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Wintering Swan Geese maximize energy intake through substrate foraging depth when feeding on buried *Vallisneria natans* tubers

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Abstract

Background: Foraging theory predicts that animals select patches that offer the highest net rate of energy gain. Hence, prey distribution patterns and spatiotemporal heterogeneity play important roles in determining animal feeding patch selection. For waterfowl foraging on buried aquatic plant tubers, the distribution and biomass of these plant organs vary with depth in the substrate. Since excavation costs also increase with depth, the energy intake of the animals foraging on these plants is highly sediment depth dependent.

Methods: Here, using observations of Swan Geese (*Anser cygnoides*) foraging on *Vallisneria natans* tubers, we test our hypothesis that geese feeding on tubers buried at intermediate sediment depth maximize their daily energy intake because of the interaction between tuber size and abundance with depth. To do this, we measured the distribution patterns of buried *Vallisneria* tubers under both undisturbed conditions and post-exploitation by geese (i.e. giving-up conditions). We investigated the relationship between tuber size and burial depth, and total tuber biomass within each sediment layer in undisturbed and exploited plots. Finally, we compared modelled Swan Goose daily energy intake feeding on *Vallisneria* tubers buried at different sediment layers (1–10, 11–20 and 21–30 cm below the surface).

Results: Dry weight of *Vallisneria* tubers linearly increased with burial depth, while average total dry weight density of tubers showed a unimodal relationship, peaking at intermediate levels. Not surprisingly, Swan Geese foraged most intensively on tubers buried at intermediate sediment depths, where they maximize their daily energy intake. Our results support our hypothesis that Swan Geese feeding on tubers at intermediate depths maximize their daily energy intake.

Conclusions: Our study is the first to quantify foraging strategies of Swan Geese during the wintering period, emphasizing the importance of plant traits on foraging selection of belowground foragers.

Keywords: Energetic trade-off, Optimal foraging, Shengjin Lake, Substrate, Tuber burial depth, Yangtze River

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Background

Animals need to satisfy their daily energy needs, but finding food is energetically costly, so consumers tend to select feeding patches which support the highest energetic intake rates (Murakami 1998), following the energy-maximizing hypothesis (Charnov 1976; Jeschke et al. 2002). Hence, prey or plant distribution patterns and their heterogeneity play an important role in determining densities of foraging predators and herbivores (the aggregative response, e.g., Rowcliffe et al. 1999). For example, herbivores feeding on highly digestible energy-rich tubers of plants aggregate in areas with the highest tuber densities, although this relationship is influenced by other factors affecting availability (Klaassen and Nolet 2007; Nolet and Gyimesi 2013).

Several waterfowl species feed on buried, over-wintering tubers of aquatic plants in underwater substrates, which may contribute to regulate the populations of these plants (Sponberg and Lodge 2005). The extraction costs associated with foraging on tubers increase with increasing tuber burial depth (Richman and Lovvorn 2009), so there is a selection pressure for tubers to be buried deeper in the substrate to avoid predation. However, for a given tuber size, the chance of germinating and sprouting to the surface successfully decreases with burial depth (Klaassen and Nolet 2007; Hamberg et al. 2017). For this reason, we would predict that plants balance the costs of such an avoidance strategy amongst deeply buried tubers by increasing their energy content to enhance the likelihood of successful germination and growth to the surface (Jokela et al. 2000). Hence, larger tubers are often found at deepest levels in the sediment, because costs of germination, shoot initiation and penetration to the surface increase with increasing burial depth (Santamaria and Rodriguez-Girones 2002).

Given this heterogeneity in size class distribution within the sediment, how the foraging strategies of tuber-feeding waterfowl respond to the belowground distribution patterns of over-wintering tubers is of great interest. Herbivores feeding on such belowground tubers may have a trade-off feeding on abundant, low quality tubers at shallow depths *versus* fewer but more profitable tubers deeper within the substrate, which cost more energy to extract. For example, despite a positive relationship between Fennel Pondweed (*Potamogeton pectinatus*) tuber size and burial depth, tuber density peaks at intermediate depths. Hence, among observed Bewick's Swans (*Cygnus columbianus*) feeding on Fennel Pondweed tubers, studies showed that it was most profitable for swans to forage at intermediate depths (Santamaria and Rodriguez-Girones 2002; Hidding et al. 2009).

The Swan Goose (*Anser cygnoides*) is a globally vulnerable species, which mainly breeds in Russia, Mongolia

and China and overwinters now almost exclusively in China where it is largely restricted to the Yangtze flood plain (Kear 2005; Cao et al. 2008). During winter, when the water level drops below the substrate surface they excavate pits in the substrate from which they extract tubers (Zhang et al. 2011; Kim et al. 2013), although they have also been observed grazing on sedges, *Carex* and grasses (Fox et al. 2008). In this study, we test the hypothesis that Swan Geese feeding on belowground tubers of *Vallisneria* mostly extract tubers buried at intermediate sediment depth, because these layers offer the greatest net intake of energy.

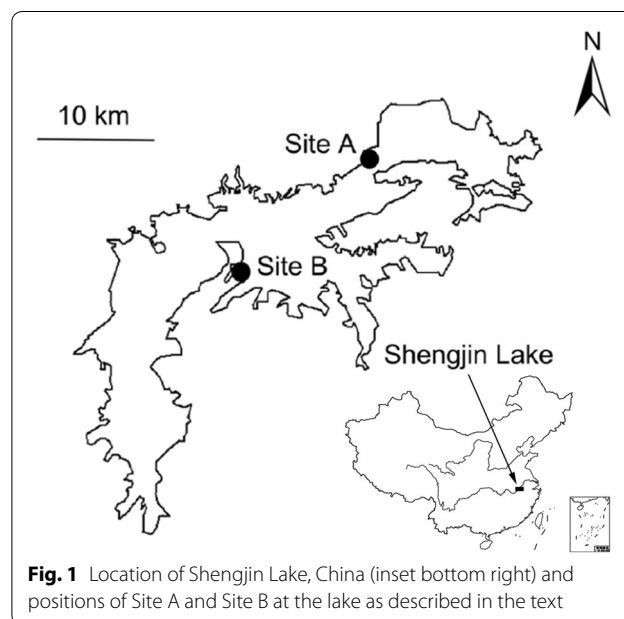
Methods

Study area

Shengjin Lake National Nature Reserve (30°15'–30°30'N; 116°55'–117°15'E), is situated south of the Yangtze River. It is a seasonally inundated freshwater lake of ca. 140 km² and a shoreline of 156 km in winter (Fig. 1). During the wet season, water level increases to ca. 17 m a.s.l. and falls to lower than 10 m a.s.l. in the dry season. A sluice built in 1965 is used to regulate water flow between Shengjin Lake and the Yangtze River, allowing water retention in winter when river levels fall. Average annual precipitation is 1600 mm, with most rain during April to August. Average annual temperature is 16 °C and average January temperature is 4 °C.

Study sites

Data presented in these analyses were collected at Sites A and B at Shengjin Lake from mid-December 2008



to early February 2009 (Fig. 1). Site A (30°22′01.47″N; 117°04′10.99″E) was an open flat area covered by water until late November. After early winter water level recession, this site was used by Swan Geese during early December. From mid-December, this site was abandoned because of the combined effects of rapidly receding water levels and dry weather conditions, resulting in a larger area of unexploited habitat. Site B (30°22′01.47″N; 117°04′10.99″E) is a relatively enclosed bay ca. 80 m wide, heavily used by Swan Geese from mid-December 2008 to early February 2009. At both sites, the sediment type is clay and *Vallisneria natans* was the dominant aquatic plant over-wintering in the form of tubers buried in the muddy lake substrate.

Diet composition

In winter 2008/2009, Swan Goose faeces were collected at the two sites, separately stored in paper bags and oven-dried at 50 °C for 48 h using an oven (DHG-9053A, Shanghai). At least 20 faecal pellets from the same day and site were pooled and mixed thoroughly by hand. Vegetation samples were also collected at each site. Dicotyledonous plant epidermis patterns were derived by coating leaves with nail polish, the layer peeled off when dry and photographs of the impressions of cell patterns were taken under a microscope. Sub-samples of faeces were diluted with water in a petri dish, and drops taken from this suspension, placed on a glass slide, spread out evenly and covered with a cover slip. From each slide, 20 fields were identified using photomicrographs and area measured using a grid of 0.04 mm² squares in the microscope eyepiece. However, no leaf epidermal fragments were found in the faeces, since all Swan Goose faeces contained fragments of *Vallisneria* tubers, readily identifiable by lack of cell structure and undifferentiated tissue, as well as compact dark flocculated fragments of tuber outer epidermis. A total of 100 fields were identified for each sample under the microscope (Owen 1975).

Determining *Vallisneria* tuber distribution

We observed the Swan Goose distribution every week at both Site A and Site B during the winter 2008/2009. The undisturbed distribution of buried *Vallisneria* tubers was determined in February 2009 at Site A. Seven 30 cm × 30 cm × 30 cm holes were excavated and tubers were extracted in situ within each of these quadrats within the substrate where they were unexploited by Swan Geese in these areas up to the sampling date. The quadrats were carefully excavated using a small shovel by removing mud layers to reveal each tuber. The vertical depth of each tuber from the substrate surface was measured to the nearest 1 cm from the surface level using a ruler. Tubers were put into separate paper

bags. By contrast, Site B was subject to intensive foraging after the sampling date (Fig. 2). Hence, after prolonged use by feeding Swan Geese, tubers were again extracted at Site B following the same method from five 30 cm × 30 cm × 30 cm sample holes in February 2009. In the laboratory, all derived *Vallisneria* tubers were washed and remaining substrate was carefully removed using a toothbrush and dried at 50 °C for 48 h (Fig. 2). The dry weight of each tuber was determined to the nearest 0.001 g using an analytic balance (Sartorius, Germany).

Excavation pit measurements

After Swan Geese had exploited the two sites for feeding on buried tubers, both areas exhibited numerous tuber excavation pits created by the birds. The largest and smallest diameters and the greatest depths of the pits dug by Swan Geese were measured to the nearest centimetre using a ruler (site A: $n = 50$, site B: $n = 28$).

Estimated Swan Goose daily energy intake

We estimated daily energy intake of Swan Geese in each layer following the method described by Fox et al. (2011). Swan Goose intake rate was determined using focal sampling. In total, 28 focal samples of individuals were observed. Daily tuber intake was estimated based



Fig. 2 Main photograph shows a view of Site B at the study area at Shengjin Lake, China, showing the excavation pits created by Swan Geese (*Anser cygnoides*) (shown in detail below left) to extract the overwintering tubers of *Vallisneria natans* (shown cleaned of sediment below right)

on the frequency of the observed goose found and swallowed the tuber. Time spent feeding was observed every 15 min using scan sampling based on the observation throughout daytime. Dropping rate was also recorded by focal sampling. Energy content for both tuber and dropping was analysed using a bomb calorimeter. In contrast to the earlier study, we further classified the tuber burial depth into three different layers (layer 1: 1–10 cm, layer 2: 11–20 cm and layer 3: 21–30 cm) and separately calculated the mean tuber dry weight within each layer. Moreover, the observed intake rate (number of tubers consumed per minute) was the average value of three layers in the analysis of Fox et al. (2011). As tuber intake rate is closely linked to tuber density, we therefore adjusted the intake rate of each layer by multiplying the percent of tubers in each layer to determine the average intake rate in each layer. Finally, the daily energy intake was estimated by subtracting the energy content of daily output in droppings from that of daily food intake.

Statistical analysis

We calculated the average tuber dry weight density (g/m^2) at each burial depth class based on the undisturbed data. To test if there was a relationship between tuber dry weight and tuber depth, a quadratic regression model was applied to ln-transformed tuber dry weight mass data from the unexploited area. A t -test was used to detect if there is a difference between undisturbed (original) and disturbed (giving-up) tuber total dry weight of each layer.

A t -test was also applied to test for differences in excavation pit greatest depth, largest and smallest diameters between Site A and Site B. The data were square root transformed to reach the assumption of normality. Statistical analyses were conducted in R 2.15.2 or SPSS 19.0.

Results

Diet analysis

Diet analysis showed that all 100 samples taken from December to January comprised 100% *Vallisneria* tuber fragments and those in February 98% (another 2% was grass), confirming that geese almost exclusively fed on *Vallisneria* tubers at these sites during these months.

Vallisneria tuber distribution

There was a positive relationship between tuber dry weight and tuber depth for undisturbed original tuber distributions down to 30 cm depth (dry weight (g) = $0.015 \times \text{depth (cm)} + 0.039$, $p < 0.001$, $r^2_{\text{adj}} = 0.26$, $n = 196$; Fig. 3). A quadratic regression model captured the relationship between mean tuber dry weight density (g/m^2) and tuber burial depth well, with highest tuber

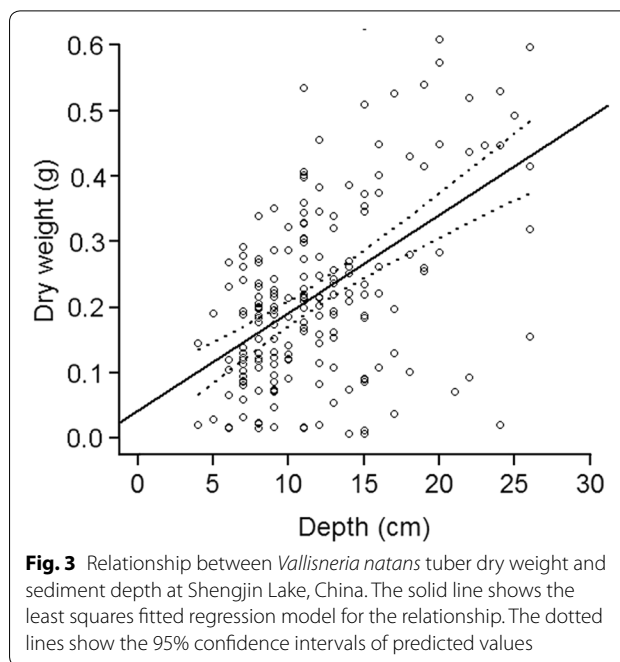


Fig. 3 Relationship between *Vallisneria natans* tuber dry weight and sediment depth at Shengjin Lake, China. The solid line shows the least squares fitted regression model for the relationship. The dotted lines show the 95% confidence intervals of predicted values

biomass densities at intermediate depths ($r^2_{\text{adj}} = 0.31$; main term: $b = 0.407$, $t = 3.292$, $p = 0.004$; squared term: $b = -0.014$, $t = -3.434$, $p < 0.03$; Fig. 4).

Comparing undisturbed (Site A) and post-feeding (Site B) total tuber dry weight in each layer indicated that the total dry weight in layer 2 was significantly less in Site B post exploitation by geese compared to site A where tubers were undisturbed ($t = 3.014$, $\text{df} = 10$, $p = 0.013$). There were no significant differences in total dry weight in layer 1 ($t = 0.867$, $\text{df} = 10$, $p = 0.406$) and layer 3 ($t = -0.033$, $\text{df} = 10$, $p = 0.974$; Fig. 5).

Excavation pit dimensions

Mean greatest depth, largest and smallest diameters of tuber pits excavated by Swan Geese were respectively 12.2 ± 0.62 , 23.9 ± 1.68 and 18.0 ± 1.06 cm (mean \pm 95% CI). There were no differences in depth ($t = 1.759$, $\text{df} = 72.207$, $p = 0.083$), long ($t = -0.070$, $\text{df} = 76$, $p = 0.945$) and short diameters ($t = 1.059$, $\text{df} = 76$, $p = 0.293$) of digging pits between site A and site B.

Daily energy intake

The average tuber dry weight of each layer from top to bottom was respectively 0.15 ± 0.02 g (mean \pm 95% CI, $n = 87$), 0.26 ± 0.03 g ($n = 97$) and 0.35 ± 0.10 g ($n = 17$). The daily energy intake rate was highest in layer 2, with 2836 kJ per day, compared to 1372 kJ in layer 1 and 663 kJ in layer 3 (Table 1).

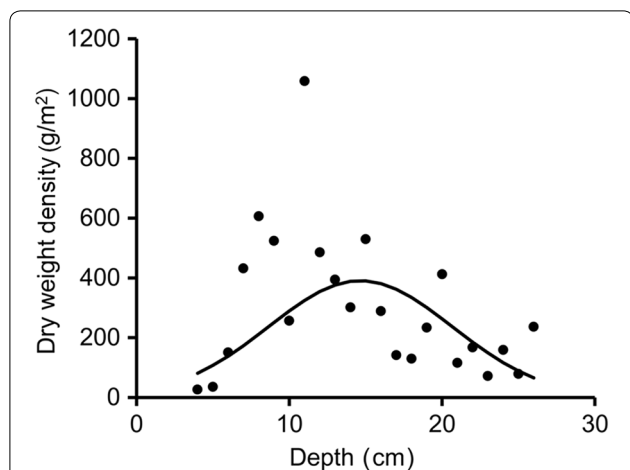


Fig. 4 Relationship between average *Vallisneria natans* tuber dry weight density (g/m^2) and tuber burial depth at Shengjin Lake, China. Predicted values (solid line) were calculated from back-transformed data on the basis of a quadratic regression on \ln -transformed tuber dry weight density values

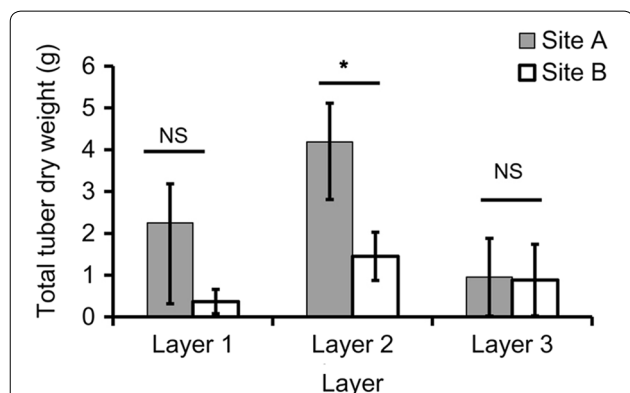


Fig. 5 Comparing undisturbed and disturbed (giving-up) *Vallisneria natans* tuber dry weight in different sediment layers at Shengjin Lake, China. Error bars show 95% confident intervals

Discussion

We demonstrated a linear relationship between *Vallisneria* tuber dry weight and burial depth, which increased with increasing burial depth in a Yangtze wetland (Fig. 3). However, the tuber dry biomass showed a different pattern, with the highest total biomass levels found at intermediate sediment depth (Fig. 4). Interestingly, we found that *Vallisneria* tubers buried at intermediate depths were also most heavily harvested by Swan Geese (based on the comparison of undisturbed versus post-feeding total tuber dry weight in different sediment layers and measuring depths of extraction pits). Our energy intake estimations also suggested that Swan geese obtained the highest levels of energy intake by extracting *Vallisneria* tubers buried at intermediate sediment depth.

The increasing dry weight of *Vallisneria* tubers with sediment depth reflects results from a study of *P. pectinatus* tubers, which showed a similar pattern (Hidding et al. 2009). Tubers buried in deep sediment can decrease their predation risk, interpreted as a herbivore avoidance strategy (Santamaria and Rodriguez-Girones 2002). However, the possibility of successful sprouting decreases with increasing burial depth for a tuber of a given size for *P. pectinatus* (Santamaria and Rodriguez-Girones 2002) and *Vallisneria americana* (Rybicki and Carter 1986), which may explain the increasing size of tubers buried in deeper sediments. Our result also revealed that *Vallisneria natans* tubers deepest within the sediment had higher dry weights compared to tubers at shallower depths. Through such a strategy, tubers likely increase their fitness by decreasing their accessibility to Swan Geese, reducing the predation risk and increasing the chances of sprouting and reaching the surface in the following spring.

Our results also suggest that the total tuber dry weight peaked at intermediate depth (11–20 cm). This result is consistent with the study on *P. pectinatus* in which the

Table 1 Comparing daily energy intake of Swan Goose feeding on the *Vallisneria natans* tuber buried at different sediment layers at Shengjin Lake, China

Sediment layers	Mean tuber dry weight (g) <i>a</i>	Total daily feeding time (min) <i>b</i>	Number of tubers	Tuber intake rate (tubers per min) <i>c</i>	Tubers consumed per day $d = b \times c$	Total tuber dry weight consumed per day $e = a \times d$	Tuber energy content (dry weight) (kJ per g) <i>f</i>	Total daily intake (kJ per day) $g = e \times f$
Layer 1 (1–10 cm)	0.15 ± 0.018 (86)	442.2	87	1.40	619.08	92.86	14.77 ± 0.14 (4)	1371.57
Layer 2 (11–20 cm)	0.26 ± 0.029 (97)		104	1.67	738.47	192.00		2835.89
Layer 3 (21–30 cm)	0.35 ± 0.100 (17)		18	0.29	128.24	44.88		662.93

Mean tuber dry weight of each layer was calculated based on tuber dry weight. The total daily feeding time and tuber energy content were obtained from Fox et al. (2011), whereas the tuber intake rate was calculated from Fox et al. (2011) using the percentage of tubers at each layer (including number of burned tubers). Values indicate means \pm 95% confidence intervals. Numbers in parentheses indicate sample size

mean tuber density was larger at a depth of 10–15 cm (Hidding et al. 2012). Although there were some larger tubers distributed in the deepest sediment, the tuber density was smaller, reducing profitability to Swan Geese in the face of mounting costs of extraction from the lowest levels. However, this result may indicate that plants have invested in deep burial of large tubers as an adaptation to herbivore predation. Such anti-herbivore strategy, achieved through phenotypic plasticity, is well known among plant species as a means to maximize relative fitness (Hanley et al. 2007; Ward et al. 2012). However, as our results are only based on 1 year of data, we are cautious about making such claims for *V. natans*, for which a long-term study is necessary to fully understand the plant's tuber anti-herbivore strategy.

Swan Goose foraging strategy and the energy intake estimation

The diet analysis showed that Swan Geese intensively feed on *Vallisneria* tubers at Shengjin Lake although our former study showed that they also grazed on grasses and sedges (Fox et al. 2008). Swan Goose feeding behaviours can be affected by water level fluctuations (Zhang et al. 2011), influencing their diet composition. Field observation showed that Swan Geese spent more time on feeding when grazing on sedges comparing to excavating *Vallisneria* tubers (Fox et al. 2008). One potential explanation could be explained by differences in food digestibility, because the fibre content of *Vallisneria* tubers is much lower than that of graminoid species. Studies have shown that energy intake rate is often limited by the food processing rate or rate of nutrient absorption in the digestive tract (Kersten and Visser 1996; Wilmshurst et al. 1999; Oudman et al. 2014), the maximum rate of energy assimilation (Weiner 1992; Ydenberg 1998). In winter, birds need to maximize their probability of survival for breeding in the next year (Caraco 1979), hence increasing foraging efficiency and predator avoidance are paramount. As time limitation, predation and disturbance risk also increase with increasing feeding time (Chudzin-ska et al. 2015), and it is essential for Swan Geese to aim to maintain the highest feeding efficiency possible. Foraging on *Vallisneria* tubers may be more efficient in terms of energy intake and time spent feeding than grazing poorer quality graminoids. Such evidence was also found for Tundra Swans that fed on Fennel Pondweed tubers, because of the high-energy assimilation rate, which these provided (90%; Klaassen and Nolet 2007).

In line with our prediction, tubers buried at intermediate depth were most heavily harvested, based on the depth of extraction pits and comparing the differences between undisturbed and disturbed tuber dry weight between layers (Fig. 5). Optimal foraging theory predicts

that animals should maximize their energy intake per unit time (Emlen 1966; Macarthur and Pianka 1966; Pyke 1984). Foraging on higher biomass patches (in this case intermediate sediment depths) can increase foraging success and increase energy intake rate (Bergman et al. 2001). To maximize fitness, animals behave as time minimizer or energy maximizer, although these may not be mutually exclusive (Langvatn and Hanley 1993). Anatidae species often use a strategy of energy maximization (Amano et al. 2004; Nolet et al. 2006; Wang et al. 2013). Digging for deeper buried tubers by Swan Geese is a time and energy-consuming process but geese benefit from the larger tuber sizes there. Our result showed that Swan Geese had a daily intake (2836 kJ) by digging for tubers at intermediate depth, where biomass density was double and fourfold compared to digging shallower or deeper layers respectively (Table 1). Daily energetic expenditure (DEE) of Swan Geese was calculated as 2200 kJ per day and the energy excreted from the production of droppings was estimated as 212 kJ per day (Fox et al. 2011). The net daily energy intake was then 2624 kJ for digging in intermediate deep sediments, as calculated from the difference between daily energy intake and energy excreted in droppings, which was higher than calculated DEE. Net energy intake acquired by digging in other layers was far less than DEE. Although we may overestimate daily energy intake as Swan Geese also fed in shallower sediments, the species can maximize their daily energy intake by foraging more at intermediate sediment depths. Migratory birds accumulate body mass in late winter in preparation for migration (Alerstam and Lindström 1990; Fox et al. 2003). By following this strategy, Swan Geese are potentially able to improve their energy balance and prepare for spring migration by active accumulation of energy stores.

Conclusions

In summary, our results are in agreement with our hypotheses that Swan Geese foraging on tubers buried at intermediate sediment depth maximize their daily energy intake. Although foraging in deeper sediments is energetically more costly, food biomass and density interact to play a critical role in determining the animals foraging selection, emphasizing the importance of plant traits on foraging selection of belowground foragers such as the Swan Goose.

Authors' contributions

YZ, ADF, and LC conceived the idea. YC and YZ conducted the field work. YC, YZ and WFD analysed the data. YZ and ADF wrote the manuscript. All authors read and approved the final manuscript.

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Competing interests

The authors declare that they have no competing interests.

Availability of data and materials

The data used and analyzed in this study are available from the corresponding authors on reasonable request.

Consent for publication

Not applicable.

Ethics approval and consent to participate

Not applicable.

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