AVIAN HERBIVORY: AN EXPERIMENT, A FIELD TEST, AND AN ALLOMETRIC COMPARISON WITH MAMMALS

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Abstract. Mechanistic studies on herbivore functional responses have largely taken place in mammals; very little has been done in herbivorous birds so far. Here we aim to fill that gap by experimentally quantifying the (short-term) functional response of a large avian herbivore, the Bewick's Swan (*Cygnus columbianus bewickii*). We explicitly distinguish between encounter-limited and handling-limited foraging by analyzing the results in the framework of the models of D. E. Spalinger and N. T. Hobbs, originally developed for mammalian herbivory. Bite size in captive swans was experimentally manipulated by varying sward height. The time interval between two bites increased with bite size, which supports the handling-limited model (process 3) and rejects the encounter-limited models (processes 1 and 2). Subsequently, we took the obtained functional response parameters into the field in order to predict, from measurements of sward height, (1) bite sizes, (2) handling times, and (3) short-term intake rates in free-ranging swans. Indeed, for all three variables, the observed values closely matched the experimentally based predictions. Finally, we review functional response parameters available in the literature on avian herbivores and scale them allometrically in relation to mammals. This analysis revealed that maximum bite sizes, and therefore maximum intake rates, in herbivorous birds are smaller than in herbivorous mammals. We hypothesize and provide evidence that birds compensate by longer daily foraging times.

Key words: allometry; Bewick's Swan; bite size; chewing; cropping; *Cygnus columbianus bewickii*; foraging; functional response; grazing; handling time; herbivory; intake rate.

INTRODUCTION

The relation between a forager's intake rate and its food supply (i.e., the functional response) plays a central role in population ecology (e.g., Vandermeer and Goldberg 2003). Therefore, a basic understanding of factors controlling a forager's intake rate seems critical for progress in this field of science. Over the past decades, Holling's disk equation (Holling 1959) has been most influential in this respect (Jeschke et al. 2002). In this short-term functional response model (i.e., dealing explicitly with the constraints acting while foraging; Bergman et al. 2001), a forager alternates between searching for food and handling food (two mutually exclusive activities), yielding a Type II functional response (Holling 1966) in which intake rate increases asymptotically with food abundance. In spite of such

simplified assumptions that seem to be specific for true predators feeding on discrete prey items, the model not only fits intake rates of predators (e.g., Piersma et al. 1995), but often fits short-term intake rates of herbivorous consumers as well (e.g., Augustine et al. 1998, Nolet et al. 2001). However, as pointed out and explored by Spalinger and Hobbs (1992), several alternative mechanisms, other than the trade-off between searching and handling, could account for Type II functional responses seen so often in herbivores.

Central in the herbivore models developed by Spalinger and Hobbs (1992) is the decomposition of handling time into two sequential stages that are typical for herbivorous foraging: cropping (i.e., the act biting off plant tissue) and chewing (i.e., the act of processing the bite in the mouth until swallowing it). These authors further assume that (1) cropping and chewing are mutually exclusive (a mouth can only perform one function at any given time; but see Ginnett and Demment 1995), (2) cropping slows down searching (but does not exclude it), and (3) chewing and searching are entirely non-mutually exclusive. Based on spatial and morphological characteristics of plants, these assumptions enabled Spalinger and Hobbs to distinguish three possible mechanisms applying to herbivore foraging. In process 1, herbivores feed on spatially dispersed, hidden plants and are therefore either searching or

Manuscript received 31 May 2006; revised 8 February 2007; accepted 20 February 2007. Corresponding Editor: B. P. Kotler.

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FIG. 1. A free-ranging Bewick's Swan taking a large bite of grass. The study was conducted in Heteren, The Netherlands. Photo credit: Paul Cools.

handling or doing both at the same time (due to this latter activity this process differs from Holling's disk equation). In process 2, herbivores feed on spatially dispersed, apparent plants and are therefore either moving toward a new bite or handling or doing both at the same time. In process 3, herbivores feed on spatially concentrated, apparent plants and are therefore always handling their bites.

Up to now, the models developed by Spalinger and Hobbs have mainly been tested and verified in mammalian herbivores, for which they were originally developed (e.g., Gross et al. 1993, Bradbury et al. 1996, Illius et al. 2002, Hobbs et al. 2003, Searle et al. 2005). However, as shown by Hewitt and Kirkpatrick (1996) and Durant et al. (2003), the models seem to apply to avian herbivory under experimental conditions as well. Whether they apply to free-ranging avian herbivores remains as yet untested, but seems highly probable. For example, free-ranging Brent Geese (*Branta bernicla*) feeding on respectively *Zostera* and *Plantago* showed Type II functional responses (Charman 1979, Prop 1991), which is highly suggestive. By mechanistically unraveling such responses, models on population dynamics of avian herbivores and their food resources, which in the past were often based on phenomenological asymptotic functional responses (Lang et al. 1998, Pettifor et al. 2000), could produce more realistic predictions. In addition, deviations from a Type II response, such as the "dome-shaped" functional response recently report-

ed in a range of relatively small avian herbivores (Van der Wal et al. 1998, Therkildsen and Madsen 2000, Lang and Black 2001, Bos et al. 2004), may be better understood in the light of the proposed competition between cropping and chewing on the one hand and between cropping and searching on the other.

In this paper, we focus on short-term or so-called instantaneous intake rates by explicitly distinguishing between the encounter-limited (process 1 and 2) and the handling-limited (process 3) Spalinger and Hobbs models in a large grass-eating avian herbivore, the Bewick's Swan (*Cygnus columbianus bewickii*; see Fig. 1 and Plate 1). We do so by experimentally manipulating bite size in captive swans (through varying sward height). Subsequently, we take the obtained functional response parameters into the field to see whether we can predict short-term intake rates in free-ranging swans from measurements of naturally available sward heights. Finally, we review functional response parameters available in the literature on avian herbivores and scale them allometrically in relation to mammals.

DISTINGUISHING ENCOUNTER-LIMITED FORAGING FROM HANDLING-LIMITED FORAGING

Because in the Spalinger-Hobbs models searching time (T_s) and handling time (T_h) can completely overlap (in contrast to the disk equation), foraging time T_f between two bites is simply determined by whichever activity takes longest:

FIG. 2. Sward height increases as a function of experimental treatment (time since mowing; $N = 23$ sample plots). These box-and-whisker plots give mean (circle), median (horizontal line within box), interquartile range (box), and range (bars). The line gives the generalized linear model regression.

$$T_f = \max(T_s, T_h). \quad (1)$$

An increase in bite size S increases handling time linearly, but does not affect searching time. Therefore, a positive (and linear) correlation between T_f and S is diagnostic for process 3 foraging. According to Spalinger and Hobbs, handling time T_h is affected by S in the following manner:

$$T_h = T_c + T_p = T_c + \frac{S}{R_{\max}} \quad (2)$$

where T_c is cropping time, T_p is processing (chewing) time, and $R_{\max}$ is the maximum rate of chewing (which would occur in the absence of cropping). Therefore, if process 3 holds, plotting T_f as a function of S yields an estimate of T_c (intercept) and $R_{\max}$ (inverse of the slope).

MATERIAL AND METHODS

Experimental design

In a grassland field at the Centre for Terrestrial Ecology, Netherlands Institute of Ecology, Heteren, The Netherlands, we created a mosaic of 24 plots (10×10 m each), in which we manipulated sward height into six categories, leading to a one-factor design with four replicates. Going from short to tall grass, a plot was used 1, 4, 8, 12, 16, or 20 days after it was mowed (Fig. 2). The spatial alignment of this mowing scheme followed a randomized block design, with four blocks of each six plots. Each plot was only used for a single trial, leading to 24 trials in total.

Six captive Bewick's Swans were used in this experiment (all adults; three of them were wild-caught [two males, one female]; the other three were born in captivity [one male, two females]). In each trial, the birds

were grouped into three pairs (pair 1, containing individuals AN and BD; pair 2, AP and AT; pair 3, BA and BB), each pair feeding at a fenced quarter of an experimental plot (leading to four subplots per plot, of which one served as a control subplot). Two pairs adjusted well to the daily protocol and fed normally within the experimental plots (pairs 1 and 3). Although pair 2 occasionally seemed less motivated to participate, we nevertheless maintained it in the analyses (but we will compare the results both with and without this pair). Furthermore, during one trial one of the pairs escaped (pair 3), causing anxiety among the other individuals, which is why this single trial was omitted from the analyses. Therefore, 23 trials remained for the analyses. We performed one trial per day, and each trial was recorded on video (digital video camera NV-GS15; Panasonic, Secaucus, New Jersey, USA).

As a check on our experimental treatments, we sampled sward height in the control subplot immediately after a trial had ended. We did so by measuring the length of individual plants to the nearest 0.5 cm at 10 randomly selected spots within the subplot. These measurements revealed that the manipulation of sward height worked out as originally planned (Fig. 2). As it turned out, the grass was apparently mowed down to a height of 6.1 ± 0.7 cm (intercept; mean $\pm$ SE) and grew about 0.5 ± 0.1 cm/d (slope). Henceforth, treatments differed by at least 1.6 cm from one another ($P < 0.00001$, $N = 23$; using the GLM-package in SYSTAT 10 [SYSTAT Software 2000]).

Experimental procedures

We performed trials from 07:30 to 11:00 hours four days per week (Tuesday–Friday). In order to keep the birds motivated to eat during the trials, they were given no additional food on trial days and on Mondays. Drinking water was always available. Only during weekends were they given extra food (a mixture of commercial food pellets [Natural Free Range Layer Pellets; HAVENS Graanhandel NV, Maashees, The Netherlands] and seed-based mixed grains [Van Havens Green-Line and Natural Scratching Grains; HAVENS Graanhandel NV]) in order to regain body mass lost during working days (birds were weighed daily). In order to prevent “post-weekend effects” in their feeding motivation, we never performed trials on Mondays, even though they were housed in the experimental arena on such days. During the weekend, the birds were kept pairwise in large aviaries ($5 \times 10 \times 3$ m) next to the experimental grass field.

The estimation of bite size required knowledge of the total fecal dry mass (DM) produced (see *Bite size, bite rate, and intake rate* for more details on that calculation). Therefore, we collected all droppings after each trial for each pair. This was done in two ways. (1) Directly after a trial, all droppings produced during a trial were collected from each subplot. (2) Since food retention is long in these large birds (up to 8 h; J. A. van

Gils and A. Gyimesi, *unpublished data*), the birds were kept pairwise without food for 10 h in small chambers ($1.5 \times 1 \times 1$ m), where droppings would fall through a wide mesh, allowing us to collect all droppings produced after each trial (but originating from the food intake during the trial). In spite of contending with such long retention times, we were sure all droppings originated from food intake during the 3.5-h trials only as the birds were given no other food on trial days.

Video analyses

In order to estimate interbite interval T_b , we timed each bite of each bird by replaying the videotapes using The Observer (Noldus Information Technology 1997). As we were interested in short-term intake rates during foraging bouts only, we discarded intervals between two successive bites that were due to non-feeding activities such as resting, preening, drinking, vigilance, or having social interactions. Because of the amount of video material to analyze (23 trials with six birds each trial, leading to 483 h of observations), we only analyzed one quarter of each trial. In order to spread this selection across the entire trial, we analyzed each first minute in a block of four minutes. On average, we obtained estimates for 1381 ± 89 (mean $\pm$ SE) suitable interbite intervals per pair per trial.

Field observations

During three winters (2003–2004, 2004–2005, and 2005–2006), from mid-November to mid-March, we observed foraging behavior of free-living Bewick's Swans in grasslands just north of Amersfoort, The Netherlands (Polder Arkemheen and Polder Zeldert; $52^\circ 14'$ N and $5^\circ 25'$ E). Observations were made from a car at a distance of 40–300 m using a 20–60 $\times$ spotting scope (Kowa, Chuo-Ku Tokyo, Japan) and a 60 $\times$ optolite (Meade Instruments, Irvine, California, USA). By means of focal sampling during a full hour (Martin and Bateson 1993), one observer counted each bite taken by a haphazardly selected individual (first two winters) or by a known individual carrying a neck collar (third winter; see van Gils et al. 2007 for more details). In order to estimate short-term bite rate, $1/T_b$, during foraging only, we needed to correct the total bite counts for non-feeding bouts. Therefore, we additionally scored the focal bird's behavior (i.e., foraging or not foraging) at the beginning of each minute. Short-term bite rate could then be calculated as the number of bites taken during the full hour divided by the proportion of time spent actively feeding. During the very same hour, another observer kept track of the number of fecal droppings produced. As it turned out to be hard to keep track of the same individual during a full hour (except during the third winter and during all bite scans), we applied the "hourly block method" (Bédard and Gauthier 1986) during the first two winters. This involves observing a single, haphazardly selected individual until losing contact, after which the observer

immediately switches to another haphazardly selected individual. This goes on until a full hour has passed. At the end of the day we collected dropping and grass samples at the site of observation in order to assess bite size and sward height. Each day we collected ~ 15 droppings (14.3 ± 0.4 [mean $\pm$ SE] droppings) and ~ 0.2 kg fresh mass of grass (taking intact aboveground leaves only). In the laboratory, length of individual plants was measured to the nearest millimeter in order to assess a sample's sward height (measuring 356 ± 114 [mean $\pm$ SE] leaves per sample). We observed 4.1 ± 0.4 h/d during 30 different days, spread evenly across all three field seasons (SE = 1.7 days/winter).

Bite size, bite rate, and intake rate

Bite size, S (in grams), was calculated as U/B , where U is the total amount of ingested grass dry mass (in grams) and B is the total number of bites taken. Both U and B were calculated per pair per trial (experiment) or per individual per hour (field). U was calculated as $F/(100/[100 - E])$, where F is the total amount of fecal dry matter and E is the (apparent) digestive efficiency (as a percentage). The total amount of fecal dry matter was either measured directly per pair per trial (experiment) or calculated per capita per hour (field) as the hourly defecation rate times the daily mean fecal dry mass per dropping. The digestive efficiency was calculated as $(1 - [ADF_g/ADF_f])100\%$, where ADF_g is the concentration (as a percentage) of acid detergent fiber (ADF; cellulose and lignin) in the grass and ADF_f is the ADF concentration (as a percentage) in the feces. Generally, ADF cannot be digested by herbivorous waterfowl (van Soest 1982, Prop and Vulink 1992) and is therefore often used as a marker (Durant 2003). We measured ADF in a subset of samples using the ANKOM²²⁰ Fiber Analyzer (ANKOM Technology, Macedon, New York, USA). In addition, we used near infrared spectroscopy (NIRS; multipurpose analyzer, Bruker Optics, Ettlingen, Germany) to predict ADF concentrations in the remaining samples (i.e., most samples collected in the experiment, all samples collected in the 2003–2004 winter and about half of the samples from the 2005–2006 winter; calibration for grass, $R^2 = 99.6\%$, root mean square error of estimation [RMSEE] = 0.4; feces, $R^2 = 99.1\%$, RMSEE = 0.4; cross-validation for grass, $R^2 = 74.9\%$, root mean square error of cross-validation [RMSECV] = 1.7; feces, $R^2 = 87.6\%$, RMSECV = 0.8; calibrations and cross-validations were based on the subset of samples just described; see Agnew et al. [2004] for an application of NIRS to predict ADF concentrations in grass). Estimating bite size from fecal dry mass and bite counts is an established method in waterfowl ecology (Owen et al. 1992, Durant et al. 2003). It works well when all droppings originating from the bites observed can be collected (such as in the experiment) or when bite and dropping rate are more or less constant throughout the day (such as in the field 2–3 h after the initiation of feeding [J. A. van Gils and P. P. de Vries, *unpublished*

FIG. 3. Interbite interval, T_f , increases with bite size, S (DM, dry mass). Each data point gives an estimate per pair per trial, and each line gives a pair-specific regression. For each pair a positive correlation is found, which is support for the Spalinger and Hobbs (1992) process 3 model. Henceforth, the intervals can be interpreted as handling times (T_h), composed of a cropping time and a bite-size-dependent processing time.

data], which is why nearly all field observations started after 11:00 hours).

In short vegetation, bite size is presumably limited by height of the vegetation, while in taller vegetation bill size may set the limits (Durant et al. 2003, Cope et al. 2005). Therefore, when modeling bite size, S , as a function of sward height, L , we applied two regression models (using the linear and nonlinear mixed-effects models [NLME] package in R [R Development Core Team 2005]), one in which we ignored the constraints by bill size,

$$S = aL + b \quad (3)$$

and one in which we included an asymptote (cf. Durant et al. 2003),

$$S = \frac{aL}{1 + bL} \quad (4)$$

In both models, a and b are regression coefficients. We compared Akaike Information Criterion (AIC) values (Burnham and Anderson 1998) to detect the most parsimonious model (using the ANOVA function in R).

Following Kohlmann et al. (1999), gamma distributions were fitted to the experimentally obtained distributions of intervals T_f (in seconds) between subsequent bites. We applied Kohlmann et al.'s model 1 using the NLME package in R (step sizes in the distributions were set at 0.1 s). This yielded an estimated T_f per pair per trial. This enabled the expression of the short-term bite rate (per second) as $1/T_f$ and the instantaneous intake rate (in grams per second) as S/T_f (note that this contrasts with the calculation of long-term bite rate, which would simply be the total number of bites divided by total time [including non-feeding bouts]).

RESULTS

Distinguishing encounter-limited foraging from handling-limited foraging

In the experiment, interbite interval, T_f , increased linearly with bite size, S (Fig. 3; hierarchical linear model [HLM]: $P < 0.05$, $N = 3$ level 2 observations and 69 level 1 observations using the unit of a pair as the identifier; reduced major axis [RMA] regression of T_f [in seconds] vs. S [in grams] yielded $T_f = 1.13 + 16.66S$; this positive effect remains with a similar slope and intercept, but at $P < 0.00001$, with reanalysis excluding the less-motivated pair [2]: $T_f = 1.05 + 16.57S$). Therefore, this result rejects processes 1 and 2 as potential candidate functional responses and supports the process 3 mechanism. Additionally, there was no sign for a mixture of processes operating at the same time. If the smallest bites would be so small that they would impose an encounter constraint rather than a handling constraint, then the relation plotted in Fig. 3 would be accelerating rather than linear (given Eq. 1), and this is obviously not the case. For this reason, interbite interval, T_f , can be interpreted as handling time, T_h , composed of a fixed cropping time, T_c , of 1.13 s ($= 0.02$ min) and a bite-size-dependent processing time, T_p , of 16.66 s/g DM (Fig. 3; equivalent to an $R_{\max}$ of 3.60 g DM/min).

Modeling bite size, handling time, and intake rate as a function of sward height

We modeled bite size as a function of sward height. This enabled us to predict handling time and thus intake rate from relatively simple measurements of sward height rather than from more difficult measurements of bite size.

When relating bite size to the experimentally manipulated sward height, regression parameter b did not differ from 0 in either the linear model (Eq. 3; $P > 0.95$, $AIC = -436.01$) or the asymptotic model (Eq. 4; $P > 0.6$, $AIC = -435.89$). Therefore, a linear model without an intercept is the most parsimonious and therefore most preferred model (Fig. 4A; $AIC = -441.89$). This allowed us to estimate the common slope (mean $\pm$ SE): 1.38 ± 0.09 mg DM/cm sward height (Fig. 4A; $P < 0.00001$, $N = 3$ level 2 observations and 69 level 1 observations; this result remains unaltered, at a similar P value, if we exclude pair 2: 1.39 ± 0.07 mg DM/cm).

Combining the latter parameter estimate with the observed relation between handling time, T_h (in minutes), and bite size, S (in grams) ($T_h = 0.02 + [S/3.60]$; Fig. 3) enabled us to predict S (in grams) ($S = 1.38 \times 10^{-3}L$; solid line in Fig. 4B), T_h (in minutes; $T_h = 0.02 + \{[1.38 \times 10^{-3}L]/3.60\}$; Fig. 4C), and subsequently instantaneous intake rate $I = S/T_h$ (in grams per minute) ($I = [3.60 \times 1.38 \times 10^{-3}L]/[3.60 \times 0.02 + 1.38 \times 10^{-3}L]$; Fig. 4D) as a function of sward height, L (in centimeters). While doing so, we took into account the error around each estimate (dashed lines in Fig. 4). Note that, as expected under process 3 foraging, the observed

linear relationship between bite size and sward height leads to an asymptotic relationship between intake rate, I , and sward height.

Applying functional response predictions to the field

Observed sward heights in grasslands selected by free-ranging swans ranged from 6 to 12 cm ($N = 30$; Fig. 4B–D); the longest grass lengths used in the experiment [15–20 cm] were simply not available in the field at this time of year; J. A. van Gils and P. P. de Vries, *unpublished data*). This range was used as input to predict functional response parameters in the field (Fig. 4B–D). This revealed that estimates for bite size (Fig. 4B), handling time (Fig. 4C), and intake rate $I = S/T_h$ (Fig. 4D) match well with these predictions as each estimate fell within the predicted 95% CI.

DISCUSSION

In the experiment, the time in between two bites increased with bite size (Fig. 3), which is indicative of handling-limited foraging, i.e., Spalinger and Hobbs' (1992) process 3. Thus, instantaneous intake rate in grass-eating Bewick's Swans is constrained by rates of cropping and chewing rather than by rates of encounter, leading to an asymptotic Type II functional response with the asymptote being given by $R_{\max}$. The experimentally observed quantitative dependence of bite size on sward height (Fig. 4A) was used to predict bite sizes (Fig. 4B) and subsequently handling times (Fig. 4C) and intake rates (Fig. 4D) as a function of sward height in the field. Observed bite sizes, handling times, and intake rates in the field closely matched these experiment-based predictions (Fig. 4B–D).

The fact that intake rate in grass-eating Bewick's Swans was constrained by bite mass (process 3) rather than by plant density (processes 1 and 2) may not come as a surprise. Individual grass stems (1) are not hidden and (2) are interspaced at very short distances, such that the time to move from one bite to the next bite is virtually negligible. Indeed, when applying the concept introduced by Hobbs et al. (2003), who explicitly addressed the problem of plant density on intake rate regulation, we arrive at estimated critical distances d^* between individual bites ranging from 14 cm (for the shortest sward heights of 6 cm) to 38 cm (for the longest sward heights of 17 cm), above which intake rate in grass-eating swans would be encounter-limited instead of handling-limited. (Following Hobbs et al. [2003], we calculated d^* as $SV_{\max}/R_{\max}$, using the allometric mammalian equation for $V_{\max}$ [Shiple et al. 1996], i.e., the velocity of travel in the absence of cropping at a body mass of 5.5 kg and assuming the number of leaves per bite does not vary with plant density, which is in line with observations by Lang and Black [2001]). Grass ramets are interspersed at much shorter distances than 14 cm (J. A. van Gils and P. P. de Vries, *personal observation*), and therefore handling-limited foraging was to be expected.

FIG. 4. (A) Experimental results on bite size, S (DM, dry mass), as a function of sward height. The solid line gives the hierarchical linear model regression; dashed lines give the 95% CI. Field results on (B) bite size, S , (C) handling time, T_h (= interbite interval, T_l), and (D) intake rate, I , match with experiment-based predictions (solid line, regression; dashed lines give the 95% CI). Box-and-whisker plots are as in Fig. 2, with asterisks denoting outliers.

However, Durant et al. (2003) suggested that grass eating in the smaller avian herbivores in their study (the Eurasian Wigeon [*Anas penelope*] and Barnacle Geese [*Branta leucopsis*]) shifted from handling-limited toward encounter-limited as sward heights increased. They suggested that at tall sward heights small birds need more time locating suitable bites (in addition to more time needed for cropping as found in that study). This may lead to the so-called “dome-shaped” functional response (or Holling's [1965] Type IV functional response), in which intake rate peaks at intermediate biomass (van der Wal et al. 1998, Therkildsen and

FIG. 5. Allometric scaling (note the log scales) of functional response parameters in birds (solid circles) in comparison with mammals (open circles). (A) Cropping time, T_c , does not relate to body mass and is slightly lower than in mammals. (B) Maximum bite size, $S_{\max}$ (DM, dry mass), scales to body mass with a similar slope but a lower intercept than in mammals. (C) Maximum food processing rate, $R_{\max}$, scales to body mass with a similar slope and intercept as in mammals. (D) Maximum intake rate, $I_{\max}$, scales to body mass with a similar slope but with an intercept half that in mammals. In each graph (A–D), solid lines give regressions for mammals and birds; dashed lines (B and D) give regressions through additional mammalian data reviewed by Shipley et al. (1994); dotted lines (D) give predicted $I_{\max}$ on the basis of scaling relations for T_c , $S_{\max}$, and $R_{\max}$. All mammalian data were taken from Shipley et al. (1994); avian data were taken from Jacobsen (1992), Hewitt and Kirkpatrick (1996), Hassall et al. (2001), Lang and Black (2001), Durant et al. (2003), Cope et al. (2005), Durant and Fritz (2005), and van der Graaf et al. (2005) (see Appendix A for details).

Madsen 2000, Lang and Black 2001, Bos et al. 2004). Smaller grazers may need to be more selective as the morphology of their bills seems to be a compromise between conflicting functional demands of grazing on the one hand and filter-feeding on the other (van der Leeuw et al. 2003). Larger avian herbivores, such as the Greylag Goose (*Anser anser*) and the Bewick's Swan (this study), do not seem to have such problems and therefore obey the process 3 equation across all sward heights studied.

To quantify such effects of avian body size on functional response parameters, we allometrically scaled the results of our study to parameters found in other avian herbivores and contrasted those with parameters found in mammals (Shipley et al. 1994). The avian herbivores that we included were (in increasing order of size): Ruffed Grouse (*Bonasa umbellus*; Hewitt and Kirkpatrick 1996), Eurasian Wigeon (*Anas penelope*; Jacobsen 1992, Durant et al. 2003, Durant and Fritz 2005), Brent Goose (*Branta bernicla*; Hassall et al. 2001), Barnacle Goose (*Branta leucopsis*; Lang and Black 2001, Durant et al. 2003, Cope et al. 2005, van der Graaf et al. 2005), and Greylag Goose (*Anser anser*; Durant et al. 2003) (see Appendix A for details).

As in mammals, cropping times, T_c , in birds did not scale to body mass ($P > 0.1$). The intercept however, was slightly but significantly ($P < 0.005$) lower in birds

(0.6 s) than in mammals (0.9 s). The fact that, also in birds, cropping time does not scale to body mass suggests that plant characteristics such as leaf stiffness overrule the potential effects of body size on cropping time. Maximum bite size, $S_{\max}$ (in grams DM), scaled to body mass, M (in kilograms; Fig. 5B; $P < 0.005$), with a similar slope as in mammals ($P > 0.15$), but with a lower intercept ($P < 0.00001$; mammals, $S_{\max} = 0.09M^{0.72}$, using the experimentally obtained equation by Shipley et al. [1994]; solid line in our Fig. 5B; birds, $S_{\max} = 0.004M^{0.72}$). Mammals are likely to take larger bites because their teeth may enable more plant material to be cut in a single bite, even so that a bite may extend outside their mouths (Shipley et al. 1994). Note that large avian herbivores such as geese and swans have evolved tooth-like lamellae in their bills, and it is suggested that this improved their bite size (van der Leeuw et al. 2003). The possibility of mammals having larger "beaks" enabling larger bites is precluded as beak dimensions do not differ between birds and mammals (bill widths exactly overlap with the mammalian allometric regression for incisor breadth provided by Illius and Gordon [1987], and similarly, bill lengths scale identically to body mass in birds as do jaw lengths in mammals [based on data provided by Druzinsky 1993]). Maximum processing rate, $R_{\max}$ (in grams DM per minute), scaled to body mass (in kilograms; Fig. 5C; $P <$

PLATE 1. A typical flock of free-ranging Bewick's Swans feeding in our field site near Amersfoort, The Netherlands. Photo credit: Alex Koenders.

0.05) with a similar slope ($P > 0.2$) and intercept ($P > 0.2$) as in mammals ($R_{\max} = 0.71M^{0.70}$). This may seem remarkable at first, since birds, unlike mammals, do not chew and would therefore be expected to have higher maximum processing rates. However, because they do not chew, it may take them longer to maneuver tall grass leaves that are hanging out of the bill into the mouth (Fig. 1). This so-called “spaghetti effect” (Ungar 1996) has been observed in a variety of waterfowl species (Lang and Black 2001, Durant et al. 2003). The time loss of the “spaghetti effect” in birds may be similar to the time loss of chewing in mammals, which would explain the similarity in maximum processing rate. Maximum intake rate, $I_{\max}$ (in grams DM per minute), scaled to body mass (in kilograms; Fig. 5D; $P < 0.005$) with a similar slope as in mammals ($P > 0.4$), but with an intercept two times lower ($P < 0.005$; mammals, $I_{\max} = 0.45M^{0.71}$; birds, $I_{\max} = 0.24M^{0.71}$). Note that these maximum intake rates are correctly predicted by inserting the allometric scaling relationship for T_c , $S_{\max}$, and $R_{\max}$ into Eq. 2 (yielding $I_{\max} = 0.26M^{0.71}$ for birds and comparable to $0.63M^{0.71}$ predicted by Shipley et al. [1994] for mammals; dotted lines in Fig. 5D), which is an additional support for avian herbivory to be governed

by Spalinger and Hobbs process 3 (i.e., given that T_c and $R_{\max}$ do not differ much between equally sized birds and mammals, a lower $S_{\max}$ in birds logically leads to a lower $I_{\max}$ under process 3 foraging).

In their struggle to at least maintain a balanced energy budget, there may be several ways in which birds could compensate for such lower (instantaneous) intake rates that are only half those of mammals. First of all, they could be better at digesting their food. However, this seems unlikely as evidence suggests birds have similar or even lower digestive efficiencies than mammals (Karasov 1990, Grajal 1995), possibly because the ability to fly has precluded the evolution of a complex and heavy digestive system as found in mammals (Dudley and Vermeij 1992). Secondly, birds may have lower energy requirements than mammals. Also this seems unlikely as birds generally have similar or even higher metabolic rates than mammals (Nagy 2005). Thirdly, and most likely, birds spend more time feeding per day than mammals do. Indeed, when contrasting herbivorous birds with herbivorous mammals, we found that birds allocated more than twice (2.4 times) as much time to foraging (9.7 ± 0.6 h per 24 h) (mean $\pm$ SE) than mammals did (4.1 ± 0.6 h per 24 h; $R^2 = 0.54$, $P <$

0.00001, $N = 42$; see Appendix B for studies reviewed). Note that the factor 2.4 exactly matches the ratio between the mechanistically predicted $I_{\max}$ of a mammal and that of a bird: $0.63M^{0.71}/0.26M^{0.71} = 2.4$. Further note that this analysis does not suggest that mammals are not *able* to feed longer than this. It rather suggests that, generally speaking, they do not need to feed longer in order to maintain a balanced energy budget. Of course, under more stringent conditions, such as when their population has grown to carrying capacity, short-term intake rates may fall well below $I_{\max}$ (e.g., due to competition), urging mammals to stretch their working day as well (a point of view shared by Jeschke and Tollrian [2005]).

ACKNOWLEDGMENTS

We are grateful to Pieter Coehoorn, Els Corporaal, Bert Hidding, Rik van Kraaij, Rinze de Leeuw, Daan Liefhebber, Reinder Radersma, and Peter de Vries for their observations during many long, cold, and windy hours in the field. In the lab, Dick Kuiper from the Van Hall Instituut assisted during the ADF analyses, and Harry Korthals took care of all NIRS measurements. We thank Marcel Klaassen for discussion and Olivier Duriez, Stephan G. Kohlmann, Bart A. Nolet, and two anonymous referees for constructive comments on draft manuscripts. The experiment was approved by the Dutch Animal Welfare Committee (protocol CL 03.04). This is publication 4020 of the Netherlands Institute of Ecology (NIOO-KNAW) and 481 of the Centre for Wetland Ecology.

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APPENDIX A

The method used for extracting functional response parameters from studies on avian herbivores (*Ecological Archives* E088-182-A1).

APPENDIX B

The method used for extracting daily feeding times from studies on avian and mammalian herbivores (*Ecological Archives* E088-182-A2).