GRAZING THE SALTMARSH:
BARNACLE GOOSE FORAGING BEHAVIOUR IN RELATION TO FESTUCA RUBRA QUALITY AND QUANTITY

DOCTORAL REPORT
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SUMMARY

(1) A clear temperature dependency of Festuca rubra growth was found, explaining the late switch from polder to saltmarsh in relatively cold winters compared to relatively warm winters.

(2) A level of 25% crude protein in Festuca rubra dry matter was found to be the overall limit for Barnacle goose grazing both at the end and during spring staging on the saltmarsh of Schiermonnikoog.

(3) Calculations showed that energy content of Festuca rubra was limiting Barnacle goose grazing — protein was always available in excess.

ACKNOWLEDGEMENTS

For support during this study I would like to thank Prof. Dr. Bob Jeffries, Dr. Dawn Raza, Dr. Herbert Prins, Prof. Dr. R. Brent, the staff of the Plant Ecology lab., and last but not least Gabrielle van Dinteren, Henk van der Jeugd, Martin, Edo Kneiblering and Popko Wiersema.
INTRODUCTION

The foraging activities of many herbivores have been shown to be related to the protein content of their food (Jefferies 1988; Owen 1976; Prins & Ydenberg). In the case of Barnacle geese, during the months of February, March and April on the Dutch Waddensea island Schiermonnikoog, this translates into the protein content of Festuca rubra. It has long been thought (Drent Prins Jeffries) that protein is the limiting factor for geese in food selection.

The question arises which factors influence crude protein content in Festuca rubra. In this study, several factors have been studied. Secondly, the reaction of the geese on protein content of Festuca rubra both small scale and large scale was studied. Finally, the importance of protein versus energy limitation is discussed.

Factors looked into were "site", weather conditions (field experiments) and fertilization and simulzled grazing (greenhouse experiments). Most of these have already been looked into by one or more people, one factor at a time (Ydenberg & Prins 1981; van Dinteren 1988; Wiersema 1991; Bazely et al 1991).

The site-factor was looked into because in previous years geese had been observed grazing mainly on the higher parts of the marsh early in the season, and then shifting to lower parts of the marsh later on in the season (van Dinteren 1988). Thus the question arose whether there is any relation between site and protein content, site being related to height. Height in its turn being related to moisture content of the soil and inundation frequency and thus to the onset of growth. (Bakker et al.)

Also in the field, the effect of the weather was looked into. Prins & Ydenberg (1985) had noticed a relationship between the date on which the Barnacle geese transfer their foraging activities to the saltmarsh and the rate at which the degree-days accumulate. To gain more insight in the causes of this relationship, the effect of temperature on Festuca rubra growth was studied in the field.

In other studies, it had already been noticed that the geese left the island when the weather was warm and dry for some days in a row (Faber 1985; van Dinteren 1988). The weather conditions translated into lower crude protein contents of Festuca rubra. Prins et al (1978) and Owen (1977) had noticed a relation between water content and crude protein content of Festuca rubra. In this report the factors are connected.

In the same period Bazely (1991) showed significantly higher crude protein contents in vegetation growing in areas with gull colonies and droppings. Also during spring '89, P. Wiersema had shown that artificial fertilization in the field increased crude protein contents of the
vegetation. From June '89 to June '90 a greenhouse experiment was conducted in which the effects of artificial fertilization and simulated grazing on crude protein contents were estimated. For this purpose, *Festuca rubra* clones from the saltmarsh of Schiermonnikoog were used.

Summarizing, the factors looked into in this study were:

Field experiments:
1: weather conditions
2: site

Greenhouse experiments:
3: fertilization
4: clipping (simulated grazing)

The reaction of the Barnacle geese to protein contents of *Festuca rubra* was tested on a small scale (several m²) and on a larger scale (areas of the marsh visited by distinctive groups of geese) as was done in previous years (Ydenberg & Prins 1978).

Finally, the importance of protein versus energy content of *Festuca rubra* is discussed. Prop & Vulink (in litt.) suggest energy is actually limiting, not protein content. With help of their assumptions and formulas the data in this report on protein content and behaviour of the geese were checked to see whether energy is limiting in stead of protein.
MATERIAL AND METHODS

I SITE-DESCRIPTION

On the saltmarsh, the Festuca rubra vegetation was studied on three sites. (See fig. 0). The early spring growth was studied at the Oude Beweide Kwelder.

II WEATHER CONDITIONS & GROWTH OF FESTUCA RUBRA

Data on the weather conditions collected by the University of Amsterdam were used.

II.1 TEMPERATURE-DEPENDENCY

For the temperature-dependency of growth, 42 Festuca rubra tillers were followed from Feb. 10 until April 26, 1989. For each 10 day-interval average daily temperature above 0 °C was calculated and average number of new leaves per tiller. For more details, see Pruin (1990).

II.2 QUALITY CHANGES

The sampling of Festuca rubra started when the geese were already grazing on the saltmarsh, in the first week of March 1989. At each of the three sites, a row of eight small poles was established. The poles were spaced out approximately 50 meters apart. The last pole of each row was always at the border of the Festuca rubra/ Artemisia maritima zone, and nearest to the Waddensea. The other poles were placed more towards the higher parts of the island.

From the beginning of March until the beginning of May, a Festuca sample was taken once every ten days near each pole. These samples were sorted into green and non-green portions by hand. The green portions were dried for 24 h. at 60 °C, and stored in paper bags. These samples were analysed for total nitrogen content by a modified Kjeldahl technique (see G. van Dinteren, 1988, for more information on the analyses). The crude protein content was calculated by multiplying percentage nitrogen by 6.25.

II.3 CHANGES IN STANDING CROP

The live standing crop of Festuca rubra was estimated near each pole on the first and the last sampling date. Near each pole, an area of 40 cm² was clipped to the ground. These samples were sorted into live green Festuca, dead Festuca and other species. All portions were dried for 48 h. at 60 °C, and then weighed.

II.4 GOOSE DIET

Several of the droppings collected when grass samples were taken were scored on epidermal remnants of Festuca rubra. From each
dropping a very small portion was put on a slide in some water, and then put under a microscope to score the first 100 epidermal remnants (see for more details Stewart, 1967; Dijkstra & Dijkstra-de Vlieger, 1977; and G. van Dinteren, 1988).

II.5 GRAZING PRESSURE
To estimate the reaction of the geese to the proteincontent of Festuca rubra at a certain spot and a certain moment, the number of fresh looking droppings in a 4 m² circle were counted near each pole each time grass samples were taken.

III GREENHOUSE EXPERIMENT
In May 1989, Festuca rubra tillers were taken from three different areas from the saltmarsh of Schiermonnikoog. All three of these areas are grazed by geese and/or other animals (Pruis, 1990)
A: the area of row A
M: a mown area on the marsh
P: pasture (OBK – see fig. 0)
These tillers were grown for a month and clipped in June '89. Per area, from three tillers each twelve clones were made. The clones were grown until June '90 and in the meantime received the following treatment:
1: 3 clones were fertilized
2: 3 clones were fertilized and were clipped twice
3: 3 clones were not fertilized
4: 3 clones were not fertilized and were clipped twice
The clipping was meant to simulate goose-grazing, thus only the first centimeters of the leaves were removed. In June '90, all above-ground biomass was harvested and dried for 24 hours at 60°C. Crude protein contents were estimated for one clone—all treatments—from area A and M and for three clones—all treatments—from area P. For more details on the greenhouse experiment, see Pruiss, 1990.

IV PROTEIN AND ENERGY DEMANDS
Calculations were made following Vulink & Prop, assuming:
* 85.5% of daylight hours spent feeding
* 15 g/hour intake of grass (dry weight)
* energy and protein requirements per kg exp. 0.75 as calculated by Vulink & Prop
* relationship between proteincontent and digestibility as reported by Vulink & Prop
Calculations were made for geese of several different weights consuming several different qualities of Festuca rubra.
V  STATISTICAL ANALYSIS OF DATA

All regression analyses were followed by T-tests for significance of regression/correlation.
The three different areas were compared on accumulation of standing crop, number of droppings (i.e. goosevisit) and protein content all through the season using one-way analyses of variance (ANOVA), followed by T-tests for significance of differences (de Jong, 1963). The significance of the 25% limit was tested using T-tests. The significance of differences between average crude protein content and crude protein content of a spot were tested calculating confidence intervals tested with T-tests.

fig. 0: The sites of research on the Dutch Waddenseaisland Schiermonnikoog
OBK = Oude Beweide Kwelder
A = near the Kolbedune
B = in the middle of the marsh
C = near the Willemdune
RESULTS

I EFFECTS OF WEATHER CONDITIONS

I.1 TRANSFER TO THE SALTMARSH AND EARLY SPRING GROWTH OF FESTUCA RUBRA

The switch from polder to saltmarsh showed the same relationship with the rate of accumulation of degree-days as was found by Prins & Ydenberg '85 (see fig. 9).

The number of new leaves per tiller per day was significantly related to average day-temperature above 0 degrees Celcius. Correlation coefficient 0.860 p < 0.01. (See fig. 1).

I.2 CHANGES IN CRUDE PROTEIN CONTENT

The steep decrease in crude protein contents around March 29 was related to a period of high temperatures and no percipitation. The subsequent increase in crude protein contents coincided with a period of more percipitation and lower temperatures. (See fig 2 and 4).

I.3 WATERCONTENT OF FESTUCA RUBRA SAMPLES

A strong correlation was found between the watercontent of fresh Festuca rubra samples and crude protein content.

\[ \text{% crude protein} = -0.803\times\text{% dry matter} + 46.51 \]

Correlation coefficient = -0.7992 p < 0.001 (See fig. 3).

II SITE-EFFECTS

In the C-area (at the Willemse dune) the crude proteincontent of the samples was significantly higher than average at poles 6 to 8; and significantly lower than average at poles 1 and 2. (See figure 6c).

In the B-area crude proteincontents were significantly lower than average at poles 1 and 2; and significantly higher than average at poles 3, 4, and 6. (See figure 6b).

In the A-area crude proteincontents varied the least between poles compared to area B and C. Crude proteincontents were significantly higher at poles 1 and 8; significantly lower at poles 4 and 6. (See figure 6a).

III EFFECTS OF FERTILIZATION AND CLIPPING (IN GREENHOUSE EXPERIMENT)

The effect of fertilization on each of the clones was very clear: crude proteincontents were about two times higher in fertilized clones compared to the unfertilized clones.
Clipping had an added positive effect on crude protein content in the unfertilized clones. The effect was not very large compared to the effect of fertilization. (See figure 5).

IV. RESPONSES TO VEGETATION QUALITY AND QUANTITY

IV.1 SMALL SCALE RESPONSE TO VEGETATION QUALITY AND QUANTITY

All droppings analysed had 80 or more percent Festuca rubra epidermal remnants. (See table 5).

Numbers of fresh-looking droppings were often quite low, especially in the Willemdune—area and in the middle of the marsh (area B). (See table 2).

a. VEGETATION QUALITY

There was a significant relation between number of fresh looking droppings and protein content of green Festuca rubra in area A and C. (See fig. 7a).

A: NoDR = 1.47*Crude pr — 30.2 corr.coef.=0.393  p<0.1
C: NoDR = 0.72*Crude pr — 13.1 corr.coef.=0.681  p<0.001

b. VEGETATION QUANTITY

Standing crop increased rapidly during the experiment. (See table 3). Accumulation of standing crop didn’t differ significantly between areas. There were large spot-to-spot differences in standing crop increase.

In area C (see fig 7b) there was also a significant relationship between accumulated no. of fresh-looking droppings and herbage accumulation during the same period.

IV.2 LARGE SCALE RESPONSE TO CRUDE PROTEIN CONTENTS

The geese left the Willemdune area for their breeding grounds around April 10, the population from the rest of the marsh left around April 20. Most of the geese grazed for several days on the mainland of Groningen around March 29. These events coincided with overall crude protein contents not differing significantly from or dropping below 25% (see fig 2). Except for the A—area; the geese left when average crude protein content was still significantly higher than 25% in that area. For calculation of average crude protein content per area in area C only the data from the poles 5–8 were used. This was done because only these four spots were visited by the geese for the same period as the A and B area.
V PROTEIN AND ENERGY DEMANDS

The maximum intake per day was calculated for several dates (see table 8a). The amount of grass necessary to cover protein and energy demands was calculated for different quality and different goose weight (see table 8b and c).

AVERAGE NO. OF NEW LEAVES / TILLER / DAY

fig. 1: The relationship between average number of new leaves per tiller per day and temperature for Festuca rubra tillers on the Oude Beweide Kwelder of Schiermonnikoog. Measurement between Feb. 10 and March 26 1989. n=42 corr.coefficient = 0.860 p<0.01.
 fig. 2: Average crude protein content of Festuca rubra samples in three different areas on the saltmarsh of Schiermonnikoog in 1989

- A = area near the Kobbedune n=8
- B = area in the middle of the marsh n=8
- C = area near Willemsdune n=4

significance of difference from 25%:

* p< 0.1
** p< 0.01
*** p< 0.005
fig. 3: The relationship between crude protein and dry matter content of Festuca rubra samples. $\%CP = -0.803 \times \%DM + 46.51$

$n=55$ corr.coefficient $= -0.7992$  $p<0.001$
fig. 4: (a) Percipitation and (b) daily temperatures during March and April 1989 on Schiermonnikoog.
fig. 5: Effects of fertilization and simulized grazing on crude protein content of *Festuca rubra* clones in a greenhouse experiment. n = 10 for each treatment
1: unfertilized; never clipped
2: unfertilized; twice clipped
3: fertilized; twice clipped
4: fertilized; never clipped
DIFERENCE FROM AVERAGE (% CRUDE PROTEIN IN DRY MATTER)

fig. 6: Differences from average crude protein content per sampling point
a: area A - n=5 per samp. point  significance of difference from mea
b: area B - n=6 per samp. point  *  p< 0.1
**  p< 0.05
***  p< 0.001
c: area C - n=6 per samp. point
DIFFERENCE FROM AVERAGE (% CRUDE PROTEIN IN DRY MATTER)

fig. 6c
fig. 7: (a) The relationship between numbers of fresh-looking droppings / 4 m² and crude protein content of Festuca rubra vegetation in area A and C

A: NoDR = 1.47*%CRPR - 30.2  corr.coef.=0.393  p< 0.1
C: NoDR = 0.72*%CRPR - 13.1  corr.coef.=0.681  p<0.001
Accumulated no. of fresh-looking droppings / 4 m² in relation to herbage accumulation between March 20 and May 1, 1989 in area C.

C: $\text{CUMDR} = 0.52 \times \text{HERBACC} + 2.26 \quad \text{corr. coef.} = 0.830 \ p < 0.01$
The protein content (percent of dry weight) in salt-marsh (○) and polder grass (●) on Schiermonnikoog during three years. Each point represents the mean of several samples collected within a few days of each other. The 99% confidence interval is shown for one date in the spring of 1978 when nine samples were collected simultaneously. It is shown. The protein content peaks in the spring of each year with the onset of growth, and the salt-marsh peaks slightly ahead of the polder. The residence period of barnacle geese on Schiermonnikoog is indicated by the stippled areas (light stippling — foraging in polder; heavy stippling, — foraging on saltmarsh).
fig. 9: (Prins & Ydenberg 1985) The date on which the Barnacle geese transfer their foraging activities to the salt-marsh (●) is a function of the rate at which the degree-days accumulate. The diagonal line was fitted by the least-squares method. The switch occurs later and at a lower temperature sum in cold years. '82: Faber 1985; '89: this report.
DISCUSSION

I. FACTORS INFLUENCING GROWTH AND CRUDE PROTEIN CONTENT OF FESTUCA RUBRA

1.1 WEATHER CONDITIONS

First of all, the reason behind the relationship between daily temperature and the moment of habitat switch has become more clear. Festuca rubra tillers produce more new leaves when average daily temperatures are higher. Thus if temperatures are high during January Festuca rubra biomass will be sufficient for Barnacle goose grazing earlier than when temperatures are relatively low in January.

Moisture availability was a second important factor influencing Festuca rubra growth. In the period from March to May there was an overall trend of decreasing crude protein contents of live green Festuca rubra. On the level of samples, there was a strong relationship between water content and crude protein content similar to the relationships found by Prins & Ydenberg (1978) and Owen (1977). Crude protein and water content show the aging of Festuca tillers. With age, plant tissue contains less water and less protein. In a period of high temperatures and low precipitation the water contents and crude protein contents drop because the lack of water stops growth of new leaves while leaves already present go on maturing/aging. Thus the crude protein content of the tiller as a whole drops.

1.2 FERTILIZATION AND CLIPPING

The large effects of fertilization on the crude protein content of Festuca rubra confirmed the results from the different field experiments (conducted by Prins & Ydenberg, van Dinteren, Wiersema and Bazely) where fertilization from both artificial and natural sources significantly increased crude protein content of Festuca rubra. Simulized goose-grazing on the other hand had only a slightly positive effect on crude protein contents. This confirms the idea that Barnacle geese on Schiermonnikoog can't influence the quality of their forage to the extent that other factors (such as gull-droppings, fertility of the soil etc.) can (Wiersema 1991; Bazely 1991).
1.3 SITE

In area C, the poles 1, 2 and 4 were situated relatively high compared to the other poles. Thus water availability was lower. *Festuca rubra* could probably start its growth earlier in those spots which caused them to have somewhat lower than average crude protein contents during the sampling period. Also, the lower parts of the marsh are washed by tides more often and thus accumulate more fertile mud.

In area B, the row could represent an optimization curve: spots 1 and 2 are too dry and not as fertile as the others, spots 5 and 8 are fertile but too wet, and spots 3, 4, 6, 7 represent spots that have good moisture/nutrient combinations.

In the case of area A, there might have been little difference in height between different spots. Another possibility is that the effect of fertilization by gull droppings overruled any height effects. Bazely (1991) showed how gull droppings affected crude protein contents of the vegetation on the salt marsh.

All of this remains speculative, though, because no measurements of moisture and nutrient content of the soil were taken. This experiment did show however how *Festuca rubra* quality and growth rate can vary greatly from spot to spot within a small and seemingly homogeneous area. And, as is discussed below, the geese could be seen to react to these differences in quality and growth rate.

II RESPONSE TO VEGETATION QUALITY AND QUANTITY

II.1 SMALL-SCALE

Numbers of fresh-looking droppings were often quite low, so only for the C-area could a significant relationship between number of droppings and *Festuca rubra* quality be found. As was found by Ydenberg & Prins (1981) there was a significant relationship also between accumulated numbers of droppings and increase in standing crop (areas A and C). This shows the geese reacted to both the quality and the quantity of the forage. This corresponds with the polder-saltmarsh switch: when the quality is already sufficient, the geese have to wait until enough biomass is present to forage on (as is discussed above).

II.2 LARGE-SCALE

On a larger scale, the geese could be seen to react to the crude protein levels in *Festuca rubra*. The geese left the island for their breeding grounds around April tenth (Willemsdune population) and April twentieth (other populations). Part of the geese population left the island for the Dutch mainland in the period of drought to return when the weather had changed. All of these events coincided with average crude protein contents.
dropping below a level of about 25%. In previous years, geese had also been observed leaving the island during periods of drought (G. van Dinteren). Also in previous years the geese left for their breeding grounds when crude protein contents in April were dropping below the 25% level (Prins & Yd. 1985).

III ENERGY LIMITATION VERSUS PROTEIN LIMITATION

As Prop & Vulink have found, protein itself turns out not to be the limiting factor in food selection. Protein was available in excess, energy was the limiting factor. Protein content does influence digestibility of the food, so foods high in protein are also high in energy. In early spring / end of winter daylength limits uptake. When protein content (and thus energy content) of Festuca rubra drops the energy requirements of the geese can't be met anymore. The heavier the goose, the higher quality food is needed to maintain body weight. This fits the observation that the geese leaving Schiermonnikoog for the mainland during the period of drought were the heavier geese. The lighter geese could still maintain or even increase body weight with the quality of Festuca rubra in the marsh.

At the end of the April crude protein contents drop quickly below the 25% level due to aging of the tillers, and will not return to higher levels until the next spring (Prins & Ydenberg 1985). Most of the geese in would loose weight if they would stay longer so they leave for their breeding grounds.
REFERENCES


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### Table 1.

**Crude Protein Contents of Dried Green Festuca Rubra Samples**

Area: A = Kobbedune  B = Middle of the marsh  C = Willemsduine  
Crude protein content = mg protein per g dry Festuca rubra  
1 to 8 represents 'high marsh' to 'low marsh'  

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** : almost no Barnacle geese left on the island
### Table 3.

STANDING CROP AT THE BEGINNING AND END OF THE EXPERIMENT

**LIVE** = gr live green *Festuca rubra*, dried, per square metre

**DEAD** = gr dead material and *Artemisia maritima*, dried, per square metre

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table 4.
CRUDE PROTEIN CONTENT OF FESTUCA RUBRA SAMPLES FROM GREENHOUSE EXPERIMENT
TREATMENT: 1: unfertilized, never clipped
2: unfertilized, twice clipped
3: fertilized, twice clipped
4: fertilized, never clipped

M = MOWN AREA  P = PASTURE
TREATMENT  1  2  3  4

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table 5.
ANALYSIS OF DROPPINGS
PERCENTAGE OF FRAGMENTS ORIGINATING FROM FESTUCA RUBRA

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<td>% DRY MATTER</td>
<td>CRUDE PROTEIN CONTENT (mg/g dry matter)</td>
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<td>------</td>
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### Table 7

**AVERAGE DIFFERENCES IN CRUDE PROTEIN CONTENT FROM MEAN CRUDE PROTEIN CONTENT**

**AREA A**

<table>
<thead>
<tr>
<th>SAMPLE POINT</th>
<th>AVERAGE DIFFERENCE FROM MEAN CRUDE PROT. CONTENT (g/100g dry matter)</th>
<th>STANDARD DEVIATION</th>
<th>SIGNIF. (p&lt;)</th>
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</thead>
<tbody>
<tr>
<td>1</td>
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<td>0.77</td>
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<tr>
<td>2</td>
<td>0.13</td>
<td>0.78</td>
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<td>0.98</td>
<td>N.S.</td>
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<td>0.77</td>
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<td>1.47</td>
<td>0.1</td>
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<td>0.11</td>
<td>1.43</td>
<td>N.S.</td>
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<td>1.33</td>
<td>0.05</td>
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**AREA B**

<table>
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<th>STANDARD DEVIATION</th>
<th>SIGNIF. (p&lt;)</th>
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<tbody>
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<td>0.60</td>
<td>0.0005</td>
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<tr>
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<td>2.41</td>
<td>0.1</td>
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<td>1.47</td>
<td>1.11</td>
<td>0.05</td>
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<td>-0.26</td>
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<td>1.01</td>
<td>N.S.</td>
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**AREA C**

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<th>STANDARD DEVIATION</th>
<th>SIGNIF. (p&lt;)</th>
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<tr>
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Table 2.

DAILY INTAKE OF *FESTUCA RUBRA* AND INTAKE NECESSARY TO COVER MINIMAL DAILY PROTEIN AND ENERGY DEMANDS.

(a) MAXIMAL INTAKE PER DAY

<table>
<thead>
<tr>
<th>DATE '89 (day-month)</th>
<th>DAYLENGTH (h)</th>
<th>HOURS FORAGING</th>
<th>INTAKE Fest. R./DAY (g dryweight)</th>
</tr>
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<tbody>
<tr>
<td>09-3</td>
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<td>9.08</td>
<td>137</td>
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<tr>
<td>20-3</td>
<td>11.8</td>
<td>9.74</td>
<td>146</td>
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<td>10.40</td>
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<tr>
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<td>11.72</td>
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<tr>
<td>01-5</td>
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</table>

(b) PROTEIN NEEDS

<table>
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<tr>
<th>CRUDE PROTEIN WEIGHT (% OF DRYWT) OF GOOSE (kg)</th>
<th>INTAKE NECESSARY TO COVER MINIMAL DAILY PROTEIN NEEDS (g drywt Festuca rubra)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.7</td>
<td>20.0 22.5 25.0 27.5 30.0</td>
</tr>
<tr>
<td></td>
<td>104   89  82  72  64</td>
</tr>
<tr>
<td>2.0</td>
<td>118   101  92  81  72</td>
</tr>
<tr>
<td>2.5</td>
<td>139   119  109  96  86</td>
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</tbody>
</table>

(c) ENERGY NEEDS

<table>
<thead>
<tr>
<th>CRUDE PROTEIN WEIGHT (% OF DRYWT) OF GOOSE (kg)</th>
<th>INTAKE NECESSARY TO COVER MINIMAL DAILY ENERGY NEEDS (g drywt Festuca rubra)</th>
</tr>
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<tbody>
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<td>150 143 139 128 124</td>
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<tr>
<td>2.0</td>
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<td>2.5</td>
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