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Vertebrate predation on Holm Oak, *Quercus ilex*, acorns in a fragmented habitat: effects on seedling recruitment

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Abstract

Rodent and avian consumption of Holm Oak, *Quercus ilex*, acorns were examined in central Spain during two high-production seasons, 1990–1991 and 1993–1994, in 1 and 3 large stands and in 6 and 10 small stands (0.2–12 ha) respectively, to study the effects of vertebrate predation on seedling recruitment. Previous data indicate that wood mouse abundance is much higher in small stands. Tree size, frequency of acorn-bearing oaks and acorn abundance were similar in the two sizes of forest stands. Overall acorn consumption was 33.7 times higher in the small stands compared to that in the large stands in 1991, and 3.1 times larger in 1994. Consumption of acorns by mice in the small stands was 49 and 95 times greater than that by birds in the first and second year, respectively. Seedling recruitment was significantly higher in the large stands in both study seasons. Regeneration by ramets was roughly similar in small and large stands in both seasons. Thus, predation by mice was apparently responsible for the failure of sexual reproduction in the small stands. The results suggest that vegetative regeneration might be the prevalent reproductive method of Holm Oaks in small forest tracts. © 1997 Elsevier Science B.V.

Keywords: Acorns; Forest fragmentation; Oak; Vertebrate predation; Seedlings

1. Introduction

In extensive regions of central Spain, large forests have been fragmented into small woodlots containing Holm Oak, *Quercus ilex*, embedded in an agricultural matrix (Santos et al., 1995). This is the case near Lerma, where the original forests are now represented by dispersed remnants, mainly monospecific forests of Holm Oaks.

During autumn, small mammals migrate to overwinter in these small stands and other remnants of undisturbed ground (shelterbelts, shrublands, etc.) since much of the surrounding ploughed landscape is unsuitable for the survival of these small vertebrates (Alcántara and Tellería, 1991; Tellería et al., 1991, 1992 Díaz, 1992). Concentration is due to thermoregulation and nesting needs of small mammals during the winter (Merrit, 1984; Genoud, 1988), where the unploughed areas are the only sectors with appropriate stable substrata for them to build their winter nests.

Holm Oaks flower in spring, and the acorns mature and begin to fall from mid-autumn to early spring (Ceballos and Ruiz, 1979). Hence, an important part of the crop is available to vertebrate preda-

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tors throughout autumn and winter. In Spain, acorns are consumed by many species of birds and mammals (Herrera, 1977; Alonso and Alonso, 1988; Purroy, 1988; Sáez-Royuela, 1989). The main mammalian predators in the Lerma region are Wild Boars, *Sus scrofa*, and Wood Mice, *Apodemus sylvaticus* (Tellería et al., 1991), while Tits, Chaffinches, Wood Pigeons, Robins, Nuthatches, and Jays are potentially the main avian predators.

Previous work has found an overcrowding of wintering Wood Mice in small woodland patches of three widely distributed forest archipelagoes in different years (Santos et al., 1995), suggesting that high densities are common in fragmented forests of central Spain. In the archipelago of Lerma, mice abundance was 9.4 times higher in small stands than in large stands (Tellería et al., 1991). Meaningfully, the consumption rate of experimental Holm Oak acorns and natural Spanish Juniper (*Juniperus thurifera*) seed supplies by mice has been observed to be high in the smallest remnants (Tellería et al., 1991; Santos and Tellería, 1994). Spanish Juniper reproduces only by seed (Costa et al., 1986) and has a reduced recruitment rate in the smallest fragments because of increased mouse predation (Santos and Tellería, 1994). Holm Oak is capable of both sexual and vegetative regeneration (Ceballos and Ruiz, 1979), so propagation might mainly occur by vegetative sprouting in patches with heavy acorn predation. This paper examines this prediction in the same area where the Spanish Juniper study was carried out. The reduction of the crop by vertebrate predators is examined and is expected to be higher in the small forests compared to the large forests, primarily due to predation by mice. Therefore, seedling recruitment, but not vegetative reproduction, should be higher in the large stands. The consequences of these hypothesized differences for the conservation of Holm Oak in small tracts of forests are discussed.

2. Study sites

Field work was carried out in Lerma, Spain, during autumn and winter of two abundant acorn crop seasons (1990–1991 and 1993–1994). Thirteen forest tracts surrounded by farmland were sampled, including ten small woodlots between 0.2 and 12 ha,

Table 1
Area, number of Holm Oaks sampled (*N*), and acorn crops in the small (S1–S10) and large stands (L1–L3) studied in Lerma

	Area (ha)	Autumn 1990			Autumn 1993		
		N	Score Mean (SD)	Crop Size Mean (SD)	*N*	Score Mean (SD)	Crop Size Mean (SD)
S1	0.2	5	11.2 (12.3)	8.8 (14.7)	5	25.6 (27.4)	7.2 (8.6)
S2	0.3	5	7.6 (4.6)	1.4 (1.5)	6	12.5 (14.2)	5.3 (5.3)
S3	0.3	–	–	–	6	15.0 (14.9)	1.6 (2.3)
S4	0.4	–	–	–	6	10.2 (17.2)	5.3 (7.2)
S5	0.6	9	2.3 (2.9)	2.4 (2.7)	7	16.9 (14.2)	3.2 (2.9)
S6	0.7	5	7.8 (14.2)	3.6 (5.0)	7	14.0 (11.8)	1.2 (3.0)
S7	0.8	–	–	–	7	13.9 (13.2)	1.1 (1.2)
S8	1.3	7	1.0 (1.5)	0.8 (0.5)	8	11.4 (13.1)	1.0 (1.1)
S9	2	5	4.8 (4.9)	0.5 (0.4)	8	2.3 (6.4)	0.1 (0.2)
S10	12	–	–	–	10	7.6 (6.7)	1.3 (2.2)
Average S			5.8 (3.8)	2.9 (3.1)		12.9 (6.1)	2.7 (2.4)
L1	150	–	–	–	14	9.7 (11.2)	1.8 (4.7)
L2	280	43	9.4 (10.9)	2.5 (3.2)	15	11.7 (8.9)	3.6 (2.9)
L3	350	–	–	–	15	5.6 (5.1)	2.7 (3.2)
Average L						9.0 (3.1)	2.7 (0.9)
			$t = 0.877$	$t = 0.130$		$t = 1.052$	$t = 0.799$
			$P = 0.3$	$P > 0.5$		$P = 0.3$	$P = 0.4$

Abundance scores and crop sizes (divided by 1000) are given for normal acorns. Values of 1990–1991 are analyzed using the *t*-test proposed by Sokal and Rohlf (1981) to compare a single observation with the mean of a sample.

and three large forests greater than 100 ha, which were considered to be representative of natural non-fragmented conditions (Table 1). All fragments and large stands were studied in 1993–1994, whereas only 6 fragments and one large stand were studied in 1990–1991 (Table 1). The overall cover of Holm Oaks and the mean height of trees are similar in the small and large stands, ranging from 20 to 90% for cover and from 3.4 to 6 m for height.

3. Methods

Acorn crops for each forest tract were assessed from Holm Oaks selected at random from trees having a minimum dbh of 15 cm and heights of 2–8 m. Individual trees were sampled using a cylindrical frame 30 cm in diameter and 15 cm high that was randomly placed over a branch, and the acorns found inside its dimensions were counted. Two types of acorns were identified and counted: (1) normal; and (2) aborted acorns. In mid-October 1990, eight random samples were taken from each tree from the outer edge of the crown, where acorns are located (Ceballos and Ruiz, 1979). The acorns were totalled for each tree, and a score of acorn abundance was obtained for each stand as the mean of the individual tree values. Crops were assessed from crown areas, which were estimated by fitting the crowns to a sphere (Holthuijzen and Sharik, 1985). From these values, a mean estimate of crop size was obtained for each forest stand. Acorn maturation was delayed in the 1993–1994 season, therefore sampling was delayed until early November.

Acorn consumption by vertebrates, which was not appreciable until mid-autumn, steadily increased over the winter. Cumulative consumption was measured in late February 1991 and early April 19940 by searching for acorns under the canopy of each tree. Because most bird and mammal consumers only took portions of the acorns, remnants were easily attributable to either passerines or rodents. Scores of

Table 2
Acorn consumption by mice and birds in 1990–1991 and 1993–1994. The percentages of Holm Oaks in which consumption was recorded (%HO), and scores of acorn consumption are given for each group of consumers. Scores are cumulative values measured in late winter 1991 and early spring 1994 (see Section 3). Percentages are compared by Mann-Whitney *U*-tests and scores by *t*-tests; 1990–91 scores are analyzed with the *t*-test proposed by Sokal and Rohlf (1981) (see Table 1)

	1990–1991				1993–1994			
	Mice		Birds		Mice		Birds	
	%HO	Mean (SD)	%HO	Mean (SD)	%HO	Mean (SD)	%HO	Mean (SD)
S1	100	15.6 (14.9)	0	–	100	17.6 (23.0)	0	
S2	100	19.4 (11.2)	40	1.6 (3.1)	100	23.3 (8.5)	0	–
S3	–	–	–	–	100	13.0 (9.0)	0	–
S4	–	–	–	–	100	23.7 (25.1)	16.7	0.2 (0.4)
S5	100	18.4 (14.1)	0	–	100	14.9 (10.4)	0	–
S6	100	12.4 (6.2)	0	–	100	16.7 (12.2)	14.3	0.3 (0.8)
S7	–	–	–	–	100	28.8 (7.4)	16.7	0.5 (0.8)
S8	100	8.9 (8.1)	0	–	100	4.7 (4.9)	0	–
S9	100	4.6 (4.8)	0	–	50	3.5 (4.4)	25	0.6 (1.4)
S10	–	–	–	–	100	14.4 (8.9)	11.1	0.1 (0.3)
Average S	100	13.2 (5.7)	6.7	0.3 (0.7)	95	16.1 (8.0)	8.5	0.2 (0.2)
L1	–	–	–	–	13.3	0.3 (0.8)	66.7	7.1 (15.6)
L2	28.6	0.0 [a]	83.3	0.4 (0.8)	53.3	1.7 (3.1)	73.3	3.5 (4.3)
L3	–	–	–	–	81.8	2.7 (3.4)	36.4	0.6 (1.0)
Average L					49.5	1.6 (1.2)	58.8	3.7 (3.3)
		$t = 2.13$		$t = 0.146$	$z = 2.58$	$t = 3.032$	$z = 2.525$	$t = 3.887$
		$P < 0.05$ [b]		ns	$P = 0.005$ [b]	$P = 0.006$ [b]	$P = 0.012$	$P = 0.003$

[a] Rare acorns were found out of the samples.

[b] One-tailed test.

mouse and bird acorn consumption were obtained by the same procedure used to quantify acorn abundance, using the cylinder, and consumption rates were obtained as the percentage of crop consumed, after having estimated the numbers of consumed acorns within the parental shadow (drip line). Wood Pigeons, *Columba palumbus*, and Wild Boars ingest whole acorns. Pigeons, however, were only observed in the large stands in very low numbers, exclusively during the autumn visits. An index of Wild Boar feeding activity was attempted, based on records of recent rootings under the sampled trees. Wild Boar rootings were detected in all of the large stands but only in three of the small stands. Acorn consumption by these vertebrates was therefore assumed to be lower in the small stands than in the large stands.

An index of seedling recruitment and vegetative propagation was obtained by searching for established seedlings and ramets, respectively, in mid-June 1991 and 1994 in 1 × 5-m random transects located in the same general areas where acorn sampling had taken place. Each year we examined 60 transects in large stands and 10 transects in small stands. Recent non-woody ramets and seedlings were easily distinguishable because of the acorn remnants attached to the seedlings.

4. Results

4.1. Effects of fragmentation on acorn crop

Because Holm Oak tree size affects crop size (Ceballos and Ruiz, 1979), we estimated tree size (see Section 3) in order to identify size-related differences in the fruit crop between small and large stands. No differences existed in the mean crown diameter between the Holm Oaks sampled in the large stands and those sampled in the small stands (Mann-Whitney *U*-test; sample sizes in Table 1) either in 1990 ($z = 0.506$, $P = 0.6$) or in 1993 ($z = 0.255$, $P = 0.8$). The mean frequencies of acorn-bearing trees were similar for large and small stands, both in 1990 ($z = 0.5$, $P = 0.6$) and 1993 ($z = 0$, $P = 1$); crop sizes and the scores of abundance did not differ for normal acorns (Table 1).

4.2. Patterns of mouse and bird consumption

In 1990–1991, score of acorn consumption by birds and mammals was 33.7 times higher in the small stands than in the large stands. The same pattern was recorded in 1993–1994 (Table 2), with significant differences for both the frequency of Holm Oaks affected by consumption (Mann-Whitney *U*-test: $z = 2.374$, $P = 0.018$) and the consumption score, which was 3.1 times higher in the small stands (*t*-test: $t = 2.280$, $P = 0.043$). The real incidence of mice and bird consumption on the individual acorn crops adjusted to the same trend, with consumption rates of 57.9% (1991) and 38.2% (1994) in small stands, and 6.8% (1991) and 16.6% (1994) in large stands (Table 3).

Mice were responsible for the high acorn consumption in the small stands in both study periods, in contrast with negligible (1990–1991) or low (1993–1994) consumption in the large stands (Table 2). Patterns of acorn consumption by birds were the opposite to those recorded for mice (Tables 2 and 3). More importantly, intake by mice was higher than intake by birds in the small stands in both study

Table 3
Mean rates of acorn comsumption in Lerma. Percentages of the crops consumed by mice and birds are given for the thirteen forests studied (see Table 1 for the number of Holm Oaks sampled in each forest). Percentages are compared by Mann-Whitney *U*-tests

	1990–1991		1993–1994	
	Mice	Birds	Mice	Birds
S1	45.5	0	29.4	0
S2	63.8	4	47.7	0
S3	–	–	64.7	0
S4	–	–	32.6	0.2
S5	63.4	0	35.8	0
S6	60.4	0	41.8	0.4
S7	–	–	59.2	0.8
S8	52.1	0	17.0	0
S9	58.2	0	2.8	0
S10	–	–	49.1	0.6
Average S	57.2	0.7	38.0	0.2
L1	–	–	15.0	4.8
L2	0.3	6.5	4.0	8.5
L3	–	–	0.3	17.2
Average L	0.3	6.5	6.4	10.2
			$z = 2.113$ $P = 0.015$ [a]	$z = 2.578$ $P = 0.01$

[a] One-tailed test.

Table 4
Holm Oak recruitment in Lerma. Percentages of transects in which seedlings and ramets were recorded and mean number of seedlings and ramets per transect are given for the thirteen forests studied. Averages are compared by *t*-tests (see Table 2 for 1991) and percentages by Mann-Whitney *U*-tests

	1991[a]		1994			
	Ramets		Seedlings		Ramets	
	%	Mean (SD)	%	Mean (SD)	%	Mean (SD)
S1	0	0.0	0	0.0	50	2.2 (4.3)
S2	30	0.3 (0.5)	20	0.2 (0.4)	60	1.3 (1.8)
S3	–	–	10	0.1 (0.3)	60	4.2 (9.3)
S4	–	–	0	0.0	50	1.1 (1.5)
S5	30	0.4 (0.7)	0	0.0	30	0.5 (1.0)
S6	70	3.4 (4.6)	20	0.2 (0.4)	70	2.2 (4.2)
S7	–	–	0	0.0	70	3.8 (5.1)
S8	20	0.2 (0.4)	0	0.0	50	1.8 (2.2)
S9	90	2.6 (2.7)	0	0.0	70	6.3 (4.2)
S10		–	10	0.1 (0.3)	40	1.7 (2.8)
L1	–	–	3.3	0.03 (0.2)	43.3	1.9 (4.0)
L2	35	0.7 (1.3)	40	0.83 (1.3)	20	0.4 (1.0)
L3	–	–	41.7	0.78 (1.2)	21.7	0.4 (0.8)
		$t = 0.298$	$z = 1.873$	$t = 3.613$	$z = 2.140$	$t = 1.247$
		$P > 0.2$	$P = 0.03$[b]	$P = 0.02$[b]	$P = 0.032$	$P = 0.239$

[a] Seedlings were absent from the fragments but present in the large stand in 15% of the transects (Mean = 0.19, SD = 0.512).

[b] One-tailed test.

periods (Table 2). The score of acorn consumption by mice was 49 times higher in 1991 (Mann-Whitney *U*-test: $z = 2.906$, $P = 0.004$) and 94.7 times in 1994 (*t*-test: $t = 6.277$, $P < 0.001$), and the percentage of trees affected by mice was also significantly higher in 1991 ($z = 3.015$, $P = 0.003$) and 1994 ($z = 3.780$, $P < 0.001$). Consumption rates showed a similar pattern (Table 3), both in 1991 (Mann-Whitney *U*-test, $z = 2.906$, $P = 0.004$) and 1994 ($z = 3.792$, $P = 0.0001$). Acorn consumption by mice was negatively correlated with forest size in both study periods (1991: Spearman correlation $r_s = -0.893$, $P = 0.029$, $N = 7$; 1994: $r_s = -0.736$, $P = 0.011$, $N = 13$).

4.3. Patterns of seedling recruitment and asexual regeneration

Seedlings were either absent (1991) or significantly less frequent and abundant (1994) in the fragments than in the large stands (Table 4). The mean number of seedlings per transect was 9.1 times higher in the large stands in the latter year. No differences in asexual regeneration were recorded, except in 1994, in which the frequency of ramets was significantly higher in the fragments than in the large stands (Table 4).

5. Discussion and conclusion

Fragmentation can negatively affect the seed output of plants (Nilsson and Wästljung, 1987; Smith et al., 1990; Aizen and Feisinger, 1994). In the small stands of Lerma, both tree size and the abundance of normal acorns in the early dispersal season were similar or superior to those recorded under more natural conditions in the large stands. However, acorn consumption by mice was much higher in the small stands, suggesting that the winter overcrowding of mice recorded on these forest remnants in a previous year (Tellería et al., 1991) also occurred in the study periods of this work. This, in turn, explained why the overall impact of vertebrate predators on the acorn crops was much higher in the small stands in both study years.

An increase in the numbers of rodent seed predators inhabiting patches with small, isolated populations of tree species, seems to be an effect of fragmentation common to agricultural landscapes of temperate localities (Ryszkowski, 1982; Yahner, 1982, 1983; Loman, 1991; Tellería et al., 1991; Tew and Macdonald, 1993; Santos et al., 1995). One prediction of this increase, found in some studies of temperate trees (Wästljung, 1989; Santos and Tellería, 1994; present study), is that stand size should be negatively related to seed consumption by rodents. If seed consumption tends to rise as habitat area declines, seedling recruitment will then be severely reduced or even precluded below a certain habitat size. This negative association was clear in the two study periods. Although, in 1994, seedlings were detected in 4 out of 10 small stands, recruitment failed in another 4 stands in the two study years. If, as expected, seedling recruitment is unlikely to occur in low-production years, time lags between successive recruitment events may become too long to allow forest regeneration by sexual means in many of the small stands. Large acorn production took place in the area only twice in seven years (from 1989 to 1995), which suggests that low-production years are dominant. Acorn production by Holm Oaks is, in fact, highly sensitive to climatic conditions. In addition, highland woods, such as the ones studied in Lerma, often have large production intervals of 7–8 years (Ceballos and Ruiz, 1979).

The long life span of trees can ensure their long-term conservation in severely fragmented landscapes with low recruitment (Dzwonko and Loster, 1989), particularly in species with a strong potential for asexual regeneration such as the Holm Oak (Ceballos and Ruiz, 1979). Previous work in the study area has shown that mice were responsible for a severe depletion of Spanish Juniper seeds in seven small stands (of which six were also included in this work) during a high cone production year (Santos and Tellería, 1994), and that seedling recruitment was lower in these fragments than in large stands. Seed depletion reported here for Holm Oaks was even greater, but, whereas Junipers can only reproduce by seeds (Costa et al., 1986), recruitment can still occur vegetatively in the Holm Oak (Ceballos and Ruiz, 1979). If heavy seed predation is common to small forest remnants, the effects on persistence of isolated plant populations will be more severe in species reproducing exclusively by seeds, especially in short-lived species.

Propagation exclusively by asexual means lacks, however, two key advantages such as, (1) dispersal to adequate habitat patches crossing barriers of inhospitable habitats (crop fields in fragmented landscapes; Fenner, 1985; Matlack, 1994), and (2) maintenance of genetic variation which is crucial in the long term (Loveless and Hamrick, 1984; Ledig, 1986). Although seedling recruitment was detected in fragments as small as 0.3 ha, current trends of landscape exploitation in the study area point to a progressive deterioration (felling of large, productive Holm oaks) and shrinkage of the fragments (authors' data over seven years), similar to the general trend reported in the temperate zone to produce tiny fragments (Wilcove et al., 1986). If a hypothetical minimum size for seedling recruitment exists, this trend would passively enhance the prevalence of asexual regeneration by gradually increasing the number of fragments below this threshold.

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