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Larger barnacle geese (*Branta leucopsis*) are more efficient feeders: a possible mechanism for observed body size – fitness relationships.

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Abstract

Geese have to satisfy the high energy demands of flight with a low-energy and bulky food. When feeding on food items that are concentrated and widespread, as is the case in geese, an individual's instantaneous intake rate is largely determined by its bite size. Inter-individual variation in bite size was measured in barnacle geese *Branta leucopsis*, with the hypotheses that bite size would scale with (sward height)^a, where $0 < a < 1$, and (bill length)^b, where $b = 3.0$, and that there would be a positive interaction between these explanatory variables. Using a generalized linear mixed modelling analysis, bite size was found not to vary over the measured sward heights, whilst bite size was found to scale with bill length to the power $b = 14.24$ (SE = 2.05). There was no significantly detectable interaction between these terms, indicating that barnacle geese with longer bills had larger bite sizes over the full range of sward heights studied. Bill length scaled with body mass to the power 0.21 (SE = 0.01). Combining this with the scaling of bite size to bill length, we conclude that bite size scales with body mass to the power 2.99. Our results suggest that larger barnacle geese have a disproportionately larger bite size than smaller geese, which may explain the fitness advantages of larger geese observed in other studies. However, smaller geese may resist this selection pressure by selectively consuming more nutritious plant parts or altering their bite rates.

Key words: *Branta leucopsis*, barnacle geese, grazing, intake rate, morphology, foraging efficiency, scaling, peck rate

INTRODUCTION

As herbivorous birds, migratory geese have to fuel the high energy requirements of flight with the low-energy and bulky diet of grasses. To successfully meet daily energy requirements, these birds have to spend a large proportion of the available time feeding (Ebbinge, Canters & Drent, 1975; Madsen, 1985; Black & Owen, 1989; Mooij, 1992; Giroux & Patterson, 1995). The functional response of food intake rate to sward height has been quantified in several species of goose (van der Wal, van de Koppel & Sagel, 1998; Rowcliffe, Sutherland & Watkinson, 1999; Durant *et al.*, 2003). Some studies have also focused attention on how intake rates differ between individual foragers (Black *et al.*, 1992; Hupp *et al.*, 1996; Stahl *et al.*, 2001). This inter-individual variation in the ability of geese to satisfy their daily energy requirements may affect higher order processes, such as daily energy balance in winter (Black *et al.*, 1992), accumulation of body reserves

in spring (Lang *et al.*, 1998) and breeding success (Prop & Black, 1998). Consequently, the characterization of inter-individual variation, and the understanding of the causative mechanisms for it, are important in gaining an insight into the foraging and population ecology of geese (Pettifor *et al.*, 2000).

There are two possible sources of inter-individual variation in food intake: the effect of other foragers (competition or facilitation), and the effect of intrinsic factors (foraging efficiency). Variation in foraging efficiency between individuals emerges from the situation where some individuals are better than others at finding, handling and consuming items of food (Caldow *et al.*, 1999; Stillman *et al.*, 2000). Geese forage on a widespread and abundant resource (mostly grasses), where it is possible to spend most of the day processing and swallowing food items, and only a small proportion of the day searching for them. Under these conditions, intake rate is largely determined by the size of each bite (e.g. Durant *et al.*, 2003) and the speed at which bites can be processed, which is related to the size of the bite (Spalinger & Hobbs, 1992). The objective of this

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paper is to characterize the inter-individual differences in foraging efficiency of barnacle geese by understanding how bite size varies in relation to bill length and body mass.

The size of a single bite is likely to be a function of the method of feeding, the size of the forager's mouthparts, the density of food items and interactions between these different factors. Barnacle geese feed by inserting the open bill into the grass sward from above, closing the bill and retracting it from the grass sward, removing the grass enclosed by the bill. We expect that this downward pecking action will mean that the size of the bite is determined by the length of the bill that can be lowered into the sward, the distance between the tips of the upper and lower mandibles when the bill is open (gape) and the width of the bill. Bite size should therefore be determined by bill volume, and since all the linear measures of size described above are likely to be directly proportional to one another (Gille & Salomon, 1999), any one of them may be used as an index of volume. In practice, bill length is the easiest measure to obtain from live birds, and is therefore used as the primary measure of size here. Bite size is also likely to depend on food availability, here measured by sward height. However, in the tallest swards, we would expect bill size to limit bite size, and that the relationship between bite size and sward height would therefore be approximately asymptotic. Furthermore, we would expect smaller bills to approach a maximum bite size at lower sward height than larger bills. We thus put forward the following specific hypotheses:

- (1) Bite size \propto (sward height)^{*a*}, where $0 < a < 1$, as bite size should increase with sward height, but approach an asymptote in long swards.
- (2) Bite size \propto (bill length)^{*b*}, where $b = 3.0$, describing cubic scaling from a linear measure of bill size to a volumetric measure of bite size.
- (3) There is a positive interaction between sward height and bill length on bite size, reflecting stronger constraints on shorter bills in longer swards.

METHODS

Feeding trials

Measurements of bite size were conducted at the University of Groningen, the Netherlands, using a captive flock of barnacle geese *Branta leucopsis* held at the Biology Centre, Haren. Two sets of trials (periods) were conducted, the first between October and December 1999 and the second between May and July 2001. These trials were designed to estimate the intake per bite for individual barnacle geese, over a range of food densities.

In each period, barnacle geese were put in individual aviaries with flowing water and freely available food (Anseres 2, Hope Farm, Woerden, The Netherlands). For between 1 and 3 weeks respectively for the first and second periods, the geese were trained to eat from small turfs (400–600 cm²) secured to trays. Turfs were grown

to achieve a tall sward height initially, and then used for training, thus some turfs were repeatedly grazed until they had a short sward height, whilst others were left longer. This pattern of growth, followed by repeated grazing and regrowing, replicated the situation in wild geese. The measurements of bite size were conducted following these training sessions.

The evening before a trial, pellet food was removed from the aviaries. Trials started the following day at between 09:00 and 10:00. The first step in each trial was to measure the sward height of the turf to the nearest 0.5 cm. The turf was then weighed to the nearest 0.1 g on a pan balance, placed in an empty aviary close to the trial goose for 10 min and then re-weighed. This procedure allowed the evaporative weight loss in the absence of grazing to be measured. The turf was then placed in the aviary with the trial goose for up to 10 min. During this time, a video recorder, placed outside the aviary was set to record the activity of the focal goose. At the end of the feeding trial, the turf was removed, weighed, and placed in the empty aviary for another 10 min before re-weighing. The average evaporative weight loss from the 2 periods either side of the feeding trial was subtracted from the total weight loss during the trial to derive the biomass removed from the turf by the feeding goose. This procedure was repeated for each goose with turfs of similar sward heights. Usually, each goose would undergo 2 trials each day, with 2 different sward heights. All geese were presented with a similar range of sward heights each day. Feeding trials usually finished at between 15:00 and 17:00. After the end of the day's trials, pellet food was returned to the aviaries.

At the end of the feeding trial period, all geese were sexed and had their bill lengths measured to the nearest 0.1 mm using dial calipers. Bill length was measured from the tip of the bill to the start of feathers on the upper mandible (culmen length). The geese were then released back into the captive flock.

There were slight differences in experimental design between the 2 periods (1999 and 2001). In the first period, the geese were held within chicken wire enclosures in a 3 × 2 design, whereas in the second, they were placed in a row of 6 permanent outdoor aviaries. The turfs used in the 2 periods were sourced from different locations. The turfs in the first period were dominated by *Poa spp.*, with a low proportion of *Lolium perenne*, and were 40 × 15 cm; whereas the turfs from the second period were from mature grass leys with a greater proportion of *L. perenne*, and were 20 × 20 cm. The turfs in the first experiment ranged in sward height from 4.0 to 20.0 cm (median 11.5 cm), and in the second they ranged from 1.5 to 23.0 cm (median 8.5 cm). These sward heights covered the range experienced by wild barnacle geese (Cope, 2003).

The videos were used to count the number of pecks taken from the turfs during the feeding trials. The bite size (g fresh weight intake per peck) was then calculated by measuring the change in biomass over a trial, controlling for estimated evaporative loss, divided by the number of pecks observed from the video.

Bite size analyses

Seven geese were used in the feeding trials (3 in the first period, 4 in the second). There were 5 more geese that were initially intended to be used for this study; however, they were either removed during the feeding trials due to poor health, or did not have the required biometric measurements taken. In order for a trial to be included in analysis, more than 10 bites had to be taken from the turf in 10 min. In trials with <10 bites, average evaporative weight loss (0.90 g) was greater than the estimated biomass cropped from the turf (0.77 g), suggesting a high degree of error in estimates of bite size. In total, 112 trials attained the criteria for inclusion in the analysis.

To test the hypotheses concerning the scaling of bite size, bill length, sward height and bite size were \log_{10} transformed and analysed using linear regression models. Repeated observations from the same individual are not statistically independent of one another, so we used hierarchical generalized linear mixed models (GLMMs), which allowed us to use repeated observations from the same goose (Goldstein, 1995). In this case the data were structured so that repeated trials (level 1, $n = 112$) were nested within each individual (level 2, $n = 7$) as random effects. The number of trials undertaken by each individual was not equal, making the analysis unbalanced. However, GLMMs are robust to unbalanced data (Rasbash *et al.*, 2000). Models were fitted using MLwiN v2.1a (Rasbash *et al.*, 2000). The relationship between bite size (BS) and the explanatory variables (fixed effects), namely sward height (S), bill length (BL) and the experimental period (P), was modelled as:

$$\begin{aligned} \log_{10}(\text{BS})_{ij} = & \beta_{0ij} + a. \log_{10}(\text{S}) + b. \log_{10}(\text{BL}) \\ & + c. \log_{10}(\text{S}) \times \log_{10}(\text{BL}) + d. \text{P} + f. \text{P} \\ & \times \log_{10}(\text{S}) + g. \text{P} \times \log_{10}(\text{BL}) + u_j + e_{ij} \end{aligned}$$

Where a and b are the scaling exponents for the relationships between bite size and sward height and bite size and bill length respectively; β_{0ij} is the intercept, c describes the interaction between bill length and sward height and d , f and g are the fixed effects of the experimental period and its interactions with sward height and bill length; and u_j and e_{ij} are the random effects accounting for each goose and repeated trials on each goose respectively. The significance of each term was assessed using the Wald statistic, which approximates to the χ^2 distribution. Non-significant terms were removed from the full model in a stepwise procedure until the most parsimonious model was found.

Body size in the wild

Between 1991 and 1996, wild barnacle geese were captured, measured and ringed at breeding colonies in Svalbard (78° N 15° E). Over 1400 adult barnacle geese were rounded up during the post-breeding moult, at which

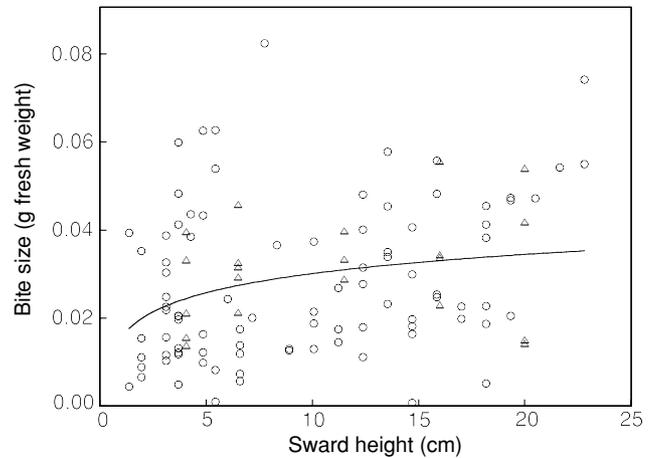


Fig. 1. Bite size of barnacle geese *Branta leucopsis* was not found to vary significant with sward height ($P = 0.062$). Each point shows bite size (untransformed), per trial, against the relevant sward height (untransformed). Open triangles = period 1 (1999), open circles = period 2 (2001). The line is a \log_{10} regression fit to all the data for illustration.

time they are flightless. Body mass was measured to the nearest 1 g, and bill length was measured to the nearest 0.1 mm. Bill length measurements and body mass measurements were \log_{10} transformed. A linear regression was conducted on these \log_{10} transformed data, with the expectation that the slope would equal 0.33 due to the relationship between linear and volumetric measures.

RESULTS

The density of grass tillers on the turfs used in the first period did not vary with sward height (parameter estimate = 0.0039, SE = 0.0051, $n = 50$, $t = 0.77$, NS), and the mean tiller density was 0.84 cm^{-2} (SE = 0.03). Tiller density was not measured in the second period; however, there were no significant differences in the bite sizes measured between the two periods (Wald $\chi^2 = 1.936$, NS). The interactions of trial period with the sward height and bill length terms were also not significant (Wald $\chi^2 = 0.023$ and 0.418 respectively, both NS). The lack of any difference in the results between the two periods suggests that the differences in design did not affect the results.

Prior to the fitting of the fixed effects, we found that the variance in our response variable (\log_{10} bite size) was split evenly between the two random effects, namely between observations within individuals (0.058 ± 0.008) and between individuals (0.050 ± 0.029). Fitting the fixed effects showed that bite size was not significantly affected by sward height (Wald $\chi^2 = 3.466$, $P = 0.062$, $a = 0.134$, SE = 0.072, 1-tailed $t = 1.86$ for greater than 0.00, NS, Fig. 1). Bill length was a highly significant determinant of bite size (Wald $\chi^2 = 48.386$, $P < 0.0001$), however, the

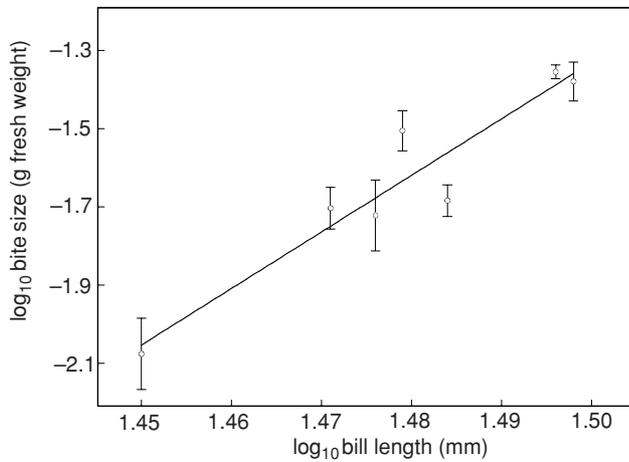


Fig. 2. The relationship between the \log_{10} transformed bite size of barnacle geese *Branta leucopsis* and the \log_{10} transformed bill length. Each point is from one individual, and shows the mean and standard error of the observed bite size measured over repeated trials. The line is a linear regression run through all data points collected from 112 valid trials for illustration. The slope of this relationship, derived from the multilevel analysis, is 14.24, indicating that intake per bite scales as bill length^{14.24}.

scaling exponent of bite size to bill length was much larger than expected ($b = 14.240$, $SE = 2.047$, 2-tailed $t = 5.49$ for a difference from 3.0, $P < 0.0001$, Fig. 2). The interaction between sward height and bill length was not significant (Wald $\chi^2 = 0.024$, NS).

Five of the seven geese used in the trials were male. Male barnacle geese are known to be larger than females, by 14% in body mass (Choudhury, Black & Owen, 1996), and 3% in bill length (Cramp & Simmons, 1984). Sex was included in the model, replacing bill length, and was found to be significant (Wald $\chi^2 = 6.749$, $P < 0.01$). However, sex dropped from significance when the bill-length term was added to the same model, indicating that bill length was a better explanatory variable than sex.

The most parsimonious model was therefore:

$$\log_{10}(\text{BS}) = -22.83 + 14.24 \times \log_{10}(\text{BL}).$$

The linear regression between \log_{10} bill length and \log_{10} body mass showed that the exponent of the relationship differed significantly from the expected value of 0.33 (parameter estimate = 0.21, $SE = 0.01$, 2-tailed $t = 9.83$ for a difference from 0.33, $P < 0.0001$). This indicates that bill length increases more slowly than expected as barnacle goose body mass increases.

DISCUSSION

The bite size of barnacle geese was not found to vary with sward height in this study (Fig. 1). This result is somewhat surprising, especially given that the trials covered the full range of sward heights that are observed in the wild

(Cope, 2003). Other workers have found an asymptotic relationship between sward height and bite size in barnacle geese (Lang & Black, 2001; Durant *et al.*, 2003), but in our study the result failed to attain significance ($P = 0.062$). On the other hand, we found that there was a large inter-individual variation in bite size, which was explained by variation in bill length between individuals.

In our study, bite size increased as $(\text{BL})^{14.24}$, rather than the expected $(\text{BL})^3$ (Fig. 2). The large disparity between the expected and the observed scaling may be due to one of two reasons. Firstly, because data from only seven geese were used in these trials, random variation in individual foraging efficiency could have caused the observed scaling. However, this seems unlikely as the results were found to be consistent even when the data were split into the two periods by including the trial period in the analysis, which suggests that the relationship is robust. The second possibility is that the observed scaling represents the real scaling, but that our predictions were overly simple. Grazing techniques differ between species of goose, from vertical pecking (e.g. barnacle geese) to horizontal scything of the sward (e.g. greylag geese *Anser anser*), and it may be possible that subtle differences in grazing technique occur between individuals of different sizes within a species. Bite mechanics may also vary with bill length between individuals: the angle of the gape may increase with bill length, or the muscles used to provide the bite strength may increase with bill length. Brain mass is known to be directly proportional to bill length in other waterfowl (Gille & Salomon, 1999), suggesting that barnacle geese with larger bills will have larger brains also. Therefore, the high scaling exponent of bill length to bite size may be due to larger geese having a higher mental capability for foraging efficiently.

No interaction between \log_{10} sward height and \log_{10} bill length was found, demonstrating that bite size is larger for geese with longer bills over the full range of sward heights. Consequently, if individual barnacle geese with shorter bills always have a smaller bite size, they may be expected to be at a disadvantage relative to others with larger bills. In a study on soay sheep, Illius *et al.* (1995) suggested that small mouthparts may be advantageous in being able to select better quality bites from a heterogeneous sward. This explanation may also hold true for barnacle geese: shorter bill length may allow geese to select only those grass leaves that are young and highly nutritious, thus giving a balancing advantage to having a short bill. Furthermore, geese with smaller bills may be at an advantage in spring and summer, where optimal grazing has been shown to require considerable selectivity, often of very different food types to grass (Prop & Black, 1989). Smaller bites will lead to higher bite rates (Spalinger & Hobbs, 1992), possibly resulting in equal intakes for large and small geese (Durant *et al.*, 2003). This possibility could also remove the advantage that large geese have over smaller ones. In this study, bite rates were not measured as the geese pecked at the trial turfs in short bouts, rather than in a consistent manner over the observation period.

In the analysis of over 1400 measurements of wild barnacle geese on Svalbard, bill length (a linear measure) was found to scale with body size (a three-dimensional measure), not as expected with an exponent of 0.33, but at a slower rate of 0.21. Taking the observed scaling of bite size with bill length, and of bill length with body mass, we expect that bite size scales with body mass with an exponent of $14.24 \times 0.21 = 2.99$, i.e. bite size \propto (body mass)^{2.99}. There is debate in the literature about the scaling of energy requirements with body mass (Schmidt-Nielsen, 1984; Nevill, 1994; Dodds, Rothman & Weitz, 2001; White & Seymour, 2003), especially as the observed scaling of body size to energy needs may be higher when measured within species than when measured between species (e.g. Kvist & Lindström, 2001 in migratory wading birds). If bite size, and therefore instantaneous intake rate, in barnacle geese scales with (body mass)^{2.99}, then we can draw three possible inferences. Firstly, energy requirements may scale intraspecifically with (body mass)^{2.99}, which is plausible if the changes in body mass are disproportionately due to changes in muscle mass, due to the high energy requirements of muscle. Secondly, energy requirements increase at a slower rate than as (body mass)^{2.99}, and larger geese can therefore spend less time in feeding, and more time in other activities. Thirdly, energy requirements may increase at a slower rate than as (body mass)^{2.99}, and the extra food that is consumed allows larger geese to put on additional fat stores. In a study of migrating barnacle geese, Butler *et al.* (1998) showed that oxygen consumption increased as (body mass)^{1.46}, suggesting that energy requirements scaled at a slower rate than (body mass)^{2.99}. This suggests that either the second or third inferences outlined above would be most likely: larger barnacle geese may be able to spend more time in activities other than feeding than smaller barnacle geese, or better able to accumulate body fat than smaller barnacle geese.

The conclusions of this study are that larger barnacle geese are at an advantage over smaller barnacle geese in terms of their biomass intake because they have larger bills, enabling them to take larger bites that overcompensate for increasing energy requirements. In food-limited conditions, it is therefore expected that larger barnacle geese would have a higher probability of survival and breeding than smaller geese. This scaling of bite size with body size provides a plausible mechanism for the observed positive relationship between female body size and clutch size, egg weight and gosling size (Larsson *et al.*, 1998) and female body size and recruitment (Choudhury *et al.*, 1996) in wild barnacle geese. These studies predicted a selection pressure for increased body size, which has, however, not been observed, probably due to density-dependent food restriction at breeding colonies constraining the heritability of body size to offspring (Black *et al.*, 1998). The results of our study lead us to suggest that breeding success and survival should be studied in relation to bill length as well as body size in barnacle geese. Whilst we have concluded that longer bills could be advantageous for barnacle geese, we believe that

there will be costs associated with having longer bills (such as reduced ability to select nutritious plant parts) that may lead to balancing selection on bill length in barnacle geese.

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