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Habitat selection by breeding waterbirds at ponds with size-structured fish populations

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Abstract Fish may significantly affect habitat use by birds, either as their prey or as competitors. Fish communities are often distinctly size-structured, but the consequences for waterbird assemblages remain poorly understood. We examined the effects of size structure of common carp (*Cyprinus carpio*) cohorts together with other biotic and abiotic pond characteristics on the distribution of breeding waterbirds in a seminatural system of monocultured ponds, where three fish age classes were separately stocked. Fish age corresponded to a distinct fish size gradient. Fish age and total biomass, macroinvertebrate and amphibian abundance, and emergent vegetation best explained the differences in bird density between ponds. Abundance of animal prey other than fish (aquatic macroinvertebrates and larval amphibians) decreased with increasing carp age in the ponds. Densities of ducks and smaller grebes were strongly negatively associated with fish age/size gradient. The largest of the grebes, the piscivorous great crested grebe (*Podiceps cristatus*), was the only species that preferred ponds with medium-sized fish and was positively associat-ed with total fish biomass. Habitat selection by bitterns and most rallids was instead strongly influenced by the relative amount of emergent vegetation cover in the ponds. Our results show that fish size structure may be an important cue for breeding habitat choice and a factor affording an opportunity for niche diversification in avian communities.

Keywords Common carp · Distant competition · Habitat selection · Size-structured interactions · Waterbird assemblages

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Introduction

The influence of ecological interactions between distantly related taxa upon patterns of habitat use is one of the focuses of ecological and evolutionary research (Levins 1979; Safina and Burger 1985; Englund et al. 1992). Interactions between fish and bird populations are known to range from predation to competition. Fish-eating birds profit from increases in fish populations (Lammens 1999), while negative effects of fish on waterbird distribution have been documented and attributed to exploitative competition (Eriksson 1979; Eadie and Keast 1982; Hurlbert et al. 1986; van Eerden et al. 1993). Fish communities frequently exhibit a distinct size structure due either to external disturbances promoting dominance of single size cohorts or to inter- and intraspecific trophic interactions between cohorts (e.g., Tonn and Magnuson 1982; Persson 1988; McParland and Paszkowski 2006). The variability in size structure of fish populations may be expected to affect the habitat choice and reproductive success of many water-birds, depending on the species involved. Larger fish can be more profitable prey for avian predators, but on the other hand, fish susceptibility to predation may decrease with

growth (Moser 1986). As most fishes are size-limited in feeding, in species with large terminal body sizes, the ability to compete with birds may increase over ontogeny. Fish may also affect the environmental context of interactions with birds, e.g., via bioturbation (Lammens 1999; Zambrano et al. 2001), and their potential for habitat alteration can be size dependent (Driver et al. 2005). However, little is known of size-structured fish–bird interactions (but see Paszkowski and Tonn 2000), as most studies have addressed avian habitat selection in relation to the presence/absence of fish (Eriksson 1979; Hurlbert et al. 1986; Allen et al. 2007) or along a fish density gradient (Hill et al. 1987; Haas et al. 2007). Since patterns of fish size structure are predictable in many natural and human-managed systems (Tonn and Magnuson 1982; Holmgren and Appelberg 2000), elucidation of size-dependent effects of fish on birds may be necessary to understand the functioning of these systems and provide practical solutions for waterbird conservation strategies.

The aim of this study was to examine how size structure of fish influences assemblage composition of pond-breeding waterbirds and what role fish size plays in determining distribution of waterbirds relative to other biological and habitat variables. We chose to work on the common carp (*Cyprinus carpio*) because carp populations frequently form strong year classes and consequently distinct size structure; predation by piscivorous birds is usually limited to the first- or second-summer cohorts (Mraz and Cooper 1957; Moser 1986). Moreover, carp commonly play a key role in structuring aquatic communities and can negatively affect food resources of waterfowl (Crivelli 1983; Haas et al. 2007; Bajer et al. 2009). We predicted that fish size structure would have a strong influence on habitat selection by some waterbirds, while on the other hand, we expected certain pond habitat features, such as emergent vegetation, to affect distribution of individual bird species among ponds. Therefore, we studied patterns of habitat selection by waterbirds at the community and individual species level, taking into account biotic and abiotic habitat properties that might influence those patterns, along a gradient of three carp age (size) classes: young-of-the-year cohorts, 1-year-old fish, and 2-year-old fish. The study system consisted of open carp ponds where fish age cohorts were stocked separately and the age of the cohorts was irregularly rotated between years. As it is difficult to manipulate habitat choice of birds exploiting spatially extensive ranges, seminatural systems such as monoculture pond fisheries offer a valuable alternative (Suter 1991; Haas et al. 2007) providing conditions for "natural experiments" sensu Diamond (1986). The clear-cut size distribution of fish age cohorts among ponds provided an excellent opportunity to examine size-structured fish–bird interactions using a whole-system approach.

Methods

Study system

The study was conducted in cooperation with the local fisheries staff at extensively managed carp ponds in southeastern Poland. During two breeding seasons, in 2002 and 2004, 39 and 46 ponds were surveyed. The ponds belonged to five pond complexes (in total 651–682 ha of water surface area) situated 10–60 km apart. The eutrophic, typically monoculture ponds in SE Poland are readily used by breeding birds and are acknowledged strongholds for waterfowl (Grimmet and Jones 1989).

The privately administered ponds formerly belonged to a single state-owned fisheries organization; hence, management practices were alike for all study sites and all carp stocks originated from the same hatchery. Three fish age classes were stocked in separate growing-on ponds, and a well-defined size gradient of fish cohorts was created. Before introduction into the ponds, all carp were weighed to establish the total stock biomass in each pond, and a large sample of fish was weighed to determine mean individual biomass. Stocking biomasses were on average similar in 1+ and 2+ ponds (225±SE 29 vs 224±28 kg/ha) but were much larger than in 0+ ponds (Table 1), where carp attained total biomass >50 kg ha only in late June. During the spring stocking period (April–May), young-of-the-year (0+; small-sized) carp were stocked at an individual weight of 1.5–3.0 mg, to reach 5–8 g (7 to 8 cm in length) within ca. 2 months; 1+ (medium-sized) carp weighed ca. 30–50 g and 2+ (large-sized) carp ca. 150–250 g. Due to substantial differences in fish size between year cohorts under pond culture conditions, carp age and the age-specific size range are considered interchangeable here. Potential carry-over effects of cohort distribution (i.e., the influence of events in pond ecosystems in past breeding seasons on the current habitat choice of birds) were minimized because in most of the ponds, the age of the carp stocks was rotated between years (albeit irregularly, each year in ca. 30–60% of the studied ponds, depending on the fish farm's current supply of the given year-class of fish). Age cohorts were alternated either by stocking different age classes in rotation in subsequent years or leaving cohorts in the same ponds for 2 years. Carp densities were within the ranges found in natural systems (Table 1; Crivelli 1983; Panek 1987). Other fish occurred in the ponds (small wild-grown and supplemental species, mainly bleak (*Leucaspius delineatus*), wels (*Silurus glanis*), or pike (*Esox lucius*)), but carp were overwhelmingly dominant (95–98% of the total fish biomass per pond; M. Filipiak and M. Sagan, personal communication). The proportion of small fish that invaded the ponds despite the screens at the water inlets was typically visually assessed

Table 1 Pond habitat variables (mean and range) sampled in 2002 and 2004, selected as potential predictors of breeding bird densities

Variable	Description	Mean (range)
Pond area	Water surface area (ha)	4.8 (0.8–26)
Fish age	0+, 1+, 2+carp cohorts	0+, 51%; 1+, 29%; 2+, 20%
Fish standing biomass	Total carp biomass (kg/ha) during the spring stocking period (April–early May)	0+, negligible at stocking (ca. 1 kg ha–); 1+, 225 (105–501); 2+, 224 (176–490)
Pond permanence	Ponds that held or gathered water over winter vs ponds which remained dry in winter and were refilled in late March to early May (treated as a categorical factor in the analyses)	Ponds wintering, 34%; flooded in spring 76%
Amphibian abundance	Relative wet weight (g/1 trap)	18.4 (0–74.8)
Macroinvertebrate abundance	Relative dry weight (mg/1 trap)	0.82 (0–8.1)
Water transparency	Secchi disk (26 cm diameter) depth (cm)	102.8 (30–180)
Emergent pond vegetation	Proportion of pond surface area covered by emergent aquatic plants	24.9 (2.5–77)
Shoreline development	The ratio of the pond perimeter to the doubled square root of the product of π and the pond surface area	1.5 (0–2.9)
Urbanized landscape	Proportion of the shoreline adjacent to urbanized habitat, i.e., roads and human settlements	0.2 (0–1.0)
Forest landscape	Proportion of the shoreline covered by forest	0.1 (0–1.0)
Agricultural landscape	Proportion of the shoreline adjacent to arable fields or pasture	0.2 (0–0.9)
Pond connectivity	Proportion of the shoreline adjacent to other ponds	0.5 (0–1.0)

For fish age and pond permanence, the percentage of ponds studied belonging to the given category is presented instead

by fish farmers during draining operations because wild fish were only occasionally collected. However, a few ponds known to develop noticeable proportions of wild-grown fish, usually following serious carp mortality episodes, were excluded from the analyses.

The ponds were similar in depth (mean values 0.7–1.3 m) but differed in emergent aquatic vegetation cover along the pond margins (mainly *Typha angustifolia* and *Phragmites australis*) and in surface area (Table 1; see Kloskowski 2009 for more details on the study system).

Bird surveys

Waterbirds were counted between April and July at ca. 10-day intervals (each pond was visited 12 times during the season). The round count method of Koskimies and Väisänen (1991) was used. We walked around the ponds and counted birds using binoculars and scopes. We counted only nonpasserine birds classified as pond breeders (nesting on ponds or pond levees) and feeding at or beneath the surface of the water. We used playback of species' calls (Bibby et al. 2000) to detect territories of little grebe (*Tachybaptus ruficollis*) and of rallids other than coot (*Fulica atra*). The vocalizations were broadcast using a tape recorder early in the morning and after sunset. Numbers of breeding pairs (breeding territories) were estimated following the method of Koskimies and Väisänen (1991), with some modifications for pond conditions

(Ranoszek 1983). Analyses were restricted to species occurring in >5% of the ponds: little grebe, great crested grebe (*Podiceps cristatus*), red-necked grebe (*Podiceps grisegena*), little bittern (*Ixobrychus minutus*), great bittern (*Botaurus stellaris*), mute swan (*Cygnus olor*), mallard (*Anas platyrhynchos*), garganey (*Anas querquedula*), pochard (*Aythya ferina*), tufted duck (*Aythya fuligula*), water rail (*Rallus aquaticus*), little crake (*Porzana parva*), moorhen (*Gallinula chloropus*), and coot. Where necessary, breeding species data were converted to densities (birds/10 ha).

Fish and habitat variables

Data on pond size, carp age, and standing biomass in individual ponds were provided by the staff of the local fisheries. Ponds were also classified by hydroperiod (ponds "wintering" vs flooded in spring). At each pond, a number of variables were measured for use in analyses predicting the community structure and responses of individual bird species. Relative abundances of amphibian larvae and aquatic invertebrates were estimated from pond surveys using funnel activity traps. In 2002 and 2004, the study sites were visited in random order from 27 April to 11 May and between 19 June and 4 July to collect the spring and summer fauna. The traps (modeled after Murkin et al. 1983; Griffiths 1985) were cylindrical with a 23-mm aperture at the narrow end of the funnel. Trapping is a reliable method of estimating the availability of nonfish prey taken by

waterfowl (Elmberg et al. 1994). Ten traps were set in each pond for 48 h (see Kloskowski 2009 for details of the trapping procedure). The traps were approximately evenly distributed in open water areas close to emergent vegetation in order to sample both habitats. Invertebrates ≥4 mm (hereafter macroinvertebrates) caught in the traps were identified (typically to family or genus). For common taxa, dry weights were predicted from length–weight regressions obtained after drying subsamples to stable weight at 50–60°C. Macroinvertebrates from rare taxa were collected and weighed after drying. Any tadpoles caught were wet-weighed in the field after drip drying. During each sampling visit, Secchi transparency was measured at the deepest parts of the ponds. The two sampling sessions spanned the time period used to establish numbers of breeding birds (Ranoszek 1983; Koskimies and Väisänen 1991), and since data collected at 2-week intervals from a smaller subset of ponds indicated that the variables measured (amphibian and macroinvertebrate abundance, water transparency) either remained stable or showed monotonic increase over late April–end of June (M. Nieoczym and J. Kloskowski, unpublished data), we used averages of the two catches/measurements in the analyses, on the assumption that they represented the variability between the ponds over the study period.

During the June–July 2002 sampling sessions, water chemistry data (electrical conductivity, pH, concentrations of dissolved oxygen, organic carbon, ammonia nitrogen NH_4-N, nitrate nitrogen NO_3-N, and available phosphate PO_4-P) were sampled (see Kloskowski 2009 for a detailed description of the methods). However, in the preliminary analyses (see "Data analysis" section), which included only the 2002 data, none of the chemical variables had a significant effect on the composition of bird assemblages or on individual species. Therefore, the analyses were conducted on data from both 2002 and 2004, omitting the chemical variables.

Emergent vegetation cover and the shoreline development index (Lind 1985) were determined by digitization from groundproofed (a planimeter was used) aerial photos. To describe the surrounding landscape characteristics for each pond, we estimated the proportion of the shoreline adjacent to urbanized habitat, to forest patches, to arable fields/pasture, and to other ponds. We restricted the landscape scale to a ca. 20–30 m buffer because all study sites were situated in agricultural landscape, with small patches of woodland (see Table 1 for a complete list of variables collected in both 2002 and 2004).

Data analysis

Canonical correspondence analysis (CCA; CANOCO 4.5; ter Braak and Šmilauer 2002) was used to determine the variables that best predicted the composition of the pond-breeding bird community. CCA is a direct gradient analysis that iteratively develops an ordination of species and sampling sites, combined with multiple regression on a series of environmental gradients. A set of environmental variables is reduced to a few orthogonal axes as composite environmental gradients structuring species distribution patterns. The significance of the relation of each environmental variable to the bird data was determined by the magnitude of the additional variation the variable explained ("conditional effects"). Stepwise forward selection was used to include significant variables ($P<0.05$) in the model. The significance of the first canonical axis and of all canonical axes together was tested by the distribution-free Monte Carlo simulation (999 permutations). Multicollinearity of the habitat variables was not excessive (variance inflation factor (VIF) <7; VIF range for variables chosen by the stepwise forward procedure 1.16–2.32). To partial out the effects of the year of sampling and study locations (pond complexes) from the model, they were included in the ordination as categorical (dummy) covariables. When a pond was sampled in both study years, we randomly selected 1 year to be excluded from the model.

Although CCA provides information on the habitat associations of individual species, its main goal is to determine the relative effects of environmental variables on the bird community as a whole. Therefore, generalized linear mixed models (GLMMs) with Poisson distribution and logarithmic link (GenStat v. 11.0) were used to identify the habitat conditions most important in determining the densities of individual bird species and bird species richness (the number of avian taxa recorded per pond) at the ponds. For bitterns, mute swan, little crake, and water rail, typically represented by no more than one breeding pair (calling individual) per pond due either to strong territorial behavior or to relatively low overall abundance, we considered presence/absence data in binomial models with logit link to be more appropriate. Also, in two species that are known to be involved in strong agonistic interactions with sympatric larger-bodied species, interspecific interactions were considered: great crested grebe presence was added to the models of red-necked grebe densities as an explanatory categorical variable and coot presence to the models of moorhen (Cramp 1985; Fjeldså 2004). The other advantage of the GLMMs was that data from all ponds surveyed in 2002 and 2004 were used, including ponds sampled twice. With regard to the close proximity distribution of the ponds clustered in pond complexes, we assumed spatial autocorrelation between data points from the same pond complexes. Therefore, the random model included year and pond identity nested within pond complex to account for lack of temporal and spatial independence of observations. We used a step-down procedure to select the final models. Starting with a full

model, the densities of each species were analyzed including all variables used in the CCA as main effects and two-way interactions. A quadratic term (fish age squared) was added to account for potential nonlinear effects of the fish age gradient. To prevent multicollinearity, the quadratic term was centered by subtracting the mean of the variable from each case's value before squaring it. We used a correlation matrix to test candidate variables for multicollinearity, and significance of predictor variables with pair-wise correlation coefficients >0.3 was tested in our models omitting the correlated variable, i.e., alternative models were constructed. We progressively simplified the model by eliminating first interactions and then main terms that were the furthest from statistical significance. To verify that significant terms had not been wrongly excluded, each dropped term was then refitted to the minimal model. Wald tests were used to assess significance of fixed terms. Fish age was fitted as a continuous variable in the models; however, for presentation of the observed patterns, carp age classes were treated as a nominal term with three levels so that means and SE could be calculated.

We did not apply the Bonferroni correction when multiple tests on different response variables (species) addressed the same hypothesis (Moran 2003). Data were log (x+1) or arcsin-transformed to improve normality before GLMM analyses. Data were not transformed for CCA.

Results

The five environmental variables included by the CCA forward selection as best differentiating habitat preferences of waterbirds were macroinvertebrate abundance (conditional importance λ_a=0.12, F=5.17, P=0.002), fish age (as an ordinal trend; λ_a=0.11, F=4.78, P=0.002), fish biomass (λ_a=0.10, F=4.47, P=0.008), amphibian abundance (λ_a=0.06, F=3.25, P=0.014), and emergent vegetation cover (λ_a=0.08, F=4.12, P=0.002; Fig. 1). Permutation tests on the trace value (0.703; F=3.219, P=0.001) and on the value of axis 1 (eigenvalue=0.234; F=8.95, P=0.001) indicated that the variables included in the model explained a significant amount of the variation in the species data. Of the variables selected by the CCA models, significant correlations (at P<0.05) were found between fish age and biomass (r=0.6353); both these variables were negatively related to macroinvertebrate abundance in activity traps (r=−0.2408 and r=−0.2707). Abundance of larval amphibians was negatively correlated with fish age (r=−0.2265; GLMM means of relative amphibian abundance in ponds with different-aged carp are presented in Table 2), but the relationship with fish biomass was not significant (r=−0.1580). Also, amphibian abundance was associated with emergent vegetation (r=0.2994).
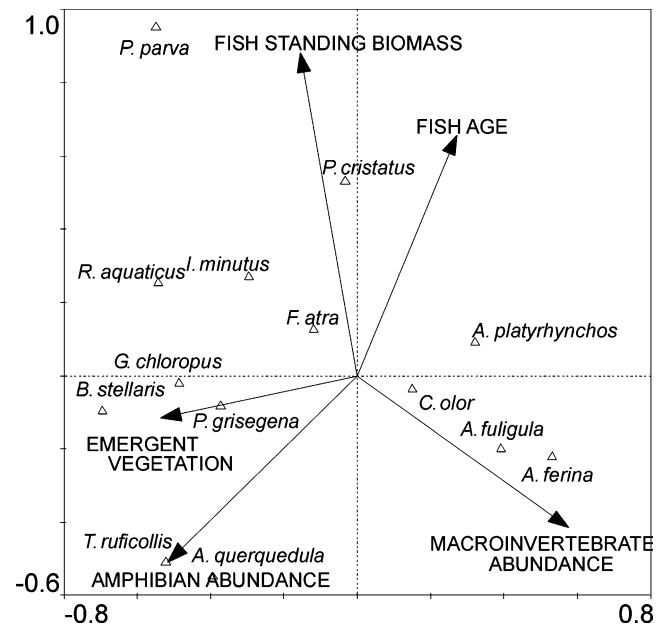
Fig. 1 Results of CCA on avian communities and environmental variables in 74 carp ponds sampled in 2002 and 2004

The inertia in the species data after fitting the covariables was 1.776. Of this, the first axis explained 12% and the second axis 6.3%. The canonical eigenvalues accounted together for 26.6% of the total variance. Correlation coefficients indicated that axis 1 of the CCA reflected trends across richly vegetated habitats (r=−0.5783) to open water habitats and those of increasing aquatic macroinvertebrate abundance (r=0.5944). Axis 2 was largely defined by the gradient of fish age (r=0.7272) and fish biomass (r=0.8889).
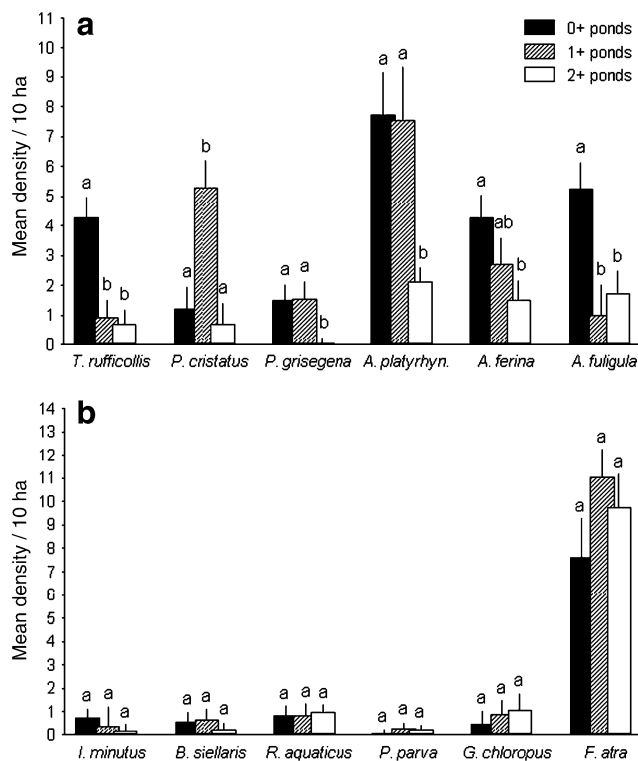
Individual ordination scores for bird species indicated that breeding habitat was selected with regard to food (macroinvertebrate or amphibian abundance, fish age, total fish biomass) and/or the proportion of emergent vegetation cover (Fig. 1). Tufted duck (r=0.4942, P<0.001) and mallard (r=0.3266, P<0.005) densities were most strongly correlated with macroinvertebrate relative abundance. The direction of the environmental vectors revealed that the presence of larger fish was negatively correlated with larval amphibian densities. Little grebe densities that correlated best with amphibian abundance (r=0.3772, P<0.001) were also negatively associated with fish age (r=−0.4337, P<0.001) and fish biomass (r=−0.3164, P<0.004). Great bittern and rallids (except moorhen) were associated with abundant emergent vegetation (r≥0.34, all P<0.003). The most common species in terms of overall occurrence, mallard (overall pond occupancy 89.4%) and coot (87.1%), but also mute swan (38.8%), tended to be clustered around the origin of the ordination, i.e., they were the most habitat generalist species.

Table 2 Effects of fish age/size structure on variables related to food availability for waterbirds (GLMM, normal error and identity link function)

	Mean (SE)			Wald χ^2 ($df=2$)	P
	0+ ponds ($N=37$)	1+ ponds ($N=22$)	2+ ponds ($N=15$)		
Amphibian abundance (g/1 trap; wet weight)	9.69[a] (2.76)	1.06[b] (0.61)	0.21[b] (0.15)	6.16	0.050
Macroinvertebrate abundance (mg/1 trap; dry weight)	0.78[a] (0.12)	0.33[b] (0.07)	0.27[b] (0.07)	14.47	<0.001
Water transparency (cm)	125.7[a] (5.6)	92.5[b] (7.2)	77.8[b] (6.6)	10.58	0.007

Unlike superscripts denote significant differences (2 standard errors of the difference=95% confidence limits)

Although some associations determined by CCA were not detected by the GLMMs, the GLMMs confirmed that habitat selection by individual species was typically influenced by either a food-related variable (most frequently the age of the fish in the pond; Fig. 2) or emergent vegetation cover (Table 3). Little grebe was the only species whose habitat selection depended on both fish age and the vegetation cover of the pond. In the case of grebes, little grebe preferred ponds with the youngest cohorts, red-necked grebe occurred in both 0+ and 1+ but was absent from 2+ ponds, and great crested grebe achieved the relatively highest breeding densities on 1+ ponds (Table 3; Fig. 2). No species was found to be positively associated with 2+ fish. Total fish biomass was correlated with carp age, but when included in the null models omitting carp age, it was positively related only to the densities of great crested grebe and pochard (Table 3). Pond area and water transparency were not selected by the CCA procedure ($\lambda_a <$ 0.06, both $P>0.1$) but were found significant for individual distribution patterns of some species by the GLMM. Water transparency was positively related to densities of coot, red-necked grebe, and great crested grebe. As indicated by the CCA correlation matrix, Secchi depth decreased with increasing fish age and total biomass ($r=-0.2969$ and $r=-0.3034$; Table 2). Also, GLMMs demonstrated the potential importance of interspecific interactions within waterbird guilds: Densities of red-necked grebe were positively related to great crested grebe presence, while moorhen showed a negative association with coot (Table 3). Total species richness was negatively related to fish age (Wald $\chi^2=4.42$, $df=1$, $P=0.0239$) and positively correlated with pond size and the proportion of emergent vegetation ($\chi^2 \geq 17.0$, $df=1$, both $P<0.001$).

Fig. 2 Breeding densities (pairs or calling males per 10 ha) of grebes, ducks (**a**), bitterns, and rallids (**b**) in carp ponds stocked with different age cohorts. 0+=young-of-the-year carp, 1+=1-year-old carp, 2+=2-year-old carp. GLMM predicted means (+SE) are shown. Note that GLMM statistics on bitterns and some rallids presented in Table 3 are derived from binomial models using species presence/absence data (see text for more details). Superscripts denote significant differences. Garganey was omitted because of its rare occurrence at ponds

Discussion

Our results show that waterbirds used two types of general cues for breeding habitat selection and two groups of species could be distinguished accordingly, although the suites of preferred habitat attributes overlapped between the groups. Densities of grebes and ducks were related to food availability (fish age and density, invertebrate or amphibian abundance; cf. Nummi et al. 1994; Haas et al. 2007). Bitterns and rallids were positively related to the amount of emergent vegetation, which might function both as shelter from predators and as a specific feeding habitat for some species (Jenkins and Ormerod 2002; Gilbert et al. 2003), while they were generally not correlated with the size structure of the fish community. The species studied have varying ability to move their young to another pond

Table 3 GLMMs (fixed part) for the estimated breeding densities or presence/absence of individual species and avian species richness at the ponds

Species	Effect	Estimate ± SE	Wald χ^2 ($df=1$)	P
Little grebe	Fish age	−0.748±0.274	7.46	0.008
	Emergent vegetation	3.265±1.088	9.00	0.005
	Amphibian abundance	0.436±0.203	4.60	0.036
Great crested grebe	Pond area	0.965±0.299	10.44	0.002
	Water transparency	0.986±0.355	7.69	0.007
	Fish squared age	−1.468±0.341	18.56	<0.001
	Pond permanence	1.276±0.528	5.85	0.018
	Fish biomass	0.195±0.046	18.04	<0.001
Red-necked grebe	Fish age	−0.614±0.296	4.28	0.038
	Water transparency	0.719±0.373	3.74	0.05
	Pond permanence	4.906±1.494	8.48	0.004
	Great crested grebe presence	1.616±0.536	9.09	0.003
Little bitern	Emergent vegetation	3.396±1.501	5.12	0.027
Great bittern	Emergent vegetation	5.500±1.530	12.92	0.001
	Pond area	1.374±0.435	9.95	0.003
Mute swan	Pond area	0.678±0.228	8.85	0.005
Mallard	Fish age	−0.344±0.153	5.09	0.027
Pochard	Fish age	−0.644±0.217	8.82	0.003
Tufted duck	Fish age	−0.781±0.309	6.38	0.013
	Fish biomass	−0.142±0.059	5.87	0.015
Water rail	Emergent vegetation	12.090±3.061	15.61	<0.001
	Pond area	2.940±0.838	12.31	0.001
Little crake	Emergent vegetation	8.477±3.115	7.41	0.009
	Pond area	2.062±0.888	5.39	0.024
Moorhen	Shoreline development	1.920±0.577	11.07	0.001
	Coot presence	−1.352±0.463	8.54	0.005
Coot	Water transparency	0.986±0.211	8.68	0.004
	Emergent vegetation	2.263±1.065	4.52	0.037
	Amphibian abundance	0.620±0.120	5.97	0.017

Garganey was omitted because it occurred in only 7% of the ponds. For the sake of brevity, the reduced models resulting from stepwise backward dropping of insignificant terms are presented. Statistics and P value of significant terms were taken from the minimal models; in great crested grebe and tufted duck, they were obtained by entering each of the intercorrelated variables into separate models

(reviewed in Elmberg et al. 1994); however, we assume that even in the "mobile" species (particularly dabbling ducks) the choice of nesting habitat is critical for breeding success because chick mortality is the highest in the early posthatching period when moving the brood seems most risky (Hill et al. 1987; reviewed by Sargeant and Raveling 1992). In great crested grebe and red-necked grebe, the preference for the early flooded ponds is probably related to grebes' inability to walk (Fjeldså 2004). After settling on ponds that are already filled, the early breeders cannot choose a different territory until the young have fledged, unless the clutch/brood fails.

The age/size of carp in the ponds significantly influenced densities of macroinvertebrates and larval amphibians. Nonfish prey of waterfowl can be heavily suppressed by fish predation (Eriksson 1979; Mallory et al. 1994). These effects may substantially depend on individual fish size due to fish capability of foraging on progressively larger prey over ontogeny (Persson 1988; Penttinen and Holopainen 1992). The size-dependent potential for predation on or competition with fish was apparently decisive for habitat choice in the "grebe-duck" assemblage. Young ducks and little and red-necked grebes feed heavily on macroinvertebrates and larval amphibians (Bandorf 1970; Hill et al. 1987; Kloskowski 2004). Therefore, breeding birds may avoid resource competition by shunning ponds with large-sized fish. The affinity to emergent vegetation among grebes was in inverse order to body size. Little grebe and red-necked grebe are well adapted for foraging both on open water and within emergent vegetation (Bandorf 1970;

Fjeldså 1982). Great crested grebes may be the least dependent on emergent vegetation as they pursue prey while diving in open water and nest even in very sparsely vegetated places (Fjeldså 2004). Females of the duck species studied can nest on pond shores or in sparse vegetation stands and thus rely more on food abundance in selecting a breeding habitat (see also Giles 1994; Nummi et al. 1994). Total fish biomass was an important factor structuring the avian community as a whole, but when individual patterns of species distribution were analyzed, it was associated only with great crested grebe and tufted duck densities. The effects of fish size and total biomass are difficult to separate in age-structured carp ponds because in spring, the biomass of young-of-the-year fish, even when stocked at high numerical densities, is naturally lower than that of older stocks. Since exceeding a critical density threshold is a prerequisite of carp impact on aquatic community (Zambrano et al. 2001; Bajer et al. 2009), density-dependent effects cannot be neglected. However, notwithstanding that 1+ and 2+ fish were stocked at similar levels of total biomass, densities of some bird species differed significantly between 1+ and 2+ ponds, indicating that the effect of carp size structure on these species was stronger than that of density.

Benthivorous fish such as carp can impact birds by elevating turbidity levels and disturbing submerged vegetation, which at high fish density induces an ecosystem shift to a macrophyte-poor turbid state (Crivelli 1983; Lammens 1999; Zambrano et al. 2001). These effects may be related to fish body size as well. Larger-sized benthivorous carp are capable of digging deeper in a substratum (Lammens and Hoogenboezem 1991) and create more turbidity via sediment and phosphorus suspension than small fish (Driver et al. 2005). The loss of macrophytes adversely affects the density of waterfowl foraging on vegetation and its associated invertebrates (cf. Hargeby et al. 1994). Elevated turbidity levels restrict the foraging efficiency of visually hunting avian predators (Cezilly 1992; Brenninkmeijer et al. 2002). However, even in the 2+ ponds (i.e., the ponds holding the oldest and largest fish), the average Secchi depth was still far from the estimated lower acceptable limit of ca. 40 cm for efficient great crested grebe predation on fish (van Eerden et al. 1993). The negative effects of fish on vegetation and water clarity can be delayed until summer (cf. Meijer et al. 1990; Haas et al. 2007), and breeding waterbirds may not be seriously affected, at least during the early breeding period. In carp ponds, the delay can be explained by low water temperature and reduced fish feeding activity in spring (Penttinen and Holopainen 1992; Richardson and Whoriskey 1992). We observed blue-green algae blooms in ≥1+ ponds only at the end of July and in August. Therefore, we suggest that the negative effects of carp on waterbirds were mainly driven by competition for food. Consequently, fish species that feed in the water column and are capable of attaining body size that allows exploitation of resources used by waterfowl may have no less potential to influence habitat suitability for birds than benthivorous fish (Eriksson 1979; Hill et al. 1987).

Bitterns and rallids rely at least in large part on animal diet, especially in the prefledging period, but only coot, being the single species that commonly acquires prey by diving (Cramp 1985), showed association with indices of food availability. However, our trapping method is likely to assess abundance of epibenthic and nektonic prey in open water habitats or open water interspersed with emergent vegetation stands, while some of the bird species dwelling in emergent vegetation are adapted for gleaning prey from emergent plants or gathering food on dry sites (Cramp 1985; Jenkins and Ormerod 2002). The piscivorous great bittern is a food opportunist that forages chiefly within dense stands of vegetation (Gilbert et al. 2003) and in pond conditions takes small wild-grown fish rather than carp (Polak 2007); thus, it may be independent of carp size structure. Among rallids, only moorhen was not related to emergent vegetation, but its distribution may be governed by agonistic competition with the more dominant coot. Moorhen is also strongly associated with terrestrial habitats around the breeding pond (Cramp 1985).

To sum up, fish individual size and factors which interact with size structure of fish populations, such as macro-invertebrate and amphibian abundance, water transparency, and pond permanence (Penttinen and Holopainen 1992; Driver et al. 2005), can play an important role in shaping distribution patterns of a significant part of the waterbird community, while avian guilds strongly associated with emergent vegetation were little responsive to variability in both fish size and density. Size structure of fish populations can also better explain niche diversification between some bird species than the fish presence/absence dichotomy. Waterfowl susceptible to competition from fish benefit from avoiding water bodies containing fish (Eriksson 1979; Giles 1994), and our data suggest that ducks tend to avoid ponds with larger fish in particular, presumably because they are more effective competitors than small fish. Small- and medium-sized piscivorous birds may prefer waters with rich populations of small-bodied fish over both habitats without fish and those dominated by large fish, i.e., invulnerable to predation (Allen et al. 2007; but see Paszkowski and Tonn 2000). Larger-bodied piscivorous species, like great crested grebe in the present study, are likely to select water bodies with bigger fish, attempting to align their size-limited predatory capacity with the better energetic return and other advantages of larger prey (Moser 1986; van Eerden et al. 1993; Paszkowski and Tonn 2000). In conditions of distinct fish size structure, e.g., in northern temperate shallow water bodies, where fish populations are regularly

structured by winter hypoxia or drought years (Tonn and Magnuson 1982; Holopainen and Hyvarinen 1985; Allen et al. 2007), individual fish size can be more significant than fish density for avian community composition. However, it should be recognized that the interplay between relative densities of fish size cohorts may be foremost in importance in more speciose assemblages with a mixture of size classes.

From a management perspective, large, heavily vegetated water bodies with small-bodied fish populations are likely to host the highest number of avian species (Elmberg et al. 1994; Weller 1999; Paszkowski and Tonn 2000). Habitats managed for breeding ducks and the smaller grebe species should harbor only small-bodied (young) fish or remain fishless (see also Giles 1994). However, water bodies dominated by populations of large-bodied fish may support relatively high avian species richness as well, provided that a considerable emergent vegetation cover is preserved. Management of habitats with size-structured fish communities can be specified to target selected bird species, e.g., by omitting piscivorous species at fisheries, to accommodate both wildlife conservation and economic interests.

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