Latitudinal patterns of species diversity, body mass and herbivory: a comparison between ectotherms and endotherms

Rosanne Beukeboom

October 15, 2013

Writing assignment master "Environmental Biology", University of Utrecht

Summary

Earth varies widely in characteristics along her latitude, like temperature, precipitation and day length. This has consequences for life along this latitude. In this research, a comparison is made between ectotherms (here fish) and endotherms (here fresh water birds) and how their distribution and plant consumption is influenced by latitudinal patterns of temperatures. I collected data from the encyclopedia of Kear (2005), an article from Wood *et al.* (2012) and a selection of research papers to create a database of 84, mostly migrating, fresh water bird species, along with their body mass, percentage of vegetal matter in their diet, average latitude and average temperature of their summer breeding area and winter non-breeding area. I compared these data with published patterns for fresh water fish from Gonzalez-Bergonzoni *et al.*, 2012. I drew four main conclusions: (1) Fish seem to follow the general latitudinal pattern of increasing species richness towards lower latitudes, while the number of species of fresh water bird species increases towards higher latitudes. (2) Fish seem to be smaller at lower latitudes, following the temperature-size rule, while no such pattern was found for water birds. (3) Heavier birds (3 kg or more) are almost exclusively herbivore, while lighter birds have a variety of diets. (4) Fish show a higher degree of herbivory towards lower latitudes. A specific part of my data of birds with a diet that consisted of at least 1%, but not more than 50% of vegetable matter, showed a pattern of a higher degree of herbivory towards higher latitudes and lower temperatures. Correlations of other birds with no or more than 50% of vegetable matter in their diet and latitude or temperature were not significant.

The reversed latitudinal gradients found for fish and water birds may be due to differences in migratory behavior and thermoregulation. Most ectotherms do not migrate, do not form a protection to extreme temperatures, and are not able to control their body temperature as well as endotherms. Both fish and birds may eat more vegetal matter when having a higher metabolism: fish at higher temperatures, because of competition and their ability to digest vegetable matter better at higher temperatures and birds at lower temperatures, because of the useful expulsion of extra C. Because of limitation in my dataset, further research is needed to confirm this.

Introduction

Earth varies widely in characteristics along her latitude, because of uneven distributed solar insolation and the rotation around her own axis. These characteristics are influenced by the effects of this uneven distribution, for example (1) the equator receives much more heat radiation than both of the poles, where mid-latitude receives more heat in summer than in winter. (2) This in turn causes extreme seasonal changes and also climate differences along latitude, from warm and wet conditions around the equator, to dry and cold conditions towards the poles. (3) Day length differs with latitude, with more days of the same length towards the equator and extreme conditions around the poles with 24 hours of light in summer and no light at all in winter (Garrison, 2010).

These characteristics have a big influence on life on earth, especially on the distribution of life. First, day length influences this distribution. An example of this is the positive correlation between lower clutch sizes in birds and shorter day lengths, because of less available time for feeding (Rose & Lyon, 2013). Secondly, the reduced solar insolation at the poles is responsible for a lower primary productivity, because of low light penetration into the water and low temperatures which reduces metabolism (Garrison, 2010). Many animals are secondary producers and rely on those primary producers as their nutrition source. This is why not much life is found around the poles, while the number of species is increasing towards the equator, where enough light and higher temperatures are present (Hillebrand, 2004). This pattern occurs from the smallest to the biggest forms of life: from bacteria, viruses and trees to invertebrates and vertebrates and occurs in endotherms as well as in ectotherms. A selection of examples are decapod species (McCallum *et al.*, 2013) such as fiddler crabs (Levinton & Mackie, 2013), dormouse tufted-tailed rats (Shi *et al.*, *in press*), fish (Hillebrand *et al.*, 2009), bats (Ramos Pereira & Palmeirim, 2013), bacterioplankton (Pommier *et al.*, 2007) and birds (Somveille *et al.,* 2013), which all show increased species richness towards the equator. Although it is clear that light and temperature are important factors that may explain this pattern, also other factors can influence the latitudinal diversity. For example, geographic boundaries (Colwell & Lees, 2000) and historical factors like niche conservatism, where organisms stay in their original habitat even when environmental conditions change (Ricklefs, 2007), can influence the latitudinal diversity gradient. Thirdly, the differences in temperature along latitude have a different effect on ectotherms (animals that rely on their environment for heat absorption to perform their metabolism) than on endotherms (animals that produce their own heat to perform their metabolism). Ectotherms are much more bound by the available heat radiation in a certain habitat than endotherms. This is an example of how temperature can influence the distribution of life.

This dependence on light and temperature, and the predictability of those factors along latitude, are responsible for more specific patterns along latitude at least for ectotherms. One pattern found in ectothermic fish is a decreasing percentage of vegetal matter in their diet towards higher latitudes (Gonzalez-Bergonzoni *et al.*, 2012). Because of their ectothermy, their body temperature increases with increasing environmental temperatures, and together with this, their metabolism increases exponentially (Brown *et al*., 2004). Since a higher metabolism requires more energy, their intake should increase too (Hillebrand, 2009; Edeline, *et al.,* 2013) or they should switch their diet to a more nutritional food source. A fish can only increase their ingestion with a certain amount, which leaves reasons enough to choose for high quality animal matter. But for some reason they do not choose for this higher quality, but for the lower quality of plants (Horn, 1989, Gonzalez-Bergonzoni *et al.*, 2012). This choice and the need for more energy at higher temperatures has effect on their body mass. Fish in tropical regions have a lower mean body mass than those of species at higher latitudes (Teixeira-de Mello *et al.*, 2012). So why are fish accepting a lower body mass by choosing for plants instead of animal matter? First, a lower mean body also seems to have advantages, especially for ectotherms in warmer regions. With a smaller surface/volume ratio, it is easier to absorb heat conform the so called temperature-size rule (Edeline *et al.,* 2013). This rule is based on the same principle of the Bergmann's rule for endotherms (Bergmann, 1847), which also seems to apply to ectotherms. Also, a lower body mass means a higher net energy gain in comparison with heavier fish (Edeline *et al.,* 2013). Second, it seems that fish perform better at higher temperatures when choosing for low quality vegetal matter (Behrens & Lafferty, 2006). The most important factor seems to be competition. As mentioned before, there are more fish species towards the equator, but also the absolute number is higher than at higher latitudes (Gonzalez-Bergonzoni *et al.*, 2012). On top of this comes the higher intake per fish at higher temperatures. This increases the predation on plants as well as on animals like crustaceans. As plants are abundant and crustaceans are not, they are forced to live on vegetal matter (Gonzalez-Bergonzoni *et al.*, 2012). But their ectothermy and the high environmental temperatures also offers them the possibility to digest vegetal matter better than at lower temperatures, as this matter is easier to digest at higher temperatures (Behrens & Lafferty, 2006). It seems there has been a selection against animal matter in the diet of fish at lower latitudes, because of competition and their dependence on external temperatures.

How do those explanations apply to endotherms, as they are not so dependent on their environmental temperature? As mentioned before, the number of endotherm species also increases towards the equator, but as their body temperature is kept constant by the body itself, they are not dependent on their surrounding temperatures for their metabolism. This also means that their metabolism does not increase with higher temperatures. Actually, their metabolism acts the opposite way at colder temperatures as they have to increase their metabolism to keep their relatively high body temperature of 36 °C to 40 °C constant (Brown *et al.,* 2004). This will have implications for their feeding strategies and body mass at different latitudes.

In this research, I used data from fresh water birds as an example of endotherms. Their habitat and diet overlaps with fresh water fish species and their body temperatures are the highest among endotherms. This leads to the highest contrast with ectotherms, which body temperatures almost never rise above 30 °C (Brown *et al.,* 2004). I tried to find possible latitudinal patterns of body mass and herbivory in endotherms and also map diversity along latitude for this group of birds. I started with a subset of waterfowl from Wood *et al*. (2012) and expanded this with two more water bird families. I used this database to test the following four hypotheses.

(1) The absolute number of fresh water bird species increases with decreasing latitude as is found for many other species (Hillebrand, 2004).

(2) Fresh water birds are heavier towards higher latitudes, because with a larger surface/volume ratio of the body, less heath is lost (Bergman, 1847; Ramirez *et al.,* 2008). This gradient is stronger in winter (non-breeding period) than in summer (breeding period), because of more extreme differences in temperature in summer than in winter (Ramirez *et al.,* 2008). Furthermore, the assumption is that they are not limited in their growth (hypothesis 3 & 4) and latitude is related to temperature with higher temperatures at lower latitudes and vice versa.

(3) Herbivory is more common in heavier fresh water birds and less common in lighter fresh water birds. This is based on three assumptions. (1) Metabolism increases with increasing body mass (Brown *et al*., 2004; McKechnie, 2008), (2) the possibility to digest vegetal matter easier, because heavier birds have a longer gut, which allows vegetal matter to stay longer in the gut and thereby more time to be digested (Kooijman, 2000, chapter 8) and (3) heavier birds can ingest larger amounts of low quality vegetal matter when needed to meet their energy requirements, because they have a bigger stomach than smaller birds (Kooijman, 2000, chapter 8).

(4) Herbivory is more common in fresh water bird species at higher latitudes and lower temperatures, with an increasing percentage of vegetal matter in diets of omnivory fresh water birds towards higher latitudes and lower temperatures. This is based on the following three assumptions.

(1) Endotherms have a higher metabolism in colder regions in order to maintain their body heat (Anderson & Jetz, 2005). (2) Vegetal matter has a high C:N ratio. The expulsion of high amounts of C is beneficial for heat production (Klaassen & Nolet, 2008). (3) Latitude is related to temperature with higher temperature at lower latitudes and vice versa.

If hypothesis two, three and four seem to be true, I have to investigate if all those hypotheses stand on their own or if one hypothesis follows logically out of any of the other hypotheses.

I collected data of 84 fresh water birds species to test the hypotheses and concluded that there is a pattern of increasing number of fresh water birds species towards higher latitudes, that body mass is not related to latitude, while there is evidence that the degree of herbivory is and that heavier birds are mostly herbivore, while lighter birds have a variety of diets.

Methods

Collecting data

To determine the presence of water fowl species (*Anseriformes)* along latitude worldwide, a distribution map of the number of species worldwide was used from the encyclopedia from Kear 2005 (p. 21). The number of species was averaged per every ten degrees of latitude. To determine the relations between herbivory, body mass, latitude and temperature, I started with the supplementary material from Wood *et al*. (2012), which consists of a list of water fowl (Geese (n=16), Swans (n=6), Sheldgeese (n=5), Ducks (n=34) and Screamers (n=3)), their mean weight and the percentage of plants (including green tissue, tubers and seeds) in their diet. The rails (*Rallidae*) from the original data set were excluded from my analysis, because it was unclear which role they played in and around the water and what water meant to their diet. I expanded this set with diet data from more species of water birds: Cormorants (*Phalacrocoracidae*, n=10) and Grebes (*Podicipedidae,* (n=10), total data set n=84). Extinct species and marine species were excluded and only diet information of adult birds was used. Data came from articles found through Google Scholar and Scopus (see Supplementary material) and the encyclopedia of Kear (2005). The worldwide distribution of every species was collected through the IUCN Red list website and the encyclopedia of Kear (2005). For every species average latitude of their breeding area (summer) and non-breeding area (winter) were determined though Google maps, where the degrees of latitude were rounded to the nearest .5 or .0 degree. There was no division made between the positive of the northern latitudes and southern negative latitudes, for example -50 on the southern hemisphere became a latitude of 50, while 50 on the northern hemisphere stayed the same. Furthermore, the average temperatures (C°) for breeding season and non-breeding season were determined through the website with climate information of the Delaware University Website (http://climate.geog.udel.edu/~climate/). The average temperature of July, 2005 was used as summer on the northern hemisphere and as winter on the southern hemisphere, where January, 2005 was used the other way around. Those months were chosen, because they had the most extreme temperatures for the season, the year 2005 was chosen because most collected data came from around this period of time.

The collected data was compared with a study from Gonzalez-Bergonzoni *et al.* (2012). They investigated the distribution of fish species along latitude and the degree of herbivory in their diet along latitude by performing a meta-analysis of published data. They included, but distinguished, fresh water, estuarine and marine ecosystems. Diet of included fish consisted of at least 1% of vegetal matter.

Statistics

To determine the relation between latitude and temperature, a Pearson correlation was performed. Because they were highly correlated (Pearson Correlation, $r=0.76$, $p<0.001$, $n=84$), I assumed that temperatures increased towards lower latitudes and therefore only included latitude in the graphs, unless temperatures were significant, where latitudes were not. Regression graphs and scatter plots were made in Excel and IBM SPSS 20.

Number of water bird species against latitude was determined by performing a Pearson correlation, using the absolute latitudes, with the outlier on 90° left out, because of too hard conditions to live in.

The relation between body mass and latitude/temperature was determined by performing Pearson correlations between different feedings modes. Because of uneven distribution of body mass as well as of the degree of herbivory, an Independent sample T-test was performed using the natural logarithm of the body mass and the herbivore data divided in two groups. One division was made between 1-50% and >50% of vegetal matter in their diet (group 1), another division was made between 0% (carnivores) and >1% (omnivores and herbivores) vegetal matter in their diet (group 2). Both groups were independently correlated with latitude and temperature in summer and winter.

The relation between body mass and the degree of herbivory was determined by performing a logistic regression with the mentioned group 1 and also the natural logarithm of the body mass. Because all the heavy birds (> 3kg) in my data set, with almost 100% of vegetal matter in their diet were belonging to the same genus of swans, I made a more specific comparison within the genus of ducks (*Anatidae*), where weights and percentage of herbivory were more distributed (min/max weight 374/2140 grams, min/max herbivory 10.5/100%).

The relation between herbivory and latitude/temperature was determined by performing a Pearson correlation in the same way as it was performed during the analysis of the relation between body mass and latitude/temperature. I performed also a binary logistic regression between the subgroups of group 2 (carnivores (0% of vegetal matter in their diet) and omnivores/herbivores (more than 1% of vegetal matter in their diet) and latitude and temperature.

Results

Number of water fowl species along latitude

The average number of water fowl species increases from low latitudes to high latitudes, with a sharp decrease around 80° till 90° on the northern hemisphere and a smaller decrease at -40° at the southern hemisphere. This increasing pattern is weaker on the southern hemisphere (Fig. 1). Those results are in contrast with fish, where the absolute number of fish is increasing towards lower latitudes (Gonzalez *et al.,* 2012; Fig. 2A). With the 90° outlier on the northern hemisphere left out, because of too cold conditions to live in, a positive significant correlation is found between an increasing number of water fowl species and increasing latitude (Pearson correlation, r=0.76, p<0.01, Fig. 2B).

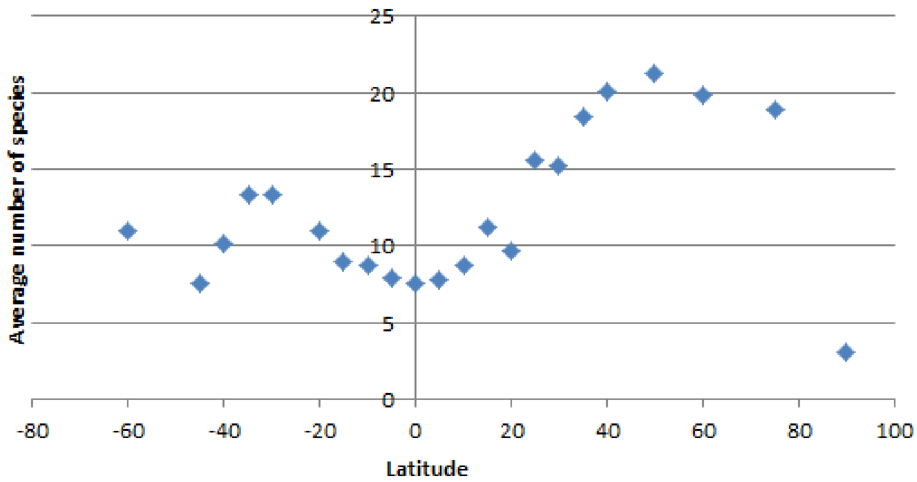

Fig. 1. Distribution of water fowl species along latitude (based on data from Kear, 2005, p. 21)

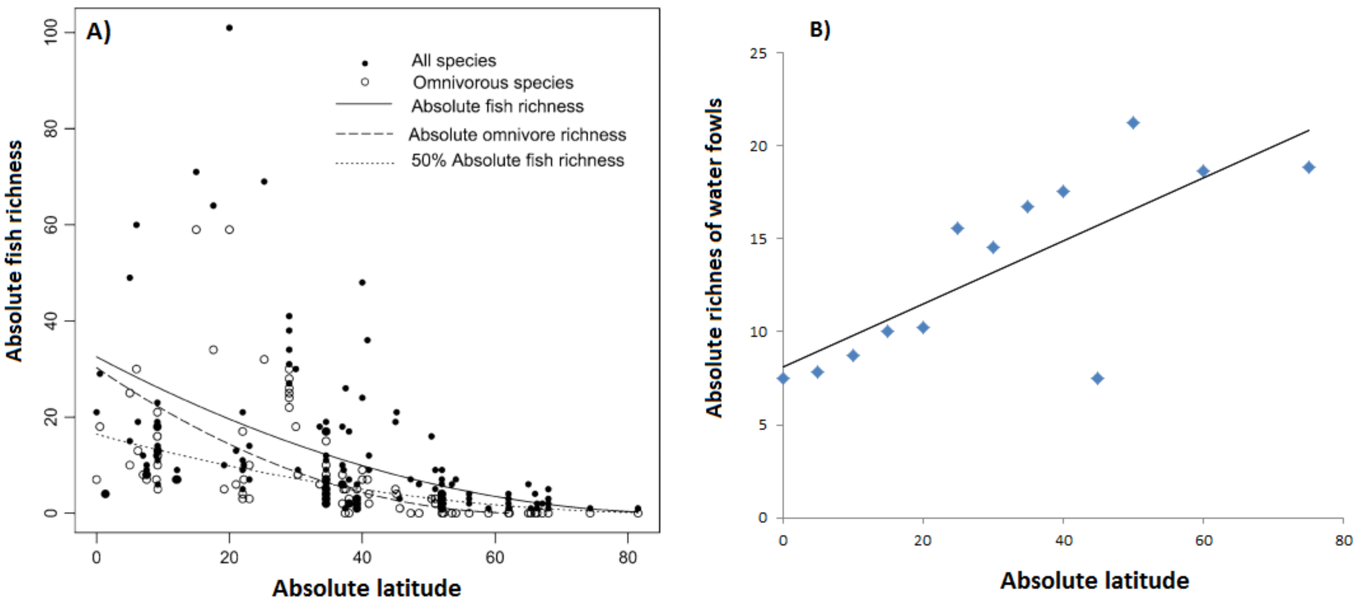

Fig. 2. Comparison of fish species and bird species which diets consist of at least 1% vegetal matter against latitude. A) Absolute fish richness against latitude (black dots, r^2=0.46, p<0.001, n=170, Gonzalez et al., 2012). B) Absolute number of water fowl species against absolute latitude (90° outlier left out, r=0,76, p<0.01) (based on data from Kear, 2005, p. 21).

Body mass along latitude and temperature

The body mass of water birds does not correlate significantly with latitude or temperature (Tab. 1; Fig 3.), which does not depend on season (summer and winter) or feeding mode (1-50% />50% herbivore or 0% / >1% herbivore).

Table 1. Pearson correlations between body mass of different groups of herbivores and latitude and temperature.

Pearson correlations		N	Latitude		Temperature (C°)	
			r	*p*	*r*	*p*
Summer	Herbi 1-50%	19	0.18	0.465	-0.31	0.199
	Herbi >50%	47	0.14	0.331	-0.17	0.245
	Herbi >1%	66	0.08	0.537	-0.18	0.137
	Herbi = 0%	17	0.00	0.993	-0.08	0.760
	Total	83	0.07	0.520	-0.18	0.107
Winter	Herbi 1-50%	19	-0.23	0.352	-0.36	0.128
	Herbi >50%	47	0.16	0.282	-0.17	0.245
	Herbi >1%	66	0.04	0.755	-0.17	0.182
	Herbi = 0%	17	0.05	0.844	-0.06	0.807
	Total	83	0.03	0.773	-0.15	0.186

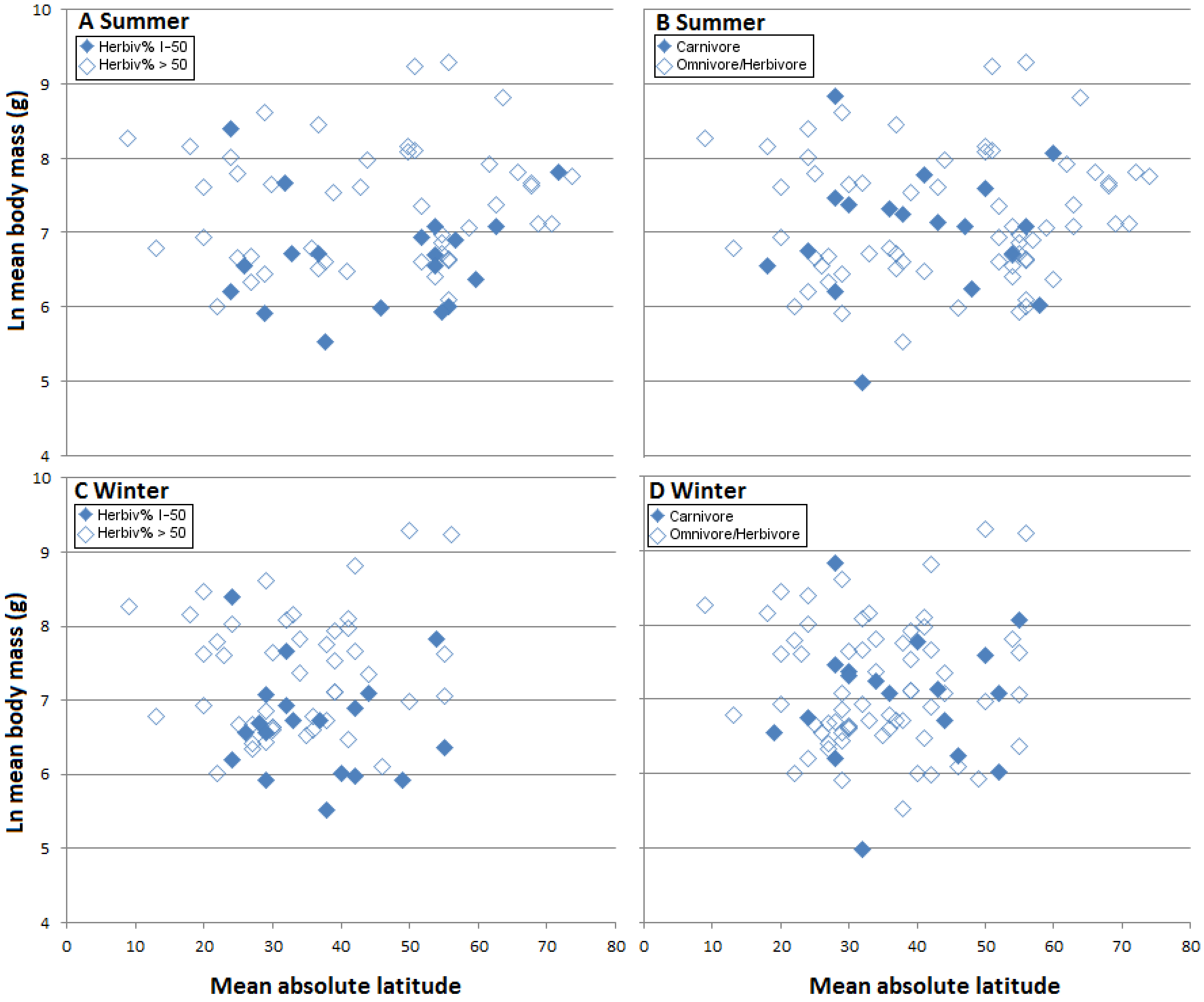

Fig. 3. The relationship between mean body mass and latitude. A) Two groups with a divided degree of herbivory against latitude. One group with a diet that consist of less than 50% vegetal matter, but at least 1% (n=19, closed diamonds), another group with a diet that consist of more than 50% vegetal matter (n=47, open diamonds) in summer (breeding season). B) Two groups with a divided degree of herbivory against latitude. One group with a diet that does consist of animal matter (n=18, closed diamonds), another group with at least 1% of vegetal matter in their diet (n=65, open diamonds) in summer (breeding season).C) Same comparison as in A, but than in winter (non-breeding season). D) Same comparison as in B, but than in winter (non-breeding season).

Herbivory and body mass

The logarithmic curve fitted between water bird body mass and the percentage of plants in their diet is significant. Heavier birds are almost completely herbivorous, while lighter birds have a variety of plant percentages in their diet (Logarithmic curve: n=66, r^2=0.28, p<0.001, Fig. 4).

Fresh water birds with more than 50% vegetal matter in their diet (n=47) are significantly heavier than fresh water birds with a diet that consist of 1% till 50% of vegetal matter (n=19) (Independent Sample T-Test, n=66, t=-4.5, p<0.001, Fig. 5A). Within the family of ducks, there is no significant difference in mean weight of ducks which consume more or less than 50% vegetal matter (Independent Sample T-Test, n=34, t=-0.9, p=0.39, Fig. 5B).

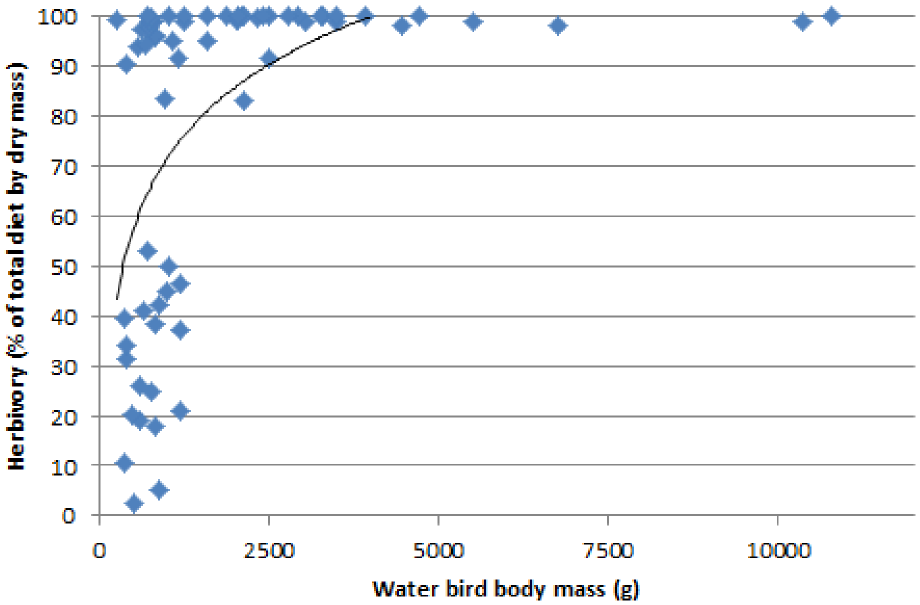

Fig. 4. Log correlation between water bird body mass (g) and percentage of vegetal matter in their diet (n=66).

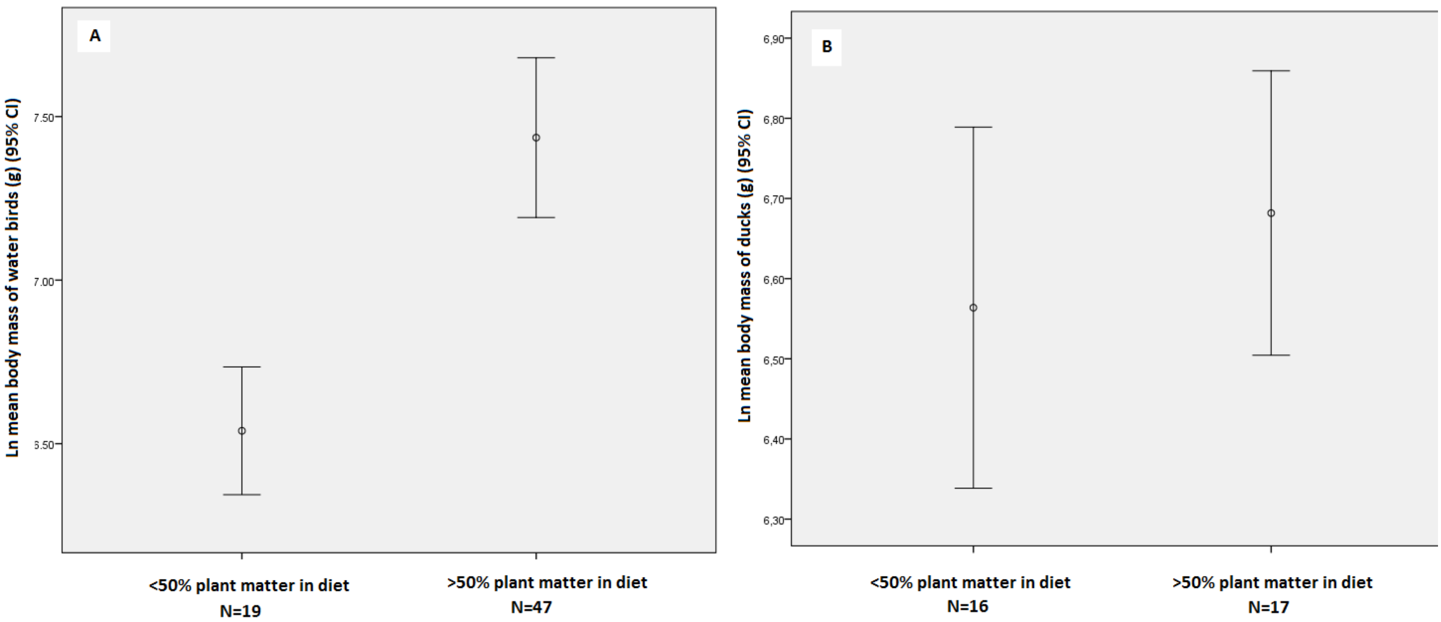

Fig. 5. 95% CI of Ln mean body mass for two groups of fresh water birds. One group with less than 50% vegetal matter in their diet, but at least 1% (n=19) and one group with more than 50% vegetal matter in their diet (n=47). A) Comparison for total water bird birds species (n=66). B) Comparison only for ducks (n=34).

Herbivory along latitude and temperature

Increasingly more fish species include plants in their diet towards the equator (Fig. 6A, Gonzalez *et al.*, 2012). Water birds (whose diet consist of 1% till 50% of vegetal matter) include increasingly more plants in their diet towards the poles (Fig. 6B, Tab. 2). There is also a significant negative correlation found within this specific group of water birds between their degree of herbivory and temperature in summer and winter (Tab. 2 & Fig. 7A&B). For all water birds a non-significant trend is visible between an increasing degree of herbivory and decreasing temperature in summer. The correlations for the other data were not significant (Tab. 2).

Another non-significant trend is visible when performing a binary logistic regression between carnivores (0% of vegetable matter in diet) and herbi/omnivores (more than 1% of vegetal matter in their diet) for temperature in summer (BLR, n=84, r^2=0.04, p=0.073; Fig. 8). No such trend was found for temperature in winter (BLR, n=84, p=0.594), latitude in summer (BLR, n=84, p=0.176) or latitude in winter (BLR, n=84, p=0.441).

Table 2. Pearson correlations between the percentage of vegetal matter in the diet of water birds and latitude and temperature in summer and winter. Significant result (*), visible trend (^).

Pearson correlations		N	Latitude		Temperature (C°)	
			r	*p*	*r*	*p*
Summer	Herbi 1-50%	19	0.48	0.038 *	-0.64	0.003 *
	Herbi >50%	47	-0.08	0.619	0.00	0.924
	Herbi >1%	66	-0.06	0.603	-0.1	0.419
	Herbi = 0%	17	-	-	-	-
	Total	66	0.07	0.518	-0.21	0.052 ^
Winter	Herbi 1-50%	19	0.24	0.320	-0.57	0.012 *
	Herbi >50%	47	0.05	0.706	-0.01	0.512
	Herbi >1%	66	-0.05	0.664	0.07	0.574
	Herbi = 0%	17	-	-	-	-
	Total	66	-0.09	0.393	0.00	0.988

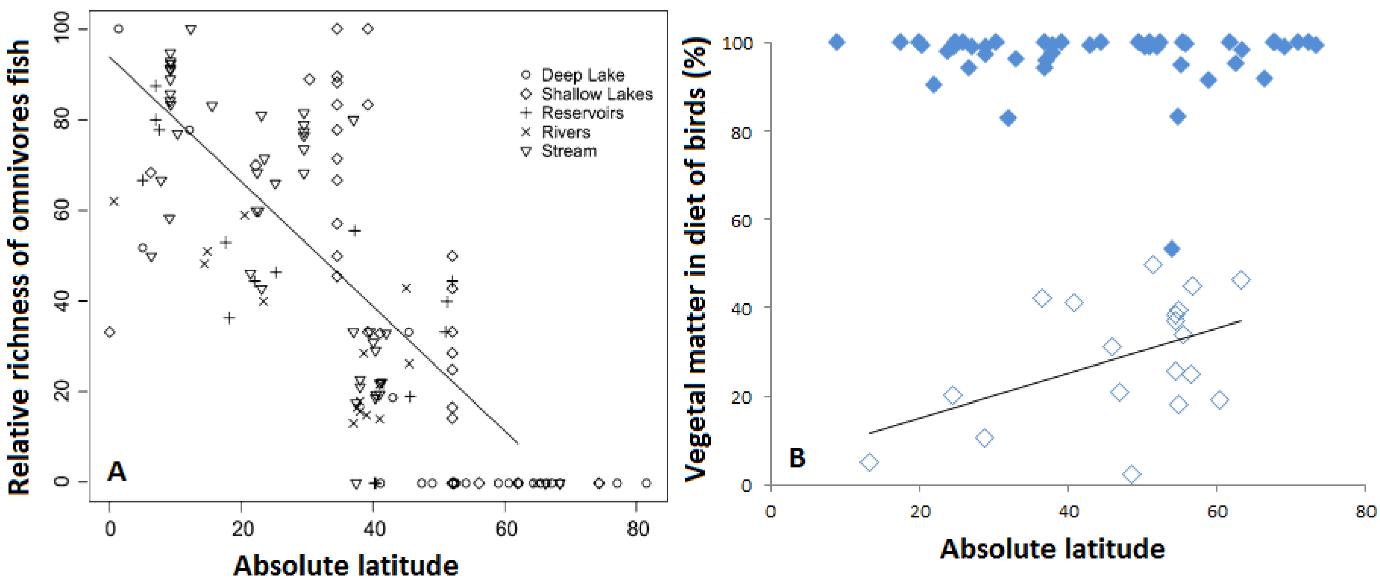

Fig. 6. A) Relative richness of omnivorous fish (at least 1% of vegetal matter in their diet) against latitude (r=0.71, p<0.001, Gonzalez et al., 2012). B) Distribution of degree of herbivory of birds against mean latitude in summer (n= 66, all diamonds). Significant increasing percentage of herbivory of birds with a diet that consist of 1-50% of vegetal matter towards higher latitudes (n= 19, r=0.48, p<0.05, open diamonds).

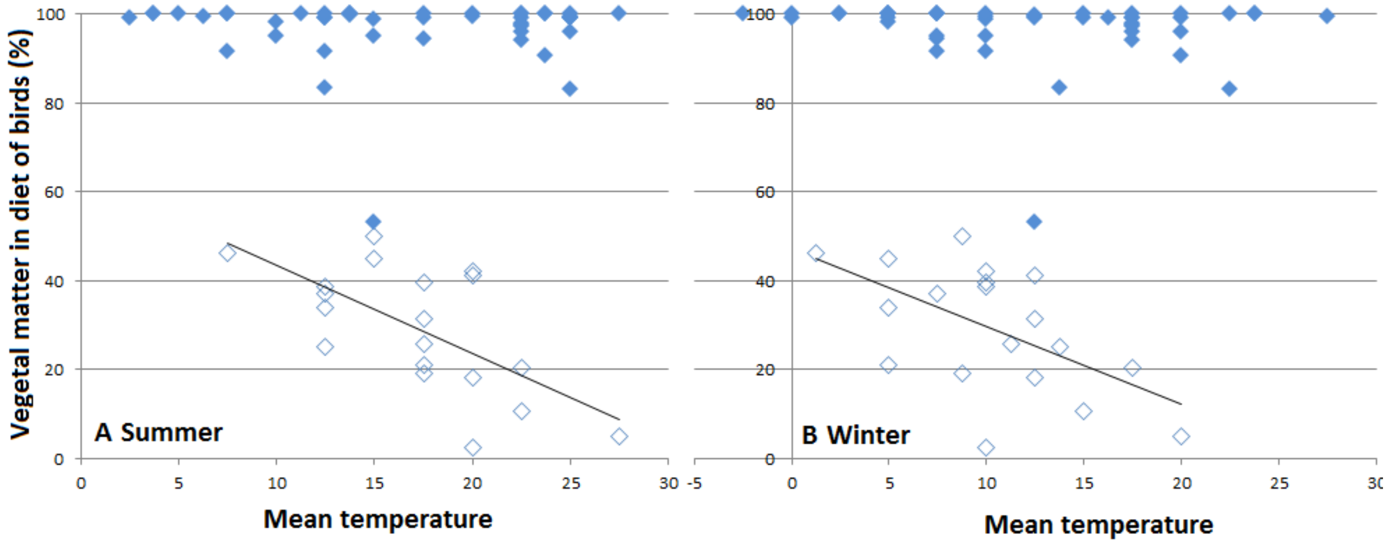

Fig. 7. A) Distribution of the degree of herbivory against temperature (all diamonds) and a significant decreasing percentage of herbivory of birds with a diet that consist of 1-50% of vegetal matter towards higher temperatures in summer (r=0.64, p<0.001, open diamonds). B) Same as A, but than in winter (r=0.57, p<0.05).

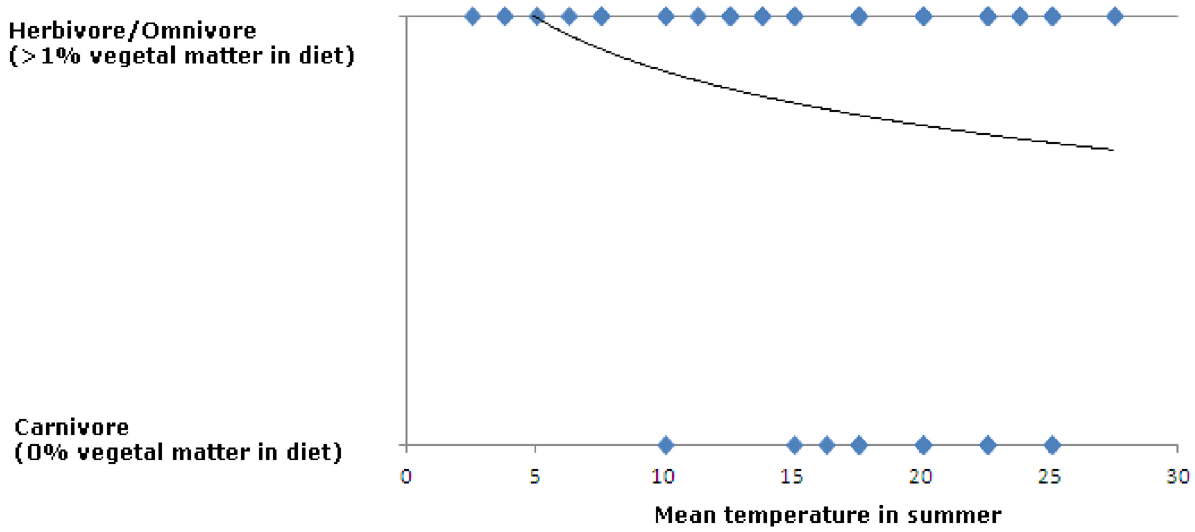

Fig. 8.Binary logistic regression between herbi/omnivores (more than 1% of vegetal matter in diet) and carnivores (0% of vegetal matter in diet) in summer.

Discussion

Number of water fowl species along latitude

The absolute number of species of water fowl increases towards higher latitudes, with a sharp decrease at the highest, hard-to-live 90°N and a smaller decrease at 40°S, because of lack of land mass. This is a reversed pattern to what is seen in many other species, which show an increase towards the equator (Hillebrand, 2004). There is a scarce selection of examples of species that also show a reversed latitudinal distribution pattern for difference reasons, but all based on geographic boundaries (Colwell and Leese, 2000). This selection includes pitcher plant communities bound by specific predation (Buckely *et al.,* 2003), saw flies bound by the abundance of their plant host group (Kouki *et al.,* 1994) and fungi, for reasons unknown (Tedersoo & Nara, 2010). Also geographical isolation can affect latitudinal distribution (Sólymos & Lele, 2012). Only one example of a reversed distribution pattern is found for vertebrates. Rabenold (1979) found this reversed pattern in an avian community in an eastern deciduous forest in North America. Therefore, it seems that birds are the only vertebrates who show this reversed latitudinal diversity gradient. Rabenold explains this mostly by the higher abundance of food at the northern hemisphere at higher latitudes in summer in comparison with lower latitudes in summer. There is only a short growing season at higher latitudes, which leads to an abundance of primary producers and smaller vertebrates in a short time span. This means that there is a higher food availability at higher latitudes in summer than around the equator in summer. This peak is so high that resident populations are not able to finish it all and there is enough food left for migrating species. The resident populations also cannot follow this oscillation all the way to the north, because of low temperatures, while migrant species can. Thus, there is one difference between this group of birds and other animals: birds can migrate, which allow them to follow seasonal patterns of food abundance (Rabenold, 1979) and thereby overcome geographic boundaries. Those explanations could be also explanatory for my research, as I found a weaker pattern on the southern hemisphere, where seasonality is weaker and fewer birds are migratory (Somveille *et al.,* 2013). This also explains why fish follow the normal latitudinal distribution pattern in the study of Gonzalez-Bergonzoni *et al.* (2012), as fish are mostly very limited in choosing their habitat and therefore bounded to it. The reversed latitudinal distribution pattern found by Rabenold (1979) on a smaller scale for birds seems also to account for a more global pattern for migratory birds.

Body mass along latitude and temperature

I did not find a relation between latitude or temperature and body mass for herbivores, nor for carnivores. This means that the birds from my dataset do not fit Bergmann's rule, which states that endotherms are bigger towards higher latitudes because of a larger surface/volume ratio that prevents excessive heat loss at colder temperatures (Bergmann, 1847). It seems that birds have other mechanisms, besides migration, to reduce heat loss at higher latitudes. They produce for example a dense coat of feathers at colder temperatures (Ricklefs, 1993) and they can actually lower their metabolism in respond to lower temperatures (West, 1972). Furthermore, in a study on rodent plateau zokors *(Eospalax baileyi)* at the Qinghai-Tibetan Plateau by Zhang *et al.* (2013), it becomes clear that also other factors than temperature can play a role. They found that those rodents are bigger at higher latitudes, but not at higher elevations, where lower temperatures are also found. This means that temperature not always drives the distribution of the body mass of endotherms along temperature ranges. Zhang *et al.* (2013) found that besides temperature, also ecological factors, like water balance and food availability (to make it possible to grow bigger, as stated in my hypothesis), could play a role in patterns of body size along latitude.

However, my results are not only in contrast with Bergmann's rule, but also with findings of Ramirez *et al.* (2008) who did find that birds are heavier at higher latitudes. Ramirez *et al.* (2008) used all kind of birds from the New World, where I used only fresh water birds, but from all over the world. There can be three possible explanations for these differences: (1) In the New World, especially in the north, seasonal temperature differences are much stronger than in the north of Europa and Asia because of the ocean circulation. This circulation brings colder water from the poles along the north of the New World and warmer water from the equator along Europe and Asia (Garrison, 2010). It is possible that because of this less extreme temperature differences in Europe and Asia, birds have no advantage in being heavier. Also, (2) water birds tend to live around water, where it is always warmer than more inland. Ramirez *et al.* used all kind of birds, which can cause the differences between their and my findings. (3) I probably have a higher percentage of migrating birds in my dataset. In this case, they possibly do not need a bigger body mass because those birds migrate easily to warmer regions (Somveille *et al.,* 2013).

Herbivory and body mass

I found that fresh water birds with a diet that consists of at least half of vegetal matter are significantly bigger than birds with less than half of vegetal matter in their diet. But I did not find this relation within a more specific genus of ducks. With caution to phylogenetic relations, I only want to conclude that heavier birds of more than three kilos have a diet of mostly vegetal matter, while lighter birds have a variety of diets. The hypothesis of bigger birds having a longer gut and therefore can digest vegetal matter better does not hold true, because also smaller birds are 100% herbivore. This means that the question no longer is why heavier birds eat plants, but what makes vegetal matter better for heavier birds in comparison with animal matter and why this is different for lighter birds. It is interesting to know if body mass is related to other factors, such as temperature. If bigger birds are also only living in colder regions, an explanation can be found in the high C-content of plants. The expelling of this extra C contributes to staying warm and then it is beneficial to be bigger and have a longer gut (Klaassen & Nolet, 2008). But, as said before, I did not find any relation between heavier birds and temperature. Thus, other factors much play a role here. A difference between body masses is the degree of metabolism, with a positive correlation between metabolism and body masses (Brown et al., 2004; McKechnie, 2008). Maybe plants contribute to something that provides a higher metabolism. Another explanation for the lack of correlation between the degree of herbivory and body mass could be the differences within vegetal matter itself. Seed is easier to digest and contains more nutritional value, while plant tissue is harder to digest and of lower nutritional value. In this research, no division was made between those two, everything was counted as vegetal matter. It still is possible that heavier birds eat more green tissue, because of their longer digestive system, while the diet of lighter birds consists of more, better digestible seeds. Further research could investigate this matter.

Herbivory along latitude and temperature

I found that birds, whose diet consist between 1 and 50% of vegetal matter, include a higher percentage of vegetal matter in their diet towards higher latitudes in summer. Within this specific group, there is also a significant pattern of increasing herbivory towards lower temperatures in summer, but also in winter. The summer significance of latitude and temperature is mainly due to the strong correlation between latitude and temperature. On the other hand, the correlation with winter temperatures is significant, while the one with winter latitudes is not. This is probably due to a wider range of mean temperatures in winter (summer 2.5 C° till +27.5 C°, winter -2.5 C° till +27.5 C°), while mean absolute latitude range is becoming smaller in winter (summer 9° till 73.5°, winter 9° till 38.5°).

Those findings are in contrast with the findings for fish (Gonzalez *et al.*, 2012), but conform my hypothesis. It seems that for fresh water birds, who have a diet that consist of 1% till 50% of vegetal matter, they choose for food, in this case plants, that consist of a higher C:N ratio in comparison with animal matter. This is probably due to the expulsion of high amounts of C what is beneficial for heat production especially at colder temperatures, like Klaassen en Nolet (2008) suggested, but further research is needed to prove this suggestion. I cannot conclude if these findings are also due to a higher metabolism, like my hypothesis stated, because I did not find any relations within birds with 0% or more than 50% of vegetal matter in their diet. This lack of correlation is probably due to a more extreme division of totally herbivores and totally carnivores in the remaining data, while the data from birds with 1-50% of vegetal matter in their diet is much more distributed along its degree of herbivory. The differences in distribution between those groups probably also cause the non-significant trend for the total data and the trend between carnivores and omni/herbivores, which show a possible higher degree of herbivory towards higher latitudes for all data. This is promising for further research. If a database is constructed that is much more distributed for the degree of herbivory, then there is great chance of finding much more significant data.

Conclusion

In this research, I tried to make a comparison between ectotherms (here fish) and endotherms (here birds) and how they are influenced by latitudinal patterns of temperatures. These are the four main findings.

(1) Fish show an increasing number of species towards lower latitudes (Gonzalez-Bergonzoni *et al.*, 2012), where migratory fresh water birds show a reversed pattern of increasing number of species towards higher latitudes (Kear, 2005; this study). This reversed pattern is probably due to a higher food peak at higher latitudes because of seasonality and only holds for migratory birds (Rabenold, 1979). Other groups of endotherms seem to follow the same pattern as in fish. This needs further investigation to be able to draw conclusions regarding the differences in distribution between ectotherms en endotherms.

(2) Fish seem to be smaller at lower latitudes (Edeline *et al.,* 2013), while I found no relation between body mass and latitude in fresh water birds and thereby temperature in my study. The fresh water birds in my data set do not seem to follow Bergmann's rule for endotherms, but they seem to have other mechanisms to prevent heat loss, like migration (Rabenold, 1979), a denser coat of feathers at lower temperatures (Ricklefs, 1993) and the possibility to actively lower their metabolism (West, 1972). It appears that temperature is not always the main factor that determines body mass. Ecological factors like food distribution also seem to be important (Zhang *et al.,* 2013). This means that there is a difference between ectotherms and endotherms on this matter. Ectotherms rarely have a chance to migrate away from

extreme temperatures (although they can move within smaller ranges), do not form a protection against extreme cold temperatures and have no constant control over their metabolism, except from moving temporarily into the sun or into the shade (Davies *et al.*, 2012). Thus, temperature has an influence on the differences in body size between ectotherms and endotherms.

(3) We have no data for fish, but I expect that there is no difference between ectotherms and endotherms regarding the relation between herbivory and body mass. In both cases, I expect that a larger body mass means a larger gut and this allows vegetal matter more time to be digested. However, I found in my study that heavier birds (3 kg or more) are almost exclusively herbivore, while lighter birds have a variety of diets. The reason why for heavier birds plants are more favorable than animal matter remains unclear, but is probably due to differences in quality and digestibility within vegetal matter itself. This may mean that my hypothesis also do not apply for ectotherms. Further investigation on the relation between fish body mass and percentages of green tissue and seeds in diet, and the relation between bird body mass and the more specific plant parts in their diet, is needed.

(4) Fish show a higher degree of herbivory towards the equator (Gonzalez-Bergonzoni *et al.*, 2012), while I found a higher degree of herbivory towards higher latitudes and colder temperatures for birds in a specific selection of my dataset, namely the group of birds with a diet that consist of at least 1%, but not more than 50% vegetal matter in their diet. The other birds with more than 50% of vegetal matter in their diet or with no vegetal matter in their diet at all, did not show any significant correlation with latitude or temperature. This is possibly due to the differences of distribution of the degree of herbivory within the data. The opposite patterns of herbivory across latitudes and temperature gradients for fish and birds may in fact point towards conformity between ectotherms and endotherms, namely a higher need for plants when metabolism is higher: fish at higher temperatures, because of competition and their ability to digest this matter better at higher temperatures and birds at lower temperatures, because the useful expulsion of extra C.

Future directions

The research I performed could not draw clear conclusions, but brought new hypothesis and suggestions for further research. For example, a remaining question is the one about the latitudinal pattern of the number of species of birds. Though I tested this pattern for mainly migratory water birds and Ramirez *et al.* (2008) tested this for all kind of birds, including migratory and non-migratory birds, it would be interesting to do an analysis for only non-migrating birds. If they follow the normal latitudinal pattern of an increasing number of species towards the equator, than the conclusions of Rabenold (1979) that migration play a major role in this reversed pattern are likely to be correct. Also more research could be done on for example migratory fish. If they show an opposite diversity gradient in contrast to their non-migrating genera members, migratory explanations may be even stronger. Besides this, this study only included fresh water birds. It would be interesting to include also other water types like brackish and marine, shallow waters to expand the data set, especially with diets of omnivores.

The interpretations of my results should be made within the context of the limitations of the data. I tried to interpret difference between ectotherms and endotherms, and thereby used birds as a model species for endotherms. Of course, more types of endotherms should be investigated on this matter. Thereby, the number of birds was not evenly distributed among the genera. Therefore it is possible that phylogeny plays a role, which in that case influenced my data. Furthermore, all heavy birds of more than three kilos with an herbivory percentage of 100% were all swans. This means that phylogeny can also play a role in this pattern found, although I tried to correct this in an extra correlation within the genus of ducks. But although this may play a role, the question remains interesting why there is only one genus that is so heavy and eating only vegetal matter. Besides those limitations, my data provide a general idea of the distribution of body mass and herbivory along latitude and temperature.

To bring this research to a broader scale, it is interesting to think what my results mean for the impact of global warming. Firstly, the strong reversed pattern of an increasing number of migratory fresh water birds species towards higher latitude, will decrease. When global warming continues, this pattern may disappear in total. This is due to less and less extreme temperature differences between the seasons, which cause less intense food peaks at higher latitudes. Secondly, global warming would not affect body mass and the degree of herbivory in the birds in my dataset, as they are both not related to temperature. For ectotherms, global warming would lead to an even higher body temperature, a higher metabolism and therefore higher competition as food intake increases even more. This could mean that more species will develop an even stronger specialization of vegetal matter in their diet. As it is clear that temperature plays an important role in the distribution of life and feeding strategies along latitude, global warming will definitely influence this distribution of life. Research could provide answers whether these changes are for better or worse.

Acknowledgements

I would like to thank Dr. Liesbeth Bakker from the Netherlands Institute for Ecology (NIOO) for guiding me through the subject, Dr. Han de Vries for his help with the statistics, Peter Benschop for correcting my English where needed and Prof. Dr. Ellen van Donk, Head of Aquatic Ecology at NIOO-KNAW and professor in Aquatic Ecology at Utrecht University for being second examiner.

References

Anderson, K.J. & W. Jetz (2005). “The broad-scale ecology of energy expenditure of endotherms” *Ecology letters*, 8: 310-318

Bergmann, Carl (1847). "Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse". *Göttinger Studien*, 3(1): 595–708

Behrens, M.D. & K.D. Lafferty (2007). “Temperature and diet effects on omnivorous fish performance: implications for the latitudinal diversity ingredient” *Canadian Journal of Fisheries and Aquatic Sciences,* 64: 867-873

Brown, J.H., J.F. Gillooly, A.P. Allen, V.M. Savage & G.B. West (2004). “Toward a metabolic theory of ecology” *Ecology* 85: 1771-1789

Buckley, H.L., Miller, T.E., Ellison, A.E. & Gotelli, N.J. (2003). “Reverse latitudinal trends in species richness of pitcher-plant food webs” *Ecology Letters,* 6:825–829.

Colwell, R.K., D.C. Lees (2000). “The mid-domain effect: geometric constraints on the geography of species richness” *Trends in Ecology and Evolution*, 15(2): 70-76

Davies, N.N., J.R. Krebs, S.A. West (2013). “An introduction to behavioural ecology” Wiley-Blackwell: West Sussex

Delaware University Website “Mean temperature for July & January 2005”: http://climate.geog.udel.edu/~climate/ (Retrieved September 25, 2013)

Edeline, E., G. Lacroix, C. Delire, N. Poulet & S. Legendre (2013). “Ecological emergence of thermal clines in body size” *Global Change Biology*, 19: 3062-3068

Garrison, T. (2010). “Oceanography. An Invitation to Marine Science” Brooks/Cole: Belmont

Gonzalez-Bergonzoni, I., M. Meerhoff,T. A. Davidson, F. Teixeira-de Mello, A. Baattrup-Pedersen & E. Jeppesen (2012). “ Meta-analysis Shows a Consistent and Strong Latitudinal Pattern in Fish Omnivory across Ecosystems” *Ecosystems,* 15: 492–503

Horn, M.H. (1989). “Biology of marine herbivorous fishes” *Oceanography and Marine Biology, An Annual Review*, 27: 167-272

Hillebrand, H. (2004). “On the Generality of the Latitudinal Diversity Gradient” *The American Naturalist,* 163(2): 192-211

Hillebrand, H., E.T. Borer, M.E.S. Bracken, B.J. Cardinale, J. Cebrian, E.E. Cleland, J.J. Elser, D.S. Gruner, W.S. Harpole, J.T. Ngai, S. Sandin, E.W. Seabloom, J.B. Shurin, J.E. Smith & M.D. Smith (2009). “ Herbivore metabolism and stoichiometry each constrain herbivory at different organizational scales across ecosystems” *Ecology Letters,* 12: 516–527

IUCN Red list of threatened species: http://www.iucnredlist.org (Retrieved September 11-25, 2013)

Kear, J. (2005). “Ducks, Geese and Swans” Oxford University Press: Oxford

Klaassen, M. & B. A. Nolet (2008). “ Stoichiometry of endothermy: shifting the quest from nitrogen to carbon” *Ecology Letters* 11: 785–792

Kooijman, S.A.L.M. (2000). “Dynamic energy and mass budget in biological systems”. Cambridge University Press: Cambridge.

Kouki, J., P. Niemelä & M. Viitasaari (1994). “Reversed latitudinal gradient in species richness of sawflies (Hymenoptera, Symphyta)” *Annales Zoologici Fennici*, 31:83-88

Levinton, J. & J. Mackie (2013). “Latitudinal diversity relationships of fiddler crabs: biogeographic differences united by temperature” *Global Ecology and Biogeography,* 22:1050–1059

McCallum, A.W., G.C.B. Poore, A. Williams, F. Althaus & Tim O’Hara (2013). “Environmental predictors of decapod species richness and turnover along an extensive Australian continental margin (13–35°S)” *Marine Ecology,* 34(3): 298-312

McKechnie, A.E. (2008). “Phenotypic flexibility in basal metabolic rate and the changing view of avian physiological diversity: a review” *Journal of Comparative Physiology B*, 178: 235-247

Pommier, T., B. Canbäck, L. Riemann, K. H. Boström, K. Simu, P. Lunberg, A. Tunlid & Å. Hagström (2007). "Global patterns of diversity and community structure in marine bacterioplankton" *Molecular Ecology,* 16: 867-880

Rabenold, K.N. (1979). "A Reversed Latitudinal Diversity Gradient in Avian Communities of Eastern Deciduous Forests" *The American Naturalist,* 114(2): 275-286

Ramirez, L., J.A.F. Diniz-Filho & B.A. Hawkins (2008). "Partitioning phylogenetic and adaptive components of the geographical body-size pattern of New World birds" *Global Ecology and Biogeography*, 17: 100-110

Ramos Pereira, M. J. & J. M. Palmeirim (2013). "Latitudinal Diversity Gradients in New World Bats: Are They a Consequence of Niche Conservatism?" *PLoS ONE,* 8(7):1-12

Ricklefs, R. E. (1993). "The Economy of Nature". W.H. Freeman: New York

Ricklefs, R.E. (2007). "History and diversity: explorations at the intersection of ecology and evolution" *The American Naturalist,* 170(S2): S56-S70

Rose, A.P. & B.E. Lyon (2013). "Day length, reproductive effort and the avian latitudinal clutch size gradient" *Ecology,* 94(6): 1327-1337

Shi, J.J., L. M. Chan, Z. Rakotomalala, A.M. Heilman, S.M. Goodman, A.D. Yoder (*In press)*. "Latitude drives diversification in Madagascar's endemic dry forest rodent Eliurus myoxinus (subfamily Nesomyinae)" *Biological Journal of the Linnean Society*

Sólymos, P. & S.R. Lele (2012). "Global pattern and local variation in species-area relationships" *Global Ecology and Biogeography*, 21: 109-120

Somveille, M., A. Manica, S.H.M. Butchart & A.S.L. Rodrigues (2013). "Mapping Global Diversity Pattern for Migratory Birds" *PLoS ONE*, 8 (8) , art. no. e70907

Tedersoo, L. & K. Nara (2010). "General latitudinal pattern of biodiversity is reversed in ectomycorrhizal fungi" *New Phytologist,* 185(2): 351-314

Teixeira-de Mello, F., M. Meerhoff, A. Baattrup-Pedersen, T. Maigaard, P.B. Kristensen, T.L. Andersen, J.M. Clemente, C. Fosalba, E.A. Kristensen, M. Masdeu, T. Riss, N. Mazzeo, E. Jeppesen (2012). "Community structure of fish in lowland streams differ substantially between subtropical and temperate climates" *Hydrobiologia*, 684: 143-160

West, G.C. (1972). "Seasonal differences in resting metabolic rate of Alaskan ptarmigan" *Comparative Biochemistry and Physiology* 42(A): 867-876

Wood, K.A., R.A. Stillman, R.T. Clarke, F. Daunt, M.T. O'Hare (2012). "The impact of waterfowl herbivory on plant standing crop: a meta-analysis" *Hydrobiology,* 686: 157-167

Zhang, T., E. Nevo, L. Tang, J. Su & G. Lin (2013). "Plateau zokors on the Qinghai-Tibetan Plateau follow Bergmann's rule latitudinally, but not altitudinally" *Mammalian Biology*, 77: 108-112