UNIVERSIDADE DE LISBOA
FACULDADE DE CIÊNCIAS

UNIVERSIDADE DO PORTO
FACULDADE DE CIÊNCIAS

Species interactions in recently established mixed colonies: Implications for conservation

"Documento Definitivo"

Doutoramento em Biodiversidade, Genética e Evolução

João Miguel Camacho Gameiro da Silva

Tese orientada por:

Doutora Inês Catry
Professora Doutora Aldina Maria Antunes Franco
Professor Doutor Jorge Manuel Mestre Marques Palmeirim

Documento especialmente elaborado para a obtenção do grau de doutor

2021

UNIVERSIDADE DE LISBOA
FACULDADE DE CIÊNCIAS

UNIVERSIDADE DO PORTO
FACULDADE DE CIÊNCIAS

Species interactions in recently established mixed colonies: Implications for conservation

Doutoramento em Biodiversidade, Genética e Evolução

João Miguel Camacho Gameiro da Silva

Tese orientada por:

Doutora Inês Catry
Professora Doutora Aldina Maria Antunes Franco
Professor Doutor Jorge Manuel Mestre Marques Palmeirim

Júri:
Presidente:
- Doutor Rui Manuel dos Santos Malhó, Professor Catedrático e Presidente do Departamento de Biologia Vegetal, da Faculdade de Ciências da Universidade de Lisboa

Vogais:
- Doutor Diego Rubolini, Asssociate Professor; Dipartimento di Scienze e Politiche Ambientali da Università degli Studi di Milano, (Itália)
- Doutor Rúben Hüttel Heleno, Professor Auxiliar, Faculdade de Ciências e Tecnologia da Universidade de Coimbra
- Doutora Rita Covas Monteiro, Investigadora Principal, Centro de Investigação em Biodiversidade e Recursos Genéticos – CIBIO, da Universidade do Porto
- Doutora Inês Catry, Investigadora Contratada ao abrigo do Decreto Lei nº57/2016, de 29 de Agosto, Centro de Investigação em Biodiversidade e Recursos Genéticos – CIBIO, da Universidade do Porto, Orientadora
- Doutor João Eduardo Gomes Rabaça, Professor Associado com Agregação, Escola de Ciências e Tecnologia da Universidade de Évora
- Doutor Luís Miguel do Carmo Rosalino, Professor Auxiliar, Faculdade de Ciências da Universidade de Lisboa

Documento especialmente elaborado para a obtenção do grau de doutor

Fundação para a Ciência e a Tecnologia
(Bolsa PD/BD/128366/2017)

2021

Nota previa: A presente tese apresenta artigos científicos já publicados ou submetidos para publicação (capítulos 2, 3 e 4), de acordo com o previsto no nº2 do artigo 25º do Regulamento de Estudos de Pós-Graduação da Universidade de Lisboa, publicado no Diário da República, 2.ª série – N.º 60 – 26 de março de 2018. Uma vez que estes trabalhos foram realizados em colaboração o candidato esclarece que participou integralmente na conceção dos trabalhos, obtenção e análise dos dados, discussão dos resultados, bem como na redação dos manuscritos.

Lisboa, julho de 2021

João Miguel Camacho Gameiro da Silva

“A certain type of perfection can only be realized through
a limitless accumulation of the imperfect”
Haruki Murakami

Table of Contents

General Introduction

Long-term persistence of conservation-reliant species: Challenges and opportunities

Influence of colony traits on ectoparasite infestation in birds breeding in mixed-species colonies

High trophic niche overlap in a bird community established in an artificial nesting landscape: implications for conservation

Is it better to be solitary or breed in heterospecific colonies? Assessing the anti-predatory benefits for a solitary bird

General discussion

ACKNOWLEDGEMENTS

Science is not a lonely endeavour, and I had the privilege to work with fantastic mentors, co-authors, colleagues, and institutions that played a huge part on the success of the research presented here and made it immensely more joyful. The other half of the smiles I carried during my PhD, and smiles ease everything, were gifted to me by the most warm-hearted and supportive friends and family I could ever have wished for. I am forever grateful to everyone who directly and indirectly accompanied me throughout this journey.

First of all, I would like to express my gratitude to *Fundação para a Ciência e a Tecnologia*, for funding my PhD. To the *Biodiv PhD programme*, *cE3c* and *UEA* for hosting and receiving me in a group with some of the most brilliant, ingenious, and hard-working minds I am fortunate to call colleagues. To *Liga para a Proteção da Natureza*, especially *Centro de Educação Ambiental do Vale Gonçalinho*, and to *Instituto da Conservação da Natureza e Florestas* for letting me wander freely and unscathed across the fields of gold of Castro Verde, and for allowing me to collect data. To all *named and unnamed reviewers* who have voluntarily improved the clarity and importance of our manuscripts. To *Sci-hub* for making those manuscripts available for everyone and giving me free access to all more than 500 research papers used to backup this thesis. To the cE3c and UEA *Science Communication and Outreach offices* for translating the scientific jargon of our manuscripts and make them accessible to a broader audience.

I am most indebted to my supervisors, for their continued support, invaluable advice, and enduring patience. *Inês Catry* was the wheel, sails, hull, and compass of this whole navigation, ever since she invited me to do a PhD with her 5 years ago. Not every student or researcher has the opportunity to do field work side-by-side with their supervisor, and I feel very privileged to have done so for a period totalling more than a year. *Aldina Franco* and *Jorge Palmeirim* have withstood me for even longer (since my Master's), and I am startled by their resilience. *Aldina* has the most creative mind and always challenged me with out-of-the-box, head-scratching questions that greatly improved my critical thinking. *Jorge* has always been a strong pillar in my academia and research paths and has this incredible ability of stepping back and look at the bigger picture. I could not neglect *Teresa Catry* and her considerable contribution. Although not an official supervisor, *Teresa* has actively help us planned, designed, and discuss every research chapter of this thesis. Oh, and she also has this neat skill where she interprets my encrypted, confusing phrases into one-line, crystal-clear sentences. All four of them have profoundly shaped, in the best sense of the word, my research and work conduct, and I could not have asked for a better mentorship. Lastly, I would like to attribute an honourable mention to *Tiago Marques* for a low-profile, yet inspiring tutorship during the first months of my PhD, and for never seemed to be annoyed by all my doubts in statistics.

I would also like to thank *Jesús Veiga*, *Francisco "Paco" Valera*, and *Estacíon Experimental de Zonas Áridas*, with their profound knowledge on parasite-host relationships and ectoparasites of hole-nesting birds. Despite my short stay in Almería, *Jesús* and *Paco* were crucial for the development of chapter 3, which was published in a Q1 scientific journal, and played a huge role on the co-mentorship of Inês Oliveira, whose Master thesis tackles some of the questions raised by this chapter. My warmest regards to them, and I sincerely hope we may share more collaborations in the near future.

To the *Tropical and Mediterranean Biodiversity* group, especially to *Birds, Bats and Snails*, for including me with the finest researchers of the whole centre and accompanying my work with so much enthusiasm. *BBS* works on so many taxa across many countries that our meetings function as this giant hub collecting high-quality knowledge about ecology and conservation, leaving any boot biologist and conservationist in awe. To *EcoComp*, albeit not being a frequent customer in the later stages of my PhD, they have happily embraced me, a boot biologist and conservationist, since even before I started this journey. They were full of the most passionate discussions about genetics, behaviour, ecology, and evolution, which kept remining me how cool and exciting science can be in a way almost no other meeting did. Both *BBS* and *EcoComp* put with my untrained presentations for more times than I can remember and their contributions with ideas, questions and picky details really pushed my research further and deeply shaped the way I propel my research. I look forward to the new and thrilling research the members of both groups will be conducting in the days to come.

To FCUL's *PhD countdown programme*. Despite feeling I was lucky or privileged to not have faced the same obstacles as others from the programme did, this psychologist-assisted course (thank you *Andreia Santos*) guided my reflexion into what mental aspects I needed to work on. For a period of around 10 weeks, sharing thoughts and struggles with PhD candidates I had not met before gave me the right tools for both work and self-related growth, which were especially useful during the pandemics. I wish all my PhD colleagues would have the same opportunity I did during this rough period.

To all people who have lend me a hand during field work: *Ana*, *Joana*, *Inês*, *Teresa*, *Marta*, *Bruno*, *Rita*, *Jethro*, *Alex*, *Emilie*, *Kate*, *James*, *Richard*, *Andrew*, *Marie*, *Claire*, *Léa*, *Aldina*, *Ana*, *Martina*, *Sara*, *Ricardo*, *Salvador*, *Edna*, *Splinter*. I had a blast having you with me, even if it was just for a couple of hours, and I hope you have learned a tiny bity something from my work. Even with all the pretty birds and all the fanciest techniques, it was you that made field work memorable. To *Birds on the Move*, for lending me most of the manpower mentioned above, and for letting me tag along with some slightly larger bird handling experience.

To my Biodiv and non-Biodiv *PhD brothers* and *sisters*. As I mentioned before, I feel very privileged to had some of the most brilliant, ingenious, and hard-working people as colleagues, and even some as friends. It made working on Mondays exciting, and doing lab or deskwork almost as good as field work (almost). I have absolutely no doubt you will push science further today and be among the top researchers tomorrow. And I will try to remain close and ride along.

To all my *friends* inside and outside academia. To *SUP*, who have embraced me for who I am since my very first days at university more than 10 years ago, and to all other friends I come to know even before that. We have done so much together and continue to do so, and there is no science that could ever explain that. Knowing I can count on you makes me feel indestructible and feel like I can accomplish anything.

To my family, whose words are inequitable to describe how grateful I am for their unconditional love and support.

ABSTRACT

Human-induced changes in the environment dramatically shape the distribution of many species by restricting their access to resources such as food or nest-sites. Ongoing biodiversity loss has prompted conservation projects and large-scale nest-site provisioning to halt species declines. While successful at recovering endangered populations, artificial nests may turn into ecological traps by attracting animals to sites that end up reducing their fitness, or into conservation traps by making populations fully reliant on continuous conservation actions. Particularly, these new artificial nesting landscapes may alter the structure and functioning of communities, and modify or promote new species interactions, with unknown consequences for the conservation of target species.

In Europe, large-scale nest-site provisioning aimed at recovering lesser kestrel (*Falco naumanni*) populations attracted several other bird species forming mixed colonies. The main objective of this thesis was to investigate the consequences of these breeding assemblages for the conservation of the lesser kestrel and the European roller (*Coracias garrulus*) in Portugal. Using long-term monitoring data and a wide range of field techniques, this thesis first addresses the challenges and opportunities of artificial nests for the successful persistence of populations. Then, it investigates how costs and benefits typically associated with group living, such as increased transmission of parasites, competition for resources, and protection from predators, may affect the conservation of lesser kestrels and rollers.

Overall, this thesis demonstrates that artificial nesting landscapes may cause target species to become fully reliant on conservation actions and could concentrate species with similar niches in supra-optimal breeding densities. Ectoparasite burden was influenced by the relative abundance of each host species, most species highly overlapped in their trophic niche, and rollers acquired clear anti-predatory benefits from nesting near lesser kestrels. Understanding the impacts of nest-provisioning beyond the recovery of target populations, by considering how they attract other species and shape the interactions between them and their resources, will help researchers and conservation managers to draw and adapt conservation actions that guarantee the long-term persistence of wildlife populations.

Keywords: artificial nests, conservation, lesser kestrels, mixed-species groups, rollers

RESUMO

Os impactos ambientais provocados pelo Homem têm alterado a distribuição de muitas espécies ao restringir o acesso a recursos como alimento ou locais de nidificação. Para tentar travar a perda de biodiversidade global, têm sido criados muitos projetos de conservação, das quais a disponibilização de ninhos artificiais é uma das medidas mais utilizadas. Apesar de eficazes na rápida recuperação de populações ameaçadas, os ninhos artificiais podem resultar em armadilhas ecológicas se atraírem animais para locais que diminuam a sua sobrevivência, ou em armadilhas de conservação se tornarem as populações totalmente dependentes de ações de conservação. Em particular, estas novas paisagens dominadas por ninhos artificiais podem alterar a estrutura e o funcionamento de comunidades, e modificar ou promover novas interações entre espécies, com consequências ainda não conhecidas para a conservação das espécies alvo. Na Europa, a disponibilização de ninhos artificias em grande escala, destinada à recuperação de francelho (*Falco naumanni*) atraiu outras espécies de aves criando colónias multiespecíficas. Utilizando dados de monitorização e uma grande variedade de técnicas de campo realizadas na Zona de Proteção Especial (ZPE) de Castro Verde, Portugal, esta tese procura perceber de que modo estas novas comunidades de aves afetam a conservação de francelhos e rolieiros (*Coracias garrulus*), através de 6 capítulos, 4 dos quais correspondem manuscritos científicos:

Capítulo 2: Viabilidade de espécies dependentes de conservação: desafios e oportunidades

Este capítulo fornece a informação base necessária para os restantes capítulos da tese, descrevendo os efetivos e tendências populacionais atuais de francelho e rolieiro na ZPE de Castro Verde, e qual o seu grau de dependência de ninhos artificiais. Em 2017, foi realizado um censo para cada espécie na área de estudo, tendo sido visitadas todos os edifícios rurais e outras infraestruturas humanas (>400) para contabilizar todos os locais de nidificação ocupados. O estado de degradação de edifícios rurais foi avaliado para estimar a longevidade deste tipo de estruturas enquanto adequadas para nidificação. Foi quantificado o número de casais a criar em cada tipo de ninho (natural ou artificial), e estimaram-se os custos necessários de substituição e disponibilização de novos ninhos de modo a manter o número atual de casais. O **capítulo 2** revela que as populações de francelho e rolieiro em Portugal tornar-se-ão totalmente dependentes de ações de conservação a curto-médio prazo. Edifícios tradicionais de taipa apresentam um tempo de vida útil de cerca de 30 anos até colapsarem, e estimase que a totalidade de ninhos naturais neste tipo de estruturas deva desaparecer até ao final do século. Apesar da população de francelhos e rolieiros ter aumentado 77% e 66%, respetivamente, desde

2004 (o ano em que foram realizados os censos de ambas as espécies), mais de 65% dos casais criou em ninhos artificiais em 2017. Esta dependência por ninhos artificiais requere financiamento constante (substituição e disponibilização de novos ninhos), estimados em 4 500 € anuais. O **capítulo 2** sugere financiar a conservação de francelhos e rolieiros utilizando as receitas provenientes do turismo rural da região, das quais grande parte resulta de atividades de turismo de Natureza como observação de aves. Esta proposta poderia criar um mecanismo de financiamento sustentável e promover a viabilidade das populações alvo.

Capítulo 3: Infestação de ectoparasitas em colónias multiespecíficas

Este capítulo explora como o tamanho, densidade, riqueza e composição das colónias podem afetar a presença e abundância de ectoparasitas em ninhos e crias de aves em colónias multiespecíficas. Estudos anteriores reportam uma correlação positiva entre o tamanho da colónia e a carga parasitária, devido ao aumento do contacto entre indivíduos, mas a maioria da investigação tem-se focado em colónias monoespecíficas. Durante a época de reprodução de 2018, amostraram-se 4 grupos de ectoparasitas, incluindo uma espécie sugadora de sangue que infesta muitas espécies de aves, em crias de mais de 250 ninhos de quatro espécies de hospedeiro: francelho, rolieiro, estorninho-preto (*Sturnus unicolor*) e pombo doméstico (*Columba livia*). O **capítulo 3** mostra que o tamanho ou densidade da colónia não afeta a carga parasitária em colónias multiespecíficas. Em vez disso, é a composição da colónia – abundância relativa de cada espécie de hospedeiro – que determina a prevalência e abundância de ectoparasitas. Colónias com mais francelhos e menos estorninhos (as duas espécies mais abundantes) apresentaram maior abundância de ectoparasitas do que colónias com mais estorninhos e menos francelhos. A presença de espécies menos suscetíveis na colónia, como estorninhos e pombos, produz um efeito de diluição que reduz a carga parasitária, favorecendo colónias multiespecíficas.

Capítulo 4: Elevada sobreposição no nicho trófico em colónias multiespecíficas

Este capítulo utiliza isótopos estáveis (azoto δ^{15}N e carbono δ^{13}C) para avaliar a sobreposição trófica interespecífica e intraespecífica (entre progenitores e crias) que nidificam nestas colónias, de modo a avaliar uma potencial competição por alimento. Durante as épocas de reprodução de 2018 e 2019 (e utilizando amostras já recolhidas em 2014 e 2016), foram recolhidas 148 amostras de penas de crias e 38 amostras de sangue de pares progenitor-cria de 6 espécies diferentes: francelho, rolieiro, estorninho, peneireiro-comum (*Falco tinnunculus*), mocho-galego (*Athene noctua*) e coruja-das-torres (*Tyto alba*). O **capítulo 4** revela uma elevada sobreposição no nicho trófico entre a maioria das espécies amostradas, particularmente entre francelhos, rolieiros e estorninhos. Existe uma segregação trófica marcada entre progenitores e

crias em todas as espécies. Estes resultados sugerem que as espécies nestas colónias ocupam nichos semelhantes que podem potenciar a competição interespecífica por alimento como gafanhotos e escaravelhos. Apesar da elevada disponibilidade de alimento na área de estudo poder garantir a coexistência destas espécies, a viabilidade destas colónias pode ficar comprometida em áreas com recursos limitados, que se prevê que aumentem com as atuais alterações ambientais e climáticas, como intensificação da agricultura ou ondas de calor extremas.

Capítulo 5: É melhor criar sozinho ou em colónias multiespecíficas? Benefícios anti predatórios para uma ave solitária

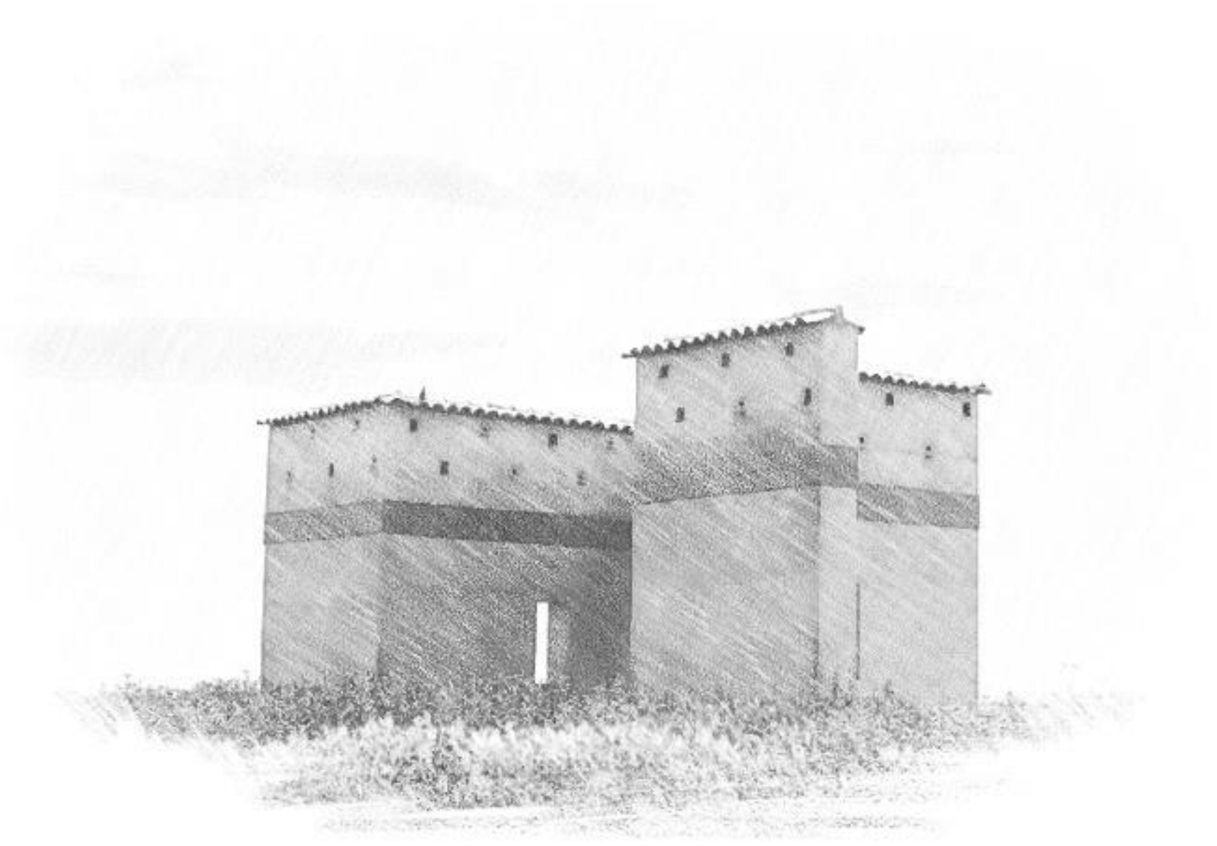
Este capítulo investiga se o rolieiro, espécie que tradicionalmente cria em ninhos isolados, adquire benefícios anti predatórios ao nidificar em colónias multiespecíficas dominadas por francelho. Entre 2017 e 2019, testou-se o comportamento de risco face a um objeto novo (neofobia) e face a um modelo de um predador (gralha-preta) em 108 casais de rolieiro, dos quais 39 criaram em ninhos isolados e 69 criaram em colónias de francelho. Adicionalmente, utilizando dados de monitorização de quase 300 eventos reprodutores em 6 anos consecutivos (2014-2019), comparam-se parâmetros reprodutores: data de postura, tamanho da postura e produtividade – e taxa de predação de ninho entre rolieiros solitários e rolieiros em colónias. O **capítulo 5** revela que rolieiros em colónias chegam ao ninho mais depressa, tanto na presença da gralha, como na presença do objeto novo, e investem menos na defesa dos ninhos. Ninhos de rolieiro em colónias também sofreram metade da predação do que ninhos solitários, mas não produziram mais crias voadoras, sugerindo que não há vantagens reprodutoras claras em criar em colónias.

Em resumo, esta tese demonstra que estas novas paisagens dominadas por ninhos artificiais podem levar a que espécies alvo se tornem totalmente dependentes de ações de conservação. Para além disso, podem agrupar espécies com nichos semelhantes em densidades supra-ótimas, exacerbando os benefícios, mas também os custos associados a grupos multiespecíficos, potencialmente afetando a eficácia de ações de conservação. Para além dos resultados imediatos na recuperação das populações alvo, é importante perceber de que maneira a disponibilização de ninhos artificiais pode atrair outras espécies e alterar as interações entre elas e os seus recursos, de modo a desenhar e adaptar medidas de conservação que garantam a viabilidade das populações naturais.

Palavras-chave: conservação, colónias multiespecíficas, francelho, ninhos artificiais, rolieiro

Chapter 1

General Introduction



GENERAL INTRODUCTION

1. CONSERVATION CHALLENGES IN THE ANTHROPOCENE

Human activities are transforming the face of the planet and causing dramatic changes to the distribution and abundance of wild species, mainly through habitat destruction, climate change, and invasive species (Scheffers et al. 2016; Dueñas et al. 2021; Winkler et al. 2021). Habitat loss and fragmentation caused by urban expansion, construction of infrastructures, intensification of agriculture, or logging, restricts species access to resources such as food and nest-sites, and reduces habitat connectivity (Fahrig 2003; Fischer & Lindenmayer 2007; Fahrgi & Rytwinski 2009). Human-mediated global warming and the increase in the occurrence of extreme weather events affect the range and distribution of species, disrupts phenology synchrony, and reduces the effectiveness of protected areas (Walther et al. 2002; Leadley et al. 2010; D'Aloia et al. 2019; Marcelino et al. 2020). Climate change impacts economic growth and agriculture productivity, further jeopardizing global biodiversity through land-cover changes (Watson 2013; Mantyka-Pringle et al. 2015; Piontek et al. 2021; Fuglie 2021). Invasive species threaten 14% of critically endangered terrestrial vertebrate species, 28% on islands, mainly through competition and predation (Dueñas et al. 2021; Soares et al. 2021). In some species, the few remaining populations face the persisting dangers of persecution (Gobush et al. 2008; Challender & MacMillan 2014; Madden et al. 2019). The footprint of humanity on biodiversity has resulted in the loss of many species. The WWF's Living Planet Index estimates an average population decline of 68% across all monitored vertebrates since 1970 (WWF 2020), and more than one thousand birds and mammals, currently classified as Endangered or Critically Endangered, will likely become extinct by the end of the century if current pressures are not halted (Johnson et al. 2017). Loss of biodiversity reverberates through ecosystems and severely compromises the services they provide, with major consequences for human well-being (Millennium Ecological Assessment 2005; Butchart et al. 2010; Cardinale et al. 2012; Johnson et al. 2017; WWF 2020).

Loss of species and degradation of ecosystems are likely to further accelerate in the coming years, demanding urgent action (Mantyka-Pringle et al. 2015; Waldron et al. 2017). Increased recognition of the magnitude of human impacts on nature has prompted world leaders, through the Convention on Biological Diversity and the Sustainable Development Goals, to commit to halt and reverse ongoing biodiversity loss (CBD 2010; United Nations 2015). However, such large-scale conservation efforts incur in high financial costs, likely hindering the achievement of international biodiversity targets so far (Hoffman et al. 2010; Tittensor et al. 2014). A total annual expense on global biodiversity was estimated at approximately 21.5 billion US dollars between 2001 and 2008 (Waldron et al. 2013). Most of these were from government expenses, of which 94% in high-income countries, leaving developing countries reliant on international aid (Waldron et al. 2013; Johnson et al. 2017; Johnson et al. 2017). Due to shortage of funds, conservation is often reactive rather than proactive: priority is given to species and populations that are already highly endangered, focusing on reversing negative impacts and rapidly restoring population sizes (Scott et al. 2010; Drechsler et al. 2011; Cardador et al. 2015). Reactive measures end up being more expensive than proactive ones (Drechsler et al. 2011) and increase the risk of turning conservation actions into ecological traps – if attracting animals to unsuitable sites that reduce their fitness, or into conservation traps – if resulting in an unsustainable need to perpetuate the implementation of those actions (Robertson & Hutto 2006; Cardador et al. 2015). It is thus fundamental for conservation policy success to accurately identify the amount of financing needed to fund conservation strategies (Waldron et al. 2013, 2017). This can be achieved by adopting evidence-based approaches, supported by long-term monitoring of wildlife populations and their response to environmental change, which then guides decision-making by evaluating past failures and successes (Johnson et al. 2017; Waldron et al. 2017; Downey et al. 2021).

Birds are amongst the most susceptible taxa to human and climate-induced environmental changes, being one of most threatened groups worldwide (Hoffman et al. 2010; Foden et al. 2013; Pacifici et al. 2015; Dueñas et al. 2021). Despite being the target of many conservation actions, many species are still declining, particularly those in human-dominated landscapes such as farmland birds (Donald et al. 2001; Newbold et al. 2016; Johnson et al. 2017). Because they are easy to monitor and sample, birds are also amongst the most studied taxa and have been used as ecological indicators to track and measure the impacts of environmental changes (Niemi & McDonald 2004; Ockendon et al. 2014; Pacifici et al. 2015).

This thesis addresses on of the most common (reactive) type of conservation actions used to restore endangered populations of birds and other taxa – artificial nest-site provisioning (Newton 1998; Sutherland et al. 2018). It examines how large-scale nest-site supplementation may re-shape the nesting landscape and alter the structure of communities by aggregating animals of multiple species in high breeding densities. This may result in costs and benefits typically associated with group living, which may have implications for the conservation of target species; here, the lesser kestrel *Falco naumanni* and the European roller *Coracias garrulus*. With this in mind, this introduction will address the challenges and opportunities of nest-site provisioning, and the ecological aspects of group living. Then, it will briefly introduce the study site and species, ending with the thesis outline and main objectives.

2. NEST-SITE PROVISIONING

While the first image that comes to most people's mind are wooden nest-boxes for songbirds, artificial nests come in many different shapes and sizes and have been successful at recovering endangered populations across many different taxa (Sutherland et al. 2018). There are insect hotels (Harris et al. 2021; Machač & Tuf 2021), metal poles and artificial mounds provided for reptiles (Sanchez 2012; Paterson et al. 2013), bat boxes (Flaquer et al. 2016) and nest boxes for non-flying mammals and marsupials (Harper et al. 2005; Lindenmayer et al. 2016; Goldingay 2017), artificial dens for small and large carnivores (Wei et al 2015; Croose et al. 2016); and a wide diversity of artificial nests adapted for different bird species (Bolton et al. 2004; Pichegru 2013; Catry et al. 2009; Olah et al. 2014; Dulle et al. 2020).

Nest-site availability is one of the main factors liming the distribution and density of natural populations (Newton 1998; Sutherland et al. 2018). Human-induced transformations to the environment has led to the loss of natural nest-sites, resulting in the decline of several hollow-nesting species, particularly secondary cavity-nesters that are unable to excavate their own cavities (Newton et al. 1994; Newton 1998; Harper et al. 2005; Catry et al. 2009). Artificial nests excel at facilitating a rapid increase in population sizes, being an effective conservation tool for recovering endangered populations facing shortage of natural nesting opportunities (Bolton et al. 2004; Harper et al. 2005; Catry et al. 2009; Finch et al. 2018; Sutherland et al. 2018). Besides their efficacy at restoring endangered populations, artificial nests have also contributed to our understanding of the biology and ecology of species, by allowing an easier access to nests or individuals (Newton et al. 1994; Beyer & Goldingay 2006; Lambrechts et al. 2010; Loretto & Vieira 2018). They allow researchers to conduct routine monitoring, easier capture or recapture of individuals, or experimental manipulations, and have helped research in a broad range of disciplines from behavioural and functional ecology, to environmental, population, and conservation biology (Lambrechts et al. 2010; Mainwaring et al. 2011).

2.1 ECOLOGICAL TRAPS

Despite being a popular and successful measure to revert shortage of natural nest-sites and increase population numbers, without planning, proper nest design, or strategic placement, artificial nest supplementation can lure individuals to unsuitable sites and result in ecological traps, impacting animals' fitness by reducing their productivity or survival (Schlaepfer et al. 2002; Battin 2004; Gottchalk et al. 2011; Rodríguez et al. 2011b; Cowan et al. 2020). Ecological traps may occur through any alteration to the environment (usually as a response to human activities) that decreases habitat quality without animals realizing it (Battin 2004; Robertson & Hutto 2006; Gilroy & Sutherland 2007; Hale et al. 2018), but they may also result from conservation actions such as habitat restoration or nest-site provisioning (Klein et al. 2007; Severns 2011; Hale & Swearer 2017). Potential ecological traps of artificial nests include: lower access to quality habitats or food sources (Schlaepfer et al. 2002; Rodrigues et al. 2011; Catry et al. 2013); higher exposure to predators (Miller 2002; Rodrigues et al. 2011) and parasites (Veiga & Valera 2020), overheating and temperature associated stress (Isaac et al. 2008; Catry et al. 2015; Bideguren et al. 2019; Crowford & O'Keefe 2021), or increased risk of collision with other human infra-structures (Garrido & Fernandez-Cruz 2003). These may decrease animal fitness by reducing breeding success, condition, or survival, which can lead to artificial nest desertion or even local extinction (Schlaepfer et al. 2002; Battin 2004; Catry et al. 2013).

Despite being used worldwide and targeting many taxa, reports on the unforeseen consequences of nest-site provisioning are still surprisingly lacking, presumably due to an absence of long-term monitoring data after achieving the desired recovery of target populations (Lambrechts et al. 2010). Many artificial nests, like the commonly used nest-boxes, may not last long and have to be frequently replaced, which may not be sustainable if their costs are high or financial resources are low (Harper et al 2005; Lindenmayer et al. 2009; Cardador et al. 2015; Mainwaring 2015). Nest-site provisioning may also re-shape animal communities by attracting species that are not the intended target of the conservation measures, and aggregate individuals at higher densities than those occurring under natural conditions (Lindenmnayer et al. 2016; Catry & Catry 2019; Stojanovic et al. 2021). Enriched artificial nesting landscapes may modify the structure and functioning of local communities and change species interactions, which may potentiate benefits, but also costs, typically associated with group living.

3. LIVING IN GROUPS

Group living is found in many taxa across the natural world and can assume many different forms, such as flocks, herds, swarms, shoals, communal roosts, etc. (Krause & Ruxton 2002). One of the most common and studied forms of group living is colonial breeding, where animals aggregate in high-density breeding areas that provide no resource other than nesting-sites

(Danchin & Wagner 1997). Colonial breeding has been reported in fish (Schütz et al. 2016), reptiles (García-Cruz et al. 2015), dinosaurs (Horner, 1982), and mammals (Fudala & Bialik 2020), but is particularly prevalent in birds, where about 13% to 19% of all species breed in colonies (Rolland et al. 1998; Papageorgiou & Farine 2021). Therefore, most research on group living done in the past few decades has been carried out in bird colonies, and most of the literature and examples used in this section are from work done with birds.

3.1 COSTS AND BENEFITS OF LIVING IN GROUPS

Living in groups may provide fitness-enhancing benefits, the most common of which are related with enhanced food finding and protection from predators (Danchin & Wagner 1997; Varela 2007). Animals in groups may increase their foraging efficiency by cueing and following and/or attracting neighbours to new food sources, particularly in areas where food is abundant but patchy and variable in space and time (Danchin & Wagner 1997; Rolland et al 1998; Jones et al. 2018; Guo et al. 2021). The main premise is that aggregations function as information centres, where animals gather and share information about where to forage - information centre hypothesis (Ward and Zahavi 1973; Bijleveld et al. 2010), as when vultures follow informed conspecifics about the location of a carcass (Harel et al. 2017). Animals in groups may also increase their foraging efficiency by adopting group hunting strategies, as in the classical examples of hunting by wolf packs or marine mammals (Ellis et al. 1993; Bailey et al. 2013; MacNutty et al. 2014; Ortiz et al. 2021).

Predation is a major force on the evolutionary history of animals, shaping their behaviour and their decision on where to breed or forage (Lima & Dill 1990; Graham & Shutler 2019), so it comes as no surprise that it may profoundly influence the structure of communities and the formation or maintenance of aggregations (Hass & Valenzuela 2002; Varela 2007; Varela et al. 2007; Lehtonen & Jaatinen 2016). Although groups may be more exposed to predation due to increased conspicuousness (Varela et al. 2007), they grant protection through group vigilance or communal defence, or through dilution and selfish herd effects (Danchin & Wagner 1997; Uetz et al. 2002; Varela et al. 2007). These mechanisms may not only reduce the chances of being caught and killed by the predator, but also reduce non-lethal effects of predation risk, as animals can allocate time from anti-predatory behaviours to other, fitness-enhancing activities such as foraging, mating, or caring for their young (Lima & Dill 1990; Frid & Dill 2002; Graham & Shutler 2019). Being in a group means that there are more eyes and hears to detect a potential threat, and consequently more signals such as alarm calls to rapidly inform neighbours of the presence and location of that threat (Beauchamp 2008; LaBarge et al. 2021). Some animals, instead of fleeing, may perform mobbing behaviour, when they harass, distract, or confuse an approaching predator by calling or lunging towards it. This decreases individual investment and risk in larger groups whilst being more effective at driving the predator off (Brown & Hoogland 1986; Arroyo et al 2001; Krams et al. 2009). Even when failing to detect a predator, the large number of individuals in a group decreases the probability of any one of them getting caught – dilution effect. Animals may even actively seek to position themselves at the centre rather than at the periphery of a group to decrease their chances of being predated – selfish-herd effect (Hamilton 1971; Uetz et al. 2002; Lehtonen & Jaatinen 2016).

Other benefits of group living include better access to mates, cooperative breeding, heat and water preservation, and energy conservation by moving together (Krause & Ruxton 2002; Goodenough et al. 2010; Ward & Webster 2016).

Group living, however, may also result in fitness-reducing costs. The increased contact among individuals facilitates the transmission of parasites, increasing their prevalence and intensity (Côté & Poulin 1995; Rifkin et al. 2012). This relationship has been found mostly in bird colonies, but also in mammals. It occurs more often in contact transmitted parasites (*e.g*., fleas, mites, lice, nematodes; Côté & Poulin 1995; Arneberg 2002; Hoi et al. 2010), than in mobile parasites (*e.g*., flies, leeches; Whiteman & Parker 2004; Fauchald et al. 2007). However, the relationship between parasitism and aggregations may not be as obvious in mammals and other taxa because many have developed behavioural coping mechanisms against parasites, including allogrooming (Clayton et al. 2010; Wilson et al. 2020) or changes in group organization and structure (Fauchald et al. 2007; Lucatelli et al. 2021). Parasites and diseases can reduce body condition and survival of offspring and adult fecundity, and shape group structure and dynamics through mate exclusion or by altering site-fidelity and avoidance, even leading to the formation and extinction of aggregations (Côté & Poulin 1995; Altizer et al. 2003; Brown & Brown 2004; Lourenço & Palmeirim 2007; Brown et al. 2017; Sanz-Aguilar et al. 2021).

Individuals in dense groups are also more likely to compete for resources such as food, nests, or mates (Danchin & Wagner 1997). Larger groups may exhaust food resources faster in the vicinity of the aggregation, particularly in the case of avian breeding colonies where birds act as central-place foragers (Ashmoles's Halo; Birt et al. 1987; Lewis et al. 2001; Bonal & Aparicio 2008). Depletion of resources may promote direct competition, producer-scrounger strategies, and kleptoparasitism (food theft) (Giraldeau et al. 1994; Arroyo & García 2002; Seiler & Robbins 2020), or force animals to spend more energy by foraging at larger distances

(Lewis et al. 2001; Bonal & Aparicio 2008). Competition for nests, food or mates may also lead to aggression (Tyack & Whitehead 1982; Huchard & Cowlishaw 2011), interference competition (when an individual prevents others from using a resource; Coulson et al. 1968; Gargen et al. 2008) alloparental care and brood parasitism (caring for unrelated young; Arroyo & García 2002), cannibalism and infanticide (Ramsay et al. 2020), or increased stress levels leading to higher susceptibility to diseases (Beldomenico et al. 2010; Kappeler et al. 2015).

Two main school of thoughts have tried to explain the evolution of animal aggregations. The economic framework views aggregations as serving a function (benefit) and predicts they are formed when the benefits of group living out balance the costs (Wittenberger & Hunt 1985; Danchin & Wagner 1997; Rolland et al. 1998; Varela 2007). This cost-benefit analysis did not provide a general answer to the evolution of group living, as assessing the costs and benefits is more complex, requires long-term studies to measure individual fitness, and likely varies according to specific, populational, or individual adaptations to local physical and biological factors (Danchin & wagner 1997; Varela et al. 2007; Clobert et al. 2009; Murthy et al. 2015). More recently, the commodity selection framework views groups as by-products of animals selecting the same commodities such as habitat or mates (Danchin & Wagner 1997; Wagner et al. 2000). This approach assumes that individuals select their mates or breeding areas (or feeding or resting areas) by observing other individuals, ending up in the same space and forming groups. Aggregations are then but a result of multiple animals attempting to benefit from the same favorable conditions, without necessarily benefiting from the group itself (Danchin & Wagner 1997; Wagner et al. 2000). In this sense, costs and benefits of group living are viewed as consequences acting on the maintenance, rather than on the formation, of aggregations. This might explain why some species have facultative social strategies, with some individuals breeding or foraging solitarily and others living in groups, something that is not yet fully understood (Banks et al. 2007; Clobert et al. 2009; Marino 2010; Dardenne et al. 2013). Regardless of the origin of groups, investigating the costs and benefits of aggregations is important to understand how human-induced changes in the environment may disrupt the equilibrium allowing their persistence, or how the re-shaping of communities and the formation of new aggregations may affect the viability of species of conservation concern (Banks et al. 2007; Varela et al. 2007; Ockendon et al. 2014; Catry & Catry 2019).

3.2 MIXED-SPECIES GROUPS

Many animal groups are composed of several different species, resulting in mixed-species aggregations (Stensland et al. 2003; Boulay et al. 2017; Goodale et al. 2017). Mixed-species associations follow the same fundamental mechanisms of single-species groups and may be formed or maintained through the acquired benefits of mutual anti-predatory avoidance, increased foraging efficiency (Sridhar & Guttal 2018) or as a by-product of habitat selection through heterospecific information transfer and copying (Seppänen et al. 2007; Quinn & Ueta 2008; Goodale et al. 2010; Sridhar & Guttal 2018).

Mixed-species groups may be more advantageous than single-species groups when the assembled species differ in their morphological, sensorial, or behavioural traits, or when grouping with conspecifics alone is insufficient to produce the benefits that only a certain group size can provide (*e.g.*, for solitary species or species forming small groups; Semeniuk & Dill, 2006; Quinn & Ueta 2008; Sridhar & Guttal 2018). Some species in a group may be more active foragers and flush more prey to others (Heymann & Buchanan-Smith; Sridhar & Guttal 2018), be more vigilant, have well-developed alarm calls that are identified by heterospecifics (Johnson et al. 2003; Vitousek et al. 2007; Goodale et al. 2019) or be more aggressive in mobbing behaviour (Quinn & Ueta 2008; Campobello et al. 2012; Dutour et al. 2017). For example, mixed-species bird flocks are often composed of smaller and more insectivorous 'follower' species, and more gregarious 'leaders' that contribute to group cohesion, resulting in increased foraging rates and reduced vigilance when compared to solitary animals or single-species flocks (Mönkkönen et al. 1996; Sridhar et al. 2009; Goodale & Beauchamp 2010). Similarly, different primate species in mixed troops occupy different strata of the vegetation (vertical segregation), and so are better at detecting predators approaching from different directions (Heymann & Buchanan-Smith 2000). When the aggregated species have different ecological niches, such as in the two examples above, mixed-species aggregations may further allow individuals to acquire group-related benefits without increasing intra-specific competition or other costs (Campobello et al. 2012; Goodale et al. 2019). This is because competition tends to increase with phenotypic similarity and so should be highest among conspecifics (Sridhar & Guttal 2018; Goodale et al. 2020). However, similarity among species may also increase the value of the aggregation – the more similar the food resources or the predators between two species, the higher the value of interspecific information share and aggregation (Seppänen et al. 2007; Sridhar & Guttal 2018). As a rule, when similarity among species increases, both the benefits and the costs of the aggregation will increase.

As with benefits, costs of mixed-species groups are like those of single-species groups. Parasites often attack multiple hosts and so the magnitude of parasitism will depend on the composition of the aggregation (Holt et al. 2003; Valera et al. 2003). Breeding with a more aggressive species may lead to higher levels of kleptoparasitism (Gaglio et al. 2018), or even predation by the protector species (Quinn & Ueta 2018). Shortage of resources may also lead to interspecific competition for nests or food (Botero-Delgadillo et al. 2015; Dalerum et al. 2016; Catry & Catry 2019).

Whether to be alone, with conspecifics, or in mixed aggregations, will likely depend on localized adaptations to specific ecological conditions, such as habitat structure, abundance of nests and food resources, or predation pressure (Wagner et al. 2000; Quinn & Uetta 2008; Marino 2010; Murthy et al. 2015; Sridhar & Guttal 2018; Liu et al. 2020). These conditions are expected to change with increasing human-made modifications through habitat loss and fragmentation, or through conservation actions such as nest-site provisioning (Banks et al. 2007; Clobert et al. 2009; Ockendon et al. 2014; Teckentrup et al. 2017; Catry & Catry 2019). This thesis addresses three of the main consequences of group living: transmission of parasites, competition for food, protection against predators. As seen throughout this section, although not the only consequences of living in groups, these are often considered to play the strongest forces in the formation or maintenance of aggregations (Varela 2007; Rifkin et al. 2012; Goodale et al. 2020).

4. STUDY AREA AND SPECIES

4.1 CASTRO VERDE SPECIAL PROTECTION AREA

All research performed for this thesis was conducted in the Castro Verde Special Protection Area (SPA; PTZPE0046), southern Portugal (37°43′N, 7°57′W) (Fig. 1.1). It was designated in 1999 and further expanded in 2008 as part of the European Natura 2000 network – the largest coordinated multi-national network of protected areas in the world (Blicharska et al. 2016; Orlikowska et al. 2016). With a total area of ca. 85 000 hectares, it is the main area for steppe bird conservation in Portugal and one of the main strongholds for several threatened farmland species in Western Europe, including great bustard *Otis tarda*, little bustard *Tetrax tetrax*, black-bellied sandgrouse *Pterocles orientalis*, stone curlew *Burhinus oedicnemus*, calandra lark *Melanocorypha calandra*, lesser kestrel *Falco naumanni* and European roller *Coracias* *garrulus*, and hosts a significant proportion of the Portuguese population of Iberian imperial eagle *Aquila adalberti* (Cabral et al. 2005; Moreira et al. 2007; LIFE Imperial 2020).

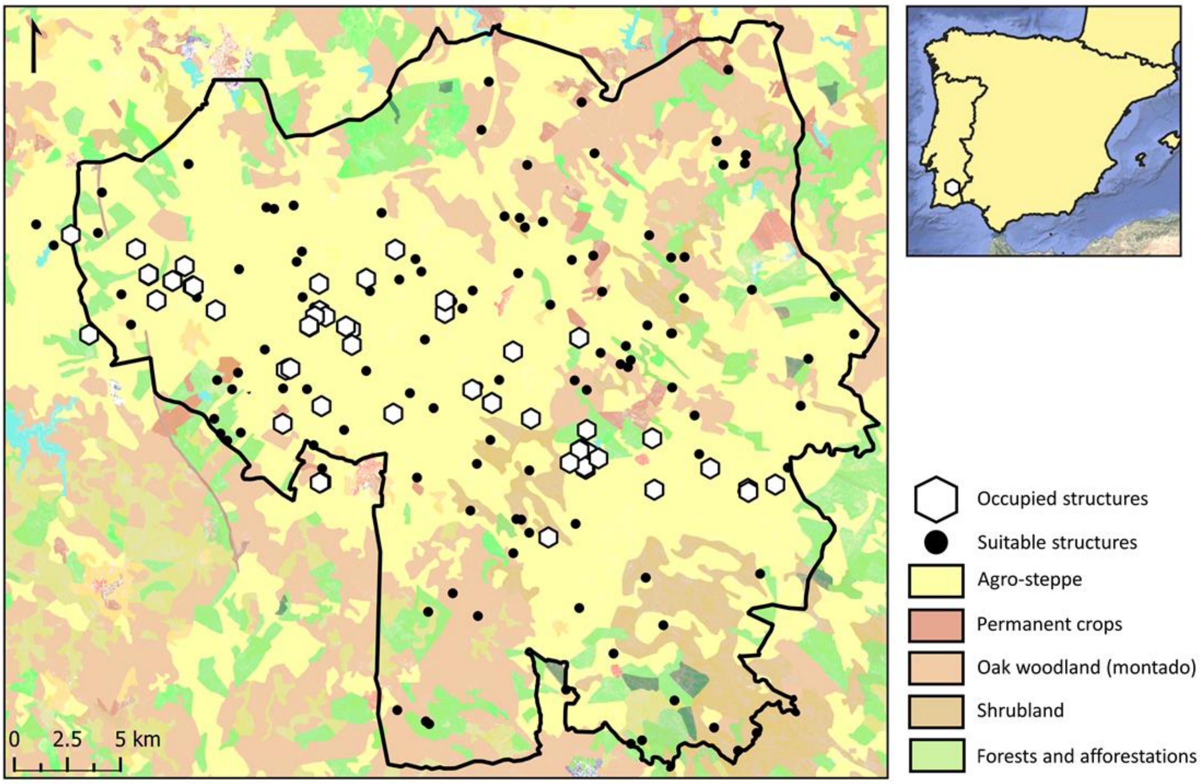


Figure 1.1: Castro Verde Special Protection Area (SPA), southeast Portugal, and all human-made structures with suitable nest-sites, including artificial nests. Black dots show suitable structures (with at least one suitable nest-site). White hexagons show structures usually occupied by lesser kestrels and/or rollers. Main land-uses retrieved from Corine Land Cover 2018 (Copernicus Land Monitoring Service 2018).

The area is characterized by a Mediterranean climate and is mainly occupied by agro-steppes (or cereal steppes) – a result of extensive cultivation of dry cereal crops in a low intensity rotating system that includes legume crops, grazed and ungrazed fallows and permanent pastures used for extensive grazing (Franco and Sutherland 2004; Moreira et al. 2007; Silva et al. 2010) (Fig. 1.1). The area includes sparse holm and cork oak woodlands (montado), vineyards and olive and almond groves, eucalyptus and pine afforestations, and shrublands (Moreira et al. 2007) (Fig.1.1).

Due to their low economic output, aggro-steppes in Portugal, and other traditional farmland systems in Europe, are threatened by land abandonment or agriculture intensification, with conversion to permanent cultures, and increase irrigation using of fertilizers and pesticides (Traba et al. 2007; Stoate 2009; Traba & Morales 2019; Gameiro et al. 2020). Major losses in agro-steppe area have been occurring throughout the Iberian Peninsula, both within and outside areas designated under the European Natura 2000 network, resulting in the recent decline of several threatened species (Palacín & Alonso, 2018; Silva et al. 2018; Bustamante e al. 2020; Gameiro et al. 2020). Despite also currently menaced by habitat loss and degradation, land use within the Castro Verde SPA has remained relatively stable in the last decades, in part due to the implementation of agri-environmental schemes and funding mechanisms that ensure high-quality foraging habitats (Silva et al. 2018; Gameiro et al. 2020). Castro Verde is thus currently working as a refuge for several threatened farmland species in Portugal and Iberia, which has contributed to its recent classification as a UNESCO Biosphere Reserve (UNESCO 2019).

While most steppe birds nest on the ground, lesser kestrels and European rollers are secondary cavity-nesters and require pre-excavated hollows to nest (del Hoyo 2001a, b). In the rather treeless landscape of Castro Verde, they occupy cavities on farmhouses scattered throughout the area (Fig. 1.1). Most of these rural buildings are built with adobe, a mixture of lime and mud, that decay with lack of maintenance and the eroding action of rain and wind, leading to the appearance of cavities in walls. The continuing degradation of these structures eventually lead to building collapse and loss of all nest-sites (Catry et al. 2009). New buildings are built with long-lasting materials, like bricks or concrete, preventing the appearance of new nesting cavities. Loss of suitable cavities, associated with the restoration of historical buildings, have contributed for the decline of lesser kestrels and rollers in the area, and likely in other regions of Portugal and Europe (Franco et al. 2004; Catry et al. 2009, 2011). To reverse the decline of the lesser kestrel, a colonial breeding raptor, large-scale nest-site provisioning started in 1994 through 4 European LIFE-Nature Projects conducted by *Liga para a Proteção da Natureza* (LIFE92/NAT/P/013900, LIFE95/NAT/P/000178, LIFE02/NAT/P/008481, and LIFE07/NAT/P/000654). Currently, more than a thousand artificial nest-sites have been provided in the Castro Verde SPA, including cavities in plastered walls (new cavities dug in existing traditional buildings), clay-pots and wooden nest-boxes placed in both traditional and new buildings, and newly built breeding walls and towers with the up 87 cavities each (Catry et al. 2009) (Fig. 1.2). Nest-site supplementation resulted in a remarkable recovery of lesser kestrels in Portugal, from approximately 150 breeding pairs in 1996 to more than 500 in 2007, and benefitted an increase of the population of the European roller, a species that lacked the attention of researchers and conservationist in Portugal until the last decade, despite being one of the seventeen breeding birds classified as Critically Endangered in the territory (Catry et al. 2009, 2011).

Figure 1.2: Types of nest-sites: traditional adobe building in advanced state of decay with suitable nest-sites (A), wooden nest-box (A), clay pot (C), artificial breeding wall (D).

Nest-site supplementation also occurred in other SPAs besides Castro Verde, but the lack of suitable foraging areas surrounding artificial nests decreased their effectiveness, supporting the idea that lesser kestrels and rollers (like most natural populations) require the sympatric availability of suitable nest-sites and high-quality habitat in other to thrive (Catry et al. 2013; Finch et al. 2018). Currently, more than 80% of the Portuguese population of lesser kestrels and rollers is concentrated within the Castro Verde SPA (Catry et al. 2009, 2011), in a nesting landscape comprised of traditional adobe buildings in various stages of degradation with nest-sites in wall cavities and under roof tiles, and artificial nests provided in traditional or newly built structures (Fig. 1.1).

4.2 LESSER KESTREL

The lesser kestrel *Falco naumanni* Fleischer 1818 is a small colonial falcon (58-72 wingspan) that undergoes trans-Saharan migrations (Cramp & Simmons 1980; del Hoyo et al. 2001a; BirdLife International 2021) (Fig 1.3). It breeds throughout the Western Palearctic from

Southern Europe and North Africa to the Middle East and Central Asia, occurring mostly in steppe-like habitats such as grasslands and extensive crops (del Hoyo et al. 2001a; Catry et al. 2013). Wintering grounds are found across Sahel, Kenya and Tanzania, to South Africa, although some populations overwinter near their breeding territories (Negro et al. 1991; Rodríguez et al. 2011a; Sàra et al. 2019). Lesser kestrels arrive to their breeding grounds in early February and lay 4-5 eggs in mid-April and May; incubation takes 28 days and chicks fledge at ca. 36 days (del Hoyo et al. 2001a; Catry et al. 2015). Adults are sexually dichromatic and dimorphic, with females being slightly larger than males (Newton 1979) (Fig. 1.3). Both sexes participate in incubation and chick rearing, but males contribute more to food provisioning (Catry et al. 2016; Hernández-Pliego et al. 2017). They feed mainly on large arthropods such as beetles and grasshoppers, and to a lesser extent on small vertebrates (Rodríguez et al. 2010; Catry et al. 2016).

Figure 1.3: Male (left) and female (right) lesser kestrels. Photo taken and generously provided by Inês Catry.

Lesser kestrels are secondary-cavity nesters and rely on previously excavated cavities (del Hoyo et al. 2001a). Although they are thought to originally occupy holes in cliffs, lesser kestrels are presently typically associated with human settlements and have been nesting in human-made buildings for at least 2000-2500 years (Negro et al. 2020). Nowadays, only a small percentage (< 5%) of the Western Palearctic populations breed in natural cliffs (Negro et al. 2020). Nests are usually located in cavities in the walls or under tiled roofs of castles and churches in urban areas, farmland houses in rural areas, or in artificial nest-sites (Catry et al. 2009; Birdlife International 2021).

The species suffered sharp population declines in its western European distribution during the 20th Century, presumably mainly due to loss of suitable nest-sites and foraging habitat degradation through agriculture intensification, or land abandonment and afforestation, and was globally classified as Vulnerable (Donazar et al. 1993; Tella et al. 1998; Franco et al. 2005; Catry et al 2009; Iñigo & Barov 2010; BirdLife International, 2021). Recent stable or slightly increasing population trends have improved its conservation status from Vulnerable to Least Concern (Birdlife International 2021), although abrupt declines have been reported in some populations in recent years, with a worrying 43% average decline in the Spanish populations in the last 10 years (Bustamante et al. 2020). Conservation actions are mostly based on nest-site provisioning and land-use management to ensure high-quality foraging areas (Iñigo & Barov 2010; Catry et al. 2013).

In Portugal, the lesser kestrel is classified as Vulnerable, after suffering a major population decline and disappearing from most of its range, possibly due to lack of suitable nesting cavities (Cabral et al. 2005; Franco et al. 2005; Catry et al. 2009). First conservation efforts in the country began in 1994 through European LIFE-Nature projects (Catry et al. 2009; see previous section). Currently, more than 80% of its population occur in the Castro Verde SPA, where more than half of the breeding pairs nest in provided artificial nests (Catry et al. 2009). It nests in cavities or under roof tiles in traditional farmland buildings, or in artificial nests, forming colonies up to 80 breeding pairs (Catry et al. 2009).

4.3 ROLLER

The European roller *Coracias garrulus* Linnaeus, 1758 (hereafter roller) is a medium-size, solitary coraciform (52-58cm wingspan) which also carries a trans-Saharan migration (Cramp & Simmons 1988; del Hoyo et al. 2001b; Birdlife International 2021) (Fig. 1.4). It has a fragmented breeding distribution concentrated in the Mediterranean and throughout the middle east from Turkey to western Himalayas (Kovacs et al. 2008), occurring in heterogenous landscapes ranging from agricultural steppes to open Mediterranean and temperate areas such as open forests or orchards (del Hoyo et al. 2001b; Kovacs 2008). Wintering grounds are found in southern Africa from Kenya to Angola, Zambia and Botswana (Finch et al. 2015). Rollers arrive to their breeding grounds at the end of April and lay 3-6 eggs mainly in May to early June; Incubation takes 17-19 days and chicks fledge at 25-30 days (del Hoyo et al. 2001b; Catry et al. 2015). Rollers have minimal morphological sexual dimorphism, and both sexes share incubation and chick rearing (Newton 1979). Like lesser kestrels, rollers feed mainly on large arthropods such as Coleoptera and Orthoptera (Avilés & Parejo 2002; Catry et al. 2019).

Natural nests are usually in abandoned woodpecker holes in old trees (especially oaks, pines, and poplars), or in cavities in sandy cliffs or banks dug by other hole nesting birds such as bee-eaters (Kovacs et al. 2008; Bouvier et al. 2014; Kiss & Tokody 2017; Valera et al. 2019). Where natural nest-sites are lacking, particularly in agricultural landscapes in the Iberian Peninsula, rollers promptly nest in cavities in abandoned human-made buildings such as farmhouses, or in artificial nest-sites (Catry et al. 2011; Rodríguez et al. 2011b; Kiss & Tokody 2017; Finch et al. 2018).

Figure 1.4: European roller. Photo taken and generously provided by Inês Catry.

The species underwent rapid population declines in late 20th – early 21st century, particularly in northern and central Europe where it became extinct in several countries, and its global status was then Near Threatened (Kovacs et al. 2008; Birdlife international 2021). The main causes for these declines include loss and degradation of suitable habitat due to agricultural intensification, loss of suitable nest-sites such as old trees with hollows, and persecution along its migratory routes (Kovacs et al. 2008; Birdlife International 2021). Although current population trends indicate that the roller is still declining, declines are occurring at a slower rate due to conservation actions and the species is now classified as Least Concern (BirdLife International 2021). Like in lesser kestrels, main conservation actions include nest-site provisioning and restoring and maintaining suitable foraging and nesting habitats, as well as understanding and reducing threats along their migratory flyways (Kovacs et al. 2008; Birdlife International 2021).

In Portugal, the roller is classified as Critically Endangered (Cabral et al. 2005). It suffered severe population contractions in its already fragmented distribution throughout the country, mainly in lowlands (Cabral et al. 2005). The population is currently estimated at no more than 100 breeding pairs and more than 80% of them are concentrated in the Castro Verde SPA. Here, more than half of the breeding pairs use artificial nests, most of which were originally provided for lesser kestrels (Catry et al. 2009; Catry et al. 2011). It nests in isolated nests in traditional buildings or isolated nest-boxes placed in trees or telephone poles, or in association with lesser kestrel colonies, where up to 4 breeding pairs per colony may occur (Catry et al. 2015).

4.4 MIXED-SPECIES COLONIES

Lack of natural nest-sites and large-scale provisioning of artificial ones attracted other species besides lesser kestrels and rollers, including both obligatory and non-obligatory cavity nesters, often forming mixed-species colonies at high breeding densities (Catry & Catry 2019) (Fig. 1.5). These include common kestrels *Falco tinnunculus,* barn owls *Tyto alba*, little owls *Athene noctua*, jackdaws *Corvus monedula*, spotless starlings *Sturnus unicolor*, and feral pigeons *Columba livia* (Fig. 1.6). All these species are resident and common throughout the Portuguese mainland and have favourable conservation status (Equipa Atlas, 2008). Common kestrels, little owls and barn owls are generally solitary breeders, while jackdaws, pigeons and starlings usually form aggregations. Although they vary in their reliance on cavities for nesting, all five species can be found nesting on rural traditional buildings in the area and promptly occupy all types of artificial nests (Catry & Catry 2019). Larger breeding structures, particularly breeding walls and towers, have high nest-site densities – up to 2-3 nests/m^2 – and usually host up to 40 breeding pairs of lesser kestrels, 15-30 pairs of starlings, some (1-10) pairs of jackdaws and pigeons, one to four pairs of common kestrel and rollers, and no more than one pair of barn owl and/or little owl (Catry & Catry 2019).

Figure 1.5: Typical landscape at the Castro Verde Special Protection Area, including an artificial breeding wall built for recovering the population of lesser kestrels *Falco naumanni*.

All species in these aggregations (including lesser kestrels and rollers) often coincide in their breeding phenology and chick rearing period, and hunt mostly in the vicinity of the colonies (Soler 1988; Johnson & Janiga 1995; Casagrande et al. 2008; Carrilo & González-Davila 2009; Šalek & Lövy 2012; Catry et al. 2013; Muriel et al. 2013; Chauson et al. 2014; Catry et al. 2017). Furthermore, their dietary habits suggest they may feed on similar resources, particularly large arthropods such as beetles or grasshoppers (Jaksić et al. 1982; Motis et al. 1997; Tomé et al. 2008; Catry et al. 2016; Orihuela-Torres et al. 2017; Catry et al. 2019). Niche similarity among these species likely potentiates the benefits, but also the costs, of mixed-species aggregations (Sridhar & Guttal 2018; Goodale et al. 2020). Recent work by Catry & Catry

(2019) revealed agonistic interspecific interactions, including interference competition and predation, among most of the species in these assemblages, likely driven by competition for nest or food resources (Fig. 1.7). However, more research is required to better understand how these new mixed-species aggregations may affect the effectiveness of the conservation actions targeting lesser kestrels and rollers.

Figure 1.6: Species usually present in the studied mixed colonies: common kestrel (A), barn owl (B), little owl (C), jackdaw (D), starling (E), and pigeon (F). Photos in C, E, and F, taken and generously provided by Inês Catry.

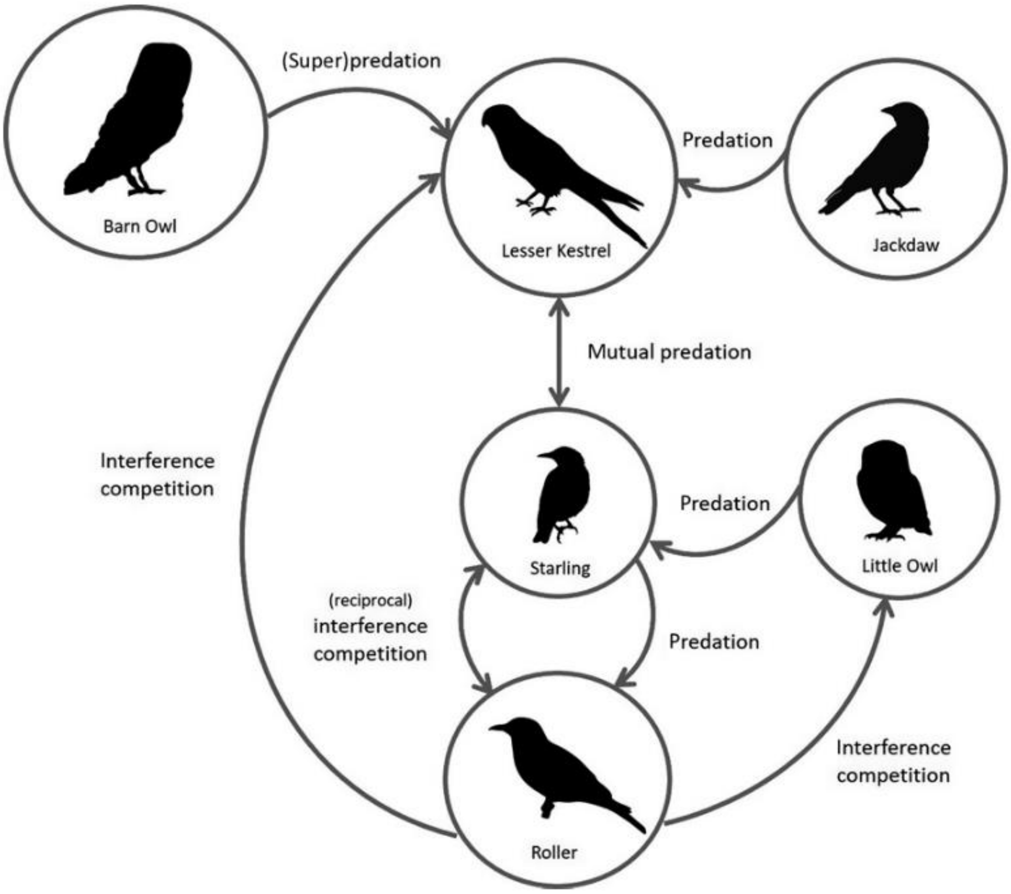


Figure 1.7: Agonistic interspecific interactions (predation and competition-driven) in mixed-species colonies established in artificial nesting structures provide in the scope of conservation projects. Extracted from "Nest-site provisioning re-shapes species interactions within bird assemblages" (Catry & Catry 2019; Ibis 161: 699-704; doi 10.1111/ibi.12731).

5. THESIS AIMS AND OUTLINE

In the Castro Verde SPA, large-scale nest provisioning, aimed at recovering lesser kestrels, attracted several other species and resulted in the formation of mixed-species colonies. While this enabled a remarkable recovery of the Portuguese populations of lesser kestrels and rollers, it is not known if these new bird assemblages will affect the long-term viability of these two species, through group related costs and benefits. These mixed-species colonies create very good opportunities to understand how changes in the nesting landscapes, through nest-site provisioning, re-shape the community and functioning of communities and promote the establishment of new interspecific interactions (Catry & Catry 2019) (Fig. 1.7).

The main objective of this thesis is to examine how costs and benefits typically associated with group living may affect the long-term persistence of these mixed-species colonies, and how these consequences may modify the effectiveness of the conservation measures targeted at lesser kestrels and rollers, two steppe bird species of conservation concern that contributed for the designation of the area as a Special Protected Area. Implications of this research is transferable not only to other conservation projects based on nest-provisioning, but also any human or climate-mediated alteration to the availability and distribution of resources that can modify the structure and dynamic of communities (Ockendon et al. 2014; Teckentrup et al. 2019).

This thesis includes four chapters, each addressing a different consequence of mixed-species aggregations through a corresponding research manuscript:

- **Chapter 2**: Long-term persistence of conservation-reliant species: challenges and opportunities;
- **Chapter 3**: Influence of colony traits on ectoparasite infestation in birds breeding in mixed-species colonies;
- **Chapter 4**: High trophic overlap in a bird community established in an artificial nesting landscape: implications for conservation;
- **Chapter 5**: Is it better to be solitary or breed in heterospecific colonies? Assessing anti-predatory benefits for a solitary bird.

Chapter 2 aims at examining whether lesser kestrels and rollers are becoming fully reliant on conservation actions such as nest-site provisioning. By visiting all more than 400 human-made rural structures in the Castro Verde SPA, it describes the current population size and trends of both species in the area, evaluates the decay of traditional adobe buildings, and estimates the conservation costs required for maintaining current population levels in the area. The results achieved in this chapter are used to highlight the challenges, but also opportunities, of having species fully reliant on artificial nest-sites, and to provide recommendations on how to secure their long-term persistence using sustainable funding sources. **Chapter 3**, **4**, and **5**, address three of the main factors commonly influenced by group living: parasitism, competition for food resources, and predation. **Chapter 3** explores the influence of multi-specific aggregations on ectoparasite prevalence and abundance. Generally, parasite burden is expected to increase with increasing group size or density, as the direct contact between individuals increases, but most studies have addressed only single-species groups, and whether the presence of other species alters parasite-host relationships has not been assessed so far. This chapter uses more than 250 nests from four different species of hosts: lesser kestres, rollers, starlings, and pigeons – to measure the influence of colony size, density, host richness, and composition, on the prevalence of four groups of ectoparasites, and on the abundance of a generalist blood-sucking fly parasitising a wide range of species. The results obtained on this chapter challenge the current knowledge on the ecological relationship between parasitism and host sociality. **Chapter 4** focuses on inter- and intraspecific competition among species breeding in these mixed-species colonies, using Stable Isotope Analysis. Species with similar ecological niches are expected to compete for the same resources, which should limit their coexistence in high-density breeding sites. Stable isotope ratios of 148 feather samples from nestlings and 38 blood samples from parent-offspring pairs from six different species: lesser kestrels, rollers, common kestrels, barn owls, little owls, and starlings – are used to assess trophic niche segregation among species, and within species between parents and their offspring. The results obtained in this chapter highlight the need to consider sympatric species and their ecological requirements when designing conservation actions. **Chapter 5** investigates whether the roller, a solitary breeding species, acquire anti-predatory benefits from breeding in mixed-species groups. Groups are considered more conspicuous but increase predator detection and deterrence while reducing individual investment in vigilance or mobbing. Using monitoring data from near 300 roller breeding attempts and behavioural experiments on 108 roller pairs, it compares the reproductive biology, nest predation rate, and risk-taking behaviour between solitary rollers and rollers nesting within mixed-colonies. This chapter provides one of the few known examples of how grouping with heterospecifics may shape the behaviour and life-history traits of a solitary breeding species. This thesis ends with a general discussion of the overall findings and their implications for the conservation of lesser kestrels and rollers. As previously mentioned, some chapters capitalize on long-term monitoring data (collected mostly by Inês Catry, this work's main supervisor), to help to support some of the questions and findings addressed here, which would not be possible by only using the data collected during this thesis' period.

6. REFERENCES

Altizer, S., Nunn, C.L., Thrall, P.H., Gitttleman, J.L., Antonovics, J., Cunningham, A.A., Dobson, A.P., Ezenwa, V., Jones, K.E., Pederse, A.B., Poss, M., Pulliam, J.R.C., 2003. Social organization and parasite risk in mammals: integrating theory and empirical studies. Annual Reviews of Ecology, Evolution, and Systematics 34: 517-547. https://doi.org/10.1146/annurev.ecolsys.34.030102.151725.

Arneberg, P., 2002. Host population density and body mass as determinants of species richness in parasite communities: comparative analyses of directely transmitted nematodes of mammals. Ecog-raphy, 25: 88-94.

Arroyo, B.E., García, J.T., 2002. Alloparental care and kleptoparasitism in the semicolonial Montagu's harrier Circus pygargus. Ibis 144: 676-679. https://doi.org/10.1046/j.1474-919X.2002.00083.x.

Arroyo, B., Mougeot, F., 2001. Colonial breeding and nest defence in Montagu's harrier (Circus pygargus). Behavioral Ecology and Sociobiology 50: 109-115. https://doi.org/10.1007/s002650100342.

Avilés, J.M., Parejo, D., 2002. Diet and prey type selection by Rollers Coracias garrulus during the breeding season in southwest of the Iberian Peninsula. Alauda 66: 313–314.

Baily, I., Myatt, J.P., Wilson, A.M., 2013. Group hunting within the carnivora: physiological, cognitive and environmental in-fluences on strategy and cooperation. Behavioural Ecology and Sociobiology 67, 1-17. https://doi.org/10.1007/s00265-012-1423-3.

Banks, S.C., Piggot, M.P., Stow, A.J., Taylor, A.C., 2007. Sex and sociality in a disconnected world: a review of the impacts of habitat fragmentation on animal social interactions. Canadian Journal of Zoology 85: 1065-1079. https://doi.org/10.1139/Z07-094.

Battin, J., 2004. When good animals love bad habitats: ecological traps and conservation of animal populations. Conservation Biology 18 (6): 1492-1491. https://doi.org/10.1113/jphysiol.1956.sp005637.

Beauchamp, G., 2008. What is the magnitude of the group-size effect on vigilance? Behavioral Ecology 19: 1361-1368. https://doi.org/10.1093/beheco/arn096.

Beldomenico, P.M., Begon, M., 2010. Disease spread, susceptibility and infection intensity: vicious circles? Trends in Ecology and Evolution 25, 21–27. https://doi.org/10.1016/j.tree.2009.06.015.

Beyer, G.L., Goldingay, R.L., 2006. The value of nest boxes in the research and management of Australian hollow-using arboreal marsupials. Wildlife Research 33: 161–174. https://doi.org/10.1071/WR04109.

Bideguren, G.M., López-Baucells, A., Puig-Montserrat, X., Mas, M., Porres, X., Flaquer, C., 2019. Bat boxes and climate change: testing the risk of over-heating in the Mediterranean region. Biodiversity and Conservation 28: 21-35. https://doi.org/10.1007/s10531-018-1634-7.

Bijleveld, A.I., Egas, M., van Gils, J.A., Piersma, T., 2010. Beyond the information centre hypothesis: communal roosting for information on food, predators, travel companions and mates? Oikos 119: 277-285. https://doi.org/10.1111/j.1600-0706.2009.17892.x.

BirdLife International, 2021. IUCN Red List for birds. Downloaded from http://www.birdlife.org on 20/06/2021.

Birt, V.L., Birt, T.P., Goulet, D., Cairns, D.K., Montevecchi, W.A., 1987. Ashmole’s Halo: direct evidence for prey depletion by a seabird. Marine Ecology (Progress Series) 40: 205-208.

Blicharska, M., Orlikowska, E.H., Roberge, J.M., Grodzinska-Jurczak, M., 2016. Contribution of social science to large scale biodiversity conservation: a review of research about the Natura 2000 network. Biological Conservation 199: 110–122. https://doi. org/10.1016/j.biocon.2016.05.007.

Bolton, M., Medeiros, R., Hothersall, B., Campos, A., 2004. The use of artificial breeding chambers as a conservation measure for cavity-nesting rocellariiform seabirds: a case study of the Madeiran storm petrel (Oceanodroma castro). Biiological Conservation116: 73-80. https://doi.org/10.1016/S0006-3207(03)00178-2.

Bonal, R., Aparicio, J.M., 2008. Evidence of prey depletion around lesser kestrel Falco naumanni colonies and its short term negative consequences. Journal of Avian Biology 39 (2): 189-197. https://doi.org/10.1111/j.2008.0908-8857.04125.x.

Botero-Delgadillo, E., Poblete, Y., Vásquez, R.A., 2015. Nestling mortality as a consequence of interspecific competition between secondary cavity nesters in the sub-Antarctic forests of Chile. The Wilson Journal of Ornithology 127 (1): 131-134. https://doi.org/10.1676/14-073.1.

Boulay, J., Aubernon, C., Ruxton, G.D., Hédouin, V., Deneubourg, J.L., Charabidzé, D., 2017. Mixed-species aggregations in arthropods. Insect Science 26: 2-19. https://doi.org/10.1111/1744-7917.12502.

Bouvier, J.C., Muller, I., Génard, M., Lescourret, F., Lavigne, C., 2014. Nest-site landscape characteristics affect the distribution of breeding pairs of European rollers Coracias garrulus in an agricultural area of southeastern France. Acta Ornithologica 49: 23-32. https://doi.org/10.3161/000164514X682869.

Brown, C.R., Brown, M.B., 2004. Empirical measurement of parasite transmission between groups in a colonial bird. Ecology 86 (6): 1619-1626. https://doi.org/10.1890/03-0206.

Brown, C.R., Hoogland, J.L., 1986. Risk in mobbing for solitary and colonial swallows. Animal Behaviour 34: 1319-1323. https://doi.org/10.1016/S0003-3472(86)80203-2.

Brown, C.R., Roche, E.A., Brown, M.B., 2017. Why come back home? Breeding-site fidelity varies with group size and parasite load in colonial bird. Animal Behaviour 132: 167-180. https://doi.org/10.1016/j.anbehav.2017.08.009.

Bustamante, J., Molina, B., del Moral., J.C., 2020. El cernícalo primilla en España, población reproductora en 2016-18 y método de censo. SEO/BirdLife Madrid.

Butchart, S.H.M., Stattersfield, A.J., Collar, N.J., 2006. How many bird extinctions have we prevented? Oryx 40: 266–278. https://doi.org/10.1017/S0030605306000950.

Butchart, S.H.M., Walpole, M., Collen, B., Strien, A. van, Scharlemann, J.P.W., Almond, R.E.A., Baillie, J.E.M., Bomhard, B., Brown, C., Bruno, J., Carpenter, K.E., Carr, G.M., Chanson, J., Chenery, A.M., Csirke, J., Davidson, N.C., Dentener, F., Foster, M., Galli, A., Galloway, J.N., Genovesi, P., Gregory, R.D., Hockings, M., Kapos, V., Lamarque, J.-F., Leverington, F., Loh, J., McGeoch, M.A., McRae, L., Minasyan, A., Morcillo, M.H., Oldfield, T.E.E., Pauly, D., Quader, S., Revenga, C., Sauer, john R., Skolnik, B., Spear, D., Stanwell-Smith, D., Stuart, S.N., Symes, A., Tierney, M., Tyrrell, T.D., Vié, J.-C., Watson, R., 2010. Global biodiversity: indicators of recent declines. Science 328, 1164–1168. https://doi.org/10.1126/science.1187512.

Cabral, M.J., Almeida, J., Almeida, P.R., Dellinger, T., Ferrand de Almeida, N., Oliveira, M.E., Palmeirim, J.M., Queiroz, A.I., Rogado, L., Santos-Reis, M., 2005. Livro Vermelho dos Vertebrados de Portugal. Instituto da Conservacão da Natureza, Lisboa.

Campobello, D., Sarà, M., Hare, J.F., 2012. Under my wing: lesser kestrels and jackdaws derive reciprocal benefits in mixed-species colonies. Behavioural Ecology 23 (2), 425-433. https://doi.org/10.1093/beheco/arr207.

Cardador, L., Brotons, L., Mougeot, F., Giralt, D., Bota, G., Pomarol, M., Arroyo, B., 2015. Conservation traps and long-term species persistence in human-dominated systems. Conservation Letters 8: 456–462. https://doi.org/10.1111/conl.12160.

Cardinale, B.J., Duffy, J.E., Gonzales, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wadrle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S., Naeem, S., 2012. Biodiversity loss and its impact on humanity. Nature 486: 59–67. https://doi.org/10.1038/nature11148.

Carrilo, J., Gonzále-Dávila, E., 2009. Latitudinal variation in breeding parameters of the common kestrel Falco tinnunculus. Ardeola 56 (29): 215-228.

Casagrande, S., Nieder, L., Di Minin, E., La Fata, I., Csermely, D., 2008. Habitat utilization and prey selection of the kestrel Falco tinnunculus in relation to small mammal abundance. Italian Journal of Zoology 75 (4): 401-409. https://doi.org/10.1080/11250000802085526.

Catry, I., Alcazar, R., Franco, A.M.A., Sutherland, W.J., 2009. Identifying the effectiveness and constraints of conservation interventions: a case study of the endangered lesser kestrel. Biological Conservation 142: 2782–2791. https://doi.org/10.1016/j.biocon.2009.07. 011.

Catry, I., Catry, T., Patto, P., Franco, A.M.A., Moreira, F., 2015. Differential heat tolerance in nestlings suggests sympatric species may face different climate change risks. Climate Research 66: 13–24. https://doi.org/10.3354/cr01329.

Catry, I., Catry, T., Alho, M., Franco, A.M.A., Moreira, F., 2016, Sexual and parent-offspring dietary segregation in a colonial raptor as revealed by stable isotopes. Journal of Zoology 299(1): 58–67. https://doi.org/10.1111/jzo.12324.

Catry, I., Franco, A.M.A., Rocha, P., Alcazar, R., Reis, S., Cordeiro, A., Ventim, R., Teodósio, J., Moreira, F., 2013. Foraging habitat quality constrains effectiveness of artificial nest-site provisioning in reversing population declines in a colonial cavity nester. PLoS One 8: 1–10. https://doi.org/10.1371/journal.pone.0058320.

Catry, I., Marcelino, J., Franco, A.M.A., Moreira, F., 2017. Landscape determinants of European roller foraging habitat: implications for the definition of agri-environmental measures for species conservation. Biodiversity & Conservation 26: 553-566. https://doi.org/10.1007/s10531-016-1241-4.

Catry, I., Sampaio, A., Silva, M.C., Moreira, F., Franco, A.M.A., Catry, T., 2019. Combining stable isotope analysis and conventional techniques to improve knowledge of the diet of the European Roller Coracias garrulus. Ibis 161: 272-285. https://doi.org/10.1111/ibi.12625.

Catry, I., Silva, J.P., Cardoso, A., Martins, A., Delgado, A., Sanches, A.R., Santos, A., Estanque, B., Cruz, C.M., Pacheco, C., Leitão, D., Pereira, E., Matilde, E., Moital, F., Romba, F., Sequeira, N., Monteiro, P., Rocha, P., Correia, R., Alcazar, R., Cangarato, R., Heleno, R., Catry, T., Silva, T., Ferro, T., 2011. Distribution and population trends of the

European Roller in pseudo-steppe areas of Portugal: results from a census in sixteen SPAs and IBAs. Airo 21, 3-14.

Catry, T., Catry, I., 2019 Nest-site provisioning re-shapes species interactions within bird assemblages. Ibis 161: 699-704. https://doi.org/10.1111/ibi.12731.

CBD, 2010. COP Decision X/2. Strategic plan for bio- diversity 2011–2020. Available at www.cbd.int/decision/cop?id=12268. Accessed July 15, 2021.

Challender, D.W.S., MacMillan, D.C., 2014. Poachin is more than an enforcement problem. Conservation Letters 7(5): 484-494. https://doi.org/10.1111/conl.12082.

Chausson, A., Henry, I., Almasi, B., Roulin, A., 2014. Barn owl (Tyto alba) breeding biology in relation to breeding season climate. Journal of Ornithology 155: 273-281. https://doi.org/10.1007/s10336-013-1012-x.

Clayton, D.H., Koop, J.A.H., Harbison, C.W., Moyer, B.R., Bush, S.E., 2010. How birds combat ectoparasites. The Open Ornithology Journal 3: 41.71. https://doi.org/10.2174/1874453201003010041.

Clobert, J., le Galliard, J.F., Cote, J., Meylan, S., Massot, M., 2009. Informed dispersal, heterogeinity in animal dispersal syndromes and the dynamics of spatially structure populations. Ecology letters 12: 197-209. https://doi.org/10.1111/j.1461-0248.2008.01267.x.

Côté, I.M., Poulin R., 1995. Parasitism and group size in social animals: a meta-analysis. Behavioral Ecology 6 (2): 159-165. https://doi.org/10.1093/beheco/6.2.159.

Cowan, M.A., Dunlop, J.A., Turner, J.M., Mooer, H.A., Nimmo, D.G., 2020. Artificial refuges to combat habitat loss for an endangered marsupial predator: how to they measure up? Conservation Science and Practice 2 (6): e204. https://doi.org/10.1111/csp2.204.

Croose, E., Birks, J.D.S., Martin, J., 2016. Den boxes as a tool for pine marten Martes martes conservation and population monitoring in a commercial forest in Scotland. Conservation Evidence 13: 57-61.

Coulson, J.C., 1968. Differences in the quality of birds nesting in the centre and on the edges of a colony. Nature 217: 478-479.

Cramp, S., Simmons, K.E.L., 1980. The Birds of the Western Palearctic. Vol. II, Oxford University Press, Oxford.

Cramp, S., Simmons, K.E.L., 1988. The Birds of the Western Palearctic. Vol. V. Oxford University Press., Oxford.

Crowford, R.D., O'Reefe, J.M., 2021. Avoiding a conservation pitfall: considering the risks of unsuitably hot bat boxes. Conservation Science and Practice. https://doi.org/10.1111/csp2.412.

D'Aloia, C., Naujokaitis-Lewis, I., Blackford, C., Chu, C., Curtis, J.M.R., Darling, E., Guichard, F., Leroux, S.J., Martesen, A.C., Rayfield, B., Sunday, J.M., Xuereb, A., Fortin, M.J., 2019. Coupled networks of permanent protected areas and dynamic conservation areas for biodiversity conservation under climate change. Frontiers in Ecology and Evolution 7: 1-8. https://doi.org/10.3389/fevo.2019.00027.

Dalerum, F., Hellström, P., Miranda, M., Nyström, J., Ekenstedt, J., 2016. Network topology of stable isotope interactions in a sub-arctic raptor guild. Oecologia 182: 511-518. https://doi.org/10.1007/s00442-016-3658-6.

Danchin, E., Wagner, R., 1997. The evolution of coloniality: the emergence of new perspectives. Trends in Ecology and Evolution 12 (9): 342-347. https://doi.org/10.1016/S0169-5347(97)01124-5.

Dardenne, S., Ducatez, S., Cote, J., Poncin, P., Stevens, V.M., 2013. Neophobia and social tolerance are related to breeding group size in a semi-colonial bird. Behavioural Ecology and Sociobilogy 67: 1317-1327. https://doi.org/10.1007/s00265-013-1560-3.

del Hoyo, J., Elliott, A., Sargatal, J., 2001a. Handbook of the birds of the world, Vol 2. New World Vultures to Guineafowl. Lynx Edn, Barcelona.

del Hoyo, J., Elliott, A., Sargatal, J., 2001b. Handbook of the birds of the world, Vol 6. Mousebirds to Hornbills. Lynx Edn, Barcelona.

Donald, P.F., Green, R.E., Heath, M.F., 2001. Agricultural intensification and the collapse of Europe's farmland bird populations. Proceedings of the Royal Society B 268: 25-29. https://doi.org/10.1098/rspb.2000.1325.

Donazar, J.A., Negro, J.J., Hiraldo, F., Hiraldo, F., 1993. Foraging habitat selection, land-use changes and population decline in the lesser kestrel Falco naumanni. Journal of Applied Ecology 30: 515-522. https://doi.org/10.2307/2404191.

Downey, H., Amano, T., Cadotte, M., Cook, C.N., Cooke, S.J., Haddaway, N.R., Jones, J.P.G., Littlewood, N., Walsh, J.C., Abrahams, M.I., Adun, G., Akasaka, M., Alves, J.A., Antwis, R.E., Arellano, E.C., Axmacher, J., Barclay, H., Batty, L., Benítez-López, A., Bennets, J.R., Berg, M.J., Bertolino, S., Biggs, S., Bolam, F.C., Bray, T., Brook, B.W., Bull, J.W., Burivalova, Z., Cabeza, M., Chauvenet, A.L.M., Christie, A.P., Cole, L., Cotton, A.J., Cotton, S., Cousins, S.A.R., Craven, D., Cresswell, W., Cusack, J.J., Dalrymple, S.E., Davies, Z.G., Diaz, A., Dodd, J.A., Felton, A., Fleishman, E., Gardner, C.J., Garside, R., Ghoddousi, A., Gilroy, J.J., Gill, D.A., Gill, J.A., Glew, L., Grainger, M.J., Grass, A.A., Greshon, S., Gundry, J., Hart, T., Hopkins, C.R., Howe, C., Johnson, A., Jones, K.W., Jordan, N.R., Kadoya, T., Kerhoas, D., Koricheva, J., Lee, T.M., Lengyel, S., Livingstone, S.W., Lyons, A., McCabe, G., Millet, J., Strevens, C.M., Moolna, A., Mossman, H.L., Mukherjee, N., Muñoz-Sáez, Negroes, N., Norfolk, O., Osawa, T., Papworth, A., Park, J.J., Pellet, J., Phillot, A.D., Plotnik, J.M., Priatna, D., Ramos, A.G., Randall, N., Richards, R.M., Ritchie, E.G., Roberts, D.L., Rcha, R., Rodríguez, J.P., Sanderson, R., Sasaki, T., Savilaakso, S., Sayer, C., Sekercioglu, C., Senzaki, M., Smith, G., Smith, R.J., Soga, M., Soulsbury, C.D., Steer, M.D., Stewart, G., Thompson, S., Thronhill, I., Trevelyan, R.K., Usieta, H.O., 2021. Training future generations to deliver evidence-based conservation and ecosystem management. Ecological Solutions and Evidence 2: 212032. https://doi.org/10.1002/2688-8319.12032.

Drechsler, M., Eppink, F.V., Wätzold, F., 2011. Does proactive biodiversity conservation save costs? Biodiversity & Conservation. 20, 1045–1055. https://doi.org/10.1007/s10531- 011-0013-4.

Dueñas, M.A., Hemming, D.J., Roberts, A., Diaz-Soltero, H., 2021. The threat of invasive species to IUCN-listed critically endangered species: a systematic review. Global Ecology and Conservation 26: 301476. https://doi.org/10.1016/j.gecco.2021.e01476.

Dulle, H.I., Seif, S.S., Mungure, S.K., Kideghesho, J.R., 2020. Growing concern for the conservation of cavity-nesting birds outside protected areas: can artificial nest boxes be effective conservation tools? In Durrant, J., Martin, E.H., Melubo, K., Jensen, R.R., Hadfiled, L.A., Hardin, P.J., Weisler, L., eds. Protected Areas in Northern Tanzania. Geotechnologies and the Environment 22. Cham: Springer.

Dutour, M., Léna, J.P., Lengagne, T., 2017. Mobbing calls: a signal transcending species boundaries. Animal behaviour 131, 3-11. https://doi.org/10.1016/j.anbehav.2017.07.004.

Ellis, D.H., Bednarz, J.C., Smith, D.G., Flemming, S.P., 1993. Social foraging classes in raptorial birds: highly developed coop-erative hunting may be important for many raptors. Bioscience, 43(1): 14-20. https://doi.org/10.2307/1312102.

Equipa Atlas, 2008. Atlas das aves nidificantes em Portugal (1999-2005). Instituto da Conservação da Natureza e da Biodiversidade, Sociedade Portuguesa para o Estudo das Aves, Parque Natural da Madeira e Secretaria Regional do Ambiente e do Mar. Lisboa: Assírio e Alvim.

Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. Annual Reviews of Ecology, Evolution and Systematics 34: 487-515. https://doi.org/10.1146/annurev.ecolsys.34.011802.132419.

Fahrig, L., Rytwinski, T., 2009. Effects of roads on animal abundance: an empirical review and synthesis. Ecology and Society 14 (1).

Fauchald, P., Rødven, R., Bårdsen, B.J., Langeland, K., Tveraa, T., Yoccoz, N.G., Ims, R.A., 2007. Escaping parasitism in the selfish herd: age, size and density dependent warble fly infestation in reindeer. Oikos 116: 491-499. https://doi.org/10.1111/j.2006.0030-1299.15390.x.

Finch, T., Branston, C., Clewlow, H., Dunning, J., Franco, A.M.A., Račinskis, E., Schwartz, T., Butler, S.J., 2018. Context-dependent conservation of the cavity-nesting European roller. Ibis. https://doi.org/10.1111/ibi.12650.

Finch, T., Saunders., Avilés, J.M., Bermejo, A., Catry, I., de la Puente, J., Emmenegger, T., Mardega, I., Mayet, P., Parejo, D., Račinskis, E., Rodríguez-Ruiz, J., Sackl, P., Schwartz, T., Tiefenbach, M., Valera, F., Hewson, C., Franco, A., Butler, S.J., 2015. A pan-European, multipopulation assessment of migratory connectivity in a near-threatened migrant bird. Diversity and Distributions 21: 1051-1062. https://doi.org/10.1111/ddi.12345.

Fischer, J., Lindenmayer, D.B., 2007. Landscape modification and habitat fragmentation: a synthesis. Global ecology and Biogeography 16: 265-280. https://doi.org/10.1111/j.1466-8238.2006.00287.x.

Foden, W.B., Butchart, S.H.M., Stuart, S.N., Vié, J.C., Akçakaya, R., Angulo, A., deVantier, L.M., Gutsche, A., Turak, E., Cao, L., Donner, S.D., Katariya, V., Bernard, R., Holland, R.A., Hughes, A.F., O'Hanlon, S.E., Garnett, S.T., Şekercioğlu,Ç., Mace, G., 2013. Identifying the World's most climate change vulnerable species: a systematic trait-based assessment of all birds, amphibians and corals. PlosOne 8: e65427. https://doi.org/10.1371/journal.pone.0065427.

Franco, A.M.A., Marques, J.T., Sutherland, W.J., 2005. Is nest-site availability limiting lesser kestrel populations? A multiple scale approach. Ibis 147 (4): 657-666. https://doi.org/10.1111/j.1474-919x.2005.00437.x.

Franco, A.M.A., Sutherland, W.J., 2004. Modelling the foraging habitat selection of lesser kestrels: conservation implications of European Agricultural Policies. Biological Conservation 120: 63–74. https://doi.org/10.1016/j.biocon.2004.01.026.

Frid, A., Dill, L., 2002. Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology 6 (1): 11

Fudala, K., Bialik, R.J., 2020. Breeding colony Dynamics of southern elephant seals at Patelnia Point, King George Island, antarctica. Remote Sensing 12 (18): 2964. https://doi.org/10.3390/rs12182964.

Fuglie, K., 2021. Climate change upsets agriculture. Nature climate change 11: 294-295. https://doi.org/10.1038/s41558-021-01017-6.

Gagern, A., Schurg, T., Michiels, N.K., Schult, G., Sprenger, D., Anthes, N., 2008. Behavioural response to interference competition in a sessile suspension feeder. Marine Ecology – Progress Series 353: 131-135.

Gaglio, D., Sherley, R.B., Cook, T.R., Ryan, P.G., Flower, T., 2018. The costs of kleptoparasitism: a study of mixed-species seabird breeding colonies. Behavioural Ecology 29: 939–947. https://doi.org/10.1093/beheco/ary050.

Gameiro, J., Silva, J.P., Franco, A.M.A., Palmeirim, J.M., 2020. Effectiveness of the European Natura 2000 network at protecting western Europe’s agro-steppes. Biological Conservation 248: 108681. https://doi.org/10.1016/j.biocon.2020.108681.

García-Cruz, M.A., Lampo, M., Peñaloza, C.L., Kendall, W.L., Solé, G., Rodríguez-Clark, K.M., 2015. Population trends and survival of nesting green sea turtles Chelonia mydas on Aves Island, Venezuela. Endangered Species Research 29: 103-116. https://doi.org/10.3354/esr00695.

Garrido, J.R., & Fernandez-Cruz, M., 2003. Effects of power lines on a white stork Ciconia Ciconia population in central. Ardeola 50, 191-200. https://doi.org/10.3354/meps07204.

Gilroy, J.J., Sutherland, W.J., 2007. Beyond ecological traps: perceptual errors and undervalued resources. Trends in Ecology and Evolution 22 (7): 351-356. https://doi.org/10.1016/j.tree.2007.03.014.

Giraldeau, L.A., Soos, C., Beauchamp, G., 1994. A test of the producer-scrounger foraging game in captive flocks of spice finches, Loncbura punctulate. Behavioral Ecology and Sociobiology 34: 251-256.

Gobush, K.S., Mutayoba, B.M., Wasser, S.K., 2008. Long-term impacts of poaching on related-ness, stress physiology, and reproductive output of adult female African elephants. Conservation Biology 22 (6): 1590-1599. https://doi.org/10.1111/j.1523-1739.2008.01035.x.

Goldingay, R.L., 2017. Does nest box use reduce the fitness of a tree-cavity dependent mammal? Ecological Research 32: 495-502. https://doi.org/10.1007/s11284-017-1461-4.

Goodale, E., Beauchamp, G., 2010. The relationship between leadership and gregariousness in mixed-species bird flocks. Journal of avian biology 41: 99-103. https://doi.org/10.1111/j.1600-048X.2009.04828.x.

Goodale, E., Beauchamp, G., Magrath, R.D., Nieh, J.C., Ruxton, G.D., 2010. Interspecific information transfer influences animal community structure. Trends in ecology and Evolution 25 (6): 354-361. http://dx.doi.org/10.1016/j.tree.2010.01.002.

Goodale, E., Beauchamp, G., Ruxton, G.D., 2017. Mixed-Species Animal Groups: Behavior, Community Structure and Conservation. Academic Press, London.

Goodale, E., Ruxton, G.D., Beauchamp, G., 2019. Predator eavesdropping in a mixed-species environment: how prey species may use grouping, confusion, and the cocktail party effect to reduce predator detection. Frontiers in Ecology and Evolution 7, 1-9. https://doi.org/10.3389/fevo.2019.00141.

Goodale, E., Sridhar, H., Sieving, K.E., Bangal, P., Colorado Z., G.J., Farine, D.R., Heymann, E.W., Jones, H.H., Krams, I., Martínez, A., Montaño-Centellas, F., Muñoz, J., Srinivasan, U., Theo, A., Shanker, K., 2020. Mixed company: a framework for understanding the composition and organization of mixed-species animal groups. Biological Reviews 95: 889-910. https://doi.org/10.1111/brv.12591.

Goodenough, J., McGuire, B., Jakob, E., 2010. Perspectives on Animal Behaviour. Third Edition. USA: John Wiley & Sons.

Gottschalk, T.K., Ekschmitt, K., Wolters, V., 2011. Journal of Raptor Research 45 (1): 1-14. https://doi.org/10.3356/JRR-09-11.1.

Graham, K.F., Shutler, D., 2019. How robust are risk-taking associations in incubating birds? A test and a review. Behavioral Ecology and Sociobiology 73 (79). https://doi.org/10.1007/s00265-019-2692-x.

Guo, D., Ding, J., Liu, H., Zhou, L., Feng, J., Luo, B., Liu, Y., 2021. Social calls influence the foraging behavior in wild big-footed myotis. Frontiers in zoology 18. https://doi.org/10.1186/s12983-020-00384-8.

Hale, R., Coleman, R., Sievers, M., Brown, T.R., Swearer, S.E., 2018. Using conservation behavior to manage ecological traps for a threatened freshwater fish. Ecosphere 9 (8). https://doi.org/10.1002/ecs2.2381.

Hale, R., Swearer, S.E., 2017. When good animals love bad restored habitats: how maladaptive habitat selection can constrain restoration. Journal of Applied Ecology 54:1478–1486. https://doi.org/10.1111/1365-2664.12829.

Hamilton, W.D., 1971. Geometry for the selfish herd. Journal of theoretical Biology 31: 295-311. https://doi.org/10.1016/0022-5193(71)90189-5.

Harel, R., Spiegel, O., Getz, W.M., Nathan. R., 2017. Social foraging and individual consistency in following behaviour: testing the information centre hypothesis in free-ranging vultures. Proc. R. Soc. B284:20162654. http://dx.doi.org/10.1098/rspb.2016.2654.

Harper, M.J., McCarthy, M.A., van der Ree, R., 2005. The use of nest boxes in urban natural vegetation remnants by vertebrate fauna. Wildlife Research 32: 509-516. https://doi.org/10.1071/WR04106.

Harris, B.A., Poole, E.M., Braman, S.K., Pennisi, S.V., 2021- Consumer-ready insect hotels: an assessment of arthropod visitation and nesting success. Journal of entomological science 56 (2): 141-155. https://doi.org/10.18474/0749-8004-56.2.141.

Hass, C.C, Valenzuela, D., 2002. Anti-predator benefits of group living in white-nosed coatis (Nasua narica). Behavioral Ecology and Sociobiology 51: 570-578. https://doi.org/10.1007/s00265-002-0463-5.

Hernández-Pliego, J., Rodríguez, C., Bustamante, J., 2017. A few long versus many shorts foraging trips: different foraging strategies of lesser kestrel sexes during breeding. Movement Ecology 5 (8): 1-16.

Heymann, E.W., Buchanan-Smith, H.M., 2000. The behavioural ecology of mixed-species troops of callitrichine primates. Biological Reviews 75: 169-190. https://doi.org/10.1111/j.1469-185X.1999.tb00044.x.

Hoffman, M., Hilton-Taylor, C., Angulo, A., Böhm, M., Brooks, Thomas M., Butchart, Stuart H.M., Carpenter, Kent E., Chanson, J., Collen, B., Cox, N.A., Darwall, W.R.T., Dulvy, N.K., Harrison, L.R., Katariya, V., Pollock, C.M., Quader, S., Richman, N.I., Rodrigues, A.S.L., Tognelli, M.F., Vié, J.-C., Aguiar, J.M., Allen, D.J., Allen, G.R., Amori, G., Ananjeva, N.B., Andreone, F., Andrew, P., Ortiz, A.L.A., Baillie, J.E.M., Baldi, R., Bell, B.D., Biju, S.D., Bird, J.P., Black-Decima, P., Blanc, J.J., Bolaños, F., Bolivar-G., W., Burfield, I.J., Burton, J.A., Capper, D.R., Castro, F., Catullo, G., Cavanagh, R.D., Channing, A., Chao, N.L., Chenery, A.M., Chiozza, F., Clausnitzer, V., Collar, N.J., Collett, L.C., Collette, B.B., Ferandez, C.F.C., Craig, M.T., Crosby, M.J., Cumberlidge, N., Cuttelod, A., Derocher, A.E., Diesmos, A.C., Donaldson, J.S., Duckworth, J.W., Dutson, G., Dutta, S.K., Emslie, R.H., Farjon, A., Fowler, S., Freyhof, J., Garshelis, D.L., Gerlach, J., Gowler, D.J., Grant, T.D., Hammerson, G.A., Harris, R.B., Heaney, L.R., Hedges, S.B., Hero, J.-M., Hughes, B., Hussain, S.A., Icochea M., J., Inger, R.F., Ishii, N., Iskandar, D.T., Jenkins, R.K.B., Kaneko, Y., Kottelat, M., Kovacs, K.M., Kuzmin, S.L., La Marca, E., Lamoreux, J.F., Lau, M.W.N., Lavilla, E.O., Leus, K., Lewison, R.L., Lichtenstein, G., Livingstone, S.R., Lukoschek, V., Mallon, D.P., McGowan, P.J.K., McIvor, A., Moehlman, P.D., Molur, S., Alonso, A.M., Musick, J.A., Nowell, K., Nussbaum, R.A., Olech, W., Orlov, N.L., Papenfuss, T.J., Parra-Olea, G., Perrin, W.F., Polidoro, B.A., Pourkazemi, M., Racey, P.A., Ragle, J.S., Ram, M., Rathbun, G., Reynolds, R.P., Rhodin, A.G.J., Richards, S.J., Rodríguez, L.O., Ron, S.R., Rondinini, C., Rylands, A.B., Sadovy de Mitcheson, Y., Sanciangco, J.C., Sanders, K.L., Santos-Barrera, G., Schipper, J., Self-Sullivan, C., Shi, Y., Shoemaker, A., Short, F.T., Sillero-Zubiri, C., Silvano, D.L., Smith, K.G., Smith, A.T., Snoeks, J., Stattersfield, A.J., Symes, A.J., Taber, A.B., Talukdar, B.K., Temple, H.J., Timmins, R., Tobias, J.A., Tsytsulina, K., Tweddle, D., Ubeda, C., Valenti, S. V., van Dijk, P.P., Veiga, L.M., Veloso, A., Wege, D.C., Wilkinson, M., Williamson, E.A., Xie, F., Young, B.E., Akçakaya, H.R., Bennun, L., Blackburn, T.M., Boitani, L., Dublin, H.T., da Fonseca, G.A.B., Gascon, C., Lacher, T.E., Mace, G.M., Mainka, S.A., McNeely, J.A., Mittermeier, R.A., Reid, G.M., Rodriguez, J.P., Rosenberg, A.A., Samways, M.J., Smart, J., Stein, B.A., Stuart, S.N., 2010. The Impact of Conservation on the Status of the World’s Vertebrates. Science 330: 1503–1509. https://doi.org/10.1126/science.1194442.

Hoi, H., Krištofík, J., Darolová, A., Hoi, C., 2010. Are parasite intensity and related costs of the milichiid fly Carnus hemapterus related to host sociality? Journal of Ornithology 151: 907-913. https://doi.org/10.1007/s10336-010-0529-5.

Holt, R.D., Dobson, A.P., Begon, M., Bowers, R.G., Schauber, E.M., 2003. Parasite establishment in host communities. Ecology Letters 6: 837–842. https://doi.org/10.1046/j.1461-0248.2003.00501.x.

Horner, J.R., 1982. Evidence of colonial nesting and “site fidelity” among Ornithischian dinosaurs. Nature 297: 675-676.

Huchard, E., Cowlishaw, G., 2011. Female-female aggression around mating: An extra cost of sociality in a multimale primate society. Behavioral Ecology 22: 1003-1011. https://doi.org/10.1093/beheco/arr083.

Iñigo, A., Barov, B., 2010. Species Action Plan for the Lesser Kestrel Falco naumanni in the European Union. SEO/BirdLife and BirdLife International for the European Commission.

Isaac, J.L., Parsons, M., Goodman, B.A., 2008. How hot do nest boxes get in the tropics? A study of nest boxes for the endangered mahogany glider. Wildlife research 35 (5): 441-445. https://doi.org/10.1071/WR08016.

Jaksić, F.M., Seib, R.L., Herrera, C.M., 1982. Predation by the Barn owl (Tyto alba) in Mediterranean habitats of Chile, Spain and California; a comparative approach. American Midland Naturalis 107: 152–159. https://doi.org/10.1007/BF00545658.

James, A., Gaston, K.J., Balmford, A., 2001. Can we afford to conserve biodiversity? Bioscience 51: 43–52. https://doi.org/10.1641/0006-3568(2001)051[0043:cwatcb] 2.0.co;2.

Johnson, C.N., Balmford, A., Brook, B.W., Buettel, J.C., Galetti M., Guangchun, L., Wilmshurst, J.M., 2017. Biodiversity losses and conservation responses in the Anthropocene. Science 356: 270-275. https://doi.org/10.1126/science.aam9317.

Johnson, F.R., McNaughton, E.J., Shelley, C.D., Blumstein, D.T., 2003. Mechanisms of heterospecific recognition in avian mobbing calls. Australian Journal of Zoology 51, 577-585. https://doi.org/10.1071/ZO03031.

Johnston, R., Janiga, M., 1995. Feral Pigeons. New York, USA: Oxford University Press.

Jones, T.B., Patricke, S.C., Arnould, J.P.Y., Rodríguez-Malagón, M.A., Wells, M.R., Green, J.A., 2018. Evidence of sociality in the timing and location of foraging in a colonial seabird. Biology Letters 14. http://dx.doi.org/10.1098/rsbl.2018.0214.

Kappeler, P.M., Cremer, S. Nunn, C.L., 2015. Sociality and health: impacts of sociality on disease susceptibility and transmission in animal and human societies. Philosophical Transactions B 370,1–10. https://doi.org/10.1098/ rstb.2014.0116.

Klein, Á., Ngy, T., Csörgő, T., Mátics, R., 2007. Exerior nest-boxes may negatively affect barn owl Tyto alba survival: an ecological trap. Bird Conservation International 17 (3): 273-281. https://doi.org/10.1017/S0959270907000792.

Kiss, O., Tokody, B., 2017. Distribution, population changes and conservation of the European roller (Coracias garrulus) in Hungary. Aquila 124: 75-90.

Kovacs, A., Barov, B., Orhun, C, Gallo-Orsi, U., 2008. International Species Action Plan for the European Roller Coracias garrulus. Besenyotelek, Hungary.

Krams, I., Bērziņš, A., Krama, T. (2009). Group effect in nest defence behaviour of breeding pied flycatchers, Ficedula hypoleuca. Animal Behaviour 77, 513-517. https://doi.org/10.1016/j.anbehav.2008.11.007.

Krause, J., Ruxton, G.D., 2002. Living in groups. Oxford Series in Ecology and Evolution. Oxford, UK: Oxford University Press.

LaBarge, L.R., Allan, A.T.L., Berman, C.M., Hill, R.A., Margulis, S.W., 2021. Extent of threat detection depends on predator type and behavioral context in wild samango monkey groups. Behavioral Ecology and Sociobiology 71 (13). https://doi.org/10.1007/s00265-020-02959-1.

Lambrechts, M.M., Adriaensen, F., Ardia, D.R., Artemyev, A.V., Atiénzar, F., Bańbura, J., Barba, E., Bouvier, J.C., Camprodon, J., Cooper, C.B., Dawson, R.D., Eens, M., Eeva, T., Faivre, B., Garamszegi, L.Z., Goodenough, A.E., Gosler, A.G., Grégoire, A., Griffith, S.C., Gustafsson, L., Johnson, L.S., Kania, W., Keišs, Llambias, P.E., Mainwaring, M.C., Mänd, R., Massa, B., Mazgajski, T.D., Møller, Moreno, J., Naef-Daenzer, B., Nilsson, J.A., Norte, A.C., Orell, M., Otter, J.A., Park, C.R., Perrins, C.M., Pinowski, J., Porkert, J., Potti, J., Remes, V., Richner, H., Rytkønen, S., Shiao, M.T., Silverin, B., Slagsvold, T., Smith, H.G., Sorace, A., Stenning, M.J., Stewart, I., Thompson, C.F., Tryjanowski, P., Török, J., van Noordwijk, A.J., Winkler, D.W., Ziane, N., 2010. The design of artificial nestboxes for the study of secondary hole-nesting birds: a review of methodological inconsistencies and potential biases. Acta Ornithologica 45 81). https://doi.org/10.3161/000164510X516047.

Leadley, P. (2010). Biodiversity scenarios: projections of 21st century change in biodiversity, and associated ecosystem services: a technical report for the global biodiversity outlook 3 (No. 50). UNEP/Earthprint.

Lehtonen J., Jaatinen, K., 2016. Safety in numbers: the dilution effect and other drivers of group in the face of danger. Behavioral Ecology and Sociobiology 70: 449-458. https://doi.org/10.1007/s00265-016-2075-5.

Lewis, S., Sherratt, T.N., Hamer, K.C., Wanless, S., 2001. Evidence of intra-specific competition for food in a pelagic seabird. Nature 412: 816-819.

LIFE Imperial, 2020. Conservação da Águia-imperial-ibérica (Aquila adalberti) em Portugal - Plano de conservação Pós-LIFE. LPN, Castro Verde, 26pp.

Lima, S.I., Dill, L.M., 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68 (4): 619-640. https://doi.org/10.1139/z90-092.

Lindenmayer, D., Crane, M., Blanchart, W., Okada, S., Montague-Drake, R., 2016. Do nest boxes in restored woodlands promote the conservation of hollow-dependent fauna? Restoration Ecology 24 (2): 244-251. https://doi.org/10.1111/rec.12306.

Lindenmayer, D.B., Welsh, A., Donnelly, C., Crane, M., Michael, D., Macgregor, C., McBurney, L., Montague-Drake, R., Gibbons, P., 2009. Are nest boxes a viable alternative source of cavities for hollow-dependent animals? Long-term monitoring of nest box occupancy, pest use and attrition. Biological Conservation 142: 33-42. https://doi.org/10.1016/j.biocon.2008.09.026.

Liu, M., Chan, S.F., Rubenstein, D.R., Sun, S.J., Chen, B.F., Shen, S.F., 2020. Ecological transitions in grouping benefits explains the paradox of environmental quality and sociality. The American Naturalist 195 (5): 818-832. https://doi.org/10.1086/708185.

Loretto, D., Vieira, M.V., 2011. Artificial nests as an alternative to studies of arboreal small mammal populations: a five-year study in the Atlantic forest, brazil. Zoologia (Curitiba) 28 (3). https://doi.org/10.1590/S1984-46702011000300013.

Lourenço, S.I., Palmeirim, J.M., 2007. Can mite parasitism affect the condition of bat hosts? Implications for the social structure of colonial bats. Journal of Zoology 272: 161-168. https://doi.org/10.1111/j.1469-7998.2007.00322.x.

Lucatelli, J., Mariano-Neto, E., Japyassú, H.F., 2021. Social interaction, and not group size, predicts parasite burden in mammals. Evolutionary Ecology 35: 115-130. https://doi.org/10.1007/s10682-020-10086-6.

Madden, K.K., Rozhon, G.C., Dwyer, J.F., 2019. Conservation Letter: Raptor persecution. Journal of raptor research 53 (2): 230-233. https://doi.org/10.3356/JRR-18-37.

Machač, O., Tuf, H., 2021. Ornithologist’s help to spiders: factors influencing spiders overwintering in bird nesting boxes. Insects 12 (5) 465. https://doi.org/10.3390/insects12050465.

MacNulty, D.R., Tallian, A, Stahler, D.R., Smith, D.W., 2014. Influence of group size on the success of wolves hunting bison. PlosOne 9 (11). https://doi.org/10.1371/journal.pone.0112884.

Mainwaring. M.C., 2011. The use of nestboxes by roosting birds during the non-breeding season: a review of the costs and benefits. Ardea 99 (2): 167-176. https://doi.org/10.5253/078.099.0206.

Mainwaring, M.C., 2015. The use of man-made structures as nesting sites by birds: A review of the costs and benefits. Journal for Nature Conservation 25: 17-22. http://dx.doi.org/10.1016/j.jnc.2015.02.007.

Mantyka-Pringle, C.S., Visconti, P., di Marco, M., Martin, T.G., Rondinini, C., Rhodes, J.R., 2015. Climate change modifies risk of global biodiversity loss due to land-cover change. Biological conservation 187: 103-111. https://doi.org/10.1016/j.biocon.2015.04.016.

Marcelino, J., Silva, J.P., Gameiro, J., Silva, A., Rego, F.C., Moreira, F., Catry, I., 2020. Extreme events are more likely to affect the breeding success of lesser kestrels than average climate change. Scientific Reports 10:7207. https://doi.org/10.1038/s41598-020-64087-0.

Marino, A., 2010. Costs and benefits of sociality differ between female guanacos living in contrasting ecological conditions. Ethology 116: 999-1010. https://doi.org/10.1111/j.1439-0310.2010.01812.x.

Millennium Ecological Assessment, 2005. Ecosystems and Human Well-being: Biodiversity Synthesis. (Washington, DC, USA).

Miller, K.E., 2002. Nesting success of the great crested flycatcher in nest boxes and in tree cavities: are nest boxes safer from nest predation? Wilson Bulletin 114 (2): 179-185.

Mönkkönen, M., Forsman, J., Helle, P., 1996. Mixed-species foraging aggregations and heterospecific attraction in boreal communities. Oikos 77 (1): 127-136.

Moreira, F., Leitão, P.J., Morgado, R., Alcazar, R., Cardoso, A., Carrapato, C., Delgado, A., Geraldes, P., Gordinho, L., Henriques, I., Lecoq, M., Leitão, D., Marques, A.T., Pedroso, R., Prego, I., Reino, L., Rocha, P., Tomé, R., Osborne, P.E., 2007. Spatial distribution patterns, habitat correlates and population estimates of steppe birds in Castro Verde. Airo 17: 5–30.

Motis, A., Estrada, J., Oro, D., 1997. Nestling diet of the Spotless starling Sturnus unicolor and the European Starling Sturnus vulgaris in a sympatric breeding area. Ornis Fennica 74 (4): 179–185

Muriel, J., Pérez-Rodríguez, L., Puerta, M., Gil, D., 2013. Differential effects of yolk testosterone and adrostenedione in embryo development and nest- ling growth in the spotless starling (Sturnus unicolor). General and Comparative Endocrinology 194, 175–182. https://doi.org/10.1016/j.ygcen.2013.09.013.

Murthy, A., Sharma, M., Amith-Kumar, U.R., Isvaran, K., 2015. Groups constrain the use of risky habitat by individuals: a new cost to sociality. Animal Behaviour 113: 167-175. https://doi.org/10.1016/j.anbehav.2015.12.027.

Negro, J.J., Prenda, J., Ferrero, J.J., Rodríguez, A., Reig-Ferrer, A., 2020. A timeline for the urbanization of wild birds: the case of the lesser kestrel. Quaternary Science Reviews 249. https://doi.org/10.1016/j.quascirev.2020.106638.

Negro, J.J., de la Riva, M., Bustamante, J., 1991. Patterns of winter distribution and abundance of lesser kestrels (Falco naumanni) in Spain. Journal of Avian Research 25 (2): 30-35.

Newbold, T., Hudson, L.N., Arnell, A.P., Contu, S., de Palma, A., Ferrier, I., Hill, S.L.L., Hoskins, A.J., Lysenko, I., Phillips, H.R.P., Burton, V.J., Chng, C.W.T., Emerson, S., Gao, D., Pask-Hale, G., Hutton, J., Jung, M., Sanchez-Ortiz, K., Simmons, B.I., Whitmee, S., Zhang, H., Scharlemann, J., Purvis, A., 2016. Has land use pushed terrestrial biodiversity beyond the planetary boundary? A global assessment 353: 288-291. https://doi.org/10.1126/science.aaf2201.

Newton I. 1979. Population ecology of raptors. Berkhamsted, Poyser.

Newton, I., 1994. The role of nest sites in limiting the numbers of hole-nesting birds: a review. Biological Conservation 70: 265–276. https://doi.org/10.1016/0006-3207(94) 90172-4.

Newton, I., 1998. Population Limitation in Birds. Academic Press, London.

Olah, G., Vigo, G., Heinsohn, R., Brightsmith, D.J., 2014. Journal for Natura Conservation 22 (2): 176-185. https://doi.org/10.1016/j.jnc.2013.11.003.

Niemi, G.J., McDonald, M.E., 2004. Application of Ecological Indicators. Annual Review of Ecology, Evolution, and Systematics 35: 8-111. https://doi.org/10.1146/annurev.ecolsys.35.112202.130132.

Ockedendon, N., Baker, D.J., Carr, J.A., White, E.C., Almond, R.E.A., Amano, T., Bertram, E., Bradbury, R.B., Bradley, C., Butchart, S.H.M., Doswald, N., Foden, W., Gill, D.J.C., Green, R.E., Sutherland, W.J., Tanner, E.V.J., Pearce-Higgins, J.W., 2014. Mechanisms underpinning climatic impacts on natural populations: altered species interactions are more important than direct effects. Global Change Biology 20: 2221-2229. https://doi.org/10.1111/gcb.12559.

Orihuela-Torres, A., Perales, P., Rosado, D., Pérez-García, J.M., 2017. Feeding ecology of the Common Kestrel Falco tinnunculus in the south of Alicante (SE Spain). Revista Catalana d'Ornitologia 33: 10–16.

Orlikowska, E.H., Roberge, J.M., Blicharska, M., Mikusiński, G., 2016. Gaps in ecological research on the world's largest internationally coordinated network of protected areas: a review of Natura 2000. Biological Conservation 200: 216–227. https://doi.org/10. 1016/j.biocon.2016.06.015.

Ortiz, S.T., Stedt, J., Midtiby, H.S., Egenmose, H.D., Wahlber, M., 2021. Group hunting in harbour porpoises (Phocoena phocoena). Canadian Journal of Zoology 99, 511-520. https://doi.org/10.1139/cjz-2020-0289.

Pacifici, M., Foden, W.B., Visconti, P., Watson, J.E.M., Butchart, S.H.M., Kovacs, K.M., Scheffers, B.R., Hole, D.G., Martin, T.G., Akçakaya, H.R., Corlett, R.T., Huntley, B., Bickford, D., Carr, J.A., Hoffmann, A.A., Midgley, G.F., Pearce-Kelly, P., Pearson, R.G., Williams, S.E., Willis, S.G., Young, B., Rondonini, C., 2015. Assessing species vulnerability to climate change. Nature Climate Change 5: 215-224. https://doi.org/10.1038/nclimate2448.

Palacín, C., Alonso, J.C., 2018. Failure of EU Biodiversity Strategy in Mediterranean farmland protected areas. Journal for Nature Conservation 42: 62-66. https://doi.org/10.1016/j.jnc.2018.02.008.

Papageorgiou, D., Farine, D.R., 2021. Multilevel societies in birds. Trends in Ecology and Evolution 36: 15-17. https://doi.org/10.1016/j.tree.2020.10.008.

Paterson, J.E., Steinberg, B.D., Litsgus, J.D., 2013. Not just any old pile of dirt: evaluating the use of artificial nesting mounds as conservation tools for freshwater turtles. Oryx 47 (4): 607-6017. https://doi.org/10.1017/S0030605312000877.

Pichegru, L., 2013. Increasing breeding success of an endangered penguin: artificial nests or culling predatory gulls? Bird Conservation international 23: 296-308. https://doi.org/10.1017/S0959270912000135.

Piontek, F., Drouet, L., Emmerling, J., Kompas, T., Méjean, A., Otto, C., Rising, J., Soergel, B., Taconet, N., Tavoni, M., 2021. Integrated perspectives on translating biophysical to economic impacts of climate change. Nature Climate Change 11: 563-572. https://doi.org/10.1038/s41558-021-01065-y.

Quinn, J.L., Ueta, M. 2008. Protective nesting associations in birds. Ibis 150, 146-167. https://doi.org/10.1111/j.1474-919X.2008.00823.x.

Ramsay, M.S., Morrison, B., Stead, S.M., 2020. Infanticide and partial cannibalism in free-ranging Coquerel's sifaka (Propithecus coquereli). Primates 61: 575-581. https://doi.org/10.1007/s10329-020-00828-z.

Rifkin, J.L., Nunn, C.L., Garamszegi, L.Z., 2012. Do animals living in larger groups experience greater parasitism? A meta-analysis. American Naturalist 180 (1): 70-82. https://doi.org/10.1086/666081.

Robertson, B.A., Hutto, R.L., 2006. A framework for under- standing ecological traps and an evaluation of existing evidence. Ecology 87: 1075–1085. https://doi.org/10.1890/0012-9658(2006)87[1075:AFFUET]2.0.CO;2.

Rolland, C., Danchin, E., de Frapoint, M., 1998. The evolution of coloniality in birds in relation to food, habitat, predation, and life-history traits: A comparative analysis. American Naturalist 151 (6): 514-529. https://doi.org/10.1086/286137.

Rodríguez, A., Alcaide, M., Negro, J.J., Pilard, P., 2011a. Using major histocompatibility complex markers to assign the geographic origin of migratory birds: Examples from the threatened lesser kestrel. Animal Conservation 14: 306–313. https://doi.org/10.1111/j.1469-1795.2010.00431.x.

Rodríguez, J., Avilés, J.M., Parejo, D., 2011b. The value of nestboxes in the conservation of Eurasian rollers Coracias garrulus in southern Spain. Ibis 153: 735-745. https://doi.org/10.1111/j.1474-919X.2011.01161.x.

Rodríguez, C., Tapia, L., Kieny, F., Bustamante, J., 2010. Temporal changes in lesser kestrel Falco naumanni diet during the breeding season in southern Spain. Journal of Raptor Research 44: 120–128. https://doi.org/10.3356/JRR-09-34.1.

Šalek, M., Lövy, M., 2012. Spatial ecology and habitat selection of little owl Athene noctua during the breeding season in central European farmland. Bird Conservation International 22: 328-338. https://doi.org/10.1017/S0959270911000268.

Sanz-Aguilar, A., Payo-Payo, A., Rotger, A., Yousfi, L., Moutallier, S., Beck, C., Dumarest, M., Igual, J.M., Miranda, M.A., Torres, M.V., Picorelli, V., Gamble, A., Boulinier, T., 2020. Infestation of small seabirds by Ornithodoros marittimus ticks: Effects on chick body condition, reproduction and associated infectious agents. Ticks and Tcik-borne Diseases 11: 101281. https://doi.org/10.1016/j.ttbdis.2019.101281.

Sarà, M., Bondi, S., Bermejo, A., Bourgeois, M., Bouzin, M., Bustamante, J., de la Puente, J., Evangelidis, A., Frassanito, A., Fulco, E., Giglio, G., Gradev, G., Griggio, M., López-Ricaurte, L., Kordopatis, P., Marin, S., Martínez, J., Mascara, R., Mellone, U., Pellegrino, S.C., Pilard, P., Podofilini, S., Romero, M., Gustin, M., Saulnier, N., Serra, L., Sfougaris, A., Urios, V., Visceglia, M., Vlachopoulos, K., Zanca, L., Cecere, J.G., Rubolini, D., 2019. Broad-front migration leads to strong migratory connectivity in the lesser kestrel (Falco naumanni). Journal of Biogeography 46 (12): 2663-2677. https://doi.org/10.1111/jbi.13713.

Scheffers, B.R., de Meester, L., Bridge, T.M.L., Hoffman, A.A., Pandolfi, J.M., Corlett, R.T., Butchart, S.H.M., Pearce-Kelly, P., Kovacs, K.M., Dudgeon, D., Pacifici, M., Rondinini, C., Foden, W.B., Martin, T.G., Mora, C., Bickford, D., Watson, J.E.M., 2016. The broad footprint of climate change from genes to biomes to people. Science 354: 6313. https://doi.org/10.1126/science.aaf7671.

Schlaepfer, M.A., Runge, M.C., Sherman, P., 2002. Ecological and evolutionary traps. Trends in Ecology and Evolution 17 (10): 474-480. https://doi.org/10.1016/S0169-5347(02)02580-6.

Schütz, D., Ocana, S.W., Maan, M.E., Taborsky, M., 2016. Sexual selection promotes colonial breeding in shell-brooding cichlid fish. Animal Behaviour 112: 153-162. https://doi.org/10.1016/j.anbehav.2015.11.022.

Scott, J.M., Goble, D.D., Haines, A.M., Wiens, J.A., Neel, M.C., 2010. Conservation-reliant species and the future of conservation. Conservation Letters 3, 91–97. https://doi.org/10.1111/j.1755-263X.2010.00096.x.

Seiler, N., Robbins, M.M., 2020. Using long-term ranging patterns to assess within-group and between-group competition in wild mountain gorillas. BMC Ecology 20. https://doi.org/10.1186/s12898-020-00306-6.

Semeniuk, C.A.D, Dill, L.M., 2006. Anti-predator benefits of mixed-species groups of cowtail stingrays (Pastinachus sephen) and whiprays (Himantura uarnak) at rest. Ethology 112, 33-43. https://doi.org/10.1111/j.1439-0310.2006.01108.x.

Seppänen, J.T., Forsman, J.T., Mönkkönen, M., Thomson, R.L., 2007. Social information use is a process across time, space, and ecology, reaching heterospecifics. Ecology 88 (7), 1622-1633. https://doi.org/10.1890/06-1757.1.

Severns, P.M., 2011. Habitat restoration facilitates an eco- logical trap for a locally rare, wetland- restricted butterfly. Insect Conservation and Diversity 4: 184–191. https://doi.org/10.1111/j.1752-4598.2010.00120.x.

Silva, J.P., Correia, R., Alonso, H., Martins, R.C., D'Amico, M., Delgado, A., Sampaio, H., Godinho, C., Moreira, F., 2018. EU protected area network did not prevent a country wide population decline in a threatened grassland bird. Peer J: 1–13. https://doi.org/10.7717/peerj.4284.

Silva, J.P., Palmeirim, J.M., Moreira, F., 2010. Higher breeding densities of the threatened little bustard Tetrax tetrax occur in larger grassland fields: implications for conservation. Biological Conservation 143: 2553–2558. https://doi.org/10.1016/j.biocon.2010.06.023.

Soares, F.C., Leal, A.I., Palmeirim, J.M., de Lima, R.F., 2021. Niche differences may reduce susceptibility to competition between native and non-native birds in oceanic islands. Diversity and Distributions 0: 1-12. https://doi.org/10.1111/ddi.13298.

Soler, M., 1988. Egg size variation in the Jackdaw Corvus monedula in Granada, Spain. Bird Study 35: 69-76. https://doi.org/10.1080/00063658809476981.

Sridhar, H., Beauchamp, G., Shanker, K., 2009. Why do bird participate in mixed-species foraging flocks? A large-scale synthesis. Animal Behaviour 78: 337-347. http://dx.doi.org/10.1016/j.anbehav.2009.05.008.

Sridhar, H., Guttal, V., 2018. Friendship across species borders: factors that facilitate and constrain heterospecific sociality. Philosophical Transactions B 373: 20170014. http://dx.doi.org/10.1098/rstb.2017.0014.

Stensland, E., Angerbjörn, A., Berggren, P., 2003. Mixed species groups in mammals. Mammal Review 33 (3): 205-223. https://doi.org/10.1046/j.1365-2907.2003.00022.x.

Stoate, C., Báldi, A., Beja, P., Boatman, N.D., Herzon, I., van Doorn, A., de Snoo, G.R., Rakosy, L., Ramwell, C., 2009. Ecological impacts of early 21st century agricultural change in Europe - a review. Journal of Environmental Managment 91: 22–46. https://doi.org/10.1016/j.jenvman.2009.07.005.

Stojanovic, D., Owens, G., Young, C.M., Alves, F., Heinsohn, R., 2021. Do nest boxes breed the target species or its competitors? A case study of a critically endangered bird. Restoration Ecology 29 (3). https://doi.org/10.1111/rec.13319.

Sutherland, W.J., Dicks, L.V., Ockendon, N., Petrovan, S.O., Smith, R.K., 2018. What Works in Conservation, Conservation Biology. Open Book Publishers, Cambridge. https://doi.org/10.11647/OBP.0131.

Tella, J.L., Forero, M.G., Hiraldo, F., Donázar, J.A., 1998. Conflicts between lesser kestrel conservation and European agricultural policies as identified by habitat use analyses. Conservation Biology 12 (3): 593-604. https://doi.org/10.1046/j.1523-1739.1998.96288.x.

Tittensor, D.P., Walpole, M., Hill, S.L.L., Boyce, D.G., Britten, G.L., Burgess, N.D., Butchart, S.H.M., Leadley, P.W., Regan, E.C., Alkemade, R., Baumung, R., Bellard, C., Bouwman, L., Bowles-Newark, N.J., Chenery, A.M., Cheung, W.W.L., Christensen, V., Cooper, H.D., Crowther, A.R., Dixon, M.J.R., Galli, A., Gaveau, V., Gregory, R.D., Gutierrez, N.L., Hirsch, T.L., Höft, R., Januchowski-Hartley, S.R., Karmann, M., Krug, C.B., Leverington, F.J., Loh, J., Lojenga, R.K., Malsch, K., Marques, A., Morgan, H.H.W., Mumby, P.J., Newbold, T., Noonan-Mooney, K., Pagad, S.N., Parks, B.C., Pereira, H.M., Robertson, I., Rondinini, C., Santini, L., Scharlemann, J.P.W., Schindler, S., Sumaila, U.R., The, L.S.L., van Kolck, J., Visconti, P., Ye, Y., 2014. A mid-term analysis of progress toward international biodiversity targets. Science 346 (6206): 241-244. https://doi.org/10.1126/science.1257484.

Tomé, R., Catry, P., Bloise, C., Korpimäki, E., 2008. Breeding density and sucess, and diet composition of little owls Athene noctua in steppe-like habitats in Portugal. Ornis Fennica 85: 22-32.

Traba, J., Morales, M.B., 2019. The decline of farmland birds in Spain is strongly associated to the loss of fallowland. Scientific Reports 9: 9473. https://doi.org/10.1038/s41598- 019-45854-0.

Traba, J., de la Morena, E.L.G., Morales, M.B., Suárez, F., 2007. Determining high value areas for steppe birds in Spain: hot spots, complementarity and the efficiency of protected areas.

Biodiversity and Conservation. 16: 3255–3275. https://doi.org/10.1007/ s10531-006-9138-2.

Tyack, P., Whitehead, H., 1982. Male competition in large groups of wintering humpback whales. Behaviour 83: 132-154.

UNESCO, 2019. Castro Verde Biosphere Reserve, Portugal. https://en.unesco.org/biosphere/eu-na/castro-verde. Assessed on 16 July, 2021.

United Nations 2015. Transforming our World: The 2030 Agenda for Sustainable Development. United Nations. https://sdgs.un.org/publications/transforming-our-world-2030-agenda-sustainable-development-17981. Assessed July 15, 2021.

Uetz, G.W., Boyle, J., Hiebert, C., Wilcox, R.S., 2002. Antipredator benefits of group living in colonial web-building spiders: the ‘early warning’ effect. Animal Behaviour 63: 445-452. https://doi.org/10.1006/anbe.2001.1918.

Valera, F., Casas-Crivillé, A., Hoi, H. 2003 Interspecific parasite exchange in a mixed colony of birds. Journal of Parasitology 89: 245–250. https://doi.org/10.1645/00223395(2003)089[0245:IPEIAM]2.0.CO;2.

Valera, F., Václav, R., Calero-Torralbo, M.A., Martínez, T., Veiga, J., 2019. Natural cavity restoration as na alternative to nest box supplementation. Restoration Ecology 27: 220-227. https://doi.org/10.1111/rec.12841.

Varela, S.A.M., 2007. Décider où et avec qui se reproduire? PhD thesis. Universite Pierre & Marie Curie, France.

Varela, S.A.M., Danchin, É., Wagner, R.H., 2007. Does predation select for or against avian coloniality? A comparative analysis. Journal of Evolutionary Biology 20: 1490-1503. https://doi.org/10.1111/j.1420-9101.2007.01334.x.

Veiga, J., Valera, F., 2020. Nest box location determines exposure of the host to ectoparasites. Avian Conservation and Ecology 15 (2): 11. https://doi.org/10.5751/ACE-01657-150211.

Vitousek, M.N., Adelman, J.S., Gregory, N.C., St Clair, J.J.H., 2007. Heterospecific alarm call recognition in a non-vocal reptile. Biology Letters 3: 632-634. https://doi.org/10.1098/rsbl.2007.0443.

Wagner, R.H., Danchin, E., Boulinier, T., Helfenstein F., 2000. Colonies as byproducts of commodity selection. Behavioral Ecology 11 (5): 572-573. https://doi.org/10.1093/beheco/11.5.572.

Waldron, A., Miller, D.C, Redding, D., Mooers, A., Kuhn, T.S., Nibbelink, N., Roberts, J.T., Tobias, J.A., Gittleman, J.L., 2017. Reductions in global biodiversity loss predicted from conservation spending. Nature 551: 364-367. https://doi.org/10.1038/nature24295.

Waldron, A., Mooers, A.O., Miller, D.C., Nibbelink, N., Redding, D., Kuhn, T.S., Roberts, J.T., Gittleman, J.L., 2013. Targeting global conservation funding to limit immediate biodiversity declines. PNAS 16 (29): 12144-12148. https://doi.org/10.1073/pnas.1221370110.

Walther, G.R., Post, R., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C, Fromentin, J.M., Hoegh-Guldber, O., Bairlein, F., 2002. Ecological responses to recent climate change. Nature 416: 389-395. https://doi.org/10.1038/416389a.

Ward, A., Webster, M., 2016. Sociality: The behaviour of Group-living animals. Switzerland Springer International Publishing.

Ward, P., Zahavi, A., 1973. The importance of certain assemblages of bird as “information centres” for food-finding. Ibis 115: 517-534

Watson, J.E.M., 2014. Human responses to climate change will seriously impact biodiversity conservation: it’s time we start planning for them. Conservation Letters 7: 1-2. https://doi.org/10.1111/conl.12083.

Wei, F., Swaisgood, R., Hu, Y., Nie., Y., Yan., L., Zhang, Z., Qi, D., Zhu, L., 2015. Progress in the ecology and conservation of giant pandas. Conservation Biology 29 (6): 1497-1507. https://doi.org/10.1111/cobi.12582.

Whiteman, N.K., parker, P.G., 2004. Effects of host sociality on ectoparasite population biology. Journal of Parasitology 90 (5): 939-947. https://doi.org/10.1645/GE-310R.

Wilson, S.N., Sindi, S.S., Brooks, H.Z., Hohn, M.E., Price, C.R., Radunskaya, A.E., Williams, N.D., Fefferman, N.H., 2020. How emergent social patterns in allogrooming combat parasite infections. Frontiers in Ecology and Evolution 31. https://doi.org/10.3389/fevo.2020.00054.

Winkler, K., Fuchs, R., Rounsevell, M., Herold, M., 2021. Global land use changes are four times greater than previously estimated. Nature Communications 12: 2501. https://doi.org/10.1038/s41467-021-22702-2.

Wittenberger, J.F., Hunt, G.L.J., 1985. The adaptive significance of coloniality in birds. In: Avian Biology (D.S. Farner, J.R. King, K.C. Parkes, eds.), pp. 1-78. Academic Press, New York.

WWF, 2020. Living Planet Report 2020 – Bending the curve of biodiversity loss. Almond, R.E.A., Grooten, M., Petersen, T. (eds). Gland, Switzerland: WWF.

Chapter 2

Long-term persistence of conservation reliant species: Challenges and opportunities

João Gameiro, Aldina M.A. Franco, Teresa Catry, Jorge M. Palmeirim & Inês Catry

Published in *Biological Conservation* (2020) DOI:10.1016/j.biocon.2020.108452

LONG-TERM PERSISTENCE OF CONSERVATION RELIANT SPECIES: CHALLENGES AND OPPORTUNITIES

ABSTRACT

"Conservation-reliant species" – those fully dependent on continued management actions – are booming and, with limited conservation budgets, securing funds to sustain their long-term viability is becoming overwhelming. This study assesses the degree of dependence on conservation actions of two obligatory cavity-nesters, the Lesser Kestrel *Falco naumanni* and the European Roller *Coracias garrulus,* whose populations in Europe were recently recovered through artificial nest-site provisioning. Using long-term monitoring data and population surveys conducted in their main Portuguese stronghold, we examined temporal changes in the availability and use of semi-natural (cavities in rural abandoned buildings) and artificial nest-sites. We further assessed the financial costs of nest-site provisioning and evaluated the potential use of tourism revenues as a conservation funding source. Following the implementation of conservation projects, the Lesser Kestrel and Roller populations have been increasing but > 65% of all breeding pairs currently nest in artificial nest-sites. Semi-natural nest-sites remain suitable for approximately 30 years and are expected to disappear by the end of this century. Lesser Kestrels and Rollers will thus become fully dependent on artificial nest-sites and sustaining their current population sizes is estimated to cost 4500€ per year. This represents < 1% of the region's lodging income, largely supported by nature-based tourism. Our findings suggest that reactive conservation measures can be very effective at recovering endangered populations but can make them fully reliant on the perpetuation of those measures. This demands long-term funding, which can be alleviated by tourism revenues in areas with high nature capital values.

Keywords: European roller; lesser kestrel; conservation; artificial nests; tourism; funding

1. INTRODUCTION

Human activities are transforming the face of the planet and causing dramatic changes to the distribution and abundance of wildlife species, mainly through habitat destruction and climate change (Pimm & Raven 2000; Sala et al. 2000). The decline of biodiversity detrimentally impacts ecosystems and the services they provide, which are essential to humans (Millenium Ecological Assessement 2005; Butchart et al. 2010; Cardinale et al. 2012; Barnosky et al. 2017). Increased recognition of the magnitude of human-mediated impacts on nature has prompted large-scale conservation efforts aiming at halting and reversing ongoing biodiversity loss, often incurring high financial costs (*e.g.*, USD 6 billion/year to manage protected areas; James et al. 2011; Butchart et al. 2006). Although conservation actions help prevent extinctions and improve population trends (Butchart et al. 2006; Rodrigues 2006; Hoffman et al. 2010), funds available are usually insufficient to offset the major drivers of extinction risk (Hoffman et al. 2010; Sebastián-González et al. 2011; Watson et al. 2014).

Often, priority is given to species and populations that are already highly endangered, focusing on reversing negative impacts in the short term (Drechsler et al. 2011; Cardador et al. 2015). Therefore, conservation approaches are often reactive rather than proactive. Generally, funding is constrained in time, limited to the duration of specific programs and/or achievement of successful results, and is then allocated to new conservation priorities (Scott et al. 2010). In the long-term, reactive conservation may be more expensive than a proactive approach (Drechsler et al. 2011) and can lead to conservation traps by promoting an unsustainable need to perpetuate the implementation of active conservation actions (Cardador et al. 2015). The number of "conservation-reliant species" – those requiring continued, long-term management actions and investment – is likely to increase, stretching even further the limited conservation budgets. Hence, cost-efficient actions that guarantee the economically sustainable conservation of threatened populations are urgently needed (Scott et al. 2010; Sebastián-González et al. 2011).

Conservation reliance may be particularly prevalent in human-dominated landscapes, where species have adapted to traditional human activities which have changed dramatically during the last century, the prime example being agriculture intensification (Green et al. 2005; Tilman et al. 2011). As a consequence of these changes, agricultural areas hold many endangered species, and birds associated with farmlands are among those declining the most (Fischer et al. 2010; Sodhi et al. 2010; Stanton et al. 2018; Socolar et al. 2019; Traba & Morales 2019). Agricultural and other human-dominated landscapes therefore have high levels of biodiversity, often establishing a strong natural and cultural heritage with high aesthetics, ecological and recreational values (Hartel et al. 2014; Schulp et al. 2019).

In areas with high biodiversity or recreational values, conservation programmes can be maintained by the financial income generated by tourism (Walpole & Leader-Williams 2002; Steven et al. 2013). Nature-based tourism, especially when paired with easy-to-see and charismatic species, has great potential to raise funds and awareness for conservation (Walpole & Leader-Williams 2002; Steven et al. 2013; Czajkowski et al. 2014). Revenues can be raised from accommodation, donations, or nature-related activities such as birdwatching. Worldwide, avitourism is a rapidly expanding subsector of the tourism industry and may foster sustainable tourism and nature conservation by reducing the need for external (*e.g.*, governmental) funding (Kiss 2004; Steven et al. 2013; Czajkowski et al. 2014).

The Lesser Kestrel (*Falco naumanni*) and the European Roller (*Coracias garrulus*, hereafter Roller) are two charismatic bird species and icons of nature conservation. Both species suffered major population declines in their European breeding ranges (ca. 46% in each decade since 1950s for Lesser Kestrels; 4-20% over three generations for Rollers) and were classified as “Vulnerable” and “Near Threatened, respectively, during the first decade of the twenty-first century (BirdLife International 2019). The observed declines triggered an increase in conservation efforts that contributed to remarkable recoveries in many European countries, with both species being downlisted to “Least Concern” (although some national populations are still declining; Bux et al. 2008; Kovacs et al. 2008; Catry et al. 2009; Rodríguez et al. 2011; Finch et al. 2018; BirdLife International 2019).

Like many bird populations in human-dominated landscapes, Lesser Kestrels and Rollers are limited by lack of suitable foraging and nesting resources and conservation strategies have focused on promoting environmentally friendly habitat management and nest-site provisioning (Newton 1998; Franco et al. 2005; Rodríguez et al. 2001; Catry et al. 2013; Finch et al. 2018). Being secondary cavity nesters, they are unable to excavate their own cavities and are thus particularly vulnerable to shortage of nest-sites. Compelling evidence has been found for the effectiveness of nest-site provisioning as a reactive conservation tool to increase population numbers of many endangered species (Newton 1994; Lambrechts et al. 2010; Mainwaring 2011; Sutherland et al. 2018). Whilst the quick success of artificial nest-site provisioning enabled the fast recovery of Lesser Kestrel and Roller populations throughout Europe, the long-term costs of increased dependency of conservation actions, essential for the persistence of these species, has never been evaluated.

In this study we assess the degree of dependence Lesser Kestrels and Rollers have on conservation actions and discuss evidence-based perspectives for their long-term conservation. Using long-term monitoring data, we estimate population trends of Portuguese Lesser Kestrels and Rollers, quantify their dependence on artificial nest-sites and understand temporal changes in the availability of semi-natural ones (cavities in rural abandoned buildings). We then calculate conservation costs associated with artificial nest-site provisioning and compare them with tourism revenues for the region. We aim at illustrating the potential challenges of relying on reactive approaches that may lead to conservation-reliant species, but also the opportunities that arise from tourism to create self-sustainable conservation strategies.

2. METHODS

2.1 STUDY AREA AND SPECIES

We focused our study in the Castro Verde Special Protection Area (SPA), located in southern Portugal (37°43′N, 7°57′W). With a total area of ca. 85 000 hectares, it is an important SPA for steppe birds at the European level and one of the main strongholds for several threatened farmland bird species in Western Europe (Moreira et al. 2007). Land use within the SPA has remained relatively stable in the last decades, in part due to the implementation of agri-environmental policy schemes and funding mechanisms that ensure high-quality foraging habitat for many farmland birds (Catry et al. 2013; Silva et al. 2018). This area harbours roughly 80% of the national breeding populations of Lesser Kestrels (418-436 pairs in 2007; Catry et al. 2009) and Rollers (52-55 pairs in 2009; Catry et al. 2011b), where both species have recently reversed declining population trends after the implementation of conservation programs (Catry et al. 2009; Catry et al. 2011b). Together with other key bird species (*e.g.*, Great Bustard (*Otis tarda*), Little Bustard (*Tetrax tetrax*), Black-bellied Sandgrouse (*Pterocles orientalis*), Iberian Imperial Eagle (*Aquila adalberti*)), Lesser Kestrels and Rollers are significant contributors to birdwatching and nature-related activities in the region.

Lesser Kestrels and Rollers are long-distance Afro-Palearctic migratory species (BirdLife International 2019) and opportunistic cavity nesters. The Lesser Kestrel – a cliff-nesting colonial raptor, benefited from the human occupancy of the landscape, both for foraging and breeding, nesting in isolated farmhouses or castles and churches in villages or towns and feeding on invertebrates in farmland areas (Catry et al. 2009). Rollers are solitary breeders, nesting in woodpecker cavities in trees or sandy banks, but can also occupy human buildings in southern latitudes, mainly where trees are lacking (Rodríguez et al. 2011). Most of the population of both species in the study area (around 300-400 and 40-50 breeding pairs of Lesser Kestrels and Rollers, respectively) have been annually monitored since 2000 by the authors and long-term demographic information (number of nests, eggs, chicks) is available.

2.1.1 SEMI-NATURAL AND ARTIFICIAL NEST-SITES

In the Castro Verde SPA, there are no records of birds breeding in the original natural nests (burrows in cliffs or hollows in trees). First known settlers nested in abandoned rural buildings (such as houses or farm sheds), traditionally built with adobe (a mixture of lime and mud) and Arabic tiles. After abandonment or lack of maintenance, these buildings decay due to the eroding action of wind and rain, leading to the formation of cavities in walls or under roof tiles, opportunistically used by both species to breed. Because these cavities are not true natural nests, we hereafter refer to them as semi-natural nest-sites. Contrarily to traditional buildings (built at least partially with adobe walls and Arabic tiles, thus potentially providing semi-natural nest-sites), new buildings are made with long lasting materials, such as bricks and concrete, that do not provide suitable cavities for nesting.

Since 1998, with the help of funding from European Union (EU) LIFE-nature conservation programmes, artificial nests have been provided to reverse declining population trends of both species (Catry et al. 2009, 2011b). New artificial nests include cavities in plastered walls (new cavities dug in existing traditional buildings that are then plastered), clay-pots and wooden nest-boxes in both traditional and new buildings, and newly built breeding walls and towers with up to 87 cavities each (Catry et al. 2009). In 2017, there were 944 artificial nest-sites available including 149 cavities in plastered walls, 663 in newly built breeding walls and towers, 65 clay-pots and 89 wooden nest-boxes. Lesser Kestrels and Rollers use all types of nests provided, can be often found in the same structures and can use the same nest-sites in alternate years (Catry et al. 2015).

2.2 SPECIES SURVEYS, POPULATION TRENDS AND OCCUPATION RATE OF ARTIFICIAL NEST-SITES

During the 2017 breeding season, the overall area to be prospected within the SPA included open/agricultural areas selected using the Corine Land Cover 2000 map. All human-made buildings (including traditional and new buildings: houses, farm sheds, churches, mills, ruins, etc) were selected from military maps at 1:25,000 scale. Buildings not reported in the military maps (*e.g.*, recent ones) but detected during fieldwork were also visited. Besides visiting buildings, all artificial nest-sites provided (including wooden nest-boxes attached to electric/telephone poles or trees) were checked for the presence of both species. Every structure was visited twice to increase the likelihood of species detection: the first visit took place between 24 April and 15 May and the second one between 16 May and 15 June. Whenever the presence of Lesser Kestrels and/or Rollers was confirmed in a structure, the number, location, and type of nests (semi-natural or artificial) was recorded. The second visit was made during the chick rearing period to confirm the number of breeding pairs (and control for late breeders or failed nesting attempts, for example), resulting in minimum and maximum estimates of breeding pairs per site. The estimated population size obtained in this survey, along with the proportion of pairs breeding in semi-natural and artificial nests, was then compared with past population censuses (Lesser Kestrel: 2003 to 2007, Catry et al. 2009; Rollers: 2004 and 2009, Catry et al. 2011b).

2.3 TEMPORAL CHANGES IN NEST-SITE AVAILABILITY

In traditional buildings holding Lesser Kestrel and Roller pairs, nest shortage is an increasing threat due to building collapse (structures are only maintained through frequent conservation interventions to secure walls and roof sections). Whilst longevity of traditional buildings is unknown, Catry et al. (2009) reported that 30% of roofs from buildings monitored for Lesser Kestrels collapsed within a 5-year period and 35% of buildings holding colonies were at high risk of collapse.

To understand how the suitability (for cavity nesters) of traditional buildings changes with time, we modelled the relationship between colony size (number of breeding pairs) and time (years) using a dataset from 14 buildings occupied by Lesser Kestrels and monitored for a period of 18 years (authors, unpublished data). Each building was classified according to its degradation level, and in some years, major walls or roofs collapse and colonies disappeared. Once a building is abandoned, we predict colony size will increase initially, as new nest-sites appear with the gradual degradation of the structure, but once a certain decay threshold is reached, the number of cavities declines and the structure begins to lose its nest-sites. We used a smoothing-splines mixed-effects model ('sme' package in R, Berk 2018) to assess changes in colony size along the building degradation process. This model uses smoothing-splines to adjust the relationship between colony size (in proportion to the maximum colony capacity) and time (years), using colony ID as a random factor (Berk 2018). The optimal model (with the correct level of smoothing) was selected according to the AIC.

Moreover, the number of future suitable traditional buildings for Lesser Kestrels and Rollers was estimated using a dataset of 175 randomly selected traditional buildings (corresponding to 56% of all traditional buildings in the area) for which suitability (presence or absence of available nest-sites) was assessed in 2008 and 2017. Buildings were considered suitable if they had at least one nest-site available (this was the only significant variable determining if a building can be used by kestrels and Rollers; see Appendix 2.1 for results on the logistic regression). Non-suitable buildings lack nest-sites and are generally inhabited by humans or in good conditions but may become suitable for nesting following decay. We quantified the number of buildings that became suitable (gained nest-sites following decay) and unsuitable (lost all nest-sites following structure restoration or collapse) from 2008 to 2017 and, assuming the rate of change between these years to be constant, determined the number of suitable buildings until the end of this century (using simple cross-multiplications).

2.4 FINANCIAL COSTS OF ARTIFICIAL NEST-SITES AND THE POTENTIAL CONTRIBUTION OF LOCAL TOURISM REVENUES

To estimate the funding required for the conservation of Lesser Kestrels and Rollers in the area, we calculated the costs associated with the provision of artificial nest-sites needed to sustain the current population size of both species (600 and 60 breeding pairs of Lesser Kestrels and Rollers, respectively), assuming the progressive disappearance of all semi-natural nest-sites (through the collapse of traditional buildings). We estimated the number and cost of nest-sites needed in each decade until the end of the century, maintaining the current proportions of each nest type (costs of each type of nest are presented in the Appendix 2.2). Calculations were made for all three types of artificial nest-sites found in the area – breeding walls, clay pots and wooden nest-boxes – considering the carrying capacity (number of pairs each structure can hold), estimated longevity, production costs and occupation rate (based on data from 2017). The longevity of wooden nest-boxes and clay pots was estimated based on their average observed longevity in the last 20 years, and concrete breeding walls were assumed to last up to 50 years. We only considered costs directly associated with the provisioning of nest-sites (material, labour, transportation). Maintenance of provided nests (cleaning nest-sites before and/or after each breeding season, adding substrate to the nest, or occasionally fixing or replacing lids) were not included in the estimated costs because they are marginal when compared to the overall costs (estimated at less than 5% of the yearly provisioning costs).

We explored if tourism revenues could contribute to fund the long-term persistence of Lesser Kestrels and Rollers in the Castro Verde SPA. Local, regional and national tourism growth rates were quantified for the period between 2001 – the year before the beginning of conservation projects in the area – and 2017. We used accommodation-related metrics as our measure of tourism. Number of guests, number of nights, and lodging income (total amount paid by guests for accommodation) were retrieved from the Portuguese National Institute of Statistics (INE, 2002, 2008). Albeit not a direct measure, accommodation related metrics are easy to interpret and thus a good indicator of tourism (Rodríguez-Rodríguez & López, 2019). We then compared the Castro Verde Lodging income with the total annual funding required to sustain the current populations of Lesser Kestrels and Rollers.

3. RESULTS

3.1 SPECIES SURVEYS, POPULATION TRENDS AND OCCUPATION OF ARTIFICIAL NEST-SITES

A total of 412 structures were surveyed in 2017 in the Castro Verde SPA, including 388 buildings, 11 breeding walls and 13 isolated wooden nest-boxes placed on electric poles or trees. Of all structures, 151 (37%) were suitable (with at least one suitable cavity) and 67 (16%) structures were occupied by Lesser Kestrels or Rollers (54 by Lesser Kestrels, 43 by Rollers).

Lesser Kestrel and Roller population sizes were estimated at 577-625 and 58-60 breeding pairs, respectively. Both species showed increasing population trends in the study area since 2004: Lesser Kestrels increased 177% and Rollers 166% (Fig. 2.1). Lesser Kestrel colony size ranged from 1 to 80 breeding-pairs and the number of Rollers nesting in the same structure varied from 1 to 3 pairs. The proportion of pairs occupying artificial nest-sites also increased substantially: in 2017, 68% of all Lesser Kestrels and 66% of all Rollers were nesting in artificial nests (Fig.

2.1). The most used artificial nest-sites were breeding walls and towers (Lesser Kestrels and Rollers) and wooden nest-boxes (Rollers) (Table 2.A3).

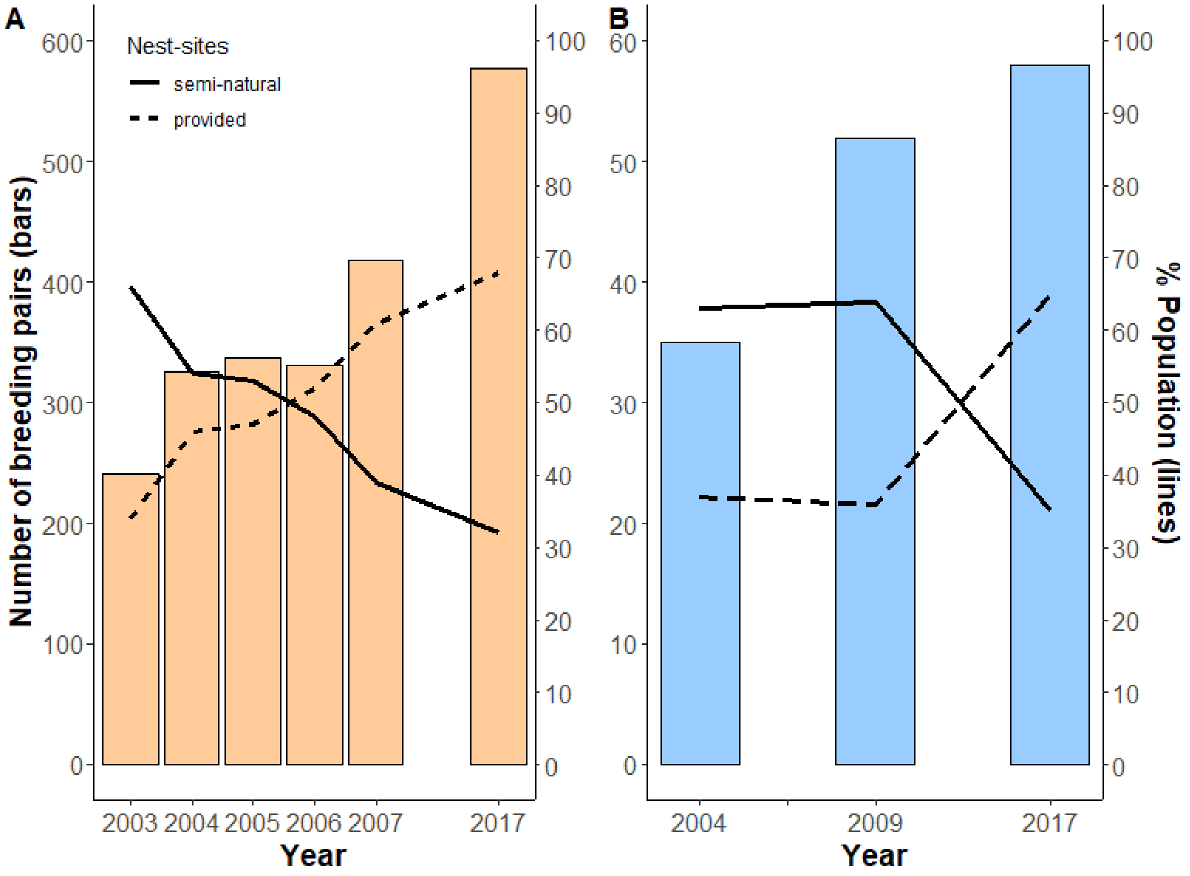


Figure 2.1: Population trends (bars) of (A) lesser kestrels and (B) European Rollers in the Castro Verde SPA, south Portugal (bars), and proportion of pairs occupying semi-natural(solid line) and artificial (dashed line) nest-sites. Presented values show minimum survey estimates.

3.2 TEMPORAL CHANGES IN NEST-SITE AVAILABILITY

Long-term data of Lesser Kestrels breeding in traditional, adobe-made, buildings suggest that these are ephemeral, hosting a Lesser Kestrel colony for an average of 30 years (Fig. 2.2). Initially, colonies grow as the structure progressively decays and offers more cavities, with the maximum number of pairs ca. 15 years after colonization. After that, the structure decays rapidly and the number of breeding pairs is reduced by 50% just five years after peaking (Fig. 2.2).

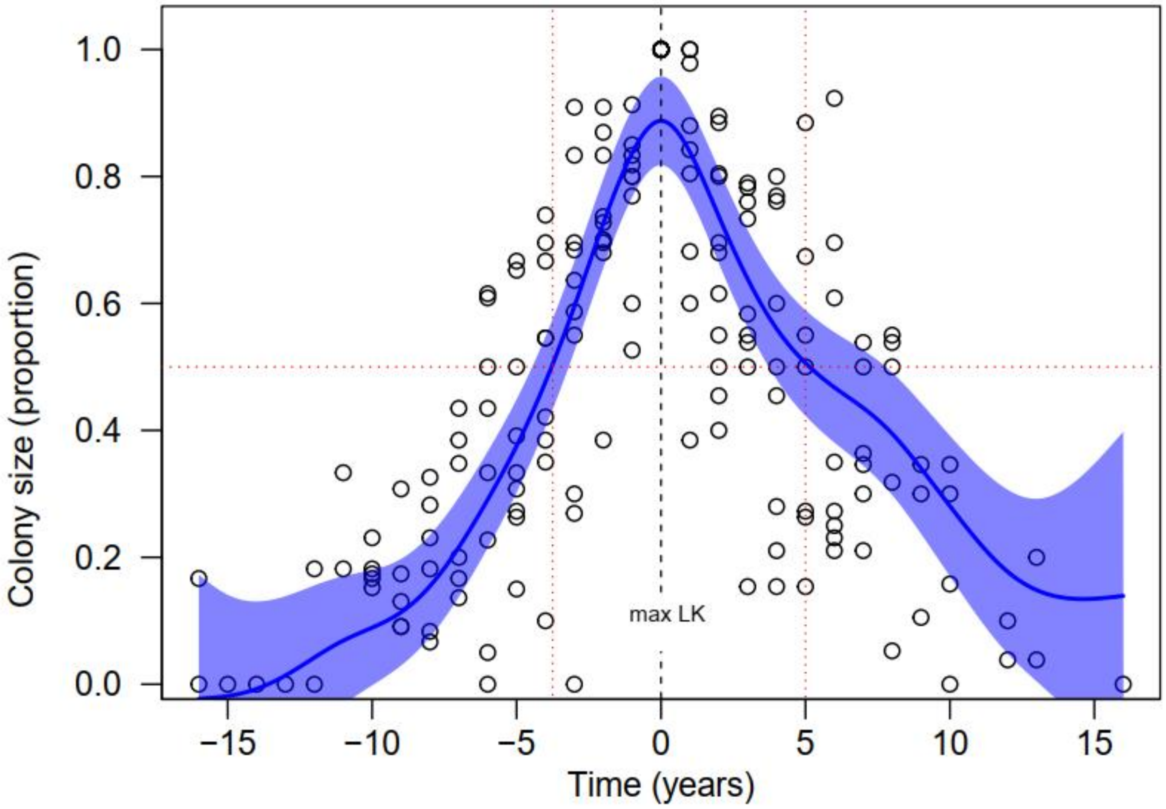


Figure 2.2: Temporal changes in size of lesser kestrel colonies (n=14) established on traditional adobe-made buildings. The trend line was estimated using a smoothing-spline mixed-effect model (loess) selected according to the AIC. Shaded area represents 95% confidence intervals. Dots represent colony size in relation to its maximum (year 0, max LK). The vertical lighter lines encompass the period when colonies were within the 50% of their maximum size. Results suggest the average longevity of a Lesser Kestrel colony in traditional buildings is less than 30 years.

From the 175 traditional buildings classified as suitable for Lesser Kestrels in 2008 and visited during 2017, 14 became unsuitable due to building collapse, 73 remained suitable, and 88 remained unsuitable but may still become suitable in the future due to ongoing or future degradation. The number of suitable buildings is expected to decrease in the future, either due to building collapse or restoration that prevents the establishment of new cavities. Based on the differences recorded between 2008 and 2017, we estimated that the number of new suitable buildings will not be able to offset those collapsing in the next couple of decades, and all traditional buildings, and hence all semi-natural nest-sites, are likely to disappear by the end of this century (Fig. 2.3).

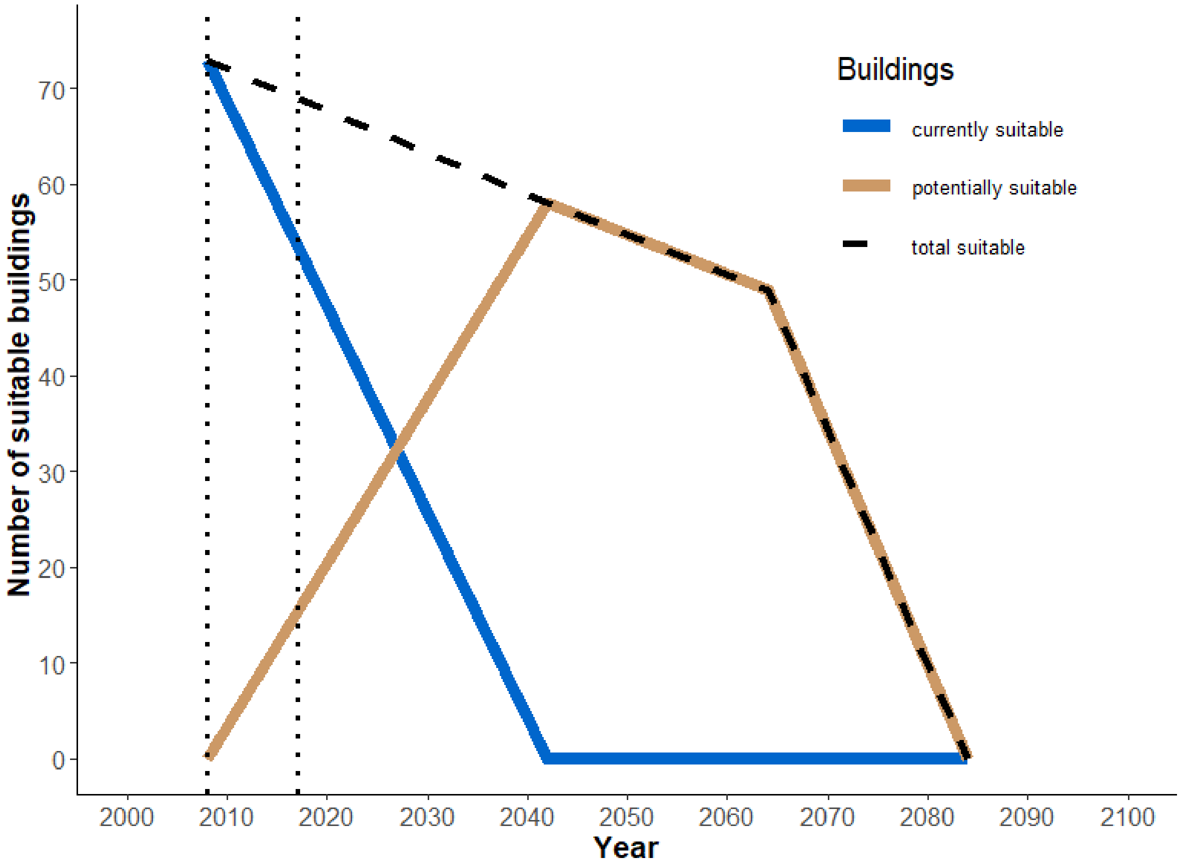


Figure 2.3. Projected changes in the availability of traditional adobe buildings, suitable for breeding Lesser Kestrels and Rollers, during the next hundred years. Potentially suitable (those currently unsuitable but likely to become suitable due to natural degradation after abandonment) are predicted to increase at first but the gradual collapse of all structures will lead to the disappearance of all semi-natural nest-sites before 2100. Projections are based on the observed rate of change of 175 buildings between 2008 and 2017 (between dotted vertical lines).

3.3 FINANCIAL COSTS OF ARTIFICIAL NEST-SITES AND THE POTENTIAL CONTRIBUTION OF LOCAL TOURISM REVENUES

Sustaining the current breeding populations of Lesser Kestrels and Rollers in artificial nests will cost approximately 4500€/year. This corresponds to 3260 artificial nest-sites that would need to be provided until the end of this century (ca. 360 000€, not accounting for inflation, Fig. 2. 4), including the replacement of existing artificial nest-sites, the provisioning of new ones, and keeping the current ratio of each artificial nest-site type (please refer to figure 2. A1 in the Appendix 2 for additional estimates considering only one type of artificial nest-site). There were differences in the cost per breeding pair between type of artificial nest provided

(Kruskal-Wallis H(2)=8.33, p-value= 0.016), with breeding walls being more expensive than clay pots (difference in 2.40€, post hoc Tuckey test: p= 0.023) (Table 2.1).

Table 2.1: Characteristics of artificial nest-sites provided in the Castro Verde SPA and estimated costs per breeding pair. The occupation rate was calculated based on the survey conducted in 2017.

Lesser Kestrel + Rollers	Number of nest-sites	Average Occupation rate 2017	Longevity (years)	Production costs (€)	Average cost/pair ± CI (€)
Breeding walls	69 (average)	0.44 ± 0.10	50	12 000	8.6 ± 1.7
Clay pots	1	0.73 ± 0.18	15	65	6.2 ± 1.7
Wooden nest-boxes	1	0.52 ± 0.19	7	30	7.3 ± 1.7
Rollers					
Isolated nest-boxes	1	0.44	7	30	10.95 (7.31 – 19.25)

Between 2001 and 2017, the number of tourist guests grew twice as fast in Castro Verde than in the South Alentejo region and 3 times higher the average of the full country, with an increase in 572.9% in lodging income (Table 2.2). In 2017, the income from lodging alone was 794 000€ in the Castro Verde area. The funds required to sustain Lesser Kestrels and Rollers in the area thus represent 0.6% of the income generated by this sub-sector of tourism.

Table 2.2: Growth rate of tourism (2001-2017) and lodging income (2017) for the Castro Verde municipality, the South Alentejo region (including Castro Verde) and mainland Portugal.

Region	Growth rate 2001-2017 (%)			Lodging income 2017 (thousand €)
	Number guests	Number nights	Lodging income	
Castro Verde	524.6	360.5	572.9	794
South Alentejo	248.8	254.8	338.9	13 201
Portugal	155.0	94.8	184.9	2 737 998

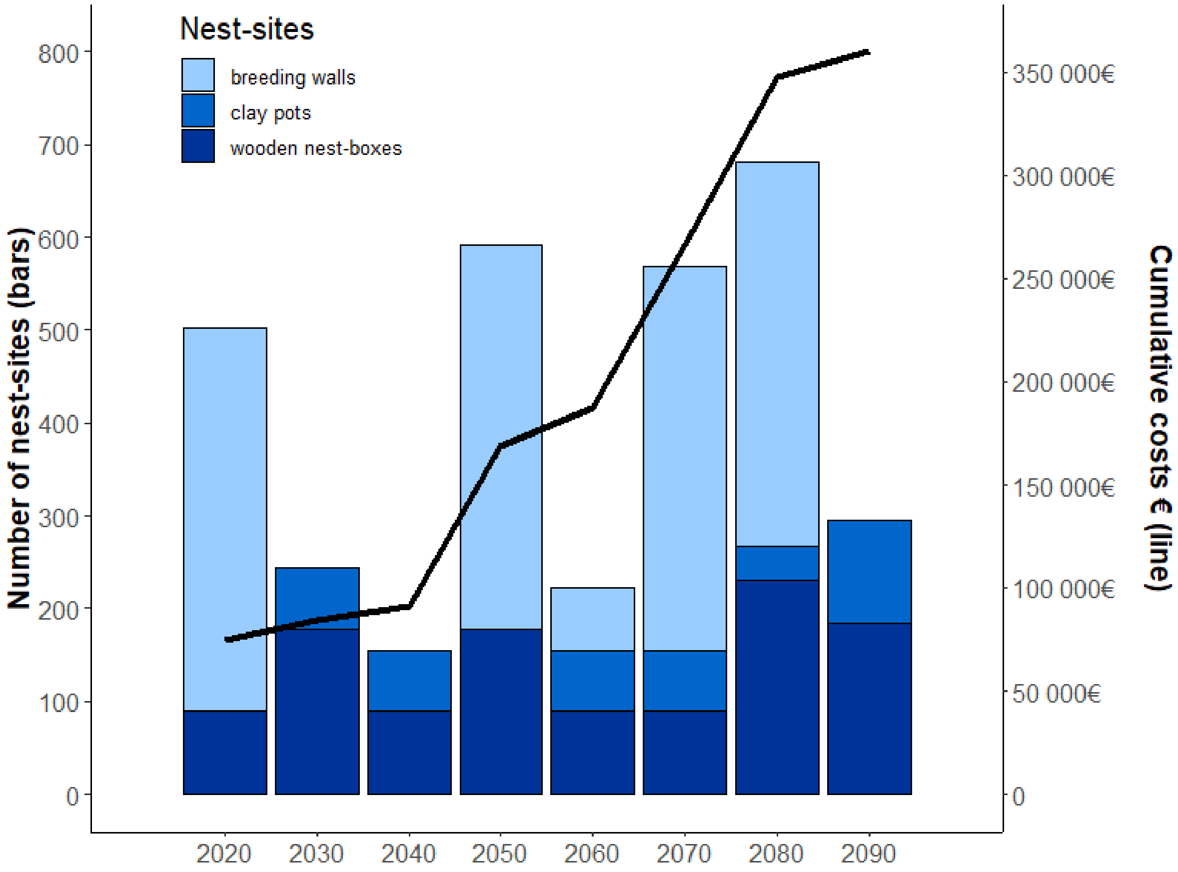


Figure 2.4: Conservation costs by decade (columns) and cumulative (black line) to sustain the current populations of Lesser Kestrels and European Rollers in the Castro Verde SPA, southern Portugal. Estimates by decade account for the replacement of provided artificial nest-sites at the end of its lifespan and new nests to accommodate all breeding pairs currently using semi-natural nests.

4. DISCUSSION

4.1 ARTIFICIAL NEST-SITES AS A REACTIVE CONSERVATION TOOL

In this study we have shown that a reactive conservation approach – artificial nest-site provisioning – enabled a fast recovery and increase of Lesser Kestrel and Roller populations but made them increasingly conservation-reliant – currently more than 65% of all breeding pairs nest in artificially provided nests. Reactive conservation approaches like this may create long-term conservation traps that have been overlooked by researchers and conservationists but have major implications for the conservation of threatened populations (Scott et al. 2010; Cardador et al. 2015). There is evidence that populations of Lesser Kestrels and Rollers across their breeding ranges could be limited by the number of available nest-sites and providing artificial nests has proven to be an effective conservation tool, responsible for observed recoveries in many European countries (Kovacs et al. 2008; Iñigo & Barov, 2010) and contributing to the down-listing of the species conservation status to Least Concern (BirdLife International 2019). We must emphasize that the availability of high-quality foraging habitats in the vicinity of the nests is also critical for maintaining positive population trends (Catry et al. 2013; Finch et al. 2018). Indeed, deterioration of foraging habitat has already been pointed out as the major driver of Lesser Kestrel's population declines outside our study area, even with the provision of artificial nest-sites (Catry et al. 2013). Whilst the extent to which both species are dependent on artificial nests across their range is unknown, other populations around Europe may face similar challenges (Kovacs et al. 2008; Rodríguez et al. 2011; Finch et al. 2018) and to maintain the population numbers of both species, artificial nests will need to be constantly provided and maintained. Our results show that the costs of maintaining healthy populations of Lesser Kestrels and Rollers could be compensated by the economic benefit provided by tourism.

4.2 EPHEMERALITY OF NATURAL NEST-SITES AND ARTIFICIAL NEST-SITES AS CONSERVATION TRAPS

Previous studies have already suggested that traditional buildings in the area represent temporary nest resources for birds, either due to their collapse or restoration (Franco et al. 2005; Catry et al. 2009). This study quantifies the longevity of traditional buildings and predicts the decline in number of semi-natural nest-sites over time. Traditional adobe buildings are only able to host Lesser Kestrels' colonies for roughly 30 years before collapsing. Indeed, in the last 2-3 years, three out of the 14 Lesser Kestrel colonies included in Figure 2.2 disappeared, and two were only sustained due the provision of artificial nests (authors' personal observation).

At the current rate of movement of people from rural to urban areas, and assuming every structure currently without cavities (mostly inhabited or in good condition) would become suitable in the future, all traditional buildings and, consequently, all semi-natural nest-sites, are expected to disappear before the end of this century. Whilst we should acknowledge some limitations to our projections due to the assumption of constant rate of degradation across time (based on the rate of change observed between 2008 and 2017), the non-reversible loss of suitable traditional buildings, and hence of all semi-natural nest-sites in the short/medium-term seems unequivocal. In fact, suitable adobe-made buildings may cease to exist even sooner, as some may be restored or collapse before the appearance of nest-sites. Adobe is no longer used as a building material in the study region, which precludes the appearance of new adobe-made buildings, potentially suitable to host new colonies in the future. Therefore, the long-term persistence of Lesser Kestrels and Rollers in Castro Verde will soon be fully reliant on artificial nest-sites. The disappearance of semi-natural nests and the logistic effort to ensure the provisioning of artificial nests and guarantee the viability of the targeted species creates a conservation trap (Cardador et al. 2015).

The estimated cost to accommodate all Roller and Lesser Kestrel breeding pairs in artificial nests within the Castro Verde SPA is 4500€/year, considering the occupation rates of breeding walls and towers, wooden nest-boxes, and clay pots. Although other solutions (*e.g.*, providing only wooden nest-boxes or clay pots) could be slightly cheaper (Table 2.1 and Figure 2.A1), previous studies carried out in the area showed that these nests can reach very high temperatures during hot days, leading to chick physiological stress and mortality (Catry et al. 2011a, 2015).

Whilst the recovery of both populations through nest-site provisioning was funded by government budgets, their future conservation may be jeopardized by the unsustainable need to perpetuate the implementation of conservation actions as well as by the lack of funds available to continue protecting both species. The recent down listing of Lesser Kestrels and Rollers to “Least Concern” may have thus been a hasty decision because both species still require continued conservation management and funding, even if their populations are no longer threatened according to IUCN criteria.

4.3 FUNDING CONSERVATION-RELIANT SPECIES: THE POTENTIAL OF TOURISM REVENUES FOR CONSERVATION

Government budgets remains the central funding source for conservation, especially in protected areas (Emerton et al. 2006; Mansourian & Dudley 2008; Steven et al. 2013). Major conservation budgets concentrate on funding nature-friendly management practices (*e.g.*, through Agri-Environmental Schemes or Paying for Ecosystem Services Schemes; Batáry et al. 2015; Chakrabarti et al. 2019), or on species-specific recovery action plans that are based on a short-term response to an identified emergency threat, and usually fail to evaluate long-term threats that may persist once funding ends (Scott et al. 2010). In the Castro Verde SPA, the provisioning of new structures for cavity nesting birds is a specific measure funded through Agri-Environmental Schemes (AESs), part of the Rural Development Programme (RDP). However, this voluntary measure had no engagement by farmers and no new nest-sites were provided under this scheme (authors’ personal observation).

Nature-based tourism has been increasingly seen as an opportunity to supplement government budget allocations (Steven et al. 2013), having the potential to generate enough local income to reduce the need for long-term external financing for conservation (albeit not entirely, Kiss 2004). Birdwatching is a significant and expanding subsector of the tourism industry, where people travel to see particular bird species or areas with high endemism or diversity (Steven et al. 2013). Although it is hard to quantify the exact contribution of nature-based tourism to total tourism revenues, the increasing attention to the high natural value of the region remains unquestionable. The number of visitors to the Environment Education Centre of the LPN at Castro Verde (a national environmental NGO) increased by 300% from 2005 to 2018, as well as the supply of birdwatching tour guides (LPN, personal communication). The recent classification of the municipality as UNESCO Biosphere Reserve, highlighting Castro Verde as one of the last refuge for many globally threatened farmland birds in western Europe (Lesser Kestrels, Rollers, Little and Great Bustards, Black-bellied Sandgrouse, Iberian Imperial Eagle), has certainly played a fundamental role in raising tourism revenues. The 4500€ required to fund the provisioning of nest-sites represents only 0.6% of the total income from lodging visitors in 2017 and highlights the great potential of using local tourism revenues to fund the conservation of threatened species in the area.

Tourism and conservation can mutually support each other, especially when recognizing the rich and varied ecosystems services provided by many species (Kiss 2004; Steven et al. 2013; Czajkowski et al. 2014; Wei et al. 2018). For example, in Poland “stork villages” generate substantial income to local communities while supporting tourism management and improving public environmental awareness (Czajkowski et al. 2014). On a much larger scale, the conservation of Giant Pandas *Ailuropoda melanoleuca* in China generates 10 to 27 times the cost of maintaining key habitats in reserves (Wei et al. 2018). The values presented in our study demonstrate the substantial economic benefits generated by bird and nature-related tourism in the study region. The Convention on Biological Diversity (CBD) has already provided guidelines for parties and other stakeholders to manage tourism activities in an ecological, economic and socially sustainable manner (CBD 2007).

In the most likely scenario in which the maintenance of Lesser Kestrels and Roller populations will require long-term management investments, finding ways to foster self-sustainable conservation is important to guarantee the viability of targeted populations in a foreseeable future. Human-made structures have been opportunistically used for nesting by bird species throughout the globe (Mainwaring 2015). In the Castro Verde SPA, first known settlers of Lesser Kestrels and Rollers, and still over 30% of the current population, nested in traditional human buildings, with no records of birds breeding in their original natural nests (burrows in cliffs or trees). Considering the nature-friendly reputation of the area and the income generated by tourism, it should be possible for the council to require that all new buildings should include cavities with the right dimensions for different cavity nesting species, a measure than should be included in the council building regulations.

The conservation implications presented here are not limited to the Portuguese populations of Lesser Kestrels and Rollers or even to bird species. Similar conservation challenges are likely widespread amongst other cavity nesting species from different taxa, whose populations have been recovered through the provisioning of nests following shortage of natural nest-sites (*e.g.*, seabirds: Bolton et al. 2004; marsupials: Beyer & Goldingay 2006; bats: Mering & Chambers 2014). Local conservationists and researchers need to consider the long-term consequences of reactive conservation measures and search for solutions to secure the funding required to guarantee the success of these measures, as well as the viability of target populations.

5. CONCLUSION

In the future, conservation reliance is likely to become even more pervasive because human activities are driving more and more species towards extinction (Scott et al., 2010). This is the case for many species, such as Lesser Kestrels and Rollers, that adapted to live in human dominated landscapes and their persistence depends on the continuation of measures that promote breeding and foraging habitats. Conserving global biodiversity is a great challenge, and the budget needed to support it is likely to grow exponentially as the ranks of conservation-reliant species increases. Here we provide evidence that nature-based tourism has the potential to generate enough income to create self-sustainable conservation. But only by including a broader spectrum of society, involving public participation and political commitment (James et al. 2001; Scott et al. 2010), can tourism revenues be translated into effective conservation measures and foster the long-term viability of wildlife populations.

6. ACKNOWLEDGMENTS

We are indebted to LPN (Liga para a Proteção da Natureza) for sharing the data regarding the number of visitors to the Environmental Education Centre (CEAVG). We would like to thank the four anonymous referees for providing valuable comments that greatly improved this manuscript. This work was supported by CESAM (UID/AMB/50017/2019), cE3c (UIBD/00329/2020) and InBIO (UID/BIA/50027/2013 and POCI-01-0145-FEDER-006821), to FCT/MCTES through national funds. Fieldwork was also financed by LPN (League for the Protection of Nature) projects LIFE02/NAT/P/8481 and LIFE07/NAT/P/654. IC and TC were supported by contracts IF/00694/2015 and DL57/2016/CP1440/CT0023, respectively, and JG by a doctoral grant (PD/BD/128366/2017) from the Portuguese Foundation for Science and Technology (FCT). The funding sources had no direct involvement in the study design or in the collection, analysis, and interpretation of data.

7. REFERENCES

Barnosky, A.D., Hadly, E.A., Gonzalez, P., Head, J., Polly, P.D., Lawing, A.M., Eronen, J.T., Ackerly, D.D., Alex, K., Biber, E., Blois, J., Brashares, J., Ceballos, G., Davis, E., Dietl, G.P., Dirzo, R., Doremus, H., Fortelius, M., Greene, H.W., Hellmann, J., Hickler, T., Jackson, S.T., Kemp, M., Koch, P.L., Kremen, C., Lindsey, E.L., Looy, C., Marshall, C.R., Mendenhall, C., Mulch, A., Mychajliw, A.M., Nowak, C., Ramakrishnan, U., Schnitzler, J., Das Shrestha, K., Solari, K., Stegner, L., Stegner, M.A., Stenseth, N.C., Wake, M.H., Zhang, Z., 2017. Merging paleobiology with conservation biology to guide the future of terrestrial ecosystems. Science (80-.). 355, 1–10. https://doi.org/10.1126/science.aah4787

Batáry, P., Dicks, L.V., Kleijn, D., Sutherland, W.J. 2015. The role of agri-environmental schemes in conservation and environmental management. Conservation Biology 29 (4): 1006-1016. DOI: 10.1111/cobi.12536

Berk, M. 2018. Smoothing-splines Mixed-effects Models in R using the sme Package: a Tutorial. Available at https://cran.r-project.org/web/packages/sme/vignettes/Tutorial.pdf (accessed on 6 December 2019)

Beyer, G.L., Goldingay, R.L. 2006. The value of nest boxes in the research and management of Australian hollow-using arboreal marsupials. Wildlife Research 33 (3): 161-174.

https://doi.org/10.1071/WR04109

BirdLife International, 2019. IUCN Red List for birds. Downloaded from http://www.birdlife.org on 21/08/2019

Bolton, M., Medeiros, R., Hothersall, B., Campos, A. 2004. The use of artificial breeding chambers as a conservation measure for cavity-nesting procelariiform seabirds: a case study of the Madeiran storm petrel (Oceanodroma castro). Biological conservation 116: 73-80. https://doi.org/10.1016/S0006-3207(03)00178-2

Butchart, S.H.M., Stattersfield, A.J., Collar, N.J., 2006. How many bird extinctions have we prevented? Oryx 40, 266–278. https://doi.org/10.1017/S0030605306000950

Butchart, S.H.M., Walpole, M., Collen, B., Strien, A. van, Scharlemann, J.P.W., Almond, R.E.A., Baillie, J.E.M., Bomhard, B., Brown, C., Bruno, J., Carpenter, K.E., Carr, G.M., Chanson, J., Chenery, A.M., Csirke, J., Davidson, N.C., Dentener, F., Foster, M., Galli, A., Galloway, J.N., Genovesi, P., Gregory, R.D., Hockings, M., Kapos, V., Lamarque, J.-F., Leverington, F., Loh, J., McGeoch, M.A., McRae, L., Minasyan, A., Morcillo, M.H., Oldfield, T.E.E., Pauly, D., Quader, S., Revenga, C., Sauer, john R., Skolnik, B., Spear, D., Stanwell-Smith, D., Stuart, S.N., Symes, A., Tierney, M., Tyrrell, T.D., Vié, J.-C., Watson, R., 2010. Global Biodiversity: Indicators of Recent Declines. Science (80-.). 328, 1164–1168. https://doi.org/10.1126/science.1187512

Bux, M., Giglio, G., Gustin, M., 2008. Nest box provision for lesser kestrel Falco naumanni populations in the Apulia region of southern Italy. Conserv. Evid. 5, 58–61.

Cardador, L., Brotons, L., Mougeot, F., Giralt, D., Bota, G., Pomarol, M., Arroyo, B., 2015. Conservation Traps and Long-Term Species Persistence in Human-Dominated Systems. Conserv. Lett. 8, 456–462. https://doi.org/10.1111/conl.12160

Cardinale, B.J., Duffy, J.E., Gonzales, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wadrle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S., Naeem, S., 2012. Biodiversity loss and its impact on humanity. Nature 486, 59–67. https://doi.org/10.1038/nature11148

Catry, I, Alcazar, R., Franco, A.M. A., Sutherland, W.J., 2009. Identifying the effectiveness and constraints of conservation interventions: A case study of the endangered lesser kestrel. Biol. Conserv. 142, 2782–2791. https://doi.org/10.1016/j.biocon.2009.07.011

Catry, I., Alcazar, R., Franco, A.M.A., Sutherland, W., 2009. Identifying the effectiveness and constraints of conservation interventions: A case study of the endangered lesser kestrel. Biol. Conserv. 142, 2782–2791. https://doi.org/10.1016/j.biocon.2009.07.011

Catry, I., Catry, T., Patto, P., Franco, A.M.A., Moreira, F., 2015. Differential heat tolerance in nestlings suggests sympatric species may face different climate change risks. Clim. Res. 66, 13–24. https://doi.org/10.3354/cr01329

Catry, I., Franco, A.M.A., Rocha, P., Alcazar, R., Reis, S., Cordeiro, A., Ventim, R., Teodósio, J., Moreira, F., 2013. Foraging Habitat Quality Constrains Effectiveness of Artificial Nest-Site Provisioning in Reversing Population Declines in a Colonial Cavity Nester. PLoS One 8, 1–10. https://doi.org/10.1371/journal.pone.0058320

Catry, I, Franco, A.M.A., Sutherland, W.J., 2011a. Adapting conservation efforts to face climate change: Modifying nest-site provisioning for lesser kestrels. Biol. Conserv. 144, 1111–1119. https://doi.org/10.1016/j.biocon.2010.12.030

Catry, I, Silva, J., Cardoso, A., Martins, A., 2011b. Distribution and population trends of the European Roller in pseudo-steppe areas of Portugal: results from a census in sixteen SPAs and IBAs. Airo 21, 3–14.

CBD (Convention on Biological Diversity), 2007. Managing Tourism & Biodiversity. User's Manual on the CBD Guidelines on Biodiversity and Tourism Development. Quebec, Canada. ISBN 92-9225-069-8.

Chakrabarti, A., Chase, L., Strong A.M., Swallow, S.K. 2019. Making markets for private provision of ecosystem services: the Bobolink project. Ecosystem services 37: https://doi.org/10.1016/j.ecoser.2019.100936

Czajkowski, M., Giergiczny, M., Kronenberg, J., Tryjanowski, P., 2014. The economic recreational value of a white stork nesting colony: Acase of "stork village" in Poland. Tour. Manag. 40, 352–360. https://doi.org/10.1016/j.tourman.2013.07.009

Deinet, S., Ieronymidou, C., McRae, L., Burfield, I.J., Foppen, R.P., Collen, B., Böhm, M., 2013. Wildlife comeback in Europe: The recovery of selected mammal and bird species. London.

Drechsler, M., Eppink, F. V., Wätzold, F., 2011. Does proactive biodiversity conservation save costs? Biodivers. Conserv. 20, 1045–1055. https://doi.org/10.1007/s10531-011-0013-4

Emerton, L., Bishop, J., Thomas, L., 2006. Sustainable financing of protected areas : a global review of challenges and options, Sustainable financing of protected areas : a global review of challenges and options. https://doi.org/10.2305/iucn.ch.2005.pag.13.en

Finch, T., Branston, C., Clewlow, H., Dunning, J., Franco, A.M., Simon, J., 2018. Context-dependent conservation of the cavity-nesting European Roller. Ibis (Lond. 1859). https://doi.org/10.1111/ibi.12650

Fischer, J., Zerger, A., Gibbons, P., Stott, J., Law, B.S., 2010. Tree decline and the future of Australian farmland biodiversity. Proc. Natl. Acad. Sci. U. S. A. 107, 19597–19602. https://doi.org/10.1073/pnas.1008476107

Flaquer, C., Torre, I., Ruiz-Jarillo, R., 2006. The value of bat-boxes in the conservation of Pipistrellus pygmaeus in wetland rice paddies. Biol. Conserv. 128, 223–230. https://doi.org/10.1016/j.biocon.2005.09.030

Franco, A.M.A., Marques, J.T., Sutherland, W.J., 2005. Is nest-site availability limiting Lesser Kestrel populations? A multiple scale approach. Ibis (Lond. 1859). 147, 657–666. https://doi.org/10.1111/j.1474-919x.2005.00437.x

Gottschalk, T.K., Ekschmitt, K., Wolters, V., 2011. Efficient Placement of Nest Boxes for the Little Owl (Athene noctua). J. Raptor Res. 45, 1–14. https://doi.org/10.3356/JRR-09-11.1

Green, R.E., Cornell, S.J., Scharlemann, J.P.W., Balmford, A., 2005. Farming and the fate of wild nature. Science (80-.). 307, 550–555. https://doi.org/10.1126/science.1106049

Harper, M.J., McCarthy, M.A., Van Der Ree, R., 2005. The use of nest boxes in urban natural vegetation remnants by vertebrate fauna. Wildl. Res. 32, 509–516. https://doi.org/10.1071/WR04106

Hartel, T., Fischer, J., Câmpeanu, C., Milcu, A.I., Hanspach, J., Fazey, I., 2014. The importance of ecosystem services for rural inhabitants in a changing cultural landscape in Romania. Ecol. Soc. 19. https://doi.org/10.5751/ES-06333-190242

Hoffman, M., Hilton-Taylor, C., Angulo, A., Böhm, M., Brooks, Thomas M., Butchart, Stuart H.M., Carpenter, Kent E., Chanson, J., Collen, B., Cox, N.A., Darwall, W.R.T., Dulvy, N.K., Harrison, L.R., Katariya, V., Pollock, C.M., Quader, S., Richman, N.I., Rodrigues, A.S.L., Tognelli, M.F., Vié, J.-C., Aguiar, J.M., Allen, D.J., Allen, G.R., Amori, G., Ananjeva, N.B., Andreone, F., Andrew, P., Ortiz, A.L.A., Baillie, J.E.M., Baldi, R., Bell, B.D., Biju, S.D., Bird, J.P., Black-Decima, P., Blanc, J.J., Bolaños, F., Bolivar-G., W., Burfield, I.J., Burton, J.A., Capper, D.R., Castro, F., Catullo, G., Cavanagh, R.D., Channing, A., Chao, N.L., Chenery, A.M., Chiozza, F., Clausnitzer, V., Collar, N.J., Collett, L.C., Collette, B.B., Ferandez, C.F.C., Craig, M.T., Crosby, M.J., Cumberlidge, N., Cuttelod, A., Derocher, A.E., Diesmos, A.C., Donaldson, J.S., Duckworth, J.W., Dutson, G., Dutta, S.K., Emslie, R.H., Farjon, A., Fowler, S., Freyhof, J., Garshelis, D.L., Gerlach, J., Gowler, D.J., Grant, T.D., Hammerson, G.A., Harris, R.B., Heaney, L.R., Hedges, S.B., Hero, J.-M., Hughes, B., Hussain, S.A., Icochea M., J., Inger, R.F., Ishii, N., Iskandar, D.T., Jenkins, R.K.B., Kaneko, Y., Kottelat, M., Kovacs, K.M., Kuzmin, S.L., La Marca, E., Lamoreux, J.F., Lau, M.W.N., Lavilla, E.O., Leus, K., Lewison, R.L., Lichtenstein, G., Livingstone, S.R., Lukoschek, V., Mallon, D.P., McGowan, P.J.K., McIvor, A., Moehlman, P.D., Molur, S., Alonso, A.M., Musick, J.A., Nowell, K., Nussbaum, R.A., Olech, W., Orlov, N.L., Papenfuss, T.J., Parra-Olea, G., Perrin, W.F., Polidoro, B.A., Pourkazemi, M., Racey, P.A., Ragle, J.S., Ram, M., Rathbun, G., Reynolds, R.P., Rhodin, A.G.J., Richards, S.J., Rodríguez, L.O., Ron, S.R., Rondinini, C., Rylands, A.B., Sadovy de Mitcheson, Y., Sanciangco, J.C., Sanders, K.L., Santos-Barrera, G., Schipper, J., Self-Sullivan, C., Shi, Y., Shoemaker, A., Short, F.T., Sillero-Zubiri, C., Silvano, D.L., Smith, K.G., Smith, A.T., Snoeks, J., Stattersfield, A.J., Symes, A.J., Taber, A.B., Talukdar, B.K., Temple, H.J., Timmins, R., Tobias, J.A., Tsytsulina, K., Tweddle, D., Ubeda, C., Valenti, S. V., van Dijk, P.P., Veiga, L.M., Veloso, A., Wege, D.C., Wilkinson, M., Williamson, E.A., Xie, F., Young, B.E., Akçakaya, H.R., Bennun, L., Blackburn, T.M., Boitani, L., Dublin, H.T., da Fonseca, G.A.B., Gascon, C., Lacher, T.E., Mace, G.M., Mainka, S.A., McNeely, J.A., Mittermeier, R.A., Reid, G.M., Rodriguez, J.P., Rosenberg, A.A., Samways, M.J., Smart, J., Stein, B.A., Stuart, S.N., 2010. The Impact of Conservation on the Status of the World's Vertebrates. Science (80-.). 330, 1503–1509. https://doi.org/10.1126/science.1194442

INE (Instituto Nacional de Estatística, I.P.), 2018. Statistical Yearbook of Alentejo Region 2017. Lisbon, Portugal. ISBN 978-989-25-0455-1

INE (Instituto Nacional de Estatística, I.P), 2002. Statistical Yearbook of Alentejo Region 2001. Lisbon, Portugal. ISBN 972-673-583-1

Iñigo, A., Barov, B., 2010. Action plan for the lesser kestrel Falco naumanni in the European Union. 55p. SEO/Bird-Life and BirdLife International for the European Commission

James, A., Gaston, K.J., Balmford, A., 2001. Can We Afford to Conserve Biodiversity? Bioscience

51, 43–52. https://doi.org/10.1641/0006-3568(2001)051[0043:cwatcb]2.0.co;2

Kiss, A., 2004. Is community-based ecotourism a good use of biodiversity conservation funds? Trends Ecol. Evol. 19, 232–237. https://doi.org/10.1016/j.tree.2004.03.010

Klein, Á́., Nagy, T., Csörgo, T., Mátics, R., 2007. Exterior nest-boxes may negatively affect Barn Owl Tyto alba survival: An ecological trap. Bird Conserv. Int. 17, 273–281. https://doi.org/10.1017/S0959270907000792

Kovacs, A., Barov, B., Orhun, C., Gallo-Orsi, U., 2008. International species action plan for the European roller Coracias garrulus garrulus. Besenyotelek, Hungary 1–52. https://doi.org/10.13140/2.1.3019.7124

Lambrechts, M.M., Adriaensen, F., Ardia, D.R., Artemyev, A. V., Atiénzar, F., Bańbura, J., Barba, E., Bouvier, J.-C., camprodon, J., Cooper, C.B., Dawson, R.D., Eens, M., Eeva, T., Faivre, B., Garamszegi, L.Z., Goodenough, A.E., Gosler, A.G., Grégoire, A., Griffith, S.C., Gustafsson, L., Johnson, L.S., Kania, W., Keišs, O., Llambias, P.E., Mainwaring, M.C., Mänd, R., Massa, B., Mazgajski, T.D., Møller, A.P., Moreno, J., Naef-Daenzer, B., Nilsson, J.-Å., Norte, A.C., Orell, M., Otter, K.A., Park, C.R., Perrins, C.M., Pinowski, J., Porkert, J., Potti, J., Remes, V., Richner, H., Rytkönen, S., Shiao, M.-T., Silverin, B., Slagsvold, T., Smith, H.G., Sorace, A., Stenning, M.J., Stewart, I., Thompson, C.F., Tryjanowski, P., Török, J., Noordwijk, A.J. van, Winkler, D.W., Ziane, N., 2010. The Design of Artificial Nestboxes for the Study of Secondary Hole-Nesting Birds: A Review of Methodological Inconsistencies and Potential Biases. Acta Ornithol. 45, 1–26. https://doi.org/10.3161/000164510X516047

MA (Millennium Ecological Assessment), 2005. Ecosystems and human well-being: biodiversity synthesis. Washington, DC, USA

Mainwaring, M.C., 2015. The use of man-made structures as nesting sites by birds: A review of the costs and benefits. J. Nat. Conserv. 25, 17–22. https://doi.org/10.1016/j.jnc.2015.02.007

Mainwaring, M.C., 2011. The use of Nestboxes by Roosting Birds during the Non-Breeding Season: A Review of the Costs and Benefits. Ardea 99, 167–176. https://doi.org/10.5253/078.099.0206

Mansourian, S., Dudley, N., 2008. Public Funds to Protected Areas Written by Stephanie Mansourian and Nigel Dudley. https://doi.org/10.13140/RG.2.1.3869.5286

Mering, E.D., Chambers, C.L. 2014. Thinking outside the box: a review of artificial roosts for bats. Wildlife Society Bulletin 38 (4). https://doi.org/10.1002/wsb.461

Moreira, F., Leitão, P.J., Morgado, R., Alcazar, R., Cardoso, A., Carrapato, C., Delgado, A., Geraldes, P., Gordinho, L., Henriques, I., Lecoq, M., Leitão, D., Marques, A.T., Pedroso, R., Prego, I., Reino, L., Rocha, P., Tomé, R., Osborne, P.E., 2007. Spatial distribution patterns, habitat correlates and population estimates of steppe birds in Castro Verde. Airo 17, 5–30.

Newton, I., 1998. Population Limitation in Birds. Academic Press, London.

Newton, I., 1994. The role of nest sites in limiting the numbers of hole-nesting birds: a review. Biol. Conserv. 70, 265–276. https://doi.org/10.1016/0006-3207(94)90172-4

Pimm, S.L., Raven, P., 2000. Extinction by numbers. Nature 403, 843–845. https://doi.org/10.1038/35002708

Rodrigues, A.S.L., 2006. Are global conservation efforts successful? Science. 313, 1051–1052. https://doi.org/10.1126/science.1131302

Rodríguez, J., Avilés, J.M., Parejo, D., 2011. The value of nestboxes in the conservation of Eurasian rollers Coracias garrulus in southern Spain. Ibis (Lond. 1859). 153, 735–745. https://doi.org/10.1111/j.1474-919X.2011.01161.x

Rodríguez-Rodríguez, D., López, I., 2019. Socioeconomic effects of protected areas in Spain across spatial scales and protection levels. Ambio. 1-13. https://doi.org/10.1007/s13280-019-01160-7

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L.R., Sykes, M.T., Walker, B.H., Walker, M., Wall, D.H., 2000. Global biodiversity scenarios for the year 2100. Science (80-.). 287, 1770–1774. https://doi.org/10.1126/science.287.5459.1770

Schlaepfer, M.A., Runge, M.C., Sherman, P., 2002. Ecological and evolutionary traps. Trends Ecol. Evol. 17, 474–480.

Schulp, C.J.E., Levers, C., Kuemmerle, T., Tieskens, K.F., Verburg, P.H., 2019. Mapping and modelling past and future land use change in Europe’s cultural landscapes. Land use policy 80, 332–344. https://doi.org/10.1016/j.landusepol.2018.04.030

Scott, J.M., Goble, D.D., Haines, A.M., Wiens, J.A., Neel, M.C., 2010. Conservation-reliant species and the future of conservation. Conserv. Lett. 3, 91–97. https://doi.org/10.1111/j.1755-263X.2010.00096.x

Sebastián-González, E., Sánchez-Zapata, J.A., Botella, F., Figuerola, J., Hiraldo, F., Wintle, B.A., 2011. Linking cost efficiency evaluation with population viability analysis to prioritize wetland bird conservation actions. Biol. Conserv. 144, 2354–2361. https://doi.org/10.1016/j.biocon.2011.06.015

Silva, J.P., Correia, R., Alonso, H., Martins, R.C., Amico, M.D., Delgado, A., Sampaio, H., Godinho, C., Moreira, F., 2018. EU protected area network did not prevent a country wide population decline in a threatened grassland bird. Peer J 1–13. https://doi.org/10.7717/peerj.4284

Socolar, J.B., Valderrama Sandoval, E.H., Wilcove, D.S., 2019. Overlooked biodiversity loss in tropical smallholder agriculture. Conserv. Biol. 00, 1–12. https://doi.org/10.1111/cobi.13344

Sodhi, N.S., Koh, L.P., Clements, R., Wanger, T.C., Hill, J.K., Hamer, K.C., Clough, Y., Tscharntke, T., Posa, M.R.C., Lee, T.M., 2010. Conserving Southeast Asian forest biodiversity in human-modified landscapes. Biol. Conserv. 143, 2375–2384. https://doi.org/10.1016/j.biocon.2009.12.029

Spring, D.A., Bevers, M., Kennedy, J.O.S., Harley, D., 2001. Economics of a nest-box program for the conservation of an endangered species: a re-appraisal. Can. J. For. Res. 31, 1992–2003. https://doi.org/10.1139/x02-142

Stanton, R.L., Morrissey, C.A., Clark, R.G., 2018. Analysis of trends and agricultural drivers of farmland bird declines in North America: A review. Agric. Ecosyst. Environ. 254, 244–254. https://doi.org/10.1016/j.agee.2017.11.028

Steven, R., Castley, J.G., Buckley, R., 2013. Tourism Revenue as a Conservation Tool for Threatened Birds in Protected Areas. PLoS One 8, 1–8. https://doi.org/10.1371/journal.pone.0062598

Sutherland, W.J., Dicks, L. V., Ockendon, N., Petrovan, S.O., Smith, R.K., 2018. What Works in Conservation, Conservation Biology. Open Book Publishers, Cambridge. https://doi.org/https://doi.org/10.11647/ OBP.0131

Tilman, D., Balzer, C., Hill, J., Befort, B.L., 2011. Global food demand and the sustainable intensification of agriculture. Proc. Natl. Acad. Sci. U. S. A. 108, 20260–20264. https://doi.org/10.1073/pnas.1116437108

Traba, J., Morales, M.B., 2019. The decline of farmland birds in Spain is strongly associated to the loss of fallowland. Sci. Rep. 9, 1–6. https://doi.org/10.1038/s41598-019-45854-0

Walpole, M.J., Leader-Williams, N., 2002. Tourism and flagship species in conservation. Biodivers. Conserv. 11, 543–547. https://doi.org/10.1023/A:1014864708777

Watson, J.E.M., Dudley, N., Segan, D.B., Hockings, M., 2014. The performance and potential of protected areas. Nature 515, 67–73. https://doi.org/10.1038/nature13947

Wei, F., Costanza, R., Dai, Q., Stoeckl, N., Gu, X., Farber, S., Nie, Y., Kubiszewski, I., Hu, Y., Swaisgood, R., Yang, X., Bruford, M., Chen, Y., Voinov, A., Qi, D., Owen, M., Yan, L., Kenny, D.C., Zhang, Z., Hou, R., Jiang, S., Liu, H., Zhan, X., Zhang, L., Yang, B., Zhao, L., Zheng, X., Zhou, W., Wen, Y., Gao, H., Zhang, W., 2018. The Value of Ecosystem Services from Giant Panda Reserves. Curr. Biol. 28, 2174-2180.e7. https://doi.org/10.1016/j.cub.2018.05.046

8. APPENDIX

In order to define what a suitable building was, we performed a binomial logistic regression for the presence/absence of each species in buildings with at least one available nest-site. We excluded isolated nest-boxes in trees or electric poles for the Lesser Kestrel model as they only very seldomly nest in these. Therefore, total sample size was 141 and 153 (out of the 412) buildings for the Lesser Kestrel and the Roller model, respectively. Explanatory variables for the Lesser Kestrel model were: human use, type of wall, type of roof, surrounding habitat, total number of available nest-sites, total number of available nest-sites, distance to nearest Lesser Kestrel colony (in meters), size of nearest Lesser Kestrel colony (number of breeding pairs), and number of species of other cavity-nesting birds. For the Roller models, we added distance to nearest structure with Rollers and number of Roller pairs in that structure, and removed type of roof, as Rollers do not nest under tiles. Variables were evaluated by model averaging using a subset based on a variation in Akaike Information Criterion by less than 2 units (ΔAIC<2) and looking at the p-values of full models and at the lower and higher confidence bounds of each variable estimate.

The total number of available nest-sites in a structure was the only variable that positively influenced the occupancy of a structure by both Lesser Kestrels and Rollers and had the highest relative importance in both models (tables 2.A1 and 2.A2). Suitable habitat was only positively selected by Lesser Kestrels, while isolated nest-boxes were selected by Rollers. All other variables, including different types of wall material and different degrees of human use, did not influence the probability of a structure being occupied by either species. We thus define a suitable structure as a structure with at least one available nest-site.

Table 2.A1: Lesser Kestrel full-model averaging using a subset of ΔAIC<2. Variables are ranked according to their relative importance (proportion of the number of times they appeared in the model. Relevant variables were the ones where confidence intervals (CI) did not include 0 (zero).

Variable	Estimate	CI	Relative importance
Total number of available nest-sites	**0.15**	**0.06 - 0.25**	**1.00**
Suitable habitat	**2.22**	**0.55 - 3.99**	**0.98**
Distance to nearest Lesser Kestrel colony	0.00	0.00 - 0.00	0.84
Roof: Arabic tiles	-0.21	-1.68 - 1.04	0.64
Roof: no roof	-1.24	-3.90 - 0.02	
Size of nearest Lesser Kestrel colony	0.00	-0.04 - 0.03	0.26
Wall: adobe walls	-0.21	-3.35 - 0.99	0.18
Wall: stone walls	-0.16	-4.44 - 2.68	
Human use: abandoned	-0.03	-2.54 - 1.52	0.06
Human use: sporadic use	-0.01	-2.04 - 1.68	
Human use: intensive use	-0.04	-2.90 - 1.49	
Intercept	-2.26	-4.78 - 0.26	

Table 2.A2**:** Roller full-model averaging using a subset of ΔAIC<2. Variables are ranked according to their relative importance (proportion of the number of times they appeared in the model. Relevant variables were the ones where confidence intervals (CI) did not include 0 (zero).

Variable	Estimate	CI	Relative importance
Total number of available nest sites	**0.17**	**0.05 - 0.29**	**1.00**
Suitable habitat	18.01	-3019.14 - 3055.58	0.99
Wall: adobe wall	3.27	-0.49 - 7.29	0.96
Wall: isolated nest-boxes	**5.31**	**1.23 - 9.88**	
Wall: stone wall	3.77	-0.79 - 8.61	
Number of Roller pairs in nearest structure with Rollers	-0.27	-1.44 - 0.28	0.46
Distance to nearest Lesser Kestrel colony	0.00	0.00 - 0.00	0.38
Size of nearest Lesser Kestrel colony	0.00	-0.02 - 0.05	0.32
Distance to nearest Roller	0.00	0.00 - 0.00	0.30
Human use: abandoned	-0.08	-3.16 - 1.24	0.08
Human use: sporadic use	-0.06	-2.90 - 1.35	
Human use: intensive use	0.00	-2.35 - 2.38	
Intercept	-22.37	-3041.70 - 2996.95	

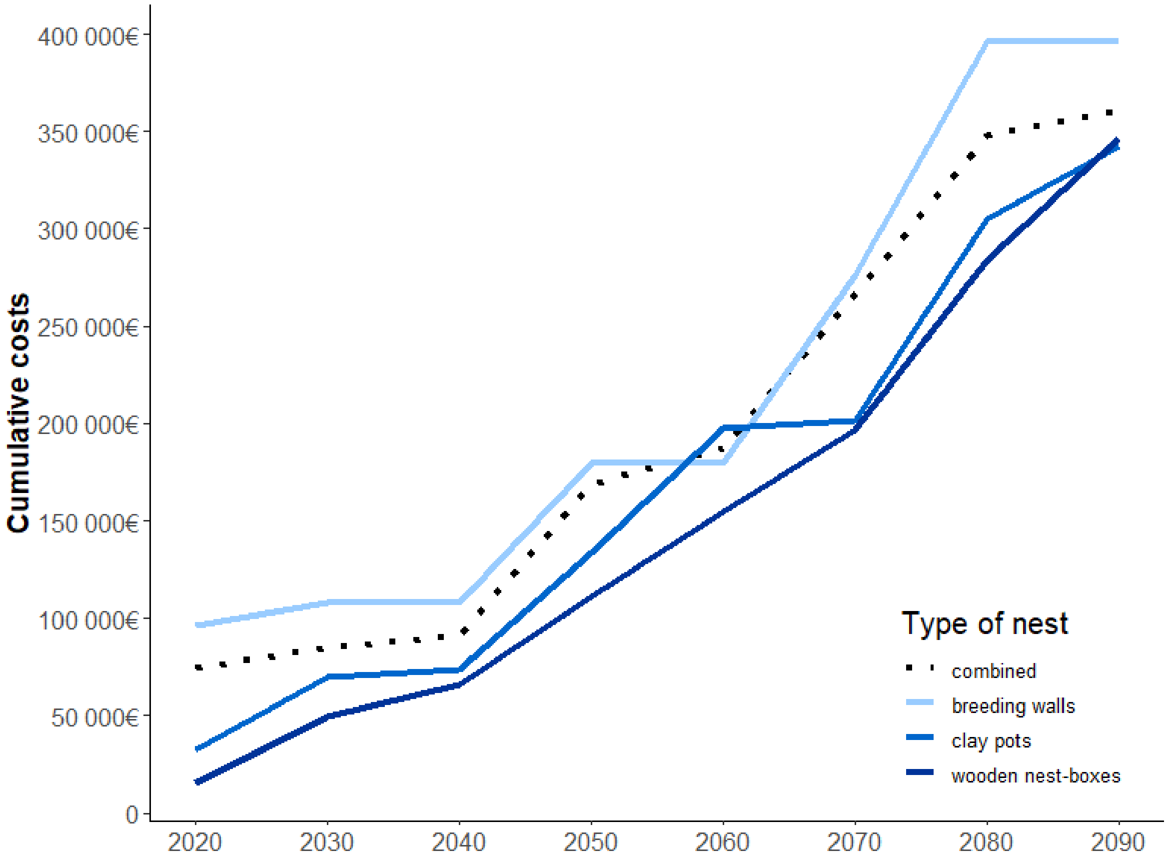


Figure 2.A1: Cumulative conservation costs to sustain the current populations of Lesser Kestrels and European Rollers in the Castro Verde SPA, southern Portugal. Different scenarios, considering the provisioning of only one type of artificial nest-sites (solid lines) and combining the three types (dotted line, the original provided in the main manuscript) are shown for comparison. Estimates by decade account for the replacement of provided artificial nest-sites at the end of its lifespan and new nests to accommodate all breeding pairs currently using semi-natural nests.

Table 2.A3: Percentage of the Lesser Kestrel and Roller populations of the Castro Verde SPA in each type of nest (2017).

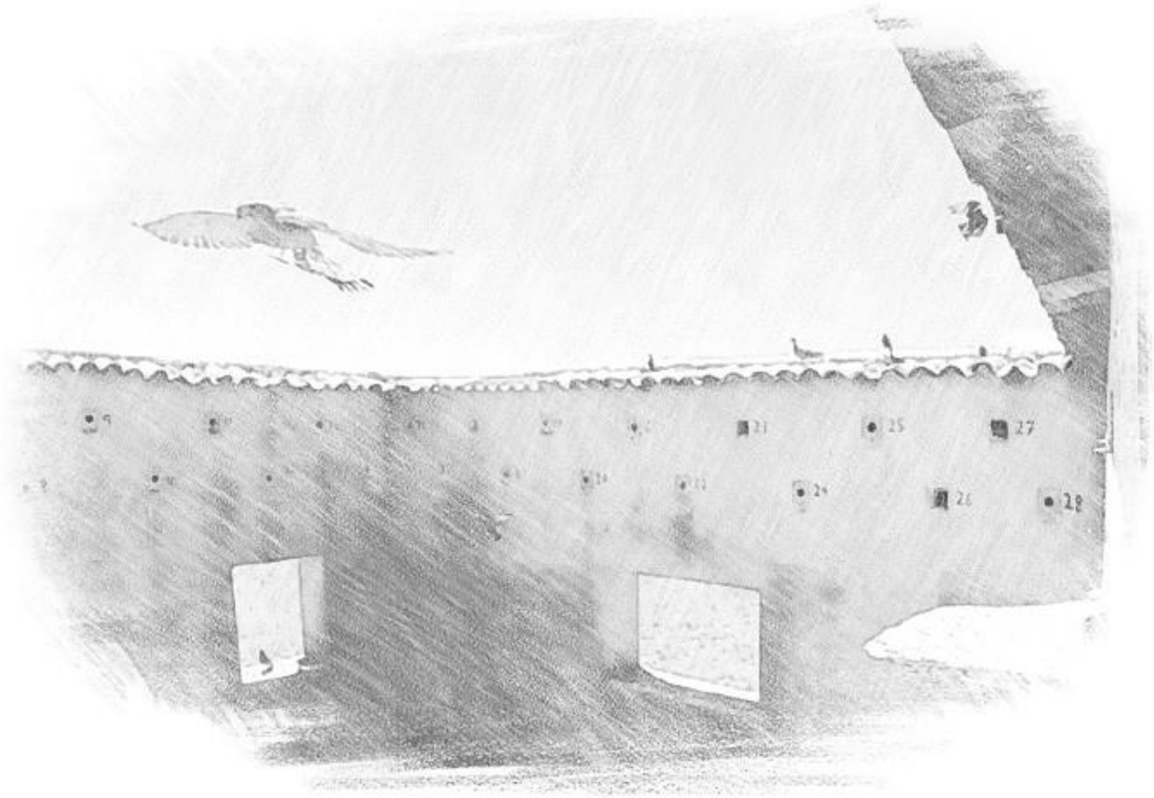
Type of nest		Lesser Kestrels (%)	European Rollers (%)
Semi-natural	Under tiles	12	0
	Semi-natural cavities	20	33
Artificial	Plastered walls	19	12
	Breeding walls/towers	36	22
	Clay pots	7	10
	Wooden nest-boxes	6	22

Chapter 3

Influence of colony traits on ectoparasite infestation in birds breeding in mixed-species colonies

João Gameiro, Jesús Veiga, Francisco Valera, Jorge M. Palmeirim & Inês Catry

Published in *Parasitology* (2021) DOI:10.1017/S0031182021000470



INFLUENCE OF COLONY TRAITS ON ECTOPARASITE INFESTATION IN BIRDS BREEDING IN MIXED-SPECIES COLONIES

ABSTRACT

Coloniality in birds is often associated with an increase in parasite burden, but whether the co-occurrence of several host species influences the prevalence and abundance of ectoparasites and their relationship with colony size or density remains poorly known. Here we studied mixed-species breeding colonies formed after the provision of artificial breeding structures for restoring the lesser kestrel (*Falco naumanni*) population in Portugal, to investigate the influence of colony traits on ectoparasite infestation. We sampled four groups of ectoparasites (carnid flies, haematophagous mites, louse flies, and chewing lice) in four hosts: lesser kestrels, European rollers (*Coracias garrulus*), feral pigeons (*Columba livia*), and spotless starlings (*Sturnus unicolor*). Each host species had a distinct infracommunity of ectoparasites, regardless of colony traits such as size, density, or host richness. The abundance of the most common ectoparasite, *Carnus hemapterus*, was influenced by colony composition – number of nests of each host species – rather than by colony size or density, with its abundance being diluted with increasing numbers of less suitable hosts such as starlings. The increased contact between multiple species of hosts in breeding colonies may complexify host-parasite interactions and challenge our current knowledge on the ecological relationships between host sociality and parasitism.

Keywords: host-parasite interaction; dilution effect, *Carnus hemapterus*, haematophagous mites, louse flies, chewing lice

1. INTRODUCTION

Avian colonial breeding is often associated with higher parasite prevalence and intensity, as the increased proximity and contact between different group members facilitates ectoparasite transmission (Brown and Brown 1986; Côté and Poulin 1995; Tella 2002; Patterson and Ruckstuhl 2013). This pattern differs according to the mode of ectoparasite transmission, with contact-transmitted parasites (*e.g.*, mites or lice) being positively correlated with group size, whereas no correlation is expected for mobile parasites (*e.g.,* biting flies, mosquitoes) due to encounter dilution effects (Patterson and Ruckstuhl 2013, but see Veiga et al. 2020). Parasites can directly or indirectly affect the reproductive and survival components of individual fitness by decreasing nestling body condition and survival, or by reducing adult fecundity (Brown and Brown 1986; Merino and Potti 1995; Arriero and Møller 2008; Hoi et al. 2018). This may consequently impact avian population dynamics, for example by decreasing breeding-site fidelity and foster both the formation and extinction of colonies (Brown and Brown 2004; Calabuig et al. 2010; Brown et al. 2017; Sanz-Aguilar et al. 2020). Group living may also result in increased physiological social stress due to increased competition for resources, which synergises with host susceptibility to parasite infestation (Beldomenico and Begon, 2010; Kappeler et al. 2015). However, most studies assessing the relationship between parasitism and colonial breeding targeted monospecific colonies or the interaction between a single host and a single parasite species, overlooking the likely interactions among different hosts, or different parasites within the same host – the parasite infracommunity (Bush et al. 1997; Holt et al. 2003; Poulin 2007; but see Whiteman and Parker 2004, Veiga and Valera 2020). In fact, bird colonies are often composed by different species, resulting in mixed-species colonies, that reshape the structure and functioning of communities through the increased interaction between the grouping species (Gaglio et al. 2018; Catry and Catry 2019). The formation of mixed-species colonies may allow species to acquire the benefits of group living while reducing the costs associated with intraspecific competition (Møller et al. 1993; Campobello et al. 2012), although multi-species associations may also result in costs through factors like kleptoparasitism or interspecific competition (Gaglio et al. 2018; Catry and Catry 2019).

In multi-species assemblages, intra and interspecific social contacts likely increase and complexify the interactions between different host and parasite species (Valera et al. 2003; Keesing et al. 2006). High host diversity could decrease infestation risk through dilution effects, as different host species may be differently susceptible and/or competent to different parasite species, but this effect may not always occur and likely depends on specific community compositions (Keesing et al. 2006; Randolph & Dobson 2012; Civitello et al. 2015; Halsey 2018; Martin et al. 2019). Mixed-species assemblages may also promote interspecific parasite exchange, especially within generalist parasite species. Whether the occurrence of several host species in bird assemblages increases or decreases the prevalence and abundance of parasites and their relationship with colony size or density remains poorly studied (Tella et al. 1998; Valera et al. 2003; Veiga et al. 2020).

Studying the ecological relationship between parasites in mixed-species colonies may be harder than in mono-specific groups due to the complexity of addressing several species and their interactions, with the solution often being to simplify the system into one-one actors. In this study, we investigate host-parasite relationships in mixed-species colonies, by considering several host and parasite species and by simultaneously looking at several colony traits that may influence the prevalence and abundance of ectoparasites. In southwestern Iberia, colonial lesser kestrels *Falco naumanni* breed in man-made structures that attract other species, including common kestrels *Falco tinnunculus*, European rollers *Coracias garrulus*, barn owls *Tyto alba*, little owls *Athene noctua*, jackdaws *Corvus monedula*, spotless starlings *Sturnus unicolor* and feral pigeons *Columba livia*; thus forming mixed-species colonies (Catry and Catry, 2019). These multi-species assemblages provide an ideal opportunity to understand the ecological relationships between multiple host and parasite species (Valera et al. 2003). Here, we study how colony traits such as colony size, host species richness, density, and composition, influence the ectoparasite infracommunities. Specifically, we aim to: (1) describe the ectoparasite infracommunity of different avian host species breeding in mixed-species colonies; (2) determine the main colony traits potentially affecting ectoparasite infracommunity composition; and (3) assess how colony traits drive the abundance of *Carnus hemapterus*, a widespread haematophagous fly parasitising at least 64 host species from 24 avian families (Grimaldi 1997; Brake 2011) and the most common ectoparasite in our study area. For this, we study the ectoparasites in nestlings and nests of the four main common bird species in 30 mixed-species colonies.

2. METHODS

2.1 STUDY SYSTEM: HOSTS AND PARASITES

This study took place in the Castro Verde Special Protection Area, Southern Portugal (~37°43′N, 7°57′W) (Fig. 3.1). In the framework of European LIFE projects to recover lesser kestrel populations, more than 800 artificial nests were provided in the study area, including new cavities opened in abandoned rural buildings, artificial cavities in newly built breeding walls and towers with up to 90 cavities, wooden nest-boxes, and clay pots (Catry et al. 2009). Given the low availability of nest-sites in the area, nest-site provisioning was very effective at increasing the lesser kestrel population and attracted other bird species to nest in these structures (Catry et al. 2009; Catry and Catry 2019; Gameiro et al. 2020).

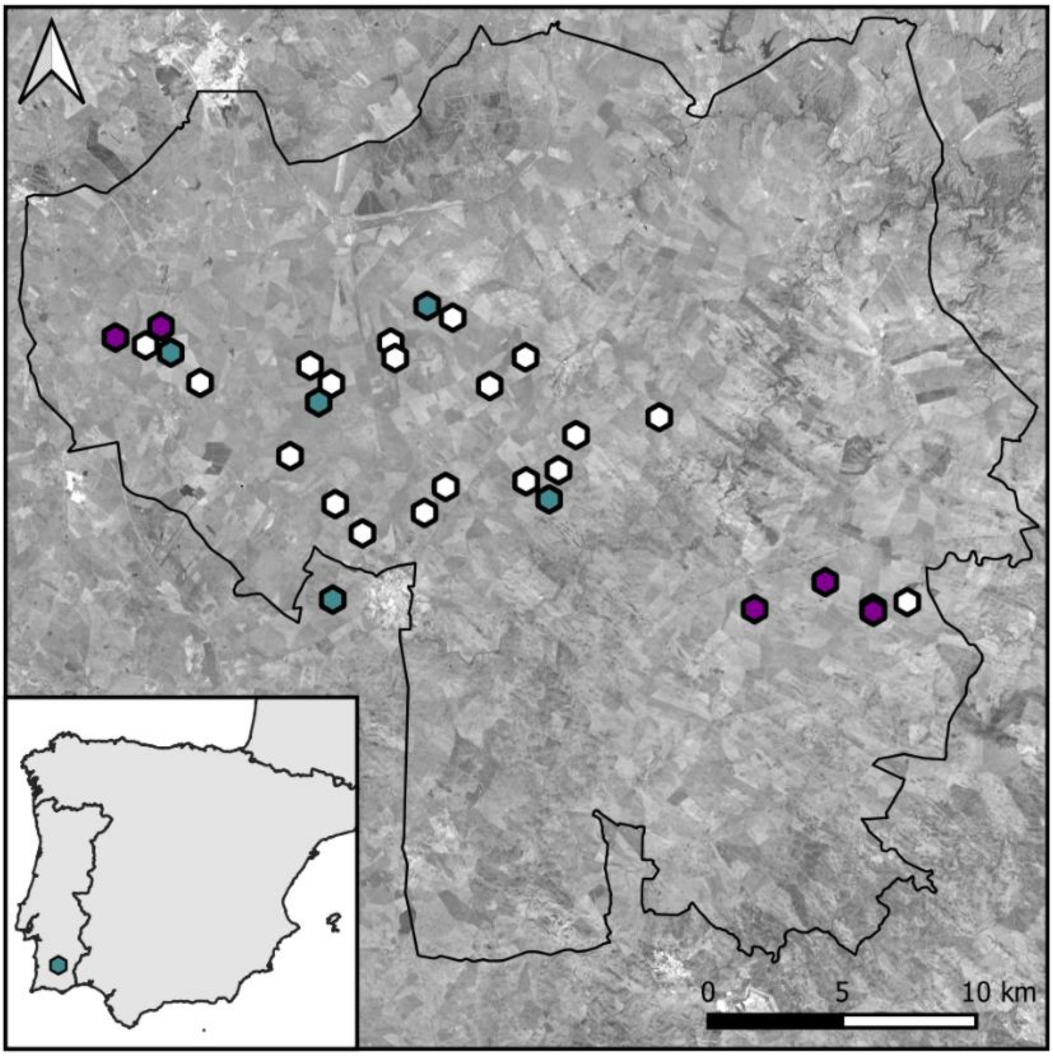


Figure 3.1: Location of the small (white), medium (light green), and large (dark green) colonies sampled in this study. Boundaries of the Castro Verde Special Protection Area (SPA) shown as a black line.

Mixed-species colonies occur in adobe-built abandoned farmhouses (nests located in cavities that appear with building degradation – 'natural cavities') or in artificial nest structures. Here, 'colony' was defined as a site with at least two active nests - usually a single building, or a main building with few smaller, annex structures (*e.g.,* a farmhouse with a separated shed). Because nests occur inside cavities, the maximum size of the colony is ultimately dependent on the number of available nest-sites, which can go from just a couple to more than a hundred cavities. Larger colonies (> 40 breeding pairs) tend to have higher density of nests and a higher richness of host species and can be dominated by either lesser kestrels or spotless starlings (Table 3.1). Larger colonies usually also hold a few pairs of jackdaws and feral pigeons, one to four common kestrels and European rollers, and one pair of barn owl and/or little owl (Catry and Catry, 2019). Distance to nearest colony was always greater than 100 meters (min = 150 m, max = 4266 m).

Table 3.1: Colony traits of small (<20 pairs), medium (21-40 pairs) and large (> 40 pairs) mixed-species colonies sampled for ectoparasites. Median (min-max) values are shown for host richness, colony size, density (average distance to the 3 active closest nests and colony composition (number of active nests).

	Small	Medium	Large
Colony host richness	3 (1 – 5)	4 (4 – 5)	5 (3 – 6)
Colony size*	6 (2 – 11)	29 (27 – 30)	49 (46 – 62)
Colony density*	6.2 (2.0 – 22.6)	2.6 (0.8 – 5.6)	0.9 (0.8 – 4.4)
Colony composition			
Lesser kestrel	4 (0 - 10)	20 (17 – 24)	22.5 (8 – 47)
Roller	1 (0 – 2)	2 (1 – 3)	1 (1 – 3)
Pigeon	0 (0 – 5)	5 (0 – 5)	4 (0 – 8)
Starling	0 (0 –1)	3 (0 – 3)	21.5 (1 – 32)
Colonies sampled	19	5	6
Nests sampled	56	61	144

*Also includes other, less abundant host species (common kestrels, jackdaws, little owls, and barn owls).

This study focused on the four most common bird species in these mixed-species colonies: lesser kestrels, European rollers (hereafter rollers), spotless starlings (hereafter starlings) and feral pigeons (hereafter pigeons). Lesser kestrels and rollers are single-brooded, secondary cavity nesting birds with a trans-Saharan migration (Catry et al. 2015). Lesser kestrels are typically colonial, with colonies reaching up to 80 breeding pairs in the study area (Catry et al.

2009). They arrive at the breeding grounds in early February and typically lay 4 to 5 eggs in April-May. Nestlings are born with a down feather coat after a 28 days incubation and usually fledge at 36 days (Catry et al. 2015). Rollers (up to four breeding pairs) are usually found breeding in lesser kestrel colonies but can also nest in isolated nests in farmhouses or in nest-boxes placed on trees or telephone poles. Egg laying is asynchronous with 3 to 6 eggs laid in May-June. Nestlings are born featherless after 17-19 days of incubation and fledge at 20-25 days (Catry et al. 2015). Starlings and pigeons are resident in the study area and lay several clutches along the breeding season. Starlings generally nest at high densities, with up to 32 breeding pairs in these mixed-species colonies (Table 3.1). Starlings lay 3 to 6 eggs, incubation takes ca. 12 days and nestlings fledge at 20-22 days old (Muriel et al. 2013). Pigeons occur at lower densities, with up to eight breeding pairs in these colonies (Table 3.1). They lay up to two eggs, incubation lasts around 18 days, and nestlings fledge at ca. 28 days old (Johnston and Janiga 1995). Contrary to lesser kestrel and roller nests, which are usually just comprised of dirt and prey remains, starlings and pigeons build their nest with sticks, straws and other vegetable material, and pigeons also accumulate droppings inside the cavity.

The most common ectoparasites found in hosts' nestlings in our study area were: carnid flies (*Carnus hemapterus,* Diptera: Carnidae), haematophagous mites (Acari: Mesostigmata), louse flies (Diptera: Hippoboscidae), and feather lice (Phthiraptera); and they were considered in this study as four separate groups since: i) identification to the species level and quantification of each species in each nest and host was not feasible, and ii) working at the species level falls beyond of this study, i.e., to investigate the influence of colony traits on the general patterns of ectoparasite infestation. Yet, some information about identified species is provided at the discussion.

The generalist *Carnus hemapterus* (hereafter *Carnus*) is a nidicolous, haematophagous fly infesting many bird taxa. *Carnus* loses its wings after finding a host, with peak infestations occurring during the mid-nestling stage, and with a resistance stage (pupa) that remains in the nest debris until the next breeding season when adult flies emerge (Valera et al. 2006a; Calero-Torralbo and Valera 2008). Despite being a mobile ectoparasite, it was found to increase with colony size and host density (Hoi et al. 2010; Veiga et al. 2020; but see Liker et al. 2001). Mites are also generalist ectoparasites, feeding mostly on blood or skin tissue of nestlings and adults. Mite populations usually grow quickly in the nest during their host's breeding season and some individuals may overwinter in the nest (Burtt et al. 1991). Being contact transmitted parasites, they are expected to increase with colony size (Davis & Brown 1999). Louse flies are also haematophagous parasites, but imagoes do not lose their wings and can fly between nests, and they have often a more restricted host range (Veiga et al. 2019). Imagoes spend most of their time feeding on the host’s body, and pupae are formed and apparently overwinter in the nest (Boyd, 1951). Louse flies are mobile parasites and should not be affected by host coloniality (Poulin 1991). Feather chewing lice are permanent ectoparasites with a host range usually confined to species within the same family or genus (Clayton et al 2008). They live on the feathers and seldom leave their host except to transfer among individuals through direct contact (e.g., between parents and their offspring), and thus are likely influenced by host sociality. (Clayton and Tompkins 1995; Rózsa et al. 1996; Whiteman & Parker, 2004; Ortego et al. 2007).

2.2 DATA COLLECTION

2.2.1 ECTOPARASITE ESTIMATION

Field work was conducted during the breeding season of 2018, from mid-April to mid-July, by sampling unclean nests occupied by the four studied host species. Colonies and nests within colonies were randomly sampled during a lesser kestrel and roller monitoring programme. A total of 30 colonies were sampled (Fig. 3.1): seven with all four hosts; four with lesser kestrels, rollers and starlings; two with lesser kestrels, rollers and pigeons; six with lesser kestrels and rollers; two with lesser kestrels and pigeons; two with rollers and pigeons; five with lesser kestrels; and two with rollers (Table 3.1). Overall, we sampled 261 nests: 141 lesser kestrel, 33 roller, 38 pigeon and, 49 starling nests. Nests were not cleaned prior to this study for two reasons: i) removing old nest detritus was not possible for most of these nests (especially for natural cavities), ii) unclean nests provide results that better resemble the natural conditions (Møller, 1989). Soiled nests may influence the prevalence and numbers of some ectoparasites in these colonies and may cause some unaccounted variability in the data, particularly when considering ectoparasites with most of their life cycle, including long diapauses, occurring in the nests (Veiga et al. 2020). Thus, this potential bias was considered in the statistical approach (see Data analysis below) and its influence was discussed.

The presence and number of ectoparasites were assessed by examining all nestlings in each host species nest. Each nest was sampled at two different periods: at mid-nestling stage (around 8-12 days old), and few days before fledging. During each of these two periods, each nestling was taken from its nest and placed in a transparent plastic bag to avoid losing mobile parasites (*e.g.*, louse flies). The nestling was then taken from the bag and the number of carnid flies and louse flies on the bag and on the body surface and sheaths of the nestling were counted twice and then averaged (Roulin, 1998; Václav et al. 2008). Feather lice were sampled by carefully scanning the nestlings' sheaths and feathers (Valera et al. 2003; Ortego et al. 2007). Mites were sampled by resting the observer's hand on the bottom of the nest for one minute and then the number of mites were counted twice and then averaged. Nestlings were then carefully placed back on the nests. The number of each ectoparasite group was calculated as the sum of parasites in all nestlings from the same brood. The maximum number of parasites from both sampling periods was selected. All work was approved by the relevant Portuguese authorities (Instituto da Conservação da Natureza e das Florestas).

2.2.2 MIXED-SPECIES COLONY TRAITS

The following variables were recorded for each sampled nest: host species identity, type of nest (natural cavities in farmhouses, artificial cavities, clay pots, wooden nest-boxes), brood size (number of nestlings), and the sampling date of the first sampling period, which was used as a proxy for ectoparasite seasonal effects (Calero-Torralbo et al. 2013). The species occupying the focal nest in the previous year was also recorded, as some ectoparasites spend most of their life cycle in the nest and their occurrence and abundance may depend on previous breeding seasons (Valera et al 2006a). Each nest was also categorized according to four main colony traits: colony host richness (number of host species in the colony); colony size (number of active nests, *i.e.*, nests with nestlings, of all species); colony density (the inverse of the average distance to the three active closest nests, in meters); colony composition (four variables, each with the number of active nests of each host species) (Table 1). Colony size was grouped into three categories: small (up to 20 nests), medium (21-40 nests), and large (more than 40 nests) (Fig. 3.1). Similarly, colony density was grouped in low (average distance to the three closest nests > 5m), medium (1-5 m), and high density (< 1m). All traits (except colony composition) acknowledged all nesting bird species, including less abundant species (common kestrels, jackdaws, little owls, and barn owls).

2.3 DATA ANALYSIS

The nest was used as the sampling unit and thus the term infracommunity refers to the community of ectoparasites in a given nest (see Veiga and Valera, 2020 for a similar approach). Accordingly, the prevalence and mean intensity of each ectoparasite group for each host species was calculated, respectively, as the proportion of infested nests amongst all nests sampled and the mean number of parasites of all infested nests. Because some nests were not sampled during both periods, prevalence and mean intensity of each parasite were calculated only for nests sampled at each parasite's peak infestation stage (assessed from our own data set and the literature; see following sentences), so that comparisons could be made between the different hosts (see Results). *Carnus* infestation peaks at mid-nestling stage (prevalence of 87% and 20% for the first and second sampling period, respectively; see also Václav et al. 2008), while feather lice and louse flies are more common in fully-grown, feathered nestlings (lice prevalence of 2% and 86%, and louse fly prevalence of 26% and 47% for the first and the second sampling period, respectively; see also Muñoz et al. 1993). The prevalence of mites did not differ between the two sampling periods in our study (23% and 19% for the first and second sampling period, respectively). Accordingly, prevalence and mean intensity values of carnid flies were obtained from all nests sampled in the first period, values for lice and louse flies from nests sampled in the second period, and values for mites were obtained from all nests (sampled both in the first and/or in the second period).

Fisher's exact tests, and Kruskal-Wallis H test followed by bootstrap 2-sample t-tests, were used for comparing parasite prevalence and mean intensity, respectively, among hosts, using 2000 replications for both estimation of confidence intervals and bootstrap t-tests (Rózsa et al. 2000; Veiga et al. 2019).

A Principal Component Analysis (PCA) was used to explore the potential correlation among the colony variables without constraints (random factors), prior to further analysis (sup. Material – Fig. 3.A1) (Borcard et al. 2011; Václav and Valera, 2018). To examine how colony traits influence the ectoparasite infracommunity composition, a partial Canonical Correspondence Analysis (CCA) was used including all sampled nests and conditioned by brood size, sampling date and colony ID (Borcard et al. 2011). The presence-absence matrix of each parasite group in each nest was used as the response variable (nests without parasites were removed; Oksanen, 2020). Host species, nest type, the species using the nest in the previous year, and colony host richness, size, density, and composition, were used as the predictive variables. The variance inflation factor (VIF) was used to assess collinearity between predictive variables (all VIFs <10, min = 1.01, max = 6.61) and forward and backward selection were performed to choose the best CCA model (Borcard et al. 2011; Václav and Valera, 2018).

To assess how colony traits (richness, size, density, and composition) influence the abundance (*i.e.*, including both infested and non-infested nests) of *Carnus*, the most common ectoparasite in our mixed-species colonies, a generalized linear mixed models (GLMMs) was used. The model followed a negative binomial distribution of errors to account for the aggregated distribution of *Carnus* among hosts (Václav and Valera, 2018). *Carnus* abundance in each nest was used as the response variable and colony ID as a random variable. The sample-to-variable ratio and the high correlation between some colony traits did now allow the inclusion of all variables in a single model (Fig. 3.A1). Because colony size, density, and host richness were correlated, the number of variables were reduced by choosing the most meaningful traits. Colony size was removed in favour of colony density because the latter reports about the nest density around each focal nest, whereas colony size attributes the same value to all nests within the same colony. Colony composition was selected instead of colony host richness because it contains information about the identity of the host and its abundance, rather than just the number of species found in a given colony. However, because the abundance of pigeons and rollers was considerably lower than the one of lesser kestrels and starlings, and both were correlated with the number of starling nests (Fig. 3.A1), colony composition was restricted to the number of nests of the most abundant hosts, i.e., lesser kestrels and starlings. Nonetheless, different combinations of variables were tested, which also included the host species using the nest in the previous year, but did not provide additional or different outputs. The results shown here refer to the most biologically meaningful model, that includes the following, non-correlated, explanatory variables: host species, brood size, sampling date, type of nest, colony density (categorical), number of lesser kestrel nests, and number of starling nests (highest VIF = 5.07, for type of nest). The number of roller and pigeon nests were also discarded as their abundance was considerably lower than the one of lesser kestrels and starlings and both were correlated with the number of starling nests (Fig. S1). A model-averaging approach based on the Akaike Information Criterion (AIC) was used to obtain weighted average estimates for fixed parameters (Grueber et al. 2011). Model averaging was performed on models with the cumulative sum of corrected AIC (AICc) weights > 0.95.

All continuous explanatory variables were scaled and centred prior to analysis. All analyses were conducted with R software 3.6.1 (R Core Team, 2016), using the packages Vegan 2.5-6 (Oksanen, 2020), nlme 3.1-148 (Pinheiro et al. 2020), lme4 1.1-23 (Bates et al. 2020) and MuMIn 1.43.17 (Bartón, 2020).

3. RESULTS

3.1 PREVALENCE AND INTENSITY OF ECTOPARASITES IN MIXED-SPECIES COLONIES

The composition of the infracommunity of ectoparasites differed among the various host species breeding in mixed-species colonies: lesser kestrels and pigeons had all four types of ectoparasites whereas starlings had no louse flies and rollers had no lice and almost no louse flies (Table 3.2).

Table 3.2: Prevalence (percentage of infested nests) and mean intensity (mean number of parasites found in infested nests) (with 95% confidence intervals in round brackets and number of infested nests/ number of sampled nests in square brackets) of ectoparasites found on nests of mixed-species colonies in southern Portugal.

Parasite		Roller	Lesser Kestrel	Pigeon	Starling
Carnid fly	Prevalence	100% (87.7 – 100) [28/28]	97.7% (93.5 – 99.5) [129/132]	41.9% (24.5 – 60.9) [13/31]	76.9% (60.7 – 88.9) [30/39]
	Mean intensity	58.3 (40.1 – 75.8)	21.4 (17.7 – 25.2)	2.9 (1.3 – 4.6)	5.6 (3.9 – 7.3)
Louse fly	Prevalence	3.0% (0 – 15.8) [1/33]	2.6% (0.5 – 7.4) [3/116]	47.4% (24.4 – 71.1) [9/19]	0.0% (0.0 – 21.8) [0 /15]
	Mean intensity	1*	1 (1 – 1)	1.8 (1.1 – 2.4)	0
Lice	Prevalence	0.0% (0 – 10.6) [0/33]	84.5% (76.6 – 90.5) [98/116]	94.7% (74.0 – 99.9) [18/19]	6.7% (0.0 – 31.9) [1/15]
	Mean intensity	0	24.3 (17.4 – 31.1)	37.9 (19.5 – 56.3)	1*
Mite	Prevalence	33.3% (18.0 – 51.8% [11/33]	15.6% (10.0 – 22.7) [22/141]	31.6% (17.5 – 48.7) [12/38]	30.6% (18.3 – 45.4) [15/49]
	Mean intensity	18 (0 – 39.9)	5.0 (1.4 – 8.6)	18.3 (4.2 – 32.3)	19.1 (9.4 – 28.7)

Carnus was the most common ectoparasite in mixed-species colonies but its prevalence differed among the four host species (Fisher test $p < 0.001$), being highest in lesser kestrels and rollers and lowest in pigeons. *Carnus* mean intensity was more than double in rollers than in lesser kestrels (bootstrap 2-sample t-test: $t = 4.22$ d.f. $= 29.65$, $p < 0.001$) and lowest in pigeons (Table 3.2). Mites were the second most common ectoparasite in mixed-species colonies, reaching the lowest prevalence and intensity in lesser kestrels (Table 2). Rollers, pigeons, and starlings had similar mite prevalence and intensity (prevalence; Fisher test: p = 0.97 intensity: Kruskal-Wallis H: 1.11, d.f. = 2, p = 0.57). Lice were almost exclusively found in lesser kestrels and pigeons, with similar prevalence and intensity (prevalence: Fisher test: p = 1.00; intensity: bootstrap 2-sample t-test: t= -1.45, d.f. = 22.65, p = 0.160) and louse flies were mostly found in pigeon nests (Table 3.2).

3.2 INFLUENCE OF COLONY TRAITS ON ECTOPARASITE INFRACOMMUNITY IN MIXED-SPECIES COLONIES

The partial Canonical Correspondence Analysis (CCA), conditioned by sampling date, brood size, and colony ID, revealed that host species was the only predictor of parasite infracommunity (in terms of presence/absence), being the only variable selected following both forward and backward selection processes (final CCA adjusted R-squared = 0.18; $X^2 = 0.2$, F = 18.2, p-value = 0.001). Conditioned and constrained partitioning explained 27.0% and 16.7% of the total inertia, respectively ("variance", total inertial = 1.11). The ectoparasite infracommunity of each host species was best described by the presence of louse flies, followed by lice and mites (Fig. 3.2). Louse flies were clearly associated with pigeons and lice commonly infested pigeons and lesser kestrels. Mites showed a positive association with starlings, rollers, and pigeons, whereas *Carnus* was negatively associated with pigeons (see also Table 3.2).

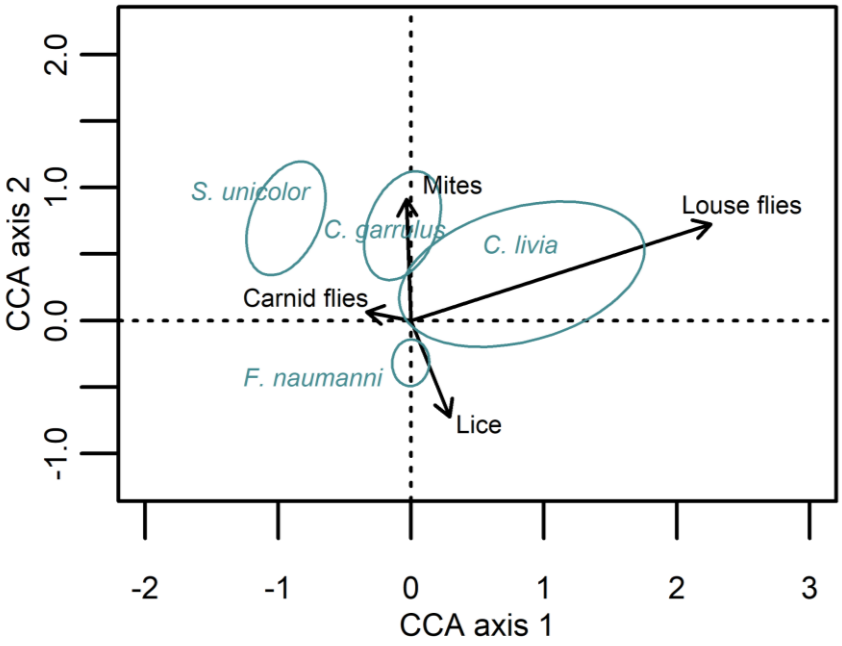


Figure 3.2: Biplot (scaling 3) of the partial Canonical Correspondence Analysis (CCA), showing the relationship between the occurrence of ectoparasites and host species, the only explanatory variable selected after forward and backward selection. Statistics: CCA1: $X^2 = 0.10$, F = 29.0, p-value = 0.001; CCA2: $X^2 = 0.08$, F = 24.9, p-value = 0.001. Sample size = 240 nests (139 lesser kestrels, 29 rollers, 33 pigeons, 39 starlings).

3.3 INFLUENCE OF COLONY TRAITS ON *CARNUS HEMAPTERUS* ABUNDANCE IN MIXED-SPECIES COLONIES

Host species had a significant influence on *Carnus* abundance, being highest in rollers and followed by lesser kestrels, starlings, and pigeons (the reference level) (Table 3.3). Model averaging revealed that *Carnus* abundance increased significantly with brood size and marginally significantly with increasing numbers of lesser kestrel nests in the colony. In contrast, it decreased significantly with increasing numbers of starlings' nests. The abundance of carnid flies also decreased, although marginally significantly, in clay pots when compared to other types of nests. Colony density had no influence on *Carnus* abundance. The models with ΔAICc <2 after model averaging and the best two models can be found in tables 3.A1 and 3.A2, respectively, in the Supplementary Material.

Table 3.3: Results of model averaging on the effect of colony traits on Carnus hemapterus abundance in mixed-species colonies using nests from all four host species (lesser kestrels, rollers, pigeons, and starlings).

Parameter	**Estimate**	**Adjusted SE**	**Z value**	**P-value**	**Relative Importance**
Intercept	0.725	0.310	2.342	0.019	
N lesser kestrel nests	0.137	0.077	1.777	0.076	0.63
N starling nests	**-0.200**	**0.089**	**2.237**	**0.025**	**0.74**
Brood size	**0.274**	**0.091**	**3.023**	**0.003**	**0.99**
Host: roller	**3.117**	**0.380**	**8.204**	**<0.001**	**1.00**
Host: lesser kestrel	**2.185**	**0.316**	**6.921**	**<0.001**	
Host: starling	**0.917**	**0.313**	**2.930**	**0.003**	
Sampling date	-0.006	0.092	0.066	0.947	0.24
Artificial cavities	-0.128	0.268	0.477	0.633	0.19
Clay pots	-0.612	0.332	1.843	0.065	
Wooden nest-boxes	-0.177	0.265	0.667	0.505	
Medium density	-0.114	0.213	0.534	0.593	0.11
High density	-0.141	0.276	0.512	0.609	

- Entry model: *Carnus* abundance ~ host species + brood size + sampling date + nest type + colony density (Cat) + number of lesser kestrel nests + number of starling nests + (1|colony ID); Sample size = 230 nests (132 lesser kestrels, 28 rollers, 31 pigeons, 39 starlings).

- Values reported are conditional averages and adjusted SE. *Carnus* abundance was studied using GLMMs following a negative binomial distribution of errors to account for its aggregated distribution among hosts. Colony ID was used as random factors. N, number of; Cat, categorical; ID, identity.

4. DISCUSSION

This study provides information on the ecology of avian parasitism in mixed-species colonies. To our knowledge, there is little information on the factors influencing host infestation by ectoparasites in colonies formed by multiple species of hosts and even less at the parasite infracomunity level. Four main ectoparasite groups – carnid flies, louse flies, lice, and mites – in four different host species were analysed, including the conservation reliant lesser kestrel and European roller (Gameiro et al. 2020). It was found that the main driver for the differences in composition of the ectoparasite infracommunity was the identity of the host species, regardless of colony traits such as size, density, or richness. Accordingly, variation in the abundance of the most common ectoparasite (*Carnus*) in these mixed-species assemblages was explained by colony composition (number of nests of each host species), rather than by overall colony size or density.

4.1 ECTOPARASITE INFRACOMMUNITY IN BIRDS BREEDING IN MIXED-SPECIES COLONIES

The importance of host species identity for ectoparasite ecology has already been described in small mammals (Krasnov et al. 2008; Lareschi and Krasnov, 2010). These results suggest that the four host species vary in their susceptibility (sensu Martin et al. 2019) to different ectoparasite groups (Keesing et al. 2006). Even the prevalence and intensity of *Carnus, the* most common and broadly considered generalist species (Veiga et al. 2019), varied considerably between hosts. Nest- and host-related characteristics may account for some of the differences found, as suggested by our results on *Carnus*. Pigeons and starlings were the least attractive hosts. These bird species use vegetable material when building their nests, which was found to be avoided by *Carnus* (Valera et al. 2006b; Valera et al. 2018). Pigeons also accumulate droppings inside the cavity that may limit the suitability of the detritus for the larval and pupal stages of this ectoparasite (Veiga et al. 2019). Carnid flies seemingly also prefer rollers to lesser kestrels since the former bird species holds more than twice as many *Carnus* as lesser kestrels. Nestling kestrels are born with a down feather coat that may hinder the access to blood by ectoparasites, when compared to the naked body of roller nestlings.

Mites also infested all host species but were less prevalent and abundant on lesser kestrels. In a dry climate like the one of the study area, the humidity required by mites (Nordenfors et al. 1999) may be secured by the vegetable material used in starling or pigeon nests, when compared to a mostly sandy substratum of lesser kestrel or roller nests. However, as rollers arrive later to the breeding grounds from their spring migration, they are likely to re-use a nest previously occupied by starlings or pigeons (hence more humid), potentially explaining why rollers had higher prevalence of mites than lesser kestrels (see below and Veiga et al. 2020).

The factors accounting for differences in prevalence of lice and louse flies among host species are not so clear and their identification goes beyond the aims of our study. Nonetheless, it is worth reporting such differences in mixed colonies where the contact among species and individuals can facilitate transmission. Lice were mostly present on lesser kestrels and pigeons, with just a single louse found on one starling nestling and none on rollers. Although lice were not identified to the species level, these ectoparasites are considered species-specific and no studies were found reporting the same lice species infecting both pigeons and lesser kestrels (Rózsa 1990; Ortego et al. 2007; Calabuig et al. 2010; Galloway and Lamb 2015). Factors such as gregariousness can explain why species like pigeons or lesser kestrels have many lice. In contrast, species usually breeding in low densities (*e.g.,* rollers) could be less appropriate for lice. Because chewing lice are mostly found on feathers, they may be more common and abundant on post-fledging juveniles or adults, when compared to young nestlings (Liker et al. 2001; Ortego et al. 2007). Louse flies were found almost exclusively on pigeons, with only three lesser kestrel and one roller nest infested and no starling nest infested. Examination of six louse flies demonstrates that at least three different species occur in our study area: *Pseudolynchia canariensis* in pigeons and lesser kestrels, *Ornithophila gestroi* in lesser kestrels, and *Hippobosca longipennis* in rollers. *Pseudolynchia canariensis* has a wide host range and is common in pigeons and in the *Falco* genus (Maa, 1966), although to the authors' knowledge this the first time *P. canariensis* is reported in lesser kestrels. *Ornithophila gestroi* has already been reported in lesser kestrels, with similar abundances but at higher prevalence than the one found in this study (Tella et al. 1997). *Hippobosca longipennis* is an ectoparasite typically found in carnivores (Maa, 1969; Mihalca et al. 2019). Besides anecdotal references, there are no clear reports of *H. longipennis* on birds, so that this finding can be also considered circumstantial. Yet, the clear pattern found (preference of louse flies for pigeons) could be explained either by a higher abundance of the louse fly species typical of this particular host and/or interspecific differences in the suitability of each host species and their nests characteristics for the co-existing louse fly species (*e.g.,* Veiga et al. 2019). Understanding the pattern of occurrence of these parasites and what factors contribute to the interspecific differences found here requires detailed knowledge of the natural history and host choice criteria of these species and goes beyond the aims of this study. Nonetheless, it is important to remark that even in situations favouring intra and interspecific parasite transmission, clear preference patterns are evident.

4.2 ECTOPARASITE ABUNDANCE IN MIXED-SPECIES COLONIES IS MOSTLY DRIVEN BY COLONY COMPOSITION RATHER THAN COLONY SIZE OR DENSITY

It has been widely acknowledged that social breeding incurs in higher risk of parasite and pathogen transmission, with larger, denser colonies, having higher prevalence and intensity of ectoparasites, even in mobile, non-contact-transmitted species (Brown and Brown 1986; Côté and Poulin 1995; Hoi et al. 1998; Kleindorfer and Dudaniec 2009; Veiga et al. 2020). Most of these studies have focused on mono-specific colonies or on single parasites species, overlooking the complex multi-species associations that often occur in nature (Valera et al. 2003). This study's results on mixed-species colonies suggest that colony size, density or richness, common characteristics used to measure host sociality, do not affect the infracommunity of ectoparasites in each host, nor the abundance of the generalist *Carnus*. Although the correlation among these variables prevented the identification of the isolated effect of each trait, none were selected using a model-averaging approach, suggesting a lack or weak effect of these variables in our study system. Instead, host species was the main predictor for *Carnus* abundance. Besides colony composition, which will be discussed below, *Carnus* abundance was found to increase with brood size. More nestlings in a nest means more food resources for ectoparasites and higher heat and CO_2 emissions that may facilitate nest detection. Thus, an increase in *Carnus* abundance with larger broods was expected (see also Veiga et al. 2020). In contrast to previous results (Calero-Torralbo et al. 2013; Veiga et al. 2020), the abundance of *Carnus* was not influenced by sampling date - a proxy of *Carnus* emergence patterns. But, contrary to these studies, the results reported here consider simultaneously different host species, so the lack of a global effect of date may be related with merging host species with different breeding phenologies, number of clutches and nestling development rates. There was also no influence of type of nest except for a marginally significant decrease in clay plots. Clay pots are shallower than cavities or nest-boxes, and some of them have a low (sometimes almost inexistent) amount of detritus, which may inhibit egg deposition or larvae development by *Carnus*.

The main finding of this study is that in mixed-species assemblages, rather than colony size or density, it is the composition of the colony – the number of nests of the various host species –

that influences the abundance of the most common ectoparasite. *Carnus* abundance decreased with increasing number of starling nests and increased with increasing numbers of lesser kestrels. Because *Carnus* mean intensity varied considerably between hosts, with lesser kestrels hosting more than three times more *Carnus* than starlings, starling-dominated colonies will have lower *Carnus* loads than lesser kestrel dominated ones. If the proportion of less competent hosts like starlings increases in a mixed colony, then the total amount of ectoparasites will decrease. A dilution effect is occurring by "adding" less competent host species, starlings (or pigeons), to the colony (Johnson and Thieltges 2010; Civitello et al. 2015). Because most *Carnus*' life stages occur in the nest (Valera et al. 2006a), *Carnus* will produce less offspring in a colony dominated by less suitable hosts than in a colony with more suitable hosts. In parallel, the number of *Carnus* will increase in colonies with increasing number of preferred hosts such as lesser kestrels and rollers. This suggests that increasing colony diversity would only result in a dilution effect – decreasing parasitism – if the added host species are less suitable for a given parasite. For instance, pigeons are avoided by *Carnus* but are preferred by *P. canariensis* (Veiga et al. 2019). Thus, having pigeons in colonies may decrease *Carnus* abundance but increase *P. canariensis* in lesser kestrel nests.

The findings of this study must be considered in the light of some limitations. Colony size, density, and host richness were correlated so that larger colonies also tended to have higher nest density and higher richness of hosts. This prevented the investigation of the effect of each colony trait, only allowing the comparison between smaller colonies (less dense and less rich) from larger ones (denser and richer). Increasing the sample size (which was not possible for this study due to logistics constrains) could potentially allow for the investigation of the correlation/interaction between colony traits and reveal other effects the authors have been unable to detect. However, because large colonies had different host species composition – some dominated by lesser kestrels and others by starlings – this study was able to untwine the effects of colony composition on ectoparasite infestation patterns. Also, as opposed to similar works (Veiga et al. 2019), nests in this study were not sanitized before sampling. As such, ectoparasites that spend most of their life cycle in the nest, such as carnid flies, were not removed, and so the prevalence and abundance (and their variability) found in this study may have been at least partially influenced by the outcome of previous breeding seasons (Valera et al 2006a). Nonetheless, results from this study suggest that the host species occupying the focal nest in the previous year had no effect (variable not selected) on the ectoparasite infracommunity nor on *Carnus* abundance. The influence of the abundance of ectoparasites during the previous season may be diluted for several reasons. For instance, *C. hemapterus* – arguably the most nest-based ectoparasite from the ones addressed – was found to rapidly colonize new (and clean) nests and to discriminate between potential hosts, favouring some of them (Veiga et al. 2019, 2020). Moreover, insect predation after the breeding season may decrease the abundance of carnid pupae (Salido et al. in press). These facts suggest that our approach may have had little impact on the results found for mobile ectoparasites (carnid flies and louse flies) and for parasites spending all their life cycle on the host's body (e.g., lice). On the other side, by examining uncleaned nests, this study reflects more closely the natural conditions than studies using sanitized nests, and thus our results are likely to apply to birds breeding in natural assemblages (Møller, 1989). Lastly, this study examines ectoparasite groups instead of individual species. This limits our capacity to establish species-specific parasite-host relationships, but it does not preclude disentangling the effects of colony traits on the general patterns of ectoparasite infestations.

4.3 FINAL CONSIDERATIONS

Previous studies on monospecific colonies have found a positive correlation between colony size and density and *C. hemapterus* infestations (Hoi et al. 1998, 2010; Veiga et al. 2020, but see Liker et al. 2001). The present study in mixed-species colonies revealed that colony traits such as size, density, richness, or composition, had no effect on ectoparasite presence, with each avian host maintaining a distinct ectoparasite infracommunity. It also revealed that colony composition, rather than colony size or density, influenced the infestation of the most common ectoparasite in these assemblages. *Carnus* can be found from North America to Europe and Asia infesting a wide range of bird species, so the implications of this study go beyond our study area (Grimaldi, 1997; Brake, 2011; Ganbold et al. 2020). The association between farmland buildings or artificial nests and secondary cavity nesters such as lesser kestrels and rollers is common in other European counties, such as Spain and Italy (Campobello et al. 2012; Negro et al. 2020). Similar natural species assemblages occur in sandstone cliffs and bridges (e.g., in south Spain), where many species, including the ones studied here (and others such as common kestrels, little owls, jackdaws, bee-eaters *Merops apiaster*, and rock sparrows *Petronia petronia*) coexist and re-use the same natural and man-made cavities (Valera et al. 2003; Veiga et al. 2020). Lesser kestrel colonies throughout Europe that rely on man-made buildings are also likely comprised by other species (Blanco & Tella 1997; Campobello et al. 2012). Densities in these "natural scenarios" are likely lower than in artificial breeding towers, but it may depend on ecological circumstances like availability of nest-sites). Our results that larger colonies do not necessarily translate into higher risk of ectoparasite transmission, and that this effect is influenced by the species composition of the colonies, are likely applicable to other mixed-species colonies of birds or even other non-bird mixed-species groups (Goodale et al., 2020). Yet, the exact outcome may vary depending on the specific parasites and hosts forming the assemblages. The interpretation of the ecological relationships between parasites and hosts should consider the interactions occurring among different hosts and their parasites and should be studied as they occur in nature, i.e., considering mixed-species assemblages, which are often overlooked despite being widespread. More studies on the natural history of ectoparasites and on host-parasite interactions in multi-species group living are clearly needed to fully understand the complex relationships between parasites and sociality.

5. ACKNOWLEDGEMENTS

We would like to thank Liga para a Proteção da Natureza (LPN) for the access to the colonies within the Castro Verde Special Protection Area, and to Instituto da Conservação da Natureza e Florestas (ICNF) for giving us the permission to sample bird’s nests. We thank all contributors who helped during field work and data collection. We would also like to thank the editor Helene Carabin and three anonymous reviewers for their valuable suggestions, which have greatly improved this manuscript. This work was supported by cE3c (UIBD/00329/2020) and InBIO (UID/BIA/50027/2013), to FCT through national funds. IC was supported by a contract DL57/2016/CP1440/CT0023 and JG by a doctoral grant (PD/BD/128366/2017) from the Portuguese Foundation for Science and Technology (FCT). F.V. received financial support from the project PGC2018-097426-B-C22 (MCIU/AEI/FEDER, UE). J.V. was funded by a predoctoral grant (BES-2015-075951) of the Spanish Ministry of Economy, Industry and Competitiveness. The funding sources had no direct involvement in the study design or in the collection, analysis, and interpretation of data.

Ethical Standards: Trapping and handling of birds during this study was approved by Instituto da Conservação da Natureza e Florestas (License 547/2018/CAPT).

6. REFERENCES

Arriero, E., Møller, A.P., 2008. Host ecology and life-history traits associated with blood parasite species richness in birds. Journal of Evolutionary Biology 21: 1504-1513. https://doi.org/10.1111/j.1420-9101.2008.01613.x

Bartón, K., 2020. MuMIn: multi-model inference. https://cran.r-project.org/web/packages/MuMIn/index.html.

Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R.H.B., Singmann, H., Dai, B., Scheipl, F., Groethendieck, G., Green, P., Fox, J., Bauer, A., Krivitsky, P., 2020. lme4: Linear mixed-effects models using "Eigen" and S4. https://cran.r-project.org/web/packages/lme4/index.html.

Beldomenico, P.M., Begon, M., 2010. Disease spread, susceptibility and infection intensity: vicious circles? Trends in Ecology and Evolution 25: 21-27. https://doi.org/10.1016/j.tree.2009.06.015.

Blanco, G., Tella, J.L., 1997. Protective association and breeding advantages of coughs nesting in lesser kestrel colonies. Animal Behaviour 54 (2): 335-342. https://doi.org/10.1006/anbe.1996.0465.

Borcard, D., Gillet, F., Legendre, P., 2011. Numerical Ecology with R. New York, USA: Springer Science and Business Media.

Boyd, E., 1951. The external Parasites of Birds: A Review. Wilson Bulletin 63, 363-369.

Brake, I., 2011. World Catalog of the Family Carnidae (Diptera, Schizophora). Myia 12, 113-169.

Brown, C.R., Brown, M.B., 2004. Group size and ectoparasitism affect daily survival probability in a colonial bird. Behavioural Ecology and Sociobiology 56: 498-511. https://doi.org/10.1007/s00265-004-0813-6.

Brown, C.R., Brown, M.B., 1986. Ectoparasitism as a cost of coloniality in Cliff Swallows (Hirundo pyrrhonota). Ecology 67, 1206-1218.

Brown, C.R., Roche, E.A., Brown, M.B., 2017. Why come back home? Breeding-site fidelity varies with group size and parasite load in a colonial bird. Animal Behaviour 132: 167-180. https://doi.org/10.1016/j.anbehav.2017.08.009.

Burtt, E.H., Chow, W., Babbit, G.A., 1991. Occurrence and demography of mites of tree swallow, house wren and eastern bluebird nests. In Loye, JE, Zuk, M (eds). Bird-Parasite interactions: Ecology, Evolution and Behaviour. Oxford, UK: Oxford University Press, pp. 104-122.

Bush, A.O., Lafferty, K.D., Lotz, J.M., Shostak, A.W., 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. Journal of Parasitology 83: 575-583.

Calabuig, G., Ortego, J., Cordero, P.J., Aparicio, J.M., 2010. Colony foundation in the lesser kestrel: Patterns and consequences of the occupation of empty habitat patches. Animal Behaviour 80: 975-982. https://doi.org/10.1016/j.anbehav.2010.08.016.

Calero-Torralbo, M.A., Václav, R., Valera, F., 2013. Intra-specific variability in life-cycle synchronization of an ectoparasitic fly to its avian host. Oikos 122: 274–284. https://doi.org/10.1111/j.1600-0706.2012.20374.x.

Calero-Torralbo, M.A., Valera, F., 2008. Synchronization of host-parasite cycles by means of diapause: Host influence and parasite response to involuntary host shifting. Parasitology 135: 1343-1352. https://doi.org/10.1017/S0031182008004885.

Campobello, D., Sarà, M., Hare, J.F., 2012. Under my wing: Lesser kestrels and jackdaws derive reciprocal benefits in mixed-species colonies. Behavioural Ecology 23: 425-433. https://doi.org/10.1093/beheco/arr207.

Catry, I., Alcazar, R., Franco, A.M.A., Sutherland, W., 2009. Identifying the effectiveness and constraints of conservation interventions: A case study of the endangered lesser kestrel. Biological Conservation 142: 2782-2791. https://doi.org/10.1016/j.biocon.2009.07.011.

Catry, I., Catry, T., Patto, P., Franco, A.M.A., Moreira, F., 2015. Differential heat tolerance in nestlings suggest sympatric species may face different climate change risks. Climate Research 66: 13-24. https://doi.org/10.3354/cr01329.

Catry, T., Catry, I., 2019. Nest-site provisioning re-shapes species interactions within bird assemblages. Ibis 161: 699-704. https://doi.org/10.1111/ibi.12731.

Civitello, D.H., Choen, J., Fatima, H., Halstead, N.T., Liriano, J., McMahon, T.A., Ortega, C.N., Sauer, E.L., Sehgal, T., Young, S., Rohr, J.R., 2015. Biodiversity inhibits parasites: Broad evidence for the dilution effect. Proceedings of the National Academy of Sciences of the United States of America 112: 8667-8671. https://doi.org/10.1073/pnas.1506279112.

Clayton, D.H., Adams, R.J., Bush, S.E., 2008. Phthiraptera, the chewing lice. In Atkinson CT, Thomas NJ, Hunter DB (eds). Parasitic diseases of wild birds. Iowa, USA, Whiley-Blackwell, 515-526.

Clayton, D.H., Tompkins, D.M., 1995. Comparative effects of mites and lice on the reproductive success of rock doves (Columba livia). Parasitology 110: 195-206.

Côté, I.M., Poulin, R., 1995. Parasitism and group size in social animals: A meta-analysis. Behavioural Ecology 6: 159-165. https://doi.org/10.1093/beheco/6.2.159.

Davis, J.A., Brown, C.R., 1999. Costs of coloniality and the effect of colony size on reproductive success in purple martins. The Condor 101: 737-745. https://doi.org/10.2307/1370060.

Gaglio, D., Sherley, R.B., Cook, T.R., Ryan, P.G., Flower, T., 2018. The costs of kleptoparasitism: A study of mixed-species seabird breeding colonies. Behavioural Ecology 29: 939-947. https://doi.org/10.1093/beheco/ary050.

Galloway, T.D., Lamb, R.J., 2015. Seasonal populations dynamics of four species of chewing lice (Phthiraptera: Menoponidae, Philopteridae) on feral pigeons (Aves: Columbiformes: Columbidae). Canadian Entomologist 147: 712-722. https://doi.org/10.4039/tce.2014.84.

Gameiro, J., Franco, A.M.A., Catry, T., Palmeirim, J.M., Catry, I., 2020. Long-term persistence of conservation-reliant species: Challenges and opportunities. Biological Conservation 243. https://doi.org/10.1016/j.biocon.2020.108452.

Ganbold, O., Azua, J., Munkhbayar, M., Khuderchuluun, O., Paek, W.K., Purevee, E., Chuluunbat, S., Reading, R.P., 2020. First records of the parasitic flies Carnus hemapterus and Ornithophilia gestroi on lesser kestrels (Falco naumanni) in Mongolia. Journal of Raptor Research 54: 66-73. https://doi.org/10.3356/0892-1016-54.1.66.

Goodale, E., Sridhar, H., Sieving, K.E., Bangal, P., Colorado Z., G.J., Farine, D.R., Heymann, E.W., Jones, H.H., Krams, I., Martínez, A.E., Montaño-Centelles, F., Muñoz, J., Srinivasan, U., Theo, A., Shanker, K., 2020. Mixed company: A framework for understanding the composition and organization of mixed-species animal groups. Biological Reviews 95: 889-910. https://doi.org/10.1111/brv.12591.

Grimaldi, D.A., 1997. The bird flies, genus Carnus: species revision, generic relationships, and a fossil Meoneura in amber (Diptera, Carnidae). American Novitates. American Museum of Natural History, New York, USA.

Grueber, C.E., Nakagawa, S., Laws, R.J., Jamieson, I.G., 2011. Multimodel inference in ecology and ecolution: Challenges and solutions. Journal of Evolutionary Biology 24: 699-711. https://doi.org/10.1111/j.1420-9101.2010.02210.x.

Halsey, S., 2018. Defuse the dilution effect debate. Nature Ecology & Evolution 3: 145-146. https://doi.org/ 10.1038/s41559-018-0764-3.

Hoi, H., Darolová, A., König, C., Krištofík, J., 1998. The relation between colony size, breeding density and ectoparasite loads of adult European bee-eaters (Merops apiaster. Ecoscience 5: 156-163. https://doi.org/10.1080/11956860.1998.11682455.

Hoi, H., Darolová, A., Krištofík, J., Hoi, C., 2018. The effect of the ectoparasite Carnus hemapterus on immune defence, condition and health of nestling European Bee-eaters. Journal of Ornithology 159: 291-302. https://doi.org/10.1007/s10336-017-1500-5.

Hoi, H., Krištofík, J., Darolová, A., Hoi, C., 2010. Are parasite intensity and related costs of the milichiid fly Carnus hemapterus related to host sociality? Journal of Ornithology 151: 907-913. https://doi.org/10.1007/s10336-010-0529-5.

Holt, R.D., Dobson, A.P., Begon, M., Bowers, R.G., Schauber, E.M., 2003. Parasite establishment in host communities. Ecology Letters 6: 837-842. https://doi.org/10.1046/j.1461-0248.2003.00501.x.

Johnson, P.T.J., Thietlges, D.W., 2010. Diversity, decoys and the dilution effect: How ecological communities affect disease risk. Journal of Experimental Biology 213: 961-970. https://doi.org/10.1242/jeb.037721.

Johnston, R., Janiga, M., 1995. Feral Pigeons. New York, USA: Oxford University Press.

Kappeler, P.M., Cremer, S., Nunn, C.L., 2015. Sociality and health: Impacts of sociality on disease susceptibility and transmission in animal and human societies. Philosophical Transactions B 370. https://doi.org/10.1098/rstb.2014.0116.

Keesing, F., Holt, R.D., Ostfeld, R.S., 2006. Effects of species diversity on disease risk. Ecology Letters 9: 485-498. https://doi.org/10.1111/j.1461-0248.2006.00885.x.

Keindorfer, S., Dudaniec, R.Y. 2009. Love thy neighbour? Social nesting pattern, host mass and nest size affect ectoparasite intensity in Darwin's tree finches. Behavioral Ecology and Sociobiology 63: 731-739. https://doi.org/10.1007/s00265-008-0706-1.

Krasnov, B.R., Korallo-Vinarskaya, N.P., Vinarksi, M.V., Shenbrot, G.I., Mouillot, D., Poulin, R., 2008. Searching for general patterns in parasite ecology: Host identity versus environmental influence on gamasid mite assemblages in small mammals. Parasitology 135: 229-242. https://doi.org/10.1017/S003118200700368X.

Lareschi, M., Krasnov, B.R., 2010. Determinants of ectoparasite assemblage structure on rodent hosts from South American marshlands: The effect of host species, locality and season. Medical and Veterinary Entomology 24: 284-292. https://doi.org/10.1111/j.1365-2915.2010.00880.x

Liker, A., Márkus, M., Vozár, A., Zemankovics, E., Rózsa, L., 2001. Distribution of Carnus hemapterus in a starling colony. Canadian Journal of Zoology 79: 574-580. https://doi.org/10.1139/cjz-79-4-574.

Maa, T.C., 1969. A revised checklist and concise host index of Hippoboscidae (Diptera). Pacific Insects Monograph 20: 261-299.

Maa, T.C., 1966. On the genus Pseudolynchia Bequart. Pacific Insects Monograph 10: 125-138.

Martin, L.B., Addison, B., Bean, A.G.D., Buchanan, K.L., Crino, O.L., Eastwood, J.R., Flies, A.S., Hamede, R., Hill, G.E., Klaassen, M., Koch, R.E., Martens, J.M., Napolitano, C., Narayan, E.J., Peacock, L., Peel, A.J., Peters, A., Raven, N., Risely, A., Roast, M.J., Rollins, L.A., Ruiz-Aravena, M., Selechnik, D., Stokes, H.S., Ujvari, B., Grogan, L.F., 2019. Extreme competence: keystone hosts of infections. Trends in Ecology and Evolution 34: 303-314. https://doi.org/10.1016/j.tree.2018.12.009.

Merino, S., Potti, J., 1995. Mites and blowflies decrease growth and survival in nestling pied flycatchers. Oikos 73: 95-103.

Mihalca, A.D., Păstrav, I.R., Sándor, A.D., Deak, G., Gherman, C.M., Sarmaşi, A., Votýpka, J., 2019. First report of the dog louse fly Hippobosca longipennis in Romania. Medical and Veterinary Entomology 33: 530-535. https://doi.org/10.1111/mve.12395.

Møller, A.P., 1989. Parasites, predators and nest boxes: facts and artefacts in nest box studies of birds? Oikos 56: 421-423.

Møller, A.P., Dufva, R., Allander, K., 1993. Parasites and the evolution of host social behaviour. In Advances in the study of behaviour Vol. 22. London, UK: Academic Press, pp. 65-102.

Muñoz, A.P., Pomarol, M., Castella, J., Gutierrez, J., Galmes, M., 1993. Ornithophilia gestroi (Rodani, 1878) (Diptera: Hippoboscidae) on Falco tinnunculus and Falco naumanni in Monegros (Aragon, Spain). Research and Reviews in Parasitology 53: 71-72.

Muriel, J., Pérez-Rodríguez, L., Puerta, M., Gil, D., 2013. Differential effects of yolk testosterone and adrostenedione in embryo development and nestling growth in the spotless starling (Sturnus unicolor). General and Comparative Endocrinology 194: 175-182. https://doi.org/10.1016/j.ygcen.2013.09.013.

Negro, J.J., Prenda, J., Ferrero, J.J., Rodríguez, A., Reig-Ferrer, A., 2020. A timeline for the urbanization of wild birds: the case of the lesser kestrel. Quaternary Science Reviews 249. https://doi.org/10.1016/j.quascirev.2020.106638.

Nordenfors, H., Höglund, J., Uggla, A., 1999. Effects of temperature and humidity on oviposition, molting, and longevity of Dermanyssus gallinae (Acari: Dermanyssidae). Journal of Medical Entomology 36: 68-72. https://doi.org/10.1093/jmedent/36.1.68.

Oksanen, J., 2020. Vegan: Community ecology package. R-package Vegan. https://cran.r-project.org/web/packages/vegan/index.html.

Ortego, J., Aparicio, J.M., Calabuig, G., Cordero, P.J., 2007. Risk of ectoparasitism and genetic diversity in a wild lesser kestrel population. Molecular Ecology 16: 3712-3720. https://doi.org/10.1111/j.1365-294X.2007.03406.x.

Patterson, J.E.H., Ruckstuhl, K.E., 2013. Parasite infection and host group size: A meta-analytical review. Parasitology 140: 803-813. https://doi.org/10.1017/S0031182012002259.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R Core Team, 2020. Nlme: linear and nonlinear mixed effects models. https://cran.r-project.org/web/packages/nlme/index.html.

Poulin, R., 1991. Group-living and infestation by ectoparasites in passerines. The Condor 2: 418-423. https://doi.org/10.2307/1368958.

Poulin, R., 2007. Are there general laws in parasite ecology? Parasitology 134: 763-776. https://doi.org/10.1017/S0031182006002150.

R Core team, 2016. A language and environment for statistical computing. https://www.r-project.org/.

Randolph, A.E., Dobson, A.D.M., 2012. Pangloss revisited: a critique of the dilution effect and the biodiversity-buffers-disease paradigm. Parasitology 139: 847-863. https://doi.org/10.1017/S0031182012000200.

Roulin, A., 1998. Cycle de reproduction et abondance du diptère parasite Carnus hemapterus dans les niches de chouettes effraies Tyto alba. Alauda 66: 265-272.

Rózsa, L., 1990. The ectoparasite fauna of feral pigeon populations in Hungary. Parasitology Hungarica 23: 115-119.

Rózsa L., Reiczigel, J., Majoros, G., 2000. Quantifying parasites in samples of hosts. Journal of parasitology 86: 228-232. https://doi.org/10.1645/0022-3395(2000)086[0228:QPISOH]2.0.CO;2.

Rózsa, L., Rékási, J., Reiczigel, J., 1996. Relationship of host coloniality to the population ecology of avian lice (Insecta: Phthiraptera). Journal of Animal Ecology 65: 242-248. https://doi.org/10.2307/5727.

Salido, A., Veiga, J., Reyes-Lopez, J.L., Nieves-Aldrey, J.L., Valera, F., 2021 Insect predation reduces the abundance of a nidicolous ectoparasite. Ecological Entomology 46 (4): 988-998. https://doi.org/10.1111/een.13036.

Sans-Aguilar, A., Payo-Payo, A., Rotger, A., Yousfi, L., Moutailler, S., Beck, C., Dumarest, M., Igual, J.M., Miranda, M.Á., Torres, M.V., Picorelli, V., Gamble, A., Boulinier, T., 2020. Infestation of small seabirds by Ornithodoros maritimus ticks: effects on chick body condition, reproduction and associated infectious agents. Ticks and Tick-borne diseases 11. https://doi.org/10.1016/j.ttbdis.2019.101281.

Tella, J.L., 2002. The evolutionary transition to coloniality promotes higher blood parasitism in birds. Journal of Evolutionary Biology 15: 32-41. https://doi.org/10.1046/j.1420-9101.2002.00375.x.

Tella, J.L., Forero, M.G., Donázar, J.Á., Negro, J.J., Hiraldo, F., 1997. Non-adaptive adoptions of nestlings in the colonial lesser kestrel: Proximate causes and fitness consequences. Behavioral Ecology and Sociobiology 40: 253-260. https://doi.org/10.1007/s002650050340.

Tella, J.L., Gajón, A., Gortázar, C., Osácar, J.J., 1998. High host specificity of Crataerina melbae (Diptera: Hippoboscidae) in a mixed colony of birds. Journal of Parasitology 84: 198-200.

Václav, R., Calero-Torralbo, M.A., Valera, F., 2008. Ectoparasite load is linked to ontogeny and cell-mediated immunity in an avian host system with pronounced hatching asynchrony. Biological Journal of the Linnean Society 94: 463-473. https://doi.org/10.1111/j.1095-8312.2008.00985.x.

Václav, R., Valera, F., 2018. Host preference of a haematophagous avian ectoparasite: A micronutrient supplementation experiment to test an evolutionary trade-off. Biological Journal of the Linnean Society 125: 171-183. https://doi.org/10.1093/BIOLINNEAN/BLY089.

Valera, F., Casas-Crivillé, A., Calero-Torralbo, M.A., 2006a. Prolonged diapause in the ectoparasite Carnus hemapterus (Diptera: Cyclorrhapha, Acalyptratae) – How frequent is it in parasites? Parasitology 133: 179-186. https://doi.org/10.1017/S0031182006009899.

Valera, F., Casas-Crivillé, A., Hoi, H., 2003. Interspecific parasite exchange in a mixed colony of birds. Journal of Parasitology 89: 245-250. https://doi.org/10.1645/0022-3395(2003)089[0245:IPEIAM]2.0.CO;2.

Valera, F., Martín-Vivaldi, M., Carles-Tolrá, M., 2006b. Life-history variation in three coexisting species of carnid flies (Diptera: Carnidae), Carnus hemapterus, Hemeromyia anthracina and Hemeromyia longirostris. European Journal of Entomology 103: 347-353. https://doi.org/10.14411/eje.2006.045.

Valera, F., Veiga, J., Sandoval, A., Moreno, E., 2018. Coexistence, habitat associations and puparia description of three dipteran species of the Family Carnidae. Parasitology Open 4: 1-9. https://doi.org/10.1017/pao.2017.23.

Veiga, J., De Oña, P., Salazar, B., Valera, F., 2019. Defining host range: host-parasite compatibility during the non-infective phase of the parasite also matters. Parasitology 146: 1-7. https://doi.org/10.1017/S0031182018001233.

Veiga, J., Václav, R., Valera, F., 2020. The effect of parasite density on host colonisation success by a mobile avian ectoparasite. Ecological Entomology 45: 867-875. https://doi.org/10.1111/een.12864.

Veiga, J., Valera, F., 2020. Nest box location determines the exposure of the host to ectoparasites. Avian Conservation and Ecology 15. https://doi.org/10.5751/ace-01657-150211.

Whiteman, N.K., Parker, P.G., 2004. Effects of host sociality on ectoparasite population biology. Journal of Parasitology 90: 939-947. https://doi.org/10.1645/GE-310R.

7. APPENDIX

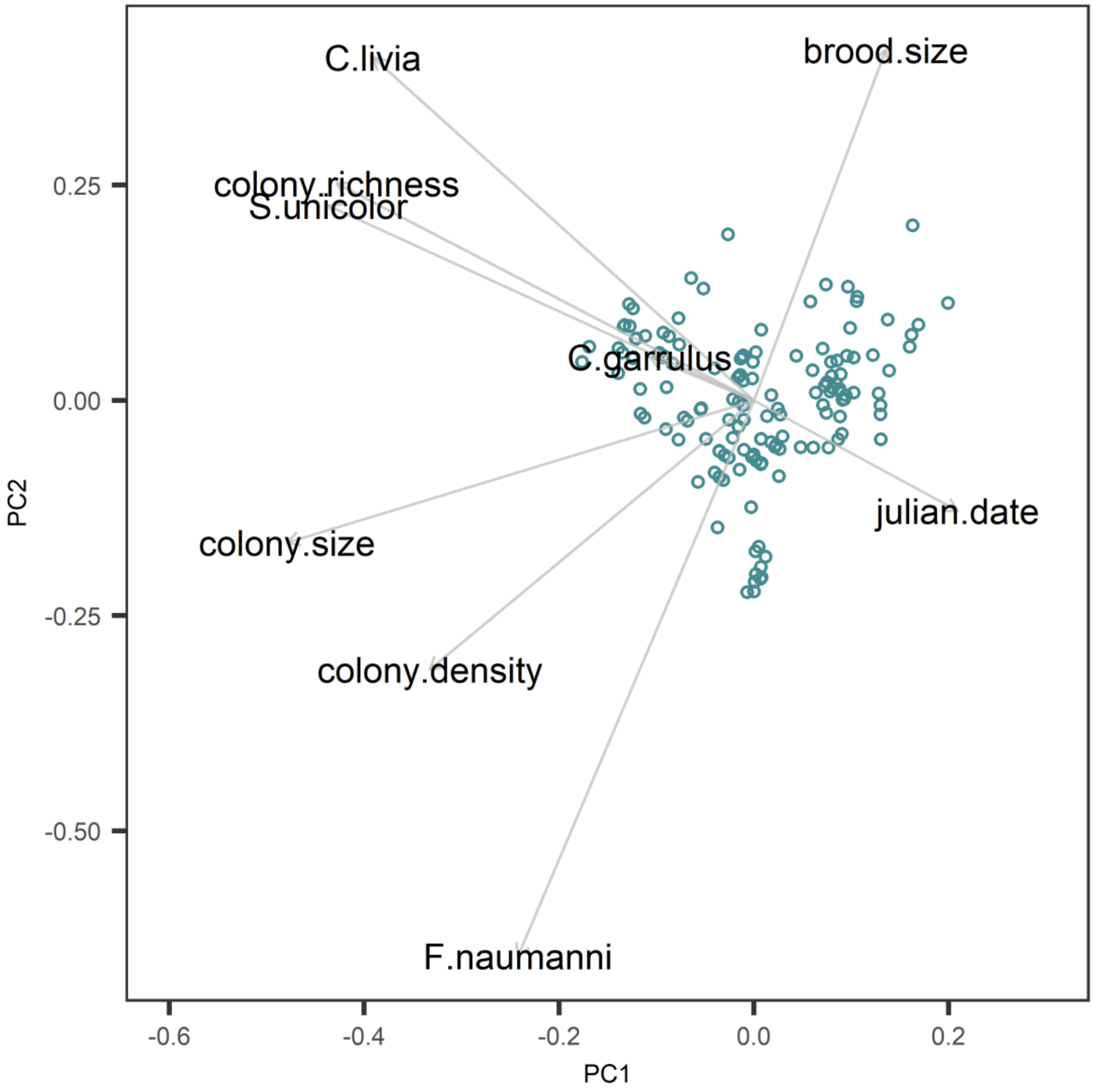


Figure 3.A1: Principal Component Analysis (PCA) correlation biplot (scaling 2) on the relationship between colony traits: richness, size, density, and composition (divided in the number of F. naumanni, C. garrulus, C. livia, and S. unicolor nests). Julian date and brood size also included. Arrows show the direction and relationship between the variables. Dots refer to individual nests.

Table 3.A1: Models with ΔAICc <2 after model averaging on the effect of colony traits on Carnus hemapterus abundance using nests from all four host species.

Models	d.f.	ΔAICc	Weight	AICc
1. Number of lesser kestrel nests + number of starling nests + number of nestlings + host species	9	0.00	0.272	1653.5
2. Number of starling nests + number of nestlings + host species	8	1.67	0.118	1655.2

Table 3.A2: Two top models on the effect of colony traits on Carnus hemapterus abundance in mixed-species colonies using nests from all four host species.

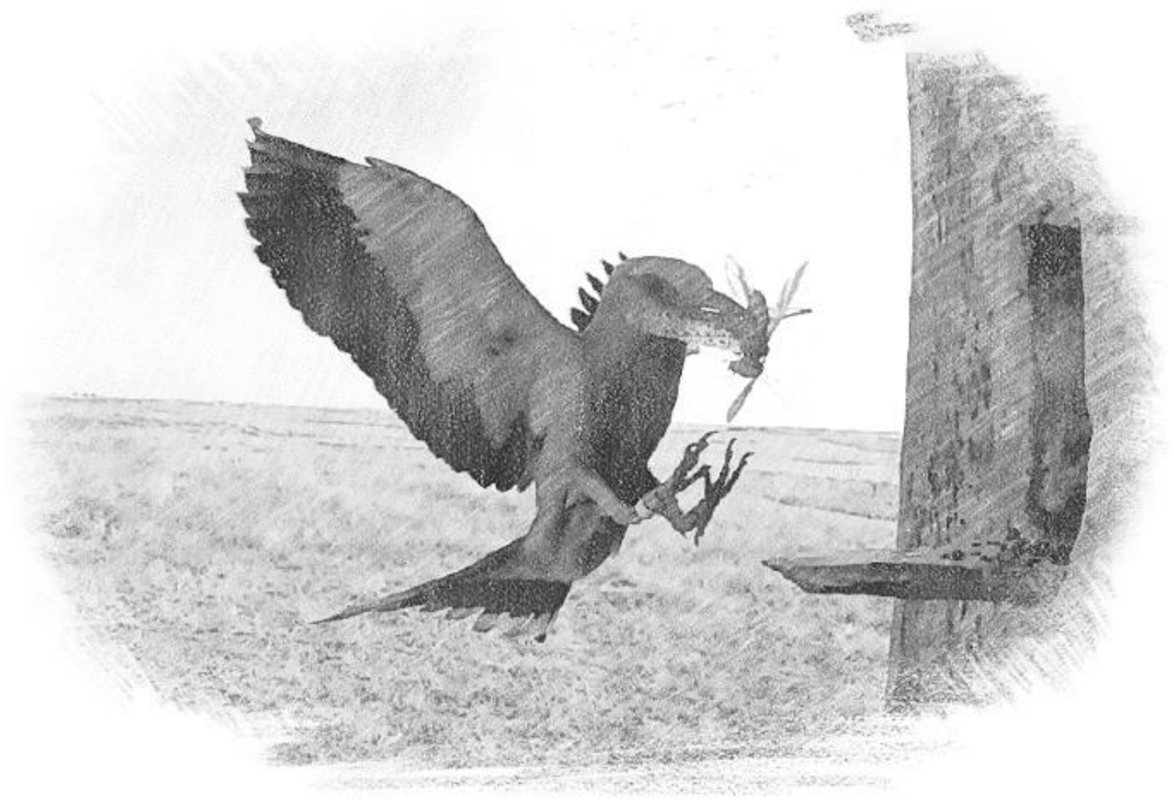
Parameter	SD	Estimate	SE	z	P-value
Model 1					
Colony ID	0.052				
Intercept		0.721	0.268	2.686	0.007
# Lesser kestrel nests		0.144	0.073	1.962	0.050
# starling nests		-0.202	0.080	-2.536	0.011
Number of nestlings		0.286	0.088	3.235	0.001
Host species roller		3.090	0.356	8.673	<0.001
Host species lesser kestrel		2.137	0.300	7.118	<0.001
Host species starling		0.911	0.306	2.982	0.003
Model 2					
Colony ID	0.109				
Intercept (host species pigeon)		0.684	0.272	2.510	0.012
# starling nests		-0.185	0.085	-2.177	0.030
Number of nestlings		0.262	0.089	2.938	0.003
Host species roller		3.065	0.363	8.443	<0.001
Host species lesser kestrel		2.191	0.304	7.203	<0.001
Host species starling		0.953	0.310	3.073	0.002

Chapter 4

High trophic niche overlap in a bird community established in an artificial nesting landscape: implications for conservation

João Gameiro, Teresa Catry, Joana Marcelino, Aldina M.A. Franco, Jorge M. Palmeirim & Inês Catry

Submitted to Biodiversity and Conservation



HIGH TROPHIC NICHE OVERLAP IN A BIRD COMMUNITY ESTABLISHED IN AN ARTIFICIAL NESTING LANDSCAPE: IMPLICATIONS FOR CONSERVATION

ABSTRACT

Although successful at recovering endangered populations, conservation projects based on nest-site provisioning seldom consider how they shape the composition of communities and alter interspecific interactions. Moreover, conservation of targeted species may be affected by the extent of dietary overlap among potential competitors. In Portugal, large-scale nest-site provisioning aimed at recovering lesser kestrel *Falco naumanni* populations attracted several bird species forming mixed-species colonies, likely promoting interspecific competition for resources during breeding. Here we used Stable Isotope Analysis ($\delta^{15}N$ and $\delta^{13}C$) to assess inter- and intraspecific dietary segregation in these mixed breeding assemblages and investigate the mechanisms allowing species coexistence. We examined resource partitioning and trophic niche overlap among lesser kestrels, common kestrel *Falco tinnunculus*, European roller *Coracias garrulus*, barn owl *Tyto alba*, little owl *Athene noctua*, and spotless starling *Sturnus unicolor*; and within species between parents and their offspring. Similar isotope ratios and highly overlapped niches, particularly among lesser kestrels, rollers, and starlings, suggest limited dietary segregation and use of similar prey. Within species, parent-offspring segregation was marked across all species. Overall, our results indicate that species breeding in these assemblages occupy similar ecological niches, despite a potential increase in competition. High-resource availability in our study area may guarantee coexistence but the viability of mixed-species groups may be compromised in areas with limited resources, which are predicted to expand with ongoing human and climate-induced changes. This study highlights that conservation practices based on nest-site provisioning need to consider the ecological niches of target and sympatric species as well as their interactions.

Keywords: isotopic niche, dietary segregation, parent-offspring segregation, interspecific competition, mixed-species colonies

1. INTRODUCTION

Human-induced changes in the environment shape the distribution of many species by restricting their access to resources such as food or nest-sites (Wiegand et al. 2005; Teckentrup et al. 2019). Ongoing biodiversity loss has prompted conservation projects and massive provisioning of artificial nest-sites to halt species decline across many taxa and regions (Harper et al. 2005; Catry et al. 2009; Olah et al. 2014; Sutherland et al. 2018), further re-shaping the nesting landscape and altering the composition and structure of communities (Duckworth et al. 2017; Catry & Catry 2019). Nest-site provisioning may modify interspecific interactions and trophic dynamics (Duckworth et al. 2017; Catry & Catry 2019), but their consequences are often overlooked by researchers or conservation managers (Mainwaring et al. 2015).

According to the niche theory and the competitive exclusion principle, species with similar niches, likely to compete with one another, are not expected to coexist (Hardin 1960; Pianka 1981). By promoting supra-optimal breeding densities with potential competitor species, artificial nest-sites may turn into ecological traps, reducing long-term individual fitness by reducing resource availability and increasing social stress associated with interspecific aggressive behaviours (Kappeler et al. 2015; Catry & Catry 2019).

To avoid competition, especially when resources are limited, coexisting species can segregate in at least one of three main axes: space, time, and diet (Pianka 1981). Segregation in spatio-temporal habitat utilisation occurs when species forage in different habitats (like in insectivorous desert bats, Razgour et al. 2011), different periods of the day (like in African carnivore communities, Schuette et al. 2013), or when they have different breeding phenologies (like in sympatric penguin species, Clewlow et al. 2019). Segregation in the dietary axis occurs when species reduce their dietary niche overlap by foraging for alternative food resources (Macarthur & Pianka 1966; Jenkins & Davoren 2020). Species may also contract their dietary niches to focus on certain prey types that become temporarily super-abundant, which increases the dietary niche overlap among species without increasing competition (Forero et al. 2004; Charter et al. 2018; Denhard et al. 2020). Dietary niche segregation can also occur within species to reduce intraspecific competition, through dietary sexual or parent-offspring segregation, especially when the potential for competitive interactions is maximum, such as for central place foragers during reproduction (Orłowski et al. 2014; Catry et al. 2016a; Reisinger et al. 2020).

Here, we investigate dietary niche overlap in a multi-specific bird community created by large-scale nest-site provisioning aimed at recovering the colonial lesser kestrel *Falco naumanni* in southern Portugal (Catry et al. 2009). In a treeless landscape with low nesting opportunities, many bird species took advantage of these artificial breeding structures – some with more than 80 cavities, forming mixed-species colonies (Catry & Catry 2019). These include lesser kestrels, common kestrels *Falco tinnunculus*, European rollers *Coracias garrulus*, barn owls *Tyto alba*, little owls *Athene noctua*, jackdaws *Corvus monedula*, spotless starling *Sturnus unicolor*, and feral pigeons *Columba livia* (Catry & Catry 2019). The dietary habits of these species suggest that their use of trophic resources may overlap to a large extent (Jaksić et al. 1982; Motis et al. 1997; Tomé et al. 2008; Catry et al. 2016a; Orihuela-Torres et al. 2017; Catry et al. 2019), especially during the breeding season, when competition for food should peak as parents need to obtain resources to fulfil their own energy requirements and those of their offspring (Orłowski et al. 2014; Antón-Tello et al. 2021). High densities of breeding pairs could lead to prey depletion in the vicinity of the colonies, further increasing inter and intraspecific competition (sensu Ashmole's halo; Birt et al. 1987; Dehnhard et al. 2020; Jenkins and Davoren, 2020).

We used Stable Isotope Analysis (SIA) to investigate inter and intraspecific overlap in the diet of six bird species breeding in mixed colonies installed in artificial breeding structures to better understand the mechanisms allowing their coexistence. Specifically, using stable isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$), we aimed to: (1) compare isotopic niche breadth and overlap among different species and (2) assess parent-offspring diet segregation of each species within the assemblages. We sampled feathers from nestlings and blood plasma from parent-offspring pairs during the breeding season, thus providing a detailed spectrum of the dietary resources used by these species. We predict species with similar diets and similar trophic positions to show higher dietary overlap, while species at the top and bottom ends of the trophic spectrum to be more segregated from the rest of the assemblage. Altogether, we aimed at understanding the extent on how dietary overlap and niche segregation among potential competitors may affect the conservation of targeted species, an issue seldom acknowledged by conservation projects.

2. METHODS

2.1 STUDY AREA AND STUDY SPECIES

This study was carried out in the Castro Verde Special Protection Area (SPA, Natura 2000), Southeast Portugal (37º41'N, 8º05'W). With ca. 85,000 ha, this is the main Portuguese area of agro-steppes – a semi-natural habitat created by low intensity farming practices – and one of the main strongholds for several threatened farmland bird species in Western Europe (Moreira et al. 2007; BirdLife International 2021). Mixed-species colonies are mostly found in artificial nesting structures provided by LIFE conservation projects target at lesser kestrels during the early 2000s (Catry et al. 2009), and to a lesser extent in abandoned farmland buildings, with nests inside wall cavities or under roof tiles. Within these breeding assemblages, we focused on species that prey mainly on small vertebrates and arthropods, as these are the ones with higher potential for having overlapped trophic niches: barn and little owls, common and lesser kestrels, European rollers (hereafter rollers) and spotless starlings (hereafter starlings). Feral pigeons and jackdaws, due to the relatively large proportion of plant sources in their diets (cereals; Murton & Westwood 1966; Högstedt 1980; Soler et al. 1990), were not included in the study.

2.2 SAMPLE COLLECTION

Feather sampling was carried out during the breeding seasons of 2014, 2016 and 2018 (Table 4.1). Nestlings of barn owls (n=12), little owls (n=19), common kestrels (n=33), lesser kestrels (n=36), rollers (n=36), and starlings (n=12) were sampled in their nests at the age of 3-4 weeks, when breast feathers are well developed. Approximately 3-5 breast feathers were plucked (keeping the feather base intact) and stored in separate plastic zip bags. Blood sampling of parent-offspring pairs – one parent and one nestling – of little owls (n=7), common kestrels (n=8), lesser kestrels (n=11), rollers (n=6), and starlings (n=6) was carried out during the breeding season of 2019 (Table 4.1). Parents and their offspring were sampled within a close temporal window (6.9 ± 6.1 days) at their nests. Approximately 150 µL of blood was collected from the brachial vein and preserved in separate vials. The blood was centrifuged for 10 min at 3400 rev/min within 3 hours of collection, to separate plasma from red blood cells, and plasma samples were frozen before being further prepared for stable isotope analysis (red blood cells were not analyzed). We were unable to sample enough barn owl adults, and so parent-offspring segregation was not investigated for this species.

Additionally, to aid the interpretation of stable isotope data, we sampled key prey types of each species in mixed-species colonies throughout the breeding season of 2018 (Table 4.2). Prey species were identified and collected inside or near the nests and were kept frozen until processed for isotope analysis. All work involving bird handling and sample collection was approved by the Instituto de Conservação da Natureza e Florestas (ICNF).

Table 4.3: Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope signatures (mean ± SD) of six bird species breeding in mixed colonies in Castro Verde, Southern Portugal. Nestling feathers and blood (plasma) from parent-offspring pairs were collected during the breeding seasons of 2014-2018 (pooled) and 2019, respectively.

	Feathers (nestlings)				**Blood**		
	$\delta^{13}C$	$\delta^{15}N$	n		$\delta^{13}C$	$\delta^{15}N$	n
Barn owl	-23.42 ± 0.58	10.64 ± 0.45	12	-	-	-	-
Little owl	-23.81 ± 1.07	10.08 ± 1.37	19	Nestling	-25.21 ± 0.45	10.03 ± 1.11	7
				Adult	-25.63 ± 0.34	11.15 ± 0.74	7
Common kestrel	-23.64 ± 0.55	8.88 ± 1.05	33	Nestling	-25.28 ± 0.34	8.77 ± 0.63	8
				Adult	-25.20 ± 0.44	10.07 ± 0.47	8
Lesser kestrel	-23.78 ± 0.25	7.76 ± 0.66	36	Nestling	-25.55 ± 0.19	7.93 ± 0.76	11
				Adult	-25.38 ± 0.40	8.94 ± 0.91	11
Roller	-23.52 ± 0.42	7.34 ± 0.69	36	Nestling	-25.42 ± 0.26	7.30 ± 0.67	6
				Adult	-25.17 ± 0.23	8.78 ± 1.14	6
Starling	-23.84 ± 0.52	8.54 ± 0.89	12	Nestling	-25.48 ± 0.26	6.62 ± 1.03	6
				Adult	-25.49 ± 0.20	8.61 ± 1.02	6

2.3 STABLE ISOTOPE ANALYSIS

Stable isotope ratios have been widely used as dietary tracers to assess the different habitats and diet resources used by consumers, providing a proxy for species or individual ecological niches using low invasive methods (Forero et al. 2004; Catry et al. 2019; Dehnhard et al. 2020). SIA of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) provides information on the trophic position of an organism in the food chain and on habitat use, respectively, allowing researchers to simultaneously examine the dietary niche segregation/overlap of multiple species or individuals within assemblages and infer on their competition for resources (Inger & Bearhop 2008; Alonso et al. 2012; Catry et al. 2016b; Reisinger et al. 2020; Jenkins and Davoren, 2020). SIA also provides information on the dietary niche at multiple temporal scales depending on the tissue sampled, as isotope ratios reflect the diet during which that tissue was metabolically active.

Here, we use feathers from nestlings of the six species to examine isotopic breadth and overlap among species, as they offer information for the period during which the feather was being formed, adequately characterising the diet of the nestlings during the breeding season (Inger & Bearhop 2008; Weiss et al. 2009). Feathers were washed in double baths of 0.25N sodium hydroxide solution alternated with baths of double distilled water to remove any surface contaminants, and were then air dried and then cut into small fragments (Catry et al. 2008). To investigate parent-offspring dietary segregation, we used blood plasma, which has a much higher metabolic turnover rate and thus reflects the averaged diet over much shorter periods (days; Inger & Bearhop 2008; Reisinger et al. 2020). Blood plasma from adult birds was also used to assess niche overlap between species in addition to nestling feathers. Information from nestling plasma was only used to examine parent-offspring segregation, as it does not add information to that obtained with nestling feathers (sample size was smaller and restricted to one year, and plasma reflects information on the birds' diet over a much shorter period). Plasma samples of birds and soft tissues (muscle) of prey were dried in an oven at 60°C for 48h and then reduced to a homogenised powder. Prey samples were then processed for lipid extraction by immersion in a 2:1 chloroform/methanol solution with a solvent volume three to five times larger than the sample volume (Logan et al. 2008). Samples were then mixed for 30s, left undisturbed for ca. 30 min, further centrifuged for 10 min at 3400rev/min, and the supernatant containing solvent and lipids were removed. This process was repeated at least three times (until the solvent was clear) and samples were then re-dried at 60ºC for 24h to remove any remaining solvent. Between 0.8 to 1.2mg of each sample (feathers, plasma, and prey) were weighted and stored in tin cups for stable carbon and nitrogen isotope assays. Isotopic ratios were determined by continuous-flow isotope ratio mass spectrometry at the "Stable Isotopes and Instrumental Analysis" facility of the faculty of Sciences, University of Lisbon. Results are presented conventionally as δ values in parts per thousand (‰) relative to the IAEA CH7 and Glucose BCR for $\delta^{13}C$, and USGS25 and USGS35 for $\delta^{15}N$. The precision of the isotope ration analysis, calculated using values from six to nine replicates of laboratory standard material (casein) interspersed among samples in every bath analysis, was 0.04-0.05‰ and 0.02-0.04‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively.

Table 4.4: Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope signatures (mean ± SD) of main prey sampled in 2018 at Castro Verde, Southern Portugal. Taxa within coleoptera and orthoptera were grouped into SIA groups according to their similarity in isotopic signatures. N = sample size.

	$\delta^{13}C$	$\delta^{15}N$	N	SIA group
Small mammals				
Apodemus sp.	-25.6 ± 0.8	7.0 ± 1.9	7	
Mus sp.	-25.3 ± 0.4	8.1 ± 0.9	3	
Soricidae	-24.9 ± 0.3	8.2 ± 1.6	2	
Birds				
Coturnix sp.	-26.1 ± 0.3	7.2 ± 0.5	2	
Sturnus unicolor	-25.3 ± 0.6	8.5 ± 1.2	3	
Reptiles				
Chalcides striatus	-25.3 ± 0.5	8.2 ± 0.8	8	
Chilopoda				
Scolopendra sp.	-25.9 ± 0.8	9.0 ± 0.7	8	
Coleoptera				
Carabidae und.	-25.5 ± 0.5	10.9 ± 3.0	3	1
Silpha sp.	-25.5 ± 0.7	10.8 ± 3.4	3	1
Tenebrionide und.	-26.3 ± 0.3	9.7 ± 0.2	2	1
Amphimllon nigrum	-26.6 ± 0.8	6.6 ± 0.9	10	2
Carabus rugosus	-26.7 ± 0.8	5.9 ± 1.0	2	2
Chrysolina bankii	-27.1 ± 0.2	7.0 ± 1.0	3	2
Pterostichus ebenus	-25.9 ± 0.1	7.0 ± 0.2	2	2
Sepidium sp.	-26.8 ± 0.8	6.5 ± 0.7	8	2
Bubas bison	-27.3 ± 0.6	8.9 ± 0.4	5	3
Netocia sp.	-23.2 ± 0.3	5.6 ± 3.7	2	4
Protaetia sp.	-23.9	7.4	1	4
Orthoptera				
Acrididae	-26.4 ± 0.7	3.8 ± 1.0	12	5
Tettigonidae	-25.3 ± 0.7	3.4 ± 1.5	14	5
Gryllotalpa sp.	-27.2 ± 0.7	6.4 ± 1.0	7	6

2.4 DATA ANALYSIS

Feather isotopic signatures for each species from all years were pooled together as the relative isotopic position of each species remained similar (Fig. 4.A1).

To compare isotopic signatures of carbon and nitrogen simultaneously among species, in both nestlings and adults, parametric and non-parametric pairwise multivariate analysis of variance (MANOVA or PERMANOVA, respectively) were performed. Parametric or non-parametric analyses of variance (ANOVA or Kruskal-Wallis, respectively) were then used to analyse differences in carbon and nitrogen separately between species, followed by pairwise comparisons using Tukey or Wilcoxon rank sum tests (for parametric and non-parametric data, respectively).

Prey items with similar isotopic signals were pooled within each taxonomic order (SIA group, Table 2), and then plotted in the isotopic biplot graph to aid the interpretation of consumer signatures using trophic discrimination factors (TEF). Due to lack of reported discrimination factors for all consumer species, we used the mean (± SD) value of trophic discrimination factors for feather and plasma samples of other bird species reported in published studies reviewed by Caut et al. (2009) (feathers: $\delta^{13}C = 2.16 \pm 1.53$, $\delta^{15}N = 2.84 \pm 1.14$; plasma: $\delta^{13}C = -0.08 \pm 0.85$, $\delta^{15}N = 2.82 \pm 0.31$).

To measure isotopic niche breadth of each species and estimate the degree of niche overlap between species, corrected and Bayesian standard ellipse areas (SEA_C and SEA_B, respectively) were calculated using the SIBER package for R (Jackson & Parnell 2020). SEA_B were used to quantitatively compare niche breadth among species, using 1 000 000 iterations, three chains, a burn-in of 1000 and thinning of 10, using a vague normal prior (Jackson & Parnell 2020). Overlap among standard ellipses (SEAc) for all pairs of species and for parents and offspring within each species were estimated to reflect the degree of trophic resources shared. For each species (i) in one pair (i,j), a value of overlap ($Ov_{[i]}$) was calculated as the ratio between the area of overlap between the two SEA_C ($A_{[I,j]}$) and its own $SEA_{[i]}$ ($A_{[i]}$), expressed as a proportion ($Ov_{]i]} = A_{[I,j]}/A_{[i]}$; Catry et al. 2016b). Average overlap per species was estimated as the average of all overlaps involving that species. Additionally, to evaluate parent-offspring segregation within each species, differences in Euclidean distances between the centroids of parents and offspring were calculated and tested using a residual permutation procedure based on Turner et al. (2010). Afterward, differences in $\delta^{15}N$ and $\delta^{13}C$ between parents and offspring were compared with t-tests or Mann-Whitney U tests for parametric and non-parametric data, respectively. Assumptions of each test were met prior analysis. All analyses were conducted in R statistical environment (R Development Core Team, 2016).

3. RESULTS

3.1 STABLE ISOTOPE SIGNATURES

Feathers were collected from a total of 148 nestlings and plasma samples from 38 parent-offspring pairs from six different species; mean (± SD) stable isotope signatures ($\delta^{13}C$, $\delta^{15}N$) for each species are presented in Table 4.1 and Figure 4.1. A PERMANOVA on $\delta^{13}C$ and $\delta^{15}N$ of nestling feathers revealed differences among species ($F_{5,142} = 23.618$, $p = 0.001$), both in $\delta^{13}C$ and in $\delta^{15}N$ (Kruskal-Wallis tests $\delta^{13}C$: $\chi^2 = 15.948$, $p = 0.007$; $\delta^{15}N$: $\chi^2 = 87.323$, $p < 0.001$). Post-hoc tests indicated that $\delta^{13}C$ only differed between lesser kestrels and rollers ($p = 0.02$). Barn owls and little owls fed at the highest trophic level (most enriched $\delta^{15}N$ values) of the community, significantly higher than all other species (all $p < 0.005$). Common kestrels had more enriched $\delta^{15}N$ values than lesser kestrels and rollers, (both $p < 0.001$), but similar values to starlings ($p = 0.257$). Starlings also had more enriched $\delta^{15}N$ than lesser kestrels ($p = 0.016$) and rollers ($p < 0.001$) and lesser kestrels had higher values than rollers ($p = 0.012$). Regarding the adult community, blood isotopic signatures were also different among species (MANOVA: $F_{4,33} = 4.97$, $p < 0.001$), but only for $\delta^{15}N$ values (ANOVA $\delta^{13}C$: $F = 2.038$, $p = 0.112$; $\delta^{15}N$: $F = 10$, $p < 0.001$). The trophic rank of adults was similar to that of nestlings. Little owls and common kestrels had the highest $\delta^{15}N$ values (adult barn owls were not sampled), with little owls being in a significantly higher position than lesser kestrels, rollers, and starlings (all $p < 0.001$), while common kestrels had only significantly higher $\delta^{15}N$ values than starlings (p-values: lesser kestrel = 0.061, roller = 0.068, starling = 0.030). Adult lesser kestrels, rollers and starlings had similar $\delta^{15}N$ values (all $p > 0.900$; Fig. 4.1B). In short, trophic position (according to $\delta^{15}N$ values) of nestlings and adults in the community was BO=LO>CK=S>LK>R and LO=CK>S=LK=R, respectively.

Isotopic signature of main prey items (corrected by TEF) can be found on Figure 4.1. The 10 potential prey groups comprise a broad isotopic space, with mean $\delta^{13}C$ values ranging from -27.3 ± 0.6 to 23.2 ± 0.3 and mean $\delta^{15}N$ from 3.4 ± 1.5 to 10.9 ± 3.0 (Table 4.2; Fig. 4.1). The relative trophic position of the six species and their relation to prey suggest that kestrels, lesser kestrels, rollers, and starlings feed their offspring mostly with Orthoptera and to a lesser extent with Coleoptera and vertebrates, while the opposite occurs in barn and little owls (Fig. 4.1A).

Regarding adults, little owls and common kestrels had closer signatures to vertebrates, while lesser kestrels, rollers, and starlings maintained a lower trophic position.

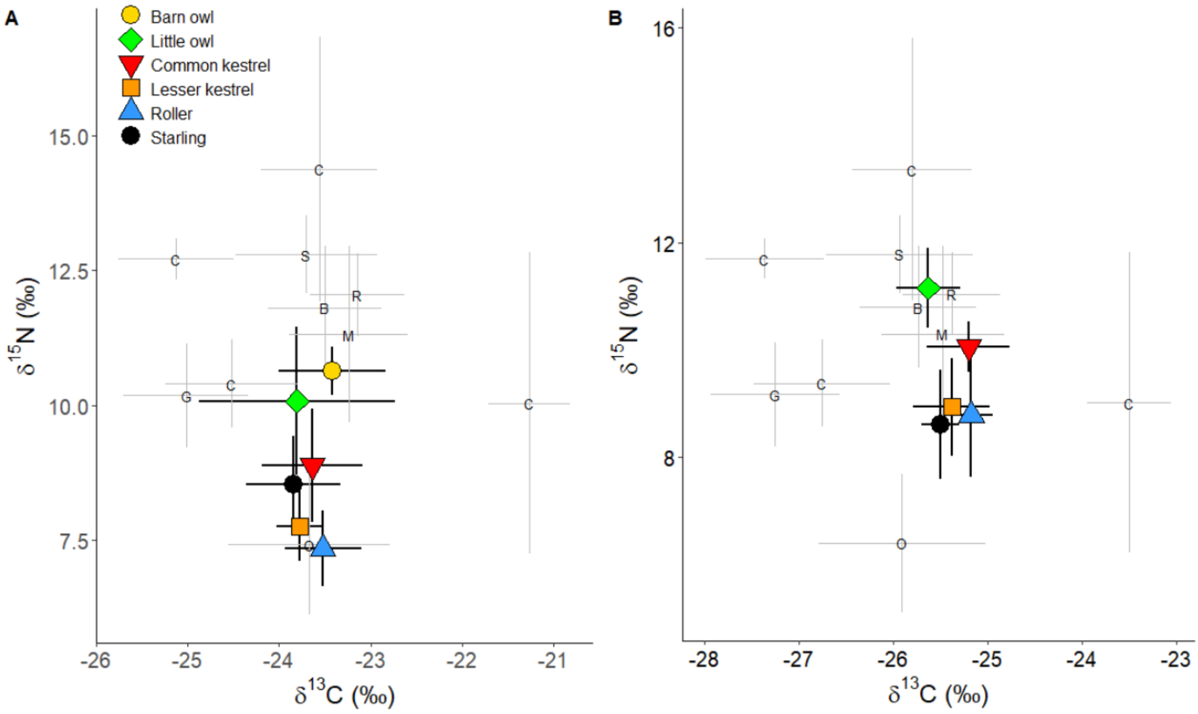


Figure 4.1: Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope signatures (mean ± SD) of nestlings (feathers collected in 2014, 2016, and 2018, pooled) (A) and adults (blood plasma collected in 2019) (B) of bird species breeding in mixed colonies in Castro Verde, Southeast Portugal. Signatures of main prey items are shown. M, small mammals; B, birds; R, reptiles; S, scolopendra; C, coleoptera; O, orthoptera; G, Gryllotalpa. Stable isotope ratios of prey items were obtained from muscle/soft tissue and corrected for the trophic discrimination factor (based on Caut et al. 2009, see methods). Because different tissues were used for nestlings and adults, direct comparisons in trophic position between the two age groups cannot be made.

3.2 INTERSPECIFIC ISOTOPIC NICHE OVERLAP

As observed for the consumers' isotopic space described above, differences in trophic niches were found mainly between species likely including vertebrates in their diet, i.e., barn owls and little owls, and those preying mostly on arthropods, such as lesser kestrels, rollers, and starlings; with common kestrels in an intermediate position (Fig. 4.2). Amongst nestlings, little owls had the widest niche breadth (SEA_B = 4.352; Table 3), only slightly overlapping with common kestrels and starlings (23% and 12%, respectively; Table 4.A1) but totally overlapping with barn owls (SEA_B = 0.755; Table 3) (Fig. 4.2A). Common kestrels and starlings also showed a high overlap with each other (63% and 75%) as well as with little owls (59% and 37%, respectively; Table 4.A1). Lesser kestrel nestlings had the smallest niche breadth (SEA_B = 0.505; Table 3) which highly overlapped with the dietary niche of rollers, common kestrels, and starlings (60%, 40% and 60%, respectively; Table 4.A1). Amongst adults, lesser kestrels, rollers, and starlings show high niche overlap, while common kestrels and little owls are clearly segregated (Fig. 4.2B; Table 4.A1).

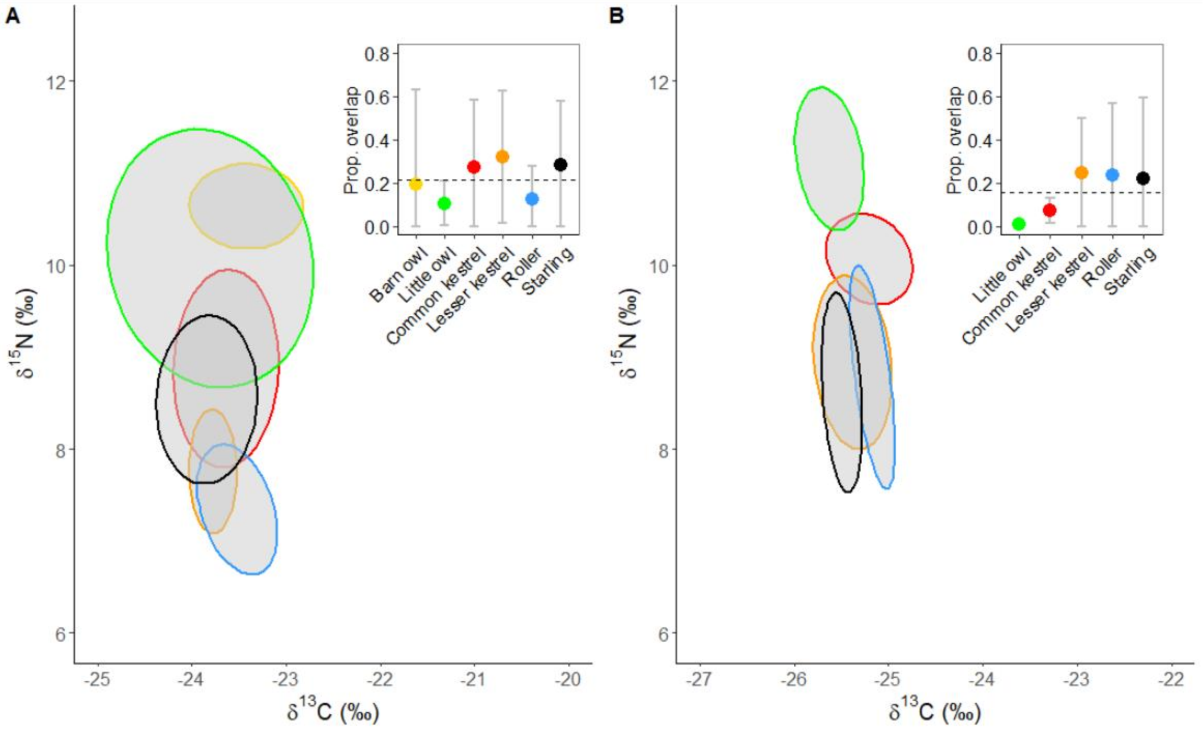


Figure 4.2: Overlap in isotopic niches (corrected standard ellipses; SEAC) among nestlings (A) and adults (B) of bird species breeding in mixed colonies. Isotope signatures were obtained from feathers and plasma for nestlings and adults, respectively. Inset plot (upper right corner) shows the mean (±SD) niche overlap for each species and the mean overlap of the community (horizontal dashed line).

3.3 PARENT-OFFSPRING SEGREGATION

Differences between adults and nestlings were found in δ^{15}N values for every species except little owls (little owl: w = 38, p = 0.097; common kestrel: w = 68, p = 0.001; lesser kestrel w = 107, p = 0.001; roller: t = 2.753, p = 0.025; starling: w = 34, p = 0.009). No differences in δ^{13}C values were found for any species (little owl: t = -1.961, p = 0.075; common kestrel: t = 0.381, p = 0.709; lesser kestrel: t = 1.256, p = 0.228; roller: t = 0.115, p = 0.115; starling: t = -0.083, p = 0.936). Despite that, Euclidean distance between centroid location of adults and nestlings was significantly different in all species (all p < 0.01; Table 4.A2), indicating a clear parent-offspring segregation in all of them (Fig. 4.3).

Table 4.5:Isotopic niche breadth of nestlings (feathers) and adults (plasma) from bird species breeding in mixed colonies, using Bayesian standard ellipse areas (SEAb, with 95% credible intervals) and sample size-corrected standard ellipse areas (SEAc). N = sample size.

Consumers	N	SEA_B (95% credible interval)	SEA_C
Nestlings (feathers)			
Barn Owl	12	0.755 (0.439-1.451)	0.899
Little Owl	19	4.352 (2.824-7.175)	4.848
Common Kestrel	33	1.763 (1.265-2.543)	1.872
Lesser Kestrel	36	0.505 (0.369-0.718)	0.535
Roller	36	0.830 (0.602-1.173)	0.871
Starling	12	1.320 (0.770-2.540)	1.575
Adults (plasma)			
Little owl	7	0.688 (0.333-1.682)	0.922
Common kestrel	8	0.558 (0.290-1.297)	0.736
Lesser kestrel	11	1.058 (0.590-2.064)	1.254
Roller	6	0.578 (0.274-1.592)	0.785
Starling	6	0.532 (0.248-1.446)	0.764

4. DISCUSSION

Identifying the dietary niche of species within assemblages is crucial to understand the mechanisms allowing the coexistence of potential competitors in a specific area and draw adequate conservation management actions. Here, we used carbon and nitrogen stable isotope ratios from nestlings and from parent-offspring pairs to provide a detailed assessment of the dietary resources used by a group of six bird species breeding in dense mixed-species colonies established as the result of an extensive nest-provisioning program (Catry et al. 2009; Catry & Catry, 2019). Overall, our results show a high intraspecific (parent-offspring) but low interspecific dietary segregation in these assemblages, suggesting a high potential for interspecific competition for resources during the breeding season.

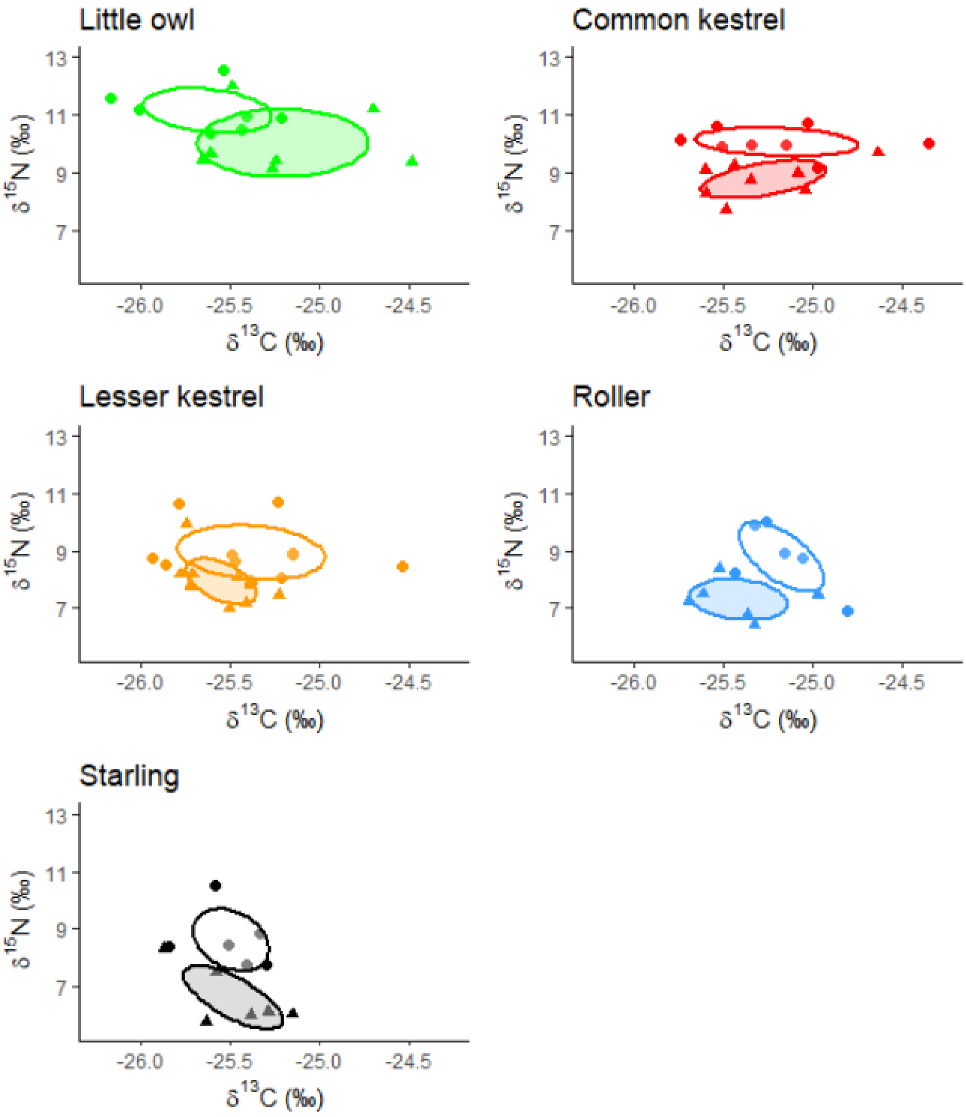


Figure 4.3: Overlap in isotopic niches (corrected standard ellipses; SEAc) between parents (clear) and offspring (filled) of bird species breeding in mixed colonies. Stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) were measured using blood plasma from 7 little owl, 8 common kestrel, 11 lesser kestrel, 6 roller, and 6 starling parent-offspring pairs (one parent and one offspring in each pair).

4.1 INTERSPECIFIC OVERLAP IN ISOTOPIC NICHES

Identical isotopic signatures and highly overlapping niches suggest that species breeding in these assemblages rely on similar prey to feed their offspring. The low $\delta^{15}N$ isotopic signatures of lesser kestrel and roller nestlings likely reflect a diet based on Orthoptera (grasshoppers and bush-crickets) as reported in previous studies (> 50% and 70% of all prey delivered to lesser kestrel and roller nestlings, respectively; Catry et al. 2016a, 2019), thus the high overlap observed between nestlings of the two species was expected. Little owl nestlings had the largest isotopic niche breadth in our study, overlapping with common kestrels but segregating from lesser kestrels and rollers. Common kestrels and little owls have more generalist diets that include vertebrates but may expand their niche to consume more abundant prey such as beetles and grasshoppers, especially during chick rearing (Tomé et al. 2008; Orihuela-Torres et al. 2017). Remains of birds, amphibians, reptiles, and small mammals, but also of Orthoptera, were frequently found in little owl and common kestrel nests in the study area during chick rearing, confirming their eclectic diet. Nestlings of barn owls had the most enriched nitrogen signatures of the assemblage, but their dietary niche breadth suggests a more specialised, vertebrated-based diet (Jacksić et al. 1982; authors pers.obs), segregating from all other species except little owls. Regarding starlings, although there is no information on their diet in our study area, in general they rely mostly on small insects such as hoverflies, ants, and on larvae of Coleoptera and Lepidoptera (Motis et al. 1997), which should give starlings a distinct isotope signature. However, in our study area starlings were often observed feeding their offspring with grasshoppers, suggesting a similar diet and explaining the observed niche overlap with the remaining community.

Isotopic characterisation of the adult community indicated a similar trophic rank, although the information retrieved from adult plasma is probably not representative of the whole breeding season, and results are based on few individuals in a single year. Adult lesser kestrels and rollers showed a high overlap with starlings, suggesting similar diets, while common kestrels and little owls had more enriched $\delta^{15}N$ values, likely reflecting the consumption of vertebrates.

4.2 PARENT-OFFSPRING DIETARY SEGREGATION

Despite the lack of significant differences when comparing $\delta^{15}N$ and $\delta^{13}C$ values between little owl adults and nestlings separately, differences in Euclidean distance suggests that all species studied in these mixed colonies (including little owls) exhibited clear parent-offspring dietary segregation during the chick-rearing period. During a season of high energy demand, parents are expected to feed their offspring with high energy items, keeping less profitable resources for themselves (Orłowski et al. 2014). While this was already reported for lesser kestrels and rollers (Catry et al. 2016a, 2019), we could not find studies addressing parent-offspring segregation in the other studied species. This study reveals that little owls, common kestrels and spotless starlings also exhibited marked parent-offspring segregation in trophic resources, reinforcing this may be a common evolutionary strategy to avoid intraspecific competition.

4.3 ECOLOGICAL NICHE THEORY APPLIED TO MIXED-SPECIES COLONIES IN ARTIFICIAL NESTING LANDSCAPES

If on one hand the competitive pressure among species breeding together in dense aggregations can be alleviated through parent-offspring partitioning in their food resources, on the other hand the low dietary segregation among species can lead to an increase of interspecific competitive interactions (Catry & Catry 2019).

These results raise questions as to the mechanisms allowing species coexistence. According to the ecological niche theory, species with high dietary overlap may still partition their niche and avoid interspecific competition through spatial or temporal segregation in habitat utilisation (Pianka 1981; Reisinger et al. 2020). In the mixed-species colonies we studied, however, there is no evidence for temporal segregation as all species highly coincide in their breeding phenology and chick rearing period (authors unpublished data). Moreover, spatial segregation is also not very likely to occur, because all species are central-place foragers and hunt in the vicinity of the colonies (Casagrande et al. 2008; Catry et al. 2012; Šalek & Lövy 2012; Catry et al. 2017a). Alternatively, high niche overlap among sympatric species may reflect high availability of resources (Pianka 1981; Charter et al. 2018; Jenkins & Davoren et al. 2020). In the Castro Verde SPA, traditional farming practices associated with agro-steppes are maintained through specific agri-environmental policy schemes, ensuring high-quality foraging habitats for many farmland species (Catry et al. 2013, 2017a; Silva et al. 2018). Large areas of low-intensity grazed fallows support a high abundance of Orthoptera, and the chick-rearing period of lesser kestrels and rollers (and likely of the whole species assemblage except barn owls) coincides with the peak abundance of grasshoppers (Catry et al. 2016a, 2017b, 2019). From mid-May, as a result of the abrupt increase in grasshopper availability (Catry et al. 2017b), species may contract their dietary niche to focus on prey that became super-abundant, increasing their overlap without necessarily increasing interspecific competition (Forero et al. 2004; Jenkins & Davoren 2020). The lack of differences in productivity between rollers breeding solitary and in mixed-species colonies, or between lesser kestrels in small or large colonies (Table S3), suggests that prey depletion around colonies in our study area is unlikely and that resources are sufficient to prevent direct costs associated with interspecific competition, allowing species with similar niches to aggregate.

4.4 CONSERVATION IMPLICATIONS

Although often successful at quickly recovering endangered populations, conservation projects based on nest-site provisioning seldom take into consideration how they may shape the composition of communities and alter interspecific interactions (Catry & Catry 2019). Moreover, the consequences of dietary overlap among potential competitors on the conservation of the targeted species has rarely been assessed. In the sequence of the implementation of European Union LIFE European projects focused on the recovery of lesser kestrels in Portugal, the provisioning of more than a thousand artificial nest-sites attracted many other avian species, possibly influencing the structure and functioning of communities. Interference competition and even predation have already been reported among most species breeding in these colonies (Catry & Catry 2019), and the high trophic overlap reported in this study may be another trigger responsible for the observed interspecific antagonistic behaviours. This may particularly affect lesser kestrels and rollers, two species of conservation concern, classified as Vulnerable and Critically endangered in Portugal, respectively, and with decreasing population trends throughout their breeding ranges (Cabral et al. 2005; BirdLife International 2021). Food resources are abundant in the study area, so interspecific competition may not be a problem here, but this situation may not be representative of most agroecosystems around the globe (Tscharntke et al. 2005; Gameiro et al. 2020). Mixed-species groups may become compromised in areas with limited resource availability, which are predicted to increase with ongoing human and climate-induced habitat changes (Tcharntke et al. 2005; Marcelino et al. 2020; Raven & Wagner 2021). Conservation practices should include monitoring of species interactions and design nest cavities to limit the occupation of artificial nests by other species, particularly generalist and abundant ones that may outcompete with the target species. Along with ensuring suitable foraging habitat with high availability of resources, these measures could help securing endangered species in new, human-shaped nesting landscapes, and promote their long-term viability.

5. ACKNOWLEDGEMENTS

This work was supported by Fundação para a Ciência e a Tecnologia (FCT) through grants to cE3c (UIBD/00329/2020), CESAM (UIDO/50017/2020 and UIDP/50017/2020), and InBIO (UID/BIA/50027/2013). JG and JM were supported by FCT doctoral grants (PD/BD/128366/2017 and SFRH/BD/114683/2016, respectively) and IC and TC by FCT contracts (IF/00694/2015 and DL57/2016/CP1440/CT0023, respectively).

6. REFERENCES

Alonso, H., Granadeiro, J. P., Paiva, V. H., Dias, A. S., Ramos, J. A., & Catry, P., 2012. Parent – offspring dietary segregation of Cory's shearwaters breeding in contrasting environments. Marine Biology, 159: 1197–1207. https://doi.org/10.1007/s00227-012-1900-2.

Antón-Tello, M., Britto, V.O., Gil-Delgado, J.A., Rico, E., Dies, J.I., Monrós, J.S., Vera, P., 2021. Unravelling diet composition and niche segregation of colonial waterbirds in a Mediterranean wetland using stable isotopes. Ibis: 1-15. https://doi.org/10.1111/ibi.12928.

Birdlife International, 2021. IUCN Red List of Birds. Accessed on 07.05.2021 from http://www.birdlife.org.

Birt, V.L., Birt, T.P., Goulet, D., Cairns, D.K., Montevecchi, W.A., 1987. Ashmole's halo: direct evidence for prey depletion by a seabird. Marine Ecology Ecology Progress Series 40: 205-208.

Casagrande, S., Nieder, L., Di Minin, E., La Fata, I., Csermely, D., 2008. Habitat utilization and prey selection of the kestrel Falco tinnunculus in relation to small mammal abundance. Italian Journal of Zoology 75 (4): 401-409. https://doi.org/10.1080/11250000802085526.

Catry, I., Alcazar, R., Franco, A. M. A., & Sutherland, W., 2009. Identifying the effectiveness and constraints of conservation interventions: A case study of the endangered lesser kestrel. Biological Conservation 142 (11): 2782–2791. https://doi.org/10.1016/j.biocon.2009.07.011.

Catry, I., Catry, T., Alho, M., Franco, A. M. A., & Moreira, F., 2016a. Sexual and parent-offspring dietary segregation in a colonial raptor as revealed by stable isotopes. Journal of Zoology 299: 58–67. https://doi.org/10.1111/jzo.12324.

Catry, I., Franco, A.M.A., Rocha, P., Alcazar, R., Reis, S., Cordeiro, A., Ventim, R., Teodósio, J., Moreira, F., 2013. Foraging Habitat Quality Constrains Effectiveness of Artificial Nest-Site Provisioning in Reversing Population Declines in a Colonial Cavity Nester. PLoS ONE 8(3): 1–10. https://doi.org/10.1371/journal.pone.0058320.

Catry, I., Marcelino, J., Franco, A.M.A., Moreira, F. 2017a. Landscape determinants of European roller foraging habitat: implications for the definition of agri-environmental measures for species conservation. Biodiversity and Conservation 26: 553-566. https://doi.org/10.1007/s10531-016-1241-4.

Catry, I., Sampaio, A., Silva, M.C., Moreira, F., Franco, A.M.A., Catry, T., 2019. Combining stable isotope analysis and conventional techniques to improve knowledge of the diet of the European Roller Coracias garrulus. Ibis 161: 272-285. doi: 10.1111/ibi.12625.

Catry, T., & Catry, I., 2019. Nest-site provisioning re-shapes species interactions within bird assemblages. Ibis 161: 699–704. https://doi.org/10.1111/ibi.12731.

Catry, T., Lourenço, P.M., Lopes, R.J., Carneiro, C., Alves, J.A., Costas, J., Rguibi-Idrissi, H., Bearhop, S., Piersma, T., Granadeiro, J.P., 2016b. Structure and functioning of intertidal food webs along na avian flyway: a comparative approach using stable isotopes. Functional Ecology 30(3): 468-478. https://doi.org/10.1111/1365-2435.12506.

Catry, T., Moreira, F., Alcazar, R., Rocha, P.A., Catry, I., 2017b. Mechanisms and fitness consequences of laying decisions in a migratory raptor. Behavioural ecology 28 (1): 222-232. https://doi.org/10.1093/beheco/arw150.

Catry, T., Ramos, J., Le Corre, M., Kojadinovic, J., Bustamante, P., 2008. The role of stable isotopes and Mercury concentrations to describe seabird foraging ecology in tropical environments. Marine Biology 155 (6): 637-647. https://doi.org/10.1007/s00227-008-1060-6.

Caut, S., Angulo, E. Courchamp, F., 2009. Variation in discrimination factors (Δ^{15}N and Δ^{13}C): the effect of diet isotopic values and applications for diet reconstruction. Journal of Applied Ecology 46: 443-453. https://doi.org/10.1111/j.1365-2664.2009.01620.x.

Charter, M., Izhaki, I., & Roulin, A., 2018. The relationship between intra–guild diet overlap and breeding in owls in Israel. Population Ecology 60(4): 397–403. https://doi.org/10.1007/s10144-018-0633-6.

Clewlow, H.L., Takahashi, A., Watanabe, S., Votier, S.C., Downie, R., Ratcliffe, N., 2019. Niche partitioning of sympatric penguins by leapfrog foraging appears to be resilient to climate change. Journal of Animal Ecology 88: 223-235. https://doi.org/10.1111/1365-2656.12919.

Dehnhard, N., Achurch, H., Clarke, J., Michel, L. N., Southwell, C., Sumner, M. D., Eens, M., Emmerson, L., 2020. High inter- and intraspecific niche overlap among three sympatrically breeding, closely related seabird species: Generalist foraging as an adaptation to a highly variable environment? Journal of Animal Ecology 89(1): 104–119. https://doi.org/10.1111/1365-2656.13078.

Duckworth, R.A., Hallinger, K.K., Hall, N., Potticary, A.L., 2017. Switch to a novel breeding resource influences coexistence of two passerine bird. Frontiers in Ecology and Evolution 5 (72): 1-11. https://doi.org/10.3389/fevo.2017.00072.

Forero, M.G., Bortolotti, G.R., Hobson, K.A., Donazar, J.A., & Bertelloti, M., 2004. High trophic overlap within the seabird community of Argentinean Patagonia: a multiscale approach. Journal of Animal Ecology 78: 789-801. https://doi.org/10.1111/j.0021-8790.2004.00852.x.

Gameiro, J., Silva, J.P., Franco, A.M.A., Palmeirim, J.M., 2020. Effectiveness of the European Natura 2000 network at protecting Western Europe’s agro-steppes. Biological Conservation 248: 1-9. https://doi.org/10.1016/j.biocon.2020.108681.

Hardin, G., 1960. The competitive exclusion principle. Science 131 (3409): 1292-1297.

Harper, M.J., McCarthey, M.A., van der Ree, R., 2005. The use of nest boxes in urban natural vegetation remnants by vertebrate fauna. Wildlife Research 32: 509-516. https://doi.org/10.1071/WR0410.

Högstedt, G., 1980. Resource partitioning in Magpie Pica pica and jackdaw Corvus monedula during the breeding season. Ornis Scandinavica 11(2): 110–115.

Inger, R., Bearhop, S., 2008. Applications of stable isotope analyses to avian ecology. Ibis 150 (3): 447–461. https://doi.org/10.1111/j.1474-919X.2008.00839.x.

Jackson, A., & Parnell, A., 2020. SIBER: Stable Isotope Bayesian Ellipses in R. Retrieved from https://cran.r-project.org/web/packages/SIBER/index.html.

Jaksić, F. M., Seib, R. L., & Herrera, C. M., 1982. Predation by the Barn owl (Tyto alba) in Mediterranean habitats of Chile, Spain and california; a comparative approach. The American Midland Naturalist, Vol. 107, pp. 152–159. https://doi.org/10.1007/BF00545658.

Jenkins, E. J., Davoren, G. K., 2020. Seabird species- and assemblage-level isotopic niche shifts associated with changing prey availability during breeding in coastal Newfoundland. Ibis. https://doi.org/10.1111/ibi.12873.

Kappeler, P. M., Cremer, S., & Nunn, C. L., 2015. Sociality and health: Impacts of sociality on disease susceptibility and transmission in animal and human societies. Philosophical Transactions of the Royal Society B, 370 (1669). https://doi.org/10.1098/rstb.2014.0116.

Logan, J. M., Jardine, T. D., Miller, T. J., Bunn, S. E., Cunjak, R. A., & Lutcavage, M. E., 2008. Lipid corrections in carbon and nitrogen stable isotope analyses: Comparison of chemical extraction and modelling methods. Journal of Animal Ecology 77 (4): 838–846. https://doi.org/10.1111/j.1365-2656.2008.01394.x.

MacArthur, R.H., Pianka, E.R., 1966. On optimal use of a patchy environment. The American Naturalist 100 (916): 603-609.

Mainwaring, M.C., 2015. The use of man-made structures as nesting sites by birds: A review of the costs and benefits. Journal for Nature Conservation 25: 17-22. https://doi.org/10.1016/j.jnc.2015.02.007.

Marcelino, J., Silva, J. P., Gameiro, J., Silva, A., Rego, F. C., Moreira, F., & Catry, I., 2020. Extreme events are more likely to affect the breeding success of lesser kestrels than average climate change. Scientific Reports 10: 1–11. https://doi.org/10.1038/s41598-020-64087-0.

Moreira, F., Leitão, P.J., Morgado, R., Alcazar, R., Cardoso, A., Carrapato, C., Delgado, A., Geraldes, P., Gordinho, L., Henriques, I., Lecoq, M., Leitão, D., Marques, A.T., Pedroso, R., Prego, I., Reino, L., Rocha, P., Tomé, R., Osborne, P.E., 2007. Spatial distribution patterns, habitat correlates and population estimates of stepe birds in Castro Verde. Airo 17: 5-30.

Motis, A., Estrada, J., & Oro, D., 1997. Nestling diet of the Spotless starling Sturnus unicolor and the European Starling Sturnus vulgaris in a sympatric breeding area. Ornis Fennica, 74 (4): 179–185.

Murton, R.K., Westwood, N. J., 1966. The foods of the rock dove and feral pigeon. Bird Study 13 (2): 130–146. https://doi.org/10.1080/00063656609476116.

Olah, G., Vigo, G., Heisohn, R., Brightsmith, D.K., 2014. Nest site selection and efficacy of artificial nests for breeding success of Scarlet macaws Ara macao macao in lowland Peru. Journal for Nature Conservation 22: 176-185. https://doi.org/10.1016/j.jnc.2013.11.003.

Orihuela-Torres, A., Perales, P., Rosado, D., & Pérez-García, J. M., 2017. Feeding ecology of the Common Kestrel Falco tinnunculus in the south of Alicante (SE Spain). Revista Catalana d'Ornitologia 33: 10–16.

Orłowski, G., Karg, J., Rłowski, G. O., Usiecki, S. R., & Arg, J. K., 2014. Partial Dietary Segregation between Adult and Nestling Bluethroats Luscinia svecica 49(1): 107–118. https://doi.org/10.3161/000164514X682931.

Pianka, E. R., 1981. Competition and niche theory. In R. M. May (Ed.), Theoretical ecology (pp. 167–196). Oxford, UK: Blackwell.

R Core Team, 2016. A Language and environment for statistical computing. Retrieved from Vienna: R Foundation for statistical computing website: https://cran.rproject.org/.

Razgour, O., Korine, C., Saltz, D., 2011. Does interspecific competition drive patterns of habitat use in desert bat communities? Oecologia 167: 493-502. https://doi.org/10.1007/s00442-011-1995-z.

Raven, P.H., Wagner, D.L., 2021. Agricultural intensification and climate change are rapidly decreasing insect biodiversity. PNAS 118 (2): 1-6. e2002548117.

Reisinger, R.R., Carpenter-Kling, T., Connan, M., Cherel, Y., & Pistorius, P.A., 2020. Foraging behaviour and habitat-use drives niche segregation in sibling seabird species: Niche segregation in giant petrels. Royal Society Open Science 7(9). https://doi.org/10.1098/rsos.200649.

Šalek, M., Lövy, M., 2012. Spatial ecology and habitat selection of little owl Athene noctua during the breeding season in central European farmland. Bird Conservation International 22: 328-338.

Schuette, P., Wagner, A.P., Wagner, M.E., Creel, S., 2013. Occupancy patterns and niche partitioning within a diverse carnivore community exposed to anthropogenic pressures. Biological Conservation 158: 301-312. https://doi.org/10.1016/j.biocon.2012.08.008.

Silva, J.P., Correira, R., Alonso, H., Martins, R.C., D'Amico, M., Delgado, A. Sampaio, H., Godinho, C., Moreira, F., 2018. EU protected area network did not prevent a country wide population decline in a threatened grassland bird. Peer J 6: 1-13. https://doi.org/10.7717/peerj.4284.

Soler, M., Alcata, N., Soler, J.J., 1990. Alimentación de la Grahilla Corvus monedula en tres zonas del sur de España. Doñana Acta Vertebrata 17: 17-48.

Sutherland, W.J., Dicks, L.V., Ockendon, N., Petrovan, S.O., Smith, R.K., 2018. What works in conservation. Cambridge, UK: Open Book Publishers, 2018. https://doi.org/10.11647/OBP.0131.

Teckentrup, L., Kramer-Schadt, S., Jeltsch, F., 2019. The risk of ignoring fear: underestimating the effects of habitat loss and fragmentation on biodiversity. Landscape Ecology 34: 2851-2868. https://doi.org/10.1007/s10980-019-00922-8.

Tomé, R., Catry, P., Bloise, C., Korpimäki, E., 2008. Breeding density and sucess, and diet composition of little owls Athene noctua in steppe-like habitats in Portugal. Ornis Fennica 85: 22-32.

Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I., Thies, C., 2005. Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. Ecology Letters 8: 857-874. https://doi.org/10.1111/j.1461-0248.2005.00782.x.

Turner, T.F., Collyer, M.L., Krabbenhoft, J., 2010. A general hypothesis-testing framework for stable isotope ratios in ecological studies. Ecology 91: 2227-2233. https://doi.org/10.1890/09-1454.1.

Wiegand, T., Revilla, E., Moloney, K.A., 2005. Effects of habitat loss and fragmentation on population dynamics. Conservation Biology 19 (1): 108-121. https://doi.org/10.1016/j.actao.2017.06.006.

Weiss, F., Furness, R. W., McGill, R. A. R., Strange, I. J., Masello, J. F., & Quillfeldt, P., 2009. Trophic segregation of Falkland Islands seabirds: Insights from stable isotope analysis. Polar Biology 32 (12): 1753–1763. https://doi.org/10.1007/s00300-009-0674-6.

7. APPENDIX

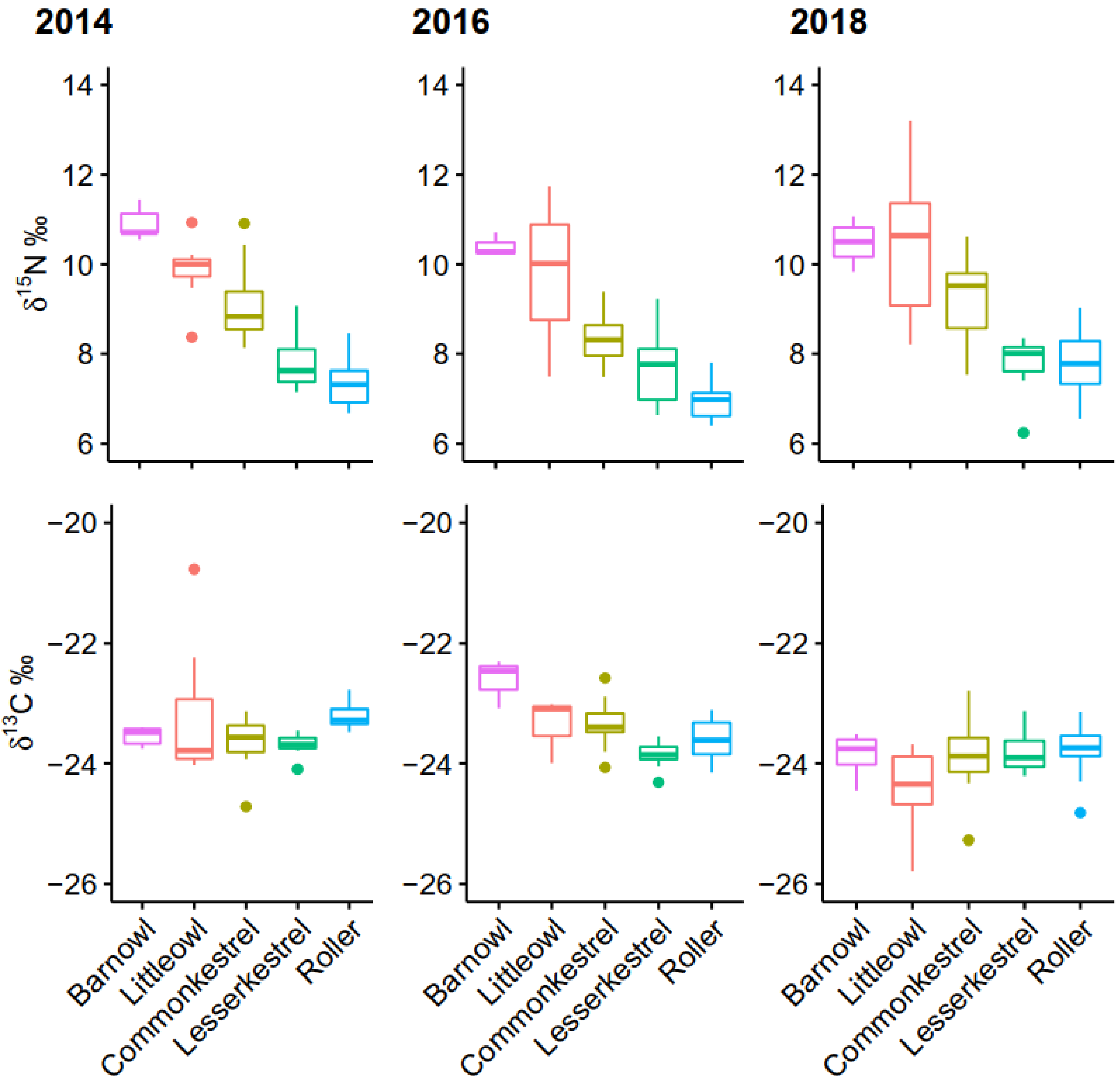


Figure 4.A1: Isotopic values ($\delta^{13}C$, $\delta^{15}N$) of each species for 2014, 2016, and 2018, based on feather samples from 12 barn owls, 19 little owls, 33 common kestrels, 36 lesser kestrels, 36 rollers, and 12 starlings.

Table 4.A1: Nestling (feathers) and adults (plasma) pairwise overlap between species expressed as the proportion of overlap in relation to the corrected standard ellipse area (SEAc) of the species in the column. Mean niche overlap (±SD) of each species was expressed as the average overlap of that species with all others (see methods).

Proportion in SEAc Overlap	Barn owl	Little owl	Common kestrel	Lesser kestrel	Roller	Starling	Mean niche overlap
Nestlings							
Barn owl	1.00	0.18	0.00	0.00	0.00	0.00	0.19 ± 0.39
Little owl	0.97	1.00	0.59	0.00	0.00	0.37	0.11 ± 0.09
Common kestrel	0.00	0.23	1.00	0.40	0.09	0.75	0.27 ± 0.28
Lesser kestrel	0.00	0.00	0.11	1.00	0.37	0.20	0.32 ± 0.27
Roller	0.00	0.00	0.04	0.60	1.00	0.09	0.12 ± 0.14
Starling	0.00	0.12	0.63	0.60	0.16	1.00	0.28 ± 0.26
Adults							
Little owl	-	1.00	0.05	0.00	0.00	0.00	0.03 ± 0.08
Common kestrel	-	0.04	1.00	0.06	0.12	0.00	0.14 ± 0.31
Lesser kestrel	-	0.00	0.10	1.00	0.73	0.78	0.28 ± 0.24
Roller	-	0.00	0.13	0.46	1.00	0.09	0.21 ± 0.26
Starling	-	0.00	0.00	0.48	0.09	1.00	0.22 ± 0.24

Table 4.A2: Test statistics and p-values for parent-offspring differences in bidimensional isoscape centroid location. P-values were generated based on a residual permutation procedure as described in Turner et al. (2010). P-values < 0.005 indicate that the Euclidean distance between centroids of parents and offspring within each species was greater than 0, and thus a statistical difference in isotopic values between the two age groups.

	Euclidean distance	p-value
Little owl	1.196	0.005
Common kestrel	1.298	0.001
Lesser kestrel	1.020	0.001
Roller	1.504	0.005
Starling	1.998	0.003

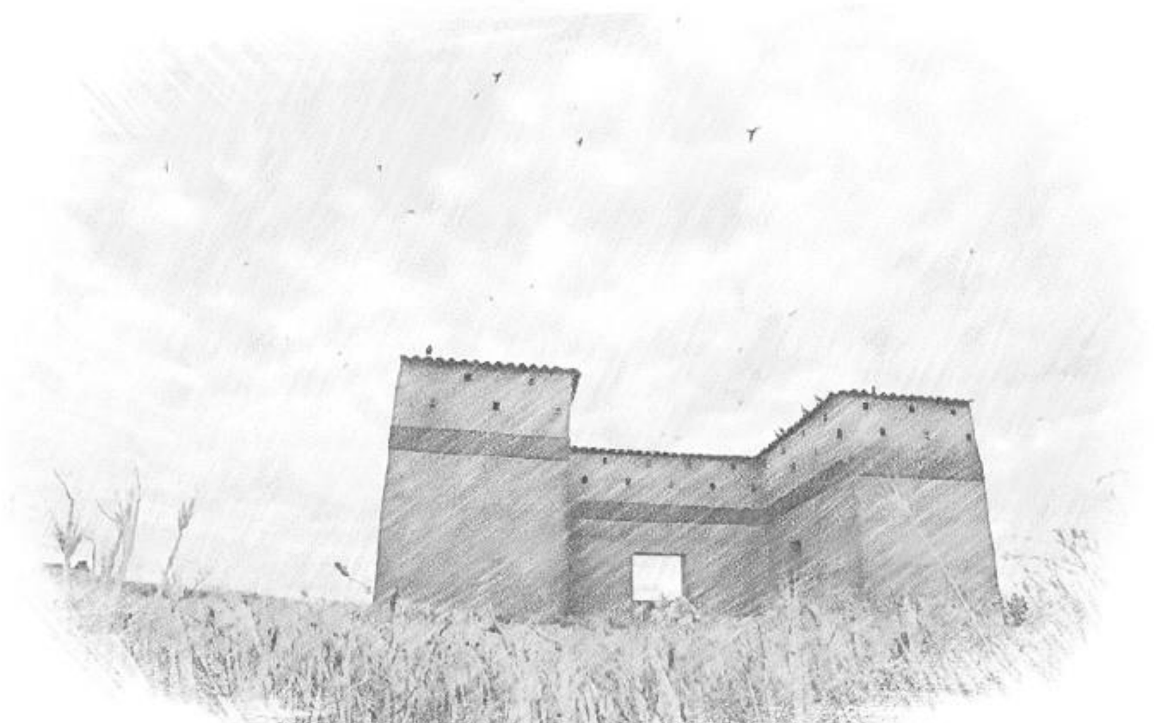
Table 4.A3: Models on the influence of coloniality on roller and lesser kestrel productivity (number of fledging nestlings), using data from 247 roller nests and 1551 lesser kestrel nests across 6 years (2014 to 2019). The roller model used social context (solitary vs colony) as a categorical fixed effect, and year as a random effect. The lesser kestrel model used colony size (number of breeding pairs) as a continuous fixed effect, and year and colony identity (ID) as random effects.

Effect	**Variance**	**estimate**	**Std. error**	**Z value**	**p-value**
Roller					
Year	0.019 (0.137)				
Intercept		1.280	0.068	18.835	<0.001
Solitary nests		-0.019	0.080	-0.237	0.813
Lesser kestrel					
Colony ID	0.047 (0.216)				
Year	0.021 (0.145)				
Intercept		0.986	0.134	7.365	<0.001
Colony size		-0.005	0.005	-1.152	0.249

Chapter 5

Is it better to be solitary or breed in heterospecific colonies? Assessing anti-predatory benefits for a solitary bird

João Gameiro, Aldina M.A. Franco, Teresa Catry, Jorge M. Palmeirim & Inês Catry



IS IT BETTER TO BE SOLITARY OR BREED IN HETEROSPECIFIC COLONIES? ASSESSING ANTI-PREDATORY BENEFITS FOR A SOLITARY BIRD

ABSTRACT

Predation risk profoundly shapes how animals behave, shifting the abundance and distribution of species and altering the structure of communities. Living in groups may provide protection from predators through increased vigilance or aggressive behaviors towards potential dangers. For some species, group living may be facultative, and individuals may live solitarily or aggregate with conspecifics or heterospecifics, but the advantages of different strategies are still poorly known. Here, we investigated whether a solitary breeding species, the European roller *Coracias garrulus*, acquires anti-predatory benefits from nesting in mixed-species colonies dominated by lesser kestrels *Falco naumanni*. We compared the risk-taking behavior of solitary rollers and rollers breeding in colonies by conducting two sets of experiments: the first measuring rollers' latency to resume incubation when presented with a novel object, and the second measuring their latency to resume chick provisioning and their investment in mobbing behavior towards a predator model. We also compared the breeding performance and nest predation rate of rollers in each social context (solitary vs colonial) using data from 300 breeding attempts across six years. We found that rollers breeding in colonies returned to their nests sooner during the presentation of both the novel object and the predator model, and attacked the predator model less frequently than solitary rollers. In addition, rollers in colonies suffered less nest predation than solitary ones, but this did not translate into a higher productivity. Future studies should investigate whether breeding in colonies provide other advantages to rollers, such as increased adult survival or fitness.

Keywords: group-living; protective nesting associations; anti-predatory behaviour; facilitation; mixed-species colonies; predation

1. INTRODUCTION

Predation is a major driving force in the evolutionary history of animals, influencing their behavior and affecting their fitness (Lima & Dill 1990; Quinn & Ueta 2008; Inbánez-Álamo et al. 2015; Graham & Shutler 2019). In addition to the obvious lethal effects of failing to escape a predator, animals may experience non-lethal effects when responding to predation risk, by redirecting time and energy from other fitness-enhancing activities such as mating, feeding, or caring for offspring (Lima & Dill 1990; Frid & Dill 2002; Cresswell 2008). Because anti-predatory strategies are costly, behaviors used by animals to evade predators are plastic and require individuals to successfully identify real threats (Frid & Dill 2002; Crane & Ferrari 2017). One way to do so is by being fearful to novel, risky stimuli, i.e., being neophobic (Cran & Ferrari 2017; Crane et al. 2020). As at the individual level, all cues from predators and non-predators are novel during the first encounter, a frightened response to new stimuli is a safe strategy to learn about real predators (Brown et al. 2013; Crane & Ferrari 2017).

Anti-predatory behavior may also be influenced by the presence of nearby animals, and predation is often considered an important factor in the evolution of sociality, influencing the structure and dynamics of communities (Lima & Dill 1990; Uetz et al. 2002; Varela et al. 2007; Lehtonen & Jaatinen 2016; Crane et al. 2020). Living in groups increases prey conspicuousness (Varela et al. 2007) but may reduce predation risk through increased efficiency in predator detection and deterrence, or simply through dilution effects (Brown & Hoogland 1986; Arroyo et al. 2001; Hass & Valenzuela 2001; Beauchamp 2008; Lehtonen & Jaatinen 2016). Individuals in groups may detect predators earlier as total time spent in vigilance increases with group size, while reducing the need for individual investment (Brown & Hoogland 1986; Beauchamp 2008; LaBarge et al. 2021). Similarly, individuals in groups engaged in mobbing – where animals harass, distract, or confuse an approaching predator by lunging or calling towards it – should face lower individual predation risk than those mobbing solitarily, whilst maintaining or increasing mobbing effectiveness (Brown & Hoogland 1986; Arroyo et al. 2001; Krams et al. 2009).

Mixed-species groups are common across many taxa and may enhance anti-predatory benefits more than single-species assemblages (Stensland et al. 2003; Sridhar & Guttal 2018; Boulay et al. 2019; Goodale et al. 2020). This may occur because species have different sensory or behavior capabilities; for example, individuals may aggregate with more vigilant, vocal, or aggressive species that are more effective at driving predators off (Quinn & Ueta, 2008; Sharpe et al. 2010; Campobello et al. 2012; Goodale et al. 2019; Gabel et al. 2021). Additionally, because niche overlap is highest among conspecifics, aggregating with other species may alleviate the costs associated with intraspecific competition (Sridhar & Guttal, 2018; but see Gaglio et al. 2018; Catry & Catry 2019). Lastly, for some species, e.g., those living solitary or in small groups, achieving a group large enough to provide anti-predatory benefits may only be possible by aggregating with heterospecifics (Semeniuk & Dill 2006; Goodale et al. 2019, 2020). Whether to live solitarily, in single, or in mixed groups may depend on localized adaptations to specific ecological conditions such as habitat structure or predation pressure (Wagner et al. 2000; Quinn & Ueda 2008; Marino 2010; Murthy et al. 2015; Liu et al. 2020). However, how predation risk favors one strategy over the other remains poorly studied.

In birds, mixed-species groups often occur as mixed-species colonies, where birds concentrate on highly dense breeding sites. Colonies are particularly susceptible to predation, as they are fixed in space and are more conspicuous through visual, acoustic, or olfactory cues (Rolland et al. 1998; Varela et al. 2007). In this study, we investigate whether a typically solitary bird species, the European roller *Coracias garrulus* (hereafter roller), acquires anti-predatory benefits from nesting in mixed-species colonies dominated by lesser kestrels *Falco naumanni*. Both species are long-distance migrants, wintering mostly in sub-Saharan Africa and breeding in the Western Palearctic (Finch et al. 2015; Sarà et al. 2019). In their southern European breeding grounds, rollers and lesser kestrels have similar dietary and nesting requirements (Catry et al. 2009, 2016, 2019; Birdlife International, 2021). Previous studies on solitary rollers found that they avoided areas with higher predation risk but did not alter parental care in the presence of a predator model (Parejo & Avilés 2011; Expósito-Granados et al. 2016). On the other hand, lesser kestrels are known for their marked mobbing behavior and have been described as the protector species in nesting associations with red-billed coughs *Pyrrhocorax pyrhocorax* (Blanco & Tella 1997) and jackdaws *Corvus monedula* (Campobello et al. 2012). In southern Portugal, rollers can be found breeding both solitarily and in association with mixed-species colonies often dominated by lesser kestrels (Catry et al. 2009; Gameiro et al. 2020). We conducted behavioral experiments examining the risk-taking behavior towards a novel object and towards a predator model in rollers breeding solitarily and rollers breeding in mixed colonies. In addition, we investigated whether potential benefits from either social breeding strategy (solitary vs colonial) translate into higher breeding success by measuring nest predation rate and breeding performance in 300 roller breeding attempts across six consecutive breeding seasons (2014 to 2019). We expect the presence and behavior of neighboring lesser kestrels would inform rollers on whether returning to the nest is safe, regulating rollers investment in nest-defensive behaviors (Seppänen et al. 2007; Quinn & Ueta 2008; Campobello et al. 2012). If nesting in colonies provides direct anti-predatory benefits, we predict rollers breeding in colonies to have lower predation rates and higher productivity.

2. METHODS

2.1 STUDY AREA AND SPECIES

This study was conducted in the Special Protection Area (SPA) of Castro Verde, Southeast Portugal (37°43′N, 7°57′W). With ca. 85 000 ha, this is one of the most important strongholds for many endangered farmland birds in Western Europe (Moreira et al. 2007), hosting more than 80% of the Portuguese populations of rollers and lesser kestrels (Catry et al. 2009, 2011; Gameiro et al. 2020). The landscape is dominated by extensive dry cereal cultivation interspersed with fallows and grasslands used for livestock, orchards, vineyards, and small afforestations (Moreira et al. 2007). Here, rollers and lesser kestrels – two secondary-cavity nesting birds – nest in cavities of abandoned farmland buildings or artificial breeding structures build in the scope of conservation programs targeting the recovery of lesser kestrels since 2000 (Catry et al. 2009; Catry et al. 2011; Gameiro et al. 2020). Artificial nests include nest-boxes, clay pots, and breeding walls and towers with up to 90 cavities (Catry et al. 2009).

Lesser kestrels arrive to the breeding grounds in early February and typically lay in April-May. Both sexes participate in incubation and chick rearing. Incubation lasts ca. 28 days and chicks fledge at 36 (del Hoyo et al. 2001a). Rollers arrive at the breeding grounds in mid-April and laying usually occurs in May-June. Both sexes engage in incubation and chick rearing. Incubation takes ca. 20 days and chicks fledge at 20-25 days (Del Hoyo et al. 2001b). Rollers can breed in isolated nests (isolated cavities in farmhouses or in nest-boxes placed on trees or telephone poles), or within mixed colonies, with up to four roller pairs per colony. Lesser kestrel colonies range from two to 80 breeding pairs. Other species can also be found breeding in these mixed-species colonies, including common kestrel *Falco tinnunculus,* barn owl *Tyto alba*, little owl *Athene noctua*, jackdaw *Corvus monedula*, spotless starling *Sturnus unicolor*, and feral pigeon *Columba livia* (Catry & Catry 2019). These species do not significantly contribute to the communal defense, and so attention was given only to lesser kestrels (see results). Potential nest/adult predators in the area include carrion crow (*Corvus corone*), Eurasian magpie (*Pica*

pica), barn owl, ladder and Monpellier snake (*Zamenis scalaris* and *Malpolon monspessulanus*, respectively), weasel (*Mustela nivalis*), garden dormhouse (*Eliomys quercinus*), and rats (*Rattus* sp.).

2.2 DATA COLLECTION

From 2017 to 2019, two sets of experiments were conducted to compare risk-taking behavior in rollers breeding solitarily and rollers breeding within mixed-species during both the incubation and chick-rearing periods.

2.2.1 RISK-TAKING BEHAVIOUR TOWARDS A NOVEL OBJECT DURING INCUBATION

This experiment, aiming to describe the latency of rollers to resume incubation during the presentation of a novel object (neophobia), was conducted in 2017 and 2018, by selecting rollers pairs at early incubation stage. One person (observer) slowly approached a nest until the incubating roller escaped, placed a GoPro Hero 4 session camera (novel object) 10cm from the nest entrance (Fig. 5.A1), and abandoned the area after 15min since the roller left the nest (to standardize the period of human disturbance across all nests). The experiment was carried out for further 90 minutes, after which the observer returned to recover the object. Flight initiation distance was not measured as it was not possible to approach the nest in a linear transect in all sites due to landscape variability, namely the presence of different structures such as walls or fences in the approach line. Latency to resume incubation was determined by analyzing the camera videos, and measured as the time, in minutes, it took one of the parents to enter the nest. A total of 75 roller pairs were tested, of which 27 were solitary (8 in 2017 and 19 in 2018) and 48 were within colonies (25 in 2017 and 23 in 2018). Rollers that failed to return to the nest during the experiment were attributed a latency of 90 minutes (15 pairs, 20%).

2.2.2 RISK-TAKING BEHAVIOUR TOWARDS A PREDATOR DURING CHICK-REARING

This experiment, aiming at investigating risk-taking behavior and nest defense by rollers in the presence of a potential predator, was conducted in 2019. A crow-like model was presented to simulate a carrion crow, a potential egg/nestling predator in the area. Previous pilot experiments tested other predator models, including common magpie, barn owl, and Montpellier’s snake, but they were not perceived as a threat (personal observation, data not shown).

Experiments were conducted when nestlings were approximately 15 days old and consisted of three sequential phases: (1) pre-demonstration, a control period before the predator model presentation (30min); (2) demonstration, during which the predator model was presented (20min); and (3) post-demonstration, after removing the predator model (40min). During the pre-demonstration phase, we recorded the provisioning rate (number of times a roller entered its nest) through direct observation, starting from the first nest entrance event, to ensure parents were actively feeding their nestlings. After the pre-demonstration phase, the crow model was placed ca. 1m above the focal nest entrance (usually on the roof or wall crevice), and the behavior of the focal rollers was recorded using a camera (GoPro Hero 4 session) placed on the floor at 10-15m from the nest to monitor the behavior of birds in a wide range (Fig. 5.A1). Video recordings were analyzed to determine: (1) rollers' latency to return to the nest-site, measured as the time elapsed until the first time a roller perched on the structure, fed their nestlings, or attacked the predator model, (2) the number of provisioning events, and (3) the number of attacks against the predator model. During the post-demonstration, we measured the time elapsed until rollers resume chick provisioning and registered the number of provisioning events. All observation and recordings were conducted when the observer was positioned >200m from the nest (inside a car), ensuring that it was not disturbing the birds. Each experiment lasted 90mins and was performed for a total of 33 roller pairs, of which 12 were solitary and 21 were in colonies.

No experiment resulted in nest abandonment from rollers.

2.2.3 BREEDING PARAMETERS AND NEST PREDATION

From 2014 to 2019, 298 roller nests (mean nests per year = 50, min = 42, max = 55), of which 88 were solitary and 210 bred within mixed-species colonies, were visited weekly to record laying date, clutch size, and productivity (number of fledged chicks per breeding attempt). Nests that lost eggs and/or nestlings with clear signs of predation such as broken eggs or dead chicks with injuries in the nest/floor were recorded as being predated.

2.3 DATA ANALYSIS

2.3.1 INFLUENCE OF SOCIAL CONTEXT IN RISK-TAKING BEHAVIOUR TOWARDS A NOVEL OBJECT

The latency of rollers to resume incubation during a neophobia event was investigated using a Gamma General Linear Mixed Model (GLMM) with latency (in minutes) as the response variable, year as a random factor, and social context (solitary vs colonial) as an explanatory variable. Laying date (Julian date, days) was also used as an explanatory variable, to control for individual traits/experience, under the assumption that early breeders are older, more experienced individuals and more risk prone (Verhulst & Nilsson 2008; Brommer et al. 2014; Winkler 2016; Poblete et al. 2021). A log-link was used as data had a right-skewed distribution.

2.3.2 INFLUENCE OF SOCIAL CONTEXT IN RISK-TAKING BEHAVIOUR TOWARDS A PREDATOR

We first confirmed that the crow model was perceived as a threat, as rollers avoided feeding their nestlings during the predator demonstration phase (Kruskal-Wallis on the provisioning rate among the three stages of the experiment: $\chi 2= 45.563$, df = 2, p-value < 0.001) (Fig. 5.1).

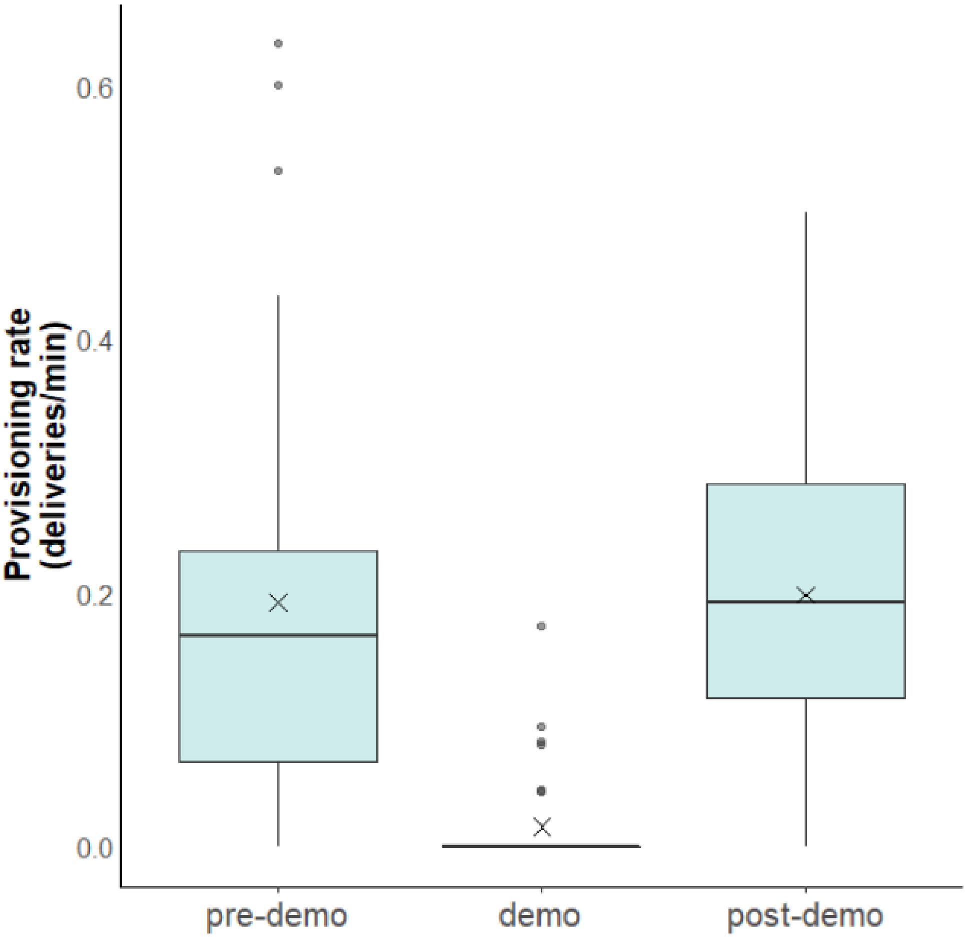


Figure 5.1: Provisioning rate of 33 roller pairs during each phase of the predator exposure experiment: pre-demonstration (pre-demo) – before placing the predator model; demonstration (demo) – during predator presentation; pos-demonstration (post-demo) – after removing the predator model.

Latency to return to the nest-site during the predator demonstration and latency to resume chick provisioning during the post-demonstration phases were investigated through log-Gamma Generalized Linear Models (GLMs) with latency (in minutes) as the response variable. Roller attack rate during predator demonstration was investigated through a zero-inflation log-Poisson GLM, using number of attacks as the response variable, with duration of the phase as an offset. For all three sets of GLMs, breeding social context (solitary vs colonial) and laying date were used as explanatory variables. To further investigate the influence of the number of lesser kestrels on roller's behavior during the predator exposure experiment, another set of similar GLMs were used for rollers breeding in colonies, using the number of lesser kestrel pairs and laying date as explanatory variables.

2.3.3 BREEDING PARAMETERS AND NEST PREDATION

To examine how breeding parameters and nest predation varied between solitary rollers and rollers breeding in colonies, four GLMMs were used, using social context and laying date as explanatory variables, and year (2014 to 2019) as a random factor. A binomial distribution was used for the predation rate model, and Poisson distributions were used for the laying date, clutch size, and productivity model. Predation (0 or 1) was additionally used as an explanatory variable for the productivity model.

All continuous variables were centered and scaled prior to analysis. All analysis were conducted with R software 3.6.1 (R Core Team, 2016).

3. RESULTS

3.1 INFLUENCE OF SOCIAL CONTEXT IN RISK-TAKING BEHAVIOUR TOWARDS A NOVEL OBJECT

Overall, rollers took an average of 40 minutes (min = 4.4, max = 90) to resume incubation during the neophobia event. Latency to resume incubation was significantly lower for rollers in colonies and decreased with increasing laying date (Table 5.1). Solitary rollers took, on average, 55.2 ± 30.3 min to resume incubation, while rollers in colonies took 31.0 ± 26.9 min (Fig. 5.2).

Table 5.1: Parameters of log-Gamma GLM investigating the effect of social breeding context (solitary rollers vs colonial rollers), laying date and year on roller's latency to resume incubation during the presentation of a novel object (GoPro camera). Data from 75 roller pairs (27 solitary and 48 in colonies) sampled during in 2017 and 2018.

Effect	SD	Estimate	SE	Z-value	P-value
Year	0.724				
Intercept [solitary]		**4.007**	**0.183**	**21.936**	**< 0.001**
Breeding context [colonial]		**-0.702**	**0.189**	**-3.717**	**< 0.001**
Laying date		**-0.229**	**0.097**	**-2.442**	**0.015**

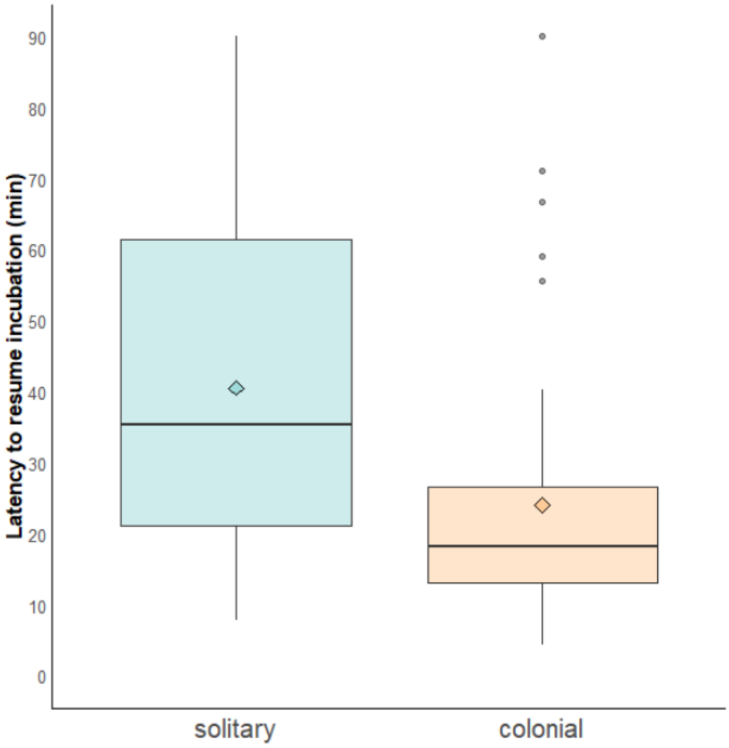


Figure 5.2: Latency to resume incubation during the presentation of a novel object (GoPro camera) in solitary rollers (solitary) and rollers breeding within lesser kestrel colonies (colonial). Boxplots show median, quantiles and range, diamonds show the mean. Data from 75 roller pairs (27 solitary and 48 in colonies) sampled during the breeding season of 2017 and 2018.

3.2 INFLUENCE OF SOCIAL CONTEXT IN RISK-TAKING BEHAVIOUR TOWARDS A PREDATOR MODEL

Twenty (60.6%) out of the 33 roller pairs tested returned to the nest-site during the predator demonstration phase (either by perching, entering the nest, or attacking the crow). GLMs revealed that roller's risk-taking behavior against the predator model was influenced by laying date, with early breeders attacking the predator model more often, but not by the breeding social context (Table 5.2).

Table 5.2: Parameters of GLMs investigating the effect of social breeding context (solitary vs colonial rollers) and laying date on roller's risk-taking behaviour during the presentation of a predator (crow model). Significant effects displayed in bold. Data from 33 roller pairs (12 solitary and 21 in colonies) sampled during the breeding season of 2019.

Effect	Estimate	SE	Z-value	p-value
Demonstration				
Attack rate				
Count model				
Intercept [solitary]	**-0.750**	**0.137**	**-5.477**	**<0.001**
Laying date	**-0.595**	**0.086**	**-6.893**	**<0.001**
Social context [colonial]	-0.184	0.160	-1.152	0.249
Zero-inflation model				
Intercept [solitary]	0.339	0.588	0.576	0.564
Laying date	-0.081	0.361	-0.226	0.821
Social context [colonial]	-0.062	0.737	-0.084	0.933
Latency to return to nest-site				
Intercept [solitary]	**2.786**	**0.154**	**18.135**	**<0.001**
Laying date	0.044	0.094	0.468	0.643
Social context [colonial]	-0.087	0.193	-0.453	0.654
Post-demonstration				
Latency to resume chick provisioning				
Intercept [solitary]	**2.966**	**0.151**	**19.593**	**<0.001**
Laying date	0.222	0.123	1.808	0.081
Social context [colonial]	-0.029	0.251	-0.117	0.908

When considering only rollers breeding within colonies, the time to return to the nest-site and the number of attacks towards the predator model decreased significantly with increasing colony size, i.e., the number of lesser kestrel pairs (Table 5.3). Rollers in larger colonies also tended to resume chick provisioning faster than rollers in smaller colonies, although this effect not significant (p = 0.078; Table 5.3).

Overall, rollers took an average of 14.2 min to return to the nesting structure (solitary: mean = 15.2, min = 4.2, max = 20; colonial: mean = 13.5, min = 1.1, max = 20), and attacked the predator model at a rate of 0.21 attacks/min (solitary: mean = 0.25, min = 0, max = 1.2; colonial: mean = 0.19, min = 0, max = 2.04). Lesser kestrels arrived sooner at 7.1 min (min = 0.4, max = 20), and attacked at an average frequency of 2.96 attacks/min (min = 0, max = 25.14). Other species participating in mobbing included common kestrels with 0.35 attacks/min (4 colonies) and jackdaws with 0.05 attacks/min (2 colonies).

Table 5.3: Parameters of GLMs investigating the effect of colony size (number of lesser kestrel pairs) and laying date on roller's the risk-taking during the presentation of a predator (crow model). Significant effects displayed in bold. Data from 21 roller pairs sampled during the breeding season of 2019.

Effect	Estimate	SE	Z-value	p-value
Demonstration				
Attack rate				
Count model				
Intercept	**-0.888**	**0.136**	**-6.539**	**<0.001**
Laying date	**-0.555**	**0.139**	**-3.981**	**<0.001**
Colony size	**-0.345**	**0.135**	**-2.558**	**0.011**
Zero-inflation model				
Intercept	0.312	0.515	0.607	0.544
Laying date	-0.107	0.563	-0.191	0.849
Colony size	-0.142	0.766	-1.097	0.057
Latency to return to nest-site				
Intercept	**2.644**	**0.132**	**19.982**	**<0.001**
Laying date	0.070	0.136	0.514	0.613
Colony size	**-0.397**	**-2.924**	**-2.924**	**0.009**
Pos-demonstration				
Latency to resume chick provisioning				
Intercept	*2.921*	*0.162*	*17.992*	*<0.001*
Laying date	0.298	0.167	1.789	0.090
Colony size	-0.311	0.167	-1.868	0.078

3.3 DOES NESTING IN COLONIES INCREASES BREEDING PERFORMANCE?

Laying date and clutch size were similar between solitary rollers and rollers breeding in lesser kestrel colonies, and clutch size decreased significantly with increasing laying date (Fig. 5.3; Table 5.A1). Predation of roller nests was significantly lower in colonies compared to solitary nests, and it was not influenced by laying date (Table 5.A1). Predation occurred in 23.3% of solitary nests and in 10.3% of nests in colonies (Fig. 5.3). Roller productivity (number of fledging chicks per breeding attempt) decreased significantly with increasing laying date and was lower in nests where predation was recorded, but did not differ with roller breeding social context (Table 5.A1).

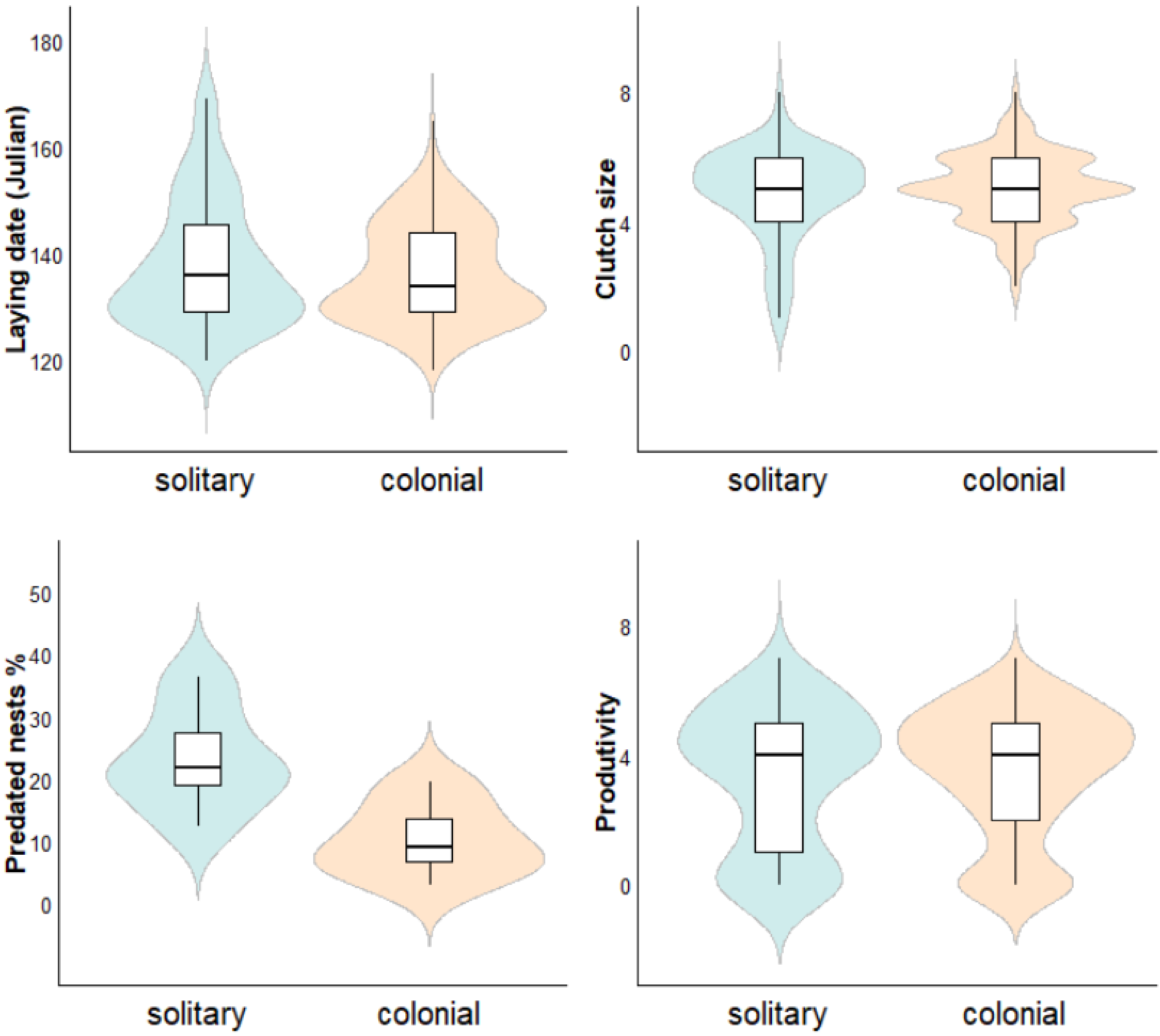


Figure 5.3: Comparison of reproductive parameters and proportion of predated nests between solitary rollers (solitary) and rollers breeding in lesser kestrel colonies (colonial). Productivity = number of chicks fledging per breeding attempt. Data from 298 roller pairs monitored from 2014 to 2019 (88 solitary, 210 colonies).

4. DISCUSSION

Living in groups may offer protection from predators, particularly when assembled individuals belong to different species that differ in their capacities to be vigilant or aggressive, or because grouping with conspecifics alone is insufficient to produce anti-predatory benefits (Sridhar & Guttal, 2018; Goodale et al. 2020). This study provides a clear example of a protective nesting association (Richardson & Bolen 1999; Quinn & Ueta 2008; Rocha et al. 2016; Burgas et al. 2021), documenting that the European roller, a solitary breeding species, gains direct anti-predatory benefits from nesting within mixed-species colonies dominated by lesser kestrels. Rollers breeding within colonies returned to their nests faster in response to a neophobic event, reduced their individual investment in mobbing behaviors towards a potential predator, and overall suffered from half the nest predation of solitary rollers. However, these apparent benefits were not reflected in a higher productivity, suggesting there are no clear reproductive advantages for breeding in colonies.

4.1 DOES NESTING WITHIN MIXED COLONIES INFLUENCE ROLLER'S RISK-TAKING BEHAVIOUR TOWARDS A NOVEL OBJECT?

During the presentation of a novel object, rollers breeding in colonies resumed incubation almost twice as fast as solitary rollers. A novel stimulus such as an unrecognizable object, sound or smell, may be perceived as a potential predation threat, and so a fearful reaction may be a plastic, adaptative strategy to avoid a potential deadly encounter (Brown et al. 2013; Crane & Ferrari 2017). Nesting near lesser kestrels may help rollers perceive the threat-level of a novel stimuli and assess whether it is safe to return to their nests by picking up cues from the responses of their heterospecific neighbors (Seppänen et al. 2007; Goodale et al. 2010; Crane et al. 2020). Heterospecific social information helps individuals acquire and share information (advertently or not) about their surroundings and potential dangers and has proven to be an advantageous mechanism in detecting and evading predators (Johnson et al. 2003; Magrath et al. 2015; Lehtonen & Jaatinen 2016). Lesser kestrels always arrived sooner to the colony, which could have facilitated the return of rollers to their nests (Rasolofoniaina et al. 2021). Solitary rollers, on the other hand, have no neighbors to which acquire information from, and so might need more time to perceive the actual risk from the novel stimuli by themselves. By returning faster to the nest-site, rollers in colonies can reduce egg's exposure to predators or adverse physical conditions (e.g., hot temperatures), while simultaneously increasing incubation time (Frid & Dill 2002).

4.2 DOES NESTING WITHIN MIXED COLONIES INFLUENCE ROLLER'S RISK-TAKING BEHAVIOUR TOWARDS A POTENTIAL PREDATOR?

Mobbing behavior is a common group defense strategy in many taxa and serves two main functions: first, it alerts con- and heterospecific neighbors about the presence of a predator and attracts them to participate in the communal defense (Goodale et al. 2010; Campobello et al. 2012; Dutour et al. 2017); second, by recruiting more mobbers, it decreases individual investment and risk of getting caught by the predator through dilution or selfish-herd effects (Brown & Hoogland 1986; Arroyo et al. 2001; Krams et al. 2009; Lehtonnen & Jaatinen 2016). It follows that the more individuals participating in mobbing the higher the success of deterring the predator, so an effective mobbing event may only be achieved at a certain group size (Krams et al. 2009). In our study, lesser kestrel mobbing behavior was only noticeable in larger colonies (> 25 breeding pairs), peaking at a rate 25 attacks/minute (Fig. 5.A2). Although we did not quantify mobbing calls, they were more frequent when mobbing was more intense (personal observation). Besides lesser kestrels, common kestrels breeding in the focal colony, but also jackdaws from nearby colonies and one Montagu's harrier were seen mobbing the predator model. The observation of an evident group mobbing behavior only at larger colonies might explain why we found no differences in risk-taking behavior between solitary rollers and rollers nesting in colonies. However, roller's mobbing intensity decreased with increasing colony size, strongly suggesting that rollers benefit from the aggressive behavior of their heterospecifics by reducing their investment and risk in defensive duties. Similar patterns were described for colonial or semi-colonial species (Arroyo et al. 2001; Krams et al. 2009), or when comparing solitary and colonial species (Brown & Hoogland 1986), but has never been described for a solitary species breeding in association with a colonial heterospecific.

4.3 WHAT OTHER FACTORS MAY INFLUENCE ROLLER'S RISK-TAKING BEHAVIOUR?

Rollers' risk-taking behavior towards the novel object and towards the predator was also influenced by laying date. In birds, early breeders are often older or more experienced individuals, selecting higher quality breeding areas, having higher reproductive success, and being more risk prone (Verhulst & Nilsson 2008; Brommer et al. 2014; Winkler 2016; Poblete et al. 2021). Our data, from six consecutive breeding seasons, showed that early breeding rollers laid more eggs and had higher productivity (number of fledging chicks) than late breeders. More experienced individuals may be better at picking up cues from their surroundings, which includes perceiving the presence and behavior of neighbors or predators (Verhulst & Nilsson 2008; Graham & Shutler 2019). This may explain why early breeding rollers in our study showed improved risk-taking responses by attacking the predator model more frequently and resuming chick provisioning earlier after predator removal, a similar result to what was reported for other bird species (Brommer et al. 2014; Poblete et al. 2021). However, our neophobia experiment revealed that early breeders took more time to resume incubation than late breeders. Rollers are single-brooded, so losing a clutch later in the season may compromise breeding for that year (Tilgar & Kikas 2009; Ghalambor et al. 2013). It is possible that the motivation to incubate for late breeders surpasses the risk of approaching a novel stimulus that may or may not end up as a real danger, as opposed to rollers presented with a predator model that is perceived as a bigger threat (Brown et al. 2013; Crane & Ferrari 2017).

In addition to the social context and timing of breeding, there are other factors that may influence roller’s risk-taking behavior that were not addressed in this study. Current brood value is expected to regulate parental investment, with parents taking higher risks when they have more offspring or when the probability of that offspring surviving increases, i.e., in older broods (Tilgar & Kikas 2008; Graham & Shutler 2019). Although we controlled for brood age, through testing rollers at similar development stages, we could not disentangle the effects of brood size from laying date due to their high correlation. Personality traits, i.e., consistent individual variation in behavior across different contexts (Biro & Stamps 2008; Brommer et al. 2014; Santos et al. 2015), may also shape individual risk-taking behavior, but these were not investigated in this study. Brood value or individual behavioral differences may have been responsible for some of the observed variability in roller’s response and could help explain the lack of social context effect on roller’s likelihood to attack the predator models, or the time it took for rollers to resume chick provisioning after predator removal.

4.4 IMPLICATIONS OF COLONIALITY FOR A SOLITARY BREEDING SPECIES

Predation is one of the strongest selective forces in nature, shaping life-history traits and the structure and dynamics of communities (Cresswell 2008; Quinn & Ueta 2008; Ibáñez-Álamo et al. 2015; Crane & Ferrari 2017). If rollers acquire direct anti-predatory benefits from breeding near lesser kestrels, one of the possible outcomes of such benefits would be to have higher productivity, as a result of higher nestling survival due to lower predation levels. However, data from near 300 breeding events across six consecutive breeding seasons show no differences in laying date, clutch size, or productivity between rollers breeding in different social contexts, suggesting there are no evident reproductive advantages of nesting within colonies. The anti-predatory advantages of nesting within colonies may be offset by costs typically inherent to group living and could explain the similar productivity levels between solitary and colonial rollers (Wagner et al. 2000; Semeniuk & Dill 2005; Gaglio et al. 2018; Catry & Catry 2019; Goodale et al. 2020). The niche similarity between two species (preying on similar resources or avoiding the same predator) increases the value of interspecific social information and may facilitate the formation of mixed-species groups, but it also increases the potential for interspecific competition, particularly when breeding at high densities (Parejo et al. 2005; Seppänen et al. 2007; Sridhar & Guttal 2018; Goodale et al, 2020). This may be the case for rollers breeding near lesser kestrels, as the two species are known to largely overlap in their trophic resources (Catry et al. 2016, 2019; Gameiro et al. submitted), and previous studies on these mixed-species colonies have reported higher parasitic burden on colonies with increasing number of lesser kestrels (Gameiro et al. 2021), all of which may reduce offspring fitness and breeding success. On the other hand, both lethal and non-lethal effects of predation may impact animals beyond their reproductive output. Parents may be killed or become impaired while defending a nest, or may exhaust their energy in anti-predatory behaviors potentially affecting their own fitness or survival in future reproductive attempts (Creel & Christianson 2008; Cresswell 2008). Offspring reared under stressful, high-predation pressure may also suffer from suboptimal growth, due to lack of parent investment in incubation or feeding, and even suffer from decreased cognitive and learning abilities that may affect later stages of life (Creel & Crhistianson 2008; Pouca et al. 2021; Oteyza et al. 2021). Even if not providing clear reproductive advantages, the protection provided by lesser kestrels in mixed colonies against predators may still result in an adaptive breeding strategy for rollers. Further studies should investigate whether breeding in mixed-species colonies provide other advantages to rollers.

5. ACKNOWLEDGEMENTS

This work was supported by Fundação para a Ciência e a Tecnologia (FCT) through grants to cE3c (UIBD/00329/2020), CESAM (UIDO/50017/2020 and UIDP/50017/2020), and InBIO (UID/BIA/50027/2013). JG was supported by a FCT doctoral grant (PD/BD/128366/2017), IC and TC by FCT contracts (DL57/2016/CP1440/CT0023 and IF/00694/2015, respectively), and AF by a Natural Environment Research Council (NERC) standard grant (NE/K006312/1).

6. REFERENCES

Arroyo, B., Mougeot, F., Bretagnolle, V., 2001. Colonial breeding and nest defence in Montagu's harrier (Circus pygargus). Behavioral Ecology and Sociobiology 50: 109-115. https://doi.org/10.1007/s002650100342.

Beauchamp, G., 2008. What is the magnitude of the group-size effect on vigilance? Behavioral Ecology 19: 1361-1368. https://doi.org/10.1093/beheco/arn096.

Birdlife international, 2021. IUCN Red List for birds. Downloaded from http://www.birdlife.org on 04/06/2021.

Biro, P.A., Stamps, J.A., 2008. Are animal personality traits linked to life-history productivity? Trends in Ecology and Evolution 23: 361–368. https://doi.org/10.1016/j.tree.2008.04.003.

Blanco, G., Tella, J.L., 1997. Protective association and breeding advantage of choughs in lesser kestrel colonies. Animial Behaviour 54: 335-342. https://doi.org/10.1006/anbe.1996.0465.

Boulay, J., Aubernon, C., Ruxton, G.D., Hédoin, V., Deneubourg, J.L., Charabidzé, D., 2019. Mixed-species aggregations in arthropods. Insect Science 26: 2-19. https://doi.org/10.1111/1744-7917.12502.

Brommer, J.E., Karell, P., Ahola, K., Karstinen, T., 2014. Residual correlations, and not individual properties, determine a nest defence boldness syndrome. Behavioral Ecology 25 (4): 802-812. https://doi.org/10.1093/beheco/aru057.

Brown, C.R., Hoogland, J.L., 1986. Risk in mobbing for solitary and colonial swallows. Animal Behaviour 34: 1319-1323.

Brown, G.E., Ferrari, M.C.O., Elvidge, C.K., Ramnarine, I., Chivers, D.P., 2013. Phenotypically plastic neophobia: a response to variable predation risk. Proceedings of the Royal Society B 280: 20122712. https://doi.org/10.1098/rspb.2012.2712.

Burgas, D., Ovaskainen, O., Blanchet, F.G., Byholm, P., 2021. The ghost of the hawk: top predator shaping bird communities in space and time. Frontiers in Ecology and Evolution 9: 1-7. https://doi.org/10.3389/fevo.2021.638039.

Campobello, D., Sarà, M., Hare, J.F., 2012. Under my wing: lesser kestrels and jackdaws derive reciprocal benefits in mixed-species colonies. Behavioral Ecology 23 (2): 425-433. https://doi.org/10.1093/beheco/arr207.

Catry, I., Alcazar, R., Franco, A.M.A., Sutherland, W.J., 2009. Identifying the effectiveness and constraints of conservation interventions: A case study of the endangered lesser kestrel. Biological Conservation 142: 2782-2791. https://doi.org/10.1016/j.biocon.2009.07.011.

Catry, I., Catry, T., Alho, M., Franco, A.M.A., Moreira, F., 2016. Sexual and parent-offspring dietary segregation in a colonial raptor as revealed by stable isotopes. Journal of Zoology 299: 57-67. https://doi.org/10.1111/jzo.12324.

Catry, I., Sampaio, A., Silva, M.C., Moreira, F., Franco, A.M.A., Catry, T., 2019. Combining stable isotope analysis and conventional techniques to improve knowledge of the diet of the European roller Coracias garrulus. Ibis 161: 272-285. https://doi.org/10.1111/ibi.12625.

Catry, I., Silva, J.P., Cardoso, A., Martins, A., Delgado, A., Sanches, A.R., Santos, A., Estanque, B., Cruz, C.M., Pacheco, C., Leitão, D., Pereira, E., Matilde, E., Moital, F., Romba, F., Sequeira, N., Monteiro, P., Rocha, P., Correia, R., Alcazar, R., Cangarato, R., Heleno, R., Catry, T., Silva, T., Ferro, T., 2011. Distribution and population trends of the European Roller in pseudo-steppe areas of Portugal: results from a census in sixteen SPAs and IBAs. Airo 21: 3-14.

Catry, T., Catry, I., 2019. Nest-site provisioning re-shapes species interactions within bird assemblages. Ibis 161: 699-704. https://doi.org/10.1111/ibi.12731.

Crane, A.L., Brown, G.E., Chivers, D.P., Ferrari, M.C.O., 2020. An ecological framework of neophobia: from cells to organisms to populations. Biological Reviews 95: 218-231. https://doi.org/10.1111/brv.12560.

Crane, A.L., Ferrari, M.C.O., 2017. Patterns of predator neophobia: a meta-analytic review Proceedings of the Royal Society B 284: 20170583. https://doi.org/10.1098/rspb.2017.0583.

Creel, S., Christianson, D., 2008. Relationships between direct predation and risk effects. Trends in Ecology and Evolution 23 (4): 194-201. https://doi.org/10.1016/j.tree.2007.12.004.

Cresswell, W., 2008. Non-lethal effects of predation in birds. Ibis 150: 3-17. https://doi.org/10.1111/j.1474-919X.2007.00793.x.

del Hoyo, J., Elliott, A., Sargatal, J., 2001a. Handbook of the birds of the world, Vol 2. New World Vultures to Guineafowl. Barcelona, Lynx Edn.

del Hoyo, J., Elliott, A., Sargatal, J., 2001b. Handbook of the birds of the world, Vol 6. Mousebirds to Hornbills. Barcelona, Lynx Edn.

Dutour, M., Léna, J.P., Lengagne, T., 2017. Mobbing calls: a signal transcending species boundaries. Animal Behaviour 131: 3-11. https://doi.org/10.1016/j.anbehav.2017.07.004.

Expósito-Granados, M., Parejo, D., Avilés, J.M., 2016. Sex-specific parental care in response to predation risk in the European roller, Coracias garrulus. Ethology 122: 72-79. https://doi.org/10.1111/eth.12444.

Finch, T., Saunders, P., Avilés, J.M., Bermejo, A., Catry, I., de la Puente, J., Emmenegger, T., Mardega, I., Mayet, P., Parejo, D., Račinskis, E., Rodríguez-Ruiz, J., Sackl, P., Schwartz, T., Tiefenbach, M., Valera, F., Hewson, C., Franco, A.M.A., Butler, S.J., 2015. A pan-European, multipopulation assessment of migratory connectivity in a near-threatened migrant bird. Diversity and Distributions 21: 1051-1062. https://doi.org/10.1111/ddi.12345.

Frid, A., Dill, L., 2002. Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology 6 (1): 2-17.

Gabel, W., Frederick, P., Zabala, J., 2021. Alligator presence influences colony site selection of long-legged wading birds through large scale facilitative nest protector relationship. Scientific Reports 11: 1-12. https://doi.org/10.1038/s41598-020-80185-5.

Gaglio, D., Sherley, R.B., Cook, T.R., Ryan, P.G., Flower, T., 2018. The costs of kleptoparasitism: a study of mixed-species seabird colonies. Behavioral Ecology 29 (4): 939-947. https://doi.org/10.1093/beheco/ary050.

Gameiro, J., Franco, A.M.A., Catry, T., Palmeirim, J.M., Catry, I., 2020. Long-term persistence of conservation-reliant species: Challenges and opportunities. Biological Conservation 243: 1-10. https://doi.org/10.1016/j.biocon.2020.108452.

Gameiro, J., Veiga, J., Valera, F., Palmeirim, J.M., Catry, I., 2021. Influence of colony traits on ectoparasite infestation in birds breeding in mixed-species colonies. Parasitology 1-9. https://doi.org/10.1017/S0031182021000470.

Ghalambor, C.K., Peluc, S.I., Martin, T.E., 2013. Plasticity of parental care under the risk of predation: how much should parents reduce care? Biological Letters. 9:1-4. https://doi.org/10.1098/rsbl.2013.0154.

Graham, K.F., Shutler, D., 2019. How robust are risk-taking associations in incubating birds? A test and a review. Behavioral Ecology and Sociobiology 73 (79): 1-9. https://doi.org/10.1007/s00265-019-2692-x.

Goodale, E., Beauchamp, G., Magrath, R.D., Nieh, J.C., Ruxton, G.D., 2010. Interspecific information transfer influences animal community structure. Trends in Ecology and Evolution 25: 354-361. https://doi.org/10.1016/j.tree.2010.01.002.

Goodale, E., Ruxton, G.D., Beauchamp, G., 2019. Predator eavesdropping in a mixed-species environment: how prey species may use grouping, confusion, and the cocktail party effect to reduce predator detection. Frontiers in Ecology and Evolution 7: 1-9. https://doi.org/10.3389/fevo.2019.00141.

Goodale E., Sridhar, H., Sieving, K.E., Bangal, P., Colorado, G.J., Farine, D.R., Heymann, E.W., Jones, H.H., Krams, I., Martínez, A.E., Montaño-Centellas, F., Muñoz, J., Srinivasan, U., Theo, A., Shanker, K., 2020. Mixed- company: a framework for understanding the composition and organization of mixed-species animal groups. Biological Reviews 95: 889-910. https://doi.org/10.1111/brv.12591.

Hass, C.C., Valenzuela, D., 2002. Anti-predator benefits of group living in white-nosed coatis (Nasua narica). Behavioral Ecology and Sociobiology 51: 570-578. https://doi.org/10.1007/s00265-002-0463-5.

Ibáñez-Álamo, J.D., Magrath, R.D., Oteyza, J.C., Chalfoun, A.D., Haff, T.M., Schmidt, K.A., Thomson, R.I., Martin, T.E., 2015. Nest predation research: recent findings and future perspectives. Journal of Ornithology 156: 247-262. https://doi.org/10.1007/s10336-015-1207-4.

Johnson, F.R., McNaughton, E.J., Shelley, C.D., Blumstein, D.T., 2003. Mechanisms of heterospecific recognition in avian mobbing calls. Australian Journal of Zoology 51: 577-585. https://doi.org/10.1071/ZO03031.

Krams, I., Bērziņš, A., Krama, T., 2009. Group effect in nest defence behaviour of breeding pied flycatchers, Ficedula hypoleuca. Animal Behaviour 77: 513-517. https://doi.org/10.1016/j.anbehav.2008.11.007.

LaBarge, L.R., Allan, A.T.L., Berman, C.M., Hill, R.A., Margulis, S.W., 2021. Extent of threat detection depends on predator type and behavioural context in wild samango monkey groups. Behavioural Ecology and Sociobiology 75 (13): 1-12. https://doi.org/10.1007/s00265-020-02959-1.

Lehtonen, J., Jaatinen, J., 2016. Safety in numbers: the dilution effect and other drivers of group life in the face of danger. Behavioural Ecology and Sociobiology 70: 449-458. https://doi.org/10.1007/s00265-016-2075-5.

Lima, S., Dill, L., 1990. Behavioural decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68 (4): 619-640. https://doi.org/10.1139/z90-092.

Liu, M., Chan, S.F., Rubenstein, D.R., Sun, S.J., Chen, B.F., Shen, S.F., 2020. Ecological transitions in grouping benefits explains the paradox of environmental quality and sociality. American Naturalist 195(5) :818-832. https://doi.org/10.1086/708185.

Magrath, R.D., Haff, T.M., Fallow, P.M., Radford, A., 2015. Eavesdropping on heterospecific alarm calls: from mechanisms to consequences. Biological Reviews 90: 560-586. https://doi.org/10.1111/brv.12122.

Marino, A., 2010. Costs and benefits of sociality differ between female guanacos living in contrasting ecological conditions. Ethology 116: 999-1010. DOI:10.1111/j.1439-0310.2010.01812.x.

Moreira, F., Leitão, P.J., Morgado, R., Alcazar, R., Cardoso, A., Carrapato, C., Delgado, A., Geraldes, P., Gordinho, L., Henriques, I., Lecoq, M., Leitão, D., Marques, A.T., Pedroso, R., Prego, I., Reino, L., Rocha, P., Tomé, R., Osborne, P.E., 2007. Spatial distribution patterns, habitat correlates and population estimates of steppe birds in Castro Verde. Airo 17: 5-30.

Murthy, A., Sharma, M., Amith-Kumar, U.R., Isvaran, K., 2015. Groups constrain the use of risky habitat by individuals: a new cost to sociality. Animal Behaviour 113: 167-175. DOI:10.1016/j.anbehav.2015.12.027.

Oteyza, J.C., Mouton, J.C., Martin, T.E., 2021. Adult survival probability and body size affect parental risk-taking across latitudes. Ecology Letters 24: 20-26. https://doi.org/10.1111/ele.13615.

Parejo, D., Avilés, J.M., 2011. Predation risk determines breeding territory choice in a Mediterranean cavity-nesting bird community. Oecologia 165: 185-191. https://doi.org/10.1007/s00442-010-1723-0.

Parejo, D., Danchin, É., Avilés, J.M., 2005. The heterospecific habitat copying hypothesis: can competitors indicate habitat quality? Behavioral Ecology 16: 96-105. https://doi.org/10.1093/beheco/arh136.

Poblete, Y., Botero-Delgadillo, E., Espíndola-Hernández, P., Vásquez, R.A., 2021. Risk-taking behaviour relates to timing of breeding in a sub-Antarctic rainforest bird. Ibis: 1-12. https://doi.org/10.1111/ibi.12941.

Pouca, C.V., Mitchell, D.J., Lefèvre, J., Vega-Trejo, R., Kotrschal, A., 2021. Early predation shapes adult learning and cognitive flexibility. Oikos 00:1-10. https://doi.org/10.1111/oik.08481.

Quinn, J.L., Ueta, M., 2008. Protective nesting associations in birds. Ibis 150: 146-167. https://doi.org/10.1111/j.1474-919X.2008.00823.x.

R Core Team, 2016. A Language and environment for statistical computing. Retrieved from Vienna: R Foundation for statistical computing website: https://cran.rproject.org/

Rasolofoniaina, B.N., Kappeler, P.M., Fichtel, C., 2021. Neophobia and social facilitation in narrow-striped mongooses. Animal Cognition 24: 165-175. https://doi.org/10.1007/s10071-020-01429-5.

Richardson, D.S., Bolen, G.M., 1999. A nesting association between semi-colonial Bullock's orioles and yellow-billed magpies: evidence for the predator protection hypothesis. Behavioral Ecology and Sociobiology. 46: 373-380. https://doi.org/10.1007/s002650050632.

Rocha, A.D., Fonseca, D., Masero, J.A., Ramos, J.A., 2016. Coastal saltpans are a good alternative breeding habitat for Kentish plover Charadrius alexandrines when umbrella species are present. Journal of Avian Biology. 47: 824.833. https://doi.org/10.1111/jav.00883.

Rolland, C., Danchin, É., de Fraipont, M., 1998. The evolution of coloniality in birds in relation to food, habitat, predation, and life-history traits: a comparative analysis. Amimal Naturalist 151 (6): 514-529. https://doi.org/10.1086/286137.

Santos, C.D., Cramer, J.F., Pârâu, L.G., Wikelski, M., Dechmann, D.K.N., 2015. Personality and morphological traits affect pigeon survival from raptor attacks. Scientific Report 5: 1-8. https://doi.org/10.1038/srep15490.

Sarà, M., Bondi, S., Bermejo, A., Bourgeois, M., Bouzin, M., Bustamante, J., de la Puente, J., Evangelidis, A., Frassanito, A., Fulco, E., Giglio, G., Gradev, G., Griggio, M., López-Ricaurte, L., Kordopatis, P., Marin, S., Martínez, J., Mascara, R., Mellone, U., Pellegrino, S.C., Pilard, P., Podofilini, S., Romero, M., Gustin, M., Saulnier, N., Serra, L., Sfougaris, A., Urios, V., Visceglia, M., Vlachopoulos, K., Zanca, L., Cecere, J.G., Rubolini, D., 2019. Broad-front migration leads to strong migratory connectivity in the lesser kestrel (Falco naumanni). Journal of Biogeography 46 (12): 2663-2677. https://doi.org/10.1111/jbi.13713.

Semeniuk, C.A.D., Dill, M.D., 2005. Cost/benefit analysis of group and solitary resting in the cowtail stingray, Pastinachus sephen. Behavioral Ecology 16: 417-426. https://doi.org/10.1093/beheco/ari005.

Semeniuk, C.A.D., Dill, L.M., 2006. Anti-predator benefits of mixed-species groups of cowtail stingrays (Pastinachus sephen) and whiprays (Himantura uarnak) at rest. Ethology 112: 33-43. https://doi.org/10.1111/j.1439-0310.2006.01108.x.

Seppänen, J.T., Forsman, J.T., Mönkkönen, M., Thomson, RL., 2007. Social information use is a process across time, space, and ecology, reaching heterospecifics. Ecology 88 (7): 1622-1633. https://doi.org/10.1890/06-1757.1.

Sharpe, L.L., Joustra, A.S., Cherry, M.I., 2010. The presence of an avian co-forager reduces vigilance in a cooperative mammal. Biological Letters 6: 475-477. https://doi.org/10.1098/rsbl.2009.1016.

Sridhar, H., Guttal, V., 2018. Friendship across species borders: factors that facilitate and constrain heterospecific sociality. Philosophical Transactions of the Royal Society B 373: 20170014. https://doi.org/10.1098/rstb.2017.0014.

Stensland, E., Angerbjörn, A., Berggren, P., 2003. Mixed species groups in mammals. Mammal Reviews. 33: 205-223. https://doi.org/10.1046/j.1365-2907.2003.00022.x.

Tilgar, V., Kikas, K., 2008. Is parental risk taking negatively related to the level of brood reduction? An experiment with pied flycatchers. Animal Behaviour 77: 43-47. https://doi.org/10.1016/j.anbehav.2008.08.027.

Uetz, G.W., Boyle, J., Hiebert, C.S., Wilcox, R.S., 2002. Antipredator benefits of group living in colonial web-building spiders: the ‘early warning’ effect. Animal Behaviour 63: 445-452. https://doi.org/10.1006/anbe.2001.1918.

Varela, S.A.M., Danchin, É., Wagner, R.H., 2007. Does predation select for or against avian coloniality? A comparative analysis. Journal of Evolutionary Biology 20: 1490-1503. https://doi.org/10.1111/j.1420-9101.2007.01334.x.

Verhulst, S., Nilsson, J.Å., 2008. The timing of birds’ breeding seasons: a review of experiments that manipulated timing of breeding. Philosophical Transactions of the Royal Society B 363: 399-410. https://doi.org/10.1098/rstb.2007.2146.

Wagner, R.H., Danchin, É., Boulinier, T., Helfenstein, F., 2000. Colonies as byproducts of commodity selection. Behavioral Ecology 11 (5): 572-573. https://doi.org/10.1093/beheco/11.5.572.

Winkler, D.W., 2016. Breeding biology of birds. In Lovetter IJ, Fitzpatrick JW (eds). Handbook of bird Biology. 408-409. Ithaca: The Cornel Lab of Ornithology.

7. APPENDIX

Figure 5.A1: Example photos of the neophobia and predator experiments: (A) novel object (GoPro Hero 4 session) placed next to nest entrance, (B) frame from video recording of that novel object, and (C) crow-like predator model placed at the top of nesting structure.

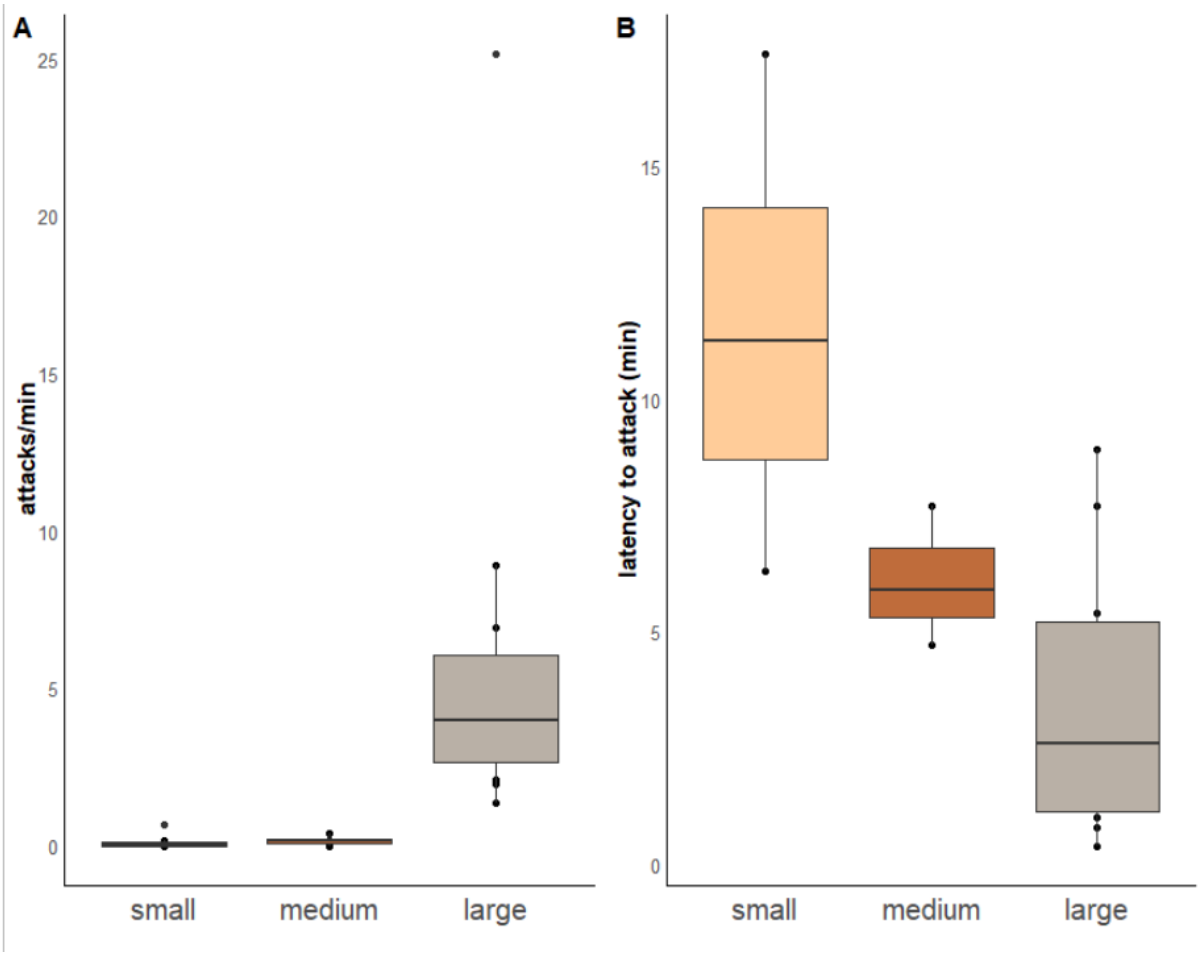


Figure 5.A2: Lesser kestrel mobbing intensity (attacks/min) and latency to initiate mobbing in small (≤10 breeding pairs), medium (11 to 24 bp) and large (≥ 25 bp) lesser kestrel colonies. Mobbing intensity was significantly higher in large than in small or medium colonies ($p < 0.001$ and $p = 0.002$, respectively; Kruskal-Wallis $X^2_2 = 16.96$, p-value < 0.001). Latency to initiate mobbing decrease only significantly from small to large colonies (p-value = 0.002; ANOVA $F_2 = 9.98$, $p = 0.003$).

Table 5.A1: Generalized Linear Mixed Models on reproductive parameters and nest predation rate of rollers breeding solitarily and in mixed-species colonies dominated by lesser kestrels (solitary vs colonial). Poisson distribution was used for the laying date, clutch size and productivity model, and binomial distribution was used for the predation model. Data from 298 breeding attempts from 2014 to 2019 (88 solitary, 210 in colonies).

Effect	**SD**	**Estimate**	**SE**	**Z-value**	**p-value**
Laying date					
Year	0.014				
Intercept [solitary]		**4.925**	**0.011**	**432.545**	**<0.001**
Social context [colonial]		-0.010	0.012	-0.854	0.393
Clutch size					
Year	0.000				
Intercept [solitary]		**1.590**	**0.051**	**30.998**	**<0.001**
Social context [colonial]		0.009	0.061	0.153	0.878
Laying date		**-0.118**	**0.029**	**-4.022**	**<0.001**
Nest Predation					
Year	0.000				
Intercept [solitary]		**-1.076**	**0.259**	**-4.151**	**<0.001**
Social context [colonial]		**-0.993**	**0.343**	**-2.86**	**0.004**
Laying date		0.232	0.159	1.464	0.143
Productivity					
Year	0.091				
Intercept [solitary]		**1.422**	**0.076**	**18.590**	**<0.001**
Social context [colonial]		-0.082	0.077	-1.106	0.269
Laying date		**-0.130**	**0.038**	**-3.433**	**0.001**
Nest predation [yes, no]		**-2.124**	**0.227**	**-9.350**	**<0.001**

Chapter 6

General discussion

GENERAL DISCUSSION

1. SPECIES INTERACTIONS IN RECENTLY ESTABLISHED MIXED COLONIES

Human induced changes in the environment, such as habitat fragmentation or climate change, shape the distribution of many species by restricting their access to resources such as food or nest-sites (Wiegand et al. 2005). Ongoing biodiversity loss has prompted conservation projects and large-scale nest-site provisioning, further re-shaping the nesting landscape (Catry & Catry 2019). Although effective at recovering endangered populations across many taxa, nest-site provisioning may create ecological traps by attracting animals to low-quality or unsuitable sites that reduces their fitness (Schlaepfer et al. 2002). Conservation projects based on nest-site provisioning seldom consider how they can re-shape the composition and functioning of communities and alter or promote new species interactions (Catry & Catry 2019). In Portugal, massive artificial nest-site provisioning, aimed at recovering lesser kestrels' populations, attracted several other species, forming mixed-species assemblages with unknown implications for the conservation of target species. Throughout this thesis, I demonstrated that, while artificial nest-site provisioning was very successful at recovering the populations of lesser kestrels and rollers in Portugal, it may result in unforeseen consequences, some linked to artificial nests themselves, and some linked to the formation of mixed-species aggregations in these new artificial nesting landscapes:

Chapter 2 revealed that lesser kestrels and rollers may soon become fully reliant on conservation actions. The collapse of traditional adobe buildings, or their restoration with long lasting materials such as concrete or bricks, prevent the appearance of new semi-natural nest-sites. While the population of both species has still been increasing since last census, more than 65% of lesser kestrels and rollers in the Castro Verde SPA – which is estimated to represent over 80% of their Portuguese population – nested in artificial nest-sites in 2017. The maintenance of these two species will thus require constant funding for replacing and providing new nests, estimated at ca. 4500€ per year, which may result in a conservation trap if funding is not secured (Cardador et al. 2015). **Chapter 2** provides a potential solution: funding conservation using the region's tourism revenues, most of which are arguably a result of nature-based tourism such as birdwatching. This may create a sustainable funding mechanism through a positive feedback loop (more conservation > higher biodiversity > more tourism > more conservation; Wei et al. 2018), promoting the long-term viability of lesser kestrels and rollers.

Chapter 3 illustrates how the presence of multiple species in an assemblage can influence the transmission patterns of ectoparasites. It reports that the identity of the host (which species), rather than colony size or density, determines the prevalence of *C. hemapterus*, louse flies, lice, and mites, on nests and chicks of the four most abundant species in mixed-species colonies studied (lesser kestrels, rollers, starlings, and pigeons). Furthermore, colonies with more lesser kestrels and less starlings (the two most abundant species in these mixed assemblages) have higher abundance of a *Carnus hemapterus*, a generalist ectoparasite, than colonies with more starlings and less lesser kestrels. **Chapter 3** shows that the presence of less susceptible species in the group, such as starlings and pigeons, produces a dilution effect that favours mixed-species aggregations by protecting them against ectoparasites. For lesser kestrels, grouping with starlings or pigeons might be more advantageous than breeding in conspecific-only colonies. However, for rollers, breeding in mixed-species colonies results in a higher ectoparasite burden when compared to breeding in solitary nests (Oliveira 2021). Furthermore, the anti-parasite benefits provided by mixed-species colonies (for some species) was only properly accessed for *Carnus hemapterus*, a blood-sucking fly infesting a wide range of hosts. Other ectoparasites (*e.g.*, *Pseudolynchia canariensis*), although less abundant, may produce different effects that were not investigated in this chapter.

Chapter 4 reveals a high trophic niche overlap among most of the species breeding in these mixed-species assemblages, particularly between lesser kestrels, rollers, and starlings, suggesting a use for similar prey resources like grasshoppers and beetles. It also shows a clear trophic niche segregation between parents and offspring of lesser kestrels, rollers, little owls, common kestrels, and starlings. High intraspecific but low interspecific segregation in resource use suggest high levels of interspecific competition for food during breeding. Although species could segregate in a spatio-temporal axis, this is highly unlikely in our mixed colonies, where all these species hunt in the vicinities of the colonies to match the high energy demand of nestlings, and coincide in their breeding phenology and chick rearing period. This suggest most of the species in these assemblages were not expected to coexist in artificial breeding structures at such high-densities but may be forced to do so due to lack of alternative nesting sites. While in the Castro Verde SPA, high-quality foraging habitats with high prey availability have been maintained through specific agri-environmental schemes, thus providing enough food for all species, agro-steppes are threatened by human and climate-induced habitat changes like agriculture intensification or extreme weather events that can reduce prey availability (Silva et al. 2018; Gameiro et al. 2020; Marcelino et al. 2020). Competition for resources may trigger aggression or other agonistic interactions among the assembled species (Catry & Catry 2019).

Chapter 5 describes how rollers acquire anti-predatory benefits from nesting in mixed-species colonies, returning faster to their nest during the presentation of a novel object and a predator model, and reducing their individual investment in mobbing during the presentation of a predator model, when compared to solitary rollers. While other species in the assemblage such as common kestrels or jackdaws may also participate, the bulk of the communal defence against a crow-like predator model was performed by lesser kestrels, with up to 25 attacks per minute. Starlings, pigeons, or owls (the latter likely due to their nocturnal habits) did not participate in nest defence, nor appeared to be affected by the presence of the predator model. For rollers, a "non-social" bird, aggregating in a mixed assemblage with a colonial, more protective species may be the only way to be in group large enough to guarantee anti-predatory benefits (Semeniuk & Dill 2006; Sridhar & Guttal 2018). Nesting with lesser kestrels might explain why rollers in colonies suffered from half as much predation rates as solitary rollers (Quinn & Ueta 2008). However, rollers in colonies did not lay earlier nor had higher productivity, suggesting there are not clear reproductive advantages for breeding in groups (Quinn & Ueta 2008). Costs associated with group living, such as the increased parasitism or competition for food reported in Chapters 3 and 4, respectively, may help explain the lack of differences in roller productivity between each social context.

1.1 ADVANCES ON THE KNOWLEDGE OF SPECIES INTERACTIONS AND GROUP LIVING

This thesis provides important new insights on interspecific interactions in mixed-species groups. Increased transmission of parasites and associated diseases is commonly seen as cost of group living, with ectoparasite prevalence and intensity increasing with colony size or density across different taxa (Rifkin et al. 2012). However, this has rarely been accessed in mixed-species groups, where specificity of the ectoparasite and/or the susceptibility of the host may vary (Valera et al. 2003). Chapter 3 demonstrated that size or density of a mixed-species colony did not shape the prevalence of four ectoparasites groups, nor the abundance of a generalist and common ectoparasite. Rather, the ectoparasite community in the nest was only determined by the identity of its occupant, and the abundance of a generalist parasite varied according with the group composition, being lower in colonies dominated by less susceptible species, and higher in colonies dominated by more susceptible species. The idea that mixed-species groups may dilute ectoparasite burden depending on the species composing the groups had been already theorised, but never proved empirically, and so chapter 3 advances the current knowledge regarding the relationship between parasitism and sociality.

Mixed-species groups are also expected to alleviate the competition for resources such as food or nests: because competition increases with increasing niche similarity between individuals (i.e., share similar resource requirements), it should be higher in single-species groups than in mixed-groups (Goodale et al. 2020). On the other hand, if two species have similar ecological niches, thus likely to compete with one another, they are not expected to coexist (Hardin 1960, Pianka 1981). It follows that mixed-species groups can only be stable aggregations if they are composed by species with complementary, mostly non-overlapping niches (Sridhar & Guttal 2018; Goodale et al. 2020). Although chapter 4 did not fully address all ways in which species in these mixed assemblages may segregate (*e.g.*, spatially, temporally, or behaviourally), their trophic resources and life-history traits suggest most of them highly overlap in their ecological niches. These species, with a high-competition potential (also evidenced in Catry & Catry 2019), not only occur sympatrically but are also forced to breed at very high-densities (up to 2-3 nests/m^2) due to lack of nesting sites, defying the known ecological mechanisms explaining their coexistence and their long-term viability as mixed aggregations.

Finally, groups result in increased vigilance, higher mobbing intensity, or dilution or selfish herd effects (Beauchamp 2008; Lehtonen & Jaatinen 2016; Goodale et al. 2020). These anti-predatory benefits have been empirically tested along different degrees of sociality within the same species (Arroyo et al. 2011), comparing solitary with colonial sister species (Brown & Hoogland 1986), or comparing mixed colonies with single-species colonies (Campobello et al. 2012). Chapter 5 is one of the first studies demonstrating how a solitary species benefits by breeding near a colonial heterospecific. It shows that the solitary species (roller) took advantage of nesting within an heterospecific colony (lesser kestrel) to acquire information on whether is safe to return to its nest and to reduce its investment in risky mobbing behaviours. Chapter 5 is also one of the few studies relating the underlying (behavioural) mechanisms of these benefits with breeding parameters and observed predation events from long-term monitoring data, providing strong evidence for the ecological importance of different social breeding strategies.

1.2 IMPLICATIONS FOR THE CONSERVATION OF LESSER KESTRELS AND ROLLERS

After several years aiming at reverse severe population declines, lesser kestrels and rollers are currently classified globally as least concern (BirdLife International 2021), but they are thought to be declining in some regions and still require conservation efforts (Bustamante et al. 2020; BirdLife International 2021). In Portugal, lesser kestrels and rollers are classified as Vulnerable and Critically Endangered, respectively (Cabral et al. 2005) and although their populations are slowly increasing, their distribution is mostly confined to the Castro Verde SPA, where they are becoming fully reliant on artificial nest-sites (chapter 2). While the long-term persistence of lesser kestrels and rollers ultimately depends on the sympatric availability of suitable nest-sites and high-quality foraging habitats, paired with safe migratory routes (Catry et al. 2013; Finch et al. 2015, 2018; Sarà et al. 2019, Negro et al. 2020), it is important to considered how the presence of other species may affect the effectiveness of their conservation.

In the studied mixed-species colonies, species like barn owls, little owls, or common kestrels may compete for resources and participate in interspecific aggression or predation (chapter 4 and Catry & Catry 2019), but their abundance in these aggregations, usually limited to one or two breeding pairs per colony, are likely insufficient to play a major role in group-associated costs or benefits. Starlings, on the other hand, are colonial and resident in Portugal, lay multiple clutches per breeding season, and obstruct nest-sites with vegetable material, being strong competitors for nests and reducing the number of suitable nest-sites for lesser kestrels and rollers. Moreover, the starling population has been increasing over the last years, being one of the most abundant species in Portugal (Alonso et al. 2021), thus representing a potential threat for lesser kestrels and rollers. In the studied mixed-species colonies, starlings are abundant (up to 32 breeding pairs per colony) and thus more likely to play a larger role in group-mediated consequences. Although starlings may dilute the abundance of ectoparasites (chapter 3), they highly overlapped in their trophic resources with the target species, suggesting high levels of interspecific competition (chapter 4). Interspecific agonistic behaviours by starlings, including predation of roller eggs, have already been reported in these colonies (Catry & Catry 2019). Because starlings do not participate in group defence against predators, they may also reduce mobbing intensity indirectly, by reducing the effect size of species that actively contribute to nest defence (colony size is ultimately dependent on the number of nest-sites; chapter 5). For rollers, group-mediated costs may not only come from starlings, but also from lesser kestrels themselves, although agonistic interactions appear to be less disruptive and often unidirectional, from rollers to lesser kestrels (Catry & Catry 2019).

The lack of differences in productivity between lesser kestrels in small and large colonies, or between rollers in solitary nests or in colonies (presented in the appendix of chapter 4 and in chapter 5), suggest that the costs of group living are not offsetting its benefits and turning these mixed-species assemblages into ecological traps (Robertson & Hutto 2006). However, these consequences could still limit lesser kestrel's and roller's population growth, reducing the effectiveness of the conservation efforts targeting them, particularly through nest competition with abundant species such as starlings or jackdaws. Ongoing and future human-induced changes in the landscape may also exacerbate the costs of mixed-species groups, by further restricting species access to their resources or concentrating them in progressively smaller patches of suitable habitat. Loss in area or quality of foraging habitats through agriculture intensification or global warming are predicted to increase in the near future (Mantyka-Pringle et al. 2015; Gameiro et al. 2020; Marcelino et al. 2020), potentiating the competition between the assembled species and jeopardizing their viability through shortage of resources. Continuing loss of natural nest-sites will force species to occupy artificial nests and other human-made structures, further concentrating them at higher-densities, and disrupting nature's equilibrium by modifying species interactions (Ockendon et al. 2014; Mainwaring 2015; Duckworth et al. 2017; Catry & Catry 2019; Teckentrup et al. 2019).

It is often suggested that ecological traps can be mitigated by improving habitat or nest quality, or by reducing their attractiveness (Schlaepfer et al. 2002; Robertson & Hutto 2006). This thesis suggests that, when providing artificial nests for target species, the attractiveness for other sympatric, non-target species also needs to be considered (Lindenmayer et al. 2016). Designing species-specific nest-sites that prevent their occupation by competitor species or reducing the number of nests or nest density per structure, could help alleviate some of the group-associated costs presented in this thesis. More importantly, new conservation measures should be followed by long-term monitoring to evaluate those measures and modify or adapt new ones that ensure the long-term viability of natural populations.

2. CHALLENGES, OPPORTUNITIES, AND FUTURE RESEARCH

The conservation recommendations presented here are built upon, and limited by, the results obtained in this thesis. To better understand the mechanism allowing the maintenance of these mixed colonies, and how they may affect the conservation of lesser kestrels and rollers, further research is required, particularly that examining other costs and benefits typically associated with group living. For example, one of the main benefits attributed to groups, besides protection against predators, is that they work as a centre where individuals share and acquire information on the best sites to breed or forage (Ward & Zahavi 1973; Seppänen et al. 2007; Bijleveld et al. 2010). Catry et al. (2014) showed that lesser kestrels follow their conspecific neighbours to the same foraging sites using direct observations, a method that could also be tested for heterospecifics. Studies further expanding on the antagonistic interactions (Catry & Catry 2019) would help to identify dominating and dominated species (which could lead to species getting excluded from colonies), and further investigate the predation levels between assembled species in more detail. For example, little owls may greatly benefit from nesting near starlings as they often prey on starling chicks. Additional studies on interspecific competition for food (chapter 4) would also provide more detail on whether species can segregate spatially, temporally, or behaviourally, for example by selecting different micro-habitats or prey of different sizes (Reisinger et al. 2020). For rollers, it is still unclear how they balance information from conspecifics or heterospecifics with breeding site fidelity (Parejo et al. 2005), factors that may shape roller's nest-site selection and dispersion patterns. For lesser kestrels, examining the main drivers for colony growth and carrying capacity would help understand how the presence of other species, through group-mediated costs and benefits, may limit or increase maximum colony size in a structure (Kildaw et al. 2005). All these questions may further help researchers and conservationists to understand whether conservation actions should promote or discourage the formation of mixed breeding aggregations, predict the number, size, and location of new structures to be provided, and analyse the growth potential of lesser kestrel's and roller's population outside of the study area.

Studying mixed-species groups or interspecific interactions may be particularly challenging because it requires a reasonable understanding of the biology of each species, increases field work and sampling effort, and complexifies data analysis and interpretation due to multiple simultaneous, often correlated factors. For example, a good understanding of the dietary requirements of each species is required to interpret isotope ratios more accurately (chapter 4).

Species also differ in their phenology and on the duration of each breeding stage, which requires colonies to be visited more frequently and each visit to last longer. We were unable to investigate parent-offspring segregation in barn owls (chapter 4) because we missed the right period to sample adults and nestlings simultaneously. Some species are also harder to sample or handle, *e.g.*, we were not able to find an effective strategy to catch adult jackdaws in their nests. Addressing several species and variables simultaneously may also prevent the investigation of each individual factor independently due to interacting effects. Chapter 3 would likely require a much larger sample size to disentangle the individual effects between colony size and colony density on the prevalence and intensity of each ectoparasite species. Finally, some results, like in chapter 5, may only be fully interpreted in the lights of individual behavioural patterns or decisions, which require individual identification of birds and the same individuals to be monitored over the years.

On the other hand, these artificial nesting structures provide excellent opportunities to understand the mechanism underlying the formation and maintenance of aggregations, and how these affect the conservation of target species, as they are easier to monitor and facilitate access to, and manipulation of, nests and animals (Lambrechts et al. 2010). In other types of conservation actions (*e.g*., habitat restoration) or any other human or climate-induced habitat alteration, measuring the effects these re-modified communities may have on endangered species might be harder to examine because monitoring individuals or populations is more challenging. This thesis utilized diverse methodologies that required: bird handling; measuring productivity and other life-history traits such as laying date, clutch and brood size; sampling and measuring parasite load; sampling feathers and blood for Stable Isotope Analysis; and filming behavioural responses and animal interactions. It also capitalized on long-term monitoring data from lesser kestrels and rollers without which many of the reported results could not have been detected. All this data would be much more difficult to collect, both logistically and mechanically, if birds bred on natural, more inaccessible, nest-sites.

3. FINAL REMARKS

This thesis documents how large-scale nest-site provisioning may attract and aggregate multiple species forming mixed colonies, resulting in unplanned group-mediated costs and benefits that may affect the conservation of target species. The main outcomes presented here are likely applicable to any environmental alteration concentrating species in progressively smaller areas, forcing them to coexist at supra-optimal densities and likely creating analogous effects to mixed-species aggregations. Human and climate-induced changes to the landscape, including urban expansion, agriculture and logging intensification, invasive species, or global warming, are predicted to increase in the near future (Mantyka-Pringle et al. 2015; Curtis et al. 2018), re-shaping the structure and functioning of communities and whole ecosystems by modifying interactions between species (Ockendon et al. 2014; Duckworth et al. 2017; Catry & Catry 2019; Teckentrup et al. 2019).

This thesis provides strong evidence of the importance of considering species interactions and mixed-species groups in ecological studies, species conservation, and population management plans. When designing conservation measures, researchers and conservationists need to consider other consequences besides the immediate recover of endangered populations, particularly how the presence and interaction with other sympatric, potentially competing species may affect the equilibrium of communities and the long-term persistence of species. For this, it is fundamental that target populations are continuously monitored after the implementation of conservation actions. Only by conducting ecological studies based on long-term monitoring data targeting multiple species and their interactions, like the ones included in this thesis, can researchers comprehend the unpredictable, yet fascinating way nature restores its balance, and find ways that safeguards the coexistence between humans and wildlife.

6. REFERENCES

Alonso, H., Coelho, C., Gouveia, C., Rethoré, G., Leitão, D., Teodósio, J., 2021. Relatório do Censo de Aves Comuns 2004-2020. Sociedade Portuguesa para o Estudo das Aves, Lisboa.

Arroyo, B., Mougeot, F., Bretagnolle, V., 2001. Colonial breeding and nest defence in Montagu's harrier (Circus pygargus). Behavioral Ecology and Sociobiology 50: 109-115. https://doi.org/10.1007/s002650100342.

Beauchamp, G., 2008. What is the magnitude of the group-size effect on vigilance? Behavioral Ecology 19: 1361-1368. https://doi.org/10.1093/beheco/arn096.

Bijleveld, A.I., Egas, M., van Gils, J.A., Piersma, T., 2010. Beyond the information centre hypothesis: communal roosting for information on food, predators, travel companions and mates? Oikos 119: 277-285. https://doi.org/10.1111/j.1600-0706.2009.17892.x.

Brown, C.R., Hoogland, J.L., 1986. Risk in mobbing for solitary and colonial swallows. Animal Behaviour 34: 1319-1323. https://doi.org/10.1016/S0003-3472(86)80203-2.

Bustamante, J., Molina, B., del Moral., J.C., 2020. El cernícalo primilla en España, población reproductora en 2016-18 y método de censo. SEO/BirdLife Madrid.

Campobello, D., Sarà, M., Hare, J.F., 2012. Under my wing: lesser kestrels and jackdaws derive reciprocal benefits in mixed-species colonies. Behavioural Ecology 23 (2), 425-433. https://doi.org/10.1093/beheco/arr207.

Cardador, L., Brotons, L., Mougeot, F., Giralt, D., Bota, G., Pomarol, M., Arroyo, B., 2015. Conservation traps and long-term species persistence in human-dominated systems. Conservation Letters 8: 456–462. https://doi.org/10.1111/conl.12160.

Catry, I., Franco, A.M.A., Rocha, P., Alcazar, R., Reis, S., Cordeiro, A., Ventim, R., Teodósio, J., Moreira, F., 2013. Foraging habitat quality constrains effectiveness of artificial nest-site provisioning in reversing population declines in a colonial cavity nester. PLoS One 8: 1–10. https://doi.org/10.1371/journal.pone.0058320.

Catry, T., Catry, I., 2019. Nest-site provisioning re-shapes species interactions within bird assemblages. Ibis 161: 699–704. https://doi.org/10.1111/ibi.12731.

Catry, I., Franco, A.M.A., Moreira, F., 2014. Easy but ephemeral food: exloring the trade-offs of agricultural practices in the foraging decisions of lesser kestrels on farmland. Bird Study 61: 447-456. http://dx.doi.org/10.1080/00063657.2014.953031.

Curtis, P.G., Slay, C.M., Harris, N.L, Tyukavina, A., Hansen, M.C., 2018. Classifying drivers of global forest loss. Science 361: 1108-1111. https://doi.org/10.1126/science.aau3445.

Duckworth, R.A., Hallinger, K.K., Hall, N., Potticary, A.L., 2017. Switch to a novel breeding resource influences coexistence of two passerine birds. Frontiers in Ecology and Evolution 5: 72. https://doi.org/10.3389/fevo.2017.00072.

Finch, T., Branston, C., Clewlow, H., Dunning, J., Franco, A.M.A., Račinskis, E., Schwartz, T., Butler, S.J., 2018. Context-dependent conservation of the cavity-nesting European roller. Ibis. https://doi.org/10.1111/ibi.12650.

Finch, T., Saunders., Avilés, J.M., Bermejo, A., Catry, I., de la Puente, J., Emmenegger, T., Mardega, I., Mayet, P., Parejo, D., Račinskis, E., Rodríguez-Ruiz, J., Sackl, P., Schwartz, T., Tiefenbach, M., Valera, F., Hewson, C., Franco, A., Butler, S.J., 2015. A pan-European, multipopulation assessment of migratory connectivity in a near-threatened mi-grant bird. Diversity and Distributions 21: 1051-1062. https://doi.org/10.1111/ddi.12345.

Gameiro, J., Silva, J.P., Franco, A.M.A., Palmeirim, J.M., 2020. Effectiveness of the European Natura 2000 network at protecting Western Europe’s agro-steppes. Biological Conservation 248: 1-9. https://doi.org/10.1016/j.biocon.2020.108681.

Goodale, E., Sridhar, H., Sieving, K.E., Bangal, P., Colorado Z., G.J., Farine, D.R., Heymann, E.W., Jones, H.H., Krams, I., Martínez, A., Montaño-Centellas, F., Muñoz, J., Srinivasan, U., Theo, A., Shanker, K., 2020. Mixed company: a framework for understanding the composition and organization of mixed-species animal groups. Biological Reviews 95: 889-910. https://doi.org/10.1111/brv.12591.

Hardin, G., 1960. The competitive exclusion principle. Science 131 (3409): 1292-1297.

Kildaw, S.D, Irons, D.B., Nysewander, D.R., Buck, C.L., 2005. Formation and growth of new seabird colonies: the significant of habitat quality. Marine Ornithology 33: 49-58.

Lambrechts, M.M., Adriaensen, F., Ardia, D.R., Artemyev, A.V., Atiénzar, F., Bańbura, J., Barba, E., Bouvier, J.C., Camprodon, J., Cooper, C.B., Dawson, R.D., Eens, M., Eeva, T., Faivre, B., Garamszegi, L.Z., Goodenough, A.E., Gosler, A.G., Grégoire, A., Griffith, S.C., Gustafsson, L., Johnson, L.S., Kania, W., Keišs, Llambias, P.E., Mainwaring, M.C., Mänd, R., Massa, B., Mazgajski, T.D., Møller, Moreno, J., Naef-Daenzer, B., Nilsson, J.A., Norte, A.C., Orell, M., Otter, J.A., Park, C.R., Perrins, C.M., Pinowski, J., Porkert, J., Potti, J., Remes, V., Richner, H., Rytkønen, S., Shiao, M.T., Silverin, B., Slagsvold, T., Smith, H.G., Sorace, A., Stenning, M.J., Stewart, I., Thompson, C.F., Tryjanowski, P., Török, J., van Noordwijk, A.J., Winkler, D.W., Ziane, N., 2010. The design of artificial nestboxes for the study of secondary hole-nesting birds: a review of methodological inconsistencies and potential biases. Acta Ornithologica 45 81).

Lehtonen J., Jaatinen, K., 2016. Safety in numbers: the dilution effect and other drivers of group in the face of danger. Behavioral Ecology and Sociobiology 70: 449-458. https://doi.org/10.1007/s00265-016-2075-5.

Mainwaring, M.C., 2015. The use of man-made structures as nesting sites by birds: a review of the costs and benefits. Journal of Nature Conservation 25: 17-22. http://dx.doi.org/10.1016/j.jnc.2015.02.007.

Mantyka-Pringle, C.S., Visconti, P., di marco, M., Martin, T.G., Rondinini, C., Rhodes, J.R., 2015. Climate change modifies risk of global biodiversity loss due to land-cover change. Biological Conservation 187: 103-111. http://dx.doi.org/10.1016/j.biocon.2015.04.016.

Marcelino, J., Silva, J.P., Gameiro, J., Silva, A., Rego, F.C., Moreira, F., Catry, I., 2020. Extreme events are more likely to affect the breeding success of lesser kestrels than average climate change. Scientific Report 10(1): 1–11. https://doi.org/10.1038/s41598-020-64087-0.

Negro, J.J., Prenda, J., Ferrero, J.J., Rodríguez, A., Reig-Ferrer, A., 2020. A timeline for the urbanization of wild birds: the case of the lesser kestrel. Quaternary Science Reviews 249. https://doi.org/10.1016/j.quascirev.2020.106638.

Ockendon, N., Baker, D.J., Carr, J.A., White, E.C., Almond, R.E.A., Amano, T., Bertram, E., Bradbury, R.B., Bradley, C., Butchart, S.H.M., Doswald, N., Foden, W., Gill, D.J.C., Green, R.E., Sutherland, W.J., Tanner, E.V.J., Pearce-Higgins, J.W., 2014. Mechanisms underpinning climatic impacts on natural populations: altered species interactions are more important than direct effects. Global Change Biology 20: 2221–2229. https://doi.org/10.1111/gcb.12559.

Oliveira, I., 2021. Influence of colonial nesting on host-parasite compatibility of the hematophagous ectoparasite *Carnus hemapterus* on two bird species in Southeast Portugal. Master Thesis. Faculdade de Ciências, Universidade de Lisboa.

Parejo, D., Danchin, E., Avilés, J.M., 2005. The heterospecific habitat copying hypothesis: can competitors indicate habitat quality? Behavioral Ecology 16: 96-105. https://doi.org/10.1093/beheco/arh136.

Pianka, E.R., 1981. Competition and niche theory. In RM May (Ed.). Theoretical ecology, pp. 167–196. Blackwell, Oxford.

Quinn, J.L., Ueta, M., 2008. Protective nesting associations in birds. Ibis 150, 146-167. https://doi.org/10.1111/j.1474-919X.2008.00823.x.

Reisinger, R.R., Carpenter-Kling, T., Connan, M., Cherel, Y., Pistorius, P.A., 2020. Foraging behaviour and habitat-use drives niche segregation in sibling seabird species. Royal Society Open Science 7: 200649. http://dx.doi.org/10.1098/rsos.200649.

Rifkin, J.L., Nunn, C.L., Garamszegi, L.Z., 2012. Do animals living in larger groups experience greater parasitism? A meta-analysis. The American Naturalist 180 (1): 70-82. https://doi.org/10.1086/666081.

Robertson, B.A., Hutto, R.L., 2006. A framework for under- standing ecological traps and an evaluation of existing evidence. Ecology 87: 1075–1085. https://doi.org/10.1890/0012-9658(2006)87[1075:AFFUET]2.0.CO;2.

Sarà, M., Bondi, S., Bermejo, A., Bourgeois, M., Bouzin, M., Bustamante, J., de la Puente, J., Evangelidis, A., Frassanito, A., Fulco, E., Giglio, G., Gradev, G., Griggio, M., López-Ricaurte, L., Kordopatis, P., Marin, S., Martínez, J., Mascara, R., Mellone, U., Pellegrino, S.C., Pilard, P., Podofilini, S., Romero, M., Gustin, M., Saulnier, N., Serra, L., Sfougaris, A., Urios, V., Visceglia, M., Vlachopoulos, K., Zanca, L., Cecere, J.G., Rubolini, D., 2019. Broad-front migration leads to strong migratory connectivity in the lesser kestrel (Falco naumanni). Journal of Biogeography 46 (12): 2663-2677. https://doi.org/10.1111/jbi.13713.

Schlaepfer, M.A., Runge, M.C., Sherman, P., 2002. Ecological and evolutionary traps. Trends in Ecology and Evolution 17 (10): 474-480. https://doi.org/10.1016/S0169-5347(02)02580-6.

Semeniuk, C.A.D, Dill, L.M., 2006. Anti-predator benefits of mixed-species groups of cowtail stingrays (Pastinachus sephen) and whiprays (Himantura uarnak) at rest. Ethology 112: 33-43. https://doi.org/10.1111/j.1439-0310.2006.01108.x.

Seppänen, J.T., Forsman, J.T., Mönkkönen, M., Thomson, R.L., 2007. Social information use is a process across time, space, and ecology, reaching heterospecifics. Ecology 88 (7), 1622-1633. https://doi.org/10.1890/06-1757.1.

Silva, J.P., Correira, R., Alonso, H., Martins, R.C., D'Amico, M., Delgado, A., Sampaio, H., Godinho, C., Moreira, F., 2018. EU protected area network did not prevent a country wide population decline in a threatened grassland bird. Peer J 6: 1-13. https://doi.org/10.7717/peerj.4284

Sridhar, H., Guttal, V., 2018. Friendship across species borders: factors that facilitate and constrain heterospecific sociality. Philosophical Transactions B 373: 20170014. http://dx.doi.org/10.1098/rstb.2017.0014.

Teckentrup, L., Kramer-Schadt, S., Jeltsch, F., 2019. The risk of ignoring fear: underestimating the effects of habitat loss and fragmentation on biodiversity. Landscape Ecology 34: 2851-2868. https://doi.org/10.1007/s10980-019-00922-8.

Valera, F., Casas-Crivillé, A., Hoi H., 2003. Interspecific parasite exchange in a mixed colony of birds. Journal of Parasitology 89, 245–250. https://doi.org/10.1645/0022-3395(2003)089[0245:IPEIAM]2.0.CO;2.

Ward, P., Zahavi, A., 1973. The importance of certain assemblages of bird as "information centres" for food-finding. Ibis 115: 517-534.

Wei, F., Costanza, R., Dai, Q., Stoeckl, N., Gu, X., Farber, S., Nie, Y., Kubiszewski, I., Hu, Y., Swaisgood, R., Yang, X., Bruford, M., Chen, Y., Voinov, A., Qi, D., Owen, M., Yan, L., Kenny, D.C., Zhang, Z., Hou, R., Jiang, S., Liu, H., Zhan, X., Zhang, L., Yang, B., Zhao, L., Zheng, X., Zhou, W., Wen, Y., Gao, H., Zhang, W., 2018. The value of ecosystem services from giant panda reserves. Current Biology 28: 2174–2180.e7. https://doi.org/10.1016/j.cub.2018.05.046.

Wiegand, T., Revilla, E., Moloney, K.A., 2005. Effects of habitat loss and fragmentation on population dynamics. Conservation Biology 19 (1): 108-121. https://doi.org/10.1016/j.actao.2017.06.006.