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Analysis of the consequences of climate change and habitat modification on migratory birds

PhD Coordinator: **Prof. Paolo Tortora**

Tutor: **Dr. Roberto Ambrosini**

PhD Candidate: **Beatrice Carlotta Sicurella**

“The ability of the birds to show us the consequences of our own actions is among their most important and least appreciated attributes.”

M. Stoneman Douglas, 1947.

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Abstract

Habitat alteration and climate change are among the most important anthropogenic factors that are currently contributing to the global decline of biodiversity.

Due to their sensitivity to environmental conditions, birds are considered excellent indicators of global environmental change. In particular, long-distance migratory birds are more likely to suffer than residents or short-distance migrants because they often experience divergent patterns of change in ecological conditions in their breeding and wintering quarters.

The aim of this thesis is to investigate the effects of climate change and habitat modification on population dynamics of long-distance migratory birds.

The first part of this thesis includes papers investigating the effects of environmental and climatic conditions experienced by two long-distance migratory species, the Barn Swallow (*Hirundo rustica*) and the Common Swift (*Apus apus*), at their breeding quarters in Northern Italy on their population dynamics. We observed that both the presence of livestock farming and the extent of hayfields within 200 m from the breeding site affected colony size of Barn Swallows, and that the recent variation occurred in these conditions has probably concurred to worsen the demographic decline that this population is currently experiencing. We also investigated the effect of the rearing environment on the survival and growth of Common Swift nestlings in a part of the breeding range of this species where these effects have not been investigated before. We observed that nestlings' growth is influenced not only by competition for resources with nest mates, but also by meteorological conditions. However, the effects we documented were different from those observed in more northern parts of the breeding range of the species, thus suggesting geographical variation in the susceptibility of this widespread species to general ecological conditions.

In the second part of this thesis we aimed at identifying migration routes and wintering quarters of small-sized birds, and we evaluated the effects of environmental conditions experienced during migration and wintering on population dynamic. We took advantage of the large number of ring recoveries available for the Barn Swallows to identify the main migration routes of individuals breeding in Europe. In addition, we applied miniaturized tracking devices to more than 100 Barn Swallows breeding in Northern Italy and Southern Switzerland. The data we collected allowed us to evaluate the impact of the application of these instruments on survival and breeding success of individuals and to obtain detailed information on timing of migration and position of their wintering areas. In a further study we combined information on wintering grounds and migration routes with long-term data on population dynamic from Northern Italy and found that environmental conditions encountered during wintering and spring migration are the factors that influence most year to year variation in the number of breeding pairs. Finally, we analyzed a long-term series of ringing data on the European Robin (*Erithacus rubecula*) and found that winter temperatures at the breeding grounds influenced spatial and temporal variation in migration propensity and distance among individuals, which were therefore affected by climate change.

Overall, our studies confirmed that global environmental change is already affecting bird populations by acting at different stages of their life-cycle. We showed that variations in ecological conditions at breeding quarters seem to influence breeding performances of individuals, while condition experienced during migration and wintering affect their survival. Effective conservation measures for migratory species should therefore aim at protecting both breeding and wintering areas as well as stopover sites during migration. The novel analytic frameworks we developed may also be suitable for investigating the effects of climate change on migration across a broad range of species.

Introduction

Habitat alteration and climate change have been identified among the most relevant anthropogenic factors that are currently contributing to the global decline of biodiversity (Gaston et al. 2003, Thomas et al. 2004, IPCC 2013). In recent decades, these two factors have led to substantial contractions in the distribution and in the consistency of several species (Pimm & Raven 2000, Warren et al. 2001, Walther et al. 2002, Parmesan & Yohe 2003, Root et al. 2003). Indeed, the loss of habitat may determine the numerical reduction and fragmentation of populations (Sodhi & Ehrlich 2010), and climate changes may alter the distribution of organisms and their phenology (Walther et al. 2002).

Although the precise mechanisms that link global environmental change to the observed decline in biodiversity have not always been clarified, several studies indicated that these factors are likely to determine the extinction of a large number of species in the future (Pimm & Raven 2000, Thomas et al. 2004, Clavero & García-Berthou, 2005).

The Intergovernmental Panel on Climate Change (IPCC) has already established that global warming is “unequivocal” and has placed on human activity a probability over 90% as its primary cause (IPCC 2013). Recent reports have estimated that the average global temperature has increased by 0.6° C over the last hundred years, with two main periods of warming between 1910 and 1945 and from 1976 onwards (Mann et al. 1998, IPCC 2013). Each of the last three decades has also been successively warmer at the Earth’s surface than any preceding decade since 1850 (IPCC 2013) and changes at an even larger scale are predicted for the future (Easterling et al. 1997). Precipitation patterns and the frequency of severe episodes of extreme weather are also expected to be altered (IPCC 2013). Recent studies have predicted that current precipitations patterns will be strengthen and that storm tracks will change, moving away from the equator toward the poles, as a result of climate change (Trenberth 2011, Marvel & Bonfils 2013).

Climatic conditions determine the structure of almost all of Earth's ecosystems, as they influence all their components at different levels, from physiology and behaviour of organisms, to population and community dynamic (Parmesan & Yohe 2003). Consequently, changes in climatic conditions have undeniable direct impact on species' behaviour, abundance and distribution (Peñuelas & Filella 2001).

The phenomenon of global warming is not without precedents in the Earth's history, however, the extent of change currently recorded, and especially that expected for the future, will probably be beyond what most of today's species has ever experienced during their evolutionary history (IPCC 2013). There is unanimous consensus in the scientific community about the fact that current climate change have already had a huge impact on biodiversity and that its importance among the causes which are leading to a gradual loss of biodiversity has exponentially grown in the last decades (Thomas et al. 2004).

Another major threat to biodiversity is the loss of habitat, which is due to all the anthropic changes to the natural ecosystems that modify the ecological conditions to which individuals have adapted over the course of their evolution (Thomas et al. 2004, Malcolm et al. 2006). Human activities can negatively impact on natural habitats in different ways, but destruction, fragmentation, and degradation are the ones that can most negatively affect biodiversity. Several studies have already emphasized the role of land-use changes as a cause of species declines and extinctions (see for example Pimm & Raven 2000, Sala et al. 2000, Dobson et al. 2014). The negative consequences of habitat loss may also exacerbate those of climate change and enhance their impact, as the ability of the species to reach new climatically suitable areas could be hampered by habitat contraction and fragmentation (Thomas et al. 2004).

The comprehension of the mechanisms that connect global environmental change and the loss of biodiversity is pivotal to plan both management and effective conservation measures (IPCC 2013), but the efforts to evaluate overall ecological effects of environmental change on biodiversity would be enormous, both in terms of time and resources required. Scientists, therefore, have to rely on some taxa that can serve as indicators for biodiversity as a whole.

Among them, birds are considered excellent indicators of environmental change (Berthold et al. 1998, Crick 2004, Møller et al. 2004, Wormworth & Şekercioğlu 2011) for several reasons. First of all, their taxonomy, distribution, ecology and life history are well known (BirdLife International 2013). Birds are also generally easy to identify, survey and monitor and are found nearly in all habitats across the world. They occupy high trophic levels and are relatively sensitive to environmental change, thus their distribution generally reflects that of many other groups, and their population trends can mirror those of other species. For all these reasons, birds have been recently defined as “winged sentinels” of global environmental change (Wormworth & Şekercioğlu, 2011).

Remarkably, birds are also one of the few animal taxa for which very long time-series of data are available. Starting from the end of the 18th century (Preuss 2001), in fact, by ringing millions of birds and gathering information on any recovery of these individuals, ornithologists have collected a huge amount of data on birds' biology and behaviour that can now be analysed for extensive studies (Møller & Fiedler 2010). Although ringing and recovery data lack of spatial and temporal homogeneity, due to the fact that ringing efforts are not even in space and time, and also do not allow a very accurate description of individual's movements, they are extremely valuable for studying birds migration. Indeed, for a long time, they will likely represent one of the very few sources of information allowing for retrospective analyses of changes in migratory behaviour over time. At continental level, ring recoveries are available thanks to the EURING databank (EDB, www.euring.org), which currently holds a very large proportion of the data that have been gathered by bird ringing schemes throughout Europe.

In recent decades, the introduction of technological tracking devices has allowed to integrate information from ringing data with more precise details on the movement behaviour of birds (Bridge et al. 2011). Although for several years, these technologies have been suitable, due to their weight, only for large-sized birds, recent technological improvements are allowing the tracking also of small-sized species (Stutchbury et al. 2009). These instruments are currently revealing unknown details on the migratory phenology and behaviour of birds. The combination of ringing and tracking data is also providing innovative developments in our understanding of bird populations and movements.

Thanks to birds' sensitivity and to the wide knowledge of different aspects of their biology and behaviour, the current literature is rich of studies that document the effects of global change on bird populations. They include, among many others, changes in survival rates and, consequently, in the size and distribution of populations (Saino et al. 2004, Both et al. 2006), as well as in the timing of reproduction and in breeding performance (e.g. nesting success, brood size and chicks' survival; Both & Visser 2001, Moss et al. 2001, Saino et al. 2004). Furthermore, extreme weather events, which are expected to increase in frequency as a result of climate change, can have catastrophic effects on entire bird populations (Newton 1998, Stenseth & Mysterud 2002).

Among bird species, long-distance migrants are more likely to suffer from environmental change than residents or short-distance migrants (Sillett et al. 2000). In fact, species that migrate over intercontinental distances often experience different patterns of change in ecological conditions in their breeding and wintering quarters, as well as in their staging areas during migration (Both et al. 2010, Saino et al. 2011). Clear examples documenting the effect of climate and habitat change specifically on migratory birds are already widespread in scientific literature. For instance, many migratory species have already altered their breeding and wintering distribution (Thomas & Lennon 1999, Valiela & Bowen 2003, Brommer 2004, Fiedler et al. 2005, Newton 2008, Visser et al. 2009, Ambrosini et al. 2011) or their migration phenology (Crick & Sparks 1999, Dunn 2004, Lehikoinen et al. 2004, Rubolini et al. 2007), with many migratory populations gradually becoming partial migrants or even residents (Berthold 1998, Sutherland 1998, Coppack & Both 2002, Visser 2009, Morganti 2014). Species that still undertake regular migratory flights have greatly advanced their return to breeding sites in spring (Gatter 1992, Bezzel & Jetz 1995, Winkel & Hudde 1997, Rubolini et al. 2007) and a general advance of the laying date and an increase in clutch size and hatching success have been observed in some species (Järvinen 1989, Abbas, Lichtman & Pober 1994, Winkel & Hudde 1997, Crick & Sparks 1999, Dunn & Winkler 1999, Przybylo, Scheldon & Merilä 2000, Both & Visser 2001, Moss et al. 2001). In addition, widespread contractions and shifts in the wintering ranges of migrant birds have been predicted for the next century according to climate suitability models applied to future climatic scenarios (Barbet-Massin et al. 2009).

Migratory birds are also mobile ecological actors that connect habitats in different parts of the world (Wormworth & Şekercioğlu, 2011). Throughout the year, they cross countries and continents, covering hundreds or even thousands of kilometres, linking different ecosystems. Organisms that have such mobile link functions can have substantial effects on ecosystem functioning and structure (Mills et al. 1993, Hahn et al. 2009), providing a multitude of different functions and playing pivotal roles on ecosystems processes (e.g. pollination, Allen-Wardell et al. 1998, or seed dispersal, Hutchins et al. 1996).

Human-induced global environmental changes that affect migratory birds, therefore, have the potential to alter the functioning of entire ecosystems across different parts of the world. Protecting these species and their environment can potentially ensure the conservation of biodiversity on a wider scale (IUCN 2014). This effort must take into account breeding areas, wintering areas, and stopover sites along migratory flyways, because the loss of any of the sites used by migratory birds during their annual cycle can have a dramatic impact on their chances of survival. However, detailed information on the timing of different phases of the life-cycle, on the precise location of wintering quarters, as well as on migration routes, is lacking for many species of long-distance migrant birds. Indeed, technological tracking devices suitable for small-sized species have become available only recently (Fiedler 2009, Bächler et al. 2010). The use of these devices, however, must be carefully evaluated and planned before undertaking studies on new population or species, because recent researches highlighted that these instruments may negatively affect survival and breeding performances of study subjects (Barron 2010; Costantini & Møller 2013, Scandolara et al. 2014).

The study of the effects of global environmental change on migratory birds could also benefit other species. Many bird species are popular and admired among people and decision-makers, and could therefore be considered flagship species for nature conservation (IUCN 2014). Despite conservation biology aims at the conservation of functional and structural characteristics of ecosystems as a whole, practical interventions are usually directed to the protection of particular species, which are awarded a particular aesthetic, cultural or economic value (Sodhi and Ehrlich 2010).

Subject of this thesis is to evaluate the effects of environmental change on the breeding biology and population dynamics of migratory bird species. Both the effects of habitat modification and climate change have been investigated and, where possible, different phases of the birds' life-cycle have been taken into account. Though the studies reported focused on a few study species, the results obtained could be easily extended to other migratory species.

Structure of the thesis

This thesis consists of two sections, each one consisting of scientific articles that have been produced during these three years of study and that have been published in or are currently submitted to international journals. The papers have been reported so to reflect the original published version as closely as possible. Only minor editorial changes concerning the position of figures and tables, were made while preparing in the present thesis. Some editorial standards have been maintained in the text and in the references, therefore there are format discrepancies between each paper and other parts of the thesis.

Each of the two sections of this thesis is preceded by a brief specific introduction. A general discussion is presented at the end of the two sections and is followed by the references of this general introduction, specific introductions of each section and discussion. The last part of the thesis contains the supplementary materials of the papers included in it, if present.

The first section presents an investigation of the effects of environmental and climatic conditions experienced by two long-distance migratory species, the Barn Swallow (*Hirundo rustica*) and the Common Swift (*Apus apus*), at their breeding quarters in Northern Italy on their population dynamics. In particular we investigate the effect of environmental variables at breeding quarters on colony size and nestlings' quality. The content of these researches has already been published in three different papers in scientific journals.

In the second section we aimed at identifying migration routes and wintering quarters of small-sized birds, and we assessed the effects of environmental conditions experienced during the whole life-cycle on population dynamic, in order to identify the more critical stages. We also evaluated the impact of the application of new tracking devices on small-sized birds on their survival and breeding. Finally, we investigate the possible effects of climate change on migration phenology of individuals from a partial migrant species, the European Robin (*Erithacus rubecula*). This section is composed of five works, three of which has been already published in scientific journals, while two are currently submitted for publication.

Study species

The study of the effects of climate change and habitat loss on a comprehensive number of migratory bird species would be very difficult to achieve, as it would require enormous amounts of time and resources. Therefore, ecological researches on these topics typically focus on some study species, which are chosen because they epitomise particular features of migrant birds and therefore are good representatives of a wide category of species. The results obtained by studying such model species are then usually assumed to be generalizable to other similar species.

The studies reported in this thesis focus on three bird species: the Barn Swallow (*Hirundo rustica*), the Common Swift (*Apus apus*) and the European Robin (*Erithacus rubecula*). These species have been chosen for several reasons.

First, the Barn Swallow and the European Robin belong to the order Passeriformes, which includes more than half of the 10,000 bird species currently identified. Conversely, the Common Swift belongs to the order Apodiformes, which consists of only about 400 species.

All three species are insectivorous, and, consequently are probably sensitive to meteorological conditions and habitat changes during their whole life-cycle, since they affect insect population availability or phenology (see e.g. Thomas et al. 2004, Conrad et al. 2006). This makes insectivorous birds good model species to investigate the effect of climate change and habitat loss.

Finally, these species have already been used in several studies on migratory behaviour and phenology. Indeed, the Barn Swallow and the Common Swift are long-distance migrants, whose totality of individuals migrates every year from Europe to sub-Saharan Africa and back. Spending their life-cycle in parts of the world located thousands of kilometres apart, they are good models to investigate the effects of habitat loss and climate change at different spatial-scales.

The migratory behaviour of the European Robin, instead, makes it a suitable model to investigate phenotypic variation in migratory behaviour among populations. In this species, in fact, migratory behaviour shows a cline according to the geographical position of the breeding range of the population, with the proportion of migrants declining from north-eastern to south-western Europe (Lack 1965, Cramp 1988).

Below is some relevant biological information on each species and further details about the reasons why they were chosen as model species in this thesis.

Barn Swallow (*Hirundo rustica,* Linnaeus 1758)

The Barn Swallow is a small (17-19 cm; wing-span 32-34 cm) passerine bird that breeds throughout the Oloarctic, from subarctic regions to the Mediterranean area, with the exception of the arctic tundra and deserts (Cramp 1998).

This species is an aerial insectivorous that feeds exclusively on insects caught on the wings (Cramp 1998), and it is also a farmland species, which preferably nests in rural buildings. Due to these features, this species has been greatly affected by the changes in agricultural practises that have occurred since the second half of the last century in Europe. These changes have resulted in shifts in land management, from a traditional agricultural mosaic to large-scale homogeneous and intensively cultivated agro-ecosystems, with low biodiversity, and in profound changes in farming practises, which include the remodelling of rural buildings (Donald et al. 2001, 2006). Consequently, food availability and nesting sites have been greatly reduced for this species, threatening different geographical populations among Europe (Møller 1994, Ambrosini et al. 2002, Tuner 2006).

The Barn Swallow is a long-distance migrant, as the large majority of individuals breeding in Europe and northwest Asia migrates to Africa, south of the Sahara (Cramp 1998). This feature probably increases its susceptibility to global change, because several studies have indicated that long-distance migrants are suffering from habitat loss and climate change more than short-distance migrants or resident species (Sanderson et al. 2006, Moller et al. 2008, Both et al. 2010).

It is also a socially monogamous species and breeding pairs lay 1-3 clutches per year; the number of eggs laid per clutch varies from 2 to 7 and is larger in first broods compared to the following ones. Incubation is performed by the female only, but rearing of offspring by both sexes. Nestlings fledge approximately 20 days after hatching (Cramp 1988), but for a few days they return at nest at night, and are still fed by their parents. This species nests exclusively in anthropic environments, mainly in rural areas (but also in some suburban and urban areas), in human-made structures such as barns, cowsheds and old houses. Individuals are also quite confident towards humans, and breeding is minimally disturbed by human presence.

For these reasons, the Barn Swallow has been chosen as model species in several ecological and behavioural studies that have clarified many fundamental aspects of the biology and ecology of this species (see Møller 1994 and Tuner 2006 for a broad discussion on the subject).

Since 1999, our research group has monitored a population of Barn Swallows breeding in Northern Italy, and has collected a large amount of data on its population dynamic and breeding biology. This long-term monitoring has allowed documenting a dramatic demographic decline of this population, which has decreased of more than 50% in the last 15 years (see Section 1). In more recent years, other populations from nearby areas in Northern Italy and Southern Switzerland have been monitored with almost identical methods by other research groups with which we are actively collaborating.

Barn Swallows from these populations have been recently equipped with the most advanced technological devices available so far to study in details the migration of small sized birds, namely light-level geolocators, which take repeated measurements of the ambient light intensity and allow the estimation of the approximate geographical position of the bird at different dates. These instruments have allowed obtaining for the first time a precise knowledge of the position of the wintering quarters of several individuals, as well as information on their timing of migration (see the second and third paper reported in Section 2).

Figure 1: adult male of Barn Swallow

Common Swift (*Apus apus,* Linnaeus 1758)

The Common Swift is a medium-sized (16–17 cm; wing-span 42–48 cm), long-lived migratory species. It is very common in Western Palearctic, from lower and upper middle latitudes to above the Arctic Circle. Like the Barn Swallow, it is a strict aerial insectivorous, and feeds almost exclusively on flying insects and airborne spiders captured in flight (Cramp 1998).

The distribution range and populations size of this species are extremely large and population trend appears to be stable throughout Europe (BirdLife International 2014).

The Common Swift is well known for being highly aerial: except when breeding, in fact, swifts spend their lives in the air and never settle voluntarily to the ground. Both adults and young are particularly sensitive to meteorological conditions, and can survive adverse weather entering a kind of torpor, which involves considerably slowing their metabolism for a few days (Lack 1951, Lyman 2013). Due to these characteristics, this species has been chosen as a model to investigate the effects of meteorological conditions on nestlings' survival and growth patterns (Lack & Lack 1951, Lack 1956, Martins & Wright 1993, Cucco & Malacarne 1996, Martins 1997)

The Common Swift nests on top of flat surfaces, under eaves of buildings or in holes in walls and has a tightly scheduled reproductive season which, in Northern Italy, lasts approximately three months. From the beginning of May, females lay only one clutch of 2-3 eggs per year, which are incubated for 20-22 days. Nestlings are fed by both parents until fledging at approximately 40 days of age, and no post-fledging parental cares are known (Cramp 1998).

All populations are migratory and winter in Africa (Cramp 1998). Recently, individuals from Swedish and British populations (Åkesson 2012, BTO 2012) have been equipped with light-level data loggers. These studies have provided for the first time an accurate knowledge of the main migration routes and the position of wintering quarters of this species.

In this thesis we took advantage of an artificial tower where swifts nest in large number and that allows an easy access to nests to study the effect of ecological conditions of the rearing environment on nestlings' survival and growth (see Section 1).

Figure 2: Common Swift in flight

European Robin (*Erithacus rubecula,* Linnaeus 1758)

The European Robin is a small (14 cm; wing span 20-22 cm) passerine bird that breeds in upper and especially middle latitudes of west Palearctic, from boreal to Mediterranean zones (Cramp 1998).

It is a socially monogamous species and breeding pairs lay clutches of 4-6 eggs. Incubation is performed only by the female for approximately 14 days. Rearing of offspring is performed by both sexes and nestlings fledge about 14 days after hatching (Cramp 1988), but for a few days they return at nest at night, and are still fed by their parents. It is an insectivorous species, which mainly takes its prey on the ground, although during winter it can also feed on seeds and small fruits (Cramp 1998).

The European Robin is currently not suffering demographic declines, as the consistency of its populations appeared to be increasing throughout its distribution range in the last decades (IUCN 2014).

Still, it is a good model species to investigate the effects of climate change on migratory behaviour, particularly as it is a partial migrant species. Indeed, in most populations individuals are short-distance migrants, with females migrating farther than males, but in the north-eastern part of their breeding range individuals are totally migratory, while they are probably largely sedentary in extreme south (Cramp 1998). This characteristic allowed the investigation of phenotypical differences among populations in migration patterns, and of the effects of climate change, which has hypothesized to be a major driver of such differences in migration behaviour.

The widespread presence of individuals of this species in Europe, has allowed the collection of about 150.000 ring recoveries over the last 70 years, which are stored in the EURING Data Bank. We used these data to investigate the effects of climate change on the migratory behaviour of the different geographical populations of this species at continental scale (see Section 2).

Figure 3: European Robin

Section 1

Introduction to section 1

This section reports three studies on the effects of habitat modification and environmental conditions in the breeding quarters on the demographic trends and breeding performances of two species of long-distance migrants, the Barn Swallow and the Common Swift.

Changes in the environmental conditions experienced by birds during the breeding season are expected to deeply influence their population dynamics because they can potentially affect several traits of their life-histories.

First, environmental conditions can affect population dynamics impacting on the survival of individuals, particularly at arrival from spring migration and at the end of the breeding season, when they approach the departure for African wintering quarters. Indeed, at arrivals to the breeding quarters, individuals have usually to recover from the long migration journey, and a favourable environment can enable them to restore better physiological conditions, which, in turn, can enhance their survival prospects and also allow a greater allocation of resources to breeding (Pilastro & Magnani 1997, Newton 2008). Furthermore, it has been demonstrated that rain and temperature at the breeding sites can affect departure decisions for wintering areas in migratory birds (Alerstam.& Lindström, 1990 Åkesson et al. 2001, Åkesson et al. 2002, Liechti et al. 2014). This timing may impact on the environmental conditions experienced by birds during migration which, in turn, may influence their chances of successfully reaching the wintering quarters (Berthold 2001, Newton 2008).

Environmental conditions are also strongly related to reproductive performances of individuals and, ultimately, to the total reproductive output at population level. For example, the length of the breeding season, which affects the number of clutches laid every year in multivoltine species, the proportion of pairs laying multiple clutches, as well as clutch and brood size, can strongly depend on weather conditions (Lack 1968, Verhulst et al. 1995, Hansson, Bensch & Hasselquist 2000). Finally, the environment experienced during the breeding season may impact population dynamics affecting the recruitment of young. Indeed, ecological conditions that nestlings experience in the first weeks after hatching may influence their phenotypic quality, their survival until fledging and their physical conditions when leaving for Africa (Perrins 1965, Richner 1989, Koskela 1998). All these factors affect their probability to be recruited later in the reproductive population.

Ecological conditions can vary at different spatial and temporal scales, ranging from e.g. climate change, which is occurring at global level, to e.g. local meteorological conditions or general habitat characteristics of the breeding sites, which can affect a rather small number of individuals and usually occur over short periods of time. In addition, reproductive performances and survival of individuals can be affected by specific variation in habitat conditions at their nesting sites (see e.g. Bryant 1978, Thessing 2000, Ambrosini & Saino 2010). The simultaneous action of all these factors can potentially produce a large impact on the dynamic of entire populations.

Given the current rate of change in climatic and habitat conditions that are occurring at the European breeding quarters of many species (Thomas et al. 2004, IPCC2013) these two factors are expected to deeply influence the population dynamics of migratory birds.

The three papers reported in the first section of this thesis aimed at investigating the effect of habitat modifications and meteorological conditions experienced at breeding quarters on the population dynamic and breeding performances of long-distance migratory birds. In the first and second paper we documented the negative effects of habitat modification on the population dynamic of Barn Swallows breeding in Northern Italy. In the third paper we investigated the effect of ecological conditions experienced by Common Swift nestlings during the first phases of life on their survival and growth.

Maintenance of livestock farming may buffer population decline of the Barn Swallow *Hirundo rustica*

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Roberto Ambrosini[1], Diego Rubolini[2], Paola Trovò[3], Giovanni Liberini[3], Marco Bandini[3], Andrea Romano[2], **Beatrice Sicurella[1]**, Chiara Scandolara[2], Maria Romano[2], Nicola Saino[2]

1. Dipartimento di Biotecnologie e Bioscienze, Università degli Studi di Milano Bicocca, Piazza della Scienza, 2 I-20126 Milano, Italy

2. Dipartimento di Bioscienze, Università degli Studi di Milano, Via Celoria, 26, I-20133 Milano, Italy.

3. Ente di gestione delle aree protette del Ticino e del Lago Maggiore, Villa Picchetta, I-28062 Cameri (NO), Italy.

Summary

Populations of farmland and long-distance migratory birds have suffered steep, often dramatic, declines in the last few decades. The Barn Swallow *Hirundo rustica* is a small migratory farmland bird that breeds synanthropically in farms, particularly where livestock is reared. Populations of this species have suffered marked declines in different parts of its European breeding range. Here, we first report a dramatic decline of 8.4% per year of the number of breeding pairs and the extinction of 19.6% of the colonies in three agricultural areas in Northern Italy, which differ in general ecological conditions. This decline was estimated on a very large sample of 190 randomly chosen farms where breeding pairs were censused both in 2001 and 2010, and occurred at different rate in the three study areas. Barn Swallows declined most (9.3% per year) in an intensively cultivated area where colonies are widespread, and least (1.3% per year) in a hilly area with a comparatively small density of colonies. Variation in livestock farming significantly influenced population dynamics. Specifically, cessation of livestock farming at a given farm between the two census years resulted in a significantly steeper decline in the number of breeding pairs compared to farms where livestock farming was maintained. Our findings highlight that European populations of Barn Swallows breeding in intensively cultivated agro-ecosystems may become significantly depleted in the next decades, and indicate that maintenance of livestock farming may contribute to buffer the population decline of this species.

Introduction

The populations of several bird species breeding in Europe have undergone marked, mostly negative, demographic changes during the last decades

(Tucker and Heath 1994, BirdLife International 2004, Donald *et al.* 2006). The sign and steepness of these trends, however, are distributed non-randomly among taxa and according to species' ecology and life-histories, as susceptibility to decline is associated with specific habitat preferences and major life-history traits such as e.g. migratory behaviour (Sanderson *et al.* 2006, Møller *et al.* 2008, Both *et al.* 2010).

Birds breeding in farmland have suffered steeper decline than forest or aquatic species, partly because of the direct impact of the changes in agricultural practices that took place in the course of the second half of the twentieth century. These changes have resulted in a rapid shift from the traditional agricultural mosaic that characterised farmland habitats for centuries, to a large-scale, homogeneous, intensively cultivated agro-ecosystem, with low biodiversity (Chamberlain *et al.* 2000, Chamberlain and Fuller 2001, Donald *et al.* 2001, 2006). For example, it has been shown that population trends of farmland birds negatively covaried with cereal yield across European countries (Donald *et al.* 2001), suggesting that agricultural intensification, determining large-scale shifts in land management, may be causally related to farmland bird decline (Chamberlain *et al.* 2000).

Long-distance trans-Saharan migratory birds have declined more than short-distance migrants and residents (Sanderson *et al.* 2006, Møller *et al.* 2008, Both *et al.* 2010). This can have several concomitant causes. The varying rate of change in ecological conditions occurring in the areas where birds spend different parts of their annual life-cycle may result in an ecological mismatch of species that are not able to track the optimal conditions for reproduction under a changing climate (Both and Visser 2001, Both *et al.* 2006, Ambrosini *et al.* 2011, Saino *et al.* 2011). Rapid changes in the ecological conditions of African wintering or stopover habitats may also negatively affect migrant survival and population trends (Sanderson *et al.* 2006, Zwarts *et al.* 2009). In particular, it has been observed that most declining species winter in open-dry habitats in Africa (Sanderson *et al.* 2006), probably due to increasing habitat degradation and loss within African drylands, such as the Sahel region, a major wintering and staging area for Afro-Palearctic migrants (Zwarts *et al.* 2009).

The Barn Swallow *Hirundo rustica* epitomises some of the risk factors that have been shown to predict demographic decline in comparative studies. It is a long-distance migrant that overwinters in open habitats south of the Sahara Desert (Cramp 1988, Møller 1994, Turner 2006). It is also a farmland bird, foraging mainly on open hayfields and pastures, and along hedgerows. In addition, it is strictly associated to traditional rural buildings for nesting. In fact, since breeding takes place most often in cowsheds and stables with cattle and horses, it can be markedly affected by rapid changes in livestock farming practices that have widely occurred in Europe during recent decades, resulting in the progressive abandonment of traditional cattle sheds in favour of modern, intensive sheds that are less suitable for Barn Swallow nesting (Møller 1994, 2001, Ambrosini *et al.* 2002, Turner 2006).

Barn Swallows breeding in farms where livestock is reared have larger reproductive success than those breeding in farms without it (Grüebler *et al.* 2010). This probably occurred as Barn Swallows benefit from warmer indoor temperatures when they nest in buildings with livestock (Ambrosini and Saino 2010). Warmer temperatures in turn allow for earlier reproduction and a larger number of pairs laying a second clutch (Grüebler *et al.* 2010). In addition, presence of livestock at a farm is usually correlated with larger food availability for the insectivorous Barn Swallow, both because manure enhances insect production, and because hayfields and pastures, which are the preferred foraging habitat of this species, are larger around farms with livestock (Møller 2001, Ambrosini *et al.* 2002, Evans *et al.* 2007, Grüebler *et al.* 2010). All these benefits result in an overall larger nestling survival in farms with livestock, particularly of second broods (Grüebler *et al.* 2010), and may explain the strong preference of nesting Barn Swallows for cowsheds, stables and, in general, for buildings where livestock is reared (Ambrosini and Saino 2010, Grüebler *et al.* 2010). Cessation of livestock farming at a farm may therefore result in lower reproductive success (Grüebler *et al.* 2010) and fewer yearlings recruited to the colony (Møller 2001).

The Barn Swallow has declined in several parts of its European range, but the extent of this decline varies widely across geographical areas (Møller 1989, Tucker and Heath 1994, Siriwardena *et al.* 1998, Robinson *et al.* 2003, BirdLife International 2004, PECBMS 2009). Several mechanisms operating in different parts of the annual life-cycle and thus in different geographical regions have been invoked as causes of the decline. Agricultural intensification and cessation of livestock farming at a farm may determine the decline of the local colony (Møller 2001, Ambrosini *et al.* 2002), whereas habitat degradation and loss on the breeding and the wintering grounds, or along migration routes probably act synergistically to determine the general decline of Barn Swallow populations (Saino *et al.* 2004, Robinson *et al.* 2008).

In the present study we first report on the population dynamics of Barn Swallows breeding in three agricultural areas in Northern Italy, which differ in general ecological conditions, such as altitude, major land use, and farming intensity, based on a very large sample of 190 farms where breeding pairs have been censused both in 2001 and 2010. Then, we analyse the effect of animal farming on local population trends to test the prediction that cessation of animal farming during the study period resulted in more negative population trends compared to conditions where animal farming did not change (i.e. it was present or absent both at the start and the end of the study period). By comparing population changes taking place at each of the three study areas, we could also explore whether the effects of animal farming differed according to general ecological conditions of the area where colonies were located.

Methods

Study areas and field methods

The study was carried out in Northern Italy, specifically in the Parco Regionale Adda Sud ('AS' hereafter, coordinates of the approximate centre: 45°19' N, 9°40' E, surface: 24.260), in the Parco Piemontese della Valle del Ticino ('TP', 45°33' N, 8°44' E, 6.561 ha), and in the Parco Regionale di Montevecchia e della Valle del Curone ('MC', 45°42' N, 9°22' E, 2.350 ha) (Figure 1). Maize fields (44%) and hayfields (32%), i.e. fields where grass or alfalfa *Medicago sativa* are not grazed but cut to produce dry feed for livestock during the winter, are the prevalent crop types in AS, which is located in the low Po Plain of Lombardy (height of monitored farms: 40-108 m a.s.l.). Woods (37%) and hayfields (25%) prevail in TP, which is in the high Po Plain in Piedmont (height of monitored farms: 99-281 m a.s.l.). MC is a hilly area (height of monitored farms: 258-442 m a.s.l.) in Lombardy where coppices (38%) and hayfields (24%) are the predominant land uses.

The size of farms, as estimated during the 2010 census and expressed as the overall area of cowsheds, stables, barns and other buildings that are accessible to Barn Swallows at each farm (see below for a definition of 'farm'), was much larger in AS (on average 3053.3 ± 288.5 SE m^2, $N = 110$) than in the other study areas (TP: 1000.8 ± 195.0 SE m^2, $N = 50$; MC: 238.1 ± 45.5 SE m^2, $N = 49$). Conversely, farm density is larger in MC (3.4 farms km^{-2}) than in AS (1.3 farms km^{-2}) or in TP (1.2 farms km^{-2}), as estimated by a complete census of all farms at each study area performed by means of detailed maps (scale 1:10,000), aerial photos, and Google Earth (Mountain View, CA).

As sample units we used groups of rural buildings (hereafter 'farms') that were separated by at least 100 m from other groups of buildings (Ambrosini *et al.* 2002).

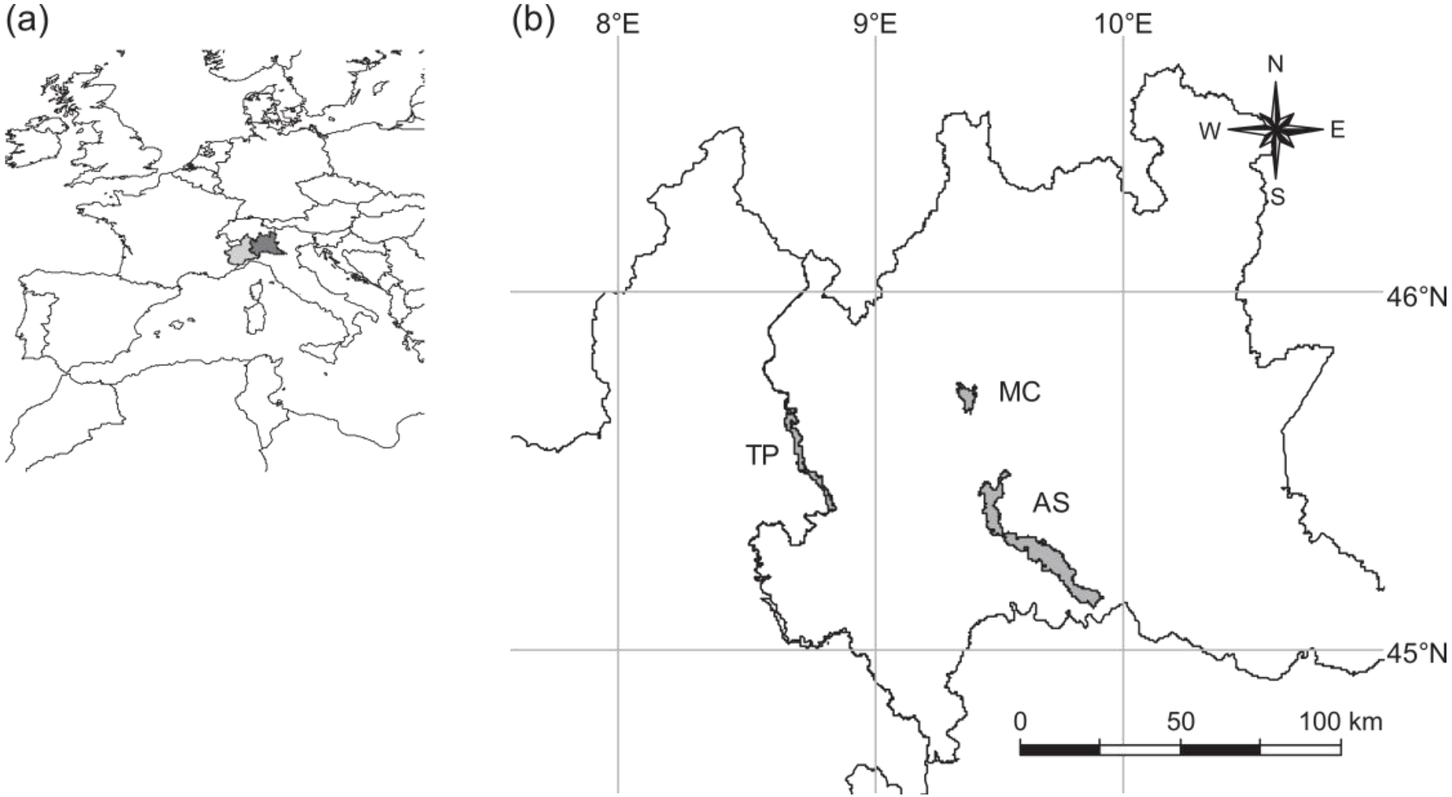
Albeit most buildings were originally farms, their use at the time of the censuses could have changed to e.g. houses, restaurants, or farm holiday centres. In AS, a long-term monitoring project of Barn Swallow populations is ongoing since 1999 in a random sample of the farms in the Park or in the surrounding area (see Ambrosini *et al.* 2002 for details). In this study area 108 farms were monitored both in 2001 and 2010 and 94 in all years in 1999-2010. In TP 56 farms within the boundaries of the Park or in the surrounding area were monitored both in 2001 and 2010. The other farms in this study area could not be censused due to inaccessibility or unwillingness of farm owners. For the same reasons, in 2010 we could not obtain reliable estimates of colony size at three farms in TP (though we could confirm that breeding took place). These farms were therefore excluded from the analyses of demographic trends and colony size, but not from those of colony extinction probability. In MC 26 randomly chosen farms were monitored both in 2001 and 2010.

In 2010 all farms at each study area were monitored according to a standardised protocol reported in detail in Ambrosini *et al.* (2002). Briefly, each farm was visited every 14 days and the content of all nests inspected. The number of pairs at a farm was then estimated as the maximum number of nests simultaneously active (i.e. with eggs or nestlings) during April-June. In 2001 farms in AS were monitored according to the same protocol as above, while farms in TP and in MC were visited monthly and all nests inspected. Colony size was estimated as above.

Data about presence of livestock at each farm were collected during the visits to the farms in each year in AS. In TP and in MC livestock data for 2010 were collected during the visits to the farms, while those for 2001 were obtained by interviewing the farmers (Ambrosini *et al.* 2002). This information was summarized in a dichotomous variable ('livestock farming') accounting for presence or absence of livestock in a farm in a given year. In addition, for each farm a three-level categorical variable ('livestock category') was generated, accounting for the presence of livestock in a farm both in 2001 and 2010 ('Present'), in none of the two years ('Absent'), or only in 2001 ('Ceased'). Three farms in AS and three in TP where livestock was reared in 2010 but not in 2001 were discarded from the analyses where this latter variable was entered as predictor.

Statistical analyses

Estimates of E from the sample of AS farms monitored in 2001 and 2010 were within the 95% confidence limits of the same parameters calculated on the AS farms sampled each year during 1999-2010 (E = 0.011, 95% CL: 0.005; 0.017; see Table 1 for estimates for 2001 and 2010).


(a)
(b)
8°E
9°E
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AS
45°N
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50
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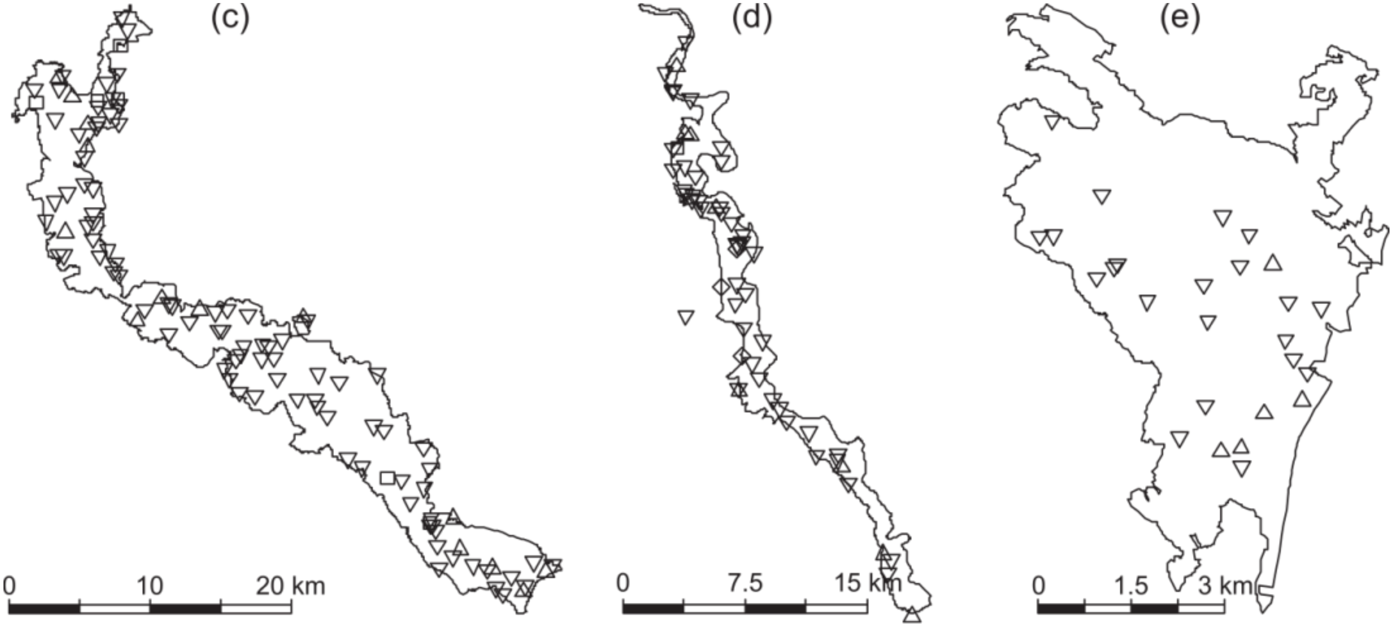

Parco Regionale Adda Sud (AS)

Parco Piemontese della Valle del Ticino (TP)

Parco Regionale di Montevecchia e della Valle del Curone (MC)

Figure 1: (a) Lombardy (dark grey) and Piedmont (light grey) in Italy and Europe. (b) The study areas in Lombardy and Piedmont: TP: Parco Piemontese della Valle del Ticino, MC: Parco Regionale di Montevecchia e della Valle del Curone, AS: Parco Regionale Adda Sud. (c-e) The monitored farms within each study area. Symbols represent the demographic trend of colonies between 2001 and 2010: Circles: farms with no Barn Swallows in both years; squares: farms with constant demographic trend, upper triangles: farms with increasing populations; lower triangles: farms with decreasing populations; diamonds: farms where only presence-absence data were available.

The value of r estimated from farms monitored in 2001 and 2010 was slightly lower than that estimated from farms monitored each year during 1999-2010 (r = -0.063, 95% CL: -0.092, -0.034). There was also no evidence of significant deviation from linearity of demographic trends estimated from Poisson regressions of annual censuses (significance of the quadratic term of year: $|t|_9 \leq 1.0$, $P \geq 0.34$ in both cases). Hence, the analysis of data from 2001 and 2010 returned estimates of decline rates and extinction risk of colonies similar to those obtained by annual censuses. We therefore focused on parameter estimates obtained by the comparison of data collected in 2001 and 2010, as these data were available for all the study areas.

Decline rates were then compared among study areas and livestock categories in Generalized Linear Models (GLM) or in Generalized Least Squares (GLS) models when variances were heterogeneous between study areas or cattle categories (Zuur *et al.* 2009). Colony extinction was coded as a dichotomous variable equal to 1 if a colony that existed in 2001 was extinct in 2010, and to 0 otherwise. This variable was then analysed in binomial GLMs to investigate whether the probability of colony extinction differed between study areas and cattle categories. Post-hoc tests (Tukey method) were also performed. We notice that the calculation of decline rates of populations allows to easily compare demographic trends calculated in all years in 1999-2010 and in years 2001 and 2010.

In order to investigate in details the effect of livestock farming on the number of breeding Barn Swallow pairs per farm, and the effect of change in livestock farming on population trends and extinction probability, we used Generalized Linear Mixed Models (GLMMs). A Poisson error distribution was assumed in the models of number of breeding swallows at farms, a binomial error distribution in models of colony extinction and a Gaussian error distribution in models of population trend.

Year (2001 or 2010, entered as a dichotomous variable) was included as a fixed effect in the GLMMs of the number of breeding pairs at each study area. In developing these models, we first investigated the most proper structure of their random part. According to Zuur *et al.* (2009), we initially included year as a random slope at the farm level, and checked whether this improved the fit of the model. In all cases, random slope models fitted the data better than models only including farm as a random factor (likelihood ratio tests (LRT): $\chi^2_2 \geq 12.3$, $P \leq 0.002$). Inclusion of year as a random slope at the farm level allows the models to control for the between-farm variation in growth rates, and avoids inflating type-I error rate (Schielzeth and Forstmeier 2009). However, inclusion of random slopes enlarges the number of random parameters that must be estimated by the models. In our GLMMs, in particular, the number of random parameters was twice the number of farms (one intercept and one slope per farm), thus equalling the total number of available observations (two years of data per farm). Hence, the inclusion of a random slope in a model where only two years of data were available per farm saturated the number of random effects that could be entered in the model, as it is not possible to estimate a number of random effects larger than the number of observations. This prevented extending the GLMM to analyse the effect of livestock farming on colony size at all study areas simultaneously. Indeed, a model of this kind would have required entering study area as an additional random factor. To obtain an overall test of the effect of livestock farming and year on the number of breeding pairs at all study areas, we therefore had to rely on a different approach, whereby we summarized the results from models for each study area by the weighted *Z*-method, a procedure that allows combining information across multiple tests of the same null hypothesis (Whitlock 2005).

Conversely, we used GLMMs with study area entered as a random factor and assuming a Gaussian or a binomial error distribution, to investigate the effect of livestock category on population trend or colony extinction probability, respectively, at all study areas. Since 'livestock category' seemed to differently affect decline rates and extinction probabilities in different study areas, we first included in the GLMMs this factor as a random slope within study area, besides as a fixed effect (Schielzeth and Forstmeier 2009). However, in all cases, models with a simpler random structure, only including the study area as a random factor, had a similar fit than random slope models (LRTs: $\chi^2_5 \leq 4.51$, $P \geq 0.48$), and were therefore preferred. Since models were underdispersed (dispersion parameter ≤ 0.70), we conservatively did not correct for overdispersion in the Poisson and binomial GLMMs (Zuur *et al.* 2009).

We used R 2.8.1 (R Development Core Team 2008) for statistical analyses, with the *nlme* procedure (Pinheiro *et al.* 2008) for GLS and Gaussian mixed models, the *lme4* procedure (Bates *et al.* 2008) for Poisson and binomial GLMMs, and the *multcomp* procedure (Bretz *et al.* 2001) for post-hoc tests.

Results

Demographic trends in the three study areas

Decline rates and extinction probabilities calculated for the three study areas by comparing the number of breeding pairs and the number of colonies recorded in 2001 and 2010 are shown in Table 1. Combining the data from the three study areas it appeared that the size of the breeding population declined by 53.1% (i.e. by 8.4% per year), and the number of colonies by 19.6%, between 2001 and 2010.

The decline rate of the breeding pairs in the colonies that existed both in 2001 and 2010 significantly differed between study areas (GLS model for inequality of variances: $F_{2,104} = 3.15$, $P < 0.001$), with a significant difference between AS and MC, while decline rates in the other comparisons were similar (Figure 2a; details not shown).

Study area also significantly explained variation in the probability of colony extinction (binomial GLM: $\chi^2_2 = 10.7$, $P = 0.005$), that was significantly higher in MC than in AS. No other significant difference was observed (Figure 2b).

Livestock farming and colony size and presence

The mean number of breeding pairs per farm was significantly larger in farms with than without livestock both in AS and TP, but not in MC (Table 2). The decline in the number of breeding pairs, that was statistically significant in all study areas (Table 2), occurred at a similar rate in farms with and without livestock, as indicated by the fact that the livestock by year interaction was never significant and was therefore removed from all models (AS: -0.43 ± 0.32 SE, $z = 1.33$, $P = 0.185$; TP: 0.57 ± 0.51, $z = 1.1$, $P = 0.27$; MC: 0.61 ± 0.77 SE, $z = 0.80$, $P = 0.43$). These findings were confirmed by pooling results from the three study areas (effect of livestock: $Z_w = -8.700$, $P < 0.001$; effect of census year: $Z_w = -7.928$, $P < 0.001$).

Livestock farming and demographic trends

Comparison of the decline rates of colonies in the farms censused both in 2001 and 2010 showed significant differences according to livestock category in TP ($F_{2,21} = 6.70$, $P = 0.006$), with colonies on farms where livestock farming ceased declining more than those in the other livestock categories (post-hoc test: $|t|_{21} \geq 2.84$, $P \leq 0.025$, Figure 3a). Marginally non-significant differences were found in AS ($F_{2,67} = 2.79$, $P = 0.068$), and MC (GLS model for inequality of variances: $F_{2,6} = 4.93$, $P = 0.054$). The mixed model analysis combining data from the three study areas revealed a significant variation of the decline rates according to livestock category ($F_{2,98} = 6.90$, $P = 0.001$). Specifically, Barn Swallow colonies in farms where livestock farming ceased were estimated to decline significantly more than in farms where livestock was always or never reared ($|z| \geq 3.29$, $P \leq 0.003$; Figure 4a).

Probability of colony extinction varied according to livestock category in AS (LRT: $\chi^2_2 = 14.8$, $P < 0.001$) and in TP (LRT: $\chi^2_2 = 7.9$, $P = 0.020$, Figure 3b), being significantly smaller in farms where livestock was reared in both years than in farms where livestock was always absent ($|z| \geq 2.40$, $P \leq 0.043$). No significant difference in the probability of colony extinction between farms in different livestock categories appeared in MC (LRT: $\chi^2_2 = 1.9$, $P = 0.383$).

The mixed model analysis of data from the three study areas revealed a highly significant difference in colony extinction probability between farms in different livestock categories (LRT: $\chi^2_2 = 25.1$, $P < 0.001$), with colonies on farms where livestock was reared in both years showing a significantly smaller estimated extinction probability than that of farms where livestock was never reared and where it ceased between 2001 and 2010 (Figure 4b).

Table 1. Summary statistics of demographic trends recorded in the different study areas. *N* is the number of censused farms; *E* is the annual extinction probability; *r* is the annual population growth rate. Numbers in brackets represent standard errors. Estimates of total population sizes were obtained by the ratio estimator, and their standard errors were corrected for small populations.

Study area	**n**	**number of colonies**			**mean number of breeding pairs per farm (SE)**			**estimated total population size (SE)**	
		2001	2010	*E*	2001	2010	*r*	2001	2010
AS	108	83	73	0.014	0.95 (1.33)	4.76 (0.66)	-0.093	3493 (117)	1518 (58)
TP	56	37	29	0.027	7.57 (1.45)*	3.89 (0.79)*	-0.074	575 (42)	296 (23)
MC	26	18	9	0.077	2.08 (0.46)	1.85 (0.64)	-0.013	166 (10)	148 (14)

* N = 53 farm

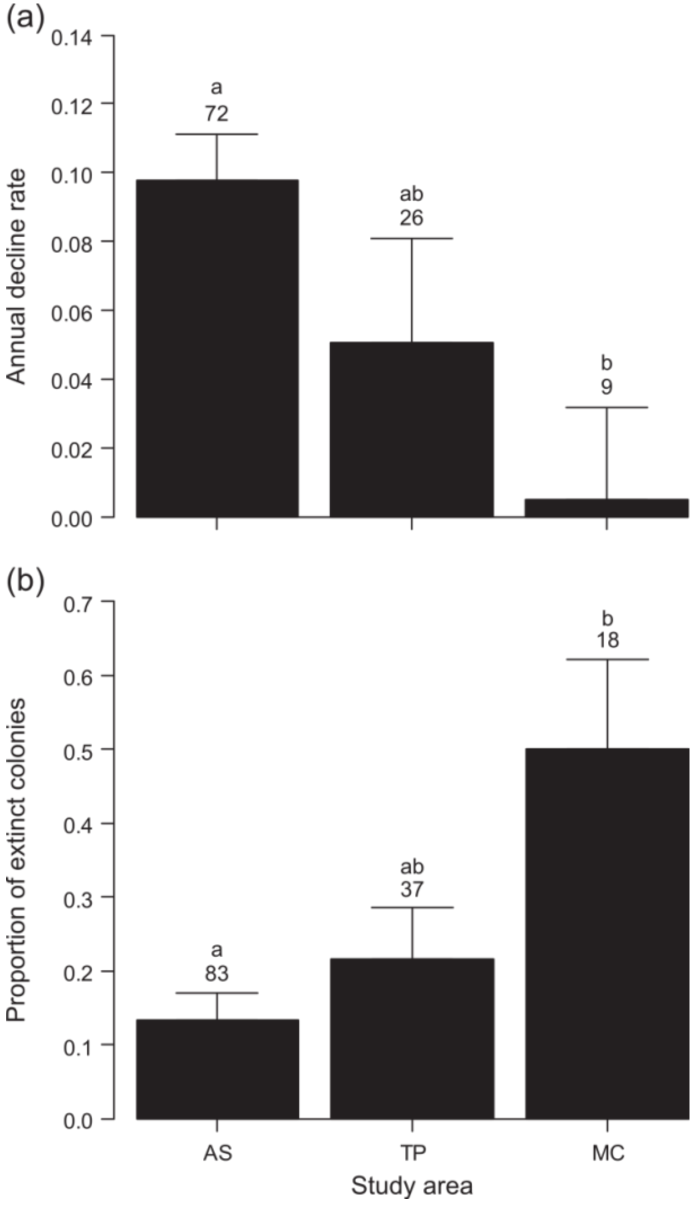

Figure 2. (a) Average annual decline rates (-*r* parameters in a population growth model) of Barn Swallow colonies and (b) proportion of colonies that went extinct between 2001 and 2010 in the Parco Regionale Adda Sud (AS), Parco Piemontese della Valle del Ticino (TP), Parco Regionale di Montevecchia e della Valle del Curone (MC). Bars represent standard errors. Numbers represent sample sizes. Bars with different letters indicate significant ($P < 0.05$) differences between study areas at post-hoc tests.

The difference in the probability of colony extinction between farms where livestock farming ceased and where livestock has never been reared was marginally non-significant (post-hoc test: $z = -1.85$, $P = 0.064$). Addition of colony size in 2001 as a covariate did not affect the results (LRT of livestock category: $\chi^2_2 = 15.8$, $P < 0.001$) and revealed that initially large colonies had a smaller extinction probability compared to small ones (coefficient: -0.170 ± 0.058 SE; LRT: $\chi^2_1 = 15.1$, $P < 0.001$). No interaction effect between livestock category and colony size in 2001 was observed (LRT of interaction: $\chi^2_2 = 4.29$, $P = 0.12$).

Table 2. Fixed effects from Poisson GLMMs of the number of breeding pairs per farm according to presence of livestock farming and census year. The livestock per year interaction was never significant (all $P \geq 0.185$), and was therefore removed from the models. In all models farm was entered as a random factor and year as a by-farm random slope.

Effect	**Coef.**	**SE**	***z***	***P***
Parco Regionale Adda Sud				
Intercept	0.270	0.240	1.12	0.261
Livestock	1.676	0.253	6.62	< 0.001
Year	-0.889	0.125	-7.09	< 0.001
Parco Piemontese della Valle del Ticino				
Intercept	-0.476	0.289	-1.64	0.100
Livestock	2.613	0.334	7.83	< 0.001
Year	-0.551	0.226	-2.44	0.015
Parco Regionale di Montevecchia e della Valle del Curone				
Intercept	0.200	0.312	0.64	0.521
Livestock	0.023	0.390	0.06	0.954
Year	-1.897	0.452	-4.20	< 0.001

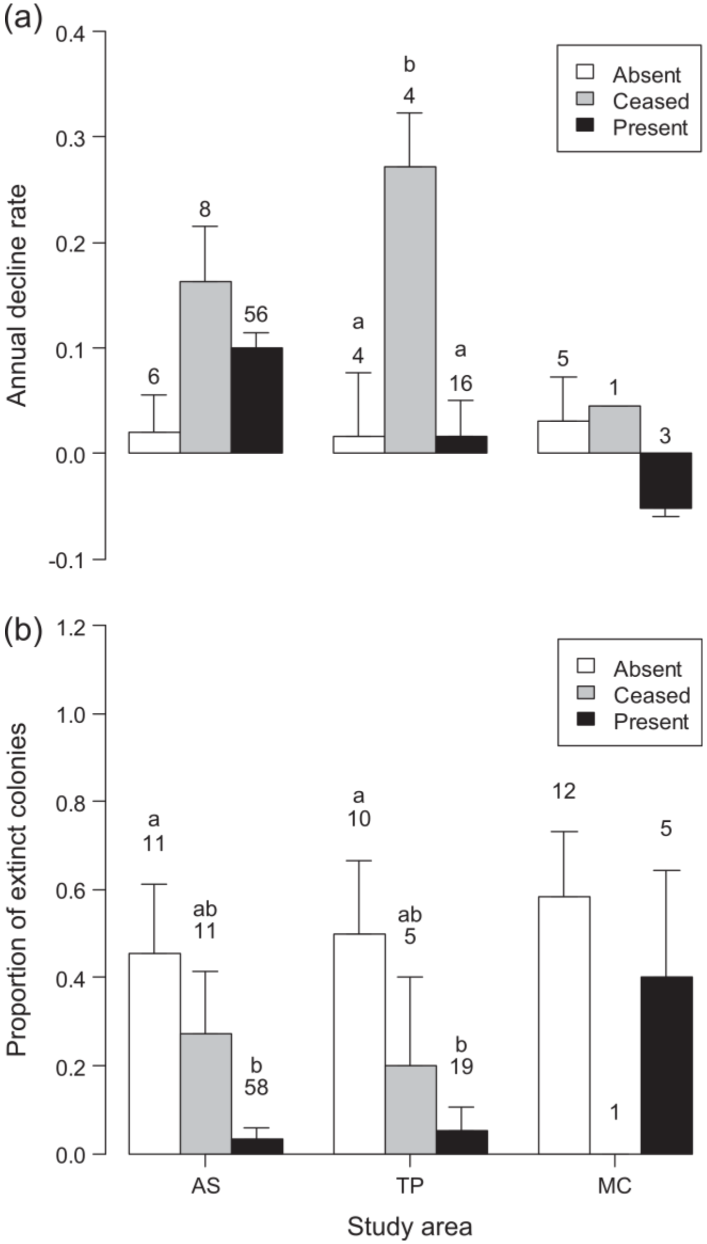

Figure 3: (a) Annual decline rates (-*r* parameter in a population growth model) of Barn Swallow colonies and (b) proportion of colonies that went extinct between 2001 and 2010 in the three livestock categories within each study area. Bars represent standard errors and numbers sample sizes. Bars with different letters indicate significant ($P < 0.05$) differences between the livestock categories within each study area at post-hoc tests.

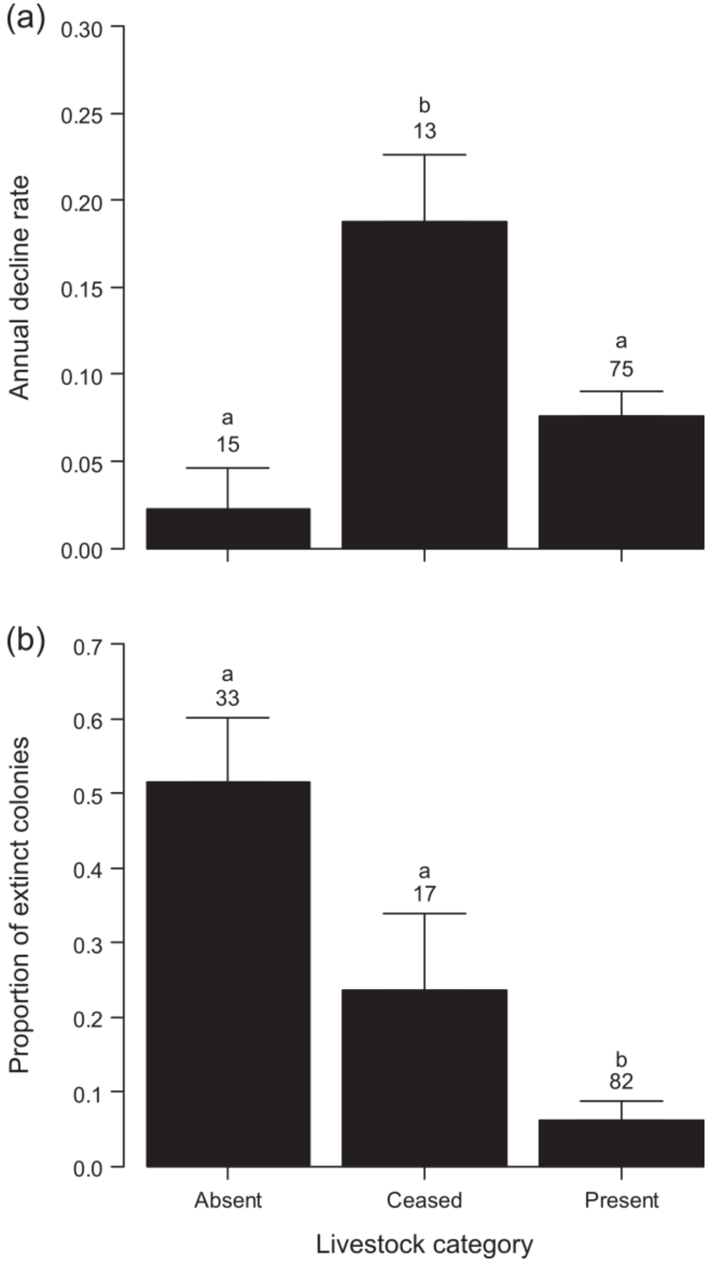

Figure 4. (a) Annual decline rates (-*r* parameter in a population growth model) of Barn Swallow colonies and (b) proportion of colonies that went extinct between 2001 and 2010 in farms in different cattle categories in the three study areas. Bars represent standard errors and numbers sample sizes. Bars with different letters indicate significant ($P < 0.05$) differences between cattle categories at post-hoc tests.

Discussion

In this study we gathered current (2010) and historical (2001) information on the size of breeding Barn Swallow populations in a very large sample of 190 farms in three study areas in Northern Italy where general ecological conditions differ. We also collected detailed information on colony size in each year between 1999 and 2010 in 94 farms in one study area, and we could therefore assess that demographic trends calculated on the basis of data from 2001 and 2010 reliably reflect those from annual censuses.

We documented a dramatic decline in the Barn Swallow population (8.4% per year), larger than that reported for the entire Lombardy (4.3% per year) by Bani *et al.* (2009) by means of point counts, and much larger than the 9% estimated for Europe by the European Bird Census Council in the period 1990-2006, corresponding to an annual decline of 1% (EBCC 2008, PECBMS 2009). This decline is however similar to that documented in a Danish population during 1970–1999 (7.6% per year), for which time to extinction was estimated in 22 years by means of stochastic population models (Engen *et al.* 2001). Differences in demographic trends among Barn Swallow populations breeding in different parts of Europe are probably due to differences in farming practices (and in their change over time) between European regions (Báldi and Batáry 2011). In addition, geographical populations of Barn Swallow segregate in different African regions during winter (Ambrosini *et al.* 2009, 2011), and therefore may be affected differently by changes in ecological conditions at their wintering grounds.

Barn Swallow populations are known to show large fluctuations at decadal scales (Siriwardena *et al.* 1998, Robinson *et al.* 2003). However, the decline of this population seems almost continuous during the 10 study years, at least in the AS, as indicated by the fact that overall population trend in the sample of farms that were monitored in all years did not deviate from linearity (see Methods). In addition, the observed decline seems, unfortunately, to reflect the steep negative demographic trend of this species in the Po plain that took place in previous years. Indeed, Selmi and Checchi (2001) reported a decline of 54.6% in the number of Barn Swallow pairs breeding in the municipality of Spilamberto (Modena province) between 1990 and 1999. This information therefore suggests that Barn Swallows in Northern Italy may have declined to one quarter of their initial population size during the last 20 years.

Barn Swallows seem to have declined at different rates in the three study areas. Before further discussing these results, two main caveats deserve consideration. First, the number of farms that were censused both in 2001 and 2010 was much lower in MC than in the other study areas. The non-significant results in the analysis comparing population size and trend at farms in different cattle categories in MC may therefore be due to the low power of statistical tests. Second, sampling protocols in 2001 (but not in 2010) differed among study areas, as farms in TP and MC were visited monthly in that year, while farms in AS every second week. We checked whether different sampling rates may have biased our estimates of colony sizes in 2001 and, consequently, of decline rates. To this end, we-assessed the number of breeding pairs at 20 randomly chosen farms in AS in 2001 *as if* we had sampled them once in a month, rather than every second week. This was simply done by considering only the data collected on each second visit at a farm. Halving the sampling rate implied a reduction of estimated decline rate at a colony by only 0.005, i.e. one order of magnitude lower than the significant difference in decline rates between AS and MC (0.09 ± 0.03 SE, Figure 2). Hence, we are confident that difference in sampling rates in different areas did not bias our general conclusions.

The decline was steeper in AS, an intensively cultivated area in the low Po plain where mean colony size was the largest, and lower in MC, a hilly area the hosted the smallest colonies, being intermediate in TP, an intensively cultivated area in the high Po plain, where mean colony size is also intermediate. Intensification of farming practices, which have been invoked to explain negative trends of Barn Swallow populations in Switzerland (Grüebler *et al.* 2010), may have occurred at different rates in the three study areas, and may therefore explain the observed differences in decline rates. Indeed AS and TP, where swallows declined the most, are more intensively cultivated than MC. However, colony extinctions have occurred at a lower rate in AS and in TP than in MC, probably due to the larger average size of colonies in the former study areas. In addition, in MC half of the colonies went extinct between 2001 and 2010, probably because several farms were remodelled in these years (R. Ambrosini, pers. obs.), and therefore have probably become unsuitable for Barn Swallow reproduction. MC may therefore be an area where Barn Swallows breed at low densities due to reduced breeding-sites availability. Farms are smaller in this study area compared to the others, and farm density is higher. In addition, climate and general ecological conditions in this hilly area differ from in the other intensively cultivated study areas on the plain. Habitats in MC may therefore be sub-optimal for this species, as suggested by the observation that in 2010 farms in MC hosted an average number of breeding pairs (1.18 ± 0.37 SE) similar to that of farms without livestock in the other study areas (AS: 1.70 ± 0.43; TP: 0.82 ± 0.34).

Presence of livestock farming at a farm positively influenced the size of Barn Swallow colonies, as expected (e.g. Møller 1994, 2001, Ambrosini *et al.* 2002, Turner 2006), in AS and TP, and in the analyses combining the results at the three study areas, but not in MC. This lack of association between livestock farming and Barn Swallow distribution at this area is difficult to explain, and may again be related to the different general ecological conditions in this area. Alternatively, it may simply be the by-product of the low power of statistical tests due to the small sample of farms at this study area.

The strong positive association between swallows and livestock explains the large negative impact that cessation of livestock farming had on their breeding populations. Indeed, colonies in the farms where livestock farming ceased declined more steeply than those in farms where livestock was always or never reared. This result is consistent with previous studies carried out in Denmark (Møller 2001), which demonstrated that cessation of livestock farming determined a lower recruitment of yearlings, leading to a rapid decline of the colony (Møller 2001). In addition, presence of livestock in the same room of the nest favours Barn Swallow reproduction (Ambrosini *et al.* 2006, Ambrosini and Saino 2010, Grüebler *et al.* 2010). However, the number of farms with livestock declined by approximately 10% between 2001 and 2010 in all three study areas (AS: 10.8%. TP: 9.09%, MC: 10.0%), so the observed variation in the decline rate of populations between these areas could not be explained by differential variation in farming practices.

Probability of colony extinction also differed among livestock categories, being largest in farms that never hosted livestock, intermediate in farms where livestock farming ceased, and smallest in farms always with livestock. In our sample, farms where livestock farming ceased between 2001 and 2010 hosted a similar number of breeding pairs in 2001 than farms where it was maintained (as assessed by a Poisson mixed model with study area as a random factor: $z = 1.75$, $P = 0.08$). The intermediate extinction probability in farms where livestock farming ceased may therefore result from a steeper decline of originally large colonies.

Presence of livestock seems therefore to enhance the number of pairs breeding at a farm, probably by a combination of direct and indirect benefits to Barn Swallow reproduction. First, flying insects are more abundant in farms with than without livestock (Møller 2001). Second, hayfields, which are the preferred foraging sites for Barn Swallows (Ambrosini *et al.* 2002, Evans *et al.* 2007), are wider around farms with livestock (+11.6% in 2010, our unpublished data) within 400 m of the farm, corresponding to the foraging range of this species (Ambrosini *et al.* 2002). Third, rooms housing livestock are significantly warmer than rooms without, and this affects nestling phenotype (Ambrosini *et al.* 2006, Ambrosini and Saino 2010) and survival (Grüebler and Naef-Daenzer 2006). All these benefits disappear after cessation of livestock farming, probably resulting in the steep decline of colony size we observed. In addition, buildings housing livestock are usually accessible to Barn Swallows for nesting, but, once farming ceases, may be rearranged and become inaccessible to swallows, thus determining nest site loss. Unfortunately, we have no detailed information on accessibility of buildings to breeding Barn Swallows in 2001 both in TP and MC. Conversely, in AS we could estimate the impact of nest site loss to breeding colonies. The rate of decline of colonies in farms where buildings that hosted breeding swallows in 2001 were remodelled or made otherwise unavailable for the swallows in 2010 (n = 54 farms), was not larger than that in farms where all nest sites were preserved (n = 16 farms) (t-test: t_{68} = 1.00, P = 0.32). The effect of nest site reduction was also not significant when the effect of cattle category was taken into account (GLM: $F_{1,66}$ = 0.14, P = 0.71, other details not shown). Hence, nest site loss does not seem to have determined the decline of colonies in AS. However, the effect of nest site loss may have been more severe in TP and MC than in AS, as average farm size is much lower in the first areas than in the latter (see Methods). Remodelling of building in a manner that denied access may therefore have concurred to the general decline of Barn Swallows in these areas.

Small colonies have also become extinct with a higher probability than large ones. These originally small colonies probably occurred in sub-optimal areas where recruitment of young individuals at their first breeding season was probably low, and became even smaller in a period of general population decline.

Three farms in AS and three in TP started livestock farming between 2001 and 2010. Colonies in two of these farms went extinct, while the other showed slightly positive demographic trends (r = +0.02 ± 0.04 SE on average, n= 4). The extinct colonies were very small in 2001 (one and two breeding pairs, respectively), and, at least in one case, extinction is probably the result of disturbance due to farm rearrangement (albeit the old cowshed was maintained at this farm). The positive trend in the other farms thus supports the hypothesis that livestock farming enhances the suitability of a farm to Barn Swallow reproduction, albeit the small sample size prevented formal statistical analyses.

Barn Swallow breeding colonies have declined at a similar rate in farms where livestock farming has either never been practiced or where cattle occurred in all years. This suggests that the general decline of breeding population is due not only to cessation of livestock farming, but also to other causes. Changes in general climatic conditions both in the breeding and the wintering grounds may be involved, as they seem to have determined a severe decline in the populations of several migratory birds

(Møller *et al.* 2008). In addition, changes in environmental conditions both in the wintering grounds and along migration routes have been shown to affect survival of migrant birds (Szép *et al.* 2006), mainly for those species inhabiting dry open habitats during winter (Sanderson *et al.* 2006). This may have profound effects on population size of several species, as adult mortality of aerial insectivores like the Barn Swallow mainly occurs during these phases of the annual life-cycle (Robinson *et al.* 2008).

Conservation implications

The Barn Swallow is currently listed as of “least concern” by IUCN (2010), but the sharp decline we documented (about 50% in ten years) calls for planning conservation strategies for this species in Italy and elsewhere (e.g. Denmark; Engen *et al.* 2001). The general negative trend observed in all three study areas, irrespective of changes in livestock farming practices, is probably due to factors acting over larger or even global geographical scales, such as climatic and environmental changes in the African wintering and passage areas, as is likely to occur for many other African wintering species (Sanderson *et al.* 2006, Møller *et al.* 2008, Both *et al.* 2009, Jones and Cresswell 2010, Saino *et al.* 2011). However, changes in farming practices occurring in the breeding quarters, such as the cessation of livestock farming, appear to have additive negative effects on Barn Swallow populations. Conservation actions aiming at buffering the global negative trends of Barn Swallows should thus favour the maintenance of livestock farming, which appears pivotal to limit the decline of the breeding populations of this species. Whether the buffering effect of livestock farming on Barn Swallows declines is due to livestock presence *per se*, possibly via its positive effects on seasonal reproductive success (Grüebler *et al.* 2010), or to habitat characteristics associated with livestock farming, such as pastures and hayfields, that represent preferential foraging sites for the species, remains to be elucidated. Agri-environment schemes (AES) specifically designed for Barn Swallow conservation should focus on the maintenance of livestock farming at farms, as swallow colonies were largest, declined the least, and had the lowest extinction risk at farms that always had livestock. However, to the best of our knowledge, we are unaware of any AES specifically designed for Barn Swallow conservation. Nevertheless, this species may benefit from implementation of AES aimed at maintaining hayfields and improving hedgerows, as these habitats are preferred foraging sites (Ambrosini *et al.* 2002, Evans *et al.* 2007, Grüebler *et al.* 2010). A less intensive approach to farming and a more wildlife-friendly agriculture, which should be promoted by the future Common Agricultural Politics, may be beneficial for farmland birds in general (Báldi and Batáry 2011) and, hopefully, also for the Barn Swallow. However, the benefit of an environmental-friendly approach to agriculture for Barn Swallow is not unequivocal, as this species was found to be more abundant in organic than in traditional farms in Denmark (Christensen *et al.* 1996), but not in the Netherlands (Kragten and de Snoo 2008, Kragten *et al.* 2009). In addition, Barn Swallows population levels were not correlated with agricultural intensification in Britain (Robinson *et al.* 2003).

At a local scale, conservation actions would be most effective in AS than in other study areas, both because population decline was steepest in this area, and because it still supports the largest population. Unfortunately, AES specifically designed for improving Barn Swallow populations seem difficult to plan in this area, as they would imply large economic costs to farmers. Indeed, cease of livestock farming and conversion of hayfields to arable fields for biomass production is currently economically advantageous for farmers (R. Ambrosini, unpubl. Data).

In conclusion, our study suggests for a careful assessment of the conservation status of the migratory Barn Swallow that showed an alarming local population decline, and indicates that plans for Barn Swallow conservation should aim to maintain livestock farming, as this may contribute to limit population declines.

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Hayfields enhance colony size of the Barn Swallow Hirundo rustica in Northern Italy

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Beatrice Sicurella[1], Manuela Caprioli[2], Andrea Romano[2], Maria Romano[2], Diego Rubolini[2], Nicola Saino[2], Roberto Ambrosini[1]

1. Dipartimento di Biotecnologie e Bioscienze, Università degli Studi di Milano-Bicocca, p.zza della Scienza 2, I-20126 Milano, Italy.

2. Dipartimento di Bioscienze, Università degli Studi di Milano, via Celoria 26, I-20133 Milano, Italy.

Abstract

The widespread decline of farmland birds is a major issue of biological conservation in European countries. The Barn Swallow *Hirundo rustica* is a flagship species for farmland bird conservation owing to its aesthetic and cultural value and to the sharp decline observed in several populations. Based on a long-term monitoring project of a population in a protected area of Northern Italy, we documented a dramatic decline of 56.6% between 1999 and 2011, corresponding to a decrease of 6.59% each year. We also showed that colonies were on average larger in farms with livestock than in those without livestock, and that colony size increased with increasing extent of hayfields within 200 m from the colony in farms without livestock, but not in those with livestock. Hayfield extent at greater distances did not influence population size or trend. Cessation of livestock farming therefore determined a decline in local colonies, but this decline may be buffered by an increase in hayfield extent within 200 m from the farm. However, variation of the ecological features of breeding sites explained only a fraction of the observed population decline, suggesting that ecological conditions during migration and wintering may be crucial in affecting population trends.

Mean hatching date of first broods advanced in recent years, but less so in farms with than without livestock. Independently of year, mean hatching date advanced more in farms with greater extent of hayfields within 200 m of the colony. Reproductive success, measured as the mean number of fledged offspring per nest, declined significantly with hatching date, but was not affected by hayfield extent. Conversely, nestling quality, in terms of body mass and feather development, improved with increasing extent of hayfields around the colony, particularly in late-hatched first clutches. Our findings suggest that conservation strategies for this declining species

should include both the maintenance of livestock farming and the enlargement of hayfields close to breeding colonies, particularly in farms where livestock farming has ceased.

Introduction

Diverse anthropogenic factors, including habitat alteration and climate change, currently concur to determine a global decline of biodiversity (Gaston *et al.* 2003, Thomas *et al.* 2004). Agricultural intensification, which occurred in Europe since the end of the Second World War, has entailed profound environmental alterations, such as habitat homogenization, loss of hedgerows and ponds, increase in the use of agrochemicals, and change in farming practices (Donald *et al.* 2001, 2006). As a consequence, birds breeding in farmlands are suffering sharper population declines than those inhabiting other environments in Europe (Donald *et al.* 2001, Murphy 2003).

Among farmland birds, the Barn Swallow *Hirundo rustica* is a flagship species for habitat conservation, owing to its aesthetic and cultural value, and to its popularity among people (Spina 1998). Several populations of this species are currently declining throughout Europe (Tucker & Heath 1994, PECBMS 2009), although the steepness of these declines largely differs among countries (Tucker & Heath 1994, Siriwardena *et al.* 1998, Engen *et al.* 2001, Robinson *et al.* 2003). Data from the Pan European Common Birds Monitoring Scheme indicate an overall population decline of about 40% in the period 1990-2006, with an annual decline rate of about 1% per year (PECBMS 2009). In Northern Italy a decrease of 53.1% since 2001, corresponding to a decline rate of 8.4% per year, much larger than that observed at continental scale, has been recently documented

(Ambrosini *et al.* 2012), so that in the near future the Barn Swallow may become a species of conservation concern in this area. A proper knowledge of the factors affecting population dynamics of this species may therefore be pivotal to plan effective conservation strategies.

The current decline of Barn Swallow populations is supposed to be the consequence of several concomitant factors. Besides agricultural intensification and habitat loss, cessation of livestock farming at nesting farms contributed to the decline of colonies (Møller 2001, Ambrosini *et al.* 2012). Indeed, Barn Swallows preferentially breed in farms where cattle, pigs or horses are reared (Møller 2001, Ambrosini *et al.* 2002), and colonies decline steeply once livestock farming ceases (Ambrosini *et al.* 2012). In addition, changes in farming practices often result in farm remodelling, with old cowsheds and barns replaced by modern buildings, less suitable to Barn Swallows' nesting (Evans *et al.* 2003). Finally, similarly to other long-distance migrant species, habitat loss and alteration both at the wintering grounds and along migration routes (Sanderson *et al.* 2006, Zwarts *et al.* 2009), as well as dissimilar rates of climate change between the breeding and the wintering quarters, may have exacerbated local population decline (Both *et al.* 2010, Saino *et al.* 2011).

The strict association between livestock farming and Barn Swallows is probably due to several concomitant factors. For example, cowsheds with livestock may provide optimal nesting sites due to warmer temperatures (Ambrosini & Saino 2010). In addition, farms with livestock are usually surrounded by a larger extent of hayfields and pastures (Møller 2001, Ambrosini *et al.* 2002, 2012), which are the favourite foraging habitat of Barn Swallows, probably because large flying insects, which are the preferred prey of this species, are more abundant on these than on other cultures (Evans *et al.* 2007, Grüebler *et al.* 2010, Orłowski & Karg 2011).

Indeed, presence of livestock enhanced nestling quality and frequency of second clutches in Denmark (Møller 2001), and nestling survival and annual offspring output of double-brooded pairs in Switzerland (Grüebler *et al.* 2010). In Northern Italy pairs breeding in cowsheds with livestock advanced laying of the first clutches and produced nestlings of better overall quality (Ambrosini *et al.* 2006). Earlier reproduction, in turn, should enhance fitness, because it increases the probability of rearing a second clutch and because breeding success declines through the breeding season (Turner 2006). In addition, early hatch increases lifespan and lifetime reproductive success (Saino *et al.* 2012).

During breeding, Barn Swallows usually forage within a very narrow range around the colony and rarely move more than 500 m (Møller 1994). In addition, the number of foraging individuals decreases steeply at increasing distance from the colony (Ambrosini *et al.* 2002). It could therefore be speculated that hayfields and pastures may be more beneficial to Barn Swallows if they are close to the breeding colony.

In the present study, taking advantage of the data collected during a long-term monitoring project in Northern Italy (Ambrosini *et al.* 2002, 2012), we investigated whether the extent of hayfields and their spatial distribution around farms influenced the number of pairs and population trends of Barn Swallows breeding at 87 farms censused each year between 1999 and 2011. We also aimed to investigate the causal mechanisms that link annual variation in extent of hayfields around farms and the demographic trend of colonies. We therefore analysed the annual variation in clutch and brood size and hatching date recorded in the same colonies during the annual censuses: if large hayfields are beneficial to Barn Swallow reproduction, we expect clutch and brood size to increase, and hatching date to advance in farms surrounded by larger extent of hayfields.

A large extent of hayfields around the colony may not only enhance reproductive success, but also nestling quality, in terms of e.g. growth or immune response, both of which may predict post-fledging survival (Møller & Saino 2004, Turner 2006). For example, foraging sites close to the nest may reduce time spent foraging, thus reducing the risk of nestling starvation, and provide greater food abundance or greater abundance of high-quality prey. To investigate this hypothesis we used a large dataset on nestling phenotypic traits collected in 2001 for a previous study (Ambrosini *et al.* 2006), in which we recorded nestlings body mass, size, and feather development, which positively influence offspring survival (Turner 2006, Grüebler & Naef-Daenzer 2010), and T cell–mediated immune response, which is a fundamental component of the acquired immune system (Saino *et al.* 1997, Christe *et al.* 2001). These data were re-analysed here with the specific aim of investigating the effect of the extent of hayfields around nesting sites on components of nestling phenotypic quality.

Methods

Study area and census methods

This study was carried out in the Parco Regionale Adda Sud, a wide (c. 240 km^2) intensively cultivated area in Northern Italy (Figure 1) where livestock farming is widespread (see Ambrosini *et al.* 2002 for a description of the study area). In 1999 all farms in this area were censused from detailed maps (scale 1:10,000) and a sample of 107 farms was randomly chosen. In the following years the number of farms monitored varied from 96 to 160 depending on our opportunities to perform field work and to farm owners' willingness to let us visit their properties. Eighty-seven farms were censused in each year since 1999 according to a standard protocol whereby we inspected all nests in a farm every second week.

All analyses of population trends were based on these 87 farms. Nest inspections started at the beginning of April, when very early first clutches are laid, and ended in mid-July, when late first clutches fledge (Ambrosini *et al.* 2002). Colony size was estimated as the maximum number of nests simultaneously active at a farm (Ambrosini *et al.* 2002).

The number of eggs and nestlings in every nest was recorded on each visit. Nestling age was estimated according to body size and plumage development (Turner 2006, see also Ambrosini & Saino 2010 for a validation of this method).

Hatching date of each brood was estimated according to nestling age, and laying date was calculated assuming that Barn Swallows lay one egg per day and incubate eggs for 14 days (Møller 1994). Brood size was expressed as the number of chicks that survived at least to the age of 10 days, as mortality after age 10 days accounts for less than 5% of total nestling mortality (N. Saino, unpubl. data).

Thus, brood size of nests observed when nestlings were eight or nine days old and not observed again before fledging was discarded. We focused on first broods only. Since Barn Swallows may change nest between first and second breeding attempts and most birds were not individually marked, we could not directly identify second broods. To avoid including possible second broods in the study, we excluded from the analyses all the nests in which the first egg was laid after the fledging of the nest that hatched first in that colony (Ambrosini *et al.* 2002, 2006). During each year we obtained information on 496-1,225 first broods, although, for practical reasons, not all information was available for all nests.

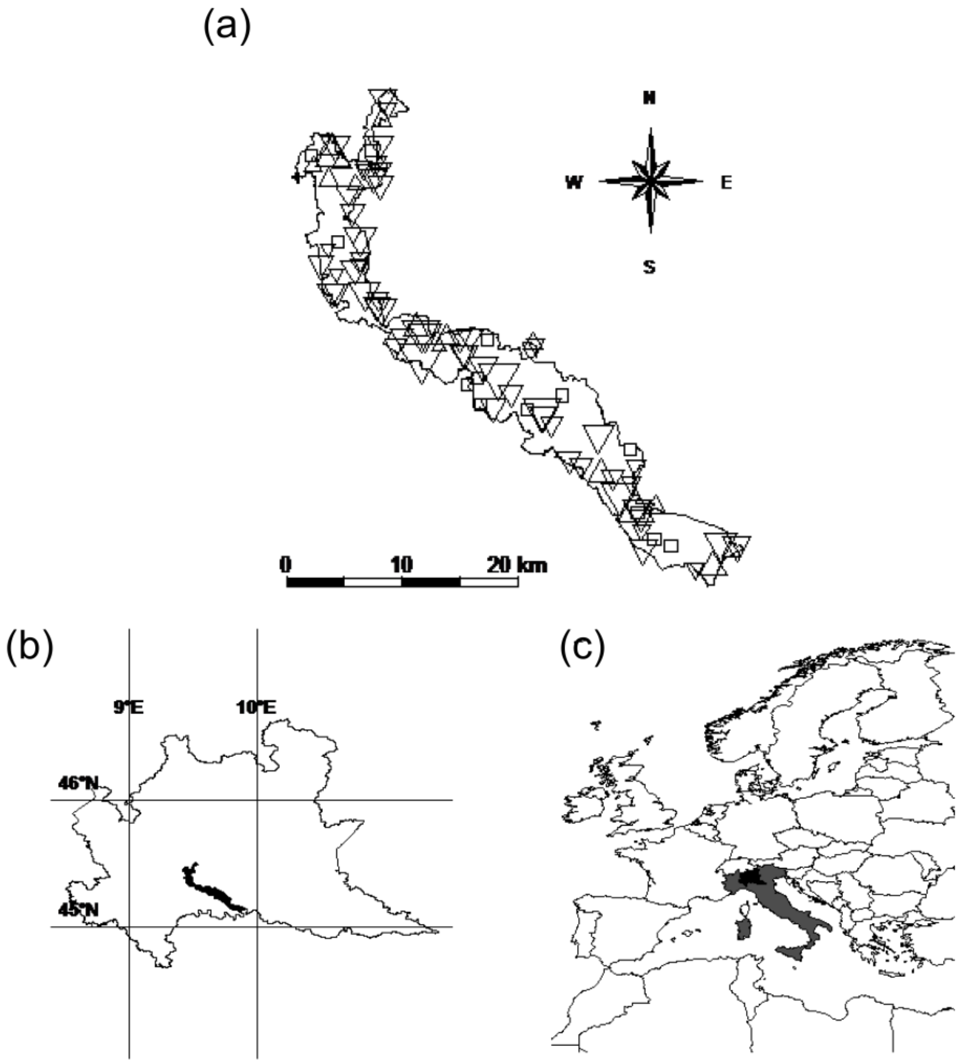

Figure 1. (a) the study area with the 87 farms included in the study. Downward triangles indicated Barn Swallow colonies with negative demographic trends, upward triangles colonies with positive trends, squares farms with no Barn Swallow in all the years of the census. Size of triangles is proportional to the absolute value of population growth rate; (b) the study area in Lombardy; (c) Lombardy in Italy and Europe.

Livestock farming and hayfield extent

Every year, we recorded the number of cows, pigs and horses reared at each farm. These data were then summarised in a dichotomous variable accounting for livestock presence or absence. Indeed, studies conducted in the same area indicated that presence of livestock at a farm is a better predictor of Barn Swallow presence and abundance than the number of head reared (Ambrosini *et al.* 2002).

The extent of different crop types was also recorded on detailed (1:10,000) maps within the foraging range of Barn Swallows (400 m from each colony; Ambrosini *et al.* 2002). Maize fields and hayfields (i.e. fields where grass or alfalfa *Medicago sativa* are not grazed but cut to produce dry feed for livestock) represent the most common land uses in the study area (on average 44% and 35% of the area, respectively). To investigate variation in the importance of crops at different distances from the colony, we quantified the extent of hayfields within 200 m from the farm and between 200 and 400 m. Hayfield extent was expressed as the proportion of the cultivated area with hayfield within each distance belt.

Recording of nestling traits

In 2001 we recorded phenotypic traits of 1,155 nestlings from 249 first broods in 57 farms. Full details of field procedures are reported in Ambrosini *et al.* (2006). Briefly, nests were visited daily to assess hatching date. Nestlings were individually marked and measured when they were 9-11 days old (23.5% were 9 day old, 50.4% 10 day old, 26.1% 11 day old), i.e. before the physiological body mass recession that occurs before fledging (c. 12 days old). We measured body mass with a spring balance (accuracy 0.1

g), right tarsus length with a calliper (accuracy 0.05 mm) and innermost left rectrix length with a ruler (accuracy 0.5 mm). On the same day we also injected the right wing web with a lectin (phytohemagglutinin, PHA) to do the PHA skin test, following the procedure described in Saino *et al.* (1997). This test is a standard method to assess T cell–mediated immune response in birds in the wild (Saino *et al.* 1997, Smits *et al.* 1999).

Statistical analyses

Population growth rate (*r* parameter) was calculated as the slope of the Poisson regression (corrected for overdispersion) of the total number of breeding pairs observed in a given year on time. Variations in mean extent of hayfields around the sampled farms and in the proportion of farms with livestock during 1999-2011 were modelled with linear regression and a binomial Generalised Linear Model (GLM), respectively.

The number of breeding pairs per farm was modelled in Generalised Linear Mixed Models (GLMM) assuming a Poisson error distribution. Year (covariate), livestock farming (dichotomous variable), the proportional extent of hayfields within a distance belt ("hayfield extent" hereafter, covariate) and the two-ways interactions between these terms were entered as predictors. Hayfield extent within each distance belt was entered in separate models because these variables were strongly and positively correlated (Pearson $r = 0.772$). Farm was entered as a random factor and year as a random slope (*sensu* Schielzeth & Forstmeier 2009) at the farm level in all models. All variables were centred to their mean values before the analyses. Collinearity of the predictors entered simultaneously in statistical models was carefully checked before any analysis (Variance Inflation Factor of predictors, including interaction terms ≤ 1.421 in all cases, |Pearson r| between predictors ≤ 0.361 in all cases). The temporal autocorrelation of observations from the same farm was accounted for by assuming an AR(1) within-farm covariance structure in all models.

We also aimed at investigating the extent to which variation in hayfields and livestock concurred in determining population trend. To this end, we re-ran the model of colony size while excluding year from the predictors, but maintaining the auto-correlation structure. Coefficients from this model should reveal the potential impact of change in farming practice on Barn Swallow population size, irrespective of the long-term trend. Analyses of colony size were done by the *glmmPQL* procedure in the *MASS* library of R 2.8.1 (R Development Core Team 2008).

Variation in mean within-farm clutch size, brood size and hatching date of first clutches was investigated in Linear Mixed Models (LMMs) assuming a Gaussian error distribution with the same random structure as the models of colony size. The same fixed predictors were entered in all models, as in models of colony size. In addition, colony size and its interaction with year were entered into models to account for potential density-dependent effects on breeding performance and their variation over time. Finally, mean hatching date and its interaction with year were entered in the models of mean clutch size and mean brood size to account for the seasonal decline in clutch and brood size (Ambrosini *et al.* 2006, Turner 2006). These models were fitted with the *lme* procedure of R 2.8.1.

Nestling quality was investigated in Gaussian LMMs. Presence of livestock farming at a farm (dichotomous variable), hayfield extent within 200 m from the colony, date at nestling measurement (“date” hereafter) and age of nestlings (covariates) were entered as fixed effects together with the interactions between date and hayfield extent and date and livestock farming. Date and age were included in the models to account for seasonal variation in nestling quality or nestling growth. Farm was entered as a random factor, date as a random slope within farm, and nest as a random factor nested within farm. Models were fitted with the *lmer* procedure in the *lme4* package in R 2.8.1. Statistics are reported together with their associated standard error, unless stated otherwise.

Results

During the 13 years of the study, the population decreased by 56.6% in the 87 farms censused each year, from the 1,142 breeding pairs censused in 1999 (13.13 ± 1.68 pairs per farm on average) to the 496 (5.70 ± 0.87) found in 2011 (Figure 2). The annual decline rate was 6.59 ± 1.14 % (95% Cl: 4.36%-8.82%). Population declined at a constant rate, as indicated by the fact that the second and the third order polynomial terms of year were never statistically significant ($|t_9| \leq 1.259$, $P \geq 0.240$). During these years eight colonies went extinct and were not recolonised, two farms were colonised by one and two breeding pairs respectively, and two farms were colonized by a single pair in some years, but hosted no breeding pairs in 2011.

Mean hayfield extent 0-200 m around the farms did not change significantly between 1999 and 2011 (estimate: 0.001 ± 0.002 proportion of hayfield × year^{-1}, $t_{11} = 0.338$, $P = 0.742$, Figure 3a) nor did that in the 200-400 m band change (0.002 ± 0.002 proportion of hayfield × year^{-1}, $t_{11} = 1.028$, $P = 0.326$).

Proportion of farms where livestock was reared declined significantly during the study period (estimate: -0.038 ± 0.018 proportion of farms ×

year^{-1}, z = -2.130, P = 0.033), from 75.9% in 1999 to 66.7% in 2011 (Figure 3b).

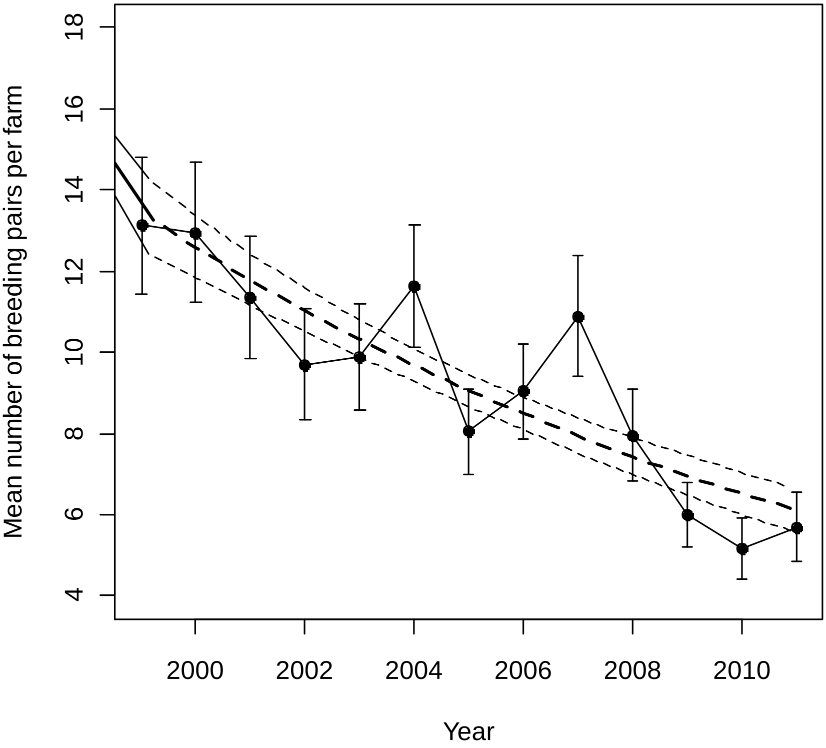

Figure 2. Mean number of breeding pairs per farm in the 87 farms monitored in all years in 1999-2011. Bars represent standard errors. Dashed lines represent population trend and its standard error estimated from a population growth model (see Methods).

Hayfield distribution and number of breeding pairs per farm

The model including hayfield extent 0-200 m from the farm indicated a significant decline in colony size over time. In addition, the interaction between hayfield extent in 0-200 m and year was significant and positive (Table 1).

Table 1. Poisson GLMMs of the number of pairs per farm. Sample size is 87 farms and 13 years. All predictors were centred to their mean values before the analyses. φ is the within-subject temporal-autocorrelation coefficient.

Effect	**Coefficient**	**S.E.**	**z**	**P**
Intercept	1.539	0.160	9.610	< 0.001
Year	-0.055	0.011	-4.944	<0.001
Livestock farming	0.083	0.039	2.141	0.032
Hayfield extent 0-200 m	0.112	0.065	1.710	0.087
Livestock farming × Year	0.013	0.015	0.914	0.360
Hayfield extent 0-200 m × Year	0.042	0.014	2.926	0.003
Hayfield extent 0-200 m × Livestock farming	-0.376	0.137	-2.747	0.006

φ = 0.619

This significant interaction can be interpreted in two non-mutually exclusive ways. First, the effect of hayfield extent 0-200 m from the farm on the number of breeding pairs has changed over time. Models run separately on data collected before and after 2005 (median year in the dataset; 2005 was excluded from the analyses) while excluding the hayfield extent by year interaction and the non-significant livestock farming by year interaction, indicated that hayfield extent had no effect on colony size before 2005 (z = -0.765, P = 0.444), while it had a significant and positive effect after 2005 (z = 3.140, P = 0.002).

Second, the rate of population decline differed between farms surrounded by different extent of hayfields. However, models run separately on farms having, on average, less or more than 50% of hayfields in 0-200 m during the 13 years of the study indicated that the number of breeding pairs per farm declined significantly both in the former (r = -0.049 ± 0.015, z = -3.251, P = 0.001, n = 60 farms) and the latter group (r = -0.051 ± 0.014, z = -3.515, P = 0.001, n = 27 farms; other details not shown).

Colonies were also on average larger in farms with than without livestock, as indicated by the positive effect of livestock farming, but declined at a similar rate, as indicated by the non-significant interaction between livestock farming and year (Table 2). Finally, the negative interaction between livestock farming and hayfield extent suggested that hayfields differentially affected colony size according to presence or absence of livestock.

In particular, the coefficients of the model (Table 2) indicated that the number of breeding pairs increased significantly with hayfield extent in farms without livestock (0.378 ± 0.131 log(pairs) × proportion hayfields^{-1}, z = 2.877, P = 0.004), while it was unaffected in farms with livestock (0.002 ± 0.066 log(pairs) × proportion hayfields^{-1}, z = 0.037, P = 0.971).

The model including hayfield extent 200-400 m only indicated that colony size declined significantly during time (r = -0.065 ± 0.010, z = - 6.699 P < 0.001), while all the other predictors were not significant ($|z| \leq 1.321$, $P \geq 0.186$; other details not shown). These results therefore suggest that hayfield extent 0-200 m from the farm, but not 200-400 m, affected colony size.

The model investigating the extent to which variation in hayfields and livestock influenced colony size indicated that colony size changed according to the combined effect of these predictors (effect of the interaction between livestock farming and hayfield extent: -0.497 ± 0.175 log(pairs) × proportion hayfields^{-1}, z = -2.844, P = 0.004). The main terms of livestock farming and hayfield extent had non-significant effects (difference in colony size between farms with and without livestock: 0.159 ± 0.087 log(pairs), z = 1.990, P = 0.067; effect of hayfield extent: 0.067 ± 0.078 log(pairs) × proportion of hayfields^{-1}, z = 0.864, P = 0.388).

The coefficients from this model allowed to calculate that the reduction in the number of farms where livestock was reared (see above) may have determined a decline of about 1.64% in the Barn Swallow population between 1999 and 2011, corresponding to 2.9% of the general decline (56.6%, see above) observed in the population during the same years.

Hayfield extent 0-200 m from the farms did not change over time (Figure 3, see also above), and therefore changes in agricultural practices should have not contributed to the observed decline. However, a future increase in the average extent of hayfields around the farms from the current 36.6% to 53.3% would determine an increase in the Barn Swallow population equal to the reduction in the number of breeding pairs due to cessation of livestock farming.

Clutch size, hatching date and number of fledged offspring

Mean size of first clutches declined significantly with mean hatching date (-0.013 ± 0.002 eggs day^{-1}, $z = -6.978$, $P < 0.001$, $n = 804$ mean within-farm and year clutch sizes). Year, livestock farming, hayfield extent 0-200 m, number of breeding pairs and the interactions between year and the other variables had no significant effects on mean clutch size ($|z| \leq 1.575$, $P \geq 0.115$ in all cases). Mean hatching date of clutches advanced significantly in recent years (-0.433 ± 0.102 days × year^{-1}, $z = -4.250$, $P < 0.001$, $n = 827$ mean within-farm and year hatching dates), but at a slower rate in farms with than without livestock (effect of the interaction between livestock farming and year: $z = 1.971$, $P = 0.049$; advancement rate in farms with livestock: -0.284 ± 0.109 days × year^{-1}; in farms without livestock: -0.796 ± 0.233 days × year^{-1}). Hatching date also advanced in farms with large hayfields within 200 m (-3.045 days × proportion of hayfields^{-1}, $z = -2.178$, $P = 0.029$).

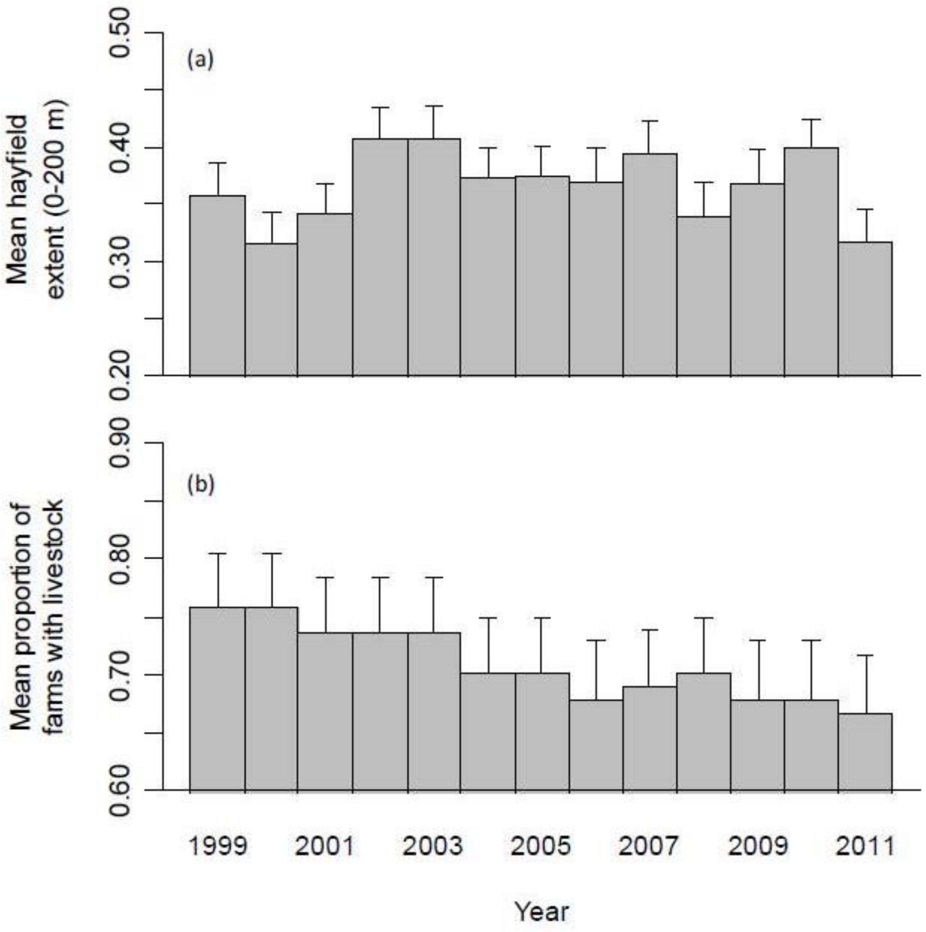

Figure 3. (a) Mean proportion of hayfields within 200 m from the colony and (b) proportion of farms with livestock at each year. Bars represent standard errors

No other variable or interaction significantly predicted mean hatching date ($|z| \leq 1.805$, $P \geq 0.071$). Mean brood size declined significantly with hatching date (-0.015 ± 0.005 nestlings × day^{-1}, $z = -2.815$, $P = 0.005$, $n = 788$ mean within-farm and year brood sizes). No other significant effect was observed ($|z| \leq 1.711$, $P \geq 0.087$). A further analysis indicated that hayfield extent did not affect mean brood size either *per se* or in interaction with other predictors, even when hatching date was removed from the model ($|z| \leq 0.940$, $P \geq 0.347$; other details not shown).

Nestling quality

Nestling body mass and feather development were significantly predicted by hayfield extent 0-200 m from the colony and in both cases the effect of hayfield extent changed during the breeding season, as indicated by the significant hayfield extent by date interaction (Table 2). Tarsus length showed a marginally non-significant tendency towards a similar pattern of variation with date, while cell-mediated immunity was unaffected by hayfield extent either *per se* or in interaction with other variables (Table 2).

To better interpret these results we re-fitted the models of body mass and rectrix length by entering date as a dichotomous variable indicating whether a given nest was measured before or after the median date at measure of all nests in the sample (4 June). These models indicated that body mass did not change with hayfield extent in early nests (-8.711 ± 6.468 g × 10 × proportion of hayfields^{-1}, $z = -1.345$, $P = 0.178$), while it increased in late nests (17.111 ± 7.911 g × 10 × proportion of hayfields^{-1}, $z = 2.162$, $P = 0.031$; Figure 4a). On the other hand, innermost rectrix length showed a weak and non-significant trend to decrease with hayfield extent in early nests (-35.438 ± 19.334 mm × 10 × proportion of hayfields^{-1}, $z = -1.833$, $P = 0.067$), and to increase in late nests (18.192 ± 13.572 mm × 10 × proportion of hayfields^{-1}, $z = -1.340$, $P = 0.180$, Figure 4b).

Cell-mediated immunity increased significantly during the breeding season, while body mass as well as tarsus and rectrix length increased with nestling age (Table 2).

Discussion

Our study population of Barn Swallows suffered a dramatic decline of more than 50% between 1999 and 2011, corresponding to an annual decrease of 6.6% This decline rate is almost identical to that estimated by Ambrosini *et al.* (2012) in a recent paper based on data collected in the same study area between 1999 and 2010 (6.3% per year) to which we refer for a discussion of demographic trends in different geographical areas. Here we only emphasize that this decline is much steeper than that observed over the whole Europe (1% per year; EBCC 2008, PECBMS 2009).

The decline of individual colonies occurred at rates that were not related to environmental features of breeding sites. Indeed, demographic trends did not differ in farms with and without livestock, and in farms having on average more or less than 50% hayfields within 200 m, as clearly indicated by the analyses run separately on these two categories of farms. However, presence of livestock and hayfield extent within 200 m from the farm influenced colony size, and their relative importance has changed over time. Indeed, presence of livestock positively influenced colony size in all years, while hayfield extent within 200 m positively influenced colony size in recent years but not in the past.

Table 2. Gaussian LMMs of nestling phenotypic traits. Date is date at nestling measurement. All predictors were centred to their mean values before the analyses.

Effect	**Coefficient**	**S.E.**	**z**	**P**
Body mass				
Intercept	203.582	1.381	147.356	< 0.001
Date	0.074	0.074	1.005	0.315
Nestling age	6.796	1.663	4.088	< 0.001
Livestock farming	-4.898	3.813	-1.284	0.199
Hayfield extent 0-200 m	5.600	5.309	1.055	0.291
Livestock farming × Date	-0.126	0.190	-0.662	0.508
Hayfield extent 0-200 m × Date	0.765	0.274	2.791	0.005
Hayfield extent 0-200 m × Livestock farm.	-20.363	14.292	-1.412	0.158
Tarsus length				
Intercept	110.864	0.322	344.356	< 0.001
Date	-0.094	0.014	-6.639	< 0.001
Nestling age	0.897	0.332	2.703	0.007
Livestock farming	1.080	0.896	1.206	0.228
Hayfield extent 0-200 m	-1.438	1.220	-1.179	0.238
Livestock farming × Date	-0.016	0.038	-0.416	0.677
Hayfield extent 0-200 m × Date	0.100	0.051	1.952	0.051
Hayfield extent 0-200 m × Livestock farm.	-4.776	3.354	-1.424	0.154
Innermost rectrix length				
Intercept	172.183	3.027	56.881	< 0.001
Date	0.630	0.164	3.838	< 0.001
Age	27.081	3.633	7.453	< 0.001
Livestock farming	11.550	8.531	1.354	0.176
Hayfield extent 0-200 m	-5.476	11.502	-0.476	0.634
Livestock farming × Date	-0.803	0.435	-1.846	0.065
Hayfield extent 0-200 m × Date	1.755	0.599	2.930	0.003
Hayfield extent 0-200 m × Livestock farm.	-12.289	32.814	-0.374	0.708
Immunocompetence index				
Intercept	150.347	5.968	25.193	< 0.001
Date	1.156	0.179	6.456	< 0.001
Age	2.905	2.607	1.114	0.265
Livestock farming	-9.189	14.330	-0.641	0.521
Hayfield extent 0-200 m	32.150	22.935	1.402	0.161
Livestock farming × Date	-0.095	0.429	-0.221	0.825
Hayfield extent 0-200 m × Date	0.277	0.692	0.401	0.689
Hayfield extent 0-200 m × Livestock farm.	47.655	38.348	-1.243	0.214

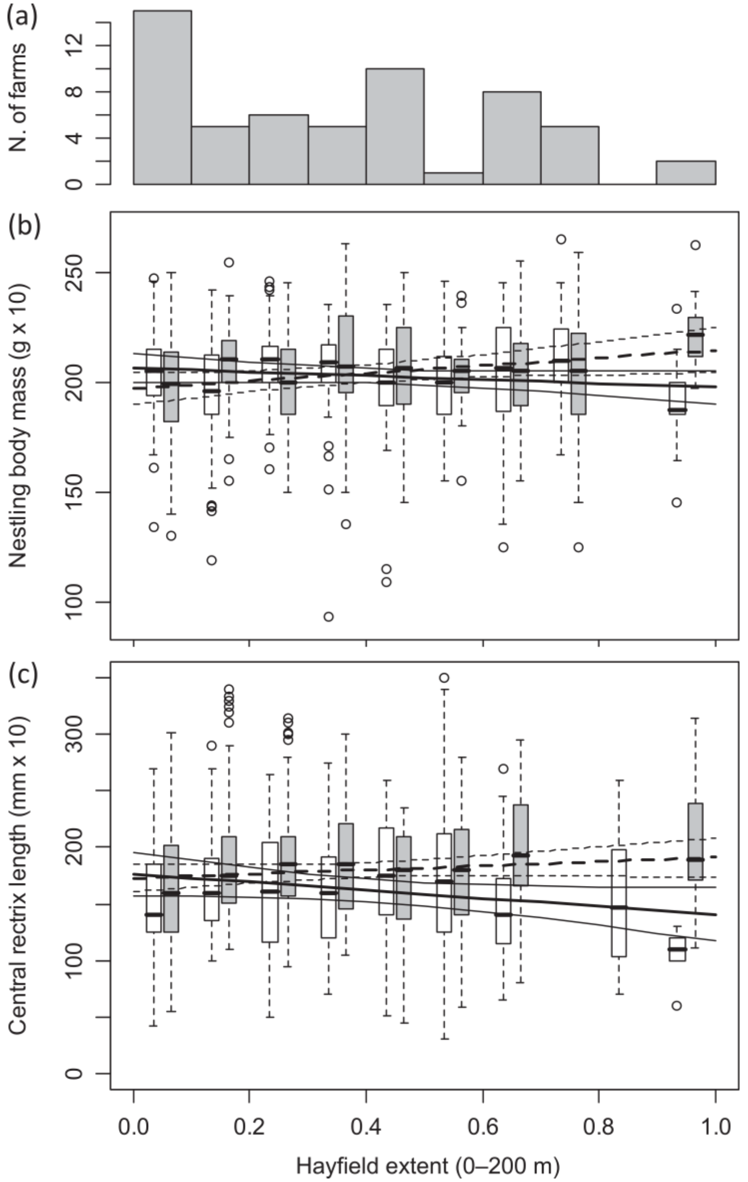

Figure 4. (a) Frequency distribution of farms with a given average proportion of hayfields within 200 m from the colony in 2001, (b) body mass and (c) innermost rectrix length of Barn Swallow nestlings in farms with different proportion of hayfields within 200 m from the colony before (open boxes and dashed lines) and after (filled boxes and solid lines) the median date at nestling measure (65 = 4 June). Boxes are drawn separately for nestlings measured before or after June 4th within 0.1 intervals of hayfields extent around farms, and slightly scattered from the median value within interval. Lines are drawn according to the coefficients of models in Table 2.

In addition, in all years hayfield extent positively affected colony size on farms without livestock, but not on farms with livestock. Conversely, hayfield extent within 200-400 m from the colonies had no significant effect on colony size.

Hayfields surrounding farms are the favourite foraging habitat of this species (Ambrosini *et al.* 2002, Evans *et al.* 2007), and therefore a positive effect of the extent of hayfields on Barn Swallow abundance is not surprising. Hayfields may offer a larger availability of prey or better quality of prey than other crops (Evans *et al.* 2007). Importantly, hayfields close to breeding farms may represent a more important source of food than those located few hundred meters away (Ambrosini *et al.* 2002), because they may reduce the energetic cost of foraging.

The positive association between livestock farming and colony size is well documented in the same study area (Ambrosini *et al.* 2002) and in other parts of Europe (Møller 2001, Turner 2006), and cessation of livestock farming usually leads to an abrupt decline in colony size (Møller 2001, Ambrosini *et al.* 2012). This was well documented in a recent paper based on data collected in the same, as well as other, study areas in Northern Italy in which colony sizes observed in 2010 were compared to those observed in the same farms in 2001, and variation in colony size was related to change in farming practices between 2001 and 2010, but not to variation in crop extent around farms, since this information was not available for all study areas (Ambrosini *et al.* 2012). The present paper, though restricted to a smaller study area, presents a more detailed investigation of the ecological variables potentially affecting demographic trends of Barn Swallow colonies, as it is based on annual censuses, and therefore year-to-year variation in colony size could be modelled on a continuum according to year-to-year variation both in farming practices and hayfield extent. In addition, by investigating the concomitant effects of hayfield extent and livestock farming on breeding success and nestling phenotype, this study provides insights into the potential mechanisms through which ecological features of breeding sites may benefit Barn Swallows.

The analyses showed that colony size increased with the extent of hayfields within 200 m on farms where livestock is not reared, while it was unaffected by hayfield extent in farms with livestock. Presence of livestock may determine abundance of flying insects at a farm, independently from the extent of hayfields in the surroundings, while large hayfields close to the colony may be an important source of food for Barn Swallows breeding in farms without livestock.

The significant interaction between the extent of hayfields within 200 m from the colony and year suggests that the effect of hayfields has changed during the 13 years of the study, as also indicated by the analyses run separately on years before and after 2005. In particular, colony size increased with hayfield extent after 2005, but not before. The importance of wide hayfields close to the colony seems therefore to have increased in recent years, concomitantly with the reduction in the number of farms with livestock in the study area.

To elucidate the possible mechanisms linking hayfield extent and colony size we first investigated the variation in mean within colony clutch or brood size, and hatching date recorded in all years between 1999 and 2011. Indeed, farms where conditions for reproduction are better, may attract a larger number of first-year breeders, which disperse from the natal colony and usually represent the large majority of individuals at a farm (Saino *et al.* 2012). We observed that mean hatching date advanced significantly during the study period, consistently with the advancement in breeding date of Barn Swallows recorded in another area of Northern Italy (Rubolini *et al.* 2007). However, hatching date advanced by c. 9.5 days in farms without livestock in 1999-2011, but only by c. 3.5 days in farms with livestock. In addition, we found that mean hatching date advanced more in farms surrounded by large hayfields. An advancement in mean hatching date may be explained by changes in the proportion of young and old individuals in the population. Indeed, cessation of livestock farming likely determines a decline in colony size via a lower recruitment of young individuals (Møller 2001). Young swallows at their first breeding attempt usually arrive and breed c. 20 days later than older individuals (Saino *et al.* 2004). If young birds are recruited in smaller numbers after cessation of livestock farming, the proportion of old early-breeding individuals at a colony should increase, and mean reproductive date advance. Conversely, the advance in breeding date with increasing extent of hayfields is probably due to earlier breeding by all individuals, irrespective of age. Indeed, the proportion of late-breeding, young individuals should not decrease in farms surrounded by large hayfields, as suggested by the fact that colony size does not decrease with hayfield extent. Alternatively, old individuals may occur at a greater proportion in farms surrounded by large hayfields because, having bred under favourable conditions, they may achieve higher survival rates.

When we investigated variation in phenotypic traits of nestlings, we observed a significant effect of hayfield extent on body mass and feather development. In particular, we found that both nestling body mass and plumage development increased with increasing extent of hayfields within 200 m from the colony in late but not in early broods, implying that large hayfields around the colony enhance the quality of offspring reared late in the breeding season. The same patterns could also be observed in tarsus length, although in this latter case the effect was marginally non-significant. In addition, the proportion of male nestlings in a brood increased with the extent of hayfields within 200 m from the colonies (Romano *et al.* 2012), but not at larger distance (A. Romano, pers. comm.).

Body mass and feather length positively predicted survival prospects of Barn Swallow nestlings (Turner 2006, Grüebler & Naef-Daenzer 2010). Large hayfields within 200 m from the colony may therefore enhance survival prospects of the offspring that hatched late in the season. Late hatched offspring, in turn, are usually produced by individuals at their first breeding attempt, which usually breed later than older individuals (Møller 1994, Turner 2006). First-year breeders may therefore base the choice of their breeding site according to hayfield extent around farms, as their offspring may benefit most by being reared on farms surrounded by large hayfields.

The offspring usually contribute only marginally to the population trend of their natal colony, as Barn Swallows rarely return to breed an the same farm where they hatched, and local recruitment rate is only about 5% and is strongly biased toward males (Møller 1994, Turner 2006). However, the concomitant effects of a general better quality of the nestlings (the present study), which enhances survival prospects, and a larger proportion of male nestlings (Romano *et al.* 2012), which are more phylopatric than females, may determine a larger number of local recruits in farms surrounded by large hayfields. Since average longevity of Barn Swallows is about 2 years (Møller 1994, Turner 2006) and one-year-old individuals always represent c. 60% of the birds of a colony (Saino *et al.* 2012), a larger recruitment rate of young individuals, both hatched in the same farms and in others, to the breeding colony may therefore be the mechanism determining the larger size of colonies surrounded by wide hayfields.

Conservation implications

The novel insights provided by the present study on the relationships linking the size of Barn Swallow colonies and the ecological features of breeding sites may have implications for the conservation of this declining species. Although the ecological variables we considered explained only a small fraction (2.9%) of the decline of the population, suggesting that ecological conditions faced by Barn Swallows during migration and wintering may be crucial in affecting population trends, we suggest some simple conservation actions that may contribute to reduce the decline of breeding colonies. Since colonies are larger in farms with livestock, maintenance of livestock farming is probably the best strategy available at the breeding quarters to buffer the decline of colonies. However, conservation actions aiming at maintaining livestock farming at farms are difficult to implement over wide geographical scales, as several farms cease livestock farming each year because of low profitability. Nevertheless, enlargement of hayfields around farms where livestock farming ceases may buffer the decline of local colonies. Conservation actions aiming at increasing the extent of hayfields around farms would have a lower cost than those aiming at maintaining livestock farming, because it would be equal to the difference in income for the farmers between hayfields and maize fields, which usually replace hayfields when livestock farming ceases at a farm. Indeed, in this area, maize fields currently provide higher income to farmers than hayfields (our unpublished data).

An even cheaper strategy to buffer colony decline of Barn Swallows would be to simply modify the position of crops around the same farm, setting hayfields preferentially close to farms, and maize fields and other crop types at larger distances. Since only hayfield extent within 200 m from the colony affects population trend, such a strategy would benefit Barn Swallows, even if the total amount of hayfields in the study area would not change. Hopefully, these strategies may contribute to reduce the sharp decline of this flagship species of agricultural habitats.

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Weather conditions, brood size and hatching order affect Common Swift *Apus apus* nestlings' survival and growth.

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Beatrice Sicurella[1], Manuela Caprioli[2], Diego Rubolini[2], Mario Caffi[3], Nicola Saino[2], Roberto Ambrosini[1].

1. Dipartimento di Biotecnologie e Bioscienze, Università degli Studi di Milano-Bicocca, p.zza della Scienza 2, I-20126 Milano, Italy.

2. Dipartimento di Bioscienze, Università degli Studi di Milano, via Celoria 26, I-20133 Milano, Italy.

3. Osservatorio Ornitologico Pianura Bresciana "Padernello", via Cavour 1, I-25022 Borgo San Giacomo, Italy.

Capsule: Hatching order negatively affected Common Swift *Apus apus* nestlings' survival, while brood size and meteorological conditions influenced their growth patterns.

Aims: To investigate the influence of hatching date, age, sex, brood size, and meteorological conditions on survival and growth of Common Swift nestlings from Northern Italy (Southern Europe), a relatively warm and dry part of the distribution range of this species.

Methods: Nestlings were weighed at regular intervals and molecularly sexed. Growth patterns were described using a double-Richards growth curve, i.e. a growth curve that also accounted for the pre-fledging mass loss. We also identified the Linear Growth Phase (i.e. when nestlings grew at the fastest rate).

Results: Mortality increased with hatching order and decreased with brood size. Mortality was highest for fourth-hatched nestlings, none of which survived. Nestlings hatched late in the season grew faster, experienced the fastest growth rate at a younger age, but reached a lower maximum weight than nestlings hatched early in the season. Nestlings from large broods reached a lower maximum weight than those of small ones. Nestlings gained more mass when temperature was slightly higher than that expected from the seasonal temperature trend, and on rainy and windy days.

Conclusion: Common Swift nestlings' growth, but not survival, was affected by meteorological conditions, with moderate rainfall, moderate winds and high temperatures favouring greater mass gain. Higher intra-brood competition resulted in slower growth and lower maximum weight. Late-hatched nestlings grew faster but reached a lower maximum weight and a lower pre-fledging mass, possibly suggesting that late-hatched nestlings adaptively tune their growth pattern to the approaching onset of migration to African wintering quarters. Our results emphasize the

importance of exploring weather effects on the breeding biology of a species in different portions of its distribution range that are characterized by contrasting climatic conditions.

INTRODUCTION

The environmental conditions experienced by an organism during ontogeny may have important long-term consequences on several traits of its life history (review in Burness *et al.* 2000). Variation in the quality of the rearing environment can result in differences in the physiological condition (Burness *et al.* 2000) or in the morphology of offspring (e.g. Boag 1987; de Kogel 1997) and in differences in their survival prospects during the early phases of life (Dijkstra *et al.* 1990; Hall *et al.* 2001), but can also have long-lasting, organizational effects, affecting adult physiology or morphology (de Kogel & Prijs 1996; Haywood & Perrins 1992; Perrins 1965; Schlutter & Gustafsson 1993). In birds, individuals raised under poor conditions often reach a smaller size, lighter body mass at fledging and have lower over-winter survival and recruitment than those raised in a more favourable environment (e.g. Perrins 1965; Boag 1987; Richner 1989; Dijkstra *et al.* 1990; Koskela 1998). In adult life, these individuals may breed in low-quality habitats (Verhulst *et al.* 1997), have lower fecundity (e.g. smaller clutch sizes; Haywood & Perrins 1992; Schlutter & Gustafsson 1993) or reduced attractiveness with respect to conspecifics (Gustafsson *et al.* 1995; de Kogel & Prijs 1996). Therefore, the environment where an individual is reared may have crucial effects on its subsequent behaviour (Rosenzweig 1984), viability and fitness (Lindström 1999).

The rearing environment of an individual is determined by both abiotic and biotic factors, which can also vary at different spatial and temporal scales.

For instance, among abiotic factors, meteorological conditions greatly affect nestlings growth in many bird species (Roldan *et al.* 2013; Chausson *et al.* 2014), because they impact on individuals both directly, e.g. by affecting thermoregulation costs and energy expenditure of nestlings (Ricklefs 1983), and indirectly, by influencing food availability or foraging efficiency of parents. Direct negative effects of temperature on growth could result either from raised energetic needs due to increased costs of thermoregulation under cold conditions or from the increase in the costs of dissipating heat when exposed to hot conditions (Speakman and Krol 2010).

Other factors may however have an equally important role in influencing the pre-fledging survival and growth. For example, the number of siblings in each brood can affect the intensity of sib-sib competition, resulting in a lower per capita food provisioning. In addition, in species where hatching asynchrony determines a hierarchy among nestlings, hatching order may affect the ability of nestlings to compete with nest mates for resources. Many studies also suggest that male and female offspring may differ in their ability to compete for food (Teather 1992), and may be differentially affected by environmental conditions (Kalmbach *et al.* 2005). Such differences have also been observed in species that are strictly monomorphic like the Alpine Swift *Thakymarptis melba* (Bize *et al.* 2005). Sex differences in competitive abilities may be exacerbated when rearing conditions deteriorate (Kalmbach & Benito 2007; Saino *et al.* 2008, Jones *et al.* 2009, Rosivall *et al.* 2010). For instance, in the Blue Tit *Cyanistes caeruleus*, female nestlings are more sensitive to adverse environmental conditions in terms of reduced fledgling size than their brothers (Råberg *et al.* 2005), while the contrary held true in the Barn Swallow *Hirundo rustica* (Boncoraglio *et al.* 2007).

Here we investigated the influence of the rearing environment on Common Swift *Apus apus* nestlings' survival and growth in a colony in Northern

Italy. The Common Swift is a medium-sized, long-lived species which lays only one clutch of two to three eggs per year, with a laying interval of two to three days, while clutches of one or four eggs are less frequent (Cramp 1998). Incubation lasts 20-22 days and eggs typically hatch asynchronously with a delay of 24 hours between each egg. Nestlings are fed by both parents until fledging. No post-fledging parental care is known in this species (Cramp 1998).

Previous studies (Lack 1956; Perrins 1964) have indicated that mortality in this species is very high before fledging and that growth patterns profoundly affect long-term fitness, because a higher body mass at fledging and a delay in the time of fledging can increase survival probability (Perrins 1965, 1988). Nestling mortality is mainly due to starvation (Lack 1956; O'Connor 1979), which, in turn, is related to inclement weather conditions (Thomson *et al.* 1996; Lack & Lack 1951; Gory 1987; Cucco *et al.* 1992). Being aerial feeders, Common Swifts are particularly sensitive to meteorological conditions because both their foraging success and the availability of invertebrate prey can be severely affected by adverse weather (Avery & Krebs 1984; Arlettaz *et al.* 2010). Indeed, adults can prolong incubation during periods of bad weather (Cramp 1998), and age at fledging strongly depends on weather conditions (Hudec 1983). Brood size and nestling features can also affect survival and growth patterns by modulating the intensity of intra-brood competition for resources. Despite the fact that the Common Swift is a monomorphic species, males and female nestlings may show different susceptibility to rearing conditions, as demonstrated in the closely-related Alpine Swift (Bize *et al.* 2005), or differ in their ability to compete with nest mates for resources.

Furthermore, the reproductive period in the Common Swift is tightly scheduled. Adults start nesting soon after their arrival at the breeding quarters and leave soon after fledging of their nestlings or even a few days before (Cramp 1998). Timing of breeding may therefore influence offspring survival, because nestlings born late in the season may suffer higher mortality due e.g. to premature nest desertion by parents (especially by inexperienced individuals at their first breeding attempt; Cramp 1998).

Because many offspring developmental traits can potentially be affected by their rearing environment, we took into account different aspects of nestlings' early stages of life. First, we investigated the influence of meteorological conditions, brood size, hatching date, position in the hatching hierarchy and age, on nestling survival. Secondly, we analysed variation in nestlings' growth patterns from hatching to fledging according to brood size, hatching date, sex and hatching order. Throughout, we refer to 'growth' as the overall gain in mass of individuals, including thus both skeletal and muscle growth (and accumulation of fat towards the pre-fledging period). In order to analyse growth patterns, we interpolated growth curves from repeated measures of nestlings' body mass to fully describe the growth trajectory of each nestling. We were interested in investigating potential differences in the entire pattern of nestling growth because the entire growth trajectory, and not just the final mass nestlings achieved, may affect their future survival (Gebhardt-Heinrich & Richner 1998). Because Common Swift nestlings experience a period of considerable body mass recession (up to 20% of their weight) before fledging, we used double-Richards (or positive-negative Richards) growth curves, which are able to fully describe both nestlings growth and their following mass recession (Oswald *et al.* 2012). Thirdly and finally, we investigated the possible effects of weather conditions on nestling growth rate and their potentially differential influence on nestlings of different sex, age and hatching order. In particular, we focused on the linear phase of nestling growth (hereafter Linear Growth Phase (LGP)) because during this phase nestlings grow at maximum rate and are maximally sensitive to short-time variation in meteorological conditions (Lack 1956).

Overall, based on previous studies, we expected mortality to increase during spells of bad weather (Lack & Lack 1951; Rajchard *et al.* 2006), and in large clutches, where the negative effects of the hatching hierarchy should be more evident. In addition, we expected nestlings to grow faster in smaller broods (Martins 1997) and, among broods, to observe a large difference between the first and last hatched sibling (Martins 1997), with the latter showing slower growth as a result of a disadvantage in the hierarchy among siblings for access to parentally delivered food. We also expected growth rates during the Linear Growth Phase to decrease during bad weather conditions. Finally, we had no clear predictions concerning sex differences in growth and environmental susceptibility because sex differences have not been taken into account in previous studies of Common nor of the closely related Pallid Swift *Apus pallidus* (Martins & Wright 1993; Cucco & Malacarne 1996; Martins 1997). However, according to previous studies on Alpine Swifts, we might expect that female nestlings are more susceptible to harsh rearing conditions (Bize *et al.* 2005).

METHODS

Study site and data collection

Fieldwork was carried out from 20 April to 2 August 2012 in colony breeding in a tower in San Paolo, Brescia, Italy (45°22’10.57” N, 10°01’34.01”E). The tower hosts 284 artificial cavities used by Common Swifts for nesting, which can be easily accessed from inside the tower.

Nests were inspected every two to four days to assess hatching date and monitor nestling growth. When a nestling was found for the first time its hatching date (and hence hatching order) was determined according to its morphological features (Jongsomjit *et al.* 2007; Tigges 2008). The mean value of hatching order was used for nestlings for which a clear size hierarchy was not evident and thus likely hatched on the same day (for example 1.5 is the hatching order of the first two siblings hatched on the same day). All newly hatched nestlings were marked with different non-toxic colours on the skin of the legs in order to be individually identified until they reached an age when they could be ringed (10-12 days) with individual metal rings.

At each visit, nestlings were weighed to the nearest 0.1 g by means of a digital balance (Constant Digital Pocket Scale 14192-97, US Balance, Vincennes, IN). At ten days of age we collected a blood sample for molecular sexing from each nestling by puncturing the brachial vein. Blood was collected in heparinized capillary tubes and stored fresh while in the field and then frozen at -20 °C within a few hours from collection.

Molecular sexing

Nestlings were sexed after PCR amplification of the sex-specific avian CHD gene. DNA extraction was performed by an alkaline lysis of blood samples with 50 mM NaOH. Between 50 and 100 ng of genomic DNA was used as template. A region of the CHD gene was amplified using the P2 and P8 primers proposed by Griffiths et al. (1998). The amplification was carried out in a total volume of 15 µl with the following final reaction conditions: 2 mM $MgCl_2$, 0.2 mM of each deoxynucleotide (dNTPS) (Fermentas, Vilnius, Lithuania), 100 ng of each primer (Sigma-Genosys, St. Louis, MO), 0.625

units of Taq polymerase (Promega, Waltham, MA) and 5X Green GoTaq Flexi Buffer. Polymerase chain reaction was carried out in a T1 thermocycler (Biometra, Goettingen, Germany) under the following conditions: 94 °C for 7 minutes, followed by 30 cycles of 48 °C for 30 seconds, 72 °C for 30 seconds and 94 °C for 60 seconds. The reaction finished with the last steps of 48 °C for 30 seconds and 72 °C for 5 minutes.

PCR products (15 µl) were digested with Hae III and Asp700I (Roche Diagnostics, Mannheim, Germany), following the procedures described in detail in Sacchi *et al.* (2004). We stress that the combined use of the two enzymes should avoid any misleading assignment. Digestion products were analysed by agarose gel electrophoresis (2% in Tris borate EDTA) and visualized under UV light after ethidium bromide staining. GeneRuler 50 bp DNA Ladder (Fermentas, Vilnius, Lithuania) was used as size marker. A single band identified a male and two different bands identified a female.
Positive controls obtained from adults of known sex were included in the sexing protocol.

Meteorological variables

Data on air temperature measured 60 m above ground level, and rainfall collected at one-hour intervals at a meteorological station located about 9 km from the colony were obtained from the Agenzia Regionale per la Protezione dell'Ambiente (ARPA, www.arpalombardia.it). Data on wind speed were obtained from the Reanalysis I Project of the National Oceanic and Atmospheric Administration (http://www.cdc.noaa.gov). We use the *NCEP.interp* procedure of the *RNCEP* package in R (Kalnay *et al.* 1996) to interpolate the mean value of both U- (East/West, variable "uwnd") and V-Wind Component (North/South, variable "vwnd") at one-hour intervals from the 1000 mb to the 925 mb pressure level (approximately from ground level up to 750 m from ground). We then calculated for each hour the total wind speed as the square root of the sum of the squared values of U-Wind and V-Wind. Finally we calculated mean daily values of wind speed. Throughout the paper dates are expressed as days from 1 January = 1.

Mortality analyses

Individual mortality was assessed at each visit by recording all nestlings found dead in the nest. In addition, all nestlings that disappeared from the nest before the age of 35 days were considered dead because this is the minimum age recorded at fledging (Cramp 1998). For each nestling we generated a dichotomous variable ("death") indicating whether it died (or disappeared prematurely; death = 1) in the days between consecutive visits at the nest (simply 'interval' hereafter), or it was present at the nest during an interval (death = 0).

We calculated the mean number of nestlings in the nest during each interval as the mean number of nestlings found in consecutive visits at the nest. This variable should account for the intensity of sibling competition for parental resources during each interval. We also calculated the mean age of each nestling during each interval. Mean date and mean nestling age at each interval were highly correlated (r = 0.79). In order to account for potential seasonal effects, we therefore included nestling age and hatching date instead of mean date of each interval among predictors. Mean temperature at each interval and nestling age were highly correlated (r = 0.66).

We therefore calculated the residuals from the regression of mean temperatures on mean dates and included this variable as covariate in the model because it was not correlated with age (r = 0.11). Hence, negative values of temperature residuals indicate lower temperatures than those expected from the seasonal trend, and positive residuals higher temperatures. Temperature residuals were negatively correlated with rainfall (r = -0.44) and with wind speed (r = -0.62), while the correlation between rainfall and wind speed was weak (r = 0.21).

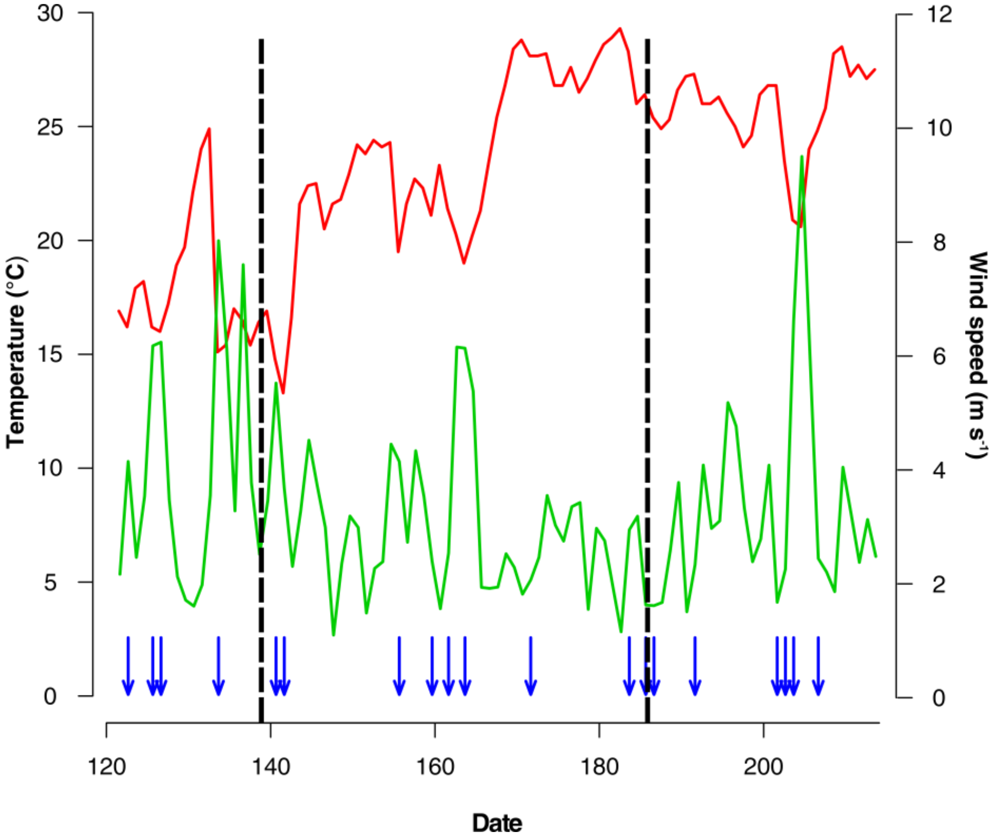

Figure 1. Meteorological conditions during the entire study period in the area in Northern Italy where our study colony of Common Swifts is located. In red: mean daily values of temperature; in green: mean daily values of wind speed: blue arrows indicate days when rainfall events occurred. Rainfall events varied between a total of 0.2 and 44.0 mm rain per day. Dashed lines delimit the period that includes the Linear Growth Phase for all nestlings of the colony. Dates are expressed as days from 1 January = 1.

To properly model death events, we built a discrete time hazard model (because death events were assessed only during visits at a nest) that also included random effects to account for repeated observations of the same nestling (up to its death or its fledging) and for clustering of nestlings within broods.

This type of model can be built using a Generalized Linear Mixed Model (GLMM) assuming a binomial error distribution (McDonald & Rosina 2001; Del Bianco & Borgoni 2006). Death events were modelled according to mean wind speed, a dichotomous variable accounting for occurrence of rainfall events during each interval (rainfall, hereafter), temperature residuals, nestling hatching date and age, and mean number of nestlings at a nest during each interval. In addition, preliminary inspection of the data suggested that probability of death steeply increased for fourth-hatched nestlings (see Figure 2a). Therefore we also included among the predictors also the interaction between mean number of nestlings and hatching order. Nest and nestling identity were included as random factors to account for repeated observations of the same nestling and for non-independence of data from the same brood. Nestling sex was not included among predictors in this analysis because 10 nestlings died at a very young age before the blood sample for molecular sexing could be taken and excluding individuals that died very young could have potentially biased the results of this analysis. The analysis was performed with the g*lmer* procedure in the *lme4* package in R 3.0.2 (R Core Team 2013).

Growth curves

We discarded from the analysis all the individuals that prematurely died or disappeared from the nest because their growth patterns may not reflect those of nestlings that successfully fledged. We also discarded from this analysis 16 nestlings from 12 nests that we were unable to molecularly sex.

To model nestling growth we used curves of the double-Richards family, which are described by the general equation:

$$y = \frac{A}{\left[1+m\, e^{-k(t-i)}\right]^{\frac{1}{m}}} + \frac{A'}{\left[1+m'\, e^{-k'(t-i')}\right]^{\frac{1}{m'}}} \qquad \text{Equation 1}$$

where *y* is the estimated mass at age *t*, *A* and *A'* are the asymptotes of both increasing and decreasing curves; *k* and *k'* are the rates at which the slope of both curves changes with age; *i* and *i'* are the inflection points, corresponding to the age at which the nestling shows its fastest growth (or weight recession); *m* and *m'* are the shape parameters of the generalized logistic curves.

The widespread application of these curves in the ornithological literature has been hampered by computational difficulties in fitting non-linear regression models. Recently, a new package called *FlexParamCurve* (Oswald *et al.* 2012) has been released for the software R (R Core Team 2013). This package allows fitting 32 possible growth curves of the double-Richards family (all possible reductions in the second curve, fixing *A'*, *k'*, *i'* or *m'* both when *m* is fixed or estimated). This package also provides automatized routines for assessing which curve, among the 32 alternative parameterizations of the double-Richard curve, best fits the data at hand.

We used the *pn.modselect.step* routine to identify the parameterization of the double-Richards curve that best fitted our data (see Oswald *et al.* 2012 for details). This routine selected a curve where parameters *A, k, i,* of Equation 1 varied among individual nestlings, while the other five were fixed to their mean value among all nestlings, (curve # 32 of the *FlexParamCurve* package).

We used a Non-Linear Mixed Model (NLMM), whereby nestling body mass at each visit was modelled as a double-Richard curve of nestling age, for investigating whether variation in the three parameters of the curve that differed among nestlings was affected by sex, hatching date, hatching order of each nestling ('nestling features' hereafter) and mean brood size. In these analyses, and differently from the other models, mean brood size was calculated as the mean number of nestlings present at *all* the visits at the nest, because only covariates that did not vary within nestling could be entered in this model. Nestling and nest were entered as random grouping factors. NLMMs allow large flexibility in the model parameterization because it is possible to model any parameter of the growth curve as a function of different predictors. This flexibility extends also to the random part of the model, because it is possible to enter different random structures for each parameter of the growth curve. However, NLMMs are challenging statistical tools. To reduce the complexity of these models we ran preliminary analyses to assess which (combination of) predictor(s) seemed to affect each of the three parameters of the growth curve that differed among nestlings.

To assess the structure of both the fixed and the random part of the NLMM we first interpolated double-Richards curves (curve #32; Oswald *et al.* 2012) to weight data of each nestling separately and noted the value of the estimated parameters. We then included each parameter as dependent variable in separate Linear Mixed Models (LMMs), where brood size, sex, hatching date and hatching order were entered as predictors, while nest was entered as a random effect. Significant predictors were noted, and these pieces of information were used to build the fixed part of the final NLMM.

We also re-ran the same models by removing the random nest effect, and compared their fit with that of LMMs by means of the Akaike's Information Criterion. If the LMM had a lower AIC than the corresponding linear model, then nest was entered as a random factor for that parameter in the final NLMM.

Finally, repeated measures of the same nestling often show temporal autocorrelation, and variance in nestling weight also usually increases with nestling age. In the final NLMM we therefore assumed a residual autocorrelation with lag up to ten days, and a variation of the variance with age according to an exponential function, as suggested in Oswald *et al.* (2012).

LMMs and LMs were fitted by the *lme* procedure and *gls* procedure in the *nlme* package (Pinheiro *et al.* 2013). NLMM was fitted by the *nlme* procedure in the *lme4* package. All the analyses were run in R 2.15.0.

Influence of weather conditions on nestling growth during the Linear Growth Phase

To objectively identify the age range of the Linear Growth Phase, which is unknown for the Common Swift, we sought to identify the age range whereby a linear function best approximated the double-Richards curve identified in previous steps. To this end, we first identified, from the growth curve obtained in the previous analysis, the age when Common Swift nestlings grow at maximum rate (maximum of the first derivative of the double-Richards curve estimated as above with parameters set to the mean values of nestling features). We then fitted a linear function to the nestling weights estimated by the growth curve (one data point per day) for all the possible age intervals including the age when maximum growth rate was attained. The Linear Growth Phase was then estimated as the longest interval in which the linear function approximated the double-Richards curve with $R^2 \geq 0.999$. This procedure indicated that the Linear Growth Phase of Common Swift nestlings spanned from age 5 to 14 days.

We then selected only weights recorded during the Linear Growth Phase of each nestling and calculated nestling daily growth rates as the differences in body mass divided by the number of days between consecutive visits. Daily growth rates of each nestling were then modelled in a LMM assuming a Gaussian error distribution, including as predictors the linear and the squared term of residuals of temperature on date, occurrence of rainfall (dichotomous variable) and mean wind speed in the interval, together with sex, age and hatching order and mean number of nestlings present at the nest during the interval. The squared value of temperature residuals was entered because preliminary analyses suggested possible non-linear effects of temperature, but not of wind speed, on nestling growth rate (details not shown). Temperature residuals were negatively correlated with rainfall ($r = -0.46$) and with wind speed ($r = -0.64$), while rainfall and wind speed were positively correlated ($r = 0.49$). Nest and nestling identity were included as random grouping factors to account for repeated observations of the same nestling and for non-independence of data from the same brood. The analysis was performed with the *lmer* procedure in the *lme4* package in R.2.15.3, with degrees of freedom set conservatively to the number of nests included in the analysis.

RESULTS

Mortality

During the 2012 breeding season, 26 nestlings from 18 nests were either found dead (16 nestlings) or disappeared prematurely from the nest (10 nestlings), while 112 nestlings from 47 nests successfully fledged. The probability that a nestling died between two consecutive visits at a nest varied according to hatching order, mean number of nestlings present at the nest during the period between the visits and the interaction between these variables (Table 1). In particular, first-hatched nestlings had lower probability of dying than late-hatched ones (Figure 2a). The probability of dying decreased with an increasing number of siblings (Figure 2b). However, closer inspection of the coefficients indicated that fourth hatched nestling had always the largest probability of dying. Furthermore, we re-ran the same analysis excluding the five nests with four nestlings. The coefficients of this model showed that the interaction between hatching order and mean number of nestlings was no longer significant, while their main effects were confirmed (details not shown), thus indicating that in the model that included all of the data, the significance of the interaction represented the steep increase in mortality of fourth-hatched nestlings. Collinearity among meteorological variables did not severely affect model coefficients, because models where each weather variable was included singly gave qualitatively similar results (details not shown).

Growth patterns

Ninety-one nestlings (46 males and 45 females) from 44 nests fledged at an age >35 days and could be molecularly sexed. Mean brood size was 2.38 ± 0.08 se and mean hatching date was 145.3 ± 0.79 se (24 May).

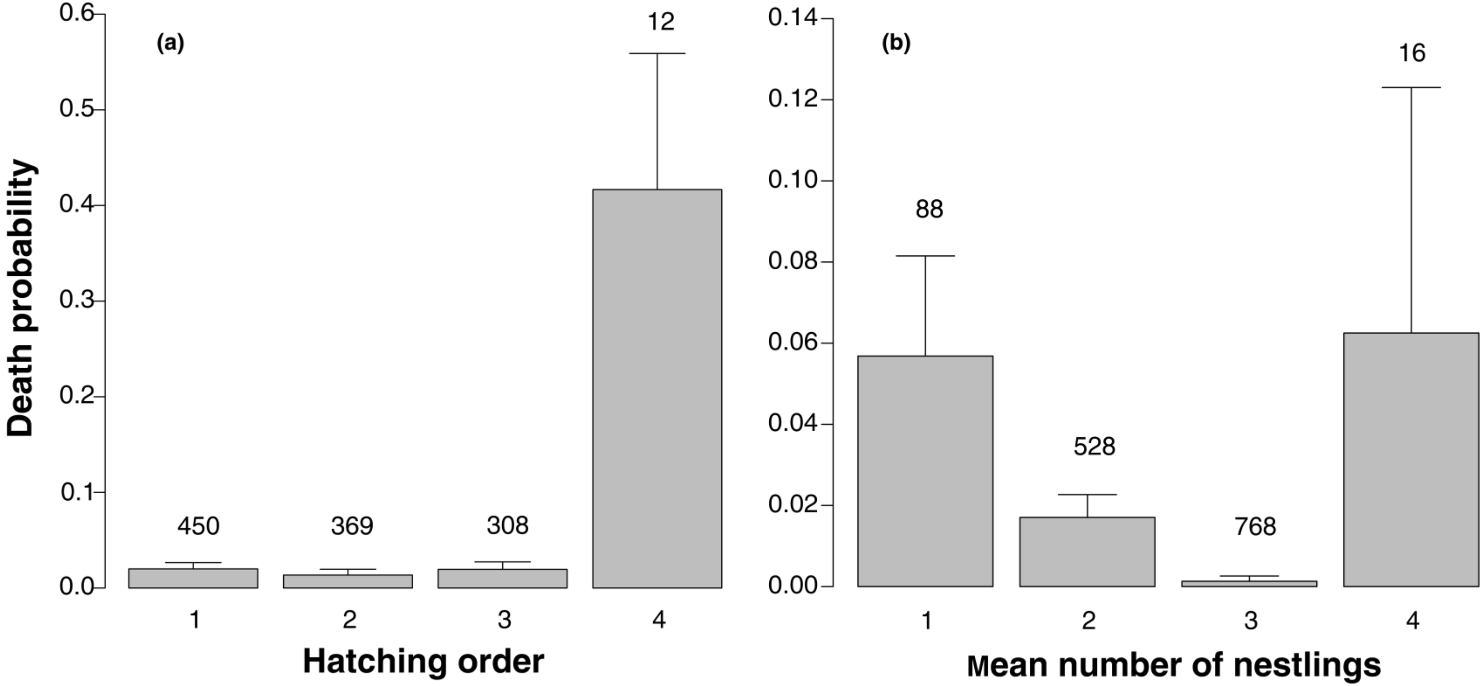

Figure 2. Mortality in relation to: A hatching order and B mean number of nestlings present in the nest. Bars represent binomial standard errors and numbers represent number of nestlings in A and number of nests in B. Only integer values of mean number of hatching order and nestlings are shown.

Growth curves interpolated separately from data from each nestling indicated that maximum weight (parameter *A* of the Double-Richards curve - see Figure 3 and Equation 1) was 50.30 ± 0.37 se g on average, the rate at which the slope of the increasing part of the curve changed with age (parameter *k*) was 0.21 ± 0.01 se g day^{-2} and mean inflection point of the curve (parameter *i*) occurred when nestlings were on average 9.54 ± 0.15 se day old (Figure 3).

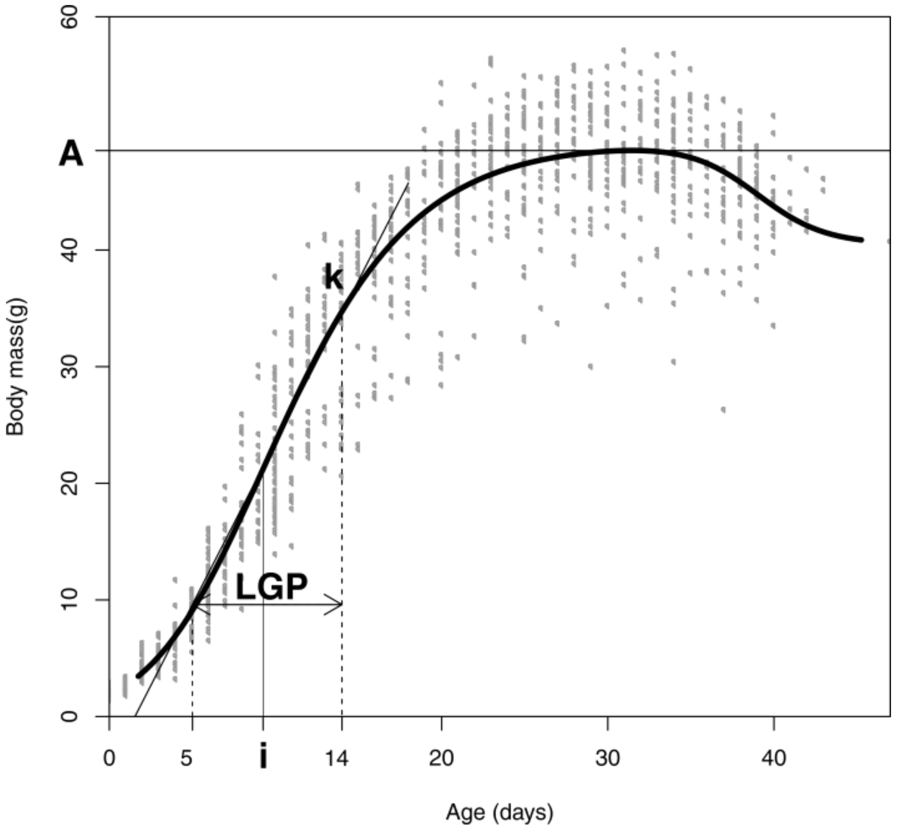

Figure 3. Body mass of nestlings that fledged successfully (light grey points) in relation to age. A double-Richards growth curve #32 (Oswald *et al.* 2012) was drawn using the coefficients of the NLMM shown in Table 2 and the mean brood size and hatching date of the population. Parameters *A*, and *i* of the double-Richards curve are shown, as well as the Linear Growth Phase (LGP).

The coefficients of the final model (Table 2) indicated that nestlings in late broods, on average, grew faster (negative effect of hatching date on parameter *k*) and experienced the fastest growth rate at a younger age (negative effect of hatching date on parameter *i*) than those of early broods (Table 2, Figure 4). These nestlings, however, reached a significantly lower maximum weight than nestlings born early in the season (negative effect of hatching date on parameter *A,* Table 2, Figure 4). In addition, the maximum weight reached by nestlings of large broods was significantly lower than that reached by nestlings of small broods (negative effect of brood size on parameter *A,* Table 2, Figure 4). Significant differences among nestlings in growth patterns, therefore, are produced by features that are shared or very similar between all siblings in a nest, namely brood size and hatching date. Indeed individual features, namely sex and hatching order, did not affect growth curve parameters.

Linear Growth Phase, weather conditions, and growth rates

The Linear Growth Phase occurred between 5 and 14 days of age for nestlings. Daily growth rates were calculated for 191 intervals from consecutive body mass measures of the 91 nestlings considered in previous analyses. Mean daily growth rate during the Linear Growth Phase was 2.97 ± 0.11 se g day^{-1} (min = 0.6 g day^{-1}, max = 7 g day^{-1}). Overall, Linear Growth Phases occurred between 18 May (day 139) and 4 July (day 186). On these days mean daily temperature was 23.6 ± 0.6 se °C, with a minimum value of 9.5 °C registered on 19 May and a maximum value of 35.0 °C registered on 1 July. Rainfall occurred in 9 out of 48 days. Mean daily wind speed was 1.45 ± 0.07 se m s^{-1}, with a maximum hourly value of 6.8 m s^{-1} recorded on 21 May.

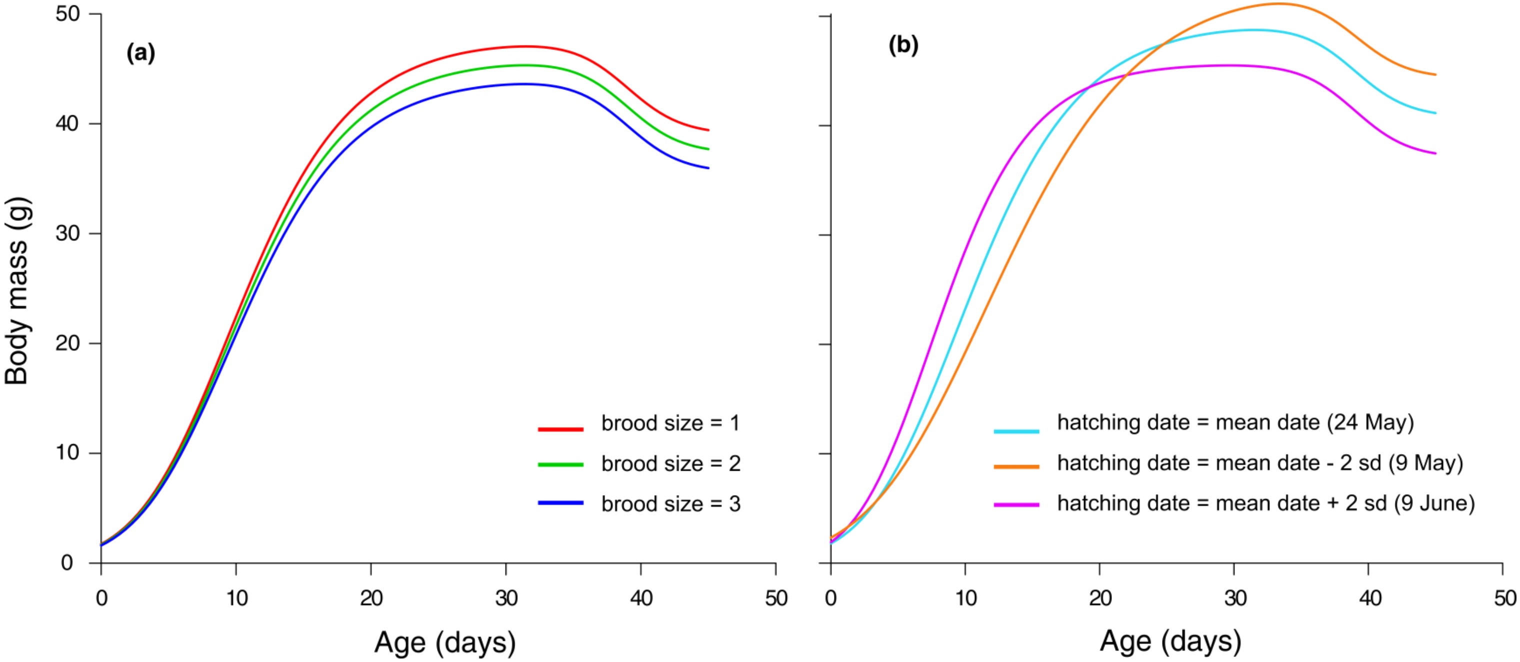

Figure 4. Double-Richards growth curves drawn using the coefficients of the NLMM (Table 2) at A) mean hatching date of all broods considered but different values of brood size and B) mean size of all broods, but different values of hatching date.

Nestling growth rate varied non-linearly with the residuals of mean temperature on date, with nestlings growing significantly faster when residuals of temperature had intermediate values (Table 3, Figure 5a). In particular, coefficients of the model indicated that nestlings grew faster when temperature was 0.52 °C higher than that expected from seasonal trend. Furthermore, significant and positive effects of rainfall and of mean wind speed indicated that nestlings grew significantly faster during intervals when wind was moderate (Table 3, Figure 5b) and when rain events occurred (Figure 5d). Collinearity among meteorological variables did not severely affect model coefficients, because models where each weather variable was included singly gave qualitatively similar results (details not shown). Finally, a negative effect of mean age suggested that, after controlling for the other effects, growth rate of *individual* nestlings significantly decreased with age (Table 3, Figure 5c).

Here we investigated the influence of the rearing environment on the first stages of life of Common Swift nestlings breeding in artificial nest boxes in Northern Italy. We analysed the possible effects of meteorological conditions, nestling features (sex and hatching date and order), and number of nestlings at a nest, which was used as a proxy for the strength of competition for resources between siblings, on nestlings' survival until fledging and growth patterns. We analysed the effect of these factors both along the entire pre-fledging period, including the physiological body mass recession that takes place before fledging, and in detail during the Linear Growth Phase, when growth rate is maximal.

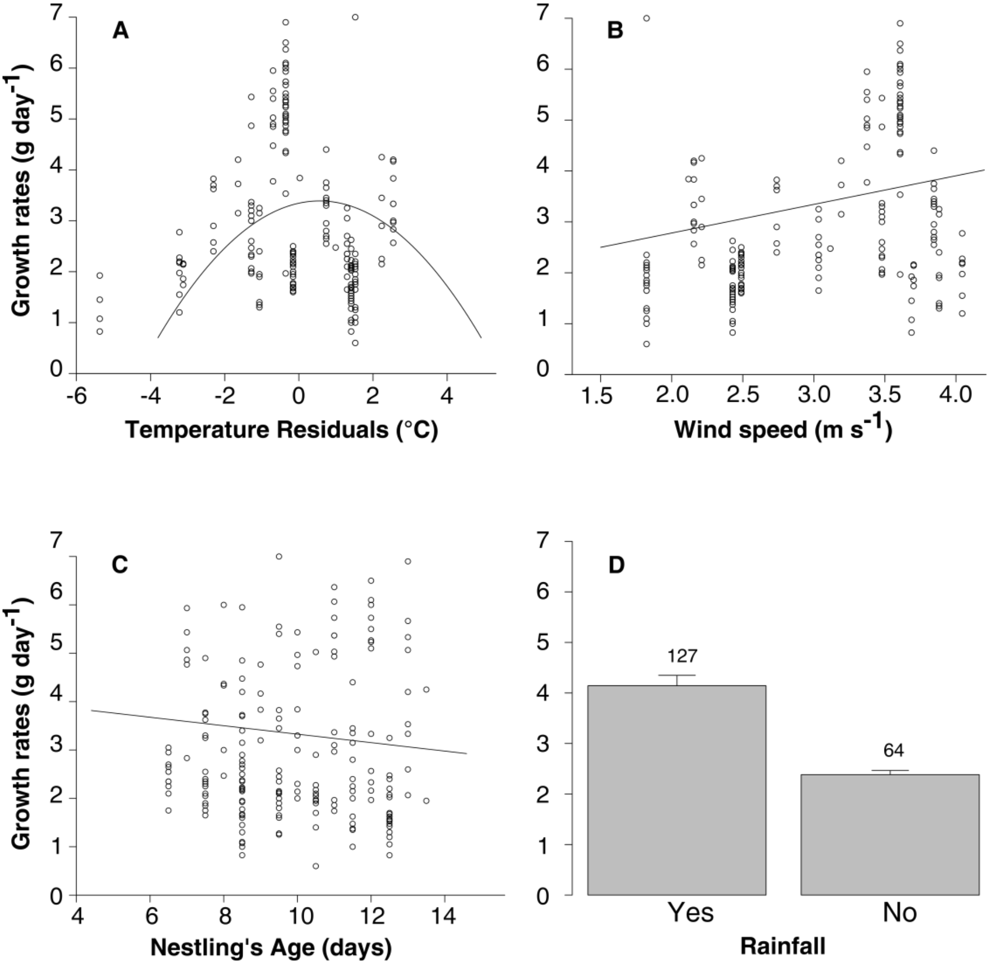

Figure 5: Growth rates in relation to A) the residuals of temperature on date; B) wind speed; C) mean nestling's age. The fitted LM curves from Table 3 are shown. D) Mean growth rates measured during intervals with and without rainfall events. Bars represent standard errors and numbers represent sample sizes.

DISCUSSION

Previous studies on Common Swifts have suggested that temperature, rainfall and wind speed negatively influenced the survival of Common Swift nestlings during the rearing period. Lack & Lack (1951) showed that nestling mortality in a breeding colony in Oxford (UK) was higher in poor weather conditions and in the same breeding colony, Martins & Wright (1993) observed a significant brood reduction event in a single year of harsh weather.

In Scotland Thomson *et al.* (1996) found that breeding success was negatively correlated with mean temperature in June. Conversely, we found no effect of rainfall, temperature and wind on nestlings' mortality. This difference in the effect of meteorological conditions on nestling mortality should however be interpreted in the light of the general climatic conditions of the Po River Plain, where our breeding colony is located. Indeed, spring is typically warm in this area (mean May temperature in the study area was 18.9 °C in 2012), summer is hot (mean July temperature was 25.9 °C in 2012, see also Figure 1 and it is one of the less windy regions in Italy (according to the Italian Interactive Wind Atlas, www.atlanteeolico.rse-web.it accessed on 10 May 2013; the range of daily average wind speeds we observed was between 1.04 m s^{-1} and 9.0 m s^{-1}, corresponding to grade 1 ("light air") to grade 5 ("fresh breeze") in the Beaufort scale, see also Figure 1). These climatic conditions differ from those of the UK, where most of the other studies on the Common Swift were conducted, where the summer is fresh and wet (in June 2012 in Oxford mean air temperature was 17.1 °C and total rainfall was 151.7 mm, according to data collected at the Radcliff Meteorological Station and available at www.geog.ox.ac.uk). Therefore, it is likely that the meteorological conditions considered in this study showed only modest variations during the period when our study was carried out, that did not affect nestlings' survival. Alternatively, the effects of weather conditions on nestling survival may vary markedly among populations breeding in different geographical areas of Europe (Rajchard *et al.* 2006), or may depend on the general climatic condition of the region where the colony is located (Salewski *et al.* 2013).

In our analysis of nestling survival we also accounted for competition for resources among siblings, the intensity of which was summarized by the number of nestlings present at a nest during the interval between two consecutive visits, for hatching order, nestling age, and hatching date which may reflect seasonal variation in parents' quality (see Hasselquist & Kempenaers 2002 for a review). We found that nestling mortality increased with hatching order, probably as a result of intra-clutch hierarchies and domination of older siblings over younger ones. O'Connor (1979) showed that in the Common Swift, nestlings hatched from last eggs had reduced survival prospects, due to failure in competition for food with older, larger siblings. This has been confirmed by behavioural observations of food distribution in the closely related Pallid Swift, which showed that last hatched nestlings obtained less food than their older siblings, and, consequently, were the more likely to die (Malacarne & Cucco 1991; Malacarne *et al.* 1994). In our study the number of siblings at a nest, however, seemed to enhance, rather than reduce, nestlings' survival prospects. This may be due to variation in parental quality, with larger broods being reared only by experienced or high quality parents (Clutton-Brock 1988; Newton 1989). However, fourth-hatched nestlings always had the lowest survival rate. This is consistent with previous observations of Common Swifts where four nestlings fledge successfully only very rarely (Martins & Wright 1993; Perrins 1964). Finally, after accounting for the effects of the other variables, we observed that nestling age did not affect survival. This result was unexpected because in birds survival usually increases with nestling age (at least up to fledging, Peak *et al.* 2004, Grant *et al.* 2005).

In the second part of our work we detected a significant inter-individual variability in growth patterns in the phase of weight increase, but not in that of the pre-fledging mass loss, as indicated by the fact that the parameters of the decreasing part of the growth curve did not vary significantly among nestlings. Moreover, nestlings from late broods, on average, grew faster and experienced the fastest growth at a younger age than those of early broods. This finding corroborates the idea that nestling growth is a flexible trait that can be adaptively modified to match environmental conditions (Mainwaring et al. 2010). Common Swifts have a tightly scheduled reproductive season (Cramp 1998): adults arrive at breeding sites in Northern Italy in mid-April and depart for Africa at the end of July together with newly-fledged nestlings, which leave for their winter quarters almost immediately after fledging (Cramp 1998). Such tightly scheduled reproductive activity may have favoured the evolution of rapid early growth in nestlings from late clutches, which may allow them to be ready to migrate in a shorter time. Indeed model coefficients indicated that a hypothetical nestling hatched on May 9 (the mean hatching date of the colony minus 2 sds) reached its maximum weight at 34 days of age, while a nestling born on June 9 (the mean hatching date of the colony plus 2 sds) reached its maximum weight at 30 days of age. However, rapid early growth may be at a cost of pre-fledging body mass. Indeed, nestlings born late in the season reached a lower maximum weight than those hatched earlier (the predicted difference in maximum weight between a nestling hatched on 9 May and one hatched on 9 June is 5.64 g corresponding to 11.2% of the mean maximum weight of nestlings estimated by the double-

Richards curve). This difference also implies that late-hatched nestlings reached a lower body mass at fledging, because body mass recession (parameter A') did not vary among nestlings in our study population. This could severely affect the fitness of late-hatched nestlings, because many studies have indicated that body mass at fledging is a good proxy of future survival in birds (Perrins 1965; Gustaffson & Sutherland 1988; Tinbergen & Boerlijst 1990; Wright *et al.* 2006).

Maximum weight was also significantly lower in fledglings from larger broods which was expected because of a higher competition for food among nest mates in larger broods. Indeed, Martins & Wright (1993), with an experimental manipulation of brood size, showed that the amount of food delivered by parents to each nestling decreased with brood size in Common Swifts. However, the difference in maximum weight among nestlings grown in broods of two or three nestlings is equal to only 1.6 g (i.e. 3.2 % of maximum weight) on average according to model-predicted values.

Finally, sex and hatching order did not affect variation of growth patterns between individuals. The fact that male and female nestlings did not show any significant difference in their growth patterns is not surprising for a sexually monomorphic species like the Common Swift, although other studies on size-monomorphic species have found some differences in growth between sexes (see for example Rosivall *et al.* 2010 on the collared flycatcher *Ficedula albicollis*).

Conversely, the finding that hatching order had no significant effect on growth trajectories was surprising, and may be due to the fact that for the analyses of growth patterns we considered only nestlings that successfully fledged and therefore excluded from the analyses all fourth-born nestlings, because none of them successfully fledged in the reproductive season of

2012. This selection could have potentially prevented our ability to reveal any effect of hatching order on growth patterns. We stress, however, that on the one hand, information on all nestlings that were found dead or that prematurely disappeared from the nest was considered in the previous analysis of mortality. On the other hand, growth trajectories of nestlings that were in very poor condition and that died prematurely were graphically inspected and appeared markedly aberrant compared to those of successfully fledged nestlings (details not shown). Their inclusion in an analysis of "normal" growth rates was therefore untenable.

We note that all the features that appear to produce significant differences in growth patterns among nestlings, namely hatching date and brood size, were shared between all siblings in a nest. Hence, our results suggest that differences in the rearing environment among broods or in parental quality are more relevant in influencing nestlings' growth then nestlings' individual quality or ability to compete for food with nest mates. Parents-offspring interactions may therefore be more important than sib-sib interactions in shaping Common Swift nestling growth trajectories.

In the last part of our study we investigated in detail the effects of weather conditions on nestling growth, focusing on the Linear Growth Phase of nestlings that successfully fledged. Growth rate is an excellent indicator of the effects of environmental condition on nestling fitness, because it varies on a temporal scale similar to that of variability in weather patterns (Richner 1989; McCarty & Winkler 1999). We found that Common Swift nestlings grew at faster rates on days when the temperature was close to that expected from the seasonal trend, whereas their growth was slower at temperatures above and below the seasonal trend. Moreover, growth was faster during rainy and windy days. Several studies have indicated that in the Common Swift the most important and critical factor affecting nestlings' growth is food supply (Lack 1947; Newton 1980; Martin 1987, 1995). In a strictly aerial insectivore like the Common Swift, flying prey availability and adults foraging effectiveness are the major determinants of the amount of food received by nestlings, and both can be strongly affected by weather conditions. Indeed, air insect abundance is influenced by flight activity in response to weather (Taylor 1963; Lewis 1967; Johnson 1969; Pedgley 1990; Peng & Sutton 1992; Poulsen 1996) and also the flight performance and general physical condition of adults can be affected by heavy rainfall (Ortega-Jimenez & Dudley 2012) or intense wind (Richardson 1978; Schmaljohann & Naef-Daenzer 2011). Thus, our findings may seem contradictory compared to the existing evidence. However, local climate conditions seem to affect the relationship between meteorological conditions and food provisioning to nestlings. For instance, in hot and sunny climates, with little or no rainfall and usually light winds, conditions which normally occur in the Po River Plain during May-July, the few moderately rainy days may trigger insect swarms because the insects may require some moisture in the air to survive (Gatehouse 1997). In addition, foraging Common Swifts may also benefit from moderate winds, because turbulent conditions may carry insects to high altitudes, where this species usually performs its foraging activity (Cramp 1998). The non-linear variation of growth rates of nestlings with temperature may reflect the natural variation of airborne insect abundance with temperature, which, for many taxa, increases with temperature up to an optimum and then shows a rapid decline (Williams 1940).

Overall, our results suggest that, in a geographical region where climate is typically hot and characterized by high humidity and very little wind, meteorological conditions such as moderate rainfall or winds, do not influence survival of Common Swift nestlings, and may positively affect their growth. Furthermore, brood size and timing of breeding, which are under parental control, played a major role in influencing offspring survival and development. In contrast, brood size and timing of breeding, were only marginally affected by features of individual nestlings, like their sex and order in the hatching hierarchy. Finally, our study highlighted that growth patterns of nestling Common Swifts show considerable seasonal plasticity, suggesting that they may be adaptively tuned to match the tight reproductive time schedule of this highly aerial species, which leaves for African wintering range by late July-early August (Akesson *et al.* 2012). However, faster growth of late hatched nestlings may not be cost-free, because it results in lower body mass at fledging, with potentially negative consequences on post-fledging survival. Indeed, during the early post-fledging phase, Common Swift fledglings may rely entirely on the energy reserves accumulated when in the nest, because parents are not known to provide care to their offspring once they have left the nest (Cramp 1998). However, the relative fitness costs and benefits of phenotypic plasticity in growth patterns remain a matter of speculation.

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Section 2

Introduction to section 2

Populations of several migratory bird species breeding in Europe are suffering sharp demographic declines in recent decades (Berthold et al. 1998, Sanderson et al. 2006), which have been often attributed to changes in land use and climatic conditions at the breeding areas (Pimm & Raven 2000, Sala et al. 2000, Both et al. 2006). However, populations of these long-distance migrants spend parts of their life in areas of the world usually thousands of kilometers apart, and therefore they are influenced also by variations in the conditions experienced in wintering quarters as well as in staging areas during migration. Furthermore, patterns of change in ecological conditions in breeding and wintering areas and along migration routes are often divergent. For instance, climate change has been shown to occur at uneven rates in different areas of the globe, usually showing a more pronounced warming at high latitudes than at the equator (Houghton et al. 2001). A resident bird species living at Northern Latitudes may therefore experience a more marked pattern of climate change through the whole year, while a long-distance migrant wintering at Southern latitudes may suffer such rapidly-changing ecological conditions only for a part of its annual life-cycle. Nonetheless, adapting to changing climatic conditions might be easier for resident species, since they must tune all the phases of their life-cycle, which are usually tightly linked to one-another, to the same rate of climate change, as they always stay in the same geographical area. Conversely, long-distance migrants might be in difficulties in adjusting their phenology according to the divergent patterns of climate change that they experience at their breeding and wintering grounds and during migration.

In order to identify the possible impact of the variation in ecological conditions on the population dynamics of migratory species, detailed information about their migratory behavior and the position of their wintering quarters is essential. For many long-distance migrants, however, migration routes and wintering quarters were only roughly identified until recently, in particular those of small sized species, which represent the large majority of migrant birds. Indeed, although new technologies for bird tracking have been widely used in the last decades, only in recent years, new miniaturized and relatively cheap devices have been introduced, which allowed the tracking of species weighting less than 100 g (Stutchbury et al. 2009).

During the last century, by collecting information on millions of ringed birds, ornithologists have gathered a huge amount of data that can be used for extensive studies of migration. Despite the fact that these data do not allow to obtain a precise identification of migration routes at individual level, for long time they will represent one of the few ways to investigate temporal pattern of variation in migratory behaviour.

In the first study reported in this chapter we took advantage of the large number of ring recoveries available for the Barn Swallows to assess timing of migration and main migration routes at continental level of individuals breeding in Europe both during autumn and spring migration. We also modelled the variation of migration phenology over time to assess the impact of climate change on the timing of migration of this species.

In the second study we applied miniaturized tracking devices to more than one hundred Barn Swallows breeding in Northern Italy and Southern Switzerland. The data we collected allowed us to obtain detailed information on timing of migration and position of their wintering areas.

In the third paper we evaluate the impact of the application of these new instruments on survival and breeding success of individuals, since recent studies have advanced the hypothesis that they could be not riskless (Barron et al. 2010, Costantini & Møller 2013).

In the fourth study we combined information on wintering grounds and migration routes obtained both from analysis of ring recoveries and the application of geolocators with long-term data on Barn Swallows population dynamic from Northern Italy. Our aims were to investigate the effect of environmental conditions encountered during different phases the whole life cycle on the year-to-year variation in the number of breeding pairs

Finally, in the fifth paper we analyzed a long-term series of ringing data on the European Robin, whose individuals exhibit different migration strategies being partially residents and partially short-distance migrants. Our aim was to evaluate the possible effect of changing climatic conditions on the spatial and temporal variation in migratory behaviour of individuals from a partial migrant species.

Modelling the Progression of Bird Migration with Conditional Autoregressive Models Applied to Ringing Data.

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Roberto Ambrosini[1], Riccardo Borgoni[2], Diego Rubolini[3], **Beatrice Sicurella[1]**, Wolfgang Fiedler[4], Franz Bairlein[5], Stephen R. Baillie[6], Robert A. Robinson[6], Jacquie A. Clark[6], Fernando Spina[7], Nicola Saino[3]

1. Dipartimento di Biotecnologie e Bioscienze, Università degli Studi di Milano-Bicocca, Milano, Italy

2. Dipartimento di Economia, Metodi quantitativi e Strategie di Impresa, Università degli Studi di Milano-Bicocca, Milano, Italy

3. Dipartimento di Bioscienze, Università degli Studi di Milano, Milano, Italy

4. Max Plank Institute for Ornithology, Vogelwarte Radolfzell, Radolfzell, Germany

5. Institute of Avian Research "Vogelwarte Helgoland", Wilhelmshaven, Germany

6. British Trust for Ornithology, Thetford, UK

7. Istituto Superiore per la Protezione e la Ricerca Ambientale, Ozzano dell'Emilia (BO), Italy

Abstract

Migration is a fundamental stage in the life history of several taxa, including birds, and is under strong selective pressure. At present, the only data that may allow for both an assessment of patterns of bird migration and for retrospective analyses of changes in migration timing are the databases of ring recoveries. We used ring recoveries of the Barn Swallow *Hirundo rustica* collected from 1908-2008 in Europe to model the calendar date at which a given proportion of birds is expected to have reached a given geographical area ('progression of migration') and to investigate the change in timing of migration over the same areas between three time periods (1908-1969, 1970-1990, 1991-2008). The analyses were conducted using binomial conditional autoregressive (CAR) mixed models. We first concentrated on data from the British Isles and then expanded the models to western Europe and north Africa. We produced maps of the progression of migration that disclosed local patterns of migration consistent with those obtained from the analyses of the movements of ringed individuals. Timing of migration estimated from our model is consistent with data on migration phenology of the Barn Swallow available in the literature, but in some cases it is later than that estimated by data collected at ringing stations, which, however, may not be representative of migration phenology over large geographical areas. The comparison of median migration date estimated over the same geographical area among time periods showed no significant advancement of spring migration over the whole of Europe, but a significant advancement of autumn migration in southern Europe. Our modelling approach can be generalized to any records of ringing date and locality of individuals including those which have not been recovered subsequently, as well as to geo-referenced databases of sightings of migratory individuals.

Introduction

Migration is widespread in nature and several taxa, from insects to fishes, amphibians, birds and mammals, undertake annual “incredible journeys” that represent key stages in their yearly cycle [1-3]. Being able to fly, birds are the taxon where migratoriness is most widespread, and on which the majority of migration studies have focused [2]. As a fundamental feature in the life-history of birds, migration is under strong selective pressures [1] However, a large amount of genetic variability in migratoriness, timing of migration, and migration strategies exists in bird populations. In addition, individuals show a high degree of phenotypic plasticity in migration strategy [4]. Genetic variability and phenotypic plasticity allow birds to adjust their migration strategies according to changes in climate and ecological conditions. Indeed, changes in the timing (phenology) of migration are considered signals of the impact of current climate changes on the biosphere [5-7]. However, many species of migrant birds are declining, probably because they are not able to sufficiently adjust the timing of their annual life-cycle to match new climatic conditions [8-10]. Studies of bird migration are hampered by the difficulty of tracking small-sized species, which represent the large majority of migratory birds. New miniaturized and cheap technological devices, like light-level geo-locators, are bridging this gap in our knowledge [11] although the information they provide must be interpreted with caution because of the impact they may have on individual fitness [12-14], and, potentially, also on migration timing and routes [12]. However, especially during the last century, by collecting information on any recovery of millions of birds that were ringed, ornithologists have collected a huge amount of data that can now be analysed for extensive studies of bird migration. Most importantly, these data, together with stable isotope analyses of museum specimens [15], will likely represent, for a long time, the only sources of information allowing for retrospective analyses of changes in bird migration strategies through time.

The analysis of ring recoveries is hampered by several difficulties, the main ones being the large spatial and temporal heterogeneity in ringing effort and in the probability of recovery of a ringed individual [16]. Nevertheless, these data have been useful to study large scale patterns of individual distribution, like migratory connectivity, and long term variation in bird distribution [17-20]. Retrospective analyses of ring recoveries may also allow us to quantify both the progression and the timing of migration. *Progression* of migration is defined here as the proportion of individuals of a given migratory population that, at any given time, have reached or have passed over a given place during migration, while migration *timing* is defined here as the date at which a given proportion of individuals have reached a given location.

In the present paper we show how ring recoveries collected throughout Europe and North Africa in 1908-2008 and stored in the EURING databank (EDB, www.euring.org) can be used to model the progression and the timing of migration of bird species, and its variation over time, using a small passerine, the Barn Swallow *Hirundo rustica,* as an example.

Progression and timing of migration can be statistically modelled by fitting the complementary log-log ('cloglog' hereafter) function [21] which is very similar to the logistic function (see Text S1), to the cumulated proportion of individuals that have reached a given site by a given date. This modelling approach has the advantage that parameters of the interpolated cloglog curve describe both the progression and the timing of migration at a given site, since the function allows us to estimate both the expected proportion of migrants that have arrived or passed at a given date, and, by model inversion, the date when a given proportion of migrants is expected to have arrived at or passed over a given site.

We first modelled progression of spring migration over the British Isles, taking advantage of the very large amount of data available for this area. We then tentatively extended the same model to Europe and north Africa, where data are sparser. Paucity of data from eastern Europe and the Middle East forced us to restrict the analysis to western Europe and the western part of north Africa (western Europe and north Africa hereafter). The same approach was also used to model autumn migration, first in the data-rich British Isles and then in western Europe and north Africa. Secondly, we modelled the variation of migration phenology over time. To this aim we divided the dataset into three periods containing approximately a similar amount of data (1908-1969, 1970-1990, and 1991-2008) and compared median migration date estimated by the cloglog functions describing progression and phenology of bird migration in different geographical areas. Also in this case analyses were run separately for the British Isles and for western Europe and north Africa and for spring and autumn migration, respectively.

Materials and Methods

Datasets

For individually ringed birds, the EDB includes information on date and locality at ringing, as well as at any subsequent encounter. These data will hereafter be defined as “ring recoveries” in order to distinguish them from records of ringing date and locality of individuals, which have not been subsequently recovered ("ringing data" hereafter). Hence ring recoveries include both ringing and finding information of any bird that has been re-encountered.

The EDB almost exclusively include ring recoveries (a few ringing data has been recently included in the EDB, but they were not considered in the present study). Before the analyses we carefully checked the consistency of data in our dataset and excluded any dubious data (details not shown).

The datasets used to model migration in the British Isles consist of 1983 ring recoveries during spring migration (March-June) and 8429 ring recoveries during autumn migration (August-October), while those used for Western Europe and North Africa consist of 11918 ring recoveries (including ring recoveries from the British Isles) collected during spring migration (February-June) and 28832 during autumn migration (August-November, Figure S1). Periods of spring and autumn migration were chosen according to Cramp [22]. Since the relevant information for this analysis is the date at which an individual was observed in a given geographical location, we used all records of individuals found either alive or dead, and retained repeated records of the same individual. Records of nestlings i.e. birds ringed at the nest and unable to fly (EURING age code equal to 1; see Speek *et al.* [23]for further details on the EURING exchange code 2000) were excluded, as well as records of individuals found dead, but not fresh (EURING code 'condition' either equal to 1 or 3 [23]) and those of individuals whose recovery date is known with an accuracy larger than 3 days either side of the reported date (EURING code 'accuracy of date' in 0-2 [23]). Date of recovery is given in days with January 1 as day 1.

Conditional autoregressive models

The British Isles were divided in 38 cells of 1.5° x 1.5° latitude x longitude, while western Europe and north Africa were divided into 67 4° x 4° cells, and each recovery was assigned to a cell (Figure S1). Only cells with ring recoveries recorded in at least four different dates were included in the analyses because interpolation of cloglog curves requires at least four data points per cell. Cell size was chosen as to maximize the geographical coverage of cells suitable for analyses. Only cells to the north of latitude 26° N and to the west of longitude 26° E were considered because data were too scattered outside this area. Some cells could not be included in all analyses due to paucity of data. For the British Isles, 27 cells were included in the spring analyses and 29 in autumn, while for western Europe and north Africa there were 59 cells in spring and 53 in autumn.

The analytical procedure interpolated the cumulated proportion of Barn Swallows recorded in a cell at each date over the periods of spring or autumn migration, by also accounting for the spatial autocorrelation of data recorded at the same time in adjacent cells. Let n_{jt} be the cumulated number of individuals observed in cell j until date t, irrespective of the year of recovery, $N_j = \sum_{t=1}^{T} n_{jt}$ be the total number of Barn Swallows in cell j and $p_{jt} = n_{jt} / N_j$ the proportion of Barn Swallows recovered until date t, t = 1, ..., T, T being the end of the period of interest (Figure S2). All recoveries were used irrespective of year as data were sparse for some cells. Ordinary binomial regression can be adopted to estimate the cumulative proportion of arrivals in cell j at any given date as a function of a set of secondary variables. We modelled the occurrences in a cell as a linear function of the date on a cloglog scale since this scale is the most appropriate to model spatial point patterns on a geographical grid [21]. To account for spatial autocorrelation and avoid biased estimates, we specified an autobinomial spatial model for arrivals by including among the linear predictors a spatial covariate obtained by calculating the weighted average proportion of Barn Swallows that, at any given date, had reached the cells immediately adjacent to any given cell. To account for potentially different cell counts, each cell in the neighbourhood was weighted by the proportion $w_k = N_k/N_{\partial j}$ of the arrivals at any cell k in the neighbourhood ∂j of cell j out of the global number of arrivals in the neighbourhood, i.e. $N_{\partial j} = \sum_{k \in \partial j} N_k$.

Cells were considered adjacent when they shared a side or a vertex ('queen' configuration; [24]). To account for the inter-cell variability in patterns of migration through time, cell identity was entered as a random grouping factor and date as a random slope at the cell level. More formally the model is specified by

$$\log\left(-\log\left(1 - E(p_{jt})\right)\right) = \alpha + \beta t + \gamma \sum_{k \in \partial j} w_k p_{kt} + A_j + G_j t$$

where $A_j \sim N\left(0, \tau^2\right)$ and $G_j \sim N\left(0, \upsilon^2\right)$, obtaining a Conditional Autoregressive (CAR) binomial Generalized Linear Mixed Model (GLMM).

Note that this model accounts for different numbers of observations at each cell in two ways. Firstly, the dependent variable p_{jt} is specified in the model as the ratio between the cumulative number of individuals that have reached cell j until time t over the total number of individuals in the cell (actually $n_{it}/(N_j - n_{it})$ in the procedure we used for analyses [25]. The variance of the dependent variable is therefore calculated by taking into account the total number of observations at a cell, thus giving larger weight to cells with more observations. Secondly, the spatial autocovariate is also calculated by giving larger weight to cells in the neighbourhood with more observations.

The ability of the model to correctly interpolate the observed proportion of Barn Swallows that had arrived or had migrated over a given cell in a given date was estimated by calculating a pseudo R^2 equal to the squared correlation coefficient between observed and estimated cumulated proportions at each cell and date for which there were observations (Efron's pseudo R^2 for binomial models; [26]). This is a measure of the predictive ability of the model, similar to common R^2 of linear models, which is undefined for binomial models [27].

These analyses were performed by the *lmer* procedure in the *lme4* package [25] in R 2.15.2 [28]. The cloglog function was interpolated by specifying the cloglog link function in the *lmer* procedure.

Model inversion and map production

The CAR model was used to predict the exact date at which a given proportion of Barn Swallows had been recovered in a given cell and used to produce contour maps of the date at which a given proportion of Barn Swallows have reached a particular geographical location. In particular, the date t at which a proportion p of swallows are estimated to have reached or have migrated over a given cell j can be calculated as

$$t_j = \left(\log\left(-\log(1-p)\right) - \alpha_j\right)/\beta_j$$

where α_j and β_j are, respectively, the values of intercept and slope estimated by the CAR binomial GLMM at cell j.

In this paper we produced maps of the calendar date at which 15%, 50% and 85% of Barn Swallows have reached a given cell during spring migration, and maps of the date at which the same percentage of Barn Swallows was still in the cell during the period of autumn migration. In addition, we estimated arrival date of the 5% of Barn Swallows, and date when 5% of Barn Swallows were still in the cell for comparison with arrival dates of the first individual and departure date of the last individual observed at ringing stations or other locations.

Contour maps allow speculations on migration flyways as the contours are isochrones that connect geographical areas showing the same phenology. If Barn Swallows follow flyways during their migration, geographical localities along the flyways might be reached by a given proportion of Barn Swallows earlier in the season than the surrounding areas where the migration movement is less intense. Hence, we expect map contours to show a reverse-U shape in the flyway direction.

Consistency of observed and model-predicted phenology

We aimed at comparing our model-predicted estimates of migration phenology with known information of phenology derived from the literature. We considered both quantitative estimates of first and mean/median arrival dates or departure dates of the last individual from time series of ringing/observation and qualitative descriptions of migration phenology (Table S1). Quantitative phenological data from time series at a given geographical location were compared to arrival/departure dates estimated by our model for the corresponding percentage and cell.

Qualitative descriptions of migration phenology were also entered in the analysis by converting them to a quantitative estimate (Table S1). We acknowledge that this procedure is based on a subjective interpretation of the qualitative description, but note that excluding these data from the analyses did not alter the results of the following analyses (details not shown).

Consistency and agreement of phenological estimates from our models and observed phenology were assessed by calculating the repeatability [29;30] between phenological estimates from the literature and those estimated by our models. Due to paucity of data, we pooled data from both autumn and spring migration. To avoid unduly inflating repeatability due to the (obvious) difference in dates among spring and autumn migration we used the following procedure to centre the data before the analysis. We calculated the mean value of both observed and estimated values for spring migration (common mean for spring migration), and the mean value of both observed and estimated values for autumn migration (common mean from autumn migration). We then subtracted the common mean for spring migration from both observed and estimated values for spring migration, and the common mean for autumn migration from both observed and estimated values for autumn migration.

Maps of ring recoveries

Maps of ring recoveries assist with the interpretation of movement patterns inferred from contour maps by showing the actual movement of individuals. Information on the movements of individuals is included in ring recoveries, but was not used in the analysis on which contour maps are based. The only information necessary to produce contour maps is indeed the date and the position where an individual has been observed.

Maps of ring recoveries were produced by connecting the positions where an individual was observed, irrespective of the year of recovery. Only records during spring or autumn migration were included. As maps of ring recoveries were used for comparison with contour maps, they only included individuals that moved a range of distances comparable to those that could be inferred from contour maps. For this reason, only individuals that moved between 1 and 8 degrees of latitude or longitude were included in maps of ring recoveries. Indeed, lines connecting the positions of individuals recovered at longer or shorter distances only complicate these maps without providing useful information on patterns of migration.

Temporal variation in migration phenology

We investigated whether median migration dates varied over time and whether changes in the timing of migration differed among geographical areas [31]. To this end, the dataset was divided into three time periods, 1908-1969, 1970-1990, and 1991-2008. Time limits for these periods were chosen to include a similar amount of data for each period (details not shown). In addition, the British Isles were divided in two latitudinal belts north or south of latitude 53° 45’ N (Figure S1), while western Europe and north Africa were divided into three latitudinal belts (northern Europe: > 50° N, central Europe: > 42° N & < 50° N, southern Europe and north Africa: < 42° N; see Figure S1). These thresholds were chosen so as to have at each belt a sufficient number of cells for statistical analyses in each period. For each cell the cumulative proportion of Barn Swallows that had been recovered by a given date within each period was then modelled as a cloglog function of date. The date when the median Barn Swallow was expected to arrive at any cell ('median migration date' or t_0 hereafter) in each period was calculated from the fitted cloglog curve ($t_0 = (\log(-\log(0.5)) - \alpha)/\beta$ where α and β are, respectively, the values of intercept and slope of the (linearized) cloglog curve fitted at each cell).

Median migration dates in each period and cell were then analysed by using CAR linear mixed models whereby period (three-level factor), belt (two-level factor in the analyses on the British Isles and three-level factor in those on western Europe and north Africa) and their interaction were entered as predictors together with a spatial autocovariate, while cell was entered as a random grouping factor. The value of the spatial autocovariate $w_{j\pi}$ for cell j in each period π was here calculated by averaging median migration dates $\mu_{k\pi}$ at period π of the $N_{\partial j\pi}$ cells in the neighbourhood $\partial_{j\pi}$ of cell j. Formally:

$$w_{j\pi} = \frac{1}{N_{\partial j\pi}} \sum_{k \in \partial j\pi} \mu_{k\pi} \,.$$

We also corrected our models for heteroscedasticity because graphical exploration showed that variance in median migration dates differed widely between periods. In these models, a significant belt by period interaction would indicate that changes in timing of bird migration between periods differed according to the geographical position of cells.

These analyses were performed with the *lme* procedure in the *nlme* package [32] in R 2.15.2. Models were corrected for heteroscedasticity by specifying an among-period *varIdent* weighting function in the *lme* procedure [32].

Results

Maps obtained from CAR models

British Isles. Maps of spring migration show a general northward progression of migration, but also show some local patterns (Figure 1A). The maps of spring migration in the British Isles indicate that Barn Swallows arrive earlier in central Ireland (estimated migration date of the first 15% of Barn Swallows at cell E1 is 109 = 19 April; see Figure S1A for cell IDs) than in the rest of the British Isles (data from southern and western Ireland were unavailable). They then appear to move northwards toward south-west Scotland, where the first 15% of Barn Swallows is expected to pass around 8 May (date = 128).

South-west England is reached by the first 15% of Barn Swallows at the beginning of May (124 = 4 May), then Barn Swallows seem to move northwards in two main directions, on the one side toward Wales and north-west England, and on the other along the western coast of northern England. Barn Swallows arrive latest in northern Scotland and the Orkney Islands (15% approximately at 140 = 20 May). The bulk of migration (50%) transits in Britain around 30 May (150), with the only exception of central Ireland, where it is earlier (128 = 8 May), and of northern Scotland, where it is later (154 = 3 June). The last Barn Swallows (85%) pass through central Ireland on around 30 May (85% is estimated at date = 150 at cell E1), then probably move north towards Scotland, which is reached by the last 85% of Barn Swallows on around 13 June (164; Figure 1A).

The CAR mixed model used to produce the map of spring migration over the British Isles interpolated the observed proportion of Barn Swallows at each cell in each date with great accuracy ($R^2 = 0.95$). In addition, the pattern of migration depicted above is consistent with the movements of individual Barn Swallows documented by ring recoveries. Indeed, Figure 2A shows movements of individuals between the Channel Islands and Ireland, thus suggesting direct movements of Barn Swallows towards Ireland.

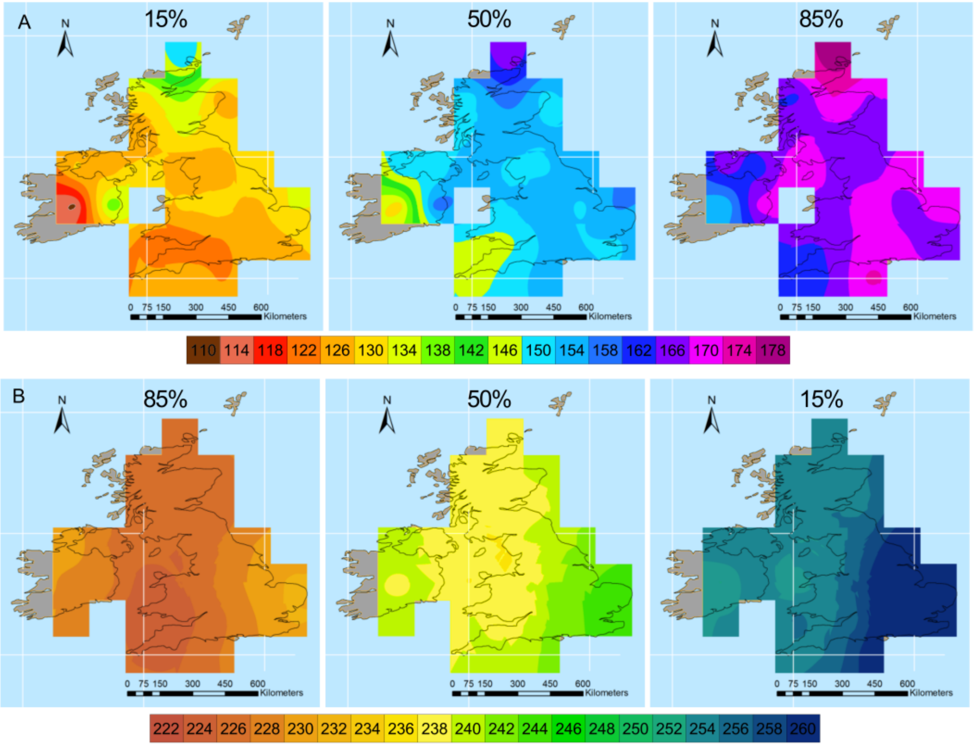

Figure 1: Progression of Barn Swallow migration in the British Isles. Contour plots of the calendar date in which the CAR model predicts that a given percentage of swallows has been recorded during (A) spring and (B) autumn migration, Contours were generated by linear kriging interpolation. Numbers in the colour scale represent the mean date for each 4-days (spring) or 2-days (autumn) colour belt (1 January = 1). For ease of interpretation we here report some reference dates: 100 = 31 March, 120 = 30 April; 150 = 30 May, 180 = 29 June, 200 = 19 July, 230 = 18 August, 260 = 17 September.

Maps of autumn migration in the British Isles showed a reverse pattern, with Barn Swallows moving south-east from Wales and Scotland. In addition, Barn Swallows seem to move through the western part of Ireland earlier than from Scotland, and leave eastern England last (Figure 1B). Migratory movements are more synchronous during autumn than spring migration, as indicated by the lower maximum difference in dates represented by isochrones on maps of the autumn compared to spring migration. In addition, autumn migration routes seem to follow a more eastward direction, as suggested by the shape of isochrones which point east in southern England. The predominant eastward movement during autumn migration is confirmed also by the maps of ring recoveries (Figure 2B). More detailed patterns are difficult to assess in this map, probably due to the synchrony of movements during autumn migration. The model used to produce the map interpolated the observed proportion of Barn Swallows at each cell in each calendar date with great accuracy ($R^2 = 0.97$).

Western Europe and North Africa. Maps of spring migration over western Europe and north Africa (Figure 3A) were based on a model that interpolated the observed data with great accuracy ($R^2 = 0.96$). They show an early transit of birds during spring migration in the Iberian peninsula, with the first 15% of Barn Swallows in southern Portugal on 1 March (60) and in central Spain and southern France on 10 April (100). They seem then to spread north-eastwards in France and the rest of northern Europe, reaching southern Sweden on 20 May (140).

The first 15% of Barn Swallows reaches southern Italy at the beginning of April, then they move towards the Balkans. Interestingly, the maps of the 15%, 50% and 85% of Barn Swallows suggest a progressive eastward shift of the northward turn of isochrones from Spain towards the Balearic Islands, thus suggesting that late migrants may embark in a more direct cross of Mediterranean than early migrants (Figure 3A).

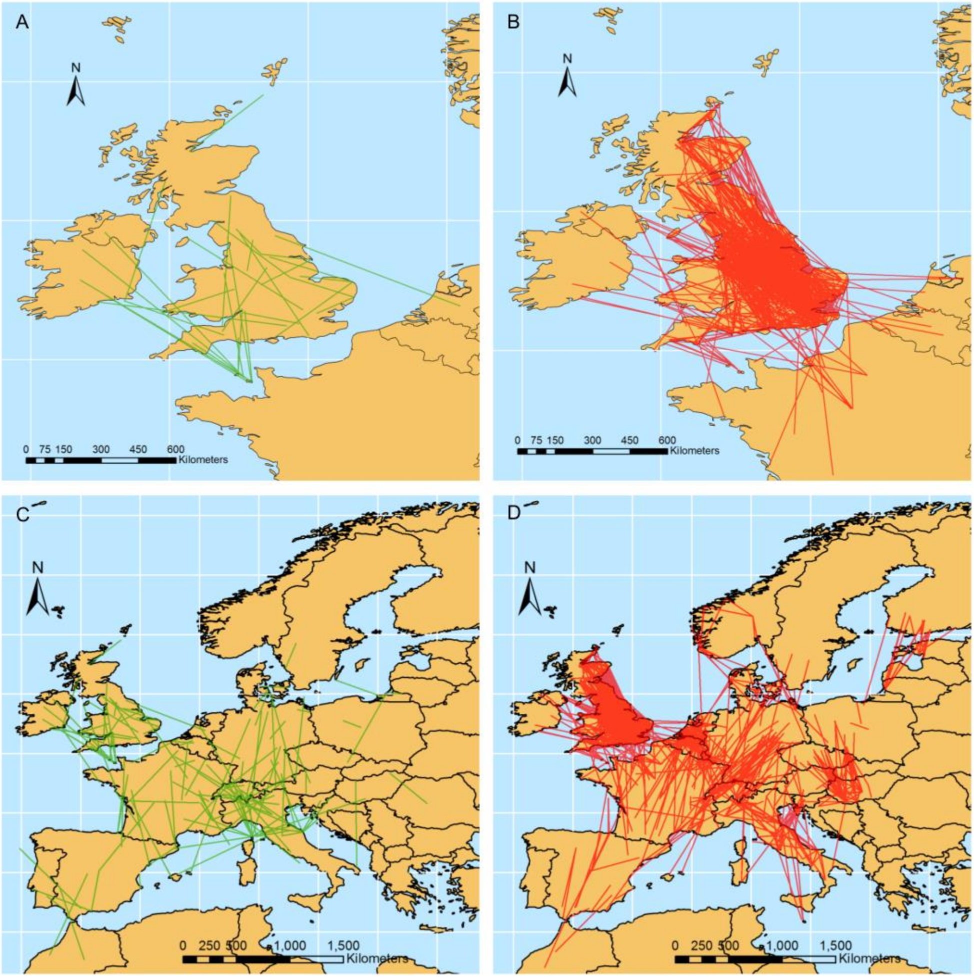

Figure 2: Maps of swallow movements. Each line connects the ring and recovery position of an individual swallows in (a) March-June and (b) August-October in the British Isles or in (c) February-June and (d) August-November in Western Europe and North Africa. To facilitate the interpretation of the figure only swallows that moved more than 1 and less than 8 degrees latitude or longitude are shown.

The maps of autumn migration were also based on a model that fitted the data with great accuracy (R^2 = 0.97). They indicate that the first 15% of Barn Swallows has already crossed Gibraltar on 18 August (230; Figure 3B). A large migration divide seems to occur in France, with Barn Swallows moving along two main migration routes, one along the Atlantic coast toward Spain and Gibraltar, and the other across Switzerland and along the Italian peninsula, with a possible crossing of the Mediterranean from central Italy toward Tunisia, thus embarking on a direct Mediterranean crossing [33]. A map of the last 15% of migrants also suggests that Barn Swallows from north-eastern Europe may move westwards across the Balkans and reach central and southern Italy, although paucity of data from Eastern Europe prevented a clear assessment of movement patterns in this area.

Phenology estimated by our model was generally consistent with that observed in different areas of Europe, as indicated by the significant repeatability among observed arrival/departure dates and those estimated by our model (Table S1, $R = 0.43 \pm 0.16$ SE, $F_{28,27} = 2.51$, $P = 0.009$). Repeatability analyses conduced on spring and autumn data separately showed a significant repeatability between observed and estimated phenology for spring migration ($R = 0.55 \pm 0.16$ SE, $F_{18,19} = 3.49$, $P = 0.005$), and a non-significant repeatability for autumn migration ($R = 0.25 \pm 0.33$ SE, $F_{8,9} = 1.68$, $P = 0.227$).

Temporal variation in migration phenology

CAR mixed models restricted to the British Isles did not show any significant variations in median date of spring migration, either according to period (Likelihood Ratio Test: $\chi^2_2 = 3.19$, $P = 0.203$), latitudinal belt ($\chi^2_1 = 1.61$, $P = 0.205$), or their interaction ($\chi^2_2 = 1.36$, $P = 0.507$, details not shown). Median autumn migration date in the British Isles did not change significantly between periods ($\chi^2_2 = 0.52$, $P = 0.770$), latitudinal belt ($\chi^2_1 =$

0.26, P = 0.607) or their interaction (χ^2_2 = 1.06, P = 0.590, details not shown).

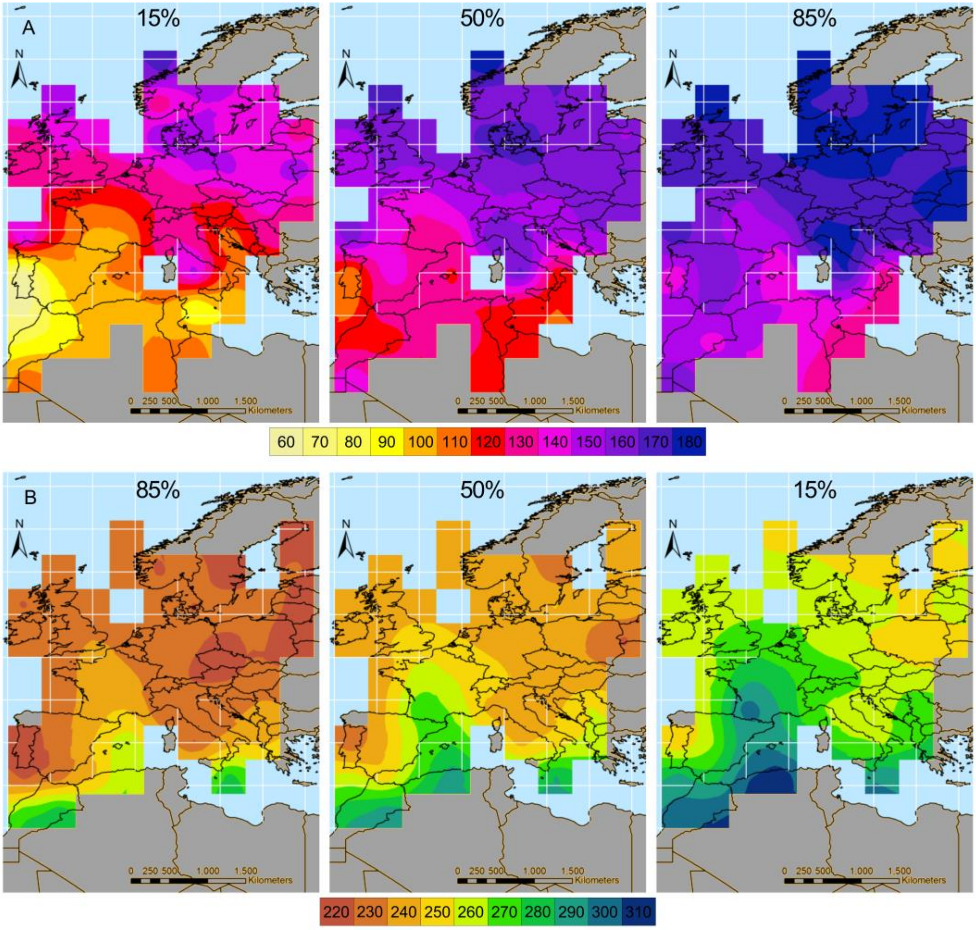

Figure 3: Progression of Barn Swallow migration in Western Europe and North Africa. Contour plots of the calendar date in which the CAR model predicts that a given percentage of swallows has been recorded during (a) spring and (b) autumn migration, Contours were generated by linear kriging interpolation. Numbers in the colour scale represent the mean date for each 10-days colour belt (1 January = 1). For ease of interpretation we here report some reference dates: 100 = 31 March, 120 = 30 April; 150 = 30 May, 180 = 29 June, 200 = 19 July, 230 = 18 August, 260 = 17 September, 300 = 27 October.

Median spring migration date changed significantly between latitudinal belts in western Europe and north Africa ($\chi^2_2 = 21.55$, $P < 0.001$), but not between periods ($\chi^2_2 = 2.07$, $P = 0.355$). The belt by period interaction was non-significant ($\chi^2_4 = 3.43$, $P = 0.488$; Figure 4A).

The model fitted to autumn data indicated that the belt by period interaction was significant ($\chi^2_4 = 11.81$, $P = 0.019$), as well as the main effect of belt ($\chi^2_2 = 20.34$, $P < 0.001$). Post-hoc tests showed that migration was later in southern than in central and northern Europe ($z \leq -3.21$, $P \leq 0.004$) and that in southern Europe autumn migration post-1990 was 13.36 ± 3.80 SE days earlier than pre-1970. There were no significant differences in the timing of autumn migration in central and northern Europe (Figure 4B).

Discussion

In this study we analysed ring recoveries spanning from 1908 to 2008 to describe patterns of bird migration and their long-term temporal trends. A first set of analyses was based on a subset of ring recoveries in the British Isles, and a second set tentatively extended the analyses to Western Europe and North Africa, where data are sparser.

We produced maps describing both spring and autumn migration phenology over the British Isles and, tentatively, over western Europe and north Africa, from which the main migration flyways could be inferred. We found no significant changes in migration phenology of the Barn Swallows in the British Isles, but an earlier timing of autumn migration in southern Europe and north Africa in 1991-2008 compared to 1908-1969. No change in autumn migration phenology was observed in central and northern

Europe as well as in spring migration phenology over the whole western Europe and north Africa.

Ring recoveries currently represent the largest and only long-term datasets on bird migration, yet they are hampered by several potential sources of bias, primarily due to large spatial and temporal variation in sampling effort. Previous studies that faced the same problem tried to account for these potential sources of bias, by re-running the analyses on different subsets of data or by including additional variables (see e.g. [18; 19]). These approaches could not be applied in this case, because this study focuses on migration periods only, and therefore analyses cannot be restricted to 'focal' periods of migration without losing important information on early and late migrants, which are relevant for modelling the progression of migration in a given area correctly. In addition, results from analyses accounting for other potential sampling biases may be difficult to interpret. For example, recovery condition of individuals, indicating, for instance, whether an individual was actively trapped or fortuitously recovered, and whether a bird was dead or alive at the time of recovery, were included in previous analyses of ringing recoveries [18]. However, trapped birds may provide early- or late-biased estimates of the timing of bird migration depending on the scheduled activities of ringing stations, which may vary between years and geographical regions. Recoveries of dead or live birds may also show different biases.

For example, if birds are more likely to be found dead early than late in spring, and late than early in autumn, analyses restricted to birds found alive or dead may bias the outcome in opposite directions. In addition, analyses restricted to subsets of data may be more prone to produce biased results due to lower power of analyses based on reduced sample size than the whole

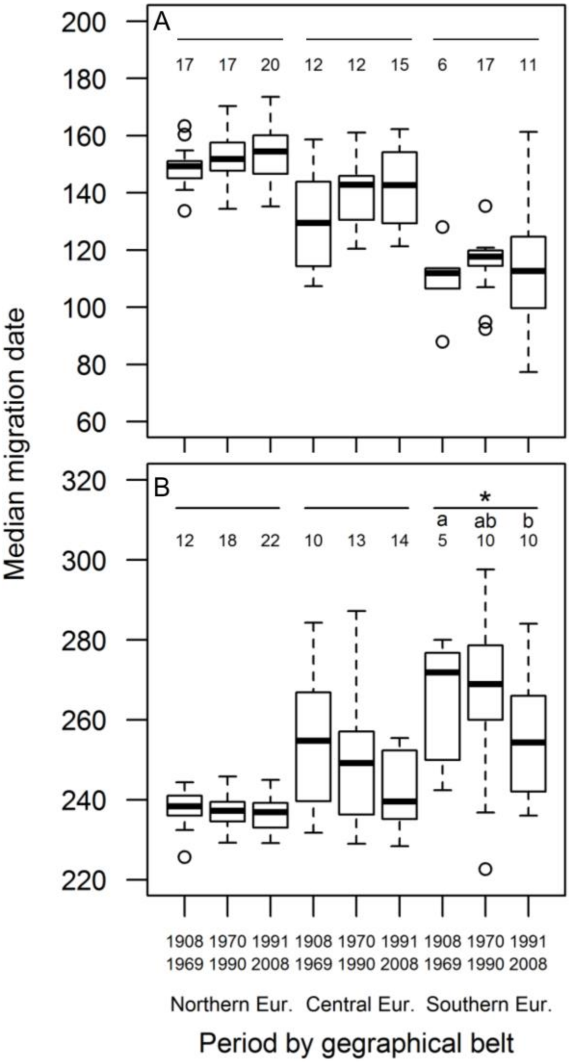

Figure 4: Boxplot of median a) spring and b) autumn migration dates in Western Europe and North Africa. Dates were estimated at each cell (t_0 parameter of cloglog curves interpolated at each cell) in all belt-by-period combinations. The solid line represent the median value, the top and the bottom of the boxes represent the first and the third quartile while whiskers approximately include 95% of data. Circles represent outliers. Numbers represent sample size (i.e. number of cells per period and belt). Asterisk denotes the belt that differs significantly from the others at Tuckey post-hoc tests ($z \leq -3.212$, $P \leq 0.004$ in all

cases). Different letters denote periods that differ significantly to each other within each latitudinal belt at Tuckey post-hoc tests (z = 3.612, P = 0.001).

dataset, which will give the most robust and the least biased results. All the analyses presented in this study therefore used the whole dataset, and all the results should be considered by keeping in mind that it was impossible to conduct additional analyses accounting for possible sources of bias.

Phenological estimates from our models were generally consistent with phenology of the spring and autumn migration described by both quantitative and qualitative observations in literature. We acknowledge that on this analysis we were forced by the scarcity of the data to cumulate information from spring and autumn migration as well as from quantitative and qualitative observations. However, repeatability of observed (from direct observation or trapping of live birds) and estimated (from our models) values was significant, thus confirming the general consistency of our estimates and the observed phenology. Closer observation of the data reported in Table S1, however, shows some differences between observed and estimated phenology. Comparison with time series of first arrival dates indicates that our model estimated that the first 5% of Barn Swallows arrive 1 (Norfolk, England [34]) to 31 days later (Leicestershire, England [35]) than the first swallow was observed. Arrival time of the first 5% of Barn Swallows should be close to but later than that of first observations. Time shifts of 21-31 days between our estimates and observation at sites like Parchim (Northern Germany; [36]), Brescia (Northern Italy; [37]), or in Leicestershire (Table S1) are therefore not negligible, even if we consider that the first Barn Swallows usually arrive much earlier than the bulk of migration[38].

Estimates of median arrival dates from our model were consistent with those of the only published time series of mean/median arrival date that was available to us (Ventotene, Southern Italy [39]; Table S1). In addition, we were able to reconstruct arrival dates of 15%, 50% and 85% of Barn Swallows in Kraghede (Denmark) [40]. In this case our model estimated phenology about one month later than that observed (Table S1), suggesting that our results may depict a somewhat later phenology than site-specific time series, at least at some geographical areas. This later estimate of timing of migration provided by our results may therefore suggest that early migrants are underrepresented in ring-recoveries, that our method underestimates the proportion of early migrants, or both. In addition, spring migration spans several months and some records may refer to Barn Swallows captured at breeding sites some times after that they have arrived. At the same time, it is questionable whether time series of arrival at single, selected localities can reliably reflect arrival dates at areas as large as four degrees latitude per longitude. This latter interpretation is suggested by the consideration that time series of arrival dates are usually collected at ringing stations, which are located at key places along migration routes, and at localities that may be close to the margins of a cell. However, our estimates are consistent with the general, qualitative description of migration phenology over larger geographical areas (Table S1).

Comparisons of results about the timing of autumn migration are more problematic, since information of autumn migration phenology is sparser than that on spring migration. Published information from Spain [41] depicts an earlier departure of Barn Swallows than that estimated by our model. However, our model estimated that the last 5% of Barn Swallows are still in central Spain (cell G2, Figure S1D) on 25 September (268), a date very close to that of 21 September reported by Gordo & Sanz [41] as the mean departure date of the last Barn Swallow from Spain. Mean autumn passage date of Barn Swallows at the Col de Bretolet (Switzerland) is 19 days later than median passage date estimated by our model (Table S1). Similarly, departure date of the last Barn Swallow at four ornithological observatories in the UK is 30 to 54 days later than the date at which only 5% of Barn Swallows are still in the area estimated by our models. Conversely, mean departure dates of Barn Swallows from northern Italy based on a short (15 years) unpublished time series (R. Ambrosini, unpublished data) are earlier than the date estimated by our model for the presence of the last 5% of Barn Swallows in the cell (Table S1). In conclusion, evidence of the ability of our model to accurately estimate autumn migration phenology is not unequivocal, but information on the timing of departure of 'extreme' individuals at selected localities may not properly represent the general timing of migration over larger geographical areas.

Different independent sources of information however confirmed the reliability of our modelling approach. The pattern of spring migration depicted in the maps of the British Isles we produced is qualitatively consistent with the south-west to north-east pattern of Barn Swallow migration progression through Britain described by Huin & Sparks [42] by using phenological records compiled before 1947. The fact that our maps indicate a migration phenology about 20 days later than that described by Huin & Sparks (e.g. 124 to 128 = 6 to 8 May in central England in our map vs. 109 = 19 April in Huin & Sparks [42]) can be explained by considering that the maps by Huin & Sparks are based on first observation dates while ours are based on the 15% of migration movements. In addition both in our maps and in the paper by Huin & Sparks the time-difference between isochrones though Britain is 20 days (Figure 1A and [42]). Hence, despite the difference in the timing of migration, both studies consistently indicated that Barn Swallows arrive in northern Scotland about 20 days later than in southern England (approximately 800 km to the south).

The second main aim of the present study was to investigate variation over time in timing of migration. No significant change in spring and autumn phenology in the British Isles was detected, which is consistent with Mason [43], who did not find a long-term trend in arrival dates of Barn Swallows between 1942 and 1991, and with Sparks & Carey [34], who found only a slight trend toward a later arrival over two centuries.

No significant change in timing of spring migration appeared neither in the analyses on western Europe and north Africa. Barn Swallows are known to have advanced first arrival dates throughout Europe. For example, Barn Swallows advanced first arrival date by 13 days in 1970-2004 in the Iberian peninsula [41], and mean/median arrival dates advanced by 0.34 days year^{-1} in 1982-2006 in northern Italy [37] and by 0.17 days year^{-1} in 1960-2006 in Europe [8]. Our model was therefore unable to capture this widespread advancement, probably because the paucity of data from ring recoveries forced us to calculate median arrival dates over periods as long as 20 years or more and because of a large heterogeneity among periods in the variance of median arrival dates in cells (despite accounting for this problem in the statistical analyses; see Methods). However, arrival dates of migrant birds, and of Barn Swallows in particular, may have varied non-linearly over the study period [41]. Indeed, Barn Swallows in Spain delayed their arrival dates during the seventies and then have advanced, reaching the same arrival dates as pre-1970 only in recent years. Our analyses are partly consistent with this pattern. Median spring arrival dates seem to have been delayed in 1970-1990 in southern Europe and have then advanced, returning to pre-1970 levels in the last decades (Figure 3A). In addition, cloglog curves interpolating arrival dates in central Spain (cell G2 of Figure

S1) pre-1970 and post-1990 almost overlap, while that for 1970-1990 was shifted towards later arrivals (Figure S3).

Parameters of the cloglog curves indicate a significant advancement in autumn migration in southern Europe and north Africa (Figure 4B). This pattern is consistent with that found by Gordo & Sanz [41], who documented an advancement in autumn migration in the Iberian Peninsula. In addition, Jenni and Kéry [44] reported a delay in mean autumn migration at the Col de Bretolet in 1970-1982 with respect to earlier years, and a subsequent advancement. Also this pattern is consistent with the results of our model, that estimated a delay of 6 days in median migration date at the cell including this Swiss locality (E5, see Figure S1) between 1970-1990 and pre-1970, and a subsequent advancement of 11 days between 1970-1990 and post-1990 (other details not shown).

In summary, in this study we propose a novel method to describe patterns of migrations and main routes followed by migratory birds based on ring recoveries. Importantly, this method does not use information on the movements of individuals between locations where they were observed at different times of their lives, but is entirely based on the information on the date at which a bird has been observed in a given place. It may therefore be possible to extend its application to other, potentially larger, datasets. For example, ringing data, which are by far much more abundant than ring recoveries, can be used for this purpose. The main disadvantage is that – so far – only a few of these data are stored in the EDB. They are therefore more difficult to access for continent-wide analyses, and they are more prone to temporal sampling biases (e.g. non-random variation in sampling effort both within and between seasons; [15]). However, they may allow detailed studies at the scale of smaller geographical areas (e.g. countries). Similarly, this method may be applied to sighting databases, such as those collected via the web (e.g. BTO BirdTrack project http://blx1.bto.org/birdtrack; the ORNITHO family portals e.g. www.ornitho.ch), which are becoming increasingly popular in recent years, and to databases of timing of flowering and leafing [45].

Ring recoveries and museum specimens provide the only available data spanning over long time periods, and thus they are the only data allowing investigation of the variation over time of migration phenology over large geographical areas. If ringing data too were available over long time periods, the increased amount of data available for the analyses may allow the use of reduced intervals so that more detailed variation in migration phenology over time can be explored.

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Timing of migration and residence areas during the non-breeding period of barn swallows *Hirundo rustica* in relation to sex and population.

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Felix Liechti[1], Chiara Scandolara[1-2], Diego Rubolini[2], Roberto Ambrosini[3], Fränzi Korner-Nievergelt[1], Steffen Hahn[1], Roberto Lardelli[1], Maria Romano[2], Manuela Caprioli[2], Andrea Romano[2], **Beatrice Sicurella**[3] & Nicola Saino[2]

1. Swiss Ornithological Institute, Seerose 1, CH-6204 Sempach, Switzerland.
2. Department of Biosciences, University of Milan, via Celoria 26, I-20133 Milano, Italy.
3. Department of Biotechnology and Biosciences, University of Milano-Bicocca, p.zza della Scienza 2, I-20126 Milano, Italy.

Abstract

We investigated sex- and year-dependent variation in the temporal and spatial movement pattern of barn swallows *Hirundo rustica* during the non-breeding period. Hundred and three individuals equipped with miniaturized light-level geolocators at three different breeding areas in southern Switzerland and northern Italy provided data for the analysis. We identified a region 1000 km in radius centred in Cameroon as the main non-breeding residence area of these three geographical populations. Five residence areas of males only were in southern Africa, south of 19°S. Most individuals occupied a single site during their stay south of the Sahara. The timing of migration broadly overlapped between sexes and all geographical breeding populations. Between the two study years there was a distinct difference of 5 to 10 d in departure dates from and arrival at the breeding sites. Remarkably, the period of residence in sub-Saharan Africa was very similar (157 d) in the two study years, but their positions in the first year (2010-2011) were about 400 km more to the north than in the second (2011-2012). Independent of the year, individuals with sub-Saharan residence areas further north and east had a shorter pre-breeding migration and arrived earlier than those staying further south and west. In addition, birds breeding in southern Switzerland arrived at their breeding colony 7-10 d later than those breeding only 100 km south, in the Po river plain. Our study provides new information on the variance in migration phenology and the distribution of residence areas in sub-Saharan Africa in relation to sex, population and year. It supports the usefulness of light-level geolocators for the study of annual routines of large samples of small birds.

Introduction

Palearctic songbirds make up the vast majority of the two billion birds migrating every autumn from Europe into sub-Saharan Africa (Hahn et al. 2009). Species-specific non-breeding ranges in sub-Saharan Africa are roughly identified, mostly by ring recoveries (Walther & Rahbek 2002), whereas population-specific whereabouts and individual histories of residences during the non-breeding period are hardly known. The recent miniaturization of individual tracking systems has now opened up the possibility to monitor the year-round movements of the small songbird species (Bridge et al. 2013).

Individual-based information is pivotal to our understanding of the evolution of migration. Such data will allow dissecting the genetic and phenotypically plastic components of migratory behaviour, and also to predict how migratory species will respond to environmental transformations, including climate change (Gienapp et al. 2007). Only for few species, population-based data on migration derived by large-scale bird ringing projects have provided general information on migration routes and phenology, and on non-breeding distribution (Tautin et al. 1999, Rubolini et al. 2002, Boulet et al. 2006, Ambrosini et al. 2011, Ryder et al. 2011). For the vast majority of migratory bird species studied so far, an individual-based description of the timing and whereabouts during the non-breeding period is not available for a considerable number of individuals from the same breeding population.

Even fundamental questions on the role of major potential sources of variation in migratory behaviour, such as sex, geographical position of the breeding area and environmental effects, are still far from being resolved. Sex-specific differential migration is well-established in several species, where males and females have been shown to adopt different migration strategies (Cristol et al. 1999, Morbey and Ydenberg 2001). A few comprehensive studies mainly show a certain degree of protandry, in the order of days/few weeks, in pre-breeding migration, based on sex-specific differences in migration timing (Swanson et al. 1999, Forstmeier 2002, Stewart et al. 2002, Rubolini et al. 2004, Saino et al. 2010b), whereas extremely little is known about post-breeding migration and/or the distribution of residence areas during the non-breeding period (but see Reudink et al. 2009).

Either sex may experience differential selective pressures during the non-breeding period (Møller 1994, Rubolini et al. 2004, Spottiswoode and Saino 2010, Morbey et al. 2012), e.g. epigamic traits such as feather ornaments may entail costs on male migration which are not, or only partly, faced by females (Barbosa and Møller 1998, Saino et al. 2010a). In general, differences in natural and sexual selection pressures may result in sex-specific strategies (Ketterson and Nolan 1983, Morbey and Ydenberg 2001, Morbey et al. 2012).

Geographical breeding populations of migratory birds are well known to differ in migration phenology, as gauged from timing of arrival and departure from the breeding grounds. This has its apparent proximate cause in latitudinal (and longitudinal) variation in timing of spring events, which are delayed farther north and, as far as continental Europe is concerned, also farther east (Hüppop and Hüppop 2003, Rubolini et al. 2007). The geographical scale at which differentiation in annual routines, and thus in migration phenology, should be expected to occur is not straightforward to predict. Sizable changes in conditions at the breeding grounds like those occurring along elevational or latitudinal gradients may produce distinctive clines of variation in breeding phenology. Even across relatively small geographic ranges gradual changes in environmental conditions can have consequences for the subsequent phenological events in the circannual cycle of migratory species (Hjernquist et al. 2009).

Inter-annual variation in ecological conditions experienced at any of the stages of the annual life-cycle may generate variation in migration phenology and non-breeding residence. The observation that migratory birds breeding in temperate and boreal biomes track annual changes in weather conditions at the breeding grounds not only by adjusting timing of reproductive events (Dunn and Winkler 2010) but also by tuning apparent timing of arrival has remained puzzling (Gordo 2007, Knudsen et al. 2011; but see Saino and Ambrosini 2008).

In the present study we equipped a large number of adults of a small, semi-colonial, trans-Saharan migratory passerine bird, the barn swallow *Hirundo rustica*, from three geographical breeding populations in southern Europe (Switzerland and northern Italy) with miniaturized individual tracking devices (light-level geolocators). The specific goals of the present study were to investigate variation in timing of migration and distribution of residence areas in sub-Saharan Africa in relation to sex and breeding location.

We tested the hypotheses that 1) the earlier arrival of males vs. females at the breeding sites (Møller 1994, 2007; NS, unpubl.) is caused by either more northerly area of residence in sub-Saharan Africa and/or a faster pre-breeding migration; 2) due to the harsher ecological conditions (higher elevation, lower temperatures) at the northernmost (Swiss) breeding site, this population should show delayed phenology of pre-breeding migration and arrival to the breeding colony compared to more southern (Italian) ones; 3) after accounting for among-population differences, the geographic position of the individual sub-Saharan residence area should predict the duration of stay at this site, because birds staying further north need less time for migration; 4) early spring arrival to the breeding area should be related to a more northern geographic position of the sub-Saharan residence area.

Methods

Study area

The study was carried out over three years (2010-2012) in three study areas, one in southern Switzerland (Magadino, hereafter N area; coordinates of the approximate centre and approximate elevation: 46°09'N, 8°55'E, 211 m a.s.l.) and two in northern Italy (Piedmont, hereafter SW area, 45°33'N, 8°44'E, 160 m a.s.l.; Lombardy, hereafter SE area, 45°19'N, 9°40'E, 60 m a.s.l.; Figure 1). All three areas consist mainly of farmland, dominated by maize and hayfields (Ambrosini et al. 2012, Scandolara et al. 2014). The N area is located in an Alpine valley floor. Despite being relatively close to each other, marked differences exist in barn swallow breeding phenology among the three study areas (see Discussion), which may be partly explained by differences in elevation of the three areas and in mean spring climate [average of mean monthly temperatures, March-June: N area, 13.96 ± 0.89 °C; SW area, 14.13 ± 0.94 °C; SE area, 14.80 ± 0.78 °C; data from the high-resolution climatological model by Brunetti et al. (2014) based on long-term (1961-1990) temperature data; the associated error is the mean of the monthly prediction intervals, as described in Brunetti et al. (2014); data kindly provided by M. Maugeri].

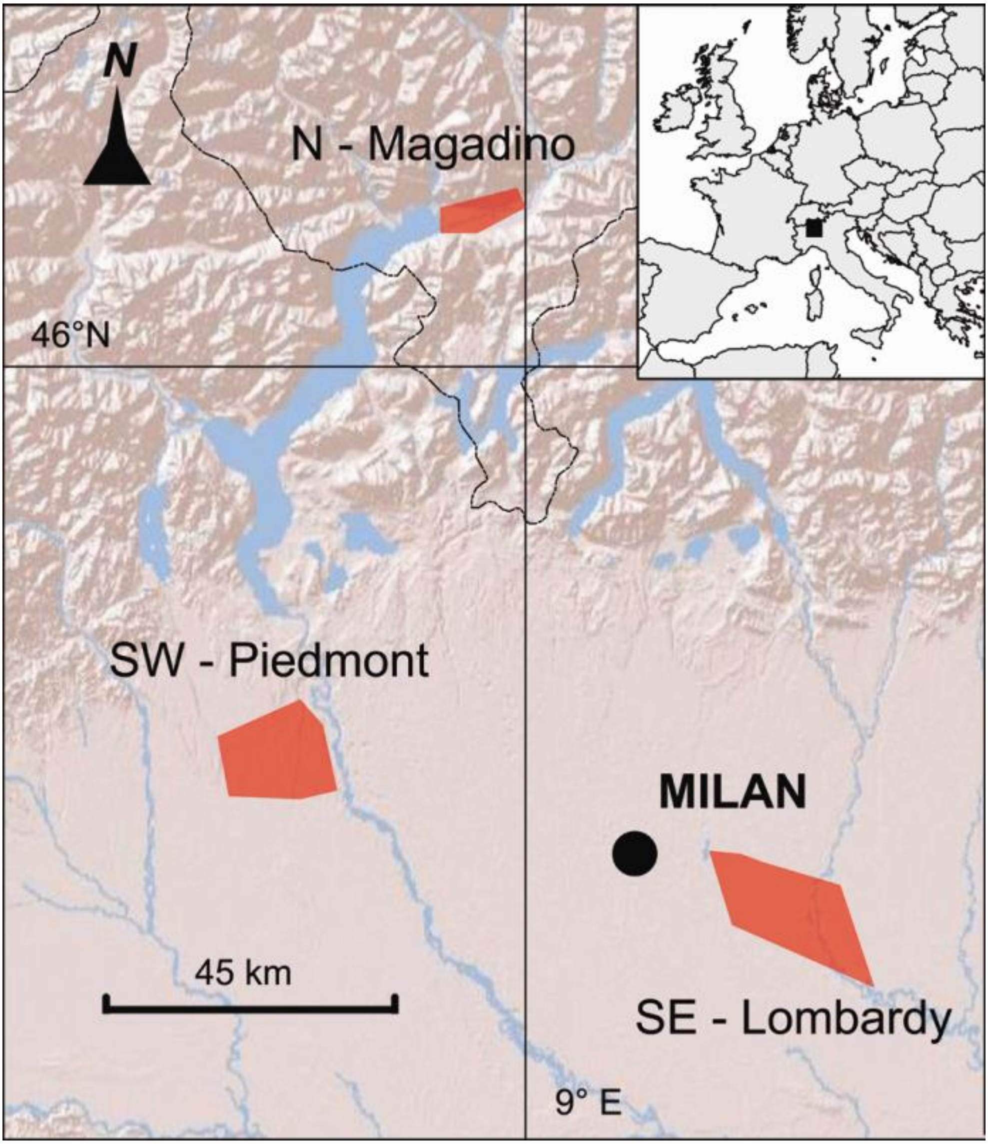

Figure 1. Geographical position of the three study areas (shaded polygons) (N – Magadino, Switzerland; SW – Piedmont, Italy; SE – Lombardy, Italy). The black line shows the border between Italy and Switzerland. Inset: position of the study areas (in black) within Europe.

Geolocator application

In July 2010, we applied 310 SOI-GDL2.10 (Swiss Ornithological Institute, http://www.vogelwarte.ch/indirect-tracking-geolocator.html) geolocators to breeding individuals (162 males, 148 females) at 21 farms, while in June-July 2011 we applied a new model (SOI-GDL2.11) to 330 breeding individuals (184 males, 146 females) at 29 farms (details in Scandolara et al. 2014). Of the tagged individuals, 162 (25%) were recaptured during the subsequent breeding period and 124 geolocators were retrieved, as 38 birds had lost the device before recapture. Geolocators were fitted using a leg-loop harness (Rappole and Tipton 1991) made of elastic silicone rubber mixture (MVQ 60 shore A). The total weight of a geolocator (including harness) differed between the two models, being lower for the 2011 model [2010: model SOI-GDL2.10 = 0.77 g (0.05 SD), n = 310; 2011: model SOI-GDL2.11 = 0.68 g (0.03 SD, n = 330)]. The 2011 model had also a shorter light stalk (Scandolara et al. 2014). The weight of geolocators relative to barn swallow body mass upon capture was below 5% (in agreement with the so-called '5 % rule'; Kenward 2001; but see Barron et al. 2010) in both years [2010: 4.14% (0.40 SD); 2011: 3.74% (0.35 SD)]. Geolocators negatively affected survival, especially of female birds, in both years, and negatively affected reproduction (delayed laying and smaller clutch size) of birds equipped with the 2010 model (Scandolara et al. 2014).

Owing to total or partial failures of the devices (e.g. battery failure), a different number of individual tracks was available for different events during the non-breeding period: the sample size of the tracks available for the different analyses is reported in Table 1.

Table 1. Sample sizes for the analyses of the phenological variables for each sex, year and geographical population group (see Methods). A total of 103 tracks are included in the analyses, but there was no event where data from all tracks were available.

	Sex		Year		Population		
	M	F	2010	2011	SW	SE	N
Departure from the breeding colony	68	33	68	33	36	16	49
Duration of post-breeding migration	62	30	60	32	33	15	44
Arrival to the sub-Saharan residence area	62	30	60	32	33	15	44
Duration of stay in the residence area	49	22	41	30	23	13	35
Departure from the residence area	51	22	41	32	24	14	35
Duration of spring migration	47	21	37	31	24	14	30
Arrival to the breeding colony[a]	47	21	37	31	24	14	30

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[a]: *size of the sample included in the analyses of the effect of SRP on phenology variables.*

Light-level data analysis

From the recorded light data a single position can be calculated for each night and day. Due to shading events caused by environment or behaviour (Lisovski and Hahn 2012), the raw positions can be highly inaccurate. We therefore processed the data going through the following steps (details are given in the Supplementary material Appendix 7).

1) We identified departure from and arrival at the breeding site manually by inspecting the variability in light levels during the day. Because all barn swallows were breeding inside barns or other buildings, visits to the buildings were clearly detectable by an abrupt decrease in the light level (Supplementary material Figure A1). We are therefore confident that these estimated departure and arrival dates in fact represent the abandonment and appearance at the nesting locations. In addition, most barn swallows, particularly early in spring (i.e. around arrival to the breeding grounds),

normally spend the night within the rural buildings where they breed, which affected the time of the onset of the recorded morning light considerably. Hence, data recorded before departure and after arrival were excluded from further analyses.

2) We determined sunrise and sunset from daily light measurements by defining a threshold which was above the baseline of nocturnal sensor values. For more than 95% of the loggers we could use the same threshold. For an unknown reason, 2 loggers had a higher nocturnal baseline. Finally, sunset and sunrise were set automatically by deploying the tailor-made software GeoLocator (Lisovski and Hahn 2012).

3) Within a running window of seven days, we calculated the residuals from a linear regression for the time of each of the two sun-events (sunset and sunrise). We applied a filter excluding sun events where the mean difference of the residuals to the earliest sunrises or latest sunsets, respectively, was larger than a given threshold of 20 min. Thus, sun events far off neighbouring events (outliers) were removed from the data set.

4) Separately, for sunset and sunrise we calculated for each event the linear trend of the seven neighbouring events before and after. If the absolute difference in the slope of the two regressions (before and after) was above 0.1 h d^{-1}, the current event was defined as a change point. In addition, change points were also determined if there was a difference of more than 0.05 h d^{-1} in consecutive events of sunrise and sunset. This procedure is based on the fact that if a bird is stationary, sunrise and sunset have a smooth natural seasonal trend in time, either rising or descending. If a bird moves to another site this natural trend is broken. Therefore, change points are determined at the end and at the beginning of a stationary period.

5) Based on the daily rate of change in sunrise and sunset (± 0.05 h d^{-1}), each period between the change points was assigned to a stationary

period or a moving period. We emphasize here that the decision on whether a time period was determined as stationary or moving was based only on the variation in the time of sun events and not on estimated geographical positions. Therefore, stationary or moving periods could also be determined in the period around the equinoxes (see below), where no or only very unreliable values for latitude can be calculated.

6) For each night and day we calculated positions using the R-package GeoLight (Lisovski and Hahn 2012). We could not use the light data from breeding range for calibrating the sun elevation angle, because of the non-natural sunset and sunrise that the birds experienced inside the buildings where they nest (see above). We therefore used for all individuals the median sun elevation angle (-2.8°) derived by the Hill-Ekstrom calibration method (Lisovski and Hahn 2012) from long non-breeding stationary periods (> 50 d) from all logger data. This sun elevation angle is slightly higher than the sun elevation angle derived from roof top calibration data from a subset of these loggers (-3.2° ± 0.2° SD, n = 10). Most likely this difference is due to a slight habitat effect at the roosting sites of the birds. During equinoxes no latitudes can be determined, and close to equinox the accuracy is very poor. Therefore, we excluded from the analysis of geographical positions the latitudes calculated in a period spanning ± 3 weeks around each equinox.

7) Finally, we merged consecutive stationary periods when the position of the centres of the kernel densities (points of highest densities) did not differ by more than 200 km. For the determination of the sub-Saharan residence area we only selected periods with a duration of at least 14 d.

For additional details, we refer to the R-code in the Supplementary material Appendix 7. From these results we extracted the time spent on migration and at stationary sites north and south of the Sahara. The first day of the first stationary period (of at least 14 d, see above) south of the Sahara (mean latitude < 23.5°N) was taken as the arrival time in the sub-Saharan residence area. Correspondingly, the last day of the last stationary period (of at least 14 d) south of the Sahara was taken as the departure time from the non-breeding residence area. For the spatial association of the sub-Saharan residence area, we calculated the centre of density (mode) and the 90% quantile for longitude and latitude, based on all stationary positions between these two dates. We defined the southern margin of the Sahara as south of 23.5°N. However, the northernmost stationary site was at ca. 14°N (Niger Delta in Mali).

In summary, throughout the study we use the following phenological variables measured at the individual track level:

Departure from the breeding colony: the Julian date (1 = 1 January) of departure from the breeding colony visually determined by inspecting light-level profile in individual days;

Duration of post-breeding migration: the number of days between departure from the breeding colony and the first day of the first stationary period south of the Sahara;

Arrival to the sub-Saharan residence area: the Julian date of the first day of the first stationary period south of the Sahara;

Sub-Saharan residence position (SRP): individual position of the centre of the density (mode) of the daily longitudinal and latitudinal positions, taking into account the stationary periods south of the Sahara;

Duration of the stay in sub-Saharan residence area: the number of days between arrival to and departure from the sub-Saharan residence area;

Departure from the sub-Saharan residence area: the Julian date of the last day of the last stationary period south of the Sahara;

Duration of pre-breeding migration: the number of days between departure from the sub-Saharan residence area and arrival to the breeding colony;

Arrival to the breeding colony: the Julian date of arrival to the breeding colony visually determined by inspecting light-level profile in individual days.

The distance (great circles) between the breeding colony and SRP was also calculated but not used in the analyses because it is very strongly correlated with latitude of the SRP ($r > -0.99$).

Importantly, throughout the study we assume that the deployment of geolocators had no effect on individual migration decisions and that it did not affect birds of different sex, breeding population or year of geolocator deployment differentially. However, the deployment of tracking devices (independently of their very nature) is known to affect behaviour (Barron et al. 2010). Unfortunately, the individual behaviour of untagged birds can hardly be monitored, and for sure not across continents. We admit that in the present study the independence of the findings from device deployment is an untested assumption.

Statistical analyses

We used standard linear regression models to analyse the association between the phenological variables and sex, year, geographical population (factors) or latitude and longitude of the SRP (covariates). As detailed in the Results section, two-way interaction terms between predictors were included in initial models where relevant and statistically feasible. Latitude and longitude of the SRP were positively correlated (either including or excluding the five deviant SRPs of males, see *Spatial distribution of individual sub-Saharan residence positions* below). Their correlation coefficient r was < 0.59, but their simultaneous inclusion did not generate an increase in multicollinearity and instability of regression coefficients (VIF values always < 2). On the other hand, the test of some two-way interaction effects was prevented by a huge increase in multicollinearity (see Results and Supplementary material Appendix 2 for details).To compare the variance in dates of departure from and arrival to the breeding and sub-Saharan residence area, we first calculated the residuals from a model with year and population as factors together with their interaction, ran on each sex separately. The residuals were first subjected to a Levene's test for the homogeneity of variances among the four phenological events (departure from breeding location, arrival at SRP, departure from SRP and arrival in breeding location) within each sex. Levene's tests were repeated between pairs of phenological events to identify specific differences in variances between events. Then, for each phenological event, homogeneity of variances between the sexes was also tested.

To investigate differences in the spatial distribution of the SRP according to sex, breeding population and year we applied a randomisation test. We assigned the individuals randomly and repeatedly (4999 times) to one of the groups in focus, calculated great-circle distances between the median locations and tested whether the observed differences between median locations of each group were significantly different from the distribution of randomized differences (Supplementary material Appendix 3).

For comparing SRP between the sexes and the breeding populations, we corrected for the observed between-year difference in SRP by shifting the locations of 2011 by 506 km to the SE (Supplementary material Appendix 3, Figure A2), so that the median geographical position of the two years coincided (Supplementary material Appendix 3). Then we performed the randomisation test on the pooled data from both years corrected for the year effect. Despite the data were not balanced according to year, sex and population (Table 1), which may have reduced the power of the tests, marked differences in SRP between sexes and breeding populations would still be detected by this approach. On the other hand, within-year comparisons between sexes and geographical populations were prevented by very low sample sizes.

For all linear models, standard diagnostic plots were used to assess whether the model assumptions were met. Sample sizes for the sex, year and population groups involved in the analyses of the various phenological variables are reported in Table 1.

In the results, either raw means or least-squares means (LSM) estimated by the models are reported together with their associated standard errors or standard deviations depending on the context.

Results

Phenology of non-breeding period events

A synopsis of the main circannual events is presented in Figure 2. Date of departure from the breeding colony differed between years and sexes but not among study areas. In 2010, departure occurred 5 d later than in 2011 (Table 2). Independently of any year effect, females deserted their breeding colony on average 3 d earlier than males.

Duration of post-breeding migration was also significantly different between years, being 10 d shorter in 2010 than in 2011 (Figure 3), with no significant variation according to sex and population. In 2010, the birds departed later from the breeding grounds, but reached their sub-Saharan residence area earlier than in 2011 (Figure 2).

Duration of stay in the sub-Saharan residence area and departure date for pre-breeding migration did not significantly vary according to sex, population or year (Table 2).

Duration of pre-breeding migration was significantly shorter (7 d) for birds tagged in 2010 than in 2011 (Figure 3) and arrival to the breeding areas was consequently earlier (9 d). In addition, arrival date was significantly later, by 7-10 d, in the study area in the Alps (area N) than in the two southern areas in the Po plain (SW and SE), although the difference was statistically significant only between the N and the SE populations. There were no statistically significant differences in arrival date between the sexes, although model estimates of mean arrival dates of males were 4 d earlier than those of females (Table 2).

Table 2. Linear models of phenological events in relation to sex, year and geographical population. Non-significant two-way interaction terms between main effects were removed from all models. Group-specific model-derived least square means (SE) are also reported. Years 2010 and 2011 are the years of geolocator deployment. Thus, for year 2010 and year 2011, duration of pre-breeding migration and date of arrival to the breeding colony refer to the spring following that of geolocator deployment, i.e. to spring 2011 and, respectively, 2012. M = males; F = females. Statistically significant (p < 0.05) effects are bolded.

	F	df	p	Least-square means (SE)		
Departure from the breeding colony						
Sex	**4.04**	**1,96**	**0.047**	**M: 250.8 (0.8)**	**F: 248.3 (1.1)**	
Year	**12.42**	**1,96**	**0.001**	**2010: 252.0 (0.9)**	**2011: 247.1 (1.1)**	
Population	0.03	2,96	0.971	SE: 249.5 (1.6)	SW: 249.7 (1.1)	N: 249.4 (0.9)
Duration of post-breeding migration						
Sex	0.52	1,87	0.472	M: 31.1 (1.4)	F: 32.7 (2.0)	
Year	**15.75**	**1,87**	**<0.001**	**2010: 27.1 (1.62)**	**2011: 36.7 (1.8)**	
Population	1.65	1,87	0.198	SE: 28.2 (2.7)	SW: 33.4 (1.9)	N: 34.1 (1.6)
Arrival to the sub-Saharan residence area						
Sex	0.30	1,87	0.585	M: 281.9 (1.2)	F: 280.9 (1.7)	
Year	**4.96**	**1,87**	**0.029**	**2010: 279.1 (1.4)**	**2011: 283.7 (1.6)**	
Population	2.22	2,87	0.115	SE: 277.7 (2.4)	SW: 283.0 (1.7)	N: 283.6 (1.4)

Duration of stay in the sub-Saharan residence area						
Sex	1.50	1,66	0.224	M: 155.0 (2.6)	F: 159.5 (3.1)	
Year	0.00	1,66	0.991	2010: 157.2 (2.6)	2011: 157.2 (2.7)	
Population	0.18	2,66	0.835	SE: 157.5 (4.1)	SW: 156.0 (3.1)	N: 158.3 (2.5)
Departure from the sub-Saharan residence area						
Sex	0.92	1,68	0.342	M: 72.7 (2.5)	F: 76.0 (3.0)	
Year	1.17	1,68	0.283	2010: 72.5 (2.5)	2011: 76.2 (2.5)	
Population	0.78	2,68	0.465	SE: 72.4 (3.8)	SW: 73.5 (2.9)	N: 77.1 (2.4)
Duration of pre-breeding migration						
Sex	0.02	1,63	0.897	M: 30.4 (1.9)	F: 30.0 (2.8)	
Year	**4.24**	**1,63**	**0.044**	**2010: 26.8 (2.4)**	**2011: 33.5 (2.3)**	
Population	0.63	1,63	0.539	SE: 27.7 (3.5)	SW: 30.5 (2.7)	N: 32.4 (2.4)
Arrival to the breeding colony						
Sex	1.31	1,63	0.257	M: 103.2 (1.8)	F: 106.8 (2.7)	
Year	**7.68**	**1,63**	**0.007**	**2010: 100.7 (2.3)**	**2011: 109.3 (2.3)**	
Population	**3.45**	**2,63**	**0.038**	**SE: 100.8[a] (3.4)**	**SW: 103.9 (2.6)**	**N:110.3[a] (2.3)**

[a] indicates significant ($p < 0.05$) pairwise difference at post-hoc tests.

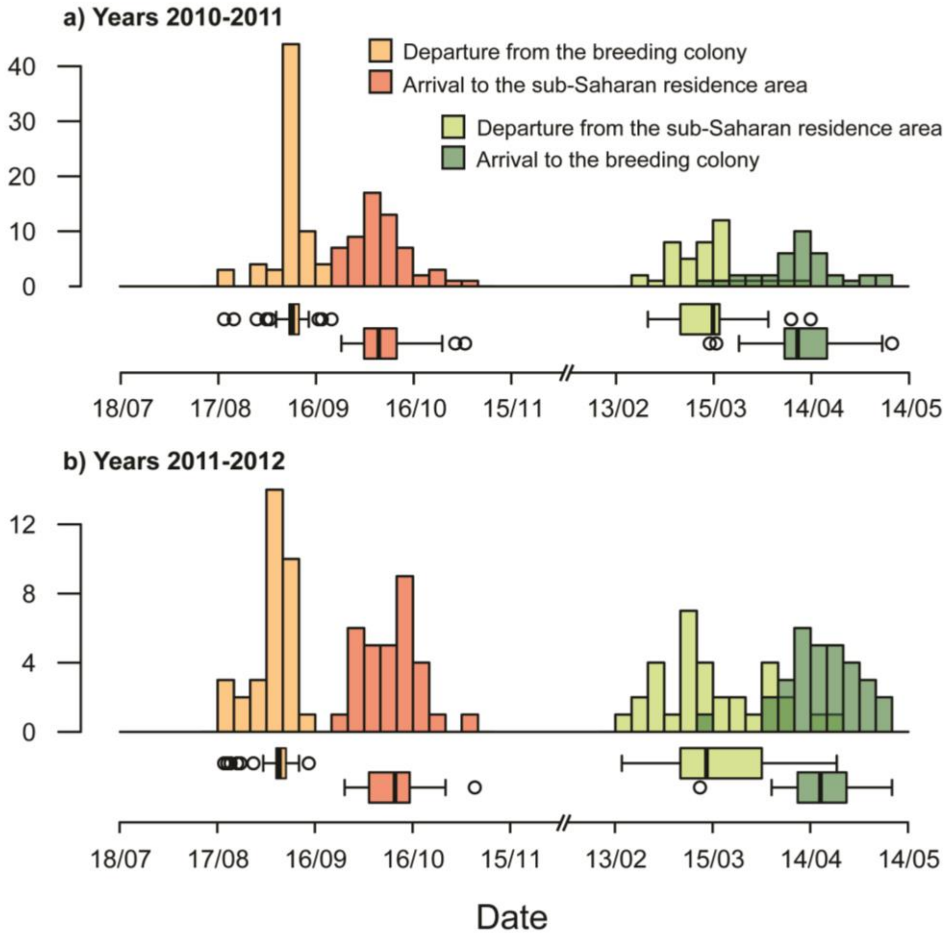

Figure 2. Phenology of autumn and spring migration of barn swallows tracked with geolocators. Upper graph shows timing of autumn and spring migration in 2010-2011. Lower graph shows timing for autumn and spring migration in 2011-2012. Boxplots show median (black line), 25% and 75% quantile (box), 90% range (whiskers) and outliers.

In both years most individuals departed from the breeding grounds within a very narrow time window (see boxplots width in Figure 2). However, the variance differed significantly among the four phenological events for males (Levene's test; $F_{3,220} = 12.74$, $p < 0.001$), and females (Levene's test; $F_{3,102} = 3.90$, $p = 0.011$). There was a general increase in variance from departure from the breeding grounds to the arrival in the next spring (Supplementary material Appendix 3, Table A1). For males, variance increased from breeding departure to arrival in the sub-Saharan residence area, and again towards departure from there, but no more towards arrival at the breeding grounds (Supplementary material Appendix 3, Table A1). For females, variances for the first two events did not differ, but was smaller than for the following two events. In addition, variance in dates of departure from the breeding colony was significantly smaller for males than females ($F_{1,99} = 6.11$, $p = 0.015$), whereas no between-sexes differences in variances existed for the dates of the other phenological events (all $p > 0.4$; see also Supplementary material Appendix 4).

Spatial distribution of individual sub-Saharan residence positions

For 92 tracks we could calculate a sub-Saharan residence position (Figure 4). The median of all residence areas was in Cameroon, at 5.8°N and 13.5°E, while mean values were 4.2°N (7.53° SD) and 12.8°E (5.70 SD).

Forty-seven per cent of all range centres were within 500 km and 88% occurred within 1000 km of the median value.

Thus, about 90% of the birds spent their non-breeding period in Cameroon and its neighbouring countries, including Nigeria, Chad, Central African Republic, Equatorial Guinea, Gabon, the Republic of the Congo and eastern Democratic Republic of Congo. Two birds (1 male, 1 female) stayed more to the west, in Mali and Senegal, while five SRPs of males were located in southern Africa, their SRPs being south of 19°S. No female moved further south than 1°S.

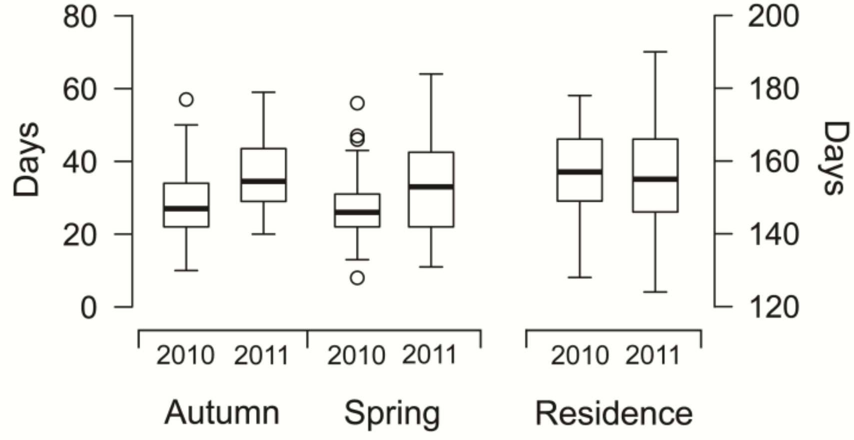

Figure 3: Boxplot of median duration of post- and pre-breeding migration (left) and of duration of stay in the sub-Saharan residence area (right) (box: interquartile range; whiskers: extreme values except dots, which are the values >1.5 times the interquartile range). Year values (2010 and 2011) refer to the year of geolocator deployment (see also Figure 2).

There was a statistically significant difference in the SRPs between the two years of the study ($p = 0.002$; Supplementary material Appendix 3). Median location of the 59 individuals tracked in 2010-2011 was 7.0°N - 12.8°E, while for the 33 individuals tracked in 2011-2012 it was 3.2°N - 15.3°E, i.e. 506 km to the SE. The limited sample size did not allow any within-year analysis of sex and population effects. Therefore, we corrected for the year effect, and pooled data from the two years (see Methods and Supplementary material Appendix 3). There were no statistically significant differences in the spatial distribution of sexes or breeding populations (all pairwise comparisons $p > 0.06$, Supplementary material Appendix 3, Table A1). The difference in the SRP was similar to the difference in the October (i.e. when barn swallows reach their non-breeding residence area) position of the intertropical convergence zone (ITCZ) between the years (Figure 4, Supplementary material Figure A3).

Out of the 66 birds that could be tracked throughout the entire non-breeding period, one third (22) had more than one stationary period, with a minimum stopover period of 14 d (Supplementary material Figure A4). Median distance between the positions of these two consecutive stationary periods was 350 km. Five out of the 22 birds returned to almost the same area (distance < 200 km) after an intermediate movement period. Among these 22 birds, there was no directional preference for the individual displacements between the consecutive non-breeding stationary periods (Rayleigh-test $r = 0.04$, $n = 22$, $p > 0.90$).

Relation of sub-Saharan residence position and phenology of non-breeding events

We tested whether the SRP was related to the timing of non-breeding events. To this end, we added latitude and longitude of the SRP to the models of duration of stay, departure date and duration of pre-breeding migration, and arrival to the breeding colony (Table 2). Since the five SRP of males that were in southern Africa could have a high influence on the results of the analyses, models were ran either including ('whole dataset') or excluding these birds ('reduced dataset'; Table 3). Duration of stay and departure from SRP were unaffected by latitude or longitude in the whole dataset (Table 3), but latitude and longitude effects emerged in the reduced dataset (Table 3). Specifically, in the reduced dataset duration of stay was shorter at more northern latitudes and more eastern longitudes, and departure from SRP was earlier in birds whose SRP was more easterly (Table 3). Duration of spring migration was shorter for those staying at northern latitudes but the effects became non-significant ($p = 0.22$) if the analyses were ran on the reduced dataset (Table 3). Arrival date to the breeding colonies was instead strongly and consistently predicted by latitude and longitude of the SRP in both datasets (Table 3). Birds from more northern and eastern locations arrived earlier (Table 3, Figure 5) than those from further south and west. Latitude of the SRP did not differentially predict the phenology of non-breeding events of either sex (details in Supplementary material Appendix 2). Finally, we tested whether the earlier arrival date in spring 2011 vs. spring 2012 (Table 2) was caused by the more northerly SRP in 2010-2011 compared to 2011-2012 (Supplementary material Appendix 2). The earlier spring arrival of birds tagged in 2010 persisted after controlling (besides for sex and population, Table 2) for latitude and longitude of the SRP (effect of year, $F_{1,61} = 5.13$, $p = 0.027$; least-square means, 2010: 101.6 ± 2.2 SE, 2011: 108.5 ± 2.1 SE) or for the distance between the breeding colony and the SRP ($F_{1,62} = 5.16$, $p = 0.027$; least-square means, 2010: 101.5 ± 2.2 SE, 2011: 108.5 ± 2.3 SE).

Table 3. Effects (slopes and SEs) of the sub-Saharan residence position (latitude and longitude) on duration of stay in the residence area, date of departure from the residence area, duration of pre-breeding migration and date of arrival to the breeding colony. Main effects of year, sex and population were also included in the models, but these are not shown for brevity (their effects are already shown in Table 2). Sample size including and excluding the data of the five males staying in southern Africa are shown. Bolded terms are statistically significant at: *: $p < 0.05$; **: $p < 0.01$.

	Duration of stay	Departure	Duration of migration	Arrival date
	(n = 71/66)	(n = 73/68)	(n= 68/63)	(n=68/63)
All data				
Latitude	0.32 (0.24)	0.04 (0.23)	**-0.66 (0.20)****	**-0.61 (0.19)****
Longitude	-0.45 (0.39)	-0.63 (0.36)	-0.10 (0.31)	**-0.79 (0.30)***
Excluding the five SRPs located south of 19°S				
Latitude	**-1.26 (0.53)***	-0.87 (0.54)	-0.62 (0.49)	**-1.44 (0.45)****
Longitude	**-0.77 (0.39)***	**-0.78 (0.37)***	-0.19 (0.33)	**-1.00 (0.31)****

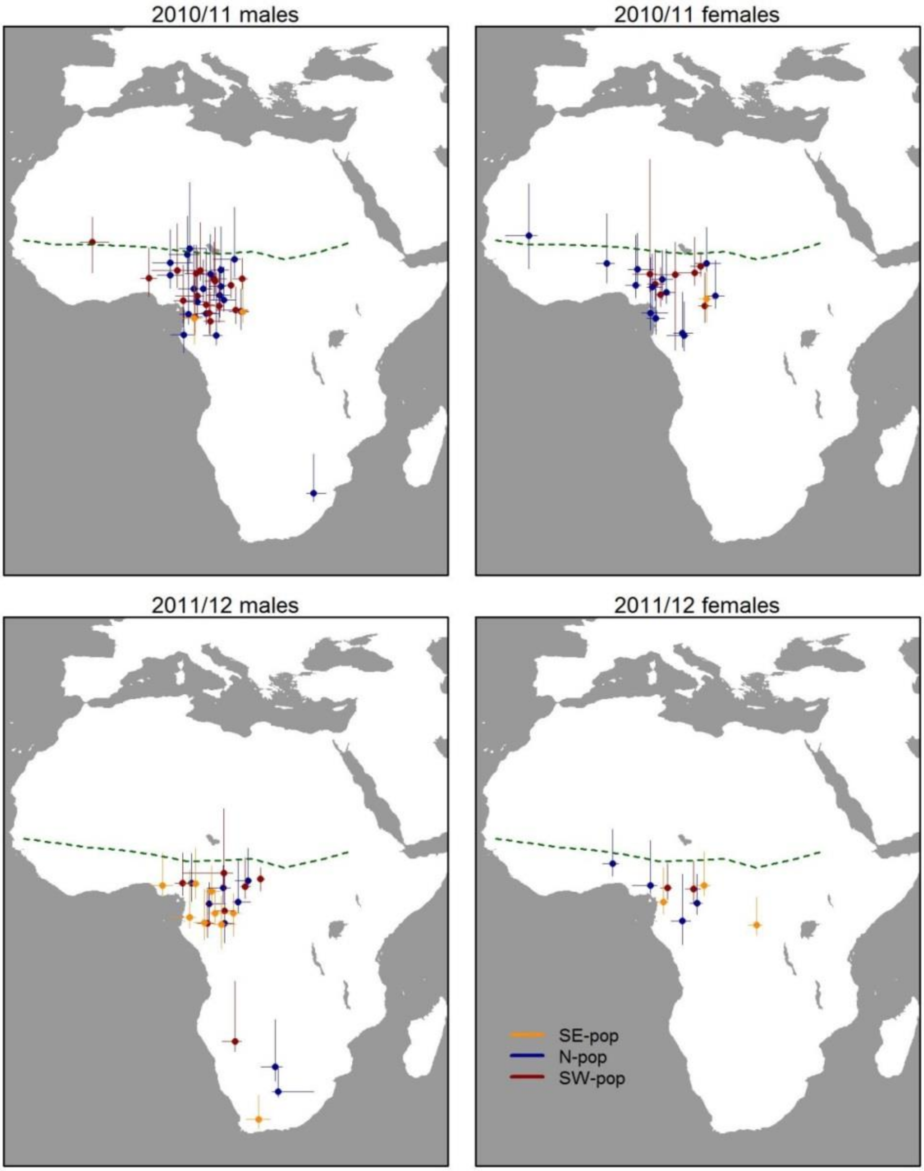

Figure 4: Spatial distribution of the individual sub-Saharan residence positions (SRP) for all individuals (n = 94 tracks). In case of more than one stationary period south of the Sahara only the longest period is represented. The centre of the density distribution and the 90% range in longitude and latitude (crossing lines) are given. The colours refer to the three breeding areas (blue = SW area; red = SE area; green = N area). Individuals are stratified in the four graphs by year and sex. The dashed green line indicates the position of the intertropical convergence zone in the last decade of October for the two years, respectively (NOAA-CPC, http://www.cpc.ncep.noaa.gov/products/fews/ITCZ/itcz.shtml).

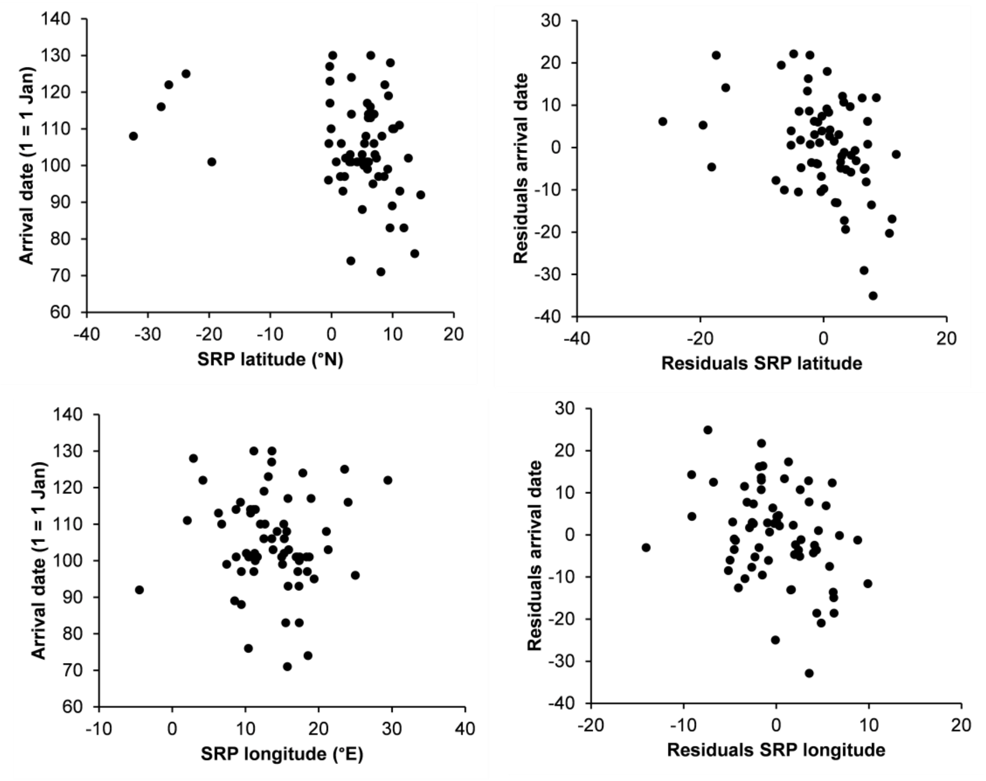

Figure 5: Arrival to the breeding colony in relation to latitude (upper panel) and longitude (lower panel) of the individual sub-Saharan residence positions (SRP, n = 68 tracks). Raw data are shown on the left. On the right residuals from the models presented in Table 3 are shown (y-axis: residuals of the dependent variable on all the other predictors in the model; x-axis: residuals of the regression of a given predictor on all the other predictors). Negative values indicate longitudes to the west of the zero meridian or latitudes in the southern hemisphere, respectively.

Discussion

This uniquely large sample of individual-based tracks of a small migratory passerine allowed to investigate sex-, population- and year-specific variation in the phenology of the non-breeding period.

Phenology of non-breeding period events

Surprisingly, there was only a statistically significant difference between the sexes in departure for post-breeding migration, but not, as expected, in the arrival at the breeding colonies in spring (Møller 1994, 2007). At least, there was a non-significant difference in the mean of the arrival dates in line with the expected trend. Indeed, while the difference in arrival dates was not statistically significant, the effect size is consistent with a statistically significant protandry of 3 d inferred from a large sample of first capture dates at the breeding colonies of two or more years old individuals (Saino et al. 2004b). We therefore assume that with a larger sample size the difference in arrival dates would be confirmed.

The mechanism and function (if any) of later departure of males from the breeding colony are unknown. One possibility is that females, being more committed to post-fledging care of the offspring, tend to leave the colony earlier following their offspring, which undergo post-fledging dispersal soon after leaving the nest. In addition, moult patterns in Africa show no evidence of sex-specific timing (Saino et al. 2013). Overall, our results suggest that at the population level sex does not seem to play a major role in shaping the phenology of the non-breeding period events.

The three geographical breeding populations we studied are, in fact, only ca. 100 km apart. However, while the N population is in an Alpine valley, the SW and SE ones are located in the Po plain. Notwithstanding a latitudinal displacement of less than 1°, the N population is known to have delayed breeding season compared to the SW and SE ones, with a difference in mean first clutch egg laying dates of approximately 6 and 16 d, respectively, in the three years encompassed by this study (RA, DR, NS, CS, unpubl.). This delay is in line with the differences between the N population and the SW and SE population in the arrival dates at the breeding sites of our tracked individuals. No other statistically significant differences in phenology were observed among populations. A close inspection of model-estimated values of phenological variables in Table 2 suggests that delayed arrival to the N population was the result of a somewhat later departure from the sub-Saharan residence area and of a longer duration of the pre-breeding migration. No difference emerged in date of departure from the breeding colony or arrival to the sub-Saharan residence area between the N and the other populations. Hence, the delayed spring arrival to the N area does not seem to be a carryover effect of overall delayed annual life cycle, but rather results from an adjustment of the pre-breeding migration schedules. These sex and population effects on phenology were independent of any year effect, as suggested by the lack of two-way statistically significant interaction effects.

The most notable difference in the phenological events during the non-breeding period was between the two years of study. Independently of any sex and population effects, the birds monitored from autumn 2010 till spring 2011 had later start of post-breeding migration (5 d), shorter post-breeding migration period (10 d), earlier arrival at the sub-Saharan residence area (5 d), shorter pre-breeding migration (7 d) and earlier arrival to the breeding colony (9 d) as compared to those tracked from post-breeding migration 2011 till spring 2012. Most strikingly in comparison with other phenological events, departure from the breeding grounds differed markedly between the years and was, in both years, highly concentrated over a few days (Figure 2). In both years the main departure from the breeding sites coincided with rainfall (MeteoSwiss 2014). In 2010 heavy rainfall events occurred in southern Switzerland and northern Italy on the 7 to 8 and 12 to 13 September. Peak departure was on the 7, and by the 13 September 90% of the tracked birds had left their breeding sites. In 2011 heavy rain was recorded on the 4 to 5 September. 60% of the tracked individuals left between 3 to 6 September, and by the 10, before the next heavy rainfall (on the 11), 32 of the 33 tracked birds had left. Food availability for aerial feeders like barn swallows is strongly impaired by heavy rain, combined with lowered temperatures and a reduced duration of daily sunshine hours (Grüebler et al. 2008). Based on two years of observations, our results can only give a good hint that local weather conditions may synchronize the final decision to leave the breeding site. Despite leaving their breeding colony later, the birds tracked in 2010-2011 managed to advance their subsequent phenology compared to those tracked in 2011-2012, including arriving earlier to their breeding colony, perhaps because of favourable weather conditions *en route* (see below).

Remarkably, the date of departure for pre-breeding migration did not significantly differ in the two monitored years and the duration of stay at the sub-Saharan residence area was identical, differently from the timing and duration of the other activities. This might support results from laboratory experiments showing that the onset of spring migration is strongly controlled by the endogenous circannual rhythm (Gwinner 1996). However, barn swallows undergo their single complete annual moult of the wing and tail feathers during the non-breeding period. The process of moulting wing feathers alone is thought to require at least 135 d (Jenni and Winkler 1994) while the mean duration of stay at the sub-Saharan residence area we observed was 157 d in both years, suggesting that moult *per se* is unlikely to constrain the onset of migration. The duration of stay could be determined by the time required to complete moult plus the time required for pre-migratory fattening, implying that the duration of stay of barn swallows in western equatorial Africa could be set by physiological constraints on the start of pre-breeding migration.

Variation in the sub-Saharan residence positions

Adult barn swallows breeding colonially in three southern European areas were found to have their individual sub-Saharan residence positions mainly within a relatively small region, of about 1000 km in radius, centred in Cameroon. Overall, barn swallows were mostly resident during wintering: even those individuals that were found to have more than one sub-Saharan residence area stayed within a region which is relatively small for a highly vagile species that can travel hundreds of km per day on foraging trips (NS, unpubl.).

Males and females appeared to broadly overlap in the SRPs, and also between populations there was no noticeable difference with respect to the location of the SRPs. The results indicate that connectivity between breeding and non-breeding ranges is weak at least with respect to our small geographical range in breeding locations. Overall, the distribution of the sub-Saharan residence areas resulting from the present data is highly consistent with the information that has been gathered from recoveries of a few tens of barn swallows ringed all over Italy during the breeding season over approximately one century (Saino et al. 2004a, Spina and Volponi 2008). Thus, on the large scale we can confirm the migratory connection of barn swallows between Italy (and presumably southern Switzerland) and mainly western equatorial Africa.

In the first study year (2010/2011) the tracked birds occupied residence areas in sub-Saharan Africa further north, they migrated faster and arrived earlier at the breeding grounds than in the second study year (2011/2012). The difference in the location of the SRPs goes along with the difference in the position of the intertropical convergence zone (ITCZ) between October 2010 and 2011. The ITCZ is a measure for the distribution of rainfall in the Sahel region (Issa Lélé and Lamb 2010). In 2010 the seasonal movement (April to October) of ITCZ was very similar to 2011, except that in October 2011 it moved much faster further south (Supplementary material Appendix 5, Figure A3). This indicates that at the time of arrival of the barn swallows (1st decade of October) in the Sahel it was more humid further north in 2010 than 2011. It seems that barn swallows opportunistically selected SRP’s further north, most probably due to favourable foraging opportunities.

It is unclear why a few males but no females showed markedly deviant decisions and spent their main residence period in austral tropical Africa, between Angola and the Republic of South Africa. These individuals might either be immigrants from populations migrating generally to southern Africa (e.g. from Britain or Scandinavia), or they might have, due to social attraction, joined conspecifics from such populations. An analysis of the genetic distances between the southern African migrants and the rest of the birds might help resolving this puzzling finding.

Besides providing an overall picture of the African non-breeding distribution of barn swallows from the southern border of the Alps, our study allowed us to test the consequences of the positions of the sub-Saharan residence areas for the timing of pre-breeding migration and return to the breeding sites. There was no statistically significant difference in the departure dates from the sub-Saharan residence areas between the years, but a distinct difference of more than a week in arrival dates at the breeding grounds. The earlier arrival in spring 2011 was independent of the more northerly distribution of SRPs in 2010-2011 vs. 2011-2012. We may speculate that the earlier arrival in spring 2011 was caused by faster migration because of more favourable *en route* conditions. Indeed, mean April (2011) temperatures in the western Mediterranean (where most of our geolocator birds migrated through, based on longitudinal positions during spring migration; RA, FL, DR, NS, CS, unpubl.) and in the breeding areas were exceptionally high (up to 4°C above the long-term average (Supplementary material Figure A5). In April 2012 temperatures were only slightly above the average (1°C), and in the western Mediterranean they were 2°C below the long-term average. Therefore, the birds might have crossed the Sahara during the same time period, but due to the favourable weather conditions in April 2011 the birds headed more directly to their breeding colonies than in 2012. More detailed analyses of the individual tracks are hampered by the fact that most of the pre-breeding migration falls into the period of equinox, with no information on latitudes.

Regardless of the year effect, birds staying further north and/or east arrived earlier at the breeding colonies (Tab. 3). However, since the SRPs stretch in northwest-southeast direction, individuals SRPs further north also were on average further west, which partially compensates the negative effect of latitude on arrival at the breeding colonies. This implies that birds from northwest Nigeria (12°N, 5°E) arrived 3 d earlier than those from southeast Cameroun (3°N, 15°E). Thus, we can conclude that early arrivals at the breeding colonies are by birds with SRPs located further north and east than those arriving late. The analyses carried out on the reduced dataset, excluding the five SRPs of males that were south of 19°S, suggest that at least part of the effect could be due to shorter duration of stay and earlier spring departure of birds whose SRP was more to the north and east. Nevertheless, this result is the first empirical evidence that long-distance migratory birds spending the non-breeding period closer to the breeding range experience measurable benefits in terms of duration of pre-breeding migration and early arrival. This suggests positive selection for spending the non-breeding period closer to the breeding range (Bearhop et al. 2005). However, the strong difference between the years also suggests that individual SRPs are markedly affected by environmental conditions, and thus that phenotypically plastic responses to contingent variation in ecological conditions may affect the choice of SRP. The distinct influence of large-scale environmental conditions in the Sahel (as gauged by differences between the years) on the SRPs and, thus, on the timing of pre-breeding migration, discloses a potential mechanism by which ecological conditions in this area may carry-over on timing of reproduction (Saino et al. 2004a).

We have previously investigated the effect of the geolocators used in this study in detail (Scandolara et al. 2014). We cannot rule out that besides the observed sex-specific geolocator effect on survival, migration speed and thus arrival dates might be more negatively affected by geolocators in males than in females. However, the extent of the sex differences in timing of arrival derived from geolocators was in line with a previous study (see above).

Overall, we found considerable variation across all phenological events, as well as for the individual SRPs. The strongest single factor explaining such variation was by far the year effect, emphasising the importance of environmental conditions. Sex- and population-specific variation was of minor importance and found only for departure and arrival events in the breeding area. Migratory connectivity was low among the three populations studied, but on the large scale it was consistent with the available information from ring recoveries, which however required one century to be accumulated. The duration of pre-breeding migration and timing of arrival to the breeding colonies suggests selection for non-breeding residence areas close to the breeding range. However, based on our two study years we cannot rule out a phenotypic adaptation to variability in the environment. To conclude, results from this study support the use of miniaturised light-level geolocators as relatively cheap devices for the study of annual routines of large samples of migratory songbirds.

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Impact of miniaturized geolocators on barn swallow *Hirundo rustica* fitness traits.

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Chiara Scandolara[1], Diego Rubolini[1], Roberto Ambrosini[2], Manuela Caprioli[1], Steffen Hahn[3], Felix Liechti[3], Andrea Romano[1], Maria Romano[1], **Beatrice Sicurella[2]**, Nicola Saino[1]

1. Dipartimento di Bioscienze, Università degli Studi di Milano, via Celoria 26, I-20133 Milano, Italy

2. Dipartimento di Biotecnologie e Bioscienze, Università degli Studi di Milano-Bicocca, p.zza della Scienza 2, I-20126 Milano

3. Swiss Ornithological Institute, Seerose 1, CH-6204 Sempach

Abstract

Miniaturized light-level geolocators may revolutionise the study of avian migration. However, there are increasing concerns that they might negatively affect fitness. We investigated the impact of two miniaturized geolocator models (SOI-GDL2.10, deployed in 2010, and SOI-GDL2.11, deployed in 2011) on fitness traits of the barn swallow (*Hirundo rustica*), one of the smallest migratory species to which geolocators have been applied to date. The 2011 model was lighter (by 0.09 g) and had a shorter light stalk compared to the 2010 model. Using data from 640 geolocator and 399 control individuals from three geographical populations, we found that geolocators reduced annual survival probabilities (control birds: 0.19-0.63; geolocator birds: 0.08-0.40, depending on year, sex, and how birds that lost the device were considered), with more markedly negative effects on females equipped with the 2010 model. In addition, among birds equipped with the 2010 model, onset of reproduction in the subsequent year was delayed (by 12 d) and females laid smaller first clutches (by 1.5 eggs, i.e. a 30% reduction) compared to controls. Equipping parents with geolocators while they were attending their brood did not affect nestling body mass or fledging success. A reduction of geolocator weight and drag by shortening the light stalk slightly enhanced the survival of females but not that of males, and mitigated the negative carry-over effects on subsequent reproduction. Our study shows that geolocators can have a negative impact on survival and reproduction, and that even minor differences in weight and drag can make the difference. We suggest that studies aiming at deploying geolocators or other year-round tagging devices should be preceded by pilot experiments to test for fitness effects.

Introduction

One of the major challenges of long-distance animal tracking is the miniaturization of tracking devices to fit the huge number of migrant species weighting below 100 g, including the thousands of species of small songbirds moving twice a year across continents (Moreau 1972, Hahn et al. 2009), that cannot be tagged with current satellite-based technologies (Bridge et al. 2011). Though they have well-known drawbacks (low accuracy of position estimates, need to retrieve the device), so far miniaturized (ca. 0.5 g) light-level geolocators constitute almost the only possibility to identify individual migration routes and wintering areas of many medium- to small-sized bird species (see Bridge et al. 2013).

The wide diffusion of geolocators, which has been favoured by the relatively low cost compared with e.g. satellite or GPS tags, easily allowing the tagging of dozens or even hundreds of individuals, and the fact that they have been deployed and will likely be deployed in the future on many different species, should prompt for a careful evaluation of their potentially harmful effects. A recent meta-analysis highlighted that attaching external devices (dataloggers and radio- or satellite-transmitters) to birds causes a significant negative impact on several fitness-related traits, most notably reducing propensity to breed and increasing energy expenditure (Barron et al. 2010). Similarly, a meta-analysis of published studies revealed that geolocator deployment negatively affects survival (Costantini and Møller 2013). Moreover, in most studies appropriate control groups to test for the effect of geolocators were lacking, and the negative survival effects reported so far in the literature are probably underestimated because researchers likely spend every effort to recapture geolocator birds (Bridge et al. 2013, Costantini and Møller 2013).

Geolocators may also have negative long-term carry-over effects on other major fitness traits, such as reproductive success (Rodriguez et al. 2009, Arlt et al. 2013). In addition, if applied to parent birds attending their broods, they may negatively affect parental food delivery rates to nestlings and impair nestling growth (Adams et al. 2009; but see Rodriguez et al. 2009, Quillfeldt et al. 2012, Gómez et al. 2013).

Here we evaluated the effects of miniaturized geolocators on fitness traits (annual survival, and laying date and clutch size in the year after deployment) of the long-distance migratory, aerially insectivorous barn swallow *Hirundo rustica*. Barn swallows were fitted with two geolocator models, which differed in their external size and shape and were deployed using leg-loop harnesses (Figure 1). We also evaluated the effects of different leg-loop harnesses on geolocator loss rate. Finally, we investigated whether applying geolocators to parents while they were attending their brood affected nestling body mass and fledging success.

Methods

Study areas, general methods and geolocator characteristics

The study was conducted in three study areas, one in southern Switzerland (Magadino) and two in northern Italy (Piedmont and Lombardy), during April–July 2010-2012 (see details in the Supplementary material Appendix 1). Nests in selected barn swallow colonies (farms) within the study areas were regularly visited (every 10-12 d) to record breeding events, laying date and clutch size (for the first clutches only; data on fledging success and subsequent clutches were not available for several individuals, years and study areas). Breeding adults were captured with mist-nets, individually marked with colour rings, and their nest identified by direct observation. Due to strong breeding philopatry and very high efficacy of capturing breeding barn swallows, we could determine whether a bird survived or not to the next breeding season with high confidence (see details in Appendix 1). Upon capture, we recorded body mass and wing length [length of the 8th primary feather (Jenni and Winkler 1989)].

Geolocators were deployed at the end of the breeding season. In July 2010, we applied 310 SOI-GDL2.10 (Swiss Ornithological Inst.) geolocators to breeding individuals (162 males, 148 females) at 21 farms, while in June-July 2011 we applied a new model (SOI-GDL2.11) to 330 breeding individuals (184 males, 146 females) at 29 farms (Table 1). Geolocators were fitted using a leg-loop harness (Rappole and Tipton 1990) made of elastic silicone rubber mixture (MVQ 60 shore A). In 2010, we decided to apply leg-loop harnesses varying in diameter (27 or 28 mm) and thickness of the leg-loop (1.00 or 1.25 mm). Since geolocators were handcrafted, their weight (harness included) varied slightly [2010: model SOI-GDL2.10 = 0.77 g (0.05 s.d.), n = 310; 2011: model SOI-GDL2.11 = 0.68 g (0.03 s.d., n = 330)]. The weight of geolocators relative to barn swallow body mass upon capture was below 5% (in agreement with the so-called ‘5 % rule’; Kenward 2001; see Barron et al. 2010) in both years [2010: 4.14% (0.40 s.d.); 2011: 3.74% (0.35 s.d.)]. Further details on the characteristics of the two models and on sex- and year-specific variation in relative geolocator weight are reported in the Appendix 2 and in the legend to Fig. 1.

In 2010, subjects were assigned to a geolocator or control treatment sequentially with the aim of maintaining a 2:1 ratio between geolocator and control subjects within each farm (odd individuals in a farm were balanced by further individuals in different farms). In 2011, protocols of geolocator deployment differed slightly between study areas: in Magadino and

Piedmont, for each geolocator subject we identified a control subject of the same sex within the same farm, captured on the same or the most close capture session, while for practical reasons in Lombardy we assigned different farms to different treatments (we had a total of 5 farms where >90% of breeding birds were equipped with geolocators, these birds being all 'geolocator' subjects, and 2 farms were no bird was equipped with geolocators, with all birds being 'control' subjects).

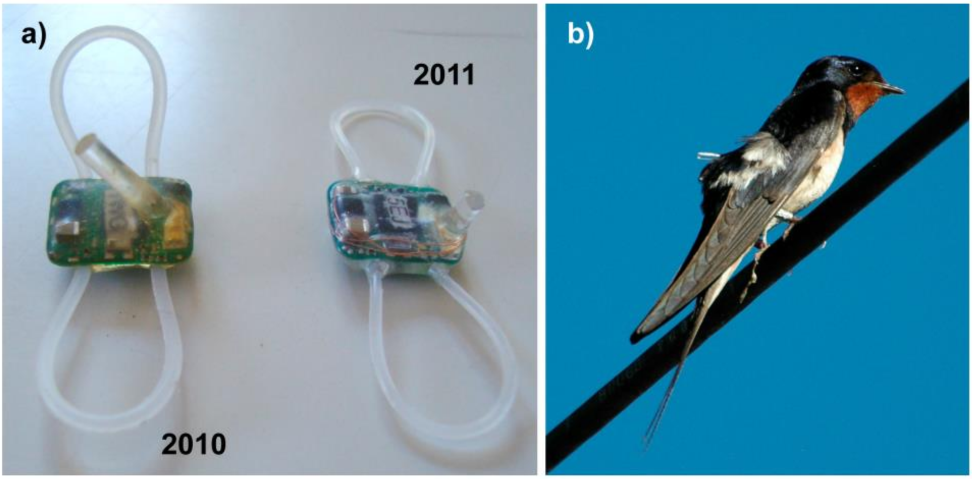

Figure 1. Picture of a) geolocator models deployed in 2010 (SOI-GDL2.10) and 2011 (SOI-GDL2.11); the difference in light stalk length and bending can be easily appreciated (see also Appendix 1); and b) a male barn swallow equipped with geolocator model SOI-GDL2.10.

In the year of geolocator deployment, geolocator and control subjects did not differ in laying date, clutch size, or age (Supplementary material Appendix 1). Deployment took only a few minutes, and we managed to handle geolocator and control subjects for the same amount of time. Devices were removed in the subsequent year, upon first capture of an individual. The detailed analyses of the information retrieved from geolocators will be reported elsewhere (Liechti et al. 2014). Preliminary inspections of African wintering sites indicated a broad overlap with the known wintering range of the study population derived from ring recoveries (Saino et al. 2004).

The short-term effects of geolocator deployment on nestling growth and fledging success (brood size at fledging) were studied in Magadino in 2010. Selected nests (see Statistical analyses) were inspected when nestlings were 6-14 d old, and each nestling was weighed and molecularly sexed using the CHD-Z and CHD-W genetic markers (see Saino et al. 2008 for details of protocols).

Statistical analyses

As detailed in the Results section, some analyses were carried out separately for each year, because our experimental treatment (geolocator deployment) differed between years due to differences in geolocator characteristics (see above).

The analyses investigating the effect of geolocator deployment on fitness are complicated by the fact that a non-negligible proportion of returning individuals lost the geolocator at an unknown time between device deployment and recapture in the subsequent breeding season (Table 1). Such individuals could therefore either be excluded from the analyses, regarded as control subjects (assuming the geolocator was lost soon after deployment) or simply treated as geolocator subjects (assuming the geolocator was lost just before recapture). Each of these alternatives has drawbacks and may cause bias, depending on when the geolocator was actually lost. Thus, analyses of survival were carried out using different datasets where the subjects that lost the geolocator were: a) excluded; b) considered as controls; or c) as ‘true’ geolocator subjects.

Table 1. Summary statistics of the number of birds assigned to the geolocator or control treatment in the two study years (2010 and 2011). The column “Surviving” shows the number of birds that survived to the subsequent year, with the proportion out of the subjects assigned to a given treatment in the year before shown in parentheses. The column “Lost” shows the number of birds that survived but returned without the geolocator (i.e. birds that lost the device), with the proportion out of the surviving birds shown in parentheses.

	Year 2010			Year 2011		
	Subjects	Surviving	Lost	Subjects	Surviving	Lost
Males						
Geolocator	162	65 (0.40)	14 (0.22)	184	36 (0.20)	1 (0.03)
Control	86	47 (0.55)	-	136	43 (0.32)	-
Females						
Geolocator	148	43 (0.29)	16 (0.37)	146	18 (0.12)	7 (0.39)
Control	81	46 (0.57)	-	96	18 (0.19)	-

The effects of geolocator configurations (diameter and thickness of the leg-loop harness) on the odds of losing the geolocator were analysed by binomial mixed models (Supplementary material Appendix 3).

The effect of geolocator deployment on survival to the subsequent year was investigated by means of binomial mixed models with survival (0 = did not survive; 1 = survived) as the binary dependent variable and geolocator deployment (hereafter treatment), sex and their interaction as predictors. Binomial mixed models were also ran to test whether geolocator weight affected survival of geolocator subjects (details in Supplementary material Appendix 3).

The effects of geolocator deployment on reproductive performance (laying date and clutch size) were analysed by Gaussian mixed models, with the within-individual difference in each trait between year (i + 1) and year i as dependent variables and treatment, sex and their interaction as predictors. The approach of comparing within-individual differences, where each subject acts as its own control when exposed to a different experimental treatment (geolocator deployment), is expected to be particularly robust as it efficiently allows ruling out confounding effects of among-population variation in mean trait size. These analyses included only geolocator birds that returned with the geolocator. Magadino data were excluded from these analyses because reproduction data for control birds were not collected in 2011 and 2012.

Study area and farm were included as random intercept effects in all mixed models to account for clustering of observations within farms and study areas. Variance explained by random effects (and the effect of random effects on fixed-effect estimates) was in most cases negligible and will not be discussed further (details not shown). Parameter estimates are reported together with their standard errors. For non-Gaussian mixed models significance tests were performed by z-scores, while for Gaussian models degrees of freedom were calculated according to the Kenward-Rogers method.

To investigate the short-term effects of geolocator deployment on nestling growth and fledging success, we ran mixed models where we compared body mass [age range 6-14 d, mean age = 10.5 (2.0 sd) days, i.e. during the linear growth period (Ferrari et al. 2006)] and fledging success (brood size at fledging) of nestlings that were attended by parents who had been equipped with geolocator (male only, female only, or both parents) at least 6 d before nestling measurement and when nestlings were a maximum of 4 d old with those whose parents were not equipped with geolocators. See Appendix 4 for further details on these analyses and sample sizes.

Mixed models were run using PROC GLIMMIX and PROC MIXED of SAS 9.1.3 (SAS Institute 2006).

Results

Geolocator design, loss rate and effects of geolocators on survival (years 2010-2011)

In 2010, we deployed geolocators on 310 barn swallows (Table 1), of which 65 males and 43 females survived to 2011. Thirty of the surviving birds lost the geolocator (Table 1). The loss rate was affected by sex and harness design, being significantly higher for females, and for geolocators with thicker and longer harnesses (Supplementary material Table A1). Wing length did not affect loss rate when added to models (including main effects of harness thickness and diameter) run separately for each sex ($p > 0.55$ in both cases, other details not shown).

We did not notice any apparent external injury or wound in birds returning with the geolocator, with the exception of the incomplete growth/moult of contour body feathers on the back-rump, just underneath the geolocator, a common feature of individuals wearing geolocators on the back/rump (see also Bridge et al. 2013).

Survival was strongly negatively affected by geolocator deployment (Table 1, 2): model-predicted probabilities of control birds surviving till the next breeding season were 0.55-0.61 for males and 0.56-0.63 for females (depending on how individuals that lost the device were considered) vs. 0.34-0.40 and 0.20-0.29 for males and females, respectively, among geolocators subjects. The negative effect of geolocator on female survival was least evident if birds that returned but lost the geolocator were considered as geolocator subjects, since females were more likely to lose the geolocator than males (Table 1, A1). Wing length or age did not differentially affect survival of geolocator and control subjects, nor did they significantly affect survival probability *per se* (Supplementary material Appendix 5).

On the whole, there was no conclusive evidence that different harness configurations affected survival independently of geolocator loss, and there was no effect of geolocator weight (either absolute or relative, expressed as % body mass) on survival (Supplementary material Appendix 6).

Effects of improved geolocators on survival (years 2011-2012)

In 2011, we deployed 330 improved geolocators (harness thickness = 1.00 mm; diameter = 27 mm; shorter light stalk and lighter weight). We successfully reduced loss rate for males, but not for females, compared to the previous year (Table 1). Survival of barn swallows was lower compared to the previous year, irrespective of geolocator deployment, and female survival was significantly lower than that of males (Table 2). The effect of treatment was negative and highly statistically significant (Table 2): model-predicted survival probabilities of control birds were 0.31-0.32 and 0.19-0.20 for males and females, respectively, while the corresponding ones for geolocator birds were 0.19-0.20 and 0.08-0.12, depending on the dataset (Table 2; see also Table 1 for actual proportions). Therefore, improvement of geolocator design reduced geolocator loss rate, but a lower geolocator weight and stalk length (see Figure 1) did not markedly reduce the negative effects of geolocator deployment on survival, as confirmed by models including data for both years, irrespective of the dataset used (treatment × sex × year: all $p > 0.22$; treatment × year: all $p > 0.09$; sex × year: all $p > 0.09$; further details not shown for brevity). However, we may qualitatively note that point estimates of odds ratios for males were very similar between the two years, while female ones in 2011 were almost half than those in 2010 (Table 2). Wing length or age did not differentially affect survival of geolocator and control subjects (Supplementary material Appendix 5). Finally, geolocator weight (either absolute or relative) did not significantly affect survival of geolocator subjects of either sex (Supplementary material Appendix 6).

Effects of geolocators on reproduction

Geolocator subjects of both sexes equipped with the 2010 model bred 11.93 (4.57 s.e.) days later than controls (Figure 2) ($F_{1,69} = 6.81$, $p = 0.011$; Table A2). In addition, the clutch size of geolocator females in the subsequent year was 1.45 (0.44 s.e.) eggs smaller than that of controls (Figure 2, Table A2). However, deployment of geolocators on males did not significantly affect the clutch size laid by their partner (Figure 2; treatment × sex, $F_{1,65} = 4.86$, $p = 0.031$; Table A2).

Such negative effects on subsequent reproduction disappeared for geolocator subjects equipped with the 2011 model (Figure 2, Table A2). Mixed models including data for both years indicated that geolocator carry-over effects did not differ statistically between years (laying date: treatment, $F_{1,123} = 4.31$, $p = 0.040$; year, $F_{1,112} = 17.86$, $p < 0.001$; treatment × year, $F_{1,106} = 1.67$, $p = 0.20$; clutch size: treatment, $F_{1,74} = 0.57$, $p = 0.45$; year, $F_{1,74} = 0.41$, $p = 0.52$; treatment × year, $F_{1,74} = 0.87$, $p = 0.35$; results were similar if data for males and females were analysed separately, details not shown).

Table 2. Binomial mixed models testing the effects of geolocator application (treatment: 0 = control birds; 1 = geolocator birds), sex (0 = female; 1 = male) and their interaction on survival to the subsequent breeding season. Estimates from predictors that were centred around their mean value are shown. Odds ratios (with geolocator subjects as the reference category) are shown for males (M) and females (F) separately even if the interaction term was non-significant, for ease of comparison between the two study seasons.

	Year 2010		Year 2011	
	Estimate (s.e.)	Odds ratio (c.l.)[a]	Estimate (s.e.)	Odds ratio (c.l.)[a]
(a) Excluding subjects that returned without the geolocator (2010, n = 447; 2011, n = 554)				
Treatment	-1.21 (0.21)**	-	-0.74 (0.25)**	-
Sex	0.42 (0.21)*	-	0.88 (0.26)**	-
Treatment × sex	0.80 (0.42)°	M: 2.92 (1.33-3.95)	0.30 (0.49)	M: 1.85 (1.07-3.19)
		F: 5.11 (2.77-9.42)		F: 2.50 (1.09-5.71)

(b) Subjects that lost the geolocator as control subjects (2010, n = 477; 2011, n = 562)				
Treatment	-1.49 (0.20)**	-	-0.95 (0.24)**	-
Sex	0.37 (0.20)	-	0.76 (0.25)**	-
Treatment × sex	0.84 (0.40)*	M: 2.98 (1.76-5.04) F: 6.89 (3.81-12.47)	0.60 (0.47)	M: 1.99 (1.15-3.43) F: 3.64 (1.65-8.04)
(c) Subjects that lost the geolocator as geolocator subjects (2010, n = 477; 2011, n = 562)				
Treatment	-0.86 (0.20)**	-	-0.51 (0.23)*	-
Sex	0.29 (0.19)	-	0.62 (0.23)**	-
Treatment × sex	0.58 (0.39)	M: 1.80 (1.06-3.05) F: 3.21 (1.82-5.66)	-0.15 (0.45)	M: 1.78 (1.04-3.05) F: 1.53 (0.73-3.20)

* = $p < 0.05$; ** = $p < 0.01$; ° = $p < 0.1$

a: geolocator subjects as reference category

Geolocator deployment on the male and/or female parents while they were attending their brood did not affect nestling body mass, controlling for nestling age, brood size, brood order, and nestling sex (Table A3, Figure A1), nor fledging success (brood size at fledging) (Table A3, Figure A1). Therefore, geolocators did not negatively affect reproduction in the short-term.

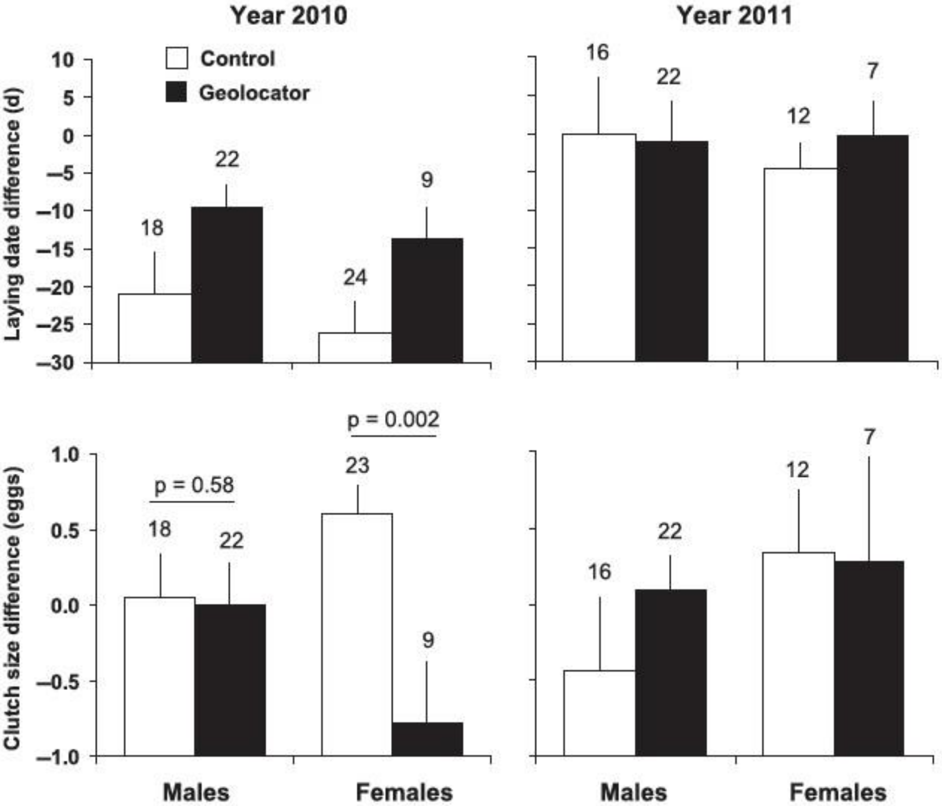

Figure 2: Within-subject differences (value in year $i + 1$ minus value in year i) of laying date and clutch size in relation to geolocator deployment and sex (mean + s.e.) in the two study years (year i) (see Table A2 for details of statistics). Numbers above bars indicate samples sizes, and may differ between traits and groups because of missing values; p-values from *post hoc* tests of the statistically significant treatment × sex interaction on the 2010 clutch size difference are shown (p-values of within-sex comparisons between geolocator and control subjects; see Table A2). Geolocator birds that returned without the device were excluded.

Discussion

Our analyses indicate that geolocator deployment on adults of the barn swallows, one of the smallest bird species equipped with geolocators so far Bridge et al. 2013), can considerably reduce survival, and may negatively affect subsequent reproduction by delaying egg laying and reducing clutch size. Negative effects on fitness showed a tendency to be sex- and geolocator type-specific: the heavier and less aerodynamic 2010 geolocator model had stronger negative effects on survival and reproduction, especially of females, compared with the 2011 model, which did not negatively affect reproduction of either sex. Lower annual survival of controls in the second compared to the first year of study (Table 1), reflecting poor ecological conditions during migration and/or wintering, may have partly obscured any reduction of the impact of the streamlined geolocator model on survival, because it may be expected that the negative effects of geolocators are exacerbated under harsh ecological conditions.

The higher susceptibility of females to geolocators, which was most obvious for the 2010 geolocator model, may be partly due to morphological differences between the sexes: female barn swallows have shorter wings than males (Møller 1994), and, during the breeding season, they have a higher wing loading (body mass/wing area) (Møller et al. 1995, our unpubl. data). These morphological characteristics may increase the cost of transportation of externally attached devices, leading to higher energy expenditure and risk of mortality during migration or other energetically demanding life stages, such as moult, and to more negative carry-over effects on the reproduction of surviving birds.

Surprisingly, within each sex, there was no correlation between the odds of geolocator birds surviving and wing length, suggesting that equipping larger individuals of each sex with geolocators may not be an efficient strategy to reduce their negative impact. In addition, small variation in geolocator weight did not affect survival (see also Barron et al. 2010). Indeed, barn swallows, like other migratory birds, can substantially increase in body mass (by up to 5-7 g compared to body mass during breeding) before and during migration (Rubolini et al. 2002). Thus, the additional geolocator load *per se* was unlikely to be the main cause of the lower fitness of geolocator birds. Rather, geolocators may have increased the drag acting on the swallow bodies during flight, resulting in higher energy expenditure while flying and shorter flight ranges (Bowlin et al. 2010). In this study, reducing the length of the light stalk did not provide a major improvement of survival, differently from previous evidence on other species (in the purple martin *Progne subis*, a reduction of the light stalk from 20 mm to 5-8 mm resulted in return rates comparable to natural ones; McKinnon et al. 2013). Future studies should also experimentally evaluate the efficacy of alternative methods of device attachment, such as wing-harnesses, which might be more suitable than leg-loop harness for aerial migrants because the geolocator might remain closer to a bird's centre of gravity (Åkesson et al. 2012), though possibly at the cost of further increasing geolocator drag (Bowlin et al. 2010).

Alternatively, geolocators, that are partly made of a reflective material, may have increased conspicuousness to aerial predators (barn swallows wearing geolocators can be easily spotted by a human observer; see also Figure 1), and impaired escape performance, especially of females, leading to higher predation and decreased annual survival. A final possibility to explain the lower survival of geolocators birds compared to controls is that the former have lower breeding site fidelity than the latter. However, this possibility can be dismissed because of the strong breeding philopatry of the barn swallow (Supplementary material Appendix 1). For example, none of the geolocator birds was found to have moved to a different colony to breed in the year following that of geolocator deployment, despite barn swallows were sampled in most nearest-neighbouring colonies.

Birds of both sexes returning with the 2010 geolocator model bred ca. 12 days later than controls, corresponding to ca. 1 s.d. of the mean laying date of controls in the same year, and females laid ca. 1.5 eggs less than controls in their first clutch, a 30% reduction compared to the mean clutch size of controls in the same year [equal to 5.11 (0.12 s.e.) eggs]. A delayed egg laying may be due to a delay of migration schedules because of heavier workload imposed by the device during migration, and/or a longer gap between arrival and egg laying. Encouragingly, negative effects on reproduction disappeared in birds returning with the 2011 streamlined model. Finally, carrying a geolocator during chick rearing did not negatively affect nestling growth or fledging success (see also Gomez et al. 2013). This latter finding was obtained when parents were equipped with the heavier and less aerodynamic 2010 model: we can thus safely exclude that the 2011 model negatively affected breeding performance in the year of deployment.

To conclude, the collective evidence derived from recent reviews (Bridge et al. 2013, Costantini and Møller 2013), together with our findings, suggests that a careful evaluation of the potentially harmful effects of geolocators on fitness traits is mandatory before embarking on extensive studies of new population or species, especially in the case of small-sized (<20 g) and aerial species (Costantini and Møller 2013). Based on our results, we can also provide insights on the sample size that allows detecting statistically significant negative effects of geolocators or other year-round tagging devices (e.g. GPS or satellite transmitters) on fitness traits in pilot studies.

For example, power analyses indicated that, in 2010, we could have detected with high confidence (power = 0.80) a statistically significant negative effect of geolocators on survival with half of the subjects (240 vs 477), using the same experimental design [simple logistic regression with $\alpha = 0.05$, two-tailed; actual proportions surviving: geolocators 0.35 (108/310), controls 0.56 (93/167)]. On the other hand, in 2011, when the negative effect of geolocators on survival was smaller [proportions surviving: geolocators 0.16 (54/330), controls 0.26 (61/232)], this number rose to 550 (vs 562) subjects. Pilot tests that aim at investigating external device effects on survival should therefore be based on large sample sizes of hundreds of birds, even in the presence of relatively large effects, as was the case in 2010. Whenever such huge sampling effort is impractical or not advisable (e.g. in the case of rare/endangered species), we suggest caution in concluding lack of effects on survival. Rather, the combined evidence of external device effects on survival and other fitness traits (e.g. breeding success, physiological traits) could be investigated. Furthermore, we emphasize that survival estimates can be heavily affected by search and recovery efforts (few species allow survival estimates as accurate and unbiased as the barn swallow), and that these should be quantified before firm conclusions about external device effects on survival can be drawn. Clearly, the design of year-round tagging devices, including geolocators, should be improved to further minimize negative impacts, as even minor differences in weight, drag and harness design can potentially make the difference.

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Environmental conditions at arrival to the wintering grounds and during spring migration affect population dynamic of barn swallows *Hirundo rustica* breeding in Northern Italy

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Beatrice Sicurella[1]**,** Federica Musitelli[1], Diego Rubolini[2], Nicola Saino[2], Roberto Ambrosini[1]

1 Dipartimento di Biotecnologie e Bioscienze, Università degli Studi di Milano-Bicocca, piazza della Scienza 2, 20126 Milano, Italy

2 Dipartimento di Bioscienze, Università degli Studi di Milano, via Celoria 26, 20133 Milano, Italy

Abstract

Several populations of long-distance migratory birds are currently suffering steep demographic declines. The identification of the causes of such declines is difficult because population changes may be driven by events that occur in distant geographical areas during different phases of the annual life-cycle of migrants. Furthermore, wintering areas and migration routes of individual populations of small-sized species are still largely unknown, with few exceptions. In this paper we identified the critical phases of the annual life-cycle that most influence the population dynamic of a small passerine, the Barn Swallow (*Hirundo rustica*). We used information on temporal dynamics of a population breeding in Northern Italy, whose wintering range and timing of migration have been recently described by miniaturised tracking dataloggers. Our results indicated that primary productivity in the wintering grounds in the month when most individuals arrive from autumn migration as well as primary productivity in an area that is probably a stopover site during spring migration, influenced population dynamics more than habitat conditions at the breeding grounds. By using annual variation in primary productivity at the wintering grounds and stopover sites as predictors, we replicated the observed interannual population changes with great accuracy. However, the steep decline suffered by the population in recent years could be replicated only by accounting for a constant annual decline, suggesting that changes in primary productivity only predicted the interannual variation around the long-term trend. Our study therefore suggests the existence of critical periods during wintering and migration that may have large impact on population fluctuations of migrant birds.

Introduction

Populations of several migratory bird species breeding in Europe are suffering sharp declines (Berthold et al 1998; Sanderson et al 2006), whose causes have been often attributed to changes in land use in the breeding areas and to unevenly distributed climate change (Pimm and Raven 2000; Sala et al 2000; Both et al 2006; Jones and Cresswell 2010). Despite long-term studies have collected large amount of information on population size in several geographical areas where migratory bird populations breed, in many cases the actual ecological determinants of the observed demographic trends are still uncertain. Indeed, the complexity of migrants' life-cycle often hampers assessing the actual causes of population changes, because such an assessment would require information on variation of ecological conditions faced by individuals at breeding and wintering grounds and along migration routes (Newton 2004; Holmes 2007). Furthermore, for the vast majority of migratory species, which are typically small-sized, detailed information on the timing of different phases of the life-cycle, on the precise location of wintering grounds, and on migration routes is lacking. Indeed, such pieces of information should ideally be available for any single population whose dynamic is to be modelled, while rarely they are actually available at such level of detail. Recently, novel technological devices are bridging this gap of knowledge, by allowing ornithologists, for the first time, to track small-sized birds during migration and wintering (Fiedler 2009; Bächler et al 2010). For example, miniaturized light-level dataloggers (geolocators) are revealing information on migration timing and routes and on the spatial distribution of wintering grounds of several small sized species (see e.g. Liechti et al. 2014).

In this paper we aim at assessing the critical stages in barn swallow *Hirundo rustica* L. life-cycle that affect population size. Detailed information on size and reproductive success of a geographical population of this species was collected during a long-term monitoring project that is ongoing in Northern Italy since 1999. We have previously shown that this population has declined by about 7% per year since then (Ambrosini et al. 2012; Sicurella et al. 2014). However, changes in habitat conditions that occurred in the breeding area during the same period accounted for only 5% of the observed decline (Sicurella et al 2014). Hence, this population seems to be mainly regulated by the ecological conditions faced during periods of the annual life-cycle other than reproduction. The deployment of miniaturized geolocators on a large sample of birds has provided a precise identification of the wintering areas of this and other two nearby geographical populations and a detailed description of the phenological events of their annual life-cycle, including time of departure from and arrival at both wintering and breeding quarters (Liechti et al 2014). Hence detailed information is available for the first time on crucial details of the life-cycle of this population out of the breeding period.

A precise description of migration routes of barn swallows is difficult to obtain even with the use of geolocators, because these instruments do not allow for reliable estimates of latitude close to equinoxes, that, unfortunately, largely coincide with the migration periods of this species. However, routes and timing of barn swallow migration can also be investigated by analysing long-term ringing data (Ambrosini et al 2014). Hence, by combining information from geolocators with the analyses of ring recoveries, it is now possible to obtain novel insights into the timing of important stages of the life-cycle, and on the geographical position of the wintering grounds and main migration routes of this geographical population of barn swallows.

The assessment of ecological conditions faced by birds during wintering and migration often involves large geographical areas of the globe and is typically made by satellite-assisted remote sensing of indices of primary productivity (Tucker 1979, 1985) In particular, the Normalized Difference Vegetation Index (NDVI), which measures photosynthetic activity and reflects the effect of rainfall on the distribution and biomass of vegetation (Boone et al 2000; Schmidt and Karnieli 2010), is widely used, and several studies indicate that it is related to bird population changes (see for example Maurer 1994; Osborne et al 2001; Bailey et al 2004; Saino et al 2004a; Szép et al 2006; Giralt and Valera 2007; Balbontín et al 2009). In particular, NDVI may be a very useful indicator of ecological conditions experienced by barn swallows during migration and wintering, because this species feeds on flying insects, whose abundance is strictly dependent on rainfall and vegetation dynamics (Saino et al 2004a, 2004b; Gordo and Sanz 2008; Balbontín et al 2009, 2012; Pillar et al 2014). We therefore used NDVI to investigate the effects of ecological conditions faced by swallows during migration and wintering on year-to-year variation in population size.

We hypothesized that inter-annual variation in population size is influenced by processes acting in different phases of the barn swallow life-cycle. In particular, we investigated the effects of ecological conditions encountered en-route during autumn and spring migration, and in the wintering quarters, since these are considered the main determinant of survival of both adult and young individuals (Saino et al 2004a, Szép and Møller 2005; Turner 2006).

We also hypothesized that ecological conditions at different times of the wintering period may have different effects on survival. For example, survival rate of white stork *Ciconia ciconia* is mainly due to variation in primary productivity at one staging area in the eastern Sahel that these birds visit from October to November, just at the end of their crossing of the Sahara, but not to variation in primary productivity at their wintering grounds (Schaub et al 2005). Hence, ecological conditions encountered at arrival from migration may have an impact on annual survival of migrant birds. Similarly, ecological condition just before departure for spring migration may affect population levels observed at the breeding grounds because only individuals that are able to accumulate sufficient fat resources can survive migration (Gordo and Sanz 2008). We therefore investigated whether ecological conditions during specific periods of wintering, and in particular at arrival to and at departure from the wintering grounds, have an impact on population fluctuations.

Finally, conditions experienced during breeding may affect the annual reproductive output at the population level, which can obviously affect population size in the following year, as returning young barn swallows mostly disperse only a few kilometres from their natal site (Scandolara et al 2014). We hypothesized that this effect may act through three different mechanisms. First, at temperate latitudes, temperature and rainfall have been demonstrated to influence the reproductive output of bird populations (Brown & Brown 1999; Dunn & Winkler 1999), likely through an indirect effect of food availability on the body condition of parents. Second, previous studies have shown that barn swallows breeding in farms where livestock is reared have larger reproductive success than those breeding in farms with no animal farming, due to both an overall larger offspring survival and a larger number of pairs laying a second clutch (Grüebler et al. 2010). Third, the extent of hayfields close to breeding sites has been identified as an important factor affecting nestling quality (Sicurella et al 2014) and, ultimately, their survival (Evans et al. 2007). We therefore accounted for temperature and rainfall, presence of livestock farming and hayfield extent at the breeding sites in our analyses of population dynamic.

Methods

Study organism and field methods

The barn swallow is a small (about 18 g) passerine bird that breeds in vast areas of the northern hemisphere. Populations breeding in Europe winter in Africa to the south of the Sahara desert (Turner 2006).

The population of barn swallows breeding in the Parco Regionale Adda Sud, a wide (24.260 ha) protected area in Northern Italy (coordinates of the approximate centre: 45°19'N, 9°40'E, see Fig. 1), has been intensively studied since 1999 (Ambrosini et al 2002). Censuses took place annually from April to June and were conducted according to a standardized protocol (Ambrosini et al 2002; Sicurella et al 2014). Briefly, all farms were visited every second week, all nests at each farm were inspected and their content recorded. The maximum number of nests simultaneously active at each farm was used to estimate colony size (Ambrosini et al 2002) and the mean number of nestlings observed at all nests when they were at least ten days old was used as an estimate of breeding success in that year. Number of farms censused in each year varied depending on our opportunities to perform field work and on farm owners' willingness to let us visit their properties. For the present study, we selected 115 farms censused for at least five years. Overall 448 to 1390 pairs bred in these farms in each year. Since the sample of farms changed from year to year (from 96 to 115 farms per year), we used the mean number of breeding pairs per farm and the mean number of nestlings in all nests in each year as a measure of population size and breeding success, respectively. In 2008 and 2010-2014 a subsample of 37-48 farms was censused also in July-August following the same protocol, to assess number of breeding pairs and breeding success during the period of second clutches.

In all years we also recorded habitat conditions at breeding sites, particularly presence of livestock farming and extent of hayfields within 200 m from each farm, because these conditions are known to influence number of breeding pairs and breeding success (Møller 2001; Turner 2006; Grüebler et al 2010; Ambrosini et al 2012; Sicurella et al 2014).

In 2011-2013 a study with miniaturized light-level geolocators provided information on wintering and migration of a total of 94 individuals from this and other two barn swallow populations breeding in Northern Italy and Southern Switzerland (Liechti et al 2014). Most of the studied individuals winter in an area of about 1000 km in radius centred in southern Cameroon (coordinates of the median point 5.8°N 13.5°E), with no significant differences in wintering areas between populations (Liechti et al 2014). In addition, geolocator data showed that the majority of individuals reach their wintering grounds in October, and depart for spring migration in March (Liechti et al 2014).

The analysis of ringing data collected over one century throughout Europe and North Africa and stored in the EURING Databank (www.euring.org) allowed us to identify two main migration routes in Western Europe followed by barn swallows during both spring and autumn migration, one through Gibraltar, and one across the Mediterranean, over Tunisia and Algeria (hereafter Tunisia, for brevity) (Ambrosini et al 2014). Importantly, exploratory analyses of geolocator data based on longitude data only (which are available from geolocators even close to the equinoxes) suggest that individuals breeding in Northern Italy follow both these migration routes during spring migration, while during autumn migration they follow only the route through Tunisia. In addition, this preliminary investigation suggests that barn swallows from this population mainly cross Tunisia in September during autumn migration and both Tunisia and Gibraltar in March during spring migration (our unpublished data).

Meteorological data

Data on air temperature and rainfall at breeding sites were obtained from the Agenzia Regionale per la Protezione dell'Ambiente (ARPA, www.arpalombardia.it). These data were collected at 1-day intervals at two meteorological stations located in the close proximity of the borders of the Parco Regionale Adda Sud (distance < 12 km; coordinates of the two stations are 45.44° N 9.50° E and 45.26° N 9.38° E). Mean temperature and total rainfall were calculated for each month from May to August in all years from mean daily temperature and rainfall data collected at these two meteorological stations.

NDVI data

We calculated monthly mean NDVI values from September to March in an area of 1000 km in radius from the median position (5.8° N 13.5° E, see Fig.1) of the wintering area identified by the geolocator study. Indeed 88% of individuals from the study populations wintered in this area (Liechti et al 2014).

We also considered monthly NDVI data recorded in Tunisia (in a squared area spanning 35-38° N and 1.5-11° E, Fig.1) and Gibraltar (in a squared area spanning 34.1-37.4° N, and 3.5°-6.5° W, Fig.1). These areas were selected on the basis of main migration routes identified by analyzing ring recoveries (Ambrosini et al. 2014).

Monthly data on NDVI were obtained from the Moderate Resolution Imaging Spectroradiometer (MODIS, http://neo.sci.gsfc.nasa.gov/). We used MODIS-NDVI dataset because recent analyses showed that these data performed better than other NDVI datasets (e.g. AVHRR-NDVI) in the African continent (Beck et al. 2011). Unfortunately, MODIS-NDVI data are not available before 2000 and this led to the exclusion from the analysis of data on barn swallows collected in 1999 and 2000.

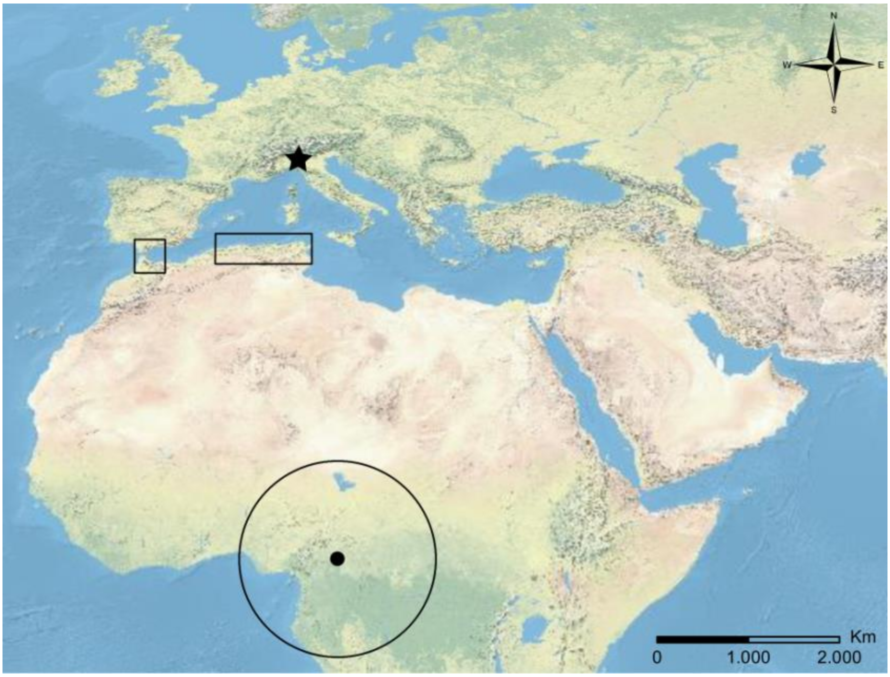

Fig 1. Geographical position of the breeding area (star), staging areas during spring and autumn migration (squared areas) and wintering quarters (circle, the dot represents its centre at 5.8°N 13.5°) of Barn Swallows from our study population.

Statistical methods

The main aim of this paper was to model the number of breeding pairs recorded in the Parco Adda Sud in each year. We hypothesized that year to year variation in the number of breeding pairs can be affected by different factors acting in different phases of the annual life-cycle of this species. Schematically, these factors are:

1. Reproductive output of the previous year
2. Ecological conditions encountered en-route during autumn migration
3. Ecological conditions in the wintering quarters
4. Ecological conditions encountered en-route during spring migration.

Reproductive output is determined by the breeding success of both first and second broods and by the proportion of pairs that produced a second brood. However, data on second broods were available to us only for a limited number of years (see above).

In a preliminary phase of the analyses we therefore tried to identify ecological variables that may account for the proportion of breeding pairs that produced a second brood and for the ratio between breeding success of second and first broods. We focused on meteorological and environmental conditions at breeding sites, which are known to influence breeding success of Hirundinidae. Any meteorological or environmental variable that affected either the proportion of breeding pairs that produced a second brood or the ratio between breeding success of second and first broods may significantly influence year to year variation in the number of breeding pairs because it influenced reproductive output of second broods. Specifically, we aimed at assessing whether reproductive output of second broods was affected by i) the monthly total precipitation and ii) the monthly average temperatures from May to July in the Parco Regionale Adda Sud, iii) by the proportion of farms with livestock farming and iv) the mean hayfield extent within 200 m from each farm. Given the few data available (only 5 years) and the large number of predictors (8 variables) whose effect we aimed at testing, the analyses were performed following an Information Theory-based approach. We modelled the proportion of breeding pairs that produced a second brood or the ratio between breeding success of second and first broods according to all possible combinations of two of the above mentioned predictors (i.e. we included in each model maximum two predictors). In this way we aimed at avoiding model over-fitting and at testing the potential effects of all predictors. We then selected all the models with a ΔAICc < 4 with respect to the model with the lowest AICc, and then averaged model coefficients.

In the following part of the analyses we aimed at identifying the determinants of year-to-year variation in population size. Mean number of breeding pairs per year showed clear temporal trend (coefficient ± SE: -0.611 ± 0.060 pairs year^{-1}, $t_{14} = -10.21$, $P < 0.001$, according to a linear regression model) and strong temporal autocorrelation ($r = 0.752$ with lag = 1). With the aim of simplifying the statistical analyses by removing both temporal trend and autocorrelation in the dependent variable, we calculated the difference in the mean number of breeding pairs per farms between one year and the preceding one. This procedure de-trended the time series of data, as indicated by the fact that the difference in the average number of breeding pairs showed no temporal trend (0.040 ± 0.092 pairs year^{-1}, $t_{13} = 0.44$, $P = 0.667$), and weak temporal autocorrelation ($r = -0.254$ with lag =1). All the following analyses were based on differences in mean number of breeding pairs per farm between consecutive years.

Given the relatively small (n = 13 years) number of data available and the large number of variables potentially affecting population dynamics, we tried to avoid model over-fitting in two ways: first, we selected the predictors according to the results of preliminary analyses on the output of second broods (see above) and to previous knowledge on the biology of barn swallows; secondly, we followed an Information Theory-based approach in the analyses.

We selected the following predictors:

1. Mean breeding success of first broods in the previous year, which represents the reproductive output of the population in the preceding year (see Results of analyses on the output of second broods);

2. NDVI in the areas of Tunisia in September, i.e. in the month when most of our swallows migrate southwards (Liechti et al 2014; Ambrosini et al 2014);

3. NDVI in the wintering area in October and March, because they are respectively the months when our population reaches its wintering grounds and when it departs for spring migration (Liechti et al 2014). The effects of these variables were also further investigated in additional analyses (see below).

4. NDVI in the areas of Gibraltar and Tunisia in March, i.e. in the month when most of the swallows of our population should reach this geographical area during spring migration (Liechti et al 2014).

Since our analyses were based on the difference in the number of breeding pairs between consecutive years, we entered as predictors in all the analyses the differences between one year and the preceding one of all the above mentioned variables (hereafter named adding ‘Δ’ to variable name for brevity, e.g. ΔNDVI). Positive values of ΔNDVI therefore indicate a higher NDVI value in year *i* than in year *i*-1. The logic behind this approach is that no variation in any predictor between years should produce no variation in the number of breeding pairs observed in the Parco Regionale Adda Sud in consecutive years.

Since MODIS NDVI data are available from February 2000, we were forced to exclude data on barn swallows collected in 1999 and 2000 from the analyses. The fact that we entered the difference in number of breeding pairs between consecutive years in all the analyses further reduced the number of data point available for the analyses to 13 only. We stress that this approach has nonetheless the merit to de-trend the data and to use reliable NDVI data for Africa.

The model selection process we adopted is similar to the one we used in the analyses of second brood output. We produced all the models including the difference in the number of breeding pairs between consecutive years as dependent variable and all the possible combinations of the above mentioned variables as predictors, by limiting to three the maximum number of predictors simultaneously included in each model. In this way we aimed at avoiding model over-fitting. We then selected the models with ΔAICc < 4 with respect to the model with the lowest AICc and finally averaged model coefficients.

In a third set of analyses we aimed at checking for the consistency of our results with respect to a possible incorrect selection of the predictors. Indeed, ΔNDVI values in the wintering grounds in October, and ΔNDVI values in Tunisia in March seemed to affect barn swallows population dynamic (see Results), but ΔNDVI values in other moths may have similar effects. We therefore ran some additional analyses to confirm that ΔNDVI values in these months have the largest effect on variation in breeding pairs. To this aim we ran all models by including ΔNDVI values in the wintering ground in each month from September to March, while keeping ΔNDVI values in Tunisia in March as the second predictor, and noted their AICc values. Similarly, we run all models by including ΔNDVI values in Tunisia in all months between February and April, while keeping ΔNDVI values in the wintering grounds in October as the second predictor, and noted their AICc values.

In the last part of the analyses, we used the final model based on differences in the number of breeding pairs between consecutive years to reproduce the population dynamic observed during annual censuses in the Parco Regionale Adda Sud. We used the number of breeding pairs observed in 2001 as the only input for this simulation. We then predicted the number of breeding pairs in the Parco Regionale Adda Sud in 2002 by summing to mean number of breeding pairs observed in 2001 the difference in breeding pairs between 2002 and 2001 predicted by the model. Number of breeding pairs in 2003 was then estimated by adding the difference in breeding pair estimated by the model to the number estimated for 2002 as above, and so on until 2014. As a measure of the ability of this procedure to correctly reproduce the observed variation in the number of breeding pairs in the Parco Regionale Adda Sud we calculated a pseudo-R^2 equal to the squared correlation coefficient between the observed mean number of pairs in each year and that estimated by this procedure.

To estimate standard errors for these predicted values, we had to account for uncertainty in the estimated of the starting value (i.e. mean number of breeding pairs observed in 2001) due to sampling, and to uncertainty in the estimate of year-to-year variation from the model due to variance in model coefficients. To this end, we re-ran the procedure exposed above by:

1. Using as starting value a random number drawn from a Gaussian distribution with mean equal to the mean number of breeding pairs observed in 2001 and variance equal to its squared standard error;
2. Estimating year-to-year variation in the number of breeding pairs while taking into account model uncertainty by drawing a random number from a Gaussian distribution with mean equal to the difference between one year and the preceding one estimated by the model and variance equal to the variance of this estimate.

This procedure was repeated 1000 times and the standard error of the number of breeding pairs estimated at each year by these 1000 simulations was used as an estimate of the standard error of the number of breeding pairs predicted by our model.

Results

Output of second broods

The model selection process indicated that the best model of the ratio between breeding success of second and first brood included only the intercept (AICc = -5), and any other model including meteorological and/or environmental variables as predictors had poorer fit (ΔAICc > 6.1 in all cases). Similarly, an intercept-only model (AICc = 3.7) fitted the proportion of breeding pairs that produced a second brood better than any other model including meteorological and/or environmental variables as predictors (ΔAICc > 5.7 in all cases).

Hence, none of the variables we included seemed to influence the reproductive output of second broods, and we therefore assumed that the number of chicks produced during first broods is a good proxy of the total annual reproductive output of the population.

Year to year variation in the number of breeding pairs

Two models were selected based on our procedure. The first included ΔNDVI in the wintering quarters in October and ΔNDVI in Tunisia in March (AICc = 47.2). The second model included only ΔNDVI in Tunisia in March (AICc = 48.7). Averaged coefficients from these models indicated that an increase in NDVI values between one year and the preceding one both in the wintering grounds in October and along migration routes in March were linked to an increase in the number of breeding swallows in the Parco Regionale Adda Sud (Table 1).

Table 1 Coefficients from the model averaging of the two best models (ΔAIC < 4) of year-to-year difference in the number of breeding Barn Swallows according to year-to-year differences in environmental conditions. Standard Errors and 95% Confidence Interval of coefficients obtained from the model averaging are also shown.

Effect	Coef.	Adjusted SE	95% CI
Intercept	-0.620	0.348	-1.302 – 0.062
ΔNDVI Tunisia March	24.521	8.317	8.220 – 40.822
ΔNDVI Wintering October	36.482	17.400	2.378 – 70.586

Pseudo-R^2 = 0.653

If other variables not included in the model had affected population dynamic, we would have expected the intercept to differ from zero, and in particular to be below zero, since barn swallows are sharply declining in our study area (Ambrosini et al 2012; Sicurella et al 2014). However, the 95% confidence interval of the intercept includes zero (Table 1).

Checking for influential periods

Additional analyses whereby we entered ΔNDVI values in the wintering area for different months clearly indicated that October was the most influential month, since ΔAICc values of models including ΔNDVI values for other months were always larger than 4 (Figure 2a). Conversely, we had little evidence that models including ΔNDVI values in Tunisia in March performed better than models including ΔNDVI values in the same area in February or April, as ΔAICc values were lower than 4 (Figure 2b). These small differences in AICc may be due to the strong positive correlation between ΔNDVI values in this area in March and in the other months we considered ($r \geq 0.785$). We therefore retained ΔNDVI values of March as geolocator data suggested that swallows from our population should mainly cross the Sahara and the Mediterranean Sea in this month (our unpublished data).

Modelling population dynamic

The population dynamic reconstructed by our procedure matched the observed population dynamic with great accuracy (pseudo-R^2 = 0.879). Standard errors of the number of breeding pairs calculated by our procedure largely overlap with standard errors of the number of breeding pairs estimated at each year by annual censuses (Figure 3).

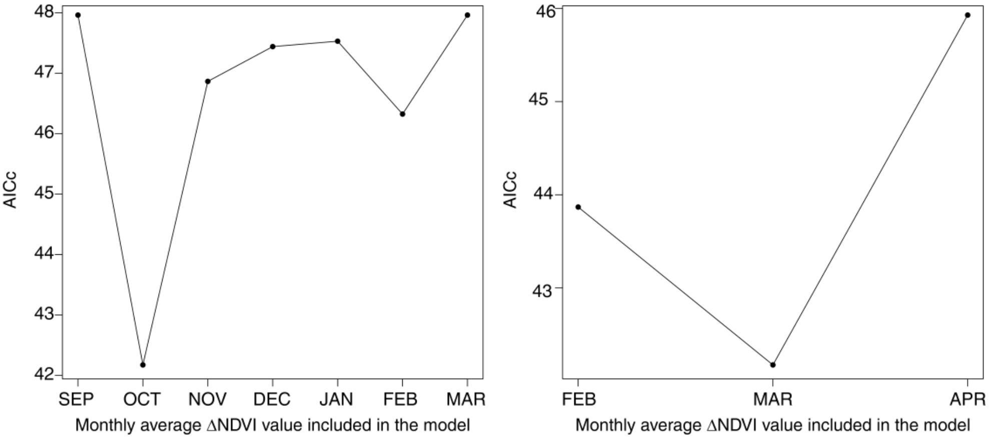

Fig 2. Variation in AICc values of models including ΔNDVI values for different months in a) the wintering areas of barn swallows, and b) the Tunisia area.

Discussion

In this work we aimed at assessing the critical stages of the annual life-cycle that limit the size of a geographical population of barn swallow breeding in Northern Italy. Our results suggest that ecological conditions encountered by individuals at their arrival at their wintering ground in sub-Saharan Africa and during spring migration in North Africa are the main determinants of year-to-year variation in population size. These findings differ from those of Ockendon et al. (2014), which investigated the effect of NDVI on population dynamic of barn swallows breeding in the United Kingdom, but did not find any effect of NDVI in the wintering quarters on annual population variation. However, the authors of this paper admit that this lack of any effect of NDVI may be consequence of the lack of information on the precise position of wintering quarters of their population, which forced them to perform the analyses at a very large spatial scale.

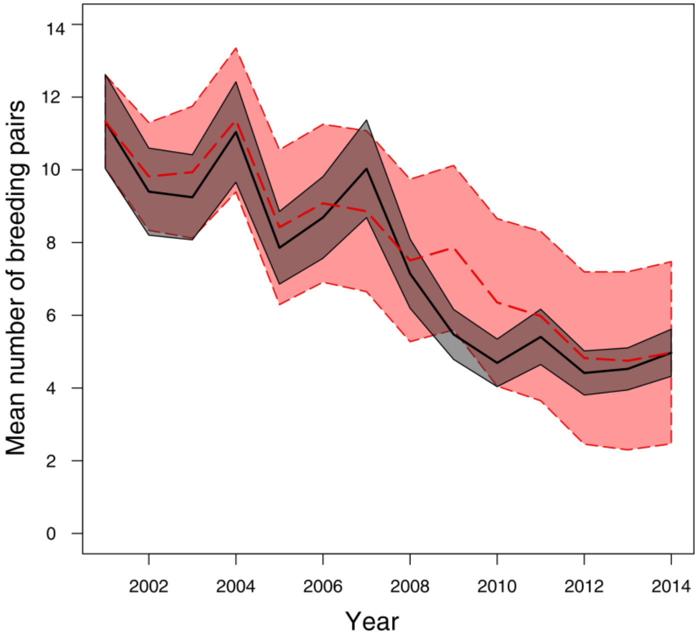

Fig 3. Mean number of breeding pairs per farm observed during annual censuses (black solid line) and estimated by the model (red dashed line). The grey solid band around the black line represents one standard error plus or minus the observed values. The red dashed band around the red line represents one standard error (estimated by 1000 simulations) plus or minus the estimated values.

Precise knowledge of the wintering areas of the geographical populations of long-distance migrants may therefore be necessary to correctly assess the relative importance of ecological conditions faced by populations in different phases of their annual life-cycle on population dynamic. Alternative explanations can however be put forward. Barn swallow populations breeding in Italy and UK are known to winter in different parts of Africa (Ambrosini et al 2009; Ambrosini et al 2011), and therefore environmental conditions faced by UK populations during wintering may influence survival to a lesser extent than those faced by Italian populations. In addition, Ockendon and co-workers used average conditions during the wintering period to model winter survival, while our analysis disclosed that the effect of NDVI markedly varied between consecutive months, so that they may have neglected the effect of environmental conditions during critical periods within wintering. Indeed, one novel finding from our work is that NDVI values at wintering grounds at arrival of barn swallows from autumn migration had a strongest influence on year-to-year variation in population size than NDVI values in other months (Figure 2a). In addition, NDVI values in the wintering grounds in October were weakly correlated with those of other months ($|r| \leq 0.10$). These findings suggest that ecological condition encountered by barn swallows at arrival in the wintering grounds from autumn migration may have a larger impact on annual survival than those faced during wintering. This may occur because at arrival birds are exhausted from the long migration journey, and may not recover under poor ecological conditions. The vast majority of the studies conducted so far on the impact of ecological conditions in the wintering grounds on population dynamic, took into account conditions during the entire winter (Boano et al 2004; Szép and Møller 2005; Gordo and Sanz 2008; Grande et al 2009) or condition immediately before departure for spring migration (Gordo and Sanz 2008). Conversely, the effect of ecological conditions at arrival to the wintering grounds has been mainly overlooked. Indeed, to the best of our knowledge, we are aware of only one previous study showing an effect of ecological conditions at arrival from crossing an ecological barrier on population dynamic of the white stork (Schaub et al 2005, see introduction). We also found that NDVI values of areas crossed by barn swallows during migration influence population size. This is coherent to the findings by Szép and Møller (2005), which found that NDVI data in northern Africa were related to annual survival rates of a Danish barn swallow population. During their migration from wintering to breeding grounds, barn swallows must fly over two main ecological barriers, the Sahara desert and the Mediterranean Sea. Tunisia is along a migration route that implies direct crossing of both these barriers, and may function as a staging area whereby swallows may refuel. Primary productivity during early spring in this area may therefore largely affect barn swallow survival. In addition, primary productivity in Tunisia in March may influence barn swallow population to a larger extent than that in Gibraltar, whose crossing implies following a route that mainly passes along the coast and over mainland. Gibraltar route may therefore be less challenging for swallows, albeit longer (at least for the population breeding in Northern Italy). In addition, a smaller proportion of individuals of the population we studied may migrate across Gibraltar than across Tunisia, thus reducing the impact of NDVI in this area on population dynamic.

Ecological conditions at the breeding grounds and during autumn migration seem not to affect population dynamic of barn swallows. This is consistent with previous investigations of the relative effect of conditions during migration and wintering in determining annual survival of this and a closely related species (the Sand Martin *Riparia riparia*; Szep and Møller 2005; see also Gordo and Sanz 2008). Indeed, also in those analyses, only condition during wintering and spring migration seemed to affect annual survival of adult barn swallows while those during autumn migration seem to have no influence.

Admittedly our study is bases on a rather short time series of data, which was further reduced by the necessity to disregard two years of data, due to unavailability of MODIS-NDVI data before 2000. Nevertheless, the model averaging procedure clearly identified only two models as the best ones, and suggested that the others were by far less supported. In addition, our model had very good performance in interpolating the difference in the mean number of breeding pairs between years (pseudo-R^2 = 0.653; Table 1) and allowed us to reconstruct the observed population dynamic with great accuracy (pseudo-R^2 = 0.879; Figure 3).

The analyses we ran also allowed us assessing the relative importance of NDVI data in different areas and months in determining population trend. Indeed, by re-running the procedure used to model population dynamic while setting one or more of the model coefficients to zero, we could simulate how population dynamic would have appeared if no change had happened in ecological conditions in a given area. The results of this exercise showed that only models including the intercept were able to capture the decline that actually occurred in the populations, while all models not including the intercept predicted an increase, rather than a decrease of the population (Figure 4). This occurred because NDVI in October in the wintering area of our barn swallow population was almost stable during the study period, NDVI in Tunisia in March increased (Figure 5), and coefficients of the final model for ΔNDVI values in both areas were positive (Table 1).

To correctly interpret the results from these simulations, it should be taken in mind that our model is based on difference in ecological conditions between consecutive years, and predicts year-to-year changes in population size.

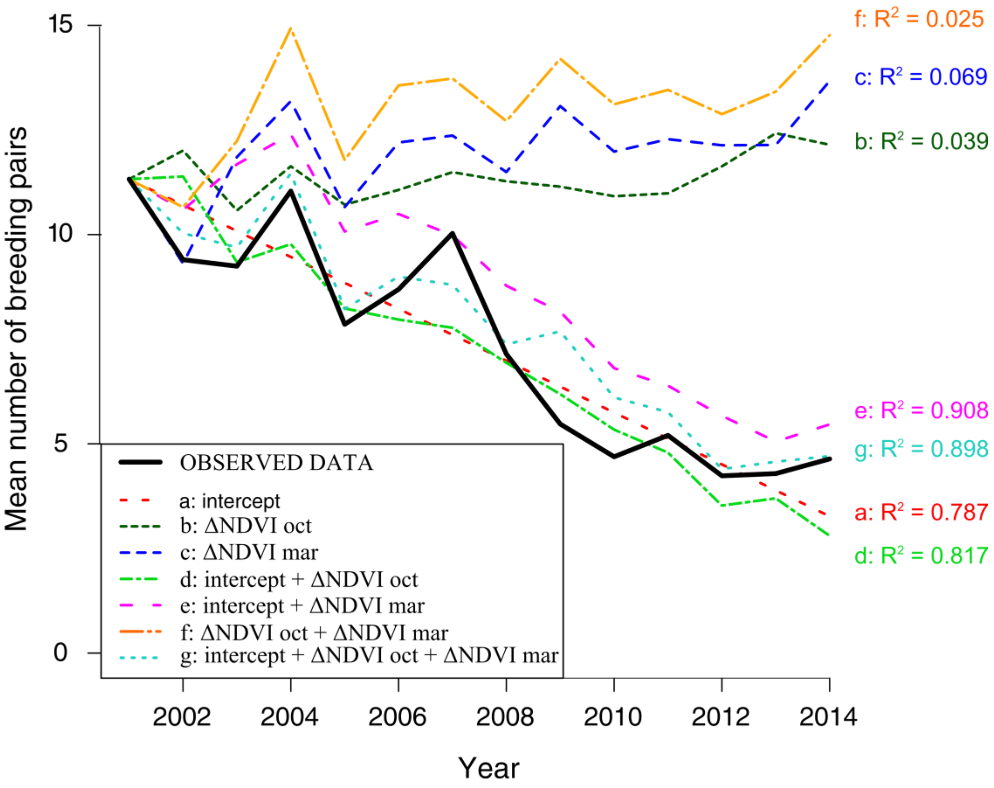

Fig 4. Predicted annual variation in the number of pairs from simulations produced setting some coefficients of the model reported in Table 1 to zero. Pseudo-R^2 of each model was calculated as the squared correlation coefficient between observed and predicted number of pairs. The legend shows the predictors included in each model.

Hence, if the ecological conditions considered in the model had been the main drivers of population dynamic, a null variation in ecological conditions would have determined a null variation in population size. These simulations clearly indicated that this was not the case, and that population declined independently from year-to-year variation in NDVI. However, models including ΔNDVI values had a better fit than the model including only the intercept, so that variation in NDVI seem to account for year-to-year variation around the general negative trend.

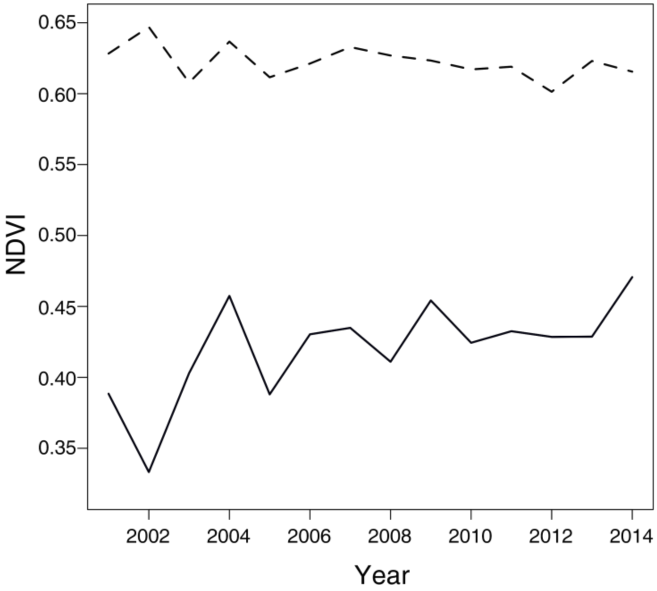

Fig 5. Annual trend of NDVI values recorded in October in the wintering quarters (dashed line) and in March in the Tunisia area (solid line).

In summary, the actual determinants of the steep decline suffered by our barn swallow population in recent years remain unclear, since the variations in NDVI values that occurred in the wintering grounds and along migration routes did not account for the observed sharp decline. Nonetheless, environmental conditions in this area seem to influence at least variation around the long-term decline at a larger extent than variation in ecological condition at the breeding grounds (Sicurella et al 2014). Conditions during spring migration seem to affect population dynamic more than those during autumn migration, and there are critical periods during wintering that affect population dynamic. For the barn swallow population we studied, this critical period coincides with the arrival at the wintering grounds, but further studies are needed to assess if this finding can be generalized to other species and to other populations of the same species. Hence, modelling population dynamic only according to average conditions faced by migrants during the whole wintering or just before departure for spring migration may prevent identifying the critical periods of the life-cycle that most influence population dynamic.

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Elevated winter temperatures decrease migration 1 propensity and migration distance of a partial migrant, the European robin *Erithacus rubecula*: a continent-wide analysis

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Roberto Ambrosini[a], José Javier Cuervo[b], Chris du Feu[c], Wolfgang Fiedler[d]
Federica Musitelli[a], Diego Rubolini[e], **Beatrice Sicurella[a]**, Fernando Spina[f], Nicola Saino[e], Anders Pape Møller[g]

a Dipartimento di Biotecnologie e Bioscienze, Università degli Studi di Milano-Bicocca, piazza della Scienza 2, 20126 Milano, Italy

b Department of Evolutionary Ecology, Museo Nacional de Ciencias Naturales, CSIC, Calle José Gutiérrez Abascal 2, E-28006 Madrid, Spain
c EURING Data Bank, Beckingham DN10 4PF, Notts, England

d Max Plank Institute for Ornithology, Vogelwarte Radolfzell, Am Obstberg 1, D-78315 Radolfzell, Germany

e Dipartimento di Bioscienze, Università degli Studi di Milano, via Celoria 26, 20133 Milano, Italy

f ISPRA, Via Cà Fornacetta 9, 40064 Ozzano dell'Emilia (BO), Italy

g Laboratoire d'Ecologie, Systématique et Evolution, CNRS UMR 8079, Université Paris-Sud, Bâtiment 362, F-91405 Orsay Cedex, France

Summary

1. Many partially migratory species have populations that are phenotypically divergent in terms of migration, with climate hypothesized to be a major driver of such divergence through the differential effects of climate on sedentary and migrant populations.

2. Based on long-term (1945-2011) bird ringing data, we analysed phenotypic differentiation in migration among geographical populations of European robins *Erithacus rubecula* across Europe.

3. We showed that clusters of populations sharing breeding and wintering ranges varied from virtually resident (British Isles and Southern Europe) to completely migratory (Scandinavia and Northern Europe).

4. Spatial and temporal variation in migration propensity and distance was inversely related to temperature during the coldest month in the breeding area. Hence, when winter temperatures were cold, a larger proportion of birds migrated and those individuals that migrated also moved a longer distance than in warm winters.

5. These findings are consistent with the hypothesis that climatic conditions are the main drivers of the temporal heterogeneity in migratory behaviour among short-distance migratory birds on a continental scale.

Introduction

Climate is changing rapidly with dramatic increases in temperature in particular at high latitudes (IPCC 2013). Because the distribution of many species closely tracks isotherms during the coldest month (e.g. Root 1988), increasing temperatures have affected distribution, phenology and migration of birds and other organisms (Parmesan & Yohe 2003; Møller, Fiedler & Berthold 2010). Some of the most dramatic effects of climate change include advances in the timing of migration by birds and other migratory organisms (review in Lehikoinen & Sparks 2010). However, the analysis of such phenotypic variation has rarely been extended to the behaviour of individuals. Amateur and professional ornithologists have ringed millions of birds for more than 100 years providing a unique database of recapture and recovery data. Surprisingly these data have only been analysed to a small extent to investigate the effects and the consequences of climate change (but see Ambrosini *et al.* 2011; 2014). A few studies on Northern Hemisphere migrants have demonstrated reductions in migration distance over time, most notably in short-distance migratory birds (Fiedler, Bairlein & Köppen 2005; Visser *et al.* 2009), but also in a long-distance migrant (Ambrosini *et al.* 2011), which are coherent with patterns of global warming. Moreover, a long-term study by Tellería (2014) on European robins *Erithacus rubecula* wintering in the Iberian Peninsula showed that the proportion of long distance winter visitors has declined from 92% to 1% between1959 and 2009. In addition, the study by Visser *et al.* (2009) provided a link between migration and climate change, as they showed that short-distance migrants wintered closer to their Dutch breeding grounds in years with milder winters. However, this study is limited to one breeding area only, while other studies lack an explicit link between migration and climate change. Migration entails significant costs, mainly in terms of mortality, but so does residency during periods of severe winter weather (Newton 2008). However, several studies suggest that a climate warming scenario should result in fewer migrants (e.g. Pulido, Berthold & van Noordwijk 1996; Pulido & Berthold 2010), but also lower mortality of residents thanks to warmer winters (e.g. Sanz- Aguilar *et al.* 2012). Indeed, populations of birds can change from partially migratory 1 to resident in a few generations, as shown by selection experiments (Pulido, Berthold & van Noordwijk 1996). Because polymorphic populations of migrants and residents are common in partial migrants (Chapman *et al.*

2011; Pulido 2011), rapid changes in current climatic conditions should equally result in rapid changes in migratory behaviour. Here we analysed an existing database on migration of individuals in order to quantify the effects of climate change on the proportion of individuals that migrated ("migration propensity" hereafter) and migration distance. To this end, we developed a novel framework for the statistical analyses of ring recoveries. The objectives of this study were to (1) identify clusters of migrants with similar migratory behaviour (i.e. similar breeding and wintering ranges); (2) identify differences in migratory propensity and migration distance among clusters; (3) link migration propensity and distance to temperature in the breeding areas during the coldest winter month. We used a large database on captures, recaptures and recoveries of the European robin (hereafter Robin) which is a model system for studies of partial migration (Adriaensen & Dhondt 1990; Tellería 2014).

Methods

Dataset

For individually ringed birds, the EURING Data Bank (EDB) includes information on date and locality at ringing, as well as at any subsequent encounter ("ring recoveries"). Hence ring recoveries include both ringing and finding information of any bird that has been re-encountered.

The EDB contains about 150,000 ring recoveries of Robins (CdF, personal communication). In 2012 we obtained 132,319 recoveries of Robins with at least one record in November-March. Before the analyses we carefully checked the consistency of data in our dataset and excluded any dubious data (e.g. individuals recovered at sea; other details not shown). From this dataset, we selected only individuals with at least one record in April-June and one record in November-February i.e.in the focal months of reproduction and wintering for Robins (Cramp *et al.* 2004). If more than one record in either the breeding or the wintering period was available for the same individual, we selected respectively the northernmost and the southernmost one (see Ambrosini, Møller & Saino 2009 and Ambrosini *et al.* 2011 for a similar approach). The final database thus consisted of two geographical locations (one for breeding and one for wintering) for 3399 Robins in the period 1945-2011.

Migration distance and migratory connectivity

We first aimed at identifying geographical populations of Robins with similar migration strategies in order to analyse variation in migration distance in relation to climate. To this end, we applied the method proposed by Ambrosini, Møller & Saino (2009) for the analysis of migratory connectivity to identify clusters of individuals that share the same breeding and wintering grounds. Migratory connectivity is the degree to which individuals from the same breeding site migrate to the same wintering site (Webster *et al.* 2002; Trierweiler *et al.* 2014). The degree of migratory connectivity was assessed by a Mantel test on great-circle (orthodromic) distance matrices between individuals calculated separately for the breeding and the wintering grounds (Ambrosini, Møller & Saino 2009). Since the analyses showed significant connectivity (see Results), we identified the main clusters in which the population could be divided with the *pam* procedure in the *cluster* library in R 3.0.2 (R Core Team 2013). The *pam* procedure is a clustering algorithm that partitions observations in a number of clusters identified a priori. As a measure of the goodness of the classification of data into a given number of clusters, the procedure returns the overall average silhouette width (*oasw*), a dimensionless coefficient ranging from -1 to 1. Increasing *oasw* values indicate better classification of data (Rousseeuw 1987), and the best number of clusters in which data can be partitioned can be chosen as the number that maximizes the *oasw*. The clusters so identified represent groups of Robins that both breed and winter close together. We emphasize that this analysis is based only on the reciprocal position of individuals both in the breeding and in the wintering grounds, and it does not take into account in any way the actual distance migrated by each individual (Ambrosini, Møller & Saino 2009). Migration distance was calculated as the great-circle (orthodrome) distance between the breeding and the wintering position of each individual. Home range of Robins was estimated to be 0.571 km in distance, corresponding to the geometric mean of natal dispersal distance in the UK (Paradis *et al.* 1998). Robins found in winter within this distance from their position during breeding were considered to be individuals that did not migrate, while those found at longer distances were considered to be migratory individuals. Since the choice of this threshold distance may be considered arbitrary, we checked for the consistency of our results by re-running the analyses with different thresholds (namely 1, 2, 3, 5, 7, 10, 20, 30, 50, 70 and 100 km).

Climatic data

We used the R library *RNCEP* (Kemp *et al.* 2011) to retrieve temperature 1 data from the NCEP/NCAR Reanalysis 1 model (parameter “air.sig995” at level= “surface” that represents air temperature at Earth surface) for November-February in Europe. The NCEP/NCAR Reanalysis 1 model provides temperature data with a global scale at a spatial resolution of 2.5 × 2.5 ° latitude × longitude (“cells” hereafter). For each cell, we calculated the mean monthly temperatures for all months between November and February, and for each winter (i.e. from November of year i to February of year $i + 1$) we selected the coldest of these months as predictor in the analyses. We then assigned to each Robin the temperature of the coldest month recorded in the cell where it was found during the breeding season for the winter period (November to February) when it was recaptured in winter. For example, if a bird was found breeding in cell A in 1989, and wintering in 1987 in cell B, we determined for cell A the temperature of the coldest month of the winter 1987 (i.e. from November 1987 to February 1988). Hereafter, we refer to these temperatures as “Winter temperatures”. The rationale behind this procedure is that individuals are expected to be faithful to their breeding grounds (at least at the coarse spatial scale of 2.5° × 2.5° latitude × longitude that we are considering), but would move longer distances from the breeding grounds according to the harshness of the climatic conditions of a given winter at the breeding grounds (Visser *et al.* 2009).

Population indices

We obtained population indices for Robins from Austria, Czech Republic, Denmark, Finland, France, Germany, Hungary, The Netherlands, Norway, Poland, Spain, Sweden (Cuervo & Møller 2013), and from United Kingdom (data kindly provided by the BTO). We then associated to each individual the population index for the country where it was observed during the breeding season and for the year when it was found on the wintering grounds (winter *i*, see above). This information was available for 1190 out of 3399 individuals (35.0%). Population indices were in all cases expressed as the proportional variation in population consistency with respect to a reference year, which however differed between countries. We rescaled these indices so that the 1 population index in the reference year always equalled zero. In this way, marginal means for the other variables estimated the effect under scrutiny at the population level in the reference year for that country.

Regression models of migration propensity and distance

We first analysed whether an individual bird stayed during winter within its breeding home-range (i.e. moved less than 0.571 km) or migrated (i.e. moved more than 0.571 km) according to Cluster, Year (the winter when an individual was recovered in the wintering grounds, see above), Winter temperature, and the interactions between Cluster and Year and between Cluster and Winter temperature by using Generalized Linear Models (GLMs) assuming a binomial error distribution. The results of this analysis thus estimated how the proportion of migratory birds (i.e. migration propensity) changed according to the above-mentioned predictors. One cluster (the German one, see below), was excluded from this analysis because all individuals in that cluster always migrated.

We also analysed distance travelled by the individuals that migrated (i.e. moved more than 0.571 km; individuals that moved less than 0.571 km were excluded) according to the same predictors in a Generalized Least Squares (GLS) model with a customized form of the variance-covariance matrix whereby variances were estimated independently for each cluster and variance in migration distance was assumed to increase exponentially with Winter temperature (technically a covariance matrix of the *varComb* class in package *nlme* of R, combining *varIdent* and *varExp* covariance matrices). This parameterization of the regression model was necessary because the data showed large heterogeneity in variance among clusters and an increase in variance at increasing values of Winter temperature. The frequency distribution of migration distances has a large excess of very small values (Figure 1), and residuals of the models showed a deviation from normality. After double square-root transformation, qq-plot of residuals showed a reasonable behaviour (details not 1 shown). However, results of the analyses run on transformed and non-transformed data were qualitatively identical (details not shown for brevity), so we reported the output of models on original data to ease interpretation of model coefficients.

Analyses accounting for effects potentially influencing migration propensity and distance

Population size may alter the proportion of migrant birds by affecting intraspecific competition for resources during winter. In addition, population size may bias the estimates of the variation in migration propensity and in distance travelled because e.g. reduced competition during winter may prompt a larger proportion of individuals to spend winter in their breeding grounds. To check the robustness of our results against this potential source of bias we re-ran models of migration propensity and distance with population indices as a covariate. Country was included as a random grouping factor to account for repeated measures of the same population index for all individuals in a country. These models were fitted using Generalized LMMs (GLMM) using binomial error distributions (migration propensity) or Linear Mixed Models (LMMs) (migration distance). Juveniles may show higher migration propensity than adults because they are usually socially subordinate and therefore less likely to acquire the best territories, which in turn offer the best chances to survive winter (Newton 2008). Individuals were therefore classified as adults (code 1) or juveniles (code 0) (variable ‘Age’ hereafter) according to their estimated age (as assessed by the ringing scheme: EURING code ‘Age scheme’) when they were recovered in winter. Individuals with Age scheme = 3 and recovered in November or December or Age scheme = 5 and recovered

January or February were considered juveniles (387 individuals = 11.4%) while those with Age scheme = 5 and recovered in November or December or Age scheme ≥ 6 were considered adults (520 individuals = 15.3%; see du

Feu *et al.* 2010 for details). Age was unknown for the remaining individuals that were therefore excluded from these analyses. Age and its interactions with Cluster and Winter temperature were entered as further predictors in the models together with all the predictors as in models of migration propensity and distance. Analyses accounting for potential reporting bias Different ringing schemes providing data to the EDB have historically adopted different procedures for processing and storing reports of birds which have been ringed and subsequently re-encountered (see http://www.euring.org/data_and_codes/obtaining_data/recovery_definitions.htm for full details on these different procedures). Differences in reporting procedures may largely affect proportion of migrant birds if e.g. birds re-encountered close to the ringing site are not reported. However, almost all ringing schemes have always reported birds found dead, so that analyses based on dead birds only should not be affected by reporting bias. We therefore re-ran all the analyses by including only birds found dead (EURING code 'condition' in 1-2; 1265 individuals = 37.2%; du Feu *et al.* 2010).

Variation in migration phenology

Changes in migration phenology may result in an apparent shift of the wintering grounds. This can be the case if birds that migrate north earlier have been found closer to their breeding grounds in recent years (Ambrosini *et al.* 2011). In addition, Winter temperature may influence phenology as well, and its effect should be disentangled from the potentially confounding effect of Year.

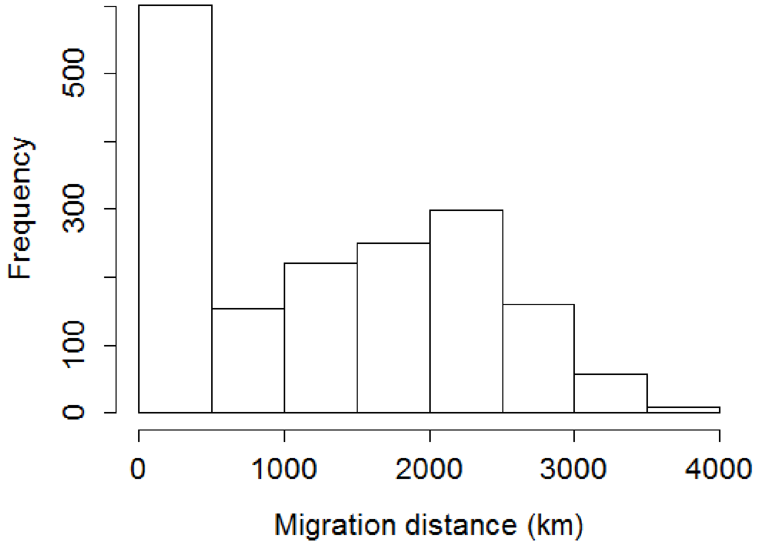

Figure 1. Frequency distribution of migration distances, defined as the great-circle distance between the ringing and the recovery sites. Only individuals that moved more than 0.571 km are reported.

To test for these effects we calculated date of recovery in each winter (1 January = 1, dates in November and December were given negative number, e.g. 3 February = 34, 13 December = -18) and then analysed temporal variation in the date of winter recovery in a linear model that included Cluster, Year, Winter temperature and the Cluster by Year and Cluster by Winter temperature interactions. Latitude and longitude of recovery were not included in the analysis because Cluster should account for the geographical position of Robins. If migration date has been advancing 1 during the study period, a significant and negative effect of Year should emerge, after statistically controlling for the other effects. All analyses were run in R 3.0.1 (R Core Team 2013) with the procedures *gls*, *lme*, *glmer*.

Results

Patterns of migratory connectivity and clustering of populations

The Mantel test disclosed significant migratory connectivity (*rM* 3 = 0.541, *P* < 0.001, 999 permutations), and cluster analysis indicated that Robins can be assigned to four clusters (*oasw* = 0.543, indicating a "reasonable" cluster structure; Rousseeuw 1987; Figure 2). The first cluster included 1795 birds, mainly from UK and The Netherlands (UK cluster hereafter), the second one 463 birds from Italy, Switzerland, Austria and southern Germany (IT cluster), and the third one 217 birds from Spain and Portugal (SP cluster). These clusters were composed of a mixture of birds that did not move during winter, and birds that migrated. Because of this, the breeding and the wintering ranges of these clusters largely overlapped (Figure 2). In contrast, the fourth cluster included no sedentary Robins (the shortest migration distance for birds in this cluster was 818.2 km). The 924 birds from this cluster bred mainly around the Baltic sea in Germany, Denmark, Poland, Norway, Sweden and Finland, and wintered in France, Spain, Portugal, and on the Mediterranean coast of Morocco and Algeria (GE cluster).

When we re-ran the Mantel test on birds found dead only, results did not change qualitatively (see Supplementary Materials). However, the cluster analysis showed the presence of two clusters only, corresponding to the UK and the GE clusters (see Supplementary Materials and Figure S1), likely because of the small sample size for the IT cluster (n = 99) and SP cluster (n = 7). For all subsequent analyses, we therefore maintained the classification of the data into four clusters.

Variation in migration propensity

The GE cluster was excluded from the analyses of migration propensity because all the individuals in this cluster migrated (see Methods). The overall difference in migration propensity between clusters was marginally non-significant (Table 1, Figure 3). Migration propensity also decreased over time in the IT and SP clusters, but not in the UK one. Milder winter temperatures 1 resulted in a decrease of migration propensity, as indicated by the significant effect of Winter temperature per se (Table 1) and by the negative sign of the coefficient in a model that did not include the Cluster by Winter temperature interaction (coef. ± SE: -0.065 ± 0.015 logit(probability) °C-1, $z = -4.452$, $P < 0.001$; other details not shown). There was weak evidence for heterogeneity in Winter temperature effects among Clusters (Table 1).

Analyses including population indices and bird age, or restricted to birds found dead, or using different thresholds for differentiating between sedentary and migratory Robins gave results generally consistent with those of the analyses on the whole dataset (see Supplementary Materials). The main exceptions were the Cluster effect *per se* and the Cluster by Winter temperature interaction that were significant in the analyses of migration propensity including population indices and in those restricted to birds fund dead. The Cluster by Winter temperature interaction was also significant in all models when the threshold used to separate sedentary from migratory birds was ≥ 2 km. In addition, the Cluster by Year interaction was not significant in the model restricted to birds found dead. Full details of these additional analyses are provided in the Supplementary Materials.

Table 1. GLM model of the proportion of migratory robins. Sample size is 2475 robins. The GE cluster was excluded because all individuals in this cluster were migrants. Covariates Year and Temperature were centred to their mean values before the analyses. Significance of each term was assessed by likelihood ratio tests (χ^2 values and associated *df* and *P*). Coefficients (marginal means) are reported for each cluster with the relative SE. Asterisks denote coefficients that differ significantly (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$) from zero, and different letters denote effects that differ significantly ($P < 0.05$) at post-hoc tests.

Effect	χ2	df	P	Cluster	Coef.	SE		
Cluster	5.58	2	0.061	1 UK	-0.488	0.057	***	
				2 IT	-0.265	0.134	*	
				3 SP	-1.223	0.429	**	
Year	0.00	1	0.959					
Winter Temp.	14.46	1	< 0.001					
Cluster x Year	70.81	2	< 0.001	1 UK	0.000	0.003		a
				2 IT	-0.056	0.008	***	b
				3 SP	-0.088	0.020	***	b
Cluster x W. Temp.	5.72	2	0.057	1 UK	-0.076	0.020	***	
				2 IT	-0.072	0.022	**	
				3 SP	0.078	0.063		

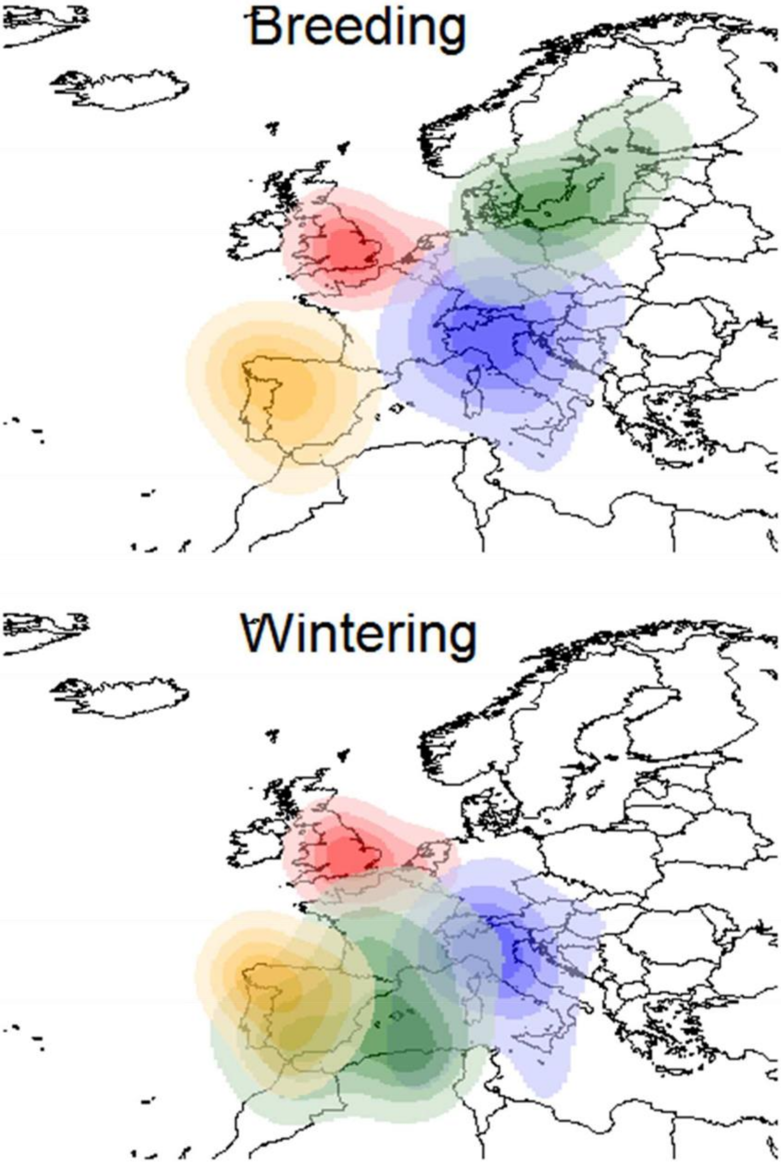

Figure 2. Kernel density plots of the clusters identified by the migratory connectivity analysis during breeding and wintering. Red: UK, blue = Italy (IT), green = Germany (GE), and orange = Spain (SP).

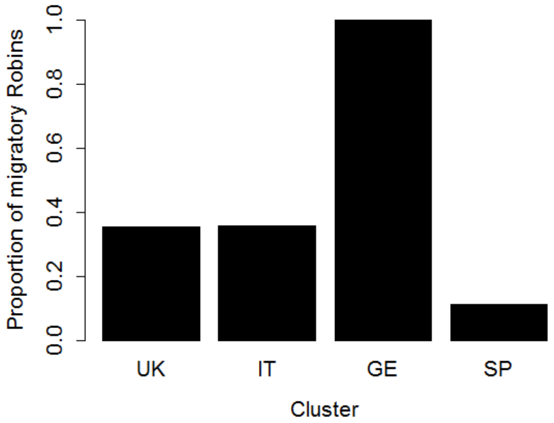

Figure 3. Proportion of migratory robins (i.e. individuals that moved more than 0.571 km) in the four geographical clusters identified by the migratory connectivity analysis.

Variation in migration distance

Similarly to migration propensity, migration distance also differed significantly between clusters, being longest in the GE cluster (Table 2). Among the other clusters, migration distance was significantly longer in the IT than in the UK cluster, while the SP cluster had an intermediate value. Migration distance also changed through time, but at different rates among clusters (Table 2). In particular, Migration distance significantly increased in the GE cluster and significantly decreased in the SP cluster, while it did not change significantly in the UK and IT cluster. Winter temperature differentially affected migration distance according to cluster (Table 2; Figure 4). Indeed, milder winter temperatures determined a larger decrease in migration distances of individuals 1 from the UK cluster than in those from the other three clusters. Also in this case, analyses including population indices and bird age, or restricted to birds found dead, or using different thresholds for differentiating between sedentary and migratory

Robins gave results generally consistent with those of the analyses on the whole dataset (see Supplementary Materials). The main exceptions were the Cluster by Winter temperature interaction, that turned non-significant in the model including population indices, and the Cluster by Year interaction, that was not significant in the model restricted to birds found dead (see the Supplementary Materials for full details on these additional analyses).

Variation in recovery phenology

Date of winter recovery did not change significantly through time (effect of Year: $F1,1736 = 2.62$, $P = 0.106$; Cluster x Year: $F3,1736 = 1.53$, $P = 0.205$), suggesting no directional temporal variation in migration phenology. We found significant differences in winter recovery date among clusters ($F3,1736 = 9.78$, $P < 0.001$). In addition, the relationship between Winter temperature and phenology varied among clusters (Cluster x winter temperature: $F1,1736 = 6.04$, $P < 0.001$). Specifically, date of recovery significantly increased with Winter temperature in the UK cluster (coef. ± SE: 1.587 ± 0.474 days °C-1, $t1736 = 3.347$, $P \leq 0.001$), significantly decreased in the GE cluster (coef ± SE: - 0.640 ± 0.308 days °C-1, $t1736 = -2.079$, $P = 0.038$) and was unaffected in the IT and SP clusters ($|t1736| \leq 0.604$, $P \geq 0.546$). Cluster and its interaction with Winter temperature did not significantly affect winter recovery date when we re-ran the analyses by also including population index as a covariate (beside Country as a random effect; likelihood ratio test: $\chi^2{}_3$.≤ 1.30, $P \geq 0.730$; all the other effects were not significant either, details not shown).

The Cluster by Year interaction was however significant in the analysis restricted 1 to birds found dead, which also indicated that only winter recovery date of the GE cluster advanced significantly (see the Supplementary Materials for full details on this analysis).

Table 2. GLS model of distance travelled by individual robins that migrated (i.e. moved longer distance than 0.571 km). Sample size is 1748 robins. Covariates Year and Temperature were centred to their mean values before the analyses. Significance of each term was assessed by likelihood ratio tests (χ^2 values associated *df* and *P*). Coefficients (marginal means) are reported for each cluster with the relative SE. Asterisks denote coefficients that differ significantly (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$) from zero, and different letters denote effects that differ significantly ($P < 0.05$) in post-hoc tests.

Effect	χ^2	*df*	*P*	Cluster	Coef.	SE	
Cluster	3969.58	3	< 0.001	1 UK	237.765	35.754	*** a
				2 IT	723.862	50.453	*** b
				3 SP	505.489	187.177	*** ab
				4 GE	2013.178	42.243	*** c
Year	0.67	1	0.414				
Winter Temp.	198.67	1	< 0.001				
Cluster x Year	25.35	3	< 0.001	1 UK	-0.483	0.591	c
				2 IT	-3.151	2.622	c
				3 SP	-22.200	6.419	*** d
				4 GE	4.486	1.336	*** e
Cluster x W. Temp.	39.01	3	< 0.001	1 UK	-55.608	3.945	*** g
				2 IT	-20.177	6.038	*** h
				3 SP	12.354	27.369	h
				4 GE	-22.784	5.714	*** h

Discussion

Many partially migratory species show evidence of phenotypic divergence in migratory behaviour among populations, with climate being hypothesized to drive such divergence through its effects on mortality (Newton 2008). Here we first showed that Robins have a high degree of migratory connectivity, based on the existence of four clusters of individuals that stay close together both during breeding and wintering (see Ambrosini, Møller & Saino 2009 for a theoretical background). These clusters identified geographical populations of Robins, showing phenotypic differentiation in migration strategy, ranging from virtually resident to completely migratory. Spatial and temporal variation in migration propensity and distance was also closely related to temperature during the coldest month in the breeding area. Indeed, increasing winter temperatures in the breeding areas were associated with smaller proportions of migratory individuals and shorter distances travelled in the UK and the IT clusters and in a reduced migration distance in the GE cluster, where all individuals were migrants. Conversely, winter temperatures seemed not to affect migration propensity and distance of Robins of the SP cluster, which was however composed mostly of sedentary individuals.

Differences among subspecies may also explain why milder winter temperatures caused a decrease in migration distance of Robins from the UK cluster that was more than twice that of Robins from the other clusters (Table 2). Such a large effect of winter temperatures on migration distance of UK Robins was confirmed also in the analyses including population indices or restricted to birds found dead. Independently of winter temperature, we also observed a decrease in migration propensity of Robins through time in the IT and SP cluster, but not in the UK cluster (Table 1), a decrease of migration distance through time in the SP cluster, and an increase in the GE cluster, 1 while migration distance of Robins in the UK and the IT cluster did not show any significant temporal trend (Table 2).

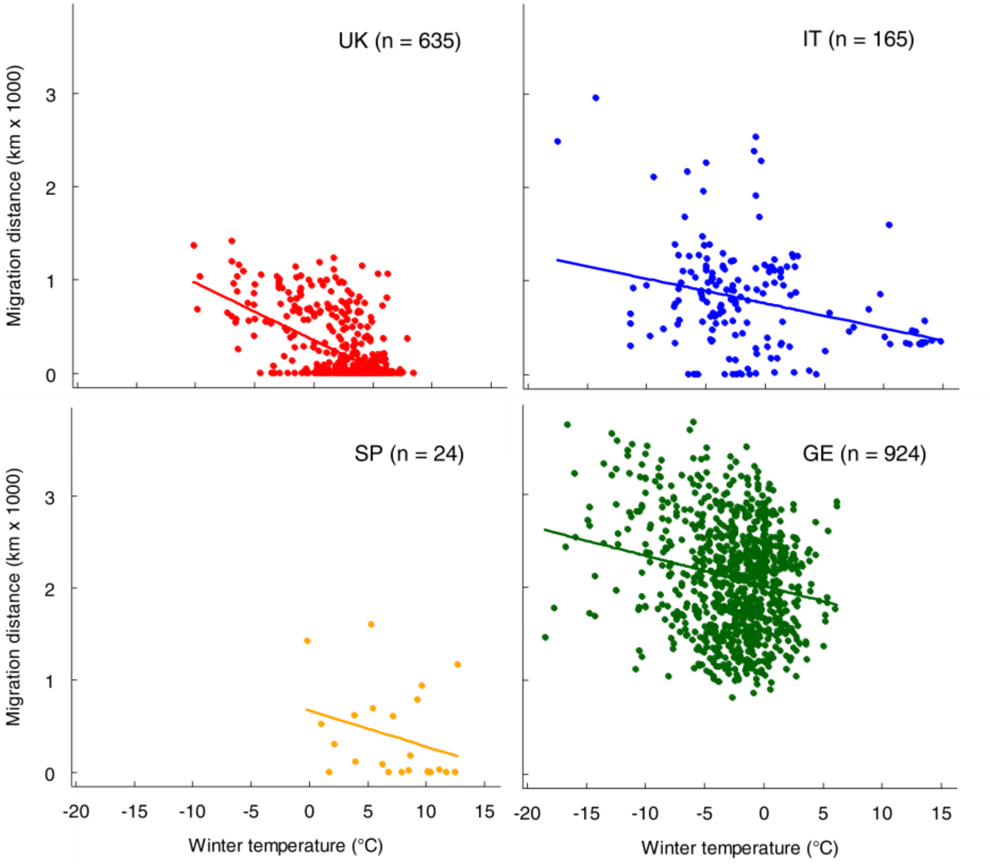

Figure 4. Migration distance (excluding birds that moved less than 0.571 m) as a function of winter temperature in the breeding areas for the four clusters of populations. Regression lines are shown to ease graph interpretation.

These differences are probably related to the strong South-West to North-East gradient in European climate and, maybe, to differences in migratory behaviour between the *melophilus* subspecies from Britain and Ireland and the nominate *rubecula* of continental Europe (despite the UK cluster also included birds from the continent, in particular from The Netherlands, see Figure 2).

These results on the one side confirm that the proportion of short-distance migrants that are becoming resident year-round is increasing (Berthold *et al.* 1992; Pulido & Berthold 2010; Morganti 2014), and also that migrant individuals tend to winter closer to their breeding range (Visser *et al.* 2009; Ambrosini *et al.* 2011; Morganti 2014). On the other side, our continent-wide analysis highlights how these processes do not occur to the same extent in all geographical populations. The 'threshold model of migration' (Pulido, Berthold & van Noordwijk 1996) states that genetic variability in migratory behaviour can be maintained in the population because migration is the dichotomous outcome of a latent underlying continuous trait, called the 'liability', which determines migration or sedentariness according to its value being higher or lower than a given threshold. The 'environmental threshold model' (Pulido 2011) extends this model by considering that the threshold is not fixed, but related to a continuous environmental variable, whose values may therefore change among populations living in different parts of the range of a species. Hence, different geographic populations may show different migration propensity according to the value of the environmental threshold in the area where the population lives, and to the proportion of the population whose liability is above the threshold. According to this model, the expression of migration or sedentariness should vary among populations living under markedly different environmental conditions and according to environmental variables. The temperature of the coldest winter month in the breeding areas is a good proxy for the harshness of winter ecological conditions, which in turn should affect migration propensity and distance. We therefore predicted that winter temperatures should affect migratory behaviour of Robins, and our results suggest that this was actually the case. However, different geographical populations not only showed differences in migration propensity and distance, but also different variation in these variables in response to winter temperature. This suggests the possibility that geographical populations of Robins showed different reaction norms to winter temperatures possibly because of differences in their underlying liability.

Migration is supposed to evolve whenever individuals can acquire a higher fitness by moving between different areas than by remaining in the same area year-round (Lack 1954). Robins are facultative partial migrants in some parts of their range (Adriensen & Dhondt 1990; Newton 2008) and full migrants in others (e.g. cluster GE in the present study, see also Cramp *et al.* 2004). Whether an individual is migratory or sedentary is considered a 'conditional strategy with unequal payoffs' (Newton 2008) for Robins; this ultimately depends on the ability of an individual to acquire a territory of a sufficient quality to ensure a high probability of winter survival: if it can do that, it can stay, otherwise it has to migrate. Socially dominant individuals are therefore more likely to be sedentary while socially subordinate ones migrate (Newton 2008). These considerations however imply that adult Robins would be less migratory than first-winter birds. However, we found no significant effect of age on migration propensity or distance. Similarly, females were found to migrate more than males because they are socially subordinate (Adriensen & Dhondt 1990). Unfortunately we could not test this latter hypothesis because sex of individuals was unknown in our study. Analyses based on ring recoveries may be affected by several sources of bias, which ultimately derive from the large spatial and temporal heterogeneity in sampling effort (Fiedler 2003; Fiedler, Bairlein & Köppen 2005; Visser *et al.* 2009). Indeed, variation in ringing and recovery effort across Europe may blur the analyses because Robin populations breeding in different parts of Europe segregate in the wintering quarters. Our analyses should however be robust with respect to this potential source of bias because clusters identified geographical populations with a connection between breeding and wintering ranges, and we incorporated this information in all analyses (see also Ambrosini *et al.* 2011 for a similar approach).

We also re-ran our analyses including indices of population size at different countries and years, and by restricting our analyses only to birds recovered dead, because they were always reported to the EDB by all national ringing schemes, which, conversely adopt heterogeneous politics for reporting live birds (see Methods). However, both kind of analyses not only strongly reduced overall sample size, but also affected sample size of each cluster differentially (e.g. the SP cluster had to be excluded from the analyses run on birds found dead because in this cluster only seven Robins were found dead). If we carefully consider this problem, we can conclude that the results of the statistical analyses were generally consistent when we included population indices or restricted the analyses to birds found dead only. Finally, we found a significant advancement in winter recovery date only in the GE cluster in the analyses based on birds found dead, while all the other analyses did not show any significant variation in winter recovery date. Thus, we can conclude that variation in migration phenology did not affect our analyses. Therefore, our findings do not appear to be heavily biased by spatial and temporal variation in recovery effort, nor by differences among sampling schemes in data recording or in migration phenology. In conclusion, we have shown that ecological conditions at the breeding grounds during winter may determine migratory decisions in a species that shows strong differences in migratory behaviour between geographical populations. In particular, milder winter temperatures in the breeding areas were associated with a larger proportion of Robins that spent the winter at their breeding grounds, and with a reduced migration distance of those birds that migrate. Climate change may therefore drive a larger part of Robin populations toward sedentariness, and toward a reduction in migration distance for those individuals that migrate. Our results are thus in agreement with those from Visser *et al.* (2009), which documented a decline in migration distance of 12 bird species breeding in The Netherlands and concluded that amelioration of winter conditions was responsible for the long-term decline in migration distance. Indeed, distance migrated decreased with increasing temperatures in the Dutch winter when the bird was recovered (Visser *et al.* 2009). The present study is an extension of previous findings by Visser *et al.* (2009) from a local to a continental scale, thus showing that climate change is affecting migratory behaviour in different part of the range of the Robin. In addition, we show that different geographical populations of this species show different reaction norms to climate change. The novel analytic framework we developed is suitable for investigating the consequences of climate change on migration, and it can be adopted across a broad range of migratory species providing much needed information on the effects of climate change at the individual level. An open question is how individual birds can anticipate overall winter harshness in autumn (October- November or earlier), when birds decide to migrate. It might be speculated that temperatures experienced shortly before migration months, or those during migration, are correlated with temperatures during the subsequent winter months. Such time-lagged correlation among temperatures (see Saino & Ambrosini 2009) may provide Robins with a proximate clue to winter harshness, allowing them to take appropriate migratory decisions.

Acknowledgements

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Discussion

The main aim of the research project presented in this thesis was to investigate the effects of habitat modification and climate change on the population dynamic of migratory birds. Overall, our studies confirmed that these two factors are already affecting populations of migrant birds, and also that they are acting at different stages of their life-cycle. In the studies reported in both sections of this thesis we documented clear examples of the impact of habitat modification and climate change on the breeding biology, migratory behaviour and demographic trends of a few model species. Some of the effects we observed could potentially be generalized to other populations of the same species as well as to other species.

The studies reported in Section 1 showed that ecological conditions experienced at the breeding quarters may influence population dynamics of long-distance migrants and their breeding performances. More in detail, in the study reported in the first paper we observed that cessation of livestock farming at breeding sites may have worsened the demographic decline recorded in recent years in three geographical populations of Barn Swallows breeding in Northern Italy. Since Barn Swallows breed mainly in cowsheds and stables with cattle or horses, the breeding performances of individuals can be markedly affected by rapid changes in livestock farming practices, and in particular by its cessation at breeding sites, probably because the presence of animals entails several advantages for both adults and nestlings (Ambrosini & Saino, 2010; Grüebler et al. 2010). Cessation of livestock farming widely occurred during the last decades, not only in Northern Italy, but also at continental scale, and is mostly related to the progressive abandonment of traditional farming practices carried out in old buildings in favor of intensive livestock farming carried out in large cowsheds, less suitable for Barn Swallow nesting (Møller 1994, 2001, Ambrosini et al.

2002, Turner 2006). Importantly, this change in farming practices entails the gradual reduction in the number of farms where livestock is reared. Our findings suggested that the maintenance of livestock farming could be an effective conservation measure for this declining species, but unfortunately it is not easy to implement as, nowadays, the maintenance of livestock farming is not economically advantageous for farmers (R. Ambrosini, unpubl. data). Luckily, the results of the second study we performed on this topic suggested an alternative conservation measure for the Barn Swallow, which may be more practical. Indeed, we showed that the worsening of the demographic decline of our population caused by the cessation of livestock farming at farms may be buffered by an increase in the extent of hayfields near the breeding sites. More in detail, our analyses revealed that colony size increased with the extent of hayfields on farms where livestock is not reared and that nestlings' phenotypic quality improved with increasing extent of hayfields around the colony. Colony size may have increased due to a higher survival rates of individuals that bred under favourable conditions, while a better nestlings’ quality, which in turn affects their survival prospects and later recrutiment (Turner 2006, Grüebler & Naef-Daenzer 2010), may positively influence the demographic trend at population level because only a very few Barn Swallow nestlings are recruited as breeding adults in the natal colony, while the vast majority disperse within some kilometre (Tuner 2006, Scandolara et al. 2014).

Although the precise mechanism underlying this beneficial effect of hayfields still needs to be elucidated, is it likely that large hayfields around breeding sites can compensate the decrease in insects availability caused by the cessation of livestock farming. In fact, previous studies have shown that flying insects of large size, which are the preferred prey of Barn Swallows, are more abundant on these than on other cultures (Evans et al. 2007, Grüebler et al. 2010, Orłowski & Karg 2011).

Based on the results of these studies, the Lega Italiana Protezione Uccelli (LIPU) has recently provided funding to the farmers of Parco Regionale Adda Sud (one of our study areas) for the maintenance and enlargement of hayfields in the immediate proximity of farms. This action may not only favour Barn Swallows, but also enhance the general quality of the agro-ecosystems of the park, since the enlargements of hayfields may have beneficial effects also for other organisms living in farmland habitats (Robinson & Sutherland 2002). The Barn Swallow can therefore be a flagship species for nature conservation in farmland areas (Spina 1998).

Our results suggested that recent variations in agricultural practices may have worsened the demographic decline of Barn Swallows in Northern Italy. Our results are supported by other studies recently conducted both at continental level (Butler et al. 2010, Donald et al. 2001) and in the UK (Fuller et al. 1995, Robinson & Sutherland 2002, Chamberlain & Fuller 2000, Eglington & Pearce-Higgins 2012), which reported that declines of several farmland species are related to changes in land-use associated with agricultural intensification.

Although the size of European Barn Swallow populations did not decrease significantly in recent year (PECBMS 2009), the steep demographic decline we documented in our study areas suggests that in the near future the Barn Swallow may become a species of conservation concern in Northern Italy. A proper knowledge of the factors affecting population dynamics of this species is therefore pivotal to plan effective conservation measures.

In the third paper reported in Section 1 we showed that both biotic and abiotic conditions of the rearing environment could affect the survival and growth of nestlings in another long-distance migrant species, the Common Swift. We demonstrated that Common Swift nestlings show considerable seasonal plasticity in their growth patterns, suggesting that these may be adaptively tuned to match variation in general ecological conditions. Our study also revealed that in our geographical area, nestlings' growth benefits from weather conditions that mitigate high temperatures and humidity, which could impair nestlings' physical condition, while their survival seemed to be not affected by climate. These results are partially in contrast with those obtained in other studies conducted on the same species, but in different geographical regions. Indeed, most of the other studies on the Common Swifts were conducted in the UK, where general climatic conditions are different from Northern Italy, and indicated that in this geographical region nestlings' survival is strongly reduced by poor weather (Lack and Lack 1951, Martins & Wright 1993, Thomson et al. 1996).

This discrepancy in the results between our and previous studies suggests that local climatic conditions could affect the breeding biology of a species, with different outcomes in different parts of its breeding range. Furthermore, since nestlings' survival and growth ultimately affect population size, these findings suggest that changes in meteorological conditions could impact the population dynamics of this species. On the one hand, the high phenotypic plasticity shown by Common Swift nestlings could facilitate an adjustment of the breeding phenology of this species in response to climate change. On the other hand, an increase in temperature such as the one predicted for the near future under climate change (Easterling et al. 1997), could severely affect the physiological conditions of both nestlings and adults and could possibly determine a northward shift of the distribution range of Common Swifts.

The effects of changes in agricultural practices we documented in the first two papers presented here only explained a small fraction of the decline observed in our Barn Swallow population, suggesting that other ecological conditions faced by birds during migration and wintering may be crucial in affecting population trends. In the studies reported in Section 2 we therefore moved our attention from the analysis of the effects of ecological conditions at breeding quarters to the identification of migrations routes and wintering ranges and to the investigation of the effects of ecological conditions experienced by long-distance migratory birds during these phases of their life-cycle on their migratory behaviour and population dynamics. We used the Barn Swallow and the European Robin as model species.

We first aimed at identifying the migration routes and the geographical position of wintering quarters of the Barn Swallow, as well as at obtaining detailed information on the phenology of those parts of its annual life-cycle that occur outside the breeding range, since they were still not accurately known so far. In the first paper of Section 2 we analyzed the large number of ring recoveries available for the Barn Swallows and we identified main migration routes and phenology of both spring and autumn migration of individuals breeding in Western Europe. We also investigated the variation over time in the timing of migration and we detected a significant advance of autumn migration in Southern Europe. This result may suggest genetic variability among populations in adjusting their migration strategies according to recent climate change (Møller et al. 2008). Remarkably, in this study we developed a novel framework for statistical analysis of ring recoveries, which represents a useful method to infer patterns of migration and main routes followed by individuals from data that are already available to ornithologists (Baillie et al. 2007).

The following papers are the results of an innovative research project aiming at applying the most advanced technological devices available so far to study in details the migration of small sized birds. By applying miniaturized light-level geolocators on about one hundred Barn Swallows form three geographical populations breeding in Northern Italy and Southern Switzerland in two consecutive years, we obtained precise information on timing of migration (particularly on arrival to and departure from the wintering grounds) and on the geographical position of their wintering quarters. Differently from the analysis of ringing data, the application of geolocators allowed obtaining information at individual level. In this way we could assess that individuals from Northern Italy winter in Central Africa where they arrive mainly in October and leave in March. Interestingly, we found a great variation between the two years of the study in the timing of different migration events as well as in the position of the wintering grounds. This suggests that environmental conditions, which vary at annual scale, have a large impact on the phenology of migration.

Since the application of small miniaturized devices has been introduced only recently in ornithological studies, and some studies have highlighted that these instruments can potentially have negative impacts on individuals (Barron 2010, Costantini & Møller 2013), we also evaluated the effect of their application on survival and breeding performances of our study species. Our study is to date one of the few in the ornithological literature that aims at quantifying the possible negative effects of these instruments on equipped individuals and, notably, to the best of our knowledge, it is one of the few studies (see for example Salewski et al. 2010) in which equipped individuals were compared to a large control group of unequipped ones breeding at the same sites and therefore under similar ecological conditions. Our results confirmed that the application of geolocator can have negative effects on individuals in terms of reduced survival prospects and breeding performance. Our study is therefore a solid, experimental confirm of the findings of recent meta-analyses, which suggested (but could not demonstrate) a negative effect of tracking devices on migratory birds by putting together pieces of information from several different studies often conducted without a proper control group of individuals (Barron et al. 2010, Costantini & Møller 2013). Still, the employment of these instruments is currently allowing ornithologists to obtain information on small-sized bird migration that may be of fundamental importance for the study and conservation of migratory species and that could be very difficult to obtain otherwise. Therefore, it is pivotal to plan any future study conducted by deploying geolocators on birds by balancing the possible negative effects associated with the use of these devices with the benefits originated by the information they can provide. These aspects must be considered even more carefully when planning studies on endangered species.

The information obtained by the analysis of data recorded by geolocators we deployed on individuals from three Barn Swallow populations gave an important contribution to the understanding of unknown details of the circannual life-cycle of this species. Since the studies in Section 1 revealed that ecological conditions at breeding sites affect the population dynamic of Barn Swallows in Northern Italy only to a minor extent, we then aimed at investigating if conditions experienced during migration and wintering could have a larger impact than those at the breeding sites on the population dynamics of this species. In a further study, we therefore combined data on migration phenology and position of staging and wintering quarters of individuals with long-term data on population dynamic of Barn Swallows from Northern Italy to assess the critical stages of the life-cycle that limit population size. We found that environmental conditions encountered at arrival from autumn migration to wintering grounds in Central Africa and during spring migration on the northern coasts of Africa are the factors that influence most year-to-year variation in the number of breeding pairs. These findings did not allow us to fully explain the long-term decline observed in our study-population, yet they highlight that environmental conditions at wintering and staging areas influence at least variation around the long-term decline at a larger extent than variation in ecological condition at the breeding grounds. Notably, this is one of the few studies suggesting that ecological condition encountered by long-distance migratory birds at arrival to the wintering grounds from autumn migration may have a larger impact on annual survival than those faced during wintering. Hence, in the life-cycle of long-distance migratory birds, there seem to be some critical periods during which the ecological conditions experienced by individuals affect most the dynamic of their population. For our study population, these critical periods seem to be the arrival to the wintering grounds and spring migration. Similar findings were recently obtained by Finch et al. (2013) and Ockendon et al. (2014), which observed that environmental conditions experienced during winter and during spring migration significantly affected breeding performances and variation in population size in several species of long-distance migrants breeding in the UK.

Population dynamic of migratory birds is therefore affected, at varying extent, by the conditions they encounter in the different parts of the world where they spent different phases of their annual life-cycle. However, distant geographical areas often show divergent pattern of variation of ecological conditions, which may hamper the ability of migratory birds to adapt to new condition. This may explain why migratory birds, particularly long-distance ones, seem particularly sensitive to climate and habitat changes. The existence of critical periods in the annual life-cycle of population when they are more sensitive to changes in ecological conditions, as suggested by our and previous study, may further amplify the effect of habitat and climate change on populations. Even if these findings need additional investigation to be further generalized to other populations or species of migratory birds, they contributed in providing a novel perspective for the conservation of migratory birds. In fact, in the light of the results we obtained and of similar ones reported in the literature (e.g. Sillet et al. 2000, Saino et al. 2004, Holmes 2007, Gordo & Sanz 2008, Barbet-Massin et al. 2009, Ockendon et al. 2014), it is evident that the planning of effective conservation measures in favor of declining populations of migratory birds, should aim at protecting both breeding and wintering areas as well as stopover sites during migration.

Finally, we analyzed an existing database on migration of individuals from a partial migrant bird species in order to quantify the effects of climate change on the proportion of individuals that migrated and on migration distance. We focused on the European Robin because it is a model species for studies of partial migration. In this study we showed, for the first time, high degree of migratory connectivity and large phenotypic differentiation in migration strategy within geographical populations of European Robins. Furthermore, our results indicated that changes observed over the years in the phenology of migration and migratory behaviour of individuals are associated to changes in winter temperature recorded in the last decades. These findings highlight once again the sensitivity of birds to weather conditions, and are consistent with the hypothesis that climate is the main driver of the difference in migratory behaviour observed in several short-distance migratory species on a continental scale (Newton 2008). In this study, we also developed an analytic framework that can be adopted across a broad range of migratory species, providing information on the effects of climate change at the individual level. The main advantage of these analyses and those developed in the first paper of section 2 is that they are based only on information routinely collected by licensed ringers. Considering the millions of birds that have been ringed in the last century and the thousands of them that every year are recovered (Baillie et al. 2007), these methods are likely to be applicable to hundreds of species and may therefore be an important tool for planning conservation strategies for declining species.

Conclusion

All the studies reported in this thesis confirmed that migratory birds are already showing responses to climate change and habitat modification. This underlies their sensitivity to ecological conditions and confirms their role of “winged sentinels” of global environmental change (Wormworth & Şekercioğlu 2011). Although at large spatial scale many species of migratory birds, including our study species, are not showing significant demographic declines, local pattern of decreasing populations should be considered as early warnings of the effects of global environmental change.

The novel frameworks for the statistical analysis of ringing data and ring recoveries that we developed in some works reported in this thesis may be a suitable tool for investigating the effects of climate and habitat change across a broad range of migratory species.

Overall, our findings suggest that long-distance migrant species may respond to global change in different ways according to the critical phases of their life-cycle during which they are more sensitive. Therefore in the design of effective conservation measures, which for some species may already be an urgent necessity, it is compulsory to identify the actual ecological determinants of populations' declines and the specific life-cycle phase in which they act.

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Supplementary materials

Supplementary materials to:

Modelling the Progression of Bird Migration with Conditional Autoregressive Models Applied to Ringing Data

The Complementary Log-Log and the Logistic Function

Binomial models can be fitted by choosing different link functions (Zuur et al. 2009). Taking our dataset as an example, the link function η defines the relationship between the expected values of the proportion p_t of swallows observed at a cell until a given calendar date t and date itself. Formally

$$\eta\left(E(p_t)\right) = \alpha + \beta t \qquad \text{Eq. 1}$$

The common choice for η is the logit function:

$$\eta(p) = \log \frac{p}{1-p} \qquad \text{Eq. 2}$$

By substituting Eq. 2 into Eq 1 with p = $E(p_t)$ and then solving for $E(p_t)$ we obtain

$$E(p_t) = \frac{e^{\alpha+\beta t}}{1+e^{\alpha+\beta t}} \qquad \text{Eq. 3}$$

Eq. 3 is the logistic function (i.e. the inverse of the logit function) and can be used to calculate the expected proportion of arrivals until a given calendar date from the coefficient of a binomial model fitted with a logistic link function.

Binomial models can also be fitted by using alternative link functions, that can be a better choice than the logistic function in particular circumstances. In particular, Baddeley *et al.* (2010) demonstrated that when spatial Poisson processes are analysed by dividing the space into pixels, the optimal estimator of the probability of occurrence (or, equally, of the proportion of occurrences) in a pixel is the complementary log-log ('cloglog') function:

$$\eta(p) = \log(-\log(1-p)) \qquad \text{Eq. 4}$$

The inverse of Eq. 4 is

$$E(p_t) = 1 - e^{-e^{\alpha+\beta t}} \qquad \text{Eq. 5}$$

We can solve Eq. 5 for t obtaining

$$t = (\log(-\log(1-p)) - \alpha)/\beta \qquad \text{Eq. 6}$$

Eq. 6 allows estimating the calendar date at which a given proportion p of swallows is expected to have been observed based on the parameters α and β of the cloglog curve.

The logistic function is symmetric about p = 0.5, while the cloglog is not, having a longer tail at the lower end (Figure R1). Both functions can be fitted to the same data by specifying the opportune link function in the binomial GLM or GLMM.

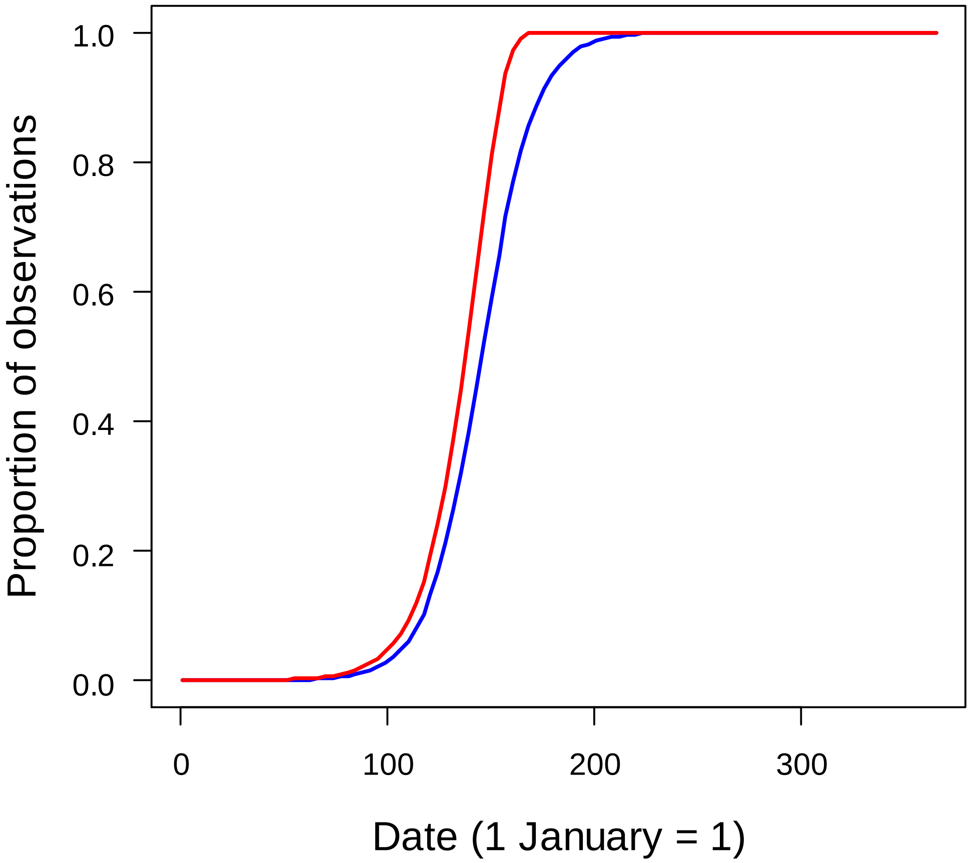

Figure R1. Logistic (blue) and complementary log-log (red) curves interpolated to spring migration data in western Europe and north Africa. Parameters of the model were estimated by binomial CAR GLMMs as specified in the main text. Both models were fitted with the *lmer* procedure in the *lme4* package (Bates et al. 2012) in R 2.15.2 (R Core Team 2012) by specifying respectively the logit and the cloglog link functions.

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Supplementary materials to:

Timing of migration and residence areas during the non-breeding period of barn swallows *Hirundo rustica* in relation to sex and population

Appendix 1. Detection of departure and arrival at the breeding site

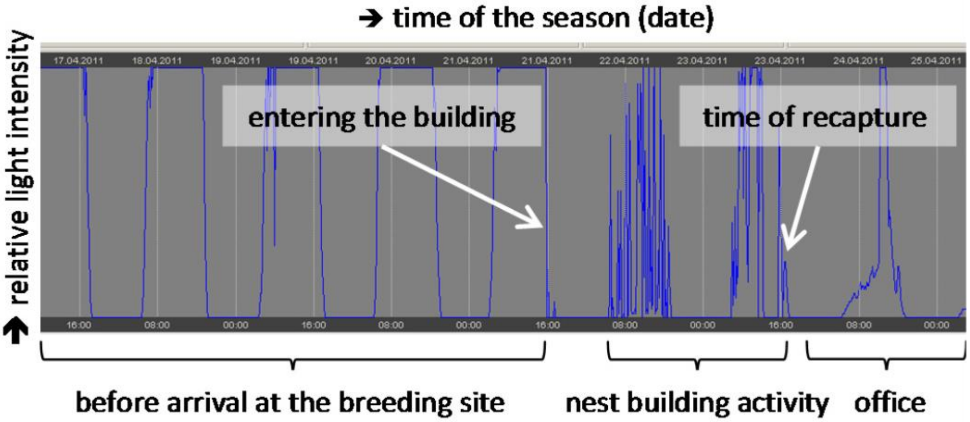

Figure A1: Example of a light curve recorded by the geolocator (SOI GDL2.11). The blue lines represent the light intensity recorded. Natural day- and night-time can be clearly recognized during the period before arrival (to the right). We assumed that the abrupt drop in light intensity on the 21.4.2011 marks the first visit to the nest site. The next two days are characterized by many artificial shading most probably due to visits to the nest. In the afternoon of the 23.4.2011 the bird was recaptured. On the 24.4.2011 the logger was laying in the office.

Appendix 2. Sex differences in the effects of the position of the sub-Saharan residence area (SRP) on phenology

We investigated whether the SRP latitude differentially affected the phenology of non-breeding events of either sex. To this end, we added to the models shown in Table 3 the statistical interaction between sex and SRP latitude, respectively. These analyses were ran only on the 'reduced' dataset, because the inclusion of the five southern wintering males strongly increased model multicollinearity (VIF > 25, details not shown) when the interaction terms were tested. Moreover, even in this reduced dataset, we could not test the interaction term between sex and longitude, again because its inclusion (either separately or simultaneously with the sex × latitude effect) raised model multicollinearity beyond acceptable levels (VIF > 10). SRP latitude did not differentially predict phenology of non-breeding events of either sex (sex × latitude effect; duration of stay in the wintering range, $F_{1,58} = 0.73$, $p = 0.39$; departure from the wintering range, $F_{1,60} = 0.33$, $p = 0.57$; duration of spring migration, $F_{1,55} = 0.58$, $p = 0.45$; arrival to the breeding colony, $F_{1,55} = 0.05$, $p = 0.82$).

Appendix 3. Comparison of the positions of the sub-Saharan residence areas (SRPs) between years, sexes and populations using a randomisation test

The median SRP of the 59 individuals tracked in 2010-2011 was 7.0° N - 12.8° E, while for the 33 individuals tracked in 2011-2012 it was 3.2° N - 15.3° E. The median SRP in 2011-2012 was thus 506 km to the SE compared to the previous year.

When assigning the year randomly to the individuals repeatedly (4999 iterations), the median distance between the SRP of the two years was 139 km. The observed distance of the median SRP between the two years (506 km) was significantly higher than expected by chance (p = 0.002, Fig. A2).

For comparing the SRP between the sexes and populations using the same randomisation procedure (i.e. assigning sexes and populations randomly to individuals, respectively; see Table A1), we therefore corrected for the between-year difference by shifting the locations of 2011 by 506 km to the SE, so that the median SRP of the two years coincided.

Table A1. Comparison of SRP median distances between sexes and populations using a randomisation test (see details above). For the six groups (3 populations x 2 sexes) differences between the median SRPs (km) of each group and p-values for differences from the randomisation test are given (M = males, F = females). There is no statistically significant difference in the median SRP between any group (all p > 0.06).

Group	SE-pop F		N-pop M		N-pop F		SW-pop M		SW-pop F	
	km	p	km	p	km	p	km	p	km	P
SE-pop M	535	0.291	429	0.156	413	0.240	456	0.135	632	0.065
SE-pop F			360	0.532	732	0.086	377	0.479	564	0.273
N-pop M					410	0.128	30	0.980	244	0.613
N-pop F							413	0.133	435	0.239
SW-pop M									215	0.700

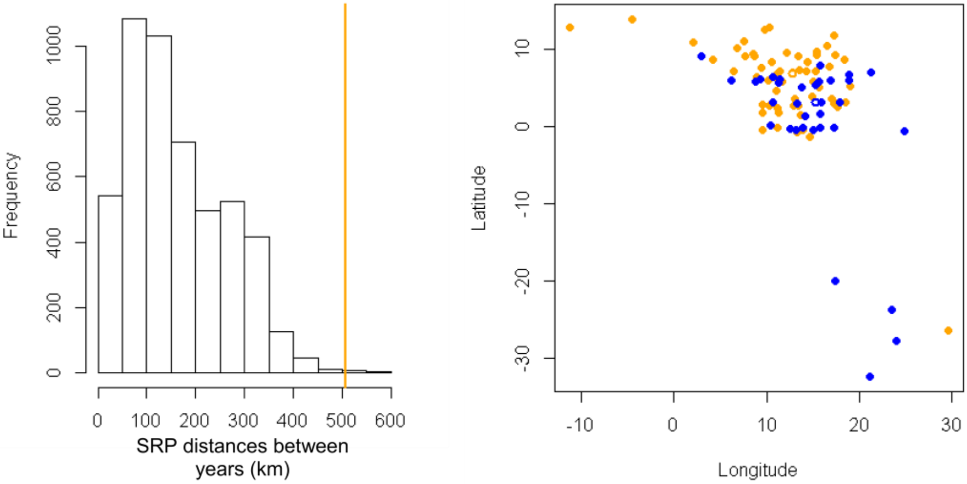

Figure A2. Left: distribution of randomised distances between median SRPs when years were assigned at random (n = 4999); orange line: observed distance between median SRPs of the two years (506 km). Right: SRP of the individuals in 2010-2011 (orange) and 2011-2012 (blue); open circles = median location.

Appendix 4: Comparison of sex-specific variances between the phenological events during the non-breeding period

For each phenological event table A2 shows the variance and results of Levene's test for differences between the sexes. Below the results (and R-code) of ANOVA for differences in variance in between sexes and between sexes for each phenological event are given.

Table A2. Sex-specific variances in the departure times from and the arrival times at the breeding grounds and sub-Saharan residence areas. The table shows the variance of the residuals from ANOVAs fitted to sex-specific data using year, population and their interaction as explanatory variables. The Levene's test for pairwise comparisons of variances between the sexes is shown.

	Males variance	Females variance	Levene's test
Departure from the breeding colony	19.8	58.6	$F_{1,99} = 6.11$, $p = 0.015$
Arrival to the sub-Saharan residence area	73.5	61.7	$F_{1,90} = 0.03$, $p = 0.87$
Departure from the the sub-Saharan residence area	132.4	198.3	$F_{1,69} = 0.72$, $p = 0.40$
Arrival to the breeding colony	128.7	123.7	$F_{1,64} = 0.02$, $p = 0.89$

Appendix 5. Variation in weather conditions between the two study years

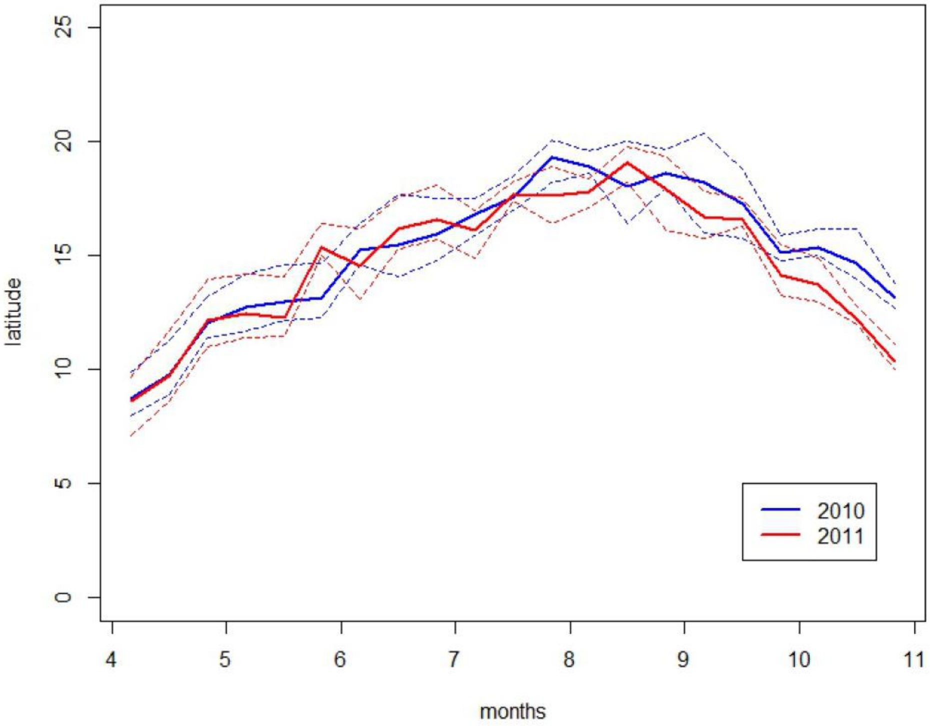

Figure A3. Movement of the intertropical convergence zone (ITCZ) in sub-Saharan Africa from April to October in the two study years (2010, 2011). Shown are the course of the mean (solid line) and the range (dashed lines) of the ITCZ latitude for the longitudinal range 2.5° – 22.5° E. Data from CPC/NOAA (http://cpc.ncep.noaa.gov/products/fews/ITCZ/itcz.shtml).

Appendix 6. Distribution of stationary sites of birds with multiple non-breeding ranges

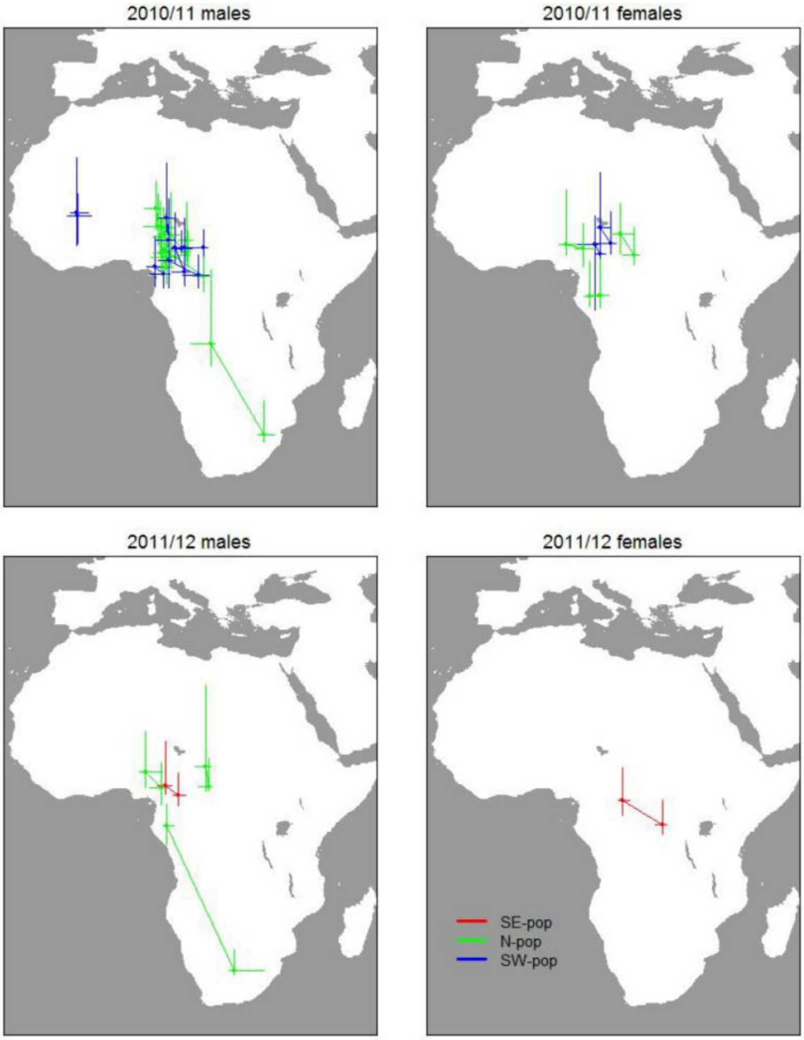

Figure A4. Distribution of stationary sites south of the Sahara (<23.5°N) of individuals with multiple non-breeding range. For each individual (n = 22) the position of the mode of the kernel densities (see Methods) (dots) and the 90% range in longitude and latitude (crossing lines) are given. Only stopover period of at least 2 weeks are shown. Stationary sites from the same individual are connected by a line. The colours refer to the breeding area(see legend). The four graphs are grouped according to year (top to bottom) and sex (left – right).

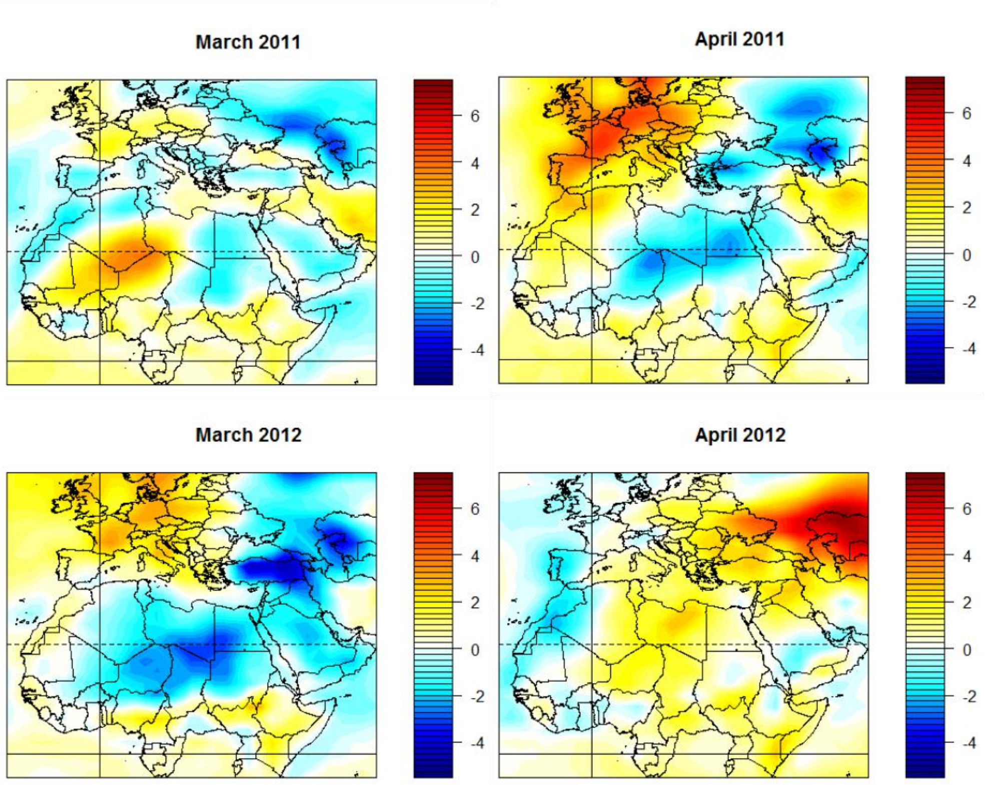

Figure A5. March-April temperature anomalies across the barn swallow wintering and migration range in the two years of study. Anomalies are expressed as the deviation (in °C) from the long-term (1970-2000) monthly mean values. Original data were gridded on a 2.5 x 2.5° grid and were downloaded from the NCEP/NCAR Reanalysis dataset provided by the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, from their Web site (http://www.esrl.noaa.gov/psd/).

Appendix 7. R-code for the data analysis of light-level geolocators

The full R-code is available at : http://www.avianbiology.org/appendix/jav-00485

Supplementary materials to :

Impact of miniaturized geolocators on barn swallow (*Hirundo rustica*) fitness traits

Appendix 1. Details of study areas and adult capture methods

Coordinates of the approximate centres of the study areas were as follows: Magadino: 46°09' N, 8°55' E, Piedmont: 45°33' N, 8°44' E, Lombardy: 45°19'N, 9°40'E. All three areas consist mainly of farmland, dominated by maize and hayfields (see Ambrosini et al. 2012; CS, unpubl. data).

In all years, we intensively captured all the adults breeding in selected farms by placing mist-nests before dawn at every exit of the buildings (mainly cowsheds and stables) where breeding individuals spend the night. We carried out 2-3 capture sessions per farm throughout the nesting season. Repeated capture sessions ensured that the vast majority of breeding individuals were captured, as confirmed by subsequent observations of birds attending the nests. We can therefore reasonably assume that the return rate of breeding adults is equal or very close to the actual survival rate of individuals at a given farm, and we will refer to survival rates hereafter (see Saino et al. 2011, 2012; see also Turner 2006 and Møller 1994 for documentation of strong breeding philopatry in the barn swallow). Moreover, since capture sessions were targeting all birds spending the night inside buildings, irrespective of whether they were equipped with geolocators or not, this ensured that recaptures were not biased towards birds wearing geolocators. Laying date and clutch size of geolocator and control subjects in the year of geolocator deployment did not differ significantly [mixed models with treatment, year, sex as fixed effect factors, and study area and farm as random effects; laying date: treatment,

$F_{1,379} = 1.48$, $p = 0.23$; year, $F_{1,154} = 16.01$, $p < 0.001$; sex, $F_{1,686} = 0.68$, $p = 0.41$; year × treatment, $F_{1,378} = 2.14$, $p = 0.14$; clutch size: treatment, $F_{1,381} = 0.14$, $p = 0.71$; year, $F_{1,176} = 1.52$, $p = 0.22$; sex, $F_{1,678} = 0.14$, $p = 0.70$; year × treatment, $F_{1,381} = 1.53$, $p = 0.22$; the 2011 Magadino data were excluded because no data for controls were collected].

In addition, for the 508 birds of known age (either because they were initially ringed as nestlings/yearlings or because they were unringed immigrants in farms where all breeding adults had been ringed in the year before; see Saino et al. 2004) that were included in the study (age ranging between 1 and 5 years), mean age did not differ significantly between geolocator and control subjects [mixed model with treatment, year, sex as fixed effect factors, and study area and farm as random effects; treatment, $F_{1,502} = 0.52$, $p = 0.47$; year, $F_{1,503} = 31.93$, $p < 0.001$; sex, $F_{1,501} = 0.06$, $p = 0.81$; year × treatment, $F_{1,502} = 0.68$, $p = 0.41$].

Appendix 2. Geolocator design and variation in absolute and relative geolocator weight

In 2010, we aimed at testing the efficacy of different harness configurations, in terms of harness thickness (1.00 or 1.25 mm thick) and leg-loop diameter (27 or 28 mm) on geolocator loss rate and survival. The choice of leg-loop diameters was based on Naef-Danzer's (2007) allometric equation relating harness size and body size among bird species. The number of geolocators deployed for each combination of thickness and diameter was as follows: 1.00-27 mm, n = 62; 1.25-27 mm, n = 181; 1.00-28 mm, n = 15; 1.25-28, n = 52.

Individual geolocators were weighted on an electronic balance (to the nearest 0.01 g) before deployment. Minor variations in device mass could arise because they were handcrafted and differed in specific harness characteristics. The overall weight of 2010 geolocators including harness (model SOI-GDL2.10) was 0.77 g (0.05 s.d., n = 310), while that of 2011 geolocators (model SOI-GDL2.11) was 0.68 g (0.03 s.d., n = 330). In 2010, geolocator weight varied according to harness thickness (thickness 1.00 mm: 0.71 g (0.03 s.d., n = 77); thickness 1.25 mm: 0.79 g (0.04 s.d., n = 233); $t_{308} = 17.0$, $p < 0.001$) but not diameter ($t_{308} = 0.21$, $p = 0.84$). The 2011 geolocators (harness diameter 27 mm and thickness 1.00 mm) were also significantly lighter (0.04 g on average) than those with the corresponding design deployed in 2010 [0.72 g (0.03 s.d.), n = 62] ($t_{390} = 8.47$, $p < 0.001$). The latter difference was partly due to a reduction in the length of the light stalk in model SOI-GDL2.11 compared to the previous model (from 10 mm, forming an angle of ca. 60° with the body axis when pointing the stalk towards the tail of the bird, to 5 mm with an angle of 90°, see Fig. 1). A reduction of the light stalk was accomplished in order to minimize geolocator drag, because wind tunnel studies suggested that a reduction of the drag of externally attached devices could be as important in affecting migration performance as reducing their size (Bowlin et al. 2010).

Relative weight of geolocators was on average 3.93% (0.43 s.d.) of swallow body mass upon capture. Only two subjects (out of 640) received a geolocator weighting > 5% of their body mass at capture (5.03% and 5.12%): notably, the one equipped with the relatively heaviest geolocator returned with the device in the subsequent year. In a two-way analysis of variance, the relative weight of geolocators varied significantly according to year and sex [year, $F_{1,624} = 205.9$, $p < 0.001$; sex, $F_{1,624} = 65.2$, $p < 0.001$; year × sex, $F_{1,624} = 3.06$, $p = 0.08$), with geolocators being relatively heavier in 2010 and for male subjects [2010, males: 4.23% (0.34 s.d., n = 157); females: 4.05% (0.45 s.d., n = 144); 2011, males: 3.87% (0.31 s.d., n = 181);

females: 3.58% (0.34 s.d., n = 146). The sex effect was due to the fact that female barn swallows, though being structurally smaller (shorter wings and tail compared to males) are heavier than males during the breeding season (Møller 1994, our unpubl. data).

Appendix 3. Analysis of factors affecting geolocator loss rate and of the effects of geolocators on survival

For the 2010 data, we investigated whether different geolocator configurations affected the odds of losing the geolocator (0 = subject survived and returned with geolocator; 1 = subject survived and returned without geolocator) in a binomial mixed model with sex, harness thickness, diameter and their interactions (up to three-ways) as predictors. Geolocator weight and harness thickness were strictly correlated (r = 0.70), and we therefore included in the analyses of loss rate harness thickness only, since it is this latter characteristic that determines geolocator weight.

Binomial mixed models were run to test whether geolocator weight affected survival of geolocator subjects, with sex and geolocator characteristics as predictors (results reported in Appendix 6). In addition, for 2010 we ran separate analyses testing the effect of harness diameter and thickness or of harness diameter and weight (either absolute or relative) on survival (we could not include geolocator weight and thickness in the same model because the variables are strictly collinear; see above; results reported in Appendix 6).

Appendix 4. Evaluating the short-term effects of geolocator deployment on parents on nestling growth and fledging success

We investigated whether equipping parents with geolocators while they were attending their brood affected nestling body mass or fledging success. Parents not equipped with geolocators, acting as controls, were captured in the same capture sessions as geolocator parents, at least 6 days before nestling measurement, but were only handled and measured. Replacement broods were excluded from these analyses. The effect of parental treatment on nestling body mass was analysed in a mixed model with male parent treatment (0 = without geolocator, 1 = with geolocator), female parent treatment and their interaction as fixed predictors, while controlling for nestling age (covariate), brood size (covariate; number of nestlings in the nest at the time of measurement), brood order (3-level factor; first, second or third) and nestling sex (covariate). Nest and farm identity were included as a random intercept effects. Farm identity was included as a random effect. Sample size (number of nests) was as follows: geolocator on the male only, n = 20 nests; on the female only, n = 18 nests; on both parents, n = 14 nests; both parents without the geolocator: n = 11 nests.

To investigate the effects on fledging success, nests were included in the analysis with similar constraints as for the analyses of nestling body mass (parents had to be equipped or not with the geolocator before hatching or during chick rearing, up to a nestling age of 4 days). However, sample size was larger since we also included additional nests for which we did not record body mass (geolocator on the male only, n = 20 nests; on the female only, n = 20; on both parents, n = 18; both parents without geolocator, n = 14).

Appendix 5. Effects of geolocator deployment, wing length and age on survival

We tested whether geolocator individuals with longer wings of each sex were more likely to survive to the subsequent breeding season. We expected larger survival of geolocator birds with longer wings, which may better sustain the additional load. Analyses were carried out separately for each sex because of morphological differences between males and females (e.g. Møller 1994). To this end, we ran binomial mixed models with wing length, treatment and their interaction as fixed effects. Wing length did not differentially affect survival probability of control and geolocator subjects in either sex (analyses carried out by excluding birds that lost the geolocator, tests performed on centred variables; 2010, males: wing length, $z = 0.05$, $p = 0.95$; treatment, $z = 3.03$, $p = 0.005$; wing length × treatment, $z = 1.08$, $p = 0.28$; females: wing length, $z = 0.15$, $p = 0.88$; treatment, $z = 5.29$, $p < 0.001$; wing length × treatment, $z = 1.55$, $p = 0.12$; 2011, males: wing length, $z = 0.01$, $p = 0.99$; treatment, $z = 2.39$, $p = 0.018$; wing length × treatment, $z = 1.71$, $p = 0.09$; females: wing length, $z = 0.13$, $p = 0.90$; treatment, $z = 2.03$, $p = 0.044$; wing length × treatment, $z = 1.55$, $p = 0.12$).

We also tested, for the sample of known-age control and geolocator birds that returned with the geolocator ($n = 192$ in 2010 and $n = 300$ in 2011) whether the survival probability of geolocator and control birds was differentially affected by age in binomial mixed models with treatment, age, sex and their two-way interactions as predictors. The treatment × age interaction was not statistically significant in either year (both $p > 0.95$), as was the main effect of age (both $p > 0.08$) (other model details not shown for brevity).

Appendix 6. Effect of variation in harness design and geolocator weight on survival

For the 2010 data, we investigated whether geolocator harness design affected survival of geolocator subjects in binomial mixed models with sex, harness thickness and diameter as predictors. Two-way interactions were included in initial models. When we excluded birds that lost the geolocator, we found a significant effect of harness thickness on survival ($z = 2.52$, $p = 0.011$), with birds bearing thinner harnesses being more likely to survive [model-predicted survival probabilities (s.e.): 1.00 mm, 0.35 (0.06); 1.25 mm, 0.20 (0.03)]. Though the effect of diameter was not significant ($z = 1.46$, $p = 0.14$), birds bearing smaller harnesses tended to be more likely to survive [model-predicted survival probabilities (s.e.): 27 mm, 0.32 (0.04); 28 mm, 0.22 (0.06)]. Two-way interactions were not significant (all $p > 0.14$) and were removed from the model (other model details not shown for brevity). However, the statistically significant effect of harness thickness disappeared ($z = 1.33$, $p = 0.18$; other model details not shown for brevity) when analyses were carried out on the entire set of surviving birds, irrespective of geolocator loss, suggesting that any effect of harness thickness on survival was confounded by non-random geolocator loss rate with respect to geolocator characteristics (see Table 2). Conclusions were similar if we included in the models harness diameter and absolute geolocator weight (instead of thickness) (details not shown), while relative geolocator weight did not significantly affect survival either if birds that lost the geolocator were included or excluded (all $p > 0.34$).

For the 2011 data, we tested whether geolocator weight (both absolute and relative) predicted survival in binomial mixed models with geolocator weight, sex and their interaction as predictors (birds that lost the geolocator were excluded). Geolocator weight did not significantly predict survival (absolute weight, z = 1.45, p = 0.15; sex, z = 2.89, p = 0.004, weight × sex, z = 0.16, p = 0.87; relative weight, z = 1.43, p = 0.15; sex, z = 2.92, p = 0.004, weight × sex, z = 0.42, p = 0.67).

Supplementary references

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Turner, A. 2006. The Barn Swallow. London, UK: T & A D Poyser

Table A1: Effects of geolocator design and sex on geolocator loss rate. Results from a binomial mixed model with loss rate (0 = subject survived and returned with geolocator; 1 = subject survived and returned without geolocator) as the binary dependent variable and sex, harness thickness and diameter as predictors (see footnotes for coding), while study area and farm were included as random effects. Results for main effects are from a model excluding the non-significant interaction terms.

Predictors	Estimate (s.e.)	z	p	Odds ratio (c.l.)
Sex[a]	-1.53 (0.58)	2.66	0.008	4.61 (1.47-14.46)[d]
Thickness[b]	1.68 (0.69)	2.44	0.015	5.33 (1.36-2.87)
Diameter[c]	2.31 (0.63)	3.69	< 0.001	10.12 (2.90-35.24)
Sex × thickness	-0.63 (1.44)	0.44	0.67	-
Sex × diameter	0.89 (1.40)	0.63	0.53	-

a: 0 = female; 1 = male

b: harness thickness: 0 = 1.00 mm; 1 = 1.25 mm

c: harness diameter: 0 = 27 mm; 1 = 28 mm

d: males as reference category

Table A2: Mixed models testing the effects of geolocator deployment (treatment: 0 = control birds; 1 = geolocator birds), sex (0 = female; 1 = male) and their interaction on laying date and clutch size. Dependent variables are expressed as within-individual differences in each trait between year (*i* + 1) and year *i*. Estimates from predictors that were centred around their mean value are shown. Sample sizes for each treatment by sex combination are shown in Fig. 2, as well as *post hoc* tests for the statistically significant treatment × sex interaction on the 2010 clutch size difference. No data from the Magadino study area were included in this analysis (see Methods). Geolocator birds that returned without the device were excluded.

	Year 2010				Year 2011			
	Estimate (s.e.)	F	d.f.	p	Estimate (s.e.)	F	d.f.	p
Laying date (days)								
Treatment	11.93 (4.57)	6.81	1, 69	0.011	3.11 (6.89)	0.20	1, 40	0.65
Sex	4.85 (4.53)	1.14	1, 69	0.29	1.03 (6.84)	0.02	1, 52	0.88
Treatment × sex	-1.11 (9.29)	0.01	1, 69	0.91	-6.45 (13.37)	0.23	1, 49	0.63
Clutch size (eggs)								
Treatment	-0.76 (0.28)	7.12	1, 67	0.010	0.24 (0.43)	0.31	1, 44	0.58
Sex	0.09 (0.28)	0.10	1, 65	0.75	-0.47 (0.43)	1.16	1, 53	0.29
Treatment × sex[a]	1.25 (0.57)	4.86	1, 65	0.031	0.58 (0.85)	0.46	1, 51	0.50

[a]: least-square means (s.e.): control males = 0.06 (0.29); geolocator males = -0.15 (0.28); control females = 0.51 (0.27) geolocator females = -0.95 (0.40)

Table A3: Mixed models of nestling body mass and fledging success analysing the effects of geolocator application to the male parent (male parent treatment: 0 = without geolocator; 1 = with geolocator) and/or the female parent (female parent treatment) (data collected in the Magadino study area, year 2010). In models of body mass, we controlled for the confounding effects of nestling age, brood size (number of nestlings), brood order (3-level factor: first, second or third brood), and nestling sex (0 = female; 1 = male), while in models of fledgling success we controlled for the confounding effects of brood. Estimates for main effects refer to models excluding the non-significant interaction terms.

Predictors	F	d.f.	p	Estimate (s.e.)
Nestling body mass (g) (n = 203 nestlings, 63 nests)				
Nestling age	4.97	1, 52.4	0.030	0.34 (0.15)
Brood size	3.70	1, 52.6	0.06	-0.53 (0.28)
Brood order	1.97	2, 56.3	0.15	-
Nestling sex	3.11	1, 167	0.08	0.58 (0.33)
Male parent treatment (MT)	0.00	1, 50.7	0.99	-0.01 (0.61)
Female parent treatment (FT)	0.86	1, 53.5	0.36	-0.52 (0.56)
MT × FT	0.05	1, 44.9	0.83	-0.25 (1.16)
Fledging success (brood size at fledging) (n = 72 nests)				
Brood order	0.45	2, 61.9	0.64	-
Male parent treatment (MT)	2.26	1, 62.4	0.14	0.44 (0.29)
Female parent treatment (FT)	0.71	1, 59.7	0.40	-0.23 (0.28)
MT × FT	1.40	1, 60.2	0.24	0.67 (0.56)

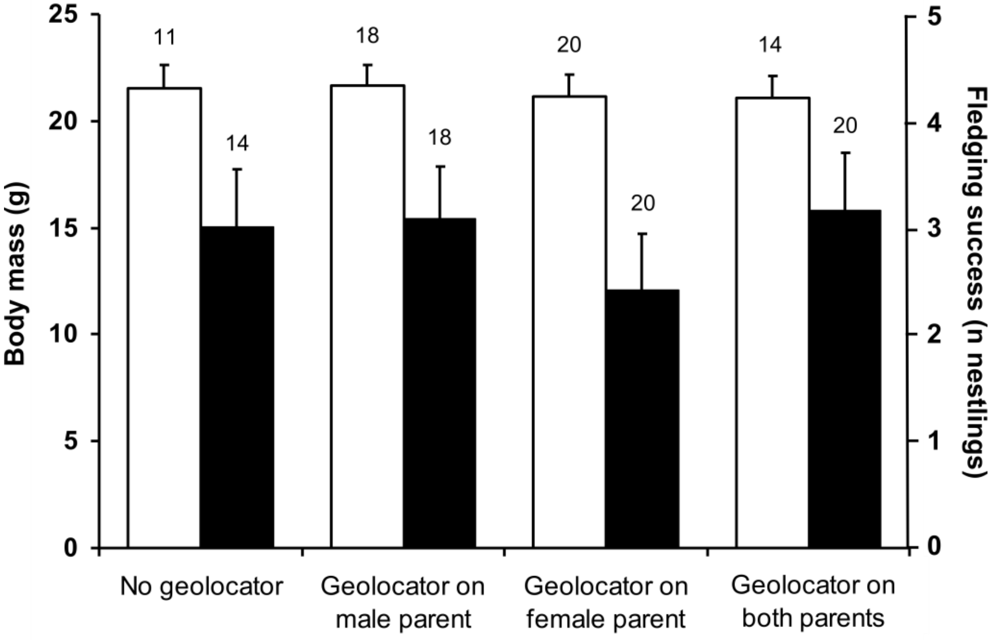

Figure A1: Nestling body mass (open bars, left axis) and fledging success (black bars, right axis) of barn swallow nests in relation to parental geolocator treatment. Values are least-square means (s.e.) obtained from the models listed in Table A3 (including the male parent treatment × female parent treatment interaction term). Numbers above bars show sample size (number of nests) for each treatment category.

Supplementary materials to:

Elevated winter temperatures decrease migration propensity and migration distance of a partial migrant, the European robin *Erithacus rubecula*: a continent-wide analysis

Patterns of migratory connectivity and clustering of populations based on recoveries of birds found dead

The Mantel test applied to birds found dead only disclosed significant migratory connectivity (rM = 0.432, $P < 0.001$, 999 permutations). Cluster analysis indicated a “weak” cluster structure with two clusters (*oasw* = 0.484; Rousseeuw, 1987; Figure S1).

Analyses of migration propensity run on different datasets and including potentially confounding effects

Analyses of migration propensity including population indices indicated that the overall difference in migration propensity between clusters was significant, and that migration propensity was larger in the IT than in the other clusters (Table S1). This analysis also confirmed the significant temporal decrease of the proportion of migratory Robins in the IT cluster, but indicated a significant temporal increase in the UK one, and no temporal change in the SP cluster (Table S1). The Cluster by Winter temperature effect was also statistically significant in this model and indicated a significant decrease in the proportion of migratory birds in the UK cluster at increasing winter temperature (Table S1).

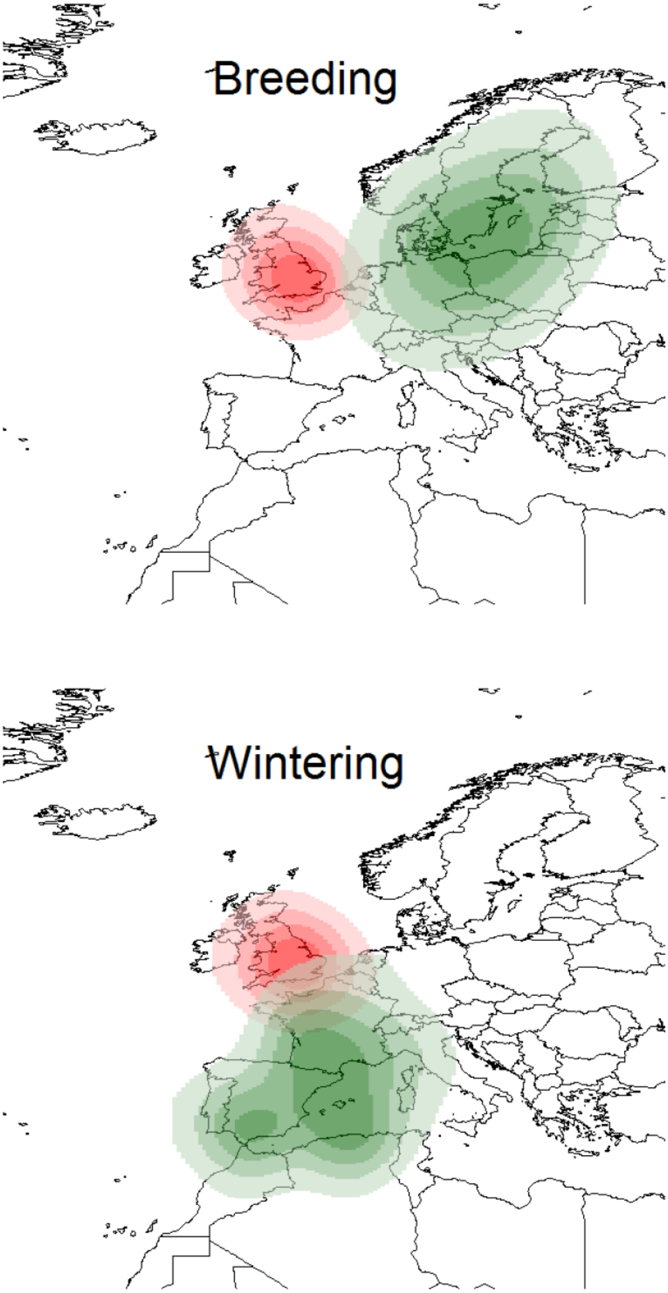

Figure S1 . Kernel density plots of the clusters identified by the migratory connectivity analysis during breeding and wintering of individuals that were recovered dead. Red: UK (n = 562), green = Germany (GE, n = 704).

The overall difference in migration propensity between clusters as well as the Cluster by Winter temperature interaction was significant (Table S2). The analysis indicated a significant effect in the UK cluster only, consistent with that highlighted by the analysis including population indices (see Table 1 in the main text). Differently from the analysis on all individuals, the Cluster by Year interaction was not significant in this model run on birds found dead only (see Table S2 in comparison with Table 1). A model fitted on birds fund dead and excluding this non-significant interaction indicated a general increase in the proportion of migratory Robins over time (coef. ± SE: 0.033 ± 0.006 logit(probability) year-124, $z = 5.281$, $P < 0.001$; other details not shown) after controlling for the effect of Winter temperature (other details not show). We note however, that the UK cluster represented 82.8% of the sample included in this latter analysis. When we re-ran the analysis of migration propensity by using different distance thresholds to differentiate between sedentary and migrant Robins, we found that all significant effects listed in Table 1 remained significant, and the Cluster by Winter temperature interaction became statistically significant when the threshold used was ≥ 2 km (other details not shown). Finally, when we analysed migration propensity in a model including age and its interactions with Cluster and Winter temperature, beside all the predictors listed in Table 1, we found no significant effect of Age or its interactions (χ29 3 ≤ 3.00, $P \geq 0.392$ in all cases). Removal of non-significant interactions from the model did not result in a significant effect of age (details not shown).

Analyses of migration distance run on different datasets and including potentially confounding effects

When we re-ran the analysis of migration distance by including population indices, the Cluster by Winter temperature interaction turned not significant (Table S3). However, the model consistently indicated a general decrease in migration distance with increasing Winter temperature (coef. ± SE: -6.423 ± 2.910 km °C-117, *t*418 = -2.173, *P* = 0.031; model excluding the non-significant Cluster by Winter temperature interaction; other details not shown). In addition, migration distance of Robins form the GE cluster significantly decreased through time, (contrary to the model run on all data; see Table S3 in comparison with Table 2).

Analyses restricted to Robins found dead confirmed the significance of the Cluster by Winter temperature interaction, but not that of the Cluster by Year (see Table S4 in comparison with Table 2). When we re-ran the analysis by using different values of the migration distance 1 threshold we observed that the Cluster by Winter temperature interaction turned non-significant when the threshold was set to ≥ 50 km, while significance of all the other effects was unchanged (details not shown).Finally, the model including Age and its interactions with Cluster and Winter temperature, beside all the other predictors, indicated no significant effect of Age or its interactions (*χ*2 6 1 ≤ 3.32, *P* ≥ 0.068 in all cases). Age was also non-significant in a model that did not include the non-significant interactions (details not shown).

Table S1. GLM models of the proportion of migratory robins including population index as a covariate. The GE cluster was excluded from the analysis because all individuals of this cluster migrated. Sample size is 1126 robins. Covariates Year and Temperature were centred to their mean values before the analyses. Significance of each term was assessed by likelihood ratio tests (χ^2 values and associated *df* and *P*). Coefficients (marginal means) are reported for each cluster with the relative SE. Asterisks denote coefficients that differ significantly (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$) from zero, and different letters denote effects that differ significantly ($P < 0.05$) in post-hoc tests.

Effect	χ^2	*df*	*P*	Cluster	Coef.	SE		
Cluster	8.87	2	0.012	1 UK	-1.624	0.619	**	a
				2 IT	-12.346	4.719	**	b
				3 SP	-1.940	1.333		a
Year	26.97	1	< 0.001					
Winter Temp.	9.71	1	0.002					
Cluster x Year	10.12	2	0.006	1 UK	0.041	0.008	***	c
				2 IT	-0.632	0.244	**	d
				3 SP	-0.047	0.059		c
Cluster x W. Temp.	8.54	2	0.014	1 UK	-0.131	0.042	**	e
				2 IT	-0.017	0.106		ef
				3 SP	0.151	0.089		f
Population Index	1.92	1	0.166		-0.902	0.655		

Table S2. General linear model of migratory propensity (proportion of individuals that moved more than 0.571 km) based only on birds recovered dead. The GE cluster was excluded from the analysis because all individuals of this cluster migrated and the SP cluster was excluded because of the low number of Robins of this cluster (n = 7) found dead. Sample size is 665 individuals. Covariates (Year and Winter Temperature) were centred to their mean values before the analyses. Significance of each term was assessed by likelihood ratio tests (χ2 6 values and associated *df* and *P*). Coefficients (marginal means) are reported for each cluster with the relative SE. Asterisks denote coefficients that differ significantly (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$) from zero, and different letters denote effects that differ significantly ($P < 0.05$) in post-hoc tests.

Effect	χ^2	*df*	*P*	Cluster	Coef.	SE	
Cluster	16.35	1	< 0.001	1 UK	0.864	0.130	** a
				2 IT	2.474	0.479	** b
Year	31.70	1	< 0.001				
Winter Temp.	19.95	1	< 0.001				
Cluster x Year	1.87	1	0.171	1 UK	0.035	0.007	***
				2 IT	0.001	0.024	
Cluster x W. Temp.	5.58	1	0.018	1 UK	-0.181	0.044	** c
				2 IT	0.008	0.070	d

Table S3. Mixed models of migration distance (distance travelled by robins that moved more than 0.571 m, see Methods) including population index as a covariate and country as a random grouping factor. Sample size is 439 robins. Covariates (Year and Winter Temperature) were centred to their mean values before the analyses. Significance of each term was assessed by likelihood ratio tests (χ^2 values and associated *df* and *P*). Coefficients (marginal means) are reported for each cluster with the relative SE. Asterisks denote coefficients that differ significantly (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$) from zero, and different letters denote effects that differ significantly ($P < 0.05$) in post-hoc tests.

Effect	χ^2	*df*	*P*	Cluster	Coef.	SE		
Cluster	156.69	3	< 0.001	1 UK	459.027	142.335	**	a
				2 IT	272.113	340.037		a
				3 SP	1406.930	239.084	***	b
				4 GE	1874.194	178.213	***	b
Year	2.13	1	0.145					
Winter Temp.	3.20	1	0.074					
Cluster x Year	24.10	3	< 0.001	1 UK	-0.821	0.563		cd
				2 IT	29.278	19.338		c
				3 SP	-39.322	9.294	***	e
				4 GE	-16.942	8.505	*	d
Cluster x W. Temp.	3.38	3	0.337	1 UK	-5.350	2.991		
				2 IT	-19.445	15.714		
				3 SP	-33.348	25.086		
				4 GE	-33.250	22.467		
Population Index	0.87	1	0.350		41.650	44.525		

Table S4. Generalized least-squares regression of migration distance (distance travelled 1 by robins that moved a longer distance than 0.571 km, see Methods) based only on birds recovered dead. Sample size is 1025 individuals. The SP cluster was excluded because of the low number of Robins of this cluster (n = 7) found dead. Covariates (Year and Winter Temperature) were centred to their mean values before the analyses. Significance of each term was assessed by likelihood ratio tests ($\chi 2$ values and associated *df* and *P*). Coefficients (marginal means) are reported for each cluster with the relative SE. Asterisks denote coefficients that differ significantly (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$) from zero, and different letters denote effects that differ significantly ($P < 0.05$) in post-hoc tests.

Effect	χ^2	*df*	*P*	Cluster	Coef.	SE	
Cluster	1834.48	2	< 0.001	1 UK	284.629	27.963	*** a
				2 IT	788.335	49.309	*** b
				4 GE	1921.176	40.536	*** c
Year	0.24	1	0.626				
Winter Temp.	132.44	1	< 0.001				
Cluster x Year	1.98	2	0.372	1 UK	-0.455	0.933	
				2 IT	2.582	3.138	
				4 GE	1.920	1.802	
Cluster x W. Temp.	16.89	2	< 0.001	1 UK	-66.956	5.818	*** d
				2 IT	-38.531	7.558	*** e
				4 GE	-31.987	7.282	*** e

Analysis of recovery phenology restricted to birds found dead

The analysis of winter recovery date restricted to birds found dead revealed a significant Cluster by Year interaction (*F*2,1016 = 5.13, *P* = 0.006), beside confirming the significance of the Cluster effect and of the Cluster by Winter temperature interaction (details not shown). A closer inspection of the model revealed that only winter recovery date of the GE cluster advanced significantly (coef. ± SE: -0.353 ± 0.110 days year-115, *t*1016 = -3.214, *P* = 0.001), while that of the UK or the IT cluster did not change significantly (|*t*1016| ≤ 1.672, *P* ≥ 0.095; other details not shown).

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