

SPATIAL VARIATION IN TUBER DEPLETION BY SWANS EXPLAINED BY DIFFERENCES IN NET INTAKE RATES

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Abstract. We tested whether the spatial variation in resource depletion by Tundra Swans (*Cygnus columbianus*) foraging on belowground tubers of sago pondweed (*Potamogeton pectinatus*) was caused by differences in net energy intake rates. The variation in giving-up densities within the confines of one lake was nearly eightfold, the giving-up density being positively related to water depth and, to a lesser extent, the silt content of the sediment. The swans' preference (measured as cumulative foraging pressure) was negatively related to these variables. We adjusted a model developed for diving birds to predict changes in the time allocation of foraging swans with changes in power requirements and harvest rate. First, we compared the behavior of free-living swans foraging in shallow and deep water, where they feed by head-dipping and up-ending, respectively. Up-ending swans had 1.3–2.1 times longer feeding times than head-dipping swans. This was contrary to our expectation, since the model predicted a decrease in feeding time with an increase in feeding power. However, up-ending swans also had 1.9 times longer trampling times than head-dipping swans. The model predicted a strong positive correlation between trampling time and feeding time, and the longer trampling times may thus have masked any effect of an increase in feeding power. Heart rate measurements showed that trampling was the most energetically costly part of foraging. However, because the feeding time and trampling time changed concurrently, the rate of energy expenditure was only slightly higher in deep water (1.03–1.06 times). This is a conservative estimate since it does not take into account that the feeding costs of up-ending are possibly higher than that of head-dipping. Second, we compared captive swans foraging on sandy and clayey sediments. We found that the harvest rate on clayey sediment was only 0.6 times that on sandy sediment and that the power requirements for foraging were 1.2–1.4 times greater. Our results are in qualitative agreement with the hypothesis that the large spatial variation in giving-up densities was caused by differences in net rates of energy intake. This potentially has important implications for the prey dynamics, because plant regrowth has been shown to be related to the same habitat factors (water depth and sediment type).

Key words: *Bewick's Swan*; *Cygnus columbianus bewickii*; energy expenditure; fennel pondweed; giving-up density; Lauwersmeer, The Netherlands; optimal foraging; patch use; plant-herbivore interaction; *Potamogeton pectinatus*; sago pondweed; Tundra Swan.

INTRODUCTION

Field studies on the resource depletion by vertebrate consumers have often found a food density below which no foraging takes place: the so-called grazing threshold or giving-up density (Drent and Prins 1987, Dolman and Sutherland 1997). The existence of such a threshold has potentially great implications for the dynamics and stability of predator-prey systems (Oaten and Murdoch 1975). A study of the factors determining the giving-up density might therefore be an important

step toward the understanding of population or even community properties from mechanisms acting at the individual level.

According to the marginal value theorem, an animal foraging in a patchy environment should leave a food patch as soon as its net energy intake rate falls below the average it can achieve in the habitat as a whole (Charnov 1976). Hence, if the net energy intake rate is solely determined by the food density, consumers should equalize resource density over all exploited patches. Brown (1988) considered the case in which patches may differ in aspects other than food density, namely harvest rate, energetic costs, predation risk, or the presence of alternative resources or foraging op-

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PLATE 1. Tundra Swans foraging on below-ground pondweed tubers in deep water in the Lauwersmeer, The Netherlands. The swan on the left is up-ending, and the one on the right is trampling.

portunities. He showed that in such a case a forager should leave a patch when the harvest rate is no longer greater than the sum of the energetic, predation, and missed opportunity costs of foraging (missed opportunity costs are the foregone fitness benefits of alternative resources or activities). His study, and most of the subsequent studies using the same approach, further concentrated on differences in predation risk between patches. These studies showed that the giving-up density was higher at more risky sites (e.g., Bowers et al. 1993).

Harvest rates and the energetic foraging costs together determine the net rate of energy intake. Changes in one or both of these factors can trigger animals to quit foraging, as has been shown for Canvasbacks (*Aythya valisineria*) diving for belowground winter buds (Lovvorn and Gillingham 1996). It was found that the remaining food biomass was largely determined by food-item size and the energy costs of descent. The ducks abandoned the study lake in early winter when foraging was no longer profitable due to a decrease in bud size and an increase in water depth.

Soil characteristics have been put forward as a potentially important environmental element affecting both the harvest rate and the energetic costs (Brown 1988). We know of two studies that experimentally investigated the effects of soil characteristics on harvest rate (Price and Heinz 1984, Van Eerden and Munsterman 1997). Both showed that harvest rate decreased with soil particle size. Van Eerden et al. (1997), studying the patch use of Tundra Swans (*Cygnus columbianus bewickii*) feeding on belowground tubers of sago pondweed (*Potamogeton pectinatus*), hypothesized that soil-type-related differences in giving-up densities were due to differences in energetic costs of foraging. In a comparison of two lakes in The Netherlands, they found a much lower giving-up density in the sandy Veluwemeer (1.9 g dry mass/m²) than in the mainly clayey Lauwersmeer (7.7 g dry mass/m²). Van Eerden et al. (1997) considered pit digging and tuber extraction to be less energetically costly for the swans in sandy sediments than in clayey soils and hypothesized that this explained the observed differences in giving-up

densities. One has to bear in mind, however, that the two lakes differ in more respects than just soil type, including the alternative food resource (Van der Winden et al. 1997).

In this study we tested whether giving-up densities differed within the confines of one lake (i.e., among patches with the same predation risk and missed opportunity costs) using the same system as Van Eerden et al. (1997). We studied the effects of silt content of the sediment and water depth in particular. We subsequently investigated whether the differences in giving-up densities could be related to differences in net rate of energy intake. We measured the time allocation of free-living swans foraging in shallow and deep water and compared the observed differences with those predicted for a change in net rate of energy intake by a model originally developed for diving birds. We further measured the harvest rate and heart rate (as a measure of energy expenditure) of captive swans foraging on sandy and clayey sediments. These we used to test for sediment-related differences in net energy intake and to parameterize the time allocation model.

STUDY SYSTEM

We studied Tundra Swans feeding on belowground tubers of the pseudo-annual sago pondweed. Upon returning to The Netherlands from their breeding grounds in the Russian tundra, the swans show a clear preference for the pondweed tubers. The swans loosen the sediment by trampling with their feet. During trampling the birds have their necks bent and waddle. In shallow water the swans subsequently dip their heads and necks under water, but in deep water they up-end (Plate 1). They extract the tubers underwater by sieving sediment through the bill. The swans can reach down to 59 and 84 cm below the water surface during head-dipping and up-ending, respectively (Owen and Cadbury 1975). The burial depth of the tubers is 5–30 cm in the sediment (L. Santamaría, *unpublished manuscript*). After a few weeks, the swans switch to sugarbeet harvest leftovers (Beekman et al. 1991).

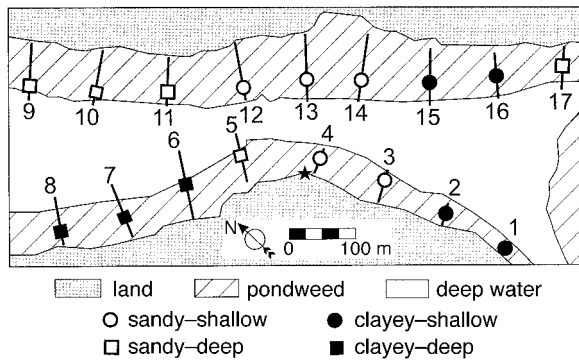


FIG. 1. Location of the transects (lines) and plots. The star indicates the position of the blind.

METHODS

Field study site

The Lauwersmeer (The Netherlands; 53°22' N, 06°13' E) is a former part of the Waddenzee (Wadden Sea) that became a shallow (<70 cm deep) freshwater lake after the embankment in 1969. The lake (750 ha) contains extensive sago pondweed beds that are visited by Tundra Swans in October and November. Our study site (800 × 300 m) comprised about half of the Babbelaar, a part of the Lauwersmeer that is closed to the public and where hunting is prohibited. The water level of the lake is regulated by sluice control.

Plant and sediment sampling

The beds of sago pondweed were mapped using aerial photography in July 1995 when aboveground plant matter was visible. In the 20–105 m wide beds, we marked 17 transects perpendicular to the shore 100 m apart with stakes. We assessed the tuber density by taking at least 30 cm deep sediment cores (10.0 cm diameter), both just before the swans arrived in the first week of October and after all swans had switched to feeding on sugarbeets or had left the area in the first half of November. In this short exploitation period, no tuber production occurs, and tuber size reduction or winter mortality is negligible; this was checked using exclosures (L. Santamaría, unpublished manuscript). In 1995, we took six cores on 1 m² every 10 m along the transects. We also classified the sediment of each sam-

pling point on a six-point scale by rubbing the sediment between our fingers. In 1996 and 1997, we marked 20 × 20 m plots on the transects (one plot per transect) with stakes and subsequently sampled them (Fig. 1); these plots were located in such a way that the tuber density (based on the 1995 sampling) varied two to three times within each depth-sediment category. In order to make the figure of the overall tuber density for 1995 comparable to that of 1996 and 1997, we only included those sampling points along the 1995 transects (two or three points per transect) that fell within the plots.

In order to determine the number of cores needed to obtain a fair estimate of the tuber density in the plot, we first took 25 cores in 10 × 10 m subplots at four different transects. We then calculated the standard error of the estimated tuber density in such a subplot for each addition of a core in a random order. The standard error generally did not fluctuate anymore after nine cores had been added. Therefore, 4 × 9 = 36 cores per 20 × 20 m plot were subsequently taken. Cores were washed through a 3-mm sieve and the dry mass (DM) of the tubers was assessed by drying for >48 h at 70°C. The distance between plots was large enough to ensure that the tuber densities were independent (linear regression of the initial tuber densities of each plot against that in the adjacent plot gave R² = 0.00004 in 1996 and R² = 0.1218 in 1997, N = 15).

Shell fragments of bivalves, remains of the former tidal area, were collected in November 1997 per subplot and weighed after being air dried.

We took one sediment core in the center of each plot in October 1996 and cut it into layers of 5 cm. The 5–10 cm and 20–25 cm layers were taken for Malvern analyses on grain size (Table 1). We described the sediment granulometric composition along a single axis using principal components analysis (PCA; SAS 1995). This axis explained 64% of the variation and was most strongly correlated with the silt fraction (grain size <63 μm) of the deep layer (R² = 0.89, N = 17). Based on the 1995 transect data, the sediment type did not change much along the transects (typically 0–2 units on our six-point scale), except along transects 3 and 4 where it changed by 3 units. Here, however, the swans only foraged on the sandy part of the transect because no

TABLE 1. Granulometric composition of sediment in the Babbelaar (Lauwersmeer, The Netherlands) and in the experimental trials (means ± 1 SE).

Location	N	<16 μm	16–<50 μm	50–<63 μm	63–<125 μm	125–<250 μm	250–<500 μm
Field							
Sandy	10	4.2 ± 0.9	6.6 ± 1.5	3.4 ± 0.5	49.4 ± 2.0	35.9 ± 3.6	0.6 ± 0.1
Clayey	7	21.5 ± 3.5	23.0 ± 1.4	5.5 ± 0.7	33.8 ± 2.9	15.7 ± 2.7	0.5 ± 0.1
Basin†							
Sandy		0.5	0.4	0.1	4.7	30.3	64.0
Clayey		12.4	8.1	0.4	3.0	21.2	55.0

† Average of four trays (standard error not given because of pseudoreplication).

plants were present on the clayey part. We could therefore regard the sediment data of the plots as representative for the corresponding transects.

We simultaneously measured the depth of the water column at the center of each plot and read the water level in the Babbelaar at a pole (that had been calibrated against a nearby fixed pole). We calculated the average water depth at each plot by taking into account the difference between the actual and average water level (-83 cm, expressed relative to The Netherlands' standard; measured during the swan exploitation in October 1996).

Foraging behavior of free-living swans

In 1995 and 1996, we made behavioral observations of the swans from a blind on a 3 m high platform, with 8–10 \times binoculars or a 20–60 \times telescope during the day and a light intensifier (LUNOS 6 \times ; Delft Instruments, Delft, The Netherlands) during moonlit nights. In 1995 and 1996, we covered 41.1% and 33.6% of the time; by concentrating our efforts on peak days, we observed an estimated 62.4% and 46.7% of the foraging swans, respectively. The swans were counted, mapped, and scanned every hour (number of scans is 158 and 121 in 1995 and 1996, respectively). We determined the positions of the flocks by measuring the angle and distance from the observatory to the swans at the boundaries of the flocks using a range finder (Geovid 7 \times 42 BDA; Leica Camera, Solms, Germany). In addition, we drew the flocks on a map using our stakes as reference points.

We transformed these data into bitmaps with each pixel representing 10 \times 10 m in the field. Usually we scanned all birds, but when the number was so large that a scan would take more than 15 min, 100 birds per flock were scanned, evenly distributed over the flock. We classified the behavior of the birds into categories (antagonistic behavior, drinking, flying, foraging, looking, preening, sleeping, swimming, and, occasionally, walking). The number of foraging swans in each flock was linked to the position of the flock, and the foraging pressure was calculated as the number of foraging swans per square meter. Summing all observations gave a foraging pressure as cumulative foraging time per area for every pixel in the bitmap. We analyzed the 1995 data with the Triangulated Irregular Network (TIN) software package within ARC/INFO (ESRI 1992) and calculated the average cumulative foraging pressure of the two to three sample points located within each 20 \times 20 m plot. For the 1996 data we directly used the bitmaps and took the average cumulative foraging pressure of the nine pixels located around each 20 \times 20 m plot. These foraging pressures were rescaled to hours per square meter using the observed total swan foraging time (16 446 h in 1995 and 34 941 h in 1996) and the total pondweed area (104 000 m²). The feeding pressure (in hours per square meter) was calculated by multiplying the foraging pressure with the proportion

of the foraging time the swans had their heads submerged (0.81 in 1995 and 0.79 in 1996), based on the focal observations.

A more detailed description of the swans' foraging behavior was obtained by making 15 min long focal observations on a handheld microcomputer (Organiser II Model LZ64; Psion plc, London, UK) using The Observer software (Noldus Information Technology, Wageningen, The Netherlands). For each focal observation, we selected another foraging swan. We distinguished the same behavioral categories as during the scans, but antagonistic behavior was now subdivided into attacking and retreating and foraging into head-dipping, up-ending, surfacing, and trampling. The duration of each behavior was determined with an accuracy of one second. A foraging bout consisted of a sequence of trampling, underwater feeding, and surfacing. If feeding consisted of a mixture of head-dipping and up-ending, the foraging bout was omitted from the analysis. Every 100 s we determined the focal swan's position using the range finder. The swan was regarded as foraging on the sediment type of the transect that it crossed during the focal observation. If the swan did not cross a transect, its focal observation was omitted unless it was feeding in between transects with a similar sediment type (difference in PCA value <1). The average of the PCA values of these transects was then used. We selected only the observations on sandy sediment (PCA > 0), because we had only a limited number of observations on clayey sediments.

Time allocation model

Houston and Carbone (1992) presented a model of the optimal allocation of time during feeding bouts in diving birds. They assumed that a diver gained a supply $x(s)$ of oxygen by spending a time s for recovery at the surface and used oxygen at a rate m_1 while traveling for a time τ and at a rate m_2 while feeding underwater for a time t . They used a Lagrange multiplier to find the optimal surface time s^* and feeding time t^* of a bird that maximizes its net rate of energetic gain subject to the constraint $x(s) = m_1\tau + m_2t$. Carbone and Houston (1994) showed that in diving birds, an increase in power requirements for feeding results in a decrease in feeding time, while not affecting the surface time. Foraging swans do not dive, and the time spent traveling is negligible. However, swans do have to dig a hole by trampling before they can eat. The major difference between a diving bird and a foraging swan is that the swan can breathe during trampling, whereas a diver cannot during traveling. The constraint thus becomes: $x(s) = m_2t$.

In the model the oxygen reserves x are replenished during surfacing as: $x(s) = K[1 - \exp(-\alpha s)]$, where K is the maximum amount of oxygen that can be stored. The cumulative metabolizable energy gain is $b \cdot t^\theta$, where b is the relative metabolizable energy intake rate and θ an exponent to model depletion. The energy ex-

penditure is $e(m_1\tau + m_2t + m_3s)$, where e converts units of oxygen to energy units, and m_3 is the rate of oxygen consumption during surfacing. The net rate of energetic gain is thus:

$$N(t, s) = \frac{bt^{\theta} - e(m_1\tau + m_2t + m_3s)}{\tau + t + s}$$

The parameterization of the model is described in Appendix A. The basic values were varied twofold in both directions to see the effects of changes in m_1 , m_2 , τ , and b on t^* and s^* .

Harvest rates and foraging costs of captive swans

The functional response of one male swan (AN) was measured in a fenced 3×3 m compartment of a basin. Before the measurements the swan was trained for 8 wk. We used wheat grains (0.05 g dry mass), similar in size to pondweed tubers from the Babbelaar, as food items. These were put out in a regular grid pattern in a tray of 1 m² filled with sand (from the IJsselmeer) and covered with a further 12.5 cm of sand. The sand was sieved through a 3-mm sieve to remove small stones, shell remains, and plant material prior to the experiments. Nine densities were used ranging from 5 to 309 g/m², offered in random order. The water depth was 52 cm, and the swan obtained the food by head-dipping. We timed until the swan had had its head submersed for a total of 2 min and then rang a bell to halt feeding. The remaining grains were collected by pumping the sediment through a 3-mm sieve. The session was videotaped and analyzed using The Observer Video-Pro software (Noldus Information Technology, Wageningen, The Netherlands). The frequency distribution of submersion times was bimodal, and on the basis of this we omitted submersion times shorter than 2 s (we assumed that these did not represent feeding). The experimental swan was accompanied by another swan at the other side of the fence in the basin to facilitate feeding behavior. This companion swan was injured in an accident during the measurement series, and it became necessary to choose a replacement companion swan. For 2 wk this caused serious restlessness in our experimental swan, and the consecutive five measurements were excluded from the analysis (see the inset of Fig. 8, open data points).

We tested whether the measured functional response was representative for the harvest rate of pondweed tubers in the field as follows. Tubers were collected in the IJsselmeer and offered in four 1-m² trays filled with either sand or 1:0.15 sand-clay mixture (Table 1) in the same compartment of the basin. The tubers were scattered and put in the tray in four layers of equal mass at burial depths of 22.5, 17.5, 12.5, and 7.5 cm in order to mimic the field situation (together ~ 40 g/m²). Four swans (AN, AP, AT, and AZ) were held together in the compartment for 1 h, and their behavior was videotaped. Water depth was 40 cm in both trials, and the birds foraged by head-dipping. AZ did not feed

during the trials and was excluded from the analysis. Only AN was trampling, and the other two birds apparently benefited from the pits AN had dug.

Of these birds, heart rate was recorded using a modified human heart rate logging system (Polar Vantage NV; Polar Electro Oy, Kempele, Finland). It consisted of a small unit that recorded the ECG signal and transmitted the heart pulse to a receiver that logged the signal. The transmitters were modified from the commercially available transmitters by removing the electronics and rehousing them in a small waterproof plastic box. The transmitter unit was attached to a harness on the back of each bird (Glahder et al. 1998). ECG leads with snap connectors were connected to the transmitter for attaching to ECG electrode pads. At both sides, an area of ~ 10 cm² just below the wings was plucked of feathers. The area was then rubbed with a light scouring paste to remove dead skin cells and finally cleaned with alcohol. The electrode pad was held in position by its own adhesive but additional adhesion was gained by adding cloth tape that had been soaked in diethyl ether. Each transmitter unit was coded so that there was no interference with the heart rate transmitted from another bird. The logging unit was in the form of a watch (41 g) that was strapped to a neck collar (69 g). The heart rate logging unit recorded mean heart rate over every 5 s. A calibration procedure carried out in the weeks before the feeding trials made it possible to convert heart rate into oxygen consumption (see Appendix B).

Statistics

We used a linear regression with stepwise selection (REG procedure; SAS 1989) to test for effects of initial tuber density, water depth, silt content of the sediment, and shell fragments on the final tuber density and swan grazing pressure, respectively. In order to be able to include an interaction term, we subsequently classified the 17 plots as sandy or clayey (PCA value of less or more than 0) and as shallow or deep (water depth less or greater than 54 cm, respectively). The latter value was based on the maximum depth Tundra Swans can reach while head-dipping (59 cm) minus the minimum burial depth of tubers (5 cm) (see *Study System*). We then used a general linear model (GLM procedure; SAS 1989) with backward elimination based on type III (i.e., partial) sum of squares with depth and sediment as class variables. We further grouped the plots into four depth-sediment categories (sandy-shallow, sandy-deep, clayey-shallow, and clayey-deep). Then plots 4 and 6 were omitted because these plots were at the extreme ends of water depth, and inclusion would have caused the plots to be confounded with respect to water depth and sediment grain size (Fig. 2). Because the final tuber density is expected to be positively correlated with the initial tuber density, we also tested for differences among depth-sediment categories by an analysis of covariance of swan consumption (i.e., the difference be-

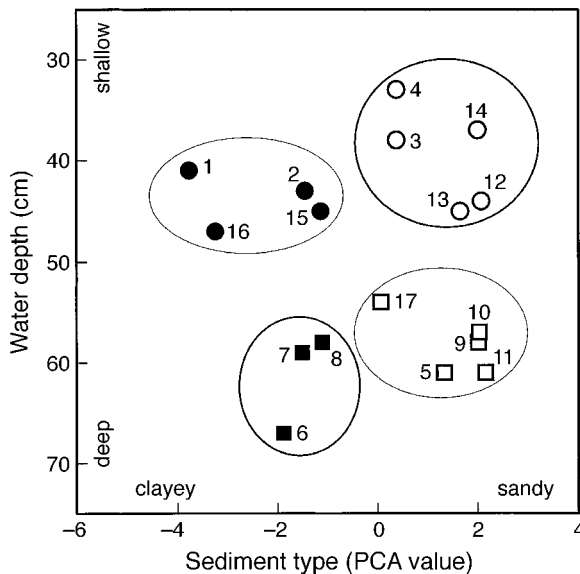


FIG. 2. Average water depths and sediment types (expressed in values along the first axis of the principal components analysis; see *Methods*) at the 17 plots in the Babelaar. Four depth-sediment categories were discriminated: (○) sandy-shallow, (□) sandy-deep, (●) clayey-shallow, and (■) clayey-deep. Plots 4 and 6 were omitted from the analyses with depth-sediment category as the class variable. Numbers next to symbols correspond to plot numbers in Fig. 1.

tween initial and final tuber density per plot) with the initial tuber density as a covariable. The interaction category \times initial tuber density was not significant, and an analysis of covariance was therefore appropriate. This method is only valid if the swan consumption is not zero, which it was in all cases (a zero consumption was only found in plot 6 in 1997, but that plot was omitted from this analysis for other reasons). The x-axis intercepts of the lines regressing swan consumption on initial tuber density is an estimate of the giving-up density per depth-sediment category.

We tested whether the time allocation during a foraging bout was significantly affected by year of observation, feeding mode, the preceding underwater

time (if applicable), and their interactions, using a general linear model. Year (1995 or 1996) and feeding mode (head-dipping or up-ending) were classification variables. The times were log transformed to normalize the variables. We did not correct for any bias in the back-transformation. In order to insure independence of data, we aggregated the 4182 foraging bouts by averaging over the focal observations ($N = 205$).

The functional response was analyzed by fitting a Type II Holling disc equation (Marquardt method in the NLIN procedure; SAS 1989) to the data of harvest rate against average resource density. In this way we derived estimates of the search area a and the handling time t_h .

Heart rates were not normally distributed, also not after log transformation. Differences in heart rates while foraging on sandy and clayey sediment were therefore tested with a median two-sample test.

RESULTS

Tuber depletion

In all three years of study, the swans exploited the pondweed tuber banks from their arrival in mid-October to the end of October when they switched to sugarbeet harvest leftovers. Peak numbers in the Babelaar were 580 on 23 October 1995, 974 on 27 October 1996, and 944 on 16 October 1997. The cumulative foraging pressure was also about twice as high in 1996 compared to 1995. In 1995, the variation in cumulative foraging pressure was to a large extent explained by the silt content of the sediment and water depth (Fig. 3a; adjusted $R^2 = 0.60$, $F_{2,14} = 13.2$, $P < 0.001$). In 1996, much less of the variation was explained (adjusted $R^2 = 0.13$, $F_{1,15} = 3.5$, $P < 0.1$), and only water depth had a marginally significant effect (Fig. 3b). These were also the models selected by stepwise multiple regression. The GLM procedure gave basically the same results. For 1995, depth class (Type III $F_{1,14} = 10.5$, $P < 0.01$) and sediment class ($F_{1,14} = 11.2$, $P < 0.005$) both contributed to the model ($R^2 = 0.59$, $F_{2,14} = 10.2$, $P < 0.005$). For 1996, only depth class ($F_{1,15} = 7.7$, $P < 0.05$) significantly contributed. The avoidance of clayey sites may seem stronger in deep

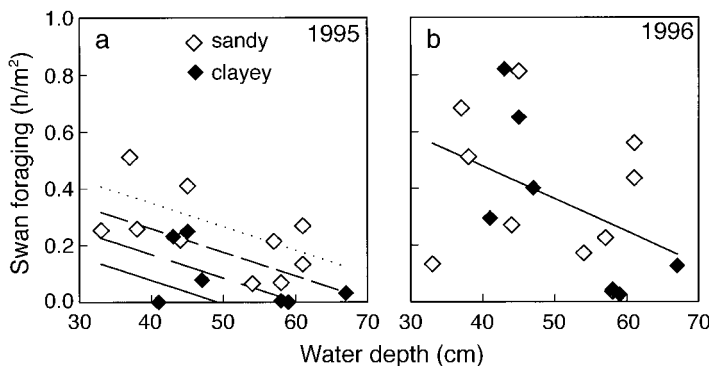


FIG. 3. Effects of water depth and silt content of the sediment on the swan foraging pressure in 1995 (Type II $F_{1,14} = 13.10$, $P < 0.005$, and $F_{1,14} = 14.55$, $P < 0.005$, respectively). Line type corresponds to sediment PCA values (Fig. 2): solid line (-4), long-dashed line (-2), short-dashed line (0), and dotted line (2). In 1996, only water depth had a marginally significant effect ($F_{1,14} = 3.45$, $P < 0.1$), and the simple linear regression line is drawn.

TABLE 2. Tuber densities (in grams dry mass per square meter; means \pm SD and range [in parentheses]) in 17 plots before and after swan exploitation.

Density	1995†	1996‡	1997‡
Initial	19.4 \pm 9.6 (6.9–42.4)	40.9 \pm 14.1 (13.9–67.3)	33.1 \pm 9.2 (15.5–50.1)
Final	14.5 \pm 9.8 (4.0–33.5)	21.2 \pm 8.8 (6.5–43.9)	18.4 \pm 10.8 (5.6–43.9)

† Sampling size = 12–18 cores per plot.
 ‡ $N = 36$ cores per plot.

than in shallow water in 1996 (Fig. 3b), but the interaction between depth class and sediment class was not significant.

The initial tuber densities varied greatly among years. The years of 1995 and 1996 were poor and rich years, respectively, with 1997 intermediate (Table 2). The spatial variation in tuber densities was also large within a year, both for the initial densities and the final densities of the plots (Table 2). This variation in final tuber density was to a large extent explained by the variables water depth and silt content of the sediment (Fig. 4; 1996: adjusted $R^2 = 0.62$, $F_{2,14} = 13.9$, $P < 0.0005$; 1997: adjusted $R^2 = 0.50$, $F_{2,14} = 9.0$, $P < 0.005$). For 1996 this was also the model selected by the stepwise multiple regression, but for 1997, the initial tuber density and depth were selected as the independent variables (adjusted $R^2 = 0.61$, $P < 0.0005$). Fig. 4 suggests that the effect of silt content is much stronger in deep than in shallow water. Indeed, the GLM procedure resulted in a model ($R^2 = 0.83$, $F_{3,13} = 21.7$, $P < 0.0001$) with depth class (Type III $F_{1,13} = 38.6$, $P < 0.0001$), sediment class ($F_{1,13} = 25.3$, $P < 0.0005$), and their interaction ($F_{1,13} = 15.2$, $P < 0.005$) as the independent variables. For 1996, the interaction term was not significant.

After accounting for the covariable initial tuber density, the effect of depth–sediment category on the swan consumption (initial minus final tuber density) was marginally significant for 1996 (Type III $F_{3,10} = 2.85$, $P < 0.1$) and significant for 1997 ($F_{3,10} = 5.03$, $P < 0.05$; Fig. 5). The calculated giving-up densities indicate that the swans tended to graze down shallow parts further than deep parts and sandy sites further than clayey sites. This latter effect was not apparent in shallow waters in 1997 (Table 3).

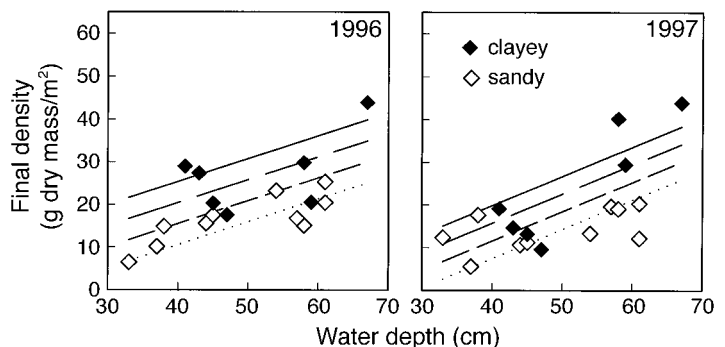
The density of shell fragments was 914 ± 1022 g/m² (mean \pm 1 SD). Despite the large variation among plots (from 58 to 3274 g/m²), the density of shell remains was not a significant predictor variable of either cumulative foraging pressure, swan consumption, or final tuber density.

Time allocation during foraging: comparing shallow and deep sites

An increase in feeding power was predicted to have a negative effect on the feeding time t (Fig. 6a). Both an increase in trampling power m_1 and, in particular, in trampling time τ were predicted to have strong positive effects on t (Fig. 6b, c). Also, a decrease in the metabolizable intake rate was predicted to result in an increase in t (Fig. 6d, read from right to left). Thus, factors that would decrease the net rate of energy intake affected t differentially. The surface time s was predicted to be rather short, but here a decrease in the net rate of energy intake led to an increase in s in all cases (Fig. 6a–d). When the original, theoretical parameter values of Houston and Carbone (1992) were used (Table 4), the same patterns were predicted by the time allocation model (not shown). These trends therefore hold for a wide parameter space.

The model predicted feeding times t in the range of the observed values (Fig. 7a). The feeding mode had a strong effect on t (Table 5), t being longer during up-ending than head-dipping. This was apparently not due to the expected higher power requirements for feeding during up-ending, since an increase in feeding power should result in a decrease in t (Fig. 6a). The t was also significantly longer in 1995 than in 1996, in particular during head-dipping (the interaction between year and feeding mode was significant; Table 5). With

FIG. 4. The effects of water depth and silt content of the sediment on the final tuber density in 1996 (Type II $F_{1,14} = 16.35$, $P < 0.005$, and $F_{1,14} = 12.89$, $P < 0.005$, respectively), and in 1997 ($F_{1,14} = 14.08$, $P < 0.005$, and $F_{1,14} = 4.76$, $P < 0.05$, respectively). Line type according to sediment PCA value: solid line (–4), long-dashed line (–2), short-dashed line (0), and dotted line (2).



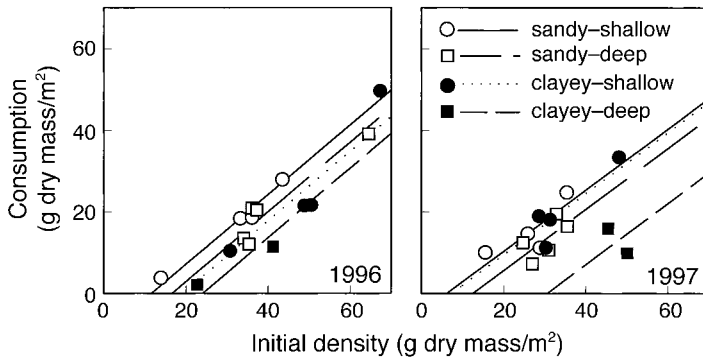


FIG. 5. The effect of depth-sediment category on the consumption (i.e., initial minus final tuber density) after accounting for the covariate initial tuber density (ANCOVA: 1996, $R^2 = 0.91$, $F_{4,10} = 25.48$, $P < 0.001$; 1997, $R^2 = 0.68$, $F_{4,10} = 5.42$, $P < 0.05$).

1995 being a poor year and 1996 a rich year, this was in accordance with our model (Fig. 6d).

The model predicted shorter surface times s than observed. As expected for underwater feeding, the surface time s was (positively) affected by t . The same held for the trampling time τ . After correcting for these effects of t , year of observation did not further contribute to the model (Table 5). During an up-ending bout, s and τ were both longer than during a head-dipping bout (Fig. 7b). Since the feeding mode affected t , part of the depicted differences in τ and s with feeding mode arise through differences in t . However, when we corrected for these effects of t , the s and τ still differed significantly between feeding modes (Table 5).

Harvest rates and heart rate: comparing sandy and clayey sites

The average heart rates during foraging on clayey sediment were 1.1–1.2 times those on sandy sediment (Table 6, except for swan AN during foraging without trampling). Because the heart rate does not increase linearly with oxygen consumption (Appendix B), the power requirements are calculated to be 1.2–1.4 times higher on clay than on sand. The few measurements we have on harvest rates suggest that harvest rates on clayey sediment were only ~ 0.6 times those on sandy sediment (Fig. 8).

DISCUSSION

Brown (1988) predicted that patches in the same microhabitat that differ in harvest rate, energy cost, or predation risk should yield different giving-up densities. This hypothesis has been successfully tested by

looking at sites that differ in predation risk. We measured giving-up densities of Tundra Swans foraging on belowground tubers within the confines of one lake. Foraging at less than ~ 10 m from the bank would yield some risk of predation by foxes (*Vulpes vulpes*), but the swans had ample opportunities to avoid that risk altogether. We could therefore rule out predation risk as the driving force.

The spatial variation in both swan foraging effort and giving-up densities was strongly related to water depth and, to a lesser extent, to the clay content of the sediment. The swans depleted shallow sites further than deep sites. They also depleted sandy sites further than clayey sites, at least in deep water. This is in broad agreement with previous work. Beekman et al. (1991) showed that swans tended to exploit pondweed stands in a fixed sequence. The northern parts in the Lauwersmeer, consisting of sandy sediments, were grazed prior to the southern parts that consist of more clayey sediments. Tundra Swans refueling on tubers at a stop-over site in the White Sea (Russia) only foraged around low tide. Nolet and Drent (1998) showed that in the course of the staging period the swans started and stopped foraging at progressively lower water levels, indicating that they exploited increasingly deeper parts of the tuber bank.

Tundra Swans forage in shallow water by head-dipping and in deep water by up-ending. We expected that the time allocation model would indicate that up-ending is more costly. The model predicted an increase in surface time with a decrease in net rate of energy intake. We indeed observed (slightly) longer surface time in up-ending swans. The model further predicted a decrease in feeding time with an increase in power requirements for feeding. However, we observed longer feeding times during the supposedly more costly up-ending than during head-dipping. Trampling times were also longer in deep water. Since, according to the model, an increase in trampling time should elicit a strong increase in feeding time, the conclusion that the longer feeding times in deep water are caused by longer trampling times seems justified. Foraging in deep water by up-ending might cause trampling behavior to be less

TABLE 3. Giving-up densities (in grams dry mass per square meter) for the four depth-sediment categories in the Bab-belaar as estimated by the x -intercept in the analysis of covariance (Fig. 5).

Category	1996	1997
Sandy-shallow	11.6	6.3
Clayey-shallow	19.2	7.4
Sandy-deep	16.6	12.5
Clayey-deep	24.0	30.6

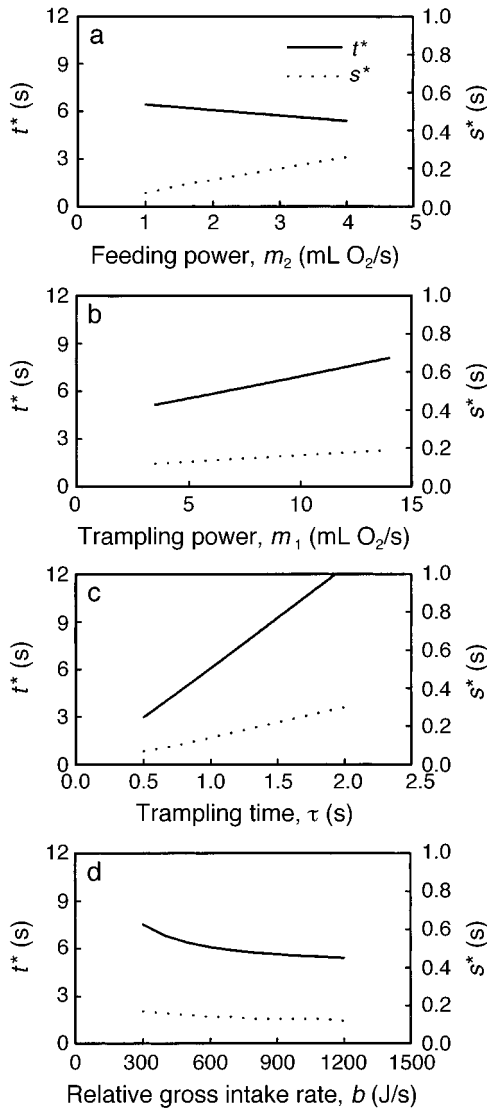


FIG. 6. The optimal feeding time (t^*) and optimal surface time (s^*) maximizing the net rate of energetic gain, subject to the constraint that the oxygen lost during feeding underwater is replaced by the oxygen stored during surfacing. The net intake rate will decrease with an increase in feeding power m_2 , trampling power m_1 , and trampling time τ , as well as with a decrease in the relative gross intake rate b . These changes will all lead to a small increase in s^* , while they affect t^* differentially. The parameter values in the basic model are given in Table 4.

effective, hence explaining the increase in trampling time. From the heart rate measurements it is clear that trampling is the most costly part of foraging. Through the reallocation of time toward longer feeding times, the swans limited the power requirements for foraging (i.e., calculated over the whole foraging bout) in deep water. Under the conservative assumption that up-ending is as costly as head-dipping, the power requirements for foraging in deep water was calculated (by combining the heart rate data from Appendix A and Fig. 7) to be only 1.06 times (1995) or 1.03 times

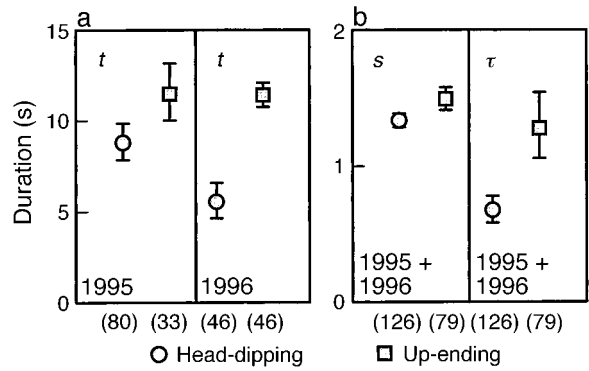


FIG. 7. (a) Back-transformed feeding time t grouped per feeding mode in 1995 and 1996 on sandy sites. (b) Surface time s and trampling time τ per feeding mode on sandy sites. The swans used head-dipping in shallow water and up-ending in deep water. Shown are the back-transformed averages and 95% confidence intervals. The number of focal observations is given below each plotted value, in parentheses.

(1996) as high as in shallow water. Of course, this difference is larger when the power requirements for up-ending are in fact greater than that of head-dipping. Harvest rates are also likely to be lower in deep water than in shallow water, because the deeper buried tubers may be beyond reach in deep water. Such an effect would further contribute to an increase in feeding times with water depth (Fig. 7d) and is also in the direction of a greater net rate of energy intake in shallow than in deep water.

We found that harvest rate was greater on sandy than on clayey sediment. This was not in accordance with

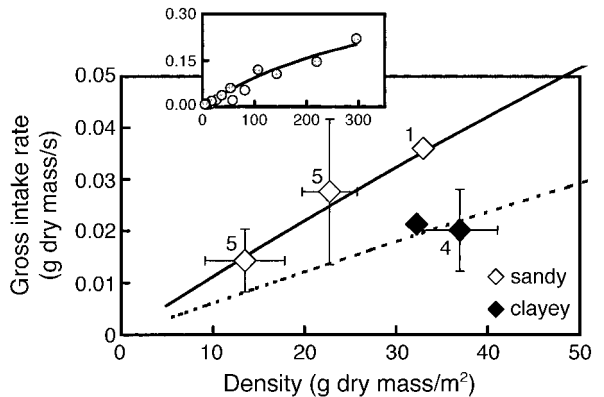


FIG. 8. Harvest rates of Tundra Swans. The inset depicts the functional response as measured on sandy sediment with wheat grain ($a = 0.00115 \text{ m}^2/\text{s}$, $t_h = 1.99 \text{ s/g dry mass}$, $R^2 = 0.98$, $N = 9$; only the gray points are included [see Methods]). The solid line is repeated in the large panel. In this panel, the data points are means $\pm 1 \text{ SE}$ of harvest rates of pondweed tubers in relation to average resource density measured in the field or in the basin (for the field data, only sample plots with an average foraging pressure of $>0.3 \text{ h/m}^2$ were included). Numbers next to symbols indicate sample size. The dashed line is the hypothetical functional response on clayey sediment.

TABLE 4. Basic parameter values of the time allocation model.

Parameter abbreviation	Definition	Original value†	Tundra Swan	Reference
K	Maximum oxygen store	10 mL O ₂	180 mL O ₂	Keijer and Butler (1982)
α	Exponent of oxygen replenishment	0.5	0.5	Houston and Carbone (1992)
m_1	\dot{V}_{O_2} during trampling	1 mL O ₂ /s	7 mL O ₂ /s	This study
m_2	\dot{V}_{O_2} during feeding underwater	1 mL O ₂ /s	2 mL O ₂ /s	This study
m_3	\dot{V}_{O_2} during surfacing	0.25 mL O ₂ /s	1 mL O ₂ /s	This study
b	Metabolizable energy intake rate	10 J/s	600 J/s	This study
θ	Exponent of depletion	1	0.83	This study
τ	Trampling time	2 s	1 s	This study (Fig. 7)
e	Energy per oxygen consumed	1 J/mL O ₂	20 J/mL O ₂	Schmidt-Nielsen (1983)

† Used in calculations by Houston and Carbone (1992).

previous work on harvest rate in relation to soil particle size (Price and Heinz 1984, Van Eerden and Munsterman 1997). In these studies, the size of the food items was somewhere intermediate between the smallest and largest soil particles tested. The harvest rate was probably reduced by the time the animals needed to separate the food and soil particles. In our study, the food items are always greater (1–20 mm) than the particle size of the sediment (maximum 0.5 mm); a similar interference of the food extraction is therefore not likely in this particular system. Based on our own experience we can state that sieving tubers out of silt takes much more time than out of sand. In addition, the power requirements for foraging on clayey sediment were slightly higher. This may at first be surprising, because smaller particles are resuspended more easily than larger ones. However, the resuspension is also strongly dependent on sediment cohesion (Blom et al. 1992). Our own experience with tuber sampling was that it was harder to extract the sampling core from clayey than from sandy sediment. Both findings indicate that the net rate of energy intake is greater on sandy than on clayey sediment.

The analysis of covariance revealed a slope of <1 (0.86 ± 0.10 in 1996 and 0.75 ± 0.19 in 1997, means ± 1 SE). This indicates that rich patches were underused relative to poor ones. The x -intercept of the analysis

of covariance thus yields the giving-up density of the poorest exploited patch within a depth–sediment category. There is more than one factor that should lead to a slope <1 (i.e., underutilization of rich patches): the extra costs of foraging, the so-called missed opportunity cost (Mitchell and Brown 1990), the incomplete knowledge of the birds about their resources (Valone and Brown 1989), or the spatial grouping of patches of similar quality (Morgan et al. 1997). Alternatively, the slope <1 is simply an artifact of the regression approach. Linear regression approaches (e.g., analysis of covariance) are useful tools to test specific hypotheses, but they minimize the least squares in the vertical (y) direction only. However, since in our case the variation occurs along both axes, geometric mean regression would give a better description of the data (Ricker 1984). Unfortunately, we do not have enough data per depth–sediment category to calculate the geometric mean regressions.

Tundra Swans feed in flocks, and the giving-up densities reported on here do not necessarily reflect decisions made at the individual level. Newly arriving swans sometimes visit a dense pondweed bed that has been already grazed upon by earlier swans (Van Eerden et al. 1997). We did not find evidence for such a second round of exploitation. However, we cannot exclude the possibility that part of the variation in final tuber den-

TABLE 5. The effects of year, feeding mode, and their interactions on log-transformed feeding time (t), surface time (s), and trampling time (τ). Given are the partial sum of squares (ss), i.e., the effect of each variable adjusted for the effects of the other variables in the model.

Variable	Feeding time, t		Surface time, s		Trampling time, τ	
	ss	F	ss	F	ss	F
Year	0.48	12.0***				
Log ₁₀ (t)	N/A†	N/A	0.09	9.9**	0.86	6.7*
Feeding mode	2.14	53.3***	0.10	10.2**	1.97	15.5***
Year \times feeding mode	0.45	11.3***				
Log ₁₀ ($t \times$ feeding mode)	N/A	N/A	0.06	6.8**		
Error	8.06		1.90		25.7	

Notes: Empty cells indicate nonsignificance. The degrees of freedom (df) = 1, except for the error term for which df = 205 - k - 1, where k is the number of included variables. For feeding time, $r^2 = 0.26$, $F = 24.0$, $P < 0.001$; for surface time, $r^2 = 0.10$, $F = 7.5$, $P < 0.001$; and for trampling time, $r^2 = 0.15$, $F = 17.9$, $P < 0.001$.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

† N/A = not applicable.

TABLE 6. Heart rates (median and mean ± SD) of captive swans foraging in a basin on sandy or clayey sediment.

Swan	Mass (kg)	Trampling	N	Heart rate (beats/min)†		P
				Sandy	Clayey	
AN	6.6	with	338	109 (113 ± 20)	121 (125 ± 20)	<0.0001
		without	154	92 (96 ± 18)	90 (91 ± 10)	<0.05
AP	4.5	without	699	89 (93 ± 17)	99 (103 ± 20)	<0.0001
AT	6.2	without	514	94 (98 ± 18)	111 (115 ± 18)	<0.0001

Note: Differences were tested with a median two-sample test.

† Excluding heart rates >200 beats/min.

sities arises from social interference (subordinates exploiting poorer patches than dominant swans; Dolman and Sutherland 1997, Van Eerden et al. 1997).

We found indications that habitat-specific giving-up densities are a consequence of differences in net rates of energy intake (Fig. 9). This is all the more interesting because the regrowth of the plant is related to the same habitat characteristics. In a laboratory experiment, the overwinter and in particular the sprouting survival of tubers proved to be significantly less in sandy sediment than in clayey sediment (L. Santamaría, unpublished manuscript). On the other hand, the maximum per capita tuber production was higher in sandy than in clayey soil, facilitating compensation during the growing season on sandy sediments (N. Jonzén, B. A. Nolet, L. Santamaría, and M. G. E. Svensson, unpublished man-

uscript). Shallow sites receive more light than deep ones (Reynolds 1984), favoring the regrowth at shallow sites. Van Vierssen et al. (1994) used the giving-up density reported by Beekman et al. (1991) to model the stability of the swan-pondweed system at different light regimes and found that enough tubers are left to safeguard a sustainable tuber bank. Our work clearly indicates the need for an extended swan-pondweed model with different giving-up densities and plant performances for combinations of water depth and sediment type.

Our results were in qualitative (but not in quantitative) agreement with the hypothesis that differences in net energy intake caused the spatial variation in giving-up densities. In Fig. 9 we assumed that the power requirements for foraging were twice as high in deep as in shallow water, but data on the feeding costs of up-ending are lacking. Hence, our findings stress the need for more conclusive and direct measurements of harvest rates and energetic costs in relation to water depth and sediment type. This will be an important next step toward unraveling the underlying mechanisms of depletion.

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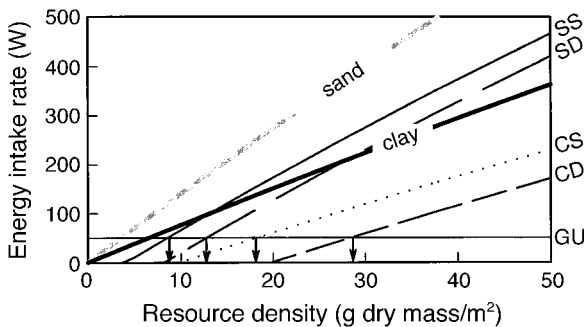


FIG. 9. The reconstructed hypothetical impact of water depth and sediment type on the relationship between the initial resource density and the rate of energy intake. The thick lines indicate the rate of metabolizable energy intake (MEI), representing the differences in harvest rate on sandy (gray line) and clayey (black line) sediments. This was calculated as $MEI = q \times e \times p \times GIR$, where GIR is the gross intake rate in grams dry mass per second (Fig. 8); q , e , and p are given in Appendix A. The net rate of energy intake is obtained after subtraction of the heat increment of feeding (0.2 MEI; Nolet and Drent 1998) and the power requirements for foraging. The latter were taken to be 1.3 times greater on clay than on sand and 2.0 times greater in deep than in shallow water. Thin lines indicate the net rate of energy intake at sandy-shallow (SS, solid line), sandy-deep (SD, long-dashed line), clayey-shallow (CS, dotted line), and clayey-deep (CD, short-dashed line) sites. The differences in harvest rate and energetic costs result in different giving-up densities among sites (arrows), at the same giving-up net energy intake rate (GU, horizontal line).

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APPENDIX A

PARAMETERIZATION OF THE TIME ALLOCATION MODEL

The maximum amount of oxygen that can be stored (K) was calculated from the size of the oxygen storage compartments in a 1.0 kg Mallard duck (*Anas platyrhynchos*) (Keijer and Butler 1982). Mallards use the same feeding modes as Tundra Swans. The measured oxygen stores (14.9, 12.3, and 1.8 mL O₂ in the circulatory, respiratory, and muscle systems, respectively) were scaled up to a 6.6 kg Tundra Swan using the mass exponents 0.91 for the respiratory system and 1.0 for the circulatory and muscle systems (Keijer and Butler 1982).

The rates of oxygen consumption were estimated from the heart rate measurements of swan AN while foraging in the basin on sandy sediment. The oxygen consumption during surfacing (m_3) was scaled up from measurements of 1.78 kg Barnacle Geese (*Branta leucopsis*) resting on the water surface (0.45 mL/s; Nolet et al. 1992). Using the body mass of AN (6.6 kg) and a mass exponent of 0.75 yields an oxygen consumption rate of 1.20 mL/s. The heart rate data of AN

(Table 5) gave estimates of its oxygen consumption during foraging without trampling (1.50 mL/s) and with trampling (1.97 mL/s). During foraging without trampling, the proportions spent surfacing and feeding underwater were 0.64 and 0.35, respectively. This gives an oxygen consumption during feeding (m_2) of 2.10 mL/s. During foraging with trampling, the proportions spent surfacing, feeding, and trampling were 0.40, 0.55, and 0.05, respectively. This gives an oxygen consumption during trampling (m_1) of 6.51 mL/s.

Based on the derived Holling disc equation (Fig. 8, inset), we calculated the cumulative metabolizable energy gain during tuber depletion from 20 to 10 g dry mass/m², using a proportion of feeding while foraging p of 0.8 (this study), an energy density e of 17.3 kJ/g, and an assimilation efficiency q of 0.9 (Nolet and Drent 1998). We then fitted a curve of the form $b \cdot r^\theta$ (PROC NLIN; SAS 1989) and obtained $b = 596$ J/s and $\theta = 0.834$.

APPENDIX B

CALIBRATION OF HEART RATE

Heart rate was calibrated by measuring heart rate and oxygen consumption simultaneously while the swans were resting in a respirometer and while walking on a treadmill.

A swan was confined on the treadmill (Marathon Type 7898.500, Heinz Kettler GMBH, Ense-Parsit, Germany) by a cage made of wire mesh. The other swans were put in front of the bird in order to put it more at ease. Before the treadmill was started, a bell was sounded to alert the bird. The bird walked for up to 15 min after which it rested for at least 30 min. Generally, a bird was walked for only 30 min each day. The swans were trained for 2 wk. We then took measurements over at least eight different speeds between 2 and 3 km/h, the sequence of which was randomly assigned.

In order to monitor the oxygen consumption of a bird while walking, a purpose-made, plastic mask (2 L) was placed over the bird's head and was sealed at the neck with foam. Air was drawn through the mask at a rate of ~ 34 L/min and dried by passing it through columns of silica gel. The main airflow was controlled and recorded by a control unit (Model 0154, Brooks Instrument, Veenendaal, The Netherlands) connected to a mass flow controller (Model 5851E, Brooks Instrument). A subsample of the main airflow was passed to an O₂ analyzer (Xentra 4102A1, Servomex, East Sussex, UK) and a CO₂ analyzer (Model 1410, Servomex). Ambient levels of oxygen and carbon dioxide were made at the start and end of each experimental run. The ambient temperature was monitored by a thermistor.

Two swans were held overnight in adjacent respirometers ($0.7 \times 0.7 \times 0.7$ m). They had free access to drinking water but were not given any food. A series of valves switched between the analyzers sampling from the respirometer and of ambient gas concentrations. Air was drawn at 20 L/min. The

air coming from each swan and the ambient gas levels were monitored for 20 min each hour.

A data logger (Squirrel 1250 series, Grant Instruments, Cambridge, UK) recorded the outputs from the gas analyzers and thermistor while a hard copy of the gas concentrations was made by also passing the signals to a pen recorder. As a further backup, a laptop computer also recorded the gas data via an A/D converter (DAQCard-A1-16E-4, National Instruments, Austin, Texas, USA). The rate of oxygen consumption (\dot{V}_{O_2}) was calculated as:

$$\dot{V}_{O_2} = \left(\frac{F_{I_{O_2}} \times (1 - F_{E_{O_2}} - F_{E_{CO_2}})}{(1 - F_{I_{O_2}} - F_{I_{CO_2}})} - F_{E_{O_2}} \right) \times \dot{V}_E$$

where F is the fraction concentration of the gas that is either entering (I subscript) or exiting (E subscript) the mask, and \dot{V}_E is the rate of flow of dry air out of the mask. The gas volumes were converted to standard conditions (273 K, 101325 Pa, dry air).

The whole system was calibrated by bleeding nitrogen into the mask at known rates (Fedak et al. 1981). The response time of the analyzers to a stepwise introduction of nitrogen was 11.5 s, while the time to full equilibration was 26.5 s. Heart rate and gas measurements were therefore synchronized by lagging the heart rate data by 20 s.

The log-log linear regressions of \dot{V}_{O_2} in milliliters per minute against heart rate (f_H) in beats per minute gave the following calibration curves for the swans that foraged in the basin:

$$\text{AN: } \dot{V}_{O_2} = 2.79 \times 10^{-2} f_H^{1.77} \quad (N = 12, R^2 = 0.95)$$

$$\text{AT: } \dot{V}_{O_2} = 5.30 \times 10^{-3} f_H^{2.07} \quad (N = 11, R^2 = 0.94).$$

AP refused to walk on the treadmill and no calibration curve was obtained for this swan.