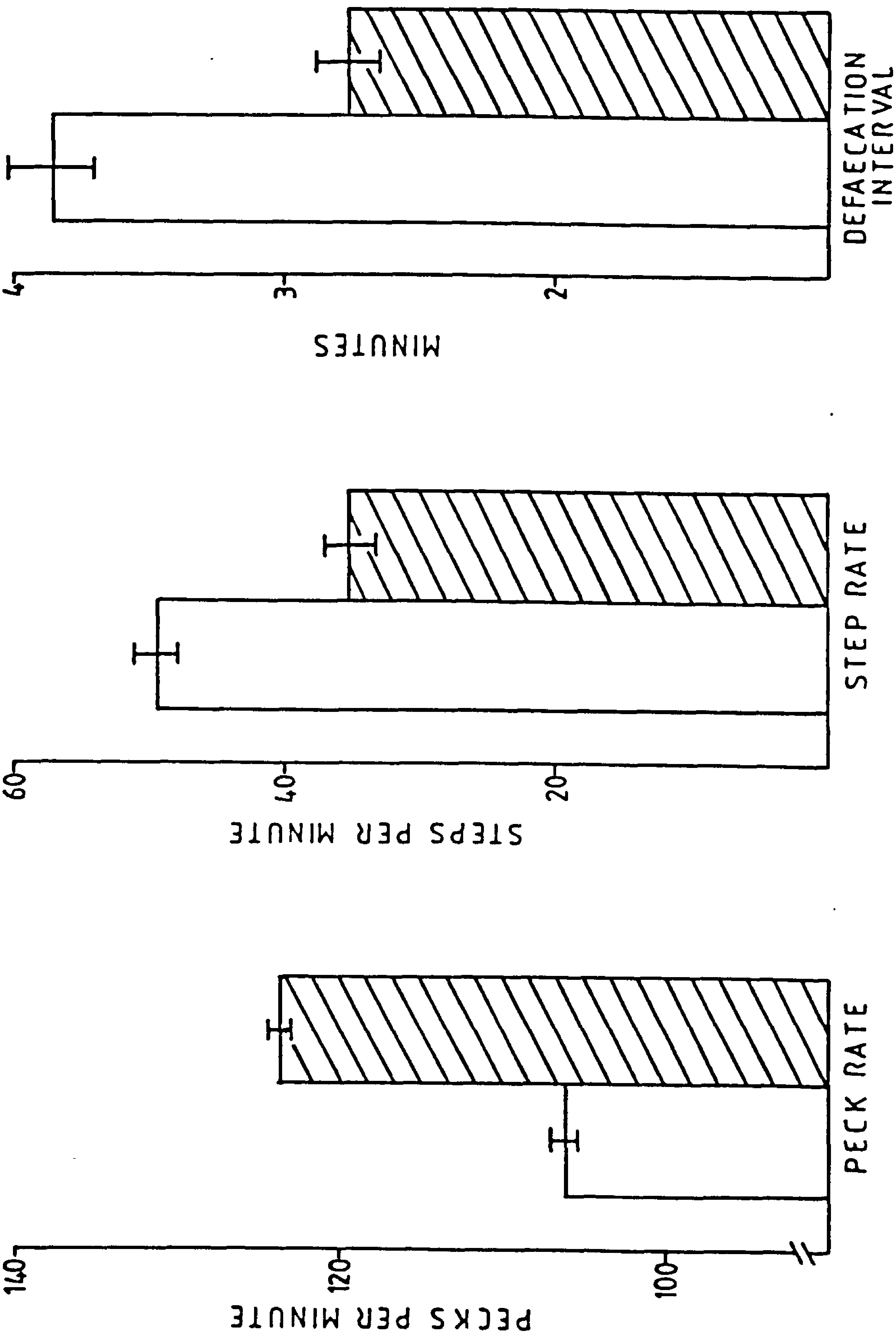
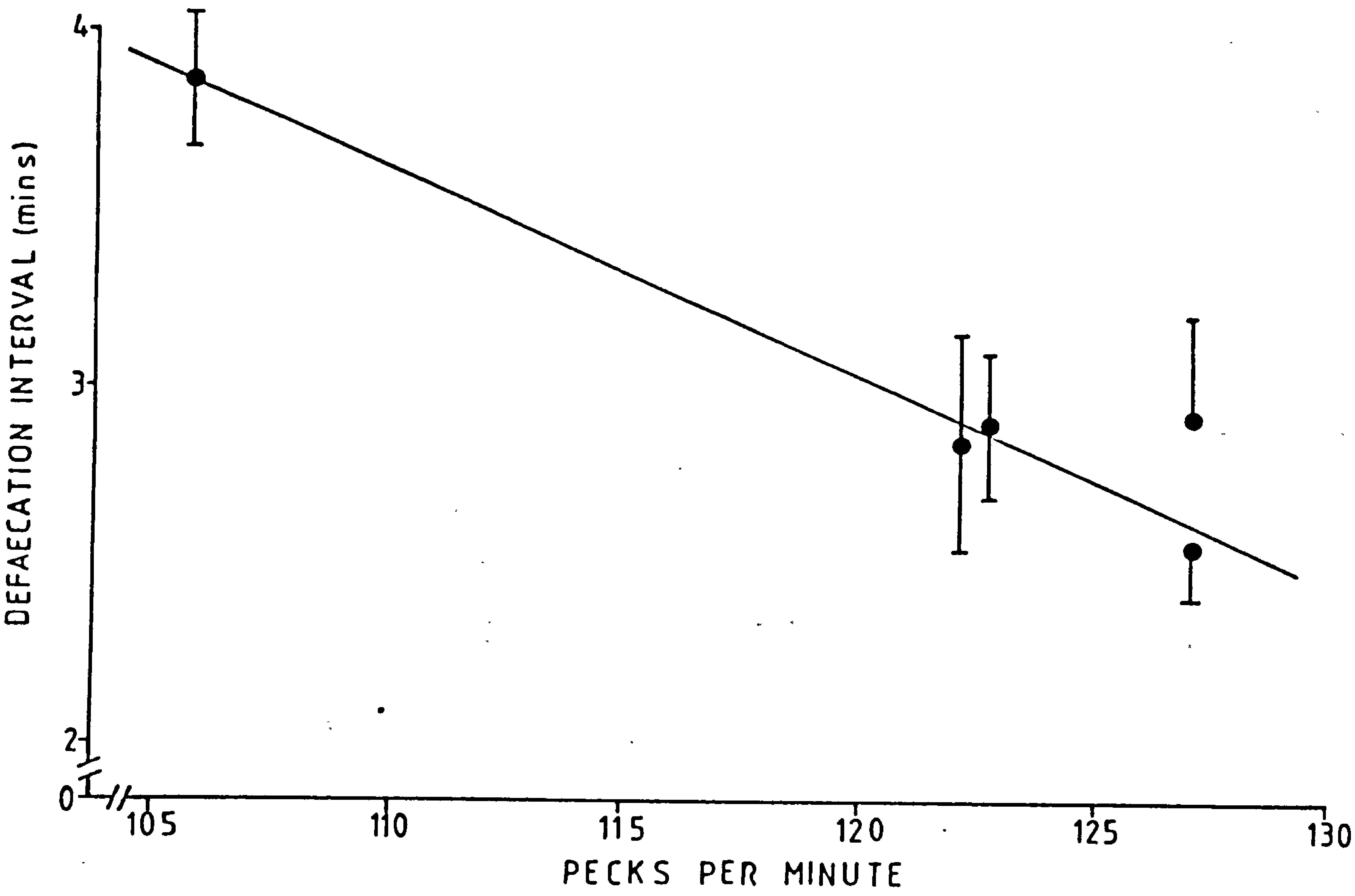

PECKS PER MINUTE
140
120
100
PECK RATE
STEPS PER MINUTE
60
40
20
STEP RATE
MINUTES
4
3
2
DEFAECATION INTERVAL

Figure 5.2

Regression of defaecation rate (mean ± 1 s.e.) on peck rate for 5 sites (for which defaecation data was available) in season 1. The equation of the line is $y=0.059x + 10.08$.


4
3
2
0
DEFAECATION INTERVAL (mins)
105
110
115
120
125
130
PECKS PER MINUTE

5.3.1 B) Season 2 studies

Since accurate records of various site variables such as grass biomass and height were recorded in season 2, data on peck rates on sites A,B,D,H and I were also collected to compare with these site variables. An attempt was made to collect at least 20 peck rate records from each site each month, although at certain times of year this proved difficult. Figure 5.3 shows the relationship between the average biomass for each site and the peck rates recorded on that site. Since biomass data was collected only from January onwards, peck rate data was likewise restricted to this time period in the analysis. The relationship was not significant (t=0.436, d.f.=211, n.s.). This result was rather puzzling in view of the season 1 study on biomass and peck rate. In order to investigate whether grass height had confused the season 2 result, the relationship between grass height on a site and peck rate was studied. In this case data from throughout the season was used, since grass height data had been collected from November onwards. The relationship was, however, not significant (t=1.55, d.f.=382, n.s.).

5.3.2 Fertilizer experiment results

During the third field season a similar behavioural study to the season 1 study reported above was carried out, but this time on artificially manipulated feeding areas. In addition, only pecking and walking rates were recorded. The areas used for the study were the fertilized and control strips set out in feeding area A (see p.25) This experiment provided an excellent opportunity to observe wigeon feeding behaviour on 'preferred' and 'rejected' feeding sites. Since these sites were adjacent, interfering factors such as disturbance and proximity to water were controlled for. As shown in Chapter 4 the fertilized strips contained higher biomass and protein levels than the control strips (Table 4.6). Records of peck and step rate were only used if the focal bird remained on the fertilized or control strip for the whole observation period. The results from this study are shown in Figure 5.4. As was the case in the season 1 study, peck rate was higher on high biomass (ie. fertilized) plots (d=4.38; $P < 0.001$) and step rate was lower (d=3.82; $P < 0.001$).

5.3.3 Captive flock results

Figure 5.5 shows the relationship between the grass height in the enclosure and the pecking rate of the captive birds. The data falls clearly into two groups. For grass taller than 30mm there are 14 points which form a highly significant regression line (t=10.25, d.f.=363, $P < 0.001$). Thus, as the birds gradually grazed down the grass over the duration of the experiment, their peck rate gradually increased. Grass shorter than 30mm has 3 points which do not fall anywhere near the line. This data was collected during the last five days of the 16 day (ie. first) experiment. By this time the grass had been grazed so low that food availability was seriously depleted. The height of the grass did not decrease during this time (as can be seen from the graph) but the amount of green leaf material did. This resulted in the birds spending longer searching for edible material, and thus their peck rate was reduced. This effect is presumably

Figure 5.3

Relationship between average biomass and peck rate (mean ± 1 s.e.) for 5 feeding sites in season 2.

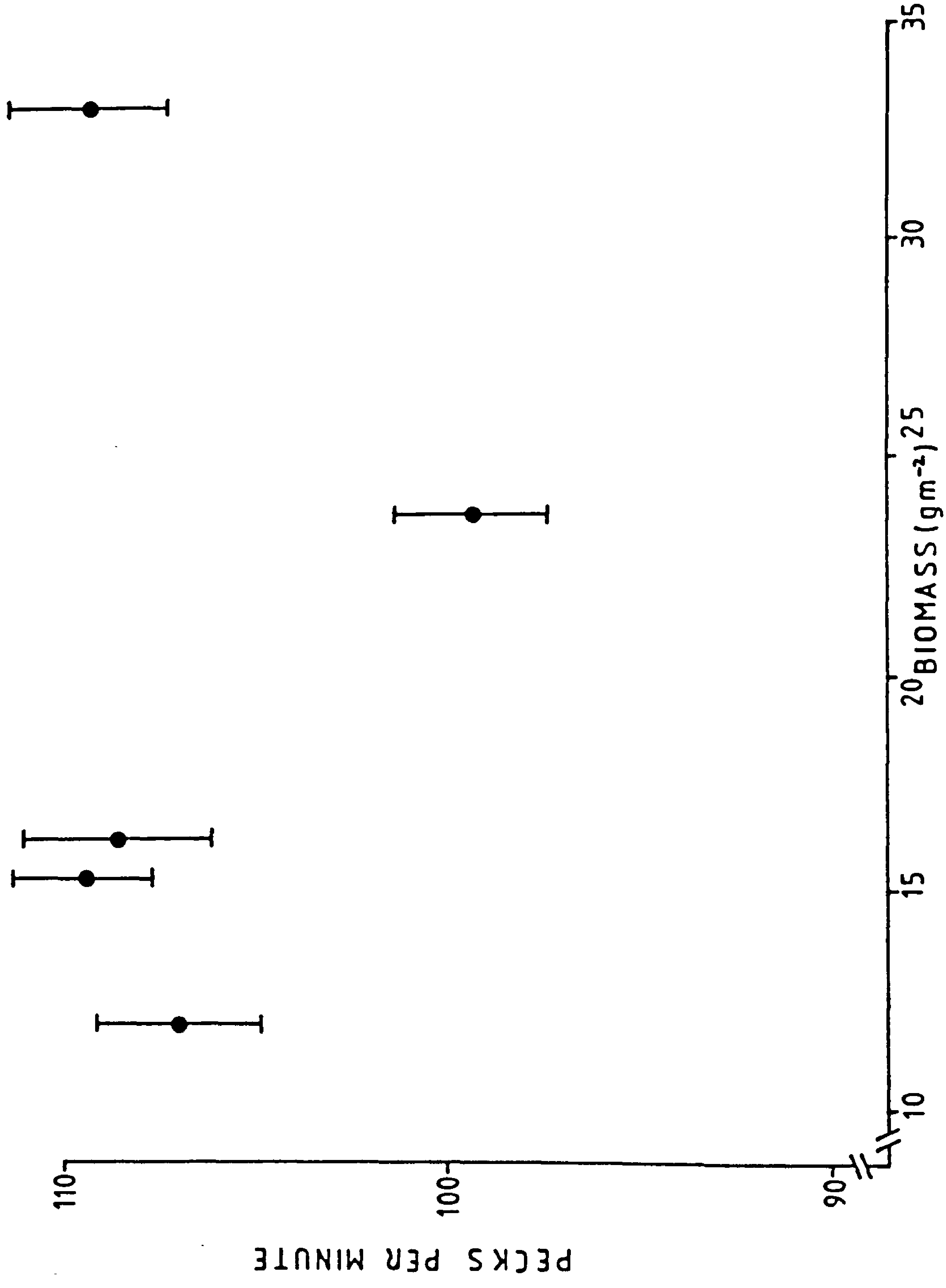

PECKS PER MINUTE
110
100
90
BIOMASS (gm⁻²)
10
15
20
25
30
35

Figure 5.4

Peck and step rate (mean ± 1 s.e.) comparisons between high biomass (fertilized) and low biomass (unfertilized) sites, (site A experiment).

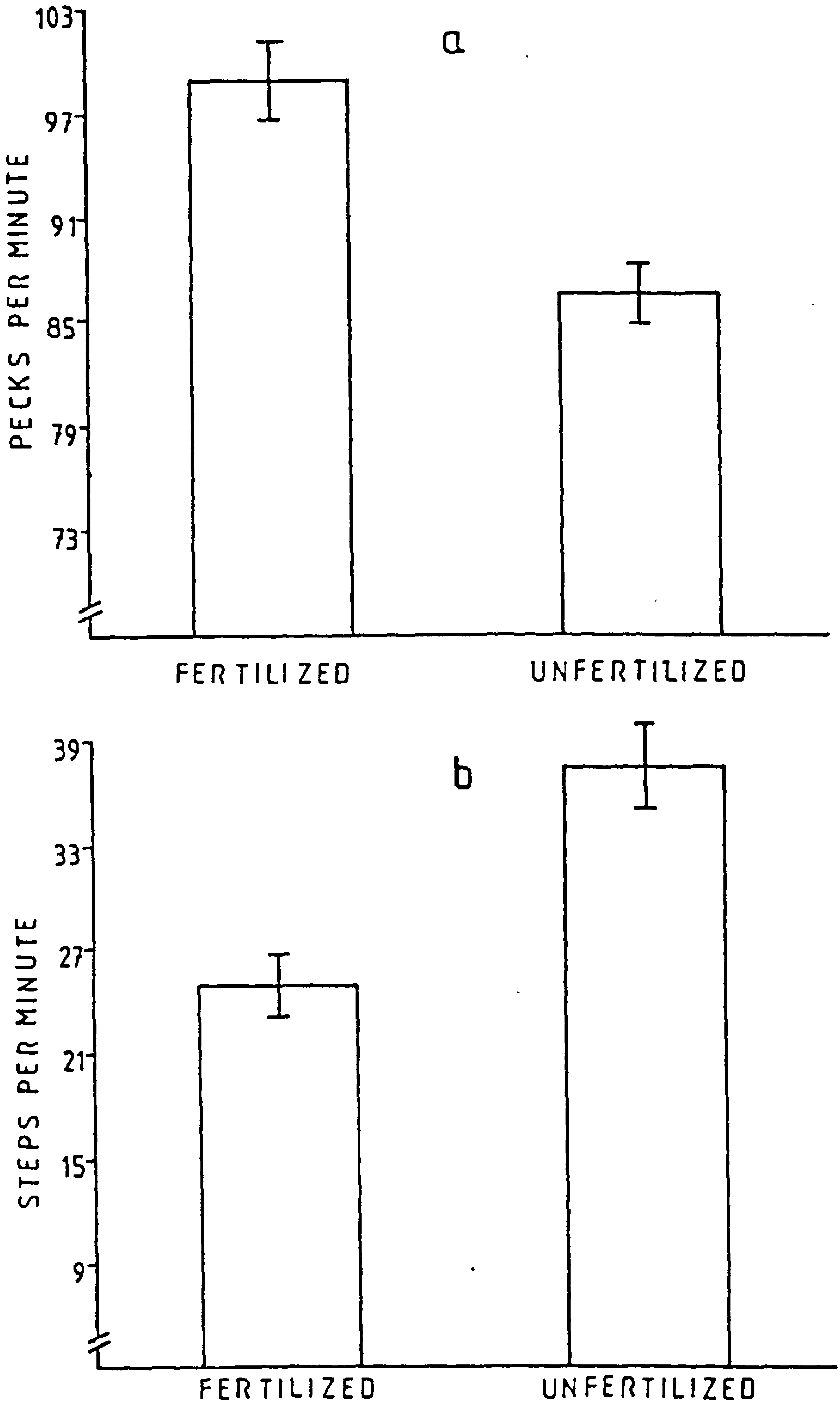
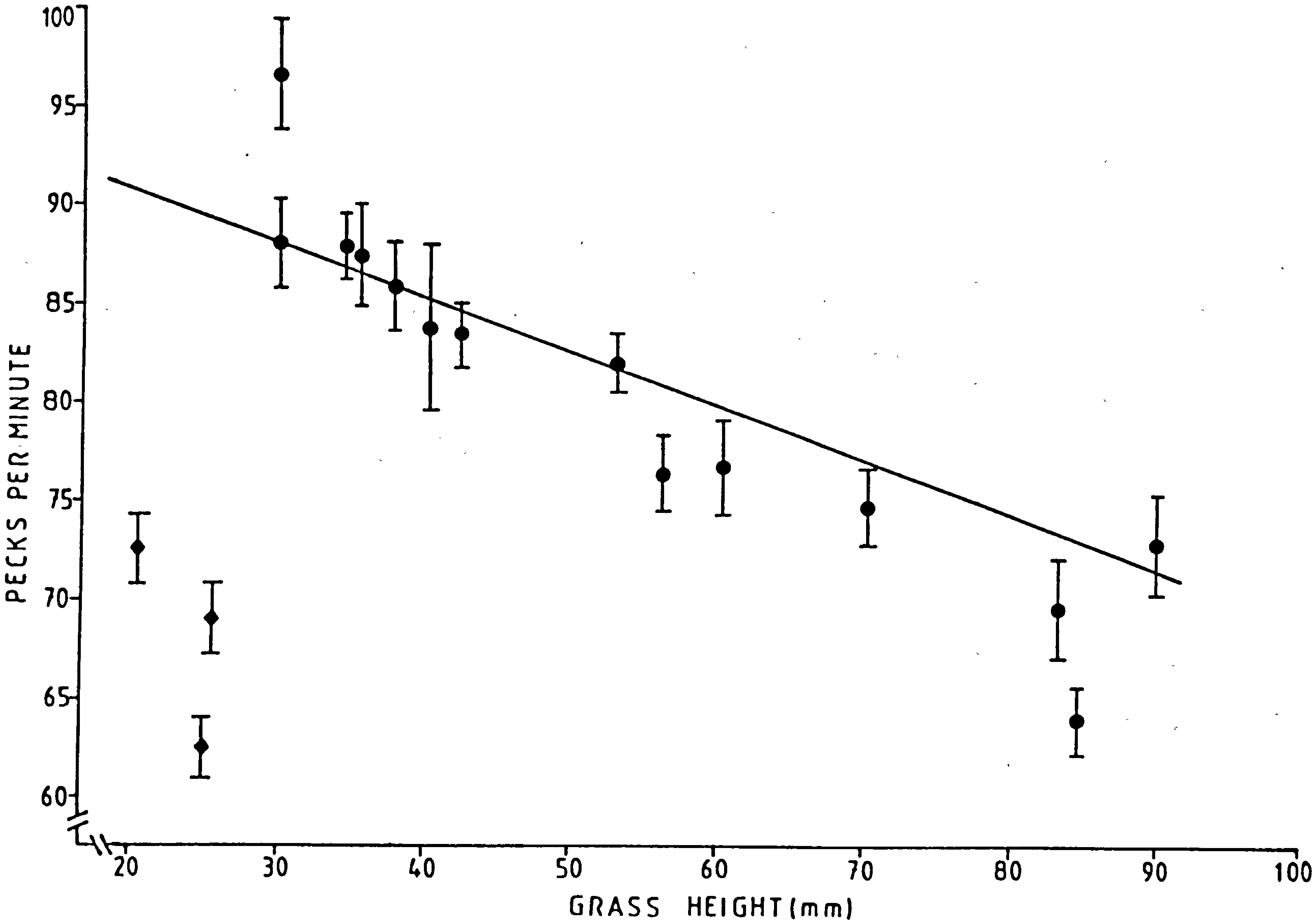

a
PECKS PER MINUTE
103
97
91
85
79
73
FERTILIZED
UNFERTILIZED
b
STEPS PER MINUTE
39
33
27
21
15
9
FERTILIZED
UNFERTILIZED

Figure 5.5

Regression of peck rate (mean ± 1 s.e.) on grass height from the captive bird experiment. The equation of the line (for points above 30mm grass height) is $y=-0.271x + 96.07$.

● points above 30mm grass height

◆ points below 30mm grass height


PECKS PER MINUTE
100
95
90
85
80
75
70
65
60
20
30
40
50
60
70
80
90
100
GRASS HEIGHT (mm)

similar to the result found with wild birds in some of the above studies, in which peck rate decreased when biomass decreased.

To summarise, the main result from this study was that peck rate shows a gradual increase as grass height decreases. Eventually a point is reached at which food availability is seriously depleted. At this point pecking rate decreases since searching time must increase. The peck rate and defaecation rates (averaged for each day) were compared to ascertain if the negative relationship between peck rate and defaecation interval found in the field study (Figure 5.2) was also operating in the captive study. Sixteen pairs of data were collected out of a total of 17 observation days. The resultant relationship was negative but not significant ($r = -0.459$, $0.1 > P > 0.05$).

5.4 DISCUSSION

5.4.1 The function of selection for high biomass feeding sites

From the results presented in Figures 5.1 and 5.4, the most likely explanation of the selection for high biomass sites in some winters and in the fertilizer experiment is that birds feed more efficiently on these sites, gaining energy at a higher rate than would be possible on a lower biomass site. Birds which forage according to this strategy are, in an evolutionary sense, more fit, since short term objectives such as maximising foraging efficiency will certainly affect a bird's survivorship and reproductive success (Krebs 1978). These results therefore lend support to the hypothesis suggested in Chapter 4 that food quantity on a site is normally of more importance to wigeon than food quality since maximising energetic intake from a bulky diet is of primary concern - a bird's main strategy when foraging will be to peck at the highest rate possible with respect to the biomass availability on the site.

However, finding that the peck rate of wigeon increases with food availability is not necessarily evidence that food intake actually increases. This would only be true if the size of each peck remained constant. This assumption is often used in studies of herbivorous birds (Murton et al 1966, Owen 1972b, Crawley 1983). Kenward and Sibly (1978) actually collected data on this subject, from captive woodpigeons (Columba palumbus) feeding on brassicas. They found that the rate of intake of birds (g min^{-1} feeding) was closely correlated with peck rate. They also found, rather counter-intuitively, that peck size (g taken in per pack) was also closely and positively correlated with peck rate. Unfortunately no similar studies have been carried out on wildfowl.

In the absence of data on intake rates, studies on defaecation rates can give a closer indication of this variable. However, they are still using an indirect measure of the amount of food passing through the gut per unit time, since dropping size may vary with defaecation rate. The results reported here on defaecation intervals do, however, support the hypothesis that peck rate provides a good measure of intake rate, since defaecation rates were significantly higher on high biomass (high peck rate) sites (Figure 5.1) and there was a significant negative correlation between peck rate and defaecation interval (Figure 5.2).

It is difficult to explain the results of Figure 5.3. While the biomass differences between sites in the season 1 study were almost certainly greater than those between sites in season 2, the biomass differences in the fertilizer experiment (Table 4.6) were about the same as those between the highest and lowest biomass sites in Figure 5.3, ie. about 20 gm^{-2}. Thus, one would at least have expected a clear difference in peck rate between low biomass and high biomass sites in Figure 5.3. It is possible that the positive correlation between grass height and biomass (Chapter 4) was having a confounding effect on peck rates, since tall grass tends to reduce peck rate (Figure 5.5). However, grass height differences between sites in season 2 were only about 0.5-1 cm, while those in the captive bird experiment were about 8 cm. In the field in season 2 therefore, sward height would have little or no effect on peck rates. This problem is heightened by the fact that no differences in defaecation rate were found between sites in season 2 (Table 4.1). Thus, throughput rates were also similar between sites and there would seem to be little selective advantage in grazing high biomass sites in season 2. The only possible explanation is that the number of factors affecting (and thus causing variation in) peck rate and defaecation rate in the field was greater than in the fertilizer experiment. Thus, larger sample sizes would be required to show up the selective advantage of high biomass feeding sites in the field, when dealing with biomass differences of only $20gm^{-2}$.

There are a number of other bird species for which an increasing food intake with increasing food biomass has been reported. Goss-Custard (1970) in a study of redshank feeding on Corophium on the Ythan estuary found that the biomass of prey taken per minute increased with the prey density in the substrate. He did not, however, find a relationship between peck rate and prey density, primarily because this species feeds in a different way from a herbivore - food is searched out rather than there being an abundant supply all around. What does happen is that the percentage of pecks which are successful (ie. result in the bird obtaining food) and also the biomass of prey per peck both increase with prey density. Barnard (1980) reports that the peck rate of house sparrows increases with barley seed density in both a cattle shed and open field environment. Murton et al (1963) found that in woodpigeons intake rate increased with food density when feeding on cereal grains on autumn and spring sowings. However, in other work on woodpigeons foraging on clover (Murton et al 1966), they found no relationship between peck rate and clover density, except at very low densities of clover (below 100 leaves ft^{-2}) when a significant positive relationship occurred.

Finally, Harwood (1975) in a study of the feeding ecology of blue geese (Anser caerulescens), found that captive goslings, grazing within an experimental enclosure, increased their peck rate and feeding bout length on fertilized grass plots. However he claimed that this change was not due to biomass differences, since he controlled for difference in biomass by mowing the vegetation before the experiments. He considered the differences to be due to the protein content of the grass, ie. birds fed more intensively and pecked faster on higher quality vegetation.

5.4.2 Mechanisms for foraging in a patchy environment

The second question addressed by this study is a causal one: "How do birds concentrate their feeding on high biomass areas?" As discussed above, these areas are likely to be of great selective advantage to wigeon. However, their feeding sites tend to be a mosaic of high and low biomass areas. In this heterogenous environment birds require some simple decision rules by which they can ensure that they remain in high biomass areas, once chanced upon.

Firstly birds need to be able to recognise they are in a good area. As suggested in Chapter 4 this could be done by simply monitoring peck rate when selecting for biomass, or monitoring the tensile strength of the grass if grass quality was most important. If a bird finds itself in an area where its peck rate is high or where the grass breaks easily, it should remain in that area. The second requirement is a simple behavioural mechanism to ensure a bird remains in that area.

One of the most commonly observed mechanisms has been termed 'area-restricted searching' (Townsend and Hughes 1981). This normally includes slower walking when in the good areas and sharp turns back into the good area when the edge is encountered. These responses have been found in, for instance, insect parasitoids, which normally use chemical stimuli to find their host (Waage 1979). They have also been found in grazing geese which almost certainly use visual and tactile clues to locate good feeding areas (Owen 1976a). For example, in Harwood's (1975) study, he found that the captive goslings reduced their walking rates as well as increasing the length of their feeding bouts on the fertilized plots. He also found that birds would turn through 180^{o} at the edge of a patch as did Owen (1975b) in a similar fertilizer experiment with wild white-fronted geese.

Unfortunately, in the fertilizer studies carried out at Caerlaverock, no observations on turning rate at the edge of patches were made. However, it has been clearly shown in Figures 5.1 and 5.4 that slower walking rates are found on high biomass/ quality patches. This would seem to be a clear response by the bird to increase the amount of time spent in the patch.

Slower walking (or hopping) in a good patch was also found by Barnard (1980) in his house-sparrow study and by Murton et al (1963) in their cereal grain study. Again, in their work on clover feeding by pigeons, Murton et al (1966) found a significant negative correlation (at certain times of the day) between clover density and walking rate.

From this discusion on walking rates and the previous one on peck rates, it would seem that a bird could forage optimally (in relation to biomass or protein) over its feeding area simply by adjusting its walking rate to its pecking rate: as pecking rate increases, so a bird should decrease its walking rate. This idea receives some support from another study in Murton et al's (1966) paper. In this case they looked at the pecking and stepping rates of birds feeding on a single clover pasture through the day. They found a highly significant negative correlation between the two. They explained this by suggesting that at certain times of the day (late afternoon) birds were being less selective in their feeding in order to fill their crops, and therefore increase their peck rate at the expense of areas searched (step rate). While this is obviously a different situation from the wigeon discusion (eg. biomass did not vary on the clover pasture) it shows that a herbivorous bird can adjust its pecking and walking rates quite intimately in relation to one another, in order to forage in the most efficient manner.

5.4.3 The effect of grass height on wigeon foraging behaviour

The final question which can be answered by these results is "How do wigeon respond to differences in the height of the grass sward on which they are grazing?" In the initial planning of the captive bird experiment, the question was more precise: "What is the optimum grass height for wigeon grazing, ie. the height at which their grazing efficiency is maximised?" However, due to the nature of the results, no clear answer can be given to this, and the former question will have to suffice.

The rationale behind the original question was as follows. In the same way that there is an optimum biomass or protein level for wigeon feeding areas, which maximises the nutrient intake of birds feeding on them, there should also be an optimum grass height (Owen 1971). With regard to protein the optimum level is simply the highest level. With regard to grass height, however, the optimum is not obvious. Owen (1973b) considered that wigeon were primarily adapted to grazing on short swards due to their short, broad bills. Their small body size would also allow greater vigilance in short grass. The idea of the experiment reported here was to answer these questions by observing food intake rates on different heights of grass.

From the feeding efficiency point of view a reduction in grass height will have two conflicting results. Firstly, due to the bird's bill morphology etc. feeding should be more efficient - a bird should be able to manipulate short blades of grass more easily and efficiently than long ones. Opposing this will be the problem that as grass length decreases, so blade size and thus weight of food per peck will decrease. The exact effect of a reduction in sward height on throughput of food through the gut is therefore not obvious.

In the study of intake on high and low biomass sites, peck rate was used as an indication of throughput rate, initially using the assumption that bite size did not change as peck rate increased, but later based on the more concrete evidence of the peck rate/ defaecation interval relationship. In this study, however, the assumption that bite size is independent of peck rate is not necessarily valid, since sward height and thus blade length are decreasing concurrently. Peck rate cannot therefore be used as an indicator of intake rate. The obvious solution is to again look at how defaecation interval changes with peck rate (and grass height). Unfortunately, the data on defaecation interval in this study are not conclusive, possibly due to the fact that sample sizes were small (normally about 10) for each sward height. This was mainly due to the difficulty of obtaining uninterrupted views of the birds when they were grazing in a fairly small pen.

On the one hand then, there is a tentative negative relationship betwen peck rate and defaecation interval (not far short of significance) which might suggest that the situation found in the field study (peck rate increase leading to defaecation interval decrease) is simply being masked by small sample size. On the other, the relationship remains not significant and a good explanation why it should not be significant does exist - short grass length results in higher peck rates but concurrent smaller bite sizes, ie. little change in gross intake rate. In the absence of further data on defaecation rates, no answer can be given to the question of an optimal grass height for wigeon. The only statement which can be made is that peck rate shows a steady and highly significant increase as grass height decreases.

Although no conclusive results on food intake in relation to grass height have been found, the fact remains that in some scientific studies (eg. Owen 1973b, Cadwalladr and Morley 1974) and also in many anecdotal reports (eg. Glegg 1943, Day 1983) wigeon are reported to prefer to graze on short grass swards. While feeding efficiency may play a part in this preference, other factors could be involved. Shorter grass may be younger or have less structural material and therefore be higher in protein content (Chapter 6 and Owen 1973b) or it may allow more efficient predator vigilance (Chapter 7).

In a very similar experiment to the one reported here, Drent and Swierstra (1977) kept a single barnacle goose in an enclosure and observed its peck rate plus foraging intensity (ie. minutes foraging per hour) throughout the day. They also collected all the droppings the bird produced throughout the day and night. This, of course, circumvented all the problems of measuring defaecation rate accurately, and even the difficulty of changing dropping size with increasing defaecation rate, since the total amount of food eaten by the goose could be calculated each day from digestive efficiency work (Chapter 3). Bite size could also be calculated from peck rate. In a very similar regression to the one shown here, they found that peck rate gradually increased as grass height decreased. Of more interest, they also found that bite size decreased with grass height, slowly at first but very rapidly below 2.5cm height. Thus, the hypothesis that as grass height decreases, peck rate increases and bite size reduces is borne out well in this study. Does this mean that grass height has no effect on intake rate since peck rate and bite size balance out (ie. there is no optimal grass height)? While this may be the case with wigeon it was not in the goose study. As sward height declined foraging intensity increased, ie. the increase in peck rate was not compensating for decreasing bite size and so the bird had to forage for longer each day to obtain sufficient food. Based on foraging intensity then, the optimal height for a goose was the tallest grass. This experiment only considered grass up to 4cm in height, however, so longer grass may result in less efficient foraging (the wigeon experiment went up to 10cm grass). How applicable this study is to wigeon is difficult to assess since the goose is a much taller bird and has a larger bill and should therefore be able to manipulate longer grass blades more efficiently. Thus, from two points of view (feeding efficiency and vigilance) a goose may prefer longer grass than a wigeon.

CHAPTER 6

THE EFFECTS OF WIGEON GRAZING ON GRASSLAND

6.1 INTRODUCTION

This chapter is concerned with the effect of wigeon grazing on the grassland on which they feed. In particular, it deals with the effect of grazing on grass biomass, height, production and quality through the winter season. Studies carried out to elucidate the mechanism by which wigeon grazing affects grass quality are also reported here.

In-depth studies of the interactions between herbivores and their food supply are a relatively recent area of research in field ecology. Certainly studies on the effect of grazing (or, very often, clipping) on grasslands, particularly from an agricultural or range management point of view, have been carried out for years (eg. Aldous 1930, Jameson 1963). However, only comparatively recently has the complex of relationships operating between plant and herbivore in natural ecosystems been investigated. The scope of this research has been very wide indeed, ranging from the relationships between herbivory and plant defence mechanisms (for a review see Janzen 1981) to the effect of grazing in actively stimulating grass growth through growth promoting substances in the herbivore's saliva, eg. thiamine (Reardon et al 1972). Indeed this type of discovery has led certain workers to suggest that the evolutionary relationship between grass and grazer is often one of mutualism rather than attack and defence (Owen & Wiegert 1981). One of the most notable studies on the relationships between grass and grazer was carred out in the Serengeti, East Africa, in which the complex interactions between the savannah vegetation and four species of grazer were elucidated during a period of over 10 years (Bell 1970, MacNaughton 1979b).

There are two main characteristics which distinguish herbivore/ plant relationships from carnivore/ prey ones (Prins et al 1980). Firstly, in the former case the food species normally survives. This means that the phenomenon of food regeneration must be taken into account. Indeed, grasses represent the pinnacle of grazing tolerance (Crawley 1983). With their meristems close to the ground, they are excellently adapted to recover from defoliation and produce new growth, either from the same tiller or through the development of new ones. Secondly, food quality tends to be far more important in herbivore/ plant interactions. Vegetable material varies greatly in nutrient content and this is often of more concern to the herbivore than is total energetic intake (Bell 1971). For these reasons, studies of the interactions between plant and herbivore and in particular the effect of the herbivore on its food supply, must include not only aspects such as the effect on total biomass availability, but also the effect on plant production and quality.

Much of the research on the effect of grazing on grass production has been stimulated by its implications for agricultural output. These studies fall into two main categories: those dealing with livestock grazing on which there is a large literature (eg. Arnold 1964, Vickery 1972); and those dealing with agricultural pests, especially geese (eg. Kear 1964b, 1970, Kuyken 1969, Patton and Frame 1981). Studies in this latter category are obviously of most relevance to the present research. However, there is no clear concensus on this subject. Some work on winter goose grazing has found no significant effects on resultant grass yields (Kear 1964b, Kuyken 1969) while others have found very significant effects (eg. Patton and Frame 1981). However, generally it seems to be the case that winter grazing has very little effect on subsequent spring and summer yields, while spring grazing (into April and May, when the grass is well into the growing season) can significantly affect later yields, either of forage or silage. Most of these studies, however, refer to the effect of winter/ spring grazing on summer/ autumn yields and are therefore not easily comparable with the present work, which deals with the effect of winter and spring grazing on spring yields.

Theoretical (as opposed to applied) studies on this subject in natural or semi-natural ecosystems are less common but more relevant to this project. Moreover, many include not only grazing effects on plant production, but effects on biomass, quality and height as well. While some studies simply catalogue the different effects of grazing on the vegetation, two studies on goose grazing (Prins et al 1980, Ydenberg & Prins 1981) are particularly interesting in that the authors hypothesise on how the effects of grazing on the plants can affect the feeding pattern and flock behaviour of the grazer. For example, in one study it was found that certain facets of the birds' behaviour, such as individual goose bite size and the flock's "inter-harvest interval" of around four days, seem to have the effect of maximising the production of Plantago (their main food plant) during the spring. Not only does the grazer affect the plant, but the plant's response affects the grazer. The idea of these complex two-way interactions between grass and grazer now forms an essential part of our understanding of the dynamics of the herbivore/ plant interface.

6.2 METHODS

6.2.1 General

Research into the effects of grazing on the grassland was based on the use of exclosure plots. This is a method commonly employed by workers in this field, with exclosures ranging from large areas fenced off from wildebeest (McNaughton 1976) to small plots of a few m^2 surrounded by chicken wire (Patton and Frame 1981, Ydenberg and Prins 1981).

The main problem with this method is that unless great care is taken over the construction of exclosure fencing or cages, the exclosure plots themselves can affect the micro-climate within the plot and thus confound the experimental results. To reduce this risk the exclosures used in this study were based on the design of Patton and Frame (1981) who carried out 'cage-effect' experiments to check on the effect of their exclosures on dry-matter production and cage micro-climate. They found that their exclosure cages had no significant effect on the above variables.

Wigeon exclosures were made by sinking four angle-iron stakes into the ground to form the corners of a rectangular plot. The walls of the plot were made from thin 2" gauge chicken wire, to a height of 0.5m. Strands of thin wire were tensioned across the top of the plot to discourage birds from flying into the exclosure. These plots were found to effectively exclude wigeon and other small herbivores, eg. rabbits and hares.

In season 2 the size of the plots was 1.5m x 1m and two plots were positioned centrally in the five main wigeon feeding areas (A, B, D, H & I) approximately 5m from the water edge. In season 3 a single larger plot (2.5m x 1m) was used, one plot being placed in each of the above five sites.

6.2.2 Season 2 measurements

Of the two exclosure plots set up on each site in season 2, one was used as a sample plot, while the other was unsampled, ie. this plot was left undisturbed throughout the winter. The 'ungrazed' biomass and grass height measurements were taken from the unsampled plot once a month. Biomass was measured with the spectrophotometer (the perceived plot radius would just fit into the exclosure plot when the sensor head was centrally positioned), while grass height was assessed in the same way as in the field (see p.9), the ruler being placed in the centre of the exclosure.

Net aerial primary production (NAPP) was estimated by measuring herbage accumulation in late winter/ spring (Ydenberg & Prins 1981). The "ungrazed" figure was defined as the increase in standing crop in the unsampled exclosure (as measured by the spectrophotometer) between the February and March biomass readings. "Grazed" NAPP was defined as the increase in standing crop (as above) plus the average amount of grass eaten by the wigeon during this period. This was estimated from droppings counts (Cargill 1981). The mean total number of droppings/ m^2 deposited during this time was calculated for the <u>inner</u> droppings quadrats (ie. <10m from water) on each of the <u>five</u> sites. The mean of several quadrats was used in preference to a single quadrat (as in the biomass and grass height grazed quadrats - see pp.66 & 67) because droppings counts were very variable betweeen quadrats. Since the average digestive efficiency (dry matter) of wigeon is 28.8% (see Chapter 8.2) and the average weight of a dropping is 0.193g (see Chapter 3) each dropping represents 0.27g of grass (dry weight). The average weight of grass removed /m^2 from the inner areas can then be calculated from this figure. Net aerial production on grazed areas is the sum of the average standing crop increase for each site plus the grass removed by wigeon grazing.

Grass quality samples (defined as % crude protein content of the green material) were collected by hand grazing once a month. Ungrazed grass was collected from an approximately 15cm x 15cm plot chosen at random within the sample exclosure. Each plot was marked after collection to prevent resampling of the same area.

Grazed grass was collected from a similar sized area, again chosen at random, outside but close by the exclosure. In both seasons (2 & 3) wigeon grazed grass was collected next to the pond, in order to minimise the effects of goose grazing, since geese tend to avoid the edge of fields (Owen 1972a, 1973a). Although barnacle geese were observed to occasionally graze near to ponds, their grazing effects were considered to be minimal compared to wigeon grazing.

6.2.3 Season 3 measurements

In the final winter, data was collected on the effect of grazing on grass quality alone. The 2.5m x 1m exclosure was divided into three sections. The first section (1m x 1m) was used as an "ungrazed" exclosure. No experimental manipulation took place on this section. The second (1m x 1m) section was used as an "ungrazed and droppings" exclosure. In an attempt to imitate the effect of nutrient leaching from wigeon droppings, 20 fresh droppings were scattered on this section once a month. This number of droppings represented a medium to high intensity of site use by wigeon (based on results from season 2). No artificial grazing took place on this section. The final exclosure section (0.5 x 1m) was termed the "artificially grazed" section. Each month this section was hand grazed in an attempt to imitate wigeon grazing. The grazing was fairly intense (ie. no long blades were left on the section after grazing) so that the effect on the plot was more severe than wigeon grazing outside the exclosure (during the early part of the season especially). This was felt justified as the method was an experimental imitation and allowed rough standardisation of the technique.

Once a month, an approximately 15cm x 15cm grass sample was taken (at random) from the "ungrazed", "ungrazed and droppings", and the "wigeon grazed" (outside and close to the exclosure) sections. Again sampled plots were marked to prevent resampling. The plucked grass from the "artificially grazed" section was also collected. All four samples were sorted and the green portion analysed for crude protein content.

6.3 RESULTS

The initial results presented in this chapter deal with the effect of grazing on grass biomass, height, aerial primary production and quality (measured by crude protein content). Thereafter, the effect of different intensities of grazing on food quality is looked at briefly. Finally, results on the mechanism by which wigeon grazing affects grass quality are reported.

6.3.1 The effect of grazing on grass

a) The effect on grass biomass.

During season 2 a comparison was made of the grass biomass in grazed and ungrazed areas. The ungrazed area used was the unsampled exclosure on each of the five sites in which exclosures had been placed. The grazed area was taken as the closest 'droppings' quadrat to this exclosure. Thus, the comparisons are based on 5 grazed/ungrazed samples for each month. Unfortunately, the spectrophotometer was not ready for use until January in season 2. Therefore the results only deal with the final 3 months of the season. Nevertheless it is fairly safe to assume that the biomass on these neighbouring plots was roughly the same at the beginning of the season, when the exclosure plots were erected. Thus, even though the data covers only half of the season, this is the most interesting period, when any grazing effects would be manifested. Figure 6.1 shows that by January the biomass on the grazed plots had been significantly reduced by wigeon grazing, and that these differences had become very significant by February/ March. Wigeon exerted a very great effect on the aerial biomass of plant material on their feeding sites, reducing food availability to around 25% of that on ungrazed sites in late February. This difference was still maintained after early spring growth during March.

b) The effect on grass height.

Using the same quadrats and exclosures as in the biomass comparison, grass height was compared on grazed and ungrazed sites. This data was collected throughout the whole of season 2 (except for the period of severe frost in December) and is shown in Figure 6.2. The results are very similar to the biomass results showing that by February/ March the wigeon had significantly reduced the height of the grass sward, in some cases to 33% of its ungrazed value.

c) The effect of grazing on grass production.

Even though the major part of this study was carried out during winter when grass growth was minimal, the effect of winter grazing on early spring production was measured. Net aerial primary production (NAPP) was estimated by measuring herbage accumulation on ungrazed sites, and herbage accumulation plus grass eaten by wigeon on grazed sites (see Methods). Table 6.1 shows the results of this analysis, the average production on ungrazed sites being 9.06gm^{-2} and on grazed 13.9gm^{-2}. The difference was significant (t=3.78 (paired t-test); d.f.=4; P<0.02). Thus the effect of grazing over the winter was to increase early spring production by an average of 53.4% over ungrazed levels.

Figure 6.1

Effect of grazing on biomass levels (mean ± 1 s.e.), season 2.

——— grazed

- - - - - ungrazed

T-test results

Jan: t=3.26, d.f.=8, $P<0.025$
Feb: t=5.40, d.f.=8, $P<0.001$
Mar: t=5.77, d.f.=8, $P<0.001$

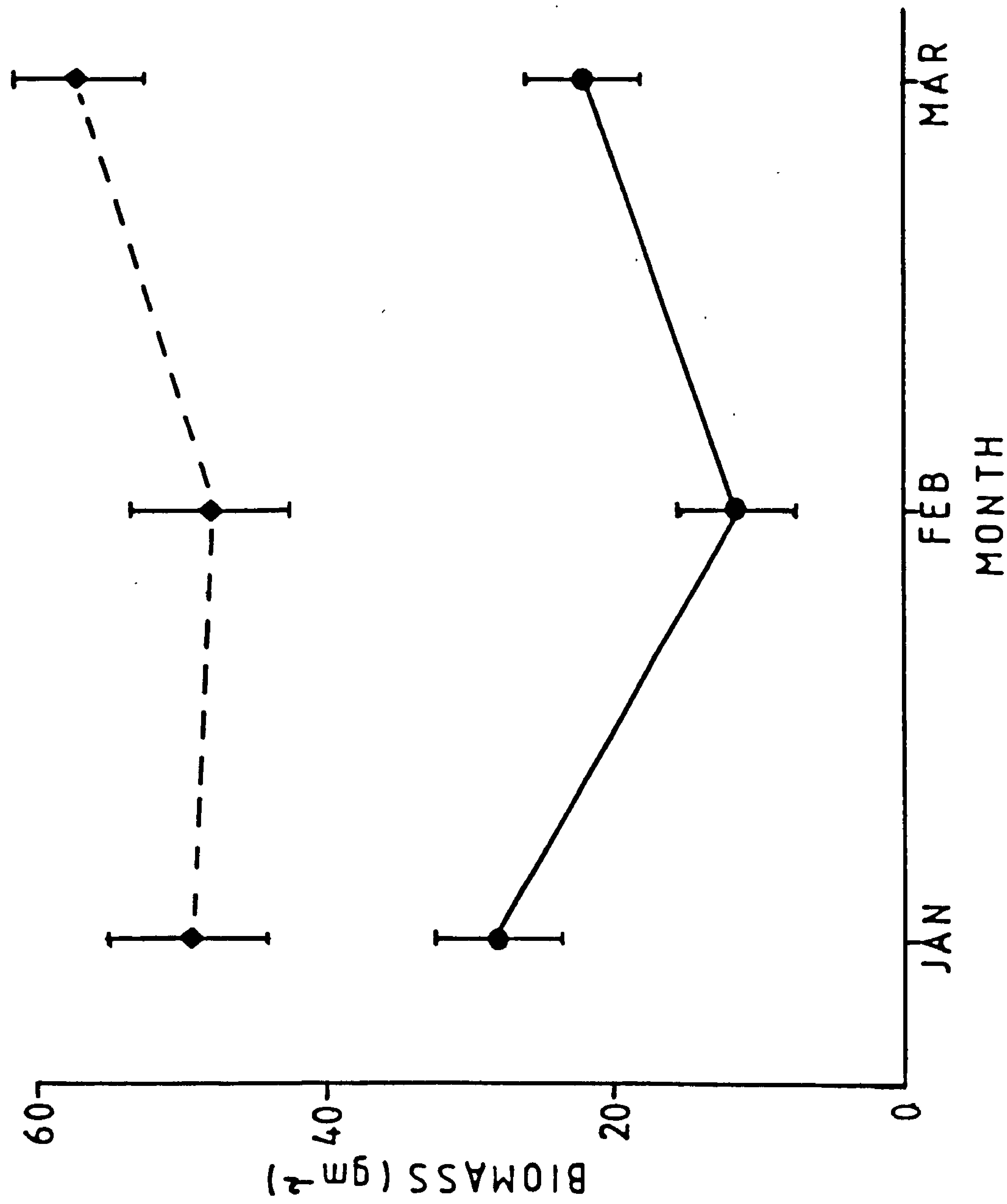

BIOMASS (gm⁻²)
60
40
20
0
JAN
FEB
MAR
MONTH

Figure 6.2

Effect of grazing on grass height (mean ± 1 s.e.), season 2.

———	grazed
– – – – –	ungrazed

T-test results

Nov: t=0.526, d.f.=8, n.s.
Jan: t=1.46, d.f.=8, n.s.
Feb: t=3.33, d.f.=8, 0.025
Mar: t=4.74, d.f.=8, 0.005

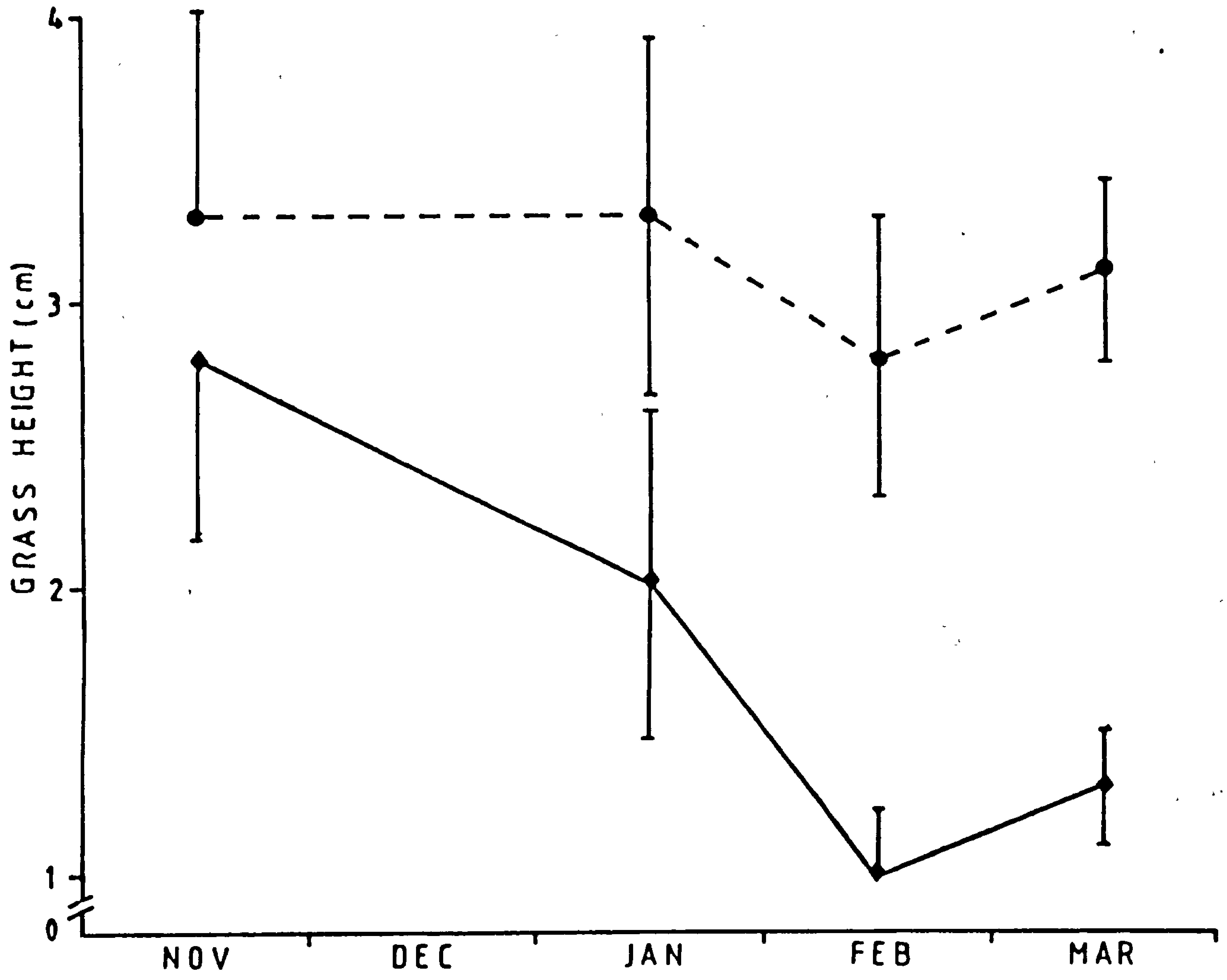

GRASS HEIGHT (cm)
4
3
2
1
0
NOV
DEC
JAN
FEB
MAR

TABLE 6.1

Effect of grazing on net aerial primary production (season 2).

(all figures gm^{-2})

A) Ungrazed

SITE	BIOMASS (FEB)	BIOMASS (MARCH)	TOTAL PRODN.	AVER. PRODN.
A	33.8	47.1	13.3	9.06
B	39.2	57.8	18.6	
D	60.4	68.4	8.0	
H	47.1	47.1	0	
I	60.4	65.8	5.4	

B) Grazed

SITE	BIOMASS (FEB)	BIOMASS (MARCH)	AVER. WT. DROPPS./m^{-2}	GRASS EQUIV.	TOTAL PRODN.	AVER. PRODN.
A	4.2	23.9	5.1	1.4	21.1	13.9
B	4.6	20.5	2.7	0.7	18.9	
D	18.8	28.5	11.2	3.0	12.7	
H	13.4	16.1	7.1	1.9	4.6	
I	21.6	31.2	7.4	2.0	11.6	

d) The effect of grazing on grass quality.

- Effect of grazing per se.

Data from the five areas with grazed and ungrazed plots were used in the second season. In season 3, however, one of the four areas with an exclosure was virtually ungrazed by wigeon. Thus, exclosure samples, ie. 'ungrazed plus droppings', 'artificially grazed' and 'ungrazed' were used as usual, but no data from the grazed samples were included in the analyses, ie. sample size was 4.

In season 2 (Figure 6.3), the protein content of both grazed and ungrazed grass tended to increase at the same rate from November to February. No significant differences were found between grazed and ungrazed samples during this period, although the quality of grazed grass did tend to be higher in later months. Between February and March the quality of both decreased rapidly, but that of ungrazed more rapidly than grazed. This resulted in a significant difference between the quality of grazed and ungrazed grass in early spring ($t=2.877$; d.f.=8; $P < 0.05$).

The pattern in season 3 was rather different (Figure 6.4). The ungrazed grass quality fluctuated around the 20% crude protein level. However, the quality of grazed grass gradually increased through the season from an initial low point of about 17%, so that by February/ March it was much higher than the ungrazed level. The differences were significant in both February and March (Feb: $t=2.517$; d.f.=7; $P < 0.05$ and March: $t=4.741$; d.f.=7; $P < 0.01$).

In season 2 the difference between grazed and ungrazed protein content in March was about 4%, while in season 3 it was about 6%. This represents an increase of almost 25% on ungrazed levels in season 2 and over 30% on ungrazed levels in season 3. Thus, the effect of wigeon grazing through the winter is to substantially increase the quality of their food supply during the late winter/ early spring period. In March this increase can amount to almost one third of ungrazed levels.

- Effect of grazing intensity.

Apart from simply dividing the grassland into the absolute categories of grazed an ungrazed areas, it is also possible to look at the effect of different grazing intensities on grass quality. For this particular analysis, the data from seasons 2 and 3 were combined. The grazing intensity on a particular site was calculated from the average total number of droppings /m^2 deposited on that site through the season (the average being the mean for all quadrats on that site). The effect on grass quality was calculated by subtracting the ungrazed protein content from the grazed grass protein content for each site for March only. This produced 9 points in all. These are plotted on Figure 6.5. While the data shows a large amount of scatter, an interesting trend does seem to be present, in that the quality stimulation tends to increase to a peak and thereafter decrease. An approximate curve is fitted by eye. While there is clearly too little data to arrive at any definite conclusions, the possibility of overgrazing, leading to a decrease in protein enhancement, is certainly hinted at. This result is most interesting in the light of MacNaughton's (1979b) results on the stimulation of grass productivity by wildebeest grazing in the Serengeti which produced a similar type of curve, and will be discussed later.

Figure 6.3

Effect of grazing on grass quality (mean ± 1 s.e.) season 2.

──────── grazed

- - - - - - ungrazed

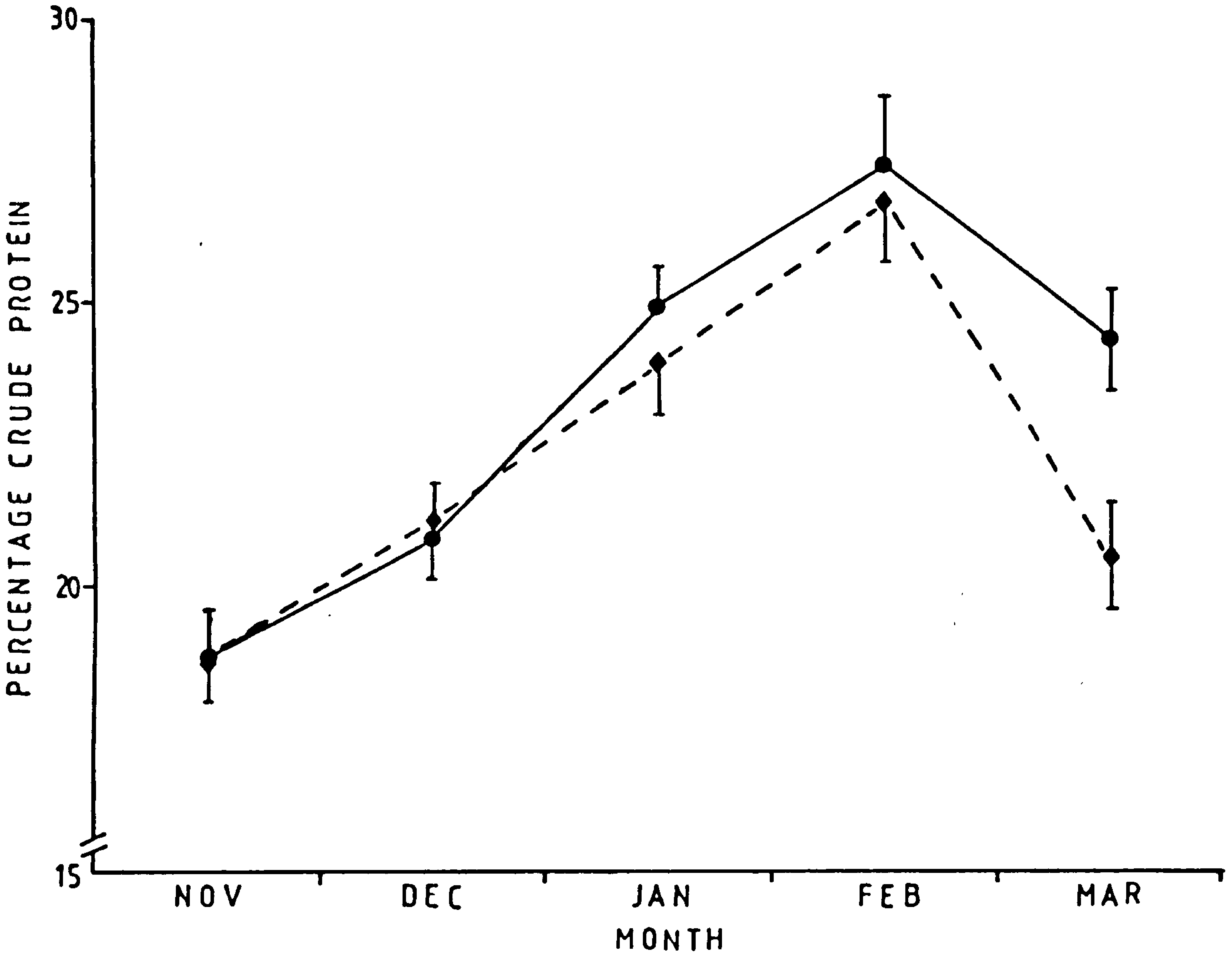

30
25
20
15
PERCENTAGE CRUDE PROTEIN
NOV
DEC
JAN
FEB
MAR
MONTH

Figure 6.4

Effect of grazing on grass quality (mean ± 1 s.e.) season 3.

——— grazed

– – – – – ungrazed

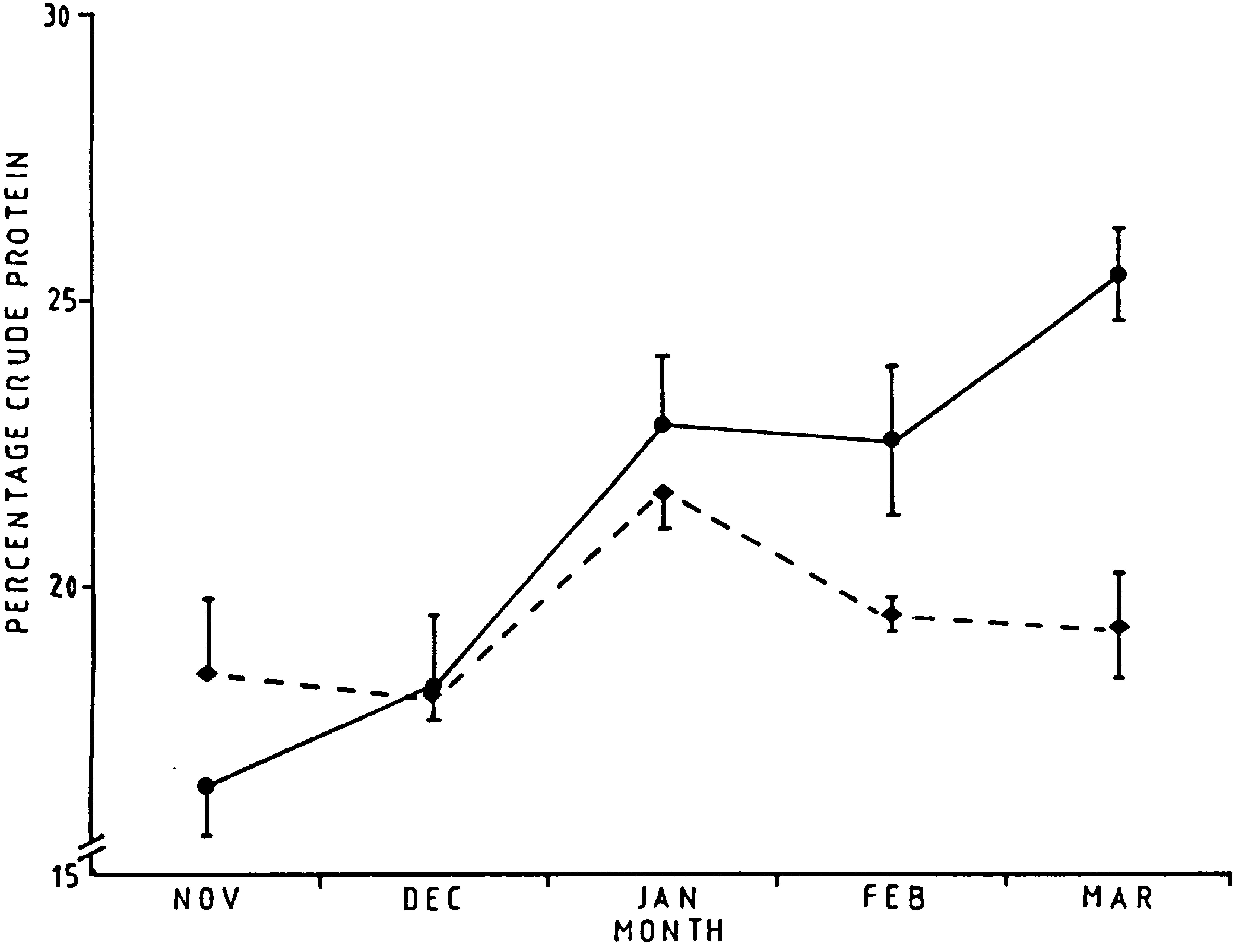
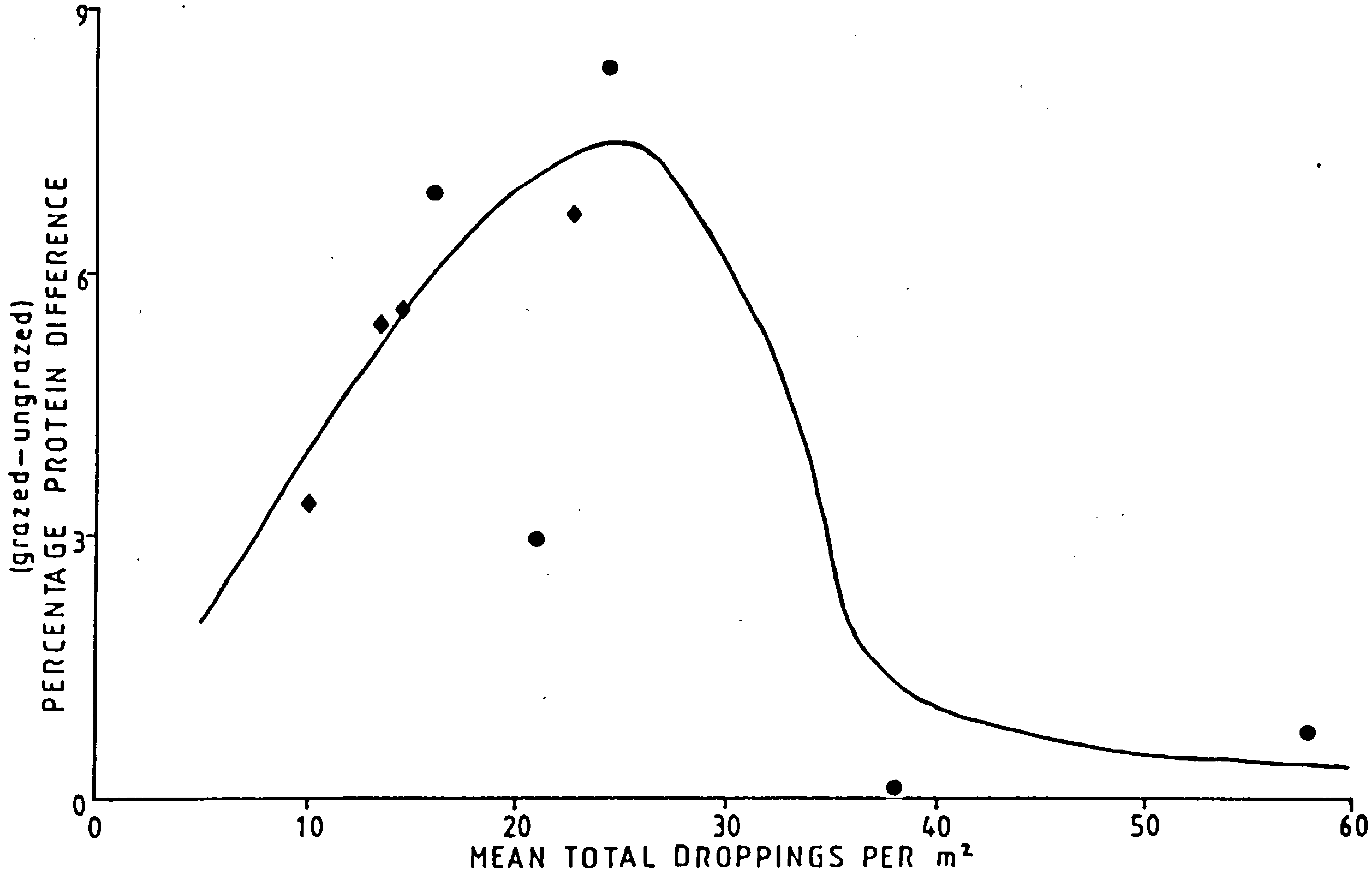

PERCENTAGE CRUDE PROTEIN
30
25
20
15
NOV
DEC
JAN
FEB
MAR
MONTH

Figure 6.5

Effect of intensity of grazing on grass quality. Grass quality figure is the difference in the % protein content for grazed and ungrazed grass for March alone. Curve fitted by eye.

● season 2

◆ season 3


9
6
3
0
PERCENTAGE PROTEIN DIFFERENCE
(grazed−ungrazed)
0
10
20
30
40
50
60
MEAN TOTAL DROPPINGS PER m²

6.3.2 The mechanism producing protein enhancement

An increase in the protein content of grazed vegetation is a well-known and well-documented phenomenon in studies on wild herbivores and in agricultural research (Ydenberg and Prins 1981, Coppock et al 1983a, Crawley 1983). There are two main mechanisms which have been cited as causing increased nutrient content in grazed vegetation: a) the effect of defoliation: grazed vegetation has a high proportion of young leaves which tend to be high in protein content and low in structural components eg. cellulose and lignin b) the effect on nutrient supply: the increased availability of soil nutrients from herbivore droppings leads to higher quality vegetation. (These hypotheses will be discussed in more detail later).

The results of the season 3 exclosure experiment were used to distinguish between these two hypotheses. The protein levels in grass grazed by wigeon and in ungrazed grass were compared with protein levels in artificially grazed grass and in ungrazed grass which had been exposed to nutrient leaching from wigeon droppings.

While the three exclosure samples (ungrazed, ungrazed and droppings, artifically grazed) were collected from all five sites each month, the wigeon grazed sample was only collected from four sites, since the birds did not graze one of the sites. The results of this analysis are presented in Figure 6.6. This diagram shows the protein content of the three experimental samples (ungrazed and droppings; artifically grazed; wigeon grazed) in comparison with the control samples (ungrazed grass). As has been shown in a previous result (Figure 6.4) the wigeon grazed grass gradually increased in protein content through the season until it was significantly different from the ungrazed grass (which fluctuated around the 20% protein level) in February and March. The artificially grazed grass follows this same trend, but more extremely, in that the protein content of these samples became significantly greater than the ungrazed samples by January and remained significantly higher for the rest of the season. The protein content of the 'ungrazed plus droppings' grass remained at or below the level of the ungrazed grass (no significant differences). Since no differences were found in these samples by February/ March (the time in the season when any differences should have appeared) it was felt pointless to spend the large amount of time required to sort and analyse the 'ungrazed and droppings' samples earlier in the season - thus no data are available for this group from November to January.

In summary it was found that grass which was artificially grazed tended to follow the trend in protein content of wigeon grazed grass, while ungrazed grass plus droppings (ie. increased nutrient supply) did not. This result would suggest that the mechanism by which wigeon grazing increases grass quality is via the mechanical removal of old leaf material (ie. defoliation) rather than by an increased level of nutrient cycling via the birds' droppings.

Figure 6.6

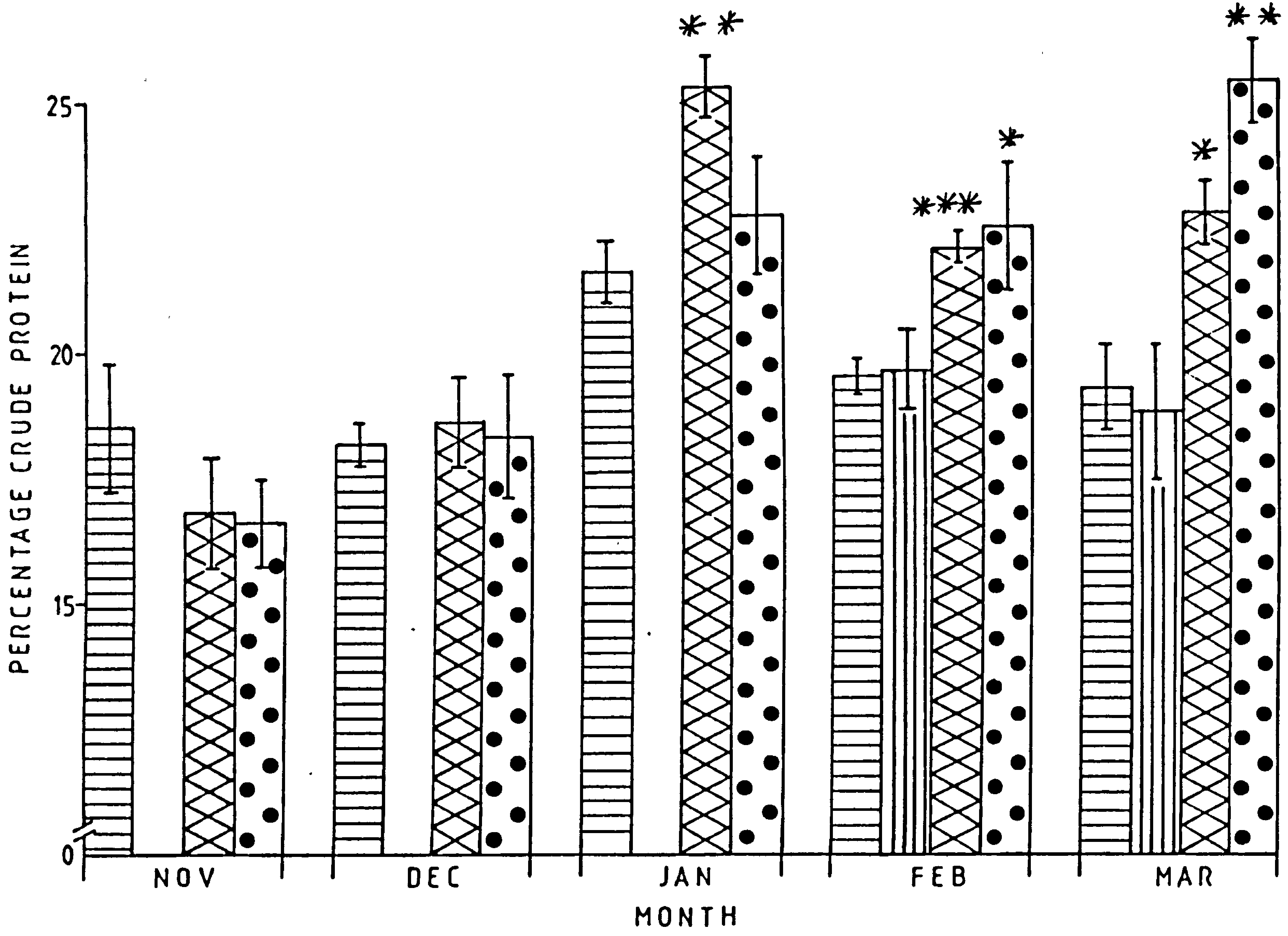
Effect of wigeon grazing, artificial grazing, and nutrient leaching from droppings on grass quality (mean ± 1 s.e.), season 3.

▤	ungrazed grass
▥	ungrazed and droppings grass
☒	artificially grazed grass
●	wigeon grazed grass

CONFIDENCE LEVELS

$p < 0.05$	*
$p < 0.01$	**
$p < 0.001$	***

ALL COMPARED WITH UNGRAZED GRASS


PERCENTAGE CRUDE PROTEIN
25
20
15
0
NOV
DEC
JAN
FEB
MAR
MONTH
**
***
*
*
**

6.4 DISCUSSION

6.4.1 The importance of grazing effects to wigeon

It is obvious that the effect an animal has on its food supply is of critical importance to its well-being. As stated in the introduction, the importance of this situation to herbivorous species is compounded by the fact that the animal's feeding can affect not only the abundance of its food supply, but also its production and quality.

There is much literature on the many and varied effects herbivorous species have on their food. Coppock et al (1983a) in a study of the effects of prairie dog grazing on a North American mixed grass prairie found that biomass was reduced to 50% of its ungrazed value; % crude protein increased from around 10.6% to 12.8%; and the dominant species of the prairie changed from graminoids in ungrazed areas to forbs and shrubs in grazed ones.

Cargill (1981) found that grazing of saltmarsh grasses and forbs in the Canadian arctic by snow geese resulted in a 30-50% increase in aerial production compared to ungrazed levels, and an increase in the crude protein content of grazed vegetation of between 6.0 and 12.5%. Harwood (1977) in the same type of situation found a 2.5% protein increase in grazed vegetation. Moss et al (1981), investigating the effects of grazing (by deer and hares) on heather, found that production decreased and crude fibre content increased in grazed areas, but the effect on nitrogen and phosphorus concentrations was variable according to soil type.

MacNaughton (1976) reported on the effects of wildebeest (Connochaetes taurinus) grazing on the vegetation of the Serengeti plains. Green biomass was reduced to 15% of its initial standing crop value, and grass height to 44% of this. However, aerial production was much higher in grazed grass. In later studies, MacNaughton (1979a,b) investigated the effect of different levels of grazing on the above ground productivity of the Serengeti grasses. He found that a graph of grazing intensity against primary production produced a bell-shaped curve, ie. light grazing stimulated production to an optimal point, but thereafter heavier grazing reduced production. He also found that the level of wildebeest grazing in the wild tended to be heavier than the optimum point for production stimulation. He suggested that this apparent over-cropping by the wildebeest could in fact maximise total nutrient yield, since more heavily grazed grass was higher in protein, etc. The reason for the shape of this grazing pressure/ production curve is not easy to determine, but possibly very heavy grazing could damage the leaf meristems or reduce the plant's stored reserves to such an extent that compensatory production is reduced. It is, however, even more difficult to suggest an adequate explanation as to how this type of relationship could extend to that found between grazing pressure and protein enhancement (Figure 6.5). One would expect that any new growth after defoliation, however slight, would contain high quality material. Possibly what was happening in this study was that grazing was so intense that virtually no new growth was taking place and samples were of older sheath material, etc. (Patton and Frame 1981). It would be very easy to hypothesise from this that, after a certain level of grazing, wigeon should stop feeding in a particular area, so as to optimise nutrient return. However, no evidence was found for this.

Two final studies are worth mentioning here, both dealing with the effect of goose grazing on vegetation. Ydenberg and Prins (1981) studied the effect of spring grazing by barnacle geese on the vegetation (almost totally Festuca rubra) of a saltmarsh island off the Dutch coast. By the end of April, after two months of grazing the protein content of grazed grass was 10% higher than that of ungrazed grass. On the same island, Prins et al (1980) found that the grazing pattern of brent geese on Plantago maritima actually maximised the production of new leaf material, unlike the situation with wildebeest and Serengeti grasses (see above).

It has been shown in this study that wigeon very significantly affect the amount of food available to them on their grazing sites, reducing it to as low as 25% of the ungrazed biomass at certain times of the year. Since it has been shown (Chapter 4) that wigeon tend to prefer feeding in areas with high grass biomasses, the fact that birds will return again and again to depleted sites later in the season seems at first rather confusing. Could there be any benefit from staying to graze on previously grazed areas? There are several possible benefits to wigeon from this feeding strategy.

Firstly, at the same time as the grass biomass is depleted by grazing, grass height is also reduced (Figure 6.2). This could result in birds finding it easier to handle the short grass on grazed sites, since peck rate tends to increase with shorter grass length (see Chapter 5). Thus, food intake per unit time could be enhanced. While this is possibly the case with initial reductions of grass height, the very severe grass height reductions of late winter tend to reduce biomass and height to the level where pecking rate and intake are hampered (Chaper 5). In other words, the reduction in grass height and availability has gone past the stage when grazing efficiency is enhanced to a point where there is so little green grass left that intake is in fact reduced.

While grazing intake is reduced, the actual producton of grass is enhanced (Table 6.1). This could be beneficial to the birds in that while the actual amount of grass available at any one time is low, production (during March at least) is greater and therefore food availability through the month is actually higher. While this theory has been shown to be the case in several studies (eg. MacNaughton 1976, Cargill 1981) it does not stand up to scrutiny in this work. While the difference in production between grazed and ungrazed sites during March was 6 gm^{-2} (13 compared to $9gm^{-2}$), the difference in overall grass availability was $35gm^{-2}$ (57 to $22gm^{-2}$). In other words increased production does not compensate for biomass loss, while the wigeon are at Caerlaverock at least.

The final possibility for a beneficial effect to wigeon of feeding on previously grazed fields is that the available food, even if greatly reduced in quantity, is high in quality compared to ungrazed grass. There are several reasons why the protein content of the grass could be of great importance to wigeon especially during late winter and early spring.

Firstly, as stated in the introduction, food quality is far more important to herbivores than carnivores. Meat eaters could conceivably select a diet on the basis of energy requirements alone and still end up with a diet balanced with respect to nutrients (Prins et al 1980). However, vegetable material is often very deficient in particular nutrients, especially proteins, and can also be highly indigestible. Thus the herbivore must confront the problem of extracting enough protein from a food supply containing abundant but obstructive carbohydrates (Bell 1971). Nutrient supply rather than energy can become the overriding factor in determining diet.

Secondly, nitrogen requirements per unit of body weight increase as overall body size gets smaller (Bell 1970, 1971). This is the same type of relationship as that between body weight and energy requirements: energy requirement is proportional to body $wt^{0.75}$ (see Chapter 3). Thus, increasingly small animals require a diet higher in protein than larger species. This is of major importance to wigeon as they are one of the smallest totally herbivorous bird species.

The third reason relates to breeding success and is especially relevant to the late winter/ early spring period, when wigeon are building up reserves for breeding. To some extent birds can be divided into those which use stored reserves to provide their energetic and nutritional requirements for breeding and those which obtain the necessary nutrition actually at the breeding grounds (Perrins and Birkhead 1983). The determining factors between these two are normally the speed of breeding after migration and the condition of the breeding grounds at the time of laying. Thus, most temperate passerine species will collect food for breeding actually at the breeding grounds, eg. the blue tit. In these species, breeding success is unrelated to body reserves. On the other hand, the arctic-nesting geese are classic cases of reserve breeders - relying on body reserves built up at wintering and staging grounds for breeding. This is primarily because these geese start breeding very early in the arctic season, when no food is available, in order that hatching time will coincide with the first flush of high protein grasses.

Ankney and MacInnes (1978) found that female lesser snow geese with larger nutrient reserves contained larger potential clutches (as measured by ovarian follicle development). This is just one example of the so-called 'condition hypothesis' (Newton 1977) which states that birds in better condition when leaving the wintering grounds will have better breeding success. Geese are not the only birds for which this seems to be the case. Milne (1976) found a significant correlation between female weight in winter and clutch size the following spring in eiders (Somateria mollisima) in Scotland, while Jones and Ward (1976) found that the protein reserves of the red-billed quelea (Quelea quelea) in

Africa determined not only the timing of breeding, but also the size of the clutch. Like arctic geese quelea need to begin laying rapidly once they find a suitable area, as they follow the rain belts moving up and down Africa. Thus, they depend on reserves rather than food available at the breeding site.

It is important to recognise that these reserves are not solely energetic, ie. stored as fat, but also protein reserves, stored in the pectoral muscles, gut, etc. Thus, McLandress and Raveling (1981) suggested that the availability of high protein new grass on the wintering grounds was essential in allowing Canada geese (Branta canadensis) to obtain the necessary body reserves for early migration and nesting before food became generally available on the breeding grounds. Ankney and MacInnes (1978) considered protein levels to be just as important as energy levels for egg production and successful breeding.

The question remains of where the ducks fit into this picture. A certain amount of evidence suggests that some species utilise proteinaceous food on the breeding grounds for egg development and laying. For instance, Serie and Swanson (1976) reported that the invertebrate portion of the diet of gadwalls increased from a normal 47% to 72% during breeding. Krapu (1981) considered that protein reserves for breeding were obtained by mallard on the breeding site by feeding on invertebrates, although most energy reserves were obtained in areas occupied before nesting. Finally, Krapu and Swanson (1975) found that pintail hens fed on wheat alone (no invertebrate food) virtually ceased egg production. However, not all ducks rely on protein gathered on the breeding site. Korschgen (1977) reports how female American eiders (Somateria mollisima dresseri) rely totally on body reserves for breeding and do not feed at all during this period. Thus, not only did overall body weight fall during the breeding season, but weights of gizzard, liver and intestine decreased as well, suggesting that these organs were being used as a protein reserve. While no similar studies have been carried out on wigeon, this species is in many respects more similar to tundra-nesting geese than temperate nesting mallard, pintail and gadwall. Admittedly, some of the European population does nest in temperate areas, eg. Scotland and mid-USSR, but the bulk nest in Scandinavian, Siberian and Icelandic tundra and northern boreal habitats (Cramp and Simmons 1977). For this reason wigeon are likely to reach their nesting grounds when they do not support large invertebrate populations and when grass growth will be only just under-way, if at all. This was, in fact, found to be the case in a study of breeding dabbling ducks (wigeon, teal, mallard and pintail) in northern Sweden (Danell and Sjoberg 1977, 1982). The authors found that the main insect food source on their study site (emerging chironomids) did not become available to the birds until after egg-laying had ceased. Thus the ducks would be dependent on body reserves built up at wintering and staging areas for their protein requirements (see also section 8.3).

There are two main mechanisms by which body condition may affect breeding success in these 'reserve' species. In many cases clutch size may be limited by poor condition (Ankney and MacInnes 1978). Alternatively, hatching success may be reduced in poor condition birds due to the increased likelihood of nest desertion and consequent nest predation (Newton and Kerbes 1974, Korschgen 1977). It is also quite possible that birds in very poor condition may not attempt to breed at all.

The above discussion has concentrated almost totally on the importance of protein reserves to breeding performance in female birds. But do males have any part to play in this? Is the attainment of adequate protein reserves important in this sex as well? Ankney (1977) hypothesised that male snow geese with larger reserves could better defend their families. This argument is, however, not applicable to wigeon as the males of most duck species desert their mates at or soon after hatching. However, Wishart (1983) found that male American wigeon (Anas americana) which were unable to obtain a mate had lower protein and lipid reserves than paired males. This could have been because a certain threshold level of condition must be attained before individuals begin investing time in mate acquisition. Thus, it is possible that access to high protein grass is important to male birds as well, though not to the same extent as females.

The final reason for the importance of a high protein intake at this time of year is that birds are building up reserves for migration. While a major part of the body reserve for migration will be in the form of lipid, to meet the energetic demands of flying as this is the most efficient energy store (Perrins and Birkhead 1983), some protein reserve will be important, especially for building up pectoral muscles for the long migration flights.

These four reasons are likely to make the grazing of previously grazed high quality grassland very attractive to wigeon, especially towards the end of the season. Several workers have found that animals will preferentially select previously grazed areas, whether this grazing was carried out by the same or other species. Bell (1970) and MacNaughton (1976) found that there was a very clear grazing succession in the Serengeti grasslands, with zebra (Equus burchelli) grazing the long coarse vegetation of the plains, followed by wildebeest and topi (Damaliscus korrigum) and finally Thomson's gazelle (Gazella thomsonii). The reason for this particular succession was that the digestive tract of the zebra was adapted to handle the stems and sheaths of the grasses, that of the wildebeest the grass leaves and that of the gazelles the higher quality dicotyledonous material, chiefly fruit, that was left behind.

A similar situation was found by Coppock et al (1983b) who reported that bison (Bison bison) tended to preferentially graze the high quality grasses of prairie dog (Cynomys ludovicianus) lawns. Willms et al (1981) found that deer tended to graze in areas which had been previously grazed by cattle. Finally, Arnold (1964) reports how sheep will normally graze in areas which they have already grazed. This can often cause problems in that ungrazed areas become less and less attractive and eventually unpalatable to the sheep, thus rendering large areas of hillside useless for sheep grazing.

While wigeon at Caerlaverock do still tend to actively select the highest biomass areas at this time of the year, at least in season 2 (Chapter 4), they do not tend to move away to completely ungrazed areas - possibly containing high biomasses but lower quality grass. This type of behaviour is also found in wigeon on the Ribble estuary which tend to restrict their feeding during spring to areas previously grazed by pink-footed geese (F Mawby, pers. comm.). This restriction of feeding areas during a time of generally low food availability could, in part, be due to the necessity for high quality forage at this time of year. The birds' strategy seems to be to select high biomass areas in which to feed, but to continue grazing on them even when biomass is low, so as to benefit from the enhanced food quality in these same areas towards the end of the season. The flock feeding habit is likely to be essential in this strategy (see Chapter 7). This situation is somewhat akin to the suggestions put forward by Prins et al (1980) and Ydenberg and Prins (1981) that barnacle geese and brent geese concentrate their grazing in certain areas and repeatedly harvest the regrowth of the same food plants so as to maximise the return of protein or new growth. They suggested that the birds were in fact 'manipulating' their food supply to obtain maximum benefit. Whether this particular verb is too anthropomorphic for a passive evolutionary process is a matter of dispute, but it remains a fact that these geese, and possibly wigeon as well have radically adapted their feeding behaviour so as to benefit from the peculiarities of grazing on a 'prey' which regrows.

6.4.2 The mechanism of protein increase

There are several mechanisms by which this enhancement of the quality of grazed grass could take place. These can be broadly separated into the effects of defoliation and the effects of nutrient supply. Defoliation can affect plants in many ways, but with regard to its effect on plant quality, the most important result is the alteration in the age structure of the leaf population (Prins et al 1980). All individual leaves on a grass plant go through a growth and senescence process, whereby an initial 'spurt' of rapid growth with high tissue nutrient concentrations is followed by a period of senescence during which increasing structural lignification and decreasing nutrient concentration occurs (Langer 1979). Eventually the leaf nutrients are extracted from the old leaf and translocated to another part of the plant and the leaf dies. The length of this process is variable, and the object of some dispute, but can be as short as ten days (D Berry, pers. comm.). The effect of regular defoliation is to reduce the overall physiological age of the leaf material since older leaves are replaced more quickly by young nutrient rich ones, ie. the turnover rate increases. Thus Prins et al (1980) found that the upper leaves of grazed Plantago had an average age of 4.9 days, while those of ungrazed plants had an age of 8.6 days. An important point with regard to this particular mechanism is that it can function over a very short time period: the effect of grazing on protein levels can be significant after a few weeks of growth.

A second mechanism by which grazing can affect plant quality which is very closely related to the above, but which operates over a longer time period, is that of the delayed maturation of the whole plant. It has been known for years that most grasses go through an annual cycle of rapid growth during spring, a mid-summer decrease in growth, and a second shorter period of rapid production in autumn before the onset of winter dormancy (Williams 1980, Kilcher 1981). This is brought about by the normal reproductive process of the plant - early and late summer flowering producing this characteristic growth cycle. As the grass plant matures and approaches flowering it produces more and more stem material. Stem, which is initially very high in quality, rapidly becomes heavily lignified (to support the flower head) and this greatly reduces the overall nutrient content of the plant (MacDonald et al 1973). Along with this, the leaf blades and sheaths gradually reduce in quality as well. The effect of grazing on this whole plant cycle is to maintain the plant in a physiologically immature state. The stem:leaf ratio is reduced, and overall plant quality increased. A common result of this is that, at a time when ungrazed areas are flowering, very few flower heads are found on grazed sites (eg. MacNaughton 1979b, Ydenberg and Prins 1981). This process is almost certainly the one producing increased protein concentrations or reduced fibre levels in several studies already mentioned (Moss et al 1981, Ydenberg and Prins 1981, MacNaughton 1979a).

A final possible effect of defoliation on plant nutrient status is that the reduced stature of frequently grazed plants can result in a concentration of the available soil nitrogen in the smaller leaf area of the plant (Coppock et al 1983a).

The deposition of faecal or urinary material in the vicinity of vegetation can greatly increase the nutrient content. This can result either from an increased rate of nutrient recycling within the ecosystem, since nutrients are released more rapidly from animal droppings than from dead vegetation (Cargill 1981) or from the net import of nutrients from other areas, eg. from the sea to sea bird nesting colonies (Smith 1978). The normal production of droppings by wildfowl on agricultural land is unlikely to significantly affect soil nutrient content (Kear 1962). However, Marriot (1973) found that, if added in sufficient quantities, Cape Barren (<u>Cereopsis novae-hollandiae</u>) goose droppings could increase grassland production (he did not measure the effect on quality). In the nutrient-deficient habitat of an arctic saltmarsh, Cargill (1981) considered that nutrient recycling via goose droppings was the most important factor leading to the very substantial increases in the NAPP and nitrogen levels which she observed in the vegetation.

In this study, it has already been shown (Figure 6.6) that nutrient changes from wigeon droppings do not seem to be the cause of the observed increase in grass protein content. Moreover, since the grass biomass in both grazed and ungrazed areas at the end of the season is low, and also since nitrogen is unlikely to be severely limited in agricultural soils, the high protein content of grazed grass is unlikely to be due to reduced dilution of available nitrogen in smaller plants. Finally, delayed maturation of the whole plant is unlikely to be operating since the time scale over which protein enhancement has been observed is too short for this process.

Many grasses, especially Lolium perenne (which is one of the commonest grasses on the study site - Table 4.3), are well known for their ability to grow through the winter if the temperature is high enough. For example, Thomas and Norris (1977) reported that L. perenne started growing in January at a low level site in mid-Wales (20m above sea level). Thus it is quite possible that during mild days, leaf extension and growth does occur at Caerlaverock throughout the winter and especially during late February/ early March. During warm periods, for instance, a very clear 'greening' of the fields could be seen even in mid-winter. By March, therefore, grass growth (and thus leaf development and eventual senescence) is likely to be well under way.

For these reasons, the most likely mechanism by which wigeon grazing increases the quality of vegetation at Caerlaverock is by decreasing the average age of the leaf population of the grass, resulting in an increase of young proteinaceous leaf material.

MacNaughton (1979) reviewed a number of possible mechanisms by which grazing can stimulate NAPP in grassland/ herbivore systems. These included increased photosynthetic rates in residual leaf tissue due to increased demand for assimilates; re-allocation of substrates from elsewhere in the plant, eg. the root system; removal of older tissues functioning at less than maximum photosynthetic level; reduction in mutual leaf shading; hormonal redistribution resulting in activation of remaining meristems; direct effects from growth promoting chemicals in herbivore saliva - this has been found to be the case in some ruminants. It is not proposed to go into these various hypotheses in great detail here, since the process of protein content enhancement is considered to be of more importance in this study. However, two points should be noted. Firstly NAPP was stimulated by wigeon grazing during early spring, though not to the same extent as found in some studies (MacNaughton 1976, Cargill 1981). Secondly, while several of the above mechanisms could be operating concurrently, it is reasonable to assume that the mechanism which stimulates protein levels is likely to be the one which stimulates production - in this situation at least. Thus, removal of older leaf material and the resultant decrease in age structure of the leaf population would not only increase nutrient levels in the remaining tissues, but would also result in very high photosynthetic rates in the newly growing leaves: aerial production would be stimulated along with protein levels.

CHAPTER 7

THE FUNCTIONS OF FLOCK FEEDING BY WIGEON

7.1 INTRODUCTION

"Wigeon are quite distinct from other ducks in their habitat and feeding requirements in that they are largely vegetarian and feed chiefly on land or exposed mud ... It is the only duck to form tight packs of grazing birds" (Prater 1981).

In much of their behaviour, wigeon are most unlike other ducks. They graze rather than dabble or dive. They feed in open marshland or fields, rather than skulking in thick aquatic vegetation or diving in open water. They spend almost all day and part of the night feeding on poor quality grasses rather than high nutrient invertebrates and seeds. Finally, as can be seen from the above quotation, they form very characteristic large feeding flocks.

With regard to this last point, one of the most influential and successful approaches to the study of the function of sociality has been the comparative approach (Davies and Krebs 1978). In this method, an attempt is made to understand divergent behaviours in similar species in terms of the environmental constraints imposed on them. This type of reasoning would suggest that the selective pressures leading to flock feeding in wigeon are to be found in their unusual diet, feeding method and feeding habitat. This chapter, therefore, is primarily an amalgam of various results which throw some light on the function of flocking in wigeon.

Historically, explanations of group feeding in birds and other vertebrates have centred on the dichotomy between anti-predator function and feeding benefits. One of the first anti-predator advantages for flocking to be put forward was Hamilton's (1971) and Vine's (1971) 'selfish herd' hypotheses. The former dealt with predation from within the group, the latter with a predator attacking from outside. The basic theory is that, by being in a group, an individual increases its survival chances by using other flock members as cover and thus decreases its 'domain of danger'. There will also be a dilution effect in a group, ie. if there are forty birds in a flock the chances are only one in forty that a particular individual will be taken.

Lazarus (1972) and Pulliam (1973) postulated a further anti-predator advantage. Most animals spend a fair portion of their time looking out for predators, time which could be spent in foraging, etc. In a group, however, vigilance can be shared, reducing the amount ot time a particular individual has to spend in this activity - the 'many eyes' hypothesis. This could therefore be a powerful force leading to flock formation. Further to this, the 'corporate' vigilance (and thus safety) of the group will, in most situations, still be higher than for a solitary animal (Bertram 1978).

Finally, several studies have shown how a group of prey can confuse a predator, leading to the escape of all individuals (eg. Sharp 1951, Neill and Cullen 1974).

The feeding benefit functions for flocking are again many, but most centre on the theme of information exchange. This information includes search image and food type (Murton 1971) and (probably more commonly) profitability of feeding area (Krebs 1974, Drent and Swierstra 1977).

It is now generally recognised that no simple dichotomy exists with regard to this subject and that the advantages of grouping will include many interactions between different benefits (Lazarus 1972, Bertram 1978). However, it remains useful to examine situations in which only one benefit can be affecting the animals in order to understand more clearly how the different requirements interact (eg. Drent and Swiestra 1977).

In conclusion, the aim of this chapter is to examine the reasons leading to flock feeding in wigeon by studying certain aspects of their feeding behaviour. These include vigilance rates in various flock sizes and changes in flock size at various distances from water. Also, results from the previous chapter on food quality enhancement by flock feeding have been brought into this discussion.

Finally, although not directly relevant to the main theme, results on sexual differences in vigilance rates are reported here.

7.2 METHODS

7.2.1 Definition of vigilance

The vigilance studies included only grazing birds (ie. grazing was the main activity of the bird, although this activity may have been punctuated by vigiliance, threats, etc.). Thus, birds which were primarily walking, preening, etc. were not observed.

A vigilant bird was defined as a grazing bird with its head up. There are several different postures which a bird can adopt when in this position. These include 'head up' - the bird raises its head so that its bill is horizontal with the ground and retains this position for several seconds; and 'extreme head up' - the bird takes up the above posture except that its neck is stretched out (Lazarus 1978). However, the most common vigiliance posture adopted by wigeon was a 'rapid head up' posture in which the bird raises its head momentarily towards the 'head up' position, but does not adopt it fully. When very rapid, this type of vigilance can resemble a head-flick type movement. This 'rapid head up' was not, however, simply the movement of the head between bites of grass. A clear scanning was observable. No distinction was made between the various head up positions when measuring vigilance time: the time spent in all three vigilance postures was simply added together to give a total vigilance estimate.

7.2.2 Observation methods

One stopwatch was used to record total observation time, while time with head up was cumulated on a second stopwatch. Total observation time was never less than one minute and never more than six minutes. The vast majority of observations were in the 1.5 to 3 minute range. While it would have been more satisfactory to use a single observation period for all birds, this was not possible, since no electronic timer was available. However, the data was checked to ensure that the variable observation time had not biased the results. No relationship was found between observation time and % vigilance, and it was concluded that the method was not affecting the results.

7.2.3 Study details

The data on average flock size and its variation through the season was collected in season 1. During this season, all birds were counted three times a day from the main observation tower (see p.7) and during these observations the size of all wigeon flocks on the study area was recorded.

The distance from water/ vigilance study was undertaken during season 3. All observations were carried out on the enclosure field by the teal pond, in order to standardise the results as much as possible. At the start of the observation, the focal bird's distance from water (the pond) was estimated on a scale of 0-10m; 10-20m; 20-30m; 30-50m; 50-70m. If the bird moved out of its distance category during the observation, the result was discarded. These distances were estimated by eye, but were considered to be reasonably accurate since the approximate length of the field was known, and the distance categories were wide. In the analysis of the results, the mid-point of each category was used. The size of the flock was also recorded. Since, on occasions, the birds could be very loosely knit and spread out, a system was used whereby the total number of birds within a 20m radius of the focal bird was counted. Thus, in the results from these observations, flock size is used in this slightly restricted sense.

The flock size/ vigilance study was carried out during the spring of season 3. Birds were observed on all grazing sites (except the enclosure) and always < 10m from water, in order to control for this variable. In this study flocks were always closely knit and never numbered more than 27, so that the total flock on the grazing site was counted.

In both studies the sex of the focal bird was recorded. Normally different sexes were observed alternately, so as to provide an approximately equal number of each sex in the sample at the end of each observation period.

7.3 RESULTS

7.3.1 Flock behaviour of wigeon

The most likely flock size in which an individual wigeon will be found is 95.4 birds. This is based on a whole winter's observations (November to April) in season 1, for which the most complete data set was available. This result was calculated from the wigeon's 'point of view', using a weighted average, rather than from the observer's or flock's viewpoint, an approach which tends towards group selectionist assumptions (Gosling and Petrie 1981). The method employed was to multiply each flock size by the number of individuals found in that flock (ie. flock size^2), sum this expression for all observations, and then derive the weighted average by dividing by the total number of individual wigeon observed (in this case, n=16,306). This is more relevant to the individual bird, than simply summing the flock sizes and dividing by the total number of flocks observed. The actual number of flocks observed for this analysis was 403. Flock size ranged from 1 to 300 birds.

The effect of time in season on flock size is shown in Figure 7.1. Flock size was calculated by the weighted average method. As can be seen from the graph, flock size tends to mirror the number of birds on the reserve. However, some regulation of flock size is taking place since the slope of the flock size line (from January to April) is not as steep as that of the number of birds line. In other words, when bird numbers on the reserve become too low, the wigeon are tending to group together more, in order to remain in an 'acceptable' size of flock.

The effect of flock size on vigilance can be seen from Figure 7.2. There is clearly a decrease in vigilance with increasing flock size (r_s = -0.720, n=200, $P < 0.001$; Spearman rank correlation). The relationship is exponential, asymptoting at about 18 birds. This would be expected, since the effect of a second bird on a single bird's vigilance rate will be very great, theoretically halving it, while at high flock numbers the addition of a single bird will result in very little change in any individual bird's vigilance.

In order to control for this group size effect in the other vigilance study (ie. distance from water effect - see Figure 4.14), only flock sizes greater than 18 birds were included in the analysis. No flock size effect was found above this number (r = 0.085, d.f.=156, n.s.)

The effect of distance from water on flock size is shown in Figure 7.3. It can be seen that a highly significant, positive relationship is found (t=98.8, d.f.=156, $P < 0.0001$). Thus, birds tend to group into larger flocks as they move further from water and into more risky areas (see Chapter 4).

7.3.2 The effect of sex on vigilance rates

Sex differences in vigilance rates were examined in both vigilance studies. In the flock size study, no significant differences were found except at a flock size of two (Table 7.1).

Figure 7.1

Effect of time in season on number of birds on reserve (see Fig. 2.1) and weighted flock size. Data from season 1.

———	no. birds on reserve
- - - - -	weighted flock size

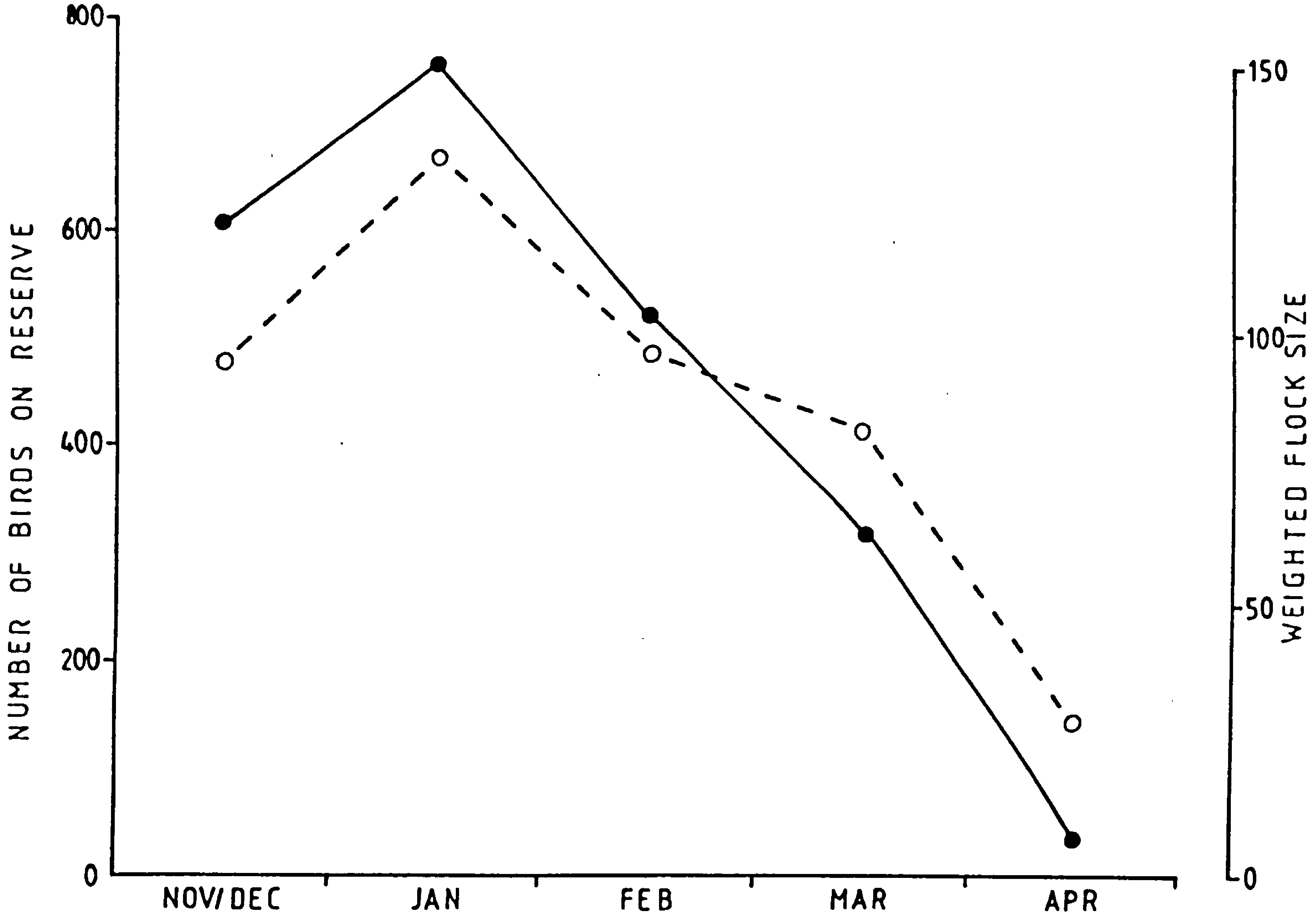

NUMBER OF BIRDS ON RESERVE
800
600
400
200
0
NOV/DEC
JAN
FEB
MAR
APR
WEIGHTED FLOCK SIZE
150
100
50
0

Figure 7.2

Effect of flock size on vigilance rates (mean ± 1 s.e.). Data from spring, season 3.

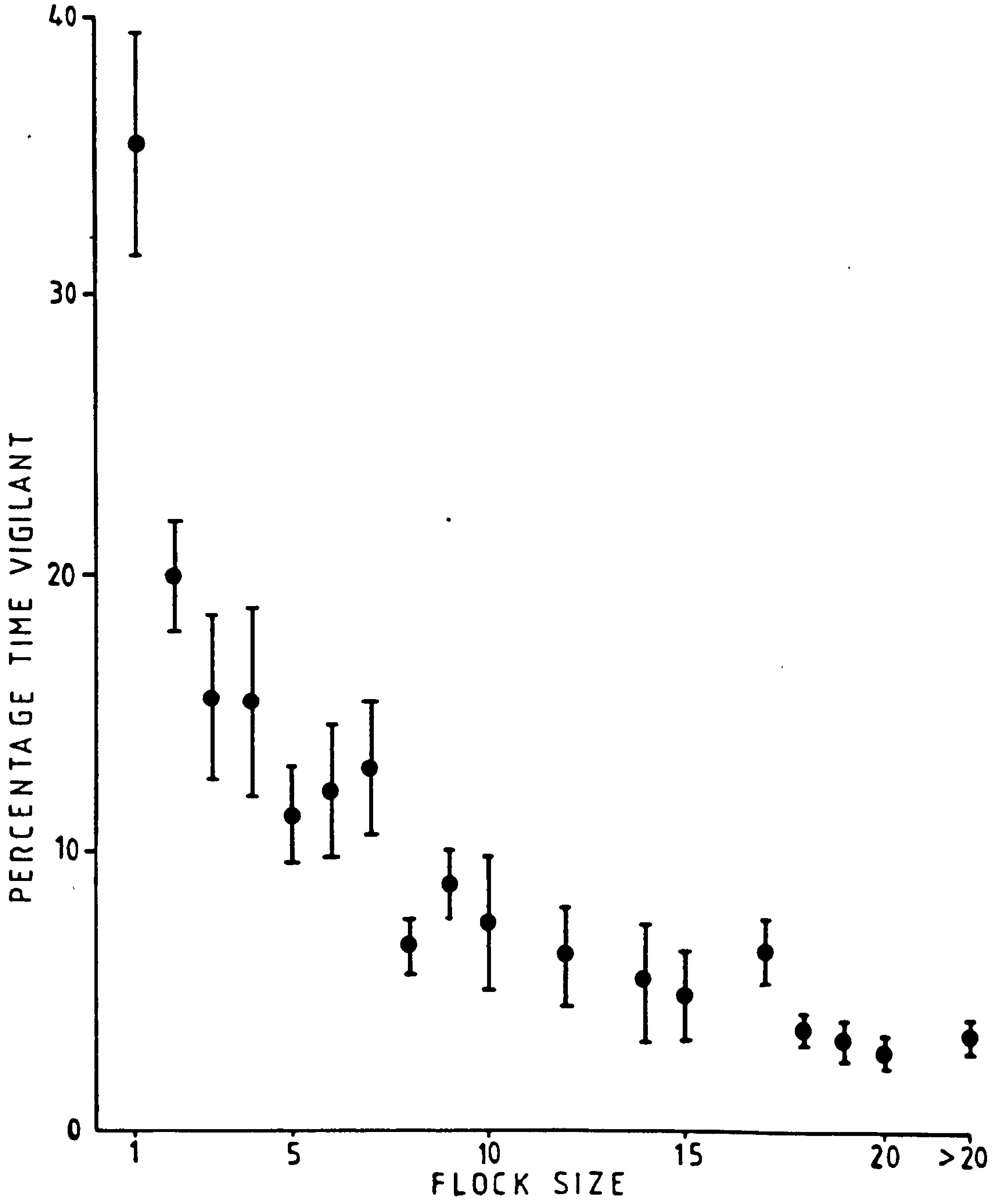
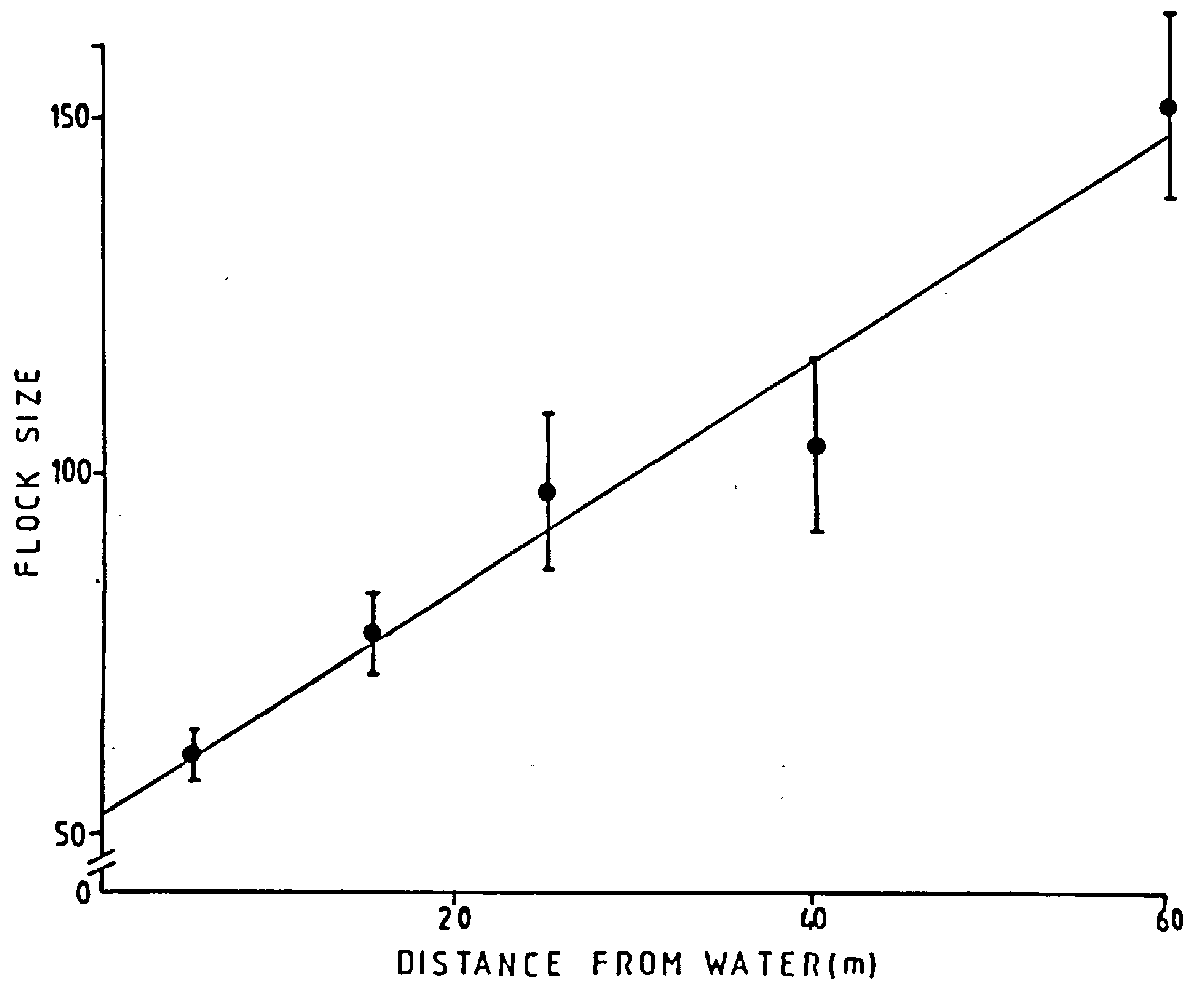

40
30
20
10
0
PERCENTAGE TIME VIGILANT
1
5
10
15
20
>20
FLOCK SIZE

Figure 7.3

Regression of flock size (mean ± 1 s.e.) on distance from water. Data from winter, season 3.
The equation of the line is $y = 1.55x + 53.44$.


FLOCK SIZE
150
100
50
0
20
40
60
DISTANCE FROM WATER(m)

Out of all the other group sizes examined (16 in all) males were more vigilant (but not significantly) in only nine cases. Thus, outside a group size of two, no clear sex difference is apparent.

TABLE 7.1

Changes in vigilance rates with flock size separated for males and females.

FLOCK SIZE	MALE	FEMALE	Significance of difference (T-test)
1	35.2	no data	-
2	26.3	12.2	P < 0.001
3	10.4	19.1	N.S.
4	9.7	21.2	N.S.
5	10.6	12.0	N.S.
6	13.1	10.9	N.S.
7	15.3	9.5	N.S.
8	8.7	5.2	N.S.
9	7.9	9.7	N.S.
10	5.6	9.2	N.S.
12	4.9	9.0	N.S.
14	6.2	4.7	N.S.
15	3.7	5.4	N.S.
17	6.9	5.8	N.S.
18	4.2	2.7	N.S.
19	4.0	2.5	N.S.
20	3.7	2.1	N.S.
>20	3.8	2.9	N.S.

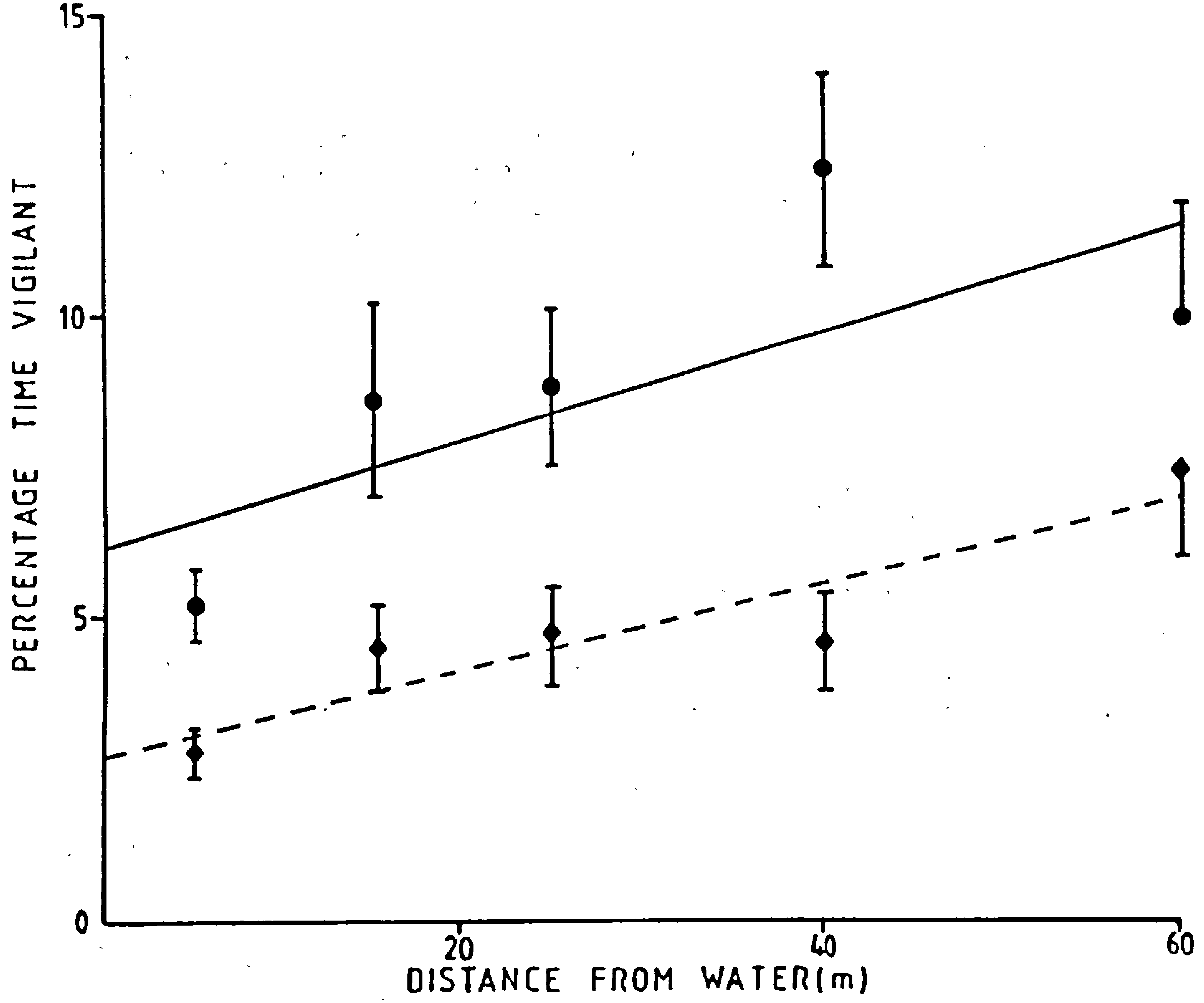
In the distance from water study however, a very obvious sex effect was found (Figure 7.4). Figure 4.14 shows the overall effect of distance from water on vigilance. Covariance analysis shows the effect of sex to be highly significant (F = 32.31; d.f.

Figure 7.4

Regression of vigilance rate (mean ± 1 s.e.) on distance from water, separated for sex. See Fig. 4.14 for overall effect.

——— male ($y = 0.09x + 6.19$)

– – – – female ($y = 0.07x + 2.76$)


PERCENTAGE TIME VIGILANT
15
10
5
0
20
40
60
DISTANCE FROM WATER(m)

= 1,155; P < 0.0001). Also, in four out of the five distances from water, there was a significant difference between males and females, using a t-test analysis. Thus, this effect is very obvious indeed. The reason for the decrease in male vigilance at a distance of 60m from water is not at all clear. A small shallow flash pond often formed in the centre of the enclosure field after rain, and wigeon would sometimes fly to this when the flash was well-formed. However, the graph of female vigilance does not show any decrease at this point, so why males alone should 'feel more secure' due to this extra pond remains unresolved.

7.4 DISCUSSION

7.4.1 The function of flock feeding in wigeon

A reduction in vigilance rate with increasing group size has been found by a large number of workers in many different species, eg. sparrows (Barnard 1980), ostriches (Struthia camelus) (Bertram 1978), barnacle geese (Drent and Swiestra 1977), white-fronted geese (Lazarus 1978), woodpigeons (Murton et al 1971), great blue herons (Ardea herodias) (Krebs 1974). While many authors explain this effect as the result of the 'selfish herd' or 'many eyes' hypotheses (see Introduction), some consider foraging information exchange to be the main cause, eg. Murton et al (1971), Krebs (1974). Indeed Krebs found that when feeding rate (which was positively correlated with group size) was taken into account, the relationship between vigilance and group size disappeared. However, in other studies, the authors seem to be basing their suggestions more on a personal preference for feeding benefit functions than on hard data. For instance, Murton et al (1971) claim that woodpigeons are gregarious in order to improve feeding efficiency, and the reason why solitary birds look around so much is because they 'feel uneasy' when not in a flock. However, this idea does not explain the very clear exponential relationships between vigilance and group size found by many workers, which so closely fit Pulliam's (1973) model (see also Elgar and Catterall 1981). Drent and Swiestra (1977) suggested that information exchange occurs in barnacle geese whereby birds are attracted to sites where other individuals are actively grazing. While this possibly does take place in wigeon flocks as well, it seems likely that, in small flocks at least, predation factors are the main cause of gregarious feeding. It would nevertheless be very interesting to carry out some of the model experiments, so crucial to Drent and Swiestra's hypothesis, on grazing wigeon.

The graph of flock size versus distance from water lends more weight to the anti-predator hypotheses, since there is no reason why there should be a reduction in food quality/ quantity (resulting in the need for more information exchange and larger flocks) at increasing distances from water. However, the distance from water/ vigilance relationship (Figure 4.14) does suggest that predation risk increases with distance from water and birds could therefore be reducing their individual risk of predation by foraging in larger flocks in more dangerous areas (Hamilton 1971). A similar result, flock size increase in the presence of a predator, was found by Caraco et al (1980b) in yellow-eyed juncos (Junco phaenotus).

A final possible function of grazing in a group relates specifically to birds feeding on a renewable resource. Flock grazing by wigeon results in the extensive removal of old vegetation over the narrow strips of grassland beside the ponds. The effect of this is that in late winter and early spring the quality of the grass is enhanced at a time of year when high protein intake is critical (Chapter 6). Obviously a single bird would not have this effect and several workers have suggested that this could be an important selection pressure leading to flock feeding in geese, through improved forage quality (Drent and Swiestra 1977, Ydenberg and Prins 1980) or increased forage production (Prins et al 1980).

Unfortunately, this last rather attractive theory faces a serious, but plausible problem. This is that since the selective advantage of food quality enhancement is a future one (the benefit is reaped in early spring by winter feeders) 'cheating' could possibly occur, since 'selfish' individuals could let the other 'altruistic' birds do the hard work of clearing off the old vegetation and then enjoying the high quality forage the next spring. High quality forage in spring is an unprotectable 'public good' (Herrera 1982). The trait of flock feeding (for this purpose) would therefore not be of selective advantage to the individual and would not spread through the population. Food quality enhancement would therefore be a consequence of flock feeding rather than a function. However, this scenario could only happen if cheating, ie. feeding in better areas while the flock feeders do the work, is possible. Could 'selfish' birds find better areas to feed in? If it is argued that wigeon are feeding on the best areas anyway, they could not. On the other hand, if it is claimed that birds forego feeding on good areas, in order to produce this effect, then problems with cheating could certainly occur. From the results in Chapter 4 it can be seen that most birds do tend to graze in the best (high biomass) areas. Thus, cheating would not be possible, and it is reasonable to hypothesise that food quality enhancement is a strong force producing the flock feeding habit of wigeon.

To sum up: four main hypotheses on the function of flock feeding in wigeon have been considered. These are:

a) the 'many eyes' hypothesis - birds in a group can spend more time in non-vigilance activities plus the 'corporate' vigilance of the group is greater.
b) the 'selfish herd' hypothesis - birds in a group are less likely to be the victim of a predator attack.
c) the feeding information hypothesis - birds in poor feeding areas can observe the feeding activities of other flock members and move to more profitable sites.
d) the food enhancement hypothesis - by feeding in a flock birds can benefit from high quality food in early spring.

Evidence for three of these hypothese (a,b and d) has been submitted. While either/ or explanations are seldom appropriate as regards this subject, it is considered likely that the 'many eyes' hypothesis is the main one leading to small flock formation in wigeon. However, an individual wigeon is most likely to be found in a flock of about 95 birds, and when overall numbers fall in late winter, average flock size does not simply follow suit, but birds attempt to keep in large groups. Thus, the other three hypotheses (including information exchange) are likely to be involved in the formation of these larger flocks, through complex interactive processes.

7.4.2 Sexual differences in vigilance rates

A higher level of alert behaviour in males compared with females has been reported for many species of wildfowl. Most of these studies concern birds during the breeding season, either before laying (eg. Fox and Madsen 1981, Kaminski and Prince 1981b) or after nesting (eg. Harwood 1975, Lazarus and Inglis 1978, Stroud 1982). The suggested hypotheses are that the former allows female birds to put on reserves for nesting and the latter allows her to make them up after long weeks of incubation. A further hypothesis for high male vigilance at this time (especially during the pre-laying phase in ducks) is to guard mates against rape attempt by other males (Kaminski and Prince 1981b, Lendrem 1983a).

Outside the breeding season, only a few records of male/ female vigilance differences exist (Bertram 1980, Lendrem 1983b), and the hypotheses explaining them are more difficult to ascertain. Lendrem (1983a) has put forward two possible explanations for this phenomenon: a) males may be looking for females to rape, and b) males (in many species) are far more conspicuous than females, and their higher vigilance rates reflect the greater risks they face. This second hypothesis seems the more likely, with good evidence for wildfowl coming from two sources. Fox and Madsen (1981) report that the male/ female difference in vigilance in breeding white-fronted geese disappears when in a flock. They suggest that this is because vigilance can now be shared by all flock members and not solely by the male. Thus, in a species with no obvious sexual dimorphism in plumage colour, males and females show similar vigilance levels, when the male is not mate-guarding. Secondly, Lendrem (1983b), amongst other lines of evidence, shows that in mallard, as predation risk increases, the male/ female divergence in vigilance increases. He suggests that this is because males are inherently more at risk from predation and are therefore more wary in riskier situations, since there is no reason why opportunities for rape should increase in riskier areas. Interestingly, the same sort of result was found in this study (Table 7.2). The male/ female vigilance divergence tends to increase as birds move to riskier areas, further from water. The fact that the difference decreases at 60m lends weight to the idea (suggested earlier) that the flash pond in the centre of the enclosure field was being used as a safe retreat by the birds - greater safety leading to a decrease in the vigilance difference between males and females.

TABLE 7.2

Difference in % vigilance (male - female) at different distances from water. (see Figure 7.4)

Distance from water (m)	5	15	25	40	60
% vigilance difference (male - female)	2.41	4.11	4.10	7.82	2.61

However, one finding goes aginst this hypothesis. In the study of group size and vigilance rates only group size 2 shows the male/ female difference (Table 7.1). This result was also found by Bertram (1980) although his highest group size was only four. This suggests that the difference is due to mate-guarding, males protecting their females from predators and conspecifics. A possible solution to this apparent contradiction is that the group size study was carried out in spring, when small wigeon flocks were more easily found. It is possible that at this time of year, mate-guarding is more prevalent, and both conspicuous plumage and mate protection are responsible for the vigilance difference. The reason that only groups of two showed this effect was possibly that these are definitely paired birds, while birds are not necessarily paired in larger groups, and so flock size constraints on vigilance are the over-riding concern. The fact that these differences remain into spring in the large flocks of the distance from water study supports this hypothesis.

In summary, the male/ female differences in vigilance rates found in large flocks in winter are probably due to the higher predation risk faced by the gaudy male birds. In spring, however, the difference is due to both gaudiness and mate-guarding.

CHAPTER 8

THE DIGESTIVE PHYSIOLOGY OF WIGEON

This chapter deals with the physiological strategies (as opposed to behavioural ones - Chapters 3-7) used by wigeon to maximise their nutrient intake. It looks at several subjects under the general theme of the digestive physiology of nutrient gathering by wigeon, physiology being used here very loosely. Firstly, some studies on the throughput time of food in the wigeon's gut are discussed. Secondly work on the digestive efficiency of wigeon is reported and, finally, results from work on changes in gut morphology with condition in wigeon are reported. It should be stressed that there is no clear connection between these different subjects outside the rather artificial title of 'physiological'. No attempt has been made to look at the effect of gut morphology on throughput time, or throughput time on digestive efficiency. While it is certainly possible to speculate on these relationships, their in-depth study would have been outwith the scope of this project. The chief aim of this part of the study has been to define the characteristics of plant digestion in wigeon which will, in turn, influence feeding behaviour.

8.1 THE THROUGHPUT TIME OF FOOD IN THE WIGEON GUT

8.1.1 Introduction

The time food spends in the gut has a profound effect on the amount of energy/ nutrients which an animal can extract from its food. Indeed digestion and food passage rates are interacting and competing processes (Robbins 1983) since a high rate of passage leads to a low digestive efficiency and, conversely, food spends much longer in the gut of animals which have a thorough digestive process. These systems can be understood as an "efficiency-velocity" continuum with different species ranked at different points along this line (Milton 1981). Bell (1971) discusses this concept and shows how the digestive processes of the Serengeti herbivores affect their feeding behaviour and ecology. The ruminant species have complex guts, slow passage rates, high digestive efficiences and are selective in their food choice, since they are unable to survive on large quantities of low quality food. The non-ruminant species have simpler guts, high rates of passage, low digestive efficiencies and feed on large quantities of low quality food.

The herbivorous wildfowl would be placed well to the velocity end of this continuum. They have an extremely simple gut (see Figure 8.4) which is consistent with the necessity for a high power-to-weight ratio in flying animals (Mattocks 1971). Thus, in common with the non-ruminant mammalian herbivores, they consume large quantities of low quality forage, have low digestive efficiencies and very rapid passage rates.

The simplicity of the wildfowl gut reduces the complexity of the rate of passage concept: there is no rumination or copraphagy to confuse the situation. Basically, food is taken in, passed straight to the gizzard, broken down mechanically, passed into the intestine and shunted out of the alimentary tract in a semi-digested state. There is no storage of food in a 'stomach', except when the oesophagus and proventriculus are used for this purpose at dusk, to provide food for digestion during the early part of the night (Owen 1972b).

8.1.2 Methods

A) General

Historically, five methods have been used to measure throughput rates in wildfowl:

1) Adding an indigestible marker to the feed (eg. Marriot & Forbes 1970, Burton et al 1979).

2) Contaminating the food with barium sulphate, and following its progress by x-ray photography (Mattocks 1971).

3) Changing the diet of the bird and recording when this change is reflected in the faeces (Mattocks 1978).

4) Calculating 'initial' throughput rates by observing geese when they first start to feed in the morning (the gut will be empty) and recording the time to first defaecation (eg. Ebbinge et al 1975, Burton et al 1979).

5) Calculating 'turnover rate' of food in the gut by dividing gut capacity by defaecation rate (Owen 1975a).

All of these techniques have advantages and drawbacks. Markers can dissociate from food, handling for x-ray photography can induce stress resulting in abnormal peristaltic movements and diet changes will affect throughput rate so that it is difficult to assess exactly what is being measured. Finally, it is difficult to know just how 'initial' throughput rates compare to normal ones on a full gut. One of the better methods is undoubtedly the calculation of turnover rate in wild birds, but it is often difficult to obtain sufficient full guts to calculate gut capacity. Moreover the amount of information gained is minimal.

In this study a radioactive tracer based on the rare earth element Ruthenium was used. This marker has the advantages of being easy to detect accurately (thus giving a great deal of information about passage rates) and binding in a non-dissociable complex to plant fibre so that it travels at the same speed as the digesta (Tan et al 1971, MacRae 1974). It has been used in at least two avian throughput studies (Gasaway et al 1975, Keast and Walsh 1979). Its main disadvantage is that birds had to be handled to administer the marker, which induced some stress.

B) Captive flock enclosures

The experiments reported here were carried out in June 1981. The captive flock of ten pinioned wigeon (see p.52) were transported from Caerlaverock to the University of Glasgow farm at Cochno, north of Glasgow. The birds were penned at night in a fox-proof enclosure on a recently-reseeded grazing pasture of Lolium perenne, Phleum pratense, Festuca spp., Poa spp. and Ranunculus. The enclosure had a large grazing area adjoining, into which the birds were released during the day. Since birds were also able to graze at night in the fox-proof enclosure, or (later in the experiment) were provided with cut grass, their whole diet consisted of grass - no grain was given during the experimental period. Water was provided from automatic poultry watering cans.

C) Isotope preparation

All direct handling of the isotope and labelled grass was carried out by Mr B Lee and Dr D Houston. ^{103}Ru-labelled tris (1, 10 - phenanthroline) Ruthenium II chloride was prepared courtesy of the Rowette Research Institute, Bucksburn, Aberdeen, using the method described by Tan et al (1971). The radioactive concentration of the stock ^{103}Ru-phen obtained from the Institute was 10 μCi/ ml. A working solution containing 0.02 μCi/ ml was made by taking 0.05 ml and making this up to 25 ml with deionised water. The stock solution could be used over several months.

D) Preparation of marked food

10 'bite size' (approximately 3 cm long) pieces of freshly cut grass (various species) were submerged in 20 ml of the working ^{103}Ru-phen solution for 1 hour at room temperature (15°C) (Lee 1984). The leaves were then removed from the solution and the excess moisture evaporated off by placing the radioactive leaf in an oven (50°C) for 5 minutes. The leaves were then pushed into a short length of soft rubber tubing. Inserted into this was a second length of harder rubber tubing to act as a 'push rod'. The tubing could then be packaged up and transported to Cochno farm. This procedure was carried out the evening before the experiment.

E) Radioactivity counting procedure

Radioactive samples (faeces) were assayed using a Nuclear Enterprises Scaler-Ratemeter SR5 coupled to a Nuclear Enterprises 663C Scintillator Counter. The scaler-ratemeter consisted of a high voltage generator, a linear pulse analyser, a ratemeter and a scaler/ timer. The scintillation counter included a 2 inch diameter, 11 stage photomultiplier tube and dynode components, housed in a tubular lead shielded case. The system was set to measure gamma radiation by having a Na I phosphor fitted.

Faecal samples were collected in disposable plastic tubes (1 cm diameter) and fitted into a well within the scintillator counter unit. The scaler/ ratemeter was preset to count to 100 seconds. This was long enough to measure the low levels of radiation within the samples to a reasonable degree of accuracy over a single count period.

After each experiment the tubes were brought back to the lab the same evening. Three background counts were taken using empty tubes, then all the experimental tubes were counted - the whole procedure taking approximately 45 minutes.

F) Experimental procedure

In all, six replicates of the throughput experiment were carried out. The first three took place on consecutive days, there was then a break of six days, and the second three were again carried out on consecutive days, ie. experiments 1-3, then a gap, then experiments 4-6.

All six experiments were carried out using the same bird (a male). This was because, when it was recognised that the bird was somewhat stressed by the experimental method, it was decided to use only one individual in the hope that this bird would to some extent habituate to the experience. The results proved this to be the case.

On the morning of the experiment, all birds were released from the night enclosure and allowed to graze for about two hours. This was to ensure that the throughput time would be a mid-feed one rather than an 'initial' one. The experimental bird was then caught by hand - a fairly quick and simple process - and taken to the experimental enclosure. This was a fenced area approximately 4 m by 2m adjacent to the grazing area. The experimental bird could at all times see the other birds, which was important as complete visual separation made the experimental bird extremely agitated.

The labelled food was administered to the experimental bird immediately so that catching-up was only carried out once per experiment. The soft rubber tube was inserted down the open mouth of the bird and approximately a quarter of the way down the oesophagus. The labelled grass was then pushed into the oesophgus. The tubes were then removed and the bird was held for a few seconds to ensure that the food was swallowed and not regurgitated. The bird was then released in the experimental enclosure and the observer moved away. This process took approximately 30 seconds.

The bird was then watched by the observer from a distance of approximately 30 m using 8x40 binoculars. No hide was used. A note was kept of when and where defaecations took place. Approximately every 20 minutes, the observer slowly approached the enclosure, entered it, and placed all voided faeces into a counting tube. He then left immediately. After several repetitions, this process had very little effect on the bird.

Apart from the faeces collection, certain feeding behaviour observations were also undertaken. In all six replicates the precise time when the experimental bird began intensive feeding was recorded. This was a clearly defined point, since up till that time the bird simply looked around. Thus, the first peck was the start of feeding. During the final two experiments (5 and 6) more detailed observations were undertaken to compare the feeding behaviour of the experimental bird and the rest of the captive flock, using a telescope. These observations were of peck rate (time for 25 pecks - as in the Chapter 5 experiment); feeding bout length; and % time feeding (using two stop-watches -

one running continuously for the observation period (approximately 5 minutes) and one used for cumulating feeding time during this period).

8.1.3 Results

It is possible to express the results of throughput time studies in many different ways, eg. the time that the marker first appears in the faeces, the time of peak throughput, the percentage of total marker recovered. Most workers on avian throughput, eg. Mattocks (1971), Owen (1975a), Ranwell and Downing (1959) have expressed throughput as a single time, ie. the first appearance of the marker in the faeces. However, due to the shortcomings of this method and also to allow comparison with other studies which describe throughput in a more detailed way, the results from these experiments were expressed in two main forms. Fig. 8.1 shows the amount of radioactivity (counts/ 100 secs.) passed out in the faeces against time for all six experiments. Each point on the graphs gives the number of counts passed out in the faeces in the previous approximately 20 minute period. Figure 8.2 shows the cumulative percentage recovery of radioactivity with time for these experiments, ie. the number of counts per 100 secs. passed out in the faeces as a percentage of the total recovered in the whole experiment. These two ways of expressing throughput allow one to calculate a number of different throughput measures: initial appearance, last appearance, peak throughput, 5%, 50%, 95% recovery of marker.

A comparison of the graphs in Figure 8.1 shows that the throughput time varied a great deal between certain experiments. Closer inspection shows that the throughput time was greatly increased in those experiments in which the experimental bird did not begin to feed until late in the experiment, ie. over 15 minutes from when the dose was administered. This was the case in experiments 1 and 4, the ones in which the bird had had little or no time to habituate to the experimental method, since the experiments were carried out in two batches (experiments 1-3 on consecutive days, a gap of 6 days, and then experiments 4-6 on consecutive days - see Methods). Thus, the experimental bird began feeding after 143 minutes and 38 minutes from the dose in experiments 1 and 4 respectively. In experiments 2,3,5 and 6, feeding always began within 14 minutes of the administration of the dose.

These results suggest that there is some form of 'push-on' effect of intensive feeding on throughput time, since food seems to be retained in the gut for longer periods if no feeding occurs. This effect is represented graphically in Figure 8.3, in which the time to the start of feeding is plotted against the time after the dose of the peak occurrence of the marker. The regression line is significant at $P < 0.02$ ($t=4.39$, d.f.$=4$).

Clearly the experimental method, which involved handling the bird, was stressful to the bird, but this stress could be reduced by repetition of the experiment. To examine just how much effect the experimental method had on the bird, certain feeding behaviours were compared between the experimental bird and the rest of the captive flock during experiments 5 and 6, ie. the

Figure 8.1

Amount of radioactivity passed out in the faeces of the experimental bird against time after the dose was administered. Arrows indicate the time when the bird started feeding (see p.92).

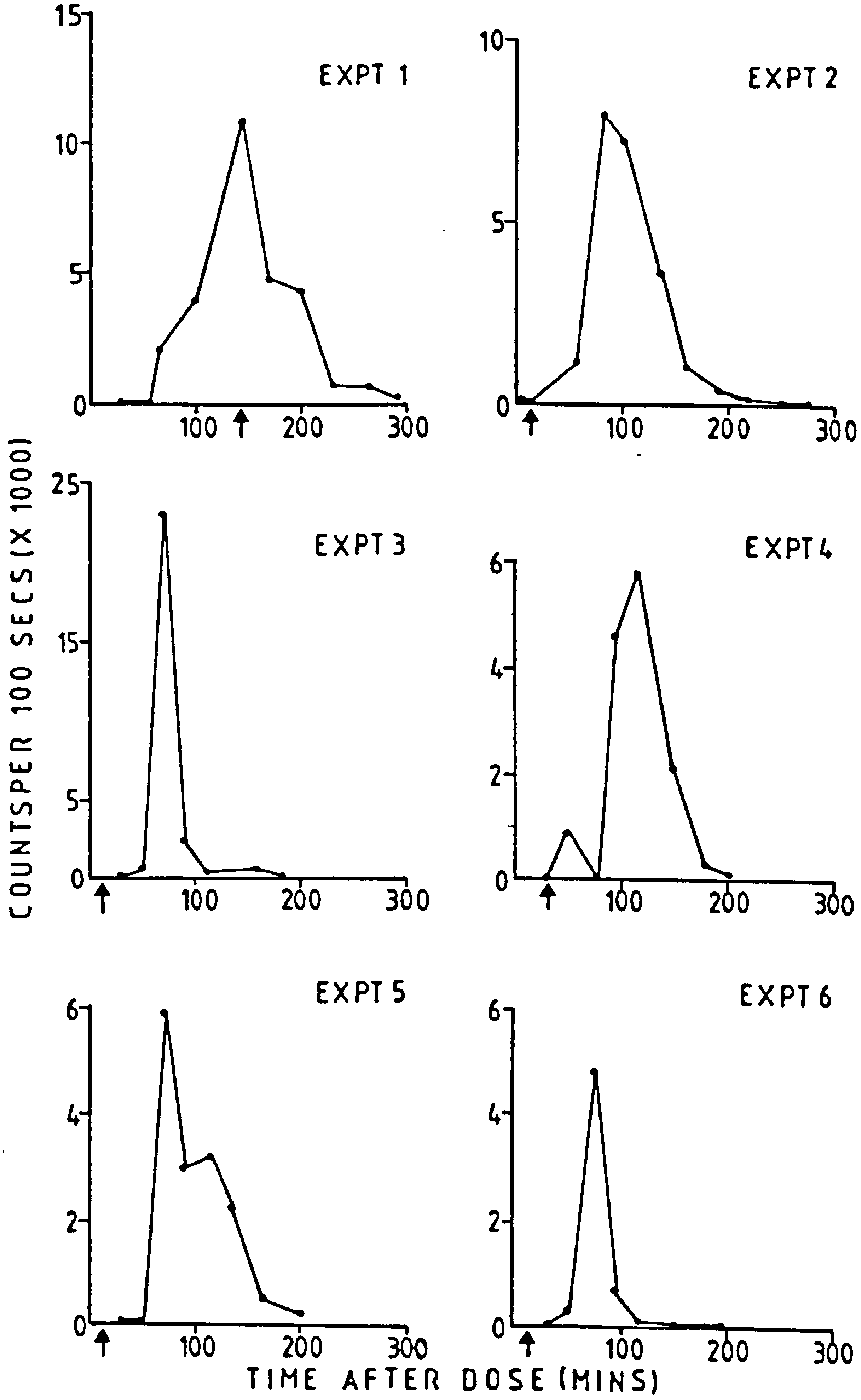

EXPT 1
15
10
5
0
100
200
300
EXPT 2
10
5
0
100
200
300
EXPT 3
25
15
5
0
100
200
300
EXPT 4
6
4
2
0
100
200
300
EXPT 5
6
4
2
0
100
200
300
EXPT 6
6
4
2
0
100
200
300
COUNTS PER 100 SECS (X 1000)
TIME AFTER DOSE (MINS)

Figure 8.2

Cumulative percentage recovery of radioactivity (ie. no. of counts/100 secs. passed out as a % of the total recovered in the whole experiment) against time after the dose was administered.

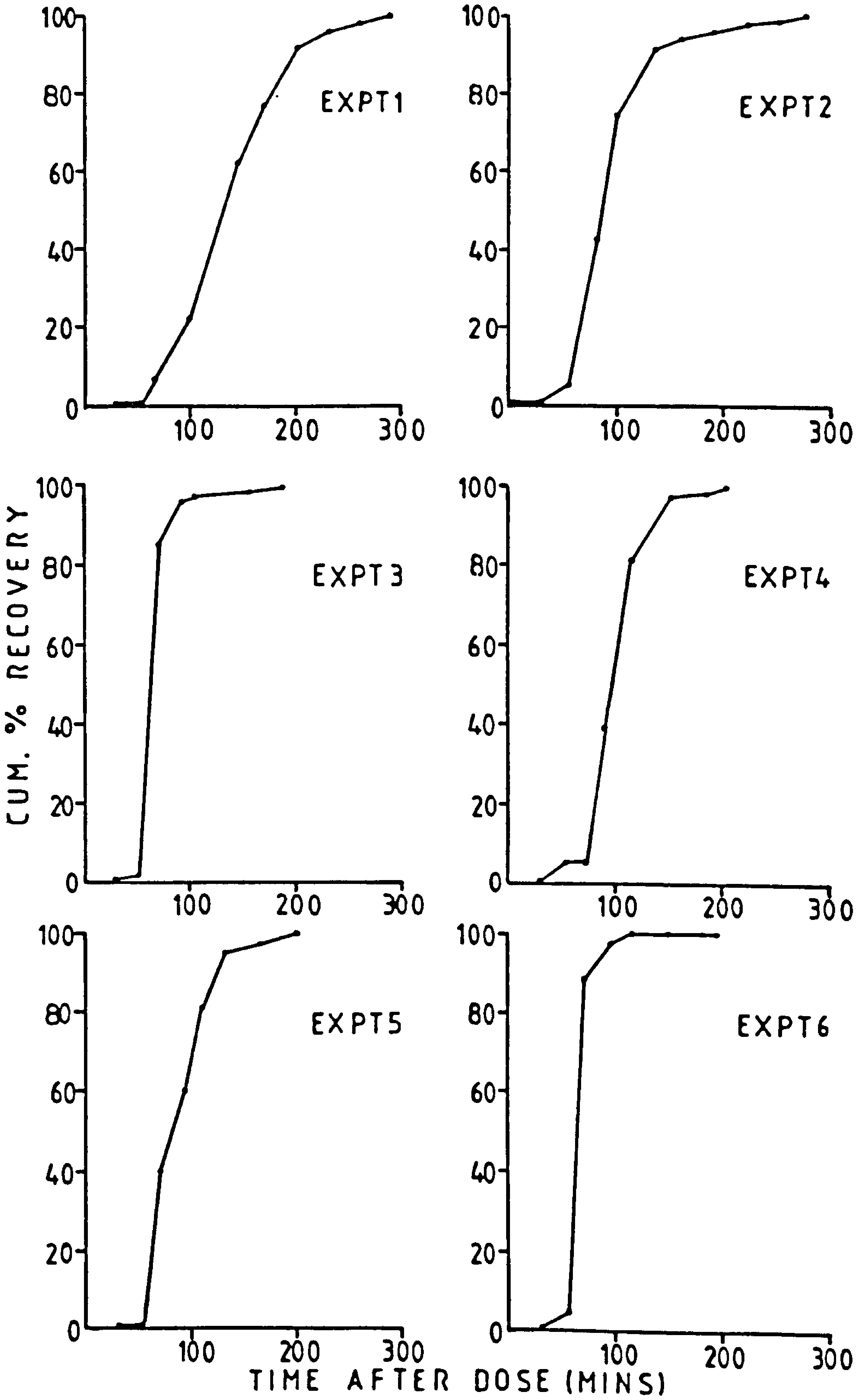
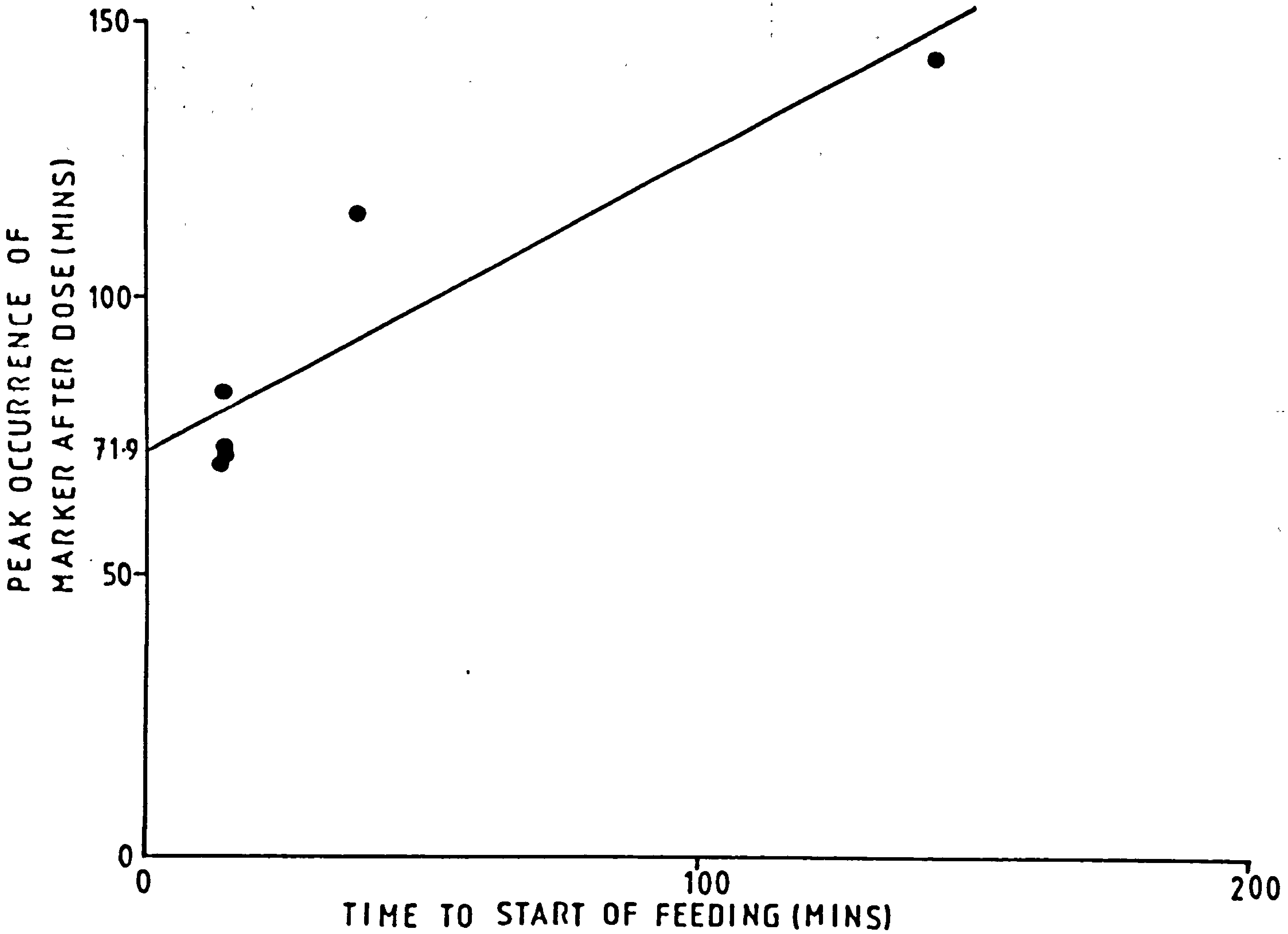

CUM. % RECOVERY
TIME AFTER DOSE (MINS)
EXPT1
EXPT2
EXPT3
EXPT4
EXPT5
EXPT6
0
20
40
60
80
100
100
200
300

Figure 8.3

Regression of peak occurrence of marker (see Fig. 8.1) on time to start of feeding for the six throughput experiments. The equation of the line is $y = 0.527x + 71.92$. The point at which the line crosses the y-axis (71.9) is the theoretical peak occurrence of the marker for a non-stressed bird (see p.93).


PEAK OCCURRENCE OF
MARKER AFTER DOSE (MINS)
150
100
71·9
50
0
0
100
200
TIME TO START OF FEEDING (MINS)

least stressful ones. Table 8.1 shows that the peck rate was significantly lower in the experimental bird, that there was little difference in feeding bout length, and that percentage time feeding was slightly lower in the experimental bird. The experimental method was clearly affecting some feeding behaviours, but having little effect on others, once the bird was more accustomed to the experience.

TABLE 8.1

Comparison of feeding behaviours between the experimental and other birds during experiments 5 and 6.

A) PECK RATE (pecks/min.)

	MEAN	S.E.	n	
EXPTL.	49.6	1.15	32	t = 2.737
OTHER	55.6	2.12	20	P < 0.01

B) FEEDING BOUT LENGTH (secs.)

	MEAN	S.E.	n	
EXPTL.	147	59.1	12	t = 1.210
OTHER	93.5	15.1	29	not significant

C) % TIME FEEDING (mins.)

	Total time feeding	Total time non-feeding	% time feeding
EXPTL.	29.4	14.9	66.4
OTHER	45.2	15.3	74.7

These results suggested two ways of reaching a figure for throughput time in captive wigeon. Firstly, one can simply take the mean of the results from the 4 experiments in which the bird was least stressed. Secondly, one can calculate a throughput figure for a theoretically non-stressed bird by using the point at which the regression line in Figure 8.3 crosses the y-axis as the throughput time figure (ie. no time to feeding - a bird which carries on feeding straight after the dose). This is done for the peak throughput time in Figure 8.3, but can be calculated for any throughput measure using the same analysis.

Table 8.2 gives figures for the initial appearance of the marker, peak occurrence of the marker, 50% cumulative recovery and 95% cumulative recovery of the marker, calculated by both the above methods. While the mean of the non-stressed birds method gives a sample of 4, the regression method obviously only gives one figure for each throughput measure. There is in fact very little difference between the two methods.

TABLE 8.2

Throughput times (mins.) for wigeon calculated from mean of unstressed birds and regression method.

	Initial appearance of marker	Peak occurrence of marker	50% cumulative recovery	95% cumulative recovery
Result from 4 non-stressed birds (mean ± s.e.)	31.3 ± 0.8	74.5 ± 2.9	73.5 ± 6.8	115 ± 16.1
Result from regression line of all birds	31.8	71.9	69.7	106.4

8.1.4 Discussion

The significant problems of an experimental technique which causes stress to the bird means that the throughput figures quoted above must be treated with a certain degree of caution. Furthermore, just how much relevance results from captive birds have for wild birds, must be questioned (this problem is dealt with more fully in Chapter 5).

However, even with these drawbacks, the methods used in this study have major advantages over simpler techniques in which only the first appearance of the marker is recorded. Even in a system as simple as the wildfowl gut, food does not simply enter the oesophagus, move through the gut, and emerge digested but intact in the faeces. The food does undergo some mixing and it is retained in the gut for variable amounts of time. Measures of throughput time from the cumulative recovery figures are, therefore, more biologically meaningful since they use two or more points on the excretion curve and therefore give a closer approximation to the average length of time that food remains in the alimentary tract (Burton et al 1979).

It is interesting to compare some of the results from this study with other research. Owen (1975a) reviews the literature on goose throughput times based on first appearance of the marker. This varies from 78 minutes to 121 minutes. In the studies on wigeon reported here, initial appearance of the marker was about 32 minutes. Burton et al (1979) quote a figure of 120 minutes for mean retention time for snow geese, while in this study 50% recovery was approximately 72 minutes and 95% recovery about 110 minutes. Wigeon therefore, in common with other wildfowl, have rapid throughput times compared to other herbivorous birds such as the Tetraonids, with throughput times of non-caecal material of around 3 hours (Gasaway et al 1975). Though in-depth comparison is difficult, and the shortcomings of this study have been pointed out, it may be the case that wigeon have shorter throughput times than even the geese.

A study of the throughput curves, Figure 8.1, suggests that the picture of the wildfowl gut as a single digestive compartment in which no mixing takes place (Owen 1975a) may not be quite correct, in wigeon at least. If this simple picture is correct, Sibly (1981) has pointed out that marked food particles would be defaecated at the same rate as they are eaten and for exactly the same length of time as that taken to eat them. While it is true that the experimental method used in this study did not allow a natural intake of food (the grass was however of normal bite size), about 90% of the marker was passed out in the faeces over a period lasting a least 40 minutes and normally 80-100 minutes. While Sibly's (1981) model is obviously over-simplified, this result does suggest that a certain degree of mixing is taking place.

Finally, the 'push-on' effect of continuous feeding on throughput of food, is probably best understood as a slowed rate of food passage when intake is reduced. This result would certainly concur with Drent et al's (1979) observation that retention time of geese increases (in their arctic breeding quarters) during rest bouts, and Sibly's (1981) hypothesis that food which is digested overnight should be retained longer in the gut, so that more energy can be extracted from it.

8.2 THE DIGESTIVE EFFICIENCY OF WIGEON

8.2.1 Introduction

The amount of energy which an animal can extract from its food is obviously of utmost importance to that animal. It affects a whole range of feeding behaviour variables including the area in which an animal will feed and the length of time for which it needs to feed.

Grazing geese are well known for their low digestive efficiences, (Marriot and Forbes 1970, Ebbinge et al 1975, Drent et al 1979). This is primarily due to their inability to digest cellulose to any great extent (Marriott and Forbes 1970, Mattocks 1971). Since many aspects of the wigeon's feeding biology eg. grazing behaviour, throughput time, diet, etc. were similar to those of the grazing geese, it was thought likely that the digestive efficiency of wigeon was also very low. In order to check on this, studies of the wigeon's digestive efficiency while feeding on grass pastures at Caerlaverock during the winter were undertaken.

8.2.2 Methods

A) Choice of method

Although the basic principles are the same, a large variety of techniques have been employed to assess digestive efficiency in wildfowl. Most of these have used captive birds and have calculated efficiency either by measuring the total food intake and the total faecal output over a number of days (Marriott and Forbes 1970, Burton et al 1979) or using a marker technique (Sugden 1973, Miller 1984). The latter technique tends to be used when it proves difficult to measure the total intake/ output of the study birds.

The captive flock was not used because firstly, it is difficult to conduct experiments on captive birds without stressing the subjects, as was found in the throughput experiments (Section 8.1). Secondly, Moss (1972) found that the caecum and small intestine of captive birds were shorter than in wild birds, and Owen (1975a) found that this also applied to gizzard, intestine and caecum in barnacle geese. Thus the digestive efficiency of captive birds is likely to be different from that of wild birds (Watson 1973). Finally, there is a simple method for assessing digestive efficiency in wild birds.

Following the methods of Moss and Parkinson (1972), Ebbinge et al (1975) and Drent et al (1979) developed techniques for assessing digestive efficiency in wild geese during studies conducted in the Netherlands. Since it is impossible to measure total intake and total output of wild birds, they used a marker technique. In principle any component of the food can be used as a reference substance. It is not essential that it is indigestable, only that the animal is in balance with respect to the marker over the period measured. Drent et al (1979) suggest four possible markers suitable for use with geese: fibre (since it is not digested), ash, magnesium (after Moss and Parkinson 1972) and chlorophyll. In this study attempts were made to use magnesium and fibre, but the techniques were fairly complex and the results inconsistent (in the case of magnesium this was possibly due to the fact that the wigeon were not in balance with respect to this element). Because of the difficulty of analysing for chlorophyll, Si-free ash was used as the marker. The silica was excluded from the ash weight because not all sand/ soil, picked up accidentally with the food samples will be removed by cleaning and (more importantly) wildfowl replace the grit in their gizzard by periodically passing it out with the faeces (M. Owen, pers. comm.).

There is however one major difficulty with this technique. Collection of food plants from the feeding area may not exactly reflect the food taken in by the bird. Errors can be minimised by collecting as much as possible only those plant parts which are being eaten by the birds, and by choosing a marker which is evenly distributed in the food plants. Even though this is probably the greatest source of error in the technique, Summers and Grieve (1982) found a difference of only 0.2% in the cell wall content of grass taken from the oesophagus of geese compared to that clipped directly from the feeding site.

B) Collection and analysis of samples

Grass and faecal samples were collected according to the techniques outlined on p.7. Samples were only collected if birds had been grazing in that area for several hours. Since throughput time in wigeon is about 1 hour (Section 8.1), the faecal samples collected in the area would very likely be from food eaten on the same site (Owen 1975a). In contrast to the collection of 'wigeon-grazed' grass for protein and fibre analysis (which was collected from a small area outside the exclosure, see Section 6.2) grass for digestive efficiency analysis was collected over the whole site, as were droppings.

In season 1, at least one sample (ie. grass and faeces) was collected each month. No account was taken of the site, as long as birds were regularly grazing there. In season 2 one sample was collected from each site once per month. In season 3 samples were collected in a similar way to season 1. In the final two seasons there was regular collection of samples to assess grass quality so that comparisons could be made between the protein/fibre content of the grass and its digestive efficiency.

Storage of samples was by the methods outlined on p.8. Samples were dried overnight at 80°C and analysed for ash and then for silica by the methods of Allen et al (1974). Two replicates of each sample were analysed, and the average of the results used. Digestive efficiency was calculated by the following formula (Drent et al 1979).

$$\text{D.E.} = 1 - \frac{(\text{concentration marker food})}{(\text{concentration marker faeces})} \times 100\%$$

8.2.3 Results

It is possible to express digestive efficiency in relation to several different variables: dry weight of the food; sand-free weight of the food; organic matter of the food (ash and sand-free). Different authors have used different terms, eg. Marriott and Forbes (1970) use dry weight, while Drent et al (1979) express digestive efficiency in relation to organic matter. The effect of these different methods is to increase or decrease average digestive efficiency in all samples by a similar amount. It does not therefore greatly affect comparisons between samples. For instance, in these results digestive efficiency (organic matter) is approximately 4% greater than digestive efficiency (dry weight). In these studies digestive efficiency is expressed in terms of dry weight because is was more useful for the studies reported in Chapter 3.

In all 32 samples were assessed for digestive efficiency: 8 from season 1, 15 from season 2, and 9 from season 3. However, in 8 of these samples the concentration of the marker (Si-free ash) was lower than in the food sample, giving a nonsense negative digestive efficiency (see Table 8.3). In these samples the food marker concentration was similar to that in normal samples, but the faecal marker concentration was greatly reduced from a normal of around 7-10% to about 3-5%. All samples giving results like this were checked with at least one more replicate, but no mistakes in the chemical analyses were found. It is difficult to explain these anomalous results. If the food marker concentration had greatly increased, one could have hypothesized that the collection of the food samples was not reflecting that taken in by the wigeon, ie. collection was too indiscriminate. However, this was not the case. Possibly the anomalous faecal samples were not from food eaten on that site. However, the faecal marker concentration was so low in these samples that no food marker concentration determined in this study would have produced a sensible result when compared with the anomalous faecal marker concentrations. Whatever the reason, these results were left out of the digestive efficiency calculations.

Table 8.3

Digestive efficiency samples for all 3 seasons. % Si-free ash figures are means of at least two replicates.

Date	% Si-Free Ash		D.E.
	Grass	Faeces	
Season 1			
11/12/80	7.47	3.62	-
18/12/80	8.58	5.06	-
22/01/81	6.53	3.50	-
05/02/81	6.95	8.81	21.1
21/02/81	5.61	8.11	30.8
04/03/81	6.32	8.00	21.0
18/03/81	5.94	8.06	26.3
01/04/81	6.59	9.56	31.1
Season 2			
09/10/81	5.94	5.19	-
10/11/81	5.79	8.28	30.1
11/11/81	5.02	5.68	11.6
11/11/81	4.12	4.85	15.1
12/11/81	4.61	8.33	44.7
24/11/81	6.28	8.67	27.6
30/12/81	6.29	3.50	-
27/01/82	5.97	7.07	15.6
Season 2 cont.			
28/01/82	5.92	7.66	22.7
02/03/82	5.50	9.45	41.8
25/03/82	5.79	8.83	34.4
30/03/82	4.82	9.35	48.4
31/03/82	6.13	8.50	27.9
31/03/82	5.41	8.85	38.9
01/04/82	5.63	8.53	33.9
Season 3			
08/10/82	5.69	10.60	46.3
03/11/82	5.91	4.24	-
05/12/82	5.68	6.40	11.3
17/12/82	4.34	3.58	-
18/01/83	6.60	8.15	19.0
19/01/83	6.62	9.40	29.6
18/02/83	6.65	10.28	35.3
02/03/83	4.30	4.26	-
06/04/83	6.22	8.49	26.7

The total sample size was therefore 24 (all positive digestive efficiency). The mean efficiency was found to be 28.8% ± 2.5.

The range was large, 11.3% to 48.4%, probably reflecting the great variety in the quality of the grass. This was checked by regressing the digestive efficiency results from seasons 2 and 3, against three measures of food quality. However, no significant relationships were found with protein content (t=0.473, d.f.=17, n.s.), grass quality (protein/ fibre) (t=1.38, d.f.=17, n.s.) or fibre (t=1.70, d.f.=17, n.s.).

8.2.4 Discussion

While there are a good number of studies quoting figures for digestive efficiency (or metabolizable energy, ie. energy obtained per gram of food) in captive wildfowl fed on artificial or semi-natural diets, only three studies give figures for digestive efficiency in wild birds using the techniques outlined above. Ebbinge et al (1975) calculated the digestive efficiency of barnacle geese to be 21.7% (dry weight calculation) and Drent et al (1979) found that brent geese digested between 31 and 37% of the organic matter of their food, dependent on food species. Finally, Summers and Grieve (1982) calculated organic matter digestive efficiency of upland and ruddy-headed geese in the Falklands to be 27-34%. According to calculations in this work, the results from the latter two studies would be equivalent to dry weight digestive efficiency of 23-33%. Sibly (1981) quotes a generalised figure of 25% (dry weight) for digestive efficiency in geese in winter. Captive geese seem to digest grass with a similar low efficiency, eg. 22-28% (dry weight) in a study of Cape Barren geese (Marriott and Forbes 1970).

It is clear therefore that with a mean dry weight digestive efficiency of 28.8% wigeon have a similar digestive ability to the grazing geese.

8.3 GUT MORPHOLOGY ALTERATION IN WIGEON

8.3.1 Introduction

The importance of throughput time and digestive efficiency to nutrient intake in wigeon is clear. The importance of gut morphology is not quite so obvious. In the last 20 years, however, a large number of studies, especially on galliforms and wildfowl, have shown that the size of the gut (measured by length or weight) may radically alter according to the type of diet. This effect was first reported as a seasonal variation in the length of the gut of certain species, eg. towhees (Pipilio erythrophthalmus) (Davis 1961) spruce grouse (Dendragapus canadensis) (Pendergast and Boag 1973) snow geese (Anser caerulescens) (Burton et al 1979) and starlings (Al Jaborae 1980). Most authors correlated these changes with seasonal alteration in the diet of the birds, which normally changed from primarily animal or fruit material in the summer to mainly foliage in the winter. Thus, a bulkier more fibrous diet was associated with longer guts. This effect was also found in purely folivorous species in which the level of fibre in the foliage increased during the winter months (eg. Burton et al 1979, Paulus 1982).

Alterations in gut morphology as a consequence of diet have also been reported in different species of closely related birds (Leopold 1953, Moss 1974) and in captive birds when fed on a high quality captive diet (Moss 1972, Owen 1975a). Several studies have also confirmed this result experimentally. For example, Miller (1975) fed diets of different fibre content to groups of captive mallard and found that gut size was larger in the high fibre diet birds. Kenward and Sibly (1978) found that captive woodpigeons eating sprout crowns had longer guts than those fed on wheat.

The exact section of the gut which alters differs from study to study. However, most authors report alterations in the size of the gizzard, small intestine and caeca. Large intestine tends to show much smaller variation if any at all.

The cause of these effects is not fully understood. An increase in fibre in the diet normally results in birds taking in more food. For example, Miller (1975) found that not only did gut length increase in mallard on a high fibre diet, but that the food consumption of these birds also increased. Thus gut length increases could simply be due to the increased diet bulk. Savoury and Gentle (1976) reported that gut size, especially caecum, of Japanese quail (Coturnix japonica) increased in size on a high fibre diet. However, Fenna and Boag (1974) working on the same species found no change in gut size with an alteration in food quality (food consumption was roughly similar) but did find an increase in intestine and caecum length with an increase in food quantity (food quantity alteration was achieved by keeping the birds in different temperature conditions, so that food quality did not need to be altered).

The functional significance of an alteration in gut size with diet is a matter of some speculation. The most likely explanation is that as diet quality decreases so digestive efficiency decreases (see section 8.2). This results in an increase in food consumption and a consequent increase in gut capacity to cope with this extra food, ie. more food can be processed each day (Sibly 1981). When food quality increases again birds reduce their gut size, since weight is at a premium in a flying animal.

Gut length, therefore, may be of great importance in a purely vegetarian species, which theoretically, should face major problems in acquiring sufficient energetic intake during the winter months. Hunter-killed wigeon were therefore collected to see whether any alterations in gut morphology with season occurred. The initial hypotheses were: 1) As the winter progresses the quality of food may decrease resulting in increased food intake and gut size, or 2) the generally lower winter temperatures may increase food intake and gut size. Data on bird condition, and size, were also collected to compare with the gut morphology results.

8.3.2 Methods

A) Sources of birds

In season 1, 20 guts were collected from hotels and guest houses in the Caerlaverock area. It was realised that the number of guts obtainable from this area was not going to be sufficient for the study and consequently, in seasons 2 and 3 birds were also bought from game dealers. No dealers handling sufficient numbers of wigeon were found in the Solway area. Contact was therefore made with dealers on the east coast, one in Duns, S E Scotland and the other in Wooler, Northumberland. The birds from Duns were shot primarily at inland flight ponds, while those from Wooler were from Lindisfarne NNR. While this obviously broadened out the study area, it was not considered a problem, since the exact source of birds shot in the Caerlaverock area was also varied, eg. foreshore and inland. Thus, the results from this study deal with birds from a variety of habitats and probably living on a range of different foods. In season 2, a total of 32 birds were examined, 15 from Caerlaverock, 5 from Wooler and 12 from Duns. In the final season, a total of 69 birds were examined, 15 from Caerlaverock, 8 from Wooler and 46 from Duns. This gave a total sample size of 121 birds over all three seasons.

B) Body measurements

Measurements from Caerlaverock birds were carried out at the hotel, and the gut extacted and retained. The eviscerated body was returned to the wildfowler. Duns and Wooler birds were kept by the dealer, frozen and wrapped in plastic until they were collected (once or twice a season). Thus all measurements were taken from defrosted birds.

The bird was weighed using a 1 kg 'pesola' balance. Then measurements were taken of:

body length - from tip of bill to tip of longest tail feather while bird was stretched on its front (to nearest mm)
total skull - from bill tip to back of head (to nearest 0.5mm)
wing span - from tip of longest primary to tip of longest primary while bird was stretched on its back (to nearest mm)
wing length - maximum chord, ie. with wing completely flattened and primaries straightened on ruler (to nearest mm)
tarsus length - (to nearest mm). this was measured in the first season, but was found not to correlate well with the other size measurements and was therefore left out in subsequent seasons.

Data on sex, age (ie. Juv/Ad.) and date shot was collected. The only difficulty with these variables was assessing age of females. This was done primarily on the basis that juvenile (ie. first year) birds have notched tail feathers until their first moult. (C. Campbell, pers. comm.).

C) Gut measurements

Guts were extracted based on the technique of Harrison (1960). However, no attempt was made to extract the oesophagus intact, as this was found to be extremely difficult. Thus the gut was severed at the proventriculus and at the point where the large intestine joins the cloaca. The intestines were freed from their mesenteries and laid along a ruler in as straight a line as could be achieved without stretching (Davis 1961). Although this technique is subject to some variability, reasonable uniformity was achieved since the same person took all the measurements.

Measurements taken were based on those of Leopold (1953). They were: (see Figure 8.4)

gizzard - opened out and contents removed. Gizzard was washed and dried and then weighed to nearest 0.5g.
small intestine - from junction with gizzard to junction with caecum (to nearest mm).
caeca - from junction with small intestine to tip (to nearest mm). Both were always measured.
large intestine - from caecal junction to junction with cloaca, excluding the cloaca itself (to nearest mm).

D) Estimation of bird size

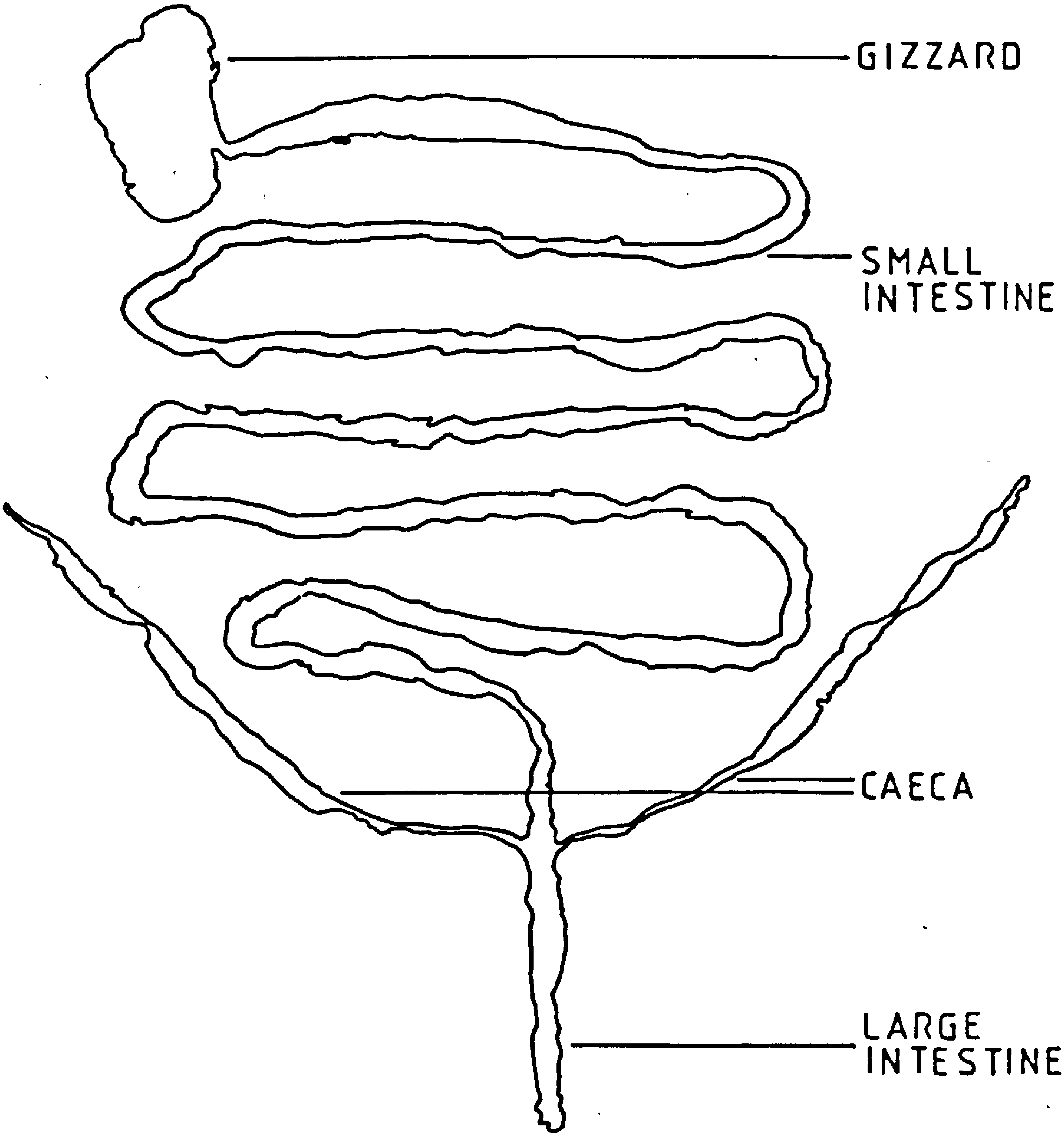
In the studies referred to in the introduction, none of the workers took individual bird size into account. Thus, the gut morphology changes which they found were not related to the structual size of the individual birds. To control for this variable, and also to allow an estimation of bird condition, a size index was calculated for each wigeon in the present study.

Several workers have used a single body measurement to assess the size of a bird, often relating this to the fat (and water)-free weight (Connel et al 1960, Ward 1969, Mascher & Marcstrom 1976). The relationship is normally very close, so that the fat-free weight can be calculated from wing or bill length and fat depots calculated from total body weight. In other studies two body measurements were used, eg. Wishart (1979) used body length and wing length in a study of American wigeon, while Davidson (1983) used wing length and bill length for several wader species.

Since in this study fat-free weights were not available, it was decided to use as much of the body size information as possible to calculate a size index for each bird. The best combination of the four recorded body measurements was calculated using factor analysis. This technique uses a correlation matrix between all variables to assess if an underlying pattern of relationships exists, and then enables the data to be represented as a 'factor score' (Nie et al 1975). To do this a 'factor score coefficient' was calculated for each body measurement variable. Thus, a variable which correlated well with other body variables will have a high 'factor score coefficient' while a variable with little relationship to the other body variables will have a low coefficient. These coefficients were 0.443 for wingspan, 0.312

Figure 8.4

Diagram of dissected wigeon gut showing the parts of the gut measured in the study (see p.102). Scale approximately 1:2.


GIZZARD
SMALL INTESTINE
CAECA
LARGE INTESTINE

for winglength, 0.220 for body length and 0.135 for total skull. These coefficients were then used to generate a 'factor score' for each bird, this being $az_1 + bz_2 + cz_3$ etc., where a, b, c, etc. are the relevant factor score coefficients and z_1, z_2, z_3, etc. are the respective standardised body variables. Standardised body variables are used as opposed to actual body measurements in order to correct for the disproportionate size of some measurements, eg. wingspan was around 10 times greater than total skull. The standardised body variable is:

$$\left(\frac{\text{variable - mean variable}}{\text{s.d. variable}} \right)$$

This 'factor score' or size index was compared with the individual body measurements in order to ascertain which was the best estimate of body size. This was done by comparing their relationships with the total body weight of each bird. Size index had the closest correlation with weight ($r=0.607$) compared to the other body measurements ($0.462<r<0.577$). Therefore, although this size index was not compared with fat-free bird weights (ie. skeletal size) it was considered to give the best available approximation to this variable.

While this linear measurement of size was considered adequate for correcting linear gut measurements, it was noted that several authors used $(\text{linear measurement})^3$ or a similar calculation to correct total weight in order to derive an estimate of condition eg. Evans and Smith (1975), Fogden and Fogden (1979), Davidson (1983). The rationale for this is that while size is a linear measurement, weight is a cubic one and so linear measurement needs to be cubed to allow comparison. However, this is not necessarily the case. For instance, Prange et al (1979) found that body mass scaled to $(\text{humerus length})^2$. In this study the relationship between weight and size index^3 ($r=0.410$) was not as good as that between weight and size index ($r=0.607$). It was therefore decided to use the linear size measurement to correct body and gizzard weights as well as gut lengths.

8.3.3 Results

A) General

In the following results, several points should be noted:

i) Individual caecum measurements exhibited similar relationships to total caecum (ie. sum of both caeca) in the following results. Thus, the results for total caecum only are given.

ii) In two of the 121 birds, the lower gut had been damaged by shot. The lower intestines ie. small intestine, caeca, large intestine, of these birds were not included in the analysis but their gizzards were.

iii) All gut sizes refer to corrected gut sizes (see below).

iv) Date of collection was separated into months, ie. September to February (the open season for wildfowl in Britain), to give six points on the axis.

v) The original data is given in Appendix 2.

B) Corrections for bird size

In order to examine whether bird size had an effect on gut size, the relationship between size index (from the factor analysis) and each gut variable was examined. The correlation coefficients are shown in Table 8.4. All showed a positive relationship with size except large intestine. Therefore each gut variable except large intestine was corrected for bird size by calculating the deviation from the size/ gut variable regression line, ie. the residual variation in gut size after bird size was taken into account.

TABLE 8.4

Correlations between gut size and size index.

GUT VARIABLE	CORRELATION WITH SIZE INDEX (r)	SIGNIFICANCE (P)	n
Gizzard	0.290	0.0006	121
Small intestine	0.314	0.0003	119
Total caecum	0.174	0.029	119
Large intestine	0.115	N.S.	119

A condition index for birds, defined as fitness for present and future needs (Owen and Cook 1977) was estimated from their weight in the same way as above, ie. the residual variation in weight, after bird size (from the size/ weight regression line) was taken into account.

C) Variation with date

The effect of date on condition index is shown in Figure 8.5. There is a general tendency for condition index to increase from September to January and then decrease in February.

The associations between gut size and date are shown in Table 8.5.

Figure 8.5

Effect of time in season on condition index (mean ± 1 s.e.) of wigeon. Condition index is weight corrected for size (see p.104).

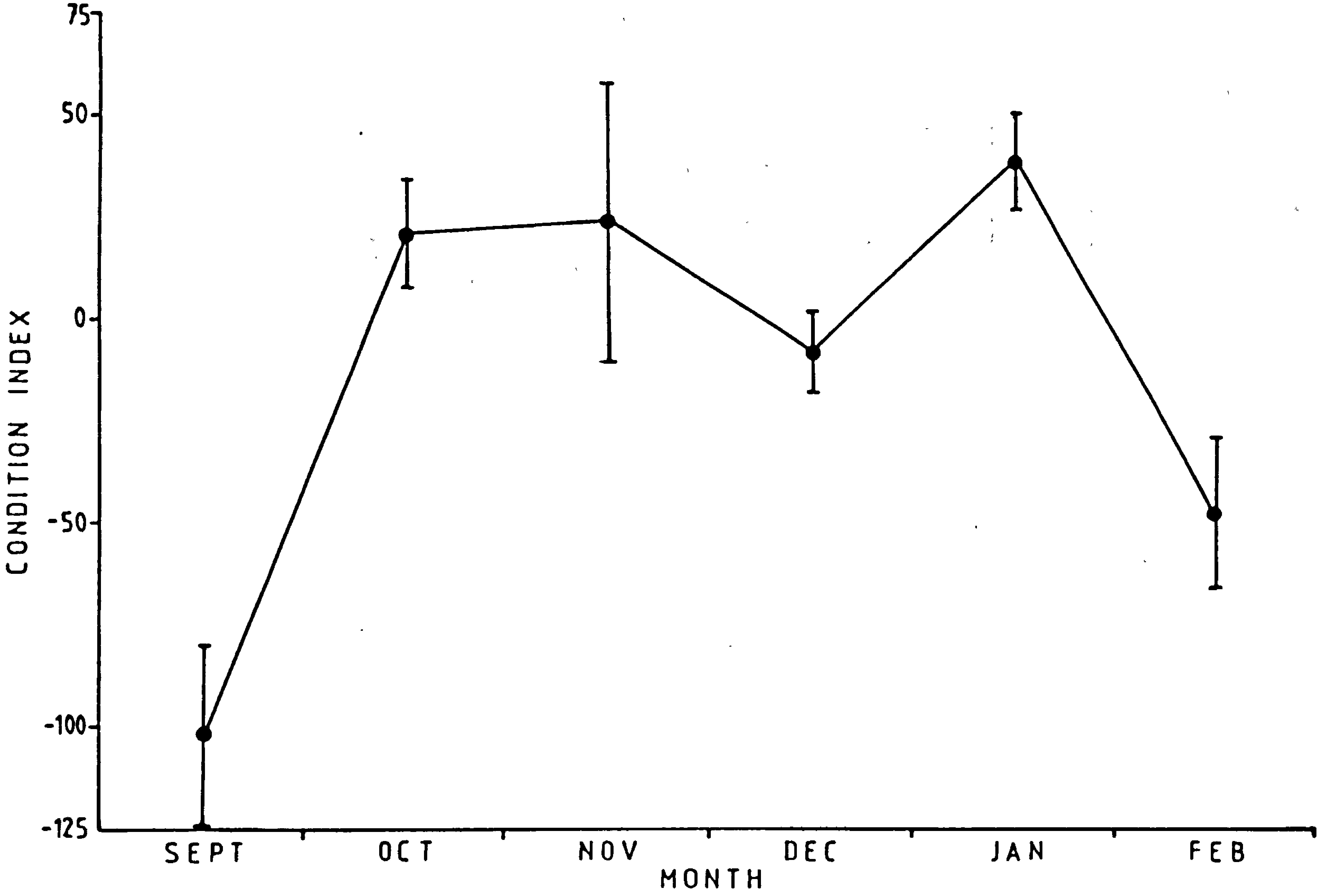

75
50
0
-50
-100
-125
CONDITION INDEX
SEPT
OCT
NOV
DEC
JAN
FEB
MONTH

TABLE 8.5

Correlations between gut size and date.

GUT VARIABLE	CORRELATION WITH DATE (r)	SIGNIFICANCE (P)	n
Gizzard	- 0.100	N.S.	121
Small intestine	- 0.032	N.S.	119
Total caecum	0.201	0.014	119
Large intestine	- 0.146	N.S.	119

None are significant except total caecum which shows a tendency to increase in length through the season. However, when an analysis of covariance was carried out on this data with caecum entered as the dependent variable, date and bird condition as covariates, and sex and age as factors (Nie et al 1975), date was found to have a non-significant effect on caecum (F=1.980, P=0.162) ie. the significant correlation was due to the confounding effects of other variables.

D) Gut size variation with condition index

The relationships between gut size and condition index are shown in Table 8.6. All gut variables showed correlations with condition index except large intestine.

TABLE 8.6

Correlations between gut size and condition index.

GUT VARIABLE	CORRELATION WITH CONDITION INDEX (r)	SIGNIFICANCE (P)	n
Gizzard	0.209	0.011	121
Small intestine	0.239	0.004	119
Total caecum	0.334	0.0001	119
Large intestine (not corrected)	0.099	N.S.	119

A check was carried out to ensure that the method of correcting for body size (which was the same for both the condition index and the gut variables) had not produced a spurious correlation between condition index and gut size. This was done by studying the relationships between size index and the gut variables plus condition index (Table 8.7). No significant relationships were found, ie. size index was not acting as a confounding variable.

TABLE 8.7

Correlations between condition index plus gut size and size index.

MEASUREMENT	CORRELATION WITH SIZE INDEX (r)	SIGNIFICANCE (P)	n
Condition index	0.00004	N.S.	121
Gizzard	- 0.00005	N.S.	121
Small intestine	0.00002	N.S.	119
Total caecum	0.00001	N.S.	119

E) Effect of sex and age on gut size/condition index relationships

The effect of sex on the gut size/ condition index relationships was studied by separating the data into males and females and looking at the relationships within these groups alone. The results are shown in Table 8.8. The effect of sex is very significant indeed: males show no significant relationships at all, while females show highly significant relationships.

TABLE 8.8

Correlations between gut size and condition index (separated for male and female).

GUT VARIABLE	MALE			FEMALE		
	CORRELATION WITH CONDITION INDEX (r)	SIGNIF. (P)	n	CORRELATION WITH CONDITION INDEX (r)	SIGNIF. (P)	n
Gizzard	0.033	N.S.	56	0.334	0.003	65
Sm. intest.	-0.006	N.S.	54	0.401	0.0005	65
Total caecum	-0.052	N.S.	54	0.532	<0.00001	65
Lg. intest.	0.122	N.S.	54	0.113	N.S.	65

The effect of age on the relationships was checked by looking at adults and juveniles independently of sex, ie. adult males, adult females, juvenile males and juvenile females - see Tables 8.9a and b. Basically, age had little effect on the relationships since all male correlations were not significant, and all female ones (except adult female gizzard) were. The relationships in adult females were, however, generally less significant than those in juvenile females.

TABLE 8.9a

Correlations between gut size and condition index (separated for sex and age).

GUT VARIABLE	ADULT MALE			JUVENILE MALE		
	CORRELATION WITH CONDITION INDEX (r)	SIGNIF. (P)	n	CORRELATION WITH CONDITION INDEX (r)	SIGNIF. (P)	n
Gizzard	0.226	N.S.	31	-0.233	N.S.	25
Sm. intest.	-0.100	N.S.	31	0.126	N.S.	23
Total caecum	0.037	N.S.	31	-0.197	N.S.	23
Lg. intest.	0.353	N.S.	31	-0.198	N.S.	23

TABLE 8.9b

GUT VARIABLE	ADULT FEMALE			JUVENILE FEMALE		
	CORRELATION WITH CONDITION INDEX (r)	SIGNIF. (P)	n	CORRELATION WITH CONDITION INDEX (r)	SIGNIF. (P)	n
Gizzard	-0.090	N.S.	24	0.483	0.001	41
Sm. intest.	0.380	0.05	24	0.521	0.0005	41
Total caecum	0.471	0.02	24	0.432	0.004	41
Lg. intest.	-0.159	N.S.	24	0.366	0.01	41

In order to study this effect of sex further, male and female weight, size, condition and gut sizes were compared (Table 8.10). The results show that, in terms of body weight, size and condition, males are significantly greater than females. In relation to gut size, the above is true only for caecum.

TABLE 8.10

Differences between sexes in body variables and gut sizes.

VARIABLE	MALE (±1s.e.)	FEMALE (±1s.e.)	T-VALUE	SIGNIF. (P)
Weight (g)	773.9 ± 9.3	674.2 ± 10.5	6.97	< 0.001
Size Index	0.560 ± 0.09	-0.483 ± 0.10	7.65	< 0.001
Condition Index (g)	20.2 ± 8.5	-17.4 ± 9.9	2.83	0.005
Gizzard (g)	0.389 ± 1.01	-0.332 ± 0.86	0.54	N.S.
Sm. Intest. (mm)	-2.08 ± 17.69	1.83 ± 18.09	0.15	N.S.
Total Caecum (mm)	14.95 ± 9.27	-12.38 ± 8.70	2.14	0.034
Lg. Intest. (mm)	98.80 ± 1.75	100.34 ± 1.71	0.63	N.S.

While these results are interesting in themselves, the sex differences in condition and gut size suggested a possible reason for the above sex effect: the condition/ gut size relationship is found only in low condition or small gutsize birds and has nothing to do with sex, ie. the fact that females show this relationship is simply due to the fact that they tend to be in poorer body condition or have smaller guts.

This theory was tested by dividing the data into birds in poor condition and those in good condition, and birds with short guts and long guts. Thus, the categories examined in this analysis were:

male: condition < 0
condition > 0
gutsize < 0
gutsize > 0

and female: condition < 0
condition > 0
gutsize < 0
gutsize > 0

The relationships between condition and gut size were then investigated in these separate categories. The results were not uniform: the condition/ gutsize correlations in males were more significant in good condition/ large gutsize birds, but in females were more significant in poor condition/ small gutsize birds. However, it was clear that the sex effect in the condition/ gutsize relationship (Table 8.8) was not caused by sexual differences in condition and gutsize. There therefore seems to be a genuine sex effect in this relationship, with females exhibiting a highly significant relationship and males showing no relationship at all.

8.3.4 Discussion

A) Variation in condition index during winter

Most studies of seasonal weight or condition change in birds (and some mammals) wintering in northern latitudes report an increase in weight during the winter months (King and Farner 1966, Pendergast and Boag 1973, Evans and Smith 1975, Davidson 1979, Smith et al 1980, Coulson et al 1983). This increase in weight is primarily due to an increase in lipid levels (Evans and Smith 1975, Davidson 1982).

Seasonal variation in the condition index of birds raises two main questions. The first of these is: what is the function of increased weight during winter? This assumes that increased weight is generally a disadvantage to an animal due to costs of maintenance of an energy reserve, increased difficulty of movement for predator escape, etc. (Pond 1981), but that during the winter the advantages of increased lipid levels outweigh the disadvantages. In wintering birds, there are currently two main hypotheses as to this function: a) the fat is stored as an insulation layer against the generally lower winter temperatures (King and Farner 1966, Coulson et al 1983); b) it is stored as an insurance against reduced food intake due to severe weather or reduced food availability (Dugan et al 1981). These hypotheses are certainly not exclusive, but suggestions as to the primary function of winter fattening can be made based on the pattern of seasonal weight changes. Thus, if hypothesis a), ie. thermoregulation, is the most important, then one would expect highest weights to be found during the months of lowest temperatures. In wigeon, as in many waders (Evans and Smith 1975, Davidson 1979) this does not seem to be the case, since wigeon weights were lowest (outside the post-moult and migration September weights) in the two coldest months - December and February (Table 8.11 and Figure 8.5).

TABLE 8.11

Mean monthly minimum temperature (1980-1983)

(from Crichton Royal Meteorological Station - c. 6 miles from Caerlaverock)

MONTH	SEPTEMBER	OCTOBER	NOVEMBER	DECEMBER	JANUARY	FEBRUARY
TEMP. (°C)	9.9	4.5	3.3	-0.5*	1.3	0.2

* mainly caused by very low temperatures in December 1981.

The second question which these seasonal weight changes raise is: if these weight increases are an insurance against low food intake (hypothesis b) then what type of environmental conditions are they insuring against? Possibilities include short daylength, low temperatures and high winds, all of which could reduce food availability or time for foraging. Some insight can be gained as to which of the above is important to each species by again studying the pattern of seasonal weight changes. Since these reserves are an insurance against poor conditions, they are likely to be genetically 'pre-programmed' to be greatest at the time of year when the most difficult conditions are most likely to occur (Dugan et al 1981). Thus, if daylength is most important one would expect weight to be highest in December (Evans and Smith 1975); if windspeed, then weights should be greatest in November/ December (Dugan et al 1981); if temperature, then weight should be highest in February (Dugan et al 1981). The wigeon condition changes reported here are not conclusive enough to identify clearly which of the above is most important. However, it seems unlikely that temperature is the main factor since birds do not have large insurance reserves in February. Again, it is unlikely that daylength is the overriding factor, since wigeon are capable of nocturnal foraging in many situations (Owen 1973b, Owen and Williams 1976, Chapter 3). These arguments would therefore suggest that wigeon lay down 'insurance' fat to cover them in times of high winds, which make feeding difficult. This result has been found in several wader species (Dugan et al 1981). However, although no data was collected on the effect of high winds on wigeon feeding, this theory does seem counter-intuitive, since a small squat bird feeding on a ubiquitous food supply is unlikely to be greatly affected by strong winds. One possibility is that high winds could stop birds flying to the best feeding sites.

There is, however, an alternative explanation for this pattern of weight change. Wigeon put on weight during winter as an insurance against difficult conditions (whatever they may be) or for thermoregulation. However, towards the end of the winter, when grass biomass is greatly reduced and temperatures low, birds tend to lose condition. Thus, wigeon are always attempting to keep their weight up during winter to a 'regulated' level, but are unable to do so in difficult conditions.

This theory is the best explanation of the available data, and would suggest that towards the end of the winter, wigeon do indeed face problems in obtaining sufficient food intake to keep their weight up to a level similar to that attained in the earlier part of the winter. Some data from brent geese support this hypothesis, since the weight of this species remains high until late March (Boudewijn 1984). Larger grazing wildfowl may therefore be able to remain in good condition more easily than smaller-sized species (see Chapter 3). This effect of reduced weight in difficult conditions in the middle to end of winter has also been found in mallard (Folk et al 1966, Owen & Cook 1977), grey plover (Dugan et al 1981) and in redshank (Davidson 1982).

B) Gut size variation with date

Although the main reason for carrying out this study had been to look for seasonal effects on gut size, no such effects were found except in caecum length. However, this latter result was found to be due to the confounding effect of body condition. The most likely reason why this relationship is not found in wigeon is that the wigeon's diet does not necessarily become more fibrous and therefore bulkier as the winter progresses. Indeed at Caerlaverock the diet tends to increase in quality as the season progresses (see Figures 6.3 and 6.4). Thus, one would not expect to find an increase in gut size, since diet bulk is not necessarily increasing as the season progresses.

C) Changes in gut size with condition index

One of the most interesting results reported in this section is the relationship between gut size and condition index found in female birds only. This relationship cannot be caused by food quality. A more plausible explanation is that birds with long guts (either genotypically or phenotypically derived) are able to attain better condition than birds with short guts, since they are able to process more food per unit time or are able to extract more nutrients from a limited amount of food (Watson 1973). However this theory does not explain the extremely obvious sex differences in this effect: the above should apply to males as much as it does to females.

Apart from these two explanations, there are three other situations reported in the literature which may lead to alternations in gut size:

i) reduced food intake can lead to increased gut size as birds attempt to extract more nutrients from their diet (Breitenbach et al 1963).
ii) gutsize may decrease in incubating female wildfowl which have no access to food, due to atrophy through disuse or active catabolism of gut proteins (Ankney 1977, Korshgen 1977).
iii) birds in a period of hyperphagia may increase gut size either to increase alimentary efficiency eg. in young birds (Kirkpatrick 1944) or so that the gut may act as a nutrient store eg. in pre-nesting female wildfowl (Ankney 1977, Korshgen 1977).

The only one of these reported effects which would fit the data on gut size/ bird condition reported here is the final one, ie. the gut is acting as a nutrient store in female wigeon. This hypothesis would explain the initially puzzling fact that this relationship is found only in females. Thus, birds which are in good condition (for whatever reason) in terms of weight (ie. lipid) are also likely to be in good condition in terms of protein levels. If a female wigeon finds itself in this situation one method of storing protein for future breeding requirements (Newton 1977) would be to enlarge the intestine or gizzard, along with, for example, the pectoral muscle. This would lead to the observed correlation between condition index and gut size. Males, on the other hand, would gain no advantage in storing protein in this way, and would in fact suffer the disadvantage of higher metabolic costs, when maintaining a large gut (Moss 1974).

Moss (1977) reports a study on intestine length in rock ptarmigan which found that female intestine length increased markedly in spring. The author suggested that the gut may act as a protein store. Korschgen (1977), in a study of eiders in N America, clearly showed that females lost significant amounts of protein (mainly from the pectoral muscles and the gut) as incubation proceeded. This was because the female eiders were unable to feed during this time. This was not simply atrophy due to disuse, but was most likely the result of active catabolism of these proteins for egg formation or metabolic requirements during incubation. The only data available on feeding by egg-laying wigeon (Danell & Sjoberg 1977, 1982) suggests that female wigeon do most probably rely on stored protein, for ovogenesis at least. Protein storage in the gut could therefore be of great importance in this species. (This theory, the 'condition hypothesis' is discussed more fully in Chapter 6).

While this hypothesis is certainly the best explanation of this very striking relationship, a problem remains. Most workers report that nutrient storage for breeding occurs in a short period of hyperphagia in the month or so before breeding (Ankney 1977, Korschgen 1977, Boudewijn 1984). This is likely due to the fact that a) food availability is greatest in mid to late spring b) there is no point in incurring the various costs of maintaining a nutrient store right through the winter, if one can collect sufficient for storage in the month before breeding. The results reported here would suggest, however, that female wigeon are storing protein in the form of gut tissue throughout the winter. One reason for this could be that, while grass biomass increases greatly in mid to late spring, grass protein content starts to decrease at this time after an initial high quality flush (Chapter 6). Thus it may be advantageous to female wigeon to store protein when it is more readily available during the winter.

D) The effect of sex on condition index

Finally, it is interesting to look briefly in more detail at the effect of sex on bird condition. Table 8.10 shows that males have a significantly higher condition index than females. In order to check that this was not due to the confounding effect of age, an analysis of co-variance was carried out with sex and age entered simultaneously as factors. The effects of gutsize and date were controlled for by entering them as covariates. The results show that sex always has a significant effect on condition but age never does (Table 8.12). It therefore seems that there is a genuine difference in condition between the sexes, with males about 20g greater than expected for their size and females about 17g under that expected for their size (Table 8.10). This effect was also found in mallard by Owen & Cook (1977) - they found that condition differences between sexes were far greater than those between different age groups.

TABLE 8.12

Analysis of variance to examine effect on bird condition of sex and age.

Variance Removed	Factors Assessed	Mean Square	F-value	Signif. (P)
Gizzard, Date	Sex Age	47086 18359	9.808 3.824	0.002 N.S.
Small Intestine, Date	Sex Age	51379 12896	10.939 2.746	0.001 N.S.
Total Caecum, Date	Sex Age	38340 11458	8.119 2.426	0.005 N.S.
Large Intestine, Date	Sex Age	54120 13243	11.080 2.716	0.001 N.S.

The most likely explanation for this effect of sex on condition is that males are dominant to females in terms of access to good feeding sites, roosting sites, etc. Male dominance on feeding sites has been reported in several bird species including crows (Houston 1977) and herring gulls (Grieg et al, in press). Moreover, Fretwell (1969) showed that fat reserves were positively related to dominance in junco flocks. Several studies have suggested that body size is an important determinant of dominance (Grieg et al, in press). Although condition index was not correlated with size index in this study (Table 8.7), males were significantly larger and heavier than females (Table 8.10). It is thus likely that body size plays some part in this hypothesised dominance of male over female wigeon.

CHAPTER 9

GENERAL DISCUSSION: STRATEGIES FOR NUTRIENT INTAKE

9.1 INTRODUCTION

This study has, in the main, been an attempt to elucidate the adaptations of an organism to its particular ecological niche. The primary question addressed by the project was formulated as "What strategies are used by wigeon to maximise their nutrient intake during winter?".

The reasons for asking this question were identified in Chapters 1 and 3. Firstly the wigeon feeds solely on coarse vegetation during the winter. Foliage presents major problems for animals which are dependent on it as a food supply. It is poor in nutrients, both energy (because of its high water content - Owen and Thomas 1979) and protein (Bell 1971), and it is very difficult to digest on account of the abundance of cell wall material (Janis 1976). Secondly, and related to the above, the wigeon, along with other anseriforms, lacks the gut adaptations necessary for microbial breakdown of its food supply. This again reduces the total amount of energy available per unit weight of food. Finally, the wigeon's small body size means that its metabolic requirements are high relative to its food intake. These factors should all act as strong selection pressures leading to the evolution of phenotypic traits in this species which increase the efficiency of nutrient intake from its low quality food source.

As discussed in Chapter 1 traits or strategies of this sort can be based on the anatomy, physiology or behaviour of an animal. With respect to adaptations to a folivorous diet, strategies of all three types are common throughout the animal kingdom, eg. anatomical (Hofmann 1973, Sibly 1981), physiological (Bayley 1978, Milton 1981) behavioural (Harwood 1975, Hoppe et al 1977). Moreover, no one group of animals is dependent on a single type of solution since, for example, anatomical adaptations will almost certainly result in behavioural changes as well. However, it is normally possible to identify the main emphasis of each strategic solution. Thus, the strategies of the ungulate herbivores, with their fermentative forestomach or hindguts harbouring symbiotic protozoa and bacteria, are primarily anatomical/ physiological adaptations. Other herbivorous mammals such as some rodents and primates again base their adaptations on fermentative gut chambers. Even some avian folivores possess symbiotic micro-organisms in their caeca. The folivorous anseriforms stand out alone among the grazing and browsing higher vertebrates in not employing this type of strategy. On account of this, their adaptations are based primarily on their behaviour rather than their anatomy or physiology (Harwood 1975).

9.2 STRATEGIES FOR NUTRIENT INTAKE FOUND IN WIGEON

Despite the fact that the main emphasis of its adaptive strategies is behavioural, the wigeon does show anatomical adaptation to its diet, when compared with other duck species. It has strong, bony jaw components, a comparatively reduced bill length to head length ratio and a high bill base. These features provide a relatively short work arm giving a more effective force at the bill tip. This suits a grazing feeding method rather than dabbling or grubbing, since the tip of the bill is used when plucking leaves from the parent plant (Olney 1965). This relationship between diet and bill morphology is also found in the geese. The grazing species have shorter bills suitable for rapid pecking, compared to the grubbing and seed-stripping species (Owen 1980).

The results of Chapter 8 show that the wigeon's physiological adaptations to its diet are fairly simple. In common with the grazing geese, the wigeon has a very simple alimentary tract and takes in very large quantities of food which pass through the gut very rapidly and are digested inefficiently. Indeed, while the wigeon's digestive efficiency is about the same as the grazing geese, its throughput time is, if anything, more rapid. This makes it very likely that there is little opportunity for any digestive process more complex than the simple absorption of cell solutes ie. proteins and soluble carbohydrates, and that there is no digestion of the cellulose comprising the plant cell walls by symbiotic micro-organisms in the caeca. This is certainly the case for the domestic goose (Anser anser) (Mattocks 1971) and the Cape Barren goose (Marriott and Forbes 1970), and has generally been assumed to be the case for most grazing geese (Owen 1972b, Harwood 1975, Drent et al 1979) and, indeed, for wigeon (Owen 1973b, Owen and Thomas 1979).

The actual amount of food passed through the gut each day is huge. Owen (1972b) calculates that a white-fronted goose ingests about 33% (wet weight) of its body weight per day. The figures in Chapter 3 suggest that a wigeon ingests around 51% of its body weight per day (assuming grass is about 75% water - Owen 1972b). Admittedly, this is a maximum figure, but it is difficult to think of another herbivorous member of the higher vertebrates which takes in around half its body weight of food each day. Clearly, this is one of the most significant effects which the combination of small body size and low quality food found in this bird has on its digestive strategy.

Even with this high food intake, it remains rather surprising that this method of meeting nutrient requirements is a competitive strategy in such a small animal. Sibly (1981) reviews the various digestive strategies found in herbivorous mammals and birds. In the ungulates, one can distinguish between two main strategies - ruminant (artiodactyls) and non-ruminant (perissodactyls). The strategy of the former is to ingest relativly small quantities of high quality forage and retain it in the gut for a long time, while species in the latter category feed on large amounts of coarser material which pass through the gut quickly and are digested poorly. Both strategies use symbiotic micro-organisms in various parts of the gut to digest cellulose. Clearly the non-ruminant strategy is closest to that of the wigeon. The effect of body size on these mammalian strategies is two-fold. Firstly all of the small ungulate species are ruminants. Bell (1971) proposes that the reason for this is that large species are better able to cope with the high quantity/ low quality diet of the non-ruminant since their lower relative but higher absolute metabolic requirements mean that they can tolerate departures in quality but not quantity in their diet. Secondly, within the ruminants, which range in body weight from 4 to 200 kg., there is a clear relationship between body size and diet, with the larger species eating primarily poor quality monocots and the smaller species feeding on higher quality dicots. One suggestion for this relationship is that the higher quality diet allows rumen weight to be kept low in the small species, since food can be digested more easily and thus more quickly. In the ungulates, then, small body size is only found in species with a digestive strategy which allows thorough digestion of a low quantity diet. Moreover, within this strategy, small size is correlated with a high quality non-gramineous diet. This contrasts strongly with the wigeon strategy in which there is poor digestion of a high quantity/ low quality gramineous diet in a species with a body size many times smaller than the smallest ruminant.

This type of comparison begs the following question: why have the grazing anseriforms not evolved microbial cellulose digestion? They would seem to be alone amongst the higher vertebrate folivores in not doing so. The normal explanation is that weight must be kept to a minimum in flying animals and so their digestive tracts must be kept simple (Mattocks 1971, Harwood 1975). This clearly explains why major gut modifications, such as the rumen, are not found in the birds. However, the Tetraonids are able to digest cellulose and lignin by fermentation primarily in the caecum (Moss 1977). Although this fibre digestion is probably a facultative ability dependent on the level of fibre in the diet (Moss and Parkinson 1972) it can be very efficient and may significantly increase the amount of nutrients extracted from a high fibre diet. The main anatomical correlate of this enhanced digestive ability is the increased size of the caeca - the caeca of the Tetraonids are about twice the size of those in Anseriforms of similar body size (Leopold 1953). Even with this ability to digest fibre, the red grouse (Lagopus lagopus scoticus) still ingests about 10% of its body weight (dry weight of heather) per day (Sibly 1981). This is slightly more than the white-fronted goose (8% dry weight) and slightly less than the wigeon (12% - dry weight). However, the food is retained for much longer in the gut - the throughput time of non-caecal material in ptarmigan (Lagopus mutus) is around 3 hours (Gasaway et al 1975). There are two possible reasons why this type of fibre digestion is not found in the Anseriforms. Firstly, the Anseriforms are more mobile than the Tetraonids: they undertake long migratory flights between breeding and wintering grounds. Thus gut weight (which may include the weight of food in the gut as well as gut tissue) may be even more critical for this group of birds. Nevertheless, it is difficult to see why about 40 cm of caecum should make so much difference - small and large intestine lengths are very similar between the groups. Possibly a more important difference is that the diet of the Tetraonids is generally much more fibrous than that of the Anseriforms, eg. 27% of some grouse diets is lignin (Moss 1977). This could mean that the modifications required for fibre digestion are more 'cost-efficient' in grouse than in ducks and geese since they have to deal with more fibre. It may be, in fact, that when feeding on highly fibrous diets some cellulose digestion does take place in the Anseriforms, in the same way that this ability is dependent on diet quality in the Tetraonids. There is no doubt that a more thorough investigation of this aspect of Anseriform digestion would be helpful.

Behavioural strategies would seem to be of most importance to wigeon in terms of maximising their nutrient intake, since their anatomical and physiological strategies are relatively undeveloped. Thus, the majority of this project is concerned with this aspect of the wigeon's feeding strategy. Behavioural strategies can, in fact, be viewed, in a purely functional sense, as a method of "outwitting" the morphological and physiological constraints placed on an animal through its phylogeny. The most obvious behavioural strategy found in wigeon is feeding for long periods. Not only is the intensity of feeding during its active hours very high (in common with other grazing species) but also the length of time it needs to remain active is considerable - about 17.5 hours per 24 hours. It needs therefore to be adapted for both diurnal and nocturnal foraging.

However, feeding for long periods is pointless if an animal is not situated in an area where sufficiently high intake rates of nutrients may be obtained. The ability to select good feeding areas is thus of critical importance to wigeon. However, the definition of a 'good' feeding area depends on which nutrient(s) is most limiting to the species concerned. Traditionally, energy or total food intake has been the factor studied in most models of feeding behaviour (Krebs 1978). However, Owen (1973b) showed that nutrient content of grass could be important in wigeon feeding site selection and Moss (1972) showed that nitrogen and phosphorus content of heather was selected for by red grouse. Belovsky (1978) found that selection for sodium was an essential part of moose (Alces alces) feeding behaviour.

The work reported here suggests that total food intake or energy is most important for wigeon feeding site selection since birds consistently selected for grass quantity in all studies of site selection, ie. between the six main feeding sites, in the fertilizer experiment and within feeding sites as birds moved away from water. This was the case even if this conflicted with selection for grass quality (ie. protein and fibre content). It seems, therefore, that the requirement for extremely high intake rates overrides food quality selection in this situation. Birds will, however, select for protein if it does not conflict with intake requirements (in early spring at least). It is also interesting to note that if general food availability is sufficiently high, wigeon may relax their selection for high biomass feeding sites. This is likely to be a successful strategy since it allows other site selection criteria to come into play if food intake is sufficient on all sites. Finally, it is clear that site selection for nutrient requirements must always be related to dangers of predation. Safety from predators is important to wigeon when selecting between sites (eg. the enclosure) and within sites. Birds will often feed on low biomass areas rather than risk predation. The most profound effect on wigeon behaviour of this requirement for safety is that this species is always tied to water when feeding on inland sites.

Site selection is not the only method that wigeon use to maintain high intake rates. Once on a high biomass site, birds generally peck more quickly thus increasing their intake rate. They also slow down their walking rate so that they are able to remain in the good area for longer periods. Thus, by altering their pecking and walking rates according to grass quantity (and possibly quality) wigeon are able to forage optimally over their heterogenous feeding sites.

One of the most characteristic feeding methods of wigeon compared to other ducks is their tight feeding flocks. There are three main selective advantages of this behavioural strategy in terms of nutrient intake. Firstly, wigeon are able to increase the time available for feeding by decreasing their vigilance rates, since their flock neighbours can look out for predators as well. This is probably most important in forming small wigeon flocks (up to 20 birds). Secondly, information on food availability can be exchanged between birds, possibly by the simple mechanism that if a bird has its head down it is in a good feeding area (Drent and Swierstra 1977). Finally, wigeon may be able to feed on higher protein grass during spring (when protein intake is most critical) by grazing in flocks during winter.

The wigeon's feeding behaviour is, therefore, well adapted to its ecological circumstances. Indeed the effect of diet and body size on this bird's behaviour is so profound that, in terms of feeding, it is more closely related to the grazing geese than other ducks. This effect is probably most noticeable when watching wigeon grazing on open fields in compact flocks. The similarity to barnacle, brent or white-fronted geese is very great indeed, while the difference from other ducks is equally noticeable. Thus, the influence of this bird's phylogeny on its feeding methods and behaviour is insignificant when compared to the influence of its ecology.

In summary, this project has investigated the adaptations of an animal to its ecological situation, primarily its diet and body size. It has shown that the anatomical and physiological adaptations found in this species are little developed. Consequently, its main adaptations are found in its feeding behaviour, which allows extremely high intake of a poor quality food type to be achieved.

9.3 THE APPLICABILITY OF AN INLAND STUDY TO A COASTAL SPECIES

Before leaving this general discussion, one possible criticism of the project requires consideration. Historically, wigeon have generally been thought of as coastal birds, restricted mainly to the mudflats on which their main food, Zostera, flourished. In only recent times have they moved inland in large numbers to feed on agricultural habitats (Owen and Williams 1976). Their feeding adaptations would, therefore, have evolved over thousands of years in a foreshore environment, and should relate primarily to this habitat and diet type. How then, can a study of feeding ecology and behaviour in an inland, agricultural situation elucidate adaptions evolved in a different environment?

The answer to this problem is two-fold. Firstly, the selection pressures acting on this bird will be similar in both environments. Moreover, the adaptive solutions are again likely to be similar. Flocking to increase feeding time and concentrating feeding effort on high quantity/ quality areas are just as relevant adaptations on mudflats as on open fields. Secondly, as noted in the introduction, wigeon have probably always fed on inland sites and non-Zostera food supplies to a far greater extent than recognised by the writers of the 19th and early 20th centuries (Glegg 1943). In historical times birds certainly regularly fed on saltmarshes and also on inland pastures when adjacent to large water bodies. In prehistoric times, when most of Europe was forested, Owen (1976b) suggests that the grazing geese fed primarily on saltmarsh, off-shore islands and inland marshes. It is likely that wigeon also used these habitats as well as estuaries. Thus, the prehistoric equivalent of the small artifical ponds at Caerlaverock, on which so much of the wigeon's feeding behaviour was based, would be semi-permanent pools and flashes on the saltmarshes and islands around the coast. The sea itself would also act as a safe 'base' from which to graze. It is quite plausible therefore, that wigeon feeding on saltmarsh would have created grazed lawns of high quality grasses in prehistoric times, and that this would have acted as a selection pressure for flock feeding in this species.

Basically then, the ancient habitat type of wigeon was quite similar in many respects to the inland feeding areas used today. Moreover, the wigeon's diet of wild Graminae and Zostera has simply been replaced by cultivated Graminae as inland grasslands have developed through agriculture (Thomas 1982). The wigeon is, in fact, pre-adapted for the artificial environment that it is coming to occupy increasingly today.

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APPENDIX 1

SPECTROPHOTOMETER PAPER

OIKOS 43: 62–67. Copenhagen 1984

An inexpensive and simple spectrophotometer for measuring grass biomass in the field

Peter W. Mayhew, Martin D. Burns and David C. Houston

Mayhew, P. W., Burns, M. D. and Houston, D. C. 1984. An inexpensive and simple spectrophotometer for measuring grass biomass in the field. – Oikos 43: 62–67.

A simple spectrophotometer design, suitable for rapid grass biomass assessment over large areas, is described. Such an instrument replaces conventional time-consuming techniques of biomass measurement in studies monitoring extensive areas, and uses inexpensive components. It measures the ratio of far red to red radiation reflected from the grass canopy, this figure being closely correlated with dry green biomass.

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Описана простая спектрофотометрическая установка, пригодная для быстрой оценки величины травяной биомассы на больших территориях. Этот аппарат заменит обычную, требующую много времени, технику измерения биомассы в работах по мониторингу обширных территорий и состоит из дешевых компонентов. Он измеряет отношение радиации дальней области красного спектра к красной радиации, отражающейся от травяного покрова, причем, эти данные близко коррелируют с величиной сухой зеленой биомассы.

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(ii)

1. Introduction

Traditional methods of standing crop measurement of grassland are both time-consuming and tedious, the usual technique being to clip all vegetation from a plot of known area and sort it into dead and live portions by hand. While this method provides an accurate measure over a small area, large scale monitoring of grassland swards (e.g. in conjunction with herbivore studies) is virtually impossible. A further disadvantage of this method is that it destroys the site being investigated, preventing the repeated monitoring of the same area.

The development of spectrophotometric remote sensing techniques for biomass estimates has greatly facilitated this aspect of ecology. However many of the instruments reported in the literature (e.g. Pearson et al. 1976, Milton 1980, Tucker et al. 1981) are expensive and may be more sophisticated than is required for vegetation biomass estimation alone.

This paper describes a spectrophotometer design which is both simple to build and inexpensive (approx. £110).

2. Materials and methods

2.1. Theory of grass spectrophotometry

The suitability of spectrophotometry for the assessment of grass biomass has been recognised since the 1950s, but has been developed mainly in the last decade. Tucker et al. (1975) reported that radiation of certain wavelengths of the electro-magnetic spectrum was either highly absorbed or highly reflected by grass canopies, and that some of these wavelengths could be closely correlated with the 'functioning green biomass' present.

Tucker (1977) selected two bandwidths which best correlated with biomass:

1) *630–690 nm* (red): This band exhibited a strong negative correlation with biomass due mainly to absorption by plant pigments.
2) *740–1000 nm* (far red): this band showed a strong positive correlation with biomass due to the lack of any appreciable absorption by plants and also to leaf scattering mechanisms.

Pearson et al. (1976) recognised that the ratio of the far red to red bandwidths should exhibit a strong positive correlation with biomass, and therefore built a hand-held spectrophotometer to test this.

A fuller account of the theory of the technique may be found in Curran (1980, 1981), Smith and Morgan (1981) and Wooley (1971).

2.2. Instrument design

The spectrophotometer used in this study was based on the above prototype, but is somewhat simpler to build and considerably cheaper.

1) The sensor head

This was constructed from two hollow, grey plastic tubes: 2.5 cm diameter and 15 cm long. In each of these was mounted a silicon photodiode-amplifier. These detectors (PFR, PR) are 5 mm² photodiodes (peak spec-

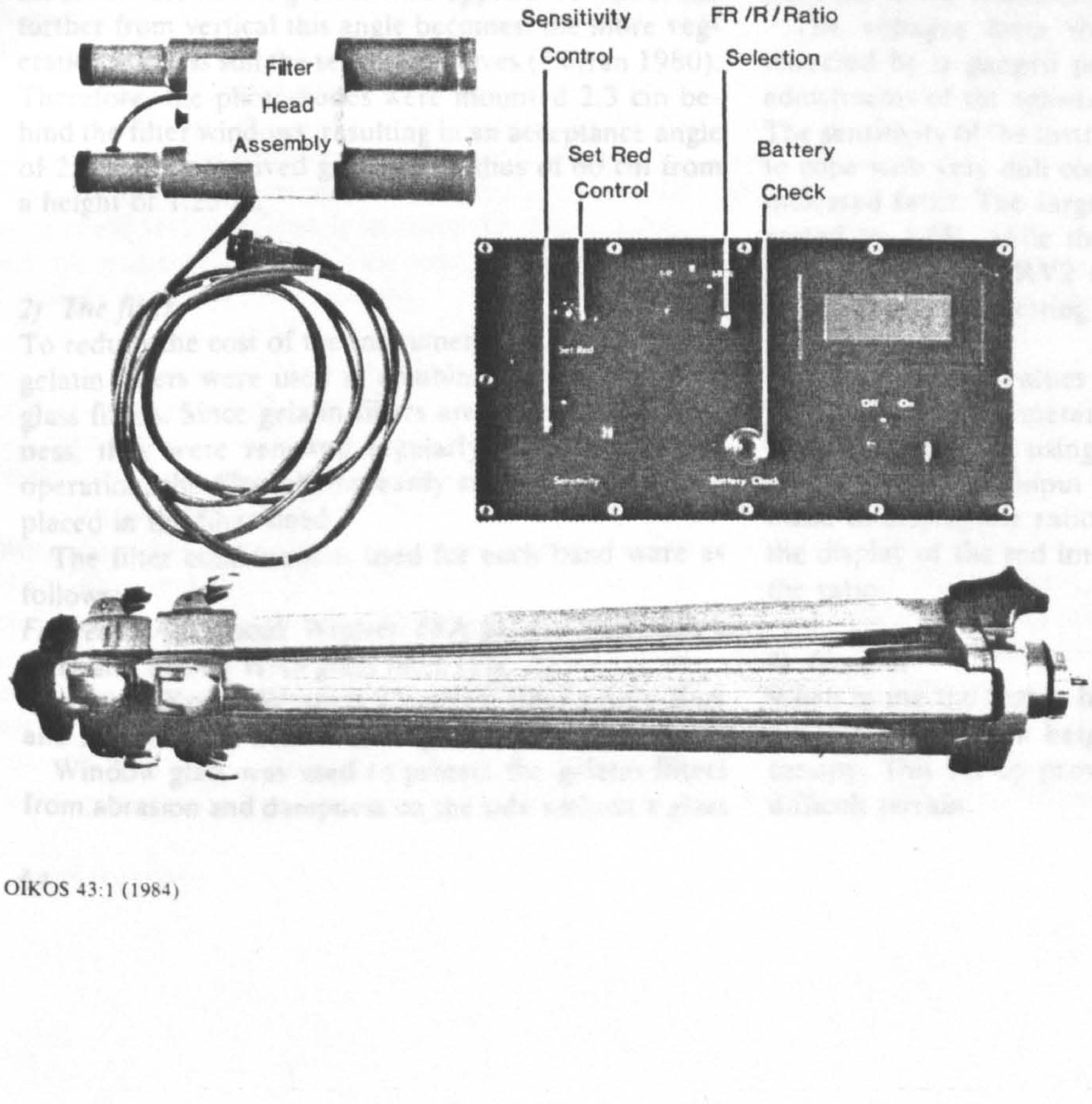

Fig. 1. Exploded view of the spectrophotometer.

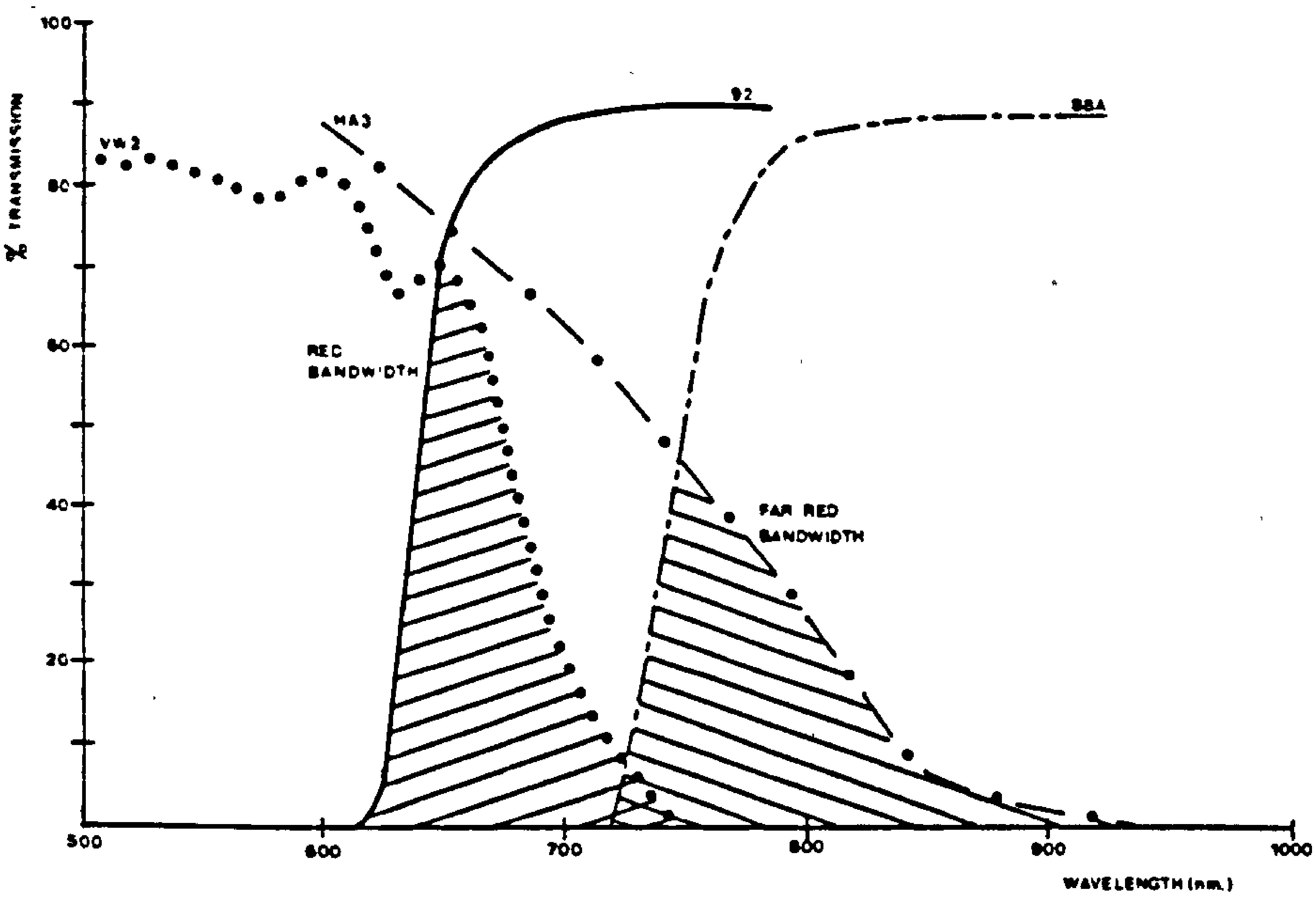

Fig. 2. % transmission of red and far red filter combinations.

tral sensitivity at 900 nm) with an integral amplifier, giving them a quoted sensitivity at 450 nm of 30 $mV/\mu V/cm^2$ They could be replaced with a photodiode and a separate operational amplifier. A possible problem with the use of these detectors is the production of a temperature sensitive dark voltage. The instrument was therefore checked in the laboratory under temperatures varying from −3°C to 28°C. No temperature effect was found.

It is important that the angle of view of the photodiodes should not be greater than approx. 30°, since the further from vertical this angle becomes, the more vegetation and less soil the sensor perceives (Curran 1980). Therefore, the photodiodes were mounted 2.3 cm behind the filter windows, resulting in an acceptance angle of 25° and a perceived grass plot radius of 60 cm from a height of 1.25 m.

2) The filters

To reduce the cost of the instrument, Kodak 'Wratten' gelatin filters were used in combination with ordinary glass filters. Since gelatin filters are affected by dampness, they were renewed regularly. This is a simple operation, the filters being easily cut to shape and replaced in the filter head.

The filter combinations used for each band were as follows:

Far red band: Kodak Wratten 88A gelatin filter with a Barr and Stroud HA3 glass filter (Fig. 2).

Red band: Kodak Wratten 92 gelatin filter with a Barr and Stroud VW2 heat reflecting filter (Fig. 2).

Window glass was used to protect the gelatin filters from abrasion and dampness on the side without a glass filter. The filter 'sandwiches' were inset into the plastic tubing and held there using a close-fitting perspex ring.

3) *The display unit* (Fig. 3)

The voltages generated in the sensor head were fed to a digital display unit. This unit could read either the red and far red voltages separately, or automatically determine the ratio of far red to red, which was extremely helpful, since (as will be discussed later) rapid changes in ambient light could affect the ratio, if the readings were not taken simultaneously.

The voltages from the photo-amplifiers were attenuated by a ganged potentiometer (RV1) allowing adjustments of the sensitivity of both channels at once. The sensitivity of the instrument could thus be increased to cope with very dull conditions, without affecting the indicated ratio. The larger far red signal was then inverted by AFR, while the red signal was inverted and amplified by AR. RV2 set the red amplification and allowed an initial setting of a convenient ratio of sensitivities.

The measured values were displayed on a liquid crystal digital panel meter (type DPM 200, based on the ICL 7106 chip). By using the normal and the reference inputs for the two input channels, this meter could be made to display the ratio of the two. Thus Sw1 selects the display of the red intensity, the far red intensity or the ratio.

4) General

When in use the sensor head was mounted on a photographic tripod, at a height of 1.25 m from the grass canopy. This set-up proved to be easily portable over difficult terrain.

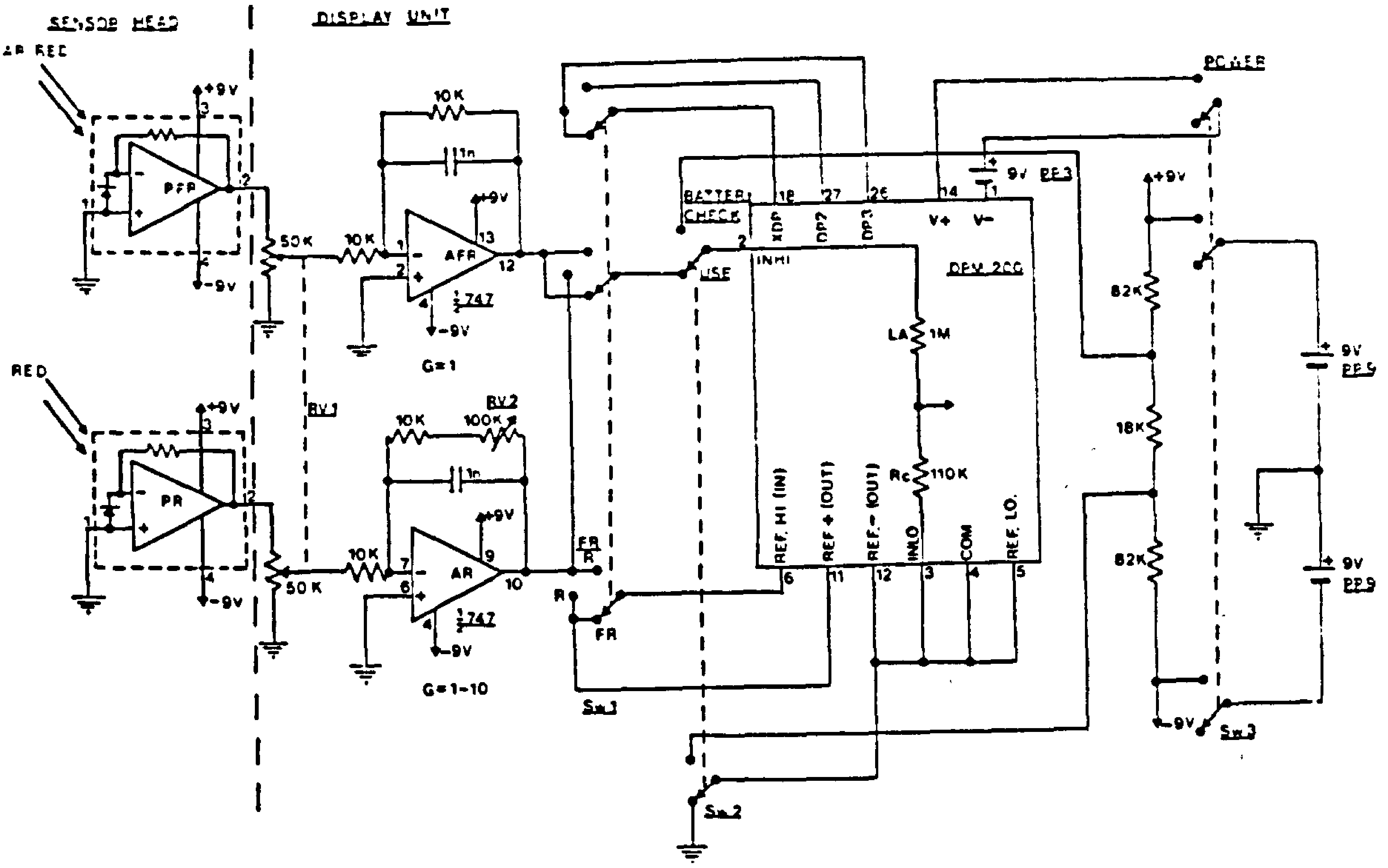

Fig. 3. Circuit diagram for sensor head and display unit. DPM 200 contains a low battery warning for its own supply. Sw3 allows checking of the voltage of the other batteries. XDP, DP2, DP3 activate the appropriate decimal point on the display. LA and Rc are resistors forming an attenuator and are internal to the DPM 200. They are altered to give the required sensitivity. G is the gain of the indicated stage.

5) Controlling for ambient light conditions

Holmes and Smith (1977) found that the effect of clouds on the red/far red ratio was only about 5%, and was due to the increased proportional contribution from scattered radiation and the selective attenuation of the red band in an atmosphere with high water content. However, in the present study it was found that cloud cover could very significantly increase the ratio reading, and this was by far the greatest source of error in the technique (see also Tucker 1980).

Thus, following the example of Milton (1980), a Kodak grey card was used as a reference card. This was mounted on the tripod 16 cm beneath the sensor head, and a reference reading was taken before every grass biomass reflectance ratio. It was found that this corrected for ambient light fluctuations only within certain limitations (possibly for the reasons stated in Palmer 1982). Thus as Milton (1981) has pointed out, the best method for controlling for changes in ambient light is to carry out observations under as uniform irradiation conditions as possible. For the situation in which this research was carried out (winter in SW Scotland) the most suitable light conditions were found to be heavy cloud.

3. Results

The instrument was calibrated against known grass biomasses at a Wildfowl Trust reserve on the Solway coast, SW Scotland. The site selected was a damp meadow of *Agrostis stolonifera, Holcus lanatus, Poa trivialis* and *Lolium perenne*.

The reflectance ratio of an area was measured, and a 25 by 25 cm plot was immediately clipped to soil level. The sample was thoroughly mixed, halved by weight, and then sorted into green and dead portions by hand. The green portion was then dried and weighed, and a green biomass per square metre figure calculated.

As can be seen from Fig. 5, the relationship between the reflectance ratio of a plot and its green biomass was direct and linear with a correlation coefficient of 0.92. Therefore, 84.6% of the variation in FR/R ratio was explained by the biomass of the plot.

Thus, a given reflectance ratio could be converted into a biomass figure by the following formula (from the regression of Y on X):

Biomass = 266.1 (Reflectance Ratio) – 203.0

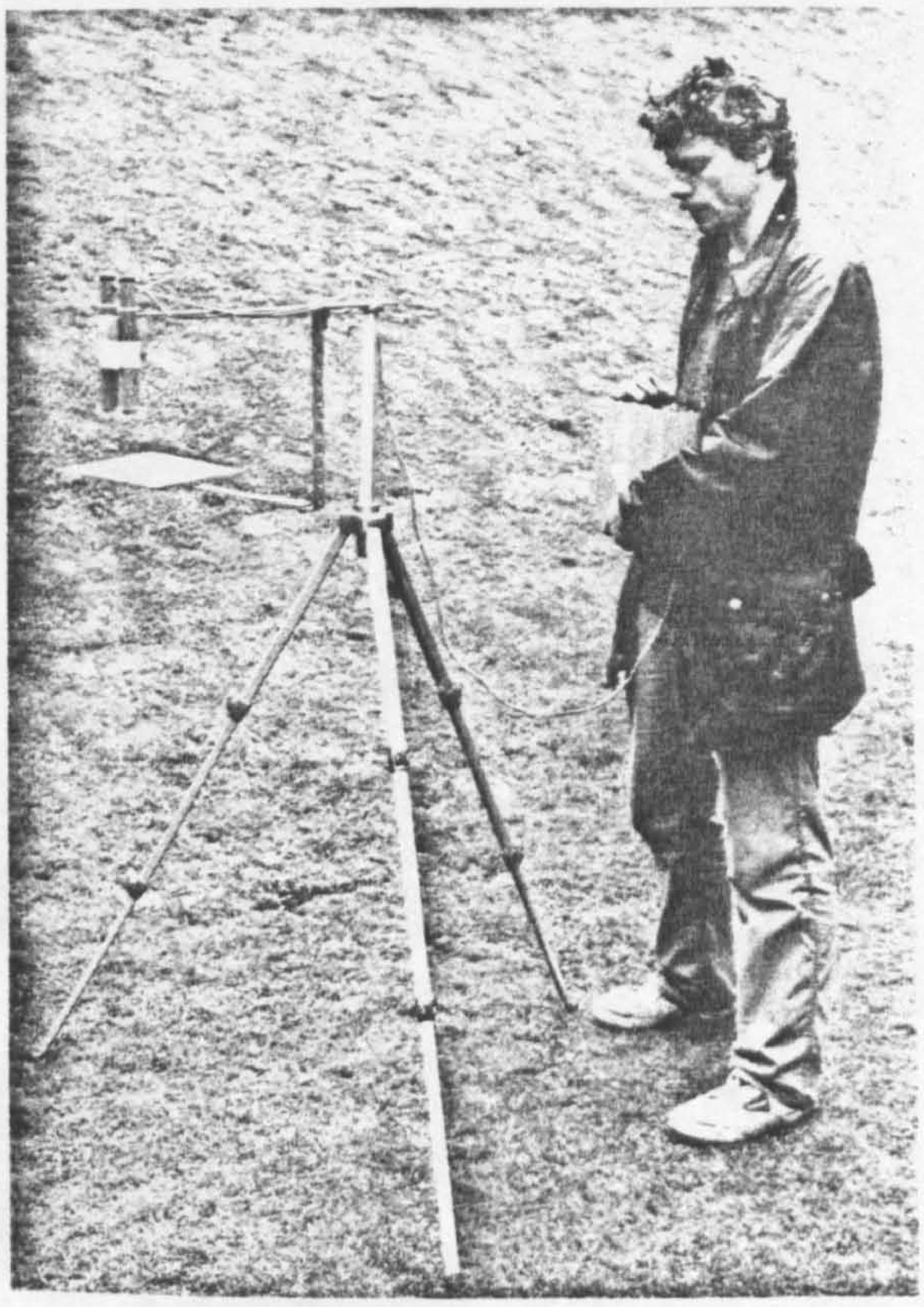

Fig. 4. Field testing the instrument.

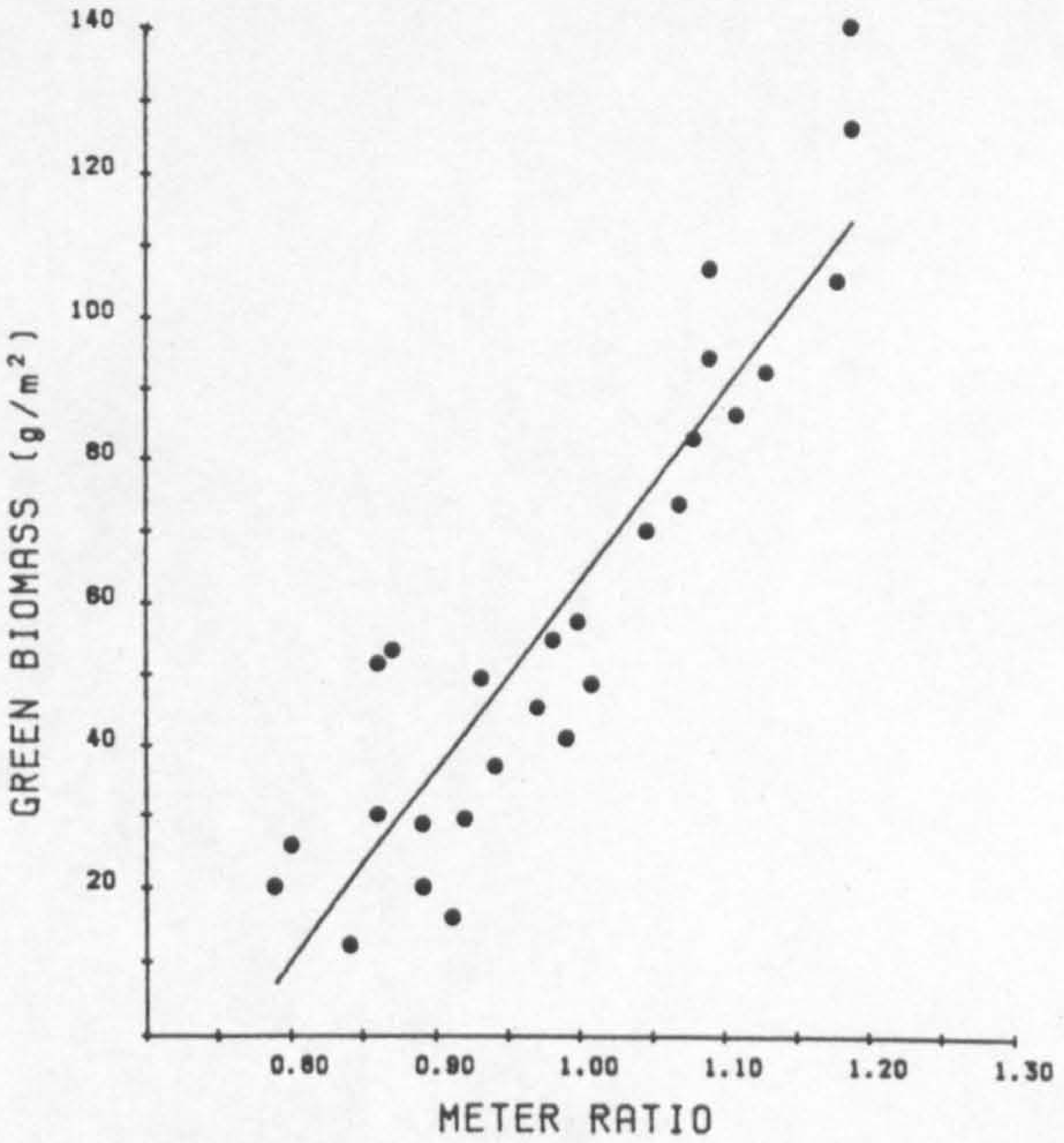

Fig. 5. The relationship between the FR/R ratio and the green biomass present on twenty-seven 625 cm² plots, (r = 0.92).

The calibration measurements were taken on seven separate days, throughout the winter, showing that adequate control can be made for the problem of fluctuating ambient light.

A different calibration curve would, of course, need to be produced for each vegetation type studied or ambient light conditions chosen.

4. Discussion

Curran (1980, 1981) reviews the effects of solar angle, soil background, senescent vegetation and productivity of the vegetation on the FR/R ratio.

The solar angle, and thus time of day, can greatly affect the reading (but correction can be made for this). However, under the heavy cloud conditions of this study, this effect was found to be minimal between approx. 0900 and 1600 hours in winter.

The colour of the soil background (if visible), may also affect the reflectance of certain wavebands. However, as Curran (1981) states, the soil/waveband combinations that are unsuitable for remote-sensing can be identified. Further, it seems that the positive relationship between vegetation amount and the FR/R ratio still holds under most soil types. This was found to be the case in one of our own study sites – a recently re-seeded field with dark soil visible between drills. However, in most semi-permanent pasture this will not be a problem.

Senescent vegetation is also reported as affecting the reading, and a 30% proportion of live:dead material is normally recommended as a minimum. However, in this study, the relationship between green biomass and FR/R ratio still held when only 10% of the vegetation was live.

Curran (1982) shows how the productivity of the vegetation can affect the reading. This could be a problem when studying spring or summer vegetation, but can again be controlled to some extent.

Lastly, it was found that the dampness of the vegetation had no effect on the ratio, permitting readings to be taken after rain.

The technique's applicability to vegetation other than grassland e.g. shrubs and forbs has been demonstrated by several authors (e.g. Thalen et al. 1980). Even though the instrument described here has only been tested on grass, there is no reason why it should not be suitable for other vegetation types.

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APPENDIX 2

RAW DATA FROM CHAPTER 8.3 - BODY AND GUT SIZES FROM WIGEON CORPSES

A) ADULT MALES

Wgt. (g)	Body Lgth (MM)	Total Skull (mm)	Wing Span (mm)	Wing Lgth (mm)	Caecum 1 (mm)	Caecum 2 (mm)	Large Intest. (mm)	Small Intest. (mm)	Gizzard (g)
745	480	86.0	822	266	284	262	100	1340	40.0
720	478	85.0	775	256	210	190	100	1195	55.0
695	486	82.0	810	251	250	228	105	1405	32.5
840	477	84.0	850	257	302	264	85	1705	56.0
785	482	83.0	812	265	223	207	91	1365	39.0
820	484	86.0	825	250	300	262	120	1540	47.0
725	497	83.5	830	260	278	240	98	1625	50.0
810	505	86.5	880	278	207	200	90	1400	55.0
840	502	87.0	865	260	255	230	110	1532	50.0
685	462	85.0	830	257	222	213	99	1402	31.0
835	495	85.5	832	258	265	245	115	1420	56.0
745	493	86.0	866	257	333	265	105	1665	48.5
870	518	88.5	860	256	246	221	97	1450	45.0
970	582	87.0	852	256	253	213	92	1390	47.0
730	497	88.5	834	261	211	199	78	1378	38.0
820	515	84.0	848	261	247	241	105	1492	45.0
675	481	83.0	854	262	270	257	107	1587	41.5
750	490	85.0	847	263	265	259	97	1623	41.5
700	497	84.5	855	268	266	235	78	1447	47.0
775	480	82.0	861	267	217	190	99	1545	44.5
860	485	90.0	852	273	221	176	116	1437	41.0
805	481	85.0	852	267	159	147	60	1116	45.0
780	489	83.0	808	255	247	240	102	1396	42.5
780	484	84.0	842	257	271	230	113	1494	42.5
820	477	85.0	867	270	170	150	112	1356	43.0
810	489	83.0	846	264	254	233	105	1737	40.0
840	499	86.0	849	259	259	239	96	1450	33.5
880	490	81.5	848	263	253	217	110	1280	42.0
865	498	89.5	874	268	184	169	115	1375	43.0
830	470	80.0	867	265	188	169	104	1366	37.5
675	495	81.5	870	273	204	190	78	1361	37.5

B) <u>JUVENILE MALES</u>

Wgt. (g)	Body Lgth	Total Skull	Wing Span	Wing Lgth	Caecum 1 (mm)	Caecum 2 (mm)	Large Intest.	Small Intest.	Gizzard
760	475	86.0	810	255	262	260	100	1450	70.0
810	490	81.0	790	258	236	236	90	1352	54.0
785	550	86.0	803	252	242	226	80	1625	50.0
765	480	84.0	803	243	259	239	105	1490	48.0
710	483	85.0	815	260	215	201	85	1360	47.0
705	487	84.5	782	210	0	0	0	0	32.5
715	497	85.0	782	244	225	201	83	1460	43.5
735	479	85.0	815	240	250	242	100	1655	49.5
865	0	84.5	825	251	240	223	87	1480	44.0
715	503	85.5	838	257	259	254	89	1547	41.0
775	502	84.0	828	247	0	0	0	0	49.0
710	492	84.5	845	259	205	202	98	1365	52.0
870	495	88.5	849	256	242	222	80	1332	43.0
795	459	83.5	818	247	208	193	82	1375	42.5
755	477	89.0	850	264	208	197	97	1402	44.5
650	486	84.5	822	253	260	259	98	1424	42.5
775	498	86.0	836	254	190	189	97	1211	37.0
725	475	85.0	837	263	205	203	108	1468	54.5
770	490	86.5	829	257	252	244	111	1525	49.0
615	473	85.5	810	230	202	178	92	1353	33.5
720	483	82.0	848	262	296	275	105	1315	52.0
830	515	85.0	865	263	242	215	117	1523	42.0
780	475	84.0	852	264	220	193	120	1701	53.0
645	495	84.0	832	258	270	244	111	1442	61.5
850	490	85.0	837	248	165	160	118	1455	35.0

C) ADULT FEMALES

Wgt. (g)	Body Lgth	Total Skull	Wing Span	Wing Lgth	Caecum 1 (mm)	Caecum 2 (mm)	Large Intest.	Small Intest.	Gizzard
780	445	83.0	770	242	240	175	74	1510	40.0
750	435	83.0	750	243	255	240	110	1510	39.0
725	438	85.0	755	247	278	235	95	890	44.0
690	467	78.0	774	242	221	196	81	1235	45.0
730	496	82.0	780	255	248	235	83	1470	41.0
745	468	83.5	852	265	295	275	120	1710	49.5
655	453	80.0	793	242	230	220	130	1360	38.0
670	477	83.0	770	242	263	255	98	1530	46.0
670	473	80.0	802	255	250	221	85	1365	42.5
705	472	82.0	815	251	285	270	103	1570	46.0
750	0	79.0	815	249	260	200	90	1430	40.5
650	452	80.5	780	240	225	200	104	1435	42.0
855	452	84.0	841	249	235	215	100	1675	40.0
730	468	82.5	793	247	264	240	102	1292	55.0
795	467	83.0	816	247	218	212	115	1532	43.5
700	460	79.5	806	249	210	193	110	1527	31.0
595	461	77.5	823	245	161	136	115	1292	47.0
625	472	83.0	821	255	167	135	105	1198	52.0
625	482	79.0	855	263	190	173	100	1474	45.5
850	467	80.0	835	259	257	239	95	1447	41.5
690	466	78.0	802	244	235	217	123	1566	38.0
640	467	80.0	815	245	216	182	115	1403	38.0
705	472	83.5	838	254	169	169	105	1325	39.0
665	479	84.5	830	259	260	241	110	1643	36.0

D) JUVENILE FEMALES

Wgt. (g)	Body Lgth	Total Skull	Wing Span	Wing Lgth	Caecum 1 (mm)	Caecum 2 (mm)	Large Intest.	Small Intest.	Gizzard
660	435	80.0	830	239	245	210	99	1540	50.0
625	438	82.0	753	232	210	210	117	1560	41.0
580	422	79.0	709	240	208	171	77	1140	37.0
615	436	80.0	767	228	250	216	85	1307	36.0
420	442	82.5	740	230	240	227	82	1091	26.0
590	458	87.0	820	243	207	176	129	1157	52.5
505	441	84.0	817	245	150	149	79	1130	33.0
635	468	87.0	830	256	198	174	114	1438	49.5
620	440	84.0	821	250	220	204	106	1475	40.0
665	456	82.0	811	235	221	214	90	1365	44.5
710	448	80.0	806	244	250	230	116	1404	42.0
865	467	83.0	859	270	220	206	95	1493	65.5
765	464	85.5	830	253	258	254	95	1508	49.5
815	467	85.0	824	252	255	245	96	1480	57.5
830	486	85.0	859	275	229	226	110	1602	58.5
655	453	84.0	794	241	227	225	118	1645	39.5
610	455	78.0	802	247	168	163	88	1260	37.5
630	459	79.5	806	247	145	145	81	1415	31.0
560	441	80.0	806	242	185	169	98	1340	38.0
710	480	83.0	809	244	191	184	103	1354	37.0
750	485	83.0	840	250	235	198	106	1582	41.0
610	458	81.0	831	249	195	163	105	1385	37.0
705	479	84.0	859	263	216	190	118	1490	38.0
570	465	80.0	824	250	185	180	77	1382	49.5
565	465	82.0	831	251	178	162	83	1535	29.5
575	464	81.5	820	247	168	159	99	1399	47.0
655	473	83.0	824	253	216	199	99	1297	41.5
620	483	82.0	823	261	145	139	89	1216	28.0
540	451	77.0	778	234	149	125	88	1152	40.5
600	444	74.0	771	239	174	154	89	1300	33.0
650	470	77.5	819	247	194	183	86	1275	37.0
750	458	81.5	824	248	268	251	123	1392	42.0
620	455	82.0	806	236	232	220	93	1250	48.5
630	462	78.5	822	244	206	190	92	1315	48.5
650	471	79.5	820	251	228	223	90	1285	43.0
670	460	82.5	795	240	195	167	92	1282	31.0
710	446	89.5	820	244	160	157	107	1229	38.0
755	482	82.0	847	257	220	210	116	1492	43.0
730	485	84.0	861	257	200	200	95	1525	40.0
730	474	79.0	837	252	215	173	118	1514	39.0
680	466	83.5	832	255	200	182	111	1389	43.0