

## Comparative breeding biology of Hen Harrier and Montagu's Harrier: an 8-year study in north-eastern France

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Hen and Montagu's Harriers breed in the same cultivated areas of eastern France. We present data from an extensive study conducted in three adjacent areas where 757 nests of the two harriers were monitored between 1993 and 2000, with the aim of comparing the breeding ecology of these two species and to evaluate their possible future trends. Breeding habitat for harriers consisted nearly exclusively of winter cereals, causing great conservation concern in this intensively farmed region. The Hen Harrier was almost absent from two of the study areas. This species showed significantly larger clutch size and higher breeding success than the Montagu's Harrier, and an earlier breeding phenology. It was thus less adversely affected by harvesting activities than Montagu's Harrier. Both species showed a reduced breeding success with increasing laying date. There was a large diet overlap between the two species, possibly leading to competitive interactions. Overall, the Montagu's Harrier should be considered as the more vulnerable of the two species, necessitating conservation measures, such as protection of nests from early harvesting activities. Nevertheless, to maintain both species in agricultural habitats, farming practices that preserve sufficient food should also be promoted.

Three species of Harriers *Circus* spp. breed in western Europe: the Marsh Harrier *C. aeruginosus*, the Hen Harrier *C. cyaneus*, and the Montagu's Harrier *C. pygargus*. As with all but one species of the genus (*C. assimilis*), they nest on the ground (del Hoyo *et al.* 1994, Clarke 1996). Over the past few decades in western Europe, all three species, but particularly Montagu's and Hen Harriers, have changed their breeding habitats from natural to cultivated areas. This habitat shift has caused great conservation concern, as chicks fledge at harvesting time and are killed by harvesting operations, making breeding success heavily dependent on direct human intervention through nest management (Arroyo & Bretagnolle 2000).

Montagu's Harrier, the lightest species of the genus (Clarke 1996), is strictly migratory, and breeds from

North Africa and Europe across to central Russia (Cramp & Simmons 1980, del Hoyo *et al.* 1994). The French population is estimated at 2500–5000 pairs (Salamolard *et al.* 1999). Together with the Spanish population, it is the largest in western Europe, representing 30–40% of the estimated species total of 6000–12000 pairs (Tucker & Heath 1994). The Hen Harrier is currently considered to be the most vulnerable harrier species of western Europe (Tucker & Heath 1994). It has also colonized cultivated areas for breeding but, at least in some regions, it is less affected by harvesting activities than Montagu's Harrier because of its earlier breeding phenology (Arroyo 1996). Partially migratory throughout its range, its numbers are estimated at 7000–12 000 pairs in western Europe, with the largest breeding population in France (2500–4000 pairs, Tucker & Heath 1994, Tombal 1999). The security of the Montagu's and Hen Harrier populations in France is therefore central to the long-term conservation status of the two species in Europe. A better knowledge of Harrier

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breeding parameters is essential to understand possible changes in demographic trends, and to set effective conservation measures (Arroyo & Bretagnolle 2000). However, very few studies have reported detailed data on breeding phenology and success in cultivated areas for either of these species, and especially few for the Hen Harrier (see Watson 1977, Butet & Leroux 1993, Arroyo 1996, Salamolard *et al.* 2000, Arroyo & Garcia 1999).

In this paper we present the results of a study conducted in north-eastern France, on breeding populations of Montagu's and Hen Harriers that nest almost exclusively in cereal fields. Although the programme started in 1987, at first it was concerned primarily with protection. The areas surveyed increased rapidly and reached a constant level in 1993. We thus present data for the period 1993–2000, representing a total of 757 nests monitored in three study areas. This is the first time that the comparative breeding biology of the two species has been studied in this habitat over many years and using a large data set. Our aims were to compare breeding ecology, diet, conservation effort and population dynamics between the different areas, years and species, in order to assess the level of competition between the two species, and their possible future trends in French cultivated areas.

## METHODS

### Study areas

The study took place within *Aube* and *Haute-Marne* départements, *Champagne-Ardenne* Region, north-eastern France (Fig. 1). Three distinct study areas were defined, according to topography and general agricultural characteristics (Fig. 1, Table 1). Breeding harriers were searched for by the same five observers during the whole study period, with a constant effort every year. The first study area (c. 600 km<sup>2</sup>) is typical of the *Champagne Crayeuse* (hereafter called *Crayeuse*). This is a low-elevation chalk plateau (< 250 m). Intensive farming in vast open fields as well as a few pine woods have replaced former sheep-grazed areas. The second and third study areas (*Barrois* 1 & 2) are also limestone plateaux, but slightly higher and more undulating (200–400 m). Between about a third and a half of the two *Barrois* areas are wooded with beech *Fagus sylvatica*. Open habitats are intensively cultivated cereal fields, vineyards and grassland or pasture fields with hedges (Fig. 1, Table 1). In the first study area (*Crayeuse*) both harrier species occur, whereas in *Barrois*, only Montagu's Harriers nest in the cereal fields, while a few Hen Harriers breed in young woodlands.

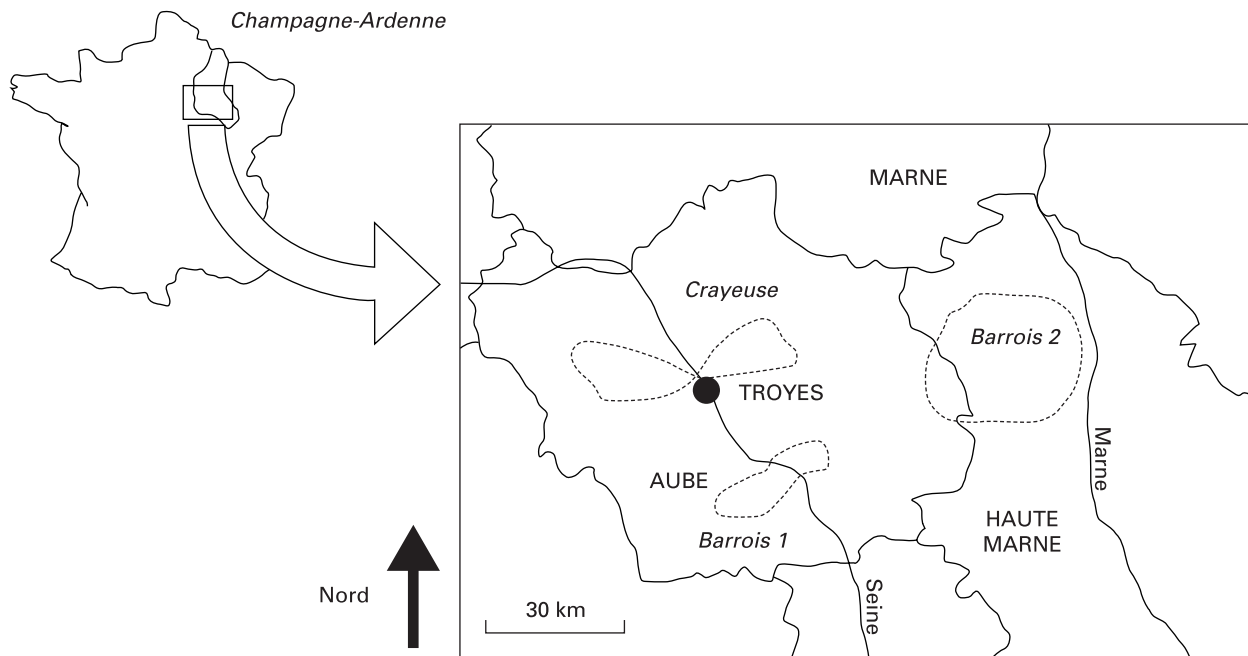


Figure 1. General map showing the three study areas and localities cited in the text.

**Table 1.** Land use characteristics of the study areas, and comparison of harrier breeding densities (breeding pairs/100 km<sup>2</sup>) and their variations from year to year (CV = 100\*sd/mean).

Study area	Area (km <sup>2</sup> )	Forest (%)	Agricultural land use (%)				Harrier density (1993–2000)			
			wheat	winter barley	meadows	other crops	Montagu's Harrier		Hen Harrier	
							Mean	CV (%)	Mean	CV (%)
<i>Crayeuse</i>	621 <sup>a</sup>	8.53	32.8	8.9	4.6	53.7	5.45	14.0	5.31	28.1
<i>Barrois 1</i>	247 <sup>b</sup>	16.6	28.5	9.3	20.7	41.5	7.37	38.3	0.24	14.8
<i>Barrois 2</i>	807	36.5	29.7	9.2	18.5	42.6	3.46	41.2	0.00	–

<sup>a</sup>This value varied from 599 to 687 according to years.

<sup>b</sup>This value varied from 223 to 260 according to years.

### Harrier censuses

Nests were located between May and July by observing male to female prey deliveries. A small number of Montagu's Harrier nests were found in forest clearings ( $n = 5$ ) or in set-aside fields ( $n = 1$ ), while a small, although not precisely known proportion of Hen Harrier nests were in young woodlands of *Barrois 2*. Most fieldwork was done in June (nest searching) and July (protection of broods from harvesting). As a result, some breeders that failed at early stages (incubation) went undetected, leading to a potential bias. In another study area in western France (1994–2000), where Montagu's Harrier nests are detected earlier, less than 15% of clutches failed to hatch ( $n = 320$ ), of which one-third were due to predation, one third to harvesting and the remaining to natural causes (V. Bretagnolle & B.E. Arroyo unpubl. data). We assumed that a similar proportion of pairs failed at incubation in Eastern France, and that this proportion was similar between the two species and years. The numbers of nests found were then converted into breeding densities (uncorrected), used in comparisons between species, study areas and years.

### Breeding phenology

Because nests were not systematically searched for from the beginning of the breeding season, egg laying dates were estimated by back-dating from hatching date. This was calculated through the age of nestlings from the length of the third primary (Arroyo 1995) and/or from plumage pattern (Pacteau & Perrotin 1991). For the Montagu's Harrier, we used an average of 30 days for incubation, and 30 days for the chick rearing period (Cramp & Simmons 1980,

Clarke 1996, pers. obs.). We used a slightly higher value for the Hen Harrier rearing period (32 days; Cramp & Simmons 1980, pers. obs.). Data on breeding phenology are presented on a weekly basis, to take into account the relative inaccuracy of the method, with week 1 being the first week of April.

### Observed and estimated clutch and brood sizes

Nests were visited one to seven times during the breeding season (but only once during incubation as Harriers are sensitive to disturbance at this time), and clutch size, hatchling and fledgling numbers were recorded during nest visits. Nests were visited mainly when we estimated that the brood was old enough to allow nest displacement as a protection measure (see below). Thus, only a few nests were visited at the egg stage (20%,  $n = 757$  nests, both species combined) and, moreover, the number of nest visits differed between nests located in wheat vs. barley because they did not require the same conservation effort. We thus estimated clutch size for nests visited at the chick stage from the number of chicks plus the number of unhatched eggs (in harriers, unhatched eggs are left within the nest). There are inherent biases in doing this (e.g. underestimation of clutch size due to early chick mortality, sample bias due to the fact that only successful clutches are used). However, this bias might have been minimal, as observed and estimated clutch sizes did not differ significantly (Kolmogorov–Smirnov two-sample test,  $D_{\max} = 0.03$ ,  $P > 0.99$ ,  $n = 443$ ;  $D_{\max} = 0.08$ ,  $P = 0.98$ ,  $n = 167$ , respectively, for Montagu's and Hen Harriers). For clarity, however, we present both actual and estimated clutch sizes separately. Unless specified otherwise, brood sizes during chick

rearing were calculated only for nests where hatching occurred, and fledged brood sizes only for nests where fledging occurred.

## Diet

Both pellets and remains were collected in June and July at nests, perching sites and roost places, and thus came from both young and adults (using a combination of pellets and remains improves harrier diet analysis: Simmons *et al.* 1991). Pellets were analysed to test for differences in the diet of the two species and between *Crayeuse* and *Barrois* (i.e. *Barrois* 1 and 2 were cumulated). Overall, 3532 pellets were collected in 1996–2000, and these accounted for 95% of 7052 identified prey items. For each pellet, the maximum number of individuals was scored (see Clarke *et al.* 1993, and Arroyo 1997 for procedure). Harrier pellets often contain remains of an unknown number of individuals, e.g. they sometimes only consist of fur or feathers, and this may introduce some bias. In such cases, we arbitrarily considered that only an individual prey was present in each pellet (see also Arroyo 1997, Salamolard *et al.* 2000). We then calculated the percentage of biomass provided by each prey type (mean mass used for each prey category was obtained from local data). Large birds or mammals are often only partially eaten by Harriers (Arroyo 1997): maximum biomass consumed per prey was thus arbitrarily 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 also Arroyo 1997).

Trophic diversity was calculated using the Shannon–Weaver index ( $H = -\sum p_i \log p_i$ , where  $P = X_i/X$ , and  $X_i$  = number of prey items taken from class  $i$ ;  $X$  = total number of prey items). Seven prey categories were considered for the calculation of the index, in order to allow comparisons between species and the two regions. Furthermore, differences between regions and species in diet were evaluated through differences in the frequency of occurrence for each prey category. We used an index of competition (MacArthur & Levins 1967, in Ricklefs 1979), which was calculated only for *Crayeuse*:  $a^{j,k} = \sum_i (P_{i,j} * P_{i,k}) / \sum_i P_{i,k}^2$  ( $P_{i,j}$  = proportion of biomass of class  $i$  for the species  $j$ ). Above 1, the index suggests that interspecific competition is weaker than intraspecific competition for species  $j$ , assuming that overlap leads to competition.

All statistical analyses were performed using SAS 8.0 (SAS 1999). Data are expressed as mean  $\pm$  sd, but were transformed for statistical analyses when

non-normally distributed. Non-parametric tests were used for small sample sizes, as well as for breeding density parameters.

## RESULTS

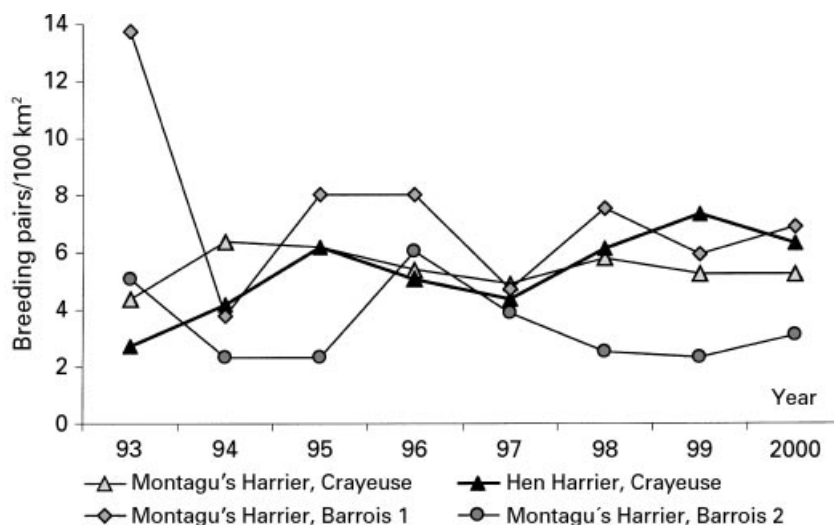
### Breeding density

The average breeding density for the Montagu's Harrier for all areas and years combined was  $4.96 \pm 0.77$  pairs/100 km<sup>2</sup> ( $n = 8$  years), and for Hen Harrier  $5.32 \pm 1.40$  (*Crayeuse* only; see Table 1). In *Crayeuse*, where both species breed in sympatry, there were no significant differences between species in density (Wilcoxon's signed ranks test,  $Z = 0.33$ ,  $P = 0.74$ ,  $n = 8$  years). Hen Harrier breeding density increased significantly during the study period (Spearman test,  $r_s = 0.81$ ,  $P = 0.01$ ,  $n = 8$  years), unlike the Montagu's Harrier in any of the study areas (see Fig. 2). However, Montagu's Harrier breeding density varied significantly among study areas (Kruskal–Wallis test,  $H = 10.68$ ,  $P = 0.04$ ,  $df = 2$ ,  $n = 24$ ; Fig. 2). The length of the study period did not allow testing for cyclicity in breeding density, as documented in some other harrier populations (Salamolard *et al.* 2000). However, *Barrois* 1 & 2 showed consistently more variability than *Crayeuse*, as revealed by the coefficients of variation for Montagu's Harrier (Table 1). Montagu's Harrier density did not covary between *Barrois* 1 and 2 ( $r_s = 0.47$ ,  $P = 0.24$ ,  $n = 8$ ), and nor did Hen Harrier and Montagu's Harrier density in *Crayeuse* ( $r_s = 0.19$ ,  $P = 0.76$ ,  $n = 8$ ).

### Breeding habitat and phenology

Overall, 97% of nests were found in cereal fields, especially winter barley and wheat (Table 2;  $n = 757$  nests, both species combined). Within the cereals, winter barley was strongly selected over wheat ( $X_1^2 = 96.2$ ,  $P < 0.001$ ), in both species (Fig. 3). There were no significant differences between Hen and Montagu's Harriers in *Crayeuse*, all years combined ( $X_1^2 = 0.63$ ,  $P = 0.43$ ). Montagu's Harriers showed a marked temporal trend in crop selection for nesting, considering the ratio of nests in wheat vs. barley ( $r_s = -0.96$ ,  $P = 0.0005$ ,  $n = 7$  weeks). The ratio was skewed towards barley in earlier breeders, and towards wheat (or other crop types) for late breeders (Fig. 3). The same trend was apparent, though not significant, for Hen Harriers ( $r_s = -0.46$ ,  $P = 0.29$ ,  $n = 7$ ).

In both species, egg-laying was spread over more than two months, between 15 April and 30 June



**Figure 2.** Harrier breeding density (pairs per 100 km<sup>2</sup>), according to species and study areas.

**Table 2.** Nest site choice according to species, area and year. Data are given as percentage of nests found per habitat type ( $n$  = number of nests monitored).

Year	Montagu's Harrier									Hen Harrier		
	Crayeuse			Barrois 1			Barrois 2			Crayeuse		
	wheat	barley	$n^a$	wheat	barley	$n^a$	wheat	barley	$n^a$	wheat	barley	$n^a$
1993	58	29	24	55	41	28	81	19	26	40	47	15
1994	46	54	35	50	38	8	75	25	12	44	48	23
1995	59	41	34	65	30	17	83	17	12	71	27	34
1996	35	65	34	65	35	17	58	39	30	41	56	31
1997	18	82	28	50	50	10	20	80	20	48	44	25
1998	61	39	33	43	57	14	69	31	13	66	29	35
1999	76	21	29	46	55	11	50	50	12	44	56	41
2000	20	73	30	40	60	15	25	75	16	28	64	36
Totals	53	44	247	57	42	120	63	37	141	56	40	240

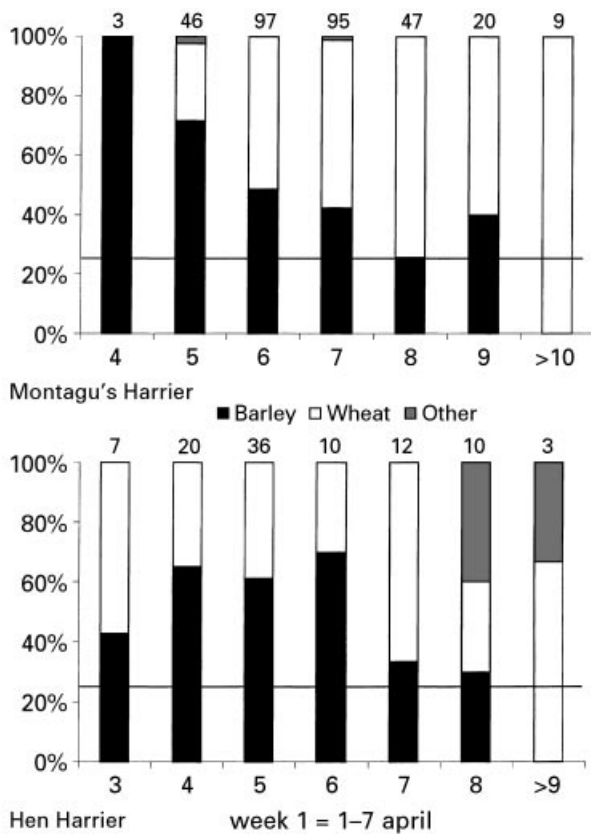
<sup>a</sup>Total numbers, including pairs that bred in other crop types than cereals.

(Fig. 4). On a weekly basis (with week 1 = 1–7 April), the Hen Harrier laid on average slightly, but significantly, earlier ( $5.45 \pm 1.55$ ,  $n = 97$ ) than Montagu's Harrier ( $6.75 \pm 1.30$ ,  $n = 317$ ; Kolmogorov–Smirnov test,  $D_{max} = 0.495$ ,  $P < 0.0001$ ; Fig. 4). This difference was more marked if median dates (week 5 vs. week 7 for Hen and Montagu's, respectively) were used, and laying was also less synchronized in Hen than in Montagu's Harriers (CV = 30% and 19%, respectively). In the Montagu's Harrier, there was a significant effect of year but not of area on laying date (two-way ANOVA, year  $F_{7,316} = 2.87$ ,  $P = 0.007$ ; area  $F_{2,316} = 1.2$ ,  $P = 0.3$ ; interaction  $F_{14,316} = 0.4$ ,

$P = 0.99$ ). In contrast, year to year variation in egg laying dates for the Hen Harrier was not statistically significant ( $F_{7,96} = 1.93$ ,  $P = 0.07$ ).

### Clutch size

In both species, clutch size ranged between one and six eggs. On average, observed clutch size was  $3.65 \pm 1.01$  for Montagu's Harrier ( $n = 111$ , CV = 28%) and  $4.15 \pm 1.27$  for Hen Harrier ( $n = 40$ , CV = 31%). Montagu's Harriers laid significantly smaller clutches than Hen Harriers in any year (two-way ANOVA, year  $F_{7,151} = 2.6$ ,  $P = 0.01$ ; species  $F_{1,151} = 14.2$ ,  $P = 0.0002$ ,

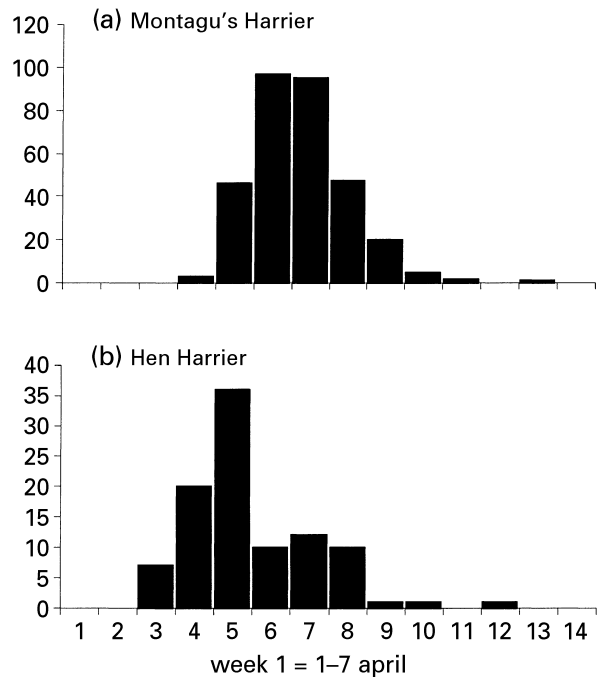


**Figure 3.** Comparative nesting habitat choice according to calendar date in the two harrier species. Data are shown as percentages. Sample sizes are indicated at the top of the columns. Only three crop categories are considered (see text). Week 1 = first week of April. The line indicates the relative availability of barley as compared to all winter cereals (23%).

interaction  $F_{7,151} = 0.8$ ,  $P = 0.59$ ). In the Montagu's Harrier, estimated clutch size varied between years but not between areas (area  $F_{2,432} = 2.19$ ,  $P = 0.11$ , year  $F_{7,432} = 7.18$ ,  $P < 0.0001$ , interaction  $F_{14,432} = 0.93$ ,  $P = 0.52$ ). However, this was due only to 1997, in which, on average, smaller clutches were laid than in 1993, 1996, 1998 and 2000 (Scheffe's test, all  $P < 0.05$ ). For the Hen Harrier, there was no significant year effect on clutch size, using estimated values ( $F_{7,167} = 0.99$ ,  $P = 0.44$ ). Estimated clutch size decreased significantly with laying date in Montagu's Harrier but not in Hen Harrier (Linear regression,  $F_{1,315} = 7.94$ ,  $P = 0.005$  and  $F_{1,94} = 0.05$ ,  $P = 0.82$ , respectively; see Fig. 5).

### Brood sizes at fledging, and nest failure

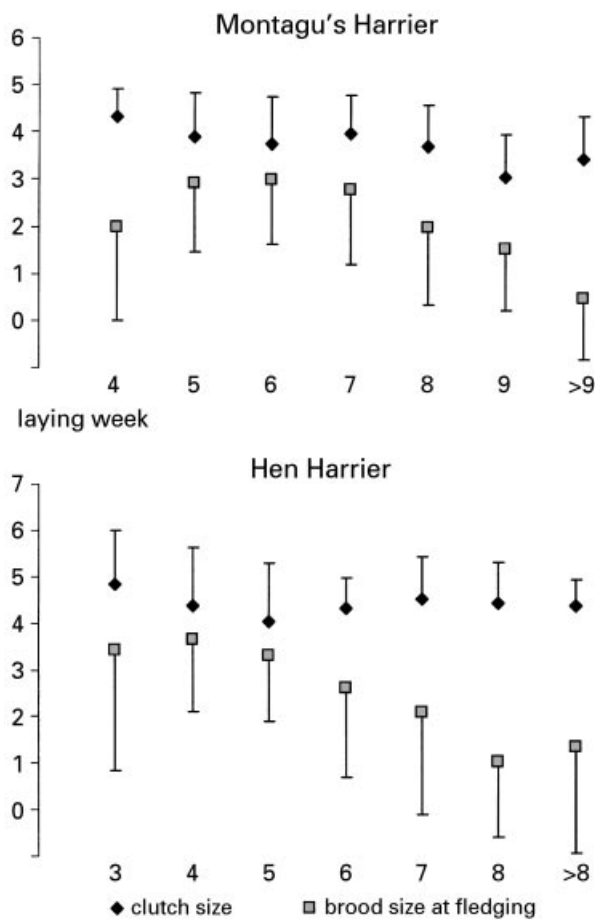
Nest failure (i.e. total failure of clutch or brood) varied between 14% and 65% according to years and



**Figure 4.** Comparative breeding chronology of Hen and Montagu's Harriers. Data are expressed as number of clutches.

species, although these are minimum values as some nests might have failed without being found. Nest failure did not differ significantly between the two harriers in *Crayeuse* (Mann-Whitney  $U$ -test,  $U = 21$ ,  $P = 0.24$ ,  $n = 8$ ), nor between years (Kruskal-Wallis test,  $H = 8$ ,  $df = 7$ ,  $P = 0.33$ ) or areas ( $H = 3$ ,  $df = 2$ ,  $P = 0.22$ ) for the Montagu's Harrier. At least 8.7% of eggs of Montagu's Harriers ( $n = 1523$ ) and 10.5% of Hen Harriers ( $n = 588$ ) failed to hatch (four clutches, transferred for conservation purposes, are excluded from this analysis). Complete infertility of a whole clutch occurred for 10 clutches (Montagu's Harrier: 2, 2, 3, 4, 5 eggs; Hen Harrier: 1, 3, 4, 4, 5 eggs).

As a likely consequence of their larger clutches, Hen Harrier brood size during the nestling period averaged higher ( $3.64 \pm 1.29$ ,  $n = 150$ ,  $CV = 36\%$ ) than for the Montagu's Harrier ( $3.33 \pm 1.09$ ,  $n = 422$ ,  $CV = 33\%$ ). This difference was significant ( $F_{1,571} = 7.82$ ,  $P = 0.005$ ). Fledged broods were, as expected, smaller:  $3.12 \pm 1.05$  and  $3.41 \pm 1.30$  for Montagu's and Hen Harriers, respectively ( $F_{1,456} = 6.36$ ,  $P = 0.01$ ). Although few nests were visited several times in the chick-rearing stage, chick mortality seemed to occur mainly in the early rearing period. Fledged brood sizes decreased with laying date in both species (ANCOVA, species  $F_{1,456} = 1.1$ ,  $P = 0.31$ , date



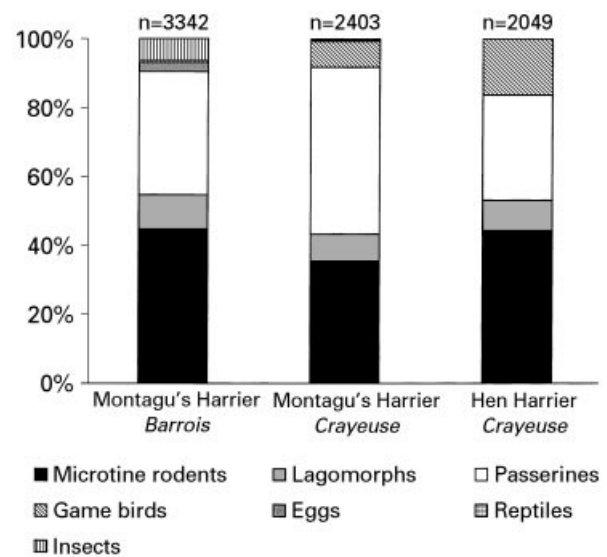
**Figure 5.** Average estimated clutch size and brood size at fledging (including unsuccessful nests) according to week of laying. Week 1 = first week of April. For sample sizes, see Fig. 3.

$F_{1,456} = 11.0$ ,  $P = 0.001$ , interaction  $F_{2,737} = 0.9$ ,  $P = 0.36$ ; Fig. 5).

There were significant effects of year and areas on fledged brood sizes in Montagu's Harrier (area  $F_{2,320} = 0.59$ ,  $P = 0.55$ , year  $F_{7,320} = 5.97$ ,  $P < 0.0001$ , interaction  $F_{14,320} = 1.0$ ,  $P = 0.46$ ). In Hen Harrier, there was also an effect of year on fledged brood sizes ( $F_{7,104} = 3.96$ ,  $P = 0.0006$ ), which was mainly due to 1997 (see Fig. 7). Variation in brood size at fledging was slightly greater in Hen Harrier (CV = 38%) than in Montagu's Harrier (CV = 33%).

## Diet

Across the whole data set, the prey species found most frequently in pellets was the Common Vole *Microtus arvalis*, which represented 53.7% of all prey (Table 3). Passerines or other non-game birds



**Figure 6.** Comparative data on diet according to species during the period 1993–2000. Data are expressed as a percentage of the estimated contribution in weight. Numbers of prey are above histograms.

were the second most important prey type, especially Skylarks *Alauda arvensis* (64% of identified passerines,  $n = 850$ ) and Yellow Wagtail *Motacilla flava* in Crayeuse. For the Montagu's Harrier, the frequency of occurrence of passerines in Barrois was lower than in Crayeuse in any year (Table 3). The frequency of occurrence of the three main prey categories (voles, passerines and others) differed significantly between the two species in Crayeuse (G-test,  $G = 97.0$ ,  $P < 0.001$ ) and between Crayeuse and Barrois for the Montagu's Harrier ( $G = 290.4$ ,  $P < 0.001$ ; see Table 3 for values). Between-year variations were significant for Montagu's Harriers in Barrois ( $G = 220.3$ ,  $P < 0.001$ ), but not in Crayeuse either for Montagu's ( $G = 13.95$ ,  $P = 0.08$ ) or for Hen Harriers ( $G = 7.04$ ,  $P = 0.53$ ).

Voies and passerines provided 76% and 83.3% of the biomass consumed by Hen Harrier and Montagu's Harrier, respectively (Fig. 6). Voies constituted the main contribution in biomass for the Montagu's Harrier in Barrois (45.5%) and for the Hen Harrier (42.7%), while passerines formed the main category for the Montagu's Harrier in Crayeuse (48.9%). Game birds accounted for more than 10% of the biomass of Hen Harrier diet (Fig. 6).

Diet diversity was similar for the Montagu's Harrier in both regions (0.496 in Barrois vs. 0.469 in Crayeuse) but was lower in Hen Harrier (0.377). The competition index, calculated with data from

**Table 3.** Comparative data on diet, according to species, study areas and year. Data are expressed as frequency of occurrence in diet ( $n = 7052$  prey items).

Study area	Montagu's Harrier					Hen Harrier									
	Barrois (1 & 2)					Crayeuse									
Year	1996	1997	1998	1999	2000	1996	1997	1998	1999	2000	1996	1997	1998	1999	2000
<b>Prey species/category</b>															
<b>Mammals</b>															
Common Vole	64.4	30.8	56.8	38.9	55.3	53.7	39.3	52.5	50.0	51.7	66.5	54.5	69.3	64.1	63.7
Lagomorphs	5.8	2.4	1.4	1.1	0.9	1	1.9	1.4	0.7	0.3	1.6	2.0	0.9	0.2	1.5
<b>Passerines</b>															
Skylark	3.4	7.8	7.6	5.8	3.6	12.9	13.1	7.0	11.7	4.7	5.9	7.7	3.7	11.0	3.8
Yellow Wagtail	0	0	0	0	0.5	4.6	4.6	3.9	2.0	4.7	4.9	4.6	1.8	2.1	1.8
Other passerines	10.4	16.5	16.6	19.4	11.8	22.0	27.9	22.1	20.8	19.6	17.4	22.3	20.6	17.8	24.3
<b>Gamebirds</b>															
Quail	0	0.3	0.3	0.3	0	0.7	2.3	0	0.7	0.3	1.4	4.2	0.5	3.2	1.5
Partridge	0.1	0	0.2	0	0	0.3	0.4	0	0.7	0.3	0.4	2.0	0	0.5	1.8
<b>Insects</b>															
Green Grasshoppers	4.7	30.7	11.7	25.8	16.1	0.6	1.3	2.0	0.3	14.8	0	0	0	0	0.4
Number of prey items	675	626	622	360	554	674	519	358	298	317	489	453	218	437	452

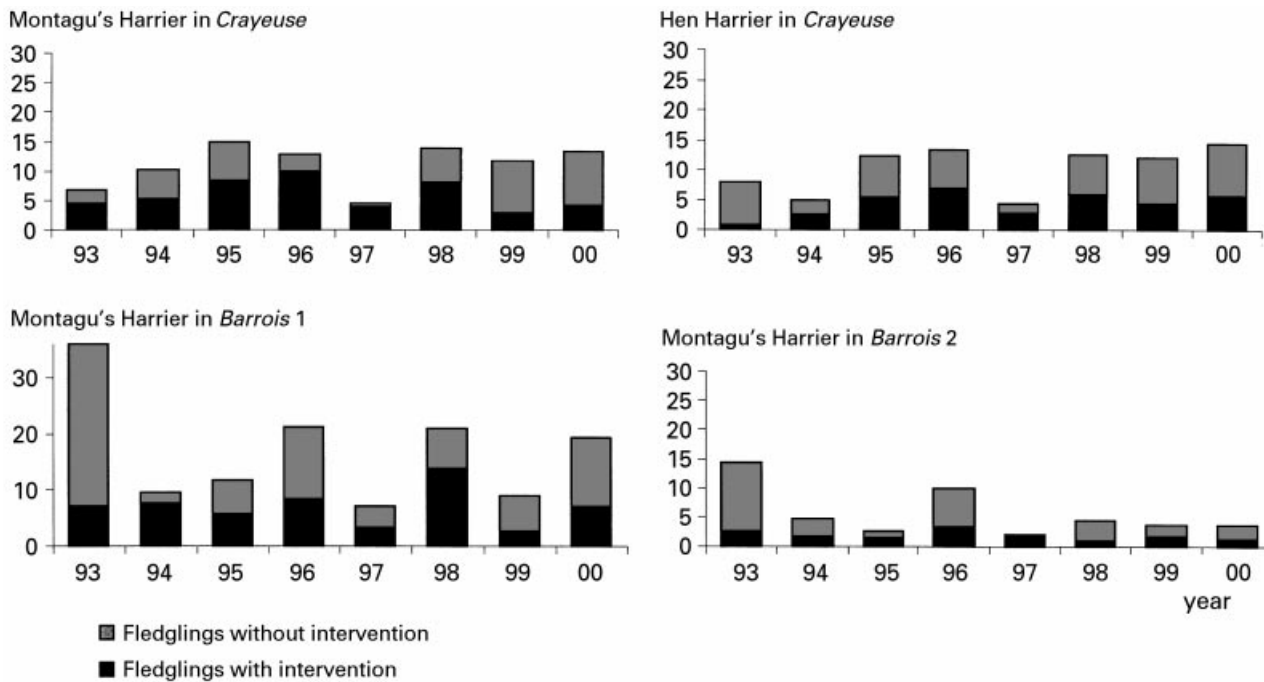
*Crayeuse*, revealed a high overlap between the two species ( $a^{\text{Montagu's, Hen}} = 1.03$ ,  $a^{\text{Hen, Montagu's}} = 0.88$ ; see also Fig. 6), while the asymmetry of index value suggests that the Montagu's Harrier suffered more inter- than intraspecific competition than did the Hen Harrier.

### Conservation effort

Types of intervention varied between areas. In *Crayeuse*, nest transfers dominated (i.e. transfer of the nestlings to an artificial nest site, generally from barley to wheat, but sometimes from wheat to potatoes, beet, sunflower or other). In the other two areas, the most common intervention technique consisted of erecting a fence around the nest (c. 1.5 m diameter), to protect nestlings during harvesting and from predators after harvesting. This technique was abandoned in *Crayeuse* because nests were too visible, and were systematically destroyed by humans after harvesting.

Combining data for both species, 666 chicks (44.9%) were saved from harvesting operations, i.e. 46.2% and 42.3% of Montagu's and Hen Harrier, respectively (Fig. 7). The difference between the two species was not significant ( $\chi^2_1 = 1.8$ ,  $P = 0.18$ ), but when considering only data from *Crayeuse*, Montagu's Harrier necessitated more intervention than Hen Harrier (respectively 54.2% and 42.3%;  $\chi^2_1 = 13.2$ ,  $P = 0.0003$ ), probably resulting from species differences in breeding phenology. There were significant differences in intervention rate between areas for the Montagu's Harrier ( $G = 27.8$ ,  $P < 0.001$ ) with *Barrois 2* requiring fewer interventions as a consequence of delayed cereal growth, resulting in both delayed harvesting and weaker nest-site selection for barley (Fig. 7). Four interventions were attempted at the egg stage, but all failed. Nests in winter barley necessitated intervention in 97.6% of cases ( $n = 211$ ) for Montagu's Harrier, and in 85% for Hen Harrier. In contrast, nests in wheat showed a more variable pattern: intervention rate varied between 17% and 55% (average = 34%) for Montagu's Harriers and 0% and 33% (19%) for Hen Harriers. Between-year variations (Fig. 7) were apparently more related to crop growth (presumably mediated by weather in spring) than to laying date, as was suggested by 1997, when a spring drought delayed wheat growth, and Harriers strongly selected barley for nesting because it was taller. All nests in other crop types (rye-grass, alfalfa, peas, rape, etc.) needed intervention ( $n = 21$ ).





**Figure 7.** Conservation effort according to year, study areas and species. Chicks fledged with intervention are compared to those fledged without intervention.

## DISCUSSION

### Comparative breeding biology of Hen and Montagu's Harriers

Between our three study areas, the distribution and breeding density of the Montagu's Harrier was homogeneous, whereas Hen Harriers were almost absent from *Barrois*. The numbers of Hen Harriers breeding in the seminatural habitat (i.e. forest) of *Barrois* have strongly declined during the last 10 years (our unpubl. data). Why Hen Harriers did not shift to crops in this area is unknown. In *Crayeuse* as well as in several other regions of France, the Hen Harrier seems to have increased in both numbers and distribution (Tombal 1999).

Both harrier species showed a strong preference for winter cereals, especially winter barley, despite its low availability. Such crop selection was particularly pronounced in the Montagu's Harrier during spring droughts, such as in 1997, and was more marked for earlier breeding pairs. Conversely, Hen Harriers did not show such a temporal pattern in habitat choice. Winter barley starts growing earlier than wheat, the latter being especially short at the time of harrier settlement, if there is no spring rain.

This may suggest that habitat choice in the Montagu's Harrier is critically dependent on crop height at laying, while Hen Harriers may be less dependent on vegetation height (see also Schipper 1978, Simmons & Smith 1985, Redpath *et al.* 1998). Hen Harriers also started laying significantly earlier than Montagu's: the difference was about eight days, as in some other areas (11 days in central Spain: Arroyo 1996). Productivity also decreased with laying date for both species. We suggest that part of the difference in breeding parameters between the two species may result from difference in breeding phenology: Hen Harriers laid more eggs and reared more fledglings than Montagu's Harriers, possibly or partly because they bred earlier.

Diet was very similar in the two species, with only minor differences in frequency of occurrence or in biomass, resulting in a large dietary overlap. Such overlap has been found elsewhere (e.g. central Spain: J.T. Garcia & B.E. Arroyo pers. comm.; Schipper 1973), though different prey were involved. Montagu's Harriers are also known to follow vole cyclical fluctuations in western France, with breeding density and clutch size being highly variable and strongly correlated with spring vole abundance (Butet & Leroux 1993, Salamolard *et al.* 2000). This is equally true for the Hen Harrier in some areas (Redpath

& Thirgood 1999, V. Bretagnolle & B.E. Arroyo unpubl. data). Because voles were an important prey in our harrier populations, we expected that Montagu's and Hen Harrier densities would vary greatly between years. Surprisingly, we only detected weak temporal variation in density of Montagu's Harrier, which was mainly due to *Barrois* areas. In this species, slight annual variations were also detected for clutch size, laying date and diet, but the clutch size coefficient of variation among years was much weaker than in western France (28% against 50%, Salamolard *et al.* 2000). Three non-exclusive hypotheses may account for this low and unexpected interannual variation. First, it is possible that vole numbers are not cyclical in this area of eastern France (however, vole abundance data are not available). Secondly, our study might have been too short to detect cycles. Thirdly, it is possible that vole densities were too low in eastern France to allow harriers to specialize there, and so they behave as generalist predators. In support of the last hypothesis, there is some evidence that harriers in eastern France are limited by food supply: harrier breeding densities were low in our study compared with other areas (e.g. > 30 breeding pairs/100 km<sup>2</sup> in peak vole years: Arroyo & Bretagnolle 2000). Moreover, first-year female Montagu's Harriers rarely bred (< 5%), very few first-year male Hen Harriers bred, and no cases of polygyny were observed in Hen Harriers. In areas where food is abundant, these three parameters are reversed (Balfour & Cadbury 1979, Salamolard *et al.* 2000, V. Bretagnolle, A.B.A. Leroux & B.E. Arroyo unpubl. data).

### Conservation and future of harriers in cultivated areas

The harrier breeding population of the *Champagne-Ardenne* region stands at about 250–500 pairs of Montagu's Harrier and 200–400 pairs of Hen Harrier (our unpubl. data), and thus is numerically one of the three most important harrier populations in France (Salamolard *et al.* 1999). Today, virtually all Montagu's Harriers in *Champagne-Ardenne* breed in cereal crops, whereas a significant proportion of the Hen Harriers still nests in natural or seminatural habitats (< 15%), especially young forest plantations, fallows or marshes. The Marsh Harrier breeds in reedbeds where it is strongly declining, and the first instance of breeding in cereal crops was recorded in 1991. Since then, one to five Marsh Harrier pairs have bred annually in cereals. Therefore, all species of

harriers in this region have shifted to some extent from natural habitats to cereal fields, as recorded elsewhere in France (Leroux 1994, Salamolard *et al.* 1999). Historically, the Montagu's Harrier was apparently the first of the western European harriers to colonize crops. In eastern France, the shift to crops might have followed the draining of its original breeding habitats, i.e. marshes and wet meadows (Paris 1906, Erard & Spitz 1964) and this may have occurred as early as the beginning of the twentieth century (Frimonnet 1925). It is likely, however, that the main shift occurred in the 1950s and 1960s, when modification of agricultural practices drastically altered the landscape (Pain & Pienkowski 1997). In Europe, the proportion of Montagu's Harriers nesting in cereals increases westward (Arroyo 1995). Polish harriers have only recently begun to shift from marshes to crops (Krogulec & Leroux 1994), while > 80% of the Russian harrier population still breeds in natural and seminatural habitats, at least in the 1980s (Flint *et al.* 1984).

The late breeding phenology of Montagu's Harrier, and the fact that almost all the breeding population nests in crops, make their future entirely dependent on conservation programmes. Without intervention, between 50% and 90% of the nests would be destroyed each year by harvesting (see also Arroyo & Bretagnolle 2000). Farming intensification has allowed earlier crop harvesting, and harriers (particularly Montagu's Harriers) are therefore of great conservation concern in Europe. Currently, more than 1000 nests are protected each year in both Spain and France. Harrier population trends are not known in these countries (Arroyo & Pinilla 1996, Salamolard *et al.* 1999), but trends observed at smaller scales suggest stability or decline (e.g. Berthemy *et al.* 1983, Armouet 1994, Krogulec & Leroux 1994, Albert 1987–1998, but see Fève 1994).

Recent changes in agricultural practices, e.g. ploughing of permanent cover or extensive use of rodenticides, are suspected to affect vole cycles. Montagu's Harrier population dynamics differed strongly between eastern and western France, but also slightly between *Crayeuse* and *Barrois*. Harriers depended more on voles in *Barrois* than in *Crayeuse*, and yearly density variations were higher in *Barrois* than in *Crayeuse*. Thus, harrier populations may exhibit different dynamics in western France, *Crayeuse* and *Barrois*. We suggest that these differences reflect a gradient of agricultural intensification from western France, *Barrois* to *Crayeuse*, along which vole fluctuations become weaker and finally disappear. Direct persecution of

chicks and adults may further affect populations, although the scale of its impact is unknown in eastern France (see Etheridge *et al.* 1997 for data on Scottish harriers). As a last potential threat, the recent increase of Hen Harriers in cultivated areas may pose a problem in the long term for the slightly smaller Montagu's Harrier. The two species seem to overlap much in their habitat, general breeding biology and diet. This may lead to interspecific competition, although we did not detect interspecific agonistic interactions. The Hen Harrier, being more sedentary, should respond better than the long-distance migrant Montagu's Harrier in cereal environments, since it is less constrained by breeding phenology, by vegetation height for nesting, and by harvesting dates.

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