Universidade de Aveiro Departamento de Biologia
2020

JOANA SOFIA DOS SANTOS COSTA

ECOLOGIA REPRODUTORA E PADRÕES MIGRATÓRIOS DE UMA AVE MIGRADORA AFRO-PALEÁRTICA INSETÍVORA, O ABELHARUCO (*MEROPS APIASTER*)

BREEDING ECOLOGY AND MIGRATION PATTERNS OF AN AFRO-PALEARCTIC MIGRATORY INSECTIVOROUS BIRD, THE BEE-EATER (*MEROPS APIASTER*)

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Tese apresentada à Universidade de Aveiro para cumprimento dos requisitos necessários à obtenção do grau de Doutor em Biologia, realizada sob a orientação científica do Doutor José Augusto Belchior Alves, Investigador Auxiliar e Professor Auxiliar Convidado do Departamento de Biologia da Universidade de Aveiro, e co-orientação do Doutor Steffen Hahn, Senior Researcher do Swiss Ornithological Institute

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agradecimentos

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palavras-chave

função discriminante, guia fotográfico, ecologia trófica, *timing* de migração, *carry-over*, produtividade, performance reprodutora, fidelidade do casal

resumo

Os habitats essenciais para a reprodução e sobrevivência animal têm vindo a ser transformados a um ritmo crescente e ao mesmo tempo, as alterações climáticas têm vindo a alterar espacialmente e temporalmente os padrões ecológicos. Muitas espécies migradoras estão, actualmente, em declínio severo devido ao facto de ocuparem áreas conectadas entre si que muitas vezes são alteradas a diferentes velocidades. Assim, para compreender os factores que influenciam a dinâmica populacional das espécies migradoras é necessário, não só, aprofundar o conhecimento sobre a sua ecologia reprodutora e os factores que determinam o sucesso reprodutor, mas também perceber de que modo os eventos que ocorrem durante um determinado período do ciclo anual se traduzem em *carry-over effects* e influenciam os eventos nas épocas subsequentes.

O principal objectivo desta tese foi aumentar o conhecimento sobre a ecologia reprodutora e padrões migratórios do Abelharuco (Merops apiaster), um migrador Afro-paleártico de longa distância. Mais concretamente, esta tese focou-se em aprofundar o conhecimento sobre a ecologia trófica, assim como investigar pela primeira vez os padrões migratórios do Abelharuco, a nível populacional e individual. Este trabalho também investigou pela primeira vez a relação entre a performance migratória e a produtividade de uma população desta espécie que nidifica na Península Ibéria. Finalmente investigou-se se a produtividade é influenciada pela idade e fidelidade do casal.

Os primeiros dois manuscritos foram desenvolvidos devido à necessidade de aplicar esses métodos nos capítulos seguintes. Primeiro, desenvolvi funções discriminantes para determinar o sexo de Abelharucos adultos. Este trabalho foi o primeiro que utilizou biometrias de Abelharucos, nos quais o sexo foi identificado molecularmente, para produzir funções discriminantes aplicáveis ao nível da população mas também para a espécie em geral. Desenvolvi também um guia de fotografias para determinar a idade das crias de Abelharuco e apresento um protocolo que propõe visitar os ninhos em intervalos de 12 dias de modo a atingir a precisão máxima na determinação da idade das crias, minimizando a perturbação e o investimento logístico.

Esta tese mostrou que a dieta do Abelharuco durante a época reprodutora varia entre colónias localizadas em habitats distintos, entre épocas e entre o que é consumido pelos adultos e fornecido às crias. Os resultados revelaram distintos padrões migratórios do Abelharuco entre três populações reprodutoras (Ibéria, Alemanha e Bulgária), indicando que os indivíduos da Bulgária migram através de uma rota este para o sul de África, enquanto as outras duas populações migram por uma rota oeste. Também demonstrou que as três populações exibem diferentes *timings* de migração.

resumo (cont.)

Ao nível individual, a partida da área de invernada e a duração da migração parecem ser os principais factores que influenciam a data de chegada à área de reprodução na Ibéria. Neste estudo, foi estabelecida uma relação positiva entre a chegada à área de reprodução e as datas de postura. Adicionalmente, a relação encontrada entre a data de postura e a produtividade variou entre anos: em 2017, o número de crias voadoras diminuiu ao longo da época reprodutora; mas tal não aconteceu em 2016, quando as datas de postura ocorreram mais cedo e a produtividade permaneceu constante ao longo da época. Finalmente, os resultados mostraram que fêmeas mais velhas (mas não machos) colocam os ovos mais cedo e têm maior produtividade do que as fêmeas que se reproduzem pela primeira vez. Adicionalmente, os casais mais velhos parecem ter a mesma probabilidade de se manter juntos durante duas épocas reprodutoras consecutivas comparado com os casais que se reproduzem pela primeira vez. A produtividade não parece ser influenciada pela manutenção do parceiro.

A variação inter-anual na produtividade pode afectar as populações a longo termo através da indução de flutuações nas taxas demográficas, se a frequência de más (ou boas) condições ambientais aumentar. Deste modo, este estudo apela à monitorização a longo prazo das populações de Abelharucos, e outros migradores afro-paleárcticos, de forma a prever as respostas das populações às alterações ambientais e optimizar medidas de conservação.

keywords

discriminant function, photographic guide, trophic ecology, migration timing, carry-over, productivity, breeding performance, pair-fidelity

abstract

Important habitats crucial to animal reproduction and survival are being transformed at an increasing rate and at the same time, climate change is altering ecological patterns in both time and space. Migratory species are currently experiencing severe declines as they move within a network of interconnected areas that are often undergoing different rates of change. Understanding the factors that influence population dynamics in migratory species therefore requires not only knowledge on breeding ecology and drivers of breeding success, but also on how events during one period of the annual cycle carry over to influence events in subsequent seasons.

The overall objective of this thesis was to increase the knowledge about the breeding ecology and migratory patterns of the European bee-eater (*Merops apiaster*), an Afro-Palearctic long-distance migrant. More specifically, this thesis focused on increasing the knowledge on trophic ecology as well as providing a first insight of bee-eater's migratory patterns, at population and individual levels. This work also explored, for the first time, the link between migratory performance and productivity in an Iberian population of this species. Finally, it was investigated if productivity is influenced by age and pair-fidelity.

The first two chapters were developed based on the need of the application of the described methods in the subsequent chapters. First, I developed discriminant functions to sex adult bee-eaters. This work was the first using biometrics of molecularly sexed birds to generate population specific, as well as, general discriminant functions for sexing adult European bee-eaters. Then, I also developed a photographic guide to estimate the age of nestling bee-eaters and presented a protocol that proposes visiting nests at 12 day intervals, while achieving the highest accuracy in nestling aging with the smallest disturbance and logistic investment.

This thesis showed that the diet of bee-eaters during the breeding season varies across colonies in distinct habitats and seasons, and between what is consumed by adults and provided to nestlings. The results revealed distinct migration patterns of European Bee-eaters from three breeding populations (Iberia, Germany and Bulgaria) showing that individuals from Bulgaria migrate on an eastern route to southern Africa while the other two populations take a western route. It also provided evidence for different timings of migration between the three populations.

abstract (cont.)

At individual level, departure from the wintering area and travel duration seemed to be the most apparent factors influencing arrival to the breeding areas in Iberia. In this study, it was reported a positive relationship between arrival and laying dates. Additionally, the relationship between laying date and productivity was year specific: in 2017, the number of fledglings decreased throughout the season, contrary to 2016, when laying was earlier in the year and productivity remained constant. Finally, the results showed that older females (but not males) lay eggs earlier and have higher productivity than first breeding females. Moreover, older couples seemed equally likely to maintain their pair bond during two consecutive seasons than first breeding pairs and productivity does not seem to be influenced by mate retention.

Inter-annual variation in productivity may affect populations in the long term if the frequency of poor (or good) environmental conditions increases, as these induce fluctuations in demographic rates. Therefore, this study urges for long-term monitoring of bee-eater populations, and other Afro-Palearctic migrants, to predict their population level responses to environmental change and optimize conservation strategies accordingly.

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Chapter 1

General introduction

General introduction

Migratory birds and global environmental changes

The world is constantly changing, but in recent decades changes have gained an impressively faster pace than before (Lindström et al. 2014). Natural habitats crucial to animal reproduction and survival are being lost at an alarming rates (Cushman 2006; Flockhart et al. 2015; Reif et al. 2010) and at the same time, climate change is altering ecological patterns in both time and space (Bartomeus et al. 2011; McDermott and DeGroote 2016; Walther et al. 2002). Migratory animals are at the forefront of impacts from environmental changes due to their characteristic use of vast distribution areas and tight links with seasonal changes in environmental conditions (Wilcove and Wikelski 2008). For example, land use changes restricting migration routes of several mammal species are leading to a decline in ungulate populations (Bolger et al. 2008), while migratory amphibians have altered the timing of their journeys due to temperature changes (Chadwick et al. 2006). For migratory avian species this is even more challenging, as the areas they occupy seasonally are often undergoing different rates of change (Wilcove and Wikelski 2008). Waders species that breed in the arctic, where warming temperatures are increasing at a higher pace than elsewhere in the globe, may have their breeding areas possibly compressed towards the northern pole (Lindström and Jep Agrell 1999; Rehfisch and Crick 2003). At the same time, the coastal wetlands they use during the non-breeding season are impacted by sea level rise or coastal developments (e.g. land claim) at varying rates (Austin and Rehfisch 2003; Yang et al. 2011). Additionally, many migratory passerines are experiencing phenological mismatches (Møller et al. 2008), and whilst some are able to advance laying at their European breeding areas in response to increasing spring temperatures earlier in the year (Bauer et al. 2010; Halupka et al. 2008), others have been unable to do so (Sanz et al. 2003; Visser et al. 1998).

Globally, since the year 1500, over 161 bird species have been lost (Birdlife International 2018). Migrant birds have suffered more severe and continued declines than non-migrants or short-term migrants (Sanderson et al. 2006; Vickery et al. 2014), with migratory population declines being reported all across the world (e.g. Baker et al. 2004; Gregory et al. 2005; Kirby et al. 2008). Unlike residents, migratory species move along a network of interconnected sites and, as a result, face spatially and temporally dynamic threats. Because of that, ascertaining the causes of population's decline of migrants is difficult (Lindström et al. 2014). For example, Afro-Palearctic migrants currently face rapid, ongoing habitat changes at their wintering and staging areas (Brink and Eva 2009; Vickery et al. 2014), while land-use and climate changes in Europe also exposes several of these species to the loss of breeding habitat (e.g. Brambilla et al. 2010) and to phenological mismatches (Both et al. 2009). In order to pinpoint where and when these populations are more vulnerable, an integrated approach must be undertaken.

Land-use changes at breeding and non-breeding areas

The degradation of breeding habitats is the factor affecting the demography of the largest number of species, particularly within agricultural systems, woodland and forests (Vickery et al. 2014). For migrants that rely on agricultural areas, the main drivers of decline are the intensification of agricultural practices, homogenization of agricultural landscapes and the loss of marginal, natural or semi-natural habitats (e.g. Benton et al. 2003; Donald et al. 2001). These factors are known to negatively impact several migrants that rely on these areas for foraging and/or nesting, like the Red-backed shrike *Lanius collurio* (Brambilla et al. 2007), European roller *Coracias garrulus* (Avilés et al. 2000) and Eurasian wryneck *Jynx torquilla* (Weisshaupt et al. 2011). Furthermore, associated with such land-use changes is the decline in insect abundance, not only due to the direct effect of habitat loss (Fox et al. 2014; Grixti et al. 2009; Hallmann et al. 2017), but also to the increased use of pesticides and climate change (Sánchez-Bayo and Wyckhuys 2019). Indeed, declines of insects are reported throughout Europe (e.g. Fox et al. 2014; Hallmann et al. 2017; Thomas et al. 2004), as well as, in other parts of the world (Grixti et al. 2009; Lister and Garcia 2018) and such declines are known to affect many bird species that depend on insects as main food source (Newton 2004; Stanton et al. 2018).

In the non-breeding areas, anthropogenic habitat degradation appears to be one of the most important factors driving declines on migratory birds (Vickery et al. 2014). For example, human-induced changes as exploitation of irrigated crops and deforestation of Sahelian wooded savannah (Gaiser et al. 2011; Walther 2016) are possibly having a significant negative impact on populations of Afro-Palearctic migrants dependent on these habitats for both wintering and staging (e.g. Atkinson et al. 2014; Wilson and Cresswell 2010). Furthermore, the quality of the habitat at the non-breeding areas is known to potentially influence migratory timings (López-Calderón et al. 2017; Marra et al. 1998) and breeding performance (Norris et al. 2004). For example, Black-tailed godwits *Limosa limosa islandica* experiencing more favorable winter conditions have higher survival rates and arrive on the breeding grounds earlier (Alves et al. 2013), while in American redstarts *Setophaga ruticilla,* winter habitat quality can influence arrival date on the breeding grounds, which in turn affect key variables associated with reproduction, including the number of young fledged (Norris et al. 2004). Such processes, termed carry-over effects, postulate that conditions experienced in one season can affect individual performance in a subsequent stage of the annual cycle (Harrison et al. 2011). Nevertheless, adverse conditions at breeding sites may counteract the potentially positive carry-over effects from the wintering and migration periods (e.g. Harrison et al. 2013). For example, for many migrant passerines breeding in the UK, breeding temperatures seem to have a stronger effect on reproductive performance than carry-over effects from wintering areas (Ockendon et al 2013).

Climate change and phenological mismatches in migratory birds

Climate change has a number of well-documented ecological effects on birds (Pearce-Higgins and Green 2014). It has led to range shifts in both breeding (Thomas and Lennon 1999) and wintering areas (Sorte and Thompson III 2007), as well as changes in population size (Both et al. 2006; Saether et al. 2000), therefore affecting distribution and demography of migratory species. In Europe, for example, climate change models predict that the potential future breeding ranges of migrants might be on average only 89% of their present range, and potential future and present distributions might only overlap by 42% (Huntley et al. 2008). In West Africa, severe drought mediated by reduced rainfall during the last decades (Nicholson 2000), potentially led to a decrease in habitat availability and a depletion of food for species wintering in this area, affecting survival and population abundance of several migrants (Peach et al. 1991; Szép 1995).

The most reported effect of climate change is, however, on phenology. Migratory movements are timed to coincide with the availability of resources (Newton 2008) at all stages of the annual cycle, but particularly at the breeding season, allowing individuals to maximize fitness (Lemke et al. 2013; Tomotani et al. 2018). But if phenology of avian species shifts at different rates from that of its main food sources, it may lead to mistiming of species seasonal activities (Visser et al. 2004), also known as “phenological mismatch”. This can occur when arrival dates at breeding locations are constrained by conditions in the wintering areas (Saino et al. 2004b) or during migration (Briedis et al. 2017; Drake et al. 2014), decoupling advancing phenology of local prey with that of migrants, potentially leading to fitness consequences of arriving and breeding too late (e.g. Bejarano and Jahn

2018). The impacts of these processes on migrant populations are difficult to predict and are likely to vary widely between regions and species (Bairlein and Hüppop 2004). In Barn swallows *Hirundo rustica*, inter-annual variation in population-level mean seasonal reproductive success is predicted by ecological conditions during winter in the sub-Saharan region, with breeding dates of the same individuals advancing (and clutch sizes being larger) following winters with high NDVI in the winter quarters (Saino et al. 2004a). However, Dutch populations of Pied flycatchers *Ficedula hypoleuca* have severely declined in areas where food for provisioning of nestlings peaked early in the season, resulting in a mismatch between resource availability and resource demand, leading to low productivity (Both et al. 2006).

The importance of ecological and tracking studies

Birds provide important ecosystem services (Sekercioglu 2011; Sekercioglu et al. 2004) and are useful indicators of ecosystem health (Gregory et al. 2005). Additionally, they are good case studies for understanding ecological patterns and processes (Sullivan et al. 2015). Although birds are probably the best studied animal group in the world (Baillie et al. 2004; Scheffers et al. 2012), bird ecology is strongly expanding and we are only now starting to reach an good understanding of the links between environment, animal behaviour, trophic ecology and demography. Ecological studies are of great importance to increase the knowledge about species interactions and the processes underlying population dynamics (Courchamp et al. 2015). For example, assessing diet composition and food availability can help to unravel potential factors influencing reproductive success (Arroyo and Garcia 2006) and predict drivers of populations decline (Margalida et al. 2012). The description of the diet composition of the Roller provided the basic information for more recent studies to suggest that traditional extensive practices of cereal cultivation, with large areas of low-intensity grazed fallows, represent a high-quality foraging habitat for this species due to higher abundance of its preferred prey (Catry et al. 2017). In addition, homogenisation and intensification of the European farmed landscape (Benton et al. 2003) could have reduced the quality of foraging habitat and contributed to the species' decline (Finch 2016).

Ecological studies often rely on widely used field techniques, but some may be difficult to apply to a particular species or group. Furthermore, some methods may provide inaccurate results due to limitations imposed by species' biology. For example, determining age of nestlings based on growth curves requires handling the birds, which may be hard to accomplish if the nests are inaccessible, if located in cliffs or trees (Fry 1984; Moritsch 1983). Or the use of morphological characters to determine the sex of individuals, which may be inaccurate for species that exhibit high overlap in biometrics or plumage coloration between sexes (Eaton 2005; Gunnarsson et al. 2006). Nevertheless, knowledge gaps in bird ecology are being progressively reduced with the continuous development and application of new techniques and development of new studies. The development of species-specific linear discriminant functions can overcome the problem of overlap in biometrics for sex differentiation (e.g. Dechaume-Moncharmont et al. 2011), while stable isotope analysis are now widely used to study trophic ecology (Catry et al. 2019) or to reveal wintering origins of migratory species (López-Calderón et al. 2017). Nevertheless, and by far, the most revolutionary advance in bird migration ecology in recent years has been the capacity to attain individual tracking data.

Until recently, knowledge of spatio-temporal distribution of individuals was limited to ring recoveries (e.g. Clark et al. 2009; Reichlin et al. 2009), which provide useful, but often imprecise, geographical and only rough temporal information. Over the last decades developments of tracking devices, for example satellite telemetry or GPS, has led to a substantial increase in the knowledge of spatio-temporal distribution of migratory birds (Berthold et al. 2004; Freeman et al. 2010; García-Ripollés et al. 2010) throughout the annual-cycle. However, the tracking of small avian migrants has only very recently become possible by the use of retrievable geolocators, which record time and light-level data allowing for the reconstruction of time-stamped latitudes and longitudes (Lemke et al. 2013; Lislevand et al. 2015). It is now possible to identify key wintering and stopover areas for many small migratory species (e.g. Common swift, Åkesson et al. 2012; Hoppoe, Bächler et al. 2010; Northern wheatear, Bairlein et al. 2012; Common redstart, Kristensen et al. 2013), assess migration phenology (e.g. Tøttrup et al. 2012) and establish levels of migratory connectivity (Cormier et al. 2013). However, studies linking migratory performance (e.g. migration timings, winter location) with breeding phenology and/or success (e.g. Drake et al. 2014; Finch et al. 2014; Norris et al. 2004; Saino et al. 2004b; Woodworth et al. 2016) remain scarce, particularly those using individual tracking (winter location, migration performance) and productivity data (e.g. Norris et al. 2004; Saino et al. 2017; Souchay et al. 2018; van Wijk et al. 2017). Indeed, estimations of productivity and survival are essential to assess population dynamic (Morrison et al. 2016), and predict the response of demographic rates to environmental change. But this data is hard to obtain, as survival rates can only be assessed through long-term monitoring of populations, while productivity estimates require a high sampling effort. This information is still currently lacking for many species, despite being crucial to predict the responses of migratory populations to environmental change and optimize conservation strategies accordingly (e.g. Green 1999; Martin et al. 2007).

The European bee-eater

Distribution and status

The European bee-eater (*Merops apiaster*) is a near-passserine migratory bird belonging to order Coraciiformes, and it is the only species of family Meropidae that naturally occurs in Europe (Fry 1984). It is a long-distance migrant that breeds from Western Europe and North Africa to western Asia, and winters in from Western Africa to southern Africa (Fry 1984). During the last decades, it has expanded its breeding range northwards into Central Europe (Fiedler 2003; Reif et al. 2010). Its population trend appears to be stable and is classified as least concern (BirdLife International 2016). Ringing recoveries of bee-eater are not common, and long-distance recaptures are extremely rare (Ramos et al. 2016), which has limited our knowledge about its spatio-temporal distribution.

In its Palearctic breeding grounds, bee-eaters occupy any type of open area, like pasture and cultivated land, but also river banks, cork-oak woods, olive-groves, scrublands and rice or cereal fields to form colonies. In its African non-breeding grounds, bee-eaters avoid the dense evergreen forests and deserts, being commonly found on savannas, steppe, lakeshores and cultivation fields (Fry 1984).

Diet and foraging ecology

The European bee-eater is an insectivore feeding mainly on medium to large-sized flying insects, with a marked preference for bees (Hymenoptera). Nevertheless, bee-eater’s diet is quite broad and it is known to consume prey according to its local availability (Fry 1984). Odonata and Coleoptera are usually well represented in bee-eaters’ diet, while insects from other orders (e.g. Hemiptera, Diptera and Orthoptera) typically represent less than 10% of the diet (Arbeiter et al. 2014; Costa 1991; Farinós-Celdrán et al. 2016; Fuisz et al. 2013; Inglisa et al. 1993; Kossenko and Fry 1998; Lourenço 2018).

Bee-eaters are single prey loaders and often seen standing on an exposed perch before flying down to take prey in mid-air. Each item is carried back to the perch for treatment (immobilization and venom removal) when needed, before being consumed. Bee-eaters also hunt on the wing, possibly consuming the prey in flight (Fry 1984).

Breeding biology

Bee-eaters are gregarious throughout the year, breeding in colonies varying between less than ten pars to several hundreds of individuals. Bee-eaters are known to be monogamous and individuals can breed on its second calendar year. Both sexes actively contribute to nest construction, digging nest holes in sloping hillsides or flat ground. Nests chambers are usually difficult to access, with burrows either straight or curving to one side, and extending for 0.7-2 m (Fry 1984). Females typically lay 4-10 eggs with a laying interval of one or two days. Although they are single-brooded, failed clutches can be replaced (Fry 1984). Incubation begins after the first egg is layed resulting in hatching asynchrony (Lessells and Avery 1989). Thus, nestling growth is asymmetric between the brood, with the first-hatched nestling often being the largest and maintaining its position in the hierarchy throughout growth (Bryant and Tatner 1990). Nestlings hatch after ca. 20 days and both parents feed the nestlings until fledging, ca. 30 days (Fry 1984).

Thesis outline

Despite the recent expansion of studies on migration patterns of Afro-Palearctic migrants, the processes driving migratory population’s demography remain poorly studied. The overall objective of this work is to increase the knowledge about the breeding ecology of the European bee-eater, as well as to provide the first insight of its migratory patterns, at population and individual level. Additionally, this work explores the links between migratory performance and productivity, using bee-eaters as study models. To achieve the overall objective, I sampled a breeding population in Portugal and obtained data of two other bee-eater populations (eastern Germany and Bulgaria). I used a combination of approaches, including linear discriminant functions, ring recoveries, light level geolocation and pellet analysis. This thesis brings together a series of six manuscripts (Chapters 2-7), including one published, one currently submitted and one accepted. These chapters are preceded by a general introduction (Chapter 1) and the thesis ends with a general discussion (Chapter 8).

Chapter 2

Joana S. Costa, Steffen Hahn, Afonso D. Rocha, Pedro M. Araújo, Juanita Olano-Marín, Tamara Emmenegger, José A. Alves (*in press*). **The discriminant power of biometrics for sex determination in European bee-eaters, *Merops apiaster*.**

In Chapter 2, I explored variation in biometrics and their suitability to discriminate sex in adult European bee-eater. Although the sex of most bee-eaters can be assigned based on sex-specific breeding plumage during the breeding season, some individuals do not display the typical sex specific colours, making this method often unreliable. A comparative study of biometrics of unambiguously sexed bee-eaters was not available and it was unknown how well combinations of biometrics could be used to discriminate sex, in fully grown individuals of this species. In order to do this, I used biometric data sampled in western Iberia (Portugal) and Central Europe (Germany), to investigate body size variation and derive population-specific and species level sex discriminant functions.

Chapter 3

Joana S. Costa, Afonso D. Rocha, Ricardo A. Correia, José A. Alves (submitted). **Developing and validating a nestling photographic aging guide for cavity-nesting birds: an example with the European Bee-eater (*Merops apiaster*)**.

In chapter 3 I constructed a photographic guide for aging European bee-eaters nestlings. Determining nestling age often requires handling the birds, and in some species nests are difficult or impossible to access, while frequent nest visits may affect nesting success. That is why reducing the frequency and length of nest visits is desirable making alternative indirect methods for estimating nestling age advantageous. Therefore, I constructed a photographic guide to determine nestling age in European bee-eaters and tested its accuracy. I also established a visiting protocol at 12 day intervals, to achieve the highest accuracy in age estimation with the smallest disturbance and logistic investment.

Chapter 4

Joana S. Costa, José A. Alves. **Variation of parental and nestling diet in an opportunistic widespread avian insectivore**

In chapter 4, I explore the variation in parental diet and provision of nestlings. Land-use changes and agriculture intensification are leading to declines in insect abundance across the globe which can be critical for bird species that depend on invertebrate prey as their main food source, as is the case of bee-eater. Although diet composition of bee-eaters is well studied in several parts of its range, diet studies are still scarce in Iberian Peninsula. I sampled pellets and assessed prey availability of bee-eaters in five colonies located in Portugal and assessed the temporal variation in diet of adult bee-eaters across the breeding season and between colonies located indistinct habitats. I also explored differences in the diet composition of nestlings and adults, during nestling rearing stage and investigated seasonal selectivity of adults across the breeding season and how selective are adults when providing their progeny. Finally, I explored the variability in the size of prey provided to nestlings thought their growth period.

Chapter 5

Steffen Hahn, José A. Alves, Kiril Bedev, Joana S. Costa, Tamara Emmenegger, Martin Schulze, Peter Tam, Pavel Zehtindjiev, Kiran L. Dhanjal-Adams (2019) **Range wide migration corridors and non-breeding areas of a northward expanding Afro-Palaearctic migrant, the European Bee-eater *Merops apiaster*.** Ibis, doi:10.1111/ibi.12752

Chapter 5 explores migration patterns of three European bee-eater populations. Different populations often use separate routes to migrate between breeding and non-breeding grounds. However it is unclear whether new populations also establish new migratory routes, non-breeding sites and migration phenology. The European bee-eater has expanded its breeding range northwards and successfully (re)colonized regions north of 47°N in central Europe, presumably benefiting from recent climatic niche expansions and land use changes. This study uses geolocators to unravel the migration corridors and non-breeding ranges of two long-established bee-eater populations (from Iberia and Bulgaria) and a recently founded population (in Germany). Moreover, it compares migration patterns of the long-established populations with the migration corridors and non-breeding range of the recently founded population.

Chapter 6

Joana S. Costa, Steffen Hahn, Miguel Araújo, Kiran L. Dhanjal-Adams, Afonso Rocha, José A. Alves. **Linking migration performance with productivity: unravelling the migration of European Bee-eaters (*Merops apiaster*) breeding in southwest Iberia.**

In Chapter 6 I use geolocators to explore migration performance and its association with productivity in European bee-eaters. As many migratory species are declining determining the spatio-temporal distribution of individuals throughout the annual cycle has become crucial to predict when and where migratory species may be most constrained. I used use a larger dataset of tracked bee-eaters to assess migratory performance and non-breeding distribution of individuals breeding in Iberia (already described in Chapter 5 for a sample of five individuals only). Additionally, I investigated timing, travel duration and travel speed between seasons and sexes and explored if non-breeding latitude, non-breeding departure date, travel duration and travel speed determine arrival date to the breeding areas. Finally, I test if timing of arrival to the breeding areas influences laying dates and productivity at the individual level.

Chapter 7

Joana S. Costa, Afonso D. Rocha, Pedro M. Araújo, José A. Alves. **The influence of pair-fidelity and age on the breeding performance of a colonial migratory near-passerine.**

In Chapter 7, I explored the influence of pair fidelity and age on breeding performance of European bee-eaters. Maintenance of pair-bonds and increased experience with age are associated with productivity in many avian species. For bee-eater, very limited information on potential effects of age on breeding parameters is published (Lessells and Krebs, 1989) and no study has ever explored the relationship between pair fidelity and productivity. Therefore, I investigate if the age of both members of the breeding pair influences laying dates and productivity and if older couples are more likely to maintain their partner than younger couples (second calendar year vs older than second calendar year). Finally, I explore if productivity is higher when pair-bond is maintained between two consecutive years.

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Chapter 2

The discriminant power of biometrics for sex determination in European bee-eaters *Merops apiaster*

Joana S. Costa, Steffen Hahn, Afonso D. Rocha, Pedro M. Araújo, Juanita Olano-Marín, Tamara Emmenegger, José A. Alves

Abstract

The degree of sexual dimorphism is highly variable among birds and many sexually dimorphic species show considerable overlap in morphological traits (e.g. plumage colours or size) of females and males. Although it is the most accurate technique for sex discrimination in monomorphic species nowadays, molecular sexing is impractical to assign sex in the field, as it requires laboratory procedures. We sampled populations of a long-distance migratory species with low sexual size dimorphism, the European bee-eater *Merops apiaster*, from colonies in western Iberia (Portugal) and Central Europe (Germany) to investigate body size variation and derive population-specific and general sex discriminant functions. Overall, male bee-eaters were larger than females while bee-eaters from Germany and Portugal did not differ in size, except for primary length and tail length. The best single measurement to discriminate sex was wing length for Portuguese and tail tip length for German birds, as in the combined dataset. Multivariate discriminant functions of head-bill, wing and tail tip lengths provided the highest discriminant accuracy, discriminating 91% of the birds from Portugal, 96% from Germany and 93% when using the combined dataset. Nonetheless, the discriminant accuracy remained high in the functions using only two variables for Portugal (head-bill and tail tip 91%, head-bill and wing 88%, wing and tail tip 88%), Germany (head-bill and tail tip 95%, wing and tail tip 97%) and in the combined dataset (head-bill and tail tip 92%, wing and tail tip 93%). Such discriminant functions can be used to assign sex of adult bee-eaters reliably and swiftly while the bird is still in the hand, highlighting the potential of these functions for rapidly sexing species with low degrees of sexual size and plumage dimorphism.

Keywords**:** sexual dimorphism; molecular sexing; discriminant function analysis; body size; morphometry

Introduction

Behavioural and ecological studies often require information on the sex of a focal individual. In sexually dichromatic species sex can be easily determined in the field (e.g. Svensson 1992, Demongin 2016). However, this is not straightforward in many bird species when plumage differences between sexes are subtle (Barraclough et al. 1995, Eaton 2005, Avilés et al. 2008, Silva et al. 2008) or when differences in plumage coloration are not apparent in younger age classes (Blasco-Zumeta and Heinze 2013a, 2013b, Demongin 2016). For species displaying low sexual dichromatism, size dimorphism may be used to assign sex (Garcia-Del-Rey et al. 2008, Katrínardóttir et al. 2013, Audet et al. 2014). Sexual size dimorphism is highly variable among bird species (Owens and Hartley 1998, Guallar et al. 2010) but even sexually dimorphic species can show considerable overlap in body size between the sexes (Gunnarsson et al. 2006, Kesler et al. 2006). Therefore, it is important to select the most discriminant characteristics when attempting to assign sex based on size traits. In addition, species with wide distribution ranges can show clinal or regional differences in body size due to spatially different environment across the range. Consequently, spatial variation in size might lead to different sets of morphological characters being useful for sexual discrimination in different parts of the range (Ellrich et al. 2010, Guallar et al. 2010, Sáez-Gómez et al. 2017).

Nowadays, molecular analyses based on PCR amplification of markers located in the sex chromosomes is the most accurate method for sexing birds (Griffiths et al. 1998, Dubiec and Zagalska-Neubauer 2006), but it is more expensive and time consuming than morphological measurements in the field – many of which are routinely taken by ringers over long periods and across continents. Discriminant functions based on biometric measurements have been used successfully to determine sex across many orders (Dechaume-Moncharmont et al. 2011) and can be a powerful tool even in cases when there is considerate overlap of measurements between sexes (Alarcos et al. 2007, Katrínardóttir et al. 2013). Thus by combining a few measurements (2 to 3) in a multivariate discriminant analysis, sex can often be assigned accurately directly in the field.

Here we explore variation in biometrics and their suitability to discriminate sex in adult European bee-eater *Merops apiaster*, a sexually dimorphic species but with considerable overlap of body size in males and females. The European bee-eater (henceforward bee-eater) is a long-distance migrant with traditional breeding areas mostly confined to southern Europe and parts of northern Africa and western Asia (Fry 1984), but it has expanded its breeding range northwards into Central Europe during the last decades (Fiedler 2003, Reif et al. 2010).

Morphological differentiation of sexes in birds often relies on plumage characteristics, brood patches and marked body size differences (Demongin 2016). Although the sex of most bee-eaters can be assigned based on sex-specific breeding plumage during the breeding season, some individuals do not display the typical sex specific colours, making this method often unreliable (Lessells and Krebs 1989, Baker 2006, Blasco-Zumeta and Heinze 2013c, Demongin 2016),particularly for second year breeding birds (JSC pers. obs.). Sexing by brood patch is also not possible since both sexes incubate (Fry 1984) and usage of a single biometric measure might give limited results owing to considerable overlap in size between sexes (Lessells and Ovenden 1989, Demongin 2016). Bee-eaters dig their nest holes in river banks or other relatively vertical surfaces, loosening the soil with their bill. This causes considerable bill wear in harder substrates (Mountfort 1957), potentially leading to differences in bill length between bee-eaters breeding at colonies with distinct substrate hardness. Unfortunately, a comparative study of biometrics of unambiguously sexed bee-eaters is still missing. Thus, it is unknown how well combinations of biometrics can be used to discriminate sex in fully grown individuals of this species.

In this study we (1) investigate sex and age specific variation in biometrics in two bee-eater populations (Iberia and Central Europe) and (2) apply a linear discriminant analysis (LDA) on multiple measures to assign sex, first at population level and finally across populations. Finally, we (3) provide discriminant functions based on several measurements and the associated levels of accuracy allowing for quick sex determination in the field.

Methods

Sampling and measuring bee-eaters

Fieldwork on both populations was conducted at four breeding colonies, two in Portugal (PT; 39.9 and 38.1°N; 7.1°W, distance 200km) and two in Germany (DE; 51.3°N, 12.0°E, distance 6km), during 10 days in end of June (PT) and the beginning of July of 2016 (DE), respectively. Despite a calendar difference in the study periods, the birds in the two populations were in the same annual period (the nestling rearing period), when the breeders had been captured using walk-in nest traps. Captured birds were ringed and aged by plumage according to Blasco-Zumeta and Heinze (2013c). We assigned birds to two age classes, either second year bird (EURING age class 5) or older than second calendar year (EURING age class 6).

The following measurements were taken from each bird: bill length (from the tip of the bill to the first feather); head-bill length (from the posterior ridge formed by the parietal–supraoccipital junction to the front edge of the bill); third primary length (p3, from base to the tip of the third primary; ascendent numbering, Svensson 1992); wing length ("maximum length", from carpal joint to tip of the longest primary, Svensson 1992); Kipp's distance (from the tip of the first secondary to the tip of the longest primary); right rectrix length (from base to the tip of the innermost right rectrix); tail length (from the base of the tail to the tip of the longest tail feather) and tail tip length (from the tip of the longest to the tip of the shortest tail feather). Birds showing plumage abrasion of tail feathers were not included in the study. Traits were grouped in relation to one of the three main structures: skull (bill and head-bill lengths); wing (p3 length, wing length and Kipp's distance) and tail (right rectrix, tail and tail tip lengths). We used rulers to measure wing and p3 lengths, Kipp's distance, right rectrix length, tail length and tail tip length (all ± 0.5 mm), and callipers to measure bill and head-bill lengths (± 0.1 mm). The measurements were taken by six different people in Portugal and one in Germany. We punctured the brachial vein with a needle, collected a blood sample with a heparinized capillary, which was immediately stored in SET buffer (0.15M NaCl, 0.01M Tris, 0.001M EDTA, pH 8.0) for later molecular sexing in the laboratory.

Molecular sex determination

DNA was extracted from blood samples with the QIAGEN DNeasy blood and tissue kit by Ecogenics GmbH (Balgach, Switzerland). Molecular sexing was performed with the primers P2/P8 from Griffiths et al. (1998) and the QIAGEN Multiplex PCR Kit in a final volume of 10 µl containing 3 µl of 1:10 diluted DNA and 200 nM of each primer. We used the following cycling profile: one activation step of 95°C for 15 min; 45 cycles of 50°C for 90 sec, 72°C for 60 sec, and 94°C for 30 sec; and one cycle of 50°C for 90 sec and 72°C for 4 min. PCR products were run with 100 V for 2 hours in a 3% agarose gel stained with GelRed® (Biotium). The gel electrophoresis yields two bands corresponding to the amplified CHD1Z and the CHD1W introns in hetero-gametic (ZW) females, while only one band corresponding to the CHD1Z intron is yielded for homogametic males (ZZ).

Statistical analysis

We measured and collected blood from 57 birds in Portugal (PT) and 113 birds in Germany (DE). Molecular sexing indicated that from the bee-eaters sampled in Portugal 23 were females (9 2nd year and 14 >2nd year) and 34 were males (18 2nd year and 16 >2nd year). In Germany, 54 bee-eaters were females (28 2nd year and 26 >2nd year) and 59 males (31 2nd year and 28 >2nd year).

We first determined if bee-eaters exhibited sexual dimorphism within each breeding population by calculating the sexual dimorphism index (SDI) for each biometric using the equation SDI=(mean male/mean female)-1, where positive values indicate that males are larger, negative values that females are larger and zero that the sexes are identical in size (Lovich and Gibbons 1992). To assess differences between sexes and age groups in Germany, we performed a 2-way-ANOVA with an interaction term. For data from Portugal, variation between the six different ringers was accounted for by including ringer as a random factor in a Generalized Linear Mixed Model (GLMM) with sex, age and its interaction as main factors. To test for differences between populations, we compared each biometric (for males and females separately) between Portugal and Germany using a GLMM with ringer as random factor. Test assumptions were confirmed by graphical inspection of standardized residuals and by plotting residuals against fitted values. GLMM was performed using the R-package “lme4” (Bates et al. 2015).

Linear discriminant analysis (LDA) assumes multivariate normality, equality of group covariance matrices and lack of multicollinearity between predictors (James et al. 2013). Therefore, we selected the biometrics from each population that met these criteria and tested for multicollinearity using Spearman’s correlation matrices and variance inflation factors (VIFs) with the R-packages “psych” and “mctest” (Figure S2.1 and S2.2; Revelle 2018, Imdad et al. 2018). When biometrics within each of the three main biometric traits groups (skull, wing and tail) correlated with a coefficient $r > 0.7$, we included only one trait of the group in the discriminant function. We considered that a VIF<3 did not suggested multicollinearity (Zuur et al. 2010). Multivariate normality was tested using function “mvn” from MVN R-package (Korkmaz et al. 2014). Accordingly, for the LDA of PT we selected wing, tail tip and head-bill lengths. We did not include bill, p3 and tail lengths due to the lack of significant differences between sexes (Table 2.1). We confirmed the assumption of multivariate normality for wing, tail tip and head-bill lengths (Royston test; Females: H=7.32, p=0.91; Males: H=5.40, p=0.144) after excluding Kipp’s distance and right rectrix length (Shapiro-Wilk test; Kipp’s distance (males): W=0.910, p<0.01; right rectrix length (males): W=0.915 p=0.01). The low VIFs (head-bill: 1.55, wing: 2.09, tail tip: 1.60) confirmed lack of multicollinearity between the selected predictors. The biometrics selected for the LDA of DE population were head-bill length, wing length, tail tip length and right rectrix length. We excluded bill length because it was highly correlated with head-bill length (r=0.89) and because bill tips are often worn, which could decrease the discriminant accuracy. P3, tail lengths and Kipp's distance did not follow a normal distribution in one of the sexes (Shapiro-Wilk test; P3 (males): W=0.916, p<0.01; tail length (females): W=0.952 p=0.03; Kipp's distance (males): W=0.957 p=0.03) and thus were also excluded. Multivariate normality was confirmed for head-bill, wing, tail tip and right rectrix lengths (Royston test, H=2.764 p=0.716). Right rectrix was correlated with wing (r=0.76) and tail tip (r = 0.89, Figure S2.2). VIF's of tail tip (6.06) and right rectrix (6.67) lengths also suggested multicollinearity. For this reason, we conducted separate LDA when using these biometrics (i.e. never included correlated biometrics in the same functions). When using tail tip and right rectrix in different functions all of the selected biometrics showed a VIF< 3 (head-bill: 1.44, wing: 2.33 tail tip: 2.08, right rectrix 2.29). The equality of group covariance matrices was then confirmed for each group of selected biometrics (Box M-test, PT: chi-sq=6.39, p=0.38; DE: chi-sq=9.88, p=0.45) using R-package "biotools" (da Silva et al. 2017). Outliers were checked using function "mvn" which detected only 3 for the DE dataset, but upon visual inspection of box plot these were retained for analysis.

We used the function "lda" from R-package MASS (Venables and Ripley 2002) to perform LDAs for predicting an individual's sex, based on biometrics. Univariate LDAs were performed to separately assess the potential of individual biometric measures in discriminating sexes. Then, all possible combinations of biometrics were used in multivariate LDAs and only those with higher or similar overall discriminant accuracy than the single biometric functions were retained. We validated the discriminant functions using leave-one-out cross-validation, where the sex of each individual in the sample was predicted from the functions calculated after that particular individual had been removed from the data set (James et al. 2013). Cross-validation results are only presented when its discriminant accuracy is lower than the one given by the training dataset. All the statistics were performed in R 3.4.3 (R Core Team 2017) .

Table 2.1. Statistical results of test for size differences between sexes and age classes in European bee-eaters. The results for Portugal are from GLMMs and for Germany from two-way ANOVAs (details see methods).

	Portugal														
	sex				age				sex*age				ringer	
	Est.	SE	*t*	*p*	Est.	SE	*t*	*p*	Est.	SE	*t*	*p*	var	sd
Bill length	0.75	0.52	1.43	n.s.	-0.54	0.55	-0.99	n.s.	0.86	0.70	1.23	n.s.	0.54	0.74
Head-bill length	1.44	0.57	2.51	0.01	-1.12	0.60	-1.86	n.s.	1.72	0.77	2.24	0.02	0.19	0.43
P3 length	2.55	1.41	1.80	n.s.	-1.05	1.48	-0.71	n.s.	0.98	1.90	0.52	n.s.	0.15	0.39
Wing length	5.53	1.00	5.48	<0.001	-2.12	1.05	-2.00	0.05	0.60	1.34	0.45	n.s.	1.88	1.37
Kipp's distance	4.40	1.19	3.69	<0.001	-0.86	1.25	-0.69	n.s.	-0.19	1.59	-0.12	n.s.	2.03	1.42
Right rectrix length	5.01	2.25	2.22	0.03	-0.94	2.37	-0.40	n.s.	1.76	3.01	0.59	n.s.	8.10	2.84
Tail length	3.38	2.12	1.59	n.s.	-2.20	2.23	-1.12	n.s.	3.58	2.84	1.26	n.s.	5.13	2.26
Tail tip length	4.30	1.46	2.93	<0.01	-1.13	1.53	-0.74	n.s.	1.78	1.96	0.90	n.s.	0.00	0.00
	Germany													
	sex				age				sex*age					
			F	*p*			F	*p*			F	*p*		
Bill length			17.30	<0.001			1.53	n.s.			0.16	n.s.		
Head-bill length			42.89	<0.001			0.90	n.s.			0.04	n.s.		
P3 length			51.41	<0.001			2.38	n.s.			0.29	n.s.		
Wing length			116.73	<0.001			0.00	n.s.			0.35	n.s.		
Kipp's distance			64.83	<0.001			0.01	n.s.			0.22	n.s.		
Right rectrix length			132.03	<0.001			0.21	n.s.			0.41	n.s.		
Tail length			64.44	<0.001			0.56	n.s.			0.27	n.s.		
Tail tip length			225.56	<0.001			1.24	n.s.			1.33	n.s.		

Results

In both populations, sexual dimorphism was low as males and females overlapped considerably in all biometrics (Figure 2.1; Table S2.1) with lowest and highest relative overlap in 40.3% and 99.1%, respectively. Nonetheless, we found that males were significantly larger than females (PT and DE) except for bill, p3 and tail lengths in PT (Table 2.1; Figure 2.1). Age classes did not differ in morphometry within each population (except wing length in PT, p = 0.05) and only head-bill from PT showed a significant interaction between age and sex (Table 2.1). Therefore, age classes were pooled for

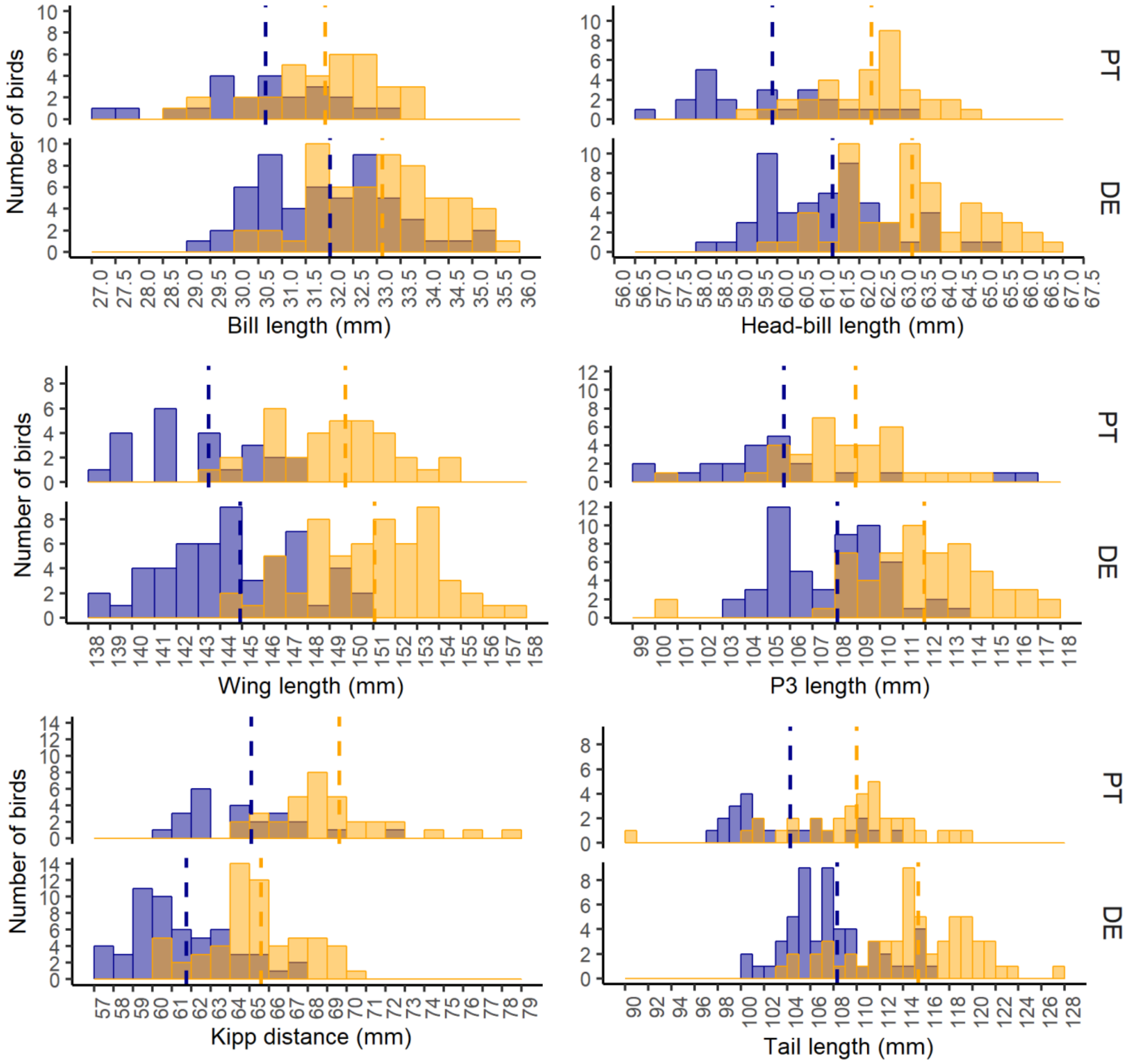

Figure 2.1. Frequency distribution of biometrics (all in mm) of females (blue) and males (yellow) from each population (PT: Portugal , DE: Germany). Dashed line represents the mean values for each sex (blue: females; yellow: males).

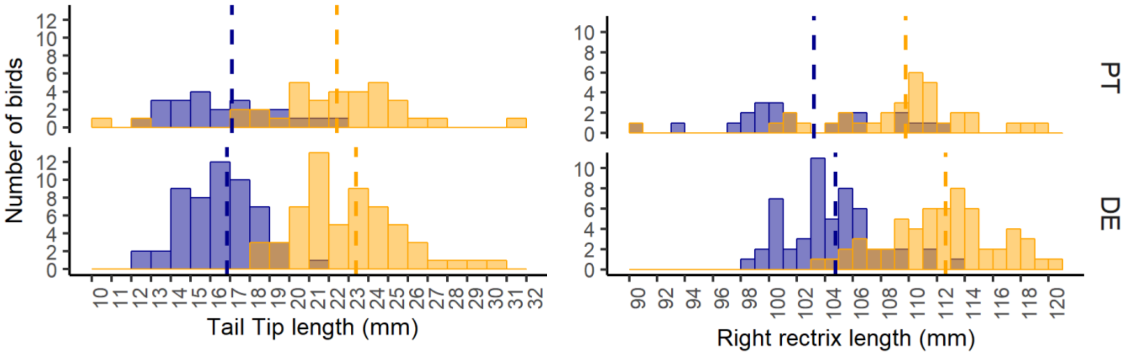

Figure 2.1. *continued.*

subsequent analysis. Additionally, we did not find significant size differences between populations except for p3 and tail lengths, with females from DE showing longer tails and males from DE having longer p3 compared to PT (Table 2.2; Figure 2.1).

The single biometric providing the highest accuracy in sex discrimination was wing length for PT (87.7%) and tail tip length for DE (93.8%). The multivariate function with the highest discriminant ability included head-bill, wing and tail tip lengths, which correctly classified 91.2% of the birds (females: 86.9%; males: 94.1%) for PT and 96.4% of the birds (females: 96.2%; males: 96.6%) for DE populations (Table 2.3). However, this function showed lower discriminant accuracy in cross-validation for PT (total: 85.9%; females: 82.6%; males: 88.2%). Using a function containing only two biometrics, head-bill length and tail tip length, classified females (86.9%) and males (94.1%) from PT with similar accuracy than the multivariate function with three biometrics (Table 2.3; Figure 2.2). Additionally, the function containing head-bill and wing lengths and the one including wing and tail tip lengths classified correctly 82.6% of females and 91.1% of males from PT (Table 2.3), with the latter equation performing worse in cross-validation (total: 84.2%; females: 82.6%; males: 85.2%). For the DE population, the discriminant function with wing and tail tip lengths allowed a correct classification of 94.9% of males and 100% of females, but performed worse for females (95%) in the cross-validation. When using head-bill and tail tip lengths, the overall classification accuracy was reduced to 94.6% in DE population (females: 96.2%; males: 93.2%; Table 2.3; Figure 2.2). Since the functions with highest discriminant power on each population were composed by head-bill, wing and tail tip lengths, we explored the ability of these biometrics to discriminate between sexes in the combined dataset (Table 2.3): Tail tip length alone (total: 88.2%; females: 88.3%;

males: 88.1%) was the single best biometric for sex discrimination; wing and tail tip lengths classified correctly 92.9% of the birds (females: 92.2%; males: 93.5%) and the equation containing head-bill and tail tip lengths sexed correctly 91.7% of birds (females: 92.2%; males: 91.3%) for the combined dataset. The three trait equation containing head-bill, wing and tail tip lengths showed the highest discriminant accuracy classifying correctly 93.5% of the birds from the combined dataset, although it had lower performance in cross-validation (total: 90.9%; females: 92.4%, males: 91.7%).

Table 2.2. Statistical results of test for size differences between populations of European bee-eaters. A GLMM was conducted separately on females and males (details see methods)

	Females					
	Est.	se	*t*	*p*	ringer	
					var	sd
Bill length	-1.45	0.82	-1.76	n.s.	0.45	0.67
Head-bill length	-1.47	0.70	-2.07	n.s.	0.28	0.53
P3 length	-2.16	1.87	-1.59	n.s.	8.71	2.95
Wing length	-1.50	1.21	-1.23	n.s.	0.77	0.88
Kipp’s distance	3.62	1.65	2.19	n.s.	1.89	1.37
Right rectrix length	-2.07	3.03	-0.68	n.s.	6.75	2.60
Tail length	-4.05	1.05	-3.84	<0.001	0.00	0.00
Tail tip length	0.26	0.54	0.49	n.s.	0.00	0.00
	Males					
	Est.	se	*t*	*p*	ringer	
					var	sd
Bill length	-1.29	0.81	-1.58	n.s.	0.48	0.69
Head-bill length	-1.08	0.65	-1.64	n.s.	0.26	0.51
P3 length	-3.04	0.66	-4.60	<0.001	0.00	0.00
Wing length	-1.60	1.43	-1.11	n.s.	1.35	1.16
Kipp’s distance	4.12	0.92	4.45	n.s.	0.41	0.64
Right rectrix length	-3.91	3.65	-1.07	n.s.	10.11	3.18
Tail length	-6.22	3.49	-1.78	n.s.	8.83	2.97
Tail tip length	-1.06	1.11	-0.95	n.s.	0.61	0.78

Table 2.3. Classification accuracy (% of correctly classified females, males and total) of univariate discriminant functions with the single biometrics providing highest scores. Multivariate discriminant functions using those biometrics and that improve overall classification accuracy are also provided. Biometrics coded as: bill length - B; head-bill length - HB; wing length - W; Kipp's distance - K; tail tip length - TT; and right rectrix length - RR. All functions can be used to determine the sex of a bird in the field with a high accuracy using a cut-off value of 0: D > 0 for males and D < 0 assigning females.

Discriminant Equation	Correctly classified (%)		
	Females	Males	Total
Portugal			
D = 0.669***HB** - 40.91	73.9	88.2	82.4
D = 0.360***W** - 52.78	82.6	91.1	87.7
D = 0.281***TT** - 5.56	69.5	88.2	80.7
D = 0.484***HB** +0.186***TT** - 33.31	86.9	94.1	91.2
D = 0.303***HB**+ 0.283***W** - 60.07	82.6	91.1	87.7
D = 0.296***W**+ 0.102***TT**- 45.52	82.6	91.1	87.7
D =0.295***HB** + 0.226***W** + 0.098***TT** - 53.27	86.9	94.1	91.2
Germany			
D = 0.633***HB** - 39.46	75.9	69.4	72.5
D = 0.333***W** - 49.35	77.7	84.7	81.4
D = 0.432***TT** - 8.68	98.1	89.8	93.8
D = 0.276***RR** - 30.03	90.7	83.0	86.7
D = 0.192***HB** + 0.395***TT** - 19.94	96.2	93.2	94.6
D = 0.160***W** + 0.338***TT** - 30.54	100	94.9	97.3
D = 0.186***HB** + 0.158***W** + 0.306***TT** - 41.26	96.2	96.6	96.4
Combined dataset			
D = 0.607***HB** - 37.57	64.9	81.7	74.1
D = 0.335***W** - 49.44	79.2	81.7	80.5
D = 0.358***TT** - 7.18	88.3	88.1	88.2
D = 0.258***HB** +0.309***TT** - 22.18	92.2	91.3	91.7
D = 0.200***W**+ 0.239***TT**- 34.29	92.2	93.5	92.9
D = 0.187***HB** + 0.179***W** + 0.219***TT** - 42.44	93.5	93.5	93.5

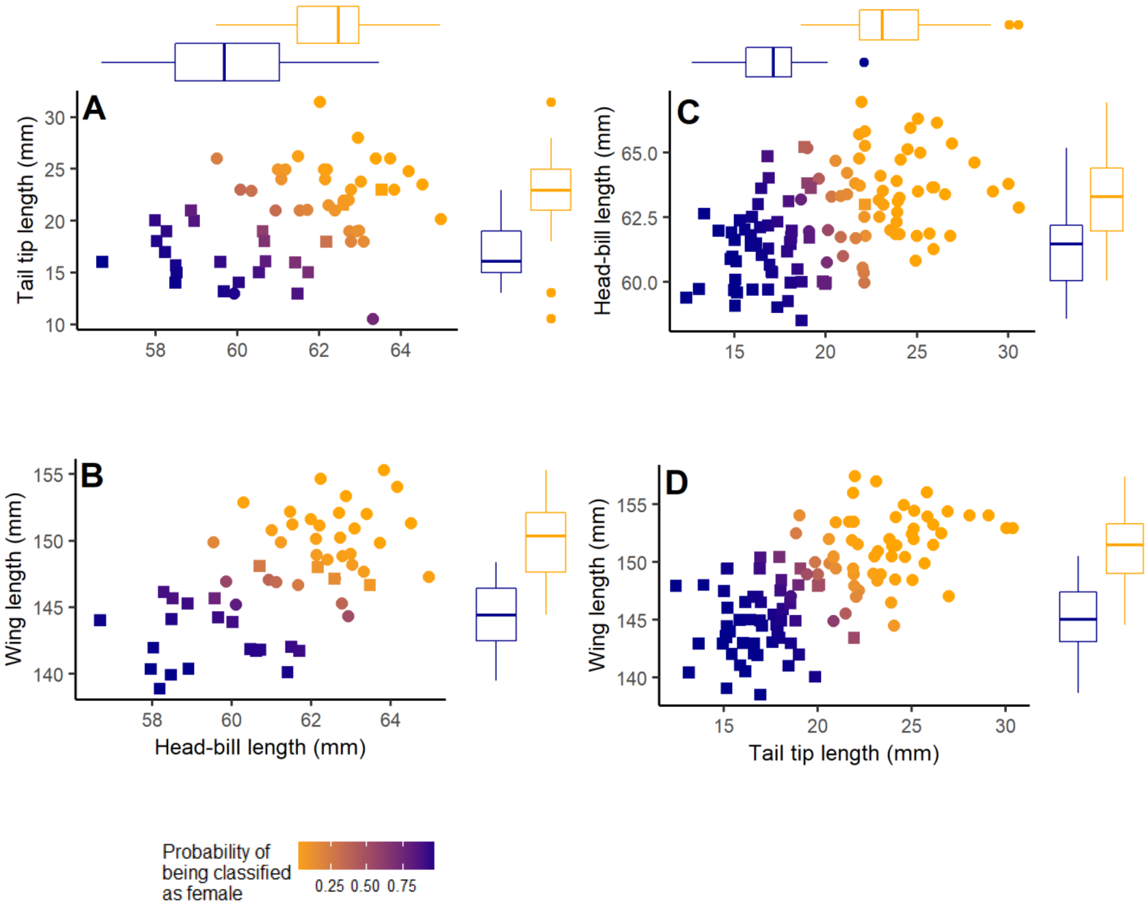

Figure 2.2. Variation in the three biometrics (all in mm) that compose the discriminant functions showing highest accuracy (TT, W, and HB; Table 3) for bee-eaters in Portugal (A-B) and Germany (C-D). Squares represent females and circles males as determined by molecular sexing. The colour gradient within the symbols shows the posterior probability of an individual being classified as female from yellow (0%) to blue (100%). Boxplots show the distribution of each biometric per sex (blue: females; yellow: males)

Discussion

Our results confirm for genetically sexed birds, that male European bee-eaters are generally larger than females in almost all biometrics while age classes do not significantly differ in size. Several studies described sex-differences of various biometrics in bee-eater before, including wing length i.e. Lessells and Ovenden (1989), Todte and Harz (2003) and complete morphometries of bill, wing, tail and tail tip lengths (e.g. Glutz and Bauer 1980, Fry 1984). The authors reported considerable overlap in biometric measures between the sexes emphasizing the difficulty of using single measurements for sexing bee-eaters. Moreover, most of the former studies could not determine the sex by methods independently from morphometry and plumage characteristics, and thus may include misclassified individuals.

The significant size differences between populations found for primary 3 length (males) and tail lengths (females) underline the benefit of applying discriminant functions on a local or regional scale and not across large geographical distances (Evans et al. 1985, Ellrich et al. 2010, Guallar et al. 2010, Sáez-Gómez et al. 2017). However, we did not find significant differences between populations for any other biometric, supporting Ramos et al. (2016) who found no population differences in wing, right rectrix and culmen lengths in Iberia and Eastern Europe/Central Asia in a dataset of unsexed birds.

Many studies have reported observer specific variation or even bias in morphological measurements (Nisbet et al. 1970, Gosler et al. 1995, Wilson 1999, Goodenough et al. 2010) which may subsequently affect the accuracy of sex determination (Henry et al. 2015). Since we accounted for potential between-ringer variation by adding this variable as a random factor in the analysis, it is unlikely that ringer bias considerably influenced the results for size differences between populations and between sexes in PT. However, between-ringer variation may have contributed to a decrease of discriminant accuracy on birds from the Portuguese population, since ringer variation was not accounted for in linear discriminant analysis. Additionally, the between-population difference in females' tail length and the lack of sex differences in tail length in PT might have been influenced by the often worn tail edges of bee-eaters in the Portuguese population (JSC pers. obs.). In further studies we encourage validation of the functions using an independent sample from the same populations. In addition, measurements should be taken by a single or few experienced ringers at each site, combined with validations of accuracy and repeatability (e.g. Harper 1994, Busse and Meissner 2015), within and between study sites and ringers.

Population specific functions allow sexing bee-eaters by morphometry with high degree of accuracy at least for Iberia or Central European populations. Because the same biometrics (i.e. head-bill, wing and tail tip lengths) had the strongest discriminant power for both populations, we used those traits to calculate general discriminant functions which can be applied in other regions of the species distribution range.

Due to the considerable overlap in various biometrics, especially in head-bill, wing and tail tip lengths (Figure 2.1, Table S2.1), discriminant functions of multiple traits discriminate sex more accurately than functions with single biometrics (Table 2.3); the best multivariate approach correctly classified 91-97% of the birds. Some discriminant functions containing two biometrics (i.e. head-bill + tail tip lengths for Portugal, wing + tail tip lengths for Germany and for the combined dataset) had similar or slightly higher discriminant power than the ones using three variables. In fact, previous studies have shown that a few characteristics to discriminate between sexes can be more powerful than the addition of extra variables (Marchi et al., 2012; van Franeker and ter Braak, 1993). This is also the case for the DE population: adding head-bill length to the equation "wing length + tail tip length" decreased the discriminant accuracy of females by 3.8%, while increasing the accuracy for males merely by 1.7%.

Similar to Blue-tailed bee-eaters (*Merops philippinus*, Siefferman et al. 2007), tail tip and wing lengths were two of the best discriminators for sexing European bee-eaters. Head-bill length was also a powerful discriminant factor and it is widely used to assign sex in other bird species, as it can be measured with a high degree of consistency (van Franeker and ter Braak 1993, Alarcos et al. 2007, Hammouda and Selmi 2013, Meissner et al. 2017). However, head-bill length strongly correlates with bill length and bee-eaters can show severely worn bill tips after nest digging (Mountfort 1957, JSC pers. obs) although the original bill length is recovered after approximately four weeks (Massa and Rizzo 2002). In this way, bill length should be used with caution as potential discriminant trait, especially for sexing birds from different colonies with different breeding cavity substrates and in different times of the year, i.e. before or after cavity digging.

This is the first study comparing morphological characteristics of molecularly sexed birds to generate population specific, as well as, general discriminant functions for sexing adult European bee-eaters. Sexing bee-eaters according to plumage colour can be achieved with the help of descriptive and photographic guides (e.g. Blasco-Zumeta and Heinze 2013c, Demongin 2016). However, it dependents of observer's training as some birds are difficult to sex due to plumage coloration overlap (Todte and Harz 2003, Blasco-Zumeta and Heinze 2013c, Demongin 2016). In addition, at the end of the breeding period few bee-eaters may have already started to moult into the non-breeding plumage (Todte and Harz 2003), with both sexes acquiring a greenish coloration which may hinder correct sex determination. Discriminant functions, on the other hand, can be used with the same statistical confidence for all individuals, independently from observer experience. Our results allow, for example, to quickly assigning sex in the field while the bird is still in hand. This can be useful for sex specific studies, for example when samples need to be collected from each sex (e.g. tissues for stable isotope analysis) or for sex specific tracking. This non-invasive sexing method also enables investigations into museum collections and post-hoc analyses of historical ringing data to derive sex related information of populations from at least Iberia and Central Europe.

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Supplementary material

Figure S2.1. Spearman's correlation matrix for biometrics from the PT population. Correlation coefficient values for each pair or biometrics is shown in the top. Plots for each pair of biometrics are shown in the bottom. Within each plot, linear regression line is showed in red. A histogram representing the distribution of each biometric is also presented along the matrix diagonal (bill length - B; head-bill length – HB; wing length - W; Kipp's distance - K; p3 length - P3; tail tip length - TT; tail length – TL; and right rectrix length – RR).

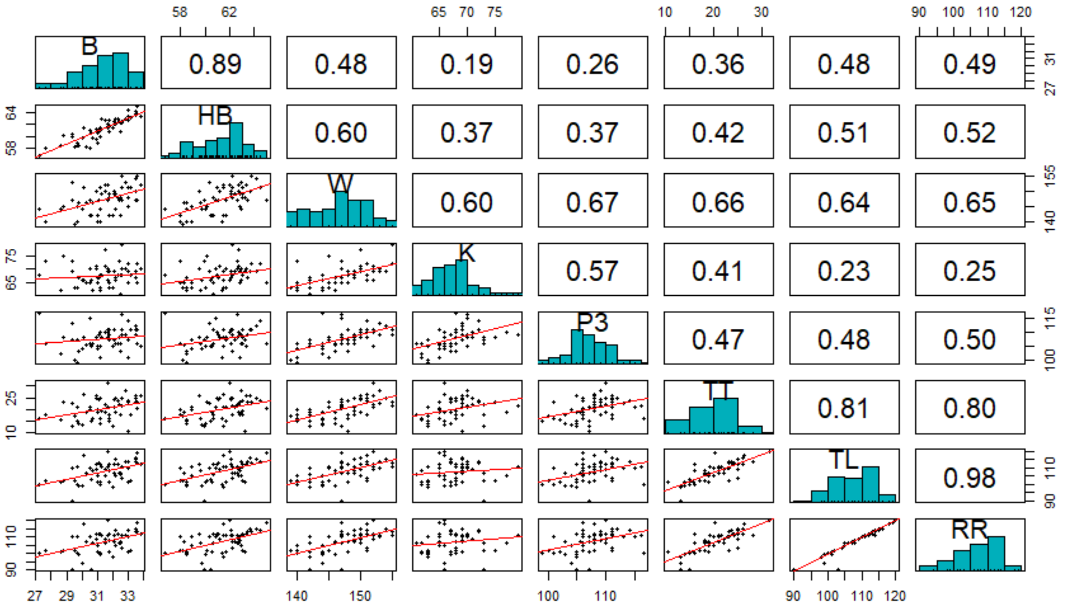

Figure S2.2. Spearman’s correlation matrix for biometrics from the DE population. Correlation coefficient values for each pair or biometrics is shown in the top. Plots for each pair of biometrics are shown in the bottom. Within each plot, linear regression line is showed in red. A histogram representing the distribution of each biometric is also presented along the matrix diagonal (bill length - B; head-bill length – HB; wing length - W; Kipp’s distance - K; p3 length - P3; tail tip length - TT; tail length – TL; and right rectrix length - RR).

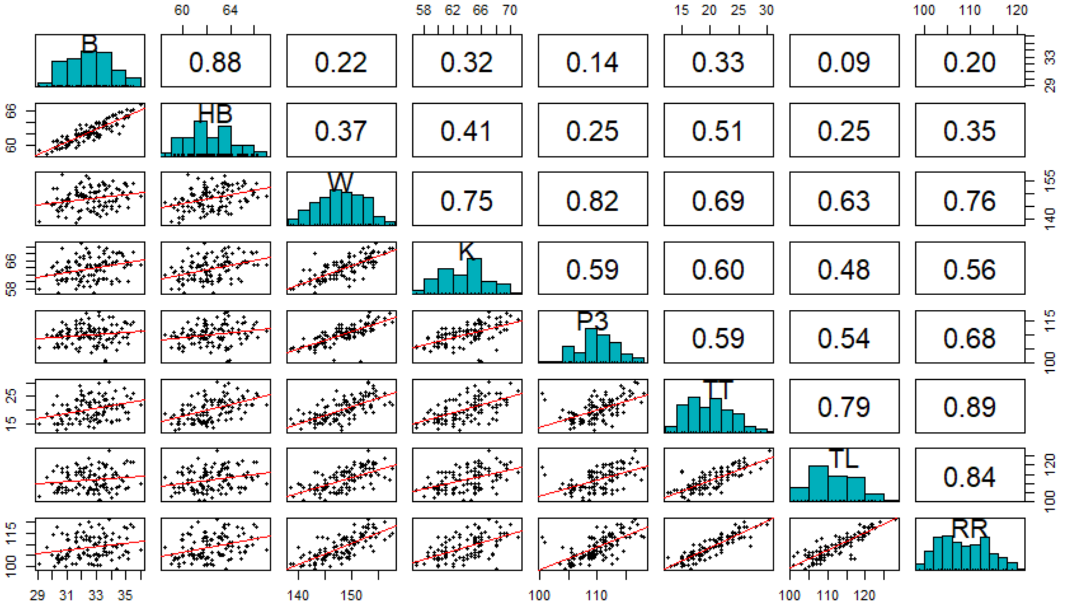

Table S2.1. Biometrics (mean, se and range, all in mm) for male and female bee-eaters breeding in Portugal and Germany, sampled in 2016. Overlap indicate the percentage of range overlap between males and females for each biometric. Positive values of Sexual Dimorphism Index (SDI) indicate that males are larger, negative values that females are larger and zero that sexes are identical in size.

	Male (n=34)			Female (n=23)			Overlap (%)	SDI
Portugal	mean	se	range	mean	se	range		
Bill length	31.9	0.2	28.8-33.8	30.6	0.3	27.2-33.5	89.4	0.04
Head-bill length	62.2	0.2	59.5-65.0	59.8	0.3	56.7-63.5	71.9	0.04
P3 length	108.9	0.4	101.0-115.0	105.7	0.8	99.0-116.5	92.2	0.03
Wing length	149.7	0.4	144.0-155.0	143.4	0.5	139.0-148.0	40.3	0.04
Kipp's distance	69.6	0.5	65.0-79.0	65.0	0.6	61.0-73.0	77.1	0.07
Right rectrix length	109.7	0.9	90.0-120.0	103.2	1.2	90.0-113.0	87.7	0.06
Tail length	110.0	1.0	90.0-120.0	104.2	1.0	98.0-114.0	87.7	0.05
Tail tip length	22.4	0.6	10.5-31.5	17.1	0.5	10.0-23.0	71.9	0.24
Germany	Male (n=59)			Female (n=54)				
Bill length	33.1	0.1	30.1-36.0	32.0	0.1	29.1-35.2	97.3	0.03
Head-bill length	63.3	0.2	60.0-67.0	61.3	0.2	58.5-65.2	99.1	0.03
P3 length	111.9	0.4	100.5-118.0	108.1	0.3	103.5-113.5	84.3	0.03
Wing length	151.0	0.3	144.5-157.5	144.9	0.4	138.5-150.5	52.1	0.04
Kipp's distance	65.5	0.3	61.0-71.0	61.7	0.3	57.0-68.0	71.3	0.06
Right rectrix length	112.6	0.5	104.0-121.0	104.7	0.4	99.0-113.5	63.1	0.07
Tail length	115.3	0.6	104.0-128.0	108.3	0.5	101.0-117.0	77.1	0.06
Tail tip length	23.3	0.3	18.5-30.5	16.8	0.2	12.5-22.0	47.3	0.28

Chapter 3

Developing and validating a nestling photographic aging guide for cavity-nesting birds: an example with the European Bee-eater (*Merops apiaster*)

Joana S. Costa, Afonso D. Rocha, Ricardo A. Correia, José A. Alves

Abstract

Accurate estimation of nestlings' age is essential in avian demography studies as well as in population ecology and conservation. For example, it can be useful for synchronizing nest visits with events of particular interest, such as the age at which young can be safely ringed, or in choosing the best period to attain the most accurate calculation of laying or hatching dates. We constructed a photographic guide for aging European bee-eaters *Merops apiaster* nestlings to 3-day age classes and evaluated the aging method by performing a validation exercise with several observers with no previous experience in aging bee-eater nestlings. The aging guide for bee-eater nestlings allowed estimating age to within 3 days with an average accuracy of 0.85. We found the optimal period for aging nestlings is between days 13-18 (with accuracy between 0.94 and 0.99), during which the status of feather development is more easily distinguishable from the preceding and subsequent age classes. During the first 3 days after hatching, nestlings can also be aged with high accuracy (0.93). The small size of the nestling in relation to the eggs and the nestling's inability to raise its head during these first days allows for good discrimination from the subsequent age class. Between days 25 and 28, nestlings were correctly aged in only half of assignments (0.55 sensitivity) and nestlings belonging to class 7 (days 7-9) were the least correctly identified (0.38 sensitivity). However, by visiting the nests at 12 days intervals it is possible to achieve the highest accuracy in age estimation with the smallest disturbance and logistic investment. This study highlights how indirect methods and a simple protocol can be established and employed to quickly estimate nestling age in cases where handling nestlings is challenging or impossible, while minimizing disturbance in and around the nest.

Keywords: Age estimation, nest visit, chick development, feather growth, image guide, plumage colour.

Introduction

Assessing bird productivity and inter-annual variation in hatching and laying dates allows linking potential phenological changes to demographic rates (e.g. Fletcher et al. 2013; Cruz-Mcdonnell and Wolf 2016; Tomotani et al. 2018). Accurate estimation of nestling age is therefore essential in avian demography studies and also in population ecology and conservation (e.g. Eeva and Lehikoinen 1996; Saunders and Ingram 1998; Marchesi et al. 2002). Establishing nestling age can also be used to synchronize subsequent nest visits with events of particular interest, such as the age at which young can be safely ringed (Fyfe and Oldendorff 1976; Tomotani et al. 2018) or in choosing the best period for attaining the most accurate back-calculation of laying or hatching dates (Marchesi et al. 2002). However, determining nestling age often requires handling the birds, and in some species nests are difficult or impossible to access, due to their location in cavities (e.g. bee-eaters; Fry 1984) or high in trees or cliffs (e.g. raptors; Moritsch 1983). In addition, frequent nest visits may affect nesting success by drawing the attention of potential predators to the nest or by changing parental behaviour. Ultimately, it can also lead to nest abandonment (Gotmark 1992). Reducing the frequency and length of nest visits (including nestling handling) is therefore very desirable and alternative indirect methods for estimating nestling age can be advantageous.

Nestlings are commonly aged using growth curves of morphological traits constructed from individuals of known age (e.g. Green and Tyler 2005; Pande et al. 2011; Saunders et al. 2015). But, estimating nestling age using directly measured biometrics alone may be inaccurate during specific periods of development (Rodway 1997; Brown et al. 2011). An alternative, or complement, is the use of guides based on photographs of nestlings with known age, together with a description of their qualitative changes in appearance, throughout the growth period (e.g. opening of the eyes, stages of feather development). This method may be used with higher success than biometric aging (Brown et al. 2013) while minimizing nest disturbance and avoiding bird handling (Moritsh 1985; Boal 1994; Saunders et al. 2015).

Here we present a photographic guide to determine nestling age in European bee-eaters *Merops apiaster*, based on visible traits that allow aging without excavation and extraction of nestlings from their burrows. The European bee-eater (hereafter bee-eater) is as Afro-Palearctic migrant that breeds colonially, digging its nest in sloping hillsides or flat ground. Nests chambers are usually difficult to access, with burrows either straight or curving to one side, and extending for 0.7-2 m (Fry 1984). Females lay 4-10 eggs in 1-2 day intervals and incubation often begins with the first egg and lasts around 20 days. This results in hatching asynchrony which can take 2-9 days, while fledging of the young occurs after 30 days (Lessells and Avery 1989). Nestlings that hatch first usually become the largest, sometimes contrasting considerably in size and developmental stage with the younger siblings that hatched later. Their relative stage regarding size and development is usually maintained throughout the nestling period (Lessells and Avery 1989).

In this study, we (1) provide a photographic guide for aging bee-eater nestlings into 3-day age classes that can be used in the field by any observer when hatching date is unknown, and (2) evaluate this aging method by performing a validation exercise on several observers with no previous experience in aging bee-eater nestlings. Finally, (3) we propose a nest visitation scheme that allows nestling age to be determined to within 3 days with high accuracy, while minimizing the number of nest visits.

Methods

Recoding nestling development

Fieldwork was conducted at two breeding colonies in Portugal (38.1N -7.0W; 38.6N -8.9W), between May and July of 2016 and 2017. We visited each nest every three days in order to minimize the intensity of the monitoring and avoid potential detrimental effects on the growth and survival of fledglings (Gotmark 1992). We inspected bee-eater nests after clutch initiation with an adapted “burrowscope” consisting of a webcam (Microsoft Lifecam HD-3000) attached to a LED light for illumination and connected to a laptop with a 2 m USB cable for image recording. In seven nests hatching date was possible to assign to within a three day period. These nests were subsequently monitored at three-day intervals until all the nestlings had fledged. During each nest visit, we recorded several photographic images of nestlings to record all noticeable aspects of their development. Since bee-eaters hatch asynchronously, we consistently targeted the oldest nestling(s), recorded and aged during the first visit following hatching, as a reference for the quantification of development, and therefore considered that nestling(s) for the production of the photographic images on each subsequent visit. The oldest nestling(s) is usually larger and tends to monopolize access to food by positioning itself in front of its siblings, inside the nest chamber (Lessells and Avery 1989). For this reason, the oldest nestling(s) is also more developed than later-hatched siblings, an order that is maintained during growth (Lessells and Avery 1989). In any case, during each visit, all nestlings were checked to ensure that the oldest nestling(s) was recorded and its development was therefore monitored. For six nests in which two nestlings hatched during the first three days, we monitored the development of the two nestlings that presented the most advanced stage of development at each visit, which was the same between them in every visit (JSC *pers. obs.*).

Photographic guide

We grouped the recorded nestling images into ten age classes at three-day intervals (1-3, 4-6, 7-9, 10-12, 13-15, 16-18, 19-21, 22-24 , 25-27 and 28-30 days; age classes henceforward indicated by the first number of the age interval), where the first interval (i.e. 1-3) corresponds to the period when the first nestling(s) of each nest hatched. We selected only good quality images from the representative nestling(s) for constructing the photographic guide. We used images from several nests and from the same nestlings at distinct development stages to illustrate each age class. For each age class, we described the most prominent characteristics and how they have changed throughout development. We selected the most identifiable characteristics based on detailed descriptions of the oldest nestling(s) and grouped them into four main features: head, plumage, relative size and behaviour. Specifically, we noted changes in the head: eye opening, bill size and colour; plumage: feather colour and stages of development (e.g. when pins emerge, unsheathing of pins); size in relation to eggs; and behaviour (e.g. being able to raise head).

Testing the nestling aging guide

In order to check the usefulness and effectiveness of the aging guide, we conducted a test with 6 observers with no prior experience in aging bee-eater nestlings but with differing levels of experience in handling other bird species. The test consisted of two stages: *learning* - the test structure was explained to all observers (see below), each having one copy of the photographic aging guide (Table S3.1). In order to evaluate how an observer would perform with little prior experience, each observer had 2 minutes to read and learn how to interpret the guide before the start of the test. The observers could consult the guide during the test (i.e. for assigning nestlings to a specific age class); *test structure* - a selection of 30 unique images from the first hatched nestling(s) (three images from each age class and different from the ones included in the guide) were randomly split into three sets of 10 images, each set composing a trial. Each image from the set was displayed during 40 seconds to all observers simultaneously, using a projector in a common room. Based on previous field experience we considered that 40 seconds would allow identifying the oldest nestling and attaining images (JSC per. obs.), therefore mimicking field conditions while minimizing disturbance. Each observer thus had 40 seconds to view the image and assign it to an age class, after which period the following image on the set was presented until all 10 images from the set had been shown and the trial ended. The three trials were run in succession and were intended to capture potential experience acquired by the observers during the test itself. Observers were not allowed to make any comments during the test and there were no intervals between trials.

Statistical analysis

The ability to correctly assign nestling age using the guide was analysed with generalized linear mixed models (GLMMs), with binomial error structure and logit link function. We included age class and trial as fixed factors and observer as random factor. We constructed full, reduced (including only one of the fixed factors) and null models (including only the random factor) that were ranked according to AICc. The model with the lowest AICc value was considered to have the best fit to our data. Models that differed by less than 2 AIC points from the best one were considered to provide similar support to the data (Burnham and Anderson 2002). For the top-ranked models, we performed pairwise comparisons between levels of each fixed factor.

In order to assess the predictive ability of our aging guide and evaluate performance accuracy within each nestling age class, we first constructed a cross-tabulation (confusion matrix) of actual and observer-assigned age classes. For each age class we constructed a 2x2 table of assignments and each assignment was categorized for each class as: true positive (TP) when the focal class (i.e. true class being shown) was correctly assigned; true negative (TN) when a different class being shown (i.e. not the focal) was correctly assigned; false positive (FP) when the focal class was incorrectly assigned while a different class was being shown; and false negative (FN) when a different class was assigned but the focal class was being shown (Table S3.2). We calculated the percentage of nestling age assignments that were correct and under- or over-estimated by one or two age classes (no incorrect under- or over-estimation was recorded beyond two classes away from the focal class, Table S3.3). Additionally, we used confusion matrices for each age class to generate five performance metrics: *Accuracy* – total proportion of correct assignments, TP+TN/TP+TN+FP+FN; *Sensitivity* – proportion of the images showing the focal class that were correctly assigned, TP/TP+FN; *Precision* – proportion of images assigned as the focal class that were in fact showing the focal class, TP/TP+FP; *False Positive Rate* – proportion of images showing different classes that were assigned as the focal class, FP/FP+TN; *False Negative Rate* – proportion of images showing the focal class that were assigned to a different class FN/TP+FN. All the analyses were performed in R 3.4.3 (R Core Team, 2017) with packages lme4 (Bates et al. 2015), emmeans (Lenth 2019) and caret (Kuhn et al. 2018).

Results

In total, 180 age estimations of bee-eater nestlings of 10 age classes were made by six participants, during the three trials of the test, resulting in 30 answers per participant, and 18 per age class. The model containing age class as the fixed factor was the most parsimonious model and ranked as the top model (Table S3.4), and the ability to correctly assign a nestling's age was significantly different between several classes (Tables 3.1 and 3.2). Specifically, class 13 received more correct answers than class 7, and class 16 presented more correct answers than classes 7, 25 and 28 (Table 3.2, Figure. S3.1). The absence of variance reported for the random factor suggests low variation in the accuracy of age class assignment between observers (Table 3.1, Figure S3.1). The difference between AICc of model 1 (including class) and model2 (including class and trial) was less than two units (AICc= 208.2, ∆AICc= 1.7, Table S3.4). However, we found no differences in the proportion of correct assignments between trials (Table S3.5; Figure S3.1).

Table 3.1. Summary table of GLMM (with a binomial error structure and logit link function) for the top-ranking model (Class + (1|observer). N = 18 age estimations per age class. Estimates, standard errors (SE), and 95% confidence intervals (95% lower and upper CI) are presented.

Fixed Effects	**Estimate**	**SE**	**Z-value**	**95% lower CI**	**95% upper CI**
Intercept	1.60	0.63	2.54	0.36	2.84
Class 4	-0.35	0.84	-0.42	0.14	2.36
Class 7	-2.06	0.79	-2.58	-1.39	0.49
Class 10	-0.65	0.82	-0.79	-0.07	1.98
Class 13	0.47	0.98	0.47	0.60	3.54
Class 16	24.60	512.00	0.04	-977.28	1029.71
Class 19	-0.35	0.84	-0.42	0.14	2.36
Class 22	-0.65	0.82	-0.79	-0.07	1.98
Class 25	-1.38	0.79	-1.75	-0.70	1.15
Class 28	-1.38	0.79	-1.75	-0.70	1.15
Random Effect			**Variance**		**SD**
Observer			0		0

Table 3.2. Pairwise comparisons between age classes following GLMM of the top-ranking model: Class + (1|observer). Estimated differences (±SE) between age classes for each pairwise comparison (row – column) are reported. Significant values are shown in bold and with (*) when p<0.01 and (**) when p<0.001.

	4	**7**	**10**	**13**	**16**	**19**	**22**	**25**	**28**
1	0.05(0.13)	0.44(0.14)	0.11(0.13)	-0.05(0.11)	-0.16(0.08)	0.05(0.13)	0.11(0.13)	0.27(0.14)	0.27(0.14)
4		0.38(0.15)	0.55(0.14)	-0.11(0.12)	-0.22(0.15)	3.96^{e-07}(0.13)	0.05(0.14)	0.22(0.15)	0.22(0.15)
7			-0.33(0.15)	**-0.50(0.13)***	**-0.61(0.11)****	-0.38(0.15)	-0.33(0.15)	-0.16(0.16)	-0.16(0.16)
10				-0.16(0.12)	-0.27(0.10)	-0.05(0.14)	1.07^{e-07}(0.14)	0.16(0.15)	0.16(0.15)
13					-0.11(0.07)	0.11(0.12)	0.16(0.12)	0.33(0.13)	0.33(0.13)
16						0.22(0.09)	0.27(0.10)	**0.44(0.11)***	**0.44(0.11)***
19							0.05(0.14)	0.22(0.15)	0.22(0.15)
22								0.16(0.15)	0.16(0.15)
25									-7.10^{e-08}(0.16)

Observers using the aging guide (Table S3.1) classified nestling age with a mean accuracy of 0.85, and seven out of ten age classes were correctly identified with an accuracy above 0.80 (Table 3.3). Most nestlings in the sample were miss-estimated by only one class and never by more than two classes (Table 3.4, Table S3.3).

The most frequently correct age classes were 1, 13 and 16 (≥0.88 sensitivity, Table 3.3), with seven classes having sensitivity of at least 0.70. Conversely, classes 25 and 28 were only correctly identified in about half of assignments (0.55 sensitivity), and class 7 was the least correctly identified (0.38 sensitivity; Table 3.3). Additionally, class 4 was correctly assigned on 77% of the events and it had both the lowest precision value (0.48) and the highest false positive rate (0.09; Table 3.3). This was reflected in a considerable proportion of nestlings from classes 7 and 10 being incorrectly assigned to class 4 (0.62 and 0.28 false negative rate, respectively; Tables 3.3 and 3.4). Classes 22, 25 and 28 were often incorrectly assigned (0.28-0.45 false negative rate and <0.68 precision; Table 3.3 and 3.4). But while class 22 was exclusively underestimated, assignment of class 25 was biased in both directions, whilst class 28 could only be underestimated (Table 3.4).

Table 3.3. Performance metrics calculated for each age class predicting the ability to correctly assign a nestling's age. FPR: false positive rate, FNR: false negative rate

Class	Accuracy	Sensitivity	Precision	FPR	FNR
1	0.93	0.88	0.80	0.02	0.12
4	0.84	0.77	0.48	0.09	0.23
7	0.68	0.38	0.70	0.02	0.62
10	0.85	0.72	0.92	0.01	0.28
13	0.94	0.88	1.00	0.00	0.12
16	0.99	1.00	0.85	0.02	0.00
19	0.87	0.77	0.73	0.03	0.23
22	0.84	0.72	0.68	0.04	0.28
25	0.75	0.55	0.58	0.04	0.45
28	0.76	0.55	0.66	0.03	0.45

Table 3.4. Percentage of nestling age estimations that were correctly estimated (center) and over- and under-estimated (right and left, respectively) by one or two age classes. Number of answers is presented in parenthesis.

Class	Under-estimated by (%)		Correctly estimated (%)	Over-estimated by (%)	
	2	1		1	2
1	-	-	88.99 (16)	5.66 (1)	5.66 (1)
4	0	16.77 (3)	77.88 (14)	5.66 (1)	0
7	5.66 (1)	55.66 (10)	38.99 (7)	0	0
10	22.22 (4)	5.66 (1)	72.22 (13)	0	0
13	0	5.66 (1)	88.99 (16)	5.66 (1)	0
16	0	0	100.00 (18)	0	0
19	0	11.11 (2)	77.88 (14)	11.11 (2)	0
22	0	27.88 (5)	72.22 (13)	0	0
25	0	16.77 (3)	55.66 (10)	27.88 (5)	0
28	5.66 (1)	38.99 (7)	55.66 (10)	-	-

Discussion

Aging guides of nestlings based on photographs have been widely developed and used for several species (e.g. Boal 1994; Fernaz et al. 2012; Amiot et al. 2014), but an assessment of age estimation accuracy has seldom been applied (but see Brown et al. 2013; Wails et al. 2014; Wilkins and Brown 2015; Brown and Alianell 2017). Here, we show that highly accurate levels of age estimation can be achieved, with only two nest visits during the entire nestling development period.

The aging guide for bee-eater nestlings allows estimating age to within 3 days with an average accuracy of 0.85. While some age classes can be estimated with an accuracy above 0.90 (classes 1, 13 and 16), others have lower accuracy (classes 7, 25 and 28, range: 0.68-0.75). This is probably due to the very distinctive characteristics of nestling in specific classes (e.g. small size of nestlings in class 1; starting of emergence or unsheathing of pins in classes 13 and 16) and the less obvious in others, as the degree of change varies during development stages.

Nevertheless, by adopting a protocol with 12 day visit intervals, nestling age can be determined to within 3 days with an accuracy of 0.85 to 0.99, with only two visits to the nest (Table 3.5). The first visit should be made during the first 12 days since hatching, to allow for a second visit before fledging in order to confirm or adjust age with high level of accuracy (>0.85). If nests are only visited after day 12, accuracy will be at least 0.94 until day 18 and at least 0.87 until day 21, although in these cases a second visit at the suggested 12 day interval would not improve accuracy (Table 3.3, Table 3.5). However, by determining hatching via observation of provisioning (i.e. adults entering the nest cavity carrying food items), a visit to the colony at 12 days intervals ensures that nests can be visited within the 12 first days since hatching.

Table 3.5. Key to attain highest accuracy in age assignment of bee-eater nestlings on a 12-day interval visit schedule. Correction on the second visit following potential misclassifications during the first visit, in accordance with most likely miss-assigned classes from Table 4.

Real age class	Assigned as (during 1st visit)	Accuracy	Visit 12 days later
1	1	0.93	confirm age estimation with 0.94 accuracy as real class is 13
	4	-	adjust age with 0.94 accuracy as real class is 13
	7	-	
4	4	0.84	confirm age with 0.99 accuracy as real class is 16
	1	-	adjust age with 0.99 accuracy as real class is 16
	7	-	
7	7	0.68	confirm age with 0.87 accuracy as real class is 19
	1	-	adjust age with 0.87 accuracy as real class is 19
	4	-	
10	10	0.85	confirm age with 0.84 accuracy as real class is 22
	4	-	adjust age with 0.84 accuracy as real class is 22

Overall, nestling age could not be estimated with the same accuracy throughout the growth period. It may thus be advantageous to visit nests for age estimation in periods that have the highest accuracy (classes 1, 13 and 16). In bee-eaters, we found the optimal period for aging nestlings to be between days 13-18 (with accuracy between 0.94 and 0.99, Table 3.3). During this period, the status of feather development is more easily distinguishable from the preceding and subsequent age classes, once there is an evident growth of pins and unsheathing of body feathers as feather colours become gradually more visible. During the first 3 days after hatching (class 1), nestlings can also be aged with high accuracy (0.93, Table 3.3), which is similarly to several passerine species (Brown and Alianell 2017). The small size of the nestling in relation to the eggs and the nestling inability to raise the head during these first days allow clear discrimination from the subsequent classes.

Aging of nestlings between 7-9 days old was most challenging and these were frequently misclassified (always as underestimation of class 4, Table 3.4). This is likely due to slow growth, and thus the lack of evident size differences between these age classes, which are only distinguishable by the appearance of a light grey coloration of the flight feathers tracts (indicating the emergence of the pins) on nestling of class 7. Additionally, the oldest bee-eater nestlings (classes 25 and 28) were frequently misclassified, similarly to what was reported in Common terns (*Sterna hirundo*, Wails et al. 2014), Eastern bluebirds (*Sialia sialis*, Wilkins and Brown 2015), House wrens (*Troglodytes aedon*, Brown et al. 2013) and Carnaby's cockatoos (*Calyptorhynchus latirostris*, Saunders et al. 2015).

In bee-eaters, the underestimation of these classes likely occurred due to the difficulty in observing the featherless patches in the ventral and anal regions, and the unsheathing of rectrices, which are characteristic of age class 25. These skin patches are only visible when nestlings are optimally positioned towards the camera. Given their age and relatively high mobility, this is more easily achieved in the field rather than in the still images displayed during the validation exercise.

The observers' ability to correctly assign age during the final stages of development might also have been influenced by variable growth rates between nestlings from different nests which were of the same age class. Differences in development rates between broods are more apparent at older ages due to several factors. Food provisioning to growing nestlings, mediated by presence of helpers (Fry 1984), and suitable weather conditions for flying insects (Arbeiter et al. 2016) are known to influence growth rate and survival of bee-eater nestlings. However, it is unlikely that weather conditions limited food availability during our study, as mean maximum temperatures were above 29°C and total precipitation below 5mm, throughout the nestling provisioning period (June/July, IPMA weather reports; Arbeiter et al. 2016). Number of nestlings per nest, paired with sibling competition, also creates additional variation in individual nestling development (Lessells and Avery 1989). However, it was not possible to account for the number of nestlings in each brood and nestlings from larger broods may develop slower than nestlings from smaller broods (Nilsson and Gårdmark 2001). Although between-brood variation of development rates might not be an issue for direct observations in the field, intra-brood variation can be relevant, as younger nestlings may develop at a slower rate than first hatched nestlings (Bryant and Tatner 1990). It is therefore recommended that the larger nestling(s) (i.e. first hatched) is targeted on each visit, in order to minimize potential differences of individual growth rates between siblings.

Although we did not find an increase in observer experience during our test trials, the percentage of correct estimations slightly increased from trial one to trial three (Figure S3.1). This suggests that training of observers can further increase age assignment accuracy, as indicated in other studies (Weinberg and Roth 1994; Brown et al. 2011; Wails et al. 2014). Longer training of the observers beyond a two minute period may further improve aging accuracy and is recommended for field studies.

It should also be noted that this test did not entirely replicate field conditions, as recorded images were displayed in a projector rather than being visualized in a laptop by the nest. In any case, besides outdoors conditions which will likely differ (e.g. temperature, light reflection) displaying projected images vs observing those in a laptop or other mobile electronic display is unlikely to increase error rate. Furthermore, when in the field, there can be ample opportunity to clarify any less obvious nestling characteristics in real time. During the experimental setup, observers were tested under stringent and fast-paced conditions, as observation time was limited to 40 seconds per photograph. It is likely that the method we propose may allow higher accuracy levels on age estimation, if observers are given enough time for detailed observation and evaluation, particularly for those age classes where lower accuracy was recorded. The images selected in the guide show (whenever possible) an example of the most and least developed phenotype within the class age days range, in order to further aid observers. In addition, the images are accompanied by a description of identifiable changes in the main developmental characteristics. The most reliable characters for age estimations are those that change at a faster rate. In the case of bee-eater nestlings this is feather development , similar to that reported in Eastern kingbirds (*Tyrannus tyrannus*) and Eastern phoebes (*Sayornis phoebe*, Murphy 1981), several species of North American passerines (Jongsomjit et al. 2007) and Barn swallows (*Hirundo rustica*, Fernaz et al. 2012). But the use of plumage development alone may lead to under- or over-estimations in age (Wails et al. 2014), as we observed in the two older classes and during the initial six days of development. Therefore, field observers should rely on a combination of developmental characteristics as much as possible (Fernaz et al. 2012; Wails et al. 2014), in order to increase the accuracy of age estimation. Considerable care must be taken when examining nests of bee-eaters, as pre-fledging nestlings and adults can get trapped in the tunnel while trying to flee the approaching camera. Thus, we recommend extra care when adults are present and to avoid nest inspection during the later stages of development whenever possible.

With this guide we were able to estimate the hatch date to within three days. We suggest visiting the colony and nests at 12 day intervals to achieve the highest accuracy metrics with the smallest disturbance and logistic investment. This study highlights how indirect methods and a simple protocol can be established and employed to quickly estimate nestling age in cases where nestling handling is complicated or impossible, while minimizing disturbance in and around the nest.

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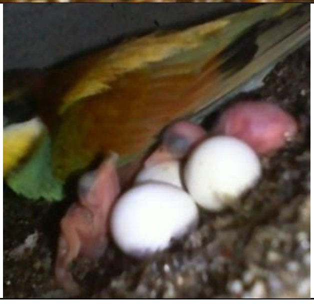
Supplementary material

Table S3.1. Photographic guide of bee-eater nestlings from hatch to fledging.

Development class (days)	**Image**	**Description**
1-3	 	**Head:** Hatchlings are blind (eyes are closed), completely naked and pink. The bill is small and pink with a grey tip. **Size/behavior:** Hatchlings have approximately the same size as an egg. They struggle to lift the head and belly.
4-6	 	**Size/behavior:** Nestlings are able to raise and support their head. Nestlings are now bigger, about 2x to 3x the size of an egg.
7-9		**Head:** The eyes begin to open. **Feathers:** Wings and tail area display a very light grey coloration, indicative of the subcutaneous alar pins (from where feathers will grow). Light grey coloration can also be visible in other parts of the body.

		
10-12	 	**Head:** The bill is longer than the rest of skull. **Feathers:** Alar pins are pressing on the skin surface: the light grey coloration on wings and tail is now dark grey. At the end of this stage, alar pins might start to emerge out of the skin.
13-15	 	**Head:** The bill is now predominantly grey and the throat is yellowish. **Feathers:** Alar pins have emerged out of skin and are clearly growing outside it. Dorsal and lateral pins also start to emerge in great number. Some feather tracts are unsheathing (colored tip at the end of some pins).

16-18	 	**Head:** Eyes are fully open. **Feathers:** Almost every part of the nestling is covered with pins, even the ventral area (but not around the cloaca). Many feathers are unsheathing; colors are more visible in the dorsal area and throat/chest region.
19-21	 	**Head:** The bill becomes black and dull. **Feathers:** Feathers continue to unsheathe and are now half grown (mainly the dorsal and wing coverts). Feather development in the head and ventral areas are delayed.
22-24		**Feathers:** Fist continuous patches of feathers (not pins) between back and wings and/or in the head.

		
25-27	 	**Head:** The bill is now shiny and the black stripe between eyes and bill is well defined. **Feathers:** Almost all feathers are fully grown, with some exceptions, usually around the cloaca or below the bill. Tail feathers might not be fully unsheathed.
28-30	 	**Feathers:** Plumage is now fully developed.

Table S3.2. Table illustrating the confusion matrix constructed for age class 7 as an example. Number in parenthesis exemplifies the number of images categorized as: true positive (TP), true negative (TN), false positive (FP) and false negative (FN).

		Image displayed - real age class (e.g. class 7)	
		Focal class (class7)	**Different class (any other class)**
Class assigned by observer	**Assigned as the focal class (class 7)**	TP - True positive (16)	FP - False Positive (4)
	Assigned as a different class (any other class)	FN - False negative (2)	TN - True negative (158)

Table S3.3. Overall confusion matrix comparing predicted age classes (rows) by the observers in the test, to the actual classes (columns) confirmed by nest inspection. Correct classifications are denoted in bold.

	1	**4**	**7**	**10**	**13**	**16**	**19**	**22**	**25**	**28**
1	**16**	3	1	0	0	0	0	0	0	0
4	1	**14**	10	4	0	0	0	0	0	0
7	1	1	**7**	1	0	0	0	0	0	0
10	0	0	0	**13**	1	0	0	0	0	0
13	0	0	0	0	**16**	0	0	0	0	0
16	0	0	0	0	1	**18**	2	0	0	0
19	0	0	0	0	0	0	**14**	5	0	0
22	0	0	0	0	0	0	2	**13**	3	1
25	0	0	0	0	0	0	0	0	**10**	7
28	0	0	0	0	0	0	0	0	5	**10**

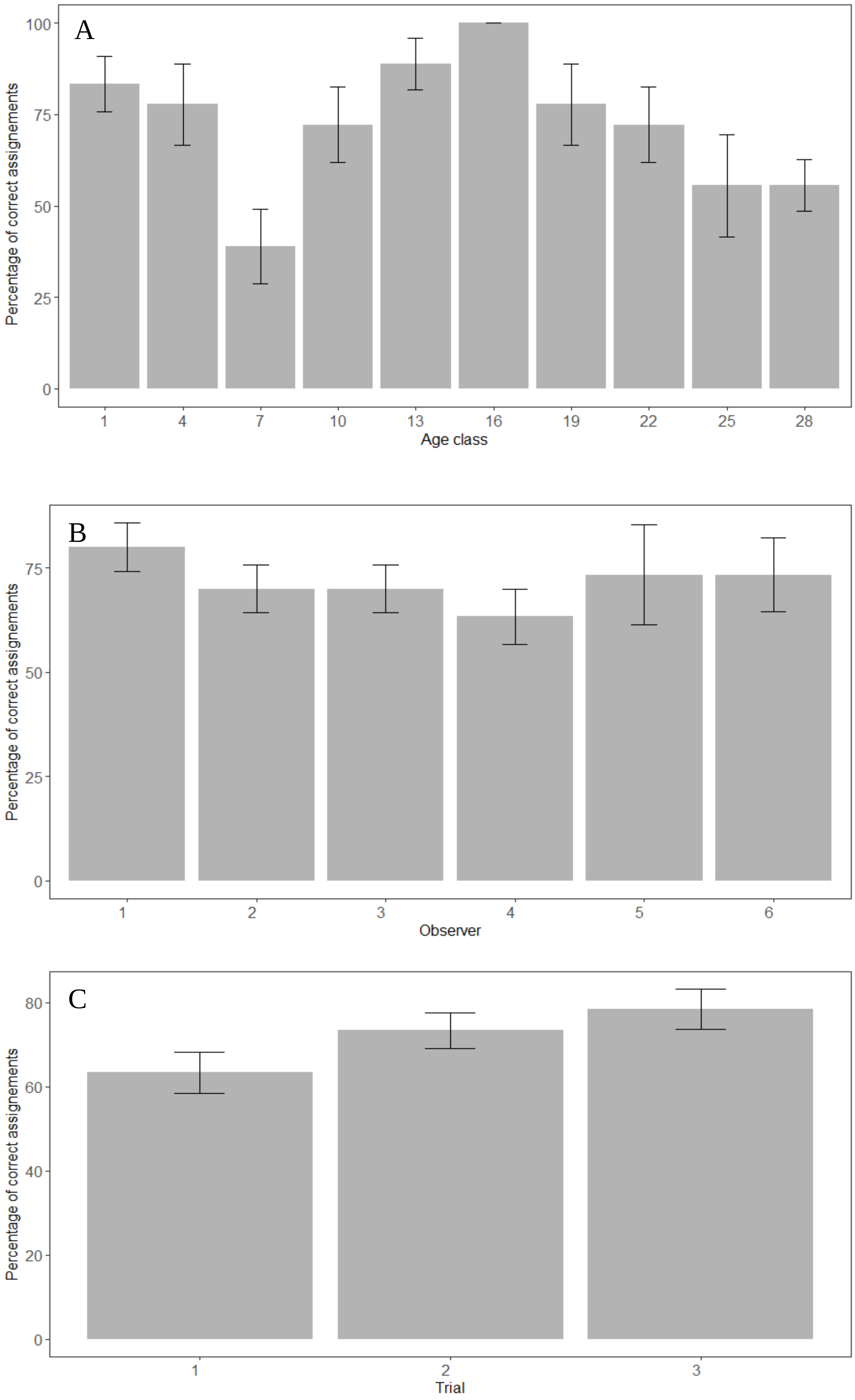
Table S3.4. Ranking of candidate models explaining the ability to predict bee-eater nestling age. AICc = Akaike information criterion for small sample size; ∆AICc = difference between AICc of the best model and reduced model; AICcw = Akaike model weights; loglik = log-likelihood; k = number of model parameters. Models with the lowest ∆AICc are shown in bold.

Model	AICc	∆AICc	AICc*w*	loglik	k
1 Class + (1|observer)	**206.54**	**0.00**	**0.690**	**-91.48**	**4**
2. Class + Trial + (1|observer)	**208.22**	**1.68**	**0.300**	**-90.01**	**5**
3. (1|observer)	216.77	10.23	0.004	-106.35	3
4. Trial + (1|observer)	218.23	11.69	0.002	-105.00	4

Table S3.5. Pairwise comparisons between trials following GLMM of the second top-ranked model: Class + Trial + (1|observer). Estimated differences (± SE) in the probability of a given observer providing a correct identification of age classes between trials for each pairwise comparison (row – column) are reported. No significant differences were found between trials.

	Trial 2	**Trial 3**
Trial 1	-0.08 (±0.08)	-0.13 (±0.08)
Trial 2		-0.05 (±0.07)

Figure S3.1. Variation on the mean percentage (±se) of correctly assigned estimates for age class (A, n=18), observer (B, n=30) and trial (C, n=10).



Chapter 4

Variation of parental and nestling diet in an opportunistic widespread avian insectivore

Joana S. Costa, José A. Alves

Abstract

Anthropogenic conversion of natural areas and intensification of agricultural practices have produced severe declines in insect abundance across the globe. This has direct consequences for many species, particularly those associated with grasslands that depend on invertebrate prey as their main food source. Although diet composition of bee-eaters is well studied in several parts of its range, diet studies are still scarce in Iberian Peninsula and none has assessed the variation of diet composition of birds breeding in different habitats and between age classes (i.e. adults and nestlings). In this study we explore temporal variation of adult bee-eater diet across the breeding season and between colonies located in distinct habitats. We also assess differences in the diet composition of nestlings and adults and investigate seasonal selectivity of adults and how selective they are when providing for their progeny. Finally, we explore the variability in the size of prey provided to nestlings thought their growth period. Hymenoptera and Coleoptera were the most important groups in the diet of both adults and nestlings. Our results show that the proportion of Hymenoptera in the diet is higher in colonies located in open habitats than in colonies surrounded by settlements and forest, where the proportion of Hymenoptera and Coleoptera in the diet is similar. This suggests that local prey availability strongly influences diet composition. Similarly, the seasonal differences found in the diet of adults are likely linked to prey availability and therefore insect phenology. Despite being opportunistic, adult bee-eaters provide nestlings with an increasing proportion of larger insects through development and seem to equally take Hymenoptera and Coleoptera for themselves and the nestlings, even when the abundance of this insects decreases, underlying the importance of these two insect orders for this opportunistic species.

Keywords: European bee-eater, *Merops apiaster*, habitat, seasonal variation, prey selection, prey availability

Introduction

Land-use changes and agriculture intensification are leading to declines in insect abundance across the globe (e.g. Fox et al. 2014; Grixti et al. 2009; Hallmann et al. 2017). This can be critical for bird species associated with grasslands that depend on invertebrate prey as their main food source (Chamberlain et al. 2000; Donald et al. 2006). A decline in the abundance and diversity of insects can lead to dietary shifts, potentially affecting breeding biology of birds (Britschgi et al. 2006; Rioux Paquette et al. 2014) and ultimately, scale up to influence demographic rates (Bowler et al. 2019). Furthermore, the interactions between birds and insects can be quite relevant and potentially influence ecosystems services, such as insect pollination (Abdu et al. 2012; Whelan et al. 2008). For example the widespread decline of bees, including honey bees, key pollinators (Pettis and Delaplane 2010; Potts et al. 2010) may even more noticeable if predators, such as bee-eaters (e.g. Fry 1983), target these species during the breeding season. Therefore, detailed knowledge on the diet composition of avian insectivores and its temporal and spatial variation is crucial in order to estimate the effects of future environmental changes on bird populations and inform the application of appropriate conservation measures.

Dietary opportunism is a common strategy adopted by several bird species (e.g. Rotenberry 1980; Post and Greenlaw 2006; Mohd-Azlan et al. 2014; Sherry et al. 2016). Foragers are considered opportunists when the composition of diet reflects the local availability of their food. Within the same species, diet can vary in space and time, being influenced by multiple factors including plant or/and prey phenology (Post and Greenlaw 2006), weather conditions (Arbeiter et al. 2016; Grüebler et al. 2008), geographic location (Duijns et al. 2013) and habitat type (Grüebler et al. 2008). Habitat type is a very strong predictor of opportunistic insectivores' diet, as prey abundance is often associated with vegetation diversity and land-use characteristics (e.g. Catry et al. 2014; Di Maggio et al. 2018). Seasonal variation in diet often follows prey phenology (e.g. Bellavance et al. 2011; Post and Greenlaw 2006), but preference or avoidance of certain insects will also influence diet composition (e.g. Kaspari and Joern 1993; Law et al. 2017). Individuals often select the most profitable prey to fulfil their energetic needs, and particularly during the breeding season, birds may select specific prey, in order to fulfil the high energetic requirements of reproduction (Naef-Daenzer et al. 2000; Wright et al. 2009). For example, males often provide more larger items to females than what they consume, before and during egg-laying (e.g. Avery et al. 1988). Nestling growth and development is similarly energetically demanding and provision of larger prey to nestlings than what adults consume, is also common (e.g. Kaspari and Joern 1993). For example, Great tits (*Parus* *major*) provide nestlings with larger caterpillars as soon as they become available, independently of their abundance (Naef-Daenzer et al. 2000); and Pied flycatchers (*Ficedula hypoleuca*) increase the size of prey provided to nestlings during growth (Wiebe and Slagsvold 2014).

The European bee-eater (*Merops apiaster*, hereafter bee-eater) is an opportunistic insectivore land-bird feeding mainly on medium to large-sized flying insects, with a marked preference for Hymenoptera. Nevertheless, its diet is quite broad and like many avian insectivores (Bellavance et al. 2011; Di Maggio et al. 2018; Post and Greenlaw 2006), bee-eaters are known to consume prey according to its availability (Fry 1984). Odonata and Coleoptera are usually well represented in bee-eaters' diet varying between 7-17% and 11-58%, respectively (Arbeiter et al. 2014; Costa 1991; Farinós-Celdrán et al. 2016; Fuisz et al. 2013; Inglisa et al. 1993; Kossenko and Fry 1998; Lourenço 2018), with Lepidoptera also being recorded as an important prey in several cases (10-12%, Krüger 2018; Lourenço 2018). Insects from other orders (e.g. Hemiptera, Diptera and Orthoptera) typically represent less than 10% of the diet. But bee-eater's preference for hymenopterans is clear, as this order seldom comprises less than 50% of its diet (e.g. Aissaoui-Marniche et al. 2007; Farinós-Celdrán et al. 2016; Kossenko and Fry 1998; Kristin 1994). Even when the availability of hymenopterans is low, bee-eaters can make this order its main food source (Inglisa et al. 1993).

Several studies have reported seasonal changes in diet of breeding bee-eaters (Kristin 1994, Inglisa et al 1993, Kruger 2018). These studies indicate that this species can take advantage of a peak of abundance of a particular prey (e.g. dung beetles Krüger 2018) or shift its diet, with adults increasing the consumption of bees and eating fewer dragonflies, during the nestling rearing period (Arbeiter et al. 2014). Other studies have reported differences in the type of prey consumed by adults and nestlings (Kristin 1994; Krüger 2018) and there is evidence that nestling bee-eaters consume larger prey than adults (Arbeiter et al. 2014; Massa and Rizzo 2002). But so far no study has explored the differences in selectivity between what adult bee-eaters consume and what is provided to nestlings. Potential differences between adult and nestling diet in terms of item size, but also in prey type, may be related to nutritional requirements of nestlings (Krebs and Avery 1984), but also to prey catchability (Brodmann and Reyer 1999). It is known that nutritional quality plays an important role in prey selection of insectivores (Razeng and Watson 2015), and for altricial birds it has been shown that the choice of food provided to nestlings by their parents, strongly influences nestling survival and/or the condition at fledging (Martin 1987; Wright et al. 2009). However, Krebs and Avery (1984) observed that bee-eaters do not feed exclusively on the most profitable prey and showed experimentally that nestlings grow more efficiently on a mixed diet of bees and dragonflies than on a pure diet of either. Additionally, at early developmental stages, nestlings may only be able to digest small and soft food items (Moser 1986). As their body size increases, total energy demand also increases and it may be more efficient to meet those demands with larger prey items (Brodmann and Reyer 1999; Kaspari and Joern 1993). Although several species have been reported to increase the size of prey provided to nestlings across the development period (e.g. Brodmann and Reyer 1999; Orłowski et al. 2015; Wiebe and Slagsvold 2014), only Kruger (2018) reported differences in dry weight of prey throughout nestling rearing period of bee-eaters in a colony at northern edge of distribution.

Being a widespread species in the Western Palearctic, bee-eaters breed in colonies surrounded by several habitats, foraging in open landscapes like grasslands, cultivated land or oak woods (Fry 1984). Bee-eaters catch their prey at a mean distance of 850 m from the nest, foraging preferentially in oak forests and riparian areas (Universidad de Extremadura 2006). Although diet composition of bee-eaters is well studied in several parts of its range (e.g. Arbeiter et al. 2014; Fuisz et al. 2013; Kossenko and Fry 1998), diet studies are still scarce in Iberian Peninsula (but see Costa 1991; Farinós-Celdrán et al. 2016; Herrera and Ramirez 1974; Lourenço 2018) and none has assessed diet variation between habitats and age classes (i.e. adults and nestlings) in this region. In this study we (1) first assess the temporal variation in the diet of adult bee-eaters during the breeding season and between colonies located in distinct habitats and (2) then explore differences between diet composition of nestlings and adults. In addition, we investigate (3) how diet selection of adults varies between two periods: before the start of incubation and during nestling rearing; and (4) explore the variation of prey size provided to nestlings throughout development.

Methods

Study area and habitat characterization

The study was carried out between April and July of 2016. We selected five bee-eater colonies surrounded by different habitats (Table S4.1). In each colony, we mapped the predominant habitat (habitat that occupied the larger area) and one or two secondary habitats (for more details see below and Table S4.1). Because bee-eaters catch prey in the vicinity of the colonies during breeding season (Fry 1984), we considered that the area within a 850 m radius from the colony as being representative of the average foraging range (University of Extremadura, 2006). We used Google Earth satellite images to create a digital habitat map of each study area. All habitats within 850 m radius from each colony were mapped using software QGIS version 2.18.24, confirmed by ground observation and subsequently adjusted if needed (i.e. if different from what was classified in the satellite image). We calculated the proportional area occupied by each habitat with the 850 m radius from the center of the colony (see Table S4.1), and named each colony according to its predominant habitat as follows: cork oak forest with extensive grazing (hereafter Oak-shrubland), cork oak forest with intensive grazing (hereafter Oak), irrigated pasture (hereafter Pasture), meadow and managed mixed forest (hereafter Forest).

Diet sample collection

Diet remains of bee-eaters were sampled at each colony during three periods: pre-incubation, incubation and nestling rearing period. Pre-incubation period is the time between the arrival of the first birds to the colony and the date of the first egg-laying. Incubation period was defined as the time from the first egg-laying until the first hatching and nestling rearing period as the time from the first hatching until the first nestlings fledge. Arrival of the first birds was determined using a sensor activated trail camera (model NUM'AXES 1027) placed at each colony well before birds arrive (10-20 days) and monitoring the main perches. Egg-laying dates were back-calculated from hatching dates (assuming 20 days of incubation), which was determined by nest inspection (Chapter 3).

Diet composition of adults was determined through analysis of pellets collected below perches, which had been placed in the colonies. At each colony, we collected several pellets every week, since arrival of the first birds to the end of the breeding season. We collected only intact pellets, ensuring these were freshly regurgitated. After each sampling session, we removed the remaining pellets and prey remains below the perches to avoid any mixing of pellets from previous sampling events. Prior to analysis, we randomly selected ten pellets from each colony and period (total thirty pellets per colony).

To assess diet composition of nestlings, we collected the nest debris from nests chambers after the nestlings had fledged, using a portable vacuum cleaner connected to a 2m hose. Prey remains from each nest were vacuumed into individual bags. Although some prey remains from the nest may belong to adults that regurgitated inside the nests during incubation, given the accumulation of a large amount of remains and the trampling of the earliest remains by the nestlings, we considered that such potential contamination was negligible. From Oak-shrubland and Pasture we sampled the content of ten nests, from Meadow, Forest and Oak we sampled seven, four and three nests, respectively. In order to standardize the volume of prey remains between nests we sub-sampled 20ml of prey remains from each nest sample.

Prey availability

In order to assess prey availability we performed 12 visual transects per colony and period (i.e. pre-incubation, incubation and nestling rearing), in which the insects we could visually detect were quantified. We focused on flying insects of the orders Coleoptera (beetles), Hymenoptera (bees), Orthoptera (grasshoppers), Hemiptera (true bugs and cicadas), which make up the majority of the bee-eater's diet previously recorded for Iberia (Costa 1991; Farinós-Celdrán et al. 2016; Herrera and Ramirez 1974). In Forest and Oak, prey availability was sampled only during rearing period. During each session, we performed eight visual transects in the predominant habitat and four transects in the secondary habitats of each colony. The starting point and direction of transects were randomly chosen within each habitat. Each transect consisted of 20 steps in a straight line and at constant speed while, counting all visible insects within three meters. Detected insects were classified as belonging to order Hymenoptera, Hemiptera, Coleoptera and Orthoptera. We did not consider the order Dermaptera because these insects were difficult to detect using this sampling method. Transects were made only during late morning (10:00-12:00), in days where min air temperature was above 25°C and without wind (Arbeiter et al. 2016, Grüebler et al. 2008).

Prey size during nestling rearing

In order to explore the variation in the size of prey provided to nestlings, we made observations of adult bee-eaters bringing food to their nestlings in three colonies: Oak-shrubland, Pasture and Meadow. The age of nestlings was assessed at each colony using a photographic guide for aging bee-eater nestlings (Chapter 3) and nests were classified in four classes of development (weeks 1-4). Incubating nests were classified as week zero. Prey observations were made each 3rd to 4th day in each colony during 15 minutes (totalling 240 minutes). During each observation a telescope was focused (zoom 30x) on one particular perch, where adults stop with prey on their bill before delivering it to nestlings. Bee-eaters are usually single-prey loaders carrying only one prey item during each feeding event (Fry 1984). This allowed observing the single item each bee-eater was carrying before it was taken to the respective nest. Each prey item was classified according to its relative length compared to the bill of each adult bee-eater. We defined that size “S” as a small dot in the tip of the bill; Size “M” corresponded to a prey up to half the size of the bill and “L” corresponded to a prey more than half the length of the bill.

Diet reconstruction

Prey remains from pellets and nest contents were sorted and identified with a magnifier to the level of order, and when possible to family, genus or species. To identify prey items we used mainly head parts (Hymenoptera, Hemiptera), wings or elytra (Coleoptera), mandibles (Orthoptera) and cerci (Dermaptera). Prey fragments were subsequently matched to determine the minimum number of individuals per prey category. We considered each head and a pair of wings, elytra, cerci or mandibles as one individual. We identified prey items with the help a guide (Chinery 2007) and a reference collection. In total, 15 prey categories were identified belonging to five insect orders: Hymenoptera, Coleoptera, Hemiptera, Dermaptera and Orthoptera. Among the Hymenoptera, we were able to assign insects to four families (Apidae, Vespidae, Formicidae and Scoliidae) and one species (*Apis mellifera*), that was considered as a separate category. From Coleoptera, we assigned insects to five families (Carabidae, Scarabaeidae, Curculionidae, Staphylinidae and Silphidae) and within Hemiptera we identified insects belonging to family Cicadidae. The prey items from Hymenoptera, Coleoptera and Hemiptera that we could not identify further than order level were respectively grouped as “other” (Table S4.2-4.4).

Statistical analysis

The diet composition was assessed as the total number, mean, standard deviation and relative frequency (number of items of a prey category divided by the total number of items). For statistical analysis, we considered only the orders comprising more than 4% of bee-eaters diet (Hymenoptera and Coleoptera). Among those, we included in the analysis only the families/species present in more than 4% of general diet of both adults and nestlings. Taxa under 4% were pooled together in the category “other” of the respective order. Therefore, we grouped Formicidae with other Hymenoptera. Similarly, the families Curculionidae, Silphidae and Staphylinidae were pooled together with other Coleoptera.

In order to test differences in diet composition between colonies we performed a Kruskal-Wallis for each prey category, having number of insects as dependent variable and colony as independent variable.

We tested for seasonal differences in the diet composition of adult bee-eaters by performing a generalised linear mixed model (GLMM, family *quasi-poisson*) for each prey category using R-package “MASS” (Venables and Ripley 2002). We defined period as fixed factor and colony as random factor. Pairwise post-hoc Tuckey comparisons were performed with R-package “emmeans” (Lenth 2016). Given that the 20 ml sub-sample of each nest content corresponded to a larger amount of prey remains compared to the volume of each pellet, in order to explore differences between diet of nestlings and adults we calculated the relative frequency of each prey category recorded in each nest content and pellets. Then, we performed a beta general linear model suitable for proportional data (bounded between 0 and 1) using R-package “betareg” (Grun et al. 2012). We defined prey category as a response variable and age class as independent variable.

To assess diet preferences we used Jacob’s selectivity index (Jacobs 1974) comparing the proportion of prey consumed with the proportion of the prey available: $I= (r-p)/(r+p-2rp)$, where r is the relative abundance in the diet and p is the relative abundance in the environment. Jacob’s Index varies from -1 (negative selection: prey consumed in lower proportion than what is available) to +1 (positive selection: prey consumed in higher proportion than what is available). Values of zero indicate that prey is selected in similar proportion than what is available in the environment. We calculated Jacob’s selectivity index for adults and nestlings considering the orders that were both sampled in the diet and in the transects: Hymenoptera, Coleoptera, Hemiptera and Orthoptera. We considered only Oak-shrubland, Meadow and Pasture for index calculation as we did not sample prey availability in Oak and Forest during pre-incubation period. As prey availability of these four orders decreased across the season (see below, Figure 4.1), we calculated Jacob’s index for adults during the pre-incubation period, when prey availability was highest, and for adults and nestlings during rearing period, when the prey availability was lowest. This allowed investigating if selectivity of adult bee-eaters changed between those. The relative abundance in diet was calculated for each order as the mean of the relative frequencies of that order in pellets (adults) or nest content (nestlings). The relative abundance in the environment was calculated for each order as the weighted mean of the relative frequencies recorded across the considered habitats in each colony.

In order to investigate if the size of prey provided to nestlings changed throughout the rearing period we performed a chi-square test on the proportion of different prey sizes across the sampling days.

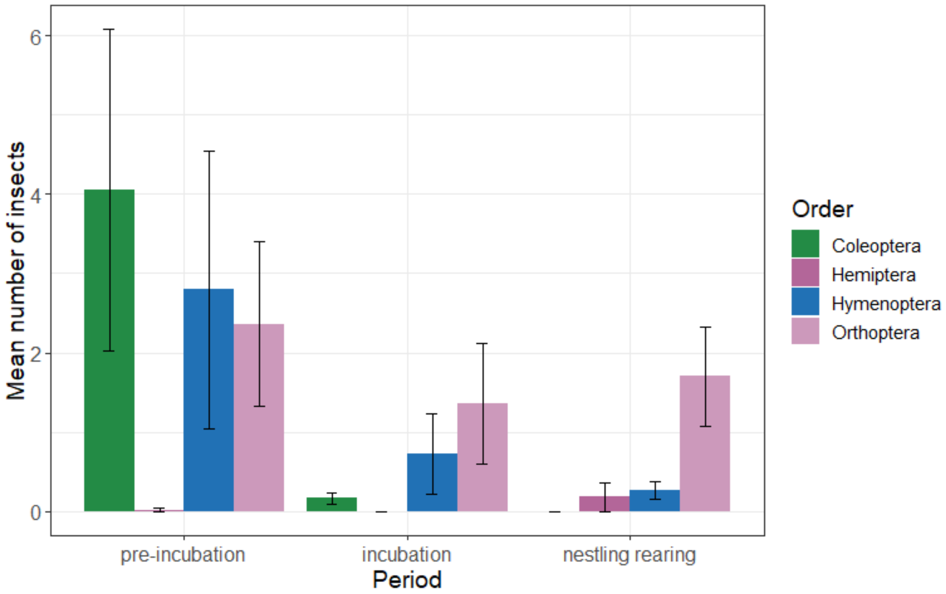


Figure 4.1. Insect availability recorded by visual transects across three sampling periods (pre-incubation, incubation and, nestling rearing) during bee-eater breeding season.

Results

Seasonal variation in adult diet

In general, prey composition varied between periods (i.e. pre-incubation, incubation and nestling rearing) with adult bee-eaters consuming different numbers of each prey category throughout the breeding season (Table 4.1, Figure 4.2). Overall, the mean number of Carabidae increased, whilst the consumption of Scarabaeidae and *Apis mellifera* decreased during incubation and nestling rearing, respectively. Other Hymenoptera were preyed in lowest proportion during incubation. We did not find any significant seasonal variation in Apidae, Vespidae and other Coleoptera (Table 4.1, Figure 4.2).

Table 4.1. Results of GLMM testing differences between main insect taxon consumed by adult bee-eaters across three periods of the breeding season (pre-incubation; incubation; nestling rearing). For post-hoc comparisons see Figure 4.2. Only those taxon representing 4% or more of diet composition are included in this analysis.

		Fixed effects				Random effect (Local)	
Prey categories		Est	SE	t	P	SD intercept	SD residual
Apis mellifera	intercept	2.067	0.154	13.399	0.000	0.239	2.154
	incubation	-0.017	0.154	-0.112	0.910		
	nest. rearing	-0.596	0.182	-3.264	**0.001**		
other Apidae	intercept	0.614	0.282	2.176	0.031	0.374	2.152
	incubation	0.132	0.304	0.434	0.664		
	nest. rearing	0.320	0.292	1.096	0.274		
Vespidae	intercept	-2.035	0.509	-3.995	<0.001	0.555	1.148
	incubation	0.738	0.531	1.391	0.166		
	nest. rearing	0.921	0.516	1.782	0.076		
other Hymenoptera	intercept	0.523	0.335	1.560	0.120	0.562	2.001
	incubation	-1.768	0.547	-3.231	**0.001**		
	nest. rearing	-0.321	0.322	-0.996	0.320		
Carabidae	intercept	-0.715	0.639	-1.118	0.265	1.083	2.293
	incubation	0.578	0.469	1.232	0.219		
	nest. rearing	1.077	0.435	2.476	**0.014**		
Scarabaeidae	intercept	1.182	0.686	1.722	0.087	1.398	3.024
	incubation	-0.742	0.309	-2.399	**0.017**		
	nest. rearing	-0.892	0.325	-2.737	**0.007**		
other Coleoptera	intercept	0.187	0.170	1.099	0.271	0.299	3.270
	incubation	-0.115	0.151	-0.761	0.446		
	nest. rearing	-0.194	0.154	-1.258	0.208		

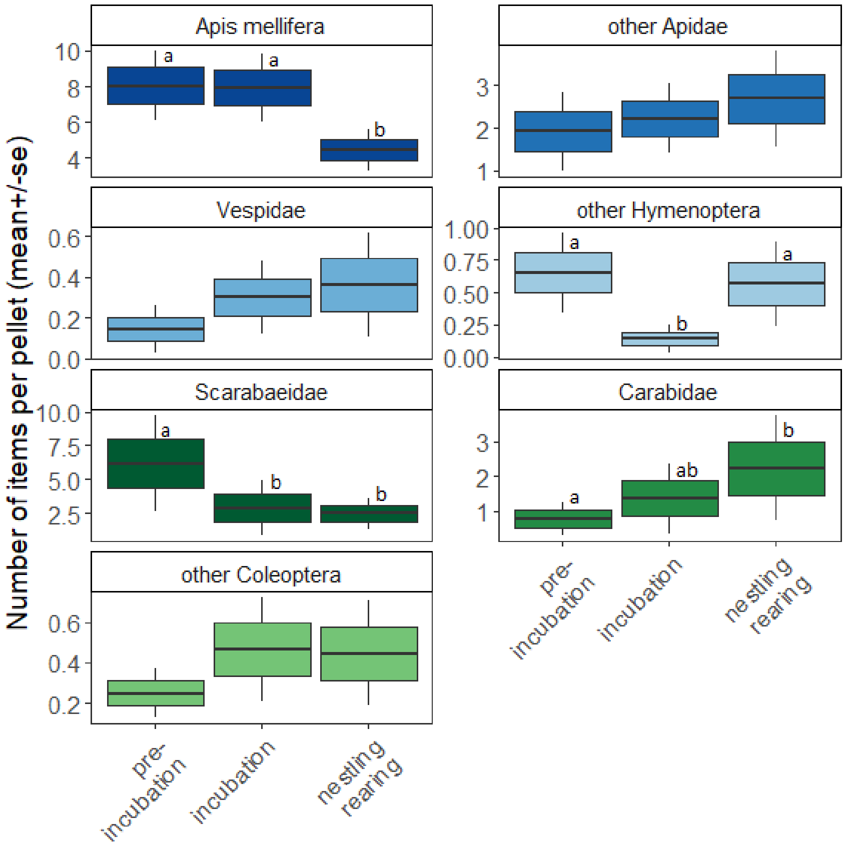


Figure 4.2. Variation on adult diet composition across three periods of the breeding season. Different letters indicate statistically significant differences from Tuckey post-hoc comparison, following GLMM (see Table 4.1). Prey taxa from order Hymenoptera are shown in blue and Coleoptera in green.

Diet composition at colonies in distinct habitats

Across all colonies bee-eaters fed mainly on Hymenoptera (adults: 58.8%, nestlings: 64.1%) and Coleoptera (adults: 37.6%, nestlings: 28.6%). Insects from orders Dermaptera, Hemiptera and Orthoptera were consumed in much lower proportions by both adults and nestlings (Table S4.2 and S4.4, Figure 4.3).

Overall, the proportions of Hymenoptera (42.4-55.7%) and Coleoptera (43.3-53.5%) consumed by bee-eaters at Oak, Pasture and Oak-shrubland colonies were similar, while at Meadow and Forest colonies Hymenoptera was by far the most preyed order (83.9% and 95.7%; Table S4.2, Figure 4.3A). Within the order Hymenoptera, adult bee-eaters preyed mainly on honeybee *Apis mellifera* (37.3%) and other species from family Apidae (12.5%), while among the order Coleoptera, families Scarabaeidae (21.0%) and Carabidae (8.0%) were the most consumed taxa by adults (Table S4.2, Figure 4.3A).

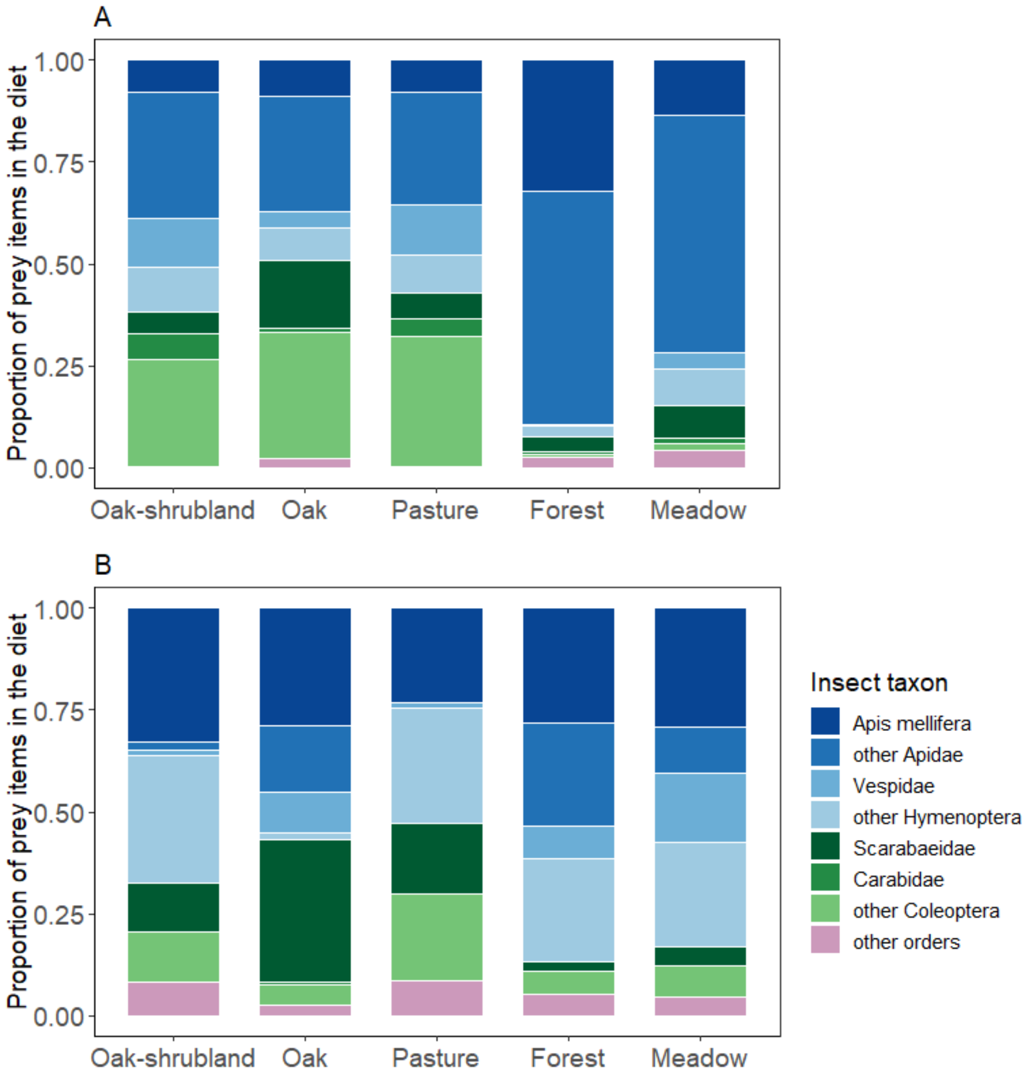


Figure 4.3. Variation in the proportion of items from several insect taxon (orders, families and *Apis mellifera*) found in the diet of (A) adult (from pellets) and (B) nestling (from nest content) bee-eaters across five colonies in distinct habitats. Taxa representing 4% or less of diet composition are pooled in “other orders”.

We found significant differences between colonies in the number per pellet of hymenopterans (*Apis mellifera*: Kruskal-Wallis chi-squared = 11.12, df = 4, p-value = 0.024; Apidae: Kruskal-Wallis chi-squared = 22.65, df = 4, p-value < 0.001; Vespidae: Kruskal-Wallis chi-squared = 11.08, df = 4, p-value = 0.025) and coleopterans (Carabidae: Kruskal-Wallis chi-squared = 17.31, df = 4, p-value = 0.001; Scarabaeidae: Kruskal-Wallis chi-squared = 59.80, df = 4, p-value < 0.001; other Coleoptera: Kruskal-Wallis chi-squared = 22.26, df = 4, p-value < 0.001) consumed by adults. The number of other hymenoptera (Kruskal-Wallis chi-squared = 3.54, df = 4, p-value = 0.470) consumed was small and did not differ between colonies (Figure 4.4A).

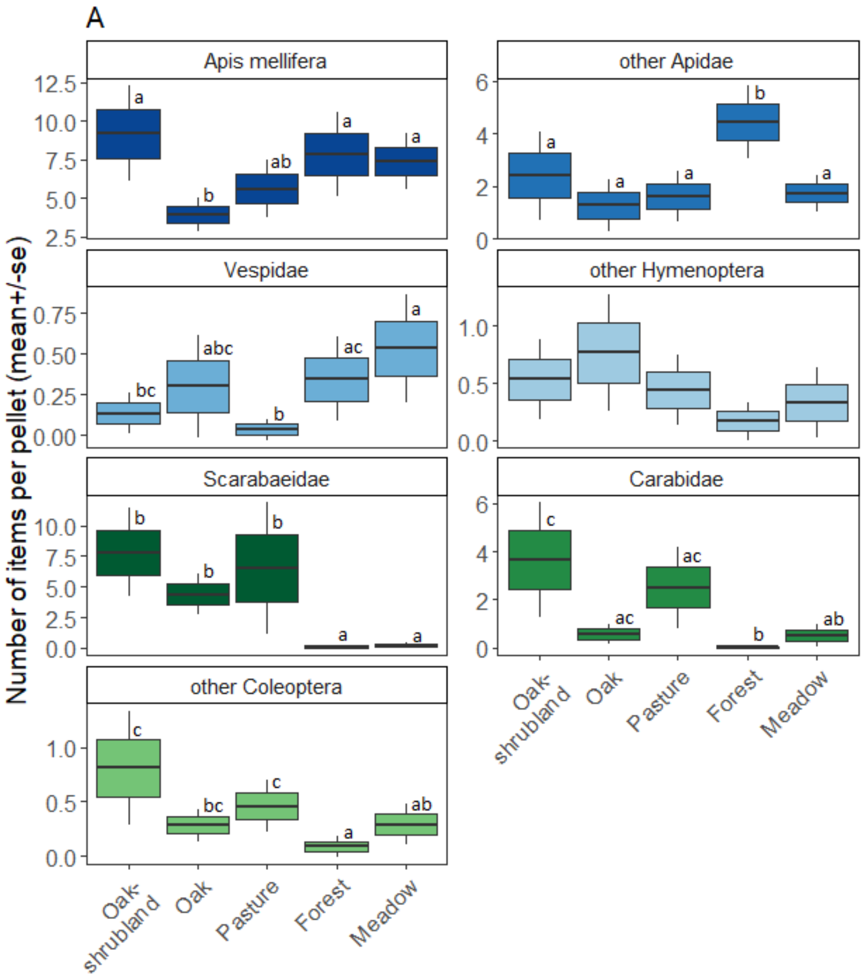


Figure 4.4. Variation in the diet composition of adult (top) and nestling (bottom) bee-eaters across five colonies in distinct habitats. Different letters indicate statistically significant differences obtained from Dunn post-hoc comparisons. Prey taxa from order Hymenoptera are shown in blue and Coleoptera in green.

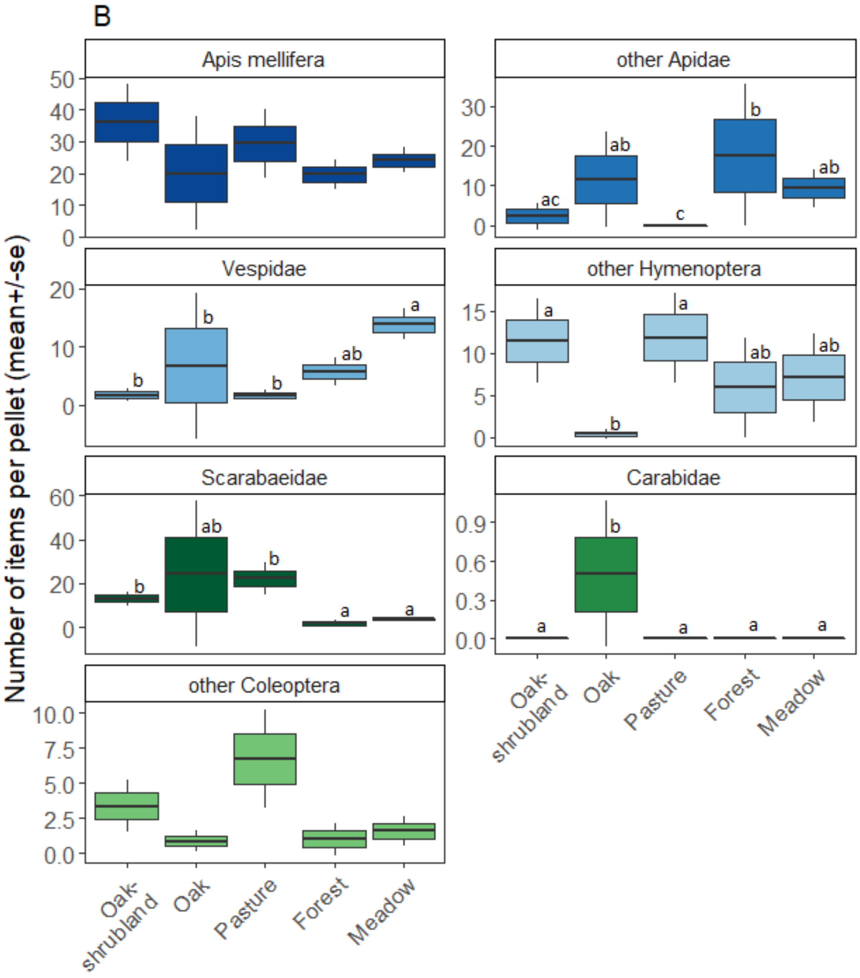


Figure 4.4. *continued*

Similarly to adult diet, Hymenoptera (52.6-86.6%) and Coleoptera (8.1-40.6%) were the main prey recorded in the diet of nestlings (Table S4.4, Figure 4.3B). Hymenoptera comprised more than 50% of the diet in all colonies with the highest proportions recorded at Meadow and Forest, as was the case for the adults (83.2%, 86.66%; Table S4.4, Figure 4.3B). Overall, when considering the order Hymenoptera, nestlings were mainly fed with honey bees (27.8%) and other Hymenoptera (22.7%). Among the order Coleoptera, Scarabaeidae (14.3%) and other Coleoptera (12.8%) were the main prey categories (Table S4.4, Figure 4.3B). We found significant differences between colonies in the consumption of hymenopterans (other Apidae: Kruskal-Wallis chi-squared = 18.74, df = 4, p-value < 0.001; Vespidae: Kruskal-Wallis chi-squared = 16.61, df = 4, p-value = 0.002, other hymenoptera: Kruskal-Wallis chi-squared = 14.08, df = 4, p-value = 0.007) and Scarabaeidae (Kruskal-Wallis chi-squared = 17.43, df = 4, p-value = 0.001) by nestling bee-eaters. Carabidae was consumed only in pasture in very small proportions (Kruskal-

Wallis chi-squared = 15.46, df = 4, p-value = 0.003). *Apis mellifera* was consistently consumed in high numbers in every colony (Kruskal-Wallis chi-squared = 4.16, df = 4, p-value = 0.384), and other Coleoptera was also an important part of nestlings diet (Kruskal-Wallis chi-squared = 1.75, df = 4, p-value = 0.781, Figure 4.4B).

Differential diet of adults and nestlings

We found significant differences in the proportions of prey taxa consumed by adults and those provided to nestlings, with the latter being fed a higher proportion of Vespidae (p = 0.01), other Hymenoptera (p < 0.001), Scarabaeidae (p = 0.01) and other Coleoptera (p = 0.03, Table 4.2). We did not find significant differences in the proportions of *Apis mellifera*, Apidae and Carabidae between adult and nestling diet, (Table 4.2, Table S4.3 and S4.4). In addition, prey sizes provided to nestlings differed during the nestling rearing period, with a higher proportion of smaller insects (size S) being recorded when most nestlings were very young (development weeks 1 and 2). But, as more nests had older nestlings (development weeks 3 and 4), adults provided their offspring with insects of larger size (size L; X-squared = 162.56, p< 0.001; Figure 4.5).

Prey selectivity

Based on Jacob's Indices of similarity, the overall preferred insect taxa were Coleoptera, Hymenoptera and Hemiptera (Figure 4.6). During pre-incubation period, when prey availability was highest (Figure 4.1), adult bee-eaters positively selected Coleoptera, Hymenoptera and Hemiptera (Figure 4.6A). As prey availability decreased across the season (Figure 4.1), adult bee-eaters continued to positively select Coleoptera and Hymenoptera for both themselves and also to provide the nestlings. However, Hemiptera was only fed to young in higher proportions that what was available, and not for adult consumption, during nestling rearing. Although the availability of Orthoptera was high across the breeding season (Figure 4.1), it was always negatively selected (Figure 4.6B).

Table 4.2. Mean and standard deviation of the proportion of each insect taxon, given as relative frequency, in the diet of adults (n=50) and nestling bee-eaters (n=35). Beta GLM output, testing differences in proportions of each prey category between adults and nestlings. Only those taxon representing 4% of more of diet composition of nestlings and adults are included in this analysis.

	Adults		Nestlings		model output				
Prey category	mean	sd	mean	sd		Est.	SE	Z	P
Apis mellifera	0.34	0.30	0.27	0.11	intercept	-0.747	0.16	-4.65	$3.32e^{-06}$
					nestlings	0.09	0.24	0.39	0.69
other Apidae	0.19	0.23	0.05	0.09	intercept	-1.44	0.17	-8.13	$4.14e^{-16}$
					nestlings	-4.43	0.23	-1.8	0.06
Vespidae	0.02	0.05	0.05	0.07	intercept	-3.37	0.16	-20.05	$< 2e^{-16}$
					nestlings	0.51	0.19	2.63	**0.01**
other Hymenoptera	0.09	0.15	0.24	0.11	intercept	-2.30	0.17	-13.49	$< 2e^{-16}$
					nestlings	1.18	0.21	5.59	**<0.001**
Carabidae	0.07	0.15	0.01	0.02	intercept	-2.64	0.17	-14.74	$<2e^{-16}$
					nestlings	-0.36	0.21	-1.68	0.09
Scarabaeidae	0.11	0.15	0.13	0.11	intercept	-2.18	0.16	-13.49	$< 2e^{-16}$
					nestlings	0.56	0.20	2.71	**0.01**
other Coleoptera	0.09	0.17	0.13	0.08	intercept	-3.30	0.11	-28.85	$<2e^{-16}$
					nestlings	0.25	0.12	2.05	**0.03**

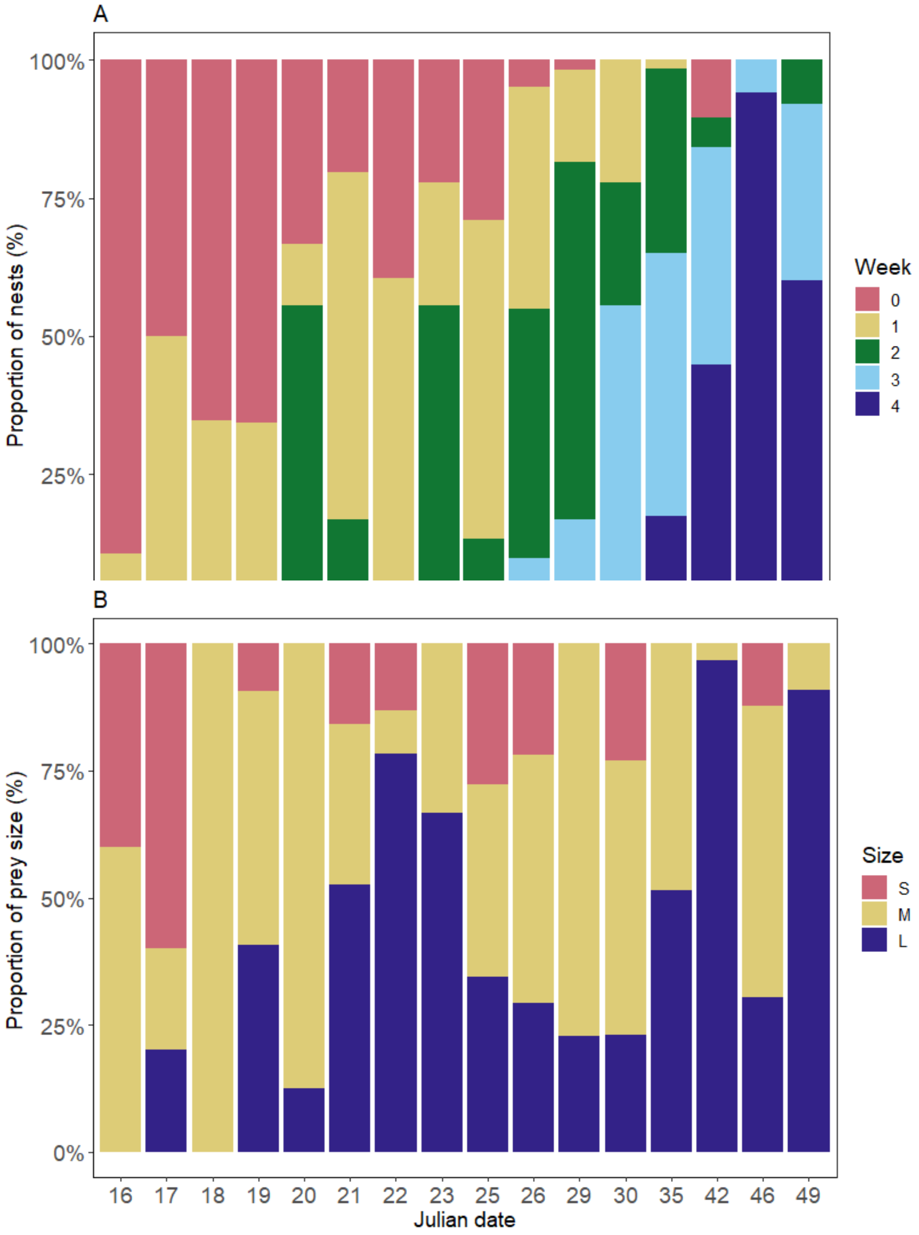


Figure 4.5. Proportion of: (A) nests with nestlings on different development weeks (week 1 to 4) recorded at each observation day (week 0 corresponds to incubating nests), and (B) prey of different size classes (S, M, L) recorded at each observation day during rearing of nestlings.

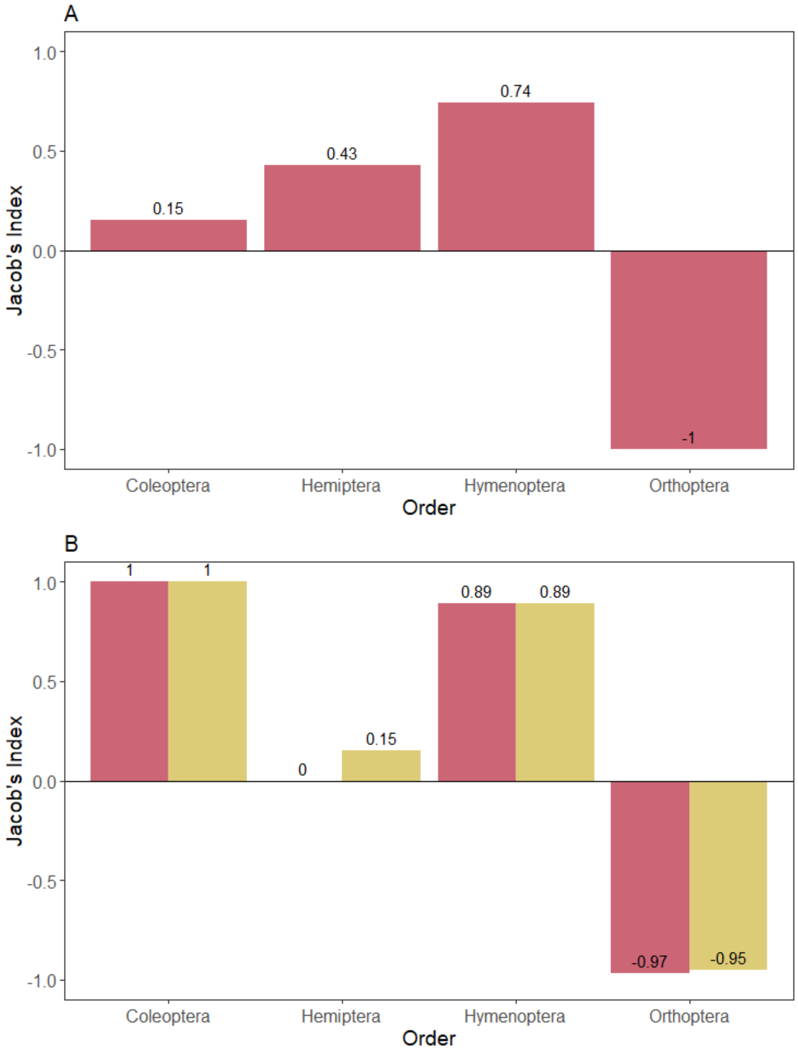


Figure 4.6. Selectivity (Jacob index) of adults (red) during: (A) pre-incubation, and (B) nestling (yellow) rearing.

Discussion

Bee-eater diet during the breeding season varies across colonies in distinct habitats, season and between what is consumed by adults and provided to nestlings. Overall, Hymenoptera and Coleoptera were the most important prey in the diet of both adults and nestlings. Our results show that the proportion of these taxa in colonies surrounded by settlements and forest is distinct from colonies located in open habitats, suggesting that prey availability in the vicinity of the colony strongly influences diet composition. Similarly, prey availability, likely linked to insect phenology, may cause the seasonal differences found in the diet of adults. Interestingly, and despite being opportunistic, as recorded in function of spatial and temporal variation in prey abundance, adult bee-eaters positively selected Hymenoptera and Coleoptera for themselves and to provide for nestlings, even when the availability of these insects was lower than other prey groups (i.e. Orthoptera and Hemiptera). Furthermore, bee-eaters seem selective, nor only regarding prey composition but also prey size, as adult also provide nestlings with an increasing proportion of larger insects through development.

Diet composition of adults and nestlings

Bee-eaters are known to feed on a wide range of flying insects, up to 300 insect species of 15 different orders (Fry 1984). The predominant prey recorded in our study was Hymenoptera (adults: 59%, nestlings: 64%) and the second most consumed prey was Coleoptera (adults: 37% nestlings: 28%), supporting what was previously described for the species in Iberia (Costa 1991). Hymenoptera and Coleoptera also formed the most abundant prey in other breeding populations across the species range, for example in Central Italy (65-70% and 17-25%, Inglisa et al. 1993), Sicily (67-96% and 2-19%, Massa and Rizzo 2002), Spain (45-85% and 6-30%, Herrera and Ramirez 1974), Southern France (58% and 32%, Christof 1990) and Central Asia (65% and 23%, Kossenko and Fry 1998). However, several studies from central Europe recorded lower proportions of Coleoptera (northern Germany: 5%, Krüger 2018; north-eastern Germany: 6%, Arbeiter et al. 2014; Hungary: 9%, Fuisz et al. 2013). This suggests that location and thus prey availability plays an important role on diet composition of bee-eaters, with Coleoptera possibly being more consumed at Mediterranean regions. Dragonflies (Odonata) play an important role in the diet of bee-eaters from north-eastern Germany (Arbeiter et al. 2014) as well as from France (Krebs and Avery 1985) and Hungary (Fuisz et al. 2013), but were completely absent in the diet at our study site. Given that occurrence of Odonata is associated with the availability of water bodies (Maravalhas and Soares 2013), and in our study sites these were scarce and dry in late spring, this could explain its absence. It should however be noted that Odonata have been recently recorded in the diet of bee-eaters in Portugal (13%, Lourenço 2018), but likely many were captured near aquatic habitats. Therefore, bee-eaters seem to be opportunistic at several spatial scales, between northern and southern breeding areas in Europe and even within the same region (Iberia), as demonstrated by our results.

Despite the vast majority of insects consumed belonging to Hymenoptera or Coleoptera (comprising 96% of adult diet and 93% of nestlings), bee-eaters also preyed on Orthoptera, Hemiptera and Dermaptera (adults: 4%; nestlings 7%). These orders have been previously recorded in the diet of bee-eaters (e.g. Costa 1991; Farinós-Celdrán et al. 2016; Herrera and Ramirez 1974; Inglisa et al. 1993; Massa and Rizzo 2002), but contrary to other studies we did not record the orders Diptera and Lepidoptera (e.g. Arbeiter et al. 2014; Fuisz et al. 2013; Lourenço 2018). However, these studies used a distinct sampling method (direct observation) that allows to identify large insects, like large butterflies, which are easily spotted in the bill of birds, whereas small insects may be overlooked (Arbeiter et al. 2014; Krüger 2018). In pellet analysis, all the insect groups whose soft bodies are highly digested will be under-represented, as is the case of Diptera and Lepidoptera. In fact, previous studies relying on the analysis of pellets recorded low proportion or absence of these two insect orders (Costa 1991; Herrera and Ramirez 1974; Kossenko and Fry 1998). In any case, the direct observations of insect size during nestling rearing, no medium or large Lepidoptera was recorded, which suggests that this order would be consumed or provided in low frequencies**.**

Dietary differences between adults and nestlings

Dietary differences between adults and nestlings are well documented for many insectivore species (Kaspari and Joern 1993; Moser 1986; Naef-Daenzer et al. 2000), including the bee-eater (Arbeiter et al. 2014; Kristin 1994; Krüger 2018; Massa and Rizzo 2002). The main differences found in previous studies on this species is in some cases the higher consumption of Odonata (Arbeiter et al. 2014; Massa and Rizzo 2002) or Lepidoptera (Krüger 2018) and in other cases, a lower consumption of Coleoptera (Kristin 1994) by nestlings. In our study, Vespidae, other Hymenoptera, Scarabaeidae and other Coleoptera had higher importance in the diet of nestlings than in adults, suggesting that adults were selectively providing their offspring with these taxa. Hymenoptera and Coleoptera have indeed high nutritional content (Razeng and Watson 2015) and it is likely that bee-eater nestlings grow more efficiently when feeding on mixed diet (Krebs and Avery 1984). But, selectivity was also found in terms of prey size. As several studies suggest, adult bee-eaters tend to feed their offspring with large items than what they consume (Arbeiter et al. 2014; Fry 1984; Kristin 1994; Massa and Rizzo 2002). This is not unusual in insectivorous birds feeding on flying insects as Tree swallows (*Tachycineta bicolor* ,McCarty and Winkler 1999), House martins (*Delichon urbica*, Bryant 1973) and Barn swallows (*Hirundo rustica,* Orłowski and Karg 2011), all showed a selectivity for larger prey when feeding young, even if smaller insects were more abundant. By directly observing the prey provided to nestlings, we recorded an increase in prey size across the rearing period, with younger nestlings receiving smaller items while older nestlings were provided with larger items. This indicates that larger items are not provided at high and similar proportions across the provision period, but that there is a gradual selection of larger items as nestlings develop and grow. This finding was contrary to what was reported in a colony at the northern edge of the species distribution, where the mean prey weight provided to nestlings decreased significantly as the nestling period progressed (Krüger 2018). The author explains this by an opportunistic strategy with adults increasing the feeding rate, independently of size of insects, in order to satisfy the ever growing demands of nestlings. However, similar to our findings, several other species are known to increase the size of prey provided to nestlings during development, for example Blue tits (*Cyanistes caeruleus*) and Pied flycacthers (Wiebe and Slagsvold 2014), Water pipits (*Anthus spinolleta*, Brodmann and Reyer 1999) and Barred warblers (*Sylvia nisoria*, Orłowski et al. 2015).

Habitat and seasonal diet variation

Many studies have linked the diet composition of birds to habitat type and land-use characteristics (Catry et al. 2014; Di Maggio et al. 2018; Orłowski and Karg 2011). Insect richness is known to increase with plant species richness, as a higher diversity of plants likely provides a more varied set of resources for a more diversified insect community (Haddad et al. 2001; Siemann et al. 1998). Therefore, native habitats with high plant diversity, like grasslands, likely harbour a higher richness of arthropods (Attwood et al. 2008; Grüebler et al. 2008; Söderström et al. 2001). In our study, we found clear differences in the diet composition of bee-eaters between colonies. More specifically, Hymenoptera was the predominant prey in Meadow and Forest colonies; while in the other colonies, bee-eaters consumed similar proportions of Hymenoptera and Coleoptera. This suggests that colonies in Oak, Oak-shrubland and Pasture habitats likely have higher plant diversity than the colonies in Meadow and Forest which also encompassed urban habitats, which may translate into higher diversity and abundance of insects overall, and of coleopterans in particular. These specific differences may also be related to the ecological requirements of the most consumed coleopteran families, as Carabidae are known to be more abundant in open habitats (da Silva et al 2008) and Scarabaeidae are usually linked to the presence of ruminants (e.g. cattle and sheep, Barbero et al. 1999), thus possibly explaining the higher availability and proportion of consumed Coleoptera in those three colonies. Meadow and Forest colonies did not have cattle or other grazing ungulates in the surroundings and were surrounded by settlements and mixed forest. This could have contributed to the lower availability of Coleoptera and therefore to a lower proportion of this order in bee-eaters' diet. Faced with a lack of coleopterans at Meadow and Forest colonies, bee-eaters consumed a higher proportion of hymenopterans. The consumption of honeybees is often dependent on the availability of beehives in the vicinity of colonies, and although it is a common taxon consumed both by adults and nestlings (e.g. Costa 1991), it does not always compose the main prey of bee-eaters (e.g. Fuisz et al. 2013). As reported by Galleoti and Inglisa (2001) bee-eaters prey on bees mainly in relation to their mean availability and in our study, the honeybee, *Apis mellifera*, was overall the most consumed Hymenoptera, as bee-eaters had access to beehives at less than 1km in all colonies. The exception was the Oak colony, where in fact the mean number of honey bees per pellet was lower in adults' diet.

Seasonal changes in the diet composition have been reported for many insectivore species (e.g. Rodríguez et al. 2010) with differences being often related to prey phenology (Bellavance et al. 2011; Post and Greenlaw 2006). The few studies that have focused on seasonal differences in the diet of bee-eaters (e.g. Arbeiter et al. 2014; Inglisa et al 1993; Krüger 2018) showed significant differences in diet composition across time, with a particular prey taxa being more predated in different periods. Although seasonal differences can be linked at some level to individual selectivity (Inglisa et al. 1993), prey phenology can also determine the availability and therefore the type of prey consumed at several stages of the breeding season. This was previously suggested by Kruger (2018) that reported bee-eaters consuming high proportion of dung beetles during one day when a mass occurrence of these insects was recorded. In our case, the mean number of Coleoptera consumed varied between periods, with Scarabaeidae decreasing and Carabidae increasing across the season. A peak in Scarabaeidae availability possibly occurred during April/May and its availability decreased across the season being potentially compensated with a moderate increase in the consumption of Carabidae. The intake of Vespidae also increased, consistent with the typical increase in abundance of this family towards the summer (Spradbery 1971). The decrease in the consumption of *A. mellifera* during nestling rearing is consistent to what was reported by Inglisa et al. (1993), although other two studies reported an increase of *A. mellifera* in the diet of bee-eaters across the breeding season (Galeotti and Inglisa 2001; Universidad de Extremadura 2007). Although Inglisa (1993) attributes the decrease in the consumption of honey bees to a depletion of bees due to bee-eaters intensive predation, this is unlikely to be a general case as several studies showed that bee-eaters do not negatively impact the survival or viability of bee-hives (e.g. Galeotti and Inglisa 2001; Massa and Rizzo 2002; Moreno-Opo et al. 2018), and the number of honey bees consumed by bee-eaters during breeding season seems to be negligible (Farinós-Celdrán et al. 2016; Galeotti and Inglisa 2001). Additionally, bee-eater predation on honey bees should not have a high impact on bees as it might depend on the availability of alternative prey. However, if natural food sources decrease at a local scale during breeding season, birds can be forced to increase honey bee consumption *in situ*, or to displace their foraging impact to other beekeeping areas, potentially having a negative effect on bee's populations.

Prey selection

Bee-eaters are known to be opportunistic but also to actively select hymenopterans, which are always predominant in diet samples across the breeding range (e.g. Aissaoui-Marniche et al. 2007; Farinós-Celdrán et al. 2016; Kossenko and Fry 1998; Kristin 1994). However, to assess prey selection it is necessary consider both diet and food availability and until now, only Inglisa et al. (1993) compared the diet of bee-eaters with prey availability, reporting selection of Hymenoptera during the entire breeding season, but of Coleoptera and Hemiptera only during the last weeks. Our results show a clear preference for Hymenoptera, Coleoptera and, to a lesser extent, for Hemiptera, disregarding Orthoptera whatever its availability. When food is abundant, aerial feeders are known to be selective but when is scarce, their selectively decreases (Lack and Owen 1955; McCarty and Winkler 1999). Interestingly, when facing a decrease in the availability of prey between pre-incubation and nestling rearing, bee-eaters continued to positively select Coleoptera and Hymenoptera. Coleopterans can be hard to digest due to its high proportion of chitin (Brodmann and Reyer 1999) but at the same time they are slow-flying insects and possibly easier to catch than fast-flying insects. Although Orthoptera was highly available during the entire breeding period, it was not selected by bee-eaters. This was not unexpected as bee-eaters are aerial feeders and grasshoppers are typically ground-dwelling insects. Hemiptera was positively selected during pre-incubation and during nestling reading, but consumed proportionally to its availability by adults during this latter period. This study shows that bee-eaters seem to equally select Hymenoptera and Coleoptera for themselves and nestlings throughout the breeding season, stressing the importance of these two insect orders for the species diet in Iberia, even at lower abundances.

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Supplementary material

Table S4.1. Description of each bee-eater colony, indicating its location and the type and proportion of the main and secondary habitats (when available), as well as, a description of the land-use characteristics surrounding each colony.

Colony		**Oak forest**		**Pasture**	**Meadow**	**Forest**
		Oak-shrubland	**Oak**			
Location		38.1°W, 7.0°W	38.7°N, -8.8°W	39.8°N, -7.1°W	38.6°N, -8.9°W	38.6°N, 9.1°W
Main Habitat	**Type**	Oak forest	Oak forest	Pasture	Meadow	Mixed forest
	Area (%)	88.98%	100%	91.27%	94.24%	100%
Secondary habitat 1	**Type**	shrubland (*Cistus ladanifer*)		pine forest (*Pinus pinea*)	Mixed forest	
	Area (%)	8.87%		6.61%	5.76%	
Secondary habitat 2	**Type**	Streams		water channels		
	Area (%)	2.15%		2.12%		
Land-use		Rotational grazing by cattle. Understory was always present in several patches during the study period.	Intensive grazing by cattle. No understory during the study period.	Extensive grazing by sheep. Irrigated only during Spring.	Meadow patches surrounded by a rural area. Hay harvested between May and June. Habitational area was not considered as potential foraging habitat.	Managed forest composed by pine and oak trees, eucalyptus and meadow patches. Surrounded by a large urban area and used as leisure space. Habitational area was not considered as potential foraging habitat.

Supplementary material Table S4.2. Diet composition of adult bee-eaters at five breeding colonies. Total number of prey items (sum), mean, standard deviation (sd) and relative frequency (FR) is shown for each insect taxon**.** For statistical analysis, only orders comprising more than 4% of bee-eaters diet (Hymenoptera and Coleoptera) and within those, only families/species present in more than 4% of the general diet of both adults and nestlings are considered.

	Oak-shrubland (n=30)				**Pasture (n=30)**				**Meadow (n=30)**			
	sum	**mean**	**sd**	**FR**	**sum**	**mean**	**sd**	**FR**	**sum**	**mean**	**sd**	**FR**
Hymenoptera	400	2.22	5.25	44.49	257	1.42	3.22	42.33	320	1.77	3.55	83.76
Apis mellifera	276	9.2	8.68	30.70	168	5.6	5.19	27.67	222	7.4	5.1	58.11
Apidae (others)	72	2.4	4.7	8.00	48	1.6	2.72	7.907	52	1.73	1.92	13.61
Vespidae	4	0.13	0.34	0.44	1	0.03	0.18	0.16	16	0.53	0.93	4.188
Formicidae	0	0	0	0	8	0.26	0.9	1.31	7	0.23	0.97	1.83
Hymenoptera (others)	48	1.6	2.6	5.33	32	1.06	2.27	5.27	23	0.76	2.31	6.02
Coleoptera	441	2.45	6	49.05	325	1.8	6.8	53.54	57	0.31	1.05	14.92
Carabidae	110	3.66	6.62	12.23	75	2.5	4.68	12.35	15	0.5	1.35	3.92
Curculionidae	38	1.26	4.26	4.22	2	0.06	0.25	0.32	4	0.13	0.57	1.04
Scarabaeidae	234	7.8	10.03	26.02	195	6.5	15.03	32.12	7	0.23	0.62	1.83
Silphidae	1	0.03	0.18	0.11	10	0.33	0.66	1.64	5	0.16	0.74	1.30
Staphylinidae	39	1.3	3.67	4.33	25	0.83	2.27	4.11	17	0.56	1.77	4.45
Coleoptera (others)	19	0.63	1.54	2.11	18	0.6	1.16	2.96	9	0.3	0.65	2.35
Dermaptera	47	1.56	5.02	5.22	10	0.33	0.99	1.64	0	0	0	0
Hemiptera	8	0.13	0.59	0.88	9	0.15	0.57	1.48	3	0.05	0.21	0.78
Cicadidae	3	0.1	0.54	0.33	1	0.03	0.18	0.16	0	0	0	0
Hemiptera (others)	5	0.16	0.64	0.55	8	0.26	0.78	1.31	3	0.1	0.3	0.78
Orthoptera	3	0.1	0.3	0.33	6	0.2	0.92	0.98	2	0.06	0.25	0.52

Supplementary material Table S4.2. *continued*.

	Forest (n=30)				Oak (n=30)				Total	
	sum	mean	sd	FR	sum	mean	sd	FR	sum	FR
Hymenoptera	382	2.19	4.52	95.73	234	1.3	2.71	55.71	1593	58.84
Apis mellifera	228	7.86	7.41	57.14	118	3.93	3.06	28.09	1012	37.38
Apidae (others)	129	4.44	3.79	32.33	38	1.26	2.8	9.04	339	12.52
Vespidae	10	0.34	0.72	2.50	9	0.3	0.87	2.14	40	1.47
Formicidae	10	0.34	1.17	2.50	0	0	0	0	25	0.92
Hymenoptera (others)	5	0.17	0.65	1.25	69	2.3	3.84	16.42	177	6.53
Coleoptera	14	0.08	0.46	3.50	182	1.01	2.52	43.33	1019	37.64
Carabidae	1	0.03	0.18	0.25	17	0.56	1.19	4.04	218	8.05
Curculionidae	2	0.06	0.37	0.50	1	0.03	0.18	0.23	47	1.73
Scarabaeidae	3	0.1	0.4	0.75	131	4.36	4.58	31.19	570	21.05
Silphidae	5	0.17	0.92	1.25	8	0.26	0.78	1.90	29	1.07
Staphylinidae	0	0	0	0	9	0.3	1.05	2.14	90	3.32
Coleoptera (others)	3	0.1	0.3	0.75	16	0.53	0.93	3.80	65	2.40
Dermaptera	0	0	0	0	1	0.03	0.18	0.23	58	2.14
Hemiptera	3	0.05	0.29	0.75	3	0.05	0.21	0.71	26	1.00
Cicadidae	0	0	0	0	1	0.03	0.18	0.23	5	0.18
Hemiptera (others)	3	0.1	0.4	0.75	2	0.06	0.25	0.47	21	0.77
Orthoptera	0	0	0	0	0	0	0	0	11	0.40

Supplementary material Table S4.3. Diet composition of adult bee-eaters during nestling rearing period. Total number of prey items (sum), mean, standard deviation (sd) and relative frequency (FR) is shown for each prey category and colony.

	Oak-shrubland (n=10)				**Pasture (n=10)**				**Meadow (n=10)**			
	sum	**mean**	**sd**	**FR**	**sum**	**mean**	**sd**	**FR**	**sum**	**mean**	**sd**	**FR**
Hymenoptera	94	1.56	3.99	31.97	97	1.61	3.42	63.39	95	1.58	2.58	85.58
Apis mellifera	51	5.1	4.3	17.34	49	4.9	5.4	32.02	59	5.9	2.99	53.15
Apidae (others)	34	3.4	7.58	11.56	23	2.3	3.68	15.03	25	2.5	1.71	22.52
Vespidae	1	0.1	0.31	0.34	0	0	0	0	9	0.9	1.37	8.10
Formicidae	0	0	0	0	8	0.8	1.47	5.22	0	0	0	0
Hymenoptera (others)	8	0.8	1.47	2.72	17	1.7	3.46	11.11	2	0.2	0.42	1.80
Coleoptera	179	2.98	6.00	60.88	43	0.71	1.71	28.10	14	0.23	0.56	12.61
Carabidae	85	8.5	9.61	28.91	20	2	3.74	13.07	4	0.4	0.69	3.60
Curculionidae	33	3.3	7.11	11.22	1	0.1	0.31	0.65	0	0	0	0
Scarabaeidae	46	4.6	5.2	15.64	10	1	1.05	6.53	5	0.5	0.97	4.50
Silphidae	0	0	0	0	5	0.5	0.84	3.26	1	0.1	0.31	0.90
Staphylinidae	4	0.4	0.96	1.36	6	0.6	0.699	3.92	1	0.1	0.31	0.90
Coleoptera (others)	11	1.1	2.6	3.74	1	0.1	0.31	0.65	3	0.3	0.48	2.70
Dermaptera	12	1.2	2.09	4.08	3	0.3	0.67	1.96	0	0	0	0
Hemiptera	6	0.3	0.92	2.04	5	0.25	0.71	3.26	0	0	0	0
Cicadidae	3	0.3	0.94	1.02	1	0.1	0.31	0.65	0	0	0	0
Hemiptera (others)	3	0.3	0.94	1.02	4	0.4	0.966	2.61	0	0	0	0
Orthoptera	3	0.3	0.48	1.02	5	0.5	1.58	3.26	2	0.2	0.42	1.80

Supplementary material Table S4.3. *continued*.

	Forest (n=10)				Oak (n=10)				Total	
	sum	**mean**	**sd**	**FR**	**sum**	**mean**	**sd**	**FR**	**sum**	**FR**
Hymenoptera	87	1.45	2.83	91.57	86	1.43	2.99	49.71	459	55.56
Apis mellifera	45	4.5	4.85	47.36	18	1.8	1.54	10.40	222	26.87
Apidae (others)	29	2.9	2.4	30.52	23	2.3	3.23	13.29	134	16.22
Vespidae	2	0.2	0.42	2.10	6	0.6	1.34	3.46	18	2.17
Formicidae	9	0.9	1.91	9.47	0	0	0	0	17	2.05
Hymenoptera (others)	2	0.2	0.63	2.10	39	3.9	5.56	22.54	68	8.23
Coleoptera	5	0.08	0.38	5.26	84	1.4	3.23	48.55	325	39.34
Carabidae	0	0	0	0	3	0.3	0.48	1.73	112	13.55
Curculionidae	2	0.2	0.63	2.10	0	0	0	0	36	4.35
Scarabaeidae	2	0.2	0.63	2.10	61	6.1	5.82	35.26	124	15.01
Silphidae	0	0	0	0	8	0.8	1.22	4.62	14	1.69
Staphylinidae	0	0	0	0	6	0.6	1.57	3.46	17	2.05
Coleoptera (others)	1	0.1	0.316	1.05	6	0.6	0.84	3.46	22	2.66
Dermaptera	0	0	0	0	1	0.1	0.31	0.57	16	1.93
Hemiptera	3	0.15	0.48	3.15	2	0.1	0.30	1.15	16	1.93
Cicadidae	0	0	0	0	0	0	0	0	4	0.48
Hemiptera (others)	3	0.3	0.67	3.15	2	0.2	0.42	1.15	12	1.45
Orthoptera	0	0	0	0	0	0	0	0	10	1.21

Supplementary material Table S4.4. Diet of nestling bee-eaters. Total number of prey items (sum), mean, standard deviation (sd) and relative frequency (FR) is shown for each prey category and colony. For statistical analysis, only orders comprising more than 4% of bee-eaters diet (Hymenoptera and Coleoptera) and within those, only families/species present in more than 4% of the general diet of both adults and nestlings are considered.

	Oak-shrubland (n=10)				**Pasture (n=10)**				**Meadow (n=7)**			
	sum	**mean**	**sd**	**FR**	**sum**	**mean**	**sd**	**FR**	**sum**	**mean**	**sd**	**FR**
Hymenoptera	742	12.36	17.06	67.57	732	11.09	16.29	52.66	412	11.44	10.55	83.23
Apis mellifera	360	36	19.65	32.78	323	29.36	18.54	23.23	145	24.1	4.85	29.29
Apidae (others)	22	2.2	5.57	2.00	0	0	0	0	56	6.33	5.88	11.31
Vespidae	17	1.7	1.63	1.54	18	1.63	1.43	1.29	83	13.83	3.31	16.76
Formicidae	53	5.3	2.7	4.82	73	6.63	4.65	5.25	2	0.33	0.81	0.40
Hymenoptera (others)	286	28.2	10.5	26.04	318	28.9	15.8	22.87	126	21	9.38	25.45
Coleoptera	265	4.41	6.59	24.13	540	8.18	12.78	38.84	60	1.66	2.42	12.12
Carabidae	0	0	0	0	0	0	0	0	0	0	0	0
Curculionidae	19	1.9	1.7	1.73	18	1.63	1.68	1.29	6	1	1.26	1.21
Scarabaeidae	130	13	4.98	11.83	244	22.1	12.27	17.55	22	3.6	0.81	4.44
Silphidae	0	0	0	0	0	0	0	0	0	0	0	0
Staphylinidae	0	0	0	0	0	0	0	0	0	0	0	0
Coleoptera (others)	116	11.6	6.7	10.56	278	25.27	10.15	20	32	5.33	2.73	6.46
Dermaptera	9	0.9	0.56	0.81	22	2	1.18	1.58	0	0	0	0
Hemiptera	65	3.25	2.26	5.91	36	1.6	2.25	2.58	18	1.5	2.19	3.63
Cicadidae	29	2.9	2.68	2.64	2	0.18	0.4	0.14	1	0.16	0.4	0.20
Hemiptera (others)	36	3.6	1.83	3.27	34	3.09	2.42	2.44	17	2.83	2.48	3.43
Orthoptera	17	1.7	1.05	1.54	60	5.45	3.32	4.31	5	0.83	0.98	1.01

Supplementary material Table S4.4. *continued*.

	Forest (n=3)				Oak (n=4)				Total	
	sum	**mean**	**sd**	**FR**	**sum**	**mean**	**sd**	**FR**	**sum**	**FR**
Hymenoptera	182	10.11	10.44	86.66	158	6.58	11.87	56.83	2226	64.13
Apis mellifera	59	19.66	4.04	28.09	80	20	18.38	28.77	967	27.85
Apidae (others)	53	17.66	15.85	25.23	46	11.5	12.26	16.54	177	5.09
Vespidae	17	5.66	2.08	8.09	27	6.75	12.84	9.71	162	4.66
Formicidae	0	0	0	0	0	0	0	0	128	3.68
Hymenoptera (others)	53	17.66	3.05	25.23	5	1.25	1.5	1.79	788	22.70
Coleoptera	17	0.94	1.79	8.09	113	4.7	15.25	40.64	995	28.66
Carabidae	0	0	0	0	2	0.5	0.57	0.71	2	0.057
Curculionidae	2	0.66	1.15	0.95	1	0.25	0.5	0.35	46	1.32
Scarabaeidae	5	1.66	1.52	2.38	97	24.25	34.09	34.89	498	14.34
Silphidae	0	0	0	0	4	1	1.15	1.43	4	0.11
Staphylinidae	0	0	0	0	0	0	0	0	0	0
Coleoptera (others)	10	3.33	3.21	4.76	9	2.25	2.21	3.23	445	12.82
Dermaptera	1	0.33	0.57	0.47	0	0	0	0	32	0.92
Hemiptera	7	1.16	1.47	3.33	3	0.27	0.74	1.07	129	3.71
Cicadidae	1	0.33	0.57	0.47	1	0.25	0.5	0.35	34	0.97
Hemiptera (others)	6	2	1.73	2.85	2	0.5	1	0.71	95	2.73
Orthoptera	3	1	1.73	1.42	4	1	2	1.43	89	2.56

Chapter 5

Range wide migration corridors and non-breeding areas of a northward expanding Afro-Palaearctic migrant, the European Bee-eater *Merops apiaster*

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Abstract

Across their ranges, different populations of migratory species often use separate routes to migrate between breeding and non-breeding grounds. Recent changes in climate and land-use have led to breeding range expansions in many species, but it is unclear whether these populations also establish new migratory routes, non-breeding sites and migration phenology.

Thus, we compared the migration patterns of European Bee-eaters *Merops apiaster* from two established western (n=5) and eastern (n=6) breeding populations in Europe, with those from a newly founded northern population (n=19). We aimed to relate the breeding populations to the two known non-breeding clusters in Africa, and to test for similarities of migration routes and timing between the old and new populations. Western Bee-eaters used the western flyway to destinations in West Africa; the eastern birds uniformly headed south to southern African non-breeding sites, confirming a complete separation in time and space between these long-established populations. The recently founded northern population, however, also used a western corridor, but crossed the Mediterranean further east than the western population and overwintered mainly in a new non-breeding area in southern Congo/northern Angola. The migration routes and the new non-breeding range overlapped only slightly with the western, but not with the eastern, population. In contrast, migration phenology appears different between the western and both the northern and the eastern populations, with tracked birds from the western population migrating earlier by 2-4 weeks. The northern population thus shares some spatial traits with western Bee-eaters, but similar phenology only with eastern population. This divergence highlights the adjustments in the timing of migration to local environmental conditions in newly founded populations, and a parallel establishment of new breeding and non-breeding sites.

Keywords: annual cycle, flyway, Meropidae, migratory connectivity, range expansion, timing of migration.

Introduction

Many long-distance migratory species have broad breeding distributions. As a result, various populations within the same species may use separate migratory routes to migrate between their breeding and non-breeding grounds. For example, Great Reed Warblers *Acrocephalus arundinaceus* and Common Reed Warblers *A. scirpa*ceus (Koleček et al. 2016, Procházka et al. 2018), Nightingales *Luscinia megarhynchos* (Hahn et al. 2013), or European Rollers *Coracias garrulus* (Finch et al. 2015) migrating between Europe and Africa, Swainson's Thrush *Catharus ustulatus* (Delmore et al. 2012) and Ovenbirds *Seiurus aurocapilla* (Hallworth et al. 2015) migrating between North and Central/South America, and Pintails *Anas acuta* (Hupp et al. 2011) and Bar-tailed Godwits *Limosa lapponica* (Battley et al. 2012) migrating between north east Asia and Australasia. Some of these migration corridors and non-breeding sites can be hundreds if not thousands of kilometres apart, with little or no overlap between populations.

Differences in migratory pathways in Holarctic species are likely to have arisen as relicts from the last glaciation, when species ranges contracted into refugia, before expanding again when the climate warmed (Newton 2008). Range expansions still remain common in birds today; prominent recent examples include Barn Swallows *Hirundo rustica* in the Nearctic/Neotropic (Winkler et al*.* 2017), and Scarlet Rosefinches *Carpodacus erythrinus* (Stjernberg 1985), Marsh Warblers *Acrocephalus palustris* (Leisler and Schulze-Hagen 2011) and Black-tailed Godwits *Limosa limosa* (Gunnarsson et al*.* 2012) in parts of the Palaearctic. Models on the impact of current climate change on bird distribution predict range shifts in many, and range expansion in some species (Huntley 2007). For migratory birds, it is often unclear how migratory behaviour might change during this process – will birds establish a new migratory corridor, or will they continue to fly along the same ‘ancient’ migratory routes? Furthermore, how quickly might they adapt their phenology to local conditions at new sites?

Migrating along different routes does not necessarily imply that the population is separated in their non-breeding ranges which would result in low migratory connectivity (Webster et al*.* 2002). Conversely, a spatial overlap in migratory routes does not necessarily mean that individuals from different populations meet each other, since final destinations and/or passage times can differ between populations, making encounters unlikely (Bauer et al*.* 2016). Understanding the level of spatiotemporal overlap in breeding, staging and non-breeding sites within and across populations can be used to understand the associated degree of migratory connectivity between populations to inform conservation planning (Dhanjal-Adams et al*.* 2017, Kramer et al*.* 2018).

Here, we investigate the migratory behaviour of three breeding populations of European bee-eater *Merops apiaster* (henceforth 'Bee-eater') along a West – North - East gradient in Europe. Bee-eaters are common in warm-temperate climates and their historical breeding distribution mainly encompassed Southern Europe delimited by the 21°July isotherm in the north (Fry 1984). In recent decades, the species has expanded its range northwards and successfully (re)colonized regions north of 47°N in central Europe, presumably benefiting from recent climatic niche expansions and land use changes (Kinzelbach et al*.* 1997, Huntley 2007). Currently, Bee-eaters form a viable breeding population with more than 1000 breeding pairs at about 51°N in central-eastern Germany (Schönbrodt and Schulze 2017). The origin(s) of founder individuals is unknown and the very few ring recoveries suggests an ongoing immigration from, or an exchange with, the southern-central European populations (Arbeiter et al*.* 2012).

Bee-eaters in the northern hemisphere are obligate long-distance migrants, and are thought to overwinter in two distinct regions: West Africa and southern Africa (Fry 1984). Surprisingly, population-specific non-breeding sites and individual migration routes remain almost unknown for the species. Recent studies on population genetics have revealed little differentiation between many European populations, pointing to historical and current exchange between populations (Ramos et al*.* 2016, Carneiro de Melo Moura et al*.* 2019). In contrast, the few ring recoveries (Ramos et al*.* 2016) and observations of Bee-eaters of unknown provenance point towards a classical migratory divide in European breeding populations, which either migrate along a western route via Iberia to west Africa, or an eastern route around the Mediterranean Sea and along the rift valley to south eastern Africa (Fry 1984), though recent genetic analyses also highlight panmixia (Carneiro de Melo Moura et al*.* 2019). The migratory divide is expected to occur in central Europe, with birds breeding in the Pannonian basin taking the easterly route and birds from France taking the westerly route. The breeding origin of the birds spending the non-breeding period in West Africa and southern Africa has not been identified yet, but likely follows these suggested western and eastern migration corridors.

In our study, we use geolocation to unravel the divergent migration corridors and the resultant disjunct non-breeding ranges of Bee-eaters from western and eastern European breeding populations (Fry 1984). Moreover, we compare migration patterns of these long-established populations with the migration corridor and non-breeding range of the recently founded northern population. We expected spatially divergent migration routes and non-breeding sites between the westernmost and the eastern European breeding populations, with no overlap and little within-population variation at continental scale (Fry 1984). Based on the currently known distant nonbreeding clusters, we expect the newly established northern population to overwinter in western Africa if these birds take the western flyway and in south-eastern Africa if they migrate along the eastern flyway. Additionally, we expect the timing of migration (i.e. departure from and arrival at residence sites) to be influenced by climatic seasonality and migratory distance, rather than by the migration corridor used (e.g. van Wijk et al*.* 2018). Thus, we expect the arrival and departure to differ between breeding regions (and thus study populations), but to be similar between populations in the same non-breeding region.

Methods

We used geolocation by light to track adult Bee-eaters from three distant and distinct breeding populations across the species' breeding range in Europe: a western breeding population in Portugal (PT; two colonies at about 39.9 and 38.1° N 7.15°W, less than 200km apart; n=5), an eastern population in Bulgaria (BG; 42.4°N 27.4°E; n=6) which is *c*. 2900 km from the western population; and a recently established northern population in Germany (DE; 51.3°N, 12.0°E; n=19) which is situated *c*. 2000 km and *c*. 1500 km from the western and the eastern populations, respectively (Figure 5.1).

Birds were captured in their nest burrows using walk-in traps (PT, DE) and mist-nets (BG) during the nestling rearing periods. Adult Bee-eaters were sexed and aged based on plumage characteristics (only for PT, DE; https://aulaenred.ibercaja.es/wp-content/uploads/284_Bee-eaterMapiaster.pdf). We equipped Bee-eaters with geolocators (SOI-GDL1/GDL2/GDL3-PAM; all Swiss Ornithological Institute) using a leg-loop harnesses made from Silicone or cord material. Geolocators including harnesses weighed between 0.84-1.56 g on average, representing 1.6-3.0% of adult body mass. Additionally, we established a control group, i.e. ringed-only birds, to check for geolocator effects on local site fidelity (PT and DE only). Local recapture rates of tagged birds varied largely between sites and years potentially according to site-specific capture effort (PT: 10%, DE: 8-14%, BG: 7%); recapture rates of controls were higher (PT: 28%, DE: 24-32%). The lower local recapture rates for tagged birds include breeding site dispersal to an unknown extent (Arbeiter et al*.* 2012). Birds from all three populations (PT, DE, and BG) were successfully tracked in 2015/16 resulting in 18 tracks and 21 non-breeding sites. We considered a longer time series to check for potential large variation in non-breeding locations in the northern population by including eight additional tracks from 2010/11, 2011/12, 2014/15 (DE only, Table 5.1).

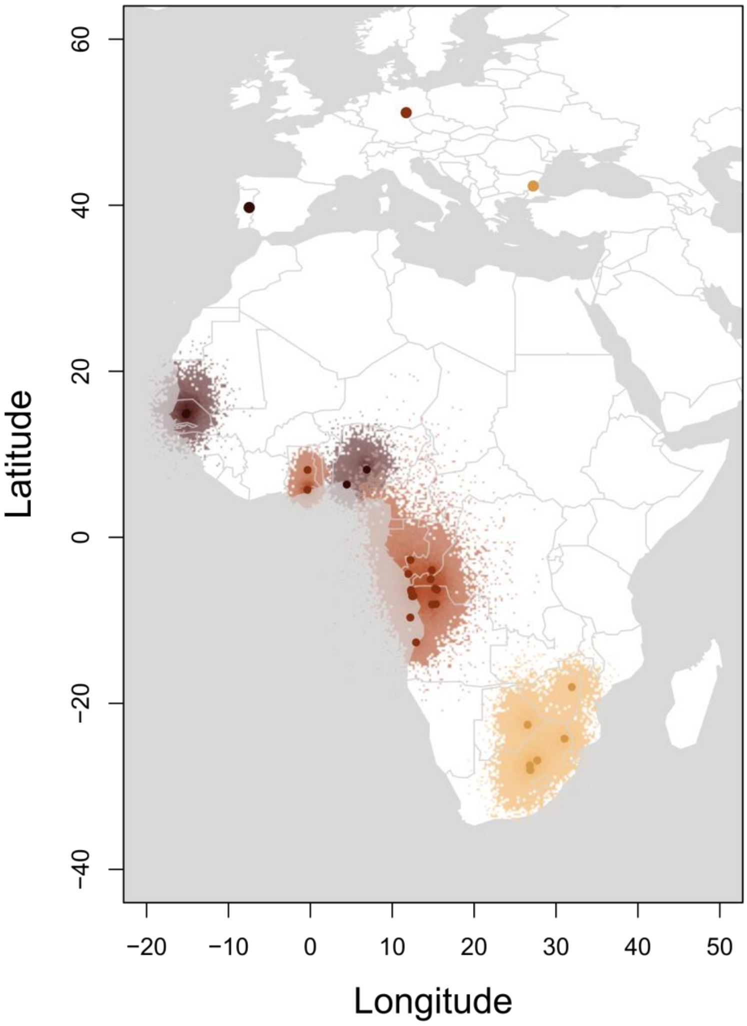

Figure 5.1. Non-breeding ranges of tracked Bee-eaters from the western (Portugal, brown, *n* = 5), the northern (Germany, red, *n* = 18), and eastern (Bulgaria, orange, *n* = 6) populations. Circles represent median positions of the main non-breeding site derived from geolocators using SGAT and while coloured regions represent the 99% probability distributions of location estimates.

Table 5.1. Number of birds per study site equipped with geolocators (#geoloc), recovered with device (N-total (males/females)) and the resultant records for autumn and spring migration and non-breeding site location.

Population (country)	Year	#geoloc	N-total (males/females)	N-autumn	N- non-breeding site	N-spring
Western (PT)	2015/16	60^{a}	6 (3/3)	2-3	5	2-3
Northern (DE)	2010/11	40^{a}	1 (1/0)	1	1	-
	2011/12	40^{a}	2 (2/0)	2	2	1
	2014/15	75^{a,c}	6 (2/4)	5	5	5
	2015/16	80^{c}	10 (6/4)	9	9	7
Eastern (BG)	2015/16	80^{bc}	6 (-/-)	6	6	3

a: SOI-GDL1 (*c*. 1.38g), b: SOI-GDL2 (*c*. 0.85g), c: SOI-GDL3 (*c*. 1.45g)

Geolocation analysis

We used *SGAT* (https://github.com/SWotherspoon/SGAT) and *GeoLight* (Lisovski and Hahn 2012) to analyse the light data from these tagged birds using a threshold method. We started by identifying sunrise and sunset events from log-transformed light intensity data (using a threshold of -8, which is the lowest light value consistently above any noise in the night-time light levels), within the R package *TwGeos* (https://github.com/slisovski/TwGeos). Because the estimate of twilight events from the geolocator differs from the theoretical twilight events by a few minutes, we used the period where the birds were still in the breeding grounds (after tagging, but before migration), and therefore in a known location, for calibration (i.e. to fit an error distribution to the data which is later used by SGAT as parameter alpha). This period varied from bird to bird, and was used to quantify the inherent measurement error of individual geolocators caused by shading from behaviour and feathers.

Because Bee-eaters breed in burrows, the sunrise and sunset times can be missed by a few minutes, and the calibration data can provide an inaccurate sun elevation angle for latitude estimation. For this reason, we used a Hill-Ekstrom calibration to correct the estimated sun elevation angle (Lisovski et al. 2012). We then used the *changeLight* function in *GeoLight* (Lisovski and Hahn 2012) to identify short stopover periods (stationary periods ranging from 1 to 3 days, a change in light probability *q* of 0.5 to 0.9 depending on data quality). The *changeLight* function uses the difference in day length to estimate movement periods given a change in probability *q*. The function is therefore sensitive to data quality and is geolocator-specific (Lisovski and Hahn 2012). We used *changeLight* in combination with the *mergeSites* function (Lisovski and Hahn 2012) to compare all stationary periods and determine what their spatial overlap was and whether they could be merged together as a single stationary period. We always started with a high *q* in *changeLight* and reduced it if the stationary periods caused *SGAT* to crash. Indeed, shading can cause two distinct stopover sites to be falsely classified as one by *changeLight,* preventing *SGAT* from converging (it is impossible to estimate one location if the sunrises and sunsets are too different). Lowering *q,* however often overestimates movement periods, but does not create incorrect stopover periods

Identifying correct stationary sites enabled us to use a grouped model in *SGAT*. This method estimates one location from multiple sunrise and sunset events, thus finding the best possible fit to the data during the identified stationary periods, and importantly, increasing the precision of the estimated location. *SGAT* uses a Bayesian framework to incorporate prior information including stopover periods, twilight error distribution (parameter alpha from the calibration), speed distribution (parameter beta) and a land mask (so that when the bird stops over, it is less likely to do so in the sea). Markov Chain Monte Carlo simulations then model the geographic probability distribution of each location where the bird is known to have stopped. We fixed the first and last location to the known capture and recapture locations where appropriate (if the sensor stopped logging light before the recapture date, the last point was not fixed). We first ran a modified Gamma model (relaxed assumptions) for 1000 iterations to initiate the model, before tuning the model with final assumptions/priors (three runs with 300 iterations). Finally, the model was run for 2000 iterations to ensure convergence. For two incomplete data sets (from Portugal and Germany), we ran SGAT only during the period where light was recorded – primarily during the non-breeding residence period (but still using the breeding site for calibration).

To calculate consistent stopovers between all birds for timing and resident period comparisons, we again used the *changeLight* function; this time with a stationary period of at least 3 days and a probability *q* of 0.8 (this avoided the aforementioned overestimation of movement periods). Once stopover periods were identified, we calculated the median location of birds during these stationary periods based on the geolocation estimates. In further analyses (e.g. Table 5.2), we considered only stopover/residence sites within the sub-Saharan non-breeding range with a spatially variable northern limit <18°N in West Africa and <12°N in Central and East Africa due to the longitudinally different southern edge of the Sahara desert. Furthermore, we distinguished between non-breeding residence periods/sites with minimum durations of >14 days and non-breeding stopover periods/sites with durations of up to 14 days.

Tracking data are available upon request from Movebank online database (https://www.movebank.org/, project IDs: 725039955 (PT), 759031657 (DE) 753257610 (BG)).

Table 5.2. Seasonal migration speed of Bee-eaters from western, northern and eastern populations in 2015/16. Speeds are given for autumn and spring as median speed (km d^{-1}) and its range, N gives sample size; the last column gives *P*-values for Mann-Whitney-U comparisons between northern and eastern populations.

Migration section	Season	Median migration speed (range, km d-1)						
		Western population	N	Northern population	N	Eastern population	N	*P*
Breeding site – first sub-Saharan site	Autumn	159 (106/212)	2	206 (189-224)	9	317 (193-465)	6	0.26
	Spring	76.5 (66/87)	2	164 (131-165)	7	147 (116-245)	3	0.99
Breeding site – main non-breeding site	Autumn	46 (37/55)	2	195 (150-207)	9	201 (157-249)	6	0.44
	Spring	50.5 (35/66)	2	133 (123-165)	7	105 (98-110)	3	0.12

Migration distance and migration speeds

We calculated migration distances as the orthodromic (great circle) distance between the breeding and non-breeding residence sites (in km, rounded to nearest 10km). Furthermore, we determined the annual cumulative travel distance (sum km a^{-1}) based on occupied sites and the movements between sites within each modelled track.

We calculated the total migration speed (km d^{-1}) between departure from breeding/non-breeding sites and arrival at the final destination. The available data on seasonal changes in body masses (Cramp 1986) indicate that European Bee-eaters do not appear to fuel before departure on migration (Fry 1984) as they are aerial foragers and thus able to feed during migration. Hence, pre-departure fattening periods do not compromise our calculation of migration duration and migration speed.

Results

Non-breeding residences

All birds from the western population (Portugal) spent the non-breeding period in West Africa between the Gambia/Senegal and Nigeria (Figure 5.1), with main residence sites occurring 3730 km (median) away from the breeding colony (25-75% = 2670-3790 km, n = 5). Two of four birds (with complete non-breeding period records) used more than a single site of residence. Sojourn time at the main sites ranged between 116 d and 154 d; total residence times averaged 186 d.

The non-breeding range of the northern breeding population (eastern Germany) stretched from eastern parts of West Africa (two birds in Ghana/Togo, one bird in Nigeria) to northern Angola, Gabon and the Republic of Congo, where 82% of the birds overwintered. Thus, the non-breeding range of the northern population overlapped occasionally (11% of 18 non-breeding residences) with those of the western population between 2°W and 5°E in eastern West Africa. The non-breeding sites were 6360 km (median) away from the breeding colony (for all years, 25-75% = 6060 – 6660 km, n = 18; for the year 2015, median = 6410km, 25-75% = 6120-6760 km). About 53% of birds used more than one residence (complete non-breeding records only). Sojourn time on the main residence site averaged 140 d (for multiple site birds) and 183 d (for single site birds); the total non-breeding residence period averaged 185d.

Birds from the eastern European population (Bulgaria) were geographically separated, with their non-breeding range being situated in southern Africa (South Africa, Botswana, and Zimbabwe) and not overlapping with the western or the northern populations. The median great circle distance between the main residence site and the breeding colony was 7550 km (25-75% = 7070-7792 km). Five birds with complete non-breeding tracks used more than a single residence site with average duration of 154 d for the main site, and a total duration of 194 d.

The migration distances from breeding to main non-breeding sites differed significantly between all populations (ANOVA, $F_{2,20} = 131.48$, $P < 0.001$; pairwise posthoc tests, all $P < 0.05$). The cumulative distance travelled within the entire year was smallest for the western population (about 5700 km), and was about 2.3 times longer in both the northern and the eastern population (ANOVA $F_{2,12} = 5.99$, $P = 0.02$; post hoc comparison North vs. West, $P = 0.80$; Figure S5.1).

Migration routes

Bee-eaters from the Western population initially headed south, crossing the Strait of Gibraltar and the desert at its western rim in West-Sahara, Mauretania and western Algeria (Figure 5.2a). Birds from the northern population headed southwest first, but then crossed the Mediterranean Sea further east between 2°W and Corsica/Sardinia, before crossing the Sahara, from Algeria heading south to Mali and western Niger (Figure 5.2b). Although migration routes spatially overlapped at about 0-2°E in some individuals from the northern and western populations (Figure 5.2a, b), we found only little simultaneous passage in this area (Figure S5.2). On the other side of the range, birds from the eastern population headed mainly south-southeast to cross the eastern Mediterranean Sea at about 20°E to Egypt. None of the tracked birds from BG made a detour across the Levant. After reaching the North African coast, the birds followed the Nile river area and the Albertine rift to their non-breeding destination (Figure 5.2c). Thus, the overlap in the migration corridors of the western and the northern populations was minimal. Only the

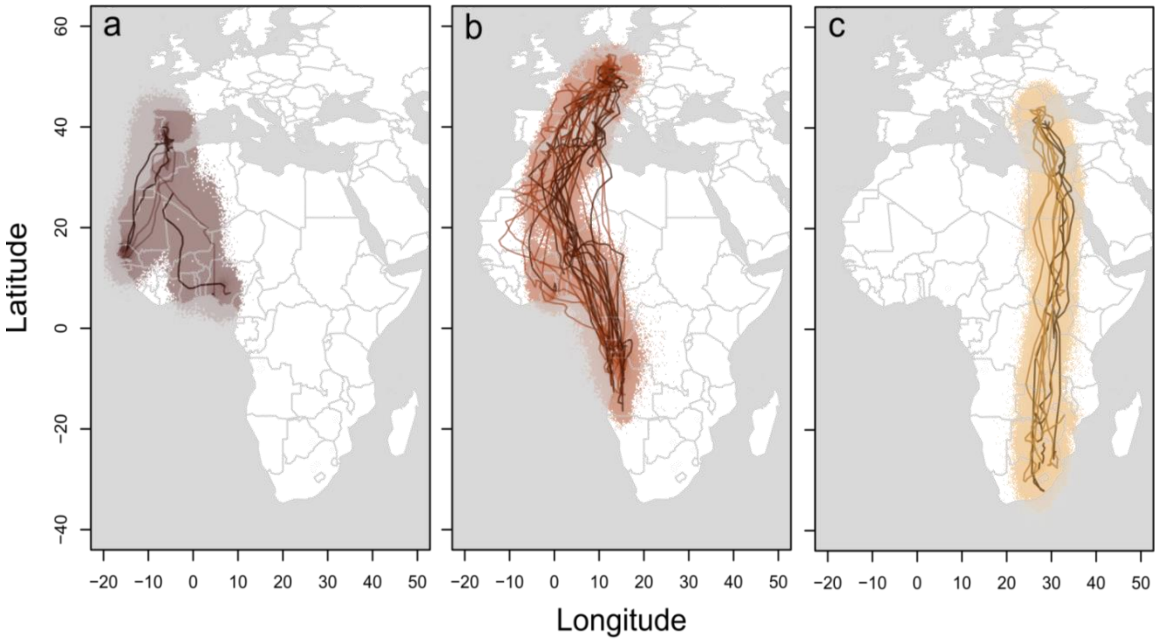

Figure 5.2. Modelled tracks of birds with complete tracking records per season from (a) the western population (Portugal, *n* = 3), (b) the northern population (Germany, *n* = 9), and (c) the eastern population (Bulgaria, *n* = 6). Shading represents the average estimate of all tracks with 99% CI. Coloured tracks represent autumn migration and black tracks represent spring migration.

eastern-most migrants from the western population overlapped with the northern population during autumn migration. The corridor used by the eastern population did not overlap with either the western or northern populations.

Timing of migration and speed

Birds from the western population departed from the breeding grounds about 2.4 weeks earlier than those from the northern and eastern populations (ANOVA, $F_{2,18}$ = 6.04, P = 0.01, Figure 5.3) and arrived at the first sub-Saharan non-breeding site about 4.4 weeks earlier than Bee-eaters from northern (t-test, t_9 = -5,98, P < 0.001) and eastern populations (t-test, t_6=-2.48, P =0.05). Additionally, departures from the last sub-Saharan non-breeding site and the arrival at breeding sites were about 1 month earlier compared to the northern and eastern populations (for details and sample sizes, see Table S5.1). The northern and eastern populations were similar in the timing of autumn migration (difference in breeding site departure: Man-Whitney-U, T_{15} = 0.41, P = 0.74; and arrival at the first sub-Saharan non-breeding site: Man-Whitney-U, T_{14} = 47.0, P = 0.95), but differed for spring migration with eastern birds departing one week later from their last sub-Saharan non-breeding site, and arriving later at the breeding sites (departure: t_9 = 2.12, P = 0.01; arrival: t_8 = 2.36, P = 0.05). Interestingly, eastern breeding birds started to move northwards from the South African non-breeding sites by about one month before the final departure from the sub-Saharan region in spring (Figure 5.3).

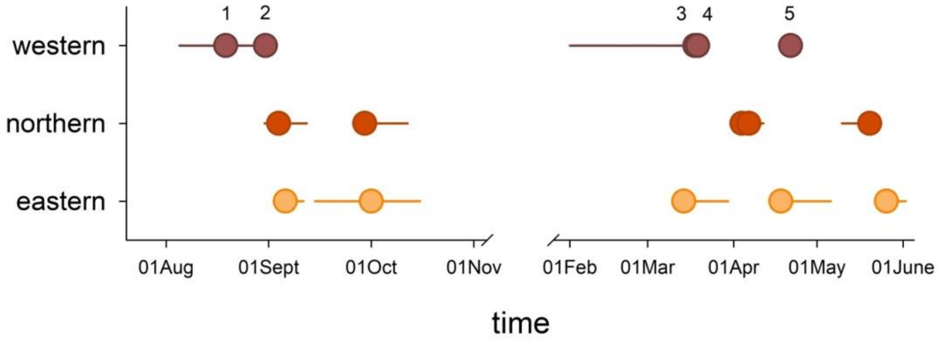

Figure 5.3. Timing of migration of Bee-eaters from western (Portugal, brown), northern (Germany, red) and eastern (Bulgaria, orange) populations during the 2015/16 season. Symbols are medians with whiskers corresponding to 25/75percentiles; the events are: 1 - the departure from the breeding site; 2 - the arrival at the first sub-Saharan non-breeding site; 3 - the departure from the main non-breeding site: 4 - the departure from the last sub-Saharan non-breeding site; and, 5 - the arrival at the breeding site.

Based on different timing and migration distance, the migration speed was consistently lower for western compared with northern and eastern populations, although sample sizes were too low for statistical comparison in the western population. There was no significant difference between northern and eastern populations (Table 5.2).

Discussion

Here, we have provided important first insights into migration patterns of European Bee-eaters, and in doing so, we have tested some of the long-standing assumptions surrounding the natural history of this iconic species. Whilst sample sizes were often small, as is typical for such exploratory studies (see Brlík et al*.* 2019 for an overview), we nonetheless have contributed significantly to the knowledge of migration routes and timing in this species. First, we have confirmed that western European breeders migrate on a western route to non-breeding regions in West Africa, and that eastern European birds migrate on an eastern route to southern Africa. Second, we have discovered that birds from the recently established northern-central European population use the western migration corridor to reach a new core non-breeding range, located between northern Angola and the southern parts of Congo. Finally, we have provided some evidence for earlier timing of migration in the western population compared to the northern and eastern populations.

Migration direction, migratory divide and non-breeding ranges

The newly established northern breeding population from eastern Germany uniformly headed westwards from their breeding sites and used a western migration corridor, similar to, but not overlapping with birds from the western population in Portugal. Because passage times differ (see below), northern birds are unlikely to encounter western birds during migration, despite using similar regions. There is no information on migration direction or flight corridor for birds from south-western Germany; the nearest population is about 4-5°west from our study site, but it seems very likely that these birds also use a western migration corridor like birds from France, which are considered as being typical western migrants (Cramp 1986). Further east, Bee-eaters breeding in the Czech Republic and Slovakia, which is about 5-10° east from the colonies in eastern Germany, are eastern migrants, as confirmed by ring recoveries of adult birds in the Balkan peninsula (Cepak et al. 2008). They might use the same corridor as the tracked eastern birds from Bulgaria which crossed the southern Balkan Peninsula and the Mediterranean Sea, but did not make a detour via the Levant (Figure 5.2). Thus, the migratory divide of the

European Bee-eater in central Europe north of the Alps must be situated east of 12°E separating the East German and the Czech/Slovakian populations, which also resembles the postglacial divide and their associated hybrids zones in many species in central Europe (Hewitt 2000). The location of the divide in southern-central Europe, i.e. south of the Alps, remains open as the few ring recoveries in Italy (Spina and Volponi 2008) and missing data from the western Balkan peninsula don't yet allow for firm conclusions to be drawn.

Our tracking data suggested that western populations, namely from Portugal, overwinter in West Africa and do not move further, neither to the main non-breeding range of the northern population in northern Angola nor to the second main non-breeding region of the species in south-eastern Africa (Fry 1984). Thus, western and eastern populations are also geographically isolated from each other during the non-breeding period, with the latter being more than 3800 km away in south-eastern Africa. A frequent exchange between the two populations during the non-breeding period seems therefore implausible (see also Cramp 1986), which is in line with a slight west-east differentiation in population genetic structure using microsatellites (Ramos et al. 2016, Carneiro de Melo Moura et al. 2019). In contrast to this rather strict ecological separation, the non-breeding range of the northern population overlapped at its western edge, from Ghana to Nigeria, with the non-breeding range of western populations (Figure 5.1). Moreover, migration routes of the birds from both populations which crossed the Sahara desert in western Algeria and Mali were very similar (Figure 5.2a,b). The fact that migration routes and non-breeding areas of the northern population were more similar to the western than eastern populations suggests exchange of individuals between those two populations. Considering the genetic similarity, such dispersal events might not be exceptional (Carneiro de Melo Moura et al. 2019).

We located the main non-breeding range of the northern population south of the Congo basin rainforest belt in southern Congo and northern Angola (Figure 5.1). However, the population did stopover between Ghana and Nigeria, with some birds overwintering in the region (11% of the tracked birds) and others continuing further southeast. Because the western population already occupies this region and arrives earlier (Figure 5.3), most birds from the later arriving northern population may be continuing southward to the Congo basin and thus establishing a kind of leap frog migration system (Bell 2005). Interestingly, this area has not been described as non-breeding range for European breeding birds (Fry 1984, Fry et al. 1988), though there is some suggestion that South African breeding birds may migrate to the region during their non-breeding season (Brooke and Herroelen 1988).

The tracked northern breeding population in eastern Germany has grown exponentially in the last two decades since it was established in 1990 (Schönbrodt and Schulze 2017). We assume that the recent non-breeding range might have been established in parallel, having been occupied in the last 10 15 years. There are no recent monitoring data from the non-breeding region, but the presence of non-breeding Bee-eaters in northern Namibia during the boreal winter (Harrison et al. 1997; http://sabap2.adu.org.za/) points towards a regular occurrence in countries of southwestern Africa.

Migration timing and speed

Routes, timing and non-breeding destinations differed largely between the western and the eastern breeding populations. Interestingly, the northern populations shared geographical features (migration direction and corridor) with the western population, including some overlap, but the migration timing and notably departure dates (Figure 5.3) and speeds (Table 5.2), were more similar to the eastern population. Indeed, the northern and eastern populations breed in pronounced seasonal climates, i.e. Köppen climate classifications Cfa and Cfb, in contrast to the less seasonal climate Csa for the western population (Peel et al. 2007), and thus they likely share similar environmental cues to trigger migration.

We therefore anticipated that the northern and eastern breeders would depart at similar times, but arrive in the non-breeding grounds at different times if travel distances differed. However, we found that the mean arrival times for the northern and eastern populations in the non-breeding grounds overlapped. In fact, even though the distances between the breeding and non-breeding grounds at first glance appear shorter for the northern than the eastern population (6360 km and 7550 km respectively), the cumulative distance travelled (Figure S5.2) during migration was on average similar (~ 7500 km; Figure S5.1), and is in some cases greater for the northern population (up to ~10’000km; Figure S5.1). Indeed, while the eastern birds followed the rift valley along the Nile in an almost straight fashion, the migratory route of the northern birds was less direct (Figure 5.2). The less straight flight routes likely allow birds to reduce the energetically demanding crossing of geographical barriers such as the Gulf of Guinea and the Mediterranean, with little thermal lift, or the Sahara, with unpredictable aerial food availability.

Peak departure dates from the breeding and the non-breeding grounds, and the corresponding arrival dates were sequential from west to east, which point towards a general and slightly shifted annual programme (Gwinner 1996) across the studied populations. However, eastern birds (which spend the non-breeding period further south) departed the main non-breeding site early to ‘pre’-migrate northwards towards Lake Victoria, before continuing towards the breeding grounds (Figure 5.3). The sequential arrival at breeding regions is consistent across the last 19 years: first observations are on average in the 4th week of March/first week of April for Portugal, and in the last week of April/first week of May for Bulgaria, and first to second week of May in Germany (https://ebird.org, period: 2000-2018, accessed at 09.11.2018).

Conclusions

In the two last decades, Bee-eaters not only established new breeding sites in northern central Europe, but also established new migratory routes and non-breeding sites in the Congo basin and northern Angola, in an intermediate area between the non-breeding ranges of western and eastern populations in West Africa and southern Africa, respectively. There was, however, a small proportion of northern birds that spent the non-breeding period in western Africa, suggesting that non-breeders in western Africa may come from breeding sites anywhere between Portugal and Germany. Thus, these populations may display lower migratory connectivity (by covering a wider nonbreeding range) than the easterly population which additionally did not overlap either spatially or temporally with the other two populations. Despite these differences in migratory pathways, there was an indication that populations have distinct migration timing. This highlights the importance of population-specific or colony-specific behaviour (Dhanjal-Adams et al. 2018) and local adaptations to environmental conditions, particularly seasonality, in shaping Bee-eaters’ annual cycles. Hence, we expect a gradual change in migration patterns, similar to population genetic structures (Ramos et al. 2016, Carneiro de Melo Moura et al. 2019) from western to eastern populations, however, the position of intermediate breeding populations, i.e. from France, Italy or the western Balkans, remains to be confirmed.

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Supplementary material

Table S5.1. Timing of main migration stages of Bee-eaters from western (PT), northern (DE) and eastern (BG) breeding populations in Europe. Times are given as median day of the year and 25-75% percentiles for the 2015/16 season for all populations, and for 2010-2015 for the northern population (annual day of year converted to the 2015/16 season). N refers to the number of individuals.

Site	Event	Western (PT)	N	Northern (DE)	N	Eastern (BG)	N
Breeding	Departure (2015)	19Aug (05Aug-01Sept)	3	04Sept (30Aug-12Sept)	10	06Sept (03-11Sept)	6
	2010-15			07Sept (31Aug-12Sept)	16		
Non-breeding	Arrival* (2015)	31Aug	2	30Sept (28Sept-13Oct)	9	02Oct (15Sept-16Oct)	6
	2010-15			14Oct (30Sept-16Oct)	17		
	Departure* (2015)	17Mar (16-19Mar)	3	04Apr (1-9Apr)	8	16Apr (12Apr-04May)	3
	2010-15			09Apr (02-14Apr)	15		
Breeding	Arrival (2016)	15Apr/2Apr	2	18May (08-20May)	8	24May (22-31May)	3
	2010-15			13May (08-19May)	13		

* refers to arrival at the first, and departure from the last, sub-Saharan non-breeding site

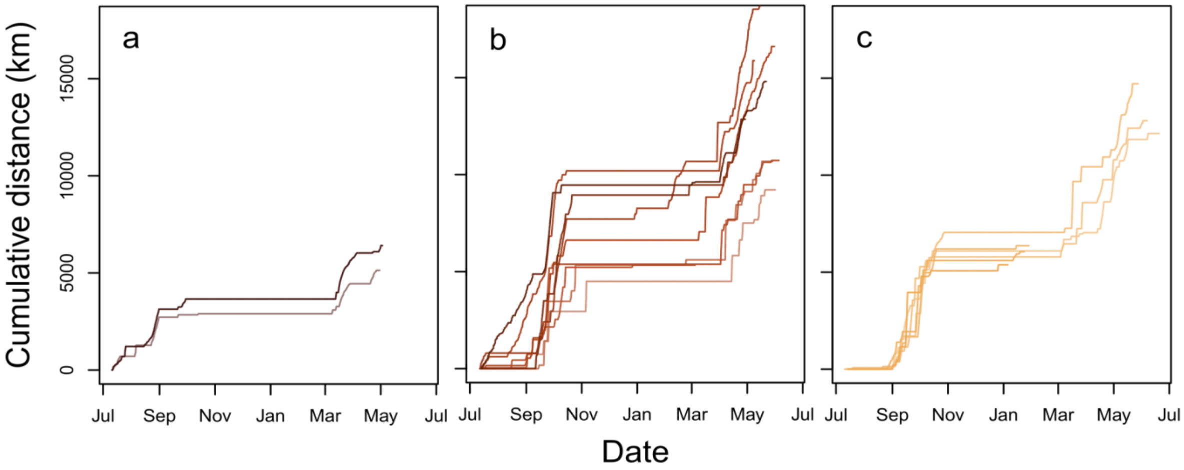

Figure S5.1. Cumulative distance travelled over time, by (a) two birds from the western population, (b) nine birds from the northern, and (c) six birds from the eastern population, all between July 2015 and July 2016.

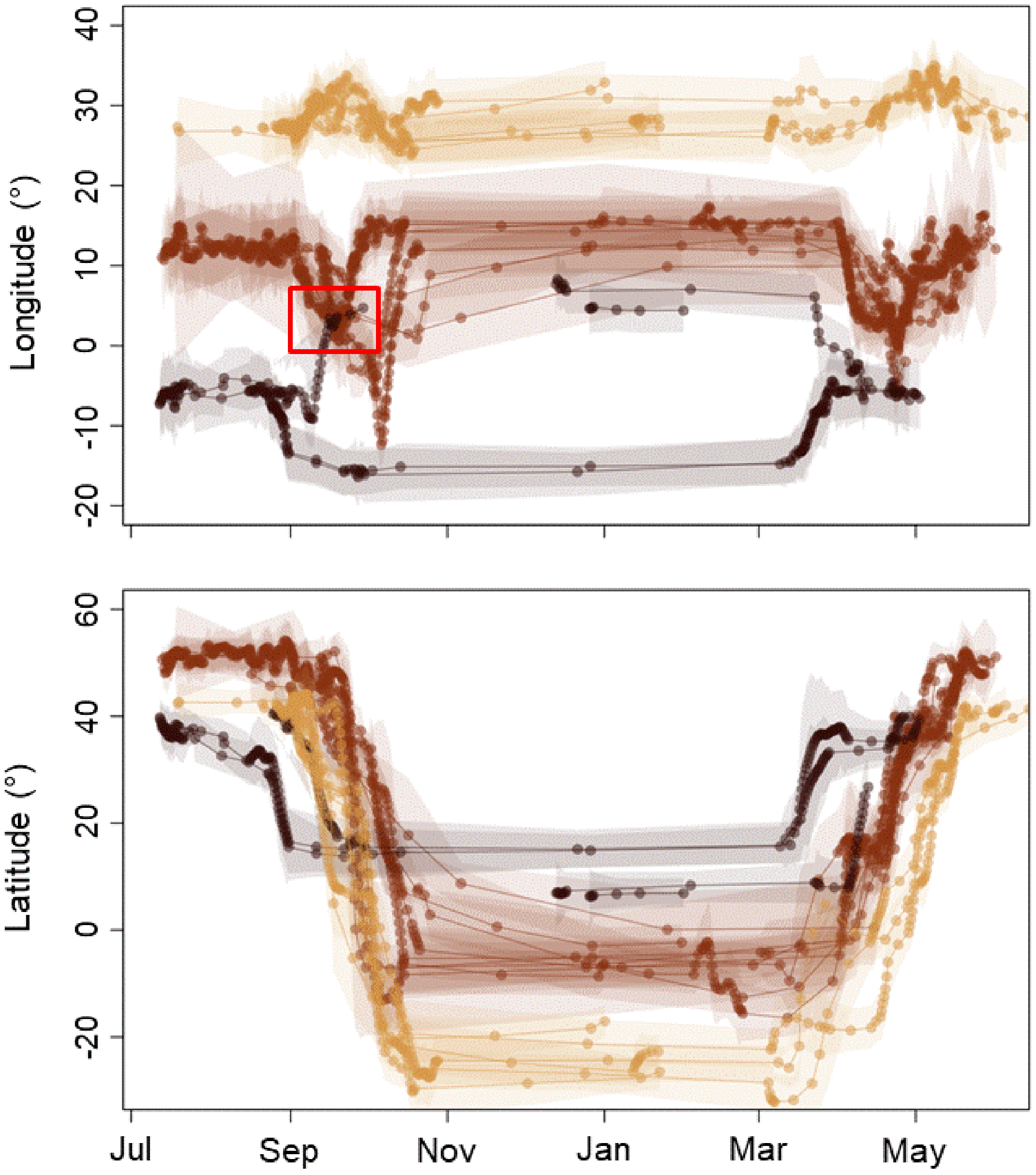

Figure S5.2. Estimated longitudes (upper panel) and latitudes (lower panel) of European Bee-eaters over the entire annual cycle of 2015/16. Data were obtained from geolocation of three populations: a western population (Portugal, dark brown), a northern population (Germany, red), and an eastern population (Bulgaria, orange). The likely encounter of a western and three northern birds is marked in red. Error range of data is given as shaded areas; see text for further details of geolocation.

Chapter 6

Linking migration performance with productivity: unravelling the migration of European Bee-eaters (*Merops apiaster*) breeding in southwest Iberia

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Abstract

Understanding the relationship between migration performance and breeding phenology, as well as its consequences for productivity, is crucial to predict the changes in population dynamics of migratory species, in light of ongoing environmental changes. In this study, we use geolocators to explore migration performance and its association with productivity in European bee-eaters at the Iberian Peninsula. Iberian bee-eaters spent the wintering period in West Africa between Senegal and Nigeria. Although we did not record differences in travel duration, travel speed and migration timings between sexes, bee-eaters had higher travel speed and shorter travel duration in spring compared to autumn. Our results show that bee-eaters either depart early or travel fast in spring. Indeed, individuals that departed earlier had longer travel duration, while late departing individuals spent fewer days on migration. Despite this, earlier and slower bee-eaters still arrived earlier at the breeding areas than later but faster individuals, in any given year. The relationship between laying date and productivity was year specific. In 2017, the number of fledglings decreased throughout the season but this was not the case in 2016, when laying was earlier in the year and productivity remained constant. Interestingly, productivity was on average higher in 2016 than in 2017, suggesting that in years when breeding conditions are favourable, early and late breeders will produce high and similar number of fledglings, but when conditions are unfavourable only early breeders will experience similar productivity levels. We urge for longer-term monitoring of bee-eater, and other Afro-Palaearctic migrants, to expand our current knowledge on inter-annual fluctuations of phenology and productivity and the potential consequences for demography.

Keywords: travel duration, geolocator, laying date, breeding arrival, carry-over effects, productivity

Introduction

Population declines are currently widespread in migratory birds across the world (e.g. Kirby et al. 2008; Sanderson et al. 2006; Vickery et al. 2014). In order to determine when (in the annual cycle) and where (across the distribution range) migratory species may be most constrained and which are the potential consequences for demography, it is essential to understand individuals' performance in time and space throughout the annual cycle (Kirby et al. 2008; Small-Lorenz et al. 2013). But exploring the potential factors affecting long-distance migrants is particularly challenging, as conditions at very distant locations, experienced in a given season, may also affect individual performance in a subsequent stage of the annual cycle at another location (i.e. carry-over effects, Harrison et al. 2011).

Migration has evolved to allow organisms to cope with seasonal changes in food availability, habitat suitability, and/or weather conditions (Newton 2008). Therefore, migratory birds must time annual cycle events according to local environmental conditions at all stages, in order to maximize fitness (Lemke et al. 2013; Tomotani et al. 2018). Timing of spring migration is often liked to breeding success, being therefore a key stage of the annual cycle. Early arrival to the breeding areas may be advantageous, by increasing the likelihood of encountering favourable environmental conditions (e.g. high food availability; Emmenegger et al. 2014), of securing high quality habitats and partners (Cooper et al. 2011; van Wijk et al. 2017) or allowing for re-nesting following potential nest failure (Morrison et al. 2019). For many species, spring migration is shorter and/or faster than autumn migration (e.g. Nilsson et al. 2013) as individuals are under high selection pressure to arrive earlier. However, early arrival and associated benefits may only be possible to those individuals which migrate shorter distances or are in better body condition to initiate migration earlier and/or travel faster (e.g. Alves et al. 2012; Nilsson et al. 2013; Saino et al. 2017). Factors influencing migration timing may differ between sexes at several stages of the annual cycle (Briedis et al. 2019), and in some cases it can lead to consequences in the subsequent season (Saino et al. 2017). For example, earlier arriving males in the breeding areas have greater chances to acquire high quality territories and have extra-pair mating opportunities (Cooper et al. 2011); while early females can benefit of paring with high-quality partners and lay eggs earlier than later arriving females (Saino et al. 2017; Smith and Moore 2005).

The distance between breeding and wintering areas often determines the time spent on migration and therefore the timing of spring arrival (e.g. Hötker 2002). However, the quality of habitat during winter may also play an important role on migratory timings (Gunnarsson et al. 2006) and subsequent breeding performance (Alves et al. 2013; Saino et al. 2004). Individuals occupying higher quality habitats during the wintering season may accumulate fuel at a faster rate, leaving the wintering grounds in better condition (Bearhop et al. 2004; Studds and Marra 2005) and earlier (Marra et al. 1998; McKinnon et al. 2015), therefore increasing the probability of raising more offspring in the breeding areas (Norris et al. 2004). Therefore, spending the winter in advantageous wintering areas and undertaking specific migratory strategies can have important consequences for individual fitness in distant breeding areas (Alves et al. 2013).

Reproductive success is also affected by local factors during the breeding season, such as weather conditions and/or food availability. Particularly for income breeders (e.g. Langin et al. 2006) that use local resources for egg production, unfavourable weather conditions upon arrival may limit food availability and delay egg-laying (Ockendon et al. 2013; Pakanen 2018). In addition, as flying insects are less active at low temperatures and during periods of rain, food shortage for insectivorous birds during nestling rearing can decrease body condition of offspring and consequently depress annual productivity (Arbeiter et al. 2016). Adverse conditions at breeding sites may therefore counteract the potentially positive carry-over effects from the wintering and migration periods (e.g. Harrison et al. 2013).

Recent technological advances of tracking devices have led to increasing numbers of studies revealing migration patterns, especially in long-distance migrants (e.g. Carneiro et al. 2019; Finch et al. 2015; Norevik et al. 2017; Robinson et al. 2010). However, studies linking migratory performance (e.g. migration timings, winter location) with breeding phenology and/or success (e.g. Drake et al. 2014; Finch et al. 2014; Norris et al. 2004; Saino et al. 2004; Woodworth et al. 2016) remain rare, particularly those using individual tracking data (winter location, migration performance) and productivity (but see: Saino et al. 2017; Souchay et al. 2018; van Wijk et al. 2017).

In this study, we use geolocators to explore migration performance and its association with productivity in European bee-eaters at the Iberian Peninsula. Although the breeding biology of the European bee-eater has been well studied (e.g. Brust et al. 2015; Lessells and Avery 1989; Lessells and Krebs 1989), little information on the spatio-temporal distribution of the species is currently available and the potential effects of migration performance on productivity have never been explored. The European bee-eater (*Merops apiaster*; hereafter bee-eater) is a long-distance migratory insectivore that breeds in open agricultural areas in the Palearctic and winters south of Sahara (Fry 1984). Bee-eaters are monogamous and both sexes actively contribute to nest (re)construction which takes approximately 10 to 20 days. Females lay the eggs in one to two days intervals and nestlings hatch after ca. 20 days. Both parents feed the young until fledging, ca. 30 days (Fry 1984). Ringing and recovery data have been widely used to track individuals across their migratory range, but bee-eater recoveries seldom occur, and long-distance recaptures are extremely rare (Ramos et al. 2016). More recently, Hahn et al (2019) reported the migratory patterns and wintering areas used by five bee-eaters of the Iberian population, which spent the winter season in West Africa (Chapter 5). Here, we use a larger dataset to (1) establish a more complete picture of migratory performance and non-breeding distribution of bee-eaters breeding in Iberia, and (2) investigate variation in timing, travel duration and travel speed between seasons and sexes throughout the annual cycle. Finally, we (3) explore if wintering latitude, wintering departure, travel duration and travel speed determine arrival date to the breeding areas and (4) if timing of arrival to the breeding areas influences laying dates and productivity, at the individual level.

Methods

Between 2015 and 2018, we used geolocation by light to track adult bee-eaters between their breeding colonies in Portugal (38.1°N, -7.0°E and 39.8°N, -7.1°E) and the wintering areas. Bee-eaters were captured in the nest burrows with walk-in traps during the nestling provisioning period, aged based on plumage characteristics (as 2nd year or older, Blasco-Zumeta and Heinze 2013) and sexed by genetic molecular analysis (n=26) or by a discriminant function (n=2, for further details see Chapter 2). Each year, we equipped 60 bee-eaters with geolocators (total 180; SOI-GDL1/GDL3; Swiss Ornithological Institute) using a leg-loop harness made from Silicone or cord material (Table 6.1). The average weight of the geolocators, including harnesses, was 1.33-1.45g, comprising less than 3% of bee-eater body mass. The annual recapture rate of birds with geolocators was 6.6% in 2016, 36.7% in 2017 and 1.6% in 2018. Additionally, we ringed birds with metal ring only (2015: 57, 2016: 213, 2017: 239) from which the recapture rates were 24.2% in 2016, 32.1% in 2017 and 13.2% in 2018. We successfully tracked 28 birds with geolocators resulting in 22 full annual tracks, 3 incomplete tracks (autumn migration only) and 28 wintering sites (Table 6.1).

Table 6.1. Number of Iberian bee-eaters equipped with geolocators and the resulting records for autumn and spring migration and wintering area location; (n total (females /males).

Year	Type	Deployed	Total recovered	Autumn	Spring	Wintering
2015/2016	GDL1	60	5(4/1)	2(1/1)	2(1/1)	5(4/1)
2016/2017	GDL3	60	22(13/9)	22(13/9)	19(13/6)	22(13/9)
2017/2018	GDL3	60	1(male)	1	1	1

Productivity and laying dates

In order to determine productivity, we visited the colonies weekly and recorded the number of pre-fledging nestlings during the third week of development using a "burrowscope". Bee-eaters take 30 days to fledge and it was assumed that the number of nestlings recorded in this last week reflects the total number of fledgling's produced (i.e. productivity). We estimated hatching date of each brood using a photographic guide for age determination of bee-eater nestlings (see Chapter 3). Laying dates were back-calculated by subtracting the incubation period of 20 days to the hatching date of the first egg. We determined the laying date and productivity of 87 nests in 2016 (including two of the tracked birds in 2015-2016) and 96 nests in 2017 (including of 19 tracked birds in 2016-2017; although in two cases productivity was not possible to quantify due to the sinuous shape of nest tunnel and chamber, which made it impossible to clearly observe the nestlings). In 2018 only the laying date of the single tracked bee-eater was determined.

Geolocation analysis

Geolocators recorded light intensity at 2 (GDL1) and 5 minute (GDL3) intervals. After log transforming the light intensity data, we used a threshold method to identify sunrise and sunset events (using a threshold of 3, except for two birds that required threshold of 8 and -5) with R package *TwGeos* (Wotherspoon et al. 2016a). This step allowed the detection of errors on twilight events and to manually correct them when necessary. Twilight events can be influenced by shading (e.g. due to clouds or foliage) potentially resulting in shorter days and affecting location estimates (Lisovski et al. 2012). Therefore, we quantified the error distribution of sunrise/sunset times by using twilights from a known location (i.e. the breeding colony). More specifically, we used the recordings from a day after the geolocator was fitted on the bird until before the start of the migration (range: 40 to 50 days) and calibrated the data by fitting an error distribution to the sunrise and sunset data, which was later used by SGAT (see below). We then plotted the estimated latitude of the bird over time with the estimated zenith from breeding calibration and if the latitude during stationary periods was not flat over time (i.e. lowest variance in latitude estimates) we used Hill-Ekstrom calibration (Lisovski et al. 2012). For Hill-Ekstrom calibration we defined a period when the bird was in the non-breeding area (usually from the first half of October to beginning of March).

We used a group model in the R package *SGAT* (Wotherspoon et al. 2016b) to estimate geographic positions. The group model uses known stationary periods to estimate a single location from multiple twilight events. This increases the accuracy of the location estimate. First, we used the *changelight* function from the package *Geolight* (Lisovski and Hahn 2012) to separate periods of residency from periods of movement, based in changes in sunrise and sunset times. The function uses the difference in day length to estimate movement periods given a change probability *q*. Due to the high probability of errors when determining stationary periods of short duration, the high sensitivity of *changelight* function to data quality and specificity to each device (Lisovski and Hahn 2012), and given the variation in data quality among individuals, we selected different parameters for each individual. More specifically, we defined stationary periods ranging from 4 to 8 days and defined a probability of change from 0.80 to 0.95. The identified stationary periods were then merged together using function *mergeSites* from *Geolight* package (Lisovski and Hahn 2012).

SGAT was used to find the best possible fit to the data and increase the precision of the estimated locations. SGAT uses a Bayesian framework incorporating prior information, such as the previously defined stopover periods, twilight error distribution (from the calibration), flight speed distribution and a spatial probability mask (to ensure that when a bird stops, it is less likely to do so in the sea). Markov Chain Monte Carlo simulations then allow the model to simulate the geographic probability distribution of each location. We fixed the first and last location to the known capture and recapture locations except for cases when the sensor stopped logging before the recapture date. We first ran a modified Gamma model (relaxed assumptions) for 1000 iterations to initiate the model, before tuning the model with final assumptions/priors (three runs with 300 iterations). Finally, the model was run for 2000 iterations to ensure convergence. For the datasets that only recorded light during a short period of the non-breeding season we ran SGAT only during the period when light was recorded.

We defined wintering residence periods as stationary periods longer than 14 days and located south of the Sahara. For birds that used more than one residency site, we defined the main wintering area as the longest stationary period south of the Sahara and used that site to calculate the latitude and longitude coordinates of the wintering area.

Migration distance, travel duration and travel speed

We calculated migration distance considering the orthodromic (great circle) line between the breeding and the wintering area (in km). For birds with more than one wintering area (n = 4; individuals with two residency periods) we considered the first residency period (for autumn migration) or the last one (for spring migration). We determined departure and arrival dates (Julian dates) from the information provided by *Geolight* (*mergesites* function). To define arrival to and departure from the wintering areas for birds with more than one wintering area, we considered the first residency period and the last one, respectively. We calculated seasonal travel duration as the number of days between departure from breeding/wintering sites and arrival at final seasonal destination. Travel speed of migratory movements was defined as the average rate of travel after departure on migration until arrival at final seasonal destination (km/day).

Statistical analysis

We used Wilcoxon tests to explore seasonal differences in travel duration and travel speed as well as differences in timing (departure from breeding, arrival to wintering, departure from wintering and arrival to breeding), travel duration and travel speed between sexes. Since we did not find significant differences between age classes (2^{nd} year birds vs older) in arrival to breeding areas (W = 56.5, p = 0.647), laying dates (W = 46, p = 0.900) and productivity (W = 33, p = 0.869), there were pooled together for analysis.

In order to explore which factors may be influencing arrival date into the breeding areas we constructed a linear model with wintering latitude, spring travel duration, spring travel speed and departure date from the wintering areas as main predictors. We ran a full model and reduced models that were ranked according to Akaike's Information Criterion for small sample sizes (AICc). Differences between models were assessed by the difference in AICc scores (ΔAICc) (R-package MuMIn; Barton 2019) from the model with the smallest AICc. Since travel speed and travel duration were strongly correlated (Spearman correlation test: S = 3423.1, $p<0.001$, rho= -0.93) we never included both predictors in the same model. Due to the low number of samples in 2015 and 2018 it was not possible to compare migration timings between years. Additionally, we constructed a linear model to test if arrival date to breeding area influences laying date at the individual level.

In order to test if productivity is influenced by laying date, we first performed a linear model using the complete dataset (i.e. tracked and non-tracked birds) and both years combined (i.e. 2016 and 2017), having laying date, year and its interaction as main predictors. As both year and the interaction term were significant, suggesting that the laying date effects on productivity differed between years, we performed a similar test for each year separately, using only laying date as main predictor. Finally, to investigate if the links between arrival, laying date and productivity were also apparent at the individual level, we ran a linear model using only the tracked individuals, having arrival date to the breeding area as predictor of productivity. Linear model assumptions were confirmed by graphical inspection of standardized residuals and by plotting residuals against fitted values. All statistical analyses were performed using R software (R Core Team 2017).

Results

All tracked bee-eaters from Iberia spent the winter in West Africa. Most (46.4%) wintered between Senegal and Guinea-Bissau (migration distance: 3009 ± 248 km; mean ± sd; n = 13); 35.7% in the region of Mali/Ivory Coast (migration distance: 3268 ± 316 km; n = 10) and the remaining 17.9% between Benin and Nigeria (migration distance: 3532 ± 109 km; n = 5; Figure 6.1). The overall mean migration distance between breeding and wintering areas was 3195 ± 319 km.

Bee-eaters departed from the breeding sites between 26 July and 31 August (13 August ± 9.8 days; mean ± sd) and arrived at their wintering sites between 1 and 25 September (10 September ± 8.4 days; Table 6.2). Furthermore, 52% of the birds had a stopover during autumn migration with a mean duration of 11.1 ± 6.8 days (n = 13). During the wintering period, bee-eaters spent a mean of 172.6 ± 16.9 days in the main wintering areas, and four birds used more than a single residency site and spent a mean of 17.0 ± 1.2 days in the secondary wintering area. Birds departed from the wintering areas between 13 March and 2 April (20 March ± 7.4 days) and arrived in the breeding areas between 27 March and 23 April (7 April ± 7.6 days; Table 6.2). As before, half of the birds stopped over during spring migration (mean stopover duration: 9.5 days ± 4.6 days; n = 11).

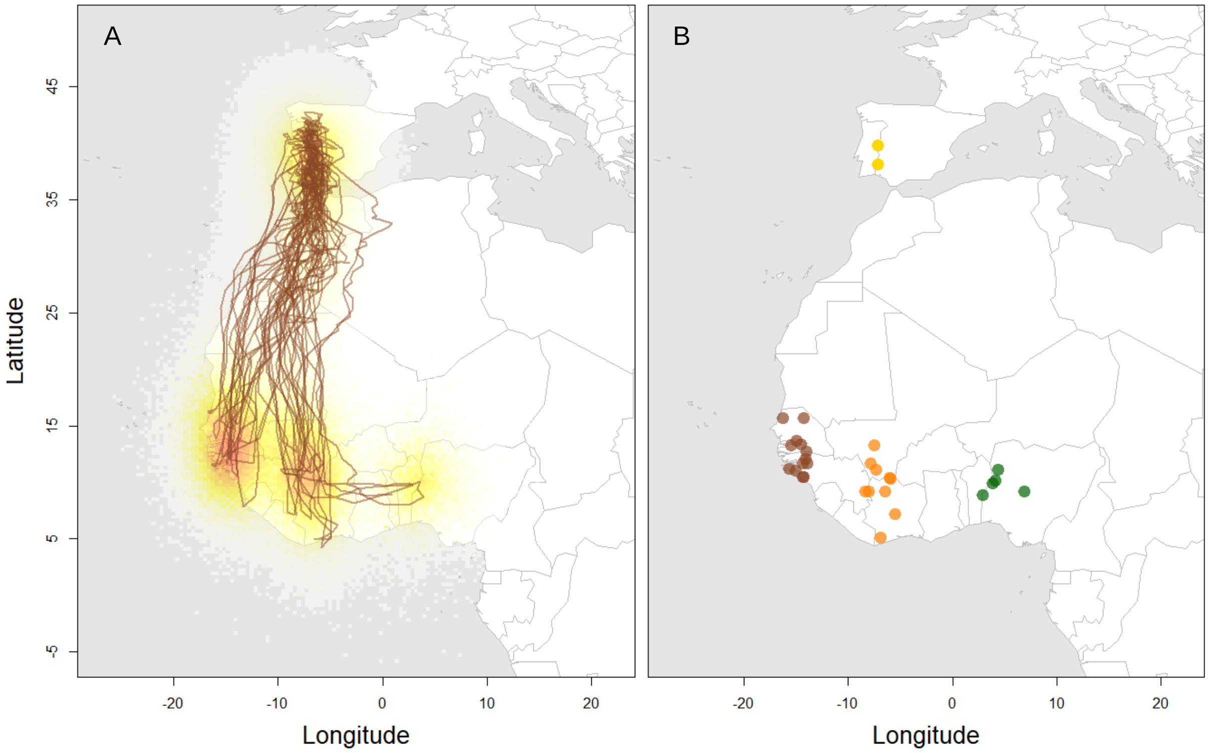

Figure 6.1. (A) Modelled tracks of Iberian bee-eaters with complete annual tracking (n = 25) and the nonbreeding ranges of all tracked birds (n = 28). Brown lines represent the median positions and coloured areas represent the 95% probability distributions of location estimates. (B) Median position of the breeding (yellow) and the wintering areas (brown: Senegal/Guinea-Bissau, orange: Mali/ Ivory Coast and green: Benin/Nigeria) of all tracked Iberian bee-eaters (n = 28).

Table 6.2. Migration parameters for female and male Iberian bee-eaters tracked in 2015-2016 (n=2), 2016-2017 (n=22) and 2017-2018 (n=1). Travel duration (days) and speed (km/day) refer to migratory periods.

	Females				Males			
	Mean	**SD**	**Min**	**Max**	**Mean**	**SD**	**Min**	**Max**
Autumn								
Departure date	13 Aug	8.6	5 Aug	1 Sep	12 Aug	11.5	26 Jul	30 Aug
Arrival date	9 Sep	8.1	1 Sep	25Sep	12 Sep	8.9	1 Sep	24 Sep
Travel duration	26.4	9.1	11	46	34.2	17.8	9	57
Travel speed	137.6	62.8	67.7	299.0	127.5	92.0	46.5	320.0
Spring								
Departure date	20 Mar	7.5	8 Mar	2 Apr	20 Mar	3.6	13 Mar	24 Mar
Arrival date	7 Apr	7.9	27 Mar	23 Apr	7 Apr	7.6	30 Mar	22 Apr
Travel duration	17.4	5.0	11	29	18.7	9.0	10	35
Travel speed	195.0	52.7	104.4	291.3	189.7	73.8	104.0	321.8

In spring, travel duration was shorter by 12.2 days on average (W = 405.5, p = 0.005; Figure 6.2A) than in autumn, and travel speed was higher by 59.8km/h (W = 136, p = 0.002; Figure 6.2B). However, we found no differences between sexes regarding seasonal travel duration (autumn: W = 73, p = 0.847; spring: W = 59, p = 0.864), travel speed (autumn: W = 83, p = 0.767; spring: W = 62, p = 0.713) or migration timing (departure breeding: W = 76, p = 0.978; arrival wintering: W = 63.5, p = 0.473; departure wintering: W = 52, p = 0.810; arrival breeding: W = 56.5, p = 1; Figure 6.3 Table 6.2).

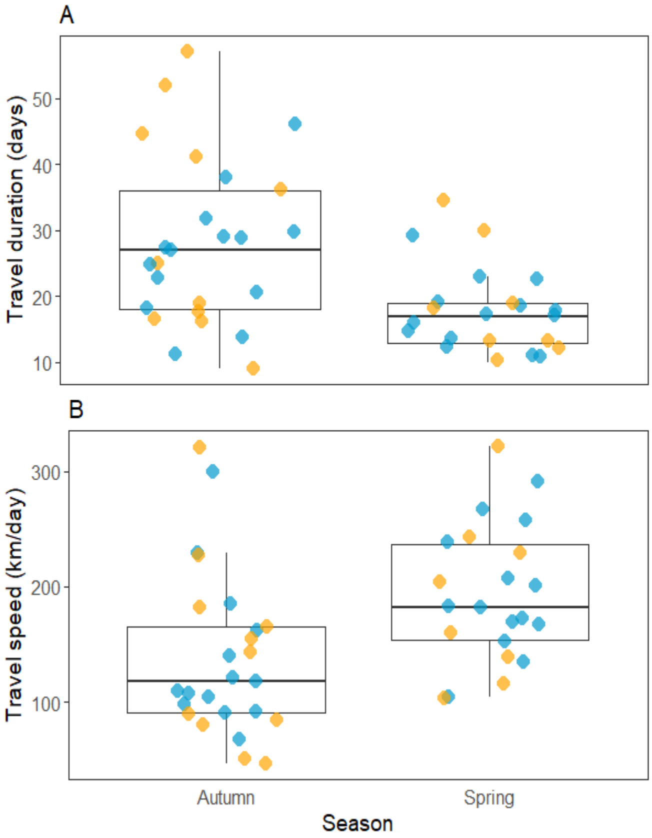

Figure 6.2. Travel duration (A) and travel speed (B) of Iberian bee-eaters during autumn and spring migration. Boxes show the median and 25-75% quartiles, whiskers extend up to 1.5 times the inter quartile range from the hinge. Points are coloured by sex (blue: females, orange: males).

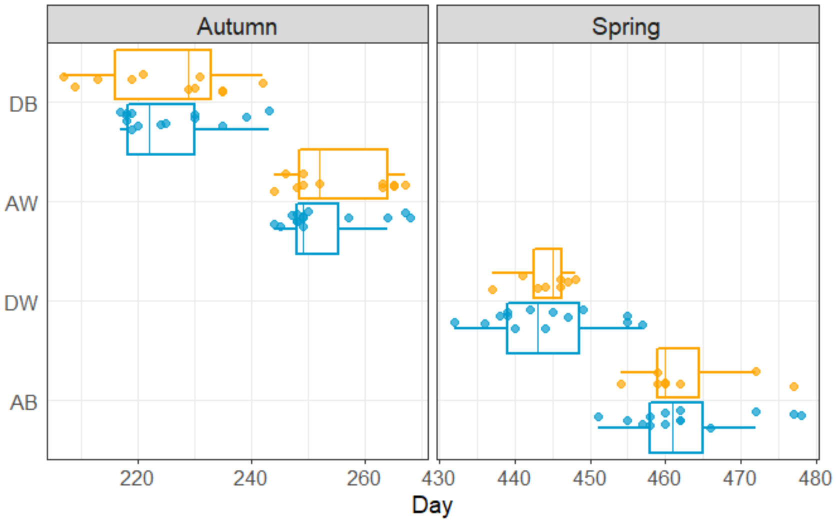

Figure 6.3. Migration timing of female (blue) and male (orange) Iberian bee-eaters in several migratory stages (DB: departure from breeding; AW: arrival to wintering; DW: departure from wintering; AB: arrival to breeding). Boxes show the median and 25-75% quartiles, whiskers extend up to 1.5 times the inter quartile range from the hinge. X-axis depicts Julian days from 1st of January.

Departure from the wintering area and travel duration were the best predictors for explaining the variation in arrival date at the breeding sites (AICc = 109.86, Table S6.1). Birds departing earlier from the wintering areas, or having shorter travel duration, tended to arrive earlier to the breeding areas (Table 6.3, Figure 6.4A and B). However, departure date was negatively correlated with travel duration, as bee-eaters departing earlier travelled for longer than conspecifics departing later (Spearman correlation, r = -0.50, p = 0.01; Figure 6.4C).

Table 6.3 – Statistical results of the top ranked linear model (wintering departure + travel duration) predicting breeding arrival time.

	Estimate	**SE**	**t**	**p**
Intercept	-1.1	3.03	-0.36	0.72
Wintering departure	1.04	0.08	12.00	<0.001
Travel duration	1.05	0.09	11.42	<0.001

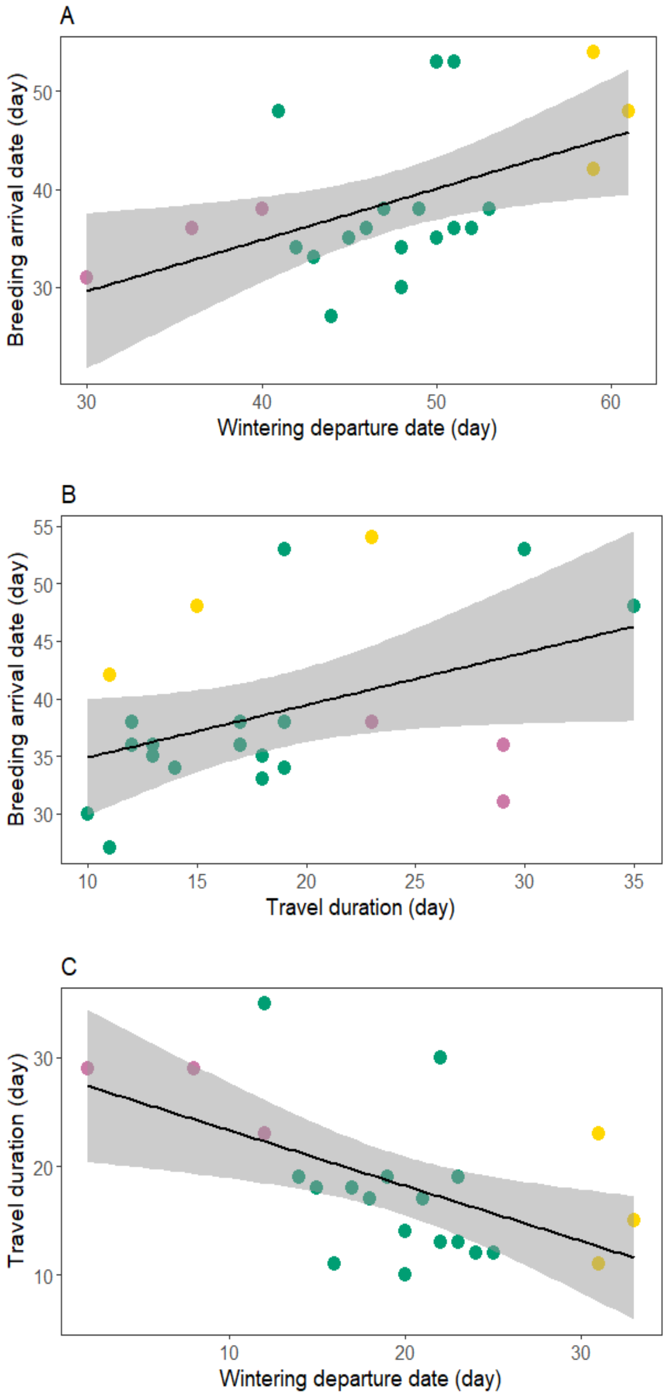

Figure 6.4. Variation on: (A) breeding arrival date and wintering departure, (B) breeding arrival and spring travel duration and (C) travel duration and wintering departure, of tracked Iberian bee-eaters. Dates are shown in Julian days from the 1st March, and linear regression lines are drawn with grey shaded area representing 95% confidence interval. First and last departing individuals are represented in pink and yellow, respectively; the remaining individuals are shown in green.

Arrival at the breeding areas positively affected laying dates, as birds arriving first laid their eggs earlier (laying date= 0.724 x arrival date + 41.211; t=3.291; p = 0.004; r^2 = 0.35; n = 19; Figure 6.5A). Productivity was significantly different between years, with birds in 2016 producing overall more fledglings (mean = 2.72 ± 0.88) than in 2017 (mean = 2.23 ± 1.85; Table 6.4, Figure 6.5B). And time of laying only influenced productivity in 2017 (Table 6.4, Figure 6.5B), as the number of fledglings decreased during the season. However, this was not the case in 2016, when productivity remained

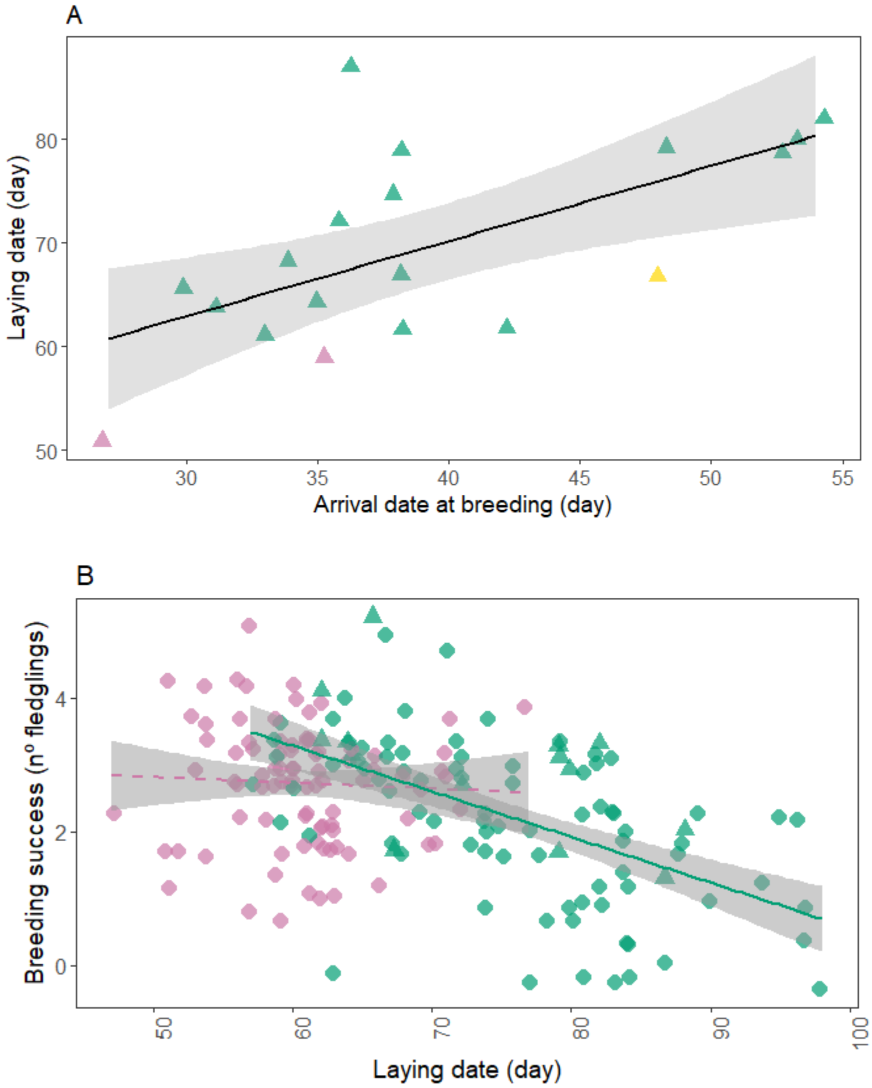

Figure 6.5. Variation on: (A) arrival date at the breeding area and laying dates of tracked Iberian bee-eaters. Pink, green and yellow show birds recaptured in 2016 (n=2), 2017 (n=16) and 2018 (n=1), respectively; and (B) laying date and productivity in 2016 (pink) and 2017 (green). Tracked birds are represented with triangles and other bee-eaters with circles. In both plots, dates are shown in Julian days from the1st March and linear regression lines (solid line shows significant differences) are drawn with grey shaded area representing 95% confidence interval.

constant throughout (Table 6.4, Figure 6.5B). We also found a negative relationship between timing of laying and productivity, when considering only the tracked bee-eaters from both years (productivity = -0.058 x laying date + 7.145; t = -2.911; p = 0.010; r2 =0.32; n = 17). It was therefore possible to establish, at the individual level, a positive effect of arrival date on laying date and a negative effect of laying date on productivity, therefore highlighting the important effects of early arrival at the breeding areas on productivity.

Table 6.4. Statistical results of the linear models testing the relationship between laying dates and productivity in 2016, 2017 and in both years combined.

		Estimate	**SE**	**t**	**p**
2016 + 2017	Intercept	3.248	1.148	2.827	0.005
	Laying date	-0.008	0.018	-0.458	0.647
	Year	4.141	1.359	3.047	**0.002**
	Laying date x Year	-0.059	0.021	-2.823	**0.005**
2016	Intercept	5.248	1.094	4.797	<0.001
	Laying date	-0.008	0.017	-0.481	0.632
2017	Intercept	7.389	0.756	9.771	<0.001
	Laying date	-0.068	0.009	-6.869	**<0.001**

Discussion

This study shows that earlier departure from the wintering areas and shorter travel duration resulted in earlier arrival of bee-eaters. This has important consequences, as individuals that arrived earlier also laid earlier and produced more offspring overall. However, the pattern is not consistent between years, indicating that local factors in the breeding areas, such as weather conditions and related food availability, also play an important role in determining annual productivity.

Non-breeding distribution

Bee-eaters from Iberia spent the winter period in West Africa between Senegal and Nigeria, confirming earlier findings based on five birds (Chapter 5), but this population’s winter distribution also included Mali/Ivory Coast - a new wintering area recorded for this breeding population, within the species distribution range (BirdLife International 2016). While most Iberian bee-eaters wintered between Senegal and Guinea-Bissau, the other two wintering areas had decreasing proportions of tagged birds, with increasing distance from the breeding area (Guinea-Bissau n = 13; Mali/Ivory Coast n = 10 and Benin/Nigeria n = 5). Interestingly, all Iberian bee-eaters migrated along the western coast of Africa. Individuals occupying more easterly longitudes (i.e. Benin/Nigeria) avoided taking the more direct inland route across the Sahara, contrary to bee-eaters from Germany (Chapter 5). If Iberian bee-eaters undertook a similar route to German bee-eaters, they would shorten the travel distance between breeding and wintering areas by ca. 15%, but would also likely face harsher conditions during migration (Strandberg et al. 2010). Several other Afro-Palearctic species breeding in Iberia are also known to adopt this migratory strategy, like Rollers (*Coracias garrulus*, Catry et al. 2014; Rodríguez-Ruiz et al. 2014) and Barn swallows (*Hirundo rustica*, Arizaga et al. 2015).

Sexual and seasonal variation in migration timing

Although sex-biased variation on migration timing has been demonstrated for several species, mainly in timing of arrival to the breeding sites in spring (e.g. Briedis et al. 2019; Saino et al. 2017), we did not find differences in travel duration, travel speed and migration timings between sexes. Early arrival seems to be particularly important in species where one of the sexes defends the breeding territory (Kokko 1999). However, bee-eaters may pair before arriving at the breeding colony and although male bee-eaters are known to select the nest site, both sexes dig the burrow (Fry 1984); hence early arrival may be equally important for both males and females. A recent study comparing migration timing between sexes on Afro-Palearctic migratory landbirds (including a sample from our study population) reported that males arrive at the breeding sites, on average only a few days, before the females (2-3 days; Briedis et al. 2019). However, that study also included a large sample of bee-eaters from another population breeding in Germany, which could drive the reported sex differences at the species level. Despite the absence of sex specific differences in migration timing we found that Iberian bee-eaters have higher travel speed and shorter travel duration in spring compared to autumn. These strategies are common in many migratory species (e.g. Nilsson et al. 2013; Tøttrup et al. 2012; van Wijk et al. 2017) since early arrival at the breeding areas is often linked to higher productivity, while early arrival to wintering areas may not be so tightly linked to apparent benefits. Indeed, for bee-eaters breeding in Iberia, early arrival promotes higher productivity, although this is modulated by conditions experienced in the breeding area.

Drivers of spring migration timing

For several species, winter departure date is a strong predictor of arrival date at the breeding site (Briedis et al. 2019; Jahn et al. 2013; Lemke et al. 2013; Saino et al. 2017), but differences in the duration of migration can also contribute to the variation in arrival dates (Briedis et al. 2017; McKinnon et al. 2016). Our results show that bee-eaters either depart early or travel faster, as individuals that departed earlier had longer travel duration, while later-departing individuals spent fewer days on migration. Despite this, earlier and slower bee-eaters still arrived to the breeding areas ahead than later but faster individuals. Therefore, traveling at a faster pace was not sufficient to fully compensate for later departure, suggesting that departure from the wintering is likely the main factor influencing arrival order to the breeding areas in this population. Faster migration by later departing individuals was also reported for several species of *Sylvia* warblers, but only during autumn migration (Fransson 1995); while in Great reed warblers (*Acrocephalus arundinaceus*), later departing individuals do not seem to compensate for their delays in spring (Lemke et al. 2013). Late departing Collared flycatchers (*Ficedula albicollis*) also show higher migration travel speed, but contrary to our findings, they seem able to partially catch up with early departing individuals and arrive at the breeding destination at a similar time (Briedis et al. 2018a). It is possible that bee-eaters can only increase travel speed to a certain limit since they are known to rely, at least partially, on a fly-and-forage strategy (Fry 1984). On the contrary, flycatchers, as many passerines, are known to fuel before migration and therefore may be able to maximize travel speed (Briedis et al. 2018a), for example in a final sprint to finish migration (Alerstam 2006).

Bee-eaters departed from the wintering areas over a relatively large period (five weeks: 13Mar - 3Apr). The variation in wintering departure, and consequently breeding arrival dates, may have been be influenced by the group dynamics characteristic of bee-eaters (Dhanjal-Adams et al. 2018). Bee-eaters are known to form groups that can prevail during one or several stages of the annual cycle or even throughout a complete annual cycle (Dhanjal-Adams et al. 2018). These associations might influence the timing of their activity, for example of when to depart (Sueur et al. 2011). Bee-eaters wintering in the regions Senegal/Guinea-Bissau and Mali/Ivory Coast departed (Senegal: 20 March ± 6 days; Mali: 15 March ± 7 days) and arrived (Senegal: 7 April ± 7 days; Mali: 5 April ± 9 days) earlier than the two tracked individuals that wintered in Benin/Nigeria, which departed (22th and 31th March) and arrived considerably later (22th and 23th of April). The late departure by the two individuals wintering in Nigeria could be explained by a late departure of the social group these individuals were part of, as in this area they overlap with bee-eaters traveling to breeding sites in Germany, which are known to depart later (although this could be driven by German bee-eaters wintering as far south as Angola; Chapter 5). Later arrival could also be due to the longer distance needed to travel from this location. However, the distance travelled by birds wintering in Senegal/Guinea Bissau or Mali/Ivory Coast differs only by ca. 260 km and by about 265 km respectively, from bee-eaters wintering in Nigeria, further suggesting that other factors like group dynamics or conditions experienced during winter, rather than distance, may play a role in determining arrival dates into the breeding areas.

Bee-eaters in spring travelled on average for 18.5 days (range 10-35 days) at a mean speed of 190 km/day (range 104-321 km/day). Although travel speed varied between individuals, it was overall low compared to other aerial insectivores migrating between Europe and Africa like Common swifts (*Apus apus*, 326km/day; Åkesson et al. 2012) or Barn swallows (approximately 320km/day; Arizaga et al. 2015; Briedis et al. 2018b). Individuals that departed earlier were possibly less timed constrained and could have had more time to forage during migration, while late departing individuals could be trying to compensate for the delay in order to arrive at the breeding areas at similar time than their conspecific. In any case, conditions during migration are also an important factor influencing migratory rates (Briedis et al. 2017), as reported in Red-backed shrikes (*Lanius collurio*) and Thrush nightingales (*Luscinia luscinia*) which showed delayed arrival at the breeding grounds, after experiencing a severe drought during migration period (Tøttrup et al. 2012).

Linking migration timing to productivity

We report an overall positive relationship between arrival and laying dates for Iberian bee-eaters. Tracked bee-eaters arriving and laying earlier also had higher productivity compared to those that laid their eggs later, in the 2017 season. Although the mechanism by which early arrival leads to earlier laying in this population is unknown, early-arriving birds are able to start laying their clutches earlier (e.g. Smith and Moore 2005), simply as they quickly find suitable nesting sites, which are nevertheless not limiting in the studied colonies (several empty nest holes were recorded each season, JSC *pers. obs.*). However, in our study, 65% of the variation observed remained unexplained and laying dates are certainly affected by other factors besides arrival date, in particular by local weather conditions. As bee-eaters are aerial insectivores, low temperatures upon arrival in the breeding areas may delay the onset of breeding (Cucco et al 1992), but this seems also not to have been the case during our study (see below).

Despite the lack of an overall effect between laying date and productivity, this relationship was year specific. In 2017, the number of fledglings decreased across the season but not in 2016, when laying was overall earlier in the season and productivity remained constant. It is possible that bee-eaters arrived earlier in 2016, as they also started laying earlier, compared to 2017. Interestingly, productivity was on average higher in 2016 compared to 2017, suggesting that in years when breeding conditions are favourable, early and late breeders will produce high and similar number of fledglings. But when facing unfavourable conditions, only early laying individuals will experience high productivity. Indeed, it is known that conditions at the breeding grounds can have a more direct effect on breeding phenology and success, than carry-over effects from previous seasons (Ockendon et al. 2013). For example, adverse weather can decrease insect availability and if such conditions occur during nestling provisioning, this can lead to high bee-eater nestlings mortality (Arbeiter et al. 2016). This was also described for other aerial insectivores like Tree swallows *(Tachycineta bicolor*, McCarty 2001; Winkler et al. 2013) and Pallid swifts (*Apus pallidus*, Cucco and Malacarne 1996), in which nestling mortality increased considerably during prolonged periods of cold weather and rain. However, in our study, low temperatures and/or precipitation were not limiting insect availability during nestling provisioning (June) in either years (2016: mean maximum air temperature 30.1°C, total precipitation 0.7mm; 2017: mean maximum air temperature 32.8°C, total precipitation 8.3mm), and therefore are unlikely to explain the lower number of nestlings fledged in 2017. On the other hand, increasing temperatures during spring can drive the advancement of insect phenology (e.g. Bartomeus et al. 2011). The mean maximum air temperature recorded at the breeding areas during spring of 2016 was 19.1 ± 2.6°C (March 16.4°C, April 18.8°C, May 21.8°C) and the mean total precipitation was 105.7 ± 57.5mm (March 40.5mm, April 127.7mm, May 149.1mm). Conversely, the spring of 2017 was hotter and drier, with the mean maximum air temperatures 22.8 ± 4.1°C (March 18.3°C, April 23.9°C, May 26.3°C) and mean total precipitation of only 38.4 ± 36.0mm (March 76.6mm, April 5.1mm, May 33.5mm, Instituto Português do Mar e da Atmosfera). Therefore, it is possible that weather conditions in 2017 led to the advancement of insect phenology and only those early arriving and laying bee-eaters could benefit from high prey available during nestling provisioning, whereas those laying later, likely had lower food availability and experienced deteriorating conditions by the end of the breeding season. Therefore, in years with harsh breeding conditions, earlier arrival and laying may lead to higher productivity, but in years with favourable conditions, there is no apparent advantage in arriving earlier. We urge for a long-term monitoring of bee-eater and other AP migrant populations in order to expand the knowledge on inter-annual fluctuations of phenology and productivity and its possible causes and consequences.

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Supplementary material

Table S6.1. Ranking of candidate models predicting arrival date to the breeding area.

Model	AIC	AICc	∆AICc
W departure + travel duration	**107.5**	**109.86**	**0**
W latitude + W departure + travel duration	108.40	112.15	2.29
W latitude + W departure + travel speed	124.32	128.07	18.21
W departure + travel speed	131.51	133.86	24.00
W latitude + W departure	148.73	151.09	41.43
W departure	150.88	152.21	42.35
W latitude + travel speed	151.58	153.93	44.07
Travel duration	152.80	154.14	44.28
Travel speed	153.20	154.53	44.67
W latitude	153.66	155.00	45.14
W latitude + travel duration	152.82	155.18	45.32

Chapter 7

The influence of pair-fidelity and age on the breeding performance of a colonial migratory near-passerine

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Abstract

Maintenance of pair-bonds across subsequent reproduction events and/or increased experience with age are often associated with productivity in many avian species. In this study, we explore the influence of pair-fidelity and age on individual breeding performance of European bee-eaters. More specifically, we investigate if the age of partners of the breeding pair influences laying dates and productivity (number of fledglings). Additionally, we determine if older and more experienced pairs are more likely to retain their partner than younger and less experienced pairs (second calendar year vs older than second calendar year), and explore if breeding performance varies when pair-bond is maintained or not between two consecutive years. We did not find significant differences in laying dates and number of fledglings between first breeder pairs, old breeder pairs and mixed pairs (pair members differ in age). However, when considering only individual age categories, the effect on laying dates and productivity is apparent, with old and more experienced females (but not males) laying earlier and having higher productivity than first breeding females. In our study, 36.8% of pairs in which both partners were recaptured in the subsequent season broke the pair bond, suggesting that divorce is common. Additionally, productivity in bee-eaters does not seem to be influenced by mate retention, as we did not record significant differences in laying dates and productivity in year *t+1* between pairs that maintained the pair bond and those that did not. Nevertheless, pair-fidelity may have other advantages than higher productivity, for example knowledge of nest locations in the breeding colony, as selecting a good quality nest site can be the difference between nest success or failure.

Keywords: European bee-eater, *Merops apiaster*, divorce, pair-bond, laying date, productivity

Introduction

Many birds are socially monogamous (Bennett and Owens 2002; Jeschke and Kokko 2008), but mate fidelity varies both within and between species (Dhondt and Adriaensen 1994). Individuals that survive to consecutive breeding season may either form a pair with the previous partner or change partner (Dhondt and Adriaensen 1994). Besides divorce, i.e. the previous partner is still alive but pair bond broke, new pairs are formed because the previous partner has died (Rowley 1983). Although the change of the partner may decrease productivity (Culina et al. 2015) it can also be advantageous for the individual that switch to a partner or territory of higher quality (Orell et al. 1994). Long-term maintenance of pair bond is common in many large long-lived bird species (Bradley et al. 1990), but also occurs in short-lived passerines (Dhondt and Adriaensen 1994; Dubois and Cézilly 2002). There is ample evidence that many species benefit from retaining the same partner in successive breeding seasons (Choudhury 1995). Benefits may include earlier onset of breeding (Gilsenan et al. 2017) and higher reproductive success (Balbontín et al. 2007; Pampus et al. 2005). However, mate fidelity is also likely to involve costs, for example for those retaining a poor quality mate (Choudhury 1995) or waiting for a delayed previous mate with consequent delays in breeding in migratory species (Gilsenan et al. 2017; Gunnarsson et al. 2004; Stutchbury et al. 2016). Mate choice should enable a bird to optimize its reproductive output and whether individuals retain, or change partner, should be determined by the previous and/or expected future reproductive performance (McNamara and Forslund 1996). Potential benefits of divorce include the acquisition of a higher-quality mate and associated increased reproductive performance, while costs involve prospecting for a new mate might include the risk to acquire a poor-quality mate, delay or skip breeding (Choudhury 1995). Therefore, pair bonds should only break if and when benefits outweigh their costs (Ens et al. 1993). Indeed, low productivity is often linked to mate switching (Dubois and Cézilly 2002), with poor breeding performance possibly leading to divorce (Dhondt and Adriaensen 1994).

In many bird species, younger individuals often have lower productivity than their older conspecifics (Curio 1983; Lozano et al. 1996). Earlier egg laying by older individuals has been linked to higher productivity, in systems where productivity declines seasonally (Robertson and Rendell 2001; Stutchbury and Robertson 1988). But such age related pattern may arise also due to several other factors, such as younger birds having a lower chance of finding a high-quality mate (Lozano et al. 1996) or caring less efficiently for eggs and nestling (Steven 1980). Generally, more experienced birds (older individuals) outperform younger conspecifics and this is the case in many aspects, for example, with adults having higher foraging experience than juveniles (e.g. Desrochers 1992; Enoksson 1988; Franks and Thorogood 2018). However, as younger individuals gain experience their performance improves (Desrochers 1992; Forslund and Larsson 1992). Several studies have also reported higher divorce rates in young breeders than in old individuals (e.g. Choudhury 1995). For example, in Blue tits (*Cyanistes caeruleus*) the annual divorce rate decreased as females became older (Dhondt and Adriaensen 1994). Divorce may be more likely to occur in colonial breeding birds (Jeschke and Kokko 2008) as alternative mates are readily available. Species in which age of breeders can be readily determined (for example via plumage characteristics), and where opportunities for mate switching are high (e.g. colonial breeders) provide an ideal system in which to explore effects of pair-fidelity and age on breeding performance.

The European bee-eater (*Merops apiaster*; hereafter bee-eater) is an Afro-Palearctic migrant described as being monogamous, with pairs breeding together each year as long as both birds survive the non-breeding period (Fry 1984). The maximum lifespan of bee-eater is currently estimated at 7 years and individuals usually start to breed in their second calendar year (Fry 1984), being readily aged by plumage characteristics (Demongin 2016). Females lay the eggs in one to two days intervals and nestlings hatch after 20 days, with both parents feeding the nestlings until fledging, ca. 30 days (Fry 1984). For this species, only very limited information on potential effects of age on breeding parameters is available (Lessells and Krebs 1989) and the relationship between pair-fidelity and productivity is yet to be explored. In this study we first (1) investigate if laying dates and productivity (number of fledglings) are influenced by age of the breeding pairs and by individual age of females and males. Additionally, (2) we determine if older and more experienced pairs are more likely to retain their partner than younger and less experienced pairs (second calendar year vs older than second calendar year) and finally (3) explore if breeding performance varies when pair-bond is maintained or not between consecutive years.

Methods

Data sampling

Fieldwork took place in two bee-eater colonies in Portugal (39.9°N and 38.1°N; 7.1°W) between June and July during five breeding seasons from 2015-2019. Bee-eaters were captured during nestling rearing periods using walk-in nest traps (Chapter 2). Captured birds were sexed and aged by plumage characteristics according to Blasco-Zumeta and Heinze (2013). When an individual did not exhibited the typical sex-specific coloration, we assigned the sex using a discriminant function (n = 32, for further details see Chapter 2). We assigned birds to two age classes, either being in the second calendar year (i.e. EURING age class 5) or older than second calendar year (EURING age class 6). The exact age of an age class 6 bird is unknown. After capture both male and female of a nest, we classified each pair according to age of both individuals as: both individuals of age 5 (hereafter, first breeders); both individuals of age 6 (hereafter, older breeders); individuals with different age classes (i.e. 5 and 6; hereafter, mixed pairs). The overall annual average recapture rate was 17 ± 8.8%, although it varied between years (2016: 12.9%; 2017: 30%, 2018: 10.1%; 2019: 15.1%).

We estimated annual pair-fidelity by considering the individuals that bred in a given year (year *t*) and returned to breed in the following year (year *t+1*) to the same colony, and for which the partner identity in years *t* and *t+1* was known*.* For simplicity, only the first recapture (and associated breeding performance) of a given individual was considered, even if the same individual was recaptured more than once (7.8%, n = 5).

We defined productivity as the total number of fledglings per nest. To do so, we recorded the number of pre-fledging nestlings during the third week of development using a “burrowscope” (Chapter 3). As bee-eaters take ca. 30 days to fledge, we assumed that the number of nestlings recorded in this final week to be the number of fledgling’s produced. We estimated hatching date of each brood using a photographic guide for age determination of bee-eaters nestling (see Chapter 3). Laying dates were back-calculated by subtracting the species incubation period (i.e. 20 days) to individual hatching dates.

Statistical analysis

In order to explore if laying date and/or productivity were influenced by pair age we performed one-way ANOVAs, with laying date or number of fledglings as depend variable and age of the pair as independent variable. In order to test if laying date and/or productivity were influenced by age of the individual we performed t-tests considering only male or female age as independent variable. Only laying dates and productivity of pairs from which the age of both the female and the male were known were included in these analysis (mixed pairs: 39; older breeders: 57; first breeders: 69). To assess if the proportion of pairs from different age groups was biased in our study system, we performed a Chi-square goodness of fit. Similarly, we assessed if among the mixed pairs, the proportion of females of age 5 and 6 differed.

To test for differences in pair-fidelity between older and younger pairs we considered only pairs composed by first breeders (n = 20) and older breeders (n = 15), for which the status of both individuals in years *t* and *t+1* was known. We then performed a Chi-square independence test considering the two age classes and the number of pairs that maintained the pair bond or not. Finally, we investigated if laying dates and productivity in year t+1 differed when pair bond was maintained, or when it was not maintained by performing a t-test. Normality was confirmed by visual inspection and all the analysis were performed in R-software (R Core Team 2017).

Results

Pairs of bee-eaters consist more frequently of first breeders (41.8%, n = 69) and older breeders (34.6%, n = 57) than mixed pairs (23.6%, n = 39, Chi-squared = 8.29, df = 2, p-value = 0.015). Pair composition did not differ between colonies (Chi-squared =4.74, df = 2, p-value = 0.093). Among mixed pairs, the proportion of first breeding females (67%, n = 26) was significantly higher than the proportion of older females (33%, n =13; Chi-squared = 4.33, df = 1, p-value = 0.037). We did not find significant differences in laying dates or number of fledglings between the three classes of pair age compositions (Table 7.1, Figure 7.1). However, considering only females, older

Table 7.1. ANOVA output comparing laying dates and productivity between age classes of European bee-eaters from Iberia.

			Laying date		
	Df	**Sum sq**	**Mean sq**	**F value**	**P**
Pair age	2	305	152.40	1.465	0.233
Residuals	206	21433	104.0		
			Productivity		
	Df	**Sum sq**	**Mean sq**	**F value**	**P**
Pair age	2	3.71	1.85	2.12	0.124
Residuals	165	144.5	0.87		

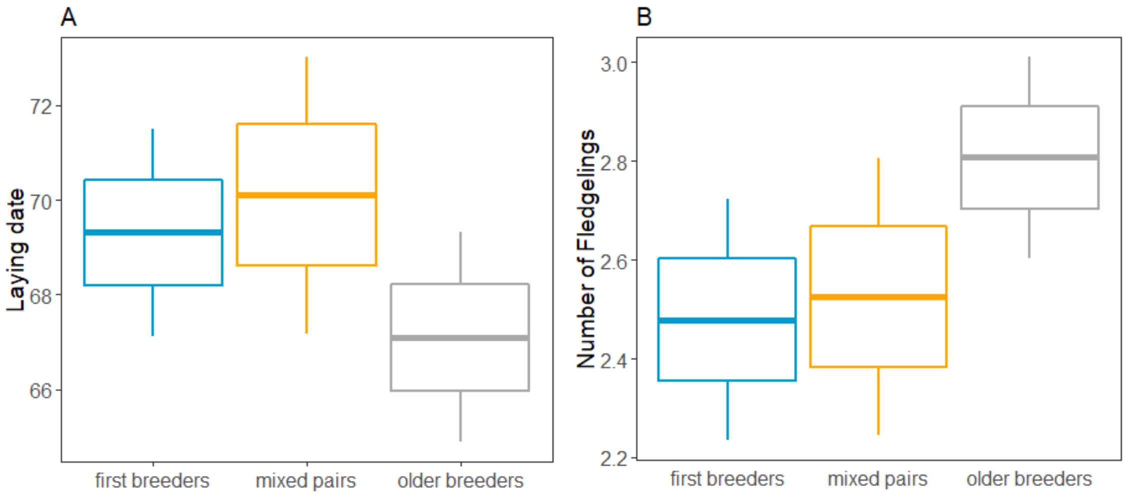

Figure 7.1. Variation on average ± SE (A) laying dates and (B) number of fledging's for bee-eater pairs of different age: first breeders, mixed pairs and older breeders. Dates are shown in Julian days from the 1st of March.

breeders showed an earlier average laying date (6 Apr ± 9.55) and higher productivity (2.8 ± 0.84), than females breeding for the first time (laying date: 9 Apr ± 10.5, t = -2.25, df = 186.81, p-value = 0.025; productivity: 2.4 ± 0.98, t = 2.40, df = 160.54, p-value = 0.017). On the other hand, there was no differences between males of different ages (laying dates: t =-0.09, df =206.22, p-value =0.92; productivity: t = 1.06, df =155.31, p-value =0.288; Figure 7.2).

We attained information about the pair bond status (maintained / not maintained) and breeding performance of 56 complete pairs for two consecutive breeding seasons. Overall, 12 pairs remained together whilst 37 pairs had a new partner in year *t+1*. Among the 19 pairs from which both individuals returned in the following year, 37% (n = 7) divorced (Figure 7.3). However, we did not find age-specific ability to maintain the pair bond in the subsequent year, as older pairs were not more likely to maintain the pair bond than first breeding pairs (Chi-squared = 0.012, df = 1, p-value = 0.99). There was also no differences in laying dates (t = -0.20, df = 23.79, p-value = 0.840) and productivity (t = -1.80, df = 17.18, p-value = 0.088) in year *t+1* between pairs that maintained the pair bond and those that did not.

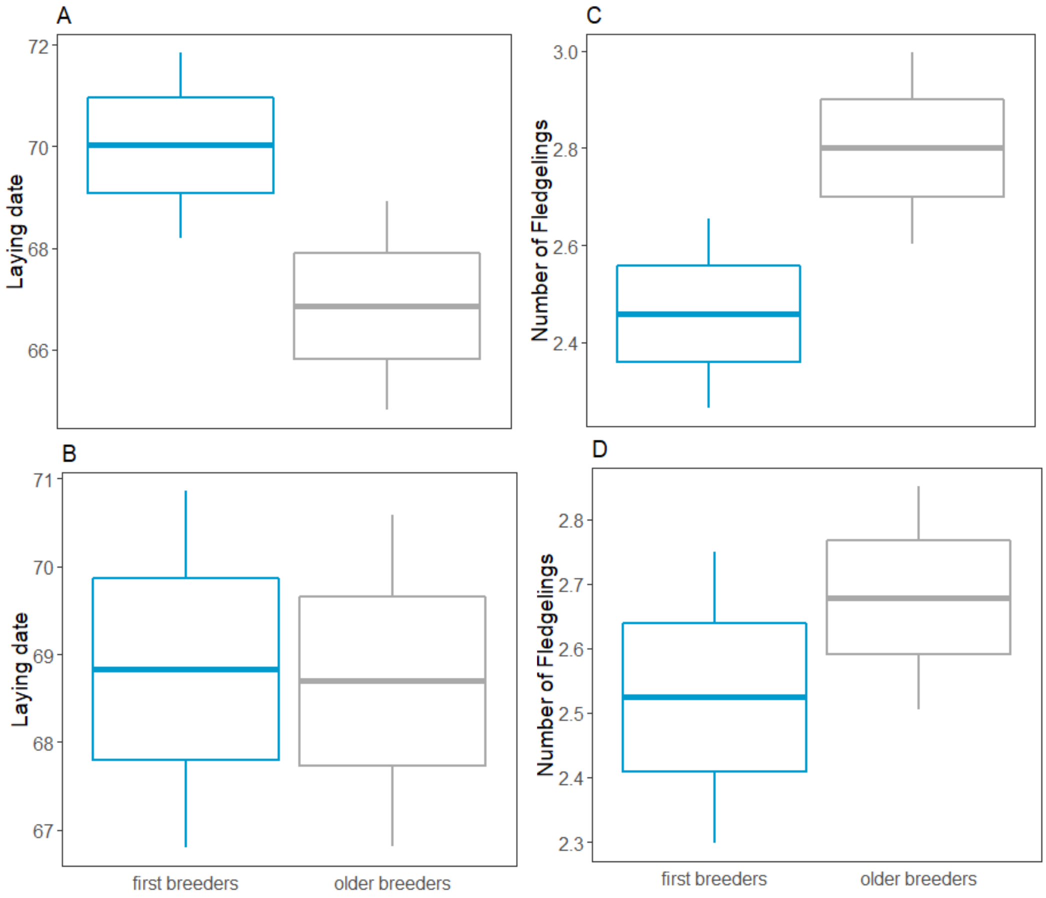

Figure 7.2. Variation on average ± SE laying date (left column) and number of fledglings (right column), for female (top row) and male (bottom row) bee-eaters of different age classes. Dates are shown in Julian days from the 1st of March.

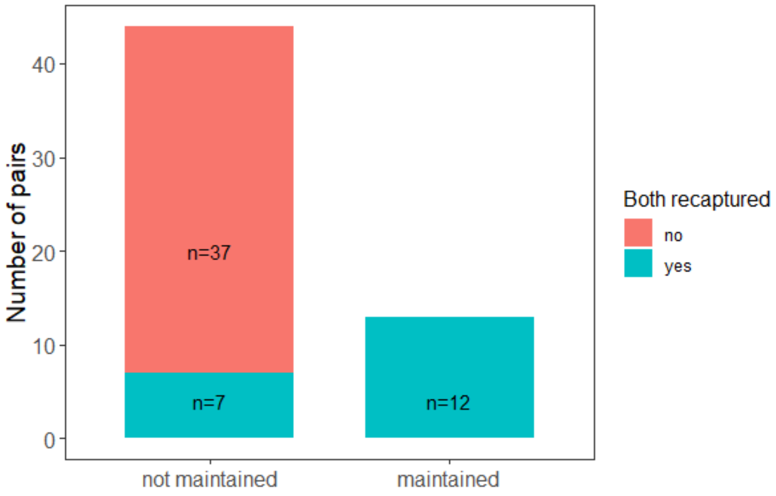

Figure 7.3. Frequency of bee-eater pairs that maintained or not the pair bond in year *t+1*. Blue shows pairs from which both individuals were recaptured, indicating those that divorced, within pairs that did not kept the pair bond.

Discussion

Influence of age on breeding performance

Reproductive performance in birds generally increases with age (e.g. Balbontín et al. 2007) up to a certain time (Robertson and Rendell 2001). Numerous studies have shown that increasing foraging and parental experience can explain this age-related increase in productivity (Balbontín et al. 2007; Curio 1983; Nol and Smith 1987; Steven 1978). In our study, however, we did not find significantly different productivity between first year breeders and older breeders. Nevertheless, there was a tendency for older breeders to produce a higher number of fledglings (2.76 ± 0.79) than mixed pairs (2.52 ± 0.93) and first breeders (2.44 ± 1.08, Figure 1). The lack of an effect may be due to several factors, for example the relatively short time series used, the grouping of all individuals aged more than class 5 into one group. Year-specific factors are also likely to influence annual variability in productivity (e.g. weather conditions, food availability and predation), which may contribute to the inability of finding such an effect.

When considering only individual age, age-dependent effects on laying dates and productivity are apparent, as older and more experienced females (but not males) layed earlier and produced more fledglings than first breeding females. Similarly, Lessells and Krebs (1989) showed that older females start breeding earlier but they could not find differences in productivity. In fact, productivity varies closely with either sex if age is considered. For example, in Barn swallows (*Hirundo rustica*), productivity increased with age of females but not males (Balbontín et al. 2007), conversely in Brown thornbills (*Acanthiza pusilla*), only male's age had a significant positive effect on annual reproductive success (Green 2001). In bee-eaters, higher productivity of older females may be related to faster establishment of the pair-bond and readiness to lay in relation to first breeding females, allowing an earlier laying, which resulted in higher productivity. By initiating laying earlier, it is possible that females increased the probability of timing nestling growth with a period of higher food abundance, contributing for the larger number of fledglings. Older bee-eater females are known to lay larger clutches (Lessells and Krebs 1989) and clutch size (not quantified in this study) is also known to reflect female condition (Slagsvold and Lifjeld 1990; Steven 1978), which is possibly linked to individual experience preparing towards laying, for example in maintaining body condition while obtaining the necessary resources for egg production. Indeed, the aerial foraging behavior of the bee-eaters seems to require considerable skills, and it may be that first-breeders are not as efficient while foraging during their first breeding season as are older individuals, and may therefore be unable to acquire the needed body condition prior to breeding and providing for nestlings as rapidly and efficiently. Low productivity due to reduced foraging skills has been suggested for other aerial insectivores like the Tree swallow (*Tachycineta bicolor*, Steven 1978) and increasing foraging ability with age has been documented on Blackbirds (*Turdus merula*, Desrochers 1992), Hihis (*Notiomystis cincta*, Franks and Thorogood 2018) and Nuthatches (*Sitta europaea*, Enoksson 1988).

Influence of pair-fidelity on breeding performance

In our study, 36.8% of pairs in which both members were recaptured in the subsequent season did not maintain their previous partners, a considerably higher proportion compared to the 12% previously reported for the species (Lessells and Krebs 1989). Although the sample size of pairs recaptured in the year after capture was small (n = 19), divorce might be more common than previously described for bee-eaters. In fact, colonial birds tend to have higher divorce rates than other species (Jeschke and Kokko 2008). The divorce rate reported in this study was lower than what was reported for other long-distance migrants like Great reed warbler (*Acrocephalus arundinaceus*, 88%) and Collared flycatcher (*Ficedula albicolis*, 92%) including several colonial passerines like the Barn swallow (58%) and House martin (*Delicon urbicum*, 100%; Dhondt and Adriaensen 1994).

Probability of divorce is often higher in first-breeders (e.g. Pampus et al. 2005) and may decrease with age (Choudhury 1995; McNamara and Forslund 1996). Our results show that older pairs of bee-eaters seem equally likely to maintain the same mate during two consecutive seasons than first breeding pairs. However, since it is not possible to determine the exact age of older birds (age 6) and the the life-span of bee-eaters is estimated to be around 6–7 years (Fry 1984), potential differences in the ability to maintain the pair bond for individuals older than age 5 remains unexplored.

Increasing levels of mate-fidelity are more apparent on long-lived than in short-lived species (Bradley et al. 1990; Harris et al. 1987), as long-lived individuals can be more mate selective, they may be more able to accommodate lower productivity early in life, if that means increased productivity during later years (McNamara and Forslund 1996). Short-lived species however, have fewer breeding attempts during their life, and may thus be less selective (McNamara and Forslund 1996), which ultimately may result in low divorce rates at younger ages. Although bee-eater can not be considered as a short-lived species (estimated life-span of 6-7 years), an urgency to increase productivity at an early age may originate the lack of differences in pair-fidelity between first breeders and older pairs.

Many species benefit from mate fidelity in successive breeding seasons (Choudhury 1995; Culina et al. 2015). For example, in Tropic birds (*Phaethon rubricauda*), productivity of faithful pairs was significantly higher than in pairs that bred together for the first time, indicating that mate-fidelity may outweigh the costs of disrupting the pair-bond (Sommerfeld et al. 2015). Similarly, in Great tits, individuals breeding together for the first time had smaller clutches than pairs which had maintained their bond in a second season (Perrins and McCleery 1985). Alternatively, disruption of pair bonds can also be beneficial for both partners if they are closely related (Hatchwell et al. 2000) or when individuals switch to a partner and/or territory of higher quality (Orell et al. 1994). However, in our study, productivity in bee-eaters does not seem to be influenced by mate-fidelity. This pattern may occur when pair disruption happens by chance and not as an adaptive strategy to increase productivity. For example, when a mate is forced away from its partner by a third individual (e.g. Choudhury 1995; Heg et al. 2003; Jeschke et al. 2007; Taborsky and Taborsky 1999) or when pairs (accidentally) split during migration or occupy distinct non-breeding areas, being unable to reunite again (Dhondt and Adriaensen 1994; Saitou 2002). But re-mating with the same partner may also occur by chance, when both partners return independently to the same breeding site and meet there again. Bee-eaters are colonial and social birds, migrating long distances in the same social group, that can or not include previous breeding partners (Dhanjal-Adams et al. 2018). Social groups can either break up or remain together during the non-breeding period (Dhanjal-Adams et al. 2018). This may influence the synchrony in the timing of arrival: if a breeding pair migrates together it should lead to synchronous arrival to the breeding areas in the following year. However, if the pair split during non-breeding period, synchrony in timing of arrival might be less likely. Consequently, asynchronous arrival can lead to a break of the pair-bond as the costs of waiting for the former partner, which may or not arrive, likely outweigh the benefits of mate fidelity and the costs of finding a new partner (Gilsenan et al. 2017; Ludwig and Becker 2006). Additionally, as colonial species have easy access to potential future partners, an effect on productivity after pair disruption may be low (Dubois et al. 1998; Jeschke and Kokko 2008). In bee-eaters, it is possible that pair-fidelity produces advantages other than productivity, for example knowledge on the best nest location, as choosing the more advantageous sites to nest may be the difference between nest success or failure (Li and Martin 1991; Mead and Pepler 1975). If maintained pair bonds do not translate to higher-productivity in Iberian bee-eaters, then pair-fidelity should be lower than what previously reported for the species (88%, Lessells and Krebs 1989). In order to achieve the highest productivity males should strive to mate with older females and females should try to lay as soon as possible.

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Chapter 8

General discussion

General discussion

Population declines have become a widespread phenomenon in a wide range of migratory birds across the world (Kirby et al. 2008; Sanderson et al. 2006; Vickery et al. 2014). In order to assess factors constraining migratory species across their range and the potential consequences for demography, it is essential to understand individuals' performance throughout the annual cycle and its relationship with productivity (Kirby et al. 2008; Small-Lorenz et al. 2013).This will allow better understand and predict how populations may respond to current and future global changes. The present thesis contributes to a wider understanding of the reproductive ecology, migratory patterns at population and individual levels and its relationship with productivity of an Afro-Palearctic insectivore, the European Bee-eater. Below, I outline the main achievements of each chapter and the study limitations. I then synthesize and discuss this thesis and suggest future research.

Development of discriminant functions for sexing bee-eaters

As in many other bird species, bee-eaters can be sexed based on sex-specific plumage characteristics (Demongin 2016). However, some individuals do not display the typical sex-specific plumage coloration, making the use of plumage for sex discrimination often unreliable. In addition, the usage of a single biometric is limited due to considerable overlap in size between sexes (Demongin 2016; Lessells and Ovenden 1989). To overcome this limitation, in **Chapter 2** I provide a comparative analysis of the sex and age specific variation in biometrics in two bee-eater populations (Iberia and Central Europe) and use several biometrics of molecularly sexed individuals to construct discriminant functions that can be used for sex determination in the field. This study is the first using biometrics of molecularly sexed birds to generate population specific, as well as, general discriminant functions, for sexing adult European bee-eaters. I develop multivariate discriminant functions containing three biometrics (head-bill, wing and tail tip lengths) that provide the highest discriminant accuracy (Portugal: 91%, Germany: 96%), although discriminant functions containing two biometric have similar discriminant power than the ones using three variables. The discriminant accuracy of the functions for the Portuguese birds is lower compared to the functions from the German population. However, in Portugal, biometrics were collected by six ringers while in Germany by a single ringer only. Variation between ringers in the biometrics included in the discriminant analysis may have contributed to a lower discriminant accuracy of birds from the Portuguese population. It is therefore recommended that biometric measurements are collected by a few experienced ringers at each site. Moreover, as discussed in Chapter 2, some biometrics should be regarded with caution as potential discriminant trait. This is the case of tail measurements, such as tail length, tail tip and right rectrix, once bee-eaters often show worn tail edges (JSC pers. obs.). Similarly, the bill can be severely worn after nest digging (Mountfort 1957; JSC pers. obs.). Nevertheless, the discriminant functions provided in this chapter can be used with the same statistical confidence for all individuals.

Photographic guide for aging nestlings

The bee-eater is a cavity-nesting bird that digs its nest in sloping hillsides or flat ground with nests chambers usually of difficult access (Fry 1984). Accurate estimation of nestling age (and associated parameters such as hatching date and predicted fledging date) is key in avian demography studies and also in population ecology and conservation (e.g. Eeva and Lehikoinen 1996; Marchesi et al. 2002; Saunders and Ingram 1998). However, determining nestling age often requires handling the birds, and in some species, nests are extremely difficult access or doing so generates high levels of disturbance or destruction; this is the case of the European bee-eater. To overcome this limitation, I develop and test the accuracy of a photographic guide to determine nestling age in this species, based on visible traits (captures with an adapted camera) that allow aging nestlings without requiring their removal from the nest (**Chapter 3**). The aging guide developed in this chapter allows estimating the age of nestling bee-eaters to within 3 days, with an average accuracy of 0.85. However, estimation of nestling age varies in accuracy throughout the growth period. Although observers tend to increase their accuracy during the experimental set up, between observer variance is small, suggesting that this guide can be used by virtually any person.

Frequent nest visits may affect nesting success by drawing the attention of potential predators to the nest or by changing parental behavior, ultimately leading to potential nest predation or abandonment (Gotmark 1992). Therefore it is desirable to reduce the frequency and length of nest visits. For this reason, in this chapter, it is also present a protocol that proposes visiting the colony and nests at 12 day intervals (maximum of two visits), allowing to achieve the highest accuracy metrics with the smallest disturbance.

Finally, it is relevant to mention that European bee-eater nestlings hatch asynchronously (Lessells and Avery 1989) and nestlings that hatch first usually become the largest individuals, sometimes contrasting considerably in size and developmental stage with its later hatched and younger siblings. As the nestling aging guide was developed based on the first hatched nestlings of each brood, it is important that these individuals are targeted on each visit, so that unbiased age estimation between nests are attained.

Variation of parental and nestling diet

Bird species associated with grassland and farmland habitats that depend on invertebrate prey as their main food source are declining at a very fast rate (Chamberlain et al. 2000; Donald et al. 2006; Vickery et al. 2014). The diet of the bee-eater, an insectivore long-distance migrant, is well studied across its breeding range. However, how its diet changes between seasons and distinct habitats, in the same population, remains poorly studied. Additionally, diet studies are still scarce in the Iberian Peninsula (but see Costa 1991; Farinós-Celdrán et al. 2016; Herrera and Ramirez 1974; Lourenço 2018) and none has previously assessed habitat and seasonal variation, as well as differences between adults and nestlings. In **Chapter 4**, I show that proportion of Hymenoptera in the diet is higher in colonies located in open habitats, compared to colonies surrounded by settlements and forest, where Hymenoptera and Coleoptera are consumed in similar proportion. This suggests that prey availability in habitats surrounding colonies influences bee-eater diet composition, which can be expected for an opportunistic species. I also report seasonal differences in the diet of adults, likely also linked to prey availability. In this chapter I show for the first time that size of prey provided to nestlings increases across the provisioning period. This chapter also brings to light how prey selection changes across the breeding season: adults have a preference for Coleoptera and Hymenoptera during pre-incubation period, and as prey availability decreases, they continue to prefer Coleoptera and Hymenoptera for themselves, as well to provide to nestlings.

Migratory patterns of three bee-eater populations

Different breeding populations of migratory species often use separate routes to migrate between breeding and non-breeding grounds. Recent changes in climate and land-use have led to breeding range expansions in many species, but it remains unclear whether these populations also establish new migratory routes, non-breeding sites and migration phenology. **Chapter 5** provide important first insights into migration patterns of European Bee-eaters by comparing the migration patterns of two traditional breeding populations in western (Iberia) and eastern (Bulgaria) areas of the breeding range, with those from a newly founded northern population (eastern Germany). This study confirms that western European breeders migrate on a western route to non-breeding area in West Africa, and that eastern European birds migrate on an eastern route to southern Africa. Bee-eaters from the recently established northern-central European population, in eastern Germany, use the western migration corridor to reach a new core non-breeding area, located between northern Angola and the southern parts of Congo. This study also provides evidence for earlier timing of migration in the western population compared to the northern and eastern populations. Although sample sizes were small, as is typical for such exploratory studies (see Brlík et al. 2019), this chapter nonetheless contributes significantly to the knowledge of migration routes and timing in this species.

Linking migratory patterns to productivity

Population declines have become a widespread phenomenon in migratory birds across the world (e.g. Kirby et al. 2008; Sanderson et al. 2006; Vickery et al. 2014). Exploring the relationship between migration performance and breeding phenology, as well as its consequences for productivity, is crucial to better predict changes in population dynamics of migratory species, in light of ongoing environmental changes. In this study, I use geolocators to explore migration performance and its association with productivity in European bee-eaters breeding in Iberia. **Chapter 6** considerably expands the information provided on Chapter 5, in terms of spatio-temporal distribution of Iberian bee-eaters and explores, for the first time, the potential effects of migration performance on productivity. This chapter brings novel information about the factors influencing arrival dates to the breeding areas in bee-eaters, showing that departure from the wintering area and travel duration are the main factors potentially influencing arrival. It also provides the first insights on the relationship between laying dates and productivity of Iberian bee-eaters, with the results suggesting that in years when breeding conditions are favourable, early and late breeders will produce high and similar number of fledglings; but when local conditions are unfavourable, individuals lay on average later and the number of fledglings decrease across the season. This chapter brings to light how carry-over from preceding seasons and environmental conditions in the breeding season might interact to influence population dynamics in the European bee-eater. The low sample size of geolocators recaptured in 2016 and 2018 did not allow comparing migration patterns between years. Indeed, the recapture rate of tracked birds (2016: 6.6%; 2017: 36.7%; 2018: 1.6%) and ringed individuals (2016: 24.2%; 2017: 32.1%; 2018: 13.2%) was very variable between years, suggesting that return rates to the colonies might also change inter-annually. Because nestling bee-eaters hatch asynchronously (Lessells and Avery 1989), correctly estimating number of fledglings requires nests to be visit before the first nestlings fledge. However, visiting too earlier may provide an inaccurate estimation because younger nestlings are prone to die of starvation (JSC pers. obs.), leading to an overestimation of the number of fledglings. These factors make productivity assessment in bee-eaters a high demanding task, as colonies need to be visit frequently. In order to reduce the number of visits, I use the aging guide developed in Chapter 3 to determine the age of nestlings and predict the date of fledging of the older nestlings, thus attaining reliable quantification of productivity. The present study provides data on productivity for two years and although the number of fledglings differed significantly between years, it is not possible yet to reasonably predict any long-term demographic effects of changing environmental conditions in this population.

Pair-fidelity and breeding performance

Maintenance of pair-bonds and increased experience (through age) are often associated with productivity in many avian species. In **Chapter 7** I explore the influence of pair-fidelity and age on productivity of European bee-eaters. For this species, only very limited information on potential effects of age on breeding parameters is available (Lessells and Krebs 1989) and the relationship between pair-fidelity and productivity has never been explored. This chapter shows that older and more experienced females lay earlier and have higher productivity than first breeding females. However this pattern is not recorded in males. Approximately 37% of pairs divorced, suggesting that divorce may be more common than what was previously described for the species (12%, Lessells and Krebs 1989). The results also show that older couples seem equally likely to maintain the same mate during two consecutive seasons than first breeding pairs, and that productivity in bee-eaters does not seem to be influenced by mate retention.

Synthesis and future directions

Declines in Afro-Paleactric migrants are likely driven by several factors including habitat loss and climatic changes at breeding locations in Europe and non-breeding sites in Africa, increased hunting pressure in southern Europe and Sahel, predation, collision with infrastructure and pesticide use (Sanderson et al. 2006; Vickery et al. 2014). These causes are likely to be both species- and population-specific (Vickery et al. 2014). Disentangling these effects is a major challenge for conservation mostly due to the current lack of data on the spatio-temporal distribution of these species and on the distinct ecological conditions experienced by individuals at several locations. These limitations arise in part because of the huge cost of performing surveys across the flyway.

Methods for studying the bee-eater

The first two manuscripts of this thesis (Chapter 2 and 3) were developed to increase knowledge on the study species, but also on the need of the application of the described methods in the subsequent chapters. The development of discriminant functions to determine the sex of individuals is now a widespread technique applied in many avian groups, from seabirds (Friars and Diamond 2011) to waders (Katrínardóttir et al. 2013), passerines (Alarcos et al. 2007) and raptors (López-López et al. 2011). However, it is not always possible to attain high levels of accuracy for species that exhibit large overlap in morphological characteristics (e.g. Meissner et al. 2018). In the European bee-eater, it is possible to discriminate between sexes with high accuracy (87.7% - 97.3%) using a combination of two to three biometrics. Therefore, one can choose the discriminant equation that best fits the data, depending, for example, on the biometrics that were sampled in the field or those that may be possible to collect in future studies. This study shows that wing and tail tip lengths are the best biometrics for sex discrimination in the European bee-eater, similar to Blue-tailed bee-eaters (Siefferman et al. 2007) and highlighting the potential use of these biometrics for discriminating sex among the Meropidae family.

The photographic aging guide (Chapter 3) provides a valuable tool for aging bee-eater nestlings without the need of handling or removing them from the nest. Aging guides based on photographs have been widely developed (e.g. Amiot et al. 2014; Boal 1994; Fernaz et al. 2012) but its accuracy has only been tested in a limited number of species, as the House wren (*Troglodytes aedon*, Brown et al. 2013), Common tern (*Sterna hirundo*, Wails et al. 2014), Eastern bluebird (*Siala sialis*, Wilkins and Brown 2015) and Tree swallow *(Tachycineta bicolor*, Brown and Alianell 2017). Similar to those studies, the aging guide presented here allows estimating age of bee-eater nestlings with an average accuracy of 85%. The validation protocol presented in this thesis can be developed and adapted for use in other species. In fact, the development of methodologies for aging nestlings according to a standardized protocol is still lacking and may be valuable as a base tool for many studies, particularly those focusing on species whose nests are difficult to access, as is the case of cavity-nesters. Discriminant functions were later applied on Chapters 6 and 7; while photographic aging guide was used on Chapters 4, 6 and 7. This provides an example of the possible future applications of those tools in distinct studies, from migration to trophic ecology and breeding biology.

Diet of the bee-eater, an opportunist with preferences

Intensive agriculture have been gradually substituting extensive farming practices and grasslands (Benton et al. 2003) leading to negative impacts on several migrants that use these habitats for foraging and/or nesting (Avilés et al. 2000; Brambilla et al. 2007; Weisshaupt et al. 2011). Chapter 4 focus on studying the diet of bee-eaters breeding in Iberia, where intensification of agriculture has been increasing in the last decades (e.g. José-María et al. 2010). The diet of Iberian bee-eaters varies between colonies surrounded by distinct habitats with Hymenoptera and Coleoptera being the main consumed prey. Diet composition also changes seasonally, most likely following the patterns in insect availability and phenology (Bellavance et al. 2011; Post and Greenlaw 2006). It is therefore undeniable that diet of bee-eaters differs at several temporal and spatial scales: across the breeding range (e.g. Inglisa et al. 1993; Krüger 2018), between years (Fuisz et al. 2013) and even spatially and temporally within the same region (Chapter 4). Such patterns are common among insectivores (e.g. Stanton et al. 2016). For example, the biomass of Diptera consumed by Tree swallows seems to decrease with increasing proportions of intensively cultivated crops (Bellavance et al. 2011), while diet of Barn swallows (*Hirundo rustica*) varies between colonies surrounded by distinct farmland habitats (Orłowski and Karg 2011). Moreover, similar to this study, Coleoptera and Hymenoptera are reported as the main consumed prey by Barn swallows, with dung beetles highly represented among coleopterans (Orłowski and Karg 2011). In the House martin (*Delichon urbicum*), the diet composition changes across the breeding season, with Hymenoptera and Hemiptera being exploited mainly during June and July (Bryant 1973). These examples outline how aerial insectivores, including the bee-eater, are typically opportunists, consuming prey according to what it is available in the environment and taking advantage of occasional peaks of certain prey types (Krüger 2018). However, it is common that opportunistic species also feed selectively (e.g. Tores et al. 2005) which seem to also be the case of the bee-eater. But the degree of selectivity may vary between populations. For example, Barn swallows breeding in Poland consume Coleoptera and Hymenoptera in higher proportion that what is potentially available (Orłowski and Karg 2011), while a population breeding in Canada are known to select mainly Diptera and Hymenoptera (Law et al. 2017). In bee-eaters breeding in Italy, Hymenoptera were selected during the entire breeding season, but Coleoptera and Hemiptera only during the last weeks (Inglisa et al. 1993). In the studied population, Hymenoptera and Coleoptera are positively selected to provide to nestlings and for own consumption, even when facing a decrease in the availability of these prey, between pre-incubation and nestling rearing. This stresses the importance of these insect taxa in the diet of bee-eaters, but also in other aerial insectivores foraging on farmlands, during the breeding season.

Insectivores are often selective not only in the type of prey but also in the size (e.g. Bryant 1973; McCarty and Winkler 1999; Orłowski and Karg 2011). Indeed, adult bee-eaters are known to feed their offspring with large items than what they consume (Arbeiter et al. 2014; Fry 1984; Kristin 1994; Massa and Rizzo 2002). This is also common for aerial insectivores species like the Tree swallow (McCarty and Winkler 1999) and the Barn swallow (Orłowski and Karg 2011). This thesis show an increase in prey size provided to nestlings across the rearing period, with younger nestlings receiving smaller items, while older nestlings were provided with larger items. This finding is contrary to what was reported in a colony at the northern edge of the species distribution, where the mean prey weight provided to nestlings decrease significantly as the nestling period progressed (Krüger 2018), suggesting that different provisioning strategies may be adopted by distinct populations, given variation on prey availability.

Although bee-eaters from the studied population feed on Hymenoptera and Coleoptera even when its availability is low, a severe decline on bees, as recorded worldwide (e.g. Pettis and Delaplane 2010; Potts et al. 2010), could lead to a diet shift with potential implications for individual fitness and productivity (Marquiss et al. 1985; Monaghan et al. 1989; Nocera et al. 2012). On the other hand, it could increase the time spent foraging for profitable prey (Britschgi et al. 2006) and negatively affect individual fitness (Martin 1987) and reduce nest attentiveness (Stanton et al. 2016). However, it remains unknown how bee-eaters would cope with a severe depletion of their preferred prey. Additionally, the diet in the non-breeding areas remains poorly studied (Fry 1984). Further studies on trophic ecology of bee-eater across breeding, but also non-breeding, areas would be essential for informing habitat management aiming to improve availability of resources.

Migratory patterns and breeding performance

Within the same species, different populations may be subject to different environmental pressures (Cresswell 2014). Indeed, breeding populations may not share the same wintering grounds, as is the case of the apparent complete lack of overlap between the bee-eater population in Bulgaria and the other two populations (Iberia and Germany;

Chapter 5). This is relevant because the environmental conditions that bee-eaters experience throughout its breeding and non-breeding ranges could potentially lead to distinct fluctuations in demographic rates at population level (Webster et al. 2002). More tracking studies are therefore required to establish migratory connectivity for distinct populations.

Similar to many species (e.g. Nilsson et al. 2013), bee-eaters breeding in Iberia seem to travel faster in spring than in autumn which suggests that individuals are under a high pressure to arrive earlier to the breeding areas (Chapter 4). This thesis demonstrates that breeding arrival seems to be mainly driven by departure dates from the wintering areas with earlier departing bee-eaters arriving earlier to the breeding areas than late departing individuals. This strategy is common among other long-distance migrants (see Briedis et al. 2019). For example, timing of departure from the wintering areas in sub-Saharan Africa determined arrival to the breeding areas in Barn swallows breeding in Italy and Switzerland (Saino et al. 2017). However, bee-eaters either depart early or travel fast in spring. Bee-eaters that depart earlier have longer travel duration, while late departing individuals spend fewer days on migration. Despite this, earlier and slower bee-eaters still arrive earlier at the breeding areas than later but faster individuals. A similar pattern was also found in Great reed warblers (*Acrocephalus arundinaceus*) with later departing individuals migrating faster in spring but not being able to compensate for their delay (Lemke et al. 2013). By the contrary, late departing Collared flycatchers (*Ficedula albicollis*) also show higher travel speed, but seem able to partially catch up with early departing individuals and arrive at the breeding destination at a similar time (Briedis et al. 2018). This distinct patterns are possibly explained by distinct migratory strategies as bee-eaters are known to rely, at least partially, on a fly-and-forage strategy (Fry 1984). On the contrary, flycatchers seem be able to maximize travel speed (Briedis et al. 2018), for example in a final sprint to finish migration (Alerstam 2006).

This thesis reports that migration timings are linked to laying dates with individuals arriving earlier also laying earlier (Chapter 6). Additionally, laying dates seem to influence productivity in two consecutive years when conditions at the breeding colonies are substantially different. In 2016, laying was overall earlier in the season and productivity remained constant while in 2017, the first individuals started laying later and number of fledglings decreased across the season. This suggests that laying earlier might be advantageous in years when conditions at the breeding grounds are poor, as was possibly the case in 2017. Although the factors behind this decrease in productivity remain unknown, it is possible that the exceptional high temperatures during the spring and summer of 2017 (mean maximum air temperature: March 18.3°C, April 23.9°C, May 26.3°C; June: 32.8°C; Instituto Português do Mar e da Atmosfera) advanced the insect phenology during the breeding period (Bartomeus et al. 2011), originating deteriorating conditions for individuals that layed later in the season. As was the case in Algeria in 2012-2013, when the number of prey brought to nestlings by adult House martins decreased from May to July, suggesting that highest temperatures during July contributed to a decrease in insect abundance (Rouaiguia et al. 2015). Conversely, studies assessing the diet of Pallid swifts (*Apus pallidus*) and Tree swallows reported an increase in the availability of flying insects across the breeding season (Dunn et al 2011, Cucco and Malacarne 1996). However, insect phenology may differ geographically according to local climate (Robinet and Roques 2010) and increasing temperatures are indeed a key factor shaping plant and insect phenology in the Mediterranean (Gordo and Sanz 2010; Gordo and Sanz 2006; Stefanescu et al. 2003) where the frequency of drought events has been increasing (Hoerling et al 2012). Nevertheless, other factors may have contributed to the differences in laying dates and productivity between years. Cavity nesting birds that dig the nest burrows in sand barriers or in the ground are usually under high predation pressure (Fry 1984; Szép et al. 2016). Predation could have been higher in 2017 compared to 2016 due to an increase in the number of predators in the surroundings, or by an indirect effect of the prolonged drought in the depletion of the alternative food sources of predators (Persson 1987). Moreover, poor conditions experienced in the wintering grounds (e.g. habitat quality, Norris et al. 2004) or during migration (e.g. weather conditions, Briedis et al. 2017) might have interacted with conditions at the breeding areas, influencing fitness of individuals and associated productivity.

Interestingly, the mean number of fledglings recorded in Iberia (Chapter 6) is relatively low (2016: 2.72 ± 0.88; 2017: 2.23 ± 1.85) compared to the mean number of fledglings reported in a population at the northern edge of the distribution, during monitoring period of 10 years (3.7 ± 1.0, Arbeiter et al. 2016). It is also relevant to note that the mean number of fledglings recorded in the dry year of 2017 (Chapter 6) is similar to the productivity recorded during a year of intensive rain in the northern colony (1.7 ± 0.86, Arbeiter et al. 2016), which suggests that different factors shaping fluctuations in productivity may be operating in distinct colonies. However, it should be noted that other factors like individual experience which increases with age, pair-fidelity (Chapter 7) and group-dynamics (Dhanjal-Adams et al. 2018) may also play an important role on productivity.

Inter-annual variation in productivity may affect populations in the long term by inducing fluctuations in demography rates if frequency of poor (or good) breeding conditions increases. However, without long-term monitoring of productivity and survival it is not possible to derive any solid conclusions (Morrison et al. 2016). Additionally, it would be relevant to compare long-term data of productivity with environmental variables such as weather conditions, prey availability and habitat suitability. Bee-eater populations in Spain appear to be stable since the last decade (SEO/BirdLife 2019), while the data available for Portugal indicates that bee-eaters have been suffering a moderate decline since 2004 (Alonso et al. 2019). Therefore, long-term monitoring of bee-eater population and productivity is fundamental in order to better understand how inter-annual fluctuations of phenology and productivity may influence demography.

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Appendix 1

A full annual perspective on sex-biased migration timing in long-distance migratory birds

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A full annual perspective on sex-biased migration timing in long-distance migratory birds

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In many taxa, the most common form of sex-biased migration timing is protandry—the earlier arrival of males at breeding areas. Here we test this concept across the annual cycle of long-distance migratory birds. Using more than 350 migration tracks of small-bodied trans-Saharan migrants, we quantify differences in male and female migration schedules and test for proximate determinants of sex-specific timing. In autumn, males started migration about 2 days earlier, but this difference did not carry over to arrival at the non-breeding sites. In spring, males on average departed from the African non-breeding sites about 3 days earlier and reached breeding sites *ca* 4 days ahead of females. A cross-species comparison revealed large variation in the level of protandry and protogyny across the annual cycle. While we found tight links between individual timing of departure and arrival within each migration season, only for males the timing of spring migration was linked to the timing of previous autumn migration. In conclusion, our results demonstrate that protandry is not exclusively a reproductive strategy but rather occurs year-round and the two main proximate determinants for the magnitude of sex-biased arrival times in autumn and spring are sex-specific differences in departure timing and migration duration.

1. Introduction

Billions of migratory animals travel vast distances between their breeding and non-breeding regions to exploit seasonal changes in resource availability and secure their survival while increasing reproductive opportunities [1–3]. Natural selection favours individuals that best match their annual schedules with the phenology of their current environment [4] and gain prime access to resources [5]. In many species, factors like intrasexual competition, sex-specific breeding roles, and individual tolerance to suboptimal environmental conditions can induce differences in migration timing between males and females [5–8].

Sex-biased migration timing has most often been demonstrated for arrival to the breeding sites in spring. Protandry—the earlier arrival of males at the breeding location—is the most common form of sex-biased migration timing in many taxa [9], while protogyny—female arrival ahead of males—is less common and typically found in some species with reversed sex roles [10–12]. Protandry and protogyny have primarily been considered as reproductive strategies and seven explanations have been brought forward of how natural selection can shape spring arrival protandry [9]. Among those, the three principal adaptive hypotheses explaining protandry in birds are: (i) the mate opportunity hypothesis, (ii) the rank advantage hypothesis, and (iii) the susceptibility hypothesis [5–7,9,13]. Under these hypotheses, protandry should prevail in territorial species with a high degree of extra-pair paternity, in species with relatively larger male body size compared to females, and in populations with male-biased sex ratio and higher fecundity for early breeding females. The level of protandry also varies with migration strategy, with smaller differences between the sexes in long-distance migrants and larger differences in facultative and short-distance migrants [13–18], suggesting that processes other than reproduction play a role.

Measuring sex biases upon arrival at the breeding sites [16,19–21] provides only brief snapshots of the full annual cycles of migratory animals. Since life-history stages of migrants are inextricably linked and shaped by environmental conditions at various locations [21–25], we need a full annual perspective to better understand the driving forces that underlie sex-biased migration timing and the consequences it may have for individuals and populations [26]. Several recent studies have looked into sex-biased migration timing also at other annual stages, e.g. [21,27–33] frequently showing earlier male departure from the non-breeding sites in spring, but ambiguous patterns for autumn migration. However, sample sizes of such case studies are often small, and confirmation of sex biases in migration timing (or lack thereof) may often be masked by low statistical power. Thus, whether sex-biased migration timing is a general pattern across the entire annual cycle of migratory birds remains to be shown [34].

Furthermore, owing to difficulties in following individual migrants year-round, the proximate causes behind sex biased spring arrival times often remain obscure [35]. With advancing tracking technologies, however, we gain more data on entire migration schedules of individual birds allowing for detailed descriptions of sex-specific migration patterns, e.g. [29,36–38], and testing for proximate causes that drive differences in spring arrival times. The three main proximate determinants, that could explain sex biases in arrival timing, are differences in (i) departure timing from non-breeding areas, (ii) migration distance, and (iii) migration speed [35]. The causes are not mutually exclusive but their relative contributions remain largely unknown for most species (but see [14,39]). If proximate causes for arrival timing are similar for autumn and spring migration, we expect a similar pattern of sex-biased arrival timing (i.e. protandry) and similar strength of the ‘domino effect’ (a situation when the timing of one annual phase affects the timing of any subsequent phase [33,40]) between migratory departure and arrival in both seasons.

To gain a general insight into migration timing of males and females across the entire annual cycle, we compiled already published and unpublished tracking data on complete annual schedules of various Afro-Palaearctic long-distance migrant landbirds.

(i) We test by how much and how consistently males migrate ahead of females in spring [5,9,13,35] and whether the timing of autumn migration is also sex biased. If protandry is solely a reproductive strategy [9], we expect it in spring, but not in autumn; if sex-biased timing prevails also in other parts of the annual cycle, additional processes besides breeding should be in play.

(ii) We evaluate multiple proximate causes—departure timing, migration distance, duration and speed—as potential drivers for sex-biased migration timing [13,35]. If departure timing is the primary proximate driver for spring arrival protandry [14,39], we expect a clear domino effect between timing of different migration stages.

2. Methods

We studied migration phenology of male and female long-distance migratory landbirds travelling within the Afro-Palaearctic bird migration system. For our analyses, we used data from studies where individual birds had been tracked between breeding and non-breeding sites using light-level geolocators or solar-powered PTT-tags (for common cuckoo *Cuculus canorus* and roller *Coracias garrulus* from Spain; see [41,42]). We included only individuals with complete annual track recordings from which information on all four major migration transition times could be extracted—departure from breeding site, arrival at (first) non-breeding site, departure from (last) non-breeding site, and arrival at breeding site. This allowed for a year-round comparison of relative migration timing of the same individuals. Since annual migration schedules can vary considerably between years in response to varying environmental conditions at breeding and non-breeding sites as well as *en route* [24,43], we only included data from years where at least one male and one female had been tracked from the same breeding population. Our dataset included 14 passerine and near-passerine species from 25 European breeding populations which had been tracked between 2009 and 2017 (electronic supplementary material, table S1). The breeding sites spanned across Europe ranging from 37° N to 60° N latitude and from 8° W to 28° E longitude (electronic supplementary material, figure S1).

(a) Compilation of individual migration data

In addition to individual migration schedules, we extracted coordinates of breeding and estimated non-breeding sites for each individual. If individuals resided at multiple non-breeding sites, we considered the first non-breeding site as the arrival site in autumn and the last non-breeding site as the departure site in spring. We calculated individual migration distances (great circle distances between individual breeding and non-breeding sites), migration duration (days) and migration speed (km day^{-1}). Because individual duration of pre-departure fuelling cannot be quantified using current tracking technologies, migration duration was defined as the time between departure and arrival at the final destination and should not be considered as total migration duration [44]. Consequently, individual migration speed is defined as migration distance divided by migration duration, which is probably an overestimate and should not be viewed as absolute migration speed *sensu stricto* [44]. Furthermore, locations of non-breeding sites as inferred from light-level geolocators inherently include positional error of up to a few hundred km [45], slightly affecting the estimates of individual migration distances and speeds.

Since we found an effect of age on the timing of autumn migration with juvenile birds migrating later than adult conspecifics ($\beta = -10.56 \pm 4.65$ s.e., $t_{1,66} = -2.27$, $p = 0.026$), we restricted our analyses to adult birds and excluded 12 juvenile hoopoes (*Upupa epops*) from the dataset. Thus, our final sample size consisted of 354 complete annual tracks (195 males; 159

females) of 340 individuals (repeated tracks: eight males, six females; electronic supplementary material, table S1).

We also compiled information on the species' morphological and ecological traits (data source: [46]), namely sexual size dimorphism (SSD; using wing length as a proxy for overall body size), moult strategy (region where complete post-breeding moult is undertaken—Europe or Africa), and foraging mode (aerial or terrestrial feeder). Phylogenetic relatedness between the species was assessed using the Ericson-backbone tree from Jetz *et al.* [47] downloaded from www.birdtree.org.

(b) Data analyses

As species and populations may differ in migration timing, distance, duration and speed, we used their relative values (Δx) as inferred from tracking data, i.e. individual migration parameters were expressed as the difference to their species-, population- and year-specific means. Values of $\Delta x < 0$ represent relatively earlier migrations, shorter distances and durations, or slower migration speeds, while $\Delta x > 0$ represent relatively later migrations, longer distances and durations, or faster migration speeds. All data analyses were done in R [48].

We first tested for differences in migration timing between males and females and then whether these differences could be explained by differences in departure time, migration duration, distance or speed. For both tests, we used mixed-effect models (LMM) and accounted for the non-independence of hierarchical data by including species, population (nested within species) and year (nested within species and population) as random factors. LMM analyses were run with the R-package 'lme4' [49]; *p*-values were obtained via R-package 'lmerTest' [50]. Finally, we also evaluated the relationship between individual migratory departure and arrival times (relative values Δx) across the annual cycle using simple linear regressions.

Using the R-package 'MCMCglmm' [51], we tested the roles of several biological species traits in explaining the average differences in male and female migration timing (in days) for each species. Foraging strategy and moulting region were included in the models as binary variables, while SSD was a continuous variable. Phylogenetic relatedness between the species was included in the model as a random effect, thus, we could account for non-independence of data owing to shared ancestry of the species. In all models, we used inverse-Gamma priors ($V = 1$, $\mathrm{nu} = 0.002$) as non-informative priors.

As the number of male and female tracks differed between species, populations and years, our ultimate sample was male-biased, which may potentially have confounded mean and relative migration parameters. To test whether this affected our results, we repeated the analyses with a reduced dataset that contained a random sample of individuals of the more common sex to match the number of the less common sex. Consequently, this reduced dataset contained a balanced number of males and females from each population and year and thus, the same total number of individuals per sex ($n = 128$ males + 128 females). To avoid effects from the identity of these individuals in the selection, we repeated the random selection and analyses 99 times. Using this reduced dataset, we recalculated the relative values for migration timing, distance, duration and speed. Results from the reduced dataset analyses are presented in the electronic supplementary material.

3. Results

(a) Annual schedules

Our analyses revealed that migration schedules of males and females differed in both migration seasons, i.e. in spring and autumn (figure 1). In autumn, males departed from their respective breeding sites on average 1.7 days earlier than females (LMM with species, population and year as random effects: $\beta = -1.73 \pm 0.85$ s.e., $t_{1,352} = -2.03$, $p = 0.043$; figure 1, electronic supplementary material, figure S2). However, we found no significant differences in relative arrival dates at the non-breeding sites between males and females originating from the same breeding sites ($\beta = 0.17 \pm 1.13$ s.e., $t_{1,352} = 0.15$, $p = 0.881$). Note that the non-breeding sites are individual-specific, and birds of the same breeding origin did not necessarily migrate to the same destination. In spring, males departed from their non-breeding sites on average 2.9 days earlier than females ($\beta = -2.94 \pm 1.16$ s.e., $t_{1,352} = -2.52$, $p = 0.012$). The difference in relative arrival times at the breeding site was even greater with males arriving on average 3.9 days earlier than females ($\beta = -3.86 \pm 0.98$ s.e., $t_{1,352} = -3.94$, $p < 0.001$).

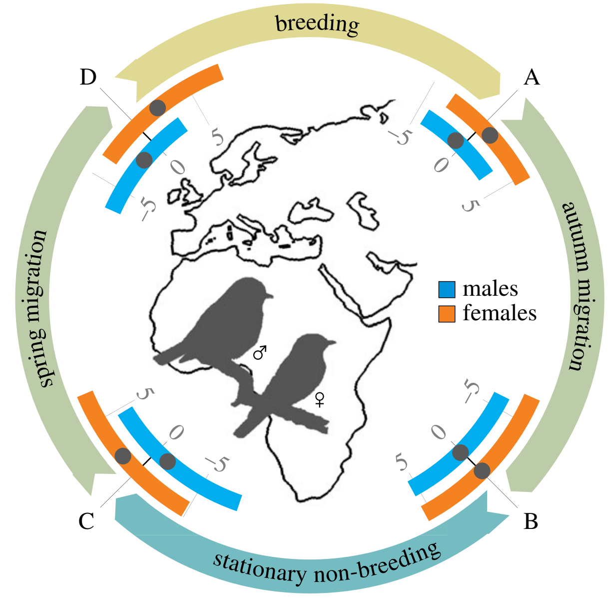

Figure 1. Differences in male (blue) and female (orange) migration timing of Afro-Palaearctic long-distance migratory birds (values below 0 correspond to earlier migration; measured in days). (A) Departure from the breeding site, (B) arrival at the non-breeding site, (C) departure from the non-breeding site, (D) arrival at the breeding site. Average values of relative migration times are indicated by black dots within interquartile ranges given as coloured bars.

The overall patterns were similar when using the reduced dataset; yet, the differences in male and female annual migration schedules were larger (average difference ± s.d.; breeding departure: 2.0 ± 0.5 days; arrival non-breeding: 0.4 ± 0.6 days (females earlier); departure non-breeding: 3.2 ± 0.7 days; arrival breeding: 4.1 ± 0.4 days; electronic supplementary material, figure S2 boxplots).

(b) Proximate causes of arrival timing

Our models identified sex-specific differences in departure timing and migration duration as the most important predictors for sex biases in arrival times (protandry or protogyny) at non-breeding and breeding sites (table 1). Migration distance and speed were similar for males and females during both migration seasons and did not account for sex-biased arrival times (table 1; figure 2).

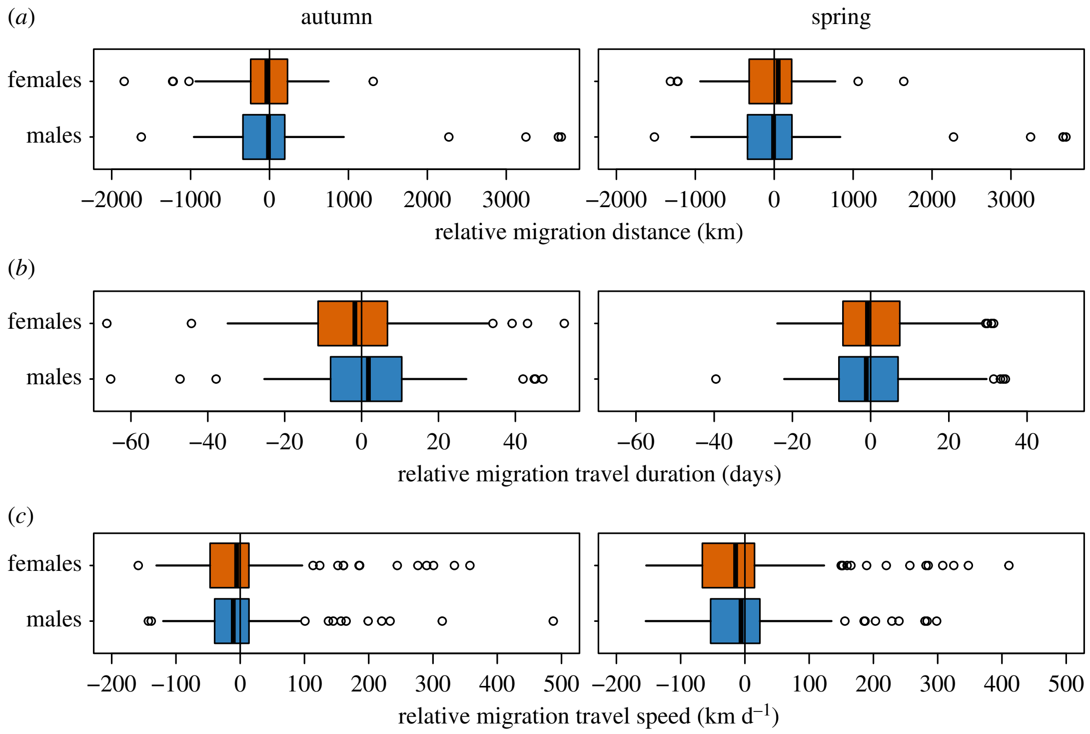

Figure 2. Comparison of relative migration (*a*) distance, (*b*) duration, and (*c*) speed between males and females in autumn and spring. Boxplots show median values with interquartile ranges (IQR; boxes), whiskers extend to 1.5 times the IQR, outliers are given as dots.

Table 1. Summary statistics of linear-mixed effects models examining proximate determinants of the magnitude of protandry (measured in days) at (*a*) autumn arrival at the non-breeding sites and (*b*) spring arrival at the breeding sites. (Species, population (nested in species) and tracking year (nested in species and population) were included in the models as random effects. All explanatory variables were scaled.)

fixed effects	estimate	s.e.	*t*-value	*p*-value
(*a*) *sex-specific differences in autumn arrival time*				
intercept	0.709	0.002	337.7	<0.001
departure time	7.254	0.003	2830.0	<0.001
migration duration	13.696	0.003	5433.2	<0.001
migration speed	0.001	0.002	0.4	0.665
migration distance	−0.001	0.002	−0.2	0.876
(*b*) *sex-specific differences in spring arrival time*				
intercept	−4.938	0.008	−605.4	<0.001
departure time	7.962	0.009	827.4	<0.001
migration duration	9.641	0.012	785.8	<0.001
migration speed	−0.006	0.011	−0.6	0.586
migration distance	0.001	0.009	0.1	0.898

The biological trait model showed that differences between male and female migration timing were greater in species with larger SSD (figure 3), particularly upon spring arrival at the breeding sites. Foraging mode was not a significant predictor of differences in male and female migration timing throughout the entire annual cycle (electronic supplementary material, figure S3). Moult strategy was only a significant predictor for departure from non-breeding sites with species undergoing complete moult in Africa showing smaller differences between male and female spring departure timing (electronic supplementary material, figure S3).

(c) Relationship between individual timing of consecutive migration episodes

We found the strongest positive relationships between breeding site departure and non-breeding site arrival time as well as between non-breeding site departure and breeding site arrival time (autumn: $\beta = 0.20 \pm 0.04$ s.e., $F_{1,352} = 25.7$, $R^2 = 0.07$, $p < 0.001$; spring: $\beta = 0.58 \pm 0.05$, $F_{1,352} = 115.6$, $R^2 = 0.25$, $p < 0.001$; figure 4). Thus, the strongest domino effect between timing of migration events was found within, rather than across, autumn and spring migrations. There were also positive relationships between arrival and

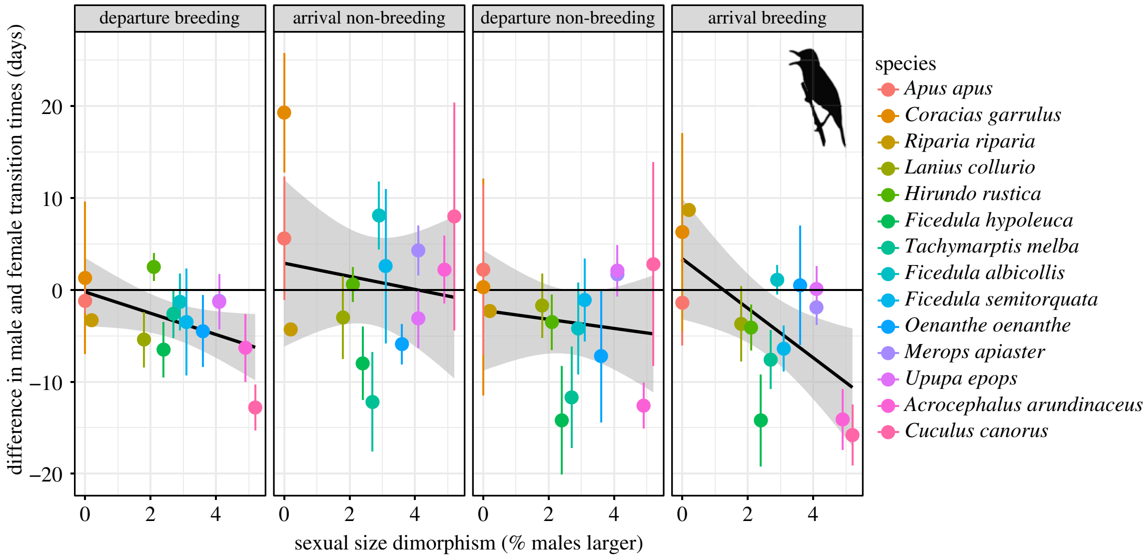

Figure 3. Differences in male and female migratory transition times among species (mean difference ± s.d.) and their relationship (±95% confidence interval—shaded area) with sexual size dimorphism as inferred from wing length. Differences below 0 denote cases of males being earlier, while values above 0 indicate females being earlier. The order of species in the figure legend corresponds to the order from left to right in the four individual plots. (Online version in colour.)

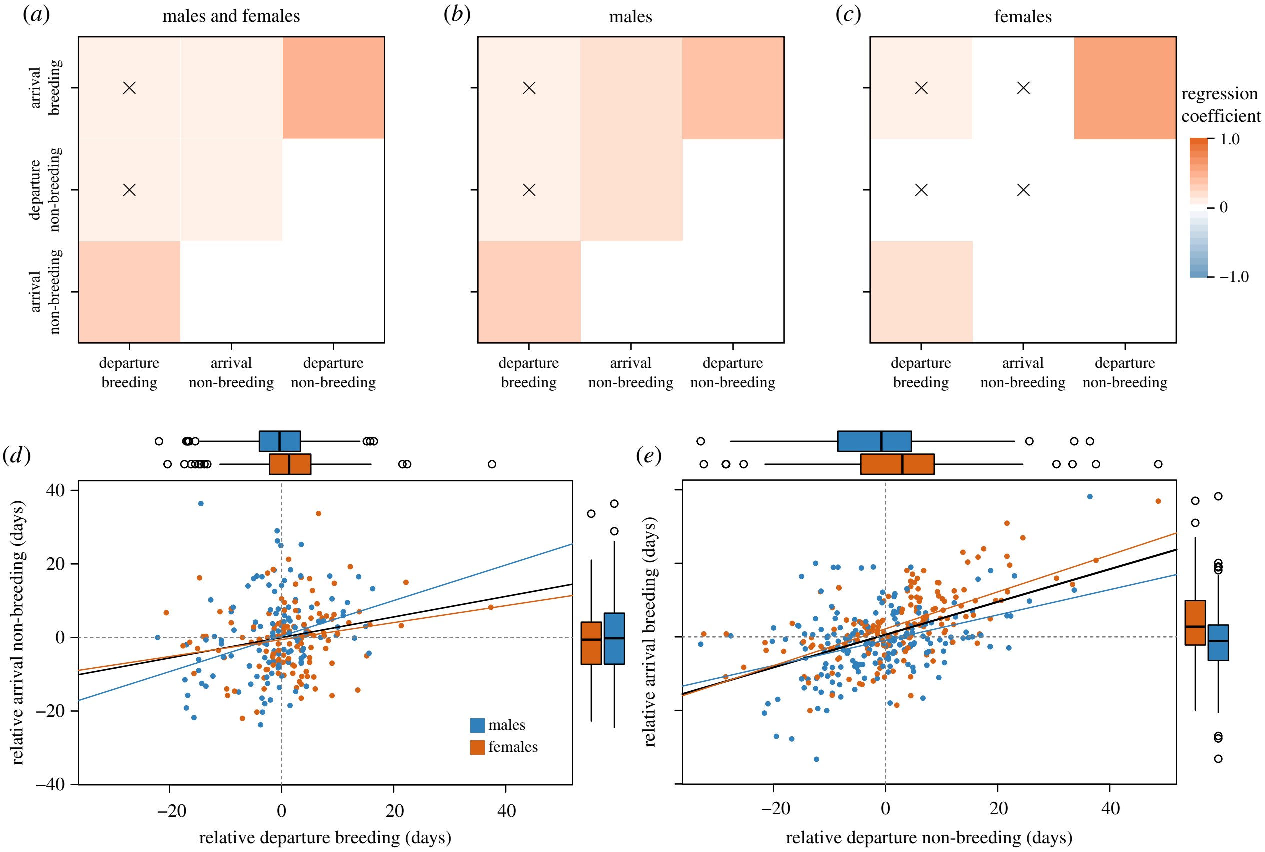

Figure 4. Relationships between individual timing of migration events. (*a*) A matrix showing simple linear regressions between individual migratory departure and arrival times in autumn and spring for males and females combined, (*b*) for males only, and (*c*) for females only. Non-significant regressions are marked with 'X'. A detailed example of the relationship between individual timing of migration departure and arrival is presented for autumn (*d*) and spring (*e*). Lines correspond to simple linear regressions: black for both sexes combined, blue—males, orange—females. Boxplots show median ± interquartile range (IQR—boxes; whiskers extend to values within 1.5 times the IQR and dots depict outliers) of *x*- and *y*-axis values for each sex.

departure time at non-breeding sites, and non-breeding site arrival and breeding site arrival time—yet, to a lesser extent (figure 4*a*). In males, domino effects of migration timing were similar to the general pattern described above with the strongest relationship between non-breeding site departure and breeding site arrival time in spring ($\beta = 0.47 \pm 0.08$, $F_{1,193} = 37.3$, $r^2 = 0.16$, $p < 0.001$; figure 4*b*). In females, migration timing in autumn and spring was not related, yet departure from non-breeding and arrival at breeding sites were strongly related ($\beta = 0.71 \pm 0.08$, $F_{1,157} = 80.3$, $r^2 = 0.33$, $p < 0.001$; figure 4*c*). Analyses of the reduced dataset yielded similar results (electronic supplementary material, figure S4).

4. Discussion

(a) Sex biases in annual schedules

Taking a full annual perspective on sex-biased timing of migration, we observed earlier male migration for three out of four main migration stages. Protandry in breeding site arrival was largely explained by an earlier departure of males from the non-breeding sites [14,35] and sex-specific differences in migration duration, whereas migration speed and distance contributed insignificantly. In autumn, males departed earlier from the breeding sites than females, but since the sexes also differed in migration duration, timing of arrival at the non-breeding sites was similar for both sexes. The species composition in our study comprise various taxonomic orders and families with variable moulting strategies, degree of territoriality, foraging modes, and SSD, and therefore, we feel confident to generalize our results to most long-distance migrants.

Our findings suggest that in Afro-Palaearctic migratory landbirds, males arrive at the breeding sites on average only a few days ahead of females. Earlier male arrival in spring has been shown in many migratory species with differences ranging between two weeks in some short-distance migrants and 2–8 days in long-distance migrants [18,20]. Furthermore, protandry in spring arrival is largely caused by males departing earlier from the non-breeding sites. This finding confirms the suggestion of several earlier case studies [14,21,27,39,52,53]. Earlier departure in males seems to be endogenously driven, as under constant day length conditions males show earlier onset of migratory restlessness than females [54]. Additionally, our findings also shed new light on sex-specific differences in migration duration as a primary contributor to sex-biased arrival timing. Migration duration is clearly an interaction between migration speed and distance, thus, these three parameters are partially masked within one another. However, the differences between average migration speed and distance of males and females were negligible, contributing only insignificantly towards sex-biased migration arrival times.

We also found that in autumn, males generally depart from the breeding sites earlier than females, but these differences ceased upon arrival at the non-breeding sites. Hitherto, our understanding of sex-biased timing of bird autumn migration has largely been based on data from ringing stations. Several of such studies reported no sex-differences or even protogyny (earlier female migration) in long-distance migrants during autumn [12,55], which would be in contrast to our results. However, an inherent pitfall of data from ringing stations is that they capture birds on passage and typically their origin and destination are unknown. Thus, any differences between the sexes that such ringing-station data might suggest, could be cofounded by variable migration timing of individuals that come from, or head to, different locations. Naturally, this is resolved in our dataset (and individual tracking data in general) and we can directly compare breeding site departure and non-breeding site arrival of individuals from the same breeding populations.

Two issues could be raised about our results and their interpretation, namely that (i) tracking devices might affect females more than males and thus delay their migration; and (ii) earlier arriving males might be easier to recapture than late arriving ones. Although it has been shown that tracking devices can have more negative effects on female rather than male apparent survival in aerial foragers [56], no sex-specific effects on the timing of migration have been found [57]. As to the recapture probability of early- and late-arriving individuals, most of our study species breed in nest-boxes or natural cavities, which are regularly inspected during the entire breeding season. Thus, late-arriving breeders are as likely to be recaptured as early-arriving breeders. However, recapture probabilities might differ if late-arriving males are unable to breed, e.g. if all territories are already occupied [21]. We recognize that a general constraint inherent to individual-based archival bio-logging devices is that the dataset contains only successfully migrating and surviving individuals and cannot infer or analyse the migration timing of unsuccessful birds.

(b) Full annual perspective on adaptive hypotheses for protandry

Protandry has primarily been considered a reproductive strategy [9] and therefore, most research has focused on sex biases in arrival times at the breeding site, largely neglecting the timing of other annual stages. We further discuss the three leading adaptive hypotheses for protandry in migratory birds [13] and put them in the context of full annual cycles.

The susceptibility hypothesis predicts that males arrive earlier in spring because they are better able to withstand adverse weather conditions (e.g. owing to their larger body size) *en route* or at the breeding sites early in the season [7]. In long-distance migrants, however, this applies only to the breeding site arrival in spring as Afro-Palaearctic migratory birds typically do not experience cold conditions at other parts of the annual cycle. Thus, the susceptibility hypothesis alone cannot explain the observed differences in male and female migration timing at other annual stages.

In the mate opportunity hypothesis, earlier arrival of males provides direct fitness benefits via polygyny, and theoretical models have convincingly demonstrated the mate opportunity hypothesis to be the most plausible explanation for spring protandry in migratory animals [6]. If males and females migrate at similar speeds and over similar distances (as shown in figure 2), this hypothesis also justifies why males should depart from the non-breeding sites ahead of females. However, applying this hypothesis to explain the protandry pattern during autumn migration is not that straightforward. Because no mating takes place after autumn migration, the mate opportunity hypothesis predicts no sex-biased arrival times at the non-breeding site which is in line with our findings. The mate opportunity hypothesis, however, fails to explain why males should leave the breeding sites earlier than females.

The rank advantage hypothesis argues that male–male competition for access to prime breeding sites is the main driver of spring arrival protandry [5]. While this hypothesis could also explain why males start spring migration earlier than females, an extension of the rank-advantage model by also including female–female competition sometimes resulted in protogyny, rather than protandry—contrasting our findings [6]. This is because early in spring, female–female competition can be stronger than male–male competition, as females compete for a resource that is relatively scarcer—territories occupied by males—than the resource contested for by males—vacant territories. Autumn migration is additionally characterized by the presence of male–female competition for access to high quality non-breeding sites, as spending the non-breeding residency period in good conditions can be of utmost importance for survival, preparing for spring migration, and future reproductive success [58]. Introducing intersexual competition in the rank-advantage model eliminates sex-biased arrival at the non-breeding sites—a pattern found in our study—as both sexes are expected to advance their arrival up to a point where increased costs of premature or excessively fast migration counteract the benefits of an even earlier arrival [5]. Competition for resources at the non-breeding sites would also lead to early departure from the breeding sites in autumn, as early-departing individuals (or populations) would gain a head-start over those who depart later [30]. Thus, both sexes should advance their departure date from the breeding sites to arrive early at the non-breeding sites. Earlier departure of males found in our study may be attributed to females investing more energy and/or time in reproduction, which delays their post-nuptial moult and preparation for migration [22]. Indeed, for species that moult before post-breeding migration, males have been shown to start post-nuptial moult earlier than females [59,60]—an important prerequisite for timely departure from the breeding sites in autumn. Thus, timing of moult might set an important constraint for timing of migration across the annual cycle generating sex-biased migration schedules (see the electronic supplementary material, figure S3).

(c) Links between consecutive annual stages

In both migratory seasons, timing of departure and arrival at the destination were positively correlated, indicating that late departure from one site cannot be fully compensated for but rather leads to late arrival at the next site with potential downstream consequences [40,61,62]. Such cascading effects have been shown in barn swallows, where females that departed early from the non-breeding areas also bred earlier and had higher fecundity; yet, no such relationships were found in males [63]. Thus, the start of spring migration bears stronger consequences for reproductive success in one sex than the other, which is in line with our finding of a tighter relationship between spring departure and arrival dates in females compared to males.

In females, spring migration schedules were not dependent on the timing of their previous autumn migration, while in males, arrival time at the non-breeding site and timing of spring migration were still positively related. Studies on short-lived migrant species suggest that effects from the previous migration season do not carry over to influence the timing of the subsequent spring migration [21,22,33,64,65]. The non-breeding period potentially serves as a buffer dissolving the rank order of individuals from the autumn migration. The sample size of these case studies, however, may sometimes be insufficient for comparing different demographic groups within the populations. Our results suggest that males and females experience different levels of domino effects between timing of consecutive migration seasons [63].

5. Conclusion

Our study has advanced the knowledge of a long-debated subject—differences in year-round migration schedules of males and females in long-distance migratory birds. We show that sex-biased timing is not restricted to spring arrival at breeding sites, but males and females differ in migration schedules across the annual cycle. The magnitude of spring arrival protandry is primarily driven by earlier male departure from the non-breeding sites and sex-specific differences in migration duration. Earlier male departure in autumn, however, does not translate into earlier arrival at the non-breeding sites. Although, our understanding of the selective advantages of spring protandry and their trade-offs has advanced during the last decades, e.g. [39,62,63,66] the ultimate causes of sex-biased autumn migration timing remain to be empirically tested. A potential prime candidate might be rank advantage in acquiring non-breeding territories or home ranges for optimal moult and maintenance of good body condition.

Data accessibility. Data are available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.t78400r [67].

Authors' contributions. M.B., S.B. and S.H. conceived the idea and study design. M.B., P.A., J.A.A., J.S.C., T.E., L.G., J.K., F.L., C.M.M., P.P. and S.H. carried out individual tracking projects, analysed and provided geolocator data. M.B. analysed the data and wrote the manuscript. All authors discussed, revised and approved the final version of the manuscript.

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Appendix 2

Weak effects of geolocators on small birds: a meta-analysis controlled for phylogeny and publication bias

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BIOLOGGING

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Weak effects of geolocators on small birds: A meta-analysis controlled for phylogeny and publication bias

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Abstract

1. Currently, the deployment of tracking devices is one of the most frequently used approaches to study movement ecology of birds. Recent miniaturization of light-level geolocators enabled studying small bird species whose migratory patterns were widely unknown. However, geolocators may reduce vital rates in tagged birds and may bias obtained movement data.
2. There is a need for a thorough assessment of the potential tag effects on small birds, as previous meta-analyses did not evaluate unpublished data and impact of multiple life-history traits, focused mainly on large species and the number of published studies tagging small birds has increased substantially.

3. We quantitatively reviewed 549 records extracted from 74 published and 48 unpublished studies on over 7,800 tagged and 17,800 control individuals to examine the effects of geolocator tagging on small bird species (body mass <100 g). We calculated the effect of tagging on apparent survival, condition, phenology and breeding performance and identified the most important predictors of the magnitude of effect sizes.
4. Even though the effects were not statistically significant in phylogenetically controlled models, we found a weak negative impact of geolocators on apparent survival. The negative effect on apparent survival was stronger with increasing relative load of the device and with geolocators attached using elastic harnesses. Moreover, tagging effects were stronger in smaller species.
5. In conclusion, we found a weak effect on apparent survival of tagged birds and managed to pinpoint key aspects and drivers of tagging effects. We provide recommendations for establishing matched control group for proper effect size assessment in future studies and outline various aspects of tagging that need further investigation. Finally, our results encourage further use of geolocators on small bird species but the ethical aspects and scientific benefits should always be considered.

KEYWORDS

condition, migration, phenology, reproduction, return rate, survival, tag effect, tracking device

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1 | INTRODUCTION

Tracking devices have brought undisputed insights into the ecology of birds. The use of these tags has enabled researchers to gather valuable information about the timing of life events across annual cycles, the year-round geographic distribution of populations and other important ecological patterns in many species whose movement ecology was widely unknown (e.g. Patchett, Finch, & Cresswell, 2018; Stanley, MacPherson, Fraser, McKinnon, & Stutchbury, 2012; Weimerskirch et al., 2002). A significant proportion of recently published tracking studies use light-level geolocators on small bird species (body mass up to 100 g; Bridge et al., 2013; McKinnon & Love, 2018); however, the increasing use of these tags on small birds raises questions about ethics of tagging and how representative the behaviour of tagged individuals is (Jewell, 2013; Wilson & McMahon, 2006).

Studies using tracking devices such as archival light-level geolocators (hereafter "geolocators") frequently report the effect of tagging. The published results on the effects of geolocator tagging are equivocal: Some found reduced apparent survival, breeding success and parental care (Arlt, Low, & Pärt, 2013; Pakanen, Rönkä, Thomson, & Koivula, 2015; Scandolara et al., 2014; Weiser et al., 2016) while others report no obvious effects (Bell, Harouchi, Hewson, & Burgess, 2017; Fairhurst et al., 2015; Peterson et al., 2015; van Wijk, Souchay, Jenni-Eiermann, Bauer, & Schaub, 2015). Recent meta-analyses evaluating the effects of geolocators (Costantini & Møller, 2013) and other tracking devices (Barron, Brawn, & Weatherhead, 2010; Bodey et al., 2018a) showed slightly negative effects on apparent survival, breeding success and parental care. These studies also discussed relative load as an aspect affecting the tagged birds (Costantini & Møller, 2013), or suggested multiple threshold values of relative load on birds (Barron et al., 2010; Bodey et al., 2018a). However, these studies involved mainly large bird species where the same additional relative load will more negatively affect surplus power and thus the flight performance than in smaller species (Caccamise & Hedin, 1985). Moreover, previous studies did not control for the effect of small-sample studies, or phylogenetic non-independence and its uncertainty. There is thus a lack of systematic and complex evaluation of geolocator effects on small birds including species' life-history and ecological traits, geolocator design, and type of attachment.

Almost all prior meta-analyses reporting effects of tagging relied only on published sources and could thus be affected by publication bias (Koricheva, Gurevitch, & Mengersen, 2013), as omitting unpublished sources in meta-analyses may obscure the result (see, e.g. Sánchez-Tójar et al., 2018). The main source of publication bias in movement ecology could be a lower probability of publishing studies based on a small sample size, including studies where no or only few tagged birds were successfully recovered due to a strong tagging effect. Additionally, geolocator effects most frequently rely on comparisons between tagged and control birds and a biased choice of control individuals may directly lead to the misestimation of the tagging effect sizes. The bias in the control groups can be due to selection of smaller birds, birds being caught in different spatiotemporal conditions, including non-territorial individuals, or different effort put into recapturing control and tagged individuals.

The number of studies tagging small birds is rapidly increasing each year even though our understanding of tag effects is incomplete. In this study, we evaluated the effects of tagging on apparent survival, condition, phenology and breeding performance for small bird species (<100 g) in a robust dataset of both published and unpublished studies to minimize the impact of publication bias. Moreover, we assess whether the tagging effects are related to species' ecological and life-history traits, type of control treatment as well as geolocator and attachment designs. We build on the most recent advances in meta-analytical statistical modelling to get unbiased estimates of the geolocator deployment effects controlled for phylogenetic non-independence and its uncertainty (Doncaster & Spake, 2018; Guillerme & Healy, 2017; Hadfield, 2010; Viechtbauer, 2010).

2 | PREDICTIONS

1. Geolocators will negatively affect apparent survival, condition, phenology and breeding performance of small birds.
2. Negative effects will be stronger in unpublished studies than in published studies.
3. Deleterious effects will be most prominent in studies establishing matched control groups compared to studies with potentially biased control groups.
4. Geolocators which constitute a higher relative load will imply stronger negative effects.
5. Geolocators with a longer light stalk/pipe will cause stronger negative effects because of increased drag in flight and thus increased energetic expenditure (Bowlin et al., 2010; Pennycuick, Fast, Ballerstädt, & Rattenborg, 2012). These effects will be stronger in aerial foragers than in other foraging guilds (Costantini & Møller, 2013).
6. Non-elastic harnesses will cause stronger negative effects than elastic harnesses, which better adjust to intra-annual body mass changes and avoid flight restriction (Blackburn et al., 2016).

3 | MATERIALS AND METHODS

3.1 | Data search

We conducted a comprehensive search for both published and unpublished studies deploying geolocators on bird species with body mass up to 100 g. We searched the Web of Science Core Collection (search terms: TS = (geoloc* AND (bird* OR avian OR migra*) OR geologg*)) and Scopus databases (search terms: TITLE-ABS-KEY (geoloc* AND (bird* OR migra*) OR geologg*)), to find published studies listed to 18 February 2018. Moreover, we searched reference lists of studies using geolocators on small birds and included studies from previous comparative studies (Bridge et al., 2013; Costantini & Møller, 2013; Weiser et al., 2016). In order to obtain information from unpublished studies, we inquired geolocator producers and the Migrant Landbird Study Group to disseminate our request for unpublished study details among their customers and members, respectively. In addition, we asked the corresponding authors of the published studies to share any unpublished data. The major geolocator producers—Biotrack, Lotek, Migrate Technology and the Swiss Ornithological Institute—sent our request to their customers. To find whether the originally unpublished studies were published over the course of this study, we inspected their status on 1 December 2018. The entire process of search and selection of studies and records (described below) is presented in a flow chart (Supporting Information Figure S1).

3.2 | Inclusion criteria; additional data requesting

We included studies that met the following criteria:

1. The study reported response variables (e.g. return rates, body masses) necessary for effect size calculation.
2. The study included a control group of birds alongside the geolocator-tagged individuals or reported a pairwise comparison of tagged birds during geolocator deployment and recovery.
3. As a control group, the study considered birds marked on the same site, of the same sex and age class without any indication of a difference in recapture effort between tagged and control groups.
4. For pairwise comparisons, the study presented correlation coefficients or raw data.
5. The variable of interest was presented outside the interaction with another variable.

In order to obtain robust and unbiased results, we asked the corresponding authors for missing data or clarification when the criteria were not met or when it was not clear whether the study complied with the criteria (70% response rate [n = 115]). In addition, we excluded birds that had lost geolocators before subsequent recapture as we did not know when the bird lost the geolocator, and excluded all individuals tagged repeatedly over years because of possible interannual carry-over effects of the devices. VBr assessed all studies for eligibility and extracted data; the final dataset was cross-checked by JK and PP. A list of all published studies included in the meta-analysis is provided in the Published Data Sources section.

3.3 | Trait categories; effect size calculation; explanatory variables

We divided all collected data into four trait categories: apparent survival, condition, phenology and breeding performance based on the response variables reported (e.g. interannual recapture rates, body mass changes, arrival dates or clutch sizes; Supporting Information Table S2). These categories represent the main traits possibly affected in the geolocator-tagged individuals. Subsequently, analyses were run separately for each trait category. We calculated the effect sizes for groups of tagged birds from the same study site and year of attachment, of the same sex (if applicable) and specific geolocator and attachment type accompanied with the corresponding control groups. For simplicity, we call these units *records* throughout the text. For each record, we extracted a contingency table with the treatment arm continuity correction (Schwarzer, Carpenter, & Rücker, 2014) or mean, variance, and sample size, to calculate the unbiased standardized mean difference—Hedges' g (Borenstein, Hedges, Higgins, & Rothstein, 2009)—and its variance with correction for the effect of small sample sizes (Doncaster & Spake, 2018). We used the equation from Sweeting, Sutton, and Lambert (2004) to calculate variance in pairwise comparisons. When raw data were not provided, we used the reported test statistics (F, t or χ^2) and sample sizes to calculate the effect size using the R package compute.es (Del Re, 2013). Besides the effect size measures, we extracted additional variables of potential interest—ecological and life-history traits per species, methodological aspects of the study, geolocator and attachment designs and harness material elasticity (Table 1).

3.4 | Accounting for dependency

We accounted for data non-independence on several levels. When multiple records shared one control group (e.g. several geolocator types and attachment designs used in one year), we split the sample size in the shared control group by the number of records to avoid a false increase in record precision. When multiple measures were available for the same individuals, we randomly chose one effect size measure in each trait category (n = 8). If the study provided both recapture and re-encounter rates, we chose the re-encounter rate as a more objective measure of apparent survival. Re-encounters included captures and observations of tagged birds, and thus, the bias towards the tagged birds caused by the potentially higher recapture effort to retrieve the geolocators should be lower. Finally, we accounted for phylogenetic non-independence between the species and the uncertainty of these relationships using 100 phylogenetic trees (Jetz, Thomas, Joy, Hartmann, & Mooers, 2012) downloaded from the BirdTree.org (www.birdtree.org) using the backbone of Hackett et al. (2008). Moreover, we used the random intercepts of species and study sites in all models, the latter to account for possible site-specific differences (such as different netting effort or other field methods used by particular research teams).

3.5 | Overall effect sizes and heterogeneity

We calculated the overall effect size for each trait category from all available records using meta-analytical null models. We employed the *MCMCglmm* function from the MCMCglmm package (Hadfield, 2010) to estimate overall effect sizes not controlled for phylogeny (model 1, Supporting Information Table S3). We then used the *mulTree* function from the mulTree package (Guillerme & Healy, 2017) to

TABLE 1 Explanatory variables used in the multivariate meta-analysis of apparent survival extracted from published and unpublished geolocator studies or from the literature. *N* presents the number of records specified as the groups of tagged birds from the same study site, year of attachment, of the same sex and the specific geolocator and the attachment type accompanied with the corresponding control groups

	Description	*N*
Methodological aspect		
Published data	Published—data from published studies (for details see Methods), data from unpublished sources from years following an already published study or data initially collected as unpublished but published by 31 August 2018	303
	Unpublished—data from unpublished studies	123
Control group	Matched—birds handled in the exactly same way as geolocator-tagged birds except for geolocator deployment	102
	Marked only—birds of the same sex, age, from the same year and study site or birds from the same site, from different years	324
Species trait		
Foraging strategy[b,c]	Aerial forager	122
	Non-aerial forager	304
Sex	Males	195
	Females	120
Geolocator specification		
Relative load	% of geolocator mass (including the harness) of the body mass of the tagged birds	418
Stalk/pipe length[a]	Length (mm) of the stalk/pipe holding the light sensor or guiding the light towards the sensor (0 mm for stalkless models)	371
Attachment specification		
Attachment type	Leg-loop harness	304
	Full-body harness	80
	Leg-flag attachment	42
Material elasticity[a]	Elastic—elastan, ethylene propylene, neoprene, rubber, silicone, silastic or Stretch Magic	235
	Non-elastic—cord, kevlar, nylon, plastic, polyester or teflon	146
Ecological trait		
Life histories	Great circle distance between geolocator deployment site and population-specific centroid of the non-breeding (or breeding) range	426
	Male body mass (g)	426
	Female body mass (g)	426
	Nest type—open/close	426
	Clutch size (number of eggs)	426
	Number of broods per year	426
	Dense habitat preference (species occurs especially in dense habitats, e.g. reeds or scrub)—yes/no	426
	Egg mass (g)—mean fresh mass[d]	426
	Clutch mass (g)—egg mass × clutch size	426

[a] Only used for harness attachments. [b] Cramp & Perrins, 1977–1994. [c] Rodewald, 2015. [d] Schönwetter, 1960–1992.

automatically fit a MCMCglmm model on each phylogenetic tree and summarised the results from all these models to obtain phylogenetically controlled overall effect size estimates (model 2, Supporting Information Table S3). We used weakly informative inverse-Gamma priors (V = 1, nu = 0.002) in all models. All fitted MCMCglmm models converged and Gelman–Rubin statistic was always <1.1 for all parameters. As our data contained many effect sizes based on small sample sizes, which could lead to a biased estimate of the overall effect size variance, all effect sizes were weighted by their mean-adjusted sampling variance (Doncaster & Spake, 2018). We considered effect sizes (Hedge's *g*) of 0.2, 0.5 and 0.8 weak, moderate and large effects, respectively. Moreover, we calculated the amount of

TABLE 2 Number of unpublished effect sizes included in the analysis and Egger's regression tests of the null model residuals against their precision to assess the presence of publication bias

	Unpublished (%)		Egger's regression			
Trait category	**Effect sizes**	***N***	**Intercept**	***t***	***SE***	***p***
Apparent survival	28.9	426	0.12	1.53	0.08	0.121
Condition	63.3	79	−0.36	−1.70	0.21	0.088
Phenology	59.1	22	−0.26	−1.28	0.21	0.217
Breeding performance	27.3	22	−0.01	−0.01	0.61	0.993

between-study heterogeneity in all null models using the equation described in Nakagawa and Santos (2012). Phylogenetic heritability (H^2) expressing the phylogenetic signal was estimated as the ratio of phylogenetic variance ($\sigma^2_{\text{phylogeny}}$) against the sum of phylogenetic and species variance ($\sigma^2_{\text{species}}$) from the models (Supporting Information Table S3; Hadfield & Nakagawa, 2010):

$$H^2 = \sigma^2_{\text{phylogeny}} / (\sigma^2_{\text{phylogeny}} + \sigma^2_{\text{species}}).$$

3.6 | Multivariate meta-analysis

To unveil the most important dependencies of the geolocator effects, we calculated three types of multivariate models: a full trait model (model 3), an ecological model (model 4) and models of publication bias (model 5, Supporting Information Table S3). In the full trait model, we used methodological, species, geolocator specification and attachment variables (Table 1) to estimate their impact on apparent survival (model 3). We did not compare the tagging effects of different attachment types due to their use in specific groups of species (e.g. the leg-flagged attachment in shorebirds or the full-body harnesses in nightjars and swifts only). Prior to fitting the ecological model, we employed a principal component analysis of the intercorrelated log continuous life-history traits and extracted the two most important ordination axes—PC1 and PC2 (Table 1). The PC1 explained 54.4% of the variability and expressed a gradient of species characterized mainly by increasing body mass, egg mass and clutch mass (Supporting Information Figure S4). The PC2 explained 18.7% of variance and was characterized mainly by increasing clutch sizes, number of broods and decreasing migration distances (Supporting Information Figure S4). These axes together with the categorical ecological traits (Table 1) were then entered into the ecological model to estimate their effect on apparent survival (model 4). Finally, we tested for differences in effect sizes between published and unpublished results in each trait category using all available records (model 5). In these models, we employed the *rma.mv* function from the R package metafor (Viechtbauer, 2010) weighted by the mean-adjusted sampling error (Doncaster & Spake, 2018). Continuous predictors were scaled and centred. None of the model residuals violated the assumptions of normal distribution. Because the phylogenetic relatedness of the species explained only a small amount of variation and the phylogenetic relatedness correlates with the life-history and ecological traits, we did not control for phylogeny in the multivariate models but incorporated the random intercepts of species and study site. We calculated R^2 for the full trait and ecological models using the residual between-study variability (τ^2_{residual}) and the total between-study variability (τ^2_{total}) according to the equation (López-López, Marín-Martínez, Sánchez-Meca, Van den Noortgate, & Viechtbauer, 2014):

$$R^2 = (1 - \tau^2_{\text{residual}} / \tau^2_{\text{total}}) \times 100.$$

3.7 | Publication bias; body mass manipulation

We used funnel plots to visually check for potential asymmetry caused by publication bias in each trait category (Supporting Information Figure S5). To quantify the level of asymmetry in each trait category, we applied the Egger's regression tests of the meta-analytical residuals from all null models of the trait categories (calculated using the *rma.mv* function) against effect size precision (1/mean-adjusted standard error; Nakagawa & Santos, 2012). An intercept significantly differing from zero suggests the presence of publication bias. In order to find differences in log body mass between the tagged and control individuals during the tagging and marking, we applied a linear mixed-effect model with species and study site as a random intercept weighted by the sample sizes. We considered all effect sizes significant when the 95% credible interval (CrI; using *MCMCglmm* function) or confidence interval (CI; using *rma.mv* function) did not overlap zero. All analyses were conducted in R version 3.3.1 (R Core Team, 2018).

4 | RESULTS

We assessed 854 records for eligibility of effect size calculation and excluded 36% of these records mainly due to a missing control group (59% of ineligible records) or missing essential values for effect size calculation (21%; Supporting Information Figure S1). Finally, a total of 122 studies containing 549 effect sizes were included in our meta-analysis wherein 35% effect sizes originated from unpublished sources (Table 2). The vast majority of the analysed effect sizes originated from Europe or North America (94%; Supporting Information Figure S6) and the data contained information about 7,829 tagged and 17,834 control individuals of 69 species from 27 families and 7 orders (Supporting Information Table S7).

We found a weak overall negative effect (Hedges' *g*: −0.2; 95% CrI −0.29, −0.11; $p < 0.001$) only on apparent survival in the model not controlled for phylogeny (model 1). Although we found no statistically significant overall tagging effects in any trait category when controlling for phylogenetic relatedness, the estimates were

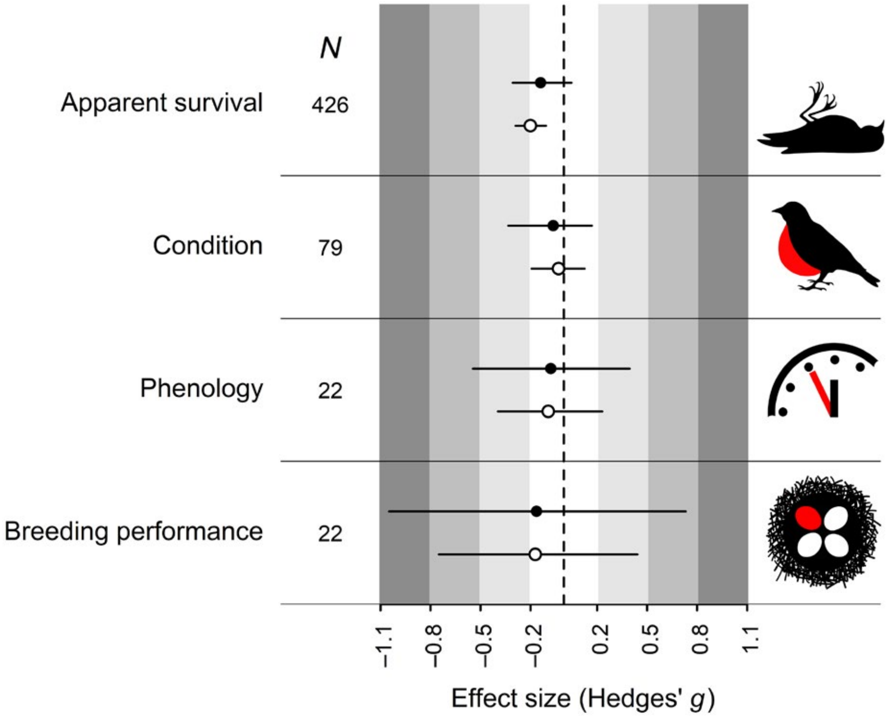

FIGURE 1 Overall effects of geolocators in the four trait categories, circles give means, horizontal lines represent 95% CrI. Filled symbols present the phylogenetically controlled overall effects, open symbols give the value from null models not accounting for phylogeny. *N* presents the number of effect sizes analysed. For the detailed description of the trait categories, see Methods and Supporting Information Table S2

TABLE 3 Summary of the full trait model ($n = 281$; model 3) and the ecological model ($n = 426$; model 4) of the geolocator effects on apparent survival. Levels contrasted against the reference level are given in parentheses

Trait	Estimate	*SE*	*Z*	95% CI	*p*
Full trait model					
Intercept	−0.25	0.10	−2.59	(−0.44; −0.06)	0.010
Published (published)	0.14	0.10	1.39	(−0.06; 0.34)	0.164
Control type (matched)	−0.05	0.09	−0.61	(−0.23; 0.12)	0.542
Foraging strategy (aerial)	−0.09	0.14	−0.61	(−0.36; 0.19)	0.540
Sex (males)	−0.07	0.05	−1.30	(−0.17; 0.03)	0.192
Relative load	−0.12	0.05	−2.36	(−0.23; −0.02)	0.018
Stalk/pipe length	0.07	0.04	1.77	(−0.01; 0.15)	0.077
Material elasticity (non-elastic)	0.19	0.08	2.21	(0.03; 0.35)	0.026
Foraging strategy (aerial) × stalk length	−0.10	0.07	−1.40	(−0.25; 0.04)	0.161
Ecological model					
Intercept	−0.26	0.08	−3.20	(−0.42; −0.10)	0.001
PC1	0.06	0.03	2.32	(0.01; 0.11)	0.026
PC2	0.02	0.03	0.47	(−0.05; 0.08)	0.638
Dense habitat (yes)	0.03	0.13	0.21	(−0.22; 0.27)	0.834
Nest type (open)	0.14	0.11	1.27	(−0.08; 0.36)	0.205

similar to those not controlled for phylogeny (model 2, Figure 1). The phylogenetic signal ($H^2 = 59\%$) was statistically significant only for apparent survival, suggesting that closely related species have more similar response to tagging than less related species, but the variances explained by phylogeny and species were very low for all models (Supporting Information Table S8).

The full trait model of apparent survival revealed that tagging effects were stronger with increasing load on tagged individuals and that geolocators with elastic harnesses affected birds more negatively than geolocators with non-elastic harnesses (Table 3, Figure 2). However, we found no statistically significant effect on apparent survival for control group type, sex, stalk length, foraging strategy or the interaction between stalk length and foraging strategy (model 3, Table 3). The ecological model suggested a relationship of apparent survival with the PC1, with negative effects being stronger with decreasing body, egg and clutch mass (model 4, Table 3).

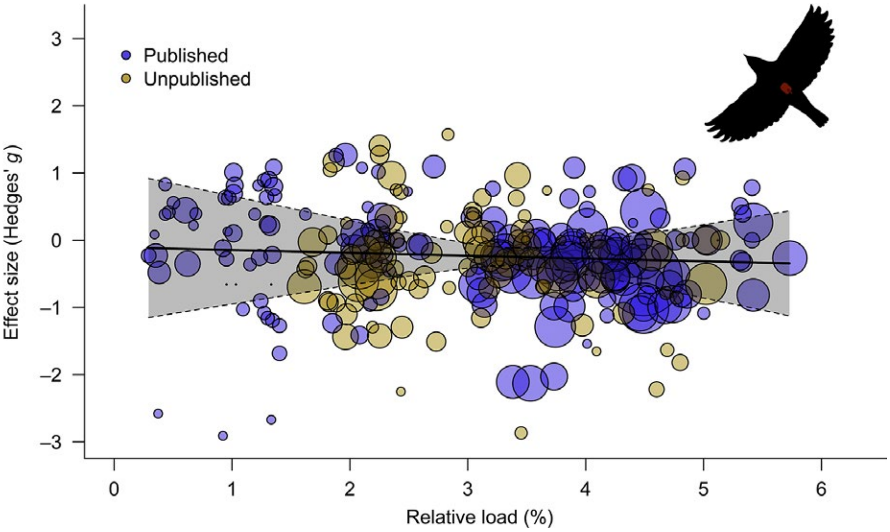

FIGURE 2 Relationship between relative load and the effect of geolocator deployment on the apparent survival of tagged birds. Size of the circles reflects the precision (1/mean-adjusted *SE*) of the effect sizes, the shaded area and dashed lines depict the 95% CI of the regression

The full trait model explained 21.1% and the ecological model 11.8% of the between-study variance.

We did not find any evidence for publication bias in any of the trait categories, either visually in the funnel plots (Supporting Information Figure S5), or using Egger's regression tests (Table 2). Moreover, there were no statistically significant differences in tagging effects between published and unpublished studies (model 5, Supporting Information Table S9). The geolocator-tagged birds were on average 3.8% heavier than control individuals prior to the geolocator deployment and marking (LMM: estimate 0.008 ± 0.003, $t = 2.47$, $p = 0.014$).

5 | DISCUSSION

Geolocator deployment has a potential to reduce a bird's apparent survival, condition, breeding performance or may delay events of the annual cycle leading to biases in movement data. By conducting a quantitative review of published studies deploying geolocators on small bird species and incorporating unpublished data, we revealed only a weak overall effect of geolocators on apparent survival of tagged birds while we found no clear overall effect on condition, phenology and breeding performance. Moreover, we found no statistically significant effects of tagging in any of trait categories when accounting for phylogenetic relationships. Tagging effects on apparent survival were stronger with a higher relative load, when the geolocators were attached with elastic harnesses and in small-bodied species.

5.1 | Overall tag effects

A negative overall effect of geolocator tagging on apparent survival found in this study seems to be prevalent across previous comparative studies of tagging effects (Barron et al., 2010; Bodey et al., 2018a, 2018b; Costantini & Møller, 2013; Trefry, Diamond, & Jesson, 2012; Weiser et al., 2016). However, unlike previous comparative (Barron et al., 2010; Bodey et al., 2018a, 2018b) and primary studies (e.g. Adams et al., 2009; Arlt et al., 2013; Snijders et al., 2017), we found no overall negative effects of tagging on variables associated with breeding performance in our analysis. We also did not find evidence for overall effects of tagging on body condition and phenology, which was consistent with equivocal results of previous studies: Some found reduced body condition (Adams et al., 2009; Elliott et al., 2012) or delayed timing of annual cycle events (Arlt et al., 2013; Scandolara et al., 2014), while others found no evidence for tagging effects on these traits (Bell et al., 2017; Fairhurst et al., 2015; Peterson et al., 2015; van Wijk et al., 2015).

Tagged individuals that returned to the study site are potentially in better condition than the tagged individuals that did not return—this potentially contributes to the weak tagging effects on condition, phenology and breeding performance. However, the lack of effect we found on phenology and breeding performance could also be an artefact of the small sample sizes, as collecting these data is probably more challenging in small avian species, which are more difficult to re-sight and recapture and have shorter life spans than the relatively heavier species included in the previous studies. Similarly, effects of tagging on condition could be underestimated in our analysis due to the initial differences we found between the body mass of tagged and control birds. Additionally, the intra-annual body mass changes could be biased in studies where timing of geolocator deployment and geolocator recovery differs. Unfortunately, the timing of captures and recaptures was rarely reported and could not be analysed in our study. Overall, the weak effects of tagging we found support several primary studies (e.g. Bell et al., 2017; Fairhurst et al., 2015; Peterson et al., 2015; van Wijk et al., 2015), indicating that geolocator tagging is both ethical and provides credible information on bird movements. On the other hand, care should be taken as the tagging effect may be specific to populations or species. For example, Weiser et al. (2016) found a negligible overall effect but significant reduction of return rates in the smallest species in their meta-analysis. The negative effect of geolocators can also vary between years (Bell et al., 2017; Scandolara et al., 2014), or be induced by occasional bad weather conditions (Snijders et al., 2017), or food shortages (Saraux et al., 2011; Wilson, Sala, Gómez-Laich, Ciancio, & Quintana, 2015).

5.2 | Inferring unbiased overall effect sizes

We minimized publication bias in our estimates of overall effects by including substantial amount of unpublished results (192 records of 38 species) and contacting authors of published studies for additional data. Still, some of these studies might get published in the future despite the delay between our data collation and the final analysis. We did not find any evidence that tagging effects differed between published and unpublished studies, suggesting that the tagging effect may not be a critical consideration for publishing a study.

Moreover, we found no support for stronger tag effects in studies with matched control individuals compared to studies with less strict control treatments. However, this result is potentially confounded by the fact that tagged birds were on average larger and in potentially better condition than control birds, which would underestimate the negative effects of tagging. We thus suggest establishing carefully matched control groups in all future studies to enable a more reliable estimation of tagging effects. Such a control group should include the following: (a) randomly selected individuals of the same species, sex and age class; (b) individuals caught at the same time of the season and year; (c) at the same time of the day; (d) of similar size and condition as tagged individuals; and (e) exclude non-territorial birds or individuals passing through the site.

5.3 | Influence of relative load and species' life histories

Our results support the current evidence (Bodey et al., 2018a, 2018b; Weiser et al., 2016) for reduced apparent survival in studies with a relatively higher tag load on treated individuals. Moreover, we found an increasing negative effect in studies tagging smaller species with smaller eggs and clutch masses. The lower body mass in these species is likely accompanied with a higher relative tag load due to technical constraints of lower tag weights. Although recent miniaturization has led to the development of smaller tags, these tags have been predominantly applied to smaller species instead of reducing tag load in larger species (Portugal & White, 2018). The various relative loads used without observed tagging effects (e.g. Bell et al., 2017; Peterson et al., 2015; van Wijk et al., 2015) indicate the absence of a generally applicable rule for all small bird species (Schacter & Jones, 2017), and we thus recommend the use of reasonably small tags despite potential disadvantages (e.g. reduced battery life span or light sensor quality).

5.4 | Harness material

Contrary to our prediction, we found higher apparent survival in birds tagged with harnesses made of non-elastic materials. Non-elastic harnesses are usually individually adjusted on each individual, whereas elastic harnesses are often prepared before attachment to fit the expected body size of the tagged individuals according to allometric equations (e.g. Naef-Daenzer, 2007). As pre-sized elastic harnesses cannot match perfectly the size of every captured individual, they may be in the end more frequently tightly fitted as some researches might tend to tag larger individuals or avoid too loose harnesses to prevent geolocator loss. Non-elastic harnesses may also be more frequently looser than elastic harnesses as researchers try to reduce the possibility of non-elastic harness getting tight when birds accumulate fat. Tight harnesses significantly reduced the return rates in whinchat (*Saxicola rubetra*; Blackburn et al., 2016), and it may be difficult to register whether elastic harnesses are restricting physical movement of birds when deploying tags. In contrast, non-elastic harnesses, which are more commonly tailored according to the actual size, are often made sufficiently loose to account for body mass changes in each individual. Prepared elastic harnesses are usually used to reduce the handling time during the geolocator deployment (Streby et al., 2015) but this advantage may be outweighed by the reduced apparent survival of geolocators with tied elastic harnesses. We thus suggest to consider stress during geolocator deployment together with the potentially reduced apparent survival and the risk of tag loss when choosing harness material.

5.5 | Variables without statistically significant impact on tagging effect

Migratory distance did not affect the magnitude of the effect sizes, contrasting with some previous findings (Bodey et al., 2018a, 2018b; Costantini & Møller, 2013). However, none of these studies used population-specific distances travelled; instead, they used latitudinal spans between ranges of occurrence (Costantini & Møller, 2013) or travelled distance categorized into three distances groups (Bodey et al., 2018a, 2018b). These types of distance measurements could greatly affect the results especially in species that migrate mainly in an east–west direction (Lislevand et al., 2015; Stach, Kullberg, Jakobsson, Ström, & Fransson, 2016) or in species whose populations largely differ in their travel distances (Bairlein et al., 2012; Schmaljohann, Buchmann, Fox, & Bairlein, 2012). Moreover, light-level geolocators were most frequently deployed to the long-distance migrants in our study and the result can be thus applicable to these species only.

Additionally, we found no overall effect of species' foraging strategy, contrary to the strong overall negative effect found for aerial foraging species (Costantini & Møller, 2013). Despite the tag shape altering the drag and thus energy expenditure during flight (Bowlin et al., 2010; Pennycuick et al., 2012), apparent survival tended to be better in individuals fitted with stalked geolocators and we found no interaction between stalk length and foraging strategy on the tagging effect size. Geolocators with longer stalks have been more frequently used in heavier birds with low relative load where the expected tag effect is weak. Moreover, previous results of strong negative effects in aerial foragers led to a preferential use of stalkless geolocators in these species and probably minimized the tagging effect in this foraging guild (Morganti et al., 2018; Scandolara et al., 2014). However, the evidence for the negative effects in non-aerial foragers is low as there is only one field study focusing on stalk length effects on the return rates (Blackburn et al., 2016).

5.6 | Future considerations

Future studies evaluating the use of geolocators on birds should focus on assessing interannual differences in tagging effects, effects of varying relative loads, different stalk lengths or different attachment methods to minimize the negative effects of tagging. We also suggest to focus on the impact of various movement strategies such as fattening and moulting schedules on the tagging effect. All future studies should carefully set matched controls and transparently report on tagging effects. Finally, our results encourage use of geolocators on small bird species but the ethical and scientific benefits should always be considered.

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AUTHORS' CONTRIBUTIONS

V.Br., J.K. and P.P. conceived the idea and designed the methodology. V.Br. reviewed the literature and collected data. J.K. and P.P. checked the data extracted for analysis. V.Br. and P.P. analysed the data. V.Br. led the writing of the manuscript with significant contributions from J.K. and P.P. M.B., S.H., D.H., M.K., J.O. and E.W. contributed with unpublished data and their comments and suggestions significantly improved the manuscript. P.A., J.A., D.A., S.B., D.B., E.B., V.Be., C.B., S.B., M.Br., B.C., D.C., N.C., J.C., V.C., T.E., K.F., O.G., M.G., M.H., C.H., F.J., J.J., T.K., D.K., M.L., T.L., S.L., C.L., K.M., P.Mar., S.M., P.Mat., C.M., B.M., J.M., R.Ne., A.N., R.No., T.P., V.P., N.P., M.P., J.R., C.R., A.R., C.S., N.S., M.T., D.T., H.O., A.W., H.W., J.W., K.W. and B.W. contributed unpublished data and critically revised the manuscript. All authors gave final approval for publication.

DATA ACCESSIBILITY

Data described in this article are available at https://doi.org/10.5281/zenodo.1886530 (Brlík et al., 2019).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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