Habitat change and climate effects on the European Roller (*Coracias garrulus*); implications for conservation

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Thesis submitted for the degree of Doctor of Philosophy at the University of East Anglia, Norwich, UK. September 2016.

Contents

Acknowledgments

It has been a privilege to spend four years studying at UEA, as part of an excellent and outgoing research group. I’d firstly like to thank my primary PhD Supervisor Aldina Franco, for giving me the opportunity to work on the project and for her unwavering guidance and support throughout. I’d also like to thank the rest of my supervisory team; Ines Catry, Simon Butler, and Phil Atkinson, for their constructive input and guidance. Special thanks also go to Derek Pomeroy and Frank Walsh, whose historic work upon Rollers in Cyprus has underpinned much of my research.

During the project I have had the good fortune to meet and work with Roller researchers from across Europe (including Deseada Parejo, Jesus Avilés, Anna Folch, Flavio Monti, Francesco Pezzo, Timothee Schwartz, and Edmunds Racinskis); their advice and input has always been gratefully received. I would particularly like to thank several of them for allowing me to use their hard-collected data in Chapter 2 of this thesis.

I am extremely grateful for the skilled guidance provided to me in the field by Chris Hewson, Teresa Catry, and members of my supervisory team. I’d also like to thank all of the field assistants and MSc students (Alli, Alessandro, Harry, and Pedro) who have assisted in data collection during the project, and who also made fieldwork a much more enjoyable and less solitary affair. Several friends (Emmi, Spyros, Christos, and Heather) also provided occasional, but much appreciated, help in the field (and even more appreciated KEOs afterwards).

A special thank you also to the staff of the Environmental Studies Centre at Kritou Tera, most especially Katerina, for the immense help they provided logistically throughout my field research. The people of Kritou Tera and outlying villages were welcoming and engaging throughout the summer seasons spent in my home away from home. Mr Doros and his family, in particular, were hospitality personified. Christina Ieronymidou’s input at the start of the project also proved extremely helpful.

The staff at BirdLife Cyprus provided essential advice throughout the project, and I would particularly like to thank Martin Hellicar for his inordinately helpful input. The dry humour and ringing assistance provided by the (much missed) Alan Crabtree and Mel Preston were also much appreciated, as was the opportunity to ring at some of their monitoring sites. Panicos Panayides of the Cyprus Game Fund provided invaluable assistance during the research permit application process, as well as

logistical support on the ground. Also thank you to Alex Kirschel for the opportunity to fondle Scops Owls.

A host of friends and colleagues at UEA have provided much appreciated guidance and support throughout my studies. Special mentions must go to James Gilroy, Cat Morrison, Jenny Gill, John Burnside, Will Nash, Ricardo Correia, Karen Hornigold, and Osgur McDermot-Long for being patient in the face of regular statistics and R-related questioning. My office mates and research group colleagues have also helped keep me sane throughout; thank you Mark, Vanessa, Karen, Nick, Nathalie, Maxim, Martin, Maira, Yoav, Elli, and Marta (and everyone else in CEEC).

Thank you to Iain Barr for both his valued friendship and his loan of ringing equipment for use in the field (plus the small matter of training me to be a certified ringer during my time at UEA). The rest of the UEA Ringing Group (most especially Dave Andrews, Will Soar, and Jen Donelan) have also provided much needed training, support, and entertainment. A special thank you must also go to my Dad and Malcolm for building forty excellent nest boxes for use in Cyprus (the Rollers and Scops Owls certainly found them to their tastes) and to my Mum, for her unconditional support, love, and cake.

I cannot sufficiently express the gratitude I feel to my current and former housemates (Oli, Will Nash, Iain, Giulia, Sara, Amy, and Matthis) for their friendship and support, both upon my arrival in Norwich and since. I wouldn’t have been able to do this without you, or the many other good friends I’ve made since moving to this Fine City (especially Peter, Jenny, Holly, Emily, Rania, and Rachel). Friends from further afield have also been a supportive presence throughout (Will Francis deserves special mention, for many reasons).

Almost last, but by no means whatsoever least, I would like to give heartfelt thanks to my good friend and Roller PhD colleague-in-arms; the inestimable Tom Finch. It’s been both a pleasure and a privilege to work and study alongside you. Tom’s Tours forever!

This study was funded by a CASE studentship from the Natural Environment Research Council (NERC), in partnership with the British Trust for Ornithology (BTO). The author was also the beneficiary of a three year A.G. Leventis Foundation Scholarship. All photographs within this thesis were taken by the author unless otherwise indicated.

Abstract

Global climate change, and associated habitat destruction and degradation, comprise 2 of the most important drivers of declines in biodiversity, and understanding their impact upon threatened taxa is an important objective for conservation initiatives. The farmland and migratory bird assemblages of Europe have both declined dramatically over the last century, and improving our understanding of the effects of climate and land use change upon them is of import when implementing successful conservation interventions. We focused upon the European Roller (Coracias garrulus), a migratory farmland species which has experienced large-scale population declines and range contractions across Europe, investigating the effects of habitat and climate change upon the species' breeding biology and distribution. We modelled the effects of climatic conditions at key phenological points in the species' annual cycle upon breeding parameters across its Mediterranean range and found that temperature comprised the key climatic correlate of clutch size and fledging success. This suggests that changing temperatures will lead to declines in Roller productivity across the Mediterranean. We produced a Habitat Suitability Model for the species on Cyprus and confirmed that the island's Protected Area network incorporates a higher proportion of high value Roller habitat than external areas. We also identified high value areas currently external to the Protected Area network. We used novel Global Positioning System technology to quantify Roller home ranges in Cyprus and to identify optimal and avoided foraging habitat types. The importance of traditional farmland and grassland habitats for Rollers was confirmed, as was the negative impact of urban habitat upon Roller productivity. Nest site selection was also investigated for Rollers in Cyprus and Portugal, with our results indicating that selection occurs at the cavity level rather than landscape scale. Rollers in both populations preferred nest sites with smaller entrances, potentially due to decreased predation risk. High levels of nest site competition were identified in Portugal, and evidence of nest site limitation in both the Cypriot and Portuguese Roller populations was observed. Key overall recommendations from the study comprise the promotion of traditional farmland and grassland habitats within European agri-environment schemes, and the extension/initialisation of artificial nest site schemes for the Roller in Cyprus and Portugal.

‘Somewhere over the rainbow, bluebirds fly…’

(Over the Rainbow, E.Y.Harburg 1939)

Chapter 1: Introduction

1.1 Global environmental change and the biodiversity crisis

Humanity's impact upon the world's biodiversity has increased disproportionately over the previous 2 centuries (Dirzo et al. 2014), with indications that we are now entering a global extinction crisis (Barnosky et al. 2011). Anthropogenic habitat loss, fragmentation, and degradation have been identified as some of the key drivers of global biodiversity decline (Butchart et al. 2010; Foley et al. 2005). These are compounded by the varied impacts of global climate change (Thomas et al. 2004), with world temperatures predicted to rise by >1.5°C within the next century (Collins et al. 2013). These drivers have a global impact, but their effects are likely to be exacerbated within the world's sensitive biodiversity hotspots, such as the Mediterranean region (Sala et al. 2000).

Monitoring the impact of global environmental change, and the effects of any subsequent conservation intervention, upon the world's biota requires the use of robust ecological indicators (Butchart et al. 2010). Birds comprise a good taxon for such a use, as they are a diverse group which can respond quickly to changes in ecosystem quality (Szabo et al. 2012; Kati et al. 2004). Several countries also have long-running national monitoring schemes in place (see www.bto.org/volunteer-surveys/bbs and www.audubon.org/conservation/science/christmas-bird-count for examples) providing an effective temporal baseline. Birds are a generally well-known, and often valued, taxon amongst the general public (Dallimer et al. 2012), and are therefore also a good group to incorporate into 'citizen science' monitoring programmes.

Our understanding of the spatial ecology and habitat requirements of threatened bird species has increased hugely over the past decade following the advent of miniaturised solar geolocators (Bridge et al. 2013) and Global Positioning Systems (Tomkiewicz et al. 2010), and globally accessible remote sensing technology (Turner et al. 2003). The use of these technologies, alongside more traditional ecological field study methods (in areas such as food and nest site availability), are now allowing researchers to integrate pressures exerted across species' entire annual cycles (Tøttrup et al. 2012) into conservation planning and policy.

1.2 Bird declines in Europe

The European bird population is well monitored via the collaborative Pan-European Common Bird Monitoring Scheme (PECBMS: www.ebcc.info/pecbm.html). PECBMS data is used to produce a variety of ornithological indicators of European ecosystem health, including the Common Bird, and the Common Farmland Bird, Indices. These show that farmland bird populations have continued to decrease (Hayhow et al. 2015), following a severe, long-term, decline during the previous century (Donald et al. 2001). Reasons for these declines are primarily focused upon the intensification of Europe's agricultural systems (Chamberlain & Fuller 2000; Donald et al. 2001), and highlight the importance of the continent's remaining traditionally managed farming landscapes (Doxa et al. 2010; Verhulst et al. 2004).

In addition to farmland species, one other group of European breeding birds has experienced severe, long-term, population declines; the trans-Saharan migrants (Sanderson et al. 2006; Vickery et al. 2014). It is unclear whether this is a consequence of habitat change or deterioration, or the cumulative effects of global climate change upon the phenology of migrant species (Knudsen et al. 2011). Several threatened European bird species, including the Turtle Dove (*Streptopelia turtur*), comprise both farmland birds and trans-Saharan migrants and are consequently subject to an increased level of threat (Hayhow et al. 2015).

1.3 European farmland conservation

Europe's agricultural landscapes are anthropogenic by definition (Stoate et al. 2001) and their strategic conservation is primarily moderated within EU member states through the provisions of the Common Agricultural Policy (CAP; European Commission 2012). The CAP incorporates 2 main routes through which agricultural landscape management can be carried out: Pillar 1, which focuses on market and income support, and Pillar 2, which promotes rural development (Poláková et al. 2011).

Historically, Pillar 2 has been identified as the main agent through which actions benefitting biodiversity can be accessed, including the promotion of sympathetic land management practises and the enactment of agri-environment schemes, aimed at improving both farmland productivity and ecosystem health (Poláková et al. 2011). Nevertheless, several Pillar 1 measures, including the education and training of farmers, and cross compliance with other non-farming specific environmental policies, may also benefit farmland ecosystems (Poláková et al. 2011).

In addition to the CAP provisions, several EU legislative measures are of relevance to farmland conservation, including the designation of Protected Areas under the auspices of the Birds and Habitats Directives (Donald et al. 2007). Public payments arising from EU LIFE+ projects (www.ec.europa.eu/environment/life/) and market based measures may also directly benefit farmland ecosystems.

1.4 The European Roller

The European Roller (*Coracias garrulus*; henceforth Roller) is the primary focus of the research incorporated within this thesis. It is a trans-Saharan migrant predominantly associated with traditional farming habitats across its European breeding range, and as such can be classified within both of the most threatened categories of birds in Europe. The following section provides an overview of the species' distribution, ecology, population trends, conservation actions, and threats, and will inform the data chapters which follow.

Ecology and distribution

The Roller is the sole European representative of the *Coraciidae* family (Fry et al. 1999) and comprises 2 migratory subspecies. The nominate subspecies breeds from Morocco, west across southern, north-eastern, and eastern Europe and Asia Minor, through to north-west Iran and south-west Siberia (Figure 1.1a; Del Hoyo et al. 2001). The *semenowi* subspecies breeds across much of Iran, Iraq, the central Asian republics, and into north-west China (Del Hoyo et al. 2001). Both subspecies mainly winter in savannah landscapes in sub-Saharan Africa (Figure 1.1b; Cramp & Simmons 1998), with part of the *semenowi* population migrating through, and occasionally wintering, in north-western and western India (Narayanan et al. 2008). The research incorporated in this thesis exclusively concerns the nominate European subspecies.

The Roller is an obligate secondary cavity nester, reliant upon other bird species (specifically woodpeckers across much of its European range) to excavate nest holes in tree trunks and branches (Cramp & Simmons 1998). In locations where primary excavators are absent, or mature trees have been removed from the landscape, the species readily adopts a range of other suitable nest types (Figure 1.2), including cavities in walls and buildings, eroding holes in river banks and cliff

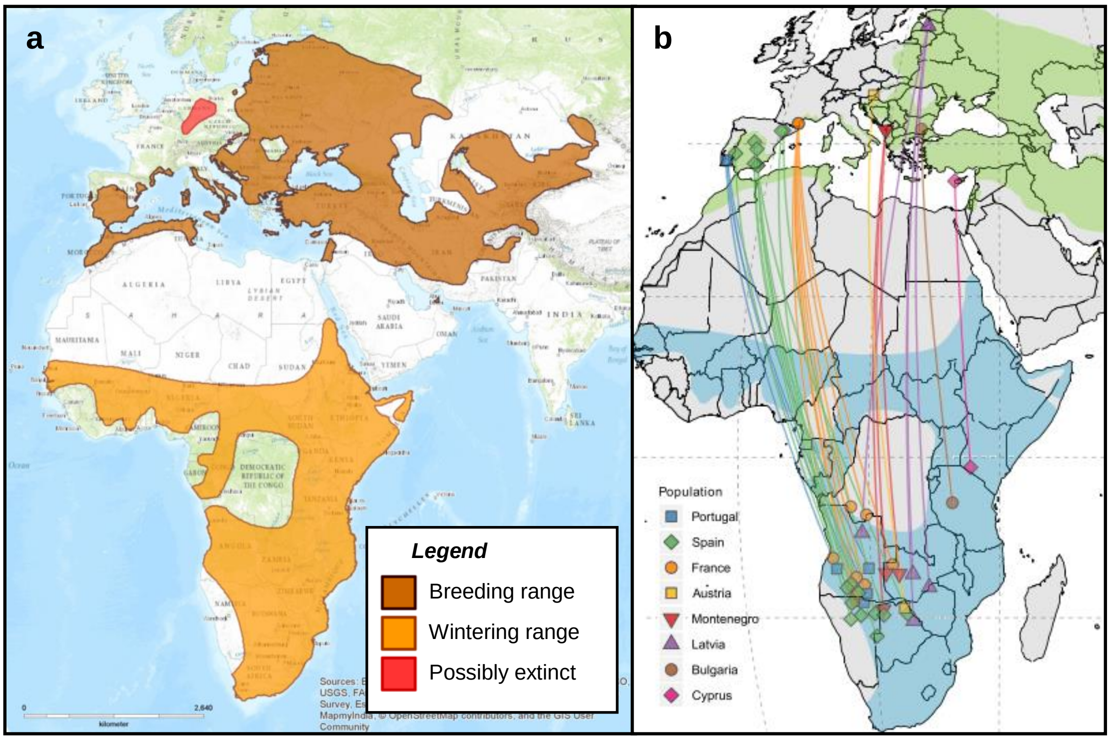

Figure 1.1: Distribution of the European Roller: (a) current global breeding and wintering range, and; (b) migratory connectivity of European populations; note the coloured lines do not denote migration routes (adapted from BirdLife International 2015 and Finch et al. 2015, respectively).

faces, natural rot holes in mature trees, and artificially provisioned nest boxes (Bouvier et al. 2014; Butler 2001; Del Hoyo et al. 2001; Rodriguez et al. 2011).

The species is primarily a sit-and-wait predator of large terrestrial invertebrate prey (Cramp & Simmons 1998), although individuals are also commonly observed sally-gleaning from taller vegetation and foraging aerially, in a similar manner to hirundines, in the presence of abundant winged invertebrate prey (Del Hoyo et al, 2001). Prey composition varies between populations, although the few studies undertaken indicate that large Orthoptera, Coleoptera, and Araneae comprise key prey taxa (Avilés & Parejo 1997; Tidmarsh 2003; Lüütsepp et al. 2011a). Additional prey items identified in the Cypriot Roller population include Scolopendrids, small to medium-sized lizards, amphibians, nestlings of other bird species, rodents, and (very rarely) fruit (Cramp & Simmons 1998; P.Saunders *unpub.data*).

Due to their requirement for abundant large invertebrate prey, and structures suitable for nesting and hunting from (Avilés & Costillo 1998), the Roller is mainly associated with traditionally managed farmland and pasture within its European range (BirdLife International 2012). Nevertheless, the species utilises a range of habitat types

Figure 1.2: Examples of typical nest sites used by Cypriot Rollers in the absence of primary cavity excavating species: (a) abandoned and partially-used buildings; (b) eroding cliff faces, and; (c) rot holes in mature carobs (Ceratonia siliqua). Disused woodpecker holes and artificial nest boxes are commonly used elsewhere in the species range.

across Europe, including open, lowland, pine woods in parts of the Mediterranean and the Baltic states (Del Hoyo et al. 2001).

Upon arrival on their European breeding grounds in spring, individuals spend several weeks in pair-bonding activities (Cramp & Simmons 1998). Nevertheless, recent research has indicated that up to approximately 6.5% of nests incorporate chicks arising from extra-pair copulation (Sanchez-Tojar et al. 2015). Egg laying occurs in late spring, followed by an approximately 2.5 week long incubation period (Cramp & Simmons 1998; Del Hoyo et al. 2001). Clutch sizes vary across the species European range, with an average of 3 to 4 eggs laid, with a 2-day interval between each egg (Cramp & Simmons 1998). Once the eggs have hatched, the chicks are provisioned in the nest for approximately 3.5 weeks prior to fledging (Figure1.3; Fry et al. 1999).

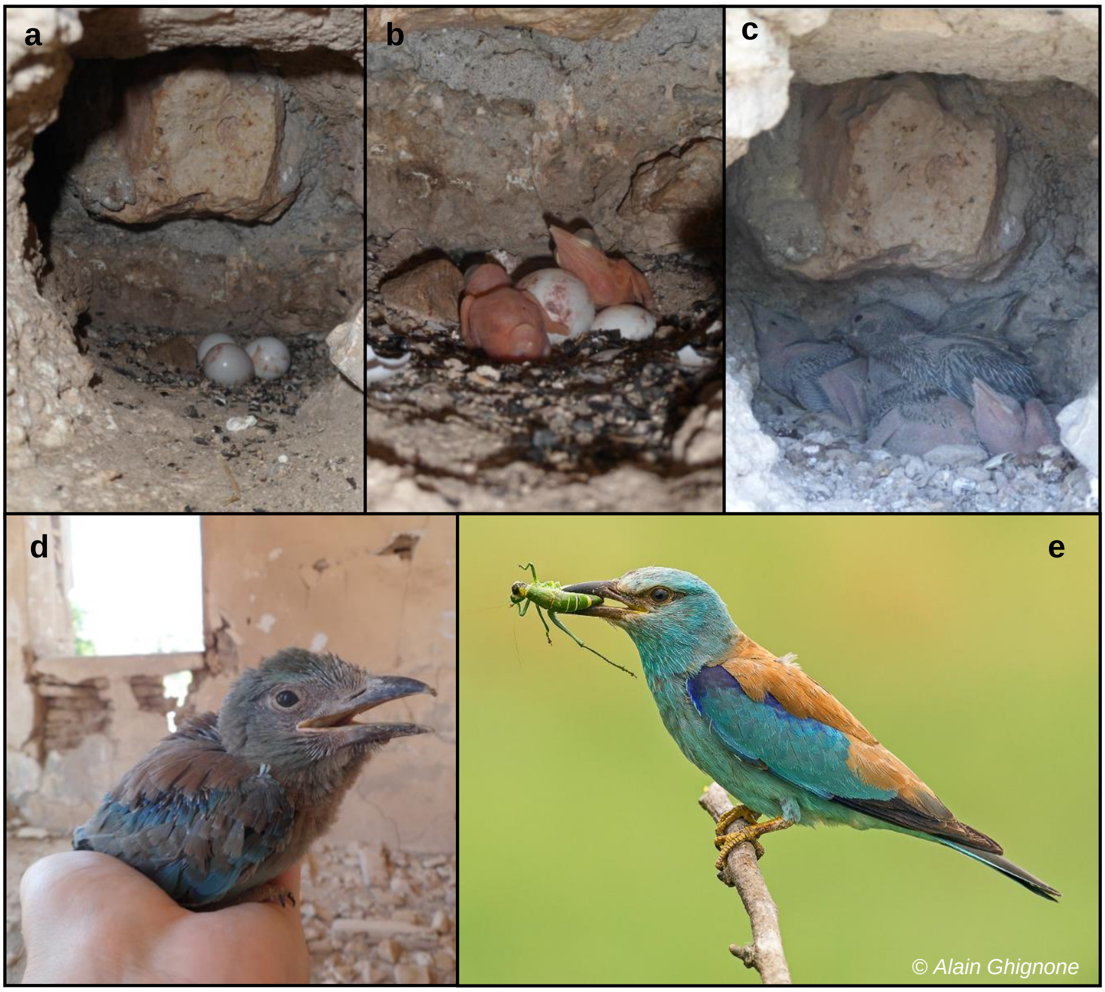

Figure 1.3: Developmental stages during the Roller breeding season: (a) Roller eggs in a semi-natural nest cavity; (b) recently hatched chicks; (c) approximately 10 day old chicks; (d) approximately 20 day old chick, and (e) adult Roller with typical prey item.

Chicks are highly susceptible to predation until the age of approximately 3 weeks, by which time they are able to protect themselves from most potential nest predators. Predators include rats (*Rattus spp*.), martens (*Martes spp*.), snakes, lizards, and corvids (Del Hoyo et al. 2001; Parejo & Avilés 2011; Lüütsepp et al. 2011).

The Roller is a diurnal migrant which usually travels in small flocks during migration. Large northward movements of the species have however been noted in early spring in east Africa (Feare 1983), and southwards alongside the eastern Black Sea in early autumn (where c.500 migrating individuals have been noted passing in a single day: https://www.facebook.com/batumiraptorcount/photos/pcb.735654573239706/735654289906401/?type=3&theater). Migration strategies differ between populations (Finch et al. 2015), with some wintering in south-west Africa and others in the east. Migration routes also vary, with some western Mediterranean populations following the north-west African coastline, whilst others directly overfly the Sahara or follow the Nile Valley (Catry et al. 2014; Emmenegger et al. 2014; Finch et al. 2015; Rodríguez-Ruiz et al. 2014). Birds from Latvia have recently been shown to undertake a ‘loop migration’, heading north through the Arabian Peninsula in spring, but following a more direct southerly autumn migration route (Finch et al. 2015). Other populations follow similar routes during both their spring and autumn migrations. Important staging sites exist for all populations in the Sahelian region, especially in the vicinity of the Lake Chad basin (Rodríguez-Ruiz et al. 2014).

European distribution and population trends

The European breeding distribution of the Roller historically ranged across much of southern, central, and eastern Europe, extending north to southern Sweden and across the Baltic states (Del Hoyo et al. 2001). However, during the last century the species underwent a long-term range contraction (Figure 1.4a), with the species now extinct in Sweden, Denmark, Germany, the Czech Republic, and Slovenia (BirdLife International 2015).

The species has almost disappeared from several of the Baltic states, with the Estonian population declining from 50 to 100 pairs in 1998 to fewer than 5 in 2012 (BirdLife International 2015; Lüütsepp et al. 2011). The Lithuanian population declined from >1,000 pairs in the 1970’s to <20 pairs in 2012, with the historically larger Latvian population undergoing a similar level of decline (BirdLife International 2015). A tiny remnant population survives in Austria (Sackl et al. 2004), and the Portuguese population has declined to fewer than 100 pairs, largely breeding in a

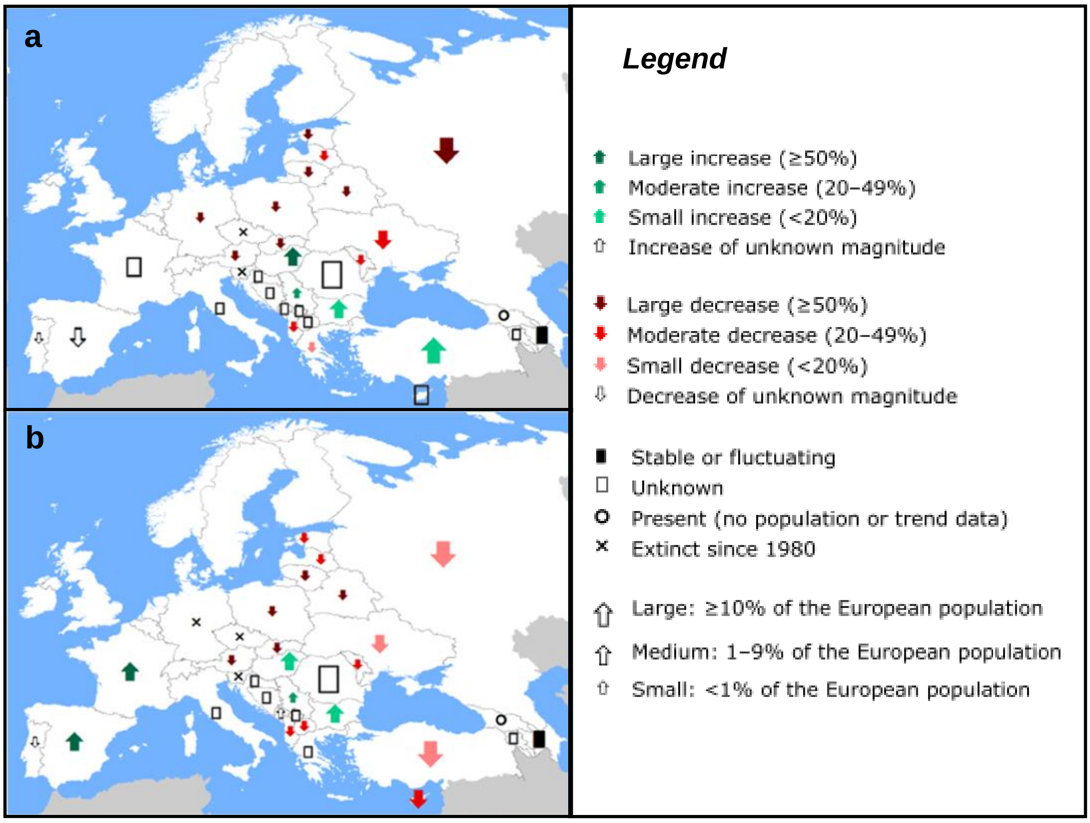

Figure 1.4: Status and trends of Roller populations across Europe: (a) long-term, and; (b) short-term (adapted from BirdLife International 2015).

single Protected Area (Catry et al. 2011). With the exceptions of Bulgaria, Hungary, Serbia, and Turkey, every population within the species' European range has either undergone a long-term decline or an unknown directional shift (BirdLife International 2015).

Short-term trends for the species vary (Figure 1.4b), with continued declines across most of Europe (supporting 40% of the species global population) bolstered by large increases in the breeding populations of Spain and France, following conservation intervention (BirdLife International 2015; Tron et al. 2008). Small increases have also been reported in the important Turkish population (comprising the largest in Europe; 12,000 to 30,000 pairs) and that in Bulgaria (2,000 to 8,000 pairs).

Nevertheless, only approximately 30% of the 32 countries within the species European range reported 'good' quality population estimates during the most recent assessment, with population estimates from Turkey, Russia, Romania, and Azerbaijan (cumulatively supporting 70% of the Roller population in Europe) described as 'poor' (BirdLife International 2015). The important Russian population (16% of the European total) is estimated to have declined by 5 to 30%, whilst the

Cypriot population (3% of the European total) has declined by 30 to 50%. No trends are provided for the important Romanian population (10% of the total; BirdLife International 2015).

Conservation status and legislative protection

Following concerns raised about the Roller's population trajectory, the species' conservation status was upgraded from Least Concern (i.e. widespread and abundant; IUCN 2012) to globally Near Threatened in 2005 (IUCN 2008). However, the most recent assessment of the species global population trend (BirdLife International 2015) resulted in the Roller being downgraded to Least Concern once more. The downgrading was based upon a deceleration in the decline of the European population (although still identified as comprising ≤20% within 3 generations), and a reassessment of the species' status in central Asia and the Middle East. The population assessments and postulated trends for the majority of central Asian populations are however identified as being of 'poor' quality and, when set against a backdrop of continued long-term and short-term declines across the majority of the species European range, the allocation of Least Concern status is perhaps premature.

The Roller is afforded legal protection in all EU countries through a variety of European conventions, namely:

- Annex I of the Bern Convention on the Conservation of European Wildlife and Natural Habitats;
- Annex I of the Council Directive on the conservation of wild birds (79/409/EEC) – the EU Birds Directive, and;
- Appendix I of the Bonn Convention on the Conservation of Migratory Species of Wild Animals.

The Birds Directive requires that special measures are taken by signatory states to protect the habitat and breeding populations of listed species, including the Roller, through the designation of Special Protection Areas (SPA's). The coverage of SPA's in terms of proportion of the Roller population varies between member states (Kovacs et al. 2008), although additional non-statutory protection is afforded additional locations through their designation as Important Bird and Biodiversity Areas (IBAs) by BirdLife International (Heath et al. 2000).

International Species Action Plan

Following the development of National Action Plans for the Roller in Hungary, Latvia, Slovakia, and parts of Spain, an International Species Action Plan was drafted in 2008 (Kovacs et al. 2008). The overarching goal of the Action Plan is to restore European populations to a favourable conservation status; a proposition redundant at the continental level following the species downgrading in 2015. Nevertheless, the Action Plan also aims to halt population declines, and to maintain a robust and stable population, across the species EU range by 2023; both objectives that are still unachieved (BirdLife International 2015).

The Action Plan identifies several key actions required to fulfil these objectives, including the filling of critical knowledge gaps and the undertaking of research upon Roller mortality, productivity, and limits to range expansion (Kovacs et al. 2008). The identification and designation of Protected Areas for the species, the integration of measures sympathetic to Rollers into agro-environmental schemes, and awareness raising amongst key stakeholders, also comprise urgently required actions across the species' European range (Kovacs et al. 2008).

Threats to the Roller

The International Species Action Plan identified a range of threats to Roller populations in Europe, each of varying importance dependent upon the population concerned. Several of these were identified as being critically important in respect to their effects upon Roller populations. Critical threats comprised: (1) land abandonment and reduced management; (2) agricultural intensification; (3) grassland conversion and management intensification, and; (4) the intensification of forest management (Kovacs et al. 2008). Most of these threats directly impact the Roller via loss of foraging habitat, whilst changes in forest management can lead to the removal of old trees and a subsequent reduction in nest site availability.

Other threats identified as critical within specific nation states include the use of pesticides (Avilés & Parejo 2004) and increased levels of natural predation (Rodriguez et al. 2011). The threat posed by hunting whilst on migration was largely unclassified in the Action Plan, although it is apparent from online resources that this emerging threat has potential to significantly affect the small and declining populations on the northern edge of the Roller's European range especially (Fig 1.5).

Figure 1.5: Recreational hunting of migrating Rollers in the Middle East is an as yet unquantified driver of population decline. Here we see a single hunting bag containing approximately 25 Rollers, in addition to several Golden Orioles (Oriolos oriolos) and Collared Doves (Streptopelia decaocto) (source: http://mekshat.com/vb/showthread.php?t=407308).

Similarly, threats to the species in its wintering areas outside of Europe, and during migration, are currently unquantified. The absence of legal protection or management proscriptions within several key stopover sites in the Sahel, most notably within the Lake Chad basin, is of particular concern.

The majority of threats posed to the Roller by habitat and land use change are also likely to be compounded by the effects of global climate change. Climate in the species' core Mediterranean range within Europe is predicted to change significantly over the coming century (Giorgi & Lionello 2008), with many areas currently supporting important populations potentially becoming climatically unsuitable for the species in the future (Huntley et al. 2007). Improving our understanding of climatic effects upon Roller distribution and breeding parameters is therefore an important objective for research upon the species.

Rollers in Cyprus and Portugal

The Roller populations of Cyprus and Portugal comprise the longitudinal extremes of the species' Mediterranean distribution (Del Hoyo et al. 2001), and exhibit markedly different population trends and conservation statuses (BirdLife International 2015). As such, the 2 populations comprise ideal candidates for a comparative study into how differences in species ecology and environment affect its conservation.

The Cypriot Roller population, in particular, has received surprisingly little research interest in light of its relative importance, comprising 3% of the European breeding population (BirdLife International 2015). The potential identification of a recent rapid decline in the Roller population in western Cyprus (Pomeroy et al. 2013) is therefore particularly concerning. Nevertheless, the Roller is still a widely distributed breeding species across the island, as well as comprising an abundant passage migrant (BirdLife Cyprus 2016).

Limited research has been carried out upon the effects of agricultural intensification and abandonment on the island's farmland bird communities, and Rollers in particular, since Cyprus joined the EU in 2004 (Hellicar 2006; Ieronymidou 2012; Pomeroy & Walsh 2006), and a detailed study of Roller habitat associations would help inform local conservation measures for the species. Several Protected Areas have been designated for Rollers on the island (Hellicar et al. 2014), although limited assessment of their conservation efficacy has been undertaken, and our understanding of the role that such sites play in the conservation of the species at the island-wide level is far from clear.

The Cypriot Roller population is also of note in comprising one of very few European study populations breeding exclusively in semi-natural cavities, rather than in artificially sited nest boxes. The absence of primary nest hole excavating species (i.e. woodpeckers) from the island, or an established nest box scheme, influences the formation and availability of Roller nest cavities, and potentially has direct implications for Roller productivity and nest predation less applicable elsewhere in the species' range.

The Portuguese Roller population differs from that in Cyprus, being both classified as Critically Endangered nationally (Marques et al. 2005) and largely restricted to a single Protected Area (Castro Verde Special Protection Area) in the south of the country (Catry et al. 2011), following a long-term population decline and range contraction. The Castro Verde population breeds in a variety of nest cavities, including some semi-natural cavities in old buildings, although artificial nest boxes and cavities in purpose built breeding walls comprise the most readily available nesting resources (Moreira et al. 2004). The landscape differs from the topographically diverse mixed farmland and scrubland communities present in Cyprus, comprising expansive low-intensity cereal rotation and pseudo-steppe habitats (Catry et al. 2011).

Portuguese Rollers share Castro Verde with a range of competitor species, including the Lesser Kestrel (*Falco naumanni*), which has been subject to a successful, and intensive, conservation intervention programme of its' own (Deinet et al. 2013). Lesser Kestrels exhibit a similar ecology to Rollers, as both are migratory, cavity-nesting, insectivores which favour low-intensity agricultural landscapes (Cramp & Simmons 1998). Nevertheless, the successful conservation interventions implemented for the Lesser Kestrel (including increased nest site provision and sympathetic landscape management (Deinet et al. 2013)) do not appear to have similarly benefitted the Roller. Understanding the reasons behind this disparity could potentially further the conservation of the Roller in Portugal. Lesser Kestrels are absent from Cyprus, except as passage migrants (BirdLife Cyprus 2016), with potential positive ramifications for the island's Roller population.

The migration routes and wintering areas of both populations have been subject to recent investigation (Catry et al. 2014; Finch et al. 2015). Results from tagging studies suggest that Portuguese Rollers predominantly winter in south-west Africa, having migrated around the north-west African coastline. Cypriot birds appear to winter further north, in east Africa, and follow a more direct north/south migratory route (although this is based upon the movements of a single bird; Finch et al. 2015). Little information is currently available on the use of, or threats to, habitat within the winter ranges of either population.

1.5 Research context and objectives

Rollers have been the subject of intensive studies in several European locations over the last 10 to 20 years, including; Portugal (Marques et al. 2005; Moreira et al. 2004; Rocha 1999), southern Spain (Avilés & Sanchez 1997; Avilés et al. 1999), southern France (Poole 2001), Austria (Sackl et al. 2004a), Lithuania (Karpuska et al. 2011), and Estonia (Lüütsepp et al. 2011a). There has also been long-term monitoring of breeding populations elsewhere in the species' northern/eastern European breeding range, including Latvia (www.putniadazos.lv/en/life-project-adazi-2006-2009) and Poland (Grzybek et al. 2009), and an EU LIFE+ project was recently established for the species in Hungary and Romania (www.rollerproject.eu). Nevertheless, the vast majority of published research on the species has focused on populations in the Iberian Peninsula, particularly Spain, with few studies carried out on the important breeding populations of south-east Europe and Asia Minor (BirdLife International 2015).

The majority of studies have centred upon breeding biology (Avilés et al. 1999; Bohus 2002; Sosnowski & Chmielewski 1996; Moreira et al. 2004) and population trends/range changes (Avilés & Sanchez 1997; Catry et al. 2011; Grzybek et al. 2009; Lüütsepp et al. 2011a; Marques et al. 2005; Tron et al. 2008), with relatively few focusing, or incorporating research, upon habitat (Avilés et al. 2000; Bouvier et al. 2014; Kiss et al. 2016; Poole 2005; Tiefenbach 2009) and nest site (Avilés et al. 2000; Bouvier et al. 2014; Butler 2001) selection. Prey composition has similarly been relatively understudied (Avilés & Parejo 1997; Avilés & Parejo 2002; Lüütsepp et al. 2011; Tidmarsh 2003).

The vast majority of Roller research has been carried out upon nest box breeding populations, with studies upon birds breeding in semi-natural cavities largely limited to tree nesting populations (Bouvier et al. 2014; Butler 2001). Following the development of miniaturised tagging technology, suitable for deployment upon Rollers, an increasing number of studies have investigated the migration ecology and wintering range distribution of the species (Catry et al. 2014; Emmenegger et al. 2014; Finch et al. 2015; Rodríguez-Ruiz et al. 2014).

Nevertheless, substantial gaps exist, both geographically and thematically, in our knowledge of Roller ecology in Europe, as identified in the International Species Action Plan (Kovacs et al. 2008). Limited research has been carried out upon the potential impacts of global climate change upon the species (Parejo et al. 2015), or the effectiveness of Protected Areas in conserving Roller populations (Catry et al. 2011). Our understanding of the key drivers of Roller population change is still developing, with little research undertaken upon the emerging threat posed by excessive hunting during migration, for example.

The specific drivers of population change, and population dynamics themselves, vary across the species European breeding range (Kovacs et al. 2008) and Roller conservation would benefit from an increase in comparative ecological studies of differing populations. Our understanding of Roller migration routes, passage, and wintering areas, as well as migratory connectivity between populations (Finch et al. 2015), is still in its infancy, and the identification of the main demographic drivers at these stages in the annual cycle is of key importance for Roller conservation.

Research objectives

The overarching objective of the research was to plug some of the existing knowledge gaps concerning the effects of climate and habitat change upon Rollers in Europe, with specific reference to the understudied Cypriot, and Critically Endangered Portuguese, populations.

Chapter 2 investigates the effects of climate upon Roller breeding parameters across the Mediterranean, using long-term monitoring datasets from 5 different countries. Specifically, it aims to:

- Identify whether individual precipitation and temperature metrics, derived from breeding locality climate data, are correlated with Roller clutch size and/or fledging success;
- Ascertain whether any observed correlations vary between key phenological periods in the Roller's annual cycle, and;
- Discuss the potential implications of projected climate change within the Mediterranean upon the region's Roller populations.

Chapter 3 focuses upon Cyprus and investigates the efficacy of the island's Protected Area network in maintaining their long-term value to Roller populations. The specific aims are to:

- Produce a Habitat Suitability Model (HSM) for the Roller on Cyprus, using the 2012 Corine Land Cover dataset and a range of other environmental parameters;
- Identify which land cover categories are most likely to support Rollers on Cyprus and to quantify changes in their extent;
- Use the HSM to investigate whether IBA's designated for their Roller populations incorporate a larger extent of high Roller occupancy probability areas than external locations, and;

- Backcast the HSM using Corine Land Cover data from 2000 to quantify changes in the area of high Roller occupancy probability in and outside of the IBA network between 2000 and 2012.

Chapter 4 again focuses on Cyprus, but at a regional scale, investigating the location of Roller home ranges within the west of the island at multiple spatial scales. Home range sizes and foraging habitat preferences during the chick rearing period are investigated through the use of novel tracking technology, and the effect of home range habitat composition upon Roller productivity is quantified. The specific aims of the chapter are to:

- Quantify the home range sizes of Rollers in western Cyprus;
- Identify whether Roller foraging habitat selection during the chick rearing period occurs at the landscape or home range scale;
- Identify preferred foraging habitats used during the chick rearing period and examine differences in prey biomass between available habitat types;
- Investigate whether habitat composition within the home range impacts Roller laying date, and fledging success, and;
- Discuss the implications of habitat change upon the Cypriot Roller population.

Chapter 5 focuses on Roller breeding biology at the nest site level and makes comparison between the Cypriot and Portuguese populations. It investigates whether surrounding habitat or individual cavity parameters are the key arbiter of nest site selection in both populations, and examines the effect of competitor species upon nest site uptake. It then aims to identify links between nest site parameters, competitor presence, and breeding parameters. It specifically aims to:

- Identify whether Rollers in either population choose their nest sites based upon surrounding habitat composition, or due to external/internal cavity parameters;
- Specify the physical parameters of Roller utilised cavities in both populations, and quantify the availability of suitable cavities;
- Investigate evidence of nest site limitation in either population through analysis of continued nest site use;
- Quantify the effect of interspecific competition on nest site availability, and;
- Investigate the effect of internal cavity metrics upon Roller fledging success.

1.6 Thesis structure

All data chapters (2 to 5) were composed in the format of journal publications. My primary PhD supervisor; Aldina Franco, and my secondary supervisors; Ines Catry, Simon Butler, and Phil Atkinson, were integral in the development of the research and made important contributions, in the form of comments and advice, during production of the chapter drafts. They are all therefore named co-authors on each of the data chapters.

Chapter 2 incorporates data kindly provided from ongoing Roller monitoring projects maintained by researchers across the Mediterranean. In addition to my supervisory team (of whom Ines Catry provided data from Portugal), all of the following researchers are therefore named co-authors on the chapter; Jesus Avilés (Spain), Tom Finch (UK/France), Anna Folch (Spain), Flavio Monti (Italy), Deseada Parejo (Spain), Francesco Pezzo (Italy), and Timothee Schwartz (France). Chapter 5 also incorporates data from Portugal collected by Ines Catry and colleagues.

Chapters 2 and 3 were written with specific journals in mind, and are planned to be submitted prior to the end of 2017. A substantial element of the field research carried out whilst collecting data for this thesis comprised the deployment and retrieval of solar geolocators from the Cypriot Roller population. However, due to the low return rates observed in the Cypriot birds, this research does not comprise an independent data chapter in the thesis. The data collected was instead included in a collaborative Europe-wide assessment of Roller migratory connectivity, published in *Diversity and Distributions*, of which I am a co-author (Finch et al. 2015).

Due to the single species focus of the research, several key papers on Roller ecology and conservation will be regularly cited throughout the thesis.

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Chapter 2: Climatic effects upon breeding parameters of the European Roller *(Coracias garrulus)* in the Mediterranean

2.1 Abstract

Global climate change comprises one of the most important drivers of biodiversity decline, with changes in climate predicted to be more extreme in fragile biodiversity hotspots, such as the Mediterranean. Bird species may be impacted by climate in different ways at varying points in their annual cycles, with migrant species particularly susceptible to negative effects due their complex breeding phenologies. Monitoring datasets exhibiting a wide temporal and geographic spread provide an important resource when seeking to understand climatic impacts upon bird populations. This study identifies key climatic variables during 3 distinct phenological periods correlated with clutch size and fledging success in 9 populations of the migratory European Roller (Coracias garrulus) in the Mediterranean. Variation in winter temperature was negatively correlated with both clutch size and fledging success the following year, whilst increasing temperature range during the chick rearing period was identified as the key climatic correlate of fledging success at that point in the cycle. The observed correlations may be explained by their impacts upon prey abundance and availability, predator and competitor behaviour, and chick physiology. Based on our results, predicted increases in temperature across the Mediterranean have potential to decrease both clutch size and fledging success, and therefore negatively impact Roller populations in the region.

2.2 Introduction

Global climate change is a key issue for biodiversity conservation (Dawson et al. 2011; Walther et al. 2002; Stephens et al. 2016), with global temperatures predicted to rise by a minimum of 1.5^{0}C above 1850 - 1900 levels over the next century (Collins et al. 2013). Climate change induced pressure upon biodiversity has increased over recent decades (Butchart et al. 2010), with >400 of the world's terrestrial bird species predicted to experience >50% reductions in their distributions by 2050, directly resulting from climate change and associated changes in land use (Jetz et al. 2007).

Climate change is forecast to have more severe consequences in sensitive biogeographic regions, where its impact is likely to be exacerbated by the cumulative impacts of changes in land use, rates of atmospheric nitrogen deposition and biotic exchange, and atmospheric carbon dioxide levels (Sala et al. 2000). The Mediterranean basin is one such location, and it is predicted to experience a pronounced decrease in precipitation levels, and a marked increase in temperature, concentrated in the summer months (Giorgi & Lionello 2008). This is in turn considered likely to lead to increased inter-annual variability in climatic conditions, and the increased incidence of extreme heat events and droughts (Giorgi & Lionello 2008) in this fragile biodiversity hotspot (Li et al. 2013).

The predicted effects of climate change upon terrestrial biodiversity are varied, and include range changes (Chen et al. 2011), habitat deterioration and fragmentation (Butchart et al. 2010), increases in disease risk (Lafferty 2009), decreasing prey availability (Durant et al. 2007), and changes in phenology (Gordo & Sanz 2006). Changes in any of these factors have potential to negatively affect species demography, through decreases in productivity and/or increased mortality. Understanding the effects of different climatic conditions upon species breeding ecology can therefore help plan for species conservation in the face of changing climates (Dawson et al. 2011). This is particularly important in areas of high biodiversity value subject to heightened climate change impacts, such as the Mediterranean basin (Li et al. 2013). The identification of key points in the annual cycle at which climatic effects have the most impact is also essential, as climate change effects may vary between different life stages (Newton 1998).

Climate change effects have the potential to affect bird species at multiple points within their annual cycles. Such effects are compounded for migratory species, whose migration phenology may be directly impacted by climate change (Cotton 2003). Phenological responses to climate change by Mediterranean birds have been shown to vary between species (Gordo & Sanz 2006), although some studies have identified potential climate-change induced range shifts (Tellería et al. 2016). Phenological mismatch between migrant arrival dates and peak prey availability have been shown to negatively affect fledging success (Both & Visser 2001; Both et al. 2006), and an inability to respond to climate change may have severe negative population level effects (Saino et al. 2011).

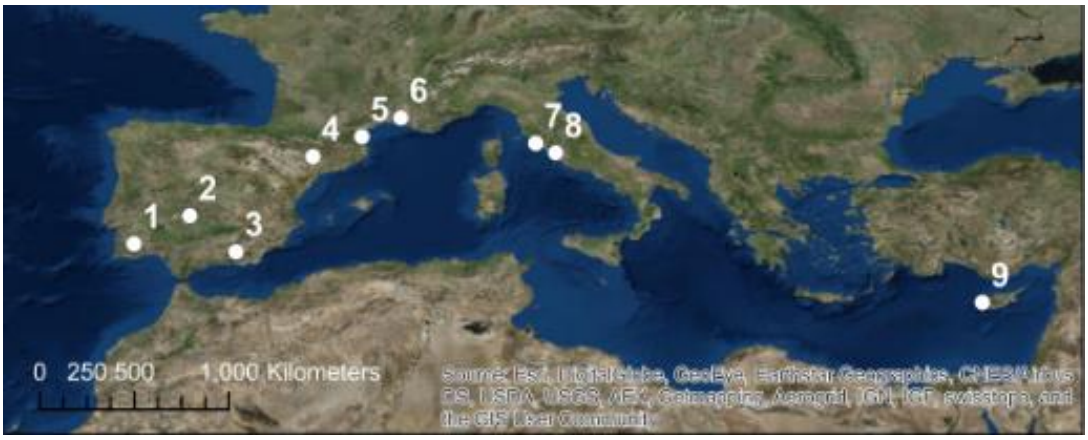
This study investigates the effects of climatic conditions during the preceding winter, pre-breeding, and chick rearing periods upon the breeding parameters of the European Roller (*Coracias garrulus*) across the species' Mediterranean range. The Roller is a sub-Saharan migrant, which may be unable to adapt its phenology to rapid changes in the Mediterranean climate. Climate may change in different ways across the species Mediterranean range, and the separate populations may therefore exhibit varied responses to it.

The study aims to identify: (1) whether the effect of climatic controls on egg laying and fledging success are visible across Mediterranean populations at a regional scale; (2) which of the key phenological periods in the Roller's annual cycle are most sensitive to climatic conditions, and; (3) to identify the potential future impacts of global climate change upon the species.

2.3 Methods

Study areas

Data was collected from 9 monitored Roller populations at locations across the width of the northern Mediterranean, each separated by at least 90km (Figure 2.1). These comprised 1 population in Portugal, 3 in Spain, 2 in France, 2 in Italy, and 1 in Cyprus. The study populations inhabited a range of Mediterranean landscape types, with low intensity agriculture and pseudo-steppe prevalent in Iberia, mixed farming and pastures alongside saltmarsh habitats in France, coastal pinewoods and agricultural areas in Italy, and mixed farming and scrubland communities in Cyprus. The majority of the study populations breed in nest boxes, although the entirety of the Cypriot population (and a small proportion of those in Portugal and Spain) breed in semi-natural cavities in buildings and cliffs.



Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community

Figure 2.1: Study locations: (1) Lower Alentejo (Portugal);(2) Extremadura (Spain); (3) Andalusia (Spain); (4) Catalonia (Spain); (5) Languedoc-Roussillon (France); (6) Provence-Alpes-Côte-d'Azur (France); (7) Tuscany (Italy); (8) Lazio (Italy), and; (9) Paphos (Republic of Cyprus).

Data collection

Breeding parameters

The number of years during which the Roller population had been continuously monitored at each of the study locations varied (Table 2.1), with 13 years (Portugal) and 2 years (Cyprus) representing the extremes. One of the Spanish study locations was however monitored, for non-consecutive periods, between 2001 and 2014. During each monitoring year, Roller breeding parameter data was collected from all accessible nest sites within each of the study locations.

The number of occupied Roller nest sites surveyed each year varied between locations, as follows: Lower Alentejo - 4 to 33; Extremadura - 13 to 33; Andalusia - 3 to 17; Catalonia - 4 to 18; Languedoc-Rousillon - 3 to 10; Provence-Alpes-Côte-d'Azur - 1 to 46; Tuscany - 2 to 15, Lazio - 7 to 27, and; Cyprus - 9 to 20 (Table S2.1 (Appendix)).

Data collected annually from all study populations comprised; (1) the total number of eggs laid, and; (2) the number of chicks successfully fledged. Additional information was collected from the majority of study locations: (3) the date that the first egg was laid (excluding both French locations and Catalonia, Spain), and (4) the number of eggs which successfully hatched (excluding Languedoc-Roussillon, France).

Table 2.1: Central co-ordinates of study locations, length of Roller monitoring period, and mean number of Roller nests monitored at each per year of study plus standard error (numbers in parentheses correspond to those in Figure 2.1).

Study location	**Latitude and Longitude (decimal degrees)**	**Monitoring period**	**ẋ no. Roller nest sites monitored / year**	**SE**
(1) Lower Alentejo (Portugal)	37.75, -8.04	2003 - 2015	16.08	2.87
(2) Extremadura (Spain)	39.03, -5.23	2005 - 2007	26.00	6.51
(3) Andalusia (Spain)	37.32, -3.03	2007 - 2015	11.38	1.60
(4) Catalonia (Spain)	41.83, 0.69	2001 - 2002 & 2013 - 2014	9.00	3.11
5) Languedoc-Roussillon (France)	42.81, 2.91	2011 - 2015	5.60	1.29
(6) Provence-Alpes-Côte-d'Azur (France)	43.70, 4.76	2004 - 2013	19.30	4.89
(7) Tuscany (Italy)	42.60, 11.13	2007 - 2014	8.00	1.56
(8) Lazio (Italy)	42.20, 11.99	2010 - 2015	14.25	4.50
(9) Paphos (Republic of Cyprus)	34.96, 32.41	2014 - 2015	14.50	5.50

Phenological periods

Three key phenological periods were identified from the breeding parameter dataset, based upon first egg laying date for those populations for which data were available Table 2.2).

Table 2.2: Dates comprising key Roller phenological periods in each of the study locations (numbers in parentheses correspond to those in Figure 2.1).

Study locations	**Winter**	**Pre-breeding**	**Chick rearing**
Portugal and southern Spain *(1 to 3)*	November to February inclusive	April	June
North-east Spain (4), France, and Italy *(5 to 8)*	November to February inclusive	Mid-April to mid-May	Mid-June to mid-July
Cyprus *(9)*	November to February inclusive	Mid-March to mid-April	Mid-May to mid-June

The three phenological periods comprised: (1) the preceding winter period, during which Rollers are absent from their breeding localities but during which the prey resource and resident competitor species will be impacted by local climatic conditions; (2) the pre-breeding period during which Rollers arrive at their breeding sites in spring, when females come into breeding condition prior to mating and egg-laying; and (3) the chick rearing period, when chicks are being actively provisioned in the nest. These phenological periods are considered those at which many seasonally breeding bird species are most susceptible to negative climatic effects (Polak & Kasprzykowski 2013).

The timing of ‘winter’ at the breeding localities was considered to be independent of Roller phenology and therefore identical for all of the study locations (November to February inclusive). The ‘pre-breeding’ and ‘chick rearing’ periods did however differ between localities. Cypriot Rollers arrive and breed earlier than Iberian birds, with Iberian birds arriving and breeding earlier than French or Italian birds (Appendix, Figure S2.1). For those populations for which laying dates were not collected (both French locations and Catalonia, Spain) a similar date to that of the closest population latitudinally was applied.

Allowing for inter-annual variation, and rare secondary nesting attempts, the Roller chick rearing stage comprises an extended period of approximately 6 weeks in each of the study populations (Avilés et al. 1999, *pers.comm*). The ‘chick rearing’ period used in the analyses therefore comprised the central 4 weeks of this extended period, when the majority of pairs were provisioning young, following approximately 2.5 weeks’ incubation (Cramp & Simmons 1998; Del Hoyo et al 2001).

Climate data

Daily 0.25 degree resolution precipitation data were downloaded from the Precipitation Estimation from Remote Sensing Information using Artificial Neural Network (PERSIANN) project (www.chrs.web.uci.edu/persiann). Eight day composite 0.05 degree resolution land surface MODIS temperature data (MOD11C2) were downloaded from the Land Process Distributed Active Archive Center (LPDAAC) (www.lpdaac/usgs/gov). These comprised the finest temporal and spatial resolution climate datasets available covering the full temporal and spatial extent of the breeding parameter datasets from the 9 study locations. The climate data was partitioned into blocks coinciding with the 3 previously identified discrete phenological periods in the Roller’s annual cycle.

Statistical analyses

The effects of ‘preceding winter’ and ‘pre-breeding’ climate upon Roller egg laying, and the effects of ‘preceding winter’, ‘pre-breeding’, and ‘chick rearing’ period climate upon Roller fledging success were modelled using a range of explanatory parameters derived from the 2 climate datasets (Table 2.3), all chosen for their potential ecological effects upon Roller breeding biology.

Table 2.3: Independent variables analysed to develop egg laying and fledging success models for the Roller within the Mediterranean region.

Fixed effects	**Description**	**Remote sensing data source**
Mean precipitation (*MeaPre*)	Mean precipitation for phenological period (mm).	PERSIANN global precipitation dataset, daily 0.25 deg resolution rasters (University of California, Irvine)
Number of rainfall days (*NRDs*)	Number of days in which precipitation ≥ 1mm during phenological period.	
Maximum consecutive number of rainfall days(*ConRDs*)	Maximum number of consecutive days in which precipitation ≥ 1mmduring phenological period.	
Number of heavy rainfall days (*NHRDs*)	Number of days during phenological period in which precipitation ≥ 20mm.	
Maximum consecutive number of heavy rainfall days (*ConHRDs*)	Maximum number of consecutive days during phenological period in which precipitation ≥ 20mm.	
Mean temperature (*MeaTem*)	Mean temperature for phenological period (ºC).	MOD11C2: MODIS global land surface temperature, 8-day 0.05 deg resolution rasters (LPDAAC, NASA)
Minimum temperature (*MinTem*)	Minimum temperature recorded on any one day of phenological period (ºC).	
Maximum temperature (*MaxTem*)	Maximum temperature recorded on any one day of phenological period (ºC).	
Temperature range (*TemRa*)	Temperature range (maximum minus minimum) of phenological period (ºC).	
Random effects		
Nest	Identifier given to each nest. Incorporated to account for repeated measurements between years and potential variation in breeding pair composition.	
Nest buffer	Individual code applied to 600m buffer surrounding each nest site. Where buffers of separate nests overlap by 10% or more, they are allocated the same code to account for overlapping foraging habitat extents.	
Area of optimal foraging habitat	Area in m^2 of the 600m nest buffer occupied by Corine Land Cover (CLC) categories comprising optimal Roller foraging habitat: *non-irrigated arable land; vineyards; pastures; annual crops associated with permanent crops; complex cultivation patterns; land principally occupied by agriculture but with significant areas of natural vegetation,* and; *natural grassland.*	CLC 2000, 2006, and 2012 250m x 250m shapefiles (European Environment Agency/Copernicus Land Monitoring Services)
Year	Calendar year. Incorporated to account for repeated visits to individual nests between years and inter-year variation.	
Temperature grid square	Grid of individually numbered cells overlapping temperature data raster (~5.6km cell size), incorporated to account for spatial autocorrelation.	
Rainfall grid square	Grid of individually numbered cells overlapping precipitation data raster (~24.64km cell size), incorporated to account for spatial autocorrelation.	

Mean precipitation was included as a variable to capture variation in rainfall in each of the 3 phenological periods, and to account for potential impacts of decreased/increased rainfall upon vegetation, soils, and invertebrate prey. The *Number of rainy days* was included to account for potential impacts upon invertebrate activity and Roller, competitor, or predator foraging behaviour. *Number of heavy rainy days* was included to account for any effect of extreme rainfall upon those same parameters, and any consequent effects upon Roller feeding rates or chick provisioning.

Mean temperature, Minimum temperature, and *Maximum temperature* were included as variables to capture variation in temperature within each of the 3 phenological periods, and to account for potential impacts of an average higher or lower temperature (or extreme high or low temperature) upon invertebrate life cycles and activity, and thermal effects upon chicks in the nest. *Temperature range* was included to capture the effect of extreme variation in temperature upon invertebrate, competitor, and predator activity, invertebrate life cycles, and thermal effects upon nestlings.

A small number of rasters (<2) in both of the climate datasets were unavailable for the 'winter' period, with any mean or cumulative values therefore derived from the available data for those years. All potential explanatory parameters were initially screened for unimodal significance prior to inclusion, with only significant variables carried forward. Pairwise correlations were then examined, with the stronger variable retained of any pair exhibiting a Pearson Correlation Coefficient of >0.7. The distribution of each dependent variable was also confirmed prior to imposition of a specific model structure.

All modelling was carried out using the lme4 and MuMIn packages in R (R Core Development Team, 2016). Due to the large number of potential explanatory parameters, individual global mixed effect models were built. Model selection was carried out using the Akaike Information Criterion adjusted for small sample sizes (AICc; Hurvichl & Tsai 1995). Due to the large number of initial explanatory parameters used, and uncertainty in model choice resulting from the large set of candidate models exhibiting a ΔAICc < 2, multimodal inference and model averaging were used to produce robust parameter estimates and calculate 95% confidence intervals (CI) using the weighted average of the corresponding coefficient in all candidate models within the top model set (Burnham & Anderson 2002). Only those parameters retained within the averaged models which exhibited 95% CI’s not spanning zero were considered statistically significant at p=<0.05.

Egg laying models

Climatic effects upon Roller egg laying (number of nests = 774) were modelled using Linear Mixed Effect Models, due to the normal distribution of the egg count data, for the ‘winter’ and ‘pre-breeding’ climate datasets. Explanatory variables comprised the range of climatic measurements detailed in Table 2.3.*Year* and nest site longitude (*Nest*) were incorporated as nested random effects to account for repeat surveying between years and inter-annual variation in breeding pair composition.

In order to minimise the effects of variation in habitat availability/quality at each nest site, the *Area of optimal foraging habitat* (comprising grassland, low-intensity agriculture, and agricultural mosaic habitat types) within 600m of each nest location was included as a random effect in the global model. These habitat types have been identified as those preferred for foraging across the Roller’s European range (Avilés & Costillo 1998; Sackl et al. 2004; Marques et al. 2005), with 500m - 600m comprising the radius within which the majority of foraging is undertaken during the breeding season (Cramp & Simmons 1998; Gray 2003, see Chapter 4).

Habitat extents were extracted from the Corine Land Cover dataset (2000, 2006, or 2012) closest to the year in question in an ArcGIS environment (ESRI 2014). *Area of optimal foraging habitat* was nested within *Nest buffer* to account for any overlapping 600m nest boundaries/foraging habitat extents in locations with more densely distributed nest sites, with any buffers overlapping >10% with one another being grouped within the same factor level.

Each precipitation/temperature dataset grid cell was allocated an individual identifier to minimise the effects of spatial autocorrelation, due to the differing spatial scales and overlapping nature of individual nest site locations and the 2 climate datasets. A nested random effect was then incorporated within the global model to account for the spatially nested structure of the data.

Fledging success models

Climatic effects upon Roller fledging success (number of nests = 592) for all 3 phenological periods were also modelled using Linear Mixed Effect Models for 8 of the 9 study sites (with data on hatching success unavailable for Languedoc-

Roussillon). An offset term was added to account for the number of eggs that successfully hatched, with the same random effects incorporated as in the egg laying models.

2.4 Results

Egg laying models

Effect of preceding winter weather at breeding sites upon Roller egg laying

Minimum temperature was collinear with *Mean temperature*, and so *Mean temperature*, *Maximum temperature*, and *Temperature range* were included in the global model as descriptors of temperature variation in the dataset. *Number of rainfall days* was collinear with *Number of heavy rainfall days*, *Number of heavy rainfall days* was collinear with *Consecutive number of heavy rainfall days*, and both *Number of rainfall days* and *Number of heavy rainfall* days were collinear with *Mean precipitation*. *Mean precipitation*, *Consecutive number of rainfall days*, and *Consecutive number of heavy rainfall days* were therefore retained in the global model as descriptors of variation in rainfall levels in the dataset.

Following removal of co-linear variables and the application of the model selection procedure, 6 models were retained within the top model set investigating the relationship between number of eggs laid and weather conditions during the preceding winter (Table 2.4). Following model averaging, *Mean temperature* (negative) and *Maximum temperature* (negative) were the only parameters exhibiting a significant negative relationship (based upon 95% CI's) with number of eggs laid (Figure 2.2a, Table S2.2 (Appendix)).

Effect of weather during the pre-breeding period upon Roller egg laying

Both *Minimum temperature* and *Maximum temperature* were collinear with *Mean temperature* and one another, and so *Mean temperature* and *Temperature range* were included in the global model as descriptors of temperature variation in the dataset. *Number of rainfall days* was collinear with *Number of heavy rainfall days*, *Number of heavy rainfall days* was collinear with *Consecutive number of heavy rainfall days*, and both *Number of rainfall days* and *Number of heavy rainfall* days were collinear with *Mean precipitation*. *Mean precipitation*, *Consecutive number of rainfall days*, and *Consecutive number of heavy rainfall days* were therefore retained in the global model as descriptors of variation in rainfall levels in the dataset.

Table 2.4: Models retained within the top model set (ΔAICc<2) following production of Generalised Linear Mixed Effect Models investigating the effect of weather conditions during the preceding winter and pre-breeding period upon the number of eggs laid by Rollers at 9 locations across the northern Mediterranean (k = no. parameters in model; AICc = Akaike Information Criterion adjusted for small sample sizes; AIC_w = Akaike model weight).

Model	***k***	***AICc***	**Δ*AICc***	***AIC_w***
Preceding winter				
MeaTem + TemRa	2	2220.70	0.00	0.10
MaxTem	1	2221.25	0.54	0.08
MaxTem + MeaTem	2	2221.94	1.24	0.06
ConHRDs + MeaTem + TemRa	3	2222.18	1.47	0.05
MeaTem	1	2222.20	1.49	0.05
ConRDs + MeaTem + TemRa	3	2222.53	1.83	0.04
Pre-breeding				
ConHRDs + MeaTem	2	2228.65	0.00	0.10
MeaPre + MeaTem	2	2229.05	0.40	0.08
MeaTem	1	2229.08	0.44	0.08
Intercept only	0	2229.26	0.61	0.07
MeaPre	1	2229.45	0.80	0.07
ConHRDs	1	2229.63	0.98	0.06
ConHRDs + MeaPre + MeaTem	3	2230.30	1.65	0.04
ConHRDs + MeaTem + TemRa	3	2230.53	1.88	0.04

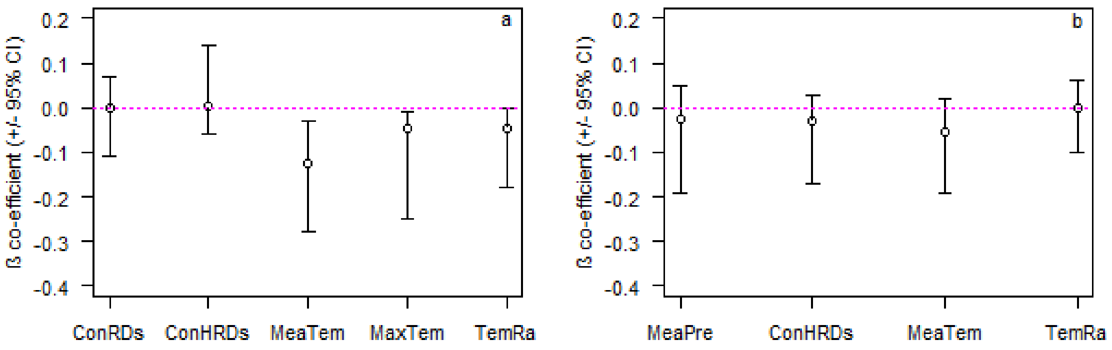


Figure 2.2: Averaged parameters and 95% confidence intervals for those models retained within the top model set investigating the effect of weather conditions during (a) the preceding winter and (b) pre-breeding periods upon the number of eggs laid by Rollers at 9 locations across the northern Mediterranean.

Following removal of co-linear variables and the application of the model selection procedure, 8 models were retained within the top model set investigating the relationship between number of eggs laid and weather conditions during the pre-breeding period (Table 2.4). Following model averaging, none of the parameters exhibiting a significant relationship (based upon 95% CI's) with number of eggs laid however (Figure 2.2b, Table S2.2 (Appendix)).

Fledging success models

Effect of preceding winter weather at the breeding site upon Roller fledging success

Minimum temperature was collinear *Mean temperature*, and so *Mean temperature*, *Maximum temperature*, and *Temperature range* were included in the global model as descriptors of temperature variation in the dataset. *Consecutive number of rainfall days* was collinear with *Number of rainfall days*, *Number of heavy rainfall days* was collinear with *Consecutive number of heavy rainfall days*, and *Consecutive number of rainfall days, Number of rainfall days*, and *Number of heavy rainfall days* were collinear with *Mean precipitation*. *Mean precipitation* and *Consecutive number of heavy rainfall days* were therefore retained in the global model as descriptors of variation in rainfall levels in the dataset.

Following removal of co-linear variables and the application of the model selection procedure, 3 models were retained within the top model set investigating the relationship between number of chicks fledged and weather conditions during the pre-breeding period (Table 2.5). Following model averaging, *Mean precipitation* (negative) and *Maximum temperature* (negative) were the only parameters exhibiting a significant relationship (based upon 95% CI's) with number of chicks fledged (Figure 2.3a, Table S2.3 (Appendix)).

Effect of weather during the pre-breeding period upon Roller fledging success

Minimum temperature was collinear with *Mean temperature* and *Maximum temperature*, and *Maximum temperature* was also collinear with *Mean temperature*. *Mean temperature* and *Temperature range* were included in the global model as descriptors of temperature variation in the dataset. *Mean precipitation* was collinear with all precipitation variables apart from *Number of rainfall days*. These 2 variables were therefore retained in the global model as descriptors of variation in rainfall levels in the dataset.

Table 2.5: Models retained within the top model set (ΔAICc<2) following production of Generalised Linear Mixed Effect Models comparing weather conditions during the preceding winter, pre-breeding, and chick rearing periods upon the number of chicks fledged by Rollers at 8 locations across the northern Mediterranean.

Model	***k***	***AICc***	***ΔAICc***	***AIC$_w$***
Preceding winter				
MaxTem + MeaPrec	2	1809.09	0.00	0.21
MaxTem	1	1810.72	1.62	0.09
ConHRDs + MaxTem + MeaPre	3	1811.04	1.95	0.08
Pre-breeding				
NRDs	1	1814.23	0.00	0.17
MeaPre	1	1814.82	0.59	0.13
NRDs + TemRa	2	1814.97	0.75	0.12
Intercept only	0	1815.47	1.24	0.09
MeaPre + TemRa	2	1815.64	1.42	0.08
Chick rearing				
TemRa	1	1807.11	0.00	0.20
ConRDs + TemRa	2	1807.65	0.54	0.15
MeaTem + TemRa	2	1808.95	1.84	0.08
ConHRDs + TemRa	2	1809.11	2.00	0.07

Following removal of co-linear variables and the application of the model selection procedure, 5 models were retained within the top model set investigating the relationship between number of chicks fledged and weather conditions during the pre-breeding period (Table 2.5). Following model averaging, none of the retained variables exhibited a significant relationship (based upon 95% CI's) with number of chicks fledged (Figure 2.3b, Table S2.3 (Appendix)).

Effect of weather during the chick rearing period upon Roller fledging success

Minimum temperature was collinear with *Mean temperature* and *Maximum temperature*, and *Maximum temperature* was also collinear with *Mean temperature*. *Mean temperature* and *Temperature range* were included in the global model as descriptors of temperature variation in the dataset. *Number of heavy rainfall days* was collinear with *Consecutive number of heavy rainfall days* and *Mean precipitation*, *Number of rainfall days* was collinear with *Mean precipitation*. *Mean*

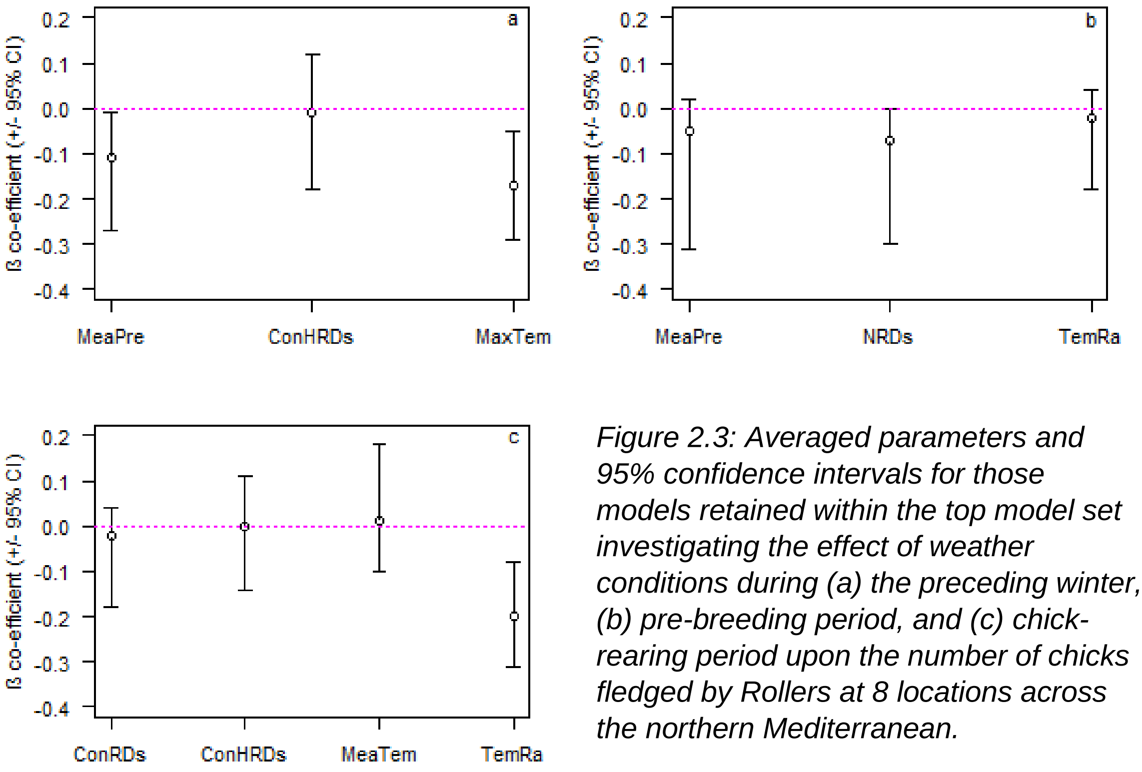


Figure 2.3: Averaged parameters and 95% confidence intervals for those models retained within the top model set investigating the effect of weather conditions during (a) the preceding winter, (b) pre-breeding period, and (c) chick-rearing period upon the number of chicks fledged by Rollers at 8 locations across the northern Mediterranean.

precipitation, *Consecutive number of rainfall days,* and *Consecutive number of heavy rainfall days* were therefore retained in the global model as descriptors of variation in rainfall levels in the dataset.

Following removal of co-linear variables and the application of the model selection procedure, 4 models were retained within the top model set investigating the relationship between number of chicks fledged and weather conditions during the chick rearing period (Table 2.5). Following model averaging, *Temperature range* (negative) was the sole parameter exhibiting a significant relationship (based upon 95% CI's) with number of chicks fledged (Figure 2.3c).

2.5 Discussion

Climatic effects on Roller egg laying

Our results indicate that temperature is the key climatic variable impacting Roller clutch size in the Mediterranean, although the relative importance of the relationship varies dependent upon the phenological period under consideration. The association between increasing winter temperature and decreasing clutch size may be explained through the impact of warmer winter months upon invertebrate prey populations. Warmer temperatures may disrupt diapause in overwintering prey species

(Harrington et al. 1999; Wallisdevries & Van Swaay 2006), or increase susceptibility to pathogens.

Warmer winters may also lead to increased vegetation growth in the spring, providing more cover for invertebrate prey and therefore decreasing Roller hunting success rates. These factors could lead to lower prey availability for Rollers upon arrival (causing poorer subsequent female condition and fecundity). Higher temperatures have been shown to depress clutch size in several bird species (Carrillo & González-Dávila 2010; Skagen & Adams 2012). Milder winters could also cause an increase in the survival of resident competitor, predator, and parasite populations (Borgman & Wolf 2016) leading to increased competition for prey items and a greater risk of nest predation.

Alternatively, the absence of any strong association between climatic conditions during the pre-breeding period and subsequent clutch size is perhaps indicative that clutch size is largely driven by carry-over effects from the preceding breeding season or experience in African wintering areas (Sedinger et al. 2011). Alternatively, female fitness may be controlled by prey availability upon arrival which is itself potentially controlled by weather during the preceding winter, as previously discussed.

Climatic effects on Roller fledging success

Our results indicate that temperature is again a key climatic variable impacting Roller fledging success in the Mediterranean. A similar potential driver of clutch size variation identified during the preceding winter period (maximum temperature) is also negatively correlated with fledging success, as is increasing mean winter precipitation. Any decrease in invertebrate prey availability, or decrease in hunting success arising from lower prey availability, increased competition, and/or denser vegetation growth, could have direct impacts upon the number of chicks fledged via reduced provisioning rates at the nest site. Provisioning rates are also potentially affected by parent bird fitness, which may be lower during years of low prey abundance/hunting success.

The absence of any strong climatic correlate of fledging success during the pre-breeding period is again indicative that fledging success may largely be driven by climatic effects experienced outside of the breeding season, or by variation in spring prey availability or hunting success driven by preceding winter weather.

The retention of temperature range as the key explanatory climatic variable during the chick rearing period is interesting, as studies on several other species report a positive relationship between increasing temperature and fledging success (Ahola et al. 2009; Eggers et al. 2015; Mihoub et al. 2012). It is possible that the negative effect observed is a function of increased minimum or maximum temperature, as excessive heat or cold conditions can negatively affect fledging success through direct chick mortality (Catry et al. 2011; Eggers et al. 2015, Newton 1998). Nevertheless, Roller nestlings in Portugal exhibit higher heat tolerances than sympatric species (Catry et al. 2015), and Rollers may therefore be less susceptible to the potential negative effects of increasing summer temperatures.

Predation levels may also be exacerbated under extreme weather conditions (Newton 1998). We would have expected heavy rainfall to be important at this point in the breeding cycle in light of the strong negative effects identified in studies on other species (Eggers et al. 2015; Polak & Kasprzykowski 2013) and the strongly negative effect on breeding success noted for Rollers in Poland (Sosnowski & Chmielewski 1996).

Future impacts on the Mediterranean Roller population

Climate change projections for the Mediterranean vary across the region, with Iberia predicted to experience increased summer and winter temperatures, wetter, winters, and drier summers, whilst Italy and south-east Europe will become warmer throughout the year, but experience drier winters and summers (Giorgi & Lionello 2008). As such, the response shown by Rollers to Mediterranean climate change is likely to differ between populations, as has been found in other study species (Sanz 2003).

Nevertheless, temperatures are predicted to increase across the Mediterranean region during both the winter and summer periods (Giorgi & Lionello 2008) and it is therefore probable, based upon our results, that Roller clutch size and fledging success across the region will decrease. The potential impacts arising from climate induced carryover effects (Sillett et al. 2000) arising in the species' African wintering areas may further affect productivity, with recent research indicating that Roller populations breeding in the Iberian Peninsula and southern France share African wintering areas (Finch et al. 2015).

Changes in the regional climate are likely to affect vegetation communities and prey availability, which will in turn impact Roller populations. The species response to climate change is nevertheless unlikely to be static (Huntley et al. 2008), and it possible that Rollers may be able to shift their climatic niche, either through changes in phenology, range, or physiology (Bellard et al. 2012). The breeding distribution of Rollers in Europe is forecast to move north-westwards under current climate predictions, with coastal Mediterranean populations moving northwards (Huntley et al. 2007).

Rollers in the Mediterranean basin are more likely to feel the negative effects of climate induced range shifts, as they comprise the most southerly breeding population on the rear edge of the species European range (Hampe & Petit 2005). Projections of Roller distribution within Europe under predicted climate change scenarios indicate that southern Iberia and France, as well as coastal areas of west-central Italy, will become unsuitable for the species by the late 21st century (Huntley et al. 2007).

Forecasting the potential effects of global climate change upon biodiversity is fraught with difficulties (Botkin et al. 2007), and any projections must consider changes in the intensity, strength, and/or direction of drivers during the predictive period (Oliver & Roy 2015). This study highlights the value of long-term monitoring programmes, and indicates that further detailed research is needed on the trophic and community interactions at play both before and during the Roller breeding season in order to understand the potential ramifications of global climate change for the species.

2.6 Acknowledgements

I’d like to thank the following collaborators for allowing me access to data from their long-term Roller monitoring datasets: Dr Jesus Aviles (*EEZA-CSIC*), Dr Ines Catry (*Universidade de Lisboa*), Tom Finch (*University of East Anglia*), Anna Folch, Dr Flavio Monti, Dr Deseada Parejo (*EEZA-CSIC/Universidad de Extremadura*), Dr Francesco Pezzo, and Timothee Schwartz (*A Rocha France*). I’d also like to thank the following people for their assistance during data collection in Cyprus: Alessandro Gravano, Harry Ewing, Drs Ines and Teresa Catry, and Dr Aldina Franco.

This research is funded through a Natural Environment Research Council Studentship Grant (No.1210309), and the author is also a beneficiary of both an A.G. Leventis Foundation Scholarship and British Trust for Ornithology CASE studentship award.

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Appendix: Supporting information

Table S2.1: Summary of annual Roller breeding parameter data from the 9 study locations used in model production.

Location	Year	No. nests monitored	Mean no. eggs laid	Range	Mean no. eggs hatched	Range	Mean no. chicks fledged	Range
Lower Alentejo (Portugal)	2003	20	4.6	2 - 7	3.6	1 - 6	3.5	1 - 6
	2004	11	4.8	3 - 6	4.2	2 - 5	3.7	2 - 5
	2005	11	4.9	4 - 6	4.6	4 - 6	4.4	4 - 6
	2006	9	5.1	4 - 7	4.3	3 - 6	4.3	3 - 6
	2007	7	5.3	4 - 7	4.4	2 - 6	4.0	2 - 6
	2008	12	5.0	4 - 6	4.6	3 - 6	4.4	3 - 6
	2009	11	4.8	3 - 6	3.8	1 - 6	3.5	1 - 5
	2010	5	4.6	3 - 6	4.4	3 - 6	3.8	3 - 5
	2011	4	5.8	5 - 6	5.3	4 -6	5.3	4 - 6
	2012	29	5.0	3 - 6	4.8	3 - 6	4.7	2 - 6
	2013	26	4.8	2 - 6	4.2	1 - 6	4.0	1 - 6
	2014	33	5.0	3 - 7	4.3	1 - 7	4.1	1 - 6
	2015	31	5.3	3 - 7	4.6	2 - 6	4.5	2 - 6
Extremadura (Spain)	2005	33	4.7	3 - 7	4.7	3 - 7	3.7	1 - 7
	2006	32	5.9	4 - 8	5.8	4 - 8	5.0	1 - 8
	2007	13	5.5	4 - 8	5.5	3 - 8	3.6	1 - 7
Andalusia (Spain)	2007	13	5.4	2 - 7	4.8	2 - 7	4.8	2 - 7
	2008	9	5.0	3 - 6	4.7	3 - 6	4.4	2 - 6
	2010	10	5.2	4 - 6	4.4	2 - 6	2.8	1 - 4
	2011	15	5.6	3 - 7	4.8	3 - 6	4.3	2 - 6
	2012	9	4.7	4 - 6	4.2	3 - 5	2.8	1 - 4
	2013	15	4.6	3 - 7	3.7	1 - 5	2.9	1 - 4

Table S2.1 (continued): Summary of annual Roller breeding parameter data from the 9 study locations used in model production.

Location	**Year**	**No. nests monitored**	**Mean no. eggs laid**	**Range**	**Mean no. eggs hatched**	**Range**	**Mean no. chicks fledged**	**Range**
Andalusia (Spain)	2014	17	4.7	3 - 6	4.1	1 - 6	3.4	1 - 5
	2015	3	5.0	4 - 6	4.0	3 - 5	3.0	-
Catalonia (Spain)	2001	4	6.0	-	5.5	5 - 6	5.0	-
	2002	8	5.5	5 - 6	5.3	5 - 6	5.3	5 - 6
	2013	6	5.3	5 - 6	5.3	5 - 6	5.3	5 - 6
	2014	18	4.3	2 - 6	4.0	2 - 6	3.8	2 - 6
Languedoc-Roussillon (France)	2011	4	4.3	1 - 6	4.3	1 - 6	3.5	1 - 6
	2012	4	5.3	5 - 6	5.0	4 - 6	4.3	2 - 5
	2013	3	5.7	4 - 7	3.3	2 - 4	3.3	2 - 4
	2014	7	5.3	5 - 6	4.3	3 - 5	3.7	2 - 5
	2015	10	5.2	4 - 8	4.5	1 - 7	4.5	1 - 7
Provence-Alpes-Côte-d'Azur (France)	2004	3	4.0	3 - 5	-	-	3.3	1 - 5
	2005	5	5.2	5 - 6	-	-	4.2	2 - 5
	2006	1	5.0	-	-	-	3.0	-
	2007	20	4.5	2 - 5	-	-	4.1	1 - 5
	2008	16	4.8	3 - 6	-	-	4.2	2 - 6
	2009	35	5.1	1 - 8	-	-	4.4	1 - 7
	2010	30	5.5	2 - 7	-	-	4.5	0 - 7
	2011	46	5.3	3 - 7	-	-	4.5	2 - 7
	2012	30	5.1	3 - 7	-	-	4.7	2 - 7
	2013	7	4.9	3 - 6	-	-	4.0	2 - 6
Tuscany (Italy)	2007	6	5.5	5 - 6	4.3	3 - 6	3.8	3 - 5
	2008	8	4.3	3 - 6	3.6	2 - 5	3.6	2 - 5

Table S2.1 (continued): Summary of annual Roller breeding parameter data from the 9 study locations used in model production.

Location	**Year**	**No. nests monitored**	**Mean no. eggs laid**	**Range**	**Mean no. eggs hatched**	**Range**	**Mean no. chicks fledged**	**Range**
Tuscany (Italy)	2009	13	5.0	3 - 6	4.2	2 - 5	3.5	0 - 5
	2010	15	4.9	2 - 6	4.3	2 - 6	4.1	2 - 6
	2011	10	5.0	4 - 6	3.7	2 - 5	3.6	2 - 5
	2012	5	4.0	3 - 5	3.8	3 - 4	3.8	3 - 4
	2013	2	4.5	4 - 5	4.0	-	4.0	-
	2014	5	5.0	4 - 7	4.2	4 - 5	4.2	4 - 5
Lazio (Italy)	2010	7	5.4	5 - 6	4.6	2 - 6	4.6	2 - 6
	2011	9	5.6	4 - 6	5.1	4 - 6	5.1	4 - 6
	2012	14	5.4	4 - 6	4.9	3 - 6	4.9	3 - 6
	2015	27	4.8	3 - 7	4.2	2 - 6	4.1	2 - 6
Paphos (Republic of Cyprus)	2014	9	4.3	4 - 5	3.7	2 - 5	2.1	0 - 5
	2015	20	4.9	4 - 6	4.1	1 - 5	3.4	1 - 5

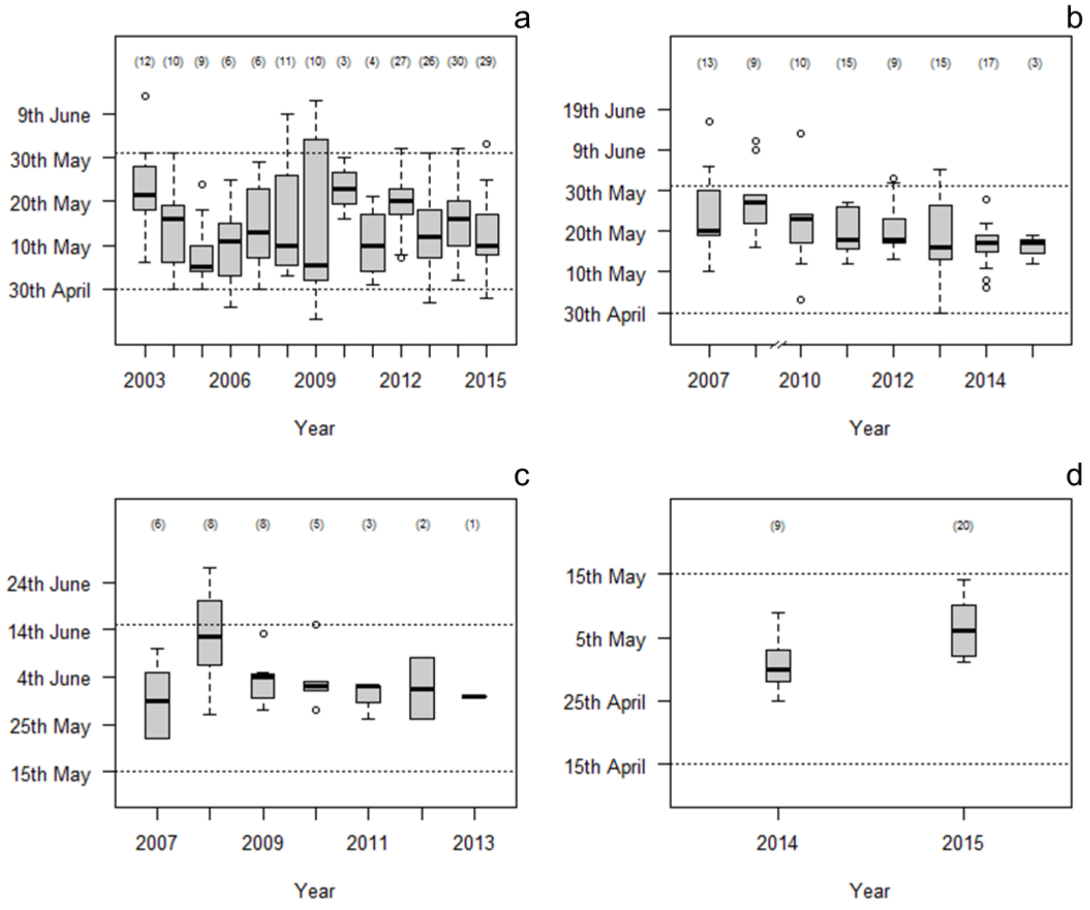

Figure S2.1: Variation in first egg laying dates for a representative sample of Roller populations used in the study; (a) Portugal, (b) southern Spain, (c) Italy, and (d) Cyprus. The lower dashed lines indicate the end of the 'pre-breeding' period during which birds arrive back in the breeding areas and come into breeding condition, and the upper dashed lines indicate the start of the 'chick rearing' period, for each of the study populations (note differing temporal periods on y axis). Numbers in parentheses correspond to the number of occupied Roller nests monitored in each year, and the figures correspond with locations 1, 3, 7, and 9 in Figure 2.1, respectively.

Table S2.2: Averaged parameters, 95% confidence intervals, and sum of Akaike weights for those models retained within the top model set investigating the effect of weather conditions during the preceding winter and pre-breeding periods upon the number of eggs laid by Rollers at 9 locations across the northern Mediterranean (MeaTem = mean temperature, TemRa = temperature range, MaxTem = maximum temperature, ConHRDs = maximum consecutive number of heavy rainfall days, ConRDs = maximum consecutive number of rainfall days, MeaPre = mean precipitation).

Parameter	***β***	***SE***	***2.5% CI***	***97.5% CI***	***ΣAIC$_W$***
Preceding winter					
Intercept	5.014	0.00	4.89	5.14	-
MeaTem	-0.125	0.02	-0.28	-0.03	0.79
TemRa	-0.048	0.02	-0.18	0.00	0.51
MaxTem	-0.047	0.04	-0.25	-0.01	0.36
ConHRDs	0.005	0.02	-0.06	0.14	0.13
ConRDS	-0.002	0.01	-0.11	0.07	0.11
Pre-breeding					
Intercept	5.000	0.00	4.84	5.15	-
ConHRDs	-0.031	0.02	-0.17	0.03	0.63
MeaTem	-0.054	0.02	-0.19	0.02	0.45
MeaPre	-0.026	0.02	-0.19	0.05	0.35
TemRa	-0.001	0.01	-0.10	0.06	0.07

Table S2.3: Averaged parameters, 95% confidence intervals, and sum of Akaike weights for those models retained within the top model set investigating the effect of weather conditions during the preceding winter, pre-breeding, and chick rearing periods upon the number of chicks fledged by Rollers at 8 locations across the northern Mediterranean (MaxTem = maximum temperature, MeaPre = mean precipitation, ConHRDs = maximum consecutive number of heavy rainfall days, NRDs = number of rainfall days, TemRa = temperature range, ConRDs = maximum consecutive number of rainfall days).

Parameter	***β***	***SE***	***2.5% CI***	***97.5% CI***	***ΣAIC_w***
Preceding winter					
Intercept	2.63	0.00	2.44	2.82	-
MaxTem	-0.17	0.00	-0.29	-0.05	1.00
MeaPre	-0.11	0.02	-0.27	-0.01	0.76
ConHRDs	-0.01	0.01	-0.18	0.12	0.21
Pre-breeding					
Intercept	2.63	0.00	2.40	2.87	-
NRDs	-0.07	0.04	-0.30	0.00	0.49
MeaPre	-0.05	0.05	-0.31	0.02	0.36
TemRa	-0.02	0.02	-0.18	0.04	0.34
Chick rearing					
Intercept	2.56	0.00	2.38	2.74	-
TemRa	-0.20	0.00	-0.31	-0.08	1.00
ConRDs	-0.02	0.02	-0.18	0.04	0.30
MeaTem	0.01	0.02	-0.10	0.18	0.16
ConHRDs	-0.003	0.01	-0.14	0.11	0.15

Chapter 3: Are Protected Areas effective at conserving the European Roller (*Coracias garrulus)* in Cyprus?

3.1 Abstract

Identifying temporal and spatial changes in the value of Protected Areas for their qualifying taxa is an important aspect of conservation management. In this paper we use Habitat Suitability Models (HSMs) and remote sensing-derived land cover datasets to evaluate the effectiveness of Important Bird and Biodiversity Areas (IBAs) in maintaining habitat suitability for the declining European Roller (Coracias garrulus) in Cyprus, which supports approximately 10% of the European Union breeding population, in the period 2000 to 2014. Our models showed that IBAs continue to incorporate a greater relative proportion of high quality Roller habitat than external areas. Negative land use changes, in the form of agricultural abandonment or intensification and urbanisation, have occurred to a greater relative extent in areas outside of IBA boundaries, coinciding with a continued decline in the Roller population across the island. Despite this decline, Roller occupancy probabilities calculated from our models remained largely static across Cyprus during the study period, and it is probable that much of the available landscape comprises suboptimal habitat. Further research is therefore required to quantify fine-scale habitat use by the species and to investigate potential negative impacts arising at other points during the species annual cycle.

3.2 Introduction

The world is in the midst of a biodiversity crisis (Butchart et al. 2010), with large-scale land use change arising from increasing resource use by human populations, compounded by the effects of global climate change (Hassan et al. 2005). The maintenance of a global network of Protected Areas under statutory mandate is identified as one of the key targets within the Convention on Biological Diversity by which populations of threatened taxa can be conserved (Marques et al. 2014). Monitoring the effectiveness of Protected Areas in conserving key taxa is an important post-designation component of this process (Caro et al. 2009). Widespread ground-based monitoring can nevertheless prove expensive and time consuming (Le Saout et al. 2013), with modelling methodologies often proving more cost-effective.

Habitat Suitability Models (HSMs) have been used to identify key areas for the conservation of a wide range of taxa (Carone et al. 2014; Prié et al. 2014; Albayrak et al. 2011). They can be used both to identify the broad environmental parameters controlling the distribution of a particular taxon, and to locate specific geographic areas which may support important populations and assist with population assessments (Syfert et al. 2014). The identification of key habitat types and environmental parameters controlling species distributions can then be directly fed into conservation management protocols.

Many bird populations are in decline across Europe, with >30% of European species exhibiting an unfavourable conservation status (BirdLife International 2015). Migratory and farmland birds have been particularly hard hit in recent decades (Donald et al. 2001; Vickery et al. 2014). The maintenance of a suite of Protected Areas has assisted in reversing these declines (Donald et al. 2007), including Special Protection Areas (SPAs) statutorily designated under the auspices of the EU Birds Directive (European Commission 2009), and a non-statutory ‘shadow list’ of Important Bird and Biodiversity Areas (IBAs) identified by BirdLife International and local partners (Heath & Evans 2000).

The management protocols required to maintain the integrity of these Protected Areas are shaped by European Union (EU) policy, with many of the conservation measures put in place to improve the status of declining European farmland bird species encoded within Pillars I and II of the EU Common Agricultural Policy (CAP) (Poláková et al. 2011). The pillars seek to safeguard farmland biodiversity within a framework which ensures productivity and openness within the European agricultural market.

The European Roller (*Coracias garrulus*; henceforth Roller) is a declining migratory bird species, largely reliant upon extensive agricultural landscapes during the breeding season (Cramp & Simmons. 1998). The species formally bred across large swathes of the Mediterranean and Eastern Europe. However, the majority of European populations, comprising 50% to 74% of the species global range, have declined sharply during the past century (BirdLife International 2015), with well-documented range contractions observed in several countries (Sackl et al. 2004; Karpuska et al. 2011; Catry et al. 2011).

The Mediterranean island of Cyprus has previously been identified as a stronghold for the Roller, and is considered to support one of the largest European populations. The species is predominantly found at elevations below 800m on the island (Flint & Stewart, 1992), with an estimated breeding population of 1,000 to 3,000 pairs identified during the last European assessment (BirdLife International 2015). This represents >8% of the Roller population within EU member states. Nevertheless, the Cypriot population exhibited a 30% to 50% decline in the period 2003 to 2013 (BirdLife International 2004; BirdLife International 2015). Another recent long-term study has indicated that the Roller population has declined dramatically (by as much as 50%) within Paphos District, in the west of the island, between 2003 and 2011 (Pomeroy et al. 2013).

The species is listed upon Annex 1 of the EU Birds Directive, with 11 IBAs identified for it between 1989 and 2014 (Hellicar et al. 2014), all of which are also (at least partially) designated as SPAs (Table S3.1 (Appendix)). An additional 2 IBAs are identified for the species within the Turkish-controlled north of the island, although neither have yet been designated as an SPA under EU legislation. Alongside these designations, Cyprus has experienced increased levels of agricultural intensification within its remaining farmland areas in recent years (BirdLife Cyprus 2006), although this has potentially been counteracted by an increase in the level of agricultural land abandonment (Ieronymidou 2012). It is therefore important to understand how these changes have affected Roller distribution on the island in and outside of designated sites.

The main aims of the study are therefore to: (1) investigate how post-2000 land use changes have affected the distribution of the Roller across Cyprus; (2) evaluate the effectiveness of the IBA network in maintaining habitat suitability for the species during the same period, via comparison with external, non-designated, sites, and; (3) to discuss the potential impact of future land use changes upon the conservation of the Cypriot Roller population.

3.3 Methods

Study Area

The study area is located in the north-west of Paphos District, within the Republic of Cyprus, and comprises the most important breeding locality for Rollers on the island (Hellicar et al, 2014). It is situated within the Akamas Peninsula IBA, which supports up to 300 breeding Roller pairs, and has exhibited a high rate of land use change since Cyprus joined the EU in 2004 (Ieronymidou 2012).

It is bounded by the Akamas Peninsula to the north-west, by the foothills of the Troodos Mountains to the east, and straddles the topographically diverse Mammonia Complex. The latter comprises a range of hills rising to approximately 670m above sea level, and also incorporates lower elevation coastal areas to the west. The area supports a range of farming land use types, representative of Cyprus, at different spatial scales. Several villages are located within the inland portion of the study area, with larger towns present at its northern and south-western coastal limits.

Field Survey

A total of 493.9km of repeated road transects were driven across the study area between 14th May and 24th June 2014. These dates covered the entire chick-rearing period for the majority of Roller nests within the study area (*pers. obs*.) Most monitored Roller nests had chicks by mid-May, and so sightings during the survey period were not biased by the absence of incubating individuals. Each survey bout was completed within a single morning, commencing half an hour after sunrise and finishing prior to 11am, when higher temperatures reduced Roller foraging activity.

Each survey was carried out by two observers seated in the front of a slow-moving vehicle (driven at c.30km/h) who each scanned both sides of the road within a 400m wide survey corridor for Roller presence. Whenever a Roller was observed, its perpendicular position relative to the road centreline was measured using a laser rangefinder and the XY co-ordinates of the road centreline location recorded.

Habitat Suitability Model

We used confirmed presence/absence data from the road transects, and remotely-sensed climatic, topographic, and land-use variables, to model the spatial distribution of the Roller across Cyprus at elevations below 800m. To develop the HSM, Roller presence and absences were marked on a 100m cell grid overlaid upon the 400m wide road survey corridor. Cells were assigned as ‘presence’ if a Roller was sighted within them at any point during the survey period, with this classification not affected by repeated or grouped observations. Cell size was selected to reflect the home range of the study species (Guisan et al. 2007) and the resolution of available remote sensing datasets, with the majority of observed foraging undertaken within 600m of the nest site (*see Chapter 4*).

Predictor Variables

Climatic, topographic, land-use, and vegetation productivity variables (Table 3.1) were related to Roller presence and absence to assess their influence on Roller foraging site selection. Temperature and precipitation datasets (at 100m x 100m and 1km x 1km resolution, respectively; LPDAAC, NASA; www.worldclim.org) were included to investigate the effect of climatic variation on an annual and monthly basis. Temperature data was available for the previous 5 years, with precipitation data available as a 30 year mean. Other, more recent, precipitation datasets are available, but not at resolutions <10km, which were considered incompatible with the scale at which Roller observations were made. The temporal resolution of the temperature dataset was maintained at the 5 year period (rather than upscaled to a 30 year mean) to increase the temporal specificity of the predictor variables incorporated in the model.

Elevation data and its derived factors (slope and aspect) were calculated from a Digital Elevation Model (DEM) at 90m x 90m resolution (SRTM, NASA). Spatial variability in primary productivity was investigated via the inclusion of a 5 year Normalized Difference Vegetation Index (NDVI) dataset at 250m x 250m resolution (LPDAAC, NASA). The inclusion of the Corine Land Cover (CLC) 2012 (the year closest to the 2014 field season) 100m x 100m resolution dataset detailed the land cover/broad-scale habitat type within each cell (Bossard,et al. 2000). 11 CLC types were identified within the survey corridor, although 3 were extremely rare and therefore lumped within similar, more abundant, types to allow extrapolation. All raster grids unavailable at the required cell size were resampled using bilinear

Table 3.1: Independent variables analysed to develop a Habitat Suitability Model for the Roller on the island of Cyprus.

Variable name	Variable type	Description	Source
Climatic			
Annual temperature	Quantitative	Mean annual temperature °C	5 year (2009 - 2013) MODIS Global temperature, 8-Day 100m resolution: MOD11A1 (LPDAAC, NASA)
January temperature	Quantitative	Mean January temperature (temperature at coldest month) °C	
August temperature	Quantitative	Mean August temperature (temperature at warmest month) in °C	
January precipitation	Quantitative	Mean January rainfall (precipitation during wettest month) in mm	30 year (1960 - 1990) precipitation dataset (WorldClim) at 30" (approx. 1km x 1km) projection
March precipitation	Quantitative	Mean March rainfall (precipitation immediately prior to breeding season) in mm	
Annual precipitation	Quantitative	Mean annual rainfall in mm	
Topographic			
Elevation	Quantitative	Mean elevation of cell in m	90m x 90m Digital Elevation Model (Shuttle Radar Topographic Mission, NASA)
Slope	Quantitative	Mean slope angle of cell in degrees	
Aspect	Categorical	Orientation (North, South, East, West) of cell	
Land use			
CLC 2012 category	Categorical	Corine Land Cover (CLC) 2012 broad habitat type within cell	CLC 2012 100m x 100m raster (European Environment Agency)
Annual crops associated with permanent crops		*Combined category comprising: (a) Annual Crops Associated With Permanent Crops, and (b) Complex Cultivation Patterns*	
Urban habitat		*Discontinuous Urban Fabric*	
Land principally occupied by agriculture		*Land Principally Occupied By Agriculture With Significant Areas Of Natural Vegetation* (consistent with Mediterranean 'mosaic' habitat types)	
Natural grassland		*Natural Grassland*	
Non-irrigated arable		*Non-irrigated Arable Land*	
Scrubland		*Sclerophylous Vegetation*	
Vineyards		*Vineyards*	
Other habitat		*Combined category comprising: (a) Coniferous Forest, (b) Permanently-irrigated Land, and (c) Mineral Extraction Sites*	
Productivity			
May NDVI	Quantitative	Mean cell Normalized Difference Vegetation Index in May (NDVI at start of chick-rearing period)	5 year (2009 - 2013) MODIS Global NDVI, 16-Day 250m resolution: MOD13Q1 (LPDAAC, NASA)
Annual NDVI	Quantitative	Mean annual cell NDVI	

interpolation at a 100m x 100m resolution within ArcGIS 10.3 (ESRI, 2014) to provide an evenly-sized and overlapping dataset prior to the extraction of cell values.

Statistical analyses and model development

All statistical analyses were carried out using R version 3.2.3 (R Development Core Team, 2016). In order to select a final list of predictor variables for inclusion in the model, all of the initial variables detailed in Table 3.1 were first assessed for the effects of multi-collinearity. Any strongly correlated variable pair (exhibiting a Pearson's Correlation coefficient >0.7) were examined, and (unless a strong ecological argument could be made for their retention) only the better performing variable within the univariate model was retained. The Variance Inflation Factor (VIF) of each variable was also calculated, with variables exhibiting a VIF of >5 (Zuur et al. 2010) removed from further analyses.

All Roller presence (*n*=108) and absence (*n*=2,415) data points from within the survey corridor were separately identified, with 70% of the presence data points (*n*=76) randomly selected for model training. The remaining random 30% of presence data points (*n*=32) were retained for model testing. A random sample of absence data points were then independently selected at a 2:1 ratio for use in model testing (*n*=152) and training (*n*=64). A Generalised Linear Model (GLM) with a binomial distribution (logit link function) was developed using the finalised input variables from the 70% model training dataset. Automated backwards stepwise selection was undertaken, using the Akaike Information Criterion (AIC) as the selection criterion (Meynard & Quinn 2007). Under this criterion only those parameters identified as significant were retained in the final stepwise selection.

The resulting logistic GLM was then applied to the retained 30% testing dataset, with the Area under the Receiver Operating Curve (AUC) calculated as a measure of the model's discriminatory power (Fielding & Bell 1997). This process was repeated for 100 iterations, with new training and testing data point combinations randomly selected at each iteration. All resultant models within the 100 iterations exhibiting an AUC >0.7 were then selected for further investigation. The use of this cut-off meant that the selected models had at least a 'fair' discriminatory ability, with AUCs >0.8 and >0.9 indicating 'good' and 'excellent' abilities, respectively.

The odds ratios of each variable within the retained models were then assessed, with any model solely exhibiting variables with odds ratio confidence intervals overlapping 1 excluded. Cohen's kappa (*k*) (Cohen 1960) was calculated for each of the remaining models, with a cut-off of >0.2 applied, indicating 'fair' prediction power. Nagelkerke R_n^2 values were also calculated to give a measure of model calibration (Nagelkerke 1991) with a cut-off of >0.2 applied, indicating 'fair' model calibration.

As each of the final model set were produced using different random combinations of the original Roller presence/absence dataset, it was not possible to average coefficients between them. Instead, predictions of Roller occupancy probability across Cyprus were produced from each of the final retained model set, with the predictions from each then back-transformed and averaged. Averaging probabilities, rather than the averaging of model coefficients, is supported in the literature and is a robust method of maximising prediction accuracy from a subsampled dataset (Araujo & New 2007), in line with ensemble forecasting methods. A map of mean 2014 Roller occupancy probability values was then produced using ArcGIS 10.3. Due to the 1:2 ratio of presence/absence data used in building the models, a 0.33 occupancy probability threshold was applied (Hosmer & Lemeshow 2004), with cells of <0.32 designated as 'low', 0.33 to 0.65 as 'medium', and >0.66 as "high" Roller occupancy probability.

The retained models used to produce the map of mean 2014 Roller occupancy probability were then used to backcast Roller occupancy probability for the year 2000. The CLC 2000 dataset was substituted at the prediction stage and a map of mean 2000 Roller occupancy probability produced by again averaging the predictions from each model. Predicted values of each 100m cell within the 2000 map were then subtracted from those within the 2014 map. The resulting values were used to produce a raster map of changes in mean Roller occupancy probability between 2000 and 2014.

Effectiveness of Cypriot IBAs in maintaining value for Rollers

To analyse the effectiveness of Cypriot IBAs in maintaining value for Rollers, the area of 'low', 'medium', and 'high' Roller occupancy probability in and outside of IBAs were calculated for both 2000 and 2014. Cells supporting CLC types in 2000 not present in the 2014 model, for which it was not possible to extrapolate, were identified as 'unknown'. Comparative figures were then produced detailing: (1) differences in the area of 'medium' and high' probability categories in and outside of relevant IBAs in 2014, and; (2) changes in the extent of these areas between 2000 and 2014. To investigate whether any observed changes were potentially driven by differences in the habitat composition and/or rate of broad-scale habitat change, the areas of all CLC types in and outside of Roller-designated IBAs were extracted from the CLC 2000 and 2012 datasets. The total area in 2010, and the rate of change in extent between 2000 and 2012, were then calculated for all relevant habitat types, comprising both those incorporated within the HSM and others indicative of agricultural land use change (i.e. abandonment or development).

3.4 Results

Habitat Suitability Model selection

Roller presence was recorded in a total of 108 100m x 100m cells within the survey corridor, with 2,415 cells recording Roller absence. 5 variables (*Annual precipitation, Aspect, Corine Land Cover 2012 category, Elevation, and Slope*) were included in the initial backwards stepwise model selection, with all other variables proving strongly collinear. *Annual precipitation* and *Elevation* did exhibit moderate collinearity, but were both retained due to their potential to control different aspects of Roller distribution. The AUC scores of the initial 100 model iterations ranged between 0.53 and 0.78, with 17 of the models exhibiting an AUC >0.7. Of these models, only 2 incorporated at least one co-efficient with OR confidence intervals non-overlapping with 1 and a Cohen’s kappa of >0.2 (fair predictive ability) and values of R_n^2 >0.2 (fair level of model calibration; Table 3.2). The outputs of these 2 models were therefore used in prediction averaging and production of model-specific occurrence probability maps (Table S3.2 & Figures S3.1 to S3.2 (Appendix)).

One of the models retained all 5 input variables, with the other retaining all variables apart from *Aspect*. The models indicated that Rollers prefer low/mid-elevation habitats, and avoid steeper slopes. Mosaics of low intensity agricultural land and semi-natural habitats are preferred, with areas of intensive agriculture, forest, scrubland, and urban areas avoided.

Effectiveness of Cypriot IBAs in maintaining value to Rollers

The 2014 map (Figure 3.1a), produced from the averaged predictions of the 2 retained models, identified two discrete areas of the island exhibiting ‘high’ (>66%) Roller occupancy probability. These comprise the eastern limit of the Karpasia Peninsula in the north-east of Cyprus, and a separate area in the north-east of the Akamas Peninsula, located in the extreme north-west of the island. Both of these

Table 3.2: Retained models used to produce a Habitat Suitability Model for the Roller on the island of Cyprus, and direction of the retained model coefficients

Model no.	**Parameters in the model**	**AUC**	***k***	R_n^2
51	Intercept - Elevation - Slope + Annual precipitation + Corine Land Cover 2012 category	0.72	0.20	0.22
75	Intercept - Elevation - Slope + Aspect + Annual precipitation + Corine Land Cover 2012 category	0.71	0.30	0.20

Model parameter	**Coefficient direction**	
	Model 51	**Model 75**
Elevation	-ve	-ve
Slope	-ve	-ve
Annual precipitation	+ve	+ve
Aspect		
North	-ve	na
South	-ve	na
West	-ve	na
Corine Land Cover 2012 category		
Annual crops associated with permanent crops	-ve	-ve
Urban habitat	-ve	-ve
Land principally occupied by agriculture	+ve	+ve
Natural grassland	-ve	-ve
Non-irrigated arable	+ve	+ve
Other habitat	-ve	-ve
Scrubland	-ve	-ve
Vineyards	-ve	-ve

locations coincide with IBAs designated for the Roller (Figure 3.1a; Figure S3.3 (Appendix)). ‘Medium’ probabilities (33 to 65%) were observed in an arc across the south-west of the island, coinciding with a concentration of IBAs designated for the species, and in areas bordering the Karpasia Peninsula IBA. Little relative change in Roller occupancy probability between 2000 and 2014 was observed across the island (Figure 3.1b), with negative changes mainly located within coastal areas, and

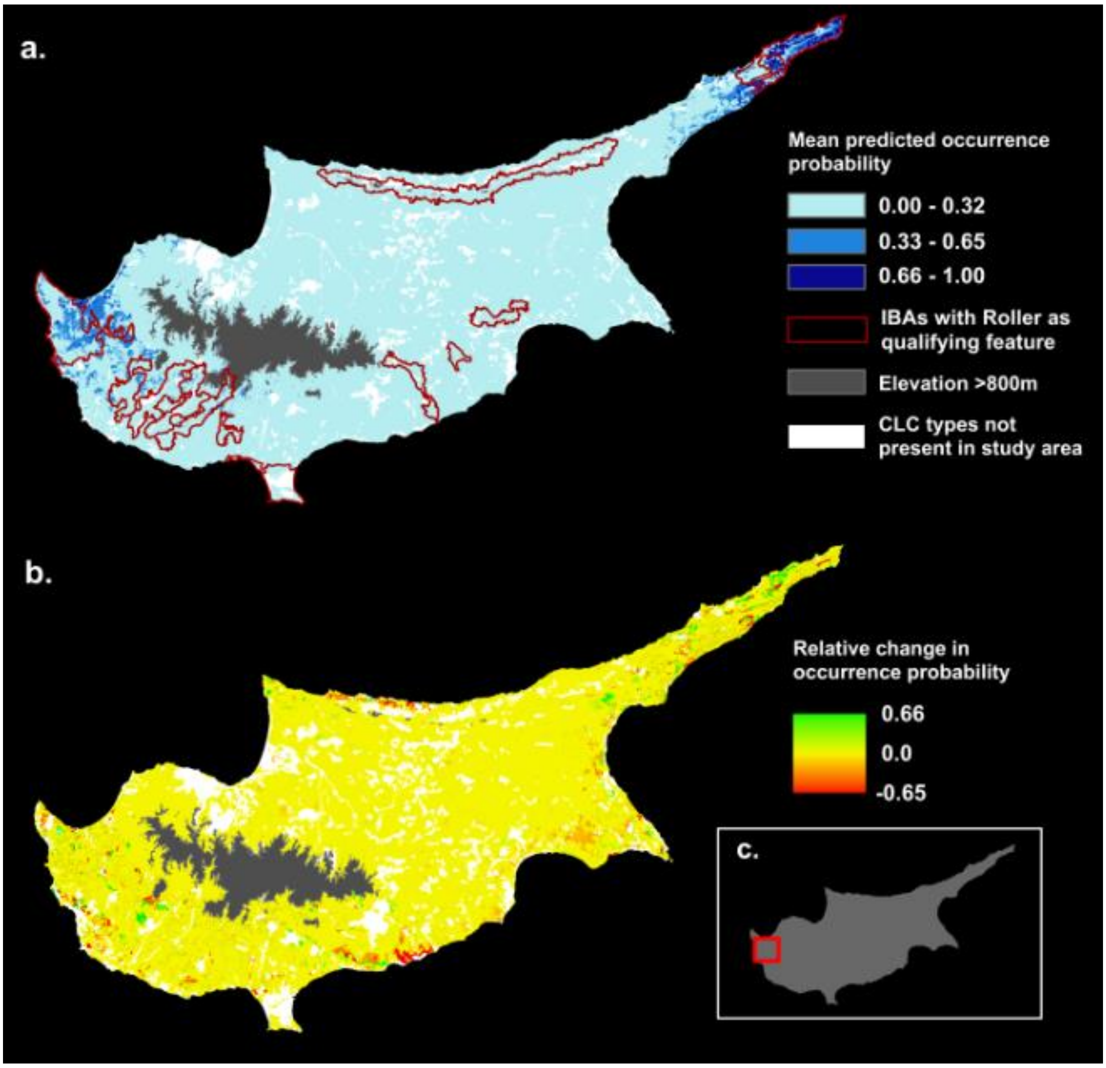

Figure 3.1: Roller occupancy probability across Cyprus and the IBA network: (a) predicted 2014 Roller occupancy probability across the island, (b) changes in Roller occupancy probability between 2000 and 2014, and (c: inset) the location of the 2014 study area.

positive changes within the south-western arc and along the Karpasia Peninsula in the north-east.

IBAs showed a larger area of suitable (i.e. ‘high’ or ‘medium’ occupancy probability) habitat in 2014 than external areas (Figure 3.2a). 16.9% of the IBA land area comprised suitable habitat, of which 5.0% showed ‘high’ occupancy probability. This compares to an area of 3.5% of suitable habitat outside of IBAs, of which only 0.5% showed ‘high’ occupancy probability. Nevertheless, these external areas still comprise 37km^2 of non-designated high occupancy probability Roller habitat.

There were relatively small changes in the relative extents of ‘high’, ‘medium’, and

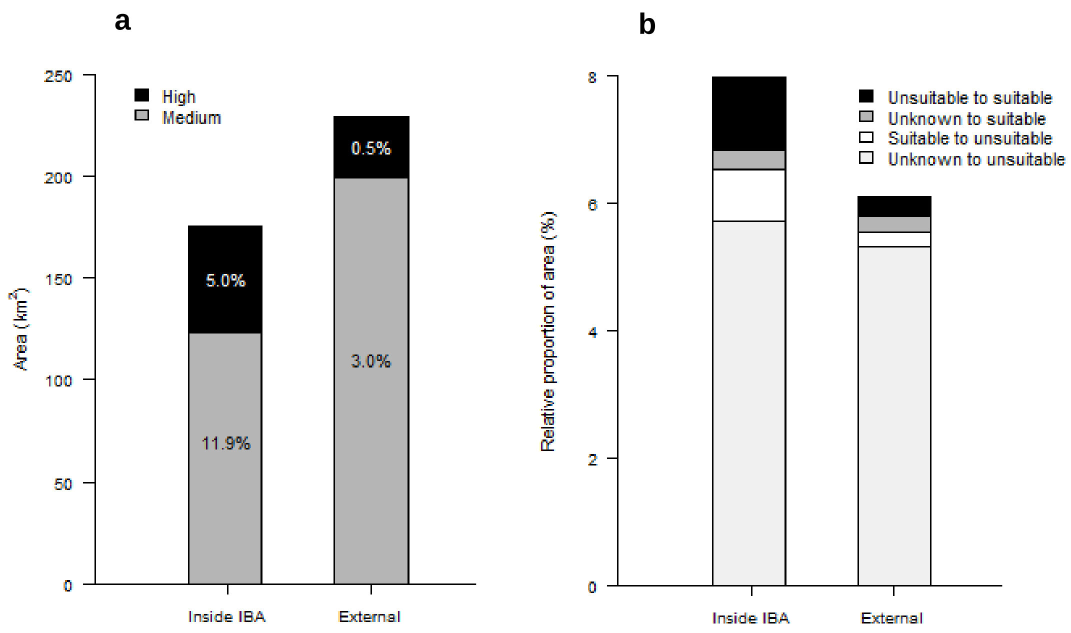

Figure 3.2: Changes in the extent of suitable Roller habitat in Cyprus, 2000 to 2014: (a) Areas of high and medium Roller occupancy probability in 2014, inside and outside of IBAs designated for the species (embedded figures comprise percentage of total respective areas: IBA area = 1162.46 km^2, external area = 7393.80 km^2), and; (b) directional changes in the extent of suitable (combined medium and high occupancy probability) habitat between 2000 and 2014 inside and outside of IBAs. Unknown habitat refers to areas for which extrapolation is not possible for 2000 due to the presence of Corine Land Cover types not represented in the 2014 model training dataset (see Methods).

‘low’ occupancy probability habitat both in and outside of IBAs between 2000 and 2014 (Figure 3.2b). 1,069.46km^2 (92.0%) of the IBA land area, and 6,942.78km^2 (93.9%) of external areas, retained the same occupancy probability during the period. Of the remaining 93.00km^2 land area within IBAs, 70.91km^2 (6.1% of the total) was classified as ‘unknown’ in 2000, corresponding with 414.05km^2 (5.6% of the total) in external areas. Proportionately a greater area of unsuitable habitat became suitable during the period within IBAs (12.79km^2, equitable to 1.1%) than in external areas (22.18km^2, equitable to 0.3%) although, when balanced against suitable to unsuitable changes, the net positive change corresponds to 3.49km^2 (0.3%) within IBAs and 7.39km^2 (0.1%) within external areas.

Larger relative proportions of urban habitat and permanently-irrigated land were present outside of IBAs in 2000 (Figure 3.3a), with external areas also supporting a

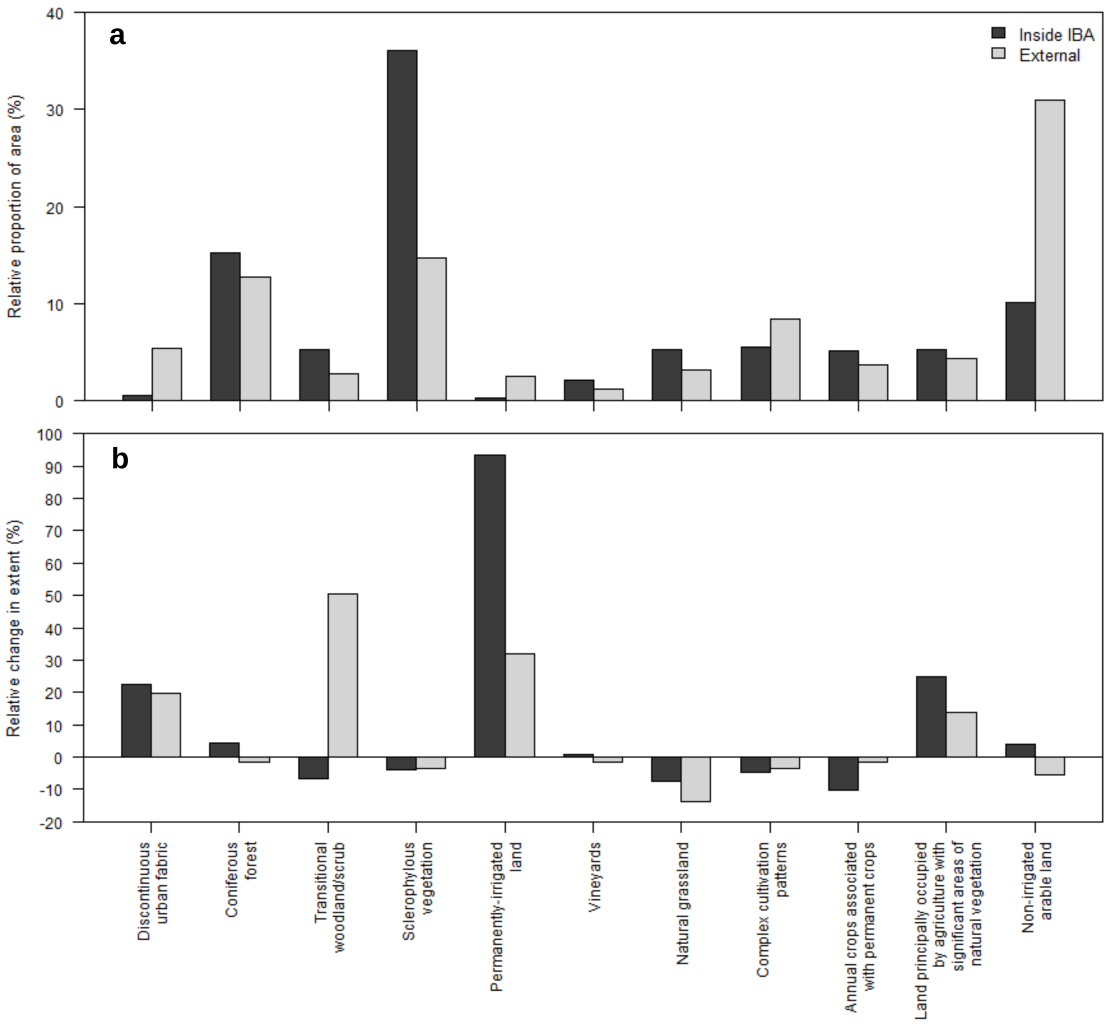

Figure 3.3: Corine Land Cover changes (CLC) in Cyprus 2000 to 2012: (a) relative composition of key CLC habitat types, below 800m elevation, in the year 2000 inside and outside of IBAs designated for the Roller, and (b) relative changes in extent of key CLC habitat types between 2000 and 2012 inside and outside of IBAs designated for the Roller (IBA area = 1162.46 km^2, external area = 7393.80 km^2). A full breakdown of island wide changes in all CLC habitat types is provided in Table S3.3 (Appendix).

much larger relative extent of non-irrigated arable land. IBAs exhibited a much larger relative proportion of scrubland habitat than external areas, with all other habitats incorporated at similar relative extents. Relative increases in the extent of urban habitat, land principally occupied by agriculture but with significant areas of natural vegetation, and permanently-irrigated land were noted within both IBAs and external areas between 2000 and 2012 (Figure 3.3b), with these increases much larger for the latter 2 CLC types within IBAs. Small decreases in the extent of scrubland habitat, natural grasslands, complex cultivation patterns, and annual crops associated with permanent crops were also observed within both areas. The relative area of non-irrigated arable land, coniferous forest, and vineyards increased slightly within IBAs, and declined slightly in external areas. The largest disparity was noted for the relative extent of transitional woodland/scrub habitats, which declined slightly within IBAs but increased to a much larger extent within external areas. Table S3.3 (Appendix) details the percentage change in all CLC types across the island in the 2000 to 2012 period, including those not found within the Roller IBA network.

3.5 Discussion

Describers of Roller occupancy

The 2014 map of potential Roller occupancy produced using the retained model set identified areas within the 2 most important IBAs designated for the species (Hellicar et al, 2014) as exhibiting the highest occupancy probability. This suggests that the retained models captured the key habitat associations of Roller distribution on the island, and supports the use of averaged model predictions.

Rollers are known to avoid higher elevations and coniferous forest areas on Cyprus (Flint & Stewart 1992), with both retained models capturing this relationship. However this study also found a positive relationship with increasing precipitation and Roller presence, possibly describing the effect of largely avoided xeric and scrubland habitats dominant along much of the Cypriot coast. A negative relationship with increasing slope can be explained by the steeper gradients found at higher elevations.

The models indicate that Rollers are positively associated with mosaics of low-intensity farmland and semi-natural vegetation, avoiding intensively managed agricultural areas and standing permanent crops. This can be explained by the species' requirement for an abundance of large invertebrate prey (Avilés & Parejo 2002; Bohus 2002), and structures (such as mature trees and abandoned buildings) suitable for use as cavity-bearing nest sites and hunting perches (Henriques et al. 2004). The negative association with urban areas could be due to a variety of factors, including a paucity of suitable foraging habitat within this land use type, or increased levels of disturbance or predation. The negative relationship with areas of natural grassland, a favoured foraging habitat within other areas of the species range (Del Hoyo et al. 2001), is best explained by the rarity of suitable hunting perches (Sackl et al. 2004) within otherwise suitable extensive grassland areas.

Land use change effects within Cyprus

The large relative declines observed in the extent of natural grasslands (both inside and outside of IBAs), and of annual crops associated with permanent crops (primarily within IBAs), is potentially indicative of the localised intensification of cereal production, as bringing extensive areas of natural grassland into rotation may be more cost effective than maintaining traditional, smaller scale, mixed farming, activities.

The increase in the extent of transitional woodland/scrub observed within external areas, and the decreases in the extent of non-irrigated arable land, is however considered indicative of increased levels of agricultural abandonment outside of IBAs and the reversion of cleared areas to semi-natural habitats. The increases observed in the extent of land principally occupied by agriculture but retaining significant areas of natural vegetation, both in and outside of IBAs, is also indicative of abandonment. Despite its positive association with Roller occupancy probability in the retained models, this land use type could be considered to comprise previously suitable Roller habitat which may be suboptimal at the landscape scale (Catry et al. 2013), and in the process of degrading further as scrub overtakes abandoned agricultural areas within it.

Rural depopulation and fiscal disincentives to maintain traditional farming practises in the face of an increasingly urbanised Cypriot population (Ieronymidou 2012) are likely to continue the agricultural abandonment process. It is considered probable that increasing urbanisation and the decreasing extent of low-intensity open farmland habitats favoured by the species are likely to negatively impact Roller populations in Cyprus. This has been the case historically elsewhere within the species' European range, with recent studies elsewhere in the Mediterranean identifying negative effects of land abandonment on a wide range of open country species (Sirami et al. 2008).

Increases in the extent of intensive agricultural land use types negatively associated with Roller occurrence in the retained models, including permanently irrigated land, are likely to continue in the face of global climate change. As annual precipitation decreases and/or becomes less predictable, and annual temperatures rise, the use of irrigated high intensity farming practises is becoming more prevalent in the marginal agricultural habitats of the Mediterranean basin (Brotons et al. 2004).

The increasing trend in levels of urbanisation within Cyprus may also negatively affect the Roller population, with the presence of urban fabric mostly negatively associated with the presence of the species in the retained model set. Ongoing urbanisation around existing towns and cities, and the continued development of coastal tourist areas, potentially explains the negative trends in Roller occupancy in many coastal areas identified in the 2000 - 2014 period.

Effectiveness of the existing IBA network for Roller conservation

Roller occupancy probability remained constant across the majority of Cyprus in the period 2000 to 2014, with quantifiable changes in Roller habitat quality (i.e. unsuitable habitat to suitable habitat, and vice versa) comprising a small proportion within both IBAs and external areas. Nevertheless, the relative area of suitable habitat within IBAs in 2014 was 4.8x larger than that within external areas, despite 37km^2 of non-designated, high quality, habitat being identified outside of IBAs. The IBAs would therefore appear to be retaining their overall value to Roller populations, in terms of occupancy potential. The continued importance of the 2 most populous IBAs for the species on the island is also notable.

Despite their retention of value to Rollers, several Cypriot IBAs are under threat, with the Akamas Peninsula IBA listed as an international ‘IBA in danger’ (BirdLife International 2016), due to the negative effects of urbanisation, tourism, and agricultural change. The key legislative protection currently afforded Cypriot IBAs is largely via proscriptions upon detrimental development projects within their SPA designated components, although non-compliance by the Cypriot authorities has been observed (BirdLife Cyprus 2013). Sympathetic Management Plans have yet to be produced for the IBAs, and are in any case legally non-binding (BirdLife Cyprus 2013). Despite this, €4 million have been committed to restoring, preserving, and enhancing ecosystems within Natura 2000 sites (including SPAs) under the 2014 - 2020 Cyprus Rural Development Plan (RDP), with 9% of agricultural land to be under ecologically friendly management contracts by the end of the period (European Commission 2016).

Nevertheless, Cyprus’ Roller population has declined during the study period (BirdLife International 2015) despite occupancy probability remaining relatively constant across large areas of the island. Occupancy probability does not directly equate to habitat quality, and it is possible that some suitable foraging areas, as identified using presence/absence data, may actually comprise suboptimal habitats for the species capable of negatively affecting breeding success (Huhta et al. 1999). The potential issues of nest site limitation, and impacts arising during migration and in the wintering areas, are also not captured in the models and may go some way to explaining the observed declines.

Ultimately, in order to further the conservation of the Roller on Cyprus, it is recommended that Cypriot conservation authorities should, as a priority, incorporate the 37km^2 of currently non-designated, high quality, Roller habitat identified in the study within newly designated areas. This should focus upon either the extension of the existing Akamas Peninsula IBA (in the north-west of the island), and the Karpasia Peninsula IBA (in the north-east), or the designation of smaller ‘satellite’ IBAs in close proximity to them (see Figure S3.3 (Appendix)). These 2 IBAs already comprise the most important designated sites for Rollers on the island (Hellicar et al. 2014), and the designation of high quality locations on their peripheries, alongside increased levels of compliance by the Cypriot authorities and the institution of sensitive management plans within the IBAs, will assist in maintaining their value to the nationally important Roller populations that they support.

3.6 Acknowledgements

I would like to thank Alessandro Gravano and Aldina Franco for their assistance in data collection during the Roller presence/absence surveys carried out in 2014. The project is funded through a Natural Environment Research Council Studentship Grant (No. 1210309), and the author is also a beneficiary of both an A.G. Leventis Foundation Scholarship and British Trust for Ornithology CASE studentship award. Ines Catry benefited from a post-doctoral grant from Fundação para a Ciência e Tecnologia (SFRH/BPD/102637/2014).

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Appendix: Supporting information

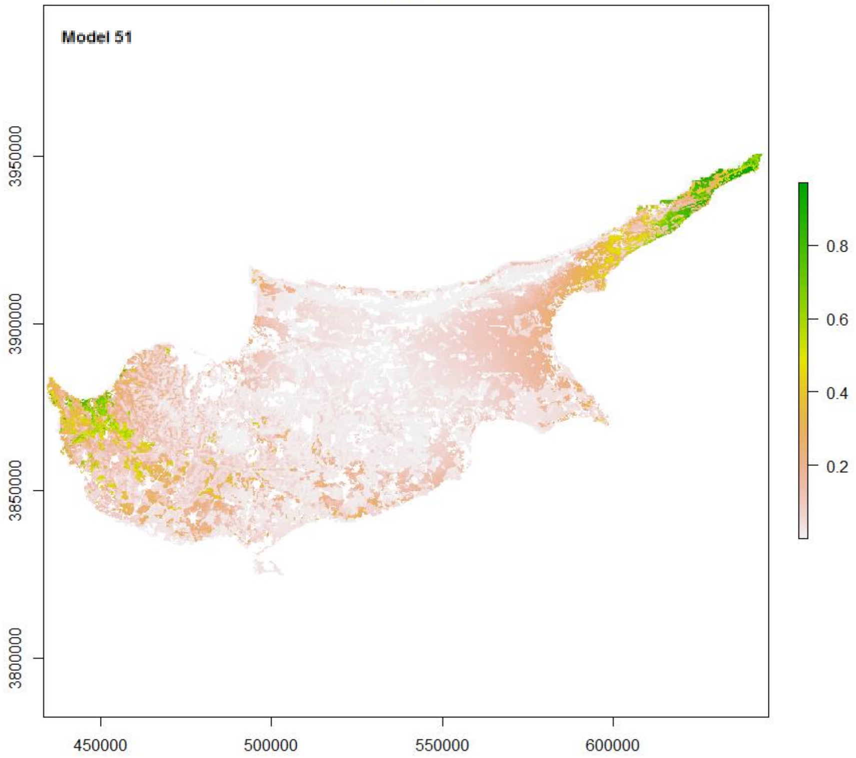
Table S3.1: Designation details of Cypriot Important Bird and Biodiversity Areas (IBA's) with Roller as a qualifying feature, and the area of each incorporated within Special Protection Areas (SPA's; Hellicar et al. 2014).

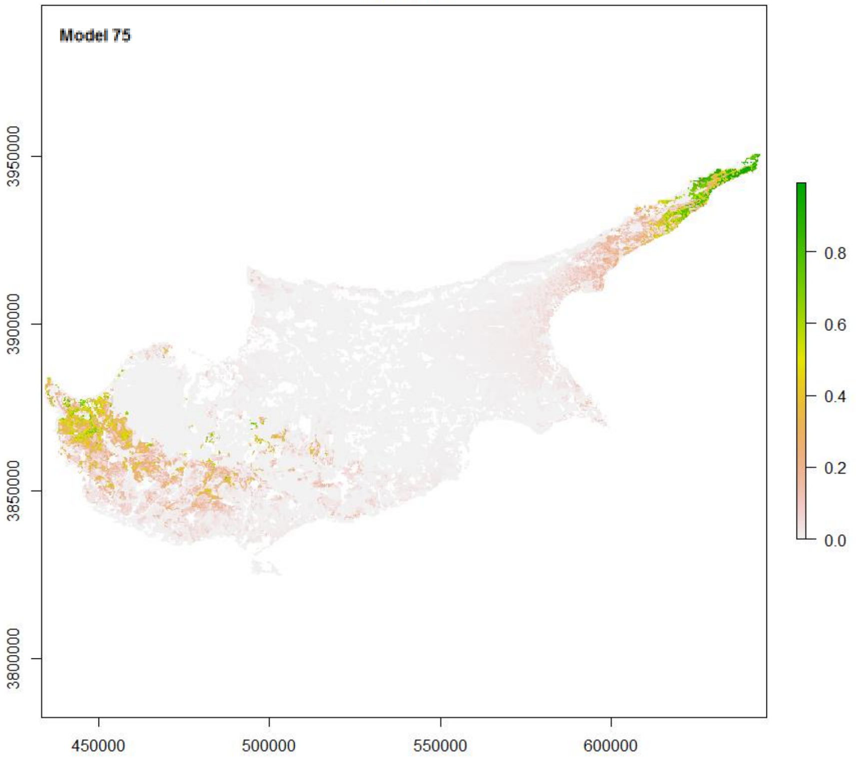
IBA full name	IBA designation year	SPA designation year	% of IBA covered by SPA	IBA Area (km^2)
Akamas and Agia Aikaterini-Agia Paraskevi Gorges	1989	2007	55	207.72
Karpasia Peninsula	1989	na	na	141.41
Xeros Valley and Hannoutaris Cliffs	1989	2005	66	95.58
Diarizos Valley	2004	2007	71	88.04
Ezousa Valley and Cliffs	2014	2007	83	74.92
Pentadaktylos Mountains	1989	na	na	263.76
Cha Potami River	2014	2007	88	78.96
Koshi-Pallourokampos and Troulloi Plain	2014	2007	82*	45.21
Paramali River and Plateau	2014	2008	76	23.49
Pentashoinos River	2014	2007	86	47.87
Saramas Valley	2014	2008	100	15.56
Panagia Stazousa River	2014	2007	100	17.45
Akrotiri Peninsula - Episkopi Cliffs	1989	2010	60	78.91

**The IBA is effectively 100% protected currently due to its partial inclusion within the UN-controlled buffer zone between the Republic of Cyprus and the occupied north of the island*

Table S3.2: Coefficients and summary information from the 2 Species Distribution Models used to produce the map of 2014 Roller occupancy probability in Cyprus.

Model No.	Variable	Estimate	Standard error	z value	Pr(>|z|)
51	Intercept	-9.18256	6.768906	-1.357	0.1749
	Elevation	-0.008455	0.00531	-1.592	0.1113
	Slope	-0.053509	0.038109	-1.404	0.1603
	Annual precipitation	0.224678	0.158123	1.421	0.1553
	Corine Land Cover 2012 category				
	Urban habitat	-2.046597	1.085125	-1.886	0.0593
	Land principally occupied by agriculture	0.831674	0.464037	1.792	0.0731
	Natural grassland	-0.761546	0.788528	-0.966	0.3342
	Non-irrigated arable	0.529426	0.49346	1.073	0.2833
	Other habitat	-1.2068	1.212154	-0.996	0.3195
	Scrubland	-1.770375	0.64929	-2.727	0.0064
	Vineyards	-1.161028	0.56588	-2.052	0.0402
75	Intercept	-15.18347	6.97891	-2.176	0.0296
	Elevation	-0.01112	0.00554	-2.007	0.0448
	Slope	-0.09033	0.04148	-2.178	0.0294
	Aspect				
	North	-0.83099	0.38971	-2.132	0.033
	South	-1.04588	0.54852	-1.907	0.0566
	West	-0.6607	0.4752	-1.39	0.1644
	Annual precipitation	0.36535	0.16423	2.225	0.0261
	Corine Land Cover 2012 category				
	Urban habitat	-1.30854	0.72341	-1.809	0.0705
	Land principally occupied by agriculture	0.80233	0.47835	1.677	0.0935
	Natural grassland	-0.22775	0.71213	-0.32	0.7491
	Non-irrigated arable	0.23798	0.48129	0.494	0.621
	Other habitat	-15.9557	878.3198	-0.018	0.9855
	Scrubland	-1.76168	0.86579	-2.035	0.0419
	Vineyards	-0.87465	0.56712	-1.542	0.123





Figures S3.1 to S3.2: Maps of 2014 Roller occupancy probability for Cyprus produced from the 2 selected Species Distribution Models, subsequently used in prediction averaging and production of a Habitat Suitability Model for the Roller on Cyprus.

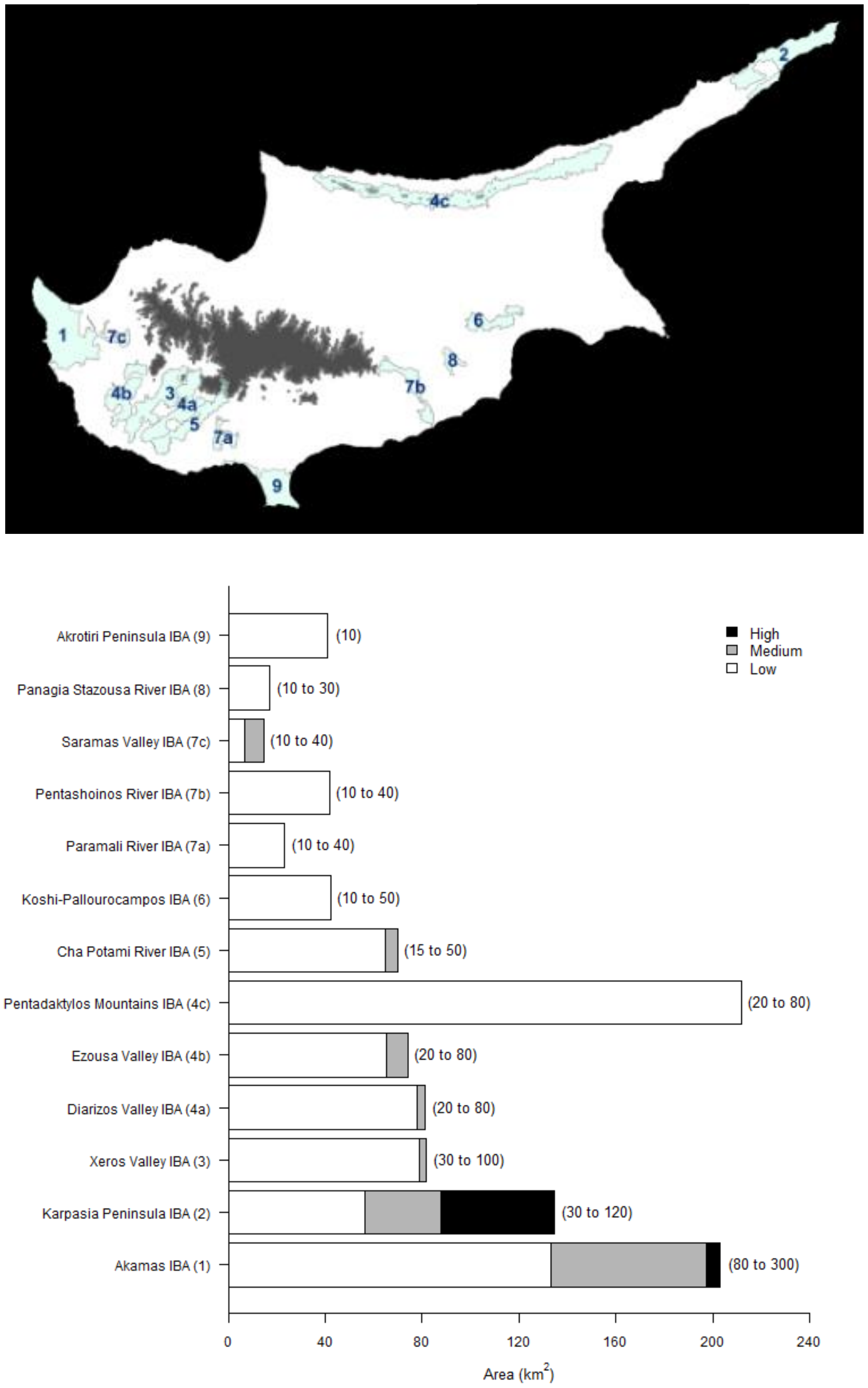


Figure S3.3: Location of IBA's citing Roller as a qualifying species and the area of high, medium, and low Roller occupancy probability (below 800m elevation) within each in 2014, ranked by breeding population size (bracketed terms refer to estimated no. of breeding pairs; Hellicar et al. 2014).

Table S3.3: Changes in extent of all Corine Land Cover types across Cyprus between 2000 and 2012.

Corine Land Cover type	**CLC 2000 land cover (km^2)**	**CLC 2012 land cover (km^2)**	**Change in land cover between 2000 and 2012 (km^2)**	**% change in relation to total land area**	**% change in relation to total area of CLC land cover type**
Airports	24.98	26.06	1.08	0.013	4.33
Annual crops associated with permanent crops	327.43	317.47	-9.96	-0.116	-3.04
Bare rock	23.61	11.91	-11.70	-0.137	-49.54
Beaches, dunes, and sand plains	50.50	45.42	-5.08	-0.059	-10.06
Broad-leaved forest	7.31	5.76	-1.55	-0.018	-21.21
Burnt areas	116.98	20.71	-96.26	-1.125	-82.29
Complex cultivation patterns	683.86	658.79	-25.07	-0.293	-3.67
Coniferous forest	1118.56	1112.96	-5.60	-0.065	-0.50
Construction sites	11.81	13.80	2.00	0.023	16.91
Continuous urban fabric	5.67	5.68	0.02	0.000	0.32
Discontinuous urban fabric	405.99	486.67	80.68	0.943	19.87
Dump sites	3.20	3.11	-0.09	-0.001	-2.73
Fruit trees and berry plantations	153.05	157.30	4.25	0.050	2.77
Green urban areas	10.81	9.97	-0.84	-0.010	-7.76
Industrial or commercial units	129.72	147.30	17.58	0.205	13.55
Inland marshes	5.20	4.97	-0.23	-0.003	-4.41
Land principally occupied by agriculture, with significant areas of natural vegetation	375.31	434.50	59.19	0.692	15.77
Mineral extraction sites	24.63	23.54	-1.10	-0.013	-4.45
Mixed forest	3.57	3.46	-0.11	-0.001	-3.10
Natural grassland	294.16	257.49	-36.67	-0.429	-12.47
Non-irrigated arable land	2402.98	2282.25	-120.72	-1.411	-5.02
Olive groves	65.03	71.25	6.22	0.073	9.56
Pastures	11.63	8.85	-2.78	-0.033	-23.93

Table S3.3 (continued): Changes in extent of all Corine Land Cover types across Cyprus between 2000 and 2012.

Corine Land Cover type	**CLC 2000 land cover (km^2)**	**CLC 2012 land cover (km^2)**	**Change in land cover between 2000 and 2012 (km^2)**	**% change in relation to total land area**	**% change in relation to total area of CLC land cover type**
Permanently irrigated land	189.59	251.89	62.30	0.728	32.86
Port areas	3.39	3.37	-0.02	0.000	-0.54
Road and rail networks and associated land	3.24	6.82	3.58	0.042	110.46
Salt marshes	19.55	19.65	0.09	0.001	0.48
Sclerophylous vegetation	1505.49	1453.30	-52.19	-0.610	-3.47
Sea and ocean	21.65	21.57	-0.07	-0.001	-0.34
Sparsely vegetated areas	116.63	118.31	1.68	0.020	1.44
Sport and leisure facilities	44.96	71.43	26.47	0.309	58.86
Transitional woodland/shrub	266.73	366.89	100.16	1.171	37.55
Vineyards	113.63	112.34	-1.29	-0.015	-1.14
Water bodies	15.43	21.22	5.79	0.068	37.49
Water courses	0.00	0.26	0.26	0.003	-

Chapter 4: Spatial ecology and habitat preferences of the European Roller (*Coracias garrulus*) in western Cyprus

4.1 Abstract

This study comprises the first of its kind in which fine-scale resolution Global Positioning System tracking devices have been deployed upon European Rollers (Coracias garrulus) to investigate the species' breeding season spatial ecology. 6 individual Rollers were tracked for between 7 and 22 days during the 2014 chick rearing period in western Cyprus, following intensive field trials of the novel tracking devices used. Mean home range size, as measured by 90% Minimum Convex Polygon (MCP) buffered to account for logger error, was 29ha (range; 14ha to 43ha). The mean distance travelled between the nest site and the MCP boundary (the Maximum Foraging Extent; MFE) was 576m (range; 298m to 835m). Rollers showed no clear preference for any particular foraging habitat type (although fallow, cereal, woody fruit crop, and grassland habitats were used in proportion to their availability), urban areas and ploughed fields were actively avoided. This reflected differences in the terrestrial invertebrate biomass of the habitat types, with grassland and fallow supporting the largest and ploughed area the lowest. Land use cover affected breeding parameters. Laying date was negatively associated with increasing area of avoided urban habitat around the nest, whilst fledging success was positively related to increasing laying date, and increasing extent of grassland, cereal, and woody fruit crop habitat surrounding the nest.

4.2 Introduction

Many of Europe’s bird species have experienced severe declines in recent decades, with farmland and migratory birds especially hard hit (Donald et al. 2001; Vickery et al. 2014). Understanding the habitat and spatial requirements of such threatened avian taxa is a key component of successful conservation interventions (Fuller 2012), and is especially important for central place foraging farmland species for which agri-environment schemes could provide effective conservation measures (Doxa et al. 2010).

Space and habitat use may vary both temporally and individually, with differing resources required dependent upon life history traits (i.e. resident versus migratory species) and time of year (e.g. breeding versus wintering; (Laube et al. 2015; Vickery et al. 2014). This can be particularly important during the chick-rearing period for altricial species, when parent birds become central place foragers and are limited by a maximum foraging extent.

In order to assess the habitat selection preferences of an organism, it is first necessary to determine the individual’s home range (Calenge 2011), as habitat selection within the wider landscape may be bound by a territorial border. The delineation of this border can be influenced by the presence of competitive congeners and topographic features (Powell & Mitchell 1998; Sovern et al. 2014). A second level of selection occurs within the established home range, whereby individuals may favour certain available foraging habitat types over others.

Once preferred habitat types have been identified, it is important to confirm whether they support a greater, and/or more easily accessible, prey resource and whether their presence is linked to increased reproductive success and/or offspring quality. Previous studies have shown that habitat composition around the nests of central-place foragers can affect pre-breeding condition (Catry et al. 2012), laying dates (Penteriani et al. 2002), and fledging success in a variety of species, with carryover effects also identified in subsequent years (Sedinger et al. 2011).

The collection of habitat selection data at high spatial and temporal resolution within breeding localities can be used to inform conservation policy and management for threatened avian species (Schlaich et al. 2015), including the identification of preferred habitat types for inclusion in agri-environment schemes

(Franco & Sutherland 2004). Recent advancements in tracking technology have allowed ornithologists to gain an increasingly detailed picture of the spatial ecology of a broad range of avian taxa, allowing large datasets to be collected with limited intervention (Tomkiewicz et al. 2010).

This study focuses on the migratory European Roller (*Coracias garrulus*; henceforth Roller) on the island of Cyprus. The Roller has experienced long-term population declines and range contractions across Europe (BirdLife International 2016), and Cyprus now supports >8% of the species population within European Union member states (BirdLife International 2015). Studies carried out elsewhere in the species Mediterranean range have identified negative impacts upon nest site selection arising from infrastructure development and agro-forestry (Rodriguez et al. 2011). Furthermore, agricultural intensification has been identified as a major threat to the species across its European range (Kovacs et al. 2008), although some studies have identified potential benefits arising from the availability of a larger prey resource within irrigated areas (Avilés et al. 2000).

Recent research indicates that the species has undergone a steep population decline in the west of the Cyprus during the last decade (Pomeroy et al. 2013), and ongoing land use changes have potential to negatively impact the species further (Ieronymidou 2012). Gaining an understanding of the Roller’s spatial requirements and preferred habitats, the reasons for any observed preferences, and their effect upon the species’ breeding success, is therefore of key importance for the conservation of this internationally important population.

The current study uses novel high temporal and spatial resolution Global Positioning System (GPS) technology to (a) quantify Roller home range size in western Cyprus; (b) identify preferred/avoided foraging habitats during the chick-rearing period; (c) identify whether preferred foraging habitats support higher invertebrate prey biomass than avoided habitat types, and; (d) assess the consequences of habitat composition, and associated prey biomass, upon Roller laying date and fledging success.

4.3 Methods

Study area

The study area is located in the north-west of Paphos District, within the Republic of Cyprus. It is topographically diverse and supports a mix of traditional, low intensity, farmland alongside areas of grassland, scrub, woodland, and more intensively managed farmland habitats. Several small villages are located within its' boundary, with larger towns situated on the periphery.

Home range estimation

Logger specification and fix quality

Novel *NanoFix^{TM}Geo* GPS loggers (www.pathtrack.co.uk/Site/nanoFix.html) were utilised in the study. Each logger was approximately 30mm x 15mm in size, reached a maximum weight of <6g (including harness material), and was recharged via a combination of internal battery and solar cells. The loggers' GPS antennae were encapsulated within a ceramic patch, to minimise damage, and a UHF antenna was incorporated within the main body. Once deployed, data was remotely downloaded to a portable base station, with effective download distance ranging between 500m and 1km, dependent upon terrain. Data was archived within each logger prior to downloading.

In addition to the 3-dimensional co-ordinates of each recorded fix, the loggers also provided an 'accuracy' measure, identifying the number of satellites used during the making of the fix, and gave a value of the voltage of the logger at the time. Any fix reporting an accuracy value of >30, or a logger voltage of <4v was considered to be spatially inaccurate by the manufacturers (Pathtrack Ltd, *pers.comm*.).

Following extensive pre-deployment field trials (see Appendix), only those fixes made using a connection to a minimum of 5 satellites, and reporting an accuracy measure of <30 and voltage of >4v, were used in any spatial analyses. The field trials also indicated that the mean location error associated with each fix was approximately 35m, which was also subsequently accounted for in all spatial analyses.

GPS logger deployment and tracking

Ten loggers were deployed upon adult Rollers from separate nest sites during May and June 2014. As this was the first time that the specific logger model had been used on Rollers, only a single bird from each pair was targeted during the study. Adult birds were caught at dawn at the nest entrance, using mist nets or a handheld landing net. Pairs were targeted either at the end of the incubation period or within the first few days of their eggs hatching.

Loggers were pre-programmed to record a fix once every 20 minutes during daylight hours (0500hrs to 2100hrs). Once caught, the birds were hooded to minimise stress, and the GPS loggers attached with 4mm Teflon tape and superglue, using the ‘backpack’ harness technique (Rodríguez-Ruiz et al. 2014). The combined logger/harness weight was <5.5% of the smallest birds’ weight, and total handling time for each bird was <30 minutes.

These measurements were within published best practise guidelines at the time of deployment. Nevertheless, a multi-population study published subsequent to the 2014 field season has identified negative effects upon Roller breeding success and return rates arising from the use of loggers >2.5% of the individuals weight (Rodriguez-Ruiz et al. 2015). No statistically significant difference was identified between the breeding parameters (no of eggs laid and number of chicks fledged) of logger and non-logger birds within the Cypriot study population in 2014, however (P. Saunders, *unpub.data*).

Post-deployment, the nest site location of each logger bird was visited at least once every 2 days, with the portable base station hidden in proximity (within 500m) to the nest cavity for a minimum of 4 hours at each site, to minimise disturbance and maximise data download potential.

Fix sampling protocol

All fixes utilised in the study were made whilst the tagged Rollers were feeding chicks in the nest, with all downloaded fixes initially screened for accuracy (<30), voltage (>4v), and number of satellite connections (≥5). Those fixes fulfilling the screening criteria were deemed ‘clean’.

In order to minimise the risk of spatial autocorrelation between the fixes for each logger bird, and to account for the reduced activity levels observed during the hottest part of the day (*pers.obs*; Poole 2005), only cleaned fixes separated by at least 1 hour, and recorded between 0500hrs and 1100hrs, and 1400hrs and 2100hrs, were used in home range estimation and foraging habitat selection analyses, alongside a single, randomly selected, daily fix between 1200hrs and 1300hrs retained for each bird.

Estimation of home range sizes

Home ranges were produced for each logger bird using Minimum Convex Polygons (MCPs; Mohr 1947). The area of the 90% MCP, and the Maximum Foraging Extent (MFE; the maximum distance from the nest to the edge of the 90% MCP), were calculated for each logger bird, using the adehabitatHR package in R (R Core development Team, 2016). The use of a 90% MCP threshold removed the influence of outlier fixes and identified the core home range of each logger bird. Following pre-deployment trials, each point was buffered by 35m to account for fix displacement error (see Appendix), resulting in a buffered 90% MCP. The MFE was considered a proxy for the maximum distance each logger bird had the potential to travel in any direction from the nest site during the chick-rearing period.

Foraging habitat selection

The nest positions of each logger bird were first buffered by the radius of the mean MFE for all 6 logger birds, using ArcGIS 10.3 (ESRI 2014). All habitats located within the mean MFE buffer, including those within the buffered 90% MCP, were then mapped in the field at the parcel scale. The habitats present were grouped into broad categories based upon their physical characteristics and/or management schedule (Table 4.1). The field maps, based on 1:5,000 scale aerial photos with precise limits of habitat categories, were then geo-referenced and digitised using ArcGIS 10.3, in order to calculate relative habitat proportions.

Type iii global selection ratios ($\hat{w}i$; Manly et al. 2002), contrasting the frequency of used habitats with those available to the individual, were then calculated for each logger bird at 2 spatial scales; landscape scale and home-range scale (see below), using the adehabitatHS package in R (Calenge 2011). The selection ratios are considered proportional to the probability that a particular habitat/resource is used/disused. A selection ratio (+/- 95% confidence intervals) of >1 indicates habitat preference, and <1 indicates avoidance, with a ratio of 1 identifying neither preference nor avoidance (‘use as available/utilised’). Any global selection ratios calculated using <5 individuals is considered tentative, with ≥5 individuals required for robust estimation (Manly et al. 2002).

Table 4.1: Broad habitat categories used in habitat selection analyses of 6 Rollers tracked in western Cyprus in 2014 (adapted for use at finer spatial scales from Corine Land Cover categories (Bossard et al. 2000)).

Broad habitat category	Description
Cereal and legumes	Cereal and legume crops grown within traditional rotation schedule. Both form a tall, dense, sward as the growing season progresses, and are harvested in late spring/early summer.
Fallow and vegetable crops	Fallow areas left as part of traditional rotation schedule, comprising mix of bare earth and patchy, low-growing, ephemerals. Also non-intensive subsistence vegetable crops, exhibiting similar mix of bare earth and sparsely vegetated areas with low-growing plants.
Grassland	All grassland areas, including extensive natural grasslands, grassland/scrub mosaic, and grassland with scattered trees. Phrygana (overgrazed grassland areas incorporating abundant spiny ruderals and patches of bare earth) also included.
Mineral extraction sites	Working quarries.
Ploughed	Fields within traditional rotation schedule, usually ploughed in late winter/early spring prior to sowing of cereal/legume crop.
Riparian and tall herbaceous vegetation	Tall patches of herbaceous vegetation forming substantial field margins. Also reed beds and marginal vegetation associated with running water.
Scrubland	Primarily garrigue and maquis communities, forming dense matrix of thorny scrub, fine grasses, bare earth, and low flowering plants on hillsides and slopes. Also areas of dense scrub along field margins.
Urban mosaic and infrastructure	Towns and villages and their associated infrastructure (gardens, outbuildings, roads, etc). Includes working farm buildings and large animal sheds, but not isolated ruins or abandoned buildings.
Woodland	All areas of continuous (mature) broad-leaved, coniferous, riparian, and mixed woodland.
Woody fruit crops and viniculture	Irrigated almonds, olives, citrus, and viniculture. Also non-irrigated, but actively managed, olives, carobs, almonds, and fruit.

Landscape scale selection

The landscape scale analysis compared those habitats present within the buffered 90% MCP with those present within the mean MFE buffer, thus providing information on the situation of home range locations within the wider landscape. The total area of each broad habitat type within the mean MFE buffer was calculated for each logger bird (constituting the ‘available’ habitat, and expressed as a percentage). The total area of each broad habitat type within the extent of the buffered 90% MCP incorporated within the mean MFE boundary (i.e. that part of the MCP intersected by the MFE, for any of the larger home ranges) was then calculated for each bird (the percentage of ‘used’ habitat at the landscape scale). Type iii global selection ratios were then calculated.

Home range scale selection

The home range scale analysis compared the number of GPS fixes recorded within each habitat type within the buffered 90% MCP (a proxy for ‘used’ habitat) with the total area of each habitat type present within the buffered 90% MCP (the ‘available’ habitat), thus identifying any preferred/avoided foraging habitat types within the established home range.

Due to the nest-guarding and provisioning behaviour exhibited by parent Rollers (*pers.obs.*), and its potential to confuse foraging habitat selection analyses, all fixes located within 70m of the nest site (accounting for 35m location error) were removed. In order to account for the innate 35m GPS location error associated with each remaining fix, the total area of all habitat types within a 35m buffer surrounding each fix was extracted. A mean value of ‘used’ habitat for each bird was then produced by dividing the sum total area of each habitat across all buffered fixes by the total number of fixes within the buffered 90% MCP. The mean values comprised the ‘used’ habitat incorporated in the home range scale analysis. The ‘available’ areas and ‘used’ fixes were converted to percentage values prior to the calculation of the global index. Type iii global selection ratios were then calculated for each bird.

Invertebrate biomass of foraging habitats

Field surveys

Invertebrate surveys were carried out during the 2014 and 2015 Roller breeding seasons, with results from the 2 survey seasons pooled, to investigate whether specific potential foraging habitats supported a higher invertebrate biomass. Surveys were carried out each year within 6 replicates of each of the open habitat types (i.e. excluding woodland) available for use by foraging Rollers within the study area (cereal stubble, fallow land, ploughed areas, scrubland (garrigue), woody fruit crops (olives/almonds), and grassland). Three structurally distinct grassland types (grassland-scrub mosaic, grassland with scattered trees, and phrygana; Table 4.1) were initially surveyed independently, but later combined following tests for significant differences between them (Student’s t-test) proved non-significant.

Areas of intensive human activity (e.g. working quarries and urban areas) unsuitable for use by foraging Rollers were excluded from the surveys. Surveys were undertaken in early, mid and late June to capture variability in food availability throughout the core chick rearing period. Each survey bout was carried out between 0700hrs and 1000hrs, to coincide with the morning Roller foraging period.

During each survey a 30m transect was walked, using the ‘pigeon step’ technique (Voisin 1980), whereby the surveyor walks at a slow pace, observing a 1m band either side of the transect line. Care was also taken to watch ahead in order to accurately record any invertebrates inadvertently flushed by the surveyor. All terrestrial invertebrates observed were identified to Order and placed within 1 of 4 length classes (<1cm, 1 - 3cm, 3 - 5cm, >5cm). In those habitats where invertebrate encounter rates were low, the transect length was increased in 10m increments (to a maximum 120m) until at least 1 invertebrate was observed in order to produce a positive metric and avoid zero inflation in the case of low density habitat types.

Ash-free dry weight

A representative sample of specimens from across the Orders observed was collected from the field sites using sweep and hand nets. These specimens were killed in 90% ethanol, and then weighed immediately. The length of each specimen was recorded, from the tip of the abdomen (excluding the ovipositor in female Orthoptera) to the front edge of the pronotum. Specimens were then dried at 90^{o}C until they reached a stable dry weight. Following this, they were heated in a muffle furnace at 450^{o}C for 24hrs until only ash residue remained. The weight of the residue was recorded, and the ash-free dry weight of each specimen calculated by subtracting the residue weight from the stable dry weight (Sutherland et al. 2005).

Biomass calculation

A linear model of ash-free dry weight ~ specimen length at time of capture was used to calculate the estimated mean biomass of the approximate mid-point value for each of the 4 invertebrate length classes used during the field surveys (5mm, 20mm, 40mm, and 75mm). The encounter rate of each length class within each transect was then multiplied by the respective weight, and then divided by the area of transect coverage (a 30m transect = 60m^2, with the area within any extended transects revised accordingly). A value of mean biomass per unit area was then produced for each of the habitat types surveyed.

Habitat effects, laying date, and fledging success

Modelling habitat effects upon laying date and fledging success

In order to assess the impact of surrounding habitat characteristics upon Roller laying date and fledging success, and to increase the sample size for incorporation within explanatory models, habitat and breeding parameter data were collected from 16 nests in the study area in 2014 (including from 5 of the logger birds) and 24 nests in 2015. All broad habitats located within a 600m buffer surrounding each nest (corresponding to the rounded mean MFE of the 6 logger birds) were mapped using the categories detailed in Table 4.1.

Clutches were monitored from the initial laying date, with the laying date back-calculated (using a 2 day laying interval per egg) if the nest was identified later in the egg laying period (Cramp & Simmons 1998; *pers.obs*). Laying date, clutch and brood size, hatching and fledging success were recorded from each monitored nest. Chicks were considered to have 'fledged' if they reached 3 weeks of age, as this comprised the immediate pre-fledging period at approximately 3.5 weeks, with chicks considered too large to be predated by this point. All checks were carried out using an endoscope, where possible, to minimise disturbance to the chicks.

Roller laying date and fledging success were modelled against a range of parameters describing habitat and nest site characteristics, including several based upon the home range scale habitat selection and invertebrate survey results (Table 4.2). All potential explanatory parameters were initially screened for unimodal significance prior to inclusion, with only significant variables carried forward. Pairwise correlations were then examined, with the stronger variable retained of any pair exhibiting a Pearson Correlation Coefficient of >0.7. The distribution of each dependent variable was also confirmed prior to imposition of a specific model structure.

All modelling was carried out using the stats and lme4 packages in R (R Core Development Team 2016). Habitat effects on laying date were investigated using a Linear Mixed Effect Model with Guassian distribution and identity link function, and incorporating *Year* as a random effect within the null model. *Nest density*

Table 4.2: Explanatory variables used within linear mixed effects models investigating the effects of surrounding habitat parameters upon the laying date of Rollers in western Cyprus.

Fixed effects	**Description**
Habitat diversity	The Shannon-Wiener diversity Index for the broad habitat categories within the 600m nest buffer.
Nest density	The number of other active Roller nests located within the 600m nest buffer.
Proportional area of strongly avoided habitat	The percentage area of the 600m nest buffer occupied by strongly avoided habitats (i.e. those identified as avoided ($\hat{w}$i <1) by ≥5 individuals during home range scale selection analyses).
Proportional area of all avoided habitats	The percentage area of the 600m nest buffer occupied by all avoided habitats (i.e. those identified as avoided ($\hat{w}i$ <1) by ≥1 individual during home range scale selection analyses).
Proportional area of strongly utilised habitats	The percentage area of the 600m nest buffer occupied by all utilised habitats (i.e. those identified as 'used as available' ($\hat{w}i$ = 1) by ≥5 individuals during home range scale selection analyses).
Proportional area of all utilised habitats	The percentage area of the 600m nest buffer occupied by all utilised habitats (i.e. those identified as 'used as available' ($\hat{w}i$ = 1) by ≥1 individual during home range scale selection analyses).
Total invertebrate biomass of strongly utilised habitats	The total invertebrate biomass (g/m^2) of each habitat type within the 600m nest buffer identified as 'strongly utilised' during home range scale selection analyses (i.e. mean invertebrate biomass/habitat multiplied by total habitat area).
Total invertebrate biomass of all utilised habitats	The total invertebrate biomass (g/m^2) of each habitat type within the 600m nest buffer identified as 'utilised' during home range scale selection analyses (i.e. mean invertebrate biomass/habitat multiplied by total habitat area).
Random effects	
Site	Geographic unit, expressed as town/location name. Incorporated to account for overlapping nest buffers within areas of high Roller nest density.
Nest ID	Identifier given to each nest. Incorporated to account for repeated measures upon same nest between years, and potential utilisation of same nest by different individuals between years.
Year	Calendar year. Incorporated to account for inter-annual variation in weather and arrival dates.

was included as a fixed effect to describe intraspecific behaviours (e.g. competition) and *Habitat diversity* (Shannon-Wiener diversity index values; Magurran 1998) incorporated to provide a metric for habitat diversity within the 600m nest buffer. Due to some of the nest sites being used by Rollers in both survey years, the potential for different individuals to use the same nest cavity between years, and the presence of several birds within 'colonies' exhibiting overlapping home ranges within the same site, *Nest ID* was nested within *Site* (i.e. individually identified areas supporting closely breeding Rollers with overlapping 600m nest buffers) as an additional random effect.

Habitat effects upon Roller fledging success were modelled using a Generalised Linear Model with Poisson distribution and log link function, as the reduced number of data points (*n* = 29) precluded the effective use of Generalised Linear Mixed Effects Models. The fledging success metric comprised the number of chicks successfully fledged from each nest, offset by the natural logarithm of the number of chicks hatched (brood size). Any nests used in the laying date models which were subsequently predated were excluded from the fledging success models. The explanatory variables used comprised those listed under 'fixed effects' in Table 4.2, in addition to *Laying date* (the Julian calendar date upon which the first egg was laid).

Model selection for both the laying date and fledging success models was carried out using the Akaike Information Criterion adjusted for small sample sizes (AICc; Hurvichl & Tsai 1995), with competing models exhibiting a ΔAICc <2 from the lowest scoring model retained in the final model set. Akaike weights (Burnham et al. 2011) were also calculated for each model.

4.4 Results

Home range estimation

Of the 10 adult Rollers upon which GPS loggers were deployed; 1 bird was not observed again after logger deployment (and was assumed to be either a prospecting passage migrant or predated); another immediately abandoned its' nest, and 2 birds had their nests predated within a few days of deployment (resulting in <12 GPS fixes). The remaining 6 birds returned sufficient fixes (20+) to enable home range and habitat selection analyses to be carried out.

The nest sites of 3 of the 6 birds were located within a densely populated 'colony' in the north-west of the study area (Figure 4.1), with the nest localities of the other 3 birds spread more widely. The buffered 90% MCP's of Birds 2 and 3 overlapped, whilst the remaining 4 buffered 90% MCPs did not. The tracking period for each bird ranged between 7 and 22 days, with the number of retained fixes per individual ranging between 26 and 46 (mean = 36.5, St.Dev = 7.42; Table 4.3).

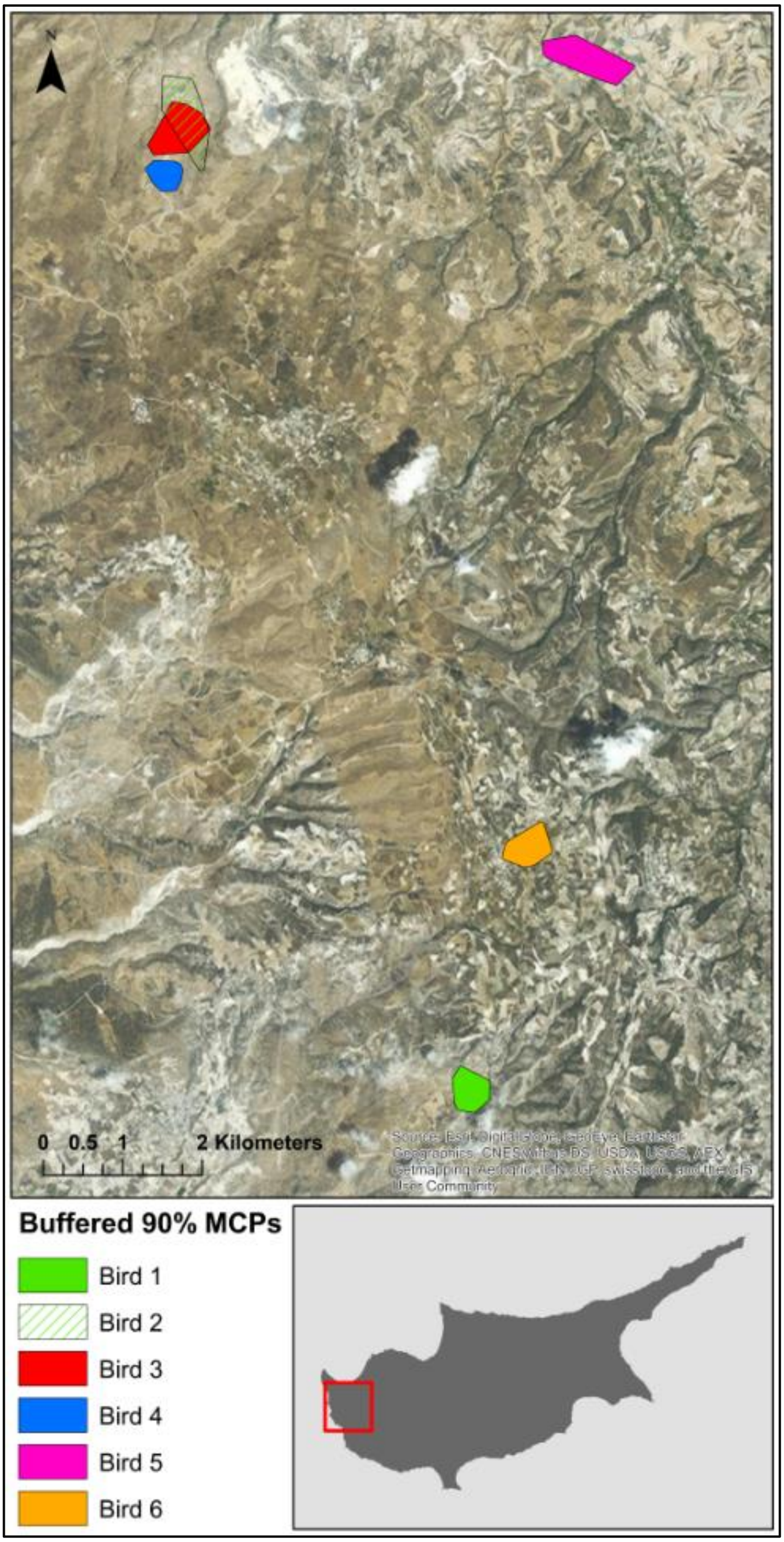


Figure 4.1: Study area (inset) and locations of buffered 90% Minimum Convex Polygons of 6 Rollers tracked in western Cyprus in 2014.

Table 4.3: Home range sizes and logger fix data from 6 adult Rollers tracked in western Cyprus during the 2014 chick rearing period.

Bird ID	**Tracking period**	**No. data-days**	**No. of fixes**	**Buffered 90% MCP area (ha)**	**Maximum Foraging Extent (MFE) from nest site to buffered 90% MCP boundary (m)**
1	24th May to 7th June	8	26	20.56	421.21
2	6th June to 13th June	8	38	43.22	835.21
3	10th June to 16th June	6	37	33.84	653.32
4	12th June to 4th July	21	42	13.89	604.04
5	9th June to 19th June	10	30	38.25	643.21
6	8th June to 18th June	10	46	22.72	297.61
	Mean	10.5	36.5	28.75	575.77

The mean buffered 90% MCP area was 28.75ha (st.dev = 11.40; range = 20.56ha to 43.22ha), whilst the mean MFE was 575.77m (st.dev = 189.70; range = 421.21 m to 835.21 m). The mean MFE value was rounded to 600m and applied as a buffer around all nests subsequently used in the landscape scale foraging selection analysis.

Foraging habitat selection

The available foraging habitat composition varied between the 6 logger birds (Table 4.4). The habitats available to Bird 1 largely comprised scrubland and grassland habitats, with those available to birds 2, 3, and 4 primarily comprising cereal and legumes, and grassland habitats. The habitats available to birds 5 and 6 were more diverse, although cereal and legumes, and woody fruit crops, were still prevalent.

Landscape scale selection

The application of a mean MFE buffer of 600m to the 6 logger bird home ranges resulted in a small proportion of the buffered 90% MCP's of Birds 2, 3, and 6 being excluded from the landscape scale analysis (3.20ha (7.4%); 0.61ha (1.8%), and; 1.00ha (4.4%) of the buffered 90% MCP, respectively).

The global selection ratios within the mean MFE buffer (Figure 4.2a) showed that logger Roller home ranges within the study area strongly avoided scrubland,

Table 4.4: Relative proportion of foraging habitat types available within the 600m nest buffer (mean Maximum Foraging Extent; MFE) and the buffered 90% Minimum Convex Polygon (MCP) of 6 Rollers tracked in western Cyprus in 2014.

	Relative % area of 600m nest buffer or 90% MCP																	
	Cereal and legumes		**Fallow and vegetable crops**		**Grassland**		**Ploughed**		**Riparian and tall herbaceous vegetation**		**Scrubland**		**Urban mosaic and infrastructure**		**Woodland**		**Woody fruit crops and viniculture**	
Bird ID	***600m***	***90% MCP***	***600m***	***90% MCP***	***600m***	***90% MCP***	***600m***	***90% MCP***	***600m***	***90% MCP***	***600m***	***90% MCP***	***600m***	***90% MCP***	***600m***	***90% MCP***	***600m***	***90% MCP***
1	-	-	1.51	0.77	15.51	35.06	0.18	0.99	-	-	78.78	48.93	2.88	13.70	-	-	1.15	0.55
2	17.05	35.14	-	-	57.41	45.82	0.28	-	-	-	2.54	0.64	13.96	18.27	5.01	-	3.76	0.13
3	20.33	53.77	-	-	60.35	37.38	0.28	-	-	-	1.29	-	9.56	5.90	4.14	-	4.04	2.96
4	40.91	77.33	1.80	-	52.33	22.67	3.89	-	-	-	0.31	-	-	-	-	-	0.76	-
5	41.97	36.89	7.34	9.20	4.82	4.97	4.14	3.30	7.46	3.14	3.40	0.11	7.39	18.87	1.17	2.39	22.30	21.14
6	9.53	10.89	5.57	13.74	33.86	15.72	0.52	-	0.68	-	0.17	-	20.11	5.16	-	-	29.56	54.50

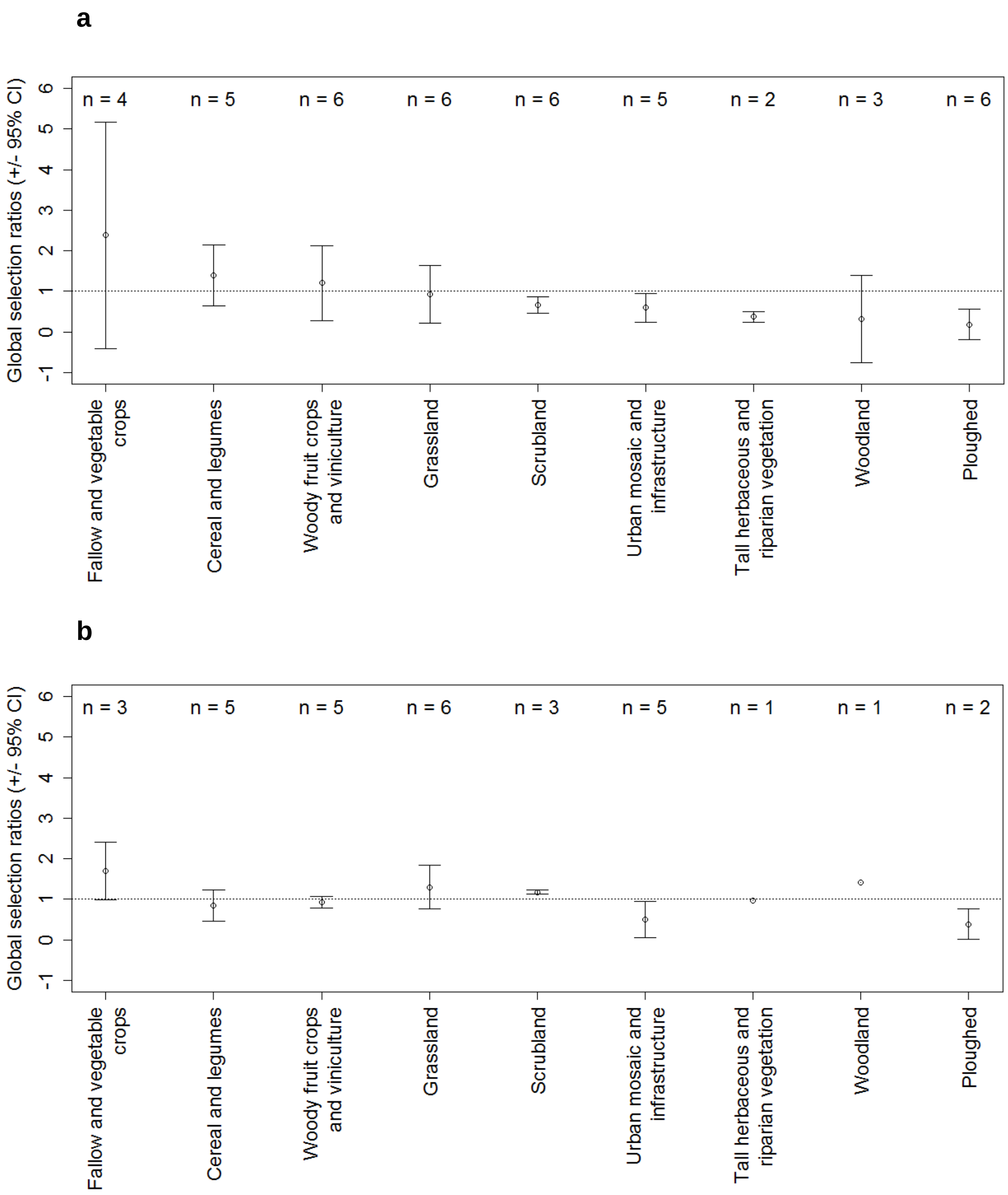


Figure 4.2: Type III Manly Selection Ratios (wi) and 95% confidence intervals for foraging habitat of 6 Rollers tracked in western Cyprus in 2014 (a) within the 600m mean Maximum Foraging Extent buffer, and (b) within the buffered 90% Minimum Convex Polygon. Dashed line indicates no preference/avoidance ('use as available/utilised").

urban, and ploughed habitats within the wider landscape (ratio +/- CI <1 for 5+ birds). Tall herbaceous and riparian vegetation appeared to be avoided, although the result was from only 2 individuals and therefore tentative.

Cereal and legumes, woody fruit crops and viniculture, and grassland areas all exhibited positive *wi* values, but the analysis indicated that these habitats were nevertheless used in proportion to availability (ratio +/- CI = 1 for 5+ birds). The analysis also suggested that fallow and vegetable crops (positive *wi*), and woodland (negative *wi*), were used as available (ratios calculated for 4 and 2 birds, respectively).

Home range scale selection

The global selection ratios within the buffered 90% MCPs (Figure 4.2b) showed that, within established home ranges, cereal and legumes and woody fruit crops and viniculture (both negative *wi*), and grassland areas (positive *wi*), were used in proportion to their availability (ratio +/- CI = 1 for 5+ birds). There were indications that fallow and vegetable crops, and scrubland, were positively selected (both positive *wi*, but with ratios calculated for 3 birds).

Urban habitats were strongly avoided (ratio calculated for 5 birds), and ploughed areas potentially were also (negative *wi*, but ratio calculated for 2 birds). Any selection for tall herbaceous vegetation or woodland could not be quantified, as the selection ratios were calculated for single birds only.

Based upon these results, fallow and vegetable crops, scrubland, cereal and legumes, woody fruit crops and viniculture, and grassland were categorised as ‘utilised’ habitats within the buffered 90% MCP (i.e. neither preferred nor avoided). The latter 3 habitat types were also categorised as ‘strongly utilised’ (ratio +/- CI = 1 for 5+ birds). Urban habitat and ploughed areas were categorised as ‘avoided habitats’, with urban identified as ‘strongly avoided’ (ratio +/- CI <1 for 5+ birds).

Invertebrate biomass of foraging habitats

Fallow and grassland habitats supported by far the largest mean invertebrate biomass during the survey periods (Table 4.5), with scrubland, woody fruit crops, and cereal (stubble) supporting sequentially decreasing biomass. Ploughed habitat supported the lowest invertebrate biomass. When plotted against the global selection ratios (*wi*) within the buffered 90% MCP of the 6 logger birds (Figure 4.3), a linear relationship was observed between mean invertebrate biomass and the *wi* value for each habitat. This suggests that habitats supporting higher invertebrate biomass may potentially be selected with priority over other, less productive, habitat types. The large confidence intervals observed in the selection ratios may therefore arise

*Table 4.5: Invertebrate biomass recorded from Roller foraging habitats in western Cyprus during the chick rearing period (*note that cereal biomass refers to stubble only, not growing crop).*

Habitat type	**Mean invertebrate biomass (g/m^2)**	**SE**	**Range (g/m^2)**
Fallow	22.61 -03	2.52 -03	4.03 -03 to 55.32 -03
Grassland	20.08 -03	1.60 -03	0.00 to 75.93 -03
Scrubland	12.92 -03	2.44 -03	0.00 to 63.52 -03
Woody fruit crops	9.46 -03	2.13 -03	0.00 to 57.53 -03
Cereal*	9.45 -03	1.12 -03	0.19 -03 to 26.07 -03
Ploughed	4.50 -03	0.74 -03	0.00 to 19.40 -03

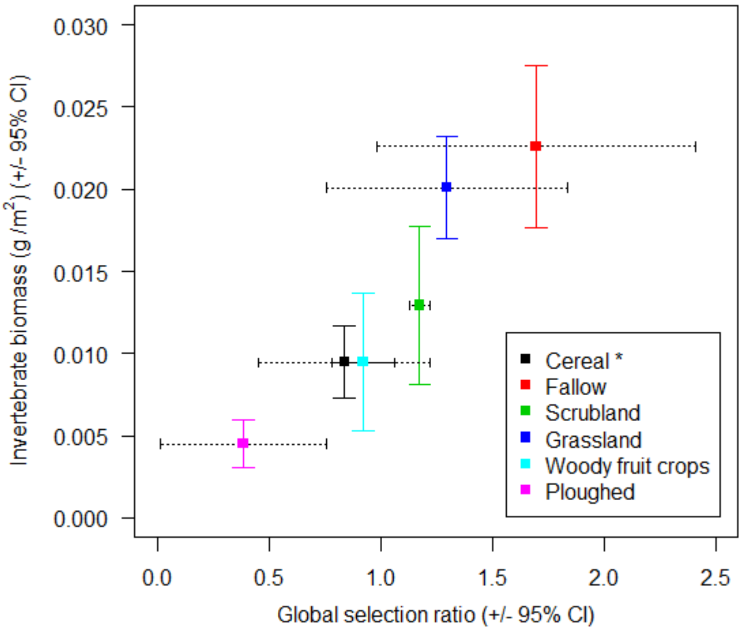


*Figure 4.3: Mean invertebrate biomass and global selection ratios (wi) for foraging habitats incorporated within the buffered 90% Minimum Convex Polygon of 6 Rollers tracked in western Cyprus during the 2014 chick-rearing period (*note that cereal biomass refers to stubble only, not growing crop).*

from the relatively small number of logger birds used in the analysis.

Habitat effects, laying date, and fledging success

Laying date

A single model was retained in the top model set (Table 4.6), with laying date negatively related to the proportional area of strongly avoided habitat (i.e. urban habitat) surrounding the nest. The Akaike weight of the top model was >2.5x greater than the intercept only model, and no other habitat or nest site metrics were incorporated in the top model set. This suggests that Roller pairs in urban sites were earlier breeders than those in more rural locations.

Table 4.6: Results from Generalised Linear Mixed Effects Model investigating the effect of habitat upon laying date in Rollers from western Cyprus (R^2_m *= marginal* R^2*;* R^2_c *= conditional* R^2*; AICc = Akaike Information criterion adjusted for small sample sizes; AICw = Akaike weight).*

Model	***B***	***exp(B)***	***df***	R^2_m	R^2_c	***AICc***	***∆AICc***	***AICw***
Proportional area of strongly avoided habitat	-1.573	0.21	34.87	0.11	0.28	244.45	0.00	0.46
Intercept only	125.104	2.15+54	35.00	0.00	0.29	246.46	2.01	0.17
Nest density	-0.824	0.44	27.32	0.03	0.28	247.97	3.52	0.08
Proportional area of utilised habitats	0.560	1.75	29.91	0.01	0.28	248.68	4.23	0.06
Total biomass of utilised habitats	0.547	1.73	24.89	0.01	0.27	248.69	4.25	0.06
Proportional area of all avoided habitats	-0.550	0.58	34.12	0.01	0.26	248.72	4.27	0.05
Habitat diversity	-0.199	0.82	21.85	0.00	0.30	249.17	4.72	0.04
Total biomass of strongly utilised habitats	0.154	1.17	22.37	0.00	0.28	249.20	4.75	0.04
Proportional area of strongly utilised habitats	0.023	1.02	23.39	2.31-05	2.87-01	249.24	4.79	0.04

Fledging success

Two models were retained in the top model set (Table 4.7). Fledging success was positively associated with a later laying date, having accounted for brood size, as was increasing extent of strongly utilised habitats (i.e. cereal and legumes, woody

Table 4.7: Results from Generalised Linear Model investigating the effect of habitat upon fledging success in Rollers from western Cyprus (R^2_m = McFadden pseudo-R^2; AICc = Akaike Information criterion adjusted for small sample sizes; AICw = Akaike weight).

Model	***B***	***exp(B)***	***df***	***R^2_m***	***AICc***	***∆AICc***	***AICw***
Laying date	0.228	1.26	27	0.04	97.22	0.00	0.32
Proportional area of strongly utilised habitats	0.197	1.22	27	0.03	98.75	1.53	0.15
Intercept only	-0.279	0.76	28	0.00	99.25	2.03	0.12
Total biomass of strongly utilised habitats	0.159	1.17	27	0.02	99.68	2.46	0.09
Proportional area of strongly avoided habitat	-0.132	0.88	27	0.02	100.09	2.87	0.08
Proportional area of all avoided habitats	-0.123	0.88	27	0.01	100.24	3.02	0.07
Total biomass of utilised habitats	0.093	1.10	27	0.01	100.88	3.66	0.05
Proportional area of utilised habitats	0.072	1.07	27	0.00	101.10	3.88	0.05
Habitat diversity	0.031	1.03	27	0.00	101.48	4.26	0.04
Nest density	-0.025	0.98	27	0.00	101.51	4.29	0.04

fruit crops and viniculture, and grassland) surrounding the nest site. Nevertheless, the Akaike weight of the laying date model is more than 2x larger than the other retained model, and laying date is likely to be the key driver of fledging success, potentially linked to the crop harvest cycle within the study area.

4.5 Discussion

Home range size and drivers of foraging habitat selection

This study represents the first time that home range size has been calculated for Rollers using high resolution GPS technology, supported by extensive field trials of logger accuracy. The 6 birds for which MCPs were produced exhibited variation in both home range size and maximum foraging extent.

Nevertheless, the landscape scale foraging selection analyses showed that the home ranges of all 6 birds were not randomly distributed within the wider landscape. Their home ranges all incorporated several farmland and grassland habitat types, but strongly avoided scrubland, urban habitats, and ploughed areas. It is possible that this constitutes active avoidance of such habitats by Rollers at the landscape scale, potentially due to a range of factors (including limited food availability, increased disturbance, or predation), as the avoidance of urban habitat is strongly supported, and the avoidance of ploughed habitat tentatively so, by the results of the home range scale selection analysis also.

However, extensive areas of scrubland in Cyprus are often found on steeper slopes and hillsides, and it may be that the landscape-scale avoidance of scrubland habitat is in reality an effect of topography, whereby foraging Rollers prefer more level areas supporting agricultural habitats (Powell & Mitchell 1998). It is important to recognise that the relative habitat composition and spatial orientation of individual home ranges, as captured by MCP’s, will not be solely influenced by Roller foraging decisions. Landscape structural elements, including topography and the proximity of foraging habitats to nests sites, have potential to directly impact GIS-derived home range boundaries.

Furthermore, the fixes returned from the loggers used in this study didn’t differentiate between perching, hunting, and flight behaviours. It is therefore possible that several of the fixes used in the habitat selection analyses do not comprise ‘foraging’ habitat selection, but may represent habitats beneath Roller flight paths, or overhead wires used as perches. This may explain the positive *wi* values produced for habitats considered unsuitable for Rollers, such as woodland. The incorporation of an accelerometer (Gilbert et al. 2016; Wilson et al. 2008) into loggers deployed upon Cypriot Rollers in future would assist in answering this question by allowing different behavioural modes to be identified within the fix dataset.

Nevertheless, whilst recognising such caveats, the results of the home range scale selection analysis indicate that Rollers in western Cyprus primarily forage within (although do not necessarily strongly prefer) areas of farmland and grassland habitats. Preferences for agricultural and grassland habitats, and avoidance of intensively farmed and scrubland areas, have been previously identified for the species elsewhere within its’ European range, including southern France (Poole 2005) , Portugal (Catry et al. 2011), Slovakia (Bohus 2002), and Austria (Tiefenbach 2009).

However, research carried out in Spain (Avilés, Sánchez, et al. 2000) suggested that foraging habitat was of lower importance than the availability of nest cavities, and in situations where nest sites are limited Rollers may use lower quality foraging habitats due to their proximity to the nest site, thus potentially confounding investigations into foraging habitat preference.

The high invertebrate biomass observed in grassland and fallow habitats, and the low biomass observed in ploughed areas, may explain the differences in selection ratios observed at the home range scale. Despite the relatively small number of logger birds used in the analysis, the results suggest that Rollers potentially select foraging habitat based, at least party, upon the habitat's invertebrate biomass. When considering these results it is nevertheless important to recognise that the selection ratios were calculated for a small number of individuals and were based upon the habitats present within 600m of the nest site, and not those within the exact home range (which was considerably smaller for 2 of the 6 birds in the study).

This may explain the variation seen in the confidence intervals surrounding the selection ratios for certain preferred habitat types which are scarce within the study area (e.g. fallow). Rollers exhibiting smaller home ranges are able to maximise their foraging within proximity to the nest site, and theoretically have no need to increase their commuting distances to more distance, albeit more productive, foraging habitat types. Rollers are also automatically constrained in the foraging habitat choice by those available in the wider landscape surrounding the nest site, with 2 of the birds nesting in areas within which fallow land was absent, for example.

Nevertheless, the utilisation of cereal habitats by breeding Rollers in the study, despite the relatively low invertebrate biomass recorded from cereal stubbles, is interesting. It is probable that standing cereal crops support a much higher invertebrate biomass prior to harvest, which Rollers are able to access during the harvest period (largely coinciding with the latter half of the Cypriot breeding season; *pers.obs;* Poole 2005; Catry et al. 2014).

Habitat effects upon laying date and fledging success

The study population displays an interesting demography, whereby birds with home ranges incorporating a greater relative proportion of strongly utilised cereal, woody fruit crops, and grassland habitat exhibit greater fledging success, but earlier laying Roller pairs are found in areas with an increasing proportion of strongly avoided urban habitat.

Later nesting birds may benefit from the increasing availability/biomass of invertebrate prey as the breeding season progresses (Figure S4.3 (Appendix);

Evans et al. 1997). They may also benefit from the availability of an ephemeral food source at harvest time, coinciding with the latter half of the chick rearing period, resulting from the harvesting of cereal crops and the prevalence of escaping invertebrate prey (Catry et al. 2014). Based upon the results of the invertebrate biomass analysis, an increasing proportion of grassland and woody fruit crop habitats within a home range could positively impact fledging success, in the absence of predation or disease, due to the higher invertebrate biomass within those habitat types.

The negative relationship observed between laying date and increasing proportion of strongly avoided urban habitat within the home range, and the positive relationship between fledging success and increasing laying date, is interesting. Earlier arriving individuals of migratory species are usually considered to be ‘higher quality’ birds (Kokko 1999), and theoretically have access to a greater choice/availability of unoccupied nest sites prior to the arrival of sympatric individuals.

The data suggests that a trade-off may occur between maximising the number of chicks fledged from a nest and that nest’s risk of predation or failure. Urban nests are potentially less susceptible to predation by terrestrial predators, even in years of overall increased predation risk, due to their location high in walls offering little purchase. Nevertheless, these nests generally fledge fewer chicks than rural nests, potentially due to their location further from optimal foraging habitats, or due to increased competition with other high quality neighbouring Roller pairs breeding within the same urban localities.

This hypothesised scenario could explain the preference of (assumed higher quality) early breeding birds for lower quality (in terms of optimal foraging habitat) urban nest sites, as the lowered risk of complete nest predation outweighs the potential for an increased number of fledglings within more rural nest locations. Nevertheless, this analysis is based upon only 2 years of breeding data, and data collection from a number of future breeding seasons would therefore be necessary before the hypothesis could be tested using robust statistical analyses.

Implications for Roller conservation

The area of traditionally farmed and grassland habitats used by foraging Rollers has declined sharply in Cyprus since its admittance to the European Union (Ieronymidou 2012), and the remaining agricultural areas are becoming more intensively managed, potentially leading to declines in invertebrate availability and biomass. Levels of urbanisation and land abandonment-induced scrub encroachment are high (Hellicar et al 2014), increasing the extent of avoided Roller habitats and further decreasing the availability of nests sites within older buildings, as these are renovated or demolished.

Maintenance of traditional farming practises, via agri-environment schemes and fiscal incentives, and limitations placed upon rural urbanisation are 2 key methods to minimise adverse effects upon Rollers in Cyprus. These issues have been previously highlighted in Cyprus' response to the UN Convention on Biological Diversity (Ministry of Agriculture, Natural Resources and Environment 2014), and control measures are identified within the Cypriot Rural Development Plan 2014 - 2020, which aims to have 9% of agricultural land under biodiversity-friendly management (European Commission 2014), as well as investing further in protected Natura 2000 sites.

Novel agri-environment schemes should focus upon those areas of high Roller densities, both within and outside of the Protected Area network (see Chapter 3), and incorporate measures that specifically promote the maintenance of traditionally farmed and grassland habitats within 600m of Roller nest locations. Such measures would particularly benefit 'urban' nesting Roller pairs, and potentially increase fledging success. The establishment of a national nest box scheme for the Roller may also prove beneficial, to counteract the loss of nest sites within older buildings. This has proven to be the case elsewhere in the species' European range, with the proviso that nest boxes are located within areas of suitable foraging habitat (Rodriguez et al. 2011) (.i.e. the preferred traditionally farmed and grassland habitats identified in this study).

4.6 Acknowledgements

I would like to thank Alessandro Gravano, Harry Ewing, Teresa Catry, Ines Catry, Chris Hewson, and Aldina Franco for their assistance in the capture of adult rollers, the deployment of GPS loggers in the field and assistance during the habitat mapping process. The project is funded through a Natural Environment Research Council Studentship Grant (No. 1210309), and the author is also a beneficiary of both an A.G. Leventis Foundation Scholarship and British Trust for Ornithology CASE studentship award.

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Appendix: Supporting information

GPS logger field trials

Prior to the commencement of the tracking study, a field trial was carried out to investigate the effect of satellite connection number upon fix location error. Thirteen loggers were placed at 2 separate locations, varying in topography, for continuous 3 day periods. The tags were deployed on the top of wooden canes c.1m in height, arranged in a 1m interval grid pattern, and programmed to attempt a fix once every 20 minutes between 0800 and 1700hrs.

Each logger location was identified using a handheld GPS unit, with any error in the subsequent fix locations recorded. This displacement error was then compared between fixes made via connections to varying satellite numbers (Figures S4.1 and S4.2). In order to minimise both location error and loss of successful fixes, a decision was made to utilise only those fixes made using a minimum of 5 satellite connections.

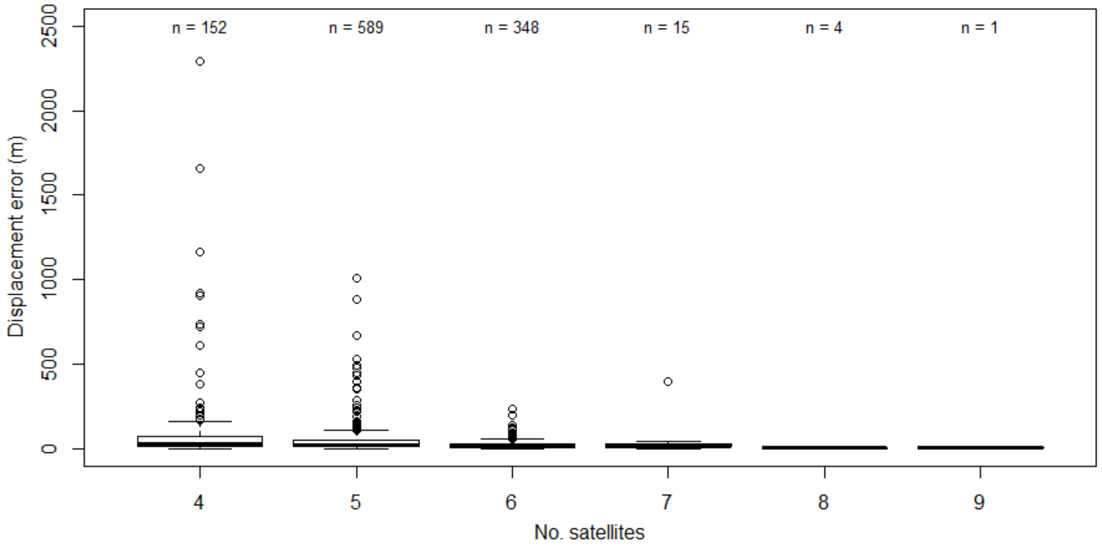

Figure S4.1: Fix displacement error vs. number of satellite connections results from logger error trials carried out at 2 locations in Cyprus over a 3 day period in the spring.

An additional trial field trial was undertaken to investigate innate logger fix location error. 4 loggers were deployed at 13 separate locations with the study area over a 3 week period to investigate fix and location error. The trial locations varied in elevation and topography, and were located in proximity to known Roller nest sites.

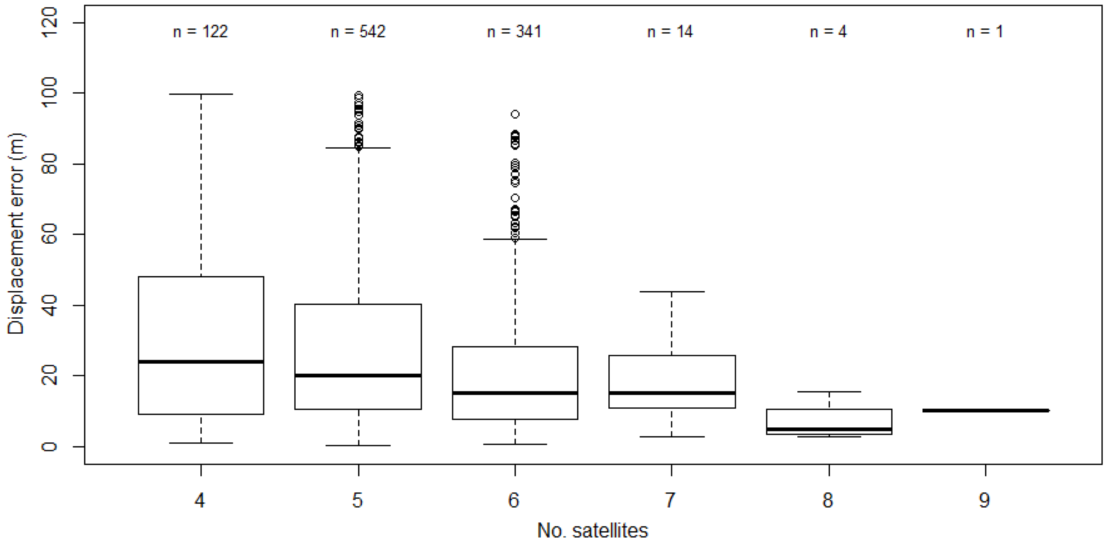

Figure S4.2: Fix displacement error with 100m threshold (outliers removed) vs. number of satellite connections results from logger error trials carried out at 2 locations in Cyprus over a 3 day period in the spring.

The 4 loggers were deployed at each locality between 0800 and 1700hrs, and were again deployed upon wooden canes, arranged in a 1m x 1m square. The central point of each trial location was identified using a handheld GPS unit, with a mean value of displacement error calculated for both trial site and individual logger (Table S4.1). The results of the 2 separate error trials were incorporated into all subsequent analyses of the GPS logger dataset.

Table S4.1: Results of large-scale GPS fix displacement error trials carried out in Cyprus over a 3 week period in the spring.

Test location	**No. fixes**	**Mean displacement (m); all tags (*n=4*)**	**Range (m)**	**Median (m)**
Akoursos	61	27.98	0.86 to 100.27	20.87
Androlikou	75	36.26	2.90 to 203.39	23.42
Arodes	78	32.78	2.41 to 819.37	14.10
Chrysochou	72	33.78	0.73 to 194.34	21.02
Evretou	58	38.37	3.39 to 399.14	21.00
Karathea Tavern	62	23.55	1.98 to 151.20	15.80
Kathikas	60	56.93	2.75 to 700.67	21.38
Pano Arkoudalia	5	10.30	4.90 to 14.54	10.57
Podromi	64	27.85	1.12 to 188.26	11.98
Pittokopos	69	19.80	0.89 to 117.20	13.42
Steni	65	45.26	1.24 to 770.95	17.54
Terra	72	20.69	0.46 to 141.46	15.61
Theletra	41	70.55	1.94 to 731.49	20.70
Overall mean		34.16		
Tag no.	**No. fixes**	**Mean displacement (m); all sites (*n=13*)**	**Range (m)**	**Median (m)**
12624	187	34.78	0.73 to 731.29	18.71
12626	208	39.73	1.35 to 819.37	19.90
12664	205	29.76	0.46 to 612.39	15.97
12671	181	33.92	1.48 to 770.95	17.78
Overall mean		34.55		

Changes in the terrestrial invertebrate biomass of Roller foraging habitat during the chick rearing period

Fallow and grassland habitats consistently supported the highest biomass of terrestrial invertebrate prey during the 3 survey periods (early, mid, and late June) (Figure S4.3), with ploughed areas consistently supporting the lowest. Scrubland, woody fruit crop, cereal, and ploughed habitats supported terrestrial invertebrate biomasses intermediate between the 2 extremes. All of the habitats exhibited an increasing biomass between the first and second survey. The biomass of fallow, cereal, and ploughed habitats continued to increase in the third survey visit, whilst that of woody fruit crops, grassland, and scrubland declined. The biomass of the latter three habitats still remained higher than during the first survey visit, however.

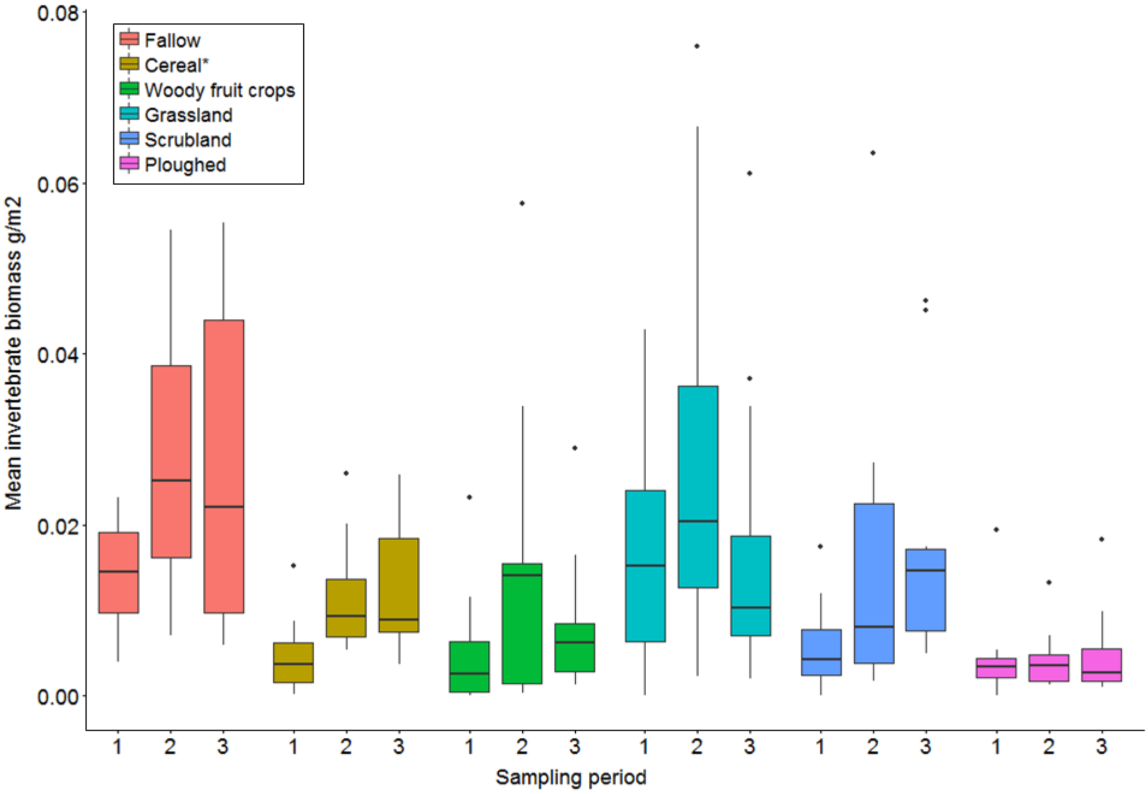

*Figure S4.3: Changes in terrestrial invertebrate biomass (combined 2014 and 2015 data) within Roller foraging habitat types during the; (1) early; (2) mid, and; (3) late chick-rearing periods. Mode, interquartile range, and outliers shown (*note that cereal biomass refers to stubble only, not growing crop).*

Do nest site selection preferences differ between eastern and western Mediterranean populations of the European Roller (*Coracias garrulus*)?

5.1 Abstract

Understanding the drivers of nest site selection in threatened bird taxa, either at the landscape scale or nest site level, is a critical component of successful conservation interventions. The use of suboptimal nest sites and breeding habitat, or the occurrence of nest site limitation, can have negative effects upon population growth. Optimal nest sites and breeding habitat may vary between populations of the same species, and it is important to identify any differences in order to make conservation management relevant at the population level. This study models nest site selection preferences (at the landscape scale and nest cavity level), and interspecies nest competition in a range of semi-natural and man-made nest sites in 2 populations of the threatened European Roller (Coracias garrulus; an obligate cavity nester) in Portugal and Cyprus, at either end of the species' Mediterranean range. The study showed that both populations selected nest sites based upon cavity parameters, rather than the extent of preferred foraging habitat surrounding the nest cavity. It also showed that Cypriot Roller cavity entrances were significantly wider, and their internal cavities significantly wider and longer, than those in Portugal. Interspecific competition was greater in Portugal than in Cyprus, with non-Roller occupied cavities in Portugal predominantly occupied by Lesser Kestrels (Falco naumanni), whilst those in Cyprus were mostly empty. The parameters of cavities occupied by other, similarly sized, species in Portugal fell within the range of those suitable for use by Rollers (based upon univariate analyses), whilst those in Cyprus did not. Our models showed that height above the ground, and entrance and cavity size, comprised the most important cavity selection parameters for the Cypriot population, with nesting structure and entrance width most important for the Portuguese population. Portuguese Rollers fledged more chicks from narrower cavities, whilst Cypriot birds did so from structures incorporating a larger number of closely-spaced cavities.

5.2 Introduction

Bird populations are limited by a range of factors, including food and nest site availability, disease, and inter/intra-specific competition (Newton 2013). At the population level, the availability of nest sites and access to food resources are key regulators (Newton 1994). In situations where either food or nest sites are limited, negative population trends can occur, with the use of suboptimal nest sites and breeding habitats having direct negative impacts upon productivity (Rodenhouse & Holmes 1992), and also often increasing predation risk (Liebezeit & George 2002). Gaining an understanding of which breeding season habitats and nest site characteristics are favoured by threatened bird species is therefore essential in order to maintain their populations at a favourable level.

Nest site selection has been widely studied in birds and consists of a complex interaction between nest site availability (Aitken & Martin 2008), inter and intraspecific competition (Martin et al. 2004), predation risk (Martin 1993), and surrounding habitat composition (Gjerdrum et al. 2005). What constitutes a ‘good’ nest site for any given species may vary across its range, due to spatial variation in biotic (e.g. competitors, predators, disturbance, and habitat) and abiotic (e.g. climatic) factors. Few studies have however attempted to capture such range-scale variation in nest site selection within a single species.

Nest sites are often limited for obligate secondary cavity nesting species (Newton 1994; Aitken & Martin 2012), as they exist within a ‘nest web’ (Martin & Eadie 1999) whereby secondary nesters are dependent upon the actions of primary excavators, or the provision of man-made cavities. Understanding the cavity parameter preferences of obligate cavity nesting species can therefore be beneficial when designing and/or siting nest boxes for use in localities where natural cavities are limited (Zingg et al. 2010).

The majority of nest cavity selection research has been undertaken upon tree or nest box-breeding species or populations, with relatively few studies carried out on species or populations breeding within cavities in buildings or cliff faces (Corrales et al. 2013; Franco et al. 2005; Catry, Silva, et al. 2011; Václav et al. 2011). In many European countries agricultural intensification has led to the replacement of older, less productive trees, with younger individuals (Moning & Müller 2009). This has resulted in many cavity nesting species relying more heavily upon nest sites in buildings and man made structures (Rodriguez et al. 2011). Understanding the role of nest sites in buildings has therefore been identified as a conservation priority for a range of threatened species (Mainwaring 2015).

This study investigates nest site selection in the migratory European Roller (*Coracias garrulus*; henceforth Roller) in Portugal and Cyprus, at the western and eastern extents of the species Mediterranean range (BirdLife International 2016a). The two populations differ, with that in Portugal having experienced a severe national decline in recent decades and now classified as Critically Endangered (www.nationalredlist.org/tag/portugal), whereas the population in Cyprus is considered to be stable, or declining slightly, and comprises >3% of the Roller population within Europe (BirdLife International 2015). Habitats within the 2 study areas also differ, with Portuguese Rollers inhabiting extensive areas of pseudo-steppe habitat subject to traditional cereal rotation, whilst Cypriot Rollers inhabit a complex Mediterranean farmland/scrub mosaic of varying topography.

Primary cavity excavators are absent from both study areas, with Rollers largely dependent upon cavities in buildings, cliff faces, and artificial nest sites (Pomeroy et al. 2013; Catry et al. 2011). The Portuguese study area also incorporates several purpose built breeding walls, in addition to other artificial nest sites in the form of wall-mounted clay pots and wooden nest boxes, installed with the aim of increasing the populations of a range of threatened cavity nesting species (Catry et al. 2013).

The majority of previously published studies on nest site selection in Rollers have focussed upon nest box and/or tree nesting populations (Avilés et al. 2000; Bouvier et al. 2014; Butler 2001; Rodriguez et al. 2011), and the current study is therefore of importance in establishing nest selection preferences for Roller populations using alternative man-made and ‘semi natural’ cavities. Furthermore, man-made structures within the 2 study areas are subject to differing development pressures, with renovation of abandoned buildings a key concern in Cyprus (Ieronymidou 2012), and building senescence and collapse an increasingly important issue in Portugal (Catry et al. 2011).

Competitor communities also differ between the two sites, with the Portuguese study area supporting a large population of colonially-nesting Lesser Kestrels (*Falco naumanni*) alongside smaller populations of other cavity nesting competitor species. Lesser kestrels are absent as a breeding species from Cyprus (BirdLife Cyprus 2016), although the island does support populations of several other cavity nesting species, including Western Jackdaws (*Corvus monedula*), Eurasian Scops Owls

(*Otus scops*), and Eurasian Kestrels (*F.tinnuculus*; BirdLife Cyprus 2016). Lesser Kestrels and Rollers share a similar ecology and are both obligate secondary cavity nesters (Cramp & Simmons 1998), and the Portuguese Lesser Kestrel population has recovered from an extremely low level in the 1990s (BirdLife International 2016b), largely due to the provision of hundreds of artificial nest sites (Catry et al. 2013). Rollers have also taken advantage of these novel sites, and the two species, now potentially compete for the available cavities.

This study therefore aims to identify whether nest site selection varies between the 2 populations and, if so, what the ramifications might be for the conservation of the species at either end of its Mediterranean range. Specifically, it examines: (1) which landscape and cavity parameters control nest site selection by Rollers in the 2 study areas; (2) whether particular cavity scale characteristics are associated with increased Roller fledging success; (3) whether increasing populations of nest site competitors may be having a detrimental effect upon the Portuguese Roller population, and; (4) whether nest site limitation is occurring in either of the study populations.

5.3 Methods

Study areas

The Cypriot study area is approximately 400km^2 in extent and is located in the north-west of Paphos District, within the Republic of Cyprus (Figure 5.1), with monitoring of its' Roller population commencing in 2013. This area of Cyprus exhibits a varied topography and supports a range of farming land use types, grassland, and scrubland habitats representative of those found across the island. It is also an area where intensification of agriculture, land abandonment, and increased urbanisation has been occurring in line with that elsewhere in Cyprus (Saunders et al. *in.prep*.).

The Portuguese study area (Figure 5.1) is approximately 600km^2 in extent and is located in the Lower Alentejo region, within the Castro Verde Special Protection Area (SPA), and its' Roller population has been monitored for approximately 9 years prior to 2013. The landscape within the SPA consists of gently rolling plains predominantly supporting extensive, low-intensity, cereal rotation (comprising a mix of cereal and fallow land) alongside isolated/abandoned buildings and man-made breeding walls.

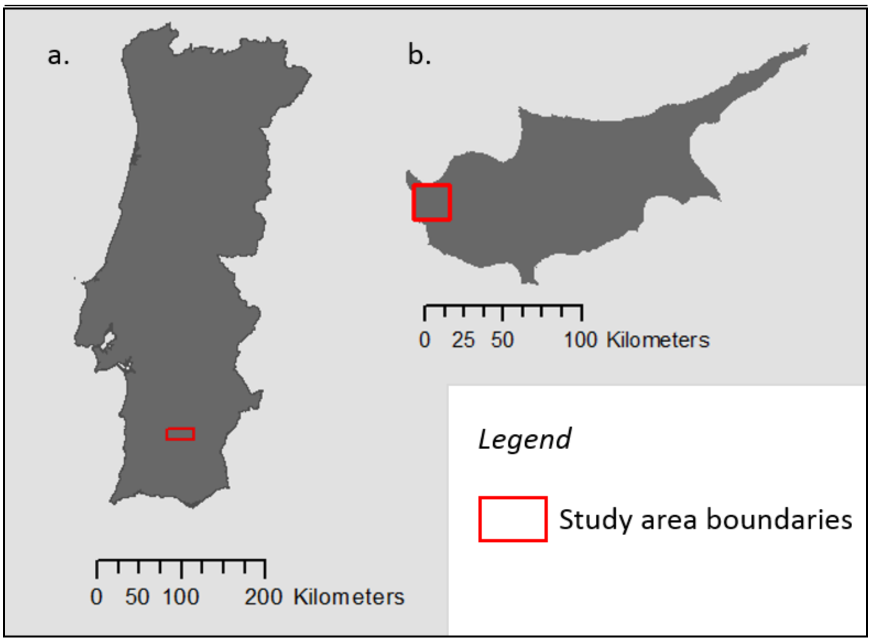

Figure 5.1: Study areas: (a) Castro Verde Important Bird Area in the Lower Alentejo of Portugal, and (b) western Paphos District in the Republic of Cyprus.

Field data collection

Cavity data

Cavity data was collected from a total of 25 cavity bearing structures in the Cypriot study area during the 2014 breeding season, with 30 cavity bearing structures surveyed in the Portuguese study area during the same year. A small number of structures within both study areas were not surveyed due to accessibility issues. All of the structures surveyed in Cyprus supported breeding Rollers, whilst those surveyed in Portugal included several structures unoccupied by the species ($n = 5$). Several structure level parameters were recorded during the surveys, including: structure type (building, breeding wall, or cliff), the maximum number of cavities within the structure, and the maximum linear distance between the furthest individual cavities within the structure.

Breeding walls were only present within the Portuguese study area, and comprise man-made stone or brick structures incorporating purpose-built cavities for use by cavity-nesting birds, and were principally created to promote Lesser Kestrel population growth (Catry et al. 2011). Due to difficulties in both access and the application of standardised cavity measurements to rot holes and hollow trunks, cavity parameter measurements were not made for the small number of confirmed Roller tree nests within the Cypriot study area.

Individual measurements were then made for each cavity present within the surveyed structure, comprising; species occupancy (or blocked/empty status), nest type (cavity, nest box, or clay pot), nest entrance orientation, and a range of detailed nest entrance and internal cavity measurements (Table 5.1).

Table 5.1: Nest site parameters collected from cavity-bearing structures within Castro Verde Special Protection Area (southern Portugal) and western Paphos district (Republic of Cyprus) during the 2014 breeding season.

Nest site parameter	**Description**
Species occupancy	Roller, competitor (identified to species level), empty, or blocked.
Structure	Building, cliff-face, or breeding wall.
Total no. of cavities	The total number of cavities within the structure.
Maximum distance between cavities	The maximum spread of cavities across the structure (i.e. how much of the structure face supports potential nest sites. Also proxy for structure size): recorded as a categorical variable <10m, 10 to 20m, and 20 to 30m.
Nest type	Cavity, nest box, or claypot.
Entrance orientation	Direction in which nest site entrance faces (north, east, south, or west).
Location	Exterior or interior (i.e. inside or outside buildings).
Height of cavity above ground	Distance between ground and bottom of nest site entrance in cm.
Entrance height	Maximum height from bottom to top of nest site entrance in cm.
Entrance width	Maximum width of nest site entrance in cm.
Distance between entrance and widest point in cavity	Distance between bottom lip of nest entrance and widest point of cavity in cm (recorded in Cyprus only)
Cavity height	Maximum internal height of nest site cavity in cm.
Cavity width	Maximum internal width of nest site cavity in cm.
Cavity length	Maximum distance between bottom lip of nest entrance and back wall of cavity in cm.

Habitat data

In addition to cavity data, the area of heavily utilised, high invertebrate biomass, foraging habitat (comprising fallow areas in Portugal (Catry et al. 2011), and combined fallow and grassland areas in Cyprus; see Chapter 4) were mapped within a 600m buffer (based upon the Mean Maximum Foraging Extent of the home range observed in Cypriot Rollers; see Chapter 4) surrounding all Roller-occupied nest structures during the 2014 breeding season, including Roller-occupied tree nests in Cyprus. The area of avoided urban habitat (see Chapter 4) within the 600m buffer surrounding all Roller-occupied structures in Cyprus was also mapped (this habitat is absent from the Portuguese study area).

Habitats surrounding an additional single Roller occupied cavity-bearing structure (from which cavity data could not be collected due to inaccessibility), and a sample of 23 non-Roller occupied cavity-bearing structures, in the Portuguese study area were also mapped. The non-Roller occupied structure data was collected for use as non-selected nest sites in the landscape-scale nest site selection analysis.

All accessible buildings and cliffs in the Cypriot study area supported breeding Rollers, and it was therefore necessary to identify additional locations for use as non-selected nest sites for the landscape scale analysis. Eighteen random points were therefore identified, using ArcGIS 10.3 (ESRI, 2014), within a 400m survey corridor centred upon those survey area access routes which had previously been exhaustively surveyed for Roller presence or absence (see Chapter 3). All areas within 1200m of known Roller nest sites or territories were excluded to minimise overlap between confirmed nest site and random point buffers. The random points were centred upon mature trees (mainly carobs *Ceratonia silique* and olives *Olea europaea*) which exhibited holes/cavities within their trunks large enough to permit access to Rollers. The random point localities were subsequently monitored throughout the 2014 and 2015 field seasons to confirm non-use by Rollers or competitor species.

Previous research has identified the importance of damp soils within the water-limited Portuguese study area upon the availability of large invertebrate prey required by Lesser Kestrels during the pre-breeding period (Catry et al. 2012). Due to their similar ecology, the effect of damp spring soils upon Roller nest site selection was therefore also considered. A measurement of water availability was made as a proxy for soil dampness for structures within the Portuguese study area, via examination of Google Earth imagery for spring 2013 (the sole period for which images were available for the entire study area). The length of all linear watercourses/ditches containing standing water within the 600m buffer were measured, as were the full/partial perimeters of all standing waterbodies (e.g. ponds). Standing water is absent from the Cypriot study area and was not therefore considered.

Roller productivity data

Roller breeding parameters were collated in order to investigate the effects of cavity parameters upon Roller productivity. The data collected comprised brood size (i.e. number of eggs within a clutch that hatched) and the number of chicks fledged (i.e. those reaching 3 weeks of age). These data were collected for each breeding season between 2013 and 2015 from each Roller occupied cavity that was subject to cavity parameters measurements during 2014, with the assumption that cavity/structure parameters would remain the same 1 year either side of the 2014 cavity survey season.

Cavity breeding assemblage census data

A census of Rollers and all other cavity breeding species was carried out annually at all potential breeding structures within the Portuguese study area between 2004 and 2013, with the number of breeding pairs of each species at each structure, and the number of cavities within each structure, recorded. Due to access issues, it was not possible to confirm exact numbers of Lesser Kestrels at every structure each year, in which case the lower limit of the breeding pair population estimate for that species was recorded.

Statistical analyses

Nest site parameters

Univariate comparisons were made between the mean internal parameters, and the height above ground, of Roller occupied cavities within the two study areas using Student’s t-tests. The potential suitability of non-Roller occupied cavities for use by Rollers was also assessed separately for the 2 study areas using univariate comparison of internal cavity parameters and cavity height above ground. The range of values of each parameter within Roller occupied cavities was first calculated, with any non-Roller occupied cavity incorporating an entire suite of assessed parameter values within the same range identified as suitable.

Landscape and cavity parameter models

Separate models of Roller nest site selection were constructed at; (1) the landscape scale and; (2) the cavity level for each of the 2 study populations, using a range of explanatory parameters. All potential explanatory parameters used within each of the models were initially screened for unimodal significance prior to inclusion, with only significant variables carried forward. Pairwise correlations were then examined, with the stronger variable retained of any pair exhibiting a Pearson Correlation Coefficient of >0.7. The distribution of each dependent variable was also confirmed prior to imposition of a specific model structure.

All modelling was carried out using the lme4 and MuMIn packages in R (R Core Development Team, 2016). Model selection was carried out using the Akaike Information Criterion adjusted for small sample sizes (AICc; Hurvichl & Tsai 1995). Due to the large number of initial explanatory parameters used, and uncertainty in model choice resulting from the large set of candidate models exhibiting a ΔAICc < 2, multimodal inference and model averaging were used to produce robust parameter estimates and calculate 95% confidence intervals (CI) using the weighted average of the corresponding coefficient in all candidate models within the top model set (Burnham & Anderson 2002). Only those parameters retained within the averaged models which exhibited 95% CI's not spanning zero were considered statistically significant at p=<0.05.

Landscape scale nest site selection

Landscape scale nest site selection was modelled separately for the Cypriot and Portuguese study areas using Logistic Mixed Effect Models with logit link function. Roller use of structure (i.e. building, breeding wall, cliff face, or tree) in 2014 was modelled against non-use of structure in the same year using a range of explanatory variables derived from data collected during field surveys (Table 5.2). *Locality* was incorporated as a random effect to account for any overlapping 600m buffers surrounding nearby structures.

Cavity selection

Two separate models of cavity selection were constructed for each of the 2 study areas: Roller occupied vs. empty cavities, and Roller occupied vs. empty cavities and those occupied by smaller, 'evictable', competitors (the latter carried out to ascertain whether competitors choose similar cavities to those used by Rollers). Evictable species were identified by their smaller size/weight (Cramp & Simmons 1998) , consultation with local experts (I.Catry, A.Franco, *pers.comm*.), and direct observation in the field. 'Evictable' species comprised the Lesser Kestrel, Little Owl (*Athene noctua*), and Spotless Starling (*Sturnus unicolor*) in Portugal, and Eurasian Scops Owl in Cyprus. Cavities that were either occupied by dominant competitors

Table 5.2 Independent variables analysed to develop landscape scale nest site selection models for the Roller in southern Portugal (P) and western Cyprus (C); use of bracketed terms denote sole use within respective study area.

Fixed effects	**Description**
Watercourse length (P)	Length (m) of all linear watercourse sections and perimeters of non-linear waterbodies within 600m nest buffer, identified from Google Earth imagery (April and May 2013).
% high quality foraging habitat surrounding nest site	The percentage area of the 600m nest buffer occupied by fallow and grassland habitats in Cyprus, and fallow habitats in Portugal.
% urban habitat surrounding nest site (C)	The percentage area of the 600m nest buffer occupied by urban areas (Cyprus only; all Portuguese nest sites are in rural areas).
Random effects	
Locality	Geographic unit, expressed as town/location name. Incorporated to account for overlapping 600m nest buffers surrounding structures used in habitat analyses.

(e.g. Eurasian Kestrel or Barn Owl (*Tyto alba*)), or blocked with nest material/debris, were considered unavailable and excluded from the analyses.

A range of potential explanatory cavity scale variables were incorporated within the 4 models (Table 5.3), describing structure type, location, size, and orientation, as well as entrance and internal cavity metrics. A structure-level random effect (*Site*) was used to account for any gross similarities between cavities within the same structure. Due to difficulties in both access and the application of standardised cavity measurements to rot holes and hollow trunks, the small number of confirmed Roller tree nests within the Cyprus study area were excluded from the cavity scale analysis. It was also not possible to measure some of the internal parameters (e.g. cavity height and width) for a small proportion of cavities in both study areas due to narrow entrances. These measurements were therefore substituted by the mean values of those parameters for all other occupied Roller nests within the respective study area.

Cavity-scale effects upon Roller productivity

Single models investigating the effect of cavity scale parameters upon Roller productivity were constructed for each of the 2 study areas using Poisson Mixed Effect Models with Log link function. The productivity metric was number of chicks fledged from each nest, offset by the natural logarithm of the number of chicks hatched (brood size). The same range of explanatory parameters used in the cavity scale nest site selection analysis (Table 5.3) were incorporated in the initial model.

Table 5.3: Independent variables analysed to cavity selection models for the Roller in Portugal (P) and Cyprus (C); use of bracketed terms denote sole use within respective study area.

Fixed effects	**Description**
Structure	Location of nest site: building, cliff-face, or tree in Cyprus, building or breeding wall in Portugal.
Total no. of cavities	The total number of cavities within all occupied structures.
Maximum distance between cavities	The maximum spread of cavities across a structure (i.e. how much of the structure face supports potential nest sites. Also proxy for structure size): <10m, 10m to 20m, and 20m to 30m.
Nest type (P)	Cavity, nest box, or claypot. All nests in Cyprus were within cavities.
Orientation	Direction in which nest site entrance faces (North, East, South, or West).
Location (C)	Exterior or interior (i.e. inside or outside buildings). All Portuguese cavities were external.
Height of cavity above ground	Distance between ground and bottom lip of nest site entrance in cm.
Entrance height	Maximum height of nest site entrance in cm.
Entrance width	Maximum width of nest site entrance in cm.
Distance between entrance and widest point in cavity (C)	Distance between bottom lip of nest entrance and widest point of cavity in cm. This parameter was not collected within the Portuguese study area.
Cavity height	Maximum height of nest site cavity in cm.
Cavity width	Maximum width of nest site cavity in cm.
Cavity length	Maximum distance between bottom lip of nest entrance and back of cavity in cm.
Random effects	
Site	Identifier given to each nest supporting structure. Incorporated to account for repeated measures between years, and presence of numerous cavities within
Year	Calendar year. Incorporated to account for inter-annual variation in habitat and breeding parameters.

Site was nested within *year* as a random effect to account for potential inter-year variation in Roller pair composition and weather/prey availability, similarities in surrounding foraging habitat composition, and repeated surveys at the same nest between years.

Effects of the increasing Lesser Kestrel population upon nest site occupation by Rollers

The effect of competitor presence on Roller nest site selection was modelled for the Portuguese study area using the 10 year Roller/Lesser Kestrel dataset and Poisson Mixed Effect Models with Log link function. Number of Roller pairs per structure was modelled against number of Lesser Kestrel pairs. Two global models were produced; (i) incorporating the total number of wall cavities (excluding spaces under roof tiles) within the nest site structure as an offset, and (ii) without the offset. The offset was included to account for variation in the number of available cavities within any given structure, and potential effects of nest site limitation. *Site* was again nested within *year* as a random effect to account for potential inter-year variation.

5.4 Results

Nest Site Parameters

Species occupancy

Forty accessible cavities occupied by Rollers were identified in the Portuguese study area in 2014, in addition to 222 cavities unused by the species (Figure 5.2a). Non-Roller occupied cavities were either empty (n=69) or used by one of 6 competitor species, with Lesser Kestrel the most commonly recorded (n=124). Rollers were the second most frequently recorded species. The majority of empty (78%) and competitor-occupied (85%) cavities nevertheless exhibited internal dimensions, and were located at heights above the ground, within the range of the Roller occupied nest cavities (Figure 5.2a; Table 5.4).

Twenty-six accessible cavities occupied by Rollers, located within 25 separate structures, were identified in the Cypriot study area in 2014 (Figure 5.2b). An additional 169 cavities unused by Rollers were also identified. Non-Roller occupied cavities were either empty (n=113), blocked by old nest material or detritus (n=29), or occupied by 1 of 2 competitor species. Rollers were the most frequently recorded species. The majority of empty (75%), blocked (83%), and competitor occupied (89%) cavities exhibited internal dimensions, and were located at heights above the ground, outside the range of the Roller occupied cavities (Figure 5.2b; Table 5.4).

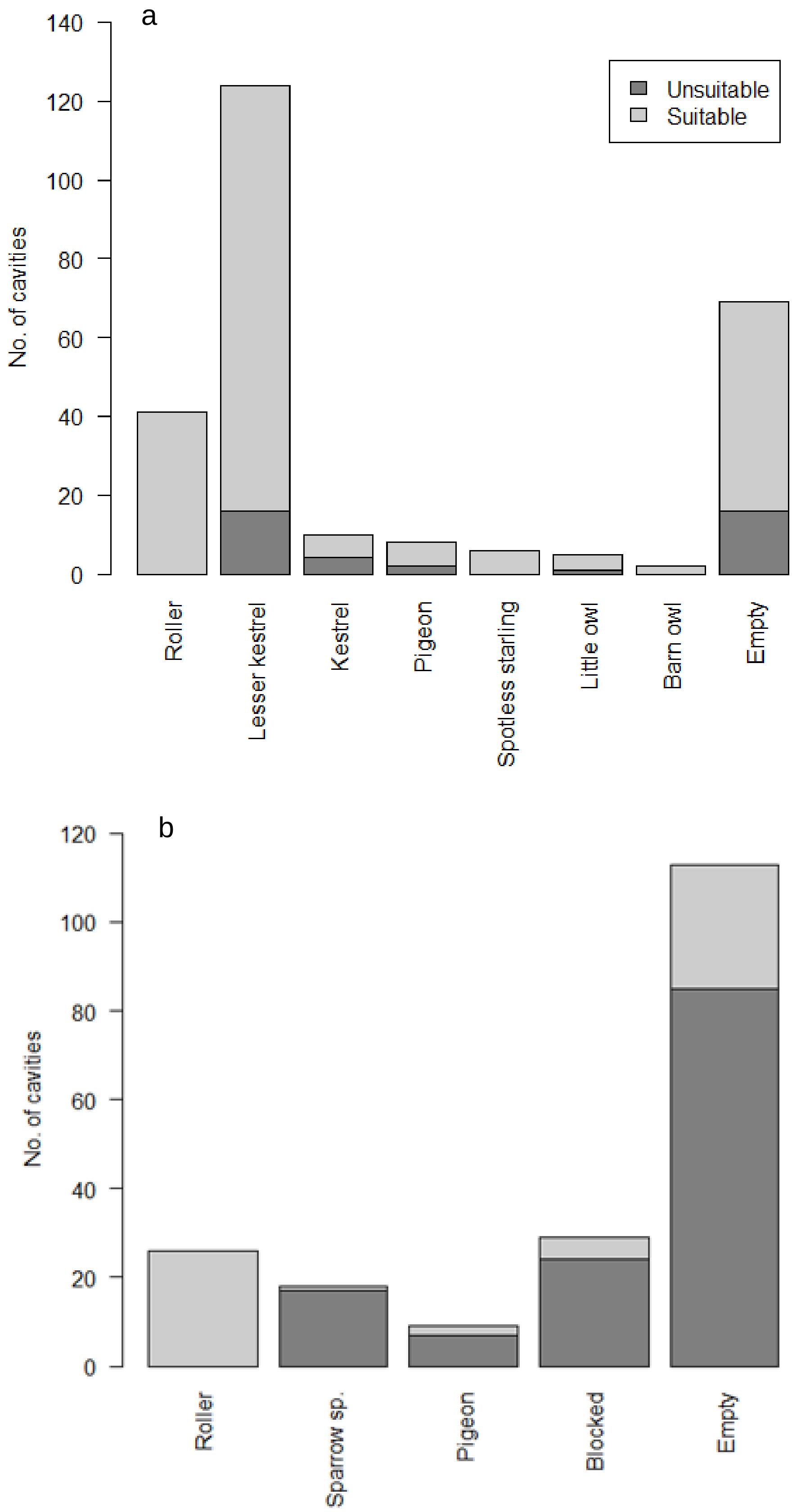

Figure 5.2: Cavity occupation by species within (a) Castro Verde SPA, southern Portugal, and (b) western Paphos district, Republic of Cyprus. All non-Roller occupied cavities were identified as suitable for use by Rollers if all of the cavity's internal and external parameters fell within the range of those exhibited by Roller-occupied cavities within the respective study area.

Table 5.4: Mean measurements and ranges of Roller occupied cavity parameters within Castro Verde SPA, southern Portugal, and western Paphos district, Republic of Cyprus.

	Portugal		**Cyprus**	
Nest site parameter	***Mean***	***Range***	***Mean***	***Range***
Height above ground (cm)	303.00	127.00 - 490.00	336.30	163.00 - 570.00
Entrance height (cm)	8.70	6.20 - 16.00	10.20	3.50 - 20.00
Entrance width (cm)	8.50	6.00 - 20.00	14.10	5.50 - 33.50
Cavity length (cm)	34.10	23.00 - 50.00	45.10	26.00 - 98.00
Cavity height (cm)	16.70	12.00 - 21.00	15.50	7.00 - 33.00
Cavity width (cm)	21.40	15.00 - 32.5	31.20	8.00 - 61.00

The number of suitable cavities identified within both the Cypriot and Portuguese study areas may still comprise an overestimate, as the univariate analyses of individual internal cavity parameters does not take into account particular combinations of cavity characteristics which may preclude use by Rollers (e.g. a potential preference for long entrances only in conjunction with larger entrances).

Supporting structure and nest type

All accessible cavities containing Roller nests within the Portuguese study area were located either within buildings, artificial breeding walls, or in nest boxes/clay pots attached to buildings, whilst all Cypriot nests were located either in buildings or cliff faces (Table 5.5). All Cypriot nests consisted of ‘semi natural’ cavities arising from erosional processes, whilst the majority of Portuguese nest sites were either located within nest boxes and clay pots installed upon buildings, or in artificial cavities within purpose built breeding walls.

Internal parameters

The internal parameters of Roller-occupied nest cavities varied between the two study areas (Figure 5.4), with Cypriot nest entrances being significantly wider (Cyprus $\dot{x}$ = 14.1cm, SE = 1.27; Portugal $\dot{x}$ = 8.5cm, SE = 0.43; $p = 2.0^{-04}$), and internal cavities being significantly wider (Cyprus $\dot{x}$ = 31.2cm, SE = 2.34; Portugal $\dot{x}$ = 21.4cm, SE = 0.75; $p = 4.0^{-04}$) and longer (Cyprus $\dot{x}$ = 45.1cm, SE = 2.99; Portugal $\dot{x}$ = 34.23cm, SE = 1.05; $p = 1.0^{-03}$). Portuguese nest sites were also located

Table 5.5: Nest type and supporting structure of Roller-occupied nest sites in Castro Verde Special Protection Area (southern Portugal) and western Paphos district (Republic of Cyprus) during the 2014 breeding season.

Supporting structure and nest type		**No. of nests**	
Structure	***Nest type***	***Portugal***	***Cyprus***
Breeding wall	Cavity	10	-
Building	Cavity	16	20
Building	Clay pot	5	-
Building	Nest box	9	-
Cliff	Cavity	-	6

significantly higher above the ground than Cypriot nest sites (Cyprus $\dot{x}$ = 270.11cm, SE =7.69; Portugal $\dot{x}$ = 305.29cm, SE = 70.06; p = 0.01). Entrance height (Cyprus $\dot{x}$ = 10.22cm, SE = 0.74; Portugal $\dot{x}$ = 8.68cm, SE = 0.42) and internal cavity height (Cyprus $\dot{x}$ = 15.45cm, SE = 1.13; Portugal $\dot{x}$ = 16.87cm, SE = 0.37) were similar within the 2 study areas (p = 0.08 and 0.24, respectively).

Landscape scale nest site selection

The sole landscape scale nest site selection model retained in the Portuguese top model set was that incorporating *watercourse length* (Table 5.6), alongside the intercept only model. Following model averaging *watercourse length* exhibited a non-significant relationship (based upon 95% CI's) with Portuguese Roller nest site selection (Table 5.7).

The intercept only model was solely retained in the top model set for Cyprus, with none of the habitat or disturbance parameters (% foraging habitat and % urban habitat surrounding the nest site) retained (Table 5.6), indicating that none of the habitats considered were either selected or avoided.

Cavity selection

Two models were retained within the top model set comparing Roller occupied nest cavities with empty cavities in the Portuguese study area (Table 5.8). Following model averaging, the only parameters exhibiting significant relationships (based

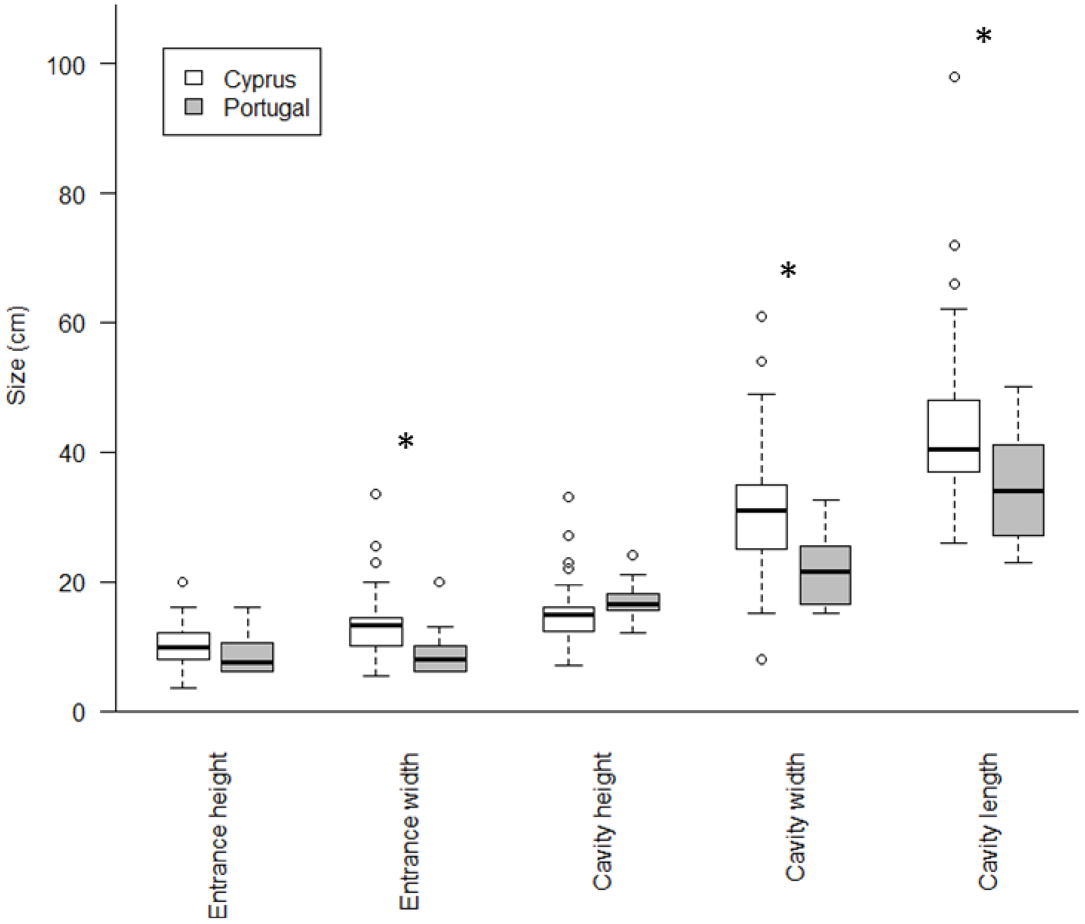

Figure 5.4: Comparison between internal parameters of Roller occupied nest cavities in western Cyprus and southern Portugal. Entrance height and width refer to the nest cavity entrance, Cavity height and width are the maxima measurements of each inside the nest cavity. Cavity length is the maximum distance between the nest cavity entrance and the back wall of the nest cavity (indicate a significant difference between the parameters of the 2 locations at p=<0.05).*

upon 95% CI's) with Portuguese Roller nest site selection were *Entrance width* (negative) and *Structure* (Table 5.9). Portuguese Rollers preferred nesting in buildings than within breeding walls, and also preferred nest sites with narrower entrances.

Ten models were retained within the top model set comparing Roller occupied nest cavities with empty cavities in the Cypriot study area (Table 5.8). Following model averaging, 5 parameters exhibited significant relationships (based upon 95% CI's): *height of cavity above ground* (positive)*; cavity length* (positive)*; entrance height* (negative); *distance between entrance and widest point* (positive), and; *(Northern)*

Table 5.6: Models retained within the top model set (∆AICc<2) following production of Generalised Linear Mixed Effect Models to investigate the effect of surrounding habitat type upon nest site selection by Rollers in southern Portugal and western Cyprus in 2014 (k = no. parameters in model; AICc = Akaike Information Criterion adjusted for small sample sizes; AIC_w = Akaike model weight).

Model	***k***	***AICc***	***∆AICc***	***AIC_w***
Portugal				
Intercept only	-	72.00	0.00	0.53
Watercourse length	1	72.26	0.26	0.47
Cyprus				
Intercept only	-	58.75	0.00	0.57

Table 5.7: Averaged parameters, 95% confidence intervals, and sum of Akaike weights for those models retained within the top model set investigating the effect of surrounding habitat type upon nest site selection by Rollers in southern Portugal in 2014.

Parameter	***β***	***SE***	***2.5% CI***	***97.5% CI***	***ΣAIC_W***
Portugal					
Intercept	-0.39	0.38	-1.11	0.33	-
Watercourse length	0.21	0.32	-0.21	1.12	0.47

Orientation (negative; Table 5.9). Cypriot Rollers preferred longer, non-northerly facing, cavities, with a greater distance between the cavity entrance and the widest internal point, with shorter entrances and situated higher from the ground.

No ‘evictable’ competitor species were recorded nesting in the Cypriot study area in 2014, and it was not therefore possible to model their effect upon Roller cavity selection. Twenty models were retained within the top model set comparing Roller occupied nest cavities with ‘evictable’ competitor occupied and empty cavities in the Portuguese study area, however (Table 5.10). Following model averaging, only 1 parameter exhibited a significant relationship (based upon 95% CI’s): *Structure* (Table 5.11), with Portuguese Rollers preferring to nest in buildings and competitor species more likely to breed in breeding walls.

Table 5.8: Models retained within the top model set (ΔAICc<2) following production of Generalised Linear Mixed Effect Models comparing parameters of Roller occupied and empty cavities in southern Portugal and western Cyprus in 2014 (AGH = height of cavity above ground; CL = cavity length; CW = cavity width; EH = entrance height; EWP; entrance to widest point; EW = entrance width; Or = Orientation; TNC = total no. cavities in structure; MDC = maximum distance between cavities, and St = structure type).

Model	***k***	***AICc***	***ΔAICc***	***AIC_w***
Portugal				
CW + EW + TNC + St	4	132.84	0.00	0.06
MDC + CW + EW + TNC + St	5	134.06	1.22	0.03
Cyprus				
AGH + CL + EH + EWP + EW + TNC	6	86.37	0.00	0.04
AGH + CL + EH + EWP + TNC	5	86.41	0.04	0.04
AGH + CL + EH + EWP + TNC + St	6	87.12	0.83	0.03
Or + AGH + CL + EH + EWP + TNC	5	87.32	0.95	0.03
AGH + CL + EH + EWP + St	5	87.40	1.03	0.03
AGH + CL + CW + EH + EWP + EW + TNC	7	87.52	1.16	0.03
AGH + CL + EH + EWP + EW + TNC + St	7	87.54	1.17	0.02
AGH + CL + EH + EWP	4	88.02	1.65	0.02
Or + AGH + CL + EH + EWP + EW + TNC	6	88.13	1.76	0.02
AGH + CL + EH + EWP + EW + St	6	88.26	1.89	0.02

Table 5.9: Averaged parameters, 95% confidence intervals, and sum of Akaike weights for those models retained within the top model set comparing parameters of Roller occupied and empty cavities in southern Portugal and western Cyprus in 2014.

Parameter	***β***	***SE***	***2.5% CI***	***97.5% CI***	***ΣAIC_W***
Portugal					
Intercept	-2.22	0.54	-3.30	-1.15	-
Entrance width	-0.80	0.38	-1.54	-0.05	1.00
Total no. cavities in structure	0.71	0.44	0.00	1.41	1.00
Structure	-	-	-	-	1.00
Building	2.83	0.84	1.16	4.49	-
Maximum distance between cavities	-	-	-	-	0.35
10m to 20m	-0.21	0.44	-1.73	0.56	-
Cavity width	0.55	0.28	0.00	1.11	1.00
Cyprus					
Intercept	2.86	0.65	-4.14	-1.58	-
Height of cavity above ground	1.29	0.40	0.50	2.08	1.00
Cavity length	0.95	0.39	0.19	1.72	1.00
Entrance height	-1.30	0.54	-2.37	-0.24	1.00
Entrance to widest point	1.03	0.42	0.20	1.86	1.00
Entrance width	-0.24	0.37	-1.28	0.24	0.47
Total no. cavities in structure	-0.75	0.63	-2.06	0.12	0.77
Structure	-	-	-	-	0.35
Cliff	0.52	0.96	-0.73	3.65	-
Orientation	-	-	-	-	0.17
North	-0.37	0.94	-4.35	-0.12	-
South	-0.26	0.73	-3.68	0.53	-
West	-0.10	0.43	-2.37	1.13	-
Cavity width	0.03	0.13	-0.28	0.94	0.09

Table 5.10: Models retained within the top model set (ΔAICc<2) following production of Generalised Linear Mixed Effect Models comparing parameters of Roller occupied and combined competitor species occupied and empty cavities in southern Portugal in 2014 (AGH = height of cavity above ground; CL = cavity length; CW = cavity width; EH = entrance height; EW = entrance width; TNC = total no. cavities in structure; MDC = maximum distance between cavities, and St = structure type).

Model	***k***	***AICc***	***ΔAICc***	***AIC_w***
Portugal				
MDC + EW + St	3	215.41	0.00	0.02
EW + St	2	215.60	0.19	0.02
MDC + EW + TNC + St	4	215.86	0.45	0.02
EH + St	2	215.90	0.49	0.02
MDC + St	2	215.91	0.50	0.02
MDC + EH + St	3	215.98	0.58	0.02
MDC + TNC + St	3	216.02	0.61	0.02
AGH + EW + St	3	216.38	0.97	0.01
MDC + EH + TNC + St	4	216.47	1.06	0.01
St	1	216.60	1.19	0.01
MDC + AGH + EW + St	4	216.61	1.21	0.01
AGH + EH + St	3	216.74	1.34	0.01
MDC + CW + EW + St	4	216.99	1.59	0.01
CW + EW + St	3	217.03	1.63	0.01
EH + EW + ST	3	217.25	1.84	0.01
MDC + AGH + EH + St	4	217.29	1.88	0.01
MDC + EH + EW + St	4	217.31	1.90	0.01
MDC + CL + EW + St	4	217.32	1.91	0.01
CL + EW + St	3	217.33	1.92	0.01
MDC + AGH + EW + TNC + St	5	217.38	1.97	0.01

Table 5.11: Averaged parameters, 95% confidence intervals, and sum of Akaike weights for those models retained within the top model set comparing parameters of Roller occupied and combined competitor species occupied and empty cavities in southern Portugal in 2014.

Parameter	***β***	***SE***	***2.5% CI***	***97.5% CI***	ΣAIC_W
Portugal					
Intercept	-.2.26	0.36	-2.98	-1.54	-
Height of cavity above ground	-0.04	0.11	-0.53	0.18	0.21
Cavity length	-0.01	0.05	-0.47	0.28	0.07
Entrance height	-0.09	0.18	-0.73	0.19	0.32
Entrance width	-0.22	0.29	-0.96	0.17	0.57
Total no. cavities in structure	0.07	0.18	-0.17	0.84	0.21
Structure	-	-	-	-	1.00
Building	1.21	0.56	0.10	2.31	-
Maximum distance between cavities	-	-	-	-	0.61
10m to 20m	-0.44	0.51	-1.66	0.23	-
Cavity width	0.01	0.08	-0.27	0.62	0.08

Cavity-scale effects upon Roller productivity

Six models were retained within the top model set investigating the relationship between Roller productivity and cavity parameters in the Portuguese study area (Table 5.12). Following model averaging, *cavity width* (negative) was the sole parameter exhibiting a significant relationship (based upon 95% CI's) with increased productivity, with Portuguese Rollers fledging more chicks from nest sites with narrower cavities (Table 5.13).

Nine models were retained within the top model set investigating the relationship between Roller productivity and cavity parameters in the Cypriot study area (Table 5.12). Following model averaging, 2 parameters exhibited a significant relationship with increased Roller productivity; *total no. of cavities in structure* (positive) and *maximum distance between cavities* (Table 5.13). Cypriot Rollers fledged more chicks from structures with a larger number of cavities and with a shorter distance between those cavities.

Table 5.12: Models retained within the top model set (∆AICc<2) following production of Generalised Linear Mixed Effect Models investigating the effect of cavity parameters upon Roller fledging success in southern Portugal and western Cyprus in 2014 (AGH = height of cavity above ground; CL = cavity length; CW = cavity width; EH = entrance height; EWP; entrance to widest point; EW = entrance width; TNC = total no. cavities in structure; MDC = maximum distance between cavities, and St = structure type).

Model	***k***	***AICc***	***∆AICc***	***AICw***
Portugal				
CW	1	205.91	0.00	0.04
CW + EH + EW	3	206.08	0.17	0.03
CW + EH	2	206.56	0.66	0.03
CL + CW + EH	3	207.04	1.13	0.02
CH + CW	2	207.22	1.32	0.02
CL + CW	2	207.30	1.40	0.02
Cyprus				
MDC + TNC	2	130.41	0.00	0.05
MDC + EW + TNC	3	130.81	0.40	0.04
Intercept only	0	130.99	0.58	0.04
MDC	1	131.24	0.83	0.03
MDC + EWP + TNC	3	131.79	1.38	0.03
MDC + CL + EWP + TNC	4	131.92	1.50	0.02
MDC + TNC + St	3	132.21	1.80	0.02
EW	1	132.37	1.96	0.02
MDC + EW	2	132.39	1.98	0.02

Nest site competition in Portugal

Cavity breeding assemblage census data

The availability of structure supporting differing numbers of cavities changed in Castro Verde SPA between 2004 and 2013 (Figure 5.5). At the start of the study period the majority of structures surveyed incorporated <10 cavities, with structures supporting large numbers of cavities (50+) the least frequently encountered. This changed dramatically during the 2007 breeding season, following the construction of several artificial breeding walls, each supporting many cavities, in 2006 (I.Catry, *pers.comm*). Since 2007 the number of structures supporting large numbers of

Table 5.13: Averaged parameters, 95% confidence intervals, and sum of Akaike weights for those models retained within the top model set investigating the effect of cavity parameters upon Roller fledging success in southern Portugal and western Cyprus in 2014.

Parameter	***β***	***SE***	***2.5% CI***	***97.5% CI***	***ΣAIC_W***
Portugal					
Intercept	-3.85	0.13	-4.11	-3.59	-
Cavity length	-0.05	0.12	-0.51	0.12	0.25
Cavity width	-0.29	0.13	-0.56	-0.02	1.00
Cavity height	-0.02	0.06	-0.37	0.11	0.12
Entrance width	-0.12	0.17	-0.56	0.08	0.52
Entrance height	0.08	0.17	-0.04	0.74	0.22
Cyprus					
Intercept	-3.49	0.17	-3.83	-3.15	-
Cavity length	0.03	0.10	-0.01	0.61	0.09
Entrance to widest point	-0.04	0.10	-0.50	0.07	0.18
Entrance width	0.06	0.12	-0.08	0.49	0.29
Total no. cavities in structure	0.30	0.31	0.01	0.98	0.60
Structure	-	-	-	-	0.08
Cliff	0.03	0.14	-0.29	1.12	-
Maximum distance between cavities	-	-	-	-	0.79
10m to 20m	1.09	0.81	0.04	2.72	-
20m to 30m	-1.15	1.11	-3.57	0.65	-

cavities has remained fairly constant, whilst those supporting a small (<10) or medium (10 to 50) number of cavities have varied in abundance (although always remaining less frequent than the larger structures within the SPA).

Numbers of Rollers and Lesser Kestrels both increased in the Portuguese study area between 2004 and 2013 (Figure 5.6a & Figure 5.7a), although Lesser Kestrels were much more abundant throughout the survey period. Despite increases in their population, the density of Lesser Kestrel breeding pairs remained relatively constant across all 3 cavity-bearing structure categories (<10, 10 to 50, and 50+ cavities per structure). Larger breeding densities were recorded in structures with a larger number of cavities, and smaller densities were recorded in structures with fewer cavities.

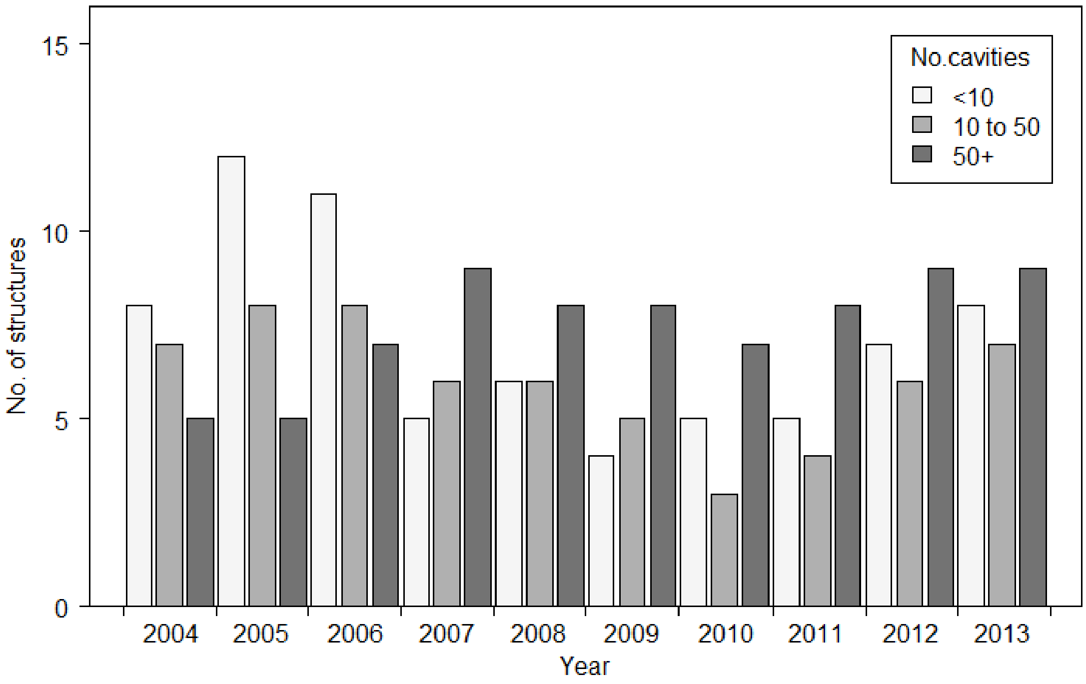

Figure 5.5: Temporal changes in the availability of structures supporting differing numbers of cavities within Castro Verde Special Protection Area, southern Portugal, between 2004 and 2013.

The density of Roller breeding pairs varied more across the study period, with larger numbers of pairs recorded in structures with a large number of cavities (50+) during the first few years (Figure 5.6b), and few Roller pairs recorded from structures with a small number of cavities. However, as the Roller population increased, mean breeding densities began to converge across all 3 cavity-bearing structure categories within the final 3 years of the census data. By the end of the study period, Roller pair densities were approximately the same across all surveyed structures, regardless of the number of cavities present.

Effects of the increasing Lesser Kestrel population upon nest site occupation by Rollers

Models including *No. of Lesser Kestrels* exhibited significantly lower AICc values than the null model, both with and without an offset of *No. available cavities* (Table 5.14). *No. of Lesser Kestrels* was significant in both the offset and non-offset model (based upon 95% CI's), with the number of Rollers present in a structure positively related to increasing Lesser Kestrel numbers in the non-offset model, and negatively related in the offset model (Table 5.15).

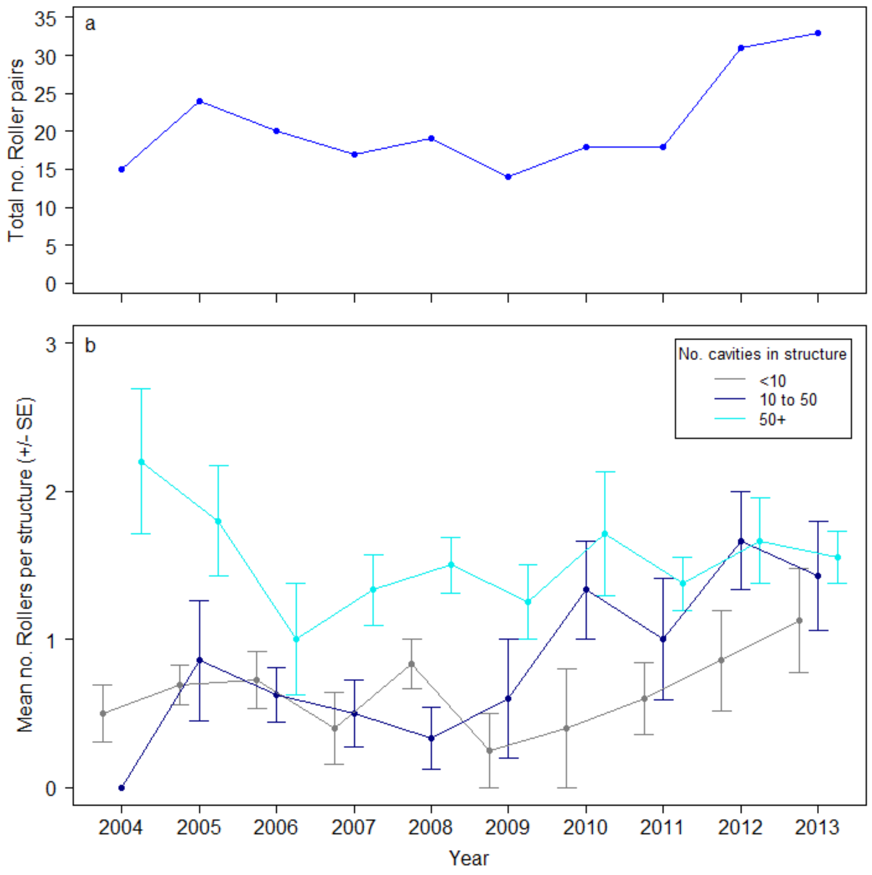

Figure 5.6: Temporal changes in the (a) total population, and (b) mean density of breeding Roller pairs in structures supporting differing numbers of cavities, within Castro Verde SPA, southern Portugal, between 2004 and 2013.

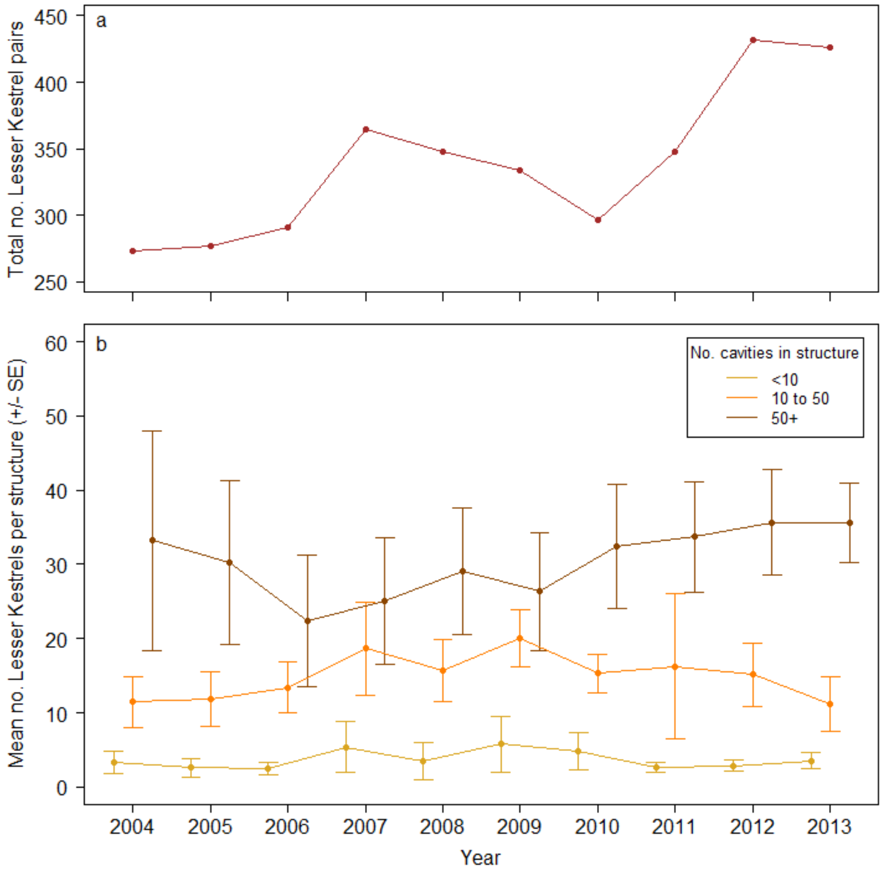

Figure 5.7: Temporal changes in the (a) total population, and (b) mean density of breeding Lesser Kestrel pairs in structures supporting differing numbers of cavities, within Castro Verde SPA, southern Portugal, between 2004 and 2013.

Table 5.14: Comparison between AICc derived model parameters of Generalised Linear mixed Effects Models investigating the effect of the increasing Lesser Kestrel population in Castro Verde Special Protection Area, southern Portugal, upon the number of Roller pairs within nest structures between 2004 and 2013. Offset comprises number of cavities within individual structures.

Model	***k***	***AICc***	***∆AICc***	***AICw***
Without offset				
No. of Lesser Kestrel pairs in structure	1	410.85	0.00	1.00
Intercept only	0	424.79	13.94	0.00
With offset				
No. of Lesser Kestrel pairs in structure	1	492.24	0.00	1.00
Intercept only	0	509.62	17.38	0.00

Table 5.15: Coefficients, standard errors, and 95% confidence intervals of Generalised Linear mixed Effects Models investigating the effect of the increasing Lesser Kestrel population in Castro Verde Special Protection Area, southern Portugal, upon the number of Roller pairs within nest structures between 2004 and 2013. Offset comprises number of cavities within individual structures.

Model	***Parameter***	***β***	***SE***	***2.5% CI***	***97.5% CI***
Without offset					
With Lesser Kestrel pairs	No. of Lesser Kestrel pairs in structure	0.23	0.06	0.10	0.34
	Intercept	0.07	0.08	-0.10	0.21
Intercept only	Intercept	0.09	0.07	-0.09	0.23
With offset					
With Lesser Kestrel pairs	No. of Lesser Kestrel pairs in structure	-3.35	0.11	-0.48	-0.14
	Intercept	-0.30	0.09	-3.59	-3.13
Intercept only	Intercept	-3.47	0.08	-3.66	-3.28

5.5 Discussion

Nest site parameters

The location of all Roller nest sites within man-made structures in the Portuguese study area is symptomatic of the local landscape, within which trees are scarce and cliffs largely absent (Catry et al. 2011). Cypriot Rollers inhabited a more diverse landscape, both topographically and with respect to habitat composition, and therefore used a wider range of nesting structures. Nevertheless, buildings were still favoured in both of the study areas, although tree nests were potentially under-represented in the Cypriot dataset due to the difficulties involved in locating them.

Portuguese Rollers also readily adopted nest sites in artificial nest boxes and clay pots, suggesting that similar structures would be adopted by the species in Cyprus. Roller populations in other parts of the species range (e.g. Spain, France, and Hungary) readily use man-made nest sites. Nest box installation should be considered in situations where nest sites are limited (Rodriguez et al. 2011; Kiss et al. 2016; Tron 2004), with the recent increase observed in the Roller population of Castro Verde SPA potentially directly linked to the provision of novel nest sites (I. Catry*, pers.comm*.).

The availability of suitable nest cavities, based on the parameters of those occupied by Rollers in the respective study areas, was far higher in Portugal than in Cyprus (taking into account the caveat that the univariate analyses may overestimate the suitability of non-occupied cavities). Nevertheless, this increased availability was offset by a greater proportion of competitor occupied cavities, with Lesser Kestrel the most commonly recorded competitor species.

Several of the competitor species recorded in Portugal are present in Cyprus (i.e. Eurasian Kestrel, Little Owl, and Barn Owl), and their absence from the Cypriot dataset is perhaps indicative of lower levels of competition within the Cypriot study area, or preference for cavities exhibiting different characteristics to those preferred by Rollers. Alternatively, Rollers may simply be more dominant over ‘evictable’ species within the Cypriot study area. The commoner competitor species present in Cyprus (i.e. Sparrows and Pigeons) occupied cavities with internal parameters outside the range of those selected by Rollers.

The significant differences in key parameters (i.e. entrance and cavity size) of Roller occupied cavities between the two study populations can potentially be explained by the larger number of artificially provisioned nest sites within the Portuguese study area. Nest boxes, clay pots, and purpose built cavities within breeding walls were purposefully designed to encourage use by Lesser Kestrels and Rollers, and to deter use by larger competitors, such as pigeons (Catry et al. 2011). Such cavities are therefore more likely to have smaller entrances and shorter/narrower internal cavities due to their design, with the ‘semi natural’ cavities within the Cypriot study area shaped more by erosional processes.

Landscape scale nest site selection

The analysis of both the Portuguese and Cypriot datasets indicated that the availability of optimal foraging habitat surrounding the nest site is not a determining factor in Roller nest site selection at the landscape scale in either study population. This suggests that Rollers are either able to access optimal foraging habitat in proximity to most cavity-supporting structures, or that nest sites are largely located within particular landscape types. The landscape within the Portuguese study area, is very uniform, with most nests sites having access to large areas of preferred fallow habitat nearby (Catry et al. 2011).

Cavity selection

Our results indicate that cavity parameters are the main driver of nest site selection by Rollers in both of the study areas (Cockle et al. 2015).The preference for nest sites in buildings in both Portugal and Cyprus may be due to their greater availability, although competition with other cavity nesters within purpose built breeding walls may negatively inform this preference in Portugal. This is further evidenced by the retention of *structure* in the combined Portuguese empty and competitor occupied cavity model. The avoidance of north-facing cavities by Cypriot Rollers is in line with other nest selection studies (Wiebe 2001; Ardia et al. 2006), which found a preference for south/easterly facing nest entrances in cavity nesting species, explained by the beneficially higher insolation levels received by chicks in the nest (Landler et al. 2014).

The selection of nest sites with smaller entrances and wider/longer cavities in the Cypriot population indicates that these may comprise the key nest selection parameters for the species (of those measured in the study) within ‘semi-natural’ nest sites. Nevertheless, with the exception of entrance width, these parameters lose their importance in Portugal, perhaps indicative of the broadly similar dimensions of the predominantly man-made cavities throughout the Portuguese study area. When competitor occupied cavities are included in the analysis, structure type becomes the sole significant describer of Portuguese Roller nest site selection, indicating that both Rollers and their competitors select nest sites with similar entrance parameters. Lesser Kestrels in particular prefer similarly sized cavities (Franco et al. 2005).

Cavities and productivity

Despite Rollers from both study areas preferentially selecting nest sites with smaller entrances and (in the case of Cyprus) larger cavities, Portuguese Rollers successfully fledged more chicks (having accounted for brood size) from nests with narrower cavities, whilst internal cavity dimensions had limited impact upon Cypriot Roller fledging success.

This may be due to nest sites within larger nest boxes, clay pots, and artificial cavities being less secure from predation than smaller natural cavities (Purcell et al. 1997), as predation is the main agent of nest failure observed in both study areas (*pers.obs*). Artificial structures are absent from the Cypriot study area, and so the higher productivity recorded from Cypriot nest sites located in structures incorporating a larger number of more densely spaced cavities may be indicative of increased predation pressure in proximity to human activity.

Competitor effects on nest site selection

The 2014 - 2015 census data indicates that the density of Roller breeding pairs across different structures within Castro Verde SPA is beginning to converge, and is indicative of the increasing Roller population potentially reaching carrying capacity in relation to the nest sites available to it. The positive relationship between Lesser Kestrel numbers within a structure and the number of Rollers also present, when no cavity offset is applied, is indicative of the fact that larger numbers of both species are present within structures within which more nest sites are available.

The negative relationship shown between increasing Lesser Kestrel numbers and Roller pair presence, when a cavity offset is applied, is suggestive of 2 different scenarios. These are; (1) Lesser Kestrels are either able to outcompete Rollers for nest sites in the Portuguese study area, or to deter them from selecting them or; (2) the selection of specific breeding structures by Rollers is density dependent, with the species preferring to nest within structures from which other Roller pairs are absent.

Lesser Kestrels arrive earlier at Portuguese breeding sites, and therefore can select cavities prior to Roller arrival. Rollers have been observed successfully evicting Lesser Kestrels from occupied cavities, although the success rate of such evictions has yet to be quantified (I. Catry, *pers.comms*). Any interaction between the 2 species is therefore considered unlikely to be driven by individual level competition for cavities, despite the preference shown by Rollers for nest sites in buildings rather than breeding walls. Despite their increasing population within Castro Verde SPA, the majority of larger structures (incorporating a large number of cavities) still only support a maximum of 2 or 3 pairs of breeding Rollers. It is therefore considered probable that Rollers actively avoid nesting within structures supporting more than 1 additional breeding Roller pairs.

Alternatively, the avoidance of breeding walls, where Lesser Kestrels and other competitors are present in larger numbers, may be due to deleterious effects arising from increased mobbing pressure (Flasskamp 1994), depletion of prey resources (Bonal & Aparicio 2008), or increased predator attraction at Lesser Kestrel colonies. Rollers may benefit from increased vigilance within large Lesser Kestrel colonies, although such protection is not necessarily directly linked to lower nest predation rates (Campobello et al. 2012).

Implications for Roller conservation

The results indicate that Rollers within the 2 study areas undertake nest site selection at the cavity scale, with surrounding habitat composition being of limited importance. Nevertheless, it is important to remember that the Cypriot study area supports an heterogeneous landscape favoured by the species elsewhere in its' range (Kiss et al. 2016), and the Portuguese study area is dominated by traditional cereal rotation identified as being of high value to Mediterranean farmland bird species (Chiatante & Meriggi 2016), and Rollers in particular (Catry et al. 2011).

As such, the 2 study areas comprise optimal examples of Roller habitat within the species Mediterranean range, and the importance of surrounding landscape upon nest site selection may therefore increase in other areas of the European range where the species' preferred foraging habitats are not so prevalent. The homogenisation of European farmlands has been identified as a critical priority for Roller conservation (Kovacs et al. 2008), and the preservation of low intensity traditional farming landscapes is therefore essential in maintaining Roller populations

(Avilés & Parejo 2004; Bouvier et al. 2014) outside of core areas, such as Castro Verde SPA.

The smaller, Critically Endangered, Portuguese population is potentially now nest site limited within Castro Verde SPA, and the provision, and maintenance (Catry et al. 2011), of additional man-made nest sites is recommended. This is a pressing issue, as many of the older buildings used by both breeding Rollers and Lesser Kestrels have collapsed in recent years, and there are indications that the species may soon be restricted to breeding walls (*I. Catry, pers.comm*.).

The importance of remaining buildings used by breeding Rollers in Cyprus is also likely to increase over the coming decades, as many older/abandoned structures are either renovated or deteriorate past suitable use (Mainwaring 2015; Catry, Silva, et al. 2011). The selection of nests sites based upon cavity parameters, rather than surrounding habitat, also suggests that any further artificial nest site provision (in Cyprus or Portugal) should target areas of optimal foraging habitat.

The importance and/or availability of nest cavities within trees in Cyprus has not been explicitly investigated, due to the difficulties involved in locating them. Whatever their specific importance to breeding Rollers, their availability is likely to decline in line with the country’s changing agricultural economy, as the mature carobs and olives favoured by the species are no longer maintained and senesce; there has been a 79% decline in the area of carob groves between 1975 and 2010 (Ieronymidou 2012).

Loss of older cavity-supporting trees has been identified as a global bird conservation issue (Manning et al. 2013), and a critical issue for Roller conservation elsewhere in the species’ range (Kovacs et al. 2008). As such, the establishment of a species-specific nest box scheme, or retention of suitable cavities within redeveloped buildings, would be highly beneficial to the long term maintenance of this important population. A small-scale nest box initiative has recently been established in the occupied north of Cyprus (http://www.kuskor.org/projects-roller.php), and its extension and integration into cross-border Roller conservation would likely benefit the island’s Roller population.

5.6 Acknowledgements

I would like to thank Alessandro Gravano, Harry Ewing, Pedro Patto, Ines Catry, and Aldina Franco for their assistance with data collection in the field. I would also thank Alessandro and Harry for their assistance during the habitat mapping process. The project is funded through a Natural Environment Research Council Studentship Grant (No. 1210309), and the author is also a beneficiary of both an A.G. Leventis Foundation Scholarship and British Trust for Ornithology CASE studentship.

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Chapter 6. Concluding remarks

6.1 Key findings

The research objectives established at the start of this thesis aimed to fill some of the key knowledge gaps identified in the International Species Action Plan (ISAP) for the Roller (Kovacs, et al. 2008), and its' findings add to the increasing body of work concerning Roller ecology and conservation within Europe. The Cypriot component of the research is of particular value, as no delegate from Cyprus was involved in the drafting of the ISAP, and detailed information on both the ecology of, and threats to, the Roller in Cyprus are absent from the publication.

The ISAP is now however on the point of revision, following the drafting of the updated Flyway Action Plan (FAP) for the European Roller (Tokody & Kiss, *in prep*.), following a meeting of the European Roller Working Group in January 2017. The author of this thesis was a delegate at the meeting and, alongside a colleague from BirdLife Cyprus, provided detailed input concerning the ecology of, and threats faced by, the Cypriot Roller population. The majority of knowledge gaps previously identified in the ISAP however remain.

The absence of data or research concerning the impact of climate change on Roller populations was identified as a highly important knowledge gap in the ISAP. The research detailed in Chapter 2 comprises one of the first attempts to increase our knowledge in this area. Temperature during the preceding winter and chick rearing periods was identified as the key climatic correlate with clutch size and fledging success in Mediterranean Roller populations. Roller productivity is therefore potentially predicted to decline across the Mediterranean, in light of these results and projected changes in climate over the coming century.

The ISAP identifies the furthering of knowledge on Roller habitat use and selection as a critical knowledge gap. Chapter 3, and Chapter 4 in particular, seek to address this for the Cypriot Roller population. In Chapter 3, a robust Habitat Suitability Model was produced for Rollers on the island, which identified key areas of high Roller occupancy probability. These locations largely coincided with high value Important Bird and Biodiversity Areas (IBAs) already designated for the species, thus confirming the models predictions, but the model also identified several areas on the periphery, and outside, of the existing IBA network which exhibited high Roller occupancy potential. The importance of the IBA network for Rollers in Cyprus was further highlighted by the finding that a greater area in IBAs than within external areas had increased in its' potential occupancy value to Rollers between 2000 and 2012.

In Chapter 4, Roller home ranges were quantified for the first time using high spatial resolution Global Positioning System technology. Analyses of foraging habitat selection preference showed that Cypriot Rollers actively avoided areas of urban and ploughed habitat, and utilised traditionally farmed and grassland areas in proportion to their availability during the chick rearing period. Furthermore, data from the small number of Rollers tracked in the study indicated that foraging habitat selection was potentially informed by the terrestrial invertebrate biomass of each habitat. It was also shown that Roller laying date was negatively associated with an increasing area of avoided urban habitat around the nest site, whilst fledging success was positively related to increasing laying date, and increasing extent of surrounding optimal foraging habitat.

In Chapter 5, it was shown that Rollers in Portugal and Cyprus selected their nest sites based upon cavity level characteristics rather than the type or composition of surrounding habitats. These findings again assist in furthering knowledge of Roller habitat use and selection, as identified in the ISAP. Cavities used by Rollers in Cyprus were significantly longer and larger than those used in Portugal, due to the prevalence of man-made nest sites in the Portuguese study area. Cavity entrance size was identified as one of the most important parameters in Roller nest site selection in both Cyprus and Portugal, potentially due to smaller entrances decreasing nest predation risk. High levels of nest site competition were identified in Portugal, and evidence of nest site limitation in both the Cypriot and Portuguese Roller populations was observed.

6.2 Conservation recommendations

It will be difficult to mitigate the potential negative impacts upon Roller productivity arising from projected climate change scenarios within the Mediterranean region. Any conservation intervention will rely upon the species initial response to changes in climate on a regional scale, as migratory bird populations are unlikely to remain static within existing breeding areas (Huntley et al. 2008).

It is possible that Roller populations on the southern extent of the species breeding distribution will shift their ranges northwards as they track a shifting climatic envelope

(Huntley et al. 2007). If such range shifts are to occur it is essential that sufficient areas of suitable habitat are available within the novel range, and that such areas are afforded policy-based or legislative protection (Thomas et al. 2012). Implementation is likely to necessitate co-operation across national boundaries, and an international commitment to conserving migratory populations, as outlined in Resolution 9.7 of the Convention on the Conservation of Migratory Species of Wild Animals.

One conservation measure that may benefit future climate-compromised populations, in the absence of any potential range shift, is supplementary feeding during the chick-rearing period. This has proved an effective method for bolstering the relict Austrian breeding population (M.Tieffenbach, *pers.comm*), and could benefit Rollers breeding in marginal habitats subject to increased temperatures, with resultant low invertebrate biomass. Such a measure would however be extremely labour intensive and likely comprise only a stop-gap approach.

Following the identification of potential areas of high value for Rollers outside of the existing Cypriot IBA network, it is recommended that these additional areas are ultimately gazetted as novel IBAs (or as extensions to existing designated sites; notably the Akamas and Karpasia Peninsula IBAs). Furthermore, it is recommended that targeted surveys are carried out in these localities, prior to designation, to accurately quantify the density of Rollers present and further inform the designation process.

The Cypriot government is currently committed to restoring, preserving, and enhancing ecosystems within Natura 2000 sites under the auspices of the Cyprus Rural Development Plan (RDP) for 2014 - 2020 (European Commission 2014). Nevertheless, the current lack of detailed Management Plans for the Cypriot IBA network, and previously observed non-compliance by the Cypriot government with respect to Natura 2000 site protection, indicate that such commitments may not hold true in reality (BirdLife Cyprus 2013).

The construction of major infrastructure projects (including wind and solar energy sites, and large-scale golf resort developments) in proximity to, or within, IBAs has been identified as a key threat to Roller conservation on the island (Tokody & Kiss, *in prep.*), and compliance with, and/or strengthening of, existing national conservation and development policy will therefore form a key component of Roller conservation in Cyprus. The value of successful implementation of conservation policy and management measures has already been shown to benefit the Portuguese study population (Tokody & Kiss, *in prep*.), for example, following the instigation of the ‘Castro Verde Zonal Plan’ in the late 1990’s and subsequent delineation of the ‘Castro Verde Integrated Territorial Intervention’ (Santana et al. 2014).

The results presented in this thesis identify the importance of traditionally managed agricultural landscapes and grassland areas for the Roller at either end of its’ Mediterranean range. The retention and/or promotion of these optimal habitats should therefore be encouraged through further integration into existing agri-environment schemes and/or fiscal incentives.

Nevertheless, such schemes are reliant upon the continuation of Pillar 2 funding for biodiversity within the EU Common Agricultural Policy (CAP), which will be cut by 18% under the new CAP for the period 2013 to 2020 (Pe’er et al. 2014). This shortfall is potentially addressed through ‘greening measures’ identified under Pillar 1, although it is considered unlikely that these will lead to increased biodiversity benefits (Pe’er et al. 2014).

The Cyprus RDP for 2007 - 2013 already incorporated several agri-environment prescriptions of potential benefit to the island’s Roller population. These comprised (i) payments for rotation (which replaced the, potentially detrimental, herbicide and fertiliser treatment of traditional crops) and; (ii) subsidised maintenance of traditional grape varieties. Both of these prescriptions also promoted the maintenance of traditionally managed farmland mosaics within the Cypriot landscape (Ieronymidou 2012).

Rotation payments, and the pesticide ban, have been retained within the updated RDP for 2014 - 2020, with emphasis placed upon the retention of at least 10% fallow land within all plots over the annual cycle (European Commission 2014). The updated RDP also includes provisions for the maintenance of boundary features and the protection of natural vegetation and landscape features (within agricultural plots) for biodiversity, and identifies a 2023 target value of having 9% of agricultural land under management contracts which support biodiversity. A potential, novel, provision arising from our research comprises the late harvesting (late June to early July) of a proportion of all cereal crops within agricultural plots. This would benefit late nesting Roller pairs and assist in maintaining invertebrate biomass throughout the Roller breeding period.

Unfortunately the updated RDP also includes several provisions considered likely to have a negative impact upon Roller populations on the island. These include subsidies paid for the afforestation of abandoned farmland and economically marginal areas (e.g. viticulture), leading to the creation of habitats largely unsuitable for use by breeding or foraging Roller pairs. There are also currently no provisions for the maintenance of traditional farming mosaics, and the issue of many 'farmers' gaining the majority of income from elsewhere (and therefore not eligible for CAP funding) is not addressed.

The nest site limitation identified within both of the study areas should be mitigated through the increased provision of man-made nest sites in both localities, targeting areas of optimal foraging habitat. The maintenance of older buildings within the 2 study areas, and the inclusion of artificial nest cavities within the walls of any newly constructed dwelling, could also be incentivised through incorporation in agri-environment schemes and national planning policy. The conservation or incorporation of such cavities would additionally benefit a range of other cavity-nesting species, including Lesser Kestrels (*Falco naumanni*) in Portugal and the endemic Cypriot Scops Owl (*Otus scops cyprius*), within cavity-limited locations.

The use of predator exclusion devices, in the form of snake and rodent prevention collars on cavity-bearing trees, and the installation of nest box plates over the entrances of larger cavities within building and cliff nest sites, would also potentially decrease nest predation in both populations. Following the identification of the Rollers preferences for smaller nest entrances, nest box plates could also be used to modify existing unsuitable cavities in buildings and cliff faces and encourage their use by breeding Roller pairs.

Nest site limitation in both populations can most easily be counteracted however by the instigation of an expanded nest box programme, with such schemes having led to increases in Roller breeding populations at several locations within the species European range (Rodriguez et al. 2011). Forty nest boxes were erected in western Paphos District between 2014 and 2015 as part of the research programme detailed in this thesis, with 2 in use by breeding Rollers in 2015.

Subsequent schemes have been initiated by the Cypriot Game Fund in the Paramali River and Plateau IBA (Tokody & Kiss, *in prep*.), and >40 nest boxes have been installed by KUŞKOR (The North Cyprus Society for the Protection of Birds and Nature) upon the Mesaoria Plain (www.kuskor.org/projects-roller.php?lang=en). Most impressively, >200 nest boxes have been erected within the Koshi - Pallourokampos and Panagias Stazousa River SPAs, in the south-east of the island, as part of the ongoing LIFE+ funded ‘Life for Birds’ project (www.lifeforbirds.eu/index.php/en/partners). It is however too early in the lifetime of these projects to assess their efficacy in increasing the Cypriot Roller population, and annual monitoring and upkeep of the nest boxes will form an important component of efforts to conserve the Roller in Cyprus.

Finally, the promotion of the Roller as a flagship species would not only highlight the threats it faces, but also potentially benefit a range of other threatened farmland bird species in Cyprus (A Rocha France 2007). The new FAP identifies a lack of public awareness as an existing knowledge gap, and the distinctive appearance and charismatic behaviour of the Roller lends itself to use as a flagship species for conservation.

6.3 Further research

The thesis identifies several key areas within which additional research would increase our understanding of Roller ecology and conservation. In light of the findings presented in Chapter 2, it is highly recommended that further research is carried out upon the effects of climate upon Roller breeding parameters and distribution. The extension of the research detailed in Chapter 2 to a larger number of monitored populations spanning the Roller’s entire Mediterranean, or European, range would further our understanding of variation in the species reactions to projected climate change. Similarly, it will be important to investigate the effects of climate in the African wintering range upon Roller breeding parameters in Europe.

Furthermore, our knowledge of the demography of the Cypriot Roller population, in particular, is still in its infancy. Prior to the commencement of our research fewer than 10 Rollers had been ringed in Cyprus (BirdLife Cyprus, 2015). Our research resulted in a further 20 adults and 108 chicks being ringed, and it is important that such ringing and monitoring effort is maintained in order to gain a better understanding of the return rates and recruitment exhibited by the Cypriot Roller population.

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