

On the ecology and evolution of partial migration: a field study on migrant and resident European blackbirds

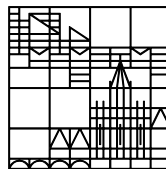
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Presented by

Daniel Sebastián Zúñiga Sepúlveda

at the

Universität
Konstanz



Faculty of Sciences,
Department of Biology

Date of oral examination: 21.11.2016
First supervisor: Prof. Dr. Martin Wikelski
Second supervisor: Prof. Dr. Michaela Hau

*“Look deep into nature, and then you will understand everything better”. -
Albert Einstein*

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Summary

Partial migration is defined as a within-population variation in migratory behaviour, meaning that some individuals migrate while others remain year-round residents in a given habitat.

Studying a partially migratory population is the ideal system to test hypotheses concerning the evolution of migration and to elucidate costs and benefits of the two strategies (migration versus residency). I studied a wild partially migratory population of European blackbirds (*Turdus merula*) using a combination of radio tracking and classic capture-mark-recapture methods.

Most of the migratory songbird species are diurnal, but they migrate at night. How these birds shift their daily rhythms from diurnal to nocturnal during the migratory seasons remains unknown. To answer this question, in the second Chapter I studied how migrant blackbirds organize their daily rhythms prior to departure in the fall. Using an automated radio telemetry system, I monitored, quantified and compared the activity of migrants and residents every 30 minutes, seven days before the departure of the migrants. I found that activity patterns between migrants and residents did not differ during daytime or night-time. Furthermore, migrants did not change their daily rhythm in a progressive manner, as previously shown in the lab, but instead shifted abruptly on the night of departure. I found no signs of nocturnal activity exhibited prior to migration.

Activity of an animal is the most basic descriptor of its behaviour. Animals vary their activity levels throughout the year in response to environmental fluctuations and the specific requirements of the different stages of the annual cycle. In the third Chapter, also using an automated radio telemetry system, I compared the seasonal activity patterns of migrants and residents when individuals of both groups were present at the breeding grounds (from spring

until fall). The main objective was to understand whether the constraints and requirements of migration as a strategy would have an effect on the activity levels of migrants after their arrival to the breeding grounds in spring, during the breeding season and prior to migration in the fall. I expected that after arrival in the spring, migrants would exhibit different activity levels compared to residents; either to recover from migration (decreased activity levels) or to compete for breeding mates and territories (increased activity levels). Similarly, during the pre-migratory period I also expected differing activity levels between migrants and residents because migrants prepare themselves for migration. Contrary to my expectations, I found that migrants and residents do not differ in their activity levels when both groups were present at the breeding grounds. Additionally I described the annual activity pattern of resident birds. Even when the photoperiod is taken into account, activity follows a seasonal pattern: there is high activity during the breeding season, decreasing activity during the moulting period, and increasing activity towards winter.

One hypothesis for the evolution and maintenance of partial migration is that migration offers individual fitness benefits. Migrants would travel during the fall to overwinter in habitats that offer better survival chances than the breeding grounds. To test whether migration offers survival benefits, I used a combination of capture-recapture and radio telemetry methods to generate a presence/absence matrix with data collected over seven years. Using multi-event survival models, I estimated seasonal and annual survival probabilities for individuals of both groups. I found that during the non-winter season (March – November) migrants and residents have a similar probability of survival. However, during the winter (November - March), migrants have higher survival probability than residents. These results support the notion that migration offers fitness benefits.

Zusammenfassung

Wenn es innerhalb einer Population eine derartige Variation bezüglich des Zugverhaltens gibt, dass manche Tiere ziehen, während andere Individuen das ganze Jahr über im Brutgebiet verweilen, so spricht man von einer teilziehenden Population. Wenn man die Evolution und Entstehung der saisonalen Wanderbewegungen im Tierreich studieren möchte, so sind solche teilziehenden Populationen ein ideales System, da man die Vor- und Nachteile beider Strategien beleuchten kann. Mittels einer Kombination aus ganzjähriger Radiotelemetrie und Rückfangmethode habe ich eine wilde, teilziehende Population der Amsel (*Turdus merula*) eingehend untersucht.

Die meisten ziehenden Singvogelarten sind tagaktiv, wechseln ihre alljährlichen Wanderungen aber üblicherweise nachts. Wie diese Tiere jedoch ihren Rhythmus von tag- zu nachtaktiv wechseln können, ist weitestgehend unbekannt. Um dieser Frage nachzugehen, habe ich im zweiten Kapitel die Tagesrhythmen von Amseln unmittelbar vor dem Herbstzug untersucht. Mithilfe eines automatisierten Radiotelemetrie-Systems konnte ich die Aktivität der Zug- und Standvögel beobachten, quantifizieren und vergleichen. Dies erfolgte alle 30 Minuten über den gesamten Zeitraum der letzten sieben Tage vor dem Herbstzug. Dabei fand ich heraus, dass sich die Aktivitätsmuster der Stand- und Zugvögel weder nachts- noch tagsüber unterscheiden. Die ziehenden Tiere zeigten nicht, wie aufgrund von Laborstudien erwartet, einen graduellen Übergang zu nächtlicher Aktivität, sondern zeigten dieses Verhalten abrupt und nur während der Zugnächte. Zuvor gab es keinerlei Anzeichen nächtlicher Aktivität bei den ziehenden Individuen.

Die Aktivität des einzelnen Individuums ist die elementarste Art, das Verhalten eines Tieres zu beschreiben. Die Aktivitätsmuster eines Tieres verändern sich im Laufe des Jahres, da sich

einhergehend mit dem Jahreszyklus' der Umwelt und des Tieres dessen Lebensabschnitte und somit Verhalten und Bedürfnissesändern. Im dritten Kapitel benutzte ich erneut das automatisierte Radiotelemetrie-System, um die Aktivitätsmuster von Amseln über den Lauf des Jahres zu quantifizieren. Hierbei interessierten mich vor allem eventuelle Unterschiede zwischen den Zug- und Standvögeln, die während der Brutzeit von Frühjahr bis Herbst im selben Gebiet verweilen. Das Hauptziel dieser Studie war es zu verstehen, welchen Einfluss der Vogelzug als Strategie mitsamt der daraus resultierenden Ansprüche und Einschränkungen auf die Aktivitätsmuster des einzelnen Individuums hat. Meine Erwartung war, dass während dreier Lebensabschnitte – nach der Ankunft der Zugvögel im Brutgebiet, während der Brutzeit, und in der Vorbereitung auf den Herbstzug – die Zugvögel in einem anderen Maße Aktivität zeigten als die Standvögel. Diese Unterschiede können dadurch zustande kommen, dass sich die Tiere vom Zug erholen (reduzierte Aktivitätslevel) oder um Partner und Territorien konkurrieren müssen (erhöhte Aktivitätslevel). Auch während der Phase unmittelbar vor dem Herbstzug erwartete ich Unterschiede in der Aktivität von Zug- und Standtieren, da sich die Zugvögel auf die Wanderung vorbereiten müssen. Entgegen meinen Erwartungen fand ich jedoch, dass es zu keinem Zeitpunkt zwischen Ankunft und Wegzug der ziehenden Individuen Unterschiede in der Aktivität zwischen den beiden Strategien gab. Zusätzlich zu diesem Vergleich habe ich auch das ganzjährige Aktivitätsmuster der Standvögel im Brutgebiet beschrieben. Selbst wenn man für die sich im Laufe des Jahres verändernde Photoperiode korrigiert, folgt die Aktivität der Tiere einem saisonalem Muster: während der Brutzeit sind Amseln besonders aktiv, in der darauf folgenden Mauserperiode sehr inaktiv. Im Winter hingegen zeigen die Tiere jedoch wieder eine zunehmende Aktivität.

Eine Hypothese für die Entstehung und dem Erhalt eines Teilzug-Phänomens ist, dass die saisonalen Wanderbewegungen den Tieren einen Fitnessvorteil verschafft. Zugtiere

verbringen den Winter in Gebieten, die ihnen höhere Überlebenschancen gegenüber den Standtieren im Brutgebiet bieten. Um zu testen, ob eine Zugstrategie den Tieren tatsächlich einen solchen Überlebensvorteil verschafft, habe ich eine Kombination auf Radiotelemetrie und Rückfangmethode benutzt und eine Präsenz/Absenz-Matrix für Daten aus sieben Jahren erstellen können. Mittels einer Ereigniszeitanalyse für multiple Ereignisse konnte ich die saisonalen und annuellen Überlebenswahrscheinlichkeiten für Individuen beider Strategien schätzen. Dabei kam heraus, dass Zug- und Standvögel von März bis November eine ähnliche Überlebenschancen hatten. Während des Winters (November bis März) hatten Zugvögel jedoch eine höhere Wahrscheinlichkeit zu überleben, als Standvögel. Diese Ergebnisse unterstützen die Annahme, dass die Strategie, saisonale Wanderbewegungen zu unternehmen, den ziehenden Tieren einen Fitnessvorteil bietet.

General Introduction

Movement is a common and widespread feature in the animal kingdom, and plays an important role in many vital ecological and evolutionary processes at individual and population levels (Nathan et al., 2008). Migration is one of the most spectacular forms of animal movement, and has fascinated and inspired multiple research efforts aimed at understanding its causes and consequences. Among the multiple forms of migration, “partial migration” is the most common type and is characterised as a within-population variation in migratory behaviour. This means only a fraction of the individuals migrate, while others remain as residents in a given habitat (Chapman et al., 2011a). This form of migration has been documented for a wide range of animals across different taxa, including fish, mammal and bird species in the wild. The most common form of partial migration is when migrants and residents breed sympatrically in a common habitat, but overwinter in different locations.

Partial migration is conceived as the intermediate point between fixed migratory and fixed sedentary strategies, and offers a unique model to study differences in behaviour, ecology and physiology between migratory and sedentary individuals (Berthold, 2001). Furthermore, it offers the possibility to test hypotheses about the evolution of migration (Berthold, 2001). Along the annual cycle, migrants and residents share some common life history stages (e.g. reproduction, moult) but differ in others (e.g. migration, stopover, overwintering). Hence, studying how these two distinct phenotypes cope with the different stages of the annual cycle can provide fundamental insight into understanding how the two strategies persist, but also to elucidate the cost and benefits of migration versus residency.

Why do some individuals migrate and others remain as residents? What are the proximate mechanisms controlling the decision to migrate or not? How are both strategies maintained? These fundamental questions have driven extensive theoretical and empirical research efforts

(Chapman et al., 2011a). Although some answers have been found, there is still a want of knowledge to fully answer these questions.

Several hypotheses explaining the ecological drivers underpinning partial migration have been proposed (see review Chapman et al., 2011a). The “arrival time” hypothesis states that if the reproductive success of one sex is influenced by acquisition of a quality territory during the early breeding season, then it is beneficial for individuals of that sex to reach the breeding grounds as early as possible (Ketterson and Nolan, 1976). The “dominance” or “competitive release” hypothesis predicts that if there is a strong intraspecific competition for limited food resources at the breeding site, the most competitive or dominant individuals would stay as residents, while subordinate individuals would migrate (Lundberg, 1985). The “fasting endurance” hypothesis postulates that when there is a seasonal food reduction, combined with potentially extreme temperatures, individuals with the greatest risk of starvation (small size, high metabolic rate) will be more likely to migrate (Chapman et al., 2011a). The “predation vulnerability” hypothesis proposes that individuals at higher risk of predation would migrate seasonally (Skov et al., 2011). Research efforts thus far have yielded empirical data supporting the following hypotheses: “arrival time” (Fudickar et al., 2013; Silverin et al., 1989); “dominance” (Lundberg, 1985; Nilsson et al., 2008); “fasting endurance” (Jahn et al., 2010) and “predation vulnerability” (Skov et al., 2013, 2011).

Regarding the evolution of partial migration, theoretical work has yielded at least two explanations. An evolutionary stable state (ESS) operating under frequency-dependent selection, where the fitness of migrants and residents equalizes, has been proposed as one possibility as to how partial migration evolves (Kaitala et al., 1993; Lundberg, 1987). Another explanation proposed is a conditional strategy operating under frequency-dependent selection, where individuals would adopt one strategy depending on specific individual phenotypes (e.g.

sex, age, dominance). This strategy would maximize their individual fitness, although it might not be the optimal strategy at the population level (Lundberg, 1988; Vélez-Espino et al., 2013). One example of conditional strategy is where juveniles migrate because they are subordinate to adults, even though at a population level, residency is the strategy that confers the most fitness benefits. Here, it is better for a given juvenile to migrate rather than stay resident, thus making the “best of a bad job” (Lundberg, 1988). Despite the theoretical frameworks developed over the years, there is a lack of empirical data supporting these hypotheses, because fitness data are hard to collect in the field.

In relation to the proximate mechanisms controlling partial migration, experimental studies in captive birds have proposed a genetic control of the propensity to migrate or not (Berthold and Querner, 1988; Berthold et al., 1990; Pulido et al., 1996). These studies have been based on artificially selecting individuals based on the amount of nocturnal restlessness (“*Zugunruhe*”) they expressed under laboratory conditions (Berthold et al., 1990; Pulido et al., 1996). It is believed that this trait represents the propensity of individuals to migrate. However, the fact that even completely sedentary species exhibit nocturnal restlessness under laboratory conditions (Helm and Gwinner, 2006; Ramenofsky et al., 2011) and the fact that the expression of *Zugunruhe* has not been observed in natural populations, reopened the discussion as to its biological significance.

The European blackbird (*Turdus merula*) has been previously used as a model system to study the ecology and evolution of partial migration (Eikenaar et al., 2015; Evans et al., 2012; Fudickar and Partecke, 2012; Fudickar et al., 2013; Lack, 1943; Lundberg and Schwabl, 1983; Lundberg, 1985; Møller et al., 2014; Partecke and Gwinner, 2007; Schwabl et al., 1984; Schwabl, 1983). Regarding the ecological drivers of partial migration, it has been suggested that blackbirds adopt an overwintering strategy based on hierarchy, such that dominant birds

remain as residents (adults and males) and subordinate individuals migrate (juveniles and females (Lundberg and Schwabl, 1983; Lundberg, 1985; Schwabl, 1983). The limitations of these studies rely on the methodology used. They based the classification of overwintering strategy on the presence or absence of banded birds. The identification and detection of specific banded birds using resighting methods can be faulty (Milligan et al., 2003) and furthermore it is difficult to distinguish between actual migration and local movement. More recently, radio telemetry technology now allows an exact classification of migrants and residents, and researchers in our lab found that female blackbirds are more likely to migrate than males, independent of age or body size (Fudickar et al., 2013). For males, it would be beneficial to remain resident at the breeding grounds during the winter to establish an early territory for the following breeding season and increase mating success. Furthermore Migratory individuals of this population travel up to 400 km nonstop throughout the night. The overwintering sites are located in west southwest Europe. never less than 300 km from the breeding grounds (Fudickar et al., 2013).

Building upon this prior knowledge, the main aim of my doctoral research was to elucidate some of the remaining major questions related to the cost and benefits of partial migration. To this end I investigated behavioural differences between migrants and residents that may arise due to the different life history stages. I studied a free-living partially migratory population of European blackbirds (*Turdus merula*) in southern Germany was previously studied by Fudickar et al. I primarily used extensive fieldwork to capture and tag individuals with radio telemetry transmitters, allowing me to track birds in their natural environments, over the entire annual cycle.

In Chapter 2, I examined the fundamental question of how nocturnal migrants shift their daily rhythm to perform their migratory journey. It has been previously shown that European

blackbirds display nocturnal restlessness (*Zugunruhe*) in captivity during the period of time that migration occurs in the wild, and individuals have been classified as migrants or residents based on the amount of *Zugunruhe* expressed (Partecke and Gwinner, 2007; Schwabl et al., 1984). It has also been described that the onset of nocturnal activity in captivity is gradual over time (Bartell and Gwinner, 2005). Using an automated radio telemetry system, I estimated the amount of activity expressed by migrants and residents every hour, 7 days before migrant departure. I compared daytime and night-time activity levels between the two groups. I showed that migrants shifted rapidly from a diurnal to nocturnal lifestyle on the night of departure. No signs of nocturnal restlessness (or elevated activity) were observed prior to migration in this wild population.

In Chapter 3, I compared daily activity levels of migrants and residents over the year. Life of an animal is divided into two stages, activity and rest (Halle and Stenseth, 2000). Activity levels can be defined as the sum of different behaviours that involve motion (foraging, locomotion, territoriality, migration and mating), while resting phases are characterized by behaviours that involved immobility (sleep, egg incubation, hibernation). Consequently, activity levels of an animal are the most basic descriptor of its behaviour (Halle and Stenseth, 2000). Throughout the year, animals must cope with environmental fluctuation imposed by the seasons and adjust their behaviour to the different stages of the annual cycle. Studying variation of activity levels in the context of the annual cycle is an effective approach to infer how animals cope with the environment. As mentioned previously, in a partially migratory population, migrants and residents have some common life stages (breeding, moulting) but others differ (pre-migratory preparation, migration, stopover, overwintering). Therefore I tested whether migrants would exhibit different activity levels than resident birds before fall migration or after spring arrival. Furthermore, we also compared activity patterns between males and females, given that their sex-specific behaviour is different during the breeding season. We found that migrants and

residents have similar activity levels during the breeding and pre-migratory period, suggesting that migration does not have an effect on activity levels in migrants.

Finally, in Chapter 4, using a 7 year capture - mark - recapture dataset in combination with radio telemetry, I tested whether migration, as a strategy, offers survival probabilities during the winter. I compared seasonal and annual survival probabilities between migrant and resident individuals. This chapter provides unique empirical data to test the hypothesis that explains the evolution and maintenance of partial migration. We found that migrants have higher survival during the winter than sedentary individuals. This result supports the hypothesis that migration offers survival benefits.

**Abrupt switch to migratory night flight in a
wild migratory songbird**

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Abstract

Every year, billions of wild diurnal songbirds migrate at night. To do so, they shift their daily rhythm from diurnality to nocturnality. In captivity this is observed as a gradual transition of daytime activity developing into nocturnal activity, but how wild birds prepare their daily rhythms for migration remains largely unknown. Using an automated radio-telemetry system, we compared activity patterns of free-living migrant and resident European blackbirds (*Turdus merula*) in a partially migratory population during the pre-migratory season. We found that activity patterns between migrant and resident birds did not differ during day and night. Migrants did not change their daily rhythm in a progressive manner as has been observed in captivity, but instead abruptly became active during the night of departure. The rapid shift in rhythmicity might be more common across migratory songbird species, but may not have been observed before in wild animals due to a lack of technology.

Introduction

Every year billions of songbirds migrate at night, largely hidden from human eyes. Migrant birds perform migratory nocturnal flights, presumably to overcome energetic constraints by flying in cooler and more laminar air (Kerlinger and Moore, 1989), to reduce their predation risk during migration (Newton, 2008) and to use celestial cues for orientation (Emlen, 1967). In order to migrate over long distances, migratory birds undergo complex changes in several physiological and behavioural traits before and during migration which are often referred to as “migratory syndrome” (Piersma et al., 2005). To reach the state of readiness for prolonged migratory flights requires dietary changes, involving hyperphagia to increase accumulation of fat as energy storage (Odum, 1960), changes in enzyme activities associated with energy metabolism (Weber, 2009), and hypertrophy of flight muscles (Dietz et al., 1999). In terms of behaviour, many diurnal migratory songbirds need to adapt their daily rhythms by adding a nocturnal phase of activity when they perform their migratory flights at night.

Under laboratory conditions, migratory behaviour of nocturnal migrant bird species is expressed by nocturnal locomotor activity (*Zugunruhe*) during the autumn and spring when migration occurs in the wild (Berthold et al., 1990; Gwinner, 1996; Pulido et al., 1996). *Zugunruhe* is composed of a set of stereotyped behaviours mostly characterized by wing whirring but also includes hopping and fluttering (Berthold et al., 2000). The amount of *Zugunruhe* has been used as a proxy for the propensity of individuals to migrate (Berthold and Querner, 1988) and has been related to genetic, physiological and behavioural aspects of bird migration (Berthold et al., 1990; Eikenaar et al., 2015, 2014a, 2014b; Gwinner, 1996; Pulido et al., 1996). The seasonal change in rhythmicity from diurnality to nocturnality that leads to the full expression of *Zugunruhe* is assumed to be controlled by endogenous circadian rhythms externally entrained by changes in photoperiod (reviewed in Coppack and Bairlein,

2011; Kumar et al., 2010). It has been assumed that two circadian oscillators – one controlling the daytime activity and the other controlling the night-time activity – are the main components of the avian circadian clock that triggers migratory nocturnality (Bartell and Gwinner, 2005; Rani et al., 2006). During migration seasons, the oscillators seem to slowly uncouple and stabilize in antiphase (Bartell and Gwinner, 2005; Rani et al., 2006) (reviewed in Kumar et al., 2010). This process can be observed as an evening or early morning component of activity which separates from the daytime activity and slowly moves into the night (Bartell and Gwinner, 2005). This shift in activity can be visualized as a gradual increase of night activity over time (Bartell and Gwinner, 2005) and has been observed in several bird species e.g. European starlings (*Sturnus vulgaris*) (Gwinner, 1975), bramblings (*Fringilla montifringilla*) (Phol, 2000), garden warblers (*Sylvia borin*) (Gwinner, 1996), common quail (*Coturnix coturnix*) (Bertin et al., 2007) and European blackbirds. In captive European blackbirds, a gradual onset of nocturnality occurs when an early morning component of activity slowly moves into the night (Fig.1 b). Individuals have previously been classified as migrants or residents based on the amount of nocturnal restlessness displayed (Partecke and Gwinner, 2007; Schwabl et al., 1984) (Fig. 1 a & b).

Although the onset of *Zugunruhe* and its underlying mechanisms have been well-studied under laboratory conditions, little attention has been devoted to how migratory birds change their daily rhythm from day- to night-time activity before their migratory journeys in the wild. A major limitation to study such migration-associated behaviours in free-living songbirds has been the lack of suitable tracking technology. Recent technical advancements have produced small and long-lived tracking devices which have led to increased research efforts investigating activity patterns of animals in the wild (Bäckman et al., 2016; Kays et al., 2015, 2011; Pagon et al., 2013; Rowcliffe et al., 2014; Steiger et al., 2013). Reports exist that during the pre-migratory phase, juvenile Eurasian reed warbler (*Acrocephalus scirpaceus*) perform

local flights around the breeding grounds (Mukhin et al., 2005). Furthermore, local nocturnal flights have also been described in Swainson's and Hermit Thrushes (*Catharus ustulatus* and *Catharus guttatus*, respectively) but in this case, during migration at stopover sites (Mills et al., 2011). However, studies so far have not focused on measuring activity at a high temporal resolution to elucidate how individuals of a diurnal bird species adjust their daily rhythm in preparation for nocturnal migration.

To test how free-living migratory songbirds extend their diurnal life style to include an additional nocturnal component while performing their migration, we studied a partially migratory population of European blackbirds using an automated radio telemetry system (Cochran et al., 1965; Kjos and Cochran, 1970; Steiger et al., 2013). Partial migration, where both migrants and year-round residents are present within the same population (Chapman et al., 2011b), provided us with an ideal study system to directly compare differences in behaviour between migrant and resident individuals (Berthold, 2001). In the population we investigated, migrants show specific characteristics that are known for classical obligate migratory bird species. Migrants accumulate fat during the pre-migratory phase as preparation for migration, while residents do not fatten up during this period of time (Fudickar et al., 2013). Furthermore, migrant European blackbirds migrate at night. Ground radio tracking data collected while following birds during their first night of the autumn migration using tracking cars show that departures from the breeding grounds occur during the first half of the night. During that first night of migration, birds fly non-stop > 200 km until they reach their first stopover site, and land just before sunrise (unpublished personal data). Data obtained from light-based geologgers indicate that migrants in this population overwinter on average 800 km west-southwest from the breeding grounds (Fudickar and Partecke, 2012).

To test whether European blackbirds prepare for migration by increasing their locomotor activity, we compared day and night activity patterns of radio-tagged migrant and resident

individuals of a partially migratory population of European blackbirds during the pre-migratory phase.

Materials and Methods

Ethical Note

All the experimental procedures were performed in accordance with the German regulation on animal experimentation. The experimental protocol was approved by the Ethical Committee of Baden-Württemberg (Regierungspräsidium Freiburg).

Study population, capture and tagging

The study population of European blackbirds inhabited a mixed coniferous/deciduous forest in south-western Germany (N 47°47', E 9°2'). Birds were captured during March and September throughout the years 2009-2012 and 2014-2015 with mist nets. Each bird was weighed (to the nearest g) and subsequently fitted with a radio transmitter (≤ 2.6 g; Sparrow Systems Fisher, IL, USA) by means of a leg loop harness. Transmitters possessed a battery life of at least one year. Recaptures of previously tagged birds were made during the last six years of the study, allowing old transmitters to be removed and renewed. The combined weight of the equipment was $<5\%$ of the mass of the individual carrying it. Leg loop harnesses were constructed of black elastic cord (1 mm thick) in a range of sizes depending on the body weight of each bird (e.g. 120 mm cord for a 75 g bird - 140 mm cord for a 90 g bird) to ensure optimal fit. Age and sex of each bird were recorded based on plumage variations (Svensson, 1992). All birds were observed post-release to confirm normal behaviour. For the present study we used 28 males (26 adults, 2 juvenile), 14 females (9 adults, 5 juveniles) and 2 juveniles of unknown sex.

Automated Receiving Unit (ARU) data collection

For the duration of the study, three to five Automated Receiving Units (ARUs; Sparrow Systems Fisher, IL, USA) attached to mounted H antennas (ATS, Isanti, MN, USA) were stationed at well-exposed sites in the study area to enable continuous reception of radio

signals of tagged individuals. ARUs searched for the frequencies of deployed radio transmitters once every 60 seconds, recording values for signal and noise. This enabled the activity of tagged individuals to be monitored on a continuous basis (Cochran et al., 1965; Crofoot et al., 2010; Kays et al., 2011; Steiger et al., 2013; Ward et al., 2014, 2013). ARUs additionally monitored the activity of static radio transmitters which were attached to stationary posts at the study site to check the normal functioning of the ARUs and to correct for the occurrence of noise.

Determination of migratory status, departure date and activity

The migratory status of each bird was determined by tracking individuals using manual radio telemetry and continuous ARU monitoring. Birds were manually tracked twice per week using a handheld three element Yagi antenna (AF Antronics, Inc., Urbana, IL, USA) and an AR 8200 MKIII handheld receiver (AOR U.S.A., Inc., Torrance, CA, USA) or a handheld H-antenna (Andreas Wagener Telemetry Systems, Köln, Germany) connected to a Yaesu handheld receiver (Vertex Standard USA, Cypress, CA, USA). Individuals whose signal was not detected by radio tracking were searched for aurally using a Cessna airplane fitted with two H-antennas and two Biotrack receivers (Lotek Wireless Inc., Newmarket, ON, Canada.). These searches covered a minimum of 20 km in radius. Due to the higher detection probability of the radio signal from the sky our aerial search method allowed us to confidently determine the presence or absence of a bird carrying a radio transmitter (Fudickar et al., 2013). If no signal was obtained for an individual after at least two aerial searches, it was defined as a migrant. An individual was defined as resident if it remained in the study site until the beginning of the next breeding season (March). We classified 9 females, 8 males and 4 birds with unknown sex as migrants; and 3 females, 19 males and 1 bird with unknown sex as residents.

To quantify the activity pattern of individual European blackbirds, we used the change (Δ) in signal strength between successive one minute recordings and applied a threshold value of 4.0 dB. An individual was either categorized as active or inactive, depending on whether the change in signal strength was above or below this threshold, respectively. To calculate this threshold, we carried out a calibration experiment in which we randomly distributed 13 radio tags throughout the study site. Each tag represented a tag on an inactive bird. ARUs recorded data from these tags for a total of one week. We then pooled the values of consecutive signal Δ between one minute intervals and used the 99% upper quantile to estimate the maximum variation in signal change occurring in an “inactive bird”. This value was taken as the threshold. Our calibrated threshold value was consistent with those of previous efforts (Steiger et al., 2013) and this method has been previously used in forested landscape (Kays et al., 2011). An individual was either categorized as active or inactive, depending on whether the change in signal strength was above or below this threshold, respectively.

ARU's have a reception range of 850 meters in our study site, although this value is subject to variation depending on topography, atmospheric conditions and position of the bird relative to the ARU antenna. Whenever the signal was absent but reappeared later, such as when the bird was out of range of the ARU, we classified these periods as ‘unknown’. For this assignment we applied a threshold to the minimum signal strength of -127.0 dB, a value that is 4 dB greater than the mean of the upper 95% quantile of the white noise recorded at the same time. We also assigned periods to be ‘unknown’ when there was less than 10 dB between signal and noise or where the value of the noise was more than -130 dB, indicating high electronic noise in the entire area, such as during thunderstorms.

The raw data were inspected visually to detect and filter artefacts produced by malfunctioning of the ARU. These artefacts were produced presumably by electromagnetic interference, for

example, due to stormy weather conditions. We also decided to filter our data based on its quality. Only daily activity budget measurements in which the uncertainty value was under 10% were used for further analysis. We decided to use this conservative approach to be sure that the activity % calculated was a representative measure of the daily activity.

We used R version 3.2.1 (R Core Team, 2015) to generate and analyse time series of binary activity data. Activity budgets were calculated as the proportion of the total number of minutes a bird was active during a 30-min period. The start of the time series was seven days before a departure event of a migrant occurred and the end of the time series was set to midnight of the night of departure. Before choosing seven days we explored the data by plotting up to 30 days before departure and we did not observe a different pattern of activity between the two groups during this period of time. In this way we aligned 24 departure events from 21 individual migrants (1 individual was included with 2 departures in different consecutive years and another bird was included with 3 departures in 3 consecutive years). The departure time was estimated by an algorithm written in R Version 3.2.1. The algorithm searched for the first time stamp after the signal in the ARU was absent permanently (the point where only unknown values were present). Visual inspection of the data was later used to confirm these estimations.

To compare migrant and resident birds, we randomly paired one migrant with one resident individual that was present at the breeding ground at the same time the departure event occurred. One resident individual was included with two departures in different consecutive years. We generated equivalent time series using data for those resident individuals.

To define day and night-time, we calculated for each day, when the morning and evening civil twilight occurred using the function “crepuscule” from the R package “maptools” (Bivand and Lewin-Koh, 2015). This function estimates for a given date and coordinate when the

geometric centre of the sun is 6° below the horizon in the morning (civil dawn) and in the evening (civil dusk). Daytime was defined as period of time between dawn and dusk, and night-time corresponded to the period of time between dusk and the consecutive dawn.

To generate the actograms presented in figure 1 a and b, we obtained raw activity data of one “captive resident” and one “captive migrant” from the study carried out by Partecke & Gwinner (Partecke and Gwinner, 2007). We did not process these data in any form but use it for visualization purposes and as an example of how *Zugunruhe* is expressed under laboratory conditions.

Statistical analysis

Statistical analyses were conducted using R 3.2.1.(R Core Team, 2015) To compare activity levels between migrants and resident individuals, we modelled the daily rhythm of activity of each phenotype during 7 days before the departure of migrants. Given the non-linear nature of the data we fitted a Generalized Additive Mixed Model (GAMM) using the function “`gamm4`” from the package “`gamm4`” (Wood and Scheipl, 2013). The flexibility of these models allows us to fit a non - linear smoothed function (smooth term) which resembles a sinusoid-like curve that describes the day and night rhythmicity of the time series. We modelled the probability of a bird being active using a binomial error distribution and a logit-link function in relation to time of the day and the migratory strategy. The dependent variable activity was expressed as minutes of activity within 30 minutes. The independent variable time of the day was expressed in hours of the day and was included as the main parameter to construct the smooth term of the GAMM. We used the default thin plate regression splines (BS= “`tp`”) parameter to construct the smooth term. We included the interaction between migratory strategy, day before departure, and time of the day in the smooth term using the argument “`by`”. This interaction resulted in one independent smooth function being fitted for

each group (migrants and residents) and for each day before departure. The choice of seven days helped with model convergence given the high number of parameters needed to be calculated. We also included migratory status as a fixed effect. As random effects we included individual identity for two reasons, first to account for repeated measurements and secondly to add a correlation structure between observations of the same bird that were close in time and therefore account for potential temporal autocorrelation of the time series. Additionally we included an observation level random factor to account for overdispersion of the binomial model. Observation level random factors, where each data point receives a unique level of a random effect that models the extra-binomial variation present in the data, are commonly employed to cope with overdispersion in binomial data(Harrison, 2014)

Given our biased sex ratio of migrant and resident birds, we did not include sex as a fixed effect. We also did not include age as a fixed effect given that we did not have enough juveniles to test for age differences.

For further analyses we ran four post hoc tests in a step wise manner. First, we tested whether the activity changed as time to departure approached. To do so, we performed the following procedure; first, we fitted another GAMM to capture the diel variation of activity. To fit this hourly GAMM we lumped the seven days before migration into a single day of 24 hours. The number of minutes active over a 30 minutes interval was modelled in relation to the time of the day in minutes as a smooth term using a binomial error with a logit-link function. The smooth term was constructed using the cyclic cubic spline “bs = cc”, to account for the cyclic nature of the data. Migratory status was included as a fixed effect and we also included the interaction between time and migratory status in the smooth term using the argument “by”. Random effects in this model were individual identity and year to account for repeated measurements and to add a correlation structure between of observations of the same bird that

were close in time. We then extracted the residual values from the hourly GAMM model and split them into day and night time observations. We calculated the mean value for daytime and night-time per individual per day before departure. This was to test whether the remaining variation left in the residuals of the hourly GAMM after accounting for the diel variation of activity, could still contain unexplained differences between migrant and resident individuals or could contain a pattern that suggested an activity change (increase or decrease) as departure approached. Using the residual values of the hourly GAMM we fitted two separate linear mixed models (LMM), one for daytime and another for night-time values respectively. In both models, the residual variation was modelled in function of time as the days before departure, migratory status and the interaction between days before departure and migratory status. Random effects in both models included individual identity and year.

Finally, the last analysis aimed to test whether the amount of nocturnal activity displayed by individuals of migrants and residents prior to the onset of migration was comparable to activity levels displayed outside the migratory season. We compared time series of the pre-migratory season with time series generated in summer. To do so we calculated the mean night activity of each individual during the ten days before departure and the mean night activity of each individual during seven days during mid-August (August 13 to 20 of each year). We then compared them using an LMM approach. Because during mid-August European blackbirds are moulting, we would not expect any nocturnal activity related to migration. The dependent variable in this LMM was the log transformed mean activity value (to account for the non-normal distribution of the variable (right-skewed)). Fixed effects included period of time as a factor (August or pre-migration), migratory status and the interaction of both. Random effects included individual identity and year to account for repeated measurements.

Before drawing conclusions in all the models, a visual residual analysis was performed to check for homogeneity of the variance, model assumptions, temporal autocorrelation and model fit. Significance was considered when p-values were smaller than alpha (0.05) or when 95% confidence intervals predicted by the model did not overlap between groups.

Results

All migratory birds departed between 23 September and 26 October (mean departure date: 14 October). All departures occurred before midnight, with mean departure time of 2.2 hours after civil dusk (min = 0.1 hour, max = 4.7 hours). Migrants were active 36.76 ± 17.48 % (mean \pm SD) during daytime, and residents were active 33.56 ± 17.36 % (mean \pm SD). During nights, migrants were active 2.28 ± 7.28 % (mean \pm SD) and resident birds 1.86 ± 6.86 % (mean \pm SD). Fig. 2 shows the mean activity value of each half hour interval of resident and migrant individuals during the seven days and nights before the departure of migrants. During the seven days prior to departure, total day and night activity of migrant and resident European blackbirds did not differ (GAMM: estimate \pm SE = -0.2088 ± 0.12 , z-value = -1.70 , $P=0.089$; Fig. 3). Mean predicted activity profiles of resident and migrant individuals exhibited similar curves and amplitudes over time (Fig. 3). Only during the night of departure did migrants show higher activity levels compared to residents during the first half of the night (Fig. 2 and Fig. 3). This is likely caused by the actual take-off of the migrants and confirms that our methods were sufficient to detect nocturnal activity differences among individuals.

To test if migrants increased their activity levels during the days before departure, we combined individual activity data during the seven pre-departure days into one 24h period. We ran a generalized additive mixed model (GAMM; referred in the method section as “hourly GAMM”) to detect possible hourly differences in activity and to account for the diel

variation in activity. The hourly GAMM did not find that activity levels were different between migrant and resident individuals (GAMM: estimate \pm SE = -0.147 ± 1.122 , z-value = -1.20 , $P = 0.23$). We then extracted the residuals of this GAMM and tested separately the residual values of daytime and night-time observations. The residual analysis of daytime observations found that the interaction between time (days before departure) and the migratory status was not significant (LMM: estimate \pm SE = 0.006 ± 0.010 , t-value = 0.63 , $P = 0.526$), which implies that daytime activity did not differ between the groups over time. Similar results were obtained for the night-time observations: night-time activity did not change over time (LMM: estimate \pm SE = -0.008 ± 0.022 , t-value = -0.382 , $P = 0.702$).

Finally, a comparison between the levels of nocturnal locomotor activity displayed by both groups in mid-August and during the pre-migratory phase was performed. The amount of nocturnal activity displayed by migrants and residents, was not different when we compared mid-August to the period prior to migration (LMM: estimate \pm SE = -0.369 ± 0.525 , t-value = -0.703 , $P = 0.487$).

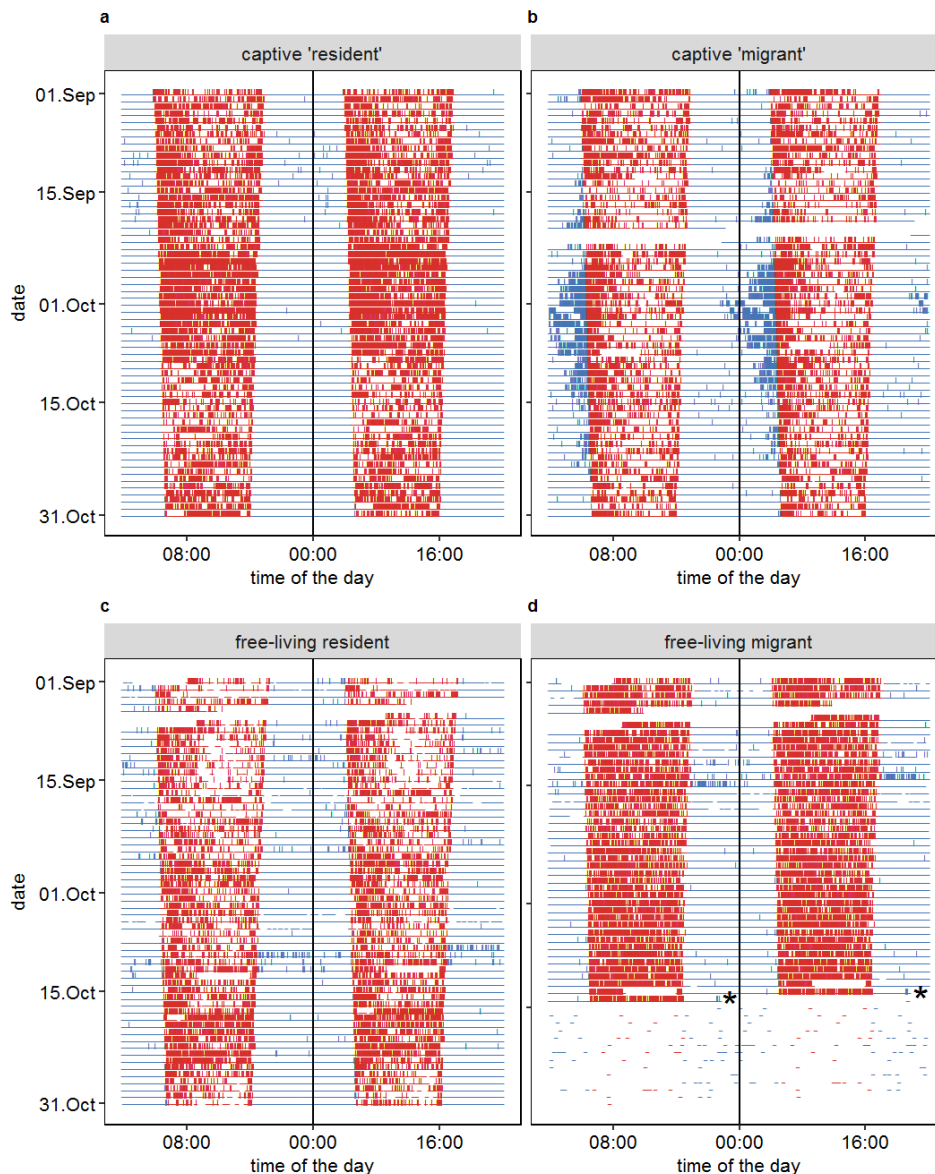


Fig. 1. Double-plotted actograms (48 hours) showing activity of a “migrant” captive, free-living resident and free-living migrant European blackbirds (*Turdus merula*) during autumn. Captive “resident” (a) and captive “migrant” (b) were exposed to natural photoperiod during the autumn (Sep. 1 – Oct. 31). These two actograms were plotted using raw data from Partecke & Gwinner (2007). In the case of the captive “migrant” (b), around mid-September a morning component of activity moves gradually into the night-time, developing nocturnal activity (*Zugunruhe*). *Zugunruhe* peaks the night of October 2. Activity of a free-living resident bird (c) was recorded using the automated telemetry system (ARU) continuously from the autumn until the consecutive spring. d) Activity of a free-living migrant bird was recorded also using the ARU, during the autumn until its departure. The departure time of the free-living migrant is indicated by *. After departure, the ARU showed some false positive inactivity due to noise in the recording. Day and night time activity coloured red and blue, respectively.

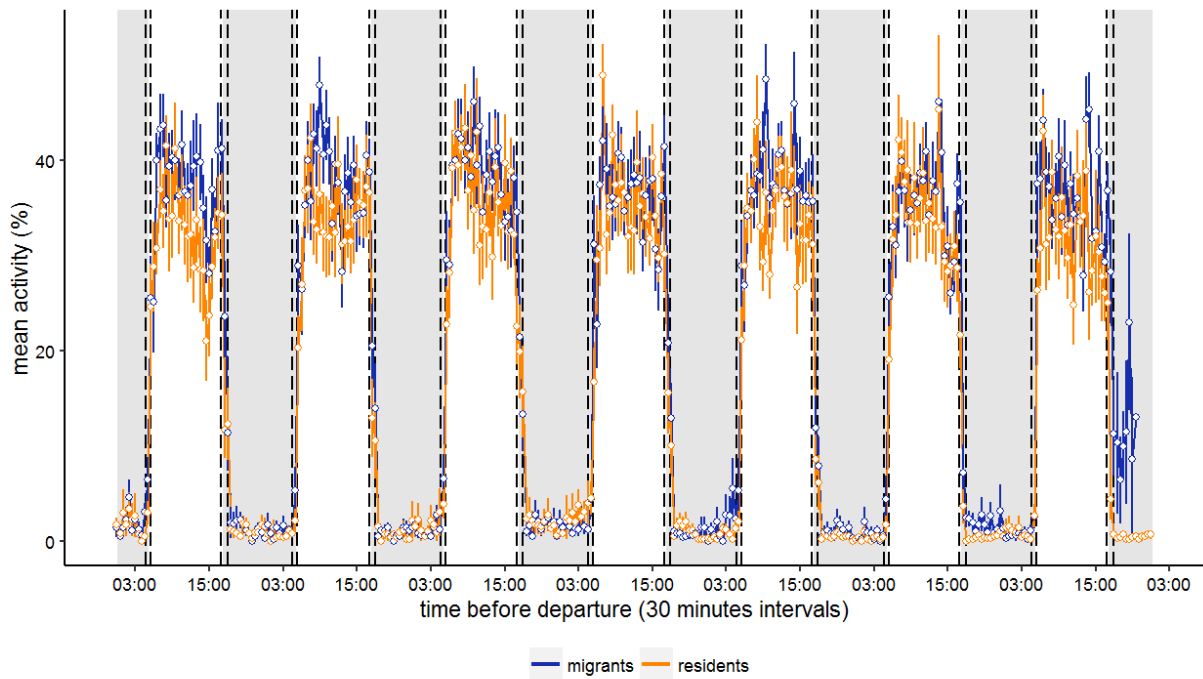


Fig 2. Activity pattern of migrant and resident birds seven days before the departure of migrants. Mean activity % and standard error of migrant (blue) and resident (orange) European blackbirds (*Turdus merula*) in 30 minute intervals seven days prior to departure. White and grey backgrounds represent mean day and night-time respectively. Dashed vertical lines represent the variation in dawn and dusk onset during the time of the study. Sample size: 21 migrant individuals (11 females, 8 males and 2 unknown sex birds; 2 individuals with multiple departure events) and 23 resident individuals (3 females and 20 males).

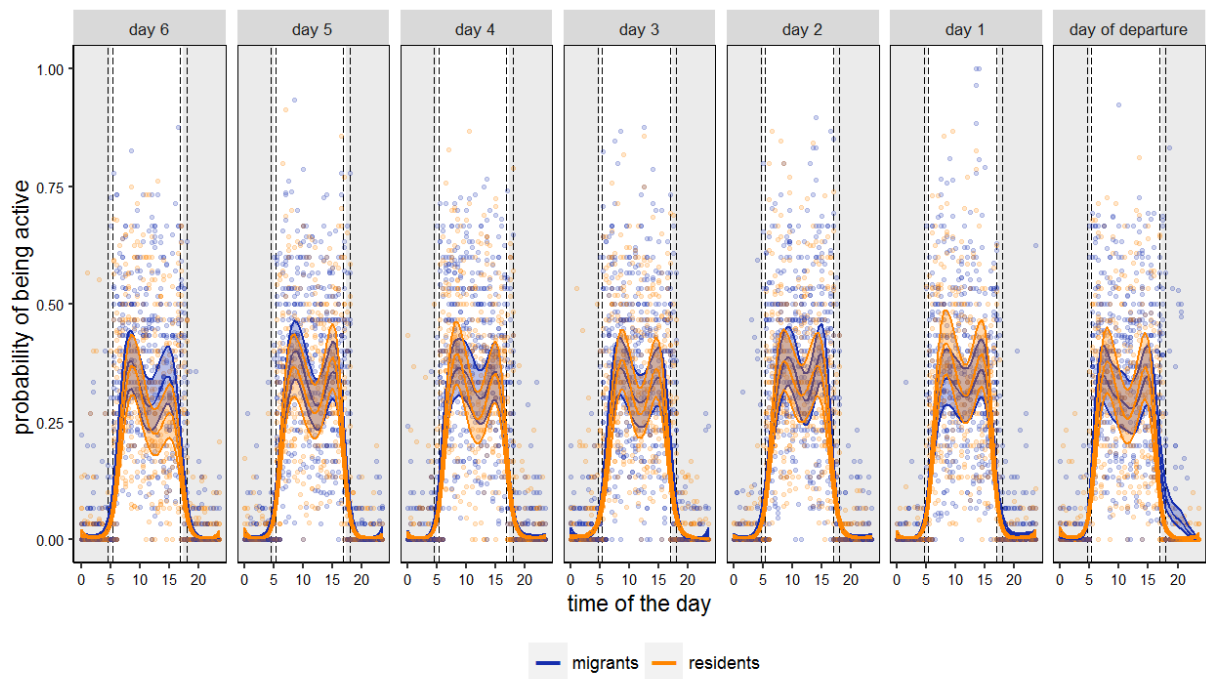


Fig. 3. Results of the Generalized Additive Mixed Model (GAMM) on daily activity seven days before the departure of migrants. Predicted daily activity pattern by GAMM of migrant (blue) and resident (orange) individuals. Solid lines represent the mean fitted values of the model (smooth term) with 95% confidence interval (shaded area). Dots correspond to the raw observations. White and grey rectangles represent mean day and night time respectively. Dashed vertical lines represent the variation of dawn and dusk onset during the time of the study

Discussion

Our results provide strong evidence that at the onset of autumn migration, European blackbirds rapidly shift from an exclusively diurnal activity pattern to migrate at night without any previous changes in their daily rhythm. We used an automated radio-telemetry system, which accurately depicted day and night cycles of activity in our wild European blackbirds. Even though, the activity patterns were biologically meaningful, we also observed bouts of activity during the night in both resident and migrant individuals without a consistent pattern (Fig 1). These bouts of “nocturnal activity” could be false positive measurements. Artefacts due to atmospheric conditions (stormy weather) or electric noise that can appear as “activity” were observed in these readings. However, there were cases where we observed short bouts of activity during the night that resembles the diurnal pattern of activity. In this case birds could have changed their roosting location or simply moved, for instance, due to presence of predators or environmental disturbances.

Very limited knowledge about the nocturnal life of birds is available and only a handful of studies have focused on this topic. Nocturnal local movements and foray behaviour have been described to take place during the breeding season in the yellow-breasted chat (*Icterina virens*) (Ward et al., 2014) and in juvenile Eurasian reed warblers. The latter exhibit nocturnal flight during the pre-migratory phase to either develop navigational skills for migration or as juvenile dispersal (Mukhin, 2004; Mukhin et al., 2005). Nocturnal flights to perform local movements have been recorded in Swainson's and Hermit Thrushes during migration at stopover sites (Mills et al., 2011). In contrast to these studies, our results clearly indicate that neither locomotor activity nor exploratory flights during night were exhibited by migratory European blackbirds prior to their migratory departure. These results support the idea that no significant amount of nocturnal locomotor activity or nocturnal exploratory flights are developed as preparation for migration in the wild. We only detected an increase of activity in

the migratory birds during the night of departure, which largely resulted from detection of actual take-off behaviour on our automated receiving system. These data provide a positive control that our recording system would have detected increased nocturnal activity if present. We also found similar low levels of nocturnal locomotor activity during August. This is well outside the migratory period and when European blackbirds are in their main moulting phase compared to the pre-migratory period. This result indicates that the amount of nocturnal locomotor activity displayed by birds of both groups is not related to the migratory season.

The rapid shift to nocturnal activity in the night of departure with all departure events occurring before midnight, appear not to match what has been observed in previous laboratory studies of nocturnal activity in migratory songbirds. In the case of European blackbirds, there is a gradual progression of an early morning component of activity into the night, at the onset of *Zugunruhe* whenever birds are kept under natural photoperiod (Fig. 1 b). The onset of nocturnality in birds during the migratory season is controlled by the circadian clock. When the two oscillators that control day and night activity respectively, slowly uncouple (Bartell and Gwinner, 2005; Rani et al., 2006), the gradual shift in activity is observed in the lab. In the wild, the rapid shift from daytime activity to nocturnal activity just during the night of departure may indicate that under natural conditions, the circadian clock might be affected by extrinsic factors. For example, a masking effect of atmospheric conditions could influence the decision to initiate the migration and suppress the expression of nocturnality prior to departure. Birds could simply wait for the right conditions to migrate and then decide to start the migratory journey very shortly afterwards. There is evidence that nocturnal migrants rely on atmospheric conditions to initiate their migratory journeys (Åkesson et al., 2002; Cochran and Wikelskli, 2005; Deppe et al., 2015). Furthermore, predator avoidance as an ultimate mechanism may also influence the expression of nocturnal activity prior to migration. Being active at night could alert potential predators and increase the risk of predation. An alternative

explanation for the possible discrepancy between lab and field data could be that a gradual increase of nocturnal activity does not happen during pre-migration but rather after departure during the course of migration. This process could be reflected by a shift in the departure time resulting in earlier departures during subsequent nights. The gradual shift could also be reflected by an increase in flight duration or efficiency resulting in a systematic increase in distance travelled each night during migration. This idea seems less plausible because during radio tracking of the first night of migration (unpublished data), migrants fly non-stop throughout the night. However more data are needed to fully test this hypothesis. Future studies using devices that quantify and store locomotor activity may be able to test whether migrants increase their flight duration or efficiency during their migratory course.

Our results provide no evidence for different activity pattern between migrant and resident European blackbirds during the pre-migratory phase in the wild, both during day and night. The lack of a difference in daytime activity between migrants and residents birds is interesting because one would expect that migrant individuals would show higher activity compared to resident birds, as a consequence of an increased foraging effort (hyperphagia) (Cornelius and Hahn, 2012). One possible explanation for the lack of a difference could be that resident birds also have to accumulate energy reserves in view of the upcoming winter. However, previous studies have shown that migrants in this population accumulate fat during the pre-migratory phase while residents do not (Fudickar et al., 2013). Moreover, residents birds accumulate fat later in the year when the winter already started (Lundberg, 1985). Another alternative is that the two groups have a similar total activity budget during the day but invest their time fulfilling different requirements. Migrants may invest more of their total time spent active in foraging at the expense of other activities (e.g., anti-predator vigilance). A similar trade-off has been described in ruddy turnstones (*Arenaria interpres*) during the pre-migratory period. Migratory individuals decreased their anti-predator vigilance, whereas non-migratory birds

showed no decrease in this activity (Metcalf and Furness, 1984). We were not able to test this hypothesis mainly due to two limitations of the automated radio tracking system we used: first is not possible to identify specific behaviours and second, the sampling resolution of 1 minute might not be sufficient to estimate the overall activity budget precisely. Furthermore, different foraging strategies between migrant and resident European blackbirds could also explain our results. Both phenotypes would invest similar amount of time foraging but migrant birds would do it more efficiently than the resident counterpart. Foraging efficiency had an effect on the amount and speed of fat deposition during the autumn pre-migratory period in gray catbirds (*Dumetella carolinensis*) (Dwyer Heise and Moore, 2003a). One could assume that foraging is the main activity in the total budget during the pre-migratory phase, at least for migrants, because migrants undergo a pre-migratory hyperphagic phase (Odum, 1960). Under this assumption the increased fat deposition in the migrants in contrast to the residents, could be explained, at least partly, by a higher efficiency of food utilization by migrants. In garden warblers, food utilization is more efficient during the pre-migratory period in autumn and spring compared with the rest of the annual cycle (Bairlein, 1985). Furthermore, optimal diet selection has been also linked with effective fat accumulation before migration with migrants selecting a diet rich in lipids and carbohydrates (Bairlein, 2002). It is also conceivable that migratory individuals lower their energy expenditure during the pauses in locomotion, similar to zebra finches in captivity that are exposed to higher workloads (Deerenberg et al., 1998).

In this study we focused on the pre-migratory phase. Further development and miniaturization of tracking devices with GPS and accelerometer sensors will make it possible to study the nocturnality of migratory songbirds during their migratory journeys and stop over sites in detail. These future studies could make use of the new technological advances to uncover further mysteries related with the fascinating phenomena of bird migration in the wild.

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**No carry-over effect of migration on activity pattern during the
breeding season: An automated radio-tracking study of wild
partially migratory European blackbirds**

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Abstract

Partial migration, where a breeding population is composed of migrant and year-round resident birds, is an ideal system to study the potential constraints that each overwintering strategy encounters throughout the annual cycle. We used daily activity levels as a reliable indicator of how animals cope with the constraints of different stages of the annual cycle. To elucidate whether and to what extent migration may affect activity, we used an automated radio-telemetry system to compare daily activity levels of radio-tagged migrant and resident European blackbirds (*Turdus merula*) at their common breeding ground. We were able to measure the activity of migrants from spring arrival to autumn departure, and throughout the entire year for residents. We found that migrants and residents exhibited similar activity levels throughout the post-migratory period in spring, as well as during the breeding season, moult, and pre-migratory period in the autumn. Furthermore, we showed that resident individuals adjust their daily activity levels throughout the year, even when accounting for photoperiod. Our results suggest migration does not cause carry-over effects on activity budgets during pre- and post-migratory periods. The fact that both overwintering strategies have similar activity budgets (at least during the breeding season) might be an indicator that both groups experience similar constraints and respond accordingly. This indicates why both strategies could evolutionarily coexist.

Introduction

For the majority of animals, life is divided into two distinct behavioural states: activity and rest (Halle and Stenseth, 2000). During the proportion of time that animals spend being active (hereafter termed 'activity'), they perform different essential tasks for the maintenance of life (e.g., locomotion, foraging, predator avoidance, mate searching, territorial defence, offspring rearing, etc.) involving body motion. Conversely, phases of inactivity correspond to periods of time when mobility and locomotion are reduced (e.g. sleep, hibernation, egg incubation, moult, etc.). Activity levels are shaped by extrinsic and intrinsic factors. Photoperiod, i.e., the fraction of light in a 24 h day, is the most predictable proximate cue that organisms use to time their daily and seasonal activities. Moreover, photoperiod is the most potent synchronizer of circadian rhythms, the endogenous mechanism that most organisms have evolved to synchronize their daily and annual events to the external environment and thus maximize their fitness (Foster and Kreitzman, 2005). Furthermore, duration and timing of activity both daily and seasonal can also be influenced by other environmental factors (e.g. food availability, weather conditions), or intrinsic factors, such as life history stages (e.g., reproduction, migration) and individual traits (e.g., age, sex, personality) (reviewed in: Dunbar et al. 2009). In addition, being active is thought to be more energetically costly than resting, primarily due to the higher energetic costs of locomotion (Halle & Stenseth 2000). Varying activity levels over time is a potent means of adapting to changing resources and climatic conditions. Therefore studying activity levels allows us to gain insight into the fundamental aspects of how animals cope with a fluctuating environment (Kays et al., 2011). A common strategy to cope with seasonal fluctuations is migration. Migration facilitates the exploitation of abundant resources in geographically distant habitats (Fryxell and Sinclair, 1988). Seasonal migration optimizes fitness by avoiding the low survival probability and potentially higher energetic costs associated with wintering in an area of limited resources and

inhospitable environmental conditions, and by increasing reproductive success in areas with abundant resources for rearing offspring (Lack, 1954).

Although migration is a widespread phenomenon among birds, at the population level, only some fraction of individuals might migrate while the rest remain at the breeding grounds as year-round residents. This phenomenon is called partial migration (Chapman et al., 2011b).

The most common form of partial migration occurs when residents and migrants breed sympatrically but over-winter in geographically distinct habitats. The annual cycle thus differs in the number of life history stages between residents and migrants. Residents typically have three stages, namely, non-breeding, breeding and moult, whereas migrants have two additional stages, autumn and spring migration. Each stage is characterized by an optimal combination of morphological, physiological and behavioural traits, with the sole purpose of optimizing fitness in response to seasonal variation of environmental conditions (Jacobs & Wingfield 2000; Dänhardt & Lindtröm 2001; Wingfield 2008). Because of the different life history stages, migratory and sedentary phenotypes may have different requirements over the course of the year.. For example, within the pre-migratory period during which birds prepare for migration, foraging becomes an essential activity to gain sufficient fat deposits to perform the subsequent migratory journey (Dwyer Heise and Moore, 2003b; Fudickar et al., 2013). Furthermore, when migrant birds return to the breeding grounds during spring, they need to arrive in optimal body condition to compete for breeding territories, which is essential to mate (Snow, 1956). In the case of residents, foraging efforts during winter become essential to accumulate sufficient fat deposits to survive the winter (Leihikoinen, 1987). When winter is over and the breeding season starts, resident birds have the advantage of already being at the breeding grounds. Consequently, if conditions are suitable, they could start to breed earlier than migrants do. Interactions between processes occurring in different life history stages are known as carry-over effects (O'Connor et al., 2014). Ascertaining in what way processes interact between life history stages of the annual cycle is crucial for understanding the factors

that influence individual fitness, population dynamics, and the evolution of alternative phenotypes, such as migratory and sedentary phenotypes in partially migratory species (Harrison et al., 2011; Norris and Marra, 2007). Timing (i.e. delays) is a widely studied mechanism through which events in one stage may have carry-over effects into the next life history stage and might influence the individual fitness of a migratory species (Malcolm et al., 1987; Mitchell et al., 2012; Newton, 2006). Our knowledge as to what extent migration, in general, has carry-over effects on traits (other than timing) in adjacent life history stages is still very limited.

Recent developments in animal tracking technologies have yielded new methods to study activity patterns of free-living animals in their natural environments (Kays et al. 2011; Pagon et al. 2013; Rowcliffe et al. 2014; Steiger et al. 2013; Kays et al. 2015). Accelerometry is one of the newest technologies currently used to study activity and energy expenditure of animals (Brown et al., 2013; Halsey et al., 2011; Wilson et al., 2006). Accelerometer devices record the acceleration purely due to the movement of an animal, termed overall dynamic body acceleration, or OBDA (Halsey et al., 2011). More recently with the miniaturization of accelerometer devices, it is possible to derive activity levels from small animals such as migratory songbirds throughout the annual cycle (Bäckman et al., 2016). Similarly, an automated radio-telemetry system (ARTS) (Kays et al., 2011) has proven an efficient and reliable method to study the activity of small wild animals.

In order to elucidate whether fall and spring migration carry over to affect other life history stages, we compared activity patterns between migrant and resident individuals of a partially migratory European blackbird (*Turdus merula*) population in southern Germany, using an automated radio-telemetry system (ARTS). Migrant birds in this population prepare themselves for migration by accumulating fat before departure (Fudickar et al., 2013). Birds who migrate do so at night, flying more than 400 km in one night (Fudickar et al., 2013) to overwinter on average 800 km west-southwest from their breeding grounds (Fudickar and Partecke 2012).

During the subsequent spring, migrants return to southern Germany to breed sympatrically with birds that remained as residents during the entire winter in that location. The use of an automated recording system allowed us to monitor activity levels of free-living individuals on a near-continuous basis while at the breeding grounds. Using this system, we investigated whether migrants and residents exhibit different activity levels, particularly after migrants' spring arrival and before their autumn departure, to elucidate potential carry over effects of migration in the breeding and moulting season. Furthermore, because we could monitor residents throughout the entire year, we characterised the annual activity pattern of resident European blackbirds within the context of the annual cycle.

Material and Methods

Study Population

European blackbirds, were captured using mist nets in a mixed coniferous/deciduous forest in southern Germany (N 47°47', E 9°2') in 2009-2012 and 2014-2015. After measuring the bird (tarsus length, wing length, muscle score, fat score, and body weight) and recording sex and age based on plumage variation (Svensson, 1992), each bird was banded and fitted with a backpack that contained a radio transmitter (≤ 2.6 g; Sparrow Systems, Fisher, IL, USA) and secured by a leg loop harness. The total weight of the backpack was $<5\%$ of the mass of the bird. The battery of the radio transmitter lasted at least one year. After release, each individual was observed to confirm normal behaviour (for more details, see Fudickar et al. 2013)

Automated radio telemetry system

An automated radio telemetry system was installed at the study site, which consisted of three to five Automated Receiving Units (ARUs; Sparrow Systems) attached to H antennas (ATS, Isanti, MN, USA) and powered by a rechargeable 12-volt battery. Each ARU was programmed to search for up to 16 different transmitters every 60 s continuously. Data were stored on an external memory chip connected to the receiver and were retrieved at regular intervals throughout the study. Static radio transmitters were attached to stationary posts at various locations at the study site to monitor the normal functioning of the ARUs.

Determination of migratory status and activity

In addition to automated monitoring, birds were also tracked manually twice per week using either a handheld three element Yagi antenna (AF Antronics, Inc., Urbana, IL, USA) and AR 8200 MKIII handheld receiver (AOR U.S.A., Inc., Torrance, CA, USA), or a handheld H antenna (Andreas Wagener Telemetry Systems, Köln, Germany) and a Yaesu VR 500 handheld receiver (Vertex Standard USA, Cypress, CA, USA). Based on the presence or absence of individuals at the breeding site, the overwintering strategy was assigned.

Individuals that departed the study site during the night within the migratory season

(September and October) were classified as migrants. Individuals that were absent during this period were subsequently radio tracked aurally using a Cessna airplane fitted with two H-antennas and two Biotrack receivers (Lotek Wireless Inc., Newmarket, ON, Canada). We conducted these searches if individuals could not be located by manual or automated radio tracking, and were at least 20 km from the study site. If a signal was absent after at least two aerial searches, the bird was classified as a migrant. Individuals that remained at the study site until the beginning of the next breeding season were classified as residents.

To determine activity of individual blackbirds, we calculated the change (Δ) in signal strength between consecutive recordings (from one minute to the next). We classified any change in signal strength that was equal to or greater than 4.0 dB as an active minute. An individual was categorized as either active (*A*) or inactive (*I*) for each minute that they were at the study site. The 4.0 dB threshold was estimated using a calibration experiment as follows; we randomly distributed 13 stationary radio tags throughout the study site that represented inactive birds and let the ARUs collect data for 1 week. We then pooled the values of consecutive signal change between one-minute intervals and used the 99% upper quantile as a threshold (4 dB). This value represents the maximum variation that the signal strength can experience in a stationary radio transmitter.

Periods of weak or absent signal, such as when a bird was out of range of an ARU, were classified as unknown values (*NA*) by applying a minimum threshold of -127.0 dB to the signal strength (this value is 4 dB greater than the mean of the upper 95% quantile of the white noise). When the signal to noise ratio of a measurement was less than 10 dB or when the value of the noise was more than -130 dB, the activity for that minute was classified as unknown (*NA*).

Data Analysis

We used R version 3.2.1 to generate and analyse time series of binary activity data. Activity budgets ($A\%$) were calculated as the proportion of total number of minutes a bird was active (A) over the total number of minutes a bird was within range of the ARU (total minutes active (A) plus total minutes inactive (I)). We also calculated the percentage of missing values ($U\%$), as a measurement of quality of each observation. Only daily activity budget measurements in which the uncertainty value ($U\%$) was $< 20\%$ were used for further analysis. The raw data were also inspected visually to detect and filter artefacts produced by malfunctioning of the ARU. These artefacts were produced by, presumably, electromagnetic interference due to stormy weather conditions.

We summarize daily activity in two periods for different analyses: 1) percentage of time active between sunrise and sunset (daytime, which was used to describe the annual pattern of resident birds, given that it takes into consideration changes in photoperiod; and 2) percentage of time active within 24 hours, which was used to compare resident and migrant individuals while both phenotypes were at the breeding grounds. We included night-time in this measurement to determine whether migrant birds would develop night-time activity before migration.

Statistical Analyses

Model to describe annual activity levels of resident birds

To describe the general annual activity pattern of resident individuals, we fitted Generalized Additive Mixed Models (GAMM) in R 3.2.3 using the function “`gamm4`” from the “`gamm4`” package (Wood and Scheipl, 2013). We choose this approach given the nonlinear nature of the data and because the flexibility of these models allowed us to fit a nonlinear smoothing function (smooth term), which can capture the variation in the activity data over time.

Observations from 46 males and 25 females were included in the model, although the sample size varied on a daily basis (summarized in Table S1). We modelled the probability of a bird being active using a binomial error distribution and a logit link function in relationship to the

day of year, temperature (mean daily temperature in °C), and precipitation (mean daily precipitation in mm) as fixed factors. We used day of the year to construct the smooth term. We included cyclic cubic regression lines (BS = "cc") as a parameter in the smooth term to account for the cyclic nature of the data. The interaction between day of the year and sex was also included in the smooth term using the argument "by", which resulted in one independent smoothing function fitted for each sex. The environmental variables were included to account for environmental effects that might explain changes in activity along the year. The environmental data were obtained from a weather station located in Konstanz, Germany (N 47°40', E 9°11'), which is operated by the German Weather Service (Deutscher Wetterdienst). This station is the closest to the study site (15.5 km of distance). We also included sex as a separate fixed effect. Given that we had very few observations of juvenile individuals over time, we did not include age in the model.

We included bird ID nested within week (Ring ID / Week) as random effect terms of the model, to account for repeated measurements and to add a correlation structure between observations of the same bird that were close in time, to account for potential temporal autocorrelation. We also included year as a random factor, given that we pooled data from 2009-2012 and 2014-2015. To account for over-dispersion of the binomial model, we included an observation-level random factor. Visual inspection of the residuals of the model was performed to assess homogeneity of the variance, model assumptions, temporal autocorrelation, and model fit.

Model to compare seasonal of activity levels between resident and migrant birds

To test for overwintering strategy-based differences in activity, a subset of the data (days 49 – 300 of the year) was used, given that individuals of the two phenotypes were both present at the breeding ground during this period. We predicted that males and females would behave differently; therefore, we fitted one GAMM for each sex independently. For females,

observations from 26 resident females and 18 migrant females were used to fit the GAMM. In the case of males, 46 resident males and 14 migrant males were used. As in the previous case, the sample size changed over time (weekly sample sizes are provided in Table S1). Each model contained a structure similar to the GAMM used to describe the annual activity pattern. In this case, we modelled the probability of being active using a binomial error distribution and a logit link function with overwintering strategy, temperature, and precipitation as a function of day of year as a smooth term. In this model, the smooth term was constructed using the default thin plate regression splines (BS= "tp") given that the time series was not cyclic. We also included the interaction between day of year and overwintering strategy in the smooth term using the argument term "by" to generate two independent smoothing functions, allowing us to test for differences between resident and migrant individuals. In both models, we included bird ID nested within week (RingID / Week) as a random term to account for non-independent observations of the same bird (repeated measurements) that were close in time and could produce temporal autocorrelation. We also included year as a random factor, given that we pooled data from 2009-2012 and 2014-2015. Finally, to account for overdispersion in both models, we included an observation-level random factor. Residual analysis was done visually to assess homogeneity of the variance, model assumptions, temporal autocorrelation, and model fit.

Results

Description of annual activity levels of resident birds

Daily activity followed a nonlinear pattern that was distinctly different for resident females and males throughout the year even when the effect of photoperiod is taken into account (Fig. 1 Upper and lower panel, orange lines, Fig. 2). In general, activity tended to be higher during the breeding season compared with the rest of the year (Fig. 2). The generalized additive mixed model confirms this nonlinear pattern. A nonlinear smooth term (day of the year) was predicted for females (GAMM smooth term significance: effective degrees of freedom (edf) = 7.433, Chi.sq=141.6, $P < 0.001$) and for males (edf = 6.764, Chi.sq=174.5, $P < 0.001$). The overall amount of activity expressed by resident females along the entire year was not significantly different from the activity showed by males (GAMM: estimate \pm SE = -0.060 ± 0.064 , z-value = 0.939, $P=0.348$, Fig. 2). However, the shape of the activity curve throughout the year (smooth term) is different for males and females (Fig 2), such that during the middle of the breeding season (days 104-159 of the year) males have higher activity than females (Fig 2).

Regarding the environmental factors that may have modified annual activity patterns, temperature had no significant effect on activity (GAMM: estimate \pm SE = 0.002 ± 0.001 , z-value = 1.407, $P=0.159$). In contrast, precipitation had a significantly positive effect on activity throughout the year (GAMM: estimate \pm SE = 0.003 ± 0.0006 , z-value = 4.749, $P < 0.001$).

Comparison of seasonal of activity levels between resident and migrant birds

In both sexes, the activity levels between migrant and resident birds did not differ (GAMM: estimate \pm SE = -0.065 ± 0.078 , z-value = -0.840 , $P=0.400$ estimates for females; GAMM:

estimate \pm SE = 0.028 ± 0.061 , z-value = 0.469, $P=0.639$ estimate for males; Fig 3). In both models (females and males), the smooth terms are significantly nonlinear for both migrants and residents, (migrant females: GAMM edf = 7.890, Chi.sq=50.56, $P < 0.001$; resident females: edf = 7.583, Chi.sq=94.73, $P < 0.001$; migrant males: edf = 4.576, Chi.sq=161.3, $P < 0.001$; resident males: edf = 6.580, Chi.sq=314.3, $P < 0.001$). Regarding the environmental factors, temperature had a positive effect on activity levels for females (GAMM: estimate \pm SE = 0.004 ± 0.002 , z-value = 2.122, $P=0.033$) and a negative effect in males (GAMM: estimate \pm SE = -0.005 ± 0.001 , z-value = -3.286, $P=0.001$). Precipitation did not have an effect on the activity in the binomial model of females (GAMM: estimate \pm SE = 0.001 ± 0.0007 , z-value = 1.798, $P=0.0722$), nor on the activity levels of males (GAMM: estimate \pm SE = 0.001 ± 0.0007 , z-value = 1.535, $P=0.124$)

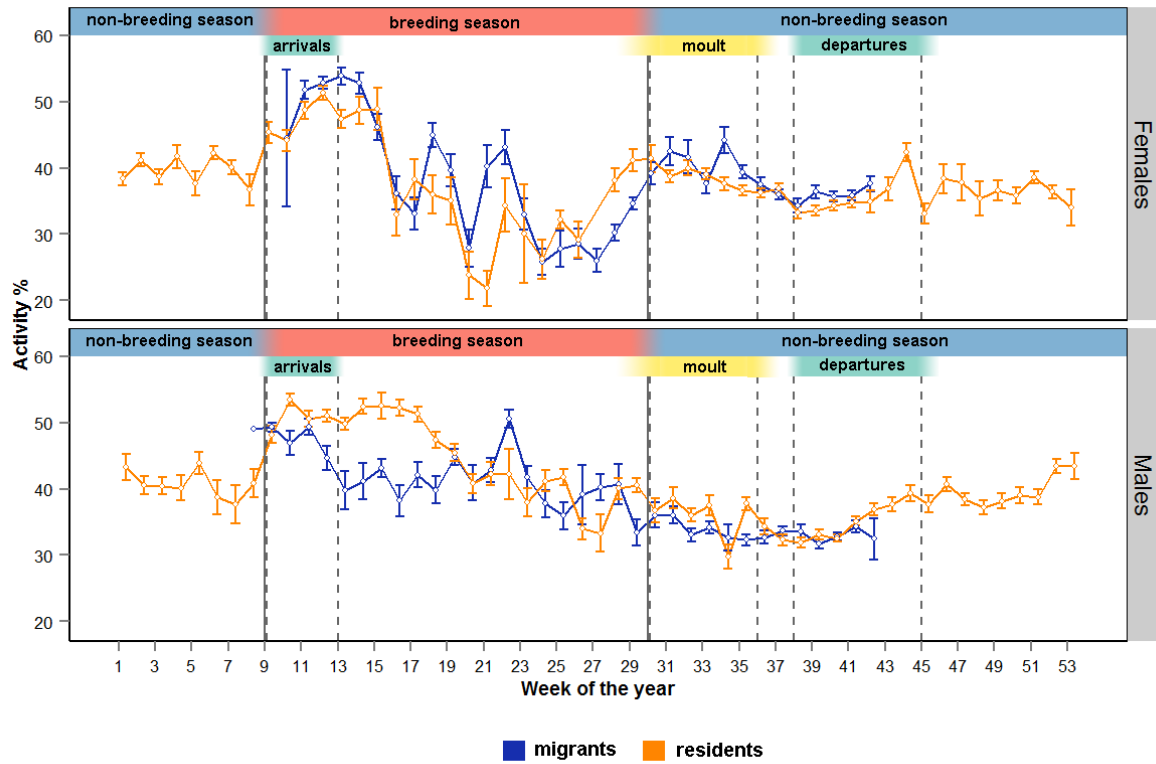


Figure 1. Seasonal variation of activity values of free-living resident (orange) and migrant (blue) European blackbirds (*Turdus merula*). Females are depicted in the upper and males in the lower panel. Activity is shown as the weekly mean percentage of daytime activity (\pm standard error). Data collected from 2009 – 2012 and 2014 – 2015.

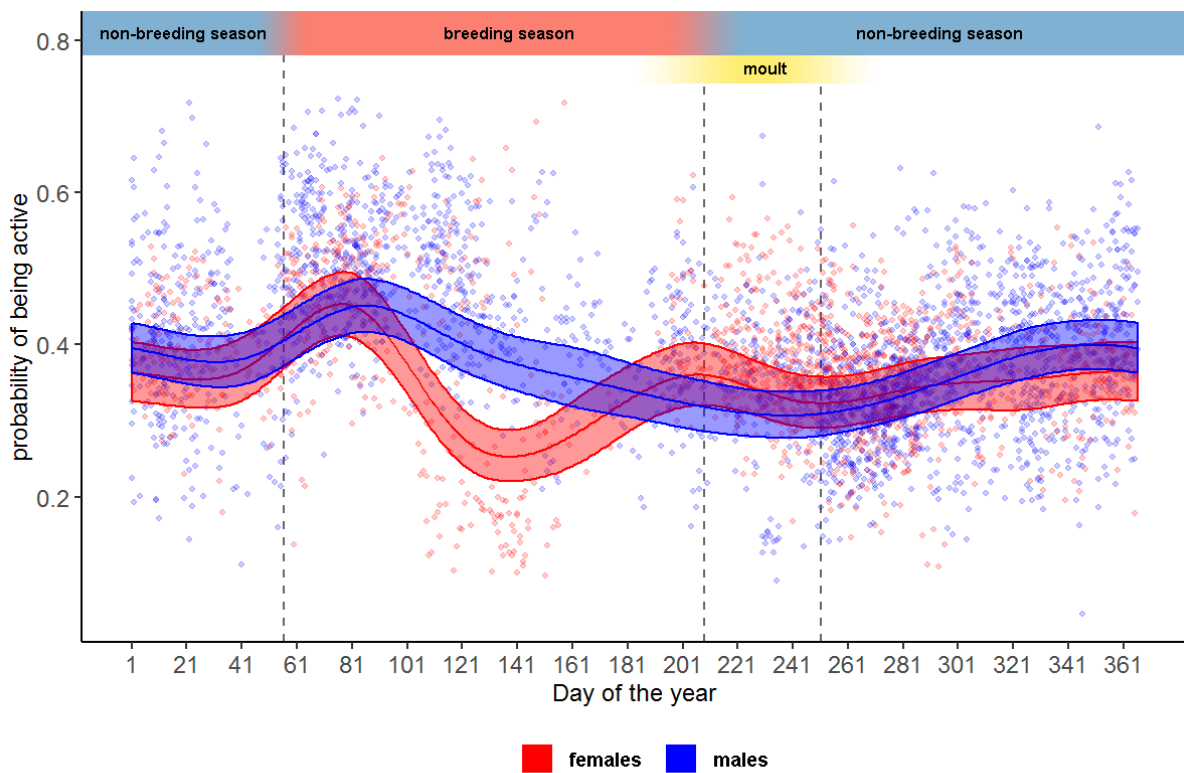


Figure 2. Seasonal activity pattern of female (red) and male (blue) resident European blackbirds (*Turdus merula*). Raw data (dots) correspond to the proportion of the daytime that birds were active. Solid line represents the results of the GAMM model (mean predicted values). Shaded area corresponds to the 95% confidence interval of the mean predicted values.

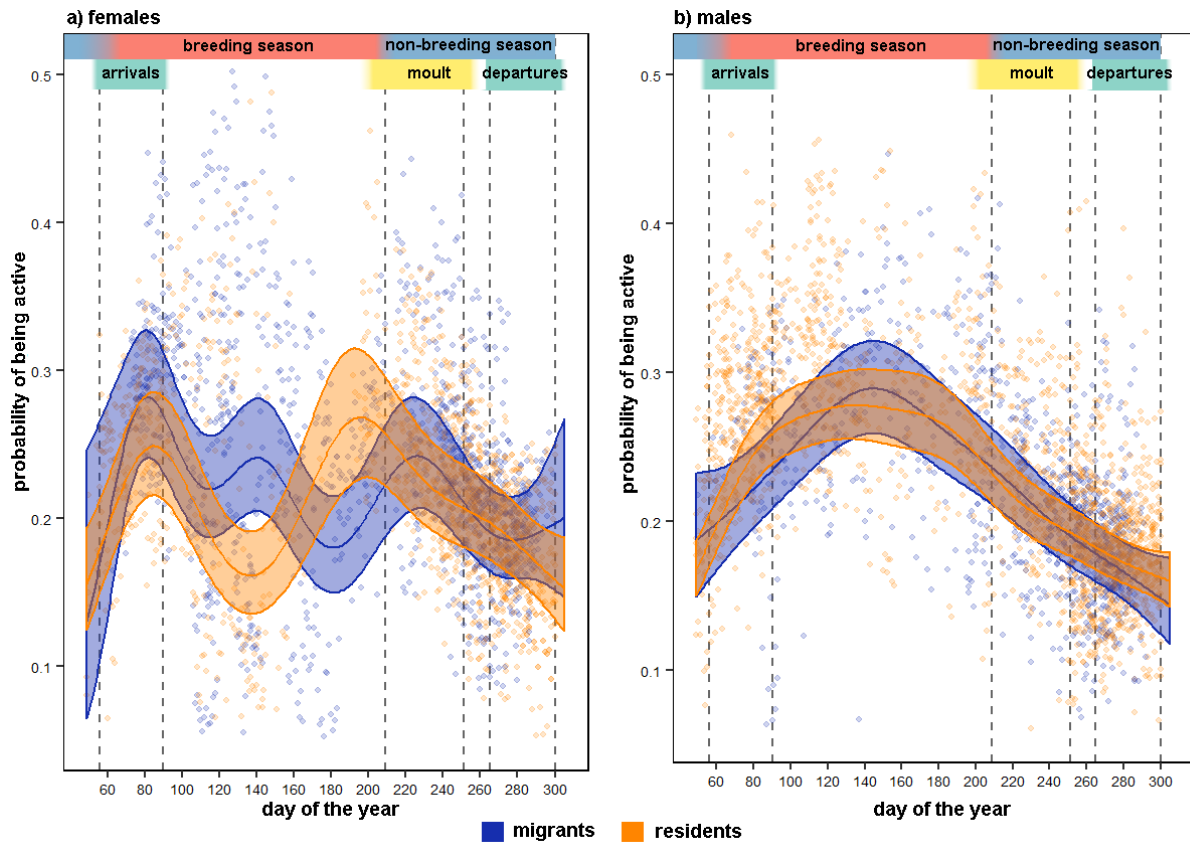


Figure 3. Activity pattern of resident (orange) and migrant (blue) females (left panel) and males (right panel). Dots correspond to the raw daily activity as a percentage of 24 hours. Solid line represents the results of the GAMMs (mean predicted values). Shaded area corresponds to the 95% confidence interval of the mean predicted values.

Table 1. Sample size per week and, migratory status and sex used to generate figure 1 and to fit the differents Generalized Additive Mixed Models				
	sedentary		migrants	
	females	males	females	males
Week of year	n	n	n	n
1	7	14	0	0
2	9	16	0	0
3	7	19	0	0
4	6	13	0	0
5	6	13	0	0
6	5	10	0	0
7	2	7	0	0
8	6	16	0	1
9	8	17	0	1
10	9	18	2	1
11	9	15	5	3
12	7	16	6	5
13	7	15	6	5
14	7	13	5	5
15	3	3	5	3
16	6	12	7	3
17	4	12	7	4
18	5	9	6	3
19	5	9	6	3
20	3	4	5	5
21	4	6	5	4
22	5	6	4	3
23	3	6	4	4
24	1	4	4	2
25	1	4	3	3
26	2	2	3	2
27	0	3	2	2
28	1	5	3	2
29	5	11	5	6
30	5	8	3	6
31	6	6	3	7
32	9	8	5	7
33	12	11	4	8
34	12	10	6	6
35	12	9	11	7
36	12	13	12	8
37	18	24	13	9
38	15	25	12	11
39	15	25	12	11
40	18	28	12	12
41	18	24	9	10
42	14	22	6	3
43	10	22	2	0
44	12	23	0	0
45	5	17	0	0
46	3	13	0	0
47	4	24	0	0
48	7	22	0	0
49	11	17	0	0
50	9	20	0	0
51	9	19	0	0
52	8	19	0	0
53	6	12	0	0

Discussion

Despite exhibiting distinct overwintering strategies and despite alteration of daily activity patterns of migrants to perform their nocturnal migratory flights, migrant and resident blackbirds did not differ in their activity levels while sympatrically breeding (from March until October). Our results suggest no carry-over effect of migration on activity levels during the breeding season. Concerning the annual activity pattern of residents, activity followed a seasonal pattern throughout the year even when photoperiod is taken into consideration, indicating that activity levels are modulated according to the specific life-history stages. Both migrants and residents increased their activity levels towards the beginning of the breeding season, decreased in the autumn, and, at least in residents, increased again during the winter. Moreover, as expected, males and females differed in activity levels during the breeding season, with females being less active than males, most likely due to egg incubation bouts. Our results concerning the annual pattern of daytime activity levels of resident individuals confirm that activity follows a seasonal pattern, even when the seasonally-changing photoperiod is taken into account. The seasonal variation in activity profiles could reflect the adaptation to the different life history events throughout the entire annual cycle. Resident males and females increased their activity, reaching peak activity during the early breeding season (March). We found the lowest activity levels of the year during the moulting period. It is well documented that during moult, the ability to fly is reduced, birds are more inconspicuous, and they shift their habitat use (Rivera et al., 1998). Subsequently, activity levels increase again in the winter. Winter is particularly challenging in terms of energy expenditure because food availability is reduced and birds need to invest energy in both thermoregulation and increased foraging effort. The increased foraging effort results in blackbirds increasing their body mass during winter (Cresswell, 1998; Macleod et al., 2005). Towards the beginning of the breeding season, activity tends to increase, reflecting the set of behavioural changes that occur during this time period, which include territorial establishment

and defence, mate acquisition, incubation and offspring rearing. These results support the assumption that the seasonal variation of activity levels reflects the constraints and requirements of the specific stages of the annual cycle; our measurements are thus biologically relevant.

After the arrival of migrants in the spring, there are three possible scenarios for locomotor activity in blackbirds of different migratory background are conceivable: i) migrant individuals could exhibit higher activity levels than resident birds due to increased efforts of territory establishment or intense partner search. In a partially migratory population, resident males are thought to be able to establish territories earlier than migratory conspecifics (Schwabl, 1983), and these territories may be better in quality (Kokko *et al.* 2006). Given that occupying a breeding territory is essential to assure mating success in blackbirds (Creighton, 2001; Snow, 1956), migrant males that arrive later may need to compete for already occupied territories. These increased reproductive efforts should translate into higher activity levels. Similarly, migrant females might need to actively seek for a mating partner in a limited period of time, which would result in an increased activity level.

Alternatively, ii) migrant individuals might exhibit lower activity than resident birds due to increased resting periods to recover from the migratory journey (Aborn and Moore, 2004). Under this situation, migrants would compensate for the high energetic demands of migration with lowered energy expenditure during the post-migratory period, and thus lower activity levels upon arrival.

Under the third scenario, iii) resident individuals, particularly males, might increase their activity as a product of territorial defence upon the arrival of migrants. However, contrary to our expectations, our results indicate that migrants and residents exhibited similar activity levels, both in males and females upon spring arrival.

Our results revealed no difference in activity levels between migrant and resident males during the breeding season, supporting the conclusion that the overwintering strategy does not

impose carry-over effects on the amount of time spent active during the breeding season. As in males, the activity levels for migrant and resident females were similar during the breeding season. During the breeding season, females of both groups displayed intermittent periods of low activity, as expected. These low activity bouts are likely related to the incubation of eggs and thus are an indication of breeding activity. No difference in the timing of these low activity bouts was observed, which could suggest that resident females do not breed earlier than migrant conspecifics, contrary to what has been previously suggested for partially migratory species (Morrissey, 2004). However, as we did not wish to disturb our study animals during this activity, we do not have breeding data for our population to test this hypothesis more precisely.

During the autumn pre-migratory phase, contrary to our expectations, the migrants and residents again showed similar activity levels. We expected two different scenarios i) differences in activity profiles between the two groups, given that migrant birds would need to prepare themselves for the energy demands of migration. Migrants display hyperphagia (Odum, 1960) and blackbirds of this population accumulate fat (Fudickar et al., 2013). In captive birds, the pre-migratory hyperphagia results in higher activity levels (Cornelius and Hahn, 2012). Alternatively, ii) wild migrant and resident birds would exhibit similar activity due to increased foraging effort in both groups, given that both migrants and residents would prepare themselves for the winter period. However, this second scenario seemed less likely because resident birds do not increase body weight or fat deposition during autumn, but during winter (Lundberg, 1985). Our results confirmed that migrant and resident birds had the same activity levels before migration, when migrants fatten up. The pre-migratory fattening of the migrant individuals could be based on different foraging efficiency (Dwyer Heise and Moore, 2003b), diet selection (Bairlein, 2002), or intrinsic changes in fat metabolism (Bairlein, 1985) between the two groups, and not purely on differences in hyperphagia-related activity levels. This is an important distinction and should be subject to experimental tests in

the future. However, it is also possible that the two phenotypes have similar daily activity levels but they invest their time differently, i.e., they perform different behaviours when active. For example, during the pre-migratory period, migrants might invest more time foraging at the expense of other activities, such as anti-predator behaviour. This trade-off has been observed previously in ruddy turnstones, where migrant individuals decreased their time budgeted for anti-predator behaviour, compared to resident individuals (Metcalf and Furness, 1984). Similarly, during the pre-migratory hyperphagic phase, migrant individuals could compensate for the higher workload by decreasing other behaviours such as flying. This behavioural compensation would result in a similar total activity budget between migrant and resident birds. A recent study showed that during the migratory hyperphagic period, birds have similar energy expenditure compared to the non-migratory phase (Guillemette et al., 2012). Explanations for this counter-intuitive fact involve behavioural and/or physiological compensation mechanisms, such as reducing flight activity and lowering of the heart rate during rest (Guillemette et al., 2012; Portugal et al., 2012). Unfortunately, our method does not allow us to distinguish specific behaviours, given that the daily activity level is calculated using body movements to test these hypotheses. Using another type of technology that allows for the identification of behaviour in time, (e.g. accelerometer loggers) one could investigate potential differences within the activity budgets between migrant and resident birds.

We argue that seasonal change in daily activity levels is an indicator of how birds cope with the demands of the different stages of the annual cycle. Under this assumption, the fact that both strategies have a similar activity pattern argues in favour of both groups experiencing similar constraints and responding accordingly, at least during the breeding season. A lack of energetic differences between migration and residency during this period could be an important argument for the evolutionary existence of the two overwintering strategies in partially migratory populations or species. To test this hypothesis is necessary to gather data

during the migration and overwintering periods to compare migrants and residents throughout the entire annual cycle. Future studies could use the newly developed accelerometer loggers by Bäckman et al. 2016, or more sophisticated bio-logging technologies such as heart rate loggers, to study energetics of both residents and migrants . An answer to this question will certainly help to further our understanding of how the two strategies are maintained.

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**Migration confers survival benefits to overcome
the winter.**

In preparation as:

Daniel Zuñiga, Yann Gager, Adam Fudickar, Andreas Schmidt, Beat Naef-Daenzer, Martin Wikelski and Jesko Partecke. Migration confers survival benefits to overcome the winter.

Abstract

One hypothesis for the evolution of seasonal migration states that migration optimizes individual fitness by avoiding the low survival probability associated with wintering in an area of limited resources and harsh climatic conditions. We monitored a partial migratory population of European blackbirds (*Turdus merula*) over 7 years and tested if migration offers survival benefits compared with residency. Using a combination of capture – mark recapture and radio telemetry we compared survival probabilities between migrants and residents using capture mark recapture multievent survival models. We found that the survival probability for winter is lower compared to non- winter season for both strategies but that survival probability was higher for migrants than resident indicating that migration offers survival benefits during the winter.

Introduction

In temperate latitudes, strong seasonal fluctuations of food resources and weather conditions can impose considerable constraints to life, particularly during the winter season. During winter, unfavourable harsh weather conditions and low food supplies reduce survival. Conversely, during spring and summer, food supplies are abundant and the most nutritionally demanding life stages (e.g. reproduction) normally overlap with this season to maximize the reproductive success (Lack, 1954). Seasonal migration is a strategy that allows migrants to cope with temporal environmental fluctuations by enabling the exploitation of abundant resources in geographically distant habitats (Fryxell and Sinclair, 1988). Therefore, seasonal migration should optimize fitness by avoiding low survival probabilities in environments where the winter is particularly harsh and increase reproductive success in areas with abundant resources to rear offspring (Lack, 1954). Migration is a wide spread strategy among various taxa (Chapman et al., 2011a) and its most common form is partial migration. Partial migration is defined as the individual variation within population in migratory behavior, meaning some individuals migrates and others remain year-around as residents at a given habitat (Lack, 1943). Hence, a partially migratory population offers a unique opportunity to study adaptive advantages of migration and residency (Berthold, 2001). The most “classical form” of partial migration is when migrants and residents breed sympatrically but overwinter apart (Chapman et al., 2011a). Partial migration is considered a polymorphic life history trait and the question of how natural selection maintains such a trait remains a fascinating mystery for evolutionary biologists and ecologists alike (Sinervo and Calsbeek, 2006). However most research on the evolution of partial migration has been theoretical, and there is a lack of empirical data supporting the theory. Theoretical efforts have yielded at least two alternative explanations for the evolution of partial migration (reviewed in Chapman et al. 2011). The first possibility is that a frequency - dependence evolutionary stable state (ESS) occurs in which the fitness of both strategies is equal at an equilibrium point (Kaitala et al., 1993;

Lundberg, 1987). The second possibility is that a conditional strategy under frequency - dependent selection occurs; in which individuals adopt the strategy that maximizes their individual fitness depending on their phenotype (e.g. age, sex, dominance), even when this strategy is suboptimal at the population level. Individuals taking the suboptimal strategy make the “best of a bad job” (Lundberg, 1988; Vélez-Espino et al., 2013). A conditional strategy also requires a form of frequency – dependence to operate. If there is no frequency – dependent selection and no fitness balance, the strategy that performs consistently less well should be lost (Kokko, 2011). More recently “transient coexistence” has been proposed as an explanation for the occurrence of partial migration (Singh and Leonardsson, 2014). Under this scenario, following the invasion of one strategy into a population, if the new strategy confers fitness benefits it will replace the previous strategy however, before this replacement occurs both strategies can be observed in the population (Singh and Leonardsson, 2014).

A vast amount of theoretical work has been done concerning the fitness related costs and benefits of remaining resident or migrating and its relation to the evolution of partial migration. However there is limited empirical data supporting these hypotheses, given that fitness data are difficult to gather. Using capture – mark – recapture and re-sighting of banded individuals Adriaensen & Dhondt 1990, showed that migrant European robins (*Erithacus rubecula*) have lower fitness (lower survival and reproductive success) than resident birds. Using similar methodology Gillis et al. 2008 reported that in a population of American dippers (*Cinclus mexicanus*) migrants have lower reproductive success and slightly higher survival than residents. In this population migrants and residents overwinter altogether but migrants move to higher altitude to breed. However recently it was shown that in this same population of dippers, migrants have similar survival probabilities than residents (Green et al., 2015). Re-sighting of banded individuals has major limitations (e.g. detection and the correct identification of a specific individual can be faulty (Lavers and Jones, 2008; Milligan et al., 2003). Moreover, the difficulty of distinguishing between migration and local movements

when individuals are not detected may lead to biased estimates of population parameters such as survival probabilities. Other methods such as radio telemetry can overcome some of these limitations because they facilitate the detection and identification of specific individuals in a population. Using a combination of capture – recapture and radio telemetry during a 7 years study, we investigated whether migration offers survival benefits during winter in a partially migratory population of European blackbirds (*Turdus merula*). In this population females migrate more often than males (Fudickar et al., 2013) and migrants overwinter on average 800 km west-southwest from the breeding grounds (Fudickar and Partecke 2012). We hypothesize that migrants will have a higher survival probability during the winter than residents. On the contrary during the non-winter while resources are plenty, both strategies should perform similarly well.

Materials and Methods

A partially migratory population of European blackbirds (*Turdus merula*) was monitored during 7 consecutive years (2009-2016). This population inhabited a mixed deciduous/coniferous forest in southern Germany (N 47° 47', E 9° 2'). A total of 572 individuals were captured and banded during the spring and summer using mist nests (Fudickar et al., 2013). Sex and age determination was done using plumage differences (Svensson, 1992) and morphological data were collected (body mass, tarsus length, wing length, muscle score, fat score). Sex of juvenile birds was determined by DNA-based sex identification (Griffiths et al., 1998). To this end a blood sample (50 ul) was collected and stored in Queen's Lysis buffer (Seutin et al. 1991). Each bird was equipped with a radio transmitter in combination with i) a light-level geolocator (Mk 10S, and Mk 12S \leq 1.2 g; British Antarctic Survey, Cambridge, UK) during 2009-2011, or ii) light-level geolocator (Intigeo-P65 \leq 1.2 g Migrate Technology, Cambridge, UK) during 2012-2013 or iii) a GPS (PinPoint GPS; \leq 2 g; Biotrack Ltd, Dorset, Uk) during 2014. During 2015 each bird was equipped just with a radio transmitter. Radio transmitters were provided in 2009-2012 and 2014-2015 by Sparrow Systems, Fisher, IL, USA and in 2014 delivered by Beat and Jan Naef-Daenzer, Sempach, Switzerland. The weight of the radio tags were \leq 2.6 g and the battery life span was at least 12 months. The tags were attached by means of leg-loop harness to the back of the birds. Whenever possible recaptures of previously tagged birds were made during the following years and the tag was removed and replaced.

Data collection

We collected presence – absence data at regular intervals through a manual and/or an automated radio telemetry system. Manual radio tracking was carried out twice per week using a handheld three element Yagi antenna (AF Antronics, Inc., Urbana, IL, USA) and AR 8200 MKIII handheld receiver (AOR U.S.A., Inc., Torrance, CA, USA) or a handheld H antenna (Andreas Wagener Telemetry Systems, Köln, Germany) and a Yaesu VR 500

handheld receiver (Vertex Standard USA, Cypress, CA, USA). The automated radio telemetry system consisted of 4 to 6 stationary automated receivers (ARU) (Sparrow Systems, Fisher, IL, USA) deployed at the study site. Each receiver was connected to an H antenna (ATS, Isanti, MN, USA) and was able to search for up to 16 different radio frequencies every 60 seconds.

The migratory status of each bird was assigned based on the presence – absence data. Birds were classified as migrants if they departed at night (determined by ARUs) from the study site during the migratory period. Birds were classified as residents if they remained present and alive at the study site until 31 November of each year were classified as residents. Individuals that were absent during this period were intensively radio tracked using a Cessna airplane fitted with two H antennas and two Biotrack receivers (Lotek Wireless Inc., Newmarket, ON, Canada) and a car mounted with a telescopic mast (6 m height) attached to a three element Yagi antenna (details). Out of 572 birds, the strategy of 288 could not be determined given that they were not present or alive during the fall and were not included in this study.

Conversely the strategy of 262 birds was assigned during the fall and. Out of these 262 birds included in the survival analysis, 192 were classified as residents (69 females: 52 adults and 17 juveniles; 123 males: 96 adults and 27 juveniles) and 70 birds were classified as migrants (45 females: 28 adults and 17 juveniles; 25 males: 17 adults and 8 juveniles). Finally 11 birds that departed from the breeding grounds during the winter and 11 birds which switch strategies over time were not included in the analysis.

Data preparation and analysis

Seasonal survival estimation.

To estimate seasonal survival probabilities, each calendar year was divided into two operationally defined “seasons”: non-winter and winter. Non-winter season was defined as the period of time between the date of the first spring arrival of a migrant bird and the date of the

last Fall departure. To define the start of the first non-winter season in 2009, the date of the very first capture (April 23rd) was used. Winter season corresponded to the period of time between the date of the last departure in the fall and the date of first arrival the subsequent spring. Based on the presence – absence data, we generated a matrix of 15 columns; each corresponding to one respective season (e.g. non-winter 2009, winter 2009-2010, non-winter 2010 etc.) and 262 rows (one for each individual). Additional columns containing the covariates sex (males and females), age at capture (juveniles and adults) and migratory status (migrants and residents) were added to the matrix.

Annual survival estimation

An operationally defined year rather than a calendar year was used for the annual survival analysis. The beginning and end of each year coincided with the arrival of migratory birds to the breeding grounds in the spring. This definition was employed so the winter period would not be divided into two different years. An annual matrix for all individuals was constructed based on the presence – absence data. This matrix contained 7 columns each corresponding to a year and 262 rows (one for each individual). Similarly to the seasonal analysis, columns containing the different covariates: sex, age at capture and migratory status were added to the matrix.

Statistical analysis.

We implemented multievent models using the software E-SURGE 1.9.0 (Choquet et al., 2009) . These models belong to the family of hidden Markov models. They assume that the individuals in a population independently transition between a finite set of N states (e.g. presence, absence) through a finite number of sampling occasions. Since the capture regime is imperfect there is uncertainty in presence or absence of each individual. Multievent models account for this uncertainty (Pradel, 2005). Multievent models allow simultaneously the estimation of the probability of survival (Φ) of a group of individuals and its detection

probability (P). Detection probability (P) is a decisive parameter because directly influences the survival estimates and in natural populations often is less than 1. Failing to account for this parameter can lead to faulty conclusions in capture mark-recapture analyses (Gimenez et al., 2008).

In addition 10 biologically meaningful models including sex, the age at capture, migratory strategy and season were fitted for the seasonal analysis. In the case of the annual analysis, 12 biologically meaningful models were fitted, including sex, the age at capture, migratory strategy and year. For both analyses model selection was performed using the Akaike Information Criterion corrected for small samples (AICc). Delta AICc (Δ AICc) was calculated and the models ranked based on this value. The best ranked model was the one that yielded the lowest AICc value and better fitted the data.

Results

Seasonal Analysis

Akaike Information Criterion corrected for small samples (AICc) indicates that when estimating survival it is important to account for different detection probabilities for migrants and residents. The first seven best ranked models include migratory strategy in the detection probability (Table 1).

Our multievent model analysis shows European blackbirds have significantly lower probability to survive the winter (Φ 0.60; \pm 95% confidence intervals (CI) = 0.55 ± 0.66) than the non-winter season (Φ 0.89; \pm 95% CI = 0.82 ± 0.94) (model 3, table 1) indicating that the bottleneck season for this species is the winter. In addition to season, the best ranked model also includes both season and migratory strategy (model 1, table 1) reflecting that the migratory strategy has a significant effect on survival probability. The best ranked model predicts that during the winter, migrants have a higher survival probability ($\Phi = 0.73$; \pm 95% CI = 0.62 ± 0.81 , fig 1) than residents ($\Phi = 0.57$; \pm 95% CI = 0.50 ± 0.63 , fig 1). This model takes into account the lower detection probability for migrants ($P = 0.19$; \pm 95% CI = 0.69 ± 0.78 , fig 1) compared to residents ($P = 0.74$; \pm 95% CI = 0.69 ± 0.78).

Interestingly models including sex as covariate were ranked lower than equivalent models without this factor (model 2 vs model 1 and model 7 vs model 6, table 1), suggesting that sex does not have an effect on the probability of survival.

Annual Analysis

Surprisingly the best ranked model based on Δ AICc, estimated survival probabilities for each year (model 1, table 2). According to this model the survival estimates for year 2009 - 2010 ($\Phi = 0.32$; \pm 95% CI = 0.20 ± 0.47 , fig2) and 2014-2015 ($\Phi = 0.19$; \pm 95% CI = 0.12 ± 0.311 , fig2) were lower than that of the other years 2010 – 2011 ($\Phi = 0.60$; \pm 95% CI = 0.44

± 0.74 , fig2); 2011-2012 ($\Phi = 0.64$; $\pm 95\%$ CI = 0.50 ± 0.75 fig2); 2012-2013 ($\Phi = 0.70$; $\pm 95\%$ CI = 0.55 ± 0.81); 2013 – 2014 ($\Phi = 0.72$; $\pm 95\%$ CI = 0.54 ± 0.85) and 2015-2016 ($\Phi = 0.51$; $\pm 95\%$ CI = 0.31 ± 0.71 ; figure 2). This model estimated an overall detection probability for the entire study period ($P = 0.69$; $\pm 95\%$ CI = 0.60 ± 0.78). The second best ranked model suggests that it is important to account for different detection probabilities each year when estimating survival probabilities (model 2, table 2). This suggestion is supported by the fact that models that included the covariate year in the detection probability (P) (models 2 – 10, table 2) ranked better than equivalent models without this covariate (Model 11 and 12, table 2). We attempted to fit a model including year as a covariate for both the survival estimate and the detection probability Φ [year]. P [year] but the software was not able to calculate all 16 parameters without convergence problems arising.

Notably, the model that did not include any covariates in the survival probability and included the covariate in the detection probability (model 2, table 2) was higher ranking (i.e. lower AICc) than models which included the covariate sex (model 3, table2), age at capture (model, table 2), migratory strategy (model 5, table 2) or the combination of these factors (model6, model7, model 8, model 9, model 10,). This result strongly suggests that sex, age at capture and migratory strategy did not have a significant effect on estimating annual survival probabilities.

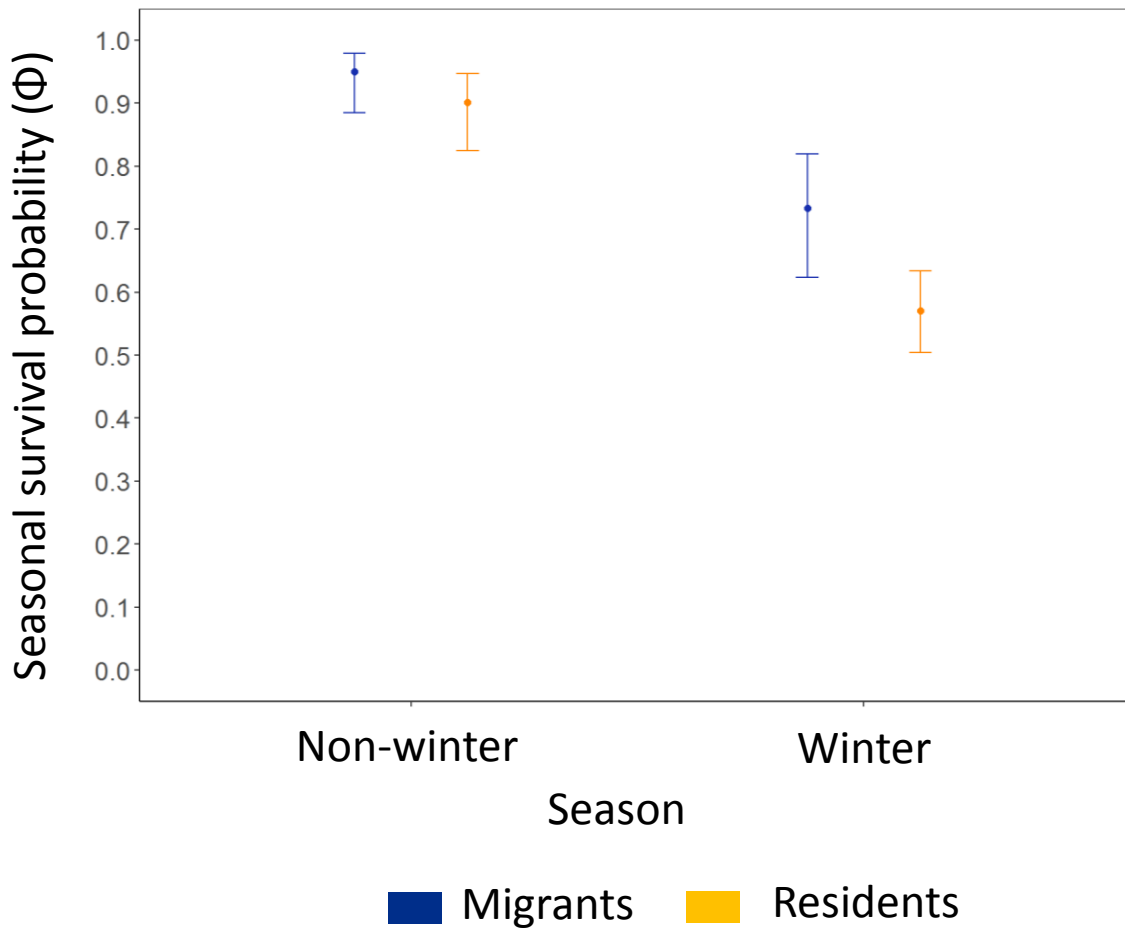


Fig1. Seasonal survival probability of migrants and residents European blackbirds.

Survival probability (Φ) and 95% confidence intervals of migrants (blue) and residents (yellow) birds estimated using the best ranked multievent capture - mark recapture model (Φ [season+migr].P[migr]). Detection probability (P) was estimated as 0.74 for residents and P = 0.19 for migrants. 262 birds were included in this analysis (192 were classified as residents and 70 were classified as migrants).

Model	Number of parameters	QAICc	Delta AICc	Deviance
(1) Φ [season+migr.].P[migr]	5	1408.3	0.00	1398.2
(2) Φ [season+migr+sex.].P[migr]	6	1409.2	0.95	1397.1
(3) Φ [season].P[migr]	4	1414.3	6.04	1406.2
(4) Φ [season+juv+ad.].P[mig]	5	1416.1	7.79	1406.0
(5) Φ [migr].P[migr]	4	1447.1	38.82	1439.0
(6) Φ [.].P[migr]	3	1448.2	39.98	1442.2
(7) Φ [sex].P[migr]	4	1449.9	41.6	1441.9
(8) Φ [season+migr].P[season]	5	1504.0	95.75	1493.9
(9) Φ [season].P[season]	5	1504.2	95.89	1494.1
(9) Φ [season+sex+migr].P[season]	6	1504.9	96.60	1492.7
(10) Φ [season+sex].P[.]	3	1530.3	122.02	1524.3

Table 1 Multievent mark-recapture models to estimate seasonal survival in a partially migratory population of European blackbirds (*Turdus merula*) Mean seasonal survival estimates are based on capture-mark-recapture and presence-absence data using radio telemetry of 262 European blackbirds. Each year was divided into two seasons: Non-winter and Winter (see methods). The models are ordered according to the Δ QAICc with lower values indicating better fit to the data. The model estimates survival probability (Φ) and detection probability (P) for the different covariates such as season (non-winter, winter), sex (males and females), age (juveniles and adults) and migratory strategy (migrant and resident).

Model	QAICc	Δ QAICc	Number of Parameters	Deviance
(1) Φ [year]. P[.]	752.8	0	8	736.5
(2) Φ [.]P[year]	778.7	25.9	8	762.4
(3) Φ [sex].P[year]	779.2	26.4	9	760.8
(4) Φ [juv+ad].P[year]	780.3	27.4	9	761.9
(5) Φ [migr].P[year]	780.8	28.0	9	762.4
(6) Φ [sex+migr].P[year]	781.2	28.4	10	760.7
(7) Φ [sex*migr].P[year]	782.4	29.5	11	759.8
(8) Φ [juv+ad+sex].P[year]	782.7	29.9	11	760.1
(9) Φ [juv+ad+migr].P[year]	784.3	31.5	11	761.7
(10) Φ [juv+ad+migr+sex].P[year]	784.7	31.9	12	760.0
(11) Φ [.]P[.]	792.5	39.7	2	788.5
(12) Φ [.]P[migr]	794.3	41.5	3	788.3

Table 2 Multievent mark-recapture models of yearly survival in a partially migratory population of European blackbirds (*Turdus merula*). Yearly survival estimates are based on capture-mark-recapture and presence-absence using radio telemetry of 262 European blackbirds. First capture occurred in April 2009 and the last presence in April 2016. The end of each year was defined as the mean date of arrival of migrants blackbirds in the Spring. The models are ordered according to the Δ QAICc, lower value indicates better fit to the data. The models estimated survival probability (Φ) and detection probability (P) including different the covariates: year, sex, age (juveniles and adults) and migratory status.

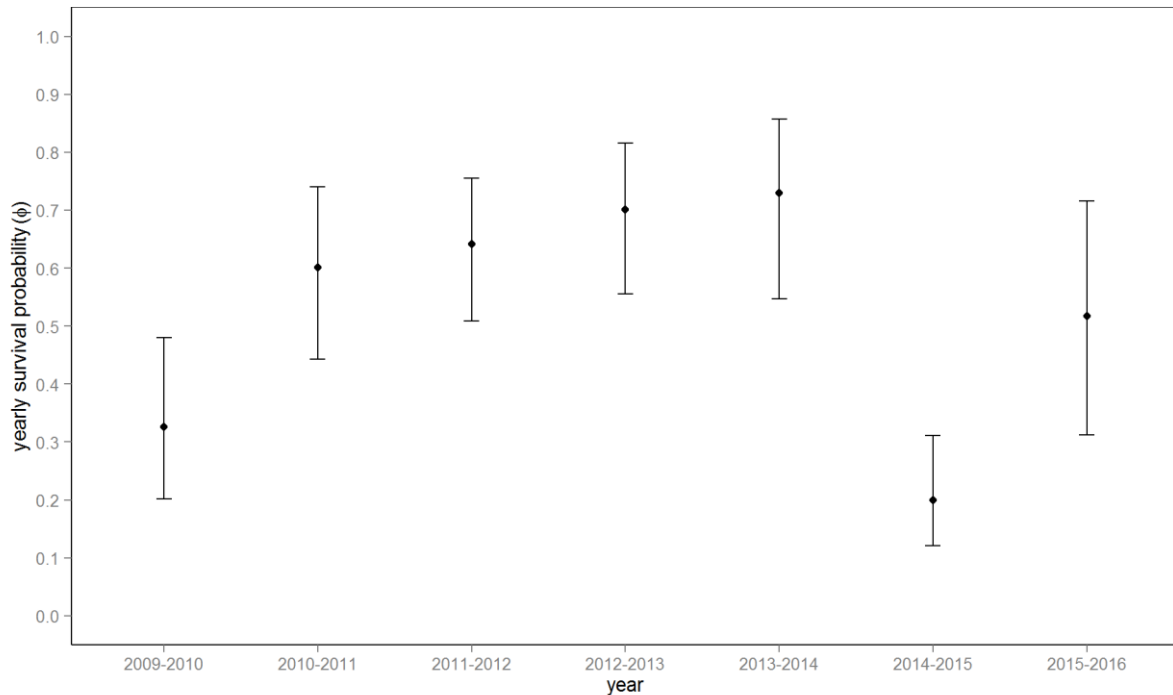


Fig 2. Yearly survival estimates of a partially migratory population of European blackbirds (*Turdus merula*). Survival probability Φ and 95% confidence intervals estimated by the best ranked model (Φ [year]. P[.]). This model was selected using Δ AICc values. A total of 262 European blackbirds were included. The best ranked model estimated survival for each year with a constant detection probability for all years (2012 -2015). Detection probability (P) estimates = 0.693; 95% confidence interval upper = 0.768 and lower = 0.606.

Discussion

We provide evidence that migrant blackbirds of a partially migratory population have higher winter survival probability than residents of the same population. This result strongly supports the hypothesis that migration confers survival benefits as a strategy to overcome the wintering season. Furthermore, our results confirm the assumption that winter is the bottleneck season for this population; survival estimates are lower during winter than during the non – winter period for both residents and migrants. Our results suggest that there is no effect of migratory strategy, age or sex on the annual survival estimates. However, we observed significant differences in survival probabilities across our study, with the first (2009-2010) and the sixth (2014 -2015) years of the study showing the lowest survival rates.

We observed that migrants are more likely to survive the winter than individuals that remained resident at the breeding grounds. This finding supports the idea that migration as a strategy, need to confer some fitness benefits to be maintained (Kokko, 2011). Larger confidence intervals of the survival estimate during winter in migrants suggest that the variation in the winter survival estimate is larger among migrants than among residents. This difference could indicate that survival in migrants is highly dependent on the success during the migratory journeys and / or the conditions at the overwintering sites. However, we cannot exclude the possibility that the greater variation in survival estimates is due to a sample size effect.

Results of previous studies on this population indicate that females migrate more often than males and that residents outnumber migrants (Fudickar et al., 2013). In our seasonal analysis we found that the survival probability during the winter is not influenced by the sex of the individuals. We argue that frequency dependent selection could provide an explanation for the tendency of females to migrate more than males even without sex-specific survival benefits.

During the winter, blackbirds form foraging flocks and an individual's access to food is related to its position within the flock hierarchy (Lundberg and Schwabl, 1983). Within winter blackbird flocks females are subordinate to males (Lundberg and Schwabl, 1983; Lundberg, 1985). Hence, females would suffer higher mortality if they remain as residents during winter, when food is limited, than if they migrate. Therefore migration represents an advantageous strategy to increase survival in females European blackbirds. Conversely, for males it would be advantageous to remain resident given that they would be present at the breeding ground as soon as the breeding season starts thereby increasing their opportunity to choose and establish a high quality breeding territory (Kokko, 2011; Kokko et al., 2006). It is essential for males to acquire a breeding territory to ensure mating success in European blackbirds (Creighton, 2001; Snow, 1956). Migrant males risk not finding an empty breeding territory upon arrival to the breeding grounds in the spring, forcing them to battle for already occupied territories.

Although our results provide evidence of the survival benefits of migration, to compare the total fitness benefits of migration and residency, data on reproductive success are needed. Comparing total fitness between migrants and residents would allow to test for different hypotheses for the evolution and maintenance of partial migration. Unfortunately, we could not collect data on reproductive success in our current study. Only a few empirical studies have related fitness data to partial migration. In blackbirds (*Turdus merula*) reproductive success of migrants and residents depend on the sex. Male residents have higher reproductive success than male migrants. On the contrary female residents and migrants have similar reproductive success (Schwabl, 1983). In skylarks (*Alauda arvensis*) the reproductive success of migrants and residents is similar (Hegemann et al., 2015). In contrast, European robins (*Erithacus rubecula*) migrants have lower fitness (lower survival and reproductive success) than residents (Adriaensen and Dhondt, 1990). Finally, in American dippers (*Cinclus mexicanus*), migrants have lower reproductive success and slightly higher survival than

residents (Gillis et al., 2008). However it has recently been reported contradictory results of this same population of American dippers, where migrants and residents have similar survival probabilities (Green et al., 2015). A limitation of these previous studies on estimating survival in partially migratory populations is that the classification of individual strategy and the presence absence data was based on capture and resighting of banded birds. There are at least two limitations of this method: First the individual detection probability is reduced and second it is difficult to distinguish between local movement and actual migration. In contrast by taking advantage of capture mark recapture combined with radio telemetry technology our approach overcome these limitations. Notably our seasonal analysis revealed that the detection probability of individuals has an important effect on their survival estimates and needs to be taken into account. During the seasonal analysis the model is informed by the presence – absence matrix that during the winter, migrants are absent from the study site and the detection probability is 0. This fact could explain the failure of previous studies in to detect a higher survival rate among migrants.

An important limitation of our study is the fact that we are not able to track the migrant blackbirds to their wintering realms. Thus the capture-mark-recapture models assume that if a bird did not return, it was dead. Future developments in tracking technologies (Wikelski et al., 2007) that allows small animals to be tracked at a global scale in real time will address this problem.

We found that neither sex nor migratory strategy have an effect on the annual survival estimates. Although this result might seem in contradiction with the results obtained in the seasonal analysis, this difference may be explained by the lower temporal resolution of the annual analysis. The annual model uses a presence – absence matrix built at a lower temporal resolution as input. Therefore, the matrix does not contain the information that migrants were

absent during winter. For this reason, the model cannot account for the importance of migratory strategy determining the detection probability of individuals. The annual analysis revealed surprising differences in survival probabilities for different years with lower survival probability occurring during years 2009-2010 and 2014-2015. The lower survival probabilities for these years could be explained by features of the tags used in 2009-2010 and 2014-2015. During the first year of the study (2009-2010) the tags deployed were bulky and the tags used in 2014-2015 were bulky and on average 0.6 g heavier than the tags used in other years. This circumstantial evidence could be an example of the potential harmful effect of tagging birds.

The fact that migration offers survival benefits for European blackbirds during winter provides a compelling explanation for the maintenance of the two phenotypes (migrants and residents) in this population. If the overall fitness of migrants and residents is equal, the two phenotypes are likely to persist as evolutionary stable strategies (ESS) due to frequency dependence selection. Alternatively if the fitness for migrants is lower than residents despite the survival benefits that migration confers, then the migratory trait is maintained as a conditional strategy operating under frequency dependence selection. Conditional strategy means that individuals given intrinsic phenotypic characteristics (sex, age, dominance) need to adopt a strategy that is suboptimal at a population level, but maximize their individual fitness. To distinguish between these two alternatives, data of reproductive success for this species is needed. Our study contributes to the ongoing efforts to fill the gap between theoretical hypotheses regarding the evolution and maintenance of partial migration (Chapman et al., 2011a). Future efforts to study the ontogeny of individuals will help to answer the question of how polymorphic traits are maintained in natural populations.

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General Discussion

Using a direct comparison between two distinct phenotypes of a partially migratory population, I worked towards teasing apart the differences in behaviour of the two distinct overwintering strategies. Furthermore I elucidated the cost and benefits of migration compared to residency. Finally, I collected empirical evidence in the field to test hypotheses explaining the evolution of partial migration.

The strength of my study system was in having a combination of extensive fieldwork and radio telemetry, allowing for: i) accurate classification of the overwintering strategies of the birds, ii) the possibility to derive long-term activity patterns of free-living individuals and iii) reliable identification and detection of individual birds to generate presence/absence dataset for a survival analysis. The combination of classic methodology used in ornithology (capture and recapture) with cutting-edge technology (automated radio-telemetry system) was the key factor to obtain our unique dataset to answer these different questions.

In Chapter 2, we provided the first evidence that free-living migratory birds do not shift gradually from a diurnal to nocturnal lifestyle when they migrate, but rather abruptly. This shift in daily rhythms has been previously observed only under laboratory conditions, when birds switched their daytime activity gradually to become night active (*Zugunruhe*) (Bartell and Gwinner, 2005; Partecke and Gwinner, 2007). Furthermore, the results of Chapter 2 indicated that no nocturnal activity occurred prior to migration. This result, together with the fact that non-migratory species exhibit nocturnal activity in the lab (Helm, 2006; Ramenofsky et al., 2011), has reopened the question regarding the biological implication of *Zugunruhe*. In this chapter, we also provided evidence that during days prior to migration, daytime activity of migrants and resident was similar. This result is interesting because one would predict that migrants should be more active during the day than residents because migrants might prepare themselves for migration (e.g. with increased foraging efforts). A limitation of our study is,

however, the impossibility to identify specific behaviours within the total daily activity budget. There is the possibility that individuals of both strategies invested their time performing different tasks, but that the total budget remained similar.

The main results of Chapter 3 indicated that daily activity levels do not differ between migrants and residents during the breeding season, moult and pre-migratory season. The seasonal variation of activity can be considered a proxy of how individuals cope with the requirements of the different life stages. Our results suggested that both strategies responded similarly to the constraints of the annual cycle. We did not find evidence that individuals would need to compensate their activity levels because of the strategy they chose. It remains possible that there are differences when comparing specific behaviours within the daily activity budget, similar to Chapter 2.

The results of Chapter 4 provided unique empirical data concerning the costs and benefits of migration versus residency; migrants have a higher probability to survive the winter. Our results suggest that independent of their migration strategy, birds have lower probabilities of surviving the winter than the rest of the year. This result confirms the assumption that winter is the bottleneck season in the system. We also provided hints regarding the potentially harmful effect of tagging birds with telemetry transmitters, given that lowest annual survival estimation are most likely due to tag effect.

To fully test the hypotheses concerning the evolution and maintenance of partial migration, ESS under frequency-dependent selection (Kaitala, Kaitala, & Lund, 1993; Per Lundberg, 1987) or conditional strategy under frequency-dependent selection (Lundberg, 1988; Vélez-Espino et al., 2013), a comparison of the overall fitness (survival and reproductive success) is needed. In our study, we could not collect data on reproductive success, however there is

breeding data available on a blackbird population that inhabits a semi-rural area less than 5 km from our study site (Schwabl, 1983). This study showed that the reproductive success of male residents was higher than that of male migrants. On the contrary, breeding success was not significantly different between resident and migrant females. This result suggests that for males, it is more advantageous to remain resident in order to increase their reproductive success. However, for females there is no cost associated with breeding success if they migrate. The fact that migration offers survival benefits and there is no cost associated with reproductive success for females would explain why females migrate more than males in our population. On the other hand, even though migration offers survival benefits for males, the reproductive success can be reduced if they only have a poor quality breeding territory, or none at all. If the risk of not obtaining a territory is high, residency should be selected for, even at risk of decreased survival (Kokko and Lundberg, 2001).

Implications and future directions

Through my doctoral work I have provided evidence that free-living migratory birds shift rapidly from a diurnal to nocturnal lifestyle on the night of their departure, when migration occurs. This result opens up new questions regarding the physiological and behavioural adaptations of migratory birds to perform their migration. Are birds active at night during stopover? Are sleep patterns prior to migration different from the rest of the year? Do migrants suffer “jet lag” due to abruptly disrupting their sleep cycles? Does the sleep-wake cycle return to normality just as abruptly upon arrival at the wintering grounds? What is the biological meaning of nocturnal restlessness in the captive birds? Is it merely a lab artefact? Certainly, future technological developments, such as smaller accelerometer loggers, will help to answer those questions related to activity. It is particularly important to answer the uncertainty as to what occurs during migration at stopover sites. Furthermore, the

miniaturization of brain activity loggers, small enough for being used in free-living migratory birds, could help to disentangle the questions related with sleep behaviour.

This study provides evidence that there are no differences in activity levels between migrant and resident individuals while both are present at the breeding grounds. However it still remains unknown as to what the migrants do during migration and at their overwintering sites. If small accelerometer loggers with long-lasting batteries were available, this question could be answered. Although variation in activity is a good indicator of how animals are adapting to their environment, future studies could measure and compare energy expenditure of individuals of both strategies. Recent technological developments have yielded heart rate loggers small enough to measure energy expenditure in free-living birds. It would be particularly interesting to test whether the energy expenditure during winter is different between migrants and residents. Although it is known that the energy expenditure is lower during the migratory flight than stop over (Wikelski et al., 2003), this study did not take into account adverse weather conditions. Combining heart rate loggers with GPS loggers could help to link energy expenditure with local environmental conditions.

Finally, my doctoral work provided empirical evidence that migration confers survival benefits. However the question still remains unanswered as to whether the overall fitness between the two strategies equalizes or not in this population. As mentioned previously, reproductive success data are needed. Future research efforts could focus on studying partially migratory bird species that are big enough to carry transmitters and or species where breeding data are easier to collect than in blackbirds. Ultimately, to understand how systems such as partial migration are maintained from an evolutionary point of view, one should study the ontogeny of individuals in natural populations. Development of tracking technologies such as

the one proposed by Wikelski et al. (2007) could make this type of studies possible in the future.

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Record of Achievement

The overall development of this project have been thought and executed by me under the supervision of Dr. Jesko Partecke.

The original idea of quantifying nocturnal activity in migrants during the pre-migratory period was developed by Dr. Jesko Partecke and Dr. Adam Fudickar. The field data collection for Chapter 2 was done by Dr. Adam Fudickar, Andreas Schmidt and I. Lab activity data was collected by Dr. Partecke and Willi Jansen. Jade Falconer and I wrote an R script to derive activity from the raw ARU data. I performed the statistical analysis and I wrote the paper. I received comments on the manuscript from Dr. Jesko Partecke, Dr. Adam Fudickar, Dr. Michaela Hau, Dr. Barbara Helm, Dr. Dina Dechmann and Dr. Wikelski

The idea of comparing seasonal activity pattern between migrants and residents (Chapter 3) was developed by my supervisor Dr. Partecke and me. Field data was collected by Dr. Adam Fudickar, Andreas Schmidt and me. I performed the statistical analysis and I wrote the manuscript. I received comments on the manuscript from Dr. Partecke and on earlier versions Dr. Barbara Helm and Dr. Davide Dominoni.

The ideas upon Chapter 4 were built were the results of discussion between Dr. Adam Fudickar, Dr. Partecke and myself at the beginning of my PhD. Dr. Adam Fudickar collected field data from 2009 until 2011. I collected field data from 2012-2015. Andreas Schmidt did most of the manual radio tracking between 2012 and 2016. I compiled the capture-recapture and radio telemetry data into a presence absence matrix to be used in the survival analysis. With the help of Yann Gager, I ran the statistical analysis for this chapter. I wrote the manuscript and I received comments from Dr. Jesko Partecke , Dr. Adam Fudickar and Yann Gager.

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List of Publications

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2016. Abrupt switch to migratory night flight in a wild migratory songbird. *Scientific Reports*.

Submitted:

Zúñiga, D., Falconer, J., Fudickar, A.M., Schmidt, A., Wikelski, M., Partecke, J. No effect of migration on activity levels during the breeding and pre-migratory season: An automated radio tracking study on partially migratory European blackbirds. *Animal Behavior*

In preparation:

Zúñiga, D., Gager, Y., Fudickar, A.M., Schmidt, A., Naef-Daenzer, B., Wikelski, M., Partecke, J.
Migration confers survival benefits to overcome the winter.

Fudickar, A.M., Linek, N., Wikelski, M., **Zúñiga, D.** Naef-Daenzer, B. Partecke, J.
Consistency and flexibility in migration strategies and schedules of partial migrants

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