Fruit abundance and trait matching determine diet type and body condition across frugivorous bird populations

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Abstract

Research on seed-dispersal mutualisms has been highly unbalanced towards the plants, largely overlooking the fitness effects of fruit resources on frugivorous animals. Moreover, despite morphological mismatches like gape limitation may reduce the abundance of fruits that are actually accessible to a frugivore species, there is very little evidence on the trait-matching implications from a frugivore's perspective. Here, we refine recent resource-provisioning models to comprehensively test the joint effects of fruit abundance and trait matching on diet type and body condition (a surrogate of fitness) across frugivorous bird populations: Sardinian warblers (*Curruca melanocephala*) inhabiting ten Mediterranean forests differing in the abundance and composition of fleshy fruits. We hypothesised the abundance of fruit resources to have positive effects on the degree of frugivory and body condition of warblers, and such effects to be more pronounced when accounting for both trait matching (accessible fruits) and resource provisioning (energy in accessible fruits). We found a sharp threshold over which warblers shifted from a diet with very little or even no fruits to a predominantly frugivorous diet with increasing the local abundance of accessible fruits. We also found a strong positive relationship between the abundance of accessible fruits and the body condition of warblers (body mass and residual body mass), an effect that was more pronounced in females than in males. Although diet type and body condition were much better predicted when accounting for trait matching, accounting for resource provisioning did not improve the explanatory power of fruit resources. The fact that we detected strong and sex-dependent effects of fruit resources on body condition just a few weeks before the breeding season suggests that fruit resources likely affect the timing and success of reproduction, a question that deserves further research. Our findings provide new insight into the fitness consequences of seed-dispersal mutualisms for frugivorous animals.

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Introduction

Seed dispersal by frugivorous animals represents one of the most outstanding mutualisms between animals and plants: frugivores benefit from the edible and nutritive pulp of fleshy fruits while plants benefit from the animal-mediated dispersal of their seeds (Snow & Snow 1988; Herrera 2002; Jordano 2013). The fitness consequences of frugivory and seed-dispersal interactions, which are key for animal nutrition and plant regeneration, can be approached through the effectiveness framework (Schupp et al. 2017). This framework considers a quantity component measured as number of interaction events; a quality component measured as a 'per capita' effect (i.e. per interaction) on animals and plants; and a total effect that can be estimated as the product of quantity and quality, which results in a measure of mutualistic effectiveness (Schupp et al. 2017).

Despite seed-dispersal mutualisms have been widely studied during the last decades, research has been highly unbalanced towards addressing the fitness consequences for the plants (Schupp et al. 2010, Schupp et al. 2017). Numerous studies have shown how distinct frugivore species can vary in the quantity of seeds they disperse, as well as in the probability of plant recruitment per dispersed seed (quality), usually related to seed treatment after ingestion and to the location or timing of seed deposition (Calviño-Cancela and Martín-Herrero 2009, Schupp et al. 2010, Escribano-Ávila et al. 2014, Rey and Alcántara 2014, Nogales et al. 2017, González-Varo et al. 2019). Accordingly, severe declines or even local extinctions of frugivore species can lead to demographic collapses of plant populations via failures in seed dispersal and subsequent seedling recruitment (Cordeiro and Howe 2003, Traveset et al. 2012, Pérez-Méndez et al. 2015, Pérez-Méndez et al. 2016). Remarkably, such failures do not necessarily result from the decline of the whole frugivore assemblage, but from the decline or extinction of the larger species that are able to consume the fruits of larger-fruited plant species (Pérez-Méndez et al. 2015, Pérez-Méndez et al. 2016, Donoso et al. 2017). This highlights that the quantity component not only depends on the abundance (González-Varo et al. 2019) and degree of frugivory of a frugivore species (Fricke et al. 2017), but also on its ability to swallow fruits from different plant species (Wheelwright 1985, Olesen et al. 2011). The latter constitutes a morphological trait matching between fruit size and frugivore's gape size, and determines whether a frugivore can swallow whole fruits and thus carry out endozoochory (Wheelwright 1985, Rey et al. 1997, González-Varo and Traveset 2016).

In contrast to the focus that plant fitness has received, the frugivore's perspective has been largely overlooked and very few studies have addressed the fitness consequences of seed-dispersal mutualisms for the frugivores in terms of resource provisioning (Quintero et al. 2020). In fact, most studies assessing the effects of fleshy fruits on animals have focused on 'fruit-resource tracking', that is, the ability of highly mobile frugivores (e.g. migratory birds or large mammals) to find and exploit vegetation patches were fruits abound (Rey 1995, García and Ortiz-Pulido 2004, Wunderle et al. 2014, Nielsen et al. 2017). Yet, only few studies have tested the importance of fleshy fruits –or the lack of them– for frugivore body condition (Foster 1977, Jordano 1988, Rey and Valera 1999, Rojas et al. 2019, Nwaogu et al. 2020), a surrogate of individual fitness in animals (Labocha and Hayes 2012, Duijns et al. 2017). For example, Rey and Valera (1999) showed that blackcaps (*Sylvia atricapilla*) wintering in olive orchards of southern Spain had a much less frugivorous diet and a lower body mass than blackcaps wintering in nearby shrublands, where wild fleshy fruits abound. This particular study is interesting because it reveals the importance of trait matching for frugivores: cultivated olives were abundant in orchards but too large (~15 mm diameter) for blackcap's gape width (~8 mm), thereby mostly inaccessible for them (see Rey and Gutiérrez 1996). It also shows an important aspect of frugivores under fruit shortage: diet plasticity (Rey and Valera 1999). Only recently, the effectiveness framework (Schupp et al. 2017) has been applied to assess resource provisioning for frugivorous animals, where the quantity component is the number of fruits ingested by a frugivore and the quality component can be measured in terms of energy or nutrients obtained per quantitative unit (Quintero et al. 2020).

In this study, we apply the effectiveness framework to estimate the abundance of fruit resources for frugivores in terms of energy content per unit area and its effects on frugivore diet and body condition. To do so, we refined resource-provisioning models (Quintero et al. 2020) by incorporating trait-matching information in the estimation of the quantity and quality components. First, trait matching can affect the quantity component because only a fraction of the total fruit abundance might be accessible for a frugivore species due to gape limitation (Rey and Gutiérrez 1996), and this fraction may vary both across and within species (González-Varo and Traveset 2016). Secondly, trait matching can determine the quality component because, for the same plant species, different frugivore species can consume fruits of different sizes (Rey et al. 1997, Galetti et al. 2013, González-Varo et al. 2014) and, thus, obtain a different amount of energy or nutrients per ingested fruit.

We used these refinements of resource-provisioning models to comprehensively test the joint effects of fruit abundance and trait matching on the diet type and body condition of a frugivorous bird: the Sardinian warbler (*Curruca melanocephala*, Sylviidae), a resident passerine that inhabits Mediterranean woodlands (Aparicio 2016) and for which, on average, fleshy fruits account for three-quarters of its diet in volume (Herrera 1995). We studied Sardinian warbler populations occurring in ten Mediterranean forests of southern Spain that differed in abundance and composition of fleshy fruits. Specifically, we hypothesised (*i*) that the abundance of fruit resources has positive effects on the degree of frugivory and body condition of Sardinian warblers; and (*ii*) that such effects are better predicted when accounting for both trait matching (i.e. accessible fruits) and resource provisioning (i.e. accessible energy per fruit).

Material and methods

Study frugivore species

The Sardinian warbler is a small (~11 g) passerine that is resident in the southern Iberian Peninsula (Aparicio 2016). This warbler plays an important role throughout the Mediterranean Basin as a seed disperser of many fleshy-fruited species (Herrera 1984, Izhaki et al. 1991). In fact, it is the most abundant resident species in avian frugivore assemblages of woodlands from our study region (González-Varo 2010). Four main characteristics make the Sardinian warbler an ideal species to test the effects of fruit abundance and trait matching on diet and body condition: (1) it shows a marked territorial and site-fidelity behaviour after juvenile dispersal (Bas et al. 2005, Aparicio 2016, González-Varo et al. 2019), thereby it is expected to be susceptible to local resource availability; (2) the contribution of fruits to Sardinian warbler's diet has been reported to vary between sites (Herrera 1995), which suggest potential diet swifts according to local resources; (3) it is a small-gaped bird, which means that it can only ingest a fraction of all fruits present in a given site owing to morphological trait matching (Wheelwright 1985, Olesen et al. 2011, González-Varo and Traveset 2016); and, finally, (4) it is a very abundant species (Tellería et al. 2005, González-Varo 2010), thus, it is relatively easy to capture many individuals per mist-netting session.

Study region and sites

The study sites were Mediterranean lowland forests located in the Guadalquivir River Valley (western Andalusia, southern Spain; Fig. A1), a large, fertile and intensively cultivated lowland (< 200 m a.s.l.) where a long history of transformation and loss of natural habitats has left just a tiny cover of Mediterranean woodlands (only ~1% outside protected areas (Aparicio 2008). The climate in the valley is typically Mediterranean (thermo-Mediterranean bioclimate), with warm dry summers and cool humid winters. Mean annual precipitation is ~550 mm and January and July temperatures average ~11°C and ~26°C, respectively (AEMET 2011).

We selected ten study sites distributed through central and southern areas of the Guadalquivir Valley that are close to the Atlantic coast, in the provinces of Cádiz and Sevilla (Fig. A1, Table A1). We knew from previous studies (González-Varo 2010) and personal observations that these sites represent a gradient in local fruit abundance. The distance between sites ranged between 3 and 120 km. Each study site consisted of a plot (mean size = 5 ha; range = 3–9 ha) located within large (>90 ha) and protected forests. The tree layer of the forests is mainly represented by stone pines (*Pinus pinea*, Pinaceae) and to a lesser extent by cork and holm oaks (*Quercus suber* and *Q. ilex* subsp. *ballota*, Fagaceae). The understorey harbours a diverse assemblage of treelets and shrubs (Fig. A1), many of which produce fleshy fruits consumed by Sardinian warblers (Herrera 1984), being *Pistacia lentiscus* (Pistaceae), *Myrtus communis* (Myrtaceae) and *Olea europaea* var. *sylvestris* (Oleaceae; hereafter, *Olea europaea*) the most common species across sites (González-Varo 2010). Due to differences in coastal proximity, local disturbance and successional processes, the identity and abundance of fleshy-fruited plants can be very different between nearby forests (González-Varo 2010).

Sampling surveys, local fruit abundance and vegetation structure

We assessed the diet and body condition of Sardinian warblers (details in the next section) through a single mist-netting survey at each study site in late February 2019. This is a winter period of decreasing fruit abundance in the woodlands of the study region after a fruiting peak between October and December (Jordano 1985). Besides, it is a period of low arthropod abundance in which fruits are the main resource for frugivorous birds (Herrera 1981, Rey and Valera 1999). We measured local fruit abundance at each site twice: in a survey conducted one month 'before' the mist-netting survey of Sardinian warblers (late January 2019) and 'during' the mist-netting survey (late February 2019). The reason for these two surveys is that fruit resources could have a delayed effect on body condition, which might be more related to previous resource abundance. A period of one month has proved suitable to detect substantial changes in body condition of other Sylviidae (Jordano 1988, Rey and Valera 1999).

We quantified fruit abundance at the study sites within eight, 10 m wide × 30 m long, fixed transects (i.e. 300 m^2 each totalling 2400 m^2 per site) evenly distributed within each study plot. Sampling in each transect was conducted by two of us (JPGV and NPM) recording the species and the estimated number of fruits per plant within the transect area (see Fig. A2). We visually estimated fruit crops per plant by counting ripe fruits in some plant branches and by extrapolating such counts to the total plant canopy. We estimated fruit crops to the nearest value one order of magnitude below the total estimate (e.g. nearest ten for hundreds of fruits, nearest hundred for thousands of fruits, etc.). For each plant species i per site j, we calculated the mean fruit density across transects (D_{ij}). For *P. lentiscus*, the most common and abundant species across sites, we visually estimated to the nearest 0.05 the proportion of black fruits in crops because: (*i*) female plants can bear full-sized black and red fruits (see Fig. A2C) throughout their whole fruiting period (Jordano 1989, González-Varo et al. 2019), (*ii*) both fruit types differ in their nutritional content (Jordano 2013), and (*iii*) birds prefer black fruits but they can consume red fruits, particularly if black fruits are depleted (Jordano 1989). We calculated the mean fruit density (D_{ijs}) for each plant species by averaging the cumulative fruit numbers of each species across transects per site i and survey s. In the case of *P. lentiscus*, we differentiated the density of black and red fruits by multiplying each individual fruit crop by either the proportion of black (p_{black}) or red fruits ($1 - p_{\text{black}}$).

In the 'during' survey, we also characterized the vegetation structure of each site by visually estimating to the nearest 5% the cover of different physiognomic elements within three 5 m wide × 10 m long rectangles chessboard distributed within each fixed transect used to quantify fruit abundance (i.e. 50 m^2 per rectangle × 3 per transect = 150 m^2 per transect × 8 transects = 1200 m^2 per site; see scheme in Fig. A1). The physiognomic elements were trees (≥ 5 m in height), tall shrubs (>1 m), low shrubs (<1 m; mainly rockroses, Cistaceae) and open ground. We calculated the mean covers of these physiognomic elements per site by averaging data per transect and then averaging transects means per site (see Table A1).

Mist netting, diet type and body condition

Between 18–27 February 2019, a median of 66 m of mist nets were operated at each site (range: 39–66 m) for a median of five hours (range: 3–9 h), between 08:30 (~30 min after sunrise) and 19:00 (sunset) local time. We initially aimed at capturing a minimum of 12 Sardinian warblers per site; thus, mist-netting duration depended on capture success. We placed two playback stations reproducing the call and song of Sardinian warblers under some mist nets in order to attract conspecifics and facilitate captures. The nets were visited every 15–20 min. Captured birds were carefully handled by expert bird ringers from our team (AO, JCI and RT), and kept inside a cotton bag until ringing. In order to obtain droppings for assessing diet type, Sardinian warblers were kept for up to 30 min inside a cotton bag with a new conical-shaped filter paper (15 cm diameter and 10 cm depth) placed at the base of the bag. We classified the content of warbler droppings into two categories: (*i*) ‘fruits’ when the droppings included defecated or regurgitated seeds, pulp and/or macroscopic pericarp remains, and (*ii*) ‘no fruits’ when the droppings showed no sign of frugivorous diet (e.g. Fig. A3). Importantly, this classification is exclusively based on frugivory, not on seed dispersal, and may thus include pulp-pecking events of large fruits to overcome gape limitation (Rey and Gutiérrez 1996).

All captured birds were ringed by AO, who also obtained the following biometric measures: body mass (g), tarsus length (mm) and wing length (mm). Body mass was measured to the nearest 0.1 g using a portable digital scale, wing length to the nearest 0.5 mm using a ruler, and tarsus length to the nearest 0.1 mm using a digital calliper. Sardinian warblers have a marked sexual dimorphism, thus, they were classified as males or females (see Fig. A3). Because sexual maturity is reached during first year of life (Aparicio 2016), all captured warblers during our survey (February) were classified either as adults born in the previous calendar year or older birds (EURING codes 5 and 6, respectively; https://euring.org/data-and-codes/euring-codes). We used two body condition measures: 'body mass (g)' and 'residual body mass (g)' expressed as the residuals of body mass regressed on tarsus length (Schulte-Hostedde et al. 2005, Labocha and Hayes 2012). Within species, body mass is a good indicator of body condition (Labocha and Hayes 2012). Residual body mass has the advantage from being uncorrelated with bird size, measured as tarsus length, as it measures deficit or excess of grams considering bird size (Schulte-Hostedde et al. 2005, Labocha and Hayes 2012). We used tarsus length as structural measure of body size because, although non-significantly, its relationship with body mass ($bm = 9.523 + 0.111 \times tl$; $P = 0.244$, $R^2 = 0.010$, $n = 135$) was slightly higher than that of wing length ($bm = 11.633 + 0.001 \times wl$; $P = 0.972$, $R^2 = 0.000$, $n = 135$).

Trait matching and fruit-resource variables

All fleshy fruits present in the study sites were spherical or ellipsoidal, thus fruit diameter is a trait that allows, or not, frugivorous birds to swallow whole fruits (Wheelwright 1985, Snow and Snow 1988). We sampled fruits from the 11 fleshy-fruited species recorded in the study sites and measured their diameter to the nearest 0.01 mm using a digital calliper. Fruits from the most common species were sampled and measured from multiple sites leading to 26 'fruit species–site' combinations. Sample sizes varied according to local fruit availability, from 25 to 191 fruits per species and site (total = 2804 fruits). We calculated the mean and standard deviation of fruit diameter per species and site, which were used to parameterise normal distributions. We used normal probability density functions to obtain the cumulative probability in fruit diameter under the mean gape width of the Sardinian warbler (6.6 mm; González-Varo and Traveset 2016), which represents the proportion of fruits (P_{ij}) that can be swallowed by warblers (i.e. accessible fruits) of each species i at each site j (see Fig. 1 and Fig. A4). This approach allows estimating very small P_{ij} values (as small as 0.0001) for species with large fruits, where observed proportions of fruits with a diameter smaller than the gape width can be zero owing to small sample size (e.g. if n measured fruits = 50, the smallest non-zero proportion is 1/50 = 0.02). Importantly, the correlation between P_{ij} values and observed proportions of fruits was nearly perfect (Pearson's $r = 0.997$, $P < 10^{-15}$, $n = 26$; see details in Fig. A5). We thus used a mixed approach to address trait matching: we accounted for intraspecific variability in fruit diameter of the fleshy-fruited species, which can vary substantially between sites (González-Varo and Traveset 2016), but we used a species-level mean value for the gape of the Sardinian warbler (Fig. 1) (see similar approach in González-Varo and Traveset 2016). The reason is that gape width is not a standard dimension measured by bird-ringers, but instead a delicate measure that exhibits strong measurer effects (see details in Appendix S1 from González-Varo and Traveset 2016). We used the mean gape width of Sardinian warblers ($n = 112$ individuals) from southern Spain and Portugal reported in González-Varo and Traveset (2016); the original data for this mean value were requested to researchers that measured this trait during frugivory studies (Herrera 1984, Jordano 1987, Costa et al. 2016). We obtained site-specific diameter data in 70% (26 of 37) of 'species–site' combinations (see Fig. A6). In those combinations with missing information (30%, 11 of 37), we performed data imputation by using the species-level means across sites of both $mean_{ij}$ and sd_{ij} to parameterize normal diameter distributions (see details in Fig. A6).

We also obtained the nutritional content and pulp dry mass of the fruits recorded in the study sites at the plant species level from Herrera (1987), which included data for black fruits of *P. lentiscus*. Additionally, we obtained the nutritional content of red fruits of *P. lentiscus* from Jordano (2013). We imputed data for *Juniperus macrocarpa* (Cupressaceae) using data of *J. oxycedrus* from Herrera (1987) because both species are sister species; in fact, *J. macrocarpa* has been considered a subspecies of *J. oxycedrus* until recently (http://www.worldfloraonline.org). We first obtained the energetic value (kJ/g) of the dry pulp of each fruit species by multiplying the relative content (proportion) of macronutrients and their energy conversion factors: 17 kJ/g for protein and carbohydrate content and 37 kJ/g for lipid content (FAO 2003). Then, we calculated the energy content per fruit (E_i: kJ/fruit) by multiplying the energetic value (kJ/g) of each fruit species fruits and the average pulp dry mass (g/fruit) of the fruits analysed (Quintero et al. 2020). Finally, for each species i, we calculated the energetic value of accessible fruits in each site j (AE_{ij}) by multiplying energy per fruit (kJ/fruit) by a ratio between the median diameter of fruits smaller than Sardinian warbler's gape width and the mean diameter of fruits analysed for macronutrients reported by Herrera (1987) and Jordano (2013). This ratio ranged from ~0.5 to ~1.0, indicating that the median diameter under gape width ranged from roughly half to roughly the same mean diameter of fruits analysed. The median diameter of fruits smaller than warbler's gape width (i.e. diameter for P_{ij} × 0.5) is a measure of central tendency that can be easily obtained from the normal probability density functions (previous paragraph) describing fruit diameter distribution of each plant species i in each site j (see details in Fig. A5). The advantage of this approach is that allows obtaining a central tendency for the diameter of accessible fruits when none of the measured fruits were under the gape width, which occurred for *Crataegus* *monogyna* (Rosaceae), *J. macrocarpa, J. phoenicea* and *Ruscus aculeatus* (Asparagaceae) (Fig. A4). Importantly, the correlation between such estimated medians and observed mean diameters under gape width was nearly complete (Pearson's $r = 0.989$, $P < 10^{-15}$, $n = 22$; see Fig. A5).

We obtained three fruit-resource variables for each site j and each sampling survey s: (*a*) total fruit density (fruits/ha) calculated as $\sum_{i=1}^{n} D_{ijs}$, that is, the sum of mean fruit densities across species (i.e.); (*b*) density of accessible fruits (fruits/ha) calculated as $\sum_{i=1}^{n} D_{ijs} \times P_{ij}$, that is, the sum of mean fruit densities multiplied by the proportion of accessible fruits across species (i.e.); and (*c*) density of accessible energy (kJ/ha) calculated as $\sum_{i=1}^{n} D_{ijs} \times P_{ij} \times AE_{ij}$, that is, the sum of the product between mean fruit densities, proportion of accessible fruits and energetic content of accessible fruits across species. The three variables represent a gradient in terms of trait matching (accounted for in *b* and *c*) and resource provisioning (only accounted for in *c*), thus, in the accuracy of the actual resources accessible to Sardinian warblers (Quintero et al. 2020).

Data analysis

We fitted generalized linear mixed models (GLMMs) to test the effects of local fruit resources on the diet type and body condition of Sardinian warblers. The frequency of frugivorous diet in warbler droppings was modelled as a Bernoulli-distributed variable with logit link function (1: fruits; 0: no fruits), whereas the two body condition measures (body mass and residual body mass) were modelled as a Gaussian variable with identity link function. All models included site identity as random factors to account for the nested data structure (i.e. individual warblers within sites). We fitted different sets of models including each of three variable types quantifying fruit resources: (*a*) total fruit density (fruits/ha), considering all fruits; (*b*) density of accessible fruits (fruits/ha) after accounting for trait matching (i.e. fruits that can be swallowed by warblers); and (*c*) density of accessible energy (kJ/ha) in fruits after accounting for trait matching; the three variables were $\log_{10}$-transformed due to huge variation among sites. For the frequency of frugivorous diet, we used the fruit-resource variables recorded in the 'during' sampling survey (i.e. three sets of models, one per fruit-resource variable). For body condition, we used the fruit-resource variables recorded either in the 'before' or the 'during' sampling surveys, leading to six sets of models: 3 fruit-resource variables × 2 surveys (we used different models owing to collinearity between the 'before' and 'during' data in the three fruit-resource variables; Pearson's $r = 0.966–0.974$). We tested both surveys because body condition might be more related to resource abundance a few weeks before than to current resource abundance, given that the gain or loss of body condition in other passerines may take several weeks (Jordano 1988, Rey and Valera 1999).

In each set of models, we tested other covariates that could potentially affect both diet type and body condition, namely bird sex, bird age (EURING code 5 or 6), Julian day of sampling, time of day and mean cover of trees, tall shrubs, low shrub and open ground at each site. We tested bird sex and its interactive effect with fruit-resource variables, not only to control for potential sex-ratio biases from acoustic playback (Lecoq and Catry 2003), but also because males and females might respond differently to local resources (e.g. Townsend et al. 2012, Wunderle et al. 2014), particularly considering that our mist-netting survey was conducted approximately *ca*. 1–2 months before the breeding season (Aparicio 2016). We also tested bird age class and its interactive effect with fruit-resource variables to control for differences among populations the frequency of second year birds. Moreover, we tested the effects of Julian day of sampling (49–58) and time of day (08:30–19:00) in order to control for inter- and intra-day temporal differences among captured warblers (sites). Finally, we tested the effects of physiognomic variables characterizing the vegetation structure of study sites, which might be relevant for Sardinian warblers (Aparicio 2016, Dagan and Izhaki

2019). In each set of models we included the corresponding fruit-resource variable as our hypothesized predictors of diet type and body condition. We then followed a forward stepwise procedure in which we tested each of the other covariates, keeping only those that both improved model fit (i.e. led to a decrease in AIC) and produced significant effects (i.e. the 95% CIs of their estimates did not overlap with zero). We assessed the goodness-of-fit of different models and different model sets containing different fruit-resource variables from their AIC and marginal R^2 values ($R^2_{\mathrm{GLMM\ (m)}}$), that is, the variance explained by the fixed effects variables (Nakagawa et al. 2013). For binomial models, $R^2_{\mathrm{GLMM\ (m)}}$ were obtained using the delta method (Nakagawa et al. 2017). All models were fitted using the R package *glmmTMB* (v. 0.2.3) (Brooks et al. 2017) and their $R^2_{\mathrm{GLMM\ (m)}}$ values were obtained with the R package *MuMIn* (v. 1.43.17) (Barton 2015). We checked for spatial structure in raw variables and the residuals from best-fit models by means of Moran's *I* correlograms (Legendre and Legendre 2012) obtained with the R package *ncf* (v. 1.2–9) (Bjornstad and Bjornstad 2020).

Results

Fruit-resource variables

We found a huge variation in total fruit density across sites, ranging between 13,208 and 2,264,917 fruits/ha in the 'before' survey and between 1062 and 751,167 fruits/ha in the 'during' survey (Fig. 2A). Four species contributed to most of the fruit density across sites and surveys: *P. lentiscus*, *M. communis*, *O. europaea* and *J. phoenicea* (Fig. 2A). The estimated proportion of accessible fruits (P_{ij}) ranged between 0.0001 and 1.0 (Table 1; see also Fig. A4). Among the most abundant species, *J. phoenicea* showed the lowest P_{ij} value, *O. europaea* and *M. communis* and showed intermediate values, while *P. lentiscus* showed the highest values across sites (Table 1). As a result, the density of accessible fruits dropped markedly in relation to total fruit density at sites where large fruits were dominant, which was most clear at one site (AL) dominated by *J. phoenicea* and two sites (GA and AS) dominated by *O. europaea* (Fig. 2B). We also estimated a large variation in terms of the energy content per accessible fruit (AE_{ij}) across species (Table 1). Among the most abundant species, red *P. lentiscus* fruits showed the lowest AE_{ij} values (~0.2 kJ/fruit) followed by *J. phoenicea* (~0.4 kJ/fruit), *M. communis* (~0.6 kJ/fruit) and black *P. lentiscus* fruits (~0.7–0.8 kJ/fruit), whereas *O. europaea* fruits (~1.4 kJ/fruit) showed by far the highest values (Table 1). As a result, the density of accessible energy dropped in relation to the density of accessible fruits at sites where red *P. lentiscus* fruits were abundant, but increased at sites where *O. europaea* fruits were abundant (Fig. 2C).

The two variables that accounted for trait matching, that is, the density of accessible fruits (Fig. 2B) and the density of accessible energy (Fig. 2C), were highly correlated in both surveys (before: Spearman's ρ = 0.94; during: ρ = 0.92). Yet, the correlation of these variables with the total fruit density (Fig. 2A) was weaker, particularly in the 'during' survey (before: ρ = 0.70–0.73; during: ρ = 0.48–0.56). This indicated that trait matching rather than energetic fruit content produced more differences among sites in the ranking of the fruit-resource variables (Fig. 2).

Captures and samples

We captured 135 individual warblers (range: 11–17 per site), 85 males (range: 7–12) and 50 females (range: 3–7), roughly one third of them born in the previous calendar year and the others were older birds (see details in Table A1). We recaptured two males and two females at different sites (Table A1), but only data from their first capture was included in body condition models. We obtained a total of 133 warbler droppings for diet-type classification (range: 10–16 per site; Table A1). Only two droppings (1.5%) belonged to recaptured birds that produced a dropping in their first capture, and these were included in diet type models.

We found a total of 100 seeds from 64 out of the 91 droppings classified as with 'fruits'; the remaining 27 droppings had pulp and pericarp remains without seeds. Among the seeds, 92 belonged to *P. lentiscus*, that is, the abundant fruit species with the smallest fruits (thus, highest P_{ij}) across sites. We also found five *M. communis* and three *O. europea* seeds (see details in Fig. A7).

Diet type

The frequency of fruits in droppings across warbler populations was strongly predicted by the density of accessible fruit resources, either fruits or energy, during the mist-netting surveys (Fig. 3). Of all covariates, including bird sex, only the time of day improved substantially all models and had positive significant effects (see details in Table A2, Table 2), indicating that birds tended to eat less fruits in the morning than in the afternoon. We thus focused on models including time of day and fruit-resource variables (Table 2). Among them, the density of accessible fruits produced the best fit followed by the density of accessible energy, and both variables had significant effects (Table 2). In contrast, the total fruit density produced the worst fit and this variable had non-significant effects (Table 2). Remarkably, the two models including accessible fruit resources explained almost all the variance (90–92%) in the frequency of frugivorous diet, nearly doubling the variance explained by the model with total fruit density (Fig. 3). Interestingly, there was a threshold response to the density of accessible resources in which warblers shifted from a predominantly frugivorous diet (frugivory = 85–100% in seven sites with >10,000 fruits/ha) to a predominantly non-frugivorous diet (frugivory = 0–8% in three sites <4000 fruits/ha). Importantly, the best model explained the existing spatial structure in frequency of frugivorous diet (Fig. A8).

Body condition

Body mass and residual body mass were also strongly predicted by the density of accessible fruit resources, either fruits or energy, and both body condition measures led to nearly identical results (Fig. 4). Interestingly, models including bird sex and its interaction with fruit-resource variables improved substantially model fit (AIC values dropped > 20; Table A3). The significant 'Fruit × Sex' interaction in the best models showed that the density of accessible fruit-resources had stronger effects on females than on males (see slopes in Fig. 4). Yet, other predictor variables had non-significant effects and did not improve model fit (Table A3). We thus focused on models with fruit-resource variables, bird sex and their interaction (Table 3). The density of accessible fruits produced the best fit followed by the density of accessible energy, and both variables had significant effects (Table 3). In contrast, the total fruit density produced a much worse fit despite its significant effects (Table 3). Moreover, models including fruit-resource variables from the 'before' sampling survey had a slightly better fit than those including the 'during' survey (Table 3). Again, the best models explained the existing spatial structure in both body condition measures (see Fig. A9). Notably, in linear scale, body condition had asymptotic response to the density of accessible fruits (Fig. A10).

Discussion

There is very little evidence on the fitness consequences of seed-dispersal mutualisms for frugivorous animals (Quintero et al. 2020) and evidence is even scarcer for the implications of trait mismatching from the frugivore's perspective (but see Rey and Valera 1999). Here, we uniquely show how local fruit abundance determines the degree of frugivory in diet and body condition of Sardinian warblers, and that fruit-abundance effects were stronger on the body condition of females. In addition, we show that trait matching plays a critical role in determining both diet type and body condition of frugivores, as these were much better predicted by the local density of accessible fruits than by the total fruit density. The latter was further supported by the identity of seeds found in warbler droppings (Fig. A7). Yet, accounting for resource provisioning did not improve the explanatory power of fruit resources. In our study system, the density of accessible fruits and that of accessible energy were strongly correlated, but this might not necessarily be the same for large-gaped frugivores in fleshy-fruited plant communities with a higher variation in fruit size and energy content (Quintero et al. 2020).

Effects of fruit resources on diet type

As far as we know, few or no studies have assessed spatial variation in frugivorous diet in relation to a gradient of fruit abundance. Interestingly, we found a sharp threshold at which warblers shifted from a predominantly non-frugivorous diet at sites with less than 4,000 accessible fruits per hectare to a predominantly frugivorous diet at sites with more than 10,000 accessible fruits per hectare (Fig. 3B and Fig. A10A). Hence, the foraging behaviour of warblers responded almost categorically (i.e. mostly frugivorous or mostly non-frugivorous) to the continuous gradient in fruit abundance of the study sites. Indeed, warblers' diet turned non-frugivorous at sites where some accessible fruits were still available. Thus, it seems that frugivory, as main diet, was not worthy for warblers where accessible fruits were scant, which is surprising because our study was conducted in a period of low arthropod abundance (Herrera 1981, Rey and Valera 1999). Because fruits tend to be more patchily distributed than invertebrates (Wunderle et al. 2014), particularly if they are scarce (Beauchamp 1998), optimal foraging might be a plausible mechanism to explain these contrasting dietary strategies (Krebs et al. 1974, Charnov 1976). Our results also suggest that pulp pecking of larger fruits was not a frequent alternative to overcome gape limitation (see Rey and Gutiérrez 1996), as exemplified by the population AL, where the frequency of fruit remains in droppings was zero despite *J. phoenicea* fruits abounded (Fig. 2 and Fig. 4).

Our study was conducted at the end of the fruiting season in Mediterranean lowland forests, when local fruit densities are shrinking (Herrera 1984, Jordano 1985). Hence, it is reasonable to assume that all warbler populations had a predominantly frugivorous diet before local fruit shortages (Fig. 2). For example, fruit resources at one of the three populations with the lowest degree of frugivory (CH) dropped from ~37,000 to ~3300 accessible fruits per hectare in one month, from the 'before' to the 'during' sampling surveys (see Fig. 2B). According to our best-fitted model (Fig. 3B and Fig. 10A), this warbler population should have been predominantly frugivorous one month before. In contrast, the population AL, where frugivory in warbler diet was 0%, already had as little as ~1300 accessible fruits per hectare in the 'before' survey. According to our model, this result suggests that this population left frugivory as a significant diet more than one month before mist netting.

Effects of fruit resources on body condition

Our results show that the local density of accessible fruits had clear effects on the body condition of Sardinian warbler populations (Fig. 4B and 4E). We obtained nearly the same results when using body mass and residual body mass as the body condition measure, which makes sense considering the absence of correlation between body mass and tarsus length. Notably, body condition was slightly better predicted by the accessible fruit resources one month before mist netting, which suggests that fruit resources have a delayed effect of a few weeks on body condition. This means that differences among warblers in body mass were mostly due to differences in reserves and muscle (Schulte-Hostedde et al. 2005, Labocha and Hayes 2012), and that bird size had a non-significant effect on the observed body masses.

Interestingly, we found that the positive effects of fruit resources were much stronger in females than in males (Fig. 4B and 4E). At the lowest density of accessible fruits, females and males had the same body condition, but females had a higher body mass than males at the highest density of accessible fruits. Given that our mist-netting surveys were conducted a few weeks before the breeding season (Aparicio 2016), these differences between sexes were likely due to female body mass gain before egg laying (Wendeln 1997, Meijer and Drent 1999, Redfern 2010). This indicates that females occurring at sites poor in accessible fruits were worse prepared for the breeding season than those occurring at sites plenty of fruit resources. Therefore, a limitation in accessible fruit resources might delay the timing of egg laying via reduced female body condition (Wendeln 1997, Redfern 2010), which is in agreement with food supplementation experiments (Meijer and Drent 1999). The latter could have strong effects on the reproductive success of multi-brooded species (Meijer and Drent 1999), like the Sardinian warbler (Aparicio 2016), because a delay in the timing of laying might determine a smaller number of broods in the breeding season. In addition, a lower female body condition can lead to a lower egg mass (Wendeln 1997), which is expected to subsequently affect offspring phenotype (Moore et al. 2019). Thus, our findings suggest that the effects of local fruit resources for Sardinian warblers might go beyond adult body condition and affect their reproductive success and the performance of the next generation, a prediction that deserves future research.

Understanding temporal dynamics from a snapshot

We acknowledge that our work represents a snapshot of the dynamics of the frugivore species and the fleshy-fruited plant communities studied. We found clear effects of fruit resources on the diet and body condition of Sardinian warblers in late winter, a period of low arthropod abundance and decreasing fruit abundance after the fruiting peak. Thus, we expect smaller effects of fruit resources earlier (autumn to early winter), when fruit abundance in all study sites was likely above the thresholds affecting diet and body condition (Fig. A10). Yet, we also expect strong effects in summer because (*i*) fruits are typically scarcer in the study region during summer (Jordano 1985), and (*ii*) summer coincides with a massive recruitment and emancipation of highly frugivorous juvenile warblers (Hampe 2001, González-Varo et al. 2019). Following the same reasoning, we expect yearly differences according to interannual variation in fruit production, both overall and in terms of species-specific relative abundances (Herrera 1998). For instance, a minority of our study sites were below the thresholds in fruit abundance that strongly affected diet and body condition during the study year, but the majority of them could be below these thresholds in a year of low fruit production.

Conclusions

This study provides new empirical evidence and further insight on the consequences of seed-dispersal mutualisms for diet and body condition of frugivorous animals. Moreover, it provides new analytical tools that allow incorporating trait matching in the estimation of the quantity and quality of local fruit resources accessible for a particular frugivore species. Indeed, our results highlight that trait matching can be of major importance in determining fruit accessibility for small-gaped frugivores, thereby in determining their diet and body condition. Our results also reveal an unexpected threshold response to local fruit abundance in the frequency of frugivory in warbler's diet, whose underlying mechanism deserves further examination. Finally, the finding that local fruit resources had stronger effects on the body condition of pre-breeding females suggests cascading effects on warbler reproduction, which also deserves future research.

Data availability statement

Data will be made available from the Dryad Digital Repository

Table 1. Range within fruit species, or single value if fruit diameter was only measured in one study site, in mean fruit diameter and two parameters used to obtain fruit-resource variables that accounted for trait matching and energetic content of fruits (P_{ij} and AE_{ij}). P_{ij} is the estimated proportion of fruits of each species *i* at each site *j* that can be swallowed by the Sardinian warbler, that is, the proportion of accessible fruits. E_i is the mean energetic content per fruit *i* calculated from energy conversion factors (FAO 2003) and macronutrient data compiled from Herrera (1987) and Jordano (2013). AE_{ij} is the energetic content per accessible fruit of each species *i* at each site *j*, calculated as the product between E_i and a size ratio (range = 0.52–1.04) between the median diameter of fruits that can be swallowed by warblers and the mean diameter of fruits analyzed for macronutrients reported by Herrera (1987) and Jordano (2013) (see Methods for details). Mean_{ij}, sd_{ij} and P_{ij} values can be found in Fig. A4.

Fruit species	Mean fruit diameter $_{ij}$ (mm)	P_{ij} (proportion)	E_i (kJ/fruit)	AE_{ij} (kJ/fruit)
Crataegus monogyna	9.74	0.0002	2.32	1.62
*Juniperus macrocarpa**	13.27	0.0001	2.36	1.51
Juniperus phoenicea	9.29	0.0004	0.50	0.39
Myrtus communis	6.75–7.04	0.3551–0.4526	0.90	0.61–0.63
Olea europaea var. *sylvestris*	7.21–7.67	0.1381–0.2230	2.03	1.44–1.44
Osyris lanceolata	7.10	0.2989	0.33	0.27
Pistacia lentiscus (black fruits)	4.43–5.55	0.9783–1.0000	0.79	0.66–0.82
Pistacia lentiscus (red fruits)	4.43–5.55	0.9783–1.0000	0.24	0.19–0.24
Rhamnus lycioides	6.31	0.6659	0.50	0.49
Rubia peregrina	4.17–5.24	0.8316–0.9970	0.19	0.13–0.15
Ruscus aculeatus	11.16	0.0041	1.97	1.02
Smilax aspera	6.58–7.42	0.2295–0.5137	0.33	0.28–0.29

* E_i imputed from *Juniperus oxycedrus* from Herrera (1987), a sister species (see Methods)

Table 2. Results of generalized linear mixed-models predicting the frequency of frugivorous diet in Sardinian warblers populations in response to fruit-resource variables (‘Fruits’; $\log_{10}$-transformed) and the time of day. Results include estimates ± se for the predictors and goodness-of-fit measures for the models (AIC, ΔAIC and $R^2_{\mathrm{GLMM}\,(m)}$). We tested three variable types quantifying fruit resources, which were sampled ‘during’ the mist-netting sessions in which we assessed warblers’ diet type: (*a*) Total fruit density (fruits/ha), considering all fruits; (*b*) Density of accessible fruits (fruits/ha) after accounting for trait matching (i.e. fruits that can be swallowed by warblers); and (*c*) Density of accessible energy (kJ/ha) in fruits after accounting for trait matching. Bold values indicate significant estimates (i.e. 95% CIs do not overlap with zero) and the goodness-of-fit measures of the model with ΔAIC = 0.

Model predictors and goodness-of-fit	(*a*) Total fruit density	(*b*) Density of accessible fruits	(*c*) Density of accessible energy
Intercept	**–25.561 ± 10.403**	**–34.444 ± 8.028**	**–30.172 ± 8.595**
Fruits	3.117 ± 1.714	**5.168 ± 1.063**	**4.376 ± 1.107**
Time of day	**1.101 ± 0.406**	**1.212 ± 0.357**	**1.322 ± 0.440**
AIC	70.4	**48.7**	52.9
ΔAIC	21.7	**0**	4.2
$R^2_{\mathrm{GLMM}\,(m)}$	0.519	**0.917**	0.896
$R^2_{\mathrm{GLMM}\,(c)}$	0.895	**0.917**	0.919

Table 3. Results of linear mixed-models predicting two measures of body condition (body mass and the residuals of a linear model 'body mass ~ tarsus length') of Sardinian warblers in response to fruit-resource variables ('Fruits'; $\log_{10}$-transformed), bird sex and their interactive effect ('Fruits × Sex'). Results include estimates ± se for the predictors and goodness-of-fit measures for the models (AIC, ΔAIC and $R^2_{\mathrm{LMM}\ (m)}$; ΔAIC was calculated across models predicting each body condition measure). We tested three variable types quantifying fruit resources sampled in two surveys: one conducted one month 'before' and the other 'during' the mist-netting sessions for measuring body condition: (*a*) Total fruit density (fruits/ha), considering all fruits; (*b*) Density of accessible fruits (fruits/ha) after accounting for trait matching (i.e. fruits that can be swallowed by warblers); and (*c*) Density of accessible energy (kJ/ha) in fruits after accounting for trait matching. Bold values indicate significant estimates (i.e. 95% CIs do not overlap with zero) and the goodness-of-fit measures of the models with ΔAIC = 0.

Response variable	Model predictors and goodness-of-fit	(*a*) Total fruit density		(*b*) Density of accessible fruits		(*c*) Density of accessible energy	
		Before	During	Before	During	Before	During
Body mass	Intercept	**9.966 ± 0.956**	**10.969 ± 0.645**	**9.509 ± 0.449**	**10.092 ± 0.379**	**9.968 ± 0.384**	**10.624 ± 0.324**
	Fruits	**0.370 ± 0.176**	0.209 ± 0.132	**0.489 ± 0.088**	**0.429 ± 0.085**	**0.433 ± 0.082**	**0.343 ± 0.080**
	Sex (male)	0.901 ± 0.737	0.389 ± 0.477	0.773 ± 0.517	0.562 ± 0.402	0.506 ± 0.437	0.267 ± 0.319
	Fruits × Sex (male)	–0.249 ± 0.135	–0.174 ± 0.098	**–0.240 ± 0.101**	**–0.228 ± 0.089**	**–0.203 ± 0.093**	**–0.179 ± 0.078**
	AIC	222.1	223.4	**206.9**	209.2	208.3	213.1
	ΔAIC	15.2	16.5	**0**	2.3	1.4	6.2
	$R^2_{\mathrm{LMM}\ (m)}$	0.176	0.150	**0.352**	0.336	0.346	0.306
	$R^2_{\mathrm{LMM}\ (c)}$	0.379	0.380	**0.380**	0.391	0.376	0.390
Residuals (bm ~ tl)	Intercept	–1.790 ± 0.951	–0.772 ± 0.640	**–2.183 ± 0.443**	**–1.611 ± 0.372**	**–1.733 ±0.374**	**–1.087 ± 0.317**
	Fruits	**0.381 ± 0.175**	0.217 ± 0.131	**0.488 ± 0.087**	**0.430 ± 0.083**	**0.434 ± 0.080**	**0.346 ± 0.078**
	Sex (male)	1.009 ± 0.728	0.455 ± 0.471	0.760 ± 0.512	0.558 ± 0.398	0.489 ± 0.433	0.264 ± 0.316
	Fruits × Sex (male)	**–0.270 ± 0.134**	**–0.189 ± 0.097**	**–0.240 ± 0.100**	**–0.229 ± 0.089**	**–0.201 ± 0.092**	**–0.181 ± 0.077**
	AIC	218.8	220.1	**203.8**	205.9	204.8	209.7
	ΔAIC	15.0	16.3	**0**	2.1	1.0	5.9
	$R^2_{\mathrm{LMM}\ (m)}$	0.184	0.158	**0.360**	0.346	0.356	0.318
	$R^2_{\mathrm{LMM}\ (c)}$	0.388	0.389	**0.386**	0.397	0.382	0.396

Figure 1. Approach used to address trait matching between the gape width of Sardinian warblers and the diameter of the fleshy fruits present in the study sites, exemplified with three hypothetical fleshy-fruited species (A, B and C). We calculated the mean and standard deviation of fruit diameter measured for different species at different sites, which were used to parameterise normal distributions. Then, we obtained the cumulative probability density under, and up to, the mean gape width of the Sardinian warbler. These probabilities represent the proportion of fruits of each plant species (P_A, P_B, and P_C) that can be swallowed by Sardinian warblers; in the example, most fruits of species A (98%), a minor fraction of species B (16%) and a negligible fraction of species C (1%).

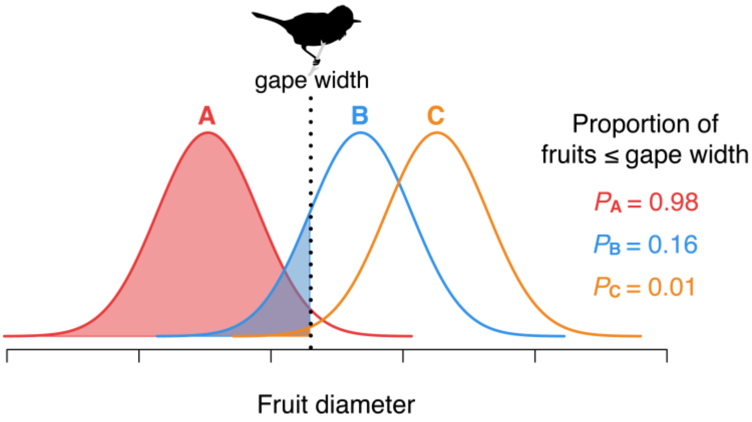


Figure 2. Mean density per site (fruits or energy per hectare) of the three variable types quantifying fruit resources sampled one month 'before' and 'during' the mist-netting sessions for measuring body condition (upper and lower panels, respectively). (A) Total fruit density (fruits/ha), considering all fruits; sites are ordered in decreasing fruit density in the 'before' survey. (B) Density of accessible fruits (fruits/ha) after accounting for trait matching (i.e. fruits that can be swallowed by warblers). (C) Density of accessible energy (kJ/ha) in fruits after accounting for trait matching. Other species: *Crataegus monogyna*, *Juniperus macrocarpa*, *Osyris lanceolata*, *Rhamnus lycioides*, *Rubia peregrina*, *Ruscus aculeatus* and *Smilax aspera*. Note that we distinguish black and red fruits of *Pistacia lentiscus* (see section 'Trait matching and fruit-resource variables').

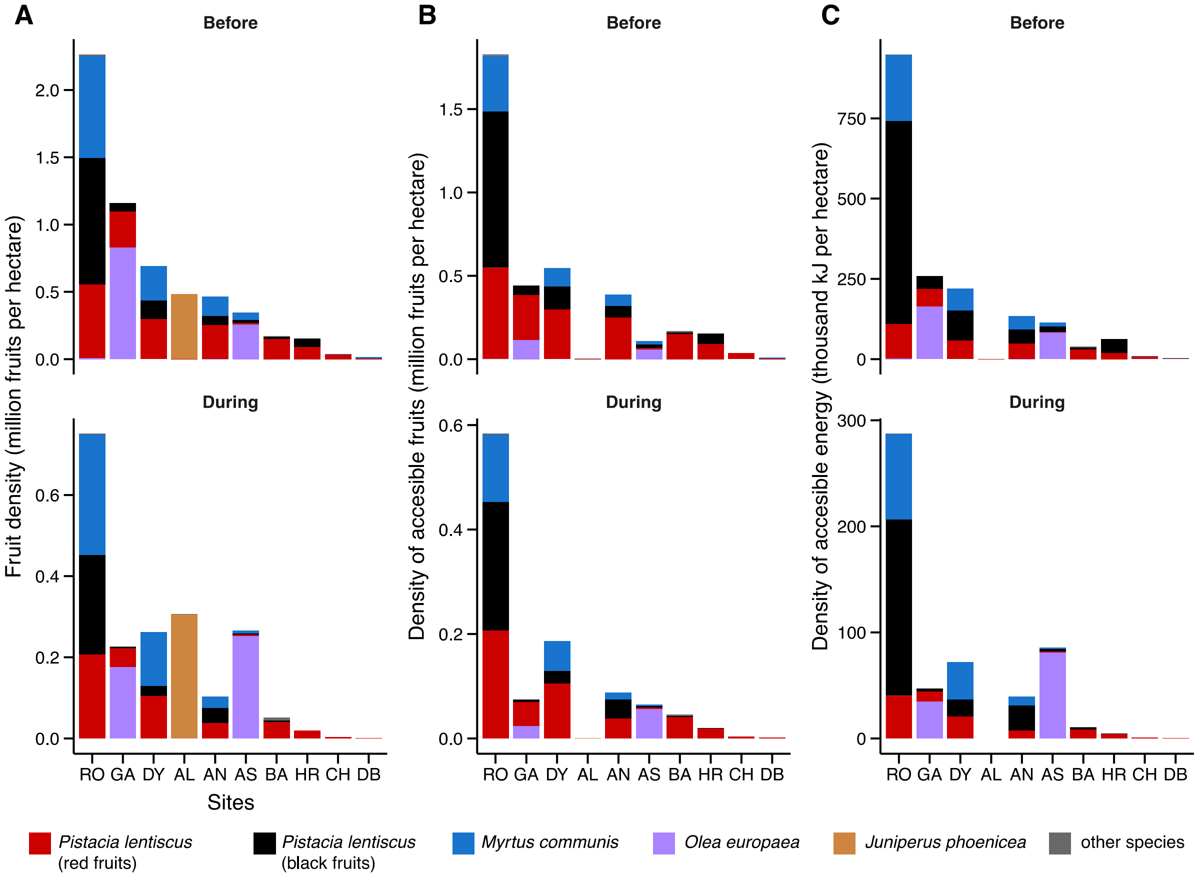


Figure 3. Frequency of fruits in droppings (i.e. frugivorous diet) in Sardinian warbler populations in response to three local fruit-resource variables ($\log_{10}$-transformed): (A) total fruit density (fruits/ha), considering all fruits; (B) density of accessible fruits (fruits/ha) after accounting for trait matching (i.e. fruits that can be swallowed by warblers); (C) density of accessible energy (kJ/ha) in fruits after accounting for trait matching. Large black circles denote population-level means, whereas small grey circles denote individual-level observations. R^2 values are $R^2_{\mathrm{GLMM}\ (m)}$ of the best-fit models, which also included time of day as a covariate in order to control for intra-day temporal differences among captured warblers (see Table 2).

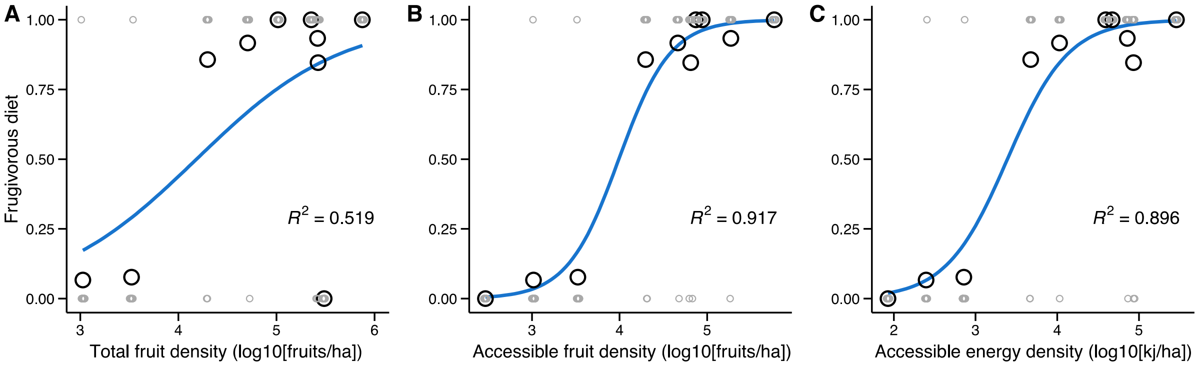
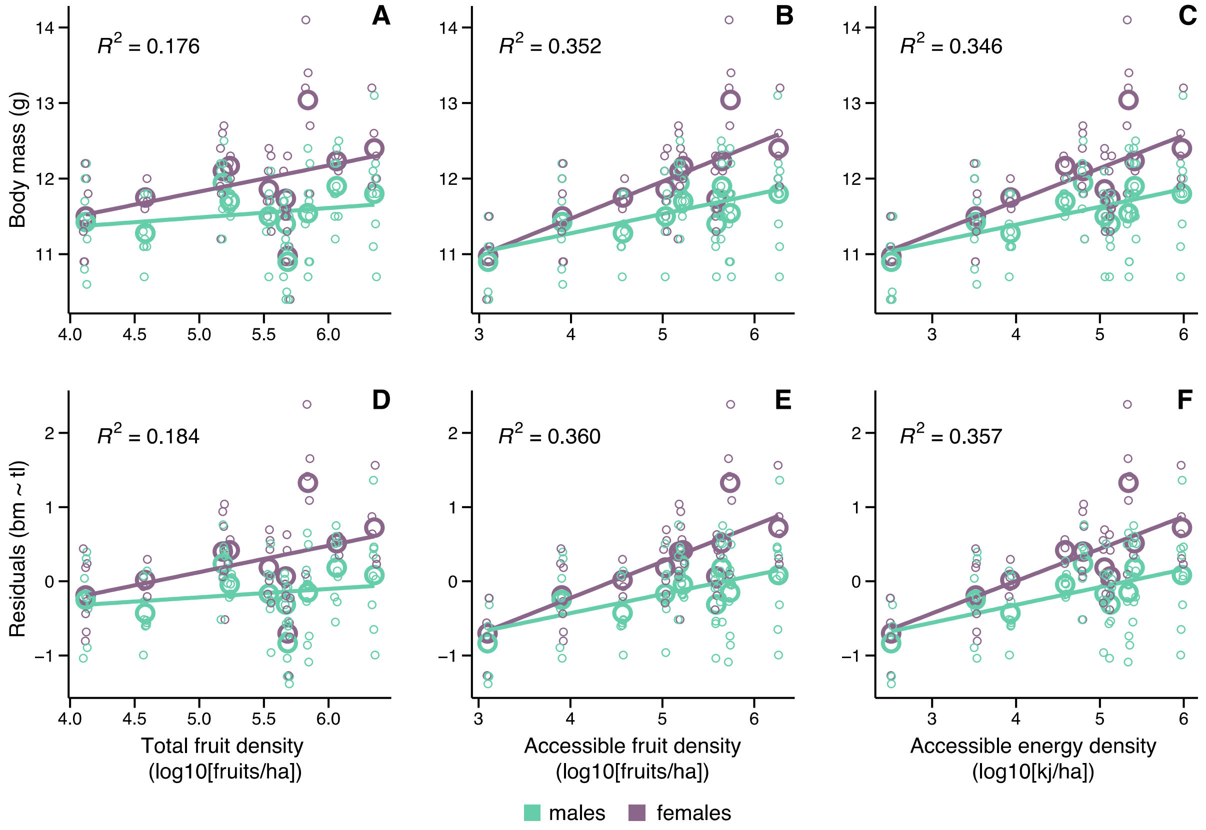


Figure 4. Body condition (body mass: upper panels; residual body mass: lower panels) of male and females Sardinian warblers in response to three local fruit-resource variables (log_{10}-transformed): (A, D) total fruit density (fruits/ha), considering all fruits. (B, E) density of accessible fruits (fruits/ha) after accounting for trait matching (i.e. fruits that can be swallowed by warblers). (C, F) density of accessible energy (kJ/ha) in fruits after accounting for trait matching. Large circles denote population-level means for males and females, whereas small circles denote individual-level observations. R^2 values are $R^2_{\mathrm{LMM}\,(m)}$ of the best-fit models including the interactive effect of fruit resources with warbler sex (see Table 3).



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Supplementary Material

Fruit abundance and trait matching determine diet type and body condition across frugivorous bird populations

Tables A1–A3

Figures A1–A10

Table A1. Location and physiognomic characteristics of the study sites, number of Sardinian warblers (*Curruca melanocephala*) captured by sex and age class (code 5: adults born in the previous calendar year; code 6: older birds; https://euring.org/data-and-codes/euring-codes), and number of samples for diet classification. Individual warblers and diet samples resulting from recaptures are shown within parentheses and brackets, respectively. Values within parentheses are not added to the sample size used for data analysis; e.g. 135 (4) denote 139 captures of 135 individuals (4 recaptures). In contrast, values within brackets are added to the sample sizes used for data analysis; e.g. 133 [2] denote 133 samples from 131 individuals [2 recaptures].

		Coordinates		Vegetation physiognomy				Warblers captured ($n_{\text{recapture}}$)					Diet samples
Site code	Site name	Long.	Lat.	Tree cover (%)	Tall shrub cover (%)	Low shrub cover (%)	Open ground cover (%)	Females (code 5)	Females (code 6)	Males (code 5)	Males (code 6)	Total	n [$n_{\text{recapture}}$]
AL	Algaida	–6.308	36.848	28.3	24.5	21.5	54.0	4	0	2	5	11	10
AN	Aznalcazar norte	-6.225	37.269	38.1	41.3	27.7	31.0	4	2	1	6	13	13
AS	Aznalcazar sur	–6.167	37.234	35.0	21.7	25.8	52.5	2	5 (1)	2	5	14 (1)	13 [1]
BA	Barbate	–5.980	36.202	51.2	19.4	15.0	65.6	0	3	0	9	12	12
CH	Chaparral	–6.284	37.243	14.4	12.9	36.7	50.4	0	4	3	6	13	13
DB	Dehesa Boyal	–6.306	37.224	22.1	22.5	34.4	43.1	2	5	1	7 (1)	15 (1)	15
DY	Dehesa Yeguas	–6.136	36.554	34.4	24.6	30.0	45.4	2	3	4	8	17	16
GA	Garrapilos	–5.949	36.659	29.0	42.5	12.3	45.2	1	2 (1)	5	5	13 (1)	13
HR	Hato Ratón	–6.337	37.171	21.0	25.2	29.8	45.0	1	5	3	4 (1)	13 (1)	14 [1]
RO	Roche	–6.141	36.335	34.6	42.9	14.4	42.7	2	3	3	6	14	14
	TOTALS	–	–	–	–	–	–	18	32 (2)	24	61 (2)	135 (4)	133 [2]

Table A2. Goodness-of-fit measures (AIC and $R^2_{\mathrm{GLMM}(m)}$) of generalized linear mixed models predicting frequency of fruit items in droppings of Sardinian warblers (*Curruca melanocephala*) in response to local fruit resources (‘Fruits’) during the mist-netting sessions; Total fruits: fruit density (fruits/ha) considering all fruits; Accessible fruits: density of accessible fruits (fruits/ha) after accounting for trait matching (i.e. fruits that can be swallowed by warblers); Accessible energy: density of accessible energy in fruits (kJ/ha) after accounting for trait matching. Colour-coded ‘■’ denote predictors included in the models. Models including the density of accessible fruits as fruit-resource variable showed the best fit, whereas models including the density of all fruits showed the worst fit. Models including ‘Bird sex’ or ‘Bird age class’ did not improve goodness-of-fit and these terms or their interactive effects with fruit resources had non-significant effects (95% CIs overlapped with zero). Time of day improved substantially all models (AIC values dropped > 10) and had significant effects, resulting in the lowest AIC value and the highest $R^2_{\mathrm{GLMM}\,(m)}$ (values shown in bold). Yet, the inclusion of other predictor variables, such as the sampling (Julian) day and variables accounting for the vegetation physiognomy of the study sites did not improve substantially model fit and all these variables had non-significant effects in the models.

	Predictors included in the models									Model fit	
Fruit-resource variable	Fruits	Bird sex	Bird age class	Julian day	Time of day	Tree cover	Tall shrub cover	Low shrub cover	Open ground cover	AIC	$R^2_{(m)}$
Total fruits	■	–	–	–	–	–	–	–	–	83.9	0.299
Total fruits	■	■	–	–	–	–	–	–	–	85.1	0.313
Total fruits	■	–	■	–	–	–	–	–	–	86.7	0.320
Total fruits	■	–	–	■	–	–	–	–	–	85.4	0.320
Total fruits	■	–	–	–	■	–	–	–	–	70.4	0.519
Total fruits	■	–	–	–	–	■	–	–	–	84.7	0.353
Total fruits	■	–	–	–	–	–	■	–	–	80.8	0.549
Total fruits	■	–	–	–	–	–	–	■	–	85.0	0.345
Total fruits	■	–	–	–	–	–	–	–	■	83.9	0.387
Accessible fruits	■	–	–	–	–	–	–	–	–	65.5	0.722
Accessible fruits	■	■	–	–	–	–	–	–	–	66.1	0.777
Accessible fruits	■	–	■	–	–	–	–	–	–	67.1	0.728
Accessible fruits	■	–	–	■	–	–	–	–	–	67.5	0.722
Accessible fruits	■	–	–	–	■	–	–	–	–	**48.7**	**0.917**
Accessible fruits	■	–	–	–	–	■	–	–	–	67.5	0.723
Accessible fruits	■	–	–	–	–	–	■	–	–	62.8	0.769
Accessible fruits	■	–	–	–	–	–	–	■	–	66.4	0.703
Accessible fruits	■	–	–	–	–	–	–	–	■	66.6	0.741
Accessible energy	■	–	–	–	–	–	–	–	–	69.9	0.656
Accessible energy	■	■	–	–	–	–	–	–	–	70.1	0.743
Accessible energy	■	–	■	–	–	–	–	–	–	72.9	0.675
Accessible energy	■	–	–	■	–	–	–	–	–	71.6	0.660
Accessible energy	■	–	–	–	■	–	–	–	–	52.9	0.896
Accessible energy	■	–	–	–	–	■	–	–	–	71.6	0.649
Accessible energy	■	–	–	–	–	–	■	–	–	68.1	0.740
Accessible energy	■	–	–	–	–	–	–	■	–	70.4	0.666
Accessible energy	■	–	–	–	–	–	–	–	■	71.6	0.664

Table A3. Goodness-of-fit measures (AIC and $R^2_{\mathrm{LMM}(m)}$) of linear mixed models predicting the body condition (body mass and residuals from regression 'body mass ~ tarsus length') of Sardinian warblers (*Curruca melanocephala*) in response to local fruit resources ('Fruits'). We tested three variable types quantifying fruit resources, which were sampled in two surveys: one conducted one month before (January 2019) and the other during the mist-netting sessions for measuring body condition (February 2019); TF: total fruit density (fruits/ha) considering all fruits; AF: density of accessible fruits (fruits/ha) after accounting for trait matching (i.e. fruits that can be swallowed by warblers); AED: density of accessible energy in fruits (kJ/ha) after accounting for trait matching. Colour-coded '■' denote predictors included in the models. Models including the fruit-resource variables from the 'before' sampling survey had a better fit than models including the 'during' sampling survey. Models including the 'Fruits × Bird sex' interaction improved substantially fit compared with models including only 'Fruits' (AIC values dropped > 20). Yet, the inclusion of other predictor variables did not improve model fit. Moreover, all these variables had non-significant effects in the models, in contrast to the significant effects of 'Fruits' and 'Fruits × Bird sex' (see Table 2). For simplicity, we omit the models with these other variables in models that included TF as fruit-resource variable, which had a much worse fit than models that included fruit-resource variables models accounting for trait matching (i.e. AF or AE as predictors). The lowest AIC values and the corresponding $R^2_{\mathrm{LMM}\,(m)}$ are shown in bold.

Type of fruit-resource variable and survey		Predictors included in the models									Response variable (model fit)			
											Body mass		Res. (bm ~ tl)	
Variable	Survey	Fruits	Bird sex	Bird age class	Julian day	Time of day	Tree cover	Tall shrub cover	Low shrub cover	Open ground cover	AIC	$R^2_{(m)}$	AIC	$R^2_{(m)}$
TF	Before	■	–	–	–	–	–	–	–	–	243.2	0.044	241.7	0.043
TF	Before	■	■	–	–	–	–	–	–	–	222.1	0.176	218.8	0.184
TF	During	■	–	–	–	–	–	–	–	–	244.2	0.019	242.7	0.019
TF	During	■	■	–	–	–	–	–	–	–	223.4	0.150	220.1	0.158
AF	Before	■	–	–	–	–	–	–	–	–	229.8	0.209	228.3	0.209
AF	**Before**	■	■	–	–	–	–	–	–	–	**206.9**	**0.352**	**203.9**	**0.360**
AF	Before	■	■	■	–	–	–	–	–	–				
AF	Before	■	■	–	■	–	–	–	–	–	207.7	0.358	204.9	0.364
AF	Before	■	■	–	–	■	–	–	–	–	208.5	0.354	205.6	0.362
AF	Before	■	■	–	–	–	■	–	–	–	208.5	0.354	205.4	0.363
AF	Before	■	■	–	–	–	–	■	–	–	207.8	0.358	204.8	0.365
AF	Before	■	■	–	–	–	–	–	■	–	208.8	0.353	205.8	0.360
AF	Before	■	■	–	–	–	–	–	–	■	207.0	0.362	204.5	0.367
AF	During	■	–	–	–	–	–	–	–	–	232.6	0.191	230.9	0.194
AF	During	■	■	–	–	–	–	–	–	–	209.2	0.336	205.9	0.346
AF	During	■	■	■	–	–	–	–	–	–	210.9	0.338	207.7	0.347
AF	During	■	■	–	■	–	–	–	–	–	210.1	0.342	207.0	0.350
AF	During	■	■	–	–	■	–	–	–	–	210.6	0.340	207.5	0.348
AF	During	■	■	–	–	–	■	–	–	–	210.0	0.346	206.4	0.357
AF	During	■	■	–	–	–	–	■	–	–	210.8	0.339	207.6	0.349
AF	During	■	■	–	–	–	–	–	■	–	211.2	0.336	207.9	0.346
AF	During	■	■	–	–	–	–	–	–	■	210.7	0.339	207.6	0.347
AE	Before	■	–	–	–	–	–	–	–	–	229.4	0.210	227.3	0.215
AE	Before	■	■	–	–	–	–	–	–	–	208.3	0.346	204.8	0.356
AE	Before	■	■	■	–	–	–	–	–	–	210.0	0.347	206.5	0.358
AE	Before	■	■	–	■	–	–	–	–	–	208.4	0.355	205.2	0.364
AE	Before	■	■	–	–	■	–	–	–	–	209.8	0.349	206.3	0.359
AE	Before	■	■	–	–	–	■	–	–	–	210.1	0.346	206.5	0.358
AE	Before	■	■	–	–	–	–	■	–	–	209.2	0.352	205.5	0.363
AE	Before	■	■	–	–	–	–	–	■	–	210.2	0.346	206.5	0.357
AE	Before	■	■	–	–	–	–	–	–	■	208.4	0.356	205.3	0.364
AE	During	■	–	–	–	–	–	–	–	–	235.2	0.169	233.2	0.174
AE	During	■	■	–	–	–	–	–	–	–	213.1	0.306	209.7	0.318
AE	During	■	■	■	–	–	–	–	–	–	214.6	0.309	211.3	0.320
AE	During	■	■	–	■	–	–	–	–	–	213.6	0.316	210.4	0.325
AE	During	■	■	–	–	■	–	–	–	–	214.0	0.313	210.9	0.323
AE	During	■	■	–	–	–	■	–	–	–	214.5	0.312	211.0	0.326
AE	During	■	■	–	–	–	–	■	–	–	214.9	0.308	211.6	0.320
AE	During	■	■	–	–	–	–	–	■	–	215.0	0.306	211.7	0.318
AE	During	■	■	–	–	–	–	–	–	■	214.8	0.309	211.6	0.319

Figure A1. (Top-left) Map of the Guadalquivir Valley (south-west Spain) with the location of the study sites (red circles). The unshaded area represents lowland areas (below 200 m in altitude), where the remaining woodland patches are shown in black; higher elevations and legally protected areas are shown in light and dark grey, respectively (the largest protected areas are labelled). (Bottom-left) Photograph showing the typical vegetation structure of the study forests. (Right) Scheme of one of the fixed transects (10 m wide × 30 m long) used to quantify fruit abundance (*n* = 8 transects per site), showing in grey the three rectangles (5 m wide × 10 m long) chessboard distributed where we estimated the cover of different vegetation elements (trees, tall shrubs, low shrubs and open ground areas).

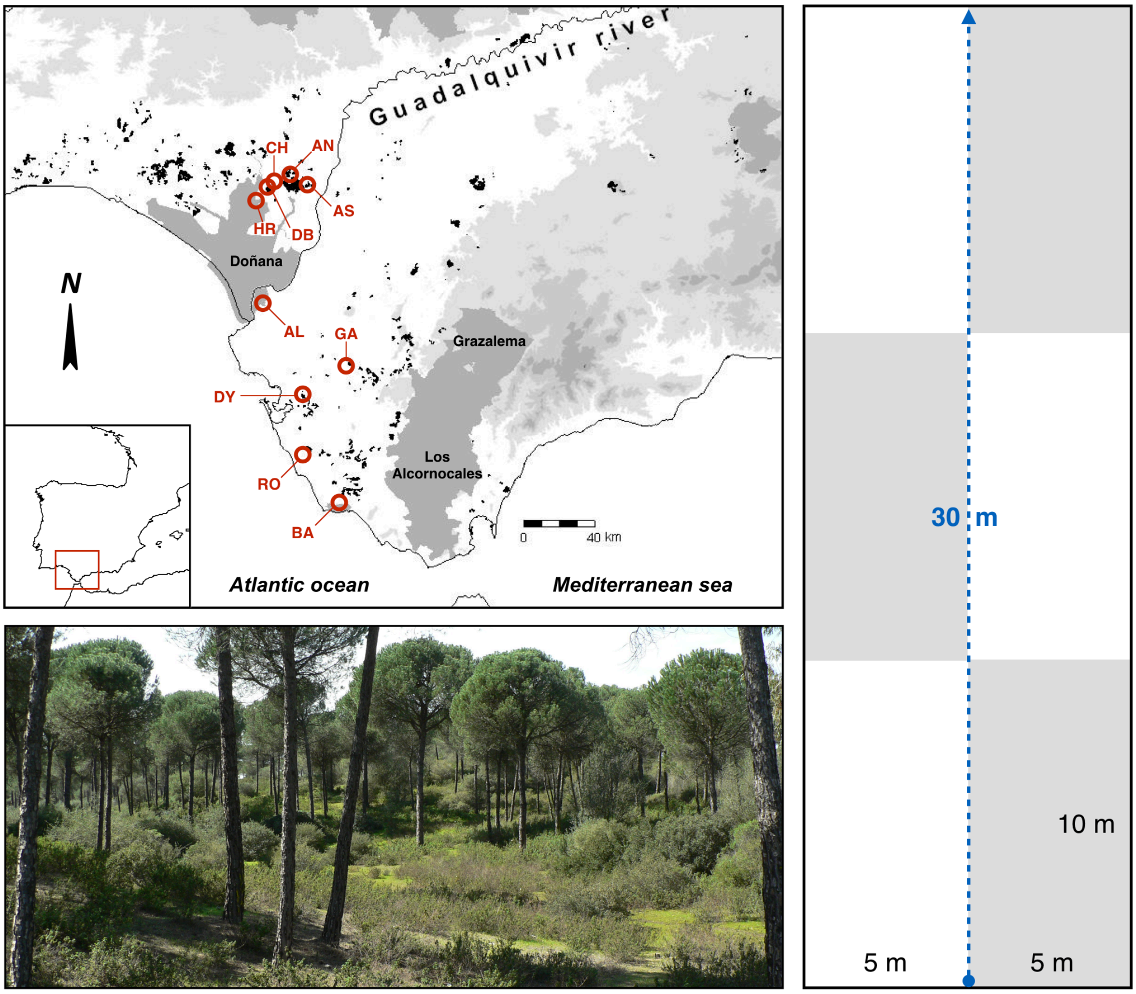


Figure A2. Photographs showing (A, B) measuring tape along fixed transects where we quantified fruit abundance and fruits of the most abundant fleshy-fruited species: (C) *Pistacia lentiscus* with black and red fruits, (D) *Myrtus communis*, (E) *Olea europaea* var. *sylvestris* and (F) *Juniperus phoenicea*.

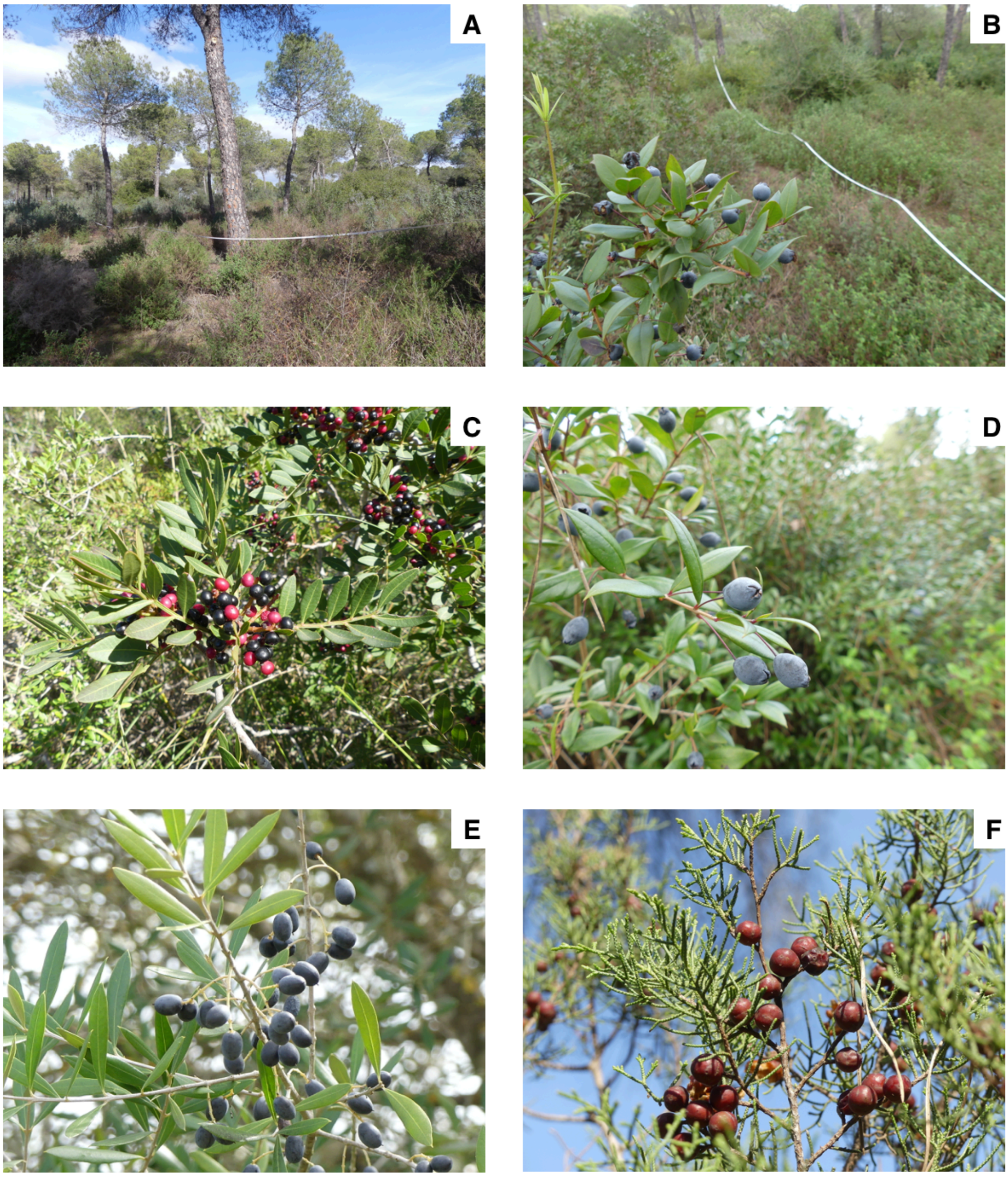


Figure A3. Photographs showing (A, B) mist nets placed between tall shrubs; (C) male and (D) female Sardinian warblers (*Curruca melanocephala*); (E) warbler dropping with fruit remains (note the pulp colour and a *Pistacia lentiscus* seed in the dropping; classified for analyses as 'fruits'); and (F) warbler dropping without fruit remains (note a beetle elytron; classified for analyses as 'no fruits').

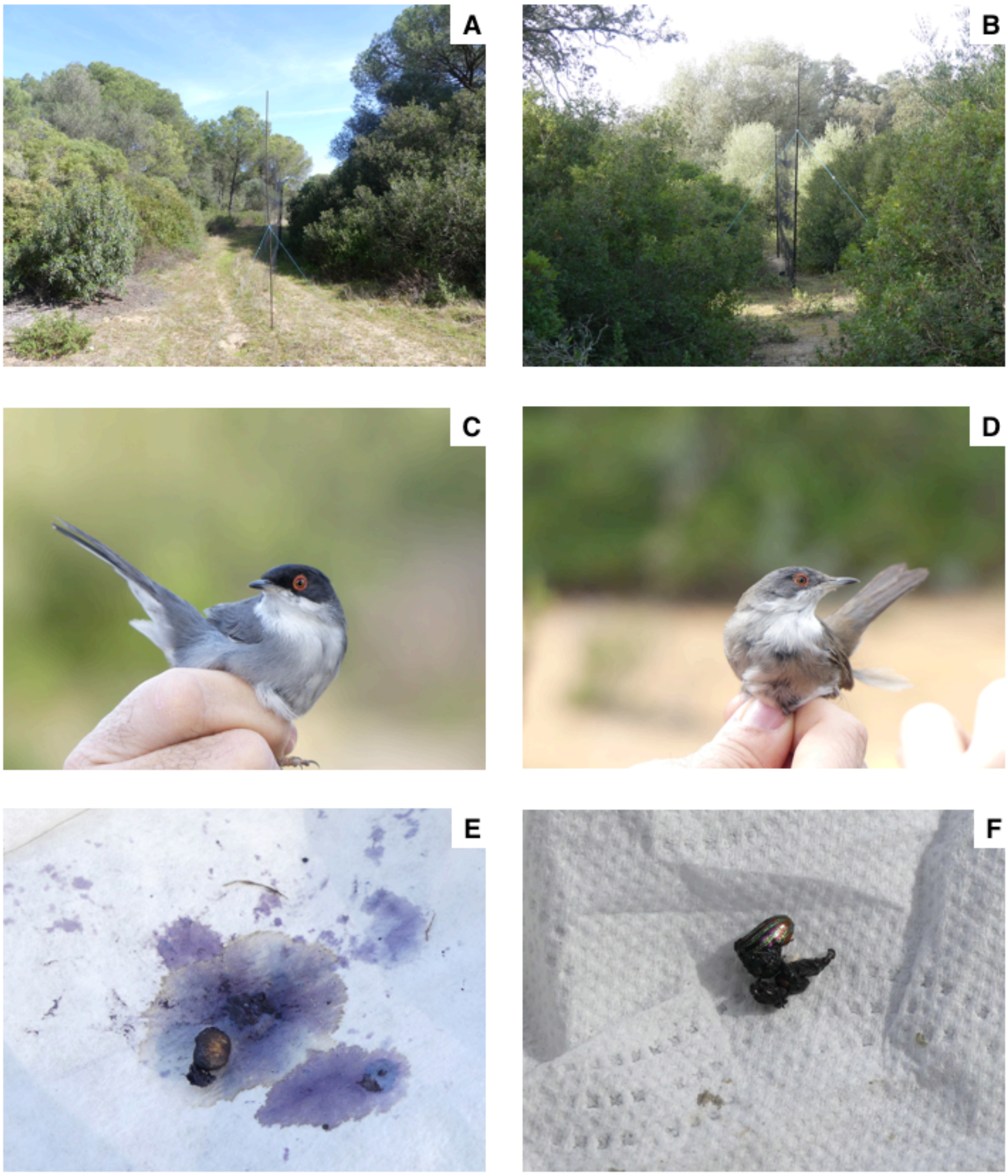


Figure A4. Histograms showing observed distributions in fruit diameter of plant species *i* at each site *j* (see site codes in Table A1 and Fig. A1) along with their normal probability density functions, parameterised with mean_{ij} and sd_{ij}. The vertical dashed line denotes the mean gape width (6.6 mm; González-Varo and Traveset 2016 Trends Ecol. Evol. 31: 700–710) of the Sardinian warbler (*Curruca melanocephala*). Bold numbers are P_{ij} values, that is, the cumulative probability in fruit diameter under the mean gape width, representing the proportion of fruits that can be swallowed by warblers (i.e. accessible fruits) of each species *i* at each site *j*. $Mean_{ij} \pm sd_{ij}$ are shown under P_{ij} values. Numbers in parentheses denote the number of fruits measured per 'species–site' combination.

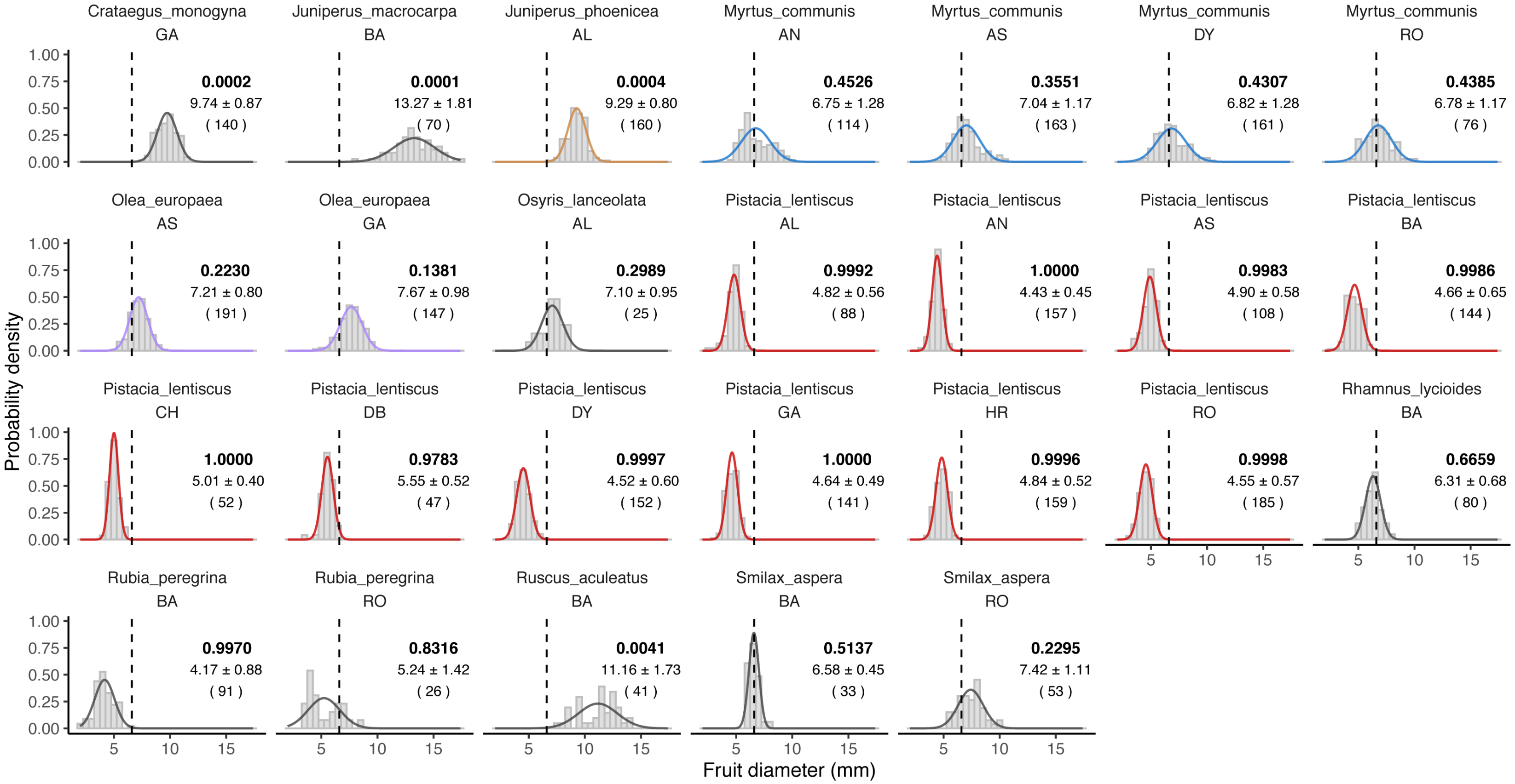


Figure A5. (A) Examples of normal probability density functions fitted to the diameter of two fleshy-fruited species *i* with small- (left panel) and large-sized (right panel) fruits at a site *j*, showing the estimated proportion of fruits (P_{ij}: the sum of both shaded areas) with diameter smaller than the mean gape width (*g*) of the Sardinian warbler (*Curruca melanocephala*) and the estimated median diameter (m_{ij}) of those fruits smaller than *g* (i.e. the diameter value for $P_{ij} \times 0.5$). (B) Relationship between estimated P_{ij} values and the observed proportion of fruits with diameter smaller than the mean gape of the Sardinian warbler (Pearson's $r = 0.997$, $P < 10^{-15}$, $n = 26$). (C) Relationship between estimated m_{ij} values and the observed mean diameter of fruits with diameter smaller than the mean gape of the Sardinian warbler (Pearson's $r = 0.989$, $P < 10^{-15}$, $n = 22$). In (B) and (C) the red line represents the $y = x$ relationship, whereas the blue line denotes a least-squares regression line (the CI 95% of both estimates overlap with 1). These results indicate that estimates (P_{ij} and m_{ij}) from empirically parameterized normal probability density functions (see Fig. A4) are an excellent proxy of proportions and central tendency measures of real data. Obtaining P_{ij} and m_{ij} from normal probability density functions has two major advantages. First, this approach allows estimating very small P_{ij} values for species with large fruits (<< 0.01), where the observed proportions of fruits with a diameter smaller than *g* can lead to zero due to small sample size (e.g. *Crataegus monogyna*, *Juniperus macrocarpa*, *J. phoenicea* and *Ruscus aculeatus* in Fig. A4). Second, this approach allows obtaining a central tendency measure for the diameter fruits smaller than *g* when none of the measured fruits were smaller than *g*, as occurred for the species mentioned before (Fig. A4).

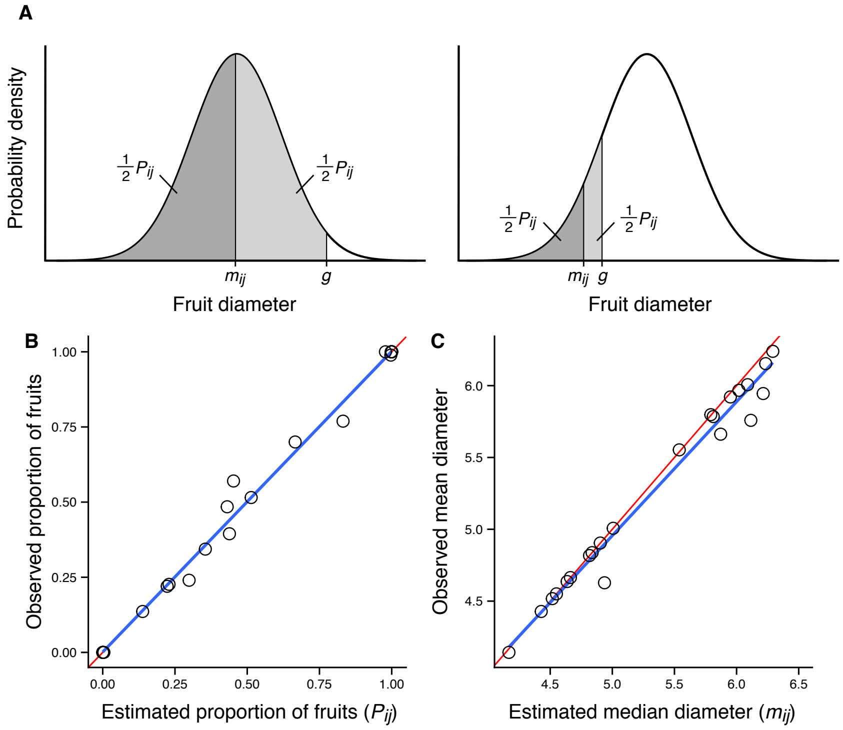
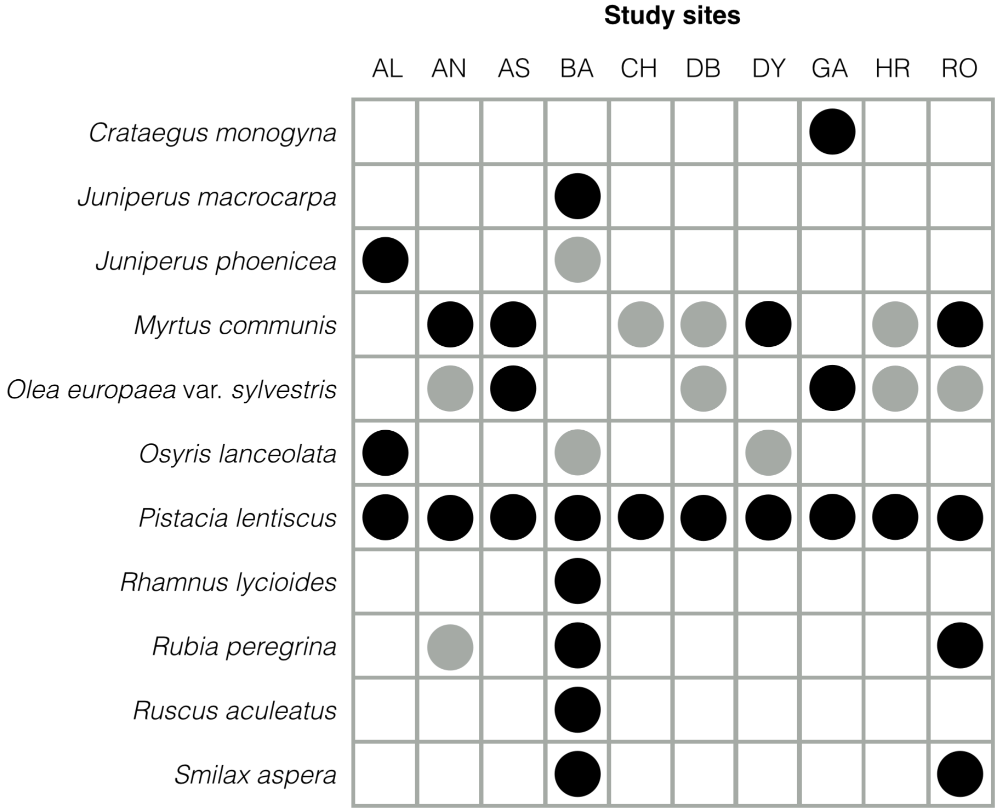


Figure A6. Matrix showing the fleshy-fruited species recorded in the sampling transects at each study site. Black circles denote 'species-site' combinations for which we obtained fruit diameter data; these were in general the most abundant fruits per site. Grey circles denote combinations of species (*i*) and sites (*j*) for which we performed data imputation by using the species-level mean of $mean_{ij}$ and sd_{ij} in fruit diameter across sites. For example, we used the means of $mean_{ij}$ and sd_{ij} of *Myrtus communis* across AN, AS, DY and RO to parameterize diameter distribution of *M. communis* at CH, DB and HR. For *Juniperus phoenicea* and *Osyris lanceolata*, because we only obtained fruit diameter data from one site, we directly imputed its $mean_{ij}$ and sd_{ij} to sites with missing data.



Study sites

	AL	AN	AS	BA	CH	DB	DY	GA	HR	RO
Crataegus monogyna								●		
Juniperus macrocarpa				●						
Juniperus phoenicea	●			○						
Myrtus communis		●	●		○	○	●		○	●
Olea europaea var. *sylvestris*		○	●			○		●	○	○
Osyris lanceolata	●			○			○			
Pistacia lentiscus	●	●	●	●	●	●	●	●	●	●
Rhamnus lycioides				●						
Rubia peregrina		○		●						●
Ruscus aculeatus				●						
Smilax aspera				●						●

Figure A7. Total number of seeds of different fruit species found in droppings of mist-netted Sardinian warblers (*Curruca melanocephala*) at each study site; no seed was found at AL. We found a total of 100 seeds from 64 droppings: 92 seeds of *P. lentiscus* across eight sites, five seeds of *M. communis* across four sites and three seeds of *O. europea* var. *sylvestris* at one site.

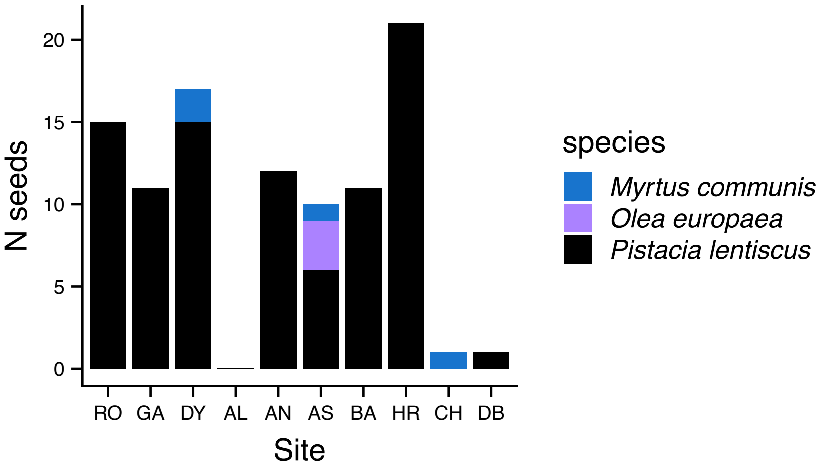


Figure A8. Spatial correlograms for the (A) density of accessible fruits when we measured body condition (predictor variable); (B) frequency of fruits in Sardinian warbler droppings (response variable); and (C) residuals of the model predicting the frequency of fruits in droppings with the density of accessible fruits as predictor. Dashed grey lines denoted intervals of Moran's *I* values = [–0.05, 0.05], that is, a negligible magnitude of spatial autocorrelation (i.e. analogous to Pearson's *r* ≤ |0.05| in collinearity analysis). The correlograms show that the predictor variable included in the model accounted for most existing spatially structured variability in frequency of fruits in diet.

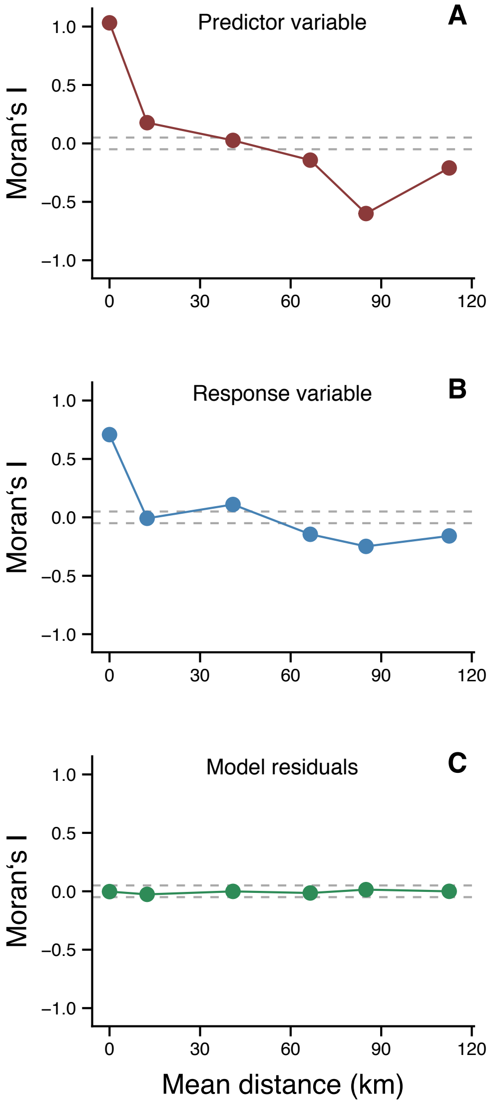


Figure A9. Spatial correlograms for the (A) density of accessible fruits one month before measuring body condition (predictor variable); (B) body mass of Sardinian warblers (response variable); (C) size-independent residual body mass (residuals of the regression 'body mass ~ tarsus length'; response variable); (D) residuals of the best model predicting body mass; and (E) residuals of the best model predicting size-independent residual body mass. The best models were the ones with lowest AIC values, which included density of accessible fruits, bird sex and their interactive effects (see Table 2). Dashed grey lines denoted intervals of Moran's *I* values = [–0.05, 0.05], that is, a negligible magnitude of spatial autocorrelation (i.e. analogous to Pearson's *r* ≤ |0.05| in collinearity analysis). The correlograms show that the predictor variables included in both models accounted for most existing spatially structured variability in body condition.

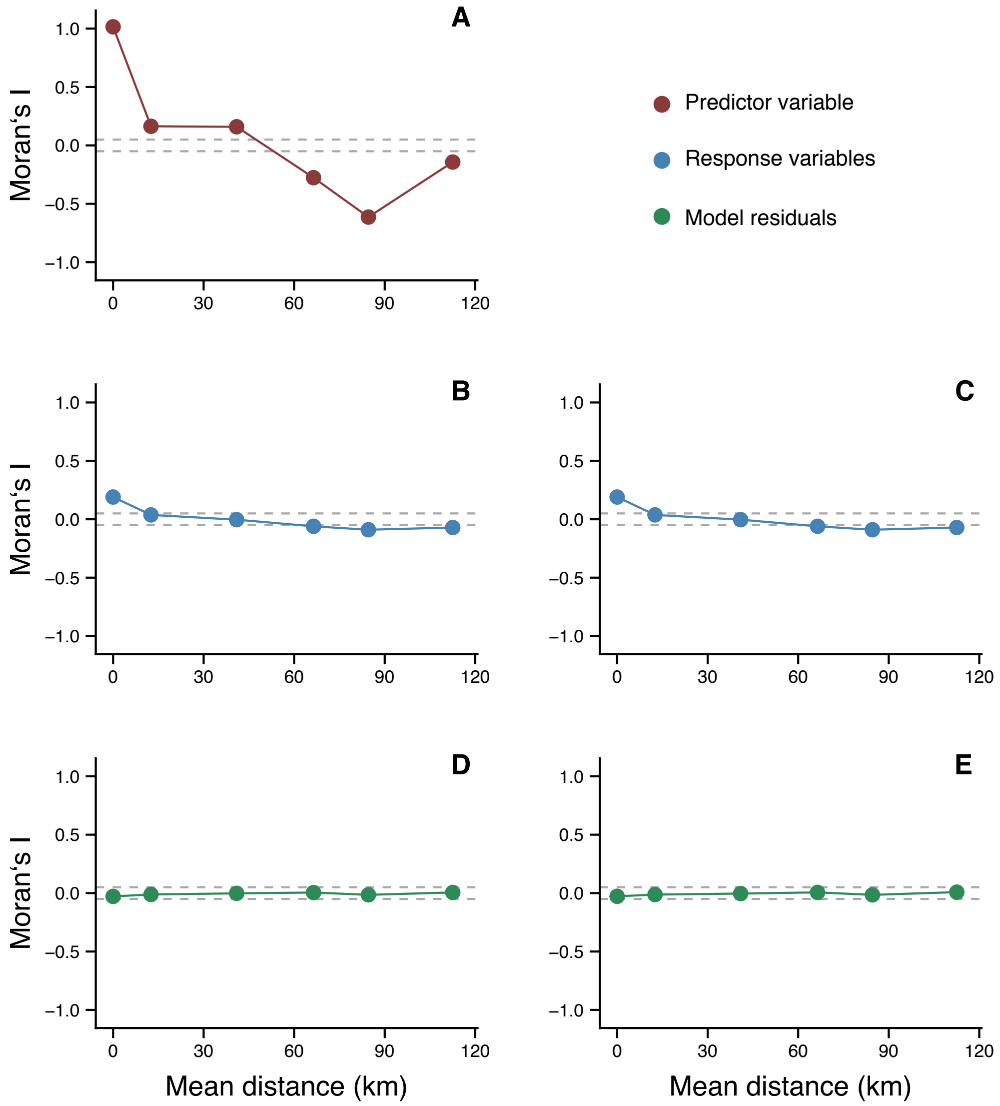


Figure A10. (A) Frequency of fruits droppings diet and (B) body mass of Sardinian warbler (*Curruca melanocephala*) in response to the density of accessible fruits (fruits/ha) after accounting for trait matching. Panels (A) and (B) contain the same data shown in Fig. 3B and Fig. 4B, respectively, but with the *x* axis here is in linear scale ($\log_{10}$ scale in Fig. 3 and Fig 4). In both panels, large circles denote population-level means, whereas small circles denote individual-level observations. Vertical, red dashed lines simply denote reference value within the threshold response to the density of accessible fruits.