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Foraging Guilds of Waterbirds Wintering in a Mediterranean Coastal Wetland

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Vasilios Liordos (2010) Foraging guilds of waterbirds wintering in a Mediterranean coastal wetland. *Zoological Studies* **49**(3): 311-323. The foraging behavior of the waterbird assemblage of a small Mediterranean coastal wetland at Vourkari inlet, Saronikos Gulf, Greece, was studied during the wintering season of 2007-2008. The foraging habitat types and feeding techniques used by each individual of 14 species were recorded during 30 sessions, each involving 4 observation points from which the entire wetland could be scanned. Seven habitat types and 11 feeding techniques were used by waterbirds during the study period. The waterbird assemblage was classified into 5 foraging guilds: stalking ardeids (1 egret and 1 heron), shallow-water divers (1 cormorant and 1 grebe), shallow-water generalists (2 ducks and 4 gulls), shallow-water plunge-divers (1 tern), and mud-peckers (3 small shorebirds). The low bidimensional niche breadth of most species, except gulls, and the low niche overlap among species of different guilds suggested a relatively high degree of specialization within this waterbird assemblage. In contrast, the overlap between species of the same guild was high, although variations in the use of habitats and mainly feeding techniques did occur. Intra-guild habitat partitioning was also observed, with diving and gull species using different zones of shallow-water areas. The 2 main habitats, shallow waters and intertidal mudflats, were the most important for waterbirds, with halophytic vegetation being important only for Little Egrets *Egretta garzetta*. The information provided herein is useful for a better understanding of birds' habitat requirements and the future management and conservation of coastal wetlands. http://zoolstud.sinica.edu.tw/Journals/49.3/311.pdf

Key words: Foraging habitat, Feeding techniques, Bidimensional niche, Community structure, Vourkari inlet.

Knowledge about the population and community ecology of animals and the study of their habitats are necessary for successful conservation strategies (Hanski and Gilpin 1997) and were investigated in many different taxa (Dagobert et al. 2008, Principe 2008, Ko et al. 2009, Mieczan 2009). The Mediterranean coast supports important wintering waterbird populations and is located in the migratory flyways of many species (BirdLife International 2004). Coastal wetlands of the Mediterranean are therefore critical foraging areas for many waterbirds during winter and migration periods, since they must build up sufficient fat reserves (Weller 1999, Kober and Bairlein 2009) which are crucial for their survival and breeding on nesting grounds (Morrison et al. 2007). Despite the documented ornithological significance of this region, studies of the structure and organization of waterbird communities in relation to biotic and abiotic factors are limited (Green 1998). In addition, many waterbird species face a steady decline in their global populations (BirdLife International 2004, Stroud et al. 2004). There is therefore an urgent need for relevant information that can fill gaps in our knowledge of the ecology of waterbird communities and will be useful in the future to better understand habitat requirements of waterbirds in coastal wetlands and provide informed conservation and management of crucial sites.

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Hutchinson (1959) first developed the idea that the boundaries of realized niches are set by competition for limited resources and assumed that groups of species sharing similar resources are common in nature because a complex trophic organization of a community is more stable than a simpler one. This approach to community ecology led to the need to divide communities in groups of lower ranks according to similarities in resource utilization. Although the term “guild” was first used by plant geographers (Schimper 1903) and plant ecologists (Clements 1905), it was a zoologist (Root 1967) who formally defined the term as “a group of species that exploit the same class of environmental resources in a similar way. This term groups together species without regard to taxonomic position, that overlap significantly in their niche requirements”. Guilds are assumed to be coevolved entities that provide important information on community structure and processes organizing communities (Pianka 1980, Jaksić and Medel 1990, Blondel 2003, López de Casenave et al. 2008). A plethora of studies followed Root’s (1967) definition, describing the guild structure of animal assemblages (Cody 1974, Holmes et al. 1979) and the ecological and evolutionary mechanisms that allow the coexistence of species in a particular guild (Landres and MacMahon 1980, Dayan et al. 1989).

Food availability is one of the most important factors determining bird distributions (Evans and Dugan 1984). Moreover, habitat structure influences waterbird foraging behavior by means of food availability and the energetic constraints of obtaining it and is associated with the adaptation potential of a species to a specific habitat type in terms of its morphology (Holmes et al. 1979, Wiens 1989). Foraging habitat use and feeding methods are therefore important factors involved in resource partitioning (Wiens 1989, Weller 1999) and can be used to assign foraging guilds to birds (Gatto et al. 2008, López de Casenave et al. 2008).

Greece is located in the eastern Mediterranean migratory flyway, and its coastal wetlands are important for many waterbird species (Goutner and Papakostas 1992, Goutner et al. 2005). Moreover, small dispersed coastal wetlands are a common pattern throughout most of Greece, and current research has demonstrated the significance of such wetlands especially as wintering and migration stopover sites for waterbirds (Ntiamoa-Baidu et al. 2000, Skagen et al. 2008). The Vourkari inlet is a small coastal wetland located in east-central mainland Greece, near the capital city of Athens. It is considered important for wintering and migrating waterbirds with over 50 species using its habitats for foraging and resting activities (V. Liordos unpubl. data). It is proposed for designation as a new wildlife refuge due to its ornithological importance and its continued exposure to anthropogenic pressures mainly because of its position within the most heavily populated district in Greece.

The aim of this paper was therefore to study the waterbird community structure of a Mediterranean coastal wetland, the Vourkari inlet, by: 1) describing the foraging habitats and feeding techniques used by waterbird species feeding within the inlet during the wintering season; 2) quantifying species’ niche breadth and overlap for the former 2 niche dimensions; and 3) classifying the waterbird assemblage into bidimensional foraging guilds.

MATERIALS AND METHODS

Study area

The study was carried out at Vourkari inlet (37°58'47"N, 23°23'17"E), Saronikos Gulf, western Attiki, Greece, a small relatively shallow coastal wetland covering 3.0 km^2 with its associated habitats (Fig. 1). It is situated about 30 km to the east of the capital city of Athens, with Salamina Island delineating its easterly oriented mouth. The wetland is < 6 m deep, and its main habitats include open water, intertidal mudflats, and a halophytic grassland dominated by glasswort *Salicornia fruticosa* and shrubby seablite *Suaeda vera* (Margaris et al. 2004). Human activities within and around the inlet include aquaculture, boat fishing, housing, and industry. The latter 2 threaten the inlet by habitat destruction through construction activities and pollution influx.

Data collection

Field foraging observations were made during the wintering season of 2007-2008, from 1st Dec. 2007 to 26th Feb. 2008. Four observation points (Fig. 1) were used, from which it was possible to scan the entire inlet. 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

3rd day from all 4 observation points, using a 25-75 × 82 fieldscope and 10 × 50 binoculars, distributed so as to include different tidal stages, hours of the day, and days. The species identity, foraging habitats, and feeding techniques of every waterbird were recorded using the initial observation method (i.e., only the 1st foraging observation of each individual was considered). This method is subject to conspicuousness bias, since the most active individuals are more likely to be discovered (Holmes and Robinson 1988, Morse 1990). However, waterbird species at Vourkari inlet were equally easy to detect due to a lack of visual obstacles and their proximity to the observer. Sequential observations (i.e., several consecutive observations of the same individual) were avoided since they are not independent because they are subject to temporal autocorrelation, i.e., each observation is usually correlated with previous ones (Morrison 1984, Hejl et al. 1990).

Seven habitat types were identified as foraging habitats for waterbirds at Vourkari inlet: shallow water (extending from the tide line to 6 m deep), mud (intertidal mudflats with muddy substrate), mud with rock (intertidal mudflats with muddy and rocky substrate), halophytic vegetation (areas covered with halophytes, mainly glasswort and shrubby seablite), tidal pools (intertidal areas holding water during low tide), tidal channels (with water channeling through a limited area in the substrate), and ditches (a 200 m long, 1.5 m wide and 0.8 m deep artificially excavated ditch, running across the western limits of the inlet, within the halophytic grassland). The approximate area of the inlet occupied by each habitat was calculated from an ortho-rectified aerial photograph (scale 1: 5000; Hellenic Ministry of Rural Development and Food) with the help of field observations. Shallow water (2.0 km^2; 66.67%) and mud (0.6 km^2; 20%) covered almost 90% of the inlet, followed by halophytic vegetation (0.24 km^2; 8%), mud with rock (0.1 km^2; 3.33%), tidal pools (0.05 km^2;

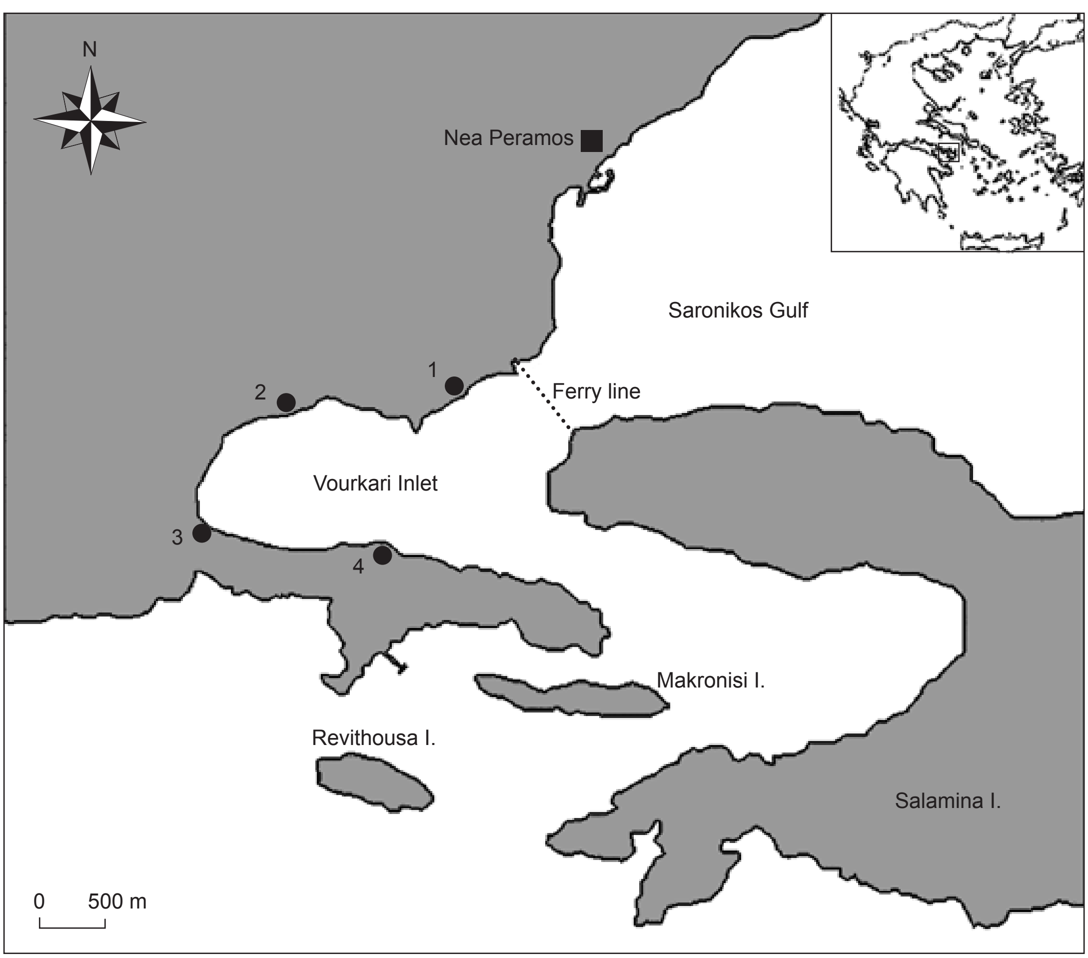

Fig. 1. Map showing the Vourkari inlet, Saronikos Gulf, Greece. Numbers indicate the observation points.

1.67%), tidal channels (0.009 km^2; 0.3%), and ditches (0.001 km^2; 0.03%). Eleven feeding techniques were used by waterbirds during the study period (following Ntiamoa-Baidu et al. 1998, Snow and Perrins 1998): pecking, probing, striking, diving, plunge-diving, surface-plunging, dip-to-surface, upending, head and neck dipping, sieving, and grazing.

Statistical analysis

Only the foraging habitats and feeding techniques of waterbird species with at least 30 foraging observations were analyzed, because this is the proposed minimum sample size required for an analysis of foraging behavior (Morrison 1984). Subsequently, data were ordered in 3 matrices, following Gatto et al. (2008): foraging habitat, feeding technique, and both dimensions together.

The 1 dimensional matrices were used to calculate foraging niche breadth and niche overlap measures. The foraging niche breadth (*FNB*) was calculated for each bird species according to Levins' (1968) formula:

$$FNB = \frac{1}{\sum_{i=1}^{n} p_i^2};$$

where p_i is the proportion of observations in each category (i) within a particular niche dimension (i.e., foraging habitat and feeding technique). A bidimensional foraging niche breadth was also calculated using 42 applicable combinations of 77 possible ones (11 techniques and 7 habitats), excluding combinations that did not make sense (e.g., mud diving). The values of this index range from 1 (a species uses only 1 niche category) to n (a species uses all niche categories in equal proportions). Foraging niche overlap (O) among every waterbird species and within each dimension was calculated using Pianka's (1973) formula:

$$O_{jk} = O_{kj} = \frac{\sum_{i=1}^{n} p_{ij}p_{ik}}{\sqrt{\sum_{i=1}^{n} p_{ij}^2 \sum_{i=1}^{n} p_{ik}^2}};$$

where p_{ij} and p_{ik} are the proportions of the i^{th} niche dimension respectively used by the j^{th} and k^{th} species. This index has values from 0 to 1, reaching 0 when niches are completely isolated from each other and 1 when niches show complete overlap. The mean overlap between each pair of species for the 2 niche dimensions examined is given.

A cluster analysis was applied to the 3rd (bidimensional) matrix to determine guild membership of waterbird species according to the use of foraging habitat and feeding technique dimensions (Jaksić and Medel 1990, López de Casenave et al. 2008). A dendrogram was thus obtained with the statistical package Statistica (vers. 6.0, StatSoft, Tulsa, OK, USA) using the unweighted pair-group algorithm (UPGMA) that relates bird species according to Euclidean distances. Guilds were then defined as those groups that were separated by more than the mean Euclidean distance (López de Casenave et al. 2008). Inter- and intra-guild comparisons of waterbirds in relation to foraging habitat, feeding techniques, and within-habitat spatial segregation were made with an analysis of similarity (ANOSIM), a non-parametric multidimensional ordination method for detecting differences between groups of community samples (Clarke 1993), using the subroutine ANOSIM in the statistical software Primer (vers. 5.1.2, PRIMER-E, Roborough, Plymouth, United Kingdom). ANOSIM generates the R statistic which ranges from 0 to 1 and gives an absolute measure of how separated groups are ($R > 0.75$, well separated; $0.25 < R < 0.75$, overlapping to some extent but different; $R < 0.25$, barely separable). The relationship between habitat area and total waterbird densities in each habitat was tested using Spearman rank correlation coefficients (r_s; Zar 1999).

RESULTS

Thirty visits were made and 120 scanning bouts were conducted at Vourkari inlet during the study period. Overall, 14 waterbird species were included in the analysis, and 11,358 foraging observations were made (Table 1). The mean population sizes of the studied species during the wintering season are also given in table 1.

More than 1/2 of the observed individuals used shallow water as a foraging habitat (6357 observations), followed by mud (3435), tidal pools (685), mud with rock (611), halophytic vegetation (225), tidal channels (37) and ditches (8). The correlation between habitat size and waterbird density in each habitat was significantly positive (Spearman $r_s = 0.857$, $p = 0.014$). Pecking was the most used feeding technique (2893 observations), followed by probing (2135), dip-to-surface (1271), upending (1259), head and neck dipping (1133), diving (931), and surface-plunging (877).

Between-species comparisons revealed that the 14 waterbirds (Fig. 2) exhibited overlapping but different use of foraging habitats (ANOSIM, $R = 0.320$, $p = 0.032$) and were well separated in the use of feeding techniques (ANOSIM, $R = 0.877$, $p < 0.001$). Both resource dimensions were therefore used in the subsequent cluster analysis which identified 5 foraging guilds (Fig. 3, Table 2). Inter-guild comparisons of habitat type showed that shallow-water generalists were similar to stalking ardeids (ANOSIM, $R = 0.031$, $p = 0.584$), shallow-water divers (ANOSIM, $R = 0.113$, $p = 0.404$), and shallow-water plunge-divers (ANOSIM, $R = 0.156$, $p = 0.301$), and overlapped with but differed from mud-peckers (ANOSIM, $R = 0.544$, $p = 0.002$). Shallow-water divers and plunge-divers used identical habitats. All other guilds were well separated from each other (pair-wise ANOSIMs, $R > 0.900$, $p < 0.001$). The statistical analysis revealed greater variations in the use of feeding techniques among the 5 guilds, with shallow-water generalists overlapping but clearly differing from mud-peckers (ANOSIM, $R = 0.463$, $p = 0.018$), and all other guilds being completely separated (pair-wise ANOSIMs, $R = 1.000$, $p < 0.001$).

The 1st guild included 2 stalking ardeid species: the Little Egret *Egretta garzetta* and Grey Heron *Ardea cinerea* (Fig. 3). Both foraged in several habitats but in different proportions (ANOSIM, $R = 0.893$, $p < 0.001$) and exclusively captured prey by striking (Fig. 2). The Little Egret mainly used halophytic vegetation (36.1%), shallow waters (30.2%), and mud (18.8%). The Grey Heron foraged mainly in shallow waters (73%) and mud (17%). The bidimensional niche breadth of the Little Egret was larger due to the use of a greater variety of foraging habitats than the Grey Heron and was also greater than the entire bird assemblage (Table 2). The mean niche overlap between these 2 species was high (Table 3).

The 2nd guild consisted of 2 shallow-water frequenters (Fig. 3) that exclusively foraged by diving: the Great Cormorant *Phalacrocorax carbo* and Great Crested Grebe *Podiceps cristatus* (Fig. 2). This guild had narrow niches in both dimensions since only 1 category of each dimension was used (Table 2), but their niche overlap was complete because they exploited the same resources (Table 3).

The 3rd guild (shallow-water generalists) grouped together 2 duck and 4 gull species (Fig. 3): the Common Shelduck *Tadorna tadorna*, Mallard *Anas platyrhynchos*, Caspian Gull *Larus cachinnans*, Slender-billed Gull *Chroicocephalus genei*, Black-headed Gull *Chroicocephalus ridibundus,* and Mediterranean Gull *Larus melanocephalus*, which varied both in foraging habitats (ANOSIM, $R = 0.529$, $p = 0.012$) and feeding techniques (ANOSIM, $R = 0.929$, $p < 0.001$). These species mainly used shallow waters, but also other habitats in lower proportions (Fig. 2). The Common Shelduck mainly used shallow waters (85.0%) but also tidal pools (10.0%) and tidal channels (5.0%). The Mallard overlapped

Table 1. Population size (mean ± SD) and number of foraging observations of 14 waterbird species during the study period (Dec. 2007 - Feb. 2008) at Vourkari inlet, Saronikos Gulf, Greece

Common name	Scientific name	Mean ± SD	Foraging observations
Little Egret	*Egretta garzetta*	18 ± 5	274
Grey Heron	*Ardea cinerea*	24 ± 15	208
Great Cormorant	*Phalacrocorax carbo*	48 ± 75	706
Great Crested Grebe	*Podiceps cristatus*	15 ± 8	225
Common Shelduck	*Tadorna tadorna*	25 ± 17	540
Mallard	*Anas platyrhynchos*	13 ± 3	76
Caspian Gull	*Larus cachinnans*	199 ± 33	1908
Slender-billed Gull	*Chroicocephalus genei*	37 ± 47	202
Black-headed Gull	*Chroicocephalus ridibundus*	978 ± 166	3816
Mediterranean Gull	*Larus melanocephalus*	295 ± 46	1239
Sandwich Tern	*Sterna sandvicensis*	12 ± 2	101
Common Redshank	*Tringa totanus*	48 ± 9	971
Little Stint	*Calidris minuta*	22 ± 4	433
Dunlin	*Calidris alpina*	33 ± 6	659

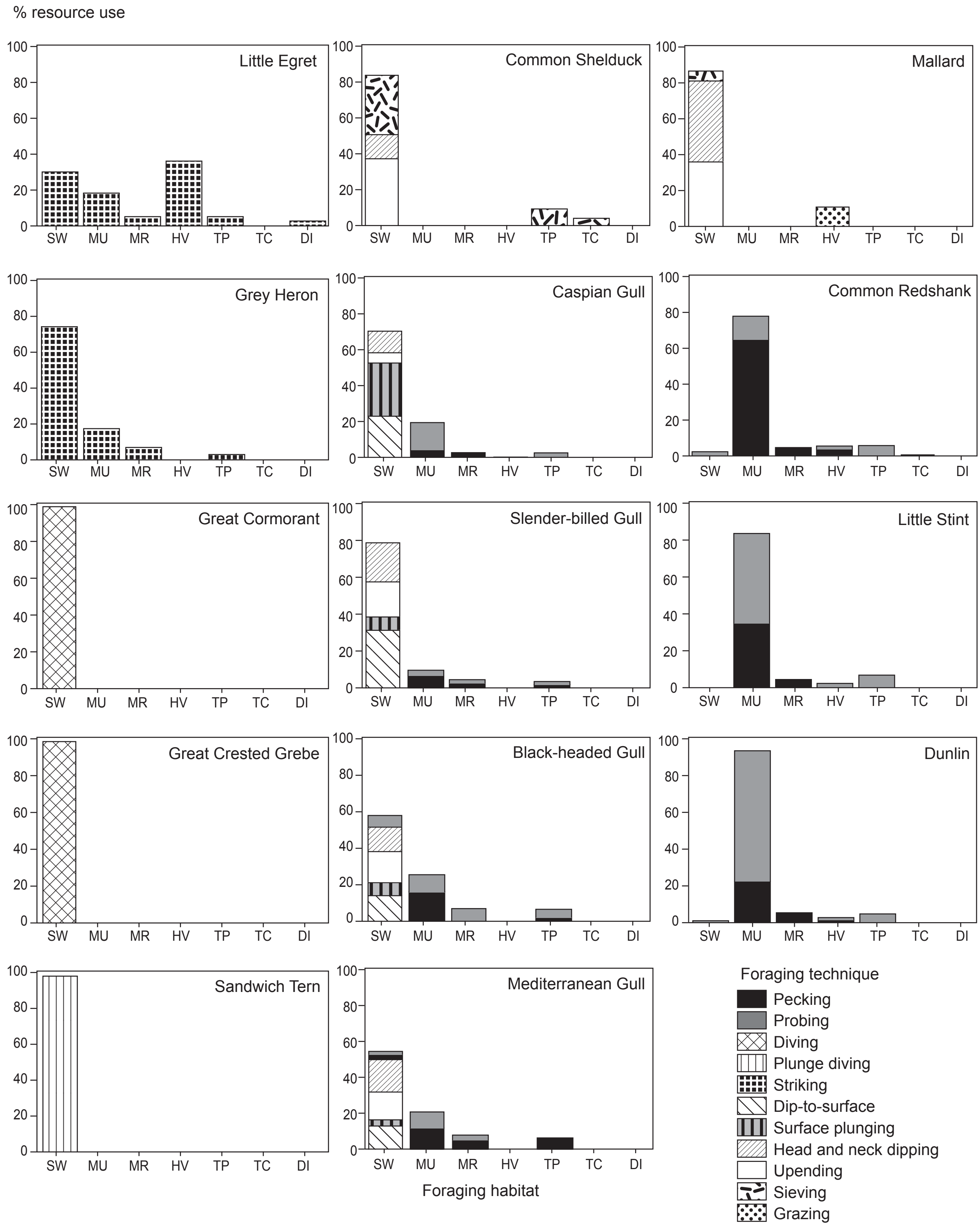

Fig. 2. Foraging habitat types and feeding techniques according to the habitat used by waterbirds during the winter of 2007-2008 at Vourkari inlet, Saronikos Gulf, Greece. Habitat codes: SW, shallow water; MU, mud; MR, mud with rock; HV, halophytic vegetation; TP, tidal pools; TC, tidal channels; DI, ditches. See “MATERIALS AND METHODS” for details.

but differed from the Common Shelduck (ANOSIM, $R = 0.411$, $p = 0.023$) by preferring shallow waters (88.1%) but also foraging on halophytic vegetation (11.9%). The gull species mainly foraged in shallow waters and mud in differing proportions (ANOSIM, $R = 0.503$, $p = 0.003$): 72.8% and 20.1% (Caspian Gull), 81.1% and 10.2% (Slender-billed Gull), 59.0% and 26.4% (Black-headed Gull), and 58.0% and 22.1% (Mediterranean Gull), respectively. Moreover, the foraging niches of gulls were further separated by spatial segregation when feeding in shallow waters (Table 4A). Caspian Gulls mainly used medium to deep (2-6 m) waters of the inlet, while Slender-billed Gulls preferred medium-depth (2-4 m) waters. At the same time, Black-headed and Mediterranean Gulls concentrated on shallower parts of the inlet (0-2 m). This guild comprised species that used a variety of feeding techniques (Fig. 2). The ducks used similar feeding techniques but in differing proportions (ANOSIM, $R = 0.953$, $p < 0.001$). The Common Shelduck used sieving (48.7%), upending (38.5%), and head and neck dipping (12.8%). The Mallard also used these techniques with respective proportions of 6.0%, 37.1%, and 45.0%, and also grazed on the halophytic grassland (11.9%). The gull species displayed an even higher diversity in the use of feeding techniques (ANOSIM, $R = 0.910$, $p < 0.001$). The Caspian Gull mainly fed by surface-plunging, dipping-to-surface, and probing with proportions of 29.4%, 24.1%, and 18.4%, respectively. The Slender-billed Gull preferred dipping-to-surface (32.3%), head and neck dipping (20.9%), and upending (20.2%). The Black-headed Gull mostly fed using the pecking (25.4%), probing (21.8%), and upending (17.4%) techniques, while the Mediterranean Gull preferred pecking (28.6%), head and neck dipping (18.7%), and probing (18.3%). This guild was characterized by a narrow to moderate foraging habitat niche and a wide feeding technique niche (Table 2). In particular, gull species displayed

Table 2. Foraging niche breadth (FNB), by species and guild, of 14 waterbird species wintering at Vourkari inlet, Saronikos Gulf, Greece

Species	Habitat ($n = 7$)	Technique ($n = 11$)	Both ($n = 42$)
Guild 1 - Stalking ardeids			
Little Egret	3.78	1.00	3.78
Grey Heron	1.76	1.00	1.76
Mean FNB	2.77	1.00	2.77
Guild 2 - Shallow-water divers			
Great Cormorant	1.00	1.00	1.00
Great Crested Grebe	1.00	1.00	1.00
Mean FNB	1.00	1.00	1.00
Guild 3 - Shallow-water generalists			
Common Shelduck	1.36	2.49	3.44
Mallard	1.27	2.79	2.79
Caspian Gull	1.75	4.84	5.20
Slender-billed Gull	1.49	4.67	4.95
Black-headed Gull	2.33	5.32	8.04
Mediterranean Gull	2.47	5.03	8.24
Mean FNB	1.78	4.27	5.44
Guild 4 - Shallow-water plunge-divers			
Sandwich Tern	1.00	1.00	1.00
Mean FNB	1.00	1.00	1.00
Guild 5 - Mud-peckers			
Common Redshank	1.59	1.15	1.59
Little Stint	1.39	1.90	2.46
Dunlin	1.50	1.74	2.51
Mean FNB	1.49	1.60	2.19

wider feeding technique niches both within their guild and the entire assemblage, resulting in a wider guild bidimensional niche. Mean niche overlap of species pairs was high within this guild (Table 3), ranging from 0.55 (Common Shelduck and Caspian Gull) to 0.99 (Black-headed Gull and Mediterranean Gull).

The 4th was a single-species guild (shallow-water plunge-divers), that contained the Sandwich Tern *Sterna sandvicensis* (Fig. 3), a species that exclusively used a single foraging habitat (shallow water; Fig. 2) and 1 feeding technique (plunge-diving; Fig. 2), thus displaying narrow niches (Table 2). Sandwich Terns shared the same foraging habitat with diving birds. However, they differentiated their niches by habitat partitioning (Table 4B). Great Cormorants were evenly spaced out, while Great Crested Grebes were concentrated at middle depths (2-4 m deep), and Sandwich Terns mostly fed in the middle to deep (2-6 m)-water parts of the inlet.

The 5th guild included 3 mud-peckers (Fig. 3): the Common Redshank *Tringa totanus*, Little Stint *Calidris minuta*, and Dunlin *Calidris alpina*, which were similar in their use of habitats (ANOSIM, $R = 0.163$, $p = 0.323$) and used the same feeding techniques although in varying proportions (ANOSIM, $R = 0.943$, $p < 0.001$). Mud was their preferred foraging habitat (Fig. 2) with proportions of 78.7%, 84.4%, and 80.9% for the Common Redshank, Little Stint, and Dunlin, respectively. The Common Redshank and Little Stint fed more by pecking (90.8% and 61.7%), followed by probing (9.2% and 38.3%, respectively) (Fig. 2). An opposite trend was displayed by the Dunlin which preferred probing (69.2%) over pecking (30.8%). This guild had small to moderate niche breadths (Table 2) but high bidimensional niche overlap (mean O = 0.75-0.95; Table 3).

The bidimensional niche overlap of within-guild species pairs, as already discussed, varied but was high (mean O = 0.55-1.00; Table 3). On the other hand inter-guild species overlap was low (mean O = 0.00-0.59), with guild 5 (Common

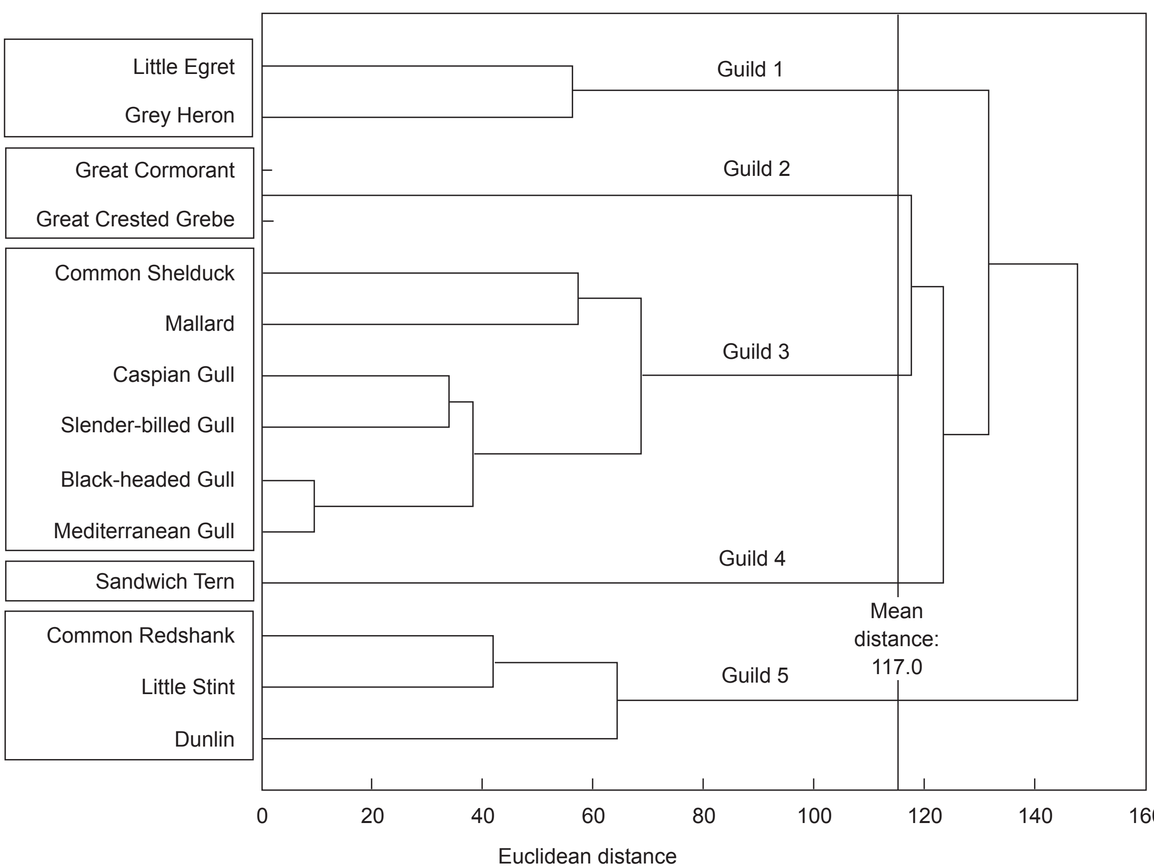

Fig. 3. Classification of the bidimensional foraging niches (foraging habitat and feeding technique) of waterbirds wintering at Vourkari inlet, Saronikos Gulf, Greece. The vertical line indicates the mean Euclidean distance between all species pairs used to define foraging guilds.

Redshank, Little Stint, and Dunlin) showing the highest degree of isolation from species of guilds 2, 3, and 4 (Great Cormorant, Great Crested Grebe, Common Shelduck, Mallard, and Sandwich Tern) with mean O values of 0.00-0.02 (Table 3). Guild 5 also displayed the highest degree of overlap with extra-guild species with mean O values of 0.51-0.59 (Black-headed and Mediterranean Gulls; Table 3).

DISCUSSION

This study provides a detailed description of the waterbird community wintering in a Mediterranean coastal wetland. The analysis categorized the 14 species into separate guilds based on the use of 2 foraging niche dimensions, 1 horizontal (foraging habitat) and 1 vertical (feeding technique), which were recorded and combined in order to aid in understanding the spatial distribution and structure of the waterbird assemblage at Vourkari inlet. Inter- and intra-guild interactions and variations were examined, and important foraging habitats were identified for each species. The acquired knowledge about the ecological requirements of these waterbirds can be used for the conservation and correct management of this and other Mediterranean coastal wetlands as well as similar areas around the world.

A variety of foraging habitat types and feeding techniques were used during the wintering season. Although interspecific variation in habitat use was considerable, the 2 main habitat types, shallow water and mud, were most utilized. However tidal pools and mud with rock, although covering small fractions of the inlet, were very important due to their use by a variety of waterbirds, namely herons, gulls, and shorebirds. In contrast, halophytic vegetation, which accounted for 8% of the area, was not used in large densities, but was however the most important feeding ground for Little Egrets. On the other hand, variations in the use of feeding techniques were higher, making them the most critical niche dimension for guild discrimination.

The assemblage was structured into 5 guilds, with all but mud-peckers preferring to forage in shallow waters while varying greatly in their feeding methods. Variations in the proportions of resource use also occurred within each guild either by habitat (stalking ardeids), feeding technique (mud-peckers), or both (shallow-water generalists). Despite these differences, each guild consisted of species with generally narrow niches and very high to complete niche overlap among them, due to the use of similar resources. The use of similar foraging habitats and feeding techniques suggested that the birds utilized similar food types (Wiens 1989) and should therefore differ in some other niche dimensions (e.g., prey size capture or substrate depth exploitation). In fact, habitat partitioning among same-guild species was observed with diving birds and gulls using different zones of the shallow-water habitat. Initially, guild structure was considered to be generated through intense interspecific competition (Pianka

Table 3. Pairwise mean overlap (O) between bidimensional foraging niches (foraging habitat and feeding technique) of 14 species of waterbirds wintering at Vourkari inlet, Saronikos Gulf, Greece

	LE	GH	GC	GCG	CS	M	CG	SG	BG	MG	ST	CR	LS
Grey Heron (GH)	0.83												
Great Cormorant (GC)	0.29	0.48											
Great Crested Grebe (GCG)	0.29	0.48	1.00										
Common Shelduck (CS)	0.30	0.48	0.50	0.50									
Mallard (M)	0.34	0.48	0.50	0.50	0.79								
Caspian Gull (CG)	0.34	0.50	0.48	0.48	0.55	0.62							
Slender-billed Gull (SG)	0.32	0.50	0.49	0.49	0.67	0.80	0.90						
Black-headed Gull (BG)	0.35	0.49	0.45	0.45	0.60	0.69	0.89	0.89					
Mediterranean Gull (MG)	0.35	0.49	0.46	0.46	0.62	0.72	0.85	0.89	0.99				
Sandwich Tern (ST)	0.29	0.48	0.50	0.50	0.50	0.50	0.48	0.49	0.45	0.46			
Common Redshank CR)	0.23	0.13	0.02	0.02	0.02	0.02	0.29	0.23	0.54	0.54	0.02		
Little Stint (LS)	0.20	0.12	0.00	0.00	0.01	0.00	0.35	0.22	0.59	0.56	0.00	0.95	
Dunlin	0.21	0.13	0.01	0.01	0.02	0.01	0.39	0.20	0.57	0.51	0.01	0.75	0.91

LE, Little Egret.

1980, Jaksić and Medel 1990). However, it was found that the opportunistic use of temporarily superabundant resources may give similar results (Wiens 1989, Blondel 2003). On the other hand, MacNally (1983) showed that guild members are usually involved in exploitative competition, especially in guilds with a moderate to small number of species, which was the case in this study. More studies on bird diet and prey abundance and availability are needed to better understand how species of the same guild partition food resources at Vourkari inlet.

On the whole, the number of foraging guilds and the generally low niche overlap among species of different guilds suggest a relatively high degree of specialization within the waterbird assemblage. It might be that the small size of the wetland does not allow for large numbers of individuals, but does allow for a diversity of species with different ecological requirements able to exploit different microhabitats and thus ease interspecific competition (Wiens 1989).

Grey Herons and Little Egrets are predominately piscivorous birds but will also take crustaceans, amphibians, reptiles, other invertebrates, and small birds and mammals (Erwin et al. 1985, Marquiss and Leitch 1990, Fasola 1994, Snow and Perrins 1998). Fasola (1994) analyzed the foraging behavior of 5 ardeid species in southern Europe and found that Grey Herons significantly overlapped with Little Egrets in foraging habitat use but not in prey type or size. Little Egrets foraged in great proportions in the halophytic grassland at Vourkari inlet suggesting the exploitation of more-diverse prey (possibly invertebrates and insects) than Grey Herons that fed mostly in shallow waters, but were also seen chasing crabs on the mud on several occasions.

Divers and plunge-divers exclusively foraged in shallow waters and shared the same food resource (fish). Great Cormorants solitarily foraged at Vourkari inlet, an indication that they mainly targeted bottom-living prey (Van Eerden and Voslamber 1995). On the other hand, Great Crested Grebes feed on fish at various depths of the water column (Gwiazda 1997), and Sandwich Terns plunge-dive for small surface-dwelling fish (Brenninkmeijer et al. 2002). Furthermore, diving birds were spatially segregated by using different zones of their foraging habitats.

Shallow-water generalists were the most numerous guild containing 6 species. It also displayed a larger niche breadth due mainly to the use of diverse feeding techniques by its members. Ducks can use a variety of feeding techniques (Snow and Perrins 1998), but Common Shelducks mainly fed by sieving from the water surface and upending, a finding similar to that of Düttmann (1992) in Germany. Mallards preferred head and neck dipping and upending but also foraged on halophytes. Green (1998) reported that Mallards mainly foraged by upending and neck dipping in Turkey. Common Shelducks are predominately carnivorous, and Olney (1965) found mainly mollusks in their stomachs and a very small fraction of plant material and seeds. On the other hand the Mallard is omnivorous and will take a wide range of animal and plant food. Mallards mainly took plant material but also seeds, invertebrates, and insects in Turkey (Green and Selva 2000). Combs and Fredrickson (1996) also found that plant material dominated the Mallard's diet but remarked that invertebrates become more important during the winter. The methods used by

Table 4. Spatial segregation of (A) gulls and (B) fish-eating divers that foraged in the shallow-water habitat at Vourkari inlet, Saronikos Gulf, Greece

	Foraging observations	Percent (%) water depth zone use			ANOSIM
		0-2 m	2-4 m	4-6 m	
(A)					
Caspian Gull	1389	3.4	32.3	64.3	$R = 0.973$,
Black-headed Gull	2251	77.0	19.7	3.3	$p < 0.001$
Mediterranean Gull	719	82.5	14.6	2.9	
Slender-billed Gull	164	26.8	65.3	7.9	
(B)					
Great Cormorant	705	27.4	35.6	37.0	$R = 0.947$,
Great Crested Grebe	225	1.8	77.3	20.9	$p < 0.001$
Sandwich Tern	101	6.9	31.7	61.4	

Mallards at Vourkari inlet implied that invertebrates were their main prey, with plant material also comprising a part of their diet.

Gulls had the widest niches among all species of the assemblage, due to exploitation of a great variety of foraging habitats and feeding techniques. They used similar habitats and techniques although in different proportions, but also spatially partitioned their main foraging habitat, shallow water. Caspian Gulls were found to feed more on fish and less on waste during the breeding season (Skórka and Wójcik 2008), but they take a more-variable diet that also includes mollusks, crustaceans, worms, and insects during the winter (Gonzáles-Solís et al. 1997). Caspian Gulls were mostly seen to surface-plunge or dip at the surface in medium to deep waters of the inlet, but they also pecked or probed on both mud and at the water's edge, an indication that they mainly took fish but also invertebrate and insect prey. Slender-billed Gulls mainly take fish and invertebrates (Snow and Perrins 1998) and were observed to mainly forage in medium-depth waters. Mollusks, crustaceans, worms, other invertebrates, and insects mainly, but also plant material, constitute the main part of the diet of Black-headed and Mediterranean Gulls (Goutner 1994, Moreira 1995, Iwamatsu et al. 2007). Both pecked and probed in muddy or water substrates most of the time suggesting the dominance of invertebrate and/or insect items in their diet.

Three shorebirds with narrow niches and high overlap among them formed the last group. According to Barbosa and Moreno (1999), Redshanks and Little Stints mainly detect their prey visually by pecking as they walk (visual continuous), while Dunlins sense prey by touch, either probing (mainly) or pecking prey (tactile continuous). Diet studies reported that Redshanks mainly feed by pecking (Goss-Custard 1969, Lourenço et al. 2008), while Little Stints and Dunlins use both pecking and probing methods (Nehls and Tiedemann 1993, Ntiamoa-Baidu et al. 1998, Lourenço et al. 2008). At Vourkari inlet, Redshanks also preferred capturing prey by pecking on muddy substrates, while Little Stints and Dunlins used both techniques, although the former foraged more by pecking and the latter by probing. Jing et al. (2007) found differences in habitat preferences between visually and tactilely foraging shorebirds. On the other hand, Kober and Bairlein (2009) reported that visually and tactilely foraging shorebirds shared the same foraging guilds. The latter was also observed at Vourkari inlet, but this also depends on the investigated set of species and the foraging niche dimensions included in each case.

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