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John Stephen Harwood

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THE GRAZING STRATEGIES OF BLUE GEESE,
<u>ANSER CAERULESCENS</u>

by

John Harwood

Zoology Department

Submitted in partial fulfillment of
the requirements for the degree of
Doctor of Philosophy

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ABSTRACT

The feeding behaviour of the blue goose (Anser caerulescens) was studied at the McConnell River breeding colony (60° 50'N, 94° 25'W) and, under more controlled conditions, in a pasture at Guelph, Ontario.

During July and August female blue geese and their goslings have a high protein requirement, due to the demands of incubation, moult and growth. Although a two kilogram goose consumes 100g of vegetation per hour of feeding, and females spend up to 80% and goslings up to 90% of the daylight hours feeding, the overall protein content of the available green vegetation in the arctic may not be high enough to meet this requirement. The components of blue goose feeding behaviour vary in a predictable way with changes in vegetation characteristic. This suggests that the behaviours may be adjusted to optimize quantity and quality of intake. A mechanism for this was suggested by experiments on a single species sward of controlled vegetation height. Blue geese spent more time feeding on plots fertilized with ammonium nitrate than on unfertilized plots. This difference is explained by an increase in the length of a feeding bout and a decreased speed of walking on the fertilized plots. The birds also pecked faster on the fertilized plots. These changes in feeding behaviour were shown to influence the intake of vegetation. Thus small, quantitative changes in feeding behaviour could serve to significantly increase protein intake.

This hypothesis is partially supported by independent data from the arctic. However, the difference between the protein content of vegetation in the oesophagi of feeding birds, and that of the available vegetation is considerably greater than that predicted by the model. This suggests the presence of additional selection mechanisms.

The impact of grazing geese on the nutrient status of the arctic tundra ecosystem, and the nature of their feeding strategies and tactics are discussed.

ACKNOWLEDGEMENTS

Successful arctic field research depends upon the co-operation of many people. I have space to acknowledge only those without whom this research would have been impossible.

Dr. C.D. MacInnes - my chief advisor for the first two years of the project - first encouraged me to study goose feeding behaviour. Without his energy and enthusiasm there would be no McConnell River field station. Dr. M.H.A. Keenleyside provided continual advice and aid for the final years of the project, and showed great tolerance of my failure to realize that I was studying the wrong Class of vertebrates.

All stages of my research and thesis have profited from my discussions with the members of my advisory committee - Drs. P.B. Cavers, L. Orloci, R.J. Planck and D.M. Scott. Dr. Planck, in particular, devoted much time and ingenuity to the design and construction of the automatic camera monitors.

Dr. F. Cooke, Queen's University kindly entrusted the geese used in the Guelph experiments to my care. Dr. D. Mullins, now of the Virginia Polytechnic Institute provided advice on, and equipment for the nitrogen analyses; Dr. J.E. Steele provided me with laboratory space. The poultry Science Department, University of Guelph supplied the pelleted goose food.

J. Izawa, S. Johnson and K. McKormick acted as field assistants in 1971 and 1973. Fellow graduate students C.D. Ankney, A. Aubin, A. Bisset and G. MacLaren provided additional assistance.

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INTRODUCTION

> "All behaviour is overt to what-is, and
> all overt relationship is behaviour"
> Martin Heidigger.

One aspect of ethological research has been traditionally and successfully concerned with elucidating the survival value of particular behaviour patterns (Tinbergen 1968). This approach may be logically extended to consider the selective advantages derived from quantitative variations in specific behavioural parameters. Not only can such information be subjected to statistical analysis, but it is also amenable to mathematical representation. Since "mathematics implies the existence of an algorithm which is more precise than ordinary language" (Bertalanffy 1973), such a representation provides a more rigorous definition of complex, inter-acting systems than does a conventional word model.

In the absence of recognized and reliable analytical procedures, it is most profitable initially to restrict the analysis of functional variations to those situations where strong natural selection for an optimal behavioural response is exerted. Since it is impossible to measure behavioural variation without error, the intrinsic "noise" of the system must be sufficiently low that the relationship between environmental and behavioural variation can be precisely delineated. Classically such analyses have been applied to various aspects of reproductive behaviour, where the cost of a sub-optimal response may be total reproductive failure. However, the process of feeding also encompasses a set of behaviours whose outcome must be optimized for survival (Schoener 1971). Additionally, feeding is a ubiquitous and year-round phenomenon in the animal kingdom, permitting the collection of large quantities of data.

Holling (1959, 1965, 1966) was able to define sets of equations that adequately describe the feeding behaviour of several predatory species under laboratory conditions. So far Holling's techniques have not been extended to field situations (Krebs 1973).

The quantitative analysis of the occurrence of any behavioural pattern is facilitated if the act is performed frequently. True geese (*Anser* and *Branta* spp) spend more than 70% of the daylight hours feeding both in summer (Lieff 1973) and winter (Owen 1972). In addition, there are convincing arguments that the feeding strategies of geese are based primarily on behavioural variation:

Birds exhibit two major types of feeding strategy, the nature of the strategy depending on the food source being used. *Predators* exploit food resources which occur as discrete items of high nutrient content, and which are clearly differentiated from their environment. The handling and ingestion of these items occupies only a small proportion of a predator's total time budget. By this definition many herbivorous species - such as seed-eaters - are essentially predatory. *Grazers* exploit a considerable proportion of their total environment for food. Objective definition of a food "item" is usually impossible, and the nutrient content per unit weight of the food is low. Grazers devote a large proportion of their activity time to the handling and ingestion of food. The vast majority of all research on avian feeding strategies has been confined to predatory species (e.g. Morse 1971; Pulliam 1971, 1973; Smith 1974a, 1974b; Baker 1974). Grazing avian herbivores are largely restricted to the orders Anseriformes and Galliformes. The feeding behaviour of several galliform species has been intensively studied in the field (Gardarsson and Moss 1970; Moss 1967, 1972; Pulliainen 1970; West 1968). Two species (*Gallus domesticus* and *Coturnix coturnix*) have been the subjects of intensive laboratory study. The feeding behaviour of grazing anseriform species has only recently been subjected to quantitative scrutiny.

While the grazing galliforms possess at least some of the morphological adaptations normally associated with herbivory in vertebrates (McBee 1971), grazing Anseriformes have remarkably simple alimentary tracts. Mattocks (1971) found no indication of cellulose breakdown in the digestive caecae of *Anser anser*. Food usually passes through the gut in two to four hours (Groebbels 1932 in Ziswiler and Farner 1972, Marriott and Forbes 1970), and large plant fragments are visible in the faeces. This rapid passage leaves little opportunity for any digestive process more complex than the simple absorbtion of cell solutes. Intestinal elaboration is probably incompatible with the long migratory flights undertaken by most ducks and geese. These species are subject to selection pressure favouring the development of behavioural traits which optimize the quality of consumed food.

Many grazing Anseriformes nest on arctic tundra grasslands; such species face an additional feeding problem. Arctic grasslands have a low annual productivity, and the nitrogen content of the vegetation tends to be low (Russell 1940, Warren-Wilson 1954, Bliss 1971). The mean protein content of green, arctic vegetation may well be close to the minimum necessary for the survival of a herbivore lacking complex physio-morphological adaptations for herbivory. Many arctic nesting geese aggravate this situation by breeding colonially or semi-colonially, thus intensifying their local impact on the vegetation. Incubation imposes an additional nutrient stress on the birds, since in at least one species (Anser caerulescens) neither member of a pair feeds to any extent during incubation. During the course of incubation, females of this species lose one third of their total body weight (Ankney 1974). Incubation is immediately followed by a major moult. Replacement of moulted feathers imposes a further protein demand on the birds' metabolic system. Moulting in passerines involves an approximately 8% increase in energy requirements (Blackmore 1969, King and Farner 1961). Thus arctic nesting geese are exposed to further selection to optimize their nutrient intake. In the absence of an elaborate digestive system this optimization must be achieved by the use of appropriate behavioural tactics.

The arctic tundra is probably the most recently evolved ecosystem (Dunbar 1968). Its boundaries have been in a continual state of flux for the last 10,000 years (Bryson, Irving and Larsen 1965; Hoffman and Taber 1967; Bryson, Baerreis and Wendland 1970; Ritchie and Hare 1971). Any species with a relatively long generation time and which habitually utilizes such an unstable environment will be subject to selection for plasticity of feeding strategy. Although such plasticity could be obtained through morphological polymorphism, arctic breeding species face a completely different feeding situation on their wintering grounds. Such an annual dichotomy in feeding requirements should favour strategies based on behavioural flexibility.

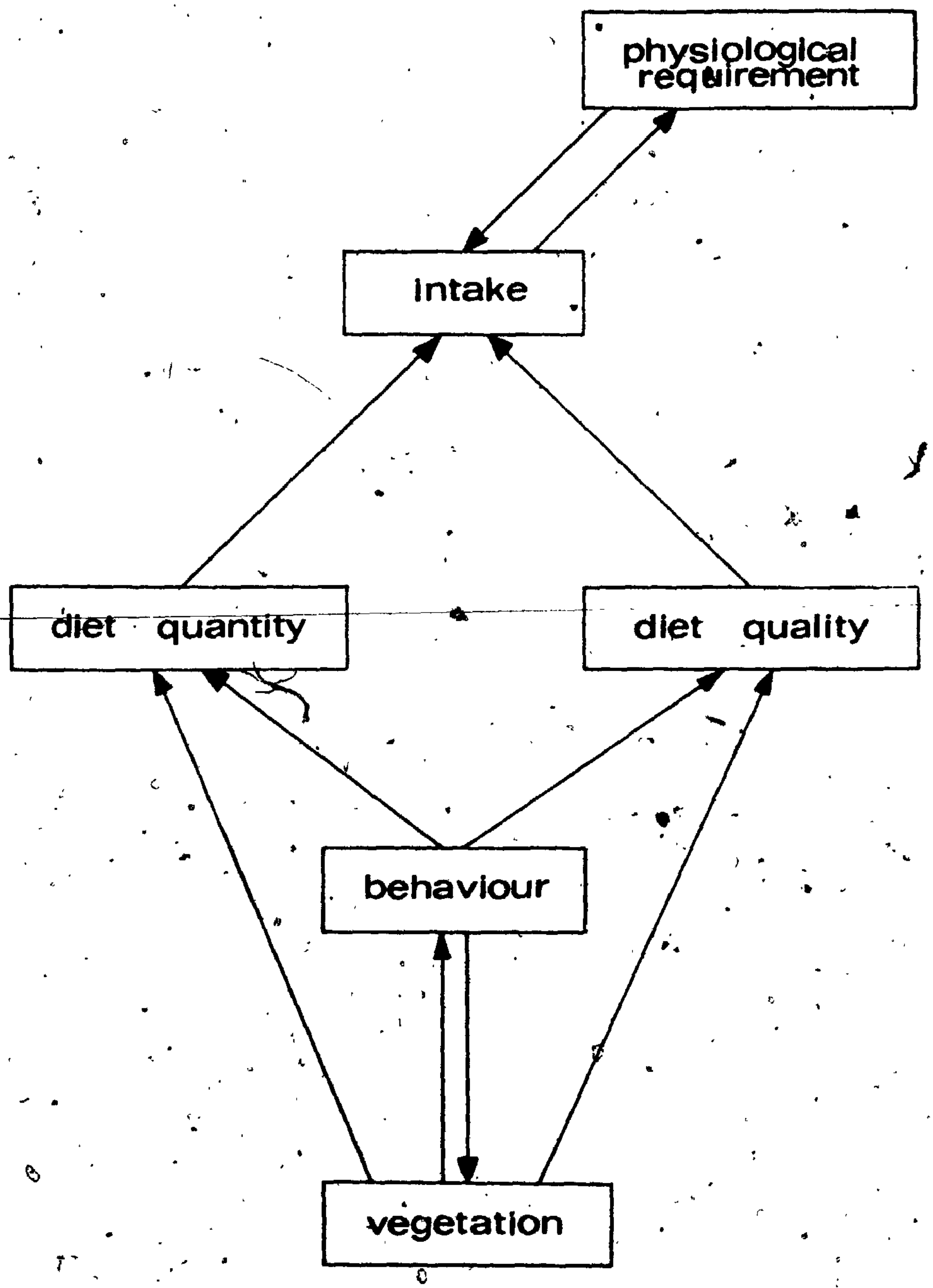
Arctic nesting, grazing Anseriformes are therefore ideal subjects for the successful study of the functional significance of quantitative variation in feeding behaviour.

This study has been concerned with the summer feeding behaviour of the blue goose (Anser caerulescens). In winter blue geese feed mainly on roots (Kear 1966). Not only is rooting behaviour difficult to observe clearly, but the standing crop of roots in an area is notoriously difficult to quantify (Alexandrova 1969). Very little rooting occurs in summer. Blue geese breed in large colonies on coastal, arctic tundra grasslands in Canada and Russia (Cooch 1962). The McConnell River colony, N.W.T. - where much of this study was conducted - has a breeding population of more than 100,000 pairs (Kerbes in Ankney 1974). It has been continuously studied for more than 15 years, and a massive amount of data on general goose biology at this site is available (MacInnes 1962, 1966; Lieff 1968, 1973; Prevett 1973; Ankney 1974). Permanent observation towers permit continuous observation of undisturbed birds for extended periods. Additionally, birds at the McConnell River tend to use traditional and relatively discrete feeding areas.

The nature of the inter-relationships studied is indicated in Figure 1. Changes in vegetation characteristics in time and space are controlled by a multiplicity of factors - including soil characteristics, drainage, microbial activity, local climate and permafrost changes - and no attempt was made to devise a predictive model of these changes in the course of the summer. The various vegetation parameters are considered as simple, exogenous variables (Goodall 1972) changing with time; these values are then used as input variables to the feeding system. Similarly the indicated relationship between physiological requirements and intake has not been quantified.

Chapter 2 gives a general description of the behaviour and

Figure 1. SYSTEMS DIAGRAM OF THE IMMEDIATE EFFECTS OF THE VARIABLES UNDER CONSIDERATION UPON EACH OTHER. ARROWS POINT FROM POTENTIAL INDEPENDENT VARIABLES TOWARDS POTENTIAL DEPENDENT VARIABLES. DIET QUANTITY IS THE ACTUAL WEIGHT OF FOOD INGESTED BY A GOOSE, DIET QUALITY IS THE CONCENTRATION OF NUTRIENTS IN THE FOOD INGESTED. INTAKE IS THE TOTAL QUANTITY OF NUTRIENTS INGESTED.


physiological requirement
intake
diet quantity
diet quality
behaviour
vegetation

overall feeding strategies of blue geese. Chapters 3 and 4 are concerned with the tactics of feeding, and develop a simple model of the relationship between vegetational variation and behavioural changes, and the influence of these behavioural changes on food intake. The predictions of this model are then tested against independently derived field data in Chapter 5.

METHODOLOGY

"The method must be purest meat
and no symbolic dressing"
Allan Ginsberg.

1.1 INTRODUCTION

The model presented in Figure 1 possesses a vagueness more suited to a conceptual aid than to an analytical tool. For the model to qualify for an analytic role it is first necessary to define mensurable and biologically valid components of the compartments labelled "vegetation" and "behaviour".

Although a plethora of vegetation parameters has been measured by ecologists at one time or another, it is doubtful whether many of these have any intimate meaning for feeding geese. Consideration was therefore limited to those features of the vegetation that might be readily apprehended by a grazing bird. This set of parameters was further restricted by logistic necessity. Since large sample sizes were required due to the intrinsically high variation in the vegetation, individual chosen components had to be amenable to rapid and accurate measurement. Quantity of vegetation per unit area, and crude protein and water content of the vegetation were measured. Although the calorific content of the vegetation must be an important factor in goose feeding, arguments have already been presented to suggest that the main nutritional requirement of post-incubation birds is the replacement of the seriously depleted body protein reserves. In addition, calorimetry of large numbers of samples is excessively time consuming, thus violating the second requirement of a suitable parameter.

The definition of units of behaviour has always been a considerable biological dilemma (e.g. Slater 1973). The general, if arbitrary policy has been to consider any measurable component as a unit until sufficient evidence to the contrary accumulates. Following this convention, feeding behaviour was divided into the following components: proportion of time devoted to feeding; rate of pecking, and rate of walking while feeding; and length of a feeding bout. Since the proportion of time that can be apportioned to feeding is determined by the time required for other essential activities, the amount of time spent in other readily recognizable behavioural activities was also recorded.

Thus the feeding system was analyzed at three levels: variation in vegetation quantity and quality; the concomitant variation in the parameters of feeding behaviour; and the effects of these variations on the quantity of food actually ingested.

A wide variety of techniques was used to determine the nature of the inter-relationships between the chosen variables. This chapter deals solely with the most general methodology and techniques. Specific details of individual experiments are given at the appropriate point in the text.

1.2 NOMENCLATURE

Botanical nomenclature follows Polunin (1959). Unless otherwise stated, the term "grass" is applied in a general sense to all species in the families Gramineae, Cyperaceae and Juncaceae. Avian nomenclature generally follows the A.O.U. checklist (1957), but the blue goose and snow goose are considered to be colour phases of <u>Anser caerulescens</u>, following Delacour and Mayr (1945). They are referred to as the blue and white phases of the blue goose respectively.

1.3 STATISTICAL METHODS

All values of parameters are presented as the mean ± the standard deviation of the mean (standard error) followed by the sample size in brackets. Simple statistical tests follow the procedures of Sokal and Rohlf (1969). More sophisticated statistical manipulations are explained at the appropriate point in the text. Statistical differences are considered to be significant if the probability of such a difference occurring by chance is less than 1 in 20. The term "highly significant" refers to probabilities of less than 1 in 100.

1.4 STUDY SITES

All field observations were made at the McConnell River delta, N.W.T. (60^{o} 50'N, 94^{o} 24'W) from May to August of 1971 and 1973. A full vegetational description of this area may be found in Lieff (1973) and MacInnes (1962). Additional, experimental data were collected from captive geese in an approximately two hectare pasture at Guelph, Ontario from June to September 1972. The pasture consisted almost entirely of awnless brome grass (Bromus inermis Leyss) and alfalfa (Medicago sativa L.). The test arena is described in Chapter 3 and Appendix 2.

1.5 VEGETATION

In all but one case, quantity of vegetation was measured by the fresh weight of green grass per unit area. Unless specifically stated, all vegetation weights refer to fresh weight. Although dry weight is a more reliable measure of the actual quantity of vegetation present at a sampling site, geese only experience the vegetation in its undried form.

An exclosure method was used to assess the changes in vegetation characteristics with time. Exclosures were constructed from 9.5 mm mesh chicken wire. McConnell River exclosures were 5m x 2m, Guelph exclosure were 0.75m square. An equal-sized, unexclosed plot was associated with each exclosure. This was randomly positioned on either the left or right side of the long axis of the rectangular exclosures, and on one of the four sides of the square exclosures in an attempt to randomize the wind-shielding effect of the wire netting.

Each sampling at the McConnell River involved the clipping to the moss level of five randomly chosen, 50cm x 20cm quadrats in each sample plot with a pair of Sunbeam electric sheep shears. Clippings were collected in a domestic dustpan. At Guelph three randomly chosen, 20 cm square quadrats in each plot were clipped to ground level with hand sheep shears. All samples were immediately sealed in polyethylene bags and frozen within six hours of collection.

Samples were later sorted by hand into green "grass", dicotyledon, and lower plant and litter components. These components were then weighed to ± 1mg on a Sartorius analytical balance. 1971 McConnell River samples were either vacuum freeze-dried to constant weight, or oven dried for 48 hours at 65°C. There is little difference in the percentage water extracted by these techniques, or the crude protein content of the samples after drying (Appendix 1). 1973 McConnell River samples were dried for 24 hours at 95°C. Guelph samples were dried for 48 hours at 65°C. All samples were reweighed after drying to determine dry weight and water content.

Samples were then ground through the 0.4mm^2 mesh screen of a Whiley mill. For each sample, three sub-samples of approximately 1mg were analyzed for total nitrogen content using the micro-Kjeldahl technique of Johnson (1941). The mean coefficient of variation for the three replicates was 8.5 ± 1.65% (n=55). Total crude protein was estimated as 6.25 times total nitrogen. Throughout the rest of the text protein refers to crude protein. Samples whose protein content was to be directly compared were always dried in the same oven run, and analyzed in the same Kjeldahl run.

In the experiments with goslings at the McConnell River (Sec. 1.6) the cover repetition method (Grieg-Smith 1964) was used to estimate the quantity of available vegetation. The goslings were tested in a 2m square enclosure, within this enclosure 100 randomly chosen samplings were made with a cover frame of four, 1.6mm diameter pins. The pins were inserted vertically into the vegetation and all pin contacts with the vegetation were recorded. Cover repetition values give an approximate index of standing crop for grass species (Grieg-Smith 1964: 8).

All faeces collected were dried for 24 hours at 95°, and analyzed in an identical manner to the vegetation samples.

1.6 EXPERIMENTAL ANIMALS

At Guelph three groups of 10, one year old geese (10 blue phase and 20 white phase) were used. These birds had been hatched at Guelph from eggs collected at the LaPerouse Bay, Manitoba colony (approximately 200 miles south of the McConnell River), and raised by blue goose foster parents. Each bird was marked with an individually coded, aluminium neck band (MacInnes, Prevett and Edney 1969) approximately one month prior to the experiments. Between experimental trials the birds had access to vegetation identical to that in the test arena, plus a grain supplement.

Experiments at the McConnell River in 1973 were performed with 18 hand-reared goslings (eight blue phase and 10 white phase). These birds were collected from the colony just after they had hatched, but before they had left the nest. For the first 21 days of life the birds were confined to a $50m^2$ pen which was moved whenever the enclosed vegetation became obviously depleted. After 21 days the birds were allowed to wander freely around the field station. They rarely moved more than 250m from the buildings. A high protein supplement (usually Miracle dog food, approximately 20% protein) of approximately 30g per bird (varying with the birds' age) was provided daily at sunset. This was invariably consumed within 10 minutes of presentation.

1.7 BEHAVIOUR

Four parameters of feeding behaviour were measured: total time spent feeding per day, mean length of a feeding bout, mean rate of pecking, and mean rate of walking while feeding. A <u>feeding bout</u> was defined as beginning when the head was lowered below the horizontal body axis, and ending when the head was raised above this axis for more than one second. The following behavioural categories were recognized:

<u>Alert</u> (Figure 2a) - the neck is held at approximately 90° to the horizontal body axis, the eyes are open.

<u>Feed</u> (Figure 2b) - the head and neck of the bird are below the horizontal body axis, repeated pecking movements are directed at the vegetation.

<u>Preen</u> (Figure 2c) - the beak is used to manipulate and rearrange the feathers.

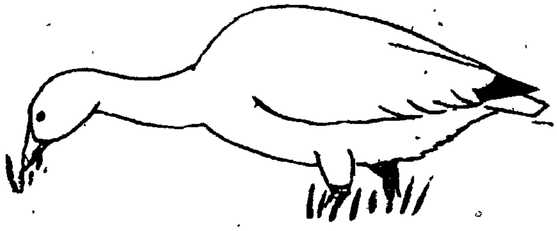
<u>Roost</u> (Figure 2d) - the ventral body surface is in contact with the ground, the head rests among the back feathers and scapulars.

Figure 2. SCHEMATIC REPRESENTATIONS OF BEHAVIOURS OF ADULT BLUE GEESE RECOGNIZED IN THIS STUDY.

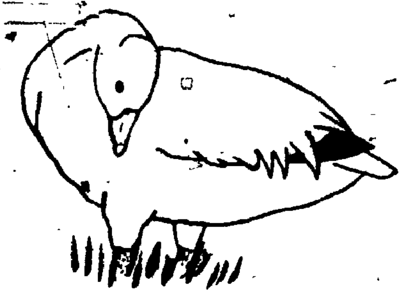
(a) ALERT (b) FEED (c) PREEN (d) ROOST

(e) BROOD

a



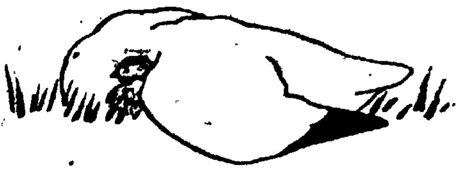
b



c

d

e



Brood (Figure 2e) - the general physiognomy of this behaviour is identical to roosting, but the goslings are kept close to the body under the arched wings. Since it proved impossible to distinguish brooding birds from roosting birds at distances greater than 250m, the two categories were combined for analysis.

Other - any behaviour which does not fall into one of the above categories. This includes drinking, bathing, swimming, running and aggressive behaviour. In any given sample period less than 5% of all observations fell into this category.

The proportion of total activity time allocated to each behaviour was estimated by "scan sampling" (Altman 1974). At regular intervals the group of birds under observation was scanned with 8x40 binoculars or a 30x telescope. As soon as a bird was visible in the field of view, its behaviour at that instant was classified and recorded on a multiple key counter. The proportion of time spent in each activity was estimated from the proportion of birds engaged in this activity at each sampling. Bout length was recorded to the nearest second. During the course of a feeding bout the total number of pecks directed at the vegetation was recorded mentally, and the total number of steps taken was recorded on a hand counter. On completion of the feeding bout , these values were transferred to a data sheet. These data were then used to calculate number of pecks and steps per minute of feeding. The method makes no assumptions about the success of individual pecks. It is similar to the method used by Murton (1963) in his study of wood pigeon (Columba palumbus) feeding. Gosling feeding bouts were so long that it was impossible to obtain a reliable count of the total number of pecks in a bout. Instead the time taken for 50 pecks, and the number of steps taken in this interval were recorded, a method used by Owen (1972) for white-fronted geese (Anser albifrons). There are no data for feeding bout length in goslings.

1.8 INTAKE

Several methods were used to estimate the quantity of vegetation ingested by grazing birds. Adults were weighed to ± 5g on a Chatilon autopsy balance. Goslings were weighed to ± 1g on an Ohaus triple-beam balance. Such accuracy is only possible with tame birds, which will sometimes sit passively on a weighing pan for a suitable length of time. Outdoor weighings at the McConnell River were performed within a small canvas tent to minimize wind effects.

Defaecation rates at the McConnell River were measured by the interval between successive defaecations for an individual whose cloaca was visible during the entire observation period. This method could not be used at Guelph where defaecation by the geese was a relatively rare event. Even Owen's (1972) method of estimating half the interval between defaecations by randomly chosing an individual and then recording the time to first defaecation proved impractical. The total number of faeces deposited in a 24 hour period by a group of 10 experimental birds within a 10m square test enclosure was counted, and this quantity was used to estimate the number of droppings produced by each individual per unit time. Each dropping was squashed after counting to prevent duplicate counting. This method has limited reliability as piles of droppings deposited while roosting are difficult to count accurately.

GENERAL FEEDING BEHAVIOUR

> "Dumplings/ Being better than flowers
> The geese are returning there?"
> Teitoku.

2.1 INTRODUCTION

Components of the model have so far been designated on the basis of their ease of measurement. For an analysis based on these variables to be more than an exercise in curve fitting, it is necessary that the components also have some specific meaning in the goose's <u>Umwelt</u> (von Uexküll 1934). If we exclude metempsychosis on practical grounds, it is only possible to infer the existence of such a meaning.

Since the chosen components of vegetation show a consistent variation during the course of the arctic summer at the McConnell River (Sec. 2.2); if it can be shown that the expression of the behavioural components varies in a predictable and concomitant fashion with this vegetational variation, it seems valid to consider that the measured components reflect some intrinsic functional process. In addition, a simple, quantitative description of the variations in feeding behaviour with time provides a broad intuitive insight into the nature of the feeding process. Such a crude analytical technique is obviously lacking in rigour but it can enhance both the realism and specificity of the hypotheses to be tested.

2.2 VARIATION IN VEGETATION PARAMETERS WITH TIME

A complete data set on the changes in vegetation quality and quantity throughout July and August is only available from 1971. However, these variations are remarkably similar to those observed by other workers at comparable sites in the western Arctic (Tieszen 1972, Haag, 1974). As they are also confirmed by the more limited data for 1973 it seems valid to consider the observed variations to be typical of arctic tundra grasslands.

Data are presented as mean values from several sites on two different study areas. Such pooling, without any testing for homogeneity, obviously precludes the drawing of precise statistical inferences. It is, however, valid for descriptive purposes; providing an indication of the overall variation in the different parameters over a wide area.

The quantity of green grass attains a maximum value in the first week of August (Figure 3). A quantitatively similar pattern of variation to that shown by the ungrazed vegetation - although with somewhat higher overall values - was found by Tieszen (1972) for a wet sedge meadow at Point Barrow, Alaska, where there are no nesting geese. The amount of vegetation removed by grazing animals - indicated by the discrepancy between the two curves of Figure 3 - is considerable. The constancy of the difference between the quantity of grazed and ungrazed vegetation throughout July and August indicates the maintenance of a balance between removal by herbivores and new growth, since geese were present throughout the entire sampling period. The fact that the decline in both grazed and ungrazed plots in August was almost identical indicates that growth was continuing longer in the grazed areas. Despite the heavy impact of grazing, the available food supply for geese was increasing until the end of the first week in August. Smaller sample sizes were used in 1973, but the variations in total standing crop of vegetation (Figure 4) indicate the occurrence of qualitatively similar changes in food availability in this year.

Figure 3. VARIATION IN DRY WEIGHT STANDING CROP OF GREEN GRASS WITH TIME AT THE McCONNELL RIVER, N.W.T. 1971. FIGURES BETWEEN CURVES INDICATE THE NUMBER OF SITES SAMPLES. VERTICAL LINES INDICATE ± ONE STANDARD ERROR.

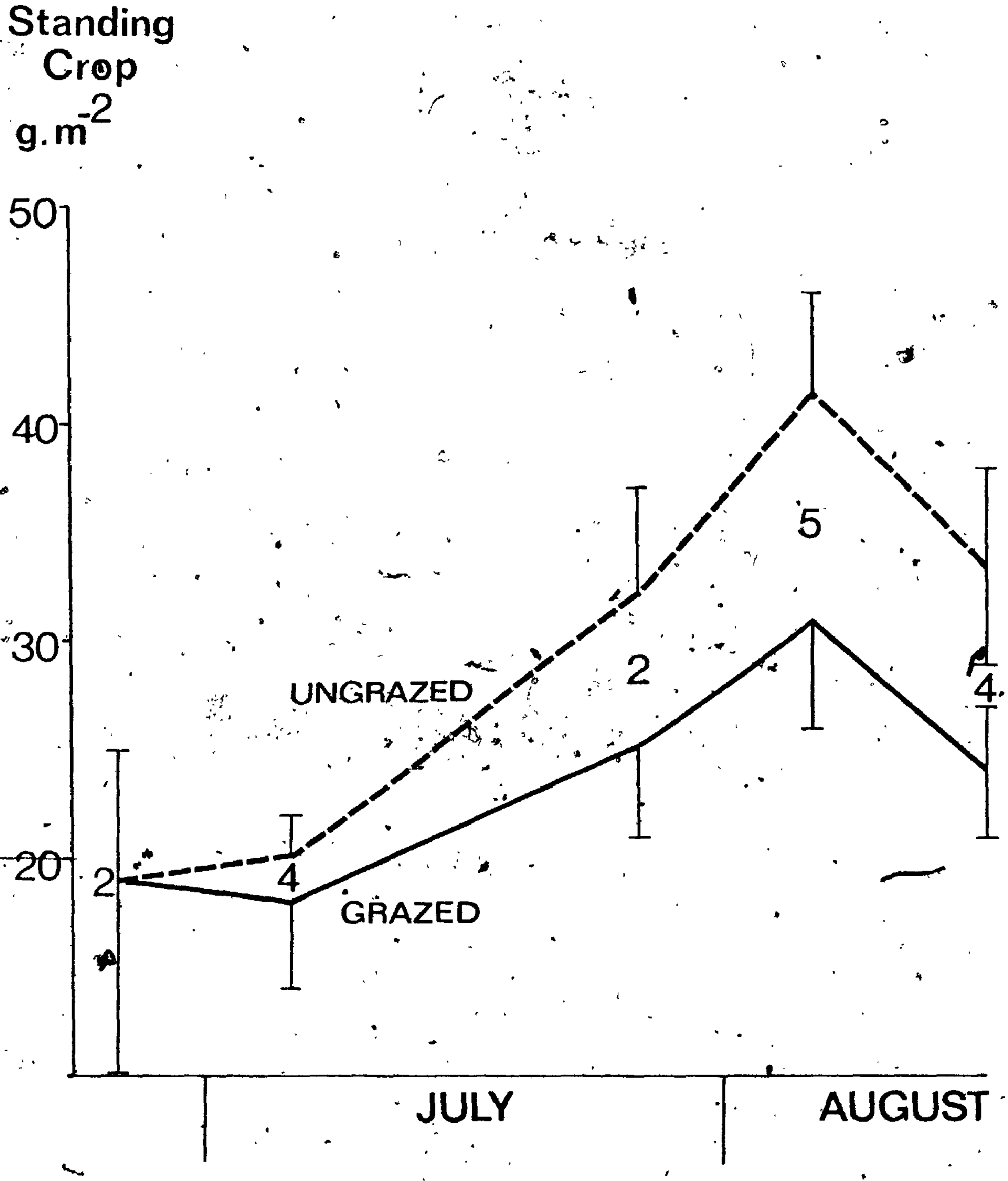
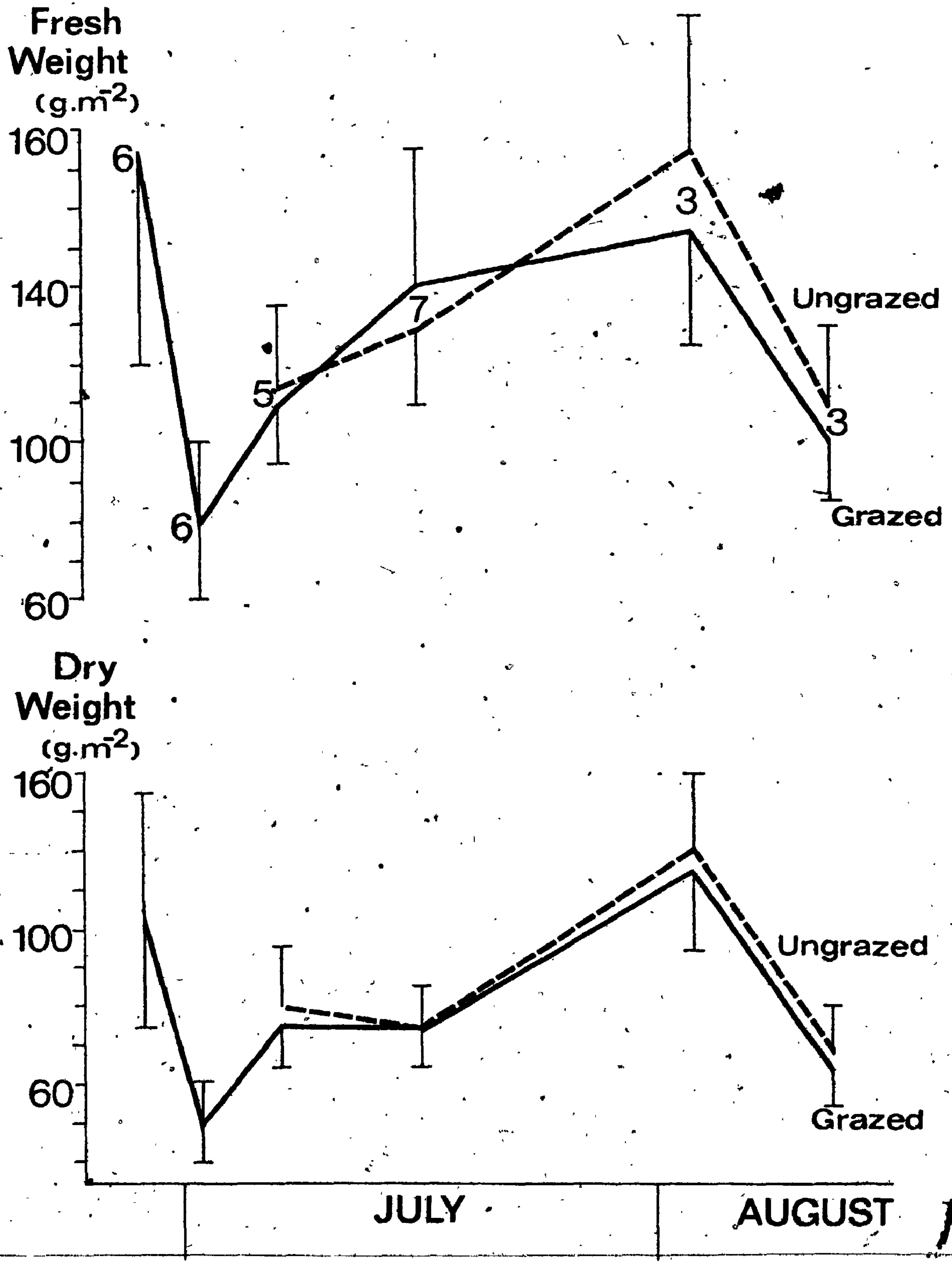

Standing
Crop
$g.m^{-2}$
50
40
30
20
UNGRAZED
GRAZED
2
4
2
5
4
JULY
AUGUST

Figure 4. VARIATION IN TOTAL STANDING CROP OF ALL VEGETATION WITH TIME AT THE McCONNELL RIVER, N.W.T. 1973. FIGURES BETWEEN CURVES INDICATE NUMBER OF SITES SAMPLED


Fresh Weight
(g.m^{-2})
160
140
100
60
6
6
5
7
3
3
Ungrazed
Grazed
Dry Weight
(g.m^{-2})
160
100
60
Ungrazed
Grazed
JULY
AUGUST

The percentage water in the grass component of the vegetation was not measured in 1971. However, in 1973 there was a highly significant, positive correlation between the mean water content of the grass at a site and the mean water content of the entire vegetation sample ($r = 0.79$, $n = 35$, $P < 0.001$). Since total water content was measured in 1971 we can use this as an index of the variation in water content of the grass. Water content remained constant for most of the summer, but declined markedly in August (Figure 5). A similar pattern of variation is evident in 1973 (Figure 6); the most noticeable feature of these data is the very low water content of the vegetation in July and August. This is probably the result of an exceptionally dry summer. Between June 25 and August 10 there was less than 0.75cm of rain. This paucity of water was exacerbated by the combination of frequent ground mists and offshore winds, which further dehydrated the area.

The protein content of exclosed vegetation reached a peak in late July in both years (Figures 7 and 8). A similar patterning was observed by Haag (1974) for a sedge meadow at Tuktoyaktuk, N.W.T., although he only sampled the vegetation three times in the course of the summer. This peak in protein content probably corresponds to the period just before maximal vegetation growth. Haag (1974) suggests that the decline in protein content in August represents the withdrawal of nitrogen and phosphorous to the root system which precedes leaf senescence. The grazed vegetation shows a rather different variation (Figures 7 and 8). Although a maximum protein content is reached by the last week of July, there is little decline in August. This fact, in conjunction with the continued productivity of the grazed vegetation in August is strong evidence that goose grazing is maintaining the vegetation in a preflowering stage which is both more nutritious, and more readily digested

Figure 5. VARIATION IN WATER CONTENT OF ALL VEGETATION WITH TIME AT THE McCONNELL RIVER, N.W.T. 1971. FIGURES BETWEEN CURVES INDICATE NUMBER OF SITES SAMPLED.

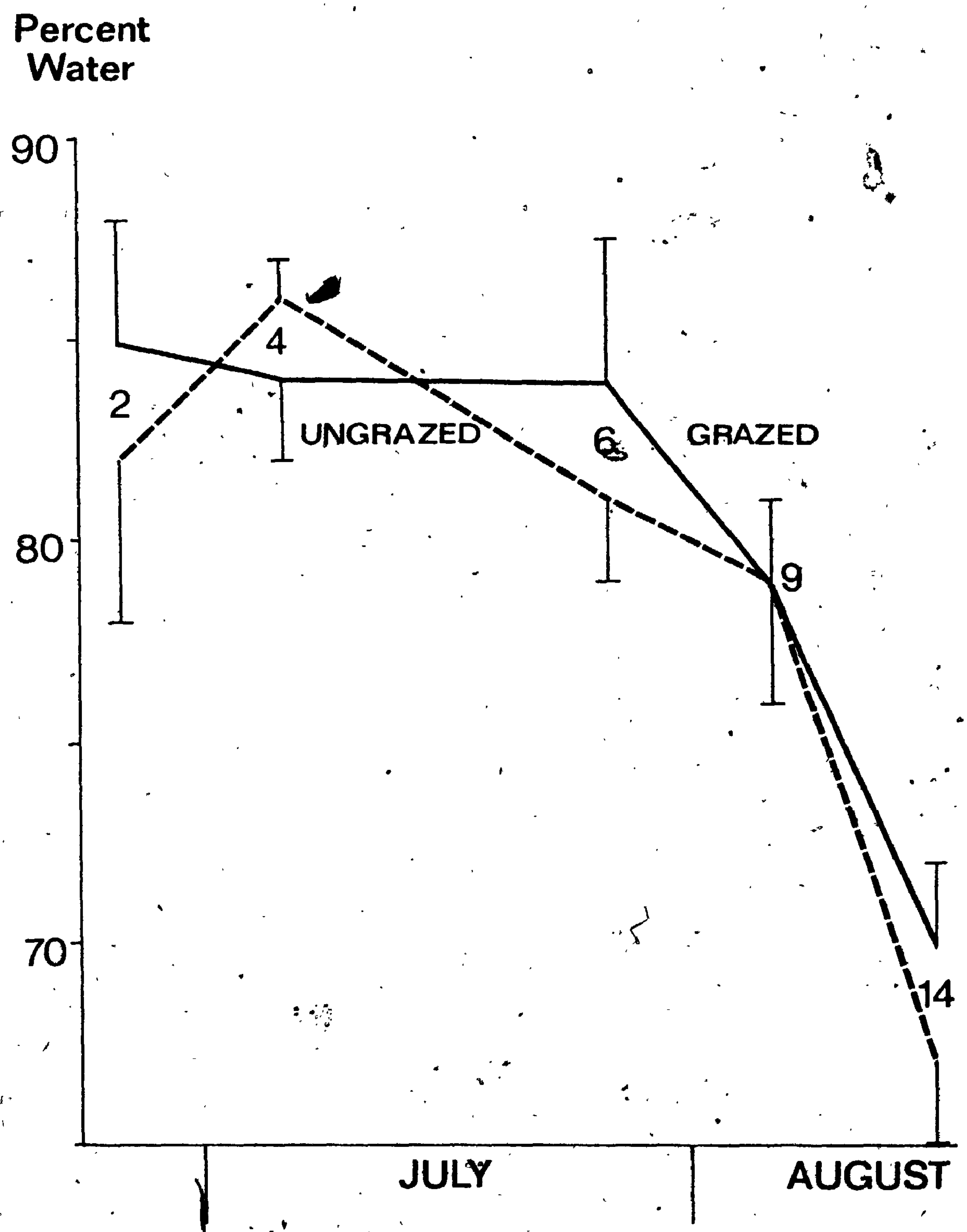

Percent Water
90
80
70
2
4
6
9
14
UNGRAZED
GRAZED
JULY
AUGUST

Figure 6. VARIATION IN WATER CONTENT OF ALL VEGETATION WITH TIME AT THE McCONNELL RIVER, N.W.T. IN 1973. FIGURES BETWEEN CURVES INDICATE NUMBER OF SITES SAMPLED.

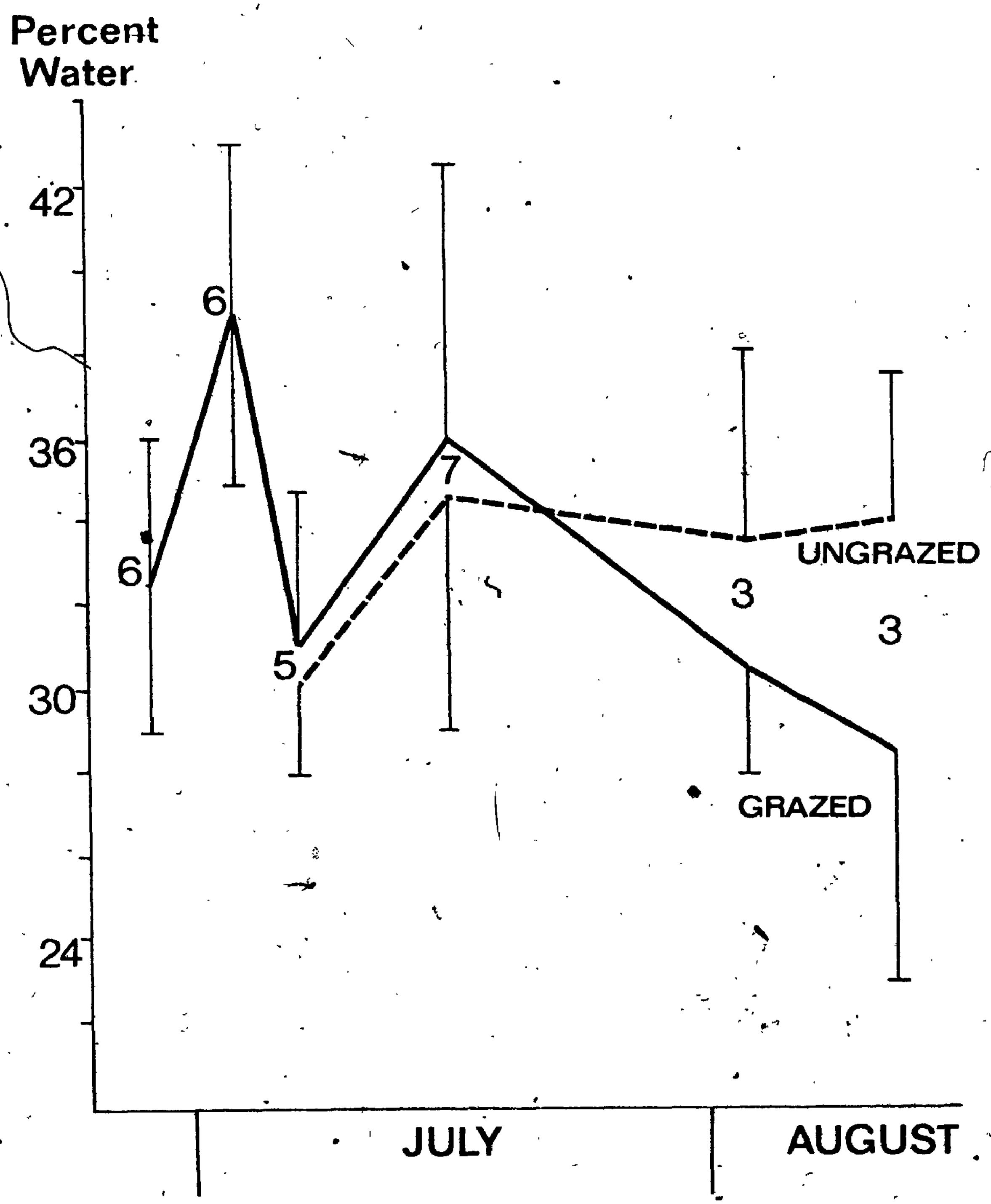

Percent Water
42
36
30
24
6
6
5
7
3
3
UNGRAZED
GRAZED
JULY
AUGUST

Figure 7. VARIATION IN CRUDE PROTEIN CONTENT OF GREEN GRASS WITH TIME AT THE McCONNELL RIVER, N.W.T. 1971. VALUES BETWEEN CURVES INDICATE NUMBER OF SITES SAMPLED

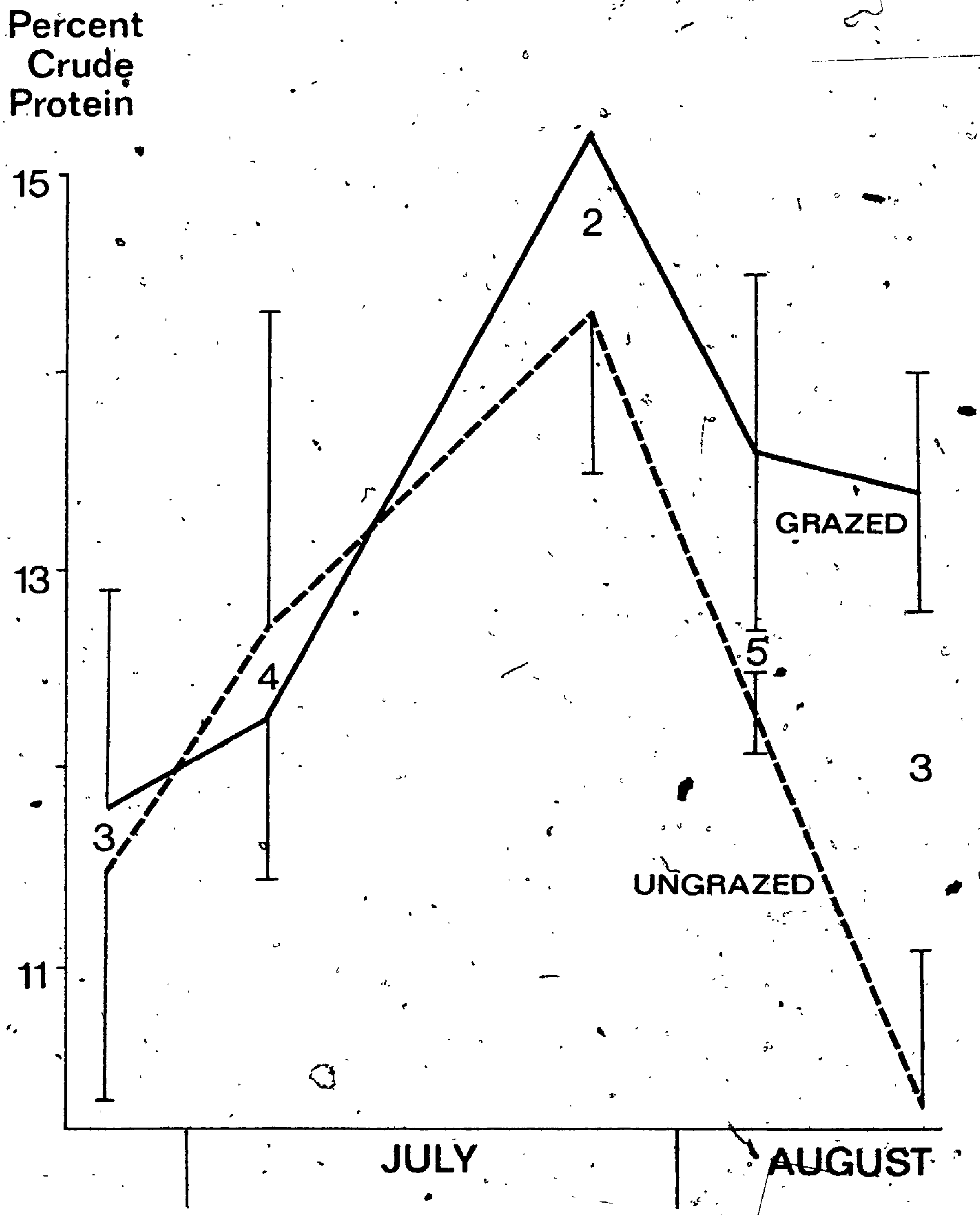
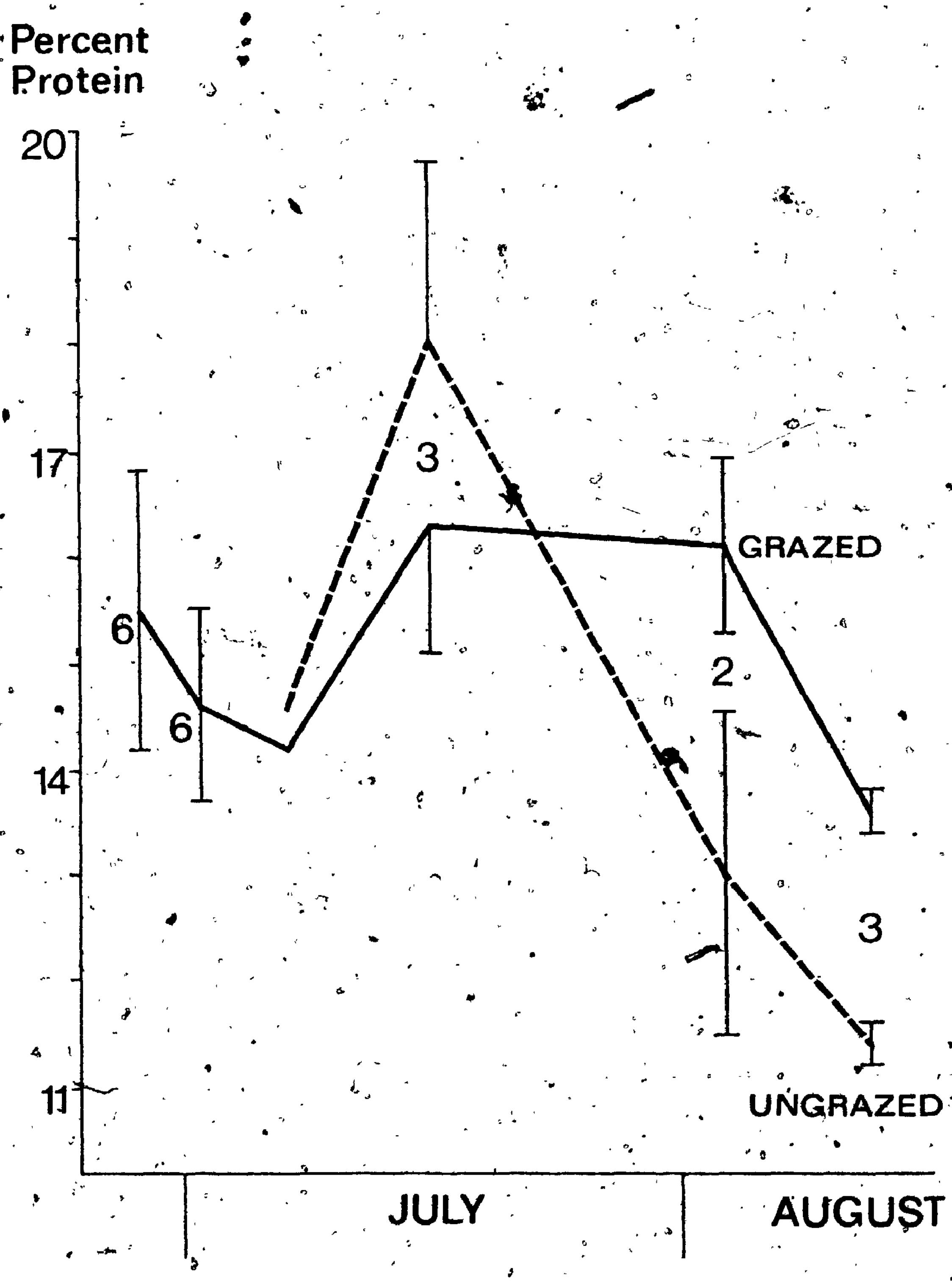

Percent
Crude
Protein
15
13
11
2
4
3
5
3
GRAZED
UNGRAZED
JULY
AUGUST

Figure 8. VARIATION IN CRUDE PROTEIN CONTENT OF GREEN GRASS WITH TIME AT THE McCONNELL RIVER, N.W.T. 1973. VALUES BETWEEN CURVES INDICATE NUMBER OF SITES SAMPLED


Percent
Protein
20
17
14
11
6
6
3
2
3
GRAZED
UNGRAZED
JULY
AUGUST

than the ungrazed vegetation. This type of mechanism was first suggested by Vesey-Fitzgerald (1960) to explain the apparently overgrazed appearance of some east African savannas, although he had no quantitative evidence. This hypothesis will be discussed more fully in Chapter 6.

Thus the geese at the McConnell River are exposed to a food source that is increasing both in quantity and quality until at least the first week of August. It is in the light of this variation that the observed variations in feeding behaviour must be considered.

2.3 THE MECHANICS OF FEEDING

Blue geese exhibit two distinct feeding modalities - grazing and rooting. Grazing is the predominant feeding mode in summer, although it is used in winter if fresh, green grass growth is available. Rooting is primarily practiced on the wintering grounds (McIlhenny 1932), where the ground is sufficiently soft for efficient probing. It is also used by all birds when they first arrive on the breeding grounds - provided suitable open ground is available - and by non-breeding adults in June and early July.

Two different grazing techniques are utilized depending on the nature of the grazing substrate. When geese feed on coarse grasses the partially open beak is inserted into the vegetation with the head tilted laterally (Figure 9a). The bill is closed, trapping vegetation along the whole length of the bill (Figure 9b), the interlocking transverse ridges of the two mandibles hold the vegetation firmly. The head is then rapidly retracted from the vegetation and the grass is torn off against the serrated shearing edge of the "grinning patch" (Figure 9c). The typical ragged grass tips produced by this tearing action can be seen throughout Figure 9. This sequence of actions constitutes a single

Figure 9a. PECKING MOVEMENTS OF MALE, WHITE PHASE BLUE GOOSE WHILE GRAZING ON *ELYMUS ARENARIUS* AT THE McCONNELL RIVER, N.W.T. 1973

INSERTION OF BEAK INTO VEGETATION

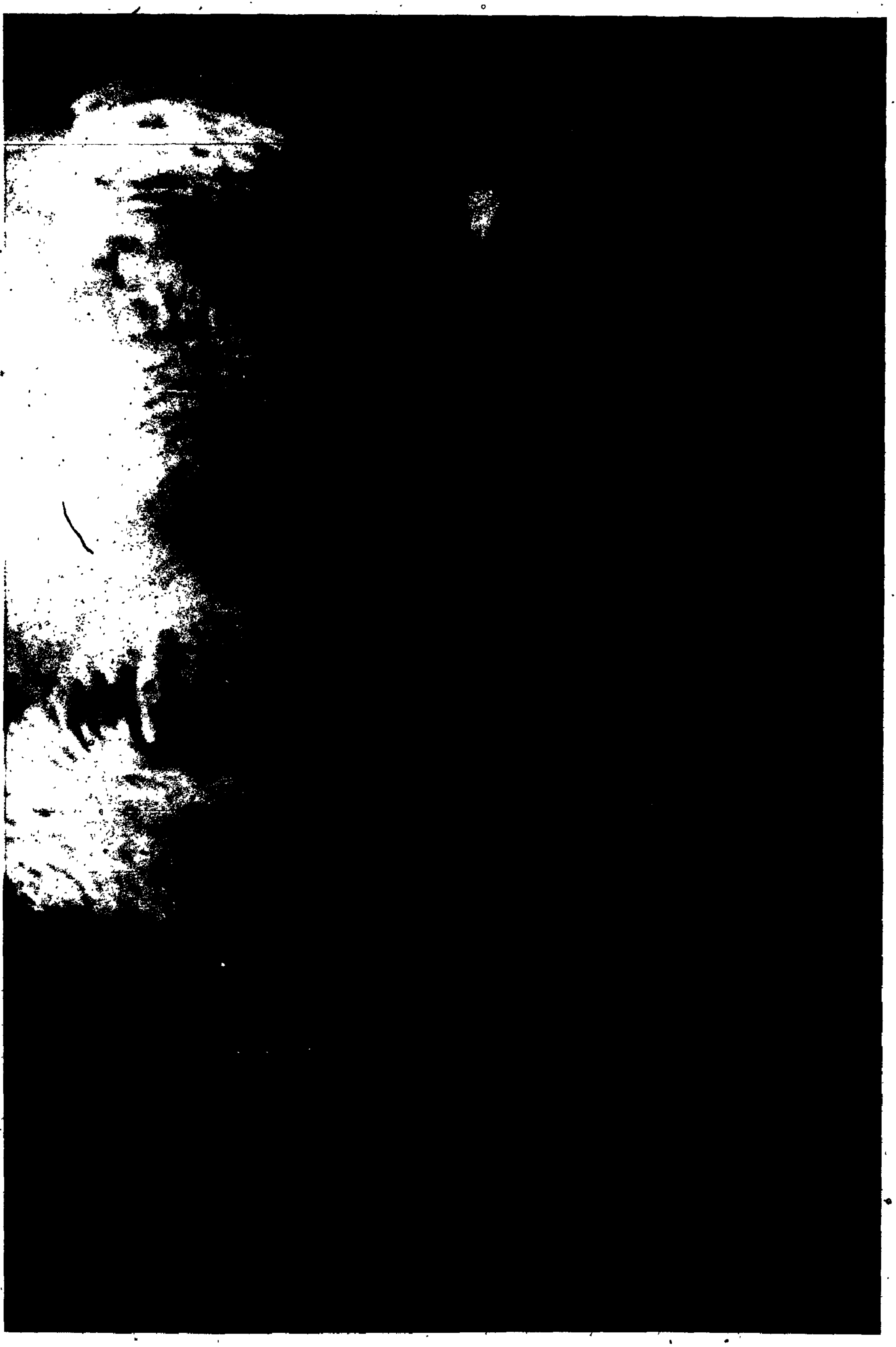


Figure 9b. PECKING MOVEMENTS OF MALE,
WHITE PHASE BLUE GOOSE WHILE GRAZING ON
ELYMUS ARENARIUS AT THE McCONNELL RIVER
N.W.T. 1973.

GRASPING OF THE VEGETATION

Figure 9c. PECKING MOVEMENTS OF MALE,
WHITE PHASE BLUE GOOSE WHILE GRAZING ON
<u>ELYMUS</u> <u>ARENARIUS</u> AT THE McCONNELL RIVER
N.W.T. 1973
INGESTION OF GRASS BLADE

"peck", which may or may not be successful in removing vegetation. Geese normally peck so fast (60-100 pecks per minute) that it is impossible to distinguish successful pecks from unsuccessful ones. Concurrent with the pecking action, already ingested vegetation is pushed down the oesophagus by the action of the tongue and the pressure of additional vegetation accumulating in the upper oesophagus (Ziswiler and Farner 1972). When feeding on fine grasses the same general procedure is used, but the beak is inserted almost perpendicularly into the vegetation and only the terminal nail of the beak is used to grasp vegetation with a forcep-like action. Very fast pecking rates - in excess of 120 per minute - are usually associated with this method, since only a small quantity of vegetation is removed by each peck. This technique is infrequently used by adult blue geese, but it is the major method used by blue goslings, and adult small-billed goose species (<u>Anser rossi</u> and <u>Branta canadensis</u> at the McConnell River).

In rooting - essentially a predatory activity - the powerful bill is thrust rhythmically into the yielding soil, presumably until the beak tip makes contact with a root. The object of desire is then withdrawn in a series of small, backward jerks which superficially resemble the pecking motions of grazing. If a particularly large root is contacted the legs are braced apart and the root may be pulled with such violence that the goose topples over when the radicle finally breaks. Root fragments up to 10cm long may be extracted by this method.

2.4 TIME SPENT IN DIFFERENT ACTIVITIES

The variation in the amount of time allocated to each of the five behaviours in the course of the summer was recorded for both adults and goslings. The methods used for pre-hatch adults, post-hatch adults and goslings differed slightly, and the respective values obtained may not be strictly comparable. Adults do feed in the period between their arrival on the breeding grounds and the inception of incubation, if suitable vegetation is available. However, most time is devoted to the acquisition and defence of a suitable nest site. There is little feeding during incubation (Ankney 1974). The female spends the vast majority of her time incubating, and the male remains in close proximity to the nest. Observation from the arrival of the birds to the first week after hatch were confined to feeding birds. Males were rarely observed to feed in this period, and usually remained alert while the female of the pair fed. The behaviour of feeding females was recorded at one minute intervals for observation periods of up to 30 minutes per individual. Such data can only provide information on the behaviour of females while away from the nest. This technique was also used to collect data on the behaviour of both species during the first week following hatch, when families were leaving the main breeding areas and journeying to the favoured feeding areas. By the second week following hatch geese were dispersed widely over the tundra in loose aggregations of several families. The behaviour of these birds was recorded from raised observation towers using the scan sample technique (Sec. 1.7). The behaviour of every bird whose whole body was clearly visible from one window of the tower was noted at five minute intervals for periods of one hour evenly distributed throughout the daylight hours.

It is almost impossible to determine the activity of small goslings at distances of greater than 200m. Instead, observations were made on the hand-raised goslings. The behaviour of these birds could not mirror exactly that of wild goslings since they had access to neither a parent bird for brooding, nor - during observation periods - sufficient water for bathing or swimming. In addition, the captive birds were given a dietary supplement (Sec. 1.6) which may have modified their behaviour. However, the information obtained from these birds is internally consistent. The behaviour of test groups of three goslings was recorded at 30 sec. intervals for observation periods of one hour, between 10:00 a.m. and 2:00 p.m.

The data are most readily assimilated by considering the variation with time in the expression of each behaviour for both adults and goslings. The percentage values used in the text and figures are means of all observations in 10 day periods. Where observations were not evenly spaced through the period, data points have been located at the median observation day.

Alert (Figure 10a)

Adults spend significantly more time being alert before hatch than after ($t=4.26$, $P < 0.001$). Feeding and being alert are the two major components of adult behaviour, the expression of one varying inversely with the variations in the other. Time spent alert is at a minimum in the first week following hatch, when considerable time must be devoted to brooding the goslings. Goslings spend less than 10% of their time being alert, this is significantly less than the time spent alert by the adults (Table 1).

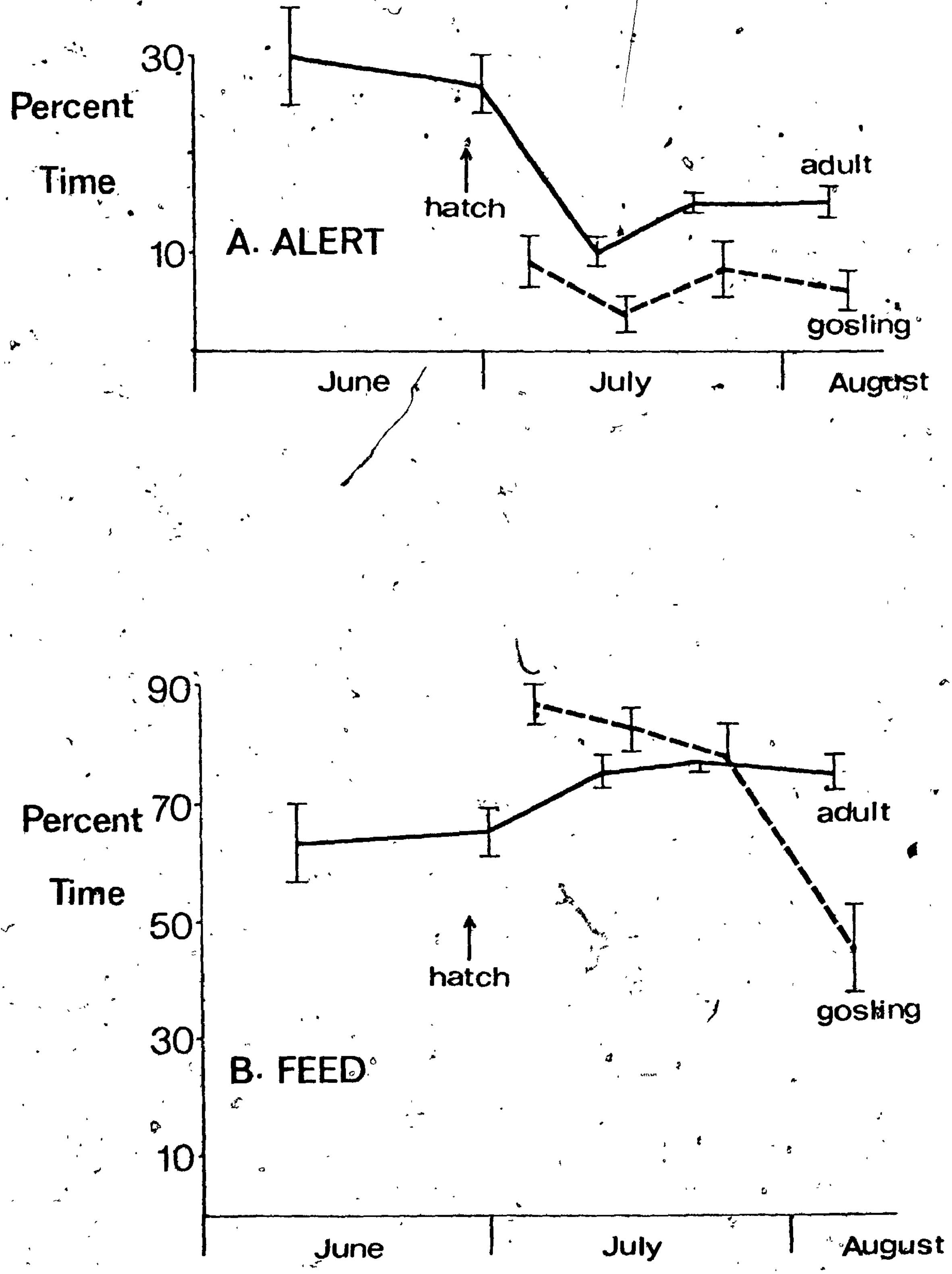
Feeding (Figure 10b)

In 1971 and 1973 the majority of resident geese arrived on the breeding grounds in the last week of May. At this time more than 40% of the area was snow covered, but females were observed rooting in

Figure 10. VARIATION IN PROPORTION OF DAYLIGHT HOURS ALLOCATED TO DIFFERENT ACTIVITIES BY BLUE GEESE AND GOSLINGS WITH TIME, AT THE McCONNELL RIVER, N.W.T. 1973

A. TIME SPENT ALERT

B. TIME SPENT FEEDING


A. ALERT
Percent Time
30
10
hatch
adult
gosling
June
July
August
B. FEED
Percent Time
90
70
50
30
10
hatch
adult
gosling
June
July
August

BEHAVIOUR	ADULT		GOSLINGS		
			ALL OBSERVATION		TO AUGUST 1
ALERT	14.9 ± 0.58	***	7.1 ± 1.20 (49)		7.6 ± 1.46 (35)
FEED	76.4 ± 0.66 (421)		71.9 ± 3.50	*	82.7 ± 2.26
PREEN	1.0 ± 0.1[illegible]	***	5.9 ± 1.16	**	2.0 ± 0.44
REST/BROOD	6.1 ± 0.42	***	14.9 ± 2.62	*	7.5 ± 1.55
OTHER	1.6 ± 0.29	***	0.2 ± 0.15		0.3 ± 0.22

Table 1. PERCENTAGE OF DAYLIGHT HOURS SPENT IN DIFFERENT ACTIVITIES BY BLUE GEESE AND GOSLINGS AT THE McCONNELL RIVER, N.W.T. IN 1973. ASTERISKS INDICATE THE PROBABILITY (FROM A t TEST) OF THE DIFFERENCE BETWEEN VALUES ON EITHER SIDE OCCURRING BY CHANCE. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. ALL TABLED VALUES ARE GIVEN AS MEAN VALUE ± ONE STANDARD ERROR, FOLLOWED BY THE SAMPLE SIZE IN BRACKETS.

suitable areas. Although incubating females rarely leave the nest, 65% of the time away from the nest is spent feeding.

After hatch both sexes feed extensively. The amount of time spend feeding increases significantly above the level during incubation ($t = 3.34$, $P < 0.01$). It remains constant at 77% of the daylight hours for the rest of the summer. This is equivalent to 15 hours feeding per day.

Goslings do not feed in the first two or three days following hatch, but survive on the remnants of the embryonic yolk sac. Once this has been completely absorbed, they spend up to 90% of their time feeding. The amount of time spent feeding decreases during August; before this it is higher than the amount of time spent feeding by the adults (Table 1). There is a significant decrease in the amount of time spent feeding in August (Table 1). This is in part an artifact. The high protein supplement resulted in the goslings attaining by mid-August a weight not normally reached by wild goslings until migration in the last week of August or first week of September. The test goslings responses were not, therefore, typical of wild birds. However, there is a significant linear correlation between date and time spent feeding for the individual observations up to August 1 ($r = -0.57$, $n = 18$, $P < 0.05$). This implies that at least some of the decrease in time spent feeding in August had a real basis. Such a decrease may have been the result of increased feeding efficiency with increased bill size and potential pecking rate.

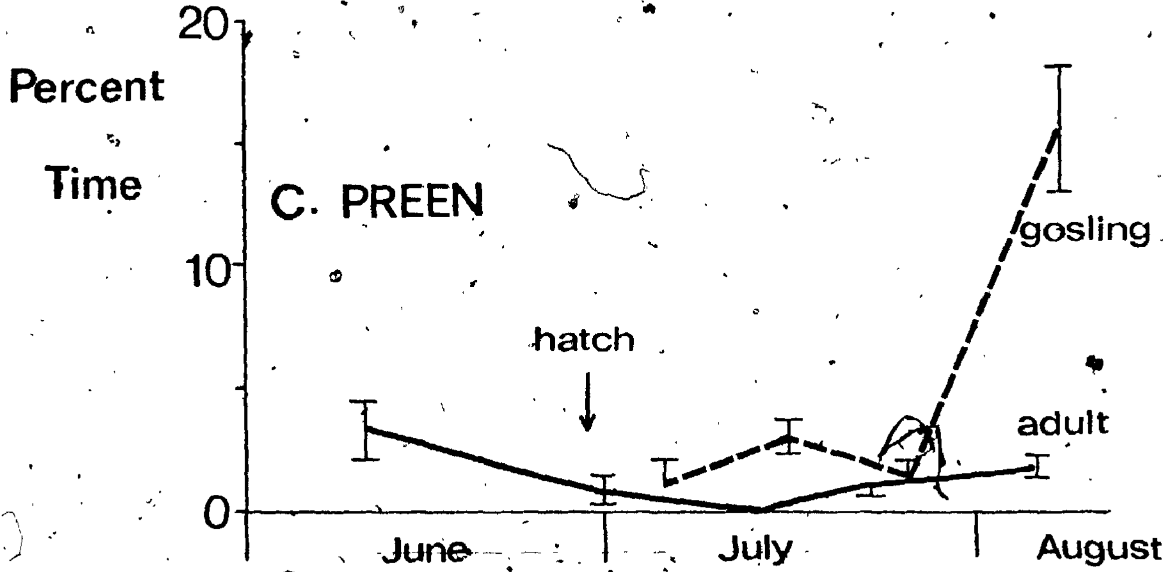
Preening (Figure 10c)

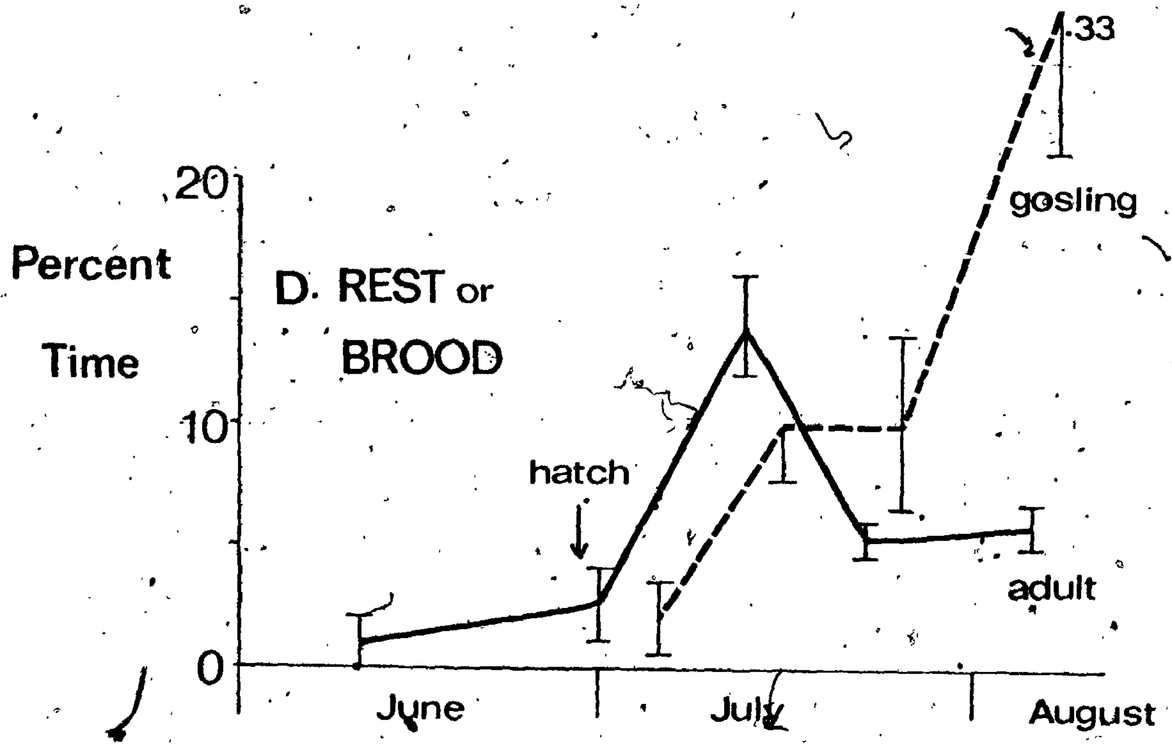
Preening activity did not change significantly during the summer; except for the fact that goslings showed an increase in this

Figure 10 cont. VARIATION IN TIME ALLOCATED TO DIFFERENT BEHAVIOURS BY BLUE GEESE AND GOSLINGS AT THE McCONNELL RIVER, N.W.T. IN 1973.

C. TIME SPENT PREENING

D. TIME SPENT ROOSTING OR BROODING


20
Percent
Time
C. PREEN
10
0
hatch
gosling
adult
June
July
August


33
20
Percent
Time
D. REST or
BROOD
10
0
hatch
gosling
adult
June
July
August

activity in August when the major flight and contour feathers were erupting. Goslings spent significantly more time preening than adults up to August 1 ($t = 2.20$, $P < 0.05$).

Roosting and Brooding (Figure 10d).

As already noted (Sec. 1.7) this is a composite category. Adult behaviour shows a peak in this activity in the first week of July. This value is significantly higher than the values for the preceeding and following 10 day periods ($t = 4.48$, and 4.33 respectively, $P < 0.01$). After the first two weeks of July the value remains constant at 5% of total time. Only in August do goslings spend significantly more time resting than adults (Figure 10d). This may be a consequence of the decrease in time spent feeding by goslings in this month. The gosling values may be lower than the appropriate values for wild goslings, as the test birds did not have access to a potentially brooding adult - although they did tend to huddle together when under thermal stress. Resting is the major alternative activity to feeding for goslings. Increase in the time spent in one activity is generally achieved by decreasing the time allocated to the other activity.

Other Activities

Other behaviours such as bathing, swimming, and inter-family aggression occurred too infrequently to be individually scored. Although adults spent significantly more time in these activities than goslings (Table 1) this has little or no biological meaning, since the goslings had no opportunity to bathe or swim during the observation periods.

2.5 LENGTH OF A FEEDING BOUT

Variations in the length of a feeding bout for both sexes are indicated in Figure 11. Males consistently fed for shorter lengths of time than females throughout July and August. This is partially explained by differences in alert behaviour between the two sexes. Being alert is an intervening behaviour either between successive bouts of the same behaviour or as part of the transition from one set of activities to another. No other behavioural category has this patterning. Thus a feeding sequence consists of strictly alternating bouts of feeding and being alert, the terminal alert act precedes the initial act of the next behavioural sequence. The difference in feeding behaviour between males and females may, therefore, be due to a simple difference in the lengths of their alert bouts while feeding. This is partially true; in a sample of ten pairs taken on the same day, male alert bouts averaged 4.8 ± 0.41 secs while females' averaged 2.5 ± 0.30 secs. This difference is highly significant ($P < 0.001$, two-way analysis of variance), but does not completely explain the observed difference in bout lengths which was more than 7 secs at the time of observation. Thus the incidence of male alert bouts must have been more frequent than female bouts. We can test this hypothesis empirically. At the time of observation, behaviours other than feeding and being alert occupied 8% of the birds' time. Assuming that alert behaviour is evenly distributed amongst all activities, then since alert behaviour occurred 15% of the time - 91% of the time was devoted to feeding sequences (77% + [15 x 0.92]%). At this time male feeding bouts averaged 19.2 secs, therefore (19.2/[19.2 + 4.8]) x 91 = 73.6% of male time should have been spent feeding. Similarly females should have spent (26.5/[26.5 + 2.5]) x 91 = 84.8% of their time feeding. Assuming an equal sex ratio, we expect all geese to have spent (84.8 + 73.6)/2 % of their time feeding. This estimate of 77.8%

lies within the 95% confidence interval of the observed value of 77.2 ± 0.66% (n=265). The arrangement has the additional advantage that - provided feeding and alert bouts are of relatively invariant length - the alert periods of the two members of a pair should never overlap, thus ensuring maximum surveillance efficiency.

The length of male and female feeding bouts increases progressively throughout July and August (Figure 11). The increase in early July is explicable in terms of the concomitant increase in total time spent feeding (Sec. 2.4). However, the later increases do not coincide with any significant changes in this variable. Vegetation quality does decline in the latter half of the summer (Sec. 2.2). Thus an individual must cover a greater area during a feeding bout in August to encounter the same overall quality of vegetation than it did in July. Since an increase in the rate of walking seems to decrease intake (Chapter 4), it would seem more profitable to increase feeding bout length and decrease pecking rate at this time. Evidence for this contention will be presented in Sec. 2.8.

2.6 RATE OF PECKING

When birds first arrive on the breeding grounds little or no vegetation is available. The roots of various monocotyledons provide the major potential food source. Pecking rates at this time are very low (Figure 12); in fact "pecking" is a misnomer for a process primarily involves probing and pulling. As new grass growth appears this becomes the predominant food item, although the leaves of certain dicotyledons are consumed. Pecking rate increases to a maximum in mid-July and then declines (Figure 12). The shape of this curve almost exactly duplicates

Figure 11. VARIATION IN LENGTH OF FEEDING BOUT WITH TIME FOR MALE AND FEMALE BLUE GEESE AT THE McCONNELL RIVER, N.W.T. 1973

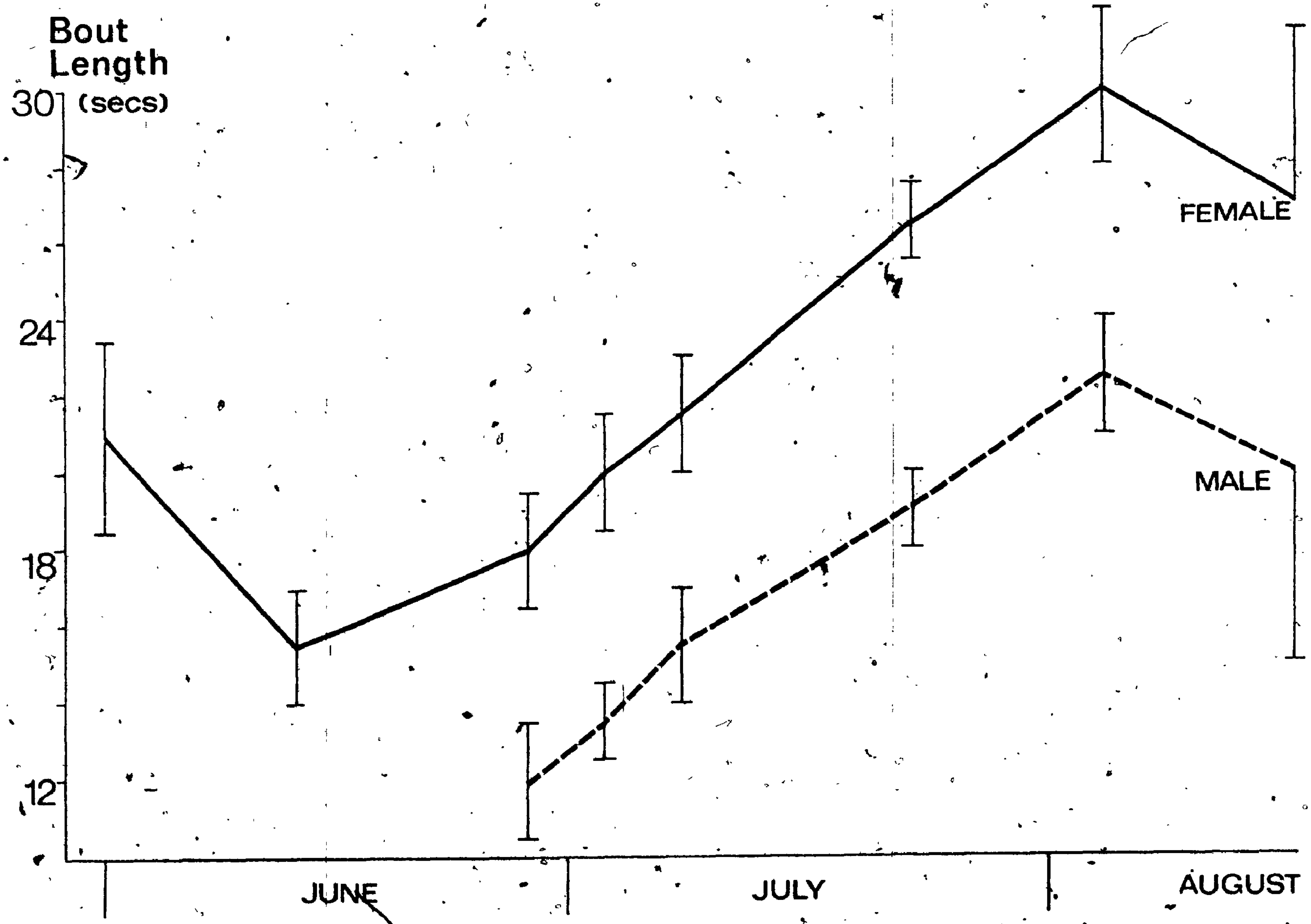
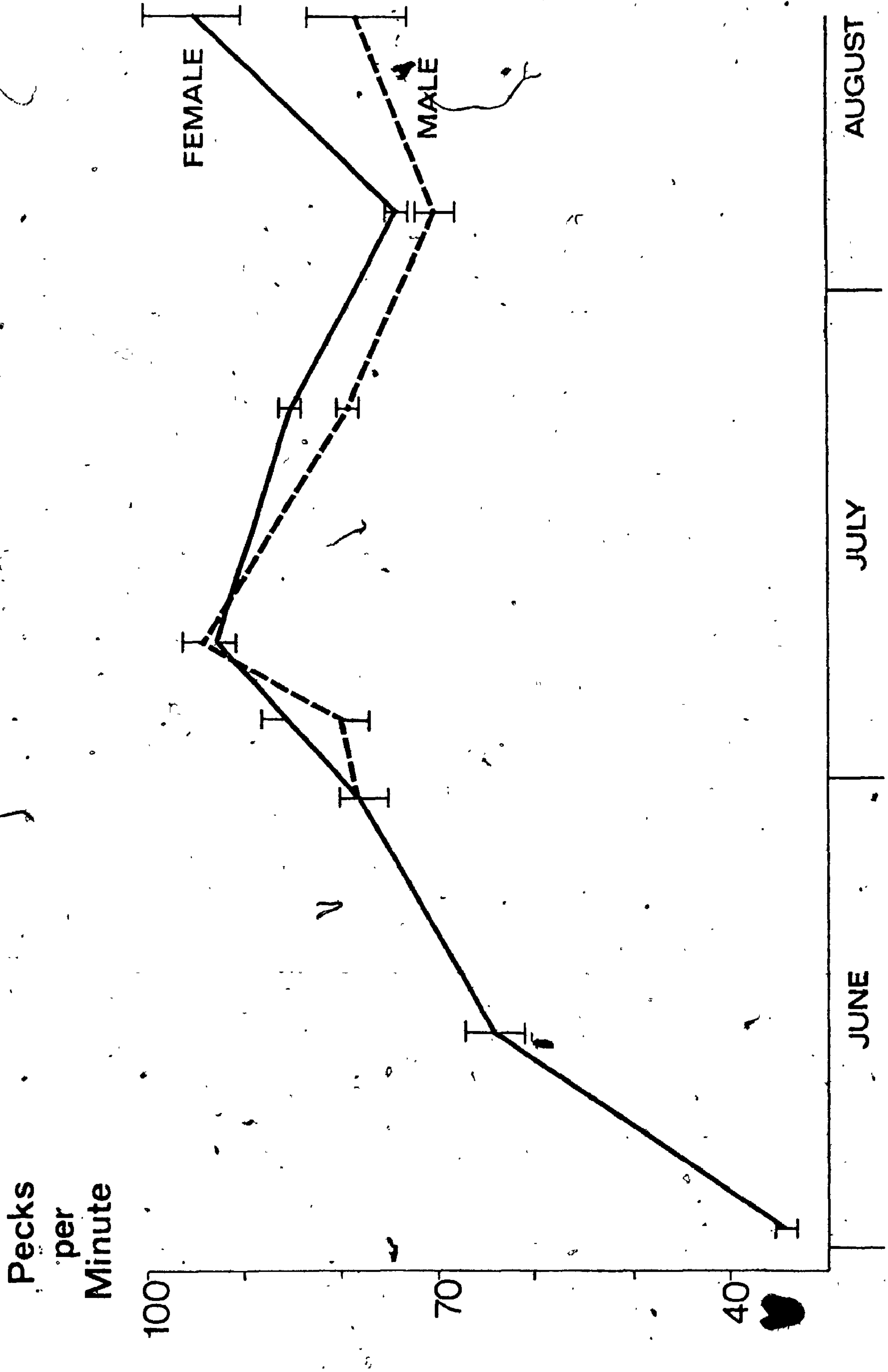

Bout Length (secs)
30
24
18
12
FEMALE
MALE
JUNE
JULY
AUGUST

Figure 12. VARIATION IN THE RATE OF PECKING WHILE FEEDING WITH TIME FOR MALE AND FEMALE BLUE GEESE AT THE McCONNELL RIVER, N.W.T. 1973


Pecks per Minute
100
70
40
JUNE
JULY
AUGUST
FEMALE
MALE

that for the variation in grass protein content (Figures 7 and 8). There is very little root feeding in August, probably because the ground is too dry for efficient probing. Males and females show identical patterns of variation, but males peck consistently slower than females (Figure 12).

Goslings show a progressive increase in pecking rate that continues throughout the whole summer (Figure 13), attaining a value in August which is in excess of the maximum recorded for adults. It is probable that goslings peck at a rate close to their physical limit.

2.7 RATE OF WALKING

The number of steps per minute taken by adults shows no obvious trend through the summer (Figure 14). Its constancy throughout July and August is consistent with the hypothesis outlined in Sec. 2.5. The very high rate shown by females in June is probably a response to newly sprouting vegetation, which is both high in nutrients (a "nutrient" is defined as "any property of the food which affects the welfare of the animal" [Westoby 1974]) and easily digestible (due to its low cellulose content), but is widely scattered. In this case the nutritional advantages would probably outweight the decrease in intake associated with rapid walking.

Goslings show a progressive decrease in the rate of walking during the summer (Figure 13). This is probably related to the concurrent growth in tarsus length, so that distance covered per unit time should have been relatively constant throughout the summer. No measurements of the variation in gosling pace length with time were made.

Figure 13. VARIATION WITH TIME IN THE RATE OF PECKING AND WALKING WHILE FEEDING FOR CAPTIVE BLUE GOSLINGS AT THE McCONNELL RIVER, N.W.T. 1973

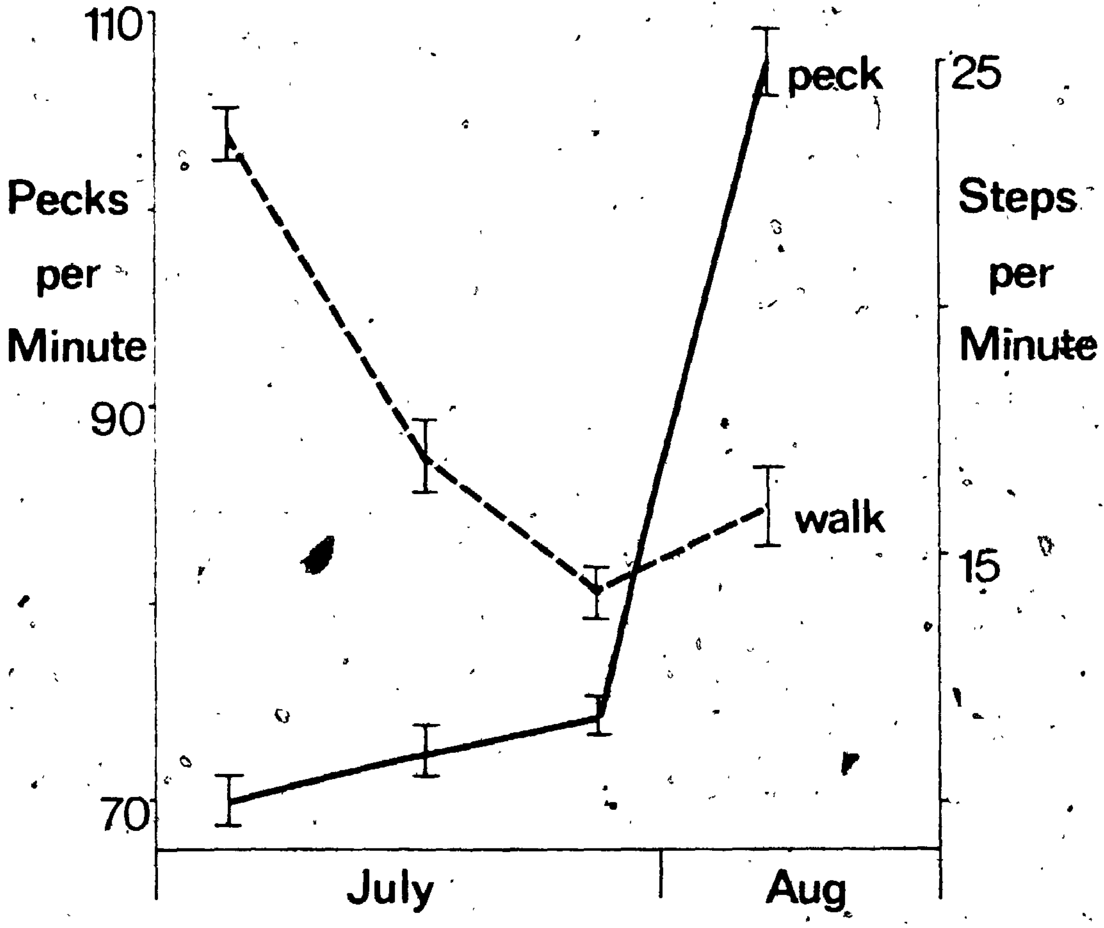
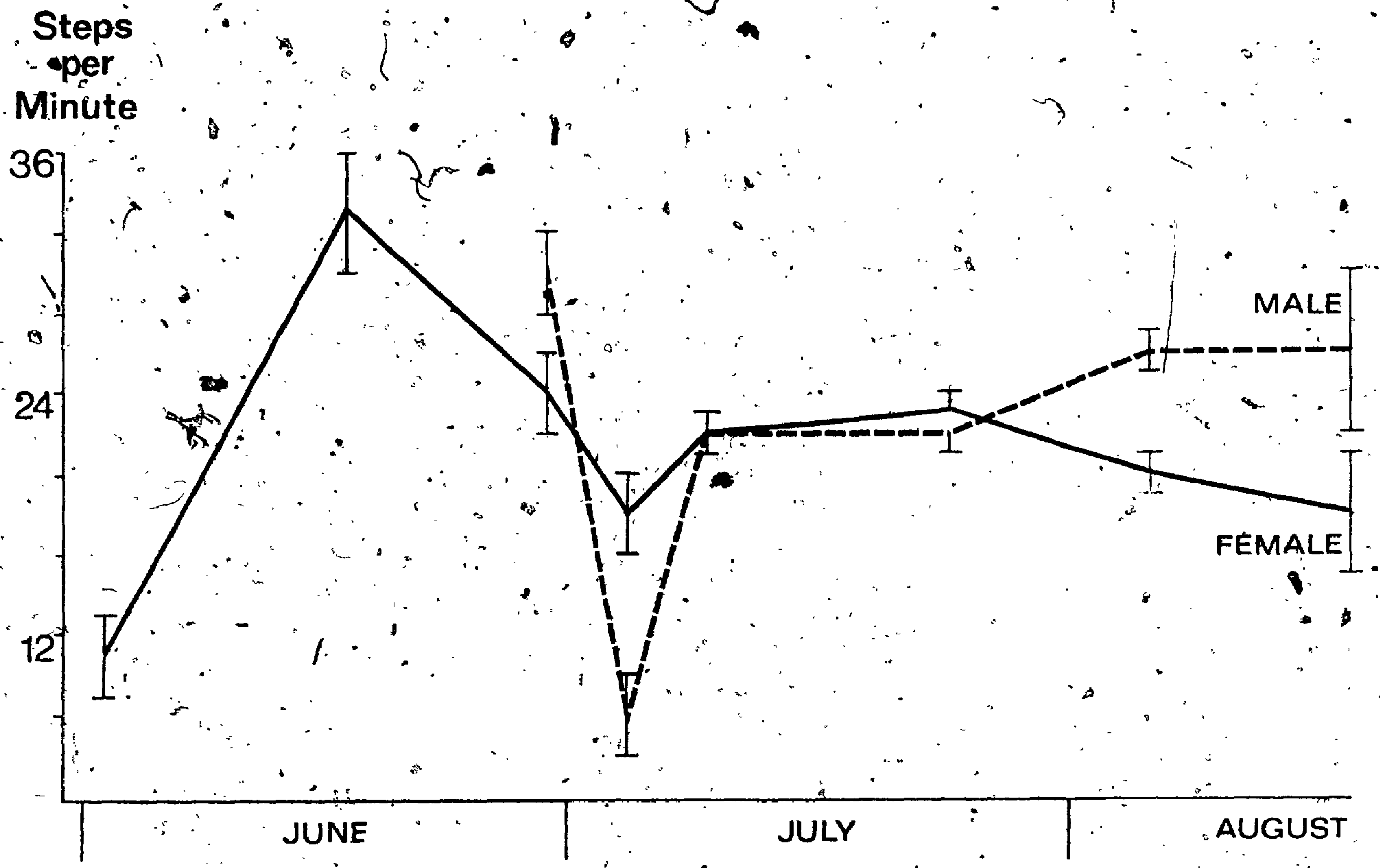

110
Pecks per Minute
90
70
25
Steps per Minute
15
peck
walk
July
Aug

Figure 14. VARIATION WITH TIME IN THE RATE OF WALKING WHILE FEEDING FOR MALE AND FEMALE BLUE GEESE AT THE McCONNELL RIVER, N.W.T., 1973



Steps per Minute
36
24
12
JUNE
JULY
AUGUST
MALE
FEMALE

2.8 DISCUSSION

The overall variations in the chosen parameters of feeding behaviour can be explained in the context of parental responsibility and the changes in vegetation quality and availability. Some enigmas remain, however. Throughout July and August daylength - and therefore the time available for feeding - is decreasing; yet during this period the proportion of time devoted to feeding remains constant (Figure 10b). Thus the actual amount of time spent feeding decreases during the summer. Some of this decrease is explained by the steady increase in vegetation protein content which continues until late July. However, after the first week of August both the quantity and the quality of the available vegetation is in decline. Again there is a partial explanation in the decline in vegetation water content at this time (Figures 5 and 6). If the volume of vegetation removed per peck remains constant, then a beakfull of vegetation at the end of the summer contains more protein per unit of fresh weight at the end of the summer than a July beakfull. In addition, it is probably impossible for the birds to increase the total time spent feeding above this level. Even small passerines feeding on short winter days do not spend more than 80% of their time feeding (Gibb 1956, 1958, 1960); a limit presumably set by the demands of other maintenance activities. Blue geese do in fact have a strategy to partially overcome this problem - by dividing the time necessarily spent alert unequally between the sexes and between adults and goslings. Alert behaviour serves mainly to protect the young, since there are few if any predators other than man capable of capturing an adult in the arctic. Adults spend nearly twice as much time as goslings alert, thus enabling the goslings to devote up to 90% of their time to feeding. A similar strategy was observed by Owen (1972) in over-wintering families of white-fronted geese in England. Additionally, males spend twice as much time alert as females, thus allowing the females to spend 85% of their time feeding. The effectiveness of this strategy is underlined by the fact that females increase their body weight by 30% in July and August, whereas male weight remains constant (Ankney 1974).

Grazing tactics - the quantitative changes in behavioural expression - vary in an obvious way with the changes in vegetation parameters until late July. At this time vegetation quality declines, but bout length continues to increase and pecking rate decreases. As the availability of high quality vegetation declines a grazing bird must cover a greater area to obtain the same amount of vegetation. This can be achieved in two ways: by walking faster, or feeding in longer bouts. It will later be shown that increasing the speed of walking adversely affects intake. Thus the optimal tactic should be to maintain the number of pecks per bout relatively constant and to increase bout length - and therefore selectivity - as vegetation quality decreases. As Table 2 indicates, the number of pecks per bout does vary less than either bout length or peck rate. This partial confirmation is gratifying but not totally convincing. An adequate explanation is only possible with a knowledge of the precise effects of variations in feeding behaviour on actual intake.

It is clear that the chosen behavioural parameters do vary in a qualitatively predictable manner with the observed changes in vegetation parameters. They thus satisfy my criterion for biological validity. However, to truly step inside the portals of science it is necessary to attempt to quantify the observed relationships. This can only readily

DATE	BOUT LENGTH (SECS)	CHANGE	PECKS/ MIN	CHANGE	PECKS/ BOUT	CHANGE
10 JULY	21.3		93.5		33.2	
		24%		11%		11%
23 JULY	26.5		83.1		36.7	
		12%		11%		1%
7 AUGUST	29.8		74.1		36.8	
		9%		29%		9%
20 AUGUST	27.2		95.4		43.2	

Table 2. PERCENTAGE CHANGE WITH TIME OF SOME FEEDING BEHAVIOUR PARAMETERS FOR FEMALE BLUE GEESE AT THE McCONNELL RIVER, N.W.T. IN JULY AND AUGUST, 1973

be achieved by imposing some control on the variations of the chosen vegetation parameters.

2.9 SUMMARY

Adult blue geese spend 14 to 17 hours per day feeding in July and August, goslings spend up to 18 hours in this activity. The major alternative activity for adults is being alert. Males are alert more frequently and for longer periods than females. This enables the females and goslings to spend a maximal amount of time feeding. Changes in feeding behaviour can be related to concurrent changes in the nature and availability of food items.

VEGETATION AND BEHAVIOUR

"In order to follow the indications of instinct, there is no need to perceive objects, it is enough to distinguish properties." Henri Bergson.

3.1 INTRODUCTION

Analytical studies of the way in which feeding behaviour varies with changes in food characteristics have predominantly employed laboratory populations of predators. In addition, they have concentrated primarily on the visual cues associated with prey objects: colour (Ginetz and Larkin 1973); contrast (Ware 1971); size (Holling 1968, Ware 1972); or abundance (Holling 1966, Ware 1972, Hardman and Turnbull 1974). A notable exception is the study by Grime et al (1970) of the role of chemical and tactile cues in the food plant preference of _Cepaea nemoralis_. Field oriented studies have similarly concentrated on the importance of visual cues to avian predators (Tinbergen et al 1962, Croze 1970, Smith 1974b). These preoccupations are understandable. Manipulation of the form of prey items is relatively easy and a subject's responses to visual cues are readily interpreted by a human observer.

Field studies of herbivores have had a strong practical bias. For vertebrates it is standard practice to compare the actual and potential diets of the studied species, either in terms of species consumed (Lieff et al 1970, Owen and Kerbes 1971, Dunnet et al 1973, Voth et al 1973), or nutrient composition (Pulliainen 1970, Moss 1972, Salo 1973), or both (Gardarsson and Moss 1970). The disproportionate representation of a particular species or nutrient component in the diet is taken to indicate selection - presumably for the item or some associated cue (Ivlev 1961). An intrinsic problem is the exact definition of the "potential diet". In addition, elucidation of the dietary cues which are modifying behaviour is difficult. Environmental manipulation has generally involved observation of the subject species' responses to partial fertilization of the food plants (Miller 1968, Thomas et al 1964). Again it is difficult to determine the cues being used because of the manifold effects of fertilization on vegetational characteristics. At a more realistic level, Owen (1972, 1973) compared the feeding behaviour of grazing white-fronted geese and wigeon (Anas penelope) on naturally occurring patches of different plant species. Moss (1972) gained some quantitative insight into the selective feeding of red grouse (Lagopus lagopus scoticus) by determining the slope of the regression line of vegetation composition on crop composition for selected nutrients. The slopes for nitrogen and phosphorous were less than unity, indicating that selection was greatest where vegetation nutrient content was lowest.

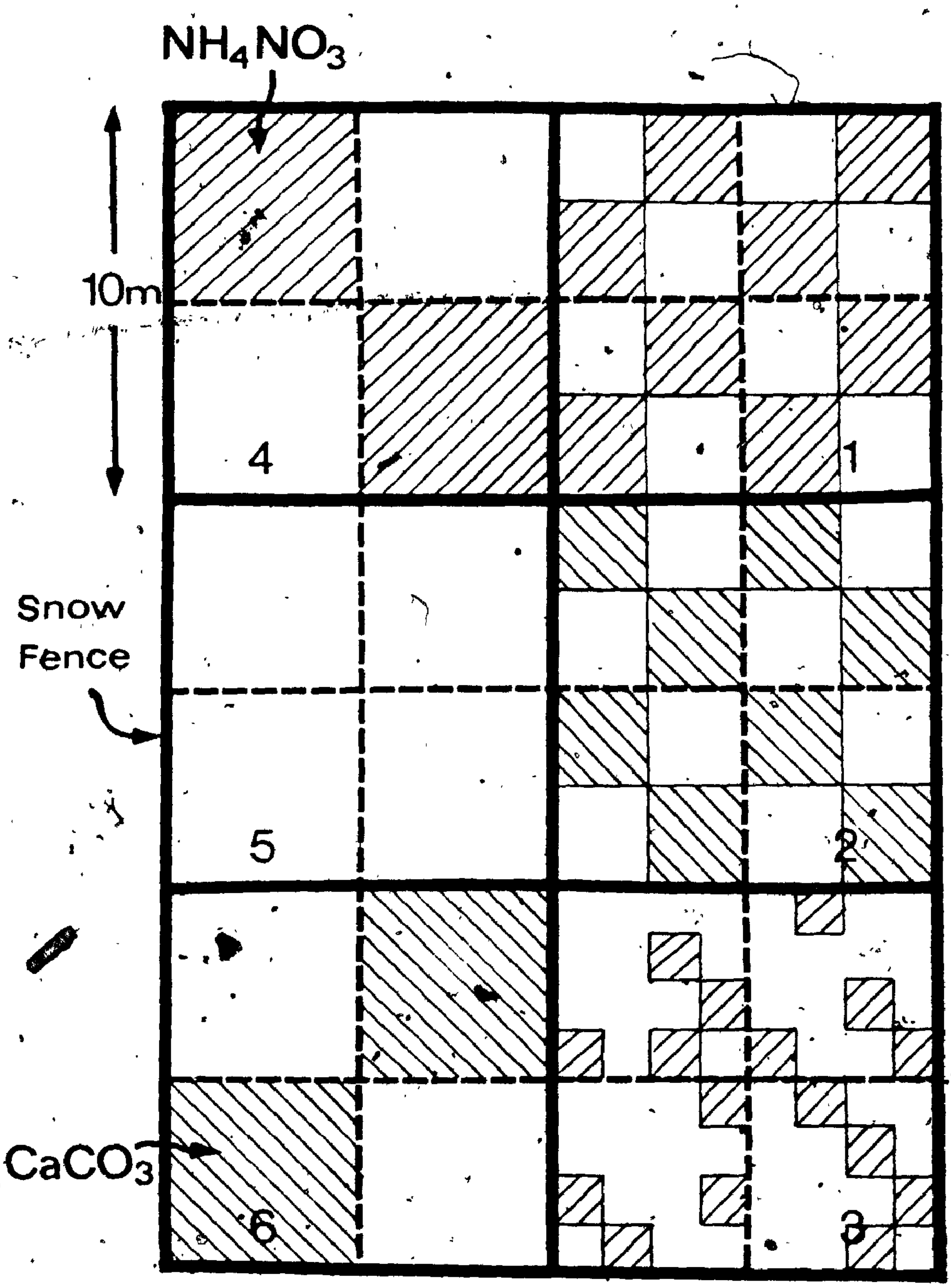
Lieff (1973) has already shown that geese at the McConnell River will feed preferentially on nitrogen fertilized vegetation. However, the fertilization procedure altered the appearance of the vegetation, making it impossible to decide exactly what cues were being responded to. The experiments described in this chapter were originally envisaged as a purely qualitative test of the response of blue geese to enhanced vegetation protein content, by eliminating as many of the secondary cues associated with fertilization as possible. However, since the fertilization had a non-uniform effect on the vegetation, it was possible to establish a quantitative relationship between the variations in vegetation quantity and quality (as previously defined) and variations in feeding behaviour.

3.2 METHODS

Three groups of 10, individually neck-banded, yearling blue geese were used. They were tested in a 30m x 20m arena which could be divided with snow fencing into six, 10m square test pens (Figure 15). Details of the soil characteristics of each pen are given in Appendix 2. Two days before a test pen was to be used, the vegetation in it was mowed to a uniform height. Initial tests were performed in each of the six pens of the untreated arena to obtain baseline behavioural data. Three randomly chosen pens were then treated with ammonium nitrate pellets (34% N) at the rate of 25g.m^{-2} (initial trials had indicated that this rate gave optimal enhancement of vegetation protein content), in an alternating pattern of 5m, 2.5m or 1.25m squares. Two other randomly chosen pens were treated with 30g.m^{-2} of lime in 5m or 2.5m squares. The sixth pen was left untreated as a control (Figure 15). The second set of trials was delayed until two rain storms had washed the fertilizer into the soil. The centre of each pen was marked with a 1.5m stake, and the corners of each square with 15cm orange pegs. These markers did not appear to influence the behaviour of the geese in any way. Water was provided in a large plastic tub at the centre of the pen. A 0.75m square exclosure was located in each quarter of the test pen. The vegetation in each quarter was sampled after the last test day. In two pens it was also sampled before the first test day. Pens were used in a random sequence, the three groups of birds being tested in a random order on consecutive days.

Each group of birds was introduced into the pen at approximately 2:00 p.m.. Observations were always made in the first three hours of daylight on the following day. Additional observations were usually

Figure 15. DESIGN OF ARENA USED TO ANALYZE GRAZING BEHAVIOUR OF YEARLING BLUE GEESE AT GUELPH, ONTARIO 1972. SHADED AREAS INDICATE DISTRIBUTION OF FERTILIZED SQUARES.


NH_4NO_3
10m
Snow
Fence
$CaCO_3$
4
1
5
2
6
3

made in the hour before sunset on the day of the birds' introduction, and between 12:00 a.m. and 2:00 p.m. on the following day. Observations were made from 10 to 20m with 8x40 binoculars. I was partially screened by the slats of the snow fencing. Data collected in the first 30 mins of observation, and during any period when the birds seemed unusually disturbed were discarded. The behaviour of each bird, and the test square it occupied were recorded at five minute intervals throughout the observation period. Feeding behaviour was measured as frequently as possible. An attempt was made to divide data collection equally among the squares of the pen; however, during each observation period the birds tended to favour one section of the pen. The design of the fertilization scheme was such that no matter what section the birds preferred, they had a choice between fertilized and unfertilized squares. Observations were, therefore, approximately equally divided between fertilized and unfertilized squares. Additionally, as many observations as possible were made of the behaviour of an individual before and after it crossed the boundary between two squares. Data were transferred from the data sheets to magnetic tape via a PDP-10 remote terminal. All data handling and calculation was performed by specially written computer programmes.

The number of droppings deposited in each square of a test pen was counted after each trial, and used as an index of the proportion of time spent by geese in each square (Owen 1971).

3.3 QUALITATIVE RESPONSE TO FERTILIZATION

Total Time Spent in Each Square

The birds spent significantly more time on the nitrate fertilized squares than on the paired unfertilized squares in all trials but one (Table 3). There is no consistent, significant difference in square usage in the control pen nor in the 2.5m lime pen, but significantly more time was spent on the unfertilized squares of the 5m lime pen (Table 3).

Percent Time Spent Feeding

Geese consistently spent more time feeding on the nitrate fertilized squares than on the unfertilized squares (Table 4); there was no consistent response to the lime treatment. Since the individual estimates were based on a small number of birds, there is an over-representation of zero values in the individual distributions and standard statistical tests cannot be applied to the data. However, a better approximation to a normal distribution was obtained by transforming every datum by taking the square root of that value plus one half. There is a highly significant difference between the amount of time spent feeding on nitrate fertilized and unfertilized squares (paired $t = 5.71$, $P < 0.001$), but no significant difference for the lime data (paired $t = 0.56$). The transformed data set is shown in Appendix 3.

Length of Feeding Bout

Feeding bouts were significantly longer on nitrate fertilized squares than on the respective unfertilized squares. There was no significant difference for the lime and control pens (Table 5).

Pecking Rate

The difference in pecking rate between unfertilized and nitrate fertilized squares is highly significant; there is no significant difference in the results for the lime treatment and control (Table 6). Birds peck fastest on nitrate fertilized squares.

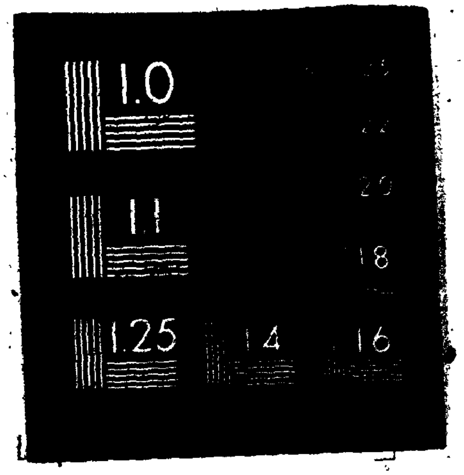
SQUARE SIZE		UNFERTILIZED	FERTILIZED	CHI-SQUARE
5m	NH_4NO_3	29	123	58.1 ***
		114	193	20.3 ***
		142	216	15.3 ***
2.5m	NH_4NO_3	205	415	71.1 ***
		238	365	26.7 ***
		165	192	2.0
1.25m	NH_4NO_3	238	369	28.3 ***
		65	132	22.8 ***
		175	357	62.3 ***
5m	$CaCO_3$	128	46	38.6 ***
		64	38	6.6 *
		130	78	13.0 **
2.5m	$CaCO_3$	74	53	3.5
		64	48	2.3
		43	63	3.8
CONTROL		144	100	7.9
		244	226	0.7
		24	107	52.6 ***

Table 3. NUMBER OF DROPPINGS DEPOSITED IN A TEST PERIOD ON EQUAL-SIZE FERTILIZATION PLOTS BY THREE GROUPS OF TEN GRAZING BLUE GEESE AT GUELPH, ONTARIO IN 1972. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

TREATMENT	SQUARE	UNFERTILIZED	FERTILIZED
		12.2 ± 3.27 (29)	26.7 ± 5.37 (27)
	5m	12.3 ± 4.47 (15)	25.0 ± 4.46 (23)
		9.5 ± 7.35 (14)	14.9 ± 3.15 (27)
		15.7 ± 3.97 (35)	34.8 ± 6.88 (34)
NH_4NO_3	2.5m	11.5 ± 3.28 (29)	38.6 ± 10.2 (20)
		4.6 ± 1.47 (31)	14.0 ± 5.39 (27)
		12.1 ± 3.60 (30)	26.2 ± 6.24 (28)
	1.2[illegible]	19.6 ± 3.77 (30)	28.1 ± 5.90 (30)
		34.9 ± 7.33 (16)	37.7 ± 8.92 (16)
		PAIRED 't' = 5.71, d.f. 8, $P < 0.001$	
		13.7 ± 3.80 (27)	21.4 ± 6.07 (25)
	5m	18.0 ± 5.83 (11)	22.2 ± 4.57 (29)
		25.3 ± 4.99 (34)	20.6 ± 4.90 (29)
$CaCO_3$			
		32.7 ± 6.01 (26)	35.0 ± 5.39 (27)
	2.5[illegible]	18.8 ± 6.22 (24)	9.7 ± 2.27 (33)
		16.0 ± 5.47 (27)	11.3 ± 3.08 (27)
		PAIRED 't' = 0.56, d.f. 5, n.s.	

Table 4. PERCENTAGE TIME SPENT FEEDING BY CAPTIVE BLUE GEESE ON PAIRED, FERTILIZED AND UNFERTILIZED VEGETATION SQUARES AT GUELPH, ONTARIO 1972.

2 OF/DE 3



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TREATMENT	SQUARE	UNFERTILIZED	FERTILIZED
NH_4NO_3	5m	14.0 ± 3.23 (15)	13.4 ± 1.77 (21)
		9.2 ± 1.72 (11)	15.5 ± 2.12 (48)
		10.0 ± 3.00 (2)	15.8 ± 1.47 (36)
	2.5m	14.4 ± 1.31 (20)	18.1 ± 1.69 (28)
		12.0 ± 1.16 (30)	11.6 ± 2.07 (17)
		11.8 ± 1.90 (14)	18.5 ± 3.14 (32)
	1.25m	12.8 ± 1.31 (22)	15.9 ± 1.81 (18)
		14.2 ± 1.57 (29)	20.6 ± 4.16 (16)
		11.7 ± 1.02 (32)	19.0 ± 2.93 (20)
		PAIRED 't' = 4.22, d.f. 8, $P < 0.01$	
$CaCO_3$	5m	10.5 ± 0.97 (38)	11.4 ± 1.82 (33)
		10.0 ± 1.73 (5)	12.2 ± 0.98 (56)
		12.8 ± 1.25 (37)	13.6 ± 1.19 (32)
	2.5m	17.1 ± 1.92 (28)	15.0 ± 1.34 (35)
		15.2 ± 2.39 (15)	9.9 ± 1.12 (22)
		13.7 ± 1.60 (17)	17.8 ± 2.99 (18)
		PAIRED 't' = -0.07, d.f. 5, n.s.	
CONTROL	5m	15.5 ± 1.17 (72)	14.8 ± 0.84 (104)

Table 5. MEAN LENGTH OF FEEDING BOUT (SECS.) FOR BLUE GEESE GRAZING ON FERTILIZED AND UNFERTILIZED VEGETATION SQUARES AT GUELPH, ONT. 1972.

TREATMENT	SQUARE	UNFERTILIZED	FERTILIZED
NH_4NO_3	5m	54.1 ± 2.67 (22)	69.2 ± 2.36 (30)
		59.2 ± 2.97 (18)	64.7 ± 1.87 (59)
		51.1 ± 0.33 (2)	60.9 ± 2.15 (42)
	2.5m	46.0 ± 3.23 (25)	59.0 ± 3.28 (32)
		54.9 ± 2.04 (33)	65.[illegible] ± 2.89 (19)
		64.2 ± 4.21 (16)	68.0 ± 3.07 (35)
	1.25m	60.0 ± 2.71 (28)	65.7 ± 2.86 (19)
		57.9 ± 3.35 (33)	72.8 ± 3.50 (23)
		70.0 ± 3.26 (35)	85.1 ± 3.50 (26)
		PAIRED 't' = 6.92, d.f. 8, $P < 0.001$	
$CaCO_3$	5m	52.3 ± 2.59 (43)	49.6 ± 2.60 (34)
		58.3 ± 3.22 (5)	57.4 ± 2.02 (62)
		60.4 ± 3.33 (41)	65.1 ± 3.28 (33)
	2.5m	67.7 ± 2.66 (42)	71.2 ± 2.58 (44)
		65.6 ± 4.21 (17)	61.4 ± 4.25 (30)
		80.3 ± 2.84 (23)	70.7 ± 3.27 (21)
		PAIRED 't' = 0.71, d.f. 5, n.s.	
CONTROL	5m	59.1 ± 1.64 (89)	59.6 ± 1.64 (108)

Table 6. MEAN RATE OF PECKING (PECKS/MIN.) OF BLUE GEESE GRAZING ON PAIRED FERTILIZED AND UNFERTILIZED VEGETATION SQUARES AT GUELPH, ONT.

Walking Rate

Geese took significantly fewer steps per minute while feeding on the nitrate fertilized squares, but showed no significant response to other treatments (Table 7).

Discussion

The yearling blue geese showed a series of statistically significant responses to the nitrate fertilized vegetation. However, these responses form an inter-related system, and some of the parameters used are obviously not independent. The increase in the amount of time spent feeding on the fertilized squares can be explained as a consequence of the increased feeding bout length and decreased rate of walking on these squares. If we make the robust assumption that the number of feeding bouts performed per unit time, and the rate of walking between feeding bouts are both independent of the vegetation being grazed, then time spent feeding on a particular vegetation type will be directly proportional to the mean bout length on that vegetation type, and inversely proportional to the mean rate of walking. Thus percentage time spent feeding on a particular vegetation type may be estimated as:

$$100 \times \frac{\text{bout length on vegetation}}{\text{mean interval between two consecutive feeding bouts}} \times \frac{\text{mean walking rate}}{\text{walk rate on vegetation}}$$

The overall mean interval between the start of two consecutive bouts was estimated as:

$$\frac{\text{overall mean bout length}}{\text{overall proportion of time spent feeding.}}$$

Using these formulae, the mean expected percentage time spent feeding on

TREATMENT	SQUARE	UNFERTILIZED	FERTILIZED
		13.5 ± 3.58 (22)	5.2 ± 1.62 (30)
	5m	15.4 ± 3.24 (18)	8.6 ± 1.63 (59)
		13.8 ± 13.8 (2)	13.2 ± 2.42 (42)
		14.3 ± 3.19 (25)	8.7 ± 2.25 (32)
NH_4NO_3	2.5m	12.5 ± 2.76 (33)	12.8 ± 2.48 (19)
		18.6 ± 5.29 (16)	14.4 ± 2.50 (35)
		10.0 ± 2.72 (28)	7.6 ± 3.15 (19)
	1.25m	18.4 ± 3.61 (13)	6.2 ± 2.30 (23)
		14.8 ± 2.46 (35)	9.0 ± 1.57 (26)
		PAIRED 't' = 3.90,	d.f. 8, $P < 0.01$
		16.1 ± 3.03 (43)	21.7 ± 3.56 (34)
	5m	2.3 ± 1.42 (5)	8.8 ± 1.71 (62)
		16.4 ± 2.35 (41)	12.0 ± 2.64 (33)
$CaCO_3$		15.1 ± 2.44 (42)	9.9 ± 1.68 (44)
	2.5m	7.6 ± 1.91 (17)	14.9 ± 3.18 (30)
		14.5 ± 2.60 (23)	17.2 ± 3.67 (2)
		PAIRED 't' = -0.92,	d.f. 5, n.s.
CONTROL	5m	15.7 ± 1.76 (89)	15.7 ± 1.43 (108)

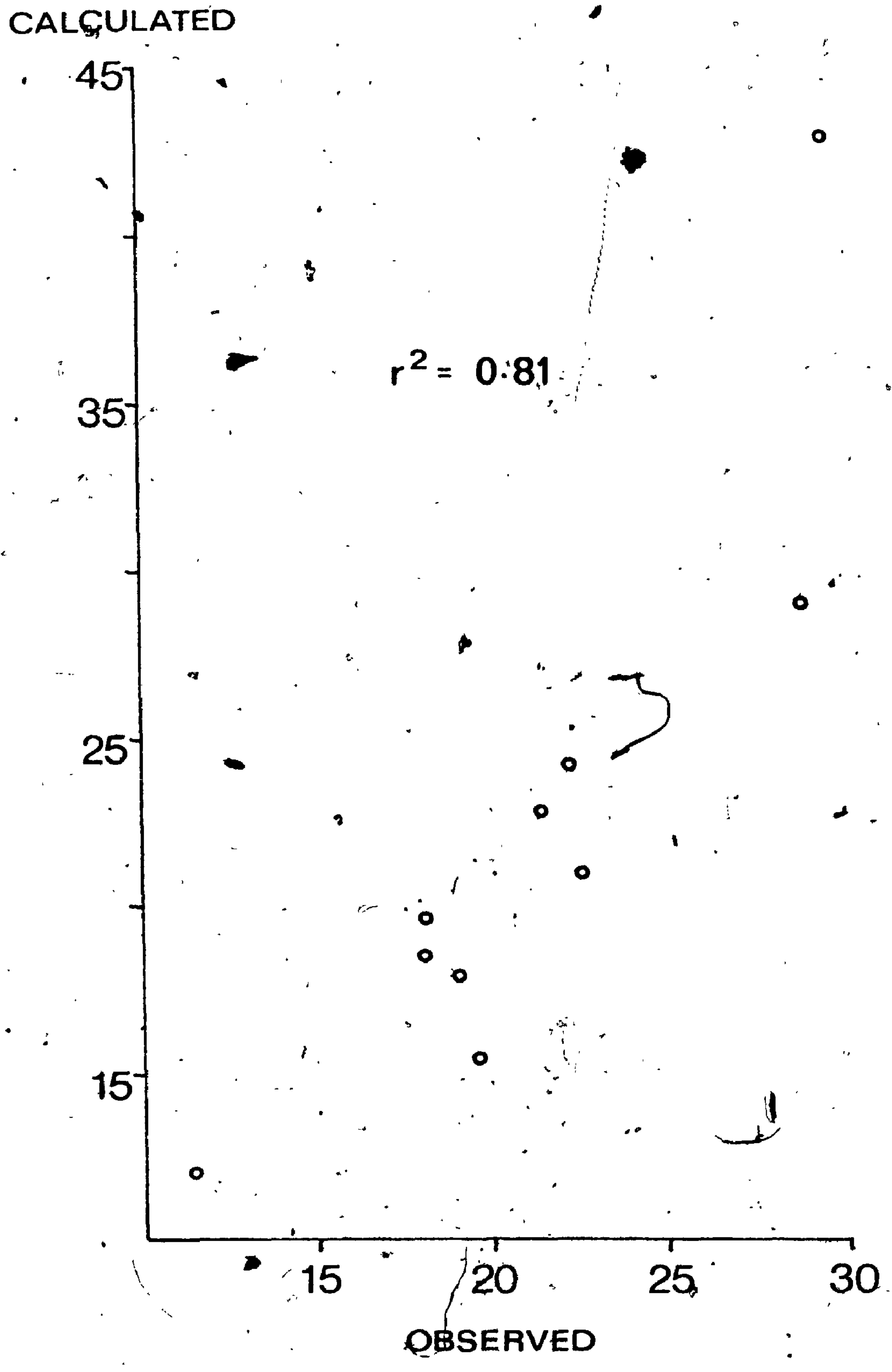
Table 7. MEAN RATE OF WALKING (STEPS/MIN) OF BLUE GEESE GRAZING ON PAIRED FERTILIZED AND UNFERTILIZED VEGETATION SQUARES, GUELPH, ONT. 1972

fertilized and unfertilized squares for each pen was calculated. As Figure 16 indicates, the relation between these values and the observed values is linear. The model explains 80% of the variation in the observed values. Since the estimates of percent time feeding are partially derived from overall percent time estimates, it may be argued that the observed correlation is the result of a correlation between overall percent time feeding for a pen and time spent feeding for the two square types of that pen. However, these values are not correlated (r = 0.45, n = 10).

If the observed responses to the nitrate fertilized vegetation have any selective advantage, then we would expect that the birds could spend less time feeding on the nitrate fertilized pens than on the other three pens. The data of Table 8 confirm this expectation. In addition, the birds spent less time feeding in the nitrate fertilized pens in the post-fertilization tests than they did in the pre-fertilization tests. The reverse is true in the other pens. Some of the observed increase in the calcium and control pens is explained by the fact that the birds were moulting during the second set of experiments, and thus probably had high nutritional requirements. This does not explain why the birds spent consistently more time feeding in the potential nitrate fertilized pens than they did in the potential lime fertilized pens in the pre-fertilization experiments (Table 9).

Since the mowing process ensured that there was no significant difference between the quantity of vegetation in the fertilized and unfertilized squares (Appendix 4), the experiments did indicate that blue geese can respond to differences in the crude protein content of vegetation, or to some highly correlated cue. However, this type of analysis

Figure 16. SCATTER DIAGRAM OF RELATION BETWEEN OBSERVED PERCENTAGE TIME SPENT FEEDING BY CAPTIVE BLUE GEESE AT GUELPH, ONTARIO AND CALCULATED PERCENTAGE TIME SPENT FEEDING BASED ON THEORETICAL CONSIDERATIONS


CALCULATED
45
35
25
15
r² = 0·81
15
20
25
30
OBSERVED

TREATMENT	SQUARE	BEFORE FERTILIZATION	AFTER FERTILIZATION
NH_4NO_3	5m	30.4 ± 4.22 (43)	21.2 ± 1.41 (192)
	2.5m	40.8 ± 3.92 (52)	19.1 ± 1.59 (192)
	1.25m	26.0 ± 1.81 (232)	21.9 ± 1.79 (171)
$CaCO_3$	5m	5.7 ± 1.36 (26)	23.4 ± 1.75 (181)
	2.5m	12.5 ± 2.19 (95)	24.6 ± 1.94 (184)
CONTROL	5m	19.8 ± 2.83 (76)	26.8 ± 1.67 (199)

Table 8. PERCENTAGE TIME SPENT FEEDING BY CAPTIVE BLUE GEESE IN 10m SQUARE TEST PENS, BEFORE AND AFTER THE APPLICATION OF FERTILIZER, GUELPH, ONT. 1972.

TREATMENT	BEFORE FERTILIZATION	AFTER FERTILIZATION
NITRATE	28.9 ± 1.56 (327)	20.7 ± 0.92 (555)
LIME AND CONTROL	14.4 ± 1.56 (197)	25.0 ± 1.03 (564)

Table 9. OVERALL EFFECT OF FERTILIZATION ON THE PERCENTAGE TIME SPENT FEEDING BY CAPTIVE BLUE GEESE AT GUELPH, ONT. 1972.

provides no quantitative information on the relationship between behavioural expression and vegetational variation. To obtain this insight we must consider the data differently.

3.4 QUANTITATIVE RESPONSE TO FERTILIZATION

Due to differences in the length of time each pen was exposed to fertilizer, and initial differences in protein composition between pens the birds were exposed to a continuum of vegetation protein content. In addition, the nitrate fertilization increased the water content, and the lime treatment in the 5m pen decreased the water content of the vegetation (Table 10). Continuous variation in the amount of available vegetation was provided by the differences in plant height and density between pens, and within each pen over the course of the three trials. It is therefore possible to make an approximate estimation of the relationship between variation in vegetation parameters and behavioural expression. The simplest model of this relationship assumes that a behavioural response is proportional to the linear summation of the important vegetational parameters of the vegetation. This model can be tested by subjecting the available data to a multiple linear regression analysis. The model for this regression is:

$$\text{Behavioural response} = a_1(\text{vegn. protein}) + a_2(\text{vegn. water}) + a_3(\text{vegn.m}^{-2}) + a_4 + e$$

Where a_i is a constant, and e is a normally distributed error term with mean zero, composed of error in the measurement of the behaviour's expression and error in the equation's estimate of the behavioural response.

TREATMENT	SQUARE	UNFERTILIZED	FERTILIZED	P^a
	5m	66.2 ± 0.89 (12)	71.1 ± 1.29 (12)	<0.01
NH_4NO_3	2.5m	74.8 ± 0.45 (6)	76.9 ± 0.51 (18)	<0.05
	1.25m	70.3 ± 1.84 (12)	74.6 ± 0.71 (12)	<0.05
$CaCO_3$	5m	59.5 ± 1.71 (12)	62.7 ± 1.64 (12)	
	2.5m	69.6 ± 0.86 (18)	64.3 ± 1.31 (6)	<0.01
CONTROL	5m	69.1 ± 1.01 (12)	70.4 ± 1.73 (12)	

Table 10. EFFECT OF FERTILIZER TREATMENTS ON THE PERCENTAGE WATER CONTENT OF THE GREEN LEAVES OF *BROMUS INERMIS*, GUELPH, ONT. 1972 (a. PROBABILITY FROM ONE-WAY ANALYSIS OF VARIANCE)

The model therefore assumes that every independent variable is measured without error. Since the values for the vegetation variables in this experiment were estimated as the mean of three samples from each quarter of the test pen, the data seem to violate this assumption. However, the error associated with each vegetation parameter estimate will tend to be normally distributed with mean zero, thus the simple sum of the errors for each variable - which is the variables' contribution to e - will very probably be normally distributed with the mean zero. In addition, the measurement errors associated with the vegetational variables are small in comparison with those of the behavioural variables. Under these conditions, ordinary least squares regression is known to give a reliable estimate of the relationship between variables (Mosbaek and Wold 1969).

For the control and 5m square pens, vegetation samples were taken in each quarter, the mean value for the three samples from each unexclosed site was used to characterize that quarter. These values were associated with the behavioural data obtained in that quarter within 24 hours of the vegetation sampling, and provided that there were more than nine behavioural observations for that quarter. For the pens with 2.5m squares, an exclosure had been randomly located in one of the squares of each quarter. Vegetation values from these exclosures were associated with the behavioural values recorded for their squares, with the same restrictions on data admissibility as the 5m squares. Due to their small size, there were few behavioural observations for each of the 1.25m squares; I therefore combined all fertilized and all unfertilized square values for this pen. In this way 19 complete data sets were extracted. The full data matrix is given in Appendix 5. This matrix was then subjected to a single least squares, step-up, multiple linear regression analysis (BMD programme 02R). The correlation half-matrix for the six variables is shown in Table 11, and the derived regression equations in Table 12. The equations for bout length and pecking rate explain approximately 50% of the observed variation in these behaviours. The equation for rate of walking is not statistically significant. All equations have the form that would be predicted from the qualitative analysis of Sec. 3.3. Bout length and pecking rate increase, and walking rate decreases with increasing vegetational protein. This suggests that - at least for bout length and pecking rate - the response to protein is absolute and continuous, rather than the result of a simple comparative process.

The water content of the vegetation is the first variable extracted by the analysis for both bout length and pecking rate, suggesting that this is the vegetation component to which the geese are responding. However, for all vegetation samples protein and water content are highly positively correlated ($r = 0.70$, $n = 60$, $P < 0.001$), so it is difficult to determine which variable is really most important. The role of vegetation quantity in these equations is small, but seems biologically meaningful. Pecking rate decreases with increasing vegetation quantity since the net yield of a peck should be positively correlated with standing crop. Similarly, bout length increases, since it should be most profitable to feed in areas of high food density.

The results of the more quantitative analysis thus confirm most of the findings of the qualitative analysis.

	PROTEIN	WATER	BOUT	PECK	STEP
VEGETATION	0.360	0.192	-0.150	-0.308	-0.230
PROTEIN		0.578**	0.455*	0.425	-0.276
WATER			0.541*	0.558	-0.220
BOUT				0.490*	-0.284
PECK					-0.349

Table 11. CORRELATION HALF-MATRIX INDICATING RELATIONSHIP BETWEEN VARIATION IN VEGETATION PARAMETERS AND ASSOCIATED VARIATION IN FEEDING BEHAVIOUR, GUELPH, ONT. 1972

VEGETATION = GRASS STANDING CROP ($g.m^{-2}$). PROTEIN = CRUDE PROTEIN CONTENT OF GREEN GRASS AS PERCENT OF DRY WEIGHT. WATER = PERCENT WATER CONTENT OF GREEN GRASS. BOUT = FEEDING BOUT LENGTH (secs.) PECK = NO. OF FEEDING PECKS PER MIN. STEP = NO. OF STEPS PER MIN.

$* \ P < 0.05$, $** \ P < 0.01$

DEPENDENT VARIABLE	CONSTANT	VEGN.	PROTEIN	WATER	R^2
BOUT LENGTH	6.10	-0.03	0.18	0.16	0.43 *
PECKING RATE	26.78	-0.13	0.56	0.55	0.56 **
WALKING RATE	25.47	-0.03	-0.19	-0.08	0.10

Table 12. COEFFICIENTS OF MULTIPLE, LINEAR REGRESSIONS EQUATIONS RELATING THE VARIATION IN INDIVIDUAL BEHAVIOURAL PARAMETERS TO VEGETATIONAL VARIATION. GUELPH, ONT. 1972.

SEE TABLE 11 FOR DEFINITION OF VARIABLES. R^2 = COEFFICIENT OF DETERMINATION. * $P < 0.05$, ** $P < 0.01$.

3.5 DISCUSSION

Captive blue geese show a set of quantitative changes in feeding behaviour when they encounter vegetation of high protein content. Are these changes likely to be adaptive for an arctic grazing species? Geese at the McConnell River are probably obtaining a nutrient intake critically close to their minimum requirements. Several females were found dead in mid-July 1973, apparently from starvation. Adult females and goslings spend almost all of the daylight hours feeding (Sec. 2.4). They cannot, therefore, afford to allocate time to a specific search for areas of high nutrient content vegetation. The goslings are flightless from hatch to mid-August, and the adults lose their primaries during the first two weeks of August; thus the birds must walk between feeding areas. The density of birds over the McConnell River area is relatively high (1 - 7 adults per hectare), and undue feeding concentration on high quality patches would soon exhaust this food supply. By feeding continuously on all available vegetation, but adjusting feeding behaviour so that more high quality vegetation is ingested when encountered (by increasing bout length and peck rate) and more time is spent on this vegetation (by decreasing the rate of walking), geese could increase their protein intake without reducing the time available for feeding. An additional, potentially favourable feeding tactic was observed (but not quantified) in the Guelph experiments. As birds reached the border of a nitrate fertilized square, they tended to turn through 180°. If such behaviour occurs in the arctic it would further tend to maintain birds in high quality areas.

There remains the problem of how geese detect variations in vegetation nutrient content. The evidence for olfactory and gustatory discrimination in birds is contradictory. Geese have a functional olfactory epithelium, which shows electrophysiological responses to chemical stimuli (Neuhaus 1957, Tucker 1965), but they cannot be classically conditioned to respond to different chemical odours (Neuhaus 1963). However, Neuhaus (1963) did find that geese show predictable changes in respiratory rate when subjected to different odours. Chicks will reject certain sugars at relatively low concentrations (Kare and Ficken 1963), and pigeons can detect some organic acids at lower concentrations than can humans (Duncan 1960). In addition, chicks show considerable individual variation in their ability to detect inorganic chlorides in solution (Ficken and Kare 1961), and Williamson (cited in Kare and Ficken 1963) has demonstrated a genetic component of this ability. Thus the ability to respond to potential chemical cues is amenable to natural selective processes. It is thus possible that geese could be responding directly to variations in the total amino acid content of the vegetation. However, Kare and Ficken (1963) found that protein deprived chicks show no response to casein in solution. Geese could also be responding to a vegetation component highly correlated with vegetation protein content.

There is evidence for a comparative element in the selective process. The most marked responses to the nitrate fertilization were in the 1.25m squares, and the least marked in the 5m squares for all behaviour parameters. Individuals were also observed to immediately turn back into fertilized squares upon encountering a boundary.

The best candidate for a correlated cue variable is vegetation water content, which was highly correlated with protein content in the Guelph experiments. The nature of the experiments made it impossible to tell if birds were selecting for high water content (and thus high digestibility) and using water or protein as a cue, or selecting for protein and using this or water as a cue, or selecting for an unmeasured, correlated variable. Protein content is also positively correlated with the reciprocal of (100 - water content) ($r = 0.70$, $n = 60$, $P < 0.001$); implying that the protein content of the vegetation as a proportion of its fresh weight was constant in all experiments, and that water variation was the major feature of the trials. However, since high water content implies high digestibility, high water content indicated high protein availability. To separate the influence of the two components it is necessary to have data from a situation where they vary independently. Such data are presented in Chapter 5.

Yearling blue geese at Guelph showed continuous changes in feeding behaviour in response to variations in vegetation quality. These changes would be expected to result in a significant increase in the quality of the vegetation ingested by the geese. However, to verify this it is necessary to know the exact effect of these behavioural variations on intake, and whether such variations actually occur in a natural situation.

3.6 SUMMARY

Yearling blue geese responded to nitrate fertilization of vegetation by increasing the length of a feeding bout, and decreasing their rate of walking while feeding on this vegetation. This increased the proportion of time spent feeding on fertilized squares. The birds also pecked faster on the fertilized vegetation. It was not possible to determine whether the birds were responding to the increased protein content of the vegetation or its increased water content (or both, or something with which these two variables were correlated).

BEHAVIOUR AND INTAKE: THE MODEL REVISITED

> "A copy of the universe is not what
> is required of science; one of the
> damned thing is ample*."
> Rebecca West

4.1 INTRODUCTION

It is satisfying that the variations in feeding behaviour observed at Guelph could be adequately explained by a small number of vegetation parameters, and that these behavioural variations intuitively appear to have survival value. However, a more complete understanding of the function of variation requires a knowledge of how it affects intake. While the behavioural data were collected at Guelph additional data were obtained on the intake of the birds. Similar data were collected from goslings at the McConnell River. The major problem was to devise a valid and convenient measure of food intake.

4.2 ESTIMATING THE INTAKE OF FREE-RANGING GEESE

Although a variety of methods have been developed to estimate the intake of wild and domestic ungulates (Van Dyne 1968), these have ~~limited applicability to geese. The Anatidae have been little studied.~~ R. Owen (1970) measured the daily food consumption of captive blue-winged teal (Anas discors) under laboratory and outdoor conditions, and Marriott and Forbes (1970) obtained similar data for the Cape Barren goose (Cereopsis novaehollandiae). However, the extrapolation of such results to field conditions is a dubious exercise. From a number of

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* the original reference is to "art", the implications extend to science.

simplifying assumptions, M. Owen (1972) estimated the daily consumption of over-wintering white-fronted geese to be 670-750g of vegetation.

Intake may be estimated directly by the amount of food eaten by caged birds; by the weight changes of feeding birds; and by shooting birds known to have been feeding for a specific length of time. It may be measured indirectly from a knowledge of digestive efficiency and defaecation rate; and by measuring the rate of vegetation removal by known numbers of birds. The last four methods were evaluated under field conditions at the McConnell River, and under more controlled conditions at Guelph. Caged birds were studied in London, Ontario.

Intake of Caged Birds

Three, two year old female geese (two white phase and one blue phase) previously used in the Guelph experiments, were held for six weeks in $1.5m^2$ cages with 2.5cm mesh wire walls and floors. Each bird was fed three different pelleted foods of known protein content for ten day periods, with an initial four day adjustment period. The weight of food removed was determined at the same time each day with an Ohaus triple-beam balance. Faeces were collected on newspaper beneath the cage, and were removed every three days then weighed fresh and after drying for 24 hours at 105°. One bird failed to adjust well to captivity, data from this bird were not used. The three foods were pelleted to the same size, and so concocted that the major variation between them was in protein and fibre content.

Daily intake and utilization efficiency are clearly related to the protein content of the diet (Table 13). It is feasible - but

DIET PROTEIN (%)	INTAKE (g d.w./DAY)	INTAKE RETENTION (%)	FAECES PROTEIN (%)	NITROGEN BALANCE
16	226. ± 7.6	35.6 ± 1.31	33.	-ve
21.	205. ± 9.4	41.2 ± 0.80	41.	-ve
26.	179. ± 11.2	44.8 ± 1.35	45.	+ve

Table 13. VARIATION IN VOLUNTARY INTAKE OF CAGED, ADULT FEMALE, WHITE PHASE BLUE GEESE WITH VARIATION IN DIETARY PROTEIN CONTENT. LONDON, ONT. INTAKE RETENTION IS

$$\frac{\text{(D.W. FOOD CONSUMED - D.W. FAECES PRODUCED)}}{\text{(D.W. FOOD CONSUMED)}}$$

potentially misleading - to use these values to estimate the minimum daily food requirements of adults at the McConnell River. The birds were kept at a mean temperature of 22°. This is considerably higher than the mean daily temperature at the McConnell River in July and August 1973 (11° - estimated as the mean of [daily maximum + daily minimum temperature]/2). R. Owen (1970) found a linear relationship between ambient temperature and energy intake for male blue-winged teal. Assuming that the slope of this line can be applied to blue geese, we can estimate their daily intake at 11°. If we further assume that intake is directly proportional to photoperiod, we obtain estimates of daily requirements for the McConnell River of 347g dry weight for a 16% protein diet, and 319g for a 21% protein diet. Since, under normal conditions, vegetation at the McConnell River contains approximately 70% water, daily vegetation requirements are 1160g and 1060g respectively. The minimum requirements of wild birds may well exceed this since grazing is more energy consuming than ingesting food pellets.

Such a tortuous conversion process can provide neither an accurate nor a precise estimate of the actual requirements of wild birds. It does, however, give a general, conservative estimate of how much food a grazing blue goose should require, and provides an index by which the realism of less direct estimates may be gauged.

Weight Changes of Feeding Birds

The temporal changes in the weight of a feeding goose may be attributed to three factors: weight of food and water ingested; weight loss due to respiration; and weight loss due to defaecation.

To estimate the intake of a feeding bird we must also estimate its respiratory and excretory expenditure. Slightly different but strictly comparable techniques were used at the McConnell River and Guelph. The McConnell birds had been hand-raised and were used to considerable human contact, and were not disturbed by manipulation. The Guelph birds had had little physical contact with people. Catching and weighing these birds usually resulted in a cessation of all feeding behaviour for 30-90 mins. For both groups respiration weight loss was estimated by the weight changes of control birds kept under identical conditions to the test birds, but without access to food. These birds were usually as active as the test birds. Each bird acted as its own control at the McConnell River. Six birds were weighed; three of these were then held without food while the other three were allowed to feed for 30 mins. All six birds were then reweighed and their roles reversed. They were then weighed a third time. The weight loss of each individual when deprived of food was used as an index of its potential weight loss while feeding. In the Guelph experiments, the controls were of the same colour and approximate weight as the test birds. Six individuals were captured and weighed; two were held without food while the others were released into a 10m square test pen (Figure 15). After approximately 90 mins., those birds which had fed consistently were recaptured, and they and the two controls were reweighed. The weight change of the controls was used to estimate the respiratory loss of the test birds. No water was provided during the test period in either set of experiments. At Guelph defaecatory weight loss was avoided by collecting all data in the two hours following dawn. The birds did not feed at night, but began feeding at first light. Food passes through the blue goose gut in approximately 90 mins (pers. obs.). It was anticipated that the birds would not defaecate during a test period. This was the case. At the McConnell River it was assumed that the defaecation rate of individuals would be approximately constant for controls and test birds. The fact that the second test group had been starved for 30 mins before testing might have biased the results. If during this period they voided the entire rectal contents, their weight loss as controls would over-estimate their actual weight loss while feeding. However, there is no significant difference in weight gain estimates between the two groups (Appendix 6).

Percentage time spent in different behaviours was estimated every minute at Guelph and every 30 secs at the McConnell River. The intake of each test bird was estimated as:

Weight change of test bird +
(Weight change of control/min) x (Interval between test bird weighings)

If this calculated intake is a reliable estimator of actual intake, it should be positively correlated with the amount of time spent feeding. The Guelph values were obtained in trials both before and after the fertilization process outlined in Chapter 3. The pre-fertilization experiments showed a high positive correlation (Figure 17), and gave an estimated intake of 1.44 ± 0.18g per minute of feeding. The post-fertilization values showed a significant, but less impressive correlation (Figure 18) and give an intake estimate of 1.87 ± 0.17g per minute. This poor fit is probably due to the marked variations in feeding behaviour between and within pens induced by the fertilization.

Figure 17. VARIATION IN QUANTITY OF VEGETATION INGESTED BY GRAZING BLUE GEESE - ESTIMATED BY WEIGHT GAIN OF TEST BIRDS + WEIGHT LOSS OF NON-FEEDING CONTROLS - WITH TIME SPENT FEEDING IN PRE-FERTILIZATION EXPERIMENTS AT GUELPH, ONT. 1972

r = CORRELATION COEFFICIENT

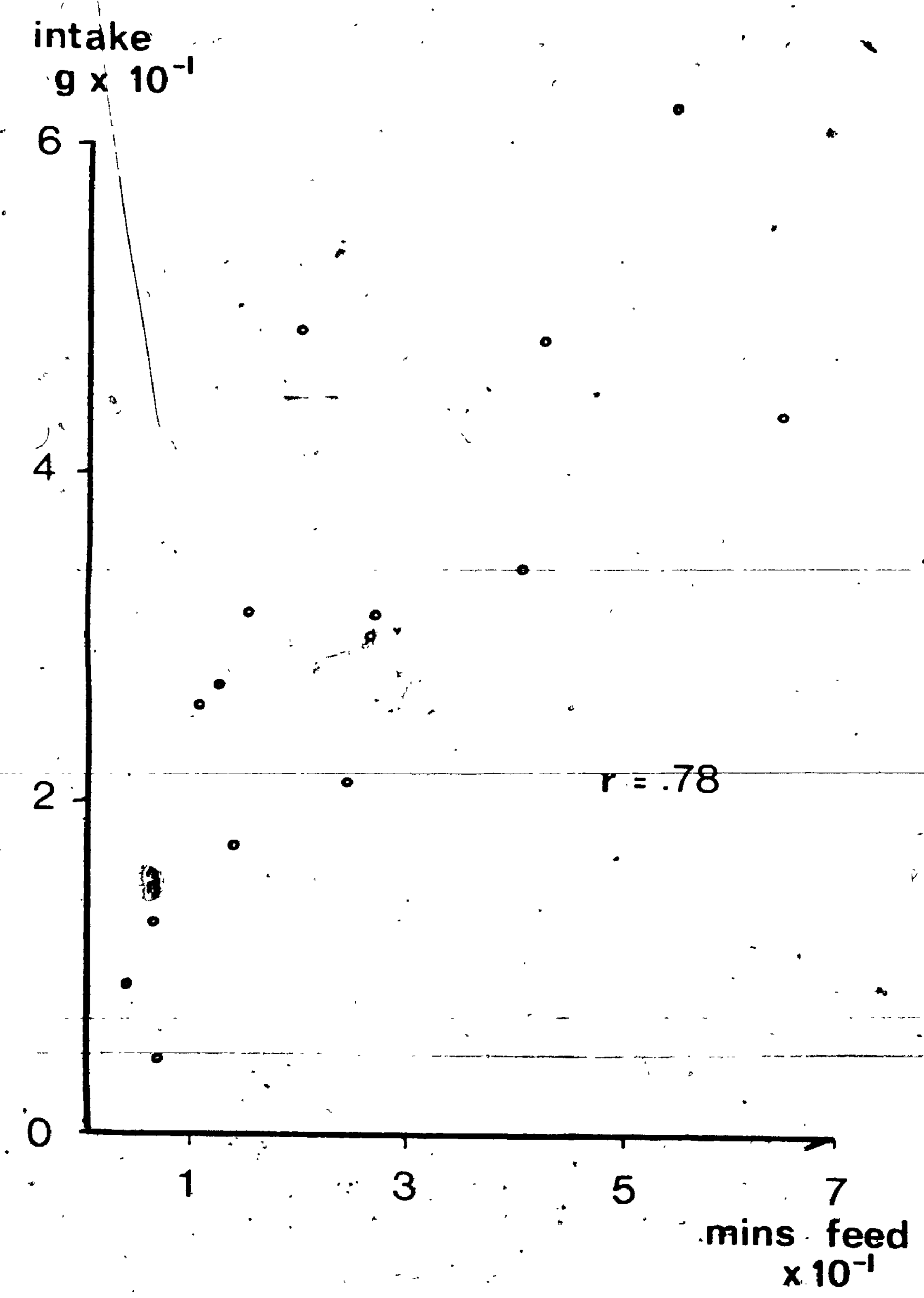
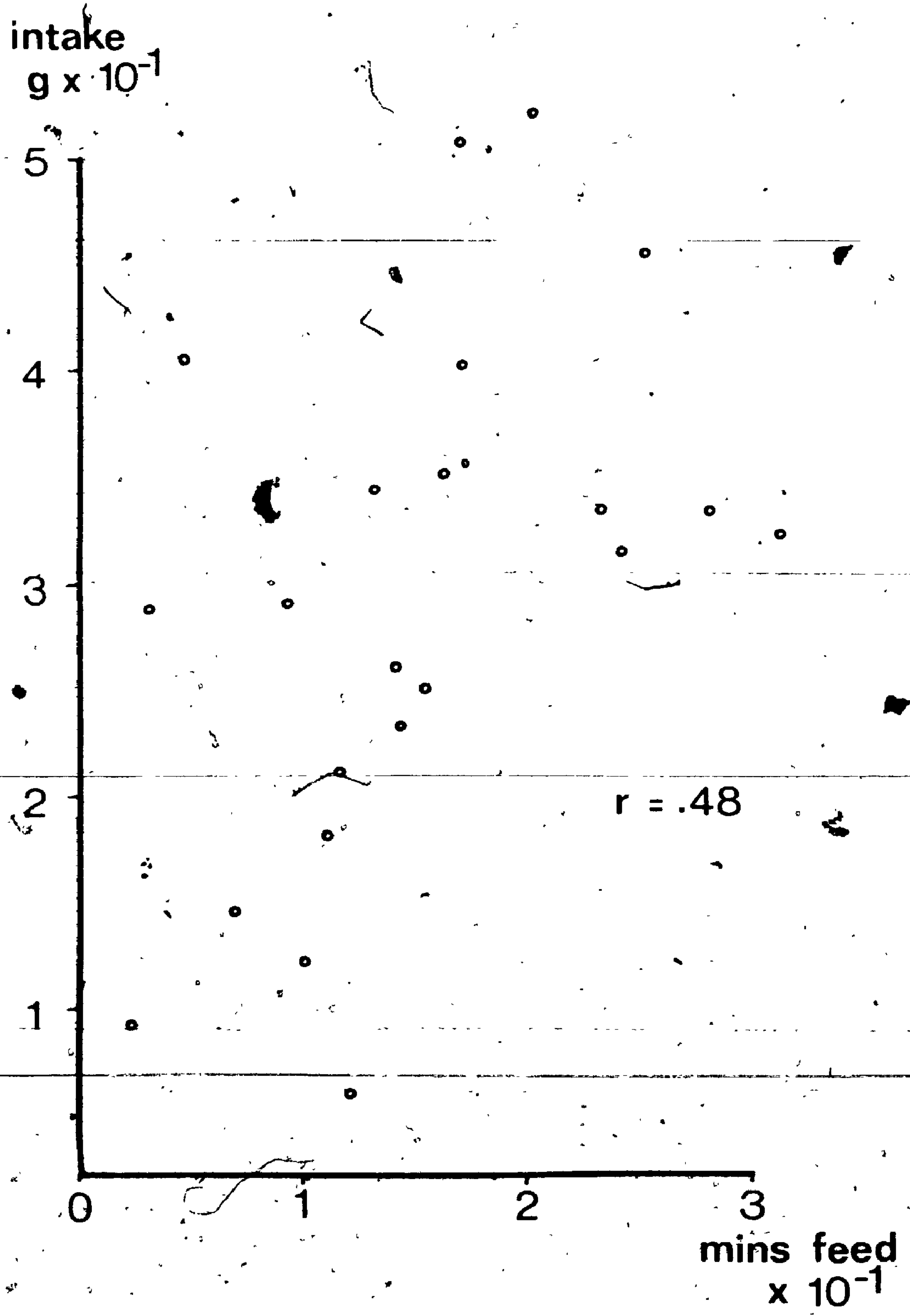

intake
g x 10^{-1}
6
4
2
0
1
3
5
7
mins feed
x 10^{-1}
r = .78

Figure 18. VARIATION IN QUANTITY OF VEGETATION INGESTED BY GRAZING BLUE GEESE - ESTIMATED BY WEIGHT GAIN OF TEST BIRDS + WEIGHT LOSS OF NON-FEEDING CONTROLS - WITH TIME SPENT FEEDING IN POST-FERTILIZATION EXPERIMENTS AT GUELPH, ONT. 1972

r = CORRELATION COEFFICIENT


intake
g x 10^{-1}
5
4
3
2
1
0
1
2
3
r = .48
mins feed
x 10^{-1}

The McConnell River values show a significant correlation for the basic data set. However, during the six weeks of experimentation the birds increased in weight by a factor of five. To compensate for this each intake value was transformed to an estimate for a 1800g bird (the mean body weight of the Guelph geese), using the cube root of body weight on the assumption that bill length determines intake and that this should-should vary as the cube root of body size. This resulted in an improved correlation (Figure 19), and yielded an intake estimate of 1.84 ± 0.10g per minute of feeding. The three estimates are not significantly different. This suggests that time spent feeding by grazing geese could be a useful indirect field estimator of total consumption.

Shooting Feeding Birds

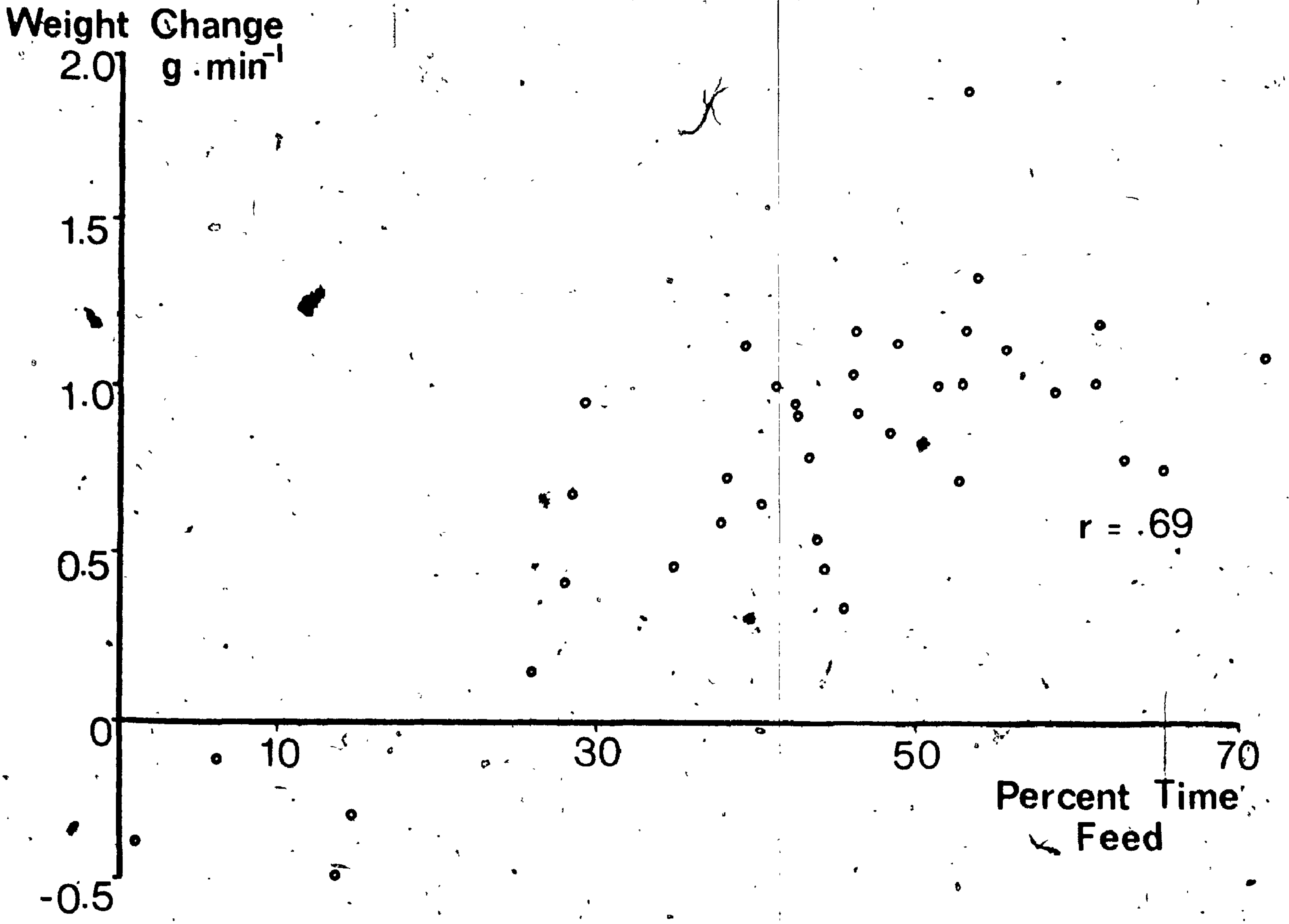
This method requires an ability to select individual, wild geese known to have empty oesophagi. Three methods were used to satisfy this empty oesophagus criterion (e.o.c.).

When incubating females are gently disturbed, they frequently begin to feed. Since incubating females do not normally feed, such birds should satisfy the e.o.c.

Immediately after hatch, families that have nested on the island between the two branches of the McConnell River (see Prevett 1973) swim across the south branch of the river on their way to the preferred feeding grounds. This crossing takes about 15 mins, and all birds begin feeding when they reach the bank. It was assumed that such birds would either satisfy the e.o.c. or have two distinct food boli in the oesophagus.

Figure 19. VARIATIONS IN QUANTITY OF VEGETATION INGESTED BY GRAZING BLUE GOSLINGS - ESTIMATED BY WEIGHT GAIN OF TEST BIRD + WEIGHT LOSS OF SAME BIRD WHEN NOT FEEDING - WITH TIME SPENT FEEDING AT McCONNELL RIVER, N.W.T. 1973. INTAKES CORRECTED FOR GROWTH OF GOSLINGS

r = CORRELATION COEFFICIENT


Weight Change
g·min^{-1}
2.0
1.5
1.0
0.5
0
-0.5
10
30
50
70
Percent Time
Feed
r = .69

During the two weeks following hatching, goslings are frequently brooded by their parents. Parents observed to brood for at least 20 mins without feeding were considered to meet the e.o.c.

Incubating females were observed by an unconcealed experimenter. For the other two methods a canvas observation blind was used. Shot birds were never more than 100m from this blind. The behaviour of each bird was recorded at 30 sec intervals, until it had fed for at least five minutes. It was then shot with a 0.222 calibre rifle. The entire oesophageal contents were immediately removed, washed in a nearby pool and sealed in a polyethylene bag. They were later sorted, weighed and dried at the research station.

The results obtained were inconsistent (Table 14). However, the three lowest values were obtained from birds which had just crossed the river (JH4, 11 and 12). These birds were feeding on fine vegetation (mainly _Carex_ _maritima_ Gunn and _Eleocharis_ _acicularis_ (L.) Reom. and Schult.) with a low standing crop (column 3, Table 14). This vegetation is rarely used by blue goose families. For the entire data set, there is a highly significant correlation between the logarithm of intake and the logarithm of vegetation standing crop (Sec. 5.2). If we exclude the three low values and the value for JH5 (which was crippled and escaped capture for 20 mins) the estimated intake of the shot birds is 1.50 ± 0.36g per minute of feeding.

Indirect Estimation from Defaecation

The rate at which food passes through a goose's intestine is sufficiently rapid that - provided that the bird feeds almost continually - rate of defaecation can be accurately measured by recording the

BIRD NO.	INTAKE (g/min)	GRASS (g/m^2)	OBSERVATION TIME (min)
JH 12	0.01	5.8	11
JH 11	0.02	7.3	10
JH 4	0.05	9.1	15
JH 5	0.06	13.7	17*
JH 3	0.43	15.1	8
JH 13	0.45	16.7**	15
JH 16	0.90	27.3	10
JH 17	1.03	12.2	7
JH 10	1.88	16.0	11
JH 14	1.91	23.7	20
JH 2	2.85	33.7	15

Table 14. INTAKE PER MINUTE OF FEEDING OF GRAZING, ADULT BLUE GEESE AT THE McCONNELL RIVER, N.W.T., 1973.

* BIRD CRIPPLED, NOT COLLECTED UNTIL c20 MINS AFTER FIRST SHOT

** BIRD FEEDING ON LEAVES OF <u>Vaccinium uliginosum</u>, VEGETATION ESTIMATED AS HALF OF STANDING CROP OF ALL DICOTYLEDONS.

interval between successive defaecations for individual birds. Average defaecation time for McConnell River adults was 4.9 ± 0.30 secs (99), and droppings averaged 1.22g (240) dry weight. The Guelph birds spent less than 30% of their time feeding on average, and individuals never remained completely visible for the interval between two defaecations. The technique outlined in Sec. 1.8 was used. Birds produced an average of 30 droppings per day, with a mean dry weight of 0.65g. Assuming that the utilization efficiency of the captive birds approximated that of the wild birds, daily intake at the McConnell River was 502g dry weight for a 21% protein diet, and 463g dry weight for a 16% protein diet. The equivalent estimate for Guelph - assuming a 26% protein diet - is 45g. This is almost impossibly low. The method assumes that feeding rate was constant for the period preceding observation as well as during the observation period. However, the birds were seriously disturbed by being caught and weighed during the experimental period. They were also subject to disturbance by stray humans. The highest number of defaecations recorded was 50, this yields a more realistic intake estimate of 75g dry weight per day.

Effect on Vegetation

The amount of vegetation removed by grazing herbivores can be estimated by comparing temporal changes in standing crop for paired grazed (unexclosed) and ungrazed (exclosed) plots. Intake may be estimated if the number of animals using the area is known. Heady (1968) has pointed out the potential errors of this method. He concluded that it was only valid for large exclosures in areas of high herbivore density. At the McConnell River 5m x 2m exclosures were used and goose numbers were assessed with an automatic camera recorder in 1971 (Appendix 7). At Guelph 0.75m square exclosures were used, and feeding intensity was measured by dropping counts.

Consumption at the McConnell River was estimated to be 1663g per day. This is an over-estimate as it was frequently impossible to detect goslings in the films from the camera recorders. The removal of vegetation by other herbivores was minimal. The two other common grazing herbivores (Branta canadensis and Rangifera tarandus) were rare in relation to blue goose numbers. Lemmings (Dicrostonyx groenlandicus) could - and did - pass through the mesh of the exclosure wire.

At Guelph there was no significant difference in the amount of vegetation inside and outside exclosures (Appendix 4). At the lowest estimated intake rate the geese should have removed 11g.m^{-2} dry weight of vegetation in a three day trial period. The mean recorded value was 2.5g.m^{-2}. Obviously the assumptions of the exclosure method did not hold true at Guelph.

Summary

Estimations of intake by the different methods are compared in Table 15. The McConnell estimates are very similar, probably because all methods are more reliable for high intake rates. The estimates of intake per hour of feeding are consistent across methods. However, considerable differences exist in the amount of work involved in each method. In particular, estimation from exclosure data was fraught with tedium and plagued by untestable assumptions. The McConnell River estimates were based on only five exclosures, yet they required over 200 hours of sampling, sorting, weighing and drying of vegetation, plus

METHOD	DAILY INTAKE (g)		INTAKE/HOUR FEEDING	
	McCONNELL	GUELPH	McCONNELL	GUELPH
CAPTIVE BIRDS	1160[1] 1060[2]	179[3]	69 63	72
DIRECT WEIGHING	1556	250	104	100
OESOPHAGEAL CONTENTS	1350		90	
DEFAECATION	1674[2] 1544[1]	250[4]	112 103	100
EXCLOSURE	1663		110	<1

Table 15. COMPARISON OF ESTIMATES OF TOTAL DAILY INTAKE, AND INTAKE PER HOUR OF FEEDING FOR GRAZING BLUE GEESE BY DIFFERENT TECHNIQUES

1. 16% PROTEIN DIET 2. 21% PROTEIN DIET 3. 26% PROTEIN DIET
4. MAXIMUM VALUE OBTAINED

further hours of film analysis.

Faeces counts gave rapid estimates but require the dubious attribution of the assimilation efficiency of captive birds to wild birds on a different diet.

In all the investigations with captive birds the direct weighing approach was used.

The shooting of feeding birds involves a considerable problem in the selection of appropriate individuals, but it was the only method for wild birds which combined reliability and practicality.

4.3 THE EFFECT OF BEHAVIOURAL VARIATION ON INTAKE

The measurement of individual pecking and walking rates, and feeding bout lengths was incorporated in the determinations of intake by direct weighing.

I used the multiple regression technique described in Sec. 3.4 to estimate the contribution of behavioural variation to the variations in intake. The mean behavioural values for all individuals in a trial were used to estimate the independent variables. The use of the regression technique is therefore subject to the criticism outlined in Sec. 3.4 (error components to the independent variables); but the same justifications for its use also apply. In this case we do not expect the effect of the behaviours to be a linear sum, but to be expressed in a multiplicative form:

$$\text{Intake} \propto \text{Time spent feeding} \times \text{Pecking rate} \times \text{Walking rate} \times \text{Vegetation quantity}$$

I therefore regressed the natural logarithms of the independent variable values on the natural logarithm of intake (raw and transformed data matrices are given in Appendices 8a and 8b respectively, a complete set of data on vegetation quantity was not available for the Guelph experiments). The correlation half-matrices and regression equations thus obtained are indicated in Tables 16-18. Both data sets give highly significant multiple correlation coefficients. The Guelph equation explains 40% of the observed variation in intake, and the McConnell equation 48%. The two equations differ substantially in their exact form. However, if we plot the changes in intake with time spent feeding for the two situations using overall mean values for the other independent variables, the two equations give virtually identical predictions (Figure 20). The curves only diverge seriously for feeding times in excess of 60 mins - i.e. for values outside the recorded range. It may be asked why the exponent for time in both equations is less than unity, since the derived equations imply that the yield from more than two hours feeding is slight. There are two possible reasons for this. Error in the measurement of independent variables tends to depress the size of the individual regression coefficients (Gilbert 1973: 30). The direct weighing technique assumes that the energy expenditure of a feeding bird is identical to that of a control. This is probably true for an individual that feeds for only a few minutes, but as time spent feeding increases the weight loss of the control will progressively underestimate the respiration loss of a feeding bird. This would tend to decrease the value of the time exponent. More reliance may be placed on the McConnell values, since the weighings were more precise than those at Guelph, the birds fed more readily, and the behavioural estimates were determined solely

	PECK	WALK	INTAKE
TIME	-0.004	0.361*	0.518**
PECK		0.045	0.041
WALK			-0.150

Table 16. CORRELATION HALF-MATRIX INDICATING RELATIONSHIP BETWEEN VARIATIONS IN FEEDING BEHAVIOUR AND VARIATION IN FOOD INTAKE

GUELPH, ONT. 1973

NOTATION AS IN TABLE 11.

	PECK	WALK	VEGETATION	INTAKE
TIME	0.255	-0.380	0.467**	0.602**
PECK		0.074	0.122	0.110
WALK			-0.227	-0.317*
VEGETATION				0.488**

Table 17. CORRELATION HALF-MATRIX OF RELATIONSHIP BETWEEN BEHAVIOURAL AND VEGETATION VARIATION AND FOOD INTAKE PER MINUTE FOR GOSLINGS AT McCONNELL R. 1973.

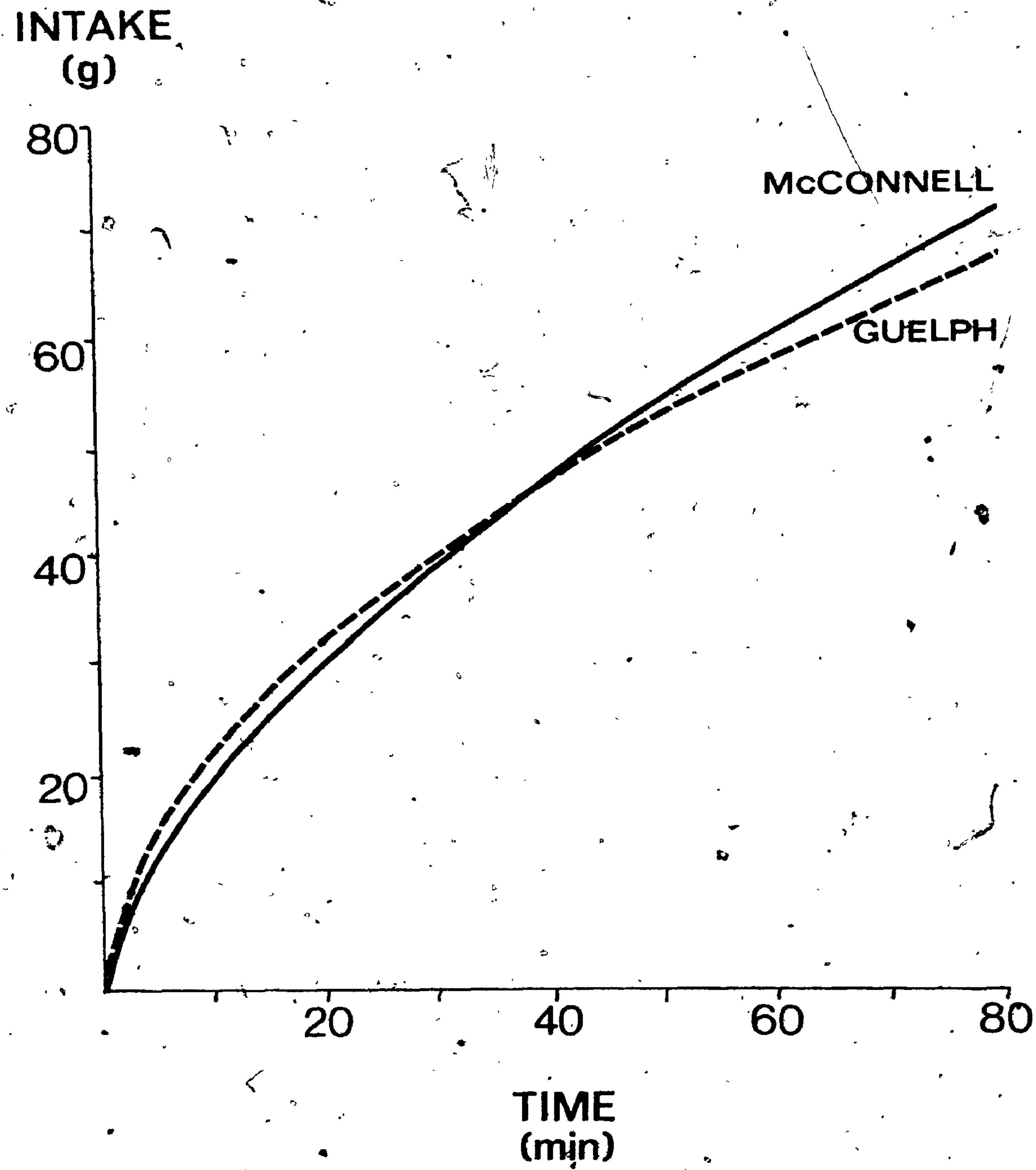
LOCATION	CONST.	TIME	PECK	WALK	VEGN.	R^2
GUELPH	9.39	0.56	0.31	-0.66		0.40 **
McCONNELL	5.42	0.66		-0.31	0.15	0.48 **

Table 18. EXPONENTS OF MULTIPLE LINEAR REGRESSION EQUATIONS RELATING VARIATIONS IN LOG.(INTAKE) OF ADULT BLUE GEESE AND BLUE GOSLINGS TO VARIATIONS IN LOG.(FEEDING PARAMETERS). NOTATION AS FOR TABLE 12, BUT VEGN. IS PERCENT COVER BY GREEN GRASS

DEPENDENT VARIABLE	CONSTANT	VEGN.	PROTEIN	WATER	R^2
BOUT LENGTH	-15.67	-0.16	2.03	0.16	0.28
PECKING RATE	58.61	-0.40	0.93	0.45	0.18
WALKING RATE	-38.61	-1.20	1.87	1.27	0.92 **

Table 19. COEFFICIENTS OF MULTIPLE, LINEAR REGRESSION EQUATIONS RELATING VARIATION IN BEHAVIOURAL PARAMETERS TO VEGETATIONAL VARIATION FOR ADULT BLUE GEESE AT THE McCONNELL R. N.W.T.

Figure 20. COMPARISON OF VARIATION IN INTAKE OF GRAZING BLUE GEESE WITH TIME SPENT FEEDING AS ESTIMATED BY REGRESSION EQUATIONS DERIVED FROM DATA COLLECTED AT GUELPH, ONT. AND McCONNELL RIVER N.W.T.


INTAKE
(g)
80
60
40
20
McCONNELL
GUELPH
20
40
60
80
TIME
(min)

for the weighed individuals.

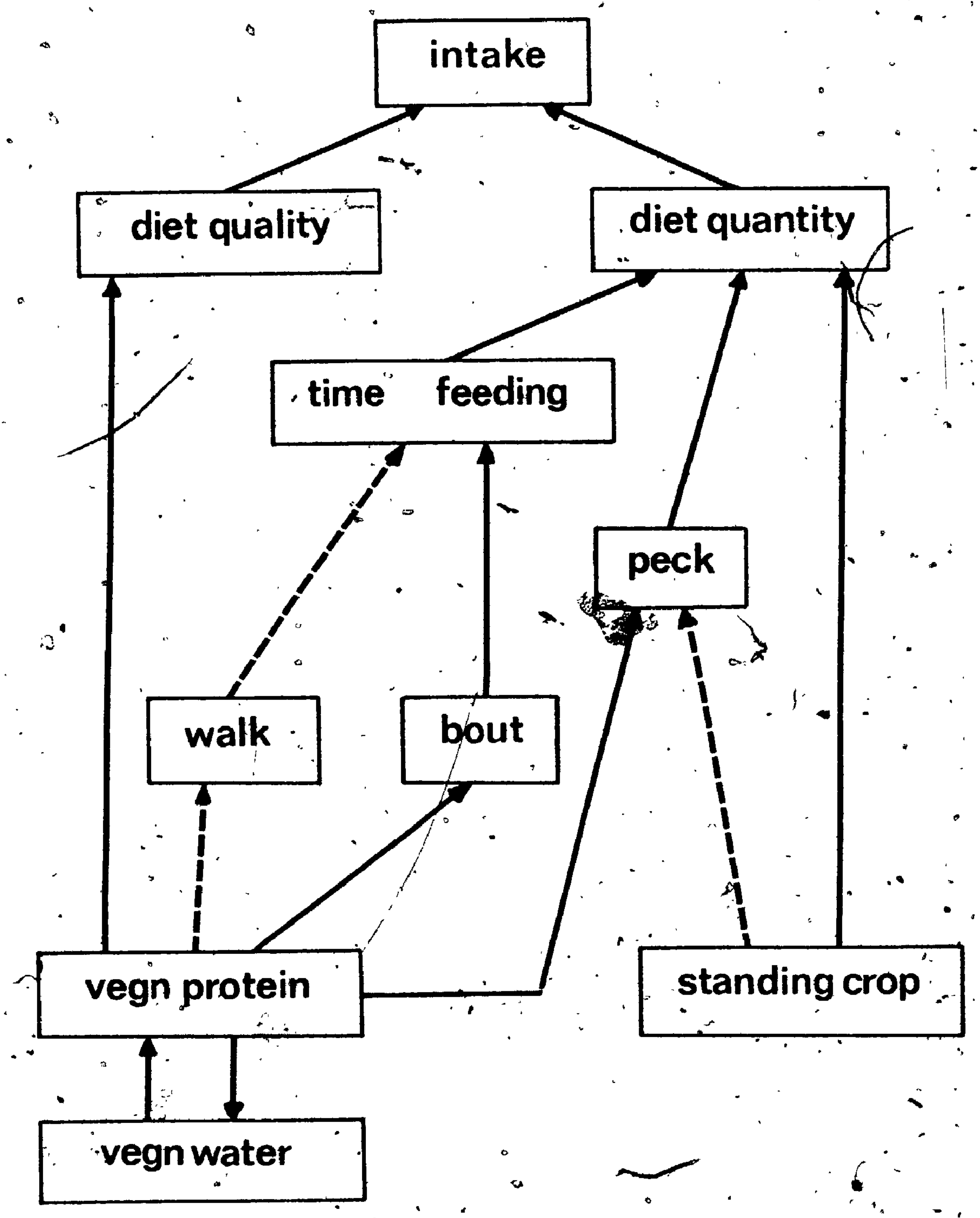
As noted in Sec. 4.2, the Guelph post-fertilization estimates showed a rather poor correlation with time spent feeding. However, the multiple correlation coefficient if the logarithms of time spent feeding and rate of walking are included is both highly significant and relatively large (r = 0.60, n = 27) for these data.

The derived regression equations are also intuitively satisfying. In both cases time spent feeding is the most important variable. At Guelph an increase in the rate of pecking leads to an increased intake. At the McConnell River, intake increases with increasing available vegetation. Thus the behavioural variations at Guelph reported in Chapter 3 can be seen to have adaptive value. An increased pecking rate enhances intake; a decreased rate of walking tends to maintain a bird in a particular area, and also increases intake (presumably because an increase in the rate of walking increases the number of unsuccessful pecks).

4.4 THE MODEL REVISITED

In the light of the analyses conducted in Secs. 3.4 and 4.3, we can define the relationships of Figure 1 with more precision. The expanded model is shown in Figure 21. It is, however, still not possible to define these relationships quantitatively since the regression equations so far defined have been determined over a narrow range of environmental variation. The extension of such equations to situations beyond their demesne is unlikely to be valid.

Figure 21. SYSTEMS DIAGRAM OF IMMEDIATE EFFECTS OF VEGETATION VARIABLES, FEEDING BEHAVIOUR AND FOOD INTAKE UPON EACH OTHER FOR GRAZING BLUE GEESE. NOTATION AS IN FIGURE 1, BUT SOLID LINES INDICATE POSITIVE CORRELATIONS AND DASHED LINED NEGATIVE CORRELATIONS


intake
diet quality
diet quantity
time feeding
peck
walk
bout
vegn protein
standing crop
vegn water

4.5 SUMMARY

The measurement of the intake of blue geese using captive birds, direct weighing of feeding birds, shooting of feeding birds, defaecation rate, and exclosure techniques yields similar estimates of intake per minute of feeding. Direct weighing is probably the most reliable technique. Defaecation rate is probably satisfactory for wild birds which spend a great proportion of their time feeding.

Variations in feeding behaviour affect intake in such a way that the responses to changes in vegetation quality previously noted would result in increased diet quality.

VERIFICATION AND ELABORATION OF THE MODEL

> "Although reality may avoid the obligation to be interesting, theories may not"
> Jorge Luis Borges.

5.1 INTRODUCTION

In the preceeding two chapters I used empirical statistical techniques to define relationships between the components of the model originally presented in Figure 1. These analyses yielded the more elaborate model of Figure 21. This seems, at least, to pass the test of that useful - if not always scientific - mentor: common sense. However, the reliance on statistical techniques to elucidate the nature of relationships is a tacit admission of ignorance (van der Steen 1970). In this chapter I shall first use the old empirical techniques in an attempt to validate the model with new data. I shall then derive a similar model from a more theoretical - and hopefully more aesthetically pleasing - basis.

5.2 VALIDATION

It was comforting that the data on the relationship between feeding behaviour and intake from both Guelph and the McConnell River yielded similar regression equations. However, it proved logistically impractical to determine the protein content of the vegetation in all of the sites used to test the McConnell River goslings. Additional data were required to confirm the predicted relations between vegetation parameters and feeding behaviour. Such data were available for the adults shot in the estimation of intake (Sec. 4.2). While these birds were under observation their feeding behaviours were recorded. After each bird was shot, three to five vegetation samples were taken from the area which the bird had traversed (the sample size depended on the extent of its perambulations). Standing crop, protein content and water content of the vegetation; and the protein content of the oesophageal contents of the bird were determined. A multiple regression technique identical to that used in Chapters 3 and 4 was applied to the data. The results are simultaneously more interesting (since the observations encompassed a wider range of vegetational and behavioural variation) and less reliable (being based on only 13 individuals) than the Guelph results. The raw data matrix is given in Appendix 9.

Vegetation and Behaviour

Of the three equations relating each behaviour to the linear sum of grass standing crop, protein content and water content, only that for walking is statistically significant (Table 19). This relationship was non-significant in the Guelph data. Rate of walking increases with increasing vegetation protein; this seems illogical in the light of previous arguments.

The failure of the linear regressions to provide an adequate explanation of the behavioural variation may be because the relationships are truly curvilinear. However, inspection of individual two dimensional plots gave no evidence of this, and rerunning the regression routine using the logarithms of all data values did not improve the fit. It seems more likely that the vegetation samples did not accurately represent the spectrum of vegetation on which the geese were feeding, especially as the location of feeding activities often had to be estimated at distances greater than 50m.

Inspection of the correlation half-matrix for all variables

(Table 20), suggested that the inclusion of percentage time spent feeding in the regression equation might improve the multiple correlation. It was hoped that time spent feeding merely provided additional information on vegetation quality. However, since it was shown in Chapter 3 that percentage time feeding could be predicted from a knowledge of bout length and walking rate, some doubt must exist as to the actual function of this variable in the regression equations. Inclusion of time spent feeding yields a significant multiple correlation coefficient for bout length, and a coefficient for pecking rate which approaches significance (Table 21). The individual coefficients of these equations are in qualitative agreement with those for the Guelph data. In particular, bout length and pecking rate increase with increasing protein content. Additionally, the effect of water content is limited.

Behaviour and Intake

The calculated regression equation for the relationship between the logarithm of intake and log (feeding behaviour) is indicated in Table 22. Although the correlation coefficient is high, there are discrepancies between this equation and those calculated from the experimental data. The major difference is in the importance of available vegetation. This made only a small contribution to the original equations. However, the experiments were carried out over a restricted range of standing crops. This restriction may have masked the influence of vegetation quality. In addition, rate of walking is positively correlated with intake. This is difficult to conceive intuitively, but makes sense analytically, since it would be advantageous if increased walking rate increased intake as the data showed a positive correlation between vegetation protein and walking rate.

DEPENDENT VARIABLE	CONSTANT	VEGN.	PROT.	WATER	TIME	R^2
BOUT LENGTH	-28.57	0.15	1.49	-0.20	0.45	0.77 **
PECKING RATE	31.82	-0.47	1.77	0.41	0.24	0.43
WALKING RATE	-38.67	-1.20	1.87	1.27		0.92 **

Table 21. COEFFICIENTS OF MULTIPLE LINEAR REGRESSION EQUATIONS RELATING VARIATION IN BEHAVIOURAL PARAMETERS TO VEGETATIONAL VARIATION, FOR ADULT BLUE GEESE AT THE McCONNELL RIVER, N.W.T. 1973. NOTATION AS FOR TABLE 20

TIME	PECK	WALK	VEGN.	R^2
0.88	2.98	0.47	3.01	0.87 **

Table 22. EXPONENTS OF MULTIPLE LINEAR REGRESSION EQUATION RELATING LOG (INTAKE) OF ADULT BLUE GEESE SHOT AT THE McCONNELL RIVER, N.W.T. TO VARIATION IN LOG.(BEHAVIOURAL PARAMETERS) AND AVAILABLE VEGETATION NOTATION AS IN TABLE 20.

	VEGETATION	PROTEIN	WATER	BOUT	PECK	WALKING RATE
TIME FEEDING	-0.028	-0.033	0.119	0.763**	0.465	0.271
VEGETATION		0.144	0.699**	0.049	-0.202	-0.308
PROTEIN			-0.177	0.367	0.217	0.001
WATER				-0.058	0.082	0.362
BOUT LENGTH					0.332	0.161
PECKING RATE						0.30[illegible]

Table 20. CORRELATION HALF-MATRIX, CORRELATION COEFFICIENTS BETWEEN FEEDING BEHAVIOURS OF ADULT BLUE GEESE AT THE McCONNELL RIVER, N.W.T. AND VEGETATION VARIABLES. NOTATION AS IN TABLE 11, BUT "TIME" IS PERCENT OF OBSERVATION TIME SPENT FEEDING.

Protein Content of the Oesophageal Samples

If the selection mechanism postulated in Chapter 4 operates among wild birds, the protein content of the vegetation in the oesophagi of feeding birds should be higher than the mean protein content of the vegetation being grazed but should fall within the vegetation's normal range of variation. Table 23 compares oesophageal protein with the 95% confidence limits for the appropriate vegetation samples. The model adequately describes less than half of the observations. These inadequacies are probably partially due to unrepresentative vegetation sampling, and partially because - by the very nature of their feeding process - geese tend to consume only the upper portions of grass blades (which have a low cuticle content). The chemical analyses for the vegetation samples were performed on all green grass in the sample. The upper 20cm of 80cm high alfalfa plants may contain 50% more protein than the whole plant (Lyttleton 1973).

Discussion

Although, the data from the shot birds confirms some of the predictions of the Guelph derived model, the agreement is far from satisfying.

5.3 THEORETICAL CONSIDERATIONS

Fitting multiple regression lines to data sets is one of the simplest forms of model testing (Gilbert 1973). The crudeness of this technique is obvious from Sec. 5.2. Additionally, it is an ecological tenet that biological relationships are rarely linear - let alone multiply linear - over more than a restricted range. It seems valid to postulate mathematically more complex, and hopefully biologically more realistic, relationships between variables. Even these relationships

BIRD NO.	OESOPHAGEAL PROTEIN	VEGETATION PROTEIN MEAN	95% CONF. LIMITS	SAMPLE SIZE
JH 3	15.7	13.1	9.1 - 17.0	4
JH 5	21.2	17.0	10.3 - 23.7	4
JH 14	18.6	15.4	11.4 - 19.4	4
JH 17	18.7	13.8	12.4 - 16.3	3
JH 2	20.8	14.6	13.5 - 15.6	5
JH 4	24.6	17.6	12.7 - 21.5	4
JH 10	28.4	20.0	12.8 - 27.2	4
JH 15	19.6	16.4	14.9 - 17.9	4
JH 16	20.6	11.0	9.2 - 12.8	4
JH 18	19.5	13.7	10.9 - 16.5	3

Table 23. COMPARISON OF CRUDE PROTEIN CONTENT OF GRASS IN OESOPHAGI OF GRAZING, ADULT BLUE GEESE AND CRUDE PROTEIN CONTENT OF AVAILABLE GRASS AT McCONNELL RIVER, N.W.T. 1973.

may involve a gross over-simplification of the biological processes involved. As van der Steen (1970) has pointed out, it is acceptable for biological hypotheses to be based on assumptions that are known to be only partially true. The problem with such a process is that it becomes difficult to distinguish errors in the hypothesis from errors associated with the premises. Having partially exonerated myself for future sins of omission, I shall now develop a more theoretical model.

Since 1966 it has become biologically fashionable to postulate mathematical models of feeding processes. However, with one exception (Westoby 1974), they have all been concerned with the feeding strategies of predators, as defined on p. 2. All these models involve the concept of optimization (Rosen 1967, Cody 1974). They hypothesize that a feeding animal attempts to optimize its gain of one nutritional element (nutrient defined as in Westoby [1974]) in the environment, within the constraints of its other nutritional requirements. To avoid difficulties in the choice of suitable units of measurement energy intake is generally considered to be the variable to be optimized. Although different authors define the variable to be optimized in more or less inclusive terms, it generally involves E_i - the net energy gain from ingesting one item of i (calorific value of i minus energy required to capture, ingest and digest i); and t_i - the average time required to locate, capture and ingest an individual of i. The predator then seeks to maximize $\sum \frac{E_i}{t_i}$ for a particular energy intake or time allocation to feeding (Schoener's (1971) time minimizers and energy maximizers respectively). These models are generally static. They assume random encounters with the different food items of the environment on the basis of the relative abundance of the items. Cody (1971) and Pulliam (1973) have, however, considered the optimal foraging paths of vertebrates. The predictions of most models have been essentially qualitative, and they have differed considerably in their degree of sophistication. MacArthur and Pianka (1966) consider all items to have the same E value, and determine graphically how a predator should minimize $\sum t_i$. Their model applies to both individual prey items and patches of prey items. However, most of the parameters of the model at present defy quantification. Emlen (1966, 1968, 1973) considers the effects of variation of individual quality within a particular class of items. His conclusions cannot easily be expanded beyond a choice between two different classes. Rapport (1971) uses the graphical, economic technique of indifference functions (which are conceptually identical to Levins' (1968) adaptive functions), to define the optimal combinations of two prey items. Such a method is conceptually difficult for more than three items. Schoener (1971) provides a succint summary and mathematical expression of many of these models.

The application of any of the above formulations to grazing geese is problematic. The parameters involved are difficult or impossible to quantify. In addition, the standard, optimal variable (energy) is probably inapplicable to the study of herbivore strategies (Westoby 1974). It is difficult to define adequately what constitutes a food item for a herbivore. Certainly, it seems unlikely that the potential food resources of a grazing herbivore can be neatly divided up into a finite set of items each possessing unique properties. Rather, a grazing animal is faced with a matrix of vegetation, varying physically in three dimensions and continuously for every nutrient parameter*. In addition, handling and searching time approach zero for most items in a grazer's diet.

---

* A true "niche ~~as multi-dimensional space~~", in the Hutchinsonian sense (Hutchinson 1957).

Jordan (1971) has pointed out that the caloric value of the vegetation components of an ecotype is relatively constant. Westoby (1974) suggests that large herbivores have a finite daily intake (determined by the cross-sectional area of the gut, and the rate of food passage through it), and that they therefore seek to optimize the nutrient content of this intake. Such reasoning, although necessarily simplistic, is applicable to grazing geese. However, I have already argued that geese in summer try to maximize daily food intake (by rapid throughput and continuous feeding) as well as dietary, nutrient content. In this respect they are the perissodactyls of the arctic tundra (see Bell 1971).

Developing a theoretical model of a system that has already been subjected to statistical analysis is a potentially circular process. It is also impossible to define numerically the hypothesized relationships without recourse to empirical data. However, if we assume that blue geese are trying to maximize their daily protein intake we can develop a comparative model of the simplest way that this can be attained. When a bird encounters a patch of high quality food it can increase its protein intake by spending longer on this patch than on other, poorer patches, up to a certain limit. Similarly intake can be increased by pecking fastest on the patches with the highest protein content. Again there is a physiological upper limit on the rate of pecking. The mathematically simplest form these relationships could take is indicated in Figures 22a and 22b. We must also estimate the effect of these behavioural changes on food intake. Intake will be assumed to be linearly related to time spent feeding; and intake per minute to be a logarithmic function of the rate of pecking - since as pecking speed increases proportionately more

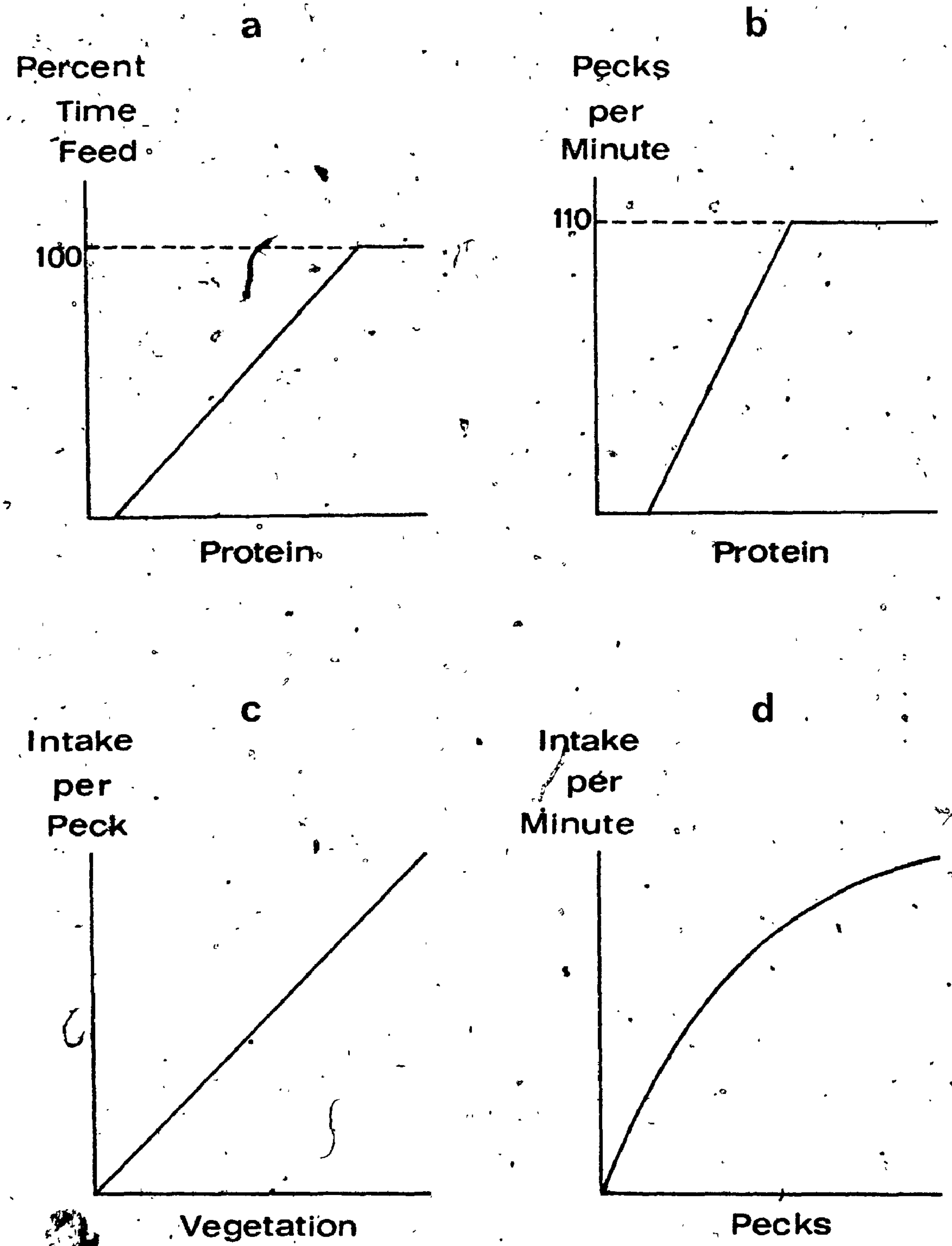
Figure 22. HYPOTHETICAL RELATIONSHIPS BETWEEN VARIABLES OF A SIMPLE MODEL OF BLUE GOOSE GRAZING BEHAVIOUR

(a) TIME SPENT FEEDING WITH VEGETATION PROTEIN CONTENT.
$\mathrm{TIME} = A_1(\mathrm{PROTEIN}) - C_1 . \quad \mathrm{TIME} \leqslant 100.$

(b) NUMBER OF FEEDING PECKS PER MINUTE WITH VEGETATION PROTEIN CONTENT.
$\mathrm{PECKS/MIN} = A_2(\mathrm{PROTEIN}) - C_2 \quad \mathrm{PECKS} \leqslant 110.$

(c) WEIGHT OF VEGETATION INGESTED PER PECK WITH STANDING CROP OF VEGETATION.
$\mathrm{INTAKE/PECK} = A_3(\mathrm{VEGETATION})$

(d) WEIGHT OF VEGETATION INGESTED PER MINUTE OF FEEDING WITH NUMBER OF PECKS PER MINUTE.
$\mathrm{INTAKE/MIN} = \mathrm{LOG}(\mathrm{PECKS/MIN})$


a
Percent Time Feed
100
Protein
b
Pecks per Minute
110
Protein
c
Intake per Peck
Vegetation
d
Intake per Minute
Pecks

pecks are likely to be unsuccessful. Intake per peck is assumed to be directly proportional to the quantity of green vegetation per unit area of the patch. The form of these relationships is illustrated in Figures 22d and 22c.

Assuming a random size distribution for patches, and random encounters with these patches, total intake will be given by:

$$\int_{P_{min}}^{P_{max}} \int_{V_{min}}^{V_{max}} f(P_iV_j).Time(P_i).Log(Peck(P_i)).A_3V_j.dV.dP$$

This can be estimated by:

$$\sum_{P_{min}}^{P_{max}} \sum_{V_{min}}^{V_{max}} f(P_iV_j).Time(P_i).Log(Peck(P_i)).A_3V_j$$

where $f(P_iV_j)$ is the observed joint frequency distribution of vegetation standing crop and protein content. Protein intake will be given by:

$$\sum_i \sum_j f(P_iV_j).Time(P_i).Log(Peck(P_i)).A_3V_j.P_i$$

Since blue geese should attempt to maximize the protein intake per unit time, and since pecking is an energy consuming process, the function to be optimized is:

$$\sum_{i}\sum_{j} f(P_iV_j) . \frac{\mathrm{Time}(P_i)}{\sum_{i}\sum_{j}\mathrm{Time}(P_i)} . \mathrm{Log}\left[\frac{\mathrm{Peck}(P_i)}{\sum_{i}\sum_{j}\mathrm{Peck}(P_i)}\right] . A_3V_j . P_i$$

To determine the nature of the optimization process I wrote a simple iterative FORTRAN programme (Appendix 10) to determine the optimal values of this function for different slopes of the peck and time lines (A_1 and A_2 in Figure 22) and different protein intercepts (C_1 and C_2, Figure 22) of 0, 5 and 10%. The upper time limit was set at 100., the upper peck limit at 110., A_3 was arbitrarily set at 0.017. I used the joint frequency distribution of green grass standing crop ($g.m^{-2}$) and the percent protein in this grass to estimate the $f(P_iV_j)$ distributions for the McConnell River in 1973 and for Guelph in 1972 (Appendix 11). The output of this programme for the McConnell River data is shown in Figure 23a, and for Guelph in Figure 23b. The results for the two locations differ markedly.

The optimal solution at the McConnell River is for birds not to feed on patches with a mean protein content less than 5%, and to feed equally on all patches with more than 11% protein. The relationship between the time spent on a patch and its protein content is shown in Figure 24. Since the mean protein content of McConnell River vegetation was 13%, most observed feeding behaviour would occur at protein levels around the inflexion of this curve. If geese pursued the optimal solution suggested by this model, it would be very difficult to detect a relationship between their feeding behaviour and vegetation protein content. This could explain the ambiguous results obtained from the shot birds.

Figure 23a. PREDICTED RELATIONSHIPS FOR GRAZING BLUE GEESE AT THE McCONNELL RIVER, N.W.T. 1973, BETWEEN PROTEIN INTAKE PER MINUTE OF FEEDING AND THE COEFFICIENTS OF THE EQUATIONS OF FIGURE 22. THE NUMBER BY EACH CURVE IS THE APPROPRIATE VALUE FOR A_1 (FIG. 22), PECKING COEFFICIENTS ARE VALUES FOR A_2 (FIG. 22)

(A) PROTEIN INTERCEPT (C_1 & C_2 OF FIG. 22) = 0.0

(B) PROTEIN INTERCEPT = 5.0

(C) PROTEIN INTERCEPT = 10.0

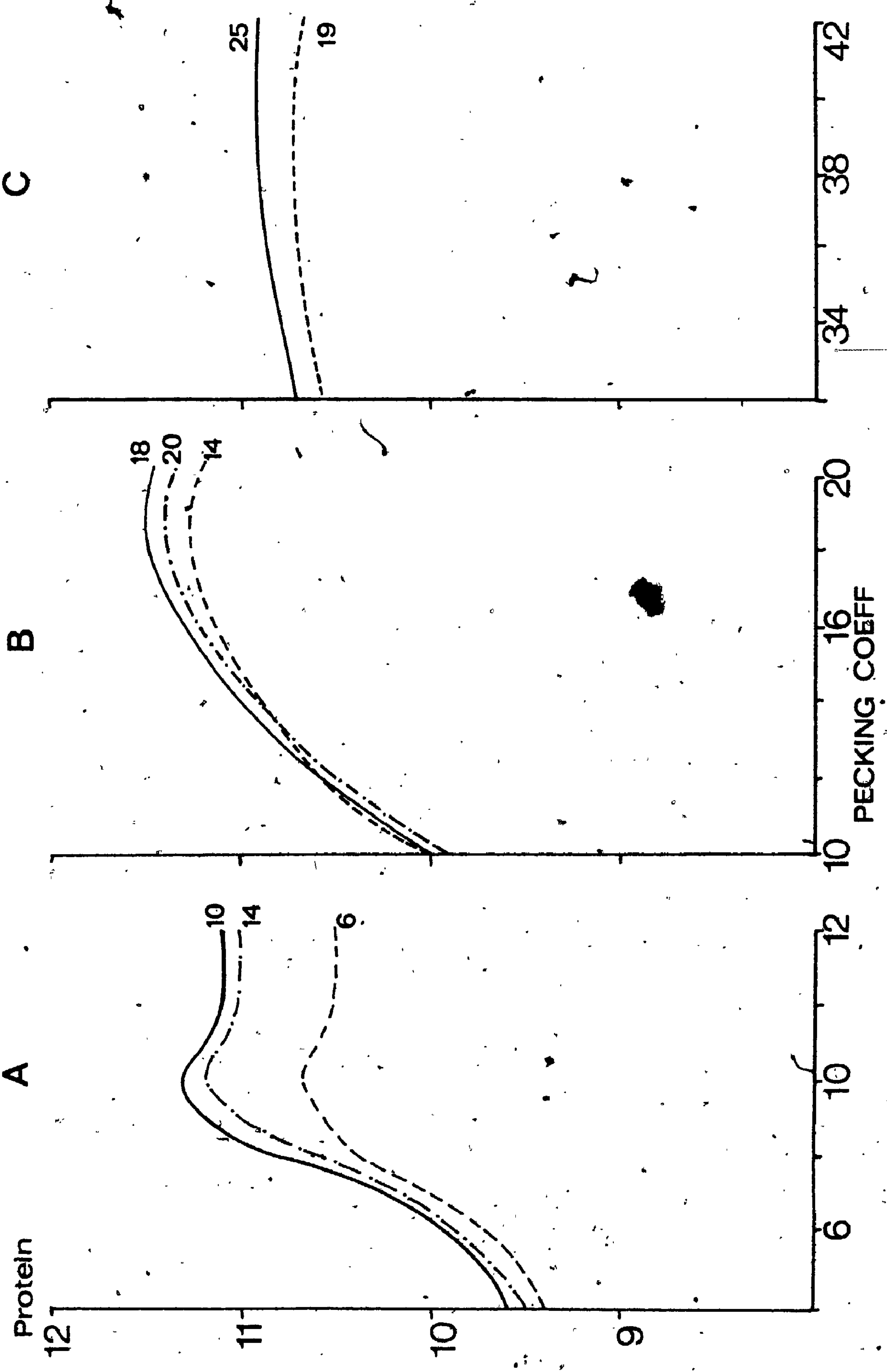
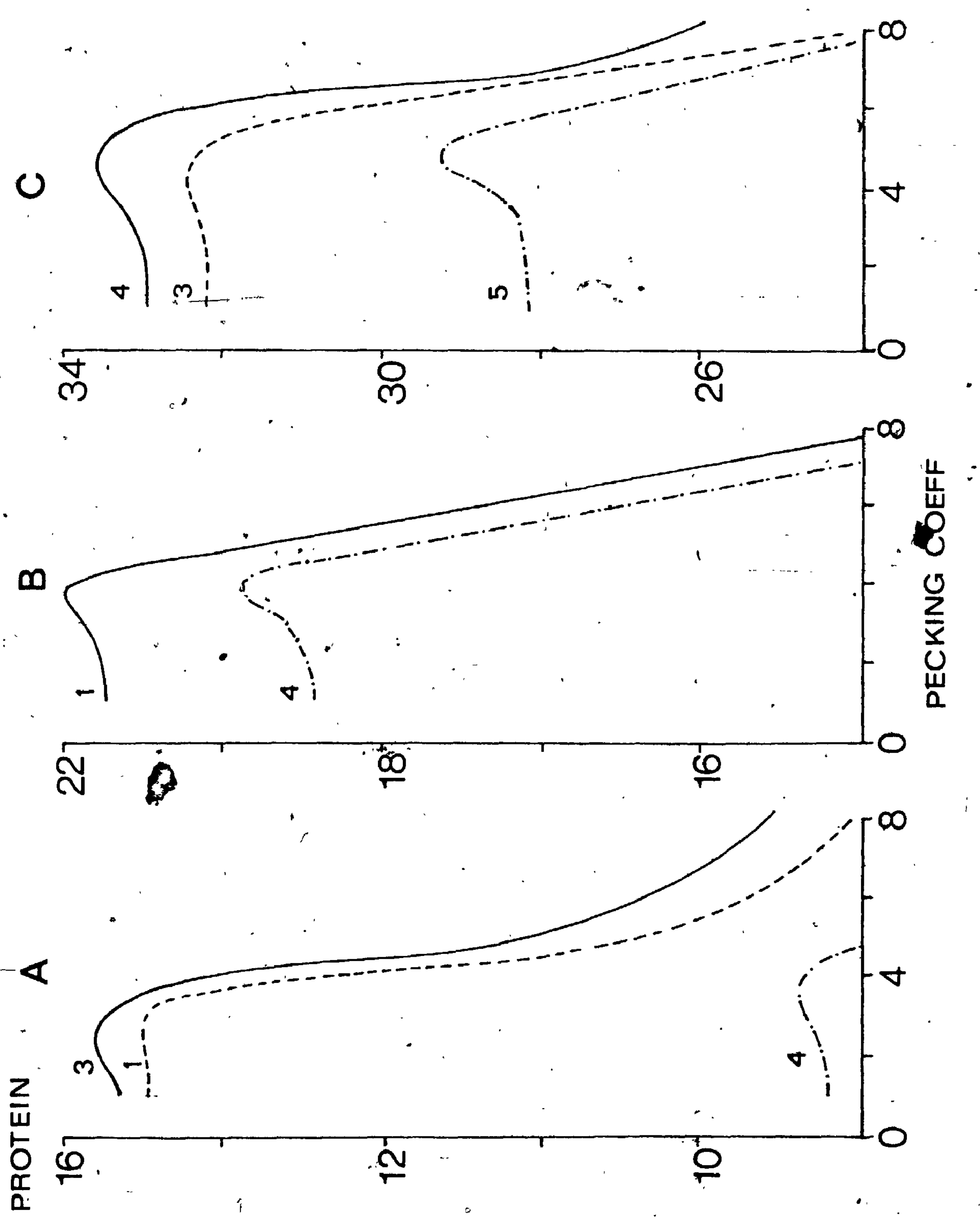

Protein
12
11
10
9
A
B
C
6
10
12
10
16
20
34
38
42
PECKING COEFF
10
14
6
18
20
14
25
19

Figure 23b. PREDICTED RELATIONSHIPS FOR GRAZING BLUE GEESE AT GUELPH, ONTARIO 1972, BETWEEN PROTEIN INTAKE PER MINUTE OF FEEDING AND THE COEFFICIENTS OF THE EQUATIONS OF FIGURE 22. NOTATION AS IN FIGURE 23a.


PROTEIN
A
16
12
10
0
4
8
3
1
4
B
22
18
16
0
8
1
4
C
34
30
26
0
4
8
4
3
5
PECKING COEFF

At Guelph the optimal solution is very different. Birds should only feed on patches containing at least 10% protein, they should gradually increase their feeding time and pecking rate with increasing vegetation protein. The relationship between time spent feeding and patch protein is indicated by the dashed line of Figure 24. Maximum pecking rate is not attained until the vegetation contains 30% protein; equal time is spent on all patches containing more than 35% protein. Since the mean vegetation protein content at Guelph was 24%, optimal feeding behaviour would show continuous variation over the observed range of protein variation, and selective feeding processes should be readily detectable.

Thus, on the basis of a small number of simple assumptions about the feeding behaviour of blue geese we can predict important aspects of the differences in their behaviour in different areas.

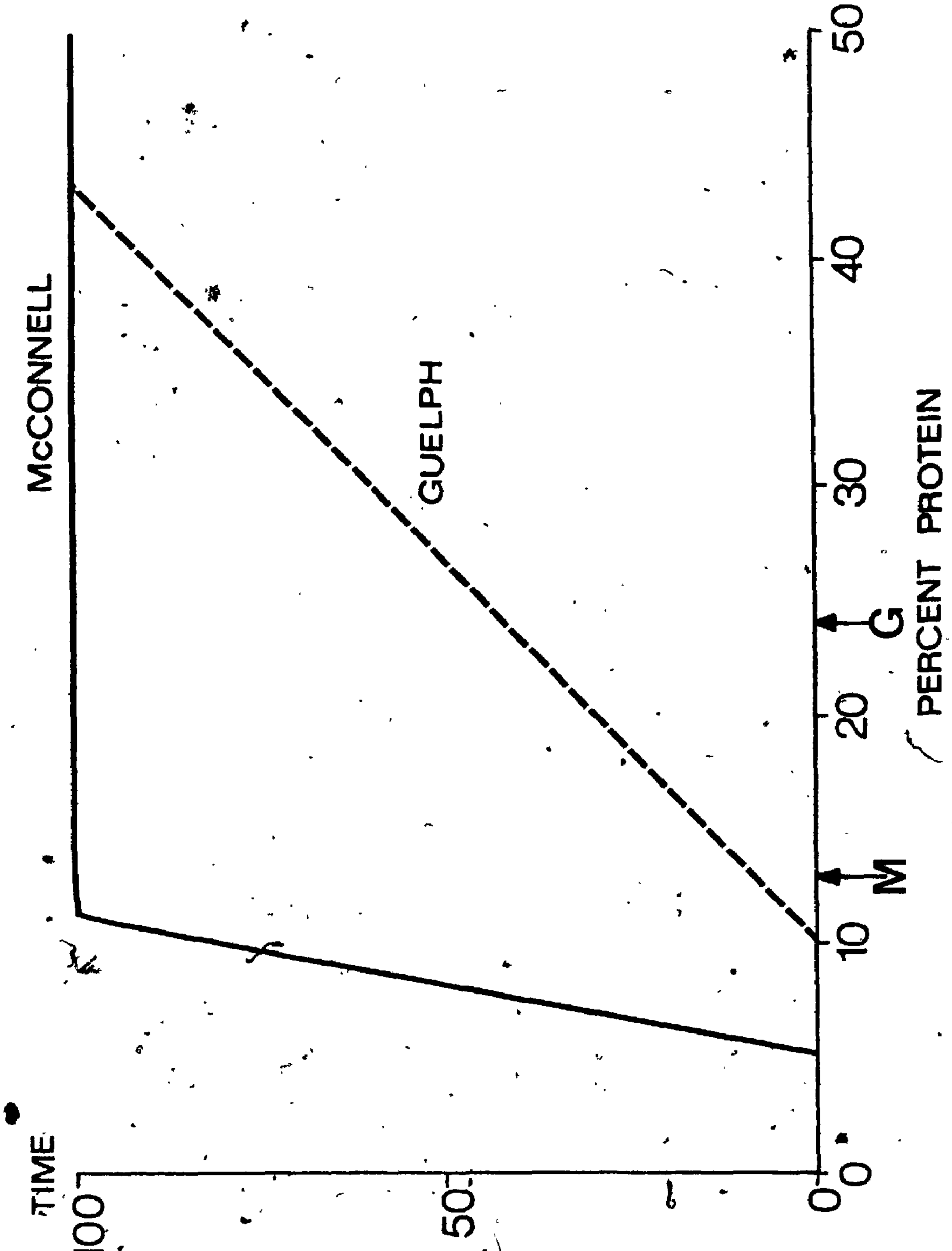
5.4 SUMMARY

The relationships suggested by the model of Chapter 4 could not be completely validated with independent data from the McConnell River. Recourse to a simple mathematical model of blue goose grazing behaviour suggested that if birds were attempting to maximize their protein intake per unit time of feeding, variation of the type observed would occur.

Figure 24. PREDICTED OPTIMAL ALLOCATION OF FEEDING TIME AMONG EQUAL-SIZED PATCHES OF DIFFERENT PROTEIN CONTENT FOR BLUE GEESE GRAZING AT THE McCONNELL RIVER AND AT GUELPH, ONT.

M - MEAN PROTEIN CONTENT OF McCONNELL RIVER VEGETATION

G - MEAN PROTEIN CONTENT OF GUELPH VEGETATION


TIME
100
50
0
0
10
20
30
40
50
PERCENT PROTEIN
M
G
McCONNELL
GUELPH

STRATEGY AND TACTICS IN BLUE GOOSE FEEDING

"...for science there is neither truth nor
reality but only the possibility of rationalization and the hope of reliability...."
J.G. Skellam.

6.1 INTRODUCTION

The tendency for biologists to explicitly consider adaptations as strategies may have its origin in the second chapter of Levins' important monograph (Levins 1968). It arises from a desire to extract unifying principles from the nexus of evolution, ecology and behaviour. The fact that completely unrelated species have evolved similar mechanisms in response to specific environmental exigencies suggests that there may only be a limited number of such strategies. If this is so, a theoretical framework for the analysis of population events in this domain may be constructed. Sophistication may be increased by distinguishing between strategies and tactics, in their original militaristic sense. Strategies are manipulations performed to determine the place and time of battle, tactics are the methods employed while in actual contact with the enemy. Smith (1974b) gives good examples of the difference between feeding strategies and feeding tactics. In this thesis, Chapter 2 was primarily concerned with strategies, and Chapter 3 specifically with tactics.

So far this analysis has been largely restricted to the quantitative relationships between the components of the model finally elaborated in Chapters 3 and 4. However, it is hardly realistic to expect an animal in so essentially ephemeral an environment as the arctic tundra to respond in the invariant manner that the model suggests. It was not therefore surprising that the results from Guelph could not be rigidly applied to the McConnell River situation. In this, final chapter I shall consider blue goose feeding behaviour in a largely qualitative fashion.

6.2 STRATEGIES

The distinction between strategy and tactic in a biological context is obviously somewhat arbitrary. However, within the original definitions of the terms it is possible to distinguish strategies as those behavioural traits concerned with the large scale spacio-temporal patterning of the environment. The distinction is one of times scale, strategies may vary seasonally but not from minute to minute.

The choice between rooting and grazing is a strategic one determined by the physiological requirements of the individual and the availability of the two food components. Kear (1966) has noted that many Anser spp are root feeders in winter and prior to migration, since at this time their primary requirement is for a high caloric content diet. In summer the basic metabolic requirement is for protein and the diet switches to green vegetation. It must be added that the chosen food items in each case are also the relatively most abundant ones in the respective environments, so that it is impossible to attribute a specific cuasality to the strategic choice.

Westoby (1974) has pointed out that the primary factor limiting a grazing herbivore's intake is the rate of passage of food through the intestinal tract. The requirements of flight have pre-adapted geese for the efficient exploitation of the relatively nutrient poor arctic vegetation. An elaborate - and therefore heavy - digestive system is incompatible with long migratory flights. Thus, of necessity, food passes rapidly through the intestinal tract, permitting continuous feeding and optimal utilization of the long arctic summer days.

The specific timing of the reproductive period is an act of strategy. The arctic tundra grasslands are characterized less by low daily primary productivity than by a very short potential growing season (Bliss 1971). As indicated in Chapter 2, high quantity and quality of vegetation at the McConnell River is restricted to July and early August. Blue geese lay their eggs and incubate in June, when food availability is low, but when nesting sites first become available. Hatch in the last week of June or first week of Jul[illegible] co-incides with the major commencement of primary production. This ensures optimal feeding conditions for the goslings at their critical period of maximum growth in the third or fourth week of life.

The role of the two sexes in parental care also involves strategic decisions. During June females lose more than one third of their body weight to the demands of egg production and incubation (Ankney 1974). They need to recover these body reserves in order to complete the major moult and migration. Similarly goslings must complete growth to near-adult size. Males lose considerably less weight than females during incubation (Ankney 1974). Thus they can energetically afford to spend more time than females in non-feeding activities after hatch. The most important non-feeding activity at this time is being alert (Sec. 2.4) to protect the goslings. The fact that males spend twice as much time alert as females confirms the intimation that they would follow an optimal strategy.

6.3 TACTICS

As implied in Sec. 6.2, tactics are concerned with the fine-grained structure of the environment, and involve the minute to minute adjustments in feeding behaviour to changes in the feeding environment. A species' tactical repertoire is obviously restricted by its initial strategic decisions.

I have argued before that blue geese should seek to maximize both their daily intake and the nutrient content of this intake. The Guelph experiments suggested a tactical mechanism for fulfilling both of these priorities, and this mechanism was at least partially confirmed by additional data. Since family parties cannot fly between feeding grounds, they must walk. It is therefore opportune for the birds to feed at all times. Feeding continuously also ensures continuous sampling of all items in the environment. This is essential if an individual is to make an optimal choice between items. By quantitatively changing the rate at which particular feeding actions are performed in response to changes in vegetation characteristics, it is possible for the birds to optimize their intake. An increase in bout length and decrease in the speed of walking ensures that the birds remain longer in high quality areas than in low quality ones. The increased rate of pecking in these areas increases the intake per unit feeding time while grazing there. If the increased rate of turning casually observed at Guelph also occurs in the arctic, this would additionally serve to maintain the birds in good areas. Experimental determinations of the influence of these behavioural changes on intake indicated that they did have the predicted effect.

It may be asked why geese feed only on arctic grasses, and effectively ignore most dicotyledons - especially since the leaves of these species are often relatively high in protein (Gardarsson and Moss 1971, Harwood unpubl. data). There seem to be three reasons. The cranial morphology of geese is not adapted to stripping the leaves from shrubs.

Most dicotyledonous plants in the arctic have thick leaf cuticles, which would resist digestion during their short residence in the goose's gut. They may also be more likely to contain noxious secondary compounds than the leaves of growing grasses (see Sec. 6.5). Dicotyledon leaves are essentially a non-renewing food source in the course of the summer. Leaves would be completely removed by feeding geese, and would not normally be replaced until the following summer. In contrast, removal of grass blade tips may result in enhanced vegetation growth during the same summer (Sec. 6.4). However, incubating geese will eat the leaves of Vaccinium uliginosum L., although this inclination disappears after hatch. The captive goslings could be persuaded to sample some dicotyledons - in particular V. uliginosum, the flowers of Astragalus alpinus L. and those of various Oxytropis spp. - up to seven days of age, although they scrupulously avoided plant leaves with thick, waxy cuticles (such as V. vitis-idaea L. and Rhodendron lapponicum (L.)). Birds older than one week were observed to consume only grasses.

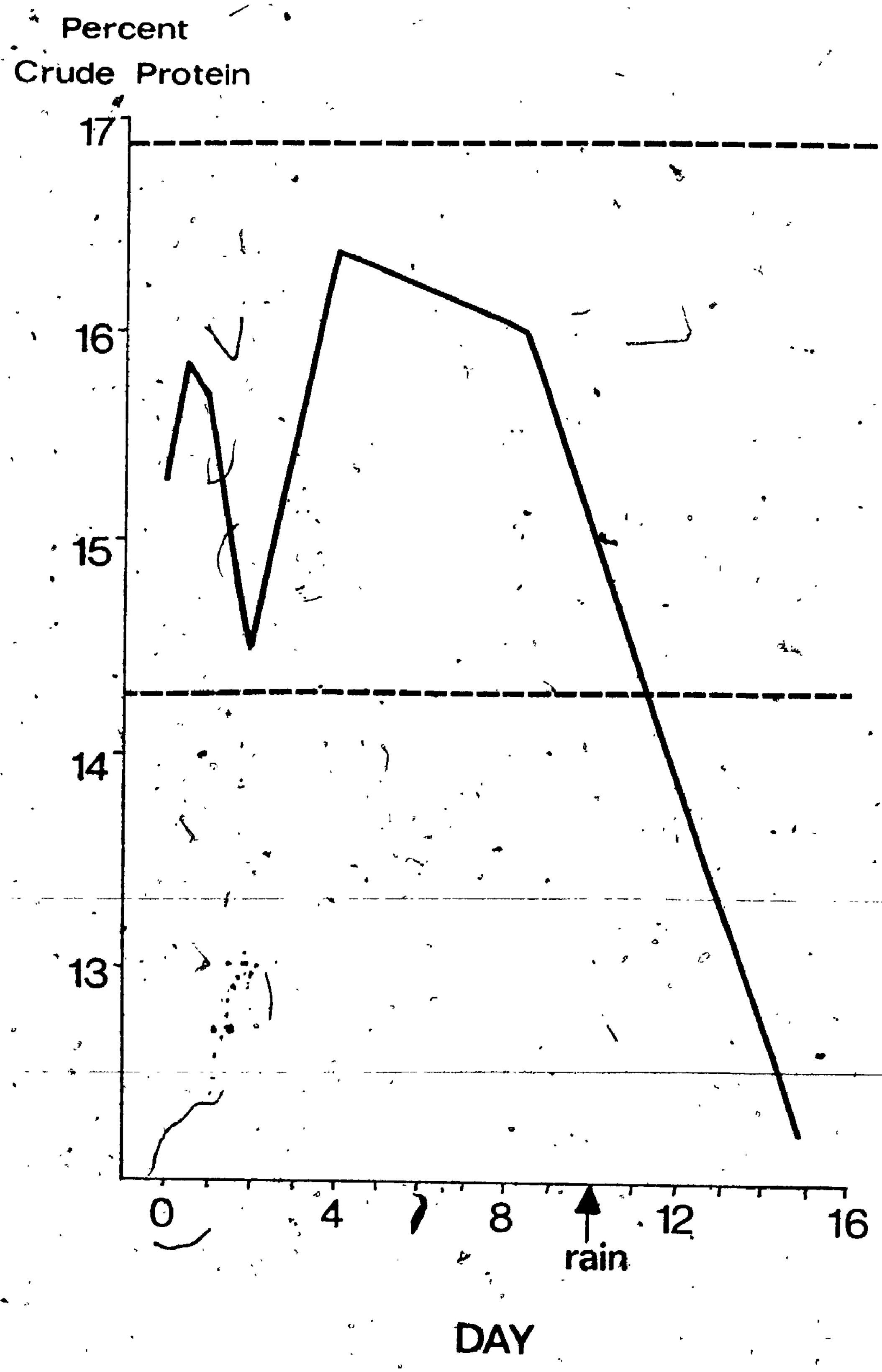
6.4 RELATIONS WITH THE ENVIRONMENT

The relationship of blue geese to their food supply involves more than a simple, one-way movement of nutrients. Otherwise it seems unlikely that colonies could occupy the same site for any extended period. The majority of gosling mortality occurs not on the breeding grounds, but is the result of hunting on the fall migration. Since almost the entire gosling is composed of nutrients extracted from the breeding grounds, this represents a massive net export of nutrients from the tundra [illegible]-system.

Remmert (1973) has suggested that large herbivores may be one of the major channels for nutrient cycling in the arctic. Normally vegetation decays very slowly in the arctic. Remmert suggests that the comminutive action of herbivores breaks the vegetation up into small fragments which, when defaecated, provide a large surface area for decomposition. Certainly blue goose faeces are composed of vast numbers of small but identifiable plant fragments. Since the food passes through the gut of geese in less than two hours, its mineral content cannot be greatly altered. To provide some information on Remmert's hypothesis, faeces were collected as they were excreted from grazing captive goslings, and frozen within 20 mins. of collection. Portions of 25g were sewn into cheese cloth bags which were pegged out on the tundra in the first week of August. Individual bags were then collected after 12 hours, 24 hours, 2 days, 4 days, 8 days and 15 days exposure, and immediately refrozen. All samples were oven dried and their nitrogen content was determined; changes in nitrogen content (expressed as "crude protein") with time are indicated in Figure 25. During the first eight days there was no rain and no appreciable change in faeces nitrogen. After less than 1cm of rain on the tenth day, the nitrogen content of the faeces dropped significantly. Since rainfall at the McConnell River normally occurs more than once every ten days, it seems that a considerable portion of the nitrogen component of blue goose faeces will be returned to the soil shortly after defaecation. Since each adult defaecates approximately 250 times per day, this is a substantial return.

There is an additional mineral input to the system. All blue goose colonies in the eastern arctic are situated on coastal lowlands. These areas have but recently emerged from Hudson Bay in the process of iso-static rebound (Walcott 1972). The area around the McConnell River

Figure 25. VARIATION IN CRUDE PROTEIN (6.25 x TOTAL NITROGEN) CONTENT OF BLUE GOOSE FAECES WITH TIME AFTER DEFAECATION AT THE McCONNELL RIVER, N.W.T. IN 1973. DASHED LINES INDICATE 99% CONFIDENCE LIMITS FOR PROTEIN BEFORE DAY 10.


Percent
Crude Protein
17
16
15
14
13
0
4
8
12
16
rain
DAY

is probably still rising about 0.6m per century (Andrews 1968). Since most of the McConnell River area is very low-lying - less than 10m above sea level (MacInnes et al 1974) - such a rapid rate of uplift will substantially increase the area of land available every decade and provide a continual external mineral input.

As noted in Chapter 2, goose grazing seems to increase and prolong primary productivity (Figures 3 and 4), and increase the protein content of the vegetation (Figures 7 and 8). Although some of this effect may be due to fertilization by the faeces, this is not an adequate explanation since many of the vegetation sites sampled contained no fresh faeces. Blue geese graze in loose aggregations of several families. Areas regularly grazed by such groups have a characteristic "bowling green" appearance. The vegetation is 2-5cm high and verdant. This is in marked contrast to some surrounding sedge meadows - especially those dominated by _Carex_ _aquatalis_ Wahlenb., agg. - where the coarse vegetation may be more than 25cm high. It seems that the intensive grazing activities of the geese may maintain the vegetation in a relatively immature stage - as suggested by Vesey-Fitzgerald (1960) for an East African grazing regime - with continued, accessible new growth (with low fibre and high protein content) and little or no flowering. The total nitrogen content of grasses is known to decrease markedly with age (Hegarty and Peterson 1973). Some circumstantial evidence for this hypothesis is provided by repeat sampling of vegetation sites at the McConnell River in 1971 (Table 24). The protein content of this artificially "grazed" vegetation is consistently higher than that of the surrounding, previously unclipped, vegetation.

SITE CODE		STANDARD SAMPLE	REPEAT SAMPLE
40A199	UNEXCLOSED	11.3	16.6
	EXCLOSED	12.3	18.4
40B252	UNEXCLOSED	12.9	14.2
	EXCLOSED	12.0	15.6

Table 24. COMPARISON OF CRUDE PROTEIN CONTENT (%) OF GREEN GRASS SAMPLED FOR THE FIRST TIME (STANDARD SAMPLE) AND SAMPLED FOR A SECOND TIME AFTER BEING PREVIOUSLY CLIPPED TO GROUND LEVEL (REPEAT SAMPLE) FOR TWO SAMPLE SITES AT THE McCONNELL R. 1971.

6.5 ANALYTICAL SHORTCOMINGS

This study has been concerned with the relationships between blue geese and grass, and specifically with two properties of the grass — its quantity and protein content. It may well be asked why other vegetation components have been ignored, and the potential influence of this ignorance on the analyses. I have argued that blue geese in summer have good cause to select for protein, and that the caloric content of the vegetation should have a trivial influence. Other nutrient minerals must be considered. Gardarsson and Moss (1971) and Moss (1972b) have shown that tetraoanids will select for high phosphorous content vegetation. However, Moss (1972b) found that phosphorus and nitrogen were positively correlated and that nitrogen was also selected for. Phosphorus has been ignored in this study primarily for logistic reasons. No facilities existed for the rapid analysis of large numbers of samples. Similar reasoning applies to the exclusion of calcium. This omission may be more important than that of phosphorus, since Ankney (1974) found that incubating female blue geese use the calcium of their long bones as a nutrient reserve. This reserve must be replenished during the summer. The failure of the Guelph birds to consistently respond to lime fertilization suggests that calcium is a less important element than nitrogen for blue geese.

As Freeland and Janzen (1974) have pointed out, the noxious and toxic effects of plant secondary compounds are major determinants of herbivore feeding strategies. Their presence is difficult to determine, and they have been virtually ignored in this study; although their presence was invoked as a possible reason for the avoidance of some dicotyledon species by geese (Sec. 6.3). It can be argued that, in an ecosystem as young as the arctic tundra, and where the depredations of grazing geese are localized, the flora will not have had time to evolve an appropriate spectrum of toxins. In this case, the arctic may be one of the few areas where geese - which cannot afford the extra weight of elaborate detoxification mechanisms - can operate efficiently as generalist herbivores.

Some mention must also be made of the lack of precision in the relationships determined between the variables of the model. A portion of this vagueness is the result of the difficulty in obtaining accurate estimates of the parameters involved. However, it is unrealistic to expect a species which operates in several different environments - all of which are, at present, temporally unstable - to exhibit rigid responses to environmental variations. It is not, therefore, surprising that the calculated relationships rarely account for more than 50% of the total variation in the appropriate dependent variable, and that their exact form varies with location.

Moss (1972a) found that the intestinal length of red grouse fed a prepared diet was significantly less than that of similar birds fed heather. It is very probable that the intestines of the Guelph birds were shorter than those of wild birds. This may have biased the results, although it is difficult to predict what this effect would be. The fact that the behaviour of these birds could be readily extrapolated to arctic conditions suggests that the effects of this abnormality were minor.

6.6 EVOLUTION

The suggestion that blue geese choose specific strategies and tactics carries the implication that they are consciously able to make decisions of statesman-like rationality. There is even less basis for making this supposition for geese than there is for the similarly named actions of military generals. It is, however, instructive to consider how such mechanisms could evolve within the strict framework of natural selection.

That an optimal feeding strategy will be favoured by natural selection is obvious. Females which feed with maximal efficiency in winter will have more available energy to channel into egg production than those that do not. Similarly, birds unable to recover the reserves lost in incubation, and to lead their goslings to areas of adequate nutrient content will be completely selected against. The problem is the explanation of the various feeding tactics. The fact that the Guelph birds exhibited these behaviours - although they had not previously had access to a wide range of food protein contents - is some evidence for a genetic component. However, the role of learning is obviously large. Goslings feed in close proximity to their parents, and are likely to mimic parental behaviour. Thus appropriate parental behaviour will lead to appropriate gosling behaviour. This imitative learning will be enhanced by delayed learning effects. If rats are made sick by X-radiation after having eaten a novel food item, they tend to avoid this item in future trials (Revusky and Bedarf 1967). Vitamin deprived rats will select for saccharin if given vitamin injections shortly after drinking saccharin (Garcia et al 1967). Similar delayed avoidance learning - in this case the avoidance of potential prey items - has been demonstrated for coyotes, <u>Canis latrans</u> (Gustavson et al 1974). Such a learning mechanism has not been shown in birds but its presence seems likely. It is therefore possible that goslings would rapidly learn which types of vegetation resulted in optimal blood protein levels, especially since parental behaviour would tend to concentrate their feeding in high quality areas. Provided the goslings could detect some cue associated with this high quality vegetation they would automatically tend to adopt optimal feeding tactics. In most years the water content of the vegetation (i.e. its "succulence") is probably an adequate cue. Water and protein content of grass were correlated at Guelph (Sec. 3.6) and at the McConnell River in 1971 ($r = 0.53$, $n = 28$, $P < 0.01$). This does not explain how the original blue goose pair came to adopt the optimal tactics, although such behaviour would confer a major selective advantage upon their genotype.

6.7 SUMMARY

Grazing blue geese show a series of behavioural strategies and tactics which seem to serve to optimize the protein intake of females and goslings. These strategies affect not only the general feeding behaviour of the birds but their impact on the tundra ecosystem. Small, quantitative changes in the expression of individual feeding behaviour parameters serve to enhance the birds' protein intake.

Although there is a net nutrient export from a blue goose colony, partial nutrient balance may be maintained through glacial uplift and rapid nutrient recycling aided by comminution.

A feasible method for the evolution of optimal feeding strategies and tactics is proposed.

APPENDIX 1

THE EFFECT OF VACUUM FREEZE DRYING AND OVEN DRYING ON THE WATER AND PROTEIN CONTENT OF GREEN GRASS

Five vegetation samples collected at the same site at the McConnell River, on the same day in 1971 were sorted into vegetation components. The grass component of each sample was divided into two, approximately equal sub-samples. One set of sub-samples was dried for 24 hours in a shelf model Virtis vacuum freeze drier, the other set was dried for 48 hours in an oven at 65°. The weight loss of each sub-~~sample~~ was determined and used to estimate its water content. The total nitrogen content of every sub-sample was then determined.

SAMPLE NO.	FREEZE DRIED	OVEN DRIED
1	50.1	54.7
2	48.2	47.3
3	50.8	56.7
4	56.1	58.4
5	53.6	55.3

Table 25. ESTIMATION OF PERCENTAGE WATER IN GREEN GRASS FROM THE McCONNELL RIVER, N.W.T. BY VACUUM FREEZE DRYING AND OVEN DRYING.

SOURCE	D.F.	SS	MS	F
BETWEEN TREATMENTS	1	18.497	18.497	5.29 n.s.
BETWEEN SAMPLES	4	97.157	24.289	6.95 n.s.
ERROR	4	13.983	3.496	
TOTAL	9	129.637		

Table 26. TWO-WAY ANALYSIS OF VARIANCE TABLE OF EFFECT OF VACUUM FREEZE DRYING AND OVEN DRYING ON THE WATER CONTENT OF GREEN GRASS FROM THE McCONNELL RIVER, N.W.T.

SAMPLE NO.	FREEZE DRIED	OVEN DRIED
1	16.4	17.1
2	14.5	14.5
3	19.4	18.4
4	15.2	16.6
5	14.1	14.3

Table 27. PERCENTAGE CRUDE PROTEIN IN GREEN GRASS FROM THE McCONNELL RIVER, N.W.T. AFTER VACUUM FREEZE DRYING AND OVEN DRYING

SOURCE	D.F.	SS	MS	F
BETWEEN TREATMENTS	1	0.169	0.169	0.43 n.s.
BETWEEN SAMPLES	4	28.920	7.230	18.35 **
ERROR	4	1.576	0.394	
TOTAL	9	30.665		

Table 28. TWO-WAY ANALYSIS OF VARIANCE TABLE OF EFFECT OF VACUUM FREEZE DRYING AND OVEN DRYING ON THE CRUDE PROTEIN CONTENT OF GREEN GRASS FROM THE McCONNELL RIVER, N.W.T.

APPENDIX 2

SOIL CHARACTERISTICS OF TEST ARENA AT GUELPH ONTARIO

OCTOBER 1972

PEN NO.	1	2	3	4	5	6
TOP-SOIL DEPTH (cm)	20	21	18	20	17	18
pH	7.5	7.4	7.4	7.5	7.5	7.5
POTASSIUM	79	69	63	63	72	79
CALCIUM	1830	1870	1830	1900	1900	1830
MAGNESIUM	571	581	603	576	565	587
PHOSPHORUS	9	9	8	11	9	8

TOP-SOIL CHARACTERISTICS OF EACH TEST PEN OF THE TEST ARENA USED AT GUELPH, ONTARIO IN 1972. EACH VALUE IS THE MEAN OF THREE SAMPLES. MINERAL VALUES ARE IN PARTS PER MILLION.

APPENDIX 3

PERCENTAGE TIME SPENT FEEDING BY CAPTIVE BLUE GEESE ON PAIRED FERTILIZED AND UNFERTILIZED VEGETATION SQUARES, GUELPH, ONT. 1972. DATA TRANSFORMED TO $\sqrt{X + 1/2}$

TREATMENT	SQUARE	UNFERTILIZED	FERTILIZED
NH_4NO_3	5m	2.57 ± 0.47 (29)	4.41 ± 0.55 (27)
		2.63 ± 0.65 (15)	4.42 ± 0.52 (15)
		1.74 ± 0.73 (14)	3.15 ± 0.46 (27)
	2.5m	2.96 ± 0.47 (35)	4.55 ± 0.66 (34)
		2.69 ± 0.41 (29)	4.62 ± 0.97 (20)
		1.66 ± 0.28 (31)	2.45 ± 0.57 (27)
	1.25m	2.49 ± 0.47 (30)	3.81 ± 0.67 (28)
		3.58 ± 0.50 (30)	4.17 ± 0.62 (30)
		5.06 ± 0.92 (16)	5.06 ± 0.81 (16)
$CaCO_3$	5m	2.84 ± 0.49 (27)	3.30 ± 0.68 (25)
		2.61 ± 0.82 (11)	3.80 ± 0.54 (29)
		3.86 ± 0.57 (34)	3.37 ± 0.59 (29)
	2.5m	4.69 ± 0.67 (26)	5.12 ± 0.60 (27)
		3.02 ± 0.67 (24)	2.41 ± 0.37 (33)
		2.63 ± 0.61 (27)	2.58 ± 0.45 (27)

APPENDIX 4

THREE-WAY ANALYSIS OF VARIANCE TABLE OF THE EFFECT OF AMMONIUM NITRATE FERTILIZATION ON THE FRESH WEIGHT STANDING CROP OF GREEN GRASS IN SQUARES OF THE TEST ARENA AT GUELPH

SOURCE	D.F.	SS	MS	F	
BETWEEN TREATMENTS	1	0.859	0.859	0.85	n.s.
BETWEEN SQUARES	4	11.047	2.762	2.74	n.s.
EXCLOSED VS UNEXCLOSED	1	0.922	0.922	0.92	n.s.
INTERACTION 1 & 2	4	80.228	20.057	19.93	***
INTERACTION 1 & 3	1	0.119	0.119	0.12	n.s.
INTERACTION 2 & 3	4	2.812	0.703	0.70	n.s.
INTERACTION 1, 2 & 3	4	4.581	1.145	1.14	n.s.
ERROR	40	40.258	1.006		
TOTAL	59	140.826			

APPENDIX 5

FEEDING RESPONSES OF CAPTIVE BLUE GEESE TO VARIATIONS IN THE QUANTITY AND QUALITY OF GREEN GRASS IN THE TEST ARENA AT GUELPH

DATE	STANDING CROP[1]	PERCENT PROTEIN	PERCENT WATER	BOUT LENGTH[2]	PECKS/ MIN	STEPS/ MIN
15 AUG	82.5	30.3	74.7	16.1	68.2	21.6
22 AUG	113.3	29.0	74.1	20.6	72.8	6.2
22 AUG	124.0	25.8	66.7	14.9	64.9	8.2
22 AUG	63.5	28.3	65.1	14.2	81.7	9.2
24 AUG	60.5	22.8	57.9	12.8	60.0	10.0
24 AUG	126.5	33.0	71.2	15.9	65.7	7.6
24 AUG	77.0	23.0	68.9	11.7	70.0	14.8
18 AUG	101.5	27.2	63.1	14.2	52.8	9.4
18 AUG	120.5	31.5	73.0	13.8	70.2	5.0
18 AUG	115.0	24.3	65.9	11.0	57.8	24.5
8 AUG	54.3	19.0	73.8	14.5	70.9	13.7
11 AUG	51.0	18.1	68.7	15.2	65.8	11.1
11 AUG	52.0	24.0	65.5	18.9	65.3	20.2
26 AUG	122.3	18.0	55.6	10.5	52.4	16.1
26 AUG	104.0	20.8	59.2	11.4	50.0	21.1
30 AUG	137.5	19.1	67.2	12.2	57.5	8.9
30 AUG	56.3	19.7	54.5	12.3	60.8	17.4
30 AUG	71.0	19.6	62.9	14.9	58.2	11.7
30 AUG	68.0	18.1	54.9	13.3	65.7	11.3

1. $g.m^{-2}$ 2. secs

APPENDIX 6

EFFECT OF TRIAL TIME ON THE ESTIMATED INTAKE PER MINUTE OF FEEDING OF BLUE GOOSE GOSLINGS AT THE McCONNELL RIVER, N.W.T. 1972

DATE	FIRST TRIAL	SECOND TRIAL
5 JULY	0.77	2.02
6 JULY	1.04	0.91
7 JULY	0.75	0.96
8 JULY	3.74	3.08
9 JULY	2.35	1.17
10 JULY	2.54	1.77
11 JULY	1.66	1.23
13 JULY	1.94	1.52
15 JULY	1.89	1.72
17 JULY	1.98	1.60
18 JULY	2.50	1.70
19 JULY	1.96	1.79
21 JULY	0.74	3.60
24 JULY	1.57	2.42
25 JULY	1.40	1.96
26 JULY	2.00	2.87
27 JULY	2.14	2.36
30 JULY	2.26	1.68

SOURCE	D.F.	SS	MS	F
BETWEEN TRIALS	1	0.035	0.035	0.08 n.s.
BETWEEN DAYS	17	10.800	0.635	1.39 n.s.
ERROR	17	7.767	0.457	
TOTAL	35	18.602		

Table 29. TWO-WAY ANALYSIS OF VARIANCE TABLE OF EFFECT OF TRIAL TIME AND DAYS ON THE ESTIMATED INTAKE OF BLUE GOSLINGS AT THE McCONNELL RIVER.

APPENDIX 7

AUTOMATIC CAMERA FOR ESTIMATING GOOSE USAGE

The camera unit was designed and built by Dr. R.J. Planck of the Zoology Department, University of Western Ontario. It resembled the unit used by Cowardin and Ashe (1965).

A Kodak Instamatic M22 Super 8 movie camera modified for single frame usage was mounted on a commercial, battery driven turntable. The turntable motor was activated at 15 minute intervals by a battery driven electric clock. Thus, every 15 minutes the turntable rotated through 360°. Stops set at 90° intervals around the circumference of the turntable platter triggered the camera's shutter mechanism. Each camera unit and each clock was housed in a separate water-tight box. Each camera could, in theory, operate for 10 days without attention.

In 1971 a unit was placed in the centre of each of the one hectare study areas. It was so adjusted that the four frames exposed every 15 minutes would together record the whole study area. By analyzing the films from each camera unit with a single frame capability super 8 projector it was possible to estimate the number of geese using each quarter of every study area, and thus the number of birds feeding in the unexclosed plot by each exclosure. However, the units proved somewhat unreliable in severe weather conditions, and only one unit ran for a whole 10 day period.

APPENDIX 8a

EFFECT OF VARIATIONS IN FEEDING BEHAVIOUR ON THE ESTIMATED INTAKE OF BLUE GEESE AND GOSLINGS - RAW DATA.

DATE	INTAKE[1]	MINS FEED	PECKS/ MIN	STEPS/ MIN
4 JULY	16.2	20.5	58.1	18.4
8 JULY	45.7	53.0	62.2	24.8
18 JUNE	40.5	17.5	50.6	15.3
19 JUNE	17.4	7.5	49.5	13.3
14 JUNE	26.2	4.0	44.8	3.2
28 JUNE	18.0	17.0	45.5	19.6
2 JULY	32.4	33.0	56.6	28.1
25 JUNE	42.2	39.0	54.1	13.3
26 JUNE	13.5	6.0	59.1	8.3
27 JUNE	27.2	12.5	54.0	16.9
11 AUGUST	31.3	31.0	53.3	11.2
12 AUGUST	32.2	23.0	58.6	12.6
14 AUGUST	45.0	25.0	66.8	15.7
18 AUGUST	32.7	28.0	69.5	12.5
19 AUGUST	34.9	14.0	64.0	13.4
20 AUGUST	10.2	10.0	76.4	12.3
23 AUGUST	41.4	22.5	62.3	9.0
24 AUGUST	26.0	14.0	64.0	13.4
26 AUGUST	12.4	7.0	76.4	12.3
15 AUGUST	50.3	19.0	62.8	8.7
16 AUGUST	50.4	13.0	63.4	10.2
17 AUGUST	39.0	5.0	60.5	13.3
8 AUGUST	16.4	21.0	63.3	14.2
10 AUGUST	21.0	14.5	67.0	15.8
27 AUGUST	16.2	11.0	51.1	18.5
28 AUGUST	37.1	15.0	57.4	8.3
30 AUGUST	31.6	17.0	62.5	14.5

Table 30a DATA FROM GUELPH, ONTARIO 1972. 1 VALUE IN G.

DATE	INTAKE[1]	MINS FEED	PECKS/ MIN	STEPS/ MIN	GREEN GRASS[2]
5 JULY	13.2	17.1	56.7	30.6	14
5 JULY	27.9	13.8	61.2	20.8	14
6 JULY	15.6	15.0	84.0	36.5	95
6 JULY	14.4	15.9	79.1	34.2	95
7 JULY	13.5	18.0	62.8	31.4	105
7 JULY	15.9	16.5	65.6	33.8	105
8 JULY	57.3	15.3	60.6	27.5	142
8 JULY	36.0	11.7	56.0	22.2	142
9 JULY	33.9	14.4	97.9	27.3	65
9 JULY	22.8	19.5	80.9	26.9	104
10 JULY	31.2	12.3	30.8	20.6	67
10 JULY	25.5	14.4	47.7	9.7	67
11 JULY	24.9	15.0	53.9	15.7	81
11 JULY	23.1	18.8	68.1	14.7	81
13 JULY	35.7	18.4	86.8	21.4	64
13 JULY	32.4	21.3	85.2	14.5	64
15 JULY	30.0	15.9	74.3	14.8	76
15 JULY	23.7	13.8	73.3	16.5	76
17 JULY	27.3	13.8	60.5	6.3	108
17 JULY	27.9	17.4	86.2	19.9	108
18 JULY	40.5	16.2	76.4	20.3	60
18 JULY	27.0	15.9	77.1	16.4	60
19 JULY	21.9	11.2	58.3	15.5	97
19 JULY	23.1	12.9	63.2	17.8	97
21 JULY	10.2	13.8	78.9	12.5	84
21 JULY	57.3	15.9	77.0	9.7	84
24 JULY	17.4	11.1	54.7	12.6	82
24 JULY	29.8	12.3	46.9	8.9	82
25 JULY	21.9	15.6	73.4	17.3	104
25 JULY	30.0	15.3	63.6	15.4	104
26 JULY	27.6	13.8	73.8	20.6	86
26 JULY	33.6	11.7	82.7	14.9	86
27 JULY	27.0	12.6	95.2	14.9	108
27 JULY	19.8	8.4	78.9	15.4	108
30 JULY	28.5	12.6	80.2	16.8	130
30 JULY	19.8	11.8	80.6	11.9	130
3 AUGUST	3.9	2.1	46.0	30.0	10
11 AUGUST	12.6	8.1	99.7	17.4	25
11 AUGUST	14.1	10.2	93.6	21.3	25
11 AUGUST	34.2	16.8	115.3	16.0	75

Table 30b DATA FROM McCONNELL RIVER, N.W.T. 1973. [1] VALUE IN G
[2] % COVER

APPENDIX 8b

EFFECT OF VARIATIONS IN FEEDING BEHAVIOUR ON THE ESTIMATED INTAKE OF BLUE GEESE AND GOSLINGS - NATURAL LOG. (DATA)

DATE	INTAKE	MINS FEED	PECKS/ MIN	STEPS/ MIN
4 JULY	2.78	3.02	4.07	3.01
8 JULY	3.82	3.97	4.15	3.32
18 JUNE	3.70	2.86	3.93	2.73
19 JUNE	2.86	2.01	3.90	2.59
14 JUNE	3.27	1.39	3.80	1.16
28 JUNE	2.89	2.83	3.82	2.98
2 JULY	3.48	3.50	4.04	3.34
25 JUNE	3.74	3.66	3.99	2.59
26 JUNE	2.60	1.79	4.08	2.12
27 JUNE	3.30	2.53	3.99	2.83
11 AUGUST	3.44	3.43	3.80	2.73
12 AUGUST	3.47	3.14	4.07	2.53
14 AUGUST	3.81	3.22	4.20	2.67
18 AUGUST	3.49	3.33	4.09	2.43
19 AUGUST	3.55	2.64	4.13	2.50
20 AUGUST	2.32	2.30	4.22	1.95
23 AUGUST	3.72	3.11	4.07	2.20
24 AUGUST	3.26	2.64	4.09	2.75
26 AUGUST	2.52	1.95	4.42	2.76
15 AUGUST	3.92	2.94	4.09	2.14
16 AUGUST	3.92	2.56	4.12	2.61
17 AUGUST	3.66	1.61	4.03	2.76
8 AUGUST	2.80	3.04	4.15	2.65
10 AUGUST	3.04	2.67	4.06	2.67
27 AUGUST	2.79	2.40	3.90	3.00
28 AUGUST	3.61	2.71	4.02	2.08
30 AUGUST	3.45	2.83	4.15	2.69

Table 31a. DATA FROM GUELPH, ONTARIO 1972.

DATE	INTAKE	MINS FEED	PECKS/ MIN	STEPS/ MIN	GREEN GRASS
5 JULY	2.58	2.84	4.04	3.42	2.64
	3.33	2.62	4.11	3.03	2.64
6 JULY	2.75	2.71	4.43	3.60	4.55
	2.67	2.77	4.37	3.53	4.55
7 JULY	2.60	2.89	4.14	3.45	4.65
	2.77	2.80	4.18	3.52	4.65
8 JULY	4.05	2.73	4.10	3.31	4.96
	3.58	2.46	4.03	3.10	4.96
9 JULY	3.52	2.67	4.58	3.31	4.17
	3.13	2.97	4.39	3.29	4.64
10 JULY	3.44	2.51	3.43	3.03	4.20
	3.24	2.67	3.86	2.27	4.20
11 JULY	3.21	2.71	3.99	2.75	4.39
	3.14	2.93	4.22	2.69	4.39
13 JULY	3.58	2.91	4.46	3.06	4.16
	3.48	3.06	4.45	2.67	4.16
15 JULY	3.40	2.77	4.31	2.69	4.33
	3.17	2.62	4.29	2.80	4.33
17 JULY	3.31	2.62	4.10	1.84	4.68
	3.33	2.86	4.46	2.99	4.68
18 JULY	3.70	2.79	4.34	3.01	4.09
	3.30	2.77	4.35	2.80	4.09
19 JULY	3.09	2.42	4.07	2.74	4.57
	3.14	2.56	4.16	2.88	4.57
21 JULY	2.32	2.62	4.37	2.53	4.43
	4.05	2.77	4.34	2.27	4.43
24 JULY	2.86	2.41	4.00	2.53	4.41
	3.39	2.51	3.85	2.19	4.41
25 JULY	3.09	2.75	4.30	2.85	4.64
	3.40	2.73	4.15	2.73	4.64
26 JULY	3.32	2.62	4.30	3.03	4.45
	3.51	2.46	4.42	2.70	4.45
27 JULY	3.30	2.53	4.36	2.70	4.68
	2.99	2.13	4.37	2.73	4.68
30 JULY	3.35	2.53	4.38	2.82	4.87
	2.99	2.47	4.39	2.48	4.87
3 AUGUST	1.36	0.74	3.83	3.40	2.30
11 AUGUST	2.53	2.09	4.60	2.86	3.22
	2.65	2.32	4.54	3.06	3.22
	3.53	2.82	4.75	2.77	4.32

Table 31b. DATA FROM McCONNELL RIVER, N.W.T. 1973.

APPENDIX 9

RAW DATA MATRIX OF VEGETATIONAL AND BEHAVIOURAL VALUES FOR ADULT BLUE GEESE SHOT AT THE McCONNELL RIVER, N.W.T. IN 1973.

CODE	INTAKE[1]	TIME[2]	TIME[3]	BOUT[4]	PECK[5]	STEP[6]	VEGN[7]	PROTEIN[8]	WATER[9]
JH 2	37.00	8.0	87	26.0	94.4	39.7	33.7	14.6	72.1
JH 3	2.20	5.0	59	7.5	73.5	26.9	15.1	13.1	44.1
JH 4	0.56	12.0	87	10.8	85.3	16.0	9.1	17.6	29.1
JH 5	0.54	10.0	59	12.8	88.9	11.3	13.7	17.0	30.2
JH10	18.81	10.0	95	41.2	88.3	32.2	26.0	17.8	46.1
JH11	0.17	7.5	75	22.8	73.3	18.2	7.3	11.4	30.0
JH12	0.03	5.0	45	8.1	83.1	36.9	5.8	15.3	45.5
JH13	4.90	11.0	73	14.3	80.0	33.4	16.7	15.1	48.3
JH14	17.16	9.0	45	14.5	90.2	9.4	23.7	15.4	36.3
JH15	6.75	8.0	55	13.7	64.1	0.9	51.2	16.4	57.1
JH16	7.19	8.0	80	17.8	86.6	13.1	27.3	11.0	53.2
JH17	6.72	6.5	93	26.2	86.5	10.9	12.2	13.8	39.3
JH18	0.76	-	95	12.3	92.8	16.9	26.6	13.7	46.4

1. g fresh weight, 2. minutes spent feeding, 3. percent of observation time feeding, 4. bout length in seconds, 5. pecks per minute, 6. steps per minute 7. standing crop of green grass grammes per square meter, 8. percent protein in green grass, 9. percent water in green grass.

APPENDIX 10

FORTRAN IV PROGRAMME TO DETERMINE OPTIMAL PROTEIN INTAKE FOR GRAZING BLUE GEESE

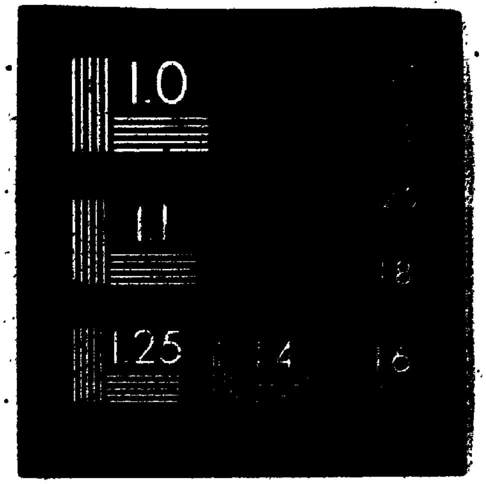
```
C       PROGRAMME TO CALCULATE PROTEIN INTAKE PER MINUTE
C       OF FEEDING FOR GRAZING BLUE GEESE
C       IV IS MATRIX OF VEGETATION FREQUENCIES, BE RECORDS
C       BEHAVIOUR VALUES
        DIMENSION  IV(10,35), BE(5,250), TOTAL(3)
C       INPUT DATA MATRIX
        DATA(IV(1,I),I=1,35)/0,0,0,0,0,0,0,0,0,0,1,0,0,
     1  2,1,0,1,0,3,1,0,0,1,2,1,1,0,0,0,0,0,1,0,1,0/

C       ETC.

        DATA(IV(10,I),I=1,35)/0,0,0,0,0,0,0,0,0,0,0,0,0,
     1  0,0,0,0,0,0,1,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0/
C       TYPE HEADINGS
        TYPE 11
C       SET VALUE OF PROTEIN INTERCEPT
        DO 99  J0 = 0,10,5
C       SET SLOPE OF TIME LINE
        DO 100 J1 = 1,5,1
C       SET SLOPE OF PECK LINE
        DO 101  J2 = 1,8,1
C       CALCULATE TIME INTERCEPT
        B1 = J1*J0
C       CALCULATE PECK INTERCEPT
        B2 = J2*J0
        IND = 0
        TOT = 0.
        POT = 0.
C       ZERO SUMMATION MATRIX
        DO 200  IA = 1,3
        TOTAL(IA) = 0.
200     CONTINUE
C       SUM OVER ALL PROTEIN VALUES
        DO 102  K1 = 1,35
        P = K1 + 5
C       SUM OVER ALL STANDING CROP VALUES
        DO 102  K2 = 1,10
        IF (IV(K2,K1).EQ.0) GO TO 102
        V = 15*(K2)
C       CALCULATE TIME SPENT FEEDING
        T = J1*P - B1
        IF (T.LE.0.) GO TO 102
        IF (T.GT.100.) T = 100.
```

```
C       CALCULATE TOTAL TIME SPENT FEEDING
        TOTAL(1) = TOTAL(1) + T
C       CALCULATE NUMBER OF PECKS
        PN = J2*P - BC
        IF (PN.LE.0.) GO TO 102
        IF (PN.GT.110.) PN = 110.
        IND = IND + 1
        BE(1,IND) = T
        BE(2,IND) = PN
C       CALCULATE TOTAL NUMBER OF PECKS
        TOTAL(2) = TOTAL(2) + PN
C       CALCULATE INTAKE PER PECK
        BE(3,IND) = 0.017*W
C       RECORD PROTEIN CONTENT OF VEG
        BE(4,IND) = F
C       RECORD FREQUENCY
        BE(5,IND) = IV(K2,K1)
102     CONTINUE
C       CALCULATE INTAKE AND PROTEIN INTAKE
        DO 103  L1 = 1,IND
        RAT = 1000.*BE(2,L1)/TOTAL(2)
        IF (RAT.LT.1.) GO TO 103
        ALGIE = ALOG10(RAT)
        GULP = (BE(1,L1)/TOTAL(1))*ALGIE*10.
        GULP = GULP*BE(3,L1)*BE(5,L1)
        PGULP = GULP*BE(4,L1)
        TOT = TOT + GULP
        POT = POT + PGULP
        DO 104  L2 = 1,4
104     BE(L2,L1) = 0.
103     CONTINUE
        IF (POT.EQ.0.) GO TO 100
        PIT = POT/TOT
101     TYPE 10,  J1,J2,TOT,POT,PIT
100     TYPE 12
99      TYPE 12
10      FORMAT (2X,2I6,3F11.2)
11      FORMAT (////3X,'  TIME   PECK   , INTAKE
     1     TOTAL PRO      % PRO'/)
12      FORMAT (2X,/)
        STOP
        END
```

3 OF/DE 3



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APPENDIX 11

JOINT FREQUENCY DISTRIBUTIONS OF GREEN GRASS STANDING CROP AND GRASS PROTEIN CONTENT FOR THE McCONNELL RIVER 1973 AND GUELPH, ONTARIO 1972.

	STANDING CROP												
PROTEIN	0	5	10	15	20	25	30	35	40	45	50	55	
8	0	0	1	0	0	0	0	0	0	0	0	0	1
9	0	0	0	0	0	0	0	1	0	0	0	0	1
10	0	0	0	0	0	0	1	0	0	0	0	0	1
11	0	1	0	1	3	1	1	0	0	0	0	0	7
12	0	0	1	1	0	1	0	1	0	0	0	0	4
13	1	1	2	1	0	0	1	0	1	1	0	0	8
14	1	1	3	0	1	1	0	1	0	0	0	0	8
15	1	0	1	0	2	0	1	0	1	0	0	1	7
16	2	1	2	1	0	0	0	0	0	1	0	0	7
17	0	0	2	0	0	0	0	0	0	0	0	1	3
18	0	0	1	0	1	0	0	0	0	0	0	0	2
19	0	1	0	0	0	0	0	0	0	0	0	0	1
20	0	1	1	0	0	0	0	0	0	0	0	0	2
21	2	0	0	0	0	0	0	0	0	0	0	0	2
22	1	0	1	0	0	0	0	0	0	0	0	0	2
23	1	0	0	0	0	0	0	0	0	0	0	0	1
	9	6	15	4	7	3	4	3	2	2	0	2	

Table 32. JOINT FREQUENCY DISTRIBUTION FOR STANDING CROP OF GREEN GRASS ($g.m^{-2}$) AND PERCENT PROTEIN IN THAT GRASS FOR THE McCONNELL RIVER 1973.

MEAN PROTEIN CONTENT = 13.2%

MEAN PROTEIN CONTENT = 24.4%

PROTEIN	STANDING CROP										
	15	30	45	60	75	90	105	120	135	150	
6	0	1	0	0	0	0	0	0	0	0	1
7	0	0	0	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0	0	0	0
15	0	1	0	0	0	0	0	0	0	0	1
16	1	0	2	1	2	0	0	0	0	0	6
17	0	3	0	0	2	0	1	0	0	0	6
18	0	0	2	5	1	1	0	0	0	0	9
19	2	6	0	4	3	0	0	0	0	0	15
20	1	4	4	2	3	3	0	0	0	0	17
21	0	0	1	1	1	0	1	0	0	0	4
22	1	4	4	2	1	1	1	0	0	0	14
23	0	4	1	5	2	0	0	0	0	0	12
24	3	1	1	2	0	2	0	0	0	0	9
25	1	1	4	1	1	1	0	0	0	1	10
26	0	1	2	5	1	0	0	0	0	0	9
27	0	1	1	0	1	0	0	0	0	0	3
28	1	2	1	3	0	1	1	0	0	0	9
29	2	4	1	4	3	0	0	0	0	0	14
30	1	1	1	2	2	1	0	1	0	0	9
31	1	3	1	2	2	1	0	0	0	0	10
32	0	1	1	2	0	0	1	0	1	0	6
33	0	2	1	2	1	0	0	2	0	0	8
34	0	0	0	3	0	0	1	0	0	0	4
35	0	0	0	0	0	0	1	0	0	0	1
36	0	0	1	0	0	0	0	0	0	0	1
37	1	0	0	0	0	0	0	0	0	0	1
38	0	0	0	0	0	0	0	0	0	0	0
39	1	0	0	0	0	0	0	0	0	0	1
40	0	0	0	0	1	0	0	0	0	0	1
	16	40	29	46	27	11	7	3	1	1	

Table 33. JOINT FREQUENCY DISTRIBUTION FOR STANDING CROP OF GREEN GRASS ($g.m^{-2}$) AND PERCENT PROTEIN IN THAT GRASS FOR GUELPH, ONT. IN 1972.

APPENDIX 12

AFFECT OF FERTILIZER TREATMENTS ON THE PERCENTAGE CRUDE PROTEIN CONTENT OF GREEN GRASS AT GUELPH, ONT. 1972.

TREATMENT	SQUARE SIZE	UNFERTILIZED	FERTILIZED	P[a]
NH_4NO_3	5m	26.8 ± 0.79 (12)	30.9 ± 1.61 (12)	0.001
	2.5m	28.4 ± 0.90 (6)	32.9 ± 0.86 (18)	0.01
	1.25m	24.3 ± 0.38 (24)	33.4 ± 0.30 (12)	0.001
$CaCO_3$	5m	18.9 ± 0.30 (24)	20.1 ± 0.37 (24)	0.05
	2.5m	27.8 ± 0.71 (18)	26.3 ± 1.02 (6)	n.s.

a. PROBABILITY (BY ONE-WAY ANALYSIS OF VARIANCE) OF DIFFERENCE BEING DUE TO CHANCE.

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