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Gregariousness and intraspecific aggression in Iberian bullfinches (*Pyrrhula pyrrhula iberiae*) throughout the year

Short title: **Social behaviour in Iberian bullfinches**

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Abstract

This study provides novel information about gregariousness and intraspecific aggression in Iberian bullfinches (*Pyrrhula pyrrhula iberiae*) in northwestern Spain. Small monospecific parties never exceeding 10 individuals were seen throughout the year, larger in winter on average. Males considerably outnumbered females within the groups. Adult flocks were frequent only in winter. In spring, many of the adult groups were mixed-sex assemblages composed of pairs plus supernumerary males. Sightings of juvenile groups, up to seven individuals, were common in summer–autumn. The vigilance role in mixed-sex assemblages, including pairs, appeared to be the responsibility of males based on sex-specific vigilance rates. The highest frequency of aggressive encounters, mainly male against male, occurred during the breeding season, associated with mate defence. Females attacked males, not the contrary, which supports reversed sexual dominance in bullfinches. Gregariousness probably acted as an anti-predatory and foraging strategy.

Keywords

agonistic behaviour, dominance, flocking, mobility, seasonal variation, vigilance.

1. Introduction

Gregariousness in birds often concerns mixed or monospecific flocks during the non-breeding season in temperate zones (e.g., Clement et al., 1993 for finches and sparrows), and its main benefits are decreased predation risk, increased foraging efficiency, and reinforcement of social interactions (Szekely et al., 1991; Clement et al., 1993; Pravosudov & Grubb, 1999; Riters et al., 2019). In monospecific groups of passerines, dominant individuals may force subordinates to occupy more disadvantageous positions where they have to keep watch comparatively longer against potential predators (Pulliam & Millikan, 1982; Pravosudov & Grubb, 1999). Reversed sexual dominance –i.e., dominance of females over males– is rare and not well understood in birds, occurring in some species of raptors, shorebirds, and *Haemorhous* finches, as well as silver-beaked tanagers (*Ramphocelus carbo*) (Mueller, 1986; Belthoff & Gowaty, 1996; Emlen & Wrege, 2004; Lebbin, 2008). For *Haemorhous* finches, whose females are no larger than males, it has been argued that males do not defend territories during the year and females have greater energetic needs and must defend their immediate nest site (Samson, 1977; Belthoff & Gauthreaux, 1991). Thus, selection may be weak for male preeminence in these finches (Samson, 1977; Belthoff & Gauthreaux, 1991; McGraw & Hill, 2002). Moreover, it is normal in birds for adult individuals to dominate, and consequently attack, juveniles (e.g., Barluenga et al., 2000; Verhulst et al., 2014 for passerines). Also, male birds usually prevent extra-pair copulation by the female through mate defence involving attacks on other males (Birkhead & Møller, 1998; Hasselquist & Sherman, 2001).

Geographical variation in behaviour within widespread vertebrate species is common, including group size and social systems in birds. This variation is often attributed to changing, interrelated population characteristics and environmental conditions (e.g., population density, predation pressure, climate, food sources), as well as evolutionary history (Herczeg & Välimäki, 2011 for fishes; Maher & Burger, 2011 for rodents; Camacho, 2012 for stone-curlews; Rohwer & Purcell, 2019 for passerines). Certain populations of Eurasian bullfinches (*Pyrrhula pyrrhula*, Fringillidae, Passeriformes, Aves, hereinafter referred to as bullfinches) (in particular some in western Europe: subspecies *europaea* from central regions, subspecies *pileata* from the the British Isles, and nominate subspecies *pyrrhula* from Scandinavia) have been described to form small parties (less than 12 birds) during the non-breeding season. This social behaviour has been hypothesized to be an anti-predation strategy, but statistical evaluations of group size are rarely provided and there is no information on the role of the sexes in vigilance (Newton, 1967; Wilkinson, 1982; Greig-Smith & Wilson, 1984; Cramp & Perrins, 1994; Hogstad, 2006; Marquiss, 2007). For the same bullfinch populations, according to some quantitative estimates, most intraspecific aggressive encounters are between individuals of the same sex, notably males linked to a large extent to mate defence (Wilkinson, 1982; Cramp & Perrins, 1994). It has been suggested that females dominate males in these populations (Wilkinson, 1982; Newton, 1985; Hogstad, 2006). Furthermore, only vague descriptions on the occurrence of gregariousness and lack of information regarding conspecific hostile behaviour are available about the very little known subspecies *P. p. iberiae* in different regions and habitats in the Iberian Peninsula (southwestern Europe) (Noval, 1971; Sanz-Zuasti & Velasco, 1999; Fernández & García, 2014). The Iberian bullfinch males outnumber females throughout the year (ÁH, unpubl. data), and they usually accompany their female partners at a short distance during the nest-building period, probably as a mate-guarding tactic (Hernández, 2020).

The bullfinch populations whose gregariousness and agonistic behaviour have been most investigated (some in continental Europe, England and Scotland) share similar habitats (forests and hedgerows), food resources (tree buds and seeds and herb seeds), and main predator (Eurasian sparrowhawk *Accipiter nisus*) (Wilkinson, 1982; Greig-Smith & Wilson, 1984; Hogstad, 2006; Marquiss, 2007). Such ecological features are also shared with the Iberian population considered in the present study (Hernández, 2018, 2021; ÁH, unpubl. data). Breeding ecology of this Iberian population is comparable, in general terms, to that previously known for continental European and British populations with regard to reproductive parameters (Hernández, 2020 and references therein), nest-site selection (Cramp & Perrins, 1994; Hernández & Zaldívar, 2021), and nest design (Biddle et al., 2017, 2018; Hernández & Zaldívar, 2021), without showing obvious territoriality (Cramp & Perrins, 1994; Hernández, 2020). Breeding density of bullfinches does not normally exceed 3 pairs/10 ha in western Europe, including Iberia, but numbers are probably underestimated if intensive methods are not used (Newton, 1985; Cramp & Perrins, 1994; Hernández, 2020; ÁH, unpubl. data). Their movements in Europe during the non-breeding season are of varying intensity depending on food availability and weather conditions, frequently leading to local changes in population density throughout the autumn–winter months (Cramp & Perrins, 1994; Fox et al., 2009; Clement, 2010; Munilla & Guitián, 2012; ÁH, unpubl. data). The body size and the distinctive, sexually dichromatic adult plumage are essentially the same for the European subspecies *pyrrhula*, *europaea*, *pileata*, and *iberiae*, with small differences between them and between the sexes (Cramp & Perrins, 1994). Bullfinches of western Europe have apparently undergone a recent, quick post-Pleistocene range expansion after the retreat of continental ice masses, the corresponding subspecies being represented by eleven very similar haplotypes (Töpfer et al., 2011).

The main aims of the present study are 1) to contribute to the knowledge of the natural history of Iberian bullfinches by providing the first detailed analysis of aggregation behavior and intraspecific aggression, and discussing their possible ecological functions, in a Mediterranean area located in northwestern Spain close to the southwestern distribution limits of the species, and 2) to compare the findings with what is already known for other western European populations. The following particular issues and their seasonal variation were assessed: 1) group size, 2) group composition with respect to age and sex, 3) vigilance behaviour, 4) flexibility in gregariousness, and 5) intraspecific attacks with respect to age and sex. Taking all the above general considerations together –related to gregariousness, dominance, and aggression–, and according to the patterns of social behaviour and population structure proposed for European bullfinch subspecies –which show little genetic, morphological and bioecological differences between them–, it can be expected that Iberian bullfinches: 1) form small flocks in autumn–winter with males outnumbering females, and 2) perform agonistic encounters principally between males but also attacks by females, acting as the dominant sex, against males. In addition, males can be expected to assume vigilance tasks if their subordinate status is confirmed, and adult birds can be expected to dominate juveniles.

2. Material and methods

2.1. Study subspecies

Iberian bullfinches (*Pyrrhula pyrrhula iberiae*) only reproduce in the northern part of the Iberian Peninsula (mainly N Spain) and are predominantly resident birds, but can perform short-medium range movements during autumn–winter (Belamendia, 2003, 2012; ÁH, unpubl. data). Records of individuals belonging to more northern subspecies arriving in the peninsula during the non-breeding season are very scarce (Tellería et al., 1999; Clement, 2010; Díaz, 2016). Iberian bullfinches are multi-brooded birds that nest from April to September, averaging 4.5 eggs per clutch (Hernández, 2020; ÁH, unpubl. data). They place their nests low above the ground –1.4 m on average– in large shrubs (Hernández & Zaldívar, 2021). Their diet consists mainly of seeds and buds, plus arthropods during spring–summer, and they forage for food in shrubs and trees or, less frequently, on the ground very close to woody vegetation (Hernández, 2021; ÁH, unpubl. data). Based on visits to the study area by myself in 2021, the bullfinches are still present and in good conservation status.

2.2. Study area

The study area covers 78 ha and is located in the middle-lower Torío river valley, between Palacio and Manzaneda (42º43’–42º44’ N, 5º30’–5º31’ W; 900 m a.s.l.; León province, Castile and León autonomous community), in northwestern Spain. Biogeographically, it forms part of the Carpetano-Leonese sector in the Mediterranean West Iberian province, in a transition zone to the Eurosiberian region, south of the Cantabrian mountain range (Rivas-Martínez, 2007). Hot summers (average temperature of ≈ 20 ºC), cold winters (≈ 4 ºC) with some snowfall, and moderate rainfall (average annual precipitation of ≈ 500 mm) with a relatively short dry summer season, characterise the area. The landscape is mainly composed of hedgerows that separate irrigated meadows grazed by livestock and cut for hay, bordered by riparian woodland on the west side, and slopes covered in Pyrenean oak (*Quercus pyrenaica*) woods interspersed with very small Scots pine (*Pinus sylvestris*) plantations on the east side. Some hedgerows border Canadian poplar (*Populus* x *canadensis*) plantations. Estimated hedgerow density is 3.3 km per 10 ha. About thirty species of broadleaved, chiefly deciduous shrubs, trees, and climbers, are found in the hedgerows.

2.3. General procedures and considerations

Fieldwork was performed using observational, non-invasive techniques which enabled sufficient data collection for the objectives of the study without threatening the welfare of the birds (see Dawkins, 2007). In the study area, bullfinches were present in all months of the year. Throughout 2001–2006 (main study period), the bullfinches were directly observed and behavioural data were collected during field trips. I conducted 41 trips in winter (December–13 trips, 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, I conducted 73 trips 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 to the extent possible, except for 2006 when the sampling effort was considerably lower. Two trips were usually needed to cover the entire area: approximately half of the area (36 ha) on one trip, and the other (42 ha) the following day. On each trip, I explored the corresponding zone by slowly walking around it, stopping frequently, following the edge of the hedgerows and marginally (≈ 10% sampling effort) the edge of the oak woods, which made it possible to detect the bulk of bullfinches. However, several factors could influence the detectability in different seasons (e.g., singing and other reproductive activities, moulting process, vegetation foliage). 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, I conducted more than 85% of field trips 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 reliable sampling. Moreover, for some analyses, data 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. I did not mark the birds individually, so their identity could not be determined. Nevertheless, records from the same sampling day most likely corresponded to different individuals, pairs, or family groups, since the birds were successively left behind during the visits. In addition, the study periods covering many years, the mentioned bullfinch movements, which can even occur during their long breeding season (Newton, 2000 for British birds), and the short life-span of this species –averaging 2 yr (Robinson, 2005)–, together ensure a high degree of independence between records. The term "pair" always refers to a male and female together. If not otherwise specified, males and females refer to individuals in apparently full adult plumage, and juveniles refer to individuals in juvenile plumage (apparently complete or already moulting) either still dependent on their parents or independent. Male, female, and juvenile bullfinches have very different plumage colourations to each other (Figure 1), which enables them to be easily differentiated in the field. Most of the individuals seen were consequently identified by sex and age. I used standard optical equipment, i.e., binoculars and a telescope, to observe birds. Temporal variation in population density and structure (age distribution and sex ratio), in the same area and time periods, is the core subject of a separate study in preparation (ÁH, unpubl. data). Therefore, these aspects are not explored in the present research, offering only some very specific reference data.

(Fig. 1 here):

a)

b)

c)

2.4. Gregariousness and mobility

To evaluate bullfinch gregariousness and mobility, I considered records collected during the main and supplementary study periods. Group is defined as all individuals performing an activity in a cohesive manner, including movement, at a short distance from each other. The size and composition of each group (number of males, females, and juveniles) correspond to the moment when the initially seen group was at its largest for no more than 10 min observation (focal sampling, see Lehner, 1992; Sutherland, 2004). Records in which the sex and age of all individuals could not be identified were considered when only the number of birds was required for the analysis (e.g., mean group size calculations). “True flocking” refers to adult groups of ≥ 2 individuals except pairs, that is, those groups in which gregariousness did not seem to be strongly affected by breeding events or pair-bond. Information on vigilance in pairs and mixed-sex assemblages (≥ 3 individuals) is provided to distinguish between the roles of males and females. An individual was considered to show vigilance behaviour if, unlike the other member(s) of the pair or group, it was less active and occupied an apparently more exposed position (a higher and/or more outer and/or more open perch), scanning its surroundings. Bullfinches normally forage and perch discreetly in shrubs and trees, avoiding exposure. Therefore, the cases that could be clearly classified as vigilance were not many in the entire study period, which did not necessarily imply that this behaviour was rare. Flexibility in gregariousness in the immediate term, that is, during 10 minutes’ observation of a specific group, occurred if it split into two or more subgroups which were then at least 25 m apart, or when individuals that had previously been at a distance of at least 25 m, joined it. With regard to mobility, on a direct observation scale (as far as the eye can reach), I distinguished two events: i) short-range movement if, during the observation time set, the individuals in the group did not fly, or flew (all of them or at least one) to a distance of less than 100 m, and ii) long-range movement if they flew to a distance of ≥ 100 m, often out of sight. Bullfinches normally formed monospecific aggregates, and in very few cases (13 of 1459, 0.9%) they accompanied other granivorous passerines. I did not consider heterospecific flocks in this study. Bullfinches mostly perched in shrubs or trees, increasing their use of ground and herbs during spring–summer, and the most frequently observed activities throughout the year were foraging and feeding, notably in winter (Hernández, 2021).

2.5. Intraspecific aggression

To better reflect the frequency of agonistic behaviour during the main study period, I considered all intraspecific aggressions seen in each season, even though some individuals likely participated in more than one aggressive encounter. Nevertheless, each group of birds (two or more individuals) was not observed for longer than 10 min for this purpose. I recorded the sex and age of the two individuals involved in each attack, as well as the size and composition –number of males and females in adult plumage, and of dependent or independent juveniles and their sex when possible to identify in moulting individuals– of the group at the time of the aggression. Not all members of each involved group necessarily participated in aggressive encounters during observation. I considered three different intensities of attack: one individual simply displacing another from its perch to occupy it immediately, short brief chase, and long sustained chase. Long attacks could involve chasing an individual until it flew away. It was not possible to clearly establish the degree of intensity of all the aggressive encounters, hence this analysis is semi-quantitative. I describe aggression sites in general terms. M→m means male attacking male, f→f female attacking female, m→f male attacking female, and f→m female attacking male, regardless of whether upper or lower case is used.

2.6. Statistical analyses

I used the chi-square test (χ^2), with Yates correction for 1 degree of freedom, to compare series of absolute frequencies, the one-way ANOVA (F), with post-hoc Tukey's test, to compare more than two means, and the Spearman's correlation coefficient (ρ) to assess association between two ranked variables; considering the two-tailed way wherever possible (Fowler et al., 1998; Lowry, 1998–2021). Standard deviation (SD) was computed. $P < 0.05$ was considered statistically significant. For large sample sizes, such as those considered in this study, the normality assumption required for parametric tests is of minor importance (see Ghasemi & Zahediasl, 2012). I pooled all years together, mainly to avoid analysing small sample sizes, so statistical tests focused on seasonality. As stated above, the sampling effort in each season was equally distributed among the years of the main study period (6 yr). The addition of data from the supplementary study period (5 yr) for some analyses further decreased the number of records per year, but contributed to providing consistent results. Long-term studies on avian and mammalian social systems allow us to establish more general patterns –even across generations– not conditioned by one or few seasons or years (e.g., Taig-Johnston et al., 2017). During the main study period, little changing environmental conditions from year to year seemed to promote steady breeding population densities, nest success and breeding productivity rates were fairly constant from one year to the next, and interannual variation in diet was not remarkable (Hernández, 2020; ÁH, unpubl. data). The coefficients of variation of the meteorological variables (e.g., monthly temperature) were relatively low throughout the main study period (Hernández, 2020). The study area features a very homogeneous landscape, resulting in a general uniformity in the distribution and abundance of the main food sources and predators (ÁH, pers. obs.), which did not allow considering a habitat stratification.

3. Results

3.1. Gregariousness and mobility

Mean size of bullfinch groups was maximum in winter (2.38 ± 1.72 individuals) and decreased in spring (2.15 ± 1.21), summer (1.99 ± 1.20), and autumn (1.95 ± 1.24), resulting in significant seasonal differences ($F_{3,\,1455} = 4.90$, $p < 0.01$) (Figure 2). Considering pairs of seasons, significant differences were only recorded between winter and summer, and between winter and autumn (Tukey's test, $p < 0.01$ in both cases). The range of group size was similar in all seasons, varying between 1–8 and 1–10 individuals. Taking into account two broad group types, one corresponding to true flocking and another composed of the remaining aggregates, there were significant seasonal differences in the frequency of both, with a high proportion of the first type in winter (≈ 40% of the groups), low in spring (≈ 25%) and autumn (≈ 15%), and almost negligible in summer (≈ 3%) ($\chi^2_3 = 151.08$, $p < 0.001$) (Figure 3). The frequency of true flocks, compared only with single adults, was significantly associated with the season, reaching 50% in both winter and spring, 37% in autumn, and 17% in summer ($\chi^2_3 = 38.85$, $p < 0.001$) (Figure 3).

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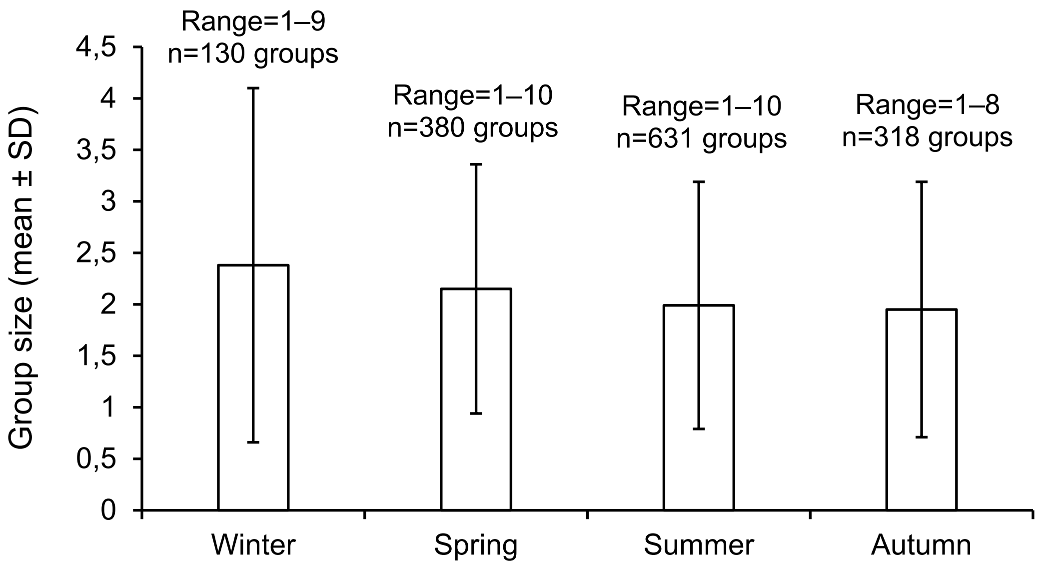

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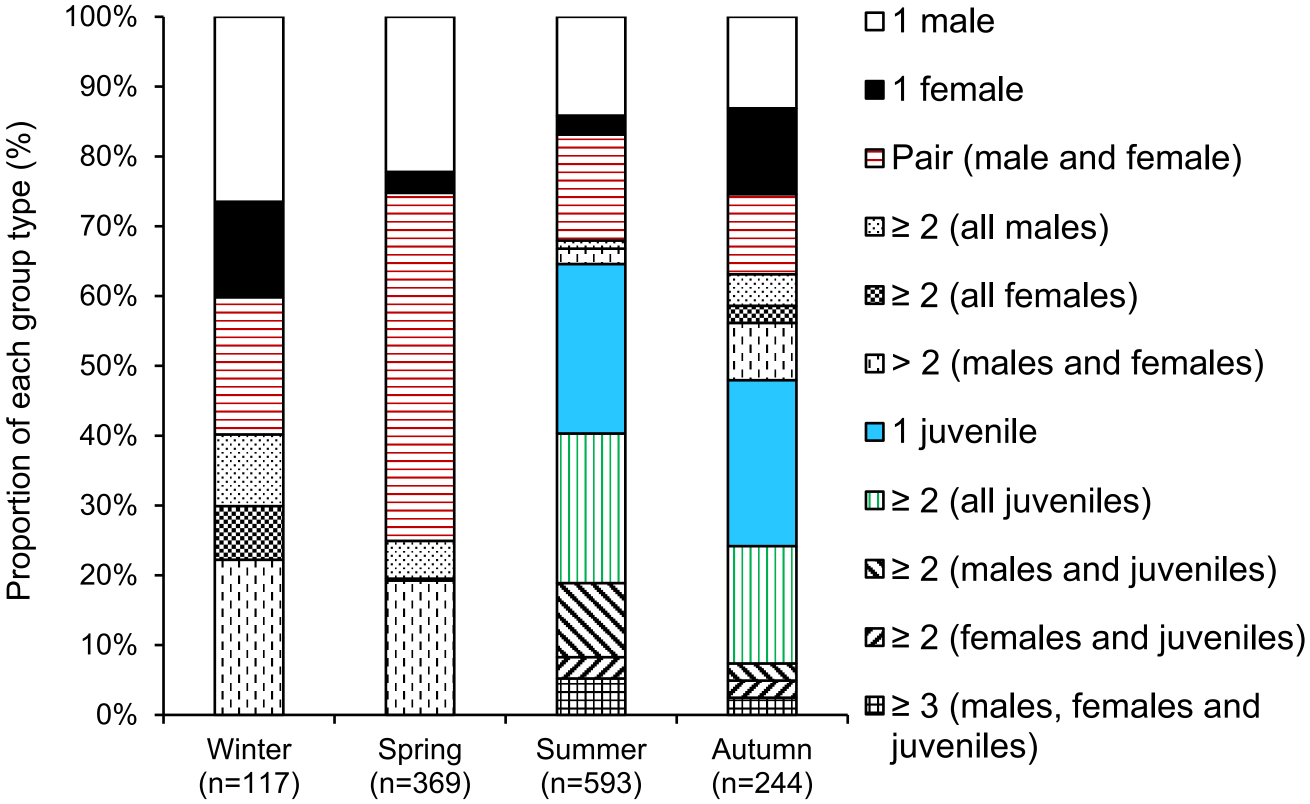
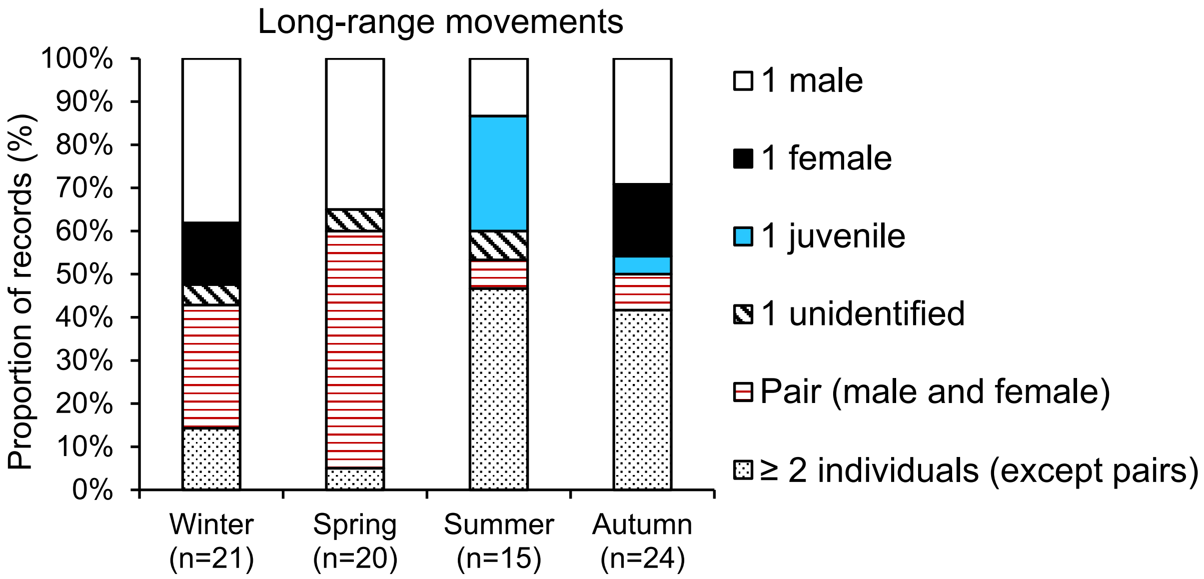


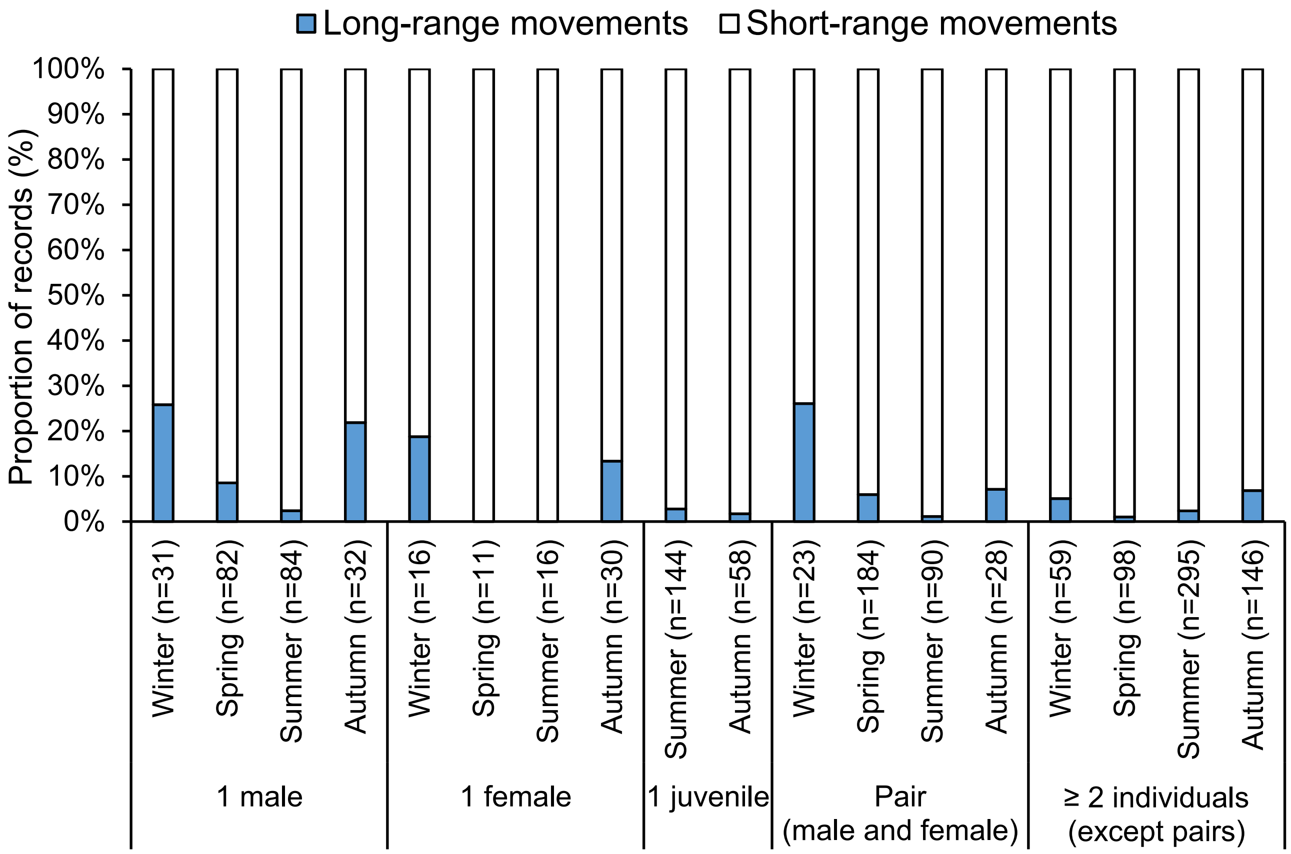
Considering more specific group types, records of single individuals were predominant (≈ 40%, with twice as many males as females) in winter, followed by pairs and mixed-sex assemblages (> 2 individuals) (≈ 20% each) (Figure 3). In spring, pairs predominated (≈ 50%), followed by single males and mixed-sex assemblages (≈ 20% each). Of 74 spring groups formed by ≥ 3 individuals, 46 (62.2%) presented supernumerary males (33 being trios), 24 (32.4%) presented parity, and only four (5.4%) presented supernumerary females. In summer and autumn, single juveniles and juvenile assemblages (≥ 2 individuals) were predominant (amounting to > 40% in each season). Single males were moderately important in both seasons, single females in autumn, pairs in both seasons, and male-juvenile groups (≥ 2 individuals) in summer (each case within the 10–16% interval). From summer to autumn, the relative contribution of assemblages composed of juveniles plus males and/or females (≥ 2 individuals) decreased from approximately 19% to 7%, and that of mixed-sex assemblages (> 2 individuals) increased from 2% to 8%.

Significant differences were observed between winter and spring groups, considering parties of ≥ 2 individuals in which males were predominant (31 and 63, respectively), of ≥ 2 individuals in which females were predominant (14 and 5), and of > 2 individuals with the same number of males and females (2 and 24) ($\chi^2_2 = 21.45$, $p < 0.001$). That is, groups formed mostly by males accounted for over 65% in both seasons, those composed mostly of females decreased from around 30% in winter to 5% in spring, and those with an equal number of males and females increased from 4% in winter to 26% in spring. Of 20 records of individuals showing clearly vigilance behaviour (10 in autumn–winter and 10 in spring–summer), 19 (95%) corresponded to males and only one to a female. A single individual kept watch, except for one case when two males seemingly did so at the same time. Nine cases occurred in pairs, mainly in spring–summer, and 11 in mixed-sex assemblages (≥ 3 individuals), mainly in autumn–winter.

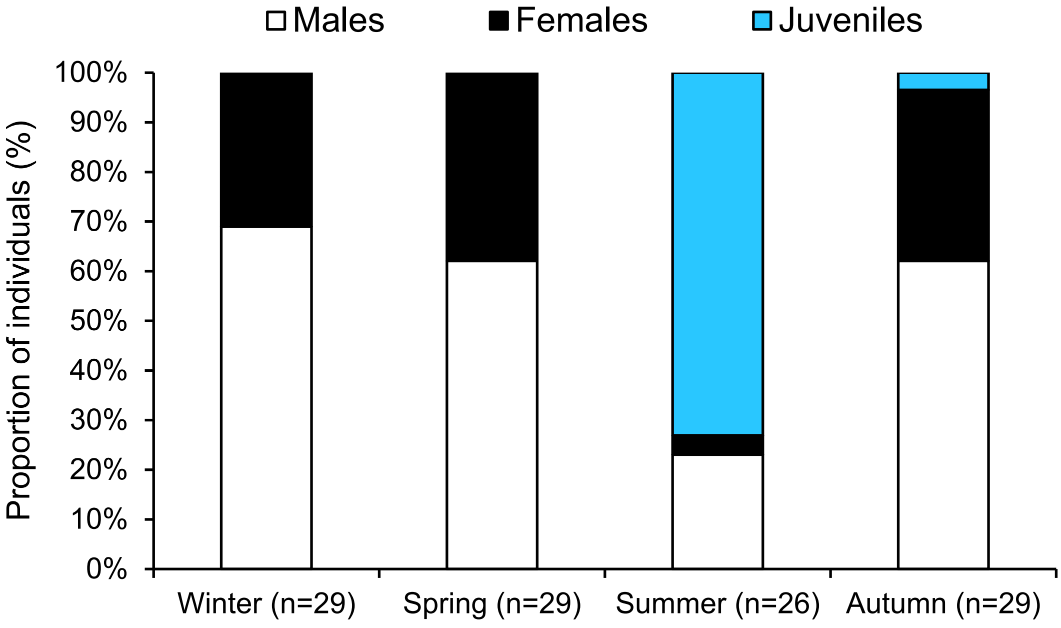
Disregarding records of single individuals and pairs, flexibility in gregariousness occurred throughout the year with significant seasonal differences, being observed in 18.6% of 59 groups in winter, 21.4% of 98 in spring, 6.1% of 295 in summer, and 4.1% of 146 in autumn ($\chi^2_3 = 31.24$, $p < 0.001$). On a direct observation scale, long-range movements were performed during the year with significant seasonal differences, involving 16.2% of all records (single individuals and groups) in winter ($N = 130$), 7.5% in autumn ($N = 318$), 5.3% in spring ($N = 380$), and 2.4% in summer ($N = 631$) ($\chi^2_3 = 42.96$, $p < 0.001$). All group formations were more mobile during autumn–winter than during spring–summer, without considering single juveniles (present only in summer–autumn). (Figure 4). The results are similar considering the number of individuals performing long-range movements: 33 of 310 (10.6%) in winter, 49 of 619 (7.9%) in autumn, 32 of 817 (3.9%) in spring, and 27 of 1258 (2.1%) in summer ($\chi^2_3 = 58.26$, $p < 0.001$). Considering only long-range movements, the proportion of them corresponding to single individuals varied between 40% in spring and almost 60% in winter, that of pairs was very high in spring (55%), and that of assemblages of ≥ 2 individuals (except pairs) in summer and autumn (approx. 45 and 40%, respectively) (Figure 4). The maximum number of individuals moving long distances together was six. By age and sex, most of the individuals performing long-range movements in summer were juveniles (≈ 73%) (the rest were males ≈ 23%, and females ≈ 4%); in the remaining seasons, the proportion of males was within the 60–70% interval, that of females within 30–40%, and juveniles represented a small percentage in autumn (3.4%) (Figure 5). Restricting this analysis to males and females (20 and 9 in winter, 18 and 11 in spring, 6 and 1 in summer, 18 and 10 in autumn, respectively), there were no significant seasonal differences ($\chi^2_3 = 1.56$, $p = 0.67$). The proportion of male to female in the population was 57–63% (depending on the season), whereas that of males involved in long-range movements, in terms of flight frequency, was 62–86%, always higher than the former in each season.

(Fig. 4 here): top and bottom:




Long-range movements
Short-range movements
Proportion of records (%)
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
Winter (n=31)
Spring (n=82)
Summer (n=84)
Autumn (n=32)
Winter (n=16)
Spring (n=11)
Summer (n=16)
Autumn (n=30)
Summer (n=144)
Autumn (n=58)
Winter (n=23)
Spring (n=184)
Summer (n=90)
Autumn (n=28)
Winter (n=59)
Spring (n=98)
Summer (n=295)
Autumn (n=146)
1 male
1 female
1 juvenile
Pair
(male and female)
≥ 2 individuals
(except pairs)

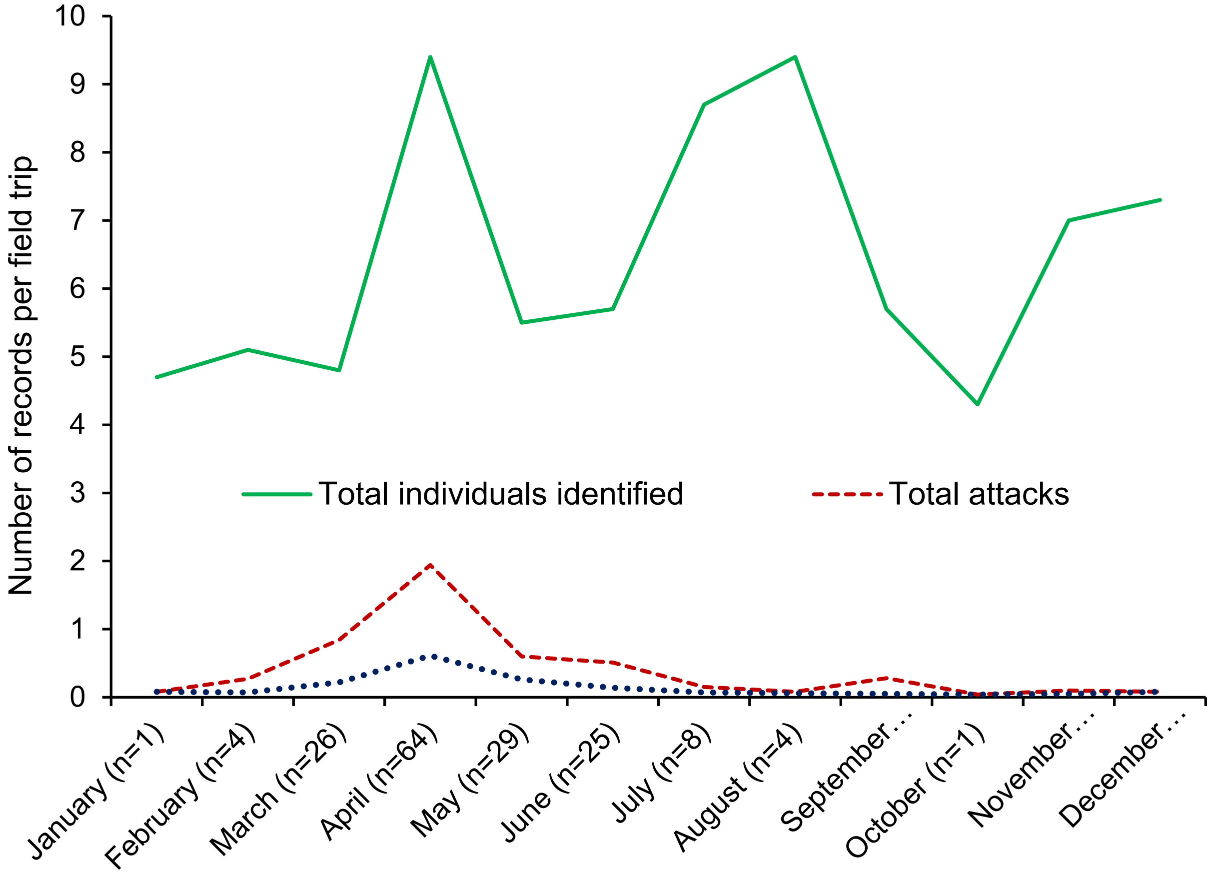
(Fig. 5 here):


Males
Females
Juveniles
Proportion of individuals (%)
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
Winter (n=29)
Spring (n=29)
Summer (n=26)
Autumn (n=29)

3.2. Intraspecific aggression

A total of 176 aggressive encounters between bullfinches in 61 groups containing a total of 218 individuals were recorded, with cases occurring in all months of the year, 81.8% of them (involving 77.0% of the groups) from March to June. Taking into account the sampling effort, both the number of attacks and number of groups involved in attacks, per systematic field trip, were also clearly higher from March to June, with a very marked peak in April (1.94 attacks/field trip, 0.61 groups/field trip) (Figure 6). There was a significant correlation between the number of groups involved in aggression and the number of attacks per field trip in each month ($\rho_{10} = 0.71$, $p < 0.01$), but not between the number of bullfinches in the population and aggression ($\rho_{10} = 0.12$, $p = 0.70$, for groups showing attacks; $\rho_{10} = 0.15$, $p = 0.65$, for individual attacks) (Figure 6). Most attacks were between adults, mainly m→m (84.7% of 176), and fewer cases of f→m (6.8%) or f→f (5.1%). A few attacks involving two moulting juvenile males, two moulting juvenile females, and one adult female on one non-moulting independent juvenile, were also observed (together amounting to 3.4%). No m→f attacks were observed. During all of the months when aggression frequency was highest (March–June), m→m always accounted for over 75% of attacks (Figure 7). Attacks normally occurred in shrubs or trees in hedgerows and poplar plantations, at very different heights, from the lower part of shrubs to tree tops (up to a height of 10 m), and rarely on the ground.

(Fig. 6 here):



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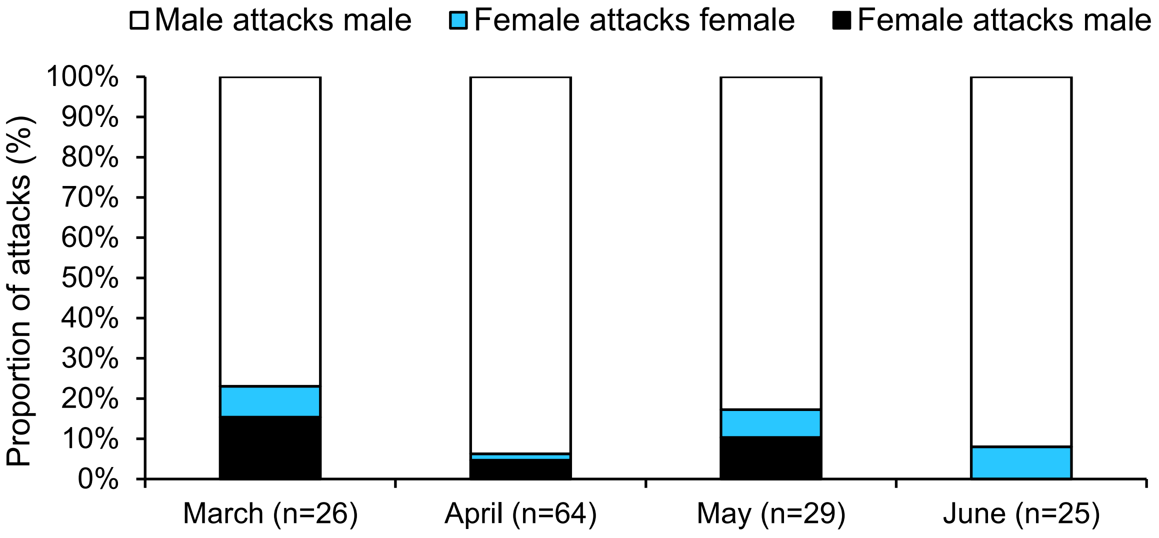

Considering adult individuals, m→m aggressions occurred between January and October, with short chases throughout this period, more frequently between March and July, and long chases during February–August, more frequently in April–May. Occasionally, males were observed just chasing each other off their perches. F→f aggressions occurred between March and June, except for one case in November, and varied in intensity to prolonged chases. F→m aggressions were concentrated in the March–May period, but also occurred in other months (August and December), and consisted of chasing each other off perches or short attacks, but no prolonged attacks were observed. The female that attacked an independent juvenile chased it off its perch in August. All aggressive encounters between moulting juveniles (m→m and f→f) were observed in September and consisted of long chases.

The overall mean size of the bullfinch parties involved in aggression was 3.57 ± 1.43 individuals (range = 2–8 individuals, $N = 61$ groups containing a total of 218 individuals). By season, the range was 3–5 individuals in winter ($N = 3$ groups), 2–8 in spring ($N = 40$), 2–4 in summer ($N = 14$) and 3–8 in autumn ($N = 4$). The recorded number of attacks per individual in these groups (sum of attacks/sum of individuals) was 0.46 (6/13) in winter, 0.84 (119/142) in spring, 0.90 (37/41) in summer, and 0.64 (14/22) in autumn. As noted earlier, not all of the members in each group necessarily took part in the aggressive encounters observed. Considering all of these groups together, 61% of the individuals were adult males, 34% adult females, and the rest (5%) non-moulting or moulting juveniles. Taking into account adult birds in the groups involved in aggression, the ratio of m→m to f→f attacks (149:9) was significantly higher than that of male to female individuals (133:74) ($\chi^2_1 = 44.37$, $p < 0.001$). Including moulting juveniles whose sex was identified, in 78.7% of these groups both sexes were represented, and in 18.0% only males, other group compositions being almost negligible (one group formed by females, one group formed by a female and two non-moulting juveniles).

4. Discussion

4.1. Gregariousness and mobility

Bullfinches showed gregarious behaviour, but only formed small groups of no more than 10 individuals throughout the year, which were larger in winter on average. Generally, males considerably outnumbered females in the groups, following the same pattern as population sex ratio. Information on gregariousness in bullfinches for other Iberian areas is often anecdotal and has not been subjected to statistical analysis, so it should be interpreted with caution. According to this information, they form monospecific groups rarely exceeding a dozen individuals, exceptionally 25, mainly from September to March (Noval, 1971, 2000; De Juana, 1972; Woutersen & Platteeuw, 1998; Sanz-Zuasti & Velasco, 1999; Fernández & García, 2014). In the center of peninsular Spain, away from the breeding grounds, sightings of up to 10 individuals have been recorded (Quirós, 2020). In regions of the western Palearctic where their social behaviour is best known, they are less sociable than other finch species, parties of fewer than a dozen birds usually being observed outside the breeding season (more specifically, mean flock sizes < 5 individuals, despite the fact that some estimates exclude single individuals; flock sizes > 20 very rare) (Newton, 1967; Wilkinson, 1982; Greig-Smith & Wilson, 1984; Cramp & Perrins, 1994; Hogstad, 2006; Marquiss, 2007). Thus, my findings on gregariousness are in agreement with previous rigorous studies –and also with anecdotal observations– of group size in other bullfinch populations.

One explanation for gregariousness is that it lowers predation risk due to increased vigilance. Flocking in bullfinches is considered an anti-predatory strategy, mainly against the sparrowhawk, their major predator in western Europe (Newton, 1986; Snow & Snow, 1988; Marquiss, 2007). Sparrowhawks are the principal predators of bullfinches in the study area during autumn–winter, with reduced predation rates during spring–summer (Hernández, 2018; ÁH, pers. obs.). The sighting rate for sparrowhawks was 0.22–0.25 birds/trip in autumn–winter and 0.13–0.15 in spring–summer over the main study period. Gregariousness is also likely to increase foraging efficiency, as proposed for fruit- and seed-eating birds, since these resources are often distributed in ephemeral patches (Orians, 1971; Pulliam & Millikan, 1982; Lindström, 1989). However, foraging success can diminish above a certain flock size (less food for each individual), and a large number of individuals is not needed for effective vigilance (Orians, 1971; Glück, 1987; Pravosudov & Grubb, 1999; Giraldeau & Caraco, 2000). This cost/benefit trade-off of foraging success and vigilance may lead to a smaller optimal group size in bullfinches, which feed in small patches.

In winter, sightings of single individuals, especially males, were as frequent as flocks, and pairs were moderately common. This was perhaps the result of flexibility in gregariousness and permanent pair-bonds (see Cramp & Perrins, 1994; Hogstad, 2006 for comments on mate fidelity in bullfinches). Similarly, in a bullfinch population in England, one individual was the predominant group size from October to February, with single males outnumbering single females (Wilkinson, 1982). Pair was the prevalent aggregate in spring in Iberian bullfinches, followed by groups containing supernumerary males, single males whose partner could be in the nest or were unpaired individuals, and mixed-sex assemblages of at least four individuals with the same number of males and females. The latter formations might represent pairs joining together. In the English population, even-numbered groups with parity between the sexes, notably pairs, were the most common aggregates in March–April (Wilkinson, 1982). Sightings containing only juvenile individuals were common in summer and autumn, independent juveniles tending to separate from adults to group together. Forest songbirds, including bullfinches, usually select particular habitats during the post-fledging period, especially those rich in dense vegetation (Jenkins et al., 2017; Hernández, 2021). I observed groups of up to 7 juveniles, highly likely from different broods as the range of bullfinch clutch size was 3–6 eggs in the study area (Hernández, 2020). I saw few females with juveniles in summer, in comparison with males with juveniles, probably because most of the females were still sitting on successive nests, but the adult sex ratio attending juveniles balanced out in autumn at the end of the breeding season. Bullfinches appear to split broods into smaller family units with each parent taking care of certain fledglings (Hernández, 2020). True flocking began to increase during autumn, presumably due to the addition of moulted hatch-year individuals.

As predicted, vigilance was the responsibility of males. During the breeding season, vigilance behaviour by the male occurred more commonly while the female collected nest material and appeared to be a function of mate-guarding (see Hernández, 2020). In other circumstances, mostly while foraging and feeding in shrubs and trees in autumn–winter, male vigilance seemed to function to prevent predation. The vigilance behaviour of male bullfinches might be linked in part to their subordinate status. Although in monospecific groups of passerines subordinate individuals have to be on the lookout for potential predators and dominant conspecifics, vigilance effort is less than if they were alone, and foraging efficiency is increased for all group members (Pravosudov & Grubb, 1999). I suggest this is also true for bullfinch groups.

Flexibility in gregariousness, and long-range movements that could be directly observed, were relatively infrequent but were evaluated in the immediate term. Presumably, the frequency of both events would have increased if the bullfinch groups had been observed for a longer time. Flexibility was lower during summer–autumn, likely due to the presence of cohesive family groups. Groups of several bullfinches congregated at points with abundant food in spring, such as large wild cherry trees (*Prunus avium*) providing buds and flowers, but these groups were not stable because while some individuals joined them, others left. Bullfinches communicated with each other all year using typical piping calls, sometimes answering from a long distance. For this species in general, gregarious behaviour is not considered to be consistent (Newton, 1967; Cramp & Perrins, 1994). However, although bullfinch flocks often split into subflocks for some minutes in a Norwegian population, they were fairly constant in size and sex composition, at least in early winter (Hogstad, 2006).

Directly observed long-range movements occurred more frequently during autumn–winter, probably reflecting behaviours commonly performed by bird species –including residents– inhabiting temperate regions, namely, juvenile dispersal (Berthold, 2001; Newton, 2008) and wandering in search of food in enlarged home ranges (e.g., Morganti et al., 2017). Juvenile Iberian bullfinches start to disperse from the end of summer, and it is usual for individuals in general to be very mobile between foraging sites throughout the non-breeding season (Noval, 1971; Munilla & Guitián, 2012; Fernández & García, 2014; Hernández, 2021). In the Norwegian population, most bullfinches roamed around during winter although some individuals were stationary (Hogstad, 2006). Furthermore, pairs were quite mobile whilst searching for nest sites, and although adult activity around the active nests was concentrated in a radius of 100 m, it was not unusual for them to move a greater distance away, even flying out of sight (Hernández, 2020). Throughout the year, the number of males performing long-range movements was clearly higher than that of females, in agreement with the pattern of population sex ratio. In addition, males appeared to be more mobile than females, perhaps because the over-representation of males made them more actively seek a potential mate. In this connection, the most mobile male house finches (*Haemorhous mexicanus*) during the non-reproductive season have more chances of finding a flock where they can achieve pairing success (Oh & Badyaev, 2010). Also, males occupied more exposed positions and are more brightly coloured than females, which presumably resulted in an increased predation risk and consequently greater need to escape. Rytkönen et al. (1998) found a significant correlation between bird vulnerability to sparrowhawks and plumage brightness.

4.2. Intraspecific aggression

In the groups of bullfinches involved in attacks, often mixed-sex, males normally outnumbered females and constituted a percentage of individuals similar to that found for the general population. The predominance of m→m attacks met the expectations, significantly exceeded the proportion of males in groups showing aggression, and was mainly recorded during the breeding season. This predominance had already been documented for bullfinches, occurring more frequently in parties with supernumerary males often formed by two males and one female (Wilkinson, 1982; Cramp & Perrins, 1994). Thus, aggression was presumably linked to a large extent to mate defence, as also suggested by Wilkinson (1982). The peak of agonistic encounters occurred in April, when the bullfinch male usually accompanied the female at a short distance during nest building, probably as a mate-guarding tactic to prevent a high risk of extra-pair paternity. During the spring, the abundance of bullfinches in the population also peaked in April, perhaps due to greater detectability and the fact that some preferred food sources (e.g., large cherry trees) could attract birds from long distances on those days. Also, some males attacked others while the female partner of the former was absent (e.g., incubating) or while the former was feeding nestlings with its female partner (ÁH, pers. obs.), perhaps also to ward off potential rivals. However, in some parties with more than one male, no m→m attacks occurred in the incubation-nestling period (May–August), at least during the observation time. Most of these cases (a dozen) consisted of two males foraging together in apparent agreement, probably benefitting from the advantages of gregariousness (e.g., improved vigilance) while the females were in the nest.

The recorded f→m attacks support the proposed dominance of females over males in bullfinches (Newton, 1985; Cramp & Perrins, 1994; Hogstad, 2006). Some factors that would strongly select for male bullfinch dominance appear to be lacking. Firstly, bullfinches show non-territorial behaviour and a monogamous mating system perhaps with longlife faithfulness (Cramp & Perrins, 1994; Hogstad, 2006; Clement, 2010). Secondly, the females presumably undertake greater parental investment as they are responsible for most of the breeding tasks until they share the feeding of nestlings with males (Cramp & Perrins, 1994; Hernández, 2020). And thirdly, there are no clear differences in size and weight between sexes (Clement et al., 1993; Cramp & Perrins, 1994).

Attacks between females were more frequent in spring, and normally in the presence of males that were apparently or almost certainly their breeding partners –e.g., both partners were in the nest-building or nestling phase– (ÁH, pers. obs.). Like the bullfinch males, perhaps the females used intrasexual aggression for the defence of mating status, and to ensure the collaboration of their partners in brood-rearing, as has already been proposed for this species (Wilkinson, 1982), and for other songbird species (Belthoff & Gauthreaux, 1991; Sandell & Smith, 1997). Aggressive encounters between an adult and a juvenile, and between juveniles, were uncommon and were within expected patterns, that is, adults attacked juveniles (a general rule for birds, as noted in the Introduction section), and juvenile males did not attack juvenile females. According to McGraw & Hill (2002), juvenile female house finches are dominant over juvenile males.

Other possible causes of antagonistic interactions between bullfinches were probably not relevant. In the study area, occasional winter food shortages may lead to an increase in interspecific and intraspecific aggression among frugivorous passerine birds, particularly legitimate seed dispersers, in both territorial species (e.g., European robin *Erithacus rubecula*) and those that usually forage in small groups (e.g., Eurasian blackcap *Sylvia atricapilla*) (Hernández, 2008). Different fleshy fruit seeds are an important component in the winter diet of bullfinches in the study area, but are complemented with other tree seeds (European ash *Fraxinus excelsior*) and tree buds (several species) (ÁH, unpubl. data). Bullfinches hardly attacked each other during the non-breeding season, and the few recorded cases could have been linked to sexual behaviour as the pair-bond has been suggested to be maintained in winter (Cramp & Perrins, 1994; Hogstad, 2006).

5. Some concluding remarks and research needs

Among the reasons why no bullfinch flock of more than 10 birds was observed in the study area during such a long time period, a relatively homogeneous spatial distribution of food sources, with availability of sufficient amount every year (ÁH, unpubl. data), could perhaps be included, but it deserves further research. In wintering flocks of yellow-throated bunting (*Emberiza elegans*), each individual attempts to forage in an optimal group size; however, if they are extremely starved, it is suggested that they adopt a conditional strategy to join a flock independently of the group size to acquire the energy necessary for survival (Yamaguchi & Yahara, 2002). Maintaining the hedgerow network of the Torío river valley in good state of conservation would likely allow bullfinches to continue to form groups that do not exceed optimal size. A low population density can be ruled out as a cause of the exclusive formation of small flocks. Estimates of breeding density in the study area (2.5–3.5 pairs/10 ha during April–May) are higher than those usually documented for other regions in northern Iberia and the western Palearctic (Cramp & Perrins, 1994; Belamendia, 2003; ÁH, unpubl. data). In winter, density changed considerably at different temporal scales (ÁH, unpubl. data). Some years, at times of heavy snowfall, bullfinch density reached 10–16 birds/ha, it being among the most abundant passerine bird species. During the non-breeding season, Iberian bullfinches often move short and medium distance, mainly downwards from mountainous regions to lower areas where shrub and tree seeds are more abundant and/or accessible (Munilla & Guitián, 2012; Fernández & García, 2014; ÁH, unpubl. data).

The apparently strong mate-guarding and considerable rate of intrasexual aggression during the breeding season, together with over-representation of males, seems to indicate that there were a high number of male floaters in this bullfinch population, that is, unpaired males able to enter the reproductive segment when a potential mate becomes available (in the sense of Penteriani et al., 2011; Moreno, 2016). Floaters could be a nuisance for paired males, but at the same time, they probably contributed to reinforcing the population. Moreover, further investigation is needed in order to clarify the bioecological significance of reversed sexual dominance in bullfinches. Likewise, the role of kinship in gregariousness and aggression among bullfinches is unknown. In simple social groups such as flocks of gregarious passerines, birds may prefer the company of their siblings even well after fledging –as is the case with house sparrows (*Passer domesticus*)–, which may facilitate kin-biased behaviours (Tóth et al., 2009).

Regarding geographical variation in behaviour, western European bullfinch populations, including those of the subspecies *iberiae*, show, as expected, little differences in the general patterns of aggregation and conspecific aggression, except for certain peculiarities, probably because they share a short evolutionary history and general ecological conditions. However, studies on such behavioural patterns in populations of Iberian bullfinches occupying habitats other than hedgerows would be relevant. It would also be interesting to investigate social behaviour in the easternmost Asian bullfinch subspecies, namely, *cineracea* and *griseiventris* (subgroups within the group of Eurasian bullfinches *P. pyrrhula* s. l.). They are spatially and genetically distanced from the European subspecies, even showing very different morphological traits (Clement et al., 1993; Clement, 2010; Töpfer et al., 2011), and their bioecology is hardly known (e.g., Yamamoto, 1971; Kolbin, 2008; Nechaev & Nechaev, 2012; Berezovikov, 2017; Balatsky, 2020; some of these authors refer to *cineracea* and *griseiventris* as species).

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Figure captions

Figure 1. Eurasian bullfinches in NW Spain. Above, a female eating ash (*Fraxinus*) seeds in January. In the centre, a male perched on a poplar (*Populus*) tree in October; note the reddish ventral part. Below, a juvenile perched on a dead branch in July; note the absence of black cap.

Figure 2. Seasonal mean number (± SD) of Eurasian bullfinch individuals per group in NW Spain. Winter: December to February. Spring: March to May. Summer: June to August. Autumn: September to November. Pooled data for 1996–2006.

Figure 3. Seasonal composition of Eurasian bullfinch groups in NW Spain, regarding sex and age. n: number of groups in each season, including records of single individuals. Winter: December to February. Spring: March to May. Summer: June to August. Autumn: September to November. Pooled data for 1996–2006.

Figure 4. Top, seasonal importance of Eurasian bullfinch single individuals, pairs (male and female), and other group formations, performing long-range movement (≥ 100 m) on a direct observation scale during the observation time (10 min per group maximum), in NW Spain. n: total number of records (single individuals and groups of individuals that moved long distance) in each season. "≥ 2 individuals (except pairs)" includes records with unidentified individuals regarding sex and age. Winter: December to February. Spring: March to May. Summer: June to August. Autumn: September to November. Pooled data for 1996–2006. Bottom, the same long-range movements considered above compared with the short-range movements recorded in the same samplings, excluding unidentified single individuals (negligible sample sizes). Short-range movement means that the individuals did not fly, or flew to a distance of less than 100 m. n: total number of records (short- plus long-range movements) in each group formation and season.

Figure 5. Seasonal characterisation of the sex and age of Eurasian bullfinch individuals performing long-range movement (≥ 100 m), on a direct observation scale during the observation time (10 min per goup maximum), in NW Spain. n: total number of identified individuals, regarding sex and age, that moved long distance in each season. Winter: December to February. Spring: March to May. Summer: June to August. Autumn: September to November. Pooled data for 1996–2006.

Figure 6. Monthly variation of bird numbers (total individuals in the population with identified sex and age) and intraspecific aggression in Eurasian bullfinches in NW Spain, in relation to number of field trips. n: total number of attacks in each month. Pooled data for 2001–2006.

Figure 7. Monthly variation of intraspecific aggression in Eurasian bullfinches in NW Spain, in relation to sexes involved. n: total number of attacks in each month. In the months shown (March to June), 144 (81.8%) of the 176 attacks observed (grand total) were recorded. Pooled data for 2001–2006.