EFFECTS OF HABITAT QUALITY ON THE ABUNDANCE, BEHAVIOUR AND BREEDING PERFORMANCE OF OWLS: BARN AND LITTLE OWLS IN AGRO-PASTORAL LANDSCAPES OF SOUTHERN EUROPE

by

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To Teresa, Sara and Clara

This thesis is based on the following publications which are referred to in the text by their Roman numerals:

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I.   Tomé, R. & Valkama, J. 2001: Seasonal variation in the abundance and habitat use of Barn Owls *Tyto alba* on lowland farmland. Ornis Fennica, 78, 109-118.

II.   Tomé, R., Bloise, C. & Korpimäki, E. 2004: Nest-site selection and nesting success of Little Owls (*Athene noctua*) in Mediterranean woodland and open habitats. Journal of Raptor Research, 38 (1), 35-46.

III.   Tomé, R., Santos, N., Cardia, P., Ferrand, N. & Korpimäki, E. 2005: Factors affecting the prevalence of blood parasites of Little Owls *Athene noctua* in southern Portugal. Ornis Fennica, 82, 63-72.

IV.   Tomé, R., Catry, P., Bloise, C. & Korpimäki, E. 2008: Breeding density and success, and diet composition of Little Owls *Athene noctua* in steppe-like habitats in Portugal. Ornis Fennica, 85, 22–32.

V.   Tomé, R., Dias, M.P., Chumbinho, A.C. & Bloise, C. 2011: Influence of perch height and vegetation structure on foraging behaviour of Little Owls *Athene noctua*: how to achieve the same success in two distinct habitats. Ardea, 99, 17-26.

CONTENTS

1. Introduction

The understanding of the processes limiting animal populations is a central issue in ecology and constitutes the basis for the practical management of wild populations, whether for conservation, sustained exploitation or plague control (Newton 1998). Bird populations are usually limited by natural ultimate factors (limiting factors), including food-supplies, nest and refuge sites, competitors, natural enemies (predators, parasites and pathogens) and weather (den Boer & Gradwell 1970, Andrewartha & Birch 1984, Begon & Mortimer 1986, Newton 1998, Begon *et al.* 2006, Brambilla *et al.* 2010). Owl and diurnal raptor populations, in particular, are often limited by the availability of food and nest-sites (Newton 1979, Korpimäki 1992a, Fargallo *et al.* 2009, Sergio *et al.* 2011).

As a consequence of an uneven distribution of resources and other limiting factors (e.g. predators or competitors), habitats vary spatially in quality, i.e., in the benefits they confer to the occupants in terms of survival and reproduction. In this way, variation in habitat quality is also proximately involved in population regulation (Newton 1998, Burgess *et al.* 2011).

According to life-history theory (e.g. Stearns 1992), individuals should prefer environments where the survival costs are low. Moreover, the heterogeneity of habitats in time and space leads organisms to develop strategies of adaptation involving trade-offs in the allocation of resources to reproduction and survival (Southwood 1977). Thus, when choosing between different environments, individuals

are expected to try to maximize their survival and reproductive success (e.g. Morris 1987, Orians & Wittenberger 1991).

Birds use habitat selection mechanisms in order to find an environment meeting the ecological requirements that are essential for their survival (ultimate factors). The proximate factors for the choice of habitat include *stimuli* that trigger the settling reaction in a habitat, but not necessarily imply a biological significance for the species. These include stimuli of, for example, landscape and terrain features, foraging or nesting sites, or the presence of competitors or predators (Hildén 1965, Carrete *et al.* 2006).

Foraging habitat selection by birds can be affected by large-scale landscape units (e.g. Korpimäki 1986, Redpath 1995, Valkama *et al.* 1995) as well as by small-scale microhabitat variables (e.g. Rice *et al.* 1984, Wiens 1985, Widén 1994). These, in turn, will condition food availability, i.e. food abundance and accessibility (Perrins & Birkhead 1983, Cody 1985, Cresswell *et al.* 2010).

As most mobile predators, birds of prey should forage preferentially in habitat patches that assure the maximum energy intake (e.g. Pyke 1984, Stephens & Krebs 1986). Selected patches should be the most advantageous in terms of prey capture rate and minimum energy costs, which is determined by prey type, density and availability. Several studies have documented the importance of e.g. perch availability and distribution, and vegetation cover and structure for habitat selection and foraging of raptors (e.g. Wakeley 1978, Baker & Brooks 1981, Bechard 1982, Janes 1984, 1985, Korpimäki 1986, Widén 1994, Ontiveros *et al.* 2005).

Because the hunting strategy of a predator may affect survival and reproduction, selection should favour the most efficient hunting behaviours (Andersson 1981a). Foraging theories have provided a set of predictions about how predators should behave in order to optimise the time spent hunting and to maximise the net energy intake (e.g. Schoener 1971, Pyke *et al.* 1977, Krebs & Davies 1978, Krebs 1980, Stephens & Krebs 1986, Terraube *et al.* 2011). Foraging behaviour is expected to be adjusted to the type and distribution of prey, to habitat characteristics and, consequently, to the resulting accessibility and vulnerability of prey (e.g. Andersson

1981a, Fitzpatrick 1981, Widén 1994, Quinn & Cresswell 2004). As prey detection is also constrained by the capacity of an animal to use different types of sensorial information (e.g. Ali 1978, Rice 1983), differences in hunting behaviour are also expected from predators using visual or acoustic signals to detect their prey (e.g. Andersson 1981a, Rice 1983, Bye *et al.* 1992, Andersson *et al.* 2008). Due to its complexity (e.g. Zach & Smith 1981), field studies on foraging behaviour are still scarce for many groups of species, including owls (but see e.g. Bye *et al.* 1992, Sonerud 1992). In particular, there is a lack of studies that evaluate how birds may change their foraging strategies in different habitats with distinct conditions of accessibility to prey and how do those changes reflect in foraging success.

Breeding success, and moreover the lifetime reproductive success, is considered as one of the most important life history traits contributing to the fitness of any individual bird (e.g. Bell 1980, Newton 1989, Partridge 1989, Korpimäki 1992b, Benton & Grant 2000). Unlike other animal classes, all birds share a similar basic life-cycle, consisting in an oviparous reproducing strategy involving the deposition of the eggs in purpose-built sites called nests. Although nests can vary greatly in form, dimensions and complexity, their function remains the same: to protect the eggs and the nestlings during the first breeding phases. Consequently, the choice of a breeding site, or nesting site, is a key component of habitat selection by birds (Hildén 1965), with important consequences for survival and reproduction of individuals (Cody 1985). Nest sites selected by a species should represent the cumulative effects of evolutionary pressures that have maximized reproductive success (Caccamise 1977).

During the different breeding stages, eggs, chicks or even incubating or brooding adults may be killed by predators or affected by adverse weather conditions (e.g. Ricklefs 1969, Newton 1998). Nest predation is a major cause of reproductive loss in many birds (e.g. Lack 1954, Ricklefs 1969, Nilsson 1984, Martin & Clobert 1996), and therefore it is considered a strong selective force in the evolution of nesting strategies (e.g. Newton 1979, Nilsson 1984, Martin 1992, 1995, Schieck & Hannon 1993, Tremblay *et al.* 1997, Hakkarainen *et al.* 2001). Nest predation rates vary with attributes of nest sites (e.g. Martin 1992, 1993, Martin & Li 1992). Therefore, nests

that are difficult to detect or are located in places that hamper the access by predators increase the likelihood of survival for their contents, i.e. reproductive success.

To reduce the risk of nest predation and losses due to adverse weather, birds have adopted strategies such as cavity nesting (e.g. von Haartman 1957, Newton 1994). Consequently, cavity nesters often have higher breeding success than open-nesting species (e.g. Lack 1954, Nice 1957, Peterson & Gauthier 1985, Korpimäki 1987). Nevertheless, high nest predation rates have also been recorded in some hole-nesting species (e.g. Flegg & Cox 1975, Dunn 1977, Eriksson 1979, Sonerud 1985a), and thus additional tactics to minimize nest predation and increase offspring production might be expected to influence nest-site selection of cavity-nesting birds. Nest-site variables, such as cavity dimensions, volume, height, and depth might be important (e.g. Stauffer & Best 1982, Van Balen *et al.* 1982, Peterson & Gauthier 1985, Belthoff & Ritchison 1990) and influence reproductive success (e.g. Karlsson & Nilsson 1977, Nilsson 1984, Korpimäki 1985, Rendell & Robertson 1989, Valkama & Korpimäki 1999). Microhabitat variables, such as tree species and density (Swallow *et al.* 1986) or the vegetation surrounding the cavity (McCallum & Gehlbach 1988, Valkama *et al.* 1995, Valkama & Korpimäki 1999) may also affect nest-site selection.

Blood parasites may affect birds by reducing their reproductive rates (Korpimäki *et al.* 1993, Dunbar *et al.* 2003), affecting their fitness (Atkinson & Van Riper III 1991, Stuht *et al.* 1999) or even by inducing mortality, in conjunction with other debilitating conditions (Peirce & Marquiss 1983, Hunter *et al.* 1997, Møller *et al.* 2009). Consequently, parasites may also impact bird populations in different ways, including the limitation of population numbers (e.g. Reid *et al.* 1978, Duncan *et al.* 1979, Begon *et al.* 2006), periodic massive reductions of population size (e.g. Newton 1998) or even decline to extinction (e.g. Warner 1968). Therefore, the role of avian parasites as morbidity and mortality factors affecting bird populations may be relevant to conservation issues, particularly when dealing with threatened bird species (e.g. Dobson & McCallum 1997, Newton 1998).

As the maintenance of immune function seems to be energetically and nutritionally costly (e.g. Demas *et al.* 1997, Lochmiller & Deerenberg 2000), prevalence of parasitism in an individual may be affected by factors such as energy reallocation during reproduction *per se* (Deerenberg *et al.* 1997, Bentley *et al.* 1998), food supply and resource levels (e.g. Wiehn & Korpimäki 1998, Appleby *et al.* 1999), hunting investment (Wiehn & Korpimäki 1998) and reproductive effort (e.g. Allander & Sundberg 1997, Wiehn *et al.* 1999). Prevalence may also vary with factors like sex (e.g. Zuk & McKean 1996, Fargallo *et al.* 2002) or individual age (e.g. Appleby *et al.* 1999, Garvin & Greiner 2003).

The degree of exposition of birds to pathogens and parasites is also affected by habitat characteristics. For example, black flies (Diptera; Simuliidae) are vectors of several species of pathogenic avian leucocytozoans (Jamnaback 1973) whose aquatic larvae and pupae require running water for their development (Crosskey 1990). Several studies have found such an association between habitat features and parasite prevalence in birds (Van Riper 1991, Moyer *et al.* 2002, Galeotti & Sacchi 2003, De Neve *et al.* 2007).

2. Aims of the thesis

In this thesis, I examine factors that affect population dynamics, habitat use and breeding success of Barn Owls *Tyto alba* and Little Owls *Athene noctua* in agro-pastoral landscapes. Although the populations of both species have decreased markedly throughout a large part of their European distribution area due to major habitat changes (Tucker & Heath 1994, BirdLife International 2004), they are still common in Central and Southern Portugal, where my research was conducted. Therefore, understanding the mechanisms and habitat variables that drive individual and population performances at these important strongholds may constitute an essential tool to develop management or recovering strategies aiming at the conservation of the species at a more general scale. In this context, I started to examine habitat use by Barn Owls in a heterogeneous lowland farmland area strongly

influenced by human activities, and including different agro-pastoral practices. Afterwards, I studied how the differences of habitat and environmental variables in two steppe-like habitats, a treeless cereal pseudo-steppe and an open Holm Oak woodland influenced the performance of Little Owls.

First, I investigated seasonal changes in the relative importance of the various habitats of Barn Owls, since they should be taken into account in any model of land management with conservation aims (paper I). I also assessed the importance of this area at a regional scale, investigating seasonal and between-year variations in the abundance of the species.

Secondly, I investigated which features influence nest site selection by Little Owls, at the site and micro-habitat scales, which could be afterwards used in management guidelines for the species conservation (II). Furthermore, because individuals should prefer nest-site features that increase reproductive success (Alatalo *et al.* 1984, Leonard and Picman 1987, Milks & Picman 1994), I also examined the relationships between nest-site variables and nesting success of owls.

Thirdly, since blood parasites may impact fitness and reproductive output of individuals (e.g. Korpimäki *et al.* 2002, Ishak *et al.* 2008), I examined the occurrence of blood parasites in Little Owls and investigated the relationships between individual host traits and the prevalence of haematozoa (III).

Fourthly, paper IV investigated the breeding density and breeding success of Little Owls in the two types of steppe-like habitats and analysed basic ecological parameters of the studied populations in a European context. In this paper I also examined which factors, including weather, body condition, diet composition, and prey and nest-site availability, could contribute to possible inter-annual and inter-area differences in breeding density and reproduction.

Finally, I investigated how Little Owls adapt their foraging behaviour to differences in habitat structure, by comparing their strategies in the two different habitats (V). In particular, I aimed to determine how the owls adapt their foraging strategies to different environmental features, such as perch height and vegetation structure, and how the selection of different behaviours influences hunting success.

3. Study species

The Barn Owl *Tyto alba* and the Little Owl *Athene noctua* are nocturnal birds of prey (order Strigiformes) which are widespread and still relatively common in Europe (BirdLife International 2004).

The medium-sized Barn Owl has a cosmopolitan distribution, being absent from the Arctic and Antarctic regions, and from big parts of Asia and North America (Mikkola 1983, Cramp 1998). It is well adapted to human presence and man modified habitats, inhabiting mainly open to semi-open landscapes including agricultural fields, pastureland, waste ground, open woodland, parkland and urban or suburban areas (Mikkola 1983, Cramp 1998). In Portugal, Barn Owls occur mostly in farmland and open woodland of Cork Oak *Quercus suber* and Holm Oak *Quercus rotundifolia* (Equipa Atlas 2008). Usual nest-sites include cavities in ruins, decrepit buildings, barns, trees and cliffs. It is a generalist and opportunistic predator, feeding typically on small mammals of orders Rodentia (mice and voles) and Insectivora (shrews), but also consuming birds, amphibians, reptiles and insects (Mikkola 1983, Cramp 1998). In Europe, the species is chiefly resident (Mikkola 1983, Cramp 1998) although during the post-breeding period juveniles can disperse more than 100 km (e.g. Bunn *et al.* 1982, de Bruijn 1994, Taylor 1994).

The Barn Owl is classified as SPEC 3 (i.e. a species whose global populations are not concentrated in Europe, but which has an Unfavourable Conservation Status in Europe; BirdLife International 2004) because of the continuous moderate decrease suffered throughout most of its European range during the last 40 years (Tucker & Heath 1994, BirdLife International 2004). This decrease was mainly due to habitat changes as consequence of new agricultural practices and expansion of urbanizations and road connections (e.g. Tucker & Heath 1994). These modifications induced the loss of suitable roost and nest-sites, as well as the loss of favourable hunting grounds (e.g. Shawyer 1987, van der Hut *et al.* 1992, de Bruijn 1994, Taylor 1994, Ramsden 1998, Martínez & Zuberogoitia 2004). Mortality and fecundity rates were also affected by the increment in the use of pesticides and in car traffic (e.g. Mendenhall

et al. 1983*,* Shawyer 1987, Newton *et al.* 1991*,* van der Hut *et al.* 1992, de Bruijn 1994, Taylor 1994, Ramsden 1998, Fajardo 2001).

The Little Owl is a smaller, mostly sedentary, species, which shows crepuscular and nocturnal habits (Schönn *et al.* 1991, Exo 1992, Van Nieuwenhuyse *et al.* 2008, Sunde *et al.* 2009) but that also may hunt during daytime, especially during the breeding period (e.g. Negro *et al.* 1990). It shows a Turkestanian-Mediterranean distribution (Voous 1960, Mikkola 1983), being present along a vast geographical range including most of Western, Central and Southern Europe, North of Africa, Middle East and a wide band along Central Asia (Mikkola 1983, Van Nieuwenhuyse *et al.* 2008). Depending on the region, its diet may be based on invertebrates (mostly insects) or small mammals (e.g. Mikkola 1983, Van Nieuwenhuyse *et al.* 2008).

Little Owls are mostly associated with open to semi-open landscapes, including steppes, farmland, groves of different kinds and open woodland (Van Nieuwenhuyse *et al.* 2008). In Portugal, they occur mainly in agricultural mosaics, groves of Olive Trees *Olea europaea*, Carob Trees *Cerationia siliqua* or Almond Trees *Prunus dulcis*, cereal pseudo-steppes and open woodland of Holm Oak (Equipa Atlas 2008). Essential habitat elements for the species are year-round availability and accessibility to prey, and presence of suitable nest-sites (e.g. Loske 1986, Exo 1992, Bultot *et al.* 2001, Van Nieuwenhuyse *et al.* 2008). Nesting occurs in cavities in trees, walls, stone piles, buildings or even in the ground (e.g. Schönn *et al.* 1991, Van Nieuwenhuyse *et al.* 2008). The method of hunting is associated with the type of vegetation and prey (e.g. Schönn *et al.* 1991), but frequently includes perch-hunting (e.g. Fajardo *et al.* 1998), using a "perch and pounce" (Génot & Van Nieuwenhuyse 2002) or pause-travel (*sensu* Andersson 1981a, Bye *et al.* 1992) technique. Hunting occurs predominantly in twilight and at night (Exo 1989, Schönn *et al.* 1991, Van Nieuwenhuyse *et al.* 2008), but Little Owls may also hunt in daytime, especially during the breeding season (e.g. Negro *et al.* 1990).

Due to a moderate continued decline in the European populations over the last decades, Little Owls are now considered to have an unfavourable conservation status in Europe (SPEC 3; BirdLife International 2004). This decrease was caused by large-scale habitat changes associated with the intensification and mechanization of agriculture (e.g. Tucker & Heath 1994, Van Nieuwenhuyse *et al.* 2008), involving the loss of suitable nest-sites, decrease in prey abundance and detrimental effects of pesticides on breeding success (Schönn *et al.* 1991, Exo 1992, Tucker and Heath 1994, Van Nieuwenhuyse *et al.* 2008, Thorup *et al.* 2010). Recent research has shown that habitat changes may affect the demographic rates of Little Owls (such as survival and immigration rates), but the resultant impact on the local populations of the species depends on their spatial extent and degree of isolation (Schaub *et al.* 2006).

4. Study areas

This research took place in study areas located in the Centre and South of Portugal (Figure 1). Both the studied locations shared a flat topography and a mainly agricultural use that resulted in a mosaic of different cultures, pastures and fallows.

The Barn Owl study (I) was conducted from October 1991 to December 1993 in Ponta da Erva (*ca.* 38° 50' N, 8° 58' W), an alluvial floodplain (designated in Portuguese as "*lezíria*") with *ca.* 62.19 km². This area is located in the southern margin of the estuary of the river Tagus, just 12 km to the Northeast of the Portuguese capital, Lisbon. Climate in this region is characterized by mild and wet winters and hot and dry summers. Average annual precipitation is *ca.* 645 mm (Leitão *et al.* 1998). The area is fully occupied by cultivations and pastures for cattle, separated by a vast system of draining ditches and fences (Figure 2). Natural vegetation subsists only in narrow field edges, ditch margins and some pastures. It includes mainly herbaceous plants and a single perennial species, the Shrubby Sea-blite *Suaeda vera* (Leitão *et al.* 1998). At the time of the study, agricultural fields were mostly occupied with cereal, silage, sunflower and maize. During the last years,

however, a significant proportion of those plots, together with pastureland, were reconverted to rice fields.
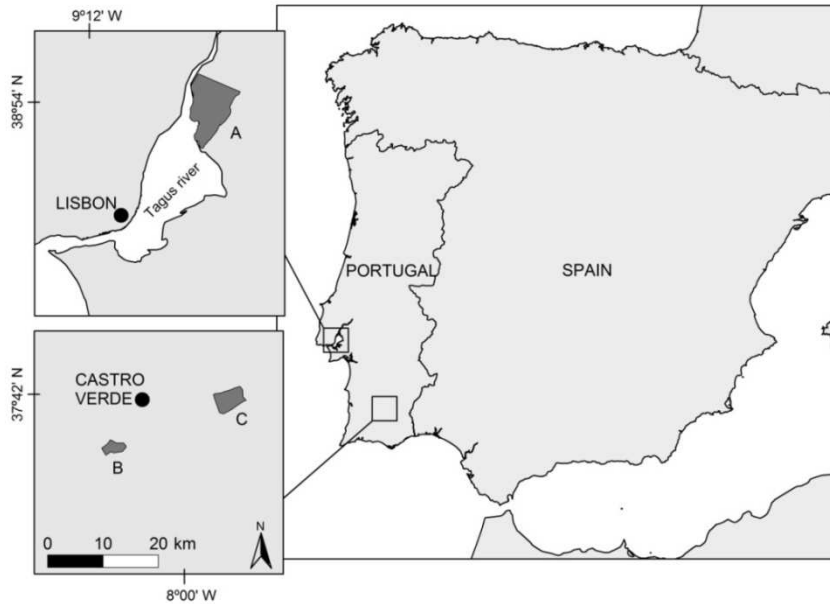
Figure 1 - Study areas: A – Ponta da Erva, where the Ban Owl study was conducted; B – Cabeça da Serra and C – São Marcos da Atabueira, where the Little Owls research was conducted.

The study area is crossed by numerous minor roads, that are used for farming purposes. While human activities related with agriculture practices are frequent, constructions are reduced to a few houses and barns and traffic is low. The area is totally included in the Special Protection Area for Birds (Directive 79/409/EC) and partially in the Nature Reserve of the Tejo estuary, one of most important wetlands in Europe that holds regularly more than 100 000 wintering aquatic birds (Leitão *et al.* 1998, Costa *et al.* 2003).

Figure 2 - Pastures bounded by fences in the Ponta da Erva study area (photo: Paulo Cardoso).

Little Owls were studied (II, III, IV and V) between 1997 and 1999 in two steppe-like areas located approximately 22 km apart, in the Baixo Alentejo region, Southern Portugal: Cabeça da Serra (ca. 37° 37' N, 8° 08' W) and São Marcos da Atabueira (ca. 37° 41' N, 7° 54' W). In this region climate is dry, with an average annual precipitation under 600 mm (DRAA 2000). Nonetheless, there is marked inter-annual variation in precipitation (Rivas-Martinez 1981, Reis & Gonçalves 1987, DRAA 2000). Streams are mostly temporary, drying up during half of the year. Only a few major streams and some reservoirs remain as permanent water bodies in the region. Temperature is mild in winter (monthly average ca. 11° C) and high during summer (monthly average over 25° C, with maximum values exceeding 40° C; DRAA 2000).

Cabeça da Serra comprises 6.1 km² of parkland-like, very open old Holm Oak *Quercus ilex rotundifolia* woodland (0.25 – 16.5 trees/ha (IV); Figure 3). During the study period, most of the area was used as pasture for cattle and sheep, whereas a smaller proportion (5%–30%) was used for cereal cultivation. A small part was covered by a young forestation of Stone Pine *Pinus pinea*.

São Marcos da Atabueira is an open pseudo-steppe area (cereal steppe; Suárez *et al.* 1997, Moreira 1999) of 16.8 km², where trees are practically absent, with the exception of a small (0.3 km²) plantation of Blue Gum *Eucalyptus globulus*. During

the study, most of the area was also used for cattle and sheep pasture, while a smaller percentage (15%-25%) was occupied by cereal fields (Delgado & Moreira 2000). Characteristic landscape features are the numerous man-made stone piles that resulted from stone gathering during agricultural practices (Figure 4).

In both areas, agriculture and cattle farming are carried out in traditional ways, maintaining a rotation every 4-5 years between cereal fields and fallows used as pastures (Suárez et al. 1997, Moreira 1999).

Figure 3 - Open Holm Oak woodland in the Cabeça da Serra study area.

Figure 4 - Man-made stone piles in the pseudo-steppe of São Marcos da Atabueira study area.

Due to their landscape and bioclimatic features, steppic areas of Portugal and western Spain are relatively unique in Europe (Valverde 1958). Cereal steppes originated mostly from the clearance of the natural oak *Quercus* spp. forests (Moreira 1999), and therefore open oak woodlands in the same regions share already some of the same steppic characteristics. Iberian pseudo-steppes hold significant proportions of the European populations of several threatened bird species, such as the Great Bustard *Otis tarda*, Little Bustard *Tetrax tetrax*, Lesser Kestrel *Falco naumanni* and Montagu's Harrier *Circus pygargus* (e.g. De Juana *et al.* 1988, Tucker 1991, Tucker & Heath 1994, Costa *et al.* 2003). Nevertheless, the maintenance of these landscapes is threatened by changes in the agricultural and land-use practices (leading to the abandonment or conversion of agricultural fields or to the intensification of agriculture) introduced by the European Union Common

Agricultural Policy reforms in last decades (e.g. Baldock 1991, Moreira & Leitão 1996).

The whole area of São Marcos da Atabueira and a small part of Cabeça da Serra area are classified as Special Protection Areas for Birds (Directive 79/409/EC). Most of São Marcos da Atabueira area is also managed with nature conservation purposes by a national environmental NGO (LPN – Liga para a Protecção da Natureza). Moreover, both São Marcos da Atabueira and Cabeça da Serra areas are included in the proposed network of Vital Sign monitoring areas for evaluating population trends and key habitat components for Little Owls (Van Nieuwenhuyse *et al.* 2008).

5. Methods

5.1. Owl abundance and distribution

Different methods were used to assess owls' abundance and distribution in the study areas, according with local specificities of landscape features and species-specific behavioural characteristics.

Nocturnal car transects (e.g. Fuller & Mosher 1981) were used to locate Barn Owls in the open farmland areas of Ponta da Erva, where they benefited from the existent wide system of wire fences, hunting very frequently from fence poles to nearby ditches and road margins (I) (Figure 5). From October 1991 to December 1993, 76 car transects (average three transects/month) were conducted and Barn Owls were detected with the help of the car head lights (full beam) and a hand torch. Every location of an owl was mapped and a Kilometric Index of Abundance (I.K.A.; e.g. Fuller & Mosher 1981, Ricci 1989a, 1989b, Bibby *et al.* 1992) was calculated for each transect.

To identify and map all Little Owl territories in the Holm Oak woodland and pseudo-steppe areas, we monitored them almost continuously from February to mid-August during 1997–1999 (IV). Little Owl territories were mapped based on responses to playbacks (mainly between February and April; Zuberogoitia & Campos 1998, Centili 2001), and observations of individuals and their movements, both

during day and night. Supplementary information from telemetry was also used (A. Chumbinho & R. Tomé, unpubl. data).

5.2. Captures and colour-ringing

Owls were captured for measurements and colour-ringed (Figure 6) as an auxiliary to estimate the number of individuals and territory distribution (e.g. Bibby *et al.* 1992, Sutherland *et al.* 2004).

Barn Owls were captured at night, between August 1992 and October 1993 (I). They were attracted to the ground using a simulated mouse lure, flashed with the car head lights and a flashlight and captured with a sweep net (Tomé 1994; see also Bull 1987). Age of captured individuals was ascertained based on moult pattern (Taylor 1993) and ringed birds were intensively looked for in transects conducted subsequently at the study area.

Little Owls were captured between March 1997 and August 1999 using mist-nets, *bal-chatri* and other trap baited with a live mouse (R. Tomé, unpubl.) during day, and a flashlight and a sweep net at night (Bub 1991) (III, IV). Captured owls were aged with basis on plumage features (Juillard 1979, Cramp 1985) and several measurements were taken, including body mass and wing length (IV). Sex was also determined for a sample of birds through molecular methods (Ellegren & Sheldon 1997, Griffiths *et al.* 1998) (III).

Figure 5 - Barn Owl detected during a car transect while hunting from a pole in Ponta da Erva area (photo: Faísca).

Figure 6 - Colour-ringed Little Owl in São Marcos da Atabueira area (photo: Ricardo Guerreiro).

5.3. Ecto- and endo-parasites

Little Owls that were captured between February and August 1999 were also inspected externally for the presence of ectoparasites (e.g. lice and ticks) and blood sampled to examine the presence of blood parasites (III). Blood samples were obtained by piercing the brachial vein, drawing blood into a capillary tube and smearing it onto a glass slide. Later, smears were scanned in the laboratory at 1000 X magnification and the prevalence of blood parasites was inspected (e.g. Bennett 1962, Fedynich *et al.* 1993, Fedynich & Rhodes 1995, Leppert *et al.* 2004).

5.4. Environmental variables and habitat types

Habitat variables were measured at distinct scales (see e.g. Sutherland *et al.* 2004) in the different study areas. In the Barn Owl study (I), we characterized periodically land use types in the farming plots adjacent to the transects during the period between October 1991 and June 1993. Five main types of land use were considered: herbaceous pastures periodically used by cattle, silage and cereal fields, irrigated sunflower and maize cultivations, tillage and reed beds.

For Cabeça da Serra and São Marcos da Atabueira areas, where Little Owls were studied, we obtained data on monthly precipitation during 1997-1999 (IV). Vegetation features were measured in spring during the same study years, in 10 Little Owl territories randomly selected in each area (IV, V). In each territory, vegetation characteristics were measured in eight sample-plots, located at 20 m and 40 m from the nest or territory centre in a north, south, east and west direction. A sample quadrat (50 cm x 50 cm) was used within each plot to estimate the percentage cover of ground vegetation. A profile board with 8 horizontal bands was used to calculate the horizontal density of vegetation (Hays *et al.* 1981). We also calculated an Index of Vegetation Volume (IVV) for each sample plot by multiplying the % ground vegetation cover by the average horizontal density of vegetation (IV), and an Index of Vegetation Cover (IVC; e.g. Thiollay & Clobert 1988), by multiplying the % ground vegetation cover by the average vegetation height (V).

The same 20 randomly selected territories were used to estimate perch availability and the average available perch height in each area (V), by counting and measuring to the maximum height all perches ≥ 50 cm present in a 100 m radius area around the nest or territory centre.

In the study on hunting behaviour of Little Owls (V), we determined for each focal observation period: the average percentage of ground vegetation coverage, estimated from three 1 m² squares randomly distributed throughout the area where attacks took place; the average ground vegetation height, estimated from measurements of the nearest plants to the corners of the same squares (e.g. Thiollay & Clobert 1988); and the IVC value.

5.5. Diet and prey availability

Little Owl diet was studied by analysing pellets collected between February and May 1998 (IV). Pellets were collected in 10–15 territories in the Holm Oak woodland and the pseudo-steppe areas.

Prey availability was studied in the same study sites in spring, between 1997 and 1999 (IV, V). To obtain estimates of prey availability we sampled in June the same 10

territories sampled for vegetation in each area. The availability of ground invertebrates was sampled using four pitfall traps (e.g. Sutherland 1996) in each territory. These traps were kept open during three nights plus a continuous 48-h period. Sweep-netting was used to sample invertebrates in standing vegetation (e.g. Sutherland 1996). A series of ten sweeping movements was performed while walking from the pitfall trap location toward the north, south, east and west.

The abundance of small mammals was also sampled setting eight snap-traps per territory, which were left open during four nights. Additionally, the abundance of birds was sampled in 1998, from 150-m linear transects crossing each territory.

5.6. Habitat use

Habitat use by Barn Owls in the Ponta da Erva area (I) was analysed using data collected during car transects conducted between October 1991 and June 1993. Only roads with similar features of bordering fences and ditches were considered, as well as we included only observations of owls that were hunting and already emancipated from their parents. The exact location of each observed owl was mapped and associated to the land use type present in the adjacent farming plot. Due to the narrowness of the roads (*ca.* 6 m), Barn Owls could quickly abandon poles at one roadside to others in the opposite margin, exploring easily hunting patches on both sides (and in fact they were regularly seen doing so). Therefore, if habitats differed on both sides of the transect, we considered for each observed owl the probability associated with foraging in each patch (i.e., 0.5 in each).

To determine the availability of each habitat in each transect, we summed the length of all farming plots with that habitat sampled along the transect.

The relationship between Little Owls and the structure of their habitat was also studied in the woodland area (IV). In this case, we investigated the relationship between the number of territories and the density of trees, applying a grid to aerial photographs and subdividing the area into plots of 20.25 ha. In each plot, we counted the number of trees and the number of Little Owl territories, based on the presence

of detected nests (II) or territory centres (a tree or a group of trees where an owl pair had previously been frequently observed).

5.7. Nest-site selection

Little Owls nests were searched for during the breeding seasons of 1997–1999, by following male owls taking prey to incubating or brooding females or young, or by inspecting cavities frequently utilized by the owls (II). In the Holm Oak woodland area, 36 nests were found in 26 territories, whereas in the pseudo-steppe area, 37 nests were found in 30 territories during the study period. We included some different nests found in the same territories, because at least one of the parent owls changed in most of the territories during the study period (R. Tomé unpubl. data) (see e.g. Belthoff & Ritchison 1990, Sedgwick & Knopf 1990).

For each detected nest (in trees or stone piles), the following variables were measured: habitat, tree species, tree dimensions (height and diameter at breast height), stone pile dimensions (height, length and width), stone pile type (classified as "tower", "wall", hide for hunters, etc.), stone pile stability, mean dimensions of stones composing stone piles (long and short diameters of ten randomly selected stones), distance to ground of nest entrances, dimensions (long and short diameters), inclination (in degrees) and orientation of nest entrances, percentage of coverage of nest entrance (for nests in trees) and place in tree (trunk, base of branch, branch). We also checked for the existence of alternative entrance holes to the same nest and for the presence of potential predator signs (e.g., feces of mustelids, foxes, rats or jeweled lizards *Lacerta lepida*).

Additionally, we measured the distances from the nest to the nearest road, pathway, human habitation, reservoir, and permanent stream. Habitat type and the number and type of available perches and of available nesting cavities within a 100-m radius of each nest site were also recorded.

To investigate what variables were related with the choice of certain cavities for nest sites by Little Owls, we compared the sample of used nests with a selection of 44

randomly selected cavities that were not used during the study period (22 in each area).

5.8. Breeding success

We investigated breeding success of Little Owls between 1997 and 1999 (II, IV). Breeding success was usually determined from the number of fledged young observed near the entrance of each nest. The depth and complexity of nest cavities (e.g. Glue and Scott 1980) hampered a meticulous inspection of nest chambers in most cases and therefore we obtained scanty data on clutch size, accurate laying date and cause of failure (II, IV).

In the study aiming the comparison of breeding success between the two areas, a random sub-sample of territories was selected and monitored systematically (IV). This was done to avoid bias in the determination of breeding success, due to effects of higher detectability of successful nests compared to that of unsuccessful nests (e.g. Sutherland *et al.* 2004).

5.9. Behavioural observations

While monitoring the Holm Oak woodland and the pseudo-steppe areas during the diurnal period between January and August 1999, we actively searched for Little Owls that were hunting (V). When we detected an owl that was actively hunting, we started a 40 min. period of continuous observation ("focal animal sampling"; e.g. Altmann 1974, Martin & Bateson 1993). Observations were made with binoculars and/or telescope from a minimum distance of 30 m (from inside a car) to a maximum of several hundred meters. Each focal period began after the owl perched following an attack (irrespectively of its success). If the owl abandoned a perch due to disturbance (e.g. caused by raptors or people) or changed its behaviour (e.g. started roosting), the sampling period was not considered.

Fourteen (pseudo-steppe) and fifteen (woodland) focal observation periods were obtained in different territories, the majority (66 %) during breeding season (April-

June). All prey items captured by Little Owls during the observation periods were invertebrates.

During the observation periods, we measured detection and giving-up times (e.g. Bye *et al.* 1992) to the nearest second. Detection times corresponded to the period spent on a perch before a hunting attempt, and giving-up times corresponded to the period spent on a perch before abandoning it to another. The success of each attack attempt was also recorded.

After each observation period, all used perches and the distances flown by the owls were measured to the nearest cm (e.g. Hays *et al.* 1981). Perches were classified as detection perches (from which a hunting attempt was launched; *sensu* Carlson 1985, Bye *et al.* 1992) or giving-up perches (perches abandoned for other perches, without a hunting attempt being launched; *sensu* Andersson 1981, Moreno 1984, Bye *et al.* 1992).

5.10. Statistical analyses

In the different studies, statistical tests were two-tailed and corrected for ties when appropriate. Log- or square-root transformations were used to meet the normality and homoscedasticity assumptions for parametric tests (Sokal & Rohlf 1981, Zar 1996). When data were not normally distributed even after transformations we used non-parametric tests (Siegel & Castellan 1988). Contingency analyses were used to compare the distributions of categorical variables (Zar 1996). Data were analysed using SPSS statistical package (Norusis 1993) or R statistical software (R Development Core Team 2009).

To investigate if Barn Owls foraged in different habitats non-randomly (I), we compared the proportion of owls observed in each habitat with the proportion that these habitats represented in each transect. Since proportions of habitat types always sum to 1 and are not inter-independent (unit-sum constraint; see Aitchison 1986), we used compositional analysis to examine our data. This method renders the proportions independent and approximately normally distributed (Aebischer & Robertson 1992) by log-ratio transformation based on one of the proportions as

denominator, after replacing zero values with 0.01. Using MANOVA and a suitable statistic (Wilk's lambda, Λ), it was then possible to assess whether log-ratio differences (utilized - available) differ significantly from 0 (random habitat use) over all the transects. In the end, a rank of the habitats can be composed, based on the relative use of each type, indicating also when different ranks represent statistically significant differences in the habitats relative utilization (Aitchison 1986, Aebischer & Robertson 1992, Aebischer *et al.* 1993).

Logistic regression was used to evaluate simultaneously the effect of different variables and their interactions on nest-site selection (nests vs. random cavities) and nesting success (successful vs. failed nests) of Little Owls (II). All variables that had a univariate *P*-value < 0.25 entered the initial multivariate model, together with their first-order interactions (Hosmer and Lemeshow 1989). Non-significant interactions and main effects were gradually removed from the model, starting from the least significant variable. At the end, only significant effects and interactions remained in the final model (e.g. Christensen 1990, Tremblay *et al.* 1997, Valkama *et al.* 1998). Logistic regressions were used to analyze the effect of variables in both study areas independently, because the different nature of tree and stone pile cavities resulted in basic scale and categorical differences among most variables measured.

To investigate the relationships between prevalence of blood parasites and body measurements or plumage features (III), we used data from all captured adult owls. In the analysis concerning the relationships between age or sex and prevalence, only data from owls captured in different territories were used, to avoid possible pseudo-replication effects concerning the likelihood of owls occupying the same territories being more or less susceptible to infections. In this study, logistic regression was again used to evaluate the effect of different variables on parasites prevalence in Little Owls. In the end, the area under the receiver-operating characteristic curve (AUC) was calculated, to assess the model's performance (e.g. Fielding & Bell 1997, Pearce & Ferrier 2000, Manel *et al.* 2001). Since several variables were only measured in adults, logistic regression analyses were conducted separately on data from all owls captured and on data from adults.

The body mass of Little Owls captured in different years and in both study areas was compared (IV) using analysis of covariance (ANCOVA), for adult birds (including wing length as a covariate to correct body mass for size; e.g., García-Berthou 2001), and two-way ANOVA, for juveniles.

For the comparison of vegetation variables (IV), vegetation measures taken from sample-plots (% vegetation cover, vegetation horizontal density and IVV) were used to calculate mean values for each habitat (fallow or cereal field) that occurred within a sampled territory.

For the analysis regarding the availability of invertebrate prey (Coleoptera and Orthoptera) (IV), we combined the samples obtained in each pitfall trap and the associated sweep-net series. Consequently, four samples of invertebrate prey were used to calculate an average for each sampled territory.

Two-way ANOVA models were used to examine the similarity in average IVV, invertebrate prey availability and the number of fledglings in successful nests, between years and areas (IV). The effect of area and year on breeding success was analysed with a Generalized Linear Model (GLM) with a Poisson error term and log link function. A logistic regression was also used to evaluate the effect of area and year on the success of breeding attempts (nests with at least one fledged juvenile vs. nests with no fledged juvenile).

In the study on hunting behaviour of Little Owls (V), we compared habitat variables (perch and vegetation characteristics and prey availability) in random territories in the woodland and pseudo-steppe areas using Mann-Whitney U-tests. To analyse the availability of invertebrates, we combined the four samples obtained in each pitfall trap and in the associated sweep-netting, to calculate an average for each sampled territory.

In comparisons involving focal samplings (V) we used average values for each variable, calculated from all measurements made during the same focal period per territory. Chi-square and likelihood ratio tests were used to compare the utilization of different perch types by the owls with those available in random territories. In the same study (V), differences in the number and height of perches and in variables

associated to hunting success between areas or between samples from focal observations and random territories were tested with Mann-Whitney U-tests or *t*-tests. For comparisons between detection vs. giving-up variables within the same area we used paired tests per territory (Wilcoxon test), whereas Mann-Whitney tests were again used in inter-area comparisons. Spearman correlations were used to test for relationships between behavioural variables, while multiple linear regressions were used to investigate the relationships between vegetation characteristics and behavioural variables.

6. Main findings of the thesis

6.1. Variation in Barn Owl abundance in lowland farmland (I)

The Barn Owl is considered as a mainly resident species, despite dispersive movements involving mostly juvenile individuals. These movements are more relevant in Central Europe and the number of individuals involved and the average extension of the movements may change considerably between years, apparently due to the combined influence of harsh weather conditions during the post-breeding phase and high breeding productivity related with periodic cycles of prey abundance (Mikkola 1983, Cramp 1985, Taylor 1994, Roulin 2002; see also Altwegg *et al.* 2003). In Southern Europe, e.g. in Portugal and Spain, Barn Owls are also generally considered as residents and the occurrence of significant variations in the local abundance of the species has not been described (Díaz *et al.* 1996, Catry *et al.* 2010).

In our study, we detected marked seasonal variations in the abundance of Barn Owls in the Ponta da Erva farmland area (estuary of the river Tejo), clearly related to different phases of their annual cycle. Abundance was highest after the breeding period, from late summer to mid-autumn, coinciding with the main period of juvenile dispersal (August-November; e.g. Cramp 1985, Baudvin 1986, de Bruijn 1994, Taylor 1994). Maximum abundance was registered in mid-September or mid-October, when up to 70 individuals were observed during the execution of car transects, representing almost 2.5 owls per kilometre. Abundance decreased

thereafter during autumn and winter, becoming very low during the first stages of the breeding period (winter and early spring; e.g. Bunn *et. al.* 1982, Mikkola 1983, Cramp 1985, Rufino 1989, Roque 2003, Catry *et al.* 2010). The small resident breeding population in the study area was estimated at 7 to 10 pairs (i.e. *ca.* 1 pair per 6.3 km²).

Barn Owls occurring in the study area during the abundance peak were almost exclusively 1st year birds, certainly involved in post-breeding dispersal movements. The very low proportion of visual recaptures of individuals marked with colour rings indicated a high turn-over of individuals during this period or/and the occurrence of a large population. Most of the owls probably came from areas surrounding the Tejo estuary, since the average juvenile dispersal distance for Barn Owls is reported to be less than 50 km in most European regions (e.g. Bunn *et al.* 1982, de Bruijn 1994, Taylor 1994). High turn-over rates and/or the fact that most birds abandoned the area until January may be a consequence of movements in search for suitable nesting sites, since Barn Owls usually breed when they are one year old (Cramp 1985, Roulin 2002) and the few rural buildings that existed in the area were already mostly occupied by adult birds.

Extensive farmland (e.g. van der Hut *et al.* 1992, de Bruijn 1994, Taylor 1994, Butet *et al.* 2006), and the presence of landscape elements such as ditches and fences bordered by dense strips of vegetation (e.g. Hardy 1992, Taylor 1994, Burel 1996, Michel *et al.* 2007, Arlettaz *et al.* 2010) usually support high densities of small mammals. Additionally, the existence of hunting perches (e.g. poles) may be also important, especially during winter, when energetic constraints increase (Village 1983, Masman *et al.* 1988, Taylor 1994). All these factors probably contribute to the high number of dispersing Barn Owls occurring in our study area and to the relatively long period during which owl abundance was high. Good hunting areas are essential for young owls, since a high percentage of their mortality is due to starvation and diseases as a consequence of bad hunting performances (e.g. Newton *et al.* 1991, de Bruijn 1994, Taylor 1994). Consequently, lowland farmland may increase the survival of a large number of individuals in autumn, when juvenile

mortality may be highest (e.g. de Fajardo 1990, Bruijn 1994), and might contribute decisively to the population dynamics of the species, at least on a local scale.

The fact that the area is located in an estuary might have also contributed to the high numbers observed. Natural hedges, one of the most important habitats for the owls in terms of food supply (e.g. van der Hut *et al.* 1992, de Bruijn 1994, Taylor 1994, Roulin 2002), are more frequent along river courses and it is possible that juvenile Barn Owls tend to follow rivers in order to obtain favourable hunting habitats.

6.2. Habitat use by Barn Owls (I)

The importance of distinct habitats for foraging Barn Owls changed throughout the year. During summer, owls selected pastures, winter cultures (cereal and silage cultivations) and tilled fields, while summer cultures (irrigated sunflower and maize fields) were significantly less used. Habitat use was random in one of the studied autumns (1991), while in the next fall, summer cultures were the most selected habitat. Finally, during winter owls appeared to favour foraging in summer cultures, tilled fields and winter cultures. Reed beds were significantly less utilized than all other habitats during practically all seasons. The scarcity of owl observations in spring hampered an analysis of habitat use during this period.

As in other raptor species, habitat selection was most likely to be related to prey availability, i.e., prey abundance, distribution and accessibility (e.g. Cody 1985, Janes 1985, Aschwanden *et al.* 2005, Arlettaz *et al.* 2010). In our study area, Barn Owls feed almost exclusively on small mammals (especially mice *Mus* sp.; Tomé 1994) at all seasons. Although there is no available data on the abundance of small mammals in different habitats in the Ponta da Erva area, several studies have shown that it depends on several characteristics of ground cover (e.g. Bunn *et al.* 1982, Hardy 1992, van der Hut *et al.* 1992, Taylor 1994, Aschwanden *et al.* 2005, Moro & Gadal 2007, Arlettaz *et al.* 2010) and thus is affected by seasonal variations in habitat composition and structure due to farmland practices (e.g. Heroldová *et al.* 2007). On the other hand, access to prey, and consequently hunting success is also affected by

habitat and vegetation structure (e.g. Southern & Lowe 1968, Bechard 1982, Korpimäki 1986, Thiollay & Clobert 1988, Aschwanden *et al.* 2005, Andersson *et al.* 2008, Arlettaz *et al.* 2010).

In our study area, habitats with very tall or dense vegetation (reed beds and, in summer, summer cultures) were always significantly less used than all the others, because they were practically impenetrable for the owls due to high plant density, structure and height (e.g. 1.5 m and 3 m for grown-up sunflowers and maize, respectively) (see also Arlettaz *et al.* 2010). On the contrary, tilled fields, where prey was probably not abundant in most of the seasons, was one of the most used habitats throughout the study.

Pastures, which usually support high densities of small mammals (e.g. Hardy 1992, Taylor *et al.* 1992, van der Hut *et al.* 1992, Aschwanden *et al.* 2005, Arlettaz *et al.* 2010) were preferred by Barn Owls during summer. However, by late summer vegetation was almost totally destroyed by cattle, which probably conducted to a reduction in mice abundance. Consequently, pastures were used by Barn Owls significantly less than other habitats during autumn. In winter, when vegetation recovered and was again higher, importance of pastures for Barn Owls increased.

Winter cultures were especially preferred by the owls in summer, and summer cultures in autumn, after the respective harvests. Harvest leaves plenty of available plant material (seeds, stems, etc.) on the ground, which may support high densities of small mammals (e.g. Heroldová *et al.* 2007) and attracts flocks of passerines which become readily accessible for owls due to the structural simplicity of this habitats (Aschwanden *et al.* 2005). The relative importance of both types of stubble fields for the owls decreased thereafter, probably due to a decrease in prey availability.

Interestingly, habitat use was only random in the autumn of 1991, when the two most used habitats during next fall (summer cultures and tilled fields) were much less available or absent.

6.3. Nest-site selection by Little Owls (II)

In the Holm Oak woodland, Little Owls nested practically only in cavities in trees. The only measured variable that differed between utilized and randomly selected unused cavities was predator presence: faeces of potential predators for Little Owls (e.g. mustelids, rats or jeweled lizards) were present at 42% of the unused sites, while only in 11% of the utilized trees we found these types of signs.

Predation has also been reported as one of the major factors affecting the breeding success of this owl (Exo & Hennes 1980, Schönn 1986), and the avoidance of predators was identified as one of the most important factors when selecting a nesting site for other cavity-nesting species (e.g. Nilsson 1984, Nilsson *et al.* 1991, Rendell and Robertson 1989, Lawler & Edwards Jr. 2002, White Jr. *et al.* 2006, Cornelius 2008).

The main predators of Little Owl nests in our study areas were mammals such as the Stone Marten (*Martes foina*), the Common Genet (*Genetta genetta*), and the Garden Dormouse (*Eliomys quercinus*), as well as the Jewelled Lizard (Knötzsch 1978, Schönn 1986, Juillard *et al.* 1992, Génot 2001). All these species seek shelter and roost in cavities, and thus, include a number of cavities in their home ranges.

The large number of suitable natural cavities in the Holm Oak woodland of our study area makes it unlikely that nest-site availability was limiting the breeding density of Little Owls (Exo 1983, Loske 1986, Dalbek *et al.* 1999). This conclusion was supported by the very low use of 50 nest boxes that were available in our 4-yr study. Because the use of nest-boxes often indicates nest site limitation (e.g. Lundberg & Westman 1984, Brawn & Balda 1988; Knötzsch 1988, Exo 1992 for the Little Owl), this result supports the idea that nest sites were not limiting in our study area (Brush 1983), and that owls were able to select nest sites that were relatively safe from predators. This suggestion was supported by our results on the frequency of nesting failure and nest predation, which were relatively low and similar to those from studies on the Little Owl in other parts of Europe (Glue & Scott 1980, Exo 1983, Juillard 1984, Schönn 1986, Génot 2001).

In the pseudo-steppe area, Little Owls nested almost exclusively in cavities in stone piles. Compared to unused sites, selected stone piles consisted of larger stones. Moreover, the number of other suitable nesting cavities in stone piles around the selected ones was almost double of that found in the vicinity of non utilized stone piles.

Larger stones probably create more internal cavities within piles (Juillard *et al.* 1992), and also deeper cavities that owls usually prefer (Glue and Scott 1980, Exo 1981, Génot 1990, Van Nieuwenhuyse *et al.* 2008). The area of nest chambers in piles of large stones should also be bigger, and for many species of cavity nesters, this is often correlated with larger clutches and higher breeding success (e.g. Karlsson & Nilsson 1977, Korpimäki 1985, Rendell & Robertson 1989, Valkama & Korpimäki 1999). Finally, stone piles with larger stones are usually more recent, less prone to erosion, and thus, longer lasting (Juillard *et al.* 1992).

Although Little Owls often show strong nest-site fidelity (with individual variation; Glue and Scott 1980, Glutz and Bauer 1980, Ullrich 1980, Exo 1981, Sunde *et al.* 2009), they may benefit from the inclusion of alternative suitable nesting cavities in their territories. In many species of birds (Jackson 1994, Marjakangas *et al.* 1997, Valkama *et al.* 1998), including cavity-nesters (e.g. Eriksson 1979, Dow and Fredga 1983, Sonerud 1985b, Hakkarainen *et al.* 2001; but see Korpimäki 1987, 1993), individuals avoid breeding in sites where they have failed in previous attempts due to predation, probably because predators may revisit these sites. This could select for individuals that shift nest holes between breeding attempts. The inclusion of a large number of suitable cavities in a territory may also allow Little Owls to switch to alternative sites in the case of a stone pile collapse due to erosion, and provide alternative roosting places, both for adults and fledglings (Short 1979, Sedgwick and Knopf 1990, Schönn *et al.* 1991). The number of potential cavities was much larger in the woodland area than in the steppe area (on average almost the double number of suitable cavities) and probably decreased the importance of this variable in the analysis for the woodland area.

Although predator frequency (predator occurrence in randomly selected sites) seemed to be similar in the two study areas, in the steppe area Little Owls were apparently less able to select nest sites without predators. The relative lack of suitable cavities in this area possibly increases the probability of occupation of the same stone piles by both owls and predators, which may explain a larger proportion of breeding failures in the pseudo-steppe (see IV).

6.4. Breeding success and nest-site characteristics of Little Owls (II)

A considerable proportion (26 to 33%) of Little Owl nests monitored in both areas failed during the study period. Almost half (48%) of the failures could be attributed to predation, although it is likely that a considerable part of the remaining nest failures were associated with the same cause. While in the pseudo-steppe none of the measured variables differed significantly between successful and unsuccessful nests, in the woodland area, successful nests were found in trees with larger girth (i.e., larger DBH - diameter at breast height) than those that failed.

We confirmed with an infrared micro-camera that trees with a larger diameter usually held deeper cavities, with more sinuous and complex access tunnels than smaller diameter trees. By selecting those trees, owls possibly reduce the probability of a nest being found by predators and may increase the ability of adults and offspring to hide or to escape once predators have found the nest. Other studies have also demonstrated an inverse relationship between depth of nest cavity and losses due to predation (Moed and Dawson 1979).

Other variables related to nest sites might have influenced nesting success in both study areas but remained undetected. Orientation of the nest entrance, for instance, might have influenced nesting success in the woodland area, where entrances in nests that failed were mostly facing north-to-northeast. Prevailing winds and exposure to the sun may affect energy expenditure of adults and nestlings in some cavity-nesting species, and thus influence cavity entrance orientation (e.g. Lawrence 1967, Ricklefs & Hainsworth 1968, Inouye *et al.* 1981, Valkama & Korpimäki 1999). For many species of owls, cavity orientation seems to be unimportant (Forsman *et al.*

1984, Goad & Mannan 1987, McCallum & Gehlbach 1988, Belthoff & Ritchison 1990), while other Little Owl studies show that nest entrances may (Exo 1981, Génot 1990) or may not be (Juillard 1980) protected against wind and rain.

6.5. Prevalence of blood parasites in Little Owls (III)

In our study areas, *Leucocytozoon ziemanni* was the only relatively frequent (*ca.* 40% prevalence) haematozoan blood parasite of Little Owls. Additionally, a *Trypanosoma* spp. and an unidentified microfilaria were present in one sample each.

To our knowledge, this was the first study dealing with haematozoan infection in a free-living population of Little Owls. *Leucocytozoon ziemanni*, the only haematozoan species frequent in this population, has been reported in previous studies on owls, infecting e.g. Tengmalm's Owls *Aegolius funereus* (Korpimäki *et al.* 1993), Tawny Owls *Strix aluco* (Appleby *et al.* 1999, Krone *et al.* 2001) and Long-eared Owls *Asio otus* (Krone *et al.* 2001). It has also been reported in Little Owls admitted at rehabilitation centres (e.g. Muñoz *et al.* 1999). *Trypanosoma* spp. were also detected before in Little Owls (Muñoz *et al.* 1999), but, to our knowledge, there were no previous records of microfilaria in this species (but see Bedin *et al.* 2007).

Prevalence of blood parasites in European owls varies considerably, depending on species, geographical region and season (Krone *et al.* 2001). Although species-specific physiological and immunological characteristics may account for differences in prevalence levels (e.g. Forero *et al.* 1997, Deviche *et al.* 2001), geographic variation in prevalence is probably related to differences in parasite-specific vector abundance (e.g. Bennett *et al.* 1995, Merilä *et al.* 1995, Sol *et al.* 2000). The main documented vector of *Leucocytozoon* species are blood sucking black flies (Diptera; Simuliidae) (e.g. Atkinson & Van Riper III 1991, Greiner 1991), that use freshwater streams to reproduce (e.g. Super & Van Ripper III 1995, Urquhart *et al.* 1987). The predominantly dry climate in our study areas, with variable inter-annual precipitation, reduces the availability of suitable habitat for these type of vector populations compared to what occurs in Central or Northern Europe. As a consequence, ornithophilic black flies seem to be scarce in our study sites during

spring and summer (Bloise 1999, Grácio 2002, R. Tomé, own obs.), although they are known to occur in the region (Grácio 1984). This probably accounts for the lower prevalence we found in Little Owls, compared to that in other owl species at higher latitudes in Europe (e.g. Korpimäki *et al.* 1993, Appleby *et al.* 1999, Ilmonen *et al.* 1999)

Age was the only factor found to be associated with blood parasite prevalence in Little Owls in our study areas: a large majority of adult owls (82 %) were infected with *L. ziemanni*, while nearly all juveniles (91 %) were uninfected. This pattern has been found in other studies of haematozoa in wild birds (e.g. Korpimäki *et al.* 1993, Appleby *et al.* 1999, Garvin & Greiner 2003), and is usually associated to a lack of suitable insect vectors before juveniles fledge (Bennett *et al.* 1975, O'Dell & Robbins 1994) and/or to a longer exposure to vectors throughout life (Bennett & Fallis 1960, Greiner 1975).

We found a trend for higher prevalence in females than amongst males. Although males usually show higher susceptibility to parasite infections (e.g. Zuk 1990, Zuk & McKean 1996, Restif & Amos 2010) and weaker immune response (Grossman 1985, Olsen & Kovacs 1996) than females, prevalence of haematozoa may be, at least under certain conditions, higher in females. While our work was not designed to investigate this question, other studies showed that this difference could result from immune-depressive effects of reproductive effort in females (Norris *et al.* 1994, Korpimäki *et al.* 1995, Wiehn *et al.* 1999, Wilson *et al.* 2001).

Bill length was the only individual characteristic varying between parasitized (shorter billed) and unparasitized (longer billed) adult Little Owls. A relationship between bill length and characteristics of male territorial song has been found earlier in this species in the same area. Males with longer bills produced longer song units (Cardoso *et al.* 1998) and more aggressive responses to playbacks (Chumbinho 2002). Territorial song is generally accepted to represent an honest signal of male individual quality amongst birds (e.g. Andersson 1994, Ryan 1997). Hence, it is possible that Little Owls showing more aggressive territorial vocal behaviours are also less parasitized and better quality individuals.

6.6. Breeding density and breeding parameters of Little Owls (IV)

In the open Holm Oak woodland, we found one of the highest densities of territorial pairs reported in Europe (7.0 pairs/km²). The density was extremely high in a sub-area of 0.8 km² in this site, where 15 pairs were found (18.5 pairs/ km²). Higher densities have only been recorded in small study areas (up to 1 km²) in Central Europe (Exo 1988, Coppée *et al.* 1995, Van Nieuwenhuyse *et al.* 2008) or by using a different estimation method in southern Iberia (Fajardo *et al.* 1998). In the pseudo-steppe, the density of Little Owls (2.5 pairs/km²) was also among the highest values found in Europe (Fuchs 1986, Van Nieuwenhuyse *et al.* 2008).

The difference in the breeding density registered in the woodland and pseudo-steppe areas was probably associated with the variation in the availability of nest-sites (Exo 1992, Van Nieuwenhuyse *et al.* 2008). In the wooded area, where Little Owls nested mostly in oak cavities, suitable cavities for nesting were 1.9 times as numerous as in the pseudo-steppe, where trees were practically absent and the owls used stone piles as nest sites.

Within the woodland area, the number of territorial pairs peaked in areas with an intermediate density of oaks (*ca.* 5 oaks/ha), in spite of the higher number of cavities available in areas with more trees. We suggest that the lower density of Little Owls in plots with higher tree density may be due to predation risk. An avoidance of forests and forest edges by the owls has been interpreted as being a response to the presence of a woodland predator, the Tawny Owl *Strix aluco* (Schönn 1986, Zuberogoitia 2002, Zabala *et al.* 2006). In our study area, Tawny Owls are absent and the main predators of Little Owl nests are mammals, such as the Stone Marten (see also Génot 2001, Schönn *et al.* 1991) and the Common Genet. These predators seek shelter in tree cavities and seem to be more frequent in areas with higher tree density, as indicated by the fact that we found several times stone martens and genets roosting in nest-boxes only in the densest wooded areas.

In our study, clutch size (average 3.3; n = 15) was smaller than in many other Central and Eastern European countries (e.g. Glue & Scott 1980, Schönn 1986, Exo 1992). Likewise, the average number of fledged young per breeding pair varied

between 0.6 and 2.3 and was lower than those reported in the majority of studies from Central Europe; for example, 2.4 (Furrington 1998), 2.7 (Gassman & Bäumer 1993), 2.4 (Bultot *et al.* 2001) and 2.8 (Génot 1992). This poorer breeding success could be a consequence of smaller clutches, because the failure rate seems to be similar in our study areas and in Central Europe (e.g. Juillard 1984, Van Nieuwenhuyse *et al.* 2008).

The reduced size of our sample for the estimation of clutch size, together with the complexity of potential variations in breeding parameters induced by density-dependent effects (Bultot *et al.* 2001, Van Nieuwenhuyse *et al.* 2008) hampers the conclusion that low clutch sizes and numbers of fledged young in our study areas may be a consequence of geographical variation.

6.7. Diet of Little Owls (IV)

As in other sites in Mediterranean countries (Delibes *et al.* 1983, Mañez 1983, Manganaro *et al.* 2001), invertebrates – mostly insects – dominated the diet of Little Owls in our study areas, whereas small mammals were scarce, probably reflecting low availability. Beetles (Coleoptera) and grasshoppers and locusts (Orthoptera) were the most abundant prey, whereas earwigs (Dermaptera) and ants (Hymenoptera, Formicidae) were also numerous. In terms of biomass, Coleoptera, Orthoptera and vertebrates produced similar contributions. The relative importance of vertebrates in the diet of Little Owls was lower in our study areas than in most other study areas in Europe (e.g. Delibes et al. 1983, Mañez 1983, Génot & Bersuder 1995, Génot & van Nieuwehuyse 2002, Van Nieuwenhuyse *et al.* 2008).

6.8. Influence of habitat and environmental variables on the breeding performance of Little Owls (IV)

We registered a higher proportion of unsuccessful nests (that did not produce any fledglings) in the pseudo-steppe in two of the three study years. On the other hand, the number of fledglings per pair per successful breeding attempt differed significantly among years (being lower in 1998) but not between areas. Therefore,

differences in breeding success between habitats were probably not due to overall prey abundance or accessibility (i.e. vegetation growth), or body condition of adult and fledged juvenile owls, which were similar in both areas. A difference in predation rate might have been the main cause explaining why a larger proportion of nests in the pseudo-steppe failed to raise any young.

During our three-year study, annual precipitation varied considerably, being high in the winter of 1997/98 and during May 1998, and lower during 1999. Precipitation during the wet winter and spring of 1997/98 seemed to influence the body mass and breeding performance of Little Owls: adults were lighter during the pre-laying period, laying dates tended to be later, and also breeding success and fledgling condition (body mass of fledged juveniles) were relatively poor.

Other studies on Little Owl have reported poorer breeding performance and increased nestling mortality to be associated with unfavourable weather conditions, such as rainy periods (Glutz & Bauer 1980, Knötzsch 1988, Finck 1988; see also Bultot *et al.* 2001), probably because they affect food availability (Thorup *et al.* 2010). Long rainy periods decrease the activity of some types of prey, particularly insects, and make prey detection difficult, thus probably reducing hunting activity (Holsegård-Rasmussen *et al.* 2009) and hunting success of Little Owls. May 1998 was rather wet in comparison to other years, and this difference could be responsible for the low breeding output and the low body mass of fledged juveniles recorded by us. Likewise, the rainy winter of 1997/98 could have reduced the probability of prey capture for adult birds before the breeding season, leading to the low body reserves reported here, with potential repercussions in breeding performance. An effect of precipitation on vegetation development might have also be indirectly involved in the reduction of the breeding performance in 1998: fallows in both areas were much more grown up in that year, probably lowering prey detection chances and reducing hunting success (Finck 1990, Van Nieuwenhuyse *et al.* 2008; see also V).

Contrary to what happened in the rainy year of 1998, the body mass of both adult and fledged juvenile owls, and their reproductive output, was not negatively affected by dry conditions in 1999. A study on the Lesser Kestrel *Falco naumanni*, a species

that shares a similar invertebrate diet as the Little Owl (e.g. Rocha 1998), also reported a lower fledging success after the rainy spring of 1998 and a higher performance following the drier spring of 1999 in Southern Spain (Ferrero *et al.* 2001).

6.9. Hunting behavior by Little Owls in steppe-like habitats (V)

We studied the diurnal foraging behaviour of Little Owls in the Holm Oak woodland and in the pseudo-steppe in 1999, the driest year involved in our research (see IV). Both habitats differed structurally, as the woodland held generally higher perches, along with higher and denser ground vegetation, than the pseudo-steppe. The abundance of the main invertebrate groups of prey was also different, as Orthoptera were more numerous in the pseudo-steppe and Coleoptera in the woodland (see also IV).

Perch height is one the main factors that influences foraging behaviour in predators that adopt a perch-hunting strategy (e.g. Andersson 1981a, Fitzpatrick 1981, Rice 1983, Thiollay & Clobert 1988, Andersson *et al.* 2008). Perch height is particularly important in the case of species that use mostly visual cues to detect their prey, as has been suggested for Little Owls (e.g. Ille 1983, Norberg 1987, Van Nieuwenhuyse *et al.* 2008). In general, a higher perch renders a larger field of view allowing the detection of more distant prey (e.g. Greig-Smith 1983, Moreno 1984, Thiollay & Clobert 1988, Sonerud 1992; see also Andersson 1981a). If more distant prey are physically accessible, than the resulting increase in detectability will also result in increasing prey availability (e.g. Gillings 2004).

In our study, the between-habitat differences in perch height did not affect the number of prey items (invertebrates) detected by Little Owls, since we observed a similar number of prey capture attempts per hour in each area. As hunting success was also alike in both habitats, the owls achieved a similar prey capture rate per time unit. Distances at which invertebrates were captured were also similar in both areas, indicating that prey detectability for Little Owls probably did not vary. Therefore, the

increase in perch height by itself was not enough to provide increased prey detectability in the woodland.

In the woodland Little Owls utilized a wide variety of perches at different heights, including big stones on the ground. In spite of the maximum available perch height (highest branches of holm oaks) reached approximately 5 m, owls selected much lower perches (average 2.67 m). This suggests the existence of an optimal foraging height (e.g. Andersson 1981b, Carlson 1985, Andersson *et al.* 2008)*,* above which hunting would not result as rewarding. In habitats where grass is much taller than prey, vegetation hampers prey detection by predators, even from increased heights (Andersson *et al.* 2008). The facts that in the woodland we found no correlation between perch height and attack distance and that in territories with more developed ground vegetation, Little Owls produced attacks closer to their perches, corroborate the hypothesis that in this habitat vegetation was, indeed, reducing the available visual field and prey accessibility (e.g. Thiollay & Clobert 1988, Andersson *et al.* 2008).

In the pseudo-steppe, where ground vegetation was lower and less dense, Little Owls hunted from highest available hunting perches, using the tops of stone piles (average 0.77 m). Similarly to what was found in other studies (e.g. Greig-Smith 1983, Moreno 1984, Thiollay & Clobert 1988, Sonerud 1992; see also Andersson 1981a), in this habitat there was a positive correlation between perch height and distance to prey attacked. Moreover, detection perches were higher than giving-up perches, suggesting that Little Owls could benefit from choosing the highest available perches to forage, as this probably resulted in an increased chance of detecting and attacking prey. The possibility of selecting an optimal perch height in the woodland probably explains why no difference was found between the height of detection and giving-up perches in this habitat (Bye *et al.* 1992, Sonerud 1992).

In the pseudo-steppe detection perch height correlated negatively with the height of ground vegetation. This result suggests that also in this habitat vegetation may difficult visual detection of prey (Andersson *et al.* 2008), even though to a smaller extent than in the woodland due to the reduced range of variation in height. In these

cases (small prey imbedded in dense vegetation and lack of high perches), Little Owls perhaps compensate losses in visual detectability by increasing the efficiency of acoustic detection, foraging from lower heights (e.g. Rice 1983, Bye *et al.* 1992, Andersson *et al.* 2008).

In our study we collected other indications that Little Owls could be using acoustic cues while detecting prey. Search time was longer in the pseudo-steppe, although there were no inter-habitat differences in the overall abundance of invertebrate prey (and in fact Orthoptera, which are more conspicuous and diurnally active prey, were more abundant in the pseudo-steppe), a factor that may determine variations in the rate of prey detection (Fitzpatrick 1981). Instead, longer detection times may reveal that Little Owls frequently used acoustic cues to detect prey in this habitat (e.g. Bye *et al.* 1992). On the other hand, we found no positive correlation between perch height and both detection and giving-up times, in any of the studied habitats. These correlations would be expected for a predator relying mostly on visual cues, because individuals foraging from higher perches take longer to search a greater detection area and also to compensate for a reduction in detection density due to distance to prey (Andersson 1981a, Fitzpatrick 1981, Moreno 1984). Additionally, for a visual predator giving-up distance should reflect prey detectability offered by the abandoned perch (Andersson 1981a) and therefore correlate with perch height (e.g. Fitzpatrick 1981, Moreno 1984), a correlation that was not found in the woodland or in the pseudo-steppe. Finally, the selection of perches significantly lower than those available in the woodland may also indicate that Little Owls are hunting based on acoustic detection to some extent - predators relying on acoustical cues should favour lower foraging heights (e.g. Andersson 1981a, Rice 1983, Bye *et al.* 1992), due to the quadractical decline of the acoustic field of prey detection with increasing height (e.g. Rice 1983).

7. Conclusions

Although Barn Owls are mainly sedentary throughout Europe, my results show the occurrence of strong seasonal variations in their abundance at a local scale, mainly related to dispersal movements of significant numbers of juvenile individuals (I). To my knowledge, the Ponta da Erva farmland area is the only place where such a dramatic change in the abundance of this species has been observed and where such concentrations of juvenile Barn Owls take place.

The particular location of the Ponta da Erva farmland area, in an estuary, may constitute a decisive factor to the importance this area holds for Barn Owls and to the patterns of abundance variation that I detected there. Possibly, the stripes of well-conserved habitats (like natural hedges) that margin the river Tagus and its tributaries hold higher densities of prey than surrounding open fields or woodland, attracting juvenile owls and acting as dispersal corridors. Owls dispersing from territories in the vicinity of the Tagus estuary in the south/southwest direction (as frequently observed in continental Europe; Roulin 2002) would then tend to follow these favourable hunting habitats till the Ponta da Erva area, which would work as a bottleneck. The same type of pattern may be observed in other raptor species, which are almost absent in the area during the reproduction period, but extremely abundant outside the breeding season (e.g. Black-shouldered Kite *Elanus caeruelus*, Common Buzzard *Buteo buteo* and Eurasian Kestrel *Falco tinnunculus*; Leitão *et al.* 1998, Catry *et al.* 2010).

The importance of the geographic location as a determinant factor associated to the occurrence of large numbers of Barn Owls in my study area seems to be confirmed by recent observations. In fact, and despite marked habitat changes in the area during the last 15 years (namely the very significant increase in the area occupied by rice fields, replacing sunflower crops and pastures), the patterns of abundance variation and the number of owls observed during the dispersal period have remained mostly unaltered (R. Tomé, own obs., F. Machado pers. com., Rabaça *et al.* 2010, Rabaça *et al.* 2011). Ongoing telemetry studies seem also to confirm the existence of a clearly non-random pattern of dispersal of Barn Owl juveniles from

territories in the vicinity (20-40 km) in the direction of the estuary farmlands, where they may stay for a variable period of time, but usually for less than two months (I. Roque pers. com., Rabaça *et al.* 2010, Rabaça *et al.* 2011).

Landscape heterogeneity in lowland farmland, including both traditional (e.g. extensive pastures) and modern (e.g. irrigated sunflower fields) practices and a vast system of ditches and fences bordered by dense strips of vegetation seems to be extremely favourable for Barn Owls (I). This was indicated by the large number of Barn Owls observed in my study area during a considerable part of the year and by the fact that they foraged differently in distinct types of habitats throughout the year, depending on the structure and development stage of their vegetation. My study on habitat use by Barn Owls, the first involving such a high number of observations from different individuals, showed that none of the habitats was preferred at all seasons. Therefore, Barn Owls clearly benefited from a mosaic of land use types and are well adapted to explore the changes in vegetation development and prey availability associated to different agro-pastoral practices during the annual cycle. While other studies have underlined the importance of habitat mosaics for terrestrial fauna in general (e.g. Law & Dickman 1998), other Barn Owl studies in the Iberian Peninsula showed that a higher diversity of habitats is associated with a higher probability in the occurrence of breeding territories in this species (e.g. Martínez & Zuberogoitia 2004a, Roque & Tomé 2004). Nonetheless, further studies are required to show how habitat heterogeneity affects home range composition and size, and breeding success.

Other lowland farmland areas may also constitute highly favourable areas for dispersing Barn Owls, at least in Southern Europe. However, I could not find any other study reporting a similar pattern in the species occurrence. In my study site, the provision of nest boxes is likely to result in a growth of the breeding population of Barn Owls, since remaining habitat conditions seem to be very advantageous (Martínez & Zuberogoitia 2004a). Nest boxes are readily used by Barn Owls (Bunn et al. 1982, de Bruijn 1994, Ramsden 1998), and considering the high number of

juvenile birds that occur in my study area during dispersal, it is probable that the local population could increase very rapidly.

Several studies have focused on the effects of landscape or home range-scale variables on population dynamics and on the use of space by Little Owls (e.g. Van Nieuwenhuyse & Bekaert 2001, Van Nieuwenhuyse & Leysen 2001, Van Nieuwenhuyse *et al.* 2001, Ferrus *et al.* 2002, Martínez & Zuberogoitia 2004b, Sunde *et al.* 2009, Thorup *et al.* 2010). With respect to nest-site attributes, Little Owls are described as being rather eclectic, using a wide variety of cavities (Van Nieuwenhuyse *et al.* 2008). Although some studies have described the characteristics of utilized holes, there was no previous work comparing these features with those available at each site and thus investigating which variables are important in the nest-site selection process by the species. My results show that smaller-scale features associated with nest sites may be important and should be considered in the management of Little Owl habitat (II). In particular, management guidelines directed towards Little Owl conservation in habitats such as Holm Oak woodlands and pseudo-steppes, should involve the preservation of large-diameter trees and stone piles made of larger stones, as well as the maintenance of several alternative suitable cavities in the owl territories. Furthermore, my study indicates that predation pressure constitutes a major driving force in the selection of nest-site characteristics, similarly to what has been shown previously in some other secondary cavity-nesters.

Blood parasites can have negative fitness impacts on a bird host and negatively impact its reproductive success (e.g. Korpimäki *et al.* 2002, Ishak *et al.* 2008). From a global perspective, cumulative effects of blood parasites on individuals can have serious consequences on host populations (Remple 2004). Nevertheless, my research on blood parasites of Little Owls was the first on this subject on a wild population of this species (III). It revealed a large prevalence of *Leucocytozoon ziemanni*, a haematozoan found previously in Little Owls admitted at rehabilitation centres (Muñoz *et al.* 1999). This research also exposed possible relationships between the prevalence of blood parasites and other factors, such as sex and bill length, that deserve further investigation. While the first case may involve immune-depressive

effects associated to the reproductive effort of individuals, the second case may suggest, indirectly, that infection may be related to the characteristics of territorial song in Little Owls. An influence of parasite load on territorial song features, a sexually selected male trait, has been found previously in passerines (Spencer *et al.* 2005) and owls (Redpath *et al.* 2000).

Steppe-like habitats in southern Portugal, such as open Holm Oak woodlands and cereal pseudo-steppes, hold high breeding densities of Little Owls and are thus important for the species' conservation in Europe (IV). Morevover, Little Owl populations in this region occupy large, continuous areas (Equipa Atlas 2008), hence being more resilient and less prone to variation in demographic mechanisms such as local survival and immigration than more isolated or confined populations (Schaub *et al.* 2006).

The traditional practices of land-use management used in this region create a large number of suitable nest sites that sustain these high breeding densities. Breeding density was higher in the open woodland, while in the pseudo-steppe nest-site availability was probably limiting. In the more densely wooded areas, however, the owl density was lower, possibly due to a higher risk of predation by mammals. As failure and predation rates were similar to those verified in other studies, it is possible that the relatively low values of breeding success obtained in my study reflect geographical gradients observed in Europe (Van Nieuwenhuyse *et al.* 2008).

Higher predation rates seem to explain a poorer breeding performance of Little Owls in the pseudo-steppe compared to the Holm Oak woodland (IV). The fact that nest-site availability is a limiting factor in the pseudo-steppe forces Little Owls to use the same stone piles also selected as roosts by potential nest predators (II), hence increasing predation risks of eggs and chicks.

In my study sites, Little Owls preyed mainly upon invertebrates, especially beetles (Coleoptera) and grasshoppers and locusts (Orthoptera) (IV). Despite of marked structural differences between the two steppe-like habitats studied – a treeless pseudo-steppe and Holm Oak woodland - Little Owls achieved similar prey detectability and hunting success (i.e., energy intake rate; Wakeley 1978, Andersson

1981a), in both areas (V). My results showed that Little Owls present plasticity in their hunting behaviour, adopting different foraging strategies successfully adapted to distinct habitats. While in the woodland owls foraged mostly from branches of an optimal height lower than that available, in the pseudo-steppe they hunted from the highest available perches in the top of stone piles. Differences in hunting behaviour were likely to be influenced by the effect of ground vegetation in visual detection of prey and by the interaction between this effect and the range of available perch heights. Additionally, my study indicates that auditory location of prey may be more important for Little Owls than previously suggested by other authors (Van Nieuwenhuyse *et al.* 2008), which should be investigated through laboratory research. Although my study was restricted to the diurnal period, the fact that breeding success and body mass of both adults and fledged juveniles did not differ between habitats (see IV) suggests that hunting success during dusk and night should also be similar in the woodland and pseudo-steppe.

As in other studies, I confirmed that adverse weather (high precipitation) in winter and spring affects negatively the breeding performance of Little Owls (IV). On the contrary, my results indicate that this species is well adapted to the marked seasonality of precipitation and to the relative intensity of summer drought in Southern Iberia. In fact, and despite the fact that water is often considered a critical limiting ecological factor in this region (Blondel & Aronson 1999), the body condition and breeding success of Little Owls were higher in a dry year. This result is a practical confirmation that Little Owls favour warm, or even semi-arid, conditions (Van Nieuwenhuyse *et al.* 2008), like those found in the predominantly dry steppe-like Iberian habitats, which are in some aspects similar to the steppes and semi-deserts of the primary habitats in which the species may have evolved (Exo 1992). Adaptation to this type of conditions should also allow a positive response to predicted future climatic changes, leading to a possible increase in the species distribution range in Europe by the late 21st century (Huntley *et al.* 2007).

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