Conservation ecology of the European Roller

Thomas M. Finch

A thesis submitted for the degree of Doctor of Philosophy

School of Biological Sciences

University of East Anglia, UK

November 2016

Abstract

Among temperate birds, two traits in particular are associated with current population declines; an association with farmed habitats, and the strategy of long-distance migration. The European Roller *Coracias garrulus* enjoys both of these characteristics, and has declined substantially over the last few decades. Here, I investigate intra-specific variation in Roller breeding ecology and migration in an attempt to work towards conservation solutions.

I first compare the breeding ecology of Rollers from two populations; one in Latvia at the northern range limit, and one in France in the core Mediterranean range. I show that the French population is limited principally by nest-site availability, whilst foraging habitat is more important in Latvia. I also highlight the lower productivity of Latvian birds, which also varies substantially from year to year. Comparison of insect and chick feather $\delta^{13}C$ and $\delta^{15}N$ in France provides little support for specific foraging habitat preferences, providing further evidence that foraging habitat is not limiting for the French population.

Next, I provide the most comprehensive analysis of Roller migration to date, showing that Rollers from seven European countries generally occupy overlapping winter quarters. I also show that Rollers from Latvia migrate up to twice as far as their southern European counterparts. Ring recoveries provide the first chance to study the migration of juvenile Rollers, as well as non-breeding season mortality. In particular, I highlight the shooting of Rollers from eastern populations in Arabia during spring migration. Finally, I describe patterns of connectivity among 98 populations of 45 migrant land-bird species from two trans-continental flyways. As with the Roller, connectivity is generally weak, such that any non-breeding season drivers of population decline will have widespread but diffuse impacts on breeding populations.

My research highlights the utility (at least in the short-term) of nest-boxes for Roller conservation, but also demonstrates that, in more marginal parts of the range, the provisioning of nest-boxes alone is probably insufficient.

Contents

Acknowledgements

First I'd like to extend a huge thank-you to my supervisor, Simon Butler, for four years of support, enthusiasm and inspiration. Warm thanks to Aldina Franco too. I wouldn't have made it without the two of you – thanks.

My field seasons have been eventful, to say the least, but they'd have been totally disastrous without the help of lots of excellent people. Massive and special thanks to Timothée Schwartz (France) and Edmunds Račinskis (Latvia) for generously providing access to their field sites, data and knowledge. I hope I've done some justice to all your hard work, and that the collaboration has been worth your while. Additionally, many thanks to Patrick Mayet (France), Donnacha Woods (Irishman in France), Emily Wallace (Irishwoman in France), Emily Montague (Englishwoman in France), Ieva Mardeva (Latvia) and Claire Branston, Harriet Clewlow and Lourdes del Horno Sempere (UEA MSc students in France) for help in the field. And a big shout-out to Jamie Dunning for being my friend and (unpaid; sorry) field assistant for two years. I hope you got as much out of it as I did. I'm also grateful to all the landowners around Garrieux and Saint-Hippolyte for being so welcoming and taking an interest in my work. Finally, for providing me with a temporary home, I'd like to thank Patrick and Linette at Les Tourades, Natasha and Medhi in Salses and Igors in Rīga.

As well as messing up in the field, I had a lot of fun in the lab too. Thanks very much to the ENV staff & technicians for putting up with me – Paul Disdle, Alina Marca, Alina Mihailova, Graham Chilvers, Rebecca Baldwin and Bertrand Leze in particular. The BIO Teaching Technicians were amazing too, always happy to lend equipment, advice and bench-space – thank you to Kathryn Mason-Barrie and her team. Also in BIO, Dave Wright, Ellie Fairfield, Liam Crowther & Iain Barr provided helpful advice on how best to collect, store and ultimately bake / analyse genetic material. Thanks also to Dave Blomfield and Nick Griffin in the ENV electronics lab for persevering with the RFID readers. Meh.

UEA's Centre for Ecology, Evolution and Conservation has a famously excellent research vibe, without which I wouldn't have had nearly as good a time. Some particularly special CEEC contemporaries who deserve a mention include Will Nash (puns), Lilja Jóhannesdóttir (yow!), Cat Morrison (cake and R), Damian Smith (sunglasses), Karl Philips (shorts), Ellie Fairfield (mischief), Sarah 'my burger'

Marburger, Aly Lumley (invited me to her wedding in California), Phil Leftwich (fashion), Danielle Leftwich (music), Emily Fowler (remembered my Birthday), Naomi Clarke (Xmas playlist), Jo Godwin (does great presentations), Laura Hebberecht López (music too), Dave 'bumble-bee' Collins, Jen Donelan (ming), Dave Wright (beard compliments), Lewis Spurgin (clever), Tim Huggins (ale), Nathalie Gilbert (Bajadoz), Vero Méndez (east Iberian), José Alves (west Iberian), Mark Abrahams (homebrew), Karen Hornigold (microwave 'hi's), Elizabeth Duxbury (just nice), Conrad Gillet (beetles), Kat Bebbington (pets) and Mike Bolton (cool enough to be at the end). To those I've neglected to mention – sorry, and thanks.

Big thanks to the various organisers of some of the CEEC institutions – Strangles, RDG, Rebellion, etc. Also to members of the UEA Ringing Group, especially Iain – apologies for my dwindling involvement. And to Iain, Phil Leftwich, Kelly Edmunds, Harriet Jones and Jenny Gill for supporting my teaching and providing a supplementary source of income.

Various people have housed me in Norwich over the last few years – particular thanks to Dave & Laura and Dave & Jen for helping me out. Max, Christiana, Manuel, Becky, Alicia and Lilja were all excellent house-mates – cheers.

Away from UEA, I benefited from the support of virtual colleagues on Twitter, and real ones at several conferences (BOU and EOU in particular), though often these communities overlapped. Thanks to all the answerers on stackexchange.com for reducing the interaction between my head and the desk, and to the authors of all the R codes and packages I've made use of. Also to whoever put together musicforprogramming.net – excellent.

Various co-authors and collaborators from across Europe provided data, samples, ideas and feedback – I hope I've acknowledged your contributions appropriately. In particular, I'd like to extend my gratitude to Inês Catry, Jesús Avilés and Will Cresswell for their continued support and enthusiasm.

Thanks to NERC – long may you continue funding research into obscure foreign birds.

To everyone in the Cabbage Office. Thanks for the tea, coffee, cake, biscuits, hats, inflatable / stuffed animals, printer woes. What a great place it's been to work – I'll miss it lots.

To Becky, thanks and love, for everything. You were probably the first friendly face I saw on my first day, and you've seen me through to the end. Thanks for providing a home for me, as well as lots of excellent advice, good food and chuckles. Sorry I never cleaned the bathroom, and I couldn't join you in Iceland.

To Phil – another friendly face from Day 1. It's been a pleasure. Thanks for being such a smashing companion in Sweden, Extremadura, etc. Good luck for the next bit!

To Mum & Dad, thanks for believing in me, encouraging me and providing a safety net. Thanks for not making me feel bad for still being semi-dependent on you at 26, and thanks (to Zac too) for housing me and putting up with my anti-socialness during the final push.

Last but not least; To Jenn, for sticking with me all this time. Your support and love mean so much. I guess I'm now ready to join you in the real, tax-paying world – can't wait!

Author contributions

At the time of final submission, two of five data chapters presented in this thesis are published, and one is under review. Although I am lead author on all manuscripts, and made the largest contribution to each piece of work, I received data, help and advice from various co-authors. Joint authorship and author contributions are outlined below for each data chapter:

Chapter 3: Tom Finch, Claire Branston, Harriet Clewlow, Jamie Dunning, Patrick Mayet, Edmunds Račinskis, Timothée Schwarz, Aldina Franco & Simon Butler. **Intra-specific variation in the breeding ecology of the European Roller** (in prep.)

> TF conceived the study with support from SB and AF. TF led the data collection (with the support of PM and TS in France and ER in Latvia). Field data were collected by ER in Latvia (2013 and 2015) and HC and CB in France (2014). JD assisted with data collection in 2014 and 2015. TF led the data analysis and writing. SB and AF provided comments on the manuscript.

Chapter 4: Tom Finch, Claire Branston, Harriet Clewlow, Jamie Dunning, Patrick Mayet, Edmunds Račinskis, Timothée Schwarz, Aldina Franco & Simon Butler. **Insights into the foraging ecology of the European Roller from chick feather stable isotopes** (in prep.)

> TF conceived the study with support from SB and AF. TF led the data collection, assisted by ER, TS, PM, JD, HC and CB. TF conducted lab-work and led the data analysis and writing. SB and AF provided comments on the manuscript.

Chapter 5: Tom Finch, Jamie Dunning, Orsolya Kiss, Edmunds Račinskis, Timothée Schwartz, Laimonas Sniauksta, Otto Szekeres, Béla Tokody, Aldina Franco & Simon Butler. **Insights into the migration of the European Roller from ring recoveries** *Journal of Ornithology*, doi:10.1007/s10336-016-1374-y.

> TF conceived the study with support from JD, SB and AF. TF led the data collation (provided by OK, ER, TS, LS, OS and BT), data analysis and writing. All authors provided comments on the manuscript.

Chapter 6: Tom Finch, Philip Saunders, Jesús Avilés, Ana Bermejo, Inês Catry, Javier de la Puente, Tamara Emmenegger, Ieva Mardega, Patrick Mayet, Deseada Parejo, Edmunds Račinskis, Juan Rodríguez-Ruiz, Peter Sackl, Timothée Schwartz, Michael Tiefenbach, Francisco Valera, Chris Hewson, Aldina Franco & Simon Butler. **A pan-**

European, multi-population assessment of migratory connectivity in a near-threatened migrant bird *Diversity and Distributions*, **9**, 1051–1062

> TF conceived the study with support from ER, TS, AF, SB, PS, IC, PS, MT and CH; all authors contributed data, TF, JMA, JP, TE, JR, CH and SB analysed the data and TF and SB led the writing of the manuscript with support from all authors.

Chapter 7: Tom Finch, Simon Butler, Aldina Franco & Will Cresswell. **Long-distance migrants have low connectivity: good for climate change but not habitat loss** *Journal of Animal Ecology* (in review)

> TF and WC conceived the study, collected and analysed the data and wrote the paper; SB and AF provided theoretical discussion and wrote parts of the paper.

Chapter 1: The loss of avian abundance and the need for evidence-based conservation

1.1 Defaunation in the Anthropocene

In tandem with the anthropogenic alteration of the Earth's abiotic systems, the state of biodiversity is deteriorating (Waters *et al.* 2016). Current vertebrate species extinction rates are 8 to 100 times higher than the estimated background rate, making the current crisis comparable with the previous five 'mass extinction' events in geological history (Ceballos *et al.* 2015). Whilst tragic, these species extinctions – largely restricted to rare, range-restricted or insular species – are overshadowed by the decline of populations of common, widespread species (Ceballos & Ehrlich 2002; Gaston & Fuller 2007; Inger *et al.* 2014), which has serious implications for ecosystem functioning (Dirzo *et al.* 2014; Bello *et al.* 2015).

The task of preventing further declines and extinctions is generally hampered by our incomplete knowledge of the species and populations we are trying to protect. Even the most basic information, such as the number of extant species, is poorly known for many taxa (Scheffers *et al.* 2012). As a result, species are perhaps being lost faster than they can be described (Lees & Pimm 2015). For those species that have been described, data are often lacking on their numbers, distribution and ecology, preventing an accurate assessment of their conservation status and the factors limiting population size (Baillie, Hilton-Taylor & Stuart 2004).

Birds – conspicuous, ubiquitous and well-loved – are probably the best-studied animal class (Baillie *et al.* 2004; Scheffers *et al.* 2012), so as well as serving important functions in natural communities (Sekercioğlu, Daily & Ehrlich 2004), they provide useful indicators of ecosystem health (Gregory *et al.* 2005; Butler *et al.* 2012) and good case studies for understanding ecological patterns and processes (e.g. Sullivan, Newson & Pearce-Higgins 2015). Although not the most threatened animal taxon, bird populations are nevertheless declining; around 150 species have been lost since 1500 AD, and 1 in 8 species are currently threatened with extinction (Birdlife International 2008). Island endemics and species with slow life histories are, perhaps unsurprisingly, at the greatest risk of extinction (Birdlife International 2008). As above, however, an emphasis on species-level extinctions risks drawing attention away from the more insidious problem of 'defaunation'; since pre-agricultural times avian abundance has declined by an estimated 20–25 % (Gaston, Blackburn & Klein Goldewijk 2003).

Among temperate bird species, two traits in particular are associated with current declines in abundance; an association with agricultural habitats, and the strategy of migrating to tropical wintering grounds. Although these declines have been well described, their mechanistic drivers remain elusive in many cases, and probably vary both within and between species. As argued below, detailed ecological studies are necessary in order to elucidate the links between environment, animal behaviour, demography and population dynamics. Such an 'evidence base' is critical for demonstrating to policy makers, funders and other stakeholders that proposed conservation actions will deliver biodiversity gains (Sutherland *et al.* 2004).

1.2 The decline of European farmland birds

The historic appropriation of forests and wetlands for cultivation presumably paved the way for birds of open habitats – once restricted to marginal areas and more naturally open landscapes – to colonise much of Europe (Donald *et al.* 2002). Farmland now occupies almost half of Europe's land area, hosting an important and familiar community of both generalists and open-country specialists. However, European farmland birds have suffered huge losses over the last few decades, more than halving in abundance between 1980 and 2013 (**Fig. 1.1**; Donald *et al.* 2006).

'Agricultural intensification' describes a broad spectrum of synchronous changes in the intensity of farm management practices (Chamberlain *et al.* 2000). Driven by post-war technological and political advances, these developments include specialisation of farms, simplification of crop rotations, loss of non-cropped areas and increased mechanisation and agrochemical use (Benton, Vickery & Wilson 2003). As well as resulting in the general homogenisation of the European farmed landscape (Benton *et al.* 2003), agricultural intensification has reduced the quality and quantity of functional habitat for nesting and foraging (Butler *et al.* 2010).

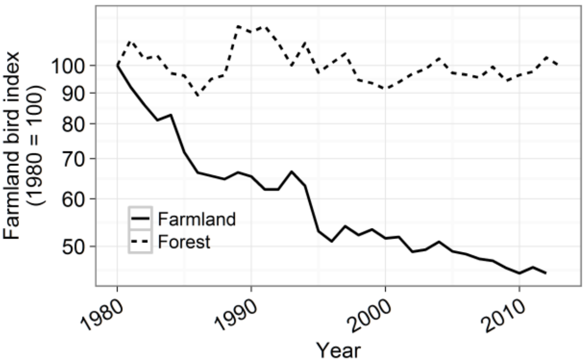


Figure 1.1 Common bird indicators for Europe, 1980–2013. These aggregated indices summarise the population trends of 39 common farmland species (solid line) and 34 common forest bird species (dashed line) across Europe. Data downloaded from PECMBS (2013).

Agricultural intensification is generally attributed as the main driver of farmland bird declines. Across Europe, for example, there is a striking negative correlation between a country's cereal yield and the overall trend of its farmland bird populations (Donald, Green & Heath 2001; Donald *et al.* 2006). Similar patterns are mirrored in the United States, where farmland (a.k.a. grassland) birds are also declining (Murphy 2003). Agricultural intensification is not the only probable driver of farmland bird declines, however. Rural abandonment, and the subsequent encroachment of forest into open areas presents an additional threat to farmland specialists, particularly in central and eastern Europe (Sanderson *et al.* 2013; Zakkak *et al.* 2015). Thus, across a gradient of agricultural intensification, the response of farmland bird populations is likely to be non-linear, with an intermediate optimum (e.g. Brambilla, Rubolini & Guidali 2007).

Despite this convincing association with agricultural intensification, the proximate cause of farmland bird declines is likely to vary from species to species, as indicated, for example, by inter-specific variation in the long-term trends of British farmland bird populations (Siriwardena *et al.* 1998). The task of identifying causal mechanisms is made difficult by the temporal synchrony of various components of agricultural intensification (Chamberlain *et al.* 2000), such that detailed ecological studies are generally necessary. These have revealed diverse environmental causes and demographic mechanisms, including; pesticide-driven reductions in prey availability and chick survival (Aebischer & Ewald 2012); direct destruction of nests and chicks by farm machinery (Green, Rocamora & Schäffer 1997); farm specialisation reducing crop diversity, so limiting the opportunity for multiple breeding attempts (Wilson *et al.* 1997) and loss of winter stubble reducing winter food availability and adult survival (Peach, Siriwardena & Gregory 1999).

Following the well-described loss of farmland biodiversity, the EU Common Environmental Policy now incentivises ‘wildlife-friendly farming’ through subsidised agri-environment schemes, though evidence that biodiversity benefits from these schemes is mixed (Kleijn & Sutherland 2003; Baker *et al.* 2012). Although widespread generalist species are expected to profit from the ‘broad-and-shallow’ amelioration of the farmed environment, evidence is currently limited (Kleijn *et al.* 2006), with the decline of common farmland birds continuing unabated. Many species will instead require more tailored (‘narrow-and-deep’) solutions (e.g. Peach *et al.* 2001; Ewald *et al.* 2010), or at least a shift towards regionally relevant and locally joined-up prescriptions (Whittingham 2006).

1.3 The decline of sub-Saharan migrant birds

Populations of birds which migrate annually between breeding areas in Europe and non-breeding areas in sub-Saharan Africa are also declining (**Fig. 1.2a**), though to a lesser and more variable extent than farmland birds. The aggregate European population index of 38 widespread sub-Saharan migrants declined by 23 % between 1980 and 2009, in contrast to the roughly stable populations of residents and short-distance migrants (Vickery *et al.* 2013). Although declines are particularly strong for migrants breeding in farmland habitats (**Fig. 1.2b**), the comparison of ecologically similar pairs of migrant and resident species indicates that migrants are declining irrespective of breeding habitat (Sanderson *et al.* 2006). As in the case of farmland birds, this decline is mirrored in North America (Robbins *et al.* 1989).

The inherent complexity of migrant life cycles – centred around the exploitation of seasonal resources at distant geographic locations – makes identifying proximal causes difficult (Hostetler, Sillett & Marra 2015). Whilst it makes intuitive sense that the reliance of individuals on multiple sites throughout the annual cycle makes migrants vulnerable during eras of environmental change (‘multiple jeopardy’, Newton 2004), we still have a relatively poor understanding of the drivers of population decline in migrant birds.

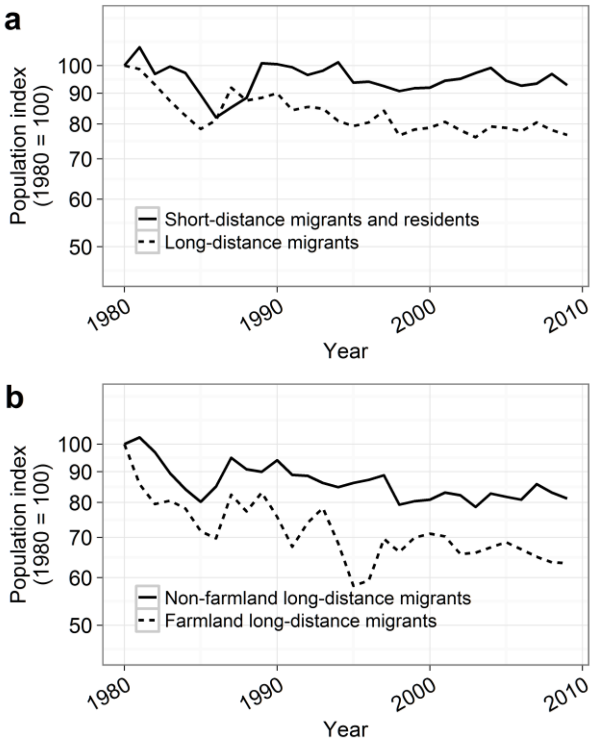


Figure 1.2 Annual variation in the aggregate population index of **a** long-distance migrant birds (dashed line) and short-distance migrant and resident birds (solid line) and **b** farmland long-distance migrant birds (dashed line) and non-farmland long-distance migrant birds (solid line). Redrawn from Vickery *et al*. (2013) using the WebPlotDigitizer application (http://arohatgi.info/WebPlotDigitizer)

The most obvious factor explaining the decline of sub-Saharan migrants (compared to residents) is the deterioration of conditions during the non-breeding season. For example, reduced rainfall in the Sahel region of West Africa is strongly correlated with inter-annual variation in the survival and population abundance of several migrant species which winter in this area (Peach, Baillie & Underhill 1991; Szep 1995). Alternatively (or additionally), migrants could face unique problems on the breeding ground, such as increased competition with residents following milder European winters (Lemoine & Bohning-Gaese 2003), or reduced ability to respond to phenological change at lower trophic levels (Both & Visser 2001). Finally, migrants may simply be more susceptible than residents to pressures operating on the breeding grounds (e.g. agricultural intensification), as suggested by the positive correlation between population trends of migrants and residents breeding in the same country (Sanderson *et al.* 2006).

In reality, different migrant populations during different time periods are probably affected by different and interacting breeding and non-breeding season drivers (Moller, Rubolini & Lehikoinen 2008; Morrison *et al.* 2013; Vickery *et al.* 2013). As with farmland birds, detailed studies are therefore required in order to diagnose the environmental processes responsible for these declines and to identify probable solutions. For migrants, the problem is compounded by our generally poor understanding of their whereabouts and ecology during the non-breeding season.

1.4 Thesis outline

I have briefly outlined the declines being suffered by biodiversity as a whole, and farmland and migratory birds in particular, as well as highlighting the importance of detailed ecological studies in identifying causes and conservation solutions. The following chapters deal with these issues in more detail, using the European Roller (*Coracias garrulus*, hereafter 'Roller') – a long-distance migrant bird, often associated with agricultural landscapes and declining across most of Europe (Birdlife International 2015) – as a case study.

First, in **Chapter 2** I describe the biology and status of the Roller, and review evidence for the potential causes of its ongoing decline. I then introduce the two main study sites; one in France, where the population is stable or increasing, and another at the species' northern limit in Latvia, where the population has undergone a massive decline.

Chapter 3 explores intra-specific variation in the breeding ecology of the Roller. Specifically, I use field data collected in France and Latvia between 2013 and 2015 to test the influence of foraging resource availability on breeding density, nest-box occupation and breeding success. This comparison reveals important differences in the factors limiting breeding density and productivity in the two populations, with implications for conservation management priorities.

In **Chapter 4** I compare the carbon and nitrogen stable isotope ratios of (1) chick feathers from across the French study site and (2) prey taxa collected from different land-uses. I generate expected prey source stable isotope ratios for all nests, and test whether variation in chick feather stable isotope ratios can be explained simply by the availability of different prey sources in the core foraging range.

Chapter 5 is the first of three chapters concerning migration. I combine all current Roller tracking data – including geolocator data from my study populations in France and Latvia – to compare the migration routes and wintering sites of birds from across Europe. This forms the first pan-European assessment of migratory connectivity for this species.

In **Chapter 6** I present a timely analysis of ring recovery data in the Roller, complementing the direct tracking data used in **Chapter 5**. This provides the first data on the migration of juvenile Rollers, as well as information relating to the causes of mortality during the non-breeding season.

In order to place the metrics of migratory connectivity measured in **Chapter 5** into context, in **Chapter 7** I collate equivalent tracking data for 98 populations of 45 migrant land-bird species from the Neotropic and Afro-Palaearctic flyways. This analysis reveals a pattern of generally weak connectivity. The consequences of this for the response of populations to environmental change are discussed.

Finally, in **Chapter 8** I synthesis and discuss my findings in the context of the Roller's decline in Europe.

1.5 References

Aebischer, N.J. & Ewald, J.A. (2012) The grey partridge in the UK: population status, research, policy and prospects. *Animal Biodiversity and Conservation*, **35**, 353–362.

Baillie, J.E.M., Hilton-Taylor, C. & Stuart, S.N. (2004) *2004 IUCN Red List of Threatened Species. A Global Species Assessment*. IUCN, Gland, Switzerland and Cambridge, UK.

Baker, D.J., Freeman, S.N., Grice, P. V. & Siriwardena, G.M. (2012) Landscape-scale responses of birds to agri-environment management: a test of the English Environmental Stewardship scheme. *Journal of Applied Ecology*, **49**, 871–882.

Bello, C., Galetti, M., Pizo, M.A., Magnago, L.F.S., Rocha, M.F., Lima, R.A.F., Peres, C.A., Ovaskainen, O. & Jordano, P. (2015) Defaunation affects carbon storage in tropical forests. *Science Advances*, e1501105.

Benton, T.G., Vickery, J.A. & Wilson, J.D. (2003) Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology and Evolution*, **18**, 182–188.

Birdlife International. (2008) *State of the World's Birds. Indicators for Our Changing World*. Cambridge, UK.

Birdlife International. (2015) *European Red List of Birds*. Cambridge, UK.

Both, C. & Visser, M.E. (2001) Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature*, **411**, 296–298.

Brambilla, M., Rubolini, D. & Guidali, F. (2007) Between land abandonment and agricultural intensification: habitat preferences of Red-backed Shrikes Lanius collurio in low-intensity farming conditions. *Bird Study*, **54**, 160–167.

Butler, S.J., Boccaccio, L., Gregory, R.D., Vorisek, P. & Norris, K. (2010) Quantifying the impact of land-use change to European farmland bird populations. *Agriculture, Ecosystems and Environment*, **137**, 348–357.

Butler, S.J., Freckleton, R.P., Renwick, A.R. & Norris, K. (2012) An objective, niche-based approach to indicator species selection. *Methods in Ecology and Evolution*, **3**, 317–326.

Ceballos, G. & Ehrlich, P.R. (2002) Mammal Population Losses and the Extinction Crisis. *Science*, **296**, 904–907.

Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M. & Palmer, T.M. (2015) Accelerated modern human–induced species losses: Entering the sixth mass extinction. *Science Advances*, e1400253.

Chamberlain, D.E., Fuller, R.J., Bunce, R.G.H., Duckworth, J.C. & Shrubb, M. (2000) Changes in the Abundance of Farmland Birds in Relation to the Timing of Agricultural Intensification in England and Wales. *Journal of Applied Ecology,* **37**, 771–788.

Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B. & Collen, B. (2014) Defaunation in the Anthropocene. *Science*, **345**, 401–406.

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 of London B: Biological Sciences*, **268**, 25–29.

Donald, P.F., Pisano, G., Rayment, M.D. & Pain, D.J. (2002) The common agricultural policy, EU enlargement and the conservation of Europe’s farmland birds. *Agriculture, Ecosystems and Environment*, **89**, 167–182.

Donald, P.F., Sanderson, F.J., Burfield, I.J. & van Bommel, F.P.J. (2006) Further evidence of continent-wide impacts of agricultural intensification on European farmland birds, 1990–2000. *Agriculture, Ecosystems & Environment*, **116**, 189–196.

Ewald, J.A., Aebischer, N.J., Richardson, S.M., Grice, P. V. & Cooke, A.I. (2010) The effect of agri-environment schemes on grey partridges at the farm level in England. *Agriculture, Ecosystems and Environment*, **138**, 55–63.

Gaston, K.J., Blackburn, T.M. & Klein Goldewijk, K. (2003) Habitat conversion and global avian biodiversity loss. *Proceedings of the Royal Society of London B: Biological Sciences*, **270**, 1293–1300.

Gaston, K.J. & Fuller, R.A. (2007) Biodiversity and extinction: losing the common and the widespread. *Progress in Physical Geography*, **31**, 213–225.

Green, R.E., Rocamora, G. & Schäffer, N. (1997) Populations, ecology and threats to the Corncrake Crex crex in Europe. *Vogelwelt*, **118**, 117–134.

Gregory, R.D., van Strien, A., Vorisek, P., Gmelig-Meyling, A.W., Noble, D.G., Foppen, R.P.B. &

Gibbons, D.W. (2005) Developing indicators for European birds. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **360**, 269–288.

Hostetler, J.A., Sillett, T.S. & Marra, P.P. (2015) Full-annual-cycle population models for migratory birds. *The Auk*, **132**, 433–449.

Inger, R., Gregory, R.D., Duffy, J.P., Stott, I., Voříšek, P. & Gaston, K.J. (2014) Common European birds are declining rapidly while less abundant species' numbers are rising. *Ecology Letters*, **18**, 28–36.

Kleijn, D., Baquero, R.A., Clough, Y., Díaz, M., De Esteban, J., Fernández, F., Gabriel, D., Herzog, F., Holzschuh, A., Jöhl, R., Knop, E., Kruess, A., Marshall, E.J.P., Steffan-Dewenter, I., Tscharntke, T., Verhulst, J., West, T.M. & Yela, J.L. (2006) Mixed biodiversity benefits of agri-environment schemes in five European countries. *Ecology Letters*, **9**, 243–254.

Kleijn, D. & Sutherland, W.J. (2003) How effective are European agri-environment schemes in conserving and promoting biodiversity? *Journal of Applied Ecology*, **40**, 947–969.

Lees, A.C. & Pimm, S.L. (2015) Species, extinct before we know them? *Current Biology*, **25**, 177–180.

Lemoine, N. & Bohning-Gaese, K. (2003) Potential Impact of Global Climate Change on Species Richness of Long-Distance Migrants. *Conservation Biology*, **17**, 577–586.

Moller, A.P., Rubolini, D. & Lehikoinen, E. (2008) Populations of migratory bird species that did not show a phenological response to climate change are declining. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 16195–16200.

Morrison, C.A., Robinson, R.A., Clark, J.A., Risely, K. & Gill, J.A. (2013) Recent population declines in Afro-Palaearctic migratory birds: the influence of breeding and non-breeding seasons. *Diversity and Distributions*, **19**, 1051–1058.

Murphy, M.T. (2003) Avian population trends within the evolving agricultural landscape of eastern and central United States. *The Auk*, **120**, 20–34.

Newton, I. (2004) Population limitation in migrants. *Ibis*, **146**, 197–226.

Peach, W.J., Baillie, S.R. & Underhill, L. (1991) Survival of British sedge warblers Acrocephalus schoenobaenus in relation to west African rainfall. *Ibis*, **133**, 300–305.

Peach, W.J., Lovett, L.J., Wotton, S.R. & Jeffs, C. (2001) Countryside stewardship delivers cirl buntings (Emberiza cirlus) in Devon, UK. *Biological Conservation*, **101**, 361–373.

Peach, W.J., Siriwardena, G.M. & Gregory, R.D. (1999) Long-term changes in over-winter survival rates explain the decline of reed buntings Emberiza schoeniclus in Britain. *Journal of Applied Ecology*, **36**, 798–811.

PECBMS. (2013) *Population Trends of Common European Breeding Birds 2013*.

Robbins, C., Sauer, J., Greenberg, R.S. & Droege, S. (1989) Population Declines in North American Birds that Migrate to the Neotropics. *Proceedings of the National Academy of Sciences of the*

United States of America, **86**, 7658–7662.

Sanderson, F.J., Donald, P.F., Pain, D.J., Burfield, I.J. & van Bommel, F.P.J. (2006) Long-term population declines in Afro-Palearctic migrant birds. *Biological Conservation*, **131**, 93–105.

Sanderson, F.J., Kucharz, M., Jobda, M. & Donald, P.F. (2013) Impacts of agricultural intensification and abandonment on farmland birds in Poland following EU accession. *Agriculture, Ecosystems and Environment*, **168**, 16–24.

Scheffers, B.R., Joppa, L.N., Pimm, S.L. & Laurance, W.F. (2012) What we know and don't know about Earth's missing biodiversity. *Trends in Ecology and Evolution*, **27**, 501–510.

Sekercioğlu, C.H., Daily, G.C. & Ehrlich, P.R. (2004) Ecosystem consequences of bird declines. *Proceedings of the National Academy of Sciences of the United States of America*, **101**, 18042–18047.

Siriwardena, G.M., Baillie, S.R., Buckland, S.T., Fewster, R.M., Marchant, J.H. & Wilson, J.D. (1998) Trends in the abundance of farmland birds: a quantitative comparison of smoothed Common Birds Census indices. *Journal of Applied Ecology*, **35**, 24–43.

Sullivan, M.J.P., Newson, S.E. & Pearce-Higgins, J.W. (2015) Evidence for the buffer effect operating in multiple species at a national scale. *Biology Letters*, **11**, 20140930.

Sutherland, W.J., Pullin, A.S., Dolman, P.M. & Knight, T.M. (2004) The need for evidence-based conservation. *Trends in Ecology and Evolution*, **19**, 305–308.

Szep, T. (1995) Relationship between west African rainfall and the survival of central European Sand Martins Riparia riparia. *Ibis*, **137**, 162–168.

Vickery, J.A., Ewing, S.R., Smith, K.W., Pain, D.J., Bairlein, F., Škorpilová, J. & Gregory, R.D. (2013) The decline of Afro-Palaearctic migrants and an assessment of potential causes. *Ibis*, **156**, 1–22.

Waters, C.N., Zalasiewicz, J., Summerhayes, C., Barnosky, A.D., Poirier, C., Ga uszka, A., Cearreta, A., Edgeworth, M., Ellis, E.C., Ellis, M., Jeandel, C., Leinfelder, R., McNeill, J.R., Richter, D. d., Steffen, W., Syvitski, J., Vidas, D., Wagreich, M., Williams, M., Zhisheng, A., Grinevald, J., Odada, E., Oreskes, N. & Wolfe, A.P. (2016) The Anthropocene is functionally and stratigraphically distinct from the Holocene. *Science*, **351**, 137–147.

Whittingham, M.J. (2006) Will agri-environment schemes deliver substantial biodiversity gain, and if not why not? *Journal of Applied Ecology*, **44**, 1–5.

Wilson, J.D., Evans, J., Browne, S.J. & King, J.R. (1997) Territory distribution and breeding success of skylarks Alauda arvensis on organic and intensive farmland in southern England. *Journal of Applied Ecology*, **34**, 1462–1478.

Zakkak, S., Radovic, A., Nikolov, S.C., Shumka, S., Kakalis, L. & Kati, V. (2015) Assessing the effect of agricultural land abandonment on bird communities in southern-eastern Europe. *Journal of Environmental Management*, **164**, 171–179.

Chapter 2: Description of the study system

2.1 The European Roller

The European Roller *Coracias garrulus* is arguably one of the most striking birds in the Western Palaearctic, sharing a place in the order Coraciiformes with other such colourful species as the European Bee-eater *Merops apiaster* and Common Kingfisher *Alcedo atthis*. Named for the spectacular rolling dives performed during courtship and territorial defence, the Roller is the only member of family Coraciidae found in Europe, where its blue and chestnut plumage is unmistakable (**Fig. 2.1**). The binomial name *Coracias garrulus* translates roughly as ‘noisy corvid’, reflecting the Roller’s crow-like form and harsh calls.

Figure 2.1 European Roller in vineyard, southern France, 2013 (Tom Finch)

Three traits combine to make the species regionally distinctive; Rollers are cavity-nesters, long-distance trans-Saharan migrants, and – across much of their range – farmland birds. Unfortunately, these characteristics probably put the Roller at risk during the current era of human-driven environmental change. In this section I give a brief overview of the natural history of the Roller, then discuss its decline and the likely causes.

2.1.1 Natural history

2.1.1.1 Distribution

The Roller's breeding distribution extends from north Africa and the Iberian Peninsula in the west through southern, eastern and north-east Europe, then east as far as Siberia and Kashmir (**Fig. 2.2**). Breeding Rollers are restricted to warm, lowland regions with stable summer climates; in western Europe they reach no further north than southern France, whereas further east, away from Atlantic influence, they breed as far north as the Baltic States (Hagemeijer & Blair 1997; Huntley *et al.* 2007). Rollers are associated with open landscapes, including mixed farmland, open forests with clearings, Mediterranean plains and steppe (Cramp 1985; Fry & Fry 1992).

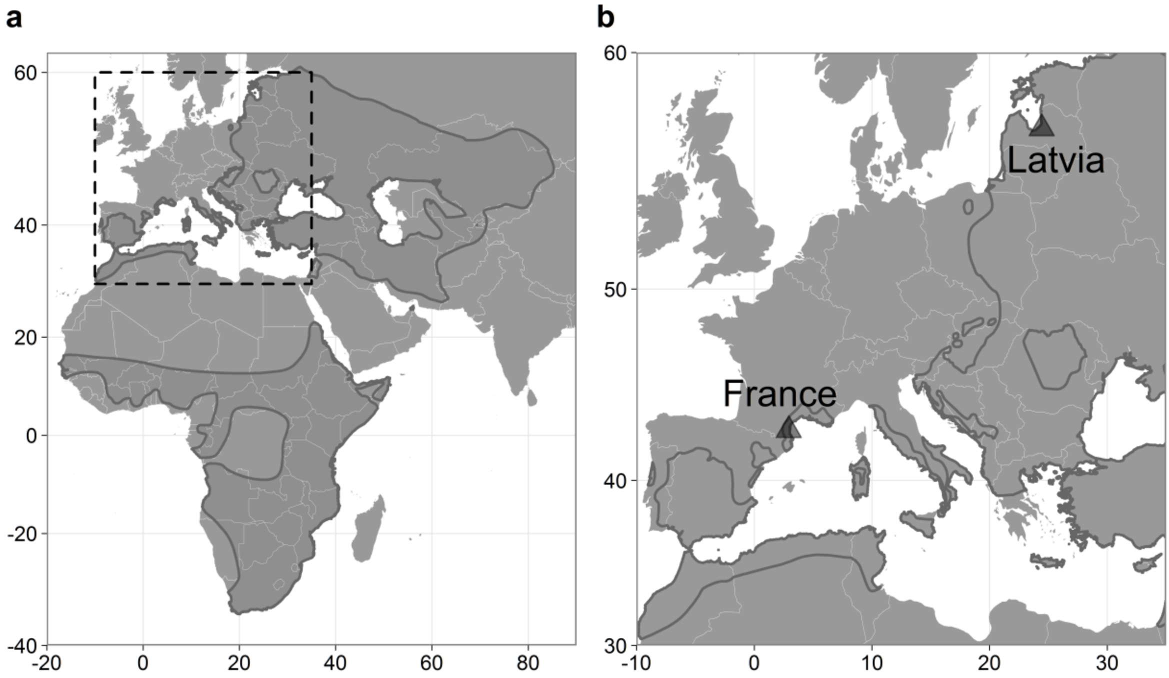


Figure 2.2 a Breeding (Eurasia) and winter (Africa) distribution of the European Roller, and **b** location of principle study sites in France and Latvia. Range map polygon from Birdlife International & NatureServe (2013). Mercator projection.

After breeding, Rollers migrate south to overwinter in the dry, wooded savannahs of sub-Saharan Africa (Fry & Fry 1992). Most aspects of their migratory movements and non-breeding ecology are poorly understand, though three recent studies have tracked Rollers from western European populations to south-west Africa (Emmenegger *et al.* 2014; Catry *et al.* 2014; Rodríguez-Ruiz *et al.* 2015).

2.1.1.2 Diet and foraging strategy

Rollers principally feed on large invertebrates, particularly beetles (order Coleoptera) to the north of their range and grasshoppers and crickets (order Orthoptera) to the south (Cramp 1985; Sosnowski & Chmielewski 1996; Avilés & Parejo 2002; Bohus & Kristin 2004; Folch, Kristin & Manosa 2004). As accomplished and opportunistic hunters, they also catch small vertebrates, as well as smaller insects (e.g. winged ants) when locally abundant (Cramp 1985; Kiss, Elek & Moskát 2014).

Their versatile hunting strategies include swallow-like aerial foraging, raptor-like quartering, and warbler-like sally-gleaning, though they are most often seen poised on an exposed perch before flying down to take prey from the ground or in mid-air (Cramp 1985; Sosnowski & Chmielewski 1996). This ‘sit-and-wait’ foraging tactic goes hand-in-hand with their association with open habitats, in which a large area can be surveyed from a single look-out post.

2.1.1.3 Breeding biology

Like other Coraciiformes, Rollers are cavity nesters but – unlike bee-eaters and kingfishers – they are unable to excavate their own nest holes (i.e. they are obligate secondary cavity-nesters). Depending on local availability, Rollers will nest in tree holes (especially those excavated by woodpeckers), masonry, sandbanks, rocky outcrops, and artificial nest boxes (Cramp 1985; Fry & Fry 1992; Avilés *et al.* 1999).

Rollers typically lay 3–5 (up to a maximum of 7) near-spherical white eggs, with a laying interval of approximately two days (Cramp 1985; Avilés *et al.* 1999). Although they are single-brooded, failed clutches may be replaced (Cramp 1985). Incubation starts before clutch completion – usually after the laying of the third egg – and lasts 17–20 days, with nestlings fledging 25–30 days after hatching (Cramp 1985; Parejo, Avilés & Rodriguez 2012). Because incubation starts before the last egg is laid, hatching is asynchronous and nestling size is often asymmetric (Sosnowski & Chmielewski 1996; Parejo, Silva & Avilés 2007; Parejo, Avilés & Expósito 2015).

Other aspects of the Roller’s reproductive behaviour have not been formally studied in much detail, with every generalisation having its exceptions:

- Rollers are largely regarded as socially monogamous (Cramp 1985), though there is anecdotal evidence of apparent cooperative breeding from Spain and Slovakia, with three adult Rollers observed feeding a single brood (Avilés & Sanchez 1999;

Bohus 2002). A recent molecular study detected extra-pair parenthood in ~ 5 % of nests in a Spanish population (Sánchez-Tójar *et al.* 2015).

- Rollers are considered territorial, and aggressive encounters (perhaps occasionally lethal) with conspecifics and other nest-site competitors are not uncommon; they are also known to evict the eggs of other species from preferred nest sites (Cramp 1985). On the other hand, Rollers sometimes breed at remarkably high densities, with adjacent pairs often separated by less than a few tens of metres (Cramp 1985; Vaclav, Valera & Martinez 2011). Similarly, they regularly tolerate the close presence of other cavity-nesting species, and may appear to 'wait' for the chicks of another species to fledge before starting a clutch of their own (Cramp 1985).
- Ringing has provided good evidence of high fidelity to natal (Rollers often return to breed within 1 km of where they hatched) and breeding sites (Avilés, Parejo & Rodríguez 2011; Vaclav *et al.* 2011), though long-distance dispersal events away from well-monitored sites are inevitably under-detected. Most Rollers do not breed until their second full year, though some breed in their first (Cramp 1985).
- The Roller is sexually dichromatic, but mostly in the UV spectrum, making field-identification of sex difficult (Silva *et al.* 2008). The nature of the division of labour between males and females is thus poorly known. Females appear to take a larger share of incubation duties (Cramp 1985) but males and females feed young at similar rates (Avilés *et al.* 2011). Pair bonds may last several years, though mate-swapping also occurs (Parejo *et al.* 2015).

In summary, breeding Rollers depend on open habitats with a good supply of large invertebrates and look-out perches, and suitable cavities for nesting. They are also long-distance migrants, crossing not only the Sahara Desert, but the equator too. So, whilst it would probably be inappropriate to describe Rollers as ecological specialists, this combination of traits certainly makes them special; and perhaps vulnerable.

2.1.2 Population status

Over the last century or so, the Roller's European range has retracted considerably, particularly in northern and central Europe. Now extinct in Sweden, Denmark, Germany, Czechoslovakia, Slovenia and Estonia (Cramp 1985; Kovacs *et al.* 2008; Lüütsepp, Kalamees & Lüütsepp 2011), the species is suffering ongoing declines across

Europe. Between 1970 and 1990, the Roller was declining in 18 out of 23 assessed European countries and increasing in just one (Tucker *et al.* 1994). This pattern continued throughout the next decade, when the Roller was declining in 20 countries, stable in 6 and increasing in 1; with an overall decline of more than 30 % the Roller was classified as ‘vulnerable’ in Europe (Burfield & van Bommel 2004). The most recent assessment period (2000–2010) saw the Roller’s decline decelerate so that in 2015 the species was reclassified as ‘least concern’ in Europe (Birdlife International 2015a). However, the Roller’s decline continues in 16 of 23 European countries for which a population trend could be estimated, though ‘good’ quality data were available for only 8 out of 33 European countries for the 2000–2010 assessment period (Birdlife International 2015a). Unsurprisingly, these well-studied populations are also some of the smallest in Europe. In contrast, little is known about the larger populations of Russia and Turkey, which together hold more than half of Europe’s Rollers. Outside of Europe, the poorly monitored Central Asian population is not thought to be in decline; the species is thus classified as ‘least concern’ globally (Birdlife International 2015b).

2.1.3 Threats

The International Species Action Plan for the European Roller (Kovacs *et al.* 2008), the result of a 2008 workshop in Hungary, compiles a list of all perceived threats to the Roller. Due to a positive association between population trend and breeding productivity (and the admitted lack of data on mortality), the report assumes that adult survival does not limit Roller population growth. Instead, it argues that the principle driver of the Roller’s decline is a reduction in the quality and quantity of foraging and nesting habitat on the breeding grounds. The six threats identified as ‘critical’ are: intensification of (1) forest and (2) grassland management, (3) increased habitat homogeneity, (4) conversion of permanent grasslands, (5) land abandonment and (6) increased insecticide use. Other potential threats include persecution on migration, nest predation, and climate change, though these have not been studied in any detail.

The conclusions of the species action plan are principally based on expert intuition, rather than any systematic, objective or evidence-based process. The primary scientific literature on Roller conservation ecology is rather limited, and key information on survival and migration is lacking almost entirely. In particular, no one has attempted to quantify whether the drivers of population limitation vary across the species’ range.

2.1.3.1 Nest site limitation

There are several instances of impressive increases in Roller numbers following the supplementation of natural nest sites with artificial nest-boxes (Rodriguez, Avilés & Parejo 2011; Vaclav *et al.* 2011; Aleman & Laurens 2013; Kiss *et al.* 2014). This quasi-experimental evidence suggests that nest-site availability is limiting the growth of some Roller populations (Newton 1994). The widespread removal of old trees (Pulido, Dõ & Hidalgo de Trucios 2001; Gibbons *et al.* 2008) and the demolition or renovation of rural structures (Franco, Marques & Sutherland 2005) are therefore good candidates in the list of processes responsible for the Roller's decline. The decline of primary excavators (e.g. Iberian Green Woodpecker *Picus sharpei* (Birdlife International 2015a)) and competition with other cavity-nesting species (e.g. Parejo, Danchin & Avilés 2005) may also have played a role.

However, the low uptake of nest-boxes in the declining Polish population (Sosnowski & Chmielewski 1996) and the failure of nest-box provisioning to halt the extinction of Rollers in Estonia (Lüütsepp *et al.* 2011), suggest that other factors are also involved. Furthermore, the success of contemporary nest-box schemes does not necessarily mean that nest-site loss was responsible for historical declines; in some cases (where good foraging opportunities exist), nest-box provisioning has facilitated the colonisation of new areas, rather than the recovery of existing populations (Aleman & Laurens 2013).

2.1.3.2 Reduced quality of foraging habitat

Studies of nest-site use have shown that Rollers often select cavities depending on the nature of the surrounding habitat, generally preferring low-intensity, insect-rich habitats over more transformed, intensive ones (Avilés & Costillo 1998; Catry *et al.* 2011; Rodriguez *et al.* 2011; Bouvier *et al.* 2014). Empirical studies of Roller foraging site selection are rare, though in Austria hunting Rollers selected perches near invertebrate-rich meadows and in areas with high edge density, avoiding maize fields and human settlements (Sackl *et al.* 2004; Tiefenbach 2009). Together, this suggests that land-use types vary in (at least) their 'perceived' foraging quality.

Only a handful of studies have tested the 'realised' quality of the habitat surrounding a nest, i.e. its influence on breeding success. In southern Spain, for example, chick mortality was highest in irrigated crops compared to less intensive habitats (Avilés & Parejo 2004). In southern Hungary, however, breeding success was higher in a farmland mosaic than in natural grassland / steppe, despite the former habitat having fewer grasshoppers (Kiss *et al.* 2014).

As a whole, these results suggest that Rollers prefer to nest near – and forage in – areas of low management intensity, where insects are both abundant and accessible, though the effect of surrounding habitat on breeding success is more ambiguous. It is easy to envisage, then, how the homogenisation and intensification of the European farmed landscape (Benton, Vickery & Wilson 2003) could have reduced the quality of Roller foraging habitat and contributed to the species' decline. In Austria, for example, the decline of Rollers coincides remarkably well with the conversion of meadows to maize fields (Samwald & Samwald 1989).

The limited evidence so far suggests that there is no singular cause of the Roller's decline. Several factors are likely to be involved, the relative importances of which probably vary across the Roller's range. Additionally, the effects of these multiple drivers might interact, such that the strength of the effect of one driver may depend on the presence or absence of others. This complex picture can only be improved by further studies of Roller ecology and demography.

2.2 Study sites

The majority of the data presented in this thesis were collected at two Roller nest-box schemes in France and Latvia (**Fig. 2.2b**). These sites vary in both geography and climate, but the main rationale behind their selection was the differing state of their Roller populations (see below). The boundaries of each site are defined by a 1 km buffer around all nest-boxes, with annual changes in site extent reflecting the loss and gain of nest-boxes.

2.2.1 Location and geography

2.2.1.1 France

The Plaine du Roussillon (42.81° N, 2.94° E) lies 13 km north of the city of Perpignan in the Pyrénées-Orientales *departement*. The field site (mean elevation = 7 m; min. = –1 m; max = 20 m) covers approximately 23.5 km^2 to the north of the plain in the *communes* of Salses-le-Châteaux and Saint-Hippolyte. The site occupies a gradient from the dry vineyard-dominated plain in the south to the orchard- and meadow-dominated landscape on the edge of the Etang du Salses (a saline lagoon surrounded by saltmarsh) in the north (**Fig. 2.3**). The principle land-cover is vineyard (35 %), followed by a semi-natural steppe-like habitat ('fallow') created from the rotational uprooting and abandonment of vineyards (24 %).

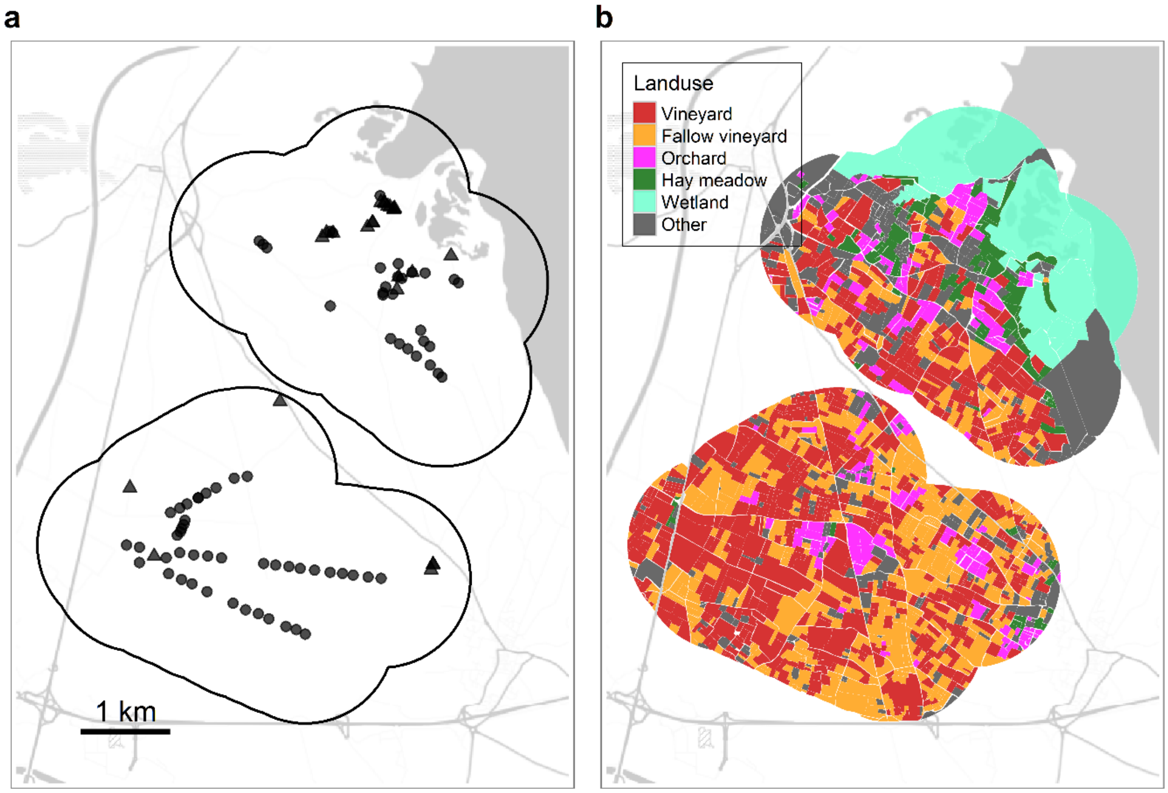


Figure 2.3 Map of French field site. **a** shows locations of nest-boxes (circles) and natural cavities (triangles) in 2015, with a 1 km radius buffer around all nest-boxes delineating the site boundary. **b** shows land-use parcels in 2015, with land-uses classes aggregated for plotting. The northern sub-site, dominated by orchards, meadows and wetland is Garrieux; the southern vineyard-dominated sub-site is St-Hippolyte.

2.2.1.2 Latvia

Some 2,000 km to the northeast, the Latvian site (57.05° N, 24.47° E) is situated on an ancient sand-dune system 20 km east of the city of Rīga. The site (mean elevation = 22 m; min. = 2 m; max = 46 m) is divided into the core Garkalne population (~ 35 km^2), with the satellite sites of Ādaži and Silakrogs a few kilometres to the north and south, respectively (**Fig. 2.4**). The sandy soil supports dry Scot's Pine *Pinus sylvestris* forest (> 50 % cover) with a low understory of moss, lichen and dwarf Ericaceous shrubs. Denser mixed forest grows in the moister depressions and open heath is maintained by forestry, military activity (a large active training area in Ādaži and abandoned Soviet military bases and stores in Garkalne and Silakrogs) and a 1992 0.6 km^2 forest fire in Garkalne. The main human impact on the landscape thus arises through forestry or military activity, in contrast to the agricultural French site. Due to access restrictions, only limited data are available from Ādaži, so I focus principally on Garkalne and Silakrogs.

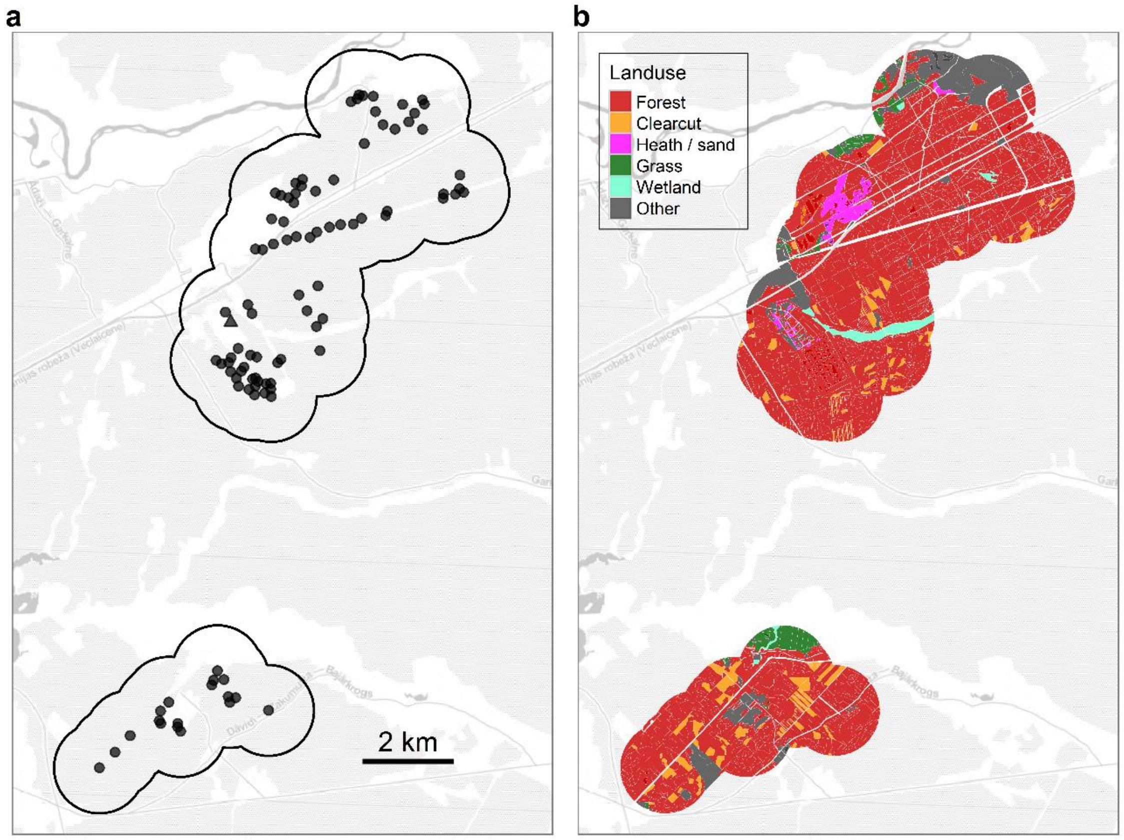


Figure 2.4 Map of Latvian field site. **a** shows locations of nest-boxes (circles) and natural cavities (triangles) in 2014, with a 1 km radius buffer around all nest-boxes delineating the site boundary. **b** shows land-use parcels in 2014, with land-uses classes aggregated for plotting. The northern sub-site is the core population of Garkalne; the satellite site of Silakrogs is to the south; the inaccessible northern satellite site of Ādaži is not shown.

2.2.2 Climate

Given that both study sites support European Rollers, their summer climates are necessarily warm, sunny and dry, though summer maximum temperatures are ~ 5 ˚C warmer in France than Latvia, and seasonality in temperature is less marked (**Fig. 3.2a**), resulting in a longer growing season. France is also drier (**Fig. 2.5b**) and has lower cloud cover on general (**Fig. 2.5c**), and the region is characterised by strong north-westerly winds (‘*Le Mistral*’; **Fig. 2.5d**).

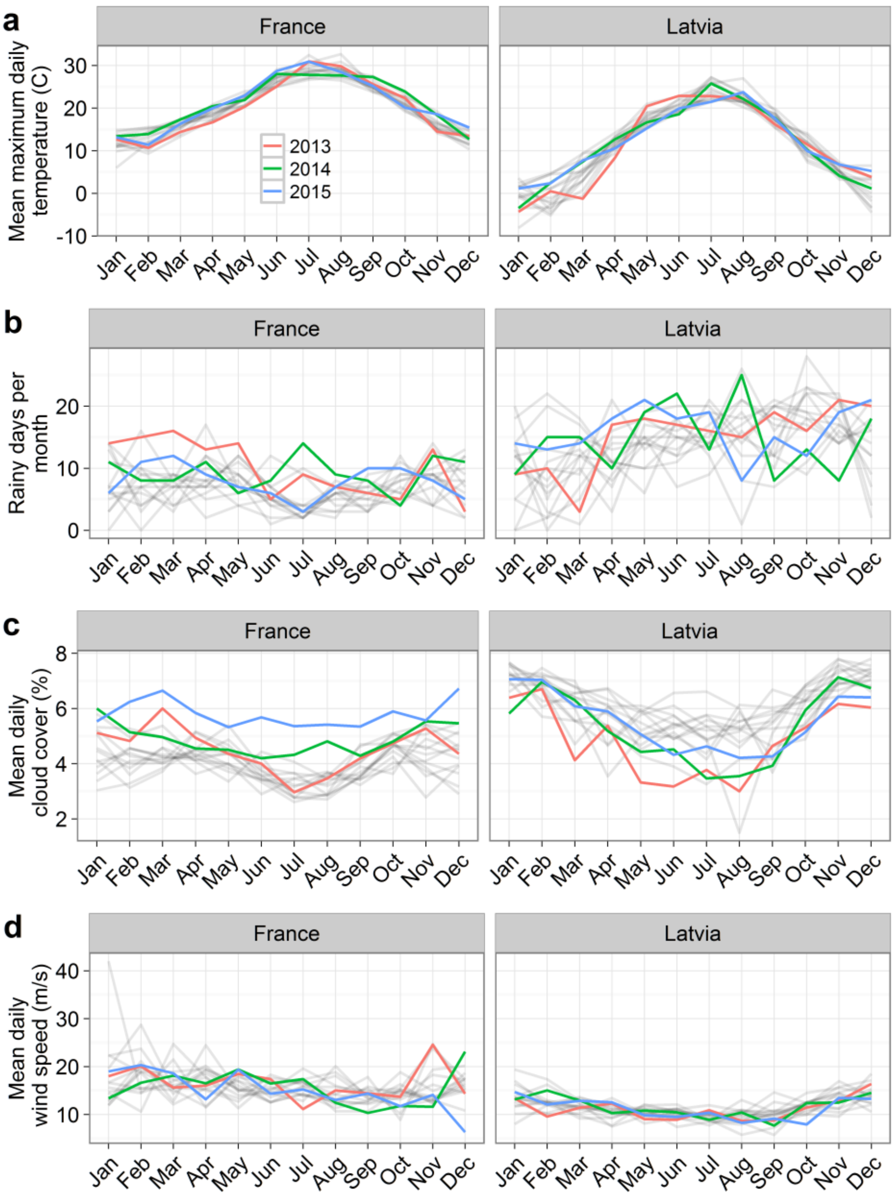


Figure 2.5 Inter- and intra-annual variation in **a** maximum daily temperature, **b**, number of rainy days per month, **c** mean cloud cover and **d** mean wind speed in France and Latvia, averaged across each month. Grey lines show data from 2000–2012, with 2013–2015 in red, green and blue. All weather data were downloaded from www.wunderground.com for the weather stations closest to the two field sites (Perpignan airport 42.74° N, 2.87° E and Rīga airport 56.92° N, 23.97° E).

2.2.3 Roller status

2.2.3.1 France

The French Roller population is likely to be increasing, with the three most recent estimates putting their numbers at 450–540 pairs in 1990 (Tucker *et al.* 1994), 520–620 in 2000 (Burfield & van Bommel 2004) and 800–1000 in 2007 (Tron *et al.* 2008). The breeding distribution is largely contiguous, following a broad arc along the

Mediterranean coast, from Pyrénées-Orientales in the south-west to Vars in the east, extending up the Rhône valley as far as Drôme (Mayet, Schwartz & Remy 2013).

Until the late 1990s the Pyrénées-Orientales supported only a small Roller population, despite apparently favourable habitat, presumably owing to a lack of suitable nesting cavities. The installation of approximately 150 nest-boxes from 1997 onwards by the Groupe Ornithologique du Roussillon preceded a substantial increase in the region's Roller population, which stood at 110–120 pairs in 2011 (Aleman & Laurens 2013). The area covered by the Plaine du Roussillon field site is described as one of the "bastions" of the department's Roller population, holding over 40 % of the known breeding pairs in 2011 (Aleman & Laurens 2013).

Although principally a nest-box-breeding population, Rollers also make use of existing natural cavities. The few trees (mostly black poplar *Populus nigran*) are restricted to the north of the site (principally planted as wind-breaks around orchards). Most cavities are old Iberian Green Woodpecker nests, though there are a handful of rotten holes suitable for Rollers. Use of other human structures for nesting was previously undocumented in this site (Aleman & Laurens 2013), though in 2015 two pairs were found breeding in farmsteads (one abandoned and one inhabited).

2.2.3.2 Latvia

In contrast to the apparently healthy state of the French population, Rollers in Latvia have declined drastically in range and abundance in recent decades, and are "one of the most rapidly disappearing species" in the country (Kerus & Račinskis 2008). This mirrors the decline observed in the other Baltic States; Rollers have not bred in Estonia since 2011 (Lüütsepp *et al.* 2011) and Lithuania now holds just a handful of breeding pairs (Laimonas Sniauksta, pers. comm.). In Latvia, Rollers were completely extirpated from the agricultural landscape sometime in the 2000s, with their distribution now restricted to the open forests around Garkalne municipality. This remnant population of approximately 10 breeding pairs increased in size following the provisioning of nest-boxes from 1999; the national population now fluctuates around 25 breeding pairs, including a handful in the satellite sites of Ādaži and Silakrogs (Edmunds Račinskis, pers. comm.). Aside from nest-boxes, Rollers make use of Black Woodpecker *Dryocopus martius* holes in Scot's Pine, and there are a handful of records of Rollers breeding in abandoned military buildings, though not during our study period.

My two principle study sites span the extremes of the Roller's existence in Europe. The apparently healthy French population is typical of many Mediterranean populations, whereas in Latvia, at the northern edge of the species' range, the study population is an isolated relict of the formerly abundant northern European population. Rollers at both sites rely on nest-boxes for breeding; the French population has increased following the installation of nest-boxes, and the Latvian population's extinction has probably been prevented (or at least delayed) thus. This makes the monitoring of breeding attempts – and, if necessary, the trapping of adults and nestlings – substantially easier. However, the use of artificial nest-boxes perhaps makes our study populations atypical compared to others in Europe (though nest-box schemes aimed at Rollers now exist across the continent) as well as the ancestral populations at our study sites. Additionally, the remnant Latvian population, having been extirpated from all farmland, now occupies a habitat – lowland heath – which was probably only of minor importance historically. Nonetheless, I expect the comparison to reveal important differences in the ecology of the two populations, which may help explain the species' decline and point to potential conservation solutions.

2.3 References

Aleman, Y. & Laurens, J. (2013) Répartition et effectifs du Rollier d'Europe (Coracias garrulus) dans les Pyrénées-Orientales en 2011. *La Mélano*, **13**, 1–11.

Avilés, J.M. & Costillo, E. (1998) Selection of breeding habitats by the Roller (Coracias garrulus) in farming areas of the southwestern Iberian peninsula. *Die Vogelwarte*, **39**, 242–247.

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*, **70**, 227–230.

Avilés, J.M. & Parejo, D. (2004) Farming practices and roller Coracias garrulus conservation in south-west Spain. *Bird Conservation International*, **14**, 173–181.

Avilés, J.M., Parejo, D. & Rodríguez, J. (2011) Parental favouritism strategies in the asynchronously hatching European Roller (Coracias garrulus). *Behavioral Ecology and Sociobiology*, **65**, 1549–1557.

Avilés, J.M. & Sanchez, J.M. (1999) Uncommon helper behaviour in the Roller Coracias garrulus. *Alauda*, **67**, 75.

Avilés, J.M., Sanchez, J.M., Sanchez, A. & Parejo, D. (1999) Breeding biology of the Roller Coracias garrulus in farming areas of the southwest Iberian Peninsula. *Bird Study*, **46**, 217–223.

Benton, T.G., Vickery, J.A. & Wilson, J.D. (2003) Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology and Evolution*, **18**, 182–188.

Birdlife International. (2015a) *European Red List of Birds*. Cambridge, UK.

Birdlife International. (2015b) *Coracias Garrulus. The IUCN Red List of Threatened Species 2015*. Cambridge, UK.

Bohus, M. (2002) On breeding biology of the Roller (Coracias garrulus) in the Komárno town surroundings (SW Slovakia, Danubian basin). *Sylvia*, **38**, 51–59.

Bohus, M. & Kristin, A. (2004) Food and foraging of the Roller (Coracias garrulus L., 1758) on the northern limit of its distribution area. *International Symposium on Ecology and Conservation of Steppe-land Birds*.

Bouvier, J.-C., Muller, I., Génard, M., Françoise, L. & Lavigne, C. (2014) Nest-Site and Landscape Characteristics Affect the Distribution of Breeding Pairs of European Rollers Coracias garullus in an Agricultural Area of Southeastern France. *Acta Ornithologica*, **49**, 23–32.

Burfield, I.J. & van Bommel, F.P.J. (2004) *Birds in Europe: Population Estimates, Trends and Conservation Status*. BirdLife International, Cambridge, UK.

Catry, I., Catry, T., Granadeiro, J.P., Franco, A.M.A. & Moreira, F. (2014) Unravelling migration routes and wintering grounds of European rollers using light-level geolocators. *Journal of Ornithology*, **155**, 1071–1075.

Catry, I., Silva, J.P., Cardoso, A., Martins, A., Delgado, A., Sanches, A.R., Santos, A., Estanque, B., Cruz, C.M., Pacheco, C., Leitao, D., Pereira, E., Matilde, E., Moital, F., Romba, F., Sequeira, N., Monteiro, P., Rocha, P., Correia, R., Alcazar, R., Congarato, 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.

Cramp, S. (1985) *The Birds of the Western Palearctic, Volume 4: Terns to Woodpeckers*. Oxford University Press, Oxford, UK.

Emmenegger, T., Mayet, P., Duriez, O. & Hahn, S. (2014) Directional shifts in migration pattern of rollers (Coracias garrulus) from a western European population. *Journal of Ornithology*, **155**, 427–433.

Folch, A., Kristin, A. & Manosa, S. (2004) Diet of European Roller (Coracias Garrulus) in northeastern Iberian Peninsula. *International Symposium on Ecology and Conservation of Steppe-land Birds*.

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**, 657–666.

Fry, K. & Fry, H. (1992) *Kingfishers, Bee-Eaters, & Rollers: A Handbook*. Princeton University Press.

Gibbons, P., Lindenmayer, D.B., Fischer, J., Manning, A.D., Weinberg, A., Seddon, J., Ryan, P. & Barrett, G. (2008) The Future of Scattered Trees in Agricultural Landscapes. *Conservation Biology*,

22, 1309–1319.

Hagemeijer, E.J.M. & Blair, M.J. (1997) *The EBCC Atlas of European Breeding Birds: Their Distribution and Abundance*. T & A.D. Poyser, London.

Huntley, B., Green, R.E., Collingham, Y.C. & Willis, S.G. (2007) *A Climatic Atlas of European Breeding Birds*. Lynx Edicions.

Kerus, V. & Račinskis, E. (2008) The second Latvian Breeding Bird Atlas 2000–2004: preliminary results. *Revista Catalana d'Ornitologia*, **24**, 100–106.

Kiss, O., Elek, Z. & Moskát, C. (2014) High breeding performance of European Rollers Coracias garrulus in heterogeneous farmland habitat in southern Hungary. *Bird Study*, **61**, 496–505.

Kovacs, A., Barov, B., Orhun, C. & Gallo-Orsi, U. (2008) *International Species Action Plan for the European Roller Coracius Garrulus Garrulus*. Besenyőtelek, Hungary.

Lüütsepp, G., Kalamees, A. & Lüütsepp, O. (2011) European Roller Coracias garrulus in Estonia 2000-2011. *Hirundo*, **24**, 61–72.

Mayet, P., Schwartz, T. & Remy, B. (2013) *Synthese Nationale Des Observations de Rollier d'Europe*.

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

Parejo, D., Avilés, J.M. & Expósito, M. (2015) Hatching Asynchrony and Spring Climatic Conditions in the European Roller. *Evolutionary Biology*, **42**, 443–451.

Parejo, D., Avilés, J.M. & Rodriguez, J. (2012) Supplemental food affects egg size but not hatching asynchrony in rollers. *Behavioral Ecology and Sociobiology*, **66**, 1097–1105.

Parejo, D., Danchin, É. & Avilés, J.M. (2005) The heterospecific habitat copying hypothesis: can competitors indicate habitat quality? *Behavioral Ecology*, **16**, 96–105.

Parejo, D., Silva, N. & Avilés, J.M. (2007) Within-brood size differences affect innate and acquired immunity in roller Coracias garrulus nestlings. *Journal of Avian Biology*, **38**, 717–725.

Pulido, F.J., Dõ, M. & Hidalgo de Trucios, S.J. (2001) Size structure and regeneration of Spanish holm oak Quercus ilex forests and dehesas: effects of agroforestry use on their long-term sustainability. *Forest Ecology and Management*, **146**, 1–13.

Rodriguez, J., Avilés, J.M. & Parejo, D. (2011) The value of nestboxes in the conservation of Eurasian Rollers Coracias garrulus in southern Spain. *Ibis*, **153**, 735–745.

Rodríguez-Ruiz, J., de la Puente, J., Parejo, D., Valera, F., Calero-Torralbo, M.Á., Reyes-González, J.M., Zajková, Z., Bermejo, A. & Avilés, J.M. (2015) Disentangling migratory routes and wintering grounds of Iberian near-threatened European rollers Coracias garrulus. *PLoS One*, **9**, e115615.

Sackl, P., Tiefenbach, M., Ilzer, W., Pfeiler, J. & Wieser, B. (2004) Monitoring the Austrian relict population of European Roller Coracias garrulus – a review of preliminary data and conservation implications. *Acrocephalus*, **25**, 51–57.

Samwald, V.O. & Samwald, F. (1989) Die Blauracke (Coracias g. garrulus) in der Steiermark - Bestandsentwicklung, Phänologie, Brutbiologie, Gefährdung. *Egretta*, **32**, 37–57.

Sánchez-Tójar, A., Parejo, D., Martínez, J.G., Rodríguezruiz, J. & Avilés, J.M. (2015) Parentage Analyses Reveal Hidden Breeding Strategies of European Rollers Coracias garrulus. *Acta Ornithologica*, **50**, 252–258.

Silva, N., Avilés, J.M., Danchin, É. & Parejo, D. (2008) Informative content of multiple plumage-coloured traits in female and male European Rollers. *Behavioural Ecology and Sociobiology*, **62**, 1969–1979.

Sosnowski, J. & Chmielewski, S. (1996) Breeding biology of the Roller Coracias garrulus in Puszcza Pilicka Forest (Central Poland). *Acta Ornithologica* , **31**, 119–131.

Tiefenbach, M. (2009) *Habitat Selection in Foraging European Rollers (Coracias Garrulus L.) in Eastern Austria*. MSc Thesis, University of Vienna.

Tron, F., Zenasni, A., Bousquet, G., Cramm, P. & Besnard, A. (2008) Réévaluation du statut du Rollier d’Europe Coracias garrulus en France. *Ornithos*, **15**, 84–89.

Tucker, G.M., Heath, M.F., Tomialojc, L. & Grimmett, R.F.A. (1994) *Birds in Europe: Their Conservation Status*. BirdLife International, Cambridge, UK.

Vaclav, R., Valera, F. & Martinez, T. (2011) Social information in nest colonisation and occupancy in a long-lived, solitary breeding bird. *Oecologia*, **165**, 617–627.

Chapter 3: Intra-specific variation in the breeding ecology of the European Roller

3.1 Abstract

Understanding the relative importance of food and nest-site limitation is important for effectively directing conservation efforts to bolster the breeding density of declining populations. Both food and nest-site limitation have been suggested as being responsible for the decline of the European Roller, but intra-specific variation in the importance of these two factors has not been formally tested. Here we compare the breeding ecology of two Roller populations – one in Latvia and one in France – to test the relative importance of food and nest-site limitation. In France – part of the core Mediterranean population – nest-box occupation is high, and we found no evidence of nest-box selection based on surrounding foraging resource availability. Furthermore, Roller breeding density increased linearly with nest-box density (but not food availability), strongly indicating nest-site limitation. In contrast, the Latvian population – at the northern range margin – had lower nest-box occupation, and showed a preference for nest-boxes in areas of higher foraging resource availability. As such, breeding density increased with food availability (but was unrelated to nest-box density), strongly indicating food limitation. We did not detect any effects of resource availability on any measure of breeding success. Overall, both resource availability and clutch size (and therefore breeding productivity) were lower and exhibited more inter-annual variation in Latvia than France. These findings provide evidence that the factors limiting breeding density vary across the Roller's range, and point towards different priorities for Roller conservation. Our results also highlight the potential vulnerability of the Latvian population to environmental change.

Supporting material can be found in ***Appendix 1****.*

3.2 Introduction

Most conservation efforts are targeted at maintaining or increasing the breeding density of threatened species. A key pre-requisite for the effective delivery of conservation management is an understanding of the factors limiting breeding density (i.e. setting the carrying capacity of a habitat). During the breeding season, bird population density at any instance will generally be limited by the availability of one of two key functional resources – nesting and foraging habitat (Newton 1998).

Evidence for food limitation comes from correlations between food availability and breeding population density in both space (Watson, Rae & Stillman 2016) and time (Karell *et al.* 2009). Experimental food supplementation studies have demonstrated a positive effect of food availability on nest-level breeding success (Wellicome *et al.* 2013; Ruffino *et al.* 2014), though this will only influence population density if breeding success (as opposed to overwinter survival, which we do not consider here) is the limiting demographic factor. Alternatively, breeding density might be limited by the availability of opportunities for nesting, especially for obligate secondary cavity nesters which rely on the pre-existence of suitable hollows for breeding (Newton 1994). As for food limitation, correlational and experimental studies have demonstrated nest-site limitation in wild populations (Fargallo *et al.* 2001; Cockle, Martin & Drever 2010).

Both food (Thorup *et al.* 2010; Aebischer & Ewald 2012) and cavity limitation (Franco, Marques & Sutherland 2005) have been implicated in recent bird population declines, and efforts to augment the availability of these resources – through the provisioning of artificial nest-boxes (Rodriguez, Avilés & Parejo 2011) or foraging habitat (Ewald *et al.* 2010) – form a key part of many conservation interventions. Understanding which resource is limiting is crucial for successfully directing conservation efforts. For example, restoration of foraging habitat makes little sense if the breeding density of a population is limited by cavity availability (though degradation of foraging habitat would likely shift the balance away from nest-site limitation). Notably, the relative importance of food and nest-site limitation can vary over time; nest-box provisioning can only increase breeding density up to a carrying capacity determined by foraging resource availability (Newton 1998).

Nest-site limitation and foraging habitat limitation have both been blamed for the decline of the European Roller (Kovacs *et al.* 2008, discussed in **Chapter 2**). The relative success of many nest-box schemes suggests that nest-site limitation is important (Vaclav, Valera & Martinez 2011; Aleman & Laurens 2013), whilst the apparent failure of others (Lüütsepp, Kalamees & Lüütsepp 2011) suggests that food limitation operates elsewhere.

Here, we compare two populations of breeding Rollers – one at the northern range edge in Latvia, and one in the core of the species' Mediterranean stronghold – in order to explore the relative importance of food and nest-site limitation. We first quantify variation in resource availability within and between sites. Dividing each site into a 1 km^2 grid, we then test whether Roller breeding density is best predicted by nest-site availability or resource availability. We go on to test whether Rollers select nest-boxes based on surrounding resource availability, and whether this influences breeding success (controlling for nearest neighbour distance and inter-annual effects, as well as nest-box condition in France). By comparing the breeding ecology of these two distant populations, we contribute to an understanding of their differing population trends.

3.3 Methods

3.3.1 Land-use mapping

Details of our two study sites – one in France and one in Latvia – are outlined in **Chapter 2**. The boundary of each site was defined by a 1 km radius buffer around each nest-box. All land parcels within this buffer were manually digitised in Quantum GIS (QGIS Development Team 2009) with reference to aerial photography and field visits, and identified in the field using the definitions in **Appendix 1** (**Tables S1.1** and **S1.2**). Land-use polygons were then converted to a 5×5 m raster (UTM projection) in R (R Development Core Team 2014).

Land-use mapping was conducted for every year of the study in France, and 2014 only in Latvia. The landscape of the Latvian field site is relatively static, with the only major inter-annual changes arising through forestry activity. Whilst it’s probable that a few clear-cuts identified in 2014 were actually forested in 2013, and that forests identified in 2014 had been harvested by 2015, clear-cuts only made up 5 % of the study area. Of this area, only a fifth was classified as ‘fresh’ (felled within 1–2 years, with saplings below knee height) in 2014, suggesting that forestry activity affects < 1 % of the total site area from year to year. All other habitats are likely to have remained stable during the three-year study period.

3.3.2 Invertebrate availability

3.3.2.1 Transect design

To quantify spatio-temporal variation in foraging resource availability, we conducted visual transects – in an attempt to mimic the hunting mode of the Roller – in each of the main land-use types in France and Latvia (**Table S1.3**). We focused on large (> 10 mm) terrestrial insects in orders Coleoptera (beetles), Orthoptera (grasshoppers and bush-crickets), Hemiptera (true bugs, principally cicadas) and Mantoidea (mantises), which make up the majority of the Roller's diet (Cramp 1985; Sosnowski & Chmielewski 1996; Avilés & Parejo 2002). Each 40 m transect was repeated once every 2 weeks throughout the season in Latvia (2014) and France (2015; **Table S1.3**). Surveyed land-use parcels were randomly selected and stratified according to the approximate proportional cover of each land-use type, and transects started at a random distance along a randomly selected parcel edge. Transects were walked perpendicular to the parcel edge at a constant slow pace of approximately 0.3 m s^{-1}, and a 1.5 m wide strip (total area = 60 m^2) was surveyed for potential Roller prey. Invertebrates were identified (generally to family, but sometimes to order or genus) and classed into 10 mm size bins. The same methodology, but over a slightly different time window and with different observers, was followed in France in 2013 and 2014, with qualitatively similar results (see **Section 3.4.1**).

3.3.2.2 Biomass estimates

To convert counts of invertebrates into biomass estimates, specimens (n = 159) belonging to each insect taxon and covering a range of body lengths were collected in the field in Latvia (2014) and France (2014 and 2015). Specimens were measured from head to tip of abdomen, then oven dried for 14 days at 60 ˚C. Dried insects were weighed, incinerated in a muffle furnace for 3 hours at 500 ˚C, then re-weighed. Ash-free dry weight (i.e. biomass) was calculated by subtracting the mass of the remaining ash from the initial (dry) mass. Specimen biomass was then modelled against body length (log-log linear regression) and taxon (a fixed factor; **Fig. S1.1**). From this model (R^2_{adj} = 0.98), biomass was predicted for the midpoint of each 10 mm size class for each taxon (**Table S1.4**). These predictions were then used to estimate the total biomass recorded on each transect, given the size class and taxon of each recorded invertebrate.

3.3.2.3 Statistical analysis

To model the variation in biomass recorded on each transect, we used a two-part hurdle model. The first model predicted the probability of recording an insect during a transect (using a GLMM with binomial error structure and logit link; 'binomial model'), and the second model predicted the biomass of recorded insects given that one or more had been recorded during a transect (GLMM with gamma error structure and log link; 'gamma model').

Binomial and gamma models were fitted using the R package *lme4* and the bobyqa optimizer (Bates *et al.* 2015), with a random intercept of transect identity to account for the pseudo-replication arising from repeating the transects through the season. We first modelled the fixed effect of land-use type, then included calendar date and its quadratic effect (both scaled and centered) to explore seasonal variations in prey biomass. In France we also included the interaction between land-use and calendar date. However, due to low invertebrate numbers recorded in Latvia, the interaction models were over-parameterised and failed to converge. Candidate models using all combinations of predictor variables were assessed using the R package *MuMIn* (Barton 2015), and predictions were model-averaged over the set of models with ΔAICc < 2 using the 'full' method in which absent variables are set to zero rather than excluded. By multiplying the predictions of the binomial and gamma models (i.e. weighting predicted biomass by the probability of observing an insect), we thus obtained predictions of insect biomass in each land-use type at a given time point over the course of the season.

Biomass predictions were then mapped onto a 5×5 m raster according to land-use cover. Surveyed land-use types covered, on average, 83 % and 76 % of land within a 250 m radius of each nest in France and Latvia, respectively. For the rarer land-use categories in which insect surveys were not conducted, we assigned insect biomass as denoted in **Tables S1.1** and **S1.2**. For each site and year, we produced rasters of predicted prey biomass at each seven-day interval starting 23 May and ending 1 Aug.

3.3.3 Foraging range size

Little published information exists on the foraging range size of the Roller. To quantify the size of the foraging range of breeding Rollers, and thus the area over which to quantify resource availability for each nest, we used radio telemetry. Breeding adult Rollers were trapped (under license) in Latvia (2014) and France (2015) at the nest just before or soon after hatching. Tags (Biotrack PIP3 Ag393, 150–151 MHz, 30 ms pulse length, 60 pulses min^{-1}) were fixed to the shaft of the central tail feather with cotton ties and cyanoacrylate glue.

Tagged birds were triangulated by two observers in radio contact, each equipped with a Sika receiver and Lintec flexible 3-element antennae (Biotrack). Subsequent fixes of the same individual were separated by at least 1 hour and, where possible, visual confirmation of locations was acquired. Non-visually-confirmed locations were inferred using the *geosphere* R package (Hijmans 2015), by intersecting the bearings from the location of each observer. Experiments with tags in known locations revealed a maximum detection distance of ~ 1 km; intersections more than 1 km from an observer were therefore discarded as unrealistic.

In order to trade-off number of individuals *vs.* number of fixes per individual, we excluded birds with fewer than 10 fixes; there was no correlation between number of fixes per individual and any metric of home range (see **Section 3.4.2**). Because we were principally interested in the foraging range of breeding Rollers, we also excluded positions recorded after breeding attempts had finished or failed. As measures of core and maximum foraging range we then calculated, for each individual, the area of the 50 % and 95 % density kernels, as well as the 50th and 95th percentiles of distance from fix to nest.

3.3.4 Nest monitoring

Potential Roller nest holes (both artificial nest-boxes and tree / building cavities) were monitored throughout the 2013–15 breeding seasons in France and Latvia. Nest contents were recorded either directly or with an inspection camera (Ridgid CA-100 with 360 cm extension) attached to a telescopic pole.

Due to logistical constraints and personnel availability, the frequency and extent of nest monitoring varied between years and sites (**Table S1.5**). In particular, the infrequency of nest controls in Latvia in 2015 likely resulted in many ‘competitor’ breeding attempts going undetected (most non-target breeders in Latvia are small passerines with short nesting periods), and the number of empty nests being overestimated. Additionally, monitoring started relatively late in Latvia in 2015 (so early failed breeders may have been missed) and finished relatively early in France in 2014 (so late breeders may have been missed).

Nest holes were categorised as Roller nests (Roller eggs or nestlings observed during a season), empty nests (no eggs or nestlings of any species observed during a season) or competitor nests (eggs or nestlings of other bird species observed during a season). If occupied by more than one species during the course of the season, a hole can be a competitor nest and a Roller nest (in that order, without exception), but never a Roller nest and an empty nest.

3.3.4.1 Breeding density

In order to explicitly explore the relative importance of nest-site and food availability in predicting breeding density we divided each site into a regular 1000 m grid (following UTM gridlines), and in each square calculated (1) the number of nest-boxes, as a measure of nest-site availability, (2) the average mid-season prey biomass, as a measure of resource availability and (3) the number of Roller breeding attempts in nest-boxes, as a measure of breeding density. In France there were 12 squares containing nest-boxes in 2013 and 2014 and 13 squares in 2015, and in Latvia there were 24 squares in all years; squares without nest-boxes were ignored.

Linear mixed models with Roller nest density as the dependent variable and nest-box density or prey biomass as the independent variable were constructed separately for each site. Data were pooled across years, so we included year (a three-level factor) as a random intercept.

3.3.4.2 Nest-box occupation

Next, we tested for predictors of Roller nest-site occupation. Due to variation in search effort for (and the general rarity of) nests in natural cavities, we modelled the occupation probability of nest-boxes only. Nest-boxes which were empty but checked only once during a season were excluded from the analysis.

To test the hypothesis that Roller nest-box use is related to surrounding foraging resource availability, we extracted predicted prey biomass averaged over all 5×5 m cells within a 250 m buffer around each nest-box (corresponding to the estimated core foraging range; see **Section 3.4.2**) for the 7-day periods starting May 23 and June 27 (corresponding to the start of the laying and chick-rearing periods, approximately). We also calculated the distance to the next-nearest known Roller nest (including those in natural cavities). Additionally, to test whether Rollers avoid the ~ 12 % of French nest-boxes with missing lids, we generated a two-level factor describing whether the lid was present (1) or absent (0).

We employed two modelling frameworks. The first approach (‘Roller–other’) compared nest-boxes occupied by Rollers (including boxes which housed a competitor then a Roller) with those not occupied by Roller, supposing that all nest-boxes are ‘available’ to Rollers, and ignoring the presence or absence of any competitor species. The second approach (‘Roller–empty’) compared nest-boxes occupied by Rollers (including boxes which housed a competitor then a Roller) with those remaining empty, excluding competitor-only nests and supposing that only empty nest-boxes are available to Rollers.

We constructed two global GLMMs each for France and Latvia (one for Roller–other and one for Roller–empty), with a binomial error structure and logit link. Independent variables were laying and chick-rearing prey biomass, distance to nearest neighbour, and (in France only) lid presence / absence. In Latvia, due to strong correlations between laying and chick-rearing prey biomass ($r > 0.99$, $p < 0.001$), we only considered the latter. A random intercept of nest-box identity was included to account for the fact that the same nest-boxes were used in multiple years. Continuous variables were scaled and centered. Candidate models using all combinations of predictor variables were assessed using the R package *MuMIn* (Barton 2015), and predictions were model-averaged over the set of models with ΔAICc < 2.

3.3.4.3 Breeding success

For all roller nests we recorded parameters relating to the circumstances, timing and success of breeding (**Table S1.6**). Differences in these parameters (clutch size, number of hatchlings, egg survival, chick survival and fledglings per breeding attempt) between France and Latvia were tested using Welch's *t*-tests.

Finally, we tested whether Roller breeding success (clutch size, egg survival and chick survival) varied according to surrounding foraging resource availability. Variations in clutch size (complete clutches only, continuous variable), hatching rate (proportion of hatchlings per egg, binomial error structure with logit link) and fledging rate (proportion of fledglings per hatchling, binomial error structure with logit link) were modelled separately for France and Latvia. Data from nest-boxes and natural cavities were combined over 2013–15, with year included as a fixed effect and nest identity as a random intercept. The main predictor variable of interest was, as above, predicted prey biomass in a 250 m buffer around each nest. The timing of each breeding attempt was known, so we extracted prey biomass for the nest-specific weeks of laying and, 35 days later, chick-rearing. As above, only chick-rearing prey biomass was included in the Latvian models, due to strong correlation with laying prey biomass ($r > 0.99$, $p < 0.001$). We also included distance to next nearest known Roller nests, again for the nest-specific weeks of laying and chick-rearing. Finally, we fitted lay date and its interaction with year (a three-level fixed factor). Continuous variables were scaled and centered, and observations were weighted according to lay date uncertainty, whereby nests with more than 10 days between minimum and maximum lay date (see **Table S1.6**) were down-weighted by a factor of 0.5. Candidate models using all combinations of predictor variables were assessed using the *MuMIn* R package, and predictions were model-averaged across the set of models with ΔAICc < 2.

3.4 Results and Discussion

3.4.1 Resource availability

The Roller is typically a sit-and-wait, ‘pounce’ hunter, and our visual surveys provided an effective way of quantifying variation in the availability of the large terrestrial invertebrates on which they prey (**Fig. 3.1**). The differences in biomass between France, (mean biomass per transect = 0.25 g) and Latvia (mean = 0.05 g) indicated a fundamental difference in resource availability between the two sites, consistent with global patterns of reduced productivity towards the poles (Gillman *et al.* 2015),.

There were also substantial variations in foraging resource availability within each site. In France there was overwhelming support for the fixed effect of land-use on both the probability of observing an invertebrate and the biomass of observed invertebrates (**Table S1.7**). Predicted biomass was more than double in hay meadow (0.31 g per transect) and fallow (0.41 g) compared to orchard (0.13 g) and vine (0.14 g; **Fig. 3.1c**). The latter two land-uses are treated with pesticides, and the uncultivated rows between crops are, in most fields, ploughed and mown throughout the season in order to control weeds. Meadows, on the other hand, appear largely unimproved and fallow, entirely unmanaged, approaches a semi-natural habitat. Our findings are therefore in line with a large body of literature demonstrating the negative impact of intensive agriculture on invertebrate abundance (Britschgi, Spaar & Arlettaz 2006; Hart *et al.* 2006; Schekkerman & Beintema 2007; Attwood *et al.* 2008; Golawski & Meissner 2008).

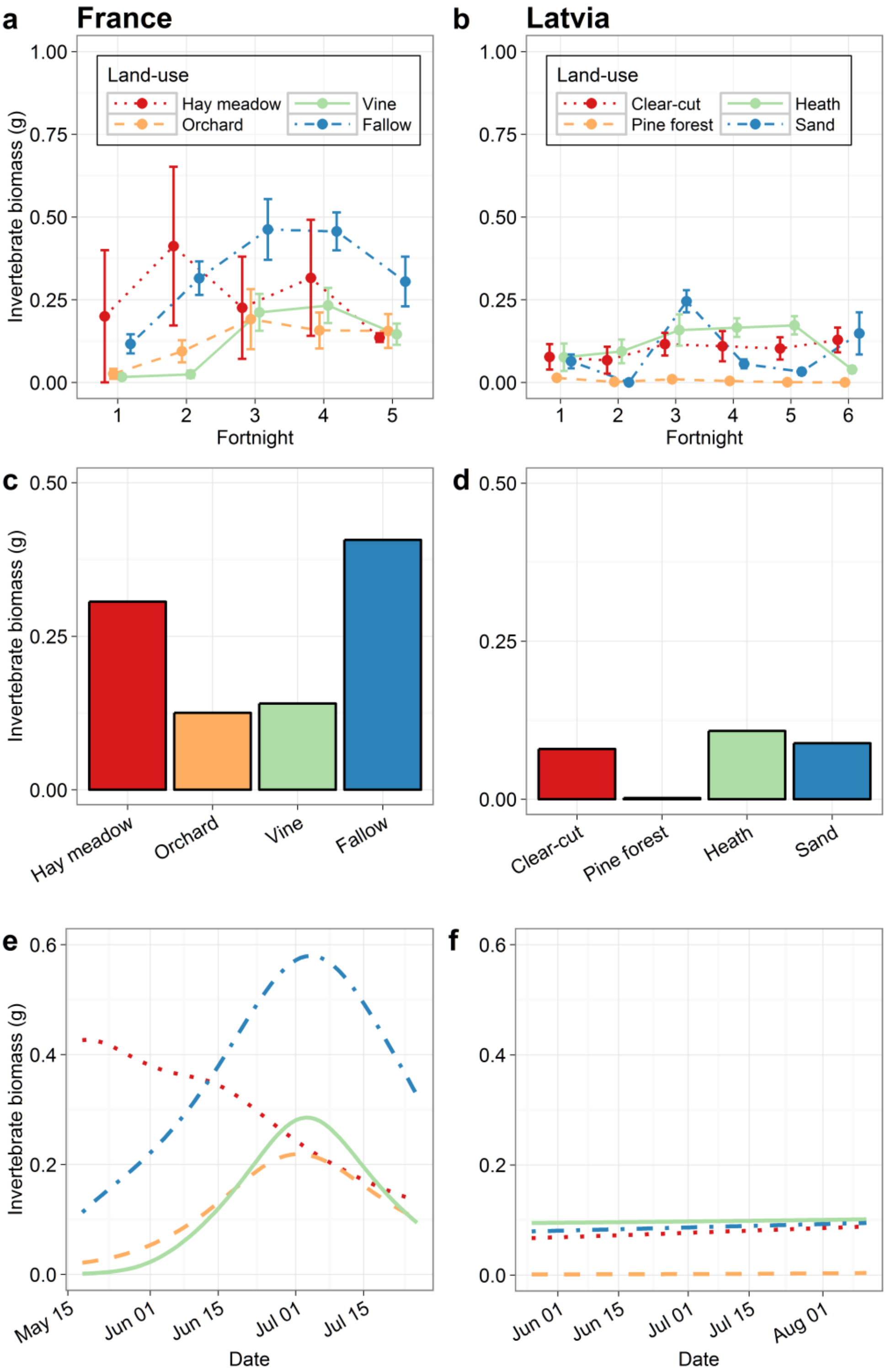


Figure 3.1 Invertebrate biomass for the four main land-use types in France (2015) and Latvia (2014). **a** and **b** show mean ± S.E. insect biomass for each 2-week survey period. Bars in **c** and **d** are the product of the predicted values from the land-use binomial (modelling the probability of observing an invertebrate) and gamma models (modelling the biomass of observed invertebrates; see text for full description). Lines in **e** and **f** are the product of the model-averaged predicted values for the seasonal binomial and gamma models.

In Latvia, whilst there was strong support for the effect of land-use on the probability of observing an invertebrate, the intercept-only model was best (i.e. lowest AICc, highest information content) at predicting the biomass of observed invertebrates (**Table S1.8**). So, after weighting by the probability of observing an invertebrate, predicted biomass was substantially higher in open (insolated) habitats – clear-cut (0.08 g), heath (0.11 g) and sand (0.09 g) – compared to pine forest (0.002 g). However, even the best Latvian land-uses were worse than the poorest French land-uses (**Fig. 3.1d**).

In France (**Table S1.9**), but not Latvia (**Table S1.10**), there was strong support for the inclusion of the quadratic effect of calendar date and its interaction with land-use. For fallow, orchard and vine, biomass peaked around early July, followed by a decline, presumably driven by the increasingly arid conditions (**Fig. 3.1e**). In contrast, biomass in hay meadow declined after mowing in early June.

Orthoptera were the most abundant taxon in both France (68 % of biomass) and Latvia (71 %), so the patterns in overall invertebrate biomass were largely driven by changes in numbers of Orthoptera (**Fig. 3.2a**, **Fig. 3.2b**). In France, the next most important taxon was Cicadidae (28 % of biomass), which emerge *en masse* in late June. Adult cicadas primarily feed on woody vegetation, so, unlike Orthoptera, were more abundant in vineyard than fallow (**Fig. 3.2c**). In Latvia, Coleoptera (28 %) were the next most important taxon after Orthoptera, reaching their highest abundance in sand, where their abundance fluctuated throughout the season (**Fig. 3.2d**).

Although our surveys focused on terrestrial invertebrates living on low-lying vegetation, Rollers are also capable of taking prey in flight or gleaning them from taller vegetation. Our surveys are likely to have underestimated the biomass of these prey sources. In France, though cicadas made up over a quarter of recorded biomass, we probably underestimated their availability by missing insects in trees and tall hedges, as well as those in flight. In Latvia, beetles – especially Scarabidae, Geotrupidae and Cerambycidae – were recorded surprisingly rarely, given their importance in the diet of northerly forest-edge Roller populations (Sosnowski & Chmielewski 1996; Lüütsepp *et al.* 2011). These taxa tended to be aggregated around their food sources (e.g. dung, flowers, wood piles), so were encountered stochastically and infrequently during our transects. It is unclear how much this bias will affect our interpretations – we have no data on the importance of non-terrestrial prey in Roller diet, though casual observations suggest that the majority of prey are captured at ground level. Besides, we suspect that land-uses which support a high density of terrestrial invertebrates will probably support more actively flying ones too.

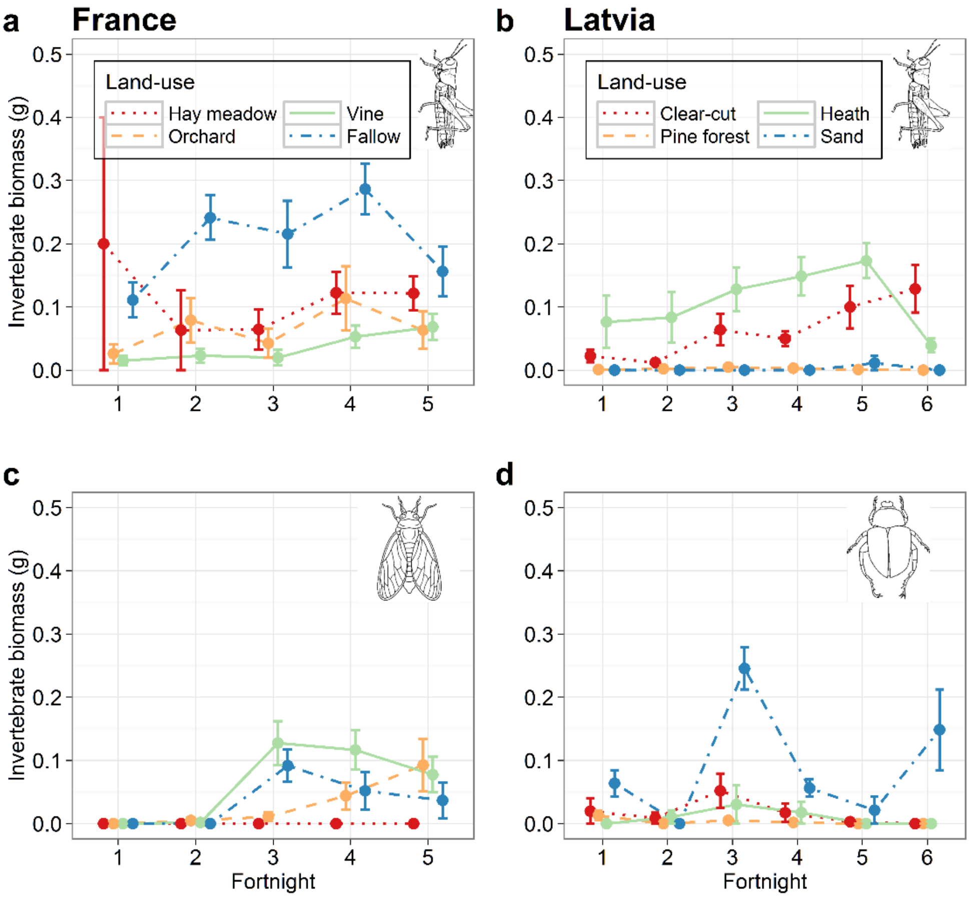


Figure 3.2 Mean ± S.E. invertebrate biomass for each 2-week period, broken down by major insect taxa in France (**a** = Orthoptera, **c** = Cicadidae) and Latvia (**b** = Orthoptera, **d** = Coleoptera).

In France, in addition to the main survey in 2015, we conducted invertebrate surveys in 2013 and 2014. Whilst observer differences probably contribute to differences in absolute biomass, relative differences between land-use types are generally consistent (**Fig. 3.3**). Fallow and hay meadow are reliably the most productive land-uses, with vine and orchard (the latter was not surveyed in 2013) having lower biomass. The high invertebrate biomass recorded in hay meadow in 2014 can probably be attributed to the comparatively earlier survey period (which perhaps underestimated the seasonal decline), and the high biomass in vine in 2013 is probably due to the comparatively late survey period (which underestimated the seasonal increase).

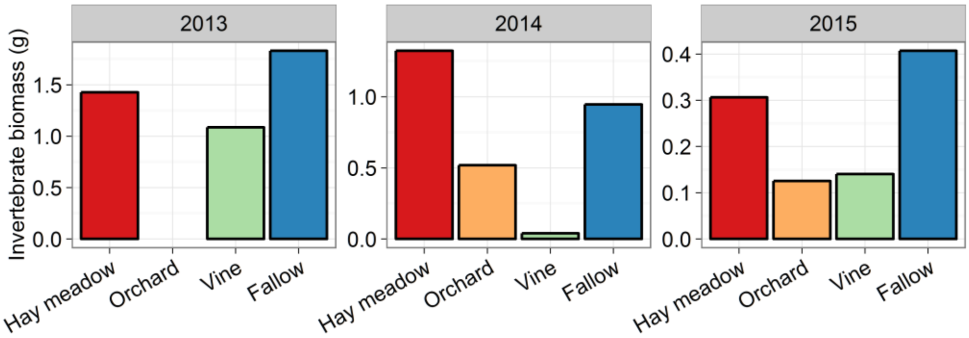


Figure 3.3 Comparison of invertebrate transect results 2013–15 in France. Bars are the product of the predicted values from the year-specific land-use-only binomial and gamma models. Note that, whilst surveys covered the whole season in 2015, they started comparatively late (and excluded orchard) in 2013 and finished comparatively early in 2014. *y*-axis scales are not equal, reflecting potential observer differences with respect to absolute biomass.

3.4.2 Home range size

Due to high rates of breeding failure (but low tag loss) in Latvia and high rates of tag loss (but low breeding failure) in France, only seven tagged breeding birds were tracked for long enough to acquire 10 fixes (**Table 3.1**). Across these seven individuals, all measures of home range correlated with one another ($r > 0.77$, $p < 0.05$), but not with either number of fixes ($r < 0.17$, $p > 0.10$) or duration of tracking ($r < 0.59$, $p > 0.10$).

Table 3.1 Summary of foraging home range metrics for 7 radio-tracked Rollers.

Site	**Kernel area (km^2)**		**Distance from nest (m)**		***n* fixes**	**Duration of tracking (days)**
	50 %	**95 %**	**50 %**	**95 %**		
France	0.11	0.70	51	647	10	6
	0.36	1.89	256	1061	22	7
	0.20	0.92	189	632	18	7
	0.12	0.63	146	509	26	14
	0.10	0.51	163	426	34	15
Latvia	0.54	3.31	480	1144	14	17
	0.13	1.09	294	764	89	17
mean =	**0.22**	**1.29**	**226**	**740**	**30**	**12**

Home ranges were generally centered on the nest-site, and often overlapping (**Fig 3.4**). Mean 50 % and 95 % kernel areas were 0.22 and 1.29 km^2 (corresponding to circles with 265 and 641 m radii), and mean 50th and 95th percentiles of distance from the nest were 226 and 740 m. From our limited data, we thus assume a core (50 %) foraging range of 250 m and a maximum (95 %) range of 750 m.

Based on direct observations, mean foraging radius has been estimated at 165 m in Spain (Avilés & Costillo 1998) and 356 m in France (Bouvier *et al.* 2014), and maximum foraging range at 1800 m in Slovakia (Bohus 2002) and 2300 m in Poland (Sosnowski & Chmielewski 1996). Although not directly comparable with our telemetry results, these estimates are at least of the right order of magnitude. Regardless, the precise value chosen for the core foraging radius matters little; across nests, predicted prey biomass in a 250 m and 750 m radius correlates strongly ($r = 0.76$, $d.f. = 226$, $p < 0.001$ for France; $r = 0.82$, $d.f. = 290$, $p < 0.001$ for Latvia).

With only two individuals successfully tracked in Latvia, we refrain from making a quantitative comparison of foraging home range between the two countries. However, we note that for all but one of the range size metrics, only one French Roller had a larger home range than either of the two Latvian Rollers.

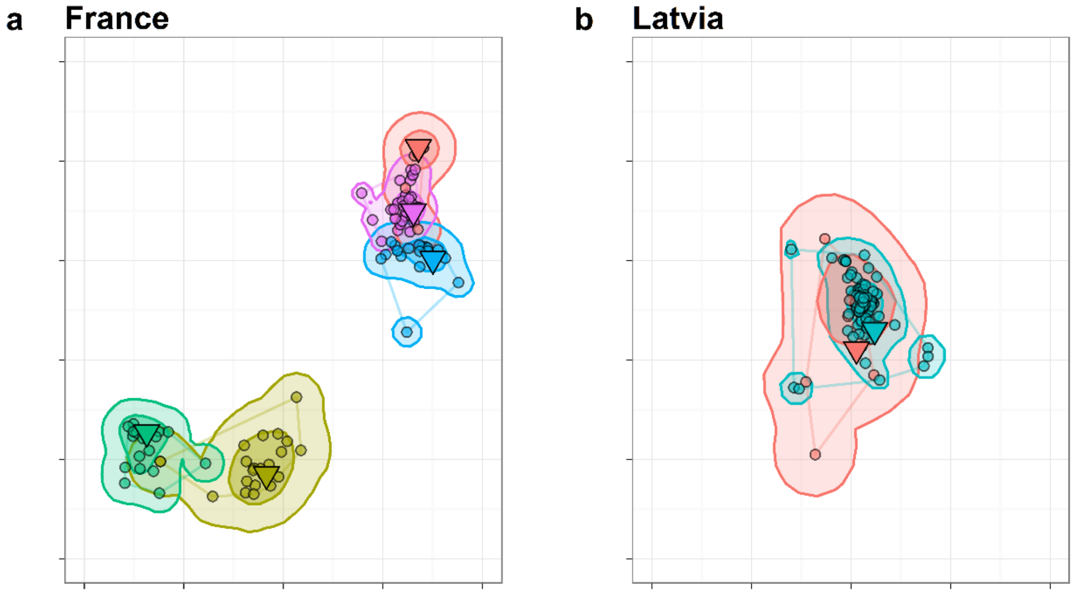


Figure 3.4 Foraging home range in **a** France and **b** Latvia. Points show individual fixes, bounded by minimum convex polygons (lines). Shaded regions denote 50 % and 95 % density kernels, and filled triangles are nest-sites. Axis tick marks are spaced 1 km apart, and the scale is equal in both panels.

3.4.3 Breeding density

Mean (± S.E.) nest-box density was higher in France (5.4 ± 0.66 boxes per km^2, range = 1–17) than Latvia (4.0 ± 0.38, 1–15), though this difference was not significant (t = 1.77, *d.f.* = 60.4, p = 0.08). Roller density, however, was substantially and significantly higher in France (2.2 ± 0.43, 0–11) than in Latvia (0.5 ± 0.09, 0–3; t = 3.9, *d.f.* = 39.6, p < 0.001).

At the 1 km^2 scale, there was a strong positive effect of nest-box density on Roller density in France ($F_{1,\,33.0}$ = 250.4, p < 0.001; **Fig 3.5a**), but not in Latvia ($F_{1,\,70}$ = 1.0, p = 0.33; **Fig 3.5b**). In contrast, there was no relationship between prey biomass and Roller density in France ($F_{1,\,19.0}$ = 0.3, p = 0.56; **Fig 3.5c**), but a significant positive relationship in Latvia ($F_{1,\,70}$ = 38.8, p < 0.001; **Fig 3.5d**). This provides convincing evidence that Rollers are nest-site limited in France but food limited in Latvia.

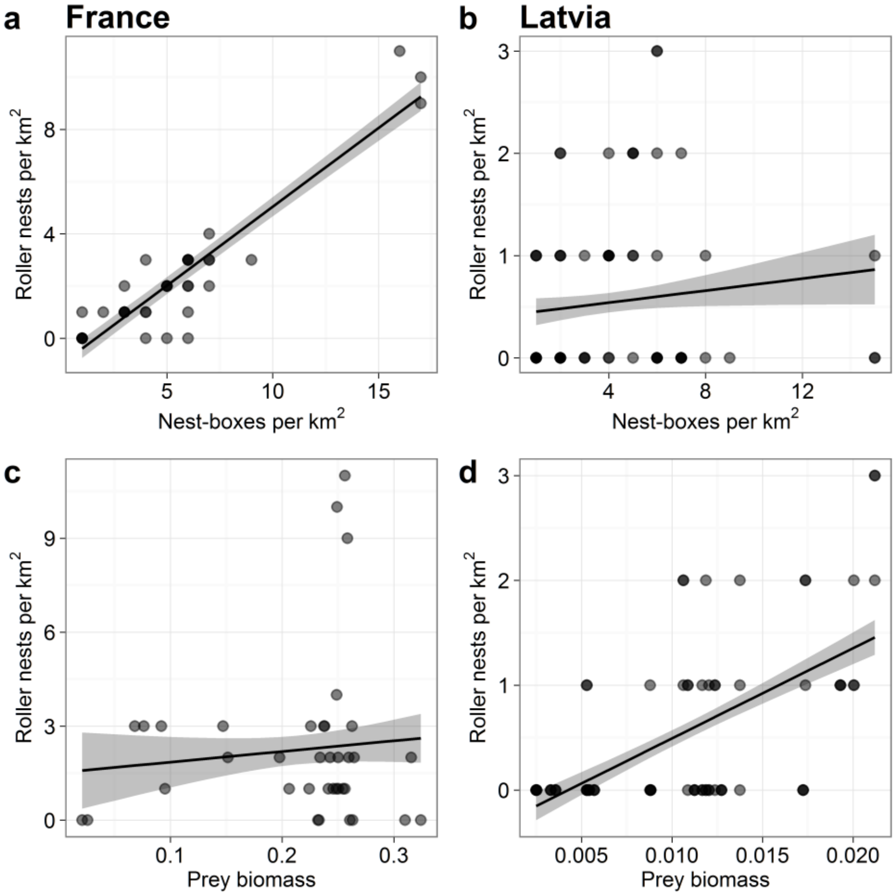


Figure 3.5 Relationship between **a**, **b** nest-box density and **c**, **d** prey biomass and Roller nest density (at a 1 km^2 scale) in France and Latvia. Line shows fitted relationship ± 1 S.E.

3.4.4 Nest-box occupation

Consistent with differences in nest-box density relative to breeding pair density, nest-box occupation was much higher in France than Latvia. In France, Rollers bred in almost every second nest-box (**Fig. 3.6a**), whereas in Latvia, despite an abundance of available nest-boxes, occupation was ~ 15 % (**Fig. 3.6b**).

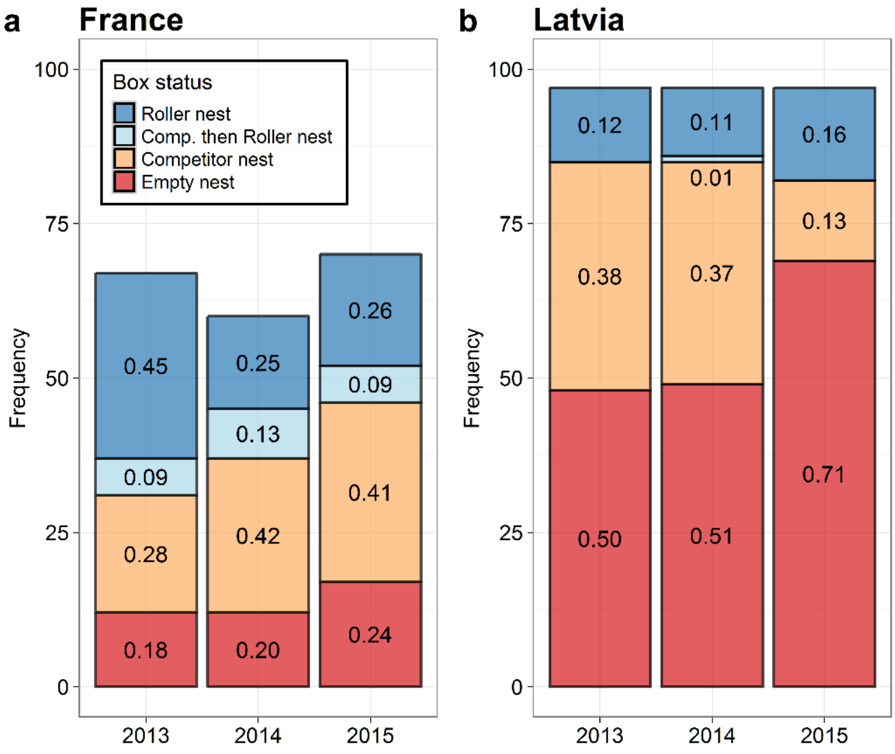


Figure 3.6 Number of nest-boxes categorised as *Roller nests*, *competitor* then *Roller nests*, *competitor nests*, and *empty nests*, in **a** France and **b** Latvia, across the three-year study period. Numbers in segments represent proportions per site/year.

Models predicting variation in nest-box occupation were generally quite poor; marginal R^2s (i.e. the proportion of variance accounted for by fixed effects) for the global models were 0.03 and 0.17 in France and < 0.01 and 0.16 in Latvia for the Roller–other and Roller–empty models, respectively.

In France, the most important variables were nest-box state and nearest neighbour distance, with no support for an effect of surrounding foraging resource availability on probability of nest-box occupation (**Table S1.11**). In Latvia, both nearest neighbour distance and surrounding prey biomass were important (**Table S1.12**). The effect of prey biomass was positive in Latvia, such that nest-boxes surrounded by land-uses with higher prey availability were more likely to be occupied by Rollers (**Fig 3.7b** and **Fig**

3.8b). These results support the coarser-scale analysis of Roller breeding density (**Section 3.4.3**) and are consistent with nest-site limitation in France and food limitation in Latvia.

The direction of the effect of nearest neighbour distance was positive in France but negative in Latvia. In France, the probability of Roller occupation was slightly higher for nest-boxes far from other Roller nests (**Fig 3.7a** and **Fig 3.8a**). In contrast, in Latvia the probability of Roller occupation was higher for nest-boxes close to other Roller nests (**Fig. 3.7b**, **Fig. 3.8b**). The mechanisms driving these apparent density-dependent effects are unclear, but we suspect that the observed patterns are inevitable consequences of (1) the lack of habitat selection in France resulting in a fairly even distribution of breeding Rollers throughout the site, possibly facilitated by intra-specific competition and (2) the preference of Latvian Rollers for high quality foraging habitats resulting in a more clustered distribution of breeding Rollers.

In France, there was a negative effect of lid absence for the Roller–empty model, but not the Roller–other model (**Table S1.11**). Across the study period, 10 out of 23 (43 %) nest-boxes without lids (and free from competitors) were occupied by Rollers compared to 92 out of 125 (74 %) nest-boxes with lids (and free from competitors). The number of Rollers using damaged nest-boxes was too low to test for differences in breeding success, but this avoidance is concerning. In 2015 we visited other nest-box sites in the Pyrénées-Orientales region which were stated by Aleman & Laurens (2013) to hold breeding Rollers; most nest-boxes were in a poor state of repair, and we found no Roller nests. Clearly, the provisioning of nest-boxes is not a sustainable long-term solution unless funds to guarantee their maintenance are guaranteed (Lindenmayer *et al.* 2009). The difference between the Roller–empty and Roller–other model suggests that Rollers, but not other avian cavity nesters, avoid nest-boxes without lids. This effect is likely to be driven by Common Kestrels *Falco tinnunculus*, which are too large to access nest-boxes otherwise, using boxes with missing lids.

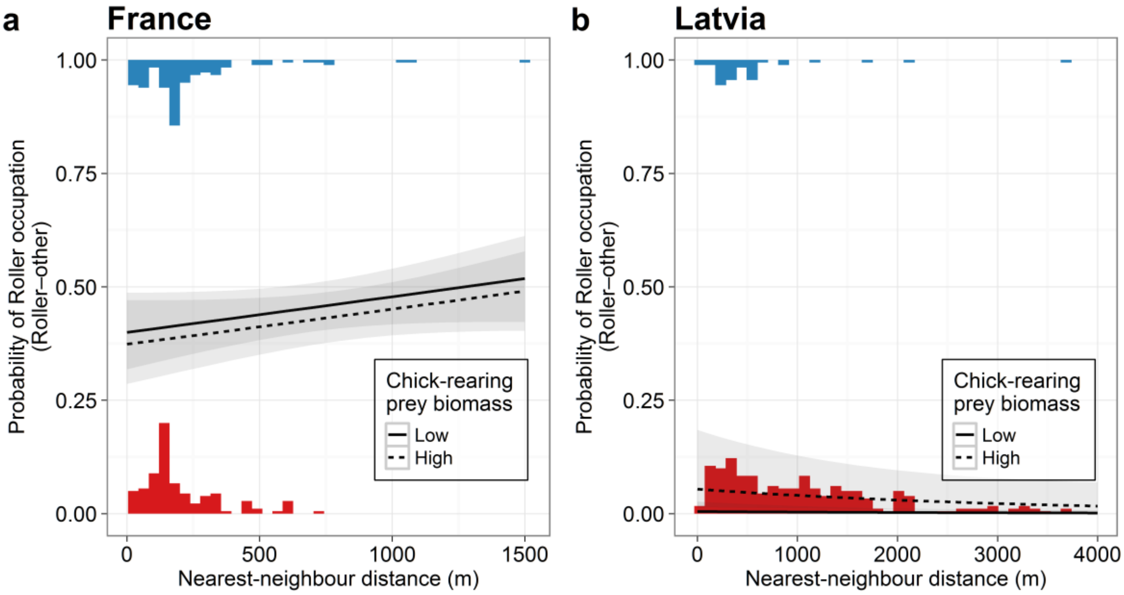


Figure 3.7 Predicted probability of Roller nest-box occupation for Roller–other model (where 0s include competitor nest-boxes as well as empty ones) in **a** France and **b** Latvia. Lines show model averaged predictor variables, with shaded regions denoting ± 1 S.E. Low and high prey biomass represent the 10th and 90th percentile values. Blue (top) and red (bottom) bars represent frequency distributions for Roller and other nest-boxes, respectively.

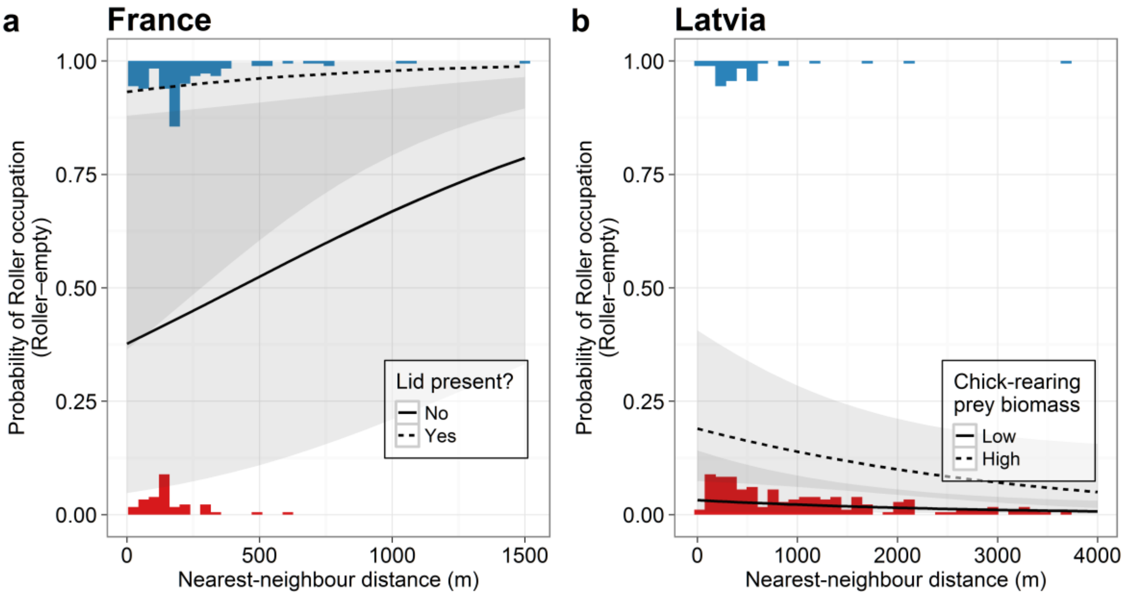


Figure 3.8 Predicted probability of Roller nest-box occupation for Roller–empty model (where 0s include empty nest-boxes only) in **a** France and **b** Latvia. Lines show model averaged predictor variables, with shaded regions denoting ± 1 S.E. In **b**, low and high prey biomass represent the 10th and 90th percentile values. Blue (top) and red (bottom) bars represent frequency distributions for Roller and other nest-boxes, respectively.

3.4.5 Breeding success

On the whole, there was little support from either site for an effect of foraging resource availability on roller clutch size, hatching success or fledging success. In fact, we were unable to detect any convincing predictors of spatial variation in breeding success (notwithstanding obvious differences between France and Latvia, and some apparent density-dependent effects), with the most important variables generally being temporal (i.e. year and lay date).

3.4.5.1 Clutch size

Clutches were, on average, larger in France (mean ± S.E. = 4.6 ± 0.11) than Latvia (4.2 ± 0.10; $t = 2.5$, $d.f. = 110.1$, $p = 0.01$). This is in line with previous studies of Rollers, which reveal a trend towards smaller clutches at higher latitudes (Sosnowski & Chmielewski 1996; Moreira *et al.* 2004; Lüütsepp *et al.* 2011; Parejo, Avilés & Rodriguez 2012; Aleman & Laurens 2013; Vincent-Martin, Gimenez & Besnard 2013; Kiss, Elek & Moskát 2014). This pattern is contrary, however, to the more general rule of clutch sizes increasing with latitude, as resource seasonality increases and overwinter survival and thus breeding density decrease (Ashmole’s hypothesis; Sanz 1997, 1998; La Sorte *et al.* 2014). Instead, our findings are consistent with Soler & Soler (1992) who argue that for single-brooded cavity nesting birds this pattern should be reversed if the disadvantages associated with large clutches are limited (due to the relative safety of the cavity) and larger eggs (traded-off against smaller clutches) are favoured in northerly populations.

Within both populations, the most important predictor of clutch size was lay date, with the latest clutches containing roughly one egg fewer than the earliest (**Fig. 3.9**, **Tables S1.13** and **S1.14**). Seasonally declining clutch size is a general pattern found across single-brooded species (Crick, Gibbons & Magrath 1993), and has been previously reported for Rollers in Spain (Avilés *et al.* 1999). The absence of second broods means that there should be no selection for Rollers to breed earlier than is optimal (i.e. clutches should be initiated such that peak resource supply and demand coincide). In France, peak resource availability (early July) occurred 5–6 weeks after the initiation of the earliest clutches (late May), approximately coinciding with the developmental mid-point of these earliest nestlings. (In Latvia, there was no detectable seasonal trend in resource availability – see **Section 3.4.1**). Pairs constrained to breed later should therefore lay fewer eggs, owing to the inevitable decline in resource availability following the seasonal peak. Alternatively, or additionally, later breeders may be of poorer quality resulting in smaller broods (Verhulst & Nilsson 2008). The absence of this seasonal decline in France in 2013 (**Fig 3.9a**) is intriguing, but difficult to explain without directly comparable invertebrate biomass data across years.

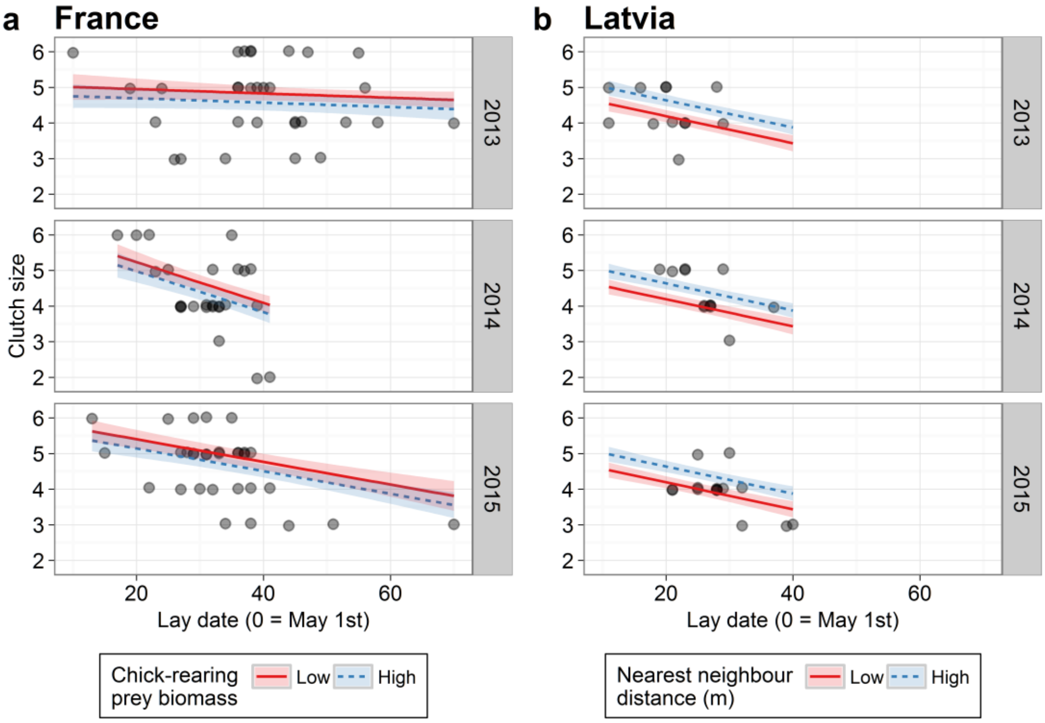


Figure 3.9 Variation in clutch size in **a** France and **b** Latvia. Lines show model-averaged fitted values (± S.E), with all other predictor variables set to their mean value. ‘Low’ and ‘high’ prey biomass (**a**) and nearest neighbour distance (**b**) are the 10th and 90th percentiles. Points are raw values, jittered slightly on the *y*-axis for readability.

We found no convincing spatial association between invertebrate availability and clutch size; in France, although there was a negative effect of chick-rearing period prey biomass on clutch size, this was neither statistically nor biologically significant (predicted clutch size for the 10th and 90th percentiles of prey biomass differed by only 0.3, with overlapping S.E. regions; **Fig. 3.9a**). In Latvia there was a weak negative density-dependent effect on clutch size, such that predicted clutch size increased by 0.45 from the 10th to 90th percentiles of nearest neighbour distance (**Fig. 3.9b**). The direction of this effect is consistent with clutch size being limited by reduced relative resource availability in areas of high Roller breeding density.

3.4.5.2 Hatching success

Hatching success was substantially higher in Latvia (mean = 0.82 ± 0.03) than France (0.57 ± 0.04; $t = 4.6$, $d.f. = 126.4$, $p < 0.001$), such that, despite the larger clutches in

France, mean number of hatchlings was actually lower (2.7 ± 0.22, compared to 3.4 ± 0.15 in Latvia; $t = 2.6$, $d.f. = 131.9$, $p = 0.01$). In France, of 79 clutches with known outcomes, 47 % suffered partial losses and 15 % suffered complete losses; in Latvia, of 39 monitored clutches, 54 % suffered partial losses and there were no complete failures. The higher failure rate in France was therefore primarily driven by complete nest failures rather than partial egg losses; when complete failures were excluded from both sites, hatching success was similar in France (0.80 ± 0.03) and Latvia (0.84 ± 0.03; $t = 1.1$, $d.f. = 96.5$, $p = 0.29$).

In the majority of cases we were unable to identify the circumstances of complete nest failures, but the most likely cause is predation (by snakes, rodents and birds, and pine martens in Latvia), followed by usurpation by both inter- and (perhaps) intra-specific competitors. Predation rates thus appear low in Latvia, consistent with a negative correlation between latitude and predation pressure (McKinnon *et al.* 2010). However, the predation pressure exerted by pine martens on bird nests has been shown to vary inversely with small mammal abundance (in line with the ‘alternative prey hypothesis’, Zárybnická, Riegert & Kouba 2015). Our three-year study period did not coincide with a year of high predation pressure in Latvia, but in previous years pine martens have had devastating effects on Roller breeding success (E Račinskis, *pers. comm.*).

In France, hatching success also declined through the season, with early clutches having a predicted success rate of ~ 0.75, compared to < 0.40 for the latest clutches (**Fig. 3.10a**, **Table S1.15**). Again, this decline was driven primarily by complete failures, and is consistent with later breeders being of lower quality, though we cannot rule out a seasonal increase in predation pressure. Avilés *et al*. (1999) demonstrated a similar seasonal decline in hatching success, though we found no such effect in Latvia, where the strongest predictor of hatching success was the fixed effect of year, primarily driven by the higher egg failure rates in 2014 and 2015 (**Fig. 3.10b**, **Table S1.16**).

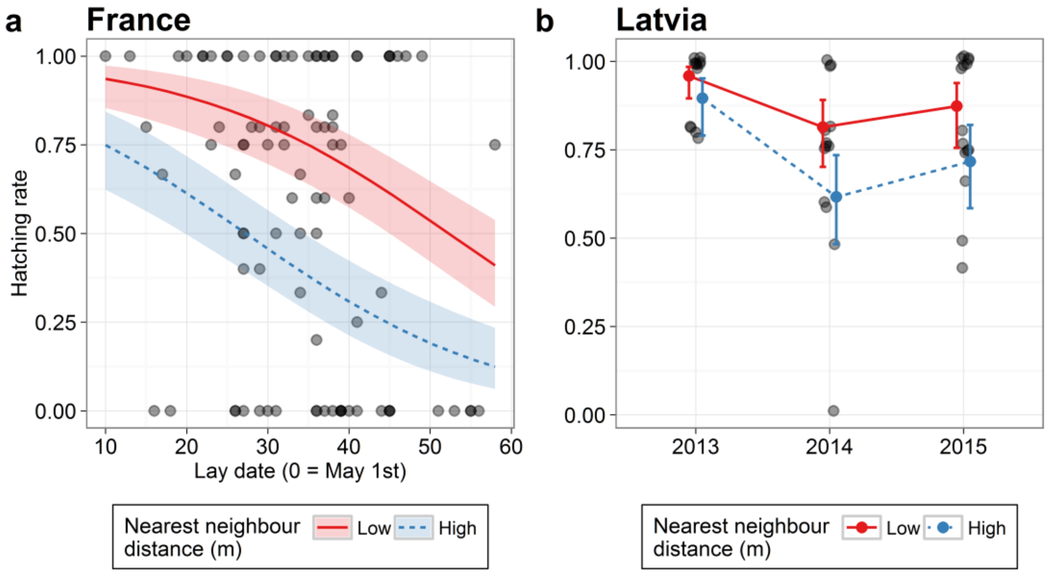


Figure 3.10 Variation in hatching rate (hatchlings per egg) in **a** France and **b** Latvia. Lines show model-averaged fitted values (± S.E), with all other predictor variables set to their mean value. ‘Low’ and ‘high’ nearest neighbour distance are the 10th and 90th percentiles. Points are raw values, jittered slightly in **b** for readability.

In both France and Latvia there was a negative effect of nearest neighbour distance on hatching success, with predicted egg survival decreasing by 0.31 (France) and 0.16 (Latvia) from the 10th to 90th percentiles of nearest neighbour distance (**Fig. 3.10a**). One possible explanation for this positive density dependence is improved defence against predators at higher nesting densities (e.g. MacDonald & Bolton 2008). Rollers readily mob avian predators and competitors, providing a potential mechanism through which this density dependence might operate. In Latvia, however, predation rates were very low during our study period, so improved defence against predators seems an unlikely explanation. Instead, the effect of neighbour distance may be an artefact of habitat quality (with higher breeding densities in better habitats) or laying date (with fewer neighbours later in the season), though we accounted for prey biomass and lay date in our models, so these explanations seem unlikely too.

3.4.5.3 Fledging success

In contrast to the lower hatching success in France, the probability of a hatched chick successfully fledging was substantially higher (mean = 0.92 ± 0.03) than in Latvia (mean = 0.68 ± 0.06; $t = 3.5$, *d.f.* = 52.7, $p = 0.001$). In France, of 78 monitored broods, 12 % suffered partial brood reduction and only 4 % of brood failed completely. In Latvia, of 39 broods, 31 % suffered partial reduction and 21% complete failure.

Variation in chick survival was low in France, and poorly explained by our predictor variables (**Fig. 3.11a**, **Table S1.17**), indicating a high and relatively constant probability of fledging successfully, comparable with data from Spain (Avilés *et al.* 1999). Roller chicks are rarely predated, perhaps due to their odorous vomit which probably serves a defensive function (Parejo *et al.* 2013). In Latvia, the only convincing predictor of variation in fledging success was the fixed effect of year, with very low chick survival in 2014 (**Fig. 3.11b**, **Table S1.18**). In other years, fledging success was comparable with France. The high mortality rate of chicks (and eggs) in 2014 was a result of a spell of unseasonally cold, wet weather during late incubation and soon after hatching.

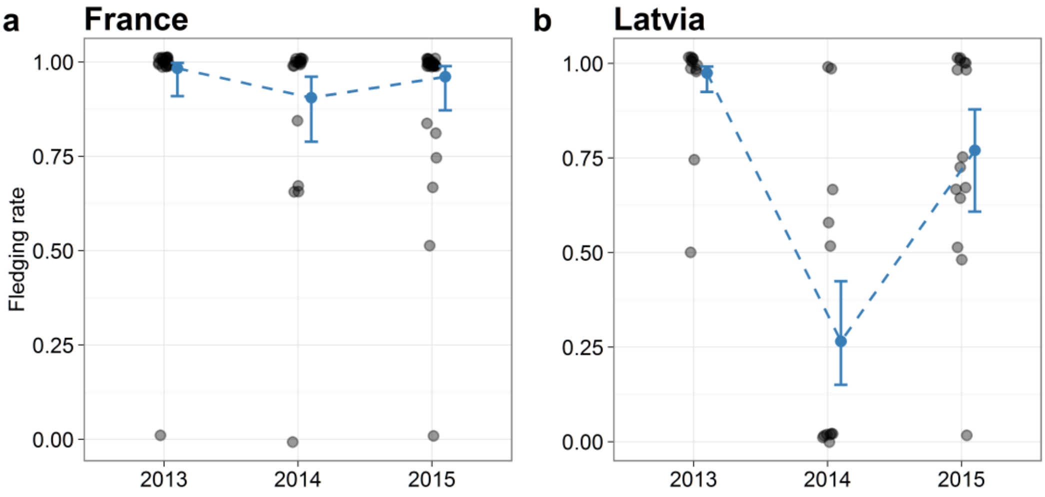


Figure 3.11 Fledging success varies annually in **a** France and **b** Latvia. Lines show model predictions, and error bars ± S.E.

Overall, these rates translate into similar nest success rates (69 % of nests fledged young in France, compared to 65 % in Latvia), but higher nest productivity in France than Latvia, with 2.6 and 1.8 fledglings per breeding attempt ($t = 2.0$, $d.f. = 134.0$, $p = 0.05$) and 3.7 and 3 fledglings per successful nest ($t = 3.0$, $d.f. = 96.0$, $p = 0.003$), respectively. Differences in hatching and fledging success balanced out, such that the probability of survival from egg to fledging was similar in both populations (0.54 in France, 0.47 in Latvia; $t = 1.0$, $d.f. = 114.1$, $p = 0.31$). The ultimate factor driving differences in productivity between the two populations was therefore clutch size.

Our results highlight four key differences between the two populations: (1) resource availability is lower in Latvia than in France, (2) nest-site availability may limit population density in France, but food may be limiting in Latvia, (3) clutch size, and therefore productivity, is lower in Latvia than in France and (4) inter-annual variation in egg and chick survival is greater in Latvia than in France (at least over our short study period).

We argue that the French population is primarily limited by the availability of cavities; nest-box occupation is high, and is poorly predicted by surrounding habitat. Furthermore, at the 1 km^2 scale, Roller density correlates remarkably well with nest-box density; even at very high nest-box densities (17 boxes per km^2), Roller breeding density shows no sign of reaching a plateau. This hypothesis is supported by the substantial increase in the local Roller population following the provisioning of nest-boxes since the late 1990s (Aleman & Laurens 2013).

On the other hand, we suggest that the Latvian population is not currently nest-site limited, given the relatively low rates of nest-box occupation and lack of correlation between nest-box and Roller density. In neighbouring Estonia, the provisioning of nest-boxes failed to prevent the extinction of breeding Rollers (Lüütsepp *et al.* 2011), again suggesting that nest-site availability is not a limiting factor in northern Europe. The fact that Roller density and nest-box occupation were both predicted by surrounding resource availability suggests that the Latvian population may instead be food limited. This is not to say that nest-boxes are unimportant; their removal would probably spell disaster for this relict population.

Previous studies of Roller nest-site selection have generally shown a preference for insect-rich habitats compared to more intensively managed ones (Avilés & Costillo 1998; Catry et al. 2011; Rodriguez et al. 2011; Bouvier et al. 2014) and a relationship between surrounding foraging resource availability and Roller breeding success (Avilés & Parejo 2004; Kiss *et al.* 2014). We did not detect these signals in France, possibly due to the relatively small spatial scale of our study. We suspect that even the ‘worst’ nest sites are still surrounded by good enough habitat – or are sufficiently close to good enough habitat – to still be suitable for breeding Rollers. The Latvian site is larger, and more variable in suitability, and we detected a preference of Rollers for nest-boxes with higher foraging resource availability. Surprisingly, however, there was no effect on breeding success, perhaps because any effect of habitat quality was swamped by the strong inter-annual variations.

Our temporally (7 day) and spatially (5×5 m) explicit predictions of insect biomass formed the basis of all analyses for which foraging resource availability (at various scales) was the main predictor variable. This process of estimating insect biomass – converting counts to biomass; predicting biomass using a two-part hurdle model; and applying predictions across the whole site – is prone to several sources of uncertainty. Nevertheless, a more basic approach based on the total cover of land-uses with high invertebrate counts would likely have yielded similar results, given the strong correlations between predicted nest-level insect biomass and the proportional cover of fallow + hay in France ($r = 0.83$, *d.f.* = 94, $p < 0.001$) and clear-cut + heath + sand in Latvia ($r = 0.95$, *d.f.* = 95, $p < 0.001$).

Our data suggests that the Latvian population – on the northern edge of the species' distribution – is more vulnerable to extinction than the French population. Already limited to ~ 25 pairs, the Latvian population, given its lower productivity, must depend on higher annual survival rates in order to maintain the same population trajectory as in France. In Latvia, there is a real chance of a 'bad' year – due to inclement weather, high pine marten predation, or both – substantially reducing the population-level productivity. In France, however, conditions are relatively reliable and, at least over the course of our study period (and, to the best of our knowledge, in general), conditions rarely deteriorate sufficiently to diminish population-level productivity.

Finally, our results highlight different priorities for Roller conservation in the two regions. In France, as long as the surrounding habitat continues to support a large number of large terrestrial invertebrates, an expansion of the nest-box scheme appears to be sufficient to maintain / increase population size. Nonetheless, unless these nest-boxes are maintained and / or replaced, this provides only a short term solution. In Latvia, although the erection of nest-boxes has almost certainly prevented the extinction of the Roller population, we found no evidence that the population is currently nest-site limited. Instead, efforts should focus on creating and protecting the open habitats which provide important foraging resources. Additionally, attempts to mitigate inter-annual stochasticity in predation rates (by protecting nest-boxes from pine martens) and weather (by supplementary feeding) should (and are being) be considered.

3.5 References

Aebischer, N.J. & Ewald, J.A. (2012) The grey partridge in the UK: population status, research, policy and prospects. *Animal Biodiversity and Conservation*, **35**, 353–362.

Aleman, Y. & Laurens, J. (2013) Répartition et effectifs du Rollier d'Europe (Coracias garrulus) dans les Pyrénées-Orientales en 2011. *La Mélano*, **13**, 1–11.

Attwood, S.J., Maron, M., House, A.P.N. & Zammit, C. (2008) Do arthropod assemblages display globally consistent responses to intensified agricultural land use and management? *Global Ecology and Biogeography*, **17**, 585–599.

Avilés, J.M. & Costillo, E. (1998) Selection of breeding habitats by the Roller (Coracias garrulus) in farming areas of the southwestern Iberian peninsula. *Die Vogelwarte*, **39**, 242–247.

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*, **70**, 227–230.

Avilés, J.M. & Parejo, D. (2004) Farming practices and roller Coracias garrulus conservation in south-west Spain. *Bird Conservation International*, **14**, 173–181.

Avilés, J.M., Sanchez, J.M., Sanchez, A. & Parejo, D. (1999) Breeding biology of the Roller Coracias garrulus in farming areas of the southwest Iberian Peninsula. *Bird Study*, **46**, 217–223.

Barton, K. (2015) MuMIn: Multi-Model Inference. R package version 1.15.1.

Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015) Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, **67**, 1–48.

Bohus, M. (2002) On breeding biology of the Roller (Coracias garrulus) in the Komárno town surroundings (SW Slovakia, Danubian basin). *Sylvia*, **38**, 51–59.

Bouvier, J.-C., Muller, I., Génard, M., Françoise, L. & Lavigne, C. (2014) Nest-Site and Landscape Characteristics Affect the Distribution of Breeding Pairs of European Rollers Coracias garullus in an Agricultural Area of Southeastern France. *Acta Ornithologica*, **49**, 23–32.

Britschgi, A., Spaar, R. & Arlettaz, R. (2006) Impact of grassland farming intensification on the breeding ecology of an indicator insectivorous passerine, the Whinchat Saxicola rubetra: Lessons for overall Alpine meadowland management. *Biological Conservation*, **130**, 193–205.

Cockle, K.L., Martin, K. & Drever, M.C. (2010) Supply of tree-holes limits nest density of cavity-nesting birds in primary and logged subtropical Atlantic forest. *Biological Conservation*, **143**, 2851–2857.

Cramp, S. (1985) *The Birds of the Western Palearctic, Volume 4: Terns to Woodpeckers*. Oxford University Press, Oxford, UK.

Crick, H.Q.P., Gibbons, D.W. & Magrath, R.D. (1993) Seasonal Changes in Clutch Size in British Birds. *Jounral of Animal Ecology*, **62**, 263–273.

Ewald, J.A., Aebischer, N.J., Richardson, S.M., Grice, P. V. & Cooke, A.I. (2010) The effect of agri-environment schemes on grey partridges at the farm level in England. *Agriculture, Ecosystems and Environment*, **138**, 55–63.

Fargallo, J., Blanco, G., Potti, J. & Vinuela, J. (2001) Nestbox provisioning in a rural population of

Eurasian Kestrels: breeding performance, nest predation and parasitism. *Bird Study*, **48**, 236–244.

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**, 657–666.

Gillman, L.N., Wright, S.D., Cusens, J., Mcbride, P.D., Malhi, Y. & Whittaker, R.J. (2015) Latitude, productivity and species richness. *Global Ecology and Biogeography*, **24**, 107–117.

Golawski, A. & Meissner, W. (2008) The influence of territory characteristics and food supply on the breeding performance of the Red-backed Shrike (Lanius collurio) in an extensively farmed region of eastern Poland. *Ecological Research*, **23**, 347–353.

Hart, J.D., Milsom, T.P., Fisher, G., Wilkins, V., Moreby, S.J., Murray, A.W.A. & Robertson, P.A. (2006) The relationship between yellowhammer breeding performance, arthropod abundance and insecticide applications on arable farmland. *Journal of Applied Ecology*, **43**, 81–91.

Hijmans, R.J. (2015) geosphere: Spherical Trigonometry. R package version 1.5-1.

Karell, P., Ahola, K., Karstinen, T., Zolei, A. & Brommer, J.E. (2009) Population dynamics in a cyclic environment: Consequences of cyclic food abundance on tawny owl reproduction and survival. *Journal of Animal Ecology*, **78**, 1050–1062.

Kiss, O., Elek, Z. & Moskát, C. (2014) High breeding performance of European Rollers Coracias garrulus in heterogeneous farmland habitat in southern Hungary. *Bird Study*, **61**, 496–505.

Kovacs, A., Barov, B., Orhun, C. & Gallo-Orsi, U. (2008) *International Species Action Plan for the European Roller Coracius Garrulus Garrulus*. Besenyőtelek, Hungary.

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.

Lüütsepp, G., Kalamees, A. & Lüütsepp, O. (2011) European Roller Coracias garrulus in Estonia 2000-2011. *Hirundo*, **24**, 61–72.

MacDonald, M.A. & Bolton, M. (2008) Predation of Lapwing Vanellus vanellus nests on lowland wet grassland in England and Wales: Effects of nest density, habitat and predator abundance. *Journal of Ornithology*, **149**, 555–563.

McKinnon, L., Smith, P. a, Nol, E., Martin, J.L., Doyle, F.I., Abraham, K.F., Gilchrist, H.G., Morrison, R.I.G. & Bêty, J. (2010) Lower predation risk for migratory birds at high latitudes. *Science*, **327**, 326–327.

Moreira, M.I., Catry, I., Henriques, I., Marques, A.T. & Reis, S. (2004) Dados preliminares sobre a biologia reprodutora do Rolieiro Caracias garrulus na ZPE de Castro Verde. *Airo*, **14**, 79–81.

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

Newton, I. (1998) *Population Limitation in Birds*. Academic Press.

Parejo, D., Avilés, J.M., Peña, A., Sánchez, L., Ruano, F., Zamora-Muñoz, C. & Martín-Vivaldi, M. (2013) Armed Rollers: Does Nestling's Vomit Function as a Defence against Predators? *PLoS One*, **8**, e68862.

Parejo, D., Avilés, J.M. & Rodriguez, J. (2012) Supplemental food affects egg size but not hatching asynchrony in rollers. *Behavioral Ecology and Sociobiology*, **66**, 1097–1105.

QGIS Development Team. (2009) QGIS Geographic Information System.

R Development Core Team. (2014) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Rodriguez, J., Avilés, J.M. & Parejo, D. (2011) The value of nestboxes in the conservation of Eurasian Rollers Coracias garrulus in southern Spain. *Ibis*, **153**, 735–745.

Ruffino, L., Salo, P., Koivisto, E., Banks, P.B. & Korpimäki, E. (2014) Reproductive responses of birds to experimental food supplementation: a meta-analysis. *Frontiers in Zoology*, **11**, 80.

Sanz, J.J. (1997) Geographic variation in breeding parameters of the Pied Flycatcher Ficedula hypoleuca. *Ibis*, **139**, 107–119.

Sanz, J.J. (1998) Effects of geographic location and habitat on breeding parameters of great tits. *The Auk*, **115**, 1034–1051.

Schekkerman, H. & Beintema, A.J. (2007) Abundance of Invertebrates and Foraging Success of Black-Tailed Godwit Limosa limosa Chicks in Relation to Agricultural Grassland Management. *Ardea*, **95**, 39–54.

Soler, M. & Soler, J.J. (1992) Latitudinal trends in clutch size in single brooded hole nesting bird species: a new hypothesis. *Ardea*, **80**, 293–300.

La Sorte, F.A., Butchart, S.H.M., Jetz, W. & Böhning-Gaese, K. (2014) Range-wide latitudinal and elevational temperature gradients for the world's terrestrial birds: Implications under global climate change. *PLoS One,* **9**, e98361.

Sosnowski, J. & Chmielewski, S. (1996) Breeding biology of the Roller Coracias garrulus in Puszcza Pilicka Forest (Central Poland). *Acta Ornithologica* , **31**, 119–131.

Thorup, K., Sunde, P., Jacobsen, L.B. & Rahbek, C. (2010) Breeding season food limitation drives population decline of the Little Owl Athene noctua in Denmark. *Ibis*, **152**, 803–814.

Vaclav, R., Valera, F. & Martinez, T. (2011) Social information in nest colonisation and occupancy in a long-lived, solitary breeding bird. *Oecologia*, **165**, 617–627.

Verhulst, S. & Nilsson, J.-A. (2008) The timing of birds' breeding seasons: a review of experiments that manipulated timing of breeding. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **363**, 399–410.

Vincent-Martin, N., Gimenez, O. & Besnard, A. (2013) Reproduction et dynamique de colonisation du rollier d'Europe en cavites artificielles. *Écologie et conservation d'une steppe méditerranéenne, La plaine de Crau* (eds L. Tatin, A. Wolff, J. Boutin, E. Colliot & T. Dutoit) Quae.

Watson, J., Rae, S. & Stillman, R. (2016) Nesting Density and Breeding Success of Golden Eagles in Relation to Food Supply in Scotland. *Journal of Animal Ecology*, **61**, 543–550.

Wellicome, T.I., Todd, L.D., Poulin, R.G., Holroyd, G.L., Fisher, R.J., Shostak, B., Cooper, J.K. & Chapman, F. (2013) Comparing food limitation among three stages of nesting: supplementation experiments with the burrowing owl. *Ecology and Evolution*, **3**, 2684–2695.

Zárybnická, M., Riegert, J. & Kouba, M. (2015) Indirect food web interactions affect predation of Tengmalm's Owls Aegolius funereus nests by Pine Martens Martes martes according to the alternative prey hypothesis. *Ibis*, **157**, 459–467.

Appendix 1: Supporting information for Chapter 3

Supplementary figures

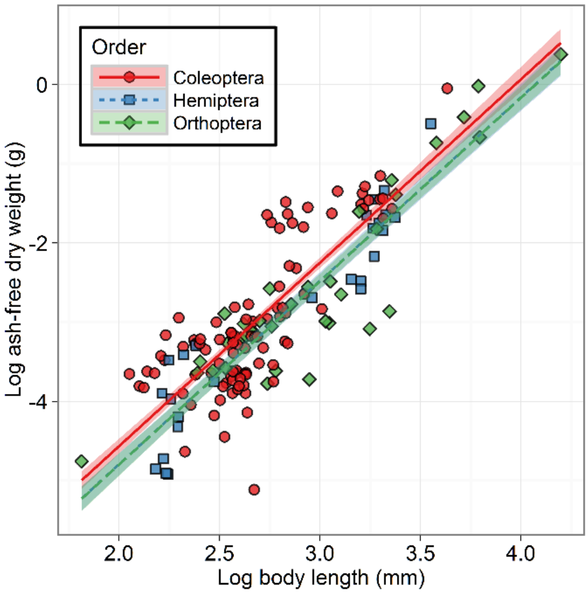


Figure S1.1 Relationship between *log_{10}* body length and *log_{10}* ash-free dry weight (i.e. biomass) of 159 insect specimens from orders Coleoptera, Hemiptera and Orthoptera

Supplementary tables

Table S1.1 Land-use categories and definitions for France. ‘Prop. cover’ gives the total cover of each land-use category in 2015. ‘Prey prediction’ denotes the treatment of each land-use category when predicting prey biomass across the field site (surveyed habitats marked with ‘=’). ‘mean’ = assigned average prey biomass across all surveyed land-uses; ‘= *land-use*’ = assigned prey biomass of corresponding land-use category; ‘0’ = assigned prey biomass of 0.

Category	Definition	Prop. cover	Prey prediction
vine	Cultivated grape vines	0.35	=
vine (fallow)	Fallow vineyard; vines usually removed, and overgrown (waist-high) with characteristic sparse herbaceous vegetation	0.24	=
saltmarsh	Marshland on edge of saline lagoon	0.06	mean
orchard	Plantation of fruit- or nut-producing trees (typically apricot, almond, olive or peach)	0.06	=
wet grass	Rank, apparently unmanaged grassland with rushes and reeds	0.05	= hay meadow
mixed	Mosaic of scrub, hay meadow and wet grass; inaccessible due to large fences.	0.05	mean
lagoon	Saline lagoon (*Etang du Salses*)	0.04	0
hay meadow	Managed grassland; mown for hay or grazed by sheep, goats or horses	0.04	=
scrub	Abandoned / fallow land with dense or scattered bushes (at least waist-high) generally separated by no more than 5 m	0.03	mean
dwelling	Inhabited dwelling, garden, allotment, greenhouse, etc.	0.03	0
vine (young)	Recently (within 2 years) planted grape vines, with woody stems shorter than knee height and surrounding earth mostly bare	0.01	0
orchard (young)	Recently (within 2 years) planted orchard, with trees shorter than waist height and surrounding earth mostly bare	0.01	0
bare	Recently (within 1 year) ploughed with < 10% vegetation cover; crop type unknown (typically either vine or orchard)	0.01	0
abandoned	Abandoned / fallow land with few or no bushes; rank vegetation; previous land-use unknown	0.01	mean
wheat	Wheat cover crop	< 0.01	= hay meadow
orchard (fallow)	Fallow orchard; trees removed and ground overgrown (waist-high) with characteristic sparse herbaceous vegetation	< 0.01	= vine (fallow)
orchard (abandoned)	Abandoned orchard, with dead / unkempt trees present and ground overgrown (waist-high) with characteristic sparse herbaceous vegetation	< 0.01	= vine (fallow)
market garden	Small-scale cultivation of annual crops, associated with Dwelling	< 0.01	0
industrial	Industrial buildings and yards, e.g. factory, quarry, land-fill etc.	< 0.01	0
forest (pine)	Plantation of *Pinus* spp., with basically no understory	< 0.01	0

Table S1.2 Land-use categories and definitions for Latvia. ‘Prop. cover’ gives the total proportional cover of each land-use category in 2014. See **Table 1** for description of ‘prey prediction’. Note that dry pine forest 1–3 were treated as a single land-use category for invertebrate transects.

Category	Definition	Prop. cover	Prey prediction
forest (dry pine 2)	Forest dominated by *Pinus sylvestris*; sparse understory including (knee high) dwarf shrubs	0.33	=
forest (dry pine 3)	Forest dominated by *Pinus sylvestris*; understory of (up to waist high) dwarf shrubs	0.16	=
forest (pine other)	Forest dominated by *Pinus sylvestris*; dense understory of (often head high) bushes and saplings	0.11	= forest
forest (dry pine 1)	Forest dominated by *Pinus sylvestris*; minimal understory of lichen and bryophytes	0.09	=
forest (pine young)	Forest dominated by young (at least head height) *Pinus sylvestris* with diameter at breast height < 20 cm	0.07	= forest
clearcut	Recently (within 5 years) felled forest; if re-planted then saplings less than head height	0.05	=
forest (birch)	Forest dominated by *Betula* spp.	0.04	= forest
dwelling	Inhabited dwelling, garden, allotment, greenhouse, etc.	0.04	0
scrub	Abandoned / fallow land with dense or scattered bushes (at least waist-high) generally separated by no more than 5 m	0.03	mean
industrial	Industrial buildings and yards, e.g. factory, quarry, land-fill etc.	0.03	0
heath	Open area with few trees, dominated by dwarf ericaceous shrubs.	0.02	=
hay meadow	Managed grassland; mown for hay or grazed by cattle or horses	0.02	mean
forest (other)	Forest dominated by species other than *Pinus sylvestris* (often *Picea* or *Abies* spp.) with very dense understory	0.02	= forest
wetland	Marshy area dominated by reeds and rushes	0.01	mean
riparian	Waterlogged forest on the edge of river	0.01	mean
sand	Open area with little vegetation cover – bare sand or thin layer of lichen or bryophytes	< 0.01	=
orchard	Plantation of fruit- or nut-producing trees	< 0.01	mean
lake	Freshwater lake	< 0.01	0
abandoned	Abandoned land, but with few or no bushes (otherwise scrub); rank vegetation; previous land-use unknown	< 0.01	mean

Table S1.3 Number of insect transects conducted in each major land-use in France and Latvia.

Site	Land-use	Transects	Repeats	First	Last	Total
France	vine	22	5	18 May	26 Jul	110
	vine (fallow)	15	5	18 May	26 Jul	75
	orchard	8	5	21 May	26 Jul	40
	hay meadow	3	5	18 May	26 Jul	15
						240
Latvia	forest (dry pine)	17 + 7*	6 / 5*	30 May	11 Aug	137
	clear-cut	14	6	26 May	11 Aug	84
	heath	4	6	1 Jun	10 Aug	24
	sand	2	6	26 May	8 Aug	12
						257

*17 transects repeated 6 times, 7 transects repeated 5 times

Table S1.4. Modelled ash-free dry weight (g) according to insect taxon (rows) and size class (columns).

Taxon	10–20 mm	20−30 mm	30–40 mm	40–50 mm	50–60 mm
CLASS					
Insecta	0.049	0.155	0.329	0.579	0.907
ORDER					
Orthoptera	0.043	0.139	0.302	0.541	0.861
Coleoptera	0.054	0.175	0.382	-	-
FAMILY					
Acrididae	0.022	0.082	0.194	0.368	0.615
Tettigonidae	0.052	0.192	0.453	0.861	1.438
Cicadidae	0.037	0.138	0.326	-	-
Carabidae-like[1]	0.042	0.156	-	-	-
Scarabidae	0.070	0.257	-	-	-
Geotrupidae-like[2]	0.121	0.448	-	-	-

[1] Includes families Carabidae, Cantharidae, Cerambycidae, Curculonidae, Silphidae and Staphylinidae
[2] Includes families Geotrupidae, Chrysomelidae and Histeridae

Table S1.5 Nest control effort across the study period in France and Latvia. Median values per nest (25th – 75th percentiles).

Site	Year	Nest-boxes / cavities controlled	First control date	Last control date	Control period (days)	Controls per box (n)	Interval between controls (days)
France	2013	67 / 3	28 May (28 – 28 May)	26 Jul (26 – 26 Jul)	59 (59 – 59)	6 (5 – 7)	10 (7 – 12)
	2014	61 / 7	18 Apr (18 – 19 Apr)	25 Jun (25 – 26 Jun)	68 (64 – 69)	21 (19 – 22)	3 (3 – 4)
	2015	71 / 20	12 May (12 – 13 May)	18 Jul (18 – 22 Jul)	67 (66 – 71)	10 (9 – 15)	6 (5 – 7)
Latvia	2013	97 / 0	22 May (2 – 27 May)	17 Jun (16 Jun – 4 Jul)	44 (21 – 55)	3 (2 – 5)	11 (7 – 13)
	2014	98 / 1	26 May (24 – 27 May)	22 Jul (18 – 24 Jul)	59 (51 – 60)	7 (5 – 8)	9 (7 – 10)
	2015	97 / 0	13 Jun (10 – 14 Jun)	14 Jun (10 Jun – 4 Jul)	0* (0 – 20)	1 (1 – 2)	0* (0 – 6)

* A control period / interval of 0 means the nest was controlled only once

Table S1.6 Definitions of parameters calculated for each Roller breeding attempt.

Variable	Values	Definition
order	1, 2	Order of avian breeding per cavity; 1 if first known avian breeding attempt of season; 2 if second
attempt	1, 2	Order of Roller breeding attempt per cavity; 1 if first known Roller breeding attempt of season; 2 if second (likely replacement clutch)
clutch size	1 – 6	Number of eggs
clutch complete	'yes', 'no', 'unknown'	'yes' if *clutch size* represent a finished clutch; 'no' if clutch failed before completion (i.e. prior to the laying of the 3rd egg); 'unknown' if clutch failed before completion could be determined or if nest was first discovered after hatching (in which case clutch size is inferred from number of hatchlings)
hatchlings	1 – 6	Number of hatchlings; includes any nestlings which died young
egg survival	0 – 1	Proportion of eggs successfully hatched; *hatchlings* / *clutch size*
fledglings (min)	1 – 6	Minimum number of fledglings, assuming that all hatchlings die unless fledging is confirmed (unlikely)
fledglings (max)	1 – 6	Maximum number of fledglings, assuming that all hatchlings live unless death is confirmed (most likely)
chick survival	0 – 1	Proportion of hatchlings successfully fledged; *fledglings (max) / hatchlings*
success	0, 1	Success of nesting attempt; 1 if *fledglings (max)* > 0, otherwise 0
lay date (min)	date	Earliest possible date of first egg; assuming a 2 day laying period, and (working back from *hatch date (min)*) a 20-day incubation period starting on the day of the third egg. 10 May if totally unknown (due to clutch failing before completion could be ascertained).
lay date (max)	date	Latest possible date of first egg; assuming a 1 day laying period, and (working back from *hatch date (max)*) a 17-day incubation period starting on the day of the third egg
hatch date (min)	date	Minimum first hatch date; last day on which eggs but no hatchlings were required; if bald and blind chicks are subsequently observed more than 7 days later then use this date minus 7 (i.e. assume bald and blind chicks couldn't have hatched more than 7 days previously).
hatch date (max)	date	Maximum first hatch date; first day on which chick(s) were observed; if feathers have emerged from pin, then subtract 7 days (i.e. assume feathered chicks must have hatched at least 7 days previously)
lay date	date	Estimated date of first egg; mid-point of *lay date (min)* and *lay date (max)*
lay date uncertainty	0 – *n*	Uncertainty of *lay date* estimate; difference between *lay date (min)* and *lay date (max)*

Table S1.7 Model summaries for France land-use only and intercept-only models predicting variation in **a**) the probability of observing an insect on a transect and **b**) the biomass of observed insects. ✓ = factor present; \ = factor absent; *k* = number of parameters in model; Δ_i = difference in AICc between i^{th} model and 'best' model; w_i = Akaike model weight. Intercept, though not shown, is present in all models.

Model	*land-use*	***k***	**AICc**	$\boldsymbol{\Delta_i}$	$\boldsymbol{w_i}$
a binomial					
1	✓	5	238.8	0.00	> 0.999
2	\	2	257.1	18.28	< 0.001
b gamma					
1	✓	6	−55.2	0.00	0.998
2	\	3	−42.6	12.63	0.002

Table S1.8 Model summaries for Latvia land-use only and intercept-only models predicting variation in **a**) the probability of observing an insect on a transect and **b**) the biomass of observed insects. ✓ = factor present; / = factor absent. Intercept, though not shown, is present in all models.

Model	*land-use*	***k***	**AICc**	$\boldsymbol{\Delta_i}$	$\boldsymbol{w_i}$
a binomial					
1	✓	5	180.8	0.00	> 0.999
2	/	2	224.8	44.03	< 0.001
b gamma					
1	/	3	−232.2	0.00	0.945
2	✓	6	−226.5	5.67	0.055

Table S1.9 Model summaries for France seasonal models predicting variation in **a**) the probability of observing an insect on a transect and **b**) the biomass of observed insects. Results are presented only for models with $\Delta_i < 2$, but w_i is calculated across all models (though only across those with $\Delta_i < 2$ for the purposes of model averaging). Parameter estimates are shown for continuous variables only. ✓ = factor present; / = variable absent. Intercept, though not shown, is present in all models.

Model	*land-use*	*date*	*date*^{2}	*land-use* × *date*	*land-use* × *date*^{2}	***k***	**AICc**	$\boldsymbol{\Delta_i}$	$\boldsymbol{w_i}$
a binomial									
1	✓	−8.80	15.19	✓	✓	13	197.3	0.00	0.499
2	✓	4.57	−3.40	/	/	7	198.1	0.76	0.341
b gamma									
1	✓	−0.69	2.43	✓	✓	14	−87.2	0.00	0.889

Table S1.10 Model summaries for Latvia seasonal models predicting variation in **a**) the probability of observing an insect on a transect and **b**) the biomass of observed insects. Results are presented only for models with $\Delta_i < 2$, but w_i is calculated across all models. Parameter estimates are shown for continuous variables only. ✓ = factor present; / = variable absent. Intercept, though not shown, is present in all models.

Model	*land-use*	*date*	*date*^{2}	***k***	**AICc**	$\boldsymbol{\Delta_i}$	$\boldsymbol{w_i}$
a binomial							
1	✓	0.40	/	6	179.7	0.00	0.348
2	✓	/	0.40	6	179.8	0.10	0.332
3	✓	/	/	5	180.8	1.11	0.199
b gamma							
1	/	/	/	3	−232.2	0.00	0.497
2	/	−0.38	/	4	−230.7	1.48	0.237
3	/	/	−0.26	4	−230.4	1.85	0.197

Table S1.11. Summary of ‘top’ **a** Roller–other and **b** Roller–empty nest-box occupation models in France. Results are presented only for models with $\Delta_i < 2$, but w_i is calculated across all models. Parameter estimates are shown for continuous variables only. ✓ = factor present; / = variable absent. Intercept, though not shown, is present in all models.

Model	*neighbour distance*	*prey (laying)*	*prey (chick-rearing)*	*state*	***k***	**AICc**	Δ_i	w_i
a Roller–other								
1	0.25	/	/	/	3	310.7	0.00	0.156
2	/	/	/	/	2	311.1	0.32	0.132
3	0.30	/	–0.21	/	4	311.3	0.58	0.116
4	0.24	/	/	✓	4	312.1	1.34	0.080
5	/	/	/	✓	3	312.2	1.44	0.076
6	/	/	–0.15	/	3	312.3	1.53	0.072
b Roller–empty								
1	0.81	/	/	✓	4	169.4	0.00	0.272
2	/	/	0.72	✓	4	170.4	0.94	0.171
3	0.74	/	0.33	✓	5	170.6	1.16	0.152

Table S1.12 Summary of ‘top’ **a** Roller–other and **b** Roller–empty nest-box occupation models in Latvia. Results are presented only for models with $\Delta_i < 2$, but w_i is calculated across all models. Parameter estimates are shown for continuous variables only. ✓ = factor present; / = variable absent. Intercept, though not shown, is present in all models.

Model	*neighbour distance*	*prey (chick-rearing)*	***k***	**AICc**	Δ_i	w_i
a Roller–other						
1	–0.63	1.15	4	187.6	0.00	0.468
2	/	1.38	3	188.3	0.63	0.341
b Roller–empty						
1	–0.68	0.89	4	176.4	0.00	0.566
2	/	1.18	3	177.7	1.29	0.297

Table S1.13. Summary of 'top' clutch size models in France. Results are presented only for models with $\Delta_i < 2$, but w_i is calculated across all models. Parameter estimates are shown for continuous variables only. ✓ = factor present; / = variable absent. Intercept, though not shown, is present in all models.

Model	*year*	*prey (laying)*	*prey (chick-rearing)*	*neighbour distance (laying)*	*neighbour distance (chick-rearing)*	*lay date*	*year × lay date*	$\boldsymbol{k}$	**AICc**	$\boldsymbol{\Delta_i}$	$\boldsymbol{w_i}$
1	✓	/	–0.20	/	/	–0.13	✓	9	239.2	0.00	0.242
2	✓	/	/	/	/	–0.07	✓	8	240.3	1.14	0.137

Table S1.14. Summary of 'top' clutch size models in Latvia. Results are presented only for models with $\Delta_i < 2$, but w_i is calculated across all models. Parameter estimates are shown for continuous variables only. ✓ = factor present; / = variable absent. Intercept, though not shown, is present in all models.

Model	*year*	*prey (chick-rearing)*	*neighbour distance (laying)*	*neighbour distance (chick-rearing)*	*lay date*	*year × lay date*	$\boldsymbol{k}$	**AICc**	$\boldsymbol{\Delta_i}$	$\boldsymbol{w_i}$
1	/	/	/	0.23	–0.33	/	5	72.8	0.00	0.296
2	/	0.12	/	0.21	–0.32	/	6	74.2	1.42	0.145

Table S1.15 Summary of ‘top’ hatching success models in France. Results are presented only for models with $\Delta_i < 2$, but w_i is calculated across all models. Parameter estimates are shown for continuous variables only. ✓ = factor present; / = variable absent. Intercept, though not shown, is present in all models.

Model	*year*	*prey (laying)*	*prey (chick-rearing)*	*neighbour distance (laying)*	*neighbour distance (chick-rearing)*	*lay date*	*year × lay date*	***k***	**AICc**	Δ_i	w_i
1	/	/	/	–0.73	/	–0.83	/	4	306.7	0.00	0.185
2	/	0.46	–0.46	–0.97	/	–1.17	/	6	307.3	0.62	0.136
3	/	/	–0.23	–0.70	/	–0.83	/	5	307.8	1.13	0.105
4	/	0.21	/	–0.87	/	–0.98	/	5	308.1	1.40	0.092
5	/	/	/	–0.69	–0.23	–0.79	/	5	308.2	1.50	0.088

Table S1.16. Summary of ‘top’ hatching success models in Latvia. Results are presented only for models with $\Delta_i < 2$, but w_i is calculated across all models. Parameter estimates are shown for continuous variables only. ✓ = factor present; / = variable absent. Intercept, though not shown, is present in all models.

Model	*year*	*prey (chick-rearing)*	*neighbour distance (laying)*	*neighbour distance (chick-rearing)*	*lay date*	*year × lay date*	***k***	**AICc**	Δ_i	w_i
1	✓	/	–0.55	/	/	/	5	69.8	0.00	0.143
2	✓	–0.36	–0.69	/	/	/	6	70.5	0.70	0.101
3	✓	/	–0.64	/	0.51	/	6	70.6	0.74	0.098
4	✓	/	/	–0.51	/	/	5	71.1	1.25	0.076

Table S1.17 Summary of ‘top’ fledging success models in France. Results are presented only for models with $\Delta_i < 2$, but w_i is calculated across all models. Parameter estimates are shown for continuous variables only. ✓ = factor present; / = variable absent. Intercept, though not shown, is present in all models.

Model	*year*	*prey (laying)*	*prey (chick-rearing)*	*neighbour distance (laying)*	*neighbour distance (chick-rearing)*	*lay date*	*year × lay date*	***k***	**AICc**	Δ_i	w_i
1	✓	/	/	/	/	/	/	4	90.0	0.00	0.082
2	✓	/	/	/	/	–0.62	/	5	90.3	0.35	0.069
3	✓	/	/	0.64	/	/	/	5	90.4	0.41	0.067
4	/	/	/	/	/	/	/	2	90.6	0.57	0.062
5	✓	/	–0.34	/	/	/	/	5	91.1	1.16	0.046
6	/	/	–0.30	/	/	/	/	3	91.7	1.76	0.034
7	✓	/	–0.41	0.66	/	/	/	6	91.9	1.90	0.032
8	✓	/	/	0.50	/	–0.53	/	6	91.9	1.92	0.032

Table S1.18 Summary of ‘top’ fledging success models in Latvia. Results are presented only for models with $\Delta_i < 2$, but w_i is calculated across all models. Parameter estimates are shown for continuous variables only. ✓ = factor present; / = variable absent. Intercept, though not shown, is present in all models.

Model	*year*	*prey (chick-rearing)*	*neighbour distance (laying)*	*neighbour distance (chick-rearing)*	*lay date*	*year × lay date*	***k***	**AICc**	$\boldsymbol{\Delta_i}$	$\boldsymbol{w_i}$
1	✓	/	/	/	/	/	4	73.2	0.00	0.219
2	✓	–0.58	/	/	/	/	5	74.0	0.77	0.149
3	✓	/	/	/	0.55	/	5	74.6	1.43	0.107
4	✓	/	/	–0.32	/	/	5	75.2	1.97	0.082

Chapter 4: Insights into the foraging ecology of the European Roller from chick feather stable isotopes

4.1 Abstract

Having previously demonstrated that the French study population is not limited by foraging habitat availability, we here use carbon and nitrogen stable isotope signatures to explore signals of foraging habitat selection. Within the French study area, we detected striking patterns in chick feather $\delta^{15}N$ and $\delta^{13}C$ values, with chicks in the Garrieux site being ^{15}N enriched and ^{13}C depleted compared to those in Saint-Hippolyte, just a few kilometres to the south. In an attempt to explain these patterns, we compared chick feather stable isotope ratios with those measured from potential prey items collected from the main land-use types in each site. We estimated availability-weighted average $\delta^{15}N$ and $\delta^{13}C$ values for a randomly selected prey item at both the site and nest level. We hypothesised that, if Rollers are indifferent to foraging habitat, differences in chick feather stable isotope ratios will simply reflect variations in the stable isotope signature of locally available prey sources. Inter-site differences in chick feather $\delta^{15}N$ values corresponded exactly with differences in mean estimated prey source $\delta^{15}N$, and at the nest level, estimated prey source $\delta^{13}C$ was convincingly correlated with observed chick feather $\delta^{13}C$. Both of these observations point towards Rollers foraging on available prey sources rather than selecting specific ones, though we refrain from estimating the contribution of different prey sources to Roller diet. Nevertheless, our results suggest that Rollers may consume more vineyard-derived nutrients than expected, perhaps because of high prey accessibility in this land-use. The site-specific variation in prey and consumer $\delta^{15}N$ and $\delta^{13}C$ values has concerning implications for larger-scale geographical assignment studies, but shows promise for the study of short-distance dispersal.

*Supporting material can be found in **Appendix 2**.*

4.2 Introduction

Natural variations in the abundance of different stable isotopes have been used by ecologists to answer a wide range of questions (Inger & Bearhop 2008). Many natural stable isotope ratios – representing the relative enrichment or depletion of the heavier, rarer isotope – vary along biogeographical gradients within habitats, ecosystems and continents (Bowen 2010; Hobson *et al.* 2012b). A record of these differences can be found in consumer tissues, which provide a time-integrated chemical record (shifted to some degree by trophic enrichment) of where or what an animal consumed around the time of tissue synthesis (Bearhop *et al.* 2002; Hobson & Bairlein 2003). In other words, “you are what you eat, plus a few ‰”. Thus, by sampling tissues with different lifespans and turnover rates, researchers can gain an insight into the ecology of birds over various temporal and spatial scales (Rubenstein & Hobson 2004; Beaulieu & Sockman 2012).

In avian ecology, recent emphasis has been placed on using stable isotopes to infer the origin of migratory birds, making use of continent-wide gradients in $\delta^{13}C$, $\delta^{15}N$, $\delta^{2}H$ values (e.g. Hobson *et al.* 2012a; Garcia-Perez & Hobson 2014; Veen *et al.* 2014). However, the spatial resolution of these attempts at geographical assignment is often dissatisfying, and large-scale gradients may be rendered less useful by small-scale, site-specific variations associated with habitat choice or diet (e.g. Oppel *et al.* 2011). Instead, stable isotopes have been used more successfully to quantify variation in foraging habitat associations (rather than location *per se*), both during the breeding season (e.g. Girard *et al.* 2012) and overwinter (e.g. Marra, Hobson & Holmes 1998; Bearhop *et al.* 2004; Gunnarsson *et al.* 2005), as well as to estimate the nutrient contribution of different dietary sources (e.g. Inger *et al.* 2006; Cross *et al.* 2014).

Agricultural intensification and the affiliated reductions in the quality and extent of foraging habitat – as well as the spatial separation of nesting habitat from foraging habitat – has been blamed for the decline of many open-habitat species (Thorup *et al.* 2010; Aebischer & Ewald 2012; Catry *et al.* 2013). In order to devise conservation management plans and to predict the effect of future land-use change, an understanding of individual foraging habitat requirements is required (Franco & Sutherland 2004; Barbaro *et al.* 2008; Catry *et al.* 2012).

In **Chapter 3**, we provided evidence that the local density of breeding Rollers at our study site in southern France is strongly associated with nest-site availability. We found no associations between surrounding prey biomass and either breeding density, nest-box occupation probability or breeding success. An understanding of the foraging ecology underlying this finding is crucial. On the one hand, Rollers may rely on particularly rich 'honeypot' habitats (e.g. fallow) which are currently sufficiently abundant across the study area so as to be available to most breeding pairs. Alternatively, Rollers might use whatever habitat is immediately available to them in their home range, with even relatively poor habitats (e.g. vine) still being 'good enough'. Understanding the relative importance of a few rich patches *vs.* more widespread but poorer quality patches has important consequences for land management and Roller conservation, and essentially represents a small scale land-spring–land-sharing scenario.

In the absence of direct data on Roller foraging behaviour, we use carbon and nitrogen stable isotope signatures as tracers of dietary nutrients, in an attempt to detect signals of foraging habitat selection. We make use of a striking gradient in $\delta^{15}N$ and (to a lesser extent) $\delta^{13}C$ values across the French study area. We first test whether inter-site differences in $\delta^{15}N$ and $\delta^{13}C$ values can be explained simply by Rollers deriving nutrients from different prey sources in proportion to their availability (consistent with, though not proving, an absence of foraging habitat preference). We then examine whether expected prey source $\delta^{15}N$ and $\delta^{13}C$ values within the 250 m core foraging range – again based on random prey selection – predict variation in chick feather $\delta^{15}N$ and $\delta^{13}C$ values.

4.3 Methods

4.3.1 Study sites

Our study was conducted in the Plaine du Roussillon (42.81° N, 2.94° E) in the Pyrénées-Orientales *departement* in southern France (see **Chapter 2** for a more detailed description of the site). Due to the positioning of nest-boxes, our main study site naturally divides into two; Garrieux and Saint-Hippolyte. Garrieux is the northerly of the two sites, in the orchard- and meadow-dominated landscape on the edge of the Etang du Salses (a saline lagoon surrounded by saltmarsh). A few kilometres to the south, Saint-Hippolyte is dominated by vineyards and fallow.

4.3.2 Tissue sample collection

During the standard ringing of nestlings, 2–3 body feathers were collected from 122 individuals between 2013 and 2015. In total, 37 nests were sampled, 15 in Garrieux and 22 in Saint-Hippolyte. Feathers were collected between June 24 and July 26 (mean = July 14, IQR = July 8–22) from chicks 32–51 days after the estimated first egg date, corresponding to a nestling age of ~ 9–28 days (mean = 19.5, IQR = 16–23).

Insects of order Orthoptera (grasshoppers / crickets) and family Cicadidae (cicadas) – the main prey items of Rollers in southern Europe (Cramp 1985; Avilés & Parejo 2002) – were collected by hand in early July 2015. Five sampling points, two in Garrieux and three in Saint Hippolyte, were chosen at random. At each sampling point, ~ 5 specimens of each taxon were collected from the nearest orchard, vine, fallow and (in Garrieux only) hay field. These four land-uses make up, on average, 80 % of the area within 250 m of each sampled nest. In total, 143 insects were collected from 17 fields (74 Orthoptera and 69 cicadas).

4.3.3 Chemical analysis

Analysis of stable isotope ratios was carried at the University of East Anglia. Feathers were washed in a 2:1 chloroform/methanol solution, left to dry in a fume cupboard overnight, then cut into small (~2 mm) sections. Insect specimens were rinsed in distilled water, air-dried, and then had their appendages removed (legs, wings and heads; body parts which are generally removed or regurgitated by Rollers and so rarely metabolised). Insects were then desiccated in a freeze drier and powdered with a pestle and mortar.

Each sample of ~ 0.5 mg was weighed into a tin capsule. These were crimped (expelling all air) and loaded into a combustion Costech elemental analyser coupled to a Thermo Scientific Delta XP continuous flow mass spectrometer with a Conflo III interface. All samples were measured alongside in-house references (casein) and standards (collagen). Across all batches, the mean precision of $\delta^{15}N$ and $\delta^{13}C$ values was 0.11 ‰ and 0.47 ‰, respectively. Stable isotope ratios are expressed as deviations from international standards (AIR for nitrogen and V-PDB for carbon), and reported in per mil (‰) units.

4.3.4 Variation in chick feather stable isotope ratios

We first compared within- and between-brood variation in nitrogen and carbon stable isotope ratios using ANOVA, with brood identity as the grouping variable. Within-brood variation was negligible, so we used brood-mean data for all further analyses. Differences in brood-mean $\delta^{15}N$ and $\delta^{13}C$ values between sites (a 2-level fixed factor) and years (a 3-level fixed factor) were tested using linear models. Candidate models for each isotope were constructed using all combinations of site, year and intercept, and were compared based on AICc values (**Table S2.1**). To compare the carbon–nitrogen niche space of chicks in Garrieux and Saint-Hippolyte, we estimated standard ellipses (corrected for sample size) and their area of overlap using the *siar* R package (Parnell & Jackson 2013).

4.3.5 Variation in prey source stable isotope ratios

Variations in raw prey source isotope values were explored using separate linear models for $\delta^{15}N$ and $\delta^{13}C$. We first compared the univariate effects of site (a 2-level factor), land-use (3 levels in Saint-Hippolyte, 4 in Garrieux) and taxa (a 2-level factor) based on AICc values (**Table S2.2**). We then constructed a global model with fixed effects of site, land-use and taxa, as well as all pair-wise interactions (i.e. site × land-use, site × taxa and land-use × taxa). Candidate models were created using all combinations of predictor variables, and were compared based on AICc values (**Table S2.3**).

Because there were no systematic effects of land-use or taxa on insect stable isotope ratios, we defined ‘prey sources’ as all unique combinations of site, land-use and taxa (**Fig. 4.1**). However, not all prey sources are equally ‘available’ across the study area; for example, fallow is rare in Garrieux (< 2 % cover), orchard is rare in Saint-Hippolyte (< 9 % cover), and Cicadidae make up a larger proportion of biomass in vine (~ 85 %) than do Orthoptera (~ 15 %). Because insect collection was targeted so as to sample a representative range of prey sources, rather than to sample prey sources in proportion to their availability, simply comparing raw prey source isotope values may give an inaccurate estimate of ‘available’ dietary isotope values. In order to estimate the average stable isotope signature of a randomly selected prey item, we calculated availability-weighted mean prey source $\delta^{15}N$ and $\delta^{13}C$ at three levels:

1. The site level, by weighting prey source isotope values by the proportional biomass of each taxon in each land-use and the proportional cover of each land-

use across each site. This represents the average estimated isotope value of a prey source selected randomly from each site (horizontal dashed lines in **Figs. 4.1**, **4.2** and **4.3**). Land-use proportional cover was calculated as the site-level mean proportional cover of the four land-uses around each nest (250 m radius), and proportional biomass was the relative ratio of biomass accounted for by Orthoptera and Cicadidae between 16 June and 16 July (based on transect data described in **Chapter 3**).

2. The land-use level, by weighting prey source isotope values by the proportional biomass of each taxon in each land-use. This represents the average estimated isotope value of a prey source selected randomly from each land-use in each site (**Fig. 4.2**).
3. The taxon level, weighting the prey source isotope values by the proportional biomass contribution of each land-use for each taxon and the proportional cover each land-use across each site. This represents the average estimated isotope value of a prey source selected randomly from each taxon in each site (**Fig. 4.3**).

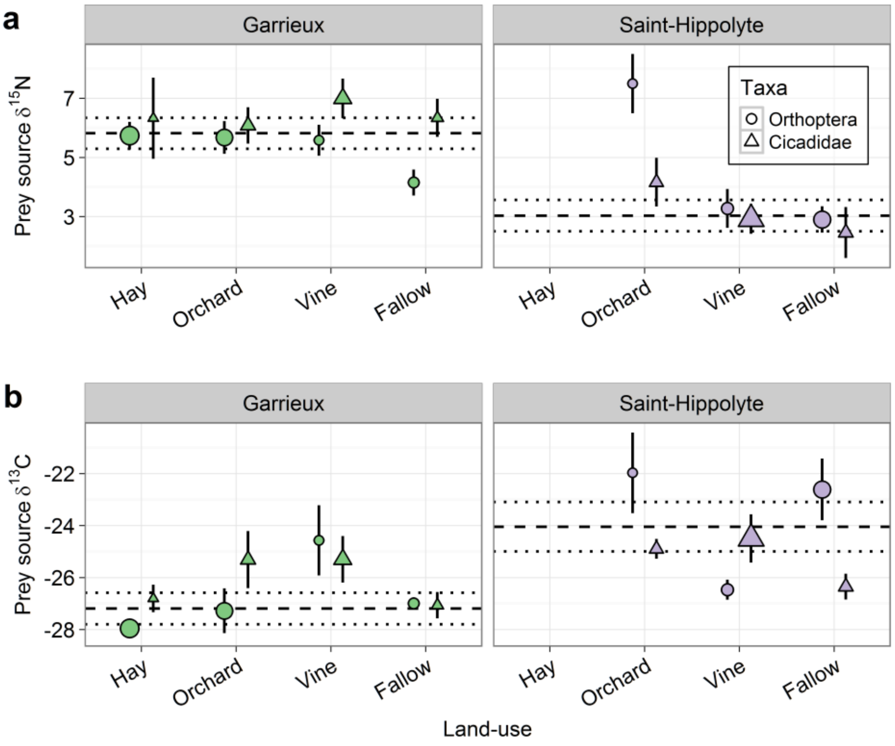


Figure 4.1 Raw prey source δ^{15}N and δ^{13}C values for all unique combinations of site, land-use and taxa. Points show mean values ± S.E. Dashed horizontal lines show weighted site-level means (± S.E). Point size is proportional to relative availability of each prey source per site (i.e. their contribution to the site-level mean).

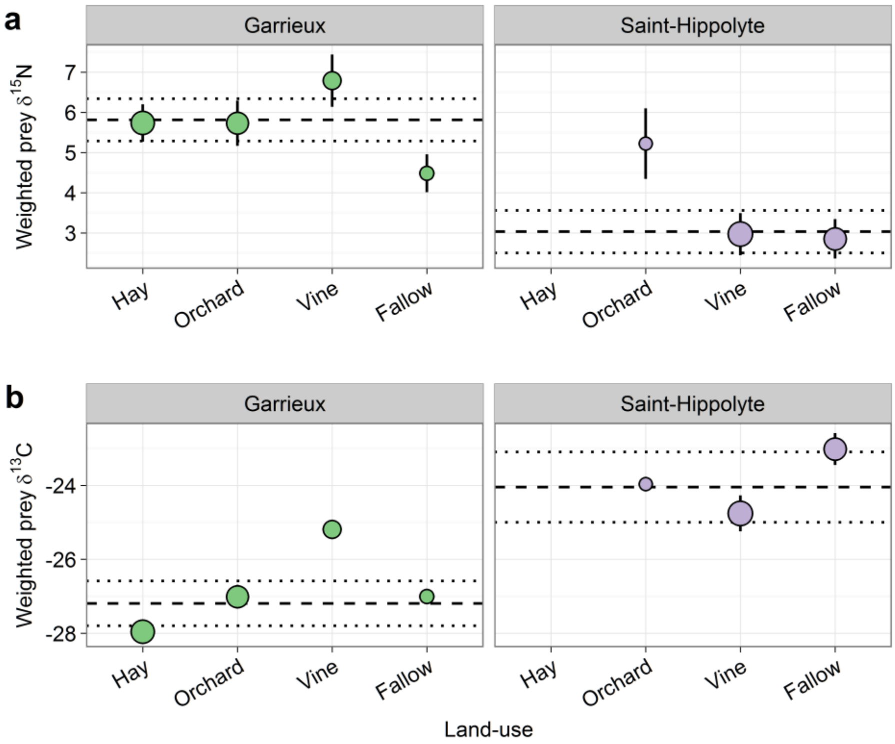


Figure 4.2 Weighted prey source δ^{15}N and δ^{13}C values pooled across land-uses. Points show weighted mean values ± S.E. Dashed horizontal lines show weighted site-level means (± S.E). Point size is proportional to relative availability of each prey source per site.

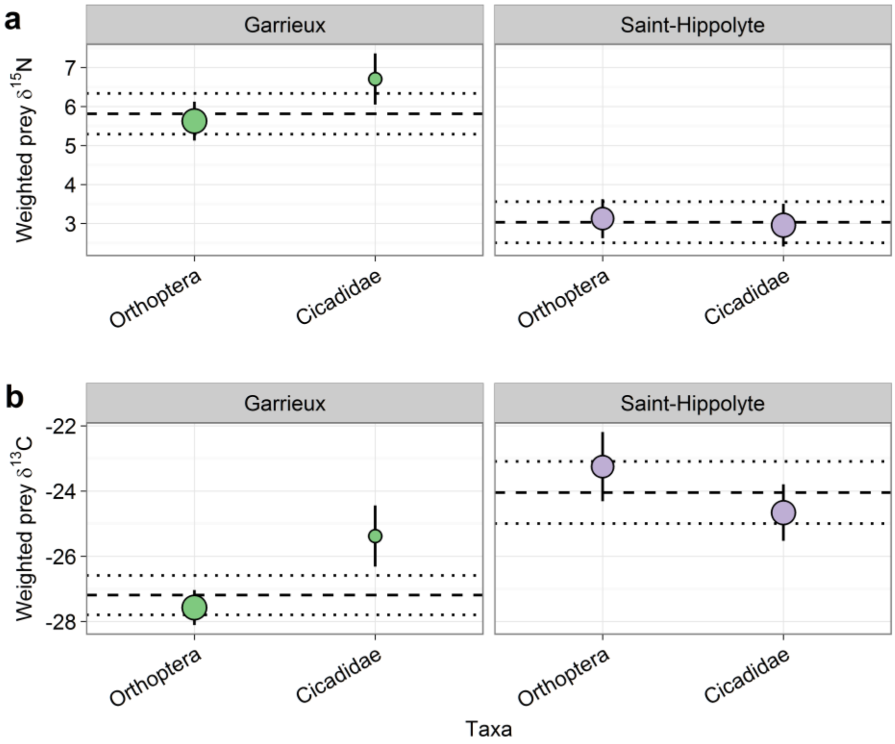


Figure 4.3 Weighted prey source δ^{15}N and δ^{13}C values pooled across taxa. Points show weighted mean values ± S.E. Dashed horizontal lines show weighted site-level means (± S.E). Point size is proportional to relative availability of each prey source per site.

4.3.6 Site-level expected prey isotope values

We first tested whether inter-site differences in chick feather $\delta^{15}N$ and $\delta^{13}C$ values matched inter-site differences in estimated average prey source $\delta^{15}N$ and $\delta^{13}C$ values. We used linear regression to estimate the slope of the relationship between site-level average prey source (i.e. horizontal dashed lines in **Figs. 4.1**, **4.2** and **4.3**) and chick feather $\delta^{15}N$ and $\delta^{13}C$ values.

Absolute differences between diet and consumer stable isotope ratios result from trophic enrichment, and are described by ‘trophic discrimination factors’ (TDFs), which have not been quantified for the European Roller. Instead, we estimate TDFs for $\delta^{15}N$ and $\delta^{13}C$ using *DEsiR*, a Bayesian imputation approach to estimating species- and tissue-specific TDFs from a comprehensive meta-analysis of published values (Healy *et al.* 2016). We thus judged whether Roller chicks were ^{15}N or ^{13}C enriched or depleted relative to expected prey, using these estimated TDFs.

Our null expectation – a fitted slope not different to 1, with an intercept approximating the estimated TDF – is consistent with Rollers deriving nutrients from the ‘average’ available prey source, rather than consuming more of a particular prey source. Deviations from this expected relationship were interpreted with reference to prey source isotope values in **Figs. 4.1**–**4.3**.

4.3.7 Nest-level expected prey isotope values

Next, we estimated the availability-weighted mean prey source $\delta^{15}N$ and $\delta^{13}C$ values for each nest by weighting prey source isotope values by the proportional cover of each land-use type in a 250 m radius and the proportional biomass of each taxon in each land-use type. This represents the average estimated stable isotope ratio of a prey source selected randomly from within the core foraging range (see **Chapter 3**).

To test the null hypothesis that chick feather nutrients are derived simply from average available prey sources, we ran linear regressions separately for $\delta^{15}N$ and $\delta^{13}C$ in each site. Chick feather isotope value was the dependent variable, and predicted nest-level dietary isotope value was the predictor variable. As above, our null expectation was a positive relationship (with slope = 1), indicating that Roller chicks derive nutrients from different prey sources in proportion to their availability.

4.4 Results

4.4.1 Variation in chick feather isotope stable isotope ratios

Compared to variation between broods, within-brood variation in feather stable isotope ratios was negligible (ANOVA; $F_{36, 85} = 89.8$, $p < 0.001$ for δ^{15}N; $F_{36, 85} = 30.1$, $p < 0.001$ for δ^{13}C), indicating that, within a nest, all chicks derive nutrients from isotopically similar dietary sources. There was no support for the effect of year on δ^{15}N values (**Table S2.1**), but δ^{13}C values varied significantly between years, with higher values in 2015 compared to 2013 and 2014 ($F_{2, 33} = 15.1$, $p < 0.001$; **Table S2.1**). Inferred nestling age did not differ between years (ANOVA, $F_{1, 35} = 1.2$, $p = 0.28$) or sites ($F_{1, 35} = 0.4$, $p = 0.53$), and had no effect on either δ^{15}N ($F_{1, 35} = 1.4$, $p = 0.25$) or δ^{13}C ($F_{1, 35} = 0.1$, $p = 0.75$).

Even over the small scale of our study area there was strong spatial variation in chick feather stable isotope ratios, with support for the effect of site on both δ^{15}N and δ^{13}C values (**Table S2.1**). Roller chicks from Garrieux and Saint-Hippolyte were completely non-overlapping in isotopic space (estimated standard ellipse overlap = 1.1×10^{-16}; **Fig. 4.4**), despite being separated by only 2 km at their closest point. Between-site differences were most striking for δ^{15}N ($F_{1, 33} = 170.0$, $p < 0.001$), but were also significant for δ^{13}C ($F_{1, 33} = 22.1$, $p < 0.001$); chick feathers were ^{15}N enriched (mean ± S.E. = 9.1 ± 0.17 ‰) and ^{13}C depleted (–23.2 ± 0.10 ‰) in Garrieux compared to Saint-Hippolyte (δ^{15}N = 6.4 ± 0.13 ‰; δ^{13}C = –22.5 ± 0.14 ‰).

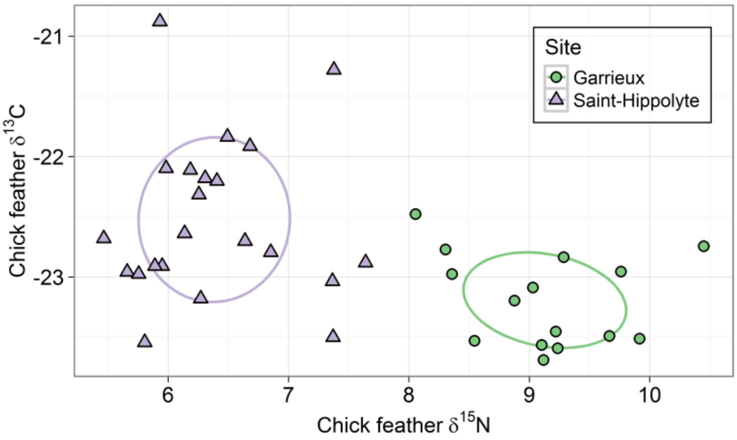


Figure 4.4 Chicks from Garrieux and Saint-Hippolyte do not overlap in carbon-nitrogen niche space. Points show brood-average δ^{15}N and δ^{13}C feathers values, with small-sample-size-corrected standard ellipse.

4.4.2 Variation in insect isotope stable isotope ratios

Overwhelmingly, the strongest univariate predictor of variation in insect $\delta^{15}N$ and $\delta^{13}C$ values was site (**Table S2.2**). Insects were generally ^{15}N enriched and ^{13}C depleted in Garrieux, with no systematic effects of land-use or taxa (**Fig. 4.1**). The ratio of inter- to intra-site variation was higher for $\delta^{15}N$ ($F_{1, 141} = 24.7$, $p < 0.001$) than $\delta^{13}C$ ($F_{1, 141} = 13.7$, $p < 0.001$), the latter thus being more variable within each site. The effects of site were not, however, totally consistent across all land-uses and taxa; for $\delta^{15}N$ there was strong support for site × land-use and site × taxa interactions, and for $\delta^{13}C$ there was strong support for site × taxa interactions (**Table S2.3** and **Fig. 4.1**).

4.4.3 Site-level expected prey isotope values

After weighting all prey sources by their estimated availability in each site, mean $\delta^{15}N$ was 2.8 ‰ higher and mean $\delta^{13}C$ 3.1 ‰ lower in Garrieux than Saint-Hippolyte. In other words, a randomly sampled insect would be ^{15}N enriched and ^{13}C depleted in Garrieux.

For $\delta^{15}N$, there was thus almost perfect correspondence between the inter-site difference in expected prey source $\delta^{15}N$ (2.8 ‰) and chick feather $\delta^{15}N$ (2.7 ‰). As such, the slope of the regression line between site-level expected prey and observed chick $\delta^{15}N$ was almost exactly one ($\beta = 0.99$, 95 % C.I. = 0.83–1.14; **Fig 4.5a**). The absolute difference between expected prey source $\delta^{15}N$ and chick feather $\delta^{15}N$ was therefore similar in Garrieux (+3.3 ‰) and Saint-Hippolyte (+3.4 ‰). These differences are slightly higher than the estimated TDF (median = +2.5 ‰), but well within the 95 % limits (0.06–4.8; **Fig 4.5a**).

For $\delta^{13}C$, the inter-site difference in expected prey source $\delta^{13}C$ (3.1 ‰) was substantially greater than for chick feathers, which were only 0.7 ‰ ^{13}C enriched in Saint-Hippolyte compared to Garrieux. The slope of the regression line between expected prey and observed chick $\delta^{13}C$ was therefore significantly less than one, though still positive ($\beta = 0.21$, 95 % C.I. = 0.09–0.34; **Fig 4.5b**). The absolute difference between expected prey source $\delta^{13}C$ and chick feather $\delta^{13}C$ was substantially higher in Garrieux (+4.0 ‰) compared to both Saint-Hippolyte (+1.5 ‰) and the estimated median TDF of +1.3 ‰ (95 % C.I. = –1.8–4.2).

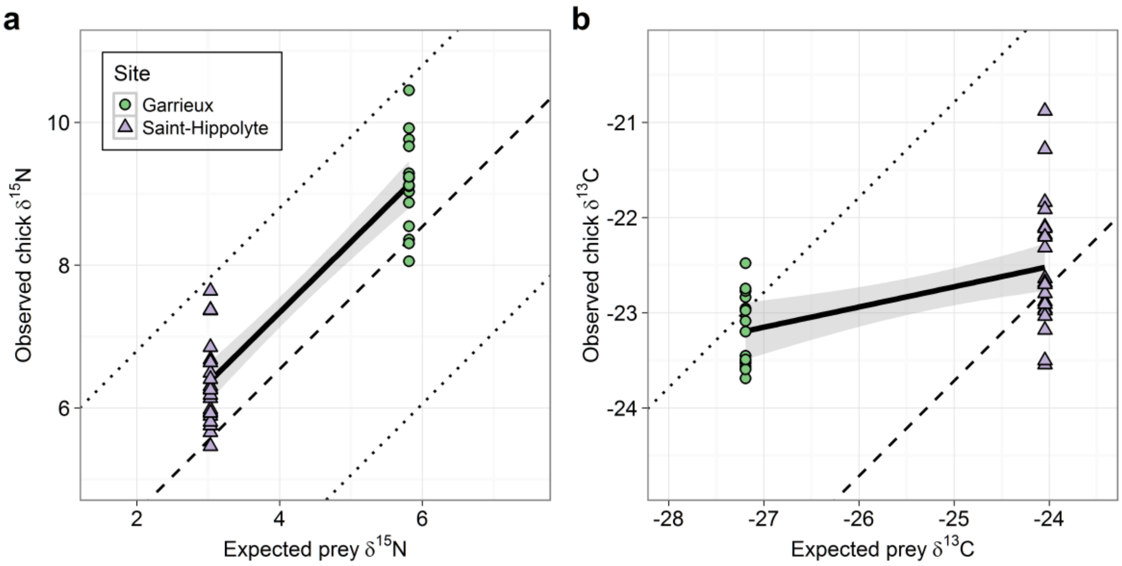


Figure 4.5 Inter-site relationship between expected prey and observed chick feather **a** δ^{15}N and **b** δ^{13}C values. Solid lines are the fitted regression lines (± S.E.) and points are brood-average values. The dashed line has a slope of one and intercepts the *y*-axis at the TDF, representing the relationship expected if consumers derive nutrients from the expected prey sources. Dotted lines represent the 95 % confidence limits of the estimated TDF.

4.4.4 Nest-level expected prey isotope values

Within sites, variation in chick feather δ^{15}N values was, at best, weakly related to nest-level expected prey source δ^{15}N values ($F_{1,20} = 6.0$, $p = 0.02$ in Saint-Hippolyte; $F_{1,13} = 0.04$, $p = 0.85$ in Garrieux). In other words, nests with a high predicted availability of ^{15}N enriched prey sources did not necessarily have high chick feather δ^{15}N values (**Fig. 4.6a** and **b**).

For δ^{13}C, however, there was a significant positive relationship between expected prey and observed chick δ^{13}C values in both Saint-Hippolyte ($F_{1,20} = 8.9$, $p = 0.007$) and Garrieux ($F_{1,20} = 11.6$, $p = 0.005$). The fitted slopes of these relationships were close to one (β = 1.05, 95 % C.I. = 0.32–1.79 in Saint-Hippolyte; β = 0.62, 0.23–1.02 in Garrieux). Thus, within each site, nests surrounded by land-uses with high predicted prey δ^{13}C values tended to have high chick feather δ^{13}C values (**Fig. 4.6c** and **d**).

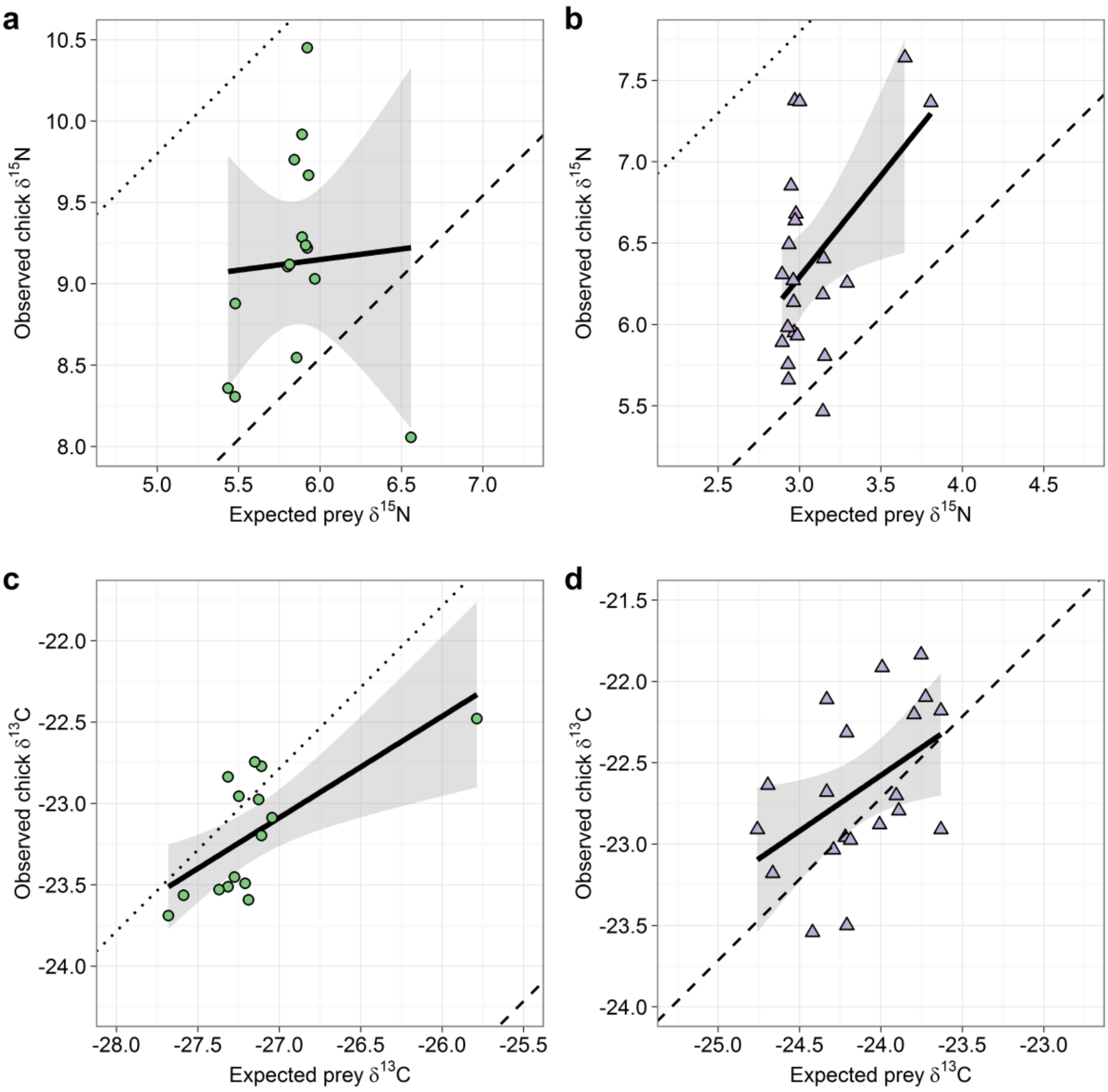


Figure 4.6 Relationship between predicted and observed **a**, **b** δ^{15}N and **c**, **d** δ^{13}C values within each site. Lines show fitted relationship (± S.E.) and points show brood-average values. Dashed line has a slope of 1 and intercepts *x*-axis at the isotope-specific median estimated trophic discrimination factor (dotted lines are 95 % confidence intervals).

4.5 Discussion

Chick feathers collected from nests in Garrieux and Saint-Hippolyte – separated by only a few kilometres – were completely non-overlapping in isotopic space. This difference in chick feather stable isotope values across such a small spatial scale is striking, indicating that chicks in the two sites derive nutrients from isotopically distinct prey sources. The principal aim of this study was to explain this isotopic segregation, providing insights into Roller foraging ecology.

4.5.1 Nitrogen stable isotope ratios

The main driver of inter-site differences in chick feather isotope values was the relative ^{15}N enrichment (+2.7 ‰) of chicks in Garrieux. This pattern was matched almost exactly by inter-site differences in mean expected insect δ^{15}N values (+2.8 ‰). This strongly suggests that the ^{15}N enrichment of chicks from Garrieux is driven simply by their deriving nutrients from available prey sources which are also ^{15}N enriched, rather than a preference for specific prey sources which are ^{15}N enriched. In other words, δ^{15}N appears to provide a signal of site membership. This is supported by the fact that δ^{15}N values were invariable between years and, within each site, relatively consistent across prey sources. Thus, at the nest level, there was no correspondence between expected prey source δ^{15}N and chick feather δ^{15}N.

The marked variation in δ^{15}N values – of prey and consumers alike – over such a small spatial scale requires an explanation. In ecological studies, δ^{15}N has typically been used as an indicator of dietary trophic level (Beaulieu & Sockman 2012; Resano-Mayor *et al.* 2014) or broad gradients in precipitation and aridity (Chamberlain *et al.* 2000; Drake *et al.* 2013). Here we show that, between two sites separated by just a few kilometres, prey sources belonging to the same taxa and exposed to the same topographical and climatic conditions differ, on average, by almost 3 ‰. This difference was largely independent of land-use type, suggesting that soil management plays little role in driving the inter-site difference. Our best guess is that insect δ^{15}N reflects differences in underlying soil δ^{15}N, perhaps driven by the proximity of Garrieux to the saline lagoon (Etang du Salses). Indeed, within Saint-Hippolyte there was a near-significant negative correlation between distance to the shore and chick feather δ^{15}N values ($r = -0.40$, $d.f. = 20$, $p = 0.07$).

The absolute differences between expected prey source δ^{15}N and chick feather δ^{15}N within each site were slightly higher than the estimated TDF for δ^{15}N (as demonstrated by the fitted line sitting above the dashed line in **Fig. 5a**). Given (1) that TDFs have not yet been quantified for the Roller and (2) the large uncertainty surrounding estimated TDFs, we are reluctant to draw inferences based on these estimates. However, assuming that the median TDF is correct for our population, Rollers in both Garrieux and Saint-Hippolyte are ^{15}N enriched relative to mean expected prey source. This suggests a preference for ^{15}N enriched prey sources. However, no prey sources are ^{15}N enriched (relative to the site average) in both sites, so this would require a site-specific preference for Cicadidae- or vine-derived nutrients in Garrieux and orchard-derived nutrients in

Saint-Hippolyte (**Figs. 4.2** and **4.3**). A global preference for some un-measured prey source consistently ^{15}N-enriched across sites (e.g. small vertebrates) may be more likely. Our impression though, given the tight correspondence between expected mean prey source δ^{15}N and chick feather δ^{15}N, is that the TDF has probably been slightly underestimated.

4.5.2 Carbon stable isotope ratios

Patterns of variation differed quite markedly for carbon stable isotope ratios. Compared to δ^{15}N values, chick feather δ^{13}C values varied more between years but less between sites, and prey source δ^{13}C values varied more within sites. Furthermore, there was quite a convincing correspondence between nest-level expected prey source δ^{13}C values and observed chick feather δ^{13}C values. This suggests that – unlike δ^{15}N, which appears to be an indicator of site-membership only – δ^{13}C combines (site-specific) information on land-use and/or prey taxa.

The inter-site difference in mean expected prey source δ^{13}C (3.1 ‰) was much larger than for chick feathers, which were only 0.7 ‰ ^{13}C enriched in Saint-Hippolyte compared to Garrieux. In other words, the random selection of prey sources in proportion to their estimated availability would have resulted in larger inter-site differences than observed for chick feather δ^{13}C values. The absolute difference between expected prey source δ^{13}C and chick feather δ^{13}C closely matched the estimated TDF in Saint-Hippolyte, but was well above the estimated TDF in Garrieux (see position of the fitted line relative to the dashed line in **Figure 5b**). Given the size of this discrepancy compared to TDF uncertainty, we are confident that chicks in Garrieux are ^{13}C enriched relative to expected mean prey, rather than chicks in Saint-Hippolyte being ^{13}C depleted, though a combination of the two may also be likely. Only three prey sources have higher ^{13}C than average in Garrieux; Cicadidae in orchard and vine and Orthoptera in vine. An increase in the proportion of either of these prey sources in the diet of Rollers would thus increase dietary δ^{13}C in Garrieux relative to Saint-Hippolyte (though an increase in Cicadidae in vine would also increase δ^{15}N values in Garrieux). Increased use of vine-derived nutrients seems the most plausible explanation for this difference. Whilst insect biomass is relatively low in vineyards, the abundance of perches combined with sparse vegetation cover is likely to improve the accessibility of prey (Butler & Gillings 2004; Tome *et al.* 2011). An association with vineyards is consistent with anecdotal observations of foraging Rollers, though this hypothesis needs confirming with more quantitative measures. Alternatively, the ^{13}C enrichment of chicks in Garrieux could represent an under-estimation of the availability of high $\delta^{13}C$ prey sources, rather than a foraging preference. Although our insect transects were very efficient at surveying Orthoptera (almost entirely terrestrial), it is possible that we underestimated the availability of Cicadas, which are often airborne or on tall vegetation.

The correlation between nest-level expected prey source $\delta^{13}C$ and chick feather $\delta^{13}C$ is intriguing. Intra-site variation in prey source $\delta^{13}C$ was primarily driven by (1) ^{13}C enrichment of insects from vine and ^{13}C depletion of those from hay in Garrieux and (2) ^{13}C enrichment of insects from fallow and ^{13}C depletion of those from vine in Saint-Hippolyte. That nests with high expected prey source $\delta^{13}C$ tended also to have high chick feather $\delta^{13}C$ strongly suggests that Rollers derive nutrients from different land-uses in proportion to their availability. If, on the other hand, Rollers specialised on a particular prey type (e.g. grasshoppers in fallow) we might expect no relationship between expected prey source $\delta^{13}C$ and chick feather $\delta^{13}C$; instead, all nests would show a similar signal associated with the preferred prey type.

It is unclear why $\delta^{13}C$ values varied between years, particularly given that this increase occurred in both sites, and no single prey source was relatively ^{13}C enriched in both sites. 2015 was a bumper year for Cicadidae (though without robust insect survey data from 2013 and 2014 we cannot quantify this increase), and an increase in the proportion of cicadas in the diet would result in ^{13}C enrichment in Garriuex, though not in Saint-Hippolyte. Another possible driver of the increased $\delta^{13}C$ values in 2015 is a weather-driven increase in the relative proportion of C_4 to C_3 plants (Lajtha & Marshall 1994), though we have no evidence for this. Regardless, the inter-annual variation in chick feather $\delta^{13}C$ values suggests that they represent something more interesting than simply site membership.

Most isotope studies of avian diet have focused on large-bodied species with wide foraging ranges and diverse diets spanning a range of trophic levels and / or biomes (Inger *et al.* 2006; El-Hacen *et al.* 2014; Resano-Mayor *et al.* 2014). Fewer have examined insectivorous birds with smaller foraging ranges (e.g. Girard *et al.* 2012; Cross *et al.* 2014), in which dietary sources may be less isotopically distinct. We avoided placing too much emphasis on estimating the dietary contribution of specific prey sources, partly due to their overlapping isotopic values and partly because of uncertainty surrounding estimated trophic discrimination factors. For these reasons, we chose not to employ isotope mixing models, which are increasingly used in stable isotope dietary studies (e.g. Parnell *et al.* 2010; Bond & Diamond 2011; Phillips *et al.* 2014).

Instead, we were interested in whether the spatial patterns of availability-weighted prey source stable isotope ratios were consistent with patterns in chick feather stable isotopes ratio. Feather carbon stable isotope ratios provide evidence that Rollers derive nutrients from different prey sources in proportion to their availability. Feather nitrogen stable isotope ratios provided a signal primarily of site membership, and the inter-site differences in availability weighted average prey source δ^{15}N corresponded exactly with inter-site differences in chick feather δ^{15}N. The removal of vine-derived nutrients, for example, would have reduced the correspondence between inter-site differences in dietary isotope values and chick feather isotope values. Our results are therefore generally consistent with the French study population not being limited by food availability, instead deriving nutrients from prey sources in proportion to their availability. Specifically, we suggest that vineyards make up for their lower prey abundance by providing high accessibility, so might provide an important foraging resource for Rollers, though this hypothesis needs further confirmation.

Unfortunately, we were unable to collect sufficient data from Latvia to perform comparative analyses, principally due to the high chick mortality rate in 2014 when the main data collection was conducted. However, based on data from 5 nests (**Fig. S2.1**), δ^{15}N values are lower and less variable in Latvia than France, whereas δ^{13}C values are comparable. Our prediction would be that in Latvia, where Rollers are likely to be food limited, chick feather stable isotope values will be more consistent across the study area as Rollers concentrate their foraging efforts in the few high quality areas.

Our results contribute to a growing body of literature highlighting the magnitude of small-scale variation in stable isotope values (Wunder *et al.* 2005; Oppel *et al.* 2011; Charmantier *et al.* 2014). This has concerning implications for the use of broad-scale patterns in stable isotope values for the geographical assignment of migrant birds (Hobson *et al.* 2012b). In reality, small scale decisions relating to local site choice may overwhelm broader geographic signals (Oppel *et al.* 2011). These site-specific stable isotope signatures might instead prove useful in studies of natal dispersal, if 1st year breeders (retaining feathers grown in the nest) can be assigned to their natal site (Charmantier *et al.* 2014).

4.6 References

Aebischer, N.J. & Ewald, J.A. (2012) The grey partridge in the UK: population status, research, policy and prospects. *Animal Biodiversity and Conservation*, **35**, 353–362.

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*, **70**, 227–230.

Barbaro, L., Couzi, L., Bretagnolle, V., Nezan, J. & Vetillard, F. (2008) Multi-scale habitat selection and foraging ecology of the eurasian hoopoe (Upupa epops) in pine plantations. *Biodiversity and Conservation*, **17**, 1073–1087.

Bearhop, S., Hilton, G.M., Votier, S.C. & Waldron, S. (2004) Stable isotope ratios indicate that body condition in migrating passerines is influenced by winter habitat. *Proceedings of the Royal Society of London B: Biological Sciences*, **271**, S215–S218.

Bearhop, S., Waldron, S., Votier, S.C. & Furness, R.W. (2002) Factors that influence assimilation rates and fractionation of Nitrogen and Carbon stable isotopes in avian blood and feathers. *Physiologicl and Biochemical Zoology*, **75**, 451–458.

Beaulieu, M. & Sockman, K.W. (2012) One meadow for two sparrows: Resource partitioning in a high elevation habitat. *Oecologia*, **170**, 529–540.

Bond, A.L. & Diamond, A.W. (2011) Recent Bayesian stable-isotope mixing models are highly sensitive to variation in discrimination factors. *Ecological Applications*, **21**, 1017–1023.

Bowen, G.J. (2010) Isoscapes: Spatial Pattern in Isotopic Biogeochemistry. *Annual Review of Earth and Planetary Sciences*, **38**, 161–187.

Butler, S.J. & Gillings, S. (2004) Quantifying the effects of habitat structure on prey detectability and accessibility to farmland birds. *Ibis*, **146**, 123–130.

Catry, I., Amano, T., Franco, A.M.A. & Sutherland, W.J. (2012) Influence of spatial and temporal dynamics of agricultural practices on the lesser kestrel. *Journal of Applied Ecology*, **49**, 99–108.

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**, e58320.

Chamberlain, C.P., Bensch, S., Feng, X., Åkesson, S. & Andersson, T. (2000) Stable isotopes examined across a migratory divide in Scandinavian willow warblers (Phylloscopus trochilus trochilus and Phylloscopus trochilus acredula) reflect their African winter quarters. *Proceedings of the Royal Society of London B: Biological Sciences*, **267**, 43–48.

Charmantier, A., Blondel, J., Perret, P., Harmelin-Vivien, M. & Fletcher, R. (2014) Tracing site-specific isotopic signatures along a Blue Tit Cyanistes caeruleus food chain. *Ibis*, **156**, 165–175.

Cramp, S. (1985) *The Birds of the Western Palearctic, Volume 4: Terns to Woodpeckers*. Oxford

University Press, Oxford, UK.

Cross, A.D.P., Hentati-Sundberg, J., Österblom, H., McGill, R.A.R. & Furness, R.W. (2014) Isotopic analysis of island House Martins Delichon urbica indicates marine provenance of nutrients (ed L Pichegru). *Ibis*, **156**, 676–681.

Drake, A., Rock, C., Quinlan, S.P. & Green, D.J. (2013) Carry-over effects of winter habitat vary with age and sex in yellow warblers Setophaga petechia. *Journal of Avian Biology*, **44**, 1–10.

El-Hacen, E.H.M., Piersma, T., Jouta, J., Overdijk, O. & Lok, T. (2014) Seasonal variation in the diet of Spoonbill chicks in the Wadden Sea: A stable isotopes approach. *Journal of Ornithology*, **155**, 611–619.

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.

Garcia-Perez, B. & Hobson, K.A. (2014) A multi-isotope (δ2H, δ13C, δ15N) approach to establishing migratory connectivity of Barn Swallow (Hirundo rustica). *Ecosphere*, **5**, 1–12.

Girard, J., Baril, A., Mineau, P. & Fahrig, L. (2012) Foraging habitat and diet of Song Sparrows (Melospiza melodia) nesting in Farmland: a stable isotope approach. *Canadian Journal of Zoology*, **90**, 1339–1350.

Gunnarsson, T.G., Gill, J.A., Newton, J., Potts, P.M. & Sutherland, W.J. (2005) Seasonal matching of habitat quality and fitness in a migratory bird. *Proceedings of the Royal Society of London B: Biological Sciences*, **272**, 2319–2323.

Healy, K., Kelly, S., Guillerme, T., Inger, R., Bearhop, S. & Jackson, A. (2016) Predicting trophic discrimination factor using Bayesian inference and phylogenetic, ecological and physiological data. DEsIR: Discrimination Estimation in R. *PeerJ Preprints*, e1950v1.

Hobson, K.A. & Bairlein, F. (2003) Isotopic fractionation and turnover in captive Garden Warblers (Sylvia borin): implications for delineating dietary and migratory associations in wild passerines. *Canadian Journal of Zoology*, **81**, 1630–1635.

Hobson, K.A., van Wilgenburg, S.L., Piersma, T. & Wassenaar, L.I. (2012a) Solving a Migration Riddle Using Isoscapes: House Martins from a Dutch Village Winter over West Africa. *PLoS One*, **7**, 1–7.

Hobson, K.A., Van Wilgenburg, S.L., Wassenaar, L.I., Powell, R.L., Still, C.J. & Craine, J.M. (2012b) A multi-isotope (δ13C, δ15N, δ2H) feather isoscape to assign Afrotropical migrant birds to origins. *Ecosphere*, **3**, 1–20.

Inger, R. & Bearhop, S. (2008) Applications of stable isotope analyses to avian ecology. *Ibis*, **150**, 447–461.

Inger, R., Ruxton, G.D., Newton, J., Colhoun, K., Robinson, J. a., Jackson, A.L. & Bearhop, S. (2006) Temporal and intrapopulation variation in prey choice of wintering geese determined by stable isotope analysis. *Journal of Animal Ecology*, **75**, 1190–1200.

Lajtha, K. & Marshall, J. (1994) Sources of variation in the stable isotopic composition of plants. *Stable Isotopes in Ecology and Environmental Science* (eds K. Lajtha & J. Marshall), pp. 1–21. Blackwell Scientific Publications.

Marra, P., Hobson, K.A. & Holmes, R.T. (1998) Linking Winter and Summer Events in a Migratory Bird by Using Stable-Carbon Isotopes. *Science*, **282**, 1884–1886.

Oppel, S., Pain, D.J., Lindsell, J.A., Lachmann, L., Diop, I., Tegetmeyer, C., Donald, P.F., Anderson, G.Q.A., Bowden, C.G.R., Tanneberger, F. & Flade, M. (2011) High variation reduces the value of feather stable isotope ratios in identifying new wintering areas for aquatic warblers Acrocephalus paludicola in West Africa. *Journal of Avian Biology*, **42**, 342–354.

Parnell, A.C., Inger, R., Bearhop, S. & Jackson, A.L. (2010) Source partitioning using stable isotopes: coping with too much variation. *PLoS One*, **5**, e9672.

Parnell, A. & Jackson, A. (2013) siar: Stable Isotope Analysis in R. R package version 4.2.

Phillips, D.L., Inger, R., Bearhop, S., Jackson, A.L., Moore, J.W., Parnell, A.C., Semmens, B.X. & Ward, E.J. (2014) Best practices for use of stable isotope mixing models in food-web studies. , **835**, 823–835.

Resano-Mayor, J., Hernández-Matías, A., Real, J., Parés, F., Inger, R. & Bearhop, S. (2014) Comparing pellet and stable isotope analyses of nestling Bonelli's Eagle Aquila fasciata diet. *Ibis*, **156**, 176–188.

Rubenstein, D.R. & Hobson, K.A. (2004) From birds to butterflies: animal movement patterns and stable isotopes. *Trends in Ecology and Evolution*, **19**, 256–263.

Thorup, K., Sunde, P., Jacobsen, L.B. & Rahbek, C. (2010) Breeding season food limitation drives population decline of the Little Owl Athene noctua in Denmark. *Ibis*, **152**, 803–814.

Tome, R., Dias, M.P., Chumbinho, A.C. & Bloise, C. (2011) Influence of perch height and vegetation structure on the foraging behaviour of Little Owls Athene noctua: how to achieve the same success in two distinct habitats. *ARDEA*, **99**, 17–27.

Veen, T., Hjernquist, M.B., Van Wilgenburg, S.L., Hobson, K.A., Folmer, E., Font, L. & Klaassen, M. (2014) Identifying the African wintering grounds of hybrid flycatchers using a multi-isotope (δ2H, δ13C, δ15N) assignment approach. *PLoS One*, **9**, e98075.

Wunder, M.B., Kester, C.L., Knopf, F.L. & Rye, R.O. (2005) A test of geographic assignment using isotope tracers in feathers of known origin. *Oecologia*, **144**, 607–617.

Appendix 2: Supporting information for Chapter 4

Supplementary tables

Table S2.1 Model summaries for the effect of site and year on chick feather (brood-mean) $\delta^{15}N$ and $\delta^{13}C$ values. k = number of parameters in model; Δ_i = difference in AICc between i^{th} model and 'best' model; w_i = Akaike model weight. ✓ = factor present; / = factor absent. Intercept, though not shown, is present in all models.

Model	*site*	*year*	***k***	**AICc**	Δ_i	w_i
$\delta^{15}N$						
1	✓	/	3	75.4	0.00	0.819
2	✓	✓	5	78.4	3.02	0.181
3	/	/	2	138.4	63.02	< 0.001
4	/	✓	4	142.1	66.69	< 0.001
$\delta^{13}C$						
1	✓	✓	5	49.3	0.00	0.997
2	/	✓	4	61.3	11.97	0.003
3	✓	/	3	68.2	18.84	< 0.001
4	/	/	2	76.9	27.56	< 0.001

Table S2.2 Model summaries for univariate effect of land-use, site and taxa on insect $\delta^{15}N$ and $\delta^{13}C$ values.

Model	*site*	*land-use*	*taxa*	***k***	**AICc**	Δ_i	w_i
$\delta^{15}N$							
1	✓	/	/	3	665.6	0.00	0.986
2	/	✓	/	5	674.1	8.49	0.014
3	/	/	/	2	686.6	20.96	< 0.001
4	/	/	✓	3	688.4	22.82	< 0.001
$\delta^{13}C$							
1	✓	/	/	3	745.2	0.00	0.990
2	/	✓	/	5	754.7	9.48	0.009
3	/	/	/	2	756.4	11.14	0.004
4	/	/	✓	3	758.3	13.06	0.001

Table S2.3 Model summaries for interactive effects of land-use, site and taxa on insect δ^{15}N and δ^{13}C values. Results are presented only for models with $\Delta_i < 2$, but w_i is calculated across all models.

Model	*land-use*	*site*	*taxa*	*land-use × site*	*land-use × taxa*	*site × taxa*	***k***	**AICc**	$\boldsymbol{\Delta_i}$	$\boldsymbol{w_i}$
δ^{15}N										
1	✓	✓	✓	✓	✓	✓	13	644.4	0.00	0.574
2	✓	✓	✓	✓	/	✓	10	645.3	0.90	0.367
δ^{13}C										
1	/	✓	✓	/	/	✓	5	743.2	0.00	0.342
2	✓	✓	✓	✓	/	✓	10	745.1	1.86	0.135

Supplementary figures

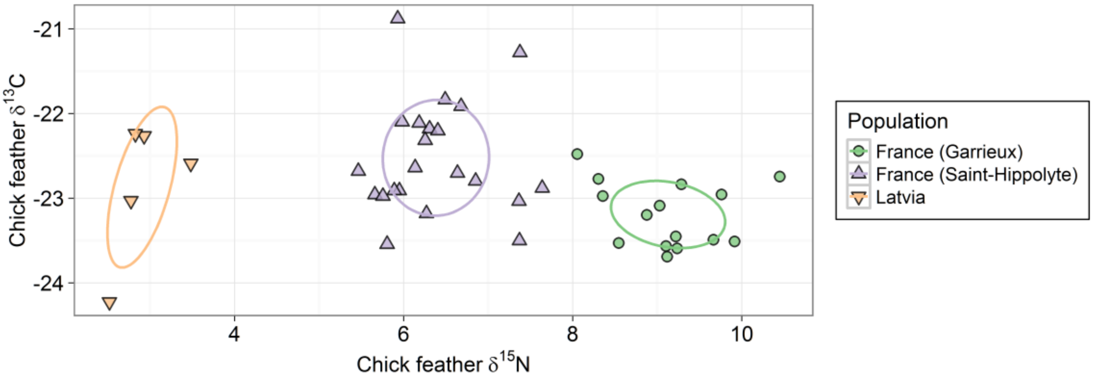


Figure S2.1 Chicks feather stable isotope ratios from Latvia and France. Points show brood-average δ^{15}N and δ^{13}C feathers values.

Chapter 5: A pan-European, multi-population assessment of migratory connectivity in a near-threatened migrant bird

A version of this chapter is published in *Diversity and Distributions*, **9**, 1051–1062

5.1 Abstract

The extent to which individuals from different breeding populations mix throughout the non-breeding season (i.e. ‘migratory connectivity’) has important consequences for population dynamics and conservation. Given recent declines of long-distance migrant birds, multi-population tracking studies are crucial in order to assess the strength of migratory connectivity and to identify key sites *en route*. Here, we present the first large-scale analysis of migration patterns and migratory connectivity in the globally near-threatened European Roller *Coracias garrulus*. We synthesise new geolocator data with existing geolocator, satellite tag and ring recovery data from eight countries across Europe. We describe routes and stopover sites, analyse the spatial pattern of winter sites with respect to breeding origin, and quantify the strength of connectivity between breeding and winter sites. We demonstrate the importance of the northern savannah zone as a stopover region and reveal the easterly spring loop (via Arabia) and leap-frog migration of Rollers from eastern populations. Whilst there was some overlap between individuals from different populations over winter, their distribution was non-random, with positive correlations between breeding and autumn/winter longitude as well as between pairwise distance matrices of breeding and winter sites. Connectivity was stronger for eastern populations than western ones. The moderate levels of connectivity detected here may increase the resilience of breeding populations to localised habitat loss on the winter quarters. We also highlight passage regions crucial for the successful conservation of Roller populations, including the Sahel / Sudan savannah for all populations, and the Horn of Africa / Arabian Peninsula for north-eastern Rollers.

Supporting information can be found in ***Appendix 3****.*

5.2 Introduction

Migratory birds are potentially more vulnerable to environmental change than sedentary species because they rely on resources at a series of sites separated by hundreds to thousands of kilometres (Newton 2004). It is therefore unsurprising that birds that migrate from temperate breeding grounds to tropical winter quarters are declining faster than their sedentary counterparts (Sanderson *et al.* 2006; Hewson & Noble 2009; Vickery *et al.* 2013). Recent evidence suggests that the mechanisms driving these declines are population-specific combinations of potentially interacting factors acting on the breeding, passage, and/or wintering grounds (Morrison *et al.* 2013; Vickery *et al.* 2013). Disentangling the mechanisms that limit migrant populations in order to guide their conservation therefore requires an understanding of their spatio-temporal distribution throughout the annual cycle.

A growing body of tracking studies are now identifying the sites used and threats encountered by migrants during the non-breeding season. These studies also reveal a range of migration strategies and patterns, including migratory divides (Reichlin *et al.* 2008), narrow- (Willemoes *et al.* 2014) and broad-front migration (Schmaljohann *et al.* 2012), leap-frog migration (Panuccio, Mellone & Muner 2013), loop migration (Tøttrup *et al.* 2012) and convergence at ecological barriers (Strandberg *et al.* 2009). Of particular value (but also scarcity) are multi-population tracking studies from across a species' range examining intraspecific variation in migration strategy. Multi-population studies also provide insight into migratory connectivity i.e., the extent of mixing of different breeding populations during the non-breeding season (Trierweiler *et al.* 2014; Stanley *et al.* 2014). Migratory connectivity is described along a continuum from complete segregation ('strong' connectivity) to complete mixing ('weak' connectivity) of different breeding populations during the non-breeding season (Webster *et al.* 2002). The strength of connectivity is expected to underpin the response of populations to habitat loss (Martin *et al.* 2007; Taylor & Norris 2009; Iwamura *et al.* 2013) with strong connectivity increasing their vulnerability, as any local deterioration in non-breeding conditions will be felt by all members of a breeding population (Dolman & Sutherland 1992; Jones *et al.* 2008; Cresswell 2014). Although migratory connectivity is typically measured between breeding and winter populations (Ryder, Fox & Marra 2011; Fraser *et al.* 2012; Cormier *et al.* 2013), the mixing of individuals *en route* and at stopover sites is arguably just as important, particularly given that mortality is often greatest during migration (Sillett & Holmes 2002; Lok, Overdijk & Piersma 2015). Connectivity across the annual cycle therefore has strong implications for conservation management, and its estimation is an important precondition for their effective delivery.

The European Roller *Coracias garrulus* (hereafter ‘Roller’) is a near-threatened long-distance migrant that has declined by 20–30 % globally over the last decade (Baillie, Hilton-Taylor & Stuart 2004). The species is classified as vulnerable in Europe, having gone extinct in several central and northern territories (Burfield & van Bommel 2004; Kovacs *et al.* 2008). Most authors attribute this decline to the degradation of the open agricultural habitats in which Rollers generally breed (e.g. Avilés & Parejo 2004; see also Kovacs *et al.* 2008). However, with ‘migration and wintering grounds’ identified as a knowledge gap for this species (Kovacs *et al.* 2008), the influence of non-breeding conditions on Roller population dynamics remains unknown. Three recent tracking studies have revealed the year-round movements of Rollers from the western extremes of the breeding range (Emmenegger *et al.* 2014; Catry *et al.* 2014; Rodríguez-Ruiz *et al.* 2015), but further tracking studies from across the range are necessary to broaden our understanding of Roller migration and population structure.

Here, we expand these single-country studies into a pan-European analysis by combining all existing published data with new data from Rollers tagged in Portugal, France, Austria, Montenegro, Latvia & Cyprus. We identify and compare migratory strategies and wintering grounds of Rollers breeding across Europe, and quantify the strength of connectivity between breeding and winter sites. This multi-population study provides a crucial step towards better understanding the population dynamics of the Roller; a prerequisite for its successful conservation.

5.3 Methods

We combine new data from 17 solar geolocators with geolocator (n = 9) and satellite tag (6) data from three existing studies (Emmenegger *et al.* 2014; Catry *et al.* 2014; Rodríguez-Ruiz *et al.* 2015), and the only sub-Saharan ring recovery. Our data yield from breeding populations in Portugal (n = 4 individuals), Spain (10), France (8, with 1 individual tracked over two years), Austria (1), Montenegro (3), Latvia (4), Bulgaria (1 ring recovery) and Cyprus (1), spanning 3600 km longitude and 2500 km latitude and providing good coverage across the western half of the Roller’s global breeding distribution (Birdlife International 2013; **Fig. 5.1**). All devices were deployed on breeding Rollers captured at or near the nest site, towards the end of incubation or during chick-rearing.

5.3.1 Geolocator data

In total, 113 solar geolocators (mass = 1.4–3.1 g; 0.7–2.9 % of adult Roller mass (Cramp 1985)) were deployed across eight countries between 2009 and 2013 (see **Appendix 3**, **Table S3.1**). After accounting for return of tagged birds (48/113 = 42 %), successful recapture (43/48 = 90 %), tag loss (13/43 = 30 %) and total electronic failure (4/30 = 13 %), data were successfully downloaded from 26 tags. Of these, three failed before the onset of spring migration, but after arrival to the winter quarters.

We employ the standard 'threshold model' of geolocation, which involves estimating latitude from day/night length and longitude from the timing of solar noon/midnight, and yields two position per 24 hour period. Sunrise and sunset (hereafter 'transitions', from which day/night length and timing of solar noon/midnight are derived) are identified when light intensity crosses a pre-defined threshold. Due to differences in light data output, the procedure for identifying sun transitions varies according to tag manufacturer. For BASTrak devices, initial data handling was conducted using the BASTrak software suite (British Antarctic Survey 2008). We used a threshold of 2 arbitrary light units and identified and removed false transitions (due to shading during daylight) by setting a minimum dark period of 4 h. Any remaining false transitions (n = 18 over 4 devices) were identified and removed manually. BASTrak devices record maximum light intensity over a model-specific logging period (2, 5 or 10 minutes), meaning that sunsets (but not sunrises) must be advanced by the length of this logging period. For SOI devices, and for all further analyses, we used the R (v3.1.2, R Development Core Team 2014) *GeoLight* package (Lisovski & Hahn 2012). A threshold of 3 units above the baseline level was used, and false transitions were filtered out by fitting a LOESS curve to the transition data, removing transitions exceeding three interquartile ranges of the curve.

In order to estimate geographical position from sun transition timings, the sun angle to which the chosen light threshold corresponds must be determined (i.e. calibration). We employed 'in-habitat calibration' (Lisovski *et al.* 2012) identifying for each tag the sun elevation angle that minimised latitudinal deviation from the known nesting location during the 21 day period following deployment (mean = –3.8°, min = –5.0°, max = –1.9°). The suitability of this angle is not necessarily constant in space and time because shading conditions (due to vegetation, cloud or topography, for example) may vary, but this technique is commonly used in geolocator studies, and alternative calibration methods (e.g. Hill-Ekstrom (Lisovski *et al.* 2012)) were not possible. We used the in-habitat angle to estimate twice-daily positions for all transition data from a given tag, but explored the influence of calibration angle on location estimates by recalculating mean winter and stopover (see next paragraph) latitudes using in-habitat angle ± 0.5° and ± 1.0° (calibration has no effect on longitude). Latitude estimates during the spring and autumn equinoxes – when latitudinal variation in day length is insufficient for successful geolocation – were discarded (mean period rejected per equinox = 20 days; min = 18, max = 52, depending on the calibration angle assigned to a given tag).

To separate stationary periods from periods of movement we used the *changeLight* function (following Emmenegger *et al.* (2014)), which fits a changepoint model to sun transitions (quantile = 0.90, minimum stationary period = 5 days), allowing the detection of stationary periods throughout the annual cycle, including during the equinoxes when geographical positions are unavailable. For each individual, spatially overlapping and temporally adjacent stationary sites were aggregated manually and the mean (± SD) position of each site, in addition to the December-January (hereafter 'winter') period was calculated. Individual route maps are presented in **Fig. S3.1** for new geolocator data only (*n* = 17).

5.3.2 Satellite tag data

Twelve 5 g solar-powered Platform Transmitting Terminals (PTT-100, Microwave Telemetry Inc., Columbia, MD, USA) were deployed on breeding adult Rollers from six sites across Spain in 2012 and 2013. After accounting for death or device failure, we were able to analyse the tracks of six individuals to their winter grounds, and one on return migration. We randomly selected one 'high quality' (up to 1.5 km accuracy) location per day, and defined stopover and winter periods (mean ± SD position) as all points reflecting less than 20 km movement in a 24 hour period. See Rodríguez-Ruiz *et al*. (2015) for full details.

5.3.3 Ring recovery data

We are aware of only one sub-Saharan ring recovery of a European Roller; a nestling ringed in Haskovo, Bulgaria in July 1936 and found in Tabora, Tanzania on 15 December 1936 (Pateff 1942). Given that all tracked birds described in this study had reached their winter sites by early December, we assume that this ringed individual had reached its final destination upon recovery (although we have no information on whether migration schedules differ between juveniles and adults).

5.3.4 Analyses

Inferences about routes and precise phenology are limited by the latitudinal uncertainty of geolocator data during movement periods (and are of course impossible with our single ring-recovery). We therefore present stopover sites (as defined above) and infer routes taken based predominantly on longitude data. Rather than presenting individual-level phenological data we show median dates (with interquartile range, IQR) of arrival to and departure from the breeding, autumn and winter sites, based on changepoint analysis of sun events (see above).

In order to examine migratory connectivity throughout the annual cycle, we combine data from all sources ($n = 33$, though lower for some analyses). Pearson's correlation coefficients were calculated between (1) longitude of breeding and post-Saharan autumn stopover site, (2) longitude of breeding and winter site (where positive coefficients indicate a 'parallel' migration pattern), (3) breeding site latitude and orthodromic (great circle) migration distance, and (4) latitude of breeding and winter site (where positive coefficients indicate sequential ('chain') migration and negative coefficients occur when northerly breeders winter furthest south ('leap-frog' migration)). We also calculated the Mantel correlation coefficient (r_M, range –1–1) between pairwise (orthodromic) distance matrices of breeding sites and winter sites, where positive correlations indicate that individuals that breed close together also winter together (i.e. migratory connectivity; Ambrosini, Møller & Saino 2009). Tests were conducted across all individuals, as well as independently for western (Portugal, Spain and France) and eastern (east from Austria) subsets.

In order to account for uncertainty around the mean geolocator-derived positions of autumn stopover and winter sites, we repeated the analyses using a randomised iterative process, sampling new positions from the error distribution about mean positions (see **Appendix 3** for details). Furthermore, to explore the implications of sample size for our analyses, we conducted resampling experiments in which each statistical test was performed on sequentially reduced datasets (see **Appendix 3** for details).

5.4 Results

5.4.1 Autumn migration

Median departure date from the breeding site was 21th August (IQR: 3rd Aug – 6th Sep). In the west, two autumn routes were apparent; Rollers from south-west Iberia took a westerly route along the Atlantic coast of west Africa before bearing east along the savannah belt, whereas those from north-east Spain and southern France flew directly across the Sahara (**Fig. 5.2, Fig. S3.1**). In the east, Rollers migrated south over the Mediterranean Sea and Sahara Desert; for Latvian birds, this southwards movement occurred on a broad front with several Mediterranean crossing points.

Stopovers were detected in south-east Europe for Latvian Rollers and west Africa for Rollers from south-west Iberia, and all birds made a prolonged autumn stopover in the northern savannah (**Table 5.1**; median arrival = 20st September (IQR: 8th Sep – 29th Sep); median departure = 3rd November (IQR: 26th Oct – 14th Nov)). There was a significant correlation between breeding and autumn stopover site longitude (Pearson's correlation: $r = 0.81$, $d.f. = 29$, $p < 0.001$; **Fig. 5.3a**). This association was near-significant when using data only from eastern populations ($r = 0.63$, $d.f. = 7$, $p = 0.07$) but not with data from western populations alone ($r = 0.27$, $d.f. = 20$, $p = 0.22$). In addition to the main autumn stopover, some individuals also stopped south of the equator prior to reaching their winter quarters. Median arrival to the winter quarters was 14th November (IQR: 3rd Nov – 21st Nov).

5.4.2 Winter quarters

All individuals spent the winter period in southern Africa, between the equator and 20–25° S (**Table 5.1, Fig. 5.1**). Data from the PTT devices suggests that at least some individuals make small-scale movements during the winter period (mean winter site SD = 46 km for latitude; 50 km for longitude) which are too small to be detected by geolocators. There is no evidence of substantial variation in winter distribution between years (data not shown).

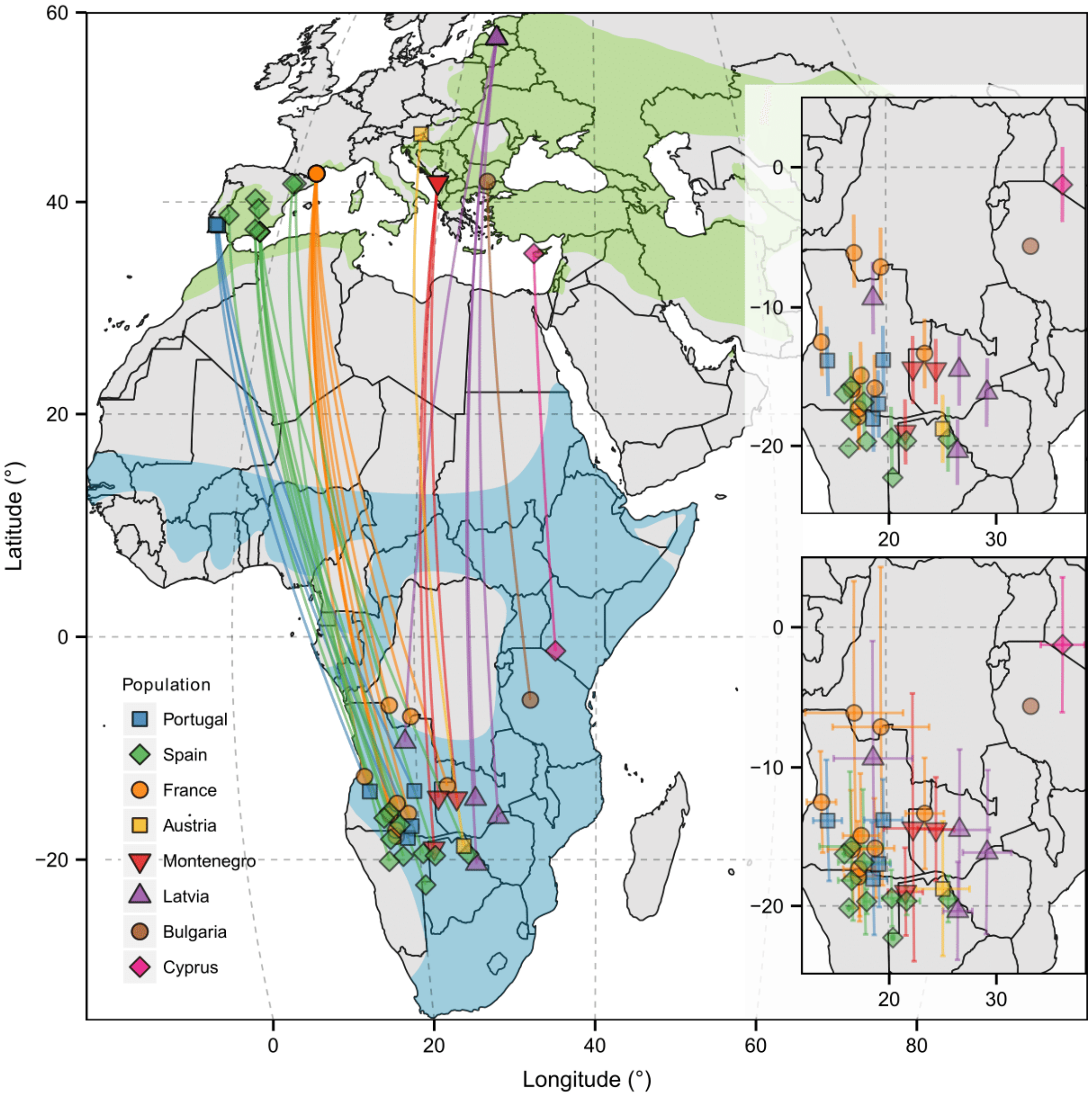


Figure 5.1 Migratory connectivity in the European Roller (*Coracias garrulus*) revealed by geolocators, satellite tags and a ring recovery (Mollweide equal-area projection). Loxodromic lines (not intended to represent routes taken) connect breeding and winter sites of 33 European Rollers from eight countries. Shaded areas show global breeding (green) and winter (blue) distribution of the European Roller, from BirdLife International and NatureServe (2013). The south-east quarter of the breeding distribution, from Iraq and southern Iran to southern Kazakhstan, is occupied by the *semenowi* subspecies. **Inset top**: verticle lines represent latitudinal shift in mean winter position resulting from ± 1.0° to sun elevation angle. **Inset bottom**: bars show variation (S.D.) surrounding mean winter locations.

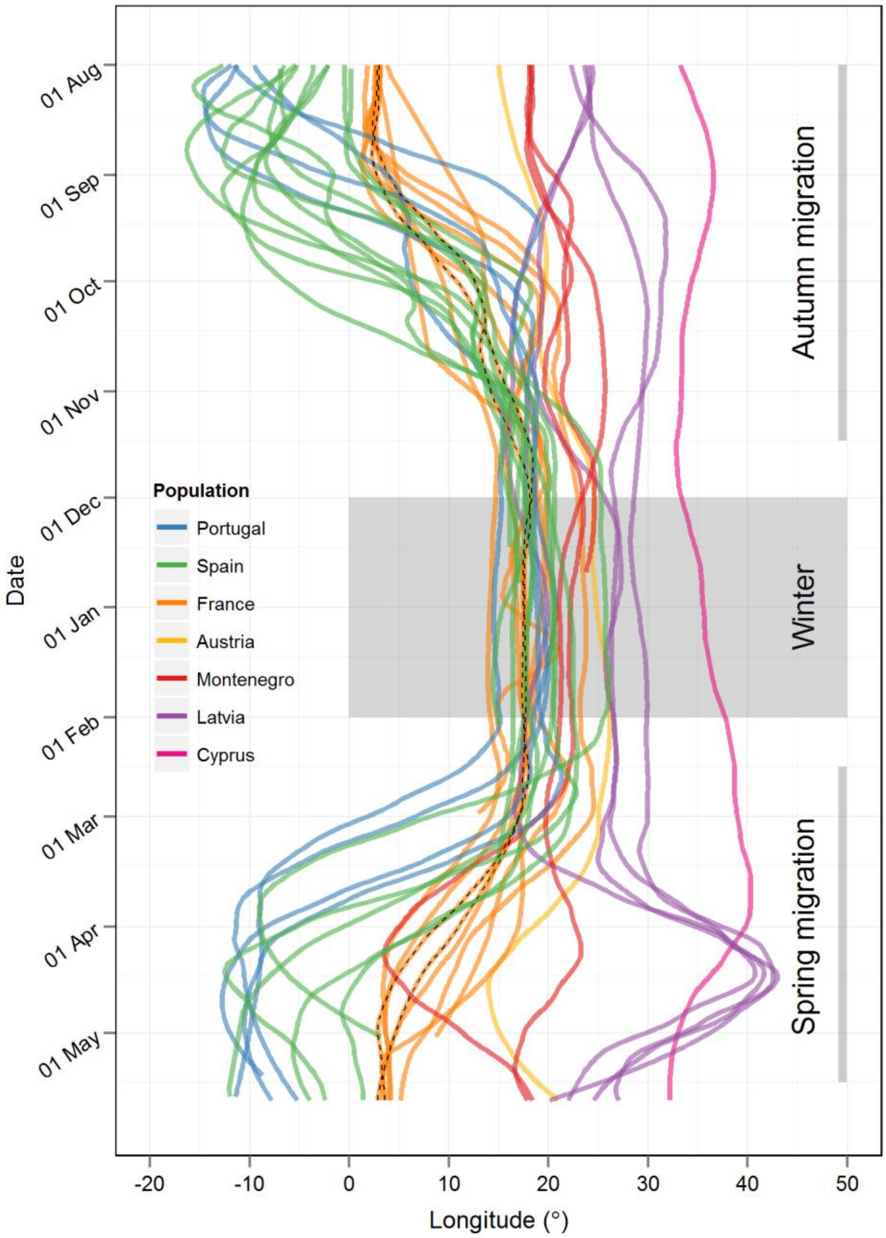


Figure 5.2 Smoothed longitudinal tracks of 32 European Rollers (*Coracias garrulus*) from seven countries (LOESS regression, α = 0.25). Note that time is on the y-axis, latitude is not represented and that, for obvious reasons, the Bulgarian ring recovery is not represented in this figure. Shaded box denotes winter period (Dec–Jan) and bars indicate approximate periods of autumn and spring migration. Dashed lines show the migration of a French Roller tracked across two consecutive years.

Table 5.1 Country-level summary of the migration of 33 European Rollers (*Coracias garrulus*) revealed by geolocators (GLS), satellite tags (PTT) and a ring recovery. Migration distance is measured as mean great circle distance between breeding and winter site. Spring–autumn displacement is the mean longitudinal difference between autumn and spring routes, with negative values indicating a westerly (clockwise) spring loop.

Country	**n**	**Migration distance (km ± SD)**	**Sub-Saharan stopover**	**Winter quarters**	**Spring–autumn displacement (° ± SD)**
Portugal	4 GLS	6550 ± 271	Cameroon, Libya, Congo	Angola, Namibia	–5.4 ± 6.7
Spain	4 GLS 6 PTT	6800 ± 371	Nigeria, Cameroon, Niger, Chad	Namibia, Angola, Botswana	+2.2 ± 6.0
France	9 GLS	6450 ± 458	Chad, Niger, Nigeria, CAR	Angola, DRC, Namibia, Zambia	–4.2 ± 3.6
Austria	1 GLS	7350	Chad	Botswana	–4.0
Montenegro	3 GLS	6450 ± 287	Libya	Zambia, Botswana	–8.3 ± 5.3
Latvia	4 GLS	8050 ± 503	Chad, Sudan, Libya	Zambia, Botswana, Zimbabwe, Angola	+12.2 ± 5.0
Bulgaria	1 ring	5350	-	Tanzania	-
Cyprus	1 GLS	4050	Sudan	Kenya	+4.0

Great circle distances between breeding and winter sites (ignoring any deviations from the orthodromic route) ranged from 4050 to 8625 km (**Table 5.1**) and were greater for individuals from more northerly breeding grounds ($r = 0.66$, $d.f. = 31$, $p < 0.001$). When data for Rollers from eastern and western Europe were tested separately, this association was significant for the eastern ($r = 0.90$, $d.f. = 8$, $p < 0.001$), but not the western subset ($r = –0.04$, $d.f. = 21$, $p = 0.85$), which is perhaps unsurprising given the limited latitudinal variation between western breeding sites. There was no overall correlation between breeding and wintering ground latitude ($r = 0.01$, $d.f. = 31$, $p = 0.94$). For western populations this association was near-significant and positive ($r = 0.37$, $d.f. = 21$, $p = 0.08$) and for eastern populations it was non-significant but negative ($r = –0.45$, $d.f. = 8$, $p = 0.19$).

Rather than occupying discrete areas, the winter quarters of different breeding populations were large and often overlapping. However, there was a strong overall correlation between breeding and winter site longitude ($r = 0.75$, $d.f. = 31$, $p < 0.001$; **Fig. 5.3b**). When this analysis was repeated on data from just the eastern or western populations it was significant for the former ($r = 0.69$, $d.f. = 8$, $p = 0.03$) but not the latter ($r = 0.02$, $d.f. = 21$, $p = 0.92$). There was also a strong correlation between pairwise distance matrices of breeding and winter sites (Mantel test; $r_M = 0.50$, $p = 0.001$), indicating that individuals which breed close together also winter close together. Again, when eastern and western populations were considered separately, the Mantel test was significant for the former ($r_M = 0.36$, $p = 0.02$) but not the latter ($r_M = –0.3$, $p = 0.68$).

5.4.3 Spring migration

Median departure date from the winter quarters was 5th March (IQR: 14th Feb – 17th Mar). Spring routes differed from autumn routes for all individuals (**Table 5.1**), most strikingly for Latvian Rollers, whose spring ‘loop’ reached as far as 45° E (**Fig. 5.2, Fig. S3.1**). Spring stopover sites were often difficult to identify given their close proximity to the vernal equinox. Nevertheless, all individuals stopped before reaching Europe, and in most cases these stopovers appear to be in the sub-Saharan savannah zone (in others, latitudinal uncertainty was too large to tell; **Fig. S3.1**). Additional spring stopovers were made north of the Sahara by some individuals, as well as in west Africa by Rollers from south-west Iberia. Median arrival date to the breeding grounds was 4th May (IQR: 29th Apr – 8th May), so Rollers spent on average more than eight months away from their breeding grounds.

We only successfully tracked one individual across multiple years, so are unable to make any quantitative conclusions regarding within-individual repeatability. However, the migration of this individual appears to be repeatable in space (see **Fig. S3.1b** and **f**) and dashed lines in **Fig. 5.2**) and time; departure and arrival to and from winter and breeding grounds were consistent to within 6 days (but note the potential uncertainty of geolocator-derived phenological information).

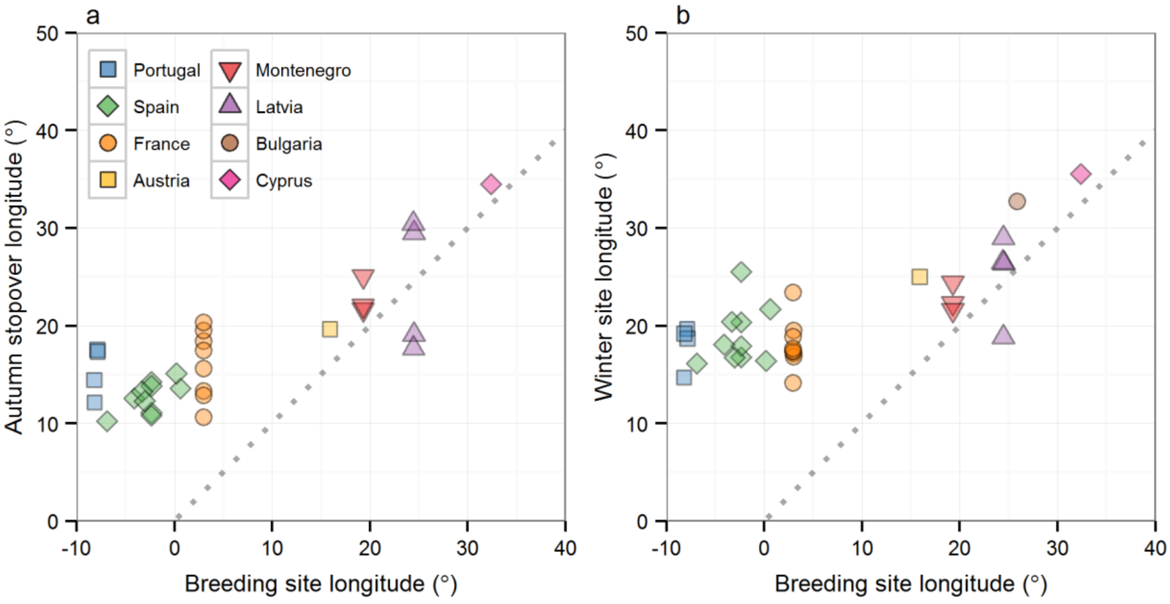


Figure 5.3 Relationship between **a** longitude of breeding site and first sub-Saharan autumn stopover (Pearson correlation; $r = 0.81$, $d.f. = 29$, $p < 0.001$) and **b** longitude of breeding site and winter site($r = 0.75$, $d.f. = 31$, $p < 0.001$). Dashed lines represent $x = y$

Geolocator-derived locations are inherently imprecise and potentially inaccurate, so an evaluation of the sensitivity of our conclusions to this source of uncertainty is crucial. Imprecision in estimated winter locations (SD = 540 km for latitude, 214 km for longitude) was small relative to the cross-hemisphere movements of this long-distance migrant, and our randomisation tests show that our conclusions based on mean autumn and winter positions are robust; on only one occasion did an originally significant ($p < 0.05$) test have 95 % confidence intervals overlapping zero, and this was only marginal (**Appendix 3**). Confidence intervals were wider for outputs of tests incorporating latitudinal information than those based on longitude only, owing to the greater imprecision of the former. Whilst it is not possible to quantify the potential inaccuracy arising from the application of an inappropriate sun elevation angle, altering the chosen in-habitat sun angle by ± 0.5° and ± 1.0° resulted in average latitudinal displacements in mean winter position to the north (angle decrease) or south (angle increase) of 138 km and 275 km respectively. Finally, our resampling experiments suggest that test coefficients stabilise by $n \approx 10$, with the inclusion of additional samples having no effect on coefficient precision (**Appendix 3**).

5.5 Discussion

Knowledge of the year-round spatial distribution of migrant populations is critical for their conservation (Newton 2008). In order to protect a specific breeding population, it is important to know not only where they migrate to and how they get there, but to what extent they mix with individuals from other populations (e.g. Jones *et al.* 2008; Iwamura *et al.* 2013). Here we have performed the first wide-scale multi-national analysis of migratory connectivity in the European Roller, a charismatic and globally near-threatened migrant bird. New data from France and Portugal are broadly consistent with the two previous studies from these breeding populations (Emmenegger *et al.* 2014; Catry *et al.* 2014), with data on the previously unknown migration routes of Austrian, Montenegrin, Cypriot and Latvian Rollers greatly extending our knowledge of this species' year-round movements.

Our randomisation trials showed that analyses using latitudinal data were more sensitive to geolocator imprecision (arising due to day-to-day variation in shading) than those incorporating longitudinal information only, but in general our conclusions are robust to this imprecision. The second component of geolocator uncertainty is calibration error, i.e. the application of an inappropriate sun elevation angle. This inaccuracy is not possible to quantify in our study (though see Fudickar, Wikelski & Partecke 2012; Lisovski & Hahn 2012; McKinnon *et al.* 2013) but affects latitude only and is only likely to be a concern if Rollers experience considerable differences in shading conditions over winter compared to during the breeding season. We acknowledge this unknown potential for latitudinal inaccuracy (perhaps up to several hundred km), but note that our conclusions are predominantly based on east-west, rather than north-south, segregation. Finally, our resampling experiments suggest that the inclusion of additional data would not necessarily increase the robustness of our conclusions.

5.5.1 Autumn migration

In western Rollers, autumn migration occurred on two fronts; Rollers from the south-west of the region took a westerly route along the Atlantic coast of West Africa, then turned east along the savannah belt, whereas those from north-east Spain and southern France took a more direct route across the Sahara desert (Emmenegger *et al.* 2014; Catry *et al.* 2014; Rodríguez-Ruiz *et al.* 2015). This suggests a trade-off between the additional time and energy required to make a detour and the costs associated with the desert crossing, which is narrower and potentially more benign towards the coast (Alerstam 2001; Rodríguez-Ruiz *et al.* 2015). Similar detours are made by Common Swifts *Apus apus* and Common Redstarts *Phoenericus phoenericus* from northern Europe (Åkesson *et al.* 2012; Kristensen, Tøttrup & Thorup 2013), suggesting that the factors driving the selection of this route may not be unique to the Roller. Interestingly, individuals from both sides of this migratory divide eventually converged at similar autumn stopover sites, and wintered in the same region of south-west Africa. For eastern Rollers there was no evidence of any detours shortening the southward Sahara crossing.

Given that the Roller is predominantly a sit-and-wait predator (so unlikely to ‘fly-and-forage’) and an active, flapping flier, we expected migration to be punctuated by stopovers for refuelling (Alerstam & Hedenström 1998), the locations of which are clearly important from a conservation perspective. Our study supports previous work identifying the northern savannah zone, particularly the Lake Chad basin, as an important autumn stopover site for Rollers from western European populations (Emmenegger *et al.* 2014; Catry *et al.* 2014; Rodríguez-Ruiz *et al.* 2015). We also show that individuals from eastern populations make use of this area. Although the longitude of breeding and autumn stopover sites were positively correlated (indicating ‘parallel’ migration), the longitudinal spread of the latter was narrower, suggesting convergence of Rollers from across Europe. The northern savannah is an important site for many insectivorous migrants that winter further south (Morel 1973), and recent tracking studies have demonstrated its importance for species including Eleonora’s Falcon *Falco eleonora* (Mellone *et al.* 2013), Red-backed Shrike *Lanius collurio* (Tøttrup *et al.* 2012), European Bee-eater *Merops apiaster* (Arbeiter *et al.* 2012) and Common Cuckoo *Cuculus canorus* (Willemoes *et al.* 2014). Droughts in this region during the 1970s and 1980s reduced the survival and population size of several European visitors, presumably due to reduced prey abundance (e.g. Peach, Baillie & Underhill 1991; Baillie & Peach

1992). Given that Rollers from across Europe converge on this region, in both autumn and spring (see below), any environmental degradation (e.g. Held *et al.* 2005; Zwarts *et al.* 2009) would likely have widespread population consequences. Currently only the Chadian portion of Lake Chad is designated as an Important Bird Area, with no protection afforded in north east Nigeria or in the surrounding basin.

5.5.2 Winter quarters

All tracked Rollers wintered in the tropical grasslands, savannahs and shrublands (Olson *et al.* 2001) of southern Africa, 4000 to 8600 km away from their breeding sites. The Roller's arrival in southern Africa coincides with the southwards movement of the Intertropical Convergence Zone (ITCZ) and the return of the wet season to this region, whilst the northern savannahs are entering the dry season (Barry & Chorley 1992). Our data conform to the official species distribution map (**Fig. 5.1**; Birdlife International & NatureServe, 2013), though none of our tracked Rollers wintered as far south as South Africa (which is perhaps occupied by Rollers from the far east of the breeding range, including the *semenowi* subspecies). Given that none of the 24 Rollers from western Europe wintered in west Africa, we suspect that the species occurs here only on passage and suggest that a revision of the current distribution be considered. However, further research is necessary, particularly given the unknown winter quarters of the small north African breeding population.

Although the winter ranges of different (and often distant) breeding populations overlapped, the distribution of wintering Rollers with respect to their breeding origin was significantly non-random. In addition to strong longitudinal correlations between breeding and winter sites, there was a correlation between pairwise distance matrices of breeding and winter sites. These results suggest that migratory connectivity is neither absent nor strong, but somewhere in the middle of the 'weak-strong' continuum defined by Webster *et al*. (2002). This moderate level of connectivity (r_M = 0.50) is similar to that measured by Trierweiler *et al*. (2014) in their study of Montagu's Harriers *Circus pygargus* from Northern Europe (r_M = 0.56–0.60), although such interspecific comparisons should be made with caution due to the scale-dependence of connectivity measurements. The fact that Rollers from discrete breeding populations spread out over a larger area during the non-breeding season may increase their (population-level) resilience to deterioration of local environmental conditions on the non-breeding grounds. On the other hand, it could dilute the strength of interseasonal density effects (Norris & Marra 2007). For instance, if a population suffers a locally catastrophic breeding season but mixes with individuals from across Europe over winter, the expected density-dependent reduction in per-capita overwinter mortality may not be realised.

Migratory connectivity appears to be stronger for eastern populations compared to western ones, as demonstrated by significant correlations between (1) breeding and winter site longitude and (2) pairwise distance matrices of breeding and winter sites for the former but not the latter. Similarly, Rodríguez-Ruiz *et al*. (2015) found no evidence for connectivity in Spanish Rollers. Whilst these differences may reflect the different spatial structure of eastern (mean pairwise distance between breeding sites = 1202 km) versus western (536 km) study sites, an alternative explanation for this disruption to connectivity in the west may be the easterly circumnavigation of the Gulf of Guinea. In contrast, eastern birds are able to make a southerly, ‘parallel’ migration, thus maintaining their longitudinal structure. This intriguing possibility points to the potential importance of continental configuration as a driver of connectivity patterns in other species. Stronger connectivity in eastern populations may increase their vulnerability to loss of non-breeding habitat compared to western ones (Jones *et al.* 2008), a possibility which deserves attention in the face of strong population declines in the east (Kerus & Račinskis 2008; Kovacs *et al.* 2008).

There was no overall relationship between breeding and winter site latitude, but the non-significant tendency for high-latitude eastern breeders to winter at more southerly latitudes suggests a leap-frog migration, with a significant positive relationship between breeding latitude and migration distance. Rollers from the relict (Kerus & Račinskis 2008) Latvian population wintered 800–2000 km south of the Roller from the increasing (Burfield & van Bommel 2004; but see Pomeroy, Walsh & Richardson 2013) Cypriot population, despite breeding ~ 2400 km further north. Whilst this conclusion largely relies on a single data point from Cyprus, and is based on latitudinal patterns which are prone to uncertainty, the Bulgarian ring recovery adds further support to our hypothesis. Leap-frog patterns have been described in a number of migrants, including many wader species (e.g. Duijns *et al.* 2012) Yellow Wagtail *Motacilla flava* (Bell 1996) and Barn Swallow *Hirundo rustica* (Ambrosini *et al.* 2009), and may reflect competitive differences or different optimal time allocation strategies between northern and southern breeding populations (Greenberg 1980; Bell 1996; Alerstam & Hedenström 1998). Further multi-population tracking studies are necessary to explore the generality of leap-frog migration, in addition to its causes and consequences.

5.5.3 Spring migration

The northern savannah zone also appears to be used on spring migration, when stopovers were generally south of their autumn equivalents (though note large latitudinal uncertainty due to proximity to equinox and equator), as expected given that the northern savannah becomes increasingly dry over winter. All individuals exhibited, to some extent, a loop migration. French and Montenegrin Rollers had a small clockwise loop, whereas Latvian Rollers had a large anti-clockwise loop, taking them to the Horn of Africa and along the Arabian Peninsula. This route, proposed by Hogg *et al*. (1984) and presumably driven by regional variation in foraging and/or wind conditions (Pearson & Lack 1992), is supported by the recovery of a Latvian-ringed Roller on spring migration in Saudi Arabia (data not shown). The recovery of ringed Serbian and Hungarian Rollers in Arabia suggests that other eastern populations also use this route (Stanković 2011, Tokody, B. pers. comm.; see **Chapter 6**). Recent tracking of red-backed shrikes (Tøttrup *et al.* 2012) and Eleonora's falcons (Mellone *et al.* 2013) show that this route is not unique to Rollers, but may be important for many insectivorous migrants. In contrast, common cuckoos (Willemoes *et al.* 2014) and Montagu's harriers (Trierweiler *et al.* 2014) display a clockwise loop, with spring migration displaced to the west. All three ringed Rollers recovered in Arabia were shot, and anecdotal evidence suggests that large numbers of Rollers are killed by hunters in this region (e.g. del Hoyo, Elliott & Sargatal 2001). Having been separated by up to 1000 km on autumn migration and over winter, the spring migration of Latvian Rollers occurred in a synchronous and narrow-front, so any threats present in this region will likely affect all members of the population.

5.5.4 Conclusions

Our study supports existing data on the migration of Rollers from western Europe, and describes new routes from eastern Europe, including a large synchronous loop migration (via Arabia) performed by Latvian Rollers, and a putative leap-frog pattern in the east. It also highlights the importance of the northern savannah zone as a stopover region for this species. We perform the first pan-European quantification of migratory connectivity in this species, finding a non-random spatial structure despite some mixing of individuals from different breeding populations. Any conservation actions in southern Africa would therefore have wide-ranging but diffuse effects. Connectivity appears to be stronger for eastern populations, many of which have undergone severe declines in recent decades. Whilst it is unclear exactly what the consequences of the level of connectivity detected here will be for Roller population dynamics, we are now in a position to start exploring explicit hypotheses.

Although our findings appear robust to the inherent imprecision of geolocator data and our relatively small sample sizes, future studies should aim at more precisely elucidating the sites used; we are currently limited to making only large, international-scale conservation recommendations. We expect many of our findings to be consistent across other flapping, insectivorous, terrestrial birds faced with similar environmental constraints. For example, if driven by prey availability and weather conditions, migration routes (e.g. detours to shorten the Sahara crossing, stopovers in the northern savannah) should be fairly conserved across species. More broadly, we suggest that continental configuration plays a role in shaping patterns of connectivity (see **Chapter 7**). The development of migration strategies at the individual level is also predicted to be important in determining connectivity patterns (Cresswell 2014), so studies of juvenile migration (see **Chapter 6**) and adult route fidelity are crucial. We also recommend research into differential migration in relation to sex, and spatial and temporal patterns of mortality during the non-breeding season. This information should be combined with genetic analyses to examine the interplay between migratory connectivity and the structure and isolation of breeding populations to further inform conservation management.

5.6 References

Åkesson, S., Klaassen, R.H.G., Holmgren, J., Fox, J.W. & Hedenström, A. (2012) Migration routes and strategies in a highly aerial migrant, the common swift Apus apus, revealed by light-level geolocators. *PLoS One*, **7**, e41195.

Alerstam, T. (2001) Detours in bird migration. *Journal of Theoretical Biology*, **209**, 319–331.

Alerstam, T. & Hedenström, A. (1998) The development of bird migration theory. *Journal of Avian Biology*, **29**, 343–369.

Ambrosini, R., Møller, A.P. & Saino, N. (2009) A quantitative measure of migratory connectivity. *Journal of theoretical biology*, **257**, 203–211.

Arbeiter, S., Schulze, M., Todte, I. & Hahn, S. (2012) Das Zugverhalten und die Ausbreitung von in Sachsen-Anhalt brütenden Bienenfressern (Merops apiaster). *Berichte Vogelwarte Hiddensee*, **21**, 33–41.

Avilés, J.M. & Parejo, D. (2004) Farming practices and roller Coracias garrulus conservation in south-west Spain. *Bird Conservation International*, **14**, 173–181.

Baillie, J.E.M., Hilton-Taylor, C. & Stuart, S.N. (2004) *2004 IUCN Red List of Threatened Species. A*

Global Species Assessment. IUCN, Gland, Switzerland and Cambridge, UK.

Baillie, S.R. & Peach, W.J. (1992) Population limitation in Palaearctic-African migrant passerines. *Ibis*, **134**, 120–132.

Barry, R.G. & Chorley, R.J. (1992) *Atmosphere, Weather and Climate*. Routledge, London.

Bell, C.P. (1996) Seasonality and time allocation as causes of leap-frog migration in the Yellow Wagtail Motacilla flava. *Journal of Avian Biology*, **27**, 334–342.

Birdlife International. (2013) *Bird Species Distribution Maps of the World*. BirdLife International, Cambridge, UK, NatureServe, Arlington, USA.

British Antarctic Survey. (2008) *Geolocator Manual v8*. British Antarctic Survey, Cambridge.

Burfield, I.J. & van Bommel, F.P.J. (2004) *Birds in Europe: Population Estimates, Trends and Conservation Status*. BirdLife International, Cambridge, UK.

Catry, I., Catry, T., Granadeiro, J.P., Franco, A.M.A. & Moreira, F. (2014) Unravelling migration routes and wintering grounds of European rollers using light-level geolocators. *Journal of Ornithology*, **155**, 1071–1075.

Cormier, R.L., Humple, D.L., Gardali, T. & Seavy, N.E. (2013) Light-jevel geolocators reveal strong migratory connectivity and within-winter movements for a coastal California Swainson’s thrush (Catharus ustulatus) population. *The Auk*, **130**, 283–290.

Cramp, S. (1985) *The Birds of the Western Palearctic, Volume 4: Terns to Woodpeckers*. Oxford University Press, Oxford, UK.

Cresswell, W. (2014) Migratory connectivity of Palaearctic-African migratory birds and their responses to environmental change: the serial residency hypothesis (ed S Bauer). *Ibis*, **156**, 493–510.

Dolman, P.M. & Sutherland, W.J. (1992) The response of bird populations to habitat loss. *Ibis*, **137**, S38–S46.

Duijns, S., Jukema, J., Spaans, B., Horssen, P. Van & Piersma, T. (2012) Revisiting the proposed leap-frog migration of bar-tailed godwits along the east-Atlantic flyway. *Ardea*, **100**, 37–43.

Emmenegger, T., Mayet, P., Duriez, O. & Hahn, S. (2014) Directional shifts in migration pattern of rollers (Coracias garrulus) from a western European population. *Journal of Ornithology*, **155**, 427–433.

Fraser, K.C., Stutchbury, B.J.M., Silverio, C., Kramer, P.M., Barrow, J., Newstead, D., Mickle, N., Cousens, B.F., Lee, J.C., Morrison, D.M., Shaheen, T., Mammenga, P., Applegate, K. & Tautin, J. (2012) Continent-wide tracking to determine migratory connectivity and tropical habitat associations of a declining aerial insectivore. *Proceedings of the Royal Society of London B: Biological Sciences*, **279**, 4901–4906.

Fudickar, A.M., Wikelski, M. & Partecke, J. (2012) Tracking migratory songbirds: Accuracy of light-level loggers (geolocators) in forest habitats. *Methods in Ecology and Evolution*, **3**, 47–52.

Greenberg, R.S. (1980) Demographic aspects of long-distance migration. *Migrant birds in the neotropics* (eds A. Keast & E. Morton), pp. 493–504. Smithsonian Institution Press, Washington, D. C.

Held, I.M., Delworth, T.L., Lu, J., Findell, K.L. & Knutson, T.R. (2005) Simulation of Sahel drought in the 20th and 21st centuries. *Proceedings of the National Academy of Sciences of the United States of America*, **102**, 17891–17896.

Hewson, C.M. & Noble, D.G. (2009) Population trends of breeding birds in British woodlands over a 32-year period: relationships with food, habitat use and migratory behaviour. *Ibis*, **151**, 464–486.

Hogg, P., Dare, P.J. & Rintoul, J. V. (1984) Palaearctic migrants in the central Sudan. *Ibis*, **126**, 307–331.

del Hoyo, J., Elliott, A. & Sargatal, J. (2001) *Handbook of the Birds of the World Volume VI Mousebirds to Hornbills*. Lynx Edicions, Barcelona, Spain.

Iwamura, T., Possingham, H.P., Chade, I., Murray, N.J., Rogers, D.I., Treml, E.A., Fuller, R.A., Minton, C., Nj, M. & Di, R. (2013) Migratory connectivity magnifies the consequences of habitat loss from sea-level rise for shorebird populations. *Proceedings of the Royal Society of London B: Biological Sciences*, **280**, 20130325.

Jones, J., Norris, D.R., Girvan, M.K., Barg, J.J., Kyser, T.K. & Robertson, R.J. (2008) Migratory connectivity and rate of population decline in a vulnerable songbird. *The Condor*, **110**, 538–544.

Kerus, V. & Račinskis, E. (2008) The second Latvian Breeding Bird Atlas 2000–2004: preliminary results. *Revista Catalana d'Ornitologia*, **24**, 100–106.

Kovacs, A., Barov, B., Orhun, C. & Gallo-Orsi, U. (2008) *International Species Action Plan for the European Roller Coracius Garrulus Garrulus*. Besenyőtelek, Hungary.

Kristensen, M.W., Tøttrup, A.P. & Thorup, K. (2013) Migration of the common redstart (Phoenicurus phoenicurus): A Eurasian songbird wintering in highly seasonal conditions in the West African Sahel. *The Auk*, **130**, 258–264.

Lisovski, S. & Hahn, S. (2012) GeoLight - processing and analysing light-based geolocator data in R. *Methods in Ecology and Evolution*, **3**, 1055–1059.

Lisovski, S., Hewson, C.M., Klaassen, R.H.G., Korner-Nievergelt, F., Kristensen, M.W. & Hahn, S. (2012) Geolocation by light: accuracy and precision affected by environmental factors. *Methods in Ecology and Evolution*, **3**, 603–612.

Lok, T., Overdijk, O. & Piersma, T. (2015) The cost of migration: spoonbills suffer higher mortality during trans-Saharan spring migrations only. *Biology Letters*, **11**, 20140944.

Martin, T.G., Chadès, I., Arcese, P., Marra, P.P., Possingham, H.P. & Norris, D.R. (2007) Optimal conservation of migratory species. *PLoS One*, **2**, e751.

McKinnon, E.A., Stanley, C.Q., Fraser, K.C., MacPherson, M.M., Casbourn, G., Marra, P.P., Studds, C.E., Diggs, N.E. & Stutchbury, B.J.M. (2013) Estimating geolocator accuracy for a migratory songbird using live ground-truthing in tropical forest. *Animal Migration*, **1**, 31–38.

Mellone, U., López-López, P., Limiñana, R., Piasevoli, G. & Urios, V. (2013) The trans-equatorial loop migration system of Eleonora's falcon: differences in migration patterns between age classes, regions and seasons. *Journal of Avian Biology*, **44**, 471–426.

Morel, G. (1973) The Sahel Zone as an environment for Palaearctic migrants. *Ibis*, **115**, 413–417.

Morrison, C.A., Robinson, R.A., Clark, J.A., Risely, K. & Gill, J.A. (2013) Recent population declines in Afro-Palaearctic migratory birds: the influence of breeding and non-breeding seasons. *Diversity and Distributions*, **19**, 1051–1058.

Newton, I. (2004) Population limitation in migrants. *Ibis*, **146**, 197–226.

Newton, I. (2008) *The Migration Ecology of Birds*. Academic Press, London.

Norris, D.R. & Marra, P.P. (2007) Seasonal interactions, habitat quality, and population dynamics in migratory birds. *The Condor*, **109**, 535–547.

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P. & Kassem, K.R. (2001) Terrestrial ecoregions of the world: A new map of life on Earth. *BioScience*, **51**, 933–938.

Panuccio, M., Mellone, U. & Muner, L. (2013) Differential wintering area selection in Eurasian marsh harrier (Circus aeruginosus): A ringing recoveries analysis. *Bird Study*, **60**, 52–59.

Pateff, P. (1942) Die von der Kgl. Ornithologischen Zentrale in Sofia beringten und rückgemeldeten Vogel. Bericht über die Jahre 1928-1941. *Bulletin des Institutions Royales d'Histoire Naturelle Sofia*, **15**, 235–251.

Peach, W.J., Baillie, S.R. & Underhill, L. (1991) Survival of British sedge warblers Acrocephalus schoenobaenus in relation to west African rainfall. *Ibis*, **133**, 300–305.

Pearson, D.J. & Lack, P.C. (1992) Migration patterns and habitat use by passerine and near-passerine migrant birds in eastern Africa. *Ibis*, **134**, suppl. 1, 89–98.

Pomeroy, D., Walsh, F. & Richardson, C. (2013) Documenting the status of the European roller (Coracias garrulus) in western Cyprus. *Sandgrouse*, **35**, 20–25.

R Development Core Team. (2014) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Reichlin, T.S., Schaub, M., Menz, M.H.M., Mermod, M., Portner, P., Arlettaz, R. & Jenni, L. (2008) Migration patterns of hoopoe Upupa epops and wryneck Jynx torquilla: an analysis of European ring recoveries. *Journal of Ornithology*, **150**, 393–400.

Rodríguez-Ruiz, J., de la Puente, J., Parejo, D., Valera, F., Calero-Torralbo, M.Á., Reyes-González, J.M., Zajková, Z., Bermejo, A. & Avilés, J.M. (2015) Disentangling migratory routes and wintering grounds of Iberian near-threatened European rollers Coracias garrulus. *PLoS One*, **9**, e115615.

Ryder, T.B., Fox, J.W. & Marra, P.P. (2011) Estimating migratory connectivity of gray catbirds (Dumetella carolinensis) using geolocator and mark-recapture data. *The Auk*, **128**, 448–453.

Sanderson, F.J., Donald, P.F., Pain, D.J., Burfield, I.J. & van Bommel, F.P.J. (2006) Long-term population declines in Afro-Palearctic migrant birds. *Biological Conservation*, **131**, 93–105.

Schmaljohann, H., Buchmann, M., Fox, J.W. & Bairlein, F. (2012) Tracking migration routes and the annual cycle of a trans-Sahara songbird migrant. *Behavioral Ecology and Sociobiology*, **66**, 915–922.

Sillett, T.S. & Holmes, R.T. (2002) Variation in survivorship of a migratory songbird throughout its annual cycle. *Journal of Animal Ecology*, **71**, 296–308.

Stanković, D. (2011) Eleventh report of Centre for Animal Marking. *Ciconia*, **20**, 104–119.

Stanley, C.Q., McKinnon, E.A., Fraser, K.C., Macpherson, M.P., Casbourn, G., Friesen, L., Marra, P.P., Studds, C.E., Ryder, T.B., Diggs, N.E. & Stutchbury, B.J.M. (2014) Connectivity of wood thrush breeding, wintering, and migration sites based on range-wide tracking. *Conservation Biology*, **29**, 164–174.

Strandberg, R., Klaassen, R.H.G., Hake, M., Olofsson, P. & Alerstam, T. (2009) Converging migration routes of Eurasian hobbies Falco subbuteo crossing the African equatorial rain forest. *Proceedings* *of the Royal Society of London B: Biological Sciences*, **276**, 727–733.

Taylor, C.M. & Norris, D.R. (2009) Population dynamics in migratory networks. *Theoretical Ecology*, **3**, 65–73.

Tøttrup, A.P., Klaassen, R.H.G., Strandberg, R., Thorup, K., Kristensen, M.W., Jørgensen, P.S., Fox, J.W., Afanasyev, V., Rahbek, C. & Alerstam, T. (2012) The annual cycle of a trans-equatorial Eurasian-African passerine migrant: different spatio-temporal strategies for autumn and spring migration. *Proceedings of the Royal Society of London B: Biological Sciences*, **279**, 1008–1016.

Trierweiler, C., Klaassen, R.H.G., Drent, R.H., Exo, K., Komdeur, J., Bairlein, F. & Koks, B.J. (2014) Migratory connectivity and population-specific migration routes in a long-distance migratory bird. *Proceedings of the Royal Society of London B: Biological Sciences*, **281**, 20132897.

Vickery, J.A., Ewing, S.R., Smith, K.W., Pain, D.J., Bairlein, F., Škorpilová, J. & Gregory, R.D. (2013) The decline of Afro-Palaearctic migrants and an assessment of potential causes. *Ibis*, **156**, 1–22.

Webster, M.S., Marra, P.P., Haig, S.M., Bensch, S. & Holmes, R.T. (2002) Links between worlds: unravelling migratory connectivity. *Trends in Ecology and Evolution*, **17**, 76–83.

Willemoes, M., Strandberg, R., Klaassen, R.H.G., Tøttrup, A.P., Vardanis, Y., Howey, P.W., Thorup, K., Wikelski, M. & Alerstam, T. (2014) Narrow-front loop migration in a population of the common cuckoo Cuculus canorus, as revealed by satellite telemetry. *PLoS One*, **9**, e83515.

Zwarts, L., Bijlsma, R.G., van der Kamp, J. & Wymenga, E. (2009) *Living on the Edge: Wetlands and Birds in a Changing Sahel*. KNNV Publishing, Zeist, The Netherlands.

Appendix 3: Supporting information for Chapter 5

Supplementary tables

Table S3.1 Summary of solar geolocator deployment and recovery. Tags were deployed across eight countries between 2009 and 2013.

Deployment year	**Population**	**Devices deployed**	**Birds returned (minimum)**	**Birds recaptured**	**Tags recovered**	**Data downloaded**
2009	Montenegro[1]	4	3	3	3	3*
	Austria[1]	6	1	1	1	1
2010	Montenegro[2]	5	0	0	0	0
	Austria[2]	4	1	1	1	0
2011	France (PdR)[3†]	10	7	4	4	3[‡]
2012	France (PdR)[4]	14	6	6	5	4
	France (VdB)[4]	6	2	2	0	0
	Latvia[4]	15	9	8	4[§]	4
	Portugal[4‖]	10	3	2	2	2
	Spain[5¶]	12	5	5	5	4**
2013	Cyprus[6]	9	3	3	1	1
	France (PdR)[6]	6[††]	2	2	2	2
	France (VdB)[6]	2	0	0	0	0
	Portugal[6]	10	6	6	2	2
	TOTAL	***113***	***48***	***43***	***30***	***26***

1. BASTrak MK14S; Biotrack Ltd., Wareham, Dorset, UK; 0.6 mm shrink-wrapped dyneema leg loop
2. BASTrak MK 18; 0.6 mm shrink-wrapped dyneema leg loop
3. SOI-GDL 1.0; Swiss Ornithological Institute, Sempach, Switzerland; leg loop
4. BASTrak MK5790C; 4mm Teflon ribbon leg loop
5. BASTrak MK4490C; 4mm Teflon ribbon leg loop / back harness
6. BASTrak MK7490C; 4mm Teflon ribbon leg loop

* One tag failed 21 December 2009

† Data from Emmenegger et al. (2014)

‡ One tag failed 27 December 2011

§ One tag recovered after 2 years, but failed 12 September 2013

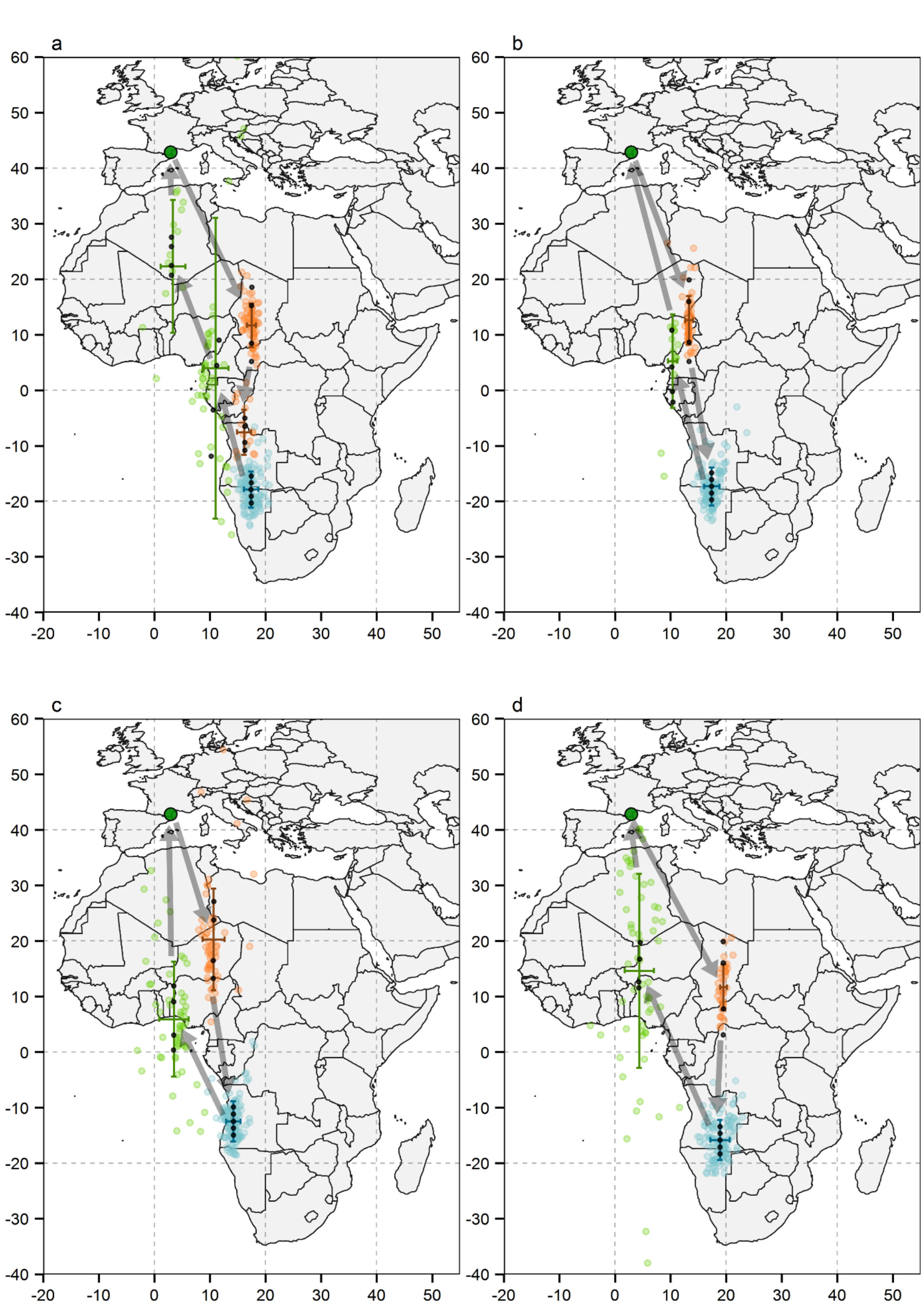
‖ Data from Catry et al. (2014)

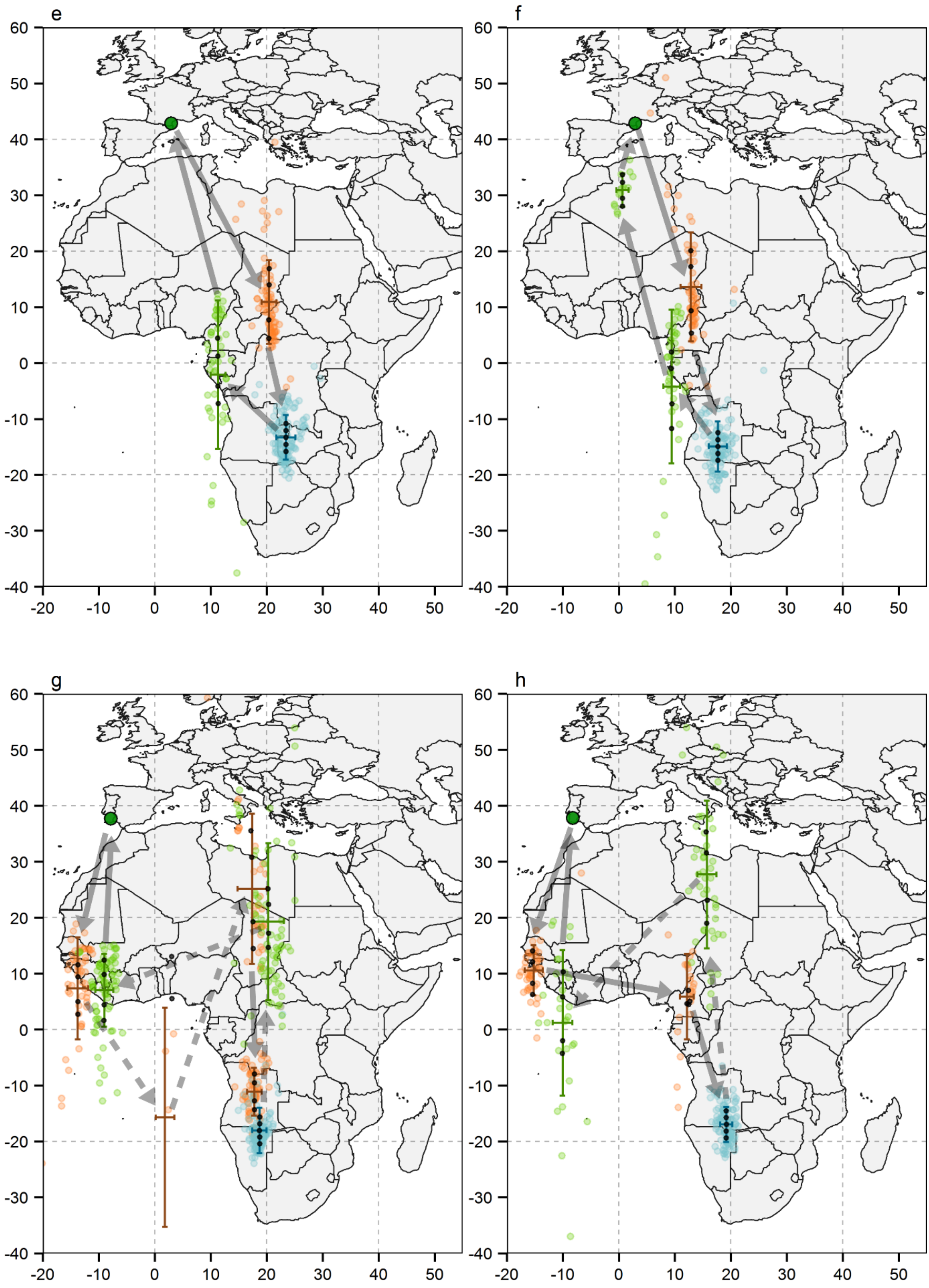
¶ Data from Rodríguez-Ruiz *et al.* (2014)

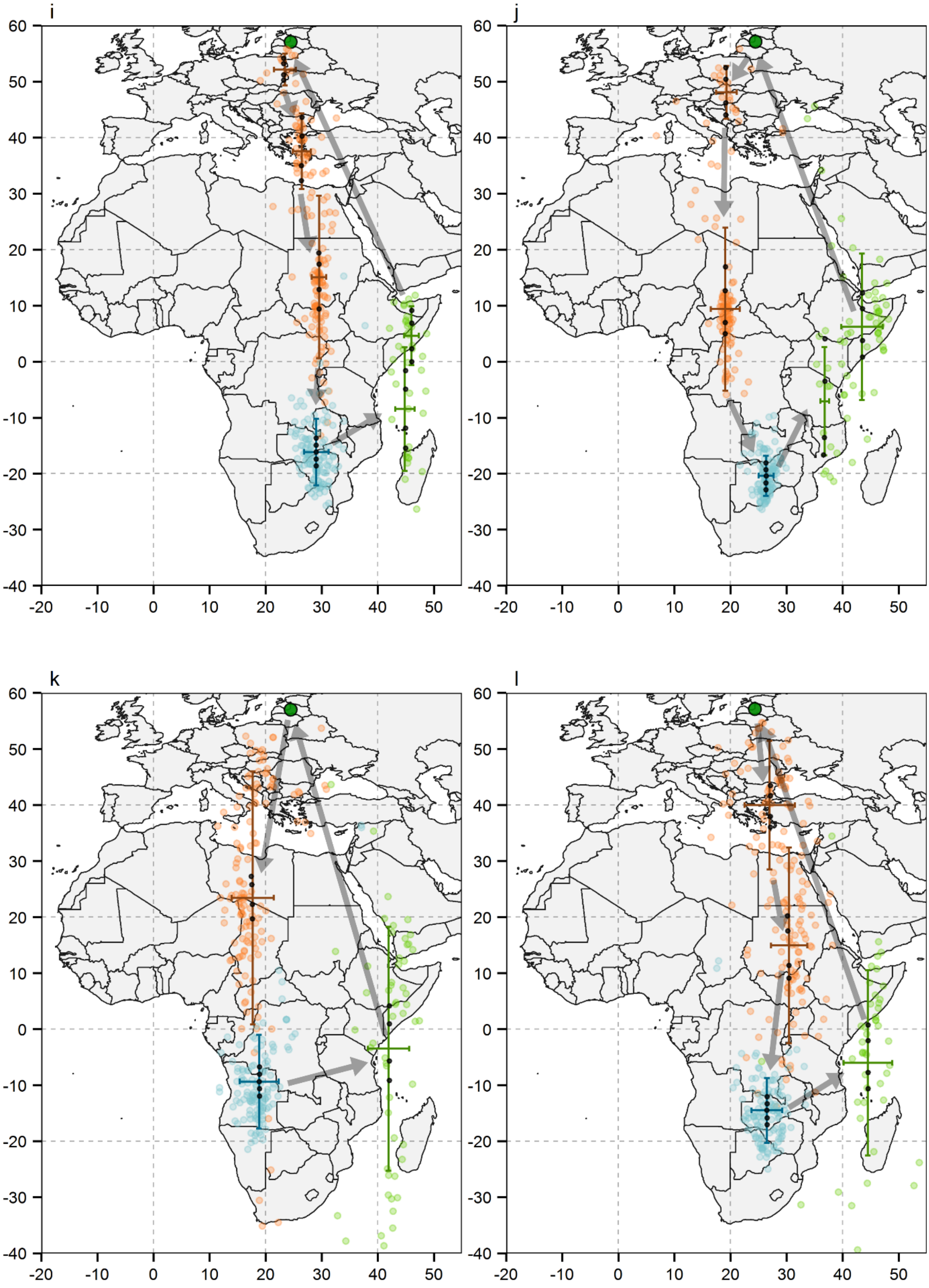
** One tag failed 24 December 2012

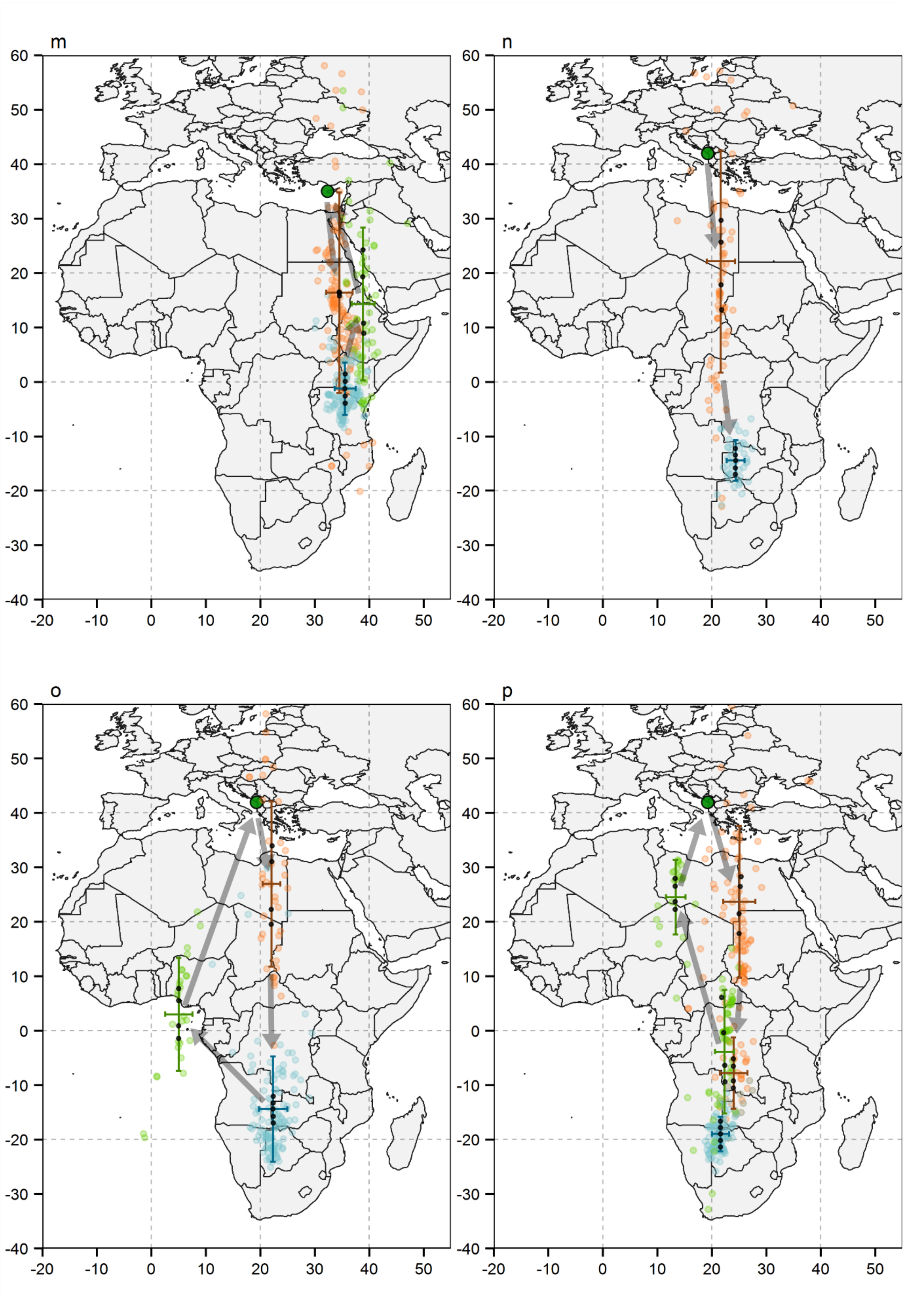
†† Includes three re-tagged 2012 individuals, one of which was recaptured, yielding two consecutive years of migration data.

Supplementary figures




e
f
g
h
60
50
40
30
20
10
0
-10
-20
-30
-40
-20
-10
0
10
20
30
40
50


i
j
k
l
60
50
40
30
20
10
0
-10
-20
-30
-40
-20
-10
0
10
20
30
40
50


m
n
o
p
60
50
40
30
20
10
0
-10
-20
-30
-40
-20
-10
0
10
20
30
40
50

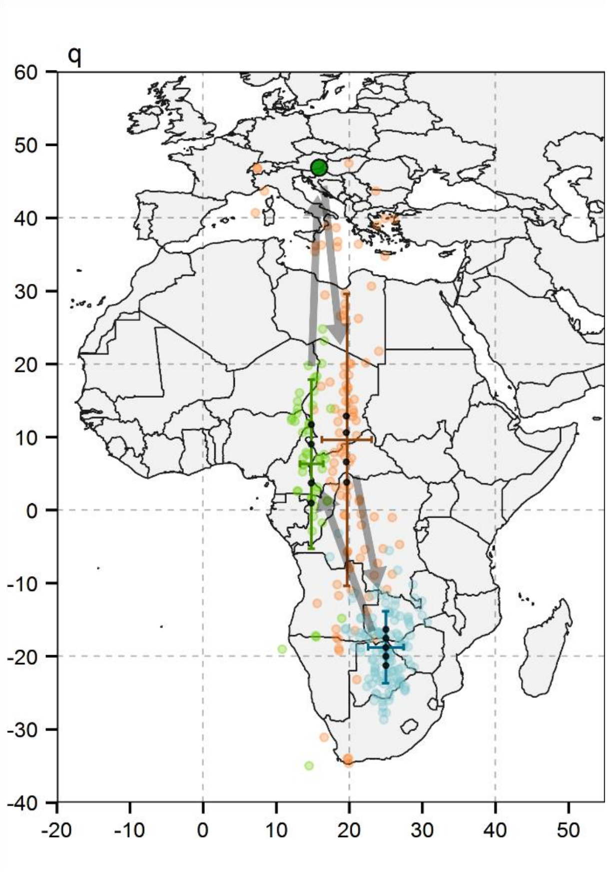


Figure S3.1 Migration route of 17 European rollers (*Coracias garrulus*) revealed by solar geolocators. **a–d** France 2012–13; **e–f** France 2013–14; **g–h** Portugal 2013–14; **i–l** Latvia 2012–13; **m** Cyprus 2013–14; **n–p** Montenegro 2009–10; **q** Austria 200910. Maps **b** and **f** are the same individual tracked over two consecutive years. Stationary periods are represented by raw twice-daily positions and standard deviation bars about the mean location. Large green points show known breeding sites, autumn stopovers are in orange, winter (DecJan) in blue, and spring in green (see main text for details). Black points show the mean winter / stopover positions for ± 0.5° and ± 1.0° sun elevation angles. Note large latitudinal uncertainty in some spring and autumn stopovers, due to proximity to the equator/equinoxes. Grey arrows simply join up consecutive stationary periods for visualisation purposes, and are not intended to represent actual routes taken. Dashed lines join stopover sites with an implausible latitudinal sequence.

Results of randomised iterative procedure exploring the sensitivity of our analyses to geolocator imprecision.

In order to account for uncertainty around the mean geolocator-derived positions used in the main analyses, we used a randomised iterative procedure to sample new positions from the error distribution about mean autumn and winter locations. For each of 10,000 iterations, a random longitude and latitude for each individual was drawn from a normal distribution approximating the scatter of points (S.D. of longitude and latitude; σ) around the mean autumn / winter position (mean of longitude and latitude; μ). For each iteration, we conducted the following statistical tests, as in the main text: Pearson's correlation between (1) longitude of breeding and post-Saharan autumn stopover site, (2) longitude of breeding and winter site, (3) breeding site latitude and migration distance and (4) latitude of breeding and winter site and (5) Mantel correlation between pairwise distance matrices of breeding and winter sites. This process was conducted across all individuals as well as separately for eastern and western populations.

In general, this procedure supports our original conclusions (**Table S3.2**). In only one instance did an originally significant test ($p < 0.05$) have confidence intervals (marginally) overlapping zero. Confidence intervals are particularly narrow for tests based on longitude, but wider for those which incorporate latitude too.

Table S3.2 Results of randomised iterative tests. Median test coefficients (with 95% confidence intervals) from this iterative process are shown alongside original test results (based on mean positions). Instances where the 95% confidence intervals do not overlap zero are highlighted in bold. The asterisk denotes the single occasion on which an originally significant test ($p < 0.05$) had confidence intervals (marginally) overlapping zero.

Test	Subset	*n*	Original test based on mean positions		Test coefficient percentiles from randomisation procedure		
			Test coefficient	*p*-value	2.5%	Median	97.5%
a breeding – autumn longitude	All	31	0.81	< 0.001	**0.63**	**0.76**	**0.85**
	East	9	0.63	0.07	**0.29**	**0.58**	**0.81**
	West	22	0.27	0.22	–0.09	0.23	0.52
b breeding – winter longitude	All	33	0.75	<0.001	**0.60**	**0.71**	**0.79**
	East	10	0.69	0.03	**0.40**	**0.65**	**0.85**
	West	23	0.02	0.92	–0.22	0.02	0.26
c breeding latitude – distance	All	33	0.66	< 0.001	**0.36**	**0.57**	**0.72**
	East	10	0.90	< 0.001	**0.62**	**0.84**	**0.94**
	West	23	–0.04	0.85	–0.31	–0.03	0.37
d breeding – winter latitude	All	33	0.01	0.94	–0.29	0.01	0.29
	East	10	–0.45	0.19	–0.74	–0.35	0.10
	West	23	0.37	0.08	–0.12	0.26	0.51
e Mantel test	All	33	0.50	0.001	**0.19**	**0.40**	**0.56**
	East	10	0.36	0.02	–0.01*	0.24	0.47
	West	23	–0.3	0.68	–0.07	–0.02	0.09

Results of resampling experiments exploring the influence of sample size on the precision of our results

In order to explore the influence of sample size on the robustness of our results, we resampled sequentially reduced datasets with $n = 3, 4, \ldots 20$. The statistical tests described in the main text which were significant when conducted across all individuals were then repeated for each reduced dataset: Pearson’s correlation between (1) longitude of breeding and post-Saharan autumn stopover site, (2) longitude of breeding and winter site and (3) breeding site latitude and orthodromic (great circle) migration distance and (4) Mantel correlation between pairwise distance matrices of breeding and winter sites. This process was iterated 30 times, with each iteration using a different combination of data points in the reduced datasets.

In all cases, the test statistic appears to stabilise around the expected value by $n \approx 10$, with the addition of further samples having little influence on the precision of our estimates (**Fig. S3.2**). We are therefore confident that our sample size is sufficient to make robust conclusions, even for the analyses restricted to eastern populations ($n = 9$, i.e. close to the threshold at which test statistics stabilise).

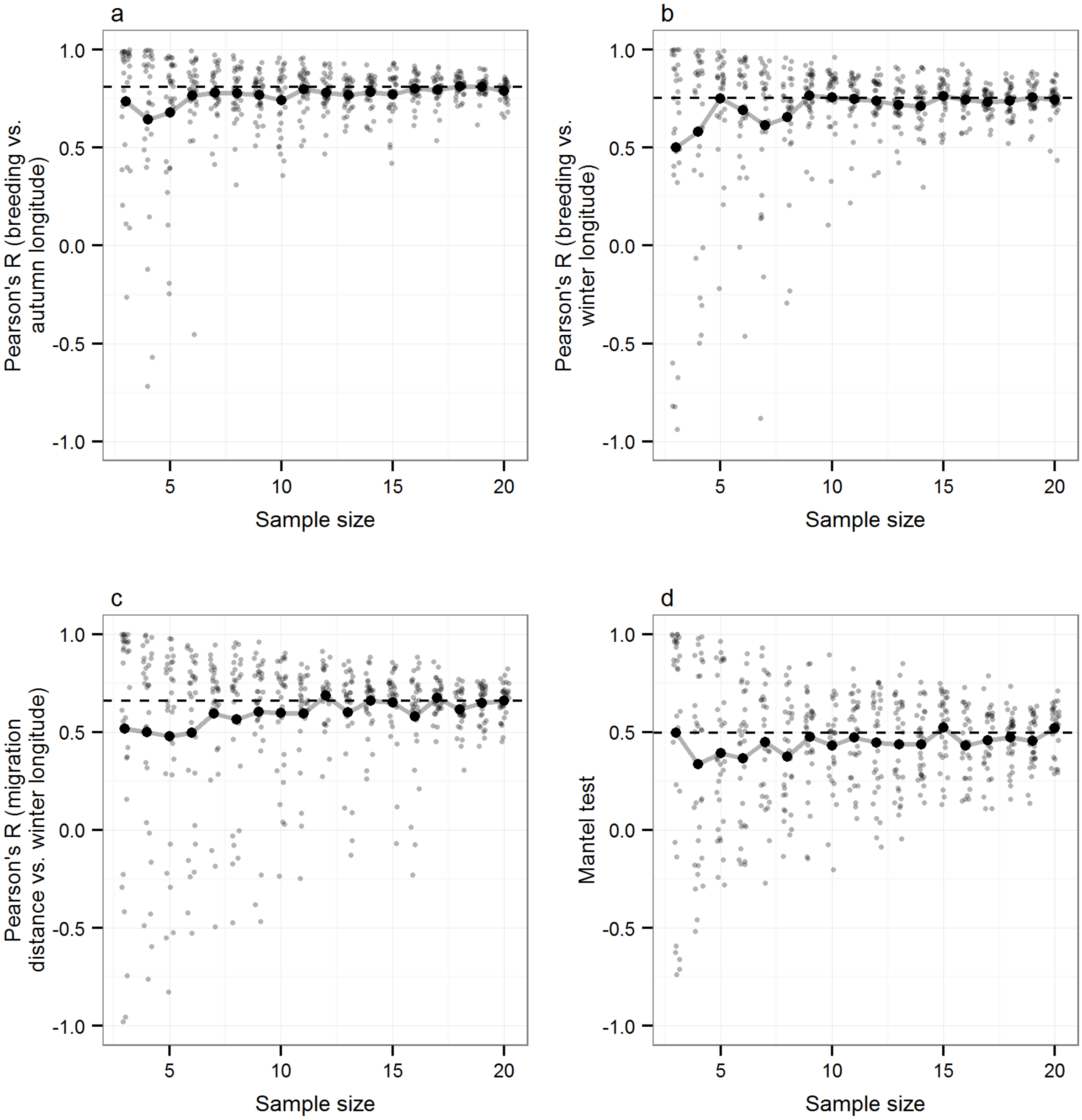


Figure S3.2 Results of resampling experiment. Small opaque dots show raw test coefficients. Solid black dots show mean values for a given sample size, and the dashed horizontal line shows the expected value (i.e. the value obtained using the whole dataset). Pearson's correlation between **a** longitude of breeding and post-Saharan autumn stopover site, **b** longitude of breeding and winter site and **c** breeding site latitude and orthodromic (great circle) migration distance and **d** Mantel correlation between pairwise distance matrices of breeding and winter sites.

Chapter 6: Insights into the migration of the European Roller from ring recoveries

A version of this chapter is published in *Journal of Ornithology* (doi:10.1007/s10336-016-1374-y)

6.1 Abstract

Despite recent advances in avian tracking technology, archival devices still present several limitations. Traditional ring recoveries provide a complementary method for studying migratory movements, particularly for cohorts of birds with a low return rate to the breeding site. Here we provide the first international analysis of ring recovery data in the European Roller *Coracias garrulus,* a long-distance migrant of conservation concern. Our data comprise 58 records of Rollers ringed during the breeding season and recovered during the non-breeding season. Most records come from Eastern Europe, half are of juveniles and over three quarters are of dead birds. Thus, ring recoveries provide migration data for cohorts of Rollers—juveniles and unsuccessful migrants—for which no information currently exists, complementing recent tracking studies. Qualitatively, our results are consistent with direct tracking studies, illustrating a broad-front migration across the Mediterranean Basin in autumn and the use of the Arabian Peninsula by Rollers from eastern populations in spring. Autumn movements were, on average, in a more southerly direction for juveniles than adults, which were more easterly. Juvenile autumn recovery direction also appeared to be more variable than in adults, though this difference was not statistically significant. This is consistent with juveniles following a naïve vector-based orientation program, and perhaps explains the ‘moderate’ migratory connectivity previously described for the Roller. In the first (qualitative) analysis of Roller non-breeding season mortality, we highlight the high prevalence of shooting. The recovery age ratio was juvenile-biased in autumn but adult-biased in spring. Although not statistically significant, this difference points towards a higher non-breeding season mortality of juveniles than adults. Our study demonstrates the complementarity of ring recoveries to direct tracking, providing an insight into the migration of juvenile Rollers and non-breeding season mortality.

6.2 Introduction

The miniaturisation of animal tracking technology is revolutionising our understanding of avian migration. Lightweight solar geolocators (Ouwehand *et al.* 2015) and GPS tags (Hallworth & Marra 2015) now allow researchers to track the migration of all but the smallest of songbirds. However, these technologies are not without limitations (Bridge *et al.* 2013). Most notably, archival loggers must be recovered for data retrieval. As a result, information on the movements of juveniles (which generally disperse further than adults, so are rarely targeted for archival tagging) and unsuccessful migrants (which, by definition, do not return to the tagging site) are rare. Most data on juvenile migration and migration-related mortality is therefore restricted to large-bodied taxa capable of bearing satellite transmitters (but see e.g. McKinnon *et al.* 2014). Traditional mark-recapture techniques therefore provide a complementary method for studying migratory movements (Reichlin *et al.* 2008; Panuccio, Mellone & Muner 2013). In particular, ring recoveries provide a good opportunity to study juvenile movements (Thorup *et al.* 2003a) and causes and rates of mortality (Mcculloch, Tucker & Baillie 1992).

Describing the spatio-temporal distribution of migrant populations at all ages and throughout their annual cycle is particularly pertinent given their widespread decline (Sanderson *et al.* 2006; Vickery *et al.* 2013). In particular, understanding the processes by which naïve first-year migrants navigate to and from their first winter site (to which they will usually return with high fidelity in subsequent years) is crucial for understanding patterns of connectivity and predicting the response of migratory populations to environmental change (Cresswell 2014). Additionally, knowing where and under what circumstances migrants die contributes to our understanding of how population size is regulated throughout the annual cycle (Strandberg *et al.* 2009; Klaassen *et al.* 2014).

The European Roller (*Coracias garrulus*, hereafter ‘Roller’) is a long-distance migrant bird of conservation concern across much of its range (Tucker *et al.* 1994; Burfield & van Bommel 2004; Birdlife International 2015). Although most authors attribute the species’ decline to agricultural change in its breeding range (e.g. Avilés & Parejo 2004), threats on migration and over winter have also been suggested (Kovacs *et al.* 2008), and the Roller is listed on Appendix II of the Convention on Migratory Species. Until recently, non-breeding season threats were difficult to assess due to our limited understanding of Roller migration. However, adult Rollers from across their European range have now been tracked to and from their south African winter sites using solar geolocators (Emmenegger *et al.* 2014; Catry *et al.* 2014) and PTT satellite tags (Rodríguez-Ruiz *et al.* 2015), revealing for the first time connectivity between breeding and wintering sites (Finch *et al.* 2015; **Chapter 5**).

Here, we complement these tracking studies with a coordinated international analysis of ring recoveries (as advocated by e.g. Bairlein (2001)), the first of its kind for this species. Specifically, we compare age related differences in autumn recovery direction, and seasonal differences in recovery age ratio. We expect juvenile autumn migration to be in a variable but, on average, southerly direction (e.g. Perdeck 1958), and the ratio of juvenile to adult recoveries to decrease between autumn and spring migration (e.g. Johnson 1973). We also describe causes of mortality during the non-breeding season.

6.3 Methods

To study the migratory movements of the Roller we collated all known records of Rollers ringed in Europe and recovered, recaptured or resighted away from their original capture site. Records acquired from the EURING Data Bank (du Feu *et al.* 2009, extracted 16/12/2015) were supplemented with additional ring recoveries from national schemes in Hungary, Latvia, France, Bulgaria, Serbia and Lithuania.

We restricted our dataset to birds ringed during the breeding season (June to August) and assume that ringing sites represent natal / breeding origin and recovery sites represent a single point along the (successful or otherwise) migration route. In the case of birds recovered after the year of ringing, we assume that Rollers are philopatric to their original ringing (i.e. hatching / breeding) site. The exclusion of birds ringed as juveniles and recaptured as adults (i.e. where breeding site is uncertain due to natal dispersal) was not possible, as these made up 88 % of adult recoveries. Although quantitative data on Roller natal philopatry is limited, we have numerous anecdotal records from populations across Europe of ringed Rollers breeding < 1 km from their natal site, and only a handful of records of Rollers dispersing to breed further afield (the record is 334 km from France to Hungary (Vincent-Martin, Gimenez & Besnard 2013)). As in other species (Paradis *et al.* 1998), breeding dispersal is believed to be substantially lower than natal dispersal, with Rollers often nesting in the same cavity in subsequent years.

Following Reichlin *et al.* (2008), we limited recoveries to those exceeding 100 km from original ringing location in an attempt to exclude short-distance pre-migratory movements. In accordance with Cramp (1985) and Finch *et al.* (2015), we assigned recoveries to one of three seasons; autumn migration (August to November, inclusive), winter (December to February) and spring migration (March to May). Recoveries in June and July were excluded, as these are unlikely to represent migratory movements. Birds recovered during their first autumn or spring migration were classed as juvenile and otherwise as adult. EURING data were read into R (R Development Core Team 2014) using the *birdring* package (Korner-Nievergelt & Robinson 2015), and recovery direction was calculated using the *geosphere* package (Hijmans 2015). Condition (dead, alive or sick) and circumstances (shot, collision (traffic or other), resighted or recaptured) were acquired when known.

We compared the relative frequency of juveniles and adults (i.e. recovery age ratio) in autumn and spring using a X^2 contingency test. Autumn recovery direction was clustered towards the south (mean = 177°) and approximately normally distributed, so was treated as a linear variable rather than circular one. We compared adult and juvenile autumn recovery angle using a Welch's *t*-test, and variance in autumn recovery angle using an ANOVA.

6.4 Results

A total of 58 recoveries met our specifications; 11 from the EURING Data Bank, and 47 from national schemes in Hungary (n = 18), Latvia (16), France (5), Bulgaria (3), Serbia (3) and Lithuania (2). Of 149 initial records from EURING, we excluded 138; 14 were ringed outside the breeding season, a further 91 were recovered during the breeding season, and of the remaining 44, 33 were recovered within 100 km of the ringing site.

The distribution of recoveries over time was distinctly bimodal, with 18 recoveries each from the 1930s and 2010s but only 22 records (mean = 3.1 records per decade) from all intervening decades. Almost all records were from easterly populations, with only 6 recoveries of birds ringed west of 15° E. The majority of recoveries (41) occurred during autumn migration, with fewer spring recoveries (16) and only one from the sub-Saharan winter area (**Table 6.1**).

Table 6.1 Numbers of ringed European Rollers recovered by age (columns) and season (rows). Totals are in boldface.

	Adult	Juvenile	**Total**
Autumn	15	26	**41**
Winter	0	1	**1**
Spring	9	7	**16**
Total	**24**	**34**	**58**

Qualitatively, the patterns of movement are comparable with those described using solar geolocators; a broad-front southerly passage through the Balkan states and eastern Mediterranean basin in autumn (mean ± S.E. direction from ringing to recovery site = 177° ± 7.3), with spring movements generally coming from further east (mean direction from recovery to ringing site = 329° ± 9.1), including several records from the Arabian Peninsula (**Fig. 6.1**).

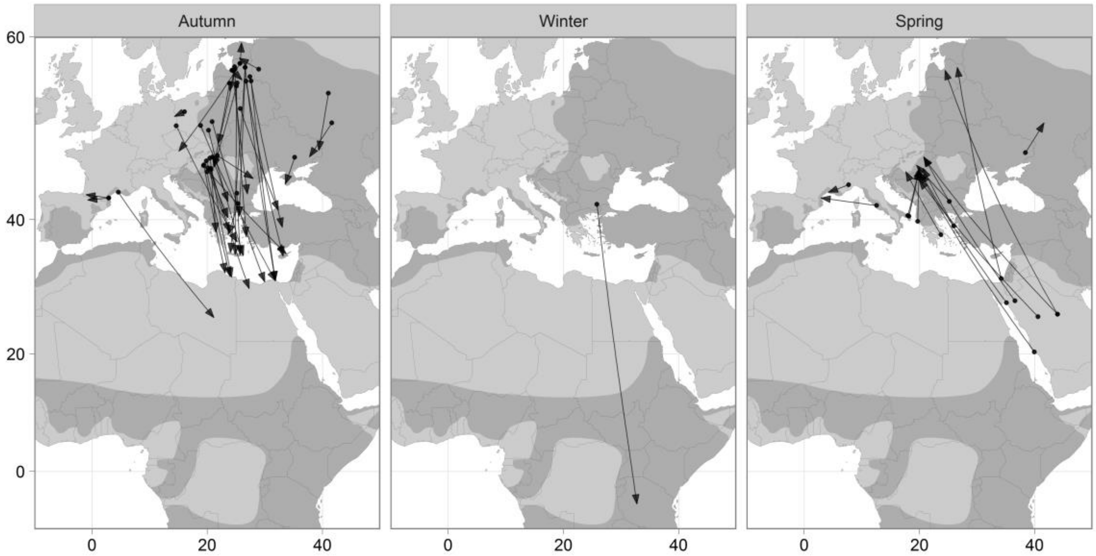


Figure 6.1 Autumn (left), winter (middle) and spring (right) recoveries of ringed European Rollers. Arrows denote direction of movement (from ringing to recovery site in autumn and winter, and recovery to ringing site in spring). Shaded regions show the Roller’s distribution during breeding (Europe) and winter (Africa) seasons (Birdlife International 2013). Mercator projection.

Juveniles made up 63 % of autumn recoveries but only 44 % of spring recoveries. The higher relative frequency of juveniles in autumn is presumably due to their higher abundance following the breeding season. The fact that this numerical advantage disappears by spring migration suggests a higher relative mortality of juveniles than adults during the non-breeding season. However, the frequency of recoveries by season and age class did not differ significantly from random (X^2 = 1.1, *d.f.* = 1, *p* = 0.29; **Table 6.1**).

Mean autumn recovery direction was more easterly in adults (mean = 154° ± 12.6) than juveniles, which migrated approximately due south (190° ± 8.0; *t* = 2.4, *d.f.* = 25.4, *p* = 0.03; **Fig. 6.2a**). There was no difference in the variance of autumn recovery direction between adults and juveniles (*F*-test; *F* = 0.7, *d.f.* = 14, 25, *p* = 0.43). However, when extreme values (Tukey method, *k* = 3; i.e. three-times the interquartile range beyond the first or third quartile) for adult and (*n* = 2) and juvenile (*n* = 1) autumn recovery direction were excluded, recovery direction was significantly more variable in juveniles than in adults (*F* = 6.5, *d.f.* = 12, 24, *p* = 0.002; **Fig. 6.2b**); recovery direction remained more southerly in juveniles than adults (*t* = 3.3, *d.f.* = 34.3, *p* = 0.002).

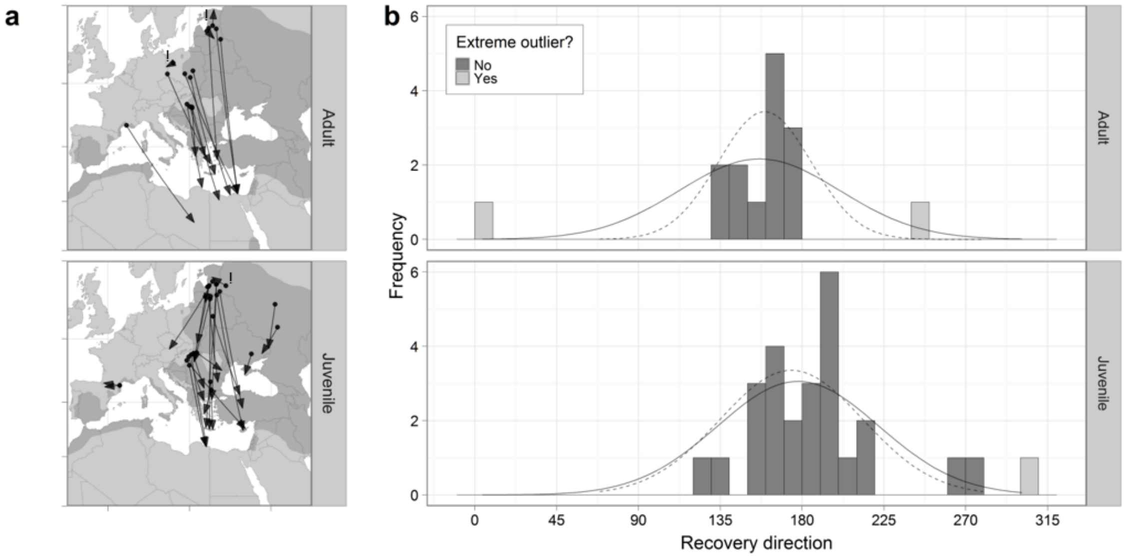


Figure 6.2 Comparison of adult (top) and juvenile (bottom) autumn migration. In **a** arrows denote direction of movement from ringing to recovery site. Recoveries identified as extreme values in terms of recovery direction (Tukey method, *k* = 3) are marked by '!'. **b** shows the frequency distribution of autumn recovery direction for adults and juveniles, with extreme values shown by light shaded bars. Curve lines represent the normal density curve with corresponding mean and S.D. for all data (solid line) and after exclusion of extreme values (dashed line).

Most recoveries (76 %) were of dead birds. Shooting was the most common cause of mortality (48 %), followed by traffic casualties (10 %) and other collisions (5 %), though circumstances were unknown for 36 % of dead birds (**Fig. 6.3**).

6.5 Discussion

We present the first Europe-wide analysis of Roller ring recovery data, complementing several recent tracking studies (Emmenegger *et al.* 2014; Catry *et al.* 2014; Finch *et al.* 2015; Rodríguez-Ruiz *et al.* 2015). We gathered 57 records of Rollers recovered on migration and one winter record. More than half of the recoveries in our data set are of juvenile migrants during their first autumn or spring migration, and over three quarters are records of dead birds. Neither juveniles nor dead migrants are represented in previous tracking studies, demonstrating the complementarity of ring recoveries to e.g. solar geolocators. We had insufficient data to compare changes in migration over time, but the recent increase in the number of recoveries (2 in the 1990s, 8 in the 2000s and 18 already in the 2010s) is encouraging.

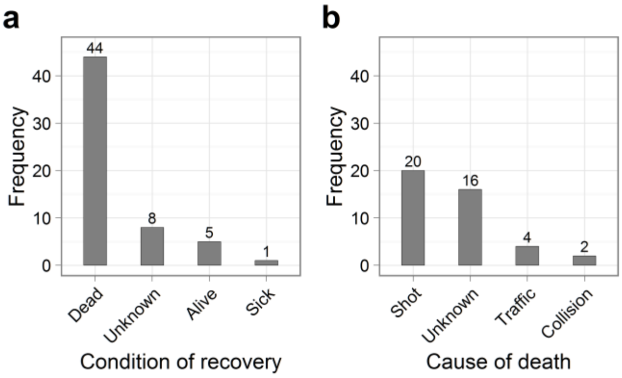


Figure 6.3 Frequency of Roller recovery records by **a** condition (dead, unknown, alive or sick) and **b** circumstances of death (shot, unknown, traffic or other collisions). Two Rollers ‘recaptured’ as dead birds were excluded from **b**.

We did not have access to data on Europe-wide ringing effort, so could not calculate the overall recovery rate. Instead, where available, we can get an indication of recovery rates from national statistics. In France, for example, 1942 Rollers were ringed between 2002 and 2013, five (0.26%) of which were recovered in circumstances which met our selection criteria. Equivalent recovery rates for Lithuania (1929 to 2015) and Serbia (2003 to 2015) were 0.63% and 0.19%, respectively. Whilst these recovery rates are higher than those reported by Robinson *et al.* (2009) for a suite of British bird species, we are nevertheless left with a rather small number of recoveries, most of which come from eastern Europe. This spatial imbalance contrasts (and therefore complements) recent direct tracking studies, in which most data came from western populations (Finch *et al.* 2015). Whilst the western bias of tracking studies is probably a general pattern reflecting funding inequalities, the eastern bias of ring recoveries is likely specific to the Roller. The Roller’s distribution in western Europe is both restricted and southerly (**Fig.**

6.1), such that the passage of western Rollers through Europe (where recovery rates are relatively high) is limited. Thus, our conclusions are principally limited to the migration of Rollers from eastern Europe.

Without quantitative data on spatio-temporal variation in recovery probability, we refrain from making a formal comparison with previous direct tracking data. However, our results are largely consistent with Finch *et al.* (2015), with autumn recoveries from the Balkan Peninsula, Libya and Egypt illustrating a broad-front migration of Rollers from central and eastern populations across the Mediterranean basin. We also demonstrate that individuals from Hungary and Serbia – in addition to Latvia, as revealed by solar geolocators (Finch *et al.* 2015) – migrate through Arabia in spring. Anecdotal evidence suggests that a large number of Rollers are shot in Arabia on spring migration (del Hoyo, Elliott & Sargatal 2001), as were four out of the six ringed Rollers recovered in this region.

Only one ringed Roller has been recovered in the sub-Saharan winter quarters. Evidently, ring-recoveries are not an effective way of describing the Roller’s winter distribution, presumably due to low encounter and / or reporting rates of ringed birds in sub-Saharan Africa (Clark, Thorup & Stroud 2009; Thorup & Conn 2009).

6.5.1 Age differences

Ring recoveries provide the first chance to study the migratory movements of juvenile Rollers which, due to their low return rate to the natal site, have yet to be tracked with archival solar geolocators (or otherwise). Autumn recovery direction was significantly higher (i.e. more southerly) for juveniles than adults and – after the exclusion of 2 adults and 1 juvenile with extreme values of autumn recovery direction – more variable for juveniles than adults. The two adult recoveries identified as extreme outliers were ringed as chicks and recovered 4–9 years after ringing and < 220 km away. We have assumed that the origin of these migratory movements is the initial ringing site, which in most cases was the natal site (because most birds were ringed as nestlings). However, given that natal dispersal is unknown, we cannot be certain that individuals recovered as adults are not migrating to / from a site removed from their place of ringing. This uncertainty is likely to influence most the direction of short distance recoveries, thus justifying the exclusion of these two individuals (in the bottom 15 % of adult autumn recovery distance, and less than the maximum recorded natal dispersal distance (Vincent-Martin *et al.* 2013)). All remaining adult recoveries fell in a narrow directional band (between 133° and 175°), whereas juvenile recoveries were more inconsistent (between 120° and 280°; **Fig. 6.2**)

These results – juveniles orientating variably but, on average, due south – are consistent with the current state of knowledge on avian navigation and orientation, though we urge caution given our limited sample size. Displacement experiments suggest that whilst adult migrants are goal-oriented (using ‘map’ information acquired on previous journeys), juveniles migrate using simple compass-based vector-navigation and are unable to compensate for artificial displacement (Perdeck 1958; Thorup, Rabøl & Erni 2007). Orientation studies have found that juvenile orientation is less precise (Holland & Helm 2013) and high-resolution tracking shows that juveniles are more susceptible to wind drift (Thorup *et al.* 2003b). As a result, the migration routes of juveniles tend to be more tortuous than adults (e.g. Mellone *et al.* 2013), and their ultimate selection of winter sites may be more stochastic (reviewed by Cresswell 2014). Assuming that successful juveniles return to their first winter site as adults, this pattern of variable juvenile orientation could explain the ‘moderate’ connectivity observed by Finch *et al.* (2015), in which individual Rollers from different breeding populations do not occupy distinct non-breeding quarters, instead overlapping with individuals from other (often distant) breeding populations.

In autumn, juvenile recoveries were 1.73 times more frequent than adult recoveries, presumably due to the greater abundance of young birds immediately following the breeding season. In spring, however, the age ratio was adult-biased (0.78). We tentatively argue that the lower relative recovery rate of juveniles in spring suggests a lower non-breeding survival in juveniles compared to adults, though these differences were not statistically significant. More formal studies of mortality during migration, though rare, generally show higher mortality in juveniles compared to adults (Johnson 1973; Owen & Black 1989; Strandberg *et al.* 2009; Guillemain *et al.* 2010; but see Grüebler, Korner-Nievergelt & Naef-Daenzer 2014).

6.5.2 Mortality

In contrast to archival solar geolocators, which record only successful migrations, 76 % of ring recoveries were of dead birds, presenting a rare opportunity to explore the causes of mortality during the migration of Rollers. Cause of death was unknown in 36 % of cases, but 48 % were shot. Due to limited sample size it is difficult to quantify spatial and temporal variation in hunting pressure, though all shot records came from eastern Europe, north Africa or Saudi Arabia.

As with all conclusions based on ring recoveries, it is important to bear in mind potential recovery biases when assessing causes of mortality. Birds dying of natural causes are less likely to be encountered and reported, so anthropogenic causes of death are probably over-represented in our database (Clark *et al.* 2009). Nevertheless, (illegal) hunting is likely to have a lower reporting rate than other anthropogenic causes of mortality, so we highlight the high prevalence of shooting in our dataset as being of real concern. A recent analysis of illegal hunting in the Mediterranean highlighted the European Roller as one of 20 species of conservation concern with the highest estimated number of birds killed (relative to population size), with the greatest numbers taken in Syria, Cyprus and Lebanon (Brochet *et al.* 2016). Hunting impact has not been estimated for Arabia, but in North Sinai (Egypt) it is estimated that over 400 Rollers are trapped annually in trammel nets; a cause of mortality not represented in our dataset (Eason, Rabia & Attum 2016).

6.5.3 Conclusion

By collating ring recovery data from across the Roller’s European range, we present the first glimpse into the autumn migration of first-year Rollers. Juveniles movements were more southerly and, after the exclusion of outliers, more variable than in adults, consistent with juveniles following a naïve vector-based orientation program. We also provide the first study of causes and rates of non-breeding season mortality, highlighting the prevalence of shooting as being of particular concern.

6.6 References

Avilés, J.M. & Parejo, D. (2004) Farming practices and roller Coracias garrulus conservation in south-west Spain. *Bird Conservation International*, **14**, 173–181.

Bairlein, F. (2001) Results of bird ringing in the study of migration routes. *Ardea*, **89**, 7–19.

Birdlife International. (2013) *Bird Species Distribution Maps of the World*. BirdLife International, Cambridge, UK, NatureServe, Arlington, USA.

Birdlife International. (2015) *European Red List of Birds*. Cambridge, UK.

Bridge, E.S., Kelly, J.F., Contina, A., Gabrielson, R.M., MacCurdy, R.B. & Winkler, D.W. (2013) Advances in tracking small migratory birds: a technical review of light-level geolocation. *Journal of Field Ornithology*, **84**, 121–137.

Brochet, A.-L., Van Den Bossche, W., Jbour, S., Ndang'ang'a, P.K., Jones, V.R., Abdou, W.A.L.I., Al-Hmoud, A.R., Asswad, N.G., Atienza, J.C., Atrash, I., Barbara, N., Bensusan, K., Bino, T., Celada, C., Cherkaoui, S.I., Costa, J., Deceuninck, B., Etayeb, K.S., Feltrup-Azafzaf, C., Figelj, J., Gustin, M., Kmecl, P., Kocevski, V., Korbeti, M., Kotrošan, D., Mula Laguna, J., Lattuada, M., Leitão, D., Lopes, P., López-Jiménez, N., Lucić, V., Micol, T., Moali, A., Perlman, Y., Piludu, N., Portolou, D., Putilin, K., Quaintenne, G., Ramadan-Jaradi, G., Ružić, M., Sandor, A., Sarajli, N., Saveljić, D., Sheldon, R.D., Shialis, T., Tsiopelas, N., Vargas, F., Thompson, C., Brunner, A., Grimmett, R. & Butchart, S.H.M. (2016) Preliminary assessment of the scope and scale of illegal killing and taking of birds in the Mediterranean. *Bird Conservation International*, **26**, 1–28.

Burfield, I.J. & van Bommel, F.P.J. (2004) *Birds in Europe: Population Estimates, Trends and Conservation Status*. BirdLife International, Cambridge, UK.

Catry, I., Catry, T., Granadeiro, J.P., Franco, A.M.A. & Moreira, F. (2014) Unravelling migration routes and wintering grounds of European rollers using light-level geolocators. *Journal of Ornithology*, **155**, 1071–1075.

Clark, J. a., Thorup, K. & Stroud, D. a. (2009) Quantifying the movement patterns of birds from ring recoveries. *Ringing & Migration*, **24**, 180–188.

Cramp, S. (1985) *The Birds of the Western Palearctic, Volume 4: Terns to Woodpeckers*. Oxford University Press, Oxford, UK.

Cresswell, W. (2014) Migratory connectivity of Palaearctic-African migratory birds and their responses to environmental change: the serial residency hypothesis (ed S Bauer). *Ibis*, **156**, 493–510.

Eason, P., Rabia, B. & Attum, O. (2016) Hunting of migratory birds in North Sinai, Egypt. *Bird Conservation International*, **26**, 39–51.

Emmenegger, T., Mayet, P., Duriez, O. & Hahn, S. (2014) Directional shifts in migration pattern of rollers (Coracias garrulus) from a western European population. *Journal of Ornithology*, **155**, 427–433.

du Feu, C., Joys, A., Clark, J., Fiedler, W., Downie, I., van Noordwijk, A., Spina, F., Wassenaar, R. & Baillie, S. (2009) EURING Data Bank geographical index 2009.

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.M., 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.

Grüebler, M.U., Korner-Nievergelt, F. & Naef-Daenzer, B. (2014) Equal nonbreeding period survival in adults and juveniles of a long-distant migrant bird. *Ecology and Evolution*, **4**, 756–765.

Guillemain, M., Bertout, J.M., Christensen, T.K., Pöysa, H., Väänänen, V.M., Triplet, P., Schricke, V. & Fox, A.D. (2010) How many juvenile Teal Anas crecca reach the wintering grounds? Flyway-scale survival rate inferred from wing age-ratios. *Journal of Ornithology*, **151**, 51–60.

Hallworth, M.T. & Marra, P.P. (2015) Miniaturized GPS Tags Identify Non-breeding Territories of a Small Breeding Migratory Songbird. *Scientific reports*, **5**, 11069.

Hijmans, R.J. (2015) geosphere: Spherical Trigonometry. R package version 1.5-1.

Holland, R. a & Helm, B. (2013) A strong magnetic pulse affects the precision of departure direction of naturally migrating adult but not juvenile birds. *Journal of the Royal Society, Interface / the Royal Society*, **10**, 20121047.

del Hoyo, J., Elliott, A. & Sargatal, J. (2001) *Handbook of the Birds of the World Volume VI Mousebirds to Hornbills*. Lynx Edicions, Barcelona, Spain.

Johnson, N.K. (1973) Spring migration of the Western Flycatcher, with notes on seasonal changes in sex and age ratios. *Bird-Banding*, **44**, 205–220.

Klaassen, R.H.G., Hake, M., Strandberg, R., Koks, B.J., Trierweiler, C., Exo, K.-M., Bairlein, F. & Alerstam, T. (2014) When and where does mortality occur in migratory birds? Direct evidence from long-term satellite tracking of raptors. *Journal of Animal Ecology*, **83**, 176–184.

Korner-Nievergelt, F. & Robinson, R. (2015) birdring: Methods to Analyse Ring Re-Encounter Data. R package version 1.3.

Kovacs, A., Barov, B., Orhun, C. & Gallo-Orsi, U. (2008) *International Species Action Plan for the European Roller Coracius Garrulus Garrulus*. Besenyőtelek, Hungary.

Mcculloch, M.N., Tucker, G.M. & Baillie, S.R. (1992) The hunting of migratory birds in Europe : a ringing recovery analysis. *Ibis*, **134**, 55–65.

McKinnon, E.A., Fraser, K.C., Stanley, C.Q. & Stutchbury, B.J.M. (2014) Tracking from the tropics reveals behaviour of juvenile songbirds on their first spring migration. *PLoS One*, **9**, e105605.

Mellone, U., López-López, P., Limiñana, R., Piasevoli, G. & Urios, V. (2013) The trans-equatorial loop migration system of Eleonora's falcon: differences in migration patterns between age classes, regions and seasons. *Journal of Avian Biology*, **44**, 471–426.

Ouwehand, J., Ahola, M.P., Ausems, A.N.M.A., Bridge, E.S., Burgess, M., Hahn, S., Hewson, C.M., Klaassen, R.H.G., Laaksonen, T., Lampe, H.M., Velmala, W. & Both, C. (2015) Light-level geolocators reveal migratory connectivity in European populations of pied flycatchers Ficedula hypoleuca. *Journal of Avian Biology*, **47**, 69–83.

Owen, B.Y.M. & Black, J.M. (1989) Factors Affecting the Survival of Barnacle Geese on Migration From the Breeding Grounds. *Journal of Animal Ecology*, **58**, 603–617.

Panuccio, M., Mellone, U. & Muner, L. (2013) Differential wintering area selection in Eurasian marsh harrier (Circus aeruginosus): A ringing recoveries analysis. *Bird Study*, **60**, 52–59.

Paradis, E., Baillie, S.R., Sutherland, W.J. & Gregory, R.D. (1998) Patterns of natal and breeding dispersal in birds. *Journal of Animal Ecology*, **67**, 518–536.

Perdeck, A. (1958) Two types of orientation in migrating Starlings, Sturnus vulgaris L., and Chaffinches, Fringilla coelebs L., as revealed by displacement experiments. *Ardea*, **46**, 1–37.

R Development Core Team. (2014) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Reichlin, T.S., Schaub, M., Menz, M.H.M., Mermod, M., Portner, P., Arlettaz, R. & Jenni, L. (2008) Migration patterns of hoopoe Upupa epops and wryneck Jynx torquilla: an analysis of European ring recoveries. *Journal of Ornithology*, **150**, 393–400.

Robinson, R. a., Grantham, M.J. & Clark, J. a. (2009) Declining rates of ring recovery in British birds. *Ringing & Migration*, **24**, 266–272.

Rodríguez-Ruiz, J., de la Puente, J., Parejo, D., Valera, F., Calero-Torralbo, M.Á., Reyes-González, J.M., Zajková, Z., Bermejo, A. & Avilés, J.M. (2015) Disentangling migratory routes and wintering grounds of Iberian near-threatened European rollers Coracias garrulus. *PLoS One*, **9**, e115615.

Sanderson, F.J., Donald, P.F., Pain, D.J., Burfield, I.J. & van Bommel, F.P.J. (2006) Long-term population declines in Afro-Palearctic migrant birds. *Biological Conservation*, **131**, 93–105.

Strandberg, R., Klaassen, R.H.G., Hake, M. & Alerstam, T. (2009) How hazardous is the Sahara Desert crossing for migratory birds? Indications from satellite tracking of raptors. *Biology letters*, **6**, 297–300.

Thorup, K., Alerstam, T., Hake, M. & Kjellen, N. (2003a) Can vector summation describe the orientation system of juvenile ospreys and honey buzzards? - An analysis of ring recoveries and satellite tracking. *Oikos*, **103**, 350–359.

Thorup, K., Alerstam, T., Hake, M. & Kjellen, N. (2003b) Bird orientation: compensation for wind drift in migrating raptors is age dependent. *Proceedings of the Royal Society of London B: Biological Sciences*, **270**, S8–S11.

Thorup, K. & Conn, P. (2009) Estimating the Seasonal Distribution of Migrant Bird Species: Can Standard Ringing Data Be Used? *Modeling Demographic Processes in Marked Populations* (eds D. Thomson, E. Cooch & M. Conroy), pp. 1107–1117. Springer.

Thorup, K., Rabøl, J. & Erni, B. (2007) Estimating variation among individuals in migration direction. *Journal of Avian Biology*, **38**, 182–189.

Tucker, G.M., Heath, M.F., Tomialojc, L. & Grimmett, R.F.A. (1994) *Birds in Europe: Their Conservation Status*. BirdLife International, Cambridge, UK.

Vickery, J.A., Ewing, S.R., Smith, K.W., Pain, D.J., Bairlein, F., Škorpilová, J. & Gregory, R.D. (2013) The decline of Afro-Palaearctic migrants and an assessment of potential causes. *Ibis*, **156**, 1–22.

Vincent-Martin, N., Gimenez, O. & Besnard, A. (2013) Reproduction et dynamique de colonisation du rollier d'Europe en cavites artificielles. *Écologie et conservation d'une steppe méditerranéenne, La* *plaine de Crau* (eds L. Tatin, A. Wolff, J. Boutin, E. Colliot & T. Dutoit) Quae.

Chapter 7: Long-distance migrants have low connectivity: good under climate change but not habitat loss

A version of this chapter is in review in *Journal of Animal Ecology*

7.1 Abstract

Estimating whether populations of long-distance migrant animals rely on specific non-breeding sites (high connectivity) is essential to understanding their population dynamics in the face of global change. Long-distance migrant bird populations (712 individuals from 98 populations of 45 species from the Neotropic and Afro-Palaearctic flyways), on average, spread out and mix over a continent-wide scale non-breeding area, with spread mainly depending simply on the availability of land to the south of the breeding location rather than species or family characteristics. Such low connectivity should engender population resilience to climate change driven shifts in habitat, but increases susceptibility to habitat loss. This leads to opposing connectivity optima: migrants cannot adapt to both, which may explain almost universal declines of migratory species.

Supporting information can be found in ***Appendix 4****.*

7.2 Introduction

Global conservation strategies to address the widespread decline of migratory animals (Bolger *et al.* 2008; Brower *et al.* 2012; Gilroy *et al.* 2016) are generally based on the premise that migrant populations have well connected breeding and non-breeding (or wintering) ranges and that the identification of these ranges is a priority (Martin *et al.* 2007; Runge *et al.* 2014, 2015). However, contemporary long-distance migration systems represent recently evolved adaptive responses to dynamic global climatic conditions (Cresswell, Satterthwaite & Sword 2011; Fryxell & Holt 2013) suggesting that, at the population level, a bet-hedging, non-deterministic migration strategy of using multiple non-breeding sites should actually be advantageous.

Understanding how breeding and non-breeding sites are connected via the trajectories of individual migrants is crucial for successfully predicting the response of migratory populations to environmental change and optimising conservation strategies (Taylor & Norris 2009). Breeding populations which spread out over a large non-breeding area (high 'migratory spread', **Fig. 7.1a**) should have greater potential to track shifting habitat (due to, for example, climate change; **Fig. 7.2a**) (Cresswell 2014) and will be affected by aggregate conditions over a wide geographical area. In contrast, low migratory spread (**Fig. 7.1b**) reduces the resilience of a breeding population to shifting non-breeding habitat, so should only be selected for when the location of non-breeding sites is highly predictable (**Fig. 7.2b**). Migratory spread also influences the degree to which individuals from different breeding populations use the same non-breeding sites, with high spread generally resulting in high 'migratory mixing' (**Fig. 7.1c** and **d** though see **e** and **f**). Populations which mix during the non-breeding season should respond equivalently to changes in non-breeding conditions, whereas segregated populations will respond only to specific local changes and maintain demographic independence (Esler 2000).

Recent advances in tagging technology have enabled the tracking of animals representing a range of migratory species and systems (Bridge *et al.* 2011), providing the opportunity to test for the first time the scale of migratory spread and the degree to which separate breeding populations mix on their non-breeding grounds (i.e. migratory connectivity (Webster *et al.* 2002)). Here, we analyze all published breeding and non-breeding locations of 712 individual migrant land-birds tracked from 98 populations of 45 species across two trans-continental flyways (Neotropic and Afro-Palaearctic; **Appendix 4**, **Table S4.1**). We show that variation in mean non-breeding spread is mostly determined simply by the availability of land to the south of the breeding area (more land, greater spread), rather than species-specific strategies, with phylogeny at any level contributing relatively little explanatory power. We also show that segregation of populations on the wintering ground is generally low, with higher levels arising only in species having a large non-breeding range allowing populations to remain segregated, rather than the constituent populations having lower spread. Our results therefore suggest that migrants have a bet-hedging strategy which can allow populations to persist during rapid climate change but that is poorly adapted to habitat loss.

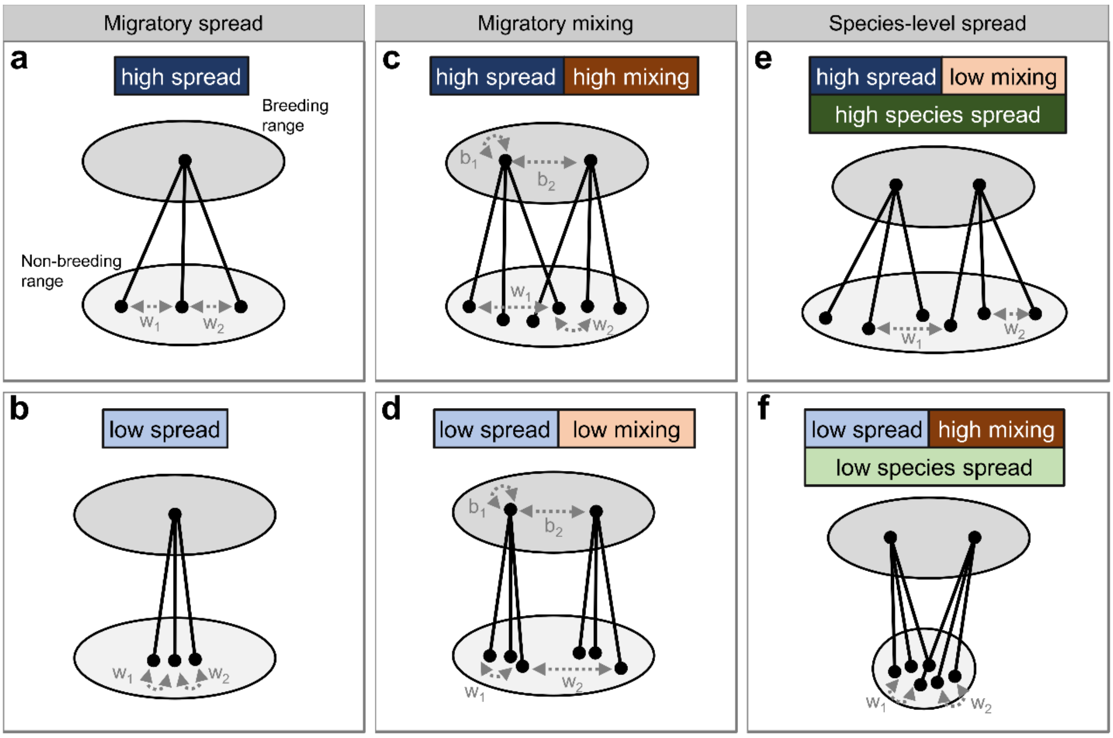


Figure. 7.1. How migratory connectivity arises through spread and mixing of populations. ‘Migratory spread’ is the degree to which a breeding population spreads out over the non-breeding area (**a**, **b**) and is measured as the mean of the distances (*w1*, *w2*, …) between non-breeding individuals from the breeding population. ‘Migratory mixing’ is the extent to which individuals from different breeding populations of a species mix in the non-breeding area (**c**, **d**) and is measured by the Mantel correlation between pairwise distances of breeding individuals (*b1*, *b2*, …) and corresponding distances of non-breeding individuals (*w1*, *w2*, …), with high positive correlations indicating low mixing. Generally, species with high population-level spread will have high mixing (**c**); those with low spread will tend to have low mixing (**d**). The relationship between migratory spread and mixing is mediated, however, by variation in the size of the non-breeding range (‘species-level spread’, or migratory dispersion (Gilroy *et al.* 2016) the mean of the distances (*w1*, *w2*, …) between all non-breeding individuals from a species regardless of breeding population). Populations with high spread will have low mixing if species-level spread is also high (**e**). Conversely, populations with low spread will have high mixing if species-level spread is also low (**f**).

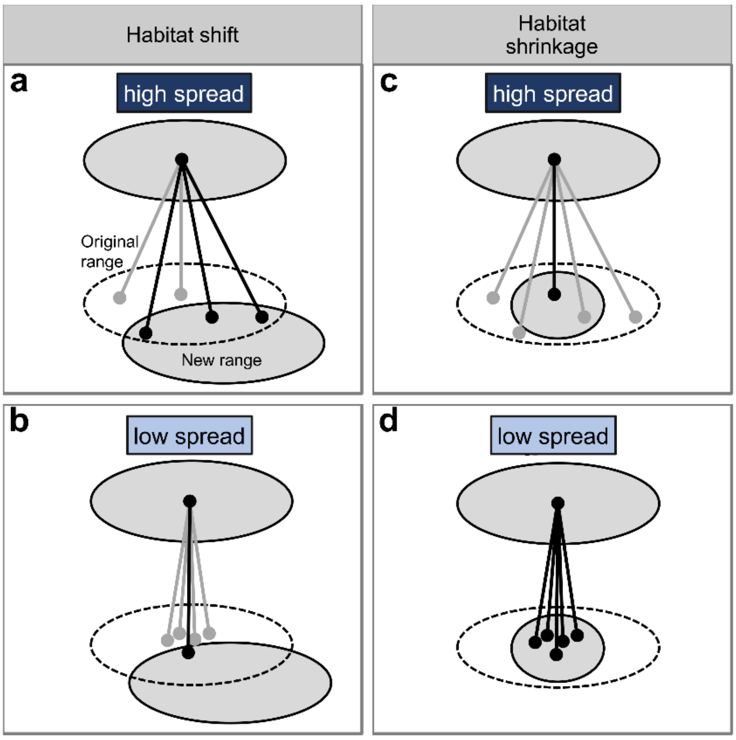


Figure 7.2. Migratory spread determines response of populations to non-breeding (e.g. wintering) habitat change. The number of individuals successfully reaching suitable non-breeding sites (black lines) following either a shift (**a**, **b**) or a reduction (**c**, **d**) in the area of suitable non-breeding habitat depends on the degree of migratory spread. A greater proportion of a population with high spread will still reach suitable habitat if its location shifts (e.g. due to climate change) compared to a low spread population (**a** and **b**), but if suitable habitat becomes less available overall (due to habitat loss) then a greater proportion of a population with high spread will miss the shrinking habitat, whereas a population with low spread may still reach the target (**c** and **d**).

7.3 Methods

7.3.1 Data acquisition

A comprehensive search of peer-reviewed tracking studies was conducted for all European and North American species classed (according to BirdLife; http://www.birdlife.org/datazone/species/search) as migratory land-birds by entering the terms *[latin name] AND migra* AND (gps OR geolo* OR satellite)* into the Web of Science online library. From these studies, breeding and non-breeding (i.e. the site where an individual spent the majority of the wintering, non-breeding period after migration) locations of individual birds were extracted (or approximated from plotted map locations using Google Earth when precise coordinates were not given). We excluded species with data from only one individual, and restricted our analyses to adult birds tagged during the breeding season. Individuals of the same species tagged within 100 km of one another (which meant tagged at the same study site in almost all cases) were grouped into 'populations', the principle unit of analysis (**Table S4.1**).

We defined the Afro-Palaearctic system as comprising all populations breeding in Europe west of 65° E and wintering in Africa south of 20° N. The African non-breeding range was divided into northern and southern zones at 4° N, the latitude at which Africa narrows at the Gulf of Guinea to reflect the main point of change in land availability. The Neotropic system was defined as all populations breeding in North America and wintering south of 30° N. The American non-breeding range was divided into northern and southern zones at 12° N, the approximate border of Central and South America, again to reflect the main point of change in land availability.

7.3.2 Migratory spread analysis

As an initial metric of population spread we calculated the maximum distance between non-breeding individuals from each breeding population. This depended inevitably on sample size and so was only used to model the asymptote of average maximum range. Four linear mixed models predicting the maximum distance between any two locations of a population on the non-breeding ground were fitted against either sample size, the natural logarithm of sample size, the quadratic of sample size or intercept only, with a random intercept of species identity (**Table S4.2**).

As a sample-size-independent metric of population-level migratory spread we calculated the mean distance between individual non-breeding sites for each population (i.e. the average distance between two individuals from the same breeding population during the non-breeding season). We tested the hypothesis (our ‘null model’) that migratory spread is determined by land availability by constructing a linear mixed model with migratory spread as the dependent variable (**Table S4.3**). Fixed effects were the three-way interaction between migration system (Afro-Palaearctic or Neotropic), wintering zone (north or south) and mean breeding longitude (centered separately for each system). We also included the two-way interaction between mean migration distance (great circle distance between mean breeding and non-breeding site) and wintering zone, because individuals departing with slight variation in bearing from a starting point will inevitably spread over a wider area with increasing migration distance (dependent on the number of stop-overs during migration). To account for the non-independence of populations of the same species, we fitted a random intercept of species, allowing us also to compare the relative explanatory power of species identity versus the fixed effects using marginal and conditional R^2s (Nakagawa & Schielzeth 2013). To test for higher-level taxonomic effects, we fitted additional models with hierarchical random intercepts of (1) species nested within family and (2) species nested within family nested within order.

7.3.3 Migratory mixing analysis

For each species tracked from more than one population, we quantified migratory mixing as the Mantel correlation between pairwise distance matrices of individual breeding and non-breeding sites (Ambrosini, Møller & Saino 2009). Strong positive Mantel coefficients indicate that individuals which breed close together also spend the non-breeding season close together, and vice versa (i.e. low mixing). To test the hypothesis that migratory mixing increases as population-level migratory spread increases, but decreases with species-level spread (i.e. migratory dispersion, **Fig. 7.1**, see Gilroy *et al*. (2016)), we constructed a linear model with Mantel correlation coefficient as the dependent variable (**Table S4.4**). Fixed effects were the mean distance between breeding sites (to control for the geographic spread of sampled breeding populations), the quadratic effect of mean distance between non-breeding sites (species-level spread) and the mean population-level migratory spread.

All linear mixed models were fitted using maximum likelihood in the R package *nlme*. Reduced models containing all possible combinations of fixed effects were evaluated according to AICc using the package *MuMIn*. We use the ‘best’ model (with lowest AICc; ΔAICc < 2 in all cases) for all predictions, interpretation and discussion, with standard errors estimated using the package *AICcmodavg* and marginal and conditional R^2s in *MuMIn*.

Our data are prone to two potential sources of error; imprecision in the translation of data from published figures to latitude-longitude coordinates via Google Earth (‘translation error’), and inaccuracy of solar geolocator-derived positions in the original published data (‘geolocator error’). The sensitivity of our results to these sources of error was explored, but results were little affected suggesting that errors were unbiased, and effects were relatively small (see **Appendix 4**).

7.4 Results

Two individuals from the same breeding population (breeding sites within 100 km) wintered, on average, 743 km apart, covering 10–20% of the maximum width of the potential non-breeding zone (**Fig. 7.3**). In turn, the average predicted maximum distance between non-breeding individuals from the same breeding population was more than 3,000 km (after accounting for sample size; **Fig. 7.4** and **Table S4.2**). This suggests that migratory spread is generally high, with most migrant populations employing a bet-hedging strategy, resulting in the use of multiple non-breeding sites.

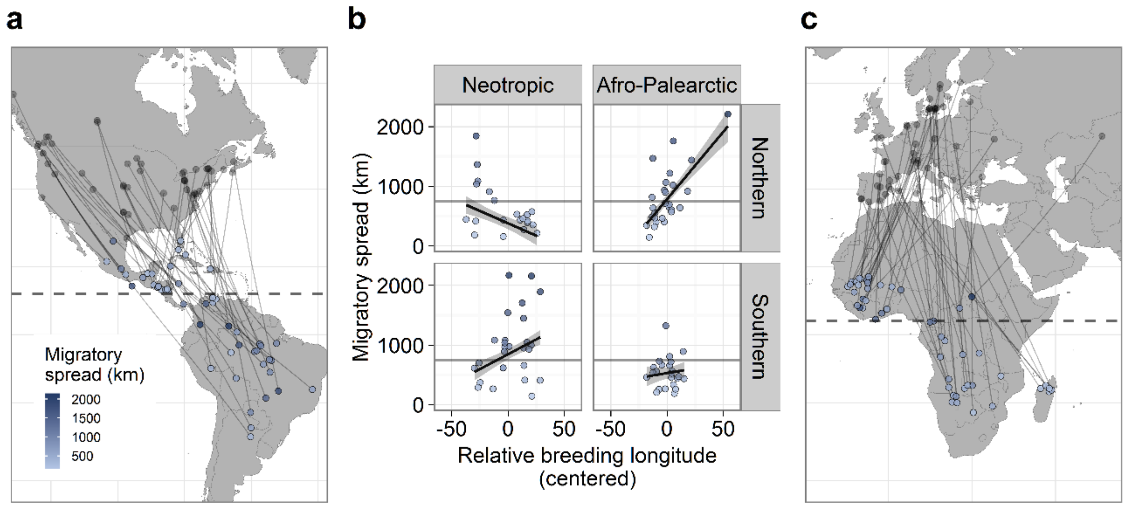


Figure 7.3. Migratory spread of populations is predicted largely by land availability. Maps show mean breeding and non-breeding (wintering) sites of 98 populations of 45 species of land birds from the Neotropic (**a**) and Afro-Palaearctic (**c**) migration systems. Horizontal dashed lines show the divide between northern and southern zones in each system. **b** shows model predictions for the interaction between breeding longitude (*x*-axis), system (columns) and zone (rows). The horizontal line intercepts the *y*-axis at mean value of migratory spread overall (average distance on the non-breeding ground between any two individuals from the same breeding population = 743 km) and shaded regions are ± S.E.

Variation in migratory spread was remarkably well predicted by a simple 'null model' of geography, where populations with greater land availability to the south of the breeding area spread out more (**Fig. 7.3** and **Table S4.3**). Thus, North American populations (**Fig. 7.3a** and **b**) wintering in the northern zone spread out more if they come from western breeding sites (because land is more limited in the Caribbean islands than in continental Central America at similar latitudes), whereas those wintering in the southern zone spread out more if they come from eastern breeding sites (because western populations are constrained by the Pacific Ocean). Likewise, in the Afro-

Palaearctic system (**Fig. 7.3b** and **c**), populations wintering in the northern zone spread out more if they come from eastern breeding sites (because western breeders are constrained by the Atlantic Ocean). For Afro-Palaearctic migrants wintering in the southern zone, spread was generally low (perhaps due to the 'funneling' effect of caused by the narrower landmass south of 4˚ N). Breeding longitude and wintering zone of a population predicted 38 % of the variance in migratory spread and species identity contributed just 25 % of the variance, ($R^2_m = 0.38$; $R^2_c = 0.63$); we found no support for higher-level phylogenetic effects. This suggests that, on the whole, the principle factor limiting migratory spread is land availability, not a species' ecology or morphology.

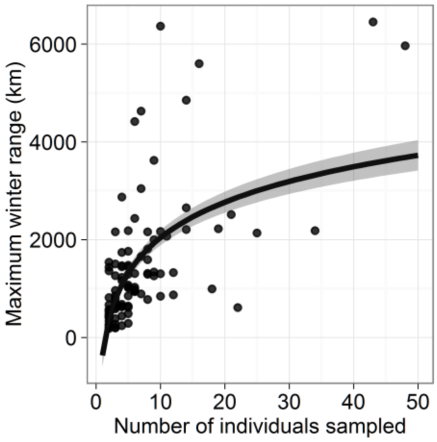


Figure 7.4. The maximum distance on the non-breeding ground between any two individuals from the same breeding population increases with sample size, levelling off at 3000–4000 km. The fitted line shows model predictions of the $log_{10}(n)$ model; shaded region is ± S.E.

As a consequence of high migratory spread, different breeding populations tended to mix during the non-breeding season. Mantel correlation coefficients, which quantify whether distances between populations on the breeding ground are maintained on the non-breeding ground (Ambrosini *et al.* 2009), were significant for only 10 out of 28 species, and above 0.5 for only 7 species (**Fig. 7.5a**). Most species therefore had "weak, diffuse, connectivity" (Ambrosini *et al.* 2009), indicating that migratory mixing is generally high. A few species had low migratory mixing, but this was principally driven by the species having a large non-breeding range ('migratory dispersion'; see (Gilroy *et al.* 2016)) allowing populations to remain segregated, rather than the constituent populations having lower spread (**Fig. 7.5b** and **Table S4.4**).

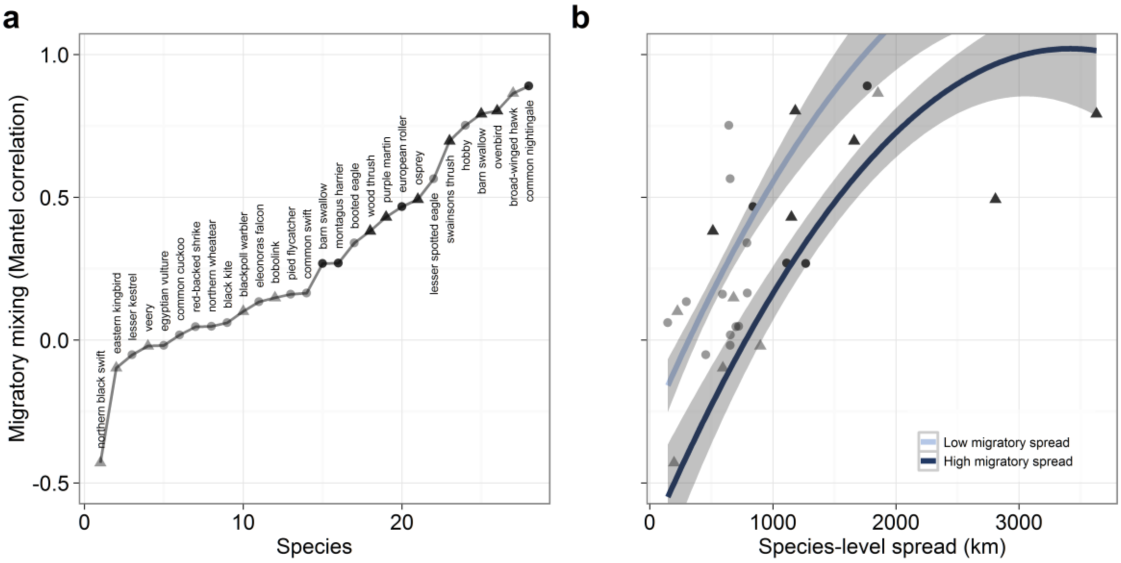


Fig. 7.5. Most species' breeding populations mix on the non-breeding ground. **a** connectivity is generally weak for 28 species of long distance migrant land bird (low values for the Mantel correlation; the strength of the correlation between pairwise distance matrices of individual breeding and non-breeding sites). **b** high values arise only in species that spread over a large area during the non-breeding season (high species-level spread), especially when population-level migratory spread is low (pale blue line). Shaded regions are ± S.E. Triangles are species from the Neotropic system and circles are those from the Afro-Palaearctic. Solid black points denote a significant ($p < 0.05$) Mantel correlation; grey points are non-significant.

7.5 Discussion

Long-distance migrant bird populations, on average, spread out and mix over a continent-wide scale non-breeding area, with spread mainly depending simply on the availability of land to the south of the breeding location rather than species or family characteristics. Our results suggest that when low mixing occurs, this is usually despite high spread (see **Fig. 7.1e**), rather than due to low spread (**Fig. 7.1d**); this highlights a limitation in the migratory connectivity nomenclature, in which 'strong connectivity' is used interchangeably to refer to both low mixing and low spread (Webster *et al.* 2002; Taylor & Norris 2009).

The general lack of population-specific non-breeding areas supports the hypothesis that a bet-hedging strategy towards non-breeding site selection is adaptive (Reilly & Reilly 2009), probably in response to large scale, relatively rapid and still dynamic climate change (Wanner *et al.* 2008; Svenning *et al.* 2015). For example, severe decadal variation in rainfall patterns across Africa (Nicholson 2001) likely favors an adaptive system that allows for rapid population-level realignment of non-breeding distribution.

Our results are consistent with existing knowledge of the mechanisms of orientation in migratory birds. Although there is good evidence for a genetic basis for many migratory traits including departure direction (Berthold *et al.* 1992), these innate controls vary between individuals and are insensitive to environmental perturbations during migration such as crosswinds (Horton *et al.* 2016). This is particularly true for naïve juvenile migrants, which do not compensate for natural or experimental displacement (Perdeck 1958; Thorup *et al.* 2003). Although adult migrants are capable of true navigation, compensating for displacement (Willemoes *et al.* 2015), they tend to be highly faithful to their first non-breeding season site (Cresswell 2014), relying on previous experience rather than innate programming. With the exception of long-lived species with extended parental care (geese, cranes, etc.) it is unlikely that juveniles are generally able to follow more experienced migrants, with adults usually migrating earlier and faster (Stewart, Francis & Massey 2002; Mellone *et al.* 2013). Thus, realized connectivity is likely the consequence of naïve juvenile migrants spreading out over the widest available area to find suitable non-breeding sites and then returning to these sites as adults if they have survived (Cresswell 2014).

Although such a bet-hedging strategy may be adaptive, and should facilitate range shifts in response to climate change, it is unlikely to be a good strategy to respond to large-scale reductions in habitat availability, because an increasing proportion of any migratory population will miss the ‘target’ (**Fig. 7.2c**). Consequently, climate-induced shifts in non-breeding habitat will select for high spread and lower connectivity, whilst suitable habitat becoming restricted to specific localized areas should favour the reverse. Whilst selection can act rapidly on mean migration direction (Berthold *et al.* 1992) we know little about the genetic basis of migratory spread (Pulido 2007; Thorup, Rabøl & Erni 2007). Even if migrants are capable of rapidly evolving more or less deterministic non-breeding site selection strategies, there is no optimum strategy in the face of the strong opposing directional selection pressures posed by climate change and habitat loss. This may help explain almost universal declines of migratory species (Bolger *et al.* 2008; Brower *et al.* 2012; Gilroy *et al.* 2016).

The conservation implications of generally low connectivity in the Afro-Palaearctic and Nearctic flyways are that the loss of any non-breeding site will have a diffuse but widespread effect on breeding populations of a species (Dolman & Sutherland 1992; Taylor & Norris 2009). Therefore, conservation of any site, at any scale, in the non-breeding area will benefit many breeding populations of European and North American migrant birds, but large-scale land-sharing or sustainable development solutions over Africa and South and Central America are needed to address large-scale migrant bird declines.

7.6 References

Ambrosini, R., Møller, A.P. & Saino, N. (2009) A quantitative measure of migratory connectivity. *Journal of theoretical biology*, **257**, 203–211.

Berthold, P., Helbig, A., Mohr, G. & Querner, U. (1992) Rapid microevolution of migratory behaviour in a wild bird species. *Nature*, **2**, 173–179.

Bolger, D.T., Newmark, W.D., Morrison, T.A. & Doak, D.F. (2008) The need for integrative approaches to understand and conserve migratory ungulates. *Ecology Letters*, **11**, 63–77.

Bridge, E.S., Thorup, K., Bowlin, M.S., Chilson, P.B., Diehl, R.H., Fléron, R.W., Hartl, P., Kays, R., Kelly, J.F., Robinson, W.D. & Wikelski, M. (2011) Technology on the Move: Recent and Forthcoming Innovations for Tracking Migratory Birds. *BioScience,* **61**, 689–698.

Brower, L.P., Taylor, O.R., Williams, E.H., Slayback, D.A., Zubieta, R.R. & Ram??rez, M.I. (2012) Decline of monarch butterflies overwintering in Mexico: Is the migratory phenomenon at risk? *Insect Conservation and Diversity*, **5**, 95–100.

Cresswell, W. (2014) Migratory connectivity of Palaearctic-African migratory birds and their responses to environmental change: the serial residency hypothesis (ed S Bauer). *Ibis*, **156**, 493–510.

Cresswell, K.A., Satterthwaite, W.H. & Sword, G.A. (2011) Understanding the evolution of migration through empirical examples. *Animal migration: a synthesis*, pp. 1–16. Oxford University Press, Oxford, UK.

Dolman, P.M. & Sutherland, W.J. (1992) The response of bird populations to habitat loss. *Ibis,* **137**, S38–S46.

Esler, D. (2000) Applying metapopulation theory to conservation of migratory birds. *Conservation Biology*, **14**, 366–372.

Fryxell, J. & Holt, R. (2013) Environmental change and the evolution of migration. *Ecology*, **94**, 1274–1279.

Gilroy, J.J., Gill, J.A., Butchart, S.H.M., Jones, V.R. & Franco, A.M.A. (2016) Migratory diversity predicts population declines in birds. *Ecology Letters*, **19**, 308–317.

Horton, K.G., Van Doren, B.M., Stepanian, P.M., Hochachka, W.M., Farnsworth, A. & Kelly, J.F. (2016) Nocturnally migrating songbirds drift when they can and compensate when they must. *Scientific Reports*, **6**, 21249.

Martin, T.G., Chadès, I., Arcese, P., Marra, P.P., Possingham, H.P. & Norris, D.R. (2007) Optimal conservation of migratory species. *PLoS One*, **2**, e751.

Mellone, U., López-López, P., Limiñana, R., Piasevoli, G. & Urios, V. (2013) The trans-equatorial loop migration system of Eleonora's falcon: differences in migration patterns between age classes, regions and seasons. *Journal of Avian Biology*, **44**, 471–426.

Nakagawa, S. & Schielzeth, H. (2013) A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, **4**, 133–142.

Nicholson, S.E. (2001) Climatic and environmental change in Africa during the last two centuries. *Climate Research*, **17**, 123–144.

Perdeck, A. (1958) Two types of orientation in migrating Starlings, Sturnus vulgaris L., and Chaffinches, Fringilla coelebs L., as revealed by displacement experiments. *Ardea*, **46**, 1–37.

Pulido, F. (2007) The Genetics and Evolution of Avian Migration. *BioScience*, **57**, 165–174.

Reilly, J.R. & Reilly, R.J. (2009) Bet-hedging and the orientation of juvenile passerines in fall migration. *Journal of Animal Ecology*, **78**, 990–1001.

Runge, C.A., Martin, T.G., Possingham, H.P., Willis, S.G. & Fuller, R.A. (2014) Conserving mobile species. *Frontiers in Ecology and the Environment*, **12**, 395–402.

Runge, C.A., Watson, J.E.M., Butchart, S.H.M., Hanson, J.O., Possingham, H.P. & Fuller, R.A. (2015) Protected areas and global conservation of migratory birds. *Science*, **350**, 1255–1258.

Stewart, R.L.M., Francis, C.M. & Massey, C. (2002) Age-Related Differential Timing of Spring Migration Within Sexes in Passerines. *The Wilson Bulletin*, **114**, 264–271.

Svenning, J.-C., Eiserhardt, W.L., Normand, S., Ordonez, A. & Sandel, B. (2015) The Influence of Paleoclimate on Present-Day Patterns in Biodiversity and Ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, **46**, 551–572.

Taylor, C.M. & Norris, D.R. (2009) Population dynamics in migratory networks. *Theoretical Ecology*, **3**, 65–73.

Thorup, K., Alerstam, T., Hake, M. & Kjellen, N. (2003) Bird orientation: compensation for wind drift in migrating raptors is age dependent. *Proceedings of the Royal Society of London B: Biological Sciences*, **270**, S8–S11.

Thorup, K., Rabøl, J. & Erni, B. (2007) Estimating variation among individuals in migration direction. *Journal of Avian Biology*, **38**, 182–189.

Wanner, H., Beer, J., Bütikofer, J., Crowley, T.J., Cubasch, U., Flückiger, J., Goosse, H., Grosjean, M., Joos, F., Kaplan, J.O., Küttel, M., Müller, S.A., Prentice, I.C., Solomina, O., Stocker, T.F., Tarasov, P., Wagner, M. & Widmann, M. (2008) Mid- to Late Holocene climate change: an overview. *Quaternary Science Reviews*, **27**, 1791–1828.

Webster, M.S., Marra, P.P., Haig, S.M., Bensch, S. & Holmes, R.T. (2002) Links between worlds:

unravelling migratory connectivity. *Trends in Ecology and Evolution*, **17**, 76–83.

Willemoes, M., Blas, J., Wikelski, M. & Thorup, K. (2015) Flexible navigation response in common cuckoos Cuculus canorus displaced experimentally during migration. *Scientific Reports*, **5**, 16402.

Appendix 4: Supporting information for Chapter 7

Supplementary tables

Table S4.1 List of species and references used in this study. n_{ind} = number of individuals per species, n_{pop} = number of populations per study. Full citations are in the supplementary bibliography

Name (common)	**Name (scientific)**	**System**	n_{ind}	n_{pop}	**Reference(s)**
Aquatic Warbler	*Acrocephalus paludicola*	Afro-Palaearctic	2	1	(Salewski *et al.* 2012)
Barn Swallow	*Hirundo rustica*	Afro-Palaearctic	95	3	(Arizaga *et al.* 2015) (Liechti *et al.* 2014)
Black Kite	*Milvus migrans*	Afro-Palaearctic	4	1	(Tanferna *et al.* 2012)
Booted Eagle	*Hieraaetus pennatus*	Afro-Palaearctic	3	1	(Chevallier *et al.* 2010) (Mellone *et al.* 2013b)
Common Cuckoo	*Cuculus canorus*	Afro-Palaearctic	6	2	(Willemoes *et al.* 2014)
Common Nightingale	*Luscinia megarhynchos*	Afro-Palaearctic	27	3	(Hahn *et al.* 2014)
Common Nightjar	*Caprimulgus europaeus*	Afro-Palaearctic	3	1	(Cresswell & Edwards 2013)
Common Redstart	*Phoenicurus phoenicurus*	Afro-Palaearctic	7	1	(Kristensen, Tøttrup & Thorup 2013)
Common Swift	*Apus Apus*	Afro-Palaearctic	7	2	(Åkesson *et al.* 2012) (Klaassen *et al.* 2014)
Egyptian Vulture	*Neophron percnopterus*	Afro-Palaearctic	4	3	(García-Ripollés, López-López & Urios 2010) (López-López, García-Ripollés & Urios 2014) (Meyburg *et al.* 2004)
Eleonora's Falcon	*Falco eleonorae*	Afro-Palaearctic	15	5	(Gschweng *et al.* 2008) (Kassara *et al.* 2012) (Mellone *et al.* 2013a)
European Hoopoe	*Upupa epops*	Afro-Palaearctic	3	1	(Bächler *et al.* 2010)
European Roller	*Coracias garrulus*	Afro-Palaearctic	26	7	(Finch *et al.* 2015)
Great Reed Warbler	*Acrocephalus arundinaceus*	Afro-Palaearctic	8	1	(Lemke *et al.* 2013)
Hobby	*Falco subuteo*	Afro-Palaearctic	3	2	(Meyburg *et al.* 2011) (Strandberg *et al.* 2009)
Honey Buzzard	*Pernis apivorus*	Afro-Palaearctic	6	1	(Hake, Kjellen & Alerstam 2003)
Lesser Kestrel	*Falco naumanni*	Afro-Palaearctic	9	2	(Catry *et al.* 2011) (Limiñana *et al.* 2012)
Lesser Spotted Eagle	*Clanga pomarina*	Afro-Palaearctic	2	2	(Meyburg, Scheller & Meyburg 1995) (Meyburg *et al.* 2007)
Marsh Harrier	*Circus aeruginosus*	Afro-Palaearctic	8	1	(Strandberg *et al.* 2008)
Montagu's Harrier	*Circus pygargus*	Afro-Palaearctic	27	4	(Limiñana, Soutullo & Urios 2007) (Trierweiler *et al.* 2007) (Trierweiler *et al.* 2008) (Trierweiler *et al.* 2014)
Northern Wheatear	*Oenanthe oenanthe*	Afro-Palaearctic	5	2	(Schmaljohann, Fox & Bairlein 2012) (van Oosten, Versluijs & van Wijk 2014)

Osprey	*Pandion haliaetus*	Afro-Palaearctic	10	1	(Alerstam, Hake & Kjellén 2006) (Hake, Kjellén & Alerstam 2001)
Pallid Harrier	*Circus macrourus*	Afro-Palaearctic	6	1	(Terraube *et al.* 2012)
Pied Flycatcher	*Ficedula hypoleuca*	Afro-Palaearctic	13	4	(Ouwehand *et al.* 2015)
Red-Backed Shrike	*Lanius collurio*	Afro-Palaearctic	9	3	(Tøttrup *et al.* 2012)
Short-Toed Eagle	*Circaetus gallicus*	Afro-Palaearctic	2	3	(Mellone *et al.* 2011) (Meyburg, Meyburg & Pacteau 1996) (Meyburg, Meyburg & Barbraud 1998) (Pavón *et al.* 2010)
Tawny Pipit	*Anthus campestris*	Afro-Palaearctic	6	1	(Briedis *et al.* 2016)
Thrush Nightingale	*Luscinia luscinia*	Afro-Palaearctic	2	1	(Stach *et al.* 2012)
Turtle Dove	*Streptopelia turtur*	Afro-Palaearctic	5	1	(Eraud *et al.* 2013)
Barn Swallow	*Hirundo rustica*	Neotropic	24	5	(Hobson *et al.* 2015)
Blackpoll Warbler	*Setophaga striata*	Neotropic	5	2	(DeLuca *et al.* 2015)
Bobolink	*Dolichonyx oryzivorus*	Neotropic	13	3	(Renfrew *et al.* 2013)
Broad-Winged Hawk	*Buteo platypterus*	Neotropic	4	2	(Haines *et al.* 2003)
Eastern Kingbird	*Tyrannus tyrannus*	Neotropic	6	2	(Jahn *et al.* 2013)
Gray Catbird	*Dumetella carolinensis*	Neotropic	6	1	(Ryder, Fox & Marra 2011)
Northern Black Swift	*Cypseloides niger*	Neotropic	2	1	(Beason *et al.* 2012)
Osprey	*Pandion haliaetus*	Neotropic	61	8	(Bedrosian *et al.* 2015) (Elliott *et al.* 2007) (Martell *et al.* 2001) (Martell *et al.* 2004)
Ovenbird	*Seiurus aurocapilla*	Neotropic	36	3	(Hallworth & Marra 2015) (Hallworth *et al.* 2015)
Purple Martin	*Progne subis*	Neotropic	95	8	(Fraser *et al.* 2012)
Red-Eyed Vireo	*Vireo olivaceus*	Neotropic	10	1	(Callo, Morton & Stutchbury 2013)
Scissor-Tailed Flycatcher	*Tyrannus forficatus*	Neotropic	3	1	(Jahn *et al.* 2013)
Swainsons Thrush	*Catharus ustulatus*	Neotropic	35	4	(Cormier *et al.* 2013) (Delmore, Fox & Irwin 2012) (Delmore & Irwin 2014)
Veery	*Catharus fuscescens*	Neotropic	34	2	(Heckscher, Halley & Stampul 2015)
Western Kingbird	*Tyrannus verticalis*	Neotropic	5	1	(Jahn *et al.* 2013)
Wood Thrush	*Hylocichla mustelina*	Neotropic	50	6	(Stanley *et al.* 2014)

Table S4.2 Model summaries for the four linear mixed models predicting the effect of sample size (n) on maximum distance recorded between any two individuals from the same breeding population on the non-breeding ground (i.e. an index of size of non-breeding range). Significant ($p < 0.05$) parameters estimates are in bold. R^2_m and R^2_c are conditional and marginal r-squared, respectively. / = variable absent

Model	**Parameter**				k	**AICc**	Δ_i	w_i	R^2_m	R^2_c
	intercept	n	n^2	$log(n)$						
1	–368.4	/	/	**1046.5**	4	1618.82	0.00	0.99	0.40	0.64
2	**408.4**	**158.5**	**–1.8**	/	5	1627.87	9.05	0.01	0.36	0.58
3	**706.1**	**89.9**	/	/	4	1629.95	11.12	0.00	0.33	0.53
4	**1280.7**	/	/	/	3	1671.91	53.08	0.00	0.00	0.32

Table S4.3 Model summaries for the top (95% confidence) set of linear mixed models predicting migratory spread. *b.lon* = mean breeding longitude; *mig.dist* = mean migration distance. Significant ($p < 0.05$) parameters estimates are in bold. k = number of parameters in model; Δ_i = difference in AICc between i^{th} model and 'best' model; w_i = Akaike model weight (calculated across all models); R^2_m and R^2_c are conditional and marginal r-squared, respectively. / = variable absent

Model	**Parameter**										***k***	**AICc**	Δ_i	w_i	R^2_m	R^2_c
	intercept	*b.lon*	*mig.dist*	*system*	*zone*	*b.lon × system*	*b.lon × zone*	*mig.dist × zone*	*system × zone*	*b.lon × system × zone*						
1	**782.9**	**22.6**	/	**–403.5**	**–252.4**	**–30.9**	**–19.4**		**719.5**	**37.6**	10	1437.8	0.00	0.487	0.38	0.63
2	512.2	**19.7**	0.1	–302.5	406.6	**–26.1**	–15.6	–0.1	**588.0**	**28.9**	12	1439.9	2.13	0.167	0.40	0.64
3	**853.5**	**23.4**	–0.02	**–423.5**	–209.0	**–32.3**	**–20.0**		**727.5**	**37.9**	11	1440.1	2.30	0.154	0.38	0.63
4	225.2	**13.4**	**0.1**	–137.5	**931.5**	**–12.3**	/	**–0.2**	**392.6**	/	10	1442.1	4.29	0.057	0.33	0.58
5	242.2	**12.3**	**0.1**	–165.2	**852.1**	**–13.1**	3.6	**–0.2**	**434.6**	/	11	1443.9	6.09	0.023	0.34	0.59
6	–72.5	**5.7**	**0.2**	/	**1293.8**	/	/	**–0.3**	/	/	7	1443.9	6.17	0.022	0.24	0.53
7	–43.2	**5.4**	**0.2**	–42.5	**1022.6**	/	/	**–0.3**	302.3	/	9	1444.1	6.31	0.021	0.29	0.56
8	6.7	**11.9**	**0.2**	73.3	**1302.9**	–9.4	/	**–0.3**	/	/	9	1445.1	7.31	0.013	0.27	0.54
9	–169.7	**5.8**	**0.2**	111.0	**1304.1**	/	/	**–0.3**	/	/	8	1445.1	7.36	0.012	0.26	0.53

Sensitivity to error

Our data are prone to two potential sources of error; imprecision in the translation of data from published figures to latitude-longitude coordinates via Google Earth (‘translation error’), and inaccuracy of solar geolocator-derived positions in the original published data (‘geolocator error’).

Translation error was estimated by first generating mock maps for each system using 50 random non–breeding sites drawn from our dataset. These points, of known location, were then translated to latitude-longitude coordinates via Google Earth (i.e. replicating the initial data extraction process), from which we calculated latitudinal and longitudinal error. To assess systematic spatial variation in translation error (due to variation in the availability of landmarks for geo-referencing e.g. coastal features, international borders) we constructed separate linear models for latitudinal and longitudinal error (both logged). Candidate models – using all combinations of system, zone, and their interaction as predictors – were assessed based on AICc. The top model for latitudinal error included only the effect of system (mean error = 0.13˚ in the Neotropic system and 0.23˚ in the Afro-Palaearctic system), whereas the top model for longitudinal error included only the intercept (mean error = 0.17˚).

For geolocator error, conservative (i.e. large) estimates of 1˚ longitude and 3˚ latitude were drawn from the literature (Phillips *et al.* 2004; Shaffer *et al.* 2005; Fudickar, Wikelski & Partecke 2012). Latitudinal error is greatest nearest the equator, where latitudinal variation in day-length is limited and so we assumed that geolocator error was inversely proportional to latitudinal variation in day-length (Lisovski *et al.* 2012). We used the R package *geosphere* to generate day-lengths for all latitudes between 50˚ S to 50˚ N, then calculated the difference in day-length with every 1˚ increment in latitude. We then calculated latitude–dependent latitudinal geolocator error, as being inversely proportional to the latitudinal difference in day-length, scaling error to 4˚ at the equator, and 2˚ at 50˚ N/S. This crude approximation of latitude-dependent geolocator error is designed to explore whether systematic spatial variation in geolocator error is likely to influence our conclusions, rather than to provide a realistic estimation of geolocator performance at different latitudes.

To estimate the sensitivity of our findings to these sources of error, we employed a simulation-based approach. We randomly shifted raw non-breeding latitudes and longitudes by a random value drawn from a normal distribution with mean 0 and standard deviation 1.235 × *error*, such that the mean deviation was equal to the mean estimated error. We repeated this process 1000 times for each of three error scenarios; (1) translation error only, (2) translation error and constant geolocator error, (3) translation error and latitude-dependent geolocator error. For each simulation, we calculated, as above, mean non-breeding spread and the Mantel correlation coefficient, and repeated the top models in **Tables S4.3** and **S4.4**, extracting model coefficients and R^2s.

Accounting for translation error alone had little influence on either our metrics of connectivity (migratory spread and Mantel correlation), or on the model coefficients or explanatory power of models predicting their variation. However, accounting for geolocator error increased the variance around all parameters, increased the magnitude of migratory spread by up to 200 km, reduced the marginal and conditional R^2s of the top model in **Table S4.3** by approximately 0.1, and increased the magnitude of the effect of population-level spread on Mantel coefficient. The simulation results for the two scenarios including geolocator error (constant or latitude-dependent) were largely the same (**Figs. S4.1** and **S4.2**).

References:

Fudickar, A.M., Wikelski, M. & Partecke, J. (2012) Tracking migratory songbirds: Accuracy of light–level loggers (geolocators) in forest habitats. *Methods in Ecology and Evolution*, **3**, 47–52.

Lisovski, S., Hewson, C.M., Klaassen, R.H.G., Korner–Nievergelt, F., Kristensen, M.W. & Hahn, S. (2012) Geolocation by light: accuracy and precision affected by environmental factors. *Methods in Ecology and Evolution*, **3**, 603–612.

Phillips, R.A., Silk, J.R.D., Croxall, J.P., Afanasyev, V. & Briggs, D.R. (2004) Accuracy of geolocation estimates for flying seabirds. *Marine Ecology Progress Series*, **266**, 265–272.

Shaffer, S.A., Tremblay, Y., Awkerman, J.A., Henry, R.W., Teo, S.L.H., Anderson, D.J., Croll, D.A., Block, B.A. & Costa, D.P. (2005) Comparison of light– and SST–based geolocation with satellite telemetry in free–ranging albatrosses. *Marine Biology*, **147**, 833–843.

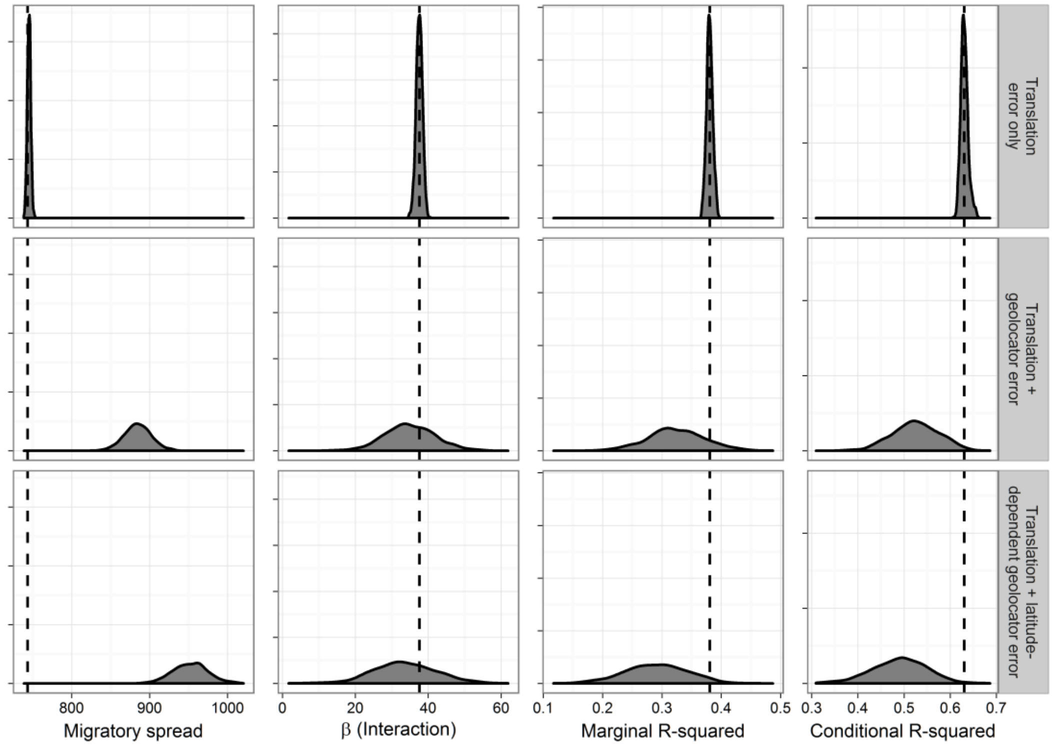


Fig. S4.1 Results of simulations testing the sensitivity of our migratory spread analysis to translation and geolocator error. Shaded curves show density of parameters (columns) calculated from 1000 simulations under each of 3 error scenarios (rows, see main text). Vertical dashed lines show parameter values calculated from the raw data.

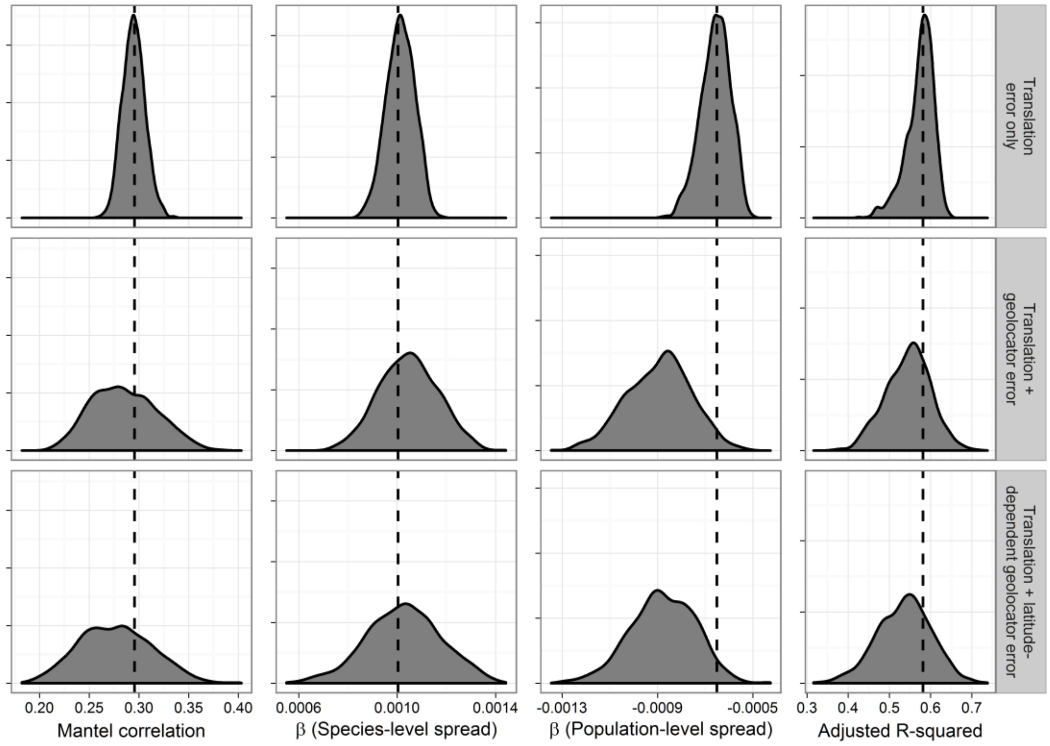


Fig. S4.2 Results of simulations testing the sensitivity of our migratory mixing analysis to translation and geolocator error. Shaded curves show density of parameters (columns) calculated from 1000 simulations under each of 3 error scenarios (rows, see main text). Vertical dashed lines show parameter values calculated from the raw data.

Supplementary bibliography

Åkesson, S., Klaassen, R.H.G., Holmgren, J., Fox, J.W. & Hedenström, A. (2012) Migration routes and strategies in a highly aerial migrant, the common swift Apus apus, revealed by light-level geolocators. *PLoS One*, **7**, e41195.

Alerstam, T., Hake, M. & Kjellén, N. (2006) Temporal and spatial patterns of repeated migratory journeys by ospreys. *Animal Behaviour*, **71**, 555–566.

Arizaga, J., Willemoes, M., Unamuno, E., Unamuno, J.M. & Thorup, K. (2015) Following year-round movements in Barn Swallows using geolocators: could breeding pairs remain together during the winter? *Bird Study*, **3657**, 1–5.

Bächler, E., Hahn, S., Schaub, M., Arlettaz, R., Jenni, L., Fox, J.W., Afanasyev, V. & Liechti, F. (2010) Year-round tracking of small trans-Saharan migrants using light-level geolocators. *PLoS One*, **5**, e9566.

Beason, J.P., Gunn, C., Potter, K.M., Sparks, R. a & Fox, J.W. (2012) The Northern Black Swift : Migration Path And Wintering Area Revealed. *The Wilson Journal Of Ornithology*, **124**, 1–8.

Bedrosian, B., Cain, S., Wolff, S. & Craighead, D. (2015) Migratory pathways, timing, and home ranges of southern greater yellowstone osprey. *Journal of Raptor Research*, **49**, 325–332.

Briedis, M., Beran, V., Hahn, S. & Adamík, P. (2016) Annual cycle and migration strategies of a habitat specialist, the Tawny Pipit Anthus campestris, revealed by geolocators. *Journal of Ornithology*, **157**, 619–626.

Callo, P.A., Morton, E.S. & Stutchbury, B.J.M. (2013) Prolonged spring migration in the Red-eyed Vireo (Vireo olivaceus). *The Auk*, **130**, 240–246.

Catry, I., Dias, M.P., Catry, T., Afanasyev, V., Fox, J.W., Franco, A.M.A. & Sutherland, W.J. (2011) Individual variation in migratory movements and winter behaviour of Iberian Lesser Kestrels Falco naumanni revealed by geolocators. *Ibis*, **153**, 154–164.

Chevallier, D., Jiguet, F., Nore, T., Baillon, F. & Cavallin, P. (2010) Satellite tracking of a Booted Eagle Aquila pennata during Migration. *Ringing & Migration*, **25**, 62–64.

Cormier, R.L., Humple, D.L., Gardali, T. & Seavy, N.E. (2013) Light-level geolocators reveal strong migratory connectivity and within-winter movements for a coastal California Swainson’s thrush (Catharus ustulatus) population. *The Auk*, **130**, 283–290.

Cresswell, B. & Edwards, D. (2013) Geolocators reveal wintering areas of European Nightjar (Caprimulgus europaeus). *Bird Study*, **60**, 77–86.

Delmore, K.E., Fox, J.W. & Irwin, D.E. (2012) Dramatic intraspecific differences in migratory routes, stopover sites and wintering areas, revealed using light-level geolocators. *Proceedings of the Royal Society of London B: Biological Sciences*, **279**, 4582–4589.

Delmore, K.E. & Irwin, D.E. (2014) Hybrid songbirds employ intermediate routes in a migratory divide. *Ecology Letters*, **17**, 1211–1218.

DeLuca, W. V, Woodworth, B.K., Rimmer, C.C., Marra, P.P., Taylor, P.D., McFarland, K.P., Mackenzie, S.A. & Norris, D.R. (2015) Transoceanic migration by a 12 g songbird. *Biology letters*, **11**, 20141045.

Elliott, J.E., Morrissey, C.A., Henny, C.J., Inzunza, E.R. & Shaw, P. (2007) Satellite telemetry and prey sampling reveal contaminant sources to Pacific Northwest Ospreys. *Ecological Applications*, **17**, 1223–1233.

Eraud, C., Rivière, M., Lormée, H., Fox, J.W., Ducamp, J.-J. & Boutin, J.-M. (2013) Migration Routes and Staging Areas of Trans-Saharan Turtle Doves Appraised from Light-Level Geolocators. *PLoS One*, **8**, e59396.

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.M., 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.

Fraser, K.C., Stutchbury, B.J.M., Silverio, C., Kramer, P.M., Barrow, J., Newstead, D., Mickle, N., Cousens, B.F., Lee, J.C., Morrison, D.M., Shaheen, T., Mammenga, P., Applegate, K. & Tautin, J. (2012) Continent-wide tracking to determine migratory connectivity and tropical habitat associations of a declining aerial insectivore. *Proceedings of the Royal Society of London B: Biological Sciences*, **279**, 4901–4906.

García-Ripollés, C., López-López, P. & Urios, V. (2010) First description of migration and wintering of adult Egyptian Vultures Neophron percnopterus tracked by GPS satellite telemetry. *Bird Study*, **57**, 261–265.

Gschweng, M., Kalko, E.K. V., Querner, U., Fiedler, W. & Berthold, P. (2008) All across Africa: highly individual migration routes of Eleonora’s falcon. *Proceedings of the Royal Society of London B: Biological Sciences*, **275**, 2887–2896.

Hahn, S., Emmenegger, T., Lisovski, S., Amrhein, V., Zehtindjiev, P. & Liechti, F. (2014) Variable detours in long-distance migration across ecological barriers and their relation to habitat availability at ground. *Ecology and Evolution*, **4**, 4150–4160.

Haines, A.M., Mcgrady, M.J., Martell, M.S., Dayton, B.J., Henke, M.B. & Seegar, W.S. (2003) Migration Routes and Wintering Locations of Broad-Winged Hawks Tracked By Satellite Telemetry. *The Wilson Bulletin*, **115**, 166–169.

Hake, M., Kjellen, N. & Alerstam, T. (2003) Age-dependent migration strategy in honey buzzards *Pernis apivorus* tracked by satellite. *Oikos*, **103**, 385–396.

Hake, M., Kjellén, N. & Alerstam, T. (2001) Satellite tracking of Swedish Ospreys Pandion haliaetus:

autumn migration routes and orientation. *Jounal of Avian Biology*, **32**, 47–56.

Hallworth, M.T. & Marra, P.P. (2015) Miniaturized GPS Tags Identify Non-breeding Territories of a Small Breeding Migratory Songbird. *Scientific reports*, **5**, 11069.

Hallworth, M.T., Sillett, T.S., Van Wilgenburg, S.L., Hobson, K.A. & Marra, P.P. (2015) Migratory connectivity of a neotropical migratory songbird revealed by archival light-level geolocators. *Ecological Applications*, **25**, 336–347.

Heckscher, C.M., Halley, M.R. & Stampul, P.M. (2015) Intratropical migration of a Nearctic-Neotropical migratory songbird (Catharus fuscescens) in South America with implications for migration theory. *Journal of Tropical Ecology*, **31**, 285–289.

Hobson, K.A., Kardynal, K.J., Van Wilgenburg, S.L., Albrecht, G., Salvadori, A., Cadman, M.D., Liechti, F. & Fox, J.W. (2015) A continent-wide migratory divide in North American breeding barn swallows (Hirundo rustica). *PLoS ONE*, **10**, e0129340.

Jahn, A.E., Cueto, V.R., Fox, J.W., Husak, M.S., Kim, D.H., Landoll, D. V., Ledezma, J.P., LePage, H.K., Levey, D.J., Murphy, M.T. & Renfrew, R.B. (2013) Migration timing and wintering areas of three species of flycatchers (Tyrannus) breeding in the Great Plains of North America. *The Auk*, **130**, 247–257.

Kassara, C., Fric, J., Gschweng, M. & Sfenthourakis, S. (2012) Complementing the puzzle of Eleonora's Falcon (Falco eleonorae) migration: New evidence from an eastern colony in the Aegean Sea. *Journal of Ornithology*, **153**, 839–848.

Klaassen, R., Klaassen, H., Berghuis, M. & Schreven, K. (2014) Trekroutes en overwinteringsgebieden van Nederlandse Gierzwaluwen ontrafeld met geolocators. *Limosa*, **87**, 173–181.

Kristensen, M.W., Tøttrup, A.P. & Thorup, K. (2013) Migration of the common redstart (Phoenicurus phoenicurus): A Eurasian songbird wintering in highly seasonal conditions in the West African Sahel. *The Auk*, **130**, 258–264.

Lemke, H.W., Tarka, M., Klaassen, R.H.G., Åkesson, M., Bensch, S., Hasselquist, D. & Hansson, B. (2013) Annual Cycle and Migration Strategies of a Trans-Saharan Migratory Songbird: A Geolocator Study in the Great Reed Warbler. *PLoS One*, **8**, e79209.

Liechti, F., Scandolara, C., Rubolini, D., Ambrosini, R., Korner-nievergelt, F., Hahn, S., Lardelli, R., Romano, M., Caprioli, M., Romano, A., Sicurella, B. & Saino, N. (2014) Timing of migration and residence areas during the non-breeding period of barn swallows Hirundo rustica in relation to sex and population. *Journal of Avian Biology*, **46**, 254–265.

Limiñana, R., Romero, M., Mellone, U. & Urios, V. (2012) Mapping the migratory routes and wintering areas of Lesser Kestrels Falco naumanni: New insights from satellite telemetry. *Ibis*, **154**, 389–399.

Limiñana, R., Soutullo, A. & Urios, V. (2007) Autumn migration of Montagu's harriers Circus pygargus tracked by satellite telemetry. *Journal of Ornithology*, **148**, 517–523.

López-López, P., García-Ripollés, C. & Urios, V. (2014) Individual repeatability in timing and spatial flexibility of migration routes of trans-Saharan migratory raptors. *Current Zoology*, **60**, 642–652.

Martell, M.S., Henny, C.J., Nye, P.E. & Solensky, M.J. (2001) Fall Migration Routes, Timing, and Wintering Sites of North American Ospreys As Determined By Satellite Telemetry. *he Condor*, **103**, 715–724.

Martell, M.S., McMillian, M., Solensky, M. & Mealey, B. (2004) Partial migration and wintering use of Florida by Ospreys. *Journal of Raptor Research*, **38**, 55–61.

Mellone, U., Limiñana, R., Mallia, E. & Urios, V. (2011) Extremely detoured migration in an inexperienced bird: Interplay of transport costs and social interactions. *Journal of Avian Biology*, **42**, 468–472.

Mellone, U., López-López, P., Limiñana, R., Piasevoli, G. & Urios, V. (2013a) The trans-equatorial loop migration system of Eleonora's falcon: differences in migration patterns between age classes, regions and seasons. *Journal of Avian Biology*, **44**, 471–426.

Mellone, U., Puente, J.D. La, López-lópez, P., Limiñana, R., Bermejo, A. & Urios, V. (2013b) Migration routes and wintering areas of Booted Eagles Aquila pennata breeding in Spain. *Bird Study*, **60**, 409–413.

Meyburg, B.-U., Gallardo, M., Meyburg, C. & Dimitrova, E. (2004) Migrations and sojourn in Africa of Egyptian vultures (Neophron percnopterus) tracked by satellite. *Journal of Ornithology*, **145**, 273–280.

Meyburg, B.-U., Howey, P.W., Meyburg, C. & Fiuczynski, K.D. (2011) Two complete migration cycles of an adult Hobby tracked by satellite. *British Birds*, **104**, 2–15.

Meyburg, B.-U., Meyburg, C. & Barbraud, J.C. (1998) Migration strategies ofan adult short-toed eagle Circaetus gallicus tracked by satellite. *Alauda*, **66**, 39–48.

Meyburg, B.-U., Meyburg, C., Matthes, J., Matthes, H., Meyburg, C., Matthes, J. & Spring, H.M. (2007) Partnerwechsel und Bruterfolg beim Schreiadler Aquila pomarina. *Vogelwelt*, **128**, 21–31.

Meyburg, B.-U., Meyburg, C. & Pacteau, C. (1996) Migration automnale d'un circaète Jean-le-Blanc Circaetus gallicus suivi par satellite. *Alauda*, **64**, 339–344.

Meyburg, B.-U., Scheller, W. & Meyburg, C. (1995) Migration and wintering of the Lesser Spotted Eagle (Aquila pomarina): a study by means of satellite telemetry. *Journal of Ornithology*, **136**, 401–422.

van Oosten, H., Versluijs, R. & van Wijk, R. (2014) Twee Nederlandse Tapuiten in de Sahel: trekroutes en winterlocaties ontrafeld. *Limosa*, **87**, 168–172.

Ouwehand, J., Ahola, M.P., Ausems, A.N.M.A., Bridge, E.S., Burgess, M., Hahn, S., Hewson, C.M., Klaassen, R.H.G., Laaksonen, T., Lampe, H.M., Velmala, W. & Both, C. (2015) Light-level geolocators reveal migratory connectivity in European populations of pied flycatchers Ficedula hypoleuca. *Journal of Avian Biology*, **47**, 69–83.

Pavón, D., Limiñana, R., Urios, V., Izquierdo, A., Yáñez, B., Ferrer, M. & de la Vega, A. (2010) Autumn migration of juvenile Short-toed Eagles Circaetus gallicus from southeastern Spain. *Ardea*, **98**, 113–117.

Renfrew, R.B., Kim, D., Perlut, N., Smith, J., Fox, J.W. & Marra, P.P. (2013) Phenological matching across hemispheres in a long-distance migratory bird. *Diversty and Distributions*, **19**, 1008–1019.

Ryder, T.B., Fox, J.W. & Marra, P.P. (2011) Estimating migratory connectivity of gray catbirds (Dumetella carolinensis) using geolocator and mark-recapture data. *The Auk*, **128**, 448–453.

Salewski, V., Flade, M., Poluda, A., Kiljan, G., Liechti, F., Lisovski, S. & Hahn, S. (2012) An unknown migration route of the "globally threatened" Aquatic Warbler revealed by geolocators. *Journal of Ornithology*, **154**, 549–552.

Schmaljohann, H., Fox, J.W. & Bairlein, F. (2012) Phenotypic response to environmental cues, orientation and migration costs in songbirds flying halfway around the world. *Animal Behaviour*, **84**, 623–640.

Stach, R., Kullberg, C., Jakobsson, S. & Fransson, T. (2012) Geolocators reveal three consecutive wintering areas in the thrush nightingale. *Animal Migration*, **1**, 1–7.

Stanley, C.Q., McKinnon, E.A., Fraser, K.C., Macpherson, M.P., Casbourn, G., Friesen, L., Marra, P.P., Studds, C.E., Ryder, T.B., Diggs, N.E. & Stutchbury, B.J.M. (2014) Connectivity of wood thrush breeding, wintering, and migration sites based on range-wide tracking. *Conservation Biology*, **29**, 164–174.

Strandberg, R., Klaassen, R.H.G., Hake, M., Olofsson, P. & Alerstam, T. (2009) Converging migration routes of Eurasian hobbies Falco subbuteo crossing the African equatorial rain forest. *Proceedings of the Royal Society of London B: Biological Sciences*, **276**, 727–733.

Strandberg, R., Klaassen, R.H.G., Hake, M., Olofsson, P., Thorup, K. & Alerstam, T. (2008) Complex timing of Marsh Harrier Circus aeruginosus migration due to pre- and post-migratory movements. *Ardea*, **96**, 159–171.

Tanferna, A., López-Jiménez, L., Blas, J., Hiraldo, F. & Sergio, F. (2012) Different Location Sampling Frequencies by Satellite Tags Yield Different Estimates of Migration Performance: Pooling Data Requires a Common Protocol. *PLoS ONE*, **7**, e49659.

Terraube, J., Mougeot, F., Cornulier, T., Verma, A., Gavrilov, A. & Arroyo, B. (2012) Broad wintering range and intercontinental migratory divide within a core population of the near-threatened pallid harrier. *Diversity and Distributions*, **18**, 401–409.

Tøttrup, A.P., Klaassen, R.H.G., Strandberg, R., Thorup, K., Kristensen, M.W., Jørgensen, P.S., Fox, J.W., Afanasyev, V., Rahbek, C. & Alerstam, T. (2012) The annual cycle of a trans-equatorial Eurasian-African passerine migrant: different spatio-temporal strategies for autumn and spring migration. *Proceedings of the Royal Society of London B: Biological Sciences*, **279**, 1008–1016.

Trierweiler, C., Drent, R.H., Komdeur, J., Exo, K.M., Bairlein, F. & Koks, B.J. (2008) De jaarcyclus van de Grauwe Kiekendief: Een leven gedreven door woelnumuizen sprinkhanen. *Limosa*, **81**, 107–115.

Trierweiler, C., Klaassen, R.H.G., Drent, R.H., Exo, K., Komdeur, J., Bairlein, F. & Koks, B.J. (2014) Migratory connectivity and population-specific migration routes in a long-distance migratory bird. *Proceedings of the Royal Society of London B: Biological Sciences*, **281**, 20132897.

Trierweiler, C., Koks, B.J., Drent, R.H., Exo, K.M., Komdeur, J., Dijkstra, C. & Bairlein, F. (2007) Satellite tracking of two Montagu's Harriers (Circus pygargus): Dual pathways during autumn migration. *Journal of Ornithology*, **148**, 513–516.

Willemoes, M., Strandberg, R., Klaassen, R.H.G., Tøttrup, A.P., Vardanis, Y., Howey, P.W., Thorup, K., Wikelski, M. & Alerstam, T. (2014) Narrow-front loop migration in a population of the common cuckoo Cuculus canorus, as revealed by satellite telemetry. *PLoS One*, **9**, e83515.

Chapter 8: Towards an understanding of the Roller's decline

Throughout this thesis, my principal motivation has been to contribute to our understanding of Roller ecology, in order to work towards a better knowledge of their decline and devise conservation solutions. My general approach was a comparative one, and I attempted to avoid relying on data from a single locale. I explored intra-specific variation in the breeding ecology of Rollers in France (a stable / increasing population in the species' core Mediterranean range) and Latvia (one of the last remnants of the once widespread Baltic population), and my migration research integrated data from additional populations throughout Europe.

8.1 Understanding the Roller's decline

As described in **Chapter 2**, qualitative information on the Roller's decline is limited. The Roller is insufficiently common to feature in the Pan-European Common Bird Monitoring Scheme, which generates annual population indices at the national level. On the other hand, in most countries it is not rare enough to be the subject of targeted national monitoring. As such, only 10 out of 33 assessed European countries have 'good' information on current population size estimates, falling to just 8 and 4 countries for short- and long-term trends, respectively (**Fig. 8.1**).

The extent of the Roller's decline is thus uncertain. The clearest pattern is the loss of numbers in central and northern Europe, where several national extinctions have already occurred and several more are looming (Birdlife International 2015). Population trajectories in southern Europe are less clear – perhaps due to the larger populations here being harder to monitor – but on the whole numbers appear to be stable or increasing (Birdlife International 2015).

The Roller's current distribution is well predicted by bioclimatic variables and future climate change is expected to result in an expansion into north and west Europe by the end of the 21st century (Huntley *et al.* 2007). Furthermore, although agricultural intensification has occurred across the continent, it is less marked in the former Soviet states where, on average, farmland birds tend to be faring better (Donald *et al.* 2006). The decline of Rollers in northern Europe – where the climate is supposedly becoming more suitable and agriculture is generally less intense – is therefore, on face value, counterintuitive.

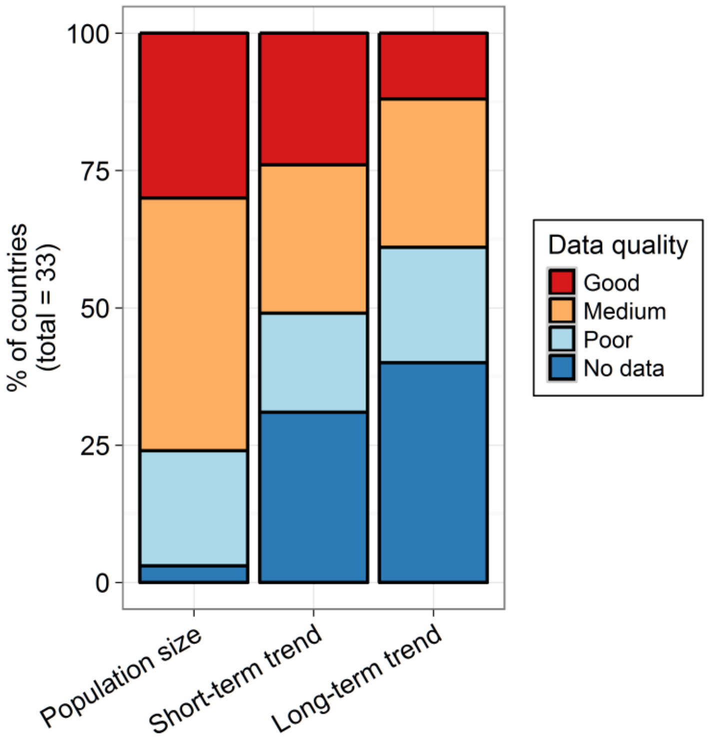


Figure 8.1 Percentage of 33 countries with good, medium, poor or no data on population size and trend at the time of the most recent assessment of the Roller's status in Europe (Birdlife International 2015).

Peripheral populations are often less abundant than those at the core of a species' range (Brown, Mehlman & Stevens 1995) and may have more variable population dynamics and higher extinction risk (Mehlman 1997; Doherty, Boulinier & Nichols 2003; Feldman *et al.* 2015). The properties of population limitation may also vary from core to edge; in the Wood Thrush *Hylocichla mustelina*, for example, core populations are regulated by density-dependent mechanisms such as habitat availability, whilst peripheral populations are influenced by density-independent mechanisms such as climate (Rushing *et al.* 2016). Thus, any population decline might be expected to hit peripheral populations hardest.

The European Roller is often thought of as a Mediterranean species (all other *Coracias* species are restricted to the tropics of Africa and Asia) and is arguably one of the more unexpected members of the Baltic avifauna. It therefore stands to reason that the northern edge populations are perhaps more ecologically marginal and thus demographically sensitive. My intra-specific comparisons highlight several key differences between the French and Latvian study populations, which I hope go some way towards explaining the increased vulnerability of northern populations (**Table 8.1**). In the following sections I summarise and synthesise these differences in the context of the Roller's decline, and provide recommendations for future research and conservation actions.

Table 8.1 Intra-specific comparison of **a** population status, **b** breeding ecology and **c** migration of Rollers in France and Latvia.

	Variable	France	Latvia	Units
a	*Population estimate**	800–1000	21	breeding pairs
	Population trend†	+30 to +70	–16 to –58	%
b	*Resource availability*	0.25	0.05	g per transect
	Breeding pair density	2.2	0.5	pairs per km^2
	Limiting factor	nest-site availability	food availability	/
	Productivity	2.6	1.8	fledglings per breeding attempt
c	*Migration route*	western Mediterranean	eastern Med. & Arabia	/
	Distance to wintering area	6450	8050	km
	Wintering area	southern Africa (west)	southern Africa (east)	/

* Population size estimate from 2015 European Red List of Birds (Birdlife International 2015) for 2006-2007 in France ('medium' quality) and 2012 in Latvia ('good' quality).

† Short term population trend estimate from 2015 European Red List of Birds (Birdlife International 2015) for 1998-2000 in France ('poor' quality) and 2001-2012 in Latvia ('good' quality).

8.2 Breeding ecology

My research in France and Latvia (**Chapter 3**) revealed striking differences in breeding density at the 1 km^2 scale. Breeding pair density was around 4 times higher in France than Latvia, despite a similar density of nest-boxes. In Latvia, Roller density bore no relationship to the number of nest-boxes per 1 km^2, but was positively correlated with estimated foraging resource availability. The reverse was true in France, where Roller density increased linearly with nest-box density but was unrelated to estimated foraging resource availability.

These differences are presumably driven by the lower resource availability in Latvia, which limits the carrying capacity of the habitat. I therefore suspect that in Latvia, where the availability of large insects is generally lower, any deterioration in foraging habitat quality – through agricultural intensification or land abandonment – will cause a reduction in Roller population size. A better handle on the foraging habitat requirements of Rollers in Latvia and other northern populations is crucial. In France, where even the most transformed habitats maintain a good supply of large insects and provide apparently sufficient foraging opportunities (**Chapter 4**), Rollers can breed successfully wherever suitable cavities exist. This is not to say that nest-site availability is trivial in Latvia, but I found no evidence that it currently limits breeding density.

Nest-boxes therefore provide a relatively straightforward conservation solution in southern Europe, provided that high quality foraging habitat is available. Indeed, many southern populations have expanded into suitable foraging habitat following the provisioning of nest-boxes over the last decade or two (Rodriguez, Avilés & Parejo 2011; Vaclav, Valera & Martinez 2011; Aleman & Laurens 2013). However, particularly in the northern part of the range, cavity provisioning may not, in isolation, be sufficient to promote recovery or prevent extinction. For example, the provisioning of nest-boxes had limited success in Poland (Sosnowski & Chmielewski 1996) and failed to prevent the extinction of Rollers in Estonia (Lüütsepp, Kalamees & Lüütsepp 2011). Instead, protection or restoration of suitable foraging habitat – open areas with an abundance of large insects – may be necessary.

Unfortunately, nest-boxes really represent a short term conservation solution; my work in France demonstrates that unmaintained nest-boxes are avoided by Rollers, such that efforts to recover populations could be wasted if funds to maintain nest-boxes cannot be guaranteed. In the medium term, mature trees must be protected, and in the long term the replanting of trees along field boundaries and water courses would be prudent. Where regionally appropriate, the preservation of abandoned agricultural buildings may also be important.

Breeding productivity was lower in Latvia, and a latitudinal decline in clutch size is consistent with previous reports from across the species' European range. Thus, in order to maintain the same population trajectory (all else being equal) northern populations must enjoy higher survival rates than southern ones. Adult survival represents a key knowledge gap for the Roller, but given the longer migration distance of Latvian Rollers (see below), I would be surprised if they were able to maintain higher non-breeding survival rates than in France (e.g. Lok, Overdijk & Piersma 2015). Breeding success also varied more from year-to-year in Latvia, such that the chances of a catastrophically bad breeding season are probably higher than in France. Given the small size of the Latvian population, we expect it to be extremely vulnerable to this kind of extrinsic stochasticity.

8.3 Migration

The narrative surrounding the Roller's decline has focused principally on processes – nest-site and foraging habitat limitation in particular – occurring during the breeding season. This is based on the assumption that reduced breeding productivity is driving the decline (Kovacs *et al.* 2008). However, as a single-brooded species with a relatively small clutch size and often not breeding until the second full year of life, Roller population growth might be expected to be quite sensitive to variations in adult survival (Wilson & Martin 2012). Thus, potential drivers of population decline away from the breeding ground – which may also act via delayed effects on breeding success (e.g. Rockwell, Bocetti & Marra 2012) – must not be ignored (Hostetler, Sillett & Marra 2015).

Whilst I fell short of addressing the influence of non-breeding season conditions on Roller demography or abundance – this would require a longer time series of data than was available to me – I have made a considerable step towards this important goal. By providing a fairly comprehensive description of the migratory movements of Rollers from across Europe, future research should focus on exploring whether / how conditions in these non-breeding areas affect population processes.

In **Chapter 5** I demonstrated that individuals from specific breeding populations spread out over a relatively large winter range, overlapping with distant breeding populations. This pattern – 'moderate migratory connectivity' or, if you prefer, 'absence of strong connectivity' – has important consequences for Roller population dynamics, because any driver of population decline acting during the non-breeding season will probably impact a large part of the European breeding population. Likewise, for a whole breeding population to be affected by problems (or solutions) in Africa, these changes need to act over large scales. More broadly, in **Chapter 7** I provide evidence that weak migratory connectivity is a general rule across a wide range of long-distance migrant land-birds. This is perhaps unsurprising given the relatively recent (post-glacial) evolution of these systems and the absence of flawlessly deterministic navigational controls in most first year migrants.

The fact that Roller population trends vary so markedly across Europe – despite Rollers from different breeding populations using broadly similar winter areas – suggests that problems in Africa are not to blame for their decline. However, this interpretation is over-simplistic. In reality, problems in Africa might interact with those in Europe such that different breeding populations exposed to the same conditions in Africa may respond differently depending on conditions experienced during the breeding season (Morrison *et al.* 2013).

I also demonstrated that Rollers from Latvia migrate substantially further than those from more southerly breeding populations. Among species, long migration distances have been associated with population declines (Jones & Cresswell 2009). The migration strategy of northern Rollers (which should be adaptive, at least in the past) may therefore present an additional cost, increasing their vulnerability to the deterioration of breeding ground conditions.

Finally, I highlighted a very tangible non-breeding season threat to Rollers from eastern breeding populations. All four tagged Latvia Rollers migrated north via the Arabian Peninsula, and ring recoveries (**Chapter 6**) show that individuals from Serbia and Hungary also use this route. Anecdotal evidence suggests that large numbers of Rollers are shot in this region during spring migration (del Hoyo, Elliott & Sargatal 2001), as were several of the ringed birds recovered here. Photos surfacing on the internet suggest that a single hunting party can easily harvest the equivalent of the entire Latvian population in a single day (**Fig 8.2**). Recent efforts to quantify hunting pressure in the Mediterranean (though not Arabia) have highlighted the Roller as being among the top 20 targeted (relative to population size) bird species of conservation concern (Brochet *et al.* 2016). The fact that hunting occurs in spring is extremely worrying, given that there is then basically no opportunity for density dependence to regulate population numbers before the start of the breeding season. However, we currently lack information on whether this pressure is contributing to the decline of eastern populations.

Figure 8.2 European Rollers (along with Golden Oriole *Oriolus oriolus* and Turtle Dove *Streptopelia turtur*) shot on spring migration through Arabia. From http://www.mekshat.com/

To conclude, my research suggests that northern Roller populations are likely to be limited by foraging habitat, meaning that, in isolation, nest-box provisioning is unlikely to lead to their recovery. A better understanding of Roller dispersal and connectivity between breeding populations is crucial for assessing the long-term viability of these isolated remnant populations. Overwinter survival represents another key knowledge gap, meaning that the demographic drivers of population declines are still basically unknown. Our understanding of the Roller's decline will improve as long-term monitoring projects mature, yielding data on Roller productivity and survival which can be linked to the conditions experienced by healthy and declining populations throughout their annual cycle.

8.4 References

Aleman, Y. & Laurens, J. (2013) Répartition et effectifs du Rollier d'Europe (Coracias garrulus) dans les Pyrénées-Orientales en 2011. *La Mélano*, **13**, 1–11.

Birdlife International. (2015) *European Red List of Birds*. Cambridge, UK.

Brochet, A.-L., Van Den Bossche, W., Jbour, S., Ndang'ang'a, P.K., Jones, V.R., Abdou, W.A.L.I., Al-Hmoud, A.R., Asswad, N.G., Atienza, J.C., Atrash, I., Barbara, N., Bensusan, K., Bino, T., Celada, C., Cherkaoui, S.I., Costa, J., Deceuninck, B., Etayeb, K.S., Feltrup-Azafzaf, C., Figelj, J., Gustin, M., Kmecl, P., Kocevski, V., Korbeti, M., Kotrošan, D., Mula Laguna, J., Lattuada, M., Leitão, D., Lopes, P., López-Jiménez, N., Lucić, V., Micol, T., Moali, A., Perlman, Y., Piludu, N., Portolou, D., Putilin, K., Quaintenne, G., Ramadan-Jaradi, G., Ružić, M., Sandor, A., Sarajli, N., Saveljić, D., Sheldon, R.D., Shialis, T., Tsiopelas, N., Vargas, F., Thompson, C., Brunner, A., Grimmett, R. & Butchart, S.H.M. (2016) Preliminary assessment of the scope and scale of illegal killing and taking of birds in the Mediterranean. *Bird Conservation International*, **26**, 1–28.

Brown, J., Mehlman, D. & Stevens, G. (1995) Spatial Variation in Abundance. *Ecology*, **76**, 2028–2043.

Doherty, P.F., Boulinier, T. & Nichols, J.D. (2003) Local extinction and turnover rates at the edge and interior of species' ranges. *Ann. Zool. Fennici*, **40**, 145–153.

Donald, P.F., Sanderson, F.J., Burfield, I.J. & van Bommel, F.P.J. (2006) Further evidence of continent-wide impacts of agricultural intensification on European farmland birds, 1990–2000. *Agriculture, Ecosystems & Environment*, **116**, 189–196.

Feldman, R.E., Anderson, M.G., Howerter, D.W. & Murray, D.L. (2015) Where does environmental stochasticity most influence population dynamics? An assessment along a regional core-periphery gradient for prairie breeding ducks. *Global Ecology and Biogeography*, 896–904.

Hostetler, J.A., Sillett, T.S. & Marra, P.P. (2015) Full-annual-cycle population models for migratory birds. *The Auk*, **132**, 433–449.

del Hoyo, J., Elliott, A. & Sargatal, J. (2001) *Handbook of the Birds of the World Volume VI Mousebirds to Hornbills*. Lynx Edicions, Barcelona, Spain.

Huntley, B., Green, R.E., Collingham, Y.C. & Willis, S.G. (2007) *A Climatic Atlas of European Breeding Birds*. Lynx Edicions.

Jones, T. & Cresswell, W. (2009) The phenology mismatch hypothesis: are declines of migrant birds linked to uneven global climate change? *Journal of Animal Ecology*, **79**, 98–108.

Kovacs, A., Barov, B., Orhun, C. & Gallo-Orsi, U. (2008) *International Species Action Plan for the European Roller Coracius Garrulus Garrulus*. Besenyőtelek, Hungary.

Lok, T., Overdijk, O. & Piersma, T. (2015) The cost of migration: spoonbills suffer higher mortality during trans-Saharan spring migrations only. *Biology Letters*, **11**, 20140944.

Lüütsepp, G., Kalamees, A. & Lüütsepp, O. (2011) European Roller Coracias garrulus in Estonia 2000-2011. *Hirundo*, **24**, 61–72.

Mehlman, D.W. (1997) Change in avian abundance across the geographic range in response to environmental change. *Ecological Applications*, **7**, 614–624.

Morrison, C.A., Robinson, R.A., Clark, J.A., Risely, K. & Gill, J.A. (2013) Recent population declines in Afro-Palaearctic migratory birds: the influence of breeding and non-breeding seasons. *Diversity and Distributions*, **19**, 1051–1058.

Rockwell, S.M., Bocetti, C.I. & Marra, P.P. (2012) Carry-over effects of winter climate on spring arrival date and reproductive success in an endangered migratory bird, Kirtland's Warbler (Setophaga kirtlandii). *The Auk*, **129**, 744–752.

Rodriguez, J., Avilés, J.M. & Parejo, D. (2011) The value of nestboxes in the conservation of Eurasian Rollers Coracias garrulus in southern Spain. *Ibis*, **153**, 735–745.

Rushing, C.S., Ryder, T.B., Marra, P.P. & Rushing, C.S. (2016) Quantifying drivers of population dynamics for a migratory bird throughout the annual cycle. *Proceedings of the Royal Society of London B: Biological Sciences*, **283**, 20152846.

Sosnowski, J. & Chmielewski, S. (1996) Breeding biology of the Roller Coracias garrulus in Puszcza Pilicka Forest (Central Poland). *Acta Ornithologica* , **31**, 119–131.

Vaclav, R., Valera, F. & Martinez, T. (2011) Social information in nest colonisation and occupancy in a long-lived, solitary breeding bird. *Oecologia*, **165**, 617–627.

Wilson, S. & Martin, K. (2012) Influence of life history strategies on sensitivity, population growth and response to climate for sympatric alpine birds. *BMC Ecology*, **12**, 9.