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Not only size matters: Acorn selection by the European jay (*Garrulus glandarius*)

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ABSTRACT

A strong selection for acorn characteristics is expected to have evolved in the mutualistic relationship between the European jay (*Garrulus glandarius*) and the oak (*Quercus* spp.). Bossema's pioneer work suggested that jays do not select acorns randomly, but rather they preferentially select some size and species. Preference for some seeds over others may have implications on plant community dynamics by conferring advantages (or disadvantages) on the selected (avoided) seed characteristics. In this paper we test to what extent jays select acorns by species and/or by size and the relation between these two traits in Mediterranean oak species. The experiments consist of a set of field tests in which acorns from four different coexisting Mediterranean oak species (*Quercus ilex*, *Quercus faginea*, *Quercus suber*, and *Quercus coccifera*) were placed in artificial feeders accessible to wild jays. The acorns were previously measured to control individual acorn characteristics. Using video-recording techniques, we followed jay activity and the fate of each acorn (sequence of acorn selection and method of transport). *Q. ilex* acorns were preferred over other acorns, and *Q. coccifera* acorns were avoided when other acorns were available. Preference for *Q. faginea* and *Q. suber* acorns was intermediate, that is, they were preferred over *Q. coccifera* acorns but not over *Q. ilex* acorns. Large acorns were also preferred although acorn species selection was stronger than size selection. Jays selected species and size both by visual means and by using acorn area as an indicator of size. Acorns wider than 17–19 mm were carried in the bill because of throat limitation. Our results confirm Bossema's study on temperate oaks and extend it to Mediterranean oak species, revealing implications on mixed oak forest dynamics.

1. Introduction

Seed size and quality play a vital role in plant life history (Venable & Brown, 1988). The dependence of offspring fitness on seed size has been extensively documented: both intra- and inter-specific studies suggest that germination, emergence, and seedling survival are higher in large seeds than in small ones (Rees, 1995; Aizen & Woodcock, 1996; Bonfil, 1998; Jakobsson and Eriksson, 2000, see Moles and Westoby, 2004 for a discussion of the seed size–survival conflict). Moreover, predation (Gómez, 2004a) and limited dispersal (Hedge et al., 1991; Schupp, 1995; Moegenburg, 1996; Moore and Swihart, 2006) may also be important for large seeds, suggesting that there could be conflicting phenotypic selection

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on seed size (Gómez, 2004b). Thus, for animal-dispersed seeds, understanding the regeneration process requires an evaluation of seed size selection by the main dispersers.

The European jay is a very efficient acorn disperser (Schuster, 1950; Chettleburgh, 1952; Bossema, 1979) and it is assumed that *Quercus* and jay have evolved a mutualistic relationship in which acorns are shaped by the selection exerted by jays and most *Quercus* seeds, especially at medium to large distances, are jay-dispersed (Bossema, 1979). Thus to fully understand the phenotypic selection on acorn size, we need to understand the direct acorn selection by the jay. Currently, there is little information on acorn size selected by jays, and most interpretations are based on a single study by Bossema (1979).

Furthermore, jay territories may include different *Quercus* species and the preferences by the jay may also have important implication for the regeneration niche of the species. For instance, the North American Blue jay (*Cyanocitta cristata*) preferentially harvests and disperses oaks with relatively small acorns (Moore & Swihart, 2006); however, the preferences for the European jay are unknown. Preferred species may have an evolutionary advantage over avoided species, and these differences may influence oak distribution patterns. To what extent differential *Quercus* occurrence is due to different dispersal capacities (regeneration niche *sensus* Grubb, 1977) that are, in turn, mediated by different jay preferences remains unknown. Certainly, acorns of different species differ in their nutritional characteristics and tannin levels (Talebbendiab et al., 1991; Shimada, 2001; Nieto et al., 2002; Cantos et al., 2003; Ferreira-Dias et al., 2003) and have shown differential selection by rodents (Briggs and Smith, 1989; Ivan and Swihart, 2000; Pons and Pausas, 2007). Thus, in mixed oak communities (Pausas et al., 2006; Pons and Pausas, 2006), we do not expect random selection by jays.

In this context we ask the following questions: (a) to what extent do jays show a preference for acorns of a given *Quercus* species; (b) to what extent do jays show an acorn size preference; and (c) which selection (size or species) is stronger. To answer these questions, we placed acorns of different oak species in artificial feeders located in a Mediterranean landscape and followed their fate using photographs and video recordings. The experiments were performed with three evergreen oak species (*Q. ilex*, *Q. suber* and *Q. coccifera*) and a semi-deciduous oak (*Q. faginea*).

2. Materials and methods

2.1. Study area

The study was performed close to the village of La Pobla Tornesa, in the eastern Iberian Peninsula (40°5′N, 0°0′W, Castelló province, València, Spain). The climate is typically Mediterranean with summer drought and mild wet winters. The vegetation is a mosaic of shrublands and pines traditionally used for pasture and wood gathering on steep slopes, together with flat areas and terraces used for agriculture (and now partially abandoned). We used acorns from four *Quercus* species present in the area: Holm oak (*Q. ilex* subsp. *rotundifolia*), Spanish oak (*Q. faginea*), Cork oak (*Q. suber*) and Kermes oak (*Q. coccifera*) (hereafter abbreviated as *Qi*, *Qf*, *Qs*, and *Qc*, respectively). Of these, Holm oak and Kermes oak (a shrub) are the most abundant oaks in the study area. Early-summer surveys revealed a minimum jay density of 0.77 pairs/km^2, with an inter-nest position of ca. 500 m (authors' unpublished data). In the study area, jays begin their reproductive period around March, and nestlings usually leave the nest between mid-June and mid-July. Family groups are seen caching acorns all autumn. Usually, by January–February few acorns remain available in the wild.

2.2. Methods

Acorns were obtained from nearby oak populations or, when necessary, from local seed banks (*Banc de Llavors*, *Generalitat Valenciana*) and conserved in a refrigerator until use. Only sound acorns were utilised in the trials and these were selected by the floating method (Bonfil, 1998) followed by tactile and visual selection. These acorns were used to perform a set of experiments (described below) designed to reveal acorn species (Experiments 1 and 2) and size (Experiment 3) selection by the jay, including an experiment testing the interaction between species and size (Experiment 4).

2.2.1. Comparing initial vs. remaining acorns

2.2.1.1. *Experiment 1.* We performed 30 trials in which 10 acorns from each of the four oak species were intermixed in a feeder (i.e., a total of 1200 acorns) during February 2005. Four feeders, separated from each other by at least 210 m, were used simultaneously. Each feeder consisted of a 40 × 40 cm tray mounted at the top of a 1.7 m pole, in order to avoid non-avian acorn consumers. The feeders were set up in places where jays are usually active, i.e., not far from high shrubs or trees, so that they would feel safe when visiting the poles. After placing the acorns on the trays, we revisited the feeders once-to-several-times a day to recover the acorns not transported by jays. On each visit we counted the number of remaining acorns and considered the trial as finished if this number was lower than 30 acorns. On the other hand, if fewer than 10 acorns remained in the feeder, the trial was discarded. The idea was to have as many trials as possible with ca. 50% of the acorns removed in order to test species selection (removed vs. non-removed).

2.2.2. Tracking individual acorns (videos)

We recorded the exact sequence of acorn removal by jays by means of a video camera hanging vertically 1.5 m over a feeder. Acorns were individually fixed (gently nailed) to the tray and separated by about 3 cm. Prior to exposing the acorns to the jays, we took digital photographs to measure acorn dimensions (length, width and area) using an image processing software (Matrox Inspector 4.0); thus, each acorn was individually identified. A total of 621 acorns were successfully tracked in 22 films. As this method allowed us to track each individual acorn fate, several trials were run for each variable tested and various different designs were used (see below, Experiments 2–4). Trials were run in spring (June) 2005 and winter (December) 2005.

2.2.2.1. Experiment 2 (multi-species trials). Ten acorns of each species (*Qi*, *Qc*, *Qs*, *Qf*) were intermixed in the feeder. In the winter trials, and to remove any possible size selection, we included only acorns between 1.30 and 1.60 cm in width and between 2.80 and 3.25 cm in length. A total of eight trials were recorded (four in each season).

2.2.2.2. Experiment 3 (single species trials, size selection). Only acorns of one species (40 acorns) were used in each trial, with variable size and random distribution in the feeder. Two trials for each species were run (a total of eight films).

2.2.2.3. Experiment 4 (shape selection). Acorns set in the feeder were previously separated into two size and shape groups. Three trials were performed: (a) *Qi* acorns were segregated into narrow (<1.4 cm wide) and wide (>1.4 cm) acorns, all with similar length (ca. 3.4 cm) (20 acorns for each shape); (b) *Qc* acorns were segregated visually into small and large acorns (20 acorns for each size); and (c) narrow and wide acorns of *Qi* were placed together with large *Qc* acorns (12, 13 and 14 acorns, respectively).

2.2.3. Transport

We reviewed all the video tapes from Experiments 2, 3 and 4, and for each jay visiting the feeder, and we noted the following information: (a) the acorns that were picked up last by the jay in each flight (usually, the last acorn picked was carried out in the bill while the remaining acorns were carried out in the throat); (b) the acorns that the jay unsuccessfully tried to swallow (acorns too large); and (c) the number of flights and the number of acorns transported in each flight. Because we knew the size of each individual acorn, we were able to compare acorn sizes between the different ways in which the acorns were transported.

2.3. Data analysis

The effect of the *Quercus* species on the number of acorns removed for each species (Experiment 1) was tested using the non-parametric Kruskal–Wallis Test (K–W hereafter). Ivlev's electivity index (Scarlett and Smith, 1991) was used to quantify jay preference for a particular acorn species. Electivity was calculated for each acorn species as $E_i = (R_i - P_i)/(R_i + P_i)$, where R_i is the number of selected acorns of the species *i*, and P_i is the number of supplied acorns of the species *i*. Thus, the index ranges from −1 to 1, with negative values indicating avoidance, positive values indicating selection, and close to 0 values indicating random selection.

The acorn removal observed in the video films (Experiments 2 and 4) was studied using a survival function, with the dependent variable (''survival'') being the acorns not removed by the jay and the independent variable being the sequence of removal (from 1 to a maximum of 40 in each video film). Survival analysis was performed for each film and each species. As there were no differences between films in the single species trials (Experiment 3), we finally aggregated the different films of the same species and obtained the mean sequence for each acorn species. Median sequence is the total number of acorns picked by the jay to reach 50% of the given acorn species, and it is an indicator of the jay's acorn species selection: the lower the value, the higher the preference. Survival functions of the different species were statistically compared by Wilcoxon (Gehan) Statistic.

To compare acorn sizes between trials performed in different seasons (Experiment 2) we used the projected area of the acorn (computed from the digital photography) as a size indicator. The statistical comparison was performed using the non-parametric Mann–Whitney *U* test (also called Wilcoxon rank-sum test).

The size selection is evaluated in the single species trials (Experiment 3) by testing the slopes of the relationship between the size of each acorn and the sequence in which the acorn was picked from the feeder by the jay. ANCOVA was used to test the effect of species and films (i.e., differences in the regression slope). The three size measures (length, width and projected area) were tested. A stepwise regression was performed to evaluate the size measure that best explained the selection sequence.

The seasonal differences in the number of acorns transported by the jay in each flight were tested using the Kolmogorov–Smirnov (K–S) test, that is, comparing the frequency distribution of the number of acorns transported by flight.

3. Results

3.1. Comparing removed vs. remaining acorns

3.1.1. Experiment 1

Jays removed 77.3% of the total of acorns ($n = 1200$ in a total of 30 trials; Table 1). Of the remaining acorns (i.e., those not removed, $n = 272$), 70.6% were *Qc* acorns, which were also the only acorn species remaining in the feeders in 63.3% of the trials (Table 1). Differences between acorns removed were significant between the four species ($n = 30$ trials, K–W $\chi^2 = 64.250$, $df = 3$, $p < 0.001$). However, when *Qc* was removed from the analysis the difference in the number of acorns of each species remaining in the feeders was not significant ($n = 11$ trials, K–W $\chi^2 = 1.366$, $df = 2$, $p < 0.505$). The mean electivity index indicates that *Qc* was clearly rejected ($E = -0.48$) by the jay, while the other three acorn species were randomly selected ($E = 0.064$, 0.106 and 0.063 for *Qi*, *Qf* and *Qs*, respectively).

3.2. Tracking individual acorns (videos)

3.2.1. Experiment 2 (multi-species trials)

Acorns of *Qi* were the most preferred (i.e., lower median sequence, Table 2) in both spring (non-controlled-size trials, Cox regression: $p < 0.001$) and winter (size controlled, Cox regression: $p < 0.001$) trials. The results were similar in both trials, even though in the spring trials *Qi* acorns were not the largest (Table 2). There was also some preference for *Qf* over *Qc* in the spring trials even though *Qf* acorns were much smaller than *Qc*.

3.2.2. Experiment 3 (single species trials)

For each acorn species, there is a clear negative relation between the acorn size and the sequence of removed acorns

Table 1 – Proportion between removed and remaining acorns of each species, the number of trials in which acorns of each species remained in the feeder, and the mean electivity index, in Experiment 1

	Qc	Qi	Qf	Qs	Total
Total acorns removed	108	274	283	263	928
Total acorn remaining	192	26	17	37	272
% Remaining	70.6	9.6	6.3	13.6	22.7
No. of trials remaining	30	7	6	8	30
Mean electivity	−0.482 b	0.064 a	0.106 a	0.063 a	

A total of 30 trials were performed with 10 acorns of each species. Similar letters denote similar mean electivity based on a multiple comparison test.

(Fig. 1, Table 3), suggesting that jays prefer larger acorns. Slopes of these trends were not different between the different films in each species, but there were differences among species (ANCOVA, Table 3). These slopes (and the associated variance) can be considered as an indicator of the strength of the size selection by jay. *Qi* is the species presenting the steepest slopes in all three size measures (Table 3). However, *Qi* was the smallest acorn set used, and thus, an increased size selection on this species due to their small size cannot be rejected (mean width (cm): *Qi*: 1.18, *Qf*: 1.52, *Qs*: 1.50, *Qc*: 1.44; mean length (cm): *Qi*: 2.79; *Qf*: 2.69, *Qs*: 2.99, *Qc*: 2.82; and mean area (cm^2): *Qi*: 2.40, *Qf*: 3.09, *Qs*: 3.51, *Qc*: 3.01). The size measure that best explained the variability in the acorn selection sequence was the area for *Qi*, *Qf* and *Qc*, and the length for *Qs*. When these variables were in the model, no additional size variables significantly increased the explained variance. When testing the four acorn species together (overall in Table 3), both area and length together entered in the regression model.

3.2.3. *Experiment 4 (shape selection)*

Jays selected big acorns over small ones for both *Qi* acorns (preferred species) and *Qc* acorns (avoided species) (Table 5). In the case of *Qi*, big and small acorns were different in width but not in length, suggesting that jays preferred wide *Qi* acorns over narrow ones. When offered big and small *Qi* and big *Qc* acorns, all varying in width but not in length, jays selected *Qi* irrespective of acorn size (Table 4).

3.3. *Acorn transport characteristics*

In a total of 22 films, we recorded 622 acorn removals by jays from our feeders. The mean number of acorns removed in each flight was 1.62 ($n = 376$ flights). By season, more acorns were transported per flight in winter than in spring–summer (mean winter = 1.91; $n = 232$ flights; mean spring = 1.26, $n = 144$ flights; K–S test $z = 3.492$, $p < 0.001$). In 61.2% of the flights, jays transported a single acorn, and the maximum number of acorns transported in a single flight was five (ca. 2%). Acorns transported in single-acorn or two-acorn flights were larger than acorns transported in multiple-acorn flights (e.g., acorns in five-acorn flights were 70% the size of those transported in two-acorn flights, Table 5).

Acorns were transported in the bill in all single-acorn transports and when the acorn was the last one picked in multiple-acorn transports. On some occasions (8%), the jay tried to swallow this acorn but could not do so and thus transported it in its bill (Fig. 2). There were significant size differences between the acorns swallowed (transported in the throat; mean width = 1.47 cm, $n = 235$) and the acorns that could not be swallowed (mean width = 1.72 cm, $n = 50$; K–S test z (width) = −7.872, $p < 0.001$). The last acorn picked by a jay was significantly larger (mean width = 1.61 cm, $n = 130$) than the previously swallowed acorns (mean width = 1.47 cm, $n = 218$; K–S test $z = -5.052$, $p < 0.001$; Table 6).

Table 2 – Mean (and SD) size (projected area, cm^2) of acorns used in the spring trials (S, non-controlled acorn size; four films, 37 filmed acorns removed) and in the winter trials (W; size controlled acorn; four films, 123 filmed acorns removed) in Experiment 2 (multi-species trials)

Acorn species	Area (cm^2)		Difference (W − S)	Median sequence				Electivity index			
	Spring (S)	Winter (W)	P	*p*	*p*	W	*p*	S	*p*	W	*p*
Qi	2.95 (0.56)	4.22 (0.47)	<0.001	13	a	9	a	0.23	a	0.57	a
Qf	2.77 (0.41)	4.02 (0.41)	<0.001	≥20	b	22	b	−0.23	b	−0.10	b
Qs	3.43 (0.86)	3.96 (0.47)	0.005	≥20	bc	30	b	−0.40	c	−0.52	c
Qc	3.55 (0.51)	3.82 (0.44)	0.009	≥20	c	32	b	−0.83	d	−0.53	c

Differences in acorn size are evaluated with the Mann–Whitney *U* test. The number of acorns used was 40 (spring) and 36 (winter). Median sequence is estimated by a survival function; the lower the value, the faster the removal. The pairwise comparison is shown with letters (from a, the fastest removal, to c, the slowest) and tested using the exact Wilcoxon (Gehan) Statistic for median sequence and the Kolmogorov–Smirnov test for the electivity index. Different letter (*p*) indicate significantly different mean values ($p < 0.05$).

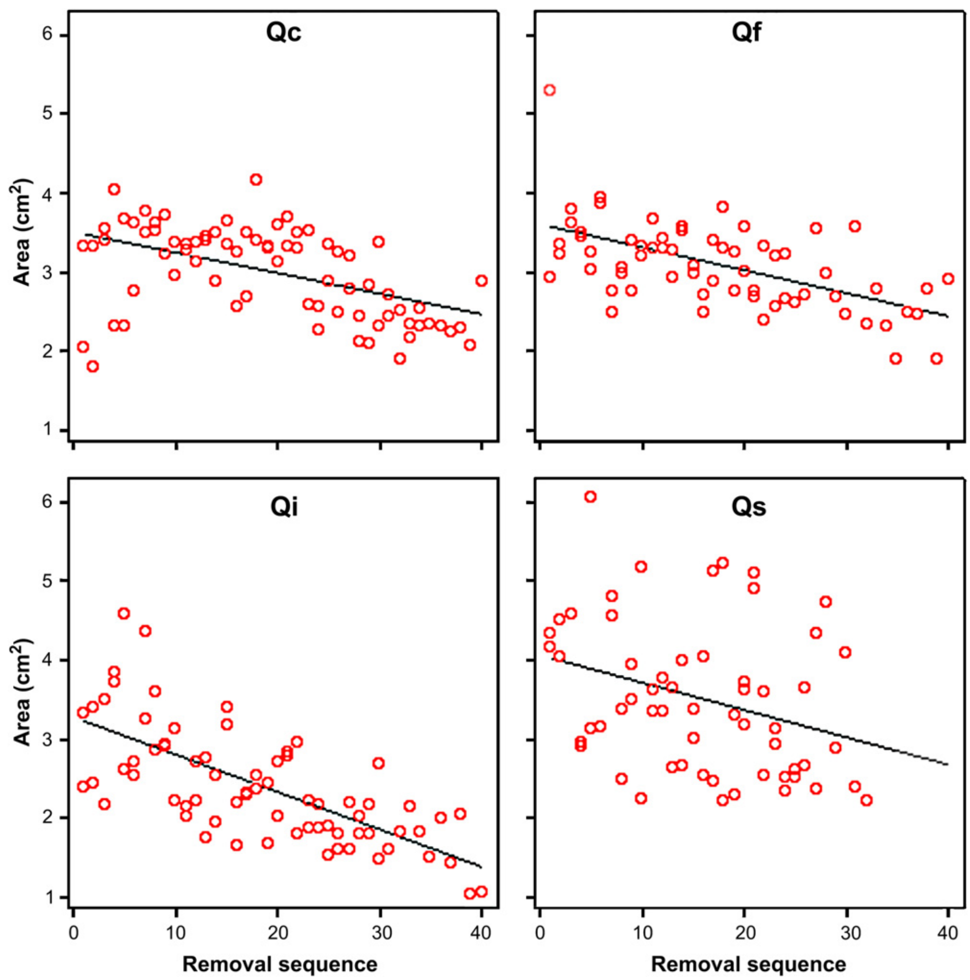

Fig. 1 – Relationship between the sequence of jay acorn removal from the feeder and acorn size (expressed as area in cm²) for the four acorn species studied (Qc = Q. *coccifera*; Qf = Q. *faginea*; Qi = Q. *ilex*; Qs = Q. *suber*). All regression lines are significant ($p < 0.01$). See the text and Tables 3 and 4 for more details.

4. Discussion

The results suggest that European jays select some acorn species over others, as has been shown for the North American Blue jay (Scarlett & Smith, 1991; Moore & Swihart, 2006). Of the four acorn species used in the trials, *Qi* was clearly preferred. Moreover, acorn species selection was stronger than acorn size selection, as: (1) *Qi* spring acorns were smaller than *Qs* and *Qc* spring acorns (Experiment 2) but were still preferred; (2) small *Qi* acorns were removed before big *Qc* acorns (Experiment 4). The lack of *Qi* selection in Experiment 1 – not acorn size controlled – could be due, in part, to the small size of *Qi* acorns compared with other acorn species. In the same way, the smaller *Qc* acorns could also be the cause of the stronger avoidance observed when comparing the results in the size-controlled experiment (Experiment 2). Size differences in the acorn pools used (see Table 2) probably reflect some species size gradient in natural acorn populations. The decreasing size from *Qs* > *Qf* > *Qc* > *Qi* has been found previously (Pascual, 2003, but with *Quercus humilis* instead of *Qf*). Altogether this suggests the jays' priority of acorn species selection over acorn size selection, with the latter acting as a modulator of the former.

The preference for *Qi* can be attributed to its higher nutritional value. In fact, *Qi* acorns have higher proportion of fat than the other three tested species (Talebbendiab et al., 1990, 1991; Afzalrafii et al., 1992; Cañellas & San Miguel, 2003; Ferreira-Dias et al., 2003). Similarly, the jays' rejection of *Qc* could be attributed to high tannin levels (Cañellas & San Miguel, 2003). Unfortunately, studies on the chemical characterization of Mediterranean acorns are scarce, despite its relevance found in other ecosystems (Johnson et al., 1993; Fleck & Woolfenden, 1997). Interestingly, *Qi* acorns were also preferred by small rodents (*Apodemus sylvaticus*) in a similar (and nearby) study area (Pons & Pausas, 2007), suggesting that *Qi* acorns are preferred over other acorns by the most important vertebrates interacting with *Quercus* in the study area (predators and dispersers). However, caution should be taken when extrapolating these results, as acorns are

Table 3 – Slopes (and SE) of the regression in size (length, width, and area) as a function of the removal sequence for each oak species and for the overall species, in the single species experiment (Experiment 3)

	n	Length				Width				Area				Best
		Slope	SE	Adj. R^2	*p*	Slope	SE	Adj.R^2	*p*	Slope	SE	Adj.R^2	*p*	
Species														
Qi	70	−0.028	0.004	0.465	***	−0.011	0.002	0.367	***	−0.047	0.006	0.484	***	Area
Qf	64	−0.007	0.002	0.103	**	−0.009	0.002	0.328	***	−0.028	0.005	0.331	***	Area
Qs	58	−0.020	0.007	0.110	**	−0.004	0.003	0.033	!	−0.035	0.014	0.084	*	Length
Qc	74	−0.010	0.003	0.155	***	−0.006	0.002	0.147	***	−0.006	0.002	0.147	***	Area
Overall	266	−0.016	0.002	0.205	***	−0.008	0.001	0.140	***	−0.035	0.004	0.213	***	Area & length
ANCOVA				0.218				0.468				0.389		
Species					***				***				***	
Film					ns				ns				ns	
Sequence					***				***				***	

Also included are the adjusted R^2 of the regression, the ANCOVA test considering species and film as factors and sequence as covariable, and the best size variable predictor of the sequence for each species (last column). Significance (*p*): !<0.1, **<0.01 ***<0.001.

morphometrically highly variable (Natividade, 1950), and thus large intra-specific variation is expected (Aizen & Woodcock, 1992).

Jays also preferentially select large acorns (Fig. 1); consequently, large acorns likely have a higher chance of being dispersed than smaller acorns. Similarly, longer dispersal distances for larger acorns have also been reported for rodents (Xiao et al., 2005). Furthermore, large acorns have increased germination rates, seedling survival, accelerated germination timing and enhanced seedling growth (Tripathi & Khan, 1990; Sonensson, 1994; Bonfil, 1998; Gómez, 2004b). Therefore, our results have implications for understanding the evolution of acorn size, as the jay-selected-and-dispersed acorns are the most likely ones to become established, and thus there may be a positive phenotypic selection on acorn size (Gómez, 2004b). Nevertheless, the positive selection pressure by the jay should not be understood strictly in terms of a linear acorn size increase as jay physical limitations for acorn handling and transport may limit the selection of very large acorns. This could lead to a stabilising or, at least, a non-linear selection (Gómez, 2004b).

Our results on jay transport characteristics confirm many of the results by Bossema (1979). Jays transported 1–5 acorns per flight, with a decreasing frequency of flights as the numbers of acorns transported increased (Table 6). The videos clearly show that most times the jays discriminate visually which acorn to carry, and after making their decision, they swallow or carry the acorn in their bill without hesitation. However, when picking up the acorn, the jay uses tactile means (pressure probably) to discard rooted or infected acorns. By these means, the jay selects the species (probably by colour and shape), the size and the quality of the acorn. In multiple-acorn flights, lower-than-throat-limit acorns are swallowed and bigger acorns are picked up last and carried in the bill. In three of the four acorn species considered, the area of the acorn was the best predictor of the acorn-size removal sequence, and this agrees with Bossema's (1979, p. 30) suggestion that jays use this parameter to estimate acorn size. However, jays suffer some size estimation error regarding their throat limit. In our trials, of the four acorn species considered, the acorn swallow capacity was around 17–19 mm in width, 31–32 mm in length and 3.6 cm^2 in area. At this limit, the jay just stopped picking up acorns and carried the unsuccessfully swallowed one in its bill. The number of acorns per trip is probably the consequence of the jay's previously planned acorn transport distance (Bossema, 1979). The lower number of acorns per trip in the spring–summer trials than in the winter ones supports this idea, as the purpose of the acorns was probably different: nestling feeding in the former and scatter hoarding in the second.

Our results have applications in forest management. It is often suggested that large acorns should be selected for afforestation projects because of their better germination and growth in the establishment phase (Montero and Cañellas, 2003). As acorn size is supposed to be genetically determined, it is probable that these planted trees would also produce big acorns. This artificial selection of large-seeded trees may be detrimental for further population expansion, as the dispersal capacity via jays of these planted trees would be deficient if acorn dimensions exceed jay throat limitations. Thus, in

Table 4 – Mean (and SD) size and median sequence for the shape selection trials (Experiment 4)

Species	Acorn type	*n*	Area (cm^2)	Length (cm)	Width (cm)	Med. sequence
Qc	Big	20	3.51 (0.27)	3.00 (0.20)	1.58 (0.10)	11
	Small	20	2.53 (0.25)	2.62 (0.17)	1.33 (0.12)	31
	P		<0.001	<0.001	<0.001	<0.001
Qi	Big	20	4.73 (0.41)	3.64 (0.17)	1.80 (0.10)	11
	Narrow	20	3.02 (0.30)	3.27 (0.19)	1.26 (0.09)	31
	P		<0.001	ns	<0.001	0.007
Qi–Qc	Qi big	13	4.23 (0.47)	3.27 (0.17)	1.74 (0.08)	10
	Qi narrow	12	3.21 (0.22)	3.24 (0.15)	1.29 (0.05)	19
	Qc big	14	3.75 (0.40)	3.04 (0.15)	1.61 (0.12)	33
	P		<0.001	ns	<0.001	0.003

One film was used for each trial. Size parameter differences were tested with the Mann–Whitney *U* test. Median sequence removals were tested using Cox regression.

Table 5 – For each type of flight (i.e., flights with a different number of transported acorns, from 1 to 5), the number (*n*), its percentage of the total recorded flights, and the mean values of acorn size (width in cm, length in cm and area in cm^2) are shown

n acorns per flight	Flights		Mean acorn size		
	n	%	Width	Length	Area
1	230	61.2	1.53	3.06	3.55
2	81	21.5	1.59	3.11	3.72
3	37	9.8	1.54	2.98	3.48
4	21	5.6	1.44	2.84	3.06
5	7	1.9	1.28	2.80	2.63
Total	376	100.0			
χ^2			18.033	17.788	21.650
p			0.001	0.001	<0.001

Comparisons of size measures between the different flight types were performed with the Kruskal–Wallis Test (χ^2).

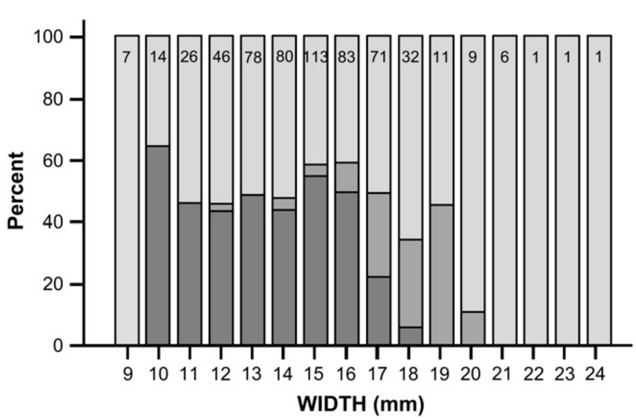

Fig. 2 – Proportion of swallowed (dark grey), unsuccessfully swallowed (grey) and bill-transported acorns with no previous attempt at swallowing (light grey) in relation to acorn width (mm). Bars correspond to 1 mm intervals. Numbers at the top of the columns indicate the number of acorns observed in each interval.

Table 6 – Comparison of mean size values (length, width and area) between the acorns last picked and the others in multiple-transport flights, and between acorns swallowed and acorns not swallowed (including single flights)

	Last			Swallowed		
	Yes	No	*p*	Yes	No	*p*
Length (cm)	3.10	2.94	***	2.93	3.08	***
Width (cm)	1.61	1.47	***	1.47	1.58	***
Area (cm^2)	3.78	3.25	***	3.25	3.69	***
n	144	236		235	344	

Significance of the mean differences is performed with the K–S test.

afforestation and restoration projects we suggest avoiding the use of acorns that exceed jay throat dimensions. We suggest that the size limit should be about 1.72 cm in width, which for *Q. suber* corresponds to acorns of about 6 g (Pascual, 2003).

In conclusion, jays select big acorns although the size of most dispersed acorns is limited by jay physical limitations (e.g., the throat). Furthermore, jays also make a species selection (e.g., *Qi* acorns are the most preferred and *Qc* the most avoided), and this selection is both stronger and prior to that of size. Altogether, this study supports the need for a multi-species approach to oak regeneration studies in order to understand oak woodland dynamics in mixed oak landscapes.

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