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Trophic niche width and overlap of two sympatric gulls in the southwestern mediterranean

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Abstract The diets of two potential competitor species, Audouin's *Larus audouinii* and yellow-legged gulls *Larus cachinnans*, were examined while they bred at the Chafarinas Islands during 1993, 1994, and 1995. Data were collected during two commercial fishing regimes: (1) trawling and purse seine fisheries, and (2) diurnal trawlers only. Since the food supply for the gulls in this area was heavily reliant on the activity of purse seine fisheries, these contrasting situations allowed us to analyze short-term effects, induced by daily changes in food supply, on niche width, dietary shift, and niche overlap between the two species. Overall, both species relied mainly on fish for food, especially Clupeiforms, in the case of Audouin's gull irrespective of the fishing situation, and in the case of the yellow-legged gull, only when purse seine fishing was in operation. When purse seine boats did not operate (food shortage), yellow-legged gulls broadened their niche, consuming equal amounts of all the feeding resources, and they showed a dietary shift toward a greater consumption of prey from refuse tips. In contrast, Audouin's gulls did not change their niche width, but showed a slight dietary shift away from the consumption of epipelagic fish, compensated by an increase in reliance on benthic-mesopelagic resources. Niche overlap was clearly higher on days when both fishing fleets operated, probably because a superabundant food resource facilitates high overlap without affecting coexistence between the two species. Since our study was developed on the basis of daily variations in food supply, and competition effects are to be expected on a longer-term basis, these changes can be seen as the outcome of the coexistence of two species in stable competitive equilibrium.

Key words Audouin's gull · yellow-legged gull · *Larus audouinii* · *Larus cachinnans* · Diet

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Introduction

Interspecific competition is a major factor determining the trophic niche width of sympatric species (MacArthur 1972; Cody 1974; Pianka 1982) at both ecological (e.g., Alatalo 1981) and evolutionary levels, in the latter case through varying selective pressures (e.g., Diamond 1978).

An abundance of resources may cause a high diet overlap between two species. When foraging resources become less abundant, diet overlap is expected to decrease, since interspecific competition becomes more intense (Lack 1947; Svärdson 1949; Cody 1974; Pianka 1982; Schoener 1982; Wiens 1989). However, if the restrictions in food supply persist, the trophic niche may once again overlap (Wiens 1989; Bell and Ford 1990).

The optimal-foraging theory, however, predicts that niche width will increase as the availability of foraging resources decreases, because the consumption of a wide range of suboptimal prey types is promoted (Svärdson 1949; MacArthur and Pianka 1966; Krebs and Davies 1981). Thus, when food is in short supply, while the trophic overlap between species should decrease, the trophic niche width of each species should increase, thus involving some degree of niche shift.

To date, changes in trophic niche and the effects of interspecific competition have been assessed from two points of view (see review in Steenhof and Kochert 1985). The first method involves a comparison of the trophic niche of a species in two areas: one in which

competitors are present and the other in which they are absent – when competitors are present, the niche overlap is less apparent. Nevertheless, changes in the trophic niche may occur due to differences in food availability in the two areas. The second method compares the same area during periods of high and low food availability. When food is in short supply, the trophic niche overlap of two sympatric species decreases, but changes in the type of food available during these periods may bias the results.

A third approach, as yet untried, would compare the trophic niches of sympatric and potential competitor species within the same area during the same period of time while changes are occurring in the availability of the main prey of these species. This is the case, for example, for seabirds that exploit commercial fisheries. Since most of the commercial fishery activity in the Mediterranean varies with sea conditions and the day of the week (Oro 1995), the availability of food changes from day to day.

On the Chafarinas Islands (southwestern Mediterranean), Audouin's gull *Larus audouinii* and the yellow-legged gull *L. cachinnans* breed sympatrically, and they exploit the foraging resources from commercial fisheries operating around the islands (Witt et al. 1981; Pedrocchi et al. 1996). The exploitation of commercial fisheries by scavenging seabirds has been carefully documented (e.g., Garthe et al. 1996 and references therein), showing that fish discards are usually the main foraging resource for some seabird populations (Blaber and Wassenberg 1989; Hamer et al. 1991).

Moreover, these two gull species fulfil the criteria recommended by Steenhof and Kochert (1985) to analyze interspecific competition and niche shifts since they show (1) a high diet overlap, due to the exploitation of fish available from commercial fisheries (Ruiz et al. 1996a), (2) a strong phylogenetic relationship, since both larids belong to the same genus, (3) enough similarity to be potential competitors, since they present morphological linear ratios (yellow-legged/Audouin's) below 1.3, and below 2.1 for body mass (Hutchinson 1959) (Table1), (4) an absence of territoriality within the foraging range, (5) low predation on adults, and (6) a major variation in food supply, as may occur in the case of seabirds showing feeding ecologies that are highly dependent on commercial fisheries (Oro et al. 1996, 1997; González-Solís et al. 1997a).

Table 1 Morphological comparison of Audouin's gull (♂ $n = 53$; ♀ $n = 51$) and yellow-legged gull (♂ $n = 10$; ♀ $n = 17$) on the Chafarinas Islands. Ratios were obtained from the means

	Yellow-legged gull	Audouin's gull	Ratio
Weight ♂ (g)	1095.78	581.24	1.89
Weight ♀ (g)	873.06	502.72	1.74
Bill length ♂ (mm)	60.63	48.63	1.25
Bill length ♀ (mm)	53.18	44.86	1.19
Wing length ♂ (mm)	454.80	407.04	1.12
Wing length ♂ (mm)	436.57	392.81	1.11
Tarsus length ♂ (mm)	70.07	59.46	1.18
Tarsus length ♀ (mm)	63.49	55.98	1.13

This paper examines the effects of changes in food availability on the trophic niche width and the interspecific diet overlap between Audouin's and yellow-legged gulls around the Chafarinas Islands colony. In this area, food supply is heavily reliant on the activity of purse seine fisheries, which attract shoaling clupeids to the surface, thus making them available to the gulls.

Material and methods

Food samples were collected at the Chafarinas Islands (southwestern Mediterranean: 35°11′N, 2°26′W) breeding site during 1993, 1994, and 1995 (May and June). The archipelago lies 4.5 km off Ras el Ma, on the eastern Moroccan coast and holds about 3500 Audouin's and 1500 yellow-legged gull nests.

Because regurgitates constitute the least biased samples for diet analysis (González-Solís et al. 1997b), we used only this kind of food sample. Furthermore, to ensure independence among samples, only one fresh regurgitate from a chick per brood and nest was collected. Since the yellow-legged gull breeds about 1 month before Audouin's gull, the chicks of the former were, on average, older.

Samples were classified depending on the activity of the purse seine fleet, which did not operate on holidays or during bad weather. The timetable of this fleet was from 0100 hours to 0800 hours. Daily catch statistics from the port of Ras el Ma were obtained from the bulletins of the fishermen's guild, and were used to assess the purse seine fishery activity. Since trawlers stopped only during very strong gales and, on such days, food samples were not collected, we assumed that trawler activity was constant during the study period. Thus, two fishing events were considered: first, when both trawlers and purse seine fisheries operated- and second, when only trawler fisheries operated.

Analytical methods and statistical procedures

Since the categorization procedures may have a marked influence on the interpretation of diet analyses (see Cooper et al. 1990 for review), two separate criteria were used to establish prey categories: taxonomy and ecologic typology. Taxonomic categories were based on order level and used to describe diets. Typologic groups were based on prey characteristics, which involve different hunting behavior, predation efforts, and/or foraging habitats (Ruiz et al. 1996b), and were used to examine ecological relationships.

The following descriptors of diet were assessed at both taxonomic and typologic levels: number of prey items (*N*), numerical percentage (%N), percentage of occurrence (percentage of sampling units containing the prey category, %P), and percentage of dry weight biomass (%B). The width of the trophic niche was measured with Brillouin's diversity index (Pielou 1975), and a jackknife procedure was used to estimate its value and associated variance (Zahl 1977). Comparisons of jackknifed diversity values were performed using the test proposed by Hutcheson (1970).

Interspecific overlap of the trophic niche within the same fishing event was estimated using the Petraitis index (Petraitis 1979) and the program provided by Ludwig and Reynolds (1988). The adjusted form of this index takes values from 0 to 1. We tested the hypothesis of 100% trophic overlap for each fishing event using the Petraitis statistic (Petraitis 1979).

For each typologic category, dietary differences between the fishing situations were assessed using their occurrence and dry-weight biomass in each regurgitate by means of the *G*-test and Mann-Whitney *U*-test of rank order, respectively.

Results

Tables 2 (taxonomic) and 3 (typology) show the diet descriptors for Audouin's and yellow-legged gull chicks in the study area. Overall, both species relied mainly on fish for food, especially Clupeiforms, in the case of Audouin's gull, irrespective of the fishing situation, and in the case of the yellow-legged gull, only when purse seine fishing was operating. Only yellow-legged gulls showed a relevant consumption of waste food, and this was clearly increased when purse seine fisheries were not operating.

Niche width values, at both the taxonomic and typologic level, for the two species and the fishing situations are given in Table 4. Niche width values were rather similar for both species. However, the change in niche width associated with the fishing situation was quite different for the two species. Tests with typologic categories showed that while there were no significant differences in the case of Audouin's gull ($t = 0.12$, $df = 280$, $P = 0.89$), the niche width of the yellow-legged gull increased significantly when purse seine fisheries did not operate ($t = -3.3$, $df = 276$, $P < 0.001$).

Table 2 Taxonomic descriptors of the chick diet of Audouin's and yellow-legged gulls on the Chafarinas Islands, according to commercial fishery activities (%N numeric percentage, %P occurrence percentage, %B biomass percentage)

	Audouin's gull						Yellow-legged gull					
	Trawler and purse seine			Trawler			Trawler and purse seine			Trawler		
Number of regurgitates	136			124			138			89		
Number of prey items	212			264			184			103		
	%N	%P	%B	%N	%P	%B	%N	%P	%B	%N	%P	%B
Clupeiformes	38.2	55.2	54.76	21.2	34.7	43.38	45.7	52.2	52.70	19.4	21.4	19.15
Perciformes	23.6	27.9	22.97	23.9	38.7	28.17	18.5	19.6	19.20	19.4	20.2	16.38
Anguiliformes	4.7	6.6	3.36	4.6	8.1	2.88	1.1	1.5	0.42	3.9	4.5	1.80
Gadiformes	3.8	5.2	5.19	9.1	10.5	16.67	6.5	8.7	4.20	7.8	9.0	4.79
Atheriniformes	4.7	2.2	3.33	–	–	–	0.5	0.7	0.06	–	–	–
Zeiformes	–	–	–	3.4	4.0	0.81	1.6	1.5	0.82	–	–	–
Gasterosteiformes	–	–	–	0.4	0.8	0.13	–	–	–	–	–	–
Selacea	–	–	–	–	–	–	0.5	0.7	0.01	–	–	–
Undetermined fish	7.6	11.8	4.88	3.8	8.1	2.65	6.5	8.7	8.30	5.8	6.7	3.58
Sepioida	1.9	2.2	2.36	11.0	8.9	4.33	0.5	0.7	0.99	4.9	5.6	8.21
Teuthoida	–	–	–	–	–	–	0.5	0.7	0.99	1.0	1.1	1.64
Stylommatophora	–	–	–	–	–	–	1.6	1.5	0.02	1.9	2.3	0.06
Decapoda	–	–	–	0.4	0.8	0.01	1.1	1.5	0.81	–	–	–
Araneae	–	–	–	–	–	–	0.5	0.7	0.01	–	–	–
Isopoda	7.1	1.5	0.58	–	–	–	–	–	–	–	–	–
Orthoptera	7.1	5.9	0.48	22.4	9.7	0.97	6.5	2.9	0.22	11.7	10.1	0.28
Hymenoptera	0.5	0.7	0.01	–	–	–	–	–	–	–	–	–
Coleoptera	–	–	–	–	–	–	1.1	1.5	0.01	6.8	2.3	0.08
Fruits, seeds	0.5	0.7	0.02	–	–	–	1.1	1.5	0.52	–	–	–
Waste food	0.5	0.7	2.05	–	–	–	6.0	8.0	10.70	17.5	20.2	44.00

Table 3 Ecological typology descriptors of the chick diet of Audouin's and yellow-legged gulls on the Chafarinas Islands, according to commercial fishery activities (%N numeric percentage, %P occurrence percentage, %B biomass percentage)

	Audouin's gull						Yellow-legged gull					
	Trawler and purse seine			Trawler			Trawler and purse seine			Trawler		
Number of regurgitates	136			124			138			89		
Number of prey items	212			264			184			103		
	%N	%P	%B	%N	%P	%B	%N	%P	%B	%N	%P	%B
Epipelagic prey	52.8	72.8	72.80	40.5	53.2	56.70	53.8	60.1	63.30	29.1	32.6	32.30
Benthic/mesopelagic	24.1	24.3	19.00	33.0	44.4	39.60	21.7	28.3	16.20	25.2	28.1	19.70
Undetermined fish	7.6	11.8	4.94	3.8	8.1	2.65	7.1	9.4	8.30	7.8	9.0	3.58
Terrestrial prey	15.3	7.3	1.14	22.4	9.7	0.97	11.4	8.7	1.50	20.4	13.5	0.43
Refuse tips	0.5	0.7	2.08	–	–	–	6.0	8.0	10.70	17.5	20.2	44.00

Table 4 Niche width (SE in parentheses) and overlap values of Audouin's and yellow-legged gulls at the Chafarinas Islands, according to commercial fishery activities, for both taxonomic and typological categories

		Niche width				Niche overlap
		Audouin's gull		Yellow-legged gull		
Trawler and purse seine	Taxonomic	2.80	(0.23)	2.70	(0.15)	
	Typologic	1.72	(0.15)	1.84	(0.10)	0.97
Trawler	Taxonomic	2.80	(0.09)	3.10	(0.16)	
	Typologic	1.74	(0.06)	2.23	(0.06)	0.85

Table 5 Dietary shift associated with commercial fishery activities shown by Audouin's and yellow-legged gulls at the Chafarinas Islands, for typologic categories. The absolute and relative (in parentheses) number of regurgitates in which the prey category occurred are provided. *G*-test values and significance are also given for each prey category

	Audouin's gull			Yellow-legged gull		
	Trawler and purse seine	Trawler	*G*-test (*p*)	Trawler and purse seine	Trawler	*G*-test (*p*)
Epipelagic prey	99 (72.8%)	66 (53.2%)	9.88 (0.002)	83 (60.1%)	29 (32.6%)	16.71 (< 0.001)
Benthic/mesopelagic	33 (24.3%)	55 (44.4%)	11.77 (< 0.001)	39 (28.3%)	25 (28.1%)	0.001 (0.98)
Undetermined fish	16 (11.8%)	10 (8.1%)	0.99 (0.32)	13 (9.4%)	8 (9.0%)	0.01 (0.91)
Terrestrial prey	10 (7.4%)	12 (9.7%)	0.45 (0.50)	12 (8.7%)	12 (13.5%)	1.28 (0.26)
Refuse tips	1 (0.7%)	0	1.30 (0.80)	11 (8.0%)	18 (20.2%)	7.10 (0.008)
Total number of regurgitates	136	124		138	89	

Niche overlap (Table 4) was higher when trawlers and purse seine fisheries operated at the same time (trawlers and purse seine: adjusted $G = 0.97$; only trawlers: adjusted $G = 0.85$). Although the overlap was significantly different from 100% for each fishing event, this difference was higher when only trawlers operated (trawlers and purse seine: $V = 12.5$, $df = 4$, $P < 0.02$; only trawlers: $V = 52.3$, $df = 4$, $P < 0.001$).

Overall, there were no differences in the median dry biomass per regurgitate according to the fishing situation, neither in Audouin's ($U = 8010$, $P = 0.55$) nor in the yellow-legged gull ($U = 5299$, $P = 0.62$). In Audouin's gull, the dietary shift associated with the lack of purse seine fishing was characterized by a significant decrease in the occurrence of epipelagic prey and a significant increase in the consumption of benthic-mesopelagic prey (Table 5). The same significant differences were also found in terms of dry biomass (epipelagic $U = 6927$, $P = 0.01$; benthic-mesopelagic $U = 6498$, $P < 0.001$). No significant shift in the consumption of the remaining categories was detected in either occurrence or biomass.

The dietary shift shown by the yellow-legged gull when purse seine fisheries did not operate was due to a significant decrease in the consumption of epipelagic prey, both in terms of occurrence (Table 5) and dry biomass ($U = 3891$, $P < 0.001$), and to a significant increase in the occurrence and biomass of food from refuse tips ($U = 4764$, $P = 0.003$, Table 5). No differences were found for the remaining typologic categories.

Discussion

Audouin's gull is considered a rather specialized nocturnal predator on shoaling clupeids (Pedrocchi et al. 1996; Ruiz et al. 1996a), while the yellow-legged gull behaves as a more generalist species, mainly dependent on food from human activities, as recorded by several studies in the Mediterranean region (Fasola et al. 1989; Bosch et al. 1994). Furthermore, Audouin's gull is a more pelagic species, with a wider foraging range than the yellow-legged gull (Arcos and Oro 1996). Nevertheless, since both species show great plasticity in their activity patterns (Oro 1995; Bosch and Sol 1996) and feeding habits (Oro et al. 1995, Oro et al. 1997), they can easily overlap in resource use, particularly when such resources are overabundant. This is the case of fish of no commercial value and/or below the minimum commercial landing size discarded by trawlers, and shoaling clupeids attracted to the surface during the night by purse seine vessels using powerful lights.

At the Chafarinas Islands, the two gull species exploited both resources, since purse seine fisheries operated around the islands. Although purse seine fisheries are particularly suitable for a nocturnal feeder such as Audouin's gull (Ruiz et al. 1996a), they are also exploited by yellow-legged gulls at dawn (González-Solís et al. 1997a). On the other hand, both Audouin's and yellow-legged gulls were also active during the day (Ruiz et al. 1996b), and able to exploit the discards from

trawling fisheries. However, even though trawlers operated continuously, they worked away from the islands and can be regarded as a much less predictable resource. Therefore, when both fisheries operated, prey were more available than when only trawlers operated (González-Solís et al. 1997a).

The reduced prey availability caused by the lack of purse seine fisheries induced different responses in terms of niche width in the two species. Audouin's gulls did not show any relevant change in this parameter because their diet continued to be dominated, though to a lesser extent, by epipelagic prey (i.e., shoaling clupeids), which were caught as they swam up to the surface during the night (Whitehead et al. 1984; Oro et al. 1997). In contrast, the yellow-legged gulls clearly broadened their niche by increasing the consumption of secondary resources, and equating their importance in their diet, which is the expected response for a generalist.

The decrease in the consumption of epipelagic prey was compensated by a different dietary shift in the two species. Audouin's gull increased the consumption of benthic/mesopelagic prey obtained from trawler discards, probably owing to their pelagic foraging abilities, which facilitated the location of trawlers operating away from the islands, whereas the yellow-legged gulls did not increase the use of this resource, but showed a huge increase in the use of food from refuse tips, which then became their main dietary resource in terms of biomass.

A superabundance of food facilitates high dietary overlap without affecting coexistence. This is probably because, in this situation, the foraging effort required was minimized by the effect of lights, which concentrated the shoaling clupeids, creating easily detectable patches of enhanced food availability (Ruiz et al. 1996a), a situation in which an ecological opportunist can be as efficient as an evolutionary specialist in using this resource. When purse seine fishery ceased, Audouin's and yellow-legged gulls increased the segregation of their trophic niches because of the dietary shift of yellow-legged gulls towards resources more accessible to an opportunist.

There is no conclusive way to ascertain whether the different responses recorded for the two gull species were related more to interspecific competition or to their varying ability to compensate for this food shortage. However, since our study was developed on the basis of daily variations in food supply, and one would expect competition effects to become apparent on a longer-term basis, it is easier to see these changes as the outcome of the coexistence of two species in stable competitive equilibrium based on their different foraging abilities (Arthur 1987).

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