

**Wild Geese of the Yangtze River:
Their Ecology and Conservation**

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Wild geese of the Yangtze River: their ecology and conservation

Yong Zhang

Thesis

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Chapter 1

General introduction

Yong Zhang

General introduction

One of the fundamental issues in ecology and conservation biology is to explain and predict the distribution of organisms. Where animals can be found is determined by their movement decisions; these decisions are in turn based on the interplay between their needs and what the environment is offering them as determined by meteorological factors, water availability, availability of food resources, human disturbance or predation risk. Despite exhaustive research efforts during the past decades, this issue remains incompletely understood, partly because distribution and abundance of animals can be determined by a variety of abiotic and biotic factors that interact and operate at different spatial scales. Moreover, biotic interactions, such as top-down and bottom-up processes, operate across trophic levels (Krebs et al. 1995), and within the same trophic level, competitive and facilitative interactions take place at the same time (Schoener 1983, Reiter and Andersen 2013, Tombre et al. 2013).

The foragers' spatial distribution is, among other factors, a consequence of adaptive foraging behaviour when foraging in a heterogeneous environment. The selection of these areas is described in, for instance, the optimal foraging theory. The optimal foraging theory (Emlen 1966, MacArthur and Pianka 1966) assumes that a predator selects preys which maximize its profitability. Thus, animals will either try to maximize energy intake or minimize time spent to obtain a fixed amount of energy (Bergman et al. 2001, Fryxell et al. 2004). For example, ungulates modified their behaviour according to a time-minimizing strategy (Kie 1999). Great tits (*Parus major*) exploited patchily distributed prey following the optimal forage theory (Cowie 1977). Starlings (*Sturnus vulgaris*) used different foraging modes to maximize the net rate of energy gain per unit of time (Bautista et al. 2001).

The ideal free distribution is frequently employed when studying animal habitat selection and distribution. This theory states that individual animals will aggregate in various patches proportionate to the amount of resources available in each patch (Fretwell and Calver 1969). For instance, ovenbird (*Seiurus aurocapilla*) density was adjusted to match the habitat condition with changing habitat size, supporting the ideal

free distribution (Hache et al. 2013). However, the ideal despotic distribution, whereby more experienced or competitive individuals occupy the habitat where they can maximize their fitness and thereby force the other individuals into the lower quality area (Petit and Petit 1996, Calsbeek and Sinervo 2002), tends to receive more support than the ideal free distribution (Rodenhouse et al. 1997, Piper 2011). Hence, when the resources are limited, interference competition becomes an important factor affecting animal habitat selection. Interference competition usually incorporates a social component, some individuals being denied access to resources by the (often aggressive) actions of others (Van Dijk et al. 2012). Through social interactions and aggressive encounters between competitors, the “superior species” may control the best patches whereas subordinates are forced to sub-optimal habitat where they experience a reduction in intake rate (Smith et al. 2001, Vahl 2006). For instance, the “subordinate species”, Greenland white-fronted geese (*Anser albifrons flavirostris*), shifted to sub-optimal feeding patches with lower food quality and increased their foraging time under competition with “superior” Canada geese (*Branta canadensis*) (Kristiansen and Jarrett 2002). The authors predicted that the Greenland white-fronted geese could compensate for the lower energy intake in this way. Hence, interference competition is an important mechanism that determines differences in feeding patch selection and intake rate in competing species.

The ideal free distribution should also take spatial differences in resource quality and quantity into account. Hassall and Lane (2005) argued that goose species should not follow the predictions derived from the ideal free distribution because they are constrained by nitrogen content of the forage. Moreover, the availability of food resources often exhibit typical spatial and temporal variation in terms of quality and quantity (Fryxell et al. 2005) that can also affect the spatial distribution and abundance of geese. In general, foods with a higher protein content and a lower fibre content have a higher digestibility (Prop and Vulink 1992) and are hence more attractive to especially smaller bodied species, whereas larger species prefer a higher intake rate, are less sensitive to variation in forage quality, and therefore select taller swards (Durant et al. 2003, Durant et al. 2004, Heuermann et al. 2011).

Several theories with regard to foraging behaviour (what to eat?) and decisions with regard to location choice (where to eat?) have been formulated based on the researches on different herbivores, such as cattle, sheep, goats and geese. The intake rate

maximization theory predicts that herbivores select patches offering the highest dry matter intake rate (Kenney and Black 1984). However, forage quality generally decreases with increasing biomass (Prins et al. 1998). When the swards grow, their quality will become poorer as the fibre content increases (Prop and Vulink 1992) and the nutrient content decreases (Hassall et al. 2001). For this reason, the forage maturation hypothesis has been formulated (Riddington et al. 1997, Heuermann et al. 2011). According to this hypothesis, herbivores should select the patches with intermediate plant biomass because under these conditions the patches not only offer higher dry matter intake but also higher nutrient intake. This hypothesis was confirmed by studies on geese (Riddington et al. 1997, Heuermann et al. 2011). Durant et al. (2004) showed that Anatidae species with different body sizes selected different feeding patches. When foraging together in a heterogeneous environment, larger species foraged on taller swards, while smaller species selected lower swards, although both species could maximize their protein intake. However, another study showed that there was no significant relationship between forage quality and grazing intensity based on results obtained from geese foraging on semi-natural areas (Si et al. 2011). The authors of the latter paper discussed that this absence of an effect of forage quality is perhaps because the grasses in their study area had such a high nutrient content that the nutrient requirements of these geese were always satisfied.

So, intake rate maximization might not offer the best strategy, as animal often face a trade-off between foraging quality and quantity, mediated by body size. The allometric scaling laws (Bell 1970, Jarman 1974) predict that animals differing in body size respond differently to environmental factors based on physiologic and digestive constraints of body size. Hence, predictions derived from foraging theories suggest that herbivores select their habitat under the influence of differences in body size (Gunnarsson et al. 2005, Hopcraft et al. 2010, Clauss et al. 2013). Herbivores with different body size normally feed on different patches, influenced by different energy and protein requirements and differences in their ability to ingest and digest. For instance, when foraging together, larger greylag goose (*Anser anser*) selected taller swards while the smaller wigeon (*Anas penelope*) selected lower swards (Durant et al. 2004). The habitat selection of the grazing ungulates in the Serengeti ecosystem was also size-related and the food availability on which ungulates optimize energy intake is a positive function of body mass (Wilmschurst et al. 2000).

However, resource spatial heterogeneity greatly affects animal habitat selection and abundance, as has been documented by several studies (Moller et al. 2010, Smith et al. 2010, Pickett and Siriwardena 2011). Herbivorous goose species, for example, generally have lower intake rates while feeding on heterogeneous, complex sward compared to homogenous single-species swards (Wilmshurst et al. 2000, Heuermann et al. 2011). Swards structure (determined principally by variations in the height of the swards, or stem/leaf fraction) affects the vertical heterogeneity in biomass availability (Courant and Fortin 2010) and thereby the foraging efficiency of grazers by influencing handling time (Searle et al. 2005, Shipley 2007). Hence, geese abundance will decrease with increasing resource heterogeneity. The smaller species, restricted by their bill morphology, have a lower bite mass but a higher bite rate, and therefore are more sensitive to the structural heterogeneity and hence select homogeneous patches.

Species abundance and density can also be affected by patch size. The individual-area relationships (IRAs), extrapolated from the theory of island biogeography, describes the relationship between animal population density and area (Connor et al. 2000). Positive IRAs are general found for birds (Connor et al. 2000, Murray et al. 2013), in line with the resource concentration hypothesis, which states that larger areas of resources should attract a larger density of herbivores (Root 1973). Thus, the size of the exposed grassland which is available for wintering herbivores is vital, as it basically determines the total amount of food and therefore indirectly the abundance and density of animals, and the time they can feed on these resources.

Hence, it is crucial to obtain a comprehensive understanding of such spatial distributions through investigating the way in which animals use patches in relation to the availability of food resources and its spatial and temporal heterogeneity (Krebs and Kacelnik, 1991, Sutherland, 1996). Moreover, it is widely recognized that human disturbances are playing an increasing role in determining spatial pattern of animal distribution and abundance. Thus, one of the main issues at present is how to balance economic development and nature conservation as they are often in conflict with each other. Human factors are rather diverse, and effects of human factors can be positive, negative or negative quadratic over different species or spatial–temporal context, and negative effects are frequently detected (Lepczyk et al. 2008). Human activities usually alter habitat selection of birds at local and landscape scale (Meager et al. 2012). The presence of roads has often a negative effect both on species richness and abundance

(Palomino and Carrascal 2007). Increasing human disturbance resulted in decreasing the mean body size of the birds, through decreasing the relative proportion of larger bodied species (De Boer et al. 2011). Thus, it is critical to better understand this influence of disturbance in combination with the influence of forage quality and quantity in order to improve management strategies.

Designating the natural reserve is an important measure to protect global biodiversity and halt the decline of many species' population sizes. However, assessments of the effectiveness of current protection policies are rare (Kleijn et al. 2011), although it is important to know whether a protection effort is really beneficial to protected species (Hoffmann et al. 2010). For instance, protection status positively affected the colonization probability of wetland birds in the UK (Hiley et al. 2013). Recently, Kleijn and co-workers showed that waterbirds increased more rapidly in Ramsar-designated wetlands in Morocco compared to unprotected wetlands (Kleijn et al. 2014). However, a comprehensive understanding of the effectiveness of conservation policies is still lacking although it is rather important to guide conservation projects.

In summary, the central questions are what affects the temporal-spatial distribution of animals and how are animals affected by a variety of bottom-up (e.g., food) and top-down factors (e.g., disturbance). Former studies concerning these topics often only focussed on a single species or one study area. However, different species often reacted differently to the environment and their reactions are also often scale-dependent (McGill 2010). A study on farmland biodiversity found that different taxa responded differently to agriculture practices on a spatial scale dependent manner (Gabriel et al. 2010). Thus, the effects of environmental changes are expected to vary over a variety of spatial and temporal scales, implying that implementation of conservation strategies should also take scale effects into account. In this thesis, I therefore studied habitat selection of several herbivorous Anatidae species that differ in body size. I analysed the impact of various top-down and bottom-up factors on these species' habitat selection and population sizes. These studies were carried out on different spatial scales, offering insight into the efficiency and spatial scales of future conservation actions.

Study area and species

This work was carried out in the wetlands of Yangtze flood plain of China. The Yangtze

floodplain (Figure 1) is globally unique for its extensive ephemeral lakes, recharged with sediments and nutrients by summer monsoonal rains. Because of the hydrological reverse flow system and large yearly variation in water levels, the Yangtze floodplain lakes are unique in their ability to produce a large biomass of plant and animal food for many waterbird species. According to the results of surveys in 2004 and 2005, the area supported in excess of one million birds (Cao et al. 2008, Cao et al. 2010). Although the distributions and abundance of birds may have some changes recently, it is still by far the most important region in China for wintering migratory waterbirds. In addition, the Yangtze watershed, within which the floodplain lies, supports 40% of China's human population and generates 40% of the national GDP. However, hydrological changes, especially from hydroelectric and water diversion projects, and the move from extensive use by local people to intensive exploitation, have severely affected the quality and sustainability of the floodplain and its lakes (Fang et al. 2006, Wu et al. 2009, Wu et al. 2010).

Several Anatidae species wintering in the wetlands of the Yangtze River floodplain were selected in this study (wigeon, bean goose *Anser fabalis*, greater white-fronted goose *Anser albifrons*, lesser white-fronted goose *Anser erythropus*, swan goose *Anser cygnoides* and tundra swan *Cygnus columbianus bewickii*). These species are all grazing herbivorous waterbirds mainly foraging on the recessional grassland during their wintering period.

Research objective

In Europe, geese numbers have dramatically increased over the last decades and have caused a large amount of agricultural concern (Madsen et al. 2014). In contrast, in China the number of geese has decreased recently and also their spatial distribution has changed greatly (Cao et al. 2010, De Boer et al. 2011). Distribution changes of geese can probably be partly explained by changes in disturbance and changes in forage abundance and forage quality of the food resources on which the geese depend. In addition, with the current economic developments, human disturbance and habitat fragmentation can also play an important role in shaping the distribution and number of wintering goose species in China. In this thesis, I aim to understand the determinants which affect the distribution and abundance of wintering herbivorous Anatidae species

in the Yangtze flood plain over different spatial scales, offering a better understanding of the effects of these determinants over different spatial scales. I analysed the effects of resource and disturbance factors, investigating the main factors determining the species' spatial distribution and abundance. Moreover, I evaluated the effectiveness of China's current protection policy, offering a scientific basis for effective protection strategies of these species in the Yangtze River flood plain.

Outline of the thesis

In Chapter 2, I studied the effects of inter-specific interactions of differently sized grazing Anatidae species on their feeding patch selection and foraging behaviour. For this purpose, we used an experimental approach where we offered tame geese of different species heterogeneously distributed feeding patches with different sward heights (1, 3, 6, 9 cm). These sward heights were maintained at different heights through mowing. In Chapter 3, I analysed the habitat selection of goose species at site level. Three research sites at Shengjin Lake National Reserve were selected to test several predictions: (1) Smaller bodied species are mainly found in lower elevation areas where forage biomass is lower but with a higher forage quality, while the larger goose species select higher areas with a larger forage quantity. (2) The density of smaller bodied species will decrease with an increase in structural heterogeneity of the swards. In Chapter 4 I analysed the effects of anthropogenic and ecological determinants on Anatidae species abundance and their spatial location at Shengjin Lake National Reserve using systemic survey data. I tested for the effect of land area, forage quantity and habitat heterogeneity on species abundance, but also for the effects of human disturbances on these two goose species that belong to the same guild but differ in body size. I offer suggestions on how management strategies can be optimized to improving habitat conditions for wintering geese in the Yangtze wetlands. In Chapter 5, I enlarged the research area to the Yangtze floodplain. Using census data from 2004 to 2012, I analysed grazing goose species distribution over several lakes in the Yangtze flood plain, comparing the distribution and abundance of goose species amongst wetlands differing in protected status and environmental variables. Chapter 6 synthesizes the conclusions that can be drawn from these preceding chapters.

Chapter 2

Experimental evidence shows the importance of behavioural plasticity and body size under competition in waterfowl

Yong Zhang, Herbert H.T. Prins, Martijn Versluijs, Rick Wessels, Lei Cao, and Willem F. de Boer

When differently sized species feed on the same resources, interference competition may occur, which may negatively affect their food intake rate. It is expected that competition between species also alters behaviour and patch selection. To assess these changes in behaviour and patch selection, we applied an experimental approach using three differently sized Anatidae species: wigeon (*Anas penelope*) (~600 g), swan goose (*Anser cygnoides*) (~2700 g) and bean goose (*Anser fabalis*) (~3200 g). We quantified the functional response for each species and then recorded their behaviour and patch selection with and without potential competitors, using different species combinations. Our results showed that all three species acquired the highest nitrogen intake at relatively tall swards (6, 9 cm) when foraging in single species flocks in the functional response experiment. When they were offered foraging patches differing in sward height with and without competitors, the mean percentage of feeding time did not change, whereas all species increased their percentage of time being vigilant except for the dominant swan goose. All species utilized strategies that increased their peck rate on patches across different sward heights, resulting in the same instantaneous and nitrogen intake rate. Our results suggest that variation in peck rate over different swards height permits Anatidae herbivores to increase nitrogen intake under competition to compensate for the loss of intake, illustrating the importance of behavioural plasticity in heterogeneous environments when competing with other species for resources.

Submitted

Introduction

Selection of feeding patches is an important process in the spatial distribution of herbivores. In this paper we experimentally test how interference interactions affect intake rate, foraging time, and patch selection. To predict patch selection a thorough understanding of the functional response of the herbivores is required. A functional response describes how the instantaneous intake rate changes with increasing food availability (Solomon 1949). Functional responses of grazing species that differ in body size are bound to be different, and understanding these allometric relationships are required to understand when competition or facilitation can occur (Prins et al. 1998, Van Langevelde et al. 2008). A Type I functional response describes a linear increase of food intake with food availability. However, a Type II functional response, which describes that instantaneous intake rate increases asymptotically with food availability, is found for most grazing herbivores (Spalinger and Hobbs 1992, Durant et al. 2003). Geese and ducks sometimes display a Type IV functional response (Bos et al. 2004, Heuermann et al. 2011), which is a dome shaped curve with a maximal intake rate at intermediate biomass densities.

In general, herbivorous Anatidae require a relatively high intake of dietary nitrogen (Ydenberg and Prins 1981, Prins and Ydenberg 1985), because of their inefficiency in converting proteins from plant food into their own body tissue. This is due to differences in amino acid profiles from plant proteins and animals proteins (Sedinger 1984, Sedinger and Raveling 1984) and low digestibility of their food (Prop and Vulink 1992). Nitrogen availability of both grasses and sedges generally decreases with increasing swards height (Hirose et al. 1989, Prop and Vulink 1992). This has been formulated as the forage maturation hypothesis, which states that nitrogen content declines during the development of plants while the total fibre content increases (Mattson 1980, Olff et al. 2002). Moreover, a hump-shaped relationship was also found between nitrogen content and plants development (van der Graaf et al. 2006). Herbivorous Anatidae therefore face a trade-off between food quantity and quality (Fryxell 1991, Wilmschurst et al. 2000). It is expected that herbivores select patches with intermediate plant biomass (for their size) which allows them to maximize their net intake rate of digestible nutrients (Wilmschurst and Fryxell 1995, Hebblewhite et al. 2008).

Body size is an important factor that affects the intake rate of herbivorous Anatidae and therefore also patch selection. Intake rate of herbivorous Anatidae species is determined by both peck rate and peck size. At lower sward heights, peck size decreases (Durant et al. 2003, Heuermann et al. 2011), and to compensate for the loss in intake rate caused by decreasing peck sizes, smaller Anatidae species generally increase their peck rate (Fox et al. 1998). However, when swards become too short, peck size will decrease to a level where a higher peck rate cannot completely compensate, and consequently intake rate decreases (Durant et al. 2003, Durant 2006). Larger species are unable to achieve their nitrogen requirements on short swards, and due to their larger bills they have a limited ability to compensate for the smaller peck sizes in short sward by increasing their peck rate (Durant et al. 2004, Heuermann et al. 2011). However, they are able to tolerate swards with lower nitrogen values (Hassall et al. 2001), which allows them to select taller, less nitrogen-rich swards, but with a larger peck size (Durant et al. 2003).

Interference competition is another important factor in determining the distribution of herbivores (Wiens 1989, Newton 1998, Kristiansen and Jarrett 2002, Gauvin and Giraldeau 2004, Prins et al. 2006, Van Dijk et al. 2012), associated with body size (Schoener 1983). According to (Wiens 1989) the necessary conditions of inter-specific competition are: (1) species must rely on the same resource and (2) joint exploitation of those resources and/or interference interactions concerning resources negatively affect either one or both species. Interference competition usually incorporates a social component, some individuals being denied access to resources by the (often aggressive) actions of others (Van Dijk et al. 2012). Through social interactions and aggressive encounters between competitors, the largest species may control the best patches whereas smaller species are forced to sub-optimal habitat where they experience a reduction in intake rate (Smith et al. 2001, Vahl 2006a). Besides, when animal spent more time on interactions, less time can be spent to foraging and therefore foraging success decreases (Cresswell 1997, Stillman et al. 1997, Vahl 2006a). Moreover, social and aggressive interactions may be very costly in terms of time and energy (Huntingford and Turner 1987). Thus, under the influences of interference competition intake rate may decrease. Kristiansen and Jarrett (2002) examined competition between moulting Canada geese (*Branta canadensis*) and Greenland white-fronted geese (*Anser albifrons flavirostris*) by field observations in Western-Greenland. They found that Greenland

white-fronted geese, the subordinate species, shifted to sub-optimal feeding patches with lower food quality and increased their foraging time. The authors predicted that they could compensate for the lower energy intake in this way. Hence, interference competition is an important mechanism that determines differences in feeding patch selection in competing species.

The aim of this study is to examine the effects of interference competition of differently sized grazing Anatidae species on their feeding patch selection and foraging behaviours. For this purpose, we used an experimental approach where we offered heterogeneously distributed feeding patches with different sward heights. These sward heights were differentially maintained through mowing. Firstly, in order to better understand the effect of interspecific competition, we quantified the functional response for each species. Then, a competition experiment was conducted with a free patch choice experiment as control. We expected that larger species are competitively superior and are expected to exclude smaller species from preferred food patches. Both superior and subordinate grazing Anatidae species are expected to increase their peck rate and/or percentage of feeding time under interference competition to compensate for the potential loss of intake rate.

Methods

Experimental trials

This experiment was carried out at the Shengjin Lake National Reserve in Eastern-China from 16 December, 2012 to 27 February, 2013. Individuals of three differently sized Anatidae species were used: wigeon (*Anas penelope*) (mean body mass of all individuals: 570 g; N = 7), swan goose (*Anser cygnoides*) (2,740 g; N = 7) and bean goose (*Anser fabalis*) (3,170 g; N = 7). We used tame birds as they were accustomed to being handled by humans, thus reducing stress. One week before the experiment, the three species were allowed to feed on nearby grassland that had a similar grass structure as the experimental area. The animals were kept in a holding pen inside a covered enclosure. The enclosure consisted of a pond where the animals could swim, eight experimental enclosures (5 × 5 m, with 2 m high wire fence) where the sedge *Carex heterolepis* was the dominant species and four holding pens where clean water was always available. All birds were individually identifiable by using different

combinations of plastic tags on the legs, and before each observation the observer recorded the ID of the bird. For the functional response experiment, the swards were mowed to four particular heights representing the natural conditions at our field sites at which geese feed (1, 3, 6, 9 cm) within the 5 × 5 m enclosures. For the free choice and competition experiment, the vegetation within the enclosures was divided into sixteen 1 × 1 m patches with small paths in between so that we were able to mow the plots to their desired height without trampling the vegetation in the patches. In each row of four patches, the sward was mowed to four different sward heights of 1, 3, 6, and 9 cm following a randomized Latin square design to eliminate the effects of environmental gradients within plots. Clean fresh water was provided at four different points in the enclosure. After each trial we raked the swards and measured the sward height. If the sward height was reduced, we started the observations in another enclosure. All observations were made inside a cabin at a distance of 40 m using a 18 – 60 × telescope (Carl Zeiss, Germany). Behavioural activities and patch selection were recorded using the software ObserverXT v10 installed on a Psion Workabout hand-held computer (Noldus Information Technology, Netherlands)

Vegetation

Sward height was determined for each of the 1 × 1 m patches on the day before we started with each repetition of the free choice and competition experiment. Sward height was estimated as the mean of 17 measurements taken according to a fixed pattern (once in the middle and four on each of the 2 perpendicular lines crossing the centre and the 2 diagonals) using a drop disc meter (DPM: diameter: 10 cm, weight: 5 g) on a graduated stick to the nearest 0.5 cm (Summers and Critchley 1990). For each enclosure, the average sward height was calculated. However, in winter sedges tend to lie flat while the tips of the leaves died off so that the leaves did not supported the weight of the drop disc. In order to correct for this effect 30 additional samples were taken and both sward height (DPM value) and leaf length (maximum length of the leaf to the soil surface) were measured by a ruler to the nearest 0.1 cm. The equation of the best-fitted line was used to adjust the measured disc pasture heights to measured leaf lengths (Fig. 2.1). All reported heights were accordingly corrected and reported as sward heights.

We measured biomass by clipping 15 squares (20 × 20 cm) to the soil level for each of the height treatment. All samples were then oven-dried at 70 °C for 48 h to determine dry weight. Dry weight was measured to the nearest 0.001 g. From each biomass sample, a mixed subsample (~8 g) was taken for the analysis of the nitrogen content (Novozamsky et al. 1983).

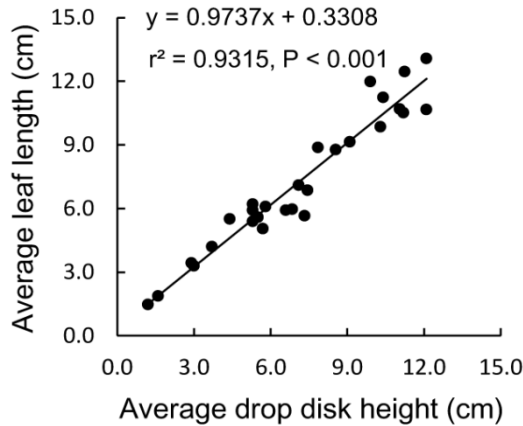


Figure 2.1 The relationship between drop disk height (cm) and leaf length (cm).

Functional response experiment

The experiments were conducted from 08:00 to 12:00h. All trials were conducted after the birds had been fasting during the previous night. During the experiment, six birds from one species were put in the experimental enclosure for 1 h with a uniform grass height at a selected height (1, 3, 6, or 9 cm, respectively). One observer recorded the behaviour for a period of two minutes using focal sampling over two behavioural classes: feeding and non-feeding behaviour. A bird was considered to be feeding when it stood with its bill pointed towards the vegetation (Van der Wal et al. 1998). When the observation started, we recorded their behaviour at a time resolution of 1 s. When an observation ended, a next focal bird was chosen randomly from the group but excluding birds from which behavioural observations had been collected already. When all individuals had been observed we started over again with all individuals in the group under observation, thus each individual was measured 3 – 5 times within a trial.

The peck rate was calculated by a separate observer by measuring the time it took for a bird to take 10 to 50 pecks using a stop watch (Durant 2006). The peck rate was

only measured for grazing individuals. All individuals were measured multiple times in 1 h.

To calculate instantaneous intake rate and nitrogen intake rate, all droppings were collected in a paper bag after the observations, and the animals were kept from foraging for at least six hours by putting them in a container with a mesh floor. All droppings in the container were also collected (Durant et al. 2003). Droppings were dried at 70 °C for 48 h.

In one day, all three species were tested, each with six birds in the enclosure. This procedure was repeated three times on three consecutive mornings. Hereafter, we cut the grass to one of the other heights. The grass was cut from the original taller grass heights to 9, 6, 3 or 1 cm and for each particular sward height we carried out our experiments with the same procedure. The order of the species in the experiment was fixed; we first tested wigeon followed by bean goose and finally swan goose.

Dry weight (DW), ash free dry weight (AFDW), nitrogen and acid detergent fibre (ADF) content were determined at the laboratory of Wageningen University. The ADF and DW were used to estimate the digestibility of the forage through the following calculation (Manseau and Gauthier 1993, Hupp et al. 1996, Wang et al. 2013a):

$$\text{Digestibility (\% AFDW)} = (1 - (ADF_{\text{sedge}} / ADF_{\text{droppings}})) \times 100$$

$$\text{Dry matter intake (g)} = \text{Dry weight droppings (g AFDW)} / (1 - \text{digestibility})$$

The instantaneous dry matter intake rate (mg/min) per animal was calculated from the total dry matter intake divided by total feeding time of all birds. The instantaneous nitrogen intake rate (mg/min) was calculated by multiplying the instantaneous dry matter intake rate with the nitrogen content.

Free choice experiment

In this experiment six individuals of one species moved freely inside the 5 × 5 m enclosure where multiple sward heights were made available. The animals were thus able to select a particular sward height for foraging. The experiments were conducted from 08:00 to 11:30 h over three consecutive days, each day measuring a different species. All trials were conducted after the birds had been fasting during the previous night. This three day series was repeated four times. The following behavioural activities were recorded for the selected bird in a 3-minute period: feeding, walking,

vigilant, drinking, sitting/sleeping, social and aggressive interactions. Peck rate was recorded as described above. The order of the species was bean goose, swan goose and wigeon.

Competition experiment

The trials were conducted between 09:00 - 11:30 h inside the 5 × 5 m enclosure on consecutive days, with one day in between two consecutive sessions. Every day we tested one combination of species, a standardized total group size of six geese was used (Table 2.1). The geese were randomly selected from the six geese available per species. Each session was repeated four times. All trials were conducted after a fasting period of one night.

Table 2.1 All species combinations used in the inter-specific competition experiment.

Combination	Species 1	n	Species 2	n	Species 3	n
1	Wigeon	3	Bean goose	3		
2	Wigeon	3	Swan goose	3		
3	Bean goose	3	Swan goose	3		
4	wigeon	2	Swan goose	2	Bean goose	2

n represent the number of individuals participating within the combination.

When the trial started, all six birds were allowed to enter the enclosure and graze freely among the patches. The 3-minute focal observations were used as above. The only difference was that aggressive interactions between individuals of the different species were also recorded and when aggressive interactions occurred, we recorded if the focal bird was the winner or loser. This way we could also determine the interspecific dominance status of the birds. Peck rate of each animal was also recorded as described above.

Statistical analysis

Vegetation

A One-Way ANOVA was used to examine differences in sward height and nitrogen content between treatments, followed by Post-hoc tests to identify differences among groups.

Functional response

A One-Way ANOVA and Post-hoc Tukey-test was used to identify differences in percentage foraging time, peck rate, instantaneous intake rate (mg min^{-1}), nitrogen intake (mg min^{-1}) and peck size for different species foraging on different swards heights.

In winter, the sedge growth rate was very low and the vegetation was short. Hence, for larger animals, intake was limited by sward height. So a linear regression model was fitted to test for a Type I functional response. With increasing sward height (Height, cm), intake rate (Intake, mg min^{-1}) might reach a maximal value and even decrease. So, to model nitrogen intake rate (mg min^{-1}) as a function of sward heights, two candidate non-linear regression models were also fitted. To test for a Type II functional response, Holling's model (1959) was used, and for a Type IV functional response, a quadratic equation was used (Durant et al. 2003). These three functional responses, differing in complexity and use of intercept, were compared using the Akaike's Information Criterion for sample size (AIC_C) for model selection.

$$\text{Intake} = a * \text{Height} + b \text{ (Type I)}$$

$$\text{Intake} = a * \text{Height} / (1 + b * \text{Height}) \text{ (Type II)}$$

$$\text{Intake} = a + b * \text{Height} - c * \text{Height}^2 \text{ (Type IV)}$$

Heuermann et al.(2011) used a Michaelis-Menten model to test the Type II functional response and a predator confusion model for the Type IV functional response. In this research, these two models were also applied, but they poorly fitted the data and are therefore not reported. We also fitted the models using the sward biomass as independent variable. By examining the R^2 value, sward height better fitted our data, so sward height was used in all final models.

Competition experiment

Per species, we tested if the three differently sized competitor species affected the percentage of time foraging and being vigilant of the focal species using a General Mixed Linear Model (GLMM). The percentage foraging and vigilance was arcsin transformed to satisfy the assumptions of normality. The GLMM was conducted with competitor and sward height as fixed factors. Session, individual and enclosure number were included as random factors. Within the model, we were especially interested in the

interaction effect between sward height and competitor, this interaction term was therefore included as a fixed factor in the model. Tukey post-hoc tests were used to identify differences in percentage foraging time over the different treatment combinations.

To determine the differences in peck rate among the three species, a GLMM was also used. Peck rate was square root transformed to satisfy the assumptions of normality. Sward height, competitor and the interaction term were included as fixed factors; session, individual and enclosure number were used as random factors. Tukey post-hoc tests were used to identify differences in peck rate over the different treatment combinations.

We also calculated the mean instantaneous intake rate and the nitrogen intake for each species when foraging alone (results from the functional response experiments) and in combinations with different competitors. One-way ANOVAs were carried out to test whether the instantaneous intake rate and the nitrogen intake differed over the different species combinations. All statistical analyses were conducted in SPSS v19 (IBM Corp, 2010) and R 2.13.0 (R Development Core Team, 2012).

Results

Vegetation

As intended, the obtained sward heights after clipping within the experimental enclosures differed between treatments (ANOVA, $F_{3,108} = 578.714$, $P < 0.001$), but slightly deviated from the target heights of 1, 3, 6, and 9 cm (Table 2.2).

Table 2.2 Desired and mean measured sward heights (\pm 95% CI) of the four different treatments. The measured swards height slightly deviated from target heights.

Desired height (cm)	Measured height (cm)	95% CI	
		Lower	upper
1	1.83	1.07	2.22
3	3.64	2.66	4.15
6	5.63	4.15	6.38
9	6.88	4.41	8.14

Nitrogen content differed between the four height treatments, as the 1 cm high swards, contained significantly less nitrogen than the taller swards and the highest

concentration of nitrogen was recorded in the 6 cm high swards (ANOVA, $F_{3,59} = 22.427$, $P < 0.001$; Fig. 2.2).

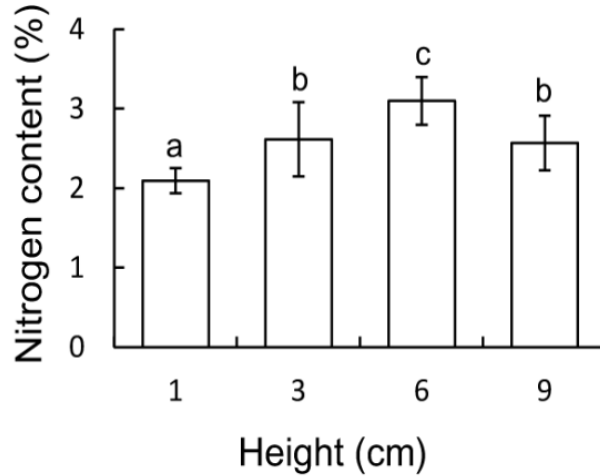


Figure 2.2 Mean values ($\pm 95\%$ CI) of the percentage nitrogen content within the four different sward heights. Letters indicate significant differences in nitrogen content between sward height on the basis of a Tukey post-hoc test.

Functional response experiment

The percentage feeding of swan goose differed significantly over the different swards heights (ANOVA, $F_{3,8} = 4.608$, $P = 0.037$; Fig. 2.3a), and the percentage feeding on 1 cm swards was significant higher than on 9 cm swards. Bean goose had a similar trend as swan goose ($F_{3,8}=17.392$, $P = 0.001$), and percentage feeding on 1 cm swards was significantly higher than on other sward heights. Wigeon had the highest percentage feeding on 6 cm ($F_{3,8} = 8.594$, $P = 0.007$); the percentage feeding on 9 cm swards was significantly lower than on other sward heights.

The highest peck rate of swan goose was found on shorter swards (ANOVA, $F_{3,8} = 42.661$, $P < 0.001$; Fig. 2.3b). Peck rate of bean goose also differed over the four different heights ($F_{3,8} = 12.844$, $P = 0.002$) and the peck rate on 9 cm swards was significantly lower than on other sward heights. There was no effect of sward height on wigeon's peck rate ($F_{3,8} = 0.894$, $P = 0.485$).

There was no effect of sward height on dry matter intake rate for swan goose (ANOVA, $F_{3,8} = 1.148$, $P = 0.387$; Fig. 2.3c) or wigeon ($F_{3,8} = 0.941$, $P = 0.465$). For

bean goose, dry matter intake on 6 cm swards was significantly higher than on 1 cm swards ($F_{3,8} = 4.878$, $P = 0.032$).

Dry matter intake/peck of swan goose and bean goose were significantly different among different swards heights (ANOVA, swan goose: $F_{3,8} = 5.944$, $P = 0.02$; bean goose: $F_{3,8} = 9.559$, $P = 0.005$), as both species had a higher dry matter intake/peck when foraging on taller swards (Fig. 2.3d). For wigeon, no significant effect was found of sward height ($F_{3,8} = 0.318$, $P = 0.812$).

Nitrogen intake rate of swan goose and wigeon was similar on different sward height (ANOVA, swan goose: $F_{3,8} = 1.990$, $P = 0.194$; wigeon: $F_{3,8} = 3.546$, $P = 0.068$; Fig. 2.3e), but nitrogen intake rate of bean goose on 6 cm swards was significantly higher than on shorter swards (ANOVA, $F_{3,8} = 7.424$, $P = 0.011$).

A Type II functional response described the relationship between sward height and nitrogen intake rate of wigeon best ($\Delta AIC_C = 2.3$; Table 2.3). A Type I functional response was the best model for the nitrogen intake rates of both swan goose ($\Delta AIC_C = 0$) and bean goose ($\Delta AIC_C = 1.9$; Table 2.3) following the rule that simpler model should be selected when ΔAIC_C is less than 2 (Burnham and Anderson 2002). The nitrogen intake rate of these two species linearly increased over the range of sward heights studied.

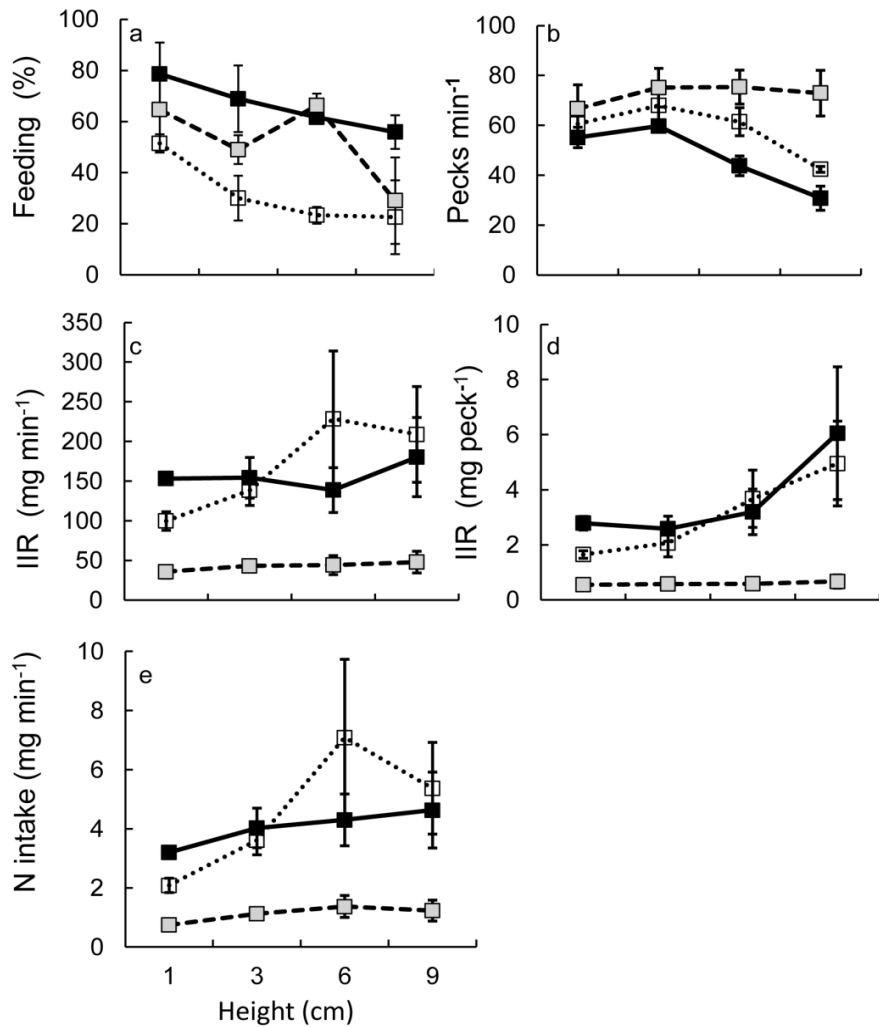


Figure 2.3 The relationship between sward height and feeding percentage (a), peck rate (b), IIR (c and d) and nitrogen intake (e). Dark filled squares: swan goose; open squares: bean goose; grey filled squares: wigeon. The error bars show the $\pm 95\%$ CIs.

Table 2.3 Comparing the functional response in relation to sward height based on nitrogen intake rate (mg/min). Type I (linear), Type II, and Type IV (quadratic). AICC values were used to decide upon the best fitting model. H = Swards height (cm).

Species	Model	Model	AIC _C	R ²
Swan goose	Type I	$0.98^{\#}H + 19.58^{\#}$	72.8	0.31
	Type II	$56.67^{\#}H / (1 + 1.98^{\#}H)$	72.8	0.43
	Type IV	$17.46^{\#} + 2.31H - 0.13H^2$	76.7	0.41
Bean goose	Type I	$2.86^{\#}H + 13.64^{\#}$	95.3	0.38
	Type II	$17.21^{\#}H / (1 + 0.35H)$	93.4	0.53
	Type IV	$-0.91 + 11.98^{\#}H - 0.91^{\#}H^2$	93.8	0.66
Wigeon	Type I	$0.35^{\#}H + 5.03^{\#}$	50.0	0.28
	Type II	$9.76^{\#}H / (1 + 1.12^{\#}H)$	47.2	0.50
	Type IV	$2.97^{\#} + 1.65^{\#}H - 0.13^{\#}H^2$	49.5	0.57

#denotes a significant coefficient ($P < 0.05$)

Table 2.4 Results of the GLMM analysis to test whether the percentage feeding time was affected by sward height and competitors. In the model both ‘sward height’ and ‘competitor’ were included as fixed factor and session, enclosure number and individual as random factors. Percentage feeding time was arcsin transformed to satisfy the assumptions of normality.

Species	Source	<i>b</i>	<i>se</i>	<i>df</i>	<i>t</i>	<i>p</i>
Swan goose	Sward height	-0.003	0.030	604	-0.592	0.554
	Competitor	-0.005	0.005	604	-0.972	0.332
	Sward height x Competitor	0.001	0.001	604	1.998	0.231
	Competitor					
Bean goose	Sward height	-0.001	0.005	526	-0.156	0.876
	Competitor	-0.002	0.005	526	-0.353	0.725
	Sward height x Competitor	-0.001	0.001	526	-0.616	0.538
	Competitor					
Wigeon	Sward height	0.006	0.005	367	1.774	0.540
	Competitor	0.001	0.007	367	0.618	0.152
	Sward height x Competitor	-0.001	0.001	367	1.367	0.201
	Competitor					

Table 2.5 Results of the GLMM analysis to test whether the percentage vigilant time was affected by sward height and competitors. In the model both ‘sward height’ and ‘competitor’ were included as fixed factor, and session, enclosure number, and individual as random factors. Peck rate was square root transformed to satisfy the assumptions of normality.

Species	Source	<i>b</i>	<i>se</i>	<i>df</i>	<i>t</i>	<i>p</i>
Swan goose	Sward height	-0.004	0.005	577	-0.861	0.389
	Competitor	-0.002	0.005	577	-0.348	0.728
	Sward height x Competitor	0.000	0.001	577	0.464	0.643
Bean goose	Sward height	0.009	0.006	484	1.510	0.132
	Competitor	-0.016	0.007	484	-2.414	0.016
	Sward height x Competitor	0.000	0.001	484	0.084	0.933
Wigeon	Sward height	0.006	0.005	397	1.132	0.259
	Competitor	-0.015	0.007	397	-1.970	0.049
	Sward height x Competitor	-0.001	0.001	397	-0.493	0.622

Table 2.6 Results of the GLMM analysis to test whether the peck rate was affected by sward height and competitors. In the model both ‘sward height’ and ‘competitor’ were included as fixed factor and session, enclosure number and individual as random factors. Peck rate was square root transformed to satisfy the assumptions of normality.

Species	Source	<i>b</i>	<i>se</i>	<i>df</i>	<i>t</i>	<i>p</i>
Swan goose	Sward height	-0.056	0.043	535	-1.297	0.195
	Competitor	-0.112	0.045	535	-2.494	0.013
	Sward height x Competitor	0.008	0.008	535	1.016	0.310
Bean goose	Sward height	-0.191	0.033	531	-5.731	<0.001
	Competitor	-0.129	0.039	531	-3.323	0.001
	Sward height x Competitor	0.023	0.006	531	3.514	<0.001
Wigeon	Sward height	-0.064	0.023	524	-2.750	0.006
	Competitor	-0.073	0.033	524	-2.178	0.030
	Sward height x Competitor	-0.002	0.005	524	-0.323	0.747

Competition experiment

The percentage of feeding time of all three species was not affected by interference competition (Table 2.4). When swan goose was feeding with bean goose, they spent less time on 6 cm high swards comparing to without competitors (Fig. 2.4a). For bean goose, when feeding with wigeon, they spent more time on 6 cm height swards (Fig. 2.4b). The percentage of feeding time of wigeon did not differ when feeding with different competitors (Fig. 2.4c).

The percentage of time being vigilant was affected when feeding with different competitors except for that of swan goose (Table 2.5). When bean goose was feeding together with competitors, they were more vigilant except when feeding on 3 cm high swards (Fig. 2.5b). Similarly, the percentage of time being vigilant of wigeon was also significantly higher when feeding with competitors except for that on 3 cm high swards.

Peck rate of all three grazing Anatidae species was affected by differently sized competitors (Table 2.6). Swan goose increased peck rate on 3 and 6 cm high swards when they feeding together with other species (Fig. 2.6a). Peck rates of bean goose on 1 and 3 cm high swards were significantly quicker when with interspecific competitors (Fig. 2.6b), compared to the control without interspecific competitors. For wigeon, when they feeding with bean goose, the peck rate on 6 cm high swards was significant quicker comparing to feed without competitors (Fig. 2.6c).

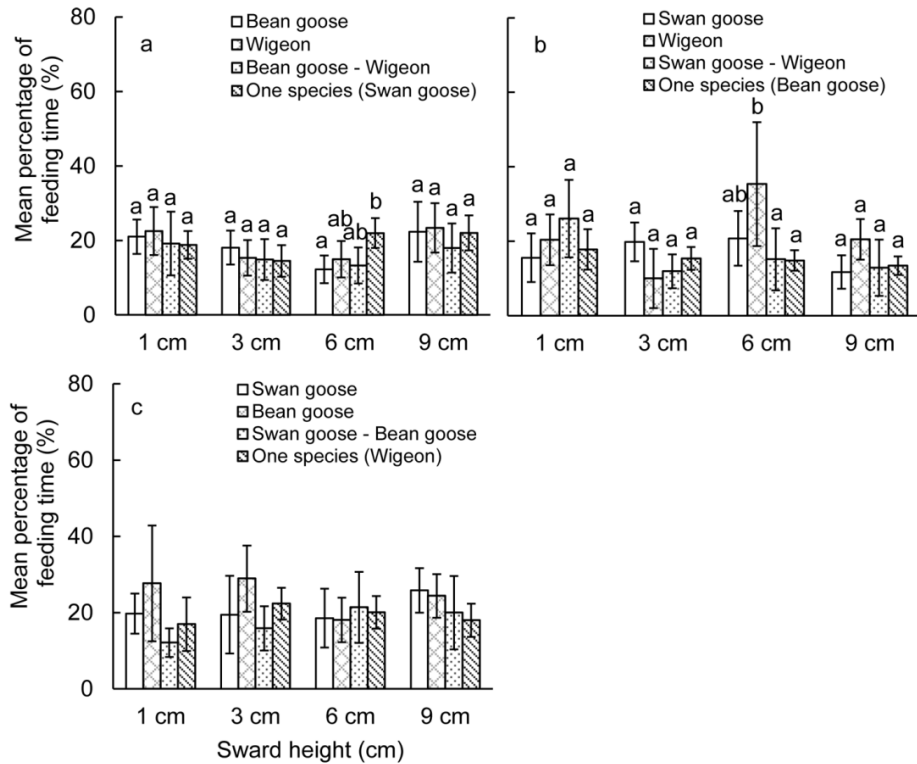


Figure 2.4 Mean percentage feeding time ($\pm 95\%$ CI, untransformed data) of swan goose (a and b), bean goose (c and d) and wigeon (e and f) in plots of different sward heights and with differently sized competitors. Different letters represent the results of the Tukey post-hoc test which indicate differences between feeding percentage between competitors within the sward height classes.

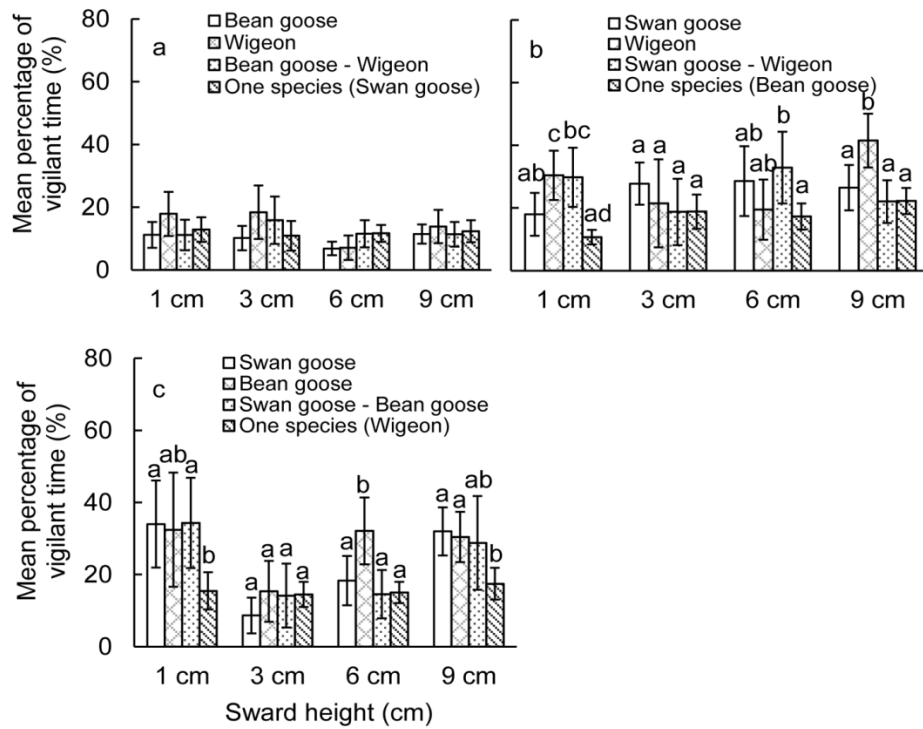


Figure 2.5 Mean percentage of time being vigilant ($\pm 95\%$ CI, untransformed data) for swan goose (a), bean goose (b) and wigeon (c) in plots of different sward heights and with differently sized competitors. Different letters represent the results of the Tukey post-hoc test, which indicate differences between peck rate between competitors within the sward height classes.

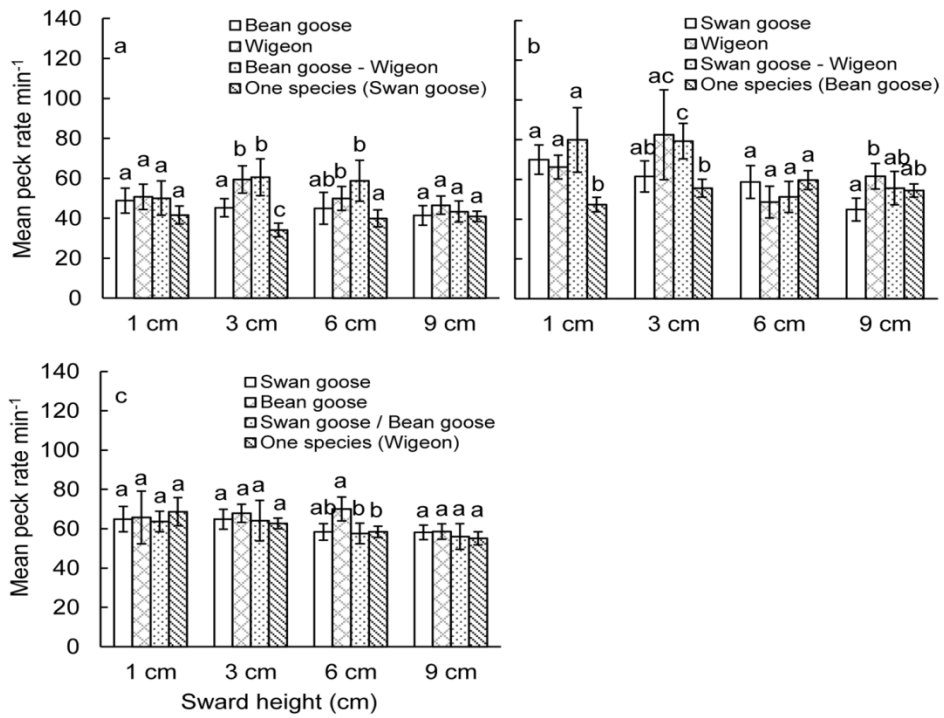


Figure 2.6 Mean peck rates per minute ($\pm 95\%$ CI) for swan goose (a), bean goose (b) and wigeon (c) in plots of different sward heights and with differently sized competitors. Different letters represent the results of the Tukey post-hoc test which indicate differences between peck rate between competitors within the sward height classes.

Instantaneous intake rate and nitrogen intake

For all species, no significant differences were found for instantaneous intake rate

(ANOVA, swan goose: $F_{3,270} = 0.791$, $P = 0.5$; bean goose: $F_{3,236} = 1.324$, $P = 0.267$;

wigeon: $F_{3,238} = 0.653$, $P = 0.582$; Fig. 2.7) and nitrogen intake (ANOVA, swan goose:

$F_{3,270} = 0.762$, $P = 0.516$; bean goose: $F_{3,236} = 0.998$, $P = 0.395$; wigeon: $F_{3,238} = 0.622$, P

$= 0.602$; Fig. 2.8) when feeding together with other species.

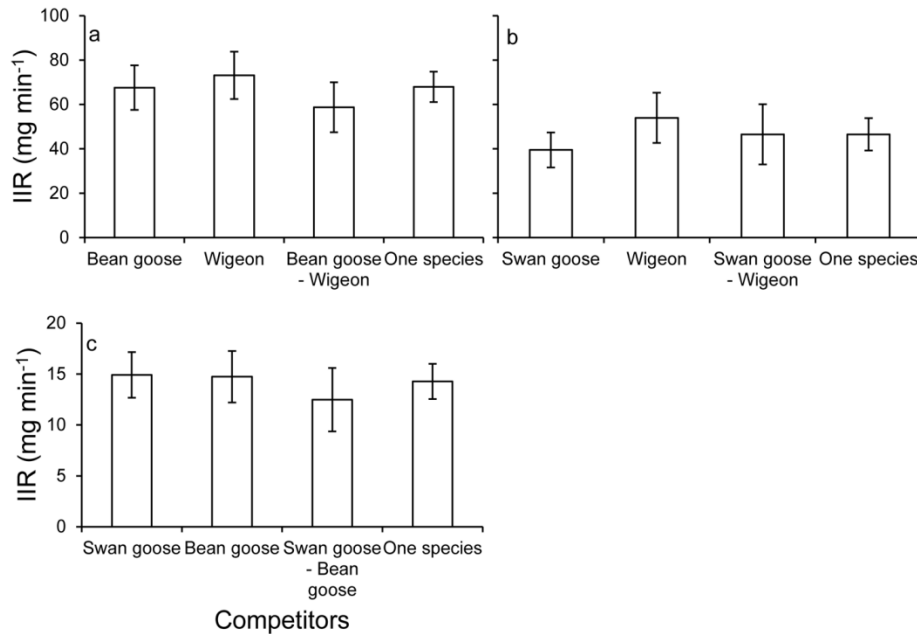


Figure 2.7 Mean instantaneous intake rate ($\pm 95\%$ CI) for swan goose (a), bean goose (b) and wigeon (c) with differently sized competitors.

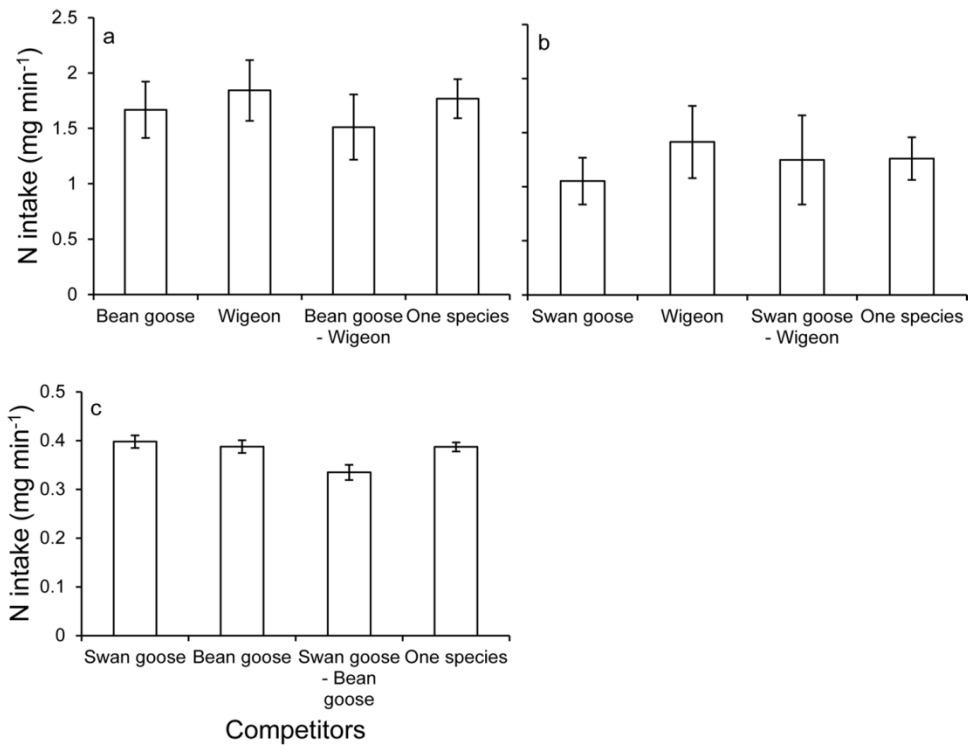


Figure 2.8 Mean nitrogen intake ($\pm 95\%$ CI) for swan goose (a), bean goose (b) and wigeon (c) with differently sized competitors.

Discussion

Our results showed that herbivorous birds use adaptive behaviours to compensate for the loss of foraging intake when under interference competition. When foraging with competitors, the mean percentage of feeding time of all studied species remained the same (Fig. 2.4), however, the mean percentage of time being vigilant increased except for the dominant swan goose (Fig. 2.5). Comparing the peck rate with and without competitors showed that the peck rate increased under competition (Fig. 2.6). Both instantaneous intake rate and nitrogen intake were not significantly different over different species combinations (Fig. 2.7, 8), indicating that herbivorous birds can change their feeding behaviour and thereby probably compensate for a loss in

intake as a results of interspecific competition. We also found that both swan goose and bean goose followed a Type I functional response, but wigeon, however, followed a Type II functional response over the range of sward heights studied (Table 3).

The nitrogen content of the vegetation is an important resource for herbivores because nitrogen is a construction element in the cell structure and it is required for all metabolic processes. Former studies often showed that the plant nitrogen content decreases with increasing plant height (Prop and Vulink 1992, Hassall et al. 2001). Our result, however, showed a dome-shaped relationship where the nitrogen content of the swards increased with the swards height until it reached a maximum at a sward height of 6 cm and then decreased, in line with the result of Van der Graaf et al. (2006). In *Carex* leaves, the nitrogen concentration drops from the top of the leaf to the leaf's base (Hirose et al. 1989). Consequently and unintentionally, we might have altered the nitrogen content in our experiments by clipping the swards to the desired heights. Nevertheless, our clipping corresponded with a natural winter situation, as in this period large numbers of herbivorous Anatidae visit these sedge meadows (Zhao et al. 2010, Zhao et al. 2012) and the grazing pressure is very high, also by livestock. Hence, herbivorous Anatidae species also modify the nitrogen distribution in sedge meadows by eating the nitrogen rich leaf tips and decreasing the sward height, as simulated in our clipping treatments.

The most common functional response in vertebrate herbivores is a Type II functional response (Spalinger and Hobbs 1992). A Type IV functional response curve, a dome shape, has been reported several times in Anatidae herbivores (Van der Wal et al. 1998, Durant et al. 2003, Bos et al. 2004, Heuermann et al. 2011). However, as shown in our results (Table 2.3, Fig. 2.3e), a Type I functional response was found for bean goose and swan goose and a Type II functional response yielded the best fit for wigeon over the range of heights studied. However, as the experiment was carried out using birds in single species flocks, these measurements do not yield interference-free functional responses. As our experiments were carried out on natural vegetation, our results may better simulate foraging intake in winter than using hand- constructed swards. With increasing sward height, peck rate of bean goose decreased (Fig. 2.3b). However, the peck size still increased with increasing sward height (Fig. 2.3d) which could compensate for the lower peck rate, triggering an increase in the instantaneous

intake rate (Fig. 2.3c). Moreover, the nitrogen content was higher in the taller swards (Fig. 2.2). As above, we could explain why a Type I functional response for nitrogen intake occurs. Hence, we suggest that bean goose prefer the taller swards. Swan goose had the lowest peck rate among the three Anatidae species and peck rate decreased with increasing sward height (Fig. 2.3b). However, the peck size of swan goose was the largest and the instantaneous intake rate was still increasing on the taller swards (Fig. 2.3c, d). As shown in Table 2.3, a Type I functional response was found which revealed that swan goose also preferred the taller swards. Wigeon was the smallest species in our research and we had predicted that the intake would follow a Type IV functional response. However, a Type II functional response fitted the data best (Table 2.3), which indicates that wigeon also preferred the tallest swards. Because of bill morphological restrictions, the peck size of wigeon was the smallest (Fig. 2.3d). Since wigeon always maintained a high peck rate, the nitrogen intake was also still increasing with increasing sward height (Fig. 2.3e). Taller swards might also limit their peck rate if we would have carried out this experiment on even taller swards, and we suggest that a Type IV functional response might still be found under a larger sward height gradient.

Interference competition between Anatidae species resulted in avoidance behaviour and aggressive interactions (Schoener 1983, Kristiansen and Jarrett 2002, Vahl 2006a). Avoidance behaviour was visible during the observations when subordinate individuals moved aside for dominant individuals of other species, whether this behaviour was costly in terms of time and energy or reduced aggressive interactions cannot be derived from our observations. However, of the 45 recorded aggressive encounters, 28 occurred between swan goose and bean goose, with swan goose as the dominant species, winning all encounters. Interspecific dominance was apparently not determined by body mass but by body height: swan goose was on average 500 gram lighter than bean goose but 14 cm taller at an upright position. It might be that body mass was affected by using tame individuals, as wild living swan goose are expected to be heavier than bean goose (Snow et al. 1998).

Aggressive interactions should be costly for both subordinate and dominant species when involved in a fight or pursuit in terms of lost foraging time, energy cost and the risk of injuries (Moore 1978, Schoener 1983, Huntingford and Turner 1987). Increasing the amount of time being vigilant will also increase the animals' energetic expenditure and therefore decrease their fitness (Black et al. 1992, Fortin et al. 2004, Nersesian et al.

2012). Hence, feeding time and/or peck rate should increase to compensate for the cost of these behavioural activities (Moore 1978, Kristiansen and Jarrett 2002, Cope 2003, Van Dijk et al. 2012). Indeed, we recorded compensation behaviour for both subordinate and dominant species by increasing their peck rate. Swan goose increased their peck rate by 10-15 pecks per minute on 3 and 6 cm high swards when feeding with other competitors. The peck rate of bean goose was quicker on 1 and 3 cm high swards under interference competition. When feeding together with bean goose, wigeon increased their peck rate on 6 cm high swards. That peck rate on 9 cm high swards did not change for all studied species under competition may be explained by increasing handling time on the taller swards and hence animals faced a bottleneck effect. In result, the instantaneous intake rate and the nitrogen intake were equal over different species combinations (Fig. 2.7 and 8), indicating that all species were able to compensate for the intake loss by this adaptive behaviour.

In conclusion, our results emphasize the importance of behavioural plasticity under interference competition. Although the mean percentage of feeding time of all studied species did not change when feeding with competitors, both dominant species (swan goose) and subordinate species (bean goose and wigeon) increased their peck rate to compensate for the negative effects of competition, such as increasing aggressive behaviour and vigilant time. This adaption behaviour may be of great important for grazing Anatidae when resources are limited, increasing their survival rate during the wintering period and the breeding success afterwards.

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Chapter 3

Elevation and sward height gradient facilitate coexistence of goose species through allometric responses in wetlands

Yong Zhang, Herbert H.T. Prins, Lei Cao, Meijuan Zhao and Willem F. De Boer

Explaining how species coexist is one of the central objectives in both basic and applied ecology. Allometric scaling law predicts that herbivores respond differently to the availability of resources, mediated by body size. Former studies concerning allometric responses often focussed on animals with a relatively large difference in body size. In this study, we hypothesized that allometric responses to the environmental gradient facilitate coexistence of species even if the body size difference is rather small. Using a correlative field study, habitat selection of two herbivorous goose species with a relatively small difference in body size was investigated. Both a generalized linear mixed model (GLMM) and a mixed logistic regression model showed that both species selected lower lying areas that became recently exposed, and as expected, the smaller species showed a stronger selection than the larger species. Sward height also influenced goose species habitat selection 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 geese habitat selection. A logistic regression model showed that structural heterogeneity of the sward had a negative effect on the patch selection of the smaller species but no effect on the larger one. In agreement with our hypotheses, the two goose species can coexist, mediated by an allometric response. We concluded that allometric responses play an important role in facilitating coexistence of species even if the difference in body size is relatively small.

Submitted for publication

Waterbirds (Accepted)

Introduction

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 favour 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 resource 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. Body size is an important species trait of animals. 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 higher quantities of food and are more tolerant of lower quality. 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. However, former studies on allometric responses often focussed on the species with relatively large difference in body size (Laca et al. 2010). Here, using two geese species that slightly differ in body size, we test our hypotheses that environmental gradients mediate species coexistence through allometric responses even if the difference in body size is relatively small.

The availability of resources often exhibits spatial and temporal variation (Fryxell et al. 2005). 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 (Wilmschurst and Fryxell 1995, Prins 1996b, Riddington et al. 1997), and factors such as plant nitrogen and fibre content are often used to predict forage selection in herbivores (Albon and Langvatn 1992, Post and Klein 1996, Van der Wal and Loonen 1998). Grazing wildfowl are sensitive to variation in forage quantity and quality (Ydenberg and Prins 1981, Sutherland and Allport 1994), whereby the nitrogen content is one of the best predictors (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 et al. 1998,

Hassall et al. 2001), whereas the fibre content increases (Gekara et al. 2005). Foragers, therefore, face a trade-off between maximizing forage quantity and quality. Foraging theory suggests that herbivores select their habitat under the influence of 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 ones prefer a higher intake rate, are less sensitive to variation in forage quality, and therefore select taller swards (Durant et al. 2003, Durant et al. 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.

Not only plant quality and quantity but also spatial heterogeneity affects the spatial distribution of herbivores. Swards structure (determined principally by variations in the height of the sward) can affect the forage efficiency of grazers by influencing handling time (Searle et al. 2005, Shipley 2007). Herbivores, for example, generally have lower intake rates while feeding on complex sward compared to homogenous swards (Wilmschurst et al. 2000, Heuermann et al. 2011). The smaller species, restricted by their bill morphology, have a lower bite mass but a higher bite rate, and therefore are more sensitive to the structural heterogeneity and hence prefer homogeneous patches (Heuermann et al. 2011).

The elevation of the grassland may play a vital role in determining forage availability for geese in wetlands, 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. During autumn and early winter, water levels drop in the Yangtze's wetlands, an important area for migrating birds, increasing the size of exposed recessional grasslands. The earlier-exposed grasslands are found on relatively higher areas, and have a longer growing period with relatively warmer temperature. Based on the above reasoning, these areas are expected to be more attractive to larger bodied goose species. The lower recessional grasslands have a shorter growing period under colder conditions, and are therefore probably more attractive to smaller bodied goose species.

In this paper, we studied the distribution of Bean Goose (*Anser fabalis*, body weight: ~ 3200 g) and the slightly smaller, Greater White-fronted Goose (*Anser albifrons*, body weight: ~ 2400 g), two species that differ in body mass and occur in wetlands of the Yangtze, to test the following hypotheses: (1) The smaller bodied species (Greater White-fronted Goose) is mainly found in the lower elevation area where forage biomass is lower but with a higher forage quality, while the larger Bean Goose select relatively higher areas. (2) An increase in the structural heterogeneity of the sward (measured by standard deviation of sward height) will have a stronger negative effect on the smaller bodied species than on the larger bodied species.

Methods

Study site

The Shengjin Lake National Nature Reserve (30°15' – 30°30' N, 116°55' – 117°15' E), with an area of 333 km², lies south of the Yangtze River. The protected area includes Shengjin Lake – a large and shallow, permanent fresh water 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.a.s.l.); during the dry season in winter when water level falls to less than 10 m.a.s.l., the lake area decreases to approximately 34 km², exposing extensive mudflats, grasslands, sedge meadows and seasonal wetlands. The dominant species of these exposed mudflats are *Carex* spp.

The climate is characterised by a subtropical monsoon with an average annual rainfall of about 1600 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 here. The majority of these are Bean Goose and Greater White-fronted Goose.

Transects and dropping count

We selected three sites that were frequently visited by these two geese species in this study. In winter, from November 2011 to March 2012, two parallel transects from the lake dyke to the water's edge were laid out at each site. Transects covered the entire

gradient from higher to lower grassland. We set short bamboo pegs at every ten steps at two of the corners to demarcate 1×1 m quadrats. Every month, we measured swards height with a disc pasture meter (DPM; 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. A mean value was calculated for each quadrat to avoid pseudoreplication.

Dropping density is a good estimate of the amount of grazing by geese (Owen 1971). Animals with different body sizes produce droppings of different sizes. Before the survey, we observed single Bean Goose and Greater White-fronted Goose flocks 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 millimetre to confirm the differences in dropping size between goose species (Bean Goose mean = 11.5 ± 1.2 mm mean \pm SD, $n = 1291$, Greater White-fronted Goose mean = 9.2 ± 0.9 mm, $n = 1430$). This method allowed us to detect the difference of droppings from the two species. Within each quadrat, we counted the number of goose droppings per species on the basis of the difference in dropping diameter every month. Droppings were removed from the quadrats after every count. With decreasing water level, the length of 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 and placed at approximately equal distances along transects. We collected leaf samples to analyze nitrogen and Acid Detergent Fibre (ADF) content within each exclosure every month. Each month, we removed and placed exclosures at a new location at equal elevation (m.a.s.l.) to account for self-shading effects and sample the plants that geese ate for chemical composition.

Measuring the relative elevation

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

Statistical analysis

For each 1×1 m quadrat, we calculated average and standard deviation of sward height (a measure of habitat heterogeneity).

As our dropping count data include many zero counts, in order to deal with data over-dispersion, we fitted a zero-inflated negative binomial GLMM with month and site as random effects for each species. Before fitting the multiple regression models, we also assessed multi-collinearity by examining the Variance Inflation Factors (VIFs) of the candidate variables, by including all candidate variables as independent variables in a regression model and dropping density as response variable. The results of a multi-collinearity test suggested little collinearity among variables (Table 3.2). Then, the final model was constructed using both forward and backward procedures for both species. For variables which 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 droppings' presence/absence data for each species. We applied both forward and backward procedures to construct the final models for both species. Then, for variables which 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 given in Table 3.1. Statistical analyses were conducted in R 3.1.2 (R Development Core Team 2014) with the packages MASS, pscl, glmmADMB and lme4. We considered results of statistical tests significant at $\alpha = 0.05$.

Table 3.1 Independent variables, abbreviations and predicted effects for the two goose species Bean Goose (BG) and Greater White-fronted Goose (GWFG).

Independent variables	Abbreviation	Note	Unit	Predicted effect	
				BG	GWFG
Relative elevation	Elev	Differences among quadrates	cm	-	--
Sward height	SH	no	cm	-	--
Nitrogen content	NC	no	%	+	++
ADF content	ADF	no	%	-	--
Habitat heterogeneity	SD	no	no	-	--

Table 3.2 Pearson correlation coefficients between independent variables, and Variance Inflation Factors (VIF); n = 623; (*P < 0.05;**p < 0.01;***p < 0.001). For abbreviations see Table 3.1.

	NC	ADF	SH	SD	VIF
Elev	-0.481***	0.102*	-0.084*	-0.287***	1.461
NC		-0.385***	0.045	0.187***	1.624
ADF			0.074	-0.104**	1.232
SH				0.217***	3.061
SD					3.116

Table 3.3 Results of the final GLMM model explaining the differences in Bean Goose and Greater White-fronted Goose dropping densities. (b = regression coefficient; SE = Standard Error of the regression coefficient; z-value; P value; VIF = Variance Inflation Factor; n = 623. For abbreviations see Table 3.1).

Species	Variables	<i>b</i>	<i>se</i>	<i>z</i>	<i>P</i>
Bean goose	Elev	-0.015	0.002	- 7.56	<0.001
	SH	-0.183	0.033	- 5.53	<0.001
	ADF	-0.046	0.021	- 2.19	0.028
Greater white-fronted goose	Elev	-0.017	0.001	- 9.17	<0.001
	SH	-0.229	0.028	-10.63	<0.001

Table 3.4 Results of the final mixed logistic regression model explaining the differences in Bean goose and Greater white-fronted goose dropping densities. (b = regression coefficient; SE = Standard Error of the regression coefficient; z-value; P value; n sample size = 623. For abbreviations see Table 3.1).

Species	Variables	<i>b</i>	<i>se</i>	<i>z</i>	<i>p</i>
Bean goose	Elev	-0.019	0.002	-8.006	<0.001
	SH	-0.205	0.036	-5.726	<0.001
	ADF	-0.071	0.028	-2.548	0.011
Greater white-fronted goose	Elev	-0.027	0.003	-9.535	<0.001
	SH	-0.266	0.061	-4.346	<0.001
	SD	-0.344	0.172	-2.004	0.045

Results

Zero-inflated negative binomial GLMM

The final models (Table 3.3) showed that relative elevation, sward height and ADF content had a significant negative effect on the dropping densities of Bean Goose and Greater White-fronted Goose.

As predicted, relative elevation (Elev) was negatively related to the density of both species (Table 3.3), suggesting that both species selected relatively lower elevation areas that became exposed later in winter. The slope of the elevation term was significantly different between species (interaction term: $z = -2.95$, $p = 0.003$). The more negative slope of Greater White-fronted Goose showed that the smaller species was more strongly selecting lower areas than the larger Bean Goose.

Sward height (SH), in line with our predictions, had a negative effect on both species (Table 3.3). The species \times sward height interaction was significant ($z = -3.25$, $p = 0.001$). The smaller species was more strongly selecting lower swards than the larger species.

ADF content (ADF) had a negative effect on Bean Goose density but no effect on Greater White-fronted Goose. Nitrogen content (NC) and structural heterogeneity of vegetation (SD) had no effect on both Bean Goose density and Greater White-fronted Goose density, which was inconsistent with our predictions (Table 3.3).

Logistic regression model

Results of the logistic regression model were similar to the zero-inflated model. Negative slopes for relative elevation (Elev) were found (Table 3.4). The effect of relative elevation was similar for the two species (interaction term: $z = 1.054$, $p = 0.282$). Sward height (SH) also had a negative effect on both species (Table 3.4). The Greater White-fronted Goose was more affected by sward height than the Bean Goose (interaction term: $z = -2.738$, $p = 0.006$).

Discussion

Our results demonstrated that landscape features and food resource affected the herbivores patch selection in different ways, mediating goose species coexistence during the wintering period in Yangtze wetlands. As predicted, factors, such as elevation and sward height negatively affected the densities of both species according to the results of the zero-inflated negative binomial GLMM and the logistic regression. As species

differences were also detected, our study hints at the importance of allometric responses in habitat selection by different goose species. Both models suggested that ADF content (ADF) had a negative effect on Bean Goose but no effect on Greater White-fronted Goose. The logistic regression model indicated that vegetation heterogeneity negatively affected Greater White-fronted Goose but had no effect on Bean Goose. For nitrogen content, however, both models failed to detect a significant effect on the two goose species (Table 3.3, 4).

Our result supports our hypothesis that both species select lower elevation areas. Water level, as estimated by relative elevation, negatively affected the densities of both species (Table 3.3, 4), which suggests that both species selected feeding patches in the lower areas closer to the water edge. This result supports the findings of previous research (Oloff et al. 1997) which showed that Brent Goose (*Branta bernicla*) reached higher densities on the lower part of an elevation gradient in salt marshes.

Sward height, an indicator of forage biomass, had a strong negative effect on the dropping density of both species. This result is in line with previous findings (De Boer and Prins 1989, Prins 1996b, Durant et al. 2003, Si et al. 2011) and our prediction. Foraging on high biomass swards increases searching and handling time, and therefore decreases intake rate (Heuermann et al. 2011). Areas with a lower above-ground biomass are therefore preferred by smaller grazing species. Since the highest dropping densities were found in the areas with a lower vegetation biomass, we suggest that food biomass was the most important factor driving geese habitat selection in our research area, as available biomass determines food intake through a functional response.

Vegetation in lower areas often has a higher quality (Oloff et al. 1997). Many experimental studies report that nitrogen content can affect herbivores' habitat selection. In our case, we failed to detect any effect of nitrogen content, similar to the study on Barnacle Goose (*Branta leucopsis*) in the Netherlands (Si et al. 2011), which was also based on field observations. They suggested that it is because of the relatively high nitrogen contents that were above the requirements of the geese. Study has shown that the presence of large herbivores can decrease the nitrogen mineralization rate in moist grassland (Schrama et al. 2013). Foraging in the lower area could, therefore, decrease the quality of the swards. We carried out our study in a natural area where nitrogen content was lower (medium = 2.3%, range from 1.17% to 4.31%, $n = 90$) than in the

Netherlands. Hence, foraging in lower quality grassland, total biomass may be more crucial in patch selection under these conditions than forage quality.

A negative effect of the structural heterogeneity of the swards was found on the dropping densities of the smaller species but no effect was found for the larger species (Table 3.4). This result partly followed 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 in order to satisfy their daily demand. However, a high heterogeneity in resource availability could decrease the bite rate and hence reduce the forage intake rate.

As allometric scaling law predicted, our study demonstrated that smaller species were 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 growth period, and consequently a higher vegetation biomass and lower quality. Consequently, the larger Bean Goose was also able to tolerate 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 result also suggests that a relatively lower sward biomass, e.g., through grazing from cattle, by mowing, or by manipulating the water heights can facilitate herbivorous geese, especially the smaller species.

Where they co-exist, herbivores often forage on the same food resource. The Yangtze 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 and we expected that competition could be important in driving their spatial distribution (Amarasekare 2002). However, our result suggested 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. Grazers that differ in body mass could apply different foraging strategies to satisfy their daily intake requirements. 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 flood plains. We suggest that an optimal hydrology regulation regime for the Yangtze flood plain could facilitate species coexistence and hence increase bird species richness.

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Chapter 4

Individual-area relationship best explains goose species density in wetlands

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Explaining and predicting animal distributions is one of the fundamental objectives in ecology and conservation biology. Animal habitat selection can be regulated by top-down and bottom-up processes, and is mediated by species interactions. Species varying in body size respond differently to top-down and bottom-up determinants, and hence understanding these allometric responses to those determinants is important for conservation. In this study, using two differently sized goose species wintering in the Yangtze floodplain, we tested the predictions derived from three different hypotheses (individual-area relationship, food resource and disturbance hypothesis) to explain the spatial and temporal variation in densities of two goose species. Using Generalized Linear Mixed Models with a Markov Chain Monte Carlo technique, we demonstrated that goose density was positive correlated with patch area size, suggesting that the individual area-relationship best predicts differences in goose densities. Moreover, the other predictions, related to food availability and disturbance, were not significant. Buffalo grazing probably facilitated greater white-fronted geese, as the number of buffalos was positively correlated to the density of this species. We concluded that patch area size is the most important factor determining the density of goose species in our study area. Patch area size is directly determined by water levels in the Yangtze floodplain, and hence modifying the hydrological regimes can enlarge the capacity of these wetlands for migratory birds.

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Introduction

Explaining and predicting animal distributions is one of the fundamental objectives in ecology and conservation biology. Despite intensive research efforts during the past decades, this issue remains incompletely understood, partly because population density of animals can be determined by a variety of abiotic and biotic determinants that interact and operate at different spatial scales. Particularly, biotic interactions, such as top-down (i.e., predation) and bottom-up (i.e., food availability and quality) factors, operate across trophic levels (Krebs et al. 1995) under influence of competitive and facilitative interactions (Schoener 1983, Reiter and Andersen 2013, Tombre et al. 2013). The effects of those determinants may vary among species through allometric responses (Laca et al. 2010). Predictions derived from allometric relationships state that animals differing in body size respond differently to top-down and bottom-up factors based on e.g., physiologic and digestive consequences of body size. Therefore, understanding the different responses among species to those determinants is crucial for conservation. In this paper, using two herbivorous goose species, we aim to answer two questions: if and how top-down and bottom-up factors affect goose density and if the effects vary between species, offering insight into the underlying factors that conservation strategies should cover.

Eastern China supports more than two million migratory waterbirds during the non-breeding seasons, of which more than one million overwinter in the Yangtze River floodplain (Cao et al. 2008). Anatidae species such as geese mainly feed on recessional grassland in the Yangtze floodplain in winter. A primary factor determining goose population density would be the extent of available habitat. The sizes of the patches of available habitat change with the water level fluctuations and thereby affect the habitat selection of these birds, which can be described by an individual-area relationship (IAR). The IRA describes the relationship between animal population size and area (Connor et al. 2000). Positive IRAs are often found (Connor et al. 2000, Murray et al. 2013), which is in line with the resource concentration hypothesis (Root 1973). The resource concentration hypothesis, introduced by researchers on herbivorous insects, states that larger areas of host plants should attract more herbivores (Root 1973). Movements of consumers between patches are also used to explain IARs (Connor et al. 2000, Skorka et al. 2009), as animals can move to larger or richer patches if this is beneficial in terms of their own net foraging success, and thereby affect the availability

of resources in patches, often resulting in a positive IAR, consistent with the ideal free distribution (Fretwell and Lucas 1970). Hence, the capacity of the Yangtze floodplains to accommodate migratory birds might be negatively affected if the availability or the size of these recessional grasslands is reduced.

Forage quantity and structural heterogeneity play an important role in determining the animal's patch selection as animals select patches offering the highest forage intake such as predicted by the optimal foraging theory (Prins 1996b, Koh et al. 2006, Crooms et al. 2009, Heuermann et al. 2011, Si et al. 2011, Pretorius et al. 2012). Goose species generally display a Type IV functional response, which is a dome-shaped curve with a maximum intake rate at intermediate forage biomass, and a decreasing intake at higher biomass densities. Smaller species tend to select lower biomass areas as their maximum intake is reached earlier than for larger species (Bos et al. 2004, Heuermann et al. 2011). In addition, habitat heterogeneity, such as horizontal variation in available forage biomass, tend to increase species richness (Bazzaz 1975, Xu et al. 2014), but the effect of habitat heterogeneity differs among species (Tews et al. 2004). Habitat heterogeneity can also negatively affect the forage efficiency of grazers by increasing searching and handling times (Searle et al. 2005, Shipley 2007). Herbivores, such as many overwintering waterbird species (e.g., *Anser* spp., *Anas* spp.), generally have a lower intake rate and consequently reach lower population size while feeding on heterogeneous swards compared to homogenous swards (Wilmshurst et al. 2000, Heuermann et al. 2011, Rosin et al. 2012).

These ecological factors are important in determining animal distribution and density. In addition, anthropogenic activities (e.g., agriculture, aquaculture and livestock breeding) are playing an increasing role (Blumstein et al. 2005, De Boer et al. 2013, Garcia-Morales et al. 2013, Zhang et al. 2013). Such activities are found to be strongly correlated with habitat selection of geese, and can have both negative or positive effects on geese densities (Fernandez-Juricic and Telleria 2000, Koh et al. 2006, Palomino and Carrascal 2007, Lepczyk et al. 2008, Meager et al. 2012).

Species normally react differently to ecological and anthropogenic factors, and this reaction is often mediated by differences in body size as indicated by allometric scaling laws (Bell 1970, Jarman 1974). The effect of forage quantity and structural heterogeneity is influenced by body size, as smaller sized species generally select areas with a lower forage quantity but with more homogenous resources (Heuermann et al.

2011). Larger species are more sensitive to human disturbances (Blumstein et al. 2005, De Boer et al. 2011). However, species can also react positively to human factors, for instance, the grazing by domestic larger grazers such as cattle or buffalo, can facilitate resource availability for smaller grazer species by changing resource structure and nutrient content (Farnsworth et al. 2002, Olff et al. 2002, Van Langevelde et al. 2008, Bakker et al. 2009). For instance, it has been reported that the density of geese was higher in areas with a higher sheep density (Loe et al. 2007).

In this paper, we analysed the effects of anthropogenic and ecological determinants on goose species density in wetland in China, using two migratory grazing goose species, namely bean goose (*Anser fabalis*, body weight: 3100 g) and greater white-fronted goose (*Anser albifrons*, body weight: 2400 g), which both rely on the same food resource and habitat in the same period. We tested several hypotheses:

- the individual-area relationship hypothesis: we predicted that goose density increases with an increasing area of the exposed land;
- the food resource hypothesis: we predicted that goose density increases with increasing forage quantity until a certain threshold. Habitat heterogeneity is expected to negatively affect goose density, and the smaller species would be more sensitive to such heterogeneity than the larger one;
- the disturbance hypothesis: we predicted a negative effect of human disturbance (i.e., the presence of domestic geese and boats) on wild goose density for both species, but with a stronger reaction for the larger species, and a positive, facilitative effect by the number of water buffalo.

Methods

Study area

Shengjin Lake National Nature Reserve (30°16′–30°25′N, 116°59′–117°12′E), located on the southern bank of the Yangtze River, is an important wetland in the Yangtze floodplain for wintering waterfowl. In summer, the maximum lake area is about 14,000 ha, in winter, as the water levels decline, the lake area decreases to about 3,400 ha. Water comes from three smaller rivers flowing directly into the lake and from the Yangtze River via the Huangpen Sluice built in 1965 (Cheng and Xu, 2005). The sluice was built to regulate the water level for facilitating agricultural activities and to control

floods. The average annual rainfall is about 1600 mm, with most rain falling from March to August, and the average annual temperature is 16.1°C, with an average January temperature of 4.0 °C.

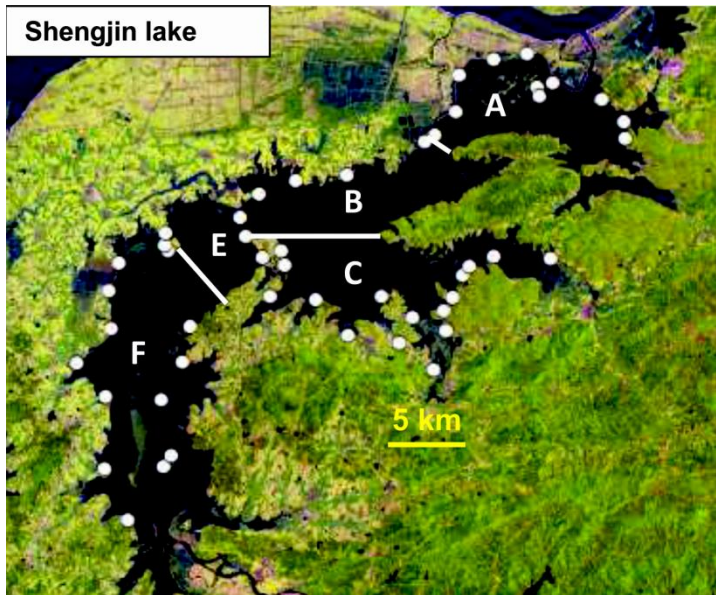


Figure 4.1 Map of Shengjin Lake and the five discrete survey areas. The white circles indicate the 56 counting points and the white lines indicate the counting area boundary.

Table 4.1 The potential predictor variables and their abbreviations used to analyse differences in goose densities. H_0 indicates expected relationship. +: positive; -: negative. NDVI: Normalized Difference Vegetation Index.

Hypothesis	Variables	Units	Explanation	Abbreviations	H_0
Individual-area hypothesis	Patch area	km ²	Calculated from satellite images	PA	+
	Total biomass	g/m ²	Calculated from NDVI data using built equation	BIO	+
Food resource hypothesis	Square of total biomass	g/m ²		BIO ²	-
	Coefficient of variation	no	Calculated by standard deviation of NDVI divided by mean NDVI	CV	-
	Number of buffaloes	no		BUFF	+
Disturbance hypothesis	Number of boats at anchor	no		BA	-
	Number of domestic goose	no		GOOSE	-

Table 4.2 Comparison of the values for the deviance information criterion (DIC) between models (MCMCglmm) that were built using a zero-inflated (zipoisson) and nonzero-inflated (poisson) distribution.

Hypothesis	DIC value			
	Bean goose		Greater white-fronted goose	
	zero-inflated	nonzero-inflated	zero-inflated	nonzero-inflated
Individual-area relationship	3796.6	3369.3	1858.8	1428.5
Food resource hypothesis	4215.5	3365.6	1874.4	1428.6
Disturbance hypothesis	4184.1	3368.3	1862.6	1426.3

Survey methods

Shengjin Lake was divided into five discrete survey areas (Fig 4.1). The major factors considered in deciding the size of a survey area was that it had clear boundaries, defined by natural and artificial features and the entire lake could be adequately surveyed by two teams of 2 persons in two days. Within each survey area, discrete sub-areas were identified by natural boundaries and features which enabled sub-areas to be completely surveyed. Each sub-area could be surveyed from a fixed counting location (Fig 4.1). The lake was surveyed every 16 days from 2008 to 2013 in winter, depending on the satellite passing and on local weather conditions. Survey areas A and B were surveyed on the same day by one group of observers, while area C was surveyed at the same time by

another group. Areas E and F were surveyed by the two groups of observers simultaneously, one surveying the west side and the other the east side of the lake. To avoid double counting, cell phone communication was used during the survey. In case of poor weather conditions, with e.g., fog or rain, an additional day was needed to complete the survey (7 out of 22 surveys). The “look-see” counting method is commonly used to count waterbirds (Bibby et al. 2000) and was therefore used in this study. For each sub-area, the number of bean goose and number of greater white-fronted goose was recorded. In case of geese moving within the sub-area, we waited until all geese had settled and no geese were flying around anymore. For both species, we recorded the sizes of the different sub-flocks as this method can reduce the error when counting large numbers of birds (Rappoldt et al. 1985). Time spent on each counting point was different, from 5-20 min, except four counting sub-area F where around 60 min was needed to count all birds. In addition, potential disturbance factors (Table 4.1) were also recorded for each sub-area. After each survey, a distribution map was drawn with reference to species, bird numbers, location and date and time. A detailed description of the survey methodology can be found in Cao et al (2011).

Satellite image processing

Normalized Difference Vegetation Index (NDVI) was calculated to represent forage quantity using Multispectral HJ-1A, Landsat Thematic Mapper (TM) and Enhanced Thematic Mapper + (ETM+) images (with a consistent spatial resolution of 30 m). We selected the images (with less than 10% cloud cover) that were recorded around our survey dates (Table S4.1, 2). Due to the sensor failure of Landsat 7 in 2003, parts of the data were lost on the edges of the ETM+ image (USGS, 2013). Fortunately, such data loss only accounted for about 5% of our study area, and a gap-filling method based on local linear histogram matching (Scaramuzza 2004) was used to fix the missing data.

After fixing the missing ETM+ data, we conducted image calibration (converting digital numbers to radiance) and atmospheric correction (using a Fast Line-of-sight Atmospheric Analysis of Hypercubes, FLAASH) (Matthew et al. 2000). Geometric correction was applied using second-order polynomials with an accuracy of less than 0.5 pixels Square Mean Root Error (SMRE). Pseudo Invariant Features (PIF) was used to normalize all images to allow for comparison between datasets (Schott et al. 1988).

We adopted the Supported Vector Machines (SVMs) method to discriminate between water and land within our study area because of their proven efficiency and accuracy in binary classification (Boyd et al. 2006). Further, we applied a NDVI threshold to distinguish between bare soil and meadows. To determine this threshold value, NDVI values were plotted against log-transformed vegetation biomass, which was measured in each winter month during 2010-2012. Eventually we selected 0.18 as the threshold to distinguish between bare soil and meadows (Fig S4.1). Image processing was performed in ENVI 4.8 and ArcGIS 10.0 software.

Statistical analysis

The independent variables that potentially affected geese habitat selection and density, their abbreviations and predicted effects are given in Table 4.1.

Vegetation biomass of the grassland is a direct indicator of forage quantity. However, field measurement of biomass is not available for each survey date, but we found a strong empirical relationship between measured total biomass (log transformed g/m^2) and NDVI (including both linear and quadratic term) using regression analysis (see Results). Hence, we calculated vegetation biomass based on NDVI data.

Generalized Linear Mixed Models using Markov Chain Monte Carlo techniques (MCMCglmm) (Hadfield 2010) were performed to separately test our predictions. A total of 22 surveys' data across five wintering periods were used depending on the satellite images quality and the passing data (Table S4.2). Because both goose species wintered in our research area from late September to the end of March, we only used the survey data from within this wintering period. The number of birds on the water was excluded from the counts, as we intended to measure the effect of the size of the patch area. We ran the analysis using zero-inflated models (family = zipoisson) and non-zero-inflated models (family = poisson) for both species separately and compared the model fit using the deviance information criterion (DIC). The model with lowest DIC was considered as the appropriate model (Spiegelhalter et al. 2002). We performed 30,000 iterations as burn-in, followed by 300,000 runs with a thinning interval of 100. The density of bean goose and greater white-fronted goose were dependent variables. The independent variables are listed in Table 1. Survey time (year and month) and site (counting points) were random factors. We checked for autocorrelation between

samples, but found that autocorrelation was of little influence (all positive values were close to zero). We also tested for spatial autocorrelation of the residuals using Moran's I index, and found little evidence for spatial autocorrelation (Table S4.3). Correlation between pairs of independent variables was weak (all pairwise correlations, $|r| < 0.01$), indicating that there was no multicollinearity problem. Statistical analyses were conducted in R 2.13.0 with the package MCMCglmm.

Results

A strong positive relationship was found between total biomass (g/m^2) and NDVI as: $\log(\text{g/m}^2 + 1) = 15.57 * \text{NDVI} - 9.77 * \text{NDVI}^2 - 1.26$ ($R^2_{\text{adj}} = 0.56$, $F_{2,232} = 152.1$, $P < 0.001$), which indicated that NDVI was a good proxy of forage biomass.

The nonzero-inflated model fitted our data best for both species according to the DIC value (Table 4.2) and was therefore used in further analysis. The predictions derived from the individual area relationship hypothesis were confirmed as patch area size (PA) had a significantly positive effect on the geese density for both species (Table 4.3, 4), whereas food and disturbance variables were not significant. Also the number of buffalos had a positive effect on the density of greater white-fronted goose (Table 4.4).

Table 4.3 Summary of the effects of dependent variables on bean goose density as generated by the MCMCglmm model for each of the hypotheses and independent variables, with coefficients and p-values. CI = confidence interval of the coefficient. For abbreviation of dependent variables see Table 4.1.

Hypothesis	Variables	Coefficient	Lower 95% CI	Upper 95% CI	<i>P</i>
Individual-area hypothesis	PA	0.962	0.106	1.866	0.036
Food resource hypothesis	BIO	-0.034	-0.108	0.045	0.373
	BIO ²	0.000	-0.001	0.001	0.496
	CV	-1.828	-8.550	3.974	0.568
Disturbance hypothesis	BA	0.066	-0.081	0.210	0.356
	GOOSE	-0.000	-0.003	0.002	0.801
	BUFF	0.012	-0.002	0.025	0.077

Table 4.4 Summary of the effects of dependent variables on greater white-fronted goose density as generated by the MCMCglmm model for each of the hypotheses and

independent variables, with coefficients and p-values. CI = confidence interval of the coefficient. For abbreviation of dependent variables see Table 4.1.

Hypothesis	Variables	Coefficient	Lower 95% CI	Upper 95% CI	<i>P</i>
Individual-area hypothesis	PA	1.739	0.669	2.939	0.003
Food resource hypothesis	BIO	-0.005	-0.116	0.096	0.930
	BIO ²	0.000	-0.001	0.001	0.704
	CV	-0.358	-10.140	8.890	0.936
Disturbance hypothesis	BA	-0.169	-0.531	0.170	0.302
	GOOSE	-0.000	-0.003	0.002	0.768
	BUFF	0.020	-0.005	0.035	0.005

Discussion

In this study, we tested the predictions derived from three hypotheses in explaining the variation in densities of two grazing goose species in Yangtze wetlands. We demonstrated that the patch area size (PA) was positively correlated with the density of both goose species, indicated that our data strongly supported the individual-area relationship. For both species, we failed to detect any support for the food resource and disturbance hypothesis, as all food and disturbance variables were not significant, although the number of domesticated buffalos had a positive effect on the density of greater white-fronted goose. Our results showed that patch area size is the most important factor in explaining spatial differences in bird distribution and densities, supporting the individual-area hypothesis, which is in line with the findings of Connor and co-workers (Connor et al. 2000). Connor et al. (2000) discussed that their analyses may be biased. We conducted our bird censuses in a systemic way, using point counts. The counting points were selected carefully to cover a certain sub-area, determined by natural and artificial boundaries. Both our study species are larger herbivores which are easily detectable. The resource concentration hypothesis, first introduced for herbivorous insects (Root 1973), is often employed to explain IARs. The hypothesis states that larger areas of host plants should attract more herbivores, because the animals are more likely to find the plants and stay longer. An alternative explanation for this relationship is that predation risk is higher in smaller patches than in larger ones (Root 1973, Risch 1981).

Our study did not find any support for the food resource hypothesis; biomass was even negatively, but not significantly, correlated with the bird densities of both species (Table 4.3, 4). These results are not consistent with the ideal free distribution which predicts that consumer density is positively related to resource availability. This may be explained by differences in forage quality and the animal's digestion system. Plant quality generally decreases over the growing season with increasing biomass (Van der Wal et al. 2000). Grazing wildfowl are sensitive to variation in forage quantity and quality (Ydenberg and Prins 1981). Goose species have a poor digestion system and may not be able to tolerate low forage quality. Vegetation heterogeneity (CV) was also negatively correlated with bean goose and greater white-fronted goose density, but this was also not significant (Table 4.3, 4). Foraging on more homogeneous area can reduce searching time (Shiple 2007) and hence offer a higher peck rate to satisfy the relatively high daily energy demands of these goose species. However, the weak negative effect indicated that vegetation heterogeneity is not the main factor that determines goose species density in these wetlands.

We also failed to detect a significant effect of disturbance related factors. As Shengjin lake is a national nature reserve in China and also one of the Ramsar wetlands, it is also relatively better managed. However, we still found negative slopes for the effects of domestic goose (GOOSE) and boats at anchor (BA) for both species, suggesting that these factors might play a weaker role in determining goose densities. Water buffalo (BUFF), the dominant livestock species in the study area, also forage on these grasslands. A positive correlation between number of buffalos and goose density was found for both species, suggested that goose density increased with number of water buffalo especially for greater white-fronted goose, indicating that water buffalos can facilitate geese. A Type IV functional response for these two goose species was found in previous studies (Durant et al. 2003, Heuermann et al. 2011), which suggests that their density is expected to decrease once a certain optimal level of forage biomass has been surpassed. Grazing livestock such as buffalos may reduce forage biomass, change the vegetation structure and increase the availability of nutritious regrowth, and thereafter facilitate goose species grazing (Van Wieren 1998, Bakker et al. 2009). Moreover, foraging with buffalos may also lead to an earlier detection of predators, such as dogs.

Our study generated strong support for the individual-area relationship, and

temporal and spatial differences in resource availability or disturbance seem to play no role in determining the differences in goose density. This result highlights the importance of patch area size in determining the animal's habitat choice. To safeguard China's wetlands biological diversity, conservation biologists and policymakers often face a dilemma in prioritizing conservations actions, as habitat selection of wetlands birds is complex, assumed to be regulated by ecological and anthropogenic factors. Our results indicate that simply increasing patch area size is an eminent management action, as one larger exposed grassland area is more attractive for migratory goose than several smaller areas with the same total area. The exposure of recessional grasslands is directly determined by fluctuations of water level. Hence, in order to enlarge the capacity of the Yangtze wetlands and better protect wintering wildfowl, hydrological regimes could be optimized. Moreover, our results support the knowledge that habitat fragmentation may negatively affect animal densities. Hence, we suggest that water level management schemes should be optimized to both address the factors that determine the wetland suitability for migratory birds, such as through a reduction in habitat fragmentation and an increase in the area of recessional grasslands, while also addressing the need for water for irrigation and aquacultural purposes and flood protection.

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Supporting information**Table S4.1** Date of acquired satellite images and total biomass data used in the analysis for predicting forage total biomass from differences in NDVI.

	HJ1A CCD2	HJ1B CCD1	HJ1B CCD2	Landsat ETM+
2010	Oct, Nov	Dec		
2011			Nov	Dec
2012	Feb			

Table S4.2 Image date and information of acquired satellite images and their corresponding survey date.

Images date	Satellite	Sensor	Survey date
02-Dec-08	Landsat	ETM+	06-Dec-08
18-Dec-08	Landsat	ETM+	15-Dec-08
31-Oct-09	HJ 1	A CCD2	31-Oct-09
05-Dec-09	Landsat	ETM+	04-Dec-09
21-Dec-09	HJ 1	A CCD1	18-Dec-09
14-Jan-10	Landsat	TM	04-Jan-10
23-Feb-10	Landsat	ETM+	16-Feb-10
19-Mar-10	Landsat	TM	16-Mar-10
31-Oct-10	HJ 1	A CCD2	21-Oct-10
06-Nov-10	HJ 1	A CCD1	05-Nov-10
22-Nov-10	Landsat	ETM+	22-Nov-10
08-Dec-10	Landsat	ETM+	08-Dec-10
21-Dec-10	HJ 1	B CCD1	23-Dec-10
25-Jan-11	Landsat	ETM+	24-Jan-11
21-Feb-11	HJ 1	B CCD2	25-Feb-11
23-Mar-11	HJ 1	A CCD1	14-Mar-11
19-Oct-11	HJ 1	B CCD2	16-Oct-11
12-Nov-11	HJ 1	B CCD2	09-Nov-11
25-Nov-11	Landsat	ETM+	25-Nov-11
11-Dec-11	Landsat	ETM+	10-Dec-11
18-Oct-12	HJ 1	B CCD2	11-Oct-12
12-Dec-12	HJ 1	A CCD1	14-Dec-12

Table S4.3 Moran's I values of residuals for the test of spatial autocorrelation in the final model both for each survey. BG = bean goose; GWFG = greater white-fronted goose. * $P < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Survey date	Moran's I value for three models					
	individual-area		Food resource model		Disturbance model	
	BG	GWFG	BG	GWFG	BG	GWFG
06-Dec-08	-0.062	-0.013	-0.156*	-0.010	0.028	0.015
15-Dec-08	-0.021	0.005	0.024	-0.018	0.015	0.078
31-Oct-09	-0.026	0.010	0.009	-0.012	-0.015	-0.059
04-Dec-09	0.095*	-0.133*	0.034	-0.031	0.008	-0.133*
18-Dec-09	-0.051	0.001	0.055	-0.042	-0.086	0.180*
04-Jan-10	-0.055	-0.010	0.065	-0.012	0.081	0.016
16-Feb-10	0.049	0.035	-0.029	0.024	0.042	0.065
16-Mar-10	0.030	-0.027	0.034	-0.014	-0.014	-0.004
21-Oct-10	-0.043	-0.021	0.064	-0.051	0.060	0.002
05-Nov-10	0.045	0.030	0.103*	0.104*	0.048	0.053
22-Nov-10	-0.023	0.005	.025	-0.022	0.087*	0.112*
08-Dec-10	0.066	-0.016	0.087	0.160*	0.062	-0.012
23-Dec-10	-0.005	0.015	0.036	-0.053	0.086	0.005
24-Jan-11	-0.026	-0.004	0.026	0.006	0.009	-0.081
25-Feb-11	-0.098	0.033	-0.004	-0.005	-0.055	0.086
14-Mar-11	0.013	-0.020	-0.041	-0.020	0.046	-0.048
16-Oct-11	-0.060	0.023	-0.032	-0.016	0.095*	-0.000
09-Nov-11	-0.042	-0.016	-0.024	-0.088	0.003	0.030
25-Nov-11	0.008	0.012	-0.035	-0.068	-0.043	-0.033
10-Dec-11	-0.051	-0.015	-0.081	.234***	-0.038	0.012
11-Oct-12	-0.101	-0.013	-0.034	0.060	-0.036	-0.036
14-Dec-12	0.027	-0.033	0.140*	0.081	0.060	-0.062

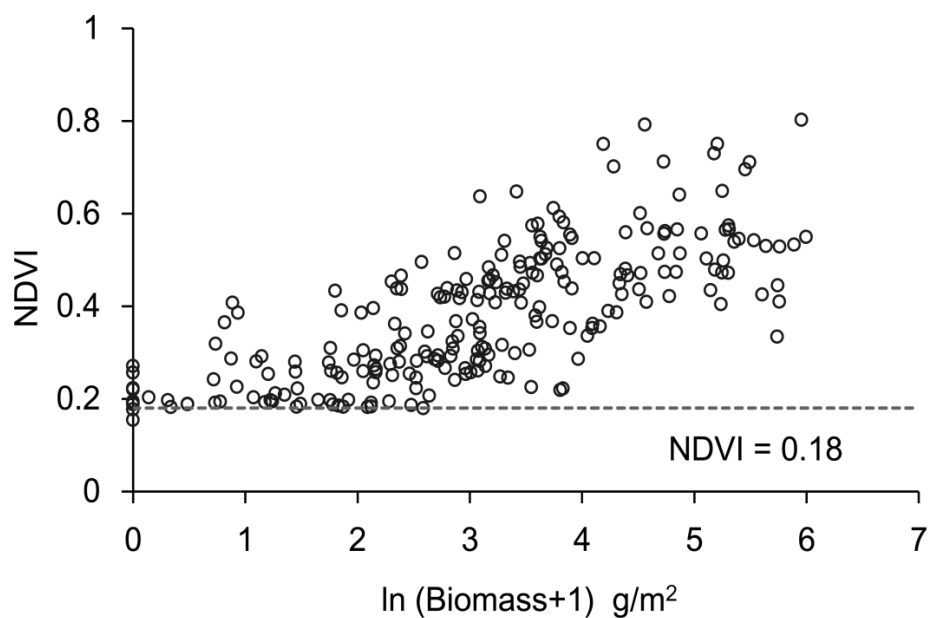


Figure S4.1 Plot of vegetation total biomass (g/m^2) and NDVI. Vegetation total biomass was log transformed

Chapter 5

Effect of protection status and ecological variables on Anatidae species population sizes in wetlands of the Yangtze River

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Forage quality and availability and wetland's conservation status of wetlands are expected to affect the density of wetlands birds, as well as the climate factors. However, the effectiveness of conservation policies is often poorly studied. Here, we tested for the effect of various ecological variables and conservation status on the density of wetland birds in China. Using census data collected from 78 wetlands in the Yangtze River flood plain, we tested for the effect of these variables on five Anatidae species (bean goose *Anser fabalis*, greater white-fronted goose *Anser albifrons*, lesser white-fronted goose *Anser erythropus*, swan goose *Anser cygnoides* and tundra swan *Cygnus columbianus bewickii*), and evaluated the effectiveness of the conservation measures by comparing population trends of these Anatidae species among wetlands that differ in conservations status. We showed that habitat feature model best explains the density of most species which climate model is the best for swan goose. The population abundances of the Anatidae species generally declined in wetlands along the Yangtze River flood plain, with a steeper decline in wetlands with a lower protection status, indicated that current conservation policies might deliver benefits for wintering Anatidae species in China, as population sizes of the studied species were buffered to some extent against decline in numbers in wetlands with a higher level protection status. Finally, we recommend several protection measures to prohibit the decline trend of these Anatidae species in the wetlands of Yangtze River Flood Plain, as it is great importance for the East Asian-Australasian Flyway.

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Introduction

Explaining and predicting animal distributions is one of the central objectives for ecologists and conservation biologists, as the species' spatial distribution is a key variable in understanding population fluctuations (Hanski 1999). Animal distribution is affected by a variety of ecological factors, such as habitat features, climatic factors and resource availability (De Boer et al. 2013). Understanding the effects of those factors on wintering waterfowl is still limited at a large scale where a network of wetlands that differ in suitability are included in the range that the wintering waterfowl use. This may result in limited effectiveness of current protection measures. This issue is of great importance because the effectiveness of conservation measures along the East Asian-Australasian Flyway, especially in China, urgently needs attention because waterfowl densities are low and still declining (De Boer et al. 2011). Comparing population trends of a species over areas with different protection statuses can provide information with regard to the effectiveness of the protection measures. However, as long-term census data often lack, the effect of protection status on population trends has been poorly studied (Kleijn et al. 2011). Using census data of five common wintering herbivores Anatidae species in 78 wetlands in the Yangtze River flood plain in China, we studied which factors appear to affect species population densities. We also analysed the species' population trends and the effect of protection status using time series census data, available for a smaller subset of these lakes, evaluating the effectiveness of the different protection statuses in these wetlands.

Analysis of animal population trends is essential for understanding a species' population status and, if required, for formulating protection strategies. For instance, population trends of farmland birds in Europe indicated that both intensification and abandonment of farmland at breeding grounds negatively affected population sizes (Wretenberg et al. 2006) but that the availability of cereal stubbles in winter had a positive effect (Gillings et al. 2005). Habitat fragmentation was found to negatively affect forest-nesting migratory birds in the United States (Donovan and Flather 2002). However, an analysis linking population trends to evaluate the effectiveness of current protection systems is generally lacking (Kleijn et al. 2011), although conservation biologists and policymakers often assume to understand and address these relationships. Recently, Klein *et al.* (2014) found that conservation “paid off”, as waterbird species

richness and abundance increased more rapidly in Ramsar wetlands than in unprotected wetlands in Morocco.

Many Anatidae species breed in the northern parts of Siberia, Europe and North America. During the wintering period, eastern China is one of the hotspots for these migrating species in the world (Dalby et al. 2014). Eastern China support around 1.1 million Anatidae birds and 80% of them use inland wetlands along the Yangtze River (Cao et al. 2010, De Boer et al. 2011). Meanwhile, these wetlands also offer food and raw materials for tens of millions of people (Cao and Fox 2009). From 1990 - 2000, 30% of China's nature wetlands have been lost due to various factors (Cyranoski 2009, Gong et al. 2010). As a consequence, birds species richness in the Yangtze floodplains severely declined (Fang et al. 2006, De Boer et al. 2011) and the number of species with a declining population has increased (Ma et al. 2009).

In this paper, using systemic survey data from wetlands along the Yangtze River in 2004 and long-term survey data (from 2001 to 2012) in four key wintering sites, we analysed the impact of abiotic and biotic factors on the densities of five Anatidae species to provide insight in the underlying causal factors for spatial and temporal changes in population trends, a prerequisite for effective conservation actions. Moreover, we tested the efficiency of conservation actions, and analysed whether the recent decline of Anatidae species is more severe in areas with a lower protection status compared to areas with a higher one. The species of interest were bean goose *Anser fabialis*, greater white-fronted goose *Anser albifrons*, lesser white-fronted goose *Anser erythropus*, swan goose *Anser cygnoides* and tundra swan *Cygnus columbianus bewickii*. Bean goose, greater and lesser white-fronted goose graze on recessionary grassland while swan goose and tundra swan mainly forage on submerged macrophytes, particularly the tubers of *Vallisneria spiralis* (Wu et al. 2009). Hence, we expected that the grazing goose species would react to changes in e.g., grass availability, but that the tuber-feeding species would not be affected by this. Instead, the tuber-feeding species were expected to be sensitive to rainfall, which changes the availability of the tubers to geese through increasing water levels.

Methods

Census data

Data from the studied species was obtained from the middle-lower Yangtze River flood plain survey carried out in February 2004, the first comprehensive survey in this area (Barter et al. 2005). All selected species are herbivorous birds wintering in the wetlands along the Yangtze River. Detailed survey methods are available in Barter *et al.* (2005). We only selected data from lakes and estuaries; shoals were excluded from the analysis. The whole dataset included 78 lakes over 5 provinces (Table S5.1). Another dataset was obtained from a systemic survey in four nature reserves (Poyang Hu, Dongting Hu, Shengjin Hu and Anqing lakes) of waterbirds in the winter of 2000/1 to 2011/12. The survey was conducted by staff of the nature reserves and by the authors using similar survey methods as reported in Barter *et al.* (2005) (Table S5.2).

Lake land and water area

Previous studies have pointed out that habitat area positively affects bird density (Connor et al. 2000). Grazing Anatidae species wintering in the Yangtze River flood plain mainly feed on recessional grasslands. The size of the grassland that is exposed, and hence available to grazing birds for foraging, increases with decreasing lake water levels and thereby affects the density of these birds. A positive correlation with area is often found when studying individual-area relationships (Connor et al. 2000), which is in line with the resource concentration hypothesis (Root 1973). We related the density of tuber-feeding birds to lake water area as they mainly forage on submerged *V. spiralis* tubers. For tuber-feeding birds a similar positive relationship was expected, although the size of the lake area is positively correlated to height of the water level, and therefore maybe negatively with the accessibility of the tubers. We measured lake land and water area of the studied 78 wetlands during the wintering survey in 2004. The data description is shown in Table 5.1, with detailed methods see Appendix S5.1 in supporting information.

Slopes

Vegetation growth is often affected by lake morphology such as littoral slopes. Littoral slopes negatively affect vegetation occurrence and biomass (Partanen et al. 2009) and thereby also the densities of herbivorous species. A gentle slope is therefore more suitable for vegetation development in wetlands (Kolada 2014). Thus, we predict that

Anatidae species densities will be negatively correlated with the mean littoral slope angle. In addition, variation of the wetlands' littoral slope angles may also affect vegetation development, as a larger variation in slope is disadvantageous for sediment deposition, negatively affecting vegetation growth and biomass (Krause-Jensen et al. 2003). We hence predicted a negative effect of the coefficient of variation (CV) of littoral slope angles on bird densities. We calculated the average and CV of littoral slope angles of each lake using Shuttle Radar Topography Mission (SRTM) digital elevation data from February 2000 (Table 5.1).

Climate data

Weather conditions can affect bird distribution and density through changing temperatures and precipitation. The abundance of wintering birds decreased with decreasing temperatures in winter (Meehan et al. 2004). Root (1988) suggested that this could be explained by the species' energy expenditure. Moreover, plant primary productivity is positively correlated with temperature. We therefore expected that bird density will be positively correlated with temperature. Precipitation positively affects plant primary productivity (Milchunas and Lauenroth 1993) but these effects often have a time lag in influencing vegetation availability of about a month (Bayliss 1989). We therefore also related mean January (previous month for most surveys) precipitation to the densities of grazing birds, expecting a positive effect. However, water level increases with increasing precipitation, and the food accessibility for tuber-feeding birds, which is dependent on water depth and the bird's neck length, therefore decreases (Owen and Cadbury 1975). Hence, we predicted that densities of tuber-feeding birds will be negatively correlated with mean precipitation. Monthly mean temperatures and precipitation were obtained from the China Meteorological Administration (Table 5.1).

Normalized Difference Vegetation Index (NDVI) and Net Primary Productivity (NPP)

Forage quantity is an important variable in determining animal distribution (Prins 1996b, Crooms et al. 2009, Heuermann et al. 2011);. Grazing Anatidae species generally follow a Type IV functional response, which is a dome-shaped curve with maximum intake rates at intermediate forage biomass, and a decreasing intake at higher

biomass densities (Heuermann et al. 2011). So NDVI and NPP were used as predictors in the density analyses of grazing birds. As functional response curves suggest that animal densities are correlated to forage biomass through a unimodal relationship, we hence included its square terms, NDVI^2 and NPP^2 , in the analysis. For tuber-feeding birds, we expected that NDVI and NPP have no effect on bird density. We calculated the mean NPP (Table 5.1) per lake, and the mean NDVI for only recessionary grasslands per lake using the satellite images (Table S5.3). The detailed image processing methods see Appendix S1 in supporting information.

Habitat heterogeneity

Studies showed that habitat heterogeneity can decrease foraging efficiency of grazers by increasing searching and handling times (Shipley 2007). Intake rates of herbivores are generally lower while feeding on heterogeneous swards compared to homogenous swards, such as shown for several overwintering waterbird species (e.g., *Anser* spp., *Anas* spp.) (Heuermann et al. 2011) and habitat heterogeneity is therefore expected to affect grazing bird densities negatively, but not affect tuber-feeding bird densities. We calculated the CV of NDVI from the different pixels in the same period (see above) as an index of the spatial heterogeneity in forage availability at these recessionary grasslands for each lake, expecting a negative correlation with bird density (Table 5.1).

Protection status

The whole purpose of wetland protection for birds is that it positively affects animal abundance. Birds species benefitted from various conservation measures in Europe (Donald et al. 2007, Hiley et al. 2013). Moreover, waterbirds increased more rapidly in Ramsar-designated wetlands in Morocco compared to unprotected wetlands (Kleijn et al. 2014).

China's protected area system includes national, provincial, city and county nature reserves, with some wetlands designated as Ramsar sites. Provincial, city and county nature reserves are often poorly managed because of reduced funding compared to national nature reserves (Liu et al. 2003). We therefore categorized our research lakes into national, provincial, and county nature reserve according to the list of China's nature reserves (State Ministry of Environmental Protection 2012). We predicted that

national reserves would have a stronger positive effect on population trends compared to the wetlands with a lower protection status.

Table 5.1 Potential predictor variables, abbreviations, data sources and resolutions used to analyse differences in species abundance in wetlands of the Yangtze River flood plain.

Variables	Abbreviation (Unit)	Source	Resolution
Lake land area	LA (km ²)	landsat TM/ ETM+	30 m
Water area	WA (km ²)	landsat TM/ ETM+	30 m
February mean air temperature	TEMP(°C)	http://www.cma.gov.cn/2011qx fw/2011qs jgx/	0.5° × 0.5°
Mean January precipitation	MP(mm)	http://www.cma.gov.cn/2011qx fw/2011qs jgx/	0.5° × 0.5°
Littoral slopes	SLOPE(°)	http://srtm.csi.cgiar.org	90 m
Coefficient of variance of littoral slopes	SLOPECV	http://srtm.csi.cgiar.org	90 m
Normalized difference vegetation index	NDVI	landsat TM/ ETM+	30 m
Net primary productivity	NPP (g/m ² month ⁻¹)	http://neo.sci.gsfc.nasa.gov/	0.1° × 0.1°
Habitat heterogeneity	NDVICV	landsat TM/ ETM+	30 m

Table 5.2 Theoretical models expected to affect the densities of Anatidae species in wetlands.

Theoretical model	LA/WA	TEMP	MP	SLOPE	SLOPECV	NDVI	NPP	NDVICV
Model I	X							
Individual-area relationship								
Model II		X	X					
Climate								
Model III				X	X			
Slope								
Model IV						X	X	
Vegetation availability								
Model V								X
Spatial heterogeneity								

Statistical analysis

Following the above reasoning we formulated a set of working hypotheses. Model I represents the effect of habitat area on the bird density of Anatidae species (Individual-area relationship). Model II, III, IV, V represent effect of climate, vegetation availability, slope and spatial heterogeneity respectively (Table 5.2).

Count data often include many zero observations. Poisson regression can be used to model the relationship between species abundance and environmental variables, but zero-inflated Poisson models often better perform than Poisson models or zero-inflated negative binomial models (Joseph et al. 2009). Hence, a zero-inflated Poisson model was applied to analyse the effects of different ecological variables on bird densities. A zero-inflated Poisson model includes two parts: a Poisson model and a zero-inflated model. The zero-inflated part provides insight on variables influencing the species' presence/absence while the Poisson part provides insight on the variables affecting the species' density. We performed a zero-inflated Poisson regression analysis for each of the hypotheses. The Akaike Information Criterion (AIC), adjusted for small sample sizes (AICC), was used to rank the competing models. Before fitting the zero-inflated Poisson models, we assessed the multi-collinearity by examining the Variance Inflation Factor (VIF) of the candidate variables. VIF values of all variables were less than 5 (Table S5.4), indicating that there was no multi-collinearity problem (O'Brien 2007). Furthermore, different mechanisms may influence the density of each species at the same time, but distinguishing their independent effect is a challenging task (Currie et al. 2004). Hence, zero-inflated Poisson models were also used to test for the combined and independent influence of the predictor variables on the densities of each species. All possible subset models were ranked according to $\Delta AICc$ and Akaike weights (ω_i) were calculated to estimate the likelihood of each model (Burnham and Anderson 2002). Model averaging was used to obtain parameter estimates for these variables. The model averaging calculation was done on the most parsimonious models using a cut-off $\Delta AICC \leq 2$ (Burnham and Anderson 2002).

To analyse population trends for each of the five waterbird species, a Generalized Additive Model (GAM) (Hastie and Tibshirani 1990) was applied using the time series survey data (2001–2012) from 25 wetlands in the four nature reserves where birds counts were carried out annually. The GAM model accommodates for smooth, nonlinear changes over time in population size (Fewster et al. 2000). In the model (Eq. 1), y_{ij} is the expected bird count at site i and year j . The expected count therefore depends on the site effect a_i and the smoother $s(j)$. The analysis was done in two parts: we first analysed the overall population trends of each species in these wetlands. Then another GAM was applied for each species but separately for the wetlands with a different protection status (national, provincial, and county). We used a GAM with a Poisson distribution and a log link function (Eq. 2).

$$\text{Log}(y_{ij}) = a_i + s(j) \quad (\text{Eq.1})$$

$$\text{Log}(\text{count}_{ij}+1) = \text{site}_i + s(\text{year}) \quad (\text{Eq.2})$$

Spatial autocorrelation is a potential problem when analysing ecological data and should be properly accounted for. We therefore explored whether there was spatial autocorrelation in birds abundances over different wetlands by calculating the Moran's I index of the residuals for each species. We found little evidence for spatial autocorrelation of studied species (all $|\text{Moran's I}| < 0.05$) which suggested that spatial autocorrelation was not a point of concern in our analysis. All statistical analyses were conducted in R 2.13.0 with the package pscl, MuMIn, mgcv, ape, and SPSS 17.

Results

Effect of the ecological variables on bird density

The distribution and abundance of the studied species is shown in Fig. S5.1 – S5.5. The majority of the variables were not significant in the zero-inflated part of the Poisson model for all species (Table 5.3). For Poisson part, most variables were significantly correlated with bird densities, although sometimes effects were not in agreement with our predictions (Table 5.3).

A negative individual-area relationship was found for all studied species (Table 5.3). Climate (temperature, rainfall) and vegetation availability (NDVI, NPP) variables had positive effects on the grazing birds. NDVI together with its square term yielded significant unimodal models for all grazing species as all these latter models had a positive main term and a negative squared term for these three species (Table S5.5). The effects on tuber-feeding birds were general negative, except for temperature that had a positive effect on tundra swan density. Slope angle variables affected bird densities differently. Slope angle was positively correlated with the grazing bird density, but negatively correlated with that of tuber-feeding birds. In contrast, the CV of slope (SLOPECV) negatively affected grazing bird density and positively affected that of tuber-feeding birds. The spatial heterogeneity (NDVICV) negatively influenced the densities of bean goose and greater white-fronted goose, but a positive correlation was found for lesser white-fronted goose. For tuber-feeding birds, there was no effect of spatial heterogeneity on swan goose density, but a marginally significant negative effect was found on tundra swan density (Table 5.3).

According to the AICc value, the slope model was the best model explaining differences in densities of all grazing birds and tundra swans. However, the climate model best explained the density of swan goose (Table 5.3).

When comparing all subset models, the most parsimonious model ($\Delta\text{AICC} \leq 2$) was often the most extensive model, including most of the predictor variables (Table 5.4). For each species, the effects of the predictor variables sometimes changed, but were generally in line with the individual predictions (Table S5.6). For example, the model averaging procedure showed that both climate variables had a negative effect on the density of the greater white-fronted goose. The results showed that different mechanisms influence the bird densities of studied species simultaneously.

Table 5.3 Predicted (H_0) and observed effects (+: positive effect; -: negative effect; NS: no effect) of different variables on the bird density of five study species tested for each competing hypotheses using a zero-inflated Poisson regression model (b = regression coefficient, se = standard error, z = calculated z-value, p = significance, AIC_c = sample size corrected Akaike Information Criterion). BG: bean goose; GWFG: greater white-fronted goose; LWFG: lesser white-fronted goose; SG: swan goose; TS: tundra swan. For variable abbreviation see Table 5.1.

	Model	Variables	H0	Poisson model				zero-inflated model				
				<i>b</i>	<i>se</i>	<i>z</i>	<i>p</i>	<i>b</i>	<i>se</i>	<i>z</i>	<i>p</i>	AIC _c
BG	I	LA	+	-0.007	0.001	-11.3	<0.001	-0.023	0.012	-1.913	0.056	8218
	II	TEMP	+	1.271	0.038	33.53	<0.001	0.161	0.397	0.406	0.685	6913
		MP	+	0.085	0.003	26.69	<0.001	-0.060	0.033	-1.848	0.065	
	III	NDVI	+	3.817	0.313	12.190	<0.001	-0.990	4.498	-0.220	0.826	8228
		NPP	+	0.007	0.001	5.311	<0.001	-0.041	0.018	-2.230	0.026	
	IV†	SLOPE	-	0.951	0.031	30.33	<0.001	-0.524	0.498	-1.053	0.293	6554
GWFG		SLOPECV	-	-3.008	0.095	-31.59	<0.001	-1.428	1.125	-1.269	0.204	
	V	NDVICV	-	-4.610	0.277	-16.67	<0.001	-2.003	4.201	-0.477	0.633	8124
	I	LA	+	-0.007	0.002	-4.583	<0.001	0.008	0.010	0.792	0.429	4157
	II	TEMP	+	0.720	0.053	13.517	<0.001	-0.483	0.339	-1.424	0.154	3922
		MP	+	0.016	0.004	4.156	<0.001	0.091	0.038	2.379	0.017	
	III	NDVI	+	12.690	0.551	23.020	<0.001	-4.038	4.554	-0.887	0.375	3611
LWFG		NPP	+	0.011	0.002	6.244	<0.001	-0.024	0.018	-1.297	0.195	
	IV†	SLOPE	-	0.788	0.039	20.04	<0.001	0.218	0.519	0.420	0.675	3453
		SLOPECV	-	-3.124	0.164	-19.04	<0.001	-0.067	1.079	-0.062	0.950	
	V	NDVICV	-	-4.999	0.568	-8.801	<0.001	-0.317	4.331	-0.073	0.942	4099
	I	LA	+	-0.008	0.001	-7.065	<0.001	-0.013	0.008	-1.558	0.119	2316
	II	TEMP	+	2.907	0.189	15.40	<0.001	-1.421	0.998	-1.424	0.154	1435
SG		MP	+	0.201	0.017	11.98	<0.001	-0.041	0.057	-0.710	0.478	
	III	NDVI	+	0.543	0.820	0.662	0.508	-18.11	6.676	-2.713	0.007	1608
		NPP	+	0.080	0.004	22.023	<0.001	0.011	0.028	0.400	0.689	
	IV†	SLOPE	-	2.261	0.074	30.51	<0.001	0.184	0.723	0.254	0.800	630
		SLOPECV	-	-2.431	0.200	-12.17	<0.001	-0.264	1.465	-0.180	0.857	
	V	NDVICV	-	2.381	0.655	3.633	<0.001	12.719	6.744	1.886	0.059	2200
TS	I	WA	+	-0.012	0.001	-17.37	<0.001	-0.006	0.004	-1.445	0.148	5129
	II†	TEMP	+	-3.659	0.085	-42.97	<0.001	0.403	0.326	1.237	0.216	1563
		MP	-	-0.134	0.004	-34.90	<0.001	-0.080	0.036	-2.228	0.026	
	III	NDVI	NS	-3.617	0.382	-9.461	<0.001	4.368	5.557	0.786	0.432	5613
		NPP	NS	0.002	0.002	0.870	0.384	-0.031	0.021	-1.474	0.140	
	IV	SLOPE	-	-3.184	0.131	-24.37	<0.001	-0.485	0.670	-0.723	0.470	3591
TS		SLOPECV	-	5.183	0.146	35.53	<0.001	-1.590	1.270	-1.253	0.210	
	V	NDVICV	NS	0.185	0.287	0.645	0.519	1.461	5.023	0.291	0.771	5708
	I	WA	+	-0.024	0.001	-20.58	<0.001	-0.010	0.008	-1.294	0.196	5027
	II	TEMP	+	0.571	0.041	13.807	<0.001	0.207	0.272	0.761	0.446	5546
		MP	-	-0.002	0.003	-0.627	0.531	-0.015	0.029	-0.514	0.607	
	III	NDVI	NS	-4.993	0.436	-11.44	<0.001	2.869	4.724	0.607	0.544	5370
TS		NPP	NS	-0.030	0.002	-18.94	<0.001	-0.037	0.019	-1.981	0.048	
	IV†	SLOPE	-	-2.057	0.076	-27.12	<0.001	-0.754	0.527	-1.432	0.152	4782
		SLOPECV	-	2.359	0.118	19.96	<0.001	-0.101	1.094	-0.092	0.926	
	V	NDVICV	NS	-0.722	0.364	-1.983	0.047	2.099	4.368	0.481	0.631	5832

†: best competing model

Table 5.4 Results from the zero-inflated Poisson model aiming to explain the effects of different variables on bird densities (AICc = sample size corrected Akaike Information Criterion. K = number of explanatory parameters in model; $\Delta AIC_c = AIC_c(i) - AIC_c(\min)$; ω_i = Akaike weights). BG: bean goose; GWFG: greater white-fronted goose; LWFG: lesser white-fronted goose; SG: swan goose; TS: tundra swan. For variable abbreviation see Table 5.1.

Species	Model	LA/WA	TEMP	MP	SLOPE	SLOPECV	NDVI	NPP	NDVICV	k	logLik	AIC _c	ΔAIC_c	ω_i
BG	1†	X	X	X	X	X		X	X	16	-2792	5625.6	0.00	0.76
	2	X	X	X	X	X	X	X	X	18	-2790	5628.2	2.62	0.21
GWFG	1†	X		X	X	X	X	X	X	16	-1096	2234.3	0.00	0.63
	2†	X	X	X	X	X	X	X	X	18	-1094	2235.7	1.39	0.32
	3	X	X	X	X	X	X		X	16	-1099	2239.4	5.07	0.05
LWFG	1†	X	X		X		X		X	12	-82	193.9	0.00	0.67
	2	X	X		X		X	X	X	14	-80	196.5	2.62	0.18
SG	1†	X	X	X	X	X	X	X	X	18	-298	643.8	0.00	0.82
	2	X	X	X	X	X	X		X	16	-302	646.7	2.97	0.18
TS	1†	X	X	X	X	X	X	X	X	18	-1446	2940.8	0.00	1.00
	2	X	X	X	X	X	X		X	16	-1464	2969.5	28.69	0.00

†: best competing model

Effect of the protection status on population trends

The overall population abundance indices from 2001 to 2012 for the five species varied strongly according to the GAM-results (Fig. 5.1). The model yielded a deviance varying from 12.5% (greater white-fronted goose) to 24.9% (bean goose). For all species, year was found to have a smoothing term significantly different from zero (Table 5.5). The abundance of bean goose and lesser white-fronted goose first showed an increasing trend and then remained stable (Fig. 5.1a, c). The population size of the greater white-fronted goose fluctuated more and showed an overall decreasing trend (Fig. 5.1b). Both swan goose and tundra swan numbers decreased, especially in recent years (Fig. 5.1d, e).

When analysing the effect of protection status, we showed that bean goose and greater white-fronted goose showed a similar patterns over the three classes (i.e., national, provincial, and county nature reserve), but fluctuations were larger in reserves under a lower protection status (Fig. 5.2a, b). Moreover, the decreasing trends of the tuber-feeding birds in recent years in county nature reserves were more rapid compared to the trends in national and provincial nature reserves (Fig. 5.2d, e; Table 5.6).

Table 5.5 Results of the Generalized Additive Model (GAM) analysing the overall changes in population sizes of five Anatidae species from 2001 to 2012 in wetlands of the Yangtze flood plain. BG: bean goose; GWFG: greater white-fronted goose; LWFG: lesser white-fronted goose; SG: swan goose; TS: tundra swan. UBRE: Un-Biased Risk Estimator; edf: effective degrees of freedom (n = 78).

Species	Smooth terms		edf	χ^2	p	Explanatory variables
	UBRE	Deviance explained (%)				site
BG	5321	24.9	8.945	40391	<0.001	<0.001
GWFG	5574	12.5	8.976	97537	<0.001	<0.001
LWFG	2155	15.6	8.973	33465	<0.001	<0.001
SG	7137	20.7	8.924	223695	<0.001	<0.001
TS	4615	12.7	8.938	49992	<0.001	<0.001

Table 5.6 Results of the Generalized Additive Model (GAM) analysing the changes in population sizes of five Anatidae species from 2001 to 2012 in 25 wetlands with different protection statuses in the Yangtze flood plain. BG: bean goose; GWFG: greater white-fronted goose; LWFG: lesser white-fronted goose; SG: swan goose; TS: tundra swan. UBRE: Un-Biased Risk Estimator; edf: effective degrees of freedom.

		Smooth terms					Explanatory variable
	Species	UBRE	Deviance explained (%)	edf	χ^2	<i>p</i>	Site
National nature reserve (n = 6)	BG	6735	22.2	8.976	20598	<0.001	<0.001
	GWFG	7570	43.7	8.992	121895	<0.001	<0.001
	LWFG	4488	17.5	8.964	22898	<0.001	<0.001
	SG	9486	51.5	8.978	174450	<0.001	<0.001
	TS	3849	54.2	8.980	115464	<0.001	<0.001
Provincial nature reserve (n = 11)	BG	6655	13.8	8.922	50873	<0.001	<0.001
	GWFG	354	45.5	8.987	11794	<0.001	<0.001
	LWFG	39	46.1	8.888	805	<0.001	<0.001
	SG	3352	11.5	8.959	33164	<0.001	<0.001
	TS	4388	10.7	8.971	20799	<0.001	<0.001
County nature reserve (n = 8)	BG	286	22.9	8.932	4616	<0.001	<0.001
	GWFG	339	24.9	8.988	5505	<0.001	<0.001
	LWFG	22	58.3	6.746	253	<0.001	<0.001
	SG	957	24.3	8.983	13950	<0.001	<0.001
	TS	2725	11.1	8.979	13923	<0.001	<0.001

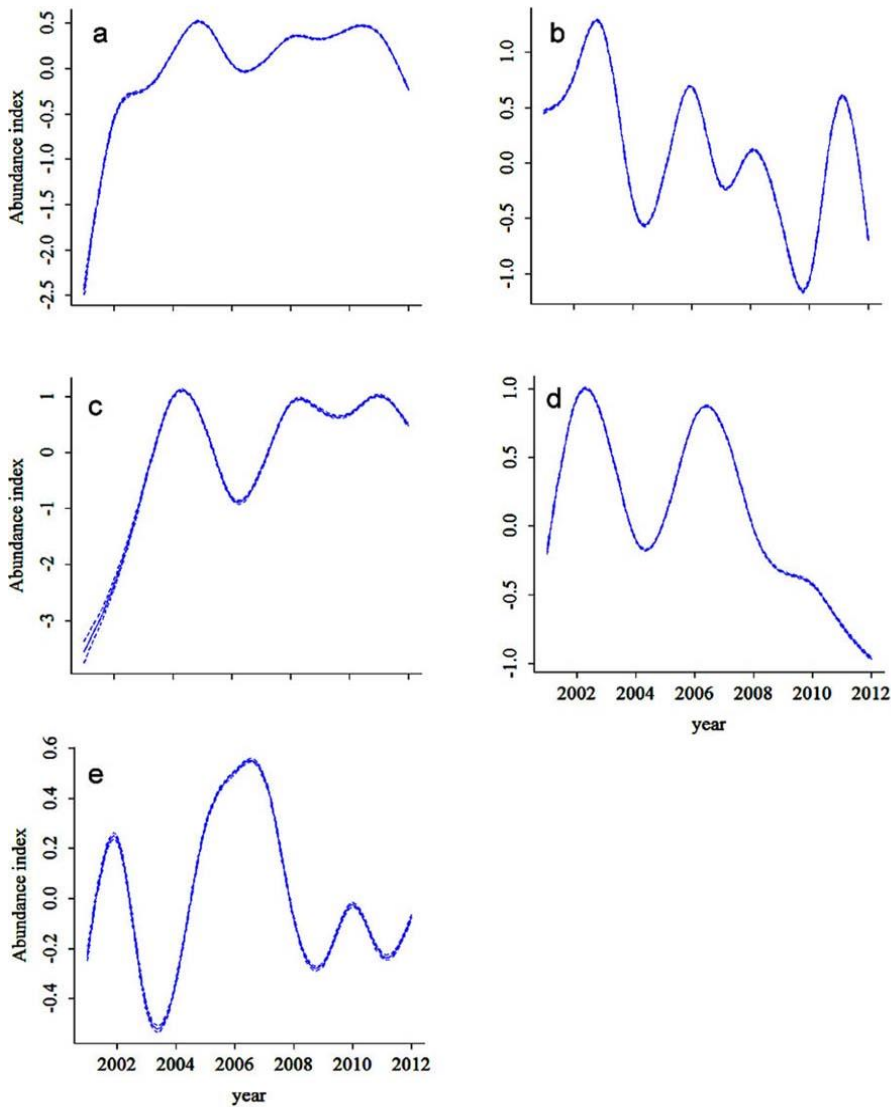


Figure 5.1: Estimated changes in population sizes of five Anatidae species from 2001 to 2014 in the Yangtze flood plain using Generalized Additive Mixed Models (GAMM). The solid line shows the population abundance index of each species and the broken lines show the 95% confidence intervals (barely visible, due to small confidence intervals). a: bean goose; b: greater white-fronted goose; c: lesser white-fronted goose; d: swan goose; e: tundra swan.

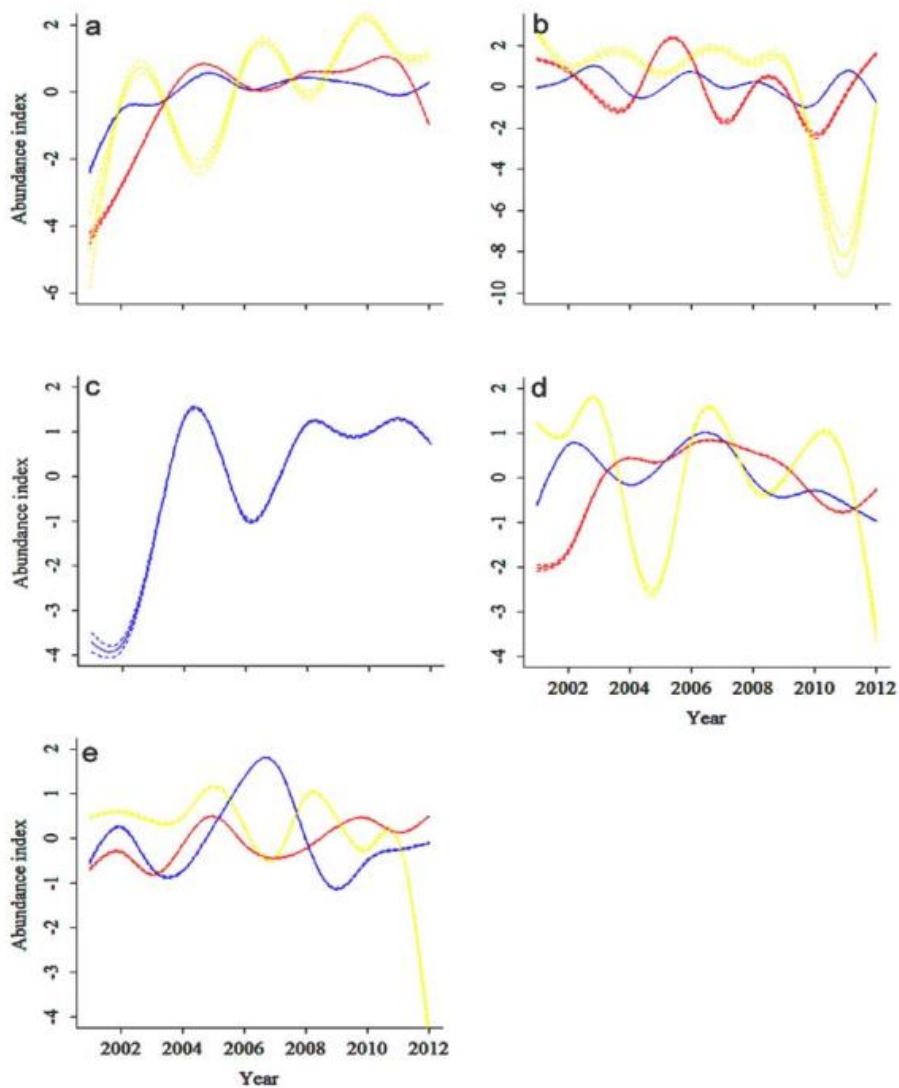


Figure 5.2: Population abundance indices of five Anatidae species from 2001 to 2012 in the 25 wetlands differing in protection status in the Yangtze flood plain using Generalized Additive Mixed Models (GAMM). Blue line: wetlands designated as national nature reserves; red line: provincial nature reserves; yellow line: county nature reserves. The solid line shows the population abundance index of each species and the broken lines show the 95% confidence intervals (barely visible, due to small confidence intervals). a: bean goose; b: greater white-fronted goose; c: lesser white-fronted goose; d: swan goose; e: tundra swan.

Discussion

In this study we demonstrated that various ecological variables affected Anatidae species densities and the most important variables were slope and climate variables. However, the presence of the Anatidae species was rarely affected by those variables, indicating that these species are widely distributed in the wetlands along the Yangtze River. However, these ecological variables also operated at the same time, as illustrated by the model averaging procedures (Table 5.4, S5.6). Most of the five studied species showed declining population trends with a steep decrease in the last years. Comparing the population trends among wetlands with different protection status suggested that the largest recent declines in Anatidae species population abundances were mainly recorded from wetlands with lower protection status, suggesting that the current conservation policy in national nature reserves might not halt the decline in birds abundance. A larger conservation effort seems required to maintain the Anatidae population, especially for wetlands with a lower level protection status.

Our results showed that majority of the potential ecological variables significantly affected Anatidae species densities in wetlands along the Yangtze River, although the effects sometimes were contrary to our predictions (Table 5.3). Slope features best explained differences in densities of all studied species except for swan goose. Partly in agreement with our hypotheses, littoral slopes had a negative effect on tuber-feeding bird density, but a positive effect on the densities of all grazing species (Table 5.3). Slope has a negative effect on aquatic vegetation occurrence and biomass (Partanen et al. 2009) and therefore probably negatively affected density of tuber-feeding birds. However, grazing birds on recessional grasslands may benefit from a gentle slope. For example, a gentle slope is important for an optimal habitat of Canada goose (Dunton and Combs 2010). A gentle slope may also offer adequate drainage (Wisz et al. 2008), which is advantageous to littoral vegetation growth in wetland (Pezeshki et al. 1998). The littoral slope in the studied wetlands was relatively flat and gentle (ranging from only $0.00 \sim 2.75^\circ$), which may explain the positive effect on grazing birds densities. However, if the range in slope angles were to extend, we expect to find dome-shaped relationships. The CV of these littoral slopes had a negative effect on the density of all grazing birds, but was positively correlated with that of tuber-feeding birds. Lakes with larger variation in slopes had a larger proportion of the area covered by aquatic

vegetation (Kolada 2014). Swan goose and tundra swan mainly forage on submerged vegetation (e.g., *Vallisneria* spp.), which may explain this positive correlation.

In line with our hypothesis, mean precipitation had a positive effect on grazing bird densities and a negative effect on swan goose density, but no effect was found on tundra swan. Also other studies found positive effects of precipitation on bird habitat use and density (Tingley et al. 2009, Barbet-Massin and Jetz 2014). Grassland bird density increased with increasing precipitation (Macias-Duarte et al. 2009). Higher precipitation increased food availability and resulted in an increase in wintering snow goose (*Anser caerulescens*) in the USA (Hobaugh 1984). However, a higher precipitation may also result in increasing water levels in wetlands, which decreases the food accessibility for tuber-feeding birds (Nolet et al. 2006). The found negative effect of precipitation on swan goose density is therefore expected to come from a reduction in availability of submerged vegetation. Precipitation had no effect on tundra swan density. Probably because tundra swans have longer necks and hence have a higher forage availability compared to swan geese.

As predicted, temperature had a positive effect on grazing birds and tundra swan densities (Table 5.3). Wintering birds tend to select warmer sites to reduce the cost of thermoregulation (Villen-Perez et al. 2013). In addition, plant primary productivity is positively correlated with temperature in grassland (Milchunas and Lauenroth 1993). Unexpectedly, we found that temperature negatively influenced densities of swan goose, suggesting that densities of swan goose might be higher in higher latitude areas where temperatures are lower. However, interference competition might also play an important role in determining the distribution of herbivores (Kristiansen and Jarrett 2002), and is mediated by body size (Smith et al. 2001). Both swan goose and tundra swan are tuber-feeding birds, and when these two species forage together, interference competition may occur. Tundra swan, having a larger body size and longer necks, is expected to be the superior species, outcompeting swan goose. Another explanation for the negative effect of temperature on swan goose may be climate warming. Climate warming was a good predictor for a northward shifts in several bird species (Melles et al. 2011). The reproductive success of waterbirds can be negatively influenced by the long distance migration from their wintering grounds to their breeding grounds (Alerstam et al. 1990). As the temperatures were relatively high during the survey period, swan goose might

decide to winter at higher latitude wetlands, and thereby minimize their migration distance.

Not in accordance with our predictions and former studies (Connor et al. 2000) was that area was negatively correlated with the bird densities for all studied species, resulting in lower bird densities in lakes with larger areas available for foraging. Human activities in larger lakes may play an important role in affecting bird densities. For example, sand mining decreased food availability for birds (Wu et al. 2007) and thereafter the density of birds in larger wetlands.

Both NDVI and NPP had a positive effect on grazing birds densities (Table 5.3). NDVI yielded significant unimodal models for all three grazing birds species (Table S5.5), so a higher bird density was found at intermediate NDVI values. Following the forage maturation hypothesis (Hassall et al. 2001), the densities of these grazing birds first increased with increasing resource availability to a maximum level and then decreased. However, for tuber-feeding birds, NDVI and NPP had negative effects. *Carex spp.*, perennial sedges that occur in dense patches, are the dominate species of these recessional wetlands in winter. In summer, *Carex spp.* beds are flooded while the roots remain buried in the soil, which may prohibit the establishment and development of *V. spiralis*, explaining the negative correlation of NDVI and NPP on densities of tuber-feeding birds.

As expected, habitat spatial heterogeneity (NDVICV) had a negative effect on bird densities of bean goose and greater white-fronted goose and no effect on the densities of tuber-feeding species. The positive effect on lesser white-fronted goose is probably influenced by its restricted distribution range, because the majority of lesser white-fronted goose was counted in East Dongting Lake National Reserve (Fig. S5.3), biasing our analysis.

The most parsimonious model was often the most extensive model, indicating that different response variables influence bird densities at the same time (Table 5.4). The derived correlation coefficients were generally similar between the single term models and the parsimonious multiple variables models. So, when testing several competing hypotheses, the interdependencies of those predictions should also be considered.

The recent decline of Anatidae species was more severe in areas with a lower protection status compared to areas with a higher one, which is in agreement with our hypothesis. Our results indicated that current conservation policies might deliver

benefits for wintering Anatidae species in China, as population sizes of the studied species were buffered to some extent against a decline in numbers in wetlands with a higher level protection status. The funding that national nature reserves receive is twice as large as that of local nature reserves (Liu et al. 2003) and the staff working in the national nature reserves have better training opportunities comparing to staff of local nature reserves (Xu and Melick 2007). Reserve staff are able to take action when more funding is received, e.g., to improve wildlife protection. Reserves with more funding and/or a higher protection status also initiate community programs and contribute to increase the local community's awareness, enhancing their sense of responsibility and acceptance of protection actions. In contrast, insufficient funding often leads to increased economic activities within reserves, such as the exploitation of natural resources (Wu et al. 2007) and tourism activities (Xu and Melick 2007).

Our results, together with the studies in Europe (Donald et al. 2007, Hiley et al. 2013) and Africa (Kleijn et al. 2014), generate a preliminary framework to evaluate the effectiveness of conservation policies. However, our analyses also had limitations as our census data were all collected from protected areas. Because of land use changes, wild birds can change their wintering site and select protected conservation areas over unprotected areas (Pouzols et al. 2014). Hence, survey efforts should be broadened to cover both protected and unprotected areas in order to acquire a better understanding of the effectiveness of conservation policies.

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Supporting information

Appendix S5.1

Satellite image processing

We used 11 Landsat images from January to February of 2004 (coinciding with the survey date) to cover the temporal and spatial scale of our study (Table S5.3).

After 2003, ETM+ images contain data duplications and loss due to the failure of the Scan Line Corrector (USGS, 2013). We therefore involved a gap-filling method based on local linear histogram matching (Scaramuzza 2004) for the four ETM+ images. Digital Number (DN) values were then calibrated to radiations before FLAASH (Fast Line-of-sight Atmospheric Analysis of Hypercubes). All Images were geometrically registered and resampled with a cubic convolution algorithm.

We firstly registered the 2004 image (path/row 121/039) as the base image. Then Radiometric Normalization for Image Mosaics (RNIM) was conducted using the registered image as the new master image to normalize the other ones (Du et al. 2001, Olthof et al. 2004). RNIM applies Principles Component Analysis (PCA) in overlap regions, with the first principal component performing a least-squares regression between overlap regions and the second principal component detecting changing elements between two scenes. By adjusting the ranges of the second principal component, we removed changed pixels until a minimum correlation coefficient of 0.9 was reached (Du et al. 2001, Olthof et al. 2004). RNIM has the unique advantage that it generates similar results regardless of the different processing orders (Du et al. 2001).

We delineated boundaries for all 78 lakes in our study area through Google Earth and field GPS records as a mask for classification. We used Supported Vector Machines (SVMs) to discriminate water and land for each lake. As pixels containing water or land are quite contrasting, we selected our training data visually from each image based on a few field survey records. Using ArcGIS 10.0, land area, average NDVI of reccessional grassland and standard deviation this NDVI value were calculated for each lake with Zonal statistic toolkit.

Reference

Du Y., Cihlar J., Beaubien J. and Latifovic R. 2001. Radiometric Normalization,

- Compositing, and Quality control for Satellite High Resolution Image Mosaics over Large Areas. IEEE Transactions on geoscience and remote sensing 39: 623-634.
- Olthof I., Pouliot D., Fernandes R. and Latifovic R. 2004. Landsat-7 ETM+ radiometric normalization comparison for northern mapping applications. Remote sensing of environment 95: 388-398.
- Scaramuzza, P., Micijevic, E., Chander, G. 2004. SLC Gap-filled Products Phase One Methodology.http://landsat.usgs.gov/documents/SLC_Gap_Fill_Methodology.pdf (Accessed date 28.05.14)
- USGS. http://landsat.usgs.gov/products_slcinfobackground.php. (Accessed date 21.05.14)

Figure S5.1 Distribution and abundance of bean goose in the Yangtze Flood Plain in 2004, with different colours for different classes of population abundances. The break values were set to 0, 1, 100, 800 (1% of estimated population size) and 4000 (5% of estimated population size).

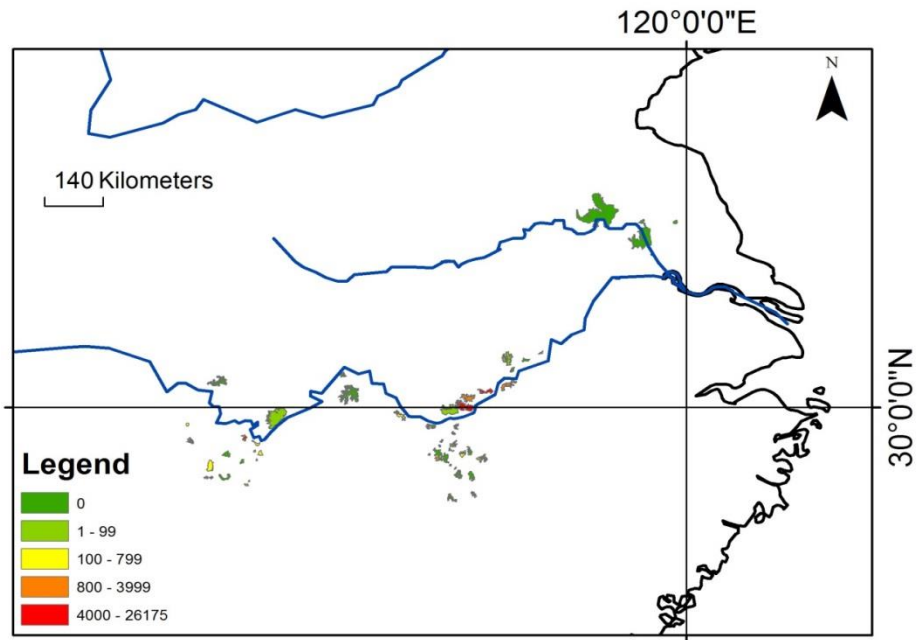


Figure S5.2 Distribution and abundance of greater white-fronted goose in the Yangtze Flood Plain in 2004, with different colours for different classes of population abundances. The break values were set to 0, 1, 100, 1800 (1% of estimated population size) and 9000 (5% of estimated population size).

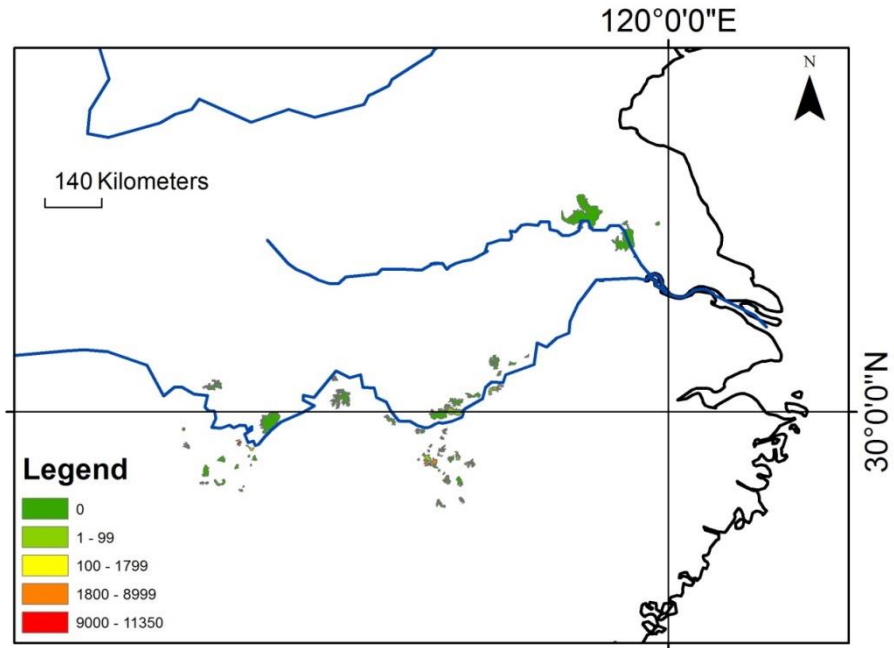


Figure S5.3 Distribution and abundance of lesser white-fronted goose in the Yangtze Flood Plain in 2004, with different colours for different classes of population abundances. The break values were set to 0, 1, 100, 200 (1% of estimated population size) and 1000 (5% of estimated population size).

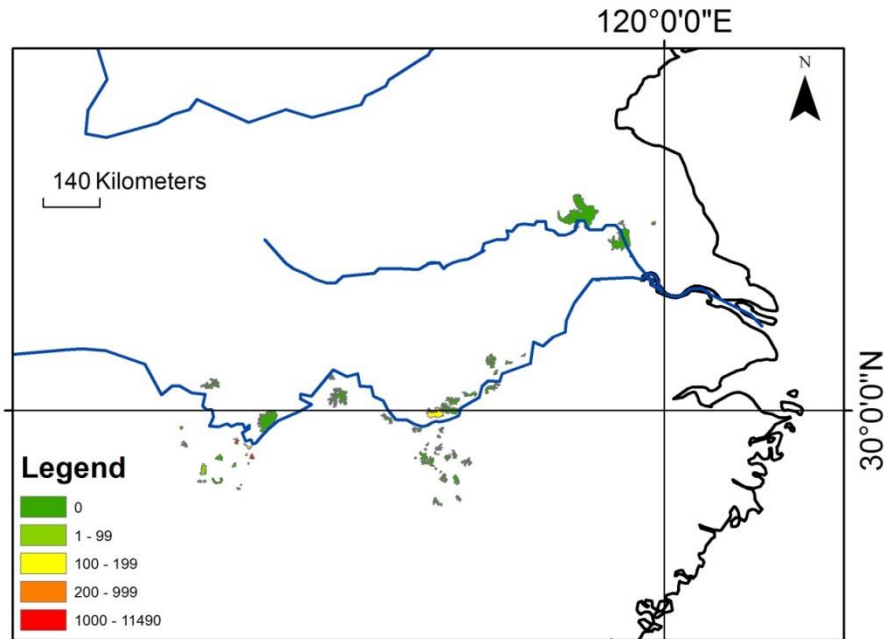


Figure S5.4 Distribution and abundance of swan goose in the Yangtze Flood Plain in 2004, with different colours for different classes of population abundances. The break values were set to 0, 1, 100, 800 (1% of estimated population size) and 4000 (5% of estimated population size).

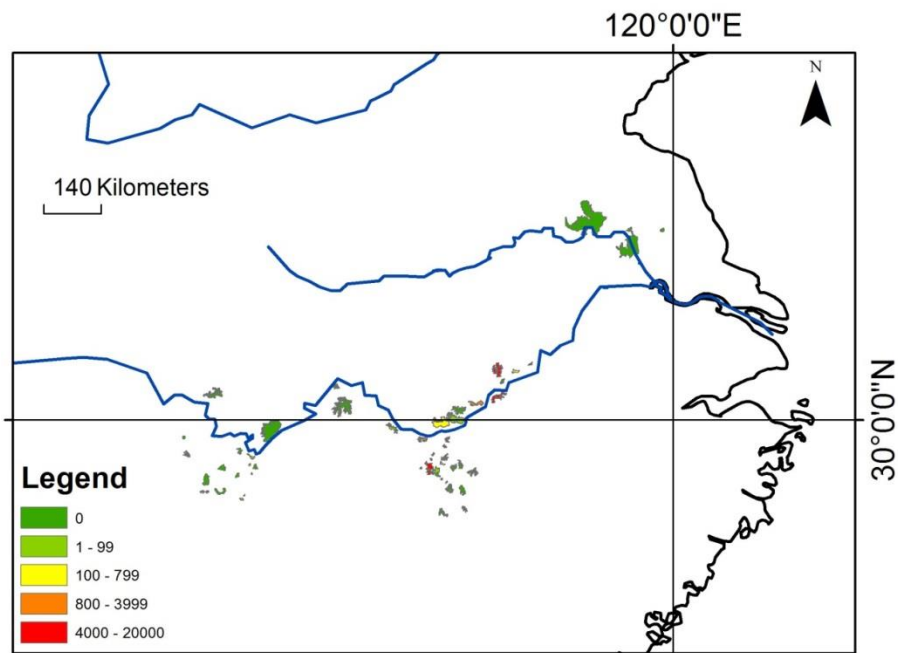


Figure S5.5 Distribution and abundance of tundra swan in the Yangtze Flood Plain in 2004, with different colours for different classes of population abundances. The break values were set to 0, 1, 100 and 920 (1% of estimated population size).

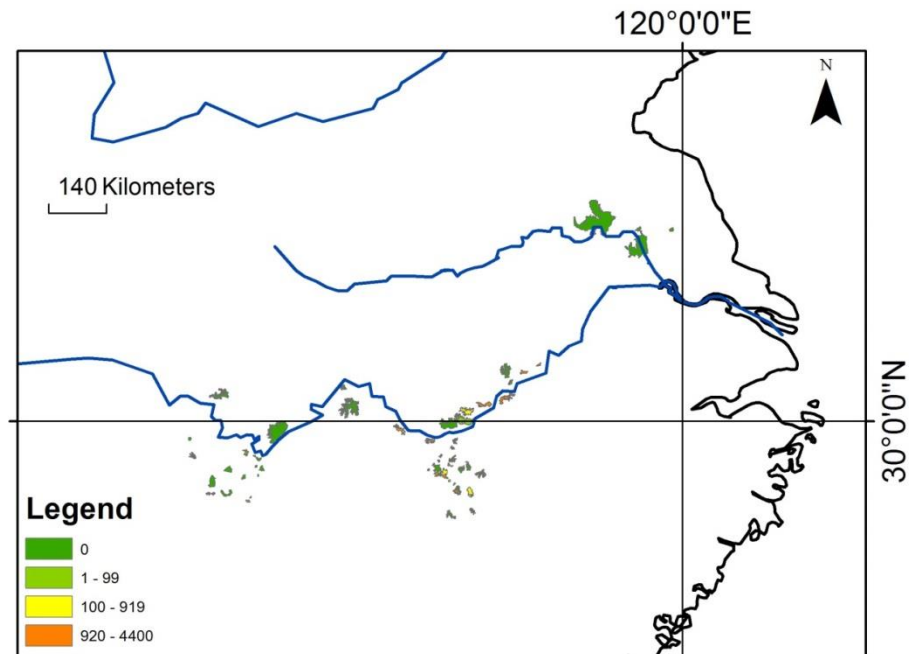


Table S5.1 Name, location and protection status of wetlands using in our analysis.

Lake Name	Province	County	Longitude	latitude	Protect status	Ramsar Site
Shengjin Hu	Anhui	Dongzhi	30° 23'54"	117° 03'45"	NNR	No
Caizi Hu	Anhui	Zongyang	30° 48'36"	117° 05'48"	PNR	No
Longgan Hu	Anhui	Susong	29° 56'36"	116° 08'41"	PNR	No
Huangda Hu	Anhui	Susong	30° 01'26"	116° 20'34"	PNR	No
Po Hu	Anhui	Taihu	30° 09'19"	116° 27'28"	PNR	No
Wuchang Hu	Anhui	Wangjiang	30° 15'35"	116° 42'48"	PNR	No
Baidang Hu	Anhui	Zongyang	30° 48'16"	117° 22'25"	PNR	No
Fengsha Hu	Anhui	Zongyang	30° 55'37"	117° 37'50"	PNR	No
Pogang Hu	Anhui	Yingjiang	30° 39'05"	117° 10'10"	PNR	No
Chang Hu	Hubei	Jinzhou	30° 26'18"	112° 26'50"	CNR	No
Liangzi Hu	Hubei	Liangzihu	30° 16'43"	114° 34'46"	PNR	No
Hong Hu	Hubei	Honghu	29° 50'47"	113° 20'54"	PNR	Yes
Wang Hu	Hubei	Xinyang	29° 51'53"	115° 19'32"	PNR	No
Shupo Hu	Hubei	Yangxin	29° 49'56"	115° 23'26"	NS	No
Maoli Hu	Hunan	Jinshi	29° 24'00"	111° 57'37"	NS	No
Beimin Hu	Hunan	Li	29° 42'55"	111° 52'36"	NS	No
Longchi Hu	Hunan	Hanshou	28° 49'19"	112° 11'05"	PNR	Yes
Anle Hu	Hunan	Hanshou	28° 49'14"	112° 11'10"	PNR	Yes
Muping Hu	Hunan	Hanshou	28° 58'58"	112° 14'23"	PNR	Yes
Wanzi Hu	Hunan	Yuanjiang	28° 49'14"	112° 29'59"	PNR	Yes
Datong Hu	Hunan	Yuanjiang	29° 12'29"	112° 30'25"	PNR	Yes
Lu Hu	Hunan	Yujiang	29° 06'07"	112° 46'55"	NNR	Yes
Hongqi Hu	Hunan	Yueyang	29° 15'31"	112° 57'45"	NNR	Yes
Fangtai Hu	Hunan	Yueyang	29° 31'05"	112° 45'56"	NNR	Yes
Chunfeng Hu	Hunan	Yueyang	29° 13'25"	113° 03'43"	NNR	Yes
Junshanhou Hu	Hunan	Yueyang	29° 22'21"	113° 00'16"	NNR	Yes
Dingzidiwai Hu	Hunan	Yueyang	29° 26'00"	112° 55'04"	NNR	Yes
Caisang Hu	Hunan	Yueyang	29° 31'06"	112° 47'46"	NNR	Yes
Daxiaoxi Hu	Hunan	Yueyang	29° 29'19"	112° 48'12"	NNR	Yes
Wangjun Hu	Hunan	Yueyang	28° 51'41"	112° 33'38"	NNR	Yes
Dong Hu	Hunan	Huarong	30° 33'40"	114° 23'56"	NS	No
Baini Hu	Hunan	Yunxi	28° 44'59"	112° 52'29"	NS	No
Helong Hu	Hunan	Xiangyin	28° 41'00"	112° 49'55"	NS	No
Beisai Hu	Hunan	Yueyang	29° 07'20"	112° 59'53"	NS	No
Hongze Hu	Jiangsu	Sihong	33° 18'19"	118° 59'53"	NNR	No
Baoying Hu	Jiangsu	Baoying	33° 08'27"	119° 18'00"	CNR	No
Gaoyou Hu	Jiangsu	Gaoyou	32° 49'51"	119° 18'05"	CNR	No
Dazong Hu	Jiangsu	Yandu	33° 08'55"	119° 48'44"	NS	No
Nan Hu	Jiangxi	De'an	29° 12'00"	115° 49'35"	CONR	Yes
Yangjia Hu	Jiangxi	Xingzi	28° 50'00"	116° 49'35"	CONR	Yes
Sixia Hu	Jiangxi	Xingzi	29° 16'35"	115° 54'00"	CONR	Yes
Shili Hu	Jiangxi	Xingzi	29° 26'27"	116° 01'30"	CONR	Yes
Liaohua Chi	Jiangxi	Xingzi	29° 20'29"	115° 59'29"	CONR	Yes
Chang Hu	Jiangxi	Xingxi	29° 11'21"	115° 54'17"	CONR	Yes

Xinmiao Hu	Jiangxi	Duchang	29° 21'29"	116° 10'55"	PNR	Yes
Duchangxi Hu	Jiangxi	Duchang	29° 14'40"	116° 28'07"	PNR	Yes
Shu Hu	Jiangxi	Duchang	29° 11'30"	116° 20'33"	PNR	Yes
Nanshan Hu	Jiangxi	Duchang	29° 15'47"	116° 11'48"	PNR	Yes
Jishan Hu	Jiangxi	Duchang	29° 17'34"	116° 08'34"	PNR	Yes
Gang Hu	Jiangxi	Hukou	29° 41'24"	116° 13'45"	CONR	Yes
Zao Hu	Jiangxi	Hukou	29° 34'17"	116° 11'24"	CONR	Yes
San Hu	Jiangxi	Nanchang	28° 53'19"	116° 16'25"	CONR	Yes
Saicheng Hu	Jiangxi	Jiujiang	29° 41'52"	115° 52'05"	CONR	Yes
Nan Hu	Jiangxi	Yugan	28° 49'07"	116° 15'21"	PNR	Yes
Linchong Hu	Jiangxi	Yugan	28° 51'14"	116° 16'16"	PNR	Yes
Xi Hu	Jiangxi	Yugan	28° 50'53"	116° 14'00"	PNR	Yes
Chengjia Hu	Jiangxi	Yugan	28° 48'08"	116° 18'11"	PNR	Yes
Caowan Hu	Jiangxi	Yugan	28° 50'50"	116° 19'07"	PNR	Yes
KangshanNei Hu	Jiangxi	Yugan	28° 51'41"	116° 29'15"	PNR	Yes
Qingshan Hu	Jiangxi	Poyang	29° 07'34"	116° 38'47"	NS	No
Chang Hu	Jiangxi	Xinjian	28° 55'32"	116° 17'22"	NNR	Yes
Sanniwan Hu	Jiangxi	Xinjian	28° 54'11"	116° 18'58"	NNR	Yes
Zhanbei Hu	Jiangxi	Xinjian	28° 54'50"	116° 16'17"	NNR	Yes
Shi Hu	Jiangxi	Xinjian	28° 52'39"	116° 18'24"	NNR	Yes
Dawu Hu	Jiangxi	Xinjian	29° 01'14"	116° 09'06"	NNR	Yes
Qinglan Hu	Jiangxi	Jinxian	28° 28'00"	116° 10'08"	PNR	Yes
Mingxi Hu	Jiangxi	Xinjian	28° 58'28"	116° 14'06"	NS	No
Candou Hu	Jiangxi	Xinjian	29° 05'55"	116° 05'15"	NNR	Yes
Xiaotan Hu	Jiangxi	Xinjian	29° 04'02"	116° 07'04"	NNR	Yes
Dahu Chi	Jiangxi	Yongxiu	29° 07'42"	115° 56'43"	NNR	Yes
Zhushi Hu	Jiangxi	Yongxiu	29° 10'36"	115° 58'20"	NNR	Yes
Changhu Chi	Jiangxi	Yongxiu	29° 08'16"	115° 59'19"	NNR	Yes
Beng Hu	Jiangxi	Xingzi	29° 13'48"	115° 57'27"	NNR	Yes
Sha Hu	Jiangxi	Xingzi	29° 10'51"	115° 55'50"	NNR	Yes
Dacha Hu	Jiangxi	Yongxiu	29° 09'27"	116° 05'07"	NNR	Yes
Zhonghu Chi	Jiangxi	Xinjian	29° 09'56"	116° 01'05"	NNR	Yes
Meixi Hu	Jiangxi	Yongxiu	29° 13'11"	116° 03'26"	NNR	Yes
Xiang Hu	Jiangxi	Xinjian	29° 06'56"	116° 00'34"	NNR	Yes

NNR=National nature reserve

PNR=Provincial nature reserve

CNR=City nature reserve

CONR=County nature reserve

NS = Not protect area

Table S5.2 Time-series census data using in our analysis in four key sites in the Yangtze.

Lake name	Province	2000/01	2001/02	2002/03	2003/04	2004/05	2005/06	2006/07	2007/08	2008/09	2009/10	2010/2011	2011/2012
Shengjin Hu	Anhui	NS	NS	NS	Feb ¹	Feb ²	Feb ³	Feb ³	Feb ⁷	Feb ⁷	Feb ⁷	Feb ⁷	Feb ⁷
Wuchang Hu	Anhui	NS	NS	NS	Feb ¹	Feb ²	Mar ⁴	Jan ⁴	Jan ⁴	Dec ⁷	Feb ⁷	Feb ⁷	Dec ⁷
Caizi Hu	Anhui	NS	NS	NS	Feb ¹	Feb ²	Mar ⁴	Jan ⁴	Jan ⁴	Dec ⁷	Feb ⁷	Feb ⁷	Dec ⁷
Baidang Hu	Anhui	NS	NS	NS	Feb ¹	Feb ²	NS	Jan ⁴	Feb ⁴	Dec ⁷	Feb ⁷	Feb ⁷	Dec ⁷
Fengsha Hu	Anhui	NS	NS	NS	Feb ¹	Feb ²	Mar ⁴	Jan ⁴	Feb ⁷	Dec ⁷	Feb ⁷	Feb ⁷	Dec ⁷
Huang Hu	Anhui	NS	NS	NS	Feb ¹	Feb ²	Mar ⁴	Jan ⁴	Jan ⁴	Dec ⁷	Feb ⁷	Feb ⁷	Dec ⁷
Po Hu	Anhui	NS	NS	NS	Feb ¹	Feb ²	Mar ⁴	Jan ⁴	Jan ⁴	Dec ⁷	Feb ⁷	Feb ⁷	Dec ⁷
Nang Hu	Jiangxi	Jan ⁵	Jan ⁵	Jan ⁵	Feb ¹	Feb ²	Dec ⁵	Dec ⁵	Jan ⁵	Feb ⁵	Feb ⁵	Feb ⁵	Feb ⁵
Shili Hu	Jiangxi	Jan ⁵	Jan ⁵	Jan ⁵	Feb ¹	Feb ²	Dec ⁵	Dec ⁵	Jan ⁵	Feb ⁵	Feb ⁵	Feb ⁵	Feb ⁵
Liaohua Chi	Jiangxi	Jan ⁵	Jan ⁵	Jan ⁵	Feb ¹	Feb ²	Dec ⁵	Dec ⁵	Jan ⁵	Feb ⁵	Feb ⁵	Feb ⁵	Feb ⁵
Chang Hu	Jiangxi	Jan ⁵	Jan ⁵	Jan ⁵	Feb ¹	Feb ²	Dec ⁵	Dec ⁵	Jan ⁵	Feb ⁵	Feb ⁵	Feb ⁵	Feb ⁵
Xingmiao Hu	Jiangxi	Jan ⁵	Jan ⁵	Jan ⁵	Feb ¹	Feb ²	Dec ⁵	Dec ⁵	Jan ⁵	Feb ⁵	Feb ⁵	Feb ⁵	Feb ⁵
Duchangxi Hu	Jiangxi	Jan ⁵	Jan ⁵	Jan ⁵	Feb ¹	Feb ²	Dec ⁵	Dec ⁵	Jan ⁵	Feb ⁵	Feb ⁵	Feb ⁵	NS
Jishan Hu	Jiangxi	Jan ⁵	Jan ⁵	Jan ⁵	Feb ¹	Feb ²	Dec ⁵	Dec ⁵	Jan ⁵	Feb ⁵	Feb ⁵	Feb ⁵	NS
Gang Hu	Jiangxi	Jan ⁵	Jan ⁵	Jan ⁵	Feb ¹	Feb ²	Dec ⁵	Dec ⁵	Jan ⁵	Feb ⁵	Feb ⁵	Feb ⁵	Feb ⁵
Zao Hu	Jiangxi	Jan ⁵	Jan ⁵	Jan ⁵	Feb ¹	Feb ²	Dec ⁵	Dec ⁵	Jan ⁵	Feb ⁵	Feb ⁵	Feb ⁵	Feb ⁵
Jiangxiangsan Hu	Jiangxi	Jan ⁵	Jan ⁵	Jan ⁵	Feb ¹	Feb ²	Dec ⁵	Dec ⁵	Jan ⁵	Feb ⁵	Feb ⁵	Feb ⁵	NS
Saicheng Hu	Jiangxi	Jan ⁵	Jan ⁵	Jan ⁵	Feb ¹	Feb ²	Dec ⁵	Dec ⁵	Jan ⁵	Feb ⁵	Feb ⁵	Feb ⁵	Feb ⁵
Linchong Hu	Jiangxi	Jan ⁵	Jan ⁵	Jan ⁵	Feb ¹	Feb ²	Dec ⁵	Dec ⁵	Jan ⁵	Feb ⁵	Feb ⁵	Feb ⁵	Feb ⁵
Chang Hu	Jiangxi	Jan ⁵	Jan ⁵	Jan ⁵	Feb ¹	Feb ²	Dec ⁵	Dec ⁵	Jan ⁵	Feb ⁵	Feb ⁵	NS	Feb ⁵
Sanniwan Hu	Jiangxi	Jan ⁵	Jan ⁵	Jan ⁵	Feb ¹	Feb ²	Dec ⁵	Dec ⁵	Jan ⁵	Feb ⁵	Feb ⁵	Feb ⁵	Feb ⁵
Dawu Hu	Jiangxi	Jan ⁵	Jan ⁵	Jan ⁵	Feb ¹	Feb ²	Dec ⁵	Dec ⁵	Jan ⁵	Feb ⁵	Feb ⁵	Feb ⁵	Feb ⁵
Qinglan Hu	Jiangxi	Jan ⁵	Jan ⁵	Jan ⁵	Feb ¹	Feb ²	Dec ⁵	Dec ⁵	Jan ⁵	Feb ⁵	Feb ⁵	Feb ⁵	Feb ⁵
Poyang Hu NNR	Jiangxi	Jan ⁵	Jan ⁵	Jan ⁵	Feb ¹	Feb ²	Dec ⁵	Dec ⁵	Jan ⁵	Feb ⁵	Feb ⁵	Feb ⁵	Feb ⁵
East Dongting NNR	Hunan	NS	NS	NS	Feb ¹	Feb ²	Jan ⁶	Jan ⁶	Feb ⁶	Feb ⁷	Feb ⁷	Feb ⁷	Jan ⁶

1 = WWF 2004 middle-lower Yangtze River floodplain survey; 2 = WWF 2004 middle-lower Yangtze River floodplain survey

3 = Shengjin Lake National Nature Reserve survey; 4 = Anqing Yanjiang Nature Reserve survey

5 = Poyang Lake National Reserve survey; 6 = Dongdongting Lake National Nature Reserve survey

7 = Survey conducted by authors; NS = No data available

Table S5.3 Information of satellite images used in this study.

Date	Path/Row	Sensor	Cloud cover (%)
2004-01-24	119/038	ETM+	0
2004-01-27	124/039	ETM+	24
2004-01-27	124/040	ETM+	16
2004-02-16	120/039	ETM+	0
2004-01-21	122/039	TM	0
2004-02-08	120/037	TM	23
2004-02-08	120/038	TM	0
2004-02-13	123/039	TM	0
2004-02-13	123/040	TM	0
2004-02-15	121/039	TM	0
2004-02-15	121/040	TM	0

Table S5.4: Pearson Correlation coefficients between independent variables, and the Variance Inflation Factors (VIF); n = 78; (* $P < 0.05$; ** $p < 0.01$; *** $p < 0.001$). For abbreviations see table 5.1.

	LA	WA	TEMP	MP	NDVI	NPP	SLOPE	SLOPECV	VIF
LA									1.914
WA	0.165								3.290
TEMP	-0.111	-0.492**							2.014
MP	0.249*	-0.115	0.035						2.275
NDVI	-0.021	-0.184	0.303**	-0.067					1.750
NPP	0.152	-0.012	-0.018	0.080	-0.034				1.923
SLOPE	0.019	0.000	0.107	0.235*	0.024	0.072			1.745
SLOPECV	0.084	-0.013	-0.031	0.246*	-0.018	0.068	0.450**		1.686
NDVICV	0.285*	-0.021	-0.158	0.086	-0.027	0.206	0.024	0.110	2.275

Table S5.5 Effect of NDVI together with its square term on the species density of grazing birds. BG: bean goose; GWFG: greater white-fronted goose; LWFG: lesser white-fronted goose; SG. For variable abbreviation see Table 5.1.

Species	Variables	Poisson model				zero-inflated model			
		b	se	z	p	b	se	z	p
BG	NDVI ²	-85.946	6.422	-13.382	<0.001	23.769	77.058	0.308	0.758
	NDVI	58.216	4.070	14.304	<0.001	-14.929	46.786	-0.319	0.750
GWFG	NDVI ²	-330.076	17.814	-18.53	<0.001	230.15	110.03	2.092	0.037
	NDVI	218.218	11.185	19.51	<0.001	-142.99	66.93	-2.136	0.033
LWFG	NDVI ²	-447.769	27.652	-16.19	<0.001	-56.361	131.270	-0.429	0.668
	NDVI	301.722	18.491	16.32	<0.001	19.395	84.254	0.230	0.818

Table S5.6 Predicted (H_0) and observed effects (+: positive effect; -: negative effect; NS: no effect) of different variables on bird density of five study species using a zero-inflated Poisson regression model based on AICc model selection with model averaging (b = regression coefficient, se = standard error, 95% CI = 95% confidence interval). BG: bean goose; GWFG: greater white-fronted goose; LWFG: lesser white-fronted goose; SG: swan goose; TS: tundra swan. For variable abbreviation see Table 5.1.

Species	Variables	H0	Poisson model			Zero-inflated model		
			b	se	95% CI	b	se	95% CI
BG	LA	+	-0.006	0.001	-0.007, -0.004	-0.017	0.012	-0.041, 0.007
	TEMP	+	0.606	0.047	0.514, 0.698	-0.328	0.437	-1.185, 0.529
	MP	+	0.074	0.003	0.067, 0.081	-0.053	0.036	-0.123, 0.018
	SLOPE	-	0.906	0.040	0.828, 0.984	-0.324	0.522	-1.347, 0.699
	SLOPECV	-	-2.588	0.121	-2.826, -2.350	-1.385	1.263	-3.861, 1.091
	NDVI	+						
	NPP	+	-0.006	0.002	-0.010, -0.002	-0.041	0.021	-0.081, -0.000
	NDVICV	-	-2.721	0.341	-3.39, -2.05	2.513	4.855	-7.002, 12.028
GWFG	LA	+	-0.045	0.004	-0.053, -0.039	-0.011	0.020	-0.053, 0.026
	TEMP	+	-0.065	0.108	-0.384, -0.009	-0.152	0.316	-1.242, 0.327
	MP	+	-0.075	0.007	-0.084, -0.056	0.070	0.042	-0.005, 0.166
	SLOPE	-	1.346	0.058	1.269, 1.492	0.356	0.601	-0.816, 1.515
	SLOPECV	-	-5.125	0.233	-5.641, -4.730	-1.365	1.489	-4.303, 1.697
	NDVI	+	28.45	0.997	26.71, 30.63	0.213	5.548	-9.985, 11.816
	NPP	+	0.010	0.003	0.003, 0.014	-0.030	0.022	-0.070, 0.014
	NDVICV	-	14.47	0.904	13.00, 16.56	3.194	6.074	-9.731, 13.678
LWFG	LA	+	-0.012	0.002	-0.017, -0.006	-0.050	0.029	-0.106, 0.006
	TEMP	+	3.970	0.301	3.380, 4.561	-1.163	1.613	-4.325, 2.000
	MP	+						
	SLOPE	-	1.742	0.073	1.599, 1.886	0.488	0.726	-0.934, 1.911
	SLOPECV	-						
	NDVI	+	17.99	1.447	15.155, 20.825	-10.30	8.262	-26.491, 5.894
	NPP	+						
	NDVICV	-	29.01	2.047	25.00, 33.02	23.591	12.31	-0.533, 47.715
SG	WA	+	-0.017	0.001	-0.018, -0.014	-0.066	0.027	-0.119, -0.013
	TEMP	+	-2.113	0.120	-2.348, -1.877	0.183	0.588	-0.970, 1.336
	MP	-	-0.145	0.005	-0.154, -0.136	-0.066	0.052	-0.168, 0.037
	SLOPE	-	-2.856	0.181	-3.210, -2.501	-1.245	1.350	-3.890, 1.400
	SLOPECV	-	6.940	0.509	5.942, 7.939	2.279	2.300	-2.228, 6.786
	NDVI	NS	5.763	0.738	4.318, 7.209	4.325	8.028	-11.41, 20.06
	NPP	NS	-0.008	0.004	-0.017, 0.001	-0.085	0.036	-0.156, -0.014
	NDVICV	NS	-6.713	0.670	-8.027, -5.399	19.452	9.453	0.925, 37.980
TS	WA	+	-0.035	0.002	-0.038, -0.031	-0.013	0.013	-0.039, 0.013
	TEMP	+	1.529	0.054	1.424, 1.634	1.855	0.705	0.473, 3.237
	MP	-	0.053	0.004	0.044, 0.062	0.060	0.045	-0.027, 0.147
	SLOPE	-	-1.379	0.080	-1.537, -1.221	-0.683	0.642	-1.940, 0.575
	SLOPECV	-	3.659	0.183	3.301, 4.018	0.751	1.508	-2.205, 3.707
	NDVI	NS	-13.33	0.595	-14.50, -12.17	1.185	5.578	-9.748, 12.118
	NPP	NS	-0.009	0.002	-0.012, -0.006	-0.036	0.023	-0.081, 0.010
	NDVICV	NS	12.19	0.633	10.957, 13.440	10.620	6.195	-1.521, 22.761

Chapter 6

Synthesis

Yong Zhang

Ecology studies the relationship between organisms and their surrounding environment. For instance, understanding the underlying mechanisms that determine the spatial and temporal distribution of organisms is a fundamental question to ecologists (Chesson 2000). Organisms' spatial-temporal distribution and abundance can be determined by a variety of abiotic and biotic factors that interact and operate at different spatial scales (Levin 1992, Barr and Babbitt 2002, McGill 2010, De Knecht et al. 2011). Unfortunately, determining the importance of the factors' impact on a species' habitat selection and abundance is complicated because of these scale effects, and the interactions between all relevant factors. Abiotic factors are among the most basic to affect the distribution and abundance of organisms as they determined a species' ecological niche where they could establish and maintain themselves (Chase and Leibold 2003). In addition, biotic interactions, such as top-down (i.e., predation) and bottom-up (i.e., food availability and quality) factors, operate across trophic levels (Krebs et al. 1995) under influence of competitive and facilitative interactions (Schoener 1983, Reiter and Andersen 2013, Tombre et al. 2013).

Distribution and abundance of organisms (particularly for herbivorous species) are also affected by their body size (Olf et al. 2002), as described by allometric scaling theory (Bell 1970, Jarman 1974). Smaller-sized herbivores are more strongly affected than larger ones by changes in forage quality, whereas larger species are more sensitive to changes in forage quantity (Prins and Ydenberg 1985, Wilmshurst et al. 2000, Durant et al. 2003, Heuermann et al. 2011, Wang et al. 2013b). Daily metabolic requirements increase with body weight at a decreasing rate, so that larger herbivores have a higher total daily demand, but smaller herbivores require a higher daily intake relative to body size (Demment and Van soest 1985, Richman et al. 2015). Furthermore, gut capacity increases in proportion to body size and hence larger herbivores have a longer gut retention time than smaller herbivores and can extract more nutrients from lower quality forage (Prop and Vulink 1992, Van Gils et al. 2008). 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 habitat selection and abundance should be used to better understand the differences in spatial distribution among species and the presence or absence of species coexistence.

The effects of these abiotic and biotic variables are often scale dependent (Brändle and Brandl 2001, McGill 2010, De Knecht et al. 2011), and different factors operate at

different spatial scales (De Knecht et al. 2011, Davidson et al. 2012). Moreover, different species respond to environmental variation differently at different scales (Olff and Ritchie 2002, Gabriel et al. 2010). Bird distributions on regional scales are largely affected by ecological factors while climatic conditions are more important on continental scales (Brändle and Brandl 2001). Local-scale vegetation gradients better explain the bird distribution than that of landscape or regional scales (Fletcher and Hutto 2008). Analyses at multiple spatial scales can greatly enhance the understanding of bird distribution (Coreau and Martin 2007). Hence, scales should be carefully considered when analysing the effects of variables on bird distribution and habitat selection.

In this thesis, I have presented several studies concerning the effects of abiotic and biotic factors on the distribution and abundance of several Anatidae species over different spatial scales. First, I studied habitat selection of three Anatidae species using an experimental approach with birds in exclosures (Chapter 2). Then, I analysed goose species habitat selection at site level using a correlative study of data collected in a single recessional grassland in Shengjin Lake (Chapter 3). In chapter 4, I studied various factors affecting Anatidae species densities at lake-level. In Chapter 5 I further expanded the study area to the whole of Yangtze River floodplain, analysing the species population trends in wetlands with different protection status and the effect of abiotic and biotic factors on Anatidae species distribution and abundance over different lakes. In this last chapter, I synthesise my results and discuss how the different environmental factors influence the habitat selection and abundance of Anatidae species differing in body size. I also discuss how the differences of these factors influence Anatidae species habitat selection and abundance at different spatial scales. In addition, I discuss the applications of my findings to wetlands management and conservation. Lastly, I draw several main conclusions and suggest a focus for future studies.

Effect of abiotic factors on Anatidae species habitat selection and abundance

Climate factors

Climate factors such as temperature and rainfall are considered as important factors in determining animal habitat selection and abundance (Hawkins et al. 2003). For instance,

temperature affects animal metabolism. Animals maintain their body temperature through physiological processes, in reaction to changes in their environment (Hertz et al. 1993, Shrestha et al. 2012, Shrestha et al. 2014). When environmental temperature is below thermoneutrality, conserving body heat becomes important for foraging birds (Swanson and Olmstead 1999). There is a strong relationship between habitat selection and thermoregulation (Compton et al. 2002, Dubois et al. 2009). Wintering birds tend to select relatively warm patches to reduce the cost of thermoregulation (Villen-Perez et al. 2013). The abundance of wintering birds decreased with decreasing temperatures in winter (Meehan et al. 2004, Zuckerberg et al. 2011). Temperature also influences plant primary productivity, and thereby forage resources for herbivorous Anatidae species (Milchunas and Lauenroth 1993, Piao et al. 2006). The sedge (e.g. *Carex* spp.) growth rate was lower in the mid-winter when the temperature was lower (Stirnemann et al. 2012, Zhao et al. 2012). Hence, a positive relationship between animal abundance and temperature can be expected. In line with former studies and my prediction, in chapter 5, I showed that temperature had a positive effect on the densities of most wintering Anatidae herbivorous species. However, a negative effect was found for the density of swan goose. I suggested two possible explanations for the negative effect of temperature on the density of swan goose: interference competition and climate warming. Interference competition will be discussed later on. Climate warming was a good predictor for the northward shifts of several bird species (Hickling et al. 2006, Melles et al. 2011) as the reproductive success of waterbirds can be negatively influenced by long distance migration from their wintering grounds to their breeding grounds (Alerstam et al. 1990). Reperant et al. (2010) suggested that waterbirds normally aggregate along cold fronts close to the 0°C isotherm where sub-zero conditions are avoided during winter so that water and forage resources remain unfrozen. As the temperatures were relatively high during the survey period, swan goose wintering at higher latitude wetlands probably reduce their migration distance and also the mortality rate.

Rainfall is considered to be one of the important drivers for animal population dynamics as it is closely related to resource availability (Georgiadis et al. 2007, Anderson et al. 2008, Lenhart et al. 2015). Rainfall influences grass growth rates and therefore quantity of grass (Van der Veen et al. 1999). Brent goose population size increased with increasing food availability as a result of higher rainfall (Ebbinge 1992). However, rainfall can also negatively affect food availability, for example increasing

water level will decrease the food accessibility for tuber-feeding birds (Nolet et al. 2006). In chapter 5, in line with these former studies and my prediction, I demonstrated that rainfall had a positive effect for all grazing wintering Anatidae species density, but had a negative effect on tuber-feeding species. My results highlighted the importance of differences between species when studying the effect of different variables on animal habitat selection and densities, and are therefore relevant for formulating appropriate conservation policies.

Topography

Habitat topography can affect animal habitat selection in various ways as illustrated by several empirical studies (Oloff et al. 1997, Genin 2004, Davies et al. 2007, Leblond et al. 2010, Di Virgilio et al. 2013). Amongst topographical factors, elevation and slope are two of the important ones. Elevation may determine the habitat selection of animals through the effects on the availability of their food availability. For example, Moorhen (*Gallinula chloropus*) abundance was negatively affected by elevation in wetland as vegetation cover was higher at lower elevation areas (Brambilla et al. 2012). Brent goose (*Branta bernicla*) reached higher densities on the lower part of an elevation gradient in salt marshes (Oloff et al. 1997). Slopes negatively affected vegetation occurrence and biomass (Andersson 2001, Partanen et al. 2009) as steep slopes are disadvantageous for sediment deposition (Kenter 1990, Hsu et al. 2013), negatively affecting vegetation growth and biomass (Krause-Jensen et al. 2003) and thus habitat selection of herbivorous species. Moreover, foraging on habitat with a gentle slope increases the ability to detect the predators (Schaible et al. 2005). In this thesis, in line with former studies, I found that goose species selected lower elevation areas closer to the water edge where the forage quality was higher (Chapter 3). I suggested that water level fluctuations play an important role on the vegetation availability and quality in wetlands and therefore determine habitat selection of grazing Anatidae species. Compared to the other competing hypotheses, the slope hypothesis was the best in explaining the observed differences in densities of most of the studied species (Chapter 5). My data partly supported the prediction that slope would be negatively correlated with abundance of herbivorous Anatidae species, but a positively effect was found for grazing species (Chapter 5). Former study showed that no effect was found when slopes

are relatively small for a foraging bird species (Fox et al. 2013). However, a positively effect was found although the slope is relatively gentle (ranging from only 0 to about 3°) in my study area. Here I argue that grazing birds on recession grasslands may benefit from a relatively steep slope because a steep slope may offer adequate drainage which could facilitate goose grazing as grassland would be waterlogged for long periods on the flat grassland, negatively affect grass growth rate in winter (Lenssen et al. 1999, Bennett et al. 2009). However, if the range in slope angles were to extend, I expect to find dome-shaped relationship. To my knowledge, studies on effect of surface slopes on habitat selection of wintering Anatidae species are scarce and how the wintering Anatidae species respond to slope gradients is still not clearly understood. Thus, more research is needed to better understand the effect of slope on the habitat selection of these wintering birds.

Effect of biotic factors on Anatidae species habitat selection and abundance

A variety of biotic factors can control animal's habitat selection and population abundance, operating across trophic levels (Krebs et al. 1995), such as top-down (i.e., predation and human disturbance) and bottom-up (i.e., food availability, quality, and vegetation heterogeneity) effects. These processes may be mediated by competitive and facilitative interactions (Schoener 1983, Reiter and Andersen 2013, Tombre et al. 2013).

Forage quantity and quality

Animals forage longer where prey is abundant and leave areas where prey is scarce (Hassell 1978). Thus, resource availability is one of the most important factors influencing an animal's habitat selection and thereby the density of a species. However, the availability of resources often varies in space and over time (Fryxell et al. 2005) and different grazer species make different choices (Durant et al. 2004, Heuermann et al. 2011) as described by species-specific functional response curves. Forage quality also plays an important role in forage patch selection (Wilmshurst and Fryxell 1995, Prins 1996a). As forage quantity increases, forage quality often decreases, such as illustrated by a decrease in nitrogen content and an increase in fibre content (Prop and Vulink 1992, Prins & Olff 1998, Olff et al. 2002,). Hence, foragers often face a trade-off

between maximizing forage quantity or maximizing forage quality, as predicted by the forage maturation hypothesis (Riddington et al. 1997). Foraging theory also predicts that herbivores select their habitat under influence of their body size (Hopcraft et al. 2010, Clauss et al. 2013): larger species are less sensitive to variation in forage quality because of a longer digestive track and therefore selected higher biomass areas, whereas smaller ones generally forage on shorter swards with a higher nutrient content (Durant et al. 2003, Durant et al. 2004, Heuermann et al. 2011).

In chapter 2, using an experimental approach by offering different sward heights, I found that the larger swan goose and bean goose followed a type I functional response, whereas wigeon followed a type II functional response. The results suggested that the intake of swan goose and bean goose increases with increasing forage availability over the range of sward heights studied. For wigeon, the intake rate will first increase with increasing forage availability and thereafter level off. The results indicated that forage quality might not affect forage intake of the studied species over the range of sward heights studied. A type IV functional response was often found when studying Anatidae species (Durant et al. 2003, Heuermann et al. 2011). I expected that the type IV would also be detected if the range of sward heights extended to a larger range. However, as I studied these functional responses using natural grasses, which were relatively short during the study period, this result may reflect the reality of the functional responses for those herbivorous Anatidae birds during this period compared to other studies.

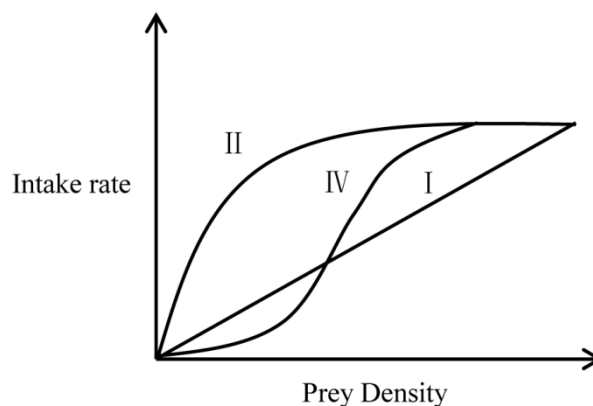


Figure 6.1: An illustration of type I, II and IV functional response curves.

In chapter 3, I studied the habitat usage of the two grazing species differing in body size at site level. In line with the foraging theories and former studies, I demonstrated that smaller species were more sensitive to the elevation gradient and to sward heights, illustrating the importance of allometric responses in habitat selection by different goose species. In chapter 4, however, I failed to find a significant effect of forage biomass on the density of the grazing goose species at lake level. This is probably because of the effect of forage quality. Grazing wildfowl are sensitive to variation in forage quantity and quality (Ydenberg and Prins 1981) and not able to tolerate low quality food because of a relatively poor digestion system (Prop and Vulink 1992), and goose species densities decreased in the patches that had a higher forage quantity. When analysing the grazing goose species densities at flood plain level (Yangtze River flood plain, chapter 5), a dome-shape relationship was found between goose densities and foraging quantity. This result indicated that higher species densities are found at areas with an intermediate foraging quantity.

Habitat heterogeneity

Habitat heterogeneity is predicted to affect bird habitat selection (Smith et al. 2010, Pickett and Siriwardena 2011), as herbivorous birds have a lower intake rate when feeding on complex swards compared to homogenous swards (Wilmschurst et al. 2000, Heuermann et al. 2011). Moreover, the effect of the habitat heterogeneity is often mediated by body size. The smaller species are more sensitive to the habitat heterogeneity and hence tend to select homogeneous patches (Heuermann et al. 2011). In chapter 3 and 5, I showed that habitat selection of the grazing Anatidae species was negatively affected by habitat heterogeneity.

Goose species normally forage at very high peck rates in order to satisfy their daily demand. For example, the peck rate of lesser white-fronted goose can reach four times per second. However, high heterogeneity in resource availability decreases the peck rate and thereby reduces forage intake rates.

Competition

Interference competition may occur when different species forage on the same resource in the same space and time (Wiens 1989, Prins 2000). The habitat selection of co-

occurring species may be profoundly affected by direct asymmetrical competition when exploiting limited resources (Keddy 2001). The “superior species” normally occupies the better habitat and out-competes the other (“sub-ordinate” or “inferior”) species. The outcome of interference competition is influenced by species body size and the larger species are often the winner (Vahl 2006b). In this thesis, I tested for the existence of interference competition among three Anatidae species differing in body size using an experimental design (chapter 2). I found that the largest species was the superior one and forced the subordinate species to forage on non-preferred patches. Meanwhile, most of the species increased their peck rate and foraging time to compensate for the energy losses. However, when studying species habitat selection in the field, these Anatidae species are often found together, foraging on the same resources (chapter 3). I found that grazing Anatidae species differing in body size co-exist, enabled by slight differences in selection of elevation and swards heights (chapter 3). However, interference competition might occur between the two tuber-feeding species (Chapter 5) as swan goose selected areas with a lower elevation compared to tundra swans. Hence, I suggest that the hydrological regimes of the different water bodies could be optimized to accommodate migratory herbivorous Anatidae species during the entire wintering period (see below).

Human factors

Human factors such as gross domestic per capita product, conservation status and human density can sometimes better predict animal population densities than differences in resources (De Boer et al. 2011, De Boer et al. 2013). Human activities such as livestock breeding and aquaculture may also, positively or negatively, affect the distribution and abundance of wintering birds. In chapter 4, the effects of human factors on goose species densities were analysed in the Shengjin Lake National Reserve. My results suggest that number of people and the number of moving boats had no effect on geese densities, while buffaloes may facilitate goose species foraging. Although I failed to find a significant effect of human densities on densities of birds, it does not necessary mean that human factors are not important in determining bird species distribution as human factors are much more diverse. For example, pollution can negatively affect birds habitat usage (Zhang et al. 2014). Land use and urbanization also play an important role in determining bird distribution (Allen and O'Connor 2000, Zuckerberg et

al. 2011). With the rapid economic development of the areas surrounding the study area, human factors such as pollution, urbanization and tourism might play an increasing role on bird habitat selection in the Yangtze River flood plain. However, as the information required to assess these threats is rarely available, a systemic analysis of the effects of human factors on birds habitat selection and population fluctuations over larger spatial and tempore scales still lacks. Hence, more research is needed in order to better understand the impact of human factors and to formulate sound protection strategies for birds in the Yangtze River flood plain.

Protection status

Conservation measures can positively affect species richness and animal abundance (Donald et al. 2007, Hiley et al. 2013, Kleijn et al. 2014). In chapter 5, I studied the effect of protection status on population trends of Anatidae species and found that the overall population trends of the Anatidae species in the wetlands along the Yangtze River flood plain were decreasing. When comparing birds population trends among wetlands with a different protection status, my results showed that wetlands with a higher protection status (“high” in terms of administrative level) may better buffer against the declining trend. This result conveys two messages: birds may benefit from current conservation measures, and current conservation measures may not stop the declining trends of Anatidae species population sizes in the Yangtze River flood plain. Unlike the reserves in Europe and Africa where increasing population trends and species richness were found, I found that birds population trends were still decreasing, even in wetlands with the highest protection status in the Yangtze. Hence, more efforts are required to improve the effectiveness of current conservation policies even though my results show that current conservation measures are not useless.

Water level

Water level fluctuations play an important role in determining food availability and accessibility and therefore indirectly determine Anatidae bird distribution and bird densities. A higher water level will reduce the forage availability for birds and hence decrease the abundance of birds. A lower water level will first offer a larger extend of reccessional grassland and increase the food accessibility 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 covered with tall and lower quality sedges that are not suitable for grazing Anatidae. Moreover, a long period of lower water levels will also decrease the food availability for tuber-feeding birds by increasing soil compaction (Clarke et al. 2008), decreasing the abundance of tuber-feeding birds (Figure 6.1). It is important to realize that in much of the Yangtze floodplain, water levels are regulated and controlled by Man through a system of canals and sluices (Wu et al. 2009, Liu and Wang 2010). Based on my study, I suggest that hydrological regimes could be optimized to provide forage during the entire wintering period for migratory herbivorous Anatidae species. Indeed, the majority of lakes along the Yangtze is connected to the Yangtze River through sluices so that management of water level heights for conservation purposes is feasible. Water level regulation can facilitate Anatidae species grazing and regrazing by carefully timing the moment of exposure of these recessional wetlands. When the water level decreases gradually, the grasslands with a relatively higher elevation will emerge firstly and thereafter the lower lying areas. Following this hydrological pattern, grazing herbivorous Anatidae species could repeatedly graze on recessional grasslands and hence increase the number of birds in these wetlands. Also for tuber-feeding birds, tubers could be exploited with the recession of water levels, maximizing tuber availability (Figure 6.2).

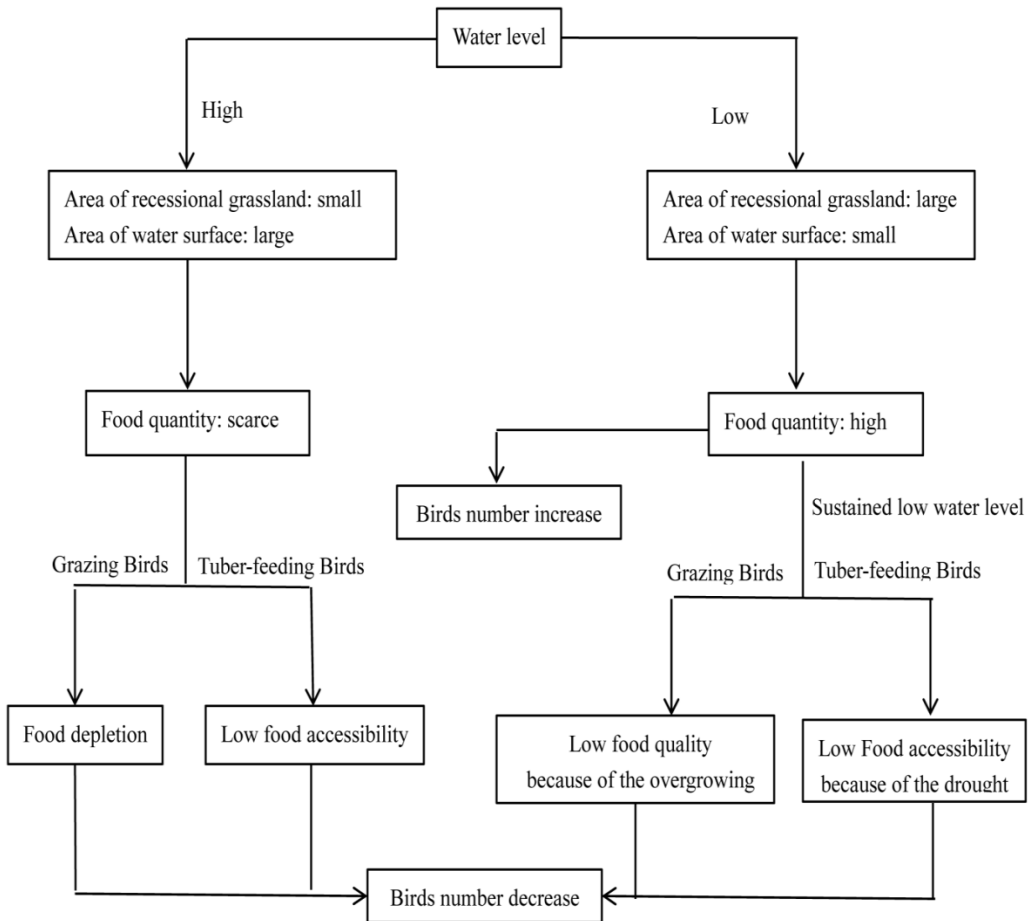


Figure 6.2: Effect of water level fluctuations on the abundance of wintering Anatidae species.

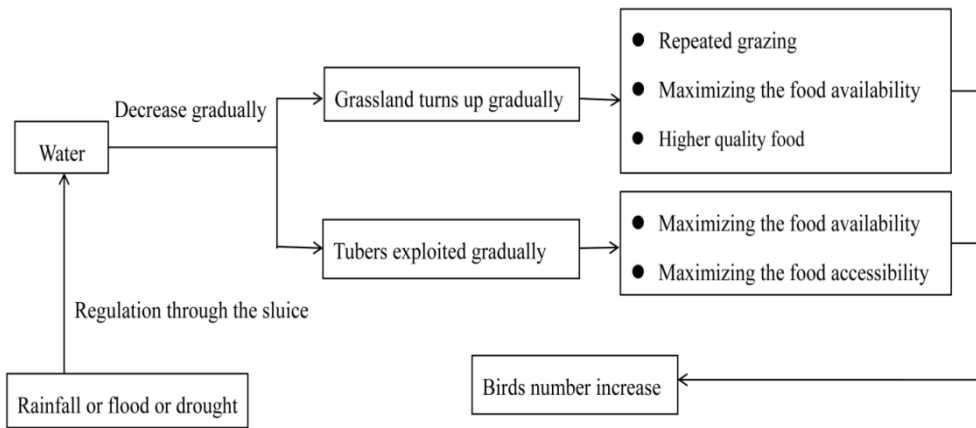


Figure 6.3: A hydrological regime that increases the number and densities of Anatidae species.

Conclusions and outlook

In this thesis I have demonstrated that the effects of various variables on the distribution and abundance of Anatidae species is mediated by body size. The results in this thesis also suggest that these effects are scale-dependent, highlighting the importance of scale when studying the effects of abiotic and biotic factors on Anatidae species distribution and abundance. Moreover, unlike Europe and Africa where conservation measures positively affected species richness and animal abundance, I have shown declining population trends of Anatidae species even in protected areas along the Yangtze River, and showed that present conservation measures may only buffer the decline trends of these birds.

In China, a comprehensive understanding of the spatial differences in densities of wintering waterfowl under influence of ecological and anthropogenic variables is still missing, reducing effectiveness of conservation activities. To better evaluate the effectiveness of such conservation activities, a systematic annual waterbirds survey should be carried out both in protected and unprotected areas in China and the data should be made freely available. For example, the North American Breeding Bird Survey (BBS) was initiated in 1966 and the survey is conducted every year. The main objective is to track the status and trends of North American bird populations and data

can be retrieved freely from a public website. In the Netherlands, SOVON in 1973 started carrying out standardised annual national bird surveys and continues till today. I strongly advocate that China starts an annual wintering birds survey, offering a basis for current and future conservation work. In that respect much can be learned from the coordinated activities of the African-Eurasian Migratory Waterbirds (AEWA), and perhaps China should even take the lead to organise waterfowl monitoring along the whole East and Central Asian flyways (encompassing countries such as Russia, Mongolia, the Koreas, Japan, China itself, but also India, Australia and the SE Asian countries).

I suggest that it is time to involve birdwatchers and volunteers in China's conservation network. Larger survey projects can strongly benefit from contributions from birdwatchers and volunteers. Birdwatchers and volunteers are often highly motivated and skilled, and can contribute to surveys. For example, thousands of volunteer birdwatchers participated in the Breeding Bird Survey in the UK. Nowadays, the number of birdwatchers is increasing in China and they can contribute to these bird surveys (Li et al. 2013) but improved organisation is needed, and called for here.

China has been undergoing a rapid process of industrialisation and urbanisation, resulting in enormous increases in habitat loss and human disturbance for the wintering bird species, especially along the middle and lower Yangtze River. However, studies linking these factors to changes in bird abundances and distributions are rare so far, reducing the effectiveness of conservation policies. Today, industry transfer is one of the basic economic policies in China. Because of unbalanced economic development, labour-intensive industries are often translocated to less developed areas, which often still support a larger number of migratory birds. Moreover, urbanisation is also often towards wetlands that are important habitats for birds, such as the plan of The Poyang Lake City Group (Huang 2009). Hence, it is urgent to study the effects of industrialisation and urbanisation on wintering bird distribution and abundance, offering a scientific base for policy-makers and managers.

Finally, I claim that nature reserves with a lower protection status ('lower' in the sense of administrative level) should also be given more attention in terms of investment, local community education and research efforts. Some lower protection status wetlands, such as the Anhui Anqing Yangtze Riverine Provincial Nature Reserve could be upgraded to a national nature reserve to increase the conservation efforts in this

important wetland. Moreover, even the national nature reserves are apparently not sufficient to stop the decline of the Anatidae birds, and thus additional measures are required. I therefore call for an in-depth investigation into the decline of Anatidae species in the East Asian-Australasian Flyway, as contrasted to the successes of the American and European counterparts.

References

- Adam, P. 1990. Saltmarsh ecology. Cambridge University Press, Cambridge.
- Albon, S. D. and R. Langvatn. 1992. Plant phenology and the benefits of migration in a temperate ungulate. *Oikos* **65**:502-513.
- Alerstam, T., D. Christie, and A. Ulfstrand. 1990. Bird migration. Cambridge University Press, Cambridge.
- Allen, A. P. and R. J. O'Connor. 2000. Interactive effects of land use and other factors on regional bird distributions. *Journal of Biogeography* **27**:889-900.
- Amarasekare, P. 2002. Interference competition and species coexistence. *Proceedings of the Royal Society B* **269**:2541-2550.
- Amarasekare, P. and R. M. Nisbet. 2001. Spatial heterogeneity, source-sink dynamics, and the local coexistence of competing species. *American Naturalist* **158**:572-584.
- Anderson, W. B., D. A. Wait, and P. Stapp. 2008. Resources from another place and time: Responses to pulses in a spatially subsidized system. *Ecology* **89**:660-670.
- Andersson, B. 2001. Macrophyte development and habitat characteristics in Sweden's large lakes. *Ambio* **30**:503-513.
- Augustine, D. J. and D. A. Frank. 2001. Effects of migratory grazers on spatial heterogeneity of soil nitrogen properties in a grassland ecosystem. *Ecology* **82**:3149-3162.
- Bakker, E. S., H. Olff, and J. M. Gleichman. 2009. Contrasting effects of large herbivore grazing on smaller herbivores. *Basic and Applied Ecology* **10**:141-150.
- Barbet-Massin, M. and W. Jetz. 2014. A 40-year, continent-wide, multispecies assessment of relevant climate predictors for species distribution modelling. *Diversity and Distributions* **20**:1285-1295.
- Barr, G. E. and K. J. Babbitt. 2002. Effects of biotic and abiotic factors on the distribution and abundance of larval two-lined salamanders (*Eurycea bislineata*) across spatial scales. *Oecologia* **133**:176-185.

- Barter, M., L. Cao, L. Chen, and G. Lei. 2005. Results of a survey for waterbirds in the lower Yangtze floodplain, China, in January-February 2004. *Forktail* **21**:1-7.
- Bautista, L. M., J. Tinbergen, and A. Kacelnik. 2001. To walk or to fly? How birds choose among foraging modes. *Proceedings of the National Academy of Sciences* **98**:1089-1094.
- Bayliss, P. 1989. Population-dynamics of Agpie Geese in relation to rainfall and density - Implications for harvest models in a fluctuating environment. *Journal of Applied Ecology* **26**:913-924.
- Bazzaz, F. A. 1975. Plant species-diversity in old-field successional ecosystems in southern illinois. *Ecology* **56**:485-488.
- Bell, R. H. V. 1970. The use of the herb layer by grazing ungulates in the Serengeti. Blackwell Scientific, Oxford.
- Bennett, S. J., E. G. Barrett-Lennard, and T. D. Colmer. 2009. Salinity and waterlogging as constraints to saltland pasture production: A review. *Agriculture Ecosystems & Environment* **129**:349-360.
- Bergman, C. M., J. M. Fryxell, C. C. Gates, and D. Fortin. 2001. Ungulate foraging strategies: energy maximizing or time minimizing? *Journal of Animal Ecology* **70**:289-300.
- Bibby, C. J., N. D. Burgess, D. A. Hill, and M. Mustoe. 2000. Bird census techniques. 2nd edition. Academic press, London.
- Black, J. M., C. Carbone, R. L. Wells, and M. Owen. 1992. Foraging dynamics in goose flocks - the cost-of-living on the edge. *Animal Behaviour* **44**:41-50.
- Blumstein, D. T., E. Fernandez-Juricic, P. A. Zollner, and S. C. Garity. 2005. Inter-specific variation in avian responses to human disturbance. *Journal of Applied Ecology* **42**:943-953.
- Bos, D., J. Van De Koppel, and F. J. Weissing. 2004. Dark-Bellied Brent Geese aggregate to cope with increased levels of primary production. *Oikos* **107**:485-496.
- Boyd, D. S., C. Sanchez-Hernandez, and G. M. Foody. 2006. Mapping a specific class for priority habitats monitoring from satellite sensor data. *International Journal of Remote Sensing* **27**:2631-2644.
- Brändle, M. and R. Brandl. 2001. Distribution, abundance and niche breadth of birds: scale matters. *Global Ecology and Biogeography* **10**:173-177.

- Brambilla, M., F. Rizzolli, and P. Pedrini. 2012. The effects of habitat and spatial features of wetland fragments on the abundance of two Rallid species with different degrees of habitat specialization. *Bird Study* **59**:279-285.
- Burnham, K. P. and D. R. Anderson. 2002. Model selection and multi-model inference : a practical information-theoretic approach. 2nd ed. edition. Springer, New York ; London.
- Calsbeek, R. and B. Sinervo. 2002. An experimental test of the ideal despotic distribution. *Journal of Animal Ecology* **71**:513-523.
- Cao, L., M. Barter, and G. Lei. 2008. New Anatidae population estimates for eastern China: Implications for current flyway estimates. *Biological Conservation* **141**:2301-2309.
- Cao, L., M. Barter, M. Zhao, H. Meng, and Y. Zhang. 2011. A systematic scheme for monitoring waterbird populations at Shengjin Lake, China: methodology and preliminary results. *Chinese Birds* **2**:1-17.
- Cao, L. and A. D. Fox. 2009. Birds and people both depend on China's wetlands. *Nature* **460**:173-173.
- Cao, L., Y. Zhang, M. Barter, and G. Lei. 2010. Anatidae in eastern China during the non-breeding season: Geographical distributions and protection status. *Biological Conservation* **143**:650-659.
- Chase, J. M. and M. A. Leibold. 2003. Ecological niches : linking classic and contemporary approaches. University of Chicago Press, London.
- Chesson, P. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* **31**:343-366.
- Clarke, M., R. Creamer, L. Deeks, D. Gowing, I. Holman, and R. Jones, et al. 2008. Scoping study to assess soil compaction affecting upland and lowland grassland in England and Wales. Final project (BD2304) report to Defra.
- Clauss, M., P. Steuer, D. W. H. Muller, D. Codron, and J. Hummel. 2013. Herbivory and body size: allometries of diet quality and gastrointestinal physiology, and implications for herbivore ecology and dinosaur gigantism. *PloS One* **8(10)**: e68714.
- Compton, B. W., J. M. Rhymer, and M. McCollough. 2002. Habitat selection by wood turtles (*Clemmys insculpta*): An application of paired logistic regression. *Ecology* **83**:833-843.

- Connor, E. F., A. C. Courtney, and J. M. Yoder. 2000. Individuals-area relationships: The relationship between animal population density and area. *Ecology* **81**:734-748.
- Cope, D. R. 2003. Variation in daily and seasonal foraging routines of non - breeding Barnacle Geese (*Branta leucopsis*): working harder does not overcome environmental constraints. *Journal of Zoology* **260**:65-71.
- Coreau, A. and J. L. Martin. 2007. Multi-scale study of bird species distribution and of their response to vegetation change: a Mediterranean example. *Landscape Ecology* **22**:747-764.
- Courant, S. and D. Fortin. 2010. Foraging decisions of bison for rapid energy gains can explain the relative risk to neighboring plants in complex swards. *Ecology* **91**:1841-1849.
- Cowie, R. J. 1977. Optimal Foraging in Great Tits (*Parus-Major*). *Nature* **268**:137-139.
- Cresswell, W. 1997. Interference competition at low competitor densities in Blackbirds *Turdus merula*. *Journal of Animal Ecology* **66**:461-471.
- Cromsigt, J. P. G. M., H. H. T. Prins, and H. Olff. 2009. Habitat heterogeneity as a driver of ungulate diversity and distribution patterns: interaction of body mass and digestive strategy. *Diversity and Distributions* **15**:513-522.
- Currie, D. J., G. G. Mittelbach, H. V. Cornell, R. Field, J. F. Guegan, and B. A. Hawkins, et al. 2004. Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters* **7**:1121-1134.
- Cyranoski, D. 2009. Putting China's wetlands on the map. *Nature* **458**:134-134.
- Dalby, L., B. J. McGill, A. D. Fox, and J. C. Svenning. 2014. Seasonality drives global-scale diversity patterns in waterfowl (*Anseriformes*) via temporal niche exploitation. *Global Ecology and Biogeography* **23**:550-562.
- Davidson, Z., M. Valeix, A. J. Loveridge, J. E. Hunt, P. J. Johnson, and H. Madzikanda, et al. 2012. Environmental determinants of habitat and kill site selection in a large carnivore: scale matters. *Journal of Mammalogy* **93**:677-685.
- Davies, R. G., C. D. L. Orme, D. Storch, V. A. Olson, G. H. Thomas, and S. G. Ross, et al. 2007. Topography, energy and the global distribution of bird species richness. *Proceedings of the Royal Society B-Biological Sciences* **274**:1189-1197.

- De Boer, W. F., L. Cao, M. Barter, X. Wang, M. M. Sun, and H. van Oeveren, et al. 2011. Comparing the community composition of european and eastern Chinese waterbirds and the influence of human factors on the China waterbird community. *Ambio* **40**:68-77.
- De Boer, W. F. and H. H. T. Prins. 1989. Decisions of cattle herdsmen in burkina-faso and optimal foraging models. *Human Ecology* **17**:445-464.
- De Boer, W. F., F. van Langevelde, H. H. T. Prins, P. C. de Ruiter, J. Blanc, and M. J. P. Vis, et al. 2013. Understanding spatial differences in African elephant densities and occurrence, a continent-wide analysis. *Biological Conservation* **159**:468-476.
- De Knegt, H. J. and F. van Langevelde and A. K. Skidmore and A. Delsink and R. Slotow and S. Henley, et al. 2011. The spatial scaling of habitat selection by African elephants. *Journal of Animal Ecology* **80**:270-281.
- Demment, M. W. and P. J. Van soest. 1985. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *American Naturalist* **125**:641-672.
- Di Virgilio, G., S. W. Laffan, and M. C. Ebach. 2013. Quantifying high resolution transitional breaks in plant and mammal distributions at regional extent and their association with climate, topography and geology. *PloS One* **8(4)**: e59227.
- Donald, P. F., F. J. Sanderson, I. J. Burfield, S. M. Bierman, R. D. Gregory, and Z. Waliczky. 2007. International conservation policy delivers benefits for birds in Europe. *Science* **317**:810-813.
- Donovan, T. M. and C. H. Flather. 2002. Relationships among north American songbird trends, habitat fragmentation, and landscape occupancy. *Ecological Applications* **12**:364-374.
- Dubois, Y., G. Blouin-Demers, B. Shipley, and D. Thomas. 2009. Thermoregulation and habitat selection in wood turtles *Glyptemys insculpta*: chasing the sun slowly. *Journal of Animal Ecology* **78**:1023-1032.
- Dunton, E. M. and D. L. Combs. 2010. Movements, habitat selection, associations, and survival of giant Canada goose broods in central Tennessee. *Human-Wildlife Interactions* **4**:192-201.
- Durant, D., H. Fritz, S. Blais, and P. Duncan. 2003. The functional response in three species of herbivorous Anatidae: effects of sward height, body mass and bill size. *Journal of Animal Ecology* **72**:220-231.

- Durant, D., H. Fritz, and P. Duncan. 2004. Feeding patch selection by herbivorous Anatidae: the influence of body size, and of plant quantity and quality. *Journal of Avian Biology* **35**:144-152.
- Durant, D., Fritz, H. 2006. Variation of pecking rate with sward height in wild Wigeon *Anas penelope*. *Journal of Ornithology* **147**:367-370.
- Ebbinge, B. S. 1992. Regulation of numbers of dark-bellied brent geese *Branta-bernicla-bernicla* on spring staging sites. *Ardea* **80**:203-228.
- Emlen, J. M. 1966. Role of time and energy in food preference. *American Naturalist* **100**:611-617.
- Fang, J., Z. H. Wang, S. Q. Zhao, Y. K. Li, Z. Y. Tang, and D. Yu, et al. 2006. Biodiversity changes in the lakes of the Central Yangtze. *Frontiers in Ecology and the Environment* **4**:369-377.
- Farnsworth, K. D., S. Focardi, and J. A. Beecham. 2002. Grassland-herbivore interactions: How do grazers coexist? *American Naturalist* **159**:24-39.
- Fernandez-Juricic, E. and J. L. Telleria. 2000. Effects of human disturbance on spatial and temporal feeding patterns of Blackbird *Turdus merula* in urban parks in Madrid, Spain. *Bird Study* **47**:13-21.
- Fewster, R. M., S. T. Buckland, G. M. Siriwardena, S. R. Baillie, and J. D. Wilson. 2000. Analysis of population trends for farmland birds using generalized additive models. *Ecology* **81**:1970-1984.
- Fletcher, R. J. and R. L. Hutto. 2008. Partitioning the multi-scale effects of human activity on the occurrence of riparian forest birds. *Landscape Ecology* **23**:727-739.
- Fortin, D., M. S. Boyce, E. H. Merrill, and J. M. Fryxell. 2004. Foraging costs of vigilance in large mammalian herbivores. *Oikos* **107**:172-180.
- Fox, A. D., J. Kahlert, and H. Ettrup. 1998. Diet and habitat use of moulting Greylag Geese *Anser anser* on the Danish island of Saltholm. *Ibis* **140**:676-683.
- Fox, B. J., W. B. Holland, F. L. Boyd, B. F. Blackwell, and J. B. Armstrong. 2013. Use of stormwater impoundments near airports by birds recognized as hazardous to aviation safety. *Landscape and Urban Planning* **119**:64-73.
- Fretwell, S. D. and J. S. Calver. 1969. On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica* **19**:37-44.

- Fretwell, S. D. and H. L. Lucas. 1970. On territorial behaviour and other factors influencing habitat distribution in birds. *Acta Biotheoretica* **19**:16-36.
- Fryxell, J. M. 1991. Forage quality and aggregation by large herbivores. *American Naturalist* **138**:478-498.
- Fryxell, J. M., J. F. Wilmschurst, and A. R. E. Sinclair. 2004. Predictive models of movement by Serengeti grazers. *Ecology* **85**:2429-2435.
- Fryxell, J. M., J. F. Wilmschurst, A. R. E. Sinclair, D. T. Haydon, R. D. Holt, and P. A. Abrams. 2005. Landscape scale, heterogeneity, and the viability of Serengeti grazers. *Ecology Letters* **8**:328-335.
- Gabriel, D., S. M. Sait, J. A. Hodgson, U. Schmutz, W. E. Kunin, and T. G. Benton. 2010. Scale matters: the impact of organic farming on biodiversity at different spatial scales. *Ecology Letters* **13**:858-869.
- Garcia-Morales, R., E. I. Badano, and C. E. Moreno. 2013. Response of neotropical bat assemblages to human land use. *Conservation Biology* **27**:1096-1106.
- Gauvin, S. and L.-A. Giraldeau. 2004. Nutmeg mannikins (*Lonchura punctulata*) reduce their feeding rates in response to simulated competition. *Oecologia* **139**:150-156.
- Gekara, O. J., E. C. Prigge, W. B. Bryan, E. L. Nestor, and G. Seidel. 2005. Influence of sward height, daily timing of concentrate supplementation, and restricted time for grazing on forage utilization by lactating beef cows. *Journal of Animal Science* **83**:1435-1444.
- Genin, A. 2004. Bio-physical coupling in the formation of zooplankton and fish aggregations over abrupt topographies. *Journal of Marine Systems* **50**:3-20.
- Georgiadis, N. J., J. G. N. Olwero, G. Ojwang, and S. S. Romanach. 2007. Savanna herbivore dynamics in a livestock-dominated landscape: I. Dependence on land use, rainfall, density, and time. *Biological Conservation* **137**:461-472.
- Gillings, S., S. E. Newson, D. G. Noble, and J. A. Vickery. 2005. Winter availability of cereal stubbles attracts declining farmland birds and positively influences breeding population trends. *Proceedings of the Royal Society B-Biological Sciences* **272**:733-739.
- Gong, P., Z. G. Niu, X. A. Cheng, K. Y. Zhao, D. M. Zhou, and J. H. Guo, et al. 2010. China's wetland change (1990-2000) determined by remote sensing. *Science China-Earth Sciences* **53**:1036-1042.

- Gunnarsson, T. G., J. A. Gill, J. Newton, P. M. Potts, and W. J. Sutherland. 2005. Seasonal matching of habitat quality and fitness in a migratory bird. *Proceedings of the Royal Society B-Biological Sciences* **272**:2319-2323.
- Hache, S., M. A. Villard, and E. M. Bayne. 2013. Experimental evidence for an ideal free distribution in a breeding population of a territorial songbird. *Ecology* **94**:861-869.
- Hadfield, J. D. 2010. MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *Journal of Statistical Software* **33**:1-22.
- Hanski, I. 1999. *Metapopulation ecology*. Oxford University Press, Oxford.
- Hassall, M. and S. J. Lane. 2005. Partial feeding preferences and the profitability of winter-feeding sites for brent geese. *Basic and Applied Ecology* **6**:559-570.
- Hassall, M., R. Riddington, and A. Helden. 2001. Foraging behaviour of Brent Geese, *Branta b. bernicla*, on grasslands: effects of sward length and nitrogen content. *Oecologia* **127**:97-104.
- Hassell, M. P. 1978. *The dynamics of arthropod predator-prey systems*. Princeton University Press, Princeton.
- Hastie, T. and R. Tibshirani. 1990. *Generalized additive models*. Chapman and Hall, London.
- Hawkins, B. A., R. Field, H. V. Cornell, D. J. Currie, J. F. Guegan, and D. M. Kaufman, et al. 2003. Energy, water, and broad-scale geographic patterns of species richness. *Ecology* **84**:3105-3117.
- Hebblewhite, M., E. Merrill, and G. Mcdermid. 2008. A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population. *Ecological Monographs* **78**:141-166.
- Hertz, P. E., R. B. Huey, and R. D. Stevenson. 1993. Evaluating temperature regulation by field-active ectotherms - the fallacy of the inappropriate question. *American Naturalist* **142**:796-818.
- Heuermann, N., F. van Langevelde, S. E. van Wieren, and H. H. T. Prins. 2011. Increased searching and handling effort in tall swards lead to a Type IV functional response in small grazing herbivores. *Oecologia* **166**:659-669.
- Hickling, R., D. B. Roy, J. K. Hill, R. Fox, and C. D. Thomas. 2006. The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology* **12**:450-455.

- Hiley, J. R., R. B. Bradbury, M. Holling, and C. D. Thomas. 2013. Protected areas act as establishment centres for species colonizing the UK. *Proceedings of the Royal Society B-Biological Sciences* **280**.
- Hirose, T., M. J. A. Werger, and J. W. A. van Rheenen. 1989. Canopy development and leaf nitrogen distribution in a stand of *Carex acutiformis*. *Ecology* **70**:1610-1618.
- Hobaugh, W. C. 1984. Habitat use by Snow Geese wintering in southeast Texas. *Journal of Wildlife Management* **48**:1085-1096.
- Hobbs, N. T., J. E. Gross, L. A. Shipley, D. E. Spalinger, and B. A. Wunder. 2003. Herbivore functional response in heterogeneous environments: A contest among models. *Ecology* **84**:666-681.
- Hoffmann, M., C. Hilton-Taylor, A. Angulo, M. Bohm, T. M. Brooks, and S. H. M. Butchart, et al. 2010. The impact of conservation on the status of the world's vertebrates. *Science* **330**:1503-1509.
- Holling, C. S. 1959. The components of predation as revealed by a study of small-mammal predation of the European Pine Sawfly. *The Canadian Entomologist* **91**:293-320.
- Hopcraft, J. G. C., H. Olff, and A. R. E. Sinclair. 2010. Herbivores, resources and risks: alternating regulation along primary environmental gradients in savannas. *Trends in Ecology & Evolution* **25**:119-128.
- Hsu, H. H., C. S. Liu, H. S. Yu, J. H. Chang, and S. C. Chen. 2013. Sediment dispersal and accumulation in tectonic accommodation across the Gaoping Slope, offshore Southwestern Taiwan. *Journal of Asian Earth Sciences* **69**:26-38.
- Huang, X. J. 2009. Poyang Lake City Group Strategic Research Development (Chinese Edition). Social Sciences Academic Press, Bei Jing.
- Huntingford, F. A. and A. K. Turner. 1987. Animal conflict. Chapman and Hall Animal Behaviour Series. Chapman and Hall: London.
- Hupp, J. W., R. G. White, J. S. Sedinger, and D. G. Robertson. 1996. Forage digestibility and intake by lesser snow geese: effects of dominance and resource heterogeneity. *Oecologia* **108**:232-240.
- Jarman, P. 1974. The social organisation of antelope in relation to their ecology. *Behaviour*:215-267.

- Joseph, L. N., C. Elkin, T. G. Martin, and H. P. Possingham. 2009. Modeling abundance using N-mixture models: the importance of considering ecological mechanisms. *Ecological Applications* **19**:631-642.
- Keddy, P. A. 2001. Competition. 2nd ed. edition. Kluwer Academic, Dordrecht ; London.
- Kenney, P. and J. Black. 1984. Factors affecting diet selection by sheep. 1. Potential intake rate and acceptability of feed. *Crop and Pasture Science* **35**:551-563.
- Kenter, J. A. M. 1990. Carbonate platform flanks - slope angle and sediment fabric. *Sedimentology* **37**:777-794.
- Kie, J. G. 1999. Optimal foraging and risk of predation: Effects on behavior and social structure in ungulates. *Journal of Mammalogy* **80**:1114-1129.
- Kleijn, D., I. Cherkaoui, P. W. Goedhart, J. van der Hout, and D. Lammertsma. 2014. Waterbirds increase more rapidly in ramsar-designated wetlands than in unprotected wetlands. *Journal of Applied Ecology* **51**:289-298.
- Kleijn, D., M. Rundlof, J. Scheper, H. G. Smith, and T. Tschardt. 2011. Does conservation on farmland contribute to halting the biodiversity decline? *Trends in Ecology & Evolution* **26**:474-481.
- Koh, C. N., P. F. Lee, and R. S. Lin. 2006. Bird species richness patterns of northern Taiwan: primary productivity, human population density, and habitat heterogeneity. *Diversity and Distributions* **12**:546-554.
- Kolada, A. 2014. The effect of lake morphology on aquatic vegetation development and changes under the influence of eutrophication. *Ecological Indicators* **38**:282-293.
- Krause-Jensen, D., M. F. Pedersen, and C. Jensen. 2003. Regulation of eelgrass (*Zostera marina*) cover along depth gradients in Danish coastal waters. *Estuaries* **26**:866-877.
- Krebs, C. J., S. Boutin, R. Boonstra, A. R. E. Sinclair, J. N. M. Smith, and M. R. T. Dale, et al. 1995. Impact of food and predation on the snowshoe hare cycle. *Science* **269**:1112-1115.
- Kristiansen, J. N. and N. S. Jarrett. 2002. Inter-specific competition between Greenland White-fronted Geese *Anser albifrons flavirostris* and Canada Geese *Branta canadensis* interior moulting in West Greenland: Mechanisms and consequences. *Ardea* **90**:1-13.

- Kuijper, D. P. J. and J. P. Bakker. 2005. Top-down control of small herbivores on salt-marsh vegetation along a productivity gradient. *Ecology* **86**:914-923.
- Laca, E. A., S. Sokolow, J. R. Galli, and C. A. Cangiano. 2010. Allometry and spatial scales of foraging in mammalian herbivores. *Ecology Letters* **13**:311-320.
- Leblond, M., C. Dussault, and J. P. Ouellet. 2010. What drives fine-scale movements of large herbivores? A case study using moose. *Ecography* **33**:1102-1112.
- Lenhart, P. A., M. D. Eubanks, and S. T. Behmer. 2015. Water stress in grasslands: dynamic responses of plants and insect herbivores. *Oikos* **124**:381-390.
- Lenssen, J. P. M., F. B. J. Menting, W. H. van der Putten, and C. W. P. M. Blom. 1999. Effects of sediment type and water level on biomass production of wetland plant species. *Aquatic Botany* **64**:151-165.
- Lepczyk, C. A., C. H. Flather, V. C. Radeloff, A. M. Pidgeon, R. B. Hammer, and J. G. Liu. 2008. Human impacts on regional avian diversity and abundance. *Conservation Biology* **22**:405-416.
- Levin, S. A. 1992. The problem of pattern and scale in ecology. *Ecology* **73**:1943-1967.
- Li, X. Y., L. Liang, P. Gong, Y. Liu, and F. F. Liang. 2013. Bird watching in China reveals bird distribution changes. *Chinese Science Bulletin* **58**:649-656.
- Liu, J. G., Z. Y. Ouyang, S. L. Pimm, P. H. Raven, X. K. Wang, and H. Miao, et al. 2003. Protecting China's biodiversity. *Science* **300**:1240-1241.
- Liu, X. Q. and Wang, H. Z. 2010. Estimation of minimum area requirement of river-connected lakes for fish diversity conservation in the Yangtze River floodplain. *Diversity and Distributions* **16**: 932-940.
- Loe, L. E., A. Myrnerud, A. Stien, H. Steen, D. M. Evans, and G. Austrheim. 2007. Positive short-term effects of sheep grazing on the alpine avifauna. *Biology Letters* **3**:109-111.
- Ma, Z. J., Y. Wang, X. J. Gan, B. Li, Y. T. Cai, and J. K. Chen. 2009. Waterbird population changes in the wetlands at Chongming Dongtan in the Yangtze River estuary, China. *Environmental Management* **43**:1187-1200.
- MacArthur, R. H. and E. R. Pianka. 1966. On optimal use of a patchy environment. *American Naturalist* **100**:603-609.

- Macias-Duarte, A., A. B. Montoya, C. E. Mendez-Gonzalez, J. R. Rodriguez-Salazar, W. G. Hunt, and P. G. Krannitz. 2009. Factors influencing habitat use by migratory grassland birds in the State of Chihuahua, Mexico. *Auk* **126**:896-905.
- Madsen, J., M. Bjerrum, and I. M. Tombre. 2014. Regional management of farmland feeding geese using an ecological prioritization tool. *Ambio*:1-9.
- Manseau, M. and G. Gauthier. 1993. Interactions between Greater Snow Geese and their rearing habitat. *Ecology* **74**:2045-2055.
- Matthew, M. W., S. M. Adler-Golden, A. Berk, S. C. Richtsmeier, R. Y. Levine, and L. S. Bernstein, et al. 2000. Status of atmospheric correction using a MODTRAN4-based algorithm. Pages 199-207 in *AeroSense 2000*. International Society for Optics and Photonics.
- Mattson, W. J. 1980. Herbivory in relation to plant nitrogen content. *Annual Review of Ecology, Evolution, and Systematics* **11**:119-161.
- McGill, B. J. 2010. Matters of scale. *Science* **328**:575-576.
- Mckay, H. V., J. D. Bishop, and D. C. Ennis. 1994. The possible importance of nutritional-requirements for Dark-Bellied Brent Geese in the seasonal shift from winter cereals to pasture. *Ardea* **82**:123-132.
- Meager, J. J., T. A. Schlacher, and T. Nielsen. 2012. Humans alter habitat selection of birds on ocean-exposed sandy beaches. *Diversity and Distributions* **18**:294-306.
- Meehan, T. D., W. Jetz, and J. H. Brown. 2004. Energetic determinants of abundance in winter landbird communities. *Ecology Letters* **7**:532-537.
- Melles, S. J., M. J. Fortin, K. Lindsay, and D. Badzinski. 2011. Expanding northward: influence of climate change, forest connectivity, and population processes on a threatened species' range shift. *Global Change Biology* **17**:17-31.
- Milchunas, D. G. and W. K. Lauenroth. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs* **63**:327-366.
- Moller, A. P., J. J. Soler, and M. M. Vivaldi. 2010. Spatial heterogeneity in distribution and ecology of Western Palearctic birds. *Ecology* **91**:2769-2782.
- Moore, F. R. 1978. Interspecific aggression: Toward whom should a mockingbird be aggressive? *Behavioral Ecology and Sociobiology* **3**:173-176.

- Murray, C. G., S. Kasel, R. H. Loyn, G. Hepworth, and A. J. Hamilton. 2013. Waterbird use of artificial wetlands in an Australian urban landscape. *Hydrobiologia* **716**:131-146.
- Murray, M. G. and A. W. Illius. 2000. Vegetation modification and resource competition in grazing ungulates. *Oikos* **89**:501-508.
- Nersesian, C. L., P. B. Banks, and C. McArthur. 2012. Behavioural responses to indirect and direct predator cues by a mammalian herbivore, the common brushtail possum. *Behavioral Ecology and Sociobiology* **66**:47-55.
- Newton, I. 1998. Population limitation in birds. Academic Press, London.
- Nolet, B. A., V. N. Fuld, and M. E. C. van Rijswijk. 2006. Foraging costs and accessibility as determinants of giving-up densities in a swan-pondweed system. *Oikos* **112**:353-362.
- Novozamsky, I., V. J. G. Houba, R. van Eck, and W. van Vark. 1983. "A novel digestion technique for multiple element plant analysis." *Communications in Soil Science and Plant Analysis* **14**:239-248.
- O'Brien, R. M. 2007. A caution regarding rules of thumb for variance inflation factors. *Quality & Quantity* **41**:673-690.
- Oloff, H., J. De Leeuw, J. P. Bakker, R. J. Platerink, H. J. Van Wijnen, and W. De Munck. 1997. Vegetation succession and herbivory in a salt marsh: changes induced by sea level rise and silt deposition along an elevational gradient. *Journal of Ecology* **85**:799-814.
- Oloff, H. and M. E. Ritchie. 2002. Fragmented nature: consequences for biodiversity. *Landscape and Urban Planning* **58**:83-92.
- Oloff, H., M. E. Ritchie, and H. H. T. Prins. 2002. Global environmental controls of diversity in large herbivores. *Nature* **415**:901-904.
- Owen-Smith, N. 2004. Functional heterogeneity in resources within landscapes and herbivore population dynamics. *Landscape Ecology* **19**:761-771.
- Owen, M. 1971. Selection of feeding site by White-Fronted Geese in winter. *Journal of Applied Ecology* **8**:905-917.
- Owen, M. and C. Cadbury. 1975. The ecology and mortality of swans at the Ouse Washes, England. *Wildfowl* **26**:31-42.

- Owen, M., M. Nugent, and N. Davies. 1977. Discrimination between grass species and nitrogen-fertilized vegetation by young barnacle geese. *Wildfowl* **28**:21-26.
- Palomino, D. and L. M. Carrascal. 2007. Threshold distances to nearby cities and roads influence the bird community of a mosaic landscape. *Biological Conservation* **140**:100-109.
- Partanen, S., M. Luoto, and S. Hellsten. 2009. Habitat level determinants of emergent macrophyte occurrence, extension and change in two large boreal lakes in Finland. *Aquatic Botany* **90**:261-268.
- Percival, S. M. 1993. The effects of reseeding, fertilizer application and disturbance on the use of grasslands by Barnacle Geese, and the implications for refuge management. *Journal of Applied Ecology* **30**:437-443.
- Petit, L. J. and D. R. Petit. 1996. Factors governing habitat selection by prothonotary warblers: Field tests of the Fretwell-Lucas models. *Ecological Monographs* **66**:367-387.
- Pezeshki, S. R., P. H. Anderson, and F. D. Shields. 1998. Effects of soil moisture regimes on growth and survival of Black Willow (*Salix nigra*) posts (cuttings). *Wetlands* **18**:460-470.
- Piao, S. L., A. Mohammat, J. Y. Fang, Q. Cai, and J. M. Feng. 2006. NDVI-based increase in growth of temperate grasslands and its responses to climate changes in China. *Global Environmental Change-Human and Policy Dimensions* **16**:340-348.
- Pickett, S. R. A. and G. M. Siriwardena. 2011. The relationship between multi-scale habitat heterogeneity and farmland bird abundance. *Ecography* **34**:955-969.
- Piper, W. H. 2011. Making habitat selection more "familiar": a review. *Behavioral Ecology and Sociobiology* **65**:1329-1351.
- Post, E. S. and D. R. Klein. 1996. Relationships between graminoid growth form and levels of grazing by Caribou (*Rangifer tarandus*) in Alaska. *Oecologia* **107**:364-372.
- Pouzols, F. M., T. Toivonen, E. Di Minin, A. S. Kukkala, P. Kullberg, and J. Kuustera, et al. 2014. Global protected area expansion is compromised by projected land-use and parochialism. *Nature* **516**:383-386.
- Pretorius, Y., J. D. Stigter, W. F. de Boer, S. E. van Wieren, C. B. de Jong, and H. J. de Knegt, et al. 2012. Diet selection of African elephant over time shows changing optimization currency. *Oikos* **121**:2110-2120.

- Prins, H. H. T. 1996a. Ecology and behaviour of the African buffalo : social inequality and decision making. Chapman & Hall, London.
- Prins, H. H. T. 1996b. Ecology and behaviour of the African buffalo: social inequality and decision making. Springer. 293 p.
- Prins, H. H. T. 2000. Competition between wildlife and livestock in Africa. Pages 51-80 Wildlife conservation by sustainable use. Springer.
- Prins, H. H. T., W. F. De Boer, H. Van Oeveren, A. Correia, J. Mafuca, and H. Olff. 2006. Co - existence and niche segregation of three small bovid species in southern Mozambique. African Journal of Ecology **44**:186-198.
- Prins, H. H. T., H. Olff, D. Newbery, and N. Brown. 1998. Species-richness of African grazer assemblages: towards a functional explanation. Pages 449-490 in Dynamics of tropical communities: the 37th symposium of the British Ecological Society, Cambridge University, 1996. Blackwell Science Ltd.
- Prins, H. H. T. and R. C. Ydenberg. 1985. Vegetation growth and a seasonal habitat shift of the barnacle goose (*Branta leucopsis*). Oecologia **66**:122-125.
- Prop, J. and T. Vulink. 1992. Digestion by barnacle geese in the annual cycle: the interplay between retention time and food quality. Functional Ecology **6**:180-189.
- Qvarnstrom, A., C. Wiley, N. Svedin, and N. Vallin. 2009. Life-history divergence facilitates regional coexistence of competing *Ficedula* flycatchers. Ecology **90**:1948-1957.
- Rappoldt, C., M. Kersten, and C. Smit. 1985. Errors in large-scale shorebird counts. Ardea **73**:13-24.
- Reiter, M. E. and D. E. Andersen. 2013. Evidence of territoriality and species interactions from spatial point-pattern analyses of subarctic-nesting geese. PLoS One **8(12)**: e81029.
- Reperant, L. A., N. S. Fuckar, A. D. M. E. Osterhaus, A. P. Dobson, and T. Kuiken. 2010. Spatial and temporal association of outbreaks of H5N1 influenza virus infection in wild birds with the 0 °C isotherm. PLoS Pathogens **6(4)**: e1000854.
- Richman, S. E., J. O. Leafloor, W. H. Karasov, and S. R. McWilliams. 2015. Ecological implications of reduced forage quality on growth and survival of sympatric geese. Journal of Animal Ecology **84**:284-298.

- Riddington, R., M. Hassall, and S. J. Lane. 1997. The selection of grass swards by brent geese *Branta b bernicla*: Interactions between food quality and quantity. *Biological Conservation* **81**:153-160.
- Risch, S. J. 1981. Insect herbivore abundance in tropical monocultures and polycultures - an experimental test of 2 hypotheses. *Ecology* **62**:1325-1340.
- Rodenhouse, N. L., T. W. Sherry, and R. T. Holmes. 1997. Site-dependent regulation of population size: A new synthesis. *Ecology* **78**:2025-2042.
- Root, R. B. 1973. Organization of a plant-arthropod association in simple and diverse habitats - Fauna of Collards (*Brassica-Oleracea*). *Ecological Monographs* **43**:95-120.
- Root, T. 1988. Energy constraints on avian distributions and abundances. *Ecology* **69**:330-339.
- Rosin, Z. M., P. Skorka, P. Wylegala, B. Krakowski, M. Tobolka, and L. Myczko, et al. 2012. Landscape structure, human disturbance and crop management affect foraging ground selection by migrating geese. *Journal of Ornithology* **153**:747-759.
- Schaible, D., C. D. Dieter, R. Losco, and P. Mammenga. 2005. Quantifying crop damage by giant Canada geese in Day County, South Dakota, 2003. Pages 259-264 in *Proceedings of the South Dakota Academy of Science*. South Dakota Academy of Sciences.
- Schoener, T. W. 1983. Field experiments on interspecific competition. *American Naturalist* **122**:240-285.
- Schott, J. R., C. Salvaggio, and W. J. Volchok. 1988. Radiometric scene normalization using pseudoinvariant features. *Remote Sensing of Environment* **26**:1-16.
- Schrama, M., P. Heijning, J. P. Bakker, H. J. van Wijnen, M. P. Berg, and H. Olf. 2013. Herbivore trampling as an alternative pathway for explaining differences in nitrogen mineralization in moist grasslands. *Oecologia* **172**:231-243.
- Searle, K. R., T. Vandervelde, N. T. Hobbs, and L. A. Shipley. 2005. Gain functions for large herbivores: tests of alternative models. *Journal of Animal Ecology* **74**:181-189.
- Sedinger, J. S. 1984. Protein and amino acid composition of tundra vegetation in relation to nutritional requirements of geese. *The Journal of Wildlife Management* **48**:1128-1136.

- Sedinger, J. S. and D. G. Raveling. 1984. Dietary selectivity in relation to availability and quality of food for goslings of Cackling geese. *The Auk* **101**:295-306.
- Shipley, L. A. 2007. The influence of bite size on foraging at larger spatial and temporal scales by mammalian herbivores. *Oikos* **116**:1964-1974.
- Shrestha, A. K., S. E. van Wieren, F. van Langevelde, A. Fuller, R. S. Hetem, and L. Meyer, et al. 2014. Larger antelopes are sensitive to heat stress throughout all seasons but smaller antelopes only during summer in an African semi-arid environment. *International Journal of Biometeorology* **58**:41-49.
- Shrestha, A. K. and S. E. van Wieren and F. van Langevelde and A. Fuller and R. S. Hetem and L. C. R. Meyer, et al. 2012. Body temperature variation of South African antelopes in two climatically contrasting environments. *Journal of Thermal Biology* **37**:171-178.
- Si, Y., A. K. Skidmore, T. Wang, W. F. de Boer, A. G. Toxopeus, and M. Schlerf, et al. 2011. Distribution of Barnacle Geese *Branta leucopsis* in relation to food resources, distance to roosts, and the location of refuges. *Ardea* **99**:217-226.
- Skellam, J. G. 1951. Random dispersal in theoretical populations. *Biometrika* **38**:196-218.
- Skorka, P., M. Lenda, R. Martyka, and S. Tworek. 2009. The use of metapopulation and optimal foraging theories to predict movement and foraging decisions of mobile animals in heterogeneous landscapes. *Landscape Ecology* **24**:599-609.
- Smith, H. G., J. Danhardt, A. Lindstrom, and M. Rundlof. 2010. Consequences of organic farming and landscape heterogeneity for species richness and abundance of farmland birds. *Oecologia* **162**:1071-1079.
- Smith, R. D., G. D. Ruxton, and W. Cresswell. 2001. Dominance and feeding interference in small groups of Blackbirds. *Behavioral Ecology* **12**:475-481.
- Snow, D., C. M. Perrins, and S. Cramp. 1998. The complete birds of the Western Palearctic on CD-ROM. Oxford CD-ROM. [Oxford University Press], [Oxford].
- Solomon, M. E. 1949. The natural control of animal populations. *Journal of Animal Ecology* **18**:1-35.
- Spalinger, D. E. and N. T. Hobbs. 1992. Mechanisms of foraging in mammalian herbivores; new models of functional response. *American Naturalist* **140**:325-348.

- Spiegelhalter, D. J., N. G. Best, B. R. Carlin, and A. van der Linde. 2002. Bayesian measures of model complexity and fit. *Journal of the Royal Statistical Society Series B-Statistical Methodology* **64**:583-616.
- Stillman, R. A., J. D. Goss-Custard, and R. W. G. Caldow. 1997. Modelling interference from basic foraging behaviour. *Journal of Animal Ecology* **66**:692-703.
- Stirnemann, R. L., J. O'Halloran, M. Ridgway, and A. Donnelly. 2012. Temperature-related increases in grass growth and greater competition for food drive earlier migrational departure of wintering Whooper Swans. *Ibis* **154**:542-553.
- Summers, R. W. and C. N. R. Critchley. 1990. Use of grassland and field selection by Brent Geese *Branta bernicla*. *Journal of Applied Ecology* **27**:834-846.
- Sutherland, W. J. and G. A. Allport. 1994. A Spatial Depletion Model of the Interaction between Bean Geese and Wigeon with the Consequences for Habitat Management. *Journal of Animal Ecology* **63**:51-59.
- Swanson, D. L. and K. L. Olmstead. 1999. Evidence for a proximate influence of winter temperature on metabolism in passerine birds. *Physiological and Biochemical Zoology* **72**:566-575.
- Tews, J., U. Brose, V. Grimm, K. Tielborger, M. C. Wichmann, and M. Schwager, et al. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography* **31**:79-92.
- Tingley, M. W., W. B. Monahan, S. R. Beissinger, and C. Moritz. 2009. Birds track their Grinnellian niche through a century of climate change. *Proceedings of the National Academy of Sciences of the United States of America* **106**:19637-19643.
- Tombre, I. M., E. Eythorsson, and J. Madsen. 2013. Towards a solution to the goose-agriculture conflict in north Norway, 1988-2012: The interplay between policy, stakeholder influence and goose population dynamics. *PloS One* **8(8)**: e71912.
- Vahl, W. K. 2006a. Interference competition among foraging waders. University of Groningen, Groningen, The Netherlands.
- Vahl, W. K. 2006b. Interference competition among foraging waders (PhD thesis). University of Groningen, Groningen, The Netherlands.
- van der Graaf, A. J., P. Coehoorn, and J. Stahl. 2006. Sward height and bite size affect the functional response of Barnacle geese *Branta leucopsis*. *Journal of Ornithology* **147**:479-484.

- Van der Veen, I., H. Van der Jeugd, and M. Loonen. 1999. Rain limits food supply of temperate breeding Barnacle Geese *Branta leucopsis*. *Wildfowl* **50**:57-67.
- Van der Wal, R. and M. J. J. E. Loonen. 1998. Goose droppings as food for reindeer. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **76**:1117-1122.
- Van der Wal, R., N. Madan, S. van Lieshout, C. Dormann, R. Langvatn, and S. D. Albon. 2000. Trading forage quality for quantity? Plant phenology and patch choice by Svalbard reindeer. *Oecologia* **123**:108-115.
- Van der Wal, R., J. van de Koppel, and M. Sagel. 1998. On the relation between herbivore foraging efficiency and plant standing crop: an experiment with barnacle geese. *Oikos* **82**:123-130.
- Van Dijk, J. G. B., S. Duijns, A. Gyimesi, W. F. de Boer, and B. A. Nolet. 2012. Mallards feed longer to maintain intake rate under competition on a natural food distribution. *Ethology* **118**:168-177.
- Van Gils, J. A., J. H. Beekman, P. Coehoorn, E. Corporaal, T. Dekkers, and M. Klaassen, et al. 2008. Longer guts and higher food quality increase energy intake in migratory swans. *Journal of Animal Ecology* **77**:1234-1241.
- Van Langevelde, F., M. Drescher, I. M. A. Heitkonig, and H. H. T. Prins. 2008. Instantaneous intake rate of herbivores as function of forage quality and mass: Effects on facilitative and competitive interactions. *Ecological Modelling* **213**:273-284.
- Van Wieren, S. E. 1998. Effects of large herbivores upon the animal community. Pages 185-214 *Grazing and conservation management*. Springer.
- Villen-Perez, S., L. M. Carrascal, and J. Seoane. 2013. Foraging patch selection in winter: A balance between predation risk and thermoregulation benefit. *PloS One* **8(7)**: e6844.
- Wang, X., A. D. Fox, P. H. Cong, and L. Cao. 2013a. Food constraints explain the restricted distribution of wintering Lesser White-fronted Geese *Anser erythropus* in China. *Ibis* **155**:576-592.
- Wang, X., Y. Zhang, M. J. Zhao, L. Cao, and A. D. Fox. 2013b. The benefits of being big: effects of body size on energy budgets of three wintering goose species grazing *carex* beds in the Yangtze River floodplain, China. *Journal of Ornithology* **154**:1095-1103.
- Wiens, J. A. 1989. The ecology of bird communities, (volume 2. Processes and variations). Cambridge Univ. Press, Cambridge.

- Wilmshurst, J. F. and J. M. Fryxell. 1995. Patch selection by red deer in relation to energy and protein-Intake - a reevaluation of langvatn and hanley (1993) results. *Oecologia* **104**:297-300.
- Wilmshurst, J. F., J. M. Fryxell, and C. M. Bergman. 2000. The allometry of patch selection in ruminants. *Proceedings of the Royal Society B-Biological Sciences* **267**:345-349.
- Wisiz, M. S., M. P. Tamstorf, J. Madsen, and M. Jespersen. 2008. Where might the western Svalbard tundra be vulnerable to pink-footed goose (*Anser brachyrhynchus*) population expansion? Clues from species distribution models. *Diversity and Distributions* **14**:26-37.
- Wretenberg, J., A. Lindstrom, S. Svensson, T. Thierfelder, and T. Part. 2006. Population trends of farmland birds in Sweden and England: similar trends but different patterns of agricultural intensification. *Journal of Applied Ecology* **43**:1110-1120.
- Wu, G., J. Leeuw, A. Skidmore, Y. Liu, and H. Prins. 2010. Comparison of extrapolation and interpolation methods for estimating daily photosynthetically active radiation (PAR). *Geo-spatial Information Science* **13**:235-242.
- Wu, G. F., J. de Leeuw, A. K. Skidmore, H. H. T. Prins, E. P. H. Best, and Y. L. Liu. 2009. Will the Three Gorges Dam affect the underwater light climate of *Vallisneria spiralis* L. and food habitat of Siberian crane in Poyang Lake? *Hydrobiologia* **623**:213-222.
- Wu, G. F., J. de Leeuw, A. K. Skidmore, H. H. T. Prins, and Y. L. Liu. 2007. Concurrent monitoring of vessels and water turbidity enhances the strength of evidence in remotely sensed dredging impact assessment. *Water Research* **41**:3271-3280.
- Xu, C., Z. Y. X. Huang, T. Chi, B. J. W. Chen, M. J. Zhang, and M. S. Liu. 2014. Can local landscape attributes explain species richness patterns at macroecological scales? *Global Ecology and Biogeography* **23**:436-445.
- Xu, J. C. and D. R. Melick. 2007. Rethinking the effectiveness of public protected areas in southwestern China. *Conservation Biology* **21**:318-328.
- Ydenberg, R. C. and H. H. T. Prins. 1981. Spring grazing and the manipulation of food quality by barnacle geese. *Journal of Applied Ecology* **18**:443-453.
- Zambatis, N., P. J. K. Zacharias, C. D. Morris, and J. F. Derry. 2006. Re-evaluation of the disc pasture meter calibration for the Kruger National Park, South Africa. *African Journal of Range & Forage Science* **23**:85-97.

- Zhang, J., W. D. Kissling, and F. L. He. 2013. Local forest structure, climate and human disturbance determine regional distribution of boreal bird species richness in Alberta, Canada. *Journal of Biogeography* **40**:1131-1142.
- Zhang, Q., J. Wu, Y. Sun, M. Zhang, B. Mai, and L. Mo, et al. 2014. Do bird assemblages predict susceptibility by E-Waste pollution? A comparative study based on species- and guild-dependent responses in China agroecosystems. *PloS One* **10**:e0122264-e0122264.
- Zhao, M., L. Cao, and A. Fox. 2010. Changes in within-winter distribution and diet of wintering Tundra Bean Geese *Anser fabalis serrirostris* at Shengjin Lake, Yangtze floodplain, China. *Wildfowl* **60**:52-63.
- Zhao, M. J., P. H. Cong, M. Barter, A. D. Fox, and L. Cao. 2012. The changing abundance and distribution of greater white-fronted geese anser albifrons in the Yangtze River floodplain: impacts of recent hydrological changes. *Bird Conservation International* **22**:135-143.
- Zuckerberg, B., D. N. Bonter, W. M. Hochachka, W. D. Koenig, A. T. DeGaetano, and J. L. Dickinson. 2011. Climatic constraints on wintering bird distributions are modified by urbanization and weather. *Journal of Animal Ecology* **80**:403-413.

Summary

Habitat selection is a process in which organisms decide to choose a suitable site for nesting, roosting or foraging. The question where the organisms are, and when they will leave are two of the fundamental questions frequently asked by ecologists. Habitat selection is affected by various abiotic and biotic determinants, varying over different spatial and temporal scales. In addition, an animal's body size, determining its daily demands and its digestion capacity, plays an important role in foraging and habitat selection. This is because forage quality often decreases with increasing forage quantity. Therefore, herbivores often face a trade-off between forage quality and quantity. Although studies on habitat selection have offered substantial insights into the effect of various ecological factors, myriad effects of habitat and its' surrounding are still not clearly understood, as former studies concerning this topic normally focus on a single species or a single spatial scale.

Migrating goose species are herbivorous with more or less similar habitat requirements and hence often mix in the field. Studying habitat selection of different goose species is attractive as they are from the same guild but differ in body size. In this thesis, I study the effects of various variables on habitat selection of different Anatidae species over different spatial scales, answering the question how ecological and anthropogenic variables affect Anatidae species habitat selection and population sizes and if these effects vary over different spatial scales.

First, I studied the habitat selection of Anatidae species under the condition with and without interference competition using an experimental approach in Chapter 2. To do this, I offered geese and ducks foraging patches with various swards heights. My results showed that all three species acquired the highest nitrogen intake at relatively tall swards (on 6 or 9 cm, but not on 3 cm) when foraging in single species flocks in the functional response experiment. When they were offered foraging patches differing in sward height with and without competitors, their mean percentage of feeding time did not change, whereas all species increased their percentage of time being vigilant except

for the dominant swan goose. All species utilized strategies that increased their peck rate on patches across different sward heights when foraging together with other species, resulting in the same instantaneous and nitrogen intake rate than when foraging in a single species flocks. My results suggest that variation in peck rate over different swards height permits Anatidae herbivores to increase nitrogen intake under competition to compensate for the loss of intake, illustrating the importance of behavioural plasticity in heterogeneous environments when competing with other species for resources.

In Chapter 3, using a correlative field study, I analysed the habitat selection of two differently sized grazing goose species at site level. I found that both species selected lower lying area where the swards became recently exposed, due to receding water levels. However, the smaller species was more sensitive to this elevation gradient. Moreover, sward height negatively affected both species habitat selection with a stronger effect on the smaller species. This result highlighted the importance of body size on facilitating species coexistence and habitat segregation. Not in agreement with the results from most experimental studies, I found that nitrogen content did not influence habitat selection of both species. This conflicting result suggests that additional factors should be carefully considered when applying outcomes from experimental studies to field situations.

In Chapter 4, I studied habitat selection of the two goose species at a lake level by analysing the effect of ecological and anthropogenic variables. My results supported the individual-area relationship as only patch area had a significant effect on both species habitat selection, and other variables that were related to food availability and disturbance, were not significant. In addition, a facilitation effect of grazing livestock on geese habitat selection was detected, indicating that larger grazing herbivores can facilitate geese foraging by removing the taller and lower quality food from the top. As patch area size in wetlands is directly linked to water levels fluctuations, this result demonstrated that modifying hydrological regimes can enlarge the capacity of wetlands for migratory birds.

In Chapter 5, I further expanded my study area to the flood plain level of the Yangtze, testing for the effect of various abiotic and biotic variables on several Anatidae species habitat selection and population trends. I showed that slope and climate factors were the most important ones affecting habitat selection and distribution of Anatidae species. Furthermore, I demonstrated that the current protection policies may not stop

the declining population trends but might buffer to some extent against a rapid decline in numbers in wetlands with a higher level protection status. This result points out that the conservation effectiveness is still low and larger conservation efforts are urgently needed to maintain the Anatidae populations, especially in wetlands with a lower level protection status. I recommend several protection measures to stop the decline of Anatidae species in wetlands of the Yangtze River flood plain and I called for more research efforts in this area in particularly, but also at a larger scale, the entire East Asian-Australasian Flyway.

In Chapter 6, I synthesized these results and draw conclusions from the preceding chapters, and highlighted the importance of spatial scales when studying the effect of abiotic and biotic variables on animals' habitat selection. I also propose to modify hydrological regimes, aimed at creating enhanced habitat and improved forage accessibility conditions over the entire wintering period for herbivorous birds species in the Yangtze River flood plain. In summary, this thesis offers a framework for the effects of various variables on habitat selection and population sizes of herbivorous Anatidae species over different spatial scales, and a scientific basis for policy-makers and managers to enhance the efficiency of conservation actions in wetlands along the Yangtze River flood plain and also for similar ecological systems.

Samenvatting

Habitatselectie is een proces waarbij organismen een bepaald habitat kiezen om zich te nestelen, te roesten of te foerageren. De vraag hoe organismen zich over de ruimte verdelen en wanneer zij een bepaalde plek verlaten zijn twee fundamentele vragen die veelvuldig door ecologen gesteld worden. Habitatselectie wordt beïnvloed door diverse abiotische en biotische factoren die variëren over verschillende ruimtelijke en temporale schalen. Daarnaast speelt de lichaamsgrootte, die de dagelijkse vraag naar voedsel en de verteringscapaciteit bepaalt, een belangrijke rol in foerageren en habitatselectie, omdat voedingskwaliteit vaak afneemt met kwantiteit. Hierdoor worden herbivoren meestal geconfronteerd met een *trade-off* tussen voedingskwaliteit en –kwantiteit. Hoewel studies over habitatselectie belangrijke inzichten hebben opgeleverd over het effect van diverse ecologische factoren, blijven een groot aantal effecten van het habitat en de omgeving grotendeels onduidelijk aangezien eerdere studies voornamelijk de nadruk legden op slechts één soort of op één ruimtelijk dimensie.

Migrerende ganzensoorten zijn herbivoren met ongeveer dezelfde habitatvereisten en mengen zich daarom vaak in het veld. Het bestuderen van habitatselectie van verschillende ganzensoorten is aantrekkelijk aangezien ze tot eenzelfdeilde behoren maar verschillen in lichaamsgrootte. In dit proefschrift bestudeer ik de effecten van diverse variabelen op de habitatselectie van verschillende Anatidae soorten over verschillende ruimtelijk schalen. Hierdoor kan ik de vraag beantwoorden hoe ecologische en antropogene variabelen de habitatselectie en populatiegroottes van deze soorten beïnvloeden en of deze effecten variëren over verschillende ruimtelijke schalen.

Eerst bestudeerde ik de habitatselectie van deze Anatidae via een experimentele aanpak waarin ik de habitatselectie bestudeerde met en zonder interferentiecompetitie (Hoofdstuk 2). Hiervoor bood ik ganzen en eenden foerageerplekken aan met verschillende grashoogtes. Mijn resultaten lieten zien dat alle drie soorten de hoogste stikstofopname kregen in een relatief hoge grasmat (van 6 of 9

cm, maar niet in die van 1 of 3 cm) wanneer zij foerageerden in groepen bestaande uit één soort tijdens het functionele respons experiment. Wanneer zij foerageerplekken aangeboden kregen met en zonder concurrenten, veranderde het gemiddelde percentage foerageertijd niet, terwijl alle soorten een toename vertoonden in de tijd dat zij waakzaam waren, met uitzondering van de dominante zwaangans. Alle soorten verhoogden hun piksnelheid op foerageerplekken van verschillende grashoogte wanneer zij foerageerden met andere soorten, wat resulteerde in dezelfde directe opnamesnelheid van stikstof dan wanneer zij foerageerden in groepen bestaande uit één soort. Mijn resultaten suggereren dat variatie in piksnelheid over verschillende grashoogtes deze Anatidae herbivoren toelaat om hun stikstofopname te compenseren voor het verlies wat optreedt onder voedselcompetitie met andere soorten. Dit illustreert het belang van plasticiteit in gedrag in heterogene omgevingen wanneer diverse soorten concurreren om hulpbronnen.

In Hoofdstuk 3, een correlatieve veldstudie, analyseerde ik de habitatselectie van twee grazende ganzensoorten van verschillende grootte op *site* niveau. Ik ontdekte dat beide soorten het lager gelegen gebied selecteerden waar het gras recent was vrij gekomen na daling van het waterpeil. De kleine ganzensoort was echter gevoeliger voor deze hoogtegradiënt. Daarnaast had grashoogte een negatief effect op de habitatselectie van beide soorten met een sterker effect op de kleinere soort. Dit resultaat illustreert het belang van lichaamsgrootte in het faciliteren van co-existentie van soorten en habitatsegregatie. Ik vond ook dat stikstofgehalte geen invloed had op habitatselectie van beide soorten, wat niet in overeenstemming is met de meeste andere experimentele studies. Deze tegenstrijdige resultaten suggereren dat bijkomende factoren zorgvuldig in overweging genomen moeten worden wanneer men resultaten van experimentele studies wil toepassen op veldsituaties.

In Hoofdstuk 4 bestudeerde ik habitatselectie van twee ganzensoorten rondom het Shengjin meer door het effect van ecologische en antropogene variabelen te analyseren. Mijn resultaten lieten zien dat enkel gebiedsgrootte een significant effect had op de habitatselectie van beide soorten en andere variabelen, die gerelateerd zijn aan voedselbeschikbaarheid en verstoring, niet significant waren. Er werd ook een facilitair effect gevonden van grazend vee op de habitatselectie van ganzen. Dit geeft aan dat grotere grazende herbivoren het foerageren van ganzen kunnen faciliteren door langer gras van mindere kwaliteit te verwijderen. Aangezien gebiedsgrootte in natte gebieden

direct verbonden is met fluctuaties in het waterpeil, toont dit resultaat aan dat het aanpassen van hydrologische regimes de capaciteit van natte gebieden voor migrerende vogels kan vergroten.

In Hoofdstuk 5 breidde ik mijn studiegebied uit naar meerdere meren langs de Yangtze, om het effect van diverse abiotische en biotische variabelen op de habitatselectie en populatie trends van verscheidene Anatidae soorten te testen. Ik toonde aan dat helling van de bodem en klimaat de belangrijkste invloeden hadden op de habitatselectie en de verspreiding van Anatidae soorten. Daarnaast demonstreerde ik dat het huidige beschermingsbeleid de afnemende populatietrends niet kan stoppen, maar mogelijk wel kan bufferen tegen snellere afnames door een hoger beschermingsniveau in te stellen. Deze resultaten tonen ook aan dat de effectiviteit van natuurbehoud in China nog steeds laag is en dat betere maatregelen dringend nodig zijn om de Anatidae populaties te behouden, voornamelijk in natte gebieden met een lager beschermingsniveau. Ik beveel verschillende beschermingsmaatregelen aan om de afname van Anatidae soorten in de natte gebieden van de Yangtze rivierbedding te remmen en ik adviseer om meer onderzoek te ondernemen in dit gebied, maar ook op een grotere schaal, namelijk de volledige vliegroute van migrerende vogels in Oost Azië en Australië.

In Hoofdstuk 6, combineer ik deze resultaten en trek ik conclusies uit de voorgaande hoofdstukken. Ik benadruk het belang van ruimtelijke schalen in de studie van abiotische en biotische factoren op habitatselectie. Ik stel ook voor om de huidige hydrologische regimes aan te passen, gericht op het creëren van uitgebreider habitat en betere voedselbeschikbaarheid tijdens de volledige winterperiode voor herbivore vogelsoorten rondom de Yangtze rivier. Samengevat, dit proefschrift biedt een omkadering om de effecten van diverse variabelen op habitatselectie en populatiegrootte van herbivore Anatidae soorten op verscheidene schalen te bestuderen, en een wetenschappelijke basis voor beleidsmakers en managers om de efficiëntie van natuurbehoudsacties in natte gebieden langs de Yangtze rivier, alsook in gelijksoortige ecologische systemen, te verbeteren.

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Curriculum vitae

Yong Zhang was born on 28 September, 1983 in Hongze, Jiangsu Province, China. In 2007, he obtained his BSc degree at Shannxi Normal University in Xi'an, China. After that, he became a MSc student at University of Science and Technology of China in Hefei, China.

For his MSc thesis project he studied swan goose distribution and behaviour ecology in the Yangtze flood plain, supervised by Prof. Dr. Lei Cao. He showed that the population size of swan goose had dramatically decreased and the decreasing trend was well explained by the collapse of submerged macrophytes.

After obtaining his MSc degree at University of Science and Technology of China in 2010, he was selected by CAS-KNAW joint PhD Training Programme and moved to Wageningen University to start a PhD at the Resource Ecology Group under the supervision of Prof. Dr. Herbert Prins and Dr. Willen Frederik De Boer. His PhD research focused on geese species habitat selection in the wetlands of Yangtze floodplain. The results of his research culminated in this thesis.



List of Publications

- Y. Zhang**, H.H.T. Prins, L. Cao, Zhao, M. J. & W.F. De Boer. Variation in elevation and sward height facilitate coexistence of goose species through allometric responses in wetlands. *Waterbirds* (Accepted).
- Y. Zhang**, Q. Jia, H.H.T. Prins, L. Cao, & W.F. De Boer. 2015. Effect of conservation efforts and ecological variables on waterbird population sizes in wetlands of the Yangtze River. *Scientific reports* 5, 17136.
- Y. Zhang**, Q. Jia, H.H.T. Prins, L. Cao, & W.F. De Boer. 2015. Individual-area relationship best explains goose species density in wetlands. *PLoS ONE* 10(5): e0124972.
- M. J. Zhao, L. Cao, M. Klaassen, **Y. Zhang** & A.D. Fox. 2015. Avoiding competition? Site use, diet and foraging behaviour in two similarly sized avian herbivores wintering in China. *Ardea* 103: 27–38.
- X. Wang, **Y. Zhang**, M.J. Zhao, L. Cao & A.D. Fox. 2013. The benefits of being big: effects of body size on energy budgets of three wintering goose species grazing *Carex* beds in the Yangtze River floodplain. *Journal of ornithology* 154: 1095–1103.
- Y. Zhang**, L. Cao, M. Barter, A.D. Fox, M.J. Zhao, M. F.J. Meng, H.Q. Shi, Y. Jiang & W.Z. Zhu. 2011. Changing distribution and abundance of Swan Geese *Anser cygnoides* in the Yangtze River floodplain: the likely loss of a very important wintering site. *Bird Conservation International* 21: 36–48.
- A.D. Fox, L. Cao, **Y. Zhang**, M. Barter, M.J. Zhao, F.J. Meng & S.L. Wang. 2011. Declines in the tuber-feeding waterbird guild at Shengjin Lake National Nature Reserve, China – a barometer of submerged macrophyte collapse. *Aquatic Conservation: Marine and Freshwater Ecosystems* 21: 82–91.
- L. Cao, M. Barter, M.J. Zhao, H.X. Meng. & **Y. Zhang**. 2011. A systematic scheme for monitoring waterbird populations at Shengjin Lake, China: methodology and preliminary results. *Chinese Birds* 2: 1–17.
- L. Cao, **Y. Zhang**, M. Barter & G. Lei. 2010. Anatidae in eastern China during the non-breeding season: geographical distributions and protection status. *Biological Conservation* 143: 650–659.

- A.D. Fox, R.D. Hearn, L. Cao, P.H. Cong, X. Wang, **Y. Zhang**, S.T. Dou, X.F. Shao, M. Barter, & E.C. Rees. 2008. Preliminary observations of diurnal feeding patterns of Swan Geese *Anser cygnoides* using two different habitats at Shengjin Lake, Anhui, Province, China. *Wildfowl* 58: 20–30.
- A.D. Fox, L. Cao, M. Barter, E.C. Rees, R.D. Hearn, P.H. Cong, X. Wang, **Y. Zhang**, S.T. Dou & X.F. Shao. 2008. The functional use of East Dongting Lake by five populations of geese. *Wildfowl* 58: 5-19.

PE&RC PhD Education Certificate

With the educational activities listed below the PhD candidate has complied with the educational requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)



Review of literature (6 ECTS)

- Forage quality and quantity of grazing herbivores (2010/2011)

Writing of project proposal (4.5 ECTS)

- The impact of water level, forage quality and quantity on Anatidae distribution.

Post-graduate courses (5.7 ECTS)

- Linear model, PE&RC (2010)
- Mixed linear model, PE&RC (2010)
- Generalized linear models, PE&RC (2010)
- The art of modelling, PE&RC (2010)
- Introduction to R for statistical analysis, PE&RC (2012)

Deficiency, refresh, brush-up courses (3 ECTS)

- Ecological methods I (2010)

Competence strengthening / skills courses (4.4 ECTS)

- PhD competence assessment, WGS (2010)
- Mobilising your scientific network, WGS (2010)
- Review a scientific paper, WGS (2012)
- Techniques for writing and presenting a scientific paper, WGS (2012)
- Scientific writing, WGS (2013)

PE&RC Annual meetings, seminars and the PE&RC weekend (1.2 ECTS)

- PE&RC Weekend, (2013)
- PE&RC Day, (2013)
- PE&RC Symposium: the search for tipping points in heterogeneous landscapes, (2013)

Discussion groups / local seminars / other scientific meetings (6 ECTS)

- Ecological theory and application, (2010/2014)
- Ecology department meetings (University of Science & Technology of China. USTC), (2010/2013)
- Wageningen Evolutionary and Ecology Seminar (WEES) (2010/2014)

International symposia, workshops and conferences (6.6 ECTS)

- International Conference on Individual Differences, Groningen, the Netherlands (poster presentation) (2013)
- Netherlands Annual Ecology Meeting (NAEM), Lunteren, the Netherlands (poster presentation) (2013)
- The 16th meeting of the Goose Specialist Group, Beijing, China (oral talk) (2014)

Supervision of MSc student; 180 days (3 ECTS)

- Feeding patch selection and intake rate by herbivores Anatidae species: the influence of inter-specific competition (Martijn Versluijs)
- Feeding patch selection in differently sized geese species in relation to swards height and nitrogen content (Rick Wessels)

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