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Diet and grit characteristics in young Eurasian Bullfinches (*Pyrrhula pyrrhula*) inhabiting Iberian hedgerows

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For the first time, the diet of young Iberian Bullfinches (*Pyrrhula pyrrhula iberiae*) is studied, specifically in a hedgerow habitat in northwestern Spain, through stomach (younger nestlings up to 8 days of age, which died without researcher intervention) and faecal sac (older nestlings) analysis, and secondarily direct observation (nestlings and dependent juveniles). Also, for the first time, grit use by bullfinch nestlings is described in some detail. Bullfinches fed their young with a mixture of seeds and invertebrates, with greater quantitative importance of the former. The identity of the seeds varied considerably between spring and summer, and animal fraction gradually decreased from May to July for older nestlings, in both cases presumably because of the seasonal changes in food availability. Caterpillars and spiders were the most important arthropod prey in the diet. Apparently, the young were not fed non-arthropod invertebrates. The relative importance of invertebrates, which are very rich in proteins, was greater for younger nestlings than for older ones. Difficult to digest hard-bodied prey, such as beetles, were not present in the stomachs of the youngest nestlings. The frequency of occurrence and amount of grit in stomachs increased with nestling age, along with the need to grind food. There were no remarkable differences in number of units, size, or number of colour types of gastroliths between months. The high floristic diversity in the study area, which has great overall conservation value, provides a wide range of resources for bullfinches, including plenty of food for their young.

1. Introduction

The diet of finch (Fringillidae) nestlings in Europe usually consists of a mixture of seeds and invertebrates in variable proportions, the latter being the main source of proteins to favour growth, except for species in the subfamily Fringillinae whose nestlings are fed almost entirely on invertebrates, and some species in the subfamily Carduelinae whose nestlings are fed almost entirely on seeds (Newton 1967a, 1985, Cramp & Perrins 1994, Valera *et al.* 2005, Gil-Delgado *et al.* 2009).

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Granivorous passerines select specific plant foods, mostly seeds in the broader sense, based mainly on their bill size and shape, including feeding of finch nestlings (Newton 1967a, 1985, Willson 1971, Pulliam 1985, review by Díaz 1996). Furthermore, the high proportion of caterpillars (Lepidoptera larvae) and spiders in the diet of passerine nestlings in wooded habitats in temperate and Mediterranean regions has been underlined (Pagani-Núñez *et al.* 2011, Ceia *et al.* 2016, Serrano-Davies & Sanz 2017, Nyffeler *et al.* 2018). In connection with avian diet, ingestion of small stones to break down food in the gizzard and enable digestion is widespread in granivorous, insectivorous, and omnivorous species (McLelland 1979, Best & Gionfriddo 1991, Gionfriddo & Best 1996, 1999, Luttik & de Snoo 2004, Møller & Erritzøe 2010), and parents provide this grit for their nestlings (Barrentine 1980, Alonso 1985, Marques *et al.* 2003, Orłowski *et al.* 2009, Ottens *et al.* 2014). Other secondary functions of bird gastroliths have been suggested, namely, as a supply of minerals such as calcium and potential detoxifying action (see Barrentine 1980, Orłowski *et al.* 2009, Møller & Erritzøe 2010).

Eurasian Bullfinches (*Pyrrhula pyrrhula*) (Carduelinae, Fringillidae) (hereinafter referred to as bullfinches) are considered generalist forest birds that readily accept heterogeneous semi-open landscapes (Cramp & Perrins 1994, Wilson *et al.* 2009, Clement 2010, Hernández 2021). Currently, there are nine recognized bullfinch subspecies, of which *iberiae* occupies southwest France (Pyrenees) and the mountains of northern Portugal and Spain (Clement 2010). The nestling diet composition of certain populations of the species, particularly those in northern, central and western Europe, including the British Isles, is known to some degree, at least with regard to main food types (Newton 1967b, 1985, Cramp & Perrins 1994). Summarizing this knowledge, bullfinches feed their nestlings mostly a mixture of seeds, insects, and spiders, and occasionally include some small terrestrial gastropods. The amount of invertebrates given tends to decrease in the final days of growth (less necessary proteins), at the end of the breeding season (lower availability of invertebrates), and in open country (lower availability of invertebrates than in woodland). Also, there may be some differences in diet composition between broods, even in the same habitat and time, due to very local environment variations, since adults generally forage near the nest. Compared to nestlings, food of plant origin forms the bulk of adult bullfinch diet. According to Newton (1967b), young bullfinches receive grit and free water from their parents, along with food, without providing further details. By contrast, to date, information available on nestling diet in the Iberian subspecies is practically non-existent, except for vague and imprecise references to the probable contribution of herb seeds and some invertebrates (Noval 2000, Díaz 2016). Occasionally, bullfinches have been observed pecking cherries and then feeding fledglings with pieces of pulp in northern Spain (Hernández 2008). Bernis (1957) found grit in the stomach of an adult male bullfinch from Galicia (NW Spain). However, according to the literature reviewed, no information has been published for Iberian bullfinch nestlings in this regard.

Cardueline finches swallow food and then regurgitate it to nestlings without predigesting it (Newton 1967a, 1985). Differential digestion rates of dietary items, with soft items being digested more rapidly (*e.g.*, soft-bodied insects vs. hard seeds) and different passage times, with large hard items persisting for longer, impose the highest risk of bias in any study of bird gut contents (Rosenberg & Cooper 1990, Sutherland 2004). Nevertheless, gut content analysis is considered appropriate for reliably determining the presence of prey items in the nestling diet of small insect-eating songbirds (Kleintjes & Dahlsten 1992). Normally, 10 or fewer stomachs are adequate for assessing species-specific bird diets at particular sites within a collection period (Rosenberg & Cooper 1990, but see Kleintjes & Dahlsten 1992). Regarding bird dropping analysis, one of its disadvantages is the high degree of fragmentation and digestion of samples, making the identification of remains more difficult than stomach contents, together with unequal digestibility between food items (Rosenberg & Cooper 1990, Pulido & Díaz 1994, Stoate *et al.* 1998, Sutherland 2004). Nevertheless, no major differences have been found between the results – range of food items encountered – of the faecal and stomach analysis in passerines, and nestlings typically have lower digestive efficiency than adults, which, comparatively, enables better identification of fragments (Ralph *et al.* 1985, Rosenberg & Cooper 1990, Sutherland 2004). Faecal analysis is a feasible procedure to obtain a rough assessment of diet composition and relative proportion of prey items in nestlings of small insectivorous passerines (Kleintjes & Dahlsten 1992, Poulsen & Aebischer 1995, Moreby & Stoate 2000, Michalski *et al.* 2011). Obviously, dropping analysis is less intrusive than stomach analysis if the latter involves deliberately killing the birds. The direct observation technique is appropriate for assessing the diet and foraging tactics of frugivorous and granivorous birds that feed above the ground, for which species of food plants may be identified, but is less useful for insectivorous birds, especially in detecting inconspicuous prey (Rosenberg & Cooper 1990, Sutherland 2004, Yoshikawa & Osada 2015). Bullfinches accumulate food collected for their young, or for the female in the case of mate-feeding, in special pouches under the lower jaw (up to 1 cm^3 of food), with the consequent bulging of the throat (Newton 1967b, Hernández 2020, Á. Hernández pers. obs.).

The main aim of this study is to provide a first approach to the diet of bullfinch nestlings in an area located in northwestern Mediterranean Spain, close to the southwestern distribution limits of the species. The target population occupied a single general habitat, specifically a dense network of well-grown hedgerows surrounded by woodland. Well-tried techniques in avian research, namely, stomach content analysis – applied to nestlings found dead –, faecal sac analysis, and direct observation, following the usual procedures for each technique (Rosenberg & Cooper 1990, Hernández 1993, Hódar 1994, Sutherland 2004), were used to determine the diet of young bullfinches.

The following issues on nestling diet were assessed quantitatively: (1) relative importance of plant and animal fractions, (2) diversity of foods within these fractions, and (3) variations associated with timing of breeding and nestling age. Direct observation allowed some data on the diet of dependent juveniles to be obtained. Additionally, (4) the results obtained through the different analysis methods were compared, and (5) the relevance of the mineral fraction in stomachs was evaluated and the gastroliths found were described. Important bioecological aspects of this bullfinch population are already known, some of which are closely related to nestling diet, namely feeding habits of adults and independent juveniles (self-feeding), habitat use and space preferences, and breeding, including nestling stage characteristics except for diet composition (Hernández 2020, 2021, 2022, Hernández & Zaldívar 2021). Using part of this information, a secondary aim of the present study is to compare the general young provisioning diet with self-feeding.

Based on the background information set out above, the diet of nestling Iberian bullfinches is expected to be diverse (seeds plus invertebrates) with seasonal and age-related changes in composition, including a higher contribution of animal matter in younger nestlings and at the onset of the breeding season, certain food types being selected according to their size. No notable differences are expected between the general dietary patterns of young Iberian bullfinches and those of other European subspecies, but certain peculiarities associated with the regional and local ecological community are expected in the more detailed range of foods consumed. Caterpillars and spiders are expected to play an important role in nestling diet. The contribution of invertebrates should be greater in nestling diet than in self-feeding. Stomach analysis is expected to provide the most comprehensive results on diet in terms of taxonomic accuracy, and to allow grit use to be properly assessed, but the other techniques are expected to provide a reliable view of the major food categories.

2. Material and 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 (42º 43’–42º 44’ N, 5º 30’–5º 31’ W; 900 m a.s.l.; León province, Castile and León autonomous community), in northwest Spain. Biogeographically, it forms part of the Carpetano-Leonese sector in the Mediterranean West Iberian province (Rivas-Martínez 2007). Hot summers (average temperature of *ca.* 20 ºC), cold winters (*ca.* 4 ºC) with some snowfall, and moderate rainfall (average annual precipitation of *ca.* 500 mm) with a relatively short dry summer season characterize the area. Details on the weather during the study period are available in 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 plantations of Scots Pine (*Pinus sylvestris*) on the east side (see Supplementary Material Fig. S1). Some hedgerows border Canadian Poplar (*Populus* x *canadensis*) plantations. Estimated hedgerow density is 3.3 km per 10 ha. The area is located in a transition zone to the Eurosiberian region, south of the Cantabrian Mountain range, in an extensive hedgerow network of great conservation value for flora and fauna (Hernández 2009, 2018, Hernández & Zaldívar 2013). 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.

2.2. General considerations

All the fieldwork was performed using 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 live birds nor active nests were manipulated (see Dawkins 2007). Throughout 2001–2006, the bullfinches directly observed in the area and maximum details of these sightings were recorded during field trips conducted to investigate various aspects of their ecology. Bullfinches inhabited the area all year round. In particular, general fieldwork to study their breeding ecology was conducted between the months of March (when the first signs of probable breeding were observed) to October (when the last sightings of adults with dependent young were made) (Hernández 2020). In a systematic way, 113 trips were conducted in spring (March: 31, April: 33, May: 49), 155 in summer (June: 49, July: 54, August: 52), and 65 in autumn (September: 39, October: 26). The total number of trips in each season was equally distributed among the years of study as far as possible, except for 2006 when the sampling effort was considerably lower. Two trips were usually needed to cover the entire area: approximately half of the area (36 ha) on one trip, and the other (42 ha) the following day. On each trip, the corresponding zone was explored by slowly walking around it, stopping frequently, following the edge of the hedgerows and marginally (≈10% sampling effort) the edge of the oak woods. Small European birds generally show a bimodal pattern of daily locomotor activity, but mobility tends to decrease throughout the day (Bas *et al.* 2007). 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. Standard optical equipment was used to observe birds, *i.e.*, binoculars and a telescope. Bullfinch density in the area and study period was approximately 2.5–3.5 pairs/10 ha during April–May (Hernández 2020). As far as the current situation is concerned, recent visits to the study area for other purposes in 2022 revealed that the bullfinches are still present and apparently in good conservation status.

More specifically, nests were searched for, found and monitored during April–August of the period 2001–2005 (n=56 nests found). 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. 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. The observer kept the maximum distance possible when visiting the nests to determine their content by visual inspection, with the help of a long-handle mirror if necessary. 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 researcher did not apparently interfere in nest success. The earliest date of nest building was within 11–30 April for all years, and fledglings were recorded leaving the nest during all the ten-day periods from the end of May to mid-August (Hernández 2020; but a nest found in 2021, very close to the study area at the edge of the forest, contained nestlings until early September). 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 4.6 eggs. Bullfinches chose nesting zones with greater shrub and tree cover than that available, and nests were normally placed in hedgerows approximately 1.5 m above the ground, on a wide variety of plant species, but thorny species were selected (Hernández & Zaldívar 2021). Adult activity around the active nests was concentrated in a radius of 100 m, although it was not rare for them to move beyond this distance, sometimes flying out of sight (Hernández 2020).

Nesting success, *i.e.*, at least one young fledged, increased progressively from April–May (4% of 25 nests) to June–July (61% of 28) and August (100% of 3) (Hernández 2020). The principal proximate causes of nest failure were egg desertion/predation (18 of 35 failed nests, 51%), nest desertion during nest building (20%), and nestling desertion/predation (17%). In complete clutches with a known size (n=32), approximately half of the eggs became fledglings leaving the nest, no significant seasonal differences being observed for this parameter. In such clutches, individual losses (n=71) were due to deserted/predated eggs (49%), deserted/predated nestlings (31%), unhatched eggs (18%), and marginally natural death in nestlings in successful nests (<2%) (Hernández 2020).

Both males and females fed nestlings, fledglings, and dependent juveniles. Considering the total number of visits by males and females, parents visited the nest at intervals of *ca.* 17–23 min, resulting in 40–55 times a day (Hernández 2020). Concerning self-feeding, there was no significant difference between males and females in the frequency of plant and animal food records in spring, or in summer between males, females, and juveniles (Hernández 2022). In all, 84% of self-feeding records during spring–summer corresponded to plants (1046 of 1247) and 16% to arthropods, these values being used for comparison with those of parental provisioning of young. Self-feeding records were obtained by direct observation, similar to how the young provisioning records were obtained by direct observation (see below).

2.3. Nestling diet determination

2.3.1. Stomach content analysis

In all, the stomach contents of 13 nestling bullfinches from 5 nests were analysed. By month of death, 9 nestlings from 3 nests corresponded to May, and 4 from 2 to July. By year, 4 nestlings from 1 nest corresponded to 2001, 4 from 1 to 2002, and 5 from 3 to 2003. The nestlings died without researcher intervention in unsuccessful nests (*i.e.*, they were apparently nestlings abandoned due to factors such as weather or predation, so none of them fledged), except for one that died in a successful nest due to natural causes (the rest of the young fledged). None of the nestlings had reached 9 days old when they died, that is, some had, at most, slightly exceeded half of their growth period, as the nestling stage in bullfinches lasts 14–17 days (Hernández 2020). Nestlings with an estimated age of <5 days were differentiated from those with an estimated age of 5–8 days, through visual inspection of their body size and plumage development, and taking into account the approximate hatching date, if known. Nestlings of both ages were recorded in May and July. After verifying that nests were no longer active, dead nestlings were removed and placed in a labelled container with 70% ethanol. In the laboratory, the stomach of each nestling was removed using a scalpel and fine-tip scissors and preserved under the same conditions in individual labelled containers until their contents were analysed. The stomachs were then opened using the same surgical material, and the contents spread on a thin sheet of water in a Petri dish to identify and count food items by examining them under a Motic® SMZ-168 (7.5x–50x magnification range) trinocular stereo microscope equipped with a Moticam 580 (5.0 MP) digital camera. Photographs were taken so that analysis could continue later without depending on physical samples and microscope (as shown in Supplementary Material Fig. S2).

Three main components were considered, namely, plant remains, animal remains, and mineral fraction. For each stomach, plant, animal, and mineral contribution, in terms of volume, was visually estimated with 5% accuracy. Plant remains were mostly whole seeds/fruits, some fragmented, as well as skins and small fibrous pieces, presumably belonging to seeds/fruits ingested. The term "seed" will be used from now on in a broad sense (*e.g.*, it includes whole achene-type fruits found in the stomachs). For each stomach, all of the seeds were counted, the number of different seed types (at species/genus level) was estimated according to their morphology and size, and an attempt was made to identify them. Seeds were identifed by comparing them with pictures (photos/drawings) in botanical encyclopedias or guides (*e.g.*, Castroviejo 1986–2017, Torroba *et al.* 2013) and well-known online media file repositories (*e.g.*, Wikimedia Commons 2004–2021, Alamy 1999–2021, Arkive 2013–2019), together with prior knowledge of the flora in the study area and many of their fruits and seeds (Hernández & Zaldívar 2013, Hernández 2021, Á. Hernández pers. obs.). A large number of the seeds, but not all of them, were identified at species/genus level; thus, the analysis carried out at this level is not quantitative but semi-quantitative. Seed length attributed to each stomach is the mean value of the respective length range found.

All of the animal remains found belonged to small arthropods, and were identified to order level when possible. They were mainly heads, jaws, thoraxes, wings, elytra, legs, and long hairs, in the case of insects; and prosomata, chelicerae, and spinnerets, in the case of spiders. Some prey, such as caterpillars, were found almost whole. The stomachs also contained unidentifiable tiny fragments of arthropods. The contribution of the different arthropod orders was estimated as frequency of occurrence in stomachs.

Mineral fraction was formed by small stones, *i.e.*, gastroliths. For each stomach, all of the gastroliths were counted and the number of gastrolith colours estimated, differentiating between colourless (translucent), whitish, pinkish, reddish, brownish, and blackish, *i.e.*, the six differentiated colour types found in the stomachs as a whole. Gastrolith length attributed to each stomach is the mean value of the respective length range found. Tiny mineral fragments, resembling fine sand, found in one stomach were excluded from the analysis.

2.3.2. Faecal sac analysis

In all, the content of 103 faecal sacs from 15 nests was analysed. The faecal sacs came from a maximum of 46 nestlings. In the case of nests containing more nestlings than faecal sacs collected, the number of faecal sacs was taken as the maximum number of nestlings involved. Faecal sacs were assigned to 20 May–10 June (47 sacs from a maximum of 13 nestlings, 4 nests), 11–30 June (34, 16, 6), and 1–31 July (22, 17, 5), corresponding to the years 2002 (5 nests), 2003 (6), 2004 (2), and 2005 (2). For 14 successful nests, the date assigned was the estimated day when the young fledged, and the faecal sacs were collected when the nest was no longer active. For the remaining nest, which was unsuccessful, it was the day when it was verified that the nestlings, which were at least half-grown, had been predated. Faecal sacs were collected from the nest rim, where the droppings of more developed mobile European finch nestlings, including bullfinches, usually accumulate as parents no longer remove them at the end of the nestling stage (Newton 1985, Ferguson-Lees *et al.* 2011, Hernández 2020). Therefore, the faecal sacs corresponded to older nestlings. Each one was collected with fine-tip tweezers and placed in a small labelled plastic bag. In the laboratory, they were removed from the bags, placed on absorbent paper, left to dry at room temperature and then returned to their respective bags until analysis. Each sac was placed and broken up on a thin sheet of water in a Petri dish for purposes of identification of food items using the same optical equipment as that described for stomach content analysis.

The analysis only considered two main components, namely, plant remains and animal remains, as the presence of small stones was negligible (a few were found in only one faecal sac). For each faecal sac, plant and animal contribution, in terms of volume, was visually estimated with 5% accuracy. Plant remains were above all vegetable matter, highly fragmented by digestion, small fibrous pieces, and, very exceptionally, some small seeds whole or in pieces (a few were found in two faecal sacs). The plant remains were not taxonomically identified.

All of the animal remains found belonged to small arthropods, and were identified to order level when possible. They were mainly heads, antennae, jaws, wings, elytra, hemelytra, legs/leg segments, abdomen segments, and long hairs, in the case of insects; and prosomata, chelicerae, legs/leg segments, and opisthosomata, in the case of spiders. The faecal sacs also contained unidentifiable tiny arthropod fragments. The contribution of the different arthropod orders was estimated as frequency of occurrence in faecal sacs.

2.3.3. Direct observation

Sightings of adults searching for food, filling their buccal pouches, and immediately feeding nestlings or dependent juveniles (all this in a maximum time of 10 min), were recorded during the fieldwork period in 2001–2006 (June: 9 records, July: 36, August: 15). Focal sampling, *i.e.*, watching foraging individual birds for a specific time, is a standard method in studies on avian feeding habits (Sutherland 2004). Each record refers to an individual, differentiating between male and female, entering a nest to feed nestlings or feeding juveniles that had left the nest, regardless of number of nestlings or juveniles fed on each feeding visit. More than one record could occur for the same individual if it collected more than one food type during 10 min prior to feeding. As far as possible, the records were independent of one another, at least those for each sampling day, since the birds were successively left behind during the visits. In addition, the study period covering many years, bullfinch movements – which can even affect some pairs during their long breeding season (Newton 2000 for British birds) – and the short lifespan of this species, averaging 2 years (Robinson 2005), together ensure a high degree of independence between records. The records came from 20 males and 19 females, considering the sum of apparently different individuals from each sampling day.

For each record, food was identified a) visually while the birds ate (*e.g.*, fleshy fruits), b) by inspection immediately after *in situ* (*e.g.*, caterpillars that build communal silken nests), and/or c) by collecting a sample and identifying it in the laboratory (*e.g.*, most herbs). In all cases, it was confirmed whether the food was vegetable or animal (arthropods), but not always identified to lower taxonomic levels. It cannot be completely ruled out that the bullfinches used part of the food collected in this way for self-feeding or to feed females (in the case of males).

2.4. Statistical analysis

The *Z*-score test was used to compare two independent proportions; the Mann–Whitney *U* test to compare two mean ranks of two independent groups; the Kruskal–Wallis test (*H*) to compare three mean ranks of three independent groups; the chi-square test (χ^2), with Yates correction for one degree of freedom, to compare series of absolute frequencies for two variables; 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, Lowry 1998–2022). For rows by columns chi-square tests, the total sample size was not smaller than 50, at least 80% of the cells had an expected frequency equal to or greater than 5, and no cell had an expected frequency smaller than 1. In addition, for 2 x 2 tables, the chi-square test was only used if all expected cell frequencies were equal to or greater than 5. Consequently, for 2 x 2 tables, two-tailed Fisher's exact test was used instead of the chi-square test if any the above requirements were not met (Lowry 1998–2022). In some comparisons between techniques for determining diet, percentages relating to volume were assumed to be sufficiently equivalent to those relating to feeding records and both were considered as absolute frequencies, although this should be taken with caution. For several comparisons in the stomach content analysis, the ratio between two means was used so as not to overuse statistical tests having small sample sizes. The ratio between two means simply refers to the division of the mean with the highest value by the other. Standard deviation (SD) was estimated as a measurement of dispersion. Probability $p<0.05$ was considered statistically significant. All years were pooled together, mainly to avoid analysing small sample sizes. As stated above, the sampling effort in each season was equally distributed among the years of study. Also, little changing environmental conditions from year to year seemed to promote steady breeding population densities during the main study period, nest success and breeding productivity rates were fairly constant from one year to the next, and interannual variation in adult and independent juvenile diet was not remarkable (Hernández 2020, 2022, Á. Hernández unpubl.). All of the nests were in an area characterized by a landscape invariably composed of hedgerows between meadows, which did not allow considering a habitat stratification.

3. Results

3.1. Stomach content analysis

All nestling stomachs contained both plant and arthropod remains (Table 1). Frequency of occurrence of grit was similar in May (56% of 9 stomachs) and July (50% of 4) (*Z*-score = 0.18, p=0.85), but much less in nestlings <5 days old (14% of 7 stomachs) than 5–8 days old nestlings (100% of 6) (*Z*-score = –3.09, p=0.002) (Table 1).

Taking all of the stomachs into account (n=13), mean percent volume was 66 ± 26% (range = 10–90%) for plant remains, 31 ± 26% (range = 5–90%) for animal remains, and 3 ± 3% (range = 0–10%) for grit. Mean percent volume ratio between May and July was low for plant (1.2), animal (1.3), and mineral (1.3) fractions (Fig. 1). Comparing ages, such ratio was low for plant (1.2) and animal (1.2) fractions, but high for mineral fraction (8.3), grit accounting for less than 1% on average in nestlings <5 days old and almost 6% in those aged 5–8 days (*U*=2.5 , p<0.01, n=7 and 6 stomachs respectively) (Fig. 1).

Regarding plant remains for the 14 total stomachs, the mean number of seed types was 4, mean number of seeds approximately 70, and mean seed length slightly over 2 mm (Fig. 2). Mean ratios between months (May and July) and between ages (<5 d and 5–8 d old nestlings) were low or moderately low for these variables (seed types: 1.3 and 1.2, respectively; number of seeds: 1.8 and 2.3; size: 1.4 and 1.3) (Fig. 2). Fourteen seed species belonging to 10 families (Asteraceae, Caprifoliaceae, Caryophyllaceae, Fabaceae, Geraniaceae, Polygonaceae, Ranunculaceae, Rosaceae, Urticaceae, Violaceae) were identified. Most of the seeds corresponded to dry fruits of herb species, except for a few Common Honeysuckle

	Nest	Nestling	Plant remains	Animal remains	Gastroliths
<5 days old	Nest 1 (May 2002)	1	85	15	0
		2	90	10	0
		3	85	15	0
		4	90	10	0
	Nest 2 (July 2003)	1	50	50	0
		2	10	90	0
		3	90	5	5
5−8 days old	Nest 3 (May 2001)	1	45	50	5
		2	55	40	5
		3	40	55	5
		4	50	45	5
	Nest 4 (May 2003)	1	85	10	5
	Nest 5 (July 2003)	1	85	5	10

Table 1. Individualized percent volume of plant, animal, and mineral fractions in stomachs of Iberian bullfinch nestlings in northwest Spain, regarding estimated age at death, and month and year of death. For each stomach, plant, animal, and mineral contribution was visually estimated with 5% accuracy.

(*Lonicera periclymenum*) and Bramble (*Rubus* spp.) seeds (fleshy fruits of shrub species). In May, seeds appearing in a higher number of stomachs and/or in greater quantity were Daisy (*Bellis perennis*), Mouse-eared Chickweed (*Cerastium fontanum*), Chickweed (*Stellaria media*), Dandelion (*Taraxacum* gr. *officinale*), Common Nettle (*Urtica dioica*), and Violet (*Viola* spp.). In July stomachs, the seeds of Cranesbill (*Geranium* spp.) predominated, but those of Common Honeysuckle, Medick (*Medicago* spp.), Buttercup (*Ranunculus* spp.), Dock (*Rumex* spp.), and Common Nettle were also found. Dandelion seeds were particularly abundant in some May stomachs (as many as 130 units in one). Only two seed types (Cranesbill and Common Nettle) coincided in May and July stomachs. However, five seed types coincided in the stomachs of <5 days and 5–8 days old nestlings, namely, Bramble, Chickweed, Dandelion, Common Nettle, and Violet.

Both insects and spiders were found in ≥75% of stomachs in any month and at any age, with no significant differences in the occurrence of either prey types between May and July (Fisher's exact test, $p=0.99$) or between nestlings <5 days and 5–8 days old (Fisher's exact test, $p=0.99$) (Fig. 3). Insects could only be identified at the order level in May stomachs (Fig. 3). Lepidoptera remains, belonging to caterpillars, appeared very frequently in this month (8 of 9 stomachs, 89%) regardless of nestling age. Coleoptera remains, belonging to adult beetles, were only found for nestlings 5–8 days old (4 of 6 stomachs, 67%). Diptera remains, belonging to adult flies, only appeared in the stomach of one nestling <5 days old. As for the relative abundance of remains of different arthropod orders in particular stomachs, in some cases where this could be established with certain consistency, spiders predominated, or caterpillars and spiders in equal proportion, with lower number of beetles and negligible proportion of flies. Individual prey could not usually be counted accurately due to fragmentation, but, for example, at least eight caterpillars were found in one stomach.

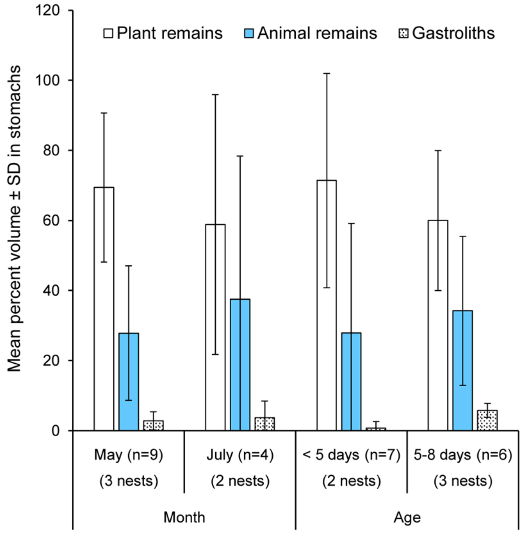

Fig. 1. Mean percent volume of plant, animal, and mineral fractions in stomachs of Iberian bullfinch nestlings in northwest Spain, regarding month of death and estimated age at death. Sample size (n) is the number of nestlings. For each stomach, plant, animal, and mineral contribution was visually estimated with 5% accuracy. Pooled data for 2001–2003.

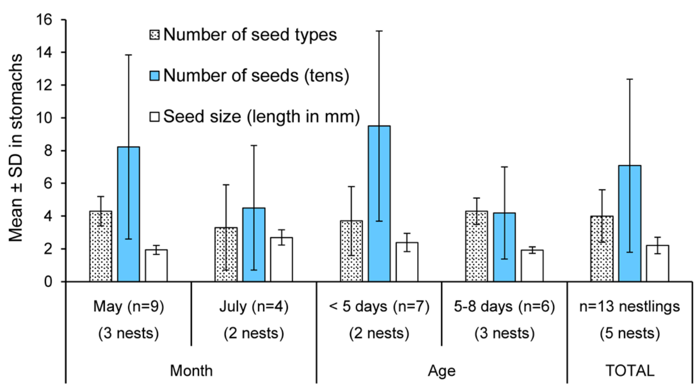

Fig. 2. General attributes of seed presence in stomachs of Iberian bullfinch nestlings in northwest Spain, regarding month of death and estimated age at death. Sample size (n) is the number of nestlings. Seed types refers to the number of plant species. The number of seeds is expressed as the number of tens (groups of 10 seeds). Pooled data for 2001–2003.

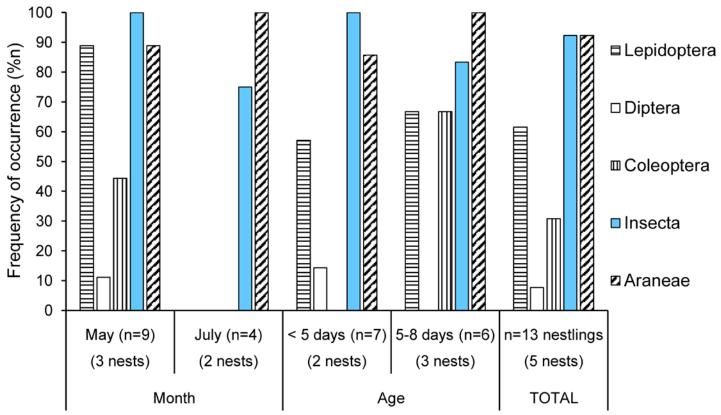

Fig. 3. Frequency of occurrence of arthropod remains in stomachs of Iberian bullfinch nestlings in northwest Spain, regarding month of death and estimated age at death. Sample size (n) is the number of nestlings. Insecta includes all stomachs containing remains of insects, whether or not identified to order level. All stomachs contained arthropod remains. Pooled data for 2001–2003.

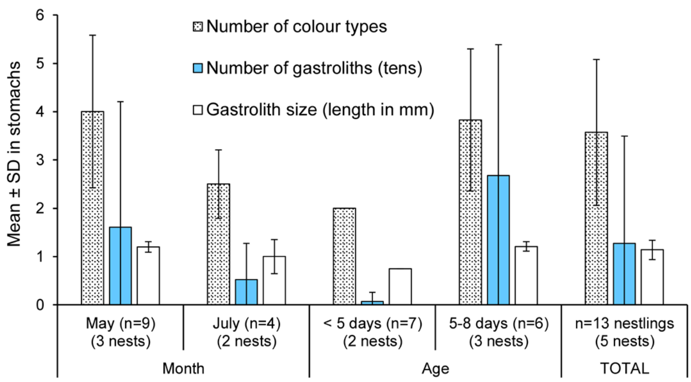

Fig. 4. General attributes of gastrolith presence in stomachs of Iberian bullfinch nestlings in northwest Spain, regarding month of death and estimated age at death. Sample size (n) is the number of nestlings. Possible colour types: colourless (translucent), whitish, pink, reddish, brownish, and blackish. Restrictions: no gastroliths were found in 6 of the 13 total stomachs. These stomachs were included in the calculation of the number of gastroliths (with a value of 0), but not in that of size and colour type. Therefore, the sample size for these two variables is n=5 nestlings from 2 nests (May); n=2 nestlings from 2 nests (July); n=1 nestling from 1 nest, SD=0 (<5 d old); n=6 nestlings from 3 nests (5–8 d old). The number of gastroliths is expressed as the number of tens (groups of 10 gastroliths). Pooled data for 2001–2003.

With regard to mineral fraction for total stomachs (n=13), the mean number of gastroliths was approximately 12 (range = 0–81), and, considering only stomachs containing them (n=7), mean gastrolith length was just over 1 mm and mean number of gastrolith colours just under 4 (Fig. 4). The mean number of gastroliths in the stomachs containing them was 23.7 ± 24.2 (range = 5−81, n=7). Mean ratios between months (May and July) and between ages (<5 d and 5–8 d old nestlings) were generally low or moderate for these variables (colour types: 1.6 and 1.9, respectively; size: 1.2 and 1.7; number of units: 3.2 between months), but mean ratio between ages was very high for number of gastroliths (38.3), grit accounting for 0.7 units on average in nestlings <5 days old and 26.8 in those aged 5–8 days (U=0, p<0.01, n=7 and 6 stomachs respectively) (Fig. 4). The number of colour types in the grit was positively and significantly correlated with the number of grit particles (r_s=0.95, p=0.001, n=7 stomachs). Six colour types were observed in the stomach containing the most grit particles (n=81 gastroliths). Gastroliths were irregular in shape, but compact and not very elongated, some even almost spherical.

3.2. Faecal sac analysis

Significant differences were observed in percent volume of plant and animal remains among faecal sacs from different periods of the breeding season (H_2=6.29, p=0.04, n=4, 6, and 5 nests; both for plant and animal remains), with a progressive decrease in the importance of animal fraction, from a mean of just over 10% during 20 May–10 June to approximately 4% in July (Fig. 5). Plant remains were found in all faecal sacs in all time periods (n=103). Arthropod remains were found in all of the 20 May–10 June faecal sacs (n=47), in 82% of the 34 corresponding to 11–30 June, and in 64% of the 22 corresponding to July (Fig. 6). Similarly, the frequency of occurrence of the main arthropod orders, *i.e.*, Lepidoptera (caterpillars), Coleoptera (adults), and Araneae, decreased from May–early June to July (Fig. 6). Nevertheless, in all nests (n=15), at least part of the faecal sacs removed contained arthropod remains. Taking into account the frequency of occurrence in faecal sacs, there was no significant association between time periods (the three already mentioned) and main prey types (insects and spiders) (χ^2_2=2.72, p=0.25), even though the relative importance of spiders tended to increase and that of insects to decrease from May–early June to July (from 44% to 62%, and from 56% to 38%, respectively). Considering three prey types (lepidopteran caterpillars, the remaining insects identified at the order level together, and spiders), this same analysis also resulted in non-significant association (χ^2_4=5.72, p=0.22).

3.3. Direct observation

According to direct observations, bullfinches provisioned the young (nestlings and dependent juveniles) with plant (82% of 60 feeding visits) and animal (18%) food. They used at least 10 plant species belonging to 6 families (Asteraceae, Caprifoliaceae, Geraniaceae, Polygonaceae, Ranunculaceae, Rosaceae), mainly seeds corresponding to dry fruits of herb species, but also flower buds of herb species and seeds/pulp of fleshy fruits of shrub/tree species (Table 2).

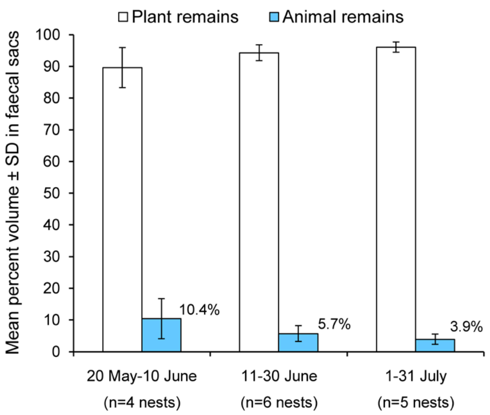

Fig. 5. Mean percent volume of plant and animal remains in faecal sacs of Iberian bullfinch nestlings in northwest Spain during the breeding season. The faecal sacs belonged to older nestlings. Sample size (n) is the number of occupied nests. For each faecal sac, plant and animal contribution was visually estimated with 5% accuracy. The volume values (plant vs. animal) for each nest are the mean values corresponding to its respective faecal sacs. 20 May–10 June: 47 faecal sacs from a maximum of 13 nestlings; 11–30 June: 34 faecal sacs from a maximum of 16 nestlings; 1–31 July: 22 faecal sacs from a maximum of 17 nestlings. Pooled data for 2002–2005.

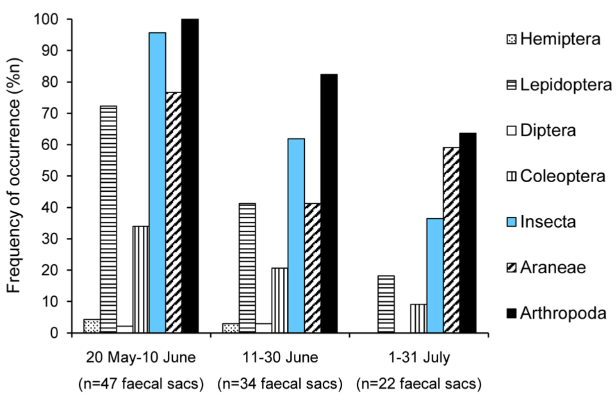

Fig. 6. Frequency of occurrence of arthropod remains in faecal sacs of Iberian bullfinch nestlings in northwest Spain during the breeding season. The faecal sacs belonged to older nestlings. Sample size (n) is the number of faecal sacs. All faecal sacs collected are considered, including those containing plant remains only. In the case of Insecta, all faecal sacs containing insect remains are considered, whether or not identified to order level. In the case of Arthropoda, all faecal sacs containing arthropod remains are considered, whether or not identified to order level. 20 May–10 June: faecal sacs from a maximum of 13 nestlings, 4 nests; 11–30 June: faecal sacs from a maximum of 16 nestlings, 6 nests; 1–31 July: faecal sacs from a maximum of 17 nestlings, 5 nests. Pooled data for 2002–2005.

Table 2. Direct observations of adult Iberian bullfinches searching for food, filling their buccal pouches, and immediately feeding nestlings or dependent juveniles, in northwest Spain during summer months. Each record corresponds to one adult, distinguishing between male and female, entering a nest to feed nestlings or feeding juveniles outside the nest, regardless of number of nestlings and juveniles fed on each visit. One adult could produce more than one record if it collected more than one food type during a maximum of 10 min foraging prior to feeding nestlings or juveniles. Data for June (9 records), July (36 records), and August (15 records). Pooled data for 2001–2006.

Food types	Males		Females	
	Feeding nestlings (%n)	Feeding juveniles (%n)	Feeding nestlings (%n)	Feeding juveniles (%n)
Prunus avium (pulp)	0.0	16.8	0.0	0.0
Lonicera periclymenum (seeds)	0.0	0.0	0.0	29.3
Unidentified fleshy fruit	0.0	0.0	0.0	11.8
Rumex spp. (seeds)	0.0	0.0	9.1	0.0
Polygonum bistorta (seeds)	0.0	27.9	0.0	5.9
Ranunculus spp. (seeds)	21.5	0.0	9.1	5.9
Filipendula ulmaria (seeds)	7.1	0.0	9.1	5.9
Geum urbanum (seeds)	21.5	22.2	27.2	23.5
Geranium molle (seeds)	7.1	11.1	9.1	0.0
Lactuca serriola (seeds)	7.1	0.0	9.1	0.0
Unidentified herb seeds	7.1	5.5	9.1	0.0
Agrimonia eupatoria (flower buds)	0.0	0.0	9.1	0.0
Total food of plant origin	71.4	83.5	89.9	82.3
Hemiptera nymphs	0.0	5.5	0.0	5.9
Lepidoptera caterpillars	0.0	5.5	0.0	5.9
Unidentified arthropods	28.6	5.5	9.1	5.9
Total food of animal origin	28.6	16.5	9.1	17.7
Number of records (n)	14	18	11	17

Regarding arthropod prey, only hemipteran nymphs and lepidopteran caterpillars were identified at order level. There was no significant association between food type (plant vs. animal origin) and sex of the adult (male vs. female) that fed the young (χ^2_1=0.18, p=0.67, nestlings and dependent juveniles together), or between food type (the same types) and age of the young birds (nestlings vs. dependent juveniles) (Fisher's exact test, p=1, males and females together).

3.4. Comparison between techniques

Considering only plant and animal fractions, *i.e.*, ignoring grit, their relative importance in the young provisioning diet was 68% vs. 32% (overall mean percent volume), respectively, according to the stomach analysis (n=13 stomachs), 93% vs. 7% (overall mean percent volume) according to the faecal analysis (n=3 time periods, encompassing 103 droppings belonging to a maximum of 46 nestlings in 15 nests), and 82% vs. 18% (percentage of records) according to direct observations (n=60 feeding visits), resulting in significant differences between techniques when percentage values are considered as absolute frequencies (overall: χ^2_2=20.40, p<0.001; for each couple of techniques: χ^2_1, p<0.05). Plant remains were found in all stomachs (n=13) and all faecal sacs (n=103), and arthropod remains in all stomachs and 86% of faecal sacs. No significant differences were observed between stomachs and faecal sacs in frequency of occurrence (occurrence vs. no occurrence) of insect remains (Fisher's exact test, p=0.18), but they were observed for spiders (Fisher's exact test, p=0.03). Both prey types were found in a higher percentage of stomachs than faecal sacs (insects: 92% of 13 stomachs, 72% of 103 faecal sacs; spiders: 92% and 61%, respectively). Gastroliths were found in just over half of the stomachs (7 of 13, 54%), but their occurrence in faecal sacs was negligible (1 of 103, <1%).

3.5. Comparison between young provisioning diet and self-feeding

Self-feeding during spring–summer (84% plants and 16% arthropods, relating to feeding records, as stated in the methods section) was significantly different to the young provisioning diet when compared with stomach analysis (68% and 32%, respectively, by volume) (χ^2_1=6.17, p=0.01), but not when compared with faecal analysis (93% and 7%, respectively, by volume) (χ^2_1=3.14, p=0.08) or, especially, direct observation (82% and 18%, respectively, relating to feeding records) (χ^2_1=0.04, p=0.85), considering percentage values as absolute frequencies. Nor were there significant differences in the latter comparison considering actual absolute frequencies, with very similar statistical results (self-feeding: 1046 plants and 201 arthropods; young provisioning according to direct observation: 49 plants and 11 arthropods; χ^2_1=0.08, p=0.78). Self-feeding during spring–summer and young provisioning diet, considering all of the different techniques used as a whole, coincided in 11 plant taxa at species/genus level with regard to seeds consumed.

4. Discussion

Of the three methods used to determine the diet of young Iberian bullfinches in a hedgerow habitat, faecal sac analysis provided the best results, weighing advantages (relatively non-invasive, large sample sizes) against drawbacks (lack of detail in taxonomic identification due to digestion). As expected, their diet was formed by a blend of seeds and invertebrates, and the importance of the animal fraction decreased during the breeding season and with age. Dietary changes were apparently associated with seasonal variations in the availability of different food types and with variations in the requirements (*e.g.*, protein intake) or handicaps (*e.g.*, difficulty digesting hard-bodied prey) of growing nestlings. For the first time, a qualitative and quantitative characterization of grit use by bullfinch nestlings is provided. Gastrolith occurrence and abundance was positively related to nestling age, probably owing to an increasing need to crush food. As expected, the importance of arthropod prey was higher in the diet of younger nestlings than in that of adults or independent juveniles during spring–summer.

4.1. Effects of the techniques used on findings about diet

The values obtained by faecal analysis in estimating the contribution of the animal fraction were lower (overall percent volume averaged only 7%) than those for stomach analysis and direct observation. Assuming that faecal sacs corresponded exclusively to older nestlings, these results could partly reflect an age-related variation in diet, as bullfinch nestlings are fed on fewer invertebrates towards the end of their growth period, even on seeds alone during the last days prior to leaving the nest, according to research from Britain (Newton 1967b, 1985). A distorting effect of the method used should not be ruled out, since soft-bodied insects and spiders are digested more easily and quickly than seeds (Rosenberg & Cooper 1990, Sutherland 2004), and therefore the presence of their remains could be more unlikely in faecal sacs than in stomachs. However, faecal analysis provides similar results to other techniques, such as neck collars or gut analysis, when used simultaneously on the same passerine nestlings, in regard to important groups of invertebrates (Kleintjes & Dahlsten 1992, Poulsen & Aebischer 1995, Moreby & Stoate 2000). Insects and spiders appeared in a higher proportion of stomachs than droppings, but differences were not significant for the former. Using direct observation, a high percentage of plant food items were identified at genus or species level, but animal foods could usually only be identified as arthropods, and to a lesser extent to insect order – they were not reliably observed to catch spiders – as could be expected from this technique (Rosenberg & Cooper 1990, Sutherland 2004, Yoshikawa & Osada 2015, see methods section).

In sum, faecal analysis enabled large sample sizes to be obtained relatively rapidly and effortlessly, and their analysis provided sufficiently reliable and accurate results for major food categories, in line with findings for nestlings of other passerine bird species. Faecal sacs could be collected directly from younger nestlings in the nest, but it is nevertheless advisable to collect those of older nestlings on the nest-rim after fledging, as they tend to jump out of the nest prematurely ("exploding") over the age of 10 days if disturbed (Cramp & Perrins 1994, Ferguson-Lees *et al.* 2011). Younger bullfinch nestlings digest insects more easily than seeds, many of the latter being passed whole into the droppings (Newton 1967b, 1985), which could not be verified in the present study since the faecal sacs analysed were from older nestlings and contained seeds that were not normally recognisable.

Stomach analysis was, as expected, the most reliable and accurate method at a more detailed level, but it is unpredictable in its application if it only relies, as ethics advises, on dead nestlings without researcher intervention, and direct observations were costly to obtain and imprecise in the determination of animal food. In contrast, over half of the plant species recorded by direct observation as nestling food were not found in stomachs, including soft food that bullfinches probably digest readily, such as Wild Cherry (*Prunus avium*) pulp, Common Agrimony (*Agrimonia eupatoria*) flower buds, and Meadowsweet (*Filipendula ulmaria*) seeds, some of which were unripe when consumed. Logically, stomach analysis was the only useful technique for studying gastroliths. Birds replace grit from time to time, often every few days in the case of small passerines, because it wears out progressively (McLelland 1979, Alonso 1985, Gionfriddo & Best 1995), so its appearance in droppings seems to be rare.

4.2. Seasonal and age-related variations in diet

Overall, bullfinches fed their young with a mixture of seeds and invertebrates, with greater quantitative importance of the former, as is usual in finches and expected in this species (Newton 1985, Cramp & Perrins 1994). Animal fraction decreased gradually and significantly, considering both frequency of occurrence and percent volume, from May to July for older nestlings (faecal analysis). This result is largely in agreement with what Newton (1967b) observed in British bullfinches, that is, a decline in the proportion of invertebrates in nestling diet at the end of the breeding season associated with lower availability. In the case of stomach contents (younger nestlings), there were apparently no noticeable monthly differences in this respect, but without a consistent statistical basis due to the small sample sizes. Perhaps bullfinches actually fed younger nestlings with invertebrates regardless of the month, despite the increasing effort to obtain them as the breeding season progressed, due to their higher protein requirements. It should not be ruled out that the most frequent invertebrates in the July diet, *i.e.*, spiders, probably reflecting their temporal availability, were still underestimated in faecal sacs as they were more easily digested. According to Pulido and Díaz (1994), spiders are amongst the most difficult soft-bodied arthropods to detect in the droppings of insectivorous passerines. On the contrary, in the May–June diet, insects as a whole were the most commonly found arthropods, in particular caterpillars and beetles. Similarly, in England, caterpillars predominated in the June diet of bullfinch nestlings among invertebrates, whereas spiders (as well as small slugs and snails) did so in the July diet (Newton 1967b by using neck collars, which allow identifying food not yet completely ingested by nestlings). In temperate and Mediterranean forest ecosystems, abundance and biomass of insects and spiders reach their peak in spring (May–June), followed in summer by a marked decrease in insects, but less so in spiders (Southwood *et al.* 2004, Cardoso *et al.* 2007). Both are an optimal diet for passerine birds, especially nestlings, on account of their high protein content and, in the case of spiders, high taurine content, both organic compounds playing a vital role in their early development (see reviews by Gunnarsson 2007, Nyffeler *et al.* 2018).

Regarding the apparent non-consumption of small non-arthropod invertebrates by young Iberian bullfinches, perhaps the techniques used overlooked them, since neck collars were not placed, or their absence was actually due to very sporadic use of this food resource. No remains of snail shells were found either in the examination of the building materials of 23 bullfinch nests that were already inactive (Hernández & Zaldívar 2021). Species richness and abundance of terrestrial gastropods in the study area is unknown, although they are indeed present. Most passerines need calcium-rich materials, in addition to their normal food, for eggshell formation and growth of nestling skeleton, making use mainly of snail shells and calcareous grit (Barrentine 1980, Graveland & van Gijzen 1994). Some specific prey, such as woodlice (Isopoda) and millipedes (Diplopoda), can also fulfill this function (Bureš & Weidinger 2003). Paradoxically, according to Newton (1967b), bullfinches remove the shells from snails, by handling them in the bill, before feeding the nestlings. Therefore, the role of gastropods and gastroliths as calcium sources for bullfinch nestlings needs to be investigated.

In the study area, herb seed availability increased from early spring to summer (Hernández & Zaldívar 2013), as did their general consumption by bullfinches (Hernández 2022), which could have led to a progressive increase in their use to feed nestling. According to stomach analysis, most of the seed types making up the diet of bullfinch nestlings in spring were not present in their summer diet, and vice versa, largely reflecting seasonal variation in the presence/fruiting of herb species in the study area (Hernández & Zaldívar 2013, Á. Hernández pers. obs.). Temporal variation in the diet of nestling passerines is common, and is generally associated with seasonal changes in the abundance and affordability of food at different taxonomic levels (Hernández 1993, Iglesias *et al.* 1993, Marques *et al.* 2003, Zeng & Lu 2009). Even so, the mean length of the seeds was consistently less than 3 mm. Granivorous passerines choose plant foods based principally on their bill size and shape (review by Díaz 1996). Some genera and species of seeds found in the diet of the young Iberian bullfinches match those found in that of subspecies of the western Palearctic further north (*e.g.*, *Taraxacum*, *Stellaria media*), but some others do not, presumably due primarily to geographic variations in floristic composition. For example, Spruce (*Picea*) and Blueberry (*Vaccinium*) seeds may be common in the diet of bullfinch nestlings from central Europe and western Russia (Cramp & Perrins 1994), but these plants are absent from the study area, the former due to its global distribution and the latter only inhabiting the valley at somewhat higher elevations.

With regard to age-related variation, as noted above, the relative importance of invertebrates was lower in faecal sacs (older nestlings) than stomachs (younger nestlings), but apparently there were no remarkable differences between stomachs belonging to nestlings <5 days and 5–8 days old in the percent volume of the plant and animal fractions. This pattern is in line with findings by Newton (1967b, 1985) for Britain, where the percent volume of animal matter in the food of nestling bullfinches did not clearly decrease until day 11 or 12. According to this author, protein requirements for nestling growth are better supplied by animal than vegetable matter, particularly during the first days, when young digest arthropods more effectively than seeds in overall terms. The relative contribution of invertebrates to the diet of nestlings of granivorous passerines, including several finches and sparrows, usually decreases markedly with age, and after about the tenth day they often receive seeds only (Newton 1967b, 1985, MacMillan 1981, Klvaňová *et al.* 2012). A relative uniformity in the general diet of the nestling bullfinches until day 8 was also the case for main types of invertebrates (frequency of occurrence of insects and spiders), and for seeds (quantity, range of variety, and identity). More specifically, however, hard-bodied prey such as beetles were found in the stomachs of nestlings aged 5–8 days but not in those aged <5 days. According to Orłowski *et al.* (2015), the youngest Barred Warbler (*Sylvia nisoria*) nestlings, which received the highest proportions in number and biomass of soft-bodied prey, may be physiologically limited as regards their ability to digest more heavily chitinised arthropods.

4.3. Seasonal and age-related variations in gastrolith presence

Considering both number of gastroliths and volume, the frequency of occurrence and amount of grit in stomachs were clearly associated with nestling age and not with season. Although parents may begin to provide the nestlings with grit practically after hatching in passerine birds, it has been found that the percentage of stomachs containing it increases with nestling age, and there is also a positive correlation between nestling age/weight and number of gastroliths in the stomach (Barrentine 1980 for Barn Swallows (*Hirundo rustica*), Alonso 1985 for Spanish Sparrows (*Passer hispaniolensis*), Orłowski *et al.* 2009 for Rooks (*Corvus frugilegus*)). Alonso (1985) noted a positive correlation between nestling age and the mean size of grit particles. There may be several reasons for greater importance of grit in older passerine nestlings, mainly retention of some grit in stomachs as age increases, and changes in diet (increasing number and mean size of food elements) (Alonso 1985, Orłowski *et al.* 2009). In the case of bullfinch nestlings, the progressive increase in the hardness of the arthropods ingested perhaps influenced the increasing role of grit for more efficient grinding action. It should also be considered that nestlings ingest most calcium-rich items at a time of maximum skeletal growth (Graveland & van Gijzen 1994, Bureš & Weidinger 2003). For birds in general, gizzards of granivores normally contain more and larger grit particles than those of insectivores, omnivores and frugivores, linked to food hardness and coarseness (Gionfriddo & Best 1996, Luttik & de Snoo 2004). In adult and nestling sparrows, the digestion of soft-bodied insects (*e.g.*, caterpillars, aphids) may require relatively little grit, whereas the breakdown of hard plant food and hard-bodied insects (*e.g.*, adult coleopterans) may require large amounts (Gionfriddo & Best 1995 and references therein, Marques *et al.* 2003).

Avian species that change their diet composition seasonally can also change the corresponding grit use (Gionfriddo & Best 1995, 1996 and references therein), which did not occur in bullfinch nestlings presumably because there were no significant monthly variations in the main food types received by nestlings up to 8 days old. Seeds ingested by these nestlings changed quite a bit taxonomically from May to July, but the difference in their mean length between both months was less than 1 mm. Also, at first glance the hardness of the food items in general did not seem to vary considerably from one month to another, but this quality was not assessed quantitatively.

The number and size of gastroliths generally correlate positively with the body size of bird species (Best & Gionfriddo 1991, Gionfriddo & Best 1996, Luttik & de Snoo 2004). Compared to other small songbirds, the mean number of gastroliths per stomach, without differentiating ages, was higher in bullfinch nestlings (≈12) than in wholly insectivorous Barn Swallow nestlings (≈5) (Barrentine 1980 for USA), but lower, differentiating between ages, than in largely insectivorous Spanish Sparrow nestlings (≈1 vs. 8 for nestlings *ca.* <5 days old, ≈26 vs. 90 for nestlings *ca.* 5–10 days old) (Alonso 1985 for Spain). In another study of Spanish Sparrows, the mean number of gastroliths in nestlings aged 5–10 days was only 2.2 (Marques *et al.* 2003 for Portugal), not referring to stomachs but to samples obtained using the ligature method, that is, restricted feeding events. In terms of size, mean gastrolith length is usually within 1.0–1.5 mm in small passerine nestlings, namely, Barn Swallow (Barrentine 1980), Spanish Sparrow (Alonso 1985), Eurasian Skylark (*Alauda arvensis*) (Ottens *et al.* 2014 for The Netherlands), and bullfinch (present study). This is probably an optimal size for them. Therefore, among small songbird species, the number of grit particles given to nestlings seems more flexible than the size of each one. The number of grit colours per nestling stomach was high (averaging approximately 4 out of 6 possible), with no seasonal variations to note, and increased with the number of gastroliths. There was no apparent predominance of any particular colour types in frequency of occurrence or quantity, and the selection of colours, with respect to those available in the field, was not evaluated. The shape of bird gastroliths usually ranges from spherical to, more commonly, slightly oblong, with sub-rounded corners (Best & Gionfriddo 1991, Gionfriddo & Best 1996, present study).

4.4. Nestling diet vs. self-feeding

Arthropods contributed significantly more to the diet of younger nestlings (stomach analysis) than to self-feeding (direct observation) during spring–summer, which is normal in other bullfinch subspecies and several European finch species (Newton 1967b, 1985, Cramp & Perrins 1994, Clement *et al.* 1993, Del Hoyo *et al.* 2010). Most temperate-zone passerines, including many typical seed-eaters, feed their young a protein-rich diet dominated by insects, at least for the first few days of life (Winkler 2004). The similarity found between self-feeding and diet of older nestlings or dependent juveniles was due to the decrease in importance of arthropod prey for the latter two in comparison with younger nestlings. Nevertheless, estimated diet composition of bullfinches in spring and summer by direct observation, both for nestlings and dependent juveniles and for adults, is not completely accurate as it was not always possible to determine whether or not they stored food for their young in the buccal pouches whilst eating – the bulging throat was only visible under optimal watching conditions – and neither was it possible to verify whether all of the food collected while they filled their pouches was destined for young individuals. According to Newton (1967b, 1985), British bullfinches normally only capture invertebrate prey to provide their young with a diet rich in proteins, which promotes growth, but in the study area their consumption was not necessarily associated with nestlings/fledglings, as adults regularly ate arthropods in autumn, after the breeding season, and independent juveniles in summer–autumn (Hernández 2022).

Nestlings, independent juveniles, and adults all fed on small insects and spiders, and coincided in the consumption of many seed species. According to Newton (1976b), adult bullfinches consume the same seed types that they feed their nestlings on. Although tree buds were an important component of the spring diet of adult bulfinches in March–April, when seed abundance was lower, they consumed very few from May onwards (Hernández 2022) and they were not found in the nestling diet. Bullfinches clearly preferred certain plant species, and avoided others, as a food resource in each season, and favourite herb seeds were generally contained in small achenes and capsules, probably easy to handle and dehusk (Hernández 2022, present study).

It is interesting to note that parent bullfinches often eat the faecal sacs removed from the nest, particularly during the first days of the nestling stage, seemingly implying the reuse of food that had not been digested by younger nestlings, mainly seeds – then they usually attach the sacs to branches and twigs and later ignore them – (Newton 1967b, 1985, Hernández 2020). In this way, the dividing line between the diet of nestlings and adults becomes even more diffuse. Removing faeces from the nest is common behaviour in passerines for nest-cleaning purposes or to hide the nest from predators, the parents also benefitting from ingesting the sacs (*e.g.*, energetically or nutritionally), which they can do even without leaving the nest (Hurd *et al.* 1991, McGowan 1995, Düttmann *et al.* 1998, Winkler 2004, Quan *et al.* 2015). The specific reasons for parental consumption of nestling faeces in bullfinches remain to be determined.

4.5. Brief comment on conservation

The high floristic diversity of the dense hedgerow network in the study area provides a wide range of resources for bullfinches, including plenty of suitable nest sites (Hernández & Zaldívar 2021) and food for their young. Its conservation and that of the rest of the valley with similar landscape characteristics, where bullfinches also live, is therefore highly advisable. For many typical passerine bird species in forested areas, hedgerows play an important role as foraging habitats or steppingstones for movement between woods, even providing the necessary resources both during and outside the breeding season (Gregory & Baillie 1998, Newton 1998, Robinson & Sutherland 1999, Hinsley & Bellamy 2000, Tellería *et al.* 2008, Wilson *et al.* 2009).

Nuorten Iberian punatulkkujen ruokavaliosta

Tässä tutkimuksessa dokumentoin ensimmäistä kertaa Iberian punatulkun (*Pyrrhula pyrrhula iberiae*) ruokavaliota pensaikkoympäristössä

luoteis-Espanjassa. Tutkittava aineisto koostui pienten (alle kahdeksan päivän ikäisten) poikasten vatsasisällöistä, ulostepussinsisällöistä (vanhemmat poikaset), sekä lisäksi suorista havainnoista (vanhemmat poikaset ja nuoret yksilöt). Dokumentoin myös ensimmäistä kertaa yksityiskohtaisemmin punatulkkupoikasten soran (tai mahalaukun kivien) käyttöä osana ruokavaliota. Punatulkut ruokkivat poikasiaan erilaisilla siemenillä ja selkärangattomilla, siementen ollessa merkittävämmässä roolissa poikasten ruokavaliossa. Erilaisten siementen käyttö vaihteli huomattavasti kevään ja kesän välillä, samoin kuin selkärangattomien osuus pieneni toukokuusta heinäkuuhun. Havaitut muutokset johtuvat todennäköisesti ravinnon saatavuudesta. Hämähäkit ja perhostoukat olivat tärkeimpiä niveljalkaisravintoa. Poikasille ei ilmeisesti syötetty niveljalkaisten lisäksi muita selkärangattomia. Runsasproteiiniset selkärangattomat olivat lisäksi suhteellisesti tärkeämpää ravintoa nuoremmille verrattuna vanhempiin poikaisiin. Kovakuoriaisia, jotka ovat vaikeasti sulatettavia, ei löytynyt pienimpien poikasten vatsoista lainkaan. Soraa havaittiin vatsojen sisällössä sitä enemmän, mitä vanhempia poikaset olivat. Mahalaukun kivien määrässä, koossa tai värissä ei havaittu eroja eri ajankohtina. Tutkimusalueen kasvillisuuden vaihtelevuus ja monimuotoisuus tarjoaa punatulkuille laajan valikoiman ravintoa poikasille, mikä myös nostaa alueen suojeluarvoa.

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Online supplementary material

Supplementary material available in the online version includes Figs. S1 and S2.