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Abstract.—Allometric scaling law predicts that herbivores respond differently to the availability of resources, mediated by body size. However, studies of allometric responses have often focused on animals with a relatively large difference in body size. Here, using a correlative field study, habitat use by two herbivorous species, the Bean Goose (*Anser fabalis*) and the Greater White-fronted Goose (*A. albifrons*), with a relatively small difference in body size was investigated during the wintering period. Both a generalized linear mixed model and a mixed logistic regression model showed that both species selected lower lying areas that were recently exposed, and, as expected, the smaller Greater White-fronted Goose showed a stronger selection of foraging habitat than the larger Bean Goose. Sward height also influenced habitat selection by both species, and the smaller species selected shorter swards than the larger species. In terms of forage quality, both models failed to detect a significant effect of nitrogen content on goose habitat selection. A logistic regression model showed that structural heterogeneity of the sward negatively correlated with the patch selection of the smaller species, but for the larger species such a correlation was not found. In agreement with our hypotheses, our results provide some preliminary indication that coexistence of the two goose species studied here might be mediated by an allometric response even if the difference in body size is relatively small. *Received 31 March 2015, accepted 3 October 2015.*

Key words.—*Anser albifrons*, *Anser fabalis*, Bean Goose, body size, forage quality, forage quantity, grassland, Greater White-fronted Goose, habitat selection, heterogeneity.

Explaining how species coexist is one of the central objectives in both basic and applied ecology. Coexistence of similar species may occur if fluctuations in environmental conditions favor different species at different times or places (Amarasekare and Nisbet 2001). A life-history trade-off is often used to illustrate species coexistence when competition for resources is asymmetric (Skellam 1951; Qvarnstrom *et al.* 2009). For species having a rather similar life-history, resource partitioning and environmental heterogeneity may mediate species coexistence. However, the underlying mechanisms are still not clear. The Jarman-Bell Principle (Bell 1970; Jarman 1974) proposed an ecophysiological explanation for the coexistence of herbivores differing in body size. They assumed that smaller herbivore species require higher quality food than larger species due to their higher metabolic demands, while larger species require larger quantities of food and are more tolerant of lower quality food. According to the allometric scaling theory, species differing in body size should respond differently to the environment, and hence body size differences facilitate species coexistence (Prins and Olff 1998). However, older studies on allometric responses often focused on species with relatively large differences in body size (Laca *et al.* 2010).

The availability of resources often exhibits spatial and temporal variation (Fryxell *et al.* 2005; Zhang *et al.* 2015). Vegetation height is often regarded as an important index for the variation in forage quantity, and hence different grazer species specialize in different foraging heights (Murray and Illius 2000; Durant *et al.* 2004; Heuermann *et al.* 2011). Forage quality is another factor affecting forage patch selection (Wilmshurst and Fryxell 1995; Prins 1996; Riddington *et al.* 1997), and factors such as plant nitrogen and fiber content are often used to predict forage selection in herbivores (Albon and Langvatn 1992; Post and Klein 1996; van der Wal and Loonen 1998). Anatidae species are sensitive to variation in forage quantity and

quality (Ydenberg and Prins 1981; Sutherland and Allport 1994), whereby nitrogen content is one of the best predictors for their habitat selection (Owen *et al.* 1977; Percival 1993; McKay *et al.* 1994). Plant quality generally decreases over the growing season with increasing plant height and biomass (van der Wal *et al.* 2000). With increasing plant height, the nitrogen content decreases (Prins and Olff 1998; Hassall *et al.* 2001), whereas the fiber content increases (Gekara *et al.* 2005). Foragers face a trade-off between maximizing forage quantity and quality. Foraging theory suggests that herbivores select their habitat based on differences in body size (Gunnarsson *et al.* 2005; Hopcraft *et al.* 2010; Clauss *et al.* 2013); smaller bodied species generally forage on shorter swards that contain a higher nutrient content, whereas larger species exhibit a higher intake rate and are less sensitive to variation in forage quality, and therefore select taller swards (Durant *et al.* 2003, 2004; Heuermann *et al.* 2011). Hence, body size plays a pivotal role in habitat selection in relation to forage quality and quantity, and the effect of these forage variables on differences in species abundance could be used to understand the differences in spatial distribution of the species and species coexistence.

The elevation of the grassland in wetlands may play a vital role in determining forage availability for geese in these areas, as it is directly related to inundation frequency and exposure of recessional grassland (Adam 1990; Olff *et al.* 1997). Forage quality and quantity and sward structure depend to some extent on inundation patterns (Kuijper and Bakker 2005), and hence spatial differences in forage quantity and quality along the elevation gradient are expected to influence the abundance of different herbivorous species.

In China, the wetlands of the Yangtze River comprise an important area for migrating birds. During autumn and early winter, water levels drop in these wetlands, thus increasing the size of exposed recessional grasslands. As water levels drop, higher elevation areas experience relatively warmer air temperatures and have a longer growing period than areas at lower elevations.

We studied Bean Goose (*Anser fabalis*: body weight: ~3,200 g, bill length: ~63 mm; Kear 2005; Ruokonen *et al.* 2008) and the slightly smaller Greater White-fronted Goose (*Anser albifrons*: ~2,400 g, ~46 mm; Beer and Boyd 1963; Kear 2005), which both occur in wetlands of the Yangtze River. We tested the following hypotheses: 1) both species will mainly be found in lower elevation areas where forage biomass is lower but with a higher forage quality, while the smaller Greater White-fronted Goose will be more sensitive to elevation and select relatively lower lying areas compared to the larger Bean Goose; and 2) an increase in the structural heterogeneity of the sward (measured by the standard deviation of sward height) will have a stronger negative effect on the smaller bodied species than on the larger bodied species.

Methods

Study Area

The Shengjin Lake National Nature Reserve (30° 15' to 30° 30' N, 116° 55' to 117° 15' E), with an area of 333 km², lies south of the Yangtze River in the Anhui Province of China. The protected area includes Shengjin Lake, a large and shallow, permanent freshwater lake with a 165-km shoreline. Water comes from three rivers flowing directly into the lake and from the Yangtze River via a sluice built in 1965. During the wet season in summer, the maximum lake area is 140 km² (water level = 17 m above sea level). During the dry season in winter when the water level falls to less than 10 m above sea level, the lake area decreases to approximately 34 km², exposing extensive mudflats, grasslands, sedge (*Carex* spp.) meadows and seasonal wetlands. The dominant species of the exposed mudflats are sedges. The climate is characterized by a subtropical monsoon with an average annual rainfall of about 1,600 mm. Average annual temperature and average January temperature are 16.1 °C and 4.0 °C, respectively. The Shengjin Lake National Nature Reserve is an important wintering site for wildfowl, as every year more than 50,000 geese overwinter there (Cheng *et al.* 2009). The majority of these are Bean and Greater White-fronted geese.

Transects and Dropping Counts

We selected three sites that were frequently visited by the two geese species (Fig. 1). In winter, from November 2011 to March 2012, two parallel transects from the lake dyke to the water's edge were established at each site (approximate length was 200 to 300 m). Transects covered the entire gradient from higher to lower
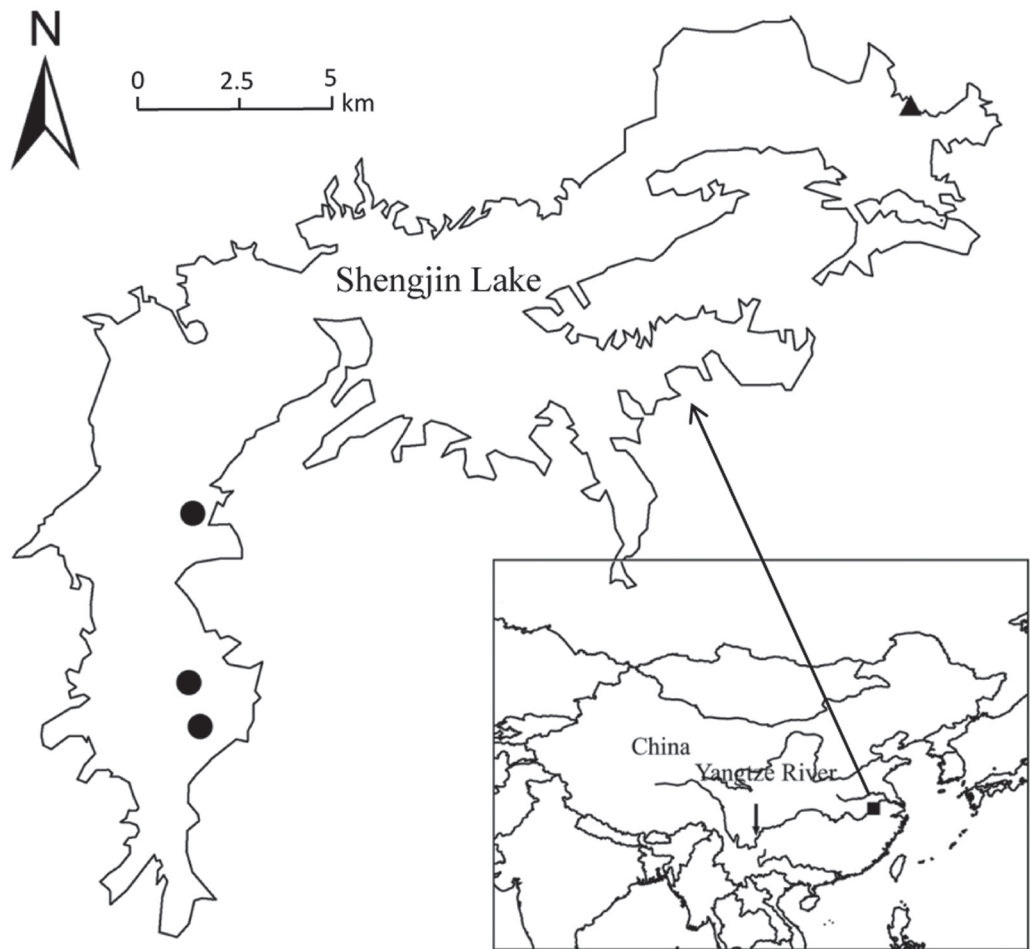
Figure 1. The geographical location of Shengjin Lake and the three study sites (black dots).

grassland. We set short bamboo pegs at every 10 steps at two of the corners to demarcate 1 × 1-m quadrats. Every month, we measured sward heights with a disc pasture meter (diameter: 10 cm, weight: 5 g) (Zambatis *et al.* 2006) within each 1 × 1-m quadrat along the transects. A total of 17 measurements were taken in each quadrat, systematically divided over the center, and horizontal, vertical and diagonal directions of each quadrat, the placement is illustrated in Fig. 2. A mean value and associated standard deviation was calculated for each quadrat to avoid pseudo-replication.

Dropping density is a good estimate of the amount of grazing by goose species (Owen 1971; Olff *et al.* 1997; Madsen *et al.* 2014). Before the survey, we observed bird flocks with only a single species (Bean or Greater White-fronted goose) within Shengjin Lake. We collected droppings from the two different species separately and measured the diameter of each dropping with a ruler to the nearest millimeter to confirm the differences in dropping size between goose species: Bean Goose mean = 11.5 ± 1.2 mm SD (n = 1,291) and Greater White-fronted Goose mean = 9.2 ± 0.9 mm SD (n = 1,430).
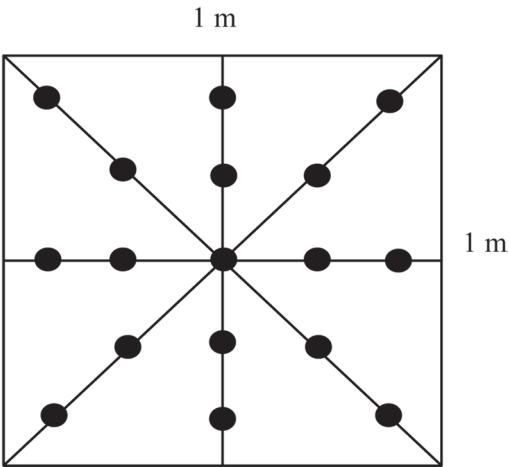

Figure 2. An illustration showing the location where the 17 measurements were taken within each 1-m × 1-m quadrate. The black dots indicate the location where sward height was measured.

This method allowed us to identify the species to which the droppings found in the field belonged. Within each quadrat, we counted the number of Bean and Greater White-fronted geese droppings per species based on this difference in dropping diameter once a month from November 2011 to March 2012 ($n = 5$). Droppings were removed from the quadrats after every count. With decreasing water level, the length of the transects and the number of quadrats were increased to cover the larger exposed area. At one site, we counted very few droppings due to high human disturbance in February and March, and hence the data during this period at this site were excluded from further analysis.

Vegetation Samples

For the duration of our study, between the two transects at each site, we constructed five 2 × 2-m exclosures placed at approximately equal distances along transects to prevent grazing by geese and other herbivores. We collected leaf samples to analyze nitrogen and acid detergent fiber (ADF) content within each exclosure every month. Biomass was not measured in these 2 × 2-m exclosures. Each month, we removed and placed exclosures at a new location at equal elevation to account for self-shading effects and sampled the plants that geese ate for chemical composition.

Measuring Plot Elevation

We measured the elevation of each 1 × 1-m quadrat at all three sites using a level instrument (DSZ2, Suzhou FOIF Co. Ltd.) in April 2012. After that, relative elevation (measuring the differences of elevation among quadrats) was calculated using the quadrat with the lowest elevation as the baseline.

Statistical Analysis

The linear regression models were first applied to detect the relationship between the potential variables and the dropping densities for each of the two goose species. Our dropping count data included many zero counts. To account for over-dispersion in the data, we fitted a zero-inflated negative binomial generalized linear mixed model (GLMM) with month and site as random effects. Before fitting the multiple regression models, we also assessed multi-collinearity by examining the variance inflation factors of the candidate variables, by including all candidate variables as independent variables in a regression model and dropping density as a response variable. The results of a multi-collinearity test suggested little collinearity among variables (Table 2). Then, the final model was constructed using both forward and backward variable-entry procedures for both species. For variables that occurred in the final models of both species, we further fitted a zero-inflated negative binomial GLMM, including the interaction terms between species and vegetation variables with month and site as random effects to detect the differences in species' responses.

We also fitted a logistic regression model with month and site as random factors using dropping presence/absence data for each species. We applied both forward and backward variable-entry procedures to construct the final models for both species. Then, for variables that occurred in the final models of both species, we also fitted a zero-inflated negative binomial GLMM, including the interaction terms between species and vegetation variables with month and site as random effects to detect the differences in species' responses.

The potential independent variables and their abbreviations are provided in Table 1. Statistical analyses were conducted in statistical program R (R Development Core Team 2012) with the packages MASS, pscl, glmmADMB and lme4. We considered results of statistical tests significant at $\alpha = 0.05$.

Results

A significant negative relationship between relative elevation, sward height and habitat heterogeneity (Table 3; Fig. 3A-F) and dropping densities of both goose species was found. The dropping densities of both Bean and Greater White-fronted geese increased with increasing nitrogen content (Table 3; Fig. 3G, H). The relationship between Bean Goose dropping density and ADF content was negatively correlated, but there was no relationship between the dropping density of Greater White-fronted Goose and ADF content (Table 3; Fig. 3I, J).

Table 1. Independent variables and predicted relationships for the Bean Goose and Greater White-fronted Goose.

Independent Variable	Note	Unit	Predicted Effect	
			Bean Goose	Greater White-fronted Goose
Relative elevation	Differences among quadrats	cm	-	- -
Sward height	The average values were calculated	cm	-	- -
Nitrogen content	Measurements of grass nitrogen content	%	+	+ +
ADF content	Measurements of grass ADF content	%	-	- -
Habitat heterogeneity	Standard deviation of sward height	no unit	-	- -

ADF = acid detergent fiber; + = positive effect; + + = strong positive effect; - = negative effect; - - = strong negative effect

Table 2. Pearson correlation coefficients between independent variables, and Variance Inflation Factors (VIF).

Variables	Nitrogen Content	ADF Content	Sward Height	Habitat Heterogeneity	VIF
Relative elevation	-0.481***	0.102*	-0.084*	-0.287***	1.461
Nitrogen content		-0.385***	0.045	0.187***	1.624
ADF content			0.074	-0.104**	1.232
Sward height				0.217***	3.061
Habitat heterogeneity					3.116

ADF = acid detergent fiber; n = 623 (*P < 0.05; **P < 0.01; ***P < 0.001).

Zero-inflated Negative Binomial GLMM

The final models (Table 4) showed that relative elevation and sward height were negatively related to dropping densities of Bean and Greater White-fronted geese. ADF content was negatively related to dropping densities of the Bean Goose but not to dropping densities of the Greater White-fronted Goose.

As predicted, relative elevation was negatively related to the fecal density of both species (Table 4), suggesting that both species used relatively lower elevation areas that became exposed later in winter. The slope of the elevation term was significantly different between species (interaction term: β = 0.006, SE = 0.002, Z = - 2.95, P = 0.003). The larger slope coefficient for the Greater White-fronted Goose showed that the smaller species used lower areas more often than the larger Bean Goose.

Sward height was negatively related to fecal density for both species (Table 4). The species × sward height interaction was significant (β = - 0.110, SE = 0.035, Z = - 3.25, P = 0.001). These results suggest the smaller Greater White-fronted Goose used shorter swards compared to the larger Bean Goose.

ADF content was negatively related to Bean Goose fecal density but was not related to fecal densities of the Greater White-fronted Goose. Nitrogen content and structural heterogeneity of the vegetation were not correlated with either Bean Goose or Greater White-fronted Goose fecal densities, which was inconsistent with our predictions (Table 4).

Logistic Regression Model

Results of the logistic regression model were similar to the zero-inflated model. Negative slopes existed between fecal densities and relative elevation (Table 5). The slopes for relative elevation were similar for the two species (interaction term: β = 0.003, SE = 0.003, Z = 1.054, P = 0.282). Sward height also was negatively related to fecal densities of both species (Table 5). As in the zero-inflated model, the slope coefficient was larger for the Greater White-fronted Goose than for the Bean Goose (interaction term: β = -0.110, SE = 0.04, Z = - 2.738, P = 0.006).

DISCUSSION

Our results demonstrate that landscape features and food resources may influence how herbivores use foraging patches. As predicted, model results suggest that factors

Table 3. Results of linear regression model between dropping densities of Bean and Greater White-fronted geese and the explanatory variables.

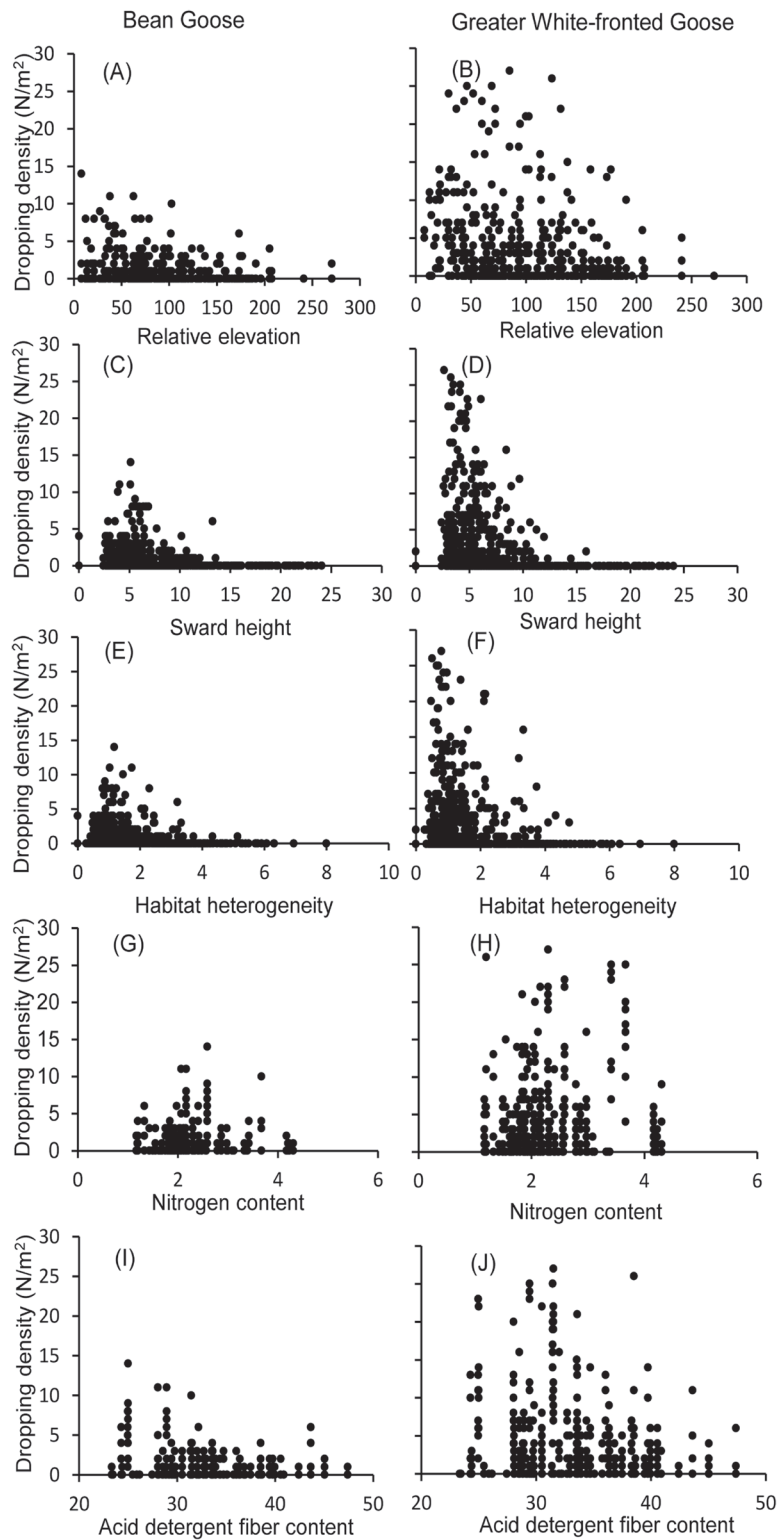| Variables (unit)	Bean Goose			Greater White-fronted Goose		
	β	R_{adj}^2	P	β	R_{adj}^2	P
Relative elevation (cm)	-0.01	0.08	< 0.001	-0.02	0.07	< 0.001
Sward height (cm)	-0.02	0.02	< 0.001	-0.32	0.07	< 0.001
Habitat heterogeneity (no unit)	-0.16	0.01	0.003	-0.83	0.04	< 0.001
Nitrogen content (%)	0.19	0.00	0.050	0.64	0.01	0.020
Acid detergent fiber content (%)	0.06	0.04	< 0.001	-0.06	0.00	0.080

Figure 3. The relationship between dropping densities of Bean Goose (left panel) and Greater White-fronted Goose (right panel) and the explanatory variables: Elevation (cm); Sward height (cm); Habitat heterogeneity (no unit, calculate the standard deviation of sward height); Nitrogen content (%); Acid detergent fiber content (%).

Table 4. Results of the final generalized linear mixed model for relationships between Bean and Greater White-fronted geese dropping densities and measured explanatory variables.

Species	Variables	β	SE	Z-value	P-value
Bean Goose	Relative elevation	-0.015	0.002	-7.56	< 0.001
	Sward height	-0.183	0.033	-5.53	< 0.001
	ADF content	-0.046	0.021	-2.19	0.028
Greater White-fronted Goose	Relative elevation	-0.017	0.001	-9.17	< 0.001
	Sward height	-0.299	0.028	-10.63	< 0.001

ADF = acid detergent fiber; β = regression coefficient; SE = standard error of the regression coefficient; $n = 623$.

such as elevation and sward height were negatively related to fecal densities of both species. However, results between models were equivocal as to the strength of the relationships between species. Although all models indicated negative relationships between fecal densities and both relative elevation and sward height, the zero-inflated model suggested differences between species for relative elevation, but the logistic regression model did not. Both models suggested that ADF content was negatively related to Bean Goose fecal densities, but not with those of the Greater White-fronted Goose. The logistic regression model indicated that vegetation heterogeneity was negatively related to fecal densities of Greater White-fronted Geese but was not related to those of Bean Goose. A similar relationship for Greater White-fronted Geese was not detected in the zero-inflated model. Variation in nitrogen content (median = 2.3%, Range = 1.17-4.31%; $n = 90$) was not related to fecal densities of either species.

Our results support our hypothesis that both species used lower elevation areas. Relative elevation was negatively correlated with the densities of both species (Tables 4 and 5), which suggests that both Bean and Greater White-fronted geese selected feeding patches in the lower areas closer to the water's edge. This result supports the findings of previous research (Olff *et al.* 1997) which showed that the Brent Goose (*Branta bernicla*) reached higher densities on the lower part of an elevation gradient in salt marshes.

Sward height, one of the important indicators of forage biomass, was negatively related to the dropping density of both species in both models used. This result is in line with previous findings (de Boer and Prins 1989; Prins 1996; Durant *et al.* 2003; Si *et al.* 2011) and our prediction. Increasing vegetation height normally results in a decrease in forage quality (van der Wal *et al.* 2000). Goose species are sensitive to forage quality (Sutherland and Allport 1994), and smaller species require a higher daily intake relative to their body size (Demment and Van Soest 1985; Richman *et al.* 2015). Areas with shorter sward heights are therefore preferred by smaller grazing species (Durant *et al.* 2004). Since the largest dropping densities were found in areas with a relatively short vegetation height, we suggest that sward height was the most important factor driving geese habitat selection in our research area.

Table 5. Results of the final mixed logistic regression model for relationships between Bean and Greater White-fronted geese dropping densities and measured explanatory variables.

Species	Variables	β	SE	Z-value	P-value
Bean Goose	Relative elevation	-0.019	0.002	-8.006	< 0.001
	Sward height	-0.205	0.036	-5.726	< 0.001
	ADF content	-0.071	0.028	-2.548	0.011
Greater White-fronted Goose	Relative elevation	-0.027	0.003	-9.535	< 0.001
	Sward height	-0.266	0.061	-4.346	< 0.001
	Habitat heterogeneity	-0.344	0.172	-2.004	0.045

ADF = acid detergent fiber; β = regression coefficient; SE = standard error of the regression coefficient; $n = 623$.

Vegetation in lower elevation areas is often of higher quality (Olff *et al.* 1997). Many experimental studies report that nitrogen content can affect herbivore habitat selection (Hassall *et al.* 2001; Durant *et al.* 2004). In our study, we failed to detect any relationship between nitrogen content and fecal densities, similar to a study on the Barnacle Goose (*B. leucopsis*) in The Netherlands (Si *et al.* 2011), which was also based on field observations. Si *et al.* (2011) suggested that their finding was the result of the nitrogen content of the forage being higher than the requirements of the geese. Schrama *et al.* (2013) has shown that the presence of large herbivores can decrease the nitrogen mineralization rate in moist grasslands. Foraging in a lower elevation area could, therefore, decrease the quality of the swards. We conducted our study in a natural area where nitrogen content was lower than in The Netherlands (Range = 3.7-4.4%, *n* = 98; Si *et al.* 2011). Hence, when forage quality is low, sward height may be more important to geese than forage quality.

Structural heterogeneity of the swards was negatively related to dropping densities of the smaller Greater White-fronted Goose, but no relationship existed for the larger Bean Goose (Table 5). This result partially bore out our prediction. Many studies report that herbivores are sensitive to spatial heterogeneity of forage resources (Augustine and Frank 2001; Hobbs *et al.* 2003; Owen-Smith 2004; Fryxell *et al.* 2005), as forage resource heterogeneity can negatively affect bite mass (Hobbs *et al.* 2003). Small herbivores, such as geese, normally forage at very high bite rates to satisfy their daily demand (Kristiansen *et al.* 2000). However, a high heterogeneity in resource availability could decrease the bite rate and hence reduce the forage intake rate.

Our results provide some preliminary indication of possible allometric responses that smaller species are more sensitive to the elevation gradient and sward height, hinting at the importance of allometric responses in habitat selection by different goose species. The smaller species, the Greater White-fronted Goose, was found more on the lower lying and short sward areas than the larger Bean Goose. Larger species normally reach higher densities in the relatively higher biomass areas (Murray and Illius 2000; Durant *et al.* 2004), often with a relatively lower forage quality. Vegetation at higher elevation areas has a longer growing period and consequently a higher vegetation biomass and lower quality in our study area. The larger Bean Goose used taller swards than the smaller Greater White-fronted Goose. This was not only apparent from the dropping density analysis, but also from the presence/absence analysis of the droppings. Our results also suggest that a relatively lower sward height (e.g., through grazing from cattle, by mowing, or by manipulating water heights) can facilitate use of patches by herbivorous geese.

Where they coexist, herbivores often forage on the same food resource. The Yangtze River flood plains support about 80% of all Anatidae in eastern China (Cao *et al.* 2010). During the wintering period, grazing geese mainly forage on *Carex* spp. The resource availability and quality is partly determined by the number of consumers, their grazing pressure, and the competition between different species. Herbivorous birds are no exception to this rule, and we expected that competition could be important in driving their spatial distribution (Amarasekare 2002). However, our results suggest that the two species could use the same food resource if they differ in their spatial distribution. The elevation gradient along the lake shore influences the spatial pattern of the food resources through a difference in the flooding regime, and thereby affects the forage quality and quantity and the vegetation heterogeneity (Clausen 2000). Grazers that differ in body size could apply different foraging strategies to satisfy their daily intake requirements (Wang *et al.* 2013). To summarize, we conclude that variation in elevation and sward height explain the coexistence of differently sized species through an allometric response in the Yangtze River flood plains.

Water level fluctuations play an important role in determining food spatial availability

in wetlands, mediated by the elevation, and therefore indirectly determine herbivorous bird distribution. A higher water level will reduce the forage availability for herbivorous birds and hence decrease their abundance. A lower water level will first offer a larger extent of recessional grassland for herbivorous bird species, increasing the total number of birds. However, a long period with low water levels will increase the growing period of the vegetation, resulting in a large proportion of the area being covered with tall and lower quality swards that are not suitable for grazing bird species. Based on this study, to facilitate species coexistence during the wintering period and increase bird species richness, we suggest that water levels should be regulated to decrease gradually so that the grasslands with a relatively higher elevation will emerge first and thereafter the lower lying areas. This will allow species like the Bean and Greater White-fronted geese with different body sizes to select suitable foraging habitat without competition for resources. It is important to realize that in much of the Yangtze River floodplain, water levels are human-regulated and controlled through a system of canals and sluices (Wu *et al.* 2009; Liu and Wang 2010), which suggests that management of water levels for conservation purposes is feasible.

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