

Patterns of resource utilization during chick rearing season by gulls and terns breeding in a Mediterranean lagoon

J. Ignacio Dies¹ & Bosco Dies

¹ Calidad de Ambientes Acuáticos. Servicio Devesa-Albufera. CV-500 km 8,5. E46012 València. (jidades@hotmail.com).

Patterns of resource utilization, habitat use for feeding and foraging techniques within a gull and tern breeding community were evaluated in a coastal lagoon of the western Mediterranean (l'Albufera de València, E Spain) during the chick rearing season. Five habitat types were identified as foraging habitats at the study site; all were exploited to a variable extent indicating different access to food resources and foraging divergence among the species.

Our analyses suggested differences in resource exploitation and structured the species into three groups of (1) species foraging the rice paddies and the lagoon (Mediterranean gull *Larus melanocephalus*, Audouin's gull *L. audouinii*, yellow-legged gull *L. michahellis*, gull-billed tern *Gelochelidon nilotica* and whiskered tern *Chlidonias hybrida*); (2) species combining the rice paddies and the brackish marshes (black-headed gull *Chroicocephalus ridibundus*, slender-billed gull *C. genei*); and (3) species foraging the open waters, particularly at sea (sandwich tern *S. sandvicensis*, common tern *S. hirundo*, little tern *Sternula albifrons*).

Our results showed that the species with larger local breeding population (i.e., common tern, black-headed gull, sandwich tern, Audouin's gull, and gull-billed tern) were successfully exploiting the most advantageous resources (i.e., rice field marshes and marine waters) in terms of prey abundance and timing with brood rearing. The extensive transformation of natural wetland habitats at the study site and the lack of alternative, productive foraging habitats during the breeding season may endanger the thriving gull and tern colonies that came along with recent conservation efforts.

Key words: Mediterranean wetland, breeding, gulls, terns, habitat use, foraging technique, resource partitioning.

Patrons d'utilització dels recursos durant la temporada de creixement de les cries per gavines i xatracas reproductores a una llacuna mediterrània

S'avaluen els patrons d'utilització dels recursos, l'ús de l'hàbitat per a l'alimentació i les tècniques d'alimentació dins d'una comunitat de gavines i xatracas reproductores a una llacuna litoral de la Mediterrània Occidental (l'Albufera de València, est d'Espanya) durant l'estació de creixement de les seves cries. Cinc tipus d'hàbitat van ser identificats com a hàbitats d'alimentació al lloc d'estudi; tots van ser explotats en un grau variable la qual cosa indica diferent accés als recursos alimentaris i divergències d'alimentació entre les espècies.

Les nostres anàlisis van suggerir diferències d'explotació dels recursos i van assignar les espècies en tres grups: (1) alimentant-se als camps d'arròs i la llacuna (gavina capnegra *Larus melanocephalus*, gavina corsa *L. audouinii*, gavià argentat mediterrani *L. michahellis*, curroc *Gelochelidon nilotica* i fumarell de galta blanca *Chlidonias hybrida*); (2) espècies que combinen els camps d'arròs i els estanys salobrencs (gavina vulgar *Chroicocephalus ridibundus*, gavina capblanca *C. genei*); i (3) espècies alimentant-se a aigües obertes, particularment a la mar (xatrac bec llarg *S. sandvicensis*, xatrac comú *S. hirundo*, mongeta *Sternula albifrons*). Els nostres resultats van mostrar que les espècies amb les poblacions reproductores locals més grans (i.e., xatrac comú, gavina vulgar, xatrac bec llarg, gavina corsa, i curroc) explotaven amb èxit els recursos més avantatjosos (i.e., arrossars i aigües marines) en termes d'abundància de preses i de sincronització amb el creixement de les cries. L'extensa transformació dels hàbitats palustres naturals al

lloc d'estudi i la manca d'hàbitats d'alimentació alternatius i productius durant l'estació reproductora, poden posar en perill les colònies de gavines i xatracs que es van establir tot seguint esforços recents de conservació.

Mots claus: Aiguamoll mediterrani, cria, gavines, xatracs, l'ús de l'hàbitat, tècniques d'alimentació, repartició dels recursos.

Introduction

Food resources within wetlands can be diverse and vary temporally and spatially. Birds are unique among vertebrates in their ability to use wetlands dispersed over large distances in their annual range. However, they are more restricted in movement during nesting and rearing season (Weller, 1999). Local resources to accommodate new populations of seabirds probably explain some of the increases registered at various Mediterranean wetlands where the gull and tern populations have undergone increasing trends following conservation efforts of their nesting sites (Fasola & Canova, 1996; Sadoul *et al.*, 1996; Díes, 2000; Oro *et al.*, 2009). Patterns of resource utilization by birds (either food or habitat resources) are usually analyzed bearing in mind that species using a resource are potential competitors if that resource is limited, hence affecting the community structure (Armstrong & McGehee, 1980; Pöysä, 1983; Simberloff & Dayan, 1991; Pérez-Crespo *et al.*, 2013). As a result, groups of species using the same class of resources in a similar way define guilds, a concept used in environmental assessment and management (Root, 1967; Hawkins & MacMahon, 1989). In this study, we evaluate patterns of resource utilization within a gull and tern breeding community in a coastal lagoon of the western Mediterranean Sea where the natural marshes have been replaced by rice paddies. Rice cultivation has been suggested to provide important habitat for birds as a foraging resource alternative to natural marshes (Fasola & Ruiz, 1997; Tourenq *et al.*, 2001). We aimed at identifying potential competitors or partitioners of some resource within the gull and tern species breeding at the study site during the rearing season as a hint in designing management strategies. Two niche dimensions (habitat use and foraging technique)

are documented and the group composition, resource use, abundance, and habitat breadth in the study site of these sympatric breeders are discussed.

Methods

This study was carried out at l'Albufera de València (East Spain; 39° 20' N, 00° 20' W) a barrier island-lagoon complex of the western Mediterranean Sea. Data from foraging gulls (Laridae) and terns (Sternidae) at the study site was taken into consideration. Field observations were made during five breeding seasons (651 counts in total) from hatching to fledging dates in 2007 (n = 146; 22 May–26 June), 2008 (n = 97; 27 May–5 July), 2009 (n = 124; 28 May–26 June), 2010 (n = 120; 2 June–29 June) and 2011 (n = 164; 13 May–6 July). Observations were evenly distributed during daylight (from 04:50–18:30 UTC). Five habitat types were identified as foraging habitats at the study site: rice paddies (flood plain marshes converted to agricultural land through dredging and impoundment and used for rice cultivation; ca. 14.000 ha), freshwater lagoon (open water body enclosed by levees; ca. 2.800 ha), brackish marshes (salted to brackish temporary ponds; ca. 60 ha), barrier island (sandy beach strand, grassland and shrub; ca. 2.000 ha), and sea (marine inshore waters along 30 km beach barrier). Eight foraging techniques were recognized (del Hoyo *et al.*, 1996): shallow dive from air, surface grab from air, swim and pecking, walk and pecking, aerial hawking, scavenging, piracy, and predation (of eggs or chicks of waterbirds).

We used a stratified point count method (Bibby *et al.*, 1992) randomly allocating points (to the nearest access road or vantage point) in each of habitat types considered. Points were reached by car or boat and visited at least once each year. Points at sea had to be placed within two nautical miles from

shore (ca. 25 m isobath) due to practical limitations. Observations were made using 20-60×65 field scopes and 10×40 binoculars. All the gull and tern species breeding at the study site were considered: black-headed gull *Chroicocephalus ridibundus* (CHRRID), slender-billed gull *Chroicocephalus genei* (CHRGEN), Mediterranean gull *Larus melanocephalus* (LARMEL), Audouin's gull *Larus audouinii* (LARAUD), yellow-legged gull *Larus michahellis* (LARMICH), gull-billed tern *Gelochelidon nilotica* (GELNIL), sandwich tern *Sterna sandvicensis* (STESAN), common tern *Sterna hirundo* (STERHIR), and little tern *Sternula albifrons* (STEALB). An additional tern species was also considered: whiskered tern *Chlidonias hybrida* (CHLHYB) which is a common summer visitor that ceased breeding at the study site in the 1970's. Only individuals engaged in active foraging were taken into consideration and the observed feeding technique of effective prey capture by a certain individual was also recorded.

Data were pooled across years for the analysis. We tested for species under- and over-represented in our study by comparing observed and expected frequencies, using Chi square tests ($P < 0.05$). The expected values were calculated from the breeding population size at the study site (summed nesting pairs) during the same period (2007 to 2011) obtained from the official census (Generalitat Valenciana). We estimated an index of habitat breadth ($B = (1/\sum p_i^2)/5$) where p_i is the proportion of a particular species in a given habitat considering the sum in all five habitat types. The index values can range from 0 to 1, the bigger the value the higher ecologic valence of the species, providing indirect ways to explore ecological processes such as competition over shared resources (Carrascal *et al.*, 2008; Pérez-Crespo *et al.*, 2013).

Resource utilization data were grouped into two matrices: habitat type (10 species × 5 habitat variables) and foraging technique (9 species × 8 technique variables). A cluster analysis was applied to each matrix to determine group membership of species according to the use of foraging habitat and technique dimensions (López de Casenave *et al.*, 2008). Methods used for guild assignment include cluster analysis among others (Landres & MacMahon, 1980; Simberloff & Dayan, 1991).

Two dendrograms were thus obtained with the statistical package SIMFIT (vers. 6.0, Program SIMSTAT, W. G. Bardsley, University of Manchester, U.K.) using the unweighted pair group algorithm that relates bird species according to Euclidean distances (values given by the analysis). Groups were then defined as those that were separated by more than the average Euclidean distance (Gatto *et al.*, 2008; López de Casenave *et al.*, 2008). The yellow-legged gull was excluded from the cluster analysis of foraging technique due to a small sample.

Results

The distribution by species of 20.478 foraging individuals observed during our study is given in Table 1. Percentage frequency-distributions of the species totals met the expected frequencies obtained from the breeding population at the study site for the same species during the same years. The sandwich tern was the unique species showing a significant

Species	Foraging observations		Population size		B
	N	%	%	p-value	
CHRRID	5.030	25.7	17.0	NS	0.32
CHRGEN	1.214	6.2	2.2	NS	0.44
LARMEL	164	0.8	1.9	NS	0.58
LARAUD	1.595	8.2	6.3	NS	0.29
LARMIC	190	1.0	0.1	NS	0.35
GELNIL	1.396	7.2	13.9	NS	0.26
STESAN	2.464	12.6	27.4	p > 0.05	0.20
STERHIR	7.073	36.2	28.8	NS	0.21
STEALB	413	2.1	2.4	NS	0.50
CHLHYB	939	—	Not breeder	—	0.21
Total	20.478	100.0	100.0		

TABLE 1. Number of foraging individuals, relative size of breeding population (N = 28,099 pairs), discrepancy of frequencies (Chi square tests, 1 d.f. with Yates' correction, $P < 0.05$), and index of habitat breadth (B) of ten species of gulls and terns at L'Albufera de Valencia (E Spain) from 2007 to 2011 (pooled data) on chick rearing season. Species code as given in methods.

TAULA 1. Número d'individus alimentant-se, grandària relativa de la població de reproductors (N = 28.099 parelles), discrepància de freqüències (test Xi quadrat, 1 g.l. amb correccions de Yates, $P < 0,05$) i índex d'amplitud d'hàbitat (B) de deu espècies de gavines i xatracas a l'Albufera de València (E Espanya) entre 2007 i 2011 (dades agrupades) durant l'època de cria dels polls. Vegeu el codi de les espècies en mètodes.

discrepancy, with a number of observations lower than expected ($\chi^2_2 = 4.76$, $P < 0.05$) (Table 1). Habitat breadth index (B) ranged from 0.20 to 0.58 (Table 1); gulls showed the higher scores whereas terns generally showed the lowest, except for the little tern. Table 1 also shows that the species with larger local population appeared at higher frequencies and had the lower scores of habitat breadth. The matrix with the frequency of habitat use for each bird species and the subsequent cluster analysis suggested that an average Euclidean distance of 6,062 split species into three groups (Table 2, Fig. 1). The first group (H1) was composed of species foraging the rice paddies and the brackish marshes and comprised both *Chroicocephalus* species, the black-headed and the slender-billed gulls. The presence of these species at other habitats was low. The second group (H2), which included species foraging freshwater habitats at the rice paddies and the lagoon, along with barrier island habitats such as

the sandy beaches, was integrated by all three *Larus* gulls, the Mediterranean, the Audouin's and the yellow-legged gulls, and both the gull-billed and the whiskered terns, the latter two species being clearly absent from the seashore. Their lowest presence as a group occurred at the brackish marshes. The third group (H3) consisted of species foraging the open waters, particularly at sea, and embraced the sandwich, the common, and the little terns. The species of this group did not use the beach barrier habitat type (Fig. 1).

Observations of foraging techniques resulted in 1,085 events of effective prey captures by a certain individual that were later distributed by species (Table 3). A cluster analysis of the matrix with the frequency of foraging technique for each bird species suggested that an average Euclidean distance of 4,813 reliably defined three groups of species (Fig. 2). The first group (T1) embraced all the gull species, the slender-billed, the black-headed,

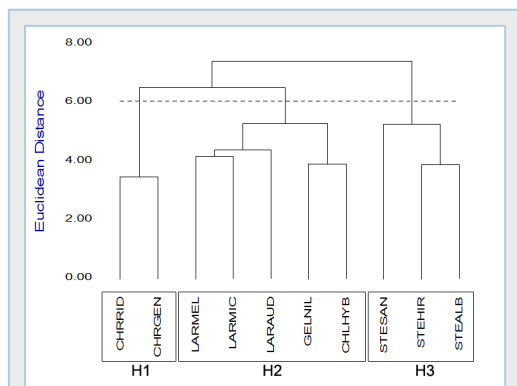


FIGURE 1. Cluster analysis of gull and tern species by habitat type dimension at l'Albufera de València (E Spain) from 2007 to 2011 (pooled data) on chick rearing season. The average Euclidean distance between all species pairs is marked with a dashed line (mean = 6.062). Group codes for habitat use are (H1) brackish- rice paddy marshes users, (H2) barrier island-freshwater habitat users, and (H3) open water users. Species code as given in methods.

FIGURA 1. Anàlisi de Cluster corresponent a la dimensió dels tipus d'hàbitat per a les diferents espècies de gavines i xatracas a l'Albufera de València (E Espanya) de 2007 a 2011 (dades agrupades) durant l'època de creixement de les seves cries. La distància euclidiana mitjana entre tots els parells d'espècies s'indica amb una línia de punts (mitjana = 6.062). Els codis de grup per a l'ús de l'hàbitat són (H1) usuaris de llacunes salobres i arrossars, (H2) usuaris dels hàbitats de restinga i d'aigua dolça, i (H3) usuaris d'aigües obertes. Vegeu el codi de les espècies en mètodes.

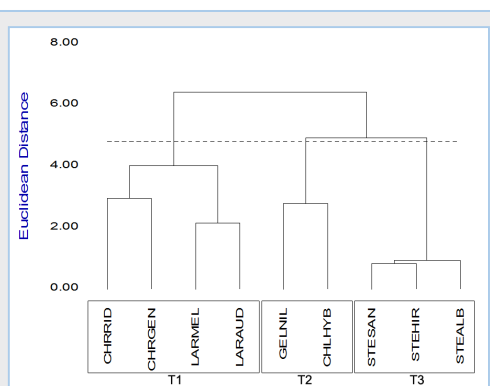


FIGURE 2. Cluster analysis of gull and tern species by foraging technique dimension at l'Albufera de València (E Spain) from 2007 to 2011 (pooled data) on chick rearing season. The average Euclidean distance between all species pairs is marked with a dashed line (mean = 4.813). Group codes for foraging technique are (T1) walk and peckers, (T2) surface grabbers from air, and (T3) plunge divers. Species code as given in methods.

FIGURA 2. Anàlisi de Cluster corresponent a la dimensió tècnica d'alimentació per a les diferents espècies de gavines i xatracas a l'Albufera de València (E Espanya) de 2007 a 2011 (dades agrupades) durant l'època de creixement de les seves cries. La distància euclidiana mitjana entre tots els parells d'espècies s'indica amb una línia de punts (mitjana = 4.813). Els codis de grup per a tècniques d'alimentació són (T1) caminadors i picadors, (T2) caçadors de superfície des de l'aire, i (T3) capturadors en picat. Vegeu el codi de les espècies en mètodes.

the Mediterranean, and the Audouin's gulls. These species mostly walked and pecked (61 % of events) to obtain food in shallow areas, muddy substrates or beaches. They were engaged in the other seven foraging techniques to a lesser degree; they all included predation of eggs or chicks and were the unique scavengers. The slender-billed and the black-headed gulls were also occupied in piracy, robbing the prey fed to chicks by common and sandwich terns, particularly around their colonies. The second group (T2), composed of surface grabbers (86 % of events), included the gull-billed and the whiskered terns, darting down, swooping or dropping from air to seize prey items from surface of water, ground or vegetation cover. They also rarely performed other techniques, including most of the events of aerial hawking on swarming insects recorded. The gull-billed tern was also engaged in predation of chicks. The third group (T3), of nearly strict plunge divers (95 % of events), was composed of the sandwich, the common, and the little terns (Fig. 2).

Discussion

Our results give the first reliable information on resource utilization by foraging gulls and terns at the study site during the rearing season that was extended from mid May to early July. All five

habitats considered were exploited to a variable extent giving some indication of different access to food resources and foraging divergence among the species in this study. As a result, rice paddies marshes and inshore marine waters hosted high numbers of foraging individuals, whereas the opposite was true for the freshwater lagoon and the barrier island habitats.

Given that the breeding species with a larger local population and greater frequencies in our study had the lower scores of habitat breadth, our deduction is therefore that these species (i.e., common tern, black-headed gull, sandwich tern, Audouin's gull, and gull-billed tern) were successfully exploiting the most advantageous resources (i.e., rice paddy marshes and marine waters) in terms of prey abundance and timing with brood rearing. The converse deduction is that limited access to these resources by the other breeding species (i.e., slender-billed gull, little tern, yellow-legged gull, and Mediterranean gull) resulted in their lower frequencies and their greater habitat breadth scores in our results. Nevertheless, habitat breadth index does not include information regarding the availability of habitats to species, resulting in lower scores for species that might have exploited more habitats had they been available (Pyron, 1999). In fact, another reading, following Ramirez *et al.* (2012), is that species with

	Rice paddy marshes		Freshwater lagoon		Brackish marshes		Barrier island		Sea	
Species	n	%	n	%	n	%	n	%	n	%
CHRRID	3855	48.2	50	12.6	1086	55.9	6	6.7	33	0.3
CHRGEN	393	4.9	5	1.3	707	36.4	2	2.2	107	1.1
LARMEL	79	1.0	2	0.5	15	0.8	18	20.0	50	0.5
LARAUD	1308	16.4	50	12.5	3	0.2	7	7.8	227	2.3
LARMIC	135	1.7	6	1.5	0	0.0	0	0.0	49	0.5
GELNIL	1221	15.3	108	27.1	8	0.4	55	61.1	4	0.0
STESAN	0	0.0	10	2.5	2	0.1	0	0.0	2452	24.4
STEHIR	11	0.1	91	22.9	78	4.0	0	0.0	6893	68.5
STEALB	74	0.9	57	14.3	41	2.1	0	0.0	241	2.4
CHLHYB	916	11.5	19	4.8	2	0.1	2	2.2	0	0.0
Total	7992	100.0	398	100.0	1942	100.0	90	100.0	10056	100.0

TABLE 2. Frequency distribution of habitat use for each bird species and the five habitat types considered in the study at L'Albufera de València (E Spain) from 2007 to 2011 (pooled data) on chick rearing season. Species code as given in methods.

TAULA 2. Distribució de freqüències d'ús d'hàbitat per cada espècie d'au i els cinc tipus d'hàbitat considerats en l'estudi a l'Albufera de València (E Espanya), entre 2007 i 2011 (dades agrupades), durant l'època de creixement dels polls. Vegeu el codi de les espècies en mètodes.

small populations can not increase because their main feeding habitat does not extend over larger areas, and alternative habitats do not meet the conditions for establishing a larger population in which the lower-ranking individuals exploit these alternative habitats (i.e., slender-billed gull), in contrast to the existence of preferential habitats for other species that mainly exploit habitats with large areas, such as the sea (i.e., common tern and sandwich tern) and the rice paddy marshes (i.e., gull-billed tern and black-headed gull).

The cluster analyses also suggested differences in resource exploitation and structured the gull and tern species into three groups (or guilds), somewhat coherent with taxonomic categories. Furthermore, certain species within the same group of habitat use were assigned to a separate group according to the foraging technique, hence apparently exploiting the same habitat but foraging upon different prey. This is the case of the gull-billed and whiskered terns belonging to the group H2 of species exploiting the barrier island and freshwater habitats, along with the gull species of the genus *Larus*, but forming their own group T2 of surface grabbers. Conversely, the black-headed and slender-billed gulls formed a separate group H1 according to the high frequencies that both species showed while foraging the brackish marshes, but were merged to other gull

species into the group T1 of walk and peckers. The common, little, and sandwich terns formed their own H3 and T3 groups, all using similar foraging habitat and techniques, as plunge divers at open waters. The frequency-distribution analysis of our species totals revealing that the sandwich tern was less recorded than expected pointed to this tern also foraging the offshore waters at sea, which were not surveyed in our study. Regular observations of sandwich terns flying directly into and from deep sea during this study supported this case and a recent study proved that the species was capable of ranging more than 50 km from its colony in a search for patchily distributed prey (Perrow *et al.* 2017).

Rice is cultivated at the study site in the great expanse of flood plain marshes which are typically flooded for sowing in late April-early May. Rice plants emerge from the water the following month and attain maximum coverage and height in August. The species that foraged the rice paddies (namely black-headed gull, Audouin's gull, gull-billed tern, and whiskered tern, as the most frequent species) gained quick access to food resources soon after flooding, though rice coverage conceals aquatic prey as season progresses. For example, Dies *et al.* (2005) showed that for the gull-billed terns, the introduced red swamp crayfish (*Procambarus clarkii*) was the main prey

Species	Shallow dive	Surface grab	Swim & pecking	Walk & pecking	Aerial hawking	Scavenging	Piracy	Predation
CHRRID	3 (1.1)	27 (9.7)	32 (44.4)	170 (46.6)	2 (12.5)	0 (0.0)	12 (35.3)	3 (25.0)
CHRGEN	2 (0.7)	8 (2.9)	34 (47.2)	83 (22.7)	0 (0.0)	9 (25.7)	15 (44.1)	1 (8.3)
LARMEL	0 (0.0)	7 (2.5)	1 (1.4)	30 (8.2)	3 (18.8)	10 (28.6)	1 (2.9)	2 (16.7)
LARAUD	2 (0.7)	25 (9.0)	3 (4.2)	72 (19.7)	1 (6.3)	16 (45.7)	2 (5.9)	3 (25.0)
LARMIC	0 (0.0)	1 (0.4)	0 (0.0)	5 (1.4)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
GELNIL	6 (2.2)	146 (52.7)	1 (1.4)	4 (1.1)	6 (37.5)	0 (0.0)	4 (11.8)	3 (25.0)
STESAN	92 (33.6)	2 (0.7)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
STEHIR	94 (34.3)	4 (1.4)	1 (1.4)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
STEALB	73 (26.6)	7 (2.5)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
CHLHYB	2 (0.7)	50 (18.1)	0 (0.0)	1 (0.3)	4 (25.0)	0 (0.0)	0 (0.0)	0 (0.0)
Total	274 (100)	277 (100)	72 (100)	365 (100)	16 (100)	35 (100)	34 (100)	12 (100)

TABLE 3. Frequency distribution of the observations (N = 1,085) of effective prey captures by a certain individual for each bird species and the eight foraging techniques considered in the study at L'Albufera de València (E Spain) from 2007 to 2011 (pooled data) on chick rearing season. Percent values into brackets. Species code as given in methods.

TABLA 3. Distribució de freqüències de les observacions (N = 1.085) de captures efectives de preses per cada espècie d'au i les vuit tècniques d'alimentació considerades en l'estudi a l'Albufera de València (E Espanya) entre 2007 i 2011 (dades agrupades) durant l'època de creixement dels polls. Percentatges entre parèntesi. Vegeu el codi de les espècies en mètodes.

species brought to colony (64% of prey items) and their chicks were fed proportionately more aquatic prey earlier in the season at the study site. Sea water along the littoral fringe reveals a number of processes associated with nutrient enrichment at large shallow areas over a wide continental shelf receiving an important input of continental water (Estrada, 1996; Salat, 1996). Species foraging the sea (i.e., sandwich tern and common tern, both tallying 93% of all individuals recorded at this habitat) preyed upon fish at shifting locations. For the sandwich tern at the study site, the prey carried to colony were mostly Clupeiformes (96% of prey items), particularly anchovy (*Engraulis encrasicolus*), and sardine (*Sardina pilchardus*) (Dies & Dies, 2005).

The salt marshes showed progressive desiccation through the season and species such as slender-billed and black-headed gulls gained access to invertebrates at the muddy substrate, particularly polychaete and chironomid species (own data). These marshes also hosted nesting colonies of Charadriiformes that were exploited by the gulls and the gull-billed tern through piracy and predation of eggs or chicks. In a previous study at this site (Dies & Dies, 2005) the most frequent and successful kleptoparasites of breeding sandwich terns were the black-headed and the slender-billed gulls. All the species foraged the lagoon at low numbers, probably owing to the hypertrophic, turbid state of the water at this habitat, due to anthropogenic eutrophication (Vicente & Miracle, 1992; Villena & Romo, 2003). The barrier island offered drier foraging habitats over sandy substrate that were mostly used by the gull-billed tern, as well as long beaches with shore drift that were explored by gulls, particularly the Mediterranean gull, seeking food and beached carrion.

Foraging segregations are thought to play an important role in the maintenance of species diversity by reducing competition and allowing birds with otherwise similar niches to coexist (Friesen, 2007). On the other hand, reproductive output of birds is likely to be influenced by how well nesting is timed to temporal patterns of food abundance, particularly during the brood rearing phase (Arzel *et al.*, 2014). Sympatric breeding seabirds, like those considered in our study, are known to segregate by feeding niche in a variety of ways, including feeding

location or targeted prey (Wiley *et al.*, 2012). These groups of species that exploit the same class of environmental resources in a similar way define guilds, grouping together species without regard to taxonomic position that overlap significantly in their niche requirements (Root, 1967). Because related species often use resources in a similar fashion, partitions into guilds probably will often reflect taxonomy, as shown in our results. To provide an accurate description of feeding guilds, more dimensions should be added to the analysis, such as data on diet (stomach contents) or availability of prey (Sarriás *et al.*, 1996).

The gulls and terns breeding at l'Albufera de València exploited food resources during the rearing season to a variable extent, resulting in increased abundance of certain species at the study site, particularly those exploiting the rice paddies and the sea which are precisely the habitats that occupy larger areas in the study site. Both rice farming operations and seawater mass processes, seem somewhat timed with the nesting and brood rearing season of the gulls and terns at the study site, thus sustaining important breeding populations. But the extensive transformation of natural wetland habitats at l'Albufera de València and the lack of alternative productive foraging habitats during the breeding season at the study site may endanger the thriving colonies of gulls and terns that came along with the conservation efforts made in recent decades.

Acknowledgements

This study was carried out as a part of the management tasks carried out at the Racó de l'Olla reserve on behalf of the Servicio Devesa-Albufera and the Oficina de Gestió Tècnica del P. N. de l'Albufera de València. We are indebted to the many helpers that eventually accompanied us, particularly Miguel Chardí and Josep Puentes, the latter also contributing to early data analysis. Toni Pradillo kindly offered his motor boat and his striking knowledge of marine fish during surveys at sea. Pablo Vera kindly commented on an earlier draft and improved the manuscript.

Bibliography

- Armstrong, R. A. & McGehee, R. 1980. Competitive exclusion. *The American Naturalist*, 115: 151–170.
- Arzel, C., Dessborn, L., Pöysä, H., Elmberg, J., Nummi, P. & Sjöberg, K. 2014. Early springs and breeding performance in two sympatric duck species with different migration strategies. *Ibis*, 156: 288–298.

- Bibby, C. J., Burgess, N. D. & Hill, D. A. 1992.** Bird Census Techniques. Academic Press, London.
- Carrascal, L. M., Palomino, D. & Polo, V. 2008.** Patrones de distribución, abundancia y riqueza de especies de la avifauna terrestre de la isla de La Palma (islas Canarias). *Graell-sia*, 64: 209-232.
- del Hoyo, J., Elliot, A. & Sangatal, J. 1996.** Handbook of the birds of the world. Vol. 3: Hoatzin to Auks. Lynx Edicions, Barcelona.
- Dies, J. I. 2000.** Habitat management for gulls and terns at l'Albufera de València (West Mediterranean). Preliminary results. In, P. Yésou and J. Sultana (Eds.): Monitoring and Conservation of Birds, Mammals and Sea Turtles of the Mediterranean and Black Seas. Procc. of the 5th MEDMARAVIS Symp., BirdLife, Malta.
- Dies, J. I. & Dies, B. 2005.** Kleptoparasitism and host responses in a Sandwich Tern colony of eastern Spain. *Waterbirds*, 28: 167-171.
- Dies, J. I., Marín, J. & Pérez, C. 2005.** Diet of nesting gull-billed terns in Eastern Spain. *Waterbirds*, 28: 106-109.
- Estrada, M. 1996.** Primary production in the northwestern Mediterranean. *Scientia Marina*, 60: 55-64.
- Fasola, M. & Canova, L. 1996.** Conservation of gull and tern colony sites in Northeastern Italy, an internationally important bird area. *Colonial Waterbirds*, 19 (Special publication 1): 59-67.
- Fasola, M. & Ruiz, X. 1997.** Rice farming and waterbirds: integrated management in an artificial landscape. *Farming and Birds in Europe*, pp. 210-235. Academic Press, London.
- Friesen, V. L., Burg, T. M. & McCoy, K. D. 2007.** Mechanisms of population differentiation in seabirds. *Molecular Ecology*, 16: 1.765-1.785.
- Gatto, A., Quintana, F. & Yorio, P. 2008.** Feeding behavior and habitat use in a waterbird assemblage at a marine wetland in coastal Patagonia, Argentina. *Waterbirds*, 31: 463-471.
- Hawkins, C. P. & MacMahon, J. A. 1989.** Guilds: the multiple meanings of a concept. *Annual Review of Entomology*, 34: 423-451.
- Landres, P. B. & MacMahon, J. A., 1980.** Guilds and community organization: analysis of an oak woodland avifauna in Sonora, Mexico. *The Auk*, 97: 351-365.
- Lopez de Casenave, J., Cueto, V. R. & Marone, L. 2008.** Seasonal dynamics of guild structure in a bird assemblage of the central Monte desert. *Basic and Applied Ecology*, 9: 78-90.
- Oro, D., Pérez-Rodríguez, A., Martínez-Vilalta, A., Bertolero, A., Vidal, F. & Genovart, M. 2009.** Interference competition in a threatened seabird community: a paradox for a successful conservation. *Biological conservation*, 142: 1830-1835.
- Pérez-Crespo, M. J., Fonseca, J., Pineda-López, R., Palacios, E. & Lara, C. 2013.** Foraging guild structure and niche characteristics of waterbirds in an epicontinental lake in Mexico. *Zoological Studies*, 52: 1-17.
- Perrow, M., Harwood, A., Berridge, R. & Skeate, E. 2017.** The foraging ecology of Sandwich Terns in north Norfolk. *British Birds*, 110: 249-308.
- Pöysä, H. 1983.** Resource utilization pattern and guild structure in a waterfowl community. *Oikos*, 295-307.
- Pyron, M. 1999.** Relationships between geographical range size, body size, local abundance, and habitat breadth in North American suckers and sunfishes. *Journal of Biogeography*, 26: 549-558.
- Ramírez, F., Navarro, J., Afán, I., Hobson, K. A., Delgado, A., & Forero, M. G. 2012.** Adapting to a changing world: unraveling the role of man-made habitats as alternative feeding areas for slender-billed gull (*Chroicocephalus genei*). *PLoS ONE*, 7(10): e47551.
- Root, R. B. 1967.** The niche exploitation pattern of the blue-gray gnatcatcher. *Ecological monographs*, 37: 317-350.
- Sadoul, N., Johnson, A. R., Walmsley, J. G. & Levéque, R. 1996.** Changes in the numbers and the distribution of colonial Charadriiformes breeding in the Camargue, Southern France. *Colonial Waterbirds*, 19: 46-58.
- Salat, J. 1996.** Review of hydrographic environmental factors that may influence anchovy habitats in northwestern Mediterranean. *Scientia marina*, 60: 21-32.
- Sarriás, A. M., Blanco, D. & De Casenave, J. L. 1996.** Estructura en gremios en un ensamble de aves acuáticas durante la estación reproductiva. *Ecología Austral*, 6: 106-114.
- Simberloff, D. & Dayan, T. 1991.** The guild concept and the structure of ecological communities. *Annual review of ecology and systematics*, 22: 115-143.
- Tourenq, C., Bennetts, R. E., Kowalski, H., Viallet, E., Lucchesi, J. L., Kayser, Y. & Isenmann, P. 2001.** Are rice-fields a good alternative to natural marshes for waterbird communities in the Camargue, southern France? *Biological Conservation*, 100: 335-343.
- Vicente, E. & Miracle, M. R. 1992.** The Coastal Lagoon Albufera de València: an ecosystem under stress. *Limnetica*, 8: 87-100.
- Villena, M. J. & Romo, S. 2003.** Phytoplankton changes in a shallow Mediterranean lake (Albufera de València, Spain) after sewage diversion. *Hydrobiologia*, 506: 281-287.
- Weller, M. W. 1999.** Wetland birds: habitat resources and conservation implications. Cambridge University Press.
- Wiley, A. E., Welch, A. J., Ostrom, P. H., James, H. F., Stricker, C. A., Fleischer, R. C., ... Gandhi, H., Adams, J., Ainley, D. G., Duvall, F., Holmes, N., Hu, D., Judge, S., Penniman, J. & Swindle, K. A. 2012.** Foraging segregation and genetic divergence between geographically proximate colonies of a highly mobile seabird. *Oecologia*, 168: 119-130.

Rebut el 31 de maig de 2017. Acceptat el 31 d'agost de 2017.