

1 **Environmental factors shaping the distribution of common wintering**

2 **waterbirds in a lake ecosystem with developed shoreline**

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14 **INTRODUCTION**

15 Metropolitan areas function as social and economic hotspots in modern societies, and it is
16 predicted that by 2030 more than 60% of the human population will dwell in cities (Grimm et al.
17 2008). As urbanization is likely to occur where biodiversity is high, its adverse impacts on
18 natural systems raise conservation issues (Liu et al. 2003). Wetlands provide a typical example:
19 people have been using shoreline habitats since early civilizations and the consequence of this is
20 that natural coastal zones are often substantially modified or eliminated (Airoldi & Beck 2007).
21 The remaining moderately intact wetlands are among the most threatened ecosystems (Mitsch &
22 Gosselink 2000), in part due to the various influences of urbanization (Brinson & Malvarez
23 2002).

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

35 Furthermore, the following studies demonstrated the influence of shoreline development
36 on the size and distribution of the populations of some waterbirds. Traut & Hostetler (2004)
37 showed that wading birds, marsh birds and ducks occurred more frequently near developed

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

54 In this study we investigated waterbird populations migrating and wintering on Lake
55 Balaton, Hungary, the largest freshwater lake in Central Europe. This lake ecosystem is ideally
56 suited to investigate the effects of urbanization on waterbird communities. Shoreline
57 development of the lake started in the 1890s with the establishment of bathing resorts, the
58 number of which has dramatically increased since World War II, resulting in a significant part of
59 the lake's shoreline being covered by urbanized areas (Buday-Sántha 2007). However, despite
60 these changes, during autumn and winter the lake is an internationally significant staging site for
61 many waterbird species (Liker & Nagy 2009; Pónyi 1994). The specific aims of this study were

62 to determine the following: (1) how the spatial distribution of 11 common waterbird species is
63 affected by shoreline urbanization, and (2) whether other habitat features such as water depth,
64 vegetation cover, food density or distance to neighbouring wetlands affect the distribution of
65 these bird species.

66

67 **METHODS**

68 **Study area**

69 Lake Balaton (46°50'N, 17°45'E) covers approximately 596 km² with a length of 78 km and
70 average width of 7 km (Fig.1). Water level has been actively regulated since the end of the 19th
71 century, with a mean water depth of 3.1 m. However, in periods of continuous drought, such as
72 between 2000-2003, the average water level can decrease by about 1 m, which leads to a
73 recession of the lake margin beyond shoreline constructions, especially on the southern shore
74 where the lake is shallower (Padisák et al. 2006).

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

83 Lake Balaton is a Ramsar site because it is a staging area for thousands of migrating
84 waterbirds (BirdLife International 2009; Pónyi 1994), accommodating up to 70 species (Nagy
85 2007). During autumn and winter the most characteristic groups of resident waterbird species in

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

89

90 **Bird census data**

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

108 coordinates (according to the Hungarian national grid system) for each census plot were noted
109 and then used to create maps with ARCGIS.

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

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

124

125 **Habitat variables**

126 For these analyses we divided the lake's shoreline into 47 standard-sized sections (Fig. 1), after
127 simplifying the shoreline by omitting piers, ferryboat docks and similar irregular artificial
128 structures. Each section was 4 km long and 2 km wide (1 km over water and 1 km over land, both
129 measured from the water's edge), and habitat variables were measured within these sections. We
130 chose to use 4 km long sections to ensure that each section contained at least one sampling point

131 used for bird census (1.5 ± 0.1 census plots per section). Furthermore, this division adequately
132 reflected the shoreline's variation in the analysed habitat variables (Table 1) and also provided a
133 reasonable sample size for the analyses. We used the terrestrial portion (4 x 1 km) of the sections
134 to measure the degree of urbanization of the shoreline and its surrounding areas. We chose 1 km
135 wide sections of water because previous observations suggested that most of the bird species we
136 included in the present study typically stayed close to shore during the censuses (Liker & Nagy
137 2009). To corroborate these data, we measured the distance from the shoreline of individual or
138 flocks of 13 bird species during two surveys conducted in September and October 2009.
139 Distances covered by these birds were measured using a VECTOR 21 high performance military
140 range finder (Vectronix AG), which can measure distances up to 10 km with ± 5 m accuracy. For
141 flocks we measured the distances of the closest and furthest individuals from the shoreline and
142 from these calculated the average distance for the entire flock.

143 For each of the 47 sections we calculated the following six habitat variables (Table 1):
144 (1) Urbanization score was calculated from three habitat features: (i) proportion of built-up land
145 area measured from a digitized landcover map (polygon layer provided by the Balaton Uplands
146 National Park); (ii) proportion of the land area covered by vegetation, which was measured from
147 infrared aerial photographs taken in 2004 (Central Transdanubian Environmental and Water
148 Authority), using the normalized difference vegetation index (NDVI) following a classification
149 procedure; and (iii) human population density, according to the data of the Hungarian Central
150 Statistical Office website. After calculating each of these variables for every section, we
151 performed a principal component analysis and extracted the first principal component which was
152 later used as the urbanization scores in the analyses (see Liker et al. (2008) and Bókonyi et al.
153 (2010) for a similar approach). The correlations between these habitat variables and their

154 loadings in the first principal component are given in Table A1 in the Appendix. Thus, a larger
155 urbanization score represents a larger built-up area, higher human population and less vegetation
156 cover (Fig. 1). Because we did not have separate data sources for the two study periods, we used
157 the same urbanization scores for all analyses.

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

165 (3) The extent of reed (*Phragmites australis*) cover was measured as a percentage of the area
166 occupied in each section. This was estimated from a digitized map of reed cover based on aerial
167 photographs (provided by the Central Transdanubian Environmental and Water Authority). Since
168 the most recent reed cover map was from 2004, we used the same coverage values for both study
169 periods. The area covered by reed was probably somewhat larger during the low water period but
170 it was shown that major changes in coverage did not occur during the study (Herodek et al.
171 2009).

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

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

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

191 (6) As an estimate of landscape-level connectivity to other waterbird habitats, we measured the
192 distance from each section to the nearest wetland. First we created a digital map that contained all
193 fish-ponds, fishing-lakes and marshes that were larger than 10 ha and situated within a radius of
194 20 km from the shore of Lake Balaton. Importantly, we made field visits to assess each of these
195 wetlands and considered all of them suitable habitats for wintering waterbirds. Then we measured
196 the distance from the centre of each section to the closest wetland. Because these wetlands
197 persisted through the whole study period, we used the same data for the two migration periods.

198 The above spatial analyses and measurements involving digitized maps were performed
199 using ARCGIS (ARCMAP 9.2) and ERDAS IMAGINE 2010 softwares.

200

201 **Statistical analyses**

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

222 In addition to analysing the abundance of individual species, we calculated a composite
223 measure of bird abundance (hereafter termed ‘combined bird abundance’), which was the first
224 component of a principal component analyses in which the average counts per section for each
225 species represented the input variables (for similar approach see Fraterrigo & Wiens 2005). Thus,

226 from this methodology we obtained a single score of bird abundance for each of the 47 sections,
227 based on the counts of the 11 species and combined bird abundance was calculated separately for
228 the low and normal water level periods.

229 We analysed relationships between bird abundances and the habitat characteristics of each
230 shoreline section by linear models (lm function in R; R Development Core Team 2011). Bird data
231 and mussel biomass were log transformed, water level data cubic transformed, and reed cover
232 data arcsine transformed before the analyses to achieve a better distribution of the model's
233 residuals. Separate models were built for each species including the following habitat variables
234 for all species; (1) urbanization score, (2) water depth, (3) reed cover and (4) distance from the
235 nearest wetland. In addition, zebra mussel biomass was included in models for species with
236 considerable mussel consumption, i.e. tufted duck, common pochard, common goldeneye and
237 eurasian coot and finally, distance from the nearest waste dump was included in the models for
238 the three gull species, which are known to use these dumps as feeding sites. In combined bird
239 abundance models we included all predictor variables. To permit model averaging (see below)
240 we did not include interactions between habitat variables in our models (Hegyi & Garamszegi
241 2011) as preliminary analyses suggested that interactions between urbanization and other habitat
242 variables had negligible impact on waterbird distribution. We used Spearman rank correlation
243 coefficients to explore correlations between habitat variables, and checked the variance inflation
244 factors (VIFs) to assess the extent of co-linearity (Zuur 2009) and found that co-linearity did not
245 pose a major concern for our dataset (max VIF: 3.04).

246 We then constructed two full model sets (low and normal water level conditions) for each
247 species and also for the combined bird abundance scores that contained all possible combinations
248 of habitat variables, then used Akaike Information Criterion corrected for small sample size
249 (AICc) for model ranking and calculating model weights (Burnham et al. 2011). Robust model

250 selection is possible if differences in AICc values between the best and the other models are
251 large, for example greater than 10 (Symonds & Moussalli 2011). However, in our analyses this
252 was never the case (see the Appendix Tables A2 – A23 for the first 10 best candidate models
253 from the full model sets for each species). Thus model averaging was used to calculate the
254 relative importance (RI) of habitat variables as the sum of weights of those models containing
255 these variables (note that RI denotes the same quantity as $w_{+}(j)$ in Burnham & Anderson 2002).
256 To further facilitate the evaluation of the importance of habitat variables, we also calculated their
257 correlation effect sizes (r) from model-averaged z-scores of the variables (Rosenthal 1991).
258 Model averaging was performed by the R package MuMIn (Bartoń 2012).

259

260 **RESULTS**

261 **Distance of birds from the shore**

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

265

266 **Responses to urbanization**

267 Although the highest ranking models contained urbanization scores for some species, other
268 models lacking urbanization scores were almost equally supported in all cases (e.g. mute swan,
269 black-headed gull, tufted duck, see Appendix). The typically low RI value of this variable also
270 suggested that urban development near the shore did not affect bird abundance for most species,
271 which was consistent between the two study periods (Table 2a-b). We only detected a higher
272 explanatory value of urbanization in the case of the black-headed gull, which had a higher

273 abundance in more urbanized shoreline sections during the normal water level period (Table 2b;
274 urbanization score $RI = 0.87$, $r = 0.347$, $\beta = 0.564$). According to the species-specific results,
275 urbanization also had low RI values in models using the combined bird abundance dependent
276 variable (Table 3).

277

278 **The effects of other habitat variables**

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

286

287 *Water depth*

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

292

293 *Reed cover*

294 Two waterfowl (mallard and mute swan) and two gull species (black-headed and caspian gulls)
295 exhibited negative responses to reed cover as indicated by the high RI values of this variable, and
296 in two of these species (i.e. mallard and caspian gull) the results were consistent between the

297 periods (Table 2a-b). In contrast, the abundance of tufted ducks was positively related to reed
298 cover only in the period of normal water level.

299

300 *Mussel biomass*

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

308

309 *Waste dump distance*

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

313

314 *Wetland distance*

315 In seven out of 11 species, distance of the shoreline sections to other wetlands emerged as an
316 important predictor of abundance, and in all cases abundance increased with proximity to
317 wetlands (Table 2a-b). Data from the low water level period indicated the importance of this
318 effect for the mallard, while six other species were significantly affected during the normal water
319 level period. The maximum relative importance which can be given for a variable (RI= 1) was
320 obtained for the great cormorant, and a high support value (RI> 0.9) was determined for the

321 common pochard, eurasian coot and caspian gull. The importance of distance from wetlands was
322 also confirmed by models using the combined bird abundance as the dependent variable (Table
323 3).

324

325 **DISCUSSION**

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

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

345 of local waste) is a likely reason for the positive association between urbanization and abundance
346 of black-headed gulls, although other factors may also be important for this species.

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

362 The majority of the species included in this study tended to stay close to the shore during
363 the day (usually < 500 m, see Fig. 2), probably to exploit available food sources or to find
364 suitable roosting sites. Thus the presence and activity of humans on urbanized shoreline sections
365 may represent a significant disturbance that could potentially influence bird distribution, i.e. birds
366 may be driven away from disturbed shorelines (Laursen et al. 2005). However, our results did not
367 support this expectation, possibly for the following reasons. Firstly, waterbirds can easily move
368 between habitat patches in close proximity to each other in response to human disturbance. Thus,

369 given the relative large size of the shoreline sections investigated in this study, such small-scale
370 changes in bird locations in response to local human disturbances may not result in quantifiable
371 effect on their distribution. Secondly, as the primary habitat of waterbirds is the water surface,
372 which is isolated from the land in terms of human access, sensitivity to the presence of human
373 activity on the shoreline may be relatively low, i.e. birds may be habituated to the presence of
374 people. Thirdly, birds may continue to use disturbed areas with high food availability, because
375 probably there is a trade-off between the survival cost of displacement versus risk-taking in good
376 foraging areas (Gill & Sutherland 2000). The latter explanation assumes that Lake Balaton may
377 offer attractive resources for these birds, otherwise they would use less urbanized/disturbed
378 wetlands around the lake.

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

387 In contrast to urbanization, several other habitat characteristics had high explanatory
388 values indicating an impact on abundances of the studied species. For instance, as in other studies
389 (e.g. Traut & Hostetler 2004), we found that the extent of reed cover was related to the
390 distributions of some species. We found that tufted ducks preferred shorelines with extensive
391 reed cover while other species (mallard, mute swan and two gull species) avoided such areas. The
392 reason for this variable response among species is unclear. A preference for reed beds by tufted

393 ducks can be related, at least in part, to the large quantities of mussels living on the submerged
394 part of the reed (this was not included in our mussel biomass estimates due to the lack of reliable
395 data). Some of those species avoiding reed beds often roost on artificial shoreline constructions
396 that are more common in developed shorelines, which may partially explain low numbers of
397 these species in areas of high reed cover. Finally, the proportion of birds using the reed beds as
398 shelter may differ between species, which may also have affected the observed relationship
399 between reed cover and abundance.

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

413 Our study also confirmed that for gull species the presence of waste dumps close to shore
414 has an important influence on the abundance of these birds, which is not surprising since it is well
415 established that numerous gull species thrive at waste dumps (Belant et al. 1998). To our
416 knowledge, however, this is the first study demonstrating a clear positive influence of waste

417 dumps on gull distribution in a large wetland ecosystem even when these dump sites are situated
418 several kilometres away from the shoreline.

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

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

439

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