Hernández, Á., Zaldívar, P. 2021. Nest-site selection and nest design of Iberian bullfinches *Pyrrhula pyrrhula iberiae* in northwestern Spain. Avian Biology Research 14 (2): 124–142.

Nest-site selection and nest design of Iberian bullfinches *Pyrrhula pyrrhula iberiae* in northwestern Spain

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Abstract

Nest-habitat selection and nest design in a Eurasian bullfinch population in the Iberian Peninsula are thoroughly addressed in this study for the first time. Hedgerows and meadows were found around all of the nests and most of them were supported by hedgerows, so bullfinches consistently used the general woody vegetation available as reproduction habitat and site. Also, poplar plantations appeared preferentially in the immediate surroundings of the nests. Partly reflecting these results, bullfinches chose zones with greater shrub and tree cover than that available. Bullfinches placed their nests on a wide variety of plant species, but showed predilection for thorny species. Overall mean height of nests above the ground was 1.43 m and large-sized shrubs/trees were preferred. The most predominant bullfinch nest orientations were S, E and centered, which arguably provided thermal benefits and protected from severe weather. In general, there were no significant temporal variations in nest-site selection. With the exception of thorny support and favourable orientation, acting jointly, there was no significant association between nest-site characteristics and nesting success, presumably because many nests were already located in the most advantageous places at each time, and because despite this, predation pressure was high. Nest external dimensions were relatively variable, whereas internal width was the least variable nest dimension. No significant monthly or interannual variations in nest weight were observed. Larger nests did not hold larger clutches. Successful nests were larger than unsuccessful ones. The bullfinch nests were of simple construction, with two clearly different regions, the outer nest and the internal cup, with no significant temporal variations in the weight of either. The outer, structural nest consisted mainly of twigs, whereas roots and herbaceous shoots were the highest fractions lining the cup. Hair was the only animal-derived material used by bullfinches.

Keywords

Building materials, Fringillidae, nest location, nest size, nesting success, vegetation structure

Introduction

Bird nests are multifunctional structures relating principally to the creation of an optimum microclimate and a safe place for parents and offspring, but also to sexual selection, through habitat choice and structural design (e.g. size, building materials).[1-3] With regard to the analysis of nest-habitat preferences, it is important to consider several spatial and temporal scales in which birds respond to different changing factors.[4-7] For many typical passerine bird species in forested areas, farmlands with hedgerows provide key habitats and resources, or at least are important in movement between woods, during the breeding season.[8-11] Unfortunately, hedgerows have declined sharply over recent decades in Europe due to the intensification of agricultural practices.[12] On the other hand, only recently has the design of bird nests –e.g. intraspecific variations or biomechanical properties of different materials in different nest parts– begun to be examined in depth, with less being known about open-cup nests built by females.[2,3,13-15] Availability of nest materials is included amongst the most important factors in avian breeding-site selection, although it does not seem to be limiting for most species.[2,4]

In passerine birds in general, especially those with a long breeding season, considerable monthly variations have been observed in nesting habitat and nesting site (e.g. nest height from the ground), linked to environmental changes (e.g. in availability of optimal habitat or weather conditions).[4,16,17] It is common for birds, including small passerines nesting in shrubs and trees, to prefer to place their nests in thorny plants and select favourable orientations, that is, they seek advantageous sites against predators and bad weather.[2,3,18,19]

As a usual rule, the dimensions of the birds' nests are determined by their body size, [4,14] and their general design is typical of each species, including finches, but there may be intraspecific variations due to different environmental scenarios in terms of geographic location, weather, and availability of particular nest materials. [14,15,20,21] Normally, the internal dimensions of passerine nests are less variable than the external ones, since they adapt the size of the cup to that of the incubating parent, as well as the set of eggs and nestlings.[14,22,23]

The effect of the different nest-habitat and nest-site features on nest success is extremely variable in passerine birds, according to the disparate results obtained in numerous investigations. In situations such as strong predation pressure or effective occupation of suitable microhabitats in which the predation risk decreases, this effect can be masked. [24,25] Nevertheless, high woody vegetation cover, thorny plants supporting the nest, large nest shrubs/trees, and hidden and inaccessible places, or against rough weather, are usually beneficial conditions associated with an increase in breeding success. [19,26-28] Although finch species that nest low normally suffer higher predation than those nesting clearly higher, since the number of potential predators increases,[29] a greater height from nest to ground is not always associated with a greater nest success in a given passerine species.[25] A larger nest size is usually correlated with a larger clutch size,[30] but it does not necessarily lead to greater breeding success, since although large nests are often built by high-quality individuals, [2,31,32] they are potentially more visible to predators, especially in open-nesting bird species. [2,4,33,34]

More particularly, Eurasian bullfinches *Pyrrhula pyrrhula* (hereinafter referred to as bullfinches) are considered to be generalist forest birds that willingly accept heterogeneous semi-open landscapes during the breeding season.[11,35] The ecology of some Eurasian subspecies and populations, notably in central and western continental Europe and the British Isles, is known in certain detail, including nest location and nest design, although no in-depth quantitative analyses are available on nest-site selection (use vs. availability).[14,35-37] In brief, females of these bullfinch subspecies generally construct their nests in thick shrubs just over 1 m from the ground, using thorny plants with some frequency, and they are composed of a base and external walls made of loosely intertwined twigs, and an internal cup made of finer, more tightly woven material, with an average weight of about 15 g for the entire nest. Until now, knowledge of the Iberian subspecies *iberiae* was limited to occasional and segmented observations, apart from geographical distribution, general habitat, and some estimations of local abundance.[38] Regarding reproduction, some reports provided brief information (clutch size, egg traits, nesting place, and nest traits), on fewer than ten nests in each, from NE Spain.[39-41] However, very recently, some aspects of the ecology of Iberian bullfinches have been carefully studied, namely, breeding ecology, and habitat use and space preferences throughout the year, without considering nest-site selection and nest design.[42,43]

In this study, nest-habitat selection –with special emphasis on nest-site selection (microscale descriptions)–[1] and nest design are thoroughly addressed for the first time in a population of bullfinches in the Iberian Peninsula. The population occupied a hedgerow-dominated landscape in northwestern Spain, in an area close to the southwest distribution limit of the species. The main characteristics analysed are: 1) habitat and vegetation structure around the nest (25–100 m radius), 2) structure type (e.g. hedgerow, isolated shrub/tree) and plant species supporting the nest, 3) spatial location of the nest within the shrub/tree, 4) nest weight and size, and 5) nest-building materials. The temporal variation in nest-associated characteristics was evaluated. Secondarily, the relationships between these features and reproductive parameters such as nesting success and clutch size, are analysed. These and other important reproductive parameters in this bullfinch population, during the same period of time, have already been assessed in detail in relation to factors such as seasonality, predatory species, and weather.[42]

Based on what is known about the bullfinch elsewhere in the western Palearctic, and about passerines in general, and taking into account the general landscape of the study area, it is expected to nest here in wide shrubs/trees in hedgerows, preferably in thorny plants, low above the ground and towards favourable orientations, with some monthly variation in some of these features as it is a multi-brooded species. Bullfinch nests are expected to have a general design similar to that already described for other subspecies, but the contribution of their different parts and the building materials used could vary to some degree throughout the breeding season. The internal linear dimensions of the nests should be less variable than the external ones, according to current knowledge.

In the event that most of the bullfinch nests were located in a small range of potentially favourable sites, and also considering that they suffered high predation rates in the study area,[42] a generalised significant association between nest-site characteristics and nesting success is not expected. Larger nests should host larger clutches, and should cause a lower nest success, although this latter pattern has not yet been clearly established.

Methods

Study area

The study area covers 78 ha and is located in the middle-lower Torío river valley, between Palacio and Manzaneda (42º43'–42º44'N, 5º30'–5º31'W; 900 m a.s.l.; León province, Castile and Leon autonomous community), in north-west Spain. Biogeographically, it forms part of the Carpetano-Leonese sector in the Mediterranean West Iberian province.[44] Hot summers (average temperature of ≈20 ºC), cold winters (≈4 ºC) with some snowfall, and moderate rainfall (average annual precipitation of ≈500 mm) with a relatively short dry summer season characterize the area.[42] The landscape is mainly composed of hedgerows separating irrigated meadows grazed by livestock and cut for hay, bordered by riparian woodland on the west side and slopes covered in Pyrenean oak *Quercus pyrenaica* woods interspersed with very small Scots pine *Pinus sylvestris* plantations on the east side. Some hedgerows border Canadian poplar *Populus* x *canadensis* plantations. Estimated hedgerow density is 3.3 km per 10 ha. The area is located in a transition zone to the Eurosiberian region, south of the Cantabrian mountain range, in an extensive hedgerow network of great conservation value for flora and fauna.[45-47] About thirty species of broadleaved, chiefly deciduous shrubs, trees, and climbers, are found in the hedgerows. The landscape and hedgerow density and structure are very similar throughout the study area and have hardly changed in recent years and decades, except for a moderate increase in the number of poplar plantations and an incipient abandonment of meadows and hedges.

Data collection

Precautions.– Only the traits of non-active (deserted, predated, or young fledged) nests were estimated as finches in general tend to abandon their nests in early breeding stages, and nestlings tend to leave the nest prematurely ("exploding"), if disturbed.[35,36]

General nesting data and procedures.– General fieldwork to study the breeding ecology of bullfinches was conducted throughout 2001–2006, between the months of March (when the first signs of probable breeding were observed) to October (when the last sightings of adults with dependent young were made).[42] In a systematic way, 113 trips were conducted in spring (March–31, April–33, May–49), 155 in summer (June–49, July–54, August–52), and 65 in autumn (September–39, October–26). The total number of trips in each season was equally distributed among the years of study as far as possible, except for 2006 when the sampling effort was considerably lower. Two trips were usually needed to cover the entire area: approximately half of the area (36 ha) on one trip, and the other (42 ha) the following day. On each trip, the corresponding zone was explored by slowly walking around it, stopping frequently, following the edge of the hedgerows and marginally (≈ 10% sampling effort) the edge of the oak woods. Small European birds generally show a bimodal pattern of daily locomotor activity, but mobility tends to decrease throughout the day.[48] Consequently, more than 85% of field trips were conducted in the morning in all seasons, and the remainder in the afternoon. The morning trips lasted from one hour after sunrise to 12:00 h (solar time) and the afternoon trips from 12:00 h (solar time) to one hour before sunset, as there was insufficient light at dawn or dusk for sampling to be carried out. In particular, nests were searched for, found and monitored during April–August of the period 2001–2005. Direct nest searching ("cold searching") is not usually effective for bird species that hide their nests,[49] which is the case of the bullfinch. Thus, the search for nests was mainly by following adults showing signs of nest attendance.[42] Apart from field trips made systematically to cover the entire area, as described above, short visits were made to increase the monitoring of active nests in an effort to identify, weekly at least, the breeding stage of each nest. In addition to these samplings, the necessary fieldwork was carried out to collect diverse data related to nest site and nest design.

Bullfinch density in the area and study period was approximately 2.5–3.5 pairs/10 ha during April–May.[42] As far as the current situation is concerned, recent visits to the study area for other purposes in 2021 revealed that the bullfinches are still present and apparently in good conservation status. Although active nests belonging to different pairs could be located very close to each other (as close as ≈25 m), some had been constructed in close vicinity (at a distance of ≈2–50 m) to others that had failed, and were probably replacement nests. Even though bullfinch pairs usually breed solitarily, several can coincide in a small area as they are not territorial, like other European cardueline finches.[35,36] Adult activity around the active nests was concentrated in a radius of 100 m, although it was common for them to move beyond this distance, sometimes flying out of sight.[42]

Nesting success is the percentage of nests in which at least one young fledged, though not all eggs hatched and/or not all nestlings survived. Clutch size refers to complete clutches. In nests found with nestlings, clutch size was estimated as the number of nestlings plus, where applicable, the number of unhatched eggs. It is assumed that parents were unable to remove unhatched eggs or dead nestlings from the nest, since it was verified that they remained inside with the live nestlings. In complete clutches, individual losses (n=71) were due to deserted/predated eggs (49.3%), deserted/predated nestlings (31.0%), unhatched eggs (18.3%), and marginally dead nestlings (1.4%).[42] Newly built nests are those completed that at most reached the incubation stage, in contrast with those that contained nestlings (whether fledging occurred or not). Apart from nests that were found and monitored (n=56), that is, nests in which activity had been checked at some time, a few other inactive ones were found (n=7), undoubtedly bullfinch, with an unknown breeding history. Because of their size, general external appearance, and location, bullfinch nests could not be confused with those of any other passerine bird in the study area. Not all of the nests (n=63) were used for all analyses, the most appropriate sample being selected in each case (e.g. those seven additional nests were not used for analyses related to timing of breeding or nesting success, but were included to estimate the overall average height of the nests above the ground). Normally, data collection on nest site and the collection of completed (definitely or very likely) and apparently whole (well-preserved) nests, measured straightaway (weight and linear dimensions) in the field and later taken to the laboratory to analyse building materials, were carried out approximately one week after there was no reproductive activity in them. Some nests were collected a few days later if it rained during this period of time to allow them to dry.

Nest site.– The following features were assessed for each nest: 1) occurrence of habitat components in a 25 and 100 m radius, 2) percent cover of vegetation strata in a 50 m radius, 3) supporting structure type and its orientation (north-south or east-west, applicable in particular to hedgerows), 4) supporting plant species (considering individual plants in direct contact with the nest), and 5) nest location within the shrub/tree and size of nest shrub/tree (i-height above the ground, ii-height of shrub/tree where the nest is located –homogenous mass without considering isolated trunks or branches protruding upwards–, iii-width of shrub/tree at nest height, iv-nest position within the shrub/tree with relation to orientation –N, S, E, W, centered–, v-nest visibility, and vi-nest accessibility). E and S were considered favourable directions within the shrub/tree, as E orientation enables moderate warming at dawn when morning sunlight appears, and S/E orientations counteract prevailing westerly winds and frontal systems, intense afternoon sunlight, and cold, northern exposure. Habitat components considered were hedgerow-meadow (by far the main component of the landscape in the study area), oak woodland, riverside woodland, brushwood, poplar plantation, and fruit orchard. Vegetation strata considered were herb, shrub and tree (forming the canopy) layer; vegetation cover was visually estimated, rounded to the nearest percent, considering aerial view, that is, the sum of herb, shrub and tree cover is 100%. Supporting structure types considered were: hedgerow, small patch of woody vegetation (distinguishing among next to hedgerow, to oak woodland, and to riverside woodland), wild rose shrub within poplar plantation, and tree in apple orchard. To estimate nest visibility, each nest was attributed a value, according to visual assessment, between 1 (clearly visible) and 5 (not visible), with 0.5 accuracy (1, 1.5, …, 4.5, 5), and the same for nest accessibility (between 1–easily accesible and 5–hardly accessible). Values for visibility and accessibility were assigned from the "human" perspective, probably not extrapolable to all potential predators, especially flying and climbing predators.

Plant species availability for supporting the nests was estimated by conducting eight sampling days within the period 28 September–15 October 2005, when approximately 9 km of hedgerows were covered (≈35% of all the hedgerows, evenly distributed in the study area), recording the presence-absence, but not the number of individuals of each species (shrubs, trees, climbers) in 2 m-long fragments (*n*=330 fragments) situated every 25 m –modified from a previous study in the area–.[50] Multispecific complexes of *Populus* poplars (*P. nigra*, *P.* x *canadensis*, *P. tremula*), *Salix* willows (mainly *S. fragilis*, also *S. atrocinerea*, *S.* x *secalliana*), *Rubus* brambles (mainly *R. ulmifolius*, also *R. caesius*), *Rosa* roses (mainly *R. canina*), and *Malus* apples (*M. domestica*, some *M. sylvestris*), were classified as single species. *Pyrus communis* included *P. communis* var. *pyraster*; *Prunus spinosa* included *P. insititia* and *P. domestica*. Selection of each plant species was estimated by the Jacobs' index: $S=(u-a)/(u+a-2ua)$,[51] where u (use) is the proportion of occurrence as nest support of a given plant species in relation to the total nest support occurrences, and a (availability) the proportion of occurrences of that plant species in the hedgerows in relation to the total occurrences of all plant species. Correction of u and a values for a total of 1 is required for calculations. This index varies between -1 (maximum negative selection) and 1 (maximum positive selection), with a value 0 if selection does not occur (i.e. nests were supported by the plant species according to its availability). Nevertheless, a conservative approach was taken, considering the interval between -0.2 and 0.2 to be non-selection, 0.21–0.5 (either negative or positive) moderate selection, and 0.51–1 (either negative or positive) strong selection. Other habitat components, apart from hedgerow-meadow, close (≤25 m) to the middle point of each hedge fragment, percent cover of vegetation strata (estimated as explained above) considering a 50 m radius around the middle point of each fragment, fragment orientation, the average height of each fragment, and hedge width at the middle point of the fragment at breast height (1.3 m), were also recorded (n=330 fragments/points) to compare with nest site.

Frequently, stockbreeders horizontally intertwined relatively thin green branches, cut from shrubs and trees (e.g. hazel trees, willows, poplars), in the hedges ("horizontal wooden enclosure", hereafter referred to as HWE) to close gaps and prevent livestock from escaping. For each nest, a record was made of whether, apart from live plants, a HWE contributed to supporting it, and HWE availability was estimated by conducting two sampling days (5 and 6 April, 2007), recording the presence-absence of this element and its average height above ground in the hedgerows, every 25 m, at a total of 379 points.

Nest design.– Nests were removed from the shrubs/trees very carefully so as not to lose any construction material, and any loose material that had fallen into them from shrubs/trees above (e.g. leaves) was discarded immediately. The total weight of each nest was estimated in the field, as well as the following linear dimensions: external width (nest diameter), internal width (cup diameter), external height (nest depth), and internal depth (cup depth). External and internal width of the nests was measured at the upper edge. A STANLEY® spring return pocket tape measure with an accuracy of 1 mm was used to measure the linear dimensions of the nests, and a PESOLA® spring balance (capacity: 100 g, readability: 1 g) to weigh them. Mean external width was calculated as [(external width at the longest axis+external width at the shortest axis)/2], and mean internal width in the same manner. To estimate the correlation between nest weight (mass) and overall nest size (volume), the nest was considered as an inverted cone, that is, $volume=(\pi \cdot r^2 \cdot h)/3$, r being mean external width/2 and h external height. The volume thus obtained was not considered an accurate calculation of nest volume but simply a measurement combining nest width and nest height. Mean values for the weight and linear dimensions of the nests in the study area were compared with those obtained for the same measurements of nests of the subspecies *Pyrrhula p. pileata* in Britain.[14,37]

The nests selected for examination of the building materials were placed in labelled plastic bags and frozen at -32 ºC for at least 24 h in the laboratory. Two main regions in the nests, the outer nest and internal cup, were considered because they looked different to the naked eye, and also because they were relatively easy to separate. The outer nest elements, mostly intertwined twigs, were carefully removed until only the internal cup, composed of thinner more closely interwoven elements, was left, and was, in turn, carefully disassembled. The nests were deconstructed using forceps, grouping together the pieces of each region in the following fractions: twigs, herbaceous shoots, roots, leaves, other vegetal remains, hair, and unseparated remains. Occurrence of man-made material was negligible, only one short artificial thread being found in one nest. Each piece was assigned to the corresponding fraction using the naked eye and, when necessary, with the help of a stereomicroscope. Taxonomic identification of the nest materials is not an objective of this study, and could only be carried out by simple, visual observation in some cases, thus providing additional but not exhaustive information. For example, most of the twigs were not identified because the bullfinches selected those that were dry and, therefore, showed no distinctive traits such as buds, leaf scars, and leaf vascular bundle scars; and microscopy analysis is required for the identification of hairs. Unseparated remains consisted of dust and fragments that were too small to be clearly assigned to a fraction. Elements alien to nest composition, e.g. insects, rodent droppings, or fruits and seeds carried to the nest by rodents, were discarded.

The material fractions were weighed using a SCALTEC® SPB42 electronic precision balance with 150 g capacity and 0.001 g readability, and then placed in labelled plastic bags. The size of 40 twigs from four outer nests, that is, 10 pieces randomly selected from each, was determined by measuring length (cm) using a STAEDTLER® plexiglass ruler with 1 mm resolution, and width (average diameter, mm) using a MITUTOYO® digital caliper with 0.01 mm resolution. For an approximate evaluation of hair length (cm) in each nest, distinguishing between outer nest and internal cup, the most representative ranges of length were considered, that is, the ranges in which the majority of hairs could be grouped together, and the mean (hereafter mean length) of the intermediate values of these ranges was estimated (for example, for ranges 6–8, 10–15 and 20–30 cm, intermediate values are 7, 12.5 and 25 cm, respectively). In some cases, most of the hairs could be included in a single range, but their length often varied considerably. Also, the apparently longest hair in the outer nest and internal cup of each nest was measured, and was sometimes found to be outside the most representative ranges. Hair length was estimated using a measuring tape. Hair width also varied considerably, and the presence/absence of fine, medium thickness and thick hairs was recorded by visual assessment.

Statistical analysis

The following statistical tests were used: 1) the chi-square test (χ^2), with Yates correction for one degree of freedom, to compare series of absolute frequencies for two variables, 2) log-linear analysis (G^2) to compare absolute frequencies for three variables (2 x 2 x 2 tables), 3) unpaired *t*-test to compare two means, 4) one-way ANOVA (*F*) to compare more than two means, 5) two-way ANOVA (*TWF* to differentiate it from one-way analysis) to assess whether two independent variables, in combination, are related to the mean of a dependent variable, and 6) Pearson's correlation coefficient (*r*) to measure the relationship between two continuous variables; considering the two-tailed way wherever possible.[52,53] Parametric statistical tests were not performed if the sample size was ≤5. For large sample sizes, such as those usually considered in this study, the normality assumption required for parametric tests is of minor importance.[54] Standard deviation (SD) and coefficient of variation (CV) were estimated as measures of dispersion. $P<0.05$ was considered statistically significant.

In several analyses that related nesting success with different nest-site traits, separately each, no statistically significant associations were found (chi-square test χ^2, unpaired *t*-test, $p>0.05$), with very little variation, even negligible, between successful and unsuccessful nests (e.g. ≈6% in supporting structure orientation, ≈30 cm in mean height of nests from the ground, 0.01 points both in mean visibility and accessibility). In the case of occurrence of thorns in the nest support and of nest orientation, there was also no statistical significance, but the percentages of nests located on exclusively spiny supports and of those facing east/south (favourable orientations) were considerably higher for successful nests than for unsuccessful ones (approximately 25 percentage point difference for both traits). Therefore, a log-linear analysis was used to evaluate the joint effect of these two traits on nesting success. Temporal variation in each of the location characteristics of nests was generally not statistically significant, but mean height from the ground was significantly higher for nests fully built by June–July than April–May (*t*-test, $p<0.05$). To explore this issue further, a two-way ANOVA was used for assessing wether season and nest success, in combination, were related to mean nest height above the ground. Although nest success tended to increase as the breeding season advanced,[42] there was no significant association between breeding performance (successful vs. unsuccessful nests) and the month in which nest construction was completed (April-May vs. June-July) (χ^2, $p>0.05$); therefore, nest success and season were considered to be independent variables.

If not otherwise specified, all years were pooled together, mainly to avoid analyzing small sample sizes. As stated above, the sampling effort in each season was equally distributed among the years of study. Also, little changing environmental conditions from year to year seemed to promote steady breeding population densities during the study period. Interannual variation in diet was not remarkable (ÁH, unpubl. data), and nest success and breeding productivity rates were fairly constant from one year to the next.[42]

Results

Nest-site selection

All 63 nests were surrounded by hedgerow-meadow, ≈90% by poplar plantation, ≈30% by oak woodland, ≈13% by riverside woodland, ≈11% by brushwood, and ≈6% by fruit orchard, in a 100 m radius around them. Considering this radius, most bullfinch nests (59%, 37 of 63) were located in a habitat formed exclusively by hedgerow-meadow and poplar plantation or both components plus oak woodland. Taking into account a 25 m radius, that is, the nearest habitat, hedgerow-meadow was present around all 63 nests and all of the points selected for the assessment of available habitat (n=330); poplar plantation in 46.0% and 19.1% of cases, respectively (significant difference: $\chi^2_1=19.94$, $p<0.001$); oak woodland in 3.2% and 1.8%, respectively (non-significant difference: $\chi^2_1=0.04$, $p=0.83$); and riverside woodland in 1.6% and 0.9%, respectively (non-significant difference: $\chi^2_1=0.24$, $p=0.62$).

Comparing nests (n=63) with points selected for assessing available habitat (n=330) in a 50 m radius, mean herb cover was significantly lower for the former ($t_{391}=-2.47$, $p=0.01$), mean shrub cover significantly higher for the former ($t_{391}=1.99$, $p=0.047$), and mean tree cover also significantly higher for the former ($t_{391}=2.01$, $p=0.045$) (Figure 1). Surrounding tree cover was ≥40% in 16 of 63 (25.4%) nests, mainly due to the presence of poplar plantations (14 nests). There were no significant differences in herb, shrub and tree cover between nests fully built in April–May and June–July, or between nests built in 2002 and 2003 (other years were not considered due to the small sample size), or between successful and unsuccessful nests ($p>0.05$ for all comparisons, *t*-test) (Figure 2).

[Insert Figure 1]

[Insert Figure 2]

The supporting structure for most of the nests was hedgerow (54 of 63, 86%), and to a much lesser extent, small patch of woody vegetation (9.5%), wild rose shrub within poplar plantation (3%), and tree in apple orchard (1.5%). There was no significant difference between supporting structure orientation (45.5% N-S, 54.5% E-W, n=55) and available orientation (53.0% N-S, 47.0% E-W, n=330) (χ^2_1=0.80, p=0.37). Considering nests in hedgerows in the strict sense, there was no significant association between hedgerow orientation and success/failure (31.82% success and 68.18% failure for N-S, n=22; 37.5% and 62.5%, respectively, for E-W, n=24) (χ^2_1=0.009, p=0.92).

Bullfinches used 19 (73.1%) of the 26 available plant species as nest support (Table 1). Most of the nests were supported by two (42.8%, 27 of 63) or just one species (30.2%), followed by three (22.2%) and four species (4.8%). Five species, each occurring for >20% of the nests, were the most frequently used: four thorny shrubs (*Rubus* brambles, blackthorn, wild rose, and common hawthorn) and wild privet. With regard to major species (≥5% of total occurrences in either use, availability or both), common dogwood, common hazel and poplar were very negatively selected; European spindle and field elm were moderately rejected; common hawthorn, blackthorn and common ivy were moderately selected; and wild rose, wild privet, guelder rose and *Rubus* brambles were used according to their availability (non-selection) (Table 1). Considering thorny plant species as a whole, they were moderately selected (S=0.31), and climbing plants, also considered as a whole, were used according to availability (S=0.09). In line with this, the association between plant type (thorny/non-thorny or climbing/non-climbing) and use (nest support vs. availability), considering both number of species and number of occurrences, was only significant in the case of number of occurrences of thorny/non-thorny plants (57.5% in nests vs. 41.7% available for thorny plants, 42.5% vs. 58.3% for non-thorny plants) (χ^2_1=11.50, p<0.001; p>0.05 for the remaining cases) (Figure 3).

[Insert Table 1]

[Insert Figure 3]

Occurrence of thorny plants supporting the nest (differentiating between solely thorny, solely non-thorny and mixed) was not significantly different between nests completed by April–May (36%, 18%, 46%, respectively, n=39 nests) and June–July (44%, 12%, 44%, n=16 nests) (χ^2_2=0.40, p=0.82). Neither were there any significant seasonal differences excluding the mixed category (χ^2_1=0.03, p=0.86). Few nests were supported by HWEs (7 of 63, 11.1%), which occurred to a significantly lower extent than their availability (present in 201 of 379 points, 53.0%) (χ^2_1=36.44, p<0.001). For nests as a whole (n=63), S, E and centered were the most frequent orientations (32%, 29%, 25%, respectively), whereas W and N were uncommon (9%, 5%, respectively). There was no significant association between orientation and the month when the nests were completed (χ^2_1=0.02, p=0.88), with very high percentages of frequent orientations in April–May (84.6%, 33 of 39 nests) and June–July (87.5%, 14 of 16).

Considering nest orientation (more favourable –E/S– vs. less favourable –W/N/centered–), occurrence of thorns in the nest support (solely thorny vs. non-thorny/mixed) and breeding performance (success vs. failure) together, there were significant general differences in the frequencies of bullfinch nests (G^2_4=15.05, p<0.01). More specifically, a significant association between nest orientation and occurrence of thorns was found for unsuccessful nests (n=35) (G^2_1=4.83, p<0.05), with almost half (43%) of these nests facing less favourable directions on non-thorny/mixed supports, in contrast to about a quarter (23%) of them facing more favourable directions on exclusively thorny supports. There were no significant differences for other combinations (G^2_1, p>0.05 for the remaining cases). However, it is noteworthy that half of the successful nests (50% of 20) were east/south oriented on exclusively thorny plants, in contrast to a fifth (20%) of them facing less favourable directions on non-thorny/mixed supports.

For bullfinch nests as a whole (n=63), mean height above the ground was 1.43±0.73 m (range=0.60–4.10 m), mean shrub/tree height 4.10±2.36 m (range=1.10–12.00 m), mean shrub/tree width 2.66±2.79 m (range=0.75–22.50 m), mean visibility 3.13±1.16 (range=1–5) and mean accessibility 2.57±1.15 (range=1–5). Most of the nests were within a very narrow range of heights from the ground (73% of them within 0.5–1.5 m, 87% within 0.5–2.0 m). These parameters were not significantly different comparing successful and unsuccessful nests or months, except that mean height above the ground was significantly higher for nests fully built by June–July than April–May (Table 2). Furthermore, overall mean height above the ground did not vary significantly amongst years (Table 2). There was a significant positive correlation between height above the ground and shrub/tree height (r=0.36, p=0.004, n=63), and between visibility and accessibility (r=0.57, p<0.001, n=63). Nest shrubs/trees were significantly higher (t_{391}=4.68, p<0.001) and wider (t_{391}=4.41, p<0.001) than available shrubs/trees (Figure 4). Mean height from the ground for the total number of nests (1.43 m, as stated above) was significantly greater than mean HWE height from the ground (0.67±0.22 m, range=0.10–1.15 m, n=201) (t_{262}=13.03, p<0.001).

[Insert Table 2]

[Insert Figure 4]

There was no significant combined relationship of season (month in which nest construction was completed; April–May vs. June–July) and breeding performance (successful vs. unsuccessful nests) with mean nest height above the ground ($TWF_{1,51}$=1.76, p=0.19), but there were seasonal differences when grouping successful and unsuccessful nests together ($TWF_{1,51}$=4.46, p=0.04; 1.33 m in April–May, 1.79 m in June–July). There were no differences between successful and unsuccessful nests when grouping seasons together ($TWF_{1,51}$=2.36, p=0.13; 1.26 and 1.58 m, respectively).

Nest traits

The mean dry mass of all the weighed nests (n=34) was 15.50±4.37 g (CV=28%), with no significant difference in the mean of this parameter between newly built nests and nests having contained nestlings (Table 3). The difference in mean weight between nests completed in April–May (15.13±4.92 g, range=9.0–26.0 g, n=21) and June–July (15.97±3.50 g, range=9.0–22.5 g, n=12) was not significant either (t_{31}=-0.51, p=0.61). Considering the two years with the largest sample size (2002: 7 nests; 2003: 14 nests), and without differentiating between months, there were no significant interannual differences in mean nest weight (2002: 16.13±2.03 g, 2003: 15.29±5.72 g; t_{19}=0.37, p=0.71).

[Insert Table 3]

For total nests, the CV in external width was 12% (at both shortest and longest axis), 9% in internal width (at both shortest and longest axis), 13% in external height, and 16% in internal depth (Table 3). Nests containing nestlings had a significantly greater mean external and internal width than newly built ones; however, there were no significant differences between the two types of nest in mean external height or internal depth (Table 3). Compared with nests in Britain, those in the study area as a whole were similar in weight, had smaller horizontal dimensions (widths), except for the similar external width at the longest axis, and greater vertical dimensions (external height and internal depth) (Table 3). There was no significant correlation between nest external height and weight (r=0.31, p=0.80, n=32), but there was between nest mean external width and weight (r=0.36, p=0.04, n=32), and a closer correlation between nest volume and weight (r=0.55, p=0.001, n=32). There was no significant correlation between nest mean internal width and clutch size (r=-0.20, p=0.36, n=24), or between nest volume and clutch size (r=-0.22, p=0.31, n=24), considering all nests for which these parameters were available. The volume of successful nests (306.10±55.68 cm^3, range=196.35–394.85 cm^3, n=17) was significantly higher than unsuccessful nests (260.62±68.20 cm^3, range=180.96–448.71 cm^3, n=22) (t_{37}=2.23, p=0.03).

Overall, the outer part of the nest was not tightly packed. It was mostly composed of loosely intertwined twigs and some herbaceous shoots, whereas the internal cup was comprised principally of tightly rolled and interwoven thin roots and herbaceous shoots (Figure 5). Considering the weight of nests by region, 10.81±3.82 g (CV=35%, n=23 nests selected for the building material analysis) corresponded to the outer nest and 4.06±1.47 g (CV=36%, n=23) to the internal cup. The outer nest accounted for over 65% of the total weight in 78.3% (18 of 23) of the nests. There were no significant differences between the mean outer nest weight of nests completed in April–May (10.34±4.39 g, n=15) and those completed in June–July (11.67±2.43 g, n=8) (t_{21}=-0.79, p=0.44), or mean internal cup weight (April–May: 3.92±1.68 g, n=15; June–July: 4.34±1.00 g, n=8; t_{21}=-0.65, p=0.52). Considering average percentages, seasonal differences in the contribution of each region in terms of weight were not significant either (outer nest: April–May: 71.5±12.1%, n=15, June–July: 72.6±5.7%, n=8; internal cup: April–May: 28.5±12.1%, n=15, June–July: 27.4±5.7%, n=8; t_{21}=0.25, p=0.80 for both regions). Considering the two years with the largest sample size (2002: 7 nests; 2003: 10 nests), and without differentiating between months, there were no significant interannual differences in the mean percentage of the weight of each region (outer nest: 2002: 72.6±11.4%, 2003: 76.2±9.3%; internal cup: 2002: 27.4±11.4%, 2003: 23.8.±9.3%; t_{15}=0.72, p=0.48 for both).

[Insert Figure 5]

All of the considered fractions appeared in over 90% (21 of 23) of the nests, and only leaves were missing in the other two. Regarding quantitative importance of fractions within each region, outer nest consisted mainly of twigs, averaging 82% (CV=10%) by weight, and secondarily herbaceous shoots (13%, CV=65%), the remaining fractions being much less used (<3% each), whereas internal cup consisted mainly of roots (53%, CV=31%) and herbaceous shoots (27%, CV=59%), with relatively low importance of twigs (8%, CV=75%) and hair (7%, CV=117%) and very low importance of the other fractions (<3% each) (Figures 6 and 7). The contribution of hair to the internal cup was very variable throughout the breeding season, but there were no significant differences between the mean weight of this fraction in April–May internal cups (0.28±0.38 g, CV=135%, *n*=15) and in June–July internal cups (0.29±0.24 g, CV=81%, *n*=8) (t_{21}=-0.08, *p*=0.94).

[Insert Figure 6]

[Insert Figure 7]

All of the twigs used to construct the outer nest and internal cup belonged to eudicot species, with no gymnosperm twigs being found. Taxa identified for outer nest in order of frequency of occurrence were as follows: *Lonicera periclymenum* (74% of nests), *Rosa* spp. (70%), *Crataegus monogyna* (26%), *Prunus spinosa* (26%), *Rubus* spp. (17%), and to a lesser extent, *Salix* spp., *Quercus pyrenaica*, *Berberis vulgaris* and *Viburnum opulus*. Most of the twigs were thornless, some thorny or prickly types less frequently being found. In the outer nest, their mean length was 11.48±2.86 cm (*n*=40, range=6.0–18.0 cm) and mean width 1.34±0.35 mm (*n*=40, range=0.82–2.61 mm), and they were usually curved or with short ramifications. Roots were not identified. Generally, they were thin, long, twisted, and easy to use to achieve the round shape of the cup. Herbaceous shoots were mainly from eudicot species and hardly any grasses (Poaceae) were found. Only *Galium* stems, *Bryonia dioica* tendrils and crucifer stems were identified among the remains. Amongst whole leaves and leaf parts, the following taxa were recognised: *Rosa* spp. (occurring in 30% of outer nests), *Crataegus monogyna* (22% of both outer nests and internal cups), and to a lesser extent, *Euonymus europaeus*, *Quercus* spp., *Rubus* spp. and *Ligustrum vulgare*. Other vegetal remains included Salicaceae empty capsules and seed wool in 17% of outer nests, and occasionally, small pieces of moss, lichen and bark.

Hair was the only material of animal origin found in all of the nests, normally accounting for more weight in internal cup than outer nest. The mean and maximum length of the hairs used to construct the outer nest (4.96±1.27 cm, range=3.0–8.5 cm, *n*=23; 12.74±6.99 cm, range=4.0–33.0 cm, *n*=23) were significantly lower, respectively, than those of the internal cup (12.46±6.98 cm, range=3.5–26.0 cm, *n*=22; 38.23±28.06 cm, range=6.0–112.0 cm, *n*=22; t_{43}=-5.07, *p*<0.001 for mean length; t_{43}=-4.22, *p*<0.001 for maximum length). Considering the years with the largest sample sizes (2002: n=7 outer nests and 7 internal cups, 2003: *n*=10 outer nests and 9 internal cups), there were no significant interannual differences in the mean and maximum length of the hairs in both regions ($t_{14–15}$=0.27–1.48, *p*=0.16–0.79, depending on the case). Fine hairs were more commonly found in outer nests than internal cups (22 of 23 nests, 95.7% vs. 15 of 22 nests, 68.2%), the opposite occurring in the case of medium thickness (43.5% vs. 63.6%) and thick (21.7% vs. 81.8%) hairs (χ^2_2=8.27, *p*=0.01). Many of the hairs very likely belonged to domestic ungulates, and the very long (up to over 1 m), thick strong ones, rolled several times, typically found in the internal cup, were clearly horse hairs.

Discussion

Nest-site selection

Hedgerows and meadows, which make up the more prevalent landscape component in the study area, surrounded all of the nests and most of them were supported by hedges, that is, bullfinches consistently used the general woody vegetation available as reproduction habitat/site. Also, poplar plantations frequently appeared in the area surrounding the nests, although none were built directly in a poplar tree within a plantation. Partly reflecting these results, bullfinches selected areas with higher shrub and tree cover than was available, the pattern of cover distribution around the nests being maintained from year to year. Several nests belonging to different pairs concentrated in defined spots characterised by high woody vegetation cover mainly due to high hedgerow density –length/area–, brushwood and/or poplar plantations, even in consecutive years (ÁH, pers. obs.). In non-colonial passerine species, several pairs can coincide in a small area when selecting the most suitable places in patchy environments or for other reasons such as conspecific attraction.[55] One bullfinch nest was found in the same hedge and practically the same place in three different years (2002, 2004 and 2005), supported mainly by hawthorn branches, and was successful in all three cases. Interannual breeding-site fidelity is common in passerines, particularly if nesting was successful the previous year.[5,56] Bullfinches occupy a broad spectrum of wooded habitats during the breeding season in the Iberian Peninsula and the rest of their geographic range, including mosaics of mixed land use in which hedgerows with large shrubs and trees are an important part and provide appropriate support structure for nests.[8,35,57-59] In the study area and surroundings, bullfinches did not construct their nests in oak woods on the valley slopes, presumably because they are quite dry and have little undergrowth cover, preferring the bottom of the main valley and small transverse ones (ÁH, pers. obs.).

Although not statistically significant, mean herb cover decreased by approximately 7% and mean tree cover increased by 7.5% between April–May and June–July bullfinch nests, that is, there appeared to be a propensity towards increasing the use of more wooded and shadier nest-zones as the breeding season progressed, which was quite significant when considering habitat selection by juvenile and adult individuals, probably because they provide more shelter (a much-needed requirement during post-fledging and moult periods), food and shade in summertime.[43] In other passerines, particularly multi-brooded species, seasonal variations have also been observed in nest habitat, coinciding with temporary changes in habitat resource availability and distribution.[17]

In the study area, bullfinches placed their nests in a very wide variety of plant species, but showed great preference for thorny shrubs. Countless plant species of different types support the nests of this fringillid within its wide distribution range, including Iberia, usually typical shrubs and trees preferentially thick, perennial or deciduous, conifer or broadleaf, climbing or non-climbing, thorny or sharp-leaved species being relatively preponderant.[35,36,40,41] Many small passerine bird species use and even positively select thorny plants as nest support, especially dense *Rubus* brambles, both in the study valley (e.g. *Lanius* shrikes, long-tailed tits *Aegithalos caudatus*)[60,61] and worldwide.[19,22] Few HWEs supported nests partly due to the fact that they are used to close gaps in thinner hedges, and bullfinches positively selected wider ones, or that they preferred to nest in higher places from the ground than HWEs, several of which had already deteriorated and fallen somewhat (ÁH, pers. obs.). The most predominant bullfinch nest orientations probably provided thermal benefits and protected from severe weather. *Lanius* shrikes also preferred E to W and S to N orientations in the study valley.[60] The predilection of birds for certain nest orientations, which can vary considerably depending on different factors including the climate of the region and timing of breeding, has often been demonstrated.[2,4,18]

In agreement with our findings, bullfinches generally construct their nests at mean heights of between 1 and 2 m above the ground, so values close to 5 m are rare and anything clearly higher, exceptional.[35,36,38,40] In the study area, this parameter increased as the breeding season progressed. The height of bird nests from the ground can vary seasonally, and, in fact, in other passerine species, including the yellowhammer *Emberiza citrinella*, a characteristic songbird in hedgerows in Europe, it increases progressively from spring to summer, earlier nests being constructed at lower heights for protection against weather extremes.[4,16]

The present study confirms bullfinches' preference for taller, wider shrubs/trees, arguably to conceal their nests well, which has already been suggested by other authors.[35,36,62] Similarity between mean plant height where breeding was recorded in the study area (4.1 m) and that in an area in England (4.5 m)[62] should be underlined. Apart from the presence/abundance of trees, hedge size is a crucial factor positively associated with species richness and abundance of breeding birds in hedgerows, as it is related to food and nest-site supply.[10,62] Although the spring–summer diet of bullfinches was largely composed of herb seeds, hedgerow shrubs and trees provided them with other plant and animal food sources during this period (ÁH, unpubl. data).

Nesting success was unrelated, statistically, to most nest-habitat and nest-site features, with the exception of occurrence of thorny plants supporting the nest and orientation within the shrub/tree acting in combination. Several authors have also found no association between nest success and nest-placement characteristics in other passerine species, attributing this to a number of causes, including very high predation, due to a diversity of predators, not avoidable by breeding-site selection, or previous occupation of microhabitats with comparatively lower predation risk which outweighs later analyses.[18,24,25,63] In contrast, in some scenarios where less favourable microhabitats are occupied, nesting success may be associated with nest-site features.[25] In the study area, overall bullfinch nesting success was low, slightly higher than 35% of nests, mainly due to the effect of a rich community of proven and potential predators.[42] Moreover, bullfinches showed a strong predilection, resulting in extensive use, towards seemingly favourable nest-site traits against predators, including immediate surroundings with high shrub and tree cover, thorny plants as nest support, tall wide nest shrubs/trees, and places that are relatively inconspicuous and difficult to access, or against disadvantageous weather conditions such as appropriate nest orientations. Some authors have related these traits with an increase in breeding success of passerines.[19,26-28] A tendency towards greater success was observed for almost all of these apparently favourable nest-site features in bullfinches, although not significantly for several of them.

Bullfinch nesting success tended to gradually increase between spring and summer according to a parallel study, which has been explained by environmental seasonality, that is, lower predation pressure (decreasing predator density, increasing foliage density) and better weather conditions.[42] In this connection, spatial characteristics studied in this paper that possibly favour nest success (tree cover, thorny plants as nest support, nest-shrub/tree width) tended to be reinforced in June–July. Nest height from the ground increased as the breeding season progressed, but this parameter was not significantly associated with nest success; perhaps the difference in height, less than half a metre between the mean for April–May and June–July, made no difference to the impact of predators. Finch species that nest low, for instance the bullfinch, suffer higher predation than those nesting noticeably higher, because they are vulnerable to more predator species.[29] Nevertheless, for a given passerine species, nesting at a greater height from the ground does not necessarily imply greater nest survival, even though it shows a preference for high nest sites.[25]

Nest traits

The estimated external dimensions of bullfinch nests from the study area are slightly larger than in NE Iberia, but the internal dimensions are similar, according to values provided for an undetermined but probably very low number of nests from the Spanish Pyrenees (external width=10.0–11.0 cm, internal width=all 6.5 cm, external height=5.5–6.0 cm, internal depth=3.0–3.5 cm).[40] Comparing size ranges of nests from the study area with size variation in nests from the western Palearctic,[35,64] values overlap considerably, with external width and external height showing very wide ranges. Similarity in average weight and external width at the longest axis between total nests in the Iberian subspecies (*iberiae*) and British subspecies (*pileata*) is probably due to the fact that they are similar in size.[35,65] Clear positive correlations have been observed between body mass and nest dimensions in passerine birds including finches.[4,14] Differences in some nest dimensions could partly depend on whether they housed nestlings or not, particular nest supports and/or construction materials used, or even measurement biases associated with the researcher.

Internal width was the least variable linear dimension of bullfinch nests according to its CV, coinciding with the results reported for nests of this species in Britain,[14] whereas external dimensions were, in comparison, relatively variable, presumably due to the need to fit the nest into smaller or larger spaces or to attach it to more or less robust branches, adapting the width and height of the structural layer to the corresponding nest support but keeping the diameter of the inner cup stable to properly accommodate the incubating female, eggs and nestlings. Normally, birds in general build their nests from the inside, shaping the cup with body movements and making it a perfect fit for the incubating parents,[22,66] as we have personally witnessed. In the study area, some exceptionally large and heavy bullfinch nests (≈25 g) were built in the middle of very open fragile structures (ÁH, pers. obs.). In finches in general and other passerine birds, nest external dimensions usually show more variability than internal dimensions.[14]

Nests constructed in June–July were no lighter than those constructed in April–May. Therefore, if later nests were built in fewer days to adjust optimal reproduction time,[42] they did not weigh less as a result. It has been verified in other European small passerine birds –some tit (Paridae) species and the long-tailed tit (Aegithalidae)– that females usually construct their nests more rapidly as the season advances, with a decrease in total nest mass in some cases, but not in others.[15,67,68] In all cases, temperatures experienced by females during nest construction are inversely related to total nest mass, irrespective of the laying date, probably to maintain an optimal microclimate for the developing embryos and nestlings.[15,20,67] Tit and long-tailed tit breeding season is relatively short (March–May) but much longer in the case of bullfinches (April–August), therefore ambient temperature must clearly increase with laying date in the latter. The apparent lack of association between air temperature and nest weight in bullfinches is discussed below in relation to building materials. Nests occupied by chicks were significantly wider internally and externally than newly built ones, presumably because older heavier and more mobile nestlings can deform the nest to a certain degree.

Larger nests did not contain larger clutches, despite the fact that these two characteristics generally have a positive correlation in both open-nesting and hole-nesting bird species, suggesting plasticity of clutch size in response to nest size.[4,30] Nevertheless, the results obtained in this study for bullfinch should be considered with caution, as the contribution of newly constructed nests, before the chicks could alter their width, to sample size was very small (five nests). Successful nests were larger than unsuccessful ones, which contradicts findings by several authors who state that when nest size increases in some passerine bird species, the likelihood that they will be discovered by predators also increases and incubation efficiency decreases, especially in open-nesters.[2,4,33,34] However, it has been verified for open-cup nesting passerines inhabiting a given area that predation can differ between species-specific nest sites, but not between large and small nests.[69] The role of nest mass in determining the success of incubation and/or rearing in songbirds has yet to be clarified.[22] Also, nest size can reflect individual phenotypic condition in passerine birds, as nest construction is an expensive process; thus, high-quality males or females (i.e. older and more experienced and/or those with better body condition) build larger nests which result in greater breeding success.[2,31,32] Perhaps large bullfinch nests adapted to very open fragile supporting structures, apparently more difficult to construct, belonged to high-quality expert females.

The general design of bullfinch nests in the study area was similar to that described for other subspecies in Europe, basically an uneven structural layer of dry twigs (outer nest) and a very differentiated internal lining of dry, fine materials such as rootlets, herbs, and hair (internal cup), fresh green vegetation and feathers not being used.[14,35,37] The majority of avian nests are constructed from a variety of materials which can generally be classified as being either structural, the function of which is still not clear, but could probably be multiple (physical support, thermoregulation, camouflage), or lining, with an undoubted thermoregulatory role.[2,4,22] Therefore, bullfinch nests are extremely simple and, together with hawfinch *Coccothraustes coccothraustes* nests, are built using the smallest variety of type of material amongst European finches, especially the outer nest, which may reflect nest location or the particular characteristics of the materials used.[14]

The outer nests analysed were constructed with twigs belonging to at least 9 of the 26 (35%) shrub, tree and climber species in hedgerows, although they were difficult to identify visually; in addition, dry *Ulmus minor* twigs were cut directly from the tree by a female and then transported (ÁH, pers. obs). Other authors report a majority of twigs used from both broadleaf (both thorny and thornless) and conifer species in bullfinch outer nests, depending on the floristic composition of each nesting zone.[35,40,64] It seems normal for bullfinches to collect dry twigs in trees rather than from the ground.[35,64] Information available on the taxonomic identity of the plants used by bullfinches for nest building is generally scarce, but presumably very diverse in their wide distribution range as they are considered generalist forest birds that occupy all types of shrub/tree formations.[35,65]

Composition of avian nests is a species-specific characteristic in terms of fraction types involved, but reports suggest that birds are opportunistic in their use of materials within each type, as long as they have the right dimensions and properties (e.g. diameter, mass, flexibility) for the nest region being constructed at the time.[13,14,70,71] Relatively little is known about nest-construction behaviour in birds, including the bullfinch, in the natural environment, but the structure and composition of this finch nest indicates that first it builds the outer nest, a strong platform and side walls, with significantly thicker materials than the internal cup, which is constructed subsequently.[37] Direct observations in the study area support this idea, since the most rigid and thickest material (twigs) was collected preferably at the start of nest construction and the softest and thinnest material (e.g. herbs) towards the end.[42] Twig mean length of the outer nests was somewhat longer than that estimated for outer nests of British bullfinches (approx. 11.5 cm vs. 8.0 cm) but mean width was very similar (approx. 1.3 mm in both cases).[37] The considerable robustness of the twigs used in the outer nest, especially at the base, could be because they are normally constructed on outer branches, with weak support from underneath, away from a trunk or a large branch.[70] Similarly, many nests were placed on relatively thin branches in shrubs without well-defined trunks in the study area (ÁH, pers. obs.).

Herbaceous shoots, used largely in the internal cup, were mainly from eudicot species, in contrast with bullfinch nests in other parts of Europe with a predominance of grasses,[14,35,37,64] perhaps due to the combination of habitat components. Only on hedgerow edges, April–August vegetation samplings revealed a total of 44 herb taxa in the study area, mostly eudicot, potential forest species.[47] All European finches, including bullfinches, use leaves to construct the outer nest and internal cup, but in a low proportion,[14] in agreement with the present study.

Hairs were found in all of the nests, and those in the internal cup were longer, wider and contributed more mass. However, their relative importance within this region showed very high variability throughout the breeding season. Although they are a common construction material in the nests of this fringilid species, they are not always present.[14,36,40,64] About three quarters of European passerines regularly use hair as nest material, and its availability during building, at least in recent times, can depend on the presence of domestic livestock in the surroundings.[15] In the study area, populations of domestic ungulates (cattle, sheep, horses) were small and farmers frequently moved them from one plot to another (ÁH, pers. obs.), but bullfinches apparently used their hairs regularly during the breeding season in all years.

In European passerines, the varying compositions of the outer nest may play a role in camouflage, arthropod silk, moss and lichen being relatively common materials in the outer layers of finch nests, except bullfinch and hawfinch,[14] in line with our findings. It has been demonstrated that songbirds build camouflaged nests and that materials such as lichen and spider cocoons may reduce the visual detectability of nests by predators.[72-74] Maybe the inconspicuous colour of outer nest and characteristics of nest sites chosen by bullfinches, e.g. tall wide nest plants and immediate surroundings with high shrub/tree cover, enable sufficient concealment and special camouflage materials need not be added to the nests.

As in the case of the entire nest weight, the general variation in weight of the outer nest and internal cup was moderate and there were no significant temporal differences in their relative contribution, outer nest accounting for some three quarters of the total nest mass. In certain European parid and aegithalid species, relative mass of nest regions does not usually change between years or, in some cases, during the breeding season, but as a general rule, the relative contribution of cup lining material (feather fraction in the case of long-tailed tit domed nests) decreases as ambient temperature increases.[15,20,67,68] Unlike bullfinches and hawfinches, most European fringilids normally use feathers and, in comparison, much more hair in the cup lining,[14] as we have personally observed. In the study area, the absence of feathers in bullfinch nests cannot be attributed to low availability of this material since, as a very clear example, breeding density of long-tailed tits is high[61] and they construct their nests with a huge quantity of feathers (ÁH, pers. obs.). Animal-derived materials, especially feathers, and moss provide the best thermal insulation.[75-78] Perhaps bullfinches do not need to seasonally regulate the total mass of their nests or the relative importance of their different regions due to the low contribution of animal materials and insignificance of moss. Also, mean weight of hair fraction hardly varied seasonally in the nests in the study area. Measurements obtained by infrared thermography and temperature loggers showed that insulation of bullfinch nests is low in contrast to that of most European songbirds.[78-80] The mud cup in *Turdus* thrush nests is a good insulator.[80] Also, among open-nesters the risk of predation is expected to reach a very high level with the visual cue of even a few feathers and, in fact, they use them less than hole-nesters like parids; nevertheless, both circumstances, cavity-nesting and use of feathers, increase the risk of hyperthermia during the late nestling period.[75]

Roots, herbaceous stems and some hair in cup lining of bullfinch nests may not provide as great thermal insulation as feathers and moss but may still provide enough, as well as a softer substrate than twigs. Small-sized bird species have feathers in their nests more often than large-sized ones, presumably because they have higher metabolic demands due to their proportionately larger surface.[75] Nevertheless, songbirds as small as European robins *Erithacus rubecula* appear to be able to use plant-derived, mainly leaves in this species, rather than animal-derived materials to effectively insulate their nests.[81] Also, the particular features of the nest sites preferred by bullfinches, e.g. favourable orientations, probably create a comfortable nest microclimate. Moreover, the construction of austere nests can provide advantages, including savings in the energetic cost of this activity and an easier replacement following a loss.[2,82]

Conclusion

Bullfinches used and selected breeding habitat at different spatial scales, 1) occupying the bottom of the valley, which is cooler and provides adequate shrubby vegetation alternating with meadows, the latter being important for foraging, 2) selecting places with higher shrub and tree cover, 3) constructing nests mainly in wider and taller hedges, 4) preferring thorny plant species as direct support for their nests, and 5) placing the bulk of their nests facing S or W or in a centered position. Generally, there were no significant temporal variations in nest-site selection, except that they were higher from the ground in June–July than April–May. Neither was there a significant association between each of the bullfinch nest-site characteristics and nest success, presumably because most of the nests were already located in the most appropriate places at each time and because, despite this, predation pressure was high. However, a joint effect of the occurrence of thorny supports and orientation on nesting success was found. Bullfinch nests were simple in structure and composition, made up principally of plant-derived materials, without feathers and with a modest amount of hair, but apparently efficient in providing, to the extent necessary, an optimum microclimate and safe place for parents and offspring. The preservation of this outstanding hedgerow network, without cutting hedges excessively, would continue to provide bullfinches with a suitable breeding habitat, numerous nest sites and sufficient nest materials.

Acknowledgements

We wish to thank José Luis Robles for his valuable comments on the submitted version of the manuscript and the two anonymous referees for their helpful suggestions for improvement of the manuscript in the review process. This paper is a research contribution of the Ecology and Conservation of Flora and Fauna Group at Valladolid University, Spain.

Declaration of conflicting interests

The authors declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

Funding

The authors received no financial support for the research, authorship, and/or publication of this article.

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Table 1. Frequency of occurrence and selection of plant species for nest support by Iberian bullfinches in NW Spain, considering individual plants in direct contact with the nest. (t): typical thorny species, (c): typical climbing species. More than one plant species could be used to support each nest. Frequency of occurrence: proportion of nests supported by each plant species. Use: proportion of each used plant species in relation to total nest support occurrences (*n*=127). Availability: proportion of each plant species in relation to the total occurrences of all plant species in the habitat (*n*=1817). Selection index (*S*: Jacobs' index) varies between -1 (maximum negative selection) and 1 (maximum positive selection), with a value 0 if selection does not occur (i.e. nests were supported by the plant species according to its availability).[51] In bold: moderate positive selection (0.21 to 0.50). In italics: moderate negative selection (-0.21 to -0.50). In italics and underlined: strong negative selection (-0.51 to -1). Only values for plant species of certain importance are highlighted: %*n*≥5, for their use, availability or both. The nests were located during 2001–2005. See Methods for details on availability assessment.

Plant	Frequency of occurrence (%*n*)	Selection analysis		
		Use (%*n*)	Availability (%*n*)	Selection (*S*)
Rubus spp. (t)	33.3	16.5	16.2	0.01
Prunus spinosa (t)	28.6	14.2	8.0	**0.31**
Rosa spp. (t)	27.0	13.4	10.1	0.16
Crataegus monogyna (t)	25.4	12.6	6.9	**0.32**
Ligustrum vulgare	23.8	11.8	9.7	0.11
Hedera helix (c)	14.3	7.1	4.6	**0.23**
Viburnum opulus	12.7	6.3	6.0	0.02
Salix spp.	6.3	3.1	3.2	-0.02
Ulmus minor	6.3	3.1	5.3	*-0.27*
Euonymus europaeus	4.8	2.3	5.1	*-0.39*
Lonicera periclymenum (c)	3.2	1.6	1.5	0.03
Populus spp.	3.2	1.6	5.0	<u>*-0.53*</u>
Corylus avellana	3.2	1.6	5.9	<u>*-0.59*</u>
Ribes uva-crispa (t)	1.6	0.8	0.2	0.60
Malus spp.	1.6	0.8	0.3	0.46
Sambucus nigra	1.6	0.8	0.7	0.07
Quercus pyrenaica	1.6	0.8	0.8	0.00
Prunus avium	1.6	0.8	0.8	0.00
Fraxinus excelsior	1.6	0.8	1.05	-0.14
Pyrus communis	0.0	0.0	0.05	-1
Juglans regia	0.0	0.0	0.2	-1
Rhamnus cathartica (t)	0.0	0.0	0.2	-1
Humulus lupulus (c)	0.0	0.0	0.2	-1
Solanum dulcamara (c)	0.0	0.0	0.2	-1
Bryonia dioica (c)	0.0	0.0	0.9	-1
Cornus sanguinea	0.0	0.0	6.9	<u>*-1*</u>
n (number of nests)	63			
n (number of occurrences)		127	1817	

Table 2. Location characteristics of Iberian bullfinch nests in NW Spain, considering the month when construction was completed (April–May, June–July), successful (observed nests that fledge at least one young) versus unsuccessful nests, and year. Heights and widths are in metres. Nest visibility varies between 1 (clearly visible) and 5 (not visible). Nest accessibility varies between 1 (easily accessible) and 5 (hardly accessible). n: number of nests with sufficient information in each case. Pooled data for 2001–2005, if the year is not specified. [a] Comparing only 2002 with 2003 (largest sample sizes): t=0.41, df=36, nsd. t: two-tailed t-test; F: ANOVA, one-way, independent samples; *: p<0.05; nsd: non-significant difference (p>0.05). See Methods for details on nest location assessment.

Nest location	April–May nests			June–July nests			Difference between means
	Mean ± SD	*n*	Range	Mean ± SD	*n*	Range	
Height above the ground	1.33 ± 0.67	39	0.60–3.96	1.79 ± 0.92	16	1.00–4.10	t=-2.07, df=53, *
Shrub/tree height	4.47 ± 2.84	39	1.10–12.00	3.30 ± 1.05	16	1.90–5.50	t=1.61, df=53, nsd
Shrub/tree width	2.32 ± 1.32	39	0.75–6.00	3.72 ± 5.07	16	1.00–22.50	t=-1.63, df=53, nsd
Nest visibility	3.18 ± 1.25	39	1.0–5.0	3.31 ± 1.05	16	2.0–5.0	t=-0.37, df=53, nsd
Nest accessibility	2.53 ± 1.22	39	1.0–4.5	2.88 ± 1.17	16	1.0–5.0	t=-0.97, df=53, nsd

	Successful nests			Unsuccessful nests			
	Mean ± SD	*n*	Range	Mean ± SD	*n*	Range	
Height above the ground	1.26 ± 0.58	20	0.60–3.45	1.58 ± 0.84	35	0.66–4.10	t=-1.48, df=53, nsd
Shrub/tree height	3.34 ± 1.88	20	1.25–9.50	4.52 ± 2.71	35	1.10–12.00	t=-1.72, df=53, nsd
Shrub/tree width	3.08 ± 4.67	20	0.80–22.50	2.55 ± 1.27	35	0.75–6.00	t=0.63, df=53, nsd
Nest visibility	3.18 ± 1.29	20	1.0–5.0	3.19 ± 1.16	35	1.0–5.0	t=-0.03, df=53, nsd
Nest accessibility	2.58 ± 1.29	20	1.0–5.0	2.59 ± 1.14	35	1.0–4.5	t=-0.03, df=53, nsd

	2001	2002	2003	2004	2005	
	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD	
[a] Height above the ground	1.24 ± 0.75 *n*=6	1.49 ± 0.75 *n*=18	1.41 ± 0.44 *n*=20	1.53 ± 0.97 *n*=9	1.40 ± 1.01 *n*=10	F=0.17, df=4,58, nsd

Table 3. Weight and size traits of Iberian bullfinch nests in NW Spain, comparing newly built nests (they did not contain nestlings) with nests having contained nestlings (15 of the 19 nests containing nestlings were successful). Weights are in grams and other measurements in centimetres. Pooled data for 2001–2005. Also, subspecies *Pyrrhula p. iberiae* is compared with *P. p. pileata*.[14,37] n: number of species in nests in each case. *t*: two-tailed *t*-test. *: $p<0.05$. **: $p<0.01$. ***: $p<0.001$. nsd: non-significant difference ($p>0.05$).

Nest weight and size traits	Newly built nests (present study)			Nests having contained nestlings (present study)			Difference between means
	Mean ± SD	*n*	Range	Mean ± SD	*n*	Range	
Weight	15.08 ± 4.68	14	9.0–26.0	15.70 ± 4.33	19	9.0–24.5	*t*=-0.39, df=31, nsd
External width at the longest axis	11.64 ± 1.36	21	9.5–14.5	12.87 ± 1.43	19	11.0–16.5	*t*=-2.77, df=38, **
External width at the shortest axis	10.48 ± 1.36	21	8.0–13.0	11.16 ± 1.10	19	9.0–13.5	*t*=-1.72, df=38, nsd
Internal width at the longest axis	6.02 ± 0.30	21	5.5–6.5	6.95 ± 0.50	19	6.5–8.0	*t*=-7.23, df=38, ***
Internal width at the shortest axis	5.74 ± 0.35	21	5.0–6.5	6.35 ± 0.56	19	5.5–7.5	*t*=-4.25, df=38, ***
External height	7.93 ± 0.88	21	7.0–9.5	8.05 ± 1.27	19	6.0–10.5	*t*=-0.36, df=38, nsd
Internal depth	3.30 ± 0.47	21	2.5–4.5	3.36 ± 0.63	19	2.0–4.5	*t*=-0.33, df=38, nsd

	Total nests (present study) Spain, *Pyrrhula pyrrhula iberiae*		Total nests Britain, *Pyrrhula pyrrhula pileata*		
	Mean ± SD	*n*	Mean ± SD	*n*	
Weight 1	15.50 ± 4.37	34	14.70 ± 5.00[37]	13	*t*=0.54, df=45, nsd
Weight 2	15.50 ± 4.37	34	12.10 ± 4.60[14]	17	*t*=2.57, df=49, *
External width at the longest axis	12.22 ± 1.51	40	12.97 ± 2.34[14]	17	*t*=-1.45, df=55, nsd
External width at the shortest axis	10.80 ± 1.28	40	11.75 ± 1.96[14]	17	*t*=-2.17, df=55, *
Internal width at the longest axis	6.46 ± 0.61	40	8.08 ± 1.21[14]	17	*t*=-6.74, df=55, ***
Internal width at the shortest axis	6.03 ± 0.55	40	6.64 ± 0.81[14]	17	*t*=-3.31, df=55, **
External height	7.99 ± 1.07	40	4.68 ± 1.13[14]	17	*t*=10.51, df=55, ***
Internal depth	3.33 ± 0.55	40	2.26 ± 0.45[14]	17	*t*=7.07, df=55, ***

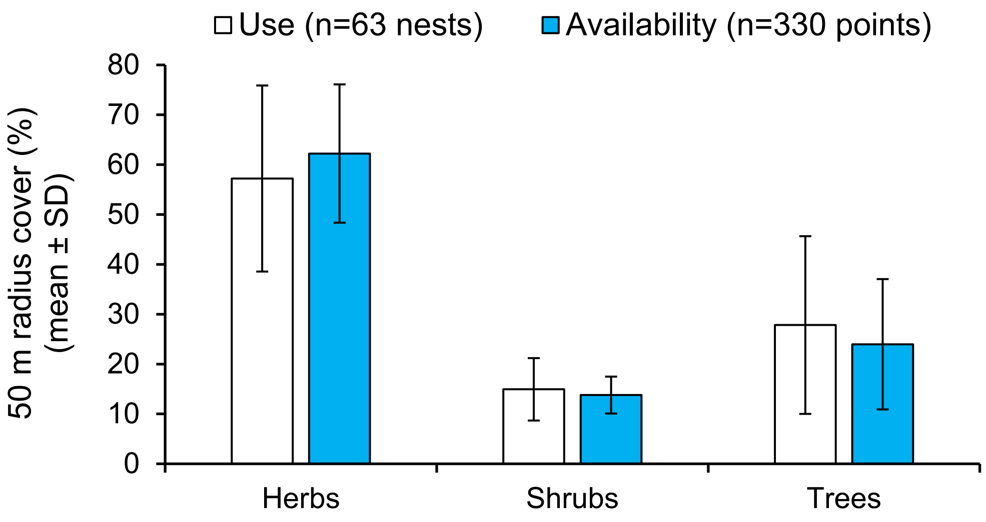

Figure 1. Proportion of area covered by vegetation strata around Iberian bullfinch nests compared with availability in the habitat, in NW Spain. Vegetation cover was estimated considering aerial view, that is, the sum of herb, shrub and tree cover is 100%. Sixty-three nests found during 2001–2005 were considered. See Methods for details on availability assessment.

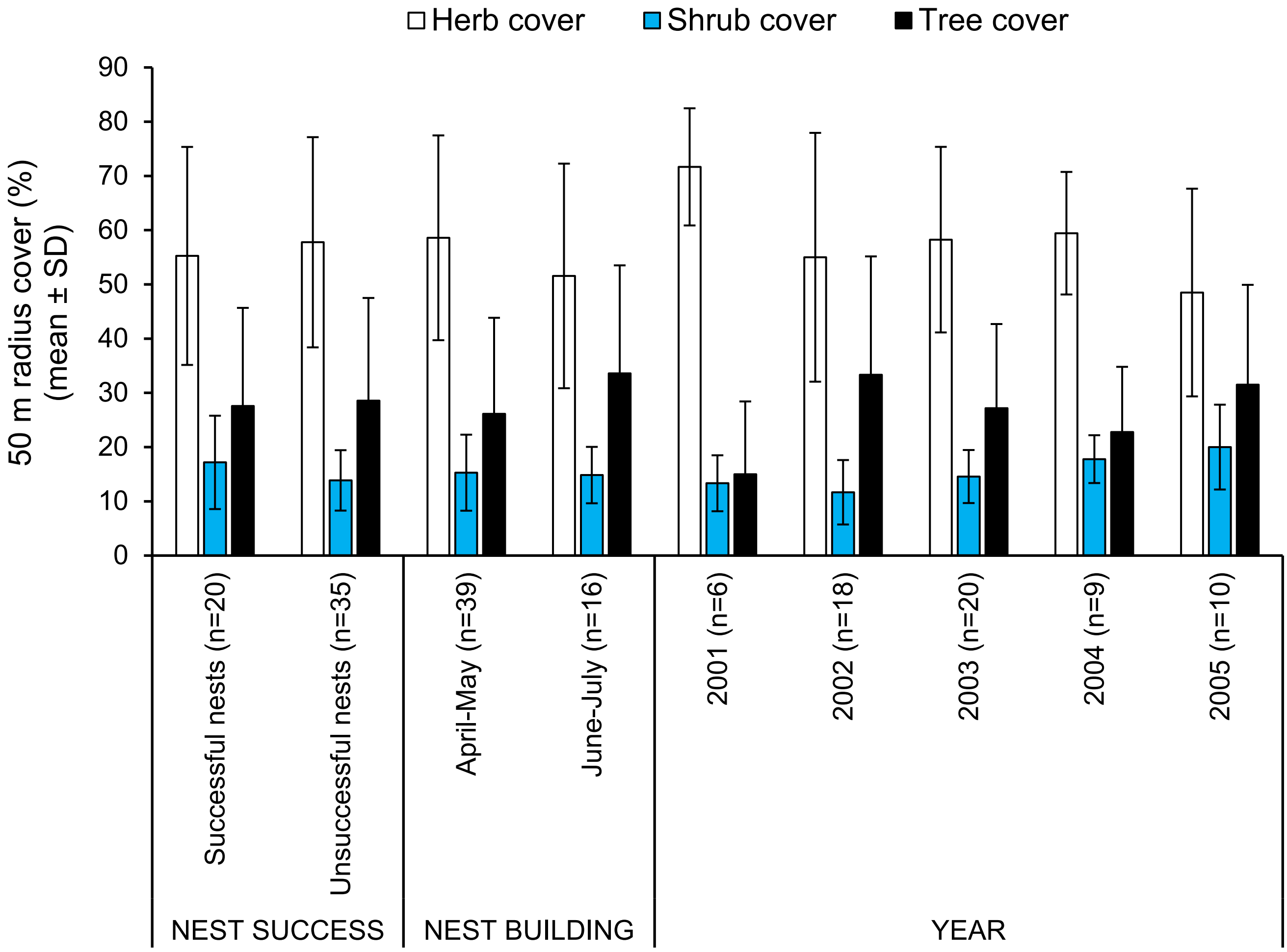

Figure 2. Proportion of area covered by vegetation strata around Iberian bullfinch nests considering successful (observed nests that fledge at least one young) versus unsuccessful nests, the month when they were completed (April–May, June–July), and year. Vegetation cover was estimated considering aerial view, that is, the sum of herb, shrub and tree cover is 100%. *n*: number of nests with sufficient information in each case. Pooled data for 2001–2005.

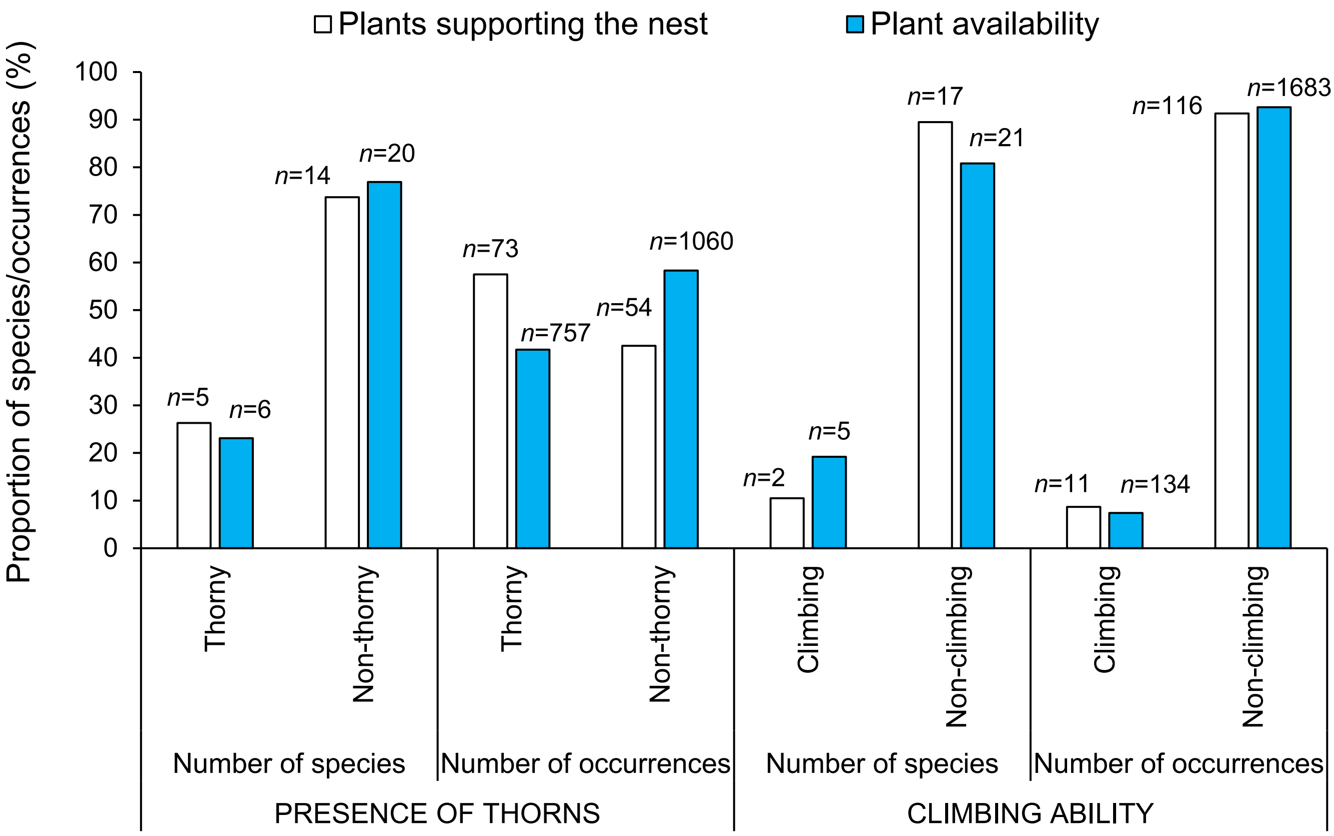

Figure 3. Importance of thorny/non-thorny and climbing/non-climbing plants as Iberian bullfinch nest support (individual plants in direct contact with the nest) in NW Spain, comparing with availability in the habitat. On the one hand, number of species used versus available species are considered, and on the other, number of occurrences of species used versus available species. Each nest could be supported by more than one plant species (63 nests, 19 total plant species supporting nests, 127 total occurrences, pooled data for 2001–2005). See Methods for details on availability assessment (330 hedge fragments, 26 total available plant species, 1817 total occurrences).

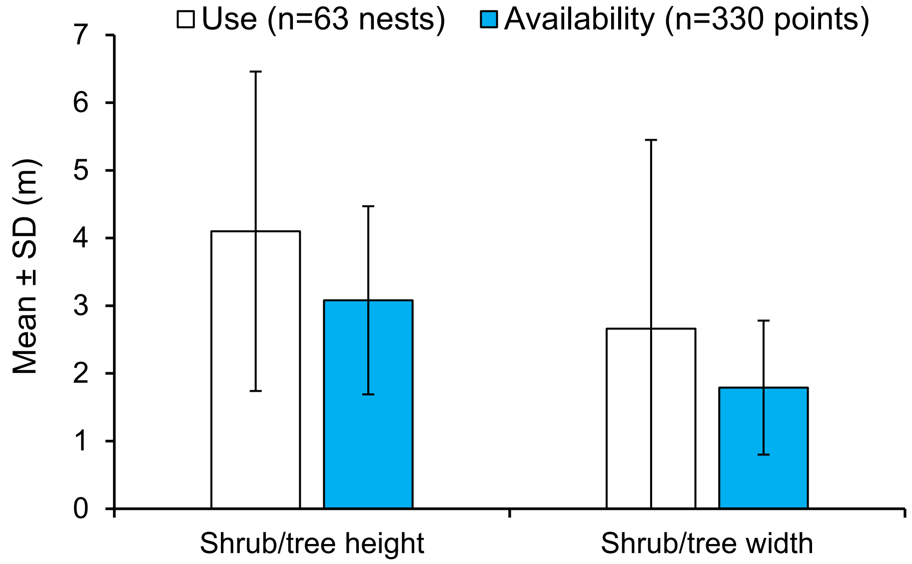

Figure 4. Height and width of the shrubs/trees where Iberian bullfinch nests were built compared with height and width of available shrubs/trees, in NW Spain. Pooled data for 2001–2005. See Methods for details on nest location and availability assessment.

A)

B)

C)

Figure 5. Iberian bullfinch nest. A) Top view of whole nest. B) Lateral view of whole nest highlighting the outer nest. C) Internal cup.

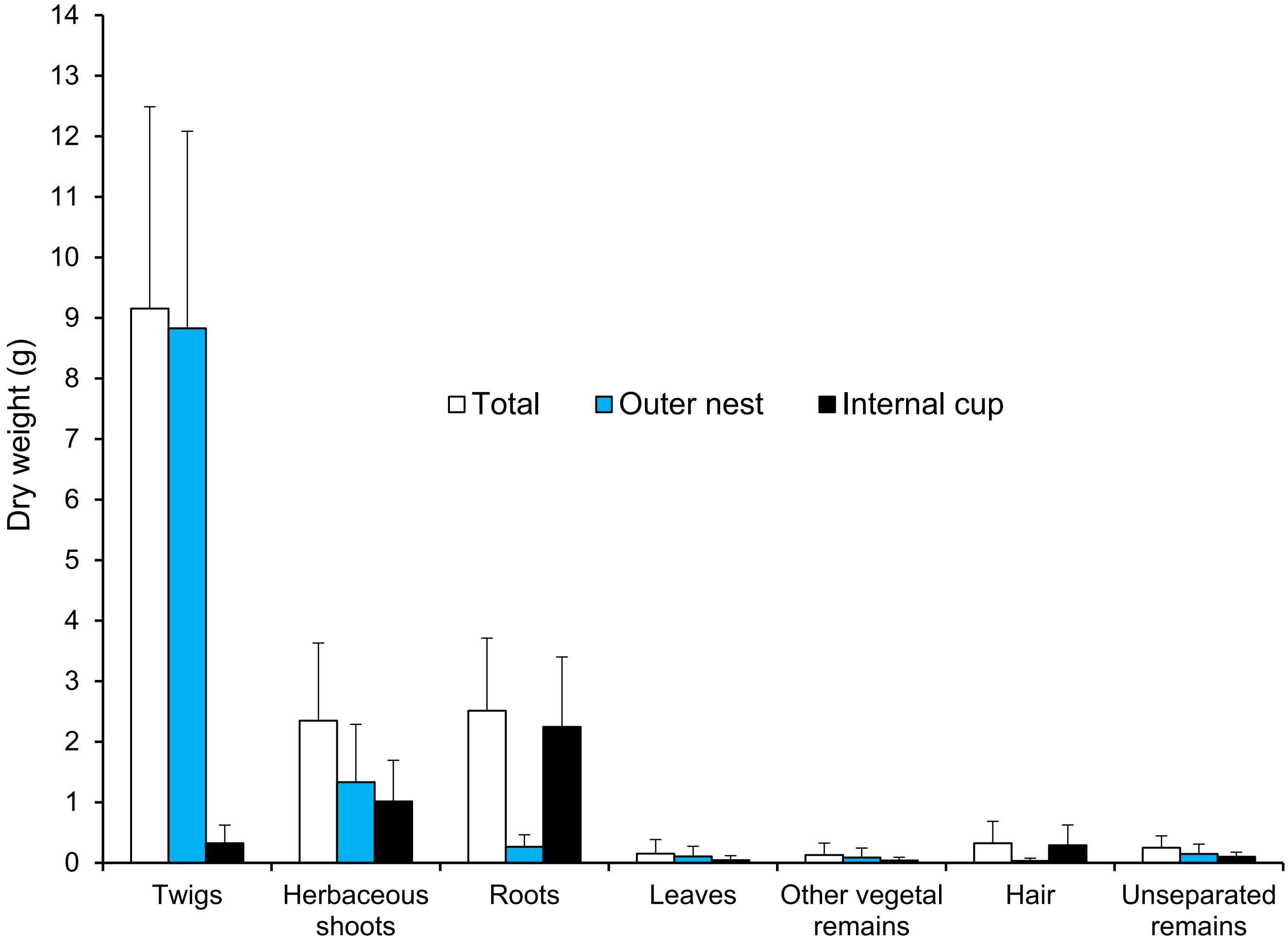

Figure 6. Mean dry weight and SD of different building materials in Iberian bullfinch nests in NW Spain. Pooled data for 23 nests built during 2001–2004.

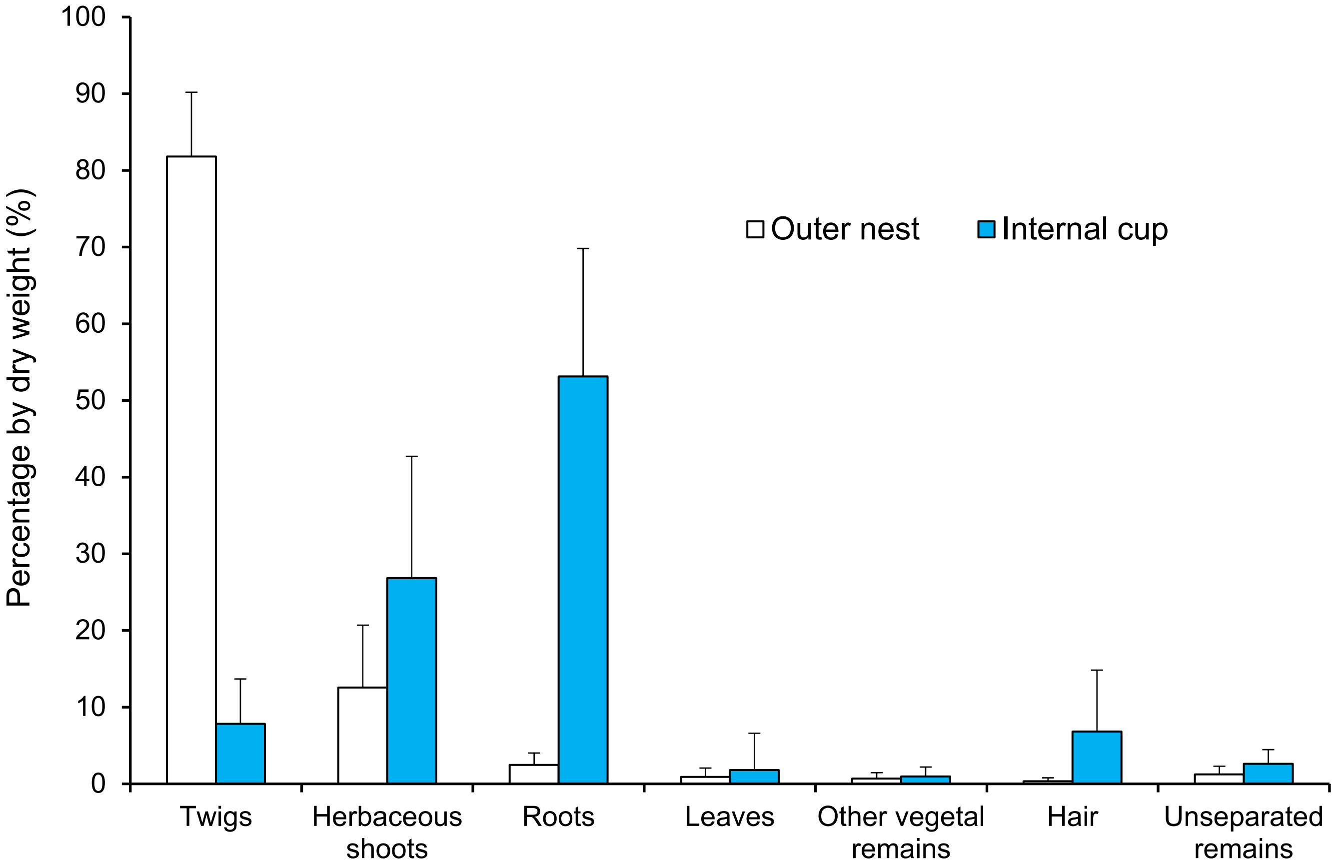

Figure 7. Mean percentage by dry weight and SD of different building materials in Iberian bullfinch nests in NW Spain. Pooled data for 23 nests built during 2001–2004.