

Food-niche differentiation in sympatric Hen *Circus cyaneus* and Montagu's Harriers *Circus pygargus*

J. T. GARCIA^{1*} & B. E. ARROYO²

¹Departamento de Biología Animal I (Zoología), Facultad de Biología, Universidad Complutense, 28040 Madrid, Spain

²CEH-Banchory, Hill of Brathens, Aberdeenshire AB31 4BW, UK

Hen Harriers *Circus cyaneus* and Montagu's Harriers *Circus pygargus* are medium-sized raptors that differ in size (Hen Harrier being slightly bigger than Montagu's Harrier) and breeding system (Montagu's Harriers are semi-colonial and Hen Harriers defend nesting-hunting territories). In contrast, the diets of the two species when in sympatry are very similar. We evaluated food-niche differentiation among these coexisting raptor species and how between-species differences in body size and social system influence interspecific relationships. We present data from a study conducted in 1997 and 1998 in northeastern Madrid province (central Spain). Diet of the two species largely overlapped (55–95%) during the breeding season, but Hen Harriers preyed more often on larger species. This segregation was observed both in the average size of the primary prey (lagomorphs) and in the alternative prey (birds for Hen Harriers vs. insects for Montagu's Harriers), and was particularly apparent late in the season. Accordingly, feeding frequency of Montagu's Harriers, but not of Hen Harriers, increased later in the season. Size differences between species in prey brought to the nest were apparent for both males and females. Foraging behaviour also differed, as Hen Harriers spent more time hunting close to the nest than did Montagu's Harriers. This implies that segregation in foraging areas may also exist. Observed niche partitioning may relax the potential for competition between these species.

The search for mechanisms that permit the coexistence of trophically similar species is a central issue of community ecology (Begon *et al.* 1990). Coexisting species are expected to develop strategies of niche differentiation, particularly when resources become scarce (May 1973, Chesson & Huntly 1997). Reduction of food-niche overlap may occur through food partitioning by type or by size of prey, or through segregation in foraging areas. Three main factors that could influence interspecific trophic relationships between species and potential mechanisms of food partitioning are the abundance of food, the body size of each species and their breeding system (i.e. the degree of territorial behaviour). The first of these is directly related to potential levels of depletion and the degree of exploitative competition between

individuals. Thus a minimization of the food-niche overlap is expected when resources decrease and the costs of overlap increase (MacArthur & Levins 1967, May 1973). Body size influences the absolute energetic requirements of each species, and the outcome of aggressive interactions. Larger body size might give an advantage in interspecific agonistic encounters (Robinson-Wolrath & Owens 2003, Shelley *et al.* 2004) but a disadvantage if food resources are limited, because larger body size implies larger food requirements (Nagy 1987, Julien-Laferriere 1999). Therefore, food partitioning by prey size might occur between species that differ in body size (Ricklefs 1973, Jaksic & Braker 1983), with larger prey expected with increasing body size of the predator (Marti *et al.* 1993). Finally, the breeding system determines whether foraging areas can be monopolized through territorial behaviour (a form of interference competition; Schoener 1983), and thus gives the possibility of food partitioning through the segregation of foraging areas.

Comparisons between sympatric species with similar ecology but different weights and social

*Corresponding author.
Email: jtgarca@bio.ucm.es

Present address: Subdirección Gral. Conservación de la Biodiversidad, Dirección General para la Biodiversidad, Ministerio de Medio Ambiente, Equipo Técnico Red Natura 2000, C/Isabel Tintero, 3. Local 2°Bis, 28005 Madrid, Spain.

behaviour are helpful in assessing the influence of energy needs or dominance on foraging strategies and food partitioning (Fedriani *et al.* 2000). The Montagu's Harrier *Circus pygargus* and the Hen Harrier *C. cyaneus* are medium-sized diurnal raptors that breed sympatrically in many areas. The diet of these species appears to be similar (Schipper 1973, Millon *et al.* 2002), as are other aspects of their breeding ecology. However, the species differ in size (with Hen Harrier being larger; Cramp & Simmons 1980) and in breeding system. Montagu's Harrier is a colonial breeder (Simmons 2000), foraging mainly away from the nest areas (Arroyo 1995, Clarke 1996), whereas the Hen Harrier breeds solitarily and defends foraging territories (Watson 1977, Picozzi 1978, Simmons 2000, García & Arroyo 2002).

The main purpose of this paper is to evaluate the nature and extent of food-niche differentiation among these coexisting raptor species, and to identify potential mechanisms that might play a role simultaneously in niche differentiation. We examine whether harriers change their food provisioning patterns and trophic overlap throughout the season (as food abundance and food needs change). We also evaluate whether differences in the food requirements of each species (estimated from their body size and brood sizes) influence food provisioning through differences in size of prey taken and/or feeding rates, and finally assess how the social system influences hunting behaviour and use of the nest area.

METHODS

Study area

The study area covered *c.* 185 km² of agricultural landscape in northeast Madrid Province (central Spain, 40°38'N, 3°30'W). The breeding populations of Montagu's and Hen Harriers in the study area had been monitored since 1991. Nests were visited to check breeding performance. Some nests were visited during laying, providing exact laying dates. Otherwise, laying onset was determined by backdating from hatching date, calculated from chick measurements (Arroyo 1995 for Montagu's Harriers, and J.T. García unpubl. data for Hen Harriers), assuming 29 days of incubation for the Montagu's Harrier and 30 days for the Hen Harrier, and a mean interval between successive eggs of 2 days (Cramp & Simmons 1980).

Diet analyses

To assess diet we analysed pellets and remains collected at nests and perching sites throughout the breeding season (mid March to mid July) in 1997 and 1998. In these years, we collected a total of 111 pellets and 58 remains from over 53 nests of Montagu's Harrier (out of 84 nests in the whole breeding population for the two years), and 67 pellets and 46 remains from 20 different nests of Hen Harrier (out of 28 nests in the whole breeding population for the two years). The proportions of pellets and remains were similar in the two species ($\chi^2_1 = 1.19$, $P = 0.2$). Pellet contents were identified when possible with the aid of reference collections (Cátedra de Vertebrados de la Facultad de Biología de la Universidad Complutense de Madrid, and personal collections), or were mounted on a microscope slide, and identified to order level using an identification key (Day 1966). Lagomorph hind feet found as prey remains were measured to compare the size of the individuals taken, but were not used in statistical analyses of diet composition to avoid biases due to different methods (pellets vs. remains). The minimum number of individuals in each pellet was scored (highest number of left jaws, right jaws, skulls or pairs of incisors in small mammals; upper or lower mandibles, left or right feet in birds; pairs of mandibles for insects), whereas fur or feathers occurring on their own were considered to have come from one individual. Prey were classed in six categories: small mammals (rodents), lagomorphs, birds, eggs, reptiles and insects. Diet data are presented in terms of percentage of identified prey and of estimated biomass. For the analysis of biomass, average weights for each prey category were obtained from local data. As large birds or mammals are often partially eaten by harriers (Arroyo 1997), the maximum biomass consumed per prey was fixed at 150 g for the Montagu's Harrier and at 250 g for the Hen Harrier, according to the size difference between these two species (see Millon *et al.* 2002, for a similar procedure).

Differences in sample size between species correspond to differences in the size of the breeding population of the two species and did not reflect differences in collection effort.

Qualitative estimators of diet

Total identified prey was also used to calculate diversity and niche overlap indices. Trophic diversity was calculated using the Shannon-Weaver index, $H = -\sum p_i * \log p_i$, where $p_i = X_i/X$, and X_i is the number

of prey items taken from class i ; X is the total number of prey items. We computed diet overlap between the two species using a symmetrical overlap index (Pianka 1973): $Ov = \sum p_i q_i / (\sum p_i^2 \cdot \sum q_i^2)^{1/2}$, where p_i and q_i are the relative occurrences of prey category i in the diets of the two species. Ov ranges from 0 to 1 (0–100% overlap).

Food abundance

The abundance of lagomorphs and birds (the main prey for both species) was estimated with point-counts in 1998. Ten transects of similar distance (c. 10 km) were determined *a priori* on 1 : 25 000 maps of the study area. Transects were chosen according to the path network, so the whole of the study area was sampled. In each transect, ten point counts were made at equivalent distances (each 1000 m). We stopped at each point for 10 min, during which we counted the number of birds and lagomorphs present within 200 m of the point. Point counts were made at dawn, and the same points were visited once a month, from March to July inclusive. As we made the transects in the last days of each month, we assumed that observations were representative of prey abundance during the period from the 15th of the month to the 15th of the following month. No quantitative data were available for estimating small mammals or insect abundance. Small mammal abundance should increase throughout the season: the reproductive season of the most abundant species in that area (Algerian Mouse *Mus spretus*) ranges from May to November (Palomo & Gisbert 2003). In the case of insects, we assumed that abundance increased throughout the season (Hugueny & Louveaux 1986, Arroyo 1995).

Feeding behaviour

Feeding behaviour was recorded during the breeding seasons of 1997 and 1998 by means of focal observations at nests of both species. Observations were carried out from late March (arrival and settlement of breeding pairs) until the end of June (end of the nestling period for most pairs). Each focal observation lasted on average 90 min (range 60–155 min). Observations were made from vantage points located 300–1000 m from the nest, which provided good visibility within 800–1000 m of the nest (because the topography of the area is almost flat, except for the few vantage points). Nests were similar in the extent of the area visible. We defined 'nest

area' as the area around the nest visible to the observer (from the nest to 800–1000 m). The birds were unaware of the presence of the observer. A total of 347 focal observations were made: 158 of 47 Montagu's Harrier nests (range 1–6 observations per nest) and 63 of 16 Hen Harrier nests (range 1–9 observations per nest) in 1997, and 82 of 29 Montagu's Harrier nests (range 1–6) and 44 of 12 Hen Harrier nests (range 1–8) in 1998. For each nest we recorded the following variables: number of prey deliveries; size of the prey in relation to the harrier's feet, when possible, as large (e.g. leverets of Iberian Hare *Lepus granatensis*, or Red-legged Partridges *Alectoris rufa*), medium (e.g. rodents or passerines) or small (e.g. orthopterans); total presence time in the nest area; and time spent hunting. We also recorded the harrier's distance from the nest when prey capture was observed. If several observations of hunting behaviour occurred during the same observation sample, hunting distance was averaged for each sex for each observation.

Statistical analysis

To evaluate how diet overlap varies through the season, we analysed differences in prey composition between the species relative to calendar date (comparing differences month by month) rather than relative to stage of breeding. At any given date, different nests are usually at different stages of breeding and so any comparison made in that way would not have been valid to test for overlap in consumption. We noted the number of items of each food category present in each pellet. Differences in diet between the species were analysed with Generalized Linear Models using STATISTICA 99 ed. (Stat Soft, Inc.), with 'species', 'period' and their interaction as categorical factors. We fitted a Poisson distribution for the dependent variables (frequency of each category of prey), and used a log-link function. Type III analyses for the effects are presented. For these analyses, we omitted prey categories that were very rarely taken by either species (e.g. eggs and reptiles, totalling less than 5% of the diet).

For the analyses of behaviour (feeding rates, hunting behaviour), we used non-parametric statistics, given that the distribution of variables strongly deviated from normal. To avoid problems linked to pseudo-replication (given that pairs were observed more than once), analyses were performed on the average values of each behavioural variable for each pair. All tests were performed using STATISTICA 99 ed.

RESULTS

Diet composition and temporal variations

The diet composition of both species throughout the breeding season is summarized in Table 1. The two harrier species hunted on the same range of prey, except for reptiles, which were never found in Hen Harrier diet (possibly due to the small sample size, and the overall rarity of this prey even in Montagu's Harrier diet). Most insects taken were orthopterans (*Acrididae* and *Tettigoniidae*). For both species, the most important prey numerically and in biomass (Table 1, Fig. 1) were young lagomorphs (mainly Iberian Hares) and birds: the largest prey types. Both harrier species took the same bird prey species (mainly passerines, particularly larks and buntings, and some gamebirds), although the small sample size of identified species for Hen Harriers prevented detailed analysis. Within the small mammal prey category, the most abundant species were Algerian Mouse and, secondarily, voles (*Microtus* sp.).

Regarding the temporal pattern of prey consumption, the frequency of small mammals in the diet showed significant differences between periods, being more frequent in the diet early in the season, but did not differ between species (Table 2). The interaction (Species \times Period) was also non-significant. Strong differences were found for the interaction Species \times Period in relation to the frequency of lagomorphs in the diet (Table 2), because the temporal patterns in hare consumption varied between species. In fact, Montagu's Harriers changed the

Table 2. Results from generalized linear models for temporal differences in the consumption of each of diet category by the two species. Type III analyses are presented.

	Main effects			
	df	log-likelihood	χ^2	P
Small mammals				
Species	1	-161.50	2.02	0.16
Period	3	-170.13	19.26	0.0002
Species \times Period	3	-163.07	5.14	0.16
Lagomorphs				
Species	1	-239.19	0.01	0.93
Period	3	-242.66	6.94	0.074
Species \times Period	3	-246.26	14.13	0.003
Birds				
Species	1	-233.57	3.96	0.047
Period	3	-247.82	32.45	> 0.0001
Species \times Period	3	-241.76	20.33	0.0001
Insects				
Species	1	-223.65	28.32	> 0.0001
Period	3	-221.07	23.17	> 0.0001
Species \times Period	3	-211.01	9.81	0.020

consumption of lagomorphs between periods (being more frequent early in the season) whereas Hen Harriers did not (Fig. 2a). The temporal pattern in the frequency of birds in the diet also differed for the two species. Only slight monthly variations were found in Hen Harrier diet (Fig. 2b), whereas a strong temporal increase was observed in the Montagu's Harrier.

Regarding the consumption of insects, we found significant differences between species and periods,

Table 1. Comparative data on diet, according to species, month and size of prey. Results are expressed as a percentage of the total number of identified prey. H index = Shannon diversity index; Diet overlap = Piankas' index of niche overlap. Indices calculated with total identified prey. n = number of identified prey.

	15 March–15 April		16 April–15 May		16 May–15 June		16 June–15 July	
	<i>C. pygargus</i> $n = 101$	<i>C. cyaneus</i> $n = 45$	<i>C. pygargus</i> $n = 78$	<i>C. cyaneus</i> $n = 35$	<i>C. pygargus</i> $n = 124$	<i>C. cyaneus</i> $n = 60$	<i>C. pygargus</i> $n = 48$	<i>C. cyaneus</i> $n = 21$
Small mammals	23	24	23	23	5	7	0	14
Lagomorphs	61	31	32	31	10	32	10	43
Birds	5	42	29	46	32	53	29	38
Eggs	6	0	3	0	2	0	0	0
Insects	4	2	12	0	52	8	58	5
Reptiles	1	0	1	0	0	0	2	0
H index	0.50	0.47	0.66	0.47	0.62	0.46	0.58	0.53
Diet overlap	0.7	0.95	0.71	0.55	87	82	100	100
Accumulated proportion of hatched clutches*	0	0	6	50	87	82	100	100

* $n = 84$ for Montagu's Harrier, and 28 for Hen Harrier.

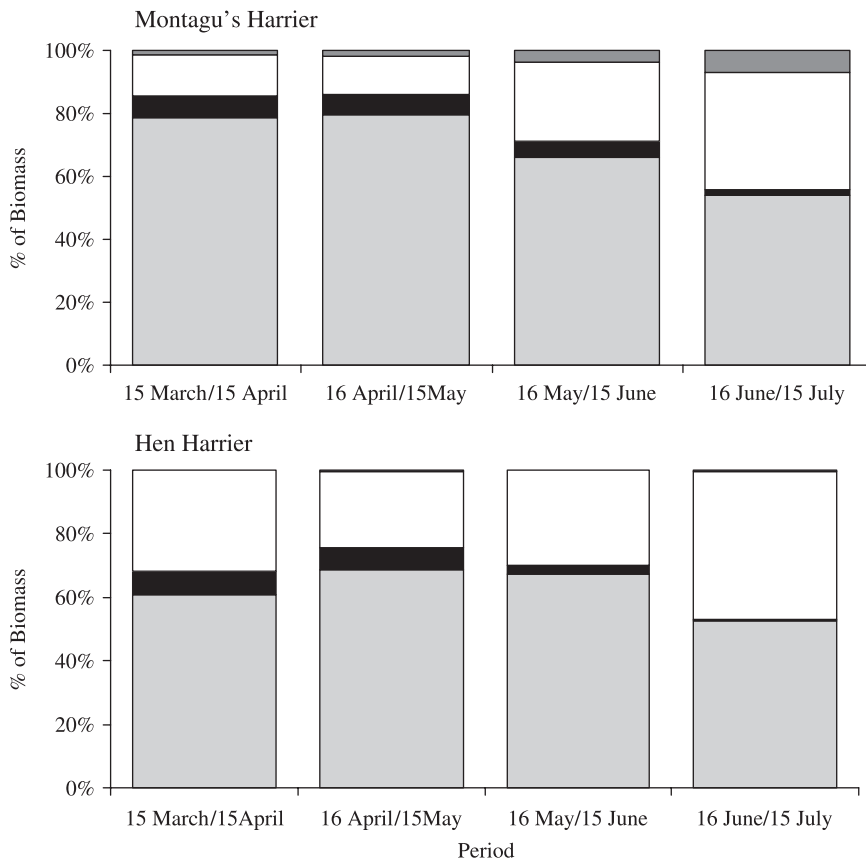


Figure 1. Seasonal variation in the occurrence of different prey categories (as percentage of total biomass) in the diets of Montagu's Harrier (above) and Hen Harrier (below). Grey bars, lagomorphs; black bars, small mammals; white bars, birds; hatched bars, others (insects and eggs).

but not for the interaction Species \times Period (Table 2). In general, Hen Harriers took few insects at any time during the breeding season, whereas Montagu's Harriers took more, particularly late in the season (Fig. 2c). These differences between species in temporal patterns were also apparent when prey types were expressed in terms of biomass (Fig. 1).

Diet diversity and overlap

Diet diversity was similar in the two harrier species (Table 1) and remained unchanged between periods. Dietary overlap between the species at this level of prey identification ranged from 55% to 95% throughout the breeding season (Table 1). Overall, dietary overlap was lowest at the end of the breeding season (Table 1). This was the time when the abundance of the main prey was lowest ($F_{3,166} = 2.92$, $P = 0.035$ for abundance of birds; $F_{3,166} = 3.04$, $P = 0.030$ for lagomorphs, Fig. 3a,b) and food requirements for the harriers were highest (as all clutches had hatched, see Table 1).

Prey size and feeding rates

No significant differences between species were found in relation to the feeding frequency of males (Mann-Whitney U -test, $U = 980$, $n = 102$, $P = 0.80$) or females ($U = 967$, $n = 102$, $P = 0.67$, Fig. 4). However, in both species females contributed food only during the nestling period, and brought only one-quarter (27% for Montagu's Harrier, 26% for Hen Harriers) of all prey items delivered during this period. In the Montagu's Harrier, prey delivery frequency was significantly higher during the nestling period (Kruskal-Wallis: $H = 6.2$, $P = 0.04$, $df = 2$), whereas in the Hen Harrier no significant differences between stages of the breeding cycle were observed (Kruskal-Wallis: $H = 0.99$, $P = 0.61$, $df = 2$; Fig. 4).

In contrast, the average size of prey delivered differed between species, mainly because they took different types of prey with different frequencies. Late in the season, when there was the lowest trophic overlap, differences between the harrier species in average prey size arose because large prey (birds and

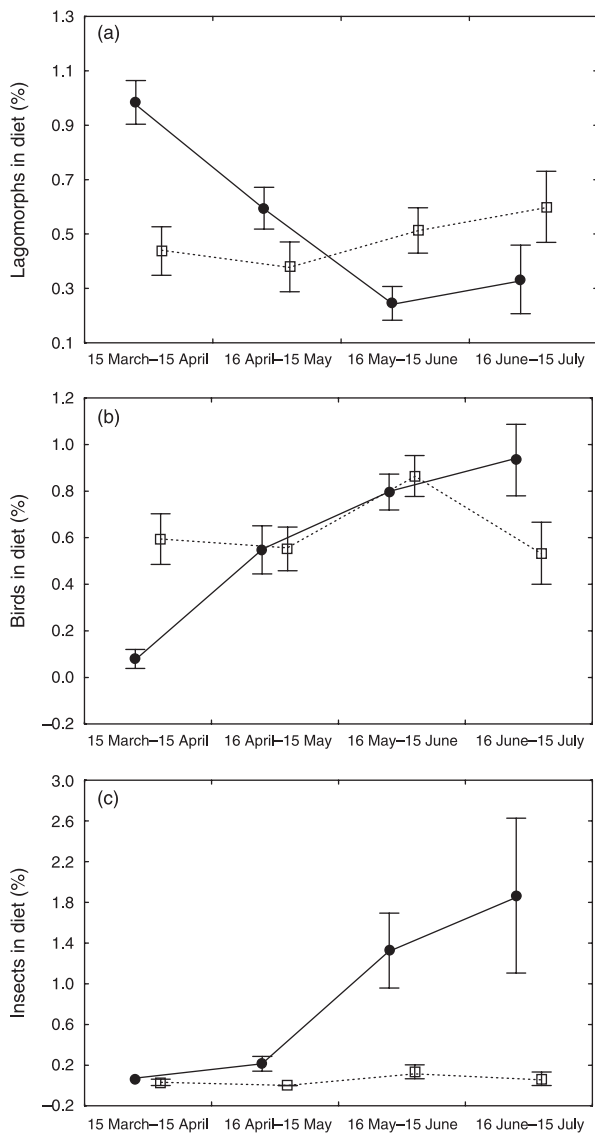


Figure 2. Frequency of occurrence (mean \pm se per pellet) of (a) lagomorphs, (b) birds and (c) insects in Montagu's Harriers (black circles) and Hen Harriers (white squares) in each of the breeding periods analysed.

lagomorphs) were more frequent in the Hen Harrier diet, and insects (small prey) in the Montagu's Harrier diet. Furthermore, within lagomorphs, Hen Harriers also preyed more frequently on larger individuals: hind feet of lagomorphs taken by Hen Harriers were on average (\pm sd) 4.9 ± 1.2 cm long ($n = 10$), and those taken by Montagu's Harriers were 3.6 ± 1.2 cm long ($n = 27$, t -test: $t_{35} = 3.14$, $P = 0.003$).

Observation also confirmed this pattern: 48% of prey brought to the nest by Montagu's Harrier males were medium-sized, and 52% were classified as

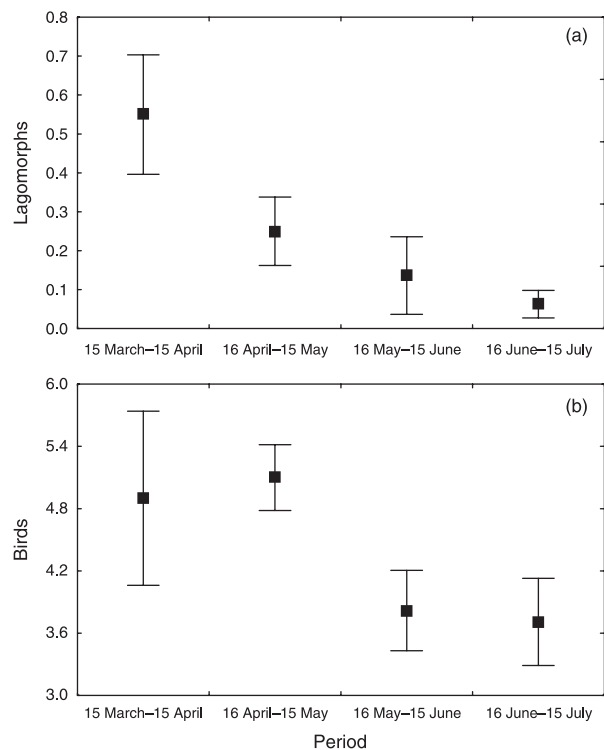


Figure 3. Temporal variation in the abundance (mean \pm se) of (a) lagomorphs and (b) birds, in the study area, estimated by point-counts during 1998 (see Methods).

small ($n = 25$). For Hen Harrier males, 28% of prey brought to the nest were large, 64% were medium-sized and only 7% were small ($n = 14$). These differences were significant ($\chi^2_2 = 12.61$, $P = 0.002$). The size of prey delivered by females to nestlings differed significantly between species: Montagu's Harrier females mainly delivered small prey (all of ten observations were small prey, probably insects as they are very common in the nestling period, Table 1). In contrast, Hen Harrier females delivered larger prey frequently (78% of 14 observations were medium-sized prey and 22% were small prey ($\chi^2_1 = 13.09$, $P = 0.0001$)). Overall therefore there was a difference between species related to prey size, with larger Hen Harriers preying more frequently on larger prey, particularly late in the season.

Between-species variation in the use of the nest area for hunting

Females spent most of their time near or at the nest in all three breeding periods (Fig. 5). Female 'presence time' varied significantly between species, being higher in the Montagu's Harrier, and, according to

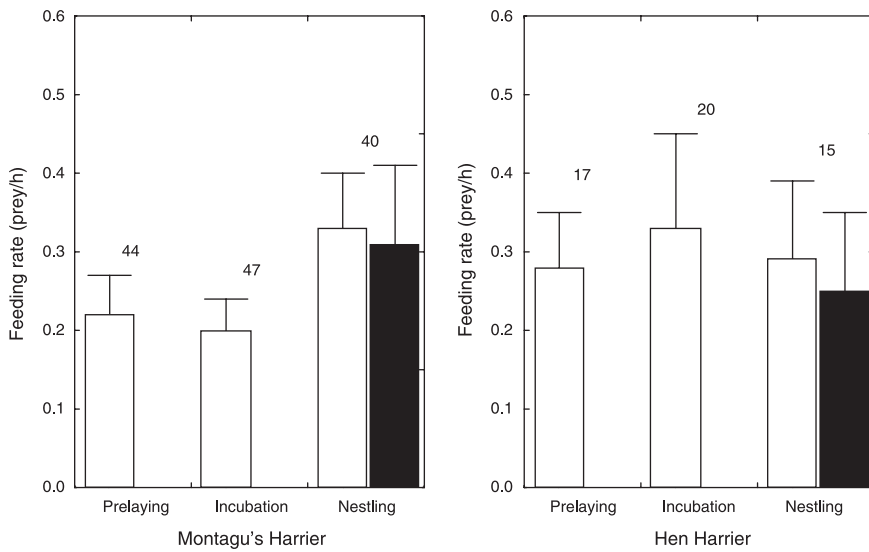


Figure 4. Mean (\pm se) food delivery rates (prey/h) for male (open bars) and female (dark bars) Hen and Montagu's Harriers throughout the breeding season. Sample sizes (number of pairs observed in each period) are shown above the histogram bars.

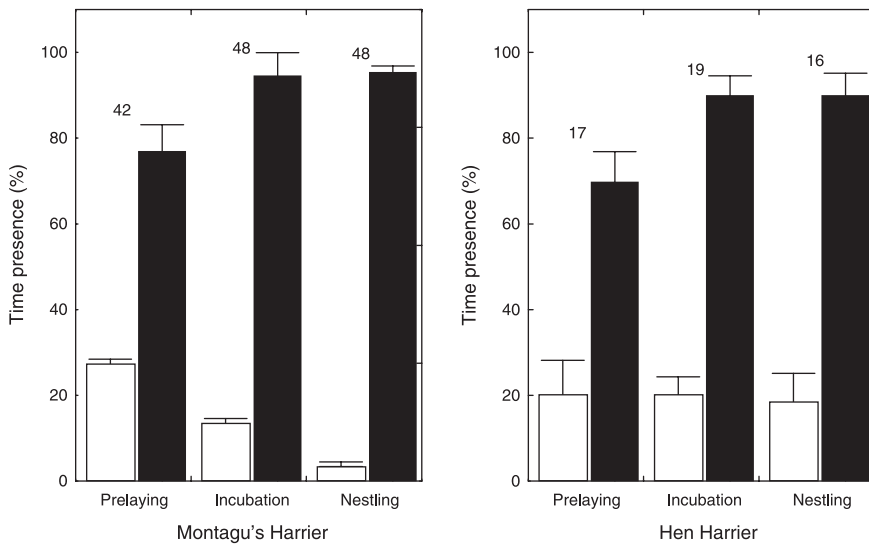


Figure 5. Mean (\pm se) presence time (in percentage) of male (open bars) and female (dark bars) Montagu's and Hen Harriers in the nest area throughout the breeding season. Sample sizes (number of pairs observed in each period) are shown above the histogram bars.

period, being lower in the prelying period in both species (Table 3 and Fig. 5). The time spent hunting by females increased significantly throughout the season, and was significantly higher in Hen Harrier than in Montagu's Harrier females in any of the periods (Fig. 6). Hen Harrier females also hunted nearer to their nests than Montagu's Harrier females (Fig. 7). Furthermore, Hen Harrier females did not vary their hunting distances during the course of the season, whereas Montagu's Harrier females hunted further from the nest during the nestling period than at earlier stages (Fig. 7, Table 3).

The two species also differed significantly in male 'presence time' (Table 3), which was higher overall in the Hen Harrier. Furthermore, the time for which

male Hen Harriers were present was relatively constant throughout the breeding season, whereas it decreased significantly through the season in the Montagu's Harrier (Table 3, Fig. 5), being only 3.5% (vs. 18.5% for the Hen Harrier) in the nestling period. While in the nest area, Hen Harrier males hunted for a significantly greater proportion of time than did Montagu's Harrier males (Table 3). Nevertheless, no significant temporal differences were found for either species in the percentage of time spent hunting in the nest area (Table 3, Fig. 6). For the hunting activities that occurred within the nest area, Hen Harriers hunted nearer to the nest than Montagu's Harriers, although the difference was not significant (Table 3 and Fig. 7). Furthermore, the

Table 3. Results of Mann–Whitney *U*-tests (for between-species differences) and of Kruskal–Wallis tests (for between-period differences) on variation in different behavioural parameters. Sample size for between-species comparisons are specified in the ‘breeding period’ columns.

Variables	Breeding period							
	Species		Montagu's Harrier			Hen Harrier		
	<i>U</i>	<i>P</i>	<i>H</i>	<i>P</i>	<i>N</i>	<i>H</i>	<i>P</i>	<i>N</i>
Male presence time	603	0.021	40.7	< 0.0001	137	1.8	0.40	52
Male hunting time	464.5	0.003	1.18	0.55	109	1.74	0.41	45
Hunting distance	226	0.17	5.9	0.05	38	3.70	0.15	32
Female presence time	547.5	0.002	18.2	< 0.0001	138	9.9	< 0.005	52
Female hunting time	570	0.04	20.4	< 0.0001	115	7.4	< 0.05	46
Hunting distance	81	0.002	13.6	< 0.005	32	1.19	0.5	22

Figure 6. Mean (\pm se) percentage time spent hunting in the nest area, when present, by Montagu's and Hen Harrier males (open bars) and females (dark bars) throughout the breeding season. Sample sizes (number of pairs observed during each period) are shown above the histogram bars.

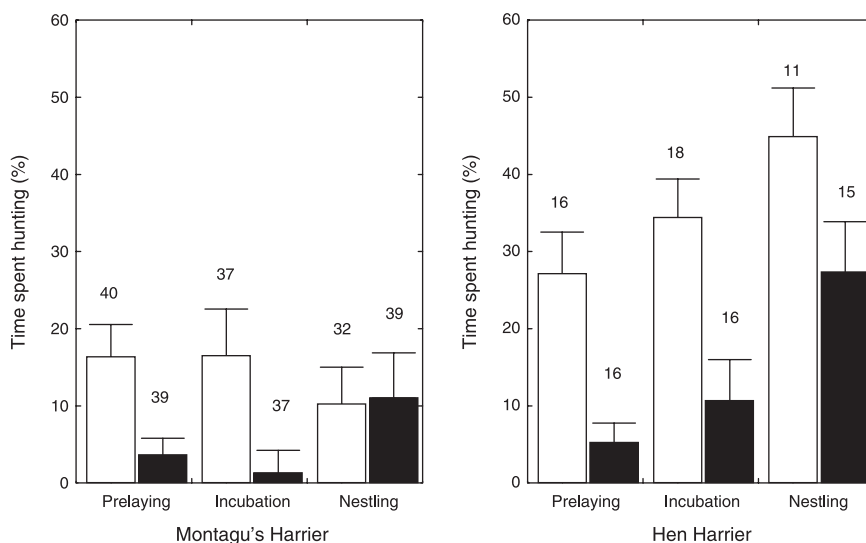
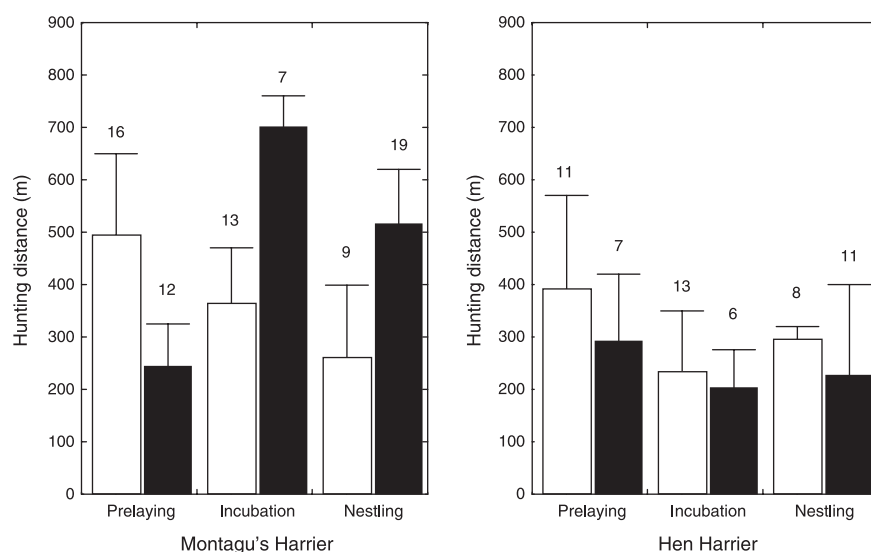


Figure 7. Mean (\pm se) distances from the nest for male (open bars) and female (dark bars) Montagu's and Hen Harriers observed hunting in the nest area throughout the breeding season. Sample sizes (number of different individuals observed hunting in each period) are shown above the histogram bars.



time for which male Hen Harriers were present was relatively constant throughout the breeding season, whereas in the Montagu's Harrier its decrease through the season was nearly significant (Table 3 and Fig. 7). Considering that the amount of time Montagu's Harriers spent away from the nest area was greater than that of Hen Harriers, differences in hunting distances between species were probably much greater than those observed.

DISCUSSION

Dietary comparisons

Diet diversity was similar in the Montagu's Harrier and Hen Harrier in each of the months of study, for the level of taxonomic precision used in this study, and trophic overlap between Hen and Montagu's Harrier during the breeding season in Madrid was high (72% in average).

Lack (1946) argued that a high food overlap between two species would occur when particular prey are exceptionally abundant. However, food-niche overlap should decrease when food abundance decreases (MacArthur & Levins 1967, May 1973). We found a temporal decline in the availability of the main prey at the end of the breeding season. Although food availability was sampled in only one of the two study years, this pattern is common in Mediterranean habitats (Hodar 1996, Duarte *et al.* 1999). Accordingly, a greater segregation of prey consumed by the two species occurred late in the breeding season, when Montagu's Harriers changed their diet towards birds and insects. It is difficult to know whether this shift was a direct response to competition or if it reflects a greater ability of one species to track certain resources. For example, insects might have been taken opportunistically according to their availability, because arthropod populations increase throughout the season (Hugueny & Louveaux 1986, Tellería *et al.* 1988). In any case, if species vary in their foraging preferences or abilities, and those differences become apparent when resources are lower, the mechanism will undoubtedly favour species being more strongly segregated.

Food requirements, size of prey and provisioning patterns

In species with similar diets, differences in the quantity of food required are determined by differences in energy needs (in absolute terms), which are

correlated positively with body mass (Julien-Laferriere 1999). Furthermore, food requirements during the breeding season are also related to brood sizes. Montagu's Harriers (280 g for males, 350 g for females; Del Hoyo *et al.* 1994) weigh on average two-thirds as much as Hen Harriers (350 g for males, 530 g for females), and Hen Harriers laid more eggs and reared more fledglings than Montagu's Harriers (García & Arroyo 2001, Millon *et al.* 2002). It follows therefore that food requirements for Hen Harriers are greater than are those for Montagu's Harriers.

Food partitioning by size between species that differ in food requirements is expected and has been observed in other species (e.g. Nilsson 1984, Gerstell & Bednarz 1999). Accordingly, within the large spectrum of prey types exploited by these two species, both observational data on prey deliveries and analyses of pellets indicated that Hen Harriers preyed more frequently on larger prey, and Montagu's Harriers on smaller prey. This segregation was observed both in the main prey (lagomorphs), and in the sizes of the most important alternative prey. Furthermore, this pattern of segregation by size was particularly marked late in the season, when food abundance decreased and food requirements increased. The larger Hen Harriers kept on preying on relatively large prey but did not vary their feeding rate. Montagu's Harriers, by contrast, turned to smaller prey during the nestling period and consequently increased their feeding rate. This study demonstrates therefore that food-niche segregation by prey size between the two harriers occurs, mainly during the most critical period when there are chicks to be fed, supporting Schipper's (1973) earlier observations.

Montagu's Harriers (the smaller species) might be forced to turn to smaller prey as a consequence of competition. However, observational data do not necessarily exclude other potential interpretations of the data on niche differentiation. Data on the diet and foraging success of each species in the absence of the other would be needed to evaluate whether observed differences in diet reflect a constraint from competition or the result of differences in efficiency between species (and thus different optimal foraging strategies).

Resource partitioning by area: hunting areas and social system

Observed differences in the use of resources increased through differences in foraging strategies related to

territorial behaviour. Foraging patterns clearly differed between territorial Hen Harriers and colonial Montagu's Harriers. Hen Harriers spent more time hunting closer to the nest than colonial Montagu's Harriers. In the Hen Harrier, although both sexes profited from food resources around the nest, females did so especially during the nestling period. During this period, females must help with chick provisioning, and it is highly profitable for them to hunt around the nest, given that they may combine hunting with nest vigilance: among raptors, females are usually the sex more involved in nest defence (Newton 1979). In the Montagu's Harrier, most hunting by males takes place far from the nests (Schipper 1977, Salamolard 1997, this study). Females did some hunting in the nestling period around the nest, but the contribution of females in terms of biomass was apparently small (as they mainly hunted small prey). Therefore, resources around the nest are probably much more important for Hen Harriers than for Montagu's Harriers.

It could be expected that Hen Harriers, and particularly females, try to force Montagu's Harriers out of their territories, particularly late in the breeding season. Hen Harriers in the study area showed relatively low rates of aggression towards Montagu's Harriers at the start of the breeding season, but this increased later, particularly from females (García & Arroyo 2002). These patterns correspond to predictions associated with competition for food (Gowaty 1981). Furthermore, Hen Harriers were much more aggressive interspecifically than were Montagu's Harriers (García & Arroyo 2002). This probably reflects the increased cost for Hen Harriers of the presence of the other species, and the greater size/dominance of the larger species (Fedriani *et al.* 2000). Nevertheless, the existence of different foraging strategies in both harrier species also led to niche segregation and possibly minimized exploitative competition for food (Gerstell & Bednarz 1999).

CONCLUSIONS

This study has shown that there is a food-niche segregation by prey size between the two harrier species, in accordance with differences in body size and presumed energy needs. This segregation by size was apparent in the main prey, but was particularly marked in the choice of alternative prey during the most critical period when nestlings were being fed. In addition, there were differences in the use of foraging areas, arising from the social system of each species.

This niche segregation may be a direct consequence of competition or be due to differences in foraging efficiency and the profitability of different resources, the abundance of which changes throughout the season. In any case, the existence of niche partitioning may relax the potential for competition, and enhance opportunities for coexistence of the two species in their area of range overlap.

Luis Palomares helped with fieldwork. Hervé Fritz provided useful thoughts on the subject. The ideas and comments of Kimberly G. Smith, Carl D. Marti, I.L. Boyd, Ian Newton, Keith Bildstein, Andrew Jenkins and two anonymous referees improved the manuscript.

REFERENCES

- Arroyo, B.E. 1995. Breeding ecology and nest dispersion of Montagu's Harrier *Circus pygargus* in central Spain. DPh thesis, University of Oxford.
- Arroyo, B.E. 1997. Diet of Montagu's Harrier *Circus pygargus* in central Spain: analysis of temporal and geographic variation. *Ibis* **139**: 664–672.
- Begon, M., Harper, J.H. & Townsend, C.R. 1990. *Ecology: Individuals, Populations and Communities*, 2nd edn. Oxford: Blackwell Scientific Publications.
- Chesson, P. & Huntly, N. 1997. The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *Am. Nat.* **150**: 519–553.
- Clarke, R. 1996. *Montagu's Harrier*. Chelmsford, UK: Arlequin Press.
- Cramp, S. & Simmons, K.E.L. (eds) 1980. *The Birds of the Western Palearctic*, Vol. 2. Oxford: Oxford University Press.
- Day, M.C. 1966. Identification of hair and feather remains in the gut and faeces of stoats and weasels. *J. Zool., Lond.* **48**: 201–217.
- Del Hoyo, J., Elliot, A. & Sargatal, J. 1994. *Handbook of the Birds of the World*, Vol. 2. Barcelona: Lynx.
- Duarte, J., Rubio, P.J., Vargas, J.M. & Rendón, M.A. 1999. Análisis del ciclo anual de abundancia de la liebre ibérica (*Lepus granatensis*) en olivares del sur de España. *Actas de 'IV Jornadas Españolas de Conservación y Estudio de Mamíferos'*. Segovia, December 1999.
- Fedriani, J.M., Fuller, T.K., Sauvajot, R.M. & York, E.C. 2000. Competition and intraguild predation among three sympatric carnivores. *Oecologia* **125**: 258–270.
- García, J.T. & Arroyo, B.E. 2001. Effect of abiotic factors on reproduction in the centre and periphery of breeding ranges: a comparative study in sympatric harriers. *Ecography* **24**: 393–403.
- García, J.T. & Arroyo, B.E. 2002. Intra- and interspecific agonistic behaviour in sympatric harriers during the breeding season. *Anim. Behav.* **64**: 77–84.
- Gerstell, A.T. & Bednarz, J.C. 1999. Competition and patterns of resource use by two sympatric raptors. *Condor* **101**: 557–565.
- Gowaty, P.A. 1981. Aggression of breeding Eastern Bluebirds, *Sialia sialis*, towards their mates and models of intra- and interspecific intruders. *Anim. Behav.* **29**: 1013–1027.

- Hodar, J.A.** 1996. Temporal variations in two cereal-crop bird assemblages in the southeastern Spain. In Fernandez Gutierrez, J. & Sanz-Zuasti, J. (eds) *Conservación de las Aves Esteparias y su Hábitat*: 173–181. Valladolid: Junta de Castilla y León.
- Hugueny, B. & Louveaux, A.** 1986. Gradient d'aridité et variation latitudinale de la taille dans les populations de *Calliptamus barbarus* (Costa, 1836) (Insecte, Orthoptère, Acrididae). *Acta Oecol.* **7**: 317–333.
- Jaksic, F.M. & Braker, H.M.** 1983. Food-niche relationships and guilds structure of diurnal birds of prey: competition versus opportunism. *Can. J. Zool.* **61**: 2230–2241.
- Julien-Laferrriere, D.** 1999. Foraging strategies and food partitioning in the neotropical frugivorous mammals *Caluromys philander* and *Potos flavus*. *J. Zool., Lond.* **247**: 71–80.
- Lack, D.** 1946. Competition for food by birds of prey. *J. Anim. Ecol.* **15**: 123–129.
- MacArthur, R.H. & Levins, R.** 1967. The limiting similarity, convergence and divergence of coexisting species. *Am. Nat.* **101**: 377–385.
- Marti, C.D., Steenhof, K., Kochert, M.N. & Marks, J.S.** 1993. Community trophic structure: the roles of diet, body size, and activity time in vertebrate predators. *Oikos* **67**: 6–19.
- May, R.M.** 1973. *Stability and Complexity in Model Ecosystems*. Princeton, NJ: Princeton University Press.
- Millon, A., Bourrioux, J.L., Riols, C. & Bretagnolle, V.** 2002. Comparative breeding biology of Hen and Montagu's Harriers: an eight-year study in north-eastern France. *Ibis* **144**: 94–105.
- Nagy, K.A.** 1987. Field metabolic rates and food requirement scaling in mammals and birds. *Ecol. Monogr.* **57**: 111–128.
- Newton, I.** 1979. *Population Ecology of Raptors*. Calton, UK: T. & A.D. Poyser.
- Nilsson, I.N.** 1984. Prey weight, food overlap, and reproductive output of potentially competing Long-eared and Tawny Owls. *Ornis Scand.* **15**: 176–182.
- Palomo, L.J. & Gisbert, J. (eds)** 2003. *Atlas de los mamíferos terrestres de España*. Madrid: Dirección General de Conservación de la Naturaleza-SECEM-SECEMU.
- Pianka, E.R.** 1973. The structure of lizard communities. *Annu. Rev. Ecol. Syst.* **4**: 53–74.
- Picozzi, N.** 1978. Dispersion, breeding and prey of the Hen Harrier *Circus cyaneus* in Glen Dye, Kincardineshire. *Ibis* **120**: 498–509.
- Ricklefs, R.E.** 1973. *Ecology*. Portland: Chiron Press.
- Robinson-Wolrath, S.I. & Owens, I.P.F.** 2003. Large size in an island-dwelling bird; intraspecific competition and the dominance hypothesis. *J. Evol. Biol.* **16**: 1106.
- Salamolard, M.** 1997. Utilisation de l'espace par le Busard cendré *Circus pygargus*. Superficie et distribution des zones de chasse. *Alauda* **65**: 307–320.
- Schipper, W.J.A.** 1973. A comparison of prey selection in sympatric harriers (*Circus*) in Western Europe. *Le Gerfaut* **63**: 17–120.
- Schipper, W.J.A.** 1977. Hunting in three European harriers (*Circus*) during the breeding season. *Ardea* **65**: 53–72.
- Schoener, T.W.** 1983. Field experiments on interspecific competition. *Am. Nat.* **122**: 240–285.
- Shelley, E.L., Tanaka, M.Y.U., Ratnathicam, A.R. & Blumstein, D.T.** 2004. Can Lanchester's laws help explain interspecific dominance in birds? *Condor* **106**: 395–400.
- Simmons, R.E. (ed.)** 2000. *Harriers of the World: Their Behaviour and Ecology*. Oxford Ornithology Series. Oxford: Oxford University Press.
- Tellería, J.L., Santos, T., Álvarez, G. & Sáez-Royuela, C.** 1988. Avifauna de los campos de cereales del interior de España. In Bernis, F. (ed.) *Aves de los Medios Urbano y Agrícola en las Mesetas Españolas*: 173–319. Madrid: SEO.
- Watson, D.** 1977. *The Hen Harrier*. Berkhamsted, UK: T. & A. D. Poyser.

Received 26 March 2003; revision accepted 6 August 2004;
 first published (online) 16 December 2004
 (doi: 10.1111/j.1474-919x.2004.00377).