RESEARCH

Identifying important habitats for waterbird conservation at a Greek Regional Nature Park

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Abstract

Background: Small coastal wetlands are vital sites for wintering waterbirds. Identifying important habitats is critical for managing waterbirds effectively. The Vourkari inlet is a small coastal wetland located near the capital Athens, within the most urbanized and industrialized area of Greece. We aimed at identifying the most important habitats for waterbirds at the Vourkari inlet during winter.

Methods: Data about habitat use and availability were collected for 14 waterbird species and for seven habitat classes. Habitat selection (Manly's selection ratio), overlap indices (Pianka's niche overlap index) and null models were calculated.

Results: All the studied waterbird species selected available habitats nonrandomly. Shallow waters (0–2 m), were used by 13 waterbirds and selected by five waterbirds. Pools and channels were used and selected by 10 species. Mud was used by nine species and selected by six species. Mud with rocky substrate was used by nine species and selected by eight species. Medium (2–4 m) and deep (4–6 m) open water habitats were used by seven species and selected by four species. Halophytic vegetation was used by six species and selected by two species. Several habitats were selected by nationally important populations: mudflat habitats (i.e., mud, mud with rocky substrate and pools and channels) by Common Redshanks (*Tringa totanus*), halophytic vegetation by Little Egrets (*Egretta garzetta*), shallow waters by Common Shelducks (*Tadorna tadorna*) and medium and deep waters by Sandwich Terns (*Thalasseus sandvicencis*), whilst shallow waters and mudflat habitats were preferred by a possibly internationally important population of Mediterranean Gulls (*Ichthyaetus melanocephalus*). Although overlap in habitat use between species was generally low, null models indicated habitat sharing and a lack of competition.

Conclusions: Waterbirds coexisted in the absence of competition for habitats at Vourkari, where they mostly used and preferred shallow water and mudflats. Small coastal wetlands are numerous, both in Greece and worldwide, therefore our findings would be useful as a basis for comparisons, both temporal at the inlet and spatial with other sites, that would help assess the importance of habitats and improve management strategies to benefit waterbirds, especially in areas with similar Mediterranean-type habitats and climate.

Keywords: Habitat selection, Habitat use, Mudflats, Niche overlap, Null models, Open water, Small coastal wetlands

Background

Understanding habitat requirements is fundamental to the effective conservation and management of animal species. In animal ecology, the habitat of a species refers to where that species lives, including the area and biotic and abiotic resources necessary for its survival and reproduction (Begon et al. 2006). Habitat use and habitat selection are the most common parameters used for understanding wildlife habitat needs in different life history stages (Cody 1985; Jones 2001). Block and Brennan (1993) defined habitat use as the way in which an individual or species uses habitats to meet its life history

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needs. Habitat selection refers to the choice of particular habitats in relation to their availability among all habitats, which may result in the disproportionate use of habitats and in individuals being nonrandomly distributed in space (Burger 1985). Jones (2001) remarked that habitat selection implies the understanding of complex behavioral and environmental processes, whereas habitat use patterns represent the actual distribution of individuals across habitats, being the end result of habitat selection processes. Competition among species plays an important role in shaping habitat selection. Svärdson (1949) noted that intraspecific competition tends to extend habitat use, whereas interspecific competition tends to limit it. Therefore, the study of habitat use and selection should involve the entire community and not only one or several species. This enables us to understand how species select between different resources to avoid competition and coexist, identifying the important habitats and informing how to implement effective conservation and management plans (Cody 1985).

Waterbirds include many different species (e.g. waterfowl, small and large waders, seabirds) which, at least at some part of their life cycle, are ecologically dependent on wetlands. The International Convention for the Conservation of Wetlands Especially as Waterfowl Habitat, signed in Ramsar, Iran in 1971 (known as the Ramsar Convention) defined wetlands, focusing on the ecological requirements of waterbirds, as "areas of marsh, fen, peatland or water, whether natural or artificial, permanent or temporary, with water that is static or flowing, fresh, brackish or salt, including areas of marine water the depth of which at low tide does not exceed six meters". Waterbird populations breeding in the north and northeastern Europe and western Siberia migrate to the south when their breeding grounds freeze and cannot thus provide them with the resources necessary for their survival. During the non-breeding season, eastern Mediterranean coastal wetlands become critically important foraging areas, hosting large numbers of waterbirds (BirdLife International 2004). Waterbirds need sufficient sources of nutrients and energy on wintering grounds to enable their survival and to invest in subsequent successful reproduction on their breeding grounds (Keddy 2010). Wetlands also offer products and services to people: habitat, flood protection, erosion control, water purification, carbon sequestration and opportunities for recreation and environmental and cultural education and research (Barbier et al. 2011). However, despite their ornithological significance and their contribution to human well-being, as wetlands occupy lowland, flat and productive lands, they have been drained worldwide and used for human activities, mostly cultivation and construction

(Keddy 2010). Davidson (2014) estimated that 87% of wetlands have been lost since the beginning of the eighteenth century. He also reported that the conversion of coastal natural wetlands accelerated more than that of inland natural wetlands in the twentieth century and also that conversion and loss is continuing in all parts of the world.

Greece is located in the eastern Mediterranean migratory flyway and its large wetland ecosystems host nationally and internationally important waterbird populations throughout the year (Goutner 1997; Liordos et al. 2014). Besides the large wetlands, small wetlands are also important for the conservation of many waterbird species, especially during the wintering and migration periods. Research has found that small wetlands serve as critical resting and refueling sites during spring and autumn migration and also offer valuable resources for the survival of wintering populations (Ntiamoa-Baidu et al. 2000; Skagen et al. 2008). There are an estimated 2,000 wetlands in Greece, both large and small (Fitoka and Keramitsoglou 2008). Of these, 805 small wetlands have been recorded in 75 islands (WWF Greece 2014) and 48 in the Region of Attiki (Greek Biotope/Wetland Centre 2017). The Vourkari Inlet Regional Nature Park is a small coastal wetland in Attiki, protected for its diverse waterbird assemblage, with species diversity and populations being the highest during the wintering period (Liordos 2011). Vourkari's habitats are constantly under pressure from human activities due to its proximity to the capital city of Athens metropolitan area.

Conserving waterbirds primarily involves conserving their habitats. Knowledge of the habitats most preferred by a species and those most selected by the entire waterbird assemblage is therefore necessary for their effective conservation and management (Keddy 2010). Therefore, numerous studies on habitat use, selection and community organization have been conducted worldwide (e.g. Jones 2001; Hamza et al. 2016; Elafri et al. 2017; Farinós-Celdrán et al. 2017; Chatterjee et al. 2020). Liordos (2010) described the structure of the waterbird assemblage at Vourkari during winter, by assigning species to foraging guilds. Few other studies have examined habitat use and community organization of waterbirds in Greek wetlands (e.g. Goutner and Papakostas 1992; Goutner 1997; Birtsas et al. 2011), whilst studies of habitat selection are lacking. In this study, we aimed at identifying important habitats for the conservation of the waterbirds wintering at the inlet by: (1) recording habitat use, measuring habitat availability and estimating habitat selection and (2) examining how patterns of habitat use differentiate or overlap among species.

Methods

Study area

The study was carried out at the Vourkari inlet (37°58′47″N, 23°23′17″E), Saronikos Gulf, western Attiki, Greece, a small coastal wetland covering 3.0 km² (Fig. 1). The less than 6 m deep wetland is situated about 30 km to the east of the capital city of Athens, with Salamina island delineating its easterly-oriented mouth. Human developments surround the wetland in close vicinity: small industries to the north, housing to the south and military and small aircraft civil airports to the west. These developments form a mosaic with pine forest (*Pinus halepensis*), shrubland, grassland and cultivation (olive and pistachio groves, vegetables). A total of 54 waterbird species have been recorded at the inlet, which is used mainly as a wintering and migration stopover area (Liordos 2011). The inlet holds nationally important wintering

populations of four waterbird species (comparisons with country-wide mid-winter counts in Liordos 2011): the Common Shelduck (*Tadorna tadorna*; 55 individuals, 1.0% of the national population), Little Egret (*Egretta garzetta*; 18 individuals, 1.0% of the national population), Common Redshank (*Tringa totanus*; 50 individuals, 2.2% of the national population) and Sandwich Tern (*Thalasseus sandvicensis*; 9 individuals, 2.2% of the national population) and 13 waterbird species have an unfavorable conservation status on the national and/or international level. Although available data is incomplete, preliminary comparisons suggested that nationally and probably internationally important populations of the Mediterranean Gull (*Ichthyaetus melanocephalus*; 400–2200 individuals) also winter at the inlet (Liordos 2012).

Vourkari inlet's location within the most heavily populated and industrialized area of Greece posed high pressures on waterbirds and their habitats. Therefore, the

Fig. 1 Map showing the Vourkari inlet, Saronikos Gulf, Greece. Solid yellow line indicates research area. Triangles indicate observation points. Satellite image: Sentinel-2 RGB: 321 (acquisition date: 15 February 2020). Inset map shows study area location within Greece (red dot)

Vourkari inlet was declared as a Regional Nature Park in 2017. Before 2017, activities that threatened the inlet included sand extraction, fishing both from the shore and on boat, collection of mollusks and crustaceans, household and industrial waste and pollution. After 2017, habitat encroachment through housing and industrial development was halted and activities such as fishing and sand extraction prohibited. The major threats that continue to threat the inlet's habitats and biodiversity are household waste and, most importantly, industrial pollution (Greek Biotope/Wetland Centre 2017).

Data collection

We studied habitat use and selection in winter, because it is the time of the year when the waterbird community is most diverse and abundant at Vourkari (Liordos 2011). We carried out 30 surveys during the wintering season of 2007–2008, every third day from 1 December 2007 to 26 February 2008. Four observation points (Fig. 1) were used, from which the scanning of the entire inlet was possible. Flock and individual bird movements were taken into account during switching between observation points to avoid collecting information on the same individual twice. A scan sampling of all feeding waterbirds (Martin and Bateson 1993) was carried out every third day from all 4 observation points, using a $25–75 \times 82$ fieldscope and 10×50 binoculars. Surveys were carried out in the morning, when birds were most active, and lasted for two to three hours (from 08:00 to 11:00 AM; GMT + 2.00). Species identity and foraging habitat of every observed individual were recorded using the initial observation method (i.e., only the first foraging observation of each individual was recorded). This method is subjected to conspicuousness bias, since the most active individuals are more likely to be discovered (Morse 1990). However, waterbird species at the Vourkari inlet were equally easy to detect due to the lack of visual obstacles and their proximity to the observer. Sequential observations (i.e., several consecutive observations from the same individual) were avoided since they are not independent; they are subjected to temporal autocorrelation, that is each observation is usually correlated with previous ones (Morrison 1984; Hejl et al. 1990). Surveys were performed by the same person (VL) to eliminate variation among researchers.

Habitat mapping

Seven habitat classes were identified at the inlet (Table 1). Field data were used together with satellite images (Sentinel-2 RGB: 321 and Google Earth) (Fig. 1) to measure the availability of each habitat class (Bobola et al. 2018). The tidal range in Greece is small, particularly in the Saronikos Gulf (mean 0.332 m; ESEAS: European Sea Level Service). Despite the small tidal range, habitat availability did vary between different tidal stages. To control for these variations, we estimated the position of the shoreline during each survey by using landmarks (e.g. buildings, trees, roads, outcrops). With the help of field observations, we drew the shoreline on satellite images and estimated habitat availability by overlapping satellite images with bathymetric maps freely available online (C-MAP Online: https://www.c-map.com/search-charts). Greater variations were observed in the availability of open water 0–2 m deep and mud habitat classes (standard error 3.5 and 2.7 respectively; Table 1). The availability of open water 2–4 m deep and open water 4–6 m deep habitat classes also varied, although to a lower degree, being lower at low than at high tide because of the increasing seafloor declivity with increasing distance from the coast (both standard errors 1.6; Table 1).

Table 1 Habitat classes identified during fieldwork and mapping at the Vourkari inlet, Saronikos Gulf, Greece

Habitat class	Habitat class availability (% ± SE)	Description
Open water (0–2 m)	38.4 ± 3.5	Shallow water from the shore to 2 m deep
Open water (2–4 m)	20.0 ± 1.6	The inlet's middle open water zone, 2–4 m deep
Open water (4–6 m)	8.3 ± 1.6	The inlet's outer open water zone, 4–6 m deep
Mud	20.0 ± 2.7	The shores of the inlet covered with mud, found mostly between halophytic vegetation and open water at the west side of the inlet
Mud with rocky substrate	3.3 ± 0.7	Areas of the mudflats with a rocky substrate
Halophytic vegetation	8.0 ± 0.0	Halophytic grassland dominated by Annual Glasswort (*Sarcocornia perennis*), Sea Rush (*Juncus maritimus*), Lesser Sea-spurrey (*Spergularia salina*) and Shrubby Seablite (*Suaeda vera*), found at the west side of the inlet
Pools and channels	2.0 ± 0.5	Small natural pools and channels formed on mudflats

Data analysis

Only the foraging habitat of waterbird species with at least 30 foraging observations were analyzed, because this is the proposed minimum sample size required for the analysis of foraging behavior (Morrison 1984). Habitat selection was studied by comparing the use and availability of each habitat class, using the selection ratio (Manly et al. 2002). For design I studies (individual animals are not identified; the habitat use and availability are measured at the scale of the population), this approach is implemented by the function widesI of the adehabitatHS R package (Calenge 2006, 2015). This function allows for testing two levels of habitat selection by each species. First, the function determined whether waterbirds used all the available habitats randomly with an overall test statistic (log-likelihood χ^2). Second, selection ratios were computed for each habitat and the differences between selection ratios were tested with pairwise Bonferroni tests. This allowed for the ranking of the relative selection of habitats by each waterbird species.

Pairwise overlap in habitat use of waterbird species was calculated using Pianka's niche overlap index (Pianka 1974). Overlap indices were computed by the piankabio function of the pgirmess R package (Giraudoux 2017). Although there are no critical levels with which overlap values can be compared, values higher than 0.60 were considered as biologically significant (Wallace 1981; Wallace and Ramsey 1983), and were classified as low (0.00–0.39), intermediate (0.40–0.60) or high (0.61–1.00), following suggestions by Grossman (1986).

Patterns of overlap in habitat use of the waterbird assemblage were calculated and tested against null models with the function niche_null_model of the EcoSimR R package (Gotelli et al. 2015). As waterbird morphology limits the habitats that can be used, the RA4 algorithm was used, because it retains the niche breadth of each species and fixes zero states to their observed values, and thus, only non-zero values are reshuffled within each row. In doing so, any differences between the observed data and the null model are above and beyond those imposed by morphological constraints (Albrecht and Gotelli 2001). The program performed 5000 Monte Carlo randomizations to create pseudo-communities, and then statistically compared the patterns (mean niche overlap values for all species pairs using Pianka's index) in these randomized communities with those in the real data matrix. Observed niche overlap that is higher than that expected by chance implies that species are sharing a niche and a lack of competition. Conversely, observed niche overlap lower than expected implies interspecific competition and resource partitioning (Albrecht and Gotelli 2001).

Habitat differentiation was further explored by comparing the use of each habitat between species using pairwise two-tailed *t*-tests after applying the Bonferroni correction for multiple comparisons (Zar 1999). This enabled the ranking of species by use within each habitat.

Analyses were performed in program R 3.6.2 (R Core Team 2019).

Results

Foraging observations and habitats

Fourteen waterbird species were observed foraging at least 30 times during the study period and were therefore included in the analyses. Their monthly breakdown is given in Table 2. The proportions of habitat use did not significantly differ between months for each habitat class and each of the 14 waterbird species ($\chi^2 > 4.605$, df = 2, $p > 0.100$). Monthly foraging observations were therefore pooled together for subsequent analyses. Open water 0–2 m deep was the most abundant habitat class at the Vourkari inlet, followed by open water 2–4 m deep and mud (Table 1, Fig. 2). Open water habitats and mud covered almost 90% of the inlet.

Habitat selection

The analysis of selection ratios showed nonrandom use of habitat classes for foraging by all 14 waterbird species (log-likelihood $\chi^2 = 131.307$–1707.654, $p < 0.001$).

Little Egrets used five habitat classes, more strongly selecting halophytic vegetation, followed by pools and channels and mud with rocky substrate, while avoiding mud and open water 0–2 m deep (Table 3, Fig. 2). Grey Herons (*Ardea cinerea*) used four habitat classes, showing a stronger selection for mud with rocky substrate and open water 0–2 m deep, followed by pools and channels, while avoiding mud. Great Cormorants (*Phalacrocorax carbo*) used three habitat classes, with a stronger selection for open water 4–6 m deep, followed by open water 2–4 m deep, while avoiding open water 0–2 m deep. Open water 2–4 m deep and open water 4–6 m deep were the most selected habitat classes, among the three used, by Great Crested Grebes (*Podiceps cristatus*), while open water 0–2 m deep was avoided. Common Shelducks showed a strong selection for the two habitat classes they used: pools and channels and open water 0–2 m deep. Mallards (*Anas platyrhynchos*) also strongly selected both habitat classes they used: open water 0–2 m deep and halophytic vegetation. Yellow-legged Gulls (*Larus michahellis*) used all available habitat classes, more strongly selecting open water 4–6 m deep, followed by pools and channels and open water 2–4 m deep, and more strongly avoiding halophytic vegetation and open water 0–2 m deep. Slender-billed Gulls (*Chroicocephalus genei*) used six habitat classes, showing a stronger

Table 2 Monthly breakdown of foraging observations (*N*) of 14 waterbird species wintering at the Vourkari inlet, Saronikos Gulf, Greece

Common name	Scientific name	December (10 surveys)		January (10 surveys)		February (10 surveys)		Total (30 surveys)	
		N	Mean ± SE	*N*	Mean ± SE	*N*	Mean ± SE	*N*	Mean ± SE
Little Egret	*Egretta garzetta*	105	10.5 ± 1.4	75	7.5 ± 1.1	94	9.4 ± 0.9	274	9.1 ± 1.0
Grey Heron	*Ardea cinerea*	117	11.7 ± 2.8	35	3.5 ± 0.6	56	5.6 ± 0.5	208	6.9 ± 2.2
Great Cormorant	*Phalacrocorax carbo*	87	8.7 ± 1.1	135	13.5 ± 3.1	484	48.4 ± 33.4	706	23.5 ± 16.7
Great Crested Grebe	*Podiceps cristatus*	12	1.2 ± 0.7	27	2.7 ± 1.7	186	18.6 ± 11.1	225	7.5 ± 5.8
Common Shelduck	*Tadorna tadorna*	43	4.3 ± 2.7	128	12.8 ± 5.4	369	36.9 ± 13.8	540	18.0 ± 6.9
Mallard	*Anas platyrhynchos*	34	3.4 ± 2.0	25	2.5 ± 1.4	17	1.7 ± 0.5	76	2.5 ± 1.3
Yellow-legged Gull	*Larus michahellis*	654	65.4 ± 20.4	670	67.0 ± 10.8	584	58.4 ± 3.8	1908	63.6 ± 9.4
Slender-billed Gull	*Chroicocephalus genei*	12	1.2 ± 0.8	10	1.0 ± 0.6	180	18.0 ± 7.8	202	6.7 ± 6.5
Black-headed Gull	*Chroicocephalus ridibundus*	1365	136.5 ± 43.8	1294	129.4 ± 20.7	1157	115.7 ± 25.0	3816	127.2 ± 37.9
Mediterranean Gull	*Ichthyaetus melanocephalus*	417	41.7 ± 19.1	437	43.7 ± 18.6	385	38.5 ± 14.1	1239	41.3 ± 18.8
Sandwich Tern	*Thalasseus sandvicensis*	36	3.6 ± 0.6	39	3.9 ± 1.1	26	2.6 ± 0.8	101	3.4 ± 0.6
Common Redshank	*Tringa totanus*	201	20.1 ± 8.3	235	23.5 ± 5.9	235	23.5 ± 4.1	671	22.4 ± 5.7
Little Stint	*Calidris minuta*	155	15.5 ± 1.6	145	14.5 ± 2.7	133	13.3 ± 3.5	433	14.4 ± 2.4
Dunlin	*Calidris alpina*	218	21.8 ± 3.5	239	23.9 ± 2.0	202	20.2 ± 4.5	659	22.0 ± 3.1

selection for open water 2–4 m deep, followed by pools and channels and mud with rocky substrate, while avoiding open water 4–6 m deep, open water 0–2 m deep and mud. Black-headed Gulls (*Chroicocephalus ridibundus*) and Mediterranean Gulls both used the same six habitat classes, also both showing a stronger selection for pools and channels and mud with rocky substrate and a stronger avoidance of open water 2–4 m deep and open water 4–6 m deep. Sandwich Terns were observed only in open water habitat classes, more strongly selecting open water 4–6 m deep, followed by open water 2–4 m deep, while avoiding open water 0–2 m deep. Common Redshanks and Dunlins (*Calidris alpina*) used five habitat classes, whereas Little Stints (*Calidris minuta*) used four habitat classes. All these small wading birds most strongly selected mud, followed by pools and channels and mud with rocky substrate, while avoiding halophytic vegetation and open water 0–2 m deep.

Habitat differentiation
Ranking of species by habitat use
Open water 0–2 m deep was the habitat class used by the most waterbird species (13), followed by pools and channels (10), mud (9), mud with rocky substrate (9), open water 2–4 m deep (7), open water 4–6 m deep (7) and halophytic vegetation (6) (Table 4).

Open water 0–2 m deep was most used by Mallards, Common Shelducks and Grey Herons, and least used by Slender-billed Gulls, Sandwich Terns, Common Redshanks, Yellow-legged Gulls, Dunlins and Great Crested Grebes. Open water 2–4 m deep was used more by

Great Crested Grebes, followed by Slender-billed Gulls, Great Cormorants, Sandwich Terns, Yellow-legged Gulls, Black-headed Gulls and Mediterranean Gulls. Open water 4–6 m deep was used more by Sandwich Terns, Yellow-legged Gulls, Great Cormorants and Great Crested Grebes, and less by Black-headed Gulls and Mediterranean Gulls. Mud was used more by Little Stints, Dunlins and Common Redshanks than by Black-headed Gulls, Mediterranean Gulls, Yellow-legged Gulls, Little Egrets, Grey Herons and Slender-billed Gulls. Mud with rocky substrate was equally used by nine waterbird species. Halophytic vegetation was used more by Little Egrets than all other species observed in this habitat class. Common Shelducks used pools and channels more than Slender-billed Gulls, Yellow-legged Gulls and Grey Herons.

Habitat overlap
Interspecific overlap in habitat class use was highly variable among the waterbird assemblage, with values being low between 47 pairs, intermediate between 18 pairs and high between 26 pairs (Table 5). Habitat overlap was higher between: (a) Common Redshanks, Little Stints and Dunlins (1.00), (b) Common Shelducks, Mallards, Black-headed Gulls, Mediterranean Gulls, Little Egrets and Grey Herons (0.58–0.99), and (c) Great Cormorants, Great Crested Grebes, Yellow-legged Gulls, Slender-billed Gulls and Sandwich Terns (0.54–0.93). On the contrary, habitat overlap was lower between species of different groups: (a) between species from the Common Redshank, Little Stint, Dunlin group and species from
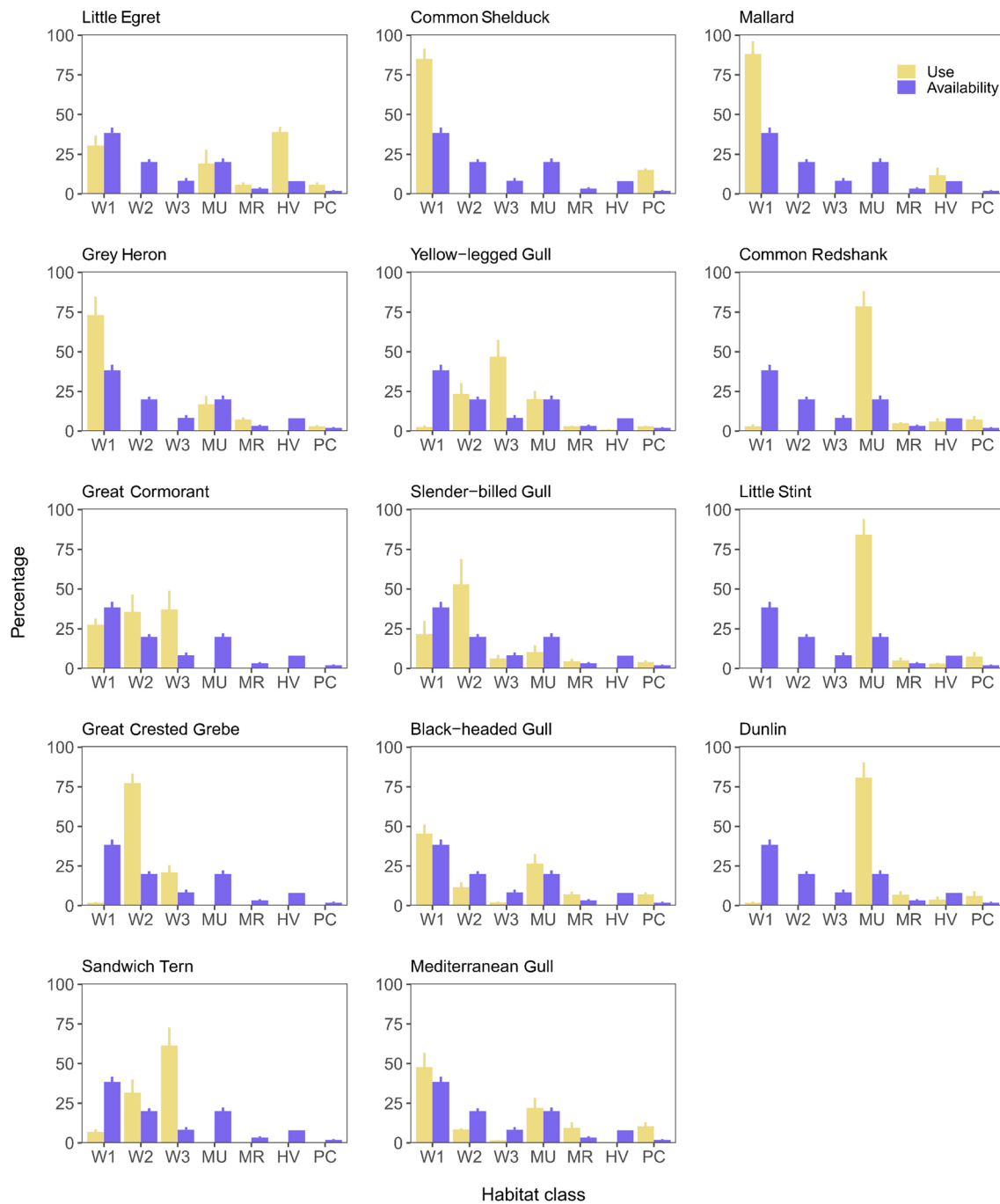
Fig. 2 Comparison of mean foraging habitat use (+ 1 SE) and habitat availability (+ 1 SE) by 14 waterbird species wintering at the Vourkari inlet, Saronikos Gulf, Greece. *W1* Open water (0–2 m), *W2* Open water (2–4 m), *W3* Open water (4–6 m), *MU* Mud, *MR* Mud with rocky substrate, *HV* Halophytic vegetation, *PC* Pools and channels

the Great Cormorant, Great Crested Grebe, Common Shelduck, Mallard, Sandwich Tern group (0.00–0.05), and (b) between species from the Great Crested Grebe,

Yellow-legged Gull, Sandwich Tern group and species from the Little Egret, Grey Heron, Mallard, Common Shelduck group (0.01–0.18).

Table 3 Manly's selection ratio (wi ± SE) of habitats used by 14 species of waterbirds wintering at the Vourkari inlet, Saronikos Gulf, Greece

Habitat class	wi ± SE	Rank	Habitat class	wi ± SE	Rank
Little Egret			Black-headed Gull		
Halophytic vegetation	4.86 ± 0.37	1	Pools and channels	3.72 ± 0.42	1
Pools and channels	2.97 ± 0.22	2	Mud with rocky substrate	2.19 ± 0.25	2
Mud with rocky substrate	1.75 ± 0.09	3	Mud	1.32 ± 0.06	3
Mud	0.95 ± 0.12	5	Open water (0–2 m)	1.19 ± 0.03	3
Open water (0–2 m)	0.79 ± 0.07	5	Open water (2–4 m)	0.58 ± 0.03	5
Grey Heron			Open water (4–6 m)	0.23 ± 0.03	6
Mud with rocky substrate	2.16 ± 0.38	1	Mediterranean Gull		
Open water (0–2 m)	1.91 ± 0.09	1	Pools and channels	5.29 ± 0.81	1
Pools and channels	1.47 ± 0.42	3	Mud with rocky substrate	2.86 ± 0.38	2
Mud	0.84 ± 0.13	4	Open water (0–2 m)	1.25 ± 0.05	3
Great Cormorant			Mud	1.11 ± 0.07	3
Open water (4–6 m)	4.44 ± 0.35	1	Open water (2–4 m)	0.42 ± 0.04	6
Open water (2–4 m)	1.78 ± 0.11	2	Open water (4–6 m)	0.20 ± 0.05	6
Open water (0–2 m)	0.78 ± 0.05	3	Sandwich Tern		
Great Crested Grebe			Open water (4–6 m)	7.37 ± 0.73	1
Open water (2–4 m)	3.87 ± 0.19	1	Open water (2–4 m)	1.58 ± 0.24	2
Open water (4–6 m)	2.51 ± 0.36	1	Open water (0–2 m)	0.18 ± 0.07	3
Open water (0–2 m)	0.38 ± 0.02	3	Common Redshank		
Common Shelduck			Mud	3.93 ± 0.16	1
Pools and channels	7.63 ± 1.26	1	Pools and channels	3.67 ± 0.63	1
Open water (0–2 m)	2.22 ± 0.06	2	Mud with rocky substrate	1.56 ± 0.26	3
Mallard			Halophytic vegetation	0.74 ± 0.11	3
Open water (0–2 m)	2.30 ± 0.11	1	Open water (0–2 m)	0.08 ± 0.01	5
Halophytic vegetation	1.47 ± 0.37	2	Little Stint		
Yellow-legged Gull			Mud	4.22 ± 0.18	1
Open water (4–6 m)	5.62 ± 0.36	1	Pools and channels	3.88 ± 0.32	2
Pools and channels	1.57 ± 0.28	2	Mud with rocky substrate	1.52 ± 0.25	3
Open water (2–4 m)	1.18 ± 0.06	2	Halophytic vegetation	0.37 ± 0.11	4
Mud	1.01 ± 0.05	2	Dunlin		
Mud with rocky substrate	0.90 ± 0.14	2	Mud	4.04 ± 0.17	1
Halophytic vegetation	0.12 ± 0.03	7	Pools and channels	3.16 ± 0.63	2
Open water (0–2 m)	0.06 ± 0.01	7	Mud with rocky substrate	2.09 ± 0.36	3
Slender-billed Gull			Halophytic vegetation	0.49 ± 0.10	4
Open water (2–4 m)	2.65 ± 0.20	1	Open water (0–2 m)	0.05 ± 0.01	5
Pools and channels	2.01 ± 0.31	2			
Mud with rocky substrate	1.34 ± 0.25	3			
Open water (4–6 m)	0.77 ± 0.21	6			
Open water (0–2 m)	0.57 ± 0.08	6			
Mud	0.52 ± 0.11	6			

The observed overlap in habitat use (mean niche overlap value for all species pairs) was 0.41, significantly higher than that expected by chance (null communities; mean overlap = 0.31; $p = 0.006$).

Discussion

Importance of habitats for waterbirds

Waterbirds wintering at Vourkari used a variety of habitats, showing significant similarities and differences in

Table 4 Foraging habitat differentiation among 14 species of waterbirds wintering at the Vourkari inlet, Saronikos Gulf, Greece

Habitat class	Species ranking by habitat use
Open water (depth 0–2 m)[1]	MA[a] > CS[a] > GH[ab] > MG[bc] > BG[bc] > LE[c] > GC[c] > SG[cd] > ST[d] > CR[d] > YG[d] > DU[d] > GG[d]
Open water (depth 2–4 m)[2]	GG[a] > SG[ab] > GC[ab] > ST[b] > YG[b] > BG[b] > MG[b]
Open water (depth 4–6 m)[2]	ST[a] > YG[a] > GC[ab] > GG[ab] > SG[bc] > BG[c] > MG[c]
Mud[3]	LS[a] > DU[a] > CR[a] > BG[b] > MG[b] > YG[b] > LE[b] > GH[b] > SG[b]
Mud with rocky substrate[3]	MG[a] > BG[a] > GH[a] > DU[a] > LE[a] > CR[a] > LS[a] > SG[a] > YG[a]
Halophytic vegetation[4]	LE[a] > MA[b] > CR[b] > DU[b] > LS[b] > YG[b]
Pools and channels[5]	CS[a] > MG[ab] > LS[ab] > BG[ab] > CR[ab] > DU[ab] > LE[ab] > SG[b] > YG[b] > GH[b]

Species were pairwise compared with two-tailed *t*-tests and ranked in descending order of use of each habitat class

Species not sharing a common letter differ significantly in the use of each habitat class. Bonferroni adjustment for multiple testing: [1]$p < 0.0006$; [2]$p < 0.0024$; [3]$p < 0.0014$; [4]$p < 0.0033$; [5]$p < 0.0011$

LE Little Egret, *GH* Grey Heron, *GC* Great Cormorant, *GG* Great Crested Grebe, *CS* Common Shelduck, *MA* Mallard, *YG* Yellow-legged Gull, *SG* Slender-billed Gull, *BG* Black-headed Gull, *MG* Mediterranean Gull, *ST* Sandwich Tern, *CR* Common Redshank, *LS* Little Stint, *DU* Dunlin

Table 5 Pairwise habitat use overlap (Pianka's niche overlap indices) of 14 species of waterbirds wintering at the Vourkari inlet, Saronikos Gulf, Greece

	LE	GH	GC	GG	CS	MA	YG	SG	BG	MG	ST	CR	LS
GH	*0.64*												
GC	0.27	0.46											
GG	0.01	0.02	*0.78*										
CS	0.58	*0.96*	0.47	0.02									
MA	*0.66*	*0.96*	0.47	0.02	*0.98*								
YG	0.18	0.13	*0.80*	*0.62*	0.05	0.05							
SG	0.29	0.41	*0.79*	*0.92*	0.38	0.37	0.55						
BG	*0.67*	*0.93*	0.54	0.23	*0.84*	*0.82*	0.34	*0.61*					
MG	*0.67*	*0.95*	0.52	0.18	*0.89*	*0.86*	0.29	0.56	*0.99*				
ST	0.06	0.10	*0.89*	*0.67*	0.10	0.10	*0.93*	0.54	0.21	0.18			
CR	0.44	0.27	0.02	0.00	0.05	0.05	0.37	0.20	0.53	0.46	0.00		
LS	0.39	0.23	0.00	0.00	0.02	0.01	0.36	0.19	0.50	0.43	0.00	*1.00*	
DU	0.41	0.26	0.01	0.00	0.04	0.03	0.37	0.20	0.52	0.45	0.00	*1.00*	*1.00*

Biologically significant overlap indices (> 0.60) are shown in italics

LE Little Egret, *GH* Grey Heron, *GC* Great Cormorant, *GG* Great Crested Grebe, *CS* Common Shelduck, *MA* Mallard, *YG* Yellow-legged Gull, *SG* Slender-billed Gull, *BG* Black-headed Gull; *MG* Mediterranean Gull, *ST* Sandwich Tern, *CR* Common Redshank, *LS* Little Stint, *DU* Dunlin

use patterns among them. Analyses also showed that all the studied waterbird species selected available habitats nonrandomly. Mallards are omnivorous generalists that may forage on water or land, mostly preferring shallow waters, mudflats and postharvest cultivations, mostly rice fields in the Mediterranean (Camargue, France, Dehorter and Tamisier 1998; Göksu Delta, Turkey, Green 1998; central Italy, Rizzo and Battisti 2009; Extremadura, Spain, Navedo et al. 2012). At Vourkari, Mallards preferably used shallow water and halophytic vegetation to exploit plant and animal food types. Common Shelducks are mostly carnivorous, predominantly using shallow waters, mudflats and saltpans (Doñana, south-west

Spain, Rendón et al. 2008; Angelochori, Thessaloniki, Greece, Birtsas et al. 2011; western France, Viain et al. 2011; Sebkhat, eastern Algeria, Bellagoune et al. 2015). Similarly, these Dabbling Ducks preferred foraging on shallow water and mudflat habitats, especially pools and channels, at Vourkari.

Grey Herons and Little Egrets mostly use shallow coastal waters, mudflats, freshwater marshes, salt-marshes, rivers, canals and rice fields in the Mediterranean (Axios Delta, Greece, Kazantzidis and Goutner 1996; Kazantzidis and Goutner 2008; central Italy, Redolfi De Zan et al. 2011; northwestern Iberian Peninsula, Regos 2011). More specifically, Little Egrets are more

generalists, using rice fields, freshwater marshes, salt-marshes and coastal shallow waters in similar proportions, whereas Grey Herons preferred coastal shallow waters (Kazantzidis and Goutner 2008; Regos 2011) and secondarily muddy habitats (Regos 2011). At Vourkari, Little Egrets used shallow water, mudflat habitats and halophytic vegetation, with a strong preference for the two latter, whereas Grey Herons used shallow water, mostly, and mudflat habitats. Although mostly piscivorous, Little Egrets and Grey Herons also feed on a variety of food types (Cramp and Simmons 1977; Kushlan and Hancock 2005) and they were often seen chasing crabs and small fish, in shallow waters or trapped in pools and channels on the inlet's mudflats (Liordos 2010). The strong preference for halophytic habitats by Little Egrets suggested a more varied diet, also consisting of amphibians, insects and other invertebrates.

Larid species use a variety of foraging habitats, from open sea and coastal wetlands to inland areas, mostly seen on water and muddy habitats of Mediterranean coastal wetlands (Adriatic Sea, Italy, Fasola et al. 1989; Alyki Kitrous, Macedonia, Greece, Goutner and Papakostas 1992; Ebro Delta and Doñana, Spain, Sanz-Aguilar et al. 2014). Mediterranean and Black-headed Gulls mainly feed on invertebrates, such as mollusks, crustaceans, worms and insects, but also consume plant material (Cramp and Simmons 1983; Goutner 1994). Yellow-legged and Slender-billed Gulls prefer feeding on fish during the breeding season (Skórka and Wójcik 2008; Sanz-Aguilar et al. 2014), whereas they take a more varied diet outside the breeding season, also including mollusks, crustaceans, worms, insects and plants (Cramp and Simmons 1983; Gonzáles-Solís et al. 1997). At Vourkari, all larid species used mudflat habitats, where they were observed feeding on aquatic plants and exposed invertebrates, crustaceans and small fish. They also used open water habitats, with Mediterranean and Black-headed Gulls preferring the shallower part and Yellow-legged and Slender-billed Gulls preferring the deeper part of the inlet. These preferences, in agreement with findings from previous studies, suggested the exploitation of a variety of habitats and food types by larids, and also the targeting of predominantly fish prey by Yellow-legged and Slender-billed Gulls.

Great Cormorants, Sandwich Terns and Great Crested Grebes are diving birds that use open water habitats (Fasola et al. 1989; Celdrán and Aymerich 2010) and feed almost exclusively on fish (Martinoli et al. 2003; Liordos and Goutner 2008; Cotin et al. 2011). Great Cormorants hunt solitarily by chasing bottom-living fish usually at depths 2–10 m (Kato et al. 2006) or in large groups targeting fish schools near the surface (Van Eerden and Voslamber 1995). At Vourkari, Great Cormorants used all open water zones, mostly preferring depths of 2–6 m, and foraged solitarily, suggesting a diet of benthic fish. Sandwich Terns feed on small surface-dwelling fish (Cotin et al. 2011) and also used all open water zones at the inlet, mostly preferring depths of 2–6 m. Great Crested Grebes target fish at various depths of the water column, primarily in the zone of 2–4 m (Martinoli et al. 2003), which was the one more strongly selected at Vourkari.

The intertidal mudflats of coastal Mediterranean wetlands are of prime importance for millions of waders that use them as foraging grounds during the non-breeding season (Masero et al. 2000; Hamza and Selmi 2015; Martins et al. 2016). At Vourkari, Dunlins, Little Stints and Common Redshanks were observed almost exclusively on mudflat habitats pecking or probing the mud for capturing their favorite invertebrate prey: polychaete worms, earthworms, dipteran flies and other insects, small gastropods, mollusks, crustaceans (Lifjeld 1984; Barbosa and Moreno 1999; Martins et al. 2013).

Competition among waterbirds

Liordos (2010) found that the waterbird assemblage at Vourkari was structured in five foraging guilds according to habitat use and feeding techniques, each consisted of species with generally narrow niches and high niche overlap between them, and generally low niche overlap between species of different guilds. The guild structure and the small number of species within each guild (1–6) could explain the generally low to medium overlap in habitat use between species pairs across the waterbird assemblage. The use of similar foraging habitats by waterbirds in the same guild suggested that they should differ in some other niche dimensions (Gotelli and Graves 1996). Diving birds foraged exclusively in open water, however, their feeding techniques suggested the use of different parts of this habitat: the bottom by Great Cormorants, the water column by Great Crested Grebes and the water surface by Sandwich Terns, further suggesting differentiation in fish prey type and size (Liordos 2010). In waders, prey size was positively correlated with body size (weight, wing length; Lifjeld 1984). Common Redshanks, Dunlins and Little Stints highly overlapped in habitat use, exploiting mudflat habitats, however they should target prey of different size as they also differ in body size, with the former being the largest and the latter the smallest. Although belonging to different guilds (Liordos 2010), Mallards and Common Shelducks highly overlapped in habitat use with Grey Herons and Little Egrets. They differentiated their niches by using different feeding techniques: sieving, upending, head and neck dipping (Dabbling Ducks) and striking (Ardeids), thus targeting different prey types and sizes (Dabbling Ducks:

small invertebrates and seeds, Ardeids: mostly fish; Cramp and Simmons 1977).

The null model analysis indicated that the observed mean overlap in habitat use, although low, was significantly higher than that expected by chance. This suggested that interspecific competition was not a significant mechanism of habitat partitioning in the waterbird community, and that the species shared the most abundant resources. However, this interpretation is controversial, as it is also possible that high overlap implies strong competition that has not yet led to segregation in habitat use (Gotelli and Graves 1996) and additional data on resource availability and species interactions is necessary for a definitive answer (Sale 1974; Connell 1980). Null models can at least indicate which direction observed patterns are in, and as such, our results indicated habitat sharing, although overlap values were small.

Conclusions

Our findings identified open water of various depths and mudflat habitats as the most important for the conservation of the waterbird assemblage at the Vourkari inlet, a Regional Nature Park located within the most urbanized and industrialized area of Greece. Although overlap in habitat use between species was generally low, null models indicated resource sharing and a lack of competition. Household and industrial pollution, the major current threats to the inlet, should be controlled for effective habitat conservation. The inlet's habitats could also be variously affected by sea level rise, which is expected to more severely affect the Mediterranean in comparison to other areas (Church et al. 2013). However, possible changes in the wetland resources necessary for the fulfillment of waterbird needs are hard to predict and understand without experimentation (McCoy et al. 2020; Serrano et al. 2020). Therefore, future research should focus on the study of species interactions and the assessment of habitat quality and suitability for waterbirds by including measures of food availability, energy intake, salinity, water quality, waste and pollution levels.

Research has shown that small coastal wetlands, such as the Vourkari inlet, are vital for the survival of waterbirds, especially as wintering and migration stopover areas (Ntiamoa-Baidu et al. 2000; Skagen et al. 2008; Liordos 2011). Such wetlands are numerous in Greece and globally. Therefore, our findings could be used as a basis for temporal, within the inlet, and spatial comparisons with other areas, especially areas with similar Mediterranean-type habitats and climate. This would allow for better identifying the importance of certain sites and habitats and to improve management strategies to benefit waterbirds.

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