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Temporal variation in the population density and structure of the Eurasian Bullfinch *Pyrrhula pyrrhula* in the Iberian Peninsula

Časovne spremembe populacijske strukture in gostote kalina *Pyrrhula pyrrhula* na Iberskem polotoku

Ángel Hernández[1,2]

[1] Zoology Area, Department of Agroforestry, University of Valladolid, E–34004 Palencia, Spain, e-mail: angel.hernandez.lazaro@uva.es
[2] University Institute for Research in Sustainable Forest Management, University of Valladolid-National Institute for Agriculture and Food Research and Technology, E–34004 Palencia, Spain

The population ecology of the Eurasian Bullfinch *Pyrrhula pyrrhula* is almost unknown in Iberia, where the subspecies *iberiae* lives. The present study provides a first approach to the population attributes of this subspecies in an area located in northern Spain, characterised by a landscape dominated by hedgerows and meadows. In particular, I analysed the population density, age distribution and sex ratio during a six-year period (2001–2006). By exploring the entire area, I estimated the density in each month, and distinguished males, females and juveniles. In winter, samplings by line transect were also used to obtain abundance indices to compare different days, months and years (1999–2005 period). Density values during the breeding season were similar between years, but winter abundances changed considerably at different temporal scales. A density peak was found in July–August, with the highest percentages of juvenile individuals occurring in August–September. Individuals clearly performing post-juvenile moult were seen during August–November. Sex ratio was markedly biased towards males throughout the year. Several biological and ecological characteristics of the Bullfinch, together with a favourable habitat and small changes of environmental conditions from year to year, seemingly promoted the relatively high stable breeding population densities estimated during the study period. The high variation in winter abundances was likely due to short-medium range movements. The high population density in late summer was a consequence of the addition of juveniles each year. The greater parental effort of females compared to males – since the former are responsible for most of the reproductive tasks and directly suffer considerable predation during incubation – was probably a root cause of the skewed sex ratio.

Key words: age distribution, bird numbers, *Pyrrhula pyrrhula iberiae*, seasonality, sex ratio
Ključne Besede: starostna porazdelitev, števila ptic, *Pyrrhula pyrrhula iberiae,* sezonskost, spolno razmerje

1. Introduction

The main factors influencing size and structure of bird populations are fecundity, mortality (or survival) and mobility (immigration/emigration) (Temple 2004, Scott 2020). These factors are, in turn, influenced by others that can be density-dependent such as predation, diseases, parasites and competition for resources (e.g., habitat, mates), or density-independent such as weather conditions, food supply and natural disasters (Ricklefs 1983, Newton 1998, Temple 2004, White 2008, Scott 2020). In short, many life-history traits, which are both interlinked and associated with variation in the environment, determine avian demography (Ricklefs 1983, Alves 2013, Scott 2020). Avian nest success varies significantly between years if one of the influencing factors such as predation or weather also varies markedly; however, long-term studies are necessary to detect these events with large effects on populations, which usually occur episodically (Winkler 2004, Crombie & Arcese 2018). At the end of each breeding season, the proportion of juveniles in bird populations is temporarily high, and age distribution, which is usually quite stable from one year to the next, is re-established prior to the start of the following breeding season (Temple 2004). Skewed juvenile sex ratios and, especially, adult sex ratios are common in wild bird populations, including passerines, and are normally male-biased, despite the fact that sex ratio in eggs, nestlings and fledglings is generally no different from equality, that is, females suffer from higher mortality due to causes not yet fully understood (McClure 1955, Breitwisch 1989, Temple 2004, Donald 2007, Payevsky 2016).

Considering overall information on some of the most studied populations of the Eurasian Bullfinch *Pyrrhula pyrrhula* (hereinafter referred to as the Bullfinch), in particular those in western Europe – central regions (subspecies *europaea*), the British Isles (subspecies *pileata*) and Scandinavia (nominate subspecies *pyrrhula*) – breeding densities vary widely at different spatial scales, and movements during autumn and winter are of varying intensity depending on the subspecies, food availability and weather conditions, although they do not seem to be particularly sensitive to severe winters (Cawthorne & Marchant 1980, Cramp & Perrins 1994A, Fox *et al.* 2009, Clement 2010). Average annual mortality of Bullfinches is about 50%, males outnumber females, the proportion of juvenile individuals gradually increases, as expected, from summer to early autumn, and adult post-breeding and post-juvenile moults occur mainly in August–October (Newton 1966, 1999A, 2000, Cramp & Perrins 1994A, Hogstad 2006). The Eurasian Sparrowhawk *Accipiter nisus* is the main predator of juvenile and adult individuals of this fringilid (Newton 1986, Marquiss 2007).

Nevertheless, in different regions and habitats in the Iberian Peninsula, occupied by the very little known subspecies *Pyrrhula pyrrhula iberiae*, only a few estimates of breeding and winter density are available, as well as incomplete information on movements during autumn and winter, and some data on its role as Eurasian Sparrowhawk prey (Noval 1971, Belamendia 2003, 2012, Carrascal & Palomino 2008, Hernández 2008, 2018, Munilla & Guitián 2012, Fernández & García 2014, Zuberogoitia 2016, Quirós 2020). In order to partly fill this knowledge gap, the main aim of this study is to provide an overview to the population size and structure of the Bullfinch in an area located in northwestern Spain, close to the south-western distribution limits of the species. The target population inhabited mainly hedgerows. The following particular issues and their variation at different temporal scales were assessed: (1) population density, (2) age distribution, and (3) sex ratio. As additional aspect, the seasonal variation in post-juvenile feather moult was briefly analysed. Regarding aspects that are not examined here, habitat, reproductive ecology, food preferences, gregariousness, intraspecific aggression and interspecific competition, are dealt with in detail in separate investigations which provide novel findings relating to this Iberian population (Hernández 2020, 2021, 2022A, B, Hernández & Zaldívar 2021, Á. H. *unpubl. data*). Overall, the Iberian Bullfinch can be considered a multi-brooded and mostly seed-eating bird – obtained from fleshy fruit and herbaceous plants – that forages for food in shrubs/trees or, less frequently, on the ground very close to woody vegetation (Díaz 2016, Hernández 2020, 2021, 2022A). It only breeds in SW France

(Pyrenees) and the mountains of N Portugal and N Spain, and is considered a sedentary bird. However, in the non-breeding season, it can move medium distance outside its breeding distribution, with some individuals reaching even the centre and south of the peninsula or as far as North Africa (Tellería *et al.* 1999, Hernández 2008, Belamendia 2012, Díaz 2016, Quirós 2020). In Spain, at the national level, it is considered that the Bullfinch breeding population was in moderate decline during 1998–2020 (Escandell & Escudero 2021A), and the wintering population in moderate increase from 2008/2009 to 2019/2020 (Escandell & Escudero 2021B). The average breeding population size is estimated at 340,000 individuals for the whole of Spain (Carrascal & Palomino 2008), and the wintering population size is unknown (Belamendia 2012).

It can be expected that the studied population shows seasonal characteristics within the normal patterns and limits known among Bullfinches and temperate zone passerines, without notable inter-annual variations, based on several assumptions: (1) habitat resources seemed to be plentiful and an absence of significant between-year variation in breeding productivity rate has been documented for this Bullfinch population (Hernández 2020, 2021, 2022A), (2) Bullfinches were secondary prey for Eurasian Sparrowhawks in the study area and, in general, predation is not a limiting factor for European songbird populations, particularly in multi-brooded species (Thomson *et al.* 1998, Hernández 2018, Roos *et al.* 2018), (3) tree-feeding birds resist very cold and snowy winters better than ground-feeders, and amongst the former, seed-eaters do so more successfully than insect-eaters (Newton 1998), and (4) most bird populations remain relatively constant in size due to homeostatic mechanisms (e.g., when density decreases, birth and immigration rates increase) (Temple 2004), unless their environment changes significantly (e.g., Rosamond et al. 2020). Although the prevailing resident lifestyle of the Iberian Bullfinch (Belamendia 2012) might seem likely to give it an advantage over migratory birds, which face unique challenges as a result of travelling, the greater dispersal capacity of the latter allows them to better escape habitat degradation and loss, thus balancing the threats (Horns & Şekercioğlu 2018). Also, based on the information above, about sex ratio in birds including the Bullfinch, it is expected that males outnumber females in this Iberian population.

This study is in line with the need to compensate for the noticeable increment in modelling and existing data analyses in biological sciences, so that ornithologists have been urged to determine the ecology of poorly investigated avian taxa by means of field investigation (Ríos-Saldaña *et al.* 2018). Bird subspecies may be of great relevance in this respect as they are generally the best representatives of genetic and ecological diversity found within species (Phillimore & Owens 2006).

2. Methods

2.1. Study area

The study area covers 78 ha and is located in the middle-lower Torío river valley, between Palacio and Manzaneda (42°43'–42°44' N, 5°30'–5°31' W; 900 m a.s.l.; León province, Castile and León 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 (average temperature of ≈ 20 °C), cold winters (≈ 4 °C) with some snowfall, and moderate rainfall (average annual precipitation of ≈ 500 mm) with a relatively short dry summer season, characterise the area (for details of weather during the study period, see Hernández 2020). 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* woods interspersed with very small Scots pine *Pinus sylvestris* plantations on the east side (Figure 1). Some hedgerows border small Canadian poplar *Populus* x *canadensis* 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 2009A, 2014, 2018, Hernández & 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 Canadian poplar plantations and an incipient abandonment of traditional hedgerow management practices.

2.2. Data collection

2.2.1 General procedures

The Bullfinch was present in the study area in all months of the year. Throughout 2001–2006, I observed the bullfinches directly during field trips conducted to investigate their general ecology, and I recorded every detail of each sighting. In a systematic way, I conducted 41 field trips in winter (13 in December, 13 in January, 15 in February), 113 in spring (31 in March, 33 in April, 49 in May), 155 in summer (49 in June, 54 in July, 52 in August), and 84 in autumn (39 in September, 26 in October, 19 in November). By year, 73 field trips were conducted in 2001, 83 in 2002, 81 in 2003, 59 in 2004, 73 in 2005, and 24 in 2006. The total number of field 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. I usually needed two field trips to cover the entire area: approximately

Figure 1: Eurasian Bullfinch subspecies *Pyrrhula pyrrhula iberiae* in northwestern Spain, and partial view of the study area. Above: female in January on the left, male in February on the right. Below: juvenile in July on the left, meadows and hedgerows in May on the right (photos: Á. Hernández)

Slika 1: Kalin podvrste *Pyrrhula pyrrhula iberiae* v severozahodni Španiji in značilna pokrajina območja raziskave. Zgoraj: levo samica v mesecu januarju, desno samec v mesecu februarju. Spodaj: levo juvenilen osebek v juliju, desno travniki in mejice v mesecu maju. (foto: Á. Hernández) half of the area (36 ha) on one field trip, and the other (42 ha) on the following day. On each field trip, I explored the corresponding zone by slowly walking around it, stopping frequently, following the edge of the hedgerows and marginally (≈ 10% sampling effort) the edge of the oak woods (area search method, in the sense of Dunn *et al.* 2006, Pascoe *et al.* 2019), which made it possible to detect the bulk of Bullfinches. Several factors could influence the detectability in different seasons (e.g., singing and other reproductive activities, moulting process, vegetation foliage), but specific research would be necessary to assess the importance of each of them. Small European birds generally show a bimodal pattern of daily locomotor activity, but mobility tends to decrease throughout the day (Bas *et al.* 2007 and references therein). Accordingly, I conducted more than 85% of field trips in the morning in all seasons, and the remainder in the afternoon. The morning field trips lasted from 1 hour after sunrise to 12:00 h (solar time) and the afternoon field trips from 12:00 h (solar time) to 1 hour before sunset, as there was insufficient light at dawn or dusk for reliable sampling. The birds were not individually marked, so their identity could not be determined. Nevertheless, records from the same sampling day most likely corresponded to different individuals, since they were successively left behind during the visits. For the longer term, the study period covering many years, the mentioned Bullfinch movements, which can even occur during their long breeding season (Newton 2000 for British birds), and the short life-span of this species –averaging 2 years (Robinson 2005) – together provide for a high degree of independence between records. If not otherwise specified, males and females refer to individuals in full adult plumage, which could have been non-moulting adults, moulting adults, or individuals recently moulted from juvenile plumage, and juveniles refer to individuals in juvenile plumage (complete or already moulting) either still dependent on their parents or independent. Male, female and juvenile Bullfinches have very different plumage colourations to each other, which enabled them to be easily differentiated in the field under good weather conditions (Figure 1). Non-moulting juveniles are predominantly brown in colour, and do not have the male's red or female's grey-buff underparts, black cap, or pale greyish-white tips of greater wing coverts, these being the most noticeable differences with adult plumage (Clement *et al.* 1993). Consequently, clearly moulting juveniles were distinguished in the field by the colouration that they progressively acquired. An "identified" Bullfinch means that its age and/or sex has been differentiated. I used standard optical equipment, i.e., binoculars and a telescope, to observe birds.

2.2.2. Population density

I estimated the Bullfinch density in each month of each year considering the census with the maximum abundance covering each established sub-area (36 and 42 ha) entirely, and then considering the sum of both abundances in relation to the total surface (78 ha). Only in 2002 and 2003 could this analysis be carried out for most months (12 and 8 months, respectively), since censuses made on bad weather days were discarded. However, I obtained reliable results for July and August, 2002, 2003, 2004 and 2005, months that plainly reflect Bullfinch breeding productivity (Hernández 2020). In the study area, active Bullfinch nests (under construction or containing eggs/nestlings) were found from April to August (Hernández 2020). In addition, a 1.6 km line transect crossing the study area was established and covered on foot from 1 hour after sunrise in different months during 1999–2005, recording the birds seen or heard in a 50 m band on either side of the transect (16 ha sampling surface). I recorded passerines (including the Bullfinch), pigeons, cuckoos and woodpeckers. In spring and summer, a singing male was considered a pair. Line transect is a widely used method for estimating bird abundances (Järvinen & Väisänen 1975, Gregory *et al.* 2004). Considering all of these years together, the number of samplings was 13 in winter, eight in spring, five in summer, and three in autumn. The sampling effort was greater in winter, when the avian community was more variable due to bird movements, increased due to episodes of adverse weather (Á. H. *pers. observ.*). In contrast to censuses covering the entire hedgerow network, I verified that samplings by line transect underestimated Bullfinch density, especially during the breeding season (values were usually below half). The Bullfinch is particularly inconspicuous when breeding, emitting contact calls and songs at fairly low volume (Newton 1985, Hernández 2020). Area search methods allow the observer to examine thicker patches of woody vegetation more closely than with transect methods, thus enabling a more efficient detection of elusive bird species (Pascoe *et al.* 2019). Also, for greater accuracy of the density results provided by a line transect it is advisable to consider bird detectability, which decreases with distance from the observer, and to achieve a minimum of about 40 registrations of the target species (Bibby *et al.* 1992, Gregory *et al.* 2004). Such requirements were not met in the present study. Therefore, I used line transects just to compare different days, months and years in winter, i.e., 13 samplings during December (three samplings), January (six) and February (four), distributed amongst 1999, 2000, 2001, 2002, 2004 and 2005, understanding the density values as abundance indices rather than as rigorous density results.

2.2.3. Population age-sex structure

To establish monthly variation in age structure, each record refers to an identified individual regarding age (adult or juvenile). Adults are males or females in adult plumage (based on colouration), and juveniles individuals in juvenile plumage, complete or already performing post-juvenile moult. To establish seasonal variation in sex structure, each record refers to an identified individual regarding sex (male or female). Males and females are the same class of individuals considered for age structure, with the addition of moulting juveniles when their sex could be determined. To establish whether the sex ratio changed from one year to the next, I evaluated interannual variation for each season considering only individuals in adult plumage, excluding cases with a sample size < 30 (males plus females), the latter occurring in all seasons in 2006, winter in 2003, 2004 and 2005, and autumn in 2005. The mean size of the samples considered for this analysis was 107.63 ± 77.60 individuals (range = 30–279 individuals, n = 16 season-year combinations: 2 different years in winter, 5 in spring, 5 in summer, 4 in autumn). I assessed monthly variation in proportion of moulting juveniles, differentiating between individuals in adult plumage, non-moulting juveniles and moulting juveniles.

2.3. Statistical analyses

Mann-Whitney U test was used to compare two mean ranks of two independent groups (different time periods) considering the two-tailed way, and the chi-square test (χ^2) (with Yates correction for 1 degree of freedom) to compare series of absolute frequencies (Fowler *et al.* 1998, Lowry 1998-2022). When comparing an observed sex ratio with a hypothetical 1:1 sex ratio, I adjusted hypothetical frequencies to the whole next number if the sample size was an odd number (for example, in a sample of 49 individuals observed, 25 males and 25 females would be considered). I estimated standard deviation (SD) as a measurement of dispersion. If not otherwise specified, all years were pooled together, mainly to avoid analysing small sample sizes. During the main study period, nest success and breeding productivity were fairly constant from one year to the next (Hernández 2020).

3. Results

3.1. Population density

Considering censuses covering the entire area and the set of years, a peak was found in the Bullfinch density in July–August (usually above 7.0 birds/10 ha) and values normally in the 4.0–6.0 birds/10 ha interval throughout the rest of the year (Figure 2). Mean densities for July–August in 2002, 2003, 2004, and 2005 were 7.4, 7.6, 7.7, and 9.2 birds/10 ha, respectively. During April-May, approximately 2.5–3.5 pairs/10 ha were estimated. Population density apparently decreased in September–October, and it increased in November. Similarly, the number of Bullfinches identified per systematic field trip decreased from August (488 individuals/52 field trips = 9.4) to September (223/39 = 5.7) and October (112/26 = 4.3), and increased in November (133/19 = 7.0), considering the entire study period (2001–2006). Statistically, there was no significant difference in density between 2002 and 2003, considering the values of all the months of the reproductive period, i.e., April–August (U = 12, n = 5 and 5, P > 0.05), but the density increased significantly from April–June to July–August grouping the values

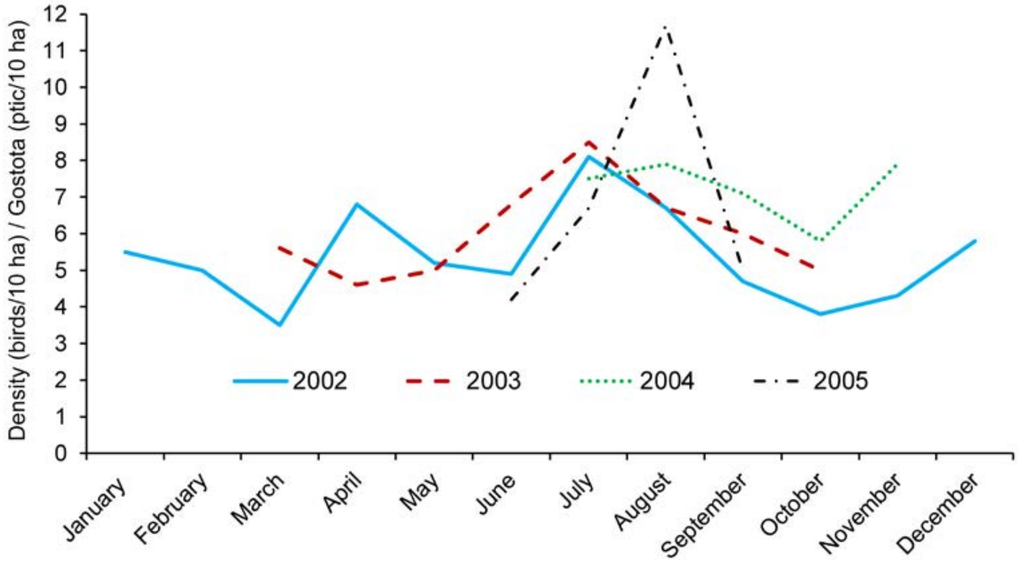

Figure 2: Monthly density of Eurasian Bullfinches in NW Spain. Maximum values for each month during the 2002–2005 period in an area of 78 ha, by inspection of its entire surface

Slika 2: Mesečne gostote kalinov v severozahodni Španiji. Maksimalne vrednosti za vsak mesec v obdobju 2002–2005 na podlagi pregleda celotnega območja raziskave (78 ha).

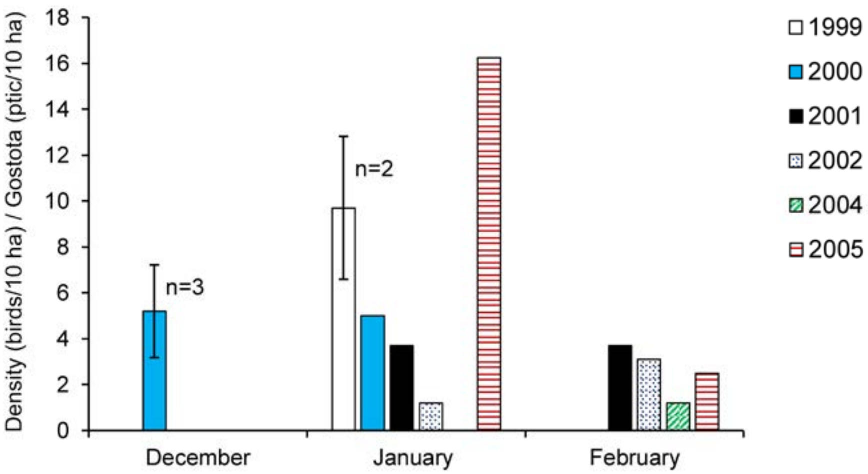

Figure 3: Comparative winter density values of Eurasian Bullfinches in northwestern Spain during different months and years. Each bar corresponds to one sampling by line transect covering an area of 16 ha, except for December 2000 (3 samplings on different days following this itinerary, mean ± SD is shown) and January 1999 (2 samplings on different days following this itinerary, mean ± SD is shown). Density values should be considered as abundance indices rather than as rigorous density results.

Slika 3: Primerjava vrednosti zimskih gostot kalinov v severozahodni Španiji v različnim mesecih in letih. Vsak stolpec ponazarja posamezno vzorčenje z linijskim transektom območja velikosti 16 ha, razen decembra 2000 (3 vzorčenja v različnih dneh po enaki metodi, podana je povprečna ± SD) in januarja 1999 (2 vzorčenji v različnih dneh po enaki metodi, podana je povprečna ± SD). Vrednosti za gostote je treba obravnavati kot indikatorje številčnosti in ne strogo kot rezultate gostot.

from 2002–2005 ($U = 6$, $n = 7$ and 8, $P < 0.05$). As for censuses by line transect, winter density varied noticeably among years from fewer than 1.5 birds/10 ha to over 16 birds/10 ha, and there were also considerable winter density fluctuations between months in the same year and even between censuses in the same month and year (Figure 3).

3.2. Population age-sex structure

The proportion of individuals in juvenile plumage increased progressively from June (≈ 30%) to July (≈ 60%) and August–September (≈ 70–75%), decreased sharply in October (< 15%), and was very low in November (< 1%) (Figure 4). For the June–October period, the difference between months in the age distribution (adults *versus* juveniles) was significant ($\chi^2_4 = 264.21$, $P < 0.001$). Considering all years together, sex ratio did not vary significantly between seasons, with males accounting for approximately 58–64% and females 36–42% ($\chi^2_3 = 3.77$, $P = 0.29$) (Figure 5). There was no significant association between abundance of each sex and year in any season, with males predominating in all cases (winter: $\chi^2_1 = 2.27$, $P = 0.13$; spring: $\chi^2_4 = 1.26$, $P = 0.87$; summer: $\chi^2_4 = 6.69$, $P = 0.15$; autumn: $\chi^2_3 = 7.10$, $P = 0.069$). In eight of 16 season-year combinations the proportion of males was within the 51–60% interval, and in the other eight above 60% (reaching 72%). In all seasons, considering all years together, observed frequencies of males and females were significantly different to those corresponding to a hypothetical 1:1 sex ratio, with increasing significance in the order autumn < winter < spring < summer ($\chi^2_1 = 4.58$, $P = 0.032$; $\chi^2_1 = 7.62$, $P = 0.006$; $\chi^2_1 = 14.39$, $P < 0.001$; $\chi^2_1 = 19.39$, $P < 0.001$; respectively). Of the 91 juveniles whose sex was identified from their body colouration, 55 (60%) were males and 36 (40%) females, but with no significant deviation

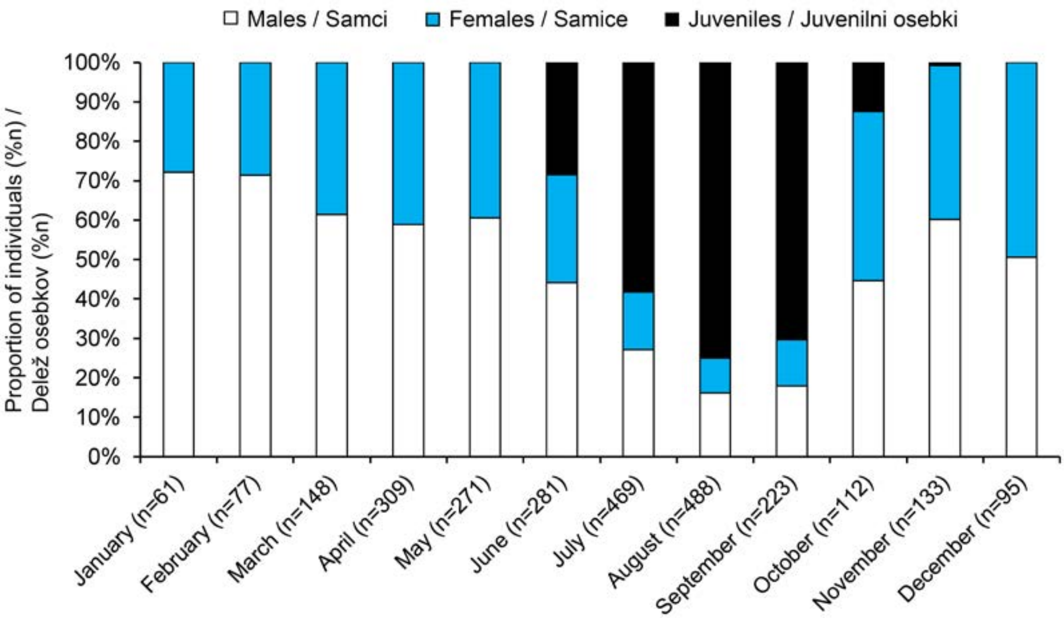

Figure 4: Monthly variation in age of Eurasian Bullfinches in northwestern Spain, by direct observation. *n:* total number of identified individuals regarding age in each month. Males and females are individuals in adult plumage. Pooled data for 2001–2006.

Slika 4: Mesečne spremembe v starosti kalinov v severozahodni Španiji. *n:* skupno število opazovanih osebkov glede na starosti v posameznem mesecu. Samci in samice so osebki v odraslem perju. Podatki zajemajo obdobje 2001–2006.

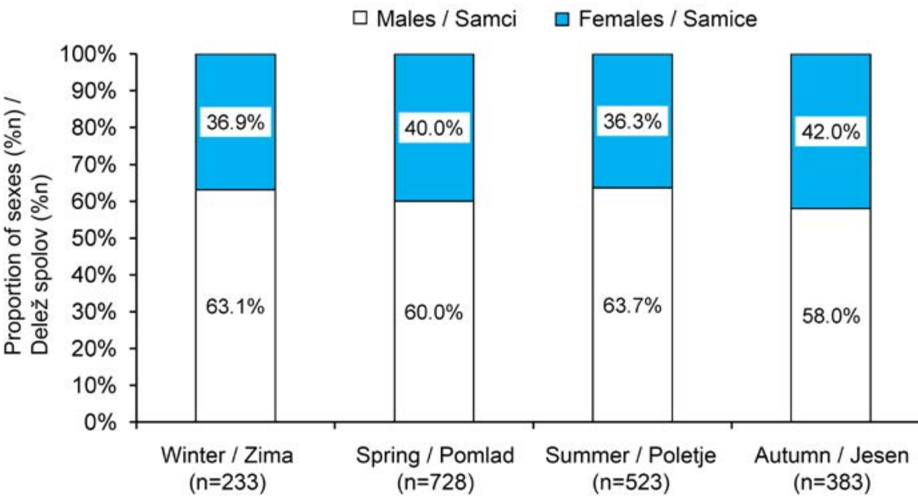

Figure 5: Seasonal variation in sex proportion of Eurasian Bullfinches in northwestern Spain, by direct observation. *n*: total number of identified individuals regarding sex, including moulting juveniles, in each season. Winter: December to February. Spring: March to May. Summer: June to August. Autumn: September to November. Pooled data for 2001–2006.

Slika 5: Sezonske spremembe v spolnem razmerju kalinov v severozahodni Španiji. n: skupno število opazovanih osebkov glede na spol, vključno z juvenilnimi osebki v času golitve, po letnih časih. Zima: december do februar. Pomlad: marec do maj. Poletje: junij do avgust. Jesen: September do November. Podatki zajemajo obdobje 2001–2006.

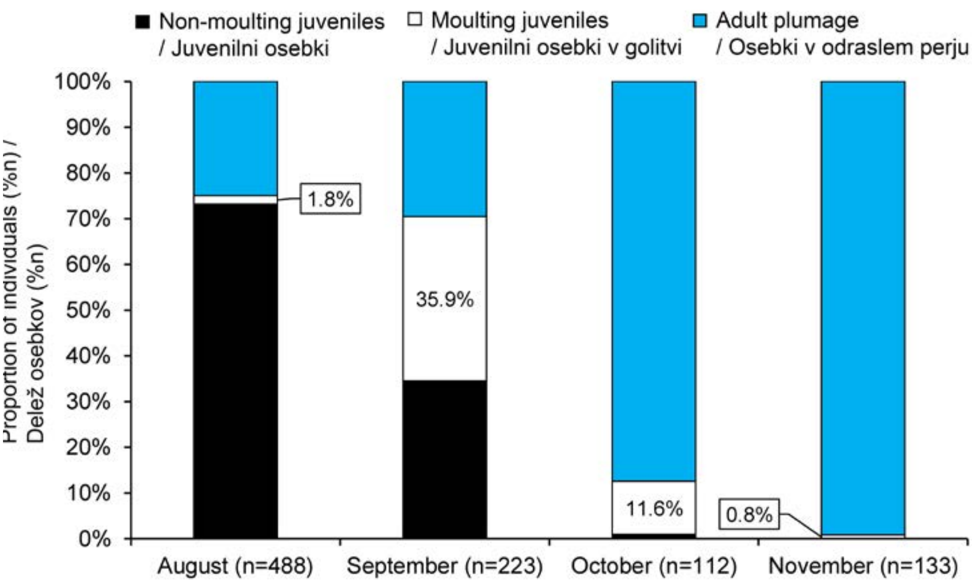

Figure 6: Monthly variation in proportion of moulting Eurasian Bullfinch juveniles in northwestern Spain, by direct observation. *n:* total number of identified individuals (non-moulting and moulting juveniles, and individuals in adult plumage) in each month. Pooled data for 2001–2006.

Slika 6: Mesečne spremembe v deležu juvenilnih kalinov v času golitve v severozahodni Španiji. *n:* skupno število opazovanih osebkov (juvenilni osebki, juvenilni osebki v času golitve in osebki v odraslem perju) po mesecih. Podatki zajemajo obdobje 2001–2006.

from a hypothetical 1:1 sex ratio ($\chi^2_1 = 1.62$, $P = 0.20$). Records of moulting juveniles increased remarkably from August (nine individuals out of 488 total Bullfinches) to September (80 out of 223), and then decreased in October (13 out of 112) and November (only one out of 133) (Figure 6).

4. Discussion

4.1. Population density

Estimates of breeding Bullfinch density in the study area (≈ 3 pairs/10 ha in April–May) are higher than those documented for other areas in León province and other regions in northern Iberia, where values in the interval 0.2–1.5 pairs/10 ha are normal and maximum values do not exceed 2.4 pairs/10 ha, appearing to be more abundant in woodland (e.g., birch, oak, beech, fir, mixed) than farmland (Costa 1993, Belamendia 2003, Carrascal & Palomino 2008, Hernández 2008, Fernández & García 2014, Díaz 2016). In its entire range, the Bullfinch occupies many types of forests and other habitats with woody vegetation and shows highly varied breeding densities, in general up to 1 pair/10 ha but it can reach almost 7 pairs/10 ha, with mean values in farmland of about 0.5 pairs/10 ha (Cramp & Perrins 1994A, Clement 2010). Density is difficult to assess in this finch as it goes unnoticed during the breeding season and is presumably underestimated if intensive specific methods have not been used (Newton 1985, Cramp & Perrins 1994A, Hernández 2008, 2020), which was also confirmed in the present study. Also, Bullfinch breeding population size can change during its prolonged breeding season, due to causes other than mortality, at different spatial scales. In the study area, nesting habitat varied as the breeding season progressed, the use of sites with more trees and shade gradually increasing (Hernández & Zaldívar 2021). 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. According to Brambilla *et al.* (2013), a large number of multi-brooded bird species are likely to show varying density and changes in species-habitat relationships between successive breeding attempts.

Logically, the Bullfinch density peak found in July–August was due to the addition of the juveniles each year. The perceptible decrease in September–October was likely linked to lower detectability during the post-fledging period and moulting process, when Bullfinches and forest passerines in general select dense vegetation, are quieter and seem to be less mobile (Noval 1971, Vitz & Rodewald 2011, Hernández 2021), apart from mortality and perhaps dispersal to an unknown range. Considering all of the years studied together, Bullfinches clearly showing post-juvenile moult were observed between August and November, but records were concentrated in September–October. Survival of songbirds during their first autumn–winter, when they are still inexperienced, is approximately 50% lower than in individuals that have reached their first breeding season (Cody 1971, von Haartman 1971, Temple 2004). In November, a certain level of increase in density coincided with the fact that almost all individuals presented adult plumage, that is, seemingly, they had moulted, and were more mobile and visible (Á. H. *pers. observ.*). Bullfinch densities from spring to autumn were quite similar from year to year. Absence of significant interannual variation in important reproductive parameters, such as nest success or breeding productivity rate, has been documented for this population, probably due to lack of interannual variation in the availability of food resources (Hernández 2020). According to visual assessment carried out at least on a monthly basis, herb seed availability was very high all years, as was shrub/tree bud and arthropod availability – buds formed part of the Bullfinch diet during late winter and spring, and insects and spiders during the breeding season– (Hernández 2022A, Á. H. *unpubl. data*). As regards general fleshy fruit availability, including the particular fruits preferred by the Bullfinch, it was consistently high or very high, except in autumn–winter 2005–2006 when it was moderate, and in autumn–winter 2006–2007 when it was very low (Hernández 2022A, Á. H. *unpubl. data*). Note that the year 2007 is not considered in this study.

Nevertheless, winter abundance changed considerably at different temporal scales. In January 1999, 2000 and 2005, with heavy snowfall in the study area, even heavier at greater altitudes in the valley, where the Bullfinch also breeds, higher densities were recorded than in the same month in 2001 and 2002 when weather conditions were milder. In the first 3 years mentioned, Bullfinch was the first (27% of total number of birds), third (8%) and second (22%) most abundant species in January samplings, respectively, whereas in the other 2 years it was the fifth (8%) and ninth (3%), respectively. Of the three samplings conducted in December 2000, the one in which higher Bullfinch density and greater relative abundance (the most abundant species, 17%) were recorded, was the only sampling that coincided with snow on the ground (on the other 2 days, it was the fourth and sixth species in abundance, 6–7%). Iberian Bullfinches are considered resident birds, but in winter they often move short and medium distances, mainly downwards from mountainous regions to lower areas where shrub and tree seeds are more abundant and/or accessible, sometimes outside their breeding range (Hernández 2008, Munilla & Guitián 2012, Fernández & García 2014). Therefore, the concentration of Bullfinches in certain places rich in favourite seeds, occupation of more open habitats, and greater tendency towards gregariousness, may result in markedly high density values during winter in Spain, exceeding 10 birds/10 ha (Belamendia 2012, Hernández 2021, 2022b, present study). Records of individuals belonging to more northern subspecies arriving in the peninsula are very scarce (Tellería *et al.* 1999, Clement 2010, Díaz 2016). Although small resident bird species generally show the largest population declines after hard winters (Newton 1998), this did not seem to affect the Bullfinch, presumably partly due to its ability to escape and trace food. In Britain, Bullfinch does not usually suffer population declines after severe winter weather (e.g., Cawthorne & Marchant 1980). According to Senar & Borras (2004), flocking and altitudinal movements are amongst the strategies developed by birds to survive winter in Iberia, and certain tree seeds are crucial for some granivorous passerines, including Bullfinches, in this season. The lack of concordance between the suggested trend of the breeding (Escandell & Escudero 2021a) and wintering (Escandell & Escudero 2021b) populations of Bullfinch during the last two decades in Spain (moderate decline and moderate increase, respectively) may be due to the limited reliability of the spring samplings, since they were not exhaustive, and the higher detectability in winter.

4.2. Population age-sex structure

The highest percentages of Bullfinches in juvenile plumage were found in August–September, which fits the timing of breeding of the population under study, whose latest fledging dates were within 11–20 August (Hernández 2020). In an area in England, the proportion of first-year individuals (identified from retained juvenile feathers) among netted Bullfinches increased progressively from July or August until October, and the highest October ratios occurred in the years when the largest proportions of pairs extended their breeding beyond July into August and September (Newton 1999b). As already stated, breeding productivity did not vary significantly from one year to the next in the study area, where there were very few late nests, and none after August (Hernández 2020).

Bullfinch sex ratio was significantly skewed towards males all year (between 1.4:1 and 1.75:1), the same tendency being found by other authors (Newton 2000, Hogstad 2006). In monogamous species, bias in favour of males between 1.1:1 and 4.8:1 has been documented, with ≥ 1.5:1 in many of them (Breitwisch 1989), and for birds in general, males outnumber females by a mean of around 33% (Donald 2007). Therefore, although estimates of avian sex ratios could be influenced by factors such as differences in ecology and behaviour between males and females not completely corrected by the sampling methods employed, survival in females after independence from their parents does actually seem to be lower in comparison with males (Breitwisch 1989, Temple 2004, Donald 2007). Accordingly, statistical significance of male-bias in Bullfinch increased progressively from autumn, when the population should have a higher percentage of first-year individuals, to the following summer, and male-bias was not significant for moulting juveniles. In a Bullfinch population in England, males tended to outnumber females throughout the year in netted samples, with the biggest divergence in the breeding season, attributed to females being confined to their nests during incubation and brooding periods, but with a sex ratio of 1.2:1 also in favour of males between November and March (Newton 2000). In Norway, Hogstad (2006) estimated a male:female ratio of 1.1:1 in Bullfinch for October–April. Perhaps in spring and summer, the combination of both higher accumulated female mortality and permanence in the nest produces the most significant skewed sex ratios in this species. Also, females show more secretive behaviour and appear to be less mobile in their daily routines than males throughout the year (Hernández 2022b). Some events at specific moments could have a certain balancing effect on the estimates, such as high detectability of females during nest building (they do most of the work, accompanied by the male) or decreased detectability of both males and females during moult, when the birds are less active and more hidden from view (Newton 1966, Hernández 2021, Á. H. *pers. observ.*). In the study area, in winter 2004 to 2005, 71% of feeding visits by Bullfinches to guelder roses *Viburnum opulus* corresponded to males and the rest to females (2.5:1) (Hernández 2009b), without this being significantly associated with sexual differences in food preferences (Hernández 2022a).

In birds in general, not enough is known about the main causes of higher mortality in females after independence from parents, or whether these causes change with age. They could be linked to the displayed level of parental effort (which may result in a delayed effect after breeding), to the risk arising from intensity in dispersal and migration (with females moving further away to worse habitats as they are usually subordinates of males), to smaller body size (particularly unfavourable under severe conditions), and even to a smaller relative brain size (associated with lower adaptability) and genetic differences (female birds are more sensitive to recessive mutations as they are the heterogametic sex) (Breitwisch 1989, Temple 2004, Donald 2007, Payevsky 2016). According to autumn–winter Bullfinch ringing results in the Madrid region, located in the centre of peninsular Spain far from its usual breeding range, sex ratio was balanced during 2000–2016 (Quirós 2020). Therefore, under-representation of female Bullfinches in northern Iberia does not seem to be primarily linked to remarkable medium- or long-range movements towards the south. On the contrary, North Eurasian Bullfinches are periodically irruptive, which is associated with weather and food supply, with females and immatures outnumbering or moving further than males and adults on their movements (Cramp & Perrins 1994a, Newton *et al.* 2006, Newton 2008, Fox *et al.* 2009, Clement 2010). The latter finding is in line with the most characteristic features of differential migration by sex among passerines, as males are normally the territorial sex and move away from breeding areas less frequently in order to reach them sooner in spring, they are usually larger than the females, and are typically the dominant sex (Newton 2008, Woodworth *et al.* 2016). However, the Bullfinch shows some distinctive features which theoretically would support what has been found for Iberian populations, namely non-territorial behaviour and a monogamous mating system with longlife faithfulness (Cramp & Perrins 1994a, Hogstad 2006, Clement 2010, Wright 2020), no clear differences in size and weight between sexes (Clement *et al.* 1993, Cramp & Perrins 1994a), and dominance of females over males (Wilkinson 1982, Hogstad 2006, Marquiss 2007, Hernández 2022b). According to Newton (1968), the body condition of Bullfinches does not deteriorate during moult, regardless of sex; to the contrary, they appear to gain weight in that process.

Therefore, greater parental investment by female Bullfinches could be a fundamental cause of skewed sex ratio in this species, as they are responsible for most of the breeding tasks until they share the feeding of nestlings with males (Cramp & Perrins 1994a, Hernández 2020). In the most immediate and extreme case, predation of females while incubating, presumably by stoats *Mustela erminea*, accounted for ≈ 10% of Bullfinch nest failure in the study area (Hernández 2020). But even nest construction is an energetically and temporally expensive activity for birds (review by Mainwaring & Hartley 2013). Although there is no full agreement on the age classes considered, average annual mortality in Bullfinches in European populations is around 50%, as many as 7 percentage points more for adult females than adult males having been found (59% versus 52%) (Haukioja 1969, Bibby 1974, Cramp & Perrins 1994A). Mortality in adult passerine birds in temperate regions occurs especially during the breeding season (Cody 1971, von Haartman 1971). Also, the number of clutches has a negative effect on the survival of adults in winter, as it implies high time and energy expenditure (Dobson 1990, Hansell 2000). Further research needs to be carried out into Bullfinch sex ratio and causes of mortality in males and females.

Bullfinches plainly showing post-juvenile moult were observed during a period of approximately 80 days between August and November. In 2004, when the latest sighting of a moulting juvenile was recorded, nestlings were also observed until later dates (interval 11–20 August) (Hernández 2020), a logical correlation already known for this species (Newton 1999A). In other Bullfinch subspecies and populations, the first moulting juveniles were recorded between mid-July and early September and the last usually during November (hardly ever December), moult lasting between 7 and 9 weeks for each individual (Newton 1966, Cramp & Perrins 1994A, Jenni & Winkler 1994). During moult, juveniles of both sexes were frequently observed together in groups and seemingly separated from adults, as occurred for juveniles in general in summer and autumn (Hernández 2022B).

4.3. Conservation concerns

Different biological and ecological characteristics of the Bullfinch, together with a favourable habitat and little changing environmental conditions from year to year, seemed to promote the relatively high and steady breeding population densities estimated during the study period. Competition with other small passerines for food resources was apparently low, and also for nest sites, since suitable hedges were a plentiful element, and interspecific aggressive encounters involving Bullfinches only occurred very occasionally (Á. H. *unpubl. data*). Differentiated microhabitat, especially by avoiding open ground, and a considerable variety of types of food eaten, with marked changes in diet throughout the year and specialised bud-eating, presumably relaxed competition between Bullfinches and other granivorous and frugivorous birds (Hernández 2021, Hernández 2022A, Á. H. *unpubl. data*). Regarding the granivorous passerines more closely related to the Bullfinch in phylogeny and ecology (see Cramp & Perrins 1994A, B), seven other fringilid and three emberizid species were recorded via line transect. The Eurasian Sparrowhawk was probably the principal predator of Bullfinches in the study area during the non-breeding season, but these did not appear to be amongst the most vulnerable birds – 4.9% of birds caught and 1.3% of biomass consumed – as the bulk of its prey were medium-sized (*Turdus* species), frequently foraging on the ground at some distance from shrubs and trees (Hernández 2018). As far as the current situation in the study area is concerned, some visits for other purposes in 2021, 2022 and 2023 revealed that the Bullfinch was still present and in good conservation status.

The principal threat to this Bullfinch population in the near future is perhaps the gradual disappearance of borders between woody vegetation and meadows, which is slowly becoming more apparent due to the spread of shrubland, the decrease in livestock activities, the increase in land surface for Canadian poplar plantations, and the loss of hedgerows. In northern Spain, the mosaics of mixed land use composed largely of hedgerows, are of great interest for the conservation of many bird species, including the Bullfinch, in both spring and winter (Tellería 1992, Tellería *et al.* 2008). In Spain in general, the two major threats facing Bullfinches are degradation and loss of habitat (Belamendia 2003). In other European countries, the causes suggested for population decline episodes in Bullfinches are very varied, affecting all stages of the life cycle (breeding and non-breeding seasons) and all ages (nestlings, first year birds, adults), but have not been clearly established, underlining how important it is to deepen in the role of habitat components and their qualities (e.g., hedgerow structure and understorey vegetation of woodlands) in the conservation of this fringilid (Siriwardena *et al.* 2001, Robinson 2005). Also, it is essential to consider landscape connectivity for sedentary passerine species that use some habitat elements in preference to others during the year (Cale 2003), as is the case in the Bullfinch.

5. Povzetek

Populacijska ekologija kalina *Pyrrhula pyrrhula* na Iberskem polotoku, kjer je razširjena podvrsta *iberiae*, je skoraj nepoznana. Pričujoča raziskava ponuja prvi opis populacijskih lastnosti te podvrste na severu Španije, kjer pokrajino na območju raziskave sestavlja preplet travnikov in mejic. Raziskava v obdobju šestih let (2001–2006) analizira populacijsko gostoto, starostno strukturo in spolno razmerje. Gostote v gnezditveni sezono so bile med leti podobne, medtem ko so se v zimskih mesecih znatno razlikovale. Najvišje gostote so bile zabeležene julija in avgusta, največji deleži juvenilnih osebkov pa avgusta in septembra. Spolno razmerje je bilo skozi vso leto izrazito v prid samcev. V raziskavi je bila ugotovljena visoka in stabilna gostota gnezditvene populacije, posledica bioloških in ekoloških značilnosti kalinov, primernega habitata in majhnih okoljskih sprememb med leti raziskave. Velika gostota v poznem poletju je bila posledica večjega števila juvenilnih osebkov, velika nihanja v številčnosti v zimskem obdobju pa so najverjetneje posledica premikov osebkov. Razlog za neenakomerno spolno razmerje lahko najbolje pojasnimo z znatno večjim starševskim naporom samic (v primerjavi s samci) in posledično večjo smrtnostjo v obdobju gnezdenja.

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6. References

Alves J. A. (2013): Avian demography in a changing world: a report on the BOU's Annual Conference held at the University of Leicester, 1–3 April. – Ibis 155: 908–911.

Bas J. M., Pons P., Gómez C. (2007): Daily activity of Sardinian warbler *Sylvia melanocephala* in the breeding season. – Ardeola 54: 335–338.

Belamendia G. (2003): Camachuelo común *Pyrrhula pyrrhula* [Eurasian bullfinch *Pyrrhula pyrrhula*]. pp. 592–593. In: Martí R., del Moral J. C. (eds): Atlas de las Aves Reproductoras de España [Spain Breeding Bird Atlas]. – DGCONA-Sociedad Española de Ornitología, Madrid. (in Spanish)

Belamendia G. (2012): Camachuelo común *Pyrrhula pyrrhula* [Eurasian bullfinch *Pyrrhula pyrrhula*]. pp. 534–535. In: del Moral J. C., Molina B., Bermejo A., Palomino D. (eds.): Atlas de las Aves en Invierno en España 2007–2010 [Spain Winter Bird Atlas 2007–2010]. –Ministerio de Agricultura, Alimentación y Medio Ambiente-SEO/BirdLife, Madrid. (in Spanish)

Bibby C. J. (1974): Bullfinch survival and populations. – Wicken Fen Group Report 5: 25–27.

Bibby C. J., Burgess N. D., Hill D. A. (1992): Bird Census Techniques. – Academic Press, London.

Brambilla M., Martino G., Pedrini P. (2013): Changes in song thrush *Turdus philomelos* density and habitat association in apple orchards during the breeding season. – Ardeola 60: 73–83.

Breitwisch R. (1989): Mortality patterns, sex ratios, and parental investment in monogamous birds. pp. 1–50. In: Power D. M. (ed.): Current Ornithology. Volume 6. – Plenum Press, New York.

Cale P. G. (2003): The influence of social behaviour, dispersal and landscape fragmentation on population structure in a sedentary bird. – Biological Conservation 109: 237–248.

Carrascal L. M., Palomino D. (2008): Las Aves Comunes Reproductoras en España: Población en 2004–2006 [Common Breeding Birds in Spain: 2004–2006 Populations]. – SEO/BirdLife, Madrid. (in Spanish)

Cawthorne R. A., Marchant J. H. (1980): The effects of the 1978/79 winter on British bird populations. – Bird Study 27: 163–172.

Clement P. (2010): Eurasian Bullfinch *Pyrrhula pyrrhula*. pp. 609–610. In: Del Hoyo J., Elliott A., Christie D. A. (eds.): Handbook of the Birds of the World. Volume 15. Weavers to New World Warblers. – Lynx Edicions, Barcelona.

Clement P., Harris A., Davis J. (1993): Finches and Sparrows. – Helm, London.

Cody M. L. (1971): Ecological aspects of reproduction. pp. 461–512. In: Farner D. S., King J. R., Parkes K. C. (eds.): Avian Biology. Volume 1. – Academic Press, New York.

Costa L. (1993): Evolución estacional de la avifauna en hayedos de la montaña cantábrica [Seasonal changes in bird community of beech forests in the Cantabrian mountains]. – Ardeola 40: 1–11. (in Spanish)

Cramp S., Perrins C. M. (eds.) (1994A): The Birds of the Western Palearctic. Volume 8. Crows to Finches. – Oxford University Press, Oxford.

Cramp S., Perrins C. M. (eds.) (1994B): The Birds of the Western Palearctic. Volume 9. Buntings and New World Warblers. – Oxford University Press, Oxford.

Crombie M. D., Arcese P. (2018): Temporal variation in the effects of individual and environmental factors on nest success. – Auk 135: 326–341.

Díaz L. (2016): Camachuelo común *Pyrrhula pyrrhula* [Eurasian bullfinch *Pyrrhula pyrrhula*]. In: Salvador A., Morales M. B. (eds.): Enciclopedia Virtual de los Vertebrados Españoles [The Online Encyclopaedia of Spanish Vertebrates]. – Museo Nacional de Ciencias Naturales, Madrid [http://www.vertebradosibericos.org/aves/pyrpyr.html], 10/01/2022. (in Spanish)

Dobson A. (1990): Survival rates and their relationship to life-history traits in some common British birds. pp. 115–146. In: Power D. M. (ed.): Current Ornithology. Volume 7. – Plenum Press, New York.

Donald P. F. (2007): Adult sex ratios in wild bird populations. – Ibis 149: 671–692.

Dunn E. H., Bart J., Collins B. T., Craig B., Dale B., Downes C. M., Francis C. M., Woodley S., Zorn P. (2006): Monitoring Bird Populations in Small Geographic Areas. Special Publication. – Canadian Wildlife Service, Ottawa.

Escandell V., Escudero E. (2021A): Tendencia de las aves en primavera [Spring bird trends]. pp. 6–15. In: SEO/BirdLife: Programas de Seguimiento y Grupos de Trabajo de SEO/BirdLife 2020 [Monitoring Programs and Working Groups, SEO/BirdLife 2020]. – SEO/BirdLife, Madrid. (in Spanish)

Escandell V., Escudero E. (2021B): Tendencia de las aves en invierno [Winter bird trends]. pp. 16–19. In: SEO/BirdLife: Programas de Seguimiento y Grupos de Trabajo de SEO/BirdLife 2020 [Monitoring Programs and Working Groups, SEO/BirdLife 2020]. – SEO/BirdLife, Madrid. (in Spanish)

Fernández M. A., García E. (2014): Camachuelo común *Pyrrhula pyrrhula* [Eurasian bullfinch *Pyrrhula pyrrhula*]. pp. 516–517. In: García E., García-Rovés P., Vigil A., Alonso L. M., Fernández M. A., Silva G., Pascual D., Álvarez D. (eds.): Atlas de las Aves Nidificantes de Asturies (1990–2010) [Asturias Breeding Bird Atlas (1990–2010)]. – Coordinadora Ornitolóxica d'Asturies-INDUROT, Avilés. (in Spanish)

Fowler J., Cohen L., Jarvis P. (1998): Practical Statistics for Field Biology. 2nd Edition. – Wiley, Chichester.

Fox A. D., Kobro S., Lehikoinen A., Lyngs P., Väisänen R. A. (2009): Northern bullfinch *Pyrrhula p. pyrrhula* irruptive behaviour linked to rowanberry *Sorbus aucuparia* abundance. – Ornis Fennica 86: 51–60.

Gregory R. D., Gibbons D. W., Donald P. F. (2004): Bird census and survey techniques. pp. 17–55. In: Sutherland W. J., Newton I., Green R. E. (eds.): Bird Ecology and Conservation. A Handbook of Techniques. – Oxford University Press, Oxford.

Hansell M. (2000): Bird Nests and Construction Behaviour. – Cambridge University Press, Cambridge.

Haukioja E. (1969): Mortality rates of some Finnish passerines. – Ornis Fennica 46: 171–178.

Hernández Á. (2008): Camachuelo común *Pyrrhula pyrrhula* [Eurasian bullfinch *Pyrrhula pyrrhula*]. pp. 271–273. In: García J., Ramos L. A., Vázquez X. (eds.): Atlas de las Aves Reproductoras de León [León Breeding Bird Atlas]. – Diputación de León, León. (in Spanish)

Hernández Á. (2009A): Summer–autumn feeding ecology of pied flycatchers *Ficedula hypoleuca* and spotted flycatchers *Muscicapa striata*: the importance of frugivory in a stopover area in north-west Iberia. – Bird Conservation International 19: 224–238.

Hernández Á. (2009B): Birds and guelder rose *Viburnum opulus*: selective consumption and dispersal via regurgitation of small-sized fruits and seeds. – Plant Ecology 203: 111–122.

Hernández Á. (2014): Seasonal habitat use in Eurasian red squirrels residing in Iberian hedgerows. – Hystrix Italian Journal of Mammalogy 25: 95–100.

Hernández Á. (2018): Diet of Eurasian sparrowhawks in a Northwest Iberian hedgerow habitat throughout the year. – Ornithological Science 17: 95–101.

Hernández Á. (2020): Breeding ecology of Eurasian bullfinches *Pyrrhula pyrrhula* in an Iberian hedgerow habitat. – Journal of Natural History 54: 2613–2645.

Hernández Á. (2021): Habitat use and space preferences of Eurasian Bullfinches *Pyrrhula pyrrhula* in northwestern Iberia throughout the year. – Avian Research 12: 8.

Hernández Á. (2022A): Seasonal feeding habits of the Iberian bullfinch *Pyrrhula pyrrhula iberiae* in northwestern Spain. – Ornithology Research 30: 155–173.

Hernández Á. (2022B): Gregariousness and intraspecific aggression in Iberian bullfinches (*Pyrrhula pyrrhula iberiae*) throughout the year. – Behaviour 159: 615–642.

Hernández Á., Zaldívar P. (2013): Epizoochory in a hedgerow habitat: seasonal variation and selective diaspore adhesion. – Ecological Research 28: 283–295.

Hernández Á., Zaldívar P. (2016): Ecology of stoats *Mustela erminea* in a valley of the Cantabrian Mountains, northwestern Spain. – Vertebrate Zoology 66: 225–238.

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

Hogstad O. (2006): Flock composition, agonistic behaviour and body condition of wintering bullfinches *Pyrrhula pyrrhula*. – Ornis Fennica 83: 131–138.

Horns J. J., Şekercioğlu Ç. H. (2018): Conservation of migratory species. – Current Biology 28: R980–R983.

Järvinen O., Väisänen R. A. (1975): Estimating relative densities of breeding birds by the line transect method. – Oikos 26: 316–322.

Lowry R. (1998-2022): VassarStats: Website for Statistical Computation. – Vassar College, Poughkeepsie [http://vassarstats.net]., 17/01/2022.

Mainwaring M. C., Hartley I. R. (2013): The energetic costs of nest building in birds. – Avian Biology Research 6: 12–17.

Marquiss M. (2007): Seasonal pattern in hawk predation on common bullfinches *Pyrrhula pyrrhula*: evidence of an interaction with habitat affecting food availability. – Bird Study 54: 1–11.

McClure H. E. (1955): Sex and age ratios of some Japanese birds. – Wilson Bulletin 67: 287–290.

Munilla I., Guitián J. (2012): Numerical response of bullfinches *Pyrrhula pyrrhula* to winter seed abundance. – Ornis Fennica 89: 197–205.

Newton I. (1966): The moult of the bullfinch *Pyrrhula pyrrhula*. – Ibis 108: 41–87.

Newton I. (1968): The temperatures, weights, and body composition of molting bullfinches. –Condor 70: 323–332.

Newton I. (1985): Finches. Limpback Edition. – Collins, London.

Newton I. (1986): The Sparrowhawk. – Poyser, Calton.

Newton I. (1998): Population Limitation in Birds. – Academic Press, San Diego.

Newton I. (1999A): An alternative approach to the measurement of seasonal trends in bird breeding success: a case study of the bullfinch *Pyrrhula pyrrhula*. – Journal of Animal Ecology 68: 698–707.

Newton I. (1999B): Age ratios in a bullfinch *Pyrrhula pyrrhula* population over six years. – Bird Study 46: 330–335.

Newton I. (2000): Movements of Bullfinches *Pyrrhula pyrrhula* within the breeding season. – Bird Study 47: 372–376.

Newton I. (2008): The Migration Ecology of Birds. – Academic Press, London.

Newton I., Hobson K. A., Fox A. D., Marquiss M. (2006): An investigation into the provenance of northern bullfinches *Pyrrhula p. pyrrhula* found in winter in Scotland and Denmark. – Journal of Avian Biology 37: 431–435.

Noval A. (1971): Movimientos estacionales y distribucion del Camachuelo común, *Pyrrhula pyrrhula*, en el norte de España [Seasonal movements and distribution of the Eurasian bullfinch, *Pyrrhula pyrrhula*, in northern Spain]. – Ardeola (special issue): 491–507. (in Spanish)

Pascoe B. A., Schlesinger C. A., Pavey C. R., Morton S. R. (2019): Effectiveness of transects, point counts and area searches for bird surveys in arid *Acacia* shrubland. – Corella 43: 31–35.

Payevsky V. A. (2016): Sex-biased survival and philopatry in birds: do they interact? – Biology Bulletin 43(8): 1–15.

Phillimore A. B, Owens I. P. F. (2006): Are subspecies useful in evolutionary and conservation biology? – Proceedings of the Royal Society B 273: 1049–1053.

Quirós Á. (2020): El camachuelo común (*Pyrrhula pyrrhula*) en la Comunidad de Madrid [The Eurasian bullfinch (*Pyrrhula pyrrhula*) in the Madrid region]. pp. 23–36. In: Juan M., de la Torre V., Pérez-Granados C. (eds.): Anuario Ornitológico de Madrid 2018 [Madrid Ornithological Yearbook 2018]. – SEO-Monticola, Madrid. (in Spanish)

Ricklefs R. E. (1983): Comparative avian demography. pp. 1–32. In: Johnston R. F. (ed.): Current Ornithology. Volume 1. – Plenum Press, New York.

Ríos-Saldaña C. A., Delibes-Mateos M., Ferreira C. C. (2018): Are fieldwork studies being relegated to second place in conservation science? – Global Ecology and Conservation 14: e00389.

Rivas-Martínez S. (2007): Mapa de series, geoseries y geopermaseries de vegetación de España [Map of series, geoseries and geopermaseries of vegetation in Spain]. – Itinera Geobotanica 17: 1–436. (in Spanish)

Robinson R. A. (2005): Bullfinch *Pyrrhula pyrrhula*. In: BirdFacts. Profiles of Birds Occurring in Britain and Ireland. – British Trust for Ornithology, Thetford [https://app.bto.org/birdfacts/results/bob17100.htm], 01/02/2022.

Roos S., Smart J., Gibbons D. W., Wilson J. D. (2018): A review of predation as a limiting factor for bird populations in mesopredator-rich landscapes: a case study of the UK. – Biological Reviews of the Cambridge Philosophical Society 93: 1915–1937.

Rosamond K. M., Goded S., Soultan A., Kaplan R. H., Glass A., Kim D. H., Arcilla N. (2020): Not singing in the rain: linking migratory songbird declines with increasing precipitation and brood parasitism vulnerability. – Frontiers in Ecology and Evolution 8: 536769.

Scott G. (2020): Essential Ornithology. 2nd Edition. – Oxford University Press, Oxford.

Senar J. C., Borras A. (2004): Sobrevivir al invierno: estrategias de las aves invernantes en la península Ibérica [Surviving to winter: strategies of wintering birds in the Iberian Peninsula]. – Ardeola 51: 133-168. (in Spanish)

Siriwardena G. M., Freeman S. N., Crick H. Q. P. (2001): The decline of the bullfinch *Pyrrhula pyrrhula* in Britain: is the mechanism known? – Acta Ornithologica 36: 143–152.

Tellería J. L. (1992): Gestión forestal y conservación de las aves en España peninsular [Forestry and the conservation of woodland birds in mainland Spain]. – Ardeola 39: 99–114. (in Spanish)

Tellería J. L., Asensio B., Díaz M. (1999): Aves Ibéricas. Volumen 2. Passeriformes [Iberian Birds. Volume 2. Passeriformes]. – Reyero, Madrid. (in Spanish)

Tellería J. L., Ramírez A., Galarza A., Carbonell R., Pérez-Tris J., Santos T. (2008): Geographical, landscape and habitat effects on birds in northern Spanish farmlands: implications for conservation. – Ardeola 55: 203–219.

Temple S. A. (2004): Individuals, populations, and communities. The ecology of birds. pp. 9.1–9.134. In: Podulka S., Rohrbaugh R. W. Jr, Bonney R. (eds.): Handbook of Bird Biology. – Cornell Lab of Ornithology-Princeton University Press, Ithaca.

Thomson D. L., Green R. E., Gregory R. D., Baillie S. R. (1998): The widespread declines of songbirds in rural Britain do not correlate with the spread of their avian predators. –Proceedings of the Royal Society B 265: 2057–2062.

Vitz A. C., Rodewald A. D. (2011): Influence of condition and habitat use on survival of post-fledging songbirds. – Condor 113: 400–411.

von Haartman L. (1971): Population dynamics. pp. 391–459. In: Farner D. S., King J. R., Parkes K. C. (eds.): Avian Biology. Volume 1. – Academic Press, New York.

White T. C. R. (2008): The role of food, weather and climate in limiting the abundance of animals. – Biological Reviews of the Cambridge Philosophical Society 83: 227–248.

Wilkinson R. (1982): Group size and composition and the frequency of social interactions in bullfinches *Pyrrhula pyrrhula*. – Ornis Scandinavica 13: 117–122.

Winkler D. W. (2004): Nests, eggs, and young: breeding biology of birds. pp. 8.1–8.152. In: Podulka S., Rohrbaugh R. W. Jr, Bonney R. (eds.): Handbook of Bird Biology. – Cornell Lab of Ornithology-Princeton University Press, Ithaca.

Woodworth B. K., Newman A. E. M., Turbek S. P., Dossman B. C., Hobson K. A., Wassenaar L. I., Mitchell G. W., Wheelwright N. T., Norris D. R. (2016): Differential migration and the link between winter latitude, timing of migration, and breeding in a songbird. – Oecologia 181: 413–22.

Wright C. (2020): Pair bonding in Eurasian Bullfinches *Pyrrhula pyrrhula*: observations from a colour-ringing study. – Ringing and Migration 35: 103–113.

Zuberogoitia I. (2016): Gavilán común *Accipiter nisus*: dieta [Eurasian Sparrowhawk *Accipiter nisus*: diet]. In: Rapaces y Carnívoros de Bizkaia [Raptors and Carnivores of Bizkaia]. – [http://depredadoresdebizkaia.blogspot.com/2016/02]. (in Spanish), 04/02/2022. (in Spanish)

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