TITLE:

Breeding ecology of Eurasian bullfinches *Pyrrhula pyrrhula* in an Iberian hedgerow habitat

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Abstract

The breeding ecology of the Iberian subspecies of the Eurasian bullfinch, *Pyrrhula pyrrhula iberiae*, is addressed for the first time. The studied population occupied a hedgerow habitat in northwestern Spain. Individuals directly watched in the study area and details of these sightings were recorded over a six-year period, and a total of 56 nests were monitored. The earliest date of nest building was within 11-30 April for all years. Fledglings were recorded leaving the nest during all the ten-day periods from the end of May to mid-August. Nest attendance, from the early building stage to when nestlings were ready to leave the nest, lasted approximately 36 days. The overall mean clutch size was 4.56 eggs. Clutch size decreased significantly at the end of the breeding season. For all egg traits, the minimum values for standard deviation were obtained in the intra-clutch analysis, and egg length was more variable than width lenght. Nesting success increased progressively from April-May to June-July and August. The main proximate cause of nest failure was egg desertion/predation, followed by nest desertion during nest building and nestling desertion/predation. Mammals were the main agents in nests where the probable predator could be identified. Approximately half of the eggs became fledglings leaving the nest, no significant seasonal differences being observed for this parameter. In August, the ratio of juveniles to adults was 2.5-4.1, juveniles representing approximately 70-80% of the individuals seen and identified that month. The absence of significant interannual variation in important reproductive parameters could have been due to lack of interannual variation in the availability of food resources. Compared to other subspecies, mean clutch size of Iberian bullfinches is the smallest recorded in the western Palearctic, and they showed an earlier start to the breeding season and shorter mean egg length than North European and Russian populations.

Keywords

Introduction

Knowledge of the breeding biology of birds contributes to our understanding of nature, helps to formulate general theories of life history evolution, can provide information on the effect of global climate change on animals, and assists in identifying demographic factors underlying population declines; therefore, ornithologists have recently been encouraged to determine reproductive parameters of poorly investigated avian taxa (Xiao et al. 2017). The relative lack of research into avian reproduction in Mediterranean contexts, that is, in intermediate latitudes between tropical and temperate northern regions, is also underlined (Moreno 2004). Furthermore, in recent decades, there has been a worrying decline in fieldwork studies involving sound observational data, in biological sciences including nature conservation, in contrast to the noticeable increment in modeling and existing data analyses, this resulting in a pressing need to

recover and revalue pivotal field studies, among which those related to avian breeding biology (Ríos-Saldaña et al. 2018).

Bird subspecies may be of considerable evolutionary significance and conservation utility as they are generally the best representatives of genetic and ecological diversity found within species (Phillimore and Owens 2006). Currently, there are nine recognized subspecies of Eurasian bullfinch *Pyrrhula pyrrhula* (Linnaeus, 1758), hereinafter referred to as the bullfinch, of which *iberiae* Voous, 1951 occupies SW France (Pyrenees) and the mountains of N Portugal and N Spain (Clement 2010). The biology and ecology (e.g. breeding, diet) of some bullfinch populations, for instance those in central and western Europe, including the British Isles, are known in certain detail (Newton 1985; reviews by Cramp and Perrins 1994 and Clement 2010). Summarizing the knowledge about reproductive aspects, bullfinches usually produce second and, occasionally, third clutches. Most of the first clutches are recorded in May, but are not rare in April. Nevertheless, in the most northern latitudes of the distribution range, breeding starts later. Nestling stage normally continues until the end of July or mid-August, although it can last until September. Females build a new nest for each brood and incubate the eggs. Modal clutch size is 5 eggs in most of the distribution range, but in the northernmost areas it is larger. Nestlings are fed by both parents. Nest success varies from 15-40% in April-May to 70% or more in July-August, and approximately half of the eggs become fledglings.

However, to date, knowledge of the Iberian subspecies has been limited to occasional and segmented observations, apart from geographical distribution, general habitat and some estimations of local abundance (review by Díaz 2016). Regarding reproduction, Mestre (1971a, b) provides brief information on fewer than ten nests from NE Spain (nest site, nest traits, clutch size, egg traits), without mentioning nest success or breeding productivity, and several authors have offered even scantier data in provincial bird atlases (e.g. Román et al. 1996; Jubete 1997).

In this study, an integral approach to the breeding ecology of a population of Iberian bullfinch subspecies is presented for the first time, through fieldwork. This population occupies a hedgerow-dominated habitat in northwestern Spain, in an area close to the southwestern distribution limit of the species. The main parameters analysed are 1) timing of the breeding stages linked to the nest (from nest building to nestlings), 2) clutch size, 3) egg traits (weight, size and colouration), 4) nesting success and breeding productivity, and 5) parental care for dependent young outside the nest. The results obtained are discussed in relation to the known patterns of these natural history traits for other subspecies. Information is also given on signs of probable breeding (apart from nest attendance, e.g. courtship display and mate-feeding), and on behaviour during nest building, egg laying, incubation and the nestling stage. The following aspects are not considered as they are dealt with in detail in other additional studies (A. Hernández in prep.): intraspecific aggressions (except brief mentions), nest design and nest-site selection, and the diet of nestlings and dependent young outside the nest, and of adults in the breeding season (except for references to mate-feeding).

Material and methods

Study area

The study area covers 78 ha and is located in the 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 (Rivas-Martínez 2007). Hot summers, cold winters with some snowfall, and moderate rainfall with a short dry summer season characterize the area. The landscape is mainly composed of hedgerows that separate 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* Willdenow, 1805 woods interspersed with very small Scots pine *Pinus sylvestris* Linnaeus, 1753 plantations on the east side. Some hedgerows border Canadian poplar *Populus* x *canadensis* Moench, 1785 plantations. Estimated hedgerow density is 3.3 km per 10 ha. This 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 (Hernández 2009, 2014, 2018; Hernández and Zaldívar 2013, 2016). 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.

Considering three months per season in the six-year study period (2001-2006), i.e. n=18 months for each season in this period, mean (± standard deviation) monthly temperature was 3.5±1.3 ºC in winter (December-February), 10.0±2.6 ºC in spring (March-May), 19.4±1.2 ºC in summer (June-August) and 11.7±4.3 ºC in autumn (September-November). Considering the three months in each season as a whole during this study period, i.e. n=6 years, mean rainfall was 130.0±63.1 mm in winter, 135.8±28.7 mm in spring, 56.5±27.6 mm in summer and 166.1±86.0 mm in autumn. Meteorological data were provided by the Agencia Estatal de Meteorología (AEMET) for the La Virgen del Camino station, situated very near to the study area at the same altitude.

Data collection

Precautions.- All the fieldwork was performed using observational, non-invasive techniques which enabled sufficient data for the objectives of the study to be obtained without threatening the welfare of the birds, as neither birds nor active nests were manipulated (see Dawkins 2007). Finches in general, including bullfinches, tend to abandon their nests in early breeding stages, and nestlings tend to jump out of the nest prematurely ("exploding"), if disturbed (Noval 1971; Cramp and Perrins 1994; Ferguson-Lees et al. 2011). Therefore, the observer kept the maximum distance possible when visiting the nests to determine their content by visual inspection. Immediately after these visits, the nests were usually checked by long-

distance observation to verify whether they were still active, which always occurred, that is, the observer did not apparently interfere in nest success. Only the traits of eggs from non-active nests were estimated.

General data.- Throughout 2001-2006, the bullfinches directly observed in the study area and the maximum details of these sightings were recorded during field trips conducted to investigate their general ecology, and more frequently in spring and summer to follow the breeding cycle adequately. In a systematic way, 41 trips were conducted in winter (December to February), 113 in spring (March to May), 155 in summer (June to August) and 84 in autumn (September to November). 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 it tends to decrease throughout the day (Bas et al. 2007 and references therein). 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.

Data collected from March (when the first signs of probable breeding were observed) to October (when the last sightings of adults with dependent young were made) were used in this study. Bullfinches are particularly inconspicuous when breeding (Newton 1985; pers. obs.), but their contact calls and songs, composed mainly of piping notes emitted at fairly low volume, enabled them to be located. Also, the observer mimicking their voices to get the birds to answer was quite a successful technique, as verified by Newton (1985).

Nesting data.- Nests were searched, found and monitored during 2001-2005, thus data on breeding ecology but not on specific nests found were considered for 2006. Direct nest searching ("cold searching") is not usually effective for bird species that hide their nests (Green 2004), which is the case of the bullfinch. Thus, the search for nests was mainly by following adults showing signs of nest attendance, more evident during building (as in other passerines, e.g. Lloyd et al. 2017) and inconspicuous during incubation and, contrary to expectations, nestling stage, as bullfinches feed their young by regurgitation, so no food is visible in their bills and the nestling feeding rate is low (Newton 1985; Ferguson-Lees et al. 2011). Bullfinches accumulate food collected for their young in special pouches under the lower jaw, but the bulging throat is only visible under optimum observation conditions at short range (Newton 1967; pers. obs.).

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. A total of 210 records for 56 nests were obtained. Although active nests belonging to different pairs could be very near to each other (as close as ≈25 m), some nests, built just after others very

close by (at a distance of ≈2-50 m) that had failed, were probably replacement nests. Bullfinch pairs usually breed solitarily, but several can coincide in a small area as they are not territorial, like other European cardueline finches (Cramp and Perrins 1994; Ferguson-Lees et al. 2011; pers. obs.). Some pairs looked after dependent young whilst also attending a new nest, that is, they tried to raise another brood, but it was not possible to determine the preceding nest.

Information was obtained on the behaviour of adults during nest building (23 nests), egg laying and incubation (32 nests) and the nestling stage (13 nests). Periods of continuous observation of some nests were carried out to obtain additional data, including number of visits made by the parents to their nest per hour, the observer being hidden in vegetation at a distance of 20-30 m. During building, three nests were observed (May-June, 5h 25 min observation in 6 days throughout the morning). During incubation three nests were observed (May-June, 3h observation on 3 days during the morning). During the nestling stage one nest was observed (June-July, 10h 30 min observation on 2 days throughout the morning and afternoon).

Assumptions, clarifications on the nature of the data and their handling, and terminology.- The records of each specific aspect are independent of one another, that is, they correspond to different individuals, pairs or family groups, at least those for each systematic sampling day to cover the entire area. Pairs looking after dependent young whilst also attending a new nest provided records on two different breeding attempts, simultaneously. Sighting rate, considering field trips, was estimated as the average number of records per trip (summation of records/number of field trips). Details recorded for one particular sighting did not necessarily coincide with those collected for another related sighting (for example, in the case of females collecting nest material, it was not always possible to identify the type of material). Frequently, nests could not be seen directly, therefore observations of individuals "entering the nest" generally means individuals "entering the shrub/tree where the nest was located", presumably to build a nest, lay, incubate eggs or feed nestlings (the same applies to "leaving the nest"). The distances between the parents and the nest, while they performed different tasks (e.g. collecting nest material or feeding the nestlings), are probably minimum values since they sometimes moved further away and were lost from sight (over 100-150 m).

The main signs of probable breeding considered, excluding nest attendance, were mate-feeding (male feeding a female), courtship display in the strict sense (mutual mating dance and caressing), copulation, pair searching for a nest site, and twig-display (partners showing nest material to one another). In the analysis of timing of breeding, only one record of a specific breeding stage (nest building, egg laying, incubation, nestlings) for each nest is considered during a specific 10-day period. The exact duration of each breeding stage or how long breeding lasted could not be determined for most of the nests, as they were not usually monitored on successive days; nevertheless, the highest verified values are provided. On-bout and off-bout refer to the time intervals spent in and outside the nest, respectively, during the incubation stage (see Mitchell et al. 2017). Date of clutch completion was established bearing in mind the reproductive moment when the nest was located, the estimated dates when the following breeding stages

began and young left the nest, as well as the average duration of breeding stages (according to Cramp and Perrins 1994; Ferguson-Lees et al. 2011; pers. obs.).

Complete clutches were used for the clutch size analyses. The clutch was considered complete when the number of eggs did not increase during at least 3 days and the nest was still active (bullfinches normally lay one egg per day, as stated below). No disappearance of eggs was detected in active nests. Clutch size in the few nests found with nestlings was estimated as the number of nestlings plus, when appropriate, the number of unhatched eggs. Eggs were collected on the same day when it was verified that the nest was no longer being used by the bullfinches. On the same day, the eggs were measured (weight and linear dimensions) if they were in good condition, and the eggshell colouration of each one (background colour and maculation) recorded. Fresh eggs are those that were weighed no later than 14 days from the estimated day when laying was completed, since bullfinches take approximately two weeks to hatch. Bird eggs start decreasing in weight as soon as they are laid but their volume does not change, and initial weight (recently laid egg) and volume can be deduced from linear dimensions (Hoyt 1979; Deeming 2002a). The mathematical formulae proposed by Hoyt (1979): volume $(cm^3)=0.51 \cdot L \cdot W^2$; initial weight $(g)=0.55 \cdot L \cdot W^2$; L being length (cm) and W width (maximum diameter, cm), were used to determine the volume and initial weight of the eggs. The constants in these formulae are mean values for 26 bird species, with very low coefficients of interspecific variation (1.44% for volume, 2.83% for initial weight). The initial weight of some eggs not weighed on the day they were collected, because they were broken, was estimated by measuring their length and width. The weight loss per day was calculated considering initial estimated weight, actual weight and time from the estimated day when laying was completed until the eggs were weighed. Egg shape index was estimated as the L/W ratio, L being length (cm) and W width (maximum diameter, cm), according to Dolenec (2004). Egg traits were assessed by considering each egg individually without differentiating clutches, and by considering one value per clutch (mean value or only value available for clutches from which only one egg was collected). The description of eggshell colouration is fundamentally qualitative and is carried out by visual assessment of mostly intact but, in some cases, fragmented eggs. In some clutches, only the colouration of one egg could be observed. It provides information on the most and least commonly observed patterns, as well as estimates on speck size.

Nesting success is the percentage of nests in which at least one young fledges. Nesting success was not corrected in relation to the breeding stage when the nests were first found (see Mayfield 1975, Shaffer 2004), since these corrections take into account the period of exposure (days) in the different breeding stages, from the date on which the nests are discovered to the date of failure, requiring very frequent visits, but bullfinch nests were visited at relatively long time intervals (one week as a reference) for precautionary reasons. Most active nests were found in the early stages of the reproductive cycle, but nevertheless the nesting success in each discovery breeding stage is provided. The main studies with which nesting success in bullfinches is compared did not use correction methods (Bijlsma 1982; Newton 1985). Hatching failure can result from either infertility or embryo mortality. However, no distinction is made between the two causes as macroscopic examination does not detect embryos that die during the first days of incubation (Hemmings et al. 2012). Breeding productivity was estimated as the proportion of young that

left the nest in relation to the number of eggs laid in complete clutches. The number of fledglings is a good indication of the number of juveniles recruited as adult breeders in bird populations (Weatherhead and Dufour 2000). Breeding productivity was estimated for each nest and, therefore, for the total number of nests, but not for each pair as the number of breeding attempts (nests) corresponding to each one could not be determined precisely. In Britain, Newton (2000) verified that, although many bullfinch pairs remain in the same locality throughout the breeding season, it is not unusual for some adult individuals to move long distances during May-August (19% ring recoveries at a distance of over 5 km, further than expected for foraging trips from the nest), and proposed that these are movements between broods. Breeding productivity was also estimated as the ratio of juveniles to adults, this index being previously used for bullfinches (Newton 1999; Proffitt et al. 2004) and applicable, without having to catch individuals, to bird species whose juveniles have very different plumage colouration to adults (Green 2004). This ratio is given for August, when the maximum value was reached almost every year, and most juveniles were apparently not in moult and could be identified correctly (only 1.8% of the total number of bullfinches identified in August were moulting juveniles, A. Hernández in prep.).

With respect to the proximate causes of nest failure, most predated nests had probably not been deserted previously (voluntarily or because one or both parents died outside the nest). However, in most cases this could not be determined, so the importance of desertion and predation are considered together. Regardless of the original cause, an attempt was made to identify the type of nest predator by signs left on the eggshell; in this respect, birds usually leave small holes, with clean edges, no teeth marks, and mammals leave crushed eggshells, sometimes with marks made by the canines (carnivores) or gnawing (rodents) (Green et al. 1987; Green 2004). Another reasonable sign of nest predation was all eggs/nestlings prematurely missing, as both avian and mammalian predators can carry them far away from the nest (Green 2004). In the case of females killed during incubation, the type of predator was identified by remains found in or just under the nest (loose feathers, parts of the body such as wing fragments), bearing in mind that mammalian carnivores bite and break the feathers when eating the birds (Bang & Dahlstrøm 2009; pers. obs.).

Each record of dependent young outside the nest refers to one young individual or several together, observed close to two adults (a pair) or just one, which were almost definitely (adults feeding young) or very likely their parents. As is widely accepted, brood division is the splitting of a brood into smaller family units, that is, each parent takes exclusive care of some of the young after fledging. To estimate the mean number of dependent young individuals per record, only sightings in which the size of the group could be quantified with a degree of certainty at the time of observation were considered. When the fledglings came out of the nest, first they stayed close to it, hidden, and did not follow their parents, which sometimes made them difficult to count.

Potential nest predators.- Several authors have emphasized how useful identifying the local community of predator species is when researching bird nest failure in a specific area (Hansell 2000; Lahti 2001; Eglington et al. 2009; Ibáñez-Álamo et al. 2015). Thus, all sightings of proven and potential predators of bullfinch eggs and individuals (raptors, shrikes, corvids, carnivores, rodents) were recorded on the field

trips carried out systematically to cover the entire area, taking into account data for spring and summer in this study. Eurasian sparrowhawks *Accipiter nisus* (Linnaeus, 1758) capture bullfinches in the study area, especially during the non-breeding season (Hernández 2018). The results corresponding to mammalian predators should be considered with some reservation as these species are generally highly active during the night and at dawn/dusk. In addition, the bird community was censused along a 1.6 km line transect that crossed the study area, covered on foot from one hour after sunrise, in spring and summer (twice in April - 2001 and 2005-, once in May -2004-, once in June -2001-, three times in July -once in 2001, twice in 2005-, once in August -2001-). Passerines (including shrikes and corvids), woodpeckers and pigeons seen or heard in a 50 m band on either side of the transect were recorded; a singing male was considered a pair. The two July-2005 samplings had already been used by Hernández (2008a) for other purposes.

Optical and measuring instruments.- Standard optical equipment was used to observe birds (binoculars and a telescope). A PHB® dental mirror with a handle (16 cm total length, with an angled mirror 2 cm in diameter) was used to observe nest content more easily. A mirror 6 cm in diameter with a handle 7 cm long was transversally attached to a wooden rod measuring 1 m in length and 1 cm in diameter to reach the highest nests. In the study area, bullfinches build open cup-shaped nests in shrubs and trees, most of which are less than 2 m above the ground (A. Hernández in prep.). A MEBA® vernier caliper with 0.1 mm accuracy was used to measure the length and maximum width of eggs in non-active nests; and a PESOLA® spring balance (up to 10 g, 0.2 g accuracy) was used to weigh them.

Statistical analysis

The chi-square test (χ^2), with Yates correction for one degree of freedom, was used to compare series of absolute frequencies; the unpaired t-test to compare two means; the one-way ANOVA (F), with post-hoc Tukey's test, to compare more than two means; and the Spearman's correlation coefficient (r_s) to assess association between two ranked variables; considering the two-tailed way wherever possible (Fowler et al. 1998). Standard deviation (SD) and coefficient of variation (CV) were estimated as measures of dispersion. $P<0.05$ was considered statistically significant. If not otherwise specified, all years were pooled together, mainly to avoid analysing small sample sizes.

Results

Breeding season density

Bullfinch densities during the breeding season were fairly similar from year to year (approx. 2.5-3.5 pairs/10 ha during April-May and 7.5-9.0 birds/10 ha during July-August).

Timing of breeding stages

Signs of probable breeding, excluding nest attendance, occurred from March to August. Most of these signs were observed during April-June (100 of 114 records, 87.7%), and the occurrence rate was also higher during these months (≈0.5-1.1 records per field trip) (Figure 1). The most frequently observed signs were mate-feeding and courtship display (99 of 114 records, 86.9%) (Figure 1).

Nest building was observed from mid-April to the end of June, egg laying-incubation from the end of April to mid-July, and nestlings from mid-May to mid-August (Figure 2). The earliest nest building date was within 21-30 April, except in 2003 when it was 11-20 April, and nestlings were observed until 21-31 July, except in 2003 and 2004 when they were observed until 11-20 August. Fledging was recorded throughout all of the ten-day periods from the end of May (21-31 May) to mid-August (11-20 August), but mainly during June (11 of 21 successful nests, 52.4%) and from the end of July to mid-August (21 July-20 August) (7 of 21 successful nests, 33.3%).

In the case of two nests, nest attendance time was established from the early stage of building to well-feathered nestlings being ready to leave the nest, 36 days in both cases (27 April-1 June; 28 April-2 June). In another nest, nest attendance from the middle of building to quite well-feathered nestlings lasted 35 days (23 June-27 July). Building time from when the nest was in the early stage to the apparently completed stage varied between 7-8 days (n=5 April-May nests). Incubation lasted at least between 8-9 days (n=6 May-June-July nests). The minimum time the chicks remained in the nest was between 13-17 days (n= 3 May and July nests).

Behaviour during breeding stages

Signs of probable breeding, excluding nest attendance.- No sexual chases or display flights were observed. Some individuals showed more than one sign uninterruptedly: mate-feeding+courtship; courtship+copulation; mate-feeding+courtship+copulation; twig-display+pair searching for a nest site. Males fed females from before nest building began and throughout the main breeding stages, but particularly during incubation, on shrubs/trees and wire fences, at a mean height of 3.3±1.3 m (range=1.5-7.0 m, n=28 records), and a mean distance from the active nest of 25.0±23.6 m (range=0.0-80.0 m, n=28). The female moved from side to side without calling when she wanted food, and flapped her wings while being fed. The male was seen ingesting mainly dandelion (*Taraxacum officinale* Wiggers, 1780) seeds or blackthorn (*Prunus spinosa* Linnaeus, 1753) buds (14 of 18 records, 77.8%) just before feeding the female, as well as black poplar (*Populus nigra* Linnaeus, 1753) seeds (from green-coloured capsules), meadowsweet (*Filipendula ulmaria* (Linnaeus) Maximowicz, 1879) seeds, bramble (*Rubus* Linnaeus, 1753) seeds, and insects captured in flight. On some occasions, the female was seen entering the nest, presumably to feed nestlings, just after being fed by the male.

Courtship display took place, with more or less intensity, when nest building had not started and during all of the principal breeding stages (from nest building to caring for dependent young outside the

nest), on shrubs/trees at a mean height of 4.5±2.3 m (range=1.5-8.5 m, n=14 records). The principal courtship rituals were lateral and vertical body movements, more clearly visible in the head and tail (recorded for both males and females), caressing the sides of the male or female with the bill, caressing each other's bills without feeding, and wing flapping (the female). Mate-feeding was often observed during courtship.

Copulation was observed on few occasions, during the stages of nest building and caring for dependent young outside the nest, on shrubs/trees at a height of between 2.5 and 8.0 m. Before copulation, the female showed the male her cloaca. During copulation, the male spent no longer than five seconds on top of the female, flapping his wings.

Pairs apparently searching for a nest site examined a hedgerow or shrubby border together at a low height, stopping at specific locations and then entering the branches (n=9 records). Twig-display was observed on few occasions, on the ground, in low-medium height hedgerows and in poplar trees in plantations, partners showing each other building materials but more often male to female.

Nest building.- Bullfinches built a new nest for each breeding attempt. It was built by the female, which usually arrived at the nest escorted by the male closely behind (28 of 32 records, 87.5%). In nests that were being built, belonging to pairs taking care of dependent young from previous broods, the female usually arrived unaccompanied by the male. The female left the nest and flew in a specific direction normally followed by the male (n=17 records), following different cardinal directions. Normally, they returned to the nest in the same direction as they had left it. While the female collected nest material, the male remained very close by, showing vigilant behaviour. Females collected material in hedgerows (29 of 38 records, 76.3%), poplar plantations (15.8%) and the edge of the oak woods (7.9%), at a mean distance from the nest of 27.3±23.6 m (range=2.0-100.0 m, n=38 records) and a mean height of 3.3±3.7 m (range=0.0-14.0 m, n=19 records). They were seen collecting apparently dry twigs from shrubs/trees (11 of 19 records, 57.9%), grass stalks (36.8%) and poplar bark fibres (5.3%). The thickest strongest material (twigs) was collected preferably during the first days of nest building and the finer softer material (herbs, bark fibres) preferably during the final days.

In one almost completely built nest, the mean visiting rate whilst carrying material was 6.5 visits/h to the nest (n=2 consecutive days, 160 min observation), in another half built one it was 6.8 visits/h (n=3 consecutive days, 135 min observation), and in another in the initial stage of building, observed on only one day, the visiting rate was 14.0 visits/h (30 min observation). These data correspond to observations made first thing in the morning, but nest building was also carried out during other times of the day, according to non-quantified sporadic observations. After entering the nest with material, the female remained there, supposedly building, for a mean time of 124.7±44.0 s (range=60-240 s, n=17 records) until she left again.

The male and female remained close together when resting from nest building. They both ate, the male sometimes feeding the female. Courtship display and copulation were observed, as well as some aggressive interpair intraspecific encounters.

Incubation.- Only the female incubated. She usually arrived at the nest accompanied by the male (9 of 13 records, 69.2%), and on two of those occasions the male also entered the nest and left shortly after. Males were seen entering the nest while the female was incubating to feed her (n=9 records). Some incubating females were linked to males caring for dependent young from a previous brood (n=2 records). Normally, when the female left the nest the male was waiting (n=12 records) on the outer branches of the same shrub/tree where the nest was located or at a maximum distance of 15 m, at a maximum height of 5 m, often emitting contact calls.

Two complete incubation on-bouts, from when the female entered the nest to when she left it, lasted 45 and 50 min, corresponding to two different nests on different days. Three complete off-bouts, from when the female left the nest to when she entered it again, lasted 2, 7 and 10 min, corresponding to three different nests on different days. During the off-bouts, the male and female stayed close together. Both of them ate, the male feeding the female on occasions. Courtship display was observed, and there were some aggressive interpair intraspecific encounters.

Nestling stage.- Both males and females fed nestlings. The female brooded the nestlings when they were small, up to approximately 4 d, with blackish dorsal down (on the head, back and wings) and their eyes were still closed. In this early stage the male apparently did not feed the nestlings directly, but passed food on to the female, part of which was used to feed them. A nest was observed in June for 210 consecutive minutes in the morning, 151 (71.9%) of which the female was brooding, in three periods of 44, 35 and 72 min, considering the intervals of time when she entered the nest and did not leave shortly afterwards. Both parents entered the nests containing older chicks with growing feathers and open eyes, not being brooded by the female. The male and female usually arrived at the nest together and entered and left it at slightly different times, the female first (9 of 14 records, 64.3%) or the male (35.7%), also moving away from the nest together.

The rate of visits by parents to a nest with three small chicks in June-July was 2.6 visits/h in 210 min of observation in the morning (1.1 by the male, perhaps to feed the brooding female, and 1.5 by the female), and when the chicks were older, 3.5 visits/h in 240 min of observation in the morning (1.75 by the male and 1.75 by the female) and 2.7 visits/h in 180 min of observation in the afternoon (1.35 by the male and 1.35 by the female). Thus, parents visited the nest at intervals of ≈17-23 min. Considering 15 daylight hours on those dates in the latitude of the study area, they visited the nest ≈40-55 times a day. Both females (n=4 records) and males (n=3 records) were seen leaving the nest carrying the faecal sacs of the chicks in their bills (apparently one sac at a time). A female ate a faecal sac while perched on a shrub 3 m from the nest, and a male attached one to a poplar tree branch at a height of 9 m, 15 m from the nest. The remaining faecal sacs were carried a considerable distance from the nest (over 50 m). During the nestling stage, the behaviour of the adults apparently not linked to nestling feeding included self-feeding, courtship display and aggressive interpair intraspecific encounters.

Clutch size

The overall mean clutch size was 4.56±0.76 eggs (range=3-6, n=32 complete clutches), the modal value being 5 eggs (20 of 32, 62.5%) (Figure 3). Comparing years, and without differentiating months, there were no significant differences in mean clutch size ($F_{4, 27}$=1.34, p=0.28). Nevertheless, the small sample sizes for several years should be considered with caution. Significant differences were observed between months in mean clutch size without differentiating years ($F_{2, 29}$=5.89, p=0.007). Considering pairs of months, there were no significant differences between May and June (p>0.05, Tukey's test), with a mean clutch size of 4.72 and 4.70 eggs, respectively, but there were between May and July, and June and July (p<0.01 for both pairs, Tukey's test), as mean clutch size decreased to 3.50 eggs in July (Figure 3). Nevertheless, the small sample size of July clutches (n=4) should be considered with caution.

Egg traits

The mean time from the estimated day when laying was completed until the lifeless eggs were collected and weighed was 16.50±8.61 d (range=8-33 d, n=28 eggs apt for weighing from 12 clutches). The mean weight of the eggs on the day they were collected was 1.89±0.27 g (range=1.3-2.3 g, n=28), that is, the heaviest egg (2.3 g) weighed 77% more than the lightest one (1.3 g). The fresh eggs weighed 1.95±0.06 g (range=1.3-2.3 g, n=16). Comparing the initial estimated weight with that obtained on the day they were collected, the mean percentage of loss was 14.47±9.56 % (range=3.8-44.9 %, n=28 eggs). The mean percentage of weight loss per day was 0.97±0.50% (range=0.24-2.63%, n=28 eggs). There was a significant positive correlation between the time interval from the estimated day when laying was completed until the day the eggs were weighed and the percentage of weight loss (r_s=0.41, p=0.03, n=28 eggs).

For all egg parameters (length, width, initial weight, volume, shape index), the minimum standard deviation values were obtained in the intra-clutch analysis, and egg length was more variable than width egg (CV values) (Table 1). The egg shape index varied between 1.25 (the longer-looking egg) and 1.56 (the wider-looking egg), pyriform to oval and subelliptical in shape.

Considering one value per clutch, there were no significant differences in initial egg weight or egg volume between clutches completed in May (initial weight =2.24±0.16 g; volume=2.08±0.15 cm^3; n=7 clutches) and June-July (initial weight =2.25±0.16 g; volume=2.09±0.14 cm^3; n=7 clutches) (initial weight: t_{12}=-0.05, p=0.96; volume: t_{12}=-0.13, p=0.90). Initial egg weight and egg volume were not compared among years due to small sample sizes. Considering one value per clutch, there was no significant correlation between initial egg weight and clutch size (r_s=0.43, p=0.14, n=13 clutches) or between egg volume and clutch size (r_s=0.48, p=0.10, the same 13 clutches).

The background colour of the observed eggshells (n=46 from 21 clutches) was usually pale light blue, but sometimes more vivid light blue, pale light blue-greenish, or pale light blue-greyish. Maculation was usually concentrated in a crown around the broad pole, with small- (<0.5 mm long), medium- (0.5-1.5 mm long) and sometimes large-sized specks (>1.5 mm, up to 3 mm long), of varied shapes (rounded, oval,

irregular), violet to brown in colour, from light to very dark. Sometimes, dark linear strokes, that can exceed 5 mm long, appear in this crown. Usually, some very small and dispersed specks, which are rarely medium-sized and somewhat more abundant, appear in the rest of the eggshell. Variation in background colour and speckling was lower among eggs of the same clutch than among eggs of different clutches.

Nesting success and breeding productivity

Nesting success increased progressively from nests found in the construction stage (4 of 27, 14.8%) to egg laying-incubaton stages (9 of 20, 45.0%) and nestling stage (8 of 9, 88.9%). Nesting success increased progressively from April-May (0.0-4.3% of nests) to June-July (54.5-64.7%) and August (100%) (Figure 4). There were no significant interannual differences in nesting success, being ≈30-40% for all years except 2004 with a value of 57.1% (χ^2_4=1.46, p=0.83) (Figure 4). Considering all nests, there were no significant differences between the mean clutch size of successful (4.40±0.82 eggs, n=20 clutches) and unsuccessful nests (4.83±0.58 eggs, n=12 clutches) (t_{30}=1.60, p=0.12). Neither were there significant differences between the mean clutch size of successful (4.60±0.70 eggs, n=10 clutches) and unsuccessful nests (4.88±0.64 eggs, n=8 clutches) (t_{16}=0.86, p=0.40), considering only nests where laying was completed in May. Similarly, there were no significant differences in the mean clutch size of successful (4.20±0.92 eggs, n=10 clutches) and unsuccessful nests (4.75±0.50 eggs, n=4 clutches) (t_{12}=1.11, p=0.29), considering nests in which laying was completed in June-July.

The principal proximate cause of nest failure was egg desertion/predation (18 of 35 failed nests, 51.4%), followed by nest desertion during nest building (20.0%) and nestling desertion/predation (17.1%). In some cases, the female died while incubating; thus, in three nests (8.6%) the remains of the female and eggs as a result of predation were found, and in another (2.9%) the female was dead and intact on the eggs which were also intact. Mammals were found to be the main agents (84.6%, 11 of 13 nests) when the probable predator was identified, birds having a lower impact (15.4%, rest of the nests). Rodents were apparently important egg predators, but carnivores killed the females in the nests and consumed the eggs being incubated at the time.

For all groups of proven and potential predators of bullfinch eggs and individuals, the sighting rate was higher in spring than in summer (Figure 5). However, the average density of corvids plus shrikes was maximum in July (9.7 birds/10 ha) according to the line transects, with values in the interval 2.4-3.7 birds/10 ha during April-June and in August. The sighting rate was higher for black kites *Milvus migrans* (Boddaert, 1783) and Eurasian sparrowhawks among raptors, carrion crows among corvids, red foxes *Vulpes vulpes* (Linnaeus, 1758) and stoats *Mustela erminea* Linnaeus, 1758 among carnivores, and Eurasian red squirrels *Sciurus vulgaris* Linnaeus, 1758 among rodents, but the red-backed shrike *Lanius collurio* Linnaeus, 1758 was the most common of all predator species (Figure 5).

Considering complete clutches with a known size (n=32), 9 (28.1%) were completely successful (all of the eggs hatched and all of the nestlings fledged), 11 (34.4%) were partially successful (some nestlings

fledged, but some eggs did not hatch/some nestlings died), and 12 (37.5%) were total failures (during the egg/nestling stage). Unhatched eggs were found in 44.0% of clutches in which hatching was verified (11 of 25), generally only one unhatched egg per clutch, maximum two. A dead nestling was found in only one (5.0%) of the successful nests (n=20) (two of the five eggs laid did not hatch, one nestling died and only two young fledged in this nest). Considering complete clutches with known clutch size (n=32) as a whole, a total of 75 fledglings left the nest from 146 eggs laid (51.4%), that is, 2.34 fledglings per nest. Considering only successful nests (n=20), 3.75 young fledged per nest. Individual losses (n=71) were due to deserted/predated eggs (49.3%), deserted/predated nestlings (31.0%), unhatched eggs (18.3%) and dead nestlings (1.4%). Considering the month when the clutch was completed, number of fledglings that left the nest in relation to number of eggs laid was similar in May (42 fledglings from 85 eggs, 49.4%) and June-July (33 from 61, 54.1%) (χ^2_1=0.15, p=0.70). Neither was there a significant association between this relationship and year (χ^2_4=5.20, p=0.26), all years except 2001 ($\approx$30%) being in the approximate range of 55-60% (Figure 6). In August, the ratio of juveniles to adults was 2.5-4.1, with no significant interannual differences (χ^2_4=4.04, p=0.40), juveniles accounting for approximately 70-80% of individuals seen and identified that month (Figure 7).

Parental care for dependent young outside the nest

The sighting rate of dependent young outside the nest was high in June ($\approx$0.7 records/field trip), maximum in July-August ($\approx$1 record/field trip), and decreased noticeably in September-October (<0.3 records/field trip) (Figure 8). Every year, there were sightings from June, generally from the first fortnight, and all years until at least the end of August, generally until September. In one case considered to be a successful nest, it was assumed that the fledglings had left the nest at the end of May, but they were neither seen nor heard on those days. The sighting rate for adults feeding young outside the nest remained fairly constant throughout June-August ($\approx$0.25-0.35 records/field trip), and non-existent in September-October (Figure 8).

There was a significant association between months (June, July, August, September-October) and types of records of dependent young outside the nest (adult male with young, adult female with young, adult pair with young), considering number of records (χ^2_6=22.43, p=0.001) (Figure 9). During June and July, most of the records corresponded to a male with young (>60%), one third to a pair with young ($\approx$33%), and only approximately 6% to a female with young. During August-October, however, percentages of records of young with either male or female were similar ($\approx$40% in each case), and those corresponding to young with pair were approximately 20%.

The mean number of dependent young individuals per record was higher in June-July than in August-October, for both young with male and young with female and young with pair (Figure 10). Comparing all the records for June-July with all those for August-October, there were significant differences in the mean number of dependent young individuals (1.92±0.91, range=1-4, n=73, in the first period; 1.39±0.67, range=1-4, n=49, in the second period; t_{120}=3.49, p=0.0007). In June-July, the mean number of dependent young individuals with pair (2.06±1.25, range=1-4, n=17) was not significantly different to with

one adult individual (1.88±0.79, range=1-4, n=56 considering young with male and with female together) (t_{73}=0.73, p=0.47). This analysis was not carried out for August-October due to the small sample size for young with pair.

Parents fed young on shrubs/trees at a mean height of 3.0±2.1 m (range=0.5-12.0 m, n=33 records). Normally, they fed only one young individual, rarely two, on each occasion. The young individual flapped its wings while feeding. Dependent young frequently emitted urgent calls which were shorter and less clear than the typical piping calls of the adults, and more insistent during feeding.

Discussion

Timing of breeding stages

In the study area, bullfinches showed signs of probable breeding prior to nest building as early as March, but mostly from April. In this monogamous species, it is common to see pairs exhibiting courtship and mate-feeding before the breaking of winter flocks; thus, pair-formation presumably occurs before the start of breeding in the strict sense (Bernis 1957; Wilkinson 1982; Cramp and Perrins 1994). Some authors suggest that pair-bond can last longer than one breeding season, remaining throughout the year, with females dominating over males, and even including courtship displays (Newton 1985; Clement 2010). In the study area, courtship rituals were not seen in winter, but females were occasionally seen attacking males in December (A. Hernández in prep.).

Bullfinches usually began building their first nests at the end of April, and the first clutches appeared mainly in early May. Limited information on the first clutches of Iberian bullfinches known to date refers to a few nests with eggs at the end of April and above all in May (Mestre 1971b; Román et al. 1996). In England and central Europe, most of the first clutches are also recorded in May, but are not rare in April (Bijlsma 1982; Newton 1999; Proffitt et al. 2004; Ferguson-Lees et al. 2011; Robinson 2018). Nevertheless, in the most northern latitudes of the distribution range, breeding starts later (Cramp and Perrins 1994). In 2003, when the earliest date for the start of nest building was recorded, the highest mean temperature in March (8.6 ºC) was also recorded and the third highest in April (9.5 ºC), for 2001-2006. This supports the idea that bullfinch breeding starts earlier due to higher ambient temperature (Bijlsma 1982; Newton 1985; Crick and Sparks 1999).

The bullfinch nestling stage normally continues until the end of July or mid-August in northern Iberia and other parts of Europe (Mestre 1971b; Bijlsma 1982; Román et al. 1996; Proffitt et al. 2004; Ferguson-Lees et al. 2011; present study), although it can last until September (Cramp and Perrins 1994; Newton 1999; Clement 2010). The two seasonal peak periods for fledglings leaving the nest probably largely correspond to first and second clutches, respectively, although two successful broods were only confirmed in cases of pairs caring for dependent young whilst attending a new nest. Bullfinches usually produce second and, occasionally, third clutches, as well as replacement ones, so a female can lay 3-5 times a year, without a clear latitudinal pattern in the number of clutches according to available information (Bijlsma

1982; Cramp and Perrins 1994; Clement 2010; Ferguson-Lees et al. 2011; Robinson 2018). Cardueline finches, including bullfinches, feed their young mainly on seeds and breed during a long season, continuously varying their diet as different plant species fructify (Newton 1985; A. Hernández in prep.). In the study area, however, there were very few late nests in the overall number of years considered, perhaps because, among other causes, at the end of the summer most of the meadows were mowed or grazed, to some extent decreasing the availability of herb seeds as food (pers. obs.).

Values recorded for the duration of the different breeding stages linked to the nest, a priori slightly underestimated, are generally somewhat lower than those typically found for bullfinches in other areas of the western Palearctic, especially for incubation (8-9 d versus 12-15 d), but the highest values recorded for nestling stage hardly differ (13-17 d versus 14-17 d) and those recorded for nest building are even slightly higher (7-8 d versus 5-7 d) (Cramp and Perrins 1994; Clement 2010; Ferguson-Lees et al. 2011; Robinson 2018). Values estimated for the total length of nest attendance (at least 35-36 d) are within the typical interval for bullfinches in other areas of the western Palearctic (31-39 d, considering the previously mentioned lowest and highest typical values for each breeding stage, respectively). It should be taken into account that bullfinches, like other passerines, usually lay one egg per day and that incubation itself usually starts when the penultimate egg has been laid, in order to attenuate hatching asynchrony (Drent 1975; Cramp and Perrins 1994; Winkler 2004; Ferguson-Lees et al. 2011; pers. obs.), thus, the 31-39 d interval would be 34-42 d adding 3 d of egg laying without incubation (assuming that incubation starts with the fourth egg, in a standard clutch of five), which also includes the total estimated length of nest attendance.

The long duration of nest building in the area is presumably because it was recorded in nests at the start of the breeding period (April-May). At temperate latitudes, passerines, including bullfinches, usually spend less time building their nests as the season advances, possibly indicating adjustment of optimal reproduction time (Hernández 1993; Cramp and Perrins 1994; Zeng and Lu 2009; Mainwaring et al. 2014). To date, the patterns and causes of variations in the length of incubation and nestling stage in bullfinches have not been analysed and, according to Newton (1985), the growth rate of young cardueline finches only varies within quite limited ranges.

Behaviour during breeding stages

Signs of probable breeding, excluding nest attendance.- The general patterns of bullfinch courtship (mutual), mate-feeding and twig-display (mutual), as well as absence of sexual chases and display flights, coincide with what is already known for this species (Newton 1985; Cramp and Perrins 1994; Clement 2010). Mate-feeding is quite frequent in passerines and responds above all to nutrition hypothesis, so it normally occurs in species in which nest building and incubation are tasks carried out exclusively by the female (energetically costly) with a mainly noncarnivorous diet (protein deficient) (Galván and Sanz 2011; Yoshikawa and Endo 2017), as happens in the bullfinch.

Nest building.- Bullfinches build a new nest for each brood, a task carried out exclusively by the female (Cramp and Perrins 1994; Clement 2010; Ferguson-Lees et al. 2011; present study). In the study area, the

frequency of visits to the nest carrying material (5-10 visits/h) are higher than in other areas of the western Palearctic (≈2-6 visits/h), but quite variable in both cases as generally occurs in cardueline finches (Newton 1985; Cramp and Perrins 1994). The highest values for the study area correspond to recently-started nests or half-built nests. During nest building, the bullfinch male usually accompanies the female a short distance (Cramp and Perrins 1994; Ferguson-Lees et al. 2011; present study). An important function of this behaviour is probably mate-guarding to prevent extra-pair copulation (EPC) with other males (see Birkhead and Møller 1998; Hasselquist and Sherman 2001). During the breeding season, aggressive interpair encounters were observed mainly among males, apparently related to mate defense (A. Hernández in prep.).

The most rigid material was collected preferably at the start of nest building, presumably to form the nest base and walls, and the softest material towards the end to line the cup. Bullfinch nests are basically made of an uneven structural layer of dry twigs (e.g. *Rubus* spp. and *Ulmus minor* Miller, 1768 in the study area) or dicot herbs and a lining of fine, dry materials such as grasses (Poaceae), rootlets and hair (Newton 1985; Ferguson-Lees et al. 2011; Biddle et al. 2017; A. Hernández and P. Zaldívar in prep.).

Incubation.- According to available information, only the female bullfinch incubates (gyneparental incubation). When called by the male, she leaves the nest and is fed by him during the recesses, but also sometimes feeds herself (Cramp and Perrins 1994; present study). Average incubation on-bouts of around 50 min and short off-bouts of no more than 10 min are normal for the species, in both the study area and the rest of its distribution range, but values of up to 2 h (on-bout) and 45 min (off-bout) have also been recorded (Cramp and Perrins 1994). In passerine species with gyneparental incubation, the female spends a mean of ≈75% of her daytime incubating, averaging ≈10 min per recess, and is fed frequently by the male (Deeming 2002b). These patterns also occur in bullfinches.

Nestling stage.- Bullfinch nestlings are fed by both parents, although during the first 4-6 days the female broods them and usually takes charge of feeding, frequently with food given to her by the male inside or outside the nest (Cramp and Perrins 1994; Clement 2010; Ferguson-Lees et al. 2011; present study). The estimated rate of visits to the nest to feed nestlings (approx. 20 min intervals, 50 visits/day) is much lower than the average found for single-item-loading passerines in the north temperate zone (300-400 visits/day) (Winkler 2004). However, multiple-item loaders, whether carrying food in their bills or feeding by regurgitation, visit the nest on fewer occasions (20-60 min intervals in cardueline finches) (Newton 1985; Winkler 2004; Ferguson-Lees et al. 2011). Male and female fed the nestlings in equal measure, coinciding with most passerine species (see Draganoiu et al. 2005).

Both males and females removed faecal sacs from the nest, which were either eaten or discarded. This is common behaviour in bullfinches and passerines in general, for nest-cleaning purposes or to hide the nest from predators, the parents also benefitting from ingesting the sacs (e.g. energetically or nutritionally) (Cramp and Perrins 1994; McGowan 1995; Düttmann et al. 1998; Winkler 2004; Quan et al. 2015). However, faecal sacs accumulated around the rim of bullfinch nests in the later stages of the

nestling period when parents ceased removing them (pers. obs.), which is usual for cardueline finches (Newton 1985; Ferguson-Lees et al. 2011).

Clutch size

To date, there are very few data on bullfinch clutch size or brood size in Iberia, referring to a small number of nests containing 4-5 eggs or nestlings (Mestre 1971a; Noval 1971; Román et al. 1996). Overall mean clutch size in the study area (4.56 eggs) is only slightly lower than that reported for the British Isles (4.62 eggs; Robinson 2018) and the Netherlands (4.67 eggs; Bijlsma 1982). In correspondence with these values, modal clutch size is 5 eggs in most of the bullfinch distribution range (Cramp and Perrins 1994; present study). However, in the northernmost areas of Europe and in Russia, clutch size is noticeably larger, e.g. averaging 5.7 eggs in Finland (Cramp and Perrins 1994; Clement 2010). According to the results for the study area and those obtained by other authors in the western Palearctic, bullfinch clutch size does not show any relevant interannual variation, although it may be somewhat higher when seed crops are exceptionally abundant, but as a rule it decreases as the breeding season progresses and clearly drops in the final months (Bijlsma 1982; Newton 1985; Cramp and Perrins 1994).

In the European temperate zone, avian clutch size usually increases towards the north and east, according to analyses that compare species and those that compare populations of the same species, explained mainly as the effect of greater seasonality of resources -higher food availability during breeding- and lower predation pressure (Cody 1971; Sanz 1998; Moreno 2004; Jetz et al. 2008; Griebeler et al. 2010). This geographic pattern is followed by the bullfinch population in the study area, which occupies the extreme SW of the species' distribution range and shows the smallest clutch size. Also, avian clutch size generally decreases at the end of the breeding season, presumably because favourable time is reduced and better quality females, relating to phenotype and/or the territory they occupy, breed earlier (Murphy and Haukioja 1986; Verhulst et al. 1995; Verhulst and Nilsson 2008; Liu et al. 2018). In the case of the bullfinch, Newton (1985) proposes that food being much more plentiful early in the breeding season is a conditioning factor.

Egg traits

Overall mean size of bullfinch eggs, taking length into account, that is, the linear dimension that can be measured most accurately, was 19.83 mm considering each egg individually without differentiating clutches, almost equal to the mean length found in NE Iberia (19.84 mm, n=28 eggs, according to Mestre 1971b) and more similar to that estimated for the subspecies *pileata* MacGillivray, 1837 (19.5 mm, n=214 eggs) and *europaea* Vieillot, 1816 (19.3 mm, n=161 eggs) than that estimated for the nominate subspecies *pyrrhula* (Linnaeus, 1758) (20.8 mm, n=238 eggs) (see Cramp and Perrins 1994). This distribution of egg sizes seems to respond to the general rule by which larger birds, subspecies in this case, lay larger eggs (Winkler 2004). The results obtained in this study also coincide with research into several bird species

related to egg size and egg shape index being more variable among the clutches of different females than those of the same female or eggs in the same clutch, thus proving to be highly heritable morphological characteristics (Hernández 1993; Bánbura and Zieliński 1998; Christians 2002; Dolenec et al. 2007). The results also coincide with egg length being more variable than egg width, so that when egg weight increases length increases rather than width (Cody 1971; Hernández 1993; Deeming 2002a; Dolenec et al. 2007).

Average weight and volume of bullfinch eggs remained fairly constant throughout the breeding season and were not associated to clutch size, as also occurs in other European passerines even without significant interannual changes (Järvinen and Ylimaunu 1986; Järvinen and Pryl 1989; Encabo et al. 2001; Mitrus and Rogala 2001; Dolenec et al. 2007). Avian egg size varies less than other reproductive parameters such as laying date, clutch size or number of broods per season, both among related species and within species (Winkler 2004).

The general patterns of egg shape and eggshell colouration coincide with what is already known for this species (Cramp and Perrins 1994; Clement 2010; Ferguson-Lees et al. 2011). Eggshell colouration pattern was less variable among eggs in the same clutch than among those of different clutches, which probably mostly belonged to different females. This widespread circumstance among avian species reflects the importance of maternal identity (Hernández 1993; Underwood and Sealy 2002; Moreno and Osorno 2003; Dearborn et al. 2012; Poláček et al. 2013).

Nesting success and breeding productivity

Bullfinch nest success increased noticeably as the breeding season progressed and nest failure was higher during nest building and egg phases than during the nestling phase, as also verified for the species in the rest of Europe (Bijlsma 1982; Newton 1985, 1999; Cramp and Perrins 1994; Proffitt et al. 2004; Clement 2010). It should be noted that some of the nests discovered during June-August in the study area already contained chickens at that time, which could influence the monthly variation in nesting success. In England and the Netherlands, there was a marked seasonal increase in nest success, from ≈15-40% in April-May to 70% or more in July-August (Bijlsma 1982; Newton 1985). Predation is thought to be the main cause of avian nest failure, including the case of bullfinch populations studied to date (Cody 1971; Cramp and Perrins 1994; Bradley and Marzluff 2003; Winkler 2004; Węgrzyn and Leniowski 2011; present study).

The predator sighting rate in the area generally decreased from spring to summer, and in England bullfinch nest success increased in the course of the breeding season attributed to a decrease in nest predation (Newton 1999). The bullfinch nest predators most frequently indicated by different authors are corvids, small mustelids and small rodents (Bocheński and Oleś 1981; Cramp and Perrins 1994; Clement 2010). Climbing carnivores, presumably stoats and maybe feral cats *Felis catus* Linnaeus, 1758, were responsible for the death of females in the nest and consumption of the eggs being incubated, and climbing rodents, presumably wood mice *Apodemus sylvaticus* (Linnaeus, 1758) and red squirrels, seemed to be

common egg predators. Predation of parent birds while incubating or brooding is considered unusual (Winkler 2004); however, in the study area it accounted for ≈10% of bullfinch nest failure. Why a female died intact whilst sitting on eggs, also intact, could not be established, but it was probably due to natural causes. In the study area, stoats were occasionally seen climbing trees or shrubs, and the stoat sighting rate was slightly higher in summer than in spring, coinciding with the usual density peak for this species in mid-late summer due to the addition of young individuals; according to a scat analysis, small- to medium-sized passerines and their eggs can be an important component of the stoat's diet in spring-summer in the valley of which the study area is a part (Hernández and Zaldívar 2016 and references therein). Some feral cats, known to be common predators of adult birds and bird nests (Loss et al. 2013; Ibáñez-Álamo et al. 2015), were seen in the hedgerows, at a distance from the villages, on occasions carrying unidentified passerines in their mouths and climbing trees and shrubs (pers. obs.).

The most abundant small rodents in hedgerows and fields in the study area are two vole species (Lusitanian pine vole *Microtus lusitanicus* (Gerbe, 1879) and common vole *M. arvalis* (Pallas, 1779)) and wood mice, but only the latter are good tree climbers, and they do so assiduously (Hernández 2008b). In Spain, wood mice prefer borders with woody vegetation (García et al. 1998). The minimum density value for European populations of wood mice, including Iberian populations, usually occurs in summer (Moreno and Kufner 1988; Montgomery 1989; Tumur et al. 2007), as for red squirrel populations (Hernández 2014 and references therein). Wood mice and red squirrels are known to consume bird eggs and nestlings to some extent, and to inspect bird nests (Bicknell et al. 2009; Hernández 2014; Bosch and Lurz 2012), and small rodents and tree squirrels in general can be important bird nest predators (Schmidt et al. 2001; Bradley and Marzluff 2003; DeGregorio et al. 2016).

The density peak of corvids plus shrikes in July was due mainly to the contribution of fledglings and juveniles to their populations in that month (pers. obs.). However, corvid density was low in spring-summer, with monthly mean values below 2 birds/10 ha for each species, except 2.2 birds/10 ha for carrion crow in July; red-backed shrikes, which reached 4.0 birds/10 ha in July, rarely capture birds in the study area, and they do so in spring (Hernández et al. 1993; Hernández 1995); and young corvids and shrikes probably had a very low impact on bullfinch nests due to their inexperience and even dependence on parents. As for other avian predators, bullfinches are occasionally captured by sparrowhawks in the study area, particularly in autumn-winter, and this raptor species only occasionally depredate passerine nestlings (Hernández 2018 and references therein). Black kites capture few small passerines during the breeding season in Spain, and avian prey are mostly young individuals that have already abandoned the nest (Arroyo 1980; Veiga and Hiraldo 1990; Viñuela and Veiga 1992).

The decrease in nest predation in bullfinches and other passerine species as the season progresses could be related not so much to variations in predator populations but to the gradual increase in foliage density around the nest, making them more difficult to locate thus decreasing predation risk (Newton 1985; Borgmann et al. 2013). In the study area, this factor was not quantitatively monitored during the breeding season, but foliage density clearly increased from March onwards (noticeably during March-April) according to visual appreciation, mainly because hedgerows are formed by broadleaved, chiefly deciduous

shrubs, trees and climbers. However, in the studied bullfinch population no significant association was found between nest-site features in general and nest success, probably because most of the nests were already located at the a priori most favourable sites (e.g. large thorny shrubs, nest orientations providing thermal benefits) and because, despite this, predation pressure was high (A. Hernández and P. Zaldívar in prep.).

Considering the 2001-2005 period as a whole, 60% of rainfall during the entire breeding season (April-August) was recorded in April-May (396.0 mm of 660.1 mm). Some years, there was even snow at the onset of breeding (pers. obs.). After predation, adverse weather conditions is the second most important cause of nest failure, both in bullfinches and birds in general, causing, for example, nest desertion if bad weather is prolonged or the death of nestlings due to hyperthermia in excessive heat conditions (Bijlsma 1982; Hernández 1993; Belda et al. 1995; Winkler 2004).

Bullfinch nest success did not vary significantly between years. However, increases in nest success have been documented in this species when good conifer seed crop has occurred in more northern European latitudes and Russia (Cramp and Perrins 1994; Clement 2010). In the study area, nestling diet was mainly composed of herb seeds and to a much lesser extent, arthropods (A. Hernández in prep.), with no apparent interannual variation in the general availability of these food resources (personal appreciation), probably because the meadows among the hedgerows were regularly irrigated during spring-summer (see Hernández and Zaldívar 2013) and therefore herb seed production was less dependent on rainfall. Avian nest success varies significantly between years if one of the influencing factors such as predation or weather also varies markedly; however, very long-term studies are necessary to detect these events with large effects on populations, which usually occur episodically (Winkler 2004; Crombie and Arcese 2018). Clutch size had no significant effect on bullfinch nest success, coinciding with what has been observed for the species in N and W Europe (Cramp and Perrins 1994).

The overall results for bullfinch breeding productivity in the study area were similar to those estimated in other central and western European regions (Germany, the Netherlands, England), namely, approximately half of the eggs became fledglings leaving the nest, the number of fledglings per nest was ≈2.2-2.4 (≈3.5-4.0 per successful nest), and the maximum annual ratio of juveniles to adults was ≈3-5 (Doerbeck 1963; Bijlsma 1982; Newton 1999). Therefore, Iberian bullfinch productivity seems comparable to that of the subspecies in mid-European latitudes.

There were no significant seasonal differences in the proportion of young bullfinches that fledged in relation to number of eggs laid, although it was slightly higher at the end of the breeding season. However, only complete clutches were considered and not nests with incomplete clutches (or nests being built, obviously), which had a high failure rate at the beginning of the breeding season. Neither were there any significant interannual differences in the number of fledglings per nest or in the ratio of juveniles to adults. In the Netherlands, the number of fledglings per nest was ≈2.0-2.5 for six consecutive years, except one year when it reached ≈3.0 coinciding with an extraordinarily abundant seed crop of conifer species (Bijlsma 1982). As stated above, interannual constancy in food availability was observed in the study area. In

England, Newton (1999) found a higher ratio of juveniles/adults for this species in years when late breeding, i.e. eggs laid from mid-July, had greater importance. As already noted, there were very few such late nests in the study area in the overall number of years considered.

Partial losses in the study area occurred in a percentage of nests similar to that recorded for the Netherlands (Bijlsma 1982), that is, ≈30-35%, in both cases due mainly to unhatched eggs, nestling mortality having very little relevance. Hatching failure, the causal attribution of which was not assessed, is common in birds, more associated in the case of infertility with poor male health/quality or copulation failure, and in the case of embryo mortality with maternal condition, environmental factors and inbreeding depression (Koenig 1982; Hernández 1993; Ponz and Gil-Delgado 2004; Hemmings et al. 2012). Nestling mortality in cardueline finches is considered rare (Newton 1985).

Parental care for dependent young outside the nest

The overall period of records of bullfinch dependent young outside the nest showed a certain delay in comparison with the overall period of young leaving the nest. When they leave the nest, neither bullfinch fledglings nor their feathers are fully grown, so they remain well hidden in the vegetation close to the nest, avoid moving, and go unnoticed (Newton 1995; pers. obs.). The last nests in which fledging took place were found during the second 10-d period of August, and the last dependent young outside the nest usually in the course of September. After leaving the nest, young passerines in general are still dependent on their parents for approximately another three weeks (Düttmann et al. 1998), and 15-20 d in the case of bullfinches (Nicolai 1956; Clement 2010). Nevertheless, from late August no further records of adult bullfinches feeding young outside the nest were obtained. In passerines, the rate of parents feeding dependent young gradually decreases until they become independent (Düttmann et al. 1998).

During June-July, only the adult male was involved with dependent young outside the nest in almost two thirds of cases, probably coinciding with when adult females attended new nests. In multi-brooded passerines, the task of looking after fledglings is normally the responsibility of the males once the females are totally dedicated to the following clutch, and the same occurs in bullfinches (Edwards 1985; Cramp and Perrins 1994; Vega Rivera et al. 1999; Rodríguez and Moreno 2008).

In contrast, from August onwards during the rest of the breeding season, in most records for dependent young outside the nest only one parent was involved but with similar male and female frequency. Brood division after fledging is common behaviour in altricial avian species, more accentuated in final broods not followed by another nesting attempt, and can sometimes even start in the nestling stage (each parent feeds specific nestlings), with different ecological implications, principally increased feeding efficiency and decreased predation risk (Edwards 1985; Anthonisen et al. 1997; Vega Rivera et al. 1999; Rodríguez and Moreno 2008; Tarwater and Brawn 2008).

The mean number of dependent young individuals per record decreased as the breeding season advanced, probably due to brood division being more associated to final broods, whereas in previous

broods all the fledglings were usually accompanied by an adult male or the pair. As expected from the high mortality rate in altricial birds during the early post-fledging period (review by Naef-Daenzer and Grüebler 2016), the mean number of dependent young individuals per record was always lower than the mean number of fledglings leaving the nest.

Concluding remarks

Bullfinch breeding ecology in this Iberian hedgerow habitat seems similar, in general terms, to that previously known for central and western Europe, including the British Isles. Nevertheless, the mean clutch size estimated is the smallest recorded in the western Palearctic, as expected from the general latitudinal and longitudinal patterns of this reproductive parameter in birds. In comparison with northern Europe and Russia, where the species has a larger body size, other differences are found, among which are the earlier start to the breeding season and a shorter mean egg length in Iberian bullfinches. The absence of significant interannual variation in important breeding parameters, such as nest success or productivity, could have been due to lack of interannual variation in the availability of food resources. The results presented correspond to a single population, and some traits, such as the number of broods per pair and season, are not solved with sufficient consistency, so it is necessary to carry out additional studies in other areas and habitats occupied by the Iberian subspecies, as well as to deepen into the different aspects of its reproductive biology.

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Figure 1. Monthly variation in signs of probable breeding of Iberian bullfinches in NW Spain, by direct observation. Nest building and subsequent nest attendance are excluded. Mate-feeding refers to male feeding a female. Courtship display refers to mutual dance and caressing. Twig-display refers to partners showing nest material to one another. n: total records per month. In brackets: number of records per field trip (31 field trips in March, 33 in April, 49 in May, 49 in June, 54 in July, 52 in August). Some individuals showed more than one sign uninterruptedly, thus the 114 grand total records correspond to 97 sightings. Pooled data for 2001-2006.

Figure 2. Temporal variation in Iberian bullfinch breeding stage, in 10-day periods, in NW Spain. For each nest, only one record of a specific breeding stage in a determined 10-day period is considered. They are records for 58 nests (56 found; 2 being built, not found). Pooled data for 2001-2006.

Figure 3. Monthly distribution of clutch size in Iberian bullfinches in NW Spain. The month refers to when the clutch was completed. n: total number of complete clutches per month. Monthly mean clutch size ± SD: 4.72 ± 0.67 in May, 4.70 ± 0.48 in June, 3.50 ± 1.00 in July. Pooled data for 2001-2005.

Figure 4. Iberian bullfinch nest success in relation to the month (above) and year (below) when success or failure was recorded, in NW Spain.

Figure 5. Spring-summer relative abundance of proven and potential predators of Iberian bullfinches in NW Spain, for a 78 ha plot. Pooled data for 2001-2006. Spring: March to May. Summer: June to August. Sighting rate was estimated as the average number of individuals seen per field trip (summation of individuals/number of field trips) multiplied by 10. n: number of field trips.

Figure 6. Yearly proportion of young Iberian bullfinches that left the nest in relation to number of eggs laid in complete clutches in NW Spain.

Figure 7. Yearly proportion of Iberian bullfinch juveniles and adults in NW Spain, according to August sightings. n: total number of identified individuals regarding age. Most juveniles had not started moult. Adults refer to males and females in adult plumage, which could have been non-moulting adults, moulting adults or (highly improbable) juveniles already moulted.

Figure 8. Temporal variation in the sighting rate of dependent young Iberian bullfinches outside the nest in NW Spain. Records of dependent young include records of adults feeding young. Each record refers to one or several young individuals together, linked to one or two (pair) adult individuals which were definitely or very likely their parents. Number of field trips each month: 49 in June, 54 in July, 52 in August, 39 in September, 26 in October. Pooled data for 2001-2006.

Figure 9. Monthly variation in sex differences in parental care for young Iberian bullfinches outside the nest in NW Spain, by direct observation. Records of dependent young include records of adults feeding young. Each record refers to only one or several young individuals together, linked to one or two (pair) adult individuals which were definitely or very likely their parents. Pooled data for 2001-2006.

Figure 10. Mean number of dependent young Iberian bullfinches per record in NW Spain, in relation to sex involved in parental care and month. Young individuals observed outside the nest were considered. n: number of records. Records of dependent young include records of adults feeding young. Each record refers to only one or several young individuals together, linked to one or two (pair) adult individuals which were definitely or very likely their parents. Records in which it was not possible to determine the number of young bullfinches with accuracy were discarded. Pooled data for 2001-2006.

Table 1. Iberian bullfinch egg traits in NW Spain. Mathematical formulas to determine initial weight and volume according to Hoyt (1979). Ratio to determine shape index according to Dolenec (2004). Pooled data for 2001-2005. Only one egg could be measured for some clutches. Only eggs from non-active nests were considered.
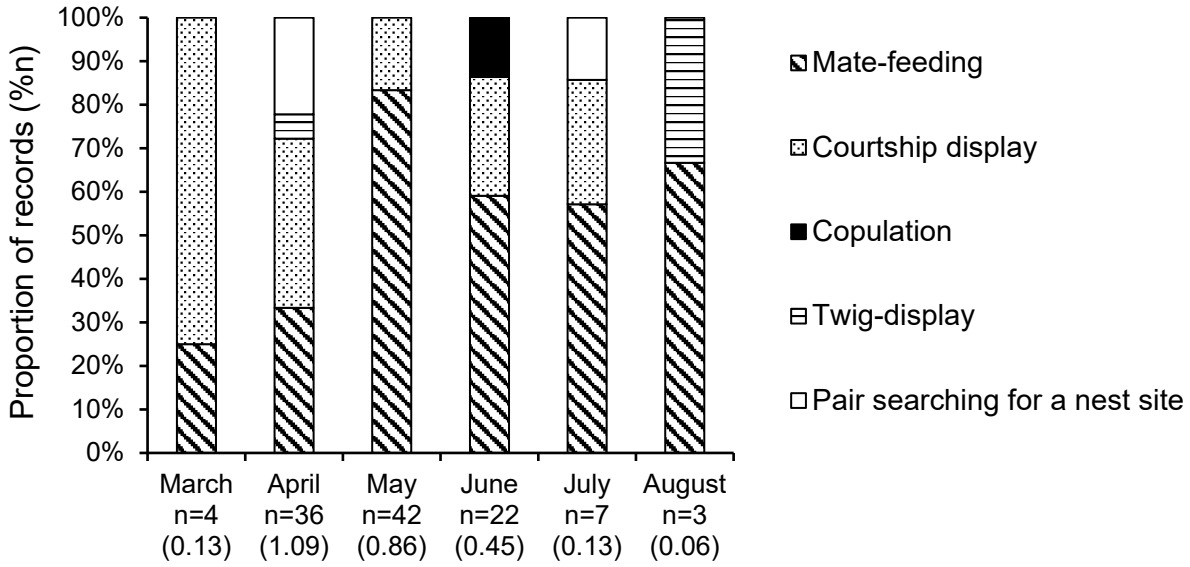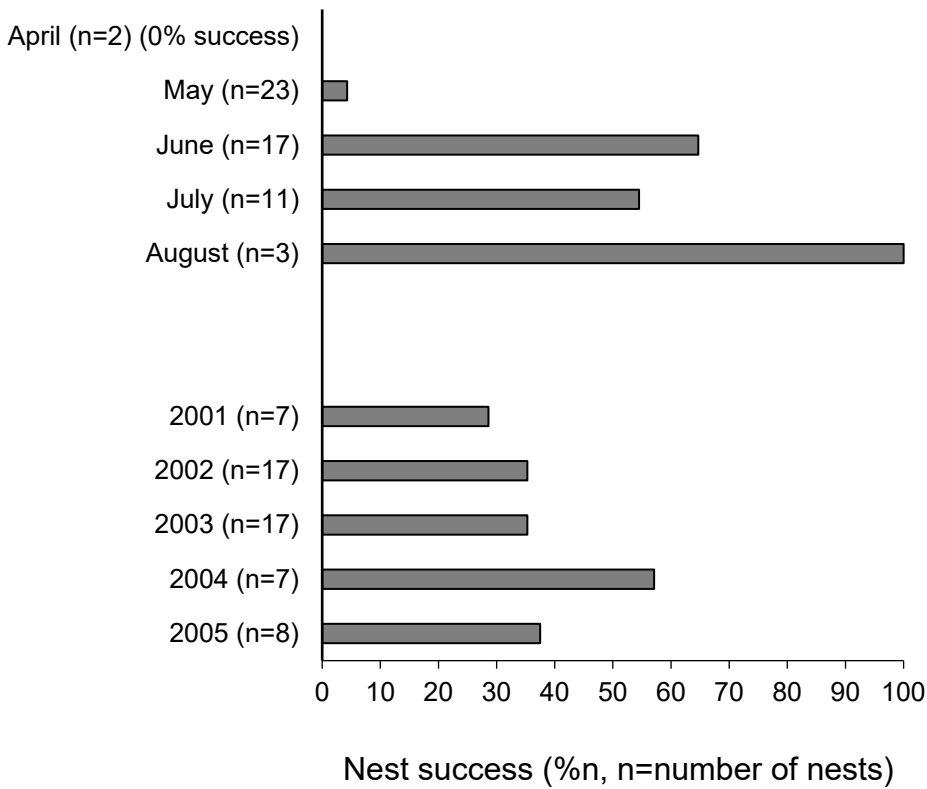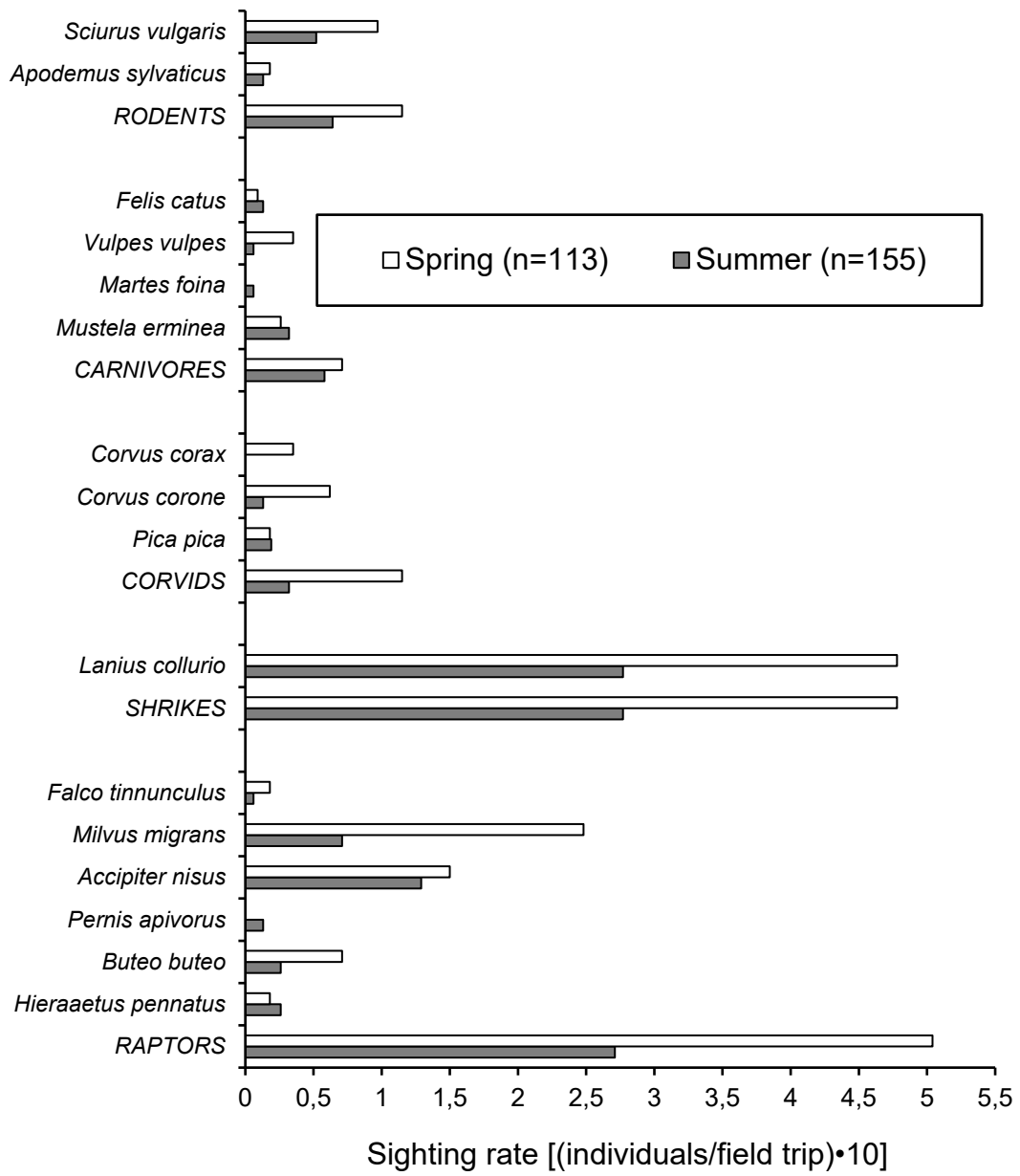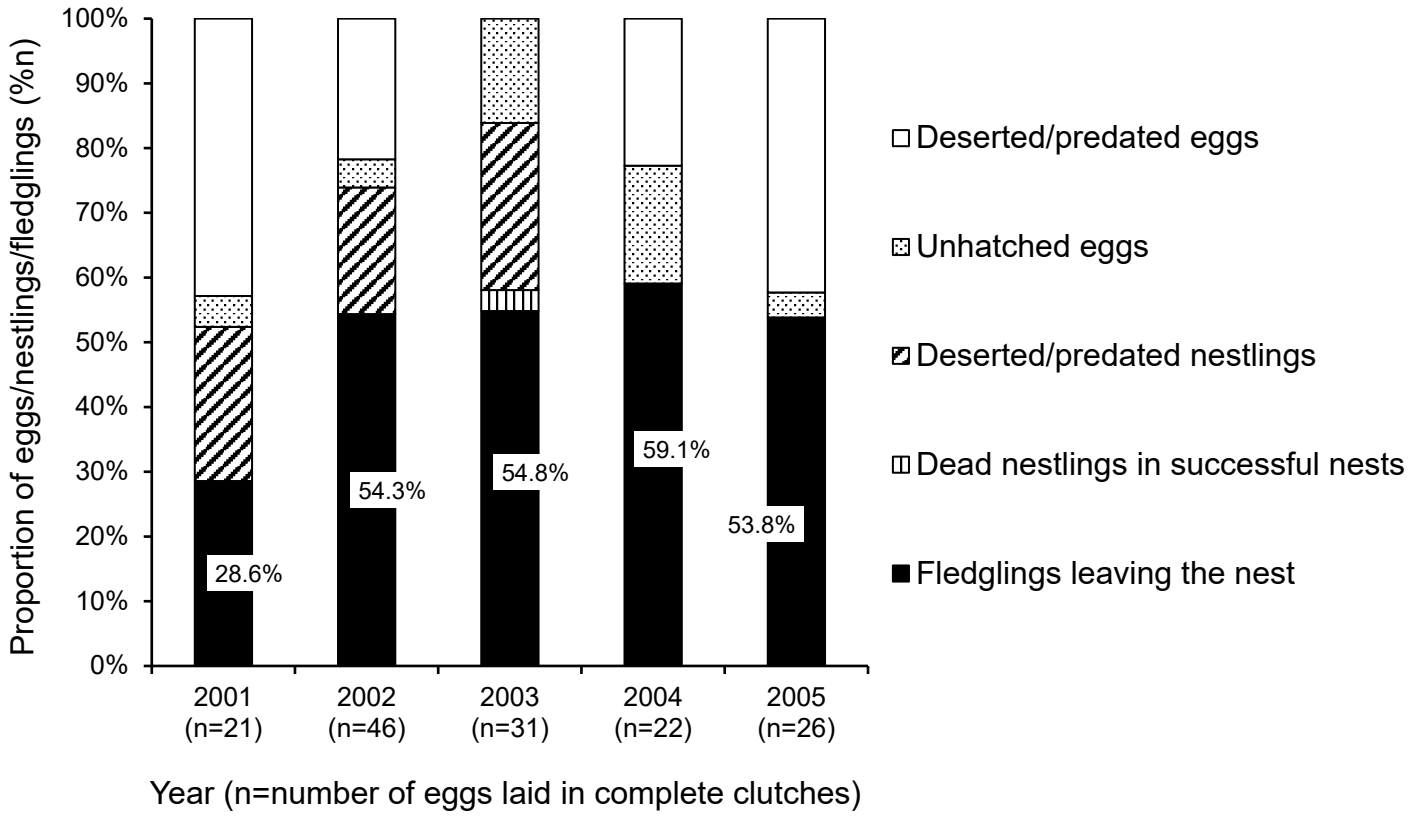
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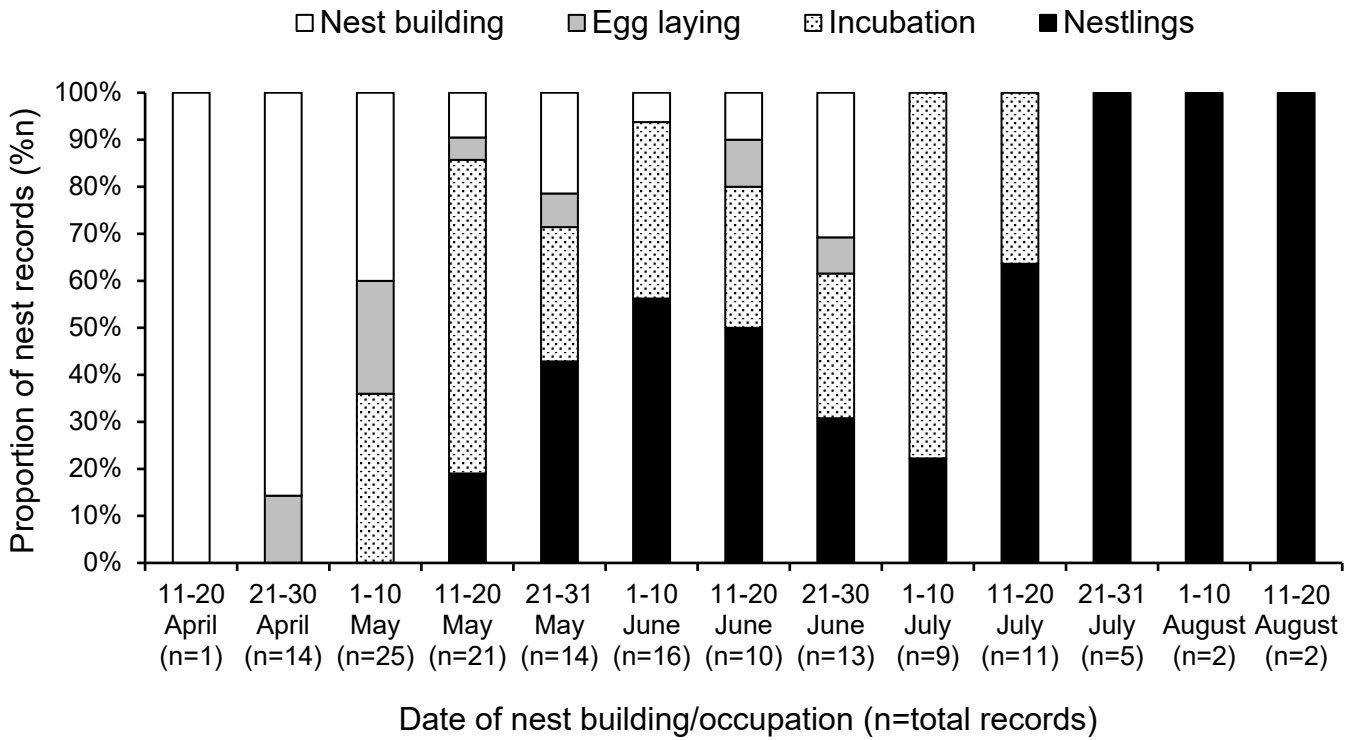
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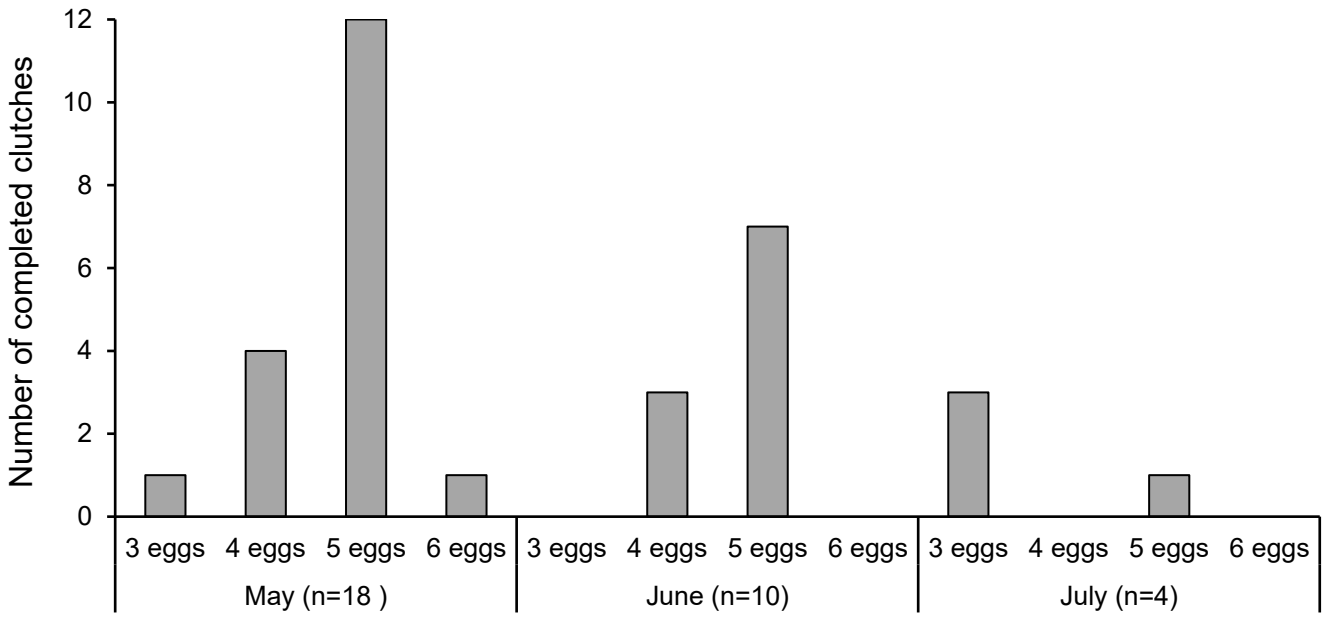
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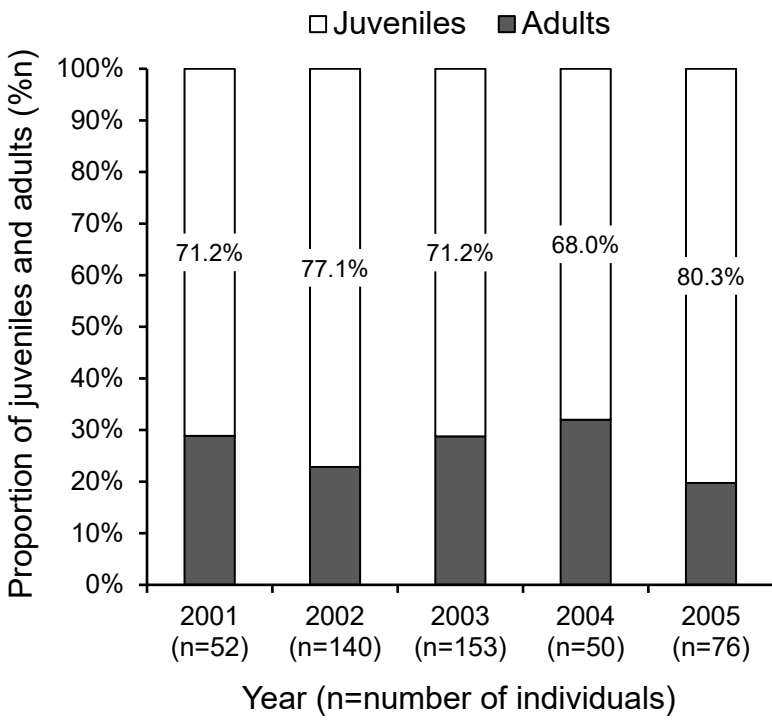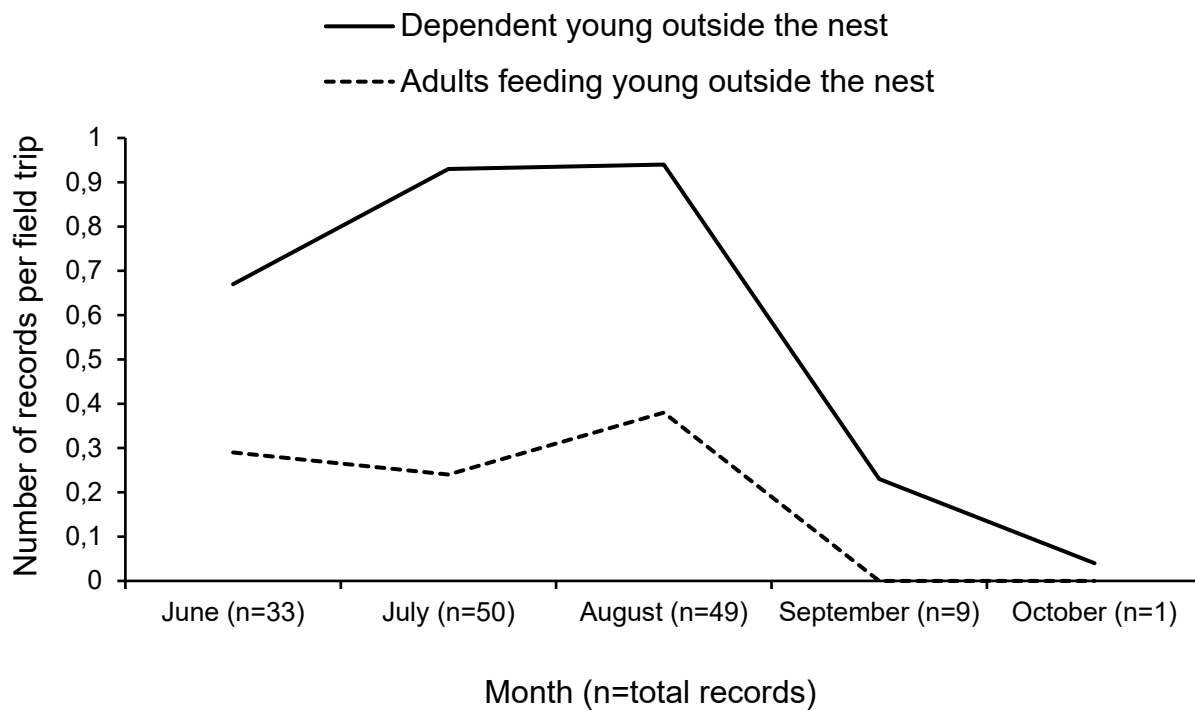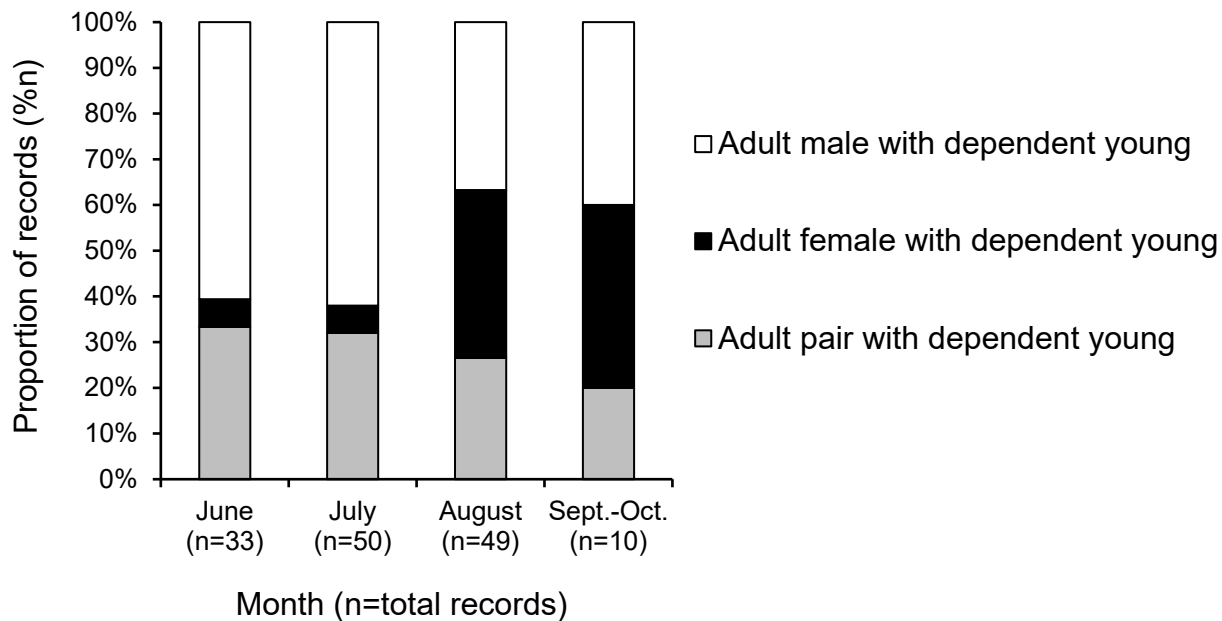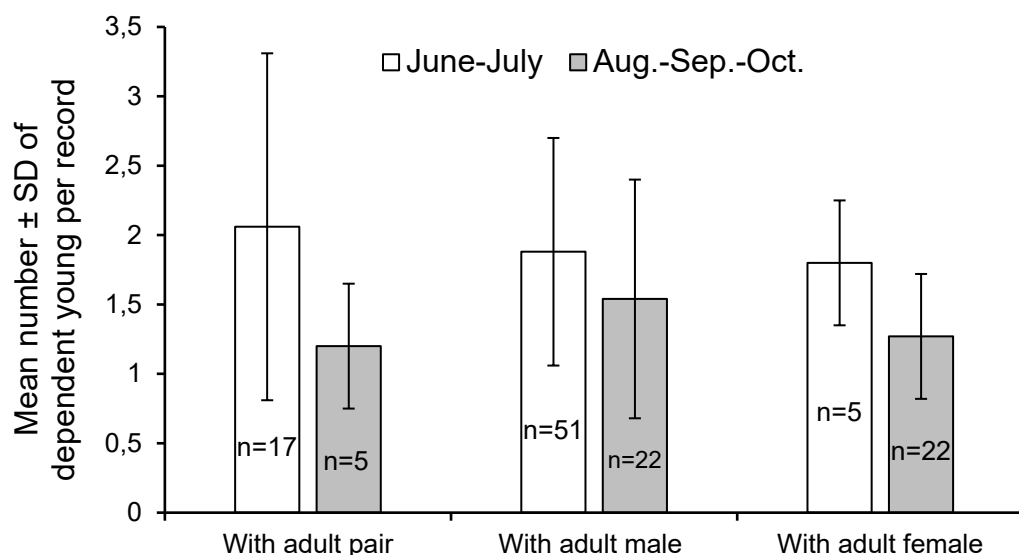

Figure 7

Figure 8

Figure 9

Figure 10

EGG TRAITS	Mean ± SD (range; CV) considering each egg individually n=33 eggs	Mean ± SD (range; CV) considering mean value for each clutch n=14 clutches	Mean ± SD (range) of intra-clutch standard deviation n=7 clutches with at least two eggs measured
Length (L) (mm)	19.83 ± 0.82 (18.30-21.50; 4.13%)	19.71 ± 0.65 (18.65-21.02; 3.30%)	0,41 ± 0.18 (0.17-0.75)
Width (W) (mm)	14.25 ± 0.43 (13.60-15.00; 3.02%)	14.38 ± 0.41 (13.80-15.00; 2.85%)	0.21 ± 0.12 (0.00-0.39)
Initial weight=0.55·LW^2 (g)	2.22 ± 0.17 (1.89-2.54; 7.66%)	2.24 ± 0.15 (1.99-2.45; 6.70%)	0.09 ± 0.05 (0.03-0.15)
Volume=0.51·LW^2 (cm^3)	2.06 ± 0.15 (1.76-2.35; 7.28%)	2.08 ± 0.14 (1.84-2.27; 6.73%)	0.08 ± 0.04 (0.03-0.13)
Shape index=length/width	1.39 ± 0.07 (1.25-1.56; 5.03%)	1.37 ± 0.06 (1.26-1.51; 4.38%)	0.03 ± 0.01 (0.00-0.04)

Table 1