Foraging efficiency in Barnacle Geese *Branta leucopsis*: a functional response to sward height and an analysis of sources of individual variation

A. Lang[1,2] & J. M. Black[3]

[1]Centre for Behavioural Biology, School of Biological Sciences, University of Bristol, Woodland Road, Bristol, BS8 1UG, U.K. Email: alison@burbleland.com
[2]Institute of Zoology, Zoological Society of London, Regent's Park, London NW1 4RY, UK
[3]Department of Wildlife, Humboldt State University, Arcata, California, 95521, U.S.A.

The functional response and variation in foraging efficiency of captive Barnacle Geese was measured on pasture sward. Intake rates were calculated for a range of grass sward heights using direct measurements of peck rate, bite height and number of leaves removed with each bite. The functional response was found to be curved reaching a maximum at 85mm and then declining. Each of the three components of intake rate responded differently to sward height. Peck rate declined steadily with increasing sward height whereas bite height increased throughout the sward heights used. The number of leaves per bite showed a curved response to sward height, increasing to a maximum at sward height of 90 mm then declining. There were significant differences between individuals for bite height and leaves taken per bite. Multiple regression analysis using age, sex, body size and bill size found that 73% of the variation in leaves taken per bite could be explained by the age of the goose, where more leaves were taken per bite by older geese. The results are discussed in relation to other studies on geese foraging on salt-marsh sward and other grazers foraging on pasture.

Key Words: herbivory, grazing efficiency, *Branta leucopsis*.

There is a long history of research on the relationship between food intake rate and some measure of food availability (known as the functional response (Solomon 1949)). Recent studies of the functional response have been central to the development of detailed population models to assist with the development of effective management strategies (eg Armstrong *et al.* 1997). Typically, an animal's food intake rate increases with increasing food availability until a plateau is reached at which point food processing ability prevents further increase (Holling 1965). In herbivores food intake rates are frequently related to plant standing crop, which is the above-ground dry weight (Crawley 1983). Grazing by sheep, goats and cattle has been extensively studied on pasture. In a homogeneous sward, intake rate has been found to be closely related to sward height (Allden & Whittaker 1970; Jamieson & Hodgson 1979; Black & Kenney 1984; Illius *et al.* 1992; Gordon *et al.* 1996). Studies on sheep also found that individual variation in intake rates could be, in part, explained by variation in the size and shape of the dental arcade (Gordon *et al.* 1996). Indeed, there is evidence of a link between incisor arcade and survival in a population of Soay Sheep during a population crash (Illius *et al.* 1995).

In birds, variation in foraging efficiency has mainly been studied in relation to age classes (Greig *et al.* 1983; Sutherland *et al.* 1986; Draulens 1987; Goss-Custard & Durrell 1987; Jansen 1990). In these examples, juveniles typically took longer to locate prey or made more unsuccessful attempts at catching prey. In a repeated measures study, Desrochers (1992) found that the foraging efficiency of individual European Blackbirds increased as they aged. This increase could, in part, be explained by an increase in bill size, but was thought to be primarily due to increased detection and handling skills.

Van der Wal *et al.* (1998) estimated intake rates for semi-captive Barnacle Geese *Branta leucopsis* feeding on the salt-marsh that is used in winter by the Siberian population of Barnacle Geese. Using a combination of peck rates and dropping rates they found that short term intake rates for pairs of geese were lowest at high plant standing crop and suggested that at high standing crop the increased dead material in the sward might cause a decreased intake rate. It is possible to measure intake rates for geese feeding on grass sward directly, but it is necessary to measure several components. Geese remove grass with each peck of the sward, and can make as many as 300 pecks per minute. With each peck a variable height of a grass tiller is removed (here termed bite height), and a goose may remove several tillers with one bite. The product of these three components gives the estimate of intake rate. This direct method of estimating intake rates is very difficult in the field because each tiller must be measured repeatedly and practise is necessary to count the high peck rates. Prop *et al.* (1998) used this method on the spring staging area of the Svalbard population of Barnacle Geese and found that total intake increased with shoot size (the summed height of all tillers). Prop & Deerenberg (1991) and Black *et al.* (1994) also used this method in the field. The effect of sward height on individual intake components has also been measured in the field. In studies on the wintering grounds of Barnacle Geese, peck rates increased as biomass decreased during winter (Owen *et al.* 1992) and increased with decreasing grass height (Black *et al.* 1992).

In this study we investigate how Barnacle Goose intake rates are affected by sward height of the sample turfs from the winter pasture that the Wildfowl & Wetlands Trust (WWT) reserve at Caerlaverock, Scotland, manage specifically for the geese (Owen *et al.* 1987). Three components of intake rate (peck rate, bite height and leaves taken per bite) were measured directly to try to detect the mechanism of the functional response to a homogeneous sward. How these components vary between individuals and whether variation between individuals can be explained by goose sex, age, body size or bill size, is investigated.

Methods

Preparation

Turfs measuring approximately 30 by 40 cm were cut from two fields at the WWT reserve at Caerlaverock in July 1996 and transported to the WWT centre at Slimbridge. The grass was mowed short then allowed to grow to the required height, measured using a foam disc sward stick. This method of regrowth was used to limit the effects of the mowing on the grass structure. The vast majority of the grass in the sward was perennial ryegrass, *Lolium perenne* (>95%) and so only shoots of this species were included in the trials. The number of perennial ryegrass shoots in 30 cm^{-2} of each turf were counted so that any variation in sward density could be accounted for in the analyses.

Thirty Barnacle Geese from the Slimbridge semi-captive flock were caught during the moult when they were unable to fly. This flock was established in the early 1960's from several wild pairs (see Black & Owen 1987 for details). The geese were colour ringed, sexed, measured and then released into a large holding pen with grass, pelleted food and running water.

Trial format

The day before each trial the leaves of 60 shoots on each of three sample turfs were measured and individually marked using small numbered wire markers. The pair or trio of geese to be used in a trial were herded quietly into the trial pen and allowed to settle with unlimited pelleted food and water for a minimum of two hours, then the food was removed for the night (see **Figure 1** for pen layout).

Immediately before each trial one pair or trio were herded into the observation half of the trial pen from where the geese could be observed and videoed from a hide less than 1 m away. The sward height was measured and then the turf was placed into the trial pen. Each trial was recorded on video. All marked shoots were re-measured immediately after the trial.

Foraging Measurements

1: Peck rates.

The number of pecks each individual took in continuous foraging bouts were counted from the video. The average peck rate was calculated from all foraging bouts.

2: Bite height.

The bite height was calculated as the original height when the turfs were marked, minus the new height after the trial, plus the average growth rate calculated from unbitten shoots.

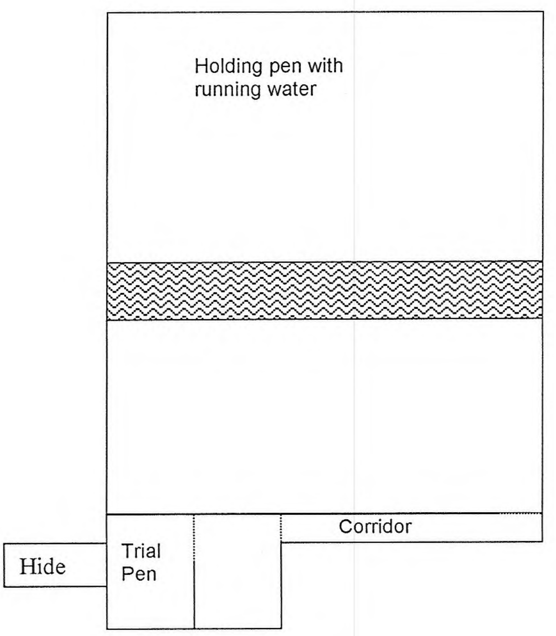

Figure 1 Diagram of the pen layout for the foraging trials. The flock remained in the holding pen (approx. 12 m x 10 m) until required for trials. The geese used in a trial were herded along the corridor into the trial pen (approx. 3 m x 4 m). The test turf was placed in the left trial pen as the trial began. Observations were made from the hide.

3: Number of leaves per bite.
Immediately after the trial the turf was examined for individual bite marks and the number of leaves taken in each bite recorded. This method was checked by counting the number of pecks made in a specially marked area of turf and comparing that to the number of leaves taken in the area. The second method is less subjective, but only rarely did the geese take a single bite from the required area. The method of bite measurement was adapted from Prop & Deerenberg (1991).

Functional response

Because these height trials took several days to complete and involved repeated disturbance, only one trio of captive geese were used. Peck rate, bite size and leaves per bite were recorded for a range of grass heights from 4 to 12 cm. Only two geese provided sufficient data for analysis. Mean values for each parameter were calculated and used in regression analyses.

Individual variation

When the geese were first caught measurements of skull, tarsus, culmen, gape, nares and bill depth were made using Vernier callipers to the nearest 0.01 cm (definition of parameters taken from Dzubin & Cooch (1992)). Because biometric data is usually highly correlated, the data were analysed using principal components analysis to provide one estimate of body size and one estimate of bill size.

Over a period of several weeks the foraging performance of all 30 geese was recorded, with each goose foraging on several sample turfs.

Results

Sward details

Analysis of variance showed that there was no significant difference in the perennial ryegrass shoot density between the two fields, $F_{1,19}$=2.36, P=0.141. The overall average shoot density was 12,666 shoots m^{-2}.

Functional response

The mean values for each component of intake rate for each individual at each sward height were used in regression analyses. Bite height was found to increase linearly with sward height (R^2=0.78, $F_{1,10}$=39.48, P<0.001), peck rate decreased linearly with sward height (R^2=0.79, $F_{2,11}$=20.77, P<0.001) and the number of leaves taken per bite increased with increasing sward height until around 90 mm above which there was a decline (R^2=0.74, $F_{2,10}$=14.52, P=0.001). The data and lines of best fit are shown in **Figure 2**. There were only significant differences between birds for the peck rate component. Combining the bite height and leaves per bite for each individual at each height gives the bite size at each sward height **Figure 3**. The plot and regression analysis show that the amount of grass a goose can take in one peck increases with increasing sward height

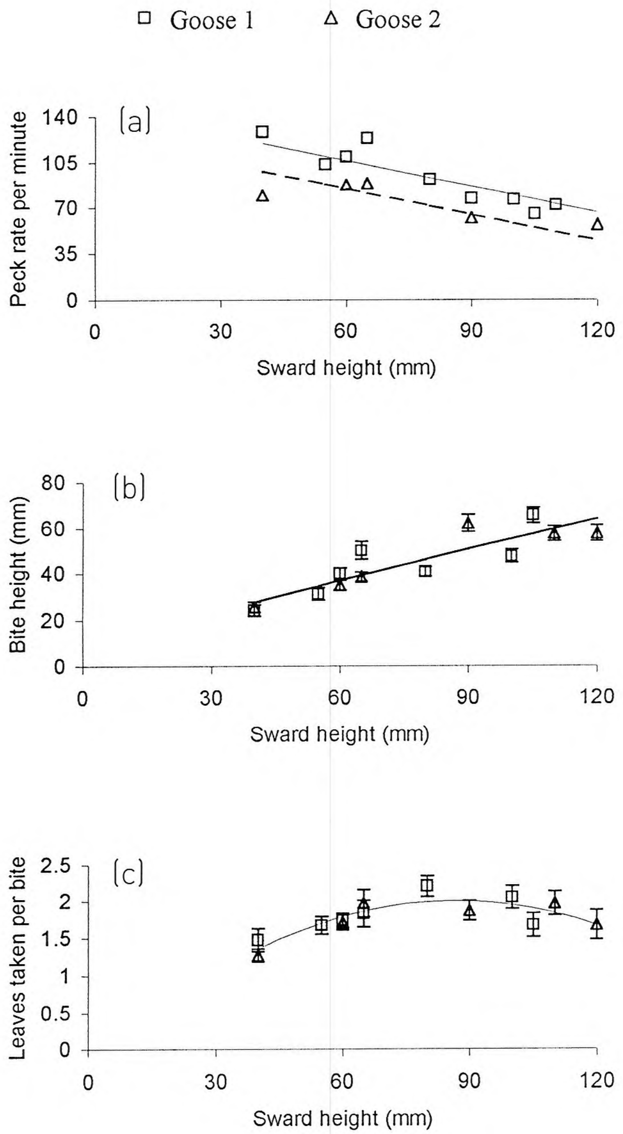

Figure 2. Variation in the components of intake rate with sward height. (a) Peck rate decreased linearly with sward height, more so for goose two (peck rate=146-0.665 x sward height-21.3 x goose; n=14, R^2=0.79, $F_{2,11}$=20.77, P<0.001). (b) Bite height increased linearly with sward height (bite height=9.78+0.455 x sward height; n=13, R^2=0.78, $F_{1,10}$=39.48, P<0.001). (c) The number of leaves taken per bite increased with increasing sward height until around 85 mm above which there was a decline (leaves= -0.262 + 0.0524 x sward height -0.000303x(sward height)^2; n=13, R^2=0.74, $F_{2,10}$=14.52, P=0.001). Mean values are plotted with standard error bars on bite height and number of leaves taken per bite.

to an asymptote above sward heights of 85mm (R^2=0.92, $F_{2,10}$=54.14, P<0.001). The mean values were then combined for all components to give an estimate of intake rate in mm.min^{-1} for each individual at each sward height (**Figure 3b**). Intake rate increases with increasing sward height until around 80 mm above which the rate declined (R^2=0.57, $F_{2,9}$=5.87, P=0.023).

Individual variation

Two principal components analyses using covariance matrices were performed using the biometric measurements taken of individual geese. A principal component incorporating the tarsus length and skull size that explained 84% of the variation between individuals was used as a general size parameter (0.857 x tarsus

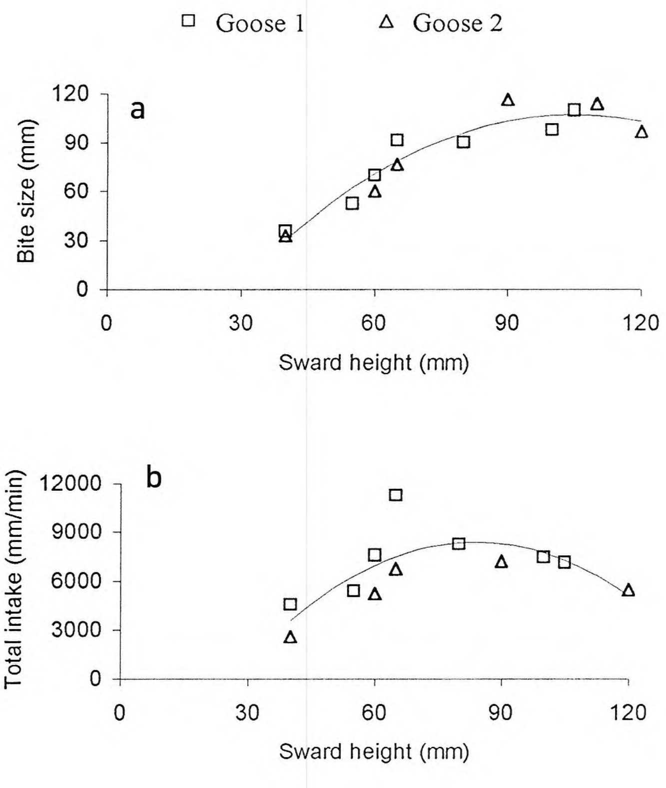

Figure 3. (a) The average bite size of the geese increased with increasing sward height to an asymptote around 80 mm (bite size=-93.3+3.83 x sward height-0.0183 x (sward height)^2; n=13, R^2=0.92, $F_{2,10}$=54.14, P<0.001). (b) The average intake rate of the geese appears to decline above 80 mm (intake=-8986+414 x sward height-2.47 x (sward height)^2; n=12, R^2=0.57, $F_{2,9}$=5.87, P=0.023).

+0.516 x skull). A second bill size parameter incorporated the remaining measurements and explained 57% of the variation (0.476 x culmen 1+0.668 x gape+0.547 x nares+0.165 x bill depth).

There were no significant within-goose differences for repeated trials and so data for each individual from several trials were combined. Analyses were only performed for individuals with more than a minimum number of samples (50 pecks rate measurements, 20 bite height measurements, 20 leaves per bite measurements). Analysis of variance showed that both the average number of leaves taken with each bite and the bite height varied significantly between individuals (**Figure 4**). **Table 1** gives a summary of the average value across individuals for each intake component. Generalised linear models were then used to investigate how the mean values for each component of intake varied with age, sex, body size and bill size, together with interaction terms. A summary of the statistics from the basic model for each component of intake is given in **Table 2**. The only significant model was of age predicting the number of leaves removed with each bite (**Figure 5**, R^2=0.73, $F_{1,14}$=37.72, P<0.001). No significant

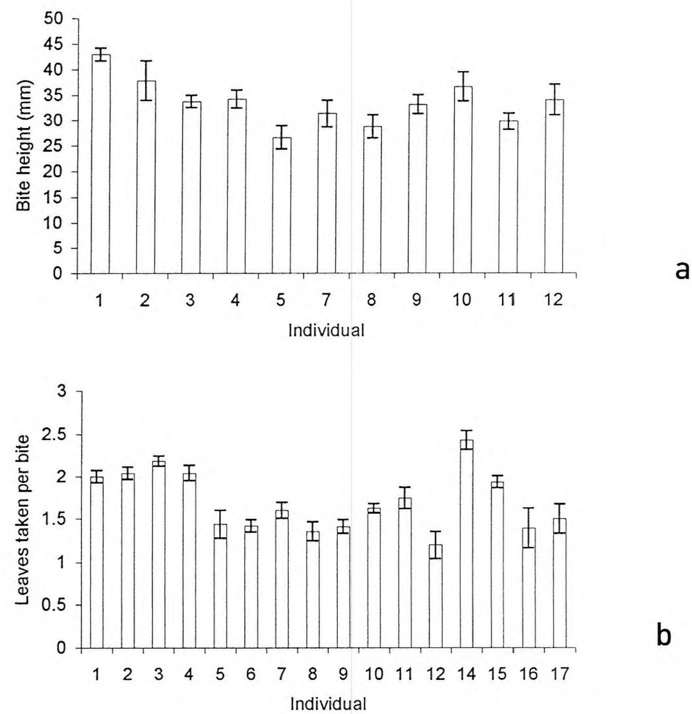

Figure 4. Two components of intake varied significantly between individuals: a) mean leaves taken per bite (n=17, $F_{15,893}$=10.16, P<0.001) and b) mean bite height (n=12, $F_{10,712}$=7.2, P<0.001). Bars indicate the standard error of the mean.

Table 1. Summary of results from variation between individuals trials.

	mean	SEM	n
Leaves taken per bite	1.7	0.4	16
Bite height (mm)	34	1.38	11
Peck rate (pecks/min)	104	4.91	14

Table 2. Summary of multiple regression statistics for the variation between individuals trials.

	Predictor	Coefficient	*t*	*P*
Mean peck rate	Constant	-338.5	-0.34	0.737
	Sex	48.91	0.6	0.557
	Age	6.113	1.31	0.214
	Body Size	16.06	1.59	0.139
	Bill Size	-25.13	-1.36	0.2
Mean bite size	Constant	31.51	0.78	0.463
	Sex	-2.377	-0.58	0.585
	Age	0.36	1.49	0.186
	Body Size	0.387	0.77	0.471
	Bill Size	-0.713	-0.82	0.441
Mean number of leaves	Constant	3.903	2.58	0.026
	Sex	-0.0652	-0.59	0.568
	Age	0.0519	6.32	0
	Body Size	-0.0196	-1.74	0.109
	Bill Size	-0.0038	-0.14	0.895

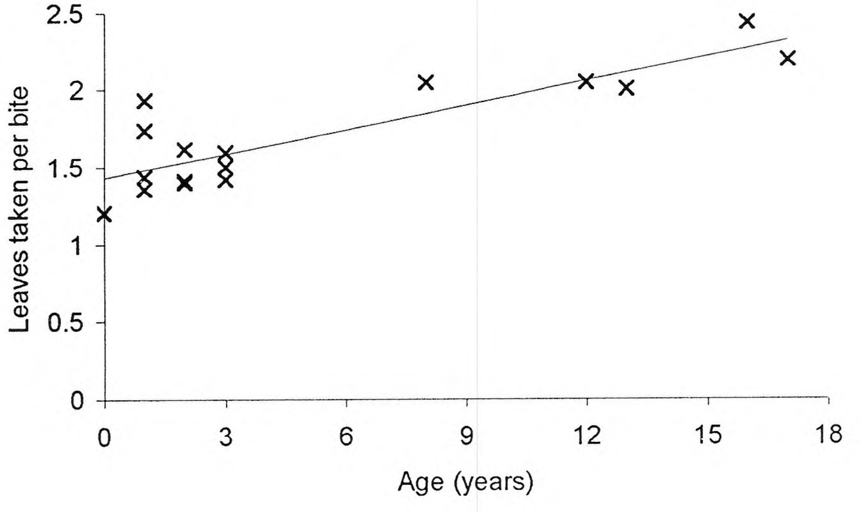

Figure 5. The mean number of leaves taken per bite increases with increasing age (mean leaves=1.43 +0.052 x age, n=16, R^2=0.73, $F_{1,14}$=37.72, P<0.001).

relationship was found between the intake rate components and the goose biometrics or sex.

Discussion

The results presented in this paper show the intake rates of the geese increased with increasing sward height to a maximum at swards of 85mm, then declining at higher sward heights. The components of intake rate that were measured each showed different variation with increasing sward height. Bite height increased throughout the sward heights used whereas leaves taken per bite decreased at the highest sward heights. The result is that bite size increases to an asymptote which when combined with a decreasing peck rate gives the observed decreasing intake rate at high sward heights. These findings correspond to similar results from experiments on sheep, goats and cattle. Several studies have found that bite depth (similar to bite height used in goose studies) increased (Milne *et al.* 1982; Barthram & Grant 1984; Burlison *et al.* 1991; Laca *et al.* 1992; Flores *et al.* 1993; Gordon *et al.* 1996) whereas bite rate declined with sward height (Black & Kenney 1984; Gross *et al.* 1993; Gordon *et al.* 1996). However, the method of feeding is very different in geese compared to mammalian grazers. The bill allows the goose to scythe grass from the side, rather than biting from above. It appears that at very low sward heights the geese have difficulty gathering more than one leaf in a single bite and so rely on a high peck rate. At intermediate sward heights the geese take more time to gather leaves together in one bite and so peck slowly. At high sward heights a single bite takes several chews to ingest leaves that are longer than the bill and so peck rate declines further: the average bill depth of the geese was 20 mm and yet they were removing up to 70 mm total grass in one bite by taking more than one leaf per bite. The difference in feeding method between geese and mammalian grazers could explain why the individual variation in bill size was not found to be related to individual variation in foraging performance. Rather than the physical size of the bill determining the amount of food in one bite, it appears that it is the increased ability of older geese to gather several leaves at once, which enhances their foraging performance. This explanation for the functional response observed assumes that the geese were maximising their intake rate throughout the trial and so peck rates decreased as a mechanistic response to long grass rather than to maintain a certain level of intake. This seems reasonable because the feeding times of the trials were short.

There are several limitations to the generality of the current study. Firstly, a functional response was generated from two geese. Unfortunately, because of the frequent disturbance necessary to complete this trial only captive geese could be used. Secondly, the specific functional response is also likely to be a function of the homogeneity of the grass sward used in the trial. Sheep trials have shown that altering the density of the sward can significantly alter the point at which intake asymptotes (Black & Kenney 1984) and this is likely to be the case in goose foraging because in dense swards the geese can take more than one leaf per bite.

As with the study by van der Wal *et al.* (1998), our results suggest that the 'best' habitat, in terms of maximizing intake rate, may not always be the habitat with the highest food availability. In the trial, geese achieved optimal intake rates when foraging on swards of between 60 mm-105 mm in height, peaking at 85 mm. Above 105 mm and below 60 mm, intake rates were much reduced. If geese choose their food based on a minimum achievable intake rate (see Ebbinge *et al.* 1975; Drent *et al.* 1979; Owen & Black 1990), they may avoid pastures with tall grass for the same reason they avoid pastures with short grass - sub-optimal intake rates. In addition, taller grass is also known to contain less protein and to be less digestible due to an increase in the amount of phenolic compounds, and dead material (Black *et al.* 1991; Fox 1993; Prop & de Vries 1993; Prop & Vulink 1992). Geese probably favour actively growing swards of intermediate height because they provide nutrients that are easily acquired and digested (*sensu* Owen 1975, 1979).

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