

## Seed predation on the ground or in the tree? Size-related differences in behavior and ecology of granivorous birds

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Perea R., Venturas M., Gil L. 2014. Seed predation on the ground or in the tree? Size-related differences in behavior and ecology of granivorous birds. *Acta Ornithol.* 49: 119–130. DOI 10.3161/000164514X682940

**Abstract.** Seed-eating birds may consume seeds in the tree (pre-dispersal predation) as well as on the ground (post-dispersal predation), usually at contrasting microhabitat conditions. We examined the foraging behaviour and contribution to seed predation of a whole assemblage of seed-eating birds (mostly Fringillidae) at both dispersal phases (pre- and post-dispersal) in a wind-dispersed tree, the European White Elm *Ulmus laevis*. We found that most seed predators were tree-feeding birds that prey upon seeds for longer periods in the tree and spend shorter periods in larger flocks foraging on the ground. We also obtained significant differences in predation speed among the seed predator species. The overall number of seeds consumed by birds, as well as the amount of time spent foraging in the tree, increased with increasing feeding heights. Seed availability increases with height, which seems to be the main reason why birds spend more time foraging on higher branches. Birds strongly differed in their perching coefficient (PC, ratio of feeding height to distance from crown edge). Small finches such as *Serinus Serinus serinus* and Goldfinches *Carduelis carduelis* had a very high value of PC in comparison to large finches such as Greenfinches *Carduelis chloris*, Chaffinches *Fringilla coelebs*, and Hawfinches *Coccothraustes coccothraustes*. In general, finches showed much higher values of PC than non-fringillid species, indicating a greater adaptation to perch and feed on more flexible stems. Birds increased their overall seed predation and the time allocated to foraging on the ground when they were in flocks. Small finches tended to follow larger finches and flock in multispecies groups when foraging on the ground. We suggest that this behaviour increases both feeding efficiency and safety. Further studies should take into account possible differences in behavior of seed-eating birds throughout the dispersal season since it may have important implications for their adaptive behavior to select new niches.

**Key words:** feeding height, flocking, foraging behaviour, Fringillidae, predation risk, granivorous bird, seed density

Received — April 2013, accepted — June 2014

### INTRODUCTION

Seed predation (i.e., granivory) is a type of plant-animal interaction in which the granivores feed mostly on the seeds of plants (Hulme & Benkman 2002). Among granivores, finches Fringillidae and other seed-eating birds are considered an important guild of seed predators (Wilson 1971, Benkman 1991, Stiles 2000). Most studies on avian seed predation have focused either on pre-dispersal seed predation (in the plant) or, more rarely, on the post-dispersal seed phase (on the ground) (but see Schluter & Repasky 1991 and references therein for ground finches). Although foraging behaviour of seed-eating birds has been extensively studied in multiple ways and from different perspectives, for instance, seed selection (Kear 1962, Getty & Pulliam 1993, Nystrand & Granström

1997), predation risk (Lindström 1990, Krams 2001, Lind & Cresswell 2005, Baker et al. 2010), habitat use (Díaz & Tellería 1994, Robinson et al. 2004, Garcia-del-Rey et al. 2009), foraging strategy (Newton 1967, Coolen et al. 2001, Baker et al. 2009, Myczko & Benkman 2011) and flock size (Newton 1967, Lindström 1989, Tellería et al. 2001), studies have neglected to compare the foraging behaviour of avian seed predators at both dispersal phases (pre and post-dispersal), despite the existence of multiple environmental differences between these phases (e.g., vegetation cover, visibility, seed density, alternative food, etc.; Janzen 1971). In addition, species-specific differences in the foraging behaviour above-ground and on the ground (after seed dispersal) are likely to occur (e.g., frequency of visits, predation speed, flock size and composition).

It is well known that seed predators must balance food acquisition and safety, usually by reducing their foraging activity under higher levels of predation risk (Lima & Dill 1990). In addition, optimal foraging theory states that birds should forage in a way to maximize their net energy intake (Stephens et al. 2007). However, seeds may not be homogeneously distributed all over the plant. Thus, seed availability within the tree can exert an important source of variation when analysing the foraging patterns of seed predator assemblages. It has also been suggested that birds perceive less predation risk at higher positions in the tree (Knight & Fitzner 1985, Datta & Pal 1993, Krams 2001) and, thus, they could be sensitive to their location in the tree. Additionally, some seed-eating birds increase their activity (e.g. singing rates) from the trunk to the outer part of the crown. Therefore, interspecific differences while foraging in the tree have been strongly based upon the different levels of predation risk within the tree crown (Suhonen 1993, Suhonen et al. 1993), concluding that foraging in the inner parts of the tree is safer, at least for tits (*Parus* sp.). We, then, expect birds to offset lower feeding heights (riskier positions) by inner perching locations to increase safety while foraging for seeds. However, few studies have combined the simultaneous effect of perching location and seed availability in order to distinguish between predator avoidance and resource tracking hypotheses (García et al. 2011). In fact, seed availability might strongly affect not only the perching location of birds but also the speed and the time allocated to seed consumption.

Importantly, many seed-eating birds tend to flock when foraging for seeds (Pulliam 1973, Pearson 1989, Benkman 1997, Baker 2010). Flocking is also considered an efficient strategy to reduce predation risk (Pulliam 1973, Thompson & Barnard 1984, Krebs & Davies 1993, Roberts 1996, Tellería et al. 2001). Nevertheless, it is far from clear whether flocking tendency and the foraging behaviour of granivores (seed intake and time allocated to consume seeds) may shift from the pre-dispersal phase to the post-dispersal phase. Additionally, very little is known about possible differences in flock species composition between both dispersal phases despite many seed-eating birds are also known to form multi-species flocks (Rubenstein et al. 1977).

In this study, we, first, evaluate seed predation in relation to bird density to know the relative contribution of each bird species to seed predation

and, then, examine the foraging behaviour (perching location, seed predation speed and flock characteristics) of a whole assemblage of seed-eating birds (mostly finches; Fringillidae) in a wind-dispersed tree, the European White Elm *Ulmus laevis* (pre-dispersal behaviour). Additionally, we also assess seed availability at different tree heights to disentangle the number of seeds consumed and the time allocated to seed predation at different positions in the tree crown. Finally we test whether post-dispersal seed predation differs from that in the tree and among the studied bird species. By integrating the whole assemblage of seed-eating birds we attempt to improve our understanding of the ecological factors involved in the interactive process of birds and seeds. We also analyse the contribution of each species to both pre- and post-dispersal seed predation, and their possible behavioural differences (intra- and inter-specific) when foraging for seeds in different parts of the tree, including beneath the tree canopy (on the ground).

## MATERIAL AND METHODS

### Study area and species

This study was conducted in a riparian forest in Madrid province, Central Spain (40°32'N, 3°40'W). The riparian forest is located within a 330 ha public domain forest, at 700 m above sea level and in a Mediterranean climate (annual precipitation of  $426 \pm 124$  mm in years 1973–2011, with a 3-month summer dry period). The riparian forest is composed mostly of European White Elms and very few ashes *Fraxinus angustifolia* and willows *Salix salviifolia* and *S. atrocinerea*, comprising an area of, approximately, 32 ha. The understory is a mosaic of evergreen shrubs, mainly Elmleaf Blackberries *Rubus ulmifolius*, tall forbs and grasses. There are 53 mature elms (diameter at breast height, d.b.h. > 10 cm) and 104 saplings spread along a small stream.

*Ulmus laevis* is mainly found in Central and Eastern Europe. In the southernmost part of its distribution (Spain) the populations are small and rare (Venturas et al. 2013). Like other elm species, *U. laevis* flowers before flushing and fruits are winged nuts (samaras) with a single seed. Natural seed fall of *U. laevis* occurs in April–June (Perea et al. 2013). Elm seeds of other European *Ulmus* (e.g. *U. minor*) are subject to post-dispersal seed predation by vertebrates (mainly rodents; Hulme & Borelli 1999). However, pre-dispersal seed

predation in elm trees has not been quantified and, thus, a variety of unknown guilds of avian seed predators may be involved (Hulme 1993). The crown of *U. laevis* is broad with a regular and sub-quadrangular shape and elm seeds are mostly located at the outer part of the branches (Navarro & Castroviejo 1993).

European finches Fringillidae are diurnal perching birds that feed mostly on seeds but also on invertebrates, especially during the breeding season (Newton 1967, Wilson et al. 1999). Many finch species frequently feed on the ground and some are even considered by some authors as ground-feeding species (e.g. Chaffinches *Fringilla coelebs*; Nystrand & Granström 1997). Six species of finches, which strongly differed in body size, were found in the study area — Hawfinch *Coccothraustes coccothraustes* (58 g), Greenfinch *Carduelis chloris* (28 g), Chaffinch *Fringilla coelebs* (24 g), Common Linnet *Carduelis cannabina* (19 g), Goldfinch *Carduelis carduelis* (17 g) and Serin *Serinus serinus* (13 g) (body masses according to Cramp & Perrins 1994).

#### Foraging behaviour in the tree

We selected three observatories within the study area. Observatories were separated at least 90 m from each other. From each observatory we could see 7–12 trees (distance of bird observation varied from 5 to 60 m, approximately). Observations were mostly performed in the mornings (8.00–10.30 a.m.) and evenings (5.30–8.00 p.m.), and always during the fruit ripening season (April–June 2010 and 2011). We spent, approximately, a total of 4360 minutes (2 years × 6 weeks × ~360 minutes/week) of field observation, of which 1602 were considered real observation of the foraging behaviour of birds up in the elm trees. We used binoculars (8 × 42), spotting scopes (20–60 × 65) and stopwatches to estimate the number of elm seeds each bird preyed and the time allocated to consume the seeds (i.e., time spent since the first seed was consumed until the bird flew away or stopped eating). Most consumed seeds were easily counted by observing the empty samaras falling from the beak. Thus, we obtained a parameter called predation speed (number of seeds consumed/time spent foraging, measured in seeds/min). We also noted the approximate branch height (m from ground level) at which the bird was feeding (hereafter feeding height) and the approximate distance (cm) from the crown edge (horizontal distance). Feeding height was estimated on the basis of previous tree height measures,

performed with a hypsometer (Vertex III, Haglöf, Sweden) with an average height of mature trees of mean ± SD = 13.0 ± 0.7 m (Venturas et al. 2014). Then, we calculated a new adimensional parameter called “perching coefficient” as the ratio of feeding height (cm) to the distance to crown edge (cm) to test the hypothesis that lower height would be compensated by inner locations in the tree while consuming seeds. When birds came in single-species flocks we noted the number of individuals per flock but observations were made only on one of these individuals, the easiest to observe. For multi-species flocks we recorded the abundance (number of individuals) of each species within the flock so that we could calculate the relative frequency (flock tendency) of each bird species to form multi and single species flocks. Observations of foraging behavior when more than one individual were feeding simultaneously (either the same species or different) were made only on one individual, the easiest to observe.

#### Foraging behaviour on the ground

In order to identify the avian seed predators, four motion-detection digital video cameras were used (Leaf River IR-5, 5 MP). We used cameras instead of direct observations because vegetation cover (tall forbs, shrubs and tall grasses) prevented us from watching the animals on the ground. Cameras were attached to elm trunks, at 1.5 m high and at, approximately 3–5 m from the center of the detection zone (in microhabitats covered only by grasses). Thus, we ensured that cameras always had similar detection zones, lower than 10–15 m<sup>2</sup> so that we could easily identify the birds and observe clearly their foraging behaviour. To avoid possible pseudoreplication, the cameras were moved among 16 different trees (distance > 50 m) every 35–60 days, and were used in April–June, coinciding with the elm seed ripening and dispersal period, in two consecutive years (2010 and 2011). We only considered those recordings that contained animals consuming elm seeds (N = 241 recordings; 181 minutes). From each video recording we identified the seed predator (bird species) and counted the individuals consuming seeds. We also obtained the predation speed of each individual (seeds/min), flock size and species composition of the flock (multi-specific flocks).

#### Bird density estimations

To address the contribution of each bird species to seed predation we estimated the density of each

bird species through a permanent linear transect in the riparian forest (470 m in length and approximately 50 m in width). Surveys were performed weekly during the seed ripening period (from late April to early June; total of 6 surveys per spring) in two consecutive years (2010 and 2011). Bird census started at approximately 8.30–9.00 am and we attempted to avoid heavy rain, poor visibility or strong wind conditions. We recorded all the birds we saw and heard following the bird survey instructions (Bibby et al. 1992).

### Seed availability in the tree

We collected a total of 15 fertile branches of similar size in five elm trees and at three different heights: low branches (2–3 m above the ground level), medium height (4–6 m) and high branches (8–11 m). We, then, counted the number of infructescences per branch and the number of seeds per infructescence. All seeds, within a tree, were collected from branches facing the same direction. We estimated the seed availability for each height by multiplying the seed density of the sampled branch by the number of fertile branches at each height and for the selected direction.

### Data analysis

We used t-tests to compare behavioural parameters (foraging time, flock size and predation speed) and  $\chi^2$ -tests (predation contribution) of each bird species in the tree vs. on the ground. To analyse the importance of each variable (feeding height, distance to crown edge and perching coefficient) on the predation speed and total number of seeds predated (response variables) we used Generalized Linear Mixed Models (GLMM) with a Poisson error distribution and a log link function. Linear Mixed Models were used when the response variable was time spent foraging. Since, for these three particular analyses, we wished to take into account the effect of seed-eating species but not interested in any species-specific effect, we included bird species as a random effect. This allows to better specify the variance and to focus on possible general patterns among avian seed predators. We used multivariate modelling (various combinations of variables) and model comparison by using the Akaike Information Criterion (AIC). We first fitted the maximal model, containing all the explanatory variables. By using a model-averaging approach with all possible models (Anderson 2008), we established the importance of each variable. Seed availability was not

included in the models since we were interested in the effect of different perching locations on seed predation. For model comparison and averaging we used the dredge function within the 'MuMIn' package of R 2.12.2 software ([www.r-project.org](http://www.r-project.org)). In all GLMM we checked for overdispersion and used quasi-likelihood when needed in order to achieve valid analysis (Crawley 2007, Zuur et al. 2009).

We used Linear Models (LM) to analyse the inter-specific differences in feeding height, distance to crown edge and perching coefficient (response variables) across the study bird species (fixed effects). We did model checking for normal distribution of residuals, linearity and constant variance. We used  $\chi^2$ -tests to compare flock composition (multi-species vs. single-species) in the tree vs. on the ground for each bird species. Estimation of the density of each bird species was obtained following Burnham et al. (1980), where all existing individuals were assumed to be recorded within the transect limits (Perea et al. 2013). We calculated the mean density of each bird species and the standard error per season ( $n=6$  surveys per season). Finally, to analyse the relationship between seed availability and feeding height we calculated the Pearson correlation coefficient between both variables. We used a t-test to analyse the significance of this correlation. All the models and tests were performed using the R software ([www.r-project.org](http://www.r-project.org)).

## RESULTS

### Overall patterns of seed predation in the tree vs. on the ground

Six bird species contributed to elm seed predation on the ground in comparison to 8 species in the tree (Table 1). Maximum activity of seed predation on the ground was obtained during the second week of June (maximum number of video recordings) whereas maximum activity in the tree (maximum number of birds observed) was seen during the third week of May. Six and four bird species of the family Fringillidae were responsible of the 97.1% ( $N = 1256$  seeds) and 98.3% ( $N = 523$  seeds) of the pre- and post-dispersal seed predation, respectively. Other bird species, mainly Wood Pigeon *Columba palumbus* and Eurasian Tree Sparrow *Passer montanus* only consumed 1.7–2.9% of the seeds (Table 1). Goldfinches showed a disproportionately lower predation of elm seeds relative to their abundance whereas Hawfinches and

Table 1. Summary of the pre- and post-dispersal seed predation by the main elm seed consumers. Shown values refer to mean  $\pm$  SE. N refers to the number of observations. Flock size include both single-species and multi-species flocks. Asterisks indicate significant differences between the arboreal and terrestrial behavioural parameters for each bird species ( $p < 0.05$ ;  $\chi^2$ -tests were used for seed predation percentages and t-tests for the other variables).

Bird species	In the tree					On the ground					Overall density estimation (ind/10 ha)		
	N	Number of seeds predated	Seed predation (%)	Predation speed (seeds/min)	Foraging time (s)	Flock size (ind.)	N	Number of seeds predated	Seed predation (%)	Predation speed (seeds/min)		Foraging time (s)	Flock size (ind.)
<b>Fringillidae birds</b>													
<i>Carduelis cannabina</i>	7	49	3.8*	5.25 $\pm$ 0.92	98.3 $\pm$ 48.5	1.3 $\pm$ 0.2	1	2	< 0.01*	6.0 $\pm$ 0.0	20.0 $\pm$ 0.0	2.0 $\pm$ 0.0	0.7 $\pm$ 0.2
<i>Carduelis carduelis</i>	15	131	10.1*	11.21 $\pm$ 1.47	66.2 $\pm$ 21.8	1.7 $\pm$ 0.1	0	0	0*	–	–	–	17.1 $\pm$ 1.8
<i>Carduelis chloris</i>	65	442	34.2	11.35 $\pm$ 0.66	43.8 $\pm$ 5.2*	1.4 $\pm$ 0.1*	48	222	42.4	11.52 $\pm$ 0.54	24.5 $\pm$ 1.1*	2.2 $\pm$ 0.3*	9.3 $\pm$ 0.7
<i>Coccothraustes coccothraustes</i>	11	195	15.1	14.03 $\pm$ 2.28	104.7 $\pm$ 44.1	1.5 $\pm$ 0.3	9	60	11.5	14.73 $\pm$ 1.95	24.0 $\pm$ 3.8*	1.6 $\pm$ 0.2	4.3 $\pm$ 0.9
<i>Fringilla coelebs</i>	30	173	13.4*	11.13 $\pm$ 1.78	138.3 $\pm$ 27.6*	1.4 $\pm$ 0.1*	64	189	36.1*	7.43 $\pm$ 0.72	21.2 $\pm$ 1.7*	2.1 $\pm$ 0.2*	28.6 $\pm$ 4.8
<i>Serinus serinus</i>	65	266	20.6*	9.33 $\pm$ 0.59	42.9 $\pm$ 5.7*	1.6 $\pm$ 0.1*	11	43	8.2*	10.01 $\pm$ 1.07	22.9 $\pm$ 2.8*	3.0 $\pm$ 0.3*	30.0 $\pm$ 1.7
<b>Non-Fringillidae birds</b>													
<i>Passer montanus</i>	15	9	0.7*	11.86 $\pm$ 1.55	53.2 $\pm$ 25.7	2.2 $\pm$ 0.5	0	0	0*	–	–	–	7.1 $\pm$ 3.1
<i>Columba palumbus</i>	4	28	2.1	12.66 $\pm$ 0.66	43.3 $\pm$ 16.7*	1.6 $\pm$ 0.3*	3	7	1.3	15.60 $\pm$ 3.12	31.2 $\pm$ 4.2*	2.7 $\pm$ 0.1*	5.0 $\pm$ 1.7

Greenfinches showed lower densities but greater rates of seed predation (Table 1). Five species (Linnet, Chaffinch, Serin, Goldfinch and Wood Pigeon) contributed differently to pre- and post-dispersal seed predation (Table 1).

Only one species, Chaffinch, showed a slower seed predation on the ground than in the tree although differences were just marginally passed the significance level ( $t = -1.84$ ; d.f. = 30.7;  $p = 0.074$ ; Table 1). However, foraging times during the pre-dispersal phase (in the tree) were clearly higher than during the post-dispersal phase (on the ground) for all studied species ( $p < 0.05$ ; Table 1). Finally, flock size was significantly higher when foraging on the ground than when foraging in the tree for most bird species (Table 1).

### Importance of each variable in the arboreal foraging behaviour

Feeding height was the most important factor when analysing the number of seeds predated by each forager (Table 2). Thus, a higher value of feeding height (within each species) caused an increase in the total number of seeds predated (Fig. 1, Table 3). Distance to crown edge was considerably less important than feeding height, but much more important than perching coefficient (Table 2). In general, the number of seeds predated decreased as the distance to crown edge increased but no significant effects were found (Table 3). Feeding height was even more important than other variables when analysing the time each bird spent foraging in the tree (Table 2). Both distance to crown edge and perching coefficient showed very little importance in the time spent foraging. Thus, the time spent by birds foraging in the tree was significantly longer for locations at higher branches ( $\chi^2_1 = 15.34$ ,  $p < 0.001$ ).

Feeding height and distance to crown edge showed similar importance in the speed at which seeds were eaten (Table 2), but the best fitting model (containing both variables) had a low value of deviance explained (0.14). In this way, predation speed was rather consistent across the studied variables (feeding height, distance to crown edge and perching coefficient) with no significant effects ( $p > 0.228$  in all cases). Moreover, interestingly, no relationship was found between predation speed and number of seeds predated (Table 3). Thus, an increasing number of predated seeds was due to an increase in the time spent foraging but not to an increase in predation speed (Table 3).

Table 2. Summary of the model ranking based on AIC (Akaike Information Criterion) to test the variables affecting the number of seeds predated, the time spent foraging and the speed at which seeds were consumed by avian seed predators. Variables: F — Feeding height, D — distance to crown edge, P — Perching coefficient. Bold type shows the relative importance of each variable (values from 0 to 1).  $k$  is the number of estimated parameters,  $\Delta AIC$  is the delta weight (difference between the AIC for a given model and the best fitting model), and  $w_i$  is the model selection probability (Akaike weights). Only models with  $w_i > 0$  are shown

Variables included	Model (response variable)								
	Number of seeds predated			Time spent foraging			Predation speed		
	$k$	$\Delta AIC$	$w_i$	$k$	$\Delta AIC$	$w_i$	$k$	$\Delta AIC$	$w_i$
F, D	4	0.00	0.479	5	4.99	0.073	4	0.00	0.464
F	3	1.55	0.221	4	0.00	0.885	3	3.81	0.069
F, D, P	5	1.57	0.218	6	11.14	0.003	5	0.12	0.438
F, P	4	3.54	0.081	5	6.24	0.039	4	5.53	0.029
Relative importance of each variable	F	D	P	F	D	P	F	D	P
	1.000	0.699	0.299	1.000	0.076	0.042	1.000	0.902	0.467

### Inter-specific differences in the foraging behaviour

We obtained significant differences in predation speed among the seed predator species ( $\chi^2_8 = 40.62$ ,  $p < 0.001$ ). Among avian seed predators, Hawfinches had the highest speed and, for example, preyed upon seeds almost five times more rapidly than Linnets (Table 1).

We obtained significant differences among avian seed predators regarding the feeding height ( $F_{8,174} = 2.40$ ;  $p = 0.017$ , Fig. 2a). For instance, Hawfinches and Linnets consumed seeds on higher branches (mean over 10 m high) whereas Tree Sparrows barely predated seeds above 6 m high (Fig. 2a). However, we found no significant differences in the distance to crown edge while

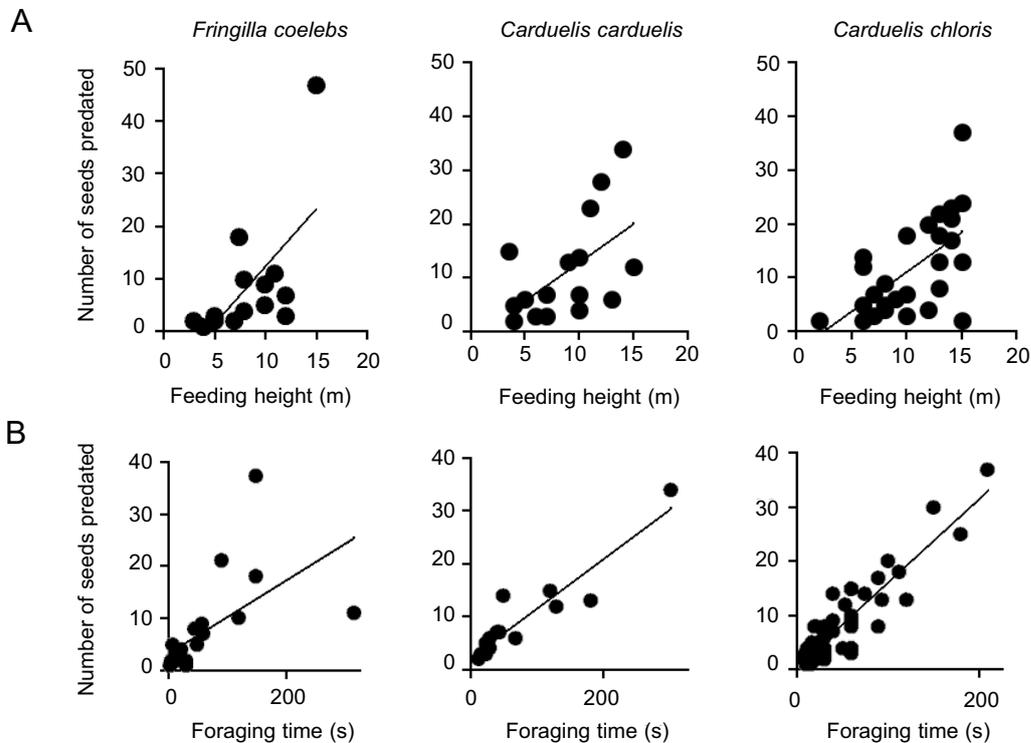


Fig. 1. Number of seeds predated in relation to feeding height (A) and foraging time (B) for three Fringillidae species at different densities: *F. coelebs* (high), *C. carduelis* (intermediate), *C. chloris* (low).

Table 3. Relationship between seed predation (number of seeds predated) and four behavioural study variables. Data for three Fringillidae species at different densities: *F. coelebs* (high), *C. carduelis* (intermediate), *C. chloris* (low). Positive and negative values of *r* indicates positive and negative correlations with seed predation, respectively.

Variables	Bird species	<i>r</i>	<i>c</i>	<i>p</i>
Feeding height (m)	<i>F. coelebs</i>	0.63	2.84	0.015
	<i>C. carduelis</i>	0.58	2.45	0.028
	<i>C. chloris</i>	0.60	3.76	< 0.001
Distance to crown edge (cm)	<i>F. coelebs</i>	-0.14	-0.62	0.541
	<i>C. carduelis</i>	-0.06	-0.21	0.837
	<i>C. chloris</i>	-0.24	-1.25	0.223
Foraging time (s)	<i>F. coelebs</i>	0.61	3.50	0.002
	<i>C. carduelis</i>	0.93	8.64	< 0.001
	<i>C. chloris</i>	0.91	16.17	< 0.001
Predation speed (seeds/min)	<i>F. coelebs</i>	0.07	0.33	0.745
	<i>C. carduelis</i>	-0.08	-0.29	0.782
	<i>C. chloris</i>	0.09	0.69	0.491

animals were consuming seeds ( $F_{8,174} = 1.09$ ,  $p = 0.369$ ). For the perching coefficient, we did obtain significant differences among the seed predators ( $F_{8,174} = 2.46$ ,  $p = 0.015$ ; Fig. 2b). For example, small finches (Serins and Goldfinches) showed values 2–4 times higher than larger finches and up to six-times higher than non-fringillidae birds (Fig. 2b).

We found a negative relationship between the percentage of video recordings (frequency of appearance on the ground) and predation speed (seeds/min) across the main seed predators ( $r = -0.64$ ; Fig. 3). Thus, Chaffinches showed the highest percentage of video recordings (52.3%) but the lowest predation speed (7.4 seeds/min), whereas Hawfinches showed a lower frequency of appearance on the ground (5.1%) but a considerable higher predation speed (14.7 seeds/min). However, this apparent negative relationship needs additional data (more species with a larger number of observations) to generalize among all Fringillidae species.

### Flocking in the tree vs. on the ground

Four species were found foraging in both microhabitats (in the tree and on the ground;  $n > 5$  observations in each microhabitat; Fig. 4). All these species except Hawfinches ( $\chi^2_1 = 0.13$ ;  $p = 0.719$ ) showed significantly higher percentage of visits in groups (i.e. tendency to flocking) when foraging on the ground ( $p < 0.001$ ; Fig. 4). Chaffinches showed the highest difference in the tendency to flocking (12.5% visits in groups in the tree vs. 75.5% on the ground;  $\chi^2_1 = 362.88$ ,  $p < 0.001$ ; Fig. 4).

All species showed higher proportion of multi-species flocks on the ground than in the tree (Fig. 4) but only two species — Serin and Hawfinch — resulted in significant differences ( $\chi^2_1 = 10.10$ ,  $p = 0.001$ ;  $\chi^2_1 = 5.36$ ,  $p = 0.021$ , respectively; Fig. 4). In the tree, all species showed similar proportion of multi-species flocks (range of 2–7%; Fig. 4a) whereas on the ground there were great differences among species (range of 7–45%; Fig. 4b), being Serins the species with the highest number of times feeding in the presence of other bird species (44.6% of multi-species flocks) as opposed to Chaffinches (6.9%; Fig. 4b). Only on the ground we found a significantly higher number of seeds predated per individual ( $\chi^2_1 = 11.43$ ,  $p < 0.001$ ) and a significantly longer foraging time ( $\chi^2_1 = 39.09$ ,  $p < 0.001$ ) when birds were feeding in flocks than when they were foraging alone. However, we found no differences in predation speed between group and individual visits ( $\chi^2_1 = 0.61$ ,  $p = 0.436$ ).

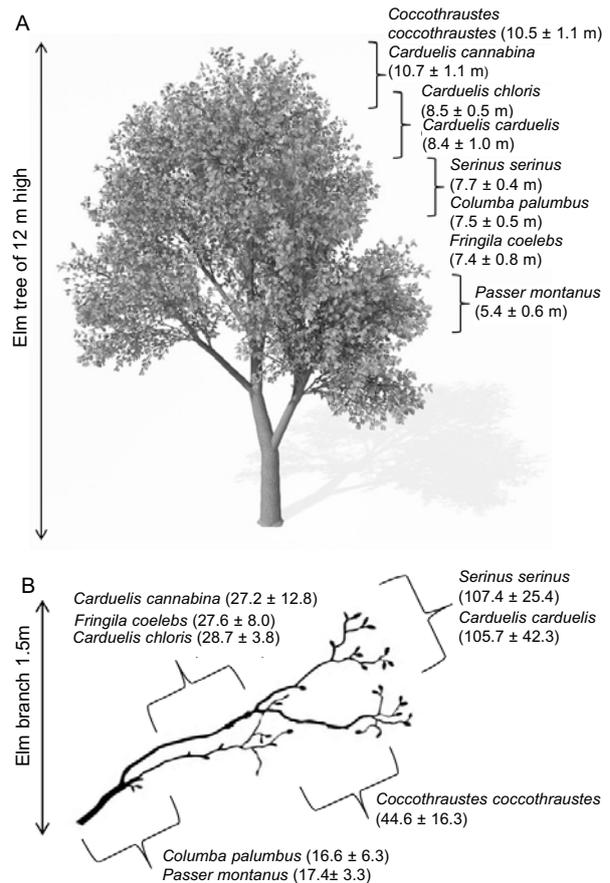


Fig. 2. Scheme of the main differences in: (A) feeding height (mean ± SD), and (B) perching coefficient (mean ± SD) for an assemblage of seed-eating birds in an elm riparian forest. Curly brackets gather those species that are not significantly different ( $p > 0.05$ ).

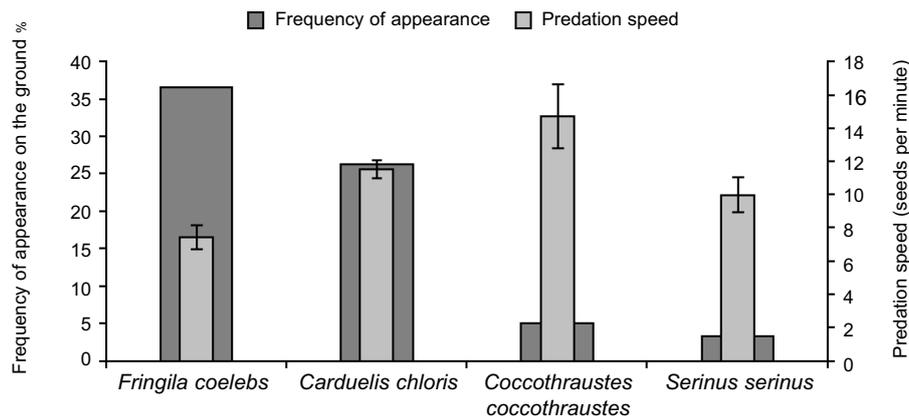


Fig. 3. Frequency of appearance on the ground for the main seed predators ( $n > 5$  recordings) and their predation speed.

### Seed availability in the tree

We found that higher branches within the same tree produced more seeds than lower branches with a positive correlation between height and

seed production ( $r = 0.79$ ,  $t = 4.76$ ; d.f. = 13,  $p < 0.0001$ ). For the same direction and individual, the highest part of the crown produced 6–35 times more seeds (mean  $\pm$  SE =  $18.2 \pm 6.8$  times; mean production = 20932 seeds; mean number of infructescences = 1507) than the lowest part (945 seeds; 96 infructescences) and 5–9 times more seeds (mean  $\pm$  SE =  $7.3 \pm 0.9$ ) than branches located at a medium height (7674 seeds; 564 infructescences).

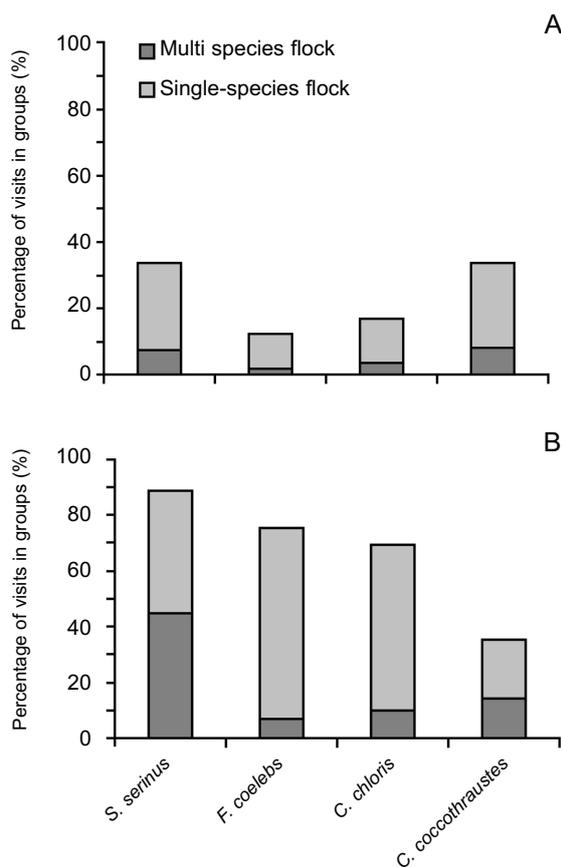


Fig. 4. Proportion of visits in groups ( $> 1$  individual) for the main seed predators in the tree (A) and on the ground (B). Data also show the proportion of one-species vs. multi-species flocks for those bird species that were found to be both pre and post-dispersal seed predators.

### DISCUSSION

#### Overall patterns of seed predation in the tree vs. on the ground

We found strong differences between the contribution of birds to seed predation in the tree and on the ground. Six finch species were the main seed consumers in the tree (97.1%) but only four of these finches were important seed predators on the ground ( $n > 5$  contacts). In addition, four common finch species (Linnet, Chaffinch, Serin and Goldfinch) contributed very differently to pre- and post-dispersal seed predation, revealing that avian seed predators can be highly affected by the environment of each dispersal phase. This study also showed that differences between both dispersal phases can affect not only the contribution of each species (overall seed predation) but also the foraging behaviour of the seed predators. Thus, we found that foraging times during the pre-dispersal phase (in the tree) were clearly higher than during the post-dispersal phase (on the ground) for all studied species (Table 1). Additionally, flock size was higher when foraging on the ground than when foraging in the tree for most bird species, revealing a differential social behaviour

between both environments. This suggests that most elm seed predators are tree-feeding birds that eat during longer periods in the tree but spend shorter times in larger flocks when foraging on the ground, probably as a strategy to reduce predation risk. Flocking is, in fact, a well-known strategy to diminish predation risk (Pulliam 1973, Thompson & Barnard 1984, McNamara & Houston 1992, Krebs & Davies 1993, Roberts 1996, Tellería et al. 2001) and, thus, tree-feeding finches tend to flock on the ground where perception of risk is higher. Alternatively, many finch species can adopt clinging and hanging positions (Kear 1962, Newton 1967), revealing their better adaptation to feed on vegetation (pre-dispersal phase).

Other variables such as predation speed were found highly variable within each bird species and, therefore, differences were null or small between both microhabitats (tree vs. ground). We expected a more rapid seed predation on the ground in agreement with the “reduced finickiness” hypothesis (Leaver & Daly 2003, Perea et al. 2011) where animals search for food more rapidly and less selectively in areas with higher levels of predation risk. Our results revealed a slower seed predation on the ground in comparison to the tree only for Chaffinches (the species more accustomed to foraging on the ground of forests; Marler 1956, Kear 1962, Newton 1967), and therefore, an increase in vigilance time on the ground could be a trait favored by selection. However, for the rest of finch species we found no differences in the speed at which seeds were consumed and, thus, did not support the “reduced finickiness” hypothesis. Interestingly, we found a negative relationship between number of visits to the ground and predation speed (Fig. 3) but further studies are needed. Apparently, birds that are more adapted to feeding on the ground (e.g. Chaffinches) resulted in more visits but lower intake whereas tree-feeding birds consumed seeds more rapidly in less visits. In accordance with Schluter & Repasky (1991), we suggest that the longer a bird remains on the ground the higher is the risk of predation.

### The importance of feeding height

Feeding height was the most important variable to explain the number of seeds predated (Table 2). We found that locations at higher branches increased the time spent by birds foraging in the trees but not the speed at which birds consumed the seeds. We suggest that finches preferred higher branches for several reasons: (1) seed

availability is greater at higher positions as has been found in this study, where feeding height and seed availability were positively correlated; (2) lower predation risk in agreement with other studies that suggest higher visibility to prevent predators attacks and allow a rapid response to fly away (Cresswell 1994, Lima 1994, Gotmark & Post 1996); (3) many finch species are well adapted to flexible twigs (e.g., Goldfinches and Serins; Newton 1967) where many other birds are not able to perch (e.g., Wood Pigeons or Tree Sparrows; Fig. 2b), decreasing a possible competition against them. This would be based on the fact that higher branches are usually more flexible because of their lower maturation (smaller diameter) and, thus, lower lignin content (Abreu et al. 1999). The higher seed density found for higher branches supports the idea that birds spend more time up in the tree not only to reduce predation risk (Datta & Pal 1993, Krams 2001) but also to increase their foraging efficiency by reducing the distance and number of movements among infructescences. This greater production of seeds for higher branches has been explained by a higher light exposure and higher probability of flowers to be pollinated (Niklas 1985, Green & Johnson 1994). Additionally, we also found that an increase in the number of seeds consumed was due to an increase in the time spent foraging but not to faster seed consumption, allocating similar times to vigilance in the different parts of the tree. This reinforces the idea of seed availability as the main biological reason of the use of different heights by granivorous birds, at least when foraging.

### Inter-specific differences in the foraging behaviour

We obtained significant differences in predation speed, feeding height and perching coefficient among the seed predator species. In that way, Hawfinches had the highest speed and, for example, preyed upon seeds almost five times more rapidly than Linnets (Table 1). Individuals of Hawfinch showed a much faster predation speed, probably due to their larger size and stronger beak, which could explain their higher ability to extract and consume the seeds (Yoshikawa et al. 2009, Myczko et al. 2013).

Interestingly, we obtained important differences among avian seed predators regarding the feeding height and the perching coefficient (Fig. 2). However, perching coefficient (PC) showed a stronger effect (wider differences) than

feeding height, probably due to the behavioural characteristics and body size of each particular bird species. For instance, Goldfinches had a very high value ( $PC = 106$ ) in comparison to Chaffinches, Hawfinches or Greenfinches ( $PC < 45$ ). In general, finches presented much higher values of PC than non-fringillidae birds (Wood Pigeon and Tree Sparrow,  $PC < 17$ ; Fig. 2b), revealing their higher adaptation to perch on more flexible stems. This new coefficient seems to be adequate to assess the bird stability and, thus, the potential ability of birds to prey upon seeds in the tree. However, we found no significant differences in the distance to crown edge while animals were consuming seeds. Birds were highly variable but especially frequent in the outer part of branches ( $< 1$  m from the edge) where, on the other hand, most seeds are located. We expected that birds would offset lower feeding heights by inner perching locations to increase safety in line with previous statements. However, perching coefficient resulted in a non-significant parameter to explain the overall seed predation. Nevertheless, further research is desirable to examine whether PC could explain other processes that are not related to specific positions in the tree (i.e. outer part of branches) such as mating or foraging for alternative food (insects, leaves, etc.).

#### **Flocking in the tree vs. on the ground**

Birds, when foraging on the ground, increased their time allocated to feed and the overall seed predation when they were in flocks. Our results agree with "group vigilance hypothesis" or "many eyes effect" (Pulliam 1973, Powell 1974, Lima 1995) where the vigilance of multiple individuals leads to a more rapid detection of predators having more time to feed (longer stays on the ground when in flocks). In addition, we found that in the tree, all species showed similar proportion of multi-species flocks (range of 2–7%; Fig. 4a) whereas on the ground there were great differences among species (range of 7–45%; Fig. 4b). Finch species that are less abundant were expected to flock in multi-species flocks, searching for more individuals to increase flock size. However, Serins, which were the most abundant bird species, tended to group in multispecies flocks more frequently (Fig. 4). We observed that Serins were mostly followers of other finch species, especially Greenfinches. Therefore, we suggest that the organization of multispecies flocks could be based on feeding efficiency, especially for the

species that act as followers in a kleptoparasitic relationship (Hino 1998). One may think that Serins might be more sensitive to predation supporting the hypothesis that those foraging birds that are more vulnerable are also more likely to form multispecies flocks (Thiollay 1999, Tellería et al. 2001). However, Gotmark & Post (1996) revealed that larger passerines (up to 40 g), such as Greenfinches are more sensitive to predation by ornithophagous raptors than small passerines such as Serins. It would be interesting to assess whether small finches tend to follow and flock with larger ones to increase not only their feeding efficiency but also their safety by flocking with more vulnerable species.

#### **Conclusions**

This study highlights that granivorous birds may forage for seeds at the two dispersal phases (pre- and post-dispersal), showing a different foraging behavior when contrasting microhabitat conditions occur (e.g. in the tree vs. on the ground). Most elm seed predators were tree-feeding birds that foraged for long periods in the tree but also spent shorter times in larger flocks when foraging on the ground, which could be seen as a possible adaptive strategy to forage in riskier environments. Here we compared a few behavioral parameters (flock tendency, flock composition, predation speed, predation rates) during the dispersal phase but further studies are needed in order to address the origin and possible implications of behavioral shifts due to strong changes in food (seed) location. As expected, rates of pre-dispersal seed predation were related to the location and density of seeds, with greater predation rates at higher and outer position of the tree where most seeds were found. However, seed-eating birds varied their positions in the tree and a new coefficient (PC) was defined, obtaining great differences not only among Fringillidae and non-Fringillidae birds but also within the Fringillidae family. This could be related to the ability of small Fringillidae birds to perch on thinner branches. This new coefficient seems to be adequate to assess the bird stability and, thus, the potential ability of birds to prey upon seeds in the tree. Further studies should take into account possible differences in the behavior of seed-eating birds throughout the seed dispersal season since it may have important implications not only for bird reproductive fitness but also for their adaptive behavior to select new potential niches.

## ACKNOWLEDGEMENTS

We would like to thank P. Sanjuanbenito, the managers of the Cuenca Alta del Río Manzanares park and the forest rangers for their support. Financial support was provided by the Comunidad de Madrid (project S2009AMB-1668). The experiments comply with the current laws of Spain, the country in which they were performed.

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