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METABOLIZABILITY AND PARTITIONING OF ENERGY AND PROTEIN IN GREEN PLANTS BY YEARLING LESSER SNOW GEESE[1]

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Abstract. We measured apparent metabolizability of organic matter, gross energy, nitrogen and cell wall constituents of pelleted alfalfa by Lesser Snow Geese (*Chen caerulescens caerulescens*. We also used simultaneous measurements of energy expenditure and apparent metabolizable energy intake to estimate heat increment of feeding and net energy for production and maintenance. Apparent metabolizability of energy was 46% as a result of substantial retention of dietary cellulose (45%). Mean slope of the relationship between energy expenditure and apparent metabolizable energy intake, which estimates heat increment at feeding, was 0.33. One minus the slope, 0.67, was our estimate of the proportion of apparent metabolizable energy available for maintenance and production. Resting metabolic rate at zero apparent metabolizable energy intake ranged from 361 $kJ \cdot kg^{-1} \cdot day^{-1}$ to 432 $kJ \cdot kg^{-1} \cdot day^{-1}$, while apparent metabolizable energy intake required for energy balance ranged from 455 $kJ \cdot kg^{-1} \cdot day^{-1}$ to 871 $kJ \cdot kg^{-1} \cdot day^{-1}$. Lesser Snow Geese (>2 kg mass) were more efficient at retaining dietary energy but possibly lost more of this energy as heat than smaller Black Brant (*Branta bernicla nigricans*)(~1 kg mass), suggesting a possible relationship between body size and processing of energy in herbivorous birds.

Key words: Apparent metabolizability; Chen caerulescens caerulescens; *energetics; heat increment of feeding; Lesser Snow Goose.*

INTRODUCTION

Energy expenditure has been extensively studied in birds (reviews in Lasiewski and Dawson 1967, Nagy 1987) but fewer studies have addressed retention of dietary energy and other nutrients, especially in herbivorous birds (see Marriott and Forbes 1970, Gasaway 1976, Halse 1984, Herd and Dawson 1984, Miller 1984, Buchsbaum et al. 1986, Joyner et al. 1987, Sedinger et al. 1989, Prop and Vulink 1992). Energy balance depends substantially on the uptake and retention of dietary energy so the paucity of such measurements limits our understanding of nutrient balance in wild animals. For herbivorous birds, a substantial proportion of gross energy in green plants is in relatively indigestible structural carbohydrates of plant cell walls (Van Soest 1982) that can be broken down only by microbial populations contained in the gut. Herbivory frequently results in enlarged sections of the gut to allow enlarged microbial populations, yet there is a strong limit on the size of the digestive tract to allow flight (Dudley and Vermeiji 1992). Thus, complex gastrointestinal structures that enable digestion of cell wall components in herbivorous mammals have not generally evolved in birds (but see Grajal et al. 1989). Furthermore, birds generally represent the smaller range of sizes for herbivores (Demment and Van Soest 1985), despite their higher metabolic rates (Calder and King 1974), thereby, increasing their mass-specific requirements for metabolizable energy intake, relative to mammals.

Despite limitations on alimentary diversity in herbivorous birds, digestion of structural carbohydrates could play an important role in the energy balance of herbivorous birds because about half the gross energy in green plants is in these compounds (Van Soest 1982). Generally, larger birds (Herd and Dawson 1984) or those with enlarged caeca (e.g., ptarmigan, Gasaway 1976) are able to digest some cellulose through micro-

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bial fermentation. Results for geese have been variable. Buchsbaum et al. (1986) reported digestion of a substantial proportion of the cellulose in green plants eaten by Atlantic Canada Geese (*Branta canadensis canadensis*). In contrast, Marriott and Forbes (1970) and Sedinger et al. (1989) detected no cellulose digestion in either Cape Barren Geese (*Cereopsis novaehollandiae*) or Black Brant (*B. bernicla nigricans*). Variation in the results of these studies indicates the need for more measurements of digestion of plant cell wall constituents to better understand the roles of these factors in energy budgets of avian herbivores and physiological adaptations associated with digestion of structural carbohydrates.

Methods for partitioning dietary nutrients, to calculate net energy, which is available for maintenance and production, were developed by animal scientists (Crampton and Harris 1969) and extended to wild mammalian herbivores (Robbins 1993). Despite their general utility, these methods have been less widely applied to birds (but see Bayley et al. 1982, Pesti et al. 1990, Sedinger et al. 1992). Within this context, few studies have attempted to estimate heat lost to digestive or metabolic inefficiency (heat increment of feeding), which can represent a substantial fraction of metabolizable energy intake (Sedinger et al. 1992). Here we use total collection trials to estimate apparent metabolizability (AM) of dietary constituents by Lesser Snow Geese (*Chen caerulescens caerulescens*) (hereafter Snow Geese) and simultaneous measurements of food intake and energy expenditure to estimate heat increment of feeding and net energy available for production.

METHODS

Snow Goose eggs were taken from nests in the Anderson River colony (Barry 1967) Northwest Territories, Canada on 27–28 June 1989. Goslings were reared on the Beaufort Sea coastal plain of the Arctic National Wildlife Refuge (70°00'N, 143°25'W) on a combination of native vegetation and poultry starter (3.2% nitrogen and 5% crude fiber). In September, after the birds fledged, they were transported to the vivarium, Institute of Arctic Biology, University of Alaska Fairbanks. Birds were fed a diet of 25% cracked corn and 75% pelleted alfalfa and they had continuous access to oyster shell grit and flowing water. We did not measure the composition of cracked corn, which generally contains 12% neutral detergent fiber (NDF, Van Soest 1982) and 1.6% nitrogen (McDonald et al. 1973). Alfalfa pellets contained 41% NDF, 3.8% nitrogen and 17.7 kJ/g gross energy (Table 1).

TABLE 1. Composition of alfalfa pellets fed to Lesser Snow Geese during apparent metabolizability trials.

Dietary constituent	% Dry mass or kJ/g ($\bar{x}$ ± SE)[a]
Energy[b]	17.7 ± 0.08
Nitrogen	3.8 ± 0.03
Phosphorus	0.31 ± <0.01
NDF	41.4 ± 0.9
ADF	26.1 ± 0.3
Cellulose	14.3 ± 0.3
Lignin	8.5 ± 0.2
Ash	15.1 ± 0.2

[a] $n = 5$.
[b] kJ/g.

We estimated AM of alfalfa pellets using total collection trials as in Sedinger et al. (1989). Briefly, methods were as follows. Individual Snow Geese each spent five days in metabolism cages before total collection trials to acclimate them to experimental conditions. Total collection trials consisted of an initial three-day equilibration period and a five-day period during which food eaten and feces produced were measured. At the beginning of the trial on 3 Nov. 1989, 4 (two males, two females) individual Snow Geese were placed in cages with 150 g of alfalfa pellets, sufficient to prevent birds from eating all of their food before dishes were refilled the next morning. Snow Geese had access to oyster-shell grit and water in their cages. Twice each day (09:00 and 17:00 hr) unconsumed food was removed and weighed, and food dishes were refilled with 150 g of alfalfa pellets. Grit and water were replenished daily. At 17:00 hr each day, feces were removed and a clean collection tray placed beneath each cage. After an equilibration period, collected feces were dried to constant mass at 59°C following collection each day. Before drying, we homogenized feces and removed a fresh 10 g subsample for determination of nitrogen and phosphorus. The fresh subsample was immediately frozen for later analysis. Geese were weighed (± 1 g) daily.

We measured gross energy in fecal and food samples using bomb calorimetry. Neutral (NDF) and acid (ADF) detergent fiber were measured using Van Soest procedures (Goering and Van Soest 1970). ADF and its components were es-

TABLE 2. Food eaten and mass dynamics of Lesser Snow Geese during apparent metabolizability trials.

Individual	Food eaten during five-day collection period (g)	Mass (g)[b] Start	Mass (g)[b] End
R56 (m)[a]	484	2,350	2,352
R64 (f)	619	2,383	2,383
R74 (m)	856	2,625	2,560
G10 (f)	801	2,230	2,297

[a] Sex.

[b] Mass at start and end of trial.

TABLE 3. Apparent metabolizability (AM) ($\bar{x}$ ± SE) of components of pelleted alfalfa by Lesser Snow Geese.

Component	AM (%)
Organic matter	46.2 ± 1.1
Energy (kJ)	46.3 ± 1.7
N	6.1 ± 4.4
P	−1.6 ± 9.3
NDF	30.9 ± 2.8
Hemicellulose	52.6 ± 2.7
ADF	16.3 ± 2.8
Cellulose	44.6 ± 6.0
Lignin	7.8 ± 6.4

timated from neutral detergent insoluble material, resulting in a sequential analysis. Lignin was estimated as the ash-free residue after treating ADF with sulfuric acid. Cellulose was estimated by subtracting lignin from ADF. Analyses of cell wall material were conducted by the Wildlife Habitat Laboratory, Washington State University. Nitrogen and phosphorus were estimated from fresh samples using a Lachat AE Flow injection inorganic analyzer. Composition of feces was measured on samples from the total feces produced by each individual each day. Total quantity of a constituent, e.g., cellulose, appearing in the feces was the sum of the estimated daily quantities produced. We also estimated the composition of food offered each day and estimated total ingestion of a dietary constituent, e.g., cellulose for each individual from daily intake and composition of food. Nitrogen and phosphorus concentrations were converted to a dry mass basis using the proportion dry matter of the entire fecal sample for that collection day. We estimated percent AM for each dietary constituent as the difference between intake and output, divided by intake, times 100 (Miller and Reinecke 1984, Sedinger et al. 1989). We estimated nitrogen intake required for balance by regressing nitrogen output against nitrogen intake. Each individual used in the total collection trials provided a single estimate of nitrogen intake and output for the five-day collection period. The regression equation was solved for the nitrogen intake that equaled nitrogen output.

Energy expenditure was estimated by measuring O_2 uptake and CO_2 production, using an open-flow system as described in Sedinger et al. (1992). We measured energy expenditure over 24 hr, three times between 11 January and 30 April 1990 on each of eight Snow Geese. Energy expenditure was measured on each individual at each of the following diet levels: ad libitum, 50% ad libitum, and fasted. Each individual was placed in a metabolism cage 24 hr before the beginning of a trial to reacclimate them to test conditions. Before the first trial each individual had spent a minimum of 14 days in a metabolism cage. At the beginning of the trial a weighed quantity of alfalfa pellets was provided consistent with one of the three dietary treatments. At the end of the 24-hr measurement, remaining food was collected, dried to constant mass and weighed. AME consumed during the measurement of energy expenditure was estimated by multiplying the amount of food eaten during the measurement by the mean AM based on total collection trials.

Apparent metabolizable energy can be partitioned into energy lost during digestion and metabolism of food (heat increment of feeding, HIF), and net energy available for maintenance and production (Crampton and Harris 1969). HIF, as a proportion of apparent metabolizable energy (AME) intake, was estimated as the slope of the regression relating energy expenditure to AME intake (McDonald et al. 1973, Sedinger et al. 1992) and proportion of AME available as net energy was estimated as one minus the slope of the regression (Robbins 1993). We used analysis of covariance (ANCOVA), with individuals as a fixed factor and AME intake as the covariant, to estimate HIF and among-individual variation in energy expenditure. The pooled slope of the relationship between energy expenditure and AME intake estimated HIF.

RESULTS

Individual Snow Geese ate between 484 and 856 g ($\bar{x}$ = 690 g) of dry alfalfa pellets during the five-day collection period (Table 2). Masses of three of four Snow Geese in the total collection trial were constant or increased during trials, while one individual lost 65g (Table 2); mean mass change was +1 g.

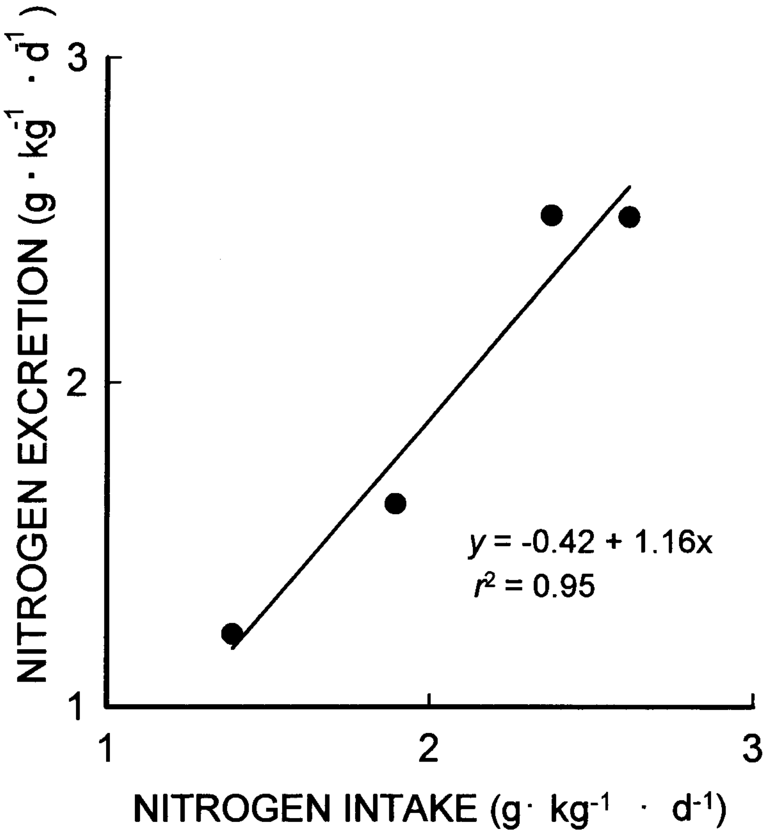

FIGURE 1. Nitrogen excretion versus nitrogen intake for individual Snow Geese. Each point represents average daily intake and excretion for an individual snow goose over a five-day collection period.

AM of organic matter and gross energy were both 46% (Table 3). Snow Geese retained 6% of dietary nitrogen. Based on the relationship between nitrogen excretion and nitrogen intake, 2.72 gN·kg^{-1}·day^{-1} were required to be in nitrogen balance (Fig. 1). Grit was spilled into collection trays, increasing the apparent total ash content of feces and ADF. We, therefore, calculated AM of cell wall components on an organic matter basis. AM of lignin was not significantly different from zero (Table 3). AM of NDF was 22%, while that for ADF and cellulose was 16% and 45%, respectively. AM of hemicellulose, which we estimated as the difference between NDF and ADF was 53%.

Energy expenditure increased significantly with increasing AME intake ($F = 8.36$, df = 1, 15, $P = 0.011$) (Fig. 2). The slope of the relationship between energy expenditure and AME intake did not vary significantly among individuals ($F = 0.82$, df = 7, 8, $P = 0.60$); pooled slope was 0.33 ± 0.11 (SE), indicating that 33% of AME was lost as heat. Net energy for production and maintenance, therefore, represented 67% (1–0.33) of AME. Daily energy expenditure, adjusted for AME intake, varied among individuals from 442 kJ·day^{-1}·kg^{-1} to 575 kJ·day^{-1}·kg^{-1} but these differences were not significant ($F = 1.69$, df = 7, 15, $P = 0.19$). Fasting metabolic rate, estimated by y-intercepts of individual regression equations relating energy expenditure to AME intake ranged from 361 kJ·kg^{-1}·day^{-1} to 432 kJ·kg^{-1}·day^{-1}.

DISCUSSION

METABOLIZABILITY OF DIETARY CONSTITUENTS

Snow Geese retained 45% of the cellulose in alfalfa pellets, which is the highest metabolizability of this cell wall component yet estimated for birds. Buchsbaum et al. (1986) estimated that Canada

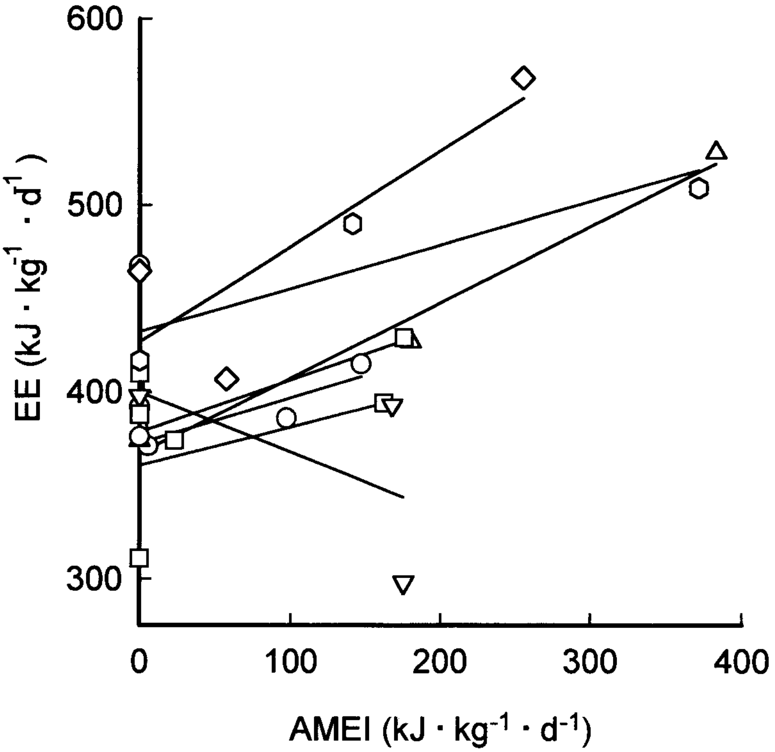

FIGURE 2. Daily energy expenditure in relation to AME intake during 24 hr. Each individual is represented by a unique symbol. Energy expenditure was measured on all individuals under fasted, 50% ration and full-ration conditions. Separate regression lines are plotted for each individual except one, which did not eat sufficient food in any trial to estimate the relationship between energy expenditure and AME intake. This individual was, however, included in the overall ANCOVA.

Geese retained about 30% of the cellulose in salt marsh grasses, while Prop and Vulink (1992) estimated that Barnacle Geese (*B. leucopsis*) retained 26% of ADF in their graminoid diet during the incubation period. Both of these studies assumed that lignin was an indigestible marker but the assumption of indigestibility of lignin was not tested. We did not detect significant retention of lignin, suggesting that estimates of AM, assuming lignin was indigestible, may not be substantially biased.

With the exception of Buchsbaum et al. (1986) and Prop and Vulink (1992), other studies of waterfowl have failed to detect digestion of cell wall components except hemicellulose (Marriott and Forbes 1970, Ebbinge et al. 1975, Summers and Grieve 1982, Miller 1984, Sedinger et al. 1989). Emus (*Dromaius novaehollandiae*), however, retained between 7 and 19% of the cellulose in experimental diets. Digestion of cellulose in Emus was attributed to a very long intestine and retention of food in the gut for >20 hr (Herd and Dawson 1984). Barnacle Geese apparently retained a significant proportion of cellulose only when rates of food intake were low and retention times were high (Prop and Vulink 1992). We did not measure retention times in our study but mean retention times for natural foods in the field for the same individual geese were <2 hr (White, Hupp and Sedinger, unpubl. data). Because cellulose digestion appears to be associated with longer retention in the gut, our data suggest that cellulose digestion may be limited in the smallest geese (e.g., Sedinger et al. 1989) by the small size of their guts and resulting shorter retention times. This hypothesis requires systematic testing by measuring cell wall digestion under standard conditions in numerous species that vary in body size.

Retention of 45% of dietary cellulose by Snow Geese increased AM of gross energy (46%) relative to smaller waterfowl (≤30%) (e.g., Sedinger et al. 1989) because about half the gross energy in green plants is in structural carbohydrates. When variation in mass-specific metabolic rate is also considered, variation in retention of structural carbohydrates will normally restrict smaller avian herbivores to diets lower in cell wall constituents, as is true for small ruminant herbivores (Demment and Van Soest 1985). Therefore, understanding the relationship between body size and AM of green plants will have important implications for understanding foraging behavior and habitat use, including the minimum quality necessary to maintain populations of avian herbivores.

Nitrogen intake required for balance in Snow Geese (2.72 $g \cdot kg^{-1} \cdot day^{-1}$) was substantially higher than for non herbivorous birds (Robbins 1993), which agrees with our findings for Black Brant (*B. bernicla nigricans,* Sedinger et al. 1989). High nitrogen excretion may be caused by high protein turnover (Welle and Nair 1990) associated with relatively high mass-specific metabolic rate in waterfowl (Zar 1969). Alternatively, geese may be inefficient at retaining dietary protein because of the imbalance of amino acids in their green plant foods (Sedinger 1984).

PARTITIONING OF METABOLIZABLE ENERGY

We estimated that 33% of AME was lost as heat by Lesser Snow Geese. Using the same techniques for Black Brant, we estimated they lost 20% of AME as heat (Sedinger et al. 1992), which did not differ significantly from our estimate for Lesser Snow Geese. Nevertheless, based on point estimates of HIF, Snow Geese may have been less efficient at using AME for maintenance and production than other waterfowl (Bayley et al. 1982, Sedinger et al. 1992) or poultry (Pesti et al. 1990). We find it intriguing that digestion of cell wall components could be inversely correlated with the energy costs of digesting and metabolizing food in Black Brant and Snow Geese. More controlled studies are needed of digestion of plant foods by geese and the proportion of AME available for maintenance.

Our results are important for modeling energy budgets because they place an upper limit on the proportion of AME available for productive processes in the thermoneutral zone. A maximum of 67% (100–33%) of AME above that required for maintenance is available for productive processes in Snow Geese. Below the thermoneutral zone a larger proportion of AME will be available for maintenance because HIF can substitute for a substantial part of the heat required for thermoregulation (Masman et al. 1989). Based on individual regressions of energy expenditure on AME intake, individual Snow Geese varied in AME intake required for energy balance from 455 to 871 ($\bar{x} = 587$) $kJ \cdot kg^{-1} \cdot day^{-1}$. Unless individuals perfectly compensate for variation in maintenance energy requirements by varying food intake, individuals will vary in their efficiency of converting AME into tissue.

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