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Breeding habitat selection in the House Martin *Delichon urbica* in the city of Valencia (Spain)

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Abstract. The distribution of breeding House Martins was examined in relation to the characteristics of the urban landscape and the structure of the buildings. The study area (73 km²) was divided into 700 × 700 m squares. 11 habitat characteristics were measured within a 300 m radius around each colony. Each nest site was classified according to nest-support-type, its height and orientation. Habitat features around colonies were compared with places at the center of those squares without colonies. Stepwise multiple regression was then used to assess the possible contribution of the independent variables to the size of the colonies. A total of 1399 nests were found, distributed in 120 colonies, mostly consisting of 1–5 nests. In the built-up area, the density reached 31.85 nests per km². House Martins selected areas with a larger proportion of old buildings and open spaces, and closer to the nearest sources of food or mud. Only the distance from colonies to the nearest mud source and the proportion of open spaces were included in the regression model. As far as nest-sites are concerned, 33% of all nests were built under eaves, 34% under the ledges of balconies with architectonic ornamentation, and 15% within balconies. Birds selected nest sites offering better adhesion of nests to the substrate; to compensate for poorer adhesion, the number of nest walls touching other nests was increased. There was a positive relation between nest site height and building height. Nests were not uniformly distributed around the circle, but no clear patterns emerged from the data.

Key words: House Martin, *Delichon urbica*, breeding ecology, habitat selection, nest-site selection

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INTRODUCTION

The House Martin is a colonially nesting species whose European breeding populations often occur in cities (Hagemeijer & Blair 1996, Snow & Perrins 1998). The breeding biology of the species is well studied (Bryant 1973, Bryant 1975, Bryant 1979, Pajuelo et al. 1992, Johnston 1993, Kamiński & Wołoskiuk 1995) including energetics (Bryant & Westerterp 1980, Bryant & Turner 1982), ectoparasitism (De Lope et al. 1993, Møller et al. 1994) and dispersal (Rheinwald & Gutscher 1975, De Lope & da Silva 1988). However, there are few studies about habitat selection. Tatner (1978) and Turner (1982) studied the relationship between

some habitat characteristics and the settling of colonies or the abundance of birds, and there are some studies about nest-site selection (Bouldin 1959, Bell 1983, Antón & Santos 1985, Indykiewicz et al. 2001). In the species, the presence and activities of conspecifics (social attraction) probably modulate the habitat selection through multiple mechanisms (Danchin & Wagner 1997). The phenomenon of coloniality have been deeply studied in other Hirundinidae species (e.g. Hoogland & Sherman 1976, Shields & Crook 1987, Brown 1988) but there are no comprehensive studies referring to House Martin's coloniality.

Variations in habitat structure, to which individual birds may respond, exist in a hierarchy of

both spatial and temporal scales (Wiens 1973, Kotliar & Wiens 1990, Orians & Wittenberger 1991). Therefore, habitat selection by House Martins was examined at two spatial scales: 1) patterns of colony site selection in the urban landscape; 2) nest site selection in relation to the structural features of buildings. The aim of this was to find what habitat features are important to House Martin and also to obtain a first insight into the interplay between coloniality and habitat selection in the species.

STUDY AREA AND METHODS

The study area (73 km²) was located at the city of Valencia and its municipality (Fig. 1). The built-up area of the city of Valencia covers about 35 km². Areas with old buildings showing architectonic ornamentation covered about 2 km², and most of them were placed in the city centre. In outskirts there were orange groves and horticultural fields (the "Huerta").

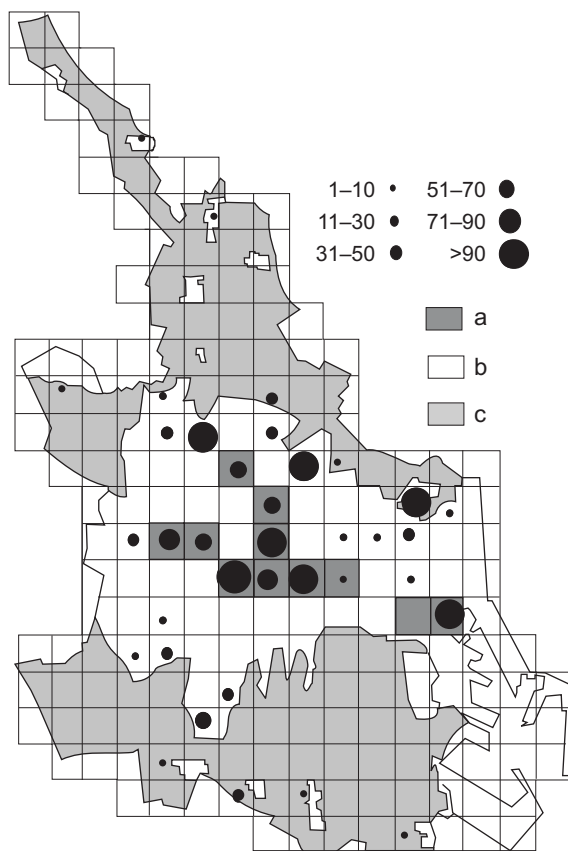


Fig. 1. Distribution of apparently occupied nests in the study area. a — presence of buildings with architectonic ornamentation, b — built-up area, c — horticultural land.

Data collection

The study area was divided into 2×2 km² squares and a search was carried out in April to July 1995. During the fieldwork on the ornithological atlas of Valencia in 1996–1998 (Murgui 1998, 2000) a small number of additional nests were found. All the nests were recorded within the new grid of 700 × 700 m squares (Fig. 1).

Following Lind (1950) a colony was defined as all nests located within 50 m of the main concentration of nests. These main concentrations of nests were selected adding all nests found on each single building, in accordance to the definition of colony of Tatner (1978). The most numerous concentration was defined as the main colony and all the nests within 50 m as sub-colonies. Nests could also appear as isolated or grouped. A nest group was defined as a cluster of attached nests. Nests were classified as apparently occupied or destroyed (i.e. clearly unsuitable for nesting).

Habitat and nest-site characteristics measurement

In total 11 habitat characteristics were measured (Table 1) within a 300 m radius around each colony, using a 1:10 000 map. Buildings were classified as showing architectonic ornamentation (henceforth old buildings) or not (new buildings). The category "other open spaces" defined stretches of derelict land or places like great squares or avenues. The places suitable for feeding or where House Martins were seen foraging were considered as "food sources". In order to determine patterns of selection, the habitat characteristics measured for active colonies were compared with those for places with no nests (henceforth "random colonies"). These measurements were made in the continuous built-up area, at the centre of the 48 squares without colonies (Fig. 1).

For each nest, ten characteristics of the nest site were measured (Table 1). Six types of nest support were distinguished (Fig. 2). The term "structure" was used for single nest support: one balcony, window and so on. The availability of a particular type of nest support was not measured. It was not measured in other studies on nest sites of House Martin, either (Bouldin 1959, Bell 1983, Antón & Santos 1985). Antón & Santos (1985) assumed that the availability of nest support types is not limited which might be not always true.

Data analysis

Unless other thing is specified, all statistical analyses were performed over the total number of nests, because it better reflects a situation without

Table 1. Measured variables describing urban landscape and nest-site characteristics.

Variables	min.–max.	$\bar{x} \pm SD$
Colony characteristics		
Colony size	1–67	9.51 ± 13.08
Distance to the city centre (km)	0.18–4.75	2.23 ± 1.07
Distance to nearest mud source (km)	0.01–0.75	0.11 ± 0.13
Distance to nearest food source (km)	0.01–0.25	0.04 ± 0.05
Percentage of old buildings	0–90.2	14.16 ± 28.22
Percentage of new buildings	2.5–100	51.81 ± 29.43
Percentage of cultivated land	0–40.21	13.75 ± 4.61
Percentage of parks and gardens	0–75.12	16.75 ± 17.83
Percentage of other open spaces	0–46.03	3.50 ± 4.81
Distance to the nearest colony (km)	0.06–2.06	0.19 ± 0.25
Size of the nearest colony	1–67	12.96 ± 15.97
Nest site characteristics		
Nest type	—	—
Nest support type	—	—
Presence of architectonic ornamentation	—	—
Orientation (o)	5–360	94
Height of buildings with nests (m)	3–54	7.19 ± 9.75
Height of nests (m)	3–54	12.39 ± 8.70
Size of nest groups	1–4	2.50 ± 2.12
Number of nest per structure	1–8	1.43 ± 0.84
Number of nest walls contacting with the substrate	2–5	3.27 ± 0.78
Number of nest walls contacting with other nests	0–5	0.50 ± 0.63

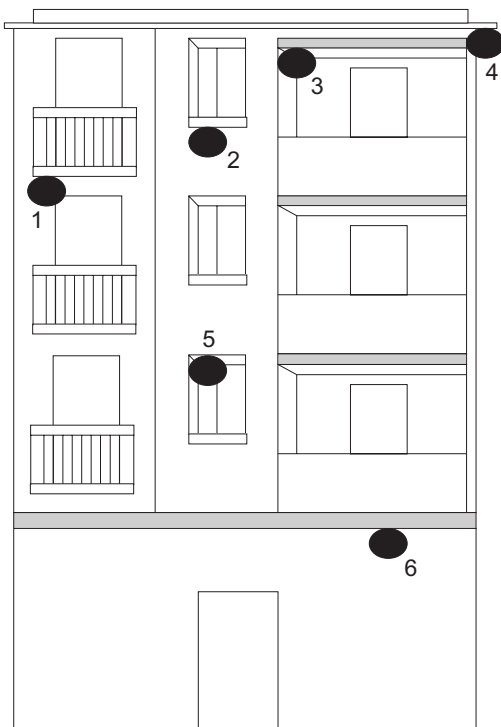


Fig. 2. Different types of nest supports. 1 — balcony ledge, 2 — window ledge, 3 — balcony frame, 4 — eaves, 5 — window frame, 6 — facade projection.

the influence of nests destruction by dwellers, an activity that is not unusual in the study area. Stepwise multiple regression (Johnson & Wichern 1992, Zar 1996) was used to assess the possible contribution of the independent variables to the size of the colonies. Circular uniformity of angles was tested by Rayleigh's test, and differences of circular distributions among colonies in old and new buildings by the Watson-Williams test (both in Zar 1996).

All variables that were not normally distributed were transformed before using them in analyses following Zar (1996) — log transformation for counts and distances, and arcsine transformation for proportions.

RESULTS

Size and distribution of the breeding population

In total 1399 nests were found of which 1101 were apparently occupied and 298 were destroyed. The density of nests for just the built-up area was $31.85/\text{km}^2$ and $15.08 \text{ nests}/\text{km}^2$ for the whole of the study area. Nests were found in 36 of the squares (Fig. 1), i.e. 18.6% of the whole of the study area and 34.3% of the built-up area.

The species was absent in the cultivated land, except areas where groups of buildings appeared (Fig. 1). In the built-up area, the spatial pattern of distribution and abundance showed two well-delimited zones. On one hand, the periphery where colonies were settled at the edge of the built-up area, very often facing cultivated fields. On the other hand, the centre of the city, where colonies were associated with old buildings and most of them were placed near an urban park along the old course of the river Turia, currently an urban park. House Martin’s nests were absent from a major part of the built-up area between these two zones.

Colony characteristics and habitat selection

During the study 120 colonies were found in total. Ten colonies were outside the urban area (Fig. 1) and probably they were part of other House Martin populations living in the surrounding towns. Therefore, they were excluded from the following analysis.

Usually, colonies were of small size (Fig. 3, Table 2). There were non-significant differences in colony size between old and new buildings, with colonies placed in new buildings being slightly smaller (Table 2).

Colonies placed on new buildings had a significantly greater proportion of overall open spaces around them ($t_{108} = 4.80, p < 0.001$, Table 2), and they were closer to mud sources than colonies on old buildings ($t_{108} = 4.80, p < 0.005$, Table 2). The difference in the distance between colony and food source was not significant (although p-level was near to 0.05) but colonies on

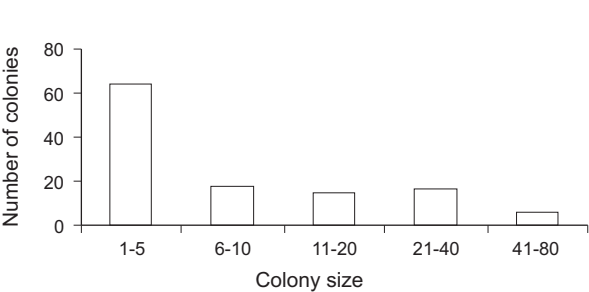


Fig. 3. Frequency distribution of colony sizes (number of nests).

old buildings were more distant than the rest. Because of these results, and the fact that nest sites of colonies placed on old buildings showed a very different structure (see next sections), only colonies placed on new buildings were compared with random ones. Random colonies had a lower proportion of open space in overall ($t_{119} = 2.39, p < 0.01$, Table 2) and in each category (Table 2) and were more distant from mud ($t_{119} = 2.48, p < 0.05$, Table 2) or food sources ($t_{119} = 2.59, p < 0.05$, Table 2) than colonies placed on new buildings.

In a multiple stepwise regression over the 110 colonies, the model included three variables (Table 3) and the amount of variation explained was very small. The analysis performed only over colonies on old buildings failed to detect any significant model. However, for colonies placed on new buildings, the distance from colony to the nearest mud source and the proportion of other open space were included in the model which explained the greater amount of variation than the previous ones (Table 3).

Table 2. Comparison of habitat variables between colonies. Means ($\bar{x} \pm SD$) of untransformed variables. p — values for the new versus old building colonies and new versus random colonies (t-tests): * $p \leq 0.05$, ** $p \leq 0.005$, *** $p \leq 0.001$.

	Location of colonies		
	New buildings (n = 75)	Old buildings (n = 35)	Random (n = 47)
Colony size	8.46 ± 12.48	11.77 ± 14.20	
Percentage of old buildings	0.0	44.51 ± 34.09 ***	0.10 ± 0.72
Percentage of new buildings	59.10 ± 24.11	36.20 ± 33.82 ***	70.44 ± 27.32 *
Percentage of parks and gardens	14.26 ± 18.36	13.82 ± 17.32	6.85 ± 10.25 *
Percentage of cultivated land	24.04 ± 24.75	0.0 ***	12.91 ± 5.12 **
Percentage of other open spaces	2.60 ± 7.17	5.45 ± 10.16 *	9.51 ± 8.10***
Percentage of overall open space	40.89 ± 24.11	19.28 ± 17.80 ***	29.27 ± 7.11**
Size of the nearest colony	11.29 ± 14.45	16.74 ± 18.43	12.54 ± 16.77
Distance to the nearest colony	0.18 ± 0.20	0.15 ± 0.11	0.66 ± 0.28
Distance to the city centre	2.70 ± 0.64	1.12 ± 0.45 ***	2.26 ± 1.11
Distance to the nearest mud source	0.09 ± 0.10	0.17 ± 0.16 **	0.24 ± 0.23 *
Distance to the nearest food source	0.03 ± 0.50	0.06 ± 0.06	0.10 ± 0.14 *

Table 3. Stepwise multiple regression of colony size against the measures of habitat. All data transformed. *** $p \leq 0.001$.

	Coefficients	
	all colonies	new colonies
Percentage of new buildings	-0.006 ***	ns
Percentage of other open spaces	0.009 ***	0.01 ***
Distance to the nearest mud source	ns	-0.31 ***
Total R ²	9.1%	14.8%
F value	$F_{2,107} = 6.50^{***}$	$F_{2,72} = 7.46^{***}$

Nest-site selection

Assuming an unlimited availability of nest supports (see Methods), the distribution of nests deviated from expected if birds choose sites randomly, both in new ($\chi^2_5 = 743.87$, $p < 0.0001$) and old buildings ($\chi^2_1 = 357.51$, $p < 0.0001$).

On new buildings, mean number of nests and mean size of nest groups was significantly greater in facade projections than on the rest of nest support types (Table 4). On old buildings there was no difference in the mean number of nests

between support types but mean size of nest groups was greater in eaves (Table 4).

On new buildings, mean number of nest walls contacting with the substrate was smaller in window ledges than in the rest of nest support types (Table 5). On old buildings, mean number of nest walls contacting with the substrate was greater in balcony ledges than in eaves (Table 5).

Among apparently occupied nests, 394 were placed on old buildings and 707 on new buildings. Therefore, density in the places with old buildings was 198 nests/km² against 26.56 nests/km² in the rest of the built-up area. Using the proportion of both types of buildings as crude measure of nest sites availability, the Electivity Index of Ivlev was calculated, and for old buildings it reached a value of 0.82, which means that House Martins showed a strong preference for old buildings. This preference could be attributed not to ornamentation but to other characteristics of support types where nests are placed. However, the quantity of nests placed in eaves and balcony-ledges of old buildings were almost opposite in the same support types of new build-

Table 4. Total number of nests, mean number of nests per structure (\bar{X} n/str \pm SD), mean nest group size per substrate type (\bar{X} g/type \pm SD) and results of statistical tests (F- and t-test) of the influence of substrate type on the parameter in question.

Substrate type	New buildings			Old buildings		
	Nests	\bar{X} n/str	\bar{X} g/type	Nests	\bar{X} n/str	\bar{X} g/type
Facade projection	97	3.34 ± 2.28	1.90 ± 1.06	—	—	—
Eaves	416	2.09 ± 4.20	1.36 ± 0.75	45	2.50 ± 1.72	1.07 ± 0.41
Balcony frames	214	1.59 ± 1.07	1.36 ± 0.77	—	—	—
Balcony ledges	26	1.44 ± 0.70	1.23 ± 0.35	477	2.40 ± 1.90	1.02 ± 0.76
Window frames	74	1.57 ± 1.03	1.17 ± 0.52	—	—	—
Window ledges	50	1.13 ± 0.46	1.08 ± 0.41	—	—	—
Tests	$F_{5,465} = 5.46$, $p < 0.001$		$F_{5,636} = 5.63$, $p < 0.001$	$t_{215} = 0.49$, ns $t_{382} = 2.13$, $p < 0.05$		

Table 5. Mean number of nest walls ($\bar{x} \pm$ SD) contacting with substrate and with other nests and results of statistical tests of the influence of substrate type on the parameter in question.

Substrate type	New buildings		Old buildings	
	Substrate	Nests	Substrate	Nests
Facade projection	2.32 ± 0.55	0.94 ± 0.63	—	—
Eaves	2.41 ± 0.58	0.49 ± 0.62	3.06 ± 0.33	0.22 ± 0.42
Balcony frames	2.60 ± 0.51	0.52 ± 0.66	—	—
Balcony ledges	2.50 ± 0.58	0.30 ± 0.55	3.34 ± 0.65	0.52 ± 0.63
Window frames	2.60 ± 0.50	0.29 ± 0.54	—	—
Window ledges	2.00 ± 0.10	0.16 ± 0.46	—	—
Tests	$F_{5,871} = 12.82$, $p < 0.001$		$t_{392} = 2.79$, $p < 0.01$	

ings (Table 4). These results suggests that there was no intrinsic advantage of using these external support types.

If bird selected old builds in order to increase the security of nests, then this selection should influence other nest-site variables. Comparing support types placed in old and new buildings mean number of nests in eaves of old buildings was greater ($t_{215} = 1.91$, $p < 0.05$, Table 4) but mean group size was smaller ($t_{342} = 2.02$, $p < 0.05$, Table 4). Consequently, mean number of nest walls contacting with the substrate was greater in old buildings ($t_{459} = 7.32$, $p < 0.0001$, Table 5) and mean number of nest walls contacting with nests was greater in new buildings ($t_{459} = 2.86$, $p < 0.005$, Table 5).

For balcony ledges, results were similar. Mean number of nests was greater in old buildings ($t_{215} = 2.10$, $p < 0.05$, Table 4), although there was no difference in the mean group size between old and new buildings ($t_{363} = 0.81$, ns, Table 4). Mean number of nest walls contacting with the substrate was greater in old buildings ($t_{501} = 7.08$, $p < 0.0001$, Table 5) but there was no difference in the mean number of nest walls contacting with nests between the two kinds of balcony ledges ($t_{501} = 1.80$, ns, Table 5).

House Martin's nests were located between 3 and 61 m from the ground level, 56% of them between 9 and 17 m. Mean height of nests in new buildings was about 15 m and 12 m in old buildings and this difference was significant ($t_{1397} = 14.12$, $p < 0.0001$). There was a positive relationship between nest's height and building's height both for new (Pearson test, $r_{877} = 0.65$, $p < 0.001$) and old buildings (Pearson test, $r_{522} = 0.58$, $p < 0.001$).

Nests were not uniformly distributed around the circle in new buildings (Mean angle = 53° ; Rayleigh's test $Z_{0.05, 877} = 10.03$, $p < 0.005$) nor in old buildings (Mean angle = 358° ; Rayleigh's test $Z_{0.05, 522} = 6.56$, $p < 0.005$). There was a significant difference between mean angles of both circular distributions (Watson-Williams test $F_{0.05 (1), 1,1397} = 309.12$, $p < 0.005$).

In new builds, orientation of nests showed a significant departure of an even distribution of nest-sites around 360° for E:S:W:N axis ($\chi^2_3 = 138.02$, $p < 0.001$). Number of nests faced to the east and the south was over the expected number, and number of nests faced to north and to the west, was below the expected number. In old builds, orientation of nests showed a significant departure of an even distribution as well ($\chi^2_3 = 31.14$, $p < 0.01$). Number of nests faced to the north

was well over the expected number, number of nests faced to south and to the west were below the expected number and number of nests faced to east was the same that the expected number.

DISCUSSION

Recruitment into House Martin populations is widely influenced by food supply composed of aerial insects, especially Hemiptera (aphids mainly) and Diptera (Bryant 1975, Snow & Perrins 1998). Turner (1982) found that vegetation cover accounted for 39% of the variation in the number of nests, probably through an increase in insect abundance, and Tatner (1975) concluded that the food from non built-up areas was the major factor controlling House Martin's distribution in Manchester. My results are in concordance with these findings. In the study area, colonies were more frequently placed in sites with greater proportion of spaces suitable for feeding than sites without colonies, and colony size was related, although weakly, with the area of other open space. On the other hand, colonies were closer to food sources than random colonies, a feature that could be important provided that House Martin is a species sensitive to the foraging site distance when feeding nestlings (Bryant & Turner 1982). All these conclusions rest, however, on an unknown relationship between habitat features and food availability, but they received some support in a study on the biology of Common Swift *Apus apus* in the city of Madrid (Bernis 1987). This author sampled directly the aerial microfauna and found that density of preys (suitable not only for swifts but to House Martins as well) is 7 times higher in the periphery than in the city centre.

Most of the variables related to food availability (specially the proportion of cultivated land) are also related with mud availability, other important resource for the species. Tatner (1975) discarded the proximity of colonies to water supply as related to the provisioning of building material because birds were able to obtain it from puddles. In Valencia, however, irrigated fields of the periphery and urban parks are the only places where birds can find mud regularly. Colonies in new buildings are closer to mud sources than random colonies, and the selection of the distance from colonies to the nearest mud source in the regression model increase the variability explained. These findings suggest that House Martins select nest sites to minimise the energy cost invested in nest building, as

occurs in Cliff Swallow *Hirundo pyrrhonota* (Gauthier & Thomas 1993).

All these relationships do not explain, however, the strong association of the species with the old buildings in the city centre where feeding resources or nest building material seem to be more difficult to obtain. Moreover, we have circumstantial evidence that after the restoration — and subsequent removal of nests — of some old buildings, birds have returned to the same place. This sort of “natural experiment” suggests a phenomenon of site tenacity (see e.g. Wiens & Rotenberry 1985) or philopatry (De Lope & da Silva 1988), that food resources or mud are not limiting factors or that there is a compensatory advantage in using those sites. This advantage could result from an increase in the security of nests because House Martins select nest support types that provide a greater adhesion with the substrate and hence tend to be very associated with buildings with architectonic ornamentation. Turner (1982) did not find greater abundance of nests in areas with old buildings (though its structural characteristics were not mentioned) but, as in my study, Antón & Santos (1985) found that birds showed a preference for complex structures where the nests could obtain a better support. Present study show also that, when the contact with the substrate is intrinsically less extensive, as in new buildings, House Martins compensated it by increasing the number of nest walls, and hence the size of nest group, contacting with other nests. A complementary benefit of this behaviour would be a reduction in the material and time required for constructing a nest. Similarly, Gauthier & Thomas (1993) found that Cliff Swallows showed a preference for sites where they could build attached nests. Despite the fact that eaves of new buildings offer a lesser number of contacts with substrate than other support types, they have more nests. This result apparently contradicts the overall picture. However, a less level of human interference in eaves and perhaps, the tendency of birds to settle in greater heights, may explain this. References about the heights at which House Martins place nests are scarce: most nests were located between 5–10 m above the ground in Durham (Bell 1983), between 10–15 m in Yecla (Martínez et al. 1996) and 76.8% between 7.6 and 16.5 m in Bydgoszcz and Grudziądz (Indykiewicz et al. 2001). Our results are similar and the differences with other studies must be due to the typology of the study area.

The fact that the mean of the angles and the number of nests faced to different orientations varied between old and new buildings suggests

that other factors are more important than orientation. In a review of the orientation of nests across six European localities Antón & Santos (1985) did not find a consistent pattern.

Patterns and processes of habitat selection in our study population seem, in general, to be consistent with previous findings. However, two factors not controlled in this study deserve much more attention in order to obtain a meaningful picture of habitat selection by House Martins. First, population dynamics and dispersal may result in intraspecific competition, which in turn can force some individuals to occupy marginal habitats (Fretwell & Lucas 1970). Secondly, coloniality, as an individual choice, could be influenced by colony characteristics through multiple processes (Hoogland and Sherman 1976, Brown 1988, but see Shields 1990, Danchin et al. 1998). The fact that the colonies in our study area are closer to other colonies than random colonies, and that a little amount of variability in colony size is explained by habitat variables suggests an influence of coloniality, but deeper studies are required to elucidate this point. On the other hand, ectoparasites impose an energy cost (De Lope et al. 1993, Møller et al. 1994) and this could promote a tendency to form small colonies in which the probability of infestation is lower, as occurs in the Cliff Swallow (Brown & Brown 1986). This scenario fits well to the House Martin sizes of the colonies of our study area, where great colonies are rare, in each single structure the number of nests is small and most nests are isolated.

Finally, some methodological weakness of our work merits attention insofar as they could have been influencing the results:

- 1) our habitat sampling method follows Bryant & Turner (1982), who found that birds, when feeding nestlings, forage at an average distance of 300 m. A more precise estimate of the foraging range in our study area may render different habitat proportions and thus different patterns. Probably more serious is the fact that habitat features that could promote the settling of a nest in a place could have changed very much in the last decades, due to urban development. Our current measure of habitat, therefore, might not reflect the habitat that birds selected in the past. This historical effect would be more pronounced in the cases of old buildings, which date back to 1900–1920. Colonies in these buildings are at least 40 years old (inf. J. A. Peris) and probably they were there when the nearby habitat was the river and not an urban park as currently is.

2) The use of the total number of nests as a measure of habitat use includes an unknown amount of unused nests, thus confounding the pattern of use between habitats or nest sites. On the other hand, the assumption that high densities are associated with high-quality habitats is often violated (van Horne 1983) and a complete test of habitat selection involves an assessment of whether the documented habitat preferences are adaptive (Jones 2001). This subject and its interplay with coloniality and demography could be easily studied in the urban populations of House Martin, compared with other species and habitats.

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STRESZCZENIE

[Wybiórczość środowiskowa oknówki w mieście Walencji, Hiszpania]

Omawiane zagadnienie jest u oknówki mało zbadane. Praca zajmuje się wybiórczością środowiskową zarówno w odniesieniu do kolonii lęgowych jak też umieszczenia poszczególnych gniazd.

Badaniem objęto teren miejski Walencji (73 km²), podzielony na kwadraty 700 × 700 m (Fig. 1). W promieniu 300 m od każdej kolonii charakteryzowano środowisko 11 wyróżnionymi cechami (Tab. 1). Dla określenia wybiórczości w podobny sposób opisywano tereny bez kolonii (określane jako „kolonie porównawcze”) w środku 48 kwadratów obszaru śródmiejskiej zabudowy. Umieszczenie każdego gniazda charakteryzowano 10 cechami, m. in. wyróżniono 6 typów jego posadowienia na budynku (Fig. 2). Budynki klasyfikowano jako mające bogatą ornamentację architektoniczną (określane umownie jako „stare”) i pozbawione jej („nowe”). Nie określano dostępności typów posadowienia oraz orientacji i wysokości budynków. Analizą objęto wszystkie gniazda, również zniszczone.

Stwierdzono 120 kolonii (Fig. 3, Tab. 2), 1399 gniazd, w tym 1101 prawdopodobnie zajętych i 298 zniszczonych. Na obszarze zabudowy (35 km²) zagęszczenie gniazd wyniosło 31.85/km², a na całym badanym terenie — 15.08/km². Kolonie w

budynkach „nowych” były mniejsze niż w starych (Tab. 2), ale różnica nie była istotna. Kolonie w „nowych” budynkach miały w stopniu istotnym częściej dostęp do otwartych przestrzeni i do miejsc z błotem wykorzystywanym przez ptaki do budowy gniazd. „Kolonie porównawcze” miały w obu kategoriach rzadziej dostęp do otwartych przestrzeni oraz były bardziej oddalone od miejsc z błotem oraz żerowisk niż kolonie „nowe”.

W wielokrotnej krokowej analizie regresji wielkości kolonii obejmującej wszystkie kolonie, przy trzech zmiennych (Tab. 3), procent zmienności wyjaśnionej był bardzo niski, ale dla samych kolonii w nowych budynkach — był wyższy.

Umiejscowienie gniazd odbiegało od prawdopodobieństwa przypadkowego. W „nowych” budynkach w stopniu istotnym było więcej gniazd na fasadzie niż innych typach posadowienia (Tab. 4). W budynkach „starych” nie było różnic w liczbie gniazd między typami posadowienia (Tab. 4), ale średnia wielkość grup gniazd była większa pod okapami dachu („eaves”). Średnia liczba ścianek gniazd przylegających do powierzchni posadowienia była w budynkach nowych mniejsza przy umieszczeniu niszy okna („window ledge”) niż przy innych typach umieszczenia, a w budynkach „starych” — była większa w niszy balkonu niż pod okapem dachu (Tab. 5).

W „starych” budynkach było 394 prawdopodobnie zajętych gniazd (198 gniazd/km² terenów z takimi budynkami), a w „nowych” — 707 (27 gniazd/km² pozostałego obszaru).

Gniazda były umieszczone na wysokości 3–61 m nad ziemią, 56% z nich między 9 i 17 m. Średnia wysokość umieszczenia w budynkach „nowych” (15 m) była w istotnym stopniu większa niż w „starych” (12 m). W obu typach budynków była ona dodatnio skorelowana ze średnią wysokością budynku. Ukierunkowanie gniazd w stosunku do stron świata wykazało istotne odchylenie od przypadkowego — w „nowych” budynkach wyniosło ono średnio 530, a w starych — 3580, przy czym różnice te były istotne.