Balancing the energy budgets of arctic-breeding geese through-out the annual cycle: a progress report

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1. The Problem

One of the obsessions of contemporary ecology is the search for the rules underlying the relations between animals and their food resources. Traditionally this work has been concentrated on polyfage songbirds, the classic subject species being the Great Tit *Parus major*, underlying both the pioneering work of L. TINBERGEN (1960) and the later work of ROYAMA (1970). Impressed by the pressures exerted by wintering flocks of geese on food stocks when replenishment is minimal and quality often low, we became interested in the link between herbivores and their food resources, and in particular in the question of the applicability of the profitability concept. We thus ask whether the small-scale shifts of geese utilizing one area, as well as the major movements in the stepping-stone like progression in the course of the year, can be explained in terms of achieving favourable energy balance with minimal effort. On the local scale, this entails testing the profitability concept put forward by ROYAMA, demanding that the geese make the „optimal" choice of feeding site and food type such that the caloric return of effort expended foraging is maximal. The large-scale movements may be dictated by differences in plant phenology throughout the range, assuring exploitation of the vegetation when the digestibility is maximal, but in addition other factors may be involved. Differences between sites in day-length and hence foraging opportunity, or in mean air temperature and hence maintenance costs, may confer advantage on movements not included in the simple profitability concept, and make a more complete analysis of costs and benefits necessary before the adaptiveness of site shifts can be evaluated. Although at times weather (especially snow cover) and disturbance by man may mask the food-driven pattern, we felt convinced that it would be feasible to analyse the movements of Barnacle Geese *Branta leucopsis* and Brent *Branta bernicla* along these lines. This demands evaluation of the food stocks over large areas, combined with a field approach to the estimation of energy intake and expenditure. Concise information on the exploitation of the vegetation by the wild geese can be obtained from direct observation supplemented by study of the droppings (microscopic examination to determine the species utilized, as described by OWEN 1975, and intensive sampling of the density of droppings to obtain grazing pressures). In order to interpret these basic data, the project has two lines of attack, 1) measuring potential food stocks (standing crop and growth rates of the vegetation, by means of scanning techniques sacrificing point accuracy in favour of a reasonable estimate of conditions over large areas), and 2)
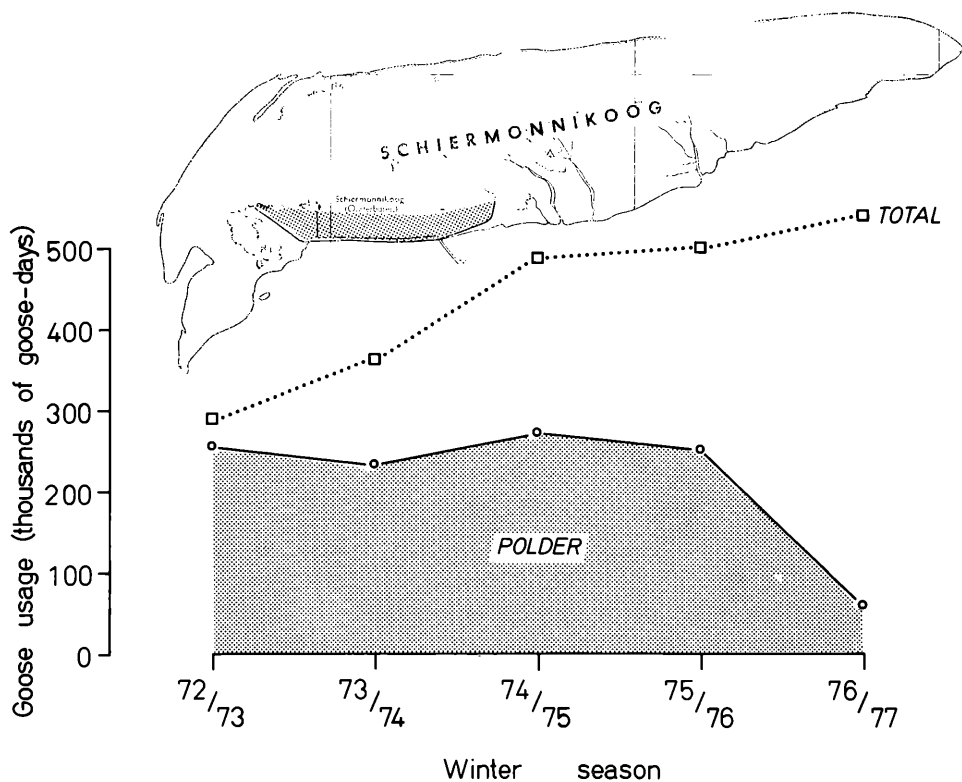
Fig. 1.

determining digestibility of the food plants encountered (using natural markers as calibrated in trials with captive geese).

Although our work is respectably theoretical, we feel it also has practical implications relating to the management problem of carrying capacity. Consideration of goose usage of our study area on the Waddensea island of Schiermonnikoog will make this point clear. The basic data on goose movements and grazing pressures are obtained by frequent direct counts of the birds in conjunction with extensive sampling of droppings (since actively grazing geese produce droppings every 3–4 minutes, this is an extremely sensitive measure of goose visitation, and in addition avoids the bias inherent in daytime counts), and are shown in Fig. 1 for the two major subdivisions of the island, polder and merse. The nearly constant cumulative goose grazing pressure scored on the enclosed „polder" grasslands (126 ha tract intensively managed for dairy cattle) in each of the first four seasons we take to represent the depletion of the winter food stock to the cut-off point, the geese then spilling over to the merse. Why then does the pattern in 1976/77 depart so widely? The summer of 1976 was exceptionally dry, and large-scale mowing of the *Festuca* sward by the desperate farmers resulted (this area of merseland had not been grazed or cut for over fifteen years). As a further departure in farming practise, a very late cut of grass was taken in the „polder" (October). When the Barnacle Geese returned, they were thus faced with a relatively depleted „polder" and a vastly enhanced *Festuca* merse, with the effect shown. If the concept

of carrying capacity is to prove useful, however, we cannot content ourselves with re-constructions after the event, but must be in a position to make accurate forecasts. A predictive ability requires rapid assessment of food stocks before the geese return, and as this has recently come within our reach we will soon have to justify our optimism.

2. Field estimation of the daily energy intake

Aside from periods when energy reserves such as fat are being built up or drawn upon, net daily energy intake is equivalent to expenditure, and we shall presently exa-mine our goose data in relation to daily existence energy (DEE) values for other bird species. The first problem is, to measure gross daily consumption regardless of how this may be expended. This can be approached either by trials with captive birds pla-ced on the vegetation used by the wild geese, or by an indirect method based on faecal output of the wild birds, again based on calibration with captive individuals. An im-portant limitation to be kept in mind when working with captive birds, is that digestive function is under the influence of diet, and in particular, the length of the gut may shor-ten when the natural grass foods are supplemented by grain. OWEN (1975) compared measurements of 9 captive Barnacle Geese that had died (not from malnutrition) with data from 27 wild specimens, and found that intestinal length in the captives was only 64–70% of the value for wild birds, while the caecum was a mere 58–63% of the wild value. Similar adjustments, with consequent loss of digestive ability, have been en-countered in other herbivores maintained in captivity (Moss, 1972; PENDERGAST & BOAG, 1971). For this reason we relied on wild-caught birds maintained on a grass sward for our work.

2.1 Weignt change of captive birds

The simplest method involves direct weighing of captive birds before and after a known foraging period at the onset of the day, making use of the fact that after a night of deprivation it will take approximately 60–90 minutes before any droppings are pro-duced, i. e. the change in body weight will reflect food intake. We say „reflect" be-cause a small correction is necessary for water loss of the bird. HARWOOD (1975) applied this method on Snow Geese *Anser caerulescens* and some data on Brent are presented in Fig. 2. The geese are placed on the same fields as their unrestrained conspecifics, and if it is assumed that digestive efficiency is unaffected, data on the time budget of the wild birds can be used in order to extrapolate from the data on captives to that for free existence.

2.2 Use of naturally occurring markers

Whenever quantitative collection of rejecta is possible, the extrapolation to intake suggests itself. Moss & PARKINSON (1972) applied this technique successfully to the he-ather-eating Red Grouse *Lagopus scoticus scoticus* and later extended this approach to ptarmigan *Lagopus mutus* (Moss, 1973), and found magnesium content to offer a re-liable digestibility marker. It is not essential that the marker be indigestible, only that the animal is in balance over the period measured. Candidate markers preferably must be a) accurately measurable without recourse to elaborate analysis methods, b)
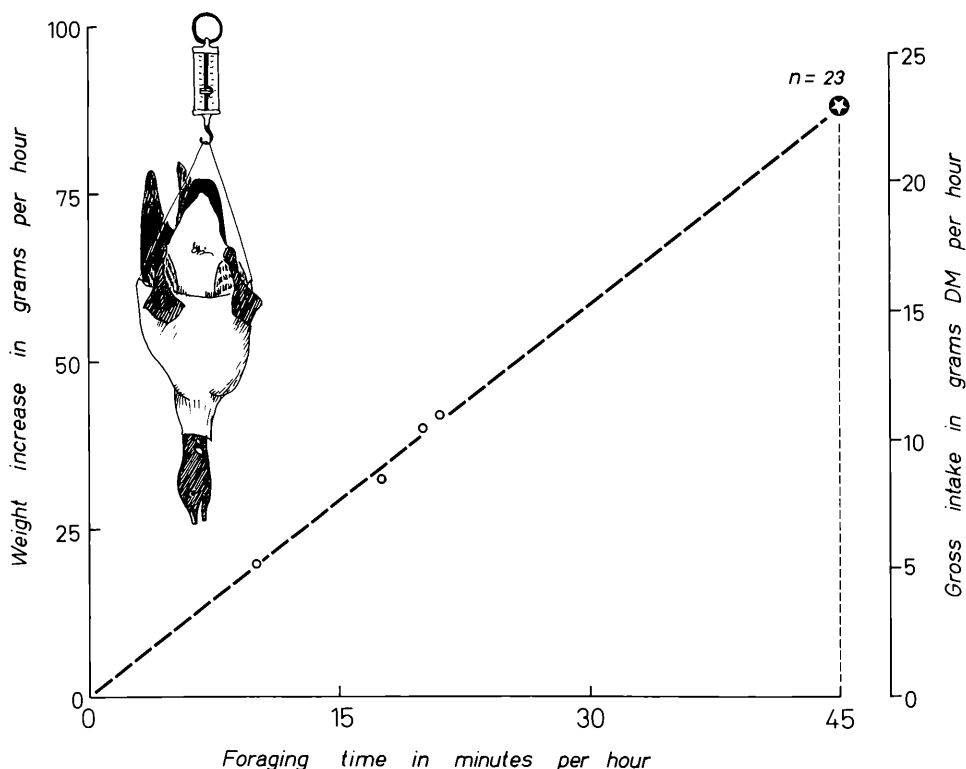
Fig. 2.

evenly distributed in the food plants to minimize errors since the exact selectivity of the birds is rarely known (crop analysis as applied in the grouse being a technique of restricted potential). WEIJAND (1976) carried out trials with four wild-caught White-fronts *Anser albifrons* to calibrate the following candidate markers: 1) crude fibre, 2) ash, 3) chlorophyll, 4) magnesium. Ash and magnesium were chosen on account of Moss' results, crude fibre as it was suspected that geese lack the ability to digest cellulose or lignine in appreciable amounts (MATTOCKS, 1971), and finally chlorophyll because in other herbivores this had proven a reliable marker (KEMMINK & DIJKSTRA, 1968).

In order to approach the natural situation, the trials were conducted in the winter months with various grasses, in part collected from fields where wild geese were feeding at the time. The subjects were held in individual cages allowing quantiative collection of droppings (trays) and were fed clipped grass in deep hampers, where spillage was minimal. Uptake could therefore be determined by weight loss of the food hampers, the weight of the droppings was measured, and weight of the subjects before and after each trial. The nitrogen balance was computed on the basis of the urine/faeces separation technique of TERPSTRA & HART (1974). Each trial was preceded by a week of adjustment to the test diet, and the period of quantitative measurement extended for five days during which time the birds were exposed to a day-night regime normal for that time of year, and housed in an unheated building. The five test diets consisted of A) 50–50 mixture of *Agrostis tenuis* and *Poa trivialis* with a slight admixture of *Holcus lanatus* (mid-October), B) same but end November, C) young *Lolium perenne,* mowed fresh daily in the Flevopolder, mid-December, D) neighbouring field with somewhat older growth *Lolium* cut 26 January, E) diet of

Table 1. Digestibility trials in the Whitefront *Anser albifrons*. Figures show digestibility of organic matter.

| | Diet | | | mean error |
	A	B	E	15 tests
gravimetric (direct)	27	37	27	standard
Markers a) crude fibre	23	36	24	0.4 (1%)
b) ash	26	32	28	2.2 (5%)
c) chlorophyll	25	35	22	1.0 (4%)

Note: Diet A = *Agrostis/Poa,* mid-October
　　　Diet C = *Lolium,* mid-December
　　　Diet E = chicken mash
The experimental values under "diet" refer to one test individual; means for all birds included for comparison.

chicken food meal for comparative purposes.   A drawback of the method is the use of mower-harvested grass, but as the food was not further ground or chopped the degree of mechanical accessibility to cell content is assumed to be comparable to shoots plucked by the geese themselves. Further details are to be found in WEIJAND et. al. (in press).

The digestibility of organic matter as measured directly on these various diets is compared in Table 1 with the predictions assuming non-digestibility (quantitative balance) of the candidate marker substances computed as shown in Fig. 3.   It will be seen that ash content, crude fibre, or chlorophyll derivatives are all three reliable markers. Since crude fibre determination involves tedious analytical procedures ash and chlorophyll are in fact the most practical candidates for field studies.   It has long been recognized that there is an inverse relation between crude fibre content and digestibility of the organic matter (see Fig. 4), and for this reason it may be good practise to send a few food samples out to laboratories equipped to perform crude fibre analyses, as the results can be used to predict digestibility.   The physiological basis for the inhibition of digestibility by the complex of substances (chiefly cellulose and lignine) separated as „crude fibre" is poorly understood (McDONALD et al., 1969), but involves far more than mere mechanical barriers to the digestive enzymes.

$$\% \text{ utilization } = \left(1 - \frac{M_f}{M_d}\right) 100 = 25$$

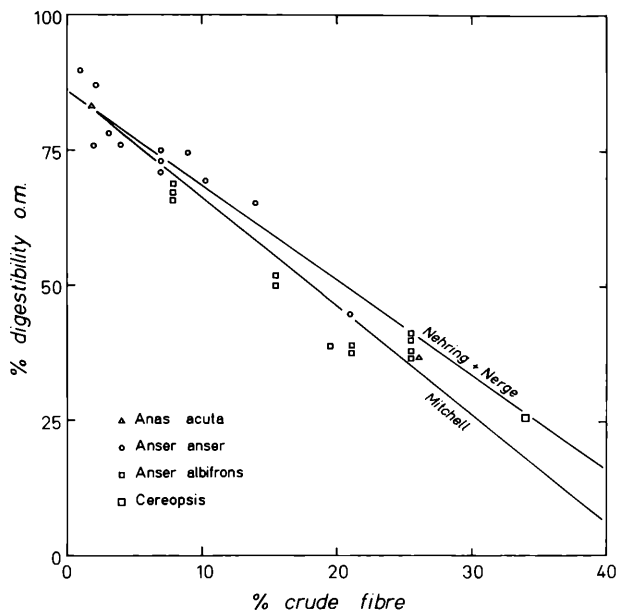food

droppings

$M_f = 1.130$

$M_d = 1.463$

Fig. 3.
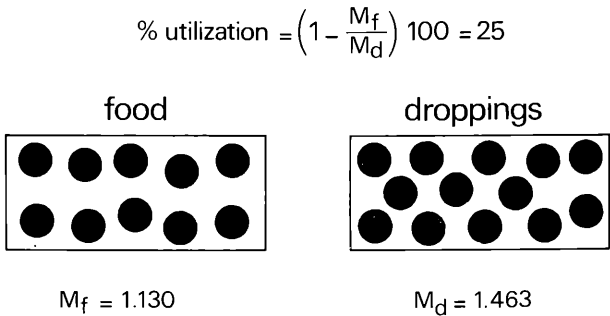
Fig. 4.

There is one important restriction to be made regarding the extrapolation to field conditions: the throughput time in the captive trials reflects a strict day-night regime with feeding limited to the daylight period, the droppings being produced every 3.5 minutes during this time. Direct observations in the continuous daylight of the arctic breeding quarters show feeding interspersed with short rest bouts resulting in a steady but much lower rate of dropping production, implying a much longer food retention time. Whether a lowered throughput time also applies to moonlit periods in the winter when the effective feeding day may be more than doubled is as yet unknown. The repercussions of throughput time on digestibility have not been investigated experimentally but this is obviously a point of some urgency.

Hourly rates of intake indicative for field conditions are collected in Table 2, and show a far-reaching similarity between the species when the data are converted to gm dry matter per metabolic kg (kg body weight to the .75 exponent). This agreement can hardly be fortuitous and suggests that there is a limit to the rate of passage of food

Table 2. Hourly rate of food uptake in wild geese.

Species	Uptake (g/bird.hr)	(g/kg$^{.75}$.hr)	Authority
Branta bernicla	19.9	15.9	this paper, Table 4
Branta leucopsis	20.4	12.6	unpubl. obs. and Table 3
Anser caerulescens	30.9	19.9	Harwood, 1975

Note: weight of food ingested is given as gross weight, including sand.

down the alimentary canal, such that an increase of intake beyond this limiting rate can only be achieved by increasing the length of the foraging period. An alternative strategy theoretically open to the geese in times of shortage is to enhance digestibility by slowing throughput time. One can speculate that in times of great demand, such as the period of egg formation and increase in mass of the flight muscles prior to spring departure or the period of the moult, a lowered rate of food passage might pay a dividend. It will be necessary to measure digestibility as a function of time using *in vitro* techniques to give these speculations a factual basis. A further complication is our ignorance of what happens to food shunted into the double caeca. A lowered throughput time obviously entails an increase in the proportion of the food treated in the caeca (See EBBINGE & EBBINGE-DALLMEIJER, 1977).

3. Estimating energy requirements from body weight in non-passerine birds

Aside from measuring digestibilities, the data on the captive Whitefronts allow reconstruction of the minimal daily ration for cage existence. As shown in Fig. 5, this information is obtained by correcting the experimental values for net energy intake for zero N balance. A vast amount of work has been devoted to measuring energy intake
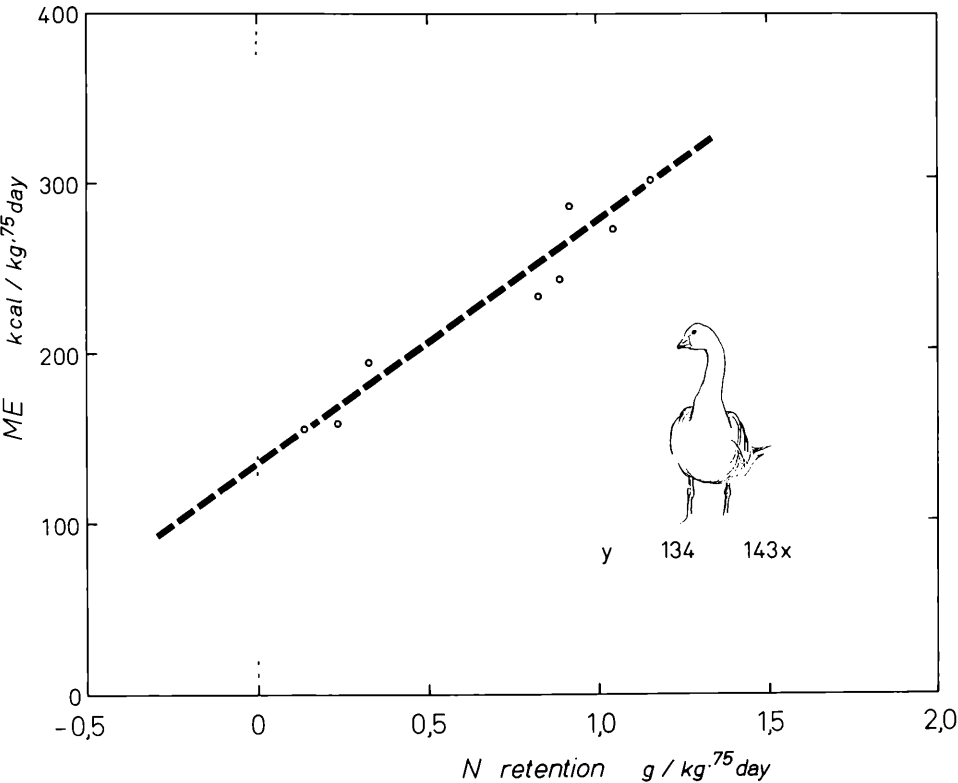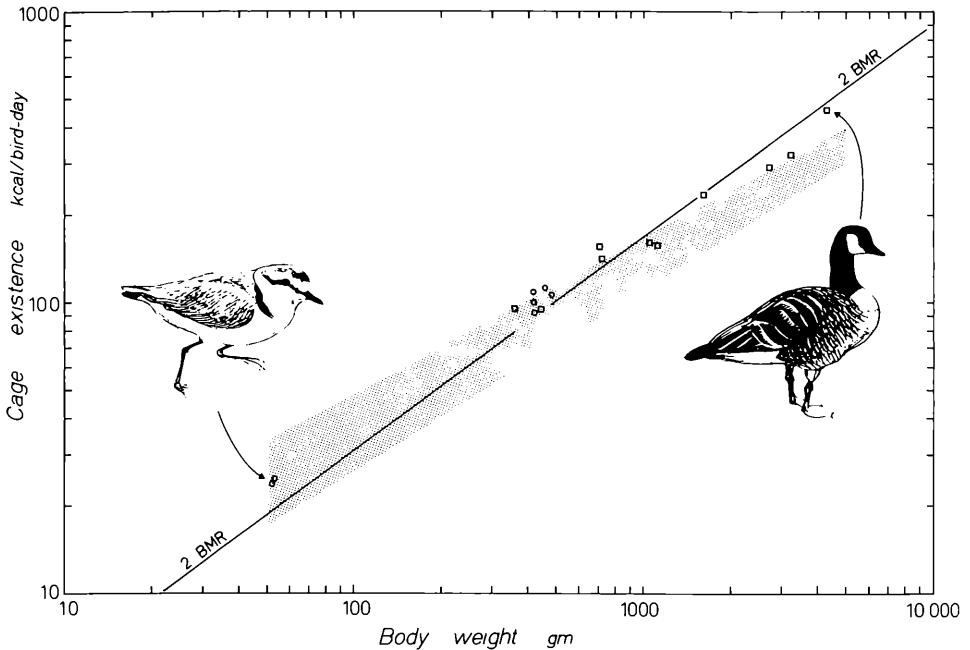

Fig. 5.

Fig. 6.

in birds kept in cages, and when body weight changes in the period of observation are small, these data are taken as indicative of balance. Fortunately KENDEIGH et al. have recently produced a massive compilation showing that the goose data presented here in fact fit rather well in with earlier studies (see Fig. 6).

The next problem is to ascertain if there is a similar exponential relation between body weight and energy expenditure for free-living, the socalled DEE (daily energy expenditure). Here we are on much less certain ground, as complete data are very scarce. Much worse, several studies make use of an extrapolation from cage to free-living by assumption (often according to the ratio 1:1.5) and the concensus on this point indicates a convergence of opinion as distinct from measurement, and means that the reported values are not entirely independent of one another. There is, however, a very considerable body of data on intake rates of fish-eating birds in terms of fresh weight captured daily. These studies are often based on estimation of meal size from individuals shot, and the problem of daily capture rate becomes the problem of defining the number of meals daily. Our criteria in selecting data were to rely on studies based on extensive sampling of wild birds, or detailed work on free-flying captives no longer in the growth stage. Only part of JUNOR's (1972) data could thus be incorporated, and several studies often quoted in this context we have had to do without, as will be explained in detail elsewhere (DRENT & DOORNBOS, in prep.).

There is obviously room for error here, but on the other hand since none of the investigators attempted to construct an energy budget from such data, these studies offer an unbiassed sample encompassing birds from 75 g to 11 300 g. We therefore derived estimates of DEE by assuming a digestive efficiency of .85 (calories retained compared to calories ingested; studies on *Uria aalge* in our group, in complete agreement with DUNN, 1975; SIEGFRIED, 1969; URAMOTO, 1961) and a

mean caloric content of fish as 1.2 kcal per g (fresh weight). We have deleted the three estimates for owls obtained by Graber (1962), since as we now know (Wijnandts, pers. comm.) the underlying assumption that no more than one pellet is produced each day is not valid, and moreover the calculations involve erroneous values for the caloric values of the prey. Finally we have included several estimates for birds subsisting on mussels and cockles, on the assumption that these foods are similarly assimilated at the rate of .85 calories ingested. There are as far as we are ware no direct digestibility trials with such foods, but there is no reason why such materials should differ from the flesh of fish or small mammals in this respect. These values for mollusc-eaters are plotted in the figure, but not included in the derivation of the regression line.
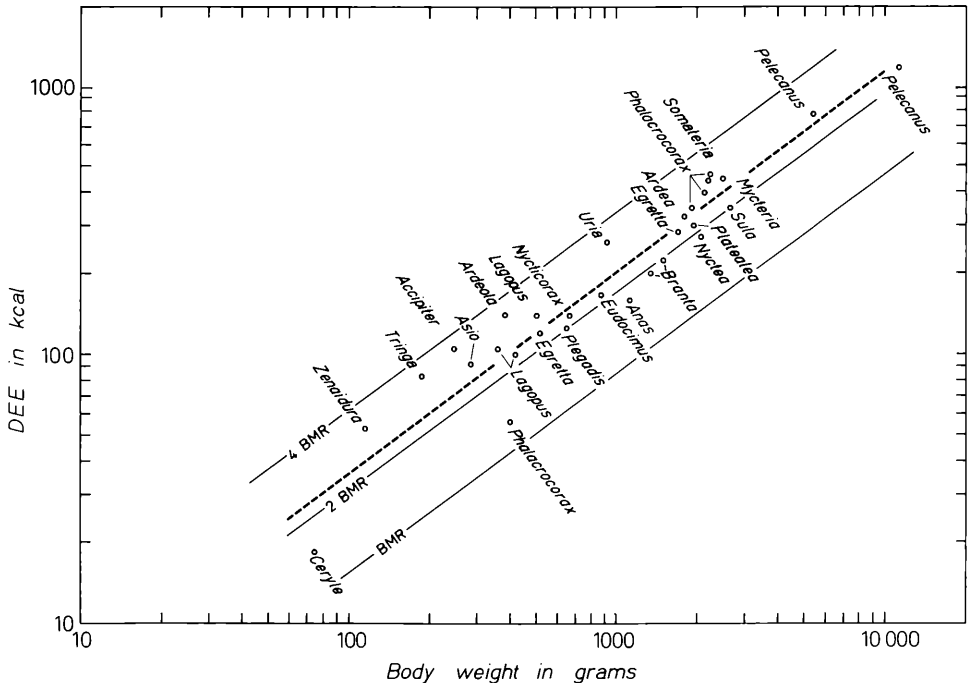

Fig. 7.

On the basis of Fig. 7, we can now narrow down King's (1974) generalisation that "non-torpid free-living homeotherms tend to operate within the range 1.5–4 BMR" to the generalisation that non-passerines heavier than about 50 g have a DEE about 2.6 BMR. The most sensitive estimate of the true ratio is to consider those species in Table 3 where BMR has been directly measured in the respirometer. We have found BMR determinations for 11 of the species in Table 3, and the mean ratio of DEE to BMR in these data is 2.6. This is closely similar to King's compilation involving primarily passerine species (for seven passerine species the DEE/BMR ratio is approximately 2.75). MacMillan & Carpenter (1977) have tabulated values for three hummingbird species, and find DEE equivalent to 3.1–3.6 BMR. The most gratifying agreement is with the data for free-living rodents tabulated by King (1974), where precisely the same level applied (39 species ranging from 9 to 607 g average DEE/BMR at 2.6). This analysis leads us to suspect that a part of the variability in results apparent in Fig. 7 is a consequence of the deviation of actual BMR from the predictive relationship with body weight. *Uria aalge* for example at first glance appears to require a DEE well in excess of that typical for other birds of that weight range, but when compa-

Table 3. Estimates of DEE = daily energy expenditure (energy metabolised daily) in wild non-passerine birds heavier than 10 g not caring for young.

Species	Body weight (g)	DEE (kcal/ bird.day)	Authority
1. Pied Kingfisher *Ceryle rudis*	75	18	TIOMLID (1973)
2. Mourning Dove *Zenaidura macroura*	115	53	SCHMID (1965)
3. Redshank *Tringa totanus*	183	83	GOSS-GUSTARD (1977)
4. Sparrow Hawk *Accipiter nisus* (♀)	246	105	TINBERGEN (1946)
5. Long-eared Owl *Asio otus*	285	92	WIJNANDTS pers. comm.
6. White-tailed Ptarmigan *Lagopus leucurus*	360	105	MOSS (1973)
7. Cattle Egret *Ardeola ibis*	383	150	SIEGFRIED (1969)
8. Reed Cormorant *Phalacrocorax africanus*	400	56	JUNOR (1972)
9. Rock Ptarmigan *Lagopus mutus*	420	100	MOSS (1973)
10. Red Grouse *Lagopus lagopus*	500	140	MOSS (1973)
11. Little Egret *Egretta garzetta*	515	120	SKOKOVA (1962)
12. Glossy Ibis *Plegadis falcinellus*	650	125	SKOKOVA (1962)
13. Night Heron *Nycticorax nycticorax*	670	140	SKOKOVA (1962)
14. American White Ibis *Eudocimus albus*	881	165	KUSHLAN (1977)
15. Guillemot *Uria aalge*	912	262	SWENNEN pers. comm.
16. Black Duck *Anas rubripes* (♂)	1180	160	WOLLEY & OWEN (1978)
17. Herring Gull *Larus argentatus*	1200	275	SPAANS (1971)
18. Brent *Branta bernicla*	1350	201	DIJKSTRA & EBBINGE pers. comm.
19. Barnacle Goose *Branta leucopsis*	1900	225	EBBINGE et al. (1975), EBBINGE (unpubl.)
20. Great White Heron *Egretta alba*	1640	285	SKOKOVA (1962)
21. Grey Heron *Ardea cinerea*	1800	325	SKOKOVA (1962)
22. White-breasted *Cormorant Phalacrocorax lucidus*	1933	350	JUNOR (1972)
23. Spoonbill *Platealea leucorodia*	1950	300	SKOKOVA (1962)
24. Snowy Owl *Nyctea scandiaca*	2086	272	GESSAMAN (1972)
25. Cormorant *Phalacrocorax carbo*	2130	400	VAN DOBBEN (1952)
26. Eider *Somateria mollisima*	2200	442	CANTIN et al.(1974) and MILNE in lit. see also SWENNEN (1976)
27. Cormorant *Phalacrocorax carbo*	2225	465	SKOKOVA (1962)
28. Wood Stork *Mycteria americana*	2500	450	KAHL (1964)
29. South African Gannet *Sula capensis*	2672	350	JARVIS (1970)
30. Pink-backed Pelican *Pelecanus rufescens*	5400	776	DIN & ELTRINGHAM (1974)
31. White Pelican *Pelecanus onocrotalus*	11300	1201	DIN & ELTRINGHAM (1974)

red to the BMR (as measured by Johnson & West, 1975) this discrepancy disappears. We feel confident that DEE representative for "average" conditions (say the mean for several weeks) for non-passerines not involved in peak efforts such as provisioning the young, at what might be termed "maintenance" conditions, can safely be stated as 2.6 BMR. It comes as something of an anticlimax to find that closely similar values have earlier been employed, and as corroborative data were at that time very scarce, these qualify as inspired guesses indeed. Thus Lauglin (1974) estimated the DEE of the Tufted Duck, *Aythya fuligula,* throughout the year as 2.5 BMR, deriving this ratio from Schmid's (1965) work on the Mourning Dove, in combination with several studies on caged birds. Cain (1973) estimated DEE in the Black-bellied Tree Duck, *Dendrocygna autumnalis,* at 2.6 BMR by assuming an increment of 25% in extrapolating from caged birds, after appropriate correction for temperature. Kendeigh, Dolnik & Gavrilov (1977) give a tentative set of equations for computing DEE (which they term DEB, the daily energy budget) in non-passerines, by extrapolation from the information on cage existence discussed earlier (see Fig. 6) by assuming that an increment of 7.1%, computed indirectly for the House Sparrow, would apply generally. Since cage existence does not parallel basal metabolism, these tentative relationships are not characterized by a single DEE/BMR ratio, but for the non-breeding conditions typical for the majority of direct measurements of DEE covered in Table 3, the predicted DEE/BMR ratio in the weight range 500–1000 g body weight where most of the cage existence data of Kendeigh et al. are clustered, averages approximately 2.3. In comparison with our compilation, the estimates of Kendeigh et al. will underestimate DEE in "heavy" non-passerines, and overestimate it in "light" non-passerines, the division between heavy and light falling at about 300 g. Extrapolating from an earlier analysis of costs for cage existence, Wiens & Scott (1975) added 40% to approximate free living, and arrived at minimal DEE at approximately 3 BMR for three species with body weights in the range covered in our Table 3 (mean weights at 787, 1022 and 2459 g).

A final generalisation is possible, and this involves identifying the portion of the increment of free-living over cage existence, due to foraging. In this analysis, the difference between DEE and cage existence is partitioned among the various activities in studies of non-breeding birds, and foraging is obtained as a difference value when other items have been accounted for. Locomotion devoted specifically to foraging (such as flights between roost and feeding areas) is included in the foraging cost (Fig. 8). The

$$\text{DEE} \qquad y = aW^?$$

foraging costs $\rightarrow$ (fc)

$$\text{EM} \qquad y = aW^{.6}$$
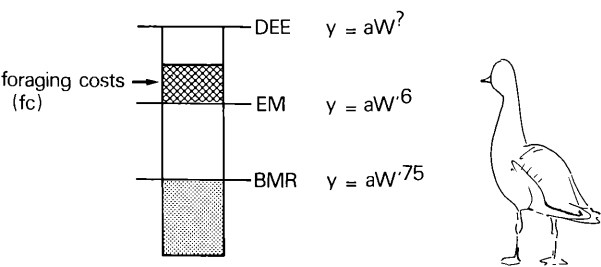
$$\text{BMR} \qquad y = aW^{.75}$$

Fig. 8.

Note: The values for fish-eating birds where ME is not stated by the author (species numbers, 1, 8, 11, 12, 13, 20, 21, 22, 23, 25, 27, 29, 30, 31) are computed from data showing fresh weight of fish consumed daily by assuming a calorific value of the food at 1.2 kcal/g freshweight, and assimilation at .85; for mollusc- and Crustacean-eaters (3, 17, 26) assimilation is likewise assumed to be .85.
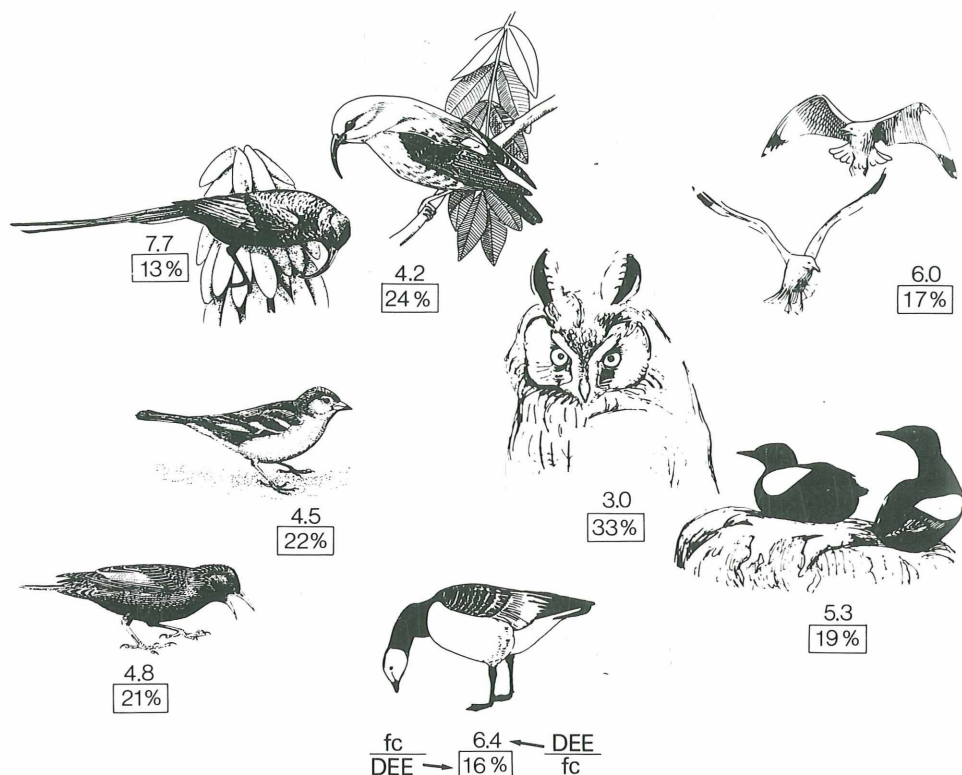
Fig. 9.

compilation (Fig. 9) expresses foraging cost as return on calories devoted to foraging (varying from 3.0 to 7.7 in metabolisable energy of food for every calorie spent foraging) or as foraging commitment, that is, daily foraging cost as compared to the total DEE. It appears that about 20% of the total DEE is devoted to foraging in non-breeding birds, in these species amounting to half of the increment of cage to free existence (see Fig. 7).

It is hard to account for the magic figure of 2.6 BMR, or for the apparent convergence in the proportion of DEE devoted to foraging and we presume this means that a further increase in energy expenditure for long periods must entail a disadvantage, for instance by increasing wear on the physiological machinery of the body and thus shortening the lifespan.

4. Food stocks and goose visitation: the small-scale pattern

4.1 Standing crop of green matter

The great variability in natural swards has defeated all but the most determined efforts to quantify above-ground biomass throughout the year, the classical method involving tedious handsorting of green material from periodic clippings (ref. IBP handbook, MILNER & HUGHES, 1968). Under the impetus of the IBP a workable indirect ap-

proach to measuring the standing crop of living grass was developed, utilizing a quantitative assessment of chlorophyll density (TUCKER et al., 1973). A highly sensitive but portable battery-powered light meter fitted with two filters (allowing passage of light at 675 and 800 nm) is all the equipment required. Measurement at 675 nm corresponds to the peak absorption of chlorophyll, and at 800 nm to the peak reflectance. The quotient of reflectance divided by absorption, each measured in the same units such as milliwatts, gives a positive "green value" or chlorophyll index showing a strong positive correlation with chlorophyll concentration and hence with living biomass. Making use of the quotient, rather than the individual wave length readings, makes the readings virtually independent of the amount of incident light, at least within rather broad limits. In our winter situation we found the "green value" to be little affected by variations in sunlight conditions at least between approximately 11.00 and 14.30 hrs, although fog must be avoided since light at 800 nm appears to be selectively attenuated under these circumstances. Calibration must be carried out for each vegetation type, and involves relating the "green value" to living biomass as determined by handsorting
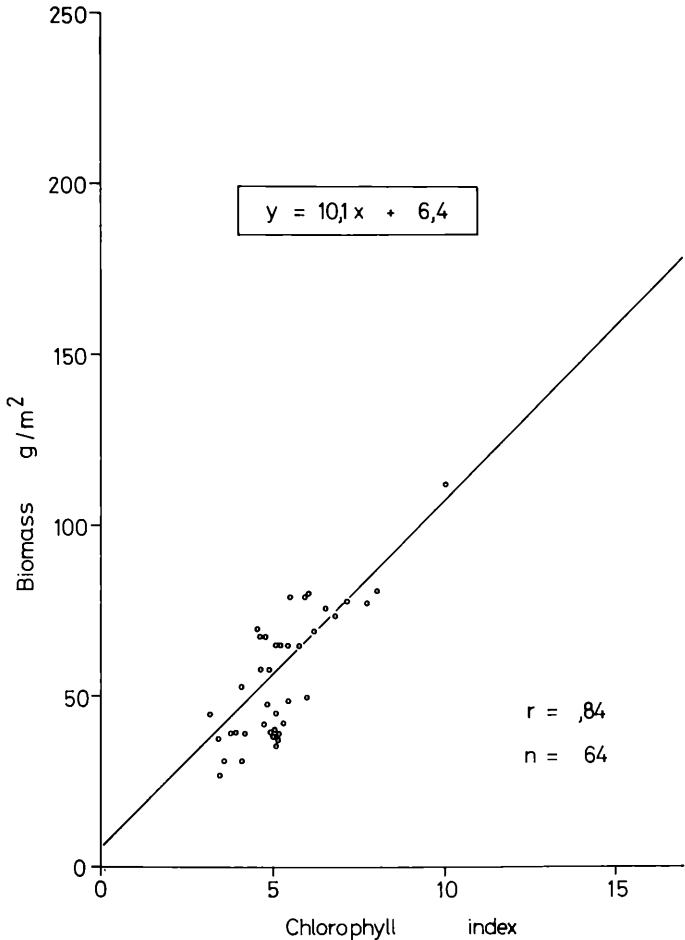

$$y = 10{,}1\,x + 6{,}4$$
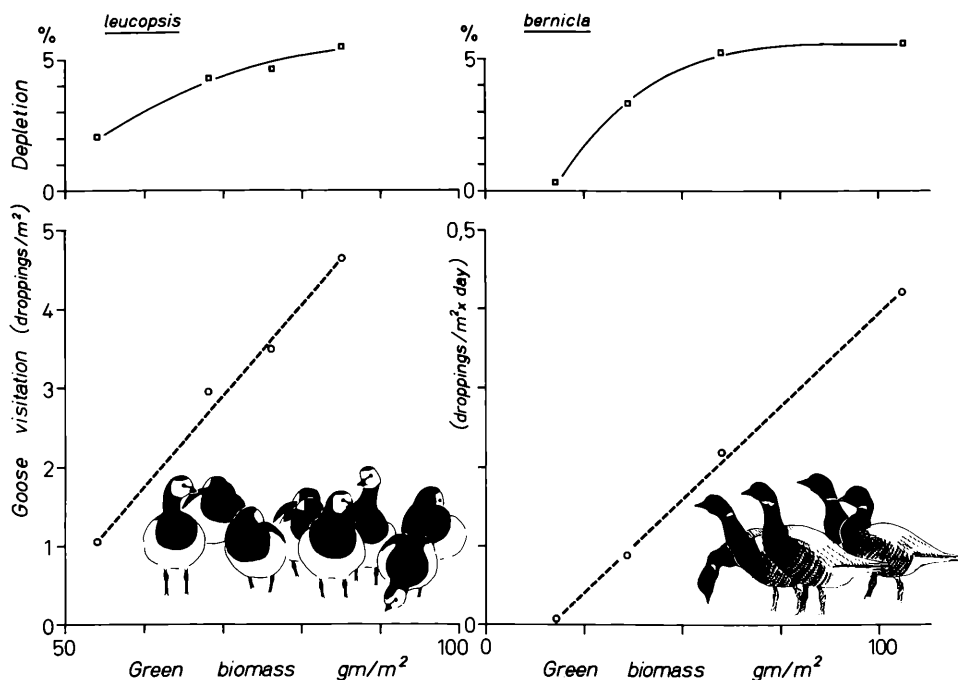
$$r = {,}84$$

$$n = 64$$

Fig. 10.

Fig. 11.

clipped samples. One does not altogether avoid drudgery therefore, but the great vir-
tue of the method is that a very large number of "green value" readings can be collected
in a short time, such that a mean biomass figure as taken from the calibration curve re-
flects an adequate sampling of the naturally occurring variation. Achieving compa-
rable values by clipped samples alone would entail a prohibitive amount of labour (see
Fig. 10). As we have applied it, the method involves a fortnightly assessment of stan-
ding stocks, entailing a day in each vegetation type, three replicate readings being ta-
ken at each of three permanent quadrants spaced twenty meters apart, with 100 meters
between the groups of three. A minimum of one kilometer per vegetation type is con-
sidered as a unit and the measurements can conveniently be combined with a collection
of droppings to assess goose visitation. Approximately every six weeks or whenever
help was available samples were taken for the calibration curve. We found it conven-
ient to take two circular cores of 15 cm diameter at each point, and these were taken
back to the field laboratory for clipping and sorting. As evinced by the healthy scatter
of points in the calibration curve (Fig. 11), the method is no panacea, but to our know-
ledge there is no alternative other than strip mowing, which is not applicable in our
case as it would alter the habitat. Undoubtedly further refinements of this scanner
technique will follow, for the present it is satisfying to note that the short merseland
swards used by both species of geese in the winter are all accomodated in the "Festuca"
calibration valid for the period October through April.

When biomass readings are taken at sites where the bulk of the sward is composed of
species utilized by the geese, we obtain a measure of available foodstocks. Goose
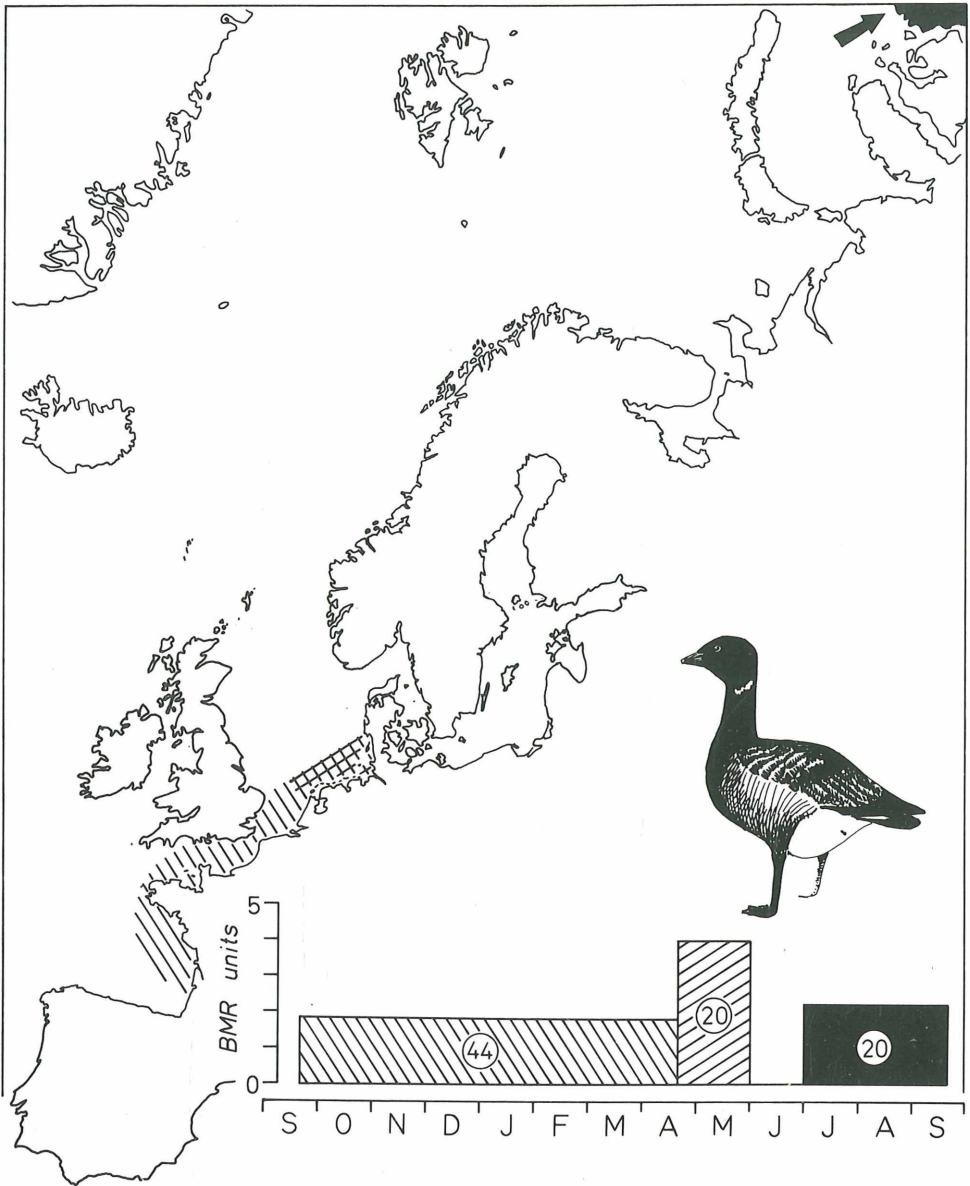usage can be related to standing crop by measuring the accumulation of droppings at

Fig. 12.

the same sites, and examples for both Brent and Barnacle Geese are collected in Fig. 12. It is important to recall that each point is the mean for a unit of vegetation covering at least 10 hectares, in each case dominated by one or more potential food species. There is clearly a very strong influence of standing crop on goose visitation. Since the analysis of marker substances in both the food species and the droppings can be used to estimate digestibility, each dropping represents a known amount of food. The density of droppings can thus be converted to the amount removed, and in this fashion

the data on depletion of the food stocks shown in the upper half of Fig. 12 have been obtained. The salient feature of this figure is the demonstration of what may be termed the grazing plateau: over a wide range of standing crop the rate of depletion of the vegetation is similar. i. e.: the better sites suffer a uniform rate of predation. The simplest interpretation of the shape of the depletion curve, is that the geese respond to two threshold values of biomass, an upper one (above which the geese do not discriminate if one considers the absolute percentage of living blades removed by grazing: the "better" areas will only differ in the total grazing offered not in the selectivity exerted on the vegetation), and a lower one (below which areas are virtually ignored). In the case of the Brent, the upper threshold can be put at about 50 g/m^2 The two vegetation types exceeding this value comprised only 19 of the total 71 hectares included in the analysis, yet accounted for upwards of 80% of total grazing. From intensive observation it appears that these two favoured areas attracted higher densities of geese than the other vegetation zones, and within the favoured areas the uniform rate of depletion is achieved by frequent passes through the area, a constant fraction of the "prey" being harvested at each pass.

Presumably the lower limit of the grazing plateau is set by unfavourable effects of declining sward height and blade density on the bite size. Tests with captive birds are being undertaken to determine if in fact sharply defined cut-off points exist. We should guard against thinking too rigidly in terms of thresholds in absolute intake, since the decision taken by the geese must always depend on the relative profitability of the vegetations open to exploitation, and limiting thesholds will only become apparent when the resources are fully utilized.

4.2 Caloric return and goose usage

As described in section 2, the nutritive quality of foods utilized by the wild geese can be estimated from the content of marker substances (acceptable candidates being crude fibre content, ash content, and chlorophyll content, all of these as related to organic dry matter in sand-free samples) in the food plants and in the droppings. The information on retention rate of the organic matter so obtained can be extended to caloric retention rate by analysis of the caloric content of samples of food and droppings (ash- and sand-free), and finally intake can be estimated from the rate of production of droppings. For several vegetation types such observations can now be assembled to yield an estimate of potential caloric gain to the geese by ingesting 100 gm of a given food species, as well as the caloric gain to be expected from one hour active grazing at rates normally observed. The data required thus comprise 1) samples of the droppings in each habitat to obtain dry sand- and ashfree weights, 2) microscopic examination of the droppings to determine the species ingested, 3) analysis of marker substances in food and droppings to obtain digestibility of the organic matter, 4) analysis of caloric content of food species and droppings, with suitable calculations for the "average" food, the caloric value of each food species entered according to its incidence in the droppings, 5) observation of the rate of production of droppings in the field, and the number of hours per day during which this rate is maintained. The basic data for Brent are collected in Table 4.

Our major difficulty in covering the various food sources utilized by Brent in winter concerned *Zostera,* as this is now rare in our study area. A fall foray into Denmark, although highly instructive, revealed heavy dependence on root stocks, thus preventing

Table 4. Basic data for computing hourly food intake rates in Brent in the Netherlands.

	Enteromorpha	Poa, Lolium (winter)	Puccinellia Plantago (spring)	Zostera
Droppings/hr	17.1 (n = 65)	17.6 (n=612)	16.2 (n = 55)	13.7 (n = 30)
Weight of droppings:				
crude dry weight (g)	0.99	0.5 −0.8	1.08	1.36
sandfree dry weight (g)	0.68	0.46−0.7	0.99	0.69
organic matter, dry (g)	0.48	0.41−0.62	0.81	0.52
Retention rate, organic matter	.34	.32	.31	.37
Caloric content, food (per g o. m.)	4.69	4.72	5.32	4.87
Caloric content, faeces (per g o. m.)	3.65	4.34	4.87	4.30

Source: compiled from v. d. Bilt et al., 1975, Dijkstra & Dijkstra-DeVlieger, Terpstra, and
Ebbinge, unpubl. obs. 1975–78. Retention rates from marker studies confirmed with
captive birds, with exception of *Zostera* with which no tests were done: see text for
derivation, making use of exclosure data in England (Charman, in press).

application of chlorophyll content as a digestibility marker when comparing food and
droppings (Dijkstra & Dijkstra-de Vlieger, unpubl). An alternative approach is possi-
ble by applying intake estimates obtained by Charman (in press) from exclosures along
the southeast coast of England, where Brent utilize almost exclusively the above-
ground leaves of *Zostera*. Charman estimated intake as 122 and 100 g dry weight per
goose-day in the two winter periods studied, and we have based our calculation on the
mean value (111 g dry-weight *Zostera* per goose-day). This we have related to our
own data from the Waddensea (dropping rate, weight, and caloric content of both food
and droppings) to complete the balance (see Table 4). Our estimate of caloric reten-
tion (= assimilation) works out at .44, the retention of organic matter being .37, in
keeping with the low crude fibre content of *Zostera* (Morehouse, 1974; Candussio,
1960). Both of these values are similar to *Enteromorpha,* and superior to values for
grassland species in winter (*Poa, Lolium*) or spring (*Puccinellia, Plantago*). Our ob-
servational parameters are virtually identical with Charman's data (Charman for
example estimates output at 130 droppings per day, whereas our estimate is 134) but
large discrepancies exist in the analytical findings, for example in the caloric determi-
nations. Our values are consistent with those of Morehouse (1974), and we suspect that
errors have been introduced into Charman's computations due to difficulties in correc-
ting for sand fractions in food and droppings, a point at present under review (Char-
man's provisional computation indicated assimilation at .75). Direct digestibility
trials with captive individuals will settle the issue.

.We can now estimate the potential yield of natural foods, and ask whether the geese
tend to select the most profitable food type, given a choice (Table 5). Particularly rele-
vant to Royama's profitability hypothesis is the computation of caloric gain per 1000 bi-
tes, taking bites as a standard measure of effort. This is unlikely to be exactly correct,
but is the best we can do at present. Two seasonal shifts in preference can now be te-

Table 5. Intake and yield of natural foods for *Branta* geese, determined from dropping, production rates and retention rates estimated from marker studies.

B. leucopsis	period	yield in kcal/100 g	hourly intake g	hourly intake kcal	kcal intake/ 1000 bites
Salicornia	Oct.	463×.40 = 185	16.9	31	9.23
Poa, Lolium	Dec.	452×.35 = 158	15.8	23	2.95
Poa, Lolium	Mar.	441×.36 = 159	15.3	23	2.27
Festuca	Dec.	462×.34 = 157	no data		——
Festuca	Mar.	449×.36 = 130	no data		——
		161			
B. bernicla					
Zostera	Oct.	364×.44 = 160	12.4	20	not applicable
Poa	Dec.–Feb.	447×.32 = 142	10.9	15.5	3.45
{ *Puccinellia*	Apr.–May	447×.37 = 165	23.7	39	4.53
{ *Plantago*					
Enteromorpha	Nov.	365×.50 = 184	15.1	27	18.33

Sources: *B. leucopsis,* EBBINGE et al. 1975, supplementes by unpubl. reports of SWIERSTRA and
VAN EERDEN and PROP;
B. bernicla from Table 4.

Note: yield refers to ME obtainable from 100 g sand-free dry matter; the fraction given is thus
assimilation hourly intake is likewise given in sand-free dry matter.

sted. In the first place, Barnacle Geese when they return to our area in October, show a strong preference for the *Salicornia* seed heads, of which vast amounts are present in the reclaimed area Lauwersmeer, and shift to grass feeding only when this resource has been depleted. As shown in Table 5, this preference follows the profitability rule, caloric gain per hour and per 1000 bites being higher on *Salicornia* than the alternative *Poa* and *Lolium* swards. Secondly, the utilisation of *Enteromorpha* by Brent can be explained along these lines. When available (in our area primarily November and again in late May) *Enteromorpha* is preferred to merse feeding, and it will be seen from the table than caloric yield per 1000 bites is clearly in favour of *Enteromorpha*. Hourly caloric yields do not differ greatly in this case however, and further data will be needed before we can conclude that the order in which plant species are depleted is always in accord with caloric profitability without regard to quality (e. g. protein content). Testing the potential profitability of sites in competition with one another as in these cases by means of droppings analyses depends on suitable observational opportunities and is only possible if use of the site in question is prolonged over several weeks. A more powerful approach is to run simultaneous digestibility trials in the competing vegetation types using tame individuals, and we are currently following this up. Likewise, the interpretation of selection within the sward at one point, a conspicuous feature of goose foraging, can only be approached by tests where all potential species are offered to captive individuals, a method followed successfully at Slimbridge as reviewed at this symposium by OWEN (p.   ). A further aspect deserving quantification is the desirability of the various sites from the point of view of disturbance (establishing the position of the various sites in the disturbance gradient (N. OWEN, 1977).

5. Large scale movements of Barnacle Geese and Brent in the course of the annual cycle in relation to food stocks

The high-arctic nesting *Branta* geese have very different migratory paths and time tables, and we here explore the possibility that these have a basis in differences in the availability of plant species offering favourable energy balance. The Barnacle Goose of all three populations leave the wintering quarters relatively early (mid-March to early April) and spend the following months at staging grounds considerably further north (Iceland, north Norway and the Baltic islands respectively for the Greenland breeding-Ireland wintering, Spitsbergen breeding-Scotland wintering and Novaya Zembla breeding-Netherlands wintering population). In two populations studied, the birds rely heavily on *Festuca* in this period, as they did in the previous early spring growth in the winter quarters, and it seems reasonable to suggest that by making the northward shift the geese are riding the crest of the wave as concerns digestibility (early growth being characterized by lower cell wall content hence higher digestibility). The postbreeding recovery again coincides with the first growth of the arctic *Festuca* and the final pre-departure fattening can be financed at the slopes fertilized by the seabird cliffs.

Turning now to the *Brent,* we are only able to construct an energy budget for part of the annual cycle. From late fall until early spring, encompassing a period of *Zostera* feeding and polder grassland in midwinter, giving way to kwelder grasses in early spring, daily ME fluctuates around 250 kcal. From mid April on, a rather spectacular improvement in return from the same intake on a dry weight basis is evident, resulting from a higher caloric density of the grass at this growth stage, coupled with an enhanced digestibility (via a decline in crude fibre, cf. data in Spedding, 1971).

Data on weight of *Brent* caught at various times on Terschelling give an indication of fat deposition in this spring period (Ebbinge, et al. in prep.). If cost of flight to the breeding grounds is estimated from Tucker's (1975) formula, with allowance being made for the wind conditions prevailing upon departure, then about 2000 kcal are required. There after we estimate that DEE of the incubating bird approximates 1.2 BMR (estimated from weight decrement of captive birds in May when deprived of food, Terpstra, pers. comm.) in accord with data available for incubating wildfowl of similar weight without access to food (Eider *Somateria mollissima* and Snow Goose). From figures on changes in carcass composition of Eider presented by Gorman & Milne (1971) and Milne (1976) it appears that the female utilizes 340 g fat and 150 g protein during the 26 day incubation period, thus approximating a DEE of 1.2 BMR if it is assumed that food intake is negligible in this period. Ankney (1974, 1977) has similar carcass analyses for the Snow Goose, showing that approximately 310 g fat and 85 g protein are expended during the 23 day incubation period, approximating 1.2 BMR. On this basis the female Brent could theoretically survive until the end of June with virtually zero intake.

It will readily be appreciated that the extent of the fat reserve, and the rate at which it is depleted, will be of paramount importance in breeding performance (Newton, 1977). For this reason, nutritional conditions at the final staging site, the top-up locale, will be of critical importance. The rate of fat accumulation in the brent observed on Terschelling and assuming an efficiency of fat deposition of 75% (i. e. it takes 13 kcal to

build one gram of fat) requires an increase in intake of about 200 kcal per day, or an increase of 80 percent over the early spring value.

6. Discussion

Breeding in the high arctic is only possible with the aid of an energy subsidy from the winter quarters. The magnitude of this subsidy is apparent in the provisional seasonal budgets for Brent in Fig. 13. Work on the breeding grounds has stressed how precarious the timetable in the far north really is. BARRY (1962) has stressed the sharp restriction on laying date imposed by the rapid deterioration of the weather at the end of summer in this stark habitat and documents how late-hatched young brent were actually frozen in because the frost set in before they were fully capable of flight. Reinforcing the need to lay as early as ice and snow conditions permit is the impossibility of combining incubation, in all geese the sole task of the female, with adequate foraging in the then still inhospitable environment. If incubation is to succeed at all, laying must commence fairly soon after arrival in the breeding quarters, otherwise the female will exhaust her energy reserves before the eggs hatch, and thus be forced to abandon her clutch. Stated another way, this means that the capacity to make a breeding attempt, and the probability of carrying through until the eggs hatch, are both dependent on the state of energy reserves, or "condition" of the female on departure from the spring fattening areas. There is some indirect evidence to support this in NEWTON & KERBES (1974) study of the Greylag breeding on the Hebrides and the work of CABOT & WEST (1973) on the Barnacle Goose population wintering in Ireland.

A closely allied point is the clarification of the adaptiveness of the choice of site where pre-breeding fattening is achieved. We have suggested that the Barnacle Goose moves northwards at this time in order to prolong the exploitation of the *Festuca* sward during the period of maximal nutritive quality (maximal digestibility of organic matter, high caloric content, and high protein content going hand in hand). Digestibility trials to test this are underway with tame geese, one group being retained on the *Festuca* vegetation used by the wild birds until departure from Schiermonnikoog in early April, the other group being transported at this time, to the *Festuca* in the Baltic area and thus as it were being allowed to accompany the wild geese. That the Brent on the contrary remain in our study area to "top up" we have linked to their utilization of *Enteromorpha* and *Nereis* on the mudflats at low water, especially in the second half of May, along with the utilization of the fresh growth of *Puccinellia* and *Plantago* on the merse, species with apparently a salt content too high for the Barnacle Goose to tolerate, but within the capability of the more maritime-adapted Brent. Obviously further trials will be called upon to verify these assumptions.

The second theme of this paper, that the utilization of the vegetation during the winter should obey the rule of preferential use of high quality (caloric return) and high biomass, and that the capacity of grassland during this period should be amenable to prior measurements, is still largely a matter of faith we must admit. We do feel, however, that further application of reflectance scanning techniques for assessing biomass, and a continuing search for suitable analytical procedures when dealing with digestibility markers, should make this approach operational within a year or two.

The experiments with captive geese have confirmed the applicability of the marker technique to obtain estimates of the gross intake of wild birds as well as the digestibility, and will make construction of a year-round energy budget feasible.   Physiological study of the functioning of the caeca must not be neglected, however, as the proportion of food processed in these organs varies with the diet (MILLER, 1976) and may have prime significance from the viewpoint of energy extraction when the bird is faced with a low-quality diet, and/or has the option of slowing the rate of food passage.

The most fascinating aspect of continuing study as we see it, is to ascertain how the geese themselves evaluate the food stocks.   Experiments to alter the sward and observe how the geese react suggest themselves, but the matter is complex as we are in fact dealing with the functioning of the flock.   It will be clear from this discussion that we are convinced that further effort will be highly profitable.

Acknowledgements

7. Summary

1) Progress is reported on study of Barnacle Geese *Branta leucopsis* and Brent *Branta bernicla,* designed to test the hypothesis that movements throughout the year are dictated to a large extent by changes in the relative profitability of the various food species.   We expect the project will yield a predictive ability to estimate carrying capacity.

2) Digestibility of natural foods as well as intake rates can be estimated from marker studies. Ash, crude fibre, and chlorophyll naturally occurring in the food are suitable markers for determining the digestibility of the organic matter, as verified in feeding trials (Table 1) with wild-caught Whitefronts *Anser albifrons*. Digestibilities can be predicted from crude fibre content of the food species (Fig. 4).

3) Intake rates in grams dry weight ingested per hour are closely similar for different food types and various species of geese (Table 2), and this finding suggests that there is a physical limit to the rate of passage of food down the alimentary canal.

4) Daily Energy Expenditure (DEE) has been estimated via the droppings for Barnacle Geese and Brent, and a compilation for non-passerine birds (Fig. 7) indicates that DEE averages 2.6 BMR.

5) The increment of DEE over cage existence values can be identified in selected species to obtain the cost of foraging for unrestrained birds; this has been expressed as foraging return (often 6 calories for every caloric expended) and foraging commitment (proportion of DEE devoted to foraging, often 20%), as shown in Figs. 8 and 9.

6) Standing crop of green matter can be estimated by hand scanner, the ratio of light reflectance of the sward at 675 nm to that of 800 nm showing a strong positive correlation with chlorophyll content (see TUCKER et al., 1974) and hence with biomass of green matter (see Fig. 10).

7) Goose usage as estimated from the accumulation of droppings in relation to foodstocks as measured in units of the natural vegetation (Fig. 12) shows what we term the grazing plateau, viz. the better sites suffer a uniform rate of depletion.

8) Small-scale site shifts corresponding to switches in food species utilized, follow the profitability rule in that caloric return per bite is highest in the preferred vegetation (Table 5). Caloric retention per hour is not always improved by such shifts, however, and study of differences in food quality in relation to requirements specific to the season is called for.

9) Breeding of Branta geese in the high arctic is only possible at the expense of fat deposit on the spring staging grounds, and provisional estimates for the magnitude of this energy subsidy are given (Fig. 13).

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