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ORIGINAL ARTICLE

Influence of habitat on nest location and reproductive output of Montagu's Harriers breeding in natural vegetation

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Abstract We examined distribution and breeding success of semi-colonial Montagu's Harriers (*Circus pygargus*) in relation to habitat in Castellón province (eastern Spain). Breeding areas used by harriers at a 1-km^2 scale were characterised by having intermediate percentages of scrub cover, their nesting habitat, and also had intermediate coverage of herbaceous crops and non-irrigated orchards. Out of all habitat variables considered, only the percentage of herbaceous crops within 500 m from individual nests had a positive and significant effect on breeding output of the species, suggesting that this habitat may be efficiently used by harriers to forage. Breeding output was also related to laying date and number of breeding neighbours within 500 m around nests, with pairs laying later and having a higher number of breeding neighbours showing lower fledged brood sizes. Number of neighbours (but not laying date) was positively related to scrub cover within 500 m and to cover of herbaceous crops within 2,000 m. Conservation actions for Montagu's Harrier in the study area should be aimed at preserving areas of scrub with nearby presence of herbaceous crops or natural grasslands. However, habitat improvement for semi-colonial species such as Montagu's Harrier may not result in a change of species distribution area, and good habitat areas may remain unoccupied, as social factors like presence of conspecifics play an important role in breeding area selection for these species.

Keywords *Circus pygargus* · Colonial species · Conservation · Natural vegetation · Spain

Zusammenfassung Wir untersuchten die Verteilung und den Bruterfolg von halb-kolonialen Wiesenweihen (*Circus pygargus*) in Bezug zum Habitat in der Provinz Castellón im Osten Spaniens. Das Brutgebiet der Wiesenweihen war, auf einer 1 km^2-Skala betrachtet, charakterisiert durch mittlere Bedeckung mit Buschwerk. Das Nesthabitat war zusätzlich bestimmt durch mittlere Bedeckung mit krautigen Pflanzen und nicht-bewässerten Obstgärten. Von allen Habitatvariablen, die wir betrachtet hatten, hatte nur der Prozentsatz der Bedeckung mit Krautpflanzen innerhalb von 500 m um die individuellen Nester einen positiven und signifikanten Effekt auf den Bruterfolg der Art. Dies lässt vermuten, dass dieses Habitat effizient von Wiesenweihen zum Furagieren genutzt wird. Der Bruterfolg war auch mit dem Legezeitpunkt korreliert, sowie mit der Anzahl von brütenden Nachbarn innerhalb eines Umkreises von 500 m um das Nest. Spät legende Paare und die mit mehr Nachbarn hatten einen niedrigeren Bruterfolg. Die Anzahl der Nachbarn (allerdings nicht der Legezeitpunkt) war positiv korreliert mit dem Grad der Bedeckung mit Buschwerk im 500 m Umkreis und mit dem Bedeckungsgrad der Krautpflanzen im Umkreis von 2,000 m um das Nest. Schutzmaßnahmen für Wiesenweihen sollten auf Gebiete mit Buschbedeckung und Präsenz von Krautpflanzen oder

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natürlichen Wiesengebieten abzielen. Jedoch sollte eine solche Habitatverbesserung für halb-kolonial brütende Arten, wie die Wiesenweihe, nicht zu einer Veränderung der Verbreitung führen. Auch können Gebiete mit gutem Habitat trotzdem nicht besiedelt werden, da soziale Faktoren wie die Präsenz von Artgenossen eine wichtige Rolle für die Wahl des Nistplatzes bei solchen Arten spielen.

Introduction

Declines of many bird populations have been linked to a reduction or degradation of their preferred habitats (Browne et al. 2004; Fernández et al. 2004; Julliard et al. 2004; Robinson et al. 2001). Both nesting and foraging habitats may play an important role in limiting bird population numbers or distribution (e.g. Newton 1998). Thus, conservation of bird species is frequently based on protection of their habitats, except in those cases when direct intervention is necessary (e.g. rescue of nestlings of a given species, supplementary food campaigns, captive breeding and release of birds in small populations, etc.; Cade and Temple 1995; Oro et al. 2008). For example, protected areas for birds (such as the Special Protection Areas—or SPAs designated under the EC Birds Directive) usually consider financial incentives for sustainable management of the land.

Like many birds, raptors are usually highly selective with respect to their habitats, especially regarding the availability of suitable nesting areas, although foraging habitats may also have an important effect at the time of choosing a site during the breeding season (Newton 1998). Breeding habitat (which include both nesting and foraging habitats) may limit species productivity or distribution (e.g. Benton et al. 2002; Soh et al. 2006; Suárez et al. 2000). In these cases, increasing availability or suitability of preferred habitats (e.g. restoring nesting habitats or increasing the availability of foraging habitats) may potentially lead to increasing population sizes (Carrete et al. 2002; Hiraldo et al. 1996). Understanding the strength of the relationships between habitat and species distribution or breeding success may be important to manage protected areas and to predict how changes in habitat may influence population dynamics, and thus contribute to the development of successful conservation programmes (López-López et al. 2006, 2007; Suárez et al. 2000; Tapia et al. 2004; Wilson et al. 2009).

However, the majority of raptor studies have been carried out on territorial species (but see García-Ripollés et al. 2005; Poirazidis et al. 2004; Sergio et al. 2003, for semi-colonial and colonial raptor species). Colonial or semi-colonial species may be atypical, because habitat selection may play a relatively smaller role in breeding spatial distribution for these species (e.g. Cornulier 2005; Cornulier and Bretagnolle 2006), whereas factors like conspecific attraction may be more important (Cornulier 2005; Sergio and Penteriani 2005; but see also Sergio et al. 2007). For these species, increasing the availability of preferred habitats might be inefficient to ensure the occupancy of given areas (see, e.g., Reed and Dobson 1993).

The Montagu's Harrier (*Circus pygargus*) is a semi-colonial ground-nesting Palaearctic raptor (Cramp and Simmons 1980). The species is considered vulnerable in France and the Iberian Peninsula (Blanco and González 1992; Salamolard et al. 1999; SNPRCN 1990), which are the strongholds of its western European populations. In western Europe, this species mainly builds nests within cereal crops (Arroyo et al. 2002), but some populations nest in natural vegetation (Cramp and Simmons 1980). The importance of protecting populations breeding in natural vegetation has been highlighted (Arroyo et al. 2002; Limiñana et al. 2006a), but most recent conservation measures have been directed towards populations breeding in agricultural habitats. One population nesting in natural vegetation is located in inland Castellón province in eastern Spain (Limiñana et al. 2006a). This population has increased exponentially from three pairs in the early 1980s to nearly 150 pairs in 2007, although population growth has slowed since 2002 (Limiñana et al. 2006a; Soutullo et al. 2006). Harrier breeding sites in Castellón face an uncertain future, as the area is currently subject to social and commercial developments, such as the recent building of an airport. A better understanding of the relationships between breeding habitat availability, harrier distribution and breeding performance would enable more effective conservation of Montagu's Harrier in this area.

In this paper, we first examine the relationship between habitat and nest occurrence, to assess the habitats preferred for breeding within the study area. Secondly, we examine the relationship between habitat, timing of breeding, number of neighbours and breeding output. We discuss the importance of habitat in explaining breeding distribution or success, and its implications for conservation in this semi-colonial species.

Methods

Study site and species

The study was carried out in Castellón province (eastern Spain; Fig. 1) where the species breeds in the inland corridors between the mountain ranges. Montagu's Harriers first bred in the study area in the early 1980s. The only nesting habitat used in this area by the species is

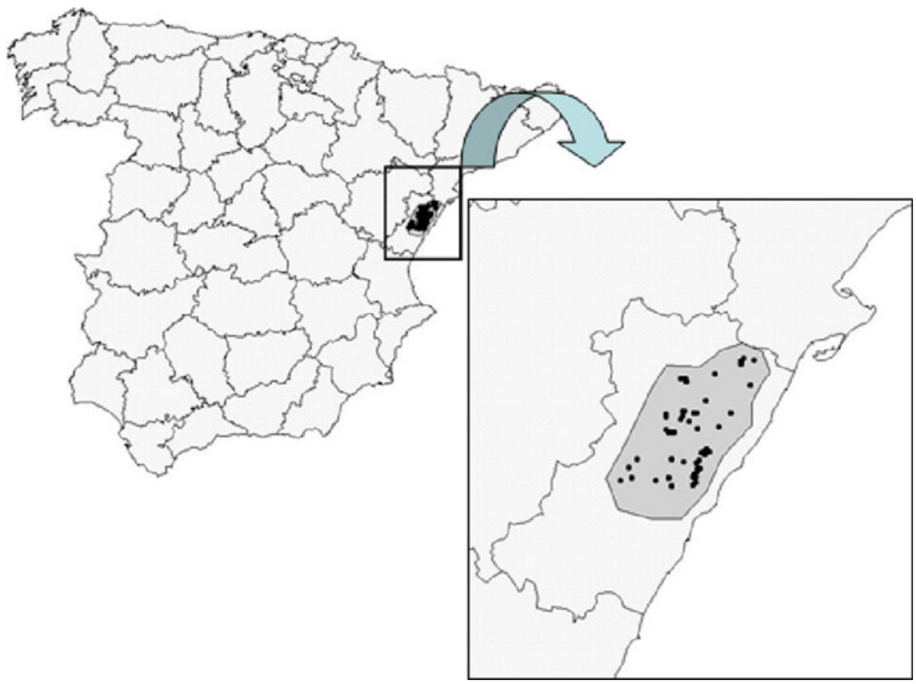

Fig. 1 Location of the study area (*grey polygon*) and overall distribution of nests of Montagu's Harriers (*Circus pygargus*)

Mediterranean scrub, dominated by Kermes Oak (*Quercus coccifera*). Other vegetation types in the region are non-irrigated crops (including cereal fields and orchards), as well as pine plantations. More details on the study area can be found in Limiñana et al. (2006a, b), and Soutullo et al. (2006). The main prey types for this Montagu's Harrier population are passerines and insects (especially orthopterans and small coleopterans), with other prey such as small mammals and lizards being taken less frequently (Limiñana et al. 2008).

This study is based on data from 2005 to 2007, when positions of located nests were recorded using a GPS. The area searched to locate Montagu's Harrier nests was ca. 1,050 km^2 (Fig. 1); field effort to locate the nests and monitor breeding performance was kept constant through the study period. Population size in the study area was stable between 2001 and 2005 at ca. 100 pairs (see Limiñana et al. 2006a; Soutullo et al. 2006). In 2006 and 2007, it increased to 129 and 145 breeding pairs, respectively. In 2005, a total of 80 Montagu's Harrier nests were located and the positions of 76 of them were recorded using a GPS. In 2006, 96 nests were located and the positions of 85 of them were recorded. In 2007, there were 101 located nests and the positions of 86 were recorded. Breeding data (number of eggs and nestlings) on these nests were recorded during nest visits. All pairs in 2005 whose nests were not located were inside known colonies, so the fact that we are not including them in the analyses of harrier nesting occurrence is not likely to strongly affect the results (as they were all in grid cells that were otherwise occupied). Some nests in 2006 and 2007 appeared in new areas for which we did not have accurate habitat data, but study of aerial photographs confirmed that these areas were similar to those included in these analyses in terms of habitat composition.

Habitat variables

Habitat composition in the study area was determined using the 1:10,000 Land Use map of the Comunidad Valenciana which is, in turn, based on recent aerial photographs (taken at the time period of the study). We had access to aerial photographs (7 × 5 km) and to the Land Use map corresponding to the areas where Montagu's Harriers nested up to 2005. We imposed a 1-km^2 UTM grid over the study area and calculated the proportion of each habitat type within each of the grid cells using a Geographic Information System (ArcView 3.2). We also evaluated (using the GIS) whether each grid cell was occupied or not by breeding harriers, and how many nests were located within each one. This scale has been extensively used in other studies of harrier occupancy (Arroyo et al. 2002, 2005; Tapia et al. 2004). To evaluate breeding performance in relation to breeding habitat, we calculated habitat composition around each nest at two different radii (500 and 2,000 m) using the GIS. The area of a circle with 500 m radius corresponds roughly to the area covered by a 1-km^2 grid cell, and also corresponds roughly to the area that a female uses for hunting around the nest, at least in Mediterranean areas (García and Arroyo 2005). We also used the 2,000-m radius since it includes a large part of the male core home range, also according to studies in southern Europe (Arroyo et al. 2008; Cornulier 2005). By using both radii, we can be sure that we are accounting for both nesting and foraging habitat in our analyses on the effect of breeding habitat on reproductive performance.

Overall, habitat variables calculated (both for circles and grid cells) were the following: percentage of scrub, percentage of forest (mainly pine plantations), percentage of herbaceous crops (mainly cereal crops) and percentage of non-irrigated orchards (mainly almond and olive). Across the study area, scrub covered 47% of the surface, orchards covered 38%, herbaceous crops 8% and forest 6%.

Statistical analyses

Hierarchical partitioning (HP) was used to identify the most likely habitat variables explaining the occurrence of Montagu's Harrier nests in the grid encompassing the study area (Chevan and Sutherland 1991). Hierarchical partitioning computes all of the possible hierarchical models that can be developed with a set of independent predictive variables; this is to say that if U, V and W are variables, HP computes single-order (U, V, W), second order (UV, UW, VW) and higher-order (UVW) models and tests whether the addition of a given variable produces an improvement in goodness of fit. For each independent variable, their explanatory power is segregated into the independent effect 'I' and the effects caused jointly with other variables 'J' (MacNally 2000). This analysis was conducted in R (R Development Core Team 2009) with the 'hier.part' package (Walsh and MacNally 2003), using logistic regression and log-likelihood as goodness-of-fit measure. As suggested by MacNally (2002), significance of the individual contribution of each variable included in the analysis was evaluated by a randomisation procedure based on 999 randomisations. Grid cell occupancy was defined as 1 = occupied (if at least one nest was present in the cell in at least 1 year), and 0 = unoccupied (if no nests were known in the cell). Only those cells for which we had information on at least 75% of its surface for habitat variables were used for the analyses. The initial model included percentages of each habitat variable: scrub, forest, herbaceous crops and orchards, as well as their quadratic terms. Quadratic terms were included since other studies of harriers have shown that percentage cover of certain habitats may be optimal at intermediate levels (Arroyo et al. 2005).

To test whether frequency of use (the number of years that a given cell had been occupied during the study) varied in relation to habitat, we used categorical modelling, with the procedure CATMOD within SAS 9.1 (SAS Institute 1999).

Secondly, we evaluated the relationship between breeding habitat and breeding output using Generalised Linear Mixed Models (GLMM). Laying date usually influences breeding output in raptors, with pairs laying later having a lower productivity (e.g. Newton and Marquiss 1984; Pietiäinen 1989). It is thus important to control for this variable when analysing factors influencing breeding output. We calculated laying date by backdating from nestling age, assuming an incubation period of 30 days (Cramp and Simmons 1980). Nestling age was estimated from length of the eighth primary wing feather following Arroyo (1995). Laying date was not known for nests that failed, since most of them failed during the incubation period (65% of total nest losses in the period 2005–2007) or before the first visit in the nestling stage (so chick age could not be assessed). To analyse breeding output in relation to habitat, we performed two separate (and complementary) analyses. We first evaluated whether breeding success (production of at least one fledged young from a nest) depended on habitat around the nest (at either 500 or 2,000 m). This binomial response variable (coded as 1 = successful nest, 0 = unsuccessful nest) was modelled using a binomial error distribution and a logit link function, with year included as a random variable. Secondly, we evaluated whether fledged brood size (number of fledglings per successful pair, modelled using a Poisson error distribution and a log link function) depended on habitat within 500 or 2,000 m, when controlling for laying date, also including year as a random variable. In semi-colonial species, local density (i.e. number of breeding neighbours) may also influence breeding output because of density-dependent competition within colonies (Arroyo 1995). Hence, we also calculated number of breeding neighbours within 500 m from each nest to include this variable in the models as a covariate. We used 500 m because this approximates the maximum distance between nests of the same semi-colony (Arroyo 1995; Cornulier and Bretagnolle 2006; Limiñana 2004). Thus, initial models included laying date (for fledged brood size only), number of breeding neighbours, and the habitat variables that had a significant contribution to harrier occurrence in the HP analysis (proportion of scrub and its quadratic term, and quadratic terms of herbaceous crops and orchards; see "Results"). Backward–forward selection and AIC comparisons were used to identify the final models (those with lower AIC values).

Because of semi-coloniality, there could be spatial correlation in results according to the position of nests (i.e. there may be lower variance within than between colonies). In fact, the variable "colony" was almost significant in models of breeding output with only colony as explanatory variable. Hence, we also used the variable "colony" as a random variable in the GLMM, to explain breeding output in relation to habitat (although in final models, this random variable was not significant in any analyses). As specified above, semi-colonies were defined based on distances between nests, with distances between closest semi-colonies being larger than 1,000 m (and thus, much larger than distances between nests within the same semi-colony).

Finally, we evaluated whether laying date or number of neighbours (assuming a normal error distribution and using an identity link function) of individual nests varied according to habitat around them. All the analyses related to breeding output were carried out using SAS 9.1.

Results

Breeding occurrence and habitat

The habitat variables that best explained the occurrence of Montagu's Harrier nests in the study area were the percentage of scrub and its quadratic term, which had each an independent contribution of more than 20% (Table 1). In addition, there was also a significant influence of the quadratic terms of percentage cover of herbaceous crops and non-irrigated orchards (Table 1). The quadratic term for scrub showed a preference for areas not entirely covered by this habitat, but with an intermediate degree of habitat diversity, as also illustrated by the significant contribution of the quadratic terms of farmland variables. Overall, cells used in at least 1 year had a higher proportion of scrub than non-occupied cells, and a lower proportion of both herbaceous crops and non-irrigated orchards (Fig. 2).

Additionally, the frequency of use (the probability that cells were used in only 1, 2 or 3 of the years of the study, or not at all) varied quadratically with scrub cover ($\chi^2_3 = 18.14$, $P = 0.0004$ for scrub cover, $\chi^2_3 = 16.15$, $P = 0.001$ for scrub cover squared), and with orchard cover ($\chi^2_3 = 7.69$, $P = 0.053$ for orchard cover, $\chi^2_3 = 9.66$, $P = 0.022$ for orchard cover squared). It was not significantly related to any other habitat variable (all $P > 0.20$). Grid cells occupied all 3 years were more likely to have between 40 and 80% of scrub cover (Fig. 3a), and between 0.1 and 60% of orchards (Fig. 3b).

Table 1 Results of hierarchical partitioning analysis performed to assess the importance of habitat on the occurrence of Montagu's Harrier (*Circus pygargus*) nests on a 1-km^2 scale in inland Castellón province (E Spain)

	I	J	Total	%I	z-score
Forest	1.02	0.67	1.69	5.86	0.65
Non-irrigated orchards	1.49	−0.06	1.43	8.52	1.35
Herbaceous crops	1.15	0.82	1.97	6.57	0.81
Scrub	3.89	1.31	5.20	22.29	4.51*
Forest	1.27	0.91	2.17	7.26	1.01
Non-irrigated orchards	2.79	0.40	3.20	16.00	3.52*
Herbaceous crops	2.26	0.94	3.20	12.95	2.39*
Scrub	3.59	−1.33	2.26	20.55	4.03*

I and *J* represent the independent and joint contribution of each habitat variable respectively. *%I* is the percentage of the total I accounted for each habitat variable. *z-score* is the randomisation test for the independent contributions of each habitat variable calculated from 999 randomisations

*$P < 0.05$

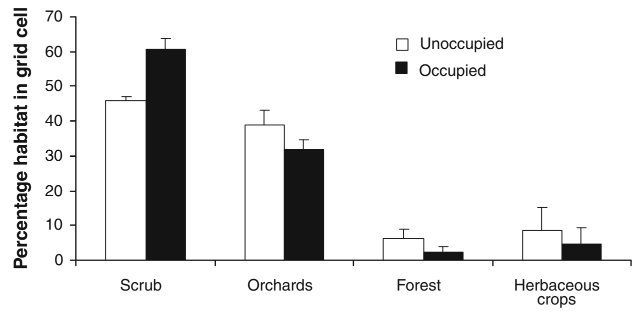

Fig. 2 Mean (±SE) percentage of different habitats in 1-km^2 grid cells occupied ($n = 53$) and unoccupied ($n = 985$) by breeding harriers in the study area

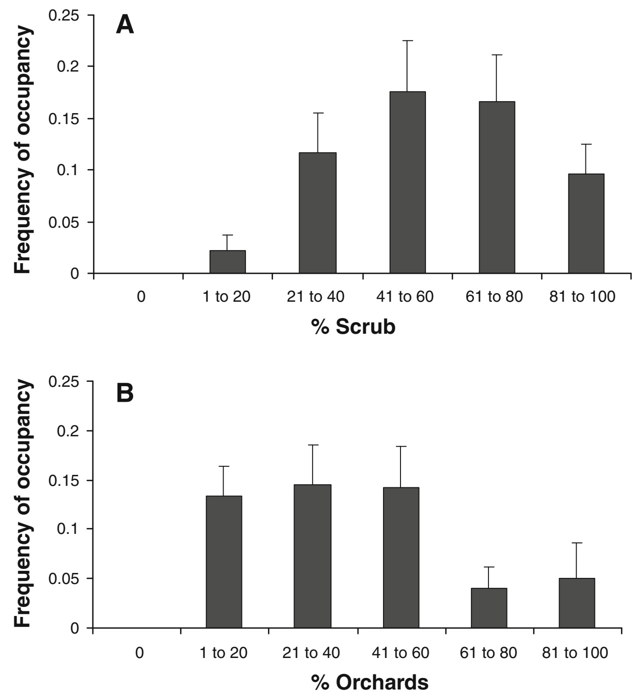

Fig. 3 Mean (±SE) frequency of occupancy (i.e. 0, 1, 2 or 3 years) of 1-km^2 grid cells in the period 2005–2007, according to scrub coverage (*above*) and orchard cover (*below*)

Breeding parameters and habitat

We found no relationship between breeding success and either number of neighbours or any habitat variable within 500 or 2,000 m (all $P > 0.2$).

When considering habitat within 500 m, fledged brood size was significantly related to laying date, number of neighbours and proportion of scrub and herbaceous crops ($F_{1,138} = 18.54$, $P < 0.0001$ for laying date; $F_{1,78} = 2.87$, $P = 0.095$ for number of neighbours; $F_{1,33} = 3.24$, $P = 0.081$ for scrub cover; $F_{1,53} = 5.15$, $P = 0.027$ for herbaceous crops cover squared). Fledged brood size decreased with laying date, number of neighbours and scrub cover, and increased with higher availability of herbaceous crops (parameter estimates: -0.01 ± 0.002; -0.015 ± 0.009; -0.003 ± 0.002 and 0.0005 ± 0.0002, respectively).

When considering habitat within 2,000 m, the only significant variables explaining fledged brood size were laying date and number of neighbours ($F_{1,150} = 21.78$, $P < 0.0001$ for laying date; $F_{1,51} = 15.92$, $P = 0.0002$ for number of neighbours) (parameter estimates: -0.01 ± 0.002; and -0.03 ± 0.01, respectively). No habitat variable was retained in the final model.

Number of breeding neighbours was significantly higher for nests placed in areas with higher scrub cover within 500 m ($F_{1,245} = 17.17$, $P < 0.0001$), or with intermediate scrub cover and relatively high herbaceous crops cover within 2,000 m ($F_{1,242} = 41.43$, $P < 0.0001$ for scrub cover, $F_{1,242} = 46.11$ $P < 0.0001$ for scrub cover squared, $F_{1,242} = 6.43$, $P = 0.009$ for herbaceous crops cover, Fig. 4).

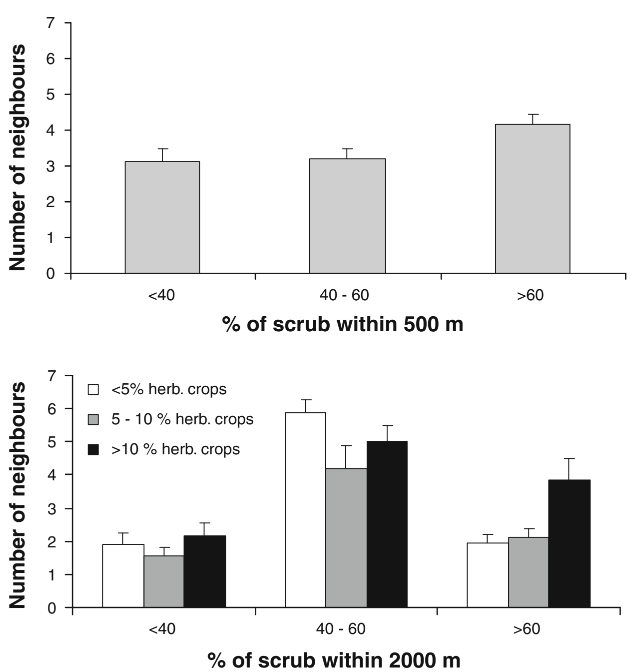

Fig. 4 Mean (±SE) number of neighbours within 500 m in relation to scrub cover within 500 m of the nest (*above*) or within scrub cover and herbaceous crops within 2,000 m of the nest (*below*)

No significant relationship between laying date and any habitat variable at either at 500 or 2,000 m was found (all $P > 0.2$).

Discussion

Our results show that the distribution of Montagu's Harrier nests within the occupied area in inland Castellón province is influenced by habitat, as found in other populations of the species or other raptors (see, e.g., Tapia et al. 2004; Wilson et al. 2009; López-Iborra et al. 2010). Probability of occurrence of harrier nests was significantly related to the availability of scrub, their nesting habitat. This relationship was not linear, but quadratic: probability and regularity of occurrence in a 1-km^2 area was greatest at intermediate levels of scrub cover. Also, the areas used by harriers for breeding had intermediate values of both herbaceous crops and non-irrigated orchards at the 1-km^2 scale. A quadratic relationship between nesting habitat and probability of occupancy was also found for Hen Harriers (*Circus cyaneus*) in Scotland. These birds use heather (*Calluna* spp.) as nesting habitat, but forage primarily over a mosaic of heather and grassland, so they favour areas with both foraging and nesting habitat to breed (Arroyo et al. 2005). Similar results were also found in Galicia, NW Spain, where Montagu's Harriers also breed in natural vegetation. There, plots occupied by harriers had a greater extent of scrub (nesting habitat) than unoccupied squares, but also a higher degree of pastureland (their preferred foraging habitat; Tapia et al. 2004). Our results thus indicate that Montagu's Harriers in Castellón prefer areas with heterogeneous land uses, where both scrub (nesting habitat) and farmland occur, and suggest that harriers probably use these non-irrigated orchards and herbaceous crops for foraging in the study area. Indeed, Montagu's Harriers in other parts of Spain often hunt in open areas with herbaceous vegetation, including grasslands and arable fields, as well as open orchards (Martínez et al. 1999; Guixé 2003; Arroyo et al. 2008). Also, Montagu's Harriers in the study area have been observed hunting in open areas with herbaceous vegetation (e.g. grasslands and cereal crops; Limiñana et al. 2008).

This result suggests that areas with intermediate scrub cover and nearby presence of orchards or herbaceous crops are optimal, but that areas with too much or too little scrub cover are suboptimal for harrier breeding, due to a lack of foraging and nesting habitat, respectively. We could thus expect that breeding output would be higher in areas with intermediate scrub and crop/orchard cover, where harriers probably assure their nesting and foraging needs in a more profitable way.

We found no effect of any of the habitat variables considered on harrier breeding success, and similarly habitat within 2,000 m of the nest did not have a significant effect on fledged brood size. However, fledged brood size was positively related to percentage cover of herbaceous crops within 500 m (and, concordantly, almost significantly negatively related to the percentage cover of scrub within 500 m). It is noteworthy that only herbaceous crops, not non-irrigated orchards, had a significant effect on breeding output, suggesting that this habitat type may be better for foraging harriers, possibly because prey are more easily captured in this habitat than in orchards (Martínez et al. 1999).

Overall, fledged brood size was mostly influenced by laying date and number of neighbours, both of which had a negative effect on breeding output of the species. Pairs laying later had a lower fledged brood size, a pattern common in many raptor species that may be related to individual quality (e.g. Newton and Marquiss 1984). However, there was no relationship between laying date and habitat, which suggests that optimal breeding sites (in terms of habitat) are not necessarily occupied before less optimal sites. This may indicate that breeding site occupancy in the species may be better explained by the ideal free model rather than by the ideal despotic distribution (Fretwell and Lucas 1970). In any case, as we are only using data from 3 years, explanations of harrier settlement and distribution in the study area derived from these models should be taken with caution (see also Soutullo et al. 2006).

Fledged brood size was also related to number of breeding neighbours, with a higher number of nearby breeding neighbours resulting in lower fledged brood sizes. This may reflect local competition for food or other resources, or a higher amount of time spent in conspecific interactions, in larger or denser nest clusters (Mougeot and Bretagnolle 2006). On the other hand, predation may also play a role in explaining this pattern, as a higher density of harriers breeding in the same scrub patch could attract more attention of predators, which may result in lower fledged brood sizes in these areas. However, predation rate of Montagu's Harrier nests in the study area is very low (e.g. a maximum of 12 nests out of 80 located nest were predated in 2005, and a maximum of 7 out of 96 nests were predated in 2006), and no effect of either habitat or number of neighbours was found on nesting success, which suggests that the effect observed refers to partial brood reduction or clutch size differences. Interestingly, the number of breeding neighbours was related to habitat, being highest in areas with high scrub cover within 500 m or with intermediate cover of scrub, and also a high percentage of herbaceous crops cover within 2,000 m. This suggests that the best habitat conditions to host large colonies are areas where scrub is very abundant at a lower scale (ca. 500 m), but intermixed with foraging areas (herbaceous crops) at a larger scale (ca. 2,000 m).

Our results thus suggest that habitat influences nest distribution in this species. However, in semi-colonial species, nest or colony location may be strongly influenced by factors like presence of conspecifics and their breeding success (Boulinier and Danchin 1997; Sergio and Penteriani 2005), which may have an even stronger effect than habitat quality (Arroyo et al. 2002; Cornulier and Bretagnolle 2006). The quality of the nesting patch (e.g. size of the scrub patch, availability of places to locate the nest or availability of nearby good feeding areas) appears to be the factor that determines the number of pairs in it (number of neighbours, thus colony size), and density within nesting patches (i.e. local competition by interference) may determine when to settle in a new patch rather than in an existing colony (Soutullo et al. 2006). Location of new colonies might be chosen at random among patches of similar quality, or determined by other factors, such as distance to occupied patches (Hanski 1999).

This means that, for this species, it may be difficult to predict the impact of small-scale habitat changes on population size or distribution at a larger scale. Improvement of breeding habitat for colonial or semi-colonial species such as Montagu's Harrier may result in higher nest numbers at the colony or semi-colony level (and even this may be affected because of interspecific competition), but it may not necessarily result in the creation of new colonies (or the occupancy of areas previously unoccupied). In these cases, it may be important to evaluate which other factors (e.g. past occurrence or productivity of breeding birds in that area, distance to other occupied sites, etc.) may influence the distribution and probability of occurrence (Arroyo et al. 2002). If protected/managed areas with good habitat are unoccupied, it may be possible to consider whether some of those parameters may be manipulated for management purposes, for example, by artificially increasing the productivity in certain areas through hacking, or by using decoys to attract them there, as has been done with the Montagu's Harrier (Pomarol 1994) or other semi-colonial species such as Osprey (*Pandion haliaetus*) (Thibault et al. 1995).

On the other hand, our results also suggest that habitat (in particular, availability of foraging areas nearby the nest) influences breeding output. Similar results were found in Hen Harriers (Amar et al. 2008). This suggests that habitat management in areas that are occupied regularly may have an impact, increasing local density (as seen above), as well as the productivity of pairs breeding there (and thus, potentially, the likelihood of that area being occupied in subsequent years). In our study area, this habitat seems to be the herbaceous crops, being an open habitat where Montagu's Harriers can easily catch their prey (e.g. Martínez et al. 1999). In that respect, it is important to note this habitat type is one of the most restricted in the study area (only 8% of the surface of the study area). Thus, an increase in its availability may enhance the suitability of the area for breeding Montagu's Harriers. However, this should ideally not be done at the expense of scrub availability, because the latter is important for harriers to choose an area to locate their nests, and important to hold high local densities (which may enhance the suitability of the area due to conspecific attraction). In the study area, the major land-use change observed in recent years is the abandonment of traditional farming practices and non-intensive agriculture for new intensive agricultural practices, mainly the transformation of herbaceous crop fields into more lucrative irrigated orchards. As well as being less well-suited to Montagu's Harrier hunting, the latter habitat may hold a lower density of prey, due to a decrease in prey habitat suitability (especially for ground-nesting passerines) and an increased use of pesticides. Hence, for species conservation in the study area, it would be useful to develop measures to encourage farmers to stop the transformation of herbaceous crops into orchards, or even encourage them to create new herbaceous crops.

In conclusion, the results of this study suggest that conservation of semi-colonial species, like Montagu's Harrier, should not be solely based on increasing availability of nesting habitat (or on protecting only these habitats), without taking into account social factors (Reed and Dobson 1993) and the importance of foraging habitats (Sergio et al. 2003; Amar et al. 2008; Arroyo et al. 2009). Habitat improvement may result in higher local densities and breeding success, but local actions aimed at preserving or enhancing nesting habitat in irregularly occupied areas for semi-colonial species may result in an inefficient investment of available conservation resources for these species. Indeed, habitat manipulation may be inefficient for changing species distribution (and thus, potentially, total breeding numbers at a regional scale). Thus, having a complete framework for a target species, including breeding habitat (both nesting and foraging), social factors and relationships between populations of the species would improve the effectiveness of conservation effort and investment. Also, protecting several core areas may be efficient for conservation of semi-colonial species (Sergio et al. 2003; Poirazidis et al. 2004), especially if such areas are regularly occupied, hold a large number of breeding pairs, or are more productive.

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