

TROPHIC AND SPATIAL RELATIONSHIPS BETWEEN WINTERING RED KITES (*MILVUS MILVUS*) AND MARSH HARRIERS (*CIRCUS AERUGINOSUS*) IN THE GUADALQUIVIR MARSHES

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Trophic and spatial relationships between wintering Red Kites (Milvus milvus) and Marsh Harriers (Circus aeruginosus) in the Guadalquivir Marshes.—Trophic and spatial variables are studied after pellet analysis from both species. Kites fed mostly on birds and insects, while Harriers fed on small mammals and Rats. Prey of Kites were small or big sized but Harriers mainly fed on medium sized prey. The aquatic habitat was the most used by both raptors. Niche breadths were always larger for Kites. Spatial niche overlap was very high but trophic niche overlaps were lower, mainly when considering the biomass of prey size classes. Factors influencing interspecific competition between both species are discussed.

Key words: Interspecific competition, *Milvus milvus*, *Circus aeruginosus*, Guadalquivir Marshes, Spain.

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INTRODUCTION

The importance of interspecific competition among similar species and the mechanisms to avoid or decrease this competition have caused much concern (see SCHOENER, 1983 and CONNELL, 1983 for revisions). In species with the same activity patterns, habitat and food type are the principal kinds of resource-partitioning differences usually observed (SCHOENER, 1974; HOLT, 1987).

For the most part, studies on wintering raptors competition have concentrated on estimating population levels, documenting habitat use, describing hunting behaviour and analyzing diets. CRAIGHEAD & CRAIGHEAD (1956) studied a raptor community in southern Michigan, and found that the extent of habitat segregation differed during the two

winters they studied the birds, with increasing overlap in years when population of Meadow Voles (*Microtus pennsylvanicus*) were low. In Iowa, wintering Red-tailed Hawk (*Buteo jamaicensis*) hunted open woods along stream bottoms, but Rough-legged Hawks (*Buteo lagopus*) used more open areas (WELLER, 1964). SCHNELL (1968) reports similar habitat segregation between these two species wintering in northern Illinois. Instead, BILDSTEIN (1987), in a study carried out in Ohio, found that for wintering Red-tailed Hawks, Rough-legged Hawks, Northern Harriers (*Circus cyaneus*) and American Kestrels (*Falco sparverius*), activity and diet, rather than habitat, were the most important niche dimensions (i.e., they exhibit the least overlap).

The Red Kite (*Milvus milvus*) and the Marsh Harrier (*Circus aeruginosus*) are the

most abundant medium sized raptors found during winter in the Guadalquivir Marshes, where they assemble in roost sites of up to 80 and 210 individuals respectively. Considering their similar size, and the fact that they apparently share the same habitats and some hunting techniques, some mechanisms to decrease or avoid competition between both species may be expected. In this paper, the tropic and spatial components of the niche of both species are analysed, and the probable factors allowing their coexistence are discussed.

STUDY AREA, MATERIAL AND METHODS

The Guadalquivir Marshes, between the provinces of Huelva and Seville (SW Spain), reach both sides of the final stretch of this river. The part lying over the right bank is almost entirely included within Doñana National Park, which has been described many times (VALVERDE, 1958; ALLIER & BRESSET, 1977; ROGERS & MYERS, 1980). The marsh on the left bank has been largely transformed into salt marshes and rice fields which still preserve a varied fauna.

To study feeding habits, 359 and 444 pellets from Red Kite and Marsh Harrier respectively were analysed. The former were collected in February 1982 under three roost sites within Doñana National Park, and the latter in November 1983, February and March 1984 in a roost site from the Brazo del Este, on the left bank of the Guadalquivir River. The climatic conditions of these periods were very similar.

The biomass of each prey was calculated by carrying out food-tests with captive Kites and Harriers. To each prey item was assigned the weight of that species, as long as it did not exceed the average daily requirements (100 g for the Red Kite and 75 g for the Marsh Harrier), deduced from these tests. For a more detailed explanation of the method see BLANCO et al. (1987) and GONZÁLEZ (1989).

To study habitat use, three types of environment have been defined: Aquatic Habi-

tat, including marshes, lagoons, rice fields and salt marshes; Scrubland, with all the types of bush and mediterranean woods of the area; and Anthropic Habitat, covering cultivated fields, waste land, and other dry, broken or transformed areas with little vegetation. We have considered that the time spent foraging by the raptors studied in these habitats is proportional to the number of prey captured in them (DELIBES, 1975, 1978). The evaluation of the habitat use was done considering the specific habitats of those prey appearing in the pellets. Insects and the most ubiquitous species were not used in these calculations.

To calculate niche breadth and overlap, LEVINS (1968) and PIANKA (1973) indexes respectively have been used, as suggested by RICKLEFS (1980) and PUTMAN & WRATTEN (1984).

Levins index:
$$B = \frac{1}{\sum_{i=1}^n p_i^2}$$

where p_i is the proportion of records for a species in each category (i) of the niche dimension. Low niche breadth: 1; great niche breadth: n (number of categories).

Pianka index:
$$O_{jk} = \frac{\sum_{i=1}^n p_{ij} p_{ik}}{\sqrt{\sum_{i=1}^n p_{ij}^2 \sum_{i=1}^n p_{ik}^2}}$$

where p_i is the proportion of the species j 's activity recorded from the category i of the niche dimension. Lowest niche overlap: 0; greatest niche overlap: 1.

For testing goodness of fit, G test (d. f. = 1) was used (SOKAL & ROHLF, 1981).

RESULTS

The number of prey items determined for the Red Kite and the Marsh Harrier were 642 and 682 respectively. Eleven types of prey were made, grouping species with common ecological traits. Results are expressed as

percentage of prey items.

Only two types of prey, fish and crustaceans, were not shared by both species. The difference between the percentage of consumption of the remaining types of prey was significant except for rallid-waders and other birds. The most frequent type of prey consumed by Kites were Anatidae (within which Geese, *Anser anser*, are of great importance), whilst the Harriers mainly ate small mammals and rats (table 1). It should be pointed out that for both raptors, almost all the prey included in Anatidae and mammals over 1000 g were consumed as carrion (BLANCO et al., 1987; SCHIPPER, 1973; GONZÁLEZ, 1989).

Prey items were grouped into five size classes, according to a geometric progression (SCHOENER, 1969). The Kites fed mainly on prey included in the extreme classes, while the Harriers fed more often on the central class, the difference in percentage being significant in all cases (table 2).

Biomass supplied by the classes of prey size provides a more accurate portray of the energetic importance for animals (ABRAMS,

Table 1. Diet of the Red Kite and the Marsh Harrier in Gualquivir Marshes during winter on percentages of prey items. n.s. Not significant; * $p < 0.05$; *** $p < 0.001$.

*Dieta del Milano Real y del Aguilucho Lagunero en las Marismas del Guadalquivir en invierno, expresadas en porcentaje del número de presas. n.s. No significativo; * $p < 0,05$; *** $p < 0,001$.*

Prey items	Red Kite	Marsh Harrier	G
Small mammals (except rats)	1.8	19.4	121.24 (***)
Rats	2.2	32.8	248.96 (***)
Mammals > 1000 g (except lagomorphs)	10.7	1.2	62.35 (***)
Lagomorphs	11.7	0.9	77.87 (***)
Anatidae	22.0	4.8	90.07 (***)
Rallids-Waders	13.6	13.5	0.00 (n.s.)
Other birds	16.4	15.4	0.22 (n.s.)
Reptiles	1.4	3.1	4.33 (*)
Insects	20.2	4.2	85.27 (***)
Fish	0.0	1.9	-
Crustacean	0.0	2.8	-

Table 2. Size of the prey consumed by Red Kites and Marsh Harriers. Results are expressed as percentages. Classes of prey size: 1. 0-15 g; 2. 16-75 g; 3. 76-375 g; 4. 376-1775 g; 5. > 1775 g; n. Number of prey items; *** $p < 0.001$.

*Tamaño de las presas consumidas por el Milano Real y el Aguilucho Lagunero. Los resultados se expresan en porcentajes. Clases de tamaño de presa: 1. 0-15 g; 2. 16-75 g; 3. 76-375 g; 4. 376-1775 g; 5. > 1775 g; n. Número de presas; *** $p < 0,001$.*

	n	Classes of prey size				
		1	2	3	4	5
Red Kite	642	23.8	5.7	17.9	26.4	26.2
Marsh Harrier	682	9.4	26.9	52.6	9.4	1.7
G		52.85 ***	114.65 ***	180.07 ***	67.18 ***	193.89 ***

1980). In the case of the Red Kite, the classes that contributed most of the biomass were the two largest. In the Harrier, the 76-375 g class contributed nearly three quarters of the total biomass (fig. 1).

The Aquatic Habitat was the most used by both species, although it was more significantly used by the Marsh Harrier (fig. 2).

Niche breadths were higher for Kites in all cases, even considering the types of prey where two more classes were included for Harriers. The minimum value of niche overlap was obtained for biomass of prey size classes. As to the habitat use, the value of niche overlap was close to the theoretical maximum of this parameter (table 3).

DISCUSSION

As we have seen, spatial niche overlap between both species was almost absolute. This result, which had already been suspected from field observations, does not allow us to deny categorically the existence of some more subtle form of spatial segregation, which would only have been noted if we had been able to investigate a larger number of

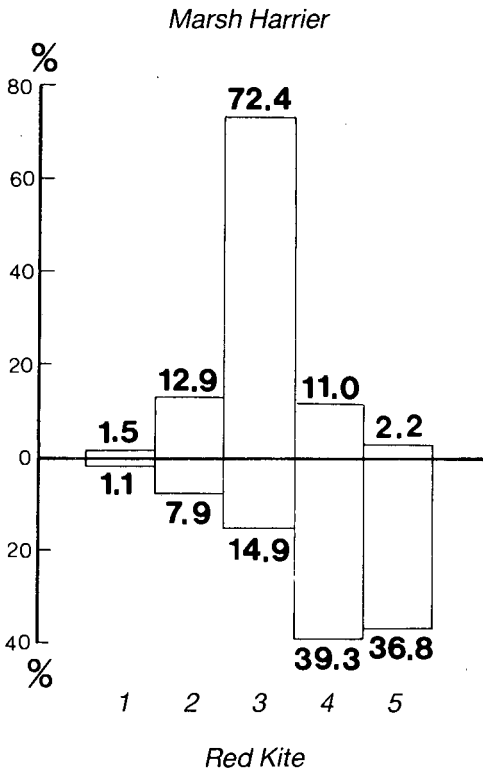


Fig. 1. Biomass, in percentages, supplied by the classes of prey size. Classes of prey as in table 2.

Biomasa, expresada en porcentajes, suministrada por las diferentes clases de tamaño de presa (véase tabla 2).

microhabitats as other authors have done in more detailed studies (e.g. PIANKA, 1975).

However, when considering the trophic niche, we do find major differences between Red Kites and Marsh Harriers, since values of trophic niche overlap goes from 0.40 to 0.55. In the Guadalquivir Marshes during winter, Red Kites feed mainly on birds during the winter, while Marsh Harriers show a higher preference for mammals. However, the greatest trophic segregation appeared when considering biomass of prey size classes. Harriers obtained 72.4% of its energy requirements from medium sized prey (76-357 g), while the Kite mainly fed on prey over 375 g

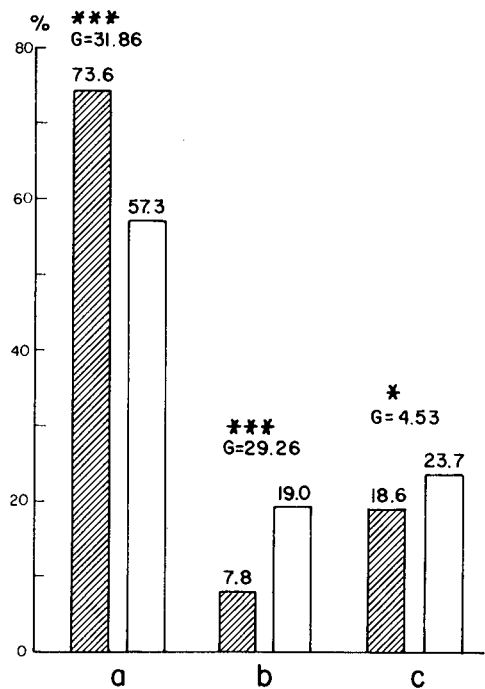


Fig. 2. Percentage of use of the three types of habitat defined: A. Aquatic Habitat; B. Scrubland; C. Anthropogenic Habitat. ▨ Marsh Harrier (n= 481); □ Red Kite (n= 631).

Porcentaje de uso de los tres tipos de hábitat definidos: A. Zonas húmedas; B. Monte; C. Hábitat antropógeno. ▨ Aguilucho Lagunero (n= 481); □ Milano Real (n= 631).

(76.1% of the biomass, fig. 1), most of which are usually eaten as carrion (BLANCO et al., 1987).

Several characteristics related to the foraging behavior allow the Kite to be more apt as carrion eater than the Harrier. One of these is the height of searching flight, which is usually directly related to the mean prey size consumed by raptors, as it has been stated by AMORES (1979). SCHIPPER (1977) observed that the Marsh Harrier spends more than 85% of its flying time at below 5 m, whilst in the Guadalquivir Marshes the Red Kite spends approximately 65% of its flying time at more than 20 m (BLANCO, 1982), flying below 10 m

Table 3. Values of niche breadth and overlap of the Red Kite and the Marsh Harrier, based on the trophic and spatial variables studied. B. Levins index; O. Pianka index; n. Number of categories.

Valores de amplitud y solapamiento de nicho en el Milano Real y el Aguilucho Lagunero, basados en las variables tróficas y espaciales estudiadas. B. Índice de Levins; O. Índice de Pianka; n. Número de categorías.

	Niche breadth				Niche overlap
	Red Kite		Marsh Harrier		O
	B	n	B	n	
Types of prey	6.23	9	5.16	11	0.43
Classes of prey size	4.34	5	2.72	5	0.55
Biomass of the classes of prey size	3.14	5	1.79	5	0.40
Habitat use	2.38	3	1.72	3	0.97

only in 12.9% of the cases (n=1377). Further, the anatomical shape of the Kite allows for greater performance for soaring than the Harrier (BROWN, 1976), so that the former is far more capable than the latter in exploring wide areas in search of carrion (HOUSTON, 1974).

However, the most important factor that may determine the decrease of interspecific competition is the great availability of food. It has been stated many times that high niche overlaps do not necessary involve competition if the abundance of the resource is greater than its demand (BIRCH, 1957; COLWELL & FUTUYMA, 1971; PIANKA, 1972, 1974). Even more, SCHOENER (1983), in a review of field experiments on interspecific competition, concludes that macrohabitat overlap is inversely related to experimentally demonstrated competition. In our particular case, we would only be able to obtain conclusive results on the possible existence of competition between these two species by carrying out experiments which would include the manipulation of abundance of the raptors under study or of the available food (SCHOENER, 1983;

CONNELL, 1983). Lacking such experimental data, we may suppose that the high availability of food in the Guadalquivir Marshes would avoid competition between the Red Kite and the Marsh Harrier, even if values of trophic niche overlap were greater than those found in this work.

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RESUMEN

Relaciones tróficas y espaciales entre los Milanos Reales (Milvus milvus) y los Aguiluchos Laguneros (Circus aeruginosus) invernantes en las Marismas del Guadalquivir.

Con objeto de aproximarse al conocimiento de los mecanismos que reducen la competencia entre las poblaciones invernantes de Milano Real y Aguilucho Lagunero en las Marismas del Guadalquivir, se estudian las relaciones tróficas y espaciales entre ambas especies, en base a los datos aportados por el análisis de egagrópilas.

El solapamiento espacial es altísimo, pero los valores de solapamiento de las variables tróficas estudiadas son muy inferiores (tabla 2). Las diferencias máximas se encuentran al considerar la biomasa aportada por las distintas clases de tamaño de presa (fig. 1). El Aguilucho obtiene el 72,4% de la biomasa de presas de tamaño medio (76-375 g), pero el Milano obtiene el 76,1% de la biomasa de presas mayores de 375 g (fig. 1), la mayor parte de las cuales son consumidas como carroña. La configuración anatómica de las alas del Milano le hace más apto para planear, lo que le permite cubrir mayor distancia en busca de carroñas. Se discuten también otros mecanismos que pueden reducir la competencia entre ambas especies, como el mayor oportunismo del Milano—que se refleja en la mayor amplitud de nicho en todas las variables estudiadas— y la gran disponibilidad de alimento existente en el área de estudio.

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