



Comparative breeding performance of Marsh Harriers *Circus aeruginosus* along a gradient of land-use intensification and implications for population management

AUDREY STERNALSKI,^{1,2*} JEAN-FRANÇOIS BLANC,¹ STEVE AUGIRON,¹ VINCENT ROCHETEAU¹ & VINCENT BRETAGNOLLE¹

¹CEBC-CNRS, Beauvoir-sur-Niort, 79360, France

²Instituto de Investigación en Recursos Cinegéticos (IREC-CSIC-UCLM-JCCM), Ronda de Toledo s/n, Ciudad Real, 13005, Spain

Assessing variation in breeding performance in relation to habitat characteristics may provide insights into predicting the consequences of land-use change on species ecology and population dynamics. We compared four Marsh Harrier *Circus aeruginosus* populations subject to similar environmental conditions, but which differed in habitat composition, ranging from natural habitats to intensively cultivated areas. Using a 6-year dataset, we characterized breeding habitat and diet in these four study sites, and analysed breeding performance in relation to this gradient of land-use intensification. There was minimal variation in breeding performance between study years but consistent variation between study sites. Unexpectedly, Marsh Harriers breeding in intensively cultivated habitats had higher reproductive success than those breeding in more natural habitats, which, however, hosted higher breeding densities, so overall net population productivity (fledglings per unit area) was similar across sites. This resulted from combined effects of density-dependence and different predation rates between study sites. The colonization of intensive farmland habitats may not necessarily impact negatively on population sustainability when breeding success and population density are traded against each other. However, our findings should not mask longer-term conservation issues for populations breeding in these intensively managed areas, and further studies should assess potential long-term negative effects of occupancy of human-altered habitat.

Keywords: breeding habitat, *Circus aeruginosus*, land-use changes, population dynamics, raptor, reproductive parameters.

Assessing variation in breeding performance in relation to habitat characteristics may provide insight for predicting the consequences of land-use changes on the ecology and population dynamics of species of conservation concern. This is especially relevant for species breeding in threatened habitats such as wetlands (Gibbs 2000) or in areas subject to major habitat transformations such as agricultural landscapes (Duncan *et al.* 1999). Habitat loss and degradation are not only a major cause of species extinction but may force individuals into

sub-optimal habitats (Bender *et al.* 1998). Habitat quality in birds is largely a function of food availability (Korpimäki 1988), predation risk (Martin 1993) and the level of intra-specific competition (Kostrzewa & Kostrzewa 1991). Each of these parameters is likely to be affected by variation in habitat composition, which in turn might affect breeding success, population density and ultimately population productivity (Newton 1998). Farmland birds have strongly declined across Europe because of agricultural intensification (Donald *et al.* 2001). Nevertheless, many farmland birds, especially ground-nesting species, still use these highly transformed landscapes for breeding,

*Corresponding author.
Email: audrey.sternalski@gmail.com

indicating that they can to some extent cope with land-use changes (Tourenq *et al.* 2004, Moreno-Mateos *et al.* 2009, Sebastián-González *et al.* 2010). The extent to which agricultural landscapes are sub-optimal habitats for these species and the population consequences of breeding in intensive farming systems compared with more natural habitats are in many cases unclear.

Habitat selection may differ between populations (i.e. when most individuals within a population use a certain habitat; e.g. Grant 1975, Pulliam & Danielson 1991). However, even when variation in breeding performance between populations is found, it is usually difficult to disentangle habitat quality *per se* and other environmental effects, particularly if study populations are separated by large distances (Mindell *et al.* 1987). The three European species of harrier (genus *Circus*; Montagu's Harrier *Circus pygargus*, Hen Harrier *Circus cyaneus* and Marsh Harrier *Circus aeruginosus*) represent case study models, as they have recently colonized intensive farmland from natural habitats (Thiollay & Bretagnolle 2004). This shift has raised conservation concern, as it exposes the species to the consequences of agricultural intensification (Arroyo *et al.* 2002). All three species, however, currently still breed both in natural and in man-made habitats, so monitoring their breeding performance within these two types of habitat would allow the investigation of variation in overall reproductive output between natural and human-modified landscapes. After a severe population decline in Europe during 1960–80, Marsh Harrier populations have recovered in recent decades and the species is currently classified as 'Least Concern' (BirdLife International 2009). However, it is still strongly impacted by habitat loss because its original wetland habitats continue to decline (Gibbs 2000). Perhaps as a consequence, this species has been recently documented breeding in agricultural landscapes and even in woodlands (Augiron *et al.* 2007, Cardador *et al.* 2011).

Here, we compare breeding performance in four Marsh Harrier populations in France that breed geographically very close to each other and which therefore experience similar climatic conditions. In contrast, their habitats vary strongly across study sites, from natural habitats to intensively cultivated farmland. This gradient of land-use across the four sites mimics, spatially, agricultural intensification (and its land-use consequences) which has occurred temporally over the last 30 years in this

region of France (Duncan *et al.* 1999). Using a 6-year dataset totalling over 500 breeding attempts, our aims were to assess the species' breeding performance along a gradient of land-use intensification, and assess whether natural and intensively managed habitats are equally productive in population terms. We first describe and quantify breeding habitat selection and diet within the four study sites. As the sites differed in habitat composition, we expected to find differences in the species' ecology. Secondly, we analyse the consequences of habitat characteristics on population breeding ecology along this land-use intensification gradient. More specifically, we investigate investment in reproduction, breeding performance and predation rates. Thirdly, to assess the consequences of land-use intensification at the population level, we compare breeding densities and the net productivity output between sites and years. We then assess the management implications of our findings for species inhabiting both natural and more artificial habitats, especially when there is a negative relationship between population density and population productivity mediated by habitat quality.

METHODS

Study sites

Data were collected over six breeding seasons (2006–11) within four study sites located in central western France (*Charente-Maritime* district; Fig. 1, Table 1): the Marais de Brouage (MB, c. 72 km², 45°51'N, 1°04'W), the Marais de Rochefort (MR, c. 30 km², 46°04'N, 0°98'W), the Ile de Ré (IR, c. 36 km², 46°20'N, 1°43'W) and the Marais Poitevin (MP, c. 65 km², 46°28'N, 1°08'W). The four study sites can be classified along a land-use intensification gradient, from natural to intensively cultivated area, according to the increasing proportion of arable land: MB (13.9%), MR (33%), IR (41.7%) and MP (76.9%; Table 2). MB and MR are wetland areas. MB is mainly composed of grasslands with, additionally, many small reed beds (in total about 1.5 km²). MR has been subject to more agriculture intensification (Butet & Leroux 2001) and reed beds are currently less abundant than in MB, but also much more fragmented, with very small remaining patches, which might affect the rate of Marsh Harrier breeding occupancy in this habitat (Cardador *et al.* 2011). In contrast, IR and MP are dominated by arable

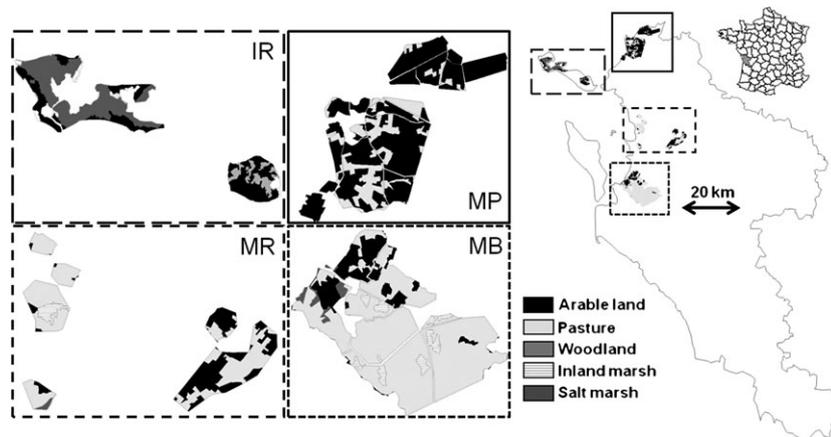


Figure 1. Map of the study area (Charente-Maritime district shaded) showing the four study sites, the Marais de Brouage (MB), the Marais de Rochefort (MR), the Ile de Ré (IR) and the Marais Poitevin (MP). Habitat occupancy at a 25-ha pixel scale was obtained from the Corine Land Cover (CLC) European database. We defined five habitat types from CLC nomenclature: arable land, pasture, woodland, salt marsh and inland marsh. The sixth category, reed bed, was derived in the field and is not shown in this figure.

Table 1. Number of Marsh Harrier nests surveyed (N) and breeding density (pairs/100 km²; D), according to study sites and years. Total number of nests and average breeding density are also presented (in bold).

Study sites Area (km ²)	MB 72*		MR 30		IR 36		MP 65		Total 203	
	N	D	N	D	N	D	N	D	N	D
2006	76	63.3	–	–	16	44.4	–	–	92	53.8
2007	–	–	–	–	19	52.7	32	49.2	51	50.9
2008	25	62.5	–	–	18	50.0	37	56.9	80	56.5
2009	37	61.7	13	43.3	17	47.2	33	50.8	100	50.7
2010	50	62.5	14	46.7	18	50.0	24	36.9	106	49.0
2011	37	61.7	16	53.3	18	50.0	28	43.1	99	52.0
Total	225	62.3	43	47.8	106	49.1	154	47.4	528	52.2

*Averaged value: in MB, surveyed area varied between years (2006: 120 km², 2008: 40 km², 2009: 60 km², 2010: 80 km² and 2011: 60 km²); yearly density was therefore calculated accounting for variation in the size of the study area.

land. IR is a large coastal island where arable crops are mainly potatoes and vineyards, and which is now managed for salt and is composed of low hills created for salt extraction, grassland and wetlands, and a few woodlands. MP is a typical intensive farmland habitat mainly cultivated for winter cereal and rape, spring-sown crops with some pasture land and other permanent or semi-permanent crops used for livestock rearing.

Diet

The Marsh Harrier is a generalist predator that has a diverse diet, consisting of birds, fish, reptiles, insects, and small- and medium-sized mammals

(Clarke 1995). However, when a particular prey-species is abundant, such as the Common Vole *Microtus arvalis*, which shows cyclical variations in abundance in western France (Salamolard *et al.* 2000), Marsh Harriers may favour this prey over other species.

Diet within each study site was assessed every year from March to July. We combined pellets, remains and visual observations, an approach that improves the analysis of raptor diet (Simmons *et al.* 1991), although some biases remain (Redpath *et al.* 2001; see Supporting Information Appendix S1). Pellets and remains were collected at nests, and we further used visual identification of prey deliveries observed when locating nests.

Table 2. Proportion (%) of available habitat (A) and percentage of Marsh Harrier nests on different habitats (U) in relation to study site, all years combined.

Study sites	MB***			MR**			IR***			MP***			Total	
	A	U	P	A	U	P	A	U	P	A	U	P	A	U
Breeding habitat type														
Arable land	13.9	3.0	--	33.0	23.3		41.7	0.0	---	76.9	85.0		41.9	29.1
Pasture	77.1	13.4	---	60.0	41.9	--	1.4	3.9		22.3	9.2	--	43.6	12.6
Woodland	–	–		1.0	4.7		8.3	17.5	+	–	–		1.5	4.6
Salt marsh	2.8	1.0		–	–		47.2	73.8	+++	–	–		9.4	15.0
Inland marsh	4.2	2.0		4.1	2.3		–	–		–	–		2.0	1.0
Reed bed	2	80.6	+++	1.9	27.8	+++	1.4	4.8		0.8	5.8		1.6	37.7

A chi-squared goodness-of-fit was used to assess statistical differences between available and used habitat types (see Methods). A global goodness-of-fit test was performed for each site (statistical significance presented on upper line of the table, ** $P < 0.01$, *** $P < 0.001$), and then a test was performed per habitat per site. Positive or negative selection and level of significance for individual habitat types are indicated (+/- $P < 0.05$, +/--- $P < 0.01$, +++/--- $P < 0.001$).

We analysed differences in the diet composition (number of prey items and biomass; Appendix S1) between the four study sites combining all sources of data. Overall, 281 pellets, 618 remains and 183 visual observations were obtained.

Habitat characteristics

We estimated available breeding habitat type within each study site using the Corine Land Cover (CLC) European database, which provides land cover at a 25-ha pixel scale. We defined five habitat types from CLC nomenclature: arable land, pasture, woodland, salt marsh and inland marsh (Fig. 1, Table 2). Reed beds, an important habitat for the Marsh Harrier, are not identified in CLC. For MB specifically, we therefore precisely recorded reed bed patches in the field and mapped them by using a geographical information system (ARCGIS 9, ESRI, France); we then calculated reed bed area and computed the proportion of this habitat type against those provided by CLC. For the three other study sites, however, we did not exactly map reed bed availability in the field, but estimated it visually in comparison with the reed bed area calculated in MB (see Table 2).

Habitat types were characterized as follows: arable land was mainly cultivated with winter cereal crops (wheat) and spring-sown crops (sunflower and corn); pastures comprised natural (not sown) vegetation, mainly grasses, flooded in winter, and essentially used for livestock rearing; woodlands were mainly composed of Holm Oak *Quercus ilex* and Scots Pine *Pinus sylvestris*, with a concentrated shrubby stratum and an herbaceous stratum

mainly composed of Bracken *Pteridium aquilinum*; within salt marshes, vegetation types of hills created for salt extraction were mainly composed of Alexanders *Smyrniolum olusatrum*, Black Mustard *Brassica nigra* and various grasses; within inland marshes (mostly present in MB), reed bed patches were almost exclusively composed of Common Reed *Phragmites australis* associated with various plant species such as nettles, grasses, blackberry bushes and rushes, which varied according to the level of flooding.

Harrier breeding parameters

Nests were searched for during the pre-laying period (March–April) within the four study sites, although nest monitoring started in different years at each site (Table 1). In total, 528 nests were located. Nests were visited as soon as possible to assess reproductive stage, and checked again 4 ± 2 times during the breeding period to collect nest pellets and food remains, and record the following reproductive parameters: clutch size, egg size, hatched and fledged brood sizes. The last allowed the derivation of parameters such as hatching success (number of hatched eggs/number of laid eggs), brood reduction (number of fledglings – number of hatched eggs; only calculated if at least one egg hatched and one chick fledged), reproductive success (number of fledglings/number of eggs laid), egg volume ($0.507 \times \text{length} \times \text{width}^2$; Hoyt 1979) and total clutch volume (sum of all egg volumes within a clutch; see Arroyo *et al.* 1998). In addition, assuming that all nests with fledglings were detected, we estimated the total

number of fledged young for a constant unit area (100 ha) by totalling all fledglings per site and per year (total productivity), and then compared breeding density, pair breeding performance (average number of fledglings per pair and per site for successful nests) and total productivity.

Sample sizes of nests varied according to parameters investigated, as not all nests were discovered at the same stage and not all parameters were equally available for all nests. In addition, as only one visit (maximum) was performed at the egg stage (Marsh Harriers are sensitive to disturbance at this stage), it was not possible to use the Mayfield method to estimate whole nest survival probabilities (see also Millon *et al.* 2002). We nonetheless estimated chick stage survival probabilities by using Aebischer's extension of the Mayfield method (Aebischer 1999).

Data analysis

We used the chi-squared test to compare the goodness-of-fit of used breeding habitat to available habitat types within each study site (Neu *et al.* 1974). Expected values were calculated as the proportion of area occupied by each habitat type in the study site times the total number of nests located within that study site. In other words, we calculated the expected number of nests in each habitat type, if nest-sites were picked at random. Hence, this chi-squared test is a goodness-of-fit test of the located nests to the expected distribution of nests if no preference or avoidance was shown by Harriers. *G*-tests were used to test for differences in available and used habitats between study sites and Kruskal–Wallis tests were used to assess differences in breeding density between years and sites. To calculate diet diversity within study sites, we used the Shannon index ($H' = -\sum p_i \log p_i$; Shannon & Weaver 1949). To test for the effects of site and year on reproductive parameters and nest predation rate, we used linear (PROC GLM in SAS 9.0, SAS Institute Inc., Cary, NC, USA) or generalized linear (PROC GENMOD, SAS/STAT User's guide, version 9 SAS Institute Inc.) models, depending on the dependent variable distribution. A normal error distribution and an identity link function were assumed for egg and clutch volumes; Poisson errors and a log link function were assumed for clutch and fledged brood sizes; binomial errors and a logit link were assumed for predation rate. Hatching success and reproductive success were analysed with a Poisson error distribution, with number of

eggs laid entered as the first independent variable, and using Type 1 errors. A similar procedure was used for brood reduction, with number of hatched eggs entered as the first independent variable. Our models were checked by analysis of residuals for normality and independence, and we checked for overdispersion when we used the Poisson error distribution.

As our samples were unbalanced between years and sites (Table 1), we ran analyses with year and site as fixed factors without an interaction term on the complete dataset (2006–11). The same models including the interaction between year and site were run only for a restricted dataset (2009–11). Birds were not marked and individual identification was not possible, and there is therefore likely to be an unknown degree of pseudoreplication in our data. All statistical analyses were performed using SAS 9.0.

RESULTS

Differences in breeding habitat and diet across study populations

Habitat availability differed between the four study sites (*G*-test: $G_{15} = 152.9$, $P < 0.001$; Fig. 1, Table 2). Similarly, habitats used by Marsh Harriers for breeding also differed between the four study sites ($G_{15} = 747.7$, $P < 0.001$; Table 2). In addition, Harriers were selective with regard to breeding habitat across all study sites (Table 2). Overall, they strongly selected reed beds, which held 38% of nests but covered < 2% of the total area. However, the proportion of nests in reed beds varied across the four sites, with marked positive selection in those sites with the highest proportions of reed bed (MB and MR; Table 2). Apart from reed bed selection, the second habitat selected for breeding was salt marsh in IR, and woodland was also positively selected on this site. Arable land was avoided in MB and IR, whereas it was used in proportion to its availability in MR and MP, and there was no apparent selection of arable land overall. Pasture was avoided at three sites – MB, MR and MP.

Harrier diet mainly comprised large and small mammals, fish and, to a lesser extent, passerines, gamebirds, insects and reptiles (Table 3). In terms of biomass, medium-sized mammals (mainly Coyote *Coypus coypus*, Rabbit *Oryctolagus cuniculus* and Brown Hare *Lepus europaeus*) represented the main prey (64%). However, diet significantly

varied between the four sites, both in terms of frequency of prey types ($G_{15} = 138.6$, $P < 0.001$) and in terms of percentage biomass provided by each prey type ($G_{15} = 160.4$, $P < 0.001$). Diet diversity differed only slightly between the four sites, being lowest in MB but similar in the three other sites (Shannon index; Table 3). Harriers consumed more mammals, followed by fish, in MP, whereas the reverse occurred in MB and MR (Table 3). In IR, diet was restricted to mammals and gamebirds (Table 3). However, the frequency of small mammals in the diet was highest in MP (47%) and MR (44%), although representing a low proportion in total biomass. In certain years, however, such as 2007 (which was a peak vole year), small mammals might account for up to 35% of total biomass in MP (J.F. Blanc unpubl. data).

Breeding parameters: variation in space and time

There was a significant site effect on breeding parameters but there was less often a year effect (see Table 4 for statistical results, Fig. 2 and Supporting Information Appendix S3 for average values per sites and years, respectively). When using the restricted dataset, in most cases there was no interaction between site and year (Supporting Information Appendix S2).

Variation in clutch size (range 1–6 eggs per clutch; mean \pm sd = 3.99 ± 0.97 eggs, $n = 299$) was significantly affected by site and by year (Table 4): clutch size increased along the gradient of land-use intensification from MB to IR (Fig. 2a)

and Harriers laid more eggs in 2007 than in other years (Appendix S3), although only the two more intensive sites (IR, MP) were monitored that year. Significant variation in egg volume (37.19 ± 4.15 cm³, $n = 1092$ eggs) was explained by site and by year (Table 4). Larger eggs were found in agricultural sites than in more natural ones (Fig. 2b) and larger eggs were laid in 2007 compared with other years (Appendix S3), although, again, only the two most agricultural sites were monitored that year. As a consequence, total clutch volume (147.30 ± 39.42 cm³, $n = 233$) was significantly higher in intensively managed sites compared with more natural sites (Fig. 2c), and was statistically only affected by site (Table 4, Appendix S2).

Hatching success (0.60 ± 0.40 , $n = 174$ clutches) was affected neither by site nor by year, although it tended to increase from natural to agricultural sites (Table 4, Fig. 2d). In contrast, fledged brood size (1.34 ± 1.44 , $n = 441$ clutches) varied with site but not with year (Table 4). As with clutch size, fledged brood size was lower in natural habitats than in more intensively managed sites (Fig. 2e). Reproductive success (0.33 ± 0.35 , $n = 284$ clutches) varied significantly with site and marginally with year (Table 4). Reproductive success was lower in more natural sites than in managed sites (Fig. 2f) and was higher in 2007 and 2006 than in other years (Appendix S3). There was also an effect of habitat type on reproductive success ($F_{4,273} = 3.54$, $P = 0.008$), with decreasing values from woodland (mean \pm sd = 3.00 ± 2.16), salt marsh (1.88 ± 1.73), arable land

Table 3. Sample size (n), percentage of sample size (%) and proportion of biomass (% in bold) of ingested prey types in relation to study site, all years combined. Shannon index (in bold), calculated both from prey categories (PC) and from prey species (PS), is presented per study site.

Study sites	MB		MR		IR		MP		Total	
Shannon index										
PC	1.28		1.44		1.36		1.46			
PS	2.43		2.68		2.21		2.83			
Ingested prey type	n (%)	%B	n (%)	%B						
Fish	121 (52)	70	33 (26)	46	6 (1)	1	69 (20)	26	229 (20)	19
Passerine	11 (5)	1	9 (7)	1	42 (9)	1	35 (10)	1	97 (8)	1
Gamebird	10 (4)	7	2 (2)	4	58 (12)	15	24 (7)	15	94 (8)	13
Mammal	16 (7)	17	13 (10)	39	219 (47)	82	47 (14)	51	295 (25)	64
Small mammal	68 (29)	4	56 (44)	9	127 (27)	1	159 (47)	7	410 (35)	3
Insect/reptile	7 (3)	1	14 (11)	1	17 (4)	0	8 (2)	0	46 (4)	0
Total	233 (100)	100	127 (100)	100	469 (100)	100	342 (100)	100	1171 (100)	100

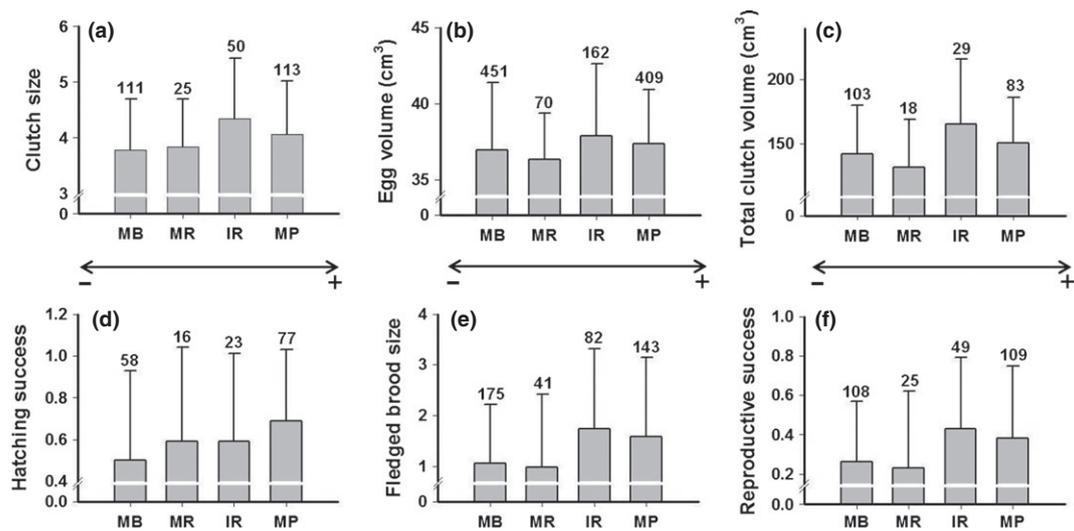


Figure 2. Variation in reproductive parameters of Marsh Harrier according to site. Reproductive parameters are separated between those related to breeding investment, as (a) clutch size, (b) egg volume and (c) total clutch volume; and those related to productivity, as: (d) hatching success, (e) fledged brood size and (f) reproductive success. The land-use intensification gradient is also indicated, from the most natural site (MB) to the most cultivated site (MP). Sample sizes are indicated above bars.

Table 4. Effects of site and year on Marsh Harrier reproductive parameters on the complete dataset (2006–11). Either linear or generalized linear models were used, depending on the dependent variable distribution (see Methods).

Source of variation	<i>n</i>	Site			Year		
		Test	df	<i>P</i>	Test	df	<i>P</i>
Breeding investment							
Clutch size	299	2.63	3, 290	0.050	2.92	5, 290	0.014
Egg volume	1092	3.40	3, 1083	0.017	4.76	5, 1083	<0.001
Total clutch volume	233	3.05	3, 224	0.029	1.14	5, 224	0.339
Reproductive output							
Hatching success	174	1.40	3, 164	0.244	0.91	5, 164	0.476
Fledged brood size	441	4.84	3, 432	0.002	1.13	5, 432	0.343
Reproductive success	284	3.07	3, 274	0.028	2.12	5, 274	0.063
Breeding failure							
Brood reduction	98	1.94	3, 88	0.129	0.84	5, 88	0.527
Predation rate	410	9.79	3	0.020	15.59	5	0.008
Egg stage	410	7.62	3	0.055	13.50	5	0.019
Chick stage	410	4.92	3	0.178	5.53	5	0.355

Test indicates the value of the test statistic (chi-squared for predation rate, *F* for all other variables). Significant effects are highlighted in bold.

(1.64 ± 1.60) to reed bed (1.03 ± 1.30) and pasture (0.97 ± 1.36).

Causes of breeding failure

Of 528 monitored nests, the fate was known for 492: in 259 (53%) of these, one or more chicks fledged. Those that failed ($n = 233$) did so for various reasons: eggs were not laid in 14%; 5% were

abandoned at the egg stage; complete infertility of the whole clutch occurred in 3%; 66% were predated (44% at the egg stage and 22% at the chick stage); 8% were destroyed during harvesting operations; 3% by herd grazing and harsh weather (in MB and MR); and three nests (1%) were deliberately destroyed by people (all in cereal crops in MP).

Overall, chick stage survival probability was affected neither by site ($\chi^2_3 = 0.23$, $P = 0.97$) nor

by year ($\chi^2_5 = 5.75$, $P = 0.33$). The intensity of brood reduction (range 0–3 chicks per clutch; mean \pm sd = 0.69 ± 0.83 , $n = 98$ clutches) was affected neither by site nor by year (Table 4). In contrast, nest predation rate varied significantly with site and year (Table 4). Predation was higher in more natural habitats (especially in MR) than in intensively managed sites (Fig. 3), and was lower in 2007 (18%) than in other years (25, 28, 47, 43 and 47%, respectively, from 2006 to 2011). This resulted from significantly higher predation rate at the egg stage (Table 4) in more natural than in more intensively managed sites (Fig. 3) and from different predation rates at the egg stage in relation to year (Table 4), especially a lower rate in 2007 (8%) compared with other years (20, 17, 30, 32 and 31%, respectively, from 2006 to 2011). Predation rates at the chick stage were similar between sites and years (Table 4, Fig. 3). Predation rates also varied with habitat type ($\chi^2_4 = 14.14$, $P = 0.007$), increasing from woodland (13%), salt-marsh (27%), arable land (32%), pasture (38%) to reed bed (47%).

Within MP, 84% of nests were found in cereal crops. Among these, 37% ($n = 48$) had to be protected from harvesting operations, the most common intervention technique being to erect a fence around the nest to protect nestlings during harvesting and after harvest from predators. Within these protected nests, 74% of young actually fledged before harvesting, whereas 26% fledged after and would have died if left unprotected. Thus, reproductive success was 0.60 ± 0.30 in protected nests compared with 0.37 ± 0.38 if we considered all

nestlings fledged after harvesting as dead. Overall, nest protection increased reproductive success from 0.28 ± 0.36 to 0.38 ± 0.37 , improving reproductive success in MP by c. 32%.

Population breeding performance in relation to population density and habitat quality

Average breeding densities of Marsh Harriers ranged from 46 ± 4 to 62 ± 2 pairs/100 km² (Table 1). Breeding densities did not vary between years (Kruskal–Wallis test: $\chi^2_5 = 1.88$, $P = 0.86$) but varied among sites ($\chi^2_3 = 10.67$, $P = 0.014$; Table 1), MB supporting the highest overall average breeding density.

Overall, increased population density resulted in a significant decrease in average pair productivity (linear regression: $F_{1,18} = 12.80$, $P = 0.002$; slope \pm se = -12.09 ± 3.38 ; Fig. 4a). However, this negative trend was counterbalanced by breeding success, which resulted in non-significant differences in the total number of fledged young per 100 ha between sites (Kruskal–Wallis test: $\chi^2_3 = 4.57$, $P = 0.206$; Fig. 4b). As a consequence, all sites reached an almost identical production of 0.60 fledglings/100 ha, being only slightly lower in MR (Fig. 4c). Removing human protection of harvested nests in MP, by considering all nestlings fledged after harvesting as dead, decreased the average number of fledged young (per 100 ha) slightly below the value of the more natural sites (MB; Fig. 4c).

DISCUSSION

The Marsh Harrier shows a high degree of plasticity in its diet and habitat choice, breeding in very different habitats, as shown by this study and others (Augiron *et al.* 2007, Molina & Martínez 2008, Cardador *et al.* 2011). This plasticity allowed us to compare breeding ecology and performance in four populations distributed along a gradient of land-use intensification, from natural wetlands to intensive farming landscape. Although the four study populations differed strongly in terms of selected breeding habitat and diet, resulting in variations in breeding ecology between study sites, there was virtually no consequence for total population productivity in terms of fledglings produced per unit area. Unexpectedly, individual Marsh Harriers did not perform better in natural habitats than in

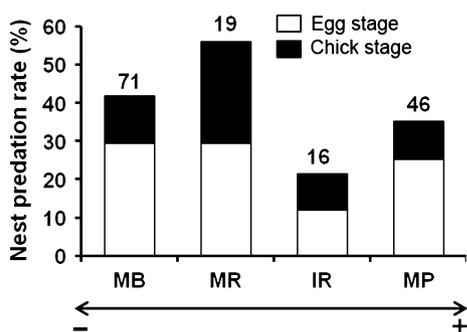


Figure 3. Nest predation rate (%) according to study site, all years combined: nest predation rate at egg (open bars) and chick (full bars) stages are shown. The land-use intensification gradient is also indicated, from the most natural site (MB) to the most cultivated site (MP). Sample size above bars refers to number of predated nests.

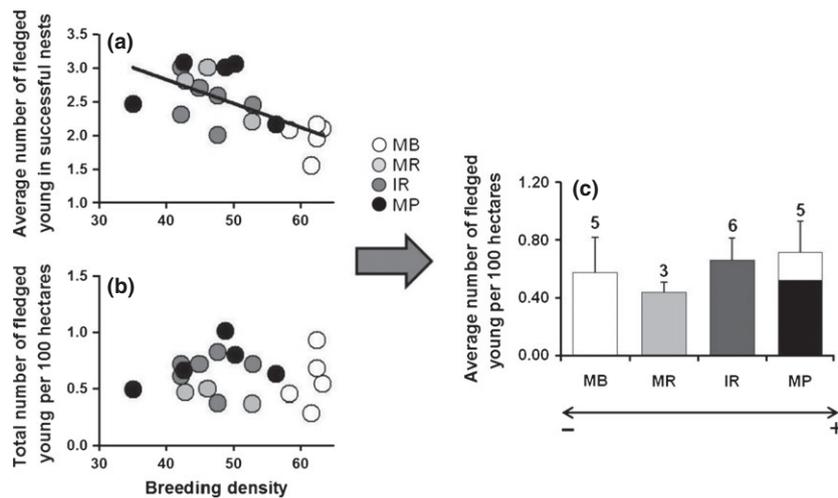


Figure 4. Marsh Harrier pair productivity (fledged young) per study site in relation to breeding density: (a) average number of fledged young per successful nest (with at least one fledged young); (b) total number of fledged young per 100 ha; (c) average number of fledged young per 100 ha. The land-use intensification gradient is also indicated, from the most natural site (MB) to the most cultivated site (MP). Sample sizes are indicated above bars. For MP, the black bar represents population productivity without nest protection by considering all nestlings fledged after harvesting as dead, while the open bar shows population productivity including protected nests. The solid line represents the fitted significant linear regression (see Results).

intensive cereal systems (Cardador *et al.* 2011). In fact, higher breeding investment and breeding success was recorded in cereal crops.

Our results for diet composition and diet diversity suggest that variation in habitat composition along the land-use intensification gradient impacts feeding resources through either prey type or food availability. Only egg volume was found to vary significantly with year, whereas nearly all breeding parameters showed significant variations with site. Overall, these results suggest that sites consistently differed in quality, or alternatively that individual quality consistently differs between sites (see below). Presumably, some sites showed higher food availability or food of better quality (i.e. richer in energy or in micronutrients; Sternalski *et al.* 2012a) leading to higher breeding investment by females, such as in IR, which showed the highest breeding investment. Food abundance may also vary to some extent with year, as exemplified by the Common Vole, which shows cyclical population dynamics (Lambin *et al.* 2006). In common with other harrier species (Sternalski *et al.* 2010), Common Vole, when abundant, is a preferred prey of Marsh Harrier. Peak vole years (as in 2007) led to particularly high Harrier population productivity in intensive farming systems.

On average, reproductive success at the individual level was lower in more natural sites,

particularly for Harriers breeding in reed beds and pasture, than in intensively managed landscapes where individuals mainly bred in cereal crops or salt marshes. In addition to potential confounded effects of individual quality on breeding performance (see below), possible mechanisms leading to such differences include: (1) differential breeding investment, (2) differences in brood reduction and (3) differences in clutch/brood predation rates.

Higher breeding densities (by *c.* 15–25%) were observed in natural landscapes, probably leading to stronger density-dependent mechanisms there, negatively affecting pair breeding performance (Bretagnolle *et al.* 2008) and resulting in lower breeding success through high intra-specific competition (Newton 1998, Bretagnolle *et al.* 2008). We observed a decrease of 12% in clutch size between natural and intensively managed landscapes, whereas there was only a 6% decrease in fledged brood size. In addition, there was no significant difference in brood reduction between natural and more intensively managed landscapes. Altogether, these results suggest a stronger negative effect of breeding density during the pre-breeding than the rearing period, and stronger intra-specific interference competition in natural than in managed sites, resulting in lowered investment in reproduction.

Nest predation is an important factor impacting reproductive success in bird populations (Newton 1998), and harriers in particular, as they are ground-nesting species. Accordingly, predation rate was the main factor affecting Marsh Harrier breeding success in this study (37% of predated nests). We found significantly higher predation rates in natural than in more managed sites (44 and 30%, respectively) and in natural habitat types such as reed bed and pasture than in more intensified ones such as salt marsh and arable land. Habitats found in managed sites, such as cereal crops in MP and salt marshes (i.e. hills created by salt extraction) in IR, showed much lower predation rates than reed beds and pastures. It is likely that in natural sites, abundance and diversity of terrestrial predators are higher, whereas in intensive farming systems, which are also used as hunting grounds for gamebirds, predation was reduced because of lower predator abundance, possibly due to human control of predators (Whittingham & Evans 2004).

Ground-nesting species, including raptors, may be particularly affected by agricultural practices (e.g. Montagu's Harrier, Arroyo *et al.* 2002). In our study, only one population was affected by harvesting, and at a low rate (5% of nest failure was actually caused by harvesting in MP, although 15% of nests would have failed due to harvesting without active human protection). There are no data available on nest destruction rates at harvesting in Marsh Harrier, but values for other harrier species in France range between 42 and 54% (Millon *et al.* 2002). It is therefore likely that, in the absence of human protection at harvesting, total productivity of fledglings in an intensive farming system (such as MP) would have been lower.

Both breeding investment and breeding success were unexpectedly higher in agricultural areas than in more natural landscapes, largely because of lower individual investment in reproduction and higher predation rates in more natural than in more intensively farmed areas. At the population scale, however, lower breeding success in natural landscapes seemed to be compensated for by higher breeding density, so that the net population productivity in natural and farmland landscapes was similar. This finding is expected under the ideal free distribution (IFD, Fretwell & Lucas 1970), in which one would expect equal pay-offs across habitats of different quality where there are density-dependent effects (Sutherland 1996).

Therefore, one could argue that the recent colonization of intensively managed habitats may not negatively impact the sustainability of the species. Indeed, Marsh Harrier populations have successfully colonized agricultural areas throughout Europe (e.g. Spain, Molina & Martínez 2008; Belgium, Derume *et al.* 2009). However, we believe that despite short-term benefits for total population size, this might actually lead to longer-term conservation problems for at least three reasons.

First, most bird species, but especially raptors and specifically Marsh Harriers in central western France, exhibit high natal philopatry (Sternalski *et al.* 2008). Thus, the possibility that in the future an even higher proportion of the population breeds in agricultural landscapes cannot be ruled out because of combined philopatric behaviour and improved breeding success, and the ongoing decrease in natural habitat availability. In this context, nest destruction during cereal harvesting, although not a major concern for this species currently, may become a major problem if harvesting continues to be carried out earlier each year (Chamberlain *et al.* 2000). Human intervention for harrier nest protection (Arroyo *et al.* 2002, Millon *et al.* 2002) necessitates the mobilization of thousands of volunteers in France. For this reason, we believe that the conservation of natural landscapes of high quality, potentially hosting higher breeding densities, is necessary for the future conservation of harriers, even if nesting in agricultural landscape currently represents a good subsidiary.

Secondly, our study lacked two important demographic components of population dynamics, the dispersal and survival components. As land-use intensification changes the availability of habitats, the proportion of individuals of a given species in any particular habitat type may be altered. In some species, surplus individuals from productive source habitats may immigrate into less productive sink habitats, where within-habitat reproduction fails to keep pace with within-habitat mortality. In such cases, alterations of the availability of source habitat may greatly affect the size of populations in other nearby habitats over a longer term than considered here (Pulliam & Danielson 1991). Therefore, despite higher fecundity, harrier populations in intensively managed habitats may show negative population growth rate: specific studies are required to test these hypotheses (Brawn & Robinson 1996).

Finally, it is possible that quality may differ between individuals occupying different site types (i.e. natural or man-made), leading to longer term fitness consequences. Little is known about the quality of individuals that breed in, or fledge from, natural vs. man-made landscapes. In the Marsh Harrier, younger adults (of lower quality) that are less competitive breed more frequently in atypical habitats such as woodland (Bavoux *et al.* 1998). As a consequence, nestlings of these poor-quality parents may themselves be of poor quality (either poor condition or immunodeficient; Sternalski *et al.* 2010, 2012a,b) and potentially suffer higher mortality rates. In addition, breeding in intensive cereal farmlands may also lead to higher exposure of chemical substances, resulting in negative health consequences, harmful physiological effects and possibly affecting long-term population sustainability in such areas (Mañosa *et al.* 2001). However, to assess these potential individual effects fully, as well as to avoid pseudo-replication in data (such as potentially occurring in our study), more detailed studies involving individually marked birds are crucial.

Most bird species inhabiting agricultural landscapes, including intensive cereal systems, also breed in more natural habitats (steppes, grassland and extensive agricultural landscapes). Therefore, with regard to the ongoing agricultural intensification and its negative consequences on farmland birds (Donald *et al.* 2001), the plasticity and positive selection shown by many species to human-altered landscapes (Moreno-Mateos *et al.* 2009) may appear at first as a welcome opportunity, but may become a serious concern in the future. Although populations newly established in intensively managed landscapes may seem viable, they should be viewed as populations that may buffer future or additional environmental changes, rather than populations that may, in the longer term, replace original populations where natural habitats are lost. In addition, in the case of Marsh Harrier and other bird species that have recently colonized intensively managed crops (e.g. Bluethroat *Luscinia svecica*, De Cornulier *et al.* 1997), and considering that their original habitats are still disappearing and/or being degraded, it may also be premature to conclude from population trends observed at national or European levels that these species are safe or of 'Least Concern' by the European Commission (BirdLife International 2009), at least until the possible longer-term negative effects

engendered by the occupancy of these new habitats are more clearly determined.

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REFERENCES

- Aebischer, N.J.** 1999. Multi-way comparisons and generalized linear models of nest success: extensions of the Mayfield method. *Bird Study* **46**: S22–S31.
- Arroyo, B., Leroux, A. & Bretagnolle, V.** 1998. Patterns of egg and clutch size variation in the Montagu's Harrier. *J. Raptor Res.* **32**: 136–142.
- Arroyo, B., García, J. & Bretagnolle, V.** 2002. Conservation of the Montagu's harrier (*Circus pygargus*) in agricultural areas. *Anim. Conserv.* **5**: 283–290.
- Augiron, S., Jacob, H., Jacob, N. & Sternalski, A.** 2007. Nidification atypique du Busard des roseaux *Circus aeruginosus* dans les bois de l'île de Ré. *Alauda* **5**: 181–183.
- Bavoux, C., Burneleau, G. & Picard, M.** 1998. La nidification du Busard des roseaux *Circus a. aeruginosus* en Charente-Maritime (France): analyse des données en fonction de l'âge des nicheurs. *Alauda* **66**: 299–305.
- Bender, D.J., Contreras, T.A. & Fahrig, L.** 1998. Habitat loss and population decline: a meta-analysis of the patch size effect. *Ecology* **79**: 517–533.
- BirdLife International.** 2009. *Birds in Europe: Population Estimates, Trends and Conservation Status*. Cambridge: Bird-Life International.
- Brawn, J.D. & Robinson, S.K.** 1996. Source-sink population dynamics may complicate the interpretation of long-term census data. *Ecology* **77**: 3–12.
- Bretagnolle, V., Mousseot, F. & Thibault, J.C.** 2008. Density dependence in a recovering osprey population: demographic and behavioural processes. *J. Anim. Ecol.* **77**: 998–1007.
- Butet, A. & Leroux, A.B.A.** 2001. Effects of agriculture development on vole dynamics and conservation of Montagu's harrier in western French wetlands. *Biol. Conserv.* **100**: 289–295.
- Cardador, L., Carrete, M. & Mañosa, S.** 2011. Can intensive agricultural landscapes favour some raptor species? The Marsh Harrier in north-eastern Spain. *Anim. Conserv.* **14**: 382–390.
- Chamberlain, D.E., Fuller, R.J., Bunce, R.G.H., Duckworth, J.C. & Shrubbs, M.** 2000. Changes in the abundance of

- farmland birds in relation to the timing of agricultural intensification in England and Wales. *J. Appl. Ecol.* **37**: 771–788.
- Clarke, R.** 1995. *The Marsh Harrier*. London: Hamlyn.
- De Cornulier, T., Bernard, R., Arroyo, B. & Bretagnolle, V.** 1997. Extension géographique et écologique de la Gorgebleue à miroir *Luscinia svecica* dans le centre-ouest de la France. *Alauda* **65**: 33–89.
- Derume, M., Guyon, J. & Bataille, B.** 2009. L'estivage des Busards des roseaux (*Circus aeruginosus*), saint-martin (*Circus cyaneus*) et cendrés (*Circus pygargus*) dans les plaines agricoles de Wallonie: premières estimations. *Aves* **46**: 49–56.
- Donald, P.F., Green, R.E. & Heath, M.F.** 2001. Agricultural intensification and the collapse of Europe's farmland bird populations. *Proc. R. Soc. Lond. B* **268**: 25–29.
- Duncan, P., Hewison, A.J.M., Houte, S., Rosoux, R., Tournebize, T., Dubs, F., Burel, F. & Bretagnolle, V.** 1999. Long-term changes in agricultural practices and wildfowling in an internationally important wetland, and their effects on the guild of wintering ducks. *J. Appl. Ecol.* **36**: 11–23.
- Fretwell, S.D. & Lucas, H.L. Jr** 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheor.* **19**: 16–36.
- Gibbs, J.P.** 2000. Wetland loss and biodiversity conservation. *Conserv. Biol.* **14**: 314–317.
- Grant, P.R.** 1975. Population performance of *Microtus pennsylvanicus* confined to woodland habitat, and a model of habitat occupancy. *Can. J. Zool.* **53**: 1447–1465.
- Hoyt, D.F.** 1979. Practical methods of estimating volume and fresh weight of bird eggs. *Auk* **96**: 73–77.
- Korpimäki, E.** 1988. Costs of reproduction and success of manipulated broods under varying food conditions in Tengmalm's owl. *J. Anim. Ecol.* **57**: 1027–1039.
- Kostrzewa, R. & Kostrzewa, A.** 1991. Winter weather, spring and summer density, and subsequent breeding success of Eurasian Kestrels, Common Buzzards, and Northern Goshawks. *Auk* **108**: 342–347.
- Lambin, X., Bretagnolle, V. & Yoccoz, N.G.** 2006. Vole population cycles in northern and southern Europe: is there a need for different explanations from single pattern? *J. Anim. Ecol.* **75**: 40–49.
- Mañosa, S., Mateo, R. & Guitart, R.** 2001. A review of the effects of agricultural and industrial contamination on the Ebro delta biota and wildlife. *Environ. Monit. Assess.* **71**: 187–205.
- Martin, T.E.** 1993. Nest predation and nest sites. *Bioscience* **43**: 523–532.
- Millon, A., Bourrioux, J.L., Riols, C. & Bretagnolle, V.** 2002. Comparative breeding biology of Hen Harrier and Montagu's Harrier: an 8-year study in north-eastern France. *Ibis* **144**: 94–105.
- Mindell, D.P., Albuquerque, J.L.B. & White, C.M.** 1987. Breeding population fluctuations in some raptors. *Oecologia* **72**: 382–388.
- Molina, B. & Martínez, F.** 2008. *El Aguilucho Lagunero en España. Población en 2006 y Métodos de Censo*. Madrid: Seo/BirdLife.
- Moreno-Mateos, D., Pedrocchi, C. & Comín, F.A.** 2009. Avian communities' preferences in recently created agricultural wetlands in irrigated landscapes of semi-arid areas. *Biodivers. Conserv.* **18**: 811–828.
- Neu, C.W., Byers, C.R. & Peek, J.M.** 1974. A technique for analysis of utilization-availability data. *J. Wildl. Manage.* **38**: 541–545.
- Newton, I.** 1998. *Population Limitation in Birds*. London: Academic Press.
- Pulliam, H.R. & Danielson, B.J.** 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. *Am. Nat.* **137**: S50–S66.
- Redpath, S.M., Clarke, R., Madders, M. & Thirgood, S.J.** 2001. Assessing raptor diet: comparing pellets, prey remains, and observational data at Hen Harrier nests. *Condor* **103**: 184–188.
- Salamolard, M., Butet, A. & Bretagnolle, V.** 2000. Responses of an avian predator to variations in prey density at a temperate latitude. *Ecology* **81**: 2428–2441.
- Sebastián-González, E., Sánchez-Zapata, J.A. & Botella, F.** 2010. Agricultural ponds as alternative habitat for waterbirds: spatial and temporal patterns of abundance and management strategies. *Eur. J. Wildl. Res.* **56**: 11–20.
- Shannon, C.E. & Weaver, W.** 1949. *The Mathematical Theory of Communication*. Urbana, IL: University of Illinois Press.
- Simmons, R.E., Avery, D.M. & Avery, G.** 1991. Biases in diets determined from pellets and remains: correction factors for a mammal and bird-eating raptor. *J. Raptor Res.* **25**: 63–67.
- Stenalski, A., Bavoux, C., Burneleau, G. & Bretagnolle, V.** 2008. Philopatry and natal dispersal in a sedentary population of western Marsh Harrier. *J. Zool.* **274**: 188–197.
- Stenalski, A., Mougeot, F., Eraud, C., Gangloff, B., Villers, A. & Bretagnolle, V.** 2010. Carotenoids in nestling Montagu's harriers: variations according to age, sex, body condition and evidence for diet-related limitations. *J. Comp. Physiol. B.* **180**: 33–43.
- Stenalski, A., Mougeot, F. & Bretagnolle, V.** 2012a. Carotenoid limitation and allocation priorities in asynchronous raptor nestlings. *Biol. J. Linn. Soc.* **105**: 13–24.
- Stenalski, A., Mougeot, F., Pérez-Rodríguez, L. & Bretagnolle, V.** 2012b. Carotenoid-based coloration, condition and immune responsiveness in the nestlings of a sexually dimorphic bird of prey. *Physiol. Biochem. Zool.* **85**: 364–375.
- Sutherland, W.J.** 1996. *From Individual Behaviour to Population Ecology*. Oxford: Oxford University Press.
- Thiollay, J.M. & Bretagnolle, V.** 2004. *Rapaces Nicheurs de France*. Paris: Delachaux & Niestlé.
- Tourenq, C., Benhamou, S., Sadoul, N., Sandoz, A., Mesléard, F., Martin, J. & Hafner, H.** 2004. Spatial relationships between tree-nesting heron colonies and rice fields in the Camargue, France. *Auk* **121**: 192–202.
- Whittingham, M.J. & Evans, K.L.** 2004. The effects of habitat structure on predation risk of birds in agricultural landscape. *Ibis* **146**: 210–220.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Additional information concerning assessment of harrier diet.

Appendix S2. Effects of study site, year and their interaction, on Marsh Harrier reproductive parameters using the restricted (balanced) dataset (2009–11).

Appendix S3. Variation in reproductive parameters of Marsh Harrier according to year (2006–11).

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