

Birds as predators of cork and holm oak pests

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Abstract The recent decline of Mediterranean oak woodlands in SW Iberian Peninsula is related to insect pests which affect both cork oak (Quercus suber) and holm oak (Quercus rotundifolia). We identified twentysix bird species as potential regular predators of twenty major pests by reviewing the diet of breeding, wintering and resident species in this ecosystem. Foraging guilds are strongly associated with predation at distinct stages of the pests' life-cycle: ground-foragers prey on overwintering pupae and larvae of seed-borers, treeforagers prey on eggs, larvae and pupae of defoliating and wood-boring pests, and aerial-sweepers prey on airborne imagines. Bird predation can cover the complete life-cycle of pest species because different species may be complementary due to a dissimilar exploitation of foraging niches and periods. Small generalist tree-foraging passerines are important pest predators given their high densities and widespread distribution in Mediterranean oak woodlands, but management practices can have a significant negative effect in their populations.

Keywords Biocontrol · Foraging guild · Insectivory · Mediterranean oak woodland · *Quercus*

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Introduction

Mediterranean oak woodlands extend over 6.3 million hectares in SW Iberian Peninsula, and are known as montados in Portugal and dehesas in Spain (Joffre et al. 1999; Fig. 1). This ecosystem is characterized by a scattered tree cover dominated by two evergreen Mediterranean oaks, cork oak (Quercus suber) and holm oak (Quercus rotundifolia), and has been structured by a systematic combination of agricultural, pastoral, and forestry uses (Marañón 1988; Pinto-Correia 1993; Plieninger and Wilbrand 2001). Traditional management has been developed for extensive livestock rearing, originally Iberian pigs but nowadays also sheep and cattle, which feed on acorns, from autumn to early spring, and herbs during the rest of the year (Joffre et al. 1988; Pinto-Correia and Mascarenhas 1999). Poor or non-agricultural land is mostly cultivated to prevent shrub invasion of grassland and to supply fodder and grain for livestock; harvesting is a secondary goal (Gómez Guttierez and Pérez Fernández 1996; Olea et al. 2005; Costa et al. 2009). Forestry management is aimed at the exploitation of cork, the most economically significant product of this system (Carvalho Mendes and Graça 2009; Ribeiro et al. 2010) and at enhancing crown coverage per tree for acorn production, as well as other side-products such as firewood.

A sustainable human usage of Mediterranean oak woodlands conceivably occurred since the Middle Age, however, in the second half of the 19th century

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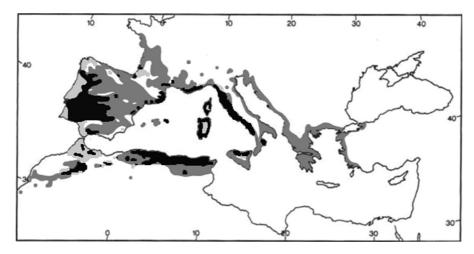


Fig. 1 Distribution of cork oak (*light grey*) and holm oak (*dark grey*) and species coexistence areas (*black*) (adapted from Costa et al. 1998)

the decline and mortality of cork and holm oaks were first recorded for trees of distinct ages (Almeida 1898; Câmara-Pestana 1898). Most of the described symptoms can still be observed in present days: trunk cankers, wounds, resinous exudates from the bark, reduced branch growth, epicormic shooting, necrosis in the root cortex, defoliation and transparency of the crown, chlorosis, dieback and finally death (Branco and Ramos 2009). Several authors linked this slow decaying process to the incidence of pathogenic fungi, mainly Phytophthora cinnamomi and Biscogniauxia mediterranea, in trees periodically exposed to soil drought and dampness (Natividade 1945; Azevedo 1958; Barbosa 1958; Torres 1985; Brasier 1993; Cobos et al. 1993; Tuset et al. 1996; Vannini et al. 1996; Gallego et al. 1999; Luque et al. 1999, 2000; Santos 2003; Martín et al. 2005; Henriques et al. 2012; Serrano et al. 2012). Furthermore, insect pests which until recently did not markedly affect these ecosystems, except for sporadic outbreaks of defoliator insects (Neves 1950), boosted the physiological instability of trees and hampered the regeneration of cork and holm oaks.

Severe tree defoliations, caused mostly by moths, reduce acorn production, stem growth and, in the case of cork oaks, also cork growth (Magnoler and Cambini 1973; Ferreira and Ferreira 1991). Trees weakened by intense defoliation are exceptionally vulnerable to xylophagous pests, whose increasing population levels may not affect exclusively trees that are stressed, weakened or decaying, but healthy and young trees as well (Sousa et al. 1995; Sousa and Debouzie 1999, 2002; Sousa and Inácio 2005). Moreover, pre-dispersive acorn predation by carpophagous insects, comprising weevils and moths with seed-boring larvae, severely constrains cork and holm oak regeneration by affecting the emergence and survival of seedlings (Nogueira 1967; Aizpúrua 1993; Soria et al. 1996, 1999a, b; Siscart et al. 1999; Branco et al. 2002a; Leiva and Fernández-Alés 2005; Jiménez et al. 2006; Bonal and Muñoz 2007; Jiménez et al. 2011).

Numerous entomopathogens and arthropods (parasitoids, predators and competitors) can contribute to restrict cork and holm oak pest populations by controlling their abundance and distribution at different stages of the life-cycle (Ferreira and Ferreira 1991; Romanyk and Cadahia 1992; Villemant and Ramzi 1995; Villemant and Andreï-Ruiz 1999). Concerning insectivorous vertebrates, birds play an important role as pest predators in several agroforestry ecosystems (e.g., Solomon et al. 1976; Holmes et al. 1979; Kroll and Fleet 1979; Campbell et al. 1983; Loyn et al. 1983; Joern 1986; Fowler et al. 1991; Bock et al. 1992; Mols and Visser 2002; Hooks et al. 2003; Fayt et al. 2005; Ji et al. 2008; Koh 2008; Van Bael et al. 2008; Whelan et al. 2008; Johnson et al. 2010; Bereczki et al. 2014). Insectivorous birds are a dominant guild of bird communities in Mediterranean oak woodlands (Herrera 1978a; Rabaça 1990; Almeida 1992a, 1997; Peris and Masa 1992; Pulido and Díaz 1992; Finlayson et al. 2002; Santos et al. 2002; Camprodon and Brotons 2006; Godinho and Rabaça 2011; Leal et al. 2011a)

but there is no comprehensive study about their role in controlling cork and holm oak pests. Actually, there are very few studies on birds' diet and foraging ecology in *montados* and *dehesas*, and these are often published in the grey literature and not in English.

The present review aims to document: (i) which bird species can regularly feed on cork and holm oak pests in Mediterranean oak woodlands of the Iberian Peninsula; (ii) the relationship between the foraging niches used by bird predators and the distinct lifecycle stages of pests; and (iii) potential correlations between birds' phenology and the biology of consumed pests. We additionally examined the effect of typical management strategies on bird assemblages and provide recommendations to enhance pest control by birds in montados and dehesas. Overall, this review provides a comprehensive framework on the role of birds as potential predators in controlling cork and holm oak insect pests (hereafter named pests), which will be particularly important to stimulate further studies on this issue.

Cork and holm oak pests

We listed twenty species of insects whose regular damages in *montados* and *dehesas* cause considerable economic losses (Table 1).

Lepidopterous larvae, particularly of Catocala spp., Euproctis chrysorrhoea, Lymantria dispar, Malacosoma neustria and Tortrix viridana, are the most important defoliators of cork and holm oak trees (Toimil 1987, 1989; Ferreira and Ferreira 1991; Villemant and Fraval 1991, 1999; Romanyk and Cadahia 1992). In some areas, extreme defoliations are also attributed to larval sawflies (*Periclista* spp.) and weevils (Orchestes spp.) (Silva 1960; Nogueira 1967; Baeta-Neves et al. 1972; Toimil 1987, 1989; Ferreira and Ferreira 1991), and larvae of Coeliodes ruber, another weevil species, dig galleries inside little branches stopping trees to burgeon (Ferreira and Ferreira 1991). Despite other phytophagous insects, such as gall inducing (e.g., gall midges and gall wasps) and sapsucker insects (e.g., aphids), often occur on trees, their damage is usually negligible (Aldrey 1981; Skuhravá et al. 1996; Villemant and Fraval 1991; Inácio et al. 2002).

Three main groups of wood-boring insects attack cork and holm oak trees: ambrosia beetles (particularly Platypus cylindrus), longhorn beetles (Cerambyx cerdo and Phymatodes testaceus) and buprestids of the genus Coraebus (Ferreira and Ferreira 1991; Villemant and Fraval 1991; Romanyk and Cadahia 1992). Ambrosia beetles are xylomycetophagous, coping with many genera of endosymbiotic fungi which will feed their larvae inside galleries in the wood, therefore acting as a vector for fungal diseases (Sousa et al. 1997; Sousa and Debouzie 2002; Henriques et al. 2009; Inácio et al. 2011). Longhorn beetles are considered secondary pests, however they open outsized holes in trees which can act as entryways for fungal infection (Soria et al. 1994a; Martín et al. 2005). Buprestids' activity can take place either on the branches or trunk of the trees; Coraebus florentinus makes longitudinal and annular larval galleries under the bark of the branches, interrupting sap flow and thus causing branch death, whilst *C. undatus* larvae feed under the trunk bark of cork oak trees, digging galleries in the cambium, where the new cork tissue is formed (Natividade 1945; Benitez Morera 1961; Merle and Attié 1992; Soria et al. 1992, 1994a; Suñer and Abós 1994). The last species accounts for the most significant economic losses in cork production (Merle and Attié 1992), although cork spoilage as a consequence of the nest construction activity of an ant species, Crematogaster scutellaris, has also been frequently reported (Natividade 1945; Montoya Oliver 1988; Villagran and Ocete 1990; Villemant and Fraval 1991; Soria et al. 1994b).

The viability of acorns can be restricted by weevils (*Curculio elephas*) and moths (*Cydia* spp.). These oviposite inside developing acorns of cork and holm oak within which the feeding larva completes growth; after seed dropping, the larva buries itself into the soil where pupation takes place (Nogueira 1967; Aizpúrua 1993; Soria et al. 1996, 1999a, b; Siscart et al. 1999; Branco et al. 2002a; Leiva and Fernández-Alés 2005; Jiménez et al. 2006; Bonal and Muñoz 2007; Jiménez et al. 2011). Even if larval activity does not directly affect the embryo in some cases, attacked acorns are more vulnerable to rotting fungi which are responsible for higher postgermination mortality (Branco et al. 2002b).

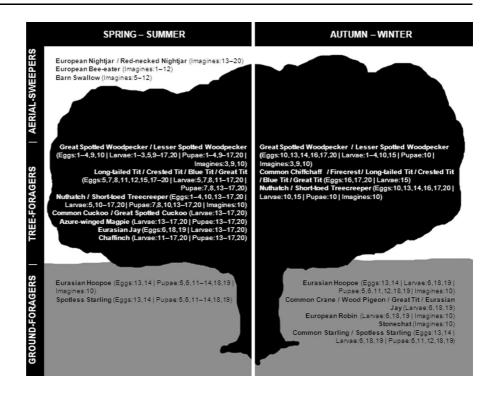
Foraging niches of bird predators

The foraging niches of bird predators were used to explore the relationship with the different life-cycle stages of pests (Fig. 2; Table 2). We identified

Table	I Insect species that	t damage	significantly cork oak and	Table 1 Insect species that damage significantly cork oak and holm oak in Mediterranean oak woodlands of SW Iberian Peninsula	s of SW Iberian Peninsula	
No.	Insect	Type	Eggs	Larvae	Pupae	Imagines
Coleoptera	ptera					
Bupr	Buprestidae (Buprestids)					
-	Coraebus florentinus	×	Branch May–Jul	Gallery inside branch Jun-May (diapause 2-4 years)	Gallery inside branch Apr-May	Airborne May-Jun
	Herbst 1801					
7	Coraebus undatus	M	Trunk May–Jul	Gallery inside trunk Jul-May (diapause	Gallery inside trunk	Airborne May-Jun
	Fabricius 1787			up to 2 years)	May-Jun	
Cerai	Cerambycidae (Longhorn beetles)	beetles)				
б	Cerambyx cerdo	M	Trunk Aug–Sep	Gallery inside trunk Sep-Jul (diapause	Gallery inside trunk	Gallery inside trunk Oct-Jul/Airborne
	Linnaeus 1758			2–3 years)	Aug-Sep	Jun-Sep
4	Phymatodes testaceus	M	Trunk or branch Jul- Sep	Gallery inside wood Sep–Apr	Gallery inside wood Mar-May	Airborne May-Aug
	Linnaeus 1758					
Curci	Curculionidae (Weevils)					
S	Coeliodes ruber	L	Leaf bud Mar–Apr	Gallery inside twig Apr-May	Soil May	Airborne May-Mar (hibernate)
	Marsham 1802					
9	Curculio elephas	S	Acorn Aug-Oct	Acom Sep-Nov	Soil Nov–Jul	Airborne Jun-Sep
	Gyllenhal 1836					
L	Orchestes erythropus	Γ	Leaf parenchyma Mar	Leaf parenchyma Mar – Leaf parenchyma Mar–May	Leaf May–Jun	Airborne Jun-Mar (hibernate)
	Germar 1821					
8	Orchestes irroratus	L	Leaf parenchyma Mar	Leaf parenchyma Mar Leaf parenchyma Mar-May	Leaf May–Jun	Airborne I Jun-Mar (hibernate)
	Kiesenwetter 1852					
6	Platypus cylindrus	M	Gallery inside wood	Gallery inside wood Apr-Aug	Gallery inside wood	Gallery inside wood! Jul-May/Airborne!
	Fabricius 1792		Mar-Jun		May-Aug	May–Jan
Hymer	Hymenoptera					
Form	Formicidae (Ants)					
10	Crematogaster scutellaris	C	Ant colony inside cork	Ant colony inside cork	Ant colony inside cork	Free-living/Airborne Jun–Jul
	Olivier 1792					

No.	Insect	Type	Eggs	Larvae	Pupae	Imagines
Tent	Tenthredinidae (Sawflies)					
11	11 Periclista andrei Konow 1906	D	Leaf parenchyma I Mar-May Leaf I Apr-Jun	Leaf Apr–Jun	Soil May-Apr (diapause 1-3 years) Airborne Mar-May	Airborne Mar-May
12	Periclista dusmeti Konow 1907	D	Leaf lower epidermis Mar- May	Leaf Apr-Jun	Soil May–Apr (diapause several months)	Airborne Mar-May
Lepidoptera Erebidae	optera idae					
13	13 Catocala nymphaea Esper 1787	D	Soil or trunk Jul-May	Leaf Apr–Jun	Leaf, trunk or soil Jun–Jul	Airborne (nocturnal) Jun-Jul
14	Catocala nymphagoga Esper 1787	D	Soil or trunk Jul–May	Leaf Apr-Jun	Leaf, trunk or soil Jun–Jul	Airborne (nocturnal) Jun–Jul
15	Euproctis chrysorrhoea Linnaeus 1758	D	Leaf lower epidermis Jun– Aug	Leaf Aug_Jul (hibernate)	Twig Jun-Jul	Airborne (nocturnal) Jun–Jul
16 Lasio	16 Lymantria dispar Linnaeus 1758 Lasiocampidae	D	Trunk or branch I Jul-Apr	Leaf Mar–Jul	Trunk or canopy May–Jul	Airborne (nocturnal, 🄉 non-flying) Jun-Aug
17 Tortri	 17 Malacosoma neustria Linnaeus 1758 Tortricidae 	D	Twig Jun–Mar	Leaf Mar–Jun	Leaf or twig May–Jun	Airborne (nocturnal) May–Jun
18	18 Cydia fagiglandanaZeller 1841	S	Acorn Jun-Oct	Acorn Jul-Dec	Soil Oct–Sep	Airborne (crepuscular) May–Oct
19	Cydia splendana Hübner 1799	S	Acorn Aug–Oct	Acorn Aug-Nov	Soil Nov-Jul	Airborne (crepuscular) Jul-Sep
20	<i>Tortrix viridana</i> Linnaeus 1758	D	Twig May–Apr	Leaf Mar–May	Leaf Apr–May	Airborne (nocturnal) Apr–Jul

1S. presented for each species (*C* cork-borer, *D* defoliator, *L* leaf-miner, *S* seed-borer, *W* wood-borer) along with information on the calendar and the substrate used by the different life-cycle stages in Mediterranean oak woodlands. References are cited in text under the section 'Cork and holm oak pests'. The bird predators of each prey are presented in Fig. 2 using the prey number indicated in this table **Fig. 2** Relationship between the seasonal foraging niches used by bird predators and the different life-cycle stages of cork oak and holm oak insect pests in SW Iberian Peninsula. Potential prey are identified by numbers which refer to species listed in Table 1. For the scientific name of birds see text or Table 2



resident, breeding and wintering bird species as potential regular predators of cork and holm oak pests in SW Iberian Peninsula whenever their diet in Mediterranean oak woodlands or elsewhere notably includes the above mentioned pests or their taxonomic counterparts.

Ground-foragers: predation on overwintering pupae and larvae of seed-borers

Insectivorous birds foraging on or in the ground may be of special relevance as predators of pests whose larvae overwinter or pupate in the soil, such as weevils (*C. ruber* and *C. elephas*), sawflies (*Periclista* spp.) and moths (*Cydia* spp.).

The Eurasian Hoopoe *Upupa epops* probes in soil with its long curved bill (5–6 cm) to forage on buried larvae and pupae (Cramp and Perrins 1998). This large insectivorous specialist species is resident in SW Iberian Peninsula though less abundant during winter (BirdLife International 2004; SEO/BirdLife 2012). At least during breeding, in spring and early summer, it is an important predator of lepidopterous larvae and pupae in various woodlands of southern Europe (Gonzalez-Cano 1981; Battisti et al. 2000; Fournier and Arlettaz 2001) where it contributes to the

regulation of forest pest populations under nonoutbreak conditions (Battisti et al. 2000).

The Common Starling Sturnus vulgaris and the Spotless Starling Sturnus unicolor are opportunistic feeders which forage largely on the ground (Cramp and Perrins 1998). Much of their food is taken below soil surface making use of a special open-bill probing technique: individuals push the closed bill into the soil, open it to create a hole, and during bill-opening, eyes can rotate forward avoiding the necessity of turning head to one side to see into the hole (Beecher 1978). Pupal and larval lepidopterous, sawflies, and weevils are described as common prey of both species during the breeding season, when starlings are mainly insectivorous (Cramp and Perrins 1998). Yet, while the worldwide distribution of the Spotless Starling is greatly restricted to the Iberian Peninsula (BirdLife International 2004), the Common Starling is essentially a winter visitor (Motis et al. 1983; Tellería et al. 1988; SEO/BirdLife 2012). In montados of SE Portugal, hymenopterous larvae and lepidopterous larvae and pupae comprised 18 and 15 %, respectively, of the items given by the Spotless Starling to nestlings (Almeida 1996a). In dehesas of W Spain, adult birds consumed many imago and larval coleopterous, hymenopterous and larval lepidopterous (Peris

Table 2 Birds feeding on cork oak and holm oak insect pests and their status in the Iberian Peninsula

ORDER/species	Niche	Phenology	Abundance	Distribution
GRUIFORMES				
Common Crane	GF	W	Uncommon	Local
Grus grus				
COLUMBIFORMES				
Wood Pigeon	GF	R	B: common	Ubiquitous
Columba palumbus			W: abundant	
CUCULIFORMES				
Common Cuckoo	FG	В	Common	Ubiquitous
Cuculus canorus				-
Great Spotted Cuckoo	FG	В	Uncommon	Scattered
Clamator glandarius				
CAPRIMULGIFORMES				
European Nightjar	ASW	В	Common	Scattered
Caprimulgus europaeus				
Red-necked Nightjar	ASW	В	Common	Scattered
Caprimulgus ruficolis				
CORACIIFORMES				
European Bee-eater	ASW	В	Common	Widespread
Merops apiaster		2	common	
Eurasian Hoopoe	GF	R	B: common	B: ubiquitous
Upupa epops			W: uncommon	W: scattered
PICIFORMES				
Great Spotted Woodpecker	BG-EX	R	Common	Widespread
Dendrocopos major				·····F
Lesser Spotted Woodpecker	BG-EX	R	Rare	Local
Dendrocopos minor				
PASSERIFORMES				
Barn Swallow	ASW	В	Abundant	Ubiquitous
Hirundo rustica		_		
European Robin	GF	R	Abundant	B: widespread
Erithacus rubecula	01		1 TO UNIQUITY	W: ubiquitou
Stonechat	GF	R	Common	Ubiquitous
Saxicola torquata	01	it it	Common	oliquitous
Common Chiffchaff	FG	R	B: uncommon	B: scattered
Phylloscopus collybita	10	it it	W: abundant	W: ubiquitou
Firecrest	FG	R	Abundant	B: scattered
Regulus ignicapillus	10	it it	rioundunt	W: ubiquitou
Long-tailed Tit	FG	R	Abundant	Widespread
Aegithalos caudatus	10	ix i	rioundant	
Crested Tit	FG	R	Abundant	Scattered
Lophophanes cristatus	10	IX	ribunudin	Scattered
Blue Tit	FG	R	Abundant	Ubiquitous
Cyanistes caeruleus	10	IX.	roundalit	Obiquitous
Great Tit	FG-GF	R	Abundant	Ubiquitous
Parus major	1'U-UF	K	Abunualit	Obiquitous

Table 2 continued

ORDER/species	Niche	Phenology	Abundance	Distribution
Nuthatch	BG	R	Abundant	Scattered
Sitta europaea				
Short-toed Treecreeper	BG	R	Abundant	Widespread
Certhia brachydactyla				
Azure-winged Magpie	FG	R	Common	Local
Cyanopica cyanus				
Eurasian Jay	FG-GF	R	Common	Widespread
Garrulus glandarius				
Common Starling	GF	R	B: common	B: local
Sturnus vulgaris			W: abundant	W: scattered
Spotless Starling	GF	R	Abundant	Ubiquitous
Sturnus unicolor				
Chaffinch	FG	R	Abundant	Ubiquitous
Fringilla coelebs				

'Niche' corresponds to the foraging categories considered in this review (*GF* ground-foraging, *FG* foliage-gleaning, *BG* barkgleaning, *EX* excavating, *ASW* aerial-sweeping). 'Phenology' (*R* resident breeding species, *B* breeding visitor, *W* winter visitor), 'Abundance' (*abundant* >1 million pairs, *common* >100,000 pairs, *uncommon* >10,000 pairs, *rare* >5,000 pairs) and 'Distribution' (*ubiquitous* >75 % of the area, *widespread* >50 % of the area, *scattered* >25 % of the area, *local* \leq 25 % of the area) of bird species in the Iberian Peninsula are presented according to Martí and Del Moral (2003), BirdLife International (2004), Equipa Atlas (2008) and SEO/BirdLife (2012)

1980a) while nestlings' diet comprised mostly larval and pupal lepidopterous and imago coleopterous (Peris 1980b). In NE Spain, although in a farmland ecosystem, larval weevils predominated in the diet of Spotless Starling adults while first year birds ate mostly imago weevils (Escartín Porta et al. 1996).

Besides being eaten by ground foraging birds while pupating in the soil, larvae of seed-borers (C. elephas and Cydia spp.) are also unintentionally preved by granivorous birds feeding on acorns (intraguild predation). Infested acorns are prematurely abscised and the larvae complete their development inside the acorns after these drop on the ground (Bonal and Muñoz 2007), making them vulnerable to predation before the insect pupates in the ground. Between November and March, fallen acorns are a main food for six to seven million wood pigeons Columba palumbus (Purroy et al. 1984; Purroy 1988; Díaz and Martín 1998; Bea and Fernández-García 2001; Bea et al. 2003) and 155,000 common cranes Grus grus (Soriguer and Herrera 1977; Almeida and Pinto 1992; Díaz et al. 1996; Cruz 1998) wintering in Iberian Peninsula, although cranes' distribution is fairly localised (Fernández-Cruz et al. 1981; Alonso and Alonso 1986; Almeida 1992b, 1996b; Prieta and Del Moral 2008; SEO/BirdLife 2012). Many corvids occurring in Mediterranean oak woodlands occasionally include acorns in their diets (Soler and Soler 1991) but only the Eurasian Jay Garrulus glandarius strongly depends on acorns for food, foraging on ground except when collecting acorns in autumn for hoarding (Bossema 1979; Gómez 2003; Pons and Pausas 2007a, b). Bird predation on infested acorns may decrease insect numbers up to the point of reducing acorn infestation rates (Drew 1987; Herrera 1989), but granivorous birds are acorn predators too. Furthermore, they have a direct negative effect on oaks' regeneration as predators of uninfested acorns, which can be selected over infested acorns by some birds (Dixon et al. 1997). Therefore, cork and holm oaks may not necessarily receive a net benefit from birds' intraguild predation on seed-borer larvae.

On the other hand, small abundant passerines may notably consume seed-borer larvae when feeding on the endosperm of cracked acorns without affecting viable ones. Fallen acorns can be extensively used by tits (Herrera 1980), particularly by the Great Tit *Parus major* which may spend 18 % of its foraging time on the ground during winter (Almeida and Granadeiro 2000). Also, wintering European robins *Erithacus* *rubecula*, which reach very high densities in the Mediterranean oak woodlands of SW Iberian Peninsula (Herrera 1978a, 1980; Tellería et al. 1988; Peris and Masa 1992; SEO/BirdLife 2012), greatly rely on acorn endosperm to increase weight (Herrera 1977), and it may represent approximately half of the diet during the mid-winter period (Debussche and Isenmann 1985).

Studies on the autumn-winter diet of groundforaging birds in Mediterranean habitats (Herrera 1977, 1978b, 1984a; Cabello et al. 1991a) pointed out the importance of ants for several species, in particular for the Eurasian Hoopoe, the European Robin and the Stonechat Saxicola torquata which present substantial winter populations in montados and dehesas (Tellería et al. 1988; Peris and Masa 1992; SEO/BirdLife 2012). Between October and February, the proportion of ants in the invertebrate fraction of the diet was 76 % for the European Robin (Herrera 1977), 54 and 63 % for the Stonechat (Herrera 1984a; Cabello et al. 1991a, respectively), and 66 % for the Eurasian Hoopoe (Herrera 1984a). Although ants of the genera Messor and Lasius were the most common in their diets (Herrera 1984a; Cabello et al. 1991a), worker ants of the cork-boring species C. scutellaris may be preyed as well.

Tree-foragers: predation on defoliators and woodborers

Three guilds of insectivores can be considered among tree-foraging birds: foliage-gleaners, bark-gleaners, and excavators. Foliage-gleaning is broadly used by birds during the spring-summer period, coinciding with the sprouting of young leaves on oak trees and the larval and pupal development of defoliator moths (Catocala spp., E. chrysorrhoea, L. dispar, M. neustria and T. viridana), sawflies (Periclista spp.) and weevils (Orchestes spp.). Since many oak pests lay eggs on the trunk, branches and twigs of trees, bark-gleaners may be relevant egg predators of defoliator moths (as well as their pupae), buprestids (Coraebus spp.) and longhorn beetles (C. cerdo and P. testaceus). Moreover, colonies of C. scutellaris may also be preyed by bark-gleaners, eating the eggs, larvae, pupae and imagines of this cork-boring ant species. The excavators' guild is represented by forest specialists, namely woodpeckers, that feed on woodboring insects (C. florentinus, C. undatus, C. cerdo, P. *testaceus* and *P. cylindrus*) when their larvae, pupae and imagines are enclosed in galleries inside wood.

Tits are the most representative group of treeforaging insectivores, accounting with four resident species in montados and dehesas: Great Tit, Blue Tit Cyanistes caeruleus, Crested Tit Lophophanes cristatus, and Long-tailed Tit Aegithalos caudatus (Herrera 1978a, c, 1979; Rabaça 1990; Almeida 1992a; Peris and Masa 1992; Almeida and Granadeiro 2000; Finlayson et al. 2002; Leal et al. 2011a). In particular, the former two species are the most important foliagegleaners both due to their high densities in Mediterranean oak woodlands (Herrera 1978a; Rabaça 1990; Peris and Masa 1992; Pulido and Díaz 1992; Díaz and Pulido 1993; Almeida 1997; Santos et al. 2002; Camprodon and Brotons 2006; Leal et al. 2011a) and their constant foraging activity on cork and holm oak trees (Herrera 1978b; Díaz and Pulido 1993; Pulido and Díaz 1994; Leal et al. 2011b, 2013), spending annually more than 65 % of their foraging time on foliage branches (Leal et al. 2013). Tits are generalist species, although during the breeding season their diet comprises around 90 % of phytophagous insects, mainly lepidopterous larvae (Cramp and Perrins 1998). Worldwide, tits have proved to be effective predators of oak defoliators, including T. viridana, Catocala spp. and Coeliodes spp. (Betts 1955; Romanyk and Cadahia 1992), in particular during the larval stage (Murakami and Nakano 2000; Sanz 2001). Foraging tits typically aggregate in areas where prey density is higher (Díaz et al. 1998) and positive numerical responses to outbreaks of defoliator moths' larvae have been described in the Iberian Peninsula (Pimentel and Nilsson 2007, 2009). With the decrease of lepidopterous larvae along the breeding season, the proportion of pupae and eggs taken by tits from branches and twigs increases in both nestlings' and adults' diet (Cramp and Perrins 1998). Summer diet of Blue Tit in dehesas showed that both young and adult birds ingested a large proportion of Coleoptera, although soft-bodied prey may be underestimated by faecal analyses (Pulido and Díaz 1994).

Four species forage exclusively on trees, the Great Spotted Woodpecker *Dendrocopos major*, the Lesser Spotted Woodpecker *D. minor*, the Nuthatch *Sitta europaea*, and the Short-toed treecreeper *Certhia brachydactyla*, gleaning most of their year-round prey from trunks and large branches (Almeida and Granadeiro 2000; Leal et al. 2011b, 2013). These species consume eggs, larvae and pupae of Lepidoptera, including T. viridana, coleopterous imagines and ants caught in bark surface, cracks and crevices (Cramp and Perrins 1998). Nuthatch's diet in dehesas was exclusively composed of invertebrates between March and August: a monthly percentage of 76–100 % of the stomachs analysed contained Coleoptera and, between March and June, 10-36 % contained Lepidoptera (Ceballos 1969). Nuthatches often hammer with bill when foraging, but apparently they are not able to chisel into wood to get wood-boring insects, unless it is rotten (Cramp and Perrins 1998). On the other hand, woodpeckers proficiently excavate wood to expose wood-borers not only in dead and decaying wood but also on trunks and branches of living hardwood trees (Solomon 1969). Due to the morphological adaptations, provided by the head and neck muscles and bones, the Great Spotted Woodpecker can drill holes up to 10 cm deep, by hammering bark and wood with lateral and vertical blows of bill. Moreover, it can probe fissures with its tongue almost twice larger than bill (\sim 4 cm), making use of a sharp tip to impale softbodied prey while harder insects adhere to tongue bristles coated with sticky saliva (Cramp and Perrins 1998). Larvae, pupae and imagines of many buprestids, bark beetles, longhorn beetles, and weevils are an essential part of woodpeckers' diet in addition to surface-dwelling insects (Cramp and Perrins 1998). For that reason, woodpeckers have been reported to play a significant role in the regulation of wood-boring pests in some forestry ecosystems in the Iberian Peninsula (Valente and Branco 2008).

During spring and summer, the Chaffinch Fringilla coelebs forages considerably on trees, although the ground is the main foraging substrate for the remainder of the year in Mediterranean oak woodlands (Herrera 1980; Almeida and Granadeiro 2000). Invertebrates represent the bulk of Chaffinch's diet during this period and nestlings are fed mainly with leaf-dwelling insects, including defoliator lepidopterous larvae (Cramp and Perrins 1998). The Eurasian Jay also feeds nestlings with a large number of lepidopterous larvae from leaves of trees, including T. viridana in oak woodlands (Bossema 1979). Accordingly, in montados of SE Portugal, lepidopterous larvae and pupae comprised 42 % of the Azure-winged Magpie Cyanopica cyanus nestlings' diet in terms of biomass (Canário et al. 2002). Two breeding migrants, the Great Spotted Cuckoo Clamator glandarius and the Common Cuckoo Cuculus *canorus*, also feed on late-instar lepidopterous larvae, including numerous colonial, hairy, and aposematic species (Valverde 1971; Gonzalez-Cano 1981; Cramp and Perrins 1998; Hoyas and López 1998). Cuckoos are highly adapted to deal with urticating caterpillars (e.g., *E. chrysorrhoea, L. dispar* and *M. neustria*) owing to their soft gizzard wall structure, and pellets of noxious hairs can be regurgitated together with chitin (Cramp and Perrins 1998). In a 36-year study of Common Cuckoo's stomach content from central Europe (Link 1889, cited in Cramp and Perrins 1998), *L. dispar* and *M. neustria* were often full with larvae of these two moth species (e.g., 173 larvae of *M. neustria* were found in a single stomach).

During the autumn-winter period, insectivorous passerines wintering or transient in Mediterranean habitats rely heavily on plant material, mainly fleshy fruits taken from shrubs and endosperm of dropped acorns, and include insects only as a minor part of their diets (Herrera 1977, 1981; Jordano 1981; Jordano and Herrera 1981; Herrera 1983, 1984b; Jordano 1987a, b, 1989; Cabello et al. 1991b; Herrera 1998). Nevertheless, the Chiffchaff Phylloscopus collybita and the Firecrest Regulus ignicapillus are tree-foraging migrants whose diet can be exclusively insectivorous while wintering in the Iberian Peninsula (Guitián 1985; Jordano 1987a). In montados and dehesas, these species forage together with resident tits at the outermost branches and twigs of cork and holm oak trees (Herrera 1979, 1980; Almeida and Granadeiro 2000; Leal et al. 2011b, 2013) where they may well glean for overwintering eggs and larvae of some lepidopterous pest species.

Aerial-sweepers: predation on airborne imagines

Aerial-sweepers are typically associated to open agroforest habitats and reach higher densities in semi-open than in dense Mediterranean oak woodlands (Herrera 1978a; Finlayson et al. 2002; Santos et al. 2002; Camprodon and Brotons 2006; Godinho and Rabaça 2011). This guild comprises a few migratory breeding species which abundantly catch insects in flight during spring and summer (Herrera 1978a), coinciding with the airborne imago stage of cork and holm oak pests.

Most European species of aerial-sweepers correspond to hirundines and swifts which are known to prey mostly on Diptera but also on flying imagines of the orders Coleoptera, Hymenoptera and Lepidoptera (Cramp and Perrins 1998). In particular, the breeding densities of the Barn Swallow *Hirundo rustica* are much higher in areas with more livestock farming and rural architecture, which contribute to provide food resources and nesting sites, respectively (Ambrosini et al. 2002), and therefore they are likely to be more abundant in *montados* and *dehesas* with these characteristics. Airborne imagines of hymenopterous and weevils may represent profitable prey given that barn swallows feed preferentially on large insects (~ 6 mm), despite their relatively lesser abundance (Turner 1982).

Nightjars are fairly specialized in the crepuscular and nocturnal predation of lepidopterous imagines (Cramp and Perrins 1998). Moths can represent >80 % biomass in the diet of adults and up to 93 % in the diet of nestlings of the European Nightjar Caprimulgus europaeus in central Europe (Sierro et al. 2001). In SW Iberian Peninsula, this species occurs together with the Red-necked Nightjar Caprimulgus ruficolis, which is more common as a breeder in this region (Cuadrado and Dominguez 1996; Santos et al. 2002; Martí and Del Moral 2003; Equipa Atlas 2008). Since the imagines of lepidopterous species damaging cork and holm oak are predominantly active at dusk and at night, these may be an important prey for nightjars in Mediterranean oak woodlands with a sparse tree cover.

The European Bee-eater *Merops apiaster* is a common breeding visitor to SW Iberian Peninsula (Martí and Del Moral 2003; Equipa Atlas 2008). Hymenoptera are the most important prey in its diet, particularly honey bees *Apis mellifera*; pellet analysis from Spanish *dehesas* showed a considerable percentage (6–28 %) of coleopterous imagines, including longhorn beetles and weevils (Herrera and Ramirez 1974; Martínez 1984; Arenas and Torres 1987). Similar results were obtained in Portuguese *montados*, where the percentage of Coleoptera in the pellets varied between 11 and 42 % and included imagines of large longhorn beetles and weevils as well (Costa 1991).

Discussion

In this review we recognize the potential of twenty-six bird species as predators of the most relevant cork and holm oak pests in the Iberian Peninsula, which correspond to more than a third of the bird assemblage of montados and dehesas (Herrera 1978a; Rabaça 1990; Almeida 1992a, 1997; Peris and Masa 1992; Pulido and Díaz 1992; Finlayson et al. 2002; Santos et al. 2002; Camprodon and Brotons 2006; Godinho and Rabaça 2011; Leal et al. 2011a). Tree-foraging birds represent the most important predatory guild, either considering the number of species involved or their abundance, because several small ubiquitous passerine species present at high densities in this ecosystem forage on trees. Throughout Europe, including Mediterranean oak woodlands, canopy defoliation occurs mainly in spring, because the larval development of most phytophagous insects coincides with the sprouting of young leaves on oak trees (Herrera 1980). During this period, foliage-gleaning birds can reduce by 22-100 % the populations of forest lepidopterous pests which they feed on (Crawford and Jennings 1989; Parry et al. 1997; Tanhuanpää et al. 2001). In autumn and winter, the predation of bark-gleaning birds on overwintering egg masses can be an important factor controlling lepidopterous pest populations in montados and dehesas given that predation rates on L. dispar egg masses can go up to 53–71 % (Higashiura 1989; Cooper and Smith 1995). Eggs of Coleoptera and Hymenoptera are also potentially taken by bark-gleaners, although they are currently not referred in their diet, possibly because of their diminutive size and reduced importance in terms of biomass. On the other hand, great and lesser spotted woodpeckers may control wood-boring Coleoptera in Mediterranean oak woodlands, as it is suggested by excavator species regulating woodborers populations in North American temperate forests (Kroll and Fleet 1979; Fayt et al. 2005; Norris and Martin 2008; Edworthy et al. 2011).

A predator community dominated by generalist species such as tits, nuthatches, treecreepers and chaffinches, may be enough to stabilize prey populations at low abundance levels, in agreement with the predictions of the generalist predation hypothesis (Murdoch and Oaten 1975), although their effect is likely to be noticeable only in non-outbreak circumstances (Crawford and Jennings 1989; Holmes 1990; Parry et al. 1997). On the other hand, specialist predation is characterized by a numerical response to the abundance of prey (Murdoch and Oaten 1975), therefore large insectivorous specialists such as cuckoos and woodpeckers, generally having broad territories and occurring at low densities, may increase their local abundances during outbreaks of prey (Fayt et al. 2005; Barber et al. 2008; Koenig et al. 2011; Edworthy et al. 2011). In most cases, an effective regulation of prey populations is achieved through a combined effect of specialist and generalist predators (Symondson et al. 2002), as we suggest for the birds in the present review. In Mediterranean oak woodlands, different species of specialist and generalist birds may be complementary in space and time, and this review suggests that distinct foraging niches and periods allow a temporal succession of predation covering the complete life-cycle of most pests.

Conclusions and management implications

Seasonal differences in bird density and species richness in Mediterranean evergreen oak forests are less marked than in more northern European forests, with a larger number of resident and migrating species owing to the mild climate, the evergreen conditions and the geographical location along the migratory routes to Africa (López-Iborra and Gil-Delgado 1999). Therefore, an appropriate management of Mediterranean oak woodlands in SW Iberian Peninsula to sustain healthy bird communities should be advantageous to keep insect populations at low levels and prevent pest outbreaks. Management is a key factor promoting bird diversity in Mediterranean oak woodlands by creating distinct habitat types (Díaz et al. 1997; Tellería 2001; Bugalho et al. 2011). However, considerable changes in taxonomic and functional diversity of bird communities take place at a local scale according to management regime (Rabaça 1990; Almeida 1992a; Pulido and Díaz 1992, 1997; Camprodon and Brotons 2006; Godinho and Rabaça 2011; Leal et al. 2011b, 2013; Pereira et al. 2014a). A decrease in natural regulation of pests by birds may outcome from common management practices, such as undergrowth clearing, tree thinning, canopy pruning and cork extraction, as these significantly reduce foraging and nesting resources for tree-foraging birds which are the most relevant guild of pest predators.

Undergrowth clearing decreases both species richness and abundance in Mediterranean oak woodlands (Rabaça 1990; Almeida 1992a; Pulido and Díaz 1992; Camprodon and Brotons 2006; Pereira et al. 2014a). This practice largely affects bird species depending directly on shrubs (e.g., *Sylvia* warblers) but there is also a considerable decline in the density and diversity of small tree-foraging passerine species which regularly seek food or refuge in the understory (Rabaça 1990; Almeida 1992a; Pulido and Díaz 1992; Camprodon and Brotons 2006; Godinho and Rabaça 2011). As most managed Mediterranean oak woodlands have understory shrubs removed, the presence of other habitat fragments, such as olive groves and riparian galleries, may help to sustain higher densities of treeforaging species in the surrounding woodland matrix, as it was observed for Great Tit, Blue Tit and Chaffinch (Leal et al. 2011a; Pereira et al. 2014b).

Tree density is generally correlated with an increase of forest bird species and a decrease of groundforagers (Tellería 2001; Santos et al. 2002; Díaz et al. 2003; Camprodon and Brotons 2006; Pereira et al. 2014a). Therefore, non-thinned woodlands are expected to favour the abundance and richness of tree-foraging species as a result of improved foraging and nesting opportunities. In fact, Blue Tit abundance in Spanish *dehesas* was strongly correlated with tree density and with the availability of tree holes for nesting (Pulido and Díaz 1997).

Cork extraction from cork oak trees is usually carried out every 9 years reducing food availability for bark-gleaners, but in the meantime a new cork layer suitable for arthropod prey is developing. Densities of both bark- (Nuthatch, Short-toed Treecreeper) and bark-foliage-gleaners (Great Tit, Blue Tit) were lower in areas with younger cork (Almeida 1992a; Godinho and Rabaça 2011; Leal et al. 2011b) and even though species richness is apparently not influenced by cork age (Leal et al. 2011b), woodpeckers and other species with broad territories or occurring in low densities can leave from recently debarked areas (Almeida 1992a). Cork exploitation regimes comprising trees with different cork ages in the same area may support high densities of bark-gleaning species, although lower than those in areas with only old cork (Leal et al. 2011b).

Maintenance pruning is often conducted on cork and holm oak trees to remove outermost branches and foliage from the canopy. This practice predominantly affects foliage-gleaning species by reducing foraging substrate and consequently the amount of available prey, although the elimination of cavities may have a negative effect on hole-nesting species (Leal et al. 2013). Leal et al. (2013) showed that densities of Great Tit, Blue Tit and wintering Chiffchaff were lower in pruned than in unpruned areas, and suggested a similar pattern for other foliage-gleaning species (Crested Tit, Long-tailed Tit and Firecrest).

Finally, artificial nest-boxes have been used in various ecosystems to control pests by increasing breeding populations of hole-nesting predators (East and Perrins 1988; Wang and Liao 1990; Sanz 2001; Mols and Visser 2002; Bouvier et al. 2005). Small abundant tree-foraging passerines (Great Tit, Blue Tit, Nuthatch and Short-toed Treecreeper) are the most common hole-nesting species occurring in *montados* and *dehesas*. If local breeding populations of these species are limited by shortage of cavities in trees, the provision of artificial nest-boxes may enhance bird predation on most cork and holm oak pests.

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