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Environmental factors shaping the distribution of common wintering waterbirds in a lake ecosystem with developed shoreline

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INTRODUCTION

Metropolitan areas function as social and economic hotspots in modern societies, and it is predicted that by 2030 more than 60% of the human population will dwell in cities (Grimm et al. 2008). As urbanization is likely to occur where biodiversity is high, its adverse impacts on natural systems raise conservation issues (Liu et al. 2003). Wetlands provide a typical example: people have been using shoreline habitats since early civilizations and the consequence of this is that natural coastal zones are often substantially modified or eliminated (Airoldi & Beck 2007). The remaining moderately intact wetlands are among the most threatened ecosystems (Mitsch & Gosselink 2000), in part due to the various influences of urbanization (Brinson & Malvarez 2002).

Pollution and nutrient release into water may be significantly higher near cities, leading to increased toxicity and eutrophication (Keatley et al. 2011). Highly developed watersheds may initiate greater water level fluctuations causing severe damage in emergent vegetation structure (Wei & Chow-Fraser 2005). Urbanization may also change food availability, both by reducing natural food sources and providing novel ones (e.g. through waste or direct provisioning by people; DeStefano & DeGraaf 2003). Predator populations may show various responses to urbanization, achieving higher densities in some cases (Rutz 2008) and lower in others (Brzezinski et al. 2012). Higher human population density can result in elevated levels of disturbance near settlements that may force some intolerant species to leave these areas, and may also have negative effects on other species (e.g. by decreasing their feeding efficiency; Severcan & Yamaç 2010).

Furthermore, the following studies demonstrated the influence of shoreline development on the size and distribution of the populations of some waterbirds. Traut & Hostetler (2004) showed that wading birds, marsh birds and ducks occurred more frequently near developed shores of small lakes, probably due to the presence of suitable habitat structures, such as lawn, which are common to those sites. Campbell (2008) found that both human presence and the physical structure of riverbanks had variable effects on the distributions of waterbirds, depending on both the species and season. Food provisioning of some species by people was a likely factor generating positive association with human habitation. While Smith & Chow-Fraser (2010) documented that urbanized locations can be important breeding sites for some generalist species, DeLuca et al. (2004) suggested that the number of specialist marsh birds decreases with increasing watershed urbanization. Studds (2012) also showed that anthropogenic activities can severely affect water quality and decrease the populations of specialist birds. Poor environmental conditions due to anthropogenic effects can also decrease the diversity of aquatic macroinvertebrate fauna that may generate parallel decreases in the diversity of their avian consumers (Getachew et al. 2012). Collectively these studies demonstrate that the effects of shoreline urbanization are highly variable, and a more complete knowledge is required if we are to predict urbanization effects in a wetland ecosystem. This is an important goal for waterbird conservation, because urban lakes and shorelines may represent the only remaining habitats for many species in developed areas.

In this study we investigated waterbird populations migrating and wintering on Lake Balaton, Hungary, the largest freshwater lake in Central Europe. This lake ecosystem is ideally suited to investigate the effects of urbanization on waterbird communities. Shoreline development of the lake started in the 1890s with the establishment of bathing resorts, the number of which has dramatically increased since World War II, resulting in a significant part of the lake's shoreline being covered by urbanized areas (Buday-Sántha 2007). However, despite these changes, during autumn and winter the lake is an internationally significant staging site for many waterbird species (Liker & Nagy 2009; Pónyi 1994). The specific aims of this study were to determine the following: (1) how the spatial distribution of 11 common waterbird species is affected by shoreline urbanization, and (2) whether other habitat features such as water depth, vegetation cover, food density or distance to neighbouring wetlands affect the distribution of these bird species.

METHODS

Study area

Lake Balaton (46°50'N, 17°45'E) covers approximately 596 km^2 with a length of 78 km and average width of 7 km (Fig.1). Water level has been actively regulated since the end of the 19th century, with a mean water depth of 3.1 m. However, in periods of continuous drought, such as between 2000-2003, the average water level can decrease by about 1 m, which leads to a recession of the lake margin beyond shoreline constructions, especially on the southern shore where the lake is shallower (Padisák et al. 2006).

A considerable part of the shoreline is situated within the boundaries of small towns and villages, with an approximate total of 100 000 resident dwellings and 70 000 holiday apartments (Buday-Sántha 2007). Between these built-up areas are remnants of the former natural shoreline habitats, which still harbour extensive reed cover (45.5% of the total shoreline, L. G-Tóth unpublished results), and marshy areas with variable amounts of woody vegetation. From June to August, the lake becomes a major tourist attraction and is densely populated by visitors, in stark contrast to the autumn and winter months when human activity levels in the area are much reduced.

Lake Balaton is a Ramsar site because it is a staging area for thousands of migrating waterbirds (BirdLife International 2009; Pónyi 1994), accommodating up to 70 species (Nagy 2007). During autumn and winter the most characteristic groups of resident waterbird species in

Lake Balaton include divers (e.g. *Gavia spp*), diving ducks (*Aythya spp., Bucephala clangula*), dabbling ducks (*Anas spp.*), grebes (*Podiceps spp.*), herons and egrets (*Ardea spp., Egretta spp.*), gulls (*Larus spp.*), geese (e.g. *Anser spp*.) and cormorants (*Phalacocorax spp.*).

Bird census data

Between 18 September 2003 and 19 April 2007 waterbird populations were surveyed by the Balaton Uplands National Park Directorate (organized by L. Nagy). Birds were counted by seven experienced field ornithologists once or occasionally twice per month (depending on the availability of time for censuses). On each census day the activities of the seven observers were synchronized and each of them counted birds within different census areas which collectively covered the entire lake. Thus, the whole shoreline of the lake was surveyed in each census and the sampling effort was the same for different parts of the shoreline. The area surveyed by each observer was a continuous section of the shoreline within which several census plots were used (i.e. the whole shoreline was divided into seven non-overlapping areas, each being surveyed by different observers). The locations of the census plots were chosen to provide as complete survey of the observers' census areas as possible. Distances between the census plots were variable (mean ± SE: 2868 ± 197 m), because both natural shore vegetation and non-public properties constrained access to suitable observation sites. Observations started early in the morning and continued for 4-6 hours depending on the number of birds present on the water. At each census plot the observers identified species using telescopes (15-45 x 65 Zeiss Diascope or 20-60 x 77 Leica ApoTelevid), and recorded the number of birds either swimming on the water or flying towards the observer (to reduce multiple counting by movements of the birds). The EOV coordinates (according to the Hungarian national grid system) for each census plot were noted and then used to create maps with ArcGIS.

During the whole study period (2003-2007) more than 470 000 birds were recorded on the lake. From this dataset, we selected the following 11 most abundant species (representing 87% of the total number of birds recorded) for our analyses, and consisting of more than 9000 recorded individuals: mallard (*Anas platyrhynchos*, mean annual number ± SE = 2354 ± 713), eurasian coot (*Fulica atra*, 3464 ± 364), black-headed gull (*Larus ridibundus*, 1393 ± 305), common goldeneye (*Bucephala clangula*, 1966 ± 108), common pochard (*Aythya ferina*, 1942 ± 113), tufted duck (*Aythya fuligula*, 1553 ± 188), caspian gull (*Larus michachellis*, 513 ± 70), mute swan (*Cygnus olor*, 361 ± 61), common gull (*Larus canus*, 844 ± 181), great cormorant (*Phalacocrax carbo*, 597 ± 95) and great-crested grebe (*Podiceps cristatus*, 300 ± 15).

We analysed census data from two migration/winter season periods (October to March) with contrasting water levels: 2003-2004 and 2006-2007, referred to as ‘low water level period’ and ‘normal water level period’ respectively. The average water depth within 1 km from the shoreline was 152 ± 4 cm during the low water level period and 219 ± 4 cm during the normal water level period.

Habitat variables

For these analyses we divided the lake’s shoreline into 47 standard-sized sections (Fig. 1), after simplifying the shoreline by omitting piers, ferryboat docks and similar irregular artificial structures. Each section was 4 km long and 2 km wide (1 km over water and 1 km over land, both measured from the water's edge), and habitat variables were measured within these sections. We chose to use 4 km long sections to ensure that each section contained at least one sampling point used for bird census (1.5 ± 0.1 census plots per section). Furthermore, this division adequately reflected the shoreline's variation in the analysed habitat variables (Table 1) and also provided a reasonable sample size for the analyses. We used the terrestrial portion (4 x 1 km) of the sections to measure the degree of urbanization of the shoreline and its surrounding areas. We chose 1 km wide sections of water because previous observations suggested that most of the bird species we included in the present study typically stayed close to shore during the censuses (Liker & Nagy 2009). To corroborate these data, we measured the distance from the shoreline of individual or flocks of 13 bird species during two surveys conducted in September and October 2009. Distances covered by these birds were measured using a VECTOR 21 high performance military range finder (Vectronix AG), which can measure distances up to 10 km with ± 5 m accuracy. For flocks we measured the distances of the closest and furthest individuals from the shoreline and from these calculated the average distance for the entire flock.

For each of the 47 sections we calculated the following six habitat variables (Table 1): (1) Urbanization score was calculated from three habitat features: (i) proportion of built-up land area measured from a digitized landcover map (polygon layer provided by the Balaton Uplands National Park); (ii) proportion of the land area covered by vegetation, which was measured from infrared aerial photographs taken in 2004 (Central Transdanubian Environmental and Water Authority), using the normalized difference vegetation index (NDVI) following a classification procedure; and (iii) human population density, according to the data of the Hungarian Central Statistical Office website. After calculating each of these variables for every section, we performed a principal component analysis and extracted the first principal component which was later used as the urbanization scores in the analyses (see Liker et al. (2008) and Bókony et al. (2010) for a similar approach). The correlations between these habitat variables and their loadings in the first principal component are given in Table A1 in the Appendix. Thus, a larger urbanization score represents a larger built-up area, higher human population and less vegetation cover (Fig. 1). Because we did not have separate data sources for the two study periods, we used the same urbanization scores for all analyses.

(2) Water depth was calculated as the average water depth in the 4 x 1 km water containing area of each section. We used a bathymetry grid which contained the elevation of the lake bed with 10 x 10 m resolution (Zlinszky et al. 2008) and used this to calculate water depth relevant for the studied period as the difference between the lake bed elevation and the elevation of actual water level recorded regularly at a standard monitoring point (Siófok, 46.92°N; 18.09°E). We calculated the average water depth (with the GIS tool zonal statistics) separately for the two study periods.

(3) The extent of reed (*Phragmites australis*) cover was measured as a percentage of the area occupied in each section. This was estimated from a digitized map of reed cover based on aerial photographs (provided by the Central Transdanubian Environmental and Water Authority). Since the most recent reed cover map was from 2004, we used the same coverage values for both study periods. The area covered by reed was probably somewhat larger during the low water period but it was shown that major changes in coverage did not occur during the study (Herodek et al. 2009).

(4) To estimate the abundance of local food sources, we collected data on the biomass of zebra mussel (*Dreissena polymorpha*), which is a major component in the diet of some of the studied species (tufted duck, common pochard, common goldeneye and eurasian coot; Pónyi 1994). The calculation was based on point samples of mussel densities measured on different underwater substrates (stones, underwater surface of boats, concrete revetments, pier pilings); details of the methods are provided in Balogh et al. (2008). Using these sample densities, we calculated the

total biomass of mussels within each section by multiplying substrate-specific biomass estimates by substrate surface area in each section (Balogh et al. 2008). Mussel biomass was calculated separately for the two study periods. We were not able to obtain reliable data for other local food sources (e.g. other invertebrate prey, fish, or macrophyte biomass) as there was no complete database for the whole lake.

(5) To estimate the availability of alternative feeding sites for gulls, we measured the distance from the centre of each shoreline section to the nearest municipal waste dumps. We created a digital map of waste dumps operating between 2003-2007 using information gathered from local environment agencies, town counties, and the Ministry of Environment and Water Policy. We only included waste dumps where organic waste such as food remains and kitchen waste was deposited from nearby cities, towns or villages. Municipal Agency personnel confirmed that many of these waste dumps were regularly visited by gulls. All dumps were considered to be of equal size and waste composition as we did not have precise data on these characteristics.

(6) As an estimate of landscape-level connectivity to other waterbird habitats, we measured the distance from each section to the nearest wetland. First we created a digital map that contained all fish-ponds, fishing-lakes and marshes that were larger than 10 ha and situated within a radius of 20 km from the shore of Lake Balaton. Importantly, we made field visits to assess each of these wetlands and considered all of them suitable habitats for wintering waterbirds. Then we measured the distance from the centre of each section to the closest wetland. Because these wetlands persisted through the whole study period, we used the same data for the two migration periods.

The above spatial analyses and measurements involving digitized maps were performed using ArcGIS (ArcMap 9.2) and ERDAS Imagine 2010 softwares.

Statistical analyses

We calculated the abundance of each of the 11 species separately for each of the 47 sections, as the mean number of individuals observed in each monthly census. Abundances were separately calculated for the two study periods. When two censuses were conducted within a month, we used the average value for that month. Those censuses performed when extensive ice cover was present on the lake were excluded from the final analysis, because this forced the birds to stay in a few ice-free areas, which did not meet the criteria of the habitat variables of interest (ice cover data from Balaton Shipping Co. and Central Transdanubian Environmental and Water Authority website). Thus, after excluding these censuses, bird abundances were estimated as the means of four (October, November, December 2003 and March 2004) and six (October, November, December 2006 and January, February, March 2007) monthly censuses for the low and normal water level period, respectively. We did not further subdivide the study periods into separate migration and wintering periods since the resulting number of observations would have been too low for a detailed statistical analysis. Although a number of factors are known to affect the results of bird censuses (e.g. weather, observation distance, differences between observers; Gregory et al. 2004), the standardisation of the census method, the synchronised data collection, and the sufficient experience of all observers probably reduced the chance that the data were influenced by sampling biases. However, one important consideration is that observations of birds from different shoreline sections were likely to have been influenced by differences in the extent of vegetation cover such as reed beds, which would have hindered visibility and although we could not correct for these effects, we discuss their potential influence on the results in the Discussion.

In addition to analysing the abundance of individual species, we calculated a composite measure of bird abundance (hereafter termed ‘combined bird abundance’), which was the first component of a principal component analyses in which the average counts per section for each species represented the input variables (for similar approach see Fraterrigo & Wiens 2005). Thus, from this methodology we obtained a single score of bird abundance for each of the 47 sections, based on the counts of the 11 species and combined bird abundance was calculated separately for the low and normal water level periods.

We analysed relationships between bird abundances and the habitat characteristics of each shoreline section by linear models (lm function in R; R Development Core Team 2011). Bird data and mussel biomass were log transformed, water level data cubic transformed, and reed cover data arcsine transformed before the analyses to achieve a better distribution of the model's residuals. Separate models were built for each species including the following habitat variables for all species; (1) urbanization score, (2) water depth, (3) reed cover and (4) distance from the nearest wetland. In addition, zebra mussel biomass was included in models for species with considerable mussel consumption, i.e. tufted duck, common pochard, common goldeneye and eurasian coot and finally, distance from the nearest waste dump was included in the models for the three gull species, which are known to use these dumps as feeding sites. In combined bird abundance models we included all predictor variables. To permit model averaging (see below) we did not include interactions between habitat variables in our models (Hegyi & Garamszegi 2011) as preliminary analyses suggested that interactions between urbanization and other habitat variables had negligible impact on waterbird distribution. We used Spearman rank correlation coefficients to explore correlations between habitat variables, and checked the variance inflation factors (VIFs) to assess the extent of co-linearity (Zuur 2009) and found that co-linearity did not pose a major concern for our dataset (max VIF: 3.04).

We then constructed two full model sets (low and normal water level conditions) for each species and also for the combined bird abundance scores that contained all possible combinations of habitat variables, then used Akaike Information Criterion corrected for small sample size (AICc) for model ranking and calculating model weights (Burnham et al. 2011). Robust model selection is possible if differences in AICc values between the best and the other models are large, for example greater than 10 (Symonds & Moussalli 2011). However, in our analyses this was never the case (see the Appendix Tables A2 – A23 for the first 10 best candidate models from the full model sets for each species). Thus model averaging was used to calculate the relative importance (RI) of habitat variables as the sum of weights of those models containing these variables (note that RI denotes the same quantity as $w_+(j)$ in Burnham & Anderson 2002). To further facilitate the evaluation of the importance of habitat variables, we also calculated their correlation effect sizes (r) from model-averaged z-scores of the variables (Rosenthal 1991). Model averaging was performed by the R package MuMIn (Bartoń 2012).

RESULTS

Distance of birds from the shore

In total, we conducted 317 distance measurements during our surveys (26.4 ± 8.2 observations per species). These data corroborated that most individuals of the studied species used a narrow shoreline section, usually < 1 km (Fig. 2).

Responses to urbanization

Although the highest ranking models contained urbanization scores for some species, other models lacking urbanization scores were almost equally supported in all cases (e.g. mute swan, black-headed gull, tufted duck, see Appendix). The typically low RI value of this variable also suggested that urban development near the shore did not affect bird abundance for most species, which was consistent between the two study periods (Table 2a-b). We only detected a higher explanatory value of urbanization in the case of the black-headed gull, which had a higher abundance in more urbanized shoreline sections during the normal water level period (Table 2b; urbanization score RI= 0.87, r= 0.347, β= 0.564). According to the species-specific results, urbanization also had low RI values in models using the combined bird abundance dependent variable (Table 3).

The effects of other habitat variables

For several species, our analyses showed high relative explanatory power for some environmental variables, which are evaluated separately in the following sections. In other cases, particularly during low water level period, the results of model-averaging did not provide clear support for any explanatory variable (uniformly low or moderate RI values and small effect sizes for all variables), and the fits of models were also typically low (as judged by R^2 values of the best models, see Table 2a-b). We presume that in these latter cases none of our habitat variables was able to adequately predict bird abundances.

Water depth

Mean water depth within 1 km of the shore had low explanatory power for all species, relative to the importance of other habitat variables (Table 2a-b). This lack of influence on bird abundance was consistent between the two study periods, despite the marked difference in the overall water level of the lake.

Reed cover

Two waterfowl (mallard and mute swan) and two gull species (black-headed and caspian gulls) exhibited negative responses to reed cover as indicated by the high RI values of this variable, and in two of these species (i.e. mallard and caspian gull) the results were consistent between the periods (Table 2a-b). In contrast, the abundance of tufted ducks was positively related to reed cover only in the period of normal water level.

Mussel biomass

We found high explanatory values for this variable for all species in which mussels represent an important dietary component. This result was particularly robust in the period of normal water level, when the densities of all four species (common pochard, tufted duck, common goldeneye and eurasian coot) were positively associated with mussel biomass, and supported by uniformly high RI values (Table 2b). During the low water level period the importance of mussel biomass was only supported in the case of the eurasian coot (Table 2a). Mussel biomass was also a reliable predictor in models using the combined bird abundance dependent variable (Table 3).

Waste dump distance

Bird abundance increased with decreasing distance to waste dumps for two out of the three gull species analysed, but this was supported statistically only for the normal water level period (caspian and black-headed gulls; Table 2b).

Wetland distance

In seven out of 11 species, distance of the shoreline sections to other wetlands emerged as an important predictor of abundance, and in all cases abundance increased with proximity to wetlands (Table 2a-b). Data from the low water level period indicated the importance of this effect for the mallard, while six other species were significantly affected during the normal water level period. The maximum relative importance which can be given for a variable (RI= 1) was obtained for the great cormorant, and a high support value (RI> 0.9) was determined for the common pochard, eurasian coot and caspian gull. The importance of distance from wetlands was also confirmed by models using the combined bird abundance as the dependent variable (Table 3).

DISCUSSION

The results of this study showed that shoreline urbanization did not significantly affect the distribution of waterbirds on Lake Balaton. We found that the urbanization score was an important component of the models only for one species during the normal water level period. We suggest several potential explanations for the lack of a general effect of urban development on waterbird distribution.

One possibility is that shoreline urbanization does not sufficiently alter the basic ecological conditions for the studied species, e.g. the availability or quality of food and predation risk. Most of the studied species roost and feed on water and do not use the land part of the shoreline in an ecologically meaningful way. Hence, urban developments on the shore could affect their food sources only indirectly, e.g. through water pollution that may influence either negatively or positively the density of food plants or animal prey like mussels and fish. However, recent pollution levels have been very low in Lake Balaton due to strict water quality regulations (Tátrai et al. 2008), which have probably resulted in negligible effects of pollution on bird food distribution. Although some of the species studied (mallard, mute swans, gulls) are regularly fed by people on the shore all year round, this seems not to have had any detectable impact on the distribution of these species. To explain this pattern we propose that (i) food provision by people is probably low during winter when tourists are largely absent, and (ii) the amount of food that could be provided in this way may represent only a small portion of food requirement of the tens of thousands of birds that are present on the lake. In contrast, food provisioning (e.g. exploitation of local waste) is a likely reason for the positive association between urbanization and abundance of black-headed gulls, although other factors may also be important for this species.

It is unknown how predation on the species may be influenced by shoreline urbanization. Because of their relatively large body sizes, the species we studied may be vulnerable only to large avian predators that can capture birds on water, such as marsh harriers (*Circus aeruginosus*) and white-tailed eagles (*Haliaeetus albicilla*). We are not aware of any study that explicitly investigated the population density or hunting frequencies/success rate of these predators in relation to habitat urbanization. Some of the studied species that occasionally occur on shore or in reeds close to shore (e.g. mallards, coots and gulls visiting lawns for feeding or roosting) may be vulnerable to terrestrial predators like feral cats (*Felis silvestris catus*), dogs (*Canis lupus*), foxes (*Vulpes vulpes*) or mustelids (*Mustelidae).* Some of these predators (e.g. cats, foxes) can reach high densities in or around urbanized areas (Sorace 2002), while others such as some mustelids avoid urbanized sites (Brzeziński et al., 2012). However, for our current study the number of birds using terrestrial areas was low compared to their total population sizes on the lake, and even individuals visiting lawns during the day may retreat to safer roosting places on the water during the night. In conclusion, we currently have no strong reason to assume that predation on waterbirds wintering on the lake is significantly influenced by shoreline urbanization.

The majority of the species included in this study tended to stay close to the shore during the day (usually < 500 m, see Fig. 2), probably to exploit available food sources or to find suitable roosting sites. Thus the presence and activity of humans on urbanized shoreline sections may represent a significant disturbance that could potentially influence bird distribution, i.e. birds may be driven away from disturbed shorelines (Laursen et al. 2005). However, our results did not support this expectation, possibly for the following reasons. Firstly, waterbirds can easily move between habitat patches in close proximity to each other in response to human disturbance. Thus, given the relative large size of the shoreline sections investigated in this study, such small-scale changes in bird locations in response to local human disturbances may not result in quantifiable effect on their distribution. Secondly, as the primary habitat of waterbirds is the water surface, which is isolated from the land in terms of human access, sensitivity to the presence of human activity on the shoreline may be relatively low, i.e. birds may be habituated to the presence of people. Thirdly, birds may continue to use disturbed areas with high food availability, because probably there is a trade-off between the survival cost of displacement versus risk-taking in good foraging areas (Gill & Sutherland 2000). The latter explanation assumes that Lake Balaton may offer attractive resources for these birds, otherwise they would use less urbanized/disturbed wetlands around the lake.

Finally, it is important to emphasize that we investigated the most abundant species in our study, which might have successfully adapted to the changed environment (e.g. may have become tolerant to disturbance, or able to cope with altered feeding or predation conditions). In contrast, the situation may be quite different for bird species rarer in Lake Balaton, which have been unable to adapt to urbanization during the last century. Unfortunately we do not have reliable information on the abundance of waterbirds from the period before the start of shoreline development, and therefore we cannot test directly whether currently common and rare species have responded differently to the urbanization process.

In contrast to urbanization, several other habitat characteristics had high explanatory values indicating an impact on abundances of the studied species. For instance, as in other studies (e.g. Traut & Hostetler 2004), we found that the extent of reed cover was related to the distributions of some species. We found that tufted ducks preferred shorelines with extensive reed cover while other species (mallard, mute swan and two gull species) avoided such areas. The reason for this variable response among species is unclear. A preference for reed beds by tufted ducks can be related, at least in part, to the large quantities of mussels living on the submerged part of the reed (this was not included in our mussel biomass estimates due to the lack of reliable data). Some of those species avoiding reed beds often roost on artificial shoreline constructions that are more common in developed shorelines, which may partially explain low numbers of these species in areas of high reed cover. Finally, the proportion of birds using the reed beds as shelter may differ between species, which may also have affected the observed relationship between reed cover and abundance.

We found that food availability also has a strong effect on waterbird distribution. For instance, there were strong positive correlations between mussel biomass and the abundance of diving ducks and coots, as found in other studies (Werner et al. 2005). However, the positive relationship between diving duck abundance and mussel biomass was significant only during the normal water level period when the entire shoreline was under water. One possible explanation for this difference between the periods might be that a significant proportion of zebra mussel substrate was not submerged during the low water level period, resulting in a reduced mussel biomass and a need to resort to alternative food sources (e.g. other mussel species that do not require hard surface). Furthermore, the effect of mussel distribution may be stronger when birds have to dive deeper for the mussels (as in years with normal water level) because in this case the food source should be abundant enough to provide sufficient calorific reward for diving. In contrast, during periods of shallow water, when energy requirements for diving are lower, then areas with lower mussel biomass may become more profitable for the birds to exploit.

Our study also confirmed that for gull species the presence of waste dumps close to shore has an important influence on the abundance of these birds, which is not surprising since is well established that numerous gull species thrive at waste dumps (Belant et al. 1998). To our knowledge, however, this is the first study demonstrating a clear positive influence of waste dumps on gull distribution in a large wetland ecosystem even when these dump sites are situated several kilometres away from the shoreline.

Finally, seven out of the 11 species examined for this study preferred shoreline sections close to other wetlands, and this was also consistently confirmed by the analyses of combined bird abundance. Factors contributing to this preference for proximity to surrounding wetlands may be that these places can serve as alternative resting sites, or as additional foraging locations. In line with our result, it has been shown by others that pond complexes around large open water areas with peripheral vegetation can offer diverse habitats that sustain the most species (Paracuellos & Telleria 2004). Additionally, Pearce et al. (2007) found that wetland clusters act like larger wetlands and may be especially attractive for waterbirds. As for the other explanatory variables, wetland distance had a stronger relationship with bird distribution during the normal than during the low water level period. This may have been because these alternative sites were less attractive for waterbirds during the low water level period caused by a reduction in feeding or roosting resources.

In summary, our study showed that urban development along lake shorelines might exhibit negligible effects on staging and wintering waterbirds if direct disturbance is low and food sources are abundant. However, we would like to emphasise the importance of investigating the less common species in future studies that may be less well adapted to urbanization and hence more strongly affected by these variables. Furthermore the results confirm that the landscape-level habitat features, such as proximity to satellite wetlands and waste dumps strongly influence the large scale distribution of waterbirds, and are thus important factors that should be considered in future conservation actions.

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