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Numerical response of Bullfinches *Pyrrhula pyrrhula* to winter seed abundance

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The main aim of our study was to investigate the coupling between the winter abundance of a seed-eater, the Bullfinch *Pyrrhula pyrrhula*, and the abundance of rowanberry *Sorbus aucuparia* seeds. We detected a numerical response of Bullfinches to temporal and spatial variation in the abundance of rowanberry seeds throughout the Cantabrian Range in northern Iberia. Data on the abundance of the Chaffinch *Fringilla coelebs*, a closely-related species were used to account for the effect of factors other than rowanberry production on Bullfinch abundance. Chaffinch did not show such an association. The changes observed in Bullfinch numbers were consistent with variation in rowanberry abundance throughout and across several spatial and temporal scales: locality, fruit-rich and fruitless sites within a given locality, and year and month. Our results suggest that rowanberry abundance may influence the timing and extent of the altitudinal movements undertaken into lowland areas by the Bullfinch populations that breed in the montane areas of Iberia.

1. Introduction

The degree to which food availability affects the dynamics and distribution of animal populations is a central issue in ecology. Fluctuation in the abundance and quality of food may strongly influence the spatial and temporal abundance of bird populations at different spatial and temporal scales (Holmes *et al.* 1986, Jones *et al.* 2003). For different bird groups, such as passerines, raptors, shorebirds and seabirds, a considerable body of evidence supports the notion that more individuals are to be found where or when their food is most plentiful (Newton 1998). While clear examples of such responses are often constrained by the difficulty of quantifying food abundance (Moegenburg & Levey 2003), fleshy-fruit-eating animals offer a solution to this problem because, from an evolutionary perspective, their food is "made to be eaten" (Snow & Snow 1980), and fleshy fruits are relatively easy to find and count accurately. Particularly avian frugivores that feed on fleshy-fruits, have provided some of the most compelling examples of food resource tracking at different spatial and temporal scales (e.g., Rey 1995, Malizia 2001, Moegenburg & Levey 2003). Similar patterns of temporal and spatial coupling between consumers and their foods, have been documented for avian seed-eaters (Newton 1998 and references therein; see also Lithner & Jönsson 2002).

Evidence for the influence of food on the distribution and numbers of birds is often based on correlations between bird density and food supply (Newton 1998). Such approaches do not necessarily reflect causality because other environmental and ecological factors influencing bird populations, such as weather, predator abundance or habitat quality, may have changed along with food (Karr & Freemak 1983, Herrera 1998, Newton 1998, Restrepo *et al.* 1999). One way to overcome the limitations of correlational approaches is experimentation; however, our ability to establish causality between resource and consumer is hampered by the fact that the numerical response of birds to food fluctuations can often only be assessed by considering patterns over large spatial and temporal extents (Herrera 1998, Levey & Benkman 1998, Curran & Leighton 2000). Therefore, an alternative approach is to use population variation in bird species that do not consume the resources of interest, as a yardstick against which to measure changes in the abundance of the species of interest (e.g., Guitián & Munilla 2008, Lehouck *et al.* 2009).

The main objective of our investigation was to assess the association between the winter abundance of a seed-eater, the Bullfinch *Pyrrhula pyrrhula*, and the abundance of rowanberry *Sorbus aucuparia* seeds. The study was conducted over a large spatial extent (the Cantabrian Range in northern Iberia), and the closely related Chaffinch *Fringilla coelebs* was used to account for the effects of factors other than seed abundance on Bullfinch numbers. The Bullfinch is the main avian consumer of rowan seeds and, as a pre-dispersal seed predator (Snow & Snow 1980, Guitián et al. 2000), it has the potential to reduce the reproductive output of rowan populations.

Moreover, this effect may depend on the ability of Bullfinches to track the seed abundance of rowan trees in time and space. In mast-fruiting populations the pattern and timing of seed predation are critical parameters to measure when assessing the effect of seed predators (Curran & Leighton 2000). The relationship between mast production and bird abundance has received considerable attention in dry-fruited species of temperate ecosystems where, despite the fact that avian consumers have to cope with large spatio-temporal variation in resource abundance and distribution, numerical responses have often been suggested (Evans 1966, Perrins 1966, Erikkson 1970, Ligon 1978, Bejer & Rudeno 1985, Smith & Scarlett 1987, Koenig & Haydock 1999, Koenig *et al.* 2009). Due to its pronounced masting behaviour, rowan is a good model to test whether masting fleshy-fruited plant species influence the density of avian consumers of its seeds, as has been suggested for disperser frugivores (Guitián & Munilla 2008). Fox *et al.* (2009) detected a link between the migratory movements of Northern Bullfinch *Pyrrhula p. pyrrhula* and rowanberry abundance.

The Iberian Bullfinch *Pyrrhula p. iberiae* occupies a broad altitudinal range (0–2,000 m) and the populations that breed at higher elevations tend to undertake altitudinal migratory movements into lowland areas (Noval 1971, Snow & Perrins 1998). Environmental conditions in mountain habitats vary in accordance to strong elevation gradients with marked effects on avian life-history traits (Badyaev 1997) and the composition of bird communities (see MacCain 2009). However, the influence of ecological drivers on bird abundance along elevation gradients remains largely unexplored. In Scotland, Bullfinches undertake progressive movements to higher elevations during winter in response to the availability of Heather seed (see Marquiss 2007 and references therein). Under the prediction that altitude could negatively affect the distribution and abundance of the Bullfinch, we aimed to investigate whether attitudinally-related differences in rowan seed abundance (above and below the lower altitudinal edge of rowan distribution which in the Cantabrian Range is about 1,000 m) were likely to reverse the expected pattern of a reduction in Bullfinch abundance with altitude.

The present study thus aims to address the following questions. (1) Is the abundance of Bullfinch associated with the temporal (annual and monthly) variation in rowanberry abundance? (2) Is the abundance of Bullfinch associated with spatial variation in rowanberry abundance? (3) Do rowanberry crops affect the altitudinal pattern of Bullfinch abundance?

2. Material and methods

2.1. The study species

We studied the association between the abundance of Bullfinch and the abundance of rowanberry seeds. In order to account for the possible effects of factors other than seed production of rowan trees on the fluctuation of Bullfinch numbers, we simultaneously recorded variation in the abundance of the Chaffinch *Fringilla coelebs*. Both species are woodland-associated cardueline finches of approximately similar size and weight (Snow & Perrins 1998), and both are common in the mountain forests of the Cantabrian Range. Both species breed across temperate Europe, where most populations are partially migratory and winter chiefly within their breeding range (Snow & Perrins 1998). Their winter food consists entirely of seeds; however, while Chaffinches seldom feed on rowan seed (e.g., Snow & Snow 1988), a large body of evidence exists to show that Bullfinches are rowan seed eaters in the Cantabrian Range and elsewhere (Snow & Snow 1988, Guitián *et al.* 2000, see Fox *et al.* 2009 and references therein). For example, of 495 observations of birds feeding on rowan seeds at four localities of the Cantabrian Range over three years, 91% concerned Bullfinch and 9% Chaffinch (Guitián *et al.* 2000).

The rowan is a small- to medium-sized tree generally less than 15 m tall, commonly found in Europe north of 40° latitude. In the Iberian Peninsula, it occurs in mountains of the northern half above 1,000 m a.s.l. Its typical habitats are heathlands, field hedgerows, woodland margins and forest gaps. It is a masting species, thus showing intermittent and synchronous production of large seed crops in certain years (i.e., mast years). Variation in fruiting is highly synchronic not only within rowan populations but also between populations, at the scale of tens of kilometres (Pías *et al.* 2007). The fruits are on average 8.2 mm in diameter and contain 2.5 small seeds of approximately 0.0014 g dry weight each (see Eriksson & Ehrlén 1991).

2.2. Study design

We used a paired-sample design that compared sites with and without rowan at eight localities extending 600 km across the Cantabrian Range. At all sampling localities, sites occupied by rowan were located at higher altitudes than sites without rowan (1,000–1,619 and 650–1,130 m a.s.l., respectively); for a given locality, differences in altitude averaged 308 m (range 202–467). At each locality, we used two 4,000 m line transects to assess the abundance of rowan berries and the abundance of Bullfinches and Chaffinches. The sampling was conducted monthly from October to January during three consecutive fruiting seasons 2002–2003, 2003–2004 and 2004–2005. For more details, see Guitián and Munilla (2008).

We assessed rowan seed abundance by counting all fruiting trees bearing more than 100 fruits within the near belt (0–25 m) of a given line transect. The area sampled in each transect was thus 20 ha, whereas seed abundance was expressed as the number of fruiting plants per 10 ha. According to the maximum number of fruiting trees recorded at each locality, the fruit production of rowan trees varied greatly in the three years of our study, from almost complete crop failure in the 2003–2004 season (only five fruiting trees at two localities) to 157.3 ± 106.4 fruiting trees/10 ha (coefficient of variation 0.676, $n = 8$ localities) in 2002–2003, and 228.2 ± 213.1 fruiting trees/10 ha (coefficient of variation 0.934, $n = 8$ localities) in 2004–2005. The three study years were ranked according to fruit-crop size as none (2003), intermediate (2002) and high (2004).

Birds observed on either side of the central line of each transect were attributed to one of two belts: 0–25 m and 25–100 m. Most birds were recorded within 25 m (Bullfinch $n = 277$, 77.3%; Chaffinch $n = 787$, 68.5%). Because we did not intend to determine actual densities, we made no adjustments for declines in detectability with distance (Bibby *et al.* 2000) and bird abundance was simply expressed as the number of birds observed per km. Analogous estimations of the relative abundances of avian frugivores have been used elsewhere (Jordano 1993; see also Guitián & Munilla 2008).

2.3. Statistical analyses

We analyzed seed-dependent variation in Bullfinch and Chaffinch abundances by means of generalized linear mixed models using the Linear

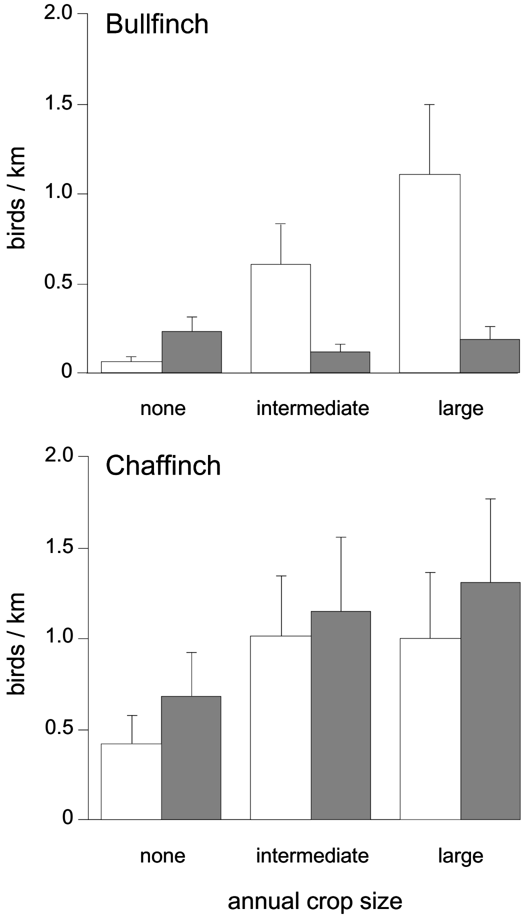

Fig. 1. Winter abundance of Bullfinch and Chaffinch at high (open bars) and low (grey bars) elevations at eight localities in the Cantabrian Range over three seasons (October–January) with different rowan crop sizes: none, intermediate and large (see text). Error bars represent standard errors of the mean.

Mixed Models procedure in SPSS Statistics 17.0. The categories describing the size of the rowanberry crop in the three fruiting seasons (i.e., years: none, intermediate and high) and the two altitudinal levels (higher elevation fruit-producing sites versus lower elevation fruitless sites) were considered as fixed factors and the identity of each locality as a random factor. We applied likelihood ratio tests, accounting for the difference in information-criterion values, to test the significance of random factors, and assessed statistical significance of the random effects using changes in the likelihood ratio of the model with and without the random effect. This difference is distributed as χ^2 (Littell *et al.* 1996).

Three types of response were tested: (a) response of Bullfinch and Chaffinch abundances to the variation in rowanberry abundance linked to the altitude and annual crop size; here, the model included the interaction between the two fixed factors (see above) and was performed separately for each species; (b) response of Bullfinch and Chaffinch abundances to variation in rowanberry abundance by locality.

For rowanberry abundance we used the peak number of fruiting rowan trees counted at a given locality and year (which corresponded with the October count at high-elevation sites). Thus, we considered rowanberry abundance as a covariate to test for a spatial response; (c) response of Bullfinch abundance to monthly variation in rowanberry abundance. For this we considered the monthly counts of Bullfinch numbers as repeated measures grouped by locality and conducted two separate analyses, one for the counts at higher and another for the counts at lower elevations.

3. Results

Bullfinch abundance varied significantly with altitude and year, and also the interaction between these factors was significant (altitude: $F_{1,35}$ = 7.459, P = 0.010; year: $F_{2,35}$ = 3.737, P = 0.034; interaction: $F_{2,35}$ = 4.399, P = 0.020; Fig. 1). In contrast, the response of the Chaffinch to the main effects and the interaction were non-significant (altitude: $F_{1,35}$ = 0.629, P = 0.433; year: $F_{2,35}$ = 1.662, P = 0.204; interaction: $F_{2,35}$ = 0.025, P = 0.976). In both cases, the likelihood ratio tests showed that the effect of the locality was not significant (Bullfinch: χ^2 = 1.699, df = 1, $P > 0.05$; Chaffinch: χ^2 = 0.002, df = 1, $P > 0.05$). (Fig. 1.)

Bullfinch abundance across localities was strongly associated with the abundance of rowanberry as measured by the density of fruiting trees, independent of the year in question (trees: $F_{1,20}$ = 6.682, P = 0.018; year: $F_{2,20}$ = 0.676, P = 0.520; Fig. 2). For the abundance of Chaffinch, the effect of rowanberry abundance was not significant ($F_{1,20}$ = 2.287, P = 0.146; Fig. 2). Again, the likelihood ratio tests failed to show a significant effect of locality (Bullfinch: χ^2 = 0.001, df = 1, $P >$

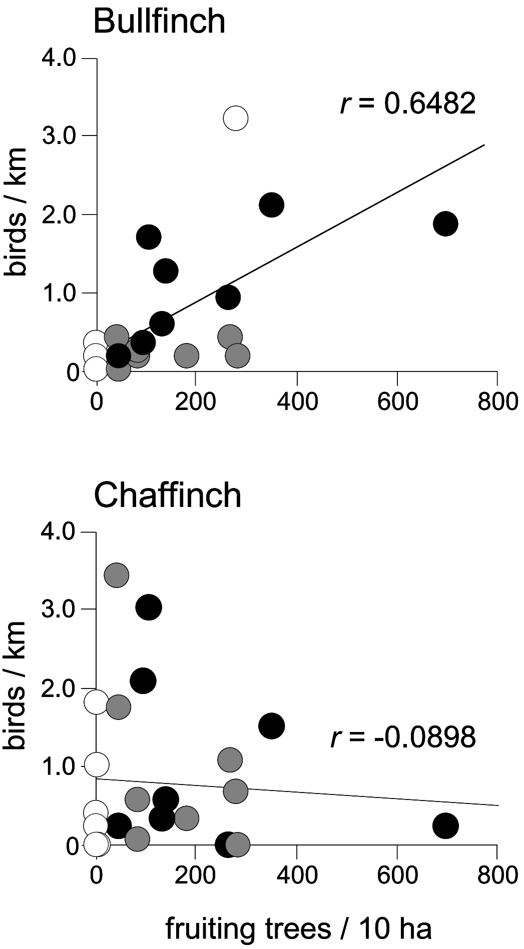

Fig. 2. Correlation between the peak abundance of rowan seed (number of fruiting trees/10 ha in October) and the winter abundance of Bullfinch and Chaffinch (total number of birds counted from October to January) at eight localities in the Cantabrian Range over three seasons with different rowan crop production: none (open dots), intermediate (grey dots) and large (closed dots).

0.05; Chaffinch: $\chi^2 = 2.319$, df = 1, $P > 0.05$).

At the low-altitude sites, the size of the annual rowanberry crop (i.e., year) did not significantly affect the repeated measures of the abundance of Bullfinches ($F_{2,26} = 0.143$, $P = 0.868$). However, that effect was highly significant at the high-altitude sites ($F_{2,26} = 5.163$, $P = 0.013$), suggesting that in years of high rowanberry production, monthly changes in Bullfinch abundance were associated with changes in rowanberry abundance over the winter months (Fig. 3).

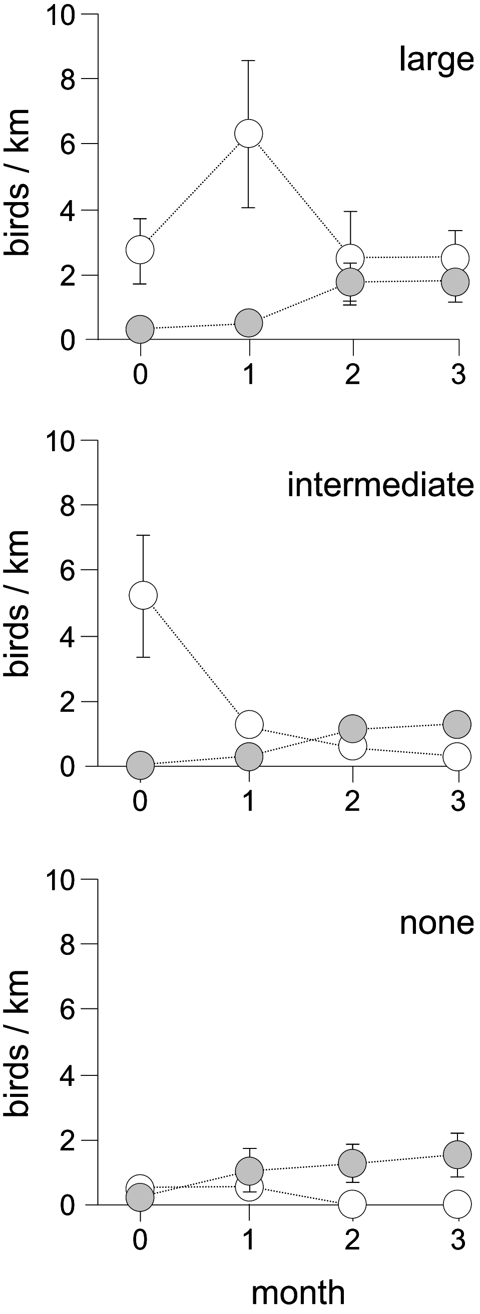

Fig. 3. Monthly variation from October to January in the abundance of Bullfinches (birds/km) at two altitudinal levels (open dots = higher elevations; grey dots = lower elevations) at eight localities in the Cantabrian Range over three seasons with different rowan crop production: none, intermediate and large. Error bars represent standard errors of the mean.

4. Discussion

We detected what is apparently a numerical response of Bullfinches to temporal and spatial variation in the abundance of rowanberry seed. Bullfinch abundance seemingly responded to interannual and monthly variation in rowan crop, whereas variation within and between localities were also associated with Bullfinch numbers. Although Bullfinches are granivores that prey on the seeds of rowan and do not feed on pulp, they behaved with respect to rowan fruit abundance much like "legitimate" avian frugivores that eat the whole berry and subsequently disperse the seeds (see Guitián & Munilla 2008).

Arguably, the only way to unambiguously determine whether birds respond to the abundance of discrete food resources –such as seeds or fruits – is through experimentation (Pulliam & Dunning 1987, Rey 1995, Moegenbourg & Levey 2003). Because the present study is based entirely on correlations between resource and bird abundance, we acknowledge that other uninvestigated factors may have played a role in shaping the observed pattern (e.g., other resources correlated with rowanberry abundance, weather, habitat change, fruiting and bird migration phenology; see Fuentes 1992, Noma & Yumoto 1997, Moegenbourg & Levey 2003), thus limiting conclusions about causality. However, at least two pieces of concomitant evidence suggest that Bullfinches responded principally to fluctuation in the abundance of rowanberry seeds. First, the response pattern was consistent throughout and across disparate spatial and temporal scales that were at least partially defined according to rowan crop (i.e., fruit-producing or fruitless sites). Secondly, the abundance of Chaffinch, a fringillid that shares many ecological and biological features with Bullfinches and is also widespread and common in the mountain habitats of our study, did not show such an association. In addition to the use of the Chaffinch to account for factors other than rowanberry abundance, it should be noted that the apparent response of Bullfinches was analogous to the pattern exhibited at the time in the Cantabrian Range by the guild of avian seed dispersers (see Guitián & Munilla 2008).

According to Newton (1998), correlations between bird numbers and food supplies can be divided into three main types: (1) short-term associations between birds and resources either simultaneously (increasing bird density more or less immediately) or in a delayed fashion (by means of survival or reproductive success); (2) long-term changes in birds associated with long-term changes in food resources (for example, through long-term landscape change); and (3) consistent geographic differences in bird density associated with respective differences in food resources.

Our study was designed for detecting a short-term response of Bullfinch populations to rowan fruit abundance; though the existence of a large-scale (geographic) response cannot be excluded. A short-term immediate response, mostly associated with irruptive and widely fluctuating bird movements during the post-breeding period at the local scale, has been repeatedly documented for avian seed eaters, including several Palaearctic Fringillidae such as the Siskin *Carduelis spinus*, the Redpoll *Carduelis flammea*, the Red Crossbill *Loxia curvirostra* and the Brambling *Fringilla montifringilla* (Newton 1998). The ability to track crops of masting tree species is a common feature in different ecological and taxonomic bird groups, including seed-dispersing frugivores (see Guitián & Munilla 2008 and references therein) and, especially, seed-eating frugivores (Reinikainen 1937, Haapanen 1965, Newton 1972, Bock & Lepthien 1976). Indirect evidence (e.g., Fox *et al.* 2009), as well as feeding records collected throughout the range of the Bullfinch (Erkamo 1948, Pulliainen 1978, Snow & Snow 1988, Guitián *et al.* 2000) support the idea that rowanberry seeds are favoured winter food for this species. Accordingly, our findings suggest that rowanberry seed can be an important winter food resource for Bullfinches in the Cantabrian Range.

Fox *et al.* (2009) tested the hypothesis that poor rowanberry production in normal wintering areas was responsible for the efflux of Bullfinches of the subspecies *pyrrhula* ("Northern Bullfinch") to other areas and their results supported the prediction of highest bird irruptions in years of lowest rowanberry abundance. Mobile specialist and opportunistic resident consumers represent two common strategies among animal consumers that use pulsed resources (Yang *et al.* 2008 and references therein). Mobile specialists often travel long distances in order to utilize patchy and asynchronously pulsed resources; in contrast, opportunistic residents are often widespread in their distribution and sufficiently generalists in their diet to recognize and use an infrequently available resource. Whereas the results of Fox *et al.* (2009) suggest that the Northern Bullfinch may be representative of the mobile strategy, Iberian Bullfinch populations are probably better understood as opportunistic residents. Interestingly, Bullfinches in Scotland are relatively sedentary and respond opportunistically to heather seed availability (Marquiss 2007).

The Iberian Bullfinch subspecies *iberiae* is thought to be highly sedentary with those breeding at high elevations tending to undertake short-range post-breeding movements into more favourable lower areas (Noval 1971, Snow & Perrins 1998). Although our results conform with this pattern in the year when the rowanberry crop failed, in the two good fruiting years of rowanberry, Bullfinches were consistently more abundant at higher than at lower elevations (>1,000 versus <1,000 m a.s.l.). In addition, this altitudinal shift was only maintained as long as the rowanberry crop was not depleted, as shown by variation in Bullfinch density over the winter months.

Our results thus suggest a facultative response in the timing and magnitude of altitudinal movements with birds remaining longer in montane areas in good fruiting years. This behaviour mirrors the latitudinal pattern described for the Northern Bullfinch (Fox *et al.* 2009) and the Fieldfare *Turdus pilaris* (Tyrväinen 1975), both in relation to rowanberry abundance.

Thus, our study supports the idea that a single food resource may have the potential to drive and modulate post-breeding movements, whether they are latitudinal or altitudinal, of certain bird species. Given that fruit availability is subject to substantial variation in space and time, strong interactions between birds and plants can only be expected if birds are able to track changes in fruit abundance. However, such resource tracking by non-mutualist avian frugivores has rarely been considered from this perspective, although the guild of seed-eater birds has the potential to play an important role in the ecology of many plants that rely on avian seed dispersal.

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Punatulkun runsauden suhde talvisiin siemenmääriin

Työmme tarkoitus oli selvittää siemeniä pääravintonaan käyttävän punatulkun (*Pyrrhula pyrrhula*) talviaikaista runsautta suhteessa pihlajan (*Sorbus aucuparia*) marjasatoon. Havaitsimme punatulkun numeerisen vasteen paikalliseen ja ajalliseen pihlajan marjasadon vaihteluun Cantabriassa Pohjois-Espanjassa. Punatulkun lähilajia peippoa (*Fringilla coelebs*) käytettiin muun kuin pihlajan siemensadon vaikutuksien kontrolloimiseen, eikä tällä lajilla havaittu samanlaista vastetta. Punatulkun runsausvaihtelu oli säännönmukaista pihlajanmarjojen määrään nähden riippumatta tarkastelun ajallisesta tai tilamittakaavasta (tutkimuspaikka, marjattomien ja runsasmarjaisten paikkojen suhde, vuosi ja kuukausi). Lisäksi tuloksemme viittaavat siihen, että pihlajanmarjojen määrä voi vaikuttaa Iberian vuoristoissa pesivien punatulkkujen siirtymiseen korkealta alemmas ajoittumiseen ja laajuuteen.

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