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INSECT PREDATION BY BIRDS IN MEDITERRANEAN OAK WOODLANDS AND ITS IMPORTANCE IN THE CONTROL OF DEFOLIATOR PESTS

Tese de Doutoramento em Biociências, ramo de especialização em Ecologia, orientada por Jaime Albino Ramos e apresentada no Departamento de Ciências da Vida da Universidade de Coimbra

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Insect predation by birds in Mediterranean oak woodlands and its importance in the control of defoliator pests

Thesis submitted for the degree of Doctor of Philosophy in Biosciences (scientific area of Ecology) presented to the University of Coimbra, supervised by Jaime Albino Ramos.

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To my parents

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TABLE OF CONTENTS

ABSTRACT

A systematic investigation on insect predation by birds was conducted in Mediterranean oak woodlands of southwestern Iberian Peninsula with the purpose of assessing the services provided by insectivorous birds in the control of cork oak (*Quercus suber*) and holm oak (*Q. rotundifolia*) pests, particularly defoliators.

Through a literature review concerning foraging ecology and diet of breeding, wintering and resident birds in southwestern Iberian Peninsula, twenty-six species were listed as potential regular predators of the main cork and holm oak pests. A strong interaction was found between bird foraging guilds and the biology of consumed pests: ground-foragers prey on overwintering pupae and larvae of seed-borers, tree-foragers prey on eggs, larvae and pupae of defoliator and wood-boring pests, and aerial-sweepers prey on airborne imagines. Regarding defoliators, spring-summer was recognized as the period when bird predation is supposed to have the greatest impact on their populations because caterpillars, throughout their development on foliage, are highly vulnerable to predation by various tree-foraging passerine species which occur in high densities and are widespread in Mediterranean oak woodlands.

Such prediction was validated in the field at the same time that tree selection between cork oak and holm oak by insectivorous birds was studied with respect to dominant tree species of Mediterranean oak woodlands. Approximately 95% of arthropod predation by birds on trees was carried out by only seven passerine species, which, by themselves, represented more than 60% of total bird abundance: blue tit (*Cyanistes caeruleus*), great tit (*Parus major*), crested tit (*Lophophanes cristatus*), chaffinch (*Fringilla coelebs*), Sardinian warbler (*Sylvia melanocephala*), nuthatch (*Sitta europaea*) and short-toed treecreeper (*Certhia brachydactyla*). Local scale variation in cork oak- and holm oak-dominance had little effect on breeding bird communities, although bark-gleaners moderately preferred cork oak. It was also suggested, via statistical modeling of the time spent by foraging birds on each tree, that some characteristics regarding morphology, phenology and physiological condition of cork and holm oak trees can be used to predict habitat quality for insectivorous forest birds.

Numerical and functional responses of the tree-foraging guild to localized larval outbreaks of two major defoliator pests – gypsy moth (*Lymantria dispar*) and the sawfly *Periclista andrei* – in cork oak woodlands were compared with a non-infested control. Four species evidenced positive responses to defoliator outbreaks: densities of nuthatch and chaffinch were higher in the outbreak areas of gypsy moth and *P. andrei*, respectively (numerical responses), and blue tits and crested tits spent a significantly larger amount of time foraging on trees infested with gypsy moth (functional responses). These results are consistent with predictions of the generalist predator hypothesis and drawed attention to the importance of natural biological control by birds, namely through density-dependent mechanisms of pest regulation.

Bird predation on defoliator caterpillars was estimated in non-outbreak conditions, through identification of food given to nestlings by three hole-nesting passerine species which forage on different niches of trees: blue tit (*Cyanistes caeruleus*; foliage-gleaner), great tit (*Parus major*; bark-foliage-gleaner) and nuthatch (*Sitta europaea*; bark-gleaner). Their specific roles were compared using breeding densities, size and composition of preyed caterpillars and provisioning rates to nestlings reared in nest-boxes. Caterpillars were the most, or second-most, common prey consumed by nestlings of the three species. Blue tits, in particular, consumed a significantly higher percentage of caterpillars than the other two passerine species, and showed a significantly higher removal rate of caterpillars at the habitat scale. On the other hand, the supply of caterpillar biomass to each species showed little differences at the habitat scale due to caterpillar size segregation between blue tit and the other two species, which preyed on early and late instars of caterpillars, respectively. Finally, a before-after control-impact (BACI) experience used to test the increase of the breeding density of hole-nesting passerines by setting nest-boxes, achieved a significant increase in the density of blue tit in manipulated nest-box plots compared with control plots (+ 38.2%) while it also contributed for a considerable increase in breeding populations of great tit and nuthatch (+ 26.8% and + 14.3%, respectively).

On the whole, this thesis shows the importance of natural biological control by common resident passerine species in Mediterranean oak woodlands and calls on landowners to consider the effect of management interventions on their populations in order to prevent pest outbreaks.

Keywords: bark-gleaning, foliage-gleaning, foraging ecology, insectivory, natural biological control, nest-box, tree-foraging guild

RESUMO

As aves insectívoras foram o objecto desta investigação sistemática realizada no montado com o propósito de determinar a sua importância no controlo de pragas de sobreiro (*Quercus suber*) e azinheira (*Q. rotundifolia*), nomeadamente desfolhadores.

Numa revisão bibliográfica focada na dieta e ecologia alimentar das aves reprodutoras, invernantes e residentes no sudoeste da Península Ibérica foram identificadas vinte e seis espécies como potenciais predadores regulares das principais pragas de sobreiro e azinheira. Os nichos alimentares destas aves mostraram uma relação com a biologia das pragas consumidas: aves que se alimentam no solo ingerem pupas e larvas de insectos carpófagos, aves que se alimentam nas árvores consomem ovos, larvas e pupas de desfolhadores e de insectos xilófagos, e aves que se alimentam em voo capturam insectos voadores na fase adulta. No que respeita aos desfolhadores, o impacto das aves nas suas populações supõe-se maior durante a Primavera-Verão, coincidindo com a fase de desenvolvimento larvar nas folhas na qual estes estão particularmente expostos à predação por várias espécies de passeriformes arborícolas que ocorrem em densidades elevadas e apresentam uma larga distribuição no montado.

Este princípio foi verificado no terreno, ao mesmo tempo que a selecção entre sobreiro e azinheira pelas aves insectívoras foi investigada tendo em conta a espécie arbórea dominante no montado. Quase 95% da predação de artrópodes pelas aves nas árvores foi efectuada por apenas sete espécies de passeriformes, que, por sua vez, representaram mais de 60% da abundância total de aves: chapim-azul (*Cyanistes caeruleus*), chapim-real (*Parus major*), chapim-de-crista (*Lophophanes cristatus*), tentilhão (*Fringilla coelebs*), toutinegra-de-cabeça-preta (*Sylvia melanocephala*), trepadeira-azul (*Sitta europaea*) e trepadeira-comum (*Certhia brachydactyla*). As variações na dominância de sobreiro e azinheira tiveram pouca influência nas comunidades de aves nidificantes do montado, contudo as aves que se alimentam na casca preferiram moderadamente o sobreiro. Também foi sugerido, via modelação estatística do tempo dispendido pelas aves em alimentação em cada árvore, que algumas características morfológicas, fenológicas e fisiológicas relacionadas com a abundância de artrópodes nos sobreiros e azinheiras podem ser utilizadas para avaliar a qualidade do habitat para as aves insectívoras florestais.

As respostas numéricas e funcionais das aves insectívoras a surtos localizados de larvas de duas importantes pragas de desfolhadores, a lagarta-do-sobreiro (*Lymantria* *dispar*) e a lagarta-verde (*Periclista andrei*), em montados de sobro foram comparadas com uma área-controlo não-infestada. Quatro espécies responderam positivamente aos surtos de desfolhadores: as densidades de trepadeira-azul e de tentilhão foram superiores nas áreas atacadas por lagarta-do-sobreiro e lagarta-verde, respectivamente (respostas numéricas), e o chapim-azul e o chapim-de-crista passaram mais tempo em alimentação nas árvores infestadas por lagarta-do-sobreiro (respostas funcionais). Estes resultados estão de acordo com as teorias de predação generalista e salientam a importância do controlo biológico natural pelas aves, nomeadamente através de mecanismos de regulação dependentes da densidade das pragas.

A função das aves como predadores de larvas de desfolhadores foi avaliada em diferentes nichos das árvores na ausência de surtos, comparando a densidade, o tamanho e a composição das lagartas capturadas e a frequência de alimentação de crias em caixas-ninho de três espécies-chave: chapim-azul, chapim-real e trepadeira-azul. As lagartas foram a principal ou a segunda principal presa consumida pelas crias das três espécies. Em particular, o chapim-azul consumiu uma percentagem de lagartas significativamente mais elevada do que as outras espécies, e apresentou igualmente uma taxa de remoção de lagartas significativamente maior à escala do habitat. Por outro lado, não se verificaram diferenças entre as três espécies na provisão de biomassa de lagartas à escala do habitat devido a uma predação complementar dos *instars* iniciais e finais das lagartas pelo chapim-azul e pelas outras duas espécies, respectivamente. Por fim, numa experiência onde se testou o aumento da densidade reprodutora de passeriformes por intermédio da colocação de caixas-ninho, foi registado um aumento significativo na densidade de chapim-azul nas parcelas onde foram colocadas caixas-ninho em comparação com as parcelas-controlo (+ 38.2%), tendo as caixas-ninho contribuído também para um aumento considerável das populações nidificantes de chapim-real e trepadeira-azul (+ 26.8% e + 14.3%, respectivamente).

No geral, esta tese afirma a importância do controlo biológico natural proporcionado por espécies comuns de passeriformes residentes no montado e apela aos proprietários para considerarem o efeito das práticas de gestão nas populações destas aves de modo a prevenir surtos de pragas.

Palavras-chave: caixa-ninho, chapim, controlo biológico natural, ecologia alimentar, insectivoria, passeriformes arborícolas, trepadeira

GENERAL INTRODUCTION

MEDITERRANEAN OAK WOODLANDS

ECOLOGICAL IMPORTANCE

Evergreen oaks, such as cork oak (*Quercus suber*) and holm oak (both *Q. ilex* and *Q. rotundifolia*), thrive under the Mediterranean climate of long, hot, dry summers (daily maximum temperature often reaches 40ºC) and mild, humid winters (average rainfall of 500–650 mm) (INMG 1991). The world distribution of these two species is basically restricted to countries of southern Europe and northern Africa situated in the western Mediterranean basin (Fig. 1). The largest Mediterranean oak woodlands are located in southwestern Iberian Peninsula, where they extend over an area of 3.1–6.3 million hectares, depending on the authors (Campos 1992, 1993, Joffre *et al.* 1999, Pereira & Pires da Fonseca 2003, Olea & San Miguel-Ayanz 2006). They are locally known as *montados* or *dehesas*, the Portuguese and Spanish names, respectively (hereafter referred by the general designation of Mediterranean oak woodlands).

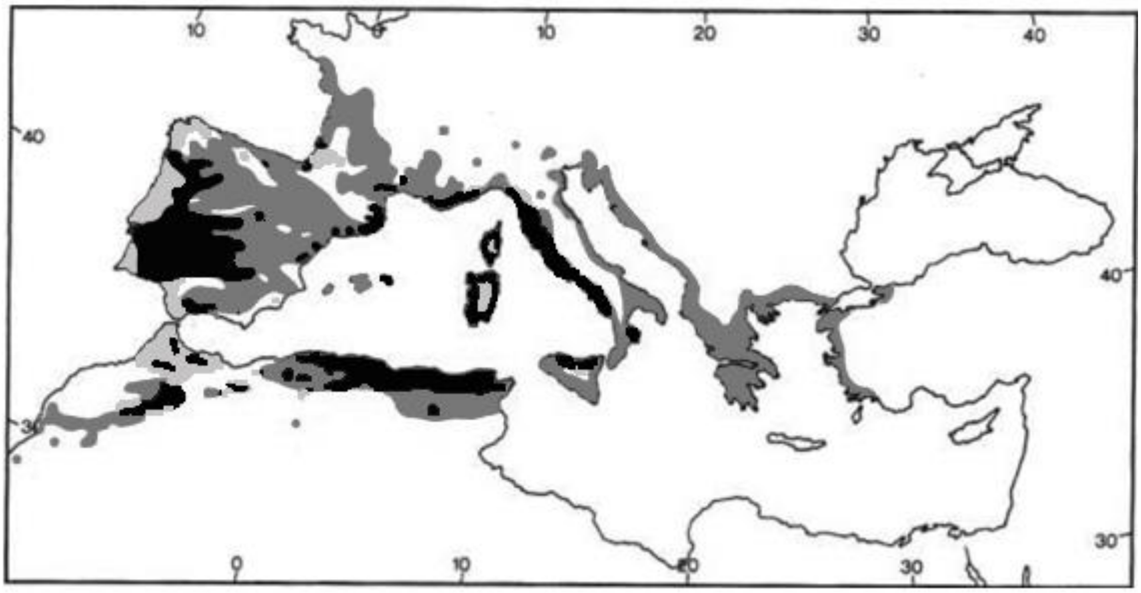

Figure 1. Distribution of cork oak (light grey) and holm oak (dark grey) and species coexistence areas (black) (adapted from Costa *et al.* 1998).

Mediterranean oak woodlands have evolved through major geological and climatic changes that took place during the Pleistocene period and constitute a special mixture of nature and nurture in the Mediterranean region (di Castri 1981, Blondel & Aronson 1999, Pereira & Pires da Fonseca 2003). Cork and holm oaks rather present a complementary distribution in the Iberian Peninsula as a consequence of different ecological preferences: cork oaks occupy areas with mild oceanic climate, relatively high humidity and a low incidence of frost; while holm oaks are basically distributed in areas of more extreme continental climate due to their higher tolerance to water deficit, cold and temperature contrasts (Gómez 1997, Rey Benayas & Scheiner 2002, Pereira & Paulo 2004). However, in some areas, the unequal distribution of these two spontaneous tree species is mainly due to anthropic reasons than to edaphoclimatic preferences (Natividade 1950). Long-term human presence and related activities gradually transformed this ecosystem, and the successive clearing of evergreen oak forests and shrublands shaped its distinctive scattered tree physiognomy (Fig. 2), with densities varying from 20 to 80 trees per hectare (Joffre *et al.* 1999, Pinto-Correia & Mascarenhas 1999).

Figure 2. Typical physiognomy of Mediterranean oak woodlands with scattered trees distributed on extensive flat or hilly areas (photograph by R. Ceia).

Even though Mediterranean oak woodlands show up as monospecific cork-holm oak ecosystems, their floristic composition (Ojeda *et al.* 1995, Pérez-Latorre 1996, Lourenço *et al.* 1998) is identical to that of the mid-Holocene Mediterranean forests (Carrión *et al.* 2000), with the exception that many of those plant species are nowadays restricted to streamside tracks of land, stony uncultivated areas or quickset hedges. Indeed, of the total Iberian flora and fauna, Mediterranean oak woodlands support approximately 30% of the plant species, 40% of the bird species and 60% of both mammal and reptile species (Pineda & Montalvo 1995). It is also the habitat of many protected animal species, namely Iberian lynx (*Lynx pardinus*), Iberian imperial eagle (*Aquila adalberti*), Bonelli's eagle (*Aquila fasciatus*), black-shouldered kite (*Elanus caeruleus*), black vulture (*Aegypius monachus*), black stork (*Ciconia nigra*), crane (*Grus grus*), Iberian Cabrera's vole (*Microtus cabrerae*), and many others, including invertebrate species (Tellería 2001, Carrete & Donázar 2005, Olea & San Miguel-Ayanz 2006, da Silva *et al.* 2008, Mira *et al.* 2008, Godinho *et al.* 2011).

Distinct agroforestry land uses within Mediterranean oak woodlands create different selection pressures on species and, even if low-diversity woodlands are common, they help building a mosaic landscape crucial for many wide-ranging species. Blondel and Aronson (1999) emphasized this high biodiversity taking into consideration both α and γ diversity components of this ecosystem, *i.e.*, high number of species both at community level and at landscape level. According to Belo *et al.* (2009), the main causes for the high biological diversity in cork-holm oak woodlands are: (1) dominant tree species (cork and holm oak) are autochthonous and long-lived; (2) invertebrate fauna is also autochthonous, rich and abundant; (3) trees are preserved continuously, although their structure can be conditioned; (4) human activities follow traditional and less disturbing models; (5) vegetation structure is much distinct both vertically (understory composed by small shrubs, high shrubs, cultivated areas, fallows and grasslands) and horizontally (mosaics of distinct understory and/or tree density); (6) cork and holm oak boast numerous natural holes in their trunks; and (7) Mediterranean oak woodlands typically correspond to very extensive non-fragmented areas.

The ecological importance of Mediterranean oak woodlands was stated with their classification as protected habitats in the framework of the European Union Natura 2000 Network (92/43/EEC Habitats Directive). Moreover, they are considered high nature value farming systems, according to the classification proposed by the European Environmental Agency (Paracchini *et al.* 2008). The coevolution of man and nature, both acting as main drivers of the high structural and biological diversity in this ecosystem (di Castri 1981, Blondel & Aronson 1999, Pereira & Pires da Fonseca 2003), is deeply linked to stability in this ecosystem, thus management should be taken into account as a conservation tool.

SOCIOECONOMIC IMPORTANCE

Human use of Mediterranean oak woodlands shaped this ecosystem to the present day (Joffre *et al.* 1999, Rey Benayas & Scheiner 2002). Romans likely used it to rear pigs, and the origin of the Portuguese word *montado* goes back to the Middle Ages, when *montar* was the term for exploiting communal hills, either for pasturing, timber harvesting, wooding and hunting (Fonseca 2004, Coelho 2007). The harsh Mediterranean climate and the low fertility of soils (particularly scarce in phosphorous and calcium) established complementary agroforestry uses as an adequate productive and sustainable system (Olea & San Miguel-Ayanz 2006). Traditional management of Mediterranean oak woodlands consisted of selective tree clearing to enhance herb growth and to increase tree crown coverage in order to provide a regular yield of edible, high-quality acorns (Rupérez 1957). Poor or non-agricultural lands were mostly cultivated to prevent shrub invasion of grasslands and to supply fodder and grain for livestock, harvesting being a secondary goal (San Miguel-Ayanz 1994, Montero *et al.* 2000, San Miguel-Ayanz 2005).

Management systems have been developed for extensive livestock rearing, originally Iberian pigs but nowadays also sheep and cattle (Fig. 3), which feed on acorns, from early autumn to late spring, and grasses, during most of the year (Campos 1984, Campos & Martín 1987). Forestry is not aimed at timber production but mainly at the exploitation of other products, of which cork oaks provide the most economically significant product which is the cork (Ribeiro *et al.* 2010; Fig. 4). Portugal is the world leader-country in cork production and exportation, being responsible for 54% (at a mean annual production of 157 000 T) of the world production of this good (APCOR 2007). Cork industry has a very important role in the Portuguese economy, representing 3% of the Gross Domestic Product (Tinoco *et al.* 2009) and employing around 15 000 persons in the transformation sector (APCOR 2007).

Notwithstanding its direct socioeconomic value, Mediterranean oak woodlands also provide other economical incomes and a wide variety of ecosystem services: structural and biological diversity, environmental stability (erosion, climate, nutrient and water cycles, fire, carbon storage), landscape, leisure activities, hunting, tourism, and cultural heritage, among others (Belo *et al.* 2009).

Figure 3. Extensive livestock rearing in Mediterranean oak woodlands: black Iberian pigs (above), sheep (middle) and cattle (below) (photographs by R. Ceia).

Instead of taking full advantage of the output of a particular product, the use of every natural resource (multiple, scarce and unevenly distributed in time and space) within Mediterranean oak woodlands is optimized with a minimum input of energy and materials (Olea & San Miguel-Ayanz 2006). It is due to this versatility that this ecosystem has been able to successfully satisfy human requirements from the Middle Ages to the 21st century.

Figure 4. Cork harvesting takes place in mature cork oak trees (>30 years old) at approximately nine years intervals and brings in the most important income for landowners (photographs by R. Ceia).

INSECT PESTS AND THE DECLINE OF MEDITERRANEAN OAK WOODLANDS

In the second half of the 19th century, the decline and mortality of cork and holm oaks was first recorded in trees of distinct ages (Almeida 1898, Câmara-Pestana 1898). Most described symptoms, identical to those of trees under drought conditions, 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 & Ramos 2009). Tree decaying is usually a slow process that can last for several months or years, but occasionally, in late summer and early autumn, sudden dying-off can occur in few weeks (Belo *et al.* 2009). Various authors associated this slow decaying process to the incidence of pathogenic fungi, mainly *Phytophthora cinnamomi* and *Biscogniauxia mediterranea*, in trees often exposed to soil drought and dampness (Natividade 1950, 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). Moreover, various defoliators, xylophagous and carpophagous insects that did not markedly affect Mediterranean oak woodlands until recently, can decrease the vigour of cork and holm oak trees and constrain their natural regeneration (Cabral & Santos 1992, Ferreira & Ferreira 1989, Sousa 1995, Sousa *et al*. 1995; Figs. 5 and 6).

Insect herbivores are an essential part of terrestrial ecosystems wherein they contribute to the flow of energy and matter through the consumption of plant material (Seastedt & Crossley 1984). On the other hand, insect herbivores critically affect plant performance (Crawley 1989) and, in managed ecosystems, they are classified as pests whenever their potential damage on plants is associated with economic loss. The regulation of insect pests is mostly achieved by the labour of natural enemies, *i.e.*, entomopathogens, parasitoids, and predators, which retain pest population levels below those causing economic injury (van Driesch *et al.* 2008). There is however a propensity of some pest species to display outbreaking population dynamics, which seems to relate with certain life history traits such as poor female flying ability (Hunter 1995) or absence of adult feeding (Tammaru & Haukioja 1996). Outbreaks of such species are often caused by a reduction in natural biological control services, in consequence of natural and anthropogenic perturbations that could have an effect on the abundance of various species within a system (Yodzis 1988, Johnson *et al.* 1996).

CHEMICAL PEST CONTROL IN MEDITERRANEAN OAK WOODLANDS

Chemical control of insect pests in Mediterranean oak woodlands started in the first half of the 20th century. The ease of use of DDT and arsenates following World War II strongly encouraged their application against defoliator insects. Chemical spraying was however ineffective against xylophagous and carpophagous insects since their larvae and pupae are concealed and adult emergence is not synchronized (Ferreira & Ferreira 1991).

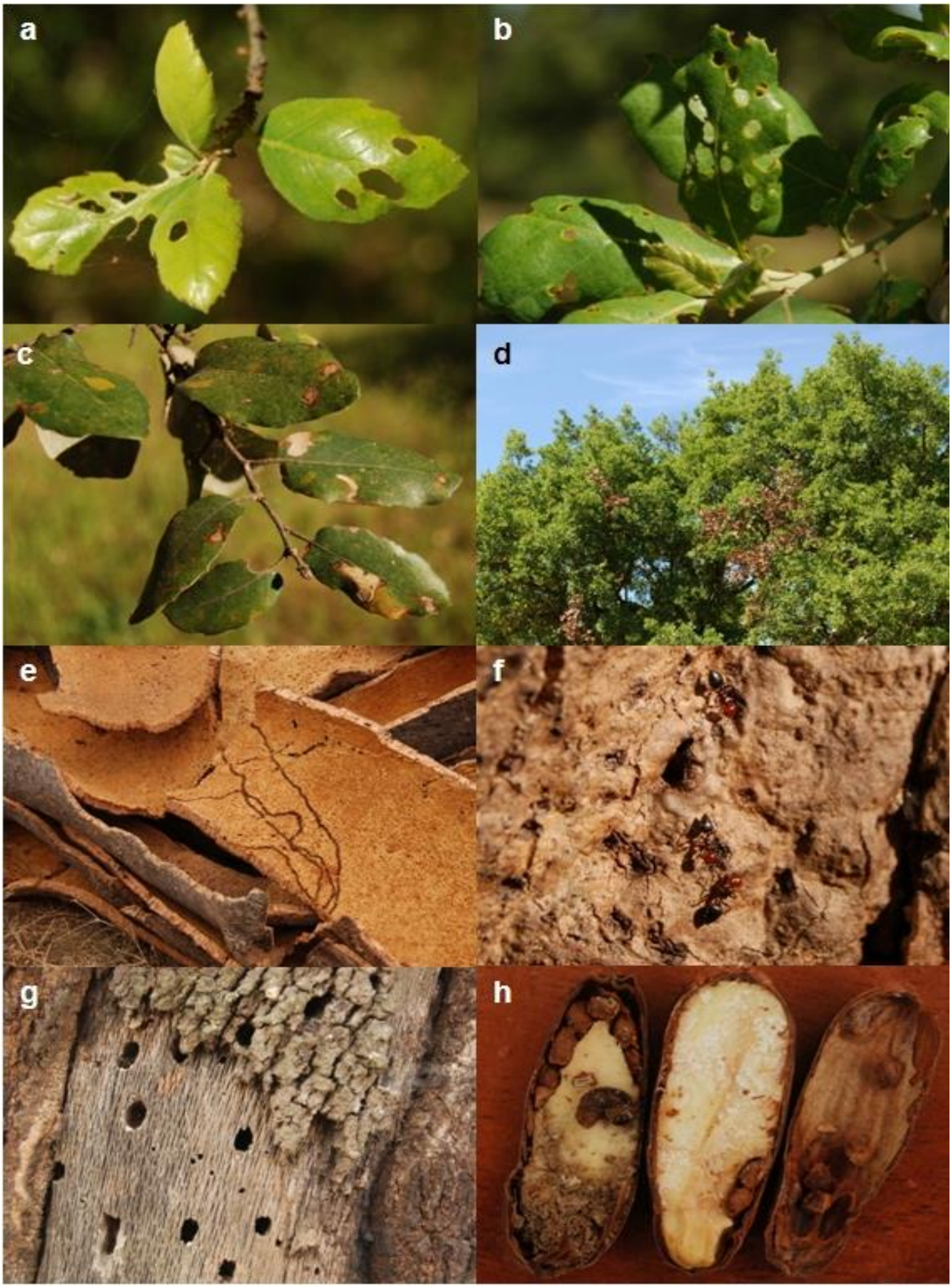

Figure 5. Damages caused by insects on cork oak and holm oak: (a) leaves eaten by larvae of gypsy moth (*Lymantria dispar*); (b) leaves eaten by larvae of the sawfly *Periclista andrei*; (c) leaves consumed by leaf-mining larvae of weevils; (d) dead branches due to interruption of sap flow by the feeding activity of larvae of the buprestid *Coraebus florentinus*; (e) harvested cork boards with galleries excavated by larvae of the buprestid *Coraebus undatus*; (f) ant colony of *Crematogaster scutellaris* with nest built inside cork; (g) exit holes on the trunk produced by imago emergence of insects with wood-boring larvae; (h) acorns consumed by seed-boring larvae of weevils and moths (photographs by R. Ceia).

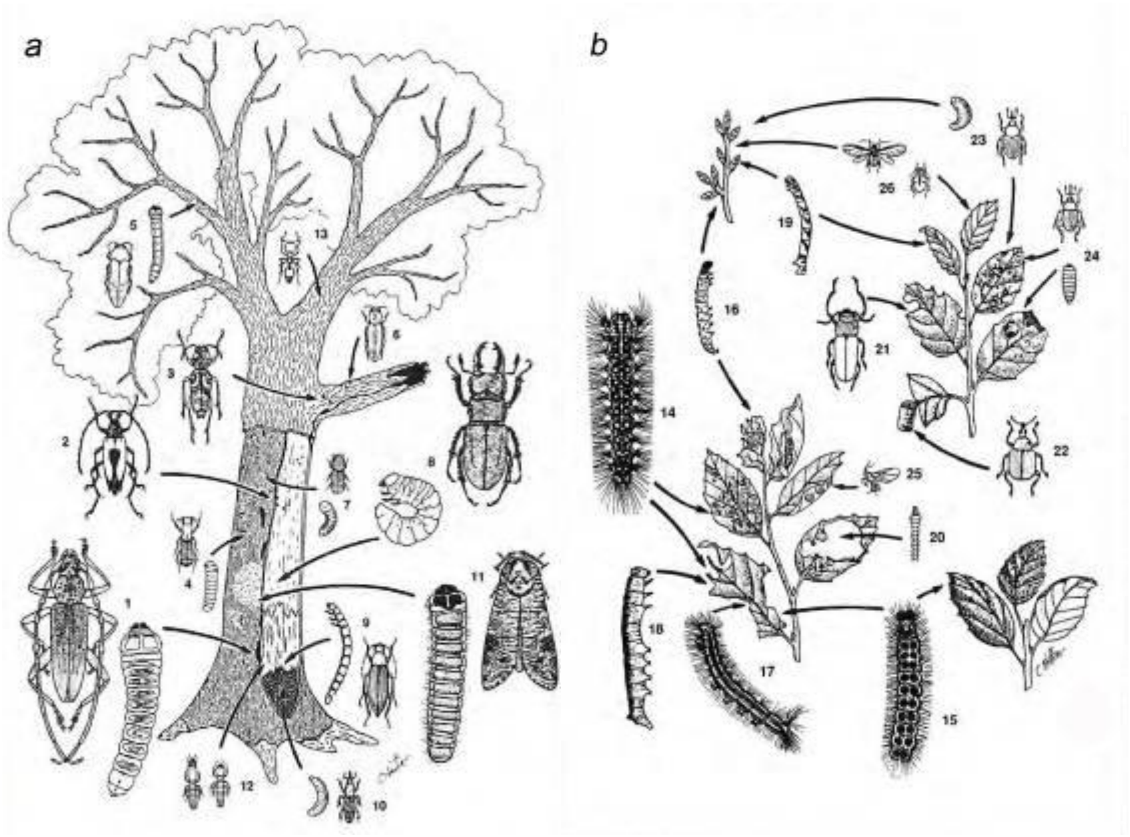

Figure 6. Main insects which attack cork oak throughout its geographical distribution (a – wood- and cork-borers, b – defoliators and leaf-miners): 1 – *Cerambyx cerdo* (Coleoptera: Cerambycidae), 2 – *Stictoleptura cordigera* (Coleoptera: Cerambycidae), 3 – *Xylotrechus antilope* (Coleoptera: Cerambycidae), 4 – *Platypus cylindrus* (Coleoptera: Curculionidae), 5 – *Coraebus florentinus* (Coleoptera: Buprestidae), 6 – *Coraebus undatus* (Coleoptera: Buprestidae), 7 – *Agrilus hastulifer* (Coleoptera: Buprestidae), 8 – *Lucanus tetraodon* (Coleoptera: Lucanidae), 9 – *Allecula morio* (Coleoptera: Tenebrionidae), 10 – *Rhyncolus ater* (Coleoptera: Curculionidae), 11 – *Cossus cossus* (Lepidoptera: Cossidae), 12 – *Kalotermes flavicollis* (Isoptera: Kalotermitidae), 13 – *Crematogaster scutellaris* (Hymenoptera: Formicidae), 14 – *Lymantria dispar* (Lepidoptera: Erebidae), 15 – *Euproctis chrysorrhoea* (Lepidoptera: Erebidae), 16 – *Tortrix viridana* (Lepidoptera: Tortricidae), 17 – *Malacosoma neustria* (Lepidoptera: Lasiocampidae), 18 – *Catocala nymphagoga* (Lepidoptera: Erebidae), 19 – *Eupithecia massiliata* (Lepidoptera: Geometridae), 20 – *Phyllonorycter messaniella* (Lepidoptera: Gracillariidae), 21 – *Labidostomis taxicornis* (Coleoptera: Chrysomelidae), 22 – *Attelabus nitens* (Coleoptera: Attelabidae), 23 – *Coeliodes ilicis* (Coleoptera: Curculionidae), 24 – *Orchestes irroratus* (Coleoptera: Curculionidae), 25 – *Neuroterus lanuginosus* (Hymenoptera: Cynipidae), 26 – *Thelaxes dryophila* (Hemiptera: Aphididae) (reproduced from Villemant & Fraval 1993).

In Portugal, first pest control campaigns occurred in the period 1945–58 in response to high population levels of gypsy moth (*Lymantria dispar*), and approximately 80 000 ha were sprayed with DDT (Nogueira 1967, Figo 1972; Fig. 7). However, DDT spraying against gypsy moth caused, simultaneously, the outbreak of other perniciousdefoliator pests, such as brown-tail moth (*Euproctis chrysorrhoea*), green oak moth (*Tortrix viridana*) and buff-tip moth (*Phalera bucephala*) (Natividade 1950, Neves 1950, Silva 1960). Continuous chemical control of defoliator species in the subsequent years likely created a deeper disequilibrium in the ecosystem, and previously innocuous sawfly species (*Periclista andrei* and *P. dusmeti*) caused severe defoliations in the decade of 1960 (Silva 1960, Nogueira 1967). Chemical spraying had a small impact on sawfly populations because of the short duration of the larval stage (20–30 days), followed by ground burrowing for a 10–34 months pupal diapause (Ferreira & Ferreira 1991). In the decade of 1970, other defoliator Lepidoptera species (*e.g.*, *Catocala nymphagoga* and *Archips xylosteana*), which had low-density populations until then, reached high numbers in several areas (Nogueira & Ferreira 1972).

Figure 7. Aerial spraying with DDT during pest control campaigns against gypsy moth in Portugal (photograph from ICNF historic archives).

Broad-spectrum insecticides were interdicted in most European countries in the 1980's, because of their high toxicity and long environmental persistence. Recent control methods in Mediterranean oak woodlands involve the aerial spraying with diflurobenzuron, an insect growth regulator, or *Bacillus thuringiensis* (*Bt*), a microbial insecticide (Martin *et al.* 2002, Serrão 2002, Basri *et al.* 2005, Luciano & Lentini 2012, Ruiu *et al.* 2014). Both methods have been fairly recommended against defoliator Lepidoptera (Ferreira & Ferreira 1991), although the action of *Bt* bacteria can apparently be inhibited when in contact with oak leaf epidermis (Martin *et al.* 2002, Heitor & Pereira 2004). Biological control strategies include also pheromone traps, although these have been mainly used to monitor defoliator populations since they cannot carry massive captures and thus are ineffective during outbreaks (Serrão 2002). Promising results have been reported from field tests using host-specific viruses (Cerboneschi 2012a, 2012b) and entomophagous fungi (Contarini *et al.* 2014) against gypsy moth in Sardinia, but further research on their effectiveness and hazards is needed before extending these methods to other Mediterranean oak woodlands.

THE IMPORTANCE OF INSECTIVOROUS BIRDS IN PEST CONTROL

The role of natural enemies in the control of pest populations depends on the strength of density-dependent responses across a range of prey densities and on whether these responses can determine the stability of a population (May 1986). While parasitoids and pathogens are relatively important in reducing outbreak populations of forest pests (Doane 1976, Anderson & May 1981, Myers 1988, Elkinton & Liebhold 1990, Berryman 1995), several studies indicate that birds are the main agents of regulation in low-density populations (Holmes *et al.* 1979, Furuta 1982, Campbell & Torgersen 1983, Campbell *et al.* 1983, Crawford & Jennings 1989, Parry *et al.* 1997, Murakami & Nakano 2000, Tanhuanpää *et al.* 2001, Medina & Barbosa 2002).

Bird predation on pests has demonstrated an exceptional importance in various agroforestry systems (Solomon *et al.* 1976, Holmes *et al.* 1979, Kroll & Fleet 1979, Campbell *et al.* 1983, Loyn *et al.* 1983, Joern 1986, Fowler *et al.* 1991, Bock *et al.* 1992, Mols & 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 can promote the performance of the plants on which they forage by feeding on insect herbivores and, to support this significance, three examples from oak forests are worth mentioning. Marquis and Whelan (1994), working in Missouri (USA), found that using cages to exclude birds from white oak (*Quercus alba*) saplings significantly increased density of defoliator insects and leaf damage, which in turn decreased production of new biomass in the following growing season. Murakami and Nakano (2000) used “canopy” enclosures to control the presence of great tit (*Parus major*) and nuthatch (*Sitta europaea*) in a Mongolian oak (*Quercus crispula*) forest in Hokkaido (Japan). These authors found that the two bird species could have distinct trophic-cascading effects on trees: great tits had a direct negative effect on the density of Lepidoptera larvae (herbivores) and an indirect positive effect on oak trees (producers) but had no impact on ants (intermediate predators), whereas nuthatches reduced ants by *ca.* 60% but had an overall neutral effect on Lepidoptera larvae and oak trees. Sanz (2001) experimentally increased breeding populations of insectivorous birds by providing nest-boxes in a Pyrenean oak (*Quercus pyrenaica*) forest in central Spain. Breeding density of insectivorous birds in the manipulated plot was more than three times that in the control plot, and this increase was associated with a significant reduction of Lepidoptera larvae density and leaf damage to oak trees.

Although insectivorous birds are the dominant guild in Mediterranean oak woodlands and their role as predators of cork and holm oak pests is unanimously assumed as positive, only in recent years this interaction has been object of scientific studies (Godinho & Rabaça 2011, Pereira *et al.* 2014a). The effect of birds on cork and holm oak pest populations, mainly on defoliator pests, can potentially establish, or support, a pest control program in Mediterranean oak woodlands, although the elaboration of a forest management plan involving birds should be preceeded by studies on the impacts of birds on pest populations and their outbreak dynamics.

THESIS OBJECTIVES

The broad framework of this thesis is centered on understanding the role of insect predation by birds in the ecosystem functioning of Mediterranean oak woodlands. The main focus was to estimate the services provided by insectivorous birds in the control of cork and holm oak pests, particularly defoliators. To achieve the proposed goal, this thesis addressed the following specific objectives:

(1) to evaluate the potential of bird predation on cork and holm oak pests in southwestern Iberian Peninsula based on published literature about diet of

breeding, wintering and resident bird species, and by relating their foraging niches and phenology with the biology of consumed pests;

(2) to detail the foraging ecology of insectivorous birds in Mediterranean oak woodlands and to determine whether local scale differences in cork oak- and holm oak-dominance have an influence on tree-foraging bird communities;

(3) to examine how birds from the tree-foraging guild respond to localized larval outbreaks of two different defoliator species (gypsy moth and *P. andrei*) in cork oak woodlands;

(4) to estimate the importance of Lepidoptera larvae in nestling diet of three key insectivorous passerine species, blue tit (*Cyanistes caeruleus*), great tit (*P. major*) and nuthatch (*S. europaea*), in a Mediterranean oak woodland under non-outbreak circumstances, and to test if their breeding densities can be increased by providing nest-boxes.

STUDY AREA

Field data collection was carried out at three locations in southern Portugal (Fig. 8). Most fieldwork was conducted in the Herdade do Freixo do Meio (38º42’ N, 8º19’ W), a farm that manages 1140 ha of cork-holm oak woodlands in Foros de Vale Figueira, Montemor-o-Novo. However, in order to evaluate bird responses to defoliator outbreaks (Chapter 3), fieldwork was carried out in two other sites: Herdade do Adaíl (37º47’N 8º44’W), a cork oak woodland with 170 ha located in the municipality of Sines (where there was an outbreak of gypsy moth); and Herdade do Areeiro e Caneira (39º02’N 8º34’W), a cork oak woodland with 800 ha located in the municipality of Coruche (where there was an outbreak of the sawfly *P. andrei*).

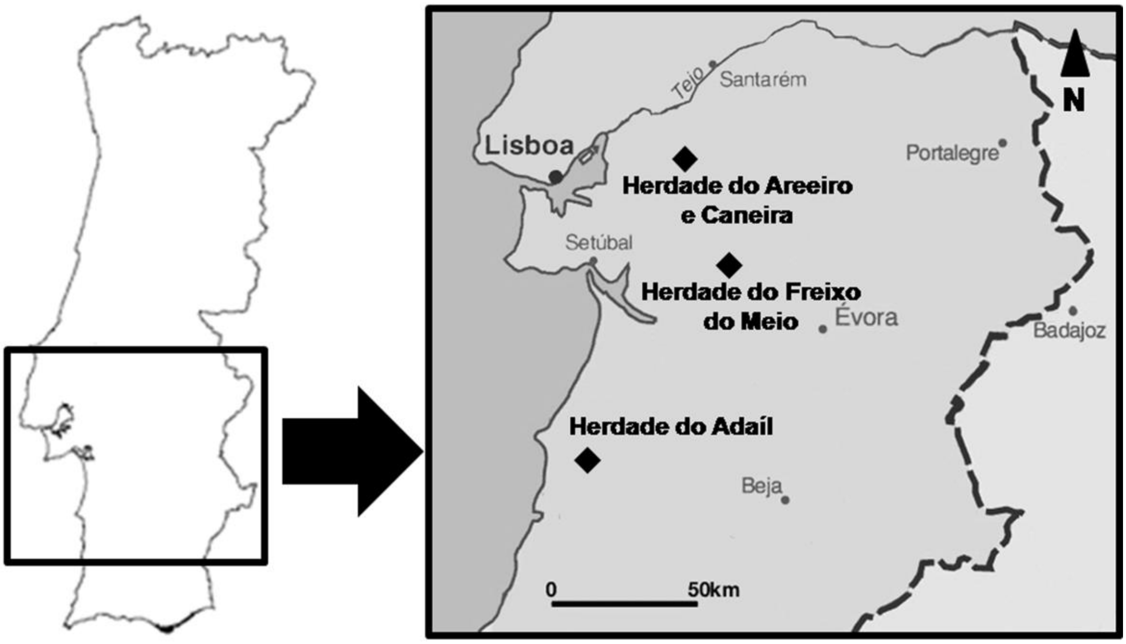

Figure 8. Map of the study area in southern Portugal with the location of the three fieldwork sites.

CHAPTER 1

Birds as predators of cork and holm oak pests

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ABSTRACT

The recent decline of Mediterranean oak woodlands in southwestern Iberian Peninsula is related to insect pests which affect both cork oak (*Quercus suber*) and holm oak (*Q. rotundifolia*). Twenty-six bird species were identified as potential regular predators of twenty major pests by reviewing 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, tree-foragers prey on eggs, larvae and pupae of defoliator 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.

INTRODUCTION

Mediterranean oak woodlands extend over 6.3 million hectares in southwestern Iberian Peninsula, and are known as *montados* in Portugal and *dehesas* in Spain (Joffre *et al.* 1999). This ecosystem is characterized by a scattered tree cover dominated by two evergreen Mediterranean oaks, cork oak (*Quercus suber*) and holm oak (*Q. rotundifolia*), and has been structured by a systematic combination of agricultural, pastoral, and forestry uses (Marañón 1988, Pinto-Correia 1993, Plieninger & 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 & 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 Guttiérez & 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 & 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 Ages, however, in the second half of the 19th century the decline and mortality of cork and holm oaks were first recorded for trees of distinct ages (Almeida 1898, Câmara-Pestana 1898). Most 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 & 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 1950, 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 Lepidoptera, reduce acorn production, stem growth and, in the case of cork oaks, also cork growth (Magnoler & Cambini 1973, Ferreira & 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 & Debouzie 1999, 2002, Sousa & 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, Siscart *et al.* 1999, Soria *et al.* 1999a, 1999b, Branco *et al.* 2002a, Leiva & Fernández-Alés 2005, Jiménez *et al.* 2006, Bonal & 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 & Ferreira 1991, Romanyk & Cadahia 1992, Villemant & Ramzi 1995, Villemant & Andreï-Ruiz 1999; see Appendix A for a list of parasitoids and insect predators of cork and holm oak pests). Concerning insectivorous vertebrates, birds play an important role as pest predators in several agroforestry ecosystems (Solomon *et al.* 1976, Holmes *et al.* 1979, Kroll & Fleet 1979, Campbell *et al.* 1983, Loyn *et al.* 1983, Joern 1986, Fowler *et al.* 1991, Bock *et al.* 1992, Mols & 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, Peris & Masa 1992, Pulido & Díaz 1992, Almeida 1997, Finlayson *et al.* 2002, Santos *et al.* 2002, Camprodon & Brotons 2006, Godinho & 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 bird diet and foraging ecology in Mediterranean oak woodlands, and these are often published in the grey literature and not in English.

The present review aims to document: (1) which bird species can regularly feed on cork and holm oak pests in Mediterranean oak woodlands of the Iberian Peninsula; (2) relationships between foraging niches used by bird predators and distinct life-cycle stages of pests; and (3) potential correlations between bird phenology and the biology of consumed pests. Additionally, it is examined the effect of typical management strategies on bird assemblages and recommendations are given to enhance pest control by birds in Mediterranean oak woodlands. 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

There are twenty species of insects whose regular damage causes considerable economic losses in Mediterranean oak woodlands of southwestern Iberian Peninsula (Table 1).

Table 1. Insect species that damage significantly cork oak and holm oak in Mediterranean oak woodlands of southwestern Iberian Peninsula. With the exception of *Coraebus* spp. and *Crematogaster scutellaris* that affect exclusively cork oak, all other insect pests attack both cork and holm oak. Type of damage is 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 each life-cycle stage in Mediterranean oak woodlands. References are cited in text under the section 'Cork and holm oak pests'. Bird predators of each prey are presented in Fig. 9 using prey numbers indicated in this table.

No.	Insect	Type	Eggs	Larvae	Pupae	Imagines
COLEOPTERA						
Buprestidae (Buprestids)						
1	*Coraebus florentinus* Herbst 1801	W	Branch | May–Jul	Gallery inside branch | Jun–May (diapause 2–4 yrs)	Gallery inside branch | Apr–May	Airborne | May–Jun
2	*Coraebus undatus* Fabricius 1787	W	Trunk | May–Jul	Gallery inside trunk | Jul–May (diapause up to 2 yrs)	Gallery inside trunk | May–Jun	Airborne | May–Jun
Cerambycidae (Longhorn beetles)						
3	*Cerambyx cerdo* Linnaeus 1758	W	Trunk | Aug–Sep	Gallery inside trunk | Sep–Jul (diapause 2–3 yrs)	Gallery inside trunk | Aug–Sep	Gallery inside trunk | Oct–Jul / Airborne | Jun–Sep
4	*Phymatodes testaceus* Linnaeus 1758	W	Trunk or branch | Jul–Sep	Gallery inside wood | Sep–Apr	Gallery inside wood | Mar–May	Airborne | May–Aug
Curculionidae (Weevils)						
5	*Coeliodes ruber* Marsham 1802	L	Leaf bud | Mar–Apr	Gallery inside twig | Apr–May	Soil | May	Airborne | May–Mar (hibernate)
6	*Curculio elephas* Gyllenhal 1836	S	Acorn | Aug–Oct	Acorn | Sep–Nov	Soil | Nov–Jul	Airborne | Jun–Sep
7	*Orchestes erythropus* Germar 1821	L	Leaf parenchyma | Mar	Leaf parenchyma | Mar–May	Leaf | May–Jun	Airborne | Jun–Mar (hibernate)
8	*Orchestes irroratus* Kiesenwetter 1852	L	Leaf parenchyma | Mar	Leaf parenchyma | Mar–May	Leaf | May–Jun	Airborne | Jun–Mar (hibernate)
9	*Platypus cylindrus* Fabricius 1792	W	Gallery inside wood | Mar–Jun	Gallery inside wood | Apr–Aug	Gallery inside wood | May–Aug	Gallery inside wood | Jul–May / Airborne | May–Jan

HYMENOPTERA						
Formicidae (Ants)						
10	*Crematogaster scutellaris* Olivier 1792	C	Ant colony inside cork	Ant colony inside cork	Ant colony inside cork	Free-living / Airborne | Jun–Jul
Tenthredinidae (Sawflies)						
11	*Periclista andrei* Konow 1906	D	Leaf parenchyma | Mar–May	Leaf | Apr–Jun	Soil | May–Apr (diapause 1–3 yrs)	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						
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	*Lymantria dispar* Linnaeus 1758	D	Trunk or branch | Jul–Apr	Leaf | Mar–Jul	Trunk or canopy | May–Jul	Airborne (nocturnal, ♀ non-flying) | Jun–Aug
Lasiocampidae						
17	*Malacosoma neustria* Linnaeus 1758	D	Twig | Jun–Mar	Leaf | Mar–Jun	Leaf or twig | May–Jun	Airborne (nocturnal) | May–Jun
Tortricidae						
18	*Cydia fagiglandana* Zeller 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	*Tortrix viridana* Linnaeus 1758	D	Twig | May–Apr	Leaf | Mar–May	Leaf | Apr–May	Airborne (nocturnal) | Apr–Jul

Lepidoptera 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 1987a, 1989, Ferreira & Ferreira 1991, Villemant & Fraval 1991, Romanyk & Cadahia 1992, Villemant & Fraval 1999). 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 1987a, 1989, Ferreira & Ferreira 1991), and larvae of *Coeliodes ruber*, another weevil species, dig galleries inside little branches stopping trees to burgeon (Ferreira & 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 & 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 & Ferreira 1991, Villemant & Fraval 1991, Romanyk & Cadahia 1992). Ambrosia beetles are xylomycetophagous, coping with many genera of endosimbiotic fungi which will feed their larvae inside galleries in the wood, therefore acting as a vector for fungal diseases (Sousa *et al.* 1997, Sousa & 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). Buprestid activity can take place either on branches or the trunk of trees; *Coraebus florentinus* makes longitudinal and annular larval galleries under the bark of branches, interrupting sap flow and thus causing branch death, whilst *C. undatus* larvae feed under the trunk bark of cork oak trees, diging galleries in the cambium, where new cork tissue is formed (Natividade 1950, Benitez Morera 1961, Merle & Attié 1992, Soria *et al.* 1992, 1994a, Suñer & Abós 1994). The last species accounts for the most significant economic losses in cork production (Merle & Attié 1992), although cork spoilage as a consequence of nest construction by an ant species, *Crematogaster scutellaris*, has also been frequently reported (Natividade 1950, Montoya Oliver 1988, Villagran & Ocete 1990, Villemant & 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, Siscart *et al.* 1999, Soria *et al.* 1999a, 1999b, Branco *et al.* 2002a, Leiva & Fernández-Alés 2005, Jiménez *et al.* 2006; Bonal & 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

Foraging niches of bird predators were used to explore the relationship with different life-cycle stages of pests (Table 2; Fig. 9). Resident, breeding and wintering bird species were identified as potential regular predators of cork and holm oak pests in southwestern Iberian Peninsula whenever their diet in Mediterranean oak woodlands or elsewhere notably includes species listed in Table 1 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.).

Eurasian hoopoe (*Upupa epops*) probes in soil with its long curved bill (5–6 cm) to forage on buried larvae and pupae (Cramp & Perrins 1998). This large insectivorous specialist species is resident in southwestern 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 Lepidoptera larvae and pupae in various woodlands of southern Europe (González-Cano 1981, Battisti *et al.* 2000, Fournier & Arlettaz 2001) where it contributes to the regulation of forest pest populations under non-outbreak conditions (Battisti *et al.* 2000).

Table 2. Birds feeding on cork oak and holm oak insect pests and their status in the Iberian Peninsula. 'Niche' corresponds to the foraging categories considered in this review (*GF* ground-foraging, *FG* foliage-gleaning, *BG* bark-gleaning, *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* >5000 pairs) and 'Distribution' (*ubiquitous* >75% of the area, *widespread* >50% of the area, *scattered* >25% of the area, *local* ≤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).

ORDER/Species	**Niche**	**Phenology**	**Abundance**	**Distribution**
GRUIFORMES				
Common crane *Grus grus*	GF	W	uncommon	local
COLUMBIFORMES				
Wood pigeon *Columba palumbus*	GF	R	B: common W: abundant	ubiquitous
CUCULIFORMES				
Common cuckoo *Cuculus canorus*	FG	B	common	ubiquitous
Great spotted cuckoo *Clamator glandarius*	FG	B	uncommon	scattered
CAPRIMULGIFORMES				
European nightjar *Caprimulgus europaeus*	ASW	B	common	scattered
Red-necked nightjar *Caprimulgus ruficolis*	ASW	B	common	scattered
CORACIIFORMES				
European bee-eater *Merops apiaster*	ASW	B	common	widespread
Eurasian hoopoe *Upupa epops*	GF	R	B: common W: uncommon	B: ubiquitous W: scattered
PICIFORMES				
Great spotted woodpecker *Dendrocopos major*	BG-EX	R	common	widespread
Lesser spotted woodpecker *Dendrocopos minor*	BG-EX	R	rare	local
PASSERIFORMES				
Barn swallow *Hirundo rustica*	ASW	B	abundant	ubiquitous
European robin *Erithacus rubecula*	GF	R	abundant	B: widespread W: ubiquitous
Stonechat *Saxicola torquata*	GF	R	common	ubiquitous
Common chiffchaff *Phylloscopus collybita*	FG	R	B: uncommon W: abundant	B: scattered W: ubiquitous

Firecrest *Regulus ignicapillus*	FG	R	abundant	B: scattered W: ubiquitous
Long-tailed tit *Aegithalos caudatus*	FG	R	abundant	widespread
Crested tit *Lophophanes cristatus*	FG	R	abundant	scattered
Blue tit *Cyanistes caeruleus*	FG	R	abundant	ubiquitous
Great tit *Parus major*	FG-GF	R	abundant	ubiquitous
Nuthatch *Sitta europaea*	BG	R	abundant	scattered
Short-toed treecreeper *Certhia brachydactyla*	BG	R	abundant	widespread
Azure-winged magpie *Cyanopica cyanus*	FG	R	common	local
Eurasian jay *Garrulus glandarius*	FG-GF	R	common	widespread
Common starling *Sturnus vulgaris*	GF	R	B: common W: abundant	B: local W: scattered
Spotless starling *Sturnus unicolor*	GF	R	abundant	ubiquitous
Chaffinch *Fringilla coelebs*	FG	R	abundant	ubiquitous

Common starling (*Sturnus vulgaris*) and spotless starling (*Sturnus unicolor*) are opportunistic feeders which forage largely on the ground (Cramp & 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). Pupae and larvae of Lepidoptera, sawflies, and weevils are described as common prey of both species during breeding season, when starlings are mainly insectivorous (Cramp & Perrins 1998). Yet, while the world distribution of spotless starling is greatly restricted to the Iberian Peninsula (BirdLife International 2004), common starling is essentially a winter visitor (Motis *et al.* 1983, Tellería *et al.* 1988, SEO/BirdLife 2012). In *montados* of southeastern Portugal, Hymenoptera larvae and Lepidoptera larvae and pupae comprised 18% and 15%, respectively, of the items given by spotless starling to nestlings (Almeida 1996a). In *dehesas* of western Spain, adult birds consumed many imago and larval Coleoptera, Hymenoptera and larvae of Lepidoptera (Peris 1980a) while nestling diet comprised mostly larval and pupal Lepidoptera and imago Coleoptera (Peris 1980b). In northeastern 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 preyed by granivorous birds feeding on acorns (intraguild predation). Infested acorns are prematurely abscised and larvae complete their development inside the acorns after these drop on the ground (Bonal & 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, 1988, Díaz & Martín 1998, Bea & Fernández-García 2001, Bea *et al.* 2003) and 155,000 common cranes *Grus grus* (Soriguer & Herrera 1977, Almeida & Pinto 1992, Díaz *et al.* 1996, Cruz 1998) wintering in the Iberian Peninsula, although crane distribution is fairly localized (Fernández-Cruz *et al.* 1981, Alonso & Alonso 1986, Almeida 1992b, 1996b, Prieta & Del Moral 2008, SEO/BirdLife 2012). Many corvids occurring in Mediterranean oak woodlands occasionally include acorns in their diets (Soler & Soler 1991) but only 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 & Pausas 2007a, 2007b). 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 oak 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 bird 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 great tit (*Parus major*) which may spend 18% of its foraging time on the ground during winter (Almeida & Granadeiro 2000). Also, wintering European robins (*Erithacus rubecula*), which reach very high densities in Mediterranean oak woodlands of southwestern Iberian Peninsula (Herrera 1978a, 1980, Tellería *et al.* 1988, Peris & 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 & Isenmann 1985).

Studies on autumn-winter diet of ground-foraging birds in Mediterranean habitats (Herrera 1977, 1978b, 1984a, Cabello *et al.* 1991a) pointed out the importance of ants for several species, in particular for Eurasian hoopoe, European robin and stonechat (*Saxicola torquata*) which present substantial winter populations in Mediterranean oak woodlands of southwestern Iberian Peninsula (Tellería *et al.* 1988, Peris & Masa 1992, SEO/BirdLife 2012). Between October and February, the proportion of ants in the invertebrate fraction of the diet was 76% for European robin (Herrera 1977), 54% and 63% for stonechat (Herrera 1984a and Cabello *et al.* 1991a, respectively), and 66% for 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.

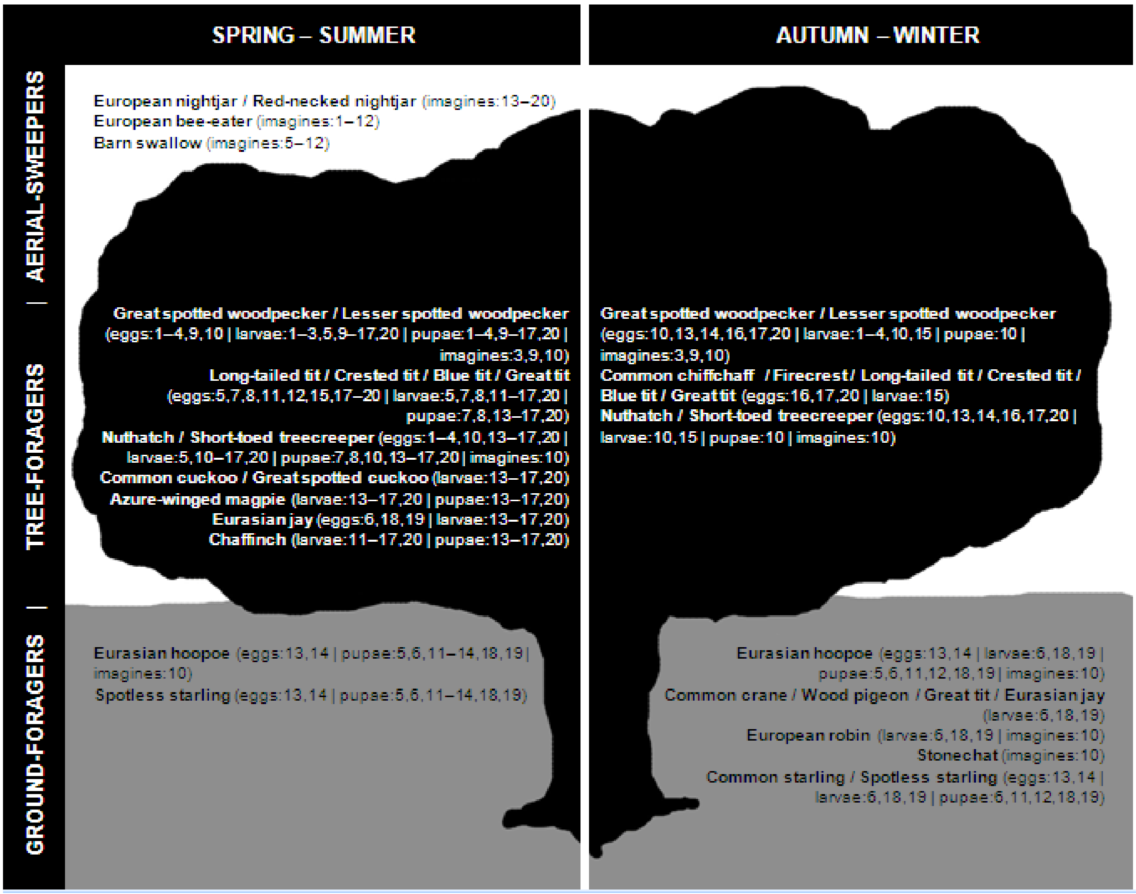

Figure 9. Relationship between seasonal foraging niches used by bird predators and life-cycle stages of cork oak and holm oak insect pests in southwestern Iberian Peninsula. Potential prey are identified by numbers which refer to species listed in Table 1. For scientific names of birds see text or Table 2.

TREE-FORAGERS: PREDATION ON DEFOLIATORS AND WOOD-BORERS

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 eggs, larvae, pupae and imagines of this cork-boring ant species. The excavator guild is represented by forest specialists, namely woodpeckers, that feed on wood-boring 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 tree-foraging insectivores, accounting with four resident species in Mediterranean oak woodlands of southwestern Iberian Peninsula: great tit, blue tit (*Cyanistes caeruleus*), crested tit (*Lophophanes cristatus*), and long-tailed tit (*Aegithalos caudatus*) (Herrera 1978a, 1978c, 1979, Rabaça 1990, Almeida 1992a, Peris & Masa 1992, Almeida & Granadeiro 2000, Finlayson *et al.* 2002, Leal *et al.* 2011a). In particular, the former two species are the most important foliage-gleaners both due to their high densities in Mediterranean oak woodlands (Herrera 1978a, Rabaça 1990, Peris & Masa 1992, Pulido & Díaz 1992, Díaz & Pulido 1993, Almeida 1997, Santos *et al.* 2002, Camprodon & Brotons 2006, Leal *et al.* 2011a) and constant foraging activity on cork and holm oak trees (Herrera 1978b, Díaz & Pulido 1993, Pulido & 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 breeding season their diet comprises around 90% of phytophagous insects, mainly Lepidoptera larvae (Cramp & Perrins 1998). Worldwide, tits have proved to be effective predators of oak defoliators, including *T. viridana*, *Catocala* spp. and *Coeliodes* spp. (Betts 1955, Romanyk & Cadahia 1992), in particular during the larval stage (Murakami & 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 moth larvae have been described in the

Iberian Peninsula (Pimentel & Nilsson 2007, 2009). With the decrease of Lepidoptera larvae along breeding season, the proportion of pupae and eggs taken by tits from branches and twigs increases in both nestling and adult diet (Cramp & 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 & Díaz 1994).

Four species forage exclusively on trees, great spotted woodpecker (*Dendrocopos major*), lesser spotted woodpecker (*D. minor*), nuthatch (*Sitta europaea*) and short-toed treecreeper (*Certhia brachycdactyla*), gleaning most of their year-round prey from trunks and large branches (Almeida & Granadeiro 2000, Leal *et al.* 2011b, 2013). These species consume eggs, larvae and pupae of Lepidoptera, including *T. viridana*, Coleoptera imagines and ants caught in bark surface, cracks and crevices (Cramp & Perrins 1998). Nuthatch diet in *dehesas* was exclusively composed of invertebrates between March and August: 76–100% of the stomachs analysed monthly 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 & Perrins 1998). On the other hand, woodpeckers proficiently excavate wood to expose wood-borers not only in dead and decaying wood but also on the trunk and branches of living hardwood trees (Solomon 1969). Due to morphological adaptations, provided by head and neck muscles and bones, 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 (~4 cm), making use of a sharp tip to impale soft-bodied prey while harder insects adhere to tongue bristles coated with sticky saliva (Cramp & Perrins 1998). Larvae, pupae and imagines of many buprestids, bark beetles, longhorn beetles, and weevils are an essential part of woodpecker diet in addition to surface-dwelling insects (Cramp & Perrins 1998). For that reason, woodpeckers have been reported to play a significant role in the regulation of wood-boring pests in some forestry systems in the Iberian Peninsula (Valente & Branco 2008).

During spring and summer, chaffinch (*Fringilla coelebs*) forages considerably on trees, although ground is the main foraging substrate for the remainder of the year in Mediterranean oak woodlands (Herrera 1980, Almeida & Granadeiro 2000). Invertebrates represent the bulk of chaffinch diet during this period and nestlings are fed mainly with leaf-dwelling insects, including defoliator Lepidoptera larvae (Cramp & Perrins 1998). Eurasian jay also feeds nestlings with a large number of Lepidoptera larvae from leaves of trees, including *T. viridana* in oak woodlands (Bossema 1979). Accordingly, in *montados* of southeastern Portugal, Lepidoptera larvae and pupae comprised 42% of the azure-winged magpie (*Cyanopica cyanus*) nestling diet in terms of biomass (Canário *et al.* 2002). Two breeding migrants, great spotted cuckoo (*Clamator glandarius*) and common cuckoo (*Cuculus canorus*), also feed on late-instar Lepidoptera larvae, including numerous colonial, hairy, and aposematic species (Valverde 1971, González-Cano 1981, Cramp & Perrins 1998, Hoyas & 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 & Perrins 1998). In a 36-year study of common cuckoo stomach contents from central Europe (Link 1889, cited in Cramp & Perrins 1998), *L. dispar* and *M. neustria* were important prey and stomachs 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 diet (Herrera 1977, 1981, Jordano 1981, Jordano & Herrera 1981, Herrera 1983, 1984b, Jordano 1987a, 1987b, 1989, Cabello *et al.* 1991b, Herrera 1998). Nevertheless, chiffchaff (*Phylloscopus collybita*) and firecrest (*Regulus ignicapillus*) are tree-foraging migrants whose diet can be exclusively insectivorous while wintering in the Iberian Peninsula (Guitián 1985, Jordano 1987a). In Mediterranean oak woodlands, these species forage together with resident tits at the outermost branches and twigs of cork and holm oak trees (Herrera 1979, 1980, Almeida & Granadeiro 2000, Leal *et al.* 2011b, 2013) where they may well glean for overwintering eggs and larvae of some Lepidoptera pest species.

AERIAL-SWEEPERS: PREDATION ON AIRBORNE IMAGINES

Aerial-sweepers are typically associated to open agro-forest 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 & Brotons 2006, Godinho

& 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 & Perrins 1998). In particular, 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 Mediterranean oak woodlands with these characteristics. Airborne imagines of Hymenoptera 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 crepuscular and nocturnal predation of Lepidoptera imagines (Cramp & Perrins 1998). Moths can represent >80% biomass in the diet of adults and up to 93% in the diet of nestlings of European nightjar (*Caprimulgus europaeus*) in central Europe (Sierro *et al.* 2001). In southwestern Iberian Peninsula, this species occurs together with red-necked nightjar (*Caprimulgus ruficolis*), which is more common as a breeder in this region (Cuadrado & Dominguez 1996, Santos *et al.* 2002, Martí & Del Moral 2003, Equipa Atlas 2008). Since imagines of Lepidoptera 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.

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

DISCUSSION

In this review it is recognized 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 Mediterranean oak woodlands (Herrera 1978a, Rabaça 1990, Almeida 1992a, Peris & Masa 1992, Pulido & Díaz 1992, Almeida 1997, Finlayson *et al.* 2002, Santos *et al.* 2002, Camprodon & Brotons 2006, Godinho & 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 Lepidoptera pests which they feed on (Crawford & Jennings 1989, Parry *et al.* 1997, Tanhuanpää *et al.* 2001). In autumn and winter, predation of bark-gleaning birds on overwintering egg masses can be an important factor controlling Lepidoptera pest populations in Mediterranean oak woodlands given that predation rates on *L. dispar* egg masses can go up to 53–71% (Higashiura 1989, Cooper & 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 diminute 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 wood-borers populations in North American temperate forests (Kroll & Fleet 1979, Fayt *et al.* 2005, Norris & Martin 2010, 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 predictions of the generalist predation hypothesis (Murdoch & Oaten 1975), although their effect is likely to be noticeable only in non-outbreak circumstances (Crawford & Jennings 1989, Holmes 1990, Parry *et al.* 1997). On the other hand, specialist predation is characterized by a numerical response to prey abundance (Murdoch & 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 it is suggested 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 & Gil-Delgado 1999). Therefore, an appropriate management of Mediterranean oak woodlands in southwestern 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 & Díaz 1992, 1997, Camprodon & Brotons 2006, Godinho & 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 & Díaz 1992, Camprodon & 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 & Díaz 1992, Camprodon & Brotons 2006, Godinho & 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 tree-foraging 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 ground-foragers (Tellería 2001, Santos *et al.* 2002, Díaz *et al.* 2003, Camprodon & Brotons 2006, Pereira *et al.* 2014a). Therefore, non-thinned woodlands are expected to favour 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 & Díaz 1997).

Cork extraction from cork oak trees is usually carried out every nine 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 & 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 densitites 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 & Perins 1988, Wang & Liao 1990, Sanz 2001, Mols & 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 Mediterranean oak woodlands. 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.

CHAPTER 2

Effects of dominant tree species on insectivorous birds breeding in Mediterranean oak woodlands

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ABSTRACT

The use of cork oak (*Quercus suber*) and holm oak (*Q. rotundifolia*) trees by insectivorous birds in Mediterranean oak woodlands was studied with respect to variation in the two dominant tree species. Point-counts were used to compare species abundance among cork oak-dominated, holm oak-dominated and mixed woodlands. Focal foraging observations were carried out to evaluate the use of cork and holm oaks in the three habitats and to relate tree characteristics with the foraging time of foliage- and bark-gleaners. Bird densities in the three habitats were not different for most foliage- and bark-gleaners. Tree preference index values and foraging time per tree showed no significant differences between tree species and foraging guilds, however bark-gleaners had positive index values for cork oak in the three habitats. It is concluded that cork and holm oak trees are equally preferred by foliage-gleaners but bark-gleaners moderately preferred cork oak. Characteristics regarding morphology, phenology and physiological condition of trees can be used to predict habitat quality for insectivorous forest birds in Mediterranean oak woodlands.

INTRODUCTION

Habitat selection is a decision-making process in which observed patterns reflect choices made by individuals (MacArthur & Pianka 1966, Cody 1985, Jones 2001). Understanding the rules that shape habitat selection has been a central focus of studies on the ecology, distribution, diversity and evolution of species for more than five decades (Hildén 1965, MacArthur 1972, Rosenzweig 1981, Orians & Wittenberger 1991, Morris 2003, Piper *et al.* 2013). Avian studies have been particularly influenced by the seminal work of Fretwell and Lucas (1970) on optimal habitat selection. Since birds are exceptionally mobile and wide ranging organisms, these authors predicted that under an ideal free distribution, aggregation in different patches is proportional to the amount of resources available in each, in order to minimize competition for resources and maximize individual fitness (Fretwell & Lucas 1970). This theory has been supported by optimal foraging studies which suggest that birds have an adaptive foraging behaviour, making sensible choices of foraging patch according to some measure of fitness, commonly expressed in terms of energy gain per unit of time (Pyke *et al.* 1977).

Research on habitat selection by birds usually focus on vegetation structure, given its known influence on species distribution and abundance (MacArthur & MacArthur 1961, James 1971, Willson 1974, Roth 1976), although the importance of floristics has been also highlighted in more recent studies (Rotenberry 1985, Bersier & Meyer 1994, López & Moro 1997, Jayapal *et al.* 2009). In forest and woodland habitats, tree species composition is one of the most important factors determining bird community structure (Rice *et al.* 1984, Peck 1989, Tellería & Santos 1994, Lee & Rotenberry 2005, Díaz 2006). These communities are largely composed by insectivorous species which often demonstrate strong foraging preferences for certain tree species based on arthropod abundance and foraging efficiency (Holmes & Robinson 1981, Parrish 1995, Gabbe *et al.* 2002, Adamík & Korňan 2004, Beltrán & Wunderle 2013). Dominant tree species may thus play a significant role in habitat selection by insectivorous birds, especially in habitats with few tree species (Balda 1969, Airola & Barrett 1985, Greenberg *et al.* 1997, Greenberg & Bichier 2005).

Mediterranean oak woodlands are scattered tree ecosystems dominated by two species of evergreen oaks, cork oak (*Quercus suber*) and holm oak (*Q. rotundifolia*), which form pure or mixed stands over 6.3 million hectares in southwestern Iberian Peninsula (Joffre *et al.* 1999). In spite of their long history of human-use, Mediterranean oak woodlands demonstrate a high importance to the preservation of biological diversity (Myers *et al.* 2000, Olson & Dinerstein 2002) which is emphasized by both α and γ diversity components (sensu Whittaker 1977) of this ecosystem (Blondel & Aronson 1999). In fact, distinct land-use regimes within Mediterranean oak woodlands helped to create a mosaic landscape on which a wide diversity of birds depends to a great extent (Díaz *et al.* 1997, Bugalho *et al.* 2011). Due to this spatial heterogeneity and the presence of ecotones from grassland, woodland and forest habitats, this ecosystem holds the highest richness in breeding passerine birds among Iberian forests (Tellería 2001). The effect of habitat structure on breeding bird communities of Mediterranean oak woodlands has been assessed in a number of studies as a consequence of traditional management practices. However, research has been carried out either on cork oak- (Rabaça 1990, Almeida 1992a, Cherkaoui *et al.* 2009, Godinho & Rabaça 2011, Leal *et al.* 2011b, 2013, Catarino *et al.* 2014, Pereira *et al.* 2014a) or holm oak-dominated areas (Pulido & Díaz 1992, Tellería 1992, Santos *et al.* 2002), and bird communities have not been compared with respect to differences in the dominant tree species of the habitat. Because the tree-foraging guild represents more than half of bird assemblages in

Mediterranean oak woodlands (Herrera 1978a, Rabaça 1990, Almeida 1992a, Pulido & Díaz 1992, Leal *et al.* 2011a, 2013), such an approach is necessary to disclose specific features of habitat selection by birds in this ecosystem.

This study compares the use of cork and holm oak trees by insectivorous birds in Mediterranean oak woodlands in order to assess potential differences in habitat quality during breeding season due to variation in the dominant tree species. There is evidence that insectivorous forest birds adhere to patterns of optimal habitat selection in scattered tree ecosystems, considering trees as patches with variable concentrations of resources (Cowie 1977, Garton 1979). On this basis, predictions on foraging habitat quality were tested by analysing the relationship between the abundance of insectivorous forest species and the dominant tree species of the habitat. However, because predictability of habitat quality may be scale-dependent (Wiens 1989, Orians & Wittenberger 1991, Lima & Zollner 1996), the selection of tree species was also examined based on individual foraging decisions. Although cork oak and holm oak are close taxonomic species with a similar structure, cork oak produces a thick cork layer in the outer bark which is periodically harvested bringing in an important income to landowners (Pinto-Correia & Mascarenhas 1999, Bugalho *et al.* 2011). Also, distinct arthropod communities are likely associated with each tree species, as it occurs with wood-boring and defoliator insects (Toimil 1987b, Ferreira & Ferreira 1991, Romanyk & Cadahia 1992). Considering the null hypothesis that cork oak and holm oak trees are equally preferred by birds, it is hypothesized that (1) the abundance of insectivorous forest species does not change with variation in the dominant tree species; (2) tree species are used by foraging birds in proportion to their availability in the habitat; and (3) the amount of foraging time that individuals spend per tree shows no differences between cork oak and holm oak trees. These hypotheses were tested for foliage- and bark-gleaners, by sorting bird species in the two guilds after carrying out observations of foraging individuals in this ecosystem. Moreover, patterns of tree selection were modeled as a function of a number of visually determined variables regarding morphology, arthropod abundance and physiological condition, in order to search for indicators of tree quality for cork oak and holm oak.

Understanding habitat selection can facilitate effective management towards bird conservation, in agreement with the classification of Mediterranean oak woodlands as High Nature Value systems (Beaufoy & Cooper 2008). This analysis is particularly important given that the economic valorization of cork oak is above that of holm oak

(Pinto-Correia & Mascarenhas 1999), and holm oak area of occupancy has been decreasing in the last five decades while new cork oak plantations thrive (AFN 2010, ICNF 2013).

METHODS

STUDY AREA

This study was carried out in the Herdade do Freixo do Meio (38º42’N 8º19’W), a farm that manages 1140 ha of cork-holm oak woodlands near Montemor-o-Novo, Portugal. As the entire area is managed principally for extensive rearing of sheep and Iberian pigs, shrubby understories are cut every few years to enhance pasture growth while some areas are cultivated to supply fodder and grain for livestock. Forestry is aimed at cork harvesting, which takes place at *ca.* nine years intervals in mature cork oak trees, but fuelwood is also periodically obtained from canopy pruning and cutting of dead and decaying trees. Throughout the study area, pruning of tree canopies and debarking of cork oak trees had taken place more than two years prior to our study. The region is characterized by a Mediterranean climate with warm and dry summers and rainfall mostly in autumn and winter (mean annual rainfall = 660 mm, mean annual temperature = 15.4 ºC, mean annual evaporation = 1760 mm; INMG 1991).

Within the study area, 15 plots (500 x 200 m, 10 ha, altitude ranging from 101–194 m a.s.l.) were outlined with aid of satellite imagery and maps (1:25 000). Plots were selected in order to represent three different levels of cork oak- and holm oak-dominance at an identical tree density. Tree density and percentage of cork oaks and holm oaks in each plot were calculated by counting the number of trees of each species via interpretation of satellite images from 25 May 2013 with the software Google Earth version 7.1.2.2041 (Google Inc. 2013). Cork oaks and holm oaks were told apart based on canopy colouration, *i.e.*, bright green for cork oaks and greyish green for holm oaks, and tree identification was then validated in the ground whenever identification based on Google Earth pictures was dubious. Fifteen plots were equally assigned to each of three types of habitat: ‘cork oak woodlands’, ‘mixed woodlands’ and ‘holm oak woodlands’. Percentages of cork oaks and holm oaks in the plots showed significant differences among habitats but tree density did not (Table 3).

Table 3. Tree density (trees.ha^{-1} ± SE) and percentage of each tree species (mean ± SE) in the three studied habitats. GLM results correspond to the analysis of habitat effect on values from 15 study plots (arcsine transformation was applied to percentages to meet the normality assumption). Significant *P* values are highlighted in bold and different letters indicate significant differences among habitats.

	Cork oak woodlands	**Mixed woodlands**	**Holm oak woodlands**	**GLM**
Tree density	42.7 ± 0.8	36.3 ± 2.0	37.2 ± 3.8	$F_{2,12} = 1.94$, $P = 0.186$
% cork oak (% holm oak)	72.5 (27.5) ± 1.7^{a}	43.4 (56.6) ± 5.6^{b}	9.4 (90.6) ± 1.2^{c}	**$F_{2,12} = 93.27$, $P < 0.001$**

All fieldwork was conducted in the springs of 2013 and 2014, *i.e.*, from 11 April to 21 May 2013 and from 8 April to 11 May 2014. Sampling was concentrated uniformly in these periods to avoid any seasonal bias in bird abundance and foraging behaviour caused, for example, by the emergence of fledglings or variation in prey availability.

FORAGING OBSERVATIONS

To evaluate the individual behaviour of birds foraging on cork and holm oak trees every plot was monitored via one permanent 1 km transect. All transects ($n = 15$) were walked once in each year between 07:30 and 12:30 GMT + 1 at a slow constant pace under favourable weather conditions. Focal observations using binoculars were carried out whenever a bird was detected on cork oak or holm oak trees, and the time it spent foraging on each tree niche (trunk and main branches, secondary branches, foliage) was recorded. Simultaneously, a characterization of used trees was performed using 13 visually determined variables, as it is indicated in Table 4. The independence of records was safeguarded by progressing on transects as birds flew away from trees where they were foraging on. Only the first observation by each focal individual was used and individuals with a foraging time lesser than 30 sec (<3% of total records) were not considered in data analysis as these could have been disturbed by the observer while positioning to carry out observation.

In order to determine whether there were differences between cork oak and holm oak trees concerning visually determined variables, a characterization was carried out on 100 random trees of each species using variables listed in Table 4.

Table 4. Variables used in the characterization of cork oak and holm oak trees and differences between the two species in the study area. Results correspond to records of 100 random trees per species and are presented as mean ± SE or percentage of occurrence in the case of binomial variables (ANT, BRA, CRE, EXD, GAL and HOL). Significant *P* values obtained with GLM are highlighted in bold.

Variable	Acronym	Cork oak	Holm oak	GLM
Trunk girth (cm) measured at a height of 130 cm or, for trunks branching lower than breast height, the sum of girths in boughs at that height	GBH	153.42 ± 4.11	138.35 ± 6.25	**$F_{1, 198}$ = 4.07, *P* = 0.045**
Percentage of discoloured leaves, *i.e.*, leaves with yellow spots of dry parenchyma, calculated from a sample of 100 observed *in situ* through binoculars	%LD	7.52 ± 1.38	0.10 ± 0.04	**$F_{1, 198}$ = 74.95, *P* < 0.001**
Percentage of leaves eaten by defoliator insects calculated from a sample of 100 observed *in situ* through binoculars	%LE	0.76 ± 0.27	0.44 ± 0.13	$F_{1, 198}$ < 0.01, *P* = 0.993
Percentage of leaves exhibiting galls, caused by gall midges (Diptera: Cecidomyiidae) or gall wasps (Hymenoptera: Cynipidae), calculated from a sample of 100 observed *in situ* through binoculars	%LG	0.04 ± 0.02	0.56 ± 0.25	**$F_{1, 198}$ = 35.16, *P* < 0.001**
Percentage of young leaves calculated from a sample of 100 observed *in situ* through binoculars	%LY	82.50 ± 2.92	72.65 ± 2.68	**$F_{1, 198}$ = 6.62, *P* = 0.011**
Percentage of the tree crown estimated to be covered with inflorescences	%FLO	14.50 ± 1.91	9.43 ± 1.68	**$F_{1, 198}$ = 4.54, *P* = 0.034**
Tree crown transparency, estimated as the percentage of sky seen through the tree canopy	%TCT	15.60 ± 1.05	12.99 ± 1.32	$F_{1, 198}$ = 3.64, *P* = 0.058
Ants on the trunk or main branches (0: absent, 1: present)	ANT	85.95 ± 3.17	63.29 ± 5.46	**$F_{1, 198}$ = 13.35, *P* < 0.001**
Dry branch extremities in the tree crown due to the occurrence of the buprestid *Coraebus florentinus* (0: absent, 1: present)	BRA	33.88 ± 4.32	0	Not applicable
Crevices on the bark of the tree (0: absent, 1: present)	CRE	79.34 ± 3.70	55.70 ± 5.62	**$F_{1, 198}$ = 10.74, *P* = 0.001**
Exudates from the bark mainly caused by pathogenic fungus (*e.g.*, *Phytophthora cinnamomi* and *Biscogniauxia mediterranea*) (0: absent, 1: present)	EXD	17.36 ± 3.46	3.80 ± 2.16	**$F_{1, 198}$ = 13.83, *P* < 0.001**
Galleries excavated on the trunk or main branches by larvae of the buprestid *Coraebus undatus* (0: absent, 1: present)	GAL	92.56 ± 2.40	0	Not applicable
Exit holes on the trunk or main branches caused by imagos of buprestids or other wood-boring insects (0: absent, 1: present)	HOL	29.75 ± 4.17	12.66 ± 3.76	**$F_{1, 198}$ = 8.00, *P* = 0.005**

POINT-COUNTS

Bird abundance was estimated in the three habitats with the point-count method (Bibby *et al.* 1992) at eight stations per plot, set approximately at 150 m intervals. Sampling was completed in all stations (n = 120) once in each year within four hours after sunrise. Counts started one minute after arriving at the point to allow birds to settle down from any disturbance caused by the observer's arrival on foot. All the individuals (of every species) heard or seen within a 50 m radius were recorded during a five-minute period. Densities of tree-foraging species and of total birds (individuals.ha^{-1}) were calculated at each station by dividing the mean number of individuals in 2013 and 2014 by the surveyed area (0.785 ha).

DATA ANALYSIS

Generalized Linear Models (GLMs) were performed to test for the effect of dominant tree species on bird density and on the number of foraging individuals per transect. The mean of 2013 and 2014 counts per station and foraging records per transect were log-transformed and included as response variables, assuming a Gaussian distribution and identity-link function, and habitat (three-level categorical variable) was used as a fixed explanatory variable.

The use of cork and holm oak trees versus their availability in the habitat was evaluated for foliage- and bark-gleaners using the Electivity Index of Ivlev (Ivlev 1961). In this study, the Electivity Index of Ivlev for the tree species i (Ei) was expressed as Ei = ri – ni / ri + ni, where ri was the percentage of foraging observations of foliage- or bark-gleaners on the tree species i, and ni was the percentage of the tree species i in the habitat. This index varies from – 1 to + 1, with negative values, particularly – 1 to – 0.5, meaning avoidance and positive values, particularly + 0.5 to + 1, indicating preference for a given tree species.

Generalized Linear Mixed-Effects Models were used to analyse Ivlev index values and the amount of foraging time that individuals spent per tree. Fixed explanatory variables were tree species (two-level categorical variable) and foraging guild (two-level categorical variable), as well as the interaction between the two variables, and habitat was included as a random effect to account for potential autocorrelation in foraging time within habitats.

Variables used in tree characterization were statistically compared between cork oak and holm oak with GLMs. Poisson distribution and log-link function were assumed for continuous variables expressed in percentages (%LD, %LE, %LG, %LY, %FLO and %TCT), following the arcsine transformation of data, and trunk girth at breast height (GBH), while a binomial distribution and logit link function were assumed for binomial variables (ANT, BRA, CRE, EXD, GAL and HOL).

GLMs were also used to test for specific effects of the 13 variables used in tree characterization on the foraging time of foliage- and bark-gleaners. Models were carried out with four data-sets, corresponding to records of foliage- and bark-gleaners in cork oak and holm oak trees. The response variable was the log-transformed foraging time per tree and a Gaussian distribution and identity-link function were assumed. Arcsine transformation was applied to the continuous explanatory variables expressed in percentages (%LD, %LE, %LG, %LY, %FLO and %TCT). Holm oak models did not include BRA and GAL as explanatory variables, as these were not observed in this tree species. Variance inflation factors and Pearson correlations were analysed, although no collinearity was found among variables. The Drop 1 selection procedure was used to obtain a single term deletions model which included only significant or nearly significant explanatory variables ($P < 0.100$).

All statistical analyses were carried out with Brodgar 2.6.6 (Highland Statistics Ltd. 2009), an interface supported by software R version 2.9.1 (R Development Core Team 2009). Dispersion parameters for all models were ≤1. Results are presented as mean ± standard error.

RESULTS

Observations of foraging birds on cork oak and holm oak trees during transects were collected for more than 16 hours (total foraging time = 988.6 minutes) and consisted of 402 individuals of 15 species (Fig. 10). A considerable percentage of tree-foraging records (94.8%) and total foraging time (93.2%) corresponded to seven species, including five foliage-gleaners – blue tit (*Cyanistes caeruleus*), chaffinch (*Fringilla coelebs*), great tit (*Parus major*), Sardinian warbler (*Sylvia melanocephala*) and crested tit (*Lophophanes cristatus*) – and two bark-gleaners – nuthatch (*Sitta europaea*) and short-toed treecreeper (*Certhia brachydactyla*). Less prominent tree-foragers included six foliage-gleaning species – long-tailed tit (*Aegithalos caudatus*), Iberian chiffchaff (*Phylloscopus ibericus*), blackcap (*Sylvia atricapilla*), nightingale (*Luscinia megarhynchos*), wren (*Troglodytes troglodytes*) and melodious warbler (*Hippolais polyglotta*) – and two bark-gleaning species – great spotted woodpecker (*Dendrocopos major*) and lesser spotted woodpecker (*Dendrocopos minor*) – which accounted for no more than five records in transects (Fig. 10).

The number of foraging birds per transect did not differ among habitats, for neither foliage- ($F_{2,\,12} = 0.03$, $P = 0.970$; Fig. 11) nor bark-gleaners ($F_{2,\,12} = 1.36$, $P = 0.293$; Fig. 11).

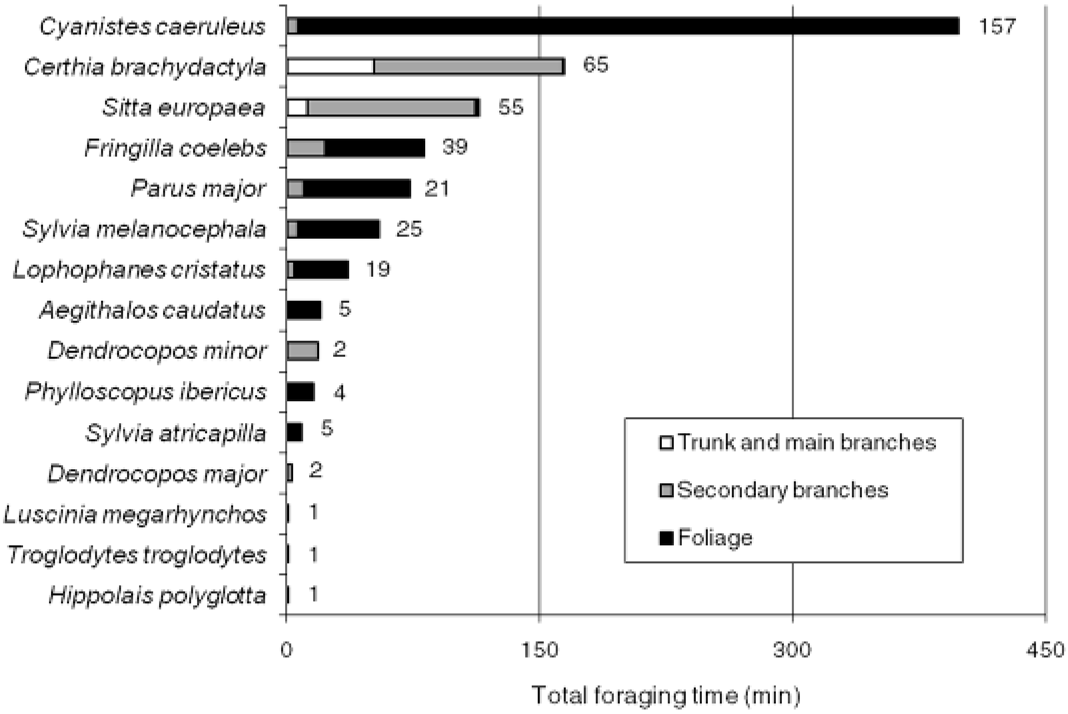

Figure 10. Total foraging time allocated per tree niche (trunk and main branches, secondary branches, foliage) of birds recorded in transects. The number of records is presented for each species on the right of the respective bar.

BIRD ABUNDANCE

A total of 54 bird species and 2658 individuals were recorded at point-count stations during the two years of this study. In each habitat, tree-foraging species represented 34.0 ± 2.0% of species richness and made up 60.8 ± 0.1% of total bird abundance (Table 5). Blue tit was the most abundant species in our study area (1.95 ± 0.09 individuals.ha^{-1}) which agrees with the fact that it had the highest number of foraging records in transects. Indeed, if we take into consideration only forest specialist species (blue tit, great tit, crested tit, short-toed treecreeper, nuthatch, and woodpeckers), there is a clear correspondence between the rank of species abundance (Table 5) and the number of foraging records in transects (Fig. 10).

Table 5. Mean density (individuals.ha^{-1} ± SE) of tree-foraging species and of total birds in the three studied habitats. Species richness (S) is indicated in parenthesis for each habitat. Tree-foraging species were sorted by foraging guild (foliage- and bark-gleaners) according with observations from transects and, within each guild, species are ordered by their overall abundance. GLM results correspond to the comparison among habitats of the density at each station using the mean of 2013 and 2014 counts. Significant *P* values are highlighted in bold and different letters indicate significant differences among habitats.

	Cork oak woodlands	**Mixed woodlands**	**Holm oak woodlands**	**GLM**
Foliage-gleaners				
Cyanistes caeruleus	1.97 ± 0.14	1.72 ± 0.13	2.16 ± 0.16	$F_{2, 117}$ = 1.69, *P* = 0.188
Fringilla coelebs	1.67 ± 0.15^{ab}	1.40 ± 0.20^{b}	2.21 ± 0.19^{a}	**$F_{2, 117}$ = 6.33, *P* = 0.002**
Sylvia melanocephala	0.86 ± 0.11	1.02 ± 0.12	0.89 ± 0.11	$F_{2, 117}$ = 0.43, *P* = 0.651
Parus major	0.65 ± 0.11	0.80 ± 0.12	0.49 ± 0.09	$F_{2, 117}$ = 2.01, *P* = 0.138
Luscinia megarhynchos	0.49 ± 0.11	0.84 ± 0.14	0.61 ± 0.11	$F_{2, 117}$ = 1.90, *P* = 0.154
Troglodytes troglodytes	0.73 ± 0.13^{a}	0.30 ± 0.08^{ab}	0.24 ± 0.09^{b}	**$F_{2, 117}$ = 6.71, *P* = 0.002**
Sylvia atricapilla	0.18 ± 0.06	0.13 ± 0.05	0.19 ± 0.06	$F_{2, 117}$ = 0.32, *P* = 0.724
Lophophanes cristatus	0.03 ± 0.02	0.06 ± 0.04	0.03 ± 0.02	$F_{2, 117}$ = 0.33, *P* = 0.721
Phylloscopus ibericus	0.03 ± 0.03	0.10 ± 0.04	0	$F_{1, 79}$ = 1.80, *P* = 0.184
Aegithalos caudatus	0.06 ± 0.04	0	0.03 ± 0.02	$F_{1, 79}$ = 0.43, *P* = 0.515
Hippolais polyglotta	0.03 ± 0.02	0.03 ± 0.02	0.02 ± 0.02	$F_{2, 117}$ = 0.20, *P* = 0.816
Bark-gleaners				
Certhia brachydactyla	1.07 ± 0.12	0.97 ± 0.09	1.02 ± 0.12	$F_{2, 117}$ = 0.02, *P* = 0.981
Sitta europaea	0.97 ± 0.13	0.78 ± 0.12	0.64 ± 0.09	$F_{2, 117}$ = 1.88, *P* = 0.157
Dendrocopos major	0.08 ± 0.03	0.03 ± 0.02	0.08 ± 0.03	$F_{2, 117}$ = 0.82, *P* = 0.441
Dendrocopos minor	0	0.02 ± 0.02	0.08 ± 0.03	$F_{1, 79}$ = 2.92, *P* = 0.092
Total birds (S)	14.54 ± 0.40 (44)	13.54 ± 0.36 (41)	14.25 ± 0.44 (39)	$F_{2, 117}$ = 1.58, *P* = 0.210

Bird densities in the three habitats were not significantly different for most foliage- and bark-gleaning species, except for chaffinch and wren (Table 5). No significant differences were also found in total bird abundance among habitats (Table 5).

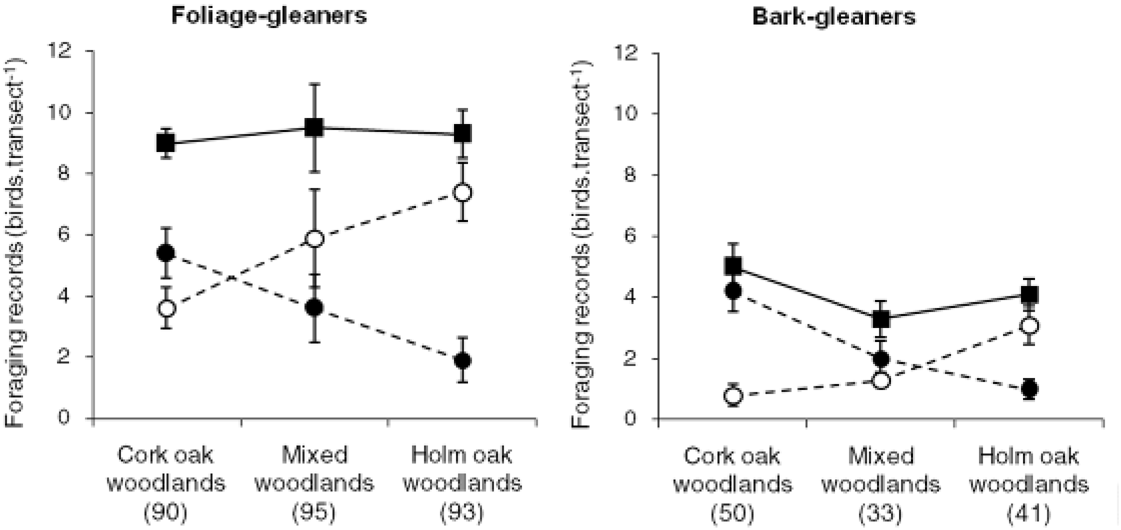

Figure 11. Number of foraging records per transect (mean ± SE) of foliage- and bark-gleaners in the three studied habitats. Dashed lines represent records obtained in cork oak trees (black circles) and holm oak trees (white circles). Solid lines and black squares represent the sum of records obtained in the two tree species. Total number of foraging records is indicated in parenthesis for each habitat.

USED VERSUS AVAILABLE TREES

Values of the Electivity Index of Ivlev ranged between – 0.27 and + 0.46 meaning that birds showed neither strong avoidance nor preference for a particular tree species (Fig. 12). However, bark-gleaners presented positive index values for cork oak in the three habitats and, according to the statistical analysis, the interaction between tree and foraging guild was significant ($F_{1,\ 114}$ = 6.62, P = 0.011). Tree species showed no significant effect on index values ($F_{1,\ 114}$ = 0.20, P = 0.655) and there were also no significant differences among foraging guilds ($F_{1,\ 114}$ = 0.48, P = 0.489).

FORAGING TIME PER TREE

Overall, the mean foraging time per tree was 2.5 ± 0.1 minutes. Statistical analysis showed no significant differences in this parameter between tree species ($F_{1,\ 398}$ = 0.01, P = 0.919) or guild ($F_{1,\ 398}$ = 0.13, P = 0.714), nor interaction between the two factors ($F_{1,\ 398}$ = 0.15, P = 0.699) (Fig. 13).

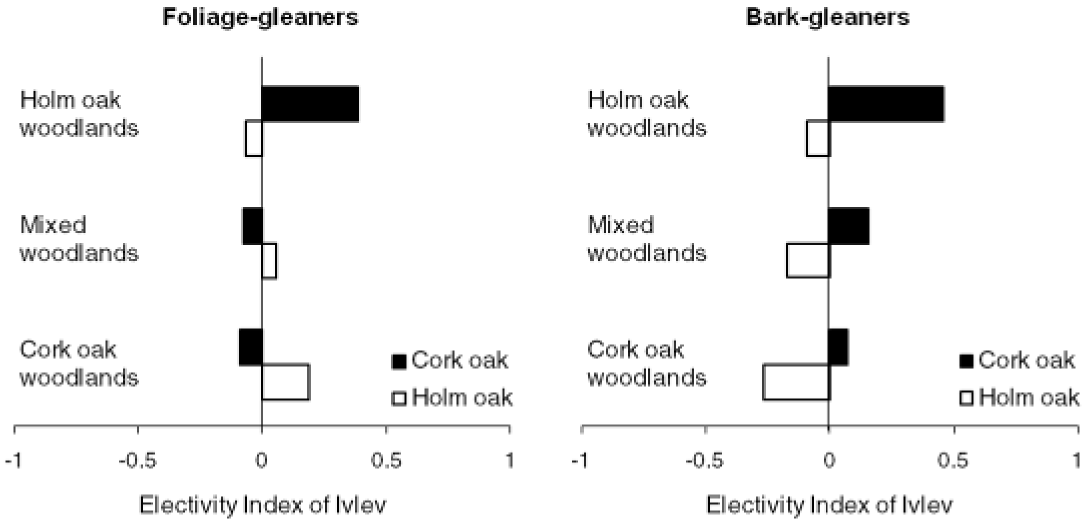

Figure 12. Tree species selection in the three studied habitats using the Electivity Index of Ivlev. Negative values indicate avoidance while positive values indicate preference for a given tree species.

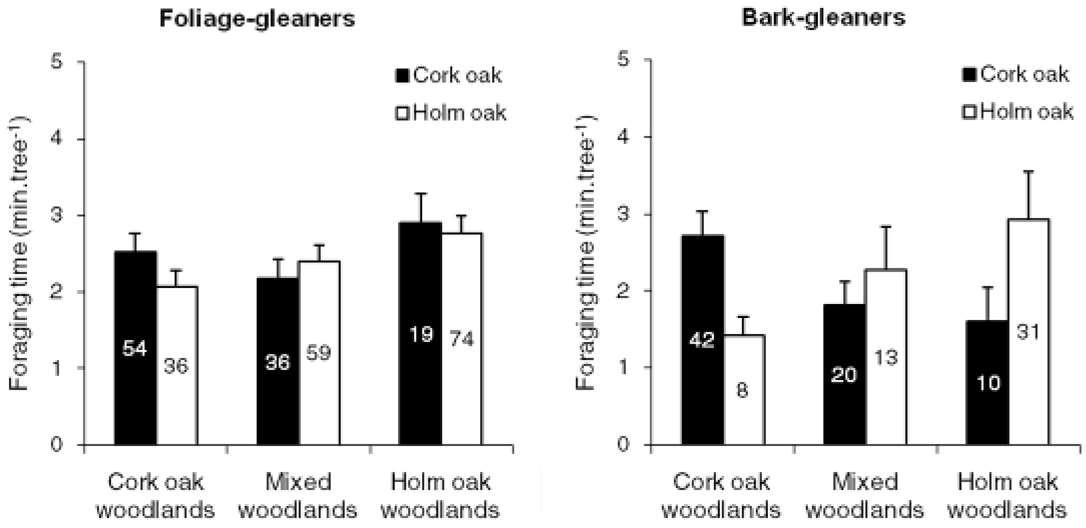

Figure 13. Foraging time per tree (mean + SE) spent by foliage- and bark-gleaners on cork oak and holm oak trees in the three studied habitats. The number of records in transects is indicated in the middle of the respective bars.

FORAGING MODELS AND INDICATORS OF TREE QUALITY

According to tree characterization in the study area, cork oak and holm oak showed significant differences in most visually determined variables (Table 4). Except for percentage of eaten leaves (%LE) and tree crown transparency (%TCT), all variables differed between the two tree species and, moreover, cork oak was the only species to present specific symptoms of *Coraebus* buprestids' activity (BRA and GAL).

A summary of the relationships between tree characteristics and the foraging time of each guild on cork oak and holm oak trees is presented in Table 6. In general, the foraging time of foliage- and bark-gleaners showed a positive relationship with characteristics associated with arthropod abundance, such as percentage of eaten leaves (%LE) and inflorescences on the tree crown (%FLO), and presence of ants (ANT), dry branch extremities (BRA) and crevices (CRE). Foraging time on holm oak was also positively related with trunk GBH. On the other hand, cork oak and holm oak trees in worse physiological conditions, *i.e.*, higher percentages of tree crown transparency (%TCT) and discoloured leaves (%LD), and presence of exudates from the bark of trees (EXD), often showed a negative correlation with the foraging time of both guilds. However, bark-gleaners' foraging time showed a positive relationship with the presence of exudates (EXD) on the bark of holm oak trees. The presence of galleries (GAL) and holes (HOL), and percentage of leaves exhibiting galls (%LG) and young leaves (%LY) were not selected in models nor did they show a significant effect on the foraging time of foliage- and bark-gleaners in either tree species.

Table 6. GLM results showing the relationship between tree characteristics and the foraging time of each guild on cork oak and holm oak trees. Models were computed using the Drop 1 selection procedure to obtain a single term deletions model which included only explanatory variables with a greater significance ($P < 0.100$) on foraging time (see methods).

Guild	Tree	Positive relationship	Negative relationship
Foliage-gleaners	Cork oak	%FLO ($F_{1, 108} = 3.63$, $P = 0.059$) BRA ($F_{1, 108} = 3.49$, $P = 0.065$)	–
Foliage-gleaners	Holm oak	GBH ($F_{1, 168} = 3.48$, $P = 0.064$)	%TCT ($F_{1, 168} = 11.43$, $P = 0.001$) EXD ($F_{1, 168} = 4.45$, $P = 0.036$)
Bark-gleaners	Cork oak	ANT ($F_{1, 71} = 3.28$, $P = 0.075$) CRE ($F_{1, 71} = 4.53$, $P = 0.037$)	%LD ($F_{1, 71} = 7.51$, $P = 0.008$)
Bark-gleaners	Holm oak	GBH ($F_{1, 51} = 4.90$, $P = 0.032$) %LE ($F_{1, 51} = 5.96$, $P = 0.018$) EXD ($F_{1, 51} = 17.37$, $P < 0.001$)	%TCT ($F_{1, 51} = 6.30$, $P = 0.016$)

DISCUSSION

This study suggests that local scale variation in the dominant tree species of Mediterranean oak woodlands have little effect on breeding bird communities. These communities are largely represented by insectivorous species associated with the tree-foraging guild (Herrera 1978a, Rabaça 1990, Almeida 1992a, Pulido & Díaz 1992, Leal *et al.* 2011a, 2013), and in this study they comprised >60% of total bird abundance in the three habitats. Breeding densities of tree-foraging species did not vary substantially between cork oak- and holm oak-dominated areas, nor when compared to mixed cork-holm oak woodlands, with the exception of chaffinch and wren, which are non-specialist forest species more engaged with other foraging substrates than trees (Cramp & Perrins 1998, Almeida & Granadeiro 2000). Even if understories were fairly similar throughout the study area, non-evaluated variation in shrub density and open ground areas among habitats probably influenced densities of chaffinch and wren, as it happened in other studies in Mediterranean oak woodlands (Rabaça 1990, Almeida 1992a, Pulido & Díaz 1992, Godinho & Rabaça 2011, Pereira *et al.* 2014a).

Under an ideal free distribution (Fretwell & Lucas 1970), it is expected that the aggregation of insectivorous forest birds in different areas is proportional to the amount of available resources on trees, as it was demonstrated with foraging tits in a Mediterranean mixed forest (Díaz *et al.* 1998). The number of foraging individuals detected along transects showed no differences among habitats for neither foliage- nor bark-gleaners, although, besides foraging on trees, forest specialist species (blue tit, great tit, crested tit, short-toed treecreeper, nuthatch, and woodpeckers) also use tree holes and cavities to nest (Cramp & Perrins 1998). If it is taken into account that both bird density and foraging opportunities were identical whichever the dominant tree species was, there are reasons to believe that cork oak and holm oak also provided similar nesting opportunities for birds in the study area.

At an individual scale, results were also consistent in showing that cork oaks and holm oaks are equally preferred by foliage-gleaners. On the other hand, bark-gleaners selectively preferred cork oaks irrespective of the dominant tree species in the habitat. Tree species selection by bark-gleaners has shown to be influenced by anatomical aspects of the bark (Adamík & Korňan 2004), given the positive relationship between coarse barks and arthropod abundance (Jackson 1979, Nicolai 1986, Mariani & Manuwal 1990). Thus, prey abundance for bark-gleaners would be predictably higher in cork oaks than in holm oaks since cork oak bark is coarser and more fissured (Natividade 1950). However, there is a significant reduction of bark arthropod abundance in cork oaks in the first years following cork debarking (Leal *et al.* 2011b), and perhaps because several cork oak trees in the study area had only 3-year-old cork, no differences were found in bark-gleaners' foraging time between cork oak and holm oak.

TREE QUALITY FOR INSECTIVOROUS BIRDS

Research on forest ecosystems worldwide demonstrated that oaks are preferred to other tree species both by foliage- and bark-gleaning birds (Balda 1969, Airola & Barrett 1985, Carrascal & Tellería 1989, Díaz *et al.* 1998, Unno 2002; see, however, Greenberg & Bichier 2005). Mediterranean oak woodlands are largely dominated by cork oak and holm oak, and both species should have an exceptionally high quality for insectivorous forest birds as this ecosystem holds the highest richness in breeding passerines among Iberian forests (Tellería 2001). Despite the fact that patterns of little selection were observed between the two tree species, there were some significant differences between cork oak and holm oak trees in a number of visually determined variables which, given the homogenous quality of the two tree species, indicates that insectivorous birds may use distinct cues to predict the quality of each tree species. Tree species selection by insectivorous birds has been largely explained by arthropod prey availability even if structural characteristics of trees can impose limitations on bird foraging efficiency (Franzreb 1978, Holmes & Robinson 1981, Robinson & Holmes 1984, Airola & Barrett 1985, Carrascal & Tellería 1989, Whelan 1989, Parrish 1995, Díaz *et al.* 1998, Hino *et al.* 2002, Greenberg & Bichier 2005, Park 2005, Strode 2009, Beltrán & Wunderle 2013). Foraging models suggest that prey availability for insectivorous birds is a function of (1) morphological and behavioural skills of foliage- and bark-gleaners to capture different types of prey in cork and holm oak trees, (2) tree structure, since prey availability increases with the area available for foraging, (3) anatomical characteristics of trees, such as bark crevices which provide sites for egg-laying and over-wintering of numerous species (Jackson 1979), (4) phenology of trees, as for instance the presence of inflorescences is strongly correlated with arthropod abundance (Díaz & Pulido 1995), and (5) physiological condition of trees, given that stressed and weakened trees provide less foraging opportunities for insectivorous forest species (Godinho & Rabaça 2011).

Furthermore, computed models highlight the importance of birds as pest predators in Mediterranean oak woodlands. A number of insect pests is related to the decline of Mediterranean oak woodlands throughout their westernmost distribution in the last decades (Toimil 1987b, Ferreira & Ferreira 1991, Romanyk & Cadahia 1992, Branco & Ramos 2009). The buprestid *Coraebus florentinus* makes longitudinal and annular larval galleries under the bark of cork oak branches, interrupting sap flow and thus causing branch death (evidenced by dry branch extremities in the tree crown of cork oaks) (Ferreira & Ferreira 1991). While concealed buprestids larva and pupa are only accessible to woodpeckers (Ceia & Ramos 2014), results show that the adult insect may be captured by foliage-gleaners on its emergence from branches during spring as there was a correlation between the occurrence of *C. florentinus* and the foraging activity of foliage-gleaners on cork oak trees. On the other hand, bark-gleaners showed a positive relationship with the percentage of eaten leaves on holm oak canopies, even if defoliator insects were present at low densities in the study area (*i.e.*, there were very low percentages of eaten leaves on both cork and holm oak). These results support the view that a predator community dominated by species with a generalist diet such as insectivorous forest birds, may be enough to stabilize pest populations at low abundance levels, in agreement with predictions of the generalist predation hypothesis (Murdoch & Oaten 1975), although their effect is likely to be noticeable only in non-outbreak circumstances (Crawford & Jennings 1989, Holmes 1990, Parry *et al.* 1997).

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

There is a long tradition of studying habitat use and selection in birds (Jones 2001 and references therein), and the effect of tree preference in habitat selection has been frequently reported for North American forests (Balda 1969, Franzreb 1978, Holmes & Robinson 1981, Airola & Barrett 1985, Parrish 1995, Gabbe *et al.* 2002, Strode 2009). In Europe, tree species foraging preferences by insectivorous birds have been only evaluated in a few studies (Ulfstrand 1976, Carrascal & Tellería 1989, Peck 1989, Díaz *et al.* 1998, Adamík & Korňan 2004) and this study is the first to do it in Mediterranean oak woodlands. These are protected habitats in the framework of the European Union Natura 2000 Network (92/43/EEC Habitats Directive) and are classified as High Nature Value systems based on the sustainability of management practices so that habitat quality is not jeopardized (Beaufoy & Cooper 2008). Measuring habitat quality for birds is a necessary forerunner for discerning the effects of landscape components on bird communities in order to allow informed management decisions. Even though this study advocates that cork and holm oak have a nearly identical quality for birds during breeding season, care must be taken to understand circumstances when resources are most limited or when consequences of habitat selection most influence bird populations. In this context, it would be important to evaluate if seasonal variations in species abundance and composition, and the foraging substrates used by the tree-foraging guild of Mediterranean oak woodlands (Herrera 1978a, Almeida & Granadeiro 2000) can generate patterns of tree selection that differ from spring conditions. Also, bark-gleaners are particularly sensitive to cork debarking (Almeida 1992a, Godinho & Rabaça 2011, Leal *et al.* 2011b), especially if all trees in each area are debarked in the same year as it usually happens (Leal *et al.* 2011b). Because the decline in arthropod abundance (and bark-gleaner populations) due to cork debarking should be more pronounced in cork oak woodlands than in mixed cork-holm oak woodlands, managers should carry out a non-synchronized cork harvesting in trees of cork oak-dominated areas so that foraging birds have always alternative good quality trees. At a regional scale, trends towards cork oak plantation should uphold natural levels of each tree species in Mediterranean oak woodlands and maintain the mosaic of habitats identified as a promoter of bird diversity and landscape multifunctionality (Díaz *et al.* 1997, Bugalho *et al.* 2011). As habitat quality may change over time, these recommendations should be further taken into account in the context of climate warming which is expected to change insect population dynamics due to increased drought and variability of rainfall regime in Mediterranean-type ecosystems (Christensen *et al.* 2007, Netherer & Schopf 2010).

CHAPTER 3

Numerical and functional responses of tree-foraging passerines to larval outbreaks of two defoliator species in cork oak woodlands

In: **Ceia RS**, Ramos JA. Numerical and functional responses of tree-foraging passerines to larval outbreaks of two defoliator species in cork oak woodlands. Submitted to Biological Control

ABSTRACT

Defoliation caused by gypsy moth (*Lymantria dispar*) and the sawfly *Periclista andrei* is implicated in the current decline of cork oak (*Quercus suber*) woodlands in the western Mediterranean. In order to evaluate how the bird community of cork oak woodlands responded to larval outbreaks of these defoliators, bird abundance and their foraging time per tree were determined in areas with localized outbreaks of these two insect species, and in a non-infested control area during two consecutive springs. Numerical and functional responses of tree-foraging passerines were compared among areas and there were significant individual responses of foliage- and bark-gleaning species: blue tit (*Cyanistes caeruleus*) and crested tit (*Lophophanes cristatus*) spent a larger amount of time foraging on gypsy moth infested trees; nuthatch (*Sitta europaea*) and chaffinch (*Fringilla coelebs*) abundances were higher in the outbreak areas of gypsy moth and *P. andrei*, respectively. Crypsis and urticating hairs of, respectively, *P. andrei* and gypsy moth larvae are likely to interact in determining bird responses. Results are consistent with predictions of the generalist predator hypothesis, because moderate outbreaks of defoliators in cork oak woodlands were associated with positive numerical and functional responses of generalist passerines in spring. This study shows, for the first time, that common resident passerine species of cork oak woodlands may play an important role in the control of pest populations, and calls on forest managers to find ways to enhance bird populations in order to reduce the severity of infestations.

INTRODUCTION

Leaf-eating insects (defoliators) cause significant negative economic, ecological and environmental impacts on forests (Kulman 1971, Swank *et al.* 1981, Ayres & Lombardero 2000, Lovett *et al.* 2002, Lyytikäinen-Saarenmaa & Tomppo 2002, Pimentel *et al.* 2005, Kenis *et al.* 2009, Clark *et al.* 2010, Gandhi & Herms 2010, Schäfer *et al.* 2010). Over the last decade, evergreen and deciduous oaks have been the most severely defoliated trees in Europe (ICP Forests 2013) and a number of defoliator pests is related to the recent decline of cork oak (*Quercus suber*) woodlands (Branco & Ramos 2009). Cork oak woodlands are highly biodiverse and sustainable agro-silvo-pastoral ecosystems restricted to southwestern Europe and northwestern Africa (Joffre *et al.* 1999, Bugalho *et al.* 2011). They are characterized by a sparse tree cover (20–80 trees.ha^{-1}) with only one or a few species besides cork oak, mainly holm oak (*Quercus rotundifolia*) and pines (*Pinus* spp.), and an understory which typically combines heterogeneous shrub formations with grasslands (Pinto-Correia & Mascarenhas 1999). The primary economic incentive for the management of these woodlands is cork harvesting, which takes place in mature cork oak trees (>30 years old) at *ca.* nine years intervals (Bugalho *et al.* 2011). However, cork oak defoliations decrease tree growth, acorn production and cork quality (Magnoler & Cambini 1973, Rieske & Dillaway 2008, Branco & Ramos 2009). To minimize stress to damaged trees cork should not be removed within two years after defoliation, hampering an important income for landowners (Branco & Ramos 2009). Furthermore, repeated defoliation may lead to cork oak mortality because trees weakened by defoliation are exceptionally vulnerable to xylophagous pests (Merle & Attié 1992, Martín *et al.* 2005, Sousa & Inácio 2005) and pathogenic fungi (Brasier *et al.* 1993, Vannini *et al.* 1996, Luque *et al.* 1999, Moreira & Martins 2005, Serrano *et al.* 2012).

Gypsy moth (*Lymantria dispar*, Lepidoptera: Erebidae) and the sawfly *Periclista andrei* (Hymenoptera: Tenthredinidae) (Fig. 14) are two cork oak defoliator pests responsible for major economic losses in the western Mediterranean (Luciano & Prota 1995, Villemant & Fraval 1999, Serrão 2002, Branco & Ramos 2009, Cocco *et al.* 2010). Their life-cycles follow a similar pattern: rapid larval growth in spring is followed by a pupal stage during which the larva changes into an adult, and finally the adult stage, when breeding and egg-laying takes place; while in gypsy moth the adult emerges in the same summer, in *P. andrei* the pupal stage will go through a 10–34 months diapause (Ferreira & Ferreira 1991). Damages to cork oak trees are inflicted between April and June when recently ecloded larvae feed on sprouting young leaves and then on mild stalks and leaves from the previous year (Ferreira & Ferreira 1991).

Insectivorous birds can enhance the physiological conditions of the plants on which they forage by consuming defoliator insects (Solomon *et al.* 1976, Holmes *et al.* 1979, Campbell *et al.* 1983, Atlegrim 1989, Marquis & Whelan 1994, Murakami & Nakano 2000, Strong *et al.* 2000, Sanz 2001). Foliage-gleaning birds have been able to reduce by 22–100% the populations of forest defoliator pests while feeding on them during the larval period (Crawford & Jennings 1989, Parry *et al.* 1997, Tanhuanpää *et al.* 2001). High larval densities of gypsy moth and *P. andrei* in late-April and early-May coincide with the hatching period of many tree-foraging passerine species breeding in cork oak woodlands which greatly exploit caterpillars as food for nestlings (see reviews by Cholewa & Wesołowski 2011, Ceia & Ramos 2014).

Figure 14. Larvae of gypsy moth (*Lymantria dispar*, Lepidoptera: Erebidae) (left) and the sawfly *Periclista andrei* (Hymenoptera: Tenthredinidae) (right). Note that the cryptic pattern of *P. andrei* larva matches leaf epidermis, while gypsy moth larva is very conspicuous on that same substrate (photographs by R. Ceia).

Insect populations may be limited by predation if predators consume a greater proportion of the population as prey density increases (Solomon 1949). This density-dependent response may occur in two ways: a numerical response whereby there is a change in the density of predators, and a functional response involving a change in the number of prey eaten by each predator (Solomon 1949, Holling 1961, Hassell & May 1986). The sudden abundance of defoliator caterpillars, mostly Lepidoptera, during outbreaks has been often associated with numerical and functional responses of many forest insectivorous birds in North America (Morris *et al.* 1958, Buckner & Turnock 1965, Mattson *et al.* 1968, Gage *et al.* 1970, Holmes *et al.* 1986, Crawford & Jennings 1989, Parry *et al.* 1997, Haney 1999, Gale *et al.* 2001, Barber *et al.* 2008, Koenig *et al.* 2011, Norris *et al.* 2013). In Europe, despite defoliation is much more widespread than in North America (UN-ECE/FAO 2000), this phenomenon has been less studied. So far as is known, it was only documented for northern European deciduous forests (Enemar *et al.* 1984, Wesołowski & Tomialojć 1997, Hogstad 2005) and Mediterranean pine plantations (Pimentel & Nilsson 2007, 2009) wherein the abundance of a small number of passerine species was positively related with the outbreak of defoliator larvae of Lepidoptera.

The present work aims to investigate how the bird community of cork oak woodlands responds to localized larval outbreaks of gypsy moth and *P. andrei* in two sites with moderate levels of defoliation, when compared to an undefoliated non-infested control. For this purpose, it was assessed the numerical and functional response of seven passerine species associated with the tree-foraging guild of cork oak woodlands in spring, *i.e.*, great tit (*Parus major*), blue tit (*Cyanistes caeruleus*), crested tit (*Lophophanes cristatus*), long-tailed tit (*Aegithalos caudatus*), nuthatch (*Sitta europaea*), short-toed treecreeper (*Certhia brachydactyla*) and chaffinch (*Fringilla coelebs*) (Almeida & Granadeiro 2000). Given that larval outbreaks provide a locally abundant food for these species, it was hypothesized that (1) species' abundance is higher in infested sites than in the non-infested control; (2) a greater amount of foraging time is spent on trees of infested sites than on trees of the non-infested control, in agreement with optimal foraging theory (Cowie 1977, Garton 1979, Abrams 1982); (3) less pronounced responses are found in the site infested by *P. andrei* than in the site infested by gypsy moth, based on the crypsis of *P. andrei* larvae and the fact that birds are visually hunting predators (Wickler 1968, Robinson 1969, Heinrich 1993); and (4) responses of foliage-gleaners are more obvious than those of bark-gleaners. Overall, this study contributes to the current interest in the ecological role of birds as pest predators and allows a further understanding of this in Mediterranean type-ecosystems.

MATERIALS AND METHODS

STUDY AREA

Fieldwork was carried out from 16 April to 18 May 2013 and from 8 April to 15 May 2014. Sampling was concentrated uniformly in these periods to avoid any seasonal bias, *e.g.*, insect pupation or chick fledging.

Three cork oak woodlands with identical vegetation structure and composition were chosen to represent different levels of infestation by defoliator species: two sites with exceptionally high abundances of gypsy moth and *P. andrei* larvae (GYPSY

MOTH and SAWFLY, respectively) and one site where defoliators were only present in low numbers (CONTROL). All sites were located in southern Portugal (CONTROL: 38º42'N 8º19'W, GYPSY MOTH: 37º47'N 8º44'W, SAWFLY: 39º02'N 8º34'W) and were characterized by a Mediterranean climate with warm and dry summers and rainfall mostly in autumn and winter. Management practices such as shrub removal, cork harvesting and canopy pruning can create dissimilarities on the breeding bird community of cork oak woodlands (Rabaça 1990, Almeida 1992a, Godinho & Rabaça 2011, Leal *et al.* 2011b, 2013, Pereira *et al.* 2014a). In this study, identical management regimes were run in the three field sites: canopy pruning and debarking of cork oak trees had taken place more than two years prior to this study, and, in consequence of shrubs being often cut every few years, understories were largely composed by grasses with sparse growth of low shrubs.

In each site, five 10 ha rectangular plots (ranging in altitude from 75–150 m a.s.l.) were outlined. These were considered in data analysis as pseudoreplicates of treatments. Tree density was calculated in each plot by counting the number of trees via satellite image interpretation with the software Google Earth version 7.1.2.2041 (Google Inc. 2013). Site description was further obtained from the characterization of 20 random trees per plot: trunk girth (GBH) was measured at a height of 130 cm or, for trunks branching lower than breast height, it corresponded to the sum of girths in boughs at that height; the percentage of trees infested by gypsy moth or *P. andrei* (%INF) was calculated for each plot by recording the occurrence of larvae on trees, following visual inspection of canopies with binoculars; and the percentage of defoliation (%DFL) was calculated for each tree by counting eaten leaves in a sample of 100 leaves observed *in situ* through binoculars.

NUMERICAL AND FUNCTIONAL RESPONSES

Numerical responses were assessed by comparing bird abundance in the three sites using the point-count method (Bibby *et al.* 1992) at eight stations per plot, set at approximately 150 m intervals. Sampling was completed in all stations (*n* = 120) once in each year between 07:00 and 11:00 GMT + 1. Counts started one minute after arriving at the point to allow birds to settle down from any disturbance caused by the observer's arrival. All the individuals (of every species) heard or seen within a 50 m radius were recorded during a five-minute period.

Functional responses were evaluated through the variation in time spent foraging (Hassell 1978, Abrams 1982). To determine the amount of time spent by each bird foraging on cork oak trees, every plot was monitored via one 1 km line-transect. All transects (*n* = 15) were walked once in each year between 07:30 and 12:30 GMT + 1 at a slow constant pace under favourable weather conditions. Focal observations using binoculars were carried out whenever a bird was detected on cork oak trees and the time it spent foraging on each tree niche (trunk and main branches, secondary branches, foliage) was recorded. Trunk GBH was also measured in order to control for the effect of tree size on foraging time in data analysis. The independence of records was safeguarded by progressing on transects as birds flew away from the trees where they were foraging on. Only the first observation by each focal bird was used and individuals with a foraging time lesser than 30 sec were not considered in data analysis.

DATA ANALYSIS

Statistical analyses were carried out with Generalized Linear Mixed-Effects Models (GLMMs) using the software R version 3.2.2 (lmerTest package; R Development Core Team 2015). A nested-design (plots nested within sites) was used, assuming a Gaussian distribution and lmer function, to test for differences among sites concerning tree density, GBH, %INF and %DFL (arcsine transformation was applied to percentages to meet the normality assumption). To examine bird responses in the three sites, year was added to the nested design (plots nested within sites, and plots and sites nested within year), assuming a Poisson distribution and using the glmer function in R. Numerical responses analyses were performed using bird counts per point as the response variable, whereas in functional responses analyses it was the foraging time per tree, and the GBH of each tree was included as a continuous covariate. Results are presented as mean ± standard error.

RESULTS

SITE DESCRIPTION

The three cork oak woodlands were much similar in relation to tree density and tree size (Table 7). Larvae of the two defoliator species were apparently absent from trees in the control and, accordingly, this site had significantly lower percentages of eaten leaves than the GYPSY MOTH and the SAWFLY sites, where gypsy moth and *P. andrei* larvae were found in 76% and 86% of the trees, respectively (Table 7).

Table 7. Site description. Tree density and percentage of trees infested by gypsy moth or *P. andrei* (%INF) are presented as the mean ± SE of five plots in each site, whereas trunk girth at breast height (GBH) and percentage of defoliation (%DFL) correspond to the mean ± SE of 100 random trees per site (see methods). GLMM compared sites using CONTROL as reference, and significant *P* values are highlighted in bold.

	CONTROL	**GYPSY MOTH**	**SAWFLY**	**GLMM**
Density (trees.ha^{-1})	49.1 ± 1.8	42.3 ± 2.7	41.7 ± 4.4	GYPSY MOTH: $z = 0.192$, $P = 0.848$ SAWFLY: $z = -1.214$, $P = 0.225$
GBH (cm)	149.1 ± 4.4	170.9 ± 6.9	109.8 ± 4.8	GYPSY MOTH: $z = 0.271$, $P = 0.786$ SAWFLY: $z = -0.484$, $P = 0.629$
%INF	0	76.0 ± 7.6	86.0 ± 4.8	**GYPSY MOTH: $z = 0.175$, $P = 0.002$** **SAWFLY: $z = 0.015$, $P = 0.002$**
%DFL	0.4 ± 0.2	20.4 ± 1.6	13.3 ± 1.0	**GYPSY MOTH: $z = 4.956$, $P < 0.001$** **SAWFLY: $z = 2.123$, $P = 0.034$**

NUMERICAL RESPONSES

A total of 52 bird species and 2506 individuals were recorded at point-count stations during the two years of this study. The seven passerine species of the tree-foraging guild made up 51.8 ± 1.3% of the individuals and 47.6 ± 1.1% of the species recorded at each station. Blue tit and chaffinch were the most abundant bird species in the study area (>1.31 individuals.point^{-1}; Table 8). Considering just the tree-foraging guild, crested tit and long-tailed tit had the lowest abundances in the three sites (<0.09 individuals.point^{-1}; Table 8). No differences were found in the abundance of tree-foraging passerine species among the three sites, except for chaffinch and nuthatch which had significantly higher abundances in the SAWFLY and the GYPSY MOTH sites, respectively, than in the CONTROL site (Table 8).

Table 8. Abundance of tree-foraging guild species (individuals.point^{-1} ± SE) in the three sites using 5-min point-counts within a 50 m radius. GLMM compared sites using CONTROL as reference, and significant *P* values are highlighted in bold.

	CONTROL	GYPSY MOTH	SAWFLY	GLMM
Foliage-gleaners				
Great tit	0.51 ± 0.08	0.51 ± 0.07	0.48 ± 0.07	GYPSY MOTH: *z* = 0.070, *P* = 0.944 SAWFLY: *z* = 0.005, *P* = 0.996
Blue tit	1.55 ± 0.11	1.36 ± 0.11	1.43 ± 0.09	GYPSY MOTH: *z* = -0.154, *P* = 0.878 SAWFLY: *z* = -0.472, *P* = 0.637
Crested tit	0.03 ± 0.02	0.09 ± 0.03	0.06 ± 0.03	GYPSY MOTH: *z* = 1.292, *P* = 0.196 SAWFLY: *z* = 1.061, *P* = 0.289
Long-tailed tit	0.05 ± 0.03	0.03 ± 0.03	0.05 ± 0.03	GYPSY MOTH: *z* = -1.013, *P* = 0.311 SAWFLY: *z* = 0.000, *P* = 1.000
Chaffinch	1.31 ± 0.12	1.53 ± 0.12	2.30 ± 0.10	GYPSY MOTH: *z* = 1.653, *P* = 0.098 **SAWFLY: *z* = 3.283, *P* = 0.001**
Bark-gleaners				
Nuthatch	0.76 ± 0.09	1.11 ± 0.10	0.29 ± 0.07	**GYPSY MOTH: *z* = 2.731, *P* = 0.006** SAWFLY: *z* = -0.121, *P* = 0.904
Short-toed treecreeper	0.84 ± 0.09	0.73 ± 0.09	0.60 ± 0.07	GYPSY MOTH: *z* = -0.794, *P* = 0.427 SAWFLY: *z* = -1.758, *P* = 0.079

FUNCTIONAL RESPONSES

Observations of foraging birds on cork oak trees during transects summed more than 17 hours (total foraging time = 1023 minutes) and consisted of 386 individuals of 17 species. Together, the seven studied species accounted for 93.3% of foraging records and 93.9% of total foraging time. Except for long-tailed tit, which contributed with only two observations, all studied bird species were recorded for ≥50 minutes (Table 9). Tree-canopies were largely used by blue tit, great tit and crested tit which spent virtually all their foraging time on foliage (97.0%, 95.9% and 92.4%, respectively; Table 9). Chaffinch also foraged predominantly on the canopy of cork oak trees (82.2%) but used secondary branches more often than the previous species (17.3%), while trunk and main branches were also occasionally explored (Table 9). On the other hand, nuthatch and short-toed treecreeper foraged exclusively on secondary branches (95.1% and 80.3%, respectively) or on main branches and the trunk of cork oak trees (4.9% and 19.7%, respectively) (Table 9). In particular, nuthatch foraged on secondary branches more often in the GYPSY MOTH site (98.6%) when compared with the CONTROL and the SAWFLY sites (92.8% and 83.8%, respectively) (Fig. 15).

Table 9. Percentage of time spent foraging in each tree niche (trunk and main branches, secondary branches, foliage) of tree-foraging guild species. The number of foraging birds (*n*) and total observation time (time) are indicated.

	Trunk and main branches	**Secondary branches**	**Foliage**	**(*n*; time)**
Foliage-gleaners				
Great tit	–	4.1	95.9	(30; 93 min)
Blue tit	0.2	2.8	97.0	(157; 436 min)
Crested tit	–	7.6	92.4	(15; 50 min)
Long-tailed tit	–	–	100.0	(2; 4 min)
Chaffinch	0.5	17.3	82.2	(30; 56 min)
Bark-gleaners				
Nuthatch	4.9	95.1	–	(57; 130 min)
Short-toed treecreeper	19.7	80.3	–	(69; 192 min)

GLMM results indicated a significant effect of GBH on foraging time per tree for great tit ($z = 2.125$, $P = 0.034$), blue tit ($z = 3.463$, $P < 0.001$) and short-toed treecreeper ($z = 3.986$, $P < 0.001$), but it was not significant for the other studied bird species ($[z] < 1.265$, $P > 0.206$). Blue tit was the most common tree-forager and the time it spent foraging per tree was higher in the GYPSY MOTH site and lower in the CONTROL site, with significant differences between the two sites ($z = 2.200$, $P = 0.028$; Fig. 15). Similarly, crested tit foraged for significantly longer periods on trees of the GYPSY MOTH site than on those of the CONTROL site ($z = 2.203$, $P = 0.028$; Fig. 15). No significant differences were found when comparing site variations in the mean foraging time per tree for the other species (Fig. 15).

DISCUSSION

This study demonstrates that moderate outbreaks of two distinct defoliator pests in cork oak woodlands can drive positive numerical and functional responses of some bird species that are able to act as their predators. As predicted, foliage-gleaners responded more noticeabily than bark-gleaners to the copious occurrence of defoliator larvae during two consecutive springs.

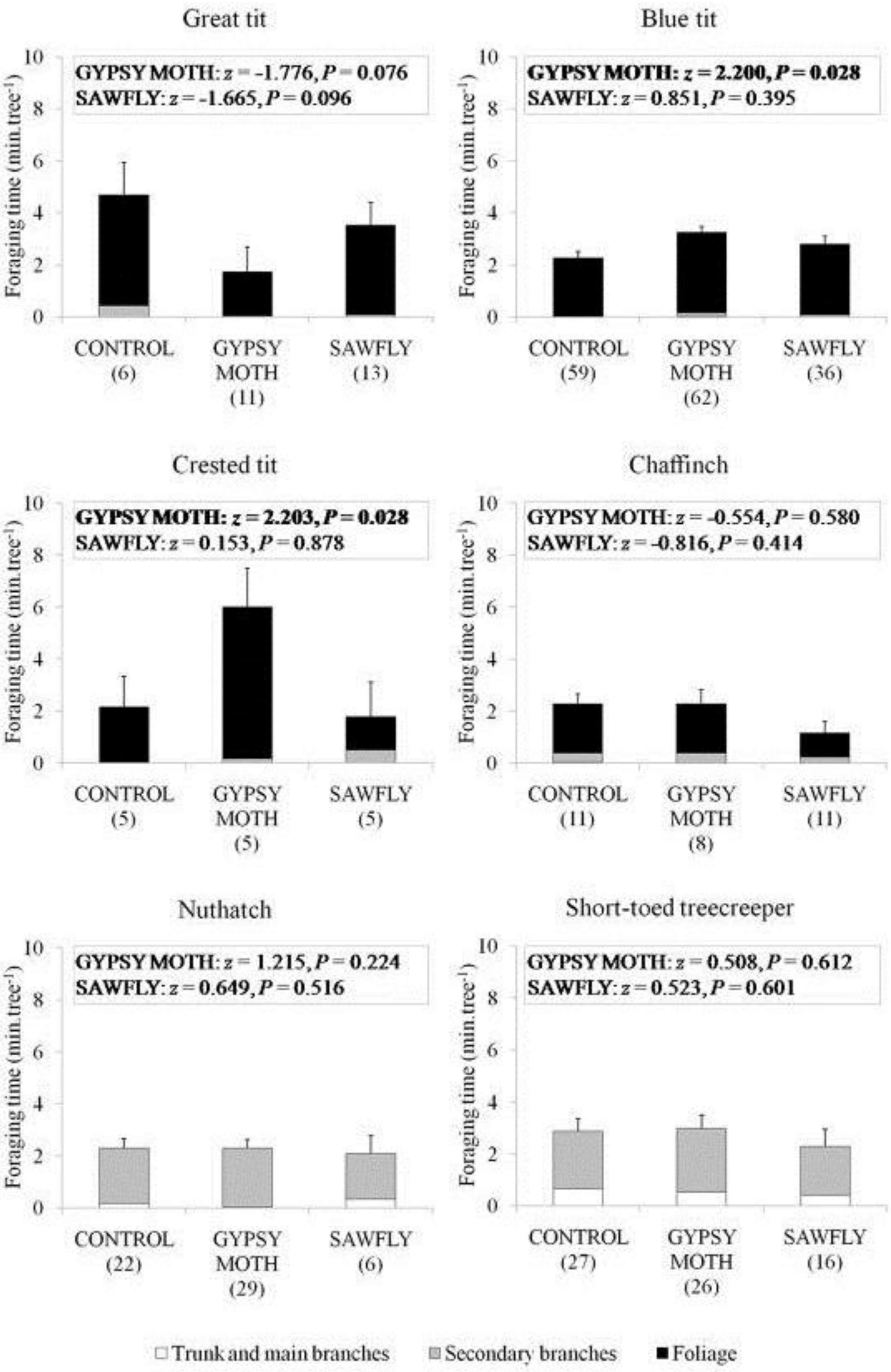

Figure 15. Foraging time per tree (mean + SE) and foraging niches (trunk and main branches, secondary branches, foliage) used by the most important tree-foraging species in the three sites. The number of foraging records is indicated in parenthesis. GLMM results of site comparison using CONTROL as reference are indicated for each species, and significant *P* values are highlighted in bold.

Blue tit was the foremost foliage-gleaning species and it spent a larger amount of time foraging on trees infested by gypsy moth and *P. andrei*, yet a significant functional response was only detected for gypsy moth, as it also happened with crested tit. Furthermore, nuthatch responded numerically to the outbreak of gypsy moth, and chaffinch, which was the most abundant species overall, expressed a numerical response to *P. andrei* outbreak.

In this section are outlined the limitations of this approach, explored the ecological function of tree-foraging passerines as pest predators in cork oak woodlands and discussed the implications of achieved results for the management of this ecosystem.

STUDY LIMITATIONS

One of the most common problems of assessing the impact of outbreaks is that it is difficult to follow rules of good experimental design, such as randomization and replication, for the reason that outbreaks are often temporarily and geographically patchy (Campbell 1973, Berryman 1987, Wallner 1987). In this study, outbreaks of gypsy moth and *P. andrei* were restricted for two years to about 150 ha of cork oak woodlands. It was not possible to replicate treatments due to the lack of infestations in nearby analogous areas during the same period. Nonetheless, the three field sites were identical in habitat structure and composition, and achieved results were consistent with tested hypotheses. This study is sufficiently robust to denote individual responses of tree-foraging passerines to high larval densities of defoliators in spring. Moreover, this is the first estimation of bird responses to defoliation in Mediterranean oak woodlands and also the first time that bird responses to different defoliators are analysed in simultaneous.

NUMERICAL AND FUNCTIONAL RESPONSES

The potential of thirteen bird species as larval predators of several cork oak defoliators, including gypsy moth and *P. andrei*, had been recognized in a recent review of the diet of birds in Mediterranean oak woodlands (Ceia & Ramos 2014). The results of this study show that, both in outbreak and non-outbreak circumstances, insectivory on cork oak trees was essentially undertaken by ubiquitous small passerine species, even though they coexisted with large insectivores such as woodpeckers and cuckoos (unpubl. data). This group of generalist resident passerines represented more than half of the breeding bird community and accounted for >93% of tree-foraging activity in our study area. These results are supported by data from other cork oak woodlands where the ratio of tree-foraging passerines in bird assemblages varied between 0.44 and 0.66 (Rabaça 1990, Almeida 1992a, Leal *et al.* 2011a, 2013, Ceia & Ramos 2015), and they were responsible for virtually all foraging on cork oak trees in spring (Almeida & Granadeiro 2000, Leal *et al.* 2013, Ceia & Ramos 2015).

There is an important difference between tree-predator community in cork oak woodlands and those in North American and northern European deciduous forests, where numerical responses of several bird species to forest pest outbreaks have been previously recorded. Breeding bird communities of those subboreal forests are dominated by migrant species and many could locate spring larval outbreaks during their northward migration or during a post-migratory nomadic phase (Buckner & Turnock 1965, Enemar *et al.* 1984, Holmes *et al.* 1986, Crawford & Jennings 1989, Parry *et al.* 1997, Haney 1999, Gale *et al.* 2001, Hogstad 2005, Barber *et al.* 2008). Short-distance movements of territorial resident species in cork oak woodlands might decrease their chance to find a localized insect outbreak. In this study, only nuthatch and chaffinch numbers correlated positively with the two defoliator outbreaks.

Nuthatch showed a significant numerical response to the outbreak of gypsy moth, confirming the importance of bark-gleaner predation on cork oak defoliator pests (Ceia & Ramos 2014). Also, in a previous study undertaken in non-outbreak cork-holm oak woodlands (Ceia & Ramos 2015), there was a positive correlation between the percentage of eaten leaves on holm oak trees and tree preferences by bark-gleaners. Although present results do not support the expansion of bark-gleaners' niche breadth, which was restricted to cork oak trunk and branches in spite of the large availability of defoliator larvae on foliage in the outbreak sites, nuthatch showed a stronger preference for foraging on smaller branches of cork oak trees in the site infested by gypsy moth.

The significant numerical response of chaffinch to cryptic larvae of *P. andrei* was somewhat contrary to expected if it is considered that chaffinch was just faintly more abundant in the gypsy moth outbreak site than in the control. Chaffinch is a non-specialist forest species and, in a different way from the other studied species, it frequently uses other foraging substrates than trees, such as ground and shrubs (Almeida & Granadeiro 2000). Even if understories were fairly similar in the three sites, non-evaluated variations in shrub density and open ground areas among sites probably influenced the abundance of chaffinch, as it happened in other studies in cork oak woodlands (Rabaça 1990, Almeida 1992a, Godinho & Rabaça 2011, Pereira *et al.* 2014a). Nevertheless, chaffinch predation on conspicuous gypsy moth larvae may be limited by the fact that it is likely not able to cope with urticating hairs found on larvae of this Lepidoptera species. So far as is known, there is no evidence for this on the literature but, in agreement with this supposition, chaffinch did not respond to high densities of the urticating pine processionary moth (*Thaumetopoea pityocampa*, Lepidoptera: Notodontidae) in Mediterranean pine plantations (Pimentel & Nillson 2009), while in northern European deciduous forests a numerical response to outbreaks of two glabrous caterpillars, the autumnal moth (*Epirrita autumnata*, Lepidoptera: Geometridae) and the winter moth (*Operophtera brumata*, Lepidoptera: Geometridae), has been detected on a close taxonomic species, the brambling (*Fringilla montfringilla*) (Enemar *et al.* 1984; Hogstad, 2005).

Tits, on the other hand, are highly adapted to feed on urticating caterpillars by discarding the urticating tegument of larvae (González-Cano 1981, Halperin 1990). The functional responses of blue tit and crested tit to gypsy moth outbreak are both worth mentioning, yet there is a pivotal importance on the response of the former species since it is by far the most demanding foliage-gleaner in cork oak woodlands (Almeida & Granadeiro 2000, Leal *et al.* 2011b, 2013, Ceia & Ramos 2015, this study). Here, achieved results agree with the formulated hypothesis that responses in the site infested by *P. andrei* would be less pronounced than in the site infested by gypsy moth. Predation on *P. andrei* is probably less successful because tits may not easily detect cryptic prey (Lawrence 1985). Although there were no significant responses of great tit to outbreaks in this study, this species has showed a positive numerical response to larval outbreaks of pine processionary moth in the Mediterranean (Pimentel & Nilsson 2007, 2009), and it should not be overlooked as a key predator of defoliator larvae in cork oak woodlands (Ceia & Ramos 2014).

GENERALIST PREDATOR HYPOTHESIS

Even if food shortage sets a potential upper limit to numbers of defoliator pests, this limit is reached only occasionally during extreme outbreaks. Research on gypsy moth and other forest defoliator pests suggests that parasitoids and pathogens are relatively important in regulating high-density populations, whereas biologically significant mortality in sparse populations is rather caused by vertebrate and invertebrate predators (Doane 1976, Campbell & Sloan 1977a, Anderson & May 1981, Furuta 1982, Campbell & Torgersen 1983, Mason & Torgersen 1983, Torgersen *et al.* 1983, Myers 1988, Elkinton & Liebhold 1990, Berryman 1995, Villemant & Ramzi 1995, Parry *et al.* 1997). Findings of the present study are consistent with these conclusions and also with predictions of the generalist predator hypothesis (Murdoch & Oaten 1975, Southwood & Comins 1976). The syntopic population model developed by Southwood and Comins (1976) predicts that functional and numerical responses by generalist predators, such as tree-foraging passerines, create a "natural enemy ravine" that retains prey populations at stable lower levels far below the carrying capacity of their environment. Any reduction in the efficiency of generalist predators due to natural variation in this complex density dependence system can result in episodic defoliator outbreaks (Beddington *et al.* 1978). Moderate outbreaks of defoliators in cork oak woodlands were associated with positive numerical and functional responses of four species of generalist passerines in spring, a time when predation is supposed to have a significant impact on pest populations as it matches the larval development of pests and the breeding season of birds. Nonetheless, bird regulation of gypsy moth and *P. andrei* populations in cork oak woodlands can only be achieved through year-round predation on the distinct life stages of insects (Ceia & Ramos 2014). Very high rates (up to 90%) of bird predation on overwintering egg masses of gypsy moth have been reported in other forests (Reichart 1958, Higashiura 1989, Cooper & Smith 1995), and predation on bare pupae is also expected to be relevant, although it has not been well documented on birds (Campbell & Sloan 1976). Because *P. andrei* lays ephemeral dispersed eggs and, as a pupa, diapauses in the soil for up to three years (Ferreira & Ferreira 1991), bird predation on larval and adult stages should have a higher importance in the regulation of populations of this insect species. Further research on the impact of birds and other enemies on populations of these pests is required to clarify the extent and influence of such interactions.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

The economic significance of defoliator damage in cork oak woodlands has justified the chemical control of these pests since early 20th century. DDT and arsenates were used until the 1980's, when they were banned in most European countries, and recent control methods in cork oak woodlands involve the aerial spraying with diflurobenzuron or *Bacillus thuringiensis*, a microbial insecticide (Martin *et al.* 2002, Serrão 2002, Basri *et al.* 2005, Luciano & Lentini 2012). Despite diflubenzuron and *Bacillus thuringiensis* are not directly toxic to vertebrates, their use to control gypsy moth populations can have an indirect negative impact on birds through a decrease in the availability of other Lepidoptera larvae (Cooper *et al.* 1990, Rodenhouse & Holmes 1992, Sample *et al.* 1993a). The chemical control of defoliator outbreaks can hence result in short-term protection and a persistence of infestations by reducing the efficiency of birds in the subsequent dampening of defoliator populations.

This study supports the ongoing evidence that birds play an important role in the control of pest populations which was here verified at moderate outbreak conditions of two distinct defoliator species in cork oak woodlands. In the context of climate warming, which is expected to increase distribution ranges and outbreaks of insect pests in the future (Logan *et al.* 2003, Netherer & Schopf 2010, Thomson *et al.* 2010), forest managers should find ways to enhance bird populations in order to reduce the severity of infestations. Also, European scenarios reflect a trend for increasing defoliation (UN-ECE/FAO 2000) and attempts should be made to understand how bird communities can maintain pest populations at low densities in other European forests.

The tree-foraging guild comprises some of the most abundant and widespread species in cork oak woodlands, however considerable changes in taxonomic and functional diversity of bird communities can occur at a local scale according to land management. A decrease in natural regulation of pests by birds may arise 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 (Rabaça 1990, Almeida 1992a, Godinho & Rabaça 2011, Leal *et al.* 2011b, 2013, Pereira *et al.* 2014a). In contrast, artificial nest-boxes have been used in various ecosystems to control pests by increasing breeding populations of hole-nesting predators (East & Perins 1988, Wang & Liao 1990, Sanz 2001, Mols & Visser 2002, Bouvier *et al.* 2005). As blue tit, great tit and nuthatch are common hole-nesting species in cork oak woodlands, the provision of artificial nest-boxes may enhance bird predation on defoliator pests if local breeding populations of these bird species are limited by shortage of tree cavities.

CHAPTER 4

Caterpillar predation by three hole-nesting passerine species and experimental increase of their densities in Mediterranean oak woodlands

In: **Ceia RS**, Machado RA, Ramos JA. Caterpillar predation by three hole-nesting passerine species and experimental increase of their densities in Mediterranean oak woodlands. Submitted to European Journal of Forest Research

ABSTRACT

This two-year study in Mediterranean oak woodlands assessed bird predation on defoliator caterpillars (Lepidoptera larvae), through identification of food given to nestlings by three hole-nesting passerine species which forage on different niches of trees: blue tit (*Cyanistes caeruleus*; foliage-gleaner), great tit (*Parus major*; bark-foliage-gleaner) and nuthatch (*Sitta europaea*; bark-gleaner). Species-specific functions were compared using breeding densities, size and composition of preyed caterpillars and caterpillar provisioning rates to nestlings, and nest-boxes were used in a before-after control-impact (BACI) design to test increase of breeding densities by providing nest-boxes. Results demonstrate a high importance of caterpillars in the nestling diet of the three passerine species, and suggest their complementary predation on early and late instars of the same Lepidoptera species. Because blue tit was more abundant than great tit and nuthatch, there were significant differences in predicted caterpillar removal rates in terms of numbers (caterpillars.ha^{-1}.day^{-1}) but not in terms of biomass (mg.ha^{-1}.day^{-1}) given that significantly smaller caterpillars were taken by blue tit than by the other two species. Finally, according to results of the BACI experiment, species' breeding density increased by providing nest-boxes, with blue tit showing the highest difference in percentage change between manipulated and control plots (38.2%, 26.8% and 14.3% for blue tit, great tit and nuthatch, respectively).

Overall, the combined function of tree-foraging guilds (foliage-, bark-foliage- and bark-gleaners) in caterpillar predation is highlighted and nest-box provision is proposed as a management method to prevent defoliator outbreaks in Mediterranean oak woodlands.

INTRODUCTION

Moth and butterfly caterpillars (Lepidoptera larvae) exclusively feed on plants, mainly on leaves, and represent the most important defoliators in forests worldwide (Gullan & Cranston 2010). Although defoliator caterpillars decisively contribute to the flow of energy and matter in forests (Seastedt & Crossley 1984), abundant species can cause significant damage to forest resources, as often happens during outbreaks of the gypsy moth (*Lymantria dispar*) (Campbell & Sloan 1977b, Schultz & Baldwin 1982, Webb *et al.* 1995, Gandhi & Herms 2010). Even if food limits numbers of defoliator caterpillars, this limit is rarely reached due to the labour of natural enemies (*i.e.*, pathogens, parasitoids and predators) which retain their populations at relatively stable lower levels far below carrying capacity (Southwood & Comins 1976, May 1986). Research on forest Lepidoptera suggests that pathogens and parasitoids are relatively important in reducing outbreak populations (Doane 1976, Anderson & May 1981, Myers 1988, Berryman 1995), whereas biologically significant mortality in low-density populations is rather caused by bird predation on caterpillars (Holmes *et al.* 1979, Furuta 1982, Campbell & Torgersen 1983, Campbell *et al.* 1983, Crawford & Jennings 1989, Parry *et al.* 1997, Murakami & Nakano 2000, Tanhuanpää *et al.* 2001, Medina & Barbosa 2002).

Because caterpillars comprise most of the food given by various hole-nesting passerine species to their nestlings (Cholewa & Wesołowski 2011), nest-boxes have been placed in some managed forests to increase breeding densities to reduce caterpillar numbers and damage to trees. But, even if many communities of hole-nesters may be strongly limited by abundance of nesting tree cavities (von Haartman 1971, Enemar & Sjostrand 1972, Perrins 1979, van Balen *et al.* 1982, East & Perrins 1988, Newton 1994, 1998, Sanz 2001, Loman 2006, Sánchez *et al.* 2007, Mänd *et al.* 2009, Miller 2010), in other cases apparently there is no such limitation (Brawn & Balda 1988, Wesołowski 1989, Carlson *et al.* 1998, Waters *et al.* 1990, Walankiewicz 1991, Aitken *et al.* 2002, Gibbons & Lindenmayer 2002, Bai *et al.* 2003, Aitken & Martin 2004, Brightsmith 2005, Wesołowski 2007, Camprodon *et al.* 2008). In addition, if there is a strong interspecific competition for nest-sites, added nest-boxes may be occupied by bird species that are less specialized predators of caterpillars. Therefore, the consequences of nest-box provision in a specific habitat should be evaluated prior to implementation of nest-box programs designed to increase populations of hole-nesting passerines.

Mediterranean oak woodlands are scattered tree ecosystems (20–80 trees.ha^{-1}) dominated by two species of sclerophyllous evergreen oaks, cork oak (*Quercus suber*) and holm oak (*Q. rotundifolia*), which form pure or mixed stands over 6.3 million hectares in the southwest Iberian Peninsula (Joffre *et al.* 1999, Pinto-Correia & Mascarenhas 1999). Evergreen oaks are amongst the most defoliated trees in Europe (ICP Forests 2013) and a number of defoliator caterpillars, including the gypsy moth, is related to the decline of this ecosystem in the last decades (Branco & Ramos 2009; see Ceia & Ramos 2014 for a list of species). Mediterranean oak woodlands constitute economically sustainable systems wherein the most important income for landowners comes from cork harvesting, a process that takes place without felling trees, at *ca.* nine years intervals in mature cork oak trees (Bugalho *et al.* 2011). Other forest products include fuelwood, obtained from canopy pruning and cutting of dead and decaying trees, and acorns, which are collected for human consumption but mainly used as food for extensively reared Iberian pigs (Joffre *et al.* 1999, Pinto-Correia & Mascarenhas 1999). Nevertheless, defoliation caused by caterpillars is responsible for decreasing tree growth, acorn production and cork quality (Magnoler & Cambini 1973, Rieske & Dillaway 2008, Branco & Ramos 2009). Furthermore, repeated defoliation may lead to tree mortality because trees weakened by defoliation are extremely vulnerable to xylophagous pests (Merle & Attié 1992, Martín *et al.* 2005, Sousa & Inácio 2005) and pathogenic fungi (Brasier *et al.* 1993, Vannini *et al.* 1996). The economic significance of damage caused by caterpillars in Mediterranean oak woodlands has resulted in chemical control of outbreaks since early 20th century. Arsenates and DDT were used until the 1980's, when they were banned in most European countries, and recent control methods involve aerial spraying with diflurobenzuron or *Bacillus thuringiensis* based insecticides (*e.g.*, Serrão 2002, Basri *et al.* 2005, Luciano & Lentini 2012). On the other hand, bird predation on caterpillars, especially by hole-nesting passerines, is not understood, although its importance has been shown in other forest ecosystems (see Whelan *et al.* 2008 for a review).

This study, in Mediterranean oak woodlands, investigated the role of three hole-nesting passerine species as caterpillar predators: blue tit (*Cyanistes caeruleus*), great tit (*Parus major*) and nuthatch (*Sitta europaea*). These are key insectivores in Mediterranean oak woodlands and, taken altogether, account for more than 55% of arthropod predation by birds on cork and holm oak trees (Leal *et al.* 2011b, 2013, Ceia & Ramos 2015). During their breeding season, which is synchronized with caterpillar availability in forest habitats (Cholewa & Wesołowski 2011), prey are almost exclusively obtained from trees, but while blue tit forages mostly on leaves, twigs and outer branches (foliage-gleaner), great tit preferentially forages on inner branches (bark-foliage-gleaner), and nuthatch captures prey on the largest branches and the trunk (bark-gleaner) (Almeida & Granadeiro 2000). Hence, these were suitable species to analyse the contribution of different tree-foraging guilds to caterpillar predation. To achieve this purpose, nestling diet and breeding densities of all three species were determined in a Mediterranean oak woodland with non-outbreak populations of defoliator caterpillars. The hypotheses were that (1) percentage of caterpillars in nestling diet and caterpillar provisioning rate to nestlings are highest for blue tit and lowest for nuthatch, given that leaf-feeding caterpillars are more exposed to predation by foliage-gleaners than by bark-gleaners; (2) caterpillar size and taxonomic composition differs among bird species in consequence of birds' different morphological and behaviour skills to capture prey and predator avoidance strategies of caterpillars (Heinrich 1979, 1993); and (3) caterpillar removal rates (number and biomass of preyed caterpillars per hectare per day by each species) are highest for blue tit and lowest for nuthatch, consistent with the first hypothesis, and because breeding densities of blue tit in Mediterranean oak woodlands are often higher than those of great tit and nuthatch (Herrera 1978a, Rabaça 1990, Pulido & Díaz 1992, Almeida 1997, Leal *et al.* 2013, Ceia & Ramos 2015; see, however, Almeida 1992a, Camprodon & Brotons 2006, Leal *et al.* 2011a). In addition, it was tested whether breeding densities could be increased by providing nest-boxes, using a before-after control-impact (BACI) design to compare plots provided with nest-boxes (manipulated) and control plots over two years. If breeding densities of foremost caterpillar predators can be increased with nest-boxes, this could be a management method to prevent defoliator outbreaks in Mediterranean oak woodlands.

METHODS

STUDY AREA

This study was carried out during the springs of 2013 and 2014 in the Herdade do Freixo do Meio (38º42'N 8º19'W), a farm that manages 1140 ha of cork-holm oak woodlands near Montemor-o-Novo, Portugal. The region is characterized by a Mediterranean climate with warm and dry summers and rainfall mostly in autumn and winter (mean annual rainfall = 660 mm, mean annual temperature = 15.4 ºC, mean annual evaporation = 1760 mm; INMG 1991). Tree density was approximately 40 trees.ha^{-1} and most trees in the study area had a diameter at breast height (DBH) greater than 45 cm. In both years of this study, damage by defoliating caterpillars affected less than 1% of leaves, as estimated by counting the number of eaten leaves in a sample of 100 leaves, observed *in situ* through binoculars, in 100 randomly selected trees of each species (cork oak and holm oak). Throughout the study area pruning of tree canopies and debarking of cork oak trees took place more than two years prior to this study.

In the year before this study, 100 nest-boxes were equally assigned to five plots, each with 5 ha. Additionally, five plot pairs were selected at that time as manipulated-control replicated pairs in a before-after control-impact (BACI) design. Each manipulated plot from a replicated pair was provided with 20 nest-boxes following the 2013 breeding season, while the control plot was devoid of nest-boxes in the two years. All plots (*n* = 15) had an identical shape (500 m x 100 m) and were similar in terms of topography, forest structure and composition. The boundaries of neighbouring plots were separated at least by 100 m. Overall, 100 and 200 nest-boxes were available during 2013 and 2014 breeding seasons, respectively, at a density of 4 nest-boxes.ha^{-1} (50 m between neighbouring nest-boxes) in each plot. Nest-boxes were made of raw pine wood, 1.5 cm thick, with 10.0 x 6.0 x 7.0 cm (height x width x depth) and an entrance hole in the front with a diameter of 2.5 cm. They were placed against the trunk or a main branch of cork and holm oak trees at a height of 2 m and randomly orientated. Nest-boxes were cleaned out in February before each new nesting season. From March to late-June in 2013 and 2014 nest-boxes were inspected on a weekly basis, by opening the roof to register developments in nest-building, egg-laying and hatching.

NESTLING DIET

Prey taken by blue tit, great tit and nuthatch were assessed by sampling nestlings reared in nest-boxes with the ligature method (Rosenberg & Cooper 1990, Mellot & Woods 1993). This method consists of positioning a cotton coated wire around the neck of nestlings (aged 5–16 days, or 5–21 days in the case of nuthatch nestlings), which prevents swallowing but allows normal breathing, and collecting food items with forceps from the throat of the nestlings. The simultaneous sampling of every nestling from a clutch was carried out from 8:00 to 20:00 GMT + 1, however ligatures were kept in place for no more than two hours at a time (mean ± SE = 81.8 ± 1.1 minutes), during which time the birds were not disturbed. Each nest-box was sampled once daily, on average during three days (mean ± SE = 2.6 ± 0.3 days). Prior to applying ligatures, each nest was checked for regurgitated invertebrates, but none were found. The nest was also checked for regurgitated items after sampling, and any that were found were also included in analyses. Therefore, all invertebrates collected from nestlings, using the ligature method, and from the nest were considered to represent prey fed to nestlings during the sampling period. Diet samples were preserved in 70% ethanol and later identified in the laboratory using a binocular microscope with 60x magnifying glass. Caterpillars were identified to family level following Chu (1949) and Viejo and Romera (2004), and body length was measured using graph paper with a precision of 0.1 mm. Body length to body mass conversion equations were used to calculate larvae biomass as described in Sample *et al.* (1993b).

BREEDING DENSITIES

From early-April to mid-May, *i.e.*, during the breeding season but prior to fledgling emergence, abundance of blue tit, great tit and nuthatch in the five manipulated-control plot pairs was estimated with the point-count method (Bibby *et al.* 1992). Bird counts were carried out at four stations per plot, set approximately at 150 m intervals. Sampling was completed in all stations (n = 40) per year within four hours after sunrise. Counts started one minute after arriving at the point to allow birds to settle down from any disturbance caused by the observer's arrival on foot. All individuals heard or seen within a 50 m radius were recorded during a five-minute period. Annual breeding densities (pairs.ha^{-1}) were calculated at each station by dividing number of individuals by the surveyed area (0.785 ha).

DATA ANALYSIS

General Linear Models (GLMs) were used to test for differences among bird species in percentage of the main prey types in nestling diet (arcsine-transformed proportions), caterpillar provisioning rate to nestlings (log-transformed data), body length of preyed caterpillars and number of occupied nest-boxes per plot. Fixed explanatory variables were bird species and year, and the interaction between these two variables.

Differences among bird species in caterpillar composition were tested by using chi-square tests to analyse number of nests with and without caterpillars belonging to each Lepidoptera family recorded in nestling diet.

To predict caterpillar removal rate per bird species in terms of numbers (caterpillars.ha^{-1}.day^{-1}) and biomass (mg.ha^{-1}.day^{-1}), caterpillar provisioning rates per nest, both in terms of numbers (caterpillars.nest^{-1}.hr^{-1}) and biomass (mg.nest^{-1}.hr^{-1}), were multiplied by species' density in the study area (mean of 2013 and 2014 pairs.ha^{-1}

in the control plots) and by number of daylight hours (14 $hr.day^{-1}$). Caterpillar removal rates in terms of numbers and in terms of biomass (log-transformed data) were then compared among species using a univariate GLM.

The effect of nest-boxes on bird densities under the BACI design was assessed using repeated-measures GLMs with manipulated-control plot pairs as subjects. Because magnitude and variability of the effects are often more informative in evaluation of impacts (Grafen & Hails 2002), results are also presented and discussed in terms of percentage change (%Δ) between manipulated (*i.e.*, provided with nest-boxes) and control plots.

Significant P values ($P < 0.050$) were compared for differences with post-hoc Tukey tests. All statistical analyses were conducted using Statistica 8.0 (StatSoft Inc. 2007). Results are presented as mean ± standard error.

RESULTS

NESTLING DIET AND CATERPILLAR PREDATION

Overall, 954 diet items were collected on 21, 23 and 24 clutches of blue tit, great tit and nuthatch. Results from nestling diet analysis are summarized in Table 10. Caterpillars (Lepidoptera larvae) were the most common prey given to nestlings of the three bird species, with the exception of nuthatch nestlings which had more beetles (Coleoptera) in 2013. Blue tit nestlings ingested a significantly higher percentage of caterpillars, up to 64.1%, compared to the other two species (Table 10). On the other hand, the diet of great tit nestlings included a significantly higher percentage of moths (Lepidoptera adults) and grasshoppers (Orthoptera) than the other two bird species, and nuthatch nestlings consumed a significantly higher percentage of beetles when compared to nestlings of blue tit and great tit (Table 10). There were also significant differences in percentage of moths and caterpillars between years, and these were highest in 2013 and 2014, respectively (Table 10). This result is consistent with the significantly higher caterpillar provisioning rates found in 2014 (Table 11). However, no differences were found among bird species or interaction between year and bird species in caterpillar provisioning rate (Table 11).

Table 10. Percentage of the main food types in nestling diet of each bird species (mean ± SE of values per nest) in the two years of this study. ‘Other items’ included insects (Dermaptera, Dictyoptera, Diptera, Hemiptera, Hymenoptera, Neuroptera, Phthiraptera), Diplopoda, Oligochaeta, Gastropoda, and vegetal items. Non-identified insects and arthropods (including eggs) were excluded from calculations. GLM compared data among species (Sp) and years (Yr), as well as the interaction between both factors (Sp*Yr). Significant *P* values are highlighted in bold and letters indicate differences from post-hoc Tukey test comparisons (see footnote).

	Blue tit		**Great tit**		**Nuthatch**		**GLM**
	2013 (*n* = 13)	2014 (*n* = 8)	2013 (*n* = 12)	2014 (*n* = 11)	2013 (*n* = 4)	2014 (*n* = 20)	
Lepidoptera	61.7 (± 11.4)	66.5 (± 11.0)	48.7 (± 9.1)	63.9 (± 9.6)	22.4 (± 7.6)	49.8 (± 7.1)	Sp: $F_{2, 65}$ = 2.68, *P* = 0.078 Yr: $F_{1, 66}$ = 3.69, *P* = 0.060 Sp*Yr: $F_{2, 62}$ = 0.34, *P* = 0.713
Larvae	57.6 (± 10.9)	64.1 (± 11.3)	30.1 (± 7.4)	56.8 (± 10.2)	14.1 (± 5.9)	46.0 (± 7.1)	**Sp: $F_{2, 65}$ = 3.51, *P* = 0.037**[a] **Yr: $F_{1, 66}$ = 6.81, *P* = 0.012**[b] Sp*Yr: $F_{2, 62}$ = 0.65, *P* = 0.527
Pupae	1.8 (± 1.8)	2.4 (± 2.4)	3.2 (± 1.7)	0.5 (± 0.5)	0.2 (± 0.2)	2.1 (± 1.5)	Sp: $F_{2, 65}$ = 0.11, *P* = 0.896 Yr: $F_{1, 66}$ = 0.03, *P* = 0.871 Sp*Yr: $F_{2, 62}$ = 0.79, *P* = 0.457
Adults	2.3 (± 2.3)	0	15.4 (± 6.1)	6.6 (± 2.4)	8.1 (± 3.5)	1.7 (± 0.8)	**Sp: $F_{2, 65}$ = 6.17, *P* = 0.004**[c] **Yr: $F_{1, 66}$ = 4.52, *P* = 0.038**[d] Sp*Yr: $F_{2, 62}$ = 0.48, *P* = 0.622
Arachnida	18.5 (± 9.0)	8.9 (± 3.8)	16.3 (± 5.1)	6.2 (± 2.7)	11.9 (± 2.7)	15.2 (± 4.1)	Sp: $F_{2, 65}$ = 0.25, *P* = 0.780 Yr: $F_{1, 66}$ = 1.66, *P* = 0.204 Sp*Yr: $F_{2, 62}$ = 0.16, *P* = 0.851
Coleoptera	0.6 (± 0.6)	0.5 (± 0.5)	1.3 (± 1.3)	6.0 (± 3.3)	31.8 (± 14.1)	16.9 (± 4.5)	**Sp: $F_{2, 65}$ = 17.60, *P* < 0.001**[e] Yr: $F_{1, 66}$ = 0.58, *P* = 0.449 Sp*Yr: $F_{2, 62}$ = 2.65, *P* = 0.079
Orthoptera	0	0	20.7 (± 10.1)	6.2 (± 4.4)	2.4 (± 2.2)	0	**Sp: $F_{2, 65}$ = 4.92, *P* = 0.011**[d] Yr: $F_{1, 66}$ = 2.54, *P* = 0.117 Sp*Yr: $F_{2, 62}$ = 1.13, *P* = 0.331
Other items	10.1 (± 5.5)	24.1 (± 9.3)	13.0 (± 5.0)	17.6 (± 6.9)	31.6 (± 7.8)	18.1 (± 6.7)	Sp: $F_{2, 65}$ = 0.81, *P* = 0.449 Yr: $F_{1, 66}$ < 0.01, *P* = 0.985 Sp*Yr: $F_{2, 62}$ = 2.07, *P* = 0.136

[a] significantly higher for blue tit than for the other two species; [b] significantly higher in 2014 than in 2013; [c] significantly higher for great tit than for the other two species; [d] significantly higher in 2013 than in 2014; [e] significantly higher for nuthatch than for the other two species

Body length of preyed caterpillars showed significant differences among bird species and both great tit and nuthatch captured larger caterpillars than blue tit (Table 11). Caterpillar size showed no differences between years, and no interaction between bird species and year (Table 11). Overall, most caterpillars in nestling diet belonged to four Lepidoptera families: Noctuidae (50.0%), Crambidae (20.8%), Geometridae (11.3%) and Erebidae (5.4%) (Fig. 16). There were no significant differences among bird species in preyed Lepidoptera families ($\chi^2 < 4.94$, $P > 0.085$), except for Noctuidae ($\chi^2 = 7.16$, $P = 0.028$) and Tischeriidae ($\chi^2 = 10.23$, $P = 0.006$) whose observed values were higher than expected for nuthatch and blue tit, respectively. In specific, gypsy moth caterpillars (family Erebidae) were captured by great tit and nuthatch and represented 2.0% and 10.8% of identified caterpillars in nestling diet of these bird species, respectively.

Table 11. Caterpillar provisioning rate (caterpillars.nest^{-1}.hr^{-1}) and body length (mm) of caterpillars given to nestlings of each bird species in the two years of this study. GLM compared data among species (Sp) and years (Yr), as well as the interaction between both factors (Sp*Yr). Significant *P* values are highlighted in bold and letters indicate differences from post-hoc Tukey test comparisons.

	Blue tit		**Great tit**		**Nuthatch**		**GLM**
	2013	2014	2013	2014	2013	2014	
Caterpillar provisioning rate	0.6 (± 0.1)	2.1 (± 0.5)	0.4 (± 0.1)	1.6 (± 0.4)	0.9 (± 0.3)	1.5 (± 0.3)	Sp: $F_{2, 65} = 0.68$, $P = 0.508$ **Yr: $F_{1, 66} = 14.45$, $P < 0.001^a$** Sp*Yr: $F_{2, 62} = 0.82$, $P = 0.447$
Body length of caterpillars	16.8 (± 1.2)	18.7 (± 1.0)	22.2 (± 0.8)	22.2 (± 1.0)	22.7 (± 1.6)	22.3 (± 1.0)	**Sp: $F_{2, 211} = 9.91$, $P < 0.001^b$** Yr: $F_{1, 212} = 0.26$, $P = 0.608$ Sp*Yr: $F_{2, 208} = 0.57$, $P = 0.566$

^{a} significantly higher in 2014 than in 2013; ^{b} significantly lower for blue tit than for the other two species

The highest caterpillar removal rates corresponded to blue tit (Fig. 17). These showed a direct relationship with species' breeding density, which in the case of blue tit was approximately fourfold that of great tit and nuthatch (blue tit: 0.86 ± 0.08 pairs.ha^{-1}, great tit: 0.21 ± 0.07 pairs.ha^{-1}, nuthatch: 0.21 ± 0.05 pairs.ha^{-1}). However, while caterpillar removal rate in terms of numbers was significantly higher for blue tit than for the other two bird species ($F_{2, 65} = 6.92$, $P = 0.002$; Fig. 17a), there were no significant differences among the three bird species in caterpillar removal rate in terms of biomass ($F_{2, 65} = 1.35$, $P = 0.267$; Fig. 17b).

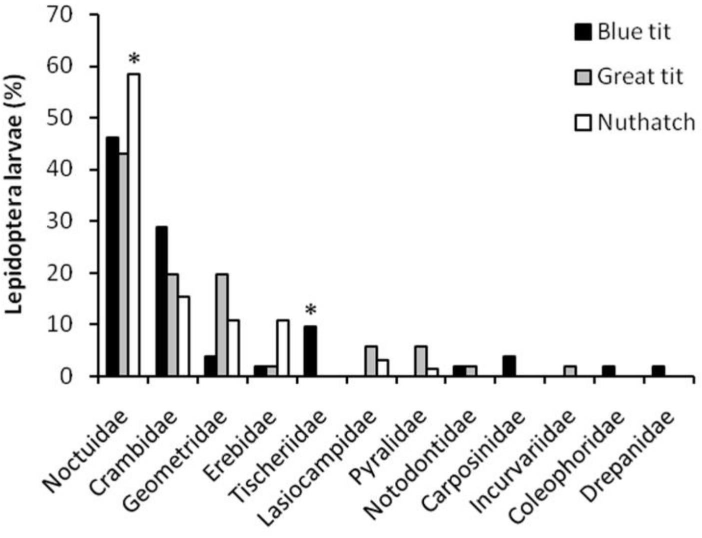

Figure 16. Percentage per Lepidoptera family of caterpillars identified in nestling diet of each bird species (*N* = 214, including 46 unidentified caterpillars). Chi-square tests were used to analyse number of nests with and without caterpillars belonging to each Lepidoptera family recorded in nestling diet, and an asterisk indicates observed values higher than expected whenever there were significant differences among bird species.

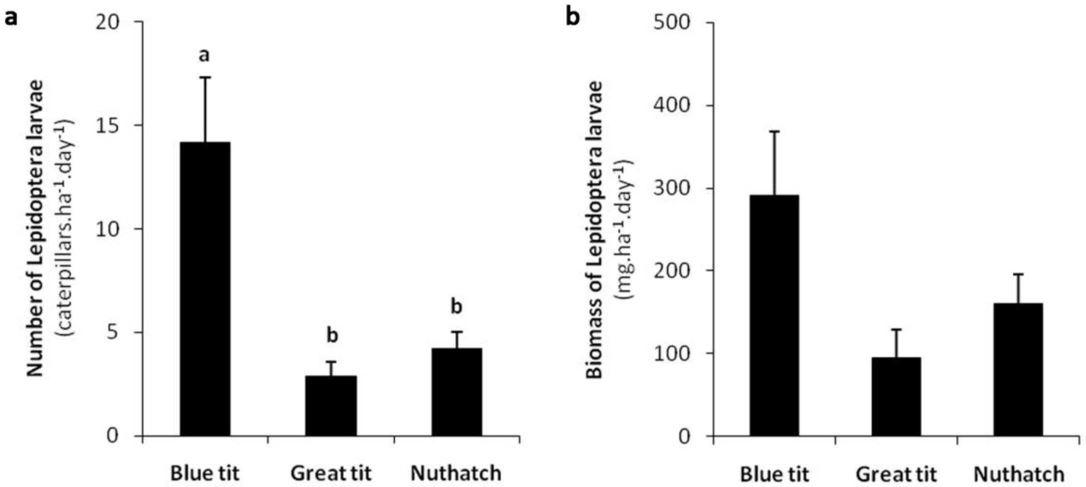

Figure 17. Caterpillar removal rates by each bird species (mean ± SE of values per nest), expressed in numbers (a) and biomass (b). See methods for details of calculations. Significant differences among species from post-hoc Tukey test following GLMs are indicated using different letters.

NEST-BOX OCCUPANCY AND THE BACI DESIGN

Nest-box occupancy per plot was 52.3 ± 3.5%. Records of occupancy (nest-boxes with ≥1 egg) corresponded essentially to great tit (38.9%), nuthatch (29.3%) and blue tit (26.1%), but rock sparrow (*Petronia petronia*) and redstart (*Phoenichuros phoenichuros*) were also recorded, respectively, in 5.1% and 0.6% of the occupied nest-boxes (*n* = 157). The number of occupied nest-boxes per plot showed no differences among the three studied species ($F_{2, 42}$ = 1.48, *P* = 0.240) or between years ($F_{1, 43}$ = 0.57, *P* = 0.456), nor interaction between the two factors ($F_{2, 39}$ = 0.73, *P* = 0.488).

Mean breeding densities of the three studied species increased or remained constant in the BACI manipulated plots from 2013 to 2014 (blue tit: $\%\Delta_{\text{manipulated}}$ = + 18.2; great tit: $\%\Delta_{\text{manipulated}}$ = + 12.5; nuthatch: $\%\Delta_{\text{manipulated}}$ = 0.0; Fig. 18), while they decreased in paired control plots (blue tit: $\%\Delta_{\text{control}}$ = – 20.0; great tit: $\%\Delta_{\text{control}}$ = – 14.3; nuthatch: $\%\Delta_{\text{control}}$ = – 14.3; Fig. 18). In 2014, percent change in breeding densities between manipulated and control plots was greatest for blue tit (38.2% for blue tit vs. 26.8% and 14.3% for great tit and nuthatch, respectively), and blue tit density in manipulated plots was significantly higher than in paired control plots ($F_{1, 38}$ = 4.69, *P* = 0.037). No significant differences were found between plot pairs for great tit ($F_{1, 38}$ = 0.14, *P* = 0.714) and nuthatch ($F_{1, 38}$ = 0.04, *P* = 0.840).

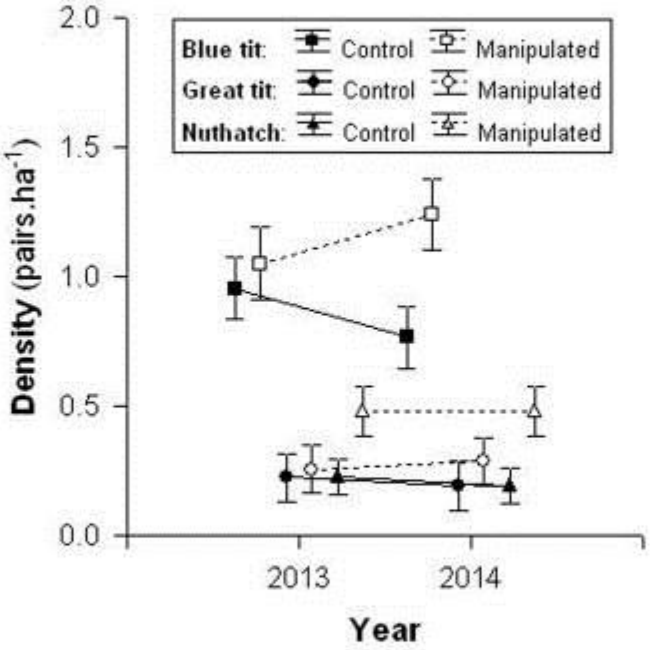

Figure 18. Response of blue tit, great tit and nuthatch densities (pairs.ha^{-1} ± SE) between control and manipulated plots under the before-after control-impact (BACI) design. Nest-boxes were installed in manipulated plots after 2013 while control plots were devoid of nest-boxes in both years.

DISCUSSION

This study demonstrates that all tree-foraging bird guilds (foliage-, bark-foliage- and bark-gleaners) are important in caterpillar predation in Mediterranean oak woodlands, even though this function has been mainly attributed to foliage-gleaners in other forest ecosystems dominated by coniferous or deciduous tree species (Crawford & Jennings 1989, Parry *et al.* 1997, Murakami & Nakano 2000). Caterpillars were the most, or second-most, common food taken each spring by studied birds of the three tree-foraging guilds to feed their nestlings. Nestling diet of foliage-gleaners (blue tit) included a significantly higher percentage of caterpillars than those of bark-foliage- (great tit) and bark-gleaners (nuthatch). However, the relative contribution of caterpillars to nestling diet of bark-foliage-gleaners did not differ significantly from that of bark-gleaners. Moreover, caterpillar provisioning rates to nestlings showed no differences among the three bird species, although their foraging niches in Mediterranean oak woodlands present a small overlap (Almeida & Granadeiro 2000).

Because preyed caterpillar composition did not differ among bird species for most preyed Lepidoptera families, results suggest that foliage-gleaners exploit earlier instars (smaller caterpillars), and bark-foliage- and bark-gleaners feed on late instars (larger caterpillars) of the same caterpillars. Both this hypothesis of caterpillar size segregation and the similar caterpillar provisioning rates found among foraging guilds agree with caterpillar development on different niches of trees. Newly hatched caterpillars start feeding on sprouting leaves and then, as they grow, move in-between branches in search of other young leaves or feed on inner leaves from the previous year. Full-grown larvae descend to pupate on lower branches, the trunk or in the soil (Ferreira & Ferreira 1991). Nevertheless, in agreement with predicted hypothesis, species-specific morphological or behavioural skills may also explain the comparatively higher number of Noctuidae and Tischeriidae caterpillars found among prey of nuthatches and blue tits, respectively. To reduce search time and increase prey profitability (*e.g.*, Hughes 1979, Houston *et al.* 1980), nuthatch may preferentially prey on conspicuous large Noctuidae caterpillars (body length = 24.5 ± 0.7 mm), while small Tischeriidae caterpillars (body length = 11.4 ± 0.8 mm) may be selected preferentially by blue tits due to a shorter handling time (Pyke *et al.* 1977).

Size differences in caterpillars taken by blue tit and great tit were also detected by Török and Tóth (1999) and have been suggested to result from interspecific competition during the breeding season. However, feeding on smaller caterpillars does not present a disadvantage for blue tits as they are more abundant. Regarding caterpillar removal rates, blue tits consumed significantly greater numbers of defoliator caterpillars at the habitat scale than great tit or nuthatch. On the other hand, the lower abundance of large caterpillars is compensated by their greater biomass. Thus, caterpillar removal rate in terms of biomass by the three species did not differ, even if the number of preyed caterpillars by great tits and nuthatches was significantly lower at the habitat scale.

CATERPILLAR PREDATION IN MEDITERRANEAN-TYPE ECOSYSTEMS

In deciduous forests of central and northern Europe, caterpillars often comprise ≥75% of the food brought to nestlings by blue tit and great tit (*e.g.*, Minot 1981, Nour *et al.* 1998, Przybylo & Merilä 2000, Wilkin *et al.* 2009), and about 30% of that brought by nuthatch (Krištín 1994). Mediterranean-type ecosystems, however, are typically dominated by evergreen trees, such as cork oak and holm oak, and development of new leaves in spring involves less than one third of foliage and occurs much later in the season than in deciduous trees (Orshan 1989). These differences are hypothesized to result in a lower abundance of defoliator caterpillars and a higher variability of this prey across space and time than in other European forest types dominated mostly by deciduous oaks (Blondel *et al.* 2010).

In this study, in evergreen Mediterranean oak woodlands, caterpillars represented on average 60%, 43% and 40% of items given to blue tit, great tit and nuthatch nestlings, respectively. Similar to these results, other studies have revealed that the overall contribution of other prey, mainly spiders and grasshoppers, to the diet of blue tit and great tit nestlings is greater in Mediterranean-type ecosystems than in other forest cover types (Blondel *et al.* 1991, Bańbura *et al.* 1994, Blondel *et al.* 2002, Ziane *et al.* 2006, Pagani-Núñez *et al.* 2011, Pagani-Núñez & Senar 2014, Pagani-Núñez *et al.* 2015). On the other hand, nuthatch nestlings were given more caterpillars in this study than in other studies in mixed coniferous-deciduous forests of central Europe (Krištín 1994) and northeastern Siberia (Pravosudov *et al.* 1996) which also used the ligature method.

So far as is known, this is the only study to assess the nestling diet of nuthatch in the last twenty years and the first for the Mediterranean region. In contrast, many studies, especially in the last few years, have evaluated nestling diet of blue tit (Blondel *et al.* 1991, Bańbura *et al.* 1994, Blondel *et al.* 2002, Tremblay *et al.* 2005, Ziane *et al.* 2006, García-Navas & Sanz 2010, 2011a, 2011b, García-Navas *et al.* 2012) or great tit (Pagani-Núñez *et al.* 2011, Pagani-Núñez & Senar 2014, Pagani-Núñez *et al.* 2015) in Mediterranean-type ecosystems. Nevertheless, interspecific comparisons between studies should be made cautiously because, as in this study, the proportion of caterpillars in nestling diets showed interannual variation at each study site.

The nestling diet of Mediterranean blue tits and great tits was compared in two other studies. Similar to this study, Massa *et al.* (2004) found a higher percentage of caterpillars in the nestling diet of blue tits than in that of great tits (74.8% and 55.5%, respectively). Although García-Navas *et al.* (2013) reported the opposite (67.2% for blue tit and 80.2% for great tit), their results agree with the findings of this study in the fact that blue tits relied more heavily on spiders than great tits did. In both studies the percentage of caterpillars in nestling diets was higher than in this study, but it was also high compared to other studied Mediterranean ecosystems on Corsica island (Blondel *et al.* 1991, Bańbura *et al.* 1994, Blondel *et al.* 2002, Tremblay *et al.* 2005) and in northeastern Spain (Pagani-Núñez *et al.* 2011, Pagani-Núñez & Senar 2014, Pagani-Núñez *et al.* 2015). Such differences are probably a result of the larger number of caterpillars available in the study areas used by Massa *et al.* (2004) and García-Navas *et al.* (2013), given the outbreaks of the green oak moth (*Tortrix viridana*). Under such outbreak scenarios, caterpillar provisioning rates were also substantially higher than those found in this study (up to 30 caterpillars.nest^{-1}.hr^{-1}; Massa *et al.* 2004, García-Navas *et al.* 2013).

EFFECT OF NEST-BOXES ON BREEDING DENSITIES

There was an increase in the breeding density of the three studied passerine species as a result of providing nest-boxes. Density of blue tits increased significantly in manipulated nest-box plots compared with control plots, and the breeding populations of great tit and nuthatch also increased moderately. However, data was collected for only one year post-next-box installation and it is hard to infer whether the observed changes in breeding densities were due to recruitment or movements of individuals between plots without and with nest boxes. If the latter, it may be challenging to use nest boxes over a large enough area to change bird density in a meaningful way. In any case, results suggest that populations of hole-nesting passerines were limited by availability of natural nest-sites at least in the manipulated plots.

Approximately half of the nest-boxes remained unoccupied in each study plot. Interspecific competition for nest-sites was probably low and only a small number of nest-boxes was occupied by rock sparrow and redstart, which have a less specialized diet on caterpillars than blue tit, great tit and nuthatch (Cramp & Perrins 1998, Cholewa & Wesołowski 2011). However, it must not be excluded the hypothesis that empty nest-boxes were unsuitable for any of the species, for instance, by being too close to conspecifics.

Availability of suitable tree cavities in forest ecosystems can be associated with management (*e.g.*, von Haartman 1971, Perrins 1979), especially if it is considered that hole-nesting passerines breeding in primeval or unmanaged forests do not experience nest-site limitations (Wesołowski 1989, Walankiewicz 1991, Carlson *et al.* 1998, Bai *et al.* 2003, Wesołowski 2007, Camprodon *et al.* 2008). In Mediterranean oak woodlands, tree thinning was extensive in the 20th century for land cultivation or to increase acorn production (Acácio & Holmgren 2014). Moreover, old and decaying trees are frequently cut for fuelwood or post-fire control strategy (Catry *et al.* 2012). Such practices, in addition to natural disturbance events (*e.g.*, stand-replacing fires, tornados), have contributed to reduced abundance of natural cavities for hole-nesting passerines. Nest-boxes help lessen a chronic lack of nesting sites in Mediterranean oak woodlands, and thus artificially increase the breeding densities of hole-nesting passerines, particularly in areas with low tree density and/or few old-aged trees.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

The findings of this study have important theoretical implications for understanding nestling diets of hole-nesting passerines and interspecific differences in caterpillar predation. They also have implications for management of Mediterranean oak woodlands. In some circumstances, increasing breeding populations of insectivorous passerines in this ecosystem may be a preventive alternative to chemical control of defoliator caterpillars during outbreaks. For example, although gypsy moth population was not under outbreak in the study area, this species represented an important percentage of bird preyed caterpillars (up to 10.8% in the case of nuthatch) which may be preventing it from reaching outbreak thresholds. Furthermore, even though diflubenzuron and *Bacillus thuringiensis* insecticides are not directly toxic to vertebrates, their use to control defoliator caterpillars can have an indirect negative impact on populations of insectivorous passerines through a decrease in food availability (Cooper *et al.* 1990, Rodenhouse & Holmes 1992, Sample *et al.* 1993a). It is known that, at least for tits, caterpillar abundance influences many traits related to reproduction, such as timing of egg laying (Perrins 1970, Blondel *et al.* 1991, Svensson & Nilsson 1995), clutch size (Nour *et al.* 1998, Blondel *et al.* 1999), nestling growth and development (Keller & van Noordwijk 1994, Tremblay *et al.* 2003) and fledging success (Tremblay *et al.* 2003), and can also directly affect adult body condition (Merilä & Wiggings 1997) and the energetic cost of parental care (Tinbergen & Dietz 1994, Thomas *et al.* 2001). Chemical control of defoliator caterpillars can thus result in short-term protection and a persistence of infestations due to a population decline of insectivorous passerines and their subsequent reduced efficiency in dampening outbreaks.

GENERAL DISCUSSION

Many investigation steps are needed for scientists to just faintly interpret the dynamics of natural systems. In this thesis, I used a variety of approaches to provide a better understanding of insect predation by birds in Mediterranean oak woodlands and its importance to ecosystem functioning. My purpose was to describe the beneficial services provided by insectivorous birds in the control of cork and holm oak pests, particularly defoliators. I will summarize the main findings of this thesis and frame them within the context of traditional management of Mediterranean oak woodlands. To end, I will open other questions that remain answered and infer on the most promising ways to approach them.

MAIN FINDINGS OF THE THESIS

The recent decline of Mediterranean oak woodlands in their westernmost distribution is related, at least in part, to insect pests. There are approximately twenty insect species which often cause significant damage to cork oak and holm oak and have serious repercussions in the economy of this ecosystem (Ferreira & Ferreira 1991, Romanyk & Cadahia 1992). In Chapter 1, a deep bibliographic survey was carried out to identify which bird species could be the most important predators of cork and holm oak insect pests in southwestern Iberian Peninsula. This review was focused on published literature about foraging ecology and diet of breeding, wintering and resident species in Mediterranean oak woodlands, including references to 26 books and 205 scientific papers published since 1889, and established the potential of birds as pest predators in this ecosystem. Twenty-six bird species were identified as regular predators of various types of cork and holm oak pests. Most of these birds are generalist, polyphagous, insectivorous predators and their foraging niches are strongly associated with pest consumption at distinct life-cycle stages: ground-foragers prey on overwintering pupae and larvae of seed-borers, tree-foragers prey on eggs, larvae and pupae of defoliator and wood-boring pests, and aerial-sweepers prey on airborne imagines. Overall, bird predation can cover the complete life-cycle of most pest species because different species may be complementary due to a dissimilar exploitation of foraging niches and periods. Regarding defoliators, spring-summer is the period when predation is supposed to have the most significant impact on their populations because caterpillars, throughout their development on foliage, are highly vulnerable to predation by several tree-foraging passerine species which occur in high densities and are widely distributed in Mediterranean oak woodlands.

In order to validate these predictions and to analyse tree selection patterns by insectivorous birds during spring, their foraging ecology was studied with respect to variation in the two dominant tree species, cork oak and holm oak, in Chapter 2. Breeding bird communities of Mediterranean oak woodlands are largely represented by insectivorous species associated with the tree-foraging guild (Herrera 1978a, Rabaça 1990, Almeida 1992a, Pulido & Díaz 1992, Leal *et al.* 2011a, 2013), and their relevance was corroborated in this intensive field survey where tree-foraging bird species comprised >60% of total bird abundance. Nearly all arthropod predation by birds on cork and holm oak trees was carried out by a small number of passerine species, including five foliage-gleaners (blue tit, great tit, crested tit, chaffinch and Sardinian warbler) and two bark-gleaners (nuthatch and short-toed treecreeper). Based on individual foraging decisions and on the relationship between the abundance of insectivorous forest species and the dominant tree species of the habitat, it was demonstrated that local scale variation in cork oak- and holm oak-dominance have little effect on breeding bird communities. Nevertheless, bark-gleaners moderately preferred cork oak, most likely due to its coarser and more fissured bark, which may entail a higher arthropod abundance. Moreover, via statistical modelation of the time spent by foraging birds on each tree, it was suggested that prey availability for insectivorous birds is determined by a combination of different characteristics regarding morphology, phenology and physiological condition of trees.

In order to evaluate responses of insectivorous birds to larval outbreaks of defoliators, field surveys in Chapter 3 additionally included two cork oak woodlands with outbreaks of two major defoliator pests, gypsy moth and the sawfly *Periclista andrei*. Numerical and functional responses of tree-foraging passerines were compared between areas as well as with the non-infested control, and four species evidenced positive responses to defoliator outbreaks: densities of nuthatch and chaffinch were higher in the outbreak areas of gypsy moth and *P. andrei*, respectively (numerical responses), and blue tits and crested tits spent a significantly larger amount of time foraging on trees infested with gypsy moth (functional responses). This was the first time that bird responses to different defoliators were analysed in simultaneous, and fewer responses were detected to *P. andrei* than to gypsy moth, since many bird species do not easily detect cryptic prey (Lawrence 1985). On the whole, this study highlights that birds are strongly implicated in pest control in Mediterranean oak woodlands, namely due to density-dependent mechanisms of regulation by common resident passerine species.

The specific role of three key insectivorous passerine species – blue tit, great tit and nuthatch – as predators of defoliator caterpillars (Lepidoptera larvae) was evaluated in Chapter 4. Because these species have distinct foraging strategies, it was possible to compare bird predation on the different niches of trees: leaves, twigs and outer branches (blue tit), inner branches (great tit), trunk and main branches (nuthatch). Moreover, as their breeding period is often dependent on synchronization with defoliating caterpillars (Cholewa & Wesołowski 2011), bird predation was assessed through identification of prey given to nestlings reared in nest-boxes. Even if defoliator abundance was very low in the study area, caterpillars were the most, or second-most, common prey consumed by nestlings of the three hole-nesting passerine species. Blue tits, in particular, consumed a significantly higher percentage of caterpillars than the other two passerine species, and showed a significantly higher removal rate of caterpillars at the habitat scale. However, given that significantly larger caterpillars were taken by great tit and nuthatch than by blue tit, caterpillar biomass supply to each species showed little differences at the habitat scale. Because preyed caterpillar composition did not differ among bird species for most Lepidoptera families, results suggest a complementary predation on early and late instars of caterpillars by the three species, which is supported by their distinct foraging niches on trees. They can also have an important regulatory effect preventing some species from reaching outbreak thresholds and, for example, gypsy moth represented 2.0% and 10.8% of identified caterpillars in nestling diet of great tit and nuthatch, respectively. Additionally, the before-after control-impact (BACI) experiment used to test the increase of the breeding density of hole-nesting passerines by providing nest-boxes, demonstrated that, with the design that was used, blue tit density in manipulated nest-box plots increased significantly when compared with control plots (+ 38.2%), while a considerable increase in the breeding populations of great tit and nuthatch was also recorded (+ 26.8% and + 14.3%, respectively).

THE IMPORTANCE OF BIRDS IN THE CONTROL OF DEFOLIATOR PESTS

The four studies presented in this thesis form a consistent group sustaining that common resident birds in Mediterranean oak woodlands are key predators of cork and holm oak pests, mainly defoliators. Birds demonstrated no strong foraging preference for either cork oak or holm oak, but the occurrence of defoliator and wood-boring insects on trees showed a positive relationship with the amount of time that birds spent foraging on trees during spring. By consuming such insects birds can enhance the physiological conditions of trees on which they forage (Holmes *et al.* 1979, Marquis & Whelan 1994, Murakami & Nakano 2000, Sanz 2001), and it was verified that trees where birds foraged for longer periods were in better physiological conditions.

Both in outbreak and non-outbreak circumstances, insectivory on cork and holm oak trees was essentially undertaken by small generalist passerine species, even though these coexisted with large specialist insectivorous species, such as cuckoos and woodpeckers. The tree-foraging guild of Mediterranean oak woodlands in spring is thus characterized by generalist species, namely tits, nuthatch, short-toed treecreeper and chaffinch, which are largely representative of breeding bird communities in this ecosystem (Herrera 1978a, Rabaça 1990, Almeida 1992a, Pulido & Díaz 1992, Leal *et al.* 2011a, 2013, Ceia & Ramos 2015). According with the generalist predation hypothesis (Murdoch & Oaten 1975, Southwood & Commins 1976), a predator community dominated by generalist species may be enough to retain prey populations at stable lower levels far below the carrying capacity of their environment. In fact, it was demonstrated that blue tit, great tit and nuthatch relied heavily on defoliator caterpillars to feed their nestlings in non-outbreak conditions. These three species should have an additive effect as predators of defoliator larvae in consequence of resource partitioning of caterpillar instars, as it had been previously suggested between blue tit and great tit (Török & Tóth 1999). Additionally, moderate larval outbreaks of defoliators in cork oak woodlands were associated with positive numerical and functional responses of four species of generalist passerines, which is in agreement with predictions of the syntopic population model of Southwood and Comins (1976).

Contrary to expected, the relative contribution of bark-gleaners as predators of defoliators in spring apparently showed no considerable differences to that of foliage-gleaners. This was demonstrated by the similar provisioning rate of caterpillars by nuthatch and great tit in comparison with blue tit. There is a relationship between caterpillar size segregation and the foraging tree-niches used by the three bird species. As caterpillars grow they have to move in-between twigs and branches in search of young leaves (Ferreira & Ferreira 1991) thus increasing their exposition to bark-gleaners. Furthermore, even though foliage-gleaners responded more noticeabily than bark-gleaners to outbreaks of defoliator larvae, there was a significant positive numerical response of nuthatch to the gypsy moth outbreak. Gypsy moth larvae, in particular, were identified in the prey given by great tit and nuthatch to nestlings in a non-outbreak area, suggesting that both guilds are able to act as their predators and help preventing pest species from reaching outbreak thresholds. Despite the fact that it is commonly assumed that blue tit avoids hairy caterpillars (Diaz & Blondel 1996, García-Navas *et al.* 2013), this species showed a significant positive functional response to gypsy moth outbreak and, although gypsy moth was not found among the prey given by blue tits to their nestlings in non-outbreak conditions, other hairy larvae of the Erebidae family were consumed by blue tits. These results contribute to sustain that blue tit is the foremost predator of defoliator larvae in Mediterranean oak woodlands.

MANAGEMENT IMPLICATIONS

Bird populations are usually limited by various factors, including food supply, nest and refuge sites, competitors, natural enemies (pathogens, parasites and predators) and weather (Andrewartha & Birch 1984, Begon & Mortimer 1986, Newton 1998, Begon *et al.* 2006). Understanding the limiting processes is a central issue in ecology and constitutes the basis for a practical management integrating bird populations, whether for conservation, sustained exploitation or pest control (Newton 1998).

As it was discussed in Chapter 1, a decrease in the natural biological control service provided by birds in Mediterranean oak woodlands may result from common practices, such as shrub removal, tree thinning, canopy pruning and cork extraction, hence these considerably reduce their food supplies and/or nesting sites (Rabaça 1990, Almeida 1992a, Pulido & Díaz 1992, 1997, Tellería 2001, Santos *et al.* 2002, Díaz *et al.* 2003, Camprodon & Brotons 2006, Godinho & Rabaça 2011, Leal *et al.* 2011b, 2013, Pereira *et al.* 2014a). In Portugal, tree thinning and undergrowth clearing were extensively carried out in Mediterranean oak woodlands during the first half of the 20th century for land cultivation or to increase tree crown for acorn production (Acácio & Holmgren 2014). Such practices are thought to be linked with the first severe defoliator outbreaks in Mediterranean oak woodlands (Sousa *et al.* 2007), as well as with the first significant attacks of wood-boring buprestids (*Coraebus florentinus* and *C. undatus*) which were also recorded around this period (Neves 1944). This unprecedented rise beyond outbreak thresholds likely occurred due to a reduction in the efficiency of natural enemies, including birds, in the complex density-dependent regulation dynamics (Southwood & Comins 1976, Beddington *et al.* 1978). The tree-foraging guild regularly seeks food or refuge in the understory, and undergrowth clearing in Mediterranean oak woodlands decreases both bird species richness and abundance (Rabaça 1990, Almeida 1992a, Pulido & Díaz 1992, Camprodon & Brotons 2006, Pereira *et al.* 2014a). Tree thinning reduces food supply for tree-foraging species even more noticeably and, furthermore, it reduces nesting opportunities for birds. As it was verified in Chapter 4, hole-nesting passerine populations may be limited by the availability of natural nesting cavities in Mediterranean oak woodlands. Nest-boxes were mainly occupied by tree-foraging passerines (blue tit, great tit and nuthatch) and the increase in breeding densities was especially significant for blue tits. Therefore, nest-box provision can be an effective measure to reduce defoliator numbers and their damage in Mediterranean oak woodlands, as it happened in other forest ecosystems (East & Perrins 1988, Sanz 2001, Mänd *et al.* 2009). The artificial increase of breeding densities of hole-nesting passerines may be particularly important in areas with low tree density and/or few old-aged trees where nesting site limitations should be stronger. However, hole-nesters may not be limited solely by the availability of nesting cavities but also by other factors, as it was suggested by the number of unoccupied nest-boxes per plot.

Another example worth mentioning is the risk of using insecticides. The sudden outbreak of different defoliator species (among other pests) in Portuguese Mediterranean oak woodlands in the second half of the 20th century was attributed to the first chemical treatments, in the decades of 1940 and 1950 (Sousa *et al.* 2007). These insecticides could often have greater effects on populations of beneficial insects (parasitoids and predators) than on those of their prey (Strong 1983), as well as direct lethal or sublethal effects on birds (Newton 1995, Burn 2000, Vos *et al.* 2000, Carere *et al.* 2010). Despite, nowadays, homologated products for chemical or biological control of defoliators are not directly toxic for birds their application reduces insect populations indiscriminantly and, therefore, raises negative consequences for insectivorous birds (Bright *et al.* 2008). Like in the past, the rupture of control dynamics by birds and other natural enemies can result in enhancement of defoliator populations, yet a recent concern may arise from the current context of climate warming in which it is expected the increase of pest outbreaks in European forests (Netherer & Schopf 2010).

Modern pest management in Mediterranean oak woodlands should give emphasis to indirect measures that discourage the development of pest populations before direct control measures are implemented. The effect of management interventions on both pests and their natural enemies needs to be considered in order to prevent pest outbreaks, while minimizing risks to economy and environment. In this context, "payment for ecosystem services" (PES) schemes could produce novel economic incentives towards the sustainable use of Mediterranean oak woodlands. Product-based PES schemes, such as the Forest Stewardship Council (FSC) certification, are already being applied to Mediterranean oak woodlands (Bugalho *et al.* 2011) but other markets of ecosystem services, *e.g.*, the Reducing Emissions from Deforestation and Forest Degradation and enhancement of carbon stocks (REDD+) program (Stickler *et al.* 2009), may additionally contribute to provide economic incentives for improved management practices. Natural biological control, among other ecosystem services, should be safeguarded if land management is explicitly required to maintain or enhance biodiversity and conservation attributes.

FUTURE RESEARCH

This work supports the ongoing evidence that birds play a pivotal role in ecosystem functioning, here demonstrated in the control of defoliator pests in Mediterranean oak woodlands. Even though previous research suggests that bird predation on caterpillars is the main factor affecting dynamics of defoliator populations (Crawford & Jennings 1989, Parry *et al.* 1997, Tanhuanpää *et al.* 2001), it should be noted that control by birds in Mediterranean oak woodlands is probably only achieved through year-round predation on distinct life stages of these insects. Bird communities of Mediterranean oak woodlands show an important seasonal variation (Herrera 1978a, Almeida & Granadeiro 2000), and their impact over defoliator eggs, pupae and adults should be evaluated in future studies. Additionally, more information is needed about bird predation on xylophagous and carpophagous pests, and on how other natural enemies (see Appendix A for examples), typically studied by different research groups, interplay as natural biological control agents in Mediterranean oak woodlands. This is essential for scientists to be able to predict, and eventually mitigate, the consequences of increasing environmental perturbations such as climate change (Logan *et al.* 2003, Netherer & Schopf 2010, Thomson *et al.* 2010).

Outbreaks offer researchers unique opportunities to increase the understanding of relationships between density-dependence and population regulation in

Mediterranean oak woodlands. Research on insectivorous bird species during outbreaks should assess their abundance and diet, as well as other parameters (*e.g.*, breeding traits), and compare them with non-outbreak conditions which should correspond preferently to pre- or post-outbreak conditions in the same area. The long-term investigation in areas where outbreaks are recurrent could give insight into dynamics of predator-prey interactions and help to ascertain the causes of outbreaks. Outbreaks could also ease studies on low-density insectivorous specialists, such as woodpeckers and cuckoos, since local abundance of these species may increase during prey outbreaks (Fayt *et al.* 2005, Barber *et al.* 2008, Koenig *et al.* 2011, Edworthy *et al.* 2011).

However, given the difficulty to follow rules of good experimental design in outbreak surveys (Campbell 1973, Berryman 1987, Wallner 1987), manipulative pest population experiments could be used instead to increase pest populations (Parry *et al.* 1997, Tanhuanpää *et al.* 2001, Bereczki *et al.* 2014). On the other hand, insectivorous birds could be manipulated using nest-boxes to increase breeding densities (Sanz 2001) or bird exclosures for branches or whole trees (Holmes *et al.* 1979, Marquis & Whelan 1994, Murakami & Nakano 2000, Strong *et al.* 2000) in order to quantify their impact on defoliator abundance and tree performance.

Looking forward, new techniques are providing ecologists the ability to expand their toolkit for the study of predator-prey interactions, and two deserve a mention here. First, stable isotopes analysis (SIA) has been used for diet reconstruction of various animal taxa (Caut *et al.* 2009). Because animals incorporate the isotopic composition (signature) of their food via tissue synthesis in a predictable manner (DeNiro & Epstein 1978, 1981), the measurement of stable isotopes in consumer and diet can allow an inference on dietary inputs from isotopically distinct sources. Although SIA does not allow a resolution to the species level, it can be useful in resolving predators' position within trophic levels, and to characterize the habitat and/or niche of provenance of prey (Gannes *et al.* 1997, Phillips & Gregg 2001, 2003, Newsome *et al.* 2007). Second, molecular techniques can yield insight into predator–prey interactions by facilitating prey identification in predator diets (Symondson 2002, King *et al.* 2008, Pompanon *et al.* 2012). Polymerase chain reaction (PCR)-based methods have been applied for detecting prey DNA in faeces, regurgitates, and stomach contents from diverse taxa (Valentini *et al.* 2009, Kress *et al.* 2015). Most interestingly, several studies have used this technique to determine the potential of both arthropod (*e.g.*, Fournier *et al.* 2008, King *et al.* 2011, Boreau de Roincé *et al.* 2012) and vertebrate predators (*e.g.*, Cleveland *et al.* 2006, Maas *et al.* 2013, Karp *et al.* 2014) in pest control.

FINAL REMARKS

Natural biological control is permanently active in ecosystems and it is the most successful, most cost effective and environmentally safest way of pest management. This ecosystem function is estimated to have a worldwide minimum value of 380 billion € per year (Costanza *et al.* 1997), which is an enormous amount compared to the 7.8 billion € annually spent on insecticides to control only a few species (Bale *et al.* 2008).

This thesis is a step toward a better understanding of the role of insectivorous birds as pest predators, an issue that only recently has begun to be investigated in Mediterranean oak woodlands (Godinho & Rabaça 2011, Pereira *et al.* 2014a). Traditionally, Mediterranean oak woodlands are agroforestry systems with low human intervention. Nevertheless, recent management techniques have driven this ecosystem to particularly artificial conditions which put at risk their continued existence, not only due to an alarming pest incidence, but also due to the absence of natural regeneration (Arosa *et al.* 2015). Management strategies that integrate insectivorous birds can be useful for the future of Mediterranean oak woodlands, in a way that they contribute holistically for their sustainability (Pereira *et al.* 2015). The role of science is now to provide information on the specificities of optimal management practices so that recommendations are flexible enough to adjust to changes in the environment, socio-economic components, harvesting products and market forces.

REFERENCES

Abrams PA (1982) Functional responses of optimal foragers. American Naturalist 120:382–390

Acácio V, Holmgren M (2014) Pathways for resilience in Mediterranean cork oak land use systems. Annals of Forest Science 71:5–13

Adamík P, Korňan M (2004) Foraging ecology of two bark foraging passerine birds in an old-growth temperate forest. Ornis Fennica 81:13–22

AFN (Autoridade Florestal Nacional) (2010) Relatório final do 5º inventário florestal nacional. Autoridade Florestal Nacional, Lisbon, Portugal

Airola DA, Barrett RH (1985) Foraging and habitat relationships of insect-gleaning birds in a Sierra Nevada mixed-conifer forest. Condor 87:205–216

Aitken KEH, Martin K (2004) Nest cavity availability and selection in aspen-conifer groves in a grassland landscape. Canadian Journal of Forest Research 34:2099–2109

Aitken KEH, Wiebe KL, Martin K (2002) Nest-site reuse patterns for a cavity-nesting bird community in interior British Columbia. Auk 119:391–402

Aizpúrua CG (1993) *Cydia fagiglandana* (Zeller, 1841). Lep. Tortricidae, en España. Boletín de Sanidad Vegetal, Plagas 19:389–400

Aldrey N (1981) Contribución al conocimiento de los cinípidios gallícolas (Hym., Cynipidae) en la encina y el alcornoque, en la provincia de Salamanca. Boletín de la Asociación Española de Entomología 5:59–74

Almeida V (1898) Àcerca dos montados de sobro. Agricultura Contemporânea 8:375–381

Almeida J (1992a) Alguns aspectos dos efeitos do maneio dos montados de sobro *Quercus suber* na avifauna nidificante. Airo 3:69–74

Almeida J (1992b) Censos de grous *Grus grus* invernantes em Portugal. Airo 3:55–58

Almeida JF (1996a) Análise da dieta de pintos de estorninho-preto *Sturnus unicolor* por aplicação do ‘método do colar’. Airo 7:63–68

Almeida J (1996b) Situation and conservation perspectives of the common crane in Portugal. Alytes 8:99–104

Almeida J (1997) Caracterização da avifauna nidificante num montado de azinho *Quercus rotundifolia* por aplicação do método dos mapas: dois anos de estudo. Airo 8:1–6

Almeida J, Granadeiro JP (2000) Seasonal variation of foraging niches in a guild of passerine birds in a cork-oak woodland. Ardea 88:243–252

Almeida J, Pinto M (1992) Selecção dos biótopos de alimentação pelo grou-comum *Grus grus*: o caso de Moura (Alentejo). Airo 3:1–8

Alonso JA, Alonso JC (1986) Demographic parameters of the common crane (*Grus g. grus*) population wintering in Iberia. Aquila 93–94:137–143

Ambrosini R, Bolzern AM, Canova L, Arieni S, Moller AP, Saino N (2002) The distribution and colony size of barn swallows in relation to agriculture land use. Journal of Applied Ecology 39:524–534

Anderson RM, May RM (1981) Infectious diseases and population cycles of forest insects. Science 210:658–661

Andrewartha HG, Birch LC (1984) The ecological web. University of Chicago Press, Chicago, USA

APCOR (Associação Portuguesa de Cortiça) (2007) Síntese de estatísticas do sector da cortiça. Associação Portuguesa de Cortiça, Santa Maria de Lamas, Portugal

Arenas R, Torres JA (1987) Apuntes sobre la dieta alimenticia del abejaruco (*Merops apiaster*) en la provincia de Córdoba. Oxyura 4:171–176

Arosa ML, Ceia RS, Costa SR, Freitas H (2015) Factors affecting cork oak (*Quercus suber*) regeneration: acorn sowing success and seedling survival under field conditions. Plant Ecology & Diversity 8:519–528

Atlegrim O (1989) Exclusion of birds from bilberry stands – impact on insect larval density and damage to the bilberry. Oecologia 79:136–139

Ayres MP, Lombardero MJ (2000) Assessing the consequences of global change for forest disturbance from herbivores and pathogens. The Science of the Total Environment 262:263–286

Azevedo NFS (1958) O carvão do entrecasco do sobreiro. Publicações da Direcção Geral dos Serviços Florestais e Aquícolas 25:159–179

Balda RP (1969) Foliage use by birds of the oak-juniper woodland and ponderosa pine forest in southeastern Arizona. Condor 71:399–412

Baeta-Neves CML, Cabral MTC, Nogueira CDS, Ferreira LJC (1972) Bio-ecologia da *Tortrix viridana* L. e combate da *Lymantria dispar* L. pela luta biológica. Instituto Superior de Agronomia, Lisbon, Portugal

Bai M-L, Wichmann F, Mühlenberg M (2003) The abundance of tree holes and their utilization by hole-nesting birds in a primeval boreal forest of Mongolia. Acta Ornithologica 38:95–102

Bale JS, van Lenteren JC, Bigler F (2008) Biological control and sustainable food production. Philosophical Transactions of the Royal Society B 363:761–776

Bańbura J, Blondel J, Wilde-Lambrechts H, Galan M-J, Maistre M (1994) Nestling diet variation in an insular Mediterranean population of blue tits *Parus caeruleus*: effects of years, territories and individuals. Oecologia 100:413–420

Barber NA, Marquis RJ, Tori WP (2008) Invasive prey impacts regional distribution of native predators. Ecology 89:2678–2683

Barbosa MA (1958) O carvão do entrecasco *Hypoxylon mediterraneum* (de Not.) Ces. et de Not.: Contribuição para o seu estudo. Publicações da Direcção Geral dos Serviços Florestais e Aquícolas 25:93–132

Basri E, El Antry S, Atay Kadiri Z (2005) Cartographie des infestations de *Lymantria dispar* et superficies traitées contre le ravageur entre 1990 et 2004 en subéraie de la Mamora (Maroc). IOBC/WPRS Bulletin 28:163–168

Battisti A, Bernardi M, Ghiraldo C (2000) Predation by the hoopoe on pupae of *Thaumetopoea pityocampa* and the likely influence on other natural enemies. Biocontrol 45:311–323

Bea A, Beitia R, Fernández JM (2003) The census and distribution of wintering woodpigeons *Columba palumbus* in the Iberian peninsula. Ornis Hungarica 12–13:157–167

Bea A, Fernández-García JM (2001) Censo y distribución de los efectivos de paloma torcaz *Columba palumbus* invernantes en la península Ibérica. Naturzale, Cuadernos de Ciencias Naturales 16:103–115

Beaufoy G, Cooper T (2008) Guidance document to the member states on the application of the High Nature Value impact indicator. Institute for European Environmental Policy, Brussels, Belgium

Beddington JR, Free CA, Lawton JH (1978) Characteristics of successful natural enemies in models of biological control. Nature 273:513–519

Begon M, Mortimer M (1986) Population ecology. Sinauer Associates, Inc., Sunderland, USA

Begon M, Townsend CR, Harper JL (2006) Ecology: from individuals to ecosystems. Blackwell Publishing. Oxford, UK

Beecher WJ (1978) Feeding adaptations and evolution in the starlings. Bulletin of the Chicago Academy of Sciences 11:269–298

Belo CC, Pereira MS, Moreira, AC, Coelho IS, Onofre N, Paulo AA (2009) Capítulo 8: Montado. In: Pereira HM, Domingos T, Vicente L, Proença V (eds.) Ecossistemas e bem-estar humano em Portugal – Avaliação para Portugal do Millenium Ecosystem Assessment. Escolar Editora, Lisbon, Portugal, pp.251–293

Beltrán W, Wunderle JM, Jr. (2013) Determinants of tree species preference for foraging by insectivorous birds in a novel *Prosopis–Leucaena* woodland in Puerto Rico: the role of foliage palatability. Biodiversity and Conservation 22:2071–2089

Benitez Morera A (1961) Los coleópteros bupréstidos del género *Coroebus* Lap. en los alcornocales de Cadiz. Boletín del Servicio de Plagas Forestales 7:55–61

Bereczki K, Ódor P, Csóka G, Mag Z, Báldi A (2014) Effects of forest heterogeneity on the efficiency of caterpillar control service provided by birds in temperate oak forests. Forest Ecology and Management 327:96–105

Berryman AA (1987) The theory and classification of outbreaks. In: Barbosa P, Schultz JC (eds.) Insect outbreaks. Academic Press, New York, USA, pp.3–30

Berryman AA (1995) What causes population cycles of forest lepidoptera? Trends in Ecology & Evolution 11:28–32

Bersier LF, Meyer DR (1994) Bird assemblages in mosaic forests: the relative importance of vegetation structure and floristic composition along the successional gradient. Acta Oecologica 15:561–576

Betts MM (1955) The food of titmice in oak woodland. Journal of Animal Ecology 24:282–323

Bibby CJ, Burgess ND, Hill DA (1992) Bird census techniques. Academic Press. London, UK

BirdLife International (2004) Birds in Europe: population estimates, trends and conservation status. BirdLife International, Cambridge, UK

Blondel J, Aronson J (1999) Biology and wildlife of the Mediterranean region. Oxford University Press, London, UK

Blondel J, Aronson J, Bodiou JY, Boeuf G (2010) The Mediterranean region: biological diversity in space and time (2nd edition). Oxford University Press, Oxford, UK

Blondel J, Dervieux A, Maistre M, Perret P (1991) Feeding ecology and life history variation of the blue tit in Mediterranean deciduous and sclerophyllous habitats. Oecologia 88:9–14

Blondel J, Dias PC, Perret P, Maistre M, Lambrechts MM (1999) Selection-based biodiversity at a small spatial scale in a low-dispersing insular bird. Science 285:1399–1402

Blondel J, Perret P, Anstett M-C, Thébaud C (2002) Evolution of sexual size dimorphism in birds: test of hypotheses using blue tits in contrasted Mediterranean habitats. Journal of Evolutionary Biology 15:440–450

Bock CE, Bock JH, Grant MC (1992) Effects of bird predation on grasshopper densities in an Arizona grassland. Ecology 73:1706–1717

Bonal R, Muñoz A (2007) Multi-trophic effects of ungulate intraguild predation on acorn weevils. Oecologia 152:533–540

Boreau de Roincé C, Lavigne C, Ricard J-M, Franck P, Bouvier J-C, Garcin A, Symondson WOC (2012) Predation by generalist predators on the codling moth versus a closely-related emerging pest the oriental fruit moth: a molecular analysis. Agricultural and Forest Entomology 14:260–269

Bouvier JC, Toubon JF, Boivin T, Sauphanor B (2005) Effects of apple orchard management strategies on the great tit (*Parus major*) in southeastern France. Environmental Toxicology and Chemistry 24:2846–2852

Bossema I (1979) Jays and oaks: an eco-ethological study of a symbiosis. Behaviour 70:1–117

Branco M, Branco C, Merouani H, Almeida MH (2002a) Effect of insect predation on the quality and storage conditions of acorns of cork oak (*Quercus suber* L.). IOBC/WPRS Bulletin 25:163–167

Branco M, Branco C, Merouani H, Almeida MH (2002b) Germination success, survival and seedling vigour of *Quercus suber* acorns in relation to insect damage. Forest Ecology and Management 166:159–164

Branco M, Ramos AP (2009) Chapter 9: Coping with pests and diseases. In: Aronson J, Pereira JS, Pausas JG (eds.) Cork oak woodlands on the edge: ecology, adaptative management, and restoration. Island Press, Washington, USA, pp.103–111

Brasier CM (1993) *Phytophthora cinnamomi* as a contributory factor in European oak declines. In: Luisi N, Lerario P, Vannini A (eds.) Recent advances in studies on oak decline. Tipolitografia Radio, Bari, Italy, pp.49–57

Brasier CM, Robredo F, Ferraz JFP (1993) Evidence for *Phytophthora cinnamomi* involvement in Iberian oak decline. Plant Pathology 42:140–145

Brawn JD, Balda RP (1988). Population biology of cavity nesters in northern Arizona: do nest sites limit breeding densities? Condor 90:61–71

Bright JA, Morris AJ, Winspear R (2008) A review of indirect effects of pesticides on birds and mitigating land-management practices. Royal Society for the Protection of Birds, The Lodge, UK

Brightsmith DJ (2005) Competition, predation and nest niche shifts among tropical cavity nesters: ecological evidence. Journal of Avian Biology 36:74–83

Buckner CH, Turnock WJ (1965) Avian predation on the larch sawfly, *Pristiphora erichsonii* (Htg.), (Hymenoptera: Tenthredinidae). Ecology 46:223–236

Bugalho MN, Caldeira MC, Pereira JS, Aronson J, Pausas JG (2011) Mediterranean cork oak savannas require human use to sustain biodiversity and ecosystem services. Frontiers in Ecology and the Environment 9:278–286

Burn AJ (2000) Pesticides and their effects on lowland farmland birds. In: Aebischer HJ, Evans AD, Grice PV, Vickery JA (eds.) Ecology and conservation of lowland farmland birds. British Ornithologist's Union, Tring, UK, pp.89–104

Cabello AM, Soler M, Soler JJ (1991a) Alimentación de la tarabilla común (*Saxicola torquata*) en el sureste de la Península Ibérica durante el período Otoño-Invierno. Ardeola 38:317–326

Cabello AM, Soler M, Soler JJ (1991b) Alimentación del acentor común (*Prunella modularis*) durante su invernada en el sureste de la Península Ibérica. Ardeola 38:305–315

Cabral MT, Santos MNS (1992) Situação sanitária do montado de sobro em Portugal. In: Instituto de Promoción del Corcho (IPROCOR) (ed.) Simpósio mediterráneo sobre regeneración del monte alcornocal. Instituto de Promoción del Corcho (IPROCOR) and Junta de Extremadura, Mérida, Spain, pp.196–199

Câmara-Pestana J (1898) Nova doença dos sobreiros. Archivo Rural 36:297–298

Campbell RW (1973) Numerical behaviour of a gypsy moth population system. Forest Science 19:162–167

Campbell RW, Sloan RJ (1976) Influence of behavioural evolution on gypsy moth pupal survival in sparse populations. Environmental Entomology 5:1211–1217

Campbell RW, Sloan RJ (1977a) Natural regulation of innocuous gypsy moth populations. Environmental Entomology 6:315–322

Campbell RW, Sloan RJ (1977b) Forest stand responses to defoliation by the gypsy moth. Forest Science, Monograph 19

Campbell RW, Torgersen TR (1983) Compensatory mortality in defoliator population dynamics. Environmental Entomology 12:630–632

Campbell RW, Torgersen TR, Srivastava N (1983) A suggested role for predaceous birds and ants in the population dynamics of the western spruce budworm. Forest Science 29:779–790

Campos P (1984) Economía y energía en la dehesa extremeña. Instituto de Estudios Agrários, Pesqueros y Alimentarios. Madrid, Spain

Campos P, Martín M (eds.) (1987) Conservación y desarrollo de las dehesas portuguesa y española. Ministerio de Agricultura, Madrid, Spain

Campos P (1992) Spain. In: Wibe S, Jones T (eds.) Forests, market and intervention failures. Five case studies. Earthscan, London, UK, pp.165–200

Campos P (1993) Valores comerciales y ambientales de las dehesas españolas. Agricultura y Sociedad 66:9–41

Camprodon J, Brotons L (2006) Effects of undergrowth clearing on the bird communities of the northwestern Mediterranean coppice holm oak forests. Forest Ecology and Management 221:72–82

Camprodon J, Salvany PJ, Soler-Zurita J (2008) The abundance and suitability of tree cavities and their impact on hole-nesting bird populations in beech forests of NE Iberian Peninsula. Acta Ornithologica 43:17–31

Canário F, Boieiro M, Vicente L (2002) The nestling diet of the Iberian azure-winged magpie *Cyanopica cyanus cooki* in southeastern Portugal. Ardeola 49:283–286

Carere C, Constantini D, Sorace A, Santucci D, Alleva E (2010) Bird populations as sentinels of endocrine disrupting chemicals. Annali dell'Istituto Superiore di Sanità 46:81–88

Carlson A, Sandström U, Olsson K (1998) Availability and use of natural tree holes by cavity nesting birds in a Swedish deciduous forest. Ardea 86:109–112

Carrascal LM, Tellería JL (1989) Comportamiento de búsqueda del alimento y selección de especies arbóreas: análisis con el agateador común (*Certhia brachydactyla*) durante el invierno. Ardeola 36:149–160

Carrete M, Donázar JA (2005) Application of central-place foraging theory shows the importance of Mediterranean *dehesas* for the conservation of the cinereous vulture, *Aegypius monachus*. Biological Conservation 126:582–590

Carrión JS, Parra I, Navarro C, Munera M (2000) Past distribution and ecology of the cork oak (*Quercus suber*) in the Iberian Peninsula: a pollen-analytical approach. Diversity and Distributions 6:29–44

Carvalho Mendes AMS, Graça JAR (2009) Chapter 5: Cork bottle stoppers and other cork products. In: Aronson J, Pereira JS, Pausas JG (eds.) Cork oak woodlands on the edge: ecology, adaptative management, and restoration. Island Press, Washington, USA, pp.59–69

Catarino L, Godinho C, Pereira P, Luís A, Rabaça JE (2014) Can birds play a role as High Nature Value indicators of *montado* system? Agroforestry Systems DOI:10.1007/s10457-014-9761-y

Catry FX, Moreira F, Pausas JG, Fernandes PM, Rego F, Cardillo E, Curt T (2012) Cork oak vulnerability to fire: the role of bark harvesting, tree characteristics and abiotic factors. Plos ONE 7:e39810

Caut S, Angulo E, Courchamp F (2009) Variation in discrimination factors (Δ^{15}N and Δ^{13}C): the effect of diet isotopic values and applications for diet reconstruction. Journal of Applied Ecology 46:443–453

Ceballos P (1969) Estudio de alimentación del trepador azul (*Sitta europaea*) en encinares durante los meses de marzo-agosto. Boletín del Servicio de Plagas Forestales 24:89–95

Ceia RS, Ramos JA (2014) Birds as predators of cork and holm oak pests. Agroforestry Systems DOI:10.1007/s10457-014-9749-7

Ceia RS, Ramos JA (2015) Effects of dominant tree species on insectivorous birds breeding in Mediterranean oak woodlands. Bird Study DOI:10.1080/00063657.2015.1136264

Cerboneschi A (2012a) First field tests with an American strain of the nucleopolyhedrosis virus for the control of *Lymantria dispar* L. in Sardinia. IOBC/WPRS Bulletin 76:143–146

Cerboneschi A (2012b) Susceptibility of third instar larvae of *Lymantria dispar* L. to an American isolate of the nuclear polyhedrosis virus. IOBC/WPRS Bulletin 76:147–150

Cherkaoui I, Selmi S, Boukhriss J, Hamid RI, Mohammed D (2009) Factors affecting bird richness in a fragmented cork oak forest in Morocco. Acta Oecologica 35:197–205

Cholewa M, Wesołowski T (2011) Nestling food of European hole-nesting passerines: do we know enough to test the adaptive hypotheses on breeding seasons? Acta Ornithologica 46:105–116

Christensen JH, Hewitson B, Busuioc A, Chen A, Gao X, Held I, Jones R, Kolli RK, Kwon W-T, Laprise R, Magaña Rueda V, Mearns L, Menéndez CG, Räisänen J, Rinke A, Sarr A, Whetton P (2007)

Regional climate projections. In: Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL (eds.) Climate Change 2007: The physical science basis. Contribution of working group I to the fourth assessment report of the Intergovernmental Panel on Climate Change, Cambridge University Press. Cambridge, UK, and New York, USA, pp.847–943

Chu HF (1949) How to know the immature insects. MC Brown Company Publishers, Dubuque, Iowa, USA

Clark KL, Skowronski N, Hom J (2010) Invasive insects impact forest carbon dynamics. Global Change Biology 16:88–101

Cleveland CJ, Betke M, Federico P, Frank JD, Hallam TG, Horn J, Lopez JD, McCracken GF, Medellín RA, Moreno-Valdez A, Sansone CG, Westbrook JK, Kunz TH (2006) Economic value of the pest control service provided by Brazilian free-tailed bats in south-central Texas. Frontiers in Ecology and the Environment 4:238–243

Cobos JM, Montoya R, Tuset JJ (1993) New damages to the *Quercus* woodlands in Spain. Preliminary evaluation of the possible implication of *Phytophthora cinnamomi*. In: Luisi N, Lerario P, Vannini A (eds.) Recent advances in studies on oak decline. Tipolitografia Radio, Bari, Italy, pp.163–169

Cocco A, Cossu AQ, Erre P, Nieddu G, Luciano P (2010) Spatial analysis of gypsy moth populations in Sardinia using geostatistical and climate models. Agricultural and Forest Entomology 12:417–426

Cody ML (ed.) (1985) Habitat selection in birds. Academic Press, New York, USA

Coelho IS (2007) A silvopastorícia, uma perspectiva histórica. In: Silva JS (ed.) Os montados – Árvores e florestas de portugal Vol. 3. Fundação Luso-Americana para o Desenvolvimento, Público, Liga para a Protecção da Natureza, Lisbon, Portugal, pp.177–209

Contarini M, Luciano P, Pilarska D (2014) Preliminary investigations to possible introduction of *Entomophaga maimaiga* in Sardinia. IOBC/WPRS Bulletin 101:227–233

Cooper RJ, Dodge KM, Martinat PJ, Donahoe SB, Whitmore RC (1990) Effect of diflubenzuron application on eastern deciduous forest birds. Journal of Wildlife Management 54:486–493

Cooper RJ, Smith HR (1995) Predation on gypsy moth (Lepidoptera: Lymantriidae) egg masses by birds. Environmental Entomology 24:571–575

Costa A, Pereira H, Madeira M (2009) Landscape dynamics in endangered cork oak woodlands in Southwestern Portugal (1958–2005). Agroforestry Systems 77:83–96

Costa LT (1991) Apiculture and the diet of breeding European Bee-eater *Merops apiaster*. Airo 2:34–42

Costa M, Morla C, Sainz H (eds.) (1998) Los bosques ibéricos, una interpretacción geobotánica. Editorial Planeta, Barcelona, Spain

Costanza R, d'Arge R, de Groot R, Farber S, Grasso M, Hannon B, Limburg K, Naeem S, O'Neil RV, Paruelo J, Raskin RG, Sutton P, van den Belt M (1997) The value of the world's ecosystem services and natural capital. Nature 387:253–260

Cowie RJ (1977) Optimal foraging in great tits (*Parus major*). Nature 268:137–139

Cramp S, Perrins CM (eds.) (1998) The complete birds of the Western Paleartic. BWP on CD-ROM. Oxford University Press, Oxford, UK

Crawford HS, Jennings DT (1989) Predation by birds on spruce budworm *Choristoneura fumiferana*: functional, numerical, and total responses. Ecology 70:152–163

Crawley MJ (1989) Insect herbivores and plant population dynamics. Annual Review of Entomology 34:531–564

Cruz CM (1998) Contribuição para o estudo da dieta de grou *Grus grus* em áreas ocidentais de invernia na Península Ibérica. Airo 9:16–18

Cuadrado M, Dominguez F (1996) Phenology and breeding success of red-necked nightjar *Caprimulgus ruficollis* in southern Spain. Journal of Ornithology 137:249–253

da Silva PM, Aguiar CAS, Niemelä J, Sousa JP, Serrano ARM (2008) Diversity patterns of ground-beetles (Coleoptera: Carabidae) along a gradient of land-use disturbance. Agriculture, Ecosystems and Environment 124:270–274

Debussche M, Isenmann P (1985) Frugivory of transient and wintering European robins *Erithacus rubecula* in a Mediterranean region and its relationship with ornithochory. Ecography 8:157–163

DeNiro MJ, Epstein S (1978) Influence of diet on the distribution of carbon isotopes in animals. Geochimica et Cosmochimica Acta 42:495–506

DeNiro MJ, Epstein S (1981) Influence of diet on the distribution of nitrogen isotopes in animals. Geochimica et Cosmochimica Acta 45:341–351

di Castri F (1981) Mediterranean-type shrublands of the world. In: di Castri F, Goodall DW, Specht RL (eds.) Mediterranean-type shrublands. Ecosystems of the World, Vol. 11. Elsevier, Amsterdam, The Netherlands, pp.1–52

Dias PC, J Blondel (1996) Breeding time, food supply and fitness components of blue tits *Parus caeruleus* in Mediterranean habitats. Ibis 138:644–649

Díaz L (2006) Influences of forest type and forest structure on bird communities in oak and pine woodlands in Spain. Forest Ecology and Management 223:54–65

Díaz M, Campos P, Pulido FJ (1997) The Spanish *dehesas*: a diversity of land use and wildlife. In: Pain D, Pienkowski M (eds.) Farming and birds in Europe. Academic Press, London, UK, pp.178–209

Díaz M, González E, Muñoz-Pulido R, Naveso MA (1996) Habitat selection patterns of common cranes *Grus grus* wintering in holm oak *Quercus ilex dehesas* of central Spain: effects of human management. Biological Conservation 75:119–123

Díaz M, Illera JC, Atienza JC (1998) Food resource matching by foraging tits *Parus* spp. during spring-summer in a Mediterranean mixed forest; evidence for an ideal free distribution. Ibis 140:654–660

Díaz M, Martín P (1998) Habitat selectivity by wintering woodpigeons (*Columba palumbus*) in Holm-Oak (*Quercus ilex*) *dehesa* of Central Spain. Gibier et Faune Sauvage 15:167–181

Díaz M, Pulido F (1993) Relaciones entre la abundancia de artrópodos y la densidad del herrerillo común (*Parus caeruleus*) en dehesas durante el período reproductor. Ardeola 40:33–38

Díaz M, Pulido FJ (1995) Relaciones entre abundancia de artrópodos y características vegetativas de la encina *Quercus ilex* L.: utilidad de su modelización empírica en la gestión forestal de las dehesas. Boletín de Sanidad Vegetal, Plagas 21:253–260

Díaz M, Pulido FJ, Marañón T (2003) Diversidad biológica y sostenibilidad ecológica y económica de los sistemas adehesados. Ecosistemas 2003/3

Dixon MD, Johnson WC, Adkisson CS (1997) Effects of weevil larvae on acorn use by blue jays. Oecologia 111:201–208

Doane CC (1976) Ecology of pathogens of the gypsy moth. In: Anderson JF, Kaya HK (eds.) Perspectives in forest entomology. Academic Press, New York, USA, pp.285–293

Drew RAI (1987) Reduction in fruit fly (Tephritidae: Dacinae) populations in their endemic rainforest habitat by frugivorous vetebrates. Australian Journal of Zoology 35:283–288

East ML, Perrins CM (1988) The effect of nestboxes on breeding populations of birds in broadleaved temperate woodlands. Ibis 130:393–401

Edworthy AB, Drever MC, Martin K (2011) Woodpeckers increase in abundance but maintain fecundity in response to an outbreak of mountain pine bark beetles. Forest Ecology and Management 261:203–210

Elkinton JS, Liebhold AM (1990) Population dynamics of gypsy moth in North America. Annual Review of Entomology 35:571–596

Enemar A, Sjostrand B (1972) Effects of the introduction of pied flycatchers, *Ficedula hypoleuca*, on the composition of a passerine bird community. Ornis Scandinavica 3:79–89

Enemar A, Nilsson L, Sjöstrand B (1984) The composition and dynamics of the passerine bird community in a subalpine birch forest, Swedish Lapland, a 20-year study. Annales Zoologici Fennici 21:321–338

Equipa Atlas (2008) Atlas das aves nidificantes em portugal (1999–2005). ICNB, SPEA, PNM, SRAM. Assírio & Alvim, Lisbon, Portugal

Escartín Porta E, Basarán Conde E, Pedrocchi Renault C (1996) Datos relativos a la alimentación del estornino negro (*Sturnus unicolor*) en la provincia de Huesca. Lucas Mallada 8:29–39

Fayt P, Machmer MM, Steeger C (2005) Regulation of spruce bark beetles by woodpeckers: a literature review. Forest Ecology and Management 206:1–14

Fernández-Cruz M, Alonso J, Garcia-Rúa A, Pereira P, Pérez-Chiscano JL, Veiga JP (1981) La migración e invernada de la grulla común *(Grus grus)* en España. Resultados del Proyecto Grus (Crane Project). Ardeola 26–27:1–164

Ferreira MC, Ferreira GWS (1989) *Platypus cylindrus* F. (Coleoptera: Platipodidae) plaga de *Quercus suber*. Boletín de Sanidad Vegetal, Plagas 4:301–306

Ferreira MC, Ferreira GWS (1991) Pragas das folhosas. Ministério da Agricultura, Pescas e Alimentação, Lisbon, Portugal

Figo MI (1972) *Lymantria díspar* L. Ensaios e meios de luta. Direcção Geral dos Serviços Florestais e Agrícolas, Lisbon, Portugal

Finlayson C, Finlayson G, Mosquera M, Fa D (2002) The breeding bird community in the cork oak woodlands of Cádiz and its significance in the context of the south and west of the Iberian Peninsula. Almoraima 27:27–31

Fonseca A (2004) O montado no Alentejo (Século XV a XVIII). Editora Colibri, Lisbon, Portugal

Fournier J, Arlettaz R (2001) Food provision to nestlings in the hoopoe *Upupa epops*: implications for the conservation of a small endangered population in the Swiss Alps. Ibis 143:2–10

Fournier V, Hagler J, Daane K, de León J, Groves R (2008) Identifying the predator complex of *Homalodisca vitripennis* (Hemiptera: Cicadellidae): a comparative study of the efficacy of an ELISA and PCR gut content assay. Oecologia 157:629–640

Fowler AC, Knight RL, George TL, McEwen LC (1991) Effects of avian predation on grasshopper populations in North Dakota grasslands. Ecology 72:1775–1781

Franzreb KE (1978) Tree species used by birds in logged and unlogged mixed coniferous forest. Wilson Bulletin 90:221–238

Fretwell SD, Lucas HL (1970) On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. Acta Biotheoretica 14:16–36

Furuta K (1982) Natural control of *Lymantria dispar* L. population at low density levels in Hokkaido (Japan). Journal of Applied Entomology 93:513–522

Gabbe AP, Robinson SK, Brawn JD (2002) Tree-species preferences of foraging insectivorous birds: implications for floodplain forest restoration. Conservation Biolo*gy* 16:462–470

Gage SH, Miller CA, Mook LJ (1970) The feeding response of some forest birds to the black-headed budworm. Canadian Journal of Zoology 48:359–366

Gale GA, DeCecco JA, Marshall MR, McClain WR, Cooper RJ (2001) Effects of gypsy moth defoliation on forest birds: an assessment using breeding bird census data. Journal of Field Ornithology 72:291–304

Gallego FJ, de Algaba AP, Fernandez-Escobar R (1999) Etiology of oak decline in Spain. European Journal of Forest Pathology 29:17–27

Gandhi KJK, Herms DA (2010) Direct and indirect effects of alien insect herbivores on ecological processes and interactions in forests of eastern North America. Biological Invasions 12:389–405

Gannes LZ, O'Brien DM, Martínez del Rio C (1997) Stable isotopes in animal ecology: assumptions, caveats and a call for more laboratory experiments. Ecology 78:1271–1276

García-Navas V, Ferrer ES, Sanz JJ (2012) Prey selectivity and parental feeding rates of blue tits *Cyanistes caeruleus* in relation to nestling age. Bird Study 59:236–242

García-Navas V, Ferrer ES, Sanz JJ (2013) Prey choice, provisioning behaviour, and effects of early nutrition on nestling phenotype of titmice. Écoscience 20:9–18

García-Navas V, Sanz JJ (2010) Flexibility in the foraging behaviour of blue tits in response to short-term manipulations of brood size. Ethology 116:744–754

García-Navas V, Sanz JJ (2011a) The importance of a main dish: nestling diet and foraging behaviour in Mediterranean blue tits in relation to prey phenology. Oecologia 165:639–649

García-Navas V, Sanz JJ (2011b) Seasonal decline in provisioning effort and nestling mass of blue tits *Cyanistes caeruleus*: experimental support for the parent quality hypothesis. Ibis 153:59–69

Garton EO (1979) Implications of optimal foraging theory for insectivorous forest birds. In: Dickson JG, Connor RN, Fleet RR, Jackson JA, Kroll JC (eds.) The role of insectivorous birds in forest ecosystems. Academic Press, Inc., New York, USA, pp.107–118

Gibbons P, Lindenmayer D (2002) Tree hollows and wildlife conservation in Australia. CSIRO Publishing, Collingwood, VIC, Australia

Godinho C, Rabaça JE (2011) Birds like it corky: the influence of habitat features and management of *montados* in breeding bird communities. Agroforestry Systems 82:183–195

Godinho S, Santos AP, Sá-Sousa P (2011) Montado management effects on the abundance and conservation of reptiles in Alentejo, Southern Portugal. Agroforestry Systems 82:197–207

Gómez F (1997) Los bosques Ibéricos: una interpretación geobotánica. Planeta, Barcelona, Spain

Gómez JM (2003) Spatial patterns in long-distance dispersal of *Quercus ilex* acorns by jays in a heterogeneous landscape. Ecography 26:573–584

Gómez Guttiérez JM, Pérez Fernández M (1996) The *dehesas*, silvopastoral systems in semiarid Mediterranean regions with poor soils, seasonal climate and extensive utilisation. In: Etienne M (ed.) Western European silvopastoral systems. INRA Editions, Paris, France, pp.55–70

González-Cano JM (1981) Predación de ‘procesionaria del pino’ por vertebrados en la zona de Mora de Rubielos (Teruel). Boletín de la Estación Central de Ecología 10:53–77

Google Inc. (2013) Google Earth (version 7.1.2.2041). Available from: http://www.google.com/earth/ (accessed 10 July 2013)

Grafen A, Hails R (2002) Modern statistics for the life sciences. Oxford University Press, Oxford, UK

Greenberg R, Bichier P, Sterling J (1997) Acacia, cattle, and migratory birds in southeastern Mexico. Biological Conservation 80:235–247

Greenberg R, Bichier P (2005) Determinants of tree species preference of birds in oak-acacia woodlands of Central America. Journal of Tropical Ecology 21:57–66

Guitián J (1985) Datos sobre el regimen alimenticio de los paseriformes de un bosque montano de la cordillera cantábrica occidental. Ardeola 32:155–172

Gullan PJ, Cranston PA (2010) Chapter 11: Insects and plants. In: Gullan PJ, Cranston PA. Insects – an outline of entomology (4th edition). Wiley-Blackwell Publishing, Chichester, West Sussex, UK, pp.279–306

Halperin J (1990) Natural enemies of *Thaumetopoea* spp. (Lep., Thaumetopoeidae) in Israel. Journal of Applied Entomology 109:425–435

Haney JC (1999) Numerical responses of birds to an irruption of elm spanworm (*Ennomos subsignarius* [Hbn.]; Geometridae: Lepidoptera) in old-growth forest of Appalachian Plateau, USA. Forest Ecology and Management 120:203–217

Hassell MP (1978) The dynamics of arthropod predator-prey systems. Princeton University Press, Princeton, New Jersey, USA

Hassell MP, May RM (1986) Generalist and specialist natural enemies in insect predator-prey interactions. Journal of Animal Ecology 55:923–940

Heinrich B (1979) Foraging strategies of caterpillars: leaf damage and possible predator avoidance strategies. Oecologia 42:325–337

Heinrich B (1993) How avian predators constrain caterpillar foraging. In: Stamp NE, Casey TM (eds.) Caterpillars. Ecological and evolutionary constrains on foraging. Chapman & Hall, New York, USA, pp.224–247

Heitor AC, Pereira S (2004) Manual das principais pragas florestais. Confederação Nacional das Cooperativas Agrícolas e do Crédito Agrícola de Portugal, CCRL (CONFAGRI), Lisbon, Portugal

Henriques J, Inácio ML, Lima A, Sousa E (2012) New outbreaks of charcoal canker on young cork oak trees in Portugal. IOBC/WPRS Bulletin 76:85–88

Henriques J, Inácio ML, Sousa E (2009) Fungi associated to *Platypus cylindrus* Fab. (Coleoptera: Platypodidae) in Cork Oak. Revista de Ciências Agrárias 32:56–66

Herrera CM (1977) Ecología alimenticia del petirrojo (*Erithacus rubecula*) durante su invernada en encinares del Sur de España. Doñana, Acta Vertebrata 4:35–59

Herrera CM (1978a) Ecological correlates of residence and non–residence in a Mediterranean passerine bird community. Journal of Animal Ecology 47:871–890

Herrera CM (1978b) Datos sobre la dieta invernal del colirrojo tizón (*Phoenicurus ochruros*) en encinares de Andalucía occidental. Doñana, Acta Vertebrata 5:61–71

Herrera CM (1978c) Niche-shift in the genus *Parus* in Southern Spain. Ibis 120:236–240

Herrera CM (1979) Ecological aspects of heterospecific flocks formation in a Mediterranean passerine bird community. Oikos 33:85–96

Herrera CM (1980). Composición y estructura de dos comunidades mediterráneas de passeriformes. Doñana, Acta Vertebrata 7:1–340

Herrera CM (1981) Fruit food of robins wintering in southern Spanish Mediterranean shrubland. Bird Study 28:115–122

Herrera CM (1983) Coevolución de plantas y frugívoros: la invernada mediterránea de algunos passeriformes. Alytes 1:177–190

Herrera CM (1984a) Significance of ants in the diet of insectivorous birds in southern Spanish Mediterranean habitats. Ardeola 30:77–81

Herrera CM (1984b) A study of avian frugivores, bird-dispersed plants and their interaction in Mediterranean shrubland. Ecological Monographs 54:1–23

Herrera CM (1989) Vertebrate frugivores and their interaction with invertebrate fruit predators: supporting evidence from a Costa Rican dry forest. Oikos 54:23–32

Herrera CM (1998) Long–term dynamics of Mediterranean frugivorous birds and fleshy fruits: a 12–year study. Ecological Monographs 68:511–538

Herrera CM, Ramirez A (1974) Food of bee-eaters in southern Spain. British Birds 67:158–164

Higashiura Y (1989) Survival of eggs in the gypsy moth *Lymantria dispar*. I. Predation by birds. Journal of Animal Ecology 58:403–412

Highland Statistics Ltd. (2009) Brodgar: Software package for data exploration, univariate analysis, multivariate analysis and time series analysis. Highland Statistics, Newburgh, New York, USA

Hildén O (1965) Habitat selection in birds: A review. Annales Zoologici Fennici 2:53–75

Hino T, Unno A, Nakano S (2002) Prey distribution and foraging preference for tits. Ornithological Science 1:82–87

Hogstad O (2005) Numerical and functional responses of breeding passerine species to mass occurrence of geometrid caterpillars in a subalpine birch forest: a 30-year study. Ibis 147:77–91

Holling CS (1961) Principles of insect predation. Annual Review of Entomology 6:163–182

Holmes RT (1990) Ecological and evolutionary impacts of bird predation on forest insects: an overview. Studies in Avian Biology 13:6–13

Holmes RT, Robinson RK (1981) Tree species preferences of foraging insectivorous birds in northern hardwoods forest. Oecologia 48:31–35

Holmes RT, Schultz JC, Nothnagle P (1979) Bird predation on forest insects: an exclosure experiment. Science 206:462–463

Holmes RT, Sherry TW, Sturges FW (1986) Bird community dynamics in a temperate deciduous forest: long-term trends at Hubbard Brook. Ecological Monographs 13:299–320

Hooks CRR, Pandey RR, Johnson MW (2003) Impact of avian and arthropod predation on lepidopteran caterpillar densities and plant productivity in an ephemeral agroecosystem. Ecological Entomology 28:522–532

Houston AI, Krebs JR, Erichsen JT (1980) Optimal prey choice and discrimination time in the great tit (*Parus major* L.). Behavioral Ecology and Sociobiology 6:169–175

Hoyas J, López F (1998) Distribución del críalo según la abundancia de procesionaria del pino. Quercus 149:20–22

Hughes RN (1979) Optimal diets under the energy maximization premise: the effects of recognition time and learning. American Naturalist 113:209–221

Hunter AF (1995) Ecology, life history, and phylogeny of outbreak and nonoutbreak species. In: Cappuccino N, Price PW (eds.) Population dynamics. new approaches and synthesis. Academic Press, New York, USA, pp.41–64

ICNF (Instituto da Conservação da Natureza e das Florestas) (2013) IFN6 – Áreas dos usos do solo e das espécies florestais de Portugal continental. Resultados preliminares. Instituto da Conservação da Natureza e das Florestas, Lisbon, Portugal

ICP Forests (International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests) (2013) The condition of forests in Europe. Executive report. Institute for World Forestry, Hamburg, Germany. Available from: http://icp-forests.net (accessed 10 December 2014)

Inácio ML, Henriques J, Sousa E (2011) Contribution of symbiotic fungi to Cork Oak colonization by *Platypus cylindrus* (Coleoptera: Platypodidae). Silva Lusitanica 19:89–99

Inácio ML, Naves P, Moreira M, Sousa EM (2002) Gall inducing insects associated with oak trees (*Quercus* spp.) in Portugal. IOBC/WPRS Bulletin 25:159–162

INMG (Instituto Nacional de Meteorologia e Geofísica) (1991) O clima de Portugal. Normais climatológicas da região de Alentejo e Algarve, correspondentes a 1951–1980, Fascículo XLIX, Vol. 4 – 4ª região. Instituto Nacional de Meteorologia e Geofísica, Lisbon, Portugal

Ivlev VS (1961) Experimental ecology on the feeding of fishes. Yale University Press, New Haven, USA

Jackson JA (1979) Tree surfaces as foraging substrates for insectivorous birds. In: Dickson JG, Conner RN, Fleet RR, Kroll JC, Jackson JA (eds.) The role of insectivorous birds in forest ecosystems. Academic Press, New York, USA, pp.69–93

James FC (1971) Ordinations of habitat relationships among breeding birds. Wilson Bulletin 83:215–236

Jayapal R, Qureshi Q, Chellam R (2009) Importance of forest structure *versus* floristics to composition of avian assemblages in tropical deciduous forests of Central Highlands, India. Forest Ecology and Management 257:2287–2295

Ji R, Simpson SJ, Yua F, He QX, Yun CJ (2008) Diets of migratory rosy starlings (Passeriformes: Sturnidae) and their effects on grasshoppers: implications for a biological agent for insect pests. Biological Control 46:547–551

Jiménez A, Maistrello L, Lopez MA, Ocete ME, Soria FJ (2011) Spatial distribution of *Cydia fagiglandana* (Zeller) in an exploited holm oak (*Quercus ilex* L.) forest. Spanish Journal of Agricultural Research 9:570–579

Jiménez A, Soria FJ, Villagrán M, Ocete ME (2006) Seguimiento del ciclo biológico de *Cydia fagigalndana* (Zeller) (Lepidoptera: Tortricidae) en un encinar del sur de España. Boletín de Sanidad Vegetal, Plagas 32:159–168

Joern A (1986) Experimental study of avian predation on coexisting grasshopper populations (Orthoptera: Acrididae) in a sandhills grassland. Oikos 46:243–249

Joffre R, Rambal S, Ratte JP (1999) The *dehesa* system of southern Spain and Portugal as a natural ecosystem mimic. Agroforestry Systems 45:57–79

Joffre R, Vacher J, De Los Llanos C, Long G (1988) The *dehesa*: an agrosilvopastoral system of the Mediterranean region with special reference to the Sierra Morena area of Spain. Agroforestry Systems 6:71–96

Johnson KH, Vogt K, Clark H, Schmitz OJ, Vogt D (1996) Biodiversity and the stability of ecosystems. Trends in Ecology and Evolution 11:372–377

Johnson MD, Kellermann JL, Stercho AM (2010) Pest reduction services by birds in shade and sun coffee in Jamaica. Animal Conservation 13:140–147

Jones J (2001) Habitat selection studies in avian ecology: a critical review. Auk 118:557–562

Jordano P (1981) Alimentación y relaciones tróficas entre los Passeriformes en paso otoñal por una localidad de Andalucía central. Doñana, Acta Vertebrata 8:103–124

Jordano P (1987a) Notas sobre la dieta no-insectívora de algunos Muscicapidae. Ardeola 34:89–98

Jordano P (1987b) Frugivory, external morphology and digestive system in mediterranean sylviid warblers *Sylvia* spp. Ibis 129:175–189

Jordano P (1989) Variación de la dieta frugívora otoño-invernal del petirrojo (*Erithacus rubecula*): Efectos sobre la condición corporal. Ardeola 36:161–183

Jordano P, Herrera CM (1981) The frugivorous diet of blackcap populations (*Sylvia attricapilla*) wintering in southern Spain. Ibis 123:502–507

Karp DS, Judson S, Daily GC, Hadly EA (2014) Molecular diagnosis of bird-mediated pest consumption in tropical farmland. SpringerPlus 3:630

Keller LF, van Noordwijk AJ (1994) Effects of local environmental conditions on nestling growth in the great tit (*Parus major* L.). Ardea 82:349–362

Kenis M, Auger-Rozenberg M-A, Roques A, Timms L, Péré C, Cock MJW, Settele J, Augustin S, Lopez-Vaamonde C (2009) Ecological effects of invasive alien insects. Biological Invasions 11:21–45

King RA, Read DS, Traugott M, Symondson WOC (2008) Molecular analysis of predation: a review of best practice for DNA-based approaches. Molecular Ecology 17:947–963

King RA, Moreno-Ripoll R, Agustí N, Shayler SP, Bell JR, Bohan DA, Symondson WOC (2011) Multiplex reactions for the molecular detection of predation on pest and nonpest invertebrates in agroecosystems. Molecular Ecology Resources 11:370–373

Koenig WD, Walters EL, Liebhold AM (2011) Effects of gypsy moth outbreaks on North American woodpeckers. Condor 113:352–361

Koh LP (2008) Birds defend oil palms from herbivorous insects. Ecological Applications 18:821–825

Kress WJ, García-Robledo C, Uriarte M, Erickson DL (2015) DNA barcodes for ecology, evolution, and conservation. Trends in Ecology and Evolution 30:25–35

Krištín A (1994) Food variability of nuthatch nestlings (*Sitta europaea)* in mixed beech forests: where are limits of its polyphagy? Biologia 39:773–779

Kroll JC, Fleet RR (1979) Impact of woodpecker predation on over-wintering within-tree populations of the southern pine beetle (*Dendroctonus frontalis*). In: Dickson JG (ed.) The role of insectivorous birds in forest ecosystems. Academic Press, New York, USA, pp.269–281

Kulman HM (1971) Effects of insect defoliation on growth and mortality of trees. Annual Review of Entomology 16:289–324

Lawrence ES (1985) Sit-and-wait predators and cryptic prey: a field study with wild birds. Journal of Animal Ecology 54:965–976

Leal AI, Correia RA, Granadeiro JP, Palmeirim JM (2011b) Impact of cork extraction on birds: Relevance for conservation of Mediterranean biodiversity. Biological Conservation 144:1655–1662

Leal AI, Correia RA, Palmeirim JM, Granadeiro JP (2013) Does canopy pruning affect foliage-gleaning birds in managed cork oak woodlands? Agroforestry Systems 87:355–363

Leal AI, Martins RC, Palmeirim JM, Granadeiro JP (2011a) Influence of habitat fragments on bird assemblages in cork oak woodlands. Bird Study 58:309–320

Lee PY, Rotenberry JT (2005) Relationships between bird species and tree species assemblages in forested habitats of eastern North America. Journal of Biogeography 32:1139–1150

Leiva MJ, Fernández-Alés R (2005) Holm-oak (*Quercus ilex* subsp. *ballota*) acorns infestation by insects in Mediterranean *dehesas* and shrublands - Its effect on acorn germination and seedling emergence. Forest Ecology and Management 212:221–229

Lima SL, Zollner PA (1996) Towards a behavioural ecology of ecological landscapes. Trends in Ecology and Evolution 11:131–135

Link JA (1889) Monatsschr. Dtsch. Ver. Schutze Vogelwelt 14:439–453 (Cited in: Cramp & Perrins 1998)

Logan JA, Régnière J, Powell JA (2003) Assessing the impacts of global warming on forest pest dynamics. Frontiers in Ecology and Environment 1:130–137

Loman J (2006) Does nest site availability limit the density of hole nesting birds in small woodland patches? Web Ecology 6:37–43

López G, Moro MJ (1997) Birds of Aleppo pine plantations in south-east Spain in relation to vegetation composition and structure. Journal of Applied Ecology 34:1257–1272

López-Iborra G, Gil-Delgado JA (1999) Composition and dynamics of bird communities. In: Rodà F, Retana J, Gracia CA, Bellot J (eds.) Ecology of Mediterranean evergreen oak forests. Springer-Verlag, Berlin, Germany, pp.355–368

Lourenço N, Pinto-Correia T, Jorge MR, Machado CR (1998) Farming strategies and land use changes in southern Portugal: land abandonment or extensification of the traditional systems? Mediterrâneo 12/13:191–208

Lovett GM, Christenson LM, Groffman PM, Jones CG, Hart JE, Mitchell MJ (2002) Insect defoliation and nitrogen cycling in forests. BioScience 52:335–341

Loyn RH, Runnalls RG, Forward GY (1983) Territorial bell miners and other birds affecting populations of insect prey. Science 221:1411–1413

Luciano P, Lentini A (2012) Ten years of microbiological control program against lepidopterous defoliators in Sardinian cork oak forests. IOBC/WPRS Bulletin 76:175–178

Luciano P, Prota R (1995) Insect pests in Sardinian cork-oak forests. IOBC/WPRS Bulletin 18:1–7

Luque J, Cohen M, Savé R, Biel C, Álvarez IF (1999) Effects of three fungal pathogens on water relations, chlorophyll fluorescence and growth of *Quercus suber* L. Annals of Forest Science 56:19–26

Luque J, Parlade J, Pera J (2000) Pathogenicity of fungi isolated from *Quercus suber* in Catalonia (NE Spain). Forest Pathology 30:247–263

Lyytikäinen-Saarenmaa P, Tomppo E (2002) Impact of sawfly defoliation on growth of Scots pine *Pinus sylvestris* (Pinaceae) and associated economic losses. Bulletin of Entomological Research 92:137–140

Maas B, Clough Y, Tscharntke T (2013) Bats and birds increase crop yield in tropical agroforestry landscapes. Ecology Letters 16:1480–1487

MacArthur R (1972) Geographical ecology: patterns in the distribution of species. Harper and Row, New York, USA

MacArthur RH, MacArthur RW (1961) On bird species diversity. Ecology 42:594–598

MacArthur RH, Pianka ER (1966) On optimal use of a patchy environment. American Naturalist 100:603–609

Magnoler A, Cambini A (1973) Radial growth of cork oak and the effects of defoliation caused by larvae of *Lymantria dispar* and *Malacosoma neustria*. Boletim do Instituto dos Produtos Florestais Cortiça 35:53–59

Mänd R, Leivits A, Leivits M, Rodenhouse NL (2009) Provision of nestboxes raises the breeding density of Great Tits *Parus major* equally in coniferous and deciduous woodland. Ibis 151:487–492

Marañón T (1988) Agro-sylvo-pastoral systems in the Iberian Peninsula: *dehesas* and *montados*. Rangel 10:255–258

Mariani JM, Manuwal DA (1990) Factors influencing brown creeper (*Certhia americana*) abundance patterns in the southern Washington Cascade Range. Studies in Avian Biology 13:53–57

Marquis RJ, Whelan CJ (1994) Insectivorous birds increase growth of white oak through consumption of leaf-chewing insects. Ecology 75:2007–2014

Martí R, Del Moral JC (eds.) (2003) Atlas de las aves reproductoras de España. SEO/BirdLife, Dirección General de Conservación de la Naturaleza, Madrid, Spain

Martín J, Cabezas J, Buyolo T, Patón D (2005) The relationship between *Cerambyx* spp. damage and subsequent *Biscogniauxia mediterranum* infection on *Quercus suber* forests. Forest Ecology and Management 216:166–174

Martin J-C, Villemant C, Mazet R (2002) Utilisation de *Bacillus thuringiensis kurstaki* 3a-3b dans la lute contre le bombyx disparate et problems poses par les migrations de chenilles. IOBC/WPRS Bulletin 25:115–122

Martínez C (1984) Notes sur l'alimentation du Guêpier d'Europe (*Merops apiaster* L.) dans une colonie du centre de l'Espagne. Alauda 52:45–50

Mason RR, Torgersen TR (1983) Mortality of larvae in stocked cohorts of the Douglas-fir tussock moth *Orgyia pseudotsugata* (McDunnough), (Lepidoptera: Lymantriidae). The Canadian Entomologist 115:1119–1127

Massa B, Lo Valvo F, Margagliotta B, Lo Valvo M (2004) Adaptive plasticity of blue tits (*Parus caeruleus*) and great tits (*Parus major*) breeding in natural and semi-natural insular habitats. Italian Journal of Zoology 71:209–217

Mattson WJ, Knight FB, Allen DC, Felts JL (1968) Vertebrate predation on the jack-pine budworm in Michigan. Journal of Economic Entomology 61:229–234

May RM (1986) When two and two do not make four: Non-linear phenomena in ecology. Proceedings of the Royal Society B 228:241–266

Medina RF, Barbosa P (2002) Predation of small and large *Orgyia leucostigma* (J.E. Smith) (Lepidoptera: Lymantriidae) larvae by vertebrate and invertebrate predators. Environmental Entomology 31:1097–1102

Mellot RS, Woods PE (1993) An improved ligature technique for dietary sampling in nestling birds. Journal of Field Ornithology 64:205–210

Merilä J, Wiggins DA (1997) Mass loss in breeding blue tits – the role of energetic stress. Journal of Animal Ecology 66:452–460

Merle P, Attié M (1992) *Coroebus undatus* (Coleoptera: Buprestidae) sur chêne-liège dans le sud-est de la France: Estimation des dégâts, relations entre ceux-ci et certains facteurs du milieu. Annales des Sciences Forestières 49:571–588

Miller KE (2010) Nest-site limitation of secondary cavity-nesting birds in even-age southern pine forests. The Wilson Journal of Ornithology 122:126–134

Minot OE (1981) Effects of interspecific competition for food in breeding blue and great tit. Journal of Animal Ecology 50:375–385

Mira A, Marques CC, Santos SM, Rosário IT, Mathias ML (2008) Environmental determinants of the distribution of the Cabrera vole (*Microtus cabrerae*) in Portugal: implications for conservation. Mammalian Biology 73:102–110

Mols CMM, Visser ME (2002) Great tits can reduce caterpillar damage in apple orchards. Journal of Applied Ecology 39:888–899

Montero G, San Miguel-Ayanz A, Cañellas I (2000) Systems of Mediterranean silviculture. La dehesa, Grafistaff, Madrid, Spain

Montoya Oliver JM (1988) Los Alcornocales (*Quercus suber* L.). Ministerio de Agricultura, Pesca y Alimentación, Madrid, Spain

Moreira AC, Martins JMS (2005) Influence of site factors on the impact of *Phytophthora cinnamomi* in cork oak stands in Portugal. Forest Pathology 35:145–162

Morris DW (2003) Toward an ecological synthesis: a case for habitat selection. Oecologia 136:1–13

Morris RF, Cheshire WF, Miller CA, Mott DG (1958) The numerical response of avian and mammalian predators during a gradation of the spruce budworm. Ecology 39:487–494

Motis A, Mestre P, Martínez A (1983) La colonización y expansión del estornino pinto (*Sturnus vulgaris* L.) y del estornino negro (*Sturnus unicolor* Temm.) en Cataluña (NE de la Península Ibérica). Miscellania Zoológica 7:131–137

Murakami M, Nakano S (2000) Species-specific bird functions in a forest-canopy food web. Proceedings of the Royal Society B 267:1597–1601

Murdoch WW, Oaten A (1975) Predation and population stability. Advances in Ecological Research 9:1–131

Myers J (1988) Can a general hypothesis explain population cycles in forest Lepidoptera? Advances in Ecological Research 18:179–242

Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858

Natividade JV (1950) Subericultura. Ministério da Economia, Direcção Geral dos Serviços Florestais e Agrícolas, Lisbon, Portugal

Netherer S, Schopf A (2010) Potential effects of climate change on insect herbivores in European forests – general aspects and the pine processionary moth as specific example. Forest Ecology and Management 259:831–838

Neves CMB (1944) Problemas suberícolas na zona pilocénica ao sul do Tejo. Boletim da Junta Nacional da Cortiça 65:193–197

Neves CM (1950) Introdução à entomologia florestal portuguesa. Livraria Sá da Costa, Lisbon, Portugal

Newsome SD, del Rio CM, Bearhop S, Phillips DL (2007) A niche for isotopic ecology. Frontiers in Ecology and Environment 5:429–436

Newton I (1994) The role of nest sites in limiting the numbers of hole-nesting birds: a review. Biological Conservation 70:265–276

Newton I (1995) The contribution of some recent research on birds to ecological understanding. Journal of Animal Ecology 64:675–696

Newton I (1998) Population limitation in birds. Academic Press, London, UK

Nicolai V (1986) The bark of trees: thermal properties, microclimate and fauna. Oecologia 69:148–160

Nogueira CDS (1967) Pragas dos montados de sobro e azinho. Revista Agronómica 5:66–74

Nogueira CDS, Ferreira LJC (1972) Distribuição das principais pragas dos montados. Instituto de Alta Cultura – Ministério de Educação Nacional, Lisbon, Portugal

Norris AR, Drever MC, Martin K (2013) Insect outbreaks increase populations and facilitate reproduction in a cavity-dependent songbird, the mountain chickadee *Poecile gambeli*. Ibis 155:165–176

Norris AR, Martin K (2008) Mountain pine beetle presence affects nest patch choice of red-breasted nuthatches. Journal of Wildlife Management 72:733–737

Nour N, Currie D, Matthysen E, Van Damme R, Dhondt AA (1998) Effects of habitat fragmentation on provisioning rates, diet and breeding success in two species of tit (great tit and blue tit). Oecologia 114:522–530

Ojeda F, Arroyo J, Marañón T (1995) Biodiversity components and conservation of Mediterranean heathlands in southern Spain. Biological Conservation 72:61–72

Olea L, López-Bellido RJ, Poblaciones MJ (2005) European types of silvopastoral systems in the Mediterranean area: *dehesa*. In: Mosquera MR, Rigueiro A, McAdam J (eds.) Silvopastoralism and sustainable land management. CABI Publishing, Wallingford, UK, pp.30–35

Olea L, San Miguel-Ayanz A (2006) The Spanish *dehesa*. A traditional Mediterranean silvopastoral system linking production and nature conservation. In: Lloveras J, González-Rodríguez A, Vázquez-Yáñez O, Piñeiro J, Santamaría O, Olea L, Poblaciones MJ (eds.) Proceedings of the 21st general meeting of the European Grassland Federation. Sociedad Española para el Estudio de los Pastos (SEEP), Madrid, Spain, pp.3–13

Olson DM, Dinerstein E (2002) The global 200: priority ecoregions for global conservation. Annals of the Missouri Botanical Garden 89:199–224

Orians GH, Wittenberger JF (1991) Spatial and temporal scales in habitat selection. American Naturalist 137:S29–S49

Orshan G (ed.) (1989) Plant pheno-morphological studies in Mediterranean type ecosystems. Kluwer Academic Publishers, Dordrecht, The Netherlands

Pagani-Núñez E, Ruiz Í, Quesada J, Negro JJ, Senar JC (2011) The diet of great tit *Parus major* nestlings in a Mediterranean Iberian forest: the important role of spiders. Animal Biodiversity and Conservation 34:355–361

Pagani-Núñez E, Senar JC (2014) Are colourful males of great tits *Parus major* better parents? Parental investment is a matter of quality. Acta Oecologica 55:23–28

Pagani-Núñez E, Valls M, Senar JC (2015) Diet specialization in a generalist population: the case of breeding great tits *Parus major* in the Mediterranean area. Oecologia 179:629–640

Paracchini ML, Petersen JE, Hoogeveen Y, Bamps C, Burfield I, van Swaay C (2008) High nature value farmland in Europe. An estimate of the distribution patterns on the basis of land cover and biodiversity data. Office for Official Publications of the European Communities, Luxembourg, Luxembourg

Park CR (2005) Tree species preference and inter-specific difference of foraging maneuver, trees and location among four canopy-dwelling birds at high-elevation temperate deciduous forest in Mt. Jumbongsan. Integrative Biosciences 9:41–46

Parrish JD (1995) Effects of needle architecture on warbler habitat selection in a coastal spruce forest. Ecology 76:1813–1820

Parry D, Spence JR, Volney WJA (1997) Responses of natural enemies to experimentally increased populations of the forest tent caterpillar, *Malacosoma disstria.* Ecological Entomology 22:97–108

Peck KM (1989) Tree species preferences shown by foraging birds in forest plantations in northern England. Biological Conservation 48:41–58

Pereira LS, Paulo AA (2004) Recursos hídricos, secas e desertificação. In: Louro V (ed.) Desertificação: sinais, dinâmicas e sociedade. Editora Piaget, Lisbon, Portugal, pp.47–62

Pereira P, Godinho C, Gomes M, Rabaça JE (2014b) The importance of the surroundings: are bird communities of riparian galleries influenced by agroforestry matrices in SW Iberian Peninsula? Annals of Forest Science 71:33–41

Pereira P, Godinho C, Roque I, Marques A, Branco M, Rabaça JE (2014a) Time to rethink the management intensity in a Mediterranean oak woodland: the response of insectivorous birds and leaf-chewing defoliators as key groups in the forest ecosystem. Annals of Forest Science 71:25–32

Pereira P, Godinho C, Roque I, Rabaça JE (2015) O montado e as aves: boas práticas para uma gestão sustentável. LabOr – Laboratório de Ornitologia/ICAAM, Universidade de Évora, Câmara Municipal de Coruche, Coruche, Portugal

Pereira PM, Pires da Fonseca M (2003) Nature vs. Nurture: the making of the *montado* ecosystem. Conservation Ecology 7:7

Pérez-Latorre AV (1996) Restauración del alcornocale en Andalucía. Elección y manejo de especies. Ecología 10:9–19

Peris SJ (1980a) Biología del estornino negro (*Sturnus unicolor* Temm.). 1. Alimentación y variación de la dieta. Ardeola 25:207–240

Peris SJ (1980b) Biología del estornino negro (*Sturnus unicolor* Temm.). 2. Dieta del pollo. Doñana, Acta Vertebrata 7:249–260

Peris SJ, Masa AI (1992) Comunidades nidificantes y invernantes de aves del encinar adehesado (*Quercus rotundifolia*) del centro-oeste de la Peninsula Iberica. Airo 3:75–82

Perrins CM (1970) The timing of birds' breeding seasons. Ibis 112:242–255

Perrins CM (1979) British tits. Collins, London, UK

Phillips DL, Gregg JW (2001) Uncertainty in source partitioning using stable isotopes. Oecologia 127:171–179

Phillips DL, Gregg JW (2003) Source partitioning using stable isotopes: coping with too many sources. Oecologia 136:261–269

Pimentel C, Nilsson JA (2007) Response of great tits *Parus major* to an irruption of a pine processionary moth *Thaumetopoea pityocampa* population with a shifted phenology. Ardea 95:191–199

Pimentel C, Nilsson JA (2009) Response of passerine birds to an irruption of a pine processionary moth *Thaumetopoea pityocampa* population with a shifted phenology. Ardeola 56:189–203

Pimentel D, Zuniga R, Morrison D (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecological Economics 52:273–288

Pineda FD, Montalvo J (1995) *Dehesa* systems in the western Mediterranean. In: Halladay P, Gilmour DA (eds.) Conserving biodiversity outside protected areas. IUCN, Gland, Switzerland, pp.117–122

Pinto-Correia T (1993) Threatened landscape in Alentejo, Portugal: the *montado* and other agro-sylvo-pastoral systems. Landscape and Urban Planning 24:43–48

Pinto-Correia T, Mascarenhas J (1999) Contribution to the extensification / intensification debate: new trends in the Portuguese *montado*. Landscape and Urban Planning 46:125–131

Piper WH, Palmer MW, Banfield N, Meyer MW (2013) Can settlement in natal-like habitat explain maladaptive habitat selection? Proceedings of the Royal Society B 280: 20130979

Plieninger T, Wilbrand C (2001) Land use, biodiversity conservation, and rural development in the *dehesas* of Cuatro Lugares, Spain. Agroforestry Systems 51:23–34

Pompanon F, Deagle BE, Symondson WOC, Brown DS, Jarmon SN, Taberlet P (2012) Who is eating what: diet assessment using next generation sequencing. Molecular Ecology 21:1931–1950

Pons J, Pausas JG (2007a) Acorn dispersal estimated by radiotracking. Oecologia 153:903–911

Pons J, Pausas JG (2007b) Not only size matters: Acorn selection by the European jay (*Garrulus glandarius*). Acta Oecologica 31:353–360

Pravosudov VV, Pravosudova EV, Zimireva EY (1996) The diet of nestling Eurasian nuthatches. Journal of Field Ornithology 67:114–118

Prieta J, Del Moral JC (2008) La grulla común invernante en España. Población en 2007 y método de censo. SEO/BirdLife, Madrid, Spain

Przybylo R, Merilä J (2000) Intersexual niche differentiation in the blue tit (*Parus caeruleus*). Biological Journal of the Linnean Society 69:233–244

Pulido F, Díaz M (1992) Relaciones entre la estructura de la vegetación y comunidades nidificantes de aves en las dehesas: influencia del manejo humano. Ardeola 39:63–72

Pulido FJ, Díaz M (1994) Diet and prey selection by adult and young blue tits (*Parus caeruleus*): the effect of correcting for prey digestibility. Ardeola 41:153–161

Pulido F, Díaz M (1997) Linking individual foraging behavior and population spatial distribution in patchy environments: a field example with Mediterranean blue tits. Oecologia 111:434–442

Purroy FJ (1988) Sobre la invernada de la paloma torcaz (*Columba palumbus*) en Iberia. In: Tellería JL (ed.) Invernada de aves en la Península Ibérica. Monografías SEO, Madrid, Spain, pp.137–151

Purroy FJ, Rodero M, Tomialojc L (1984) The ecology of woodpigeons *Columba palumbus* wintering on the Iberian Peninsula. Acta Ornithologica 20:111–146

Pyke GH, Pulliam HR, Charnov EL (1977) Optimal foraging: a selective review of theory and tests. The Quarterly Review of Biology 52:137–154

R Development Core Team (2009) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from: http://www.R-project.org (accessed 10 July 2013)

R Development Core Team (2015) R: a language and environment for statistical computing. The R Foundation for Statistical Computing, Vienna, Austria. Available from: http://www.R-project.org (accessed 10 September 2015)

Rabaça JE (1990) The influence of shrubby understory in breeding bird communities of cork oak (*Quercus suber* L.) woodlands in Portugal. Portugaliae Zoologica 1:1–6

Reichart G (1959) Birds destroying eggs of *Lymantria dispar* L. Aquila 77:315–317

Rey Benayas JM, Scheiner SM (2002) Plant diversity, biogeography and environment in Iberia: patterns and possible causal factors. Journal of Vegetation Science 13:245–258

Ribeiro NA, Surový P, Pinheiro A (2010) Adaptive management on sustainability of cork oak woodlands. In: Manos B, Paparrizos K, Matsatsinis N, Papathanasiou J (eds.) Decision support systems in agriculture, food and the environment: trends, applications and advances. IGI Global, Hershey, USA, pp.437–449

Rice J, Anderson B, Ohmart RD (1984) Comparison of the importance of different habitat attributes to avian community organization. Journal of Wildlife Management 48:895–911

Rieske LK, Dillaway DN (2008) Response of two oak species to extensive defoliation: tree growth and vigor, phytochemistry, and herbivore suitability. Forest Ecology and Management 256;121–128

Robinson MH (1969) Defenses against visually hunting predators. Evolutionary Biology 3:225–259

Robinson SK, Holmes RT (1984) Effects of plant species and foliage structure on the foraging behaviour of forest birds. Auk 101:672–685

Rodenhouse NL, Holmes RT (1992) Results of experimental and natural food reductions for breeding black-throated blue warblers. Ecology 73:357–372

Romanyk N, Cadahia D (eds.) (1992) Plagas de insectos en las masas forestales españolas, 2ª edición. Ministerio de Medio Ambiente, Madrid, Spain

Rosenberg KV, Cooper RJ (1990) Approaches to avian diet analysis. Studies in Avian Biology 13:80–90

Rosenzweig ML (1981) A theory of habitat selection. Ecology 62:327–335

Rotenberry J (1985) The role of habitat in avian community composition: physiognomy or floristics? Oecologia 67:213–217

Roth RR (1976) Spatial heterogeneity and bird species diversity. Ecology 57:773–782

Ruiu L, Mannu R, Falchi G, Braggio A, Luciano P (2014) Two years of efficacy trials with different *Bacillus thuringiensis* sv *kurstaki* formulations against *Lymantria dispar* and *Malacosoma neustria*. IOBC/WPRS Bulletin 101:205–211

Rupérez A (1957) La encina y sus tratamientos. Ediciones Selvícolas, Madrid, Spain

Sample B, Cooper RJ, Greer RD, Whitmore RC (1993b) Estimation of insect biomass by length and width. American Midland Naturalist 129:234–240

Sample BE, Cooper RJ, Whitmore RC (1993a) Dietary shifts among songbirds from a diflubenzuron-treated forest. Condor 95:616–624

San Miguel-Ayanz A (1994) La dehesa española. Origen, tipología, características y gestión. Fundación Conde del Valle de Salazar, Madrid, Spain

San Miguel-Ayanz A (2005) Mediterranean European silvopastoral systems. In: Mosquera MR, Rigueiro A, McAdam J (eds.) Silvopastoralism and sustainable land management. CABI Publishing, Wallingford, UK, pp.36–40

Sánchez S, Cuervo JJ, Moreno E (2007) Suitable cavities as a scarce resource for both cavity and non-cavity nesting birds in managed temperate forests. A case study in the Iberian Peninsula. Ardeola 54:261–274

Santos MNS (2003) Contribuição para o conhecimento das relações *Quercus suber - Biscogniauxia mediterranea* (syn. *Hypoxilon mediterraneum*). Silva Lusitanica 11:21–29

Santos T, Tellería JL, Carbonell R (2002) Bird conservation in fragmented Mediterranean forests of Spain: effects of geographical location, habitat and landscape degradation. Biological Conservation 105:113–125

Sanz JJ (2001) Experimentally increased insectivorous bird density results in a reduction of caterpillar density and leaf damage to Pyrenean oak. Ecological Research 16:387–394

Schäfer KVR, Clark KL, Skowronski N, HamerLynck EP (2010) Impact of insect defoliation on forest carbon balance as assessed with a canopy assimilation model. Global Change Biology 16:546–560

Schultz JC, Baldwin IT (1982) Oak leaf quality declines in response to defoliation by gypsy moth larvae. Science 217:149–151

Seastedt T, Crossley D, Jr. (1984) The influence of arthropods on ecosystems. Bioscience 34:157–161

SEO/BirdLife (2012) Atlas de las aves en invierno en España 2007-2010. Ministerio de Agricultura, Alimentación y Medio Ambiente, SEO/BirdLife, Madrid, Spain

Serrano MD, De Vita P, Fernández-Rebollo P, Coelho AC, Belbahri L, Sánchez ME (2012) *Phytophthora cinnamomi* and *Pythium spiculum* as main agents of *Quercus* decline in southern Spain and Portugal. IOBC/WPRS Bulletin 76:97–100

Serrão M (2002) Damage evolution and control of *Lymantria dispar* L. in a cork oak forest of southern Portugal. IOBC/WPRS Bulletin 25:109–114

Sierro A, Arlettaz R, Naef-Daenzer B, Strebel S, Zbinden N (2001) Habitat use and foraging ecology of the nightjar (*Caprimulgus europaeus*) in the Swiss Alps: towards a conservation scheme. Biological Conservation 98:325–331

Silva FA (1960) Nota sobre a *Periclista andrei* Konow, Hymenoptera, Tenthredinidae, uma praga do sobreiro, *Quercus suber* L., em Portugal. Direcção Geral dos Serviços Florestais e Aquícolas, Lisbon, Portugal

Siscart D, Diego V, Lloret F (1999) Acorn ecology. In: Rodà F, Retana J, Gracia CA, Bellot J (eds.) Ecology of Mediterranean evergreen oak forests. Springer-Verlag, Berlin, Germany, pp.89–103

Skuhravá M, Skuhravá V, Blasco-Zumeta J, Pujade J (1996) Gall midges (Diptera: Cecidomyiidae) of the Iberian Peninsula. Boletín de la Asociación Española de Entomología 20:41–61

Soler JJ, Soler M (1991) Análisis comparado del régimen alimenticio durante el período otoño-invierno de tres especies de córvidos en un área de simpatría. Ardeola 38:69–89

Solomon DM, Glen DM, Kendall DA, Milsom NF (1976) Predation on overwintering larvae of codling moth (*Cydia pomonella* (L.)) by birds. Journal of Applied Ecology 13:341–353

Solomon JD (1969) Woodpecker predation on insect borers in living hardwoods. Annals of the Entomological Society of America 62:1214–1215

Solomon ME (1949) The natural control of animal populations. Journal of Animal Ecology 18:1–35Soria FJ, Villagran M, Ocete ME (1992) Estudios poblacionales sobre *Coroebus undatus* en alcornocales de Andalucía Occidental. I: Relación infestación-bosque. Boletín de Sanidad Vegetal, Plagas 18:377–383

Soria FJ, Cano EY, Ocete ME (1996) Efectos del ataque de fitófagos perforadores en el fruto de la encina (*Quercus rotundifolia* Lam.). Boletín de Sanidad Vegetal, Plagas 22:427–432

Soria FJ, Cano E, Ocete ME (1999b) Valoración del ataque de *Curculio elephas* (Gyllenhal) (Coleoptera, Curculionidae) y *Cydia* spp. (Lepidoptera, Tortricidae) en el fruto de alcornoque (*Quercus suber* L.). Boletín de Sanidad Vegetal, Plagas 25:69–74

Soria FJ, Villagran M, Del Tio R, Ocete ME (1994a) Estudios prospectivos de los principales perforadores del alcornoque en la Sierra Norte de Sevilla. Boletín de Sanidad Vegetal, Plagas 20:643–651

Soria FJ, Villagrán M, Martín P, Ocete ME (1999a) *Curculio elephas* (Gyllenhal) (Col.: Curculionidae) y *Cydia fagiglandana* (Zeller) (Lep.: Tortricidae) en encina (*Quercus rotundifolia* Lam.): infestación y relaciones interespecíficas. Boletín de Sanidad Vegetal, Plagas 25:125–130

Soria FJ, Villagran M, Ocete ME (1994b) *Crematogaster scutellaris* Oliv. (Hym. Formicidae) en tres alcornocales del SW español. Boletín de Sanidad Vegetal, Plagas 20:637–642

Soriguer RC, Herrera C (1977) Análisis de dos contenidos estomacales de grulla común *Grus grus*. Ardeola 24:217–219

Sousa EMR (1995) Les principaux ravageurs du chêne liège au Portugal. Leurs relations avec le déclin des peuplements. IOBC/WPRS Bulletin 18:18–23

Sousa EMR, Debouzie D (1999) Distribution spatio-temporelle des attaques de *Platypus cylindrus* F. (Coleoptera : Platypodidae) dans des peuplements dus chênes-lièges au Portugal. IOBC/WPRS Bulletin 22:47–58

Sousa E, Debouzie D (2002) Contribution à la bioecologie *de Platypus cylindrus* F. au Portugal. IOBC/WPRS Bulletin 25:75–83

Sousa EMR, Debouzie D, Pereira H (1995) Le role de l'insect *Platypus cylindrus* F. (Coleoptera: Platypodidae) dans le processus de dépérissement des peuplements du chêne liège au Portugal. IOBC/WPRS Bulletin 18:43–49

Sousa E, Inácio ML (2005) New aspects of *Platypus cylindrus* Fab. (Coleoptera: Platypodidae): life history on cork oak stands in Portugal. In: Lieutier F, Ghaioule D (eds.) Entomological research in Mediterranean forest ecosystems. INRA Editions, Paris, France, pp.147–168

Sousa EMR, Santos MNS, Varela MC, Henriques J (2007) Perda de vigor dos montados de sobro e azinho: análise da situação e perspectivas. Ministério da Agricultura, do Desenvolvimento Rural e das Pescas, Direcção-Geral dos Recursos Florestais e Instituto Nacional dos Recursos Biológicos, Lisbon, Portugal

Sousa E, Tomaz IL, Moniz FA, Basto S (1997) La répartition spatiale dês champignons associés à *Platypus cylindrus* Fab. (Coleoptera: Platypodidae). Phytopathologia Mediterranea 36:145–153

Southwood TRE, Comins HN (1976) A synoptic population model. Journal of Animal Ecology 45:949–965

StatSoft Inc. (2007) STATISTICA (data analysis software system), version 8.0. http://www.statsoft.com

Stickler CM, Nepstad DC, Coe MT, McGrath DG, Rodrigues HO, Walker WS, Soares-Filho BS, Davidson EA (2009) The potential ecological costs and cobenefits of REDD: a critical review and case study from the Amazon region. Global Change Biology 15:2803–2824

Strode PK (2009) Spring tree species use by migrating yellow-rumped warblers in relation to phenology and food availability. Wilson Journal of Ornithology 121:457–468

Strong AM, Sherry TW, Holmes RTR (2000) Bird predation on herbivorous insects: indirect effects on sugar maple sapling. Oecologia 125:370–379

Strong DR (1983) Exorcising the ghost of competition past: phytophagous insects. In: Strong DR, Simberloff DS, Abele LG, Thistle AB (eds.) Ecological communities: conceptual issues and the evidence. Princeton University Press, Princeton, New Jersey, USA, pp.28–41

Suñer D, Abós L (1994) Estudio de la infestación de *Coroebus undatus* en los alcornocales catalanes. Scientia Gerundensis 20:45–53

Svensson E, Nilsson JA (1995) Food supply, territory quality, and reproductive timing in the blue tit (*Parus caeruleus*). Ecology 76:1804–1812

Swank WT, Waide JB, Crossley DA, Jr., Todd RL (1981) Insect defoliation enhances nitrate export from forest ecosystems. Oecologia 51:297–299

Symondson WOC (2002) Molecular identification of prey in predator diets. Molecular Ecology 11:627–641

Symondson WOC, Sunderland KD, Greenstone MH (2002) Can generalist predators be effective biocontrol agents? Annual Review of Entomology 47:561–594

Tammaru T, Haukioja E (1996) Capital breeders and income breeders among Lepidoptera: consequences to population dynamics. Oikos 77:561–564

Tanhuanpää M, Ruohomaki K, Uusipaikka E (2001) High larval predation rate in non-outbreaking populations of a geometrid moth. Ecology 82:281–289

Tellería JL (1992) Gestión forestal y conservación de las aves en España peninsular. Ardeola 39: 99–113

Tellería JL (2001) Passerine bird communities of Iberian *dehesas*: a review. Animal Biodiversity and Conservation 24:67–78

Tellería JL, Santos T (1994) Factors involved in the distribution of forest birds on the Iberian Peninsula. Bird Study 41:161–169

Tellería JL, Santos T, Carrascal LM (1988) La invernada de los paseriformes (O. Passeriformes) en la Peninsula Ibérica. In: Tellería JL (ed.) Invernada de aves en la Península Ibérica. Monografías SEO, Madrid, Spain, pp.153–166

Thomas DW, Blondel J, Perret P, Lambrechts MM, Speakman JR (2001) Energetic and fitness costs of mismatching resource supply and demand in seasonally breeding birds. Science 291:2598–2600

Thomson LJ, Macfadyen S, Hoffmann AA (2010) Predicting the effects of climate change on natural enemies of agricultural pests. Biological Control 52:296–306

Tinbergen JM, Dietz MW (1994) Parental energy expenditure during brood rearing in the Great Tit (*Parus major*) in relation to body mass, temperature, food availability and clutch size. Functional Ecology 8:563–572

Tinoco I, Pestana M, Nóbrega F (2009) A qualidade da cortiça versus modalidades de gestão em montado de sobro. Silva Lusitanica 17:131–158

Toimil FJ (1987a) Algunos insectos defoliadores de la encina (*Quercus ilex* L.) en la provincia de Huelva. Bolatín de Sanidad Vegetal, Plagas 13:173–188

Toimil FJ (1987b) Algunos lepidópteros defoliadores de la encina (*Q. ilex* L.) y alcornoque (*Q. suber* L.), en la provincia de Huelva. Boletín de Sanidad Vegetal, Plagas 13:331–346

Toimil FJ (1989) Comparación del período larval de las especies defoliadoras más importantes del encinar encontradas en la provincia de Huelva entre 1985 y 1988. Boletín de Sanidad Vegetal, Plagas 4:365–374

Torgersen TR, Mason RR, Paul HG (1983) Predation on pupae of Douglas-fir tussock moth, *Orgyia pseudotsugata* (McDunnough) (Lepidoptera: Lymantriidae). Environmental Entomology 12:1678–1682

Török J, Tóth L (1999) Asymmetric competition between two tit species: a reciprocal removal experiment. Journal of Animal Ecology 68:338–345

Torres J (1985) El *Hypoxylon mediterra*neum (de Not.) Mill. y su comportamiento en los encinares y alcornocales andaluces. Boletín Servicio de Defesa contra las Plagas e Inspección Fitopatológica 11:185–191

Tremblay I, Thomas D, Blondel J, Perret P, Lambrechts MM (2005) The effect of habitat quality on foraging patterns, provisioning rate and nestling growth in Corsican blue tits *Parus caeruleus*. Ibis 147:17–24

Tremblay I, Thomas D, Lambrechts MM, Blondel J, Perret P (2003) Variation in blue tit breeding performance. Ecology 84:3033–3043

Turner AK (1982) Optimal foraging by the swallow (*Hirundo rustica* L.): prey size selection. Animal Behaviour 30:862–872

Tuset JJ, Hinarejos C, Mira JL, Cobos JM (1996) Implicación de *Phytophthora cinnamomi* Rands en la enfernedad de la seca de encinas y alcornoques. Boletín de Sanidad Vegetal, Plagas 22:491–499

Ulfstrand S (1976) Feeding niches of some passerine birds in a South Swedish coniferous plantation in winter and summer. Ornis Scandinavica 7:21–27

UN-ECE/FAO (United Nations Economic Commission for Europe Food and Agriculture Organization of the United Nations) (2000) Forest resources of Europe, CIS, North-America, Australia, Japan and New Zealand. Geneva Timber and Forest Study Papers, No.17, United Nations, New York, USA and Geneva, Switzerland

Unno A (2002) Tree species preferences of insectivorous birds in a Japanese deciduous forest: the effect of different foraging techniques and seasonal change in food resources. Ornithological Science 1:133–142

Valente C, Branco M (2008) A importância dos pica-paus como inimigos naturais das brocas do eucalipto. In: Branco M, Valente C, Paiva MR (eds.) Pragas e doenças em pinhal e eucaliptal – desafios para a sua gestão integrada. ISA Press, Lisbon, Portugal, pp.147–158

Valentini A, Pompanon F, Taberlet P (2009) DNA barcoding for ecologists. Trends in Ecology and Evolution 24:110–117

Valverde JA (1971) Notas sobre la biologia reproductora del críalo *Clamator glandarius* (L.). Ardeola special number:591–647

van Bael SA, Philpott SM, Greenberg R, Bichier P, Barber NA, Mooney KA, Gruner DS (2008) Birds as predators in tropical agroforestry systems. Ecology 89:928–934

van Balen JH, Booy CJH, van Franeker JA, Osieck ER (1982) Studies on hole-nesting birds in natural nest sites. 1. Availability and occupation of natural nest sites. Ardea 70:1–24

van Driesche R, Hoddle M, Center T (2008) Control of pests and weeds by natural enemies: an introduction to biological control. Blackwell Publishing, Malden, USA, Oxford, UK, and Carlton, Australia

Vannini A, Valentini R, Luisi N (1996) Impact of drought and *Hypoxylon mediterraneum* on oak decline in the Mediterranean region. Annales des Sciences Forestières 53:753–760

Viejo JL, Romera L (2004) Lepidoptera. In: Barrientos JA (ed.) Curso práctico de Entomología. Asociación Española de Entomología, CIBIO, Universitat Autònoma de Barcelona. Barcelona, Spain, pp.705–729

Villagran M, Ocete ME (1990) Datos preliminares sobre la distribución de nidos de *Crematogaster scutellaris* Oliv., 1789 (Hym: Formicidae) en alcornocales de Andalucía Occidental. Relación con el perímetro del tronco. Boletín de Sanidad Vegetal, Plagas 16:151–157

Villemant C, Andreï-Ruiz M-C (1999) Life-cycles and biological features of eggs predators of *Lymantria dispar* (Lepidoptera: Lymantriidae) in the Mamora cork oak forest, Morocco. European Journal of Entomology 96:29–36

Villemant C, Fraval A (eds.) (1991) La faune du Chêne-Liège. Actes Editions, Rabat, Morocco

Villemant C, Fraval A (1993) Les insectes du Chêne-Liège. Insectes 88:13–16

Villemant C, Fraval A (1999) Les gradations de *Lymantria dispar* en Europe et en Afrique du Nord. IOBC/WPRS Bulletin 23:71–79

Villemant C, Ramzi H (1995) Predators of *Lymantria dispar* (Lep. Lymantriidae) egg masses: spatio-temporal variation of their impact during the 1988–89 pest generation in the Mamora cork oak forest (Morocco). Entomophaga 40:441–456

von Haartman L (1971) Population dynamics. In: Farner DS, King JR (eds.) Avian biology, Vol. 1. Academic, London, UK, pp. 391–459

Vos JG, Dybing E, Greim HÁ, Ladefoged O, Lambré C, Tarazona JV, Brandt I, Vethaak AD (2000) Health effects of endocrine-disrupting chemicals on wildlife, with special reference to the European situation. Critical Reviews in Toxicology 30:71–133

Walankiewicz W (1991) Do secondary cavity-nesting birds suffer more from competition for cavities or from predation in a primeval deciduous forest? Natural Areas Journal 11:203–212

Wallner WE (1987) Factors affecting insect population dynamics: differences between outbreak and non-outbreak species. Annual Review of Entomology 32:317–340

Wang YH, Liao YJ (1990) Attracting beneficial birds for the biological control of *Dendrolimus punctatus* (Lep. Lasiocampidae). Chinese Journal of Biological Control 6:25–26

Waters JR, Noon BR, Verner J (2010) Lack of nest site limitation in a cavity-nesting bird community. Journal of Wildlife Management 54:239–245

Webb JR, Cosby BJ, Deviney FA, Eshleman KN, Galloway JN (1995) Change in the acid-base status of an Appalachian catchment following forest defoliation by the gypsy moth. Water, Air & Soil Pollution 85:535–540

Wesołowski T (1989) Nest-sites of hole-nesters in a primaeval temperate forest (Białowieza National Park, Poland). Acta Ornithologica 25:321–351

Wesołowski T (2007) Lessons from long-term hole-nester studies in a primeval temperate forest. Journal of Ornithology 148 (Suppl. 2):S395–S405

Wesołowski T, Tomialojć L (1997) Breeding bird dynamics in a primeval temperate forest: long-term trends in Białowieza National Park (Poland). Ecography 20:432–453

Whelan CJ, Wenny DG, Marquis RJ (2008) Ecosystem services provided by birds. Annals of the New York Academy of Sciences 1134:25–60

Whittaker RH (1977) Evolution of species diversity in land communities. Evolutionary Biology 10:1–67

Wickler W (1968) Mimicry in plants and animals. World University Library, London, UK

Wiens JA (1989) Spatial scaling in ecology. Functional Ecology 3:385–397

Wilkin TA, King LE, Sheldon BC (2009) Habitat quality, nestling diet, and provisioning behaviour in great tits *Parus major*. Journal of Avian Biology 40:135–145

Willson MF (1974) Avian community organization and habitat structure. Ecology 55:1017–1029

Yodzis P (1988) The indeterminacy of ecological interactions as perceived through perturbation experiments. Ecology 69:508–515

Ziane N, Chabi Y, Lambrechts MM (2006) Breeding performance of blue tits *Cyanistes caeruleus ultramarinus* in relation to habitat richness of oak forest patches in north-eastern Algeria. Acta Ornithologica 41:163–169

APPENDIX A

Parasitoids and insect predators of cork and holm oak pests

Table 12. Parasitoids of cork and holm oak pests and parasited life-cycle stage (*E* eggs, *L* larvae, *P* pupae, *n/a* Not available) (Ferreira & Ferreira 1991, Romanyk & Cadahia 1992). For the complete scientific name of pests see Table 1 in Chapter 1.

Parasitoids	**Stage**	**Parasited species**
DIPTERA		
Bombyliidae		
Cyllenia rustica Rossi 1790	L	*P. andrei*
Muscidae		
Muscina stabulans Fallen 1817	P	*T. viridana*
Phoridae		
Megaselia rufipes Meigen 1804	n/a	*P. dusmeti*
Tachinidae		
Blepharipa pratensis Meigen 1824	L	*P. dusmeti, L. dispar*
Compsilura concinnata Meigen 1824	L	*L. dispar*
Elodia morio Fallen 1820	L	*T. viridana*
Exorista fasciata Fallen 1820	P	*M. neustria*
Exorista larvarum Linnaeus 1758	L	*E. chrysorrhoea, L. dispar*
Exorista rustica Fallen 1810	n/a	*P. dusmeti*
Exorista segregata Rondani 1859	L	*E. chrysorrhoea, L. dispar*
Nemorilla floralis Fallen 1810	P	*T. viridana*
Pales pavida Meigen 1824	n/a	*E. chrysorrhoea*
Townsendiellomyia nidicola Townsend 1908	L	*E. chrysorrhoea, L. dispar*
HYMENOPTERA		
Braconidae		
Apanteles lacteicolor Viereck 1911	n/a	*E. chrysorrhoea, L. dispar, M. neustria*
Ascogaster quadridentata Wesmael 1835	E	*C. splendana*
Bassus cingulipes Nees 1812	P	*T. viridana*
Bassus fortipes Reinhard 1867	P	*T. viridana*
Cotesia melanoscela Ratzeburg 1844	L	*E. chrysorrhoea, L. dispar, M. neustria*

Meteorus versicolor Wesmael 1835	n/a	*E. chrysorrhoea, L. dispar, M. neustria*
Protapanteles liparidis Bouche 1834	L	*E. chrysorrhoea, L. dispar, M. neustria*
Protapanteles vitripennis Curtis 1830	L	*E. chrysorrhoea, L. dispar*
Schizoprymnus sculpturatus Snoflak 1953	L	*C. elephas*
Chalcididae		
Brachymeria tibialis Walker 1834	P	*E. chrysorrhoea, L. dispar, T. viridana*
Chrysididae		
Cleptes nigritus Mercet 1904	P	*P. andrei*
Crabronidae		
Cerceris bupresticida Dufour 1841	n/a	*Coraebus undatus*
Encyrtidae		
Ooencyrtus kuvanae Howard 1910	E	*E. chrysorrhoea, L. dispar, M. neustria*
Ooencyrtus neustriae Mercet 1925	E	*M. neustria*
Eupelmidae		
Anastatus japonicus Ashmead 1904	E	*E. chrysorrhoea, L. dispar, M. neustria*
Ichneumonidae		
Agrypon clandestinum Gravenhorst 1829	P	*C. nymphaea, C. nymphagoga*
Barylypa propugnator Holmgren 1857	P	*C. nymphaea, C. nymphagoga, M. neustria*
Coelichneumon lacrymator Boyer de Fonscolombe 1847	P	*C. nymphaea, C. nymphagoga*
Coelichneumon singularis Berthoumieu 1829	P	*C. nymphaea, C. nymphagoga*
Dirophanes invisor Thunberg 1824	L-P	*M. neustria, T. viridana*
Dolichomitus populneus Ratzeburg 1848	P	*C. nymphaea, C. nymphagoga*
Echthrus reluctator Linnaeus 1758	L	*C. florentinus, C. undatus*
Endromopoda detrita Holmgren 1860	L-P	*M. neustria, C. splendana, T. viridana*
Ephialtes manifestator Linnaeus 1758	L	*T. viridana*
Ephialtes spp. Gravenhorst 1829	n/a	*C. undatus*
Gregopimpla inquisitor Scopoli 1763	L-P	*E. chrysorrhoea, L. dispar, M. neustria, T. viridana*

Itoplectis maculator Fabricius 1775	L-P	*L. dispar, M. neustria, C. splendana, T. viridana*
Itoplectis viduata Gravenhorst 1829	L-P	*L. dispar, M. neustria*
Liotryphon ascaniae Rudow 1883	L-P	*M. neustria*
Lissonota coracina Gmelin 1790	L	*C. florentinus, C. undatus, C. splendana*
Meringopus titillator Linnaeus 1758	P	*C. nymphaea, C. nymphagoga*
Monoblastus discedens Schmiedeknecht 1912	L	*P. andrei*
Pimpla rufipes Miller 1759	P	*E. chrysorrhoea, L. dispar*
Pimpla turionellae Linnaeus 1758	P	*C. nymphaea, C. nymphagoga, E. chrysorrhoea, L. dispar, M. neustria*
Scambus brevicornis Gravenhorst 1829	L-P	*M. neustria, E. chrysorrhoea, C. splendana, T. viridana*
Scambus calobatus Gravenhorst 1829	L	*C. splendana, T. viridana*
Stenarella domator Poda 1761	P	*C. nymphaea, C. nymphagoga*
Syspasis rufina Gravenhorst 1820	P	*C. nymphaea, C. nymphagoga*
Venturia canescens Gravenhorst 1829	P	*C. nymphaea, C. nymphagoga*
Scelionidae		
Telenomus spp. Haliday 1833	E	*C. nymphaea, C. nymphagoga, M. neustria*
Toryminae		
Monodontomerus aereus Walker 1834	P	*E. chrysorrhoea, L. dispar, M. neustria, T. viridana*
Trichogrammatidae		
Trichogramma spp. Westwood 1833	E	*C. splendana*

Table 13. Insect predators of cork and holm oak pests and preyed life-cycle stage (*L* larvae, *P* pupae, *n/a* Not available) (Ferreira & Ferreira 1991, Romanyk & Cadahia 1992). For the complete scientific name of pests see Table 1 in Chapter 1.

Predator	**Stage**	**Predated species**
COLEOPTERA		
Carabidae		
Calosoma inquisitor Linnaeus 1758	L	*L. dispar*
Calosoma sycophanta Linnaeus 1758	L-P	*E. chrysorrhoea, L. dispar,*
Carabus lusitanicus Fabricius 1801	n/a	*L. dispar, M. neustria*
Zopheridae		
Colydium elongatum Fabricius 1787	n/a	*P. cylindrus*
HYMENOPTERA		
Formicidae		
Camponotus spp. Mayr 1861	n/a	*L. dispar*
MECOPTERA		
Panorpidae		
Panorpa communis Linnaeus 1758	P	*T. viridana*

APPENDIX B

Other results from this PhD thesis

Ceia RS, Machado RA, Ramos JA (2016) A importância das aves no controlo de pragas de desfolhadores nos montados. In: Rangel JF, Faísca CM, Bombico S, Mourisco P (eds.) El alcornocal y el negocio corchero: una perspectiva histórica e interdisciplinar / O montado de sobro e o setor corticeiro: uma perspetiva histórica e transdisciplinar. Diputación de Badajoz, Badajoz, Spain, pp.297–312

Ceia RS, Machado RA, Ramos JA (2016) The importance of birds for the regulation of defoliator pests in *montados* [Oral communication]. 9th SPEA Ornithology Congress / 5th Iberian Ornithology Congress, Vila Real, Portugal

Ceia RS, Ramos JA (2016) Tree selection patterns between cork oak (*Quercus suber*) and holm oak (*Q. rotundifolia*) by insectivorous birds in the *montado* [Oral communication]. 9th SPEA Ornithology Congress / 5th Iberian Ornithology Congress, Vila Real, Portugal

Machado RA, Ceia RS, Ramos JA (2016) Is Stable Isotope Analysis useful to study the diet of generalist insectivorous birds? [Oral communication]. 9th SPEA Ornithology Congress / 5th Iberian Ornithology Congress, Vila Real, Portugal

Ceia RS, Ramos JA (2015) Numerical and functional responses of passerines to defoliator outbreaks in cork oak woodlands [Oral communication]. 10th Conference of the European Ornithologists' Union, Badajoz, Spain

Ceia RS, Machado RA, Ramos JA (2015) The importance of birds for the regulation of defoliator pests in *montados* [Oral communication]. International Congress "The *montado* of cork oak and the cork sector: a historical and interdisciplinary persperctive", Ponte de Sôr, Portugal

Ceia RS, Ramos JA (2014) Tritrophic interactions in the *montado*: oak trees, insect pests and tree-foraging birds [Written communication]. 8th SPEA Ornithology Congress, Almada, Portugal

Machado RA, Ceia, RS, Ramos JA (2014) Do insectivorous birds control *montado* pest species? [Written communication – Best student written communication award]. 8th SPEA Ornithology Congress, Almada, Portugal

Ceia RS, Machado RA, Ramos JA (2013) Insect predation by birds in *montados* and its importance in the control of forest pests [Written communication]. ICAAM International Conference, Évora, Portugal