Seasonal feeding habits of the Iberian bullfinch *Pyrrhula pyrrhula iberiae* in northwestern Spain

Ángel Hernández[1,2]

[1] Zoology Area, Department of Agroforestry, University of Valladolid, Avenida de Madrid 44, 34004 Palencia, Spain

[2] University Institute for Research in Sustainable Forest Management, University of Valladolid-National Institute for Agriculture and Food Research and Technology, Avenida de Madrid 44, 34004 Palencia, Spain

angel.hernandez.lazaro@uva.es

http://orcid.org/0000-0002-6282-2400

Abstract

The first comprehensive approach to the feeding ecology of Iberian bullfinches *Pyrrhula pyrrhula iberiae* is presented here. The target population inhabited hedgerows in northwestern Spain. Throughout a six-year main period, the bullfinches were directly observed whilst searching for and consuming food. Interannual variation in diet was irrelevant, so data from all years were pooled. Availability of plant species and their selection as food resource was assessed. The general categories of food consumed varied significantly between seasons, with a high contribution of fleshy fruits in autumn–winter, tree buds in spring and herb seeds in summer. The breeding-season diet included a considerable proportion of invertebrates. Generally, sex- and age-related variations in diet were not significant throughout the seasons. Bullfinches preferred specific plant species as a food resource in each season, and ignored others. The selected fleshy fruit seeds were small in size, in particular thickness, which probably made handling easier. The most consumed buds were numerous per cm of twig and were flower buds, which presumably provided, comparatively, high energy gain per unit time. Generally, favourite herb seeds were contained in small achenes, easy to handle and dehusk. Invertebrate prey identified were small insects and spiders. Bullfinches obtained most of their food while perching, regardless of sex or age, but some important fruits, and the arthropods, were frequently obtained in flight. The high diversity of woody plants and food sources found in hedgerows surely protected fruit trees from the detrimental effect of bullfinches and provided this passerine species with a wide range of habitat resources.

Keywords Age-related dietary patterns • Food selection • Foraging behaviour • Fringillidae • Sex-related dietary patterns • Temporal dietary patterns

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Author contribution The author confirms sole responsibility for the following: study conception and design, data collection, analysis and interpretation of results, and manuscript preparation.

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Ethical note All the fieldwork was performed using observational, non-invasive techniques which enabled sufficient data for the objectives of the study to be obtained without threatening the welfare of the birds.

Availability of data The main data of the study have been contained in the manuscript.

Declarations

Conflict of interest None declared.

Introduction

Food supply is among the key extrinsic determinants of bird numbers since it can influence breeding productivity, survival of full-grown individuals and immigration/emigration (Martin 1986; Newton 1998; Plummer et al. 2013; Seward et al. 2013). Bird species have evolved different life-history strategies to cope with environmental variability in food resources (Ruffino et al. 2014). In seasonal environments and for a given bird population, food may be limiting only at certain times of the year or in certain years, and winter food shortages can be particularly detrimental in this regard (Newton 1980, 1998; Elkins 2004; Senar and Borras 2004). For all vertebrates in general, a concerted effort to move beyond single season research is vital to improve our understanding of species ecology and thus favour their conservation as there currently exists severe breeding season research bias (Marra et al. 2015). Frequently, avian dietary studies do not quantify the availability of different foods in the field, making it impossible to assess the degree of selection of each one (e.g., review by Holland et al. 2006 of invertebrates and seed-bearing plants as food for farmland birds in Europe). A foraging individual has to make decisions about food quality, perhaps choosing one item over another, and about how much to eat, and sampling avian food resources is indispensable to determine how bird populations react to changes in food availability, although such sampling is a complex task (Smith and Rotenberry 1990; Scott 2020). Moreover, to compensate for the noticeable increment in modeling and existing data analyses in biological sciences, 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 and Owens 2006).

Eurasian bullfinches *Pyrrhula pyrrhula* (hereinafter referred to as bullfinches) are considered generalist forest birds that readily accept heterogeneous semi-open landscapes (Cramp and Perrins 1994; Wilson et al. 2009; Clement 2010; Hernández 2021). Currently, there are nine recognized subspecies of this passerine, of which *iberiae* occupies southwestern France (Pyrenees) and the mountains of northern Portugal and Spain (Clement 2010). In Spain, at national level, it is considered that the bullfinch breeding population was in moderate decline during 1998 – 2020 (Escandell and Escudero 2021). The average breeding population size is estimated at 340,000 individuals for the whole of Spain (Carrascal and Palomino 2008). The feeding habits of some bullfinch populations, especially those in northern, central and western Europe, including the British Isles, are known in certain detail with regard to diet composition throughout the year, though there are no thorough quantitative analyses of food selection and foraging techniques (Newton 1967a, 1985; Cramp and Perrins 1994; Marquiss 2007). Summarizing this knowledge, bullfinches are herbivores, that is, they feed largely on vegetable matter (according to the classification proposed by Lopes et al. 2016). Their diet consists mainly of shrub, tree and herb seeds, but also shrub/tree buds and, notably during the breeding season, invertebrates. They usually obtain food while perching on plants and, less frequently, on the ground. To date, knowledge on the feeding habits of the Iberian subspecies is incomplete, sometimes even anecdotal, with no precise information on seasonal diet variation, food choice, or foraging methods, and is based on small sample sizes, some authors focusing only on the consumption of particular plant species (Bernis 1957; Noval 1971; Guitián 1985; Pedrocchi-Renault 1987; Fuentes 1994; Guitián et al. 2000; Hernández 2008, 2009a, b; Munilla and Guitián 2012; Torroba et al. 2013).

To fill these knowledge gaps, this study aims to provide a comprehensive approach to the feeding habits of bullfinches in an area located in northwestern Spain, close to the southwestern distribution limits of the species. Bullfinches inhabited the study area all months of the year and appeared to be mainly sedentary. Records of individuals belonging to more northern subspecies arriving in the Iberian Peninsula during the non-breeding season are scarce (Tellería et al. 1999; Clement 2010; Díaz 2016). The target population occupied mainly hedgerows. The following particular issues were assessed quantitatively: (1) seasonal variation in diet, differentiating sexes and ages, (2) seasonal diet selection regarding vegetable food, attempting to discern favourable plant traits, and (3) seasonal foraging techniques, differentiating sexes and ages. Nestling diet is excluded from this study as it is dealt with in a separate investigation (Á. Hernández unpubl. data).

Regarding the specific bases to establish the main expectations of the present study, first of all, hedgerows play an important role as foraging habitats or a stepping stone for movement between woods for many typical passerine bird species in forested areas, even providing the necessary resources both during and outside the breeding season (Gregory and Baillie 1998; Newton 1998; Robinson and Sutherland 1999; Hinsley and Bellamy 2000; Tellería et al. 2008; Wilson et al. 2009). Secondly, the study area, characterized by strong climate seasonality, enabled bullfinches to find not only meadows and a dense network of well-grown hedgerows formed by a wide variety of herbs, shrubs and trees, but also secondary habitat components such as tree plantations, and they spatially used a considerable proportion of these structural elements with significant variations according to the season (Hernández 2021). Thirdly, temperate zone finches usually show marked seasonal variation in diet composition linked to changes in the relative abundance of the various foods that each species is adapted to eating (Newton 1967b, 1985; Cramp and Perrins 1994; Borras et al. 2003; Holland et al. 2006). The bullfinch diet is therefore expected to be diverse and to change markedly in the course of the year, specific plant species being selected and different foraging strategies used, depending on the food type.

Methods

Study area

The study area covers 78 ha and is located in the middle-lower Torío River valley, between Palacio and Manzaneda (42º43' to 42º44' N; 5º30' to 5º31' W; 900 m a.s.l.; Leon province, Castile and Leon 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 ≈ 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 characterize the area. Details on the weather during the main study period are available in Hernández (2020). The landscape is largely composed of hedgerows separating irrigated meadows grazed by livestock and cut for hay, bordered by riparian woodland on the west side and slopes covered in Pyrenean oak *Quercus pyrenaica* woods interspersed with very small Scots pine *Pinus sylvestris* plantations on the east side. Some hedgerows border small Canadian poplar *Populus* × *canadensis* plantations. Estimated hedgerow density is 3.3 km per 10 ha. About thirty species of broadleaved, chiefly deciduous shrubs, trees and climbers are found in the hedgerows.

Data collection

General procedures and terminology Throughout 2001 – 2006 (main study period), bullfinches were directly observed, and the maximum details of sightings were recorded during field trips conducted to investigate their general ecology. The direct observation method is adequate for frugivorous and granivorous birds feeding mainly on plants and provides information not only on diet but also on foraging behaviour (e.g., techniques for obtaining and handling food) (Rosenberg and Cooper 1990; Sutherland 2004; Yoshikawa and Osada 2015). In a systematic way, 41 trips were conducted in winter (December - 13, January - 13, February - 15), 113 in spring (March - 31, April - 33, May - 49), 155 in summer (June - 49, July - 54, August - 52), and 84 in autumn (September - 39, October - 26, November - 19). By year, 73 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 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 rest (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 and references therein). Consequently, more than

85% of field trips were conducted in the morning in all seasons, and the remainder in the afternoon. The morning trips lasted from one hour after sunrise to 12:00 h (solar time) and the afternoon trips from 12:00 h (solar time) to one hour before sunset, as there was insufficient light at dawn or dusk for sampling to be carried out. Moreover, a comparatively smaller number of records obtained in a non-systematic way, with regard to periodicity and surface explored, in the study area during 1996 – 2000 (supplementary study period) were added, assigning the months already indicated for the systematic sampling to each season.

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. In addition, the study periods covering many years and the short life-span of this species – averaging 2 yr (Robinson 2005) –, together ensure a high degree of independence between records. If not otherwise specified, males and females refer to individuals apparently in full adult plumage, which could have been non-moulting adults, moulting adults, or individuals recently moulted from juvenile plumage, and juveniles refers to individuals in juvenile plumage (apparently complete or already moulting) either still dependent on their parents or independent. Male (red underparts), female (grey-buff underparts) and juvenile (absence of black cap) bullfinches have different plumage colourations to each other, which enabled them to be easily differentiated in the field. Standard optical equipment was used to observe birds (binoculars and a telescope). For easier reading, shrubs, trees and climbers are hereinafter collectively referred to as trees, as opposed to low-growing herbaceous plants. In the text, the simple common names of shrubs, trees and climbers are mainly used (see Supplementary Material S1 for the corresponding scientific names).

Diet determination To establish diet, each record refers to an individual consuming a specific food type, regardless of the units (amount) ingested. More than one record could be obtained from a single individual if it consumed more than one food type during a maximum observation period of 10 min. Focal sampling, i.e., watching foraging individual birds for a certain period of time, is a commonly used method when studying avian feeding habits (Sutherland 2004). During the breeding season, no distinction was made between possible uses of the food ingested by each individual, for instance, to feed themselves, the female (in the case of males), the offspring (males and females), or perhaps different concurrent uses. For each record, food was identified (a) visually, while the birds fed (e.g., most fleshy fruits, ash samaras), (b) by immediately inspecting the plant *in situ* (e.g., some herbs that were identifiable with the naked eye), and/or (c) by collecting a sample for identification in the laboratory (e.g., most herbs, caterpillars that build communal silken nests). In all cases, it was possible to distinguish whether the food was plant (and if it belonged to trees or herbs) or animal (arthropods), but not always at species, genus or family level. It is assumed that whenever bullfinches fed on the ground, they consumed herb seeds. Bullfinches occasionally eat seeds on the ground, but whether they feed on ground-dwelling invertebrates is not documented (Newton 1967a, b; Cramp and Perrins 1994; Clement 2010). Nevertheless, obtaining grit – which is commonly used by bullfinches as gastroliths (Á. Hernández unpubl. data) – on the ground cannot be ruled out.

Five general categories of food were considered: herb seeds, buds/flowers, fleshy fruit seeds or pulp, tree non-fleshy fruit, and arthropods. Buds/flowers refers normally to trees, the majority being buds (both flower buds and leaf buds), to a lesser extent open flowers (blackthorn, cherry, poplar, willow, ash), and occasionally incipient leaves (honeysuckle and elm) and tender stems (honeysuckle). Incipient Pyrenean oak acorns were considered as tree non-fleshy fruit. The species identified for food types that appear as genera or families in some tables and figures of the results section are the following: *Populus* spp.: *P. nigra*, *P. × canadensis*, occasionally *P. tremula*; *Salix* spp.: mainly *S. fragilis*, also *S. atrocinerea*, *S. × secalliana*; *Rubus* spp.: mainly *R. ulmifolius*, also *R. caesius*; *Rosa* spp.: *R. canina*; *Malus* spp.: *M. domestica*, occasionally *M. sylvestris*; *Prunus* spp.: *P. avium*, *P. spinosa*, *P. insititia*, occasionally *P. domestica*; *Rumex* spp.: *R.acetosa*, *R. longifolius*, *R. sanguineus*, *R. obtusifolius*, *R. conglomeratus*; *Ranunculus* spp.: *R. acris*; *Trifolium* spp.: *T. repens*; Geraniaceae: *Geranium molle*.

Diet selection Tree species availability was estimated by conducting eight sampling days within the period 28 September – 15 October 2005, when approximately 9 km of hedgerows were covered (≈ 35% of all the hedgerows, evenly distributed in the study area), recording the presence or absence of each plant species in 2 m long fragments (n = 330 fragments) situated every 25 m (modified from Hernández and Alegre 1991). Multispecific complexes of *Populus* poplars, *Salix* willows*, Rubus* brambles, *Rosa* roses and *Malus* apples were classified as single species. It is assumed that species occurrence is a good indicator of food availability applied to trees in any season, since they offer resources that are potentially exploitable by bullfinches (buds, flowers, and/or fruits) throughout the year.

To estimate availability of herb taxa, vegetation along the hedgerow edges was sampled monthly during April – August 2005 (data taken from Hernández and Zaldívar 2013). At the end of August and during September some of the meadows were cut, and grazing by livestock (horses and cows) increased progressively; from the end of November to the end of March, the meadows were generally covered with short grass without flowers (Hernández and Zaldívar 2013). Bullfinches sighted on the ground or herbs were usually very close (< 3 m distance) to the woody vegetation base, mainly hedgerows (Hernández 2021). Six hedgerow sites were sampled each month: edges facing north, south, east and west bordering meadows, edge bordering a poplar plantation, and edge bordering a track. In each sampling site, a 30 × 30 cm metal quadrat was used to collect data on vegetation and was systematically placed on the ground at eight points 2 m apart, in a line along the edge of the hedgerow. The quadrat was therefore placed in 48 points (six sites × eight points) each month, at a maximum distance of 1.5 m from the base of the hedgerow. Availability of each herb taxon each month is assumed to be the mean percentage of cover (vertical projection) in the 48 sampling units, with a subsequent calculation for spring (mean for April – May) and summer (mean for June – July – August). Herb taxa were considered available only if at least one individual plant had fully grown fruit.

Plant selection by bullfinches was estimated separately for trees and herbs, considering the results for availability obtained by the previously indicated methods. Thus, selection of each plant taxon was assessed by the Jacobs' index (Jacobs 1974): $S = (u - a) \, / \, (u + a - 2ua)$, where u (use) is the proportion of feeding records for a given plant taxon in relation to the total number of feeding records, and a (availability) is the proportion of occurrences (or proportion of cover) of that plant taxon in relation to the total occurrences (or total cover) of all plant taxa considered. Correction of u and a values for a total of 1 is required for calculations. This index varies between – 1 (maximum negative selection) and 1 (maximum positive selection), with a value 0 if selection does not occur (i.e., bullfinches consumed the plant taxon according to its availability). However, a conservative approach was taken, considering non-selection the interval from – 0.2 to 0.2, moderate selection 0.21 – 0.5 (negative or positive) and strong selection 0.51 – 1 (negative or positive) (modified from Morrison 1982).

To explore the causes of food choice by bullfinches, some physical characteristics shared by the main favourite plant foods (positively selected or most consumed), which were contrary to those shared by the main discarded plant foods (abundant but avoided plants), were determined. Thus, in the case of fleshy fruits, mean number of seeds per fruit, seed mean length (mm), mean width (mm), mean thickness (mm), mean weight of groups of 10 seeds, seed hardness (soft, hard, very hard), and fruit type (structure handled or probably handled by the bullfinch when feeding: berry, drupe, drupelet, pome, hip, ariled seed) and size (small-sized fruit: normally less than 1 cm long and wide; large-sized fruit: normally over 1 cm long and wide), were taken into account. Information was taken from Torroba et al. (2013) – data for northern Iberia − and personal observations in the study area. To determine tree bud traits, 12 terminal twigs (most of them 15 – 35 cm long) of each taxon were collected from at least five different plants for 11 days in February – March throughout the 2002 – 2005 period. The mean number of buds per cm of twig (discarding the end part of the twig if it had no buds), bud length (most usual range, mm), shape (e.g., plump or elongated), hardness (from very soft to hard) and position (separate or attached from/to the twig), and twig thickness at the middle (most usual range, mm) and flexibility (from very flexible to rigid), were estimated. For some plant taxa, the main type of bud (flower bud or leaf bud) apparently predominant in February –

March was determined. Some values for bud length and twig thickness were supplemented with those provided by Herrero and Zaldívar (2001) for Iberian tree species. With regard to herbs, fruit length (structure handled or probably handled by the bullfinch when feeding, mm), type (achene, mericarp, legume, spikelet) and additional features of interest (e.g., spiny surface), were considered, according to information for Iberia compiled by Hernández and Zaldívar (2013) and personal observations in the study area.

Foraging techniques To establish general foraging techniques, each record refers to an individual taking a specific food type in a particular way (perched or in flight, according to the classification proposed by Remsen and Robinson 1990 for birds in terrestrial habitats), regardless of the units (quantity) ingested. More than one record could be obtained from the same individual if, within a maximum of 10 min observation, it took more than one food type and/or took the same food type whilst both perched and in flight. The perched technique included ground foraging. Brief information is also provided on tactics frequently used by bullfinches, according to observations made, to obtain and handle specific food types, in some cases by inspecting the plant from which they ate and/or the remains of food that fell to the ground, without carrying out a quantative analysis or disaggregating by sex and age.

Statistical analyses

The chi-square test (χ^2), with Yates' correction for one degree of freedom, was used to compare absolute frequencies for two variables, and log-linear analysis (G^2) to compare absolute frequencies for three variables (2 × 2 × 2 tables) (Fowler et al. 1998; Lowry 1998-2022 – online tool that includes statistical software). For rows by columns chi-square tests, at least 80% of the cells had an expected frequency of 5 or greater, and no cell had an expected frequency smaller than 1. For 2 × 2 tables, all expected cell frequencies were equal to or greater than 5. 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. In general, interannual variation in diet was not significant in the restricted cases where the analysis could be performed thanks to a sufficient sample size, for both main food categories and specific food types (chi-square test, P > 0.05, comparison between two years selected for each season without distinguishing the sexes and ages). According to visual assessment during the main study period, herb seed availability was high during all years, as was tree bud and arthropod availability. General fleshy fruit availability, including those most consumed by bullfinches, was consistently high in most years. General availability of tree non-fleshy fruits from year to year did not appear to vary considerably, except in the case of large seed crops produced irregularly by ash trees. The meadows among the hedgerows were regularly irrigated during spring–summer and therefore ecological productivity was less dependent on rainfall. The coefficients of variation of the meteorological variables (e.g., monthly temperature) were relatively low throughout the main study period (Hernández 2020). During the main study period, little changing environmental conditions from year to year seemed to promote steady breeding population densities estimated at around 2.5 – 3.5 pairs/10 ha during April – May, and nest success and breeding productivity rates were relatively constant from one year to the next (Hernández 2020, 2021). The study area features a homogeneous landscape, resulting in a general uniformity in the distribution and abundance of the main food sources, which did not allow considering a habitat stratification.

Results

Diet variations

Without differentiating sexes or ages, and considering general food categories, most autumn and winter feeding records corresponded to fleshy fruit (> 65% in both seasons) and buds/flowers (11% in autumn, 26% in winter), herb seeds being of some importance in autumn (9%) (Fig. 1). In spring, buds/flowers (61%) were the most recorded foods, and, secondly, herb seeds (27%). Herb seeds (56%) and fleshy fruit (19%) were the most consumed plant foods in summer, when consumption of arthropods was also substantial (24%). Excluding arthropods (not present in the winter diet), there were significant differences between seasons in the contribution of the other general categories (four plant food categories) (χ^2_9 = 1460.38, P < 0.001). There were significant differences in diet composition between the autumn–winter and spring–summer periods considering all the general food categories (χ^2_4 = 949.92, P < 0.001).

Considering the two main foods (fruits and buds, in a broad sense), sex of adult individuals (males and females), and time of year (spring–summer and autumn–winter, i.e., breeding and non-breeding seasons, respectively), there were significant general differences in the frequencies of feeding records (G^2_4 = 99.87, P < 0.001) (Supplementary Material S1). More specifically, there were highly significant differences between the breeding and non-breeding seasons in each sex (males: G^2_1 = 32.41, P < 0.001, 75.9% and 58.7% of the records corresponding to fruits in the respective seasons; females: G^2_1 = 59.86, P < 0.001, 81.7% and 54.0%), but merely significant between males and females in the non-breeding season (G^2_1 = 4.30, P < 0.05, 75.9% and 81.7% of the records corresponding to fruits, respectively) and non-significant in the breeding season (G^2_1 = 1.53, P > 0.05, 58.7% and 54.0%). Taking into account age (adults, considering both sexes together, and juveniles), season (summer and autumn), and the two main summer–autumn foods (fleshy fruits and other fruits, in a broad sense), there were significant general differences in the frequency of feeding records (G^2_4 = 355.08, P < 0.001). More specifically, there were significant differences between summer and autumn in each age (adults: G^2_1 = 164.61, P < 0.001, 24.9% and 82.0% of the records corresponding to fleshy fruits in the respective seasons; juveniles: G^2_1 = 160.19, P < 0.001, 25.5% and 89.1%), but not between adults and juveniles in each season (summer: G^2_1 = 0.03, P > 0.05, 24.9% and 25.5% of the records corresponding to fleshy fruits in the respective ages; autumn: G^2_1 = 3.36, P > 0.05, 82.0% and 89.1%). Additional information on within-season variations in diet is provided in Supplementary Material S2.

Diet selection

Plant food obtained from trees Considering the pooled sex and age data, and taking into account only relevant tree taxa (due to their availability and/or consumption), in winter bullfinches strongly selected (S = 0.51 – 1) bramble and ash as food plants, and privet and guelder rose moderately (S = 0.21 – 0.5) (Table 1). In spring, they strongly selected apple, blackthorn and cherry, and in summer cherry, bryony, privet and honeysuckle. In autumn, ash and honeysuckle were strongly selected, and bramble and privet moderately.

Fleshy fruit seeds positively selected varied in taxonomy (four different families), fruit type (from multi-seeded berries to one-seeded drupes), hardness (from soft to very hard), mean length (≈ 2.5 – 7.5 mm), mean width (≈ 1.5 – 6.5 mm), and mean weight (0.025 – 0.37 g for groups of 10 seeds), but their mean thickness was within the narrow interval of 1.10 – 1.86 mm (Table 2). Bullfinches only ate the pulp of some fleshy fruits, all of which contained a single, very hard, large (in all dimensions, with a mean thickness of 4.28 – 6.09 mm) and heavy seed.

Considering buds in a strict sense, i.e., without shoots, the most consumed throughout the seasons – each accounting for > 5% of the total number of records of bullfinches eating buds – were four Rosaceae (blackthorn: 159 of 389, 40.9%; cherry 19.0%; hawthorn 14.6%; apple 5.4%) and one Celastraceae (spindle 6.2%). According to data collected in February – March for terminal twigs, these buds were generally plump, soft and separate from the twig, which was usually rigid, but other features were more variable, such as the mean number of buds per cm of twig (0.5 – 2.5), bud length (1.5 – 10.0 mm) and twig thickness (1.5 – 4.5 mm) (Table 3). However, the two most consumed buds (blackthorn and cherry) were clearly the most numerous per cm of twig (both averaging > 2) and appeared to be mainly flower buds. On some apple trees, more terminal plump buds were missing, apparently cut off by bullfinches, than lateral buds, which were smaller, triangular, and attached to the twig.

Plant food obtained from herbs Without distinguishing the sexes and ages, and taking into account only relevant herb taxa (due to their availability and/or consumption), bullfinches strongly preferred *Taraxacum* seeds in spring (Table 4). In summer, they strongly selected *Polygonum*, *Rumex*, *Filipendula*, *Geum* and *Lactuca*, and *Ranunculus* and Geraniaceae moderately. The taxonomy of positively selected herb seeds varied (five different families), but their corresponding fruit type was usually an achene (except mericarp for *Geranium*) 2.0 – 6.0 mm long, in some cases with a hairy or spiny surface and/or a hook or pappus at the distal end (Table 5).

Plant food avoided by bullfinches Abundant but strongly avoided fleshy fruits varied in taxonomy (three different families), type (from multi-seeded hips to one-seeded drupes), seed hardness (from soft to very hard) and mean seed weight (0.16 – 1.84 g for groups of 10 seeds), and their high variability in seed size not only affected mean length (≈ 5.0 – 9.5 mm) and mean width (≈ 3.0 – 7.5 mm), but also thickness (mean values > 2 mm in all cases but within a wide interval of 2.34 – 5.31 mm) (Table 2). The buds of the three most abundant trees in hedgerows in the study area (two Rosaceae – bramble and dog rose – and one Oleaceae – privet –, ≥ 10% of relative availability each) were practically ignored by bullfinches. These buds were typically soft, few in number (a mean of 0.3 – 0.7 buds per cm of twig) and on rigid twigs (Table 3). Others of their traits were more variable, such as bud length (2.0 – 6.0 mm) and twig thickness (1.5 – 4.5 mm), but in the case of the two Rosaceae taxa, they were particularly elongated and pointed, apparently leaf buds, on spiny twigs, and privets had small lateral buds attached to the twig. Abundant but strongly avoided herb seeds varied in taxonomy (five different families) and fruit type (four different ones, in some cases with hairs, hooks and/or awns), and fruit length range was wide (1.5 – 35.0 mm) (Table 5).

Foraging techniques and food handling

General seasonal, sex-, and age-related variations in foraging technique Considering the pooled sex and age data, in winter, when bullfinches ate exclusively plants, 80% of feeding records corresponded to perched technique, and the rest to in flight (Fig. 2). During spring–summer–autumn, they obtained plant food mainly while perching (70 – 90% vs. 10 – 30% in flight) and animal food in flight (65 – 100% vs. 0 – 35% perched), producing a significant association between food type (plant or animal origin) and foraging technique (χ^2_1 = 266.02, P < 0.001, for all three seasons together). Without distinguishing food types, and taking into account age (adults, considering both sexes together, and juveniles), season (summer and autumn), and foraging technique (perched and in flight), there were significant general differences in the frequency of feeding records (G^2_4 = 82.11, P < 0.001) (Fig. 2). More specifically, there were significant differences between summer and autumn in each age (adults: G^2_1 = 19.88, P < 0.001, 59.1% and 76.0% of the records corresponding to perched in the respective seasons; juveniles: $G^2_1 = 10.08$, $P < 0.01$, 53.4% and 67.6%), but not between adults and juveniles in each season (summer: $G^2_1 = 2.33$, $P > 0.05$, 59.1% and 53.4%, respectively, corresponding to perched; autumn: $G^2_1 = 3.76$, $P > 0.05$, 76.0% and 67.6%). Without distinguishing food types, males and females differed significantly in the foraging technique used in spring ($\chi^2_1 = 5.55$, $P = 0.02$, 84.7% and 92.5% of the records corresponding to perched, respectively), but not in winter ($\chi^2_1 = 0.38$, $P = 0.54$, 81.0% and 78.7%).

Food-specific variations in foraging technique Considering the most consumed foods of plant origin at species or genus level in each season, all tree buds/flowers (hawthorn and *Prunus* and *Malus* species), guelder rose drupes and ash samaras were taken by bullfinches while perching during winter–spring, and *Filipendula* achenes in summer the same way (Fig. 3). They removed most of the privet berries while perching in autumn (99% of feeding records vs. 1% in flight) and, to a lesser degree, in winter (86% vs. 14%) ($\chi^2_1 = 7.38$, $P = 0.006$), and likewise the bramble drupelets (75% perched vs. 25% in flight in autumn, 59% vs. 41% in winter; $\chi^2_1 = 9.38$, $P = 0.002$). Most of the honeysuckle berries were removed in flight in autumn (66% vs. 34% perched). In spring, *Taraxacum* achenes were taken mainly when the bullfinches were perched (69% vs. 31% in flight), *Geum* achenes in almost the same proportion perched and in flight in summer (51% vs. 49%, respectively), and *Polygonum* achenes mainly in flight in summer (60% vs. 40% perched). Aerial manoeuvres often involved sustained hovering to take fleshy fruits, herb fruits and arthropods (both spiders and insects), according to non-quantitative observation.

Food handling Bullfinches obtained and handled food using their bills. They usually plucked the buds, the embryonic parts being eaten and the covering scales dropped. They plucked whole fleshy fruits, or removed the seeds without plucking the fruits, using both methods on each plant species. Normally, they dropped the skin and pulp of the plucked fruits, and the seed shell. Regarding herb seeds, they usually peeled them, dropping the rest of the fruit, including protruding structures such as hooks (e.g., *Geum*) and pappi (e.g., *Taraxacum*). They captured solitary caterpillars or took them from communal silken nests (e.g., *Yponomeuta* caterpillar nests on spindle). More detailed information on food handling, for both plants and invertebrates, is provided in Supplementary Material S3.

Discussion

Diet variations

The bullfinch diet was diverse in the study area, as it is in the rest of its distribution range. In short, general food categories vary significantly throughout the seasons, with a high contribution of tree fleshy and/or tree non-fleshy fruits in autumn–winter, tree buds in spring and herb seeds in summer, although buds may be important in winter, herb seeds in late spring and fleshy fruits in late summer (Newton 1964, 1967a, b; Noval 1971; Greig-Smith and Wilson 1984; Snow and Snow 1988; Cramp and Perrins 1994; Marquiss 2007; Clement 2010). A similar seasonal diet pattern has been described for the Azores bullfinch *Pyrrhula murina* (Ramos 1995). In the study area, the main tree seeds eaten by bullfinches were from fleshy fruits, except those from ash, which were of moderate importance in autumn–winter, in contrast to other places where tree non-fleshy fruits can be a key resource during the non-breeding season (e.g., *Picea* spruce, *Acer* maple, *Betula* birch and ash seeds, see Newton 1967a; Greig-Smith 1988; Cramp and Perrins 1994). In any case, bullfinches show a special ability to exploit fleshy fruits, if available (Erkamo 1948; Newton 1967b; Snow and Snow 1988; Englund 1993; Guitián et al. 2000). Invertebrates are habitually a considerable part of the bullfinch diet during the breeding season (Newton 1967a; Guitián 1985; Cramp and Perrins 1994; Marquiss 2007). According to Newton (1967a, 1985), they normally only use invertebrate prey to feed nestlings, but in the study area it was verified that their consumption was not necessarily associated to nestling diet, since adults caught and ate arthropods in autumn and juveniles in summer–autumn.

High consumption of herb seeds in late spring and a major part of summer, and buds in late winter and spring, coincided with a relatively low abundance of tree seeds during all those periods and herb seeds throughout most of the non-breeding season, derived mainly from typical seasonal variations in fruiting of plants in this area (Hernández 2007, 2009a; Hernández and Zaldívar 2013). From late summer–early autumn, when fleshy fruit supply began to be abundant, they avoided feeding close to the ground to a large extent, although some preferred herb seeds were still available in some sites (see below). The bullfinch bill is well adapted to bud consumption, and British populations may depend almost exclusively on this food resource from January to April in years of seed shortage, but seed availability in winter is probably the main factor regulating their numbers as buds are comparatively less nutritious and, consequently, less attractive (Newton 1964, 1967a, b, 1985; Summers 1982a; Greig-Smith et al. 1983; Elkins 2004). Azores bullfinches also rely heavily upon tree buds, particularly Azorean holly *Ilex azorica*, when seeds are in low supply at the end of winter (Ramos 1995).

Generally, sex- and age-related differences in diet were not significant throughout the seasons, except that females consumed a somewhat higher proportion of fruits, in a broad sense, than males during the non-breeding period, and that the proportions of the different herb seeds consumed by juvenile and adult individuals in summer were different (with a higher occurrence of *Filipendula* seeds in the juvenile diet), as with fleshy fruits in autumn (with a higher occurrence of privet and honeysuckle seeds in the juvenile diet). The literature consulted does not provide any information in this regard, apart from the bullfinch nestling diet (see Cramp and Perrins 1994). In the study area, there were no clear differences between sexes and ages in substrate use, i.e., tree use versus ground/herb use, and the significant differences found between males and females in mean perch height during spring–summer were attributable above all to non-feeding records (mostly males singing in higher places) rather than feeding records (Hernández 2021). Bullfinches are gregarious birds, and males and females have a similar morphology, which probably partly accounts for sexes having a similar diet. In his study on foraging patterns of forest passerine birds in USA, Holmes (1986) found some differences between males and females of species with morphologically similar sexes – although fewer than interspecific differences –, but he did not attribute them to resource partitioning but to the particular centres of activity of each sex (e.g., song perches for males, nests for females). However, sightings containing only juvenile bullfinches were common in summer and autumn in the study area, where they tended to separate from adults after becoming independent and group together occupying humid, shady places (Hernández 2021, 2022), precisely where *Filipendula ulmaria*, privet and honeysuckle grow. Forest songbirds usually select dense vegetation during the post-fledging period (Vitz and Rodewald 2011; Jenkins et al. 2017). Juvenile birds in general, including finches, can feed in different places, and eat different food, from those chosen by adults, often in a less proficient way (Smith 1983; Marchetti and Price 1989; Wunderle 1991).

Diet selection

Plant food obtained from trees Some of the preferred tree species for food were markedly uncommon in the study area (≤ 1.5% availability, namely ash, apple, cherry, bryony, honeysuckle), suggesting that bullfinches actively searched for them. Large trees such as ash and cherry temporarily supported plenty of food (principally samaras in autumn–winter and buds in spring, respectively, in the cases mentioned), acting as points of attraction for bullfinches, which visited them frequently and spent long periods of time eating there, several individuals often gathering in the same tree (Á. Hernández pers. obs.). Ash seeds can be a primary food resource for bullfinches in other regions, as noted above, and also cherry buds (Marquiss 2007). Although there were few fruit orchards (apple, pear, plum) in small plots, bullfinches selected their buds more positively than those of the majority of woody plant species. Bullfinches preferred the buds of cultivated fruit trees in England, because of their higher nutritional value (Newton 1964).

Under certain circumstances, the consumption of some favourite seeds by bullfinches was intense in the study area, affecting the majority of individual plants and representing a considerable proportion of total fruit removal by frugivorous birds, as happened with the guelder rose during harsh weather episodes (up to almost 35% of the fruits in February 2005, according to Hernández 2009a). High bullfinch population densities were recorded in periods of heavy snowfall in the study area – which was even heavier at greater altitudes in the valley also inhabited by them –, when this finch was among the most abundant species in bird samplings at the time, presumably due to downwards movements from mountainous areas (Á. Hernández unpubl. data). Snow and Snow (1988) and Englund (1993) have emphasized the relevance of guelder rose seeds as nourishment for bullfinches in other places in Europe. In England, 4/5 of woody species inhabiting forests and farmland constitute part of their diet, but apparently not in proportion to their availability in many cases (Newton 1967a).

The main common trait of the selected fleshy fruit seeds, in contrast to more abundant but strongly avoided ones, was their considerably smaller size and weight, particularly thickness (mean thickness < 2 mm), which probably made them easier to handle for bullfinches in their short, rounded bills. In comparison with the European greenfinch *Chloris chloris*, which is a similar size but has a larger and stronger bill, bullfinches eat smaller fleshy fruit seeds with thinner coats (Newton 1967b; Snow and Snow 1988). Abundant but hardly eaten fleshy fruits included spindle and ivy, considered particularly poisonous, also the seeds (Rivera and Obón 1991), though their degree of toxicity for bullfinches is not known. According to some authors, bullfinches consume fruit pulp rather rarely (Snow and Snow 1988; Cramp and Perrins 1994), but they regularly pecked the pulp of fleshy fruits with large, very hard, thick seeds in the study area (see also Hernández 2008). Most of the preferred fleshy fruits in each season were ripe and more abundant in that season than during the rest of the year, with the principal exception of privet fruits in summer, as they were still unripe but selected positively (Á. Hernández pers. obs.).

The largest tree seeds eaten by bullfinches were ash, coinciding with Newton (1967a) in southern England, where they chose the individual trees with seeds that had a higher fat content (Greig-Smith and Wilson 1985; Greig-Smith 1988). Ash samaras are very large, approx. 3.0 – 4.5 cm long and 7 – 11 mm wide, but with a maximum thickness of only 2 – 3 mm – right where the seed is located (Andrés 2012; Á. Hernández pers. obs. for the study area), which presumably facilitated their handling by bullfinches. Ash seeds are approx. 12 – 15 mm long, 3 – 5 mm wide and 1.5 – 2.0 mm thick (Newton 1967a; Andrés 2012; Á. Hernández pers. obs. for the study area). Very few tree species bore non-fleshy fruits suitable for bullfinches in the study area.

The main shared features of the most consumed buds, in contrast with those strongly avoided but belonging to predominant trees, were their greater abundance per cm of twig and that they were flower buds, which probably provided higher energy gain per unit of time. Some buds that were scarcely consumed or totally avoided, though not belonging to abundant plant species, showed certain traits that were perhaps in any case unattractive to bullfinches. For example, gooseberry buds are protected by spines at their base, poplar and guelder rose buds are sticky and somewhat resinous, willow and ivy buds are on very flexible twigs – which presumably affect the balance of the bullfinches as they consume the buds while perched –, and ash buds are covered in thick scales. Also, buds attached to the twig were scarcely or not eaten (willow, guelder rose, hazel, elm, dogwood, poplar, nightshade). In line with these patterns, other authors have suggested that the most profitable buds for bullfinches are those most available and easily obtainable in large quantities, but they also select buds with a higher proportion of edible and more nutritious matter, flower buds rather than leaf buds, and buds with a more pleasant flavour, amongst species or within the same species (Newton 1964; Summers 1982a; Greig-Smith et al. 1983; Greig-Smith 1985; Numazawa 1989).

Plant food obtained from herbs In spring, very few herbaceous plants had fully grown fruits and bullfinches selectively fed on *Taraxacum* seeds, which were abundant and apparently easy to obtain. In summer, the variety of herb species with a notable supply of fully grown fruits was much greater, but bullfinches showed a strong preference for only some seeds. At the start of autumn, *Polygonum* seeds had practically disappeared due to the action of bullfinches – other granivorous passerines were hardly seen feeding on them –, presumably because other favourite seeds such as *Filipendula* and *Geum* were not abundant until well into summer (Á. Hernández pers. obs.). Consumption of *Filipendula* seeds was fairly significant during September, when they were plentiful in edge zones and humid places. However, bullfinches hardly ate some of the seeds they had shown a preference for in summer still available to some extent in that month, e.g., *Rumex* and *Geum*, perhaps due to the large supply of fleshy fruit – which meant they did not have to feed close to the ground – and less use of poplar plantations, where these herbs were more abundant (Hernández 2021; Á. Hernández pers. obs.). Generally, favourite seeds were contained in small achenes, probably easy to handle and dehusk. Some abundant but highly avoided fruits were presumably too large for bullfinches (especially *Vicia* legumes and *Chaerophyllum* mericarps) and/or difficult to handle as they were covered in hooks, hairs, and awns (*Galium* mericarps, Poaceae spikelets). In woodland and farmland in England, half of the herbaceous species present formed part of the bullfinch diet, but many apparently not in proportion to their availability (Newton 1967a). Some favourite herb seeds in the study area (e.g., *Taraxacum*, *Polygonum*, *Filipendula*, *Rumex*, *Ranunculus*) had previously been mentioned as important foods for bullfinches in others, also agreeing on the minute contribution of Poaceae (Asturias-Basque Country: Noval 1971; southern England: Newton 1967a; northeastern Scotland: Marquiss 2007).

Additional discussion on selection of invertebrates, as well as on chemical, organoleptic and nutritional features of bullfinch foods and their effect on diet selection, is provided in Supplementary Material S4.

Seasonal foraging techniques and food handling

Bullfinches obtained most of their food while perching, regardless of sex or age. Nevertheless, some important fruits (particularly honeysuckle berries, *Polygonum* and *Geum* achenes) and the arthropods were captured in flight in considerable proportion. The use of aerial manoeuvres increased in summer in comparison with the rest of the year, linked to greater consumption of herb seeds and arthropods. These general patterns coincide with what has been described for other geographic areas (Newton 1967a, b; Cramp and Perrins 1994; Clement 2010), although to date, no comprehensive quantitative analyses had been carried out in this respect, except on specific fleshy fruits. In southern England, bullfinches took almost half of the honeysuckle berries in flight (Snow and Snow 1988). Probably, the fact that honeysuckles present terminal inflorescences at the end of long flexible stems made the perched technique difficult. The proportion of fleshy fruits taken in flight increased between autumn and winter in some plant species (bramble, privet), probably because those that remained were progressively less reachable if the bird was perched, as also observed by Snow and Snow (1988). Access to herbaceous plants – many of which had soft stems, terminal inflorescences, and grew at a distance from trees – using aerial manoeuvres presumably enhanced foraging efficiency. Sustained hovering while in flight is common bullfinch behaviour (Newton 1967a; Snow and Snow 1988; Cramp and Perrins 1994).

Bullfinches cut off, as was also the case in the study area, small pieces of the large soft catkins of poplar and willow trees (Newton 1967a). They can extract the seeds of fleshy fruits either without or after plucking them from the plant, and the skin and pulp are usually discarded (Snow and Snow 1988), which was confirmed in the present study. They routinely removed the hard coat of seeds/fruits, but maybe they swallowed whole unripe ones whose coats were still soft, especially smaller ones often taken in bunches, as also indicated by Newton (1967a, b). In the study area, bullfinches often fed their nestlings on small, unpeeled seeds (Á. Hernández unpubl. data).

Impact of bullfinches on plants and bullfinch conservation

In this study, the importance of different plant species in the bullfinch diet is quantitively analysed but the effect of this passerine on each one is not detailed, which is *a priori* assumed to be negative as it is mainly a bud and seed predator. Nevertheless, some signs indicated that the impact on its preferred plants must have been habitually low. For instance, in almost all years there were still some guelder rose, bramble and privet fruits left in March, even until May in some years (Á. Hernández pers. obs.), when tree buds and herb seeds were the most abundant and accessible food for bullfinches. Surprisingly, in July 2003 some bramble plants still had dry fruits from the previous year. In a separate investigation in this same area, it was estimated that feeding visits by bullfinches to guelder roses in the winter of 2004 – 2005 accounted for 8% of all visits by six species of avian frugivores – all of them seed dispersers except the bullfinch (Hernández 2009a). The community of seed-dispersing birds in the study area is rich and diverse throughout the year (e.g., Hernández 2008, 2009b). In southern England, the percentage of feeding visits by bullfinches in relation to the total number of visits by avian frugivores was 40% for honeysuckle, 33% for guelder rose, 21% for privet and 1.2% for bramble, according to Snow and Snow (1988). These authors underline that the impact is greater when considering the number of seeds as bullfinches often remain for a long time on an individual plant and destroy more fruits than a disperser takes in one visit. In Sweden, the frequently low dispersal potential of guelder rose due to heavy seed predation, mainly by bullfinches, is compensated for by sporadic massive dispersal by Bohemian waxwings *Bombycilla garrulus* in certain favourable years (Englund 1993).

Damage to fruit tree buds appeared to be limited, as bullfinch numbers were generally low (Á. Hernández unpubl. data). Besides, the considerable variety and availability of other food sources probably cushioned the impact. Also, a fraction of the fruit crop was not eaten by frugivorous animals or harvested by owners, the cultivation of fruit trees being of minor importance in the study area (Á. Hernández pers. obs.). In some places, the bullfinch has traditionally been considered a harmful bird for different tree species, particularly when they eat the buds of fruit-bearing trees (e.g., pear trees) in farmland, although production is only affected when great damage occurs, according to information mainly from England (Newton 1964, 1967a; Greig-Smith and Wilson 1984; Cramp and Perrins 1994). Lack of wild foods (e.g., ash seeds) may cause bullfinches to eat more fruit tree buds (Newton 1964), but they usually only consume a small proportion of their favourite wild seeds, and it is only when production is poor that bullfinches almost finish off the supply of these seeds (Newton 1998). A high diversity of woody plants and food sources, such as that found in hedgerows, can both protect fruit trees from the detrimental effect of bullfinches and be advantageous for this passerine species as it provides a wide range of habitat resources (e.g., varied vegetation cover and nest sites, see Hernández 2021; Hernández and Zaldívar 2021). In Britain, recent losses of understorey shrubs (e.g., brambles) from many deciduous woods and of tall thick hedgerows from farmland have represented a serious decline in both cover and food for bullfinches (Newton 2004; Marquiss 2007). Hedgerows have declined sharply in recent decades in Europe due to intensification of agricultural practices (see Cornulier et al. 2011).

Although in an unmeasured way, bullfinches could have acted as seed dispersers. They sometimes dropped some whole seeds while handling fleshy multi-seeded fruits. On one occasion, while a female bullfinch was eating *Geum* seeds at the end of July, two of them adhered to the feathers on one side and were apparently still there when she flew off, thus constituting a probable case of epizoochory. In England, bullfinches are reported to sometimes drop whole ash samaras when feeding, which could be beneficial for ashes (Greig-Smith 1988), and it has been estimated that when they eat a proportion of fruit tree buds, growth of the unaffected fruits increases (Summers 1982b). Thus, a comprehensive perspective of plant and herbivore ecology should be taken into account to properly interpret their interactions.

Temporal perspective of the results obtained

Although several years have elapsed since data collection to the present, some conditioning factors and recent observations indicate that the results obtained probably remain valid today. The landscape and hedgerow density and structure have hardly changed in recent years and decades in the study area, except for a moderate increase in the number of poplar plantations and an incipient abandonment of meadows and hedges. Visits for other purposes in 2021 and 2022 revealed that the bullfinches were still present there and apparently in good conservation status. A few nests were accidentally found in 2021. In any case, the results offered have their own value and can be compared with more recent or future field research. Some authors have emphasized the increasing necessity of investigating how overall resource availability and nutritional phenology are changing and will change for bird species in response to climate change (La Sorte et al. 2018; Shipley et al. 2022).

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Table 1 Seasonal diet selection by Iberian bullfinches in northwestern Spain referring to food of plant origin (buds, flowers, fruits) obtained in trees (including shrubs and climbers)

Plants	AV* (%*n*)	Winter		Spring		Summer		Autumn	
		U** (%*n*)	*S****	U (%*n*)	*S*	U (%*n*)	*S*	U (%*n*)	*S*
Ribes uva-crispa	0.2	0.0	-1	0.3	0.20	0.0	-1	0.0	-1
Populus spp.	5.0	2.1	*-0.42*	2.5	*-0.34*	0.7	<u>*-0.76*</u>	1.7	<u>*-0.51*</u>
Salix spp.	3.2	0.2	-0.89	1.2	-0.46	0.0	-1	3.1	-0.02
Euonymus europaeus	5.1	3.4	*-0.21*	0.6	<u>*-0.80*</u>	0.0	<u>*-1*</u>	0.6	<u>*-0.80*</u>
Cytisus scoparius	0.0	0.0	-	0.3	1	0.0	-	0.0	-
Corylus avellana	5.9	0.0	<u>*-1*</u>	0.3	<u>*-0.91*</u>	0.0	<u>*-1*</u>	0.0	<u>*-1*</u>
Quercus pyrenaica	0.8	0.0	-1	0.0	-1	3.4	0.63	0.0	-1
Juglans regia	0.2	0.0	-1	0.0	-1	0.0	-1	0.0	-1
Rubus spp.	16.2	40.9	<u>**0.56**</u>	2.8	<u>*-0.74*</u>	12.9	-0.13	30.2	**0.38**
Rosa spp.	10.1	0.0	<u>*-1*</u>	0.0	<u>*-1*</u>	0.0	<u>*-1*</u>	0.6	<u>*-0.90*</u>
Pyrus communis	0.05	0.0	-1	2.5	0.96	0.0	-1	0.0	-1
Malus spp.	0.3	0.2	-0.20	6.7	<u>**0.92**</u>	0.0	-1	0.0	-1
Crataegus monogyna	6.9	5.1	-0.16	8.6	0.12	4.1	*-0.27*	2.8	*-0.44*
Prunus spinosa	8.0	10.8	0.16	35.3	<u>**0.73**</u>	0.0	<u>*-1*</u>	0.0	<u>*-1*</u>
Prunus avium	0.8	1.0	0.11	30.7	<u>**0.96**</u>	14.3	<u>**0.91**</u>	1.7	0.36
Rhamnus cathartica	0.2	0.0	-1	0.6	0.50	0.0	-1	0.0	-1
Bryonia dioica	0.9	0.2	-0.64	0.0	-1	5.4	<u>**0.73**</u>	3.9	0.63
Ulmus minor	5.3	0.0	<u>*-1*</u>	0.6	<u>*-0.81*</u>	1.4	<u>*-0.60*</u>	3.9	-0.16
Humulus lupulus	0.2	0.0	-1	0.0	-1	0.0	-1	0.0	-1
Cornus sanguinea	6.9	0.8	<u>*-0.80*</u>	0.0	<u>*-1*</u>	0.0	<u>*-1*</u>	0.3	<u>*-0.92*</u>

Solanum dulcamara	0.2	0.5	0.43	0.0	-1	0.0	-1	0.0	-1
Fraxinus excelsior	1.05	6.5	**<u>0.74</u>**	2.5	0.41	0.0	-1	5.0	**<u>0.66</u>**
Ligustrum vulgare	9.7	14.6	**0.23**	0.0	*<u>-1</u>*	29.9	**<u>0.60</u>**	21.5	**0.44**
Lonicera periclymenum	1.5	4.4	0.50	0.3	-0.67	27.9	**<u>0.92</u>**	18.7	**<u>0.88</u>**
Sambucus nigra	0.7	0.0	-1	0.0	-1	0.0	-1	3.9	0.70
Viburnum opulus	6.0	9.0	**0.22**	4.3	-0.17	0.0	*<u>-1</u>*	2.2	*-0.48*
Hedera helix	4.6	0.3	-0.88	0.0	-1	0.0	-1	0.0	-1
n (number of records)	1817	611		326		147		358	

*Plant species availability (AV) was estimated in 2005 based on the presence or absence of each species in 2 m long hedge fragments situated every 25 m (*n* = 330 fragments)

**Feeding records (U: use) correspond to the period 1996 – 2006. Males and females were considered together in Winter and Spring; males, females and juveniles were considered together in Summer and Autumn

****S*: Jacobs' selection index (Jacobs 1974). In bold: moderate positive selection (0.21 to 0.5). In bold and underlined: strong positive selection (0.51 to 1). In italics: moderate negative selection (– 0.21 to – 0.5). In italics and underlined: strong negative selection (– 0.51 to – 1). Only values for plants with some relevance are highlighted: %n ≥ 5, in availability, use, or both

Table 2 Traits of fleshy fruits, mainly their seeds, consumed and rejected by Iberian bullfinches in northwestern Spain

Most consumed seeds	Mean number of seeds per fruit	Seed mean length (mm)	Seed mean width (mm)	Seed mean thickness (mm)	Mean weight of 10 seeds (g)	Seed hardness	Fruit type and size***
Rubus spp. (Rosaceae)	34.34**	2.59	1.69	1.10	0.025	Hard	Small drupelet
Bryonia dioica (Cucurbitaceae)	3.38	4.72	3.19	1.84	0.137	Very hard	Small berry
Ligustrum vulgare (Oleaceae)	1.71	4.52	3.10	1.86	0.147	Hard	Small berry
Lonicera periclymenum (Caprifoliaceae)	3.54	3.70	2.44	1.19	0.055	Soft	Small berry
Viburnum opulus (Caprifoliaceae)	1.00	7.63	6.59	1.61	0.370	Hard	Small drupe
Only the pulp was eaten							
Crataegus monogyna (Rosaceae)	1.00	6.41	4.74	4.61	0.787	Very hard	Small pome
Prunus avium (Rosaceae)	1.00	9.05	7.64	6.09	1.976	Very hard	Large drupe
Cornus sanguinea (Cornaceae)	1.00	4.83	4.38	4.28	0.566	Very hard	Small drupe
Abundant plants whose fruits were rejected*							
Euonymus europaeus (Celastraceae)	3.15	5.53	3.34	2.68	0.292	Soft	Small

							ariled seed
Rosa spp. (Rosaceae)	14.51	4.78	2.88	2.34	0.161	Very hard	Large hip
Prunus spinosa (Rosaceae)	1.00	9.25	7.39	5.31	1.839	Very hard	Large drupe
Hedera helix (Araliaceae)	2.14	5.23	3.60	2.69	0.289	Hard	Small berry

Fruit and seed traits according to Torroba et al. (2013) (for sample sizes and SD values, see this reference) and Á. Hernández (pers. obs.)

*Refers to plants with almost or more than 5% availability (see Table 1) whose fruits were either not eaten or eaten in insignificant numbers

**For *Rubus* spp., the mean number of seeds per fruit refers to the entire blackberry (aggregate fruit consisting of drupelets)

***Refers to the structure handled, or probably handled, by the bullfinch when feeding: whole or part of the fruit. Small-sized fruits: normally less than 1 cm long and wide. Large-sized fruits: normally more than 1 cm long and wide.

Table 3 Traits of tree buds consumed and rejected by Iberian bullfinches in northwestern Spain

Most consumed buds	Mean number ± SD of buds per cm of twig (*n* = 12 twigs)	Bud length (mm)	Bud shape	Bud hardness/ Water content	Additional features of buds	Twig thickness (mm)	Twig flexibility
Euonymus europaeus (Celastraceae)	0.8 ± 0.12	5.0 – 7.5	Chubby, round	Soft/ 71.2%	Separate from the twig	2.5 – 3.0	Rigid
Malus spp. (Rosaceae)	0.7 ± 0.17	5.0 – 10.0	Terminal buds: round Lateral buds: triangular	Fairly soft/ 55.4%	Lateral buds fairly attached to the twig	4.0 – 4.5	Slightly flexible
Crataegus monogyna (Rosaceae)	0.5 ± 0.08	3.0 – 6.0	Chubby, some elongated	Soft/ 65.2%	Separate from the twig Probably leaf buds	2.0 – 3.0	Rigid
Prunus spinosa (Rosaceae)	2.5 ± 1.14	1.5 – 2.5	Chubby, pointed	Very soft/ 71.1%	Separate from the twig Most were flower buds	1.5 – 2.5 Twigs end in a spine	Rigid
Prunus avium (Rosaceae)	2.1 ± 0.62	5.0 – 8.5	Chubby, oval	Slightly hard due to the scales/ 63.3%	Separate from the twig Most were probably flower buds	2.5 – 3.5	Fairly rigid
Abundant plants whose buds were rejected*							

Rubus spp. (Rosaceae)	0.3 ± 0.07	2.5 – 4.5	Elongated, pointed	Soft/ 57.4%	Separate from the twig Probably leaf buds	2.5 – 4.5 Twigs with many spines	Fairly rigid
Rosa spp. (Rosaceae)	0.4 ± 0.14	3.5 – 6.0	Elongated, pointed	Soft/ 62.8%	Separate from the twig Probably leaf buds	2.0 – 4.0 Twigs with some spines	Rigid
Ligustrum vulgare (Oleaceae)	0.7 ± 0.09	2.0 – 6.0 Lateral buds smaller	Chubby	Soft/ 63.8%	Lateral buds attached to the twig	1.5 – 3.0	Rigid

Traits of buds and twigs are from own data for February – March, except some values for bud length and twig thickness supplemented by Herrero and Zaldívar (2001)

*Refers to plants with almost or more than 10% availability (see Table 1) whose buds were either not eaten or eaten in insignificant numbers

Table 4 Diet selection of Iberian bullfinches in northwestern Spain referring to herb seeds in spring and summer

Plants	Spring			Summer		
	AV* (%cover)	U** (%*n*)	*S****	AV (%cover)	U (%*n*)	*S*
Urtica dioica	0.0	0.88	1	5.75	0.0	*-1*
Polygonum bistorta	0.0	0.0	-	4.42	20.33	**0.69**
Rumex spp.	0.0	0.0	-	1.94	7.87	**0.62**
Stellaria holostea	0.0	0.0	-	1.96	0.0	-1
Cucubalus baccifer	0.0	0.0	-	0.30	0.0	-1
Ranunculus ficaria	21.65	0.0	*-1*	0.0	0.0	-
Ranunculus spp.	13.10	0.0	-*1*	4.28	7.87	**0.31**
Alliaria petiolata	0.31	0.0	-1	0.09	0.0	-1
Cardamine flexuosa	0.0	1.77	1	0.0	0.0	-
Filipendula ulmaria	0.0	0.0	-	7.74	25.57	**0.61**
Alchemilla glabra	0.0	0.0	-	0.13	0.0	-1
Agrimonia eupatoria	0.0	0.0	-	1.76	0.33	-0.69
Sanguisorba minor	0.0	0.0	-	0.05	0.0	-1
Geum urbanum	5.20	0.0	*-1*	6.93	26.23	**0.65**
Geum rivale	1.98	0.0	-1	0.19	0.0	-1
Vicia sepium	0.0	0.0	-	5.87	0.0	*-1*
Medicago spp.	0.0	0.0	-	0.05	0.0	-1
Trifolium spp.	0.0	0.0	-	0.28	0.33	0.08
Geraniaceae	0.0	0.0	-	2.19	4.92	**0.40**

Malva moschata	0.0	0.0	-	0.14	0.0	-1
Hypericum perforatum	0.0	0.0	-	0.07	0.0	-1
Epilobium hirsutum	0.0	1.77	1	0.40	0.0	-1
Chaerophyllum hirsutum	0.0	0.0	-	4.98	0.0	*-1*
Anthriscus sylvestris	0.0	0.0	-	3.91	0.0	-1
Heracleum sphondylium	0.0	0.0	-	0.37	0.0	-1
Torilis japonica	0.0	0.0	-	0.71	0.0	-1
Galium aparine	7.28	0.0	*-1*	4.93	0.0	*-1*
Galeopsis tetrahit	0.0	0.0	-	0.89	0.0	-1
Lamium maculatum	1.04	0.0	-1	0.0	0.0	-
Stachys sylvatica	0.0	0.0	-	1.81	0.0	-1
Clinopodium vulgare	0.0	0.0	-	0.15	0.0	-1
Mentha longifolia	0.0	0.0	-	0.42	0.0	-1
Veronica spp.	14.59	0.0	*-1*	3.12	0.0	-1
Plantago spp.	0.0	0.0	-	1.99	0.98	-0.34
Bellis perennis	0.0	1.77	1	0.0	0.0	-
Chamaemelum nobile	0.0	0.0	-	0.0	0.66	1
Achillea millefolium	0.0	0.0	-	0.44	0.0	-1
Lapsana communis	0.0	0.0	-	1.23	0.33	-0.58
Taraxacum gr. *officinale*	34.88	92.04	**0.91**	0.62	0.33	-0.31
Senecio vulgaris	0.0	1.77	1	0.0	0.0	-
Lactuca serriola	0.0	0.0	-	0.0	4.26	**1**
Allium spp.	0.0	0.0	-	0.10	0.0	-1
Poaceae	0.0	0.0	-	29.72	0.0	*-1*
Carex spp.	0.0	0.0	-	0.03	0.0	-1

Sampling units per month	48		48	
n (number of records)		113		305

*Plant availability (AV) is the cover of species with fully grown fruits, corrected for a total of 100%, obtained in 48 sampling units per month in 2005, at a maximum distance of 1.5 m from the base of the hedgerow. Spring: mean cover in April – May. Summer: mean cover in June – July – August. Data for cover taken from Hernández and Zaldívar (2013)

**Feeding records (U: use) correspond to the period 1996 – 2006. Spring diet: March to May. Summer diet: June to August. Males and females were considered together in Spring; males, females and juveniles were considered together in Summer

****S*: Jacobs' selection index (Jacobs 1974). In bold: moderate positive selection (0.21 to 0.5). In bold and underlined: strong positive selection (0.51 to 1). In italics: moderate negative selection (– 0.21 to – 0.5). In italics and underlined: strong negative selection (– 0.51 to – 1). Only values for plants with some relevance are highlighted: %n > 5 or almost 5, in availability, use, or both

Table 5 Traits of herb fruits consumed and rejected by Iberian bullfinches in northwestern Spain

Most consumed seeds	Fruit length** (mm)	Fruit type	Additional features
Polygonum bistorta (Polygonaceae)	3.5 – 4.0	Achene	Length includes perianth surrounding achene
Rumex spp. (Polygonaceae)	4.0 – 5.0	Achene	Length includes valves surrounding achene
Ranunculus spp. (Ranunculaceae)	3.5 – 4.0	Achene	Length includes a short hook
Filipendula ulmaria (Rosaceae)	3.0 – 5.0	Achene	Spiral shaped achene
Geum urbanum (Rosaceae)	3.0 – 6.0	Achene	Hairy surface; length does not include a long hook
Geranium spp. (Geraniaceae)	2.0 – 3.0	Mericarp	Dehiscent mericarp; length refers to the seed
Taraxacum gr. *officinale* (Asteraceae)	2.0 – 3.0	Achene	Spiny surface; length does not include a very long beak ending in a pappus
Lactuca serriola (Asteraceae)	3.0 – 4.0	Achene	Length does not include a long beak ending in a pappus
Abundant plants whose fruits were rejected*			
Urtica dioica (Urticaceae)	1.5 – 2.0	Achene	Length includes perianth surrounding achene
Vicia sepium (Fabaceae)	20.0 – 35.0	Legume	Legume containing 2 – 4 seeds 3.5 – 4.0 mm long
Chaerophyllum hirsutum (Apiaceae)	8.0 – 15.0	Mericarp	Surface with longitudinal ridges and furrows
Galium aparine (Rubiaceae)	2.0 – 3.0	Mericarp	Surface covered by short hooks
Poaceae	7.0 – 8.0	Spikelet	Surface with hairs and/or awn; spikelet containing one or more seeds

Fruit trait data taken from Hernández and Zaldívar (2013) and Á. Hernández (pers. obs.)

*Refers to plants with almost or more than 5% availability (see Table 4) whose fruits were either not eaten or very scarcely eaten

**Refers to the structure that the bullfinch handled or would probably handle when feeding, as detailed in the "Additional features" column

Figures

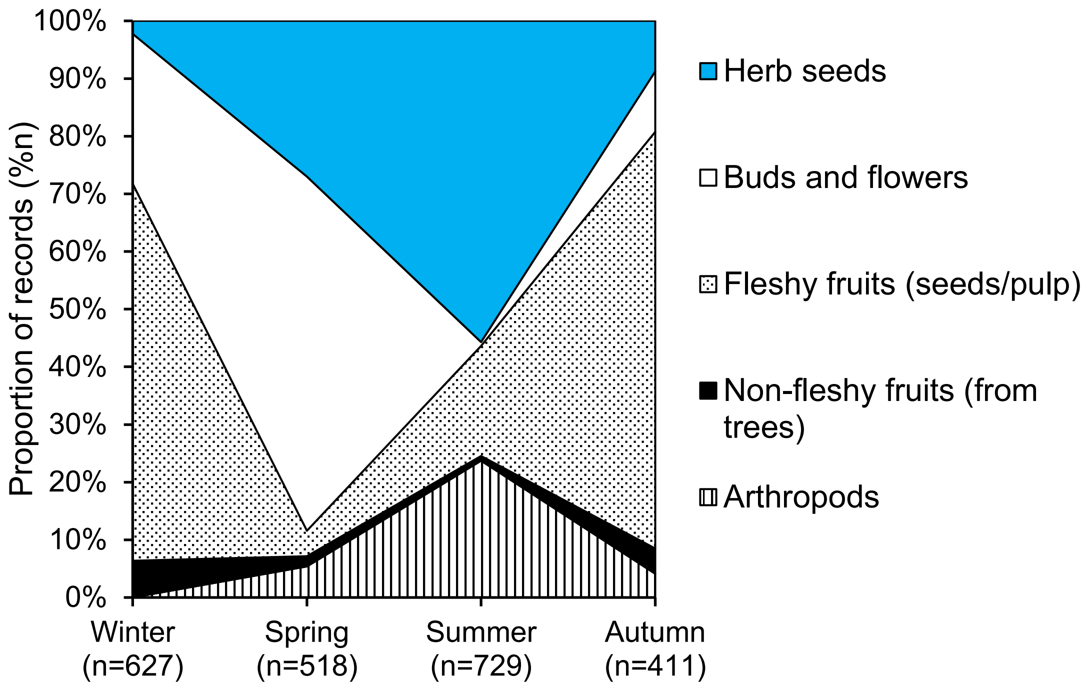
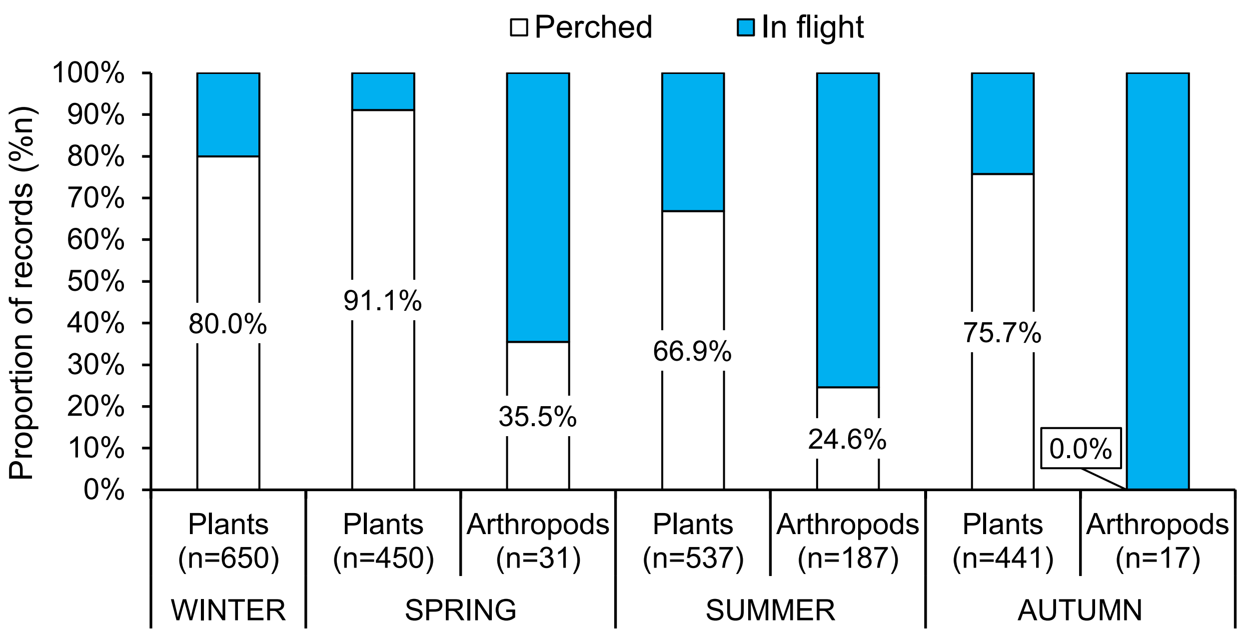
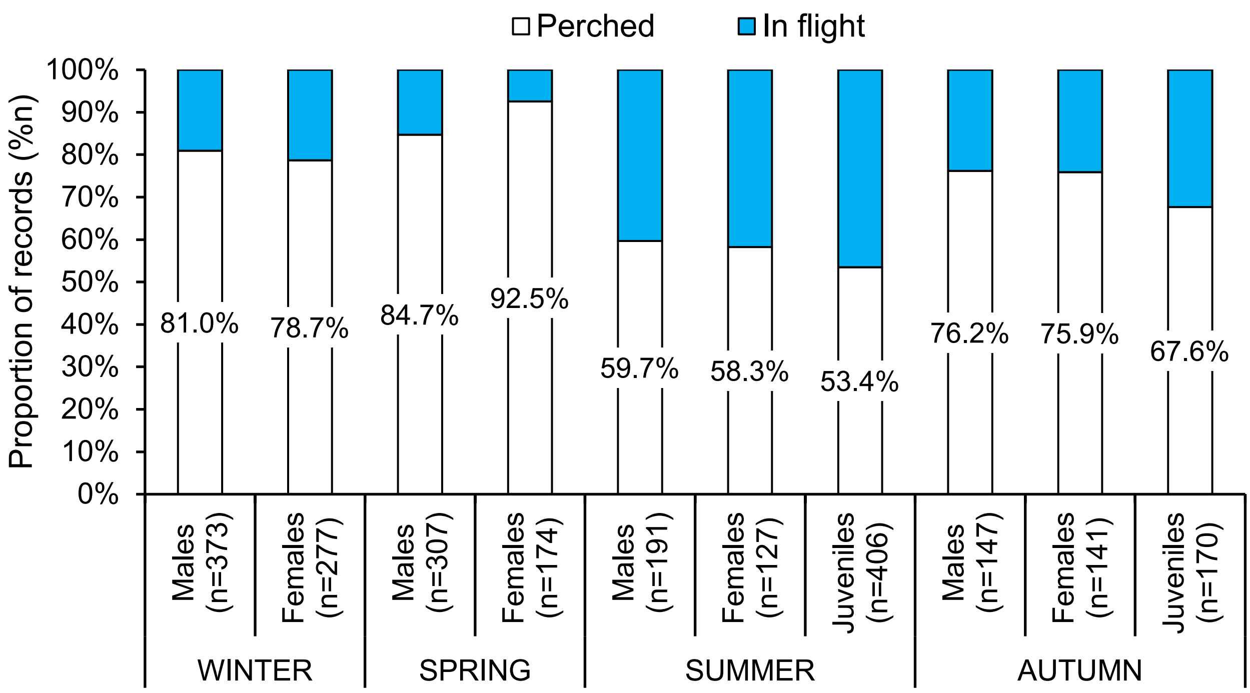


Fig. 1 Seasonal diet of Iberian bullfinches in northwestern Spain considering general food categories. Pooled data for the period 1996 – 2006. *n*: number of records per season. Each record refers to an individual eating a specific food type, regardless of the units (amount) ingested. A single individual could produce more than one record if it ate more than one food type during a maximum of 10 min observation. Males and females were considered together in winter and spring; males, females and juveniles were considered together in summer and autumn. Number of individuals observed: winter: 227 males, 199 females; spring: 268 m, 158 f; summer: 116 m, 106 f, 390 juveniles; autumn: 101 m, 91 f, 103 j



a)



b)

Fig. 2 Seasonal foraging tactics of Iberian bullfinches in northwestern Spain regarding a) foods of plant/animal origin and b) sex/age. In a), males and females were considered together in winter and spring; and males, females and juveniles were considered together in summer and autumn. Pooled data for the period 1996 – 2006. *n*: number of records. Each record refers to an individual eating a specific food type in a specific way, regardless of the units (amount) ingested. A single individual could produce more than one record if it ate more than one food type, and/or ate the same food type “perched” and “in flight”, during a maximum of 10 min observation. Only identified plants (at least tree genus and herb family) are considered. “Perched” includes on the ground

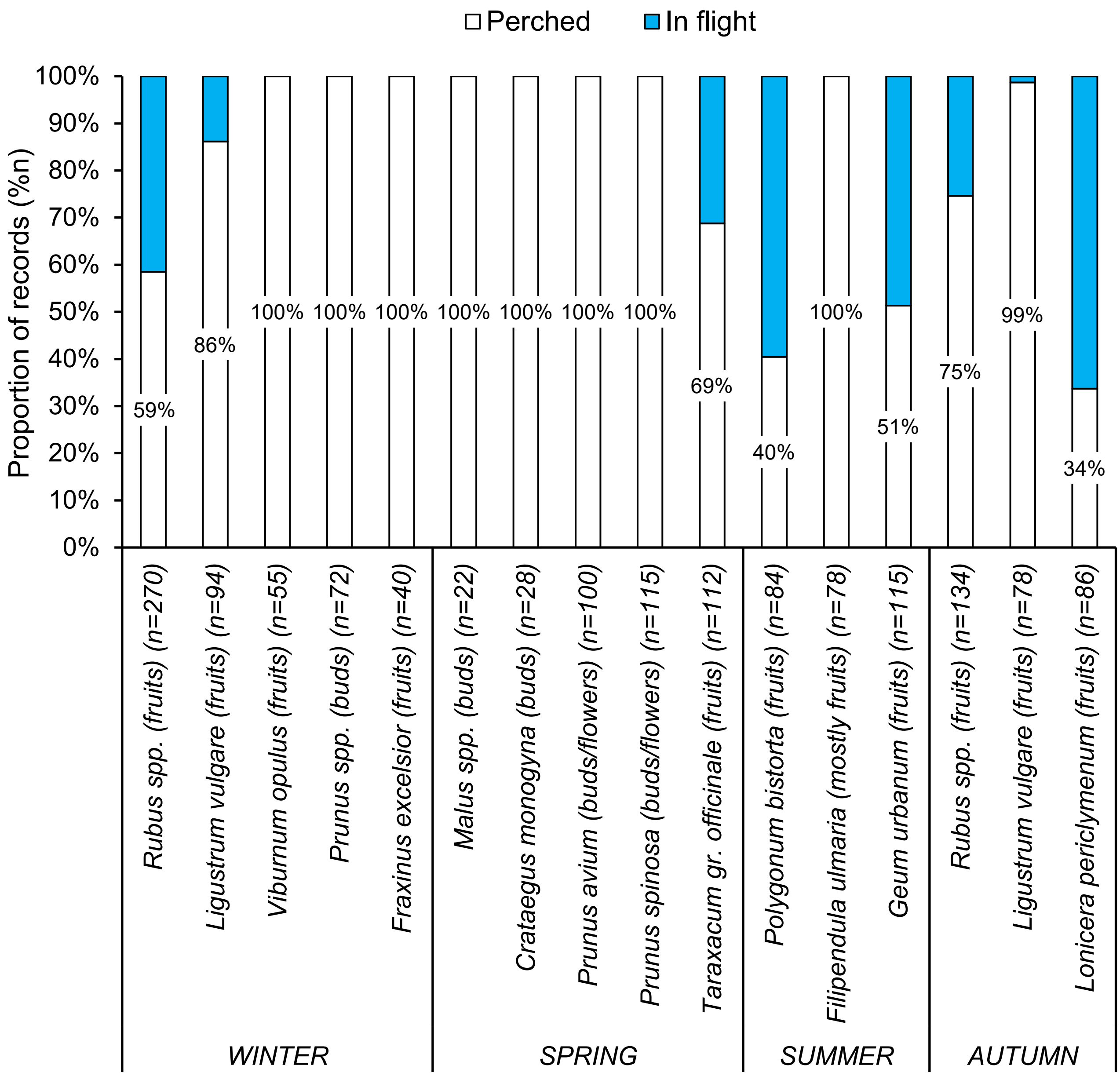


Fig. 3 Seasonal foraging tactics of Iberian bullfinches in northwestern Spain regarding principal foods of plant origin (species and genera). Pooled data for the period 1996 – 2006. *n*: number of records. Each record refers to an individual eating a specific food type in a specific way, regardless of the units (amount) ingested. An individual could produce more than one record if it ate more than one food type, and/or ate the same food type "perched" and "in flight", during a maximum of 10 min observation. Males and females were considered together in winter and spring; males, females and juveniles were considered together in summer and autumn. "Perched" includes on the ground

Ornithology Research

Seasonal feeding habits of the Iberian bullfinch *Pyrrhula pyrrhula iberiae* in northwestern Spain

Ángel Hernández[1,2]

[1] Zoology Area, Department of Agroforestry, University of Valladolid, Avenida de Madrid 44, 34004 Palencia, Spain

[2] University Institute for Research in Sustainable Forest Management, University of Valladolid-National Institute for Agriculture and Food Research and Technology, Avenida de Madrid 44, 34004 Palencia, Spain

angel.hernandez.lazaro@uva.es

http://orcid.org/0000-0002-6282-2400

Supplementary Material S1 Seasonal diet of Iberian bullfinches in northwestern Spain. Detailed information

FOOD TYPES	WINTER		SPRING		SUMMER			AUTUMN		
	M	F	M	F	M	F	J	M	F	J
	(227 i)	(199 i)	(268 i)	(158 i)	(116 i)	(106 i)	(390 i)	(101 i)	(91 i)	(103 i)
	%*n*	%*n*	%*n*	%*n*	%*n*	%*n*	%*n*	%*n*	%*n*	%*n*
Ribes uva-crispa	0.0	0.0	0.3 (b)	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Populus spp.	2.8 (b)	1.1 (b)	1.9 (s) 0.3 (b)	0.5 (s)	0.5 (s)	0.0	0.0	0.0	0.0	3.8

Salix spp.	0.3 (b)	0.0	0.6 (b)	1.0 (b)	0.0	0.0	0.0	3.1 (b)	1.6 (b)	3.2 (b)
Euonymus europaeus	3.9 (b)	2.6 (b)	0.3 (b)	0.5 (b)	0.0	0.0	0.0	0.8 (s)	0.8 (b)	0.0
Cytisus scoparius	0.0	0.0	0.0	0.5 (b)	0.0	0.0	0.0	0.0	0.0	0.0
Corylus avellana	0.0	0.0	0.3 (b)	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Quercus pyrenaica	0.0	0.0	0.0	0.0	0.5 (s)	0.8 (s)	0.7 (s)	0.0	0.0	0.0
Rubus spp.	**36.9 (s)**	**43.8 (s)**	1.9 (s)	1.5 (s)	2.5 (s)	2.4 (s)	2.7 (s)	**33.8 (s)**	**33.1 (s)**	**14.6 (s)**
Rosa spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8 (s) 0.8 (b)	0.0	0.0
Pyrus pyraster	0.0	0.0	1.5 (b)	1.5 (b)	0.0	0.0	0.0	0.0	0.0	0.0
Malus spp.	0.0	0.4 (b)	3.7 (b)	5.2 (b)	0.0	0.0	0.0	0.0	0.0	0.0
Crataegus monogyna	0.8 (p) 4.4 (b)	0.4 (p) 4.1 (b)	4.3 (b)	7.2 (b)	1.0 (p)	0.0	1.0 (p)	3.8 (p)	1.6 (p) 1.6 (b)	0.6 (p)
Prunus spinosa	**9.4 (b)**	**8.6 (b)**	**22.6 (b)**	**21.6 (b)**	0.0	0.0	0.0	0.0	0.0	0.0
Prunus avium	1.4 (b)	0.4 (b)	**18.0 (b)**	**21.6 (b)**	3.5 (p)	2.4 (p)	2.7 (p)	1.5 (b)	3.2 (b)	0.0
Prunus domestica	1.4 (b)	1.5 (b)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Rhamnus cathartica	0.0	0.0	0.3 (b)	0.5 (b)	0.0	0.0	0.0	0.0	0.0	0.0
Bryonia dioica	0.3 (s)	0.0	0.0	0.0	0.5 (s)	0.8 (s)	1.5 (s)	2.3 (s)	2.4 (s)	5.1 (s)
Ulmus minor	0.0	0.0	0.3 (s)	0.5 (s)	0.5 (b)	0.0	0.2 (b)	3.8 (b)	3.2 (b)	3.2 (b)
Cornus sanguinea	0.3 (p)	1.5 (p)	0.0	0.0	0.0	0.0	0.0	0.0	0.8 (p)	0.0
Solanum dulcamara	0.6 (s)	0.4 (s)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Fraxinus excelsior	5.0 (s)	**8.2 (s)**	1.5 (b)	1.5 (b)	0.0	0.0	0.0	7.7 (s)	6.5 (s)	0.0
Ligustrum vulgare	**13.6 (s)**	**14.6 (s)** 0.4 (b)	0.0	0.0	6.0 (s)	6.5 (s)	5.9 (s)	**15.4 (s)**	**17.0 (s)**	**22.9 (s)**
Lonicera periclymenum	0.6 (s) 5.0 (b)	2.6 (b)	0.3 (b)	0.0	6.5 (s)	6.5 (s)	5.0 (s)	**11.5 (s)**	**13.7 (s)**	**22.3 (s)**
Sambucus nigra	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8 (s)	0.0	7.0 (s) 1.3 (b)
Viburnum opulus	**10.8 (s)**	6.0 (s)	2.5 (s)	3.1 (s)	0.0	0.0	0.0	3.1 (s)	2.4 (s)	0.6 (s)
Hedera helix	0.0	0.7 (s)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Unidentified trees	0.6 (b)	0.0	3.7 (b)	4.1 (b)	0.0	0.0	0.0	0.0	0.0	0.0
TOTAL TREES	*98.1*	*97.4*	*64.4*	*71.0*	*21.5*	*19.4*	*19.9*	*89.1*	*88.0*	*84.7*
Urtica dioica	0.0	0.0	0.0	0.5 (s)	0.0	0.0	0.0	0.8 (s)	0.8 (s)	0.0
Polygonum bistorta	0.0	0.0	0.0	0.0	**11.1 (s)**	**8.9 (s)**	7.2 (s)	0.0	0.0	0.0
Rumex spp.	0.0	0.0	0.0	0.0	2.0 (s)	3.3 (s)	3.9 (s)	0.0	0.8 (s)	1.3 (s)
Ranunculus spp.	0.0	0.0	0.0	0.0	4.5 (s)	4.9 (s)	2.2 (s)	0.0	0.0	0.0

Cardamine flexuosa	0.0	0.0	0.3 (s)	0.3 (s)	0.0	0.0	0.0	0.0	0.0	0.0
Filipendula ulmaria	0.0	0.0	0.0	0.0	5.0 (s)	7.3 (s)	**14.0 (s)**	6.2 (s)	5.6 (s)	7.0 (s)
					0.5 (b)	0.8 (b)				
Agrimonia eupatoria	0.0	0.0	0.0	0.0	0.0	0.8 (b)	0.0	0.0	0.0	0.0
Geum urbanum	0.3 (s)	0.0	0.0	0.0	**10.6 (s)**	**13.8 (s)**	**10.3 (s)**	0.0	0.0	0.6 (s)
Trifolium repens	0.0	0.0	0.0	0.0	0.0	0.0	0.2 (s)	0.0	0.0	0.0
Geraniaceae	0.0	0.0	0.0	0.0	3.0 (s)	1.6 (s)	1.7 (s)	0.0	0.0	0.0
Hypericum perforatum	0.0	0.4 (s)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Epilobium hirsutum	0.8 (s)	1.1 (s)	0.3 (s)	0.5 (s)	0.0	0.0	0.0	0.0	0.0	0.0
Galium aparine	0.0	0.7 (s)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Plantago lanceolata	0.0	0.0	0.0	0.0	0.0	0.0	0.7 (s)	0.0	0.0	0.0
Bellis perennis	0.0	0.0	0.3 (b)	0.5 (b)	0.0	0.0	0.0	0.0	0.0	0.0
Chamaemelum nobile	0.0	0.0	0.0	0.0	0.5 (s)	0.8 (s)	0.0	0.0	0.0	0.0
Lapsana communis	0.0	0.0	0.0	0.0	0.0	0.0	0.2 (s)	0.0	0.0	0.0
Taraxacum gr. *officinale*	0.0	0.0	**22.6 (s)**	**15.9 (s)**	0.5 (s)	0.0	0.0	0.0	0.0	0.0
Senecio vulgaris	0.0	0.0	0.3 (b)	0.5 (b)	0.0	0.0	0.0	0.0	0.0	0.0
Lactuca serriola	0.0	0.0	0.0	0.0	2.0 (s)	2.4 (s)	1.5 (s)	0.8 (s)	2.4 (s)	0.0
Unidentified herbs	0.0	0.0	0.0	0.0	4.5 (s)	4.9 (s)	2.9 (s)	0.0	0.0	0.0
Ground feeding (probably herb seeds)	0.8	0.4	5.3	7.2	14.6	9.8	8.8	0.0	0.0	0.0
TOTAL HERBS	*1.9*	*2.6*	*29.1*	*25.4*	*58.9*	*59.5*	*53.6*	*7.8*	*9.6*	*8.9*
TOTAL PLANTS	*100.0*	*100.0*	*93.5*	*96.4*	*80.4*	*78.9*	*73.5*	*96.9*	*97.6*	*93.6*
Tetragnatha montana (Tetragnathidae, Araneae)	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Unidentified Araneae	0.0	0.0	0.6	0.0	1.5	0.0	3.4	0.0	0.0	1.9
Aphrophora alni nymphs (Aphrophoridae, Hemiptera)	0.0	0.0	1.5	0.5	0.5	1.6	0.0	0.0	0.0	0.0
Unidentified Aphididae (Hemiptera)	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0
Yponomeuta sp. larvae (Yponomeutidae, Lepidoptera)	0.0	0.0	1.2	1.0	0.5	0.0	0.0	0.0	0.0	0.0
Operophtera fagata larvae (Geometridae, Lepidoptera)	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Unidentified Lepidoptera larvae	0.0	0.0	0.0	0.0	3.0	3.3	0.0	0.0	0.0	0.0
Unidentified Arthropoda	0.0	0.0	1.9	2.1	14.0	15.4	23.1	3.1	2.4	4.5

(most were probably insects)										
TOTAL ARTHROPODS	*0.0*	*0.0*	*6.5*	*3.6*	***19.6***	***21.1***	***26.5***	*3.1*	*2.4*	*6.4*
n (number of records)	360	267	323	195	199	123	407	130	124	157

Values ≥ 8.0% in bold. Each record refers to an individual eating a specific food type, regardless of the units (amount) ingested. A single individual could produce more than one record if it ate more than one food type during a maximum of 10 min observation. M: males, F: females, J: juveniles, i: number of observed individuals, s: seeds (at different growth and ripening stages), p: pulp, b: buds/flowers. *Prunus spinosa* includes *P. insititia*. “Trees” includes shrubs and climbers. Unidentified trees were mostly Rosaceae. Pooled data for the period 1996 – 2006

Supplementary Material S2 Additional information on within-season variations in diet. Data used for statistical analyses were taken from Supplementary Material S1

In winter, both males and females ate mainly fleshy fruit (64% and 67% of feeding records, respectively, mostly seeds and occasionally pulp), and to a lesser extent tree buds/flowers (29%, 22%), ash samaras (5%, 8%) and herb seeds (2%, 3%), resulting in a non-significant difference between sexes (χ^2_3 = 6.40, P = 0.09). In spring, there were no significant differences between males and females in the frequency of plant food (94% and 96%, respectively) and animal food (arthropods) (6% and 4%) records (χ^2_1 = 1.49, P = 0.22). Excluding arthropods, neither were there significant differences between sexes for buds/flowers in general (63% and 69%, mostly trees) and seeds in general (37% and 31%, mostly herbs) (χ^2_1 = 1.60, P = 0.21).

In summer, no significant differences were observed between males, females and juveniles in the frequency of plant food (the three categories of individuals being within the 74 – 80% interval) and animal food (arthropods) (20 – 26%) records (χ^2_2 = 4.10, P = 0.13). Considering only plant food, fruits in general were the most frequently consumed by the three categories of individuals (≥ 98%), herb seeds forming approximately three quarters and fleshy fruit one quarter in the three cases. Arthropods were frequently consumed by all three categories of individuals in summer, but in many cases could not be more accurately identified, small spiders and insects being distinguished on all other occasions. In autumn, there were no significant differences between the categories of individuals in the frequency of plant food (males, females and juveniles within the 94 – 98% interval) and animal food (arthropods) (2 – 6%) records (χ^2_2 = 3.26, P = 0.20). Taking into account only plant food, males, females and juveniles consumed fruits in general more frequently than tree buds (91%, 89% and 88% vs. 9%, 11% and 12%, respectively; χ^2_2 = 0.52, P = 0.77). Considering only fruits, they consumed more tree fruits than herb seeds (91%, 89%, 89% vs. 9%, 11%, 11%; $\chi^2_2 = 0.41$, $P = 0.82$), mainly fleshy fruit (> 90% of tree fruits for the three categories of individuals, mostly seeds and much less pulp) and, to a lesser extent, ash samaras (the rest).

Considering only the three fleshy fruit seeds most recorded as winter food (all together > 95% of fleshy fruit records for both sexes), males and females consumed similar proportions of privet seeds (22% and 23%, repectively), and males slightly fewer bramble seeds than females (60%, 68%) and slightly more guelder rose seeds (18%, 9%), no significant differences between sexes being observed ($\chi^2_2 = 5.76$, $P = 0.06$). Considering only the five tree buds/flowers most consumed in winter (all together > 96% of bud/flower records for both sexes), *Prunus* species were the most important for both sexes (43% males, 50% females), followed by hawthorn (15%, 19%), honeysuckle (17%, 13%), spindle (14%, 13%), and Salicaceae (*Populus* plus *Salix*) species (11%, 5%) ($\chi^2_4 = 2.56$, $P = 0.63$).

Considering only the four tree buds/flowers most recorded as spring food (all together > 83% of bud/flower records for both sexes), differences between males and females were not significant (blackthorn: 46% males, 39% females; cherry: 37%, 39%; hawthorn: 9%, 13%; *Malus* species: 8%, 9%; $\chi^2_3 = 2.11$, $P = 0.55$). Considering only herb seeds, both sexes ate mostly *Taraxacum* seeds, with males consuming slightly more than females (79% vs. 65%).

Considering only herb seeds, approximately half of the summer feeding records corresponded to the sum of *Polygonum*, *Filipendula* and *Geum* species for the three categories (46% males, 52% females, 58% juveniles; remaining herb seeds: 54%, 48%, 42%; $\chi^2_2 = 5.05$, $P = 0.08$). However, considering only these three herb plants, males consumed more *Polygonum* (42%) and *Geum* (40%), females *Geum* (46%) and *Polygonum* (30%), and juveniles *Filipendula* (45%) and *Geum* (33%) seeds ($\chi^2_4 = 14.72$, $P = 0.005$). In the case of fleshy fruits, approximately one third of feeding records corresponded to honeysuckle seeds for the three categories (33% males, 35% females, 26% juveniles), one third to privet seeds (30%, 35%, 32%) and one third to the other fleshy-fruited species (37%, 30%, 42%, largely seeds and some pulp) ($\chi^2_4 = 1.35$, $P = 0.85$).

Considering only the three fleshy fruit seeds most recorded as autumn food (all together > 81% of fleshy fruit records for the three categories of individuals), males and females ate more bramble seeds (56% and 52%, respectively), whereas juveniles ate more privet (38%) and honeysuckle (37%) seeds ($\chi^2_4 = 21.41$, $P < 0.001$). Considering only herb seeds, over half of the feeding records corresponded to *Filipendula* for the three categories (80% males, 58% females, 79% juveniles).

Supplementary Material S3 Detailed information on food handling, for both plants and invertebrates

Food handling: plants

Regarding tree buds/flowers, bullfinches mostly consumed flower buds and fewer open flowers and leaf buds. They usually plucked the buds and handled them in their bills, the embryonic parts being eaten and the covering scales dropped. Sometimes, only recently opened flowers were eaten in the case of plants with very hard buds (e.g., ash). The basal part (ovary) of the open flowers was usually consumed and the petals discarded (e.g., blackthorn, cherry). Each bud/flower was usually plucked in one go, although some larger shoots (e.g., honeysuckle incipient leaves and tender stems) and flower clusters (e.g., poplar catkins) were consumed in several bites. Individual bullfinches often spent some time feeding on the buds/flowers of an individual plant, or of adjacent plants of the same species, moving amongst the twigs (e.g., gooseberry, poplar, willow, hawthorn, cherry, elm, ash). In the case of blackthorn, they normally consumed a large quantity of buds/flowers by slowly advancing along one twig without having to move to another, and if they could reach other twigs by stretching in different directions they would not move at all (records of up to 20, 24 and 27 bites without moving).

Bullfinches plucked whole fleshy fruits and handled them in their bills, or removed the seeds without plucking the fruits, using both methods on each plant species. Normally, they dropped the skin and pulp of the plucked fruits, and the seed shell. They rarely held a fruit against a branch with their bills to remove the seeds without using their legs (e.g., honeysuckle). They did not always consume all of the seeds of plucked multi-seeded fruits, as sometimes some whole seeds were dropped with the skin and pulp (e.g., privet). Plucked honeysuckle berries were apparently placed in the bill with the open part (basal part) facing inside the mouth, and were then squeezed to release the seeds. Although bullfinches ate the majority of fleshy fruits during autumn–winter, when ripe, they also frequently consumed unripe fruits in summer (e.g., bramble, bryony, privet, honeysuckle), showing a preference for the ripe fruits if both were available on the same plant (black bramble drupelets preferred to red ones, red honeysuckle berries preferred to green ones). They often continued consuming the seeds of fruits with semi- or completely dry pulp (e.g., bramble, guelder rose). They did not pluck the whole fruit if they only ate the pulp (hawthorn, cherry, dogwood), just pieces of pulp one after the other, sometimes from unripe fruits (e.g., hawthorn). They occasionally pecked at the pulp of fruits of which they only normally ate the seeds (e.g., guelder rose). Individual bullfinches often spent a long time eating the fleshy fruit of a single plant or adjacent plants of the same species (e.g., bramble: at least 10 consecutive minutes on various occasions, several cases of at least 15 – 20 drupelets; privet and honeysuckle: at least 10 consecutive minutes on various occasions, several cases of at least 10 – 12 berries). They frequently did not stop eating a bramble fruit (aggregate of drupelets) or a bunch of privet/honeysuckle fruits until they had finished it.

Some individuals insistently ate poplar green fruit capsules that were still closed, consuming whole clusters from which they plucked each fruit to eat the seeds, dropping the remains to the ground. Ripe ash samaras were often persistently removed and their flattened wing discarded.

When bullfinches took herb fruits in flight, they usually flew towards them from the lower branches of shrubs or trees, or from the base of wide trunks as they were able to grip the bark, a method sometimes used in poplar plantations, since the trees do not have low branches there. Without considering the consumption of fallen seeds on the ground, they used different techniques on each plant species to obtain herb fruits while perching: (i) perched on the plant without bending it (plants upright or lying on the ground, mainly due to the action of ungulates), (ii) perched on the stalk and bending the plant towards the ground, (iii) perched on a different plant to the one they were eating from (often a shrub branch), (iv) perched on the ground in the case of a very low plant. They peeled the seeds with their bills, dropping the rest of the fruit, including protruding structures such as hooks (e.g., *Geum*) and pappi (e.g., *Taraxacum*). Apart from ripe fruit seeds, even those of plants that had dried up (e.g., *Urtica*), they also fed on seeds from green, unripe fruits (e.g., *Ranunculus*, *Filipendula*, *Geum*). Whilst perched they frequently opened *Taraxacum* closed heads, an intermediate stage between flower head and seed head, to reach the developing seeds. They detached *Geranium* schizocarps whole before they split up into mericarps when mature. Sometimes they preferred green, unripe fruits to ripe ones when both were available and within reach (e.g., *Geum*). Individual birds often spent over 10 consecutive minutes eating the herb seeds of an individual plant or nearby plants of the same species (e.g., *Urtica*, *Polygonum*, *Rumex*, *Ranunculus*, *Filipendula*, *Geum*, *Taraxacum*, *Lactuca*). They usually handled each head/raceme until they finished it and often consumed several fruits at once. They ate some herb flowers/buds, using the base (ovary) and discarding the rest (e.g., *Filipendula*, *Agrimonia*, *Bellis*, *Senecio*).

Food handling: invertebrates

Bullfinches were able to catch both insects and spiders in flight, the latter from their silk threads amongst tree branches and herbs. The same athropod taxon could be captured using the perched and in flight techniques (e.g., froghopper nymphs – spittlebugs – on willows, aphids on honeysuckles). After taking *Aphrophora* spittlebugs from their foam (“cuckoo spit”), they sometimes moved their heads from side to side to remove the watery liquid. Lepidopteran caterpillars were captured from several plant species (e.g., spindle, hazel, oak, apple, blackthorn). They captured solitary caterpillars or took them from communal silken nests (e.g., *Yponomeuta* caterpillar nests on spindle). Aerial insects caught in flight were small and therefore difficult to identify, but were probably dipterans in several cases. On one occasion, a bird carrying an insect in its bill appeared to press it against a branch, perhaps to position it better, kill it, and/or remove a part of the body that it would not eat. Individual bullfinches often spent a long time eating individuals from the same prey species (e.g., spittlebugs, aphids, caterpillars, aerial insects, spiders).

Supplementary Material S4 Additional discussion on diet selection. Chemical, organoleptic and nutritional features of bullfinch foods and their effect on diet selection. Selection of invertebrates

Several of the fruits that bullfinches showed a preference for are especially rich in flavonoids and carotenoids (mostly xanthophylls), including seeds, e.g., ash, bramble, honeysuckle, guelder rose and *Filipendula ulmaria*, presumably providing antioxidant benefits as well as energy and nutrients (Goodwin 1952, 1956; Yunusova et al. 1998; Lobanova et al. 1999; Krasnov et al. 2006; Cam et al. 2007; Pukalskienė et al. 2015; Toledo-Martín et al. 2018 and references therein; Tonguç 2019). Seeds in general are a good source of xanthophyll carotenoids (Howitt and Pogson 2006). Bullfinches performing moult in the study area were mainly observed during August – November (Á. Hernández unpubl. data), when they largely fed on the seeds of several of the above-mentioned plant species. Most birds, including bullfinches, assimilate and/or store xanthophylls, and those deposited in feathers contribute to their colouring, determining sexual dichromatism and acting as an index of vigour and a sexual attractiveness (Olson and Owens 1998; Badyaev 2000; McGraw et al. 2001; Stradi et al. 2001; Cantarero and Alonso-Álvarez 2017; Maoka 2020).

European and North American granivorous passerines select specific plant foods based mainly on their bill size and shape, i.e., handling efficiency, and secondarily on availability and nutritional value, according to field and lab studies (Newton 1967a, 1985; Willson 1971; Glück 1985; Pulliam 1985; Greig-Smith and Crocker 1986; Snow and Snow 1988; Díaz 1990, 1994, 1996; Borras et al. 2003; García-del-Rey and Cresswell 2005; Valera et al. 2005; Förschler and Kalko 2006). Nevertheless, an in-depth analysis of the chemical, organoleptic and nutritional features of bullfinch foods and their effect on diet selection has yet to be carried out.

Based on information available to date, it is not possible to determine in minute detail the selection of invertebrates by bullfinches, since the taxonomic identification of their prey is not accurate and/or field sampling is insufficient to assess the availability of invertebrate taxa; nevertheless, the general rule is that they capture small insects and spiders, as well as small snails in some places (Newton 1967b; Guitián 1985; Cramp and Perrins 1994; Marquiss 2007; Clement 2010; present study).

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